Inkster-Draper, Tamara E. (2017) ***Biogeography of bats in the Australian Wet Tropics: current distribution and response to future climate change.*** **PhD thesis, James Cook University.**

Biogeography of bats in the Australian Wet Tropics:

current distribution and response to future climate change.

View over the Wet Tropics World Heritage Area from the lookout at Lamb Range.

Tamara E. Inkster-Draper
BSc (Hons)

A thesis submitted to
Centre for Tropical Biodiversity and Climate Change
Zoology and Ecology, College of Science and Engineering
James Cook University
In fulfilment of the degree of Doctor of Philosophy

Accepted August 2017

Acknowledgments

In some respects, this was the hardest part of my thesis to write. I am indebted to such a great many number of people for support, advice, kinship, and life changing experiences throughout my PhD candidature. I extend my deepest gratitude to you all. This thesis wouldn’t exist without you. I hope I have done you justice (and that I haven’t forgotten anyone!).

Thanks must first go to my supervisory team: Simon Robson, Will Edwards, Jeremy VanDerWal, and Steve Williams. Thank you all for your support, wisdom, and patience. Thank you to Steve for those undergraduate climate change lectures, invaluable support in the field, and for fun Earthwatch trips. A big thank you to Will and Jeremy who came on board half way through and helped get me over the line. Will, I greatly appreciate your thoughtful advice and patient explanations. Your comments on manuscripts were invaluable to me; they greatly strengthened this thesis and I learned immensely from your writing style. Jeremy, a huge proportion of this thesis wouldn’t have been possible without your R and modelling wisdom. Thank you for taking the time to teach me some of what you know and thank you for always being available for moral support when needed. Finally, a special thank you to Simon who was there from the beginning until the end. Thank you for all of your help, for first igniting my interests in bats in those undergraduate lectures, and thank you for Borneo!!

My first field experience during my candidature was a month long trip to survey the bats of Cape York. It was an excellent refresher in bat ecology, a great learning experience, and a hilarious (and intense!) month. Thank you to Terry Reardon, Luke Hogan, Jen Parsons, Michael Penny, and Simon Robson for being excellent field companions. Thanks for an excellent field birthday, the weirdest night of batting at Charlie’s Mine, ‘Team Dickin’, Chondro python love, and countless hours of shit-talk over the 2-way radio. Thanks also to Michael for the crash course in Pigeon which ended up coming very much in handy.

A heartfelt thank you to the people of the Huon Peninsula, Papua New Guinea. In particular, thanks must go to Jonah of Boksawin, Mala of Worin, and Keston, Henry and Francis of Gormdan. Thank you for being great field companions, for teaching me a little bit of PNG ingenuity, and in general for keeping us from getting lost. Thanks to Jonah for the songs, and to Francis for the little keepsake. Thank you to Robin who showed up with plantains and a smile when we were alone, tired and hungry. To Michella of Sapmanga, thank you for taking me in, rescuing me from the boys, and braiding my hair PNG style. Thank you also to the three women from Worin, whose

names I never got, who slowed down (way, way down) to walk with me on the afternoon of my first all day hike up the Hungapor hill from hell. Thank you to everybody that I met for truly opening my eyes to your way of life, your sense of community, and your infectious laughter. PNG was the first time I ever really made the human-faced connection to the threat of climate change. I am a changed person after having met you all and being fortunate enough to work in your lands. Special thanks to Andrew Krockenberger and Simon Robson for giving me the opportunity to visit PNG and have such an incredible experience there. Thank you to Mark Zimbicki and Gabriel Porolak for all of your in-field support and friendship whilst there. And, deep, deep thanks to April Reside for being such an excellent companion, field assistant, and friend. Thank you for keeping me sane during the trip (and throughout this PhD in general!) and for sharing the pain of Tropical Ulcers on our return!

Many, many thank you's must go to my fellow CTBCC 'Climateers'. Your support and comradery was, and is, hugely appreciated. Thank you to Marios Aristophanous, Andres Merino-Viteri, Scott Parsons, and Kyran Staunton for helping initiate me into fieldwork CTBCC style. Massive, massive thanks to Arnaud Gourret and Collin Storlie for being the best field companions a girl could ask for. Thank you for many wonderful days and nights spent wandering through the forest. It would certainly not have been the same without you both! Extra thanks to Collin for all of your support in general. The CTBCC would be nothing without Yvette Williams and I would have lost it long ago without her to lean on. Thank you immensely Yvette for your selfless moral support, sage advice, shoulder to cry on, and for always being there.

I extend my gratitude to a large number of other people who supported this journey in some way. Thank you to Professor Richard Pearson who provide excellent and constructive comment on an early version of this thesis. Thank you to my excellent field volunteers, particularly Stanley Tang, Hannah Howard, Ike and Murphy. Thank you to Jen Parsons, Deb Bower and Stewart McDonald for being great office/desk mates, for excellent conversation and for moral support. Stewart, I don't thank you for the ants! Thanks must also go to Stewart, Lauran Hodgson, April Reside, Kyran Staunton, and Collin Storlie for your incredibly patient R help. If I've come out of this knowing anything about coding it's in large part thanks to you all. Thank you to Nina Green for countless sushi dates and for always being there to listen as I unloaded. Thank you to the rest of my JCU support network, particularly Emma Coombes, Tammie Gough, Debbie Ford, Jamie Bull and Brooke Magill. Thank you also to my support networks outside of Townsville – to my Canberra (especially the wonderful Sara Nowrouzi and Kyran Staunton) and UK families in particular. Thank you to the wonderful staff of Danum Valley Research Centre, Borneo and all

creatures great and small that inhabit that area. Thank you for building my enthusiasm for science and nature, showing me that I am on the right track, and revitalising me during every stay.

I give my sincere, deep, and endless thanks to Sandra for instilling in me a love of reading and animals and to Ian for inspiring my love of nature and science. Thank you so much for your love and unconditional support which has shaped me into the person I am today. Thank you also to the entire, extended, Inkster/McKenzie/Atkinson/Edwards/Draper Clan for your love and support throughout this process and in life in general. A particular thank you to Rose for being a wonderful, strong-willed role model and for childhood holidays spent at the beach (which can probably take much of the credit for why I do what I do now).

And, last but not least, the biggest thank you, from the bottom of my heart, to Josh. You've been my rock. You've been there across years and continents, through smiles, tears, leech bites, tick checks, and various tropical diseases. Thank you for your unwavering belief in me, even when I didn't believe in myself. I'm absolutely sure I couldn't have done this without your endless love, care, support and patience. Thank you for everything. x

Cambridge, United Kingdom, August 2016

Statement of Contribution of others

Research Funding

- Australian Daintree Rainforest Observatory postgraduate student grant
- Australian Postgraduate Award Scholarship
- Ecological Society of Australia Student Travel Grant
- Skyrail Rainforest Foundation student research funding
- Wildlife Preservation Society of Australia Student Research Grant
- Department of Zoology and Ecology, James Cook University Individual Research Account

Supervision

- Associate Professor Will Edwards
- Professor Simon K. A. Robson
- Professor Jeremy VanDerWal
- Professor Stephen Williams

Statistical, analytical and modelling support

- Lauran Hodgson
- Dr Stewart McDonald
- Dr April Reside
- Professor Marcus Sheeves (ANOSIM)
- Dr Collin Storlie
- Dr Justin Welbergen (GLMMs)

Other Support (in-feild, drafting, moral, etc.)

- Professor Andrew Krockenberger (PNG)
- Professor Richard Pearson (thesis review and comment)
- Gabriel Porolak (PNG)
- Dr Mark Zimbicki (PNG)
- Fellow CTBCC students

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Thesis Abstract

Anthropogenic climate change poses a significant threat to the wellbeing of the planet. Many scientific studies have demonstrated the negative impacts climate change will have on the earths ecosystem functioning and biodiversity, ranging from disruption and alteration to, in the worst case, species extinction. Despite the fact that tropical rainforests have been acknowledged as biodiversity hotspots worldwide much of the work on the impacts of climate change to date has been conducted in temperate areas. This lack of study, coupled with high biodiversity, means more in-depth research in tropical regions is crucial to increase knowledge on how climate change will impact biodiversity globally.

This thesis focuses on a diverse taxa of mammals, echolocating insectivorous bats (order: Chiroptera), and determines current species' distributions within the Australian Wet Tropics World Heritage Area. The research presented within examines environmental factors that might explain these distributions, and combines this knowledge of current distributions with predicted changes in these environmental parameters to model future distribution change. This study begins by determining what species are present in rainforest habitats of the Wet Tropics through field surveys involving echolocation monitoring and trapping. Individual species, and regional and subregional community composition, were identified and analysis was performed to determine what environmental factors influence observed distributions. Species' probability of occurrence was found to be primarily driven by water availability (precipitation) as well as temperature and location within the region ('subregion': see Chapter 1, Figure 1.2b).

This initial research was built upon by supplementing baseline data gathered during field surveys with historical observation records (from museum and biodiversity atlases). Information on species occurrences was then combined with environmental data to produce Species Distribution Models (SDMs) for the region's bat diversity. These models provide a greater resolution of detail about climatically suitable habitat, current distributions, and the climatic variables driving each of the region's 28 bat species than just field surveys alone. Collated, these models provide information on the region's species richness overall. Rainforested areas to the centre of the region, and particularly the Atherton Uplands, were predicted to have the highest species richness while lowland coastal regions were generally predicted to be the least rich. This data was also analysed to refine methods for producing the most effective models possible. Distribution models for each of the 28 species were initially run using four different model parameters based on different levels of species occurrence data (global vs local) and background information (bias corrected vs bias-uncorrected backgrounds). The resulting outputs underwent quantitative and qualitative analysis to determine which of the four methods produced the most accurate output for each species. It was found that SDMs generally performed best using global species occurrence data against background layers that accounted for any sampling bias. This demonstrates that models built using observational data from only the focal region may misrepresent the distribution of a species, thus biasing resulting outputs. The results of this study could help to refine SDMs and provide a more accurate basis for climate modelling in the future.

To conclude, this research used refined modelling techniques and all gathered information (as outlined above) to build accurate and detailed SDMs predicting how species' distributions will alter under various future climate change scenarios. Modelling predicts that environmental conditions will become more suitable for almost half of the study species. However, conditions are predicted to become less favourable for the other half of species, resulting in distribution contractions. Total species movement is predicted to be high with species moving into upland, rainforested areas to the centre of the region and contracting out of lowland coastal areas. Modelling predicts that by 2085 the majority of bat diversity in the region will be concentrated in these upland, rainforested areas.

This research represents the first detailed description of the distributions of all echolocating bat species in the Wet Tropics World Heritage Area and presents the first models of their predicted response to climate change. Overall, this thesis concludes that climate change will impact bat species richness and diversity with almost 50% of species predicted to experience contractions in the amount of climatically suitable habitat available to them. This research adds to the growing body of evidence about the negative impacts of climate change and highlights the need for swift action to reduce emissions if we are to mitigate predicted global biodiversity loss.

Table of Contents

List of Figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Appendix 1

Appendix 2

List of Tables

Chapter 2

Chapter 3

Chapter 4

Appendix 1

Appendix 2

Chapter 1: General Introduction

The Science of climate change

Climate change is, and will be, a significant threat to the earth and its systems (e.g. Steffen *et al.*, 2011; IPCC, 2013). 'Global warming' first appeared as a scientific concern in the 1980's when the link between greenhouse gas emissions (GHG) and the hole in the ozone layer was made (Crutzen & Stoermer, 2000; Steffen *et al.*, 2011; Corlett, 2012). We now know that since the industrial revolution, increasing amounts of GHGs, and particularly carbon dioxide (CO_2), have been emitted into the atmosphere. These emissions (approximately 40%) remain in the atmosphere stopping heat from the sun, in the form of radiative forcing (the difference of radiant energy received by the earth and energy radiated back to space) from dissipating (IPCC, 2013). Positive forcing (more incoming energy) warms the system, while negative forcing (more outgoing energy) cools it (Meinshausen *et al.*, 2011). The increase in GHG concentrations have contributed to a steady increase in global temperatures since 1950, with rates of warming increasing substantially in the three decades since 1990 (IPCC, 2013; Karl *et al.*, 2015). Since the industrial revolution, the planets climate has warmed an average of almost 1°C (IPCC, 2013).

IPCC 5th assessment report

The 5th assessment report on climate change, released by the Intergovernmental Panel on Climate Change in November 2014 confirms this trend. The report states that 'the human influence on the climate system is clear' and goes on to detail observed changes and their causes, future climate change, risks, and impacts, as well as actions to be taken against climate change (IPCC, 2014). The concept of human induced warming was contested until recently when general concession among the majority of the scientific population was confirmed (Cook *et al.*, 2013; IPCC, 2013). The IPCC states it is 'extremely likely'' that the increase in average global temperature can be attributed to increased anthropogenic greenhouse gas emissions since the pre-industrial era, driven primarily by economic and population growth (IPCC, 2014). Climate change is 'beyond reasonable doubt' being amplified by human influence and we have now entered a period deemed the 'Anthropocene' where the natural environment has been irreversibly changed by the human presence (Garnaut, 2011; Steffen *et al.*, 2011; IPCC, 2013).

Climate change has had observable effects on our earth with the evidence of this being the strongest and most comprehensive for natural systems and the environment (IPCC, 2014). Changes to future climate are not limited to an increase in average global temperatures. We will also see sea level rise, unpredictable weather patterns, and an increase in extreme events such as catastrophic bushfires or devastating cyclones (IPCC, 2013). Indeed, these impacts are already beginning to be documented with climate change linked to increased incidents of devastating bushfires (e.g. Stocks *et al.*, 1998; Russell-Smith *et al.*, 2007), hurricanes and tropical storms (e.g. Knutson *et al.*, 2010), flooding (e.g. Hirabayashi *et al.*, 2013; Singh *et al.*, 2014), and severe drought (e.g. Diffenbaugh *et al.*, 2015; Trenberth *et al.*, 2015).

It has been demonstrated that this environmental change, particularly in the highly diverse tropical areas of the globe, is occurring at rates relevant to biodiversity conservation and quicker than the potential of species to adapt to change (Corlett, 2012; VanDerWal *et al.*, 2013). Climate change is no longer an abstract concept for the future but rather its impacts are already being felt and its effects are already needing to be managed. Increasing numbers of international scientists are voicing their concerns about the impacts continued and increased carbon emissions will have on the earth (e.g. Parmesan & Yohe, 2003; Beaumont *et al.*, 2011; Bellard *et al.*, 2012; Hansen *et al.*, 2013; Rummukainen, 2015). Although some of the impacts could be positive, such as increased agricultural productivity or vegetation growth in some regions, benefits would likely dissipate over time as warming increased (Mendelsohn *et al.*, 2006; McMahon *et al.*, 2010; IPCC, 2013). Overwhelmingly, the evidence suggests climate change will have negative, and is some cases deleterious, effects (IPCC, 2013).

Global climate change and its threat to biodiversity and ecosystem functioning

Until recently, deforestation was considered the biggest threat to biodiversity (Corlett, 2012). Climate change was not considered to be occurring fast enough to be of more relevance to conservation then rates of deforestation (Laurance, 2010; Corlett, 2012). However, over the last decade it has become increasingly clear that climate change is a greater and more pressing threat (IPCC, 2013; Rapacciuolo *et al.*, 2014). Loss of global biodiversity, and with it important ecosystem functions, will be one of the biggest impacts climate change will have on the earth (Surasinghe, 2010; Cahill *et al.*, 2012; Cardinale *et al.*, 2012). There is growing body of evidence to suggest that this will be the case. For example, climate change is predicted to increase warmth and acidification of the earth's oceans, lowering productivity and resulting in species losses (Halpern *et al.*, 2008; Bellard *et al.*, 2012; Gattuso *et al.*, 2015). Such losses, particular of the world's coral reefs, are predicted to negatively impact ocean systems (Gattuso *et al.*, 2015). The loss of coral biodiversity will remove important breeding and nursery grounds for many species of fish, while the loss of reef structure itself will have implications for coast lines worldwide with sea level rises and increases in wave activity expected (Gattuso *et al.*, 2015). The loss of the world's bee biodiversity is another extreme example of the impacts of climate change on ecosystem functioning. Bee populations are threatened and in decline, with climate change documented to be a primary cause of this (Brown & Paxton, 2009; Potts *et al.*, 2010; Bartomeus *et al.*, 2013b). Bees are important pollinators in many landscapes; the loss of bee biodiversity will mean that many species of plant that rely on bee pollination will also decline, including many important feed crop species (Goulson *et al.*, 2008; Brown & Paxton, 2009; Potts *et al.*, 2010; Bartomeus *et al.*, 2013a).

These are just two specific examples of how biodiversity loss will impact life on earth. The scale of biodiversity loss is only just beginning to be understood with some predicting we may be entering the sixth mass extinction, where we could lose more than three quarters of species alive today (Barnosky *et al.*, 2011). Changing and unpredictable climate may cause a decrease in overall fitness, loss of individual life, loss of genetic diversity, or local or global extinctions (Barnosky *et al.*, 2011; Bellard *et al.*, 2012). To persist under changes to preferred climatic niche individuals must be able to respond in the short term and the species as a whole adapt in the longer term. Species are predicted to respond to climate change in three, non-mutually exclusive ways; time (e.g. phenology), space (e.g. distribution) and self (e.g. physiology) (Bellard *et al*, 2012) (Figure 1.1). A species could change daily behaviours to cope with new conditions in their environment. They may feed earlier or later in a day to cope with changed temperatures or even feed on different foods (Parmesan, 2006). For example, koalas (*Phascolarctos cinereus*) have been found to choose different species of eucalypt for shelter in the day and feeding at night to cope with increased temperatures (Crowther *et al.*, 2014).

A species might alter the timing of major life events to reflect new environmental conditions. This may include earlier or later migration, hibernation, or breeding times (Root *et al.*, 2003). Australia's Common Koel (*Eudynamys scolopacea*) is among one of many species of bird found to be arriving at breeding grounds earlier than they did historically (Chambers *et al.*, 2013; Chambers *et al.*, 2014). Another study provides evidence for the impact of climate change on both early migration in American Robins (*Turdus migratorius*) and early hibernation emergence in Yellow-bellied Marmots (*Marmota flaviventris*) found to be linked to warmer springtime temperatures (Inouye *et al.*, 2000).

Finally, a species may track preferred environmental conditions, moving through space to new, more suitable habitats rather than try and acclimatise to new conditions in their current habitat.

In many cases, spatial shifts have been found to occur poleward ('latitudinally' with species moving away from the equator) or upslope ('elevationally' toward higher elevations) (Hughes, 2003; Parmesan & Yohe, 2003; Hickling *et al.*, 2006).

Shifts in species' distributions are perhaps currently the most documented impact of climate change, with latitudinal shifts being more frequently reported than elevational changes (Parmesan & Yohe, 2003; Lenoir & Svenning, 2015). Species has been found to move away from the equator at an average rate of 16.9 km per decade, and to higher elevations at a rate of 11m per decade (Chen *et al.*, 2011). An analysis of over 300 British species, including insects, fish, reptiles, birds, and mammals found that the vast majority (84%) have expanded their distribution northward during the last quarter of the 20th century (Hickling *et al.*, 2006). Vagile species like birds and butterflies have also been found to shift their distributions further north with increasing temperatures (Lenoir & Svenning, 2015). Similarly, butterfly species in Europe were found to be shifting their distributions higher in elevation with changing climatic conditions (Wilson *et al.*, 2005; Lenoir & Svenning, 2015). This elevational change in distribution was found to make these species more vulnerable to extinction as it significantly increased spatial isolation (Wilson *et al.*, 2005). Similar patterns have been found across the global with bird species in South America shifting their distributions to higher elevations (Forero-Medina *et al.*, 2011), mammal distributions in North America have shifted north (Guralnick, 2007), as have some species of insect in Asia driven by milder winter conditions (Tougou *et al.*, 2009).

Spatial changes are perhaps more restrictive to a species than changes to self or time as such movement poses hard barriers for a species, limiting capacity to track suitable conditions. Species will only be able to shift their range so far before they reach hard boundaries that cannot be crossed (Gaston, 2000). Such boundaries include reaching habitat limits (suitability or availability), temperature limits, or top of mountains restricting further movement (Thomas, 2010). For example, a species may gradually move to higher elevations on a mountain gradient as it tracks preferred environmental conditions. Once the species reaches the mountain peak there is no room left for the species to move. Then, the species must respond to altered environmental conditions through changes to self or time, or face extinction from that location.

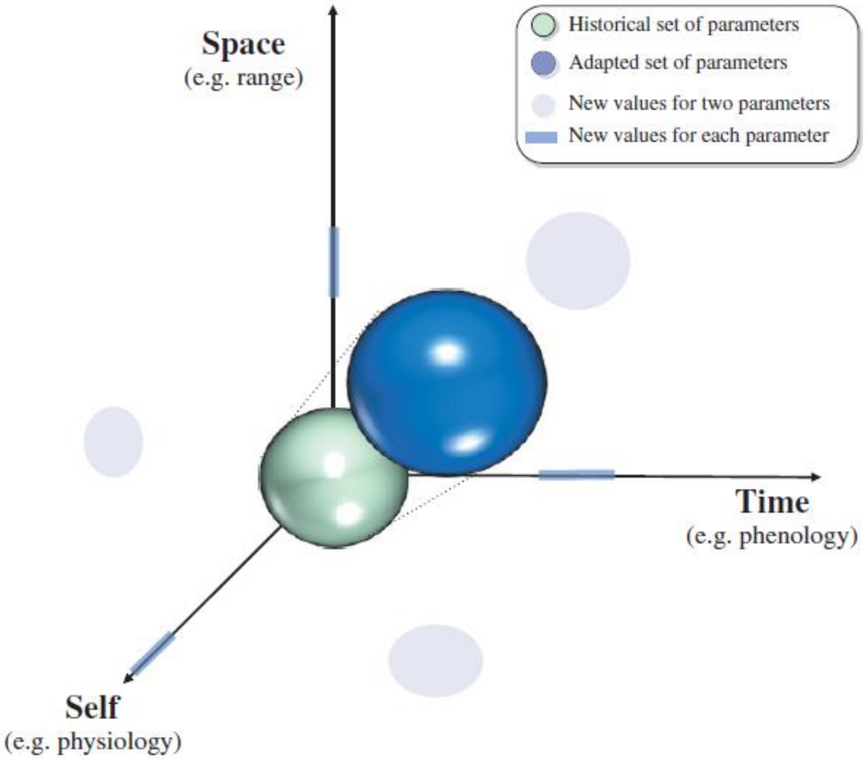


Figure 1.1 The three directions of responses to climate change through phenotypic plasticity or evolutionary responses: moving in space (dispersing to areas with suitable habitat or changing location on a microhabitat scale), shifting life history traits in time (adjusting life cycle events to match the new climatic conditions, including phenology and diurnal rhythms), or changing life history traits in its physiology to cope with new climatic conditions. Species can cope with climate change by shifting along one or several of these three axes (Bellard *et al*. 2012).

Drivers of species' distributions

Many different potential drivers of species' distribution trends have been proposed, however it is clear that climatic mechanisms have important effects on species movements (Clarke & Gaston, 2006; McCain, 2007). In general, distribution trends for most flora and fauna can be related to either temperature, water availability, or a combination of the two, with both being strongly correlated with latitude and elevation (Hawkins *et al.*, 2003; Clarke & Gaston, 2006; McCain, 2007). Shifts in species' distributions with environmental change is a well-studied phenomena (Parmesan & Yohe, 2003; Root *et al.*, 2003; Thomas, 2010; Chen *et al.*, 2011; Cahill *et al.*, 2012; Virkkala & Lehikoinen, 2014). Species' distributions generally increase poleward and upslope, primarily with increases in temperature (Parmesan & Yohe, 2003; Root *et al.*, 2003; Chen *et al.*, 2011). For elevational shifts, while temperature is the primary driver of upslope movement, there is evidence to suggest that shifts in distribution downslope may be more linked to increased precipitation (Rapacciuolo *et al.*, 2014).

Climatic factors, such as temperature and water availability, may affect species directly or indirectly. Generally, climate may limit a species' diversity or distribution as extreme conditions may act as a barrier to areas and conditions outside a species' physiological tolerance (Portner, 2002; Parmesan, 2006). It has already been established that shifts in distribution offer limited adaptation capacity for a species. Once a species reaches hard physical barriers or physiological barriers it cannot cross, if it can't respond in other ways, it will perish. This may make species that shift their distributions in response to climate change particularly vulnerable to extinction. This may be particularly true of tropical, highly biodiverse regions of the globe (Corlett, 2012).

Tropical rainforests as biodiversity strongholds

Biodiversity worldwide is under threat and facing many different challenges (Barnosky *et al.*, 2011). Tropical rainforests have been acknowledged as biodiversity hotspots worldwide (Malcolm *et al.*, 2006). Generally congregated around the equator, tropical areas cover a large portion of the world's land mass and contain a greater species richness in comparison to temperate areas. Despite this, much of the work to date on the impacts of climate change has been conducted in temperate areas and particularly North America and Europe (Lenoir & Svenning, 2015). This lack of study, coupled with high biodiversity, makes these tropical systems perfect study ecosystems. This is particularly true of Australia's Wet Tropics World Heritage area (hereafter referred to as 'the Wet Tropics'), which is currently regarded as one of the best studied tropical rainforest systems in the world (Welbergen *et al.*, 2011). The high biodiversity, relatively small geographic range, and stable paleoclimatic conditions makes this area ecologically interesting (Williams & Pearson, 1997; VanDerWal *et al.*, 2009a; Welbergen *et al.*, 2011). The biogeographic history of the region, and documented rainforest expansions and contractions, have been credited with determining the patterns of species' distribution observed today (Williams & Pearson, 1997; VanDerWal *et al.*, 2009a; Welbergen *et al.*, 2011) (Figure 1.2a and 1.2b).

Numerous studies have investigated the potential impact of climate change on the biodiversity of the Wet Tropics (Shoo *et al.*, 2006; Isaac *et al.*, 2009; VanDerWal *et al.*, 2009a). For example, herpetofauna, and microhylid frogs in particular, are predicted to be the most vulnerable Wet Tropics species to the impacts of climate change with temperature found to reduce frog populations and distributions (Williams *et al.*, 2003; Shoo & Williams, 2004; Issac, 2008; Welbergen *et al.*, 2011). Changes to patterns of bird distribution and species richness in the region have also been linked to changes in temperature (Williams *et al.*, 2010a; Anderson*,* 2011). At least 74% of these species are predicted to be threatened by mid-range climate warming, with some 30 species likely to become critically endangered (Shoo et al., 2005). Non-volant mammals are predicted to respond in similar ways too, with distributions and species richness in the Wet Tropics known to decrease to the north and south of the region (Williams, 1997).

In order to predict how species will respond to climate change on a distributional level we must first understand where species currently exist and why. Thus, many studies conducted in the Wet Tropics have focused on species' distributions and modeling preferred climatic conditions (e.g. Bateman *et al.*, 2012; Storlie *et al.*, 2013; Staunton *et al.*, 2014; Nowrouzi *et al.*, 2016). Results of these studies predict severe declines in the amount of area supporting suitable environmental niche. This decline is predicted to affect the region's species, particularly those restricted to upland mountainous areas (Williams *et al.*, 2003; Thomas *et al.*, 2004; Shoo *et al.*, 2005). Indeed, the isolation of the Wet Tropics rainforest provides little opportunity for species to shift their distributions meaning species inhabiting them may be particular vulnerable to climate change (Welbergen *et al.*, 2011). It is therefore crucial we determine how climate change may impact on species' distributions in order to appropriately conserve them.

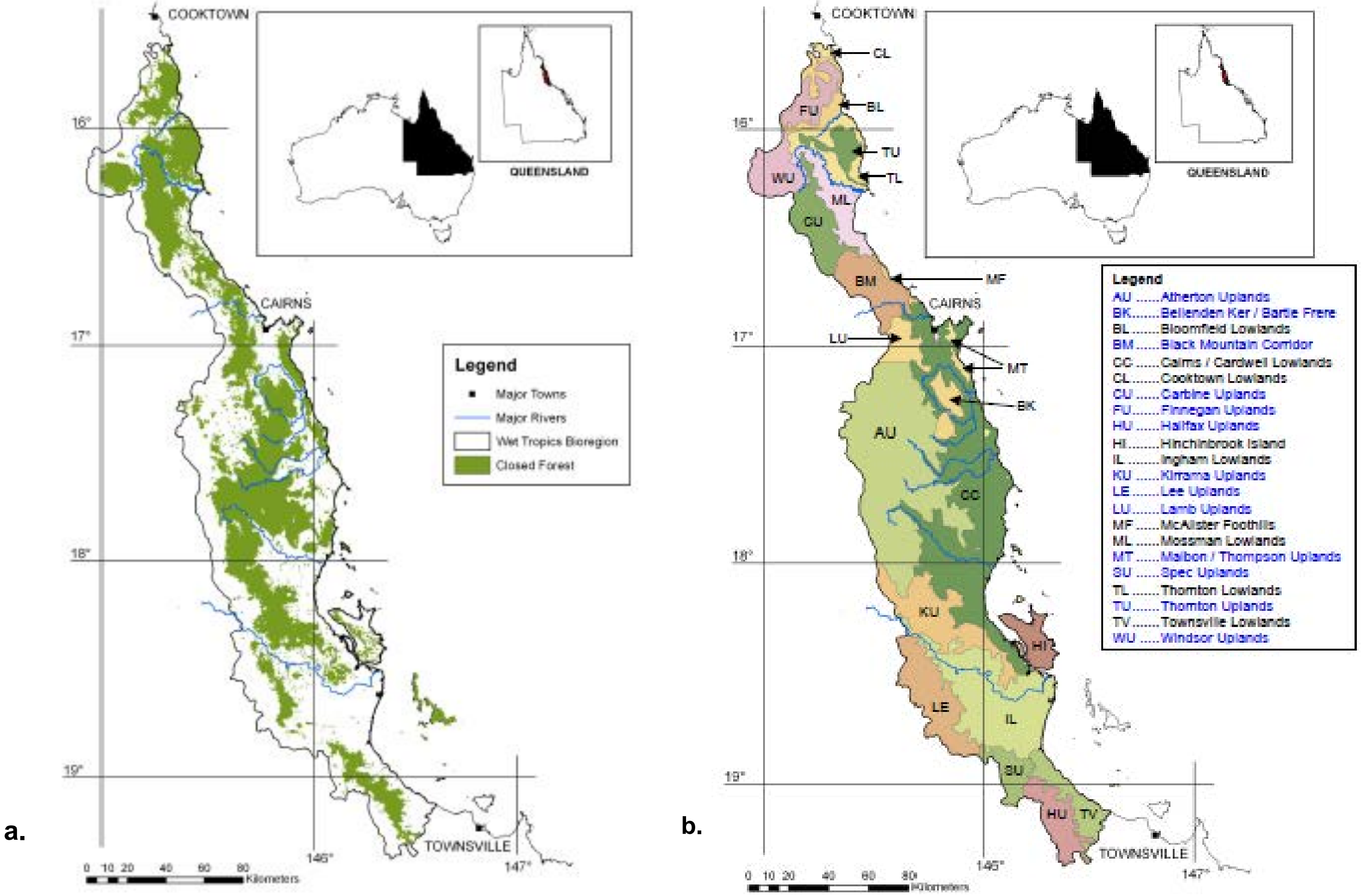


Figure 1.2a Map of the Wet Tropics showing the current extent of rainforest habitat. Figure 1.2b Map of the Wet Tropics bioregion showing the areas subregion (from Williams, 2006).

Species Distribution Modelling for biodiversity conservation

Environmental niche modelling, or Species Distribution Modelling, is a common method used to determine current and potential distributions of species (e.g. Elith *et al.*, 2006). Species Distribution Models (SDMs) assume that information about where a species is observed provides insight into the environmental limits of a species by correlating observations with environmental conditions (Phillips *et al.*, 2004). This has practical applications for species conservation and has become particular well used for predicting how biodiversity may be impacted by global climate change (Phillips *et al.*, 2004; Beaumont *et al.*, 2005; Beaumont *et al.*, 2007; Renwick *et al.*, 2012; Vasconcelos *et al.*, 2012). Possible future scenarios can be predicted by correlating what is known about a species now with possible future environmental conditions. In order to help scientist determine what such future environmental conditions and outcomes may be, the IPCC report details Representative Concentration Pathways (RCPs) (IPCC, 2013). These RCP scenarios are based on greenhouse gas emissions (GHG) concentration trajectories and describe future climatic conditions under certain amounts of GHG emission, spanning a range of years to 2100 (Meinshausen *et al.*, 2011). A number of modelling tools are available for use, each with their strengths and weaknesses. Maximum-Entropy modelling, or 'Maxent', is one of the best and most widely used species distribution modelling tools available and was chosen as the most suitable program for this analysis due to its ability to run using small sample sizes and presence only data (Phillips *et al.*, 2004; Elith *et al.*, 2006).

Modelling emphasises the fact that many environmental factors, taken in combination, define a species' distribution. This can include aspects of a species' environment such as elevational gradients, species-energy relationships and morphological characteristics, and physical barriers (Gaston, 2000). However, as established above, climate is thought to be a major driver of distribution patterns for many species. Being so strongly affected by water availability and temperature means tropical biodiversity is considerably more vulnerable to the effects of climate change than temperate biodiversity (Corlett, 2012). This is primarily due to high species diversity, already limited distributions and smaller thermal tolerance ranges (Colwell *et al.*, 2008; Cadena *et al.*, 2012).

The missing 15% - bat biodiversity and why it's important

Although the region's fauna is generally well studied, a significant gap in our understanding of overall biodiversity in the area remains. Despite accounting for approximately 15% of the region's vertebrate diversity, and over 50% of the region's mammal diversity, bats (order:

Chiroptera) have largely been omitted from biodiversity studies in the Wet Tropics. For example, an atlas of vertebrates of the Wet Tropics provides diversity and distribution information for close to 200 species in the region, none of which are bats (Williams, 2006). The limited amount of previous work conducted in the regions tend to focus on a single species (such as studies investigating the distribution of the flute-nosed bat *Murina florium* (Clague *et al*., 2000*;* Kutt & Schultz, 2000)) or a single site (such as a study, published in 1988, which characterised habitat use and community composition for 12 detected species in the Windsor Uplands (Crome & Richards, 1988)). A 2004 PhD study did look at bat community assemblage at four sites across the Wet Tropics, detecting 22 species forming 12 distinct assemblages (Clague, 2004).

The limited number of bat studies in the Wet Tropics may be due to the fact that bats are highly mobile making them somewhat difficult to survey, and it has only been in the last few decades, with the advent of echolocation monitoring equipment, that bat studies have become easier to conduct. Bats provide an interesting case study for investigating the effects of climate change due to their unique morphological characteristics (McCain, 2007). They are small endothermic organisms, with long life spans relative to their size. This, coupled with their high mobility and variety of ecological traits make them an informative case study for climate impacts research. High mobility may allow them to move to more suitable environments more readily than other small mammals. On the other hand, their longevity and lengthy reproduction cycle may mean they are less likely to genetically adapt to changes in environmental conditions in an adequate timeframe than species with shorter generation lengths. Additionally, the high species variation found in bats makes them an ideal study taxon for investigating how species' distributions may be affected by a changing climate as their unique set of traits offers comparisons with those of a variety of other taxa. Such high diversity makes them a good proxy for investigating how other taxa, and biodiversity as a whole, might be affected by environmental and climatic changes predicted to affect the Wet Tropics.

Thesis Aims

Taking the above information and rationale into consideration, the aim of this PhD research is to determine the current and future biogeography of echolocating bats in the Wet Tropics World Heritage Area and assess how bat diversity in the region may be impacted by global climate change. These research goals have been achieved by:

1. determining distribution and community composition of bats in the study region (what exists where and why this may be) by

    a. determining what species are present in the region.
    b. determining what areas of the region these species inhabit.
    c. determining what environmental factors may influence observed distributions.
2. increasing knowledge of overall biodiversity in the region by
    a. building knowledge of biodiversity in the entire region, not just in areas sampled above.
    b. producing models of potential species distribution based on known locations.
    c. determining the most accurate models for projecting future predictions on to.
3. predicting the impact of climate change on bat distributions in the Australian Wet Tropics by
    a. producing future species distribution models based on predicted future climate scenarios.
    b. commenting on the implications of this research.

Thesis Structure

Chapter 1: General Introduction.

The thesis introduction (this chapter) gives general background information of climate change, its importance and threat, and its impacts on biodiversity. Above, the research topic has been explored further and the thesis structure is now outlined.

Chapter 2: Climate, not elevation, drives bat species' distributions in the Australian Wet Tropics World Heritage Area.

This chapter investigates patterns of bat species richness and community composition in the rainforests of the Wet Tropics. Species richness is quantified and patterns are explored to determine whether species and community-level distribution patterns can be best explained by elevationally driven changes or by climatic factors. This study determined that elevation itself does not account for patterns in species' distributions. No evidence of a relationship between richness and any climatic variables, nor between richness and elevation or latitude alone was found. However, analysis indicated that patterns in bat species' probabilities of occurrences are primarily driven by temperature seasonality, with precipitation and subregion variables also being influential. Data collected during field studies outlined in this chapter provide the basis for analyses presented in Chapter 3.

Chapter 3: Improved understanding of local biodiversity using global information: a case study of bats in the Australian Wet Tropics.

Chapter 3 builds on the work presented in Chapter 2 through the production of Species Distribution Models for all species predicted to currently inhabit the Wet Tropics (not just the rainforest species recorded in Chapter 2). These models provide a more complete picture of bat diversity in the region. Crucially, however, it determines that the most accurate models of species distribution in the region contain information from the species' wider distribution and are not limited to information from the study region only. Methods and results of this chapter provide the basis of analyses presented in Chapter 4.

Chapter 4: Winners and losers: the expansion and contraction of Wet Tropics bat species' distributions with climate change.

This chapter builds on data and methods developed in previous chapters to determine how individual species, and bat species richness in the Wet Tropics as a whole, will be affected by climate change. Future species' distributions under two different climate change scenarios, and across multiple time steps into the future, are modelled. The change in, and movement of, species' distributions in the future is also explored. This study predicts that environmental conditions will become more suitable for almost half of the modelled species (46% survivors or 'winners') but less favourable, resulting in a contraction of distribution, for half of species as well (46% of species). Results of this chapter are linked to other work being conducted in the CTBCC (particularly work around 'refugia'), and comments are made around the need for global mitigation strategies.

Chapter 5: General Discussion

Chapter 5 provides a summary of the thesis and a general discussion around the major findings. This chapter focuses on the ecological impacts of climate change on the species discussed within the thesis, and what impact changes to individual species' abundances and overall species diversity may have on Wet Tropics biodiversity as a whole. This chapter concludes with a brief discussion on the merit of immediate mitigation action.

Regarding the structure of this thesis, Chapters 2, 3 and 4 present stand-alone data chapters written primarily for the purposes of peer review publication. Unfortunately, this means that there may be some repetition throughout this thesis. Efforts have been made to keep this to a minimum and links to other relevant chapters, as and where appropriate, have been included for reader ease. The following thesis contributions (included as appendices) were originally planned to be stand-alone chapters. However, for various reasons (see in text) these pieces of work did not form stand-alone chapters and thus have been submitted as appendices. This thesis contains two appendix chapters. These are:

Appendix 1: Distance of acoustic detection of ultrasonic sound in tropical rainforests.
This appendix details a pilot study designed to determine how well ultrasound, and naturally occurring bat calls, are detected in a rainforest environment. This study was originally intended to become a data methods chapter in this thesis. However, unforeseen challenges with the equipment used for this experiment resulted in a very low sample size meaning this chapter is unpublishable. Data collected during this experiment was analysed nonetheless, and the chapter was formally written, in order to hone statistical analysis and thesis writing skills. It has been included in the thesis as an appendix as it represents what could have been an important pilot study and could provide the basis for further study in the future. However, results presented within must be considered with extreme caution. How far pulses travel, and how well different pulse types (Constant frequency (CF), Frequency modulated (FM)) can be detected was measured from varying positions within the rainforest canopy using an artificial ultrasonic source (chirp board, or ‘electronic bat’). Preliminary results suggest constant frequency (CF) type pulses have a slightly better probability of detection below the canopy than FM type pulses with these results being consistent with trends found in naturally occurring bat calls. The results of this study suggest a negative association between probability of detection, distance and vegetative clutter. This pilot study could provide the basis of further study on how to optimise detection ability during field surveys.

Appendix 2: Bats of the YUS conservation Area, Papua New Guinea.
This report details work conducted in Papua New Guinea during my candidature. Data collection, analysis, and drafting of the report represent my contribution. This work was originally intended to also form a stand-alone chapter in the thesis. However, the data necessary to make this work comparable to existing chapters was not readily obtainable at the time. Nevertheless, this was a significant piece of work undertaken during this PhD candidature and is thus included in this thesis as an appendix. This study provides important baseline data on species inhabiting a newly formed conservation area in Papua New Guinea and a description of bat distributions across a complete altitudinal gradient (from sea-level to 3000m). The resulting report assembles the largest reference collection of echolocation calls for Papua New Guinean bats (22 species). This appendix contains the report in its final format, as submitted to the funder. This means that some outdated terms, such as ‘microbat’ and ‘microchiroptera’ are used within the text.

Chapter 2: Climate, not elevation, drives bat species' distributions in the Australian Wet Tropics World Heritage Area

Abstract

Understanding the processes that drive species' distributions is an important first step in mitigating biodiversity loss. Many studies have documented the correlation between elevation and/or latitude and the distributions of plant and animal species. Across numerous taxonomic groups species richness has been shown to peak at mid-elevations or to display a monotonic decline with increasing elevation. Assemblages of insectivorous, echolocating bats have also been shown to exhibit patterns of distribution associated with elevation, but these are not consistent across studies conducted at different latitudes. These relationships with elevation per se, are not causal, however. Rather, species' distributions reflect climatic and environmental variables that themselves systematically co-vary with altitude or latitude. For example, bat species richness generally decreases with elevation in the tropics, but exhibits mid-elevational peaks in temperate zones. A combination of temperature and precipitation, acting on both local and regional scales, is suggested to be the primary driver of this pattern. This study investigates patterns of bat species richness and community composition in the rainforests of the Australian Wet Tropics World Heritage Area and tests whether species and community-level distribution patterns can be best explained by elevationally driven changes or by climatic factors, or some combination of both. Echolocating bats were surveyed at 20 sites along elevational gradients of five different subregions within the Wet Tropics World Heritage Area, spanning five degrees latitude and 1300 meters elevation. Surveys were conducted via passive and active echolocation monitoring, supplemented by trapping. Echolocation call files were analysed to identify species and to provide a measure of species richness for each site. This study assesses evidence of both monotonic decline and mid-range peak patterns in two different ways. First, by examining patterns in species richness against elevation and bioclimatic variables via generalised linear models. Second, by examining community composition patterns against elevation and bioclimatic variables with the statistical approach of mvabund. Total species richness was found to be similar across all subregions. No evidence of a relationship between richness and any climatic variables, nor between richness and elevation or latitude alone was found. However, mvabund analysis indicated that patterns in bat species' probabilities of occurrences are primarily associated with temperature seasonality, with precipitation and subregion variables also being influential. Elevation itself was unable to explain differences in community composition. Individual species responses also confirmed this pattern with species' probabilities of occurrence being associated with aspects of the environment, particularly temperature seasonality, as well as latitude (subregion). These results are congruent with similar studies which attribute temperature and water availability as primary drivers of species' distribution. Results also suggest that richness itself is a poor measure of diversity, and that approaches that assess species' identities and community composition may be more sensitive in detecting distributional patterns and their causes.

Introduction

Patterns of global diversity and the species' distributions that we see today have been formed over the timeline of a species. Drivers of distribution patterns include events in the biogeographic history of the earth, evolutionary processes within a species' lineage, as well as recent and current global environmental conditions (Brown, 2001; Mittelbach *et al.*, 2007; VanDerWal *et al.*, 2009a; Pauls *et al.*, 2013). Assemblages of species (i.e. communities) in specific locations are formed as a result of regional and local processes (Ricklefs, 1987; Presley *et al.*, 2012), with their formation having been linked to environmental gradients. Specifically, changes in species' assemblages along environmental gradients have been attributed to species-specific responses to environmental conditions, including presence of suitable habitat type and appropriate climate, determining individual species distributions, which collectively form the species' assemblage in a given area (Presley *et al.*, 2012).

Studies of the processes leading to current patterns of species' distributions along environmental gradients have become increasingly common in recent decades (e.g. Hodkinson, 2005; Cadena *et al.*, 2012; Lenoir & Svenning, 2015). This is now a crucial branch of science, primarily because these studies are instructive in informing how the impacts of environmental change may determine future global biodiversity and ecosystem functioning (e.g. Hooper *et al.*, 2005; Heller & Zavaleta, 2009; Sekercioglu *et al.*, 2012; Pauls *et al.*, 2013; Urban, 2015). For example, increasing temperatures and more unpredictable rainfall patterns are common predictions of models determining the potential impacts of global climate change. These changes will almost certainly alter both the average, and the range of values, of climatic and environmental parameters that species are exposed to in their current locations (IPCC, 2013). This will have important implications for all species populations and the communities they form (Bellard *et al.*, 2012; Presley *et al.*, 2012; Virkkala & Lehikoinen, 2014).

Climatic changes will bring about variations in the extent and location of areas of suitable habitat, the availability and quantity of suitable food resources, and even changes to the timing of crucial life events such as migration, hibernation, or breeding cycles (Bellard *et al.*, 2012). Under a best-case scenario individual species will independently migrate to track these changes, potentially resulting in the realisation of different community structures. At worst, species will go extinct.

Over 120 theories have been proposed to explain species' distributions (Palmer, 1994). Although no consensus exists, it is generally agreed that patterns are not random and that some aspect of the environment, such as biomass and energy availability (Grime, 1973; Hawkins *et al.*, 2003; Buckley *et al.*, 2012), area (Gleason, 1925), or latitude and/or elevation (Connell & Orias, 1964; Terborgh, 1977; Mittelbach *et al.*, 2007) drives them. In particular, patterns in species richness have been demonstrated to reflect elevation. Evidence for this can be found across broad taxonomic groupings including vertebrate, invertebrate, and plant species (Parmesan, 2006; Chen *et al.*, 2011) with the majority of work being concentrated on birds (Rahbek, 1995; McCain, 2009; Sekercioglu *et al.*, 2012). Nevertheless, the exact nature of the relationship between species richness and elevation is not uniform across taxonomic groups, or even species within them (Rahbek, 2005). For example, a meta-analysis involving 204 datasets of plants, invertebrates and vertebrates revealed 50% of sampled studies, irrespective of species, showed richness to peak at mid-elevations while 25% show a monotonic decline in richness with increasing elevation. The remaining 25% of studies showed a variety of alternative patterns such as 'flat horizontal then decreasing', 'increasing', or 'other') (Rahbek, 2005). These differences likely reflect the fact that elevation is not the primary mechanism determining distributions. Species distributional limits reflect environmental influences associated with individual species' physiological tolerances, behaviours and mobility (Bellard *et al.*, 2012). Thus, individual studies reporting conflicting evidence for patterns associated with elevation may differ because environmental factors, which generally cause distributional limits, may show different patterns of covariation with elevation in different locations. Thus, determining whether elevation, or environmental variables associated with elevation, are most important in setting patterns of species distributions is an important step in beginning to understand how species will behave under a changing global climate.

The mountain gradients of the Wet Tropics World Heritage Area (hereafter the 'Wet Tropics') provide an excellent study region for assessing patterns of species richness against elevation and bioclimatic gradients. The region is described as a globally significant biodiversity hotspot and supports the highest biodiversity of all Australian bioregions (Stork *et al.*, 2009; Welbergen *et al.*, 2011). Decades of research investigating species' distributions across numerous floral and faunal taxa makes the distribution of biodiversity in the Wet Tropics rainforest one of the best and most comprehensively studied in the world (Stork & Turton, 2009; Welbergen *et al.*, 2011). This fact has allowed for some broad generalisations about the relationship between species richness and elevation in the region to be made. Regional patterns in diversity have been attributed to a number of factors including elevation, historical fluctuations in the size of the region's rainforest (over the last 25 000 years) and dispersal from Papua New Guinea (Williams, 1997; VanDerWal *et al.*, 2009a). For example, non-volant mammals are known to decrease in species richness with decreasing elevation and this pattern is consistent even though overall diversity decreases with latitude across the region (Williams, 1997). Here again, however, elevation cannot be inferred as the causal mechanism, because the patterns observed are potentially associated with environmental factors that vary systematically with elevation and latitude.

Despite previous studies of distribution patterns of a wide range of Wet Tropics species, a considerable gap in our knowledge of the biodiversity in the area remains. In the Wet Tropics, bats account for over 50% of the region's mammal diversity and approximately 15% of the region's total vertebrate diversity. Nevertheless, bats have largely been omitted from biodiversity studies in the region (Williams, 2006; Welbergen *et al.*, 2011). As mentioned in the introduction of this thesis, a limited number of bat focused studies have previously been conducted in the region. However, these studies tend to focus on a single species (e.g. Clague *et al.*, 2000*;* Kutt & Schultz, 2000) or a single site (e.g. Crome & Richards, 1988). A PhD study, completed by Clague in 2004, did look at habitat use and community assemblage at four sites across the Wet Tropics (Clague, 2004). The outcomes of Clague's research provided preliminary evidence that some aspects of habitat may drive the distribution of some species in the Wet Tropics (Clague, 2004). However, patterns in biodiversity of bats across the region, and the drivers behind these , remain largely unknown and this raises potential problems when inferring how bat diversity patterns will be associated with elevation or latitude.

The potential incongruity in using elevation in this way is perfectly demonstrated in studies of insectivorous, echolocating bats. Evidence suggests potentially conflicting patterns in bat species richness with elevation, contingent on latitude. A meta-analysis on global patterns of bat distribution produced a model showing that bats could follow either a monotonic decrease or a mid-elevational peaked distribution across elevation, depending on latitude (McCain, 2007)

(Figure 2.1). This has been attributed to bat distributions being fundamentally related to temperature and water availability, with richness related to differences in climatic gradients associated with individual elevational gradients. For example, richness has been found to be highest where temperature and water availability were also high. For temperate areas containing mountains with arid bases and snow-covered or equally arid peaks, the model predicts richness will peak at mid-elevation (approximately an average of 1500 meters above sea level (henceforth m a.s.l.). in the studies examined) since this corresponds to locations where temperature and water availability are simultaneously highest. In the tropics, however, mountains generally have wet, warm bases and cold wet peaks. Under these conditions, the model predicts that bat biodiversity will decline as a response to declining temperature as elevation increases, and will be less strongly associated with changes in water availability (McCain, 2007). Thus, for tropical elevation gradients, such as those in the Wet Tropics, a monotonic decrease in richness with increasing elevation is predicted.

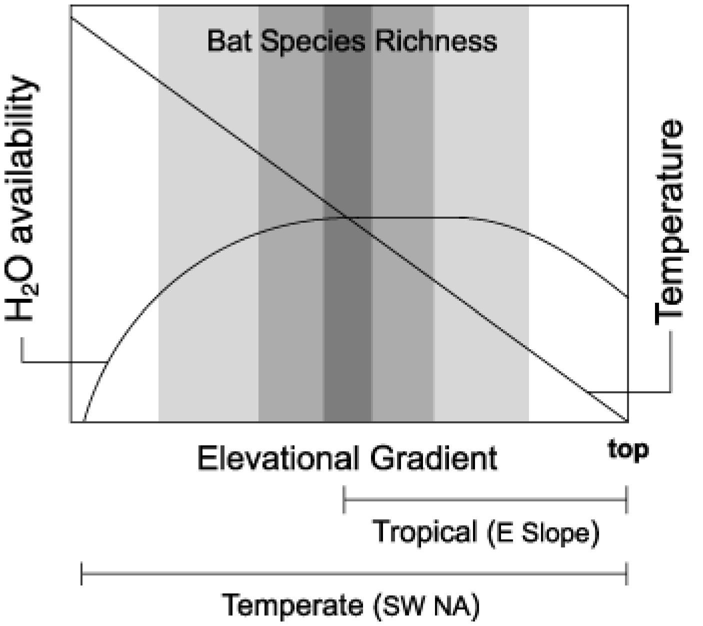


Figure 2.1 "Generalized climatic model for elevational gradients in species richness of bats, incorporating a linearly decreasing temperature gradient and a unimodal water availability gradient. Bat species richness is depicted in grey tones with darker tones indicating more species. The placements of generalized tropical and temperate elevational gradients are shown below the x-axis" (McCain, 2007).

Richness may not be the most appropriate measure for determine species' distribution patterns, however. Richness is particularly prone to bias by undersampling which is often the case when there are many rare species in the landscape. The authors of an Austrian moth study found that richness measures failed to predict moth species' distribution patterns (Fiedler & Truxa, 2012). They attributed the failure of richness as an indicator of distribution to two factors, the fragmented nature of the landscape and the high mobility of the study species. Both of these factors could also impact the result of this of this study. Rainforest habitat in the Wet Tropics are fragmented and bats are highly mobile, often covering vast distances, with the distances between rainforest sites not being inconceivable (Laurance, 1997; Churchill, 2008; Parish *et al.*, 2012). As demonstrated in Fiedler and Truxa's study (2012), this creates a problem when using richness measures to determine species distribution at any one site as site-specific distribution patterns may be 'clouded' by visiting species. Both richness (number of total species) and occurrence (detection of species in a particular space or at a particular time) measures were used to investigate the patterns of species' distribution in the Wet Tropics.

In contrast to elevation and latitude, correlations between climate variables and distribution are also continually being observed for a variety of flora and fauna (Williams, 2006; Thomas, 2010). These correlations are suggestive of causal mechanisms behind observed distribution patterns.. Climatic factors may affect species directly or indirectly. Such factors can include various aspects of temperature, and precipitation, including cloud cover and rainfall (Pounds *et al.*, 1999). Water availability tends to increase with increasing elevation, due to increased cloud stripping, while temperatures decrease toward mountain tops with increasing elevation. Changes to the climate envelope a species regularly experiences may limit expansion to, or even reduce, individual distributions or a species' diversity if change presents conditions outside a species' physiological tolerance. In such instances, climatic change could act as a barrier to distribution expansion or continued or future occupancy (Portner, 2002; Parmesan, 2006). With regard to bats specifically, climate may directly impact physiological tolerances and specific thermoregulation required for sustained flight, roosting, and breeding (McNab, 1989; Patterson *et al.*, 1996; Arlettaz *et al.*, 2000; Welbergen *et al.*, 2008). For example, extreme heat and prolonged periods of dry events have been linked to mass mortality of species who roost together, with such events negatively impacting on flight, foraging and roosting (Welbergen *et al.*, 2008). Such events are predicted to become both more frequent and more intense with changing global climates potentially causing local extinction events in some areas (Welbergen *et al.*, 2008). Although local extinction is an extreme result, it demonstrates how environmental constraints can impose 'hard barriers' to bat distributions, excluding them from locations that present unfavourable conditions (Graham, 1983). Climatic factors, and temperature fluctuations in particular, could also influence bats directly through regulation of important invertebrate food sources as shown in multiple studies across the global, including in Europe, the United States, and Asia (Bale *et al.*, 2002; Hodkinson, 2005; Wolbert *et al.*, 2014).

This study characterises the community composition and diversity of echolocating bats along elevational gradients of five subregions within Wet Tropics (Chapter 1, Figure 2.1a). The relationships between species richness and latitude, elevation, and bioclimatic variables associated with temperature and precipitation are explored. The relative merit of using 'richness' as a measure of diversity by comparing results using simple counts of richness against results from an analysis that specifically account for unique species identities in a community composition context was also assessed. Determining these outcomes should increase understanding of what environmental factors drive species' distributions providing fundamental information to inform effective biodiversity management and conservation.

Methods

Study area

The Wet Tropics bioregion is a World Heritage listed area spanning approximately 1.8 million hectares (Chapter 1, Figure 1.2a). Tropical rainforest is one of the region's predominant vegetation types, covering approximately 1 million hectares (Williams, 2006) (Chapter 1, Figure 1.2b). The region contains a number of elevational gradients (mountain ranges) ranging from sea level to 1600m a.s.l. Approximately one-third of the Wet Tropics bioregion is higher than 600m, where annual mean temperatures are generally below 22°C (Stork *et al.*, 2009). Annual rainfall throughout the Wet Tropics is high (ranging between 1500mm to 9000mm per year), with the majority of rain falling between November and April (Bonell & Callaghan, 2008).

Surveys were designed and conducted to detect and identify bat species across elevation gradients of five subregions within the Wet Tropics (between 20°S, 147°E and 15°s, 145°E). Subregions surveyed were the Windsor Uplands, Carbine Uplands, Lamb Uplands, Atherton Uplands and Spec Uplands subregions (Chapter 1, Figure 1.2a). Survey locations were selected to be representative of altitudinal and latitudinal gradients of rainforest habitats across the study region (Annex 2.1, Table 2.1.1). Surveys were conducted at 20 separate rainforest sites (5 subregions x 3 – 6 transect locations per subregion) during 2010 to 2012. As rainforest habitats were the focus of these surveys, not all elevations at each subregion were sampled due to the absence or inaccessibility of low-land tropical rainforest at some elevations. Subregions were surveyed randomly throughout the year, and at least twice throughout the study, to mitigate against any potential seasonal bias. Elevational gradients and individual sites were: Windsor Uplands (approx. 900m, 1100m, and 1300m); Carbine Uplands (approx. 100m, 400m, 600m, 800m, 1000m and 1200m); Lamb Uplands (approx. 700m, 900m, and 1100m), Atherton Uplands (approx. 200m, 400m, 600m, and 800m); and Spec Uplands (approx. 350m, 600m, 800m and 1000m) (Annex 2.1, Table 2.1.1).

Data collection

To estimate bat species presence and overall species richness passive echolocation surveying and standardised transect surveys were used, combined with flight-intercept capture data. Multiple survey methods were undertaken to generate the most complete representation of bat presence possible at each location. This also helps to reduce any potential bias in the ability of different techniques to detect different species, thus maximising the detection probabilities of all species.

Surveying trips generally surveyed one entire elevational gradient (subregion) at a time, with surveys lasting for approximately eight nights per site. AnaBat SD1 CF bat detector units (Titley Scientific, Ballina, NSW, Australia) were used to record bat presence. At each site a one kilometre transect has been constructed parallel to the elevational contour (Figure 2.2). A single AnaBat SD1 CF detector was placed within the rainforest in a position under the canopy, usually at a point approximately 200m along the sampling transect (Figure 2.2). All detectors were elevated from ground level and had their microphones angled at 45 degrees toward the canopy, allowing the maximum possible space under the canopy to be sampled (as suggested by AnaBat creator C. Corben; http://users.lmi.net/corben/). This survey method was chosen as the best way to detect the greatest range of species when conducting a standard bat survey, ensuring the most accurate picture of species richness at each survey site (see the preliminary study reported in Appendix 1 for further detail).

Detectors were calibrated and pre-programed to begin recording 30 minutes prior to sunset and to automatically shut down 30 minutes after sunrise, independent of time of year and day length. Data collected from AnaBat recorders was supplemented with flight intercept trapping (generally two 4.2m^2 two-bank harp traps) and standardised passive surveys (similar to Williams (2006) who used this survey design to survey birds, frogs, and non-volant mammals). Harp traps and mist nets were erected across or along forest tracks at sites along the 1km transect during the survey period. Generally, two large two-bank harp traps and two small five bank harp traps were erected along with four mist nets. Traps were set up at one site per night, opened at the approach of sunset, and monitored for approximately six hours. Individual bats trapped were identified to species using a variety of morphological measurements (forearm length, ear length, etc.) compared against the identification key provided in Churchill (2008). Once individuals were measured and identified to species, echolocation calls were recorded upon the release. These release calls were cross-referenced to passive recordings to help confirm the identification of recorded species. Additionally, standardised surveys, based on a single timed traverse of the one kilometre transect over a one hour period, were performed (Figure 2.2). These standardised surveys were conducted with a hand-held AnaBat detector logging the number of bat passes (calls) at each elevational site.

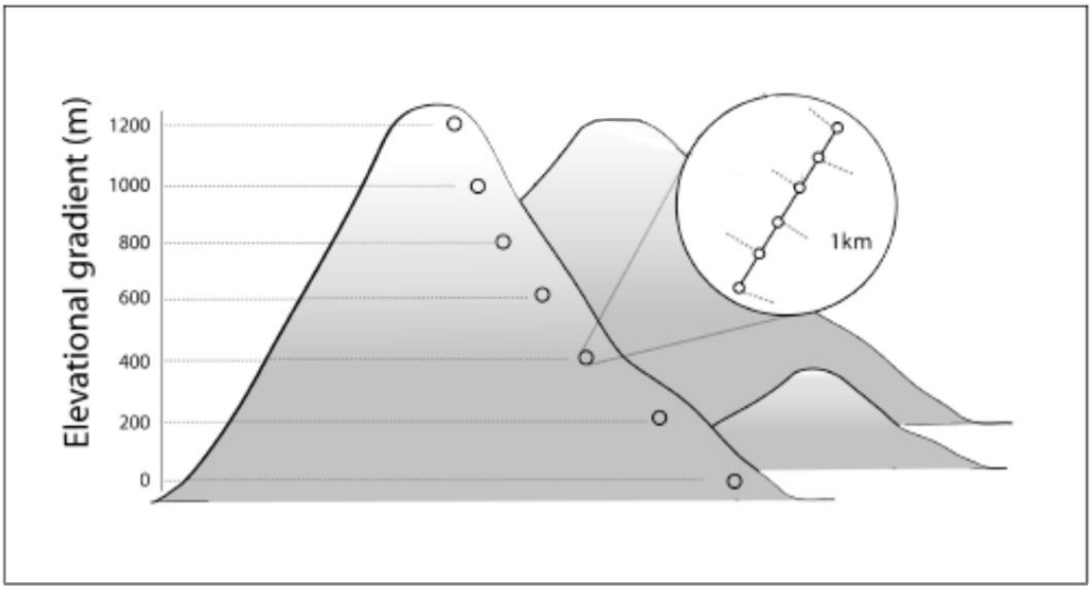


Figure 2.2 Schematic diagram indicating the sampling design used in this study. Each subregion sampled consist of an elevational gradient within the range of 100m a.s.l. to 1300m a.s.l., with survey sites along the gradient separated by 200m. Each survey site (20 in total) consisted of a 1km transect (as portrayed in the inset circle). Passive surveying was conducted at a single location (generally the second point on the transect) while active sampling was conducted along the entire 1km length (see text for details). Schematic adapted from Anderson (2011).

Species identification and data analysis

All AnaBat files were downloaded at the completion of each survey period and examined for bat calls. Files (individual sonograms) were considered to contain a call, and thus a record of species presence, when three or more pulses occurred in sequence (Corben & O'Farrell, 1999). All calls were viewed using the call-analysis program AnalookW (Version 0.3.7w, Corben 2009), and identified to species by comparing each sonogram against recorded release calls from known species (see above), and/or by reference to previously published call libraries and descriptions of known species (Crome & Richards, 1988; Reinhold *et al*., 2001; Milne, 2002; Pennay *et al*., 2004; Clague, 2004; Churchill, 2008; Inkster, 2008; Robson *et al*., 2012; Reardon *et al*., 2014). Calls that could not be confidently identified to genus or species were assigned a species code based on the shape and frequency of the call (after Corben, 2007, pers. comm). For example, a frequency modulated call (see Appendix 1 for further detail) with a characteristic frequency (the frequency at the flattest part of the call) of 16 kHz would be given a code of fm16.

Statistical analysis

Patterns in Species Richness

To investigate species richness, absolute counts of species activity (numbers of call files per species) per site, night and location were summarised and converted into presence/absence measures. Confirming that sufficient sampling effort was undertaken to accurately account for all species is an important consideration in studies such as this. Insufficient sampling effort may result in errors in under-estimating (where many rare species in the population are missed) or over-estimating (where common species bias the sample) overall species trends (Fiedler & Truxa, 2012). In order to assess whether sufficient sampling effort was conducted, the adequacy of sampling effort to produce accurate species richness estimates was explored using EstimateS (Colwell, 2004, version 8.2.0, http://viceroy.eeb.uconn.edu/EstimateS/). EstimateS is a re-sampling program that provides diversity estimates and their confidence limits based on the sampling effort performed during the study, helping to identify any confounding effects of sample size. Sampling effort is presented here in the form of species accumulation curves based on EstimateS Chao1 richness estimates and 'observed richness' based on actual counts of species detected during surveying. These curves indicate how well the methods used during this study captured the number of species observed in the sample. An idea of the appropriateness (or completeness) of sampling effort can be gained by examining the trajectory of these curves. Curves approaching an asymptote are considered to show sufficient sampling effort as they indicate that the majority of species estimated to be present in the sample have been accounted for. Accumulation curves for 'predicted' (Chao1 estimate) and 'observed' species richness were produced and assessed for approximation to asymptote, or when curves indicate the majority of samples have been reached within the sampling time.

Observed species richness values for each site and subregionwere assessed against location (elevational and latitudinal) and climatic variables to determine any potential relationship between them and species' distribution. Variables were assessed for collinearity through production of a pair-plot fitted with a smoothing (nonlinear) curve function showing correlations between all possible variable combinations. Climatic variables included four measures of temperature and four measures of precipitation for each of the 20 surveyed sites (see Table 2.1). These variables were derived from BIOCLIM datasets using mean monthly climate estimates (Nix, 1986). Bioclimatic variables representing climate data from 1976-2005 were created using the climates package (VanDerWal *et al.*, 2011a) in R (R Development Core Team, 2011, www.r-project.org). The temperature and precipitation values are based on monthly averages sourced from ANUCLIM 5.1 (McMahon *et al.*, 1995) run on a Digital Elevation Model (DEM) sourced from Geoscience Australia (v3; http://www.ga.gov.au/), created at a 250m resolution base, and georeferenced to the 20 sampling sites used in this study.

Patterns in Community Composition

As richness is a count variable, Poisson Generalised Linear Models (GLM) was used to assess the pattern in richness against all explanatory variables. Patterns in species' distribution across the region were further assessed using a GLM based approach via 'mvabund'; a multivariate generalised linear model analysis package in R (Wang et al., 2015). The mvabund approach is a substantial improvement over standard (historical) community level approaches such as Principal Component Analysis or Non-metric multidimensional scaling because the GLM approach deals with the expected mean/variance relationship and is able to account for species identity (Wang *et al.,* 2012). For this analysis, presence/absence data, for each species in each sample period, was used as it allows assessment of the probability of species' occurrence rather than treating a positive record of detection at any time period as evidence of constant presence at a location (as is implied in the use of simple richness). Because data were presence/absence binomial (logistic) family was selected for the analysis, although mvabund can also account for alternative mean/variance relationships via alternative family specifications. Models were produced using 'manyglm' (to determine best-fit model) and anova.manglm (to determine the statistical significance, and it's direction, of the model for individual species) functions.

Table 2.1 Details of elevation and bioclimatic (bc) variables selected for inclusion in linear modelling of bat species richness and community composition (mvabund) for 20 sites in the Wet Tropics region of Queensland Australia.

Variable name	Description
Elevation	Site elevation (meters above sea level (a.s.l.))
Mount	Site identity (measure of latitude by proxy)
bc01	Annual mean temperature (°C)
bc04	Temperature seasonality (°C, standard deviation *100)
bc05	Maximum temperature of the warmest month (°C)
bc06	Minimum temperature of the coldest month (°C)
bc12	Annual precipitation (mm)
bc13	Precipitation of the Wettest month (mm)
bc14	Precipitation of the driest month (mm)
bc15	Precipitation seasonality (Coefficient of Variation)

General statistical approach

For all model fitting exercises, a sequential forward-step philosophy was adopted to generate a single final model that included all (and only) significant explanatory variables (i.e. the minimum adequate model) (e.g. Annex 2.2, Table 2.2.1). This approach, and the use of mvabund in particular, was chosen as the resampling-based testing allows for assessment of which climatic variables are associated with community or species patterns taking into account correlation between species (Wang *et al.*, 2012). Modelling was performed by first testing the explanatory power and significance of each variable alone, choosing the variable that explained most deviance, then testing all other variables after the inclusion of the first. This process was iterated until a final model was constructed whereby no further terms were significant. To assess competing hypotheses of monotonic decline or unimodal ('hump shaped') patterns in richness or community composition, all analyses included individual measures of temperature and precipitation, as well as their quadratic term. Squaring the variables helps to address the possibility of a unimodal species distribution as each then has the underlying assumption of a parabolic pattern (the fit of individual variables assumes a monotonic relationship). For analysis of richness, poisson regression was used (see above). For the analysis of community composition via mvabund, binomial regression was conducted until a 'best-fit' model was reached. Variables were initially analysed individually and the variable determined to have most explanatory power (based on lowest probability of accepting null, and greatest explained deviance) was chosen (Annex 2.2, Table 2.2.1). Remaining variables were then added to a model including the terms identified above to identify the next most informative variable. This process was repeated until added variables were no longer statistically significant.

Results

Sampling effort

Sampling was conducted over a total of 317 nights, producing 281 usable sample nights (some sample nights were excluded due to equipment failure or inclement weather conditions). When combined with active sampling (27 hours of 1 hour transects) and capture effort via harp traps (approx. 90 hours) sampling effort totals over 3000 detection hours. 'Unusable' samples were not equally distributed across locations, resulting in sampling effort ranging between 38 and 82 sample nights for different elevational gradients (Annex 2.1, Table 2.1.1).

Based on the accumulation curves produced via EstimateS, mean regional species richness was estimated to be approximately 12 species (Annex 2.3, Figure 2.3.1a, Figure 2.3.1b). The upper bound of the predicted species richness for the region peaked at approximately 17 species. Mean observed species richness for the entire region was found to match the predicted richness (approximately 12 species), although no single subregion contained all richness. Accumulation curves for four of the five subregions (Carbine (9 species), Lamb (5 species), Atherton (5 species), and Spec Uplands (4 species)) show curves approaching asymptote within the sampling period, suggesting that the total number of species existing in the sample area that were possibly detected, were indeed recorded in samples (Annex 2.3, Figure 2.3.2). The Windsor Uplands (9 species) accumulation curve not stabilise within the sampling period (Annex 2.3, Figure 2.3.2).

Call analysis and species identification

The presence of 16 potentially unique bat species was confirmed during this study. Species detected in active surveying and individuals physically captured in harp nets were all from species also detected during passive surveying. Of these species, 10 could be confidently identified based on the recorded sonograms. This included the eastern horseshoe bat *Rhinolophus megaphyllus* (3292 call records, 33 captures), the little bentwing bat *Miniopterus australis* (1199 records), the eastern bentwing bat *Miniopterus orianae oceanensis* (80 records), the eastern Forest bat *Vespadelus pumulis* (24 call records, 4 captures), the eastern long-eared bat *Nyctophilus bifax* (18 call records, 5 captures), Northern freetail bat *Mormopterus lumsdenae* (18 records), the diadem leaf-nosed bat *Hipposideros diadema* (8 call records, 1 capture), the eastern Cave bat *Vespadelus troughtoni* (6 records), the flute-nosed bat *Murina florium* (4 records), and the northern broad-nosed bat *Scotorepens sanborni* (3 call records, 7 captures). Additionally, one set of calls could be identified to genus level *Vespadelus* (635 records). These calls probably represent both *V. pumulis* and *V. troughtoni* (based on geographic area and known calls from exiting call libraries). However, as the call structures and frequencies of these species can overlap, positive, distinctive identifications could not be made. Thus, this group of calls were combined and labelled *Vespadelus sp.* (Pennay *et al.*, 2004). The remaining calls (48 records) which could not be identified to species were labelled with a code detailing their call shape and frequency, for potential future identification (see above). As identification could not be confirmed to genus or species level, and unidentified calls numbered so few, coded calls are not discussed below, nor were they used in subsequent analyses.

Of the species that could be confidently identified, three species contributed to over 95% of total species records (Table 2.2). *Rhinolophus megaphyllus* was the most common and widespread species contributing 62.3% to total species records, and was found at all elevations and in all subregions (Table 2.2). *Miniopterus australis* (22.7%), and *Vespadelus sp.* (12%), also contributed high total numbers to total species records (Table 2.2). The remaining species each contributed 1.5% or less to total species records. Of the subregions sampled, bat species richness was found to be highest in the Winsdor and Carbine Uplands (9 species recorded at each) while the Spec Uplands were found to have the least species (4 species recorded) (Table 2.2). The Lamb and Atherton Uplands were intermediate, with five species each.

Patterns of species richness

Species richness across all sites ranged between one and six species with richness across subregions ranging between four and nine species present (Table 2.2; Annex 2.3, Figure 2.3.2). Few variables were found to be correlated (Annex 2.4, Figure 2.4.1). Correlations did appear to exist between latitude and longitude (correlation co-efficient = -1.0) and some climatic variables (e.g. correlation co-efficient of temperature seasonality (bc04) by latitude and longitude = -1.0 and 0.9 respectively). Elevation was found to correlate with temperature variables (bc1, bc05, and bc06) to varying degrees, although no correlation was found between elevation and temperature seasonality. Temperature variables (bc01, bc04, bc05, and bc06) were found to correlate with each other, as were the precipitation variables (bc12, bc13, bc14, and bc15) as to be expected. However, Poisson generalised linear modelling revealed no significant correlation between elevation (Z = 1.044, Pr(>Z) = 0.296) or latitude (Z = -1.740, Pr(>Z) = 0.081) and species richness (Table 2.3). Similarly, no effect of any of the bioclimatic variables on richness estimates (as expected if relationship was monotonic), nor variables squared (as expected under the assumption of a mid-range peak) was found (Table 2.3).

Patterns in Community Composition

In contrast to richness result described above, mvabund modelling, using the same bioclimatic data, revealed that overall patterns of species' probabilities of occurrence were associated with aspects of the environment, as well as latitude (subregion) (Table 2.4). This, presumably, is associated with the increase in sensitivity associated with accounting for species identities, rather than using a simple species counts (i.e. richness). For example, first pass modelling of individual explanatory variables tested alone revealed all to be significant predictors of community composition (Annex 2.2, Table 2.2.1). Step-wise selection of terms based on both significance and the amount of deviation explained resulted in a final model that included the terms: temperature seasonality (bc04) (Wald = 8.094, Pr(>Wald) = 0.001)), subregion ('Mount') (Wald = 6.389, Pr(>Wald) = 0.001), temperature seasonality squared (bc04^2) (Wald = 5.362, Pr(>Wald) = 0.001), precipitation seasonality (bc15) (Wald =3.712, Pr(>Wald) = 0.010), precipitation in the driest month squared (bc14^2) (Wald = 3.345, Pr(>Wald) = 0.021), and precipitation seasonality squared (bc15^2) (Wald =3.089, Pr(>Wald) = 0.036) (Table 2.4), added in that sequence. Thus, variables associated with both temperature and water availability were included in the final model. In terms of temperature, precipitation seasonality and precipitation in the driest month, the quadratic terms were retained in final model, indicating community composition responds to this variable in a potentially unimodal manner. Equally importantly, elevation was not required in the minimum adequate model, as it was unable to explain any deviance after the deviance explained by the above bioclimatic variables.

Table 2.2 Species presence (ordered taxonomically as per Churchill (2008) and Reardon *et al*. (2014)) at each site. Table includes total number of sites present at (presence denoted by 1), total richness per site, total number of captures per site (bracketed numbers to the right of presence notation), and total number of files recorded for each species.

Location	Elevation (a.s.l.)	*Rhinolophus megaphyllus*	*Hipposideros diadema*	*Murina florium*	*Nyctophilus bifax*	*Scotorepens sanborni*	*Vespadelus pumulis*	*Vespadelus troughtoni*	*Vespadelus sp.*	*Miniopterus australis*	*Miniopterus orianae oceanensis*	*Mormopterus lumsdenae*	*Total richness*
Windsor Uplands	900	1	0	0	1	0	1	0	1	1	1	0	6
Windsor Uplands	1100	1 (1)	1	0	1 (1)	0	1 (1)	0	1	0	0	0	5
Windsor Uplands	1300	1	0	0	0	1	0	0	1	0	1	1	5
Carbine Uplands	100	1	1	0	1	0	0	0	1	1	0	0	5
Carbine Uplands	400	1 (2)	0	0	1 (1)	0	0	1	0	0	0	0	3
Carbine Uplands	600	1 (1)	1	1	1	1 (1)	0	0	1	1	0	0	7
Carbine Uplands	800	1 (2)	1	0	1 (2)	1 (3)	0	0	1	1	0	0	6
Carbine Uplands	1000	1	0	0	0	1 (3)	1	1	1	1	1	0	7
Carbine Uplands	1200	1 (2)	1	0	0	0	1	0	1	1	1	0	6
Lamb Uplands	700	1 (19)	0	0	0	0	0	0	0	0	0	0	1
Lamb Uplands	900	1	0	0	0	0	0	0	1	1	1	0	4
Lamb Uplands	1100	1 (1)	0	0	0	0	0	1	0	1	0	0	3
Atherton Uplands	200	1 (1)	1 (1)	0	0	0	1	0	0	1	0	1	5
Atherton Uplands	400	1	0	0	0	0	0	0	0	0	0	0	1
Atherton Uplands	600	1 (4)	0	0	1 (1)	0	1 (3)	0	0	0	1	0	4
Atherton Uplands	800	1	0	0	0	0	0	0	0	0	1	0	2
Spec Uplands	350	1	0	1	0	0	0	0	0	0	0	0	2
Spec Uplands	600	1	0	1	0	0	0	0	0	0	0	0	2
Spec Uplands	800	1	0	1	0	1	0	0	0	0	0	1	4
Spec Uplands	1000	1	0	0	0	0	0	0	0	0	0	0	1
Total site presence		**20**	**6**	**4**	**7**	**5**	**6**	**3**	**9**	**9**	**7**	**3**	
Total capture #		**33**	**1**	**0**	**5**	**7**	**4**	**0**	**0**	**0**	**0**	**0**	
Total #/% call files	**5287 (100%)**	**3292 (62.3%)**	**8** (0.2%)	**4 (0.1%)**	**18 (0.3%)**	**3 (0.1%)**	**24 (0.5%)**	**6 (0.1%)**	**635 (12.0%)**	**1199 (22.7%)**	**80 (1.5%)**	**18 (0.3%)**	

Table 2.3 Summary of poisson GLM fitting for bat species richness against elevation, site and bioclimatic variable (bc) and bioclimatic variable squared. All results are single term models (i.e. richness ~ variable). No individual variable (or squared bioclimatic variable) was significant in describing richness. Thus, forward, step-wise model building was not undertaken. Bioclim variables are described in Table 2.1 above).

Variable	df	Residual deviance	Estimate	Std. Error of estimate	Z	Pr(>Z)
Elev	18	16.407	0.000	0.000	1.044	0.296
Mount	18	14.419	-0.148	0.085	-1.740	0.081
bc01	18	17.266	-0.039	0.080	-0.490	0.624
bc04	18	15.762	0.566	0.439	-1.291	0.197
bc05	18	16.929	-0.069	0.091	-0.757	0.449
bc06	18	17.365	0.027	0.072	0.384	0.701
bc12	18	17.502	0.000	0.000	0.090	0.928
bc13	18	17.038	0.001	0.001	0.695	0.487
bc14	18	16.897	-0.004	0.006	-0.769	0.442
bc15	18	16.784	1.134	1.344	8.440	0.399
$bc01^2$	18	17.316	0.000	0.000	-0.437	0.661
$bc04^2$	18	15.866	-0.094	0.075	-1.250	0.211
$bc05^2$	18	16.977	-0.001	0.001	-0.725	0.468
$bo06^2$	18	17.349	0.001	0.002	0.407	0.684
$bc12^2$	18	17.509	0.000	0.000	0.031	0.975
$bc13^2$	18	17.091	0.000	0.000	0.659	0.510
$bc14^2$	18	16.904	0.000	0.000	-0.758	0.448
$bc15^2$	18	16.933	0.616	0.816	0.755	0.451

Table 2.4 Summary of best-fit binomial GLM for bat community composition against elevation, site and bioclimatic variable (bc) and bioclimatic variable squared. Bioclim variables are described in Table 2.1 above).

Variable	df	Residual deviance	Wald	Pr(>Wald)
Mount	4	245	6.389	0.001
Bc04	1	249	8.094	0.001
$Bc04^2$	1	244	5.362	0.001
$Bc14^2$	1	242	3.345	0.021
Bc15	1	243	3.712	0.011
$Bc15^2$	1	241	3.089	0.036

When the influence of the final model on individual species' probabilities of occurrences was examined, statistically significant associations were found for four of the modelled species (*R. megaphyllus, N. bifax, Vespadelus sp., and M. australis)* (Table 2.5). This is perhaps not surprising, given that a number of species were recorded vary rarely. Thus, while all species contribute to detecting significant association in the overall analyses, when considered individually there is far too few records in some species to resolve effects. Three of those species that individually showed significant relationships with variables identified in the general analysis, *R. megaphyllus, Vespadelus sp., and M. australis* were recorded at a high proportion of sites and by large number of calls (*R. megaphyllus sites = 20, calls = 3292; Vespadelus sp. sites = 9, calls = 635; M. australis, sites = 9, calls = 1199)*, and *N. bifax,* was recorded at seven sites from only 18 calls (Table 2.2).

Temperature seasonality (bc04) was shown to be significantly related to the probability of occurrence of all four of these species (*R. megaphylus*, Wald = 2.76, Pr(>Wald) = 0.00, coefficient = -185.9; *N. bifax*, Wald = 3.89, Pr(>Wald) = 0.00, coefficient = 742.05; *Vespadelus sp.,* Wald = 3.34, Pr(>Wald) = 0.00, coefficient = 121.11; *M. australis,* Wald = 4.16, Pr(>Wald) = 0.00, coefficient = 8.05) (Table 2.5). *Rhinolophus megaphyllus'* occurrence was also found to be effected by subregion (Wald = 4.08, Pr(>Wald) = 0.00, coefficient = 2.21), temperature seasonality squared (Wald = 4.45, Pr(>Wald) = 0.00, coefficient = 29.51) and precipitation of the driest month squared (Wald = 2.81 Pr(>Wald) = 0.00, coefficient = 0.00) (Table 2.5). *Rhinolophus megaphyllus* was the only species where the probability of occurrence was significantly associated with squared variable terms. The coefficient of each variable, and its sign, indicate a positive or negative relationship. *R.* megaphyllus is shown to have a negative relationship with temperature seasonality but a positive relationship with other significant variables. *Vespadelus sp.* occurrence was found to be positively driven by annual precipitation (Wald = 2.59, Pr(>Wald) = 0.01, coefficient = 115.45) as well as temperature seasonality (Table 2.5), and *M. australis'* occurrence was found to be positively driven by subregion (Wald = 3.58, Pr(>Wald) = 0.00, coefficient = 0.66) but negatively driven by precipitation seasonality (Wald = 2.86, Pr(>Wald) = 0.01, coefficient = -33.94) (Table 2.5). Finally, probability of *N. bifax* occurrence was positively related to a single variable; temperature seasonality (Table 2.5).

Table 2.5 Summary of binomial GLM fitting for bat species occurrence against elevation, site and bioclimatic variable (bc) and bioclimatic variable squared. (bioclim variables are described in Table 2.1 above). The coefficient and its sign indicate a positive or negative relationship. Variables highlighted in grey below have a significant probability of effecting bat species occurrence in the Wet Tropics.

	Temperature seasonality (bc04)			Subregion			Temperature seasonality squared (bc04^2)			Precipitation seasonality (bc15)			Precipitation driest month squared (bc14^2)			Annual precipitation (bc15^2)		
	Wald	**Pr (>Wald)**	**Coef**	**Wald**	**Pr (>Wald)**	**Coef**	**Wald**	**Pr (>Wald)**	**Coef**	**Wald**	**Pr (>Wald)**	**Coef**	**Wald**	**Pr (>Wald)**	**Coef**	**Wald**	**Pr (>Wald)**	**Coef**
Rhinolophus megaphyllus	2.76	0.00	-185.9	4.08	0.00	2.21	4.45	0.00	29.51	1.57	0.31	14.69	2.81	0.00	0.00	0.70	0.72	-14.73
Hipposideros diadema	0.87	0.76	-328.8	0.64	0.95	0.90	0.21	1.00	54.64	0.03	0.89	303.33	0.10	0.95	0.00	0.00	0.91	-157.0
Murina florium	0.00	1.00	0.00	0.00	1.00	0.00	0.00	1.00	0.00	0.00	1.00	0.00	0.00	1.00	0.00	0.00	1.00	0.00
Nyctophilus bifax	3.89	0.00	742.05	0.13	0.95	-1.19	1.05	0.77	-138.7	0.15	0.89	4368.84	1.30	0.45	0.02	0.21	0.72	-2120.3
Scotorepens sanorni	0.72	0.83	-487.19	0.56	0.95	-8.09	0.11	1.00	90.77	0.11	0.89	584.50	0.00	0.95	0.00	0.09	0.72	-418.00
Vespadelus pumulis	1.46	0.31	279.13	0.37	0.95	-0.59	0.24	1.00	-55.29	0.39	0.89	-357.30	0.82	0.84	-0.00	1.11	0.61	184.09
Vespadelus troughtoni	0.60	0.85	-169.89	0.55	0.95	7.09	0.99	0.72	24.04	0.89	1.03	1859.76	0.95	0.35	-0.00	0.72	2.59	-1131.1
Vespadelus sp.	3.34	0.00	121.11	2.46	0.10	-1.23	0.72	0.92	-23.02	1.03	0.69	-207.38	0.35	0.95	-0.00	2.59	0.01	115.45
Miniopterus australis	4.16	0.00	8.05	3.58	0.00	0.66	0.16	1.00	-4.59	2.86	0.01	-33.94	0.66	0.88	0.00	0.92	0.72	15.01
Miniopterus orianae oceanensis	1.18	0.56	83.47	1.04	0.84	0.13	0.26	1.00	-15.81	0.72	0.81	-55.87	0.34	0.95	0.00	0.33	0.72	27.58
Mormopterus lumsdenae	0.49	0.85	-1378.4	0.66	0.95	-24.47	1.17	0.67	255.97	0.97	0.69	-305.47	0.31	0.95	0.01	0.00	0.91	146.39

Discussion

Patterns of species richness and distribution

Based on previous studies both globally and in the study region, some relationship between elevation and/or latitude and bat species richness was expected (e.g. Williams, 1997; McCain, 2007; Williams *et al.*, 2010a; Dalsgaard *et al.*, 2014). However, no support for this assumption was found. One possible cause for this result is that richness is too coarse a measure of diversity. Quantifying local diversity as raw species numbers is particularly prone to sampling effects (Fiedler and Truxa 2012). Even when extrapolation techniques have been used to estimate 'expected' species totals (i.e. Colwell *et al.*, 2004) these have been shown to fail as proxy for 'diversity' (Fiedler and Truxa 2012). This is because richness, as expressed by a simple count, fails to address changes in species' identities across sites, and can provide little insight into how individual species' occurrences might change across gradients, nor how the composition of the communities they generate change. Furthermore, there was no evidence that any bioclimatic variables could describe patterns in richness. This result too, could be due to reasons associated with using richness as a measure of diversity.

Incorporating consideration of individual species' identities (i.e. the probabilistic model of Mvabund) was able to reveal significant relationships between community-level patterns in species' probability of occurrence and all explanatory variables tested when each of these variables were tested individually. More importantly, step wise Mvabund model selection resulted in a final model based on species occurrence that did not include elevation. When investigated at the level of community composition, patterns in occurrence were shown to be primarily effected by temperature seasonality, as well as latitude (subregion), precipitation seasonality and precipitation in the driest month. While it is true that elevation was identified as a significant predictor when tested alone, it was discarded as a possible explanatory variable after bioclimatic variables were included. This finding demonstrates the inappropriateness of considering elevation per se as a meaningful, biologically important variable that in itself determines species' distributions.

Measures of temperature in particular often correlate with elevation and we would therefore expect species' distribution patterns, characterised using elevation as a proxy, to vary considerably depending on the location of the environmental gradient (McCain, 2007). This would be particularly true on a global scale but could also be true within a region at more local scales. In this study, temperature seasonality was shown to be the most significant variable predicting species occurrence. This variable represents the standard deviation of the mean monthly temperature and indicates the amount of variation in the temperature in the region (e.g. if seasonality is high this would indicate a greater difference in temperature ranges throughout the year, as expected in locations with pronounced seasons). In this case, temperature seasonality values ranged between 2.42 and 3.33 (with temperature itself ranging from 19.15 to 25.04 across the region), indicating minimal change in temperature among and across subregions throughout the year.

Subregion was also indicated to have a significant impact on patterns of species' occurrence supporting the above. Climatic variables (temperature and precipitation) coupled with site specific factors are likely to drive richness and distribution in the individual subregions. Site specific biophysical attributes that determine species presence or absence include many different aspects of the environment that combine to define habitat or niche (Speakman & Thomas, 2003; Presley *et al.*, 2012). Broadly, the significant subregional effect could result from differences in the structural complexities of forest types associated with the different mountain gradients sampled here. It is known that the distribution of some species (including this study's most abundant species *R. megaphyllus* and *V. pumulis*) do respond to vegetation complexity (Clague, 2004). Rainforest environments, particularly under dense canopies, are climatically very stable and aseasonal (Williams & Middleton, 2008; Hagger *et al.*, 2013). This may mean that species that inhabit such environments are somewhat buffered or protected from fluctuations in temperature and precipitation compared to areas that are subject to greater fluctuations. Climatic stability, coupled with life history traits of the study species (such as high dispersal and wide ranging distributions), may mean that bats are considerably less vulnerable to changes in environmental conditions (Hagger *et al.*, 2013).

Fine scale aspects of the environment are also known to be of importance to bat ecology and these may drive species' distributions more so than broad scale vegetation types. For example, precise biophysical conditions in tree hollows and caves have been shown to be of high importance for bat breeding and roosting (Rebelo *et al.*, 2010). Microhabitat conditions such as this have also been shown to limit bat species' abilities to utilise different habitats by limiting roost sites (Rebelo *et al.*, 2010) or impeding or limiting flight capabilities (Fullard *et al.*, 1991; Neuweiler, 2000). This suggests significant influence of individual ecologies of individual species that may need consideration (see below for further discussion). As possible support for this contention, a simple analysis of broad vegetation groups (based on classifications by Specht, 1970; Webb, 1978; Parsons, 2010) appears to support this hypothesis, with vegetation type found to differ between subregions (Annex 2.1, Table 2.1.1). However, a deeper understanding of how vegetation complexity, prey availability and climatic stability influence individual bat species' occurrences will require more detailed description of these variables than undertaken here. This is a potential opportunity for further study.

Richness and abundance of insectivorous bats has also been linked to prey availability, with insect abundance fluctuating with temperature and precipitation variability, but remaining relatively stable in aseasonal habitats (Richards, 1989; Williams & Middleton, 2008; Hagger *et al.*, 2013). If all these factors are indeed operating, different subregional patterns could reflect multilevel interactions between plant structural complexity, environmental stability, and invertebrate population stability.

While analysis of combined species' occurrences revealed overall significance of temperature seasonality, subregion, precipitation seasonality and precipitation in the driest month, when examined separately, individual species' responses did not necessary reflect all of these bioclimatic variables. First, of the 11 species used in Mvabund, seven species that were recorded relatively infrequently showed no individual association with these variables. Of the remaining four species, all revealed significant relationships with different combinations of them. For example, all four were individually influenced by temperature seasonality with this relationship indicated to be positive for three of these species (except *R. megaphyllus*). *Rhinolophus megaphyllus'* occurrence was also found to be positively affected by subregion, temperature seasonality (squared) and precipitation of the driest month (squared). This may indicate that likelihood of *R. megaphyllus* occurrence in the study site decreases with increasing temperature seasonality. *Vespadelus sp.* occurrence was found to be positively driven by annual precipitation as well as temperature seasonality, *M. australis* positively by subregion but negatively by precipitation seasonality, and *N. bifax* by temperature seasonality (positively) only. These results reinforce the concept that species respond individually and uniquely to environmental parameters. In this context, individual species distributions and predictions for future will require consideration of individual ecologies (outlined below).

Species' ecology and distribution

A total of 16 potentially unique species were detected during the course of this study, 10 of which could be confidential identified. This number of detected species is lower than detected during another comparable survey which detected 22 species including all 9 of the species detected in this study (Clague, 2004). Of the species detected in this study, three species (*R. megaphyllus, M. australis, and Vespadelus sp.)* accounted for over 95% of bat activity recorded across the region. *Rhinolophus megaphyllus* or the eastern horseshoe bat, was the most active and present species overall (accounting for 62% of all species records), and was found across the entire study region (all subregions and all elevations). This was not unexpected as *R. megaphyllus* is a very common species in this area and is highly suited to the environments sampled. Modelling indicates that *R. megaphyllus'* probability of occurrence is determined by temperature seasonality squared primarily, as well as subregion and precipitation of the driest month. Both temperature seasonality and temperature seasonality squared came out in the best-fit model for this species, although a negative relationship with temperature seasonality was indicated. This may suggest that distribution is likely to be unimodal and dependant on subregion and amount of precipitation in the driest months. *Rhinolophus megaphyllus* is a generalist species, inhabiting many different habitats (including rainforest, as recorded in this study), whose morphology is well suited to foraging under canopy and in dense vegetation (Churchill, 2008). An in-depth study of bat assemblage structure indicated that this species generally forages quite low within the forest structure, generally around three to 10 meters from the ground (Clague, 2004). This is also supported by preliminary data (presented in Appendix 1) showing the majority of *R. megaphyllus* recorded within this section of the rainforest structure. This species generalist nature may mean that *R. megaphyllus* could be somewhat more resilient to climate change than other less generalist species. This will be explored further in Chapter 4 of this thesis.

The second most active and present species in the study region was *Miniopterus australis,* or the eastern bentwing bat (accounting for 22.7% of all species records). This species was recorded at four of the five subregions, excluding the Spec Uplands to the south of the Wet Tropics, and at nine different sampling sites. The presence of this species was not unexpected either as this species is also common in the area, preferring 'well-timbered' habitats including rainforest; a habitat type characteristic of the region (Churchill, 2008). The species is known to forage under the canopy crown, generally within heights of 10 to 20 metres (Clague, 2004). Climatic modelling indicates that *M. australis'* probability of occurrence is positively determined by temperature seasonality primarily and subregion. A negative relationship with precipitation seasonality was indicated suggesting that likelihood of occurrence is monotonic, and decreases with increasing precipitation seasonality, depending on subregion. *Miniopterus australis* is known to be a cave dwelling species so it is likely that caves or rocky formations would need to exist near foraging areas for this species to be present in an area. Due to its cave dwelling nature this species may also be less susceptible to environmental changes outside of the stable cave environment.

Vespedalus sp. accounted for 12% of the bat activity recorded throughout the study and was found to be present at nine sites. This classification most likely contains calls recorded from *Vespadelus troughtoni* (the eastern cave bat) and *Vespadelus pumulis* (the eastern forest bat). The ultrasonic frequency of these calls overlap, meaning classification to species from call sonogram alone is extremely difficult. Both species prefer tropical rainforest or wet sclerophyll habitats over drier vegetation types like woodlands. *Vespadelus pumulis* is known to be a true forest dweller, able to forage at all heights throughout the forest structure. Conversely, *V. troughtoni* is a cave, or rocky outcrop, dwelling species, generally known to forage at mid-forest heights of between five and 30 metres (Clague, 2004; Churchill, 2008). The best-fit model for this genus indicates that distribution is monotonic and positively determined by temperature seasonality primarily, as well as annual precipitation.

Nyctophilus bifax was infrequently recorded during this study, accounting for only 0.1% of bat activity and recorded at only three sites from the two most northern subregions (Windsor and Carbine uplands). Despite its rarity in this study, modelling, based on a small number of records (26), indicated that *N. bifax'* probability of occurrence is positively associated with temperature seasonality (only). This, and the fact that this species was only recorded at the more northern subregions, may be correlated. This species is a 'forest-dwelling' species known to preference wetter habitats such as rainforest (Churchill, 2008). The tendency of this species to forage along the edge of the canopy, rather than within it, may explain the rarity of its detection in this study (Clague, 2004; Churchill, 2008). Patterns of distribution and possible impacts of future climate change on each of these species will be investigated further in the following chapters.

Caveat

The four species discussed above all preference rainforest habitats. This may hint that the survey design of this study is biased toward detecting these species. This, along with potential insufficient sampling, may explain the inability to detect the expected result of a decline in richness with increasing elevation. To be confident that this was not the case, sampling effort was analysed using species accumulation curves derived through Chao1 species richness estimates, as well as observed number of species. Analyses indicated that the majority of species estimated to be present in the regional sample were accounted for by the sampling methods used, within the sampling time. This was also confirmed for four of the five subregions (Carbine, Lamb, Atherton, and Spec Uplands) with accumulation curves stabilising within the sampling period. The Windsor Uplands proved the exception to this with the produced accumulation curve not stabilising, or reaching asymptote, within the sampling period. This may indicate that further sampling in the Windsor Uplands would provide a more accurate measure of species richness and abundance in this subregion, and the region as a whole. Indeed, compared to a previous study conducted at this subregion, a lower number of species were detected during this survey. During the original study 12 species were detected while this study detected eight species, five of which were the same across both studies (Crome & Richards, 1988).

It is important to note that the methods used to survey bat species in this study (and all similar studies) determine the number of records and thus total richness detected. Extrapolation cannot account for a techniques inability to detect some component of the community. As mentioned above, the survey design used during this study most likely bias detection to species that inhabit rainforest habitats and are suited to foraging under canopies only (Muller *et al.,* 2013). These species generally move and forage within, and under, the rainforest canopy, as evident by the ecology of the four species described above. As this study is primarily interested in species inhabiting rainforested areas of the Wet Tropics, this is not a significant issue. However, it is again important to note that species records may not be indicative of the entire suite of bats (i.e. will not include bats that were possibly not detectable under the sample regime used such as high flying species like *Saccolaimus flaviventris* and *Chaerephon jobensis*) and results should be interpreted with this in mind. A fuller picture of region wide species' distribution and diversity could be gained by increasing the scope of the sampling to additional subregions and other habitat types (e.g. wet sclerophyll forest, eucalypt woodlands, etc.) or by altering passive recording method to enable detection of species that may fly above the canopy. Additionally, as the majority of the identified species roost in caves, geological surveys of the area, mapping and targeting for sampling such characteristics as caves, casts, and mines, would provide a further indication of how other habitat variables drive species presence or absence. Finally, five potentially unique call types were excluded from analysis and discussion because identification could not be confidently made to genus or species level. These may or may not represent unique species and estimates of richness (estimated richness of 12 species) provided in this study suggest that potentially not all of them are. However, should they represent unique species this again highlights the potential neglect of this important group of mammals in the area, and more basic study to characterise all calls for bats is needed.

Relevance and implications

Currently, knowledge on echolocating bats in general is limited and information regarding individual species distributions and the mechanisms driving them is poor. Worldwide, published studies have shown that bats appear to exhibit various distribution patterns, depending on latitude with richness generally decreasing with increasing elevation in the tropics, but exhibiting mid-elevational peaks in temperate zones (McCain, 2007). This was well demonstrated by a recent study conducted by Herkt and colleagues looking at bat distribution patterns at a fine scale across the entire African continent (Herkt et al., 2016). They found that within tropical areas of the continent, predicted richness peaked near the base of mountains but for the more dry, temperate areas richness peaked further upslope or at mid-elevations (Herkt et al., 2016). Generally, bat species richness in Africa was found to increase towards the equator (Herkt et al., 2016). This study represents one of the only detailed description of the richness and community composition patterns of echolocating bats in the focal, tropical, region and gives base-line information on what might drive these distributions. In contrast to other studies conducted globally, here no support for elevation as a potential explanatory variable was found. In addition, richness was revealed to be a poor proxy of diversity.

The results of this study partially support the McCain (2007) climatic model. The fact the temperature seasonality was proposed to be one of the primary drivers of species' occurrences in the region was, perhaps, not surprising. The McCain (2007) climatic model predicts that species respond to elevational gradients, primarily because these are related to local climatic gradients (McCain, 2007). The McCain model predicts richness trends to be positively related to temperature and water availability and to be highest where temperature and water availability are also high, declining as they decreased. From her analysis, McCain produced a climatic model for predicting bat species richness along elevational gradients (2007). For the tropics, the model predicts that bat diversity will decline with declining temperature and water availability (Figure 2.1). This study determines that although elevation per say does not have any impact on richness (Figure 2.3), variation in temperature and water availability do impact species' distributions. However, McCain's climatic model does not account for seasonality of either temperature of moisture availability specifically. This may be due to a lack of data covering more than a single season of climatic measurements (McCain, 2007). Nonetheless, other studies on bat diversity patterns have also indicated seasonality to be highly correlated with distribution. For example, Stevens (2013) found seasonality to be an important predictor of bat diversity in the Atlantic Forest of South America. Steven's found that seasonality was related to changes in bat abundance commenting that it may be too 'energetically costly' for some species to occur in areas of high seasonality. Conversely, a study conducted by Lim *et al* looking at patterns of bat diversity in Malaysia did not find temperature seasonality to be an important determinant of bat diversity (Lim *et al.,* 2014). The authors themselves reference the study by Stevens (2013) and suggest that the differing results may be linked to the scale of the two studies with the study by Lim and colleagues being conducted over a much smaller seasonality gradient (Lim *et al.,* 2014). This may reinforce the idea that lack of quality seasonal data resulted in the omission of seasonality in McCain's climatic model.

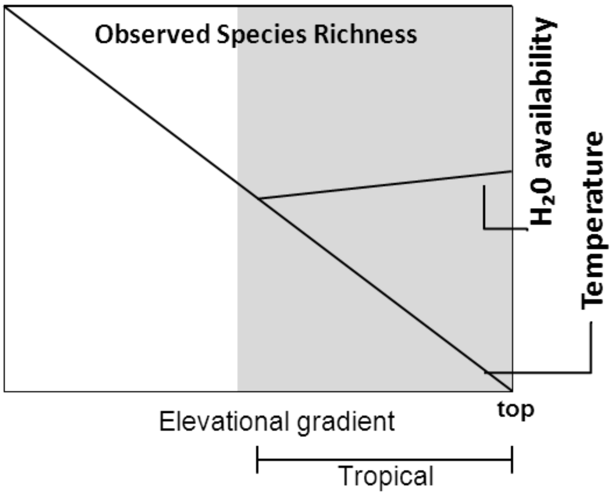


Figure 2.3 Generalised climatic model for elevational gradients in species richness of bats in the Wet Tropics incorporating a linearly decreasing temperature gradient and linear slightly increasing water availability gradient. Bat species richness is depicted in a grey tone. As richness does not change with elevation darker tones indicating more species have been omitted. The placement of a generalised tropical elevational gradient is shown below the x-axis (modelled on McCain, 2007 (see Figure 2.1)).

The results of this study align with other similar studies conducted around the world. A study conducted in South Africa also tested, and supported, the conclusions of McCain's climate model (Weier et al., 2017). They found that the occurrence of bat species in their study sites was also linked with water availability and temperature, as determined in this Wet Tropics study. However, Weier and colleagues were able to link the correlation between distribution and water availability and temperature with the mid-elevational peaks in richness in more temperate areas and a linear decrease with increasing altitude in wetter areas as predicted by the McCain model. Making this link may have been possible due to the habitat diversity in their study area allowing them to compare and contrast temperate and tropical gradients. Although not directly testing the McCain Model, a Norwegian study also determined that temperature and precipitation explained the majority of variation in bat diversity in a Norwegian study (Michaelsen, 2016). In Australia, modelling conducted by Milne and colleagues showed that amount of annual rainfall was significant in determining bat occurrence and distribution in the Northern Territory (Milne et al., 2006). In contrast to the study presented here, only one of 25 species modelled in Milne *et al's* study indicated a significant correlation to temperature variables.

The results of this study are also in line with other studies conducted in the Wet Tropics region (e.g. Williams et al., 2010a; Anderson, 2011; Staunton et al., 2014). Patterns of species' distribution in the region have been, and continue to be, well studied. The high biodiversity, relatively small geographic range, and stable paleoclimatic conditions makes this area of great interest to ecologists (Williams & Pearson, 1997; VanDerWal *et al.*, 2009a; Welbergen *et al.*, 2011). Evidence from these studies suggest that regional climate is a major driver of patterns of terrestrial distribution, including species richness and abundance, with local environmental variables such as temperature being the driving force behind their distribution patterns (Williams *et al.*, 2010b; Anderson, 2011). For example, distribution of non-volant mammals in the Wet Tropics is known to decrease in species richness to the north and south of the region, likely due to hard barriers posed by spatial constraints in the north but increased temperatures to the southern limits (Williams, 1997). Similarly, bird richness in the region has been found to be strongly linked to elevation, generally displaying mid-elevation richness peaks (600m – 1000m a.s.l.) (Williams *et al.*, 2010a). Distributions of other species in the region have also been found to be highly correlated with environmental factors; flightless ground beetles have been found to be confined to the coolest, wettest areas of the Wet tropics (Staunton *et al.*, 2014), and increasing temperature has been found to reduce populations and distributions of the region's microhylid frogs (Shoo & Williams, 2004; Issac, 2008; Welbergen *et al.*, 2011). The results of this study support this growing evidence base and again highlight the important role environmental variables play in determining species' distributions.

Effective conservation of species in the face of climate change will depend on adequate knowledge of species to be conserved. Further study is required to determine exactly how environmental variables drive bat diversity and distribution in the region. With the impending threat of climate change, greater understanding of the links between species' distributions, assemblage structure and environmental factors driving them are crucial to predicting responses of species and ecological communities to climate change. The results presented within indicate that some climatic variables influence community composition and that individual species also show significant, but different, responses to individual environmental traits. Communities are the sum (or end result) of the occurrence of individual species all reacting individually. Occurrences of individual species reflect their individual climatic limits and the changing patterns of climate through time should cause individualistic responses.

Unfortunately, the extent to which individual species' responses to climate could be resolved in this chapter was limited by the nature of the data collected in the sample. Thus, in the next chapter (Chapter 3) the available data is broadened by supplementing data from this study with museum and various biodiversity atlas datasets (see Chapter 3 for detail). This more in depth analysis will enable greater examination of individual species distributions with respect to climatic variables. Following this, Chapter 4 presents likely changes in individual species distributions expected under climate change scenarios to examine patterns in the resultant community compositions into the future.

Annex 2.1

Table 2.1.1 Total sampling effort (passive, active, and capture), and passive sampling effort, per subregion and elevation (including number of nights, hours, and percentage of overall sampling effort). Analysis of broad vegetation classifications, defined below based on Webb (1978), Specht (1970), and Parsons (2010), differed significantly between the subregions (R = 0.47, p=0.02), although vegetation classifications did not differ significantly between elevations (R = 0.002, p=0.46).

Subregion	Elevation	Veg type*	Sample nights all methods	Sample hours	Sampling %	Sampling nights passive only	Passive sample hours	Passive sampling %
Windsor Uplands	900	NVF-AG	17	204	6	15	180	6
Windsor Uplands	1100	NVF	15	180	5	11	132	5
Windsor Uplands	1300	MFF	16	192	6	14	168	6
Carbine Uplands	100	MVF	8	96	3	8	96	3
Carbine Uplands	400	MVF	7	84	2	5	60	2
Carbine Uplands	600	NVF	13	156	5	11	132	5
Carbine Uplands	800	NVF	18	216	6	15	180	6
Carbine Uplands	1000	NVF	17	204	6	15	180	6
Carbine Uplands	1200	MFF	19	228	7	16	192	7
Lamb Uplands	700	NVF	17	204	6	12	144	5
Lamb Uplands	900	NVF	14	168	5	12	144	5
Lamb Uplands	1100	NVF	15	180	5	12	144	5
Atherton Uplands	200	CS/CMVF	7	84	2	4	48	2
Atherton Uplands	400	CS/CMVF	9	108	3	8	96	3
Atherton Uplands	600	CS/CMVF	18	216	6	12	144	5
Atherton Uplands	800	CS/NVF	4	48	1	4	48	2
Spec Uplands	350	NVF	25	300	9	25	300	10
Spec Uplands	600	MOF	20	240	7	20	240	8
Spec Uplands	800	NVF	10	120	4	10	120	4
Spec Uplands	1000	A-CF	12	144	4	12	144	5
Totals			**281**	**3372**	**100%**	**241**	**2892**	**100%**

* NVF-AG = notophyll vine forest with Agathis sp. emergent; NVF = notophyll vine forest; MFF = microphyll fern forest; MVF = mesophyll vine forest; CS/CMVF = cyclone damaged/complex mesophyll vine forest; MOF = medium open forest with regenerating rainforest understory; A-CF = Acacia sp. closed forest (based on Webb (1978), Specht (1970), and Parsons (2010)).

Annex 2.2

Table 2.2.1 Variable selection and Best-fit model script determining bat species' distribution in the Wet Tropics. Red text indicates non-significant results.

Run 1: Individual variables				Run 2: (bioc04 +)				Run 3: (bioc04 + Mount +)			
Rank	Variable	Wald	Sig	Rank	Variable	Wald	Sig	Rank	Variable	Wald	Sig
1	bc04	8.094	0.001	1	mount	6.389	0.001	1	bc04^2	5.362	0.001
2	bc04^2	7.94	0.001	2	bc13^2	6.179	0.001	2	bc13^2	4.692	0.001
3	bc06^2	7.597	0.001	3	bc13	6.115	0.001	3	bc13	4.605	0.001
4	bc06	7.573	0.001	4	bc12	5.943	0.001	4	bc12^2	4.496	0.004
5	bc01^2	6.393	0.002	5	bc12^2	5.942	0.001	5	bc12	4.455	0.006
6	bc01	6.28	0.001	6	bc14	5.624	0.001	6	bc01^2	4.263	0.004
7	bc13	6.153	0.001	7	bc14^2	5.359	0.001	7	bc05^2	4.247	0.004
8	bc13^2	6.128	0.001	8	bc15	4.722	0.003	8	bc05	4.23	0.004
9	bc05^2	5.877	0.001	9	bc15^2	4.628	0.003	9	bc01	4.222	0.004
10	mount	5.845	0.008	10	bc06^2	4.488	0.010	10	bc14	4.216	0.008
11	bc05	5.828	0.002	11	bc01^2	4.474	0.006	11	bc06	4.113	0.007
12	bc12	5.69	0.003	12	bc01	4.432	0.011	12	bc14^2	4.068	0.008
13	bc12^2	5.625	0.002	13	bc06	4.420	0.012	13	bc06^2	3.862	0.022
14	Elevation	5.472	0.001	14	bc05^2	4.323	0.018	14	bc15	3.741	0.033
15	bc14^2	4.817	0.016	15	bc05	4.315	0.022	15	bc15^2	3.643	0.037
16	bc14	4.784	0.023	16	Elevation	4.097	0.041	-	Elevation	3.12	0.216
17	bc15^2	4.36	0.032	17	bc04^2	4.003	0.097				
18	bc15	4.278	0.026								

Run 4: (bioc04 + Mount + bioc04^2 +)				Run 5: (bioc04 + Mount + bioc04^2 + bioc15 +)				Run 6: (bioc04 + Mount + bioc04^2 + bioc15 + bioc14^2 +)			
Rank	Variable	Wald	Sig	Rank	Variable	Wald	Sig	Rank	Variable	Wald	Sig
1	bc15	3.712	0.005	1	bc14^2	3.345	0.025	1	bc15^2	3.089	0.032
2	bc15^2	3.615	0.013	2	bc06	3.129	0.034	-	bc05	2.966	0.062
3	bc05^2	3.584	0.012	3	bc06^2	3.119	0.044	-	bc06	2.775	0.086
4	bc06^2	3.534	0.024	4	bc01^2	3.114	0.043	-	bc01^2	2.772	0.096
5	bc13^2	3.533	0.019	5	bc12^2	3.09	0.043	-	bc06^2	2.529	0.147
6	bc12^2	3.464	0.027	6	bc15^2	3.072	0.049	-	bc13^2	2.243	0.291
7	bc13	3.447	0.023	7	bc05	3.06	0.047		bc12^2	2.222	0.322
8	bc05	3.432	0.023	8	bc13^2	3.053	0.044				
9	bc01^2	3.427	0.031	-	bc05^2	3.035	0.056				
10	bc12	3.394	0.033	-	bc13	2.947	0.056				
11	bc01	3.390	0.025	-	bc14	2.933	0.07				
12	bc14^2	3.389	0.045	-	bc01	2.895	0.102				
13	bc06	3.380	0.035	-	bc12	2.835	0.094				
14	bc14	3.264	0.035								

```
>best <- manyglm(APbats ~ preds$bioc04 + preds$Mount + preds$bioc04x2 +   preds$bioc15 + preds$bi
oc14x2 + preds$bioc15x2, family = "binomial")
> anova(best, test = "wald")
```

Annex 2.3

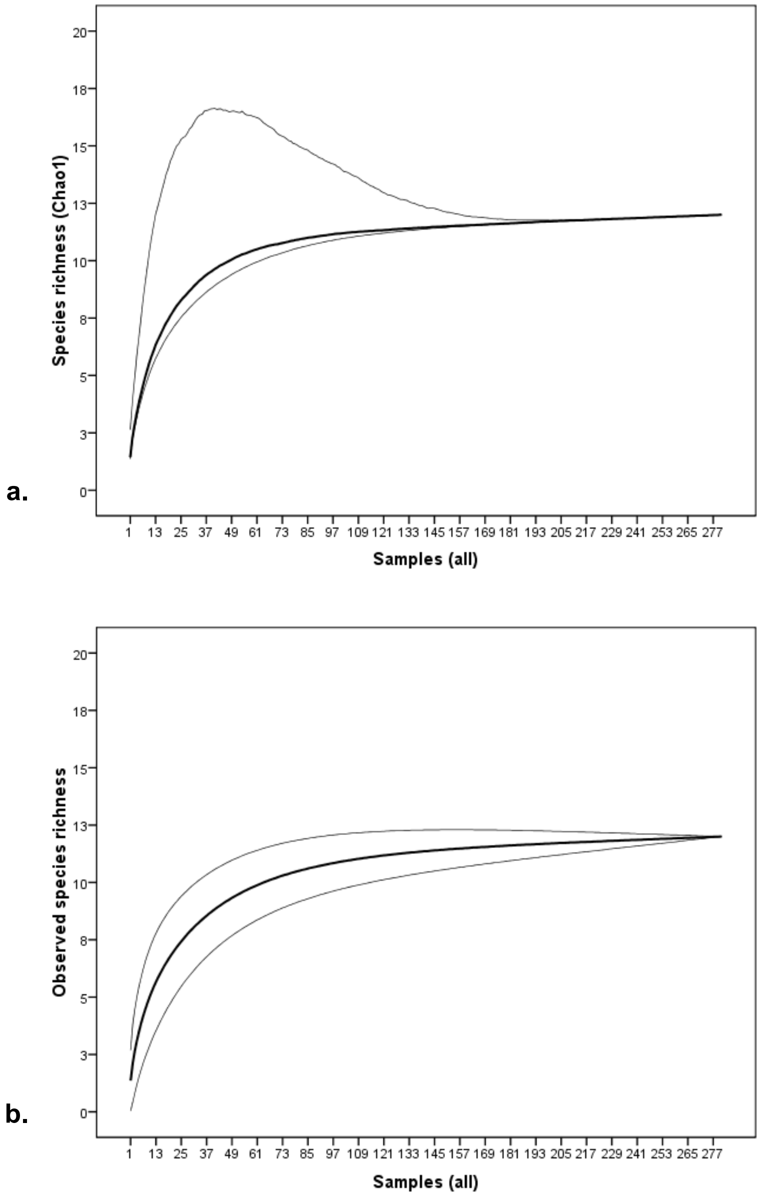


Figure 2.3.1 Accumulation curves indicating detection probability, with 95% confidence intervals over the number of samples. Curves depict Chao1 predicted species richness (1a) and observed species richness (1b).

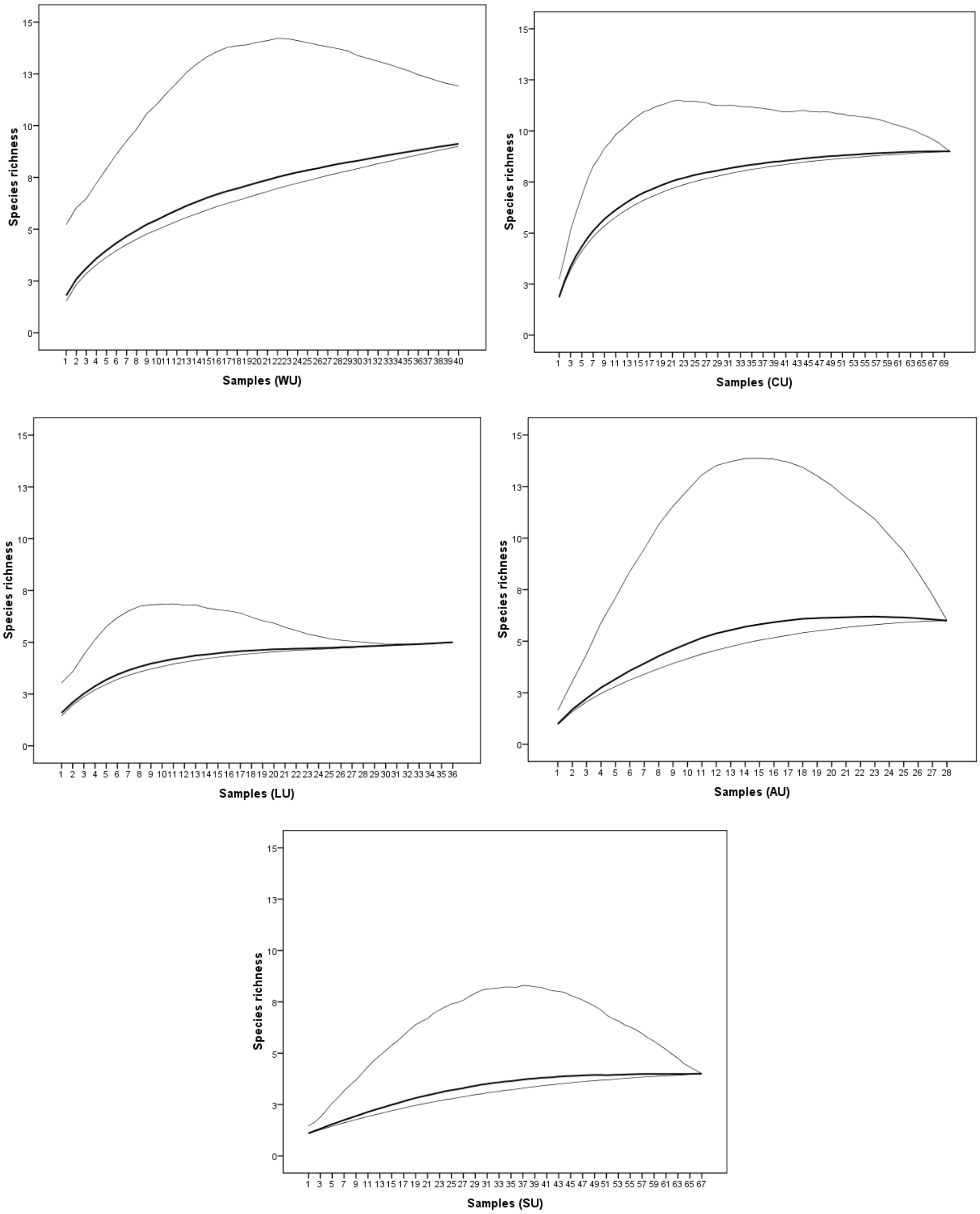


Figure 2.3.2 Accumulation curves (using Chao1 species richness) for each subregion, Windsor Uplands (WU), Carbine Uplands (CU), Lamb Uplands (LU), Atherton Uplands (AU), and Spec Uplands (SU), with 95% confidence intervals.

Annex 2.4

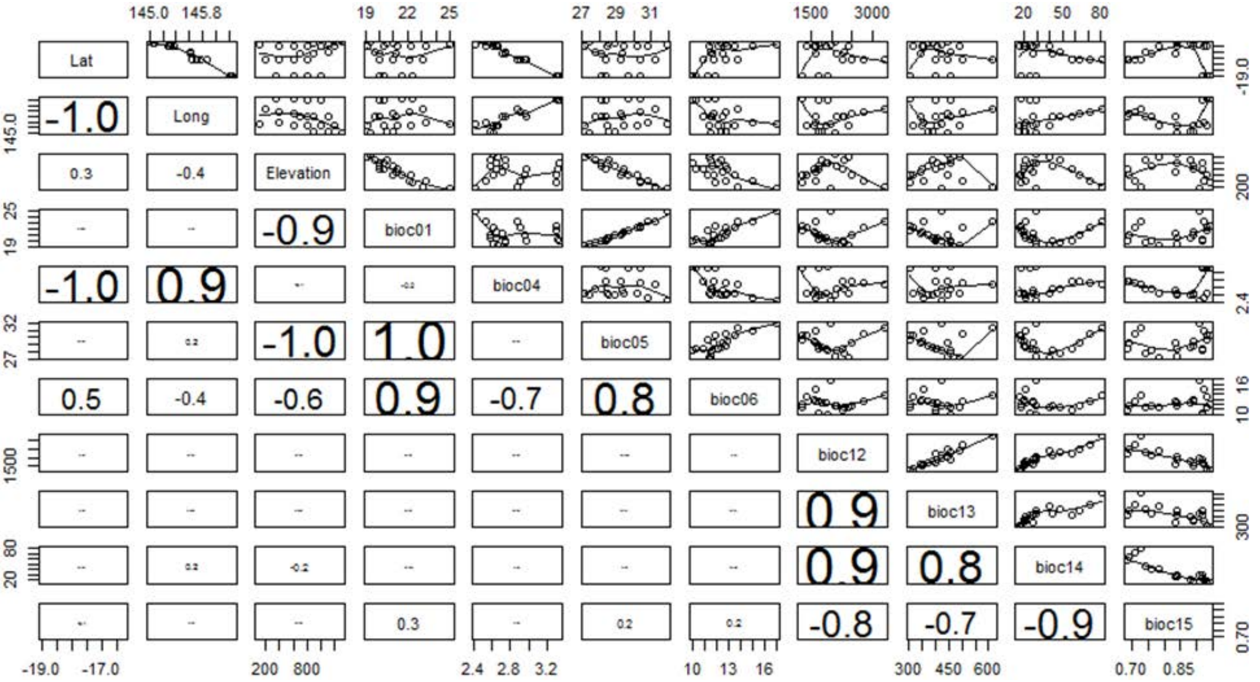


Figure 2.4.1 Pair-plot (upper) of explanatory variables and correlation coefficients (lower) for all pairwise comparisons. The line that is fitted is a smoothing (nonlinear) curve function.

Chapter 3: Improved understanding of local biodiversity using global information: a case study of bats in the Australian Wet Tropics.

Abstract

Successful conservation strategies need to be based on good understanding of 'what lives where'. With the increasing need to understand the potential distributions of species, it is common practice to use species distribution models (SDMs; also known as ecological niche models) to assess the suitability of different environments for species'. By overlapping distribution models of many species, an estimate of the biodiversity assets of a region can be generated. However, there is often a spatial mismatch between the focal region (or study area) and the wider distribution of the species examined. Typically, this is resolved by modelling the species using known information for the focal region and excluding external information. The validity of using only information from the focal region (the Wet Tropics World Heritage Area) against information from the Australia wide 'global' distribution of the study species is tested in this study. SDMs were generated for 28 species of echolocating bats known to inhabit the region, using either Australia wide 'global' data or only local Wet Tropics data, and each with two background (or pseudo-absence) options which either ignored or explicitly accounted for sampling bias in the observation data. Model performance was assessed through a combination of quantitative and qualitative analyses including assessment of model AUC values, number of data points contributing to the models, ecological relevance of environmental predictors, and how well resulting models matched what is known about the species. Over 70% of the SDMs performed best using the global data, and models that accounted for sampling bias generally outperformed models that did not (64% vs 36% respectively). This demonstrates that models built using observational data from only the focal region may misrepresent the distribution of a species. This, in turn, could misinform conservation decisions made based on this information.

Introduction

Biodiversity conservation is a key area of biological research focused around protecting the world's biodiversity (Barnosky *et al.*, 2011). However, worldwide, very little geographic space has been systematically surveyed to gain a true understanding of biodiversity at any one location, making conservation efforts challenging (Peterson, 2001; Boitani *et al.*, 2011). A study of echolocating bat species of the Wet Tropics World Heritage Area (hereafter 'Wet Tropics'; see Chapter 2 of this thesis) recorded 10 species within the study region and determined their regional richness and community composition patterns. No evidence of a relationship between overall richness and any climatic variables, nor between richness and elevation or latitude was found. However, analysis of the distribution patterns of individual species indicated that climatic variables do influence probability of a species' occurrence. Temperature seasonality was found to drive this pattern primarily, with subregion and precipitation variables also being influential. Elevation itself was unable to explain differences in community composition.

The described study (see Chapter 2) provides base-line information on what might drive species' distributions in the Wet Tropics. However, it is recognised that the combination of survey methods and study sites chosen during this study most likely bias detection to species that are primarily active under the rainforest canopy. Thus, species records are likely to not be indicative of the full assemblage of bats, limiting application of results. The study concluded that a fuller picture of region wide species' distribution and diversity could be gained by increasing the scope of the sampling to additional subregions and other habitat types. Such bias, or a general lack of information about a study species or region is not uncommon. As such, proxies are often used to supplement limited data to better inform biodiversity estimates. Such proxies can include data from nearby locations, surveys of representative taxa, and more recently, use of species distribution models to infer biodiversity based on areas identified as suitable for species (Phillips *et al.*, 2004).

Applications of species distribution models assume that information about where a species is observed provides insight into the environmental limits of a species by correlating observations with environmental conditions (Phillips *et al.*, 2004); this has been shown to work well in many examples (e.g. Beaumont *et al.* 2005; Beaumont *et al.* 2007; Vasconcelos *et al* 2012). However, this approach is based on the assumption that the observation records represent the full environmental niche (or fundamental niche) (Hutchinson & Macarthur, 1959; Araújo & Guisan, 2006). Such an assumption rarely holds true for a variety of reasons; including incomplete or biased sampling regimes or simply that only the realised niche is sampled. Developing species distribution models based on incomplete representation of a species environmental limits can restrict the ability of the model to project onto novel environments (Pearson & Dawson, 2003; Araújo & Guisan, 2006). This may be true for many studies that only use observations of a species from a study region rather than the species full distribution.

This Chapter expands the dataset presented in the previous chapter to include additional species records, from atlas and museum databases, from across the study region with the assumption that models will be strengthened if based on more species occurrence data. The validity of using observation records of species from ‘focal regions’, rather than the wider, global distributions, to generate accurate environmental envelopes and resulting distribution maps for echolocating bats of the Australian Wet Tropics World Heritage area (hereafter the ‘Wet Tropics’) is addressed through this expanded data set. Best estimates of the current distributions of 28 bat species, as modelled given two sets of observation data (local or global) and by accounting for or ignoring sampling bias, are made. This study examines evidence that SDMs should ignore artificial boundaries defining ‘focal regions’ and use all possible information to better inform biodiversity assessments.

Methods

Study area

The Wet Tropics bioregion is a World Heritage listed area of approximately 1.8 million hectares (Chapter 1, Figure 1.2a). The region contains a number of elevational gradients (mountain ranges) ranging in elevation from sea level to 1600m above sea level. Approximately one-third of the Wet Tropics bioregion is higher than 600m, where annual mean temperatures are generally below 22°C (Stork *et al.*, 2009). The area is dominated by tropical rainforest which covers approximately 1 million hectares of the region (Williams, 2006) (Chapter 1, Figure 1.2b). Annual rainfall throughout the Wet Tropics is high (ranging between 1500mm to 9000mm per year), with the majority of rain falling between November and April (Bonell & Callaghan, 2008).

Study species

For this study 28 species of bat known to, or likely to, inhabit the Wet Tropics bioregion, based on potential species distributions provided in Churchill (2008) were investigated. This expands on the number of species presented in Chapter 2 of this thesis where only 10 species were identified. The 28 species in this study cover all seven families of echolocating bats occurring in Australia (Megadermatidae, Rhinolophidae, Hipposideridae, Verspertilionidae, Miniopteridae, Molossidae, and Emballonuridae). As this study is focused on echolocating bats the only other family of bats found in Australia, the Pteropodidae or flying foxes, were not considered.

Modelling

Observations, or occurrence records, were obtained during field surveys covering an altitudinal and latitudinal gradient of the study region (see Chapter 2 and Appendix i for detailed methodology and species records). These were supplemented with observations from the

Global Biodiversity Information Facility (GBIF, www.gbif.org), the Atlas of Living Australia (ALA, www.ala.org.au), and the Online Zoological Collections of Australian Museums (OZCAM, www.ozcam.org.au). All records were vetted for positional accuracy (>1km positional accuracy) and taxonomic accuracy (nomenclature changes, identification issues, etc.) and only geographically unique observations were used for modelling. A total of 37 950 unique occurrence records representing the Australia wide (global) distributions and 730 unique records for the focal region distributions of the 28 study species were used in this analysis.

Bioclimatic variables, based on monthly temperature and rainfall values, were used to represent environmental conditions in the study area. A total of eight BIOCLIM variables were selected. These included annual mean temperature (bc01), temperature seasonality (bc04), maximum temperature of the warmest period (bc05), minimum temperature of the coldest period (bc06), annual precipitation (bc12), precipitation of the wettest month (bc13), precipitation of the driest month (bc14), and precipitation seasonality (bc15). These variables have been shown to produce sensible species distribution models for Wet Tropics mammals (VanDerWal *et al.*, 2009c; VanDerWal *et al.*, 2009b; Williams *et al.*, 2009; Staunton *et al.*, 2014). Further details of BIOCLIM and associated variables can be found in Nix (1986) and Busby (1991). Bioclimatic variables representing climate data from 1976 - 2005 were created using the climates package (VanDerWal *et al.*, 2011a) in R (R Development Core Team, 2011, www.r-project.org). Australia wide surfaces were at a 5km resolution, produced by aggregating monthly data from Australia Water Availability Project (AWAP; http://www.csiro.au/awap/). For the study region, the bioclimatic surfaces were created at a 250m resolution based on monthly averages sourced from ANUCLIM 5.1 (McMahon *et al.*, 1995) run on a 9 arc-second DEM sourced from Geoscience Australia (v3; http://www.ga.gov. au/).

Maxent (Phillips *et al.*, 2004) was used for all species distribution modelling. It has been shown to outperform other similar approaches (Araújo *et al.*, 2005; Elith *et al.*, 2006; VanDerWal *et al.*, 2009c; Merow *et al.*, 2013; García-Callejas & Araújo, 2016) and provide valuable information even with small sample sizes (Elith *et al.*, 2011). Standard Maxent settings were used to create the models (as outlined in Phillips & Dudik, 2008), with the exception of the type of background (or pseudo-absence) layer used. Maxent identifies what is unique about where the species occurs relative to what is environmentally available; as such it requires a representation of what is available, termed "background". Although the default setting in Maxent is a background selection of 10 000 random points, for this analysis approximately 20 000 random points (sampling bias-uncorrected) were chosen to more accurately represent the full environment.

However, observations of species often contain spatial bias in sampling. To attempt to account for the sampling bias in the observation records, the sampling bias in the background was simulated using a target group background (‘bias-corrected’) (Elith *et al.*, 2006; Phillips *et al.*, 2006). The target group background uses all observation data for the target taxon, in this case the 28 species of bats, independent of species to represent the environment available to the species. This allows only sampled environments to be represented with any spatial sampling bias being accounted for in both observation and background. Species’ distributions were analysed using models containing different combinations of either global or focal extent data, and bias-corrected or bias-uncorrected backgrounds, in order to test which model inputs generated the most accurate environmental envelopes and resulting distribution maps.

Four different models were run for each of the 28 species. These were:

- Model A - trained with all Australian observations (global), using all Australian bat records as background points at 5km resolution (bias-corrected background), and projected onto Wet Tropics spatial layers at 250m resolution;
- Model B - trained with all Australian observations (global), using 20 000 random background points at 5km resolution (bias-uncorrected background), and projected onto Wet Tropics spatial layers at 250m resolution;
- Model C - trained with a Wet Tropics only (focal) subset of observations, using Wet Tropics only observations of bats as background points at a 250m resolution (bias-corrected background); and
- Model D - trained with a Wet Tropics only (focal) subset of observations, using 20 000 random background points selected from within the Wet Tropics at a 250m resolution (bias-uncorrected background).

Both qualitative and quantitative assessments of model performance were conducted in order to better assess model accuracy. AUC values for each model type were produced using resulting Lambdas files projected onto a fixed set of testing points. The performance of each model was assessed and compared through analysis of each AUC value using the pROC package (Robin *et al.*, 2011) in R (R Development Core Team, 2011, www.r-project.org). Species’ distribution maps were also visually assessed to ensure sensible and realistic outputs when compared to field guides and expert opinion. A rating of 1 (very poor), 2 (poor), 3 (average), 4 (good) or 5 (very good) was assigned to projected maps based on how accurately they predicted species distribution, measured against what is known and published about the species (including published maps and habitat descriptions, see Churchill (2008)). Similar rankings were also assigned to (i) the number of species occurrence points in the model (1 = >10, 2 = >50, 3 = >500, 4 = >1000, 5 = >2000) assuming greater representation is correlated with better models; (ii) the contribution of climatic variables to the model (assessment based on ecological sense, 1 = very poor, 2 = poor, 3 = average, 4 = good or 5 = very good); (iii) the AUC value (1 = <50%, 2 = 50-64%, 3 = 65-74%, 4 = 75-84%, 5 = >85%). These scores were then averaged to give the models a 'star rating' (between 1 (poor) and 5 (best)) detailing the reliability and performance of the model. The four different models for each species were then ranked, based on performance, to determine which was the most accurate (1 = most accurate, 4 = least accurate).

Finally, overall species richness within the Wet Tropics was assessed by overlaying all 28 species distribution maps, based on the best performing model, and assessing cell occupancy. If a species was found to exist within a cell it was given a score of 1, while non-occupancy was given a score of 0. Each cell was then given a cumulative value and a total species richness map was produced.

Results

All model outputs for each species were condensed into a species specific figure (presented in Annex 3). Each species figure includes a general map of Australia indicating the number and location of occurrence records used in this study (Annex 3, Figure 3.1.1i – 3.1.28i), as well as potential species distribution maps produced from each of the model computations (Annex 3, Figure 3.1.1a-d to Figure 3.1.28a-d). Species distribution models were produced by Maxent in the form of climatic suitability maps. Each species figure also contains a table summarising data used in constructing the various models, each models' receiver-operating characteristic curve (AUC) value, the most significant climatic variables driving predicted distributions (as well as their percentage contribution and associated response curve), and model accuracy ranking.

Data synthesis and model analysis

Models generated using global occurrence points (Models A and B) were found to be the most accurate (20 species, 71% of all models deemed to be the most accurate) (Table 3.1, Table 3.2a). Additionally, models that were generated using global occurrence records coupled with a bias-corrected background (Model A) were deemed to be, in the majority of cases, more accurate (17 species, 60% of models) than all other models combined (11 species, 40% of models). For example, Model B was assessed as being most accurate in describing only three species (11%).

The accuracy of models using only records from the focal region (Models C and D) were found to be poor in comparison to those using all known records. Of these models using focal region only, Model D, that incorporated a bias-uncorrected background was deemed to be the most accurate model for seven species (25% of models). Models using only occurrence points from the focal region, projected on to a background corrected for sampling bias (Model C) were deemed to be the most accurate for just one of the 28 species (4% of models; *Macroderma gigas*).

Bioclimatic variables

Bioclimatic variables used in the Maxent SDMs were ranked according to their relative contributions to the models (Table 3.1). The three most important environmental predictors of species distribution, and their relative percentage contribution (multiple variables contributing over 75% in total, or individual variables contributing 100% of the explanation), are presented for each model in Annex 3. Response curves are also presented for each of the most important variables depicting the direction of the relationship between climatic suitability and the variable (Annex 3).

Species' distribution patterns were found to be independent of family grouping with no cohesive pattern within family found to exist. The Molossidae family, and the two species within it, was the exception to this (distributions are best characterised by Model A and precipitation variables, see Table 3.1). This lack of family pattern is particularly evident in the large Vespertilionidae family which shows considerable species variation with different species within this family exhibiting different distribution patterns (Table 3.1). Although no overall pattern was found across of within bat families, precipitation variables were found to be most important in driving species' distributions (i.e. 75% of most accurate models included some BIOCLIM parameter representing precipitation measure) (Table 3.1, Table 3.2b). Precipitation Seasonality (bc15) was the most common predicting variable across the most accurate models (29%) (Table 3.2b). Precipitation of Wettest Month (bc13) and Precipitation of Driest Month (bc14) were also found to be common predictors of species climatic distributions (21% each). Other measures of precipitation, as well as measures of temperature were less often identified as important contributors in the most accurate models (for example; Maximum Temperature of the Warmest Month (bc05, 7%), Minimum Temperature of the Coldest Month (bc06, 7%), Annual Mean Temperature (bc01, 7%), Annual Precipitation (bc12, 4%), and Temperature Seasonality (bc04, 4%) (Table 3.2b)).

Species Richness

Modelled richness of bat species in the wet tropics is predicted to be fairly high throughout the region (with most areas in Figure 3.1a coloured green indicative of greater than 18 species, with the darkest green representing a richness of greater than 24 species.). High species richness appears to coincide with upland rainforest, with the highest richness predicted to be found in mountainous, rainforested areas, particularly through the centre of the region, although not at the tops of these mountains (Figure 3.1a, 3.1b). A slightly reduced species richness can be observed at the centre of subregions with the highest elevations, for example the Winsdor (WU) and Carbine Uplands (CU) to the north where richness reduces slightly at the centre of these regions (as seen in Figure 3.1a). Lowland and coastal areas, especially between approximately -17 and -18 degrees latitude have considerably lower predicted species richness than the rest of the Wet Tropics. This region falls south of Cairns and north of Hinchinbrook around the Cairns-Cardwell subregion with areas of lowest richness correspond with lowland or non-rainforested areas (Chapter 1, Figure 1.2a; Figure 3.1a, 3.1b). The lowest species richness depicted by the models appears to coincide with the Bellenden Ker and Bartle Frere subregion, containing the highest peaks in the Wet Tropics (Chapter 1, Figure 1.2a).

Discussion

Model analysis and interpretation

Limiting the data which goes into a model will ultimately limit the accuracy, and usefulness, of the outputs (Araújo & Guisan, 2006; Merow *et al.*, 2013; Mainali *et al.*, 2015; Singer *et al.*, 2016). This study shows that more data-inclusive models generally produced stronger, more ecologically relevant species distribution models in contrast to models that ignored ‘non-focal area’ data (those that ignored the global data outside the focal region). This study highlights that although many research programs may be focused on species inhabiting a particular focal region, it is important to utilise as much data about the study species as possible, including information from outside the study region, when attempting to predict likelihood of occurrence. Using all available information allows a stronger estimate of species specific climatic suitability to be generated by the model.

Table 3.1 Summary of the most important variable contained within the most accurate species distribution model. Table shows family, species name, identity of most accurate model, model AUC value, and the most important climatic correlate and its percentage contribution to predicted species distribution. Species are ordered taxonomically as per Churchill (2008) and Reardon *et al*. (2014).

Family	Family, Species	Most accurate Model	AUC value	Climatic variable	% Model contribution
Megadermatidae	*Macroderma gigas*	C (Focal, Bias-corrected)	0.93	Temperature Seasonality (b04)	81.1
Rhinolophidae	*Rhinolophus megaphyllus*	B (Global, Bias-uncorrected)	0.63	Annual Precipitation (bc12)	55.2
	Rhinolophus robertsi	A (Global, Bias-corrected)	0.81	Precipitation Seasonality (bc 15)	55.6
Hipposideridae	*Hipposideros ater*	A (Global, Bias-corrected)	0.80	Precipitation of the Driest Month (bc14)	64.0
	Hipposideros diadema	B (Global, Bias-uncorrected)	0.81	Precipitation of the Wettest Month (bc13)	58.7
	Hipposideros semoni	D (Focal, Bias-uncorrected)	0.98	Minimum Temperature of the Coldest Month (bc06)	60.6
Vespertilionidae	*Chalinolobus gouldii*	A (Global, Bias-corrected)	0.61	Precipitation of the Wettest Month (bc13)	64.4
	Chalinolobus nigrogriseus	D (Focal, Bias-uncorrected)	0.93	Precipitation Seasonality (bc15)	46.0
	Murina florium	A (Global, Bias-corrected)	0.93	Precipitation of the Wettest Month (bc13)	56.0
	Myotis macropus	D (Focal, Bias-uncorrected)	0.86	Precipitation of the Wettest Month (bc13)	35.5
	Nyctophilus bifax	A (Global, Bias-corrected)	0.71	Precipitation Seasonality (bc15)	41.5
	Nyctophilus gouldi	A (Global, Bias-corrected)	0.96	Precipitation of the Driest Month (bc 14)	50.2
	Phoniscus papuensis	A (Global, Bias-corrected)	0.79	Precipitation Seasonality (bc15)	22.5
	Pipistrellus adamsi	D (Focal, Bias-uncorrected)	0.99	Precipitation Seasonality (bc15)	65.2
	Scoteanax rueppellii	A (Global, Bias-corrected)	0.89	Precipitation of the Driest Month (bc14)	63.2
	Scotorepens greyii	A (Global, Bias-corrected)	0.53	Maximum Temperature of the Warmest Month (bc05)	75.4
	Scotorepens orion	B (Global, Bias-uncorrected)	0.54	Precipitation of the Driest Month (bc14)	71.0
	Scotorepens sanborni	A (Global, Bias-corrected)	0.71	Precipitation Seasonality (bc15)	58.2
	Vespadelus pumulis	A (Global, Bias-corrected)	0.82	Precipitation of the Wettest Month (bc13)	43.6
	Vespadelus troughtoni	D (Focal, Bias-uncorrected)	0.89	Precipitation Seasonality (bc15)	34.8
Miniopteridae	*Miniopterus australis*	A (Global, Bias-corrected)	0.55	Precipitation of the Wettest Month (bc13)	31.4
	Miniopterus orianae oceanensis	D (Focal, Bias-uncorrected)	0.81	Precipitation of the Driest Month (bc14)	53.2
Molossidae	*Chaerephon jobensis*	A (Global, Bias-corrected)	0.89	Precipitation of the Driest Month (bc14)	50.9
	Mormopterus lumsdenae	A (Global, Bias-corrected)	0.88	Precipitation Seasonality (bc15)	40.5
Emballonuridae	*Saccolaimus flaviventris*	A (Global, Bias-corrected)	0.73	Maximum Temperature of the Warmest Month (bc05)	54.9
	Saccolaimus saccolaimus	D (Focal, Bias-uncorrected)	0.94	Annual Mean Temperature (bc01)	65.9
	Taphozous australis	A (Global, Bias-corrected)	0.88	Minimum Temperature of the Coldest Month (bc06)	40.8
	Taphozous troughtoni	A (Global, Bias-corrected)	0.90	Annual Mean Temperature (bc01)	38.1

Table 3.2a Frequency of success of most accurate model for each species. Model A (global occurrence with bias-corrected background) was the most accurate model most often. Table 3.2b Frequency of BIOCLIM parameter (environmental correlate) identified as the most important variable driving best SDM for each species. Precipitation seasonality was most correlated with species' distributions.

a) Model	Frequency	%
A	17	60
B	3	11
C	1	4
D	7	25
Total	**28**	**100**

b) Variable	Frequency	%
Precipitation seasonality (bc15)	8	29
Precipitation of wettest month (bc13)	6	21
Precipitation of driest month (bc14)	6	21
Annual precipitation (bc12)	1	4
Total Precipitation variable	**21**	**75**
Max temperature of warmest month (bc05)	2	7
Minimum temperature of coldest month (bc06)	2	7
Annual mean temperature (bc01)	2	7
Temperature seasonality (bc04)	1	4
Total temperature variable	**7**	**25**
Total	**28**	**100**

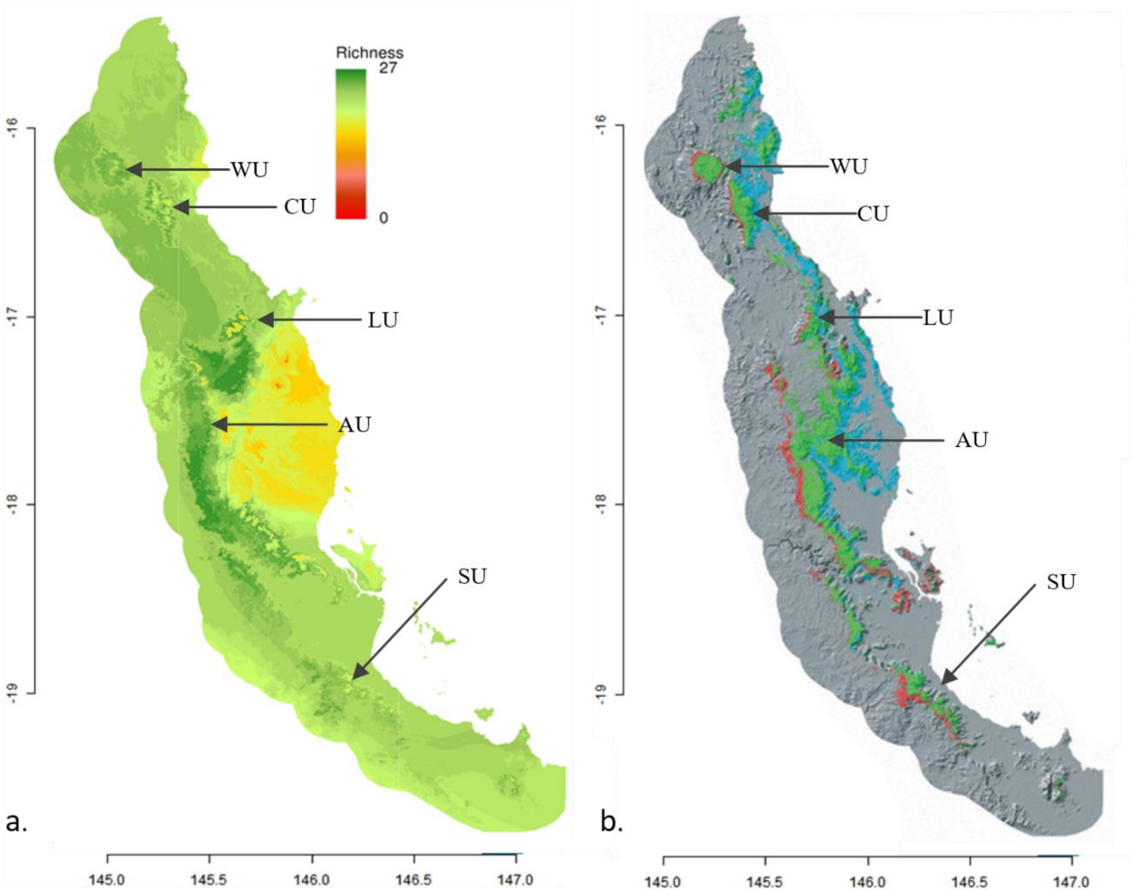


Figure 3.1 Model of the species richness, calculated by the cumulative total of the modelled distributions of 28 bats within the Wet Tropics. Richness is indicated in a gradient from red (less rich) to dark green (most rich). b. map of the pre-clearing distribution of low (blue) and high (green) elevation rainforest and adjacent wet sclerophyll forest (red) adapted from VanDerWal *et al.* (2009a).

The findings reported herein, while they agree with many other studies (e.g. Araújo & Guisan, 2006; Merow *et al.*, 2013; Mainali *et al.*, 2015; Singer *et al.*, 2016), disagree with the results of others. Vale *et al* (2014) concluded that using information from the complete range of a species may lead to overestimation of a model, particularly at range margins. Further, Stockwell and Peterson (2002) suggest that use of global data in SDMs may produce inaccurate models as some degree of regional ecological adaptation is inevitable and widespread data may not account for local distributions (Stockwell & Peterson, 2002).

Countering these arguments, this study, and other comparable studies, argue that the use of local or regional data only may provide an incomplete picture of the environmental limits to species predicted distributions (Braunisch & Suchant, 2010; Sanchez-Fernandez *et al.*, 2011). Indeed, almost half of the species modelled using focal data only were based on less than 10 occurrence records (13 species or 46% of models) with six species based on less than five records (*R. robertsi,* 2 records; *N. gouldi,* 1 record; *P. papuensis,* 2 records; *P. adamsi*, 2 records; *S. orion,* 3 records; *S. saccolaimus,* 3 records). Although it could be suggested that models based on so few records are likely to be misleading, an analysis conducted by Hernandez and colleagues (2006) indicated that a sample size of five or more records can produce adequate models. Regardless, in this study, if models based on less than five occurrence records (six species) were removed the general conclusion of this chapter remains the same with over 70% of the remaining models still being deemed more accurate based on 'global' data.

Confirming the findings of this study, the use of restricted data has been likened to not capturing 'the full species' environmental range', thus reducing the usefulness of the model (Thuiller *et al.*, 2004). For example, not taking true absences into account limits the amount of relevant information going into the model. Restricting the extent of occurrence data used places significant limitations on the resulting model outputs and ultimately leads to more conservative outputs (Thuiller *et al.*, 2004; Phillips *et al.*, 2009; Kramer-Schadt *et al.*, 2013).

To account for, and counter, where species data may be limited, this study draws on Australia wide occurrence records to increase the amount of information inputted into the models. It is recognised that some of the species included in this analysis occur outside of Australia as well. Given the general uncertainty around global bat taxonomy and phylogeny, use of these truly global records was decided against as identification accuracy could not be guaranteed (e.g. Teeling *et al.*, 2005; Reardon *et al.*, 2014).

The selection of ‘pseudo-absences’ (or background points) can have significant impacts on model accuracy and ecological realism (Phillips *et al.*, 2009; VanDerWal *et al.*, 2009c; Kramer-Schadt *et al.*, 2013). This study shows that SDMs can be strengthened by accounting for sampling bias in the background locations. The ability to quantify and account for sampling bias is a common problem for species distribution modellers as model outcomes can be sensitive to biased inputs (Araújo & Guisan, 2006; Merow *et al.*, 2013). Rather than accurately modelling the distribution of a species, heavily biased observation records can lead to an overrepresentation of particular environmental areas in the model. This may lead to the resulting model representing the spatial bias in the sample rather than accurately reflecting the species distribution (VanDerWal *et al.*, 2009c; Kramer-Schadt *et al.*, 2013). Sampling bias can be addressed by either limiting the amount of occurrence records used from an oversampled area, or through selective inclusion of background points. There is some concern that limiting the number of occurrence records may result in poor models, thus manipulation of background layers offers a more suitable solution (Kramer-Schadt *et al.*, 2013). In this study, sampling bias was accounted for by including a background layer in the model which specifically accounted for environmental preferences of the study species. The targeted background (bias-corrected, models A and C) uses all observation data available for the region, independent of species, to represent the environment available to all species. This ensured only sampled environments were included in the final model and sampling bias was accounted for. Using a bias-corrected background produced models that were characterised as more appropriate for 64% of species over those where no attempt to correct sampling bias was made.

There is a common misunderstanding over the use of AUC for SDM model accuracy; AUC does not determine the accuracy of the model but rather is a relative value for comparing different models produced using the same dataset (Yackulic *et al.*, 2013). To account for this, models’ AUC values were combined under a broader model evaluation system, rather than basing model evaluation on the AUC value alone. Other aspects of the model such us number of records inputted, sensibility of resulting distribution maps (based on what is known about the species), and ecological sensibility of climatic variables were also taken into consideration when assessing model performance. When AUC values alone were used to evaluate the best model for each species a very different pattern emerged. Models created using data from the focal region only produced more accurate distribution predictions. However, as previous studies have highlighted, that AUC values alone do not necessarily reflect the accuracy of the model. For example, in considering the modelled distribution of *C. gouldii*, AUC alone suggests that Model D (focal data, bias-uncorrected) is the best SDM (AUC = 0.980) (Annex 3, Figure 3.1.7). However, when other aspects of the model, such as number of occurrence points inputted or sensibility of determined environmental predictors, were taken into consideration Model A (global, bias-corrected) was considered to be the best model (AUC = 0.687). The ecological interpretation of input variables and resulting map of the latter model is more appropriate given the species is known to occur across most of Australia, with the exception of the far north (Churchill, 2008). Model D, using focal data only thus overestimates this species distribution by not taking information from the wider species range into account thereby over estimating the importance of rainforest habitats for this species.

There is also a growing amount of criticism around the use of summed, binary distributions of species as a surrogate of richness (Calabrese *et al.*, 2014; D'Amen *et al.*, 2015; Guillera-Arroita *et al.*, 2015). In this study, individual species distribution models are produced using continuous layers with the overall richness calculated based on binary conversion. Critics claim that richness estimates created using binary rather than continuous stacking of modelled species' distributions could lead to inaccurate, overpredicted models (D'Amen *et al.*, 2015; Guillera-Arroita *et al.*, 2015). Conversely, use of summed, binary distributions has been said to provide an easy and 'strong' way to identify the component species providing good base-line predictions on community composition (D'Amen *et al.*, 2015). Regardless, acknowledging this potential bias, a number of steps have been taken, as outlined above, to ensure that the data entered into the model is as accurate as possible to limit overestimation of species' distributions. The resulting models should thus provide good base line information on which to build further analysis of species' distribution trends in the region.

Species and variable trends

In Chapter 2 of this thesis, temperature seasonality was identified as the climatic variable that best determined probability of species occurrence, although precipitation (or water availability) in general was also found to be correlated. However, in this study, and other studies conducted in the tropics, water availability has been found to be a more important driver of species' distribution (Hawkins *et al.*, 2003; Thomas, 2010; Presley *et al.*, 2012). Two of the three most important variables identified to determine species' distributions in this study (precipitation seasonality and precipitation of the driest month) were also associated with probability of species' occurrence in Chapter 2. This suggest that when more information about a species is considered, precipitation becomes more important than temperature in determining distribution. Exceptions to this may be explained by differences in the composition of the model determined to be most accurate. For example, precipitation variables were found to be correlated with the distribution for two of the three Hipposiderid species (*H. ater* and *H. diadema)* while the distribution of the third species, *H. semoni,* was found to be primarily driven by minimum temperature of the coldest month. The most accurate distribution for *H. semoni* was based on only Wet Tropics records (Model D), of which there very few (only 6), while the models deemed to best describe the other two species used global occurrence records (181 records, Model A and 66 records, Model B respectively).

Although precipitation was found to be the main variable behind distribution of the majority of species, no obvious overall pattern between distribution and bat family or genus was found, as was the case in Chapter 2. For example, there was not a family wide distribution trend with all species in a particular family modelled to have similar distributions, with the exception of the Molossidae family and the two species with in it. Individual species within each family were modelled to have different predicted distributions, potentially responding to different variables. This is particularly the case for the large, highly diverse Vespertilionidae family which shows considerable between-species variation in important ecological dimensions such as body size, foraging style, and habitat preference, with corresponding variation in predicted distribution patterns throughout the region (Churchill, 2008) (Annex 3, Figure 3.1.7 – 3.1.20).

Species Richness

Mapping of modelled species richness shows that the upland areas in the centre of the Wet Tropics contain the highest species richness. This high species richness appears to be clustered around the Atherton Uplands (highest peak approximately 1000m elevation). This richness reduced slightly at the highest elevations throughout the area with this being particularly evident in the Winsdor and Carbine Uplands to the north. Low richness is predicted to be found in lowland and coastal regions south of Cairns. However, the lowest richness was predicted to occur on the top of the highest peaks in the region, Bellenden Ker and Bartle Frere (1600m elevation). Based on these findings, richness appears to coincide with vegetation type with the highest species richness occurring in areas vegetated by upland rainforest while lowest richness coincides with lowland or non-rainforested areas (Figure 3.1).

Upland rainforest in the region is known to be a historically stable environment type, with fluctuations in amount of rainforest vegetation being linked to precipitation (VanDerWal *et al.*, 2009a). Therefore, the correlation observed in this study between modelled bat species richness and upland rainforest may be attributable to the environmental conditions in these areas. In the case of the highest elevation, the environments generally present low temperatures with high precipitation with high amounts of low cloud cover resulting in stunted vegetation growth. These attributes combine to offer less suitable habitat for bats. In the lowlands, a reduced richness may correspond with higher temperatures and lower precipitation. As previously discussed, water availability has been demonstrated to be the primary driver of other vertebrate species richness within the Wet Tropics, especially so for species with ranges restricted to the highest elevations (e.g. Microhylid frogs) (Williams & Hero, 2001). Observed species richness trends of non-volant mammals in the region are consistent with trends reported in this study. Mammal richness is found to be highest in the central uplands (Atherton Tablelands) with a decrease in richness to the north and south of this (Williams, 1997).

Conclusion

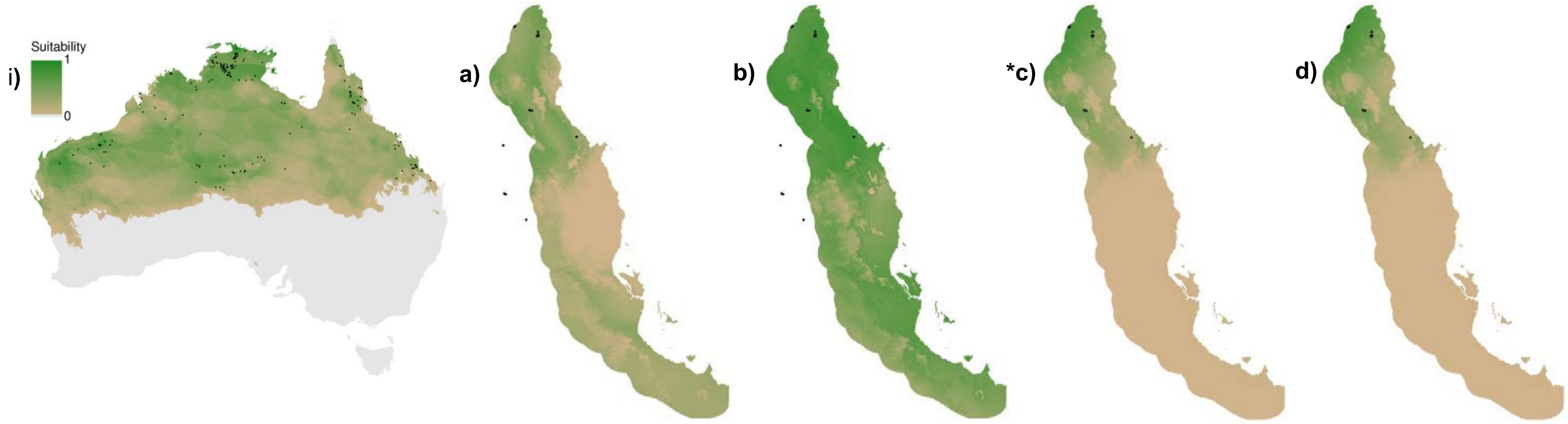
This study represents the first detailed description and analysis of the potential climatic distributions of all echolocating bat species in the focal region, and further links distributional and richness patterns of bats, a significant group of vertebrate taxa in the Wet Tropics, to climatic factors, and precipitation in particular. Being so strongly affected by water availability means tropical biodiversity may beconsiderably more vulnerable to the effects of climate change than temperate biodiversity (Tewksbury *et al.*, 2008; Corlett, 2012). This is primarily due to high species diversity, already limited distributions, and generally smaller thermal tolerances ranges in the tropics (Colwell *et al.*, 2008; Tewksbury *et al.*, 2008; Cadena *et al.*, 2012). Studies have identified this to be the case in numerous tropical species including plants and invertebrates, and many species of tropical vertebrate such as amphibians, reptiles, birds, and bats (Colwell *et al.*, 2008; Cadena *et al.*, 2012).

Crucially, this study demonstrates the importance of selecting and inputting adequate and appropriate data into models in order to provide realistic and reliable outcomes. For the vast majority of species, models based on occurrence records from the Australia wide, or ‘global’, distribution of the study species performed best. Moreover, accounting for the sampling bias (using a targeted background) produced models that generally outperformed those that ignored records outside the focal area. Based on models that were identified as most informative and most reliable, precipitation variables were determined to be most correlated with the distribution of bat species in the region. The majority of bat species diversity is shown to be clustered around upland, rainforested areas particularly in the centre of the region. Determining where species are, and why, is an important first step towards understanding how bat biodiversity in the Wet Tropics will be affected by global climate change. The results of this study support and further develop knowledge of bat biodiversity in the region (as presented in Chapter 2) as well as overall richness patterns for rainforest vertebrates and some invertebrates. This study also highlights that similar studies previously conducted could potentially be strengthened by taking all available external information into account.

Model accuracy becomes increasingly important as greater reliance is placed on techniques like SDMs to predict and inform mitigation of diversity losses due to global climate change. In such cases, inaccuracy in predictive modelling may have significant implications for species conservation efforts (Sanchez-Fernandez *et al.*, 2011; Aizpurua *et al.*, 2015). Models generated using restricted extent data have been demonstrated to produce inaccurate environmental predictions providing a poor basis for extending projections into the future. Including information on the full climatic and environmental range of a species distribution strengthens climate modelling by detailing environmental conditions where a species currently occurs or not (Thuiller *et al.*, 2004). Inaccurately determining present drivers of species' distributions makes it impossible to model changes to distributions under future change scenarios, such as global climate change. As well as providing more accurate, and thus useful, SDMs, the use of global information in this type of modelling provides a more accurate basis for future climate modelling. As such, this study informs and strengthens analyses presented in Chapter 4 which address the future impact of climate change on Wet Tropics bat biodiversity.

Annex 3

Macroderma gigas



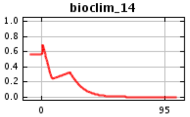
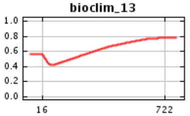
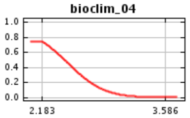
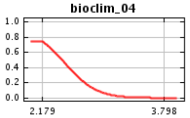
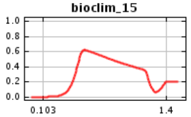
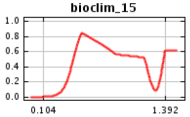
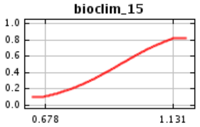
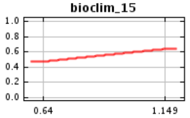
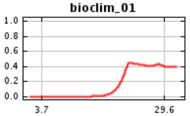
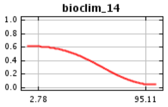
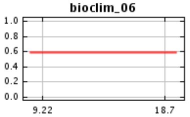
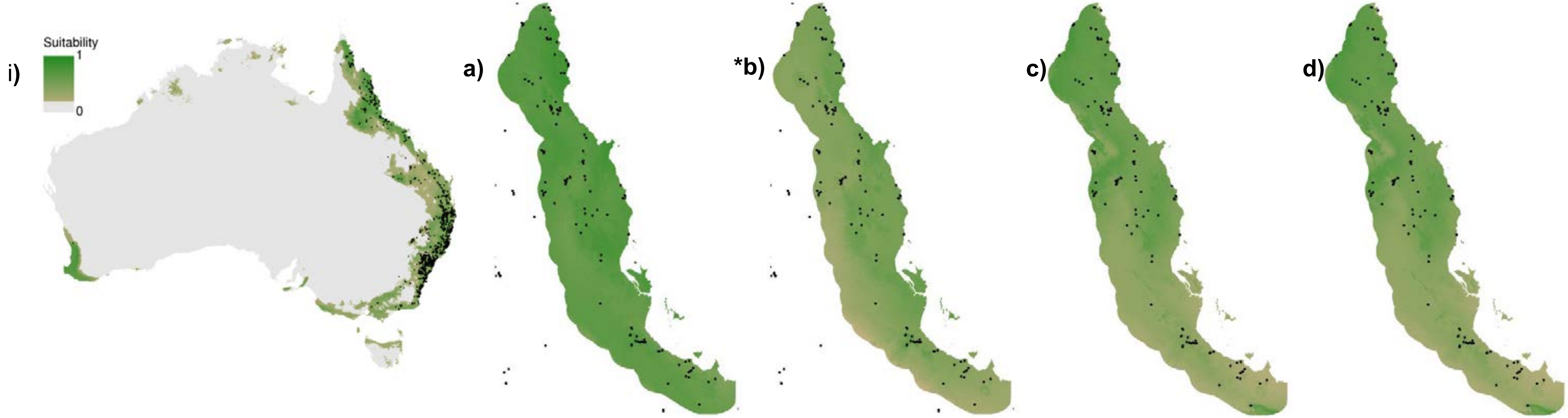
Global data, bias-corrected (a) Ranking:2 (2.75 stars)			Global data, bias-uncorrected (b) Ranking: 3 (2.75 stars)			Focal data, bias-corrected (c) Ranking: 1 (2.75 stars)			Focal data, bias-uncorrected (d) Ranking: 4 (2.5 stars)		
Model AUC	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**
0.81	272	36992	0.82	272	20475	0.93	10	728	0.93	10	20018
Variable	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**
bc14	58.3		bc13	47.4		bc04	81.1		bc04	84.3	
bc15	25.2		bc15	21.1		bc15	14.0		bc15	8.5	
bc01	7.0		bc12	12.7		bc14	4.9		bc06	3.6	
Total	**90.5**		**Total**	**81.2**		**Total**	**100**		**Total**	**96.4**	

Figure 3.1.1 Distribution of *Macroderma gigas* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Rhinolophus megaphyllus



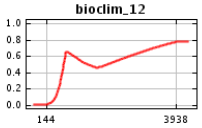
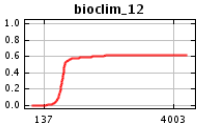
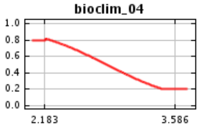
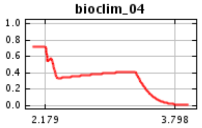
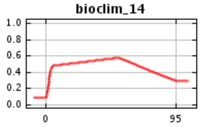
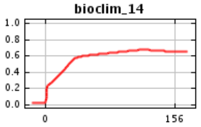
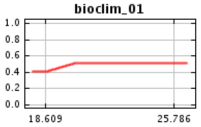
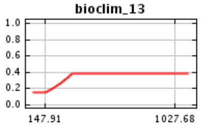
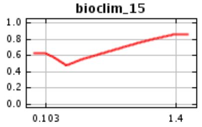
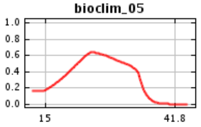
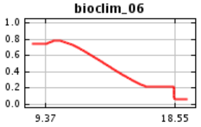
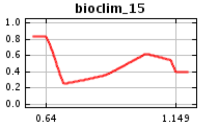
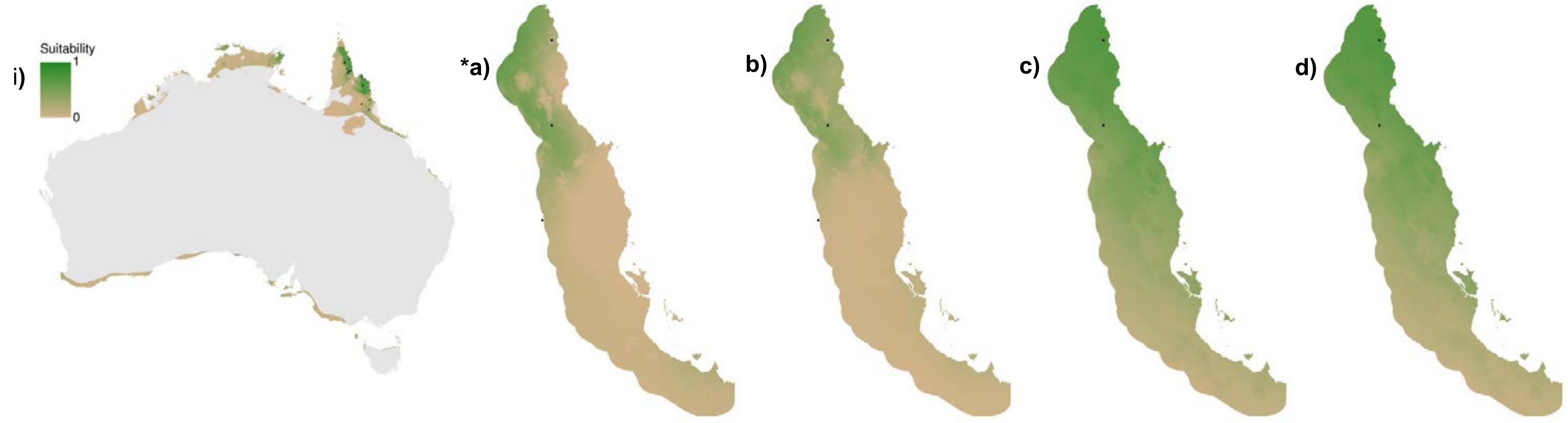
Global data, bias-corrected (a) Ranking: 2 (3.75 stars)			Global data, bias-uncorrected (b) Ranking: 1 (3.75 stars)			Focal data, bias-corrected (c) Ranking: 4 (3.25 stars)			Focal data, bias-uncorrected (d) Ranking: 3 (3.5 stars)		
Model AUC	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**
0.59	**2247**	**36992**	**0.63**	**2247**	**20475**	**0.61**	**123**	**728**	**0.77**	**123**	**20018**
Variable	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**
bc12	**53.0**		**bc12**	**55.2**		**bc04**	**53.5**		**bc04**	**38.8**	
bc14	**15.9**		**bc14**	**32.5**		**bc01**	**16.0**		**bc13**	**16.9**	
bc15	**10.0**		**bc05**	**6.9**		**bc06**	**10.4**		**bc15**	**8.4**	
Total	**78.9**		**Total**	**94.6**		**Total**	**79.9**		**Total**	**64.1**	

Figure 3.1.2 Distribution of *Rhinolophus megaphyllus* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Rhinolophus robertsi



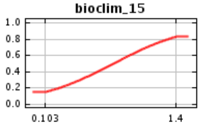
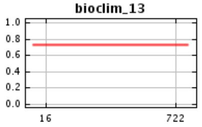
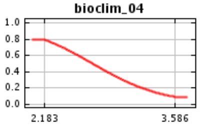
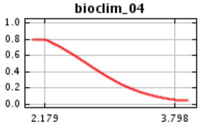
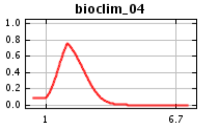
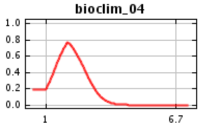
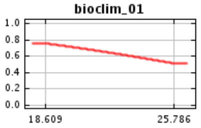
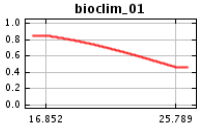
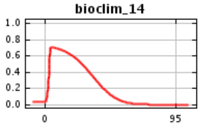
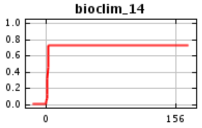
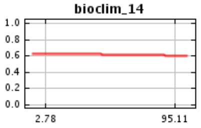
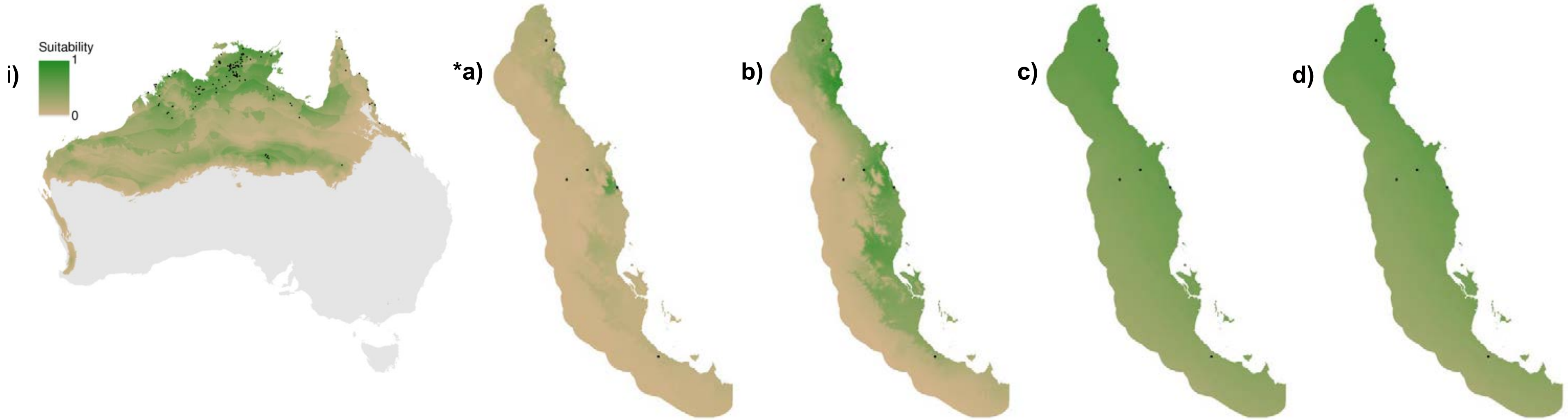
Global data, bias-corrected (a)			Global data, bias-uncorrected (b)			Focal data, bias-corrected (c)			Focal data, bias-uncorrected (d)		
Ranking: 1 (3.25 stars)			Ranking: 2 (3.25 stars)			Ranking: 3 (2.25 stars)			Ranking: 4 (2.25 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.81	28	36992	0.82	28	20475	0.87	2	728	0.87	2	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc15	55.6		bc13	36.2		bc04	93.0		bc04	91.6	
bc04	27.1		bc04	33.3		bc01	6.9		bc01	8.4	
bc14	16.1		bc14	20.6		bc14	0.1		-	-	-
Total	98.85		Total	90.1		Total	100		Total	100	

Figure 3.1.3 Distribution of *Rhinolophus robertsi* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Hipposideros ater



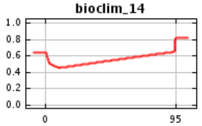
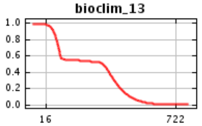
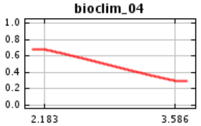
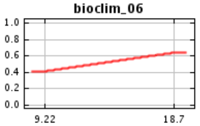
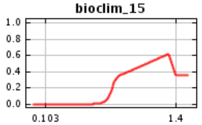
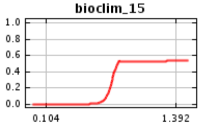
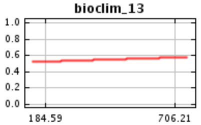
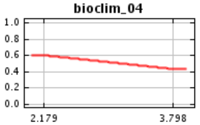
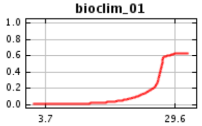
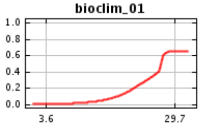
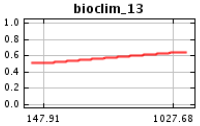
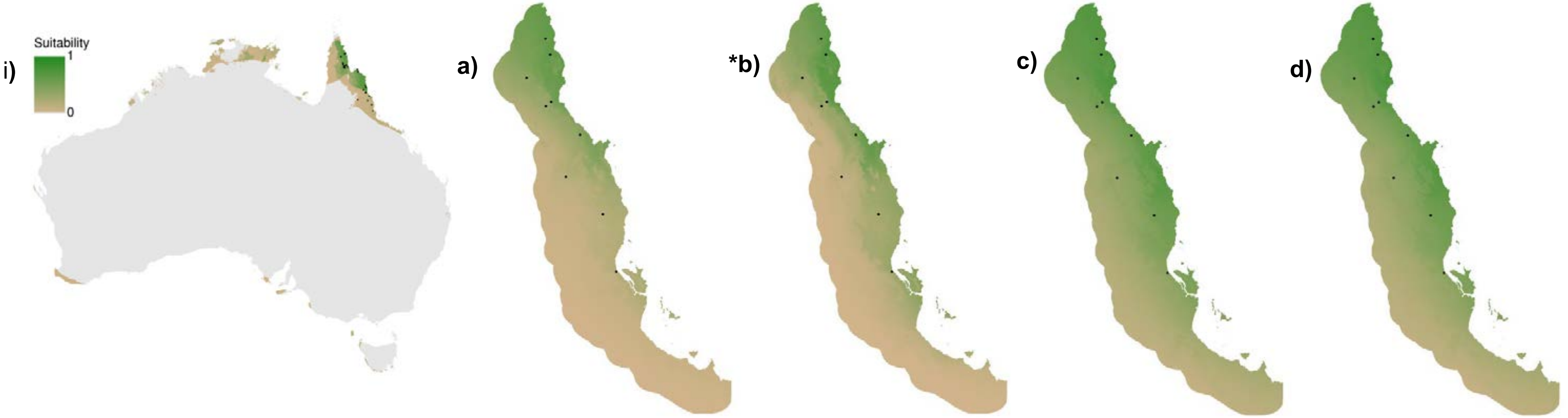
Global data, bias-corrected (a) Ranking: 1 (3.5 stars)			Global data, bias-uncorrected (b) Ranking: 2 (3.25 stars)			Focal data, bias-corrected (c) Ranking: 4 (1.5 stars)			Focal data, bias-uncorrected (d) Ranking: 3 (2.25 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.80	181	36992	0.79	181	20475	0.73	6	728	0.75	6	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc14	64.0		bc13	64.3		bc04	98.6		bc06	74.1	
bc15	22.2		bc15	11.5		bc13	1.4		bc04	22.4	
bc01	4.2		bc01	11		-	-	-	bc13	3.5	
Total	90.4		Total	86.8		Total	100		Total	100	

Figure 3.1.4 Distribution of *Hipposideros ater* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Hipposideros diadema



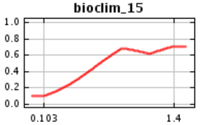
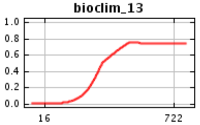
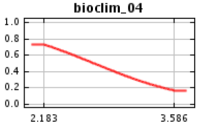
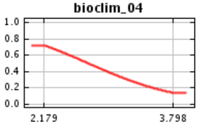
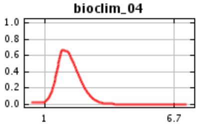
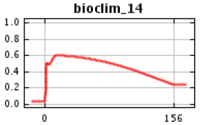
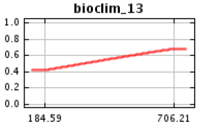
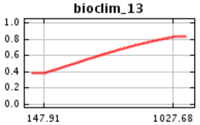
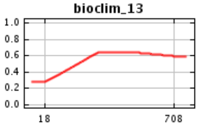
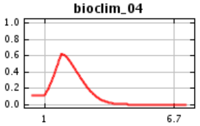
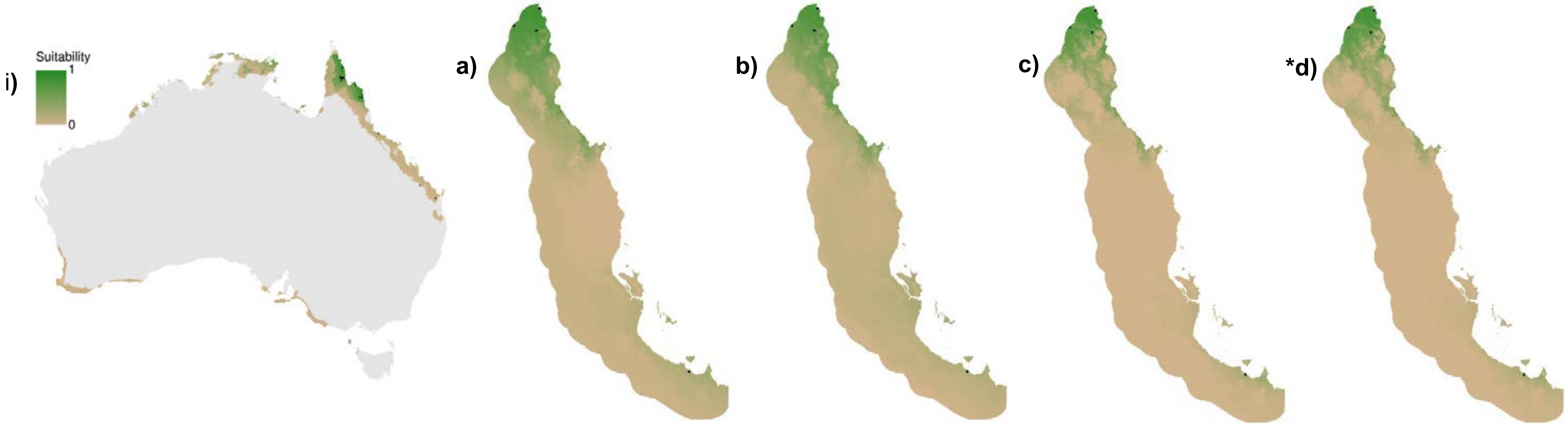
Global data, bias-corrected (a) Ranking: 2 (3.5 stars)			Global data, bias-uncorrected (b) Ranking: 1 (3.5 stars)			Focal data, bias-corrected (c) Ranking: 4 (2.25 stars)			Focal data, bias-uncorrected (d) Ranking: 3 (2.25 stars)		
Model AUC	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**
0.80	66	36992	0.81	66	20475	0.80	9	728	0.80	9	20018
Variable	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**
bc15	28.6		bc13	58.7		bc04	87.4		bc04	80.5	
bc04	24.1		bc14	17.1		bc13	12.6		bc13	19.5	
bc13	22		bc04	13.1		-	-	-	-	-	-
Total	**74.7**		**Total**	**88.9**		**Total**	**100**		**Total**	**100**	

Figure 3.1.5 Distribution of *Hipposideros diadema* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Hipposideros semoni



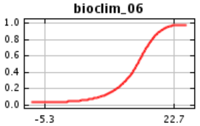
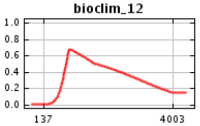
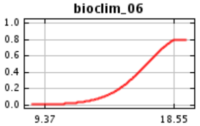
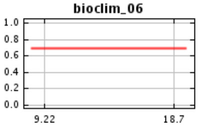
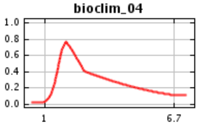
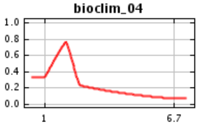
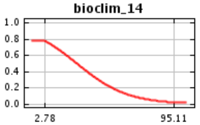
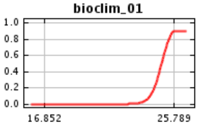
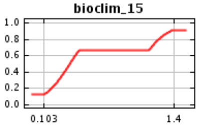
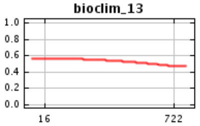
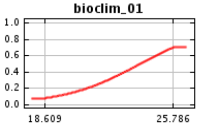
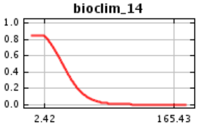
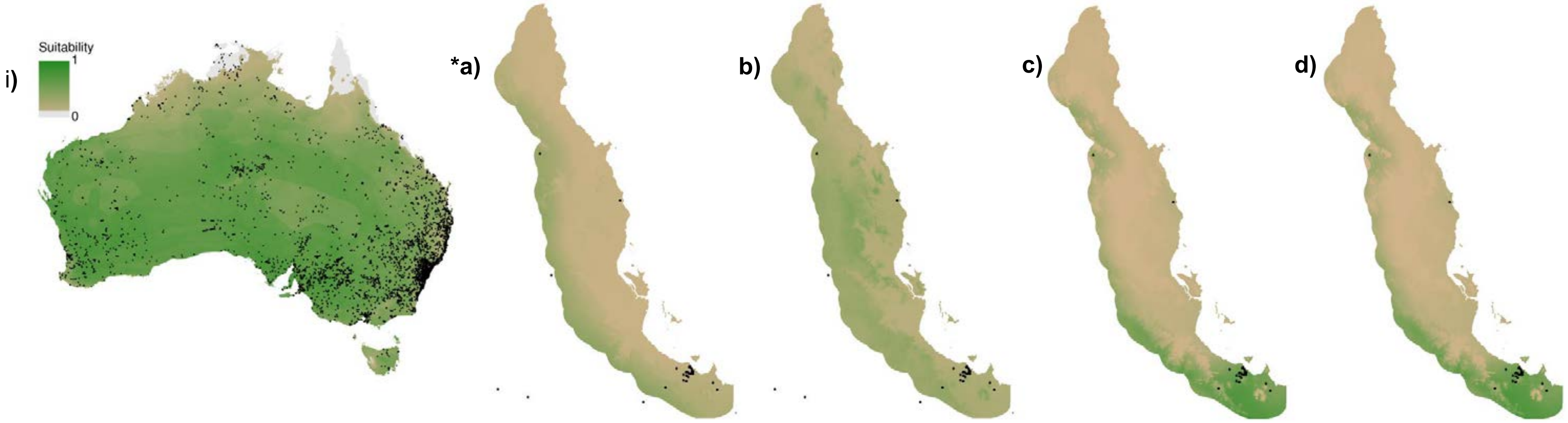
Global data, bias-corrected (a) Ranking: 2 (3.75 stars)			Global data, bias-uncorrected (b) Ranking: 3 (3.5 stars)			Focal data, bias-corrected (c) Ranking: 4 (3.25 stars)			Focal data, bias-uncorrected (d) Ranking: 1 (3.25 stars)		
Model AUC	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**
0.96	52	36992	0.95	52	20475	0.97	6	728	0.98	6	20018
Variable	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**
bc06	32.5		bc12	30.8		bc06	81.0		bc06	60.6	
bc04	25.5		bc04	22.7		bc14	14.3		bc01	25.4	
bc15	20.8		bc14	14.0		bc01	4.7		bc14	13.1	
Total	**78.5**		**Total**	**67.5**		**Total**	**100**		**Total**	**99.1**	

Figure 3.1.6 Distribution of *Hipposideros semoni* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Chalinolobus gouldii



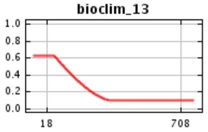
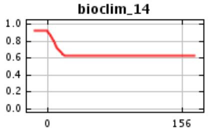
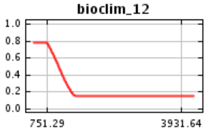
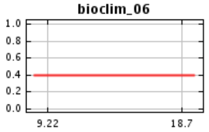
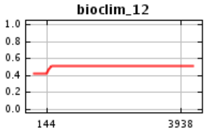
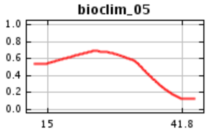
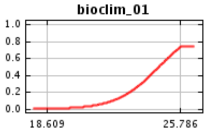
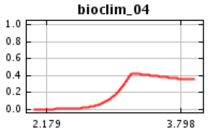
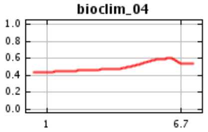
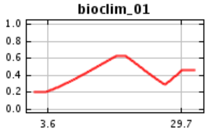
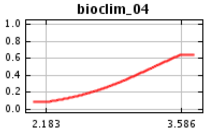
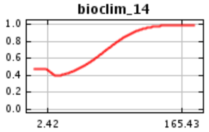
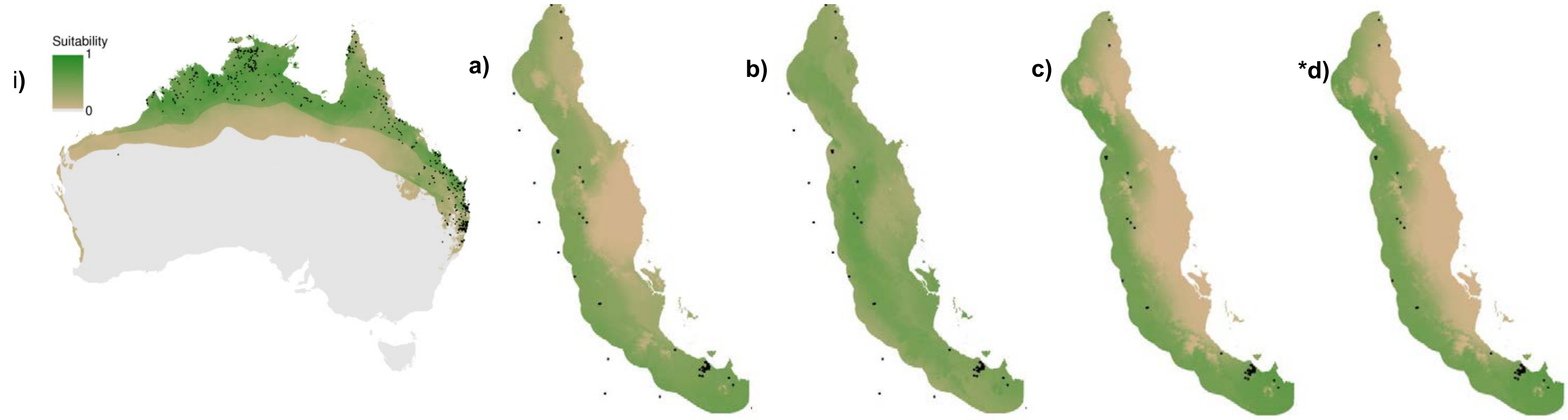
Global data, bias-corrected (a)			Global data, bias-uncorrected (b)			Focal data, bias-corrected (c)			Focal data, bias-uncorrected (d)		
Ranking: 1 (4 stars)			Ranking: 4 (3.25 stars)			Ranking: 2 (4 stars)			Ranking: 3 (3.25 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.61	7640	36992	0.59	7640	20475	0.92	26	728	0.98	26	20018
Variable	% contr.	Response curve	Variable	% contr.	Response curve	Variable	% contr.	Response curve	Variable	% contr.	Response curve
bc13	**64.4**		**bc14**	**73.0**		**bc12**	**62.3**		**bc06**	**27.0**	
bc12	**13.2**		**bc05**	**18.0**		**bc01**	**14.5**		**bc04**	**25.1**	
bc04	**5.4**		**bc01**	**3.9**		**bc04**	**14.3**		**bc14**	**18.8**	
Total	83.0		Total	94.9		Total	91.1		Total	70.90	

Figure 3.1.7 Distribution of *Chalinolobus gouldii* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Chalinolobus nigrogriseus



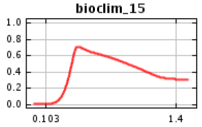
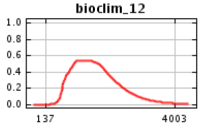
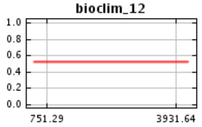
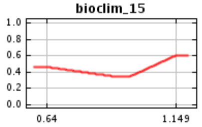
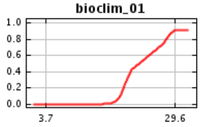
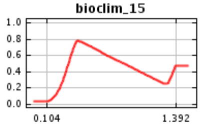
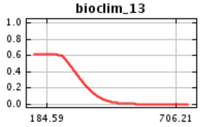
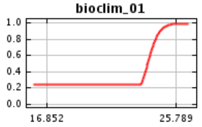
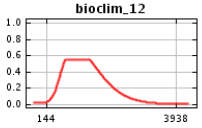
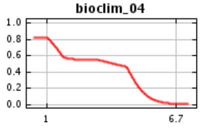
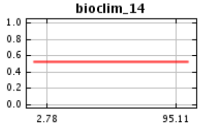
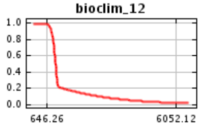
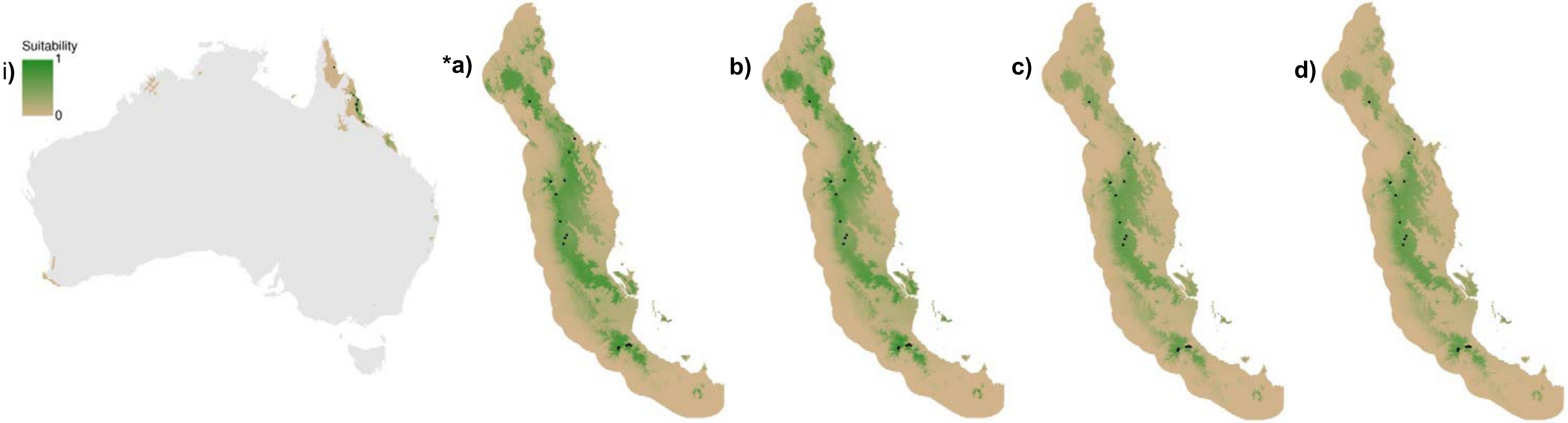
Global data, bias-corrected (a) Ranking: 2 (3.5 stars)			Global data, bias-uncorrected (b) Ranking: 4 (3 stars)			Focal data, bias-corrected (c) Ranking: 3 (3.5 stars)			Focal data, bias-uncorrected (d) Ranking: 1 (3.5 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.79	752	36992	0.59	752	20475	0.81	40	728	0.93	40	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc15	46.0		bc12	70.3		bc12	71.1		bc15	46.0	
bc01	31.3		bc15	9.8		bc13	17.0		bc01	31.3	
bc12	5.2		bc04	6.7		bc14	5.3		bc12	5.2	
Total	82.5		Total	86.8		Total	93.4		Total	82.5	

Figure 3.1.8 Distribution of *Chalinolobus nigrogriseus* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Murina florium



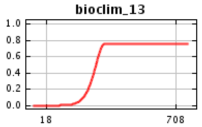
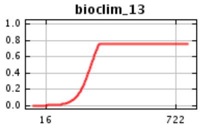
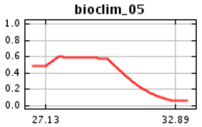
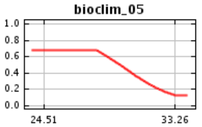
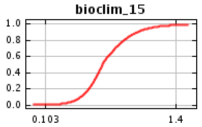
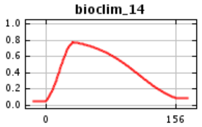
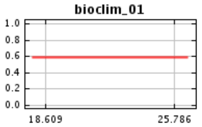
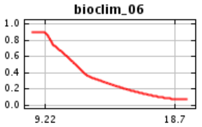
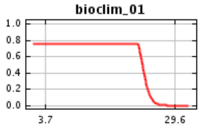
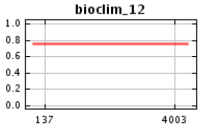
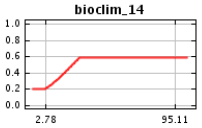
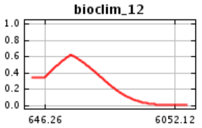
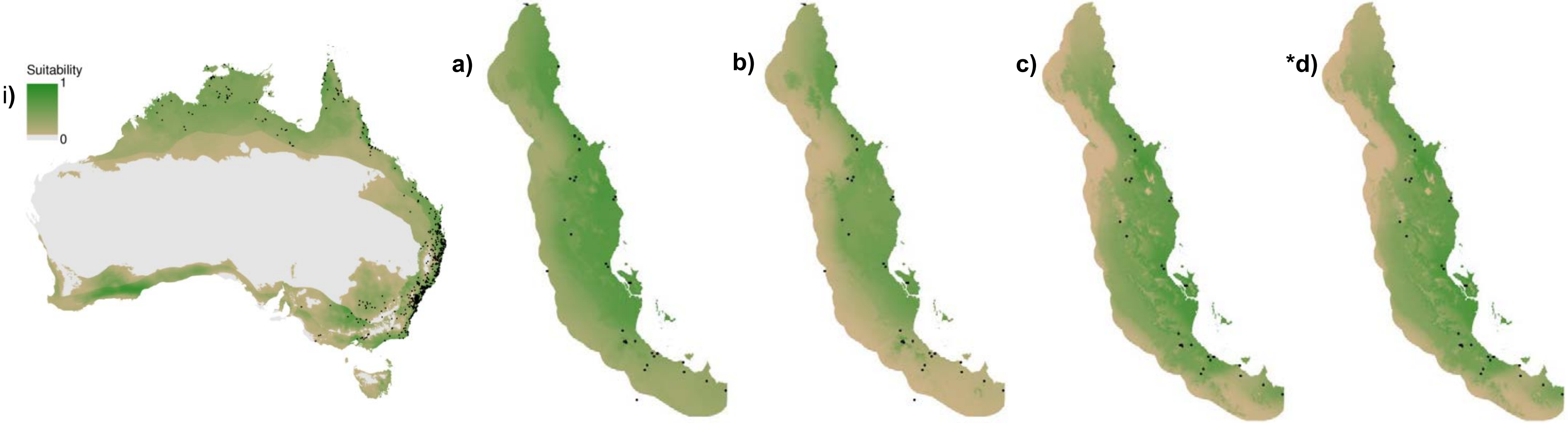
Global data, bias-corrected (a) Ranking: 1 (3.75 stars)			Global data, bias-uncorrected (b) Ranking: 2 (3.75 stars)			Focal data, bias-corrected (c) Ranking: 4 (3.5 stars)			Focal data, bias-uncorrected (d) Ranking: 3 (3.5 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.93	22	36992	0.93	22	20475	0.94	21	728	0.95	21	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc13	56.0		bc13	46.5		bc05	49.8		bc05	54.1	
bc15	17.2		bc14	25.4		bc01	23.8		bc06	18.6	
bc01	14.6		bc12	13.6		bc14	14.4		bc12	10.3	
Total	87.8		Total	85.5		Total	88.0		Total	83.0		

Figure 3.1.9 Distribution of *Murina florium* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Myotis macropus



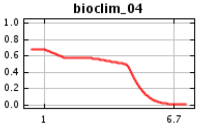
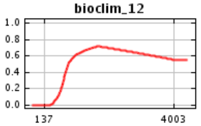
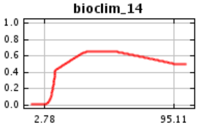
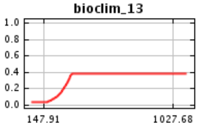
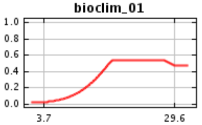
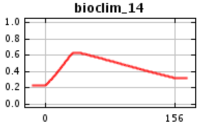
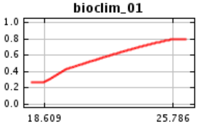
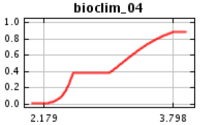
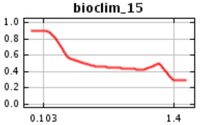
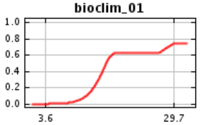
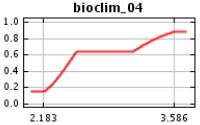
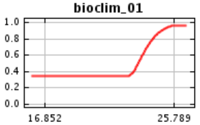
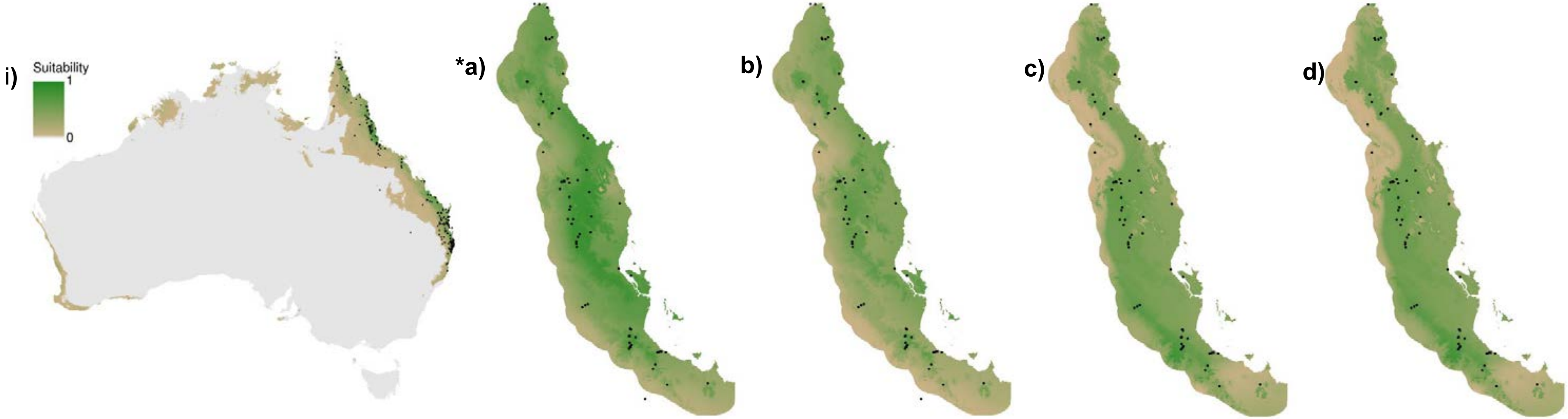
Global data, bias-corrected (a) Ranking: 4 (3 stars)			Global data, bias-uncorrected (b) Ranking: 2 (3.5 stars)			Focal data, bias-corrected (c) Ranking: 3 (3.5 stars)			Focal data, bias-uncorrected (d) Ranking: 1 (3.75 stars)		
Model AUC	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**
0.67	1313	36992	0.68	1313	20475	0.78	35	728	0.86	35	20018
Variable	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**
bc04	47.2		bc12	42.0		bc14	42.0		bc13	35.5	
bc01	18.7		bc14	41.2		bc01	16.8		bc04	19.1	
bc15	9.5		bc01	5.7		bc04	16.6		bc01	14.1	
Total	**75.4**		**Total**	**88.9**		**Total**	**75.4**		**Total**	**68.7**	

Figure 3.1.10 Distribution of *Myotis macropus* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Nyctophilus bifax



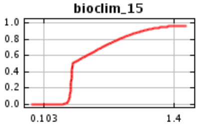
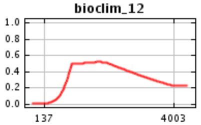
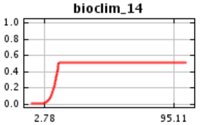
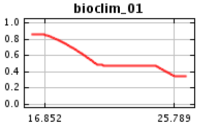
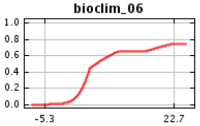
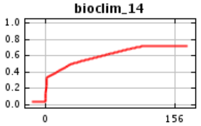
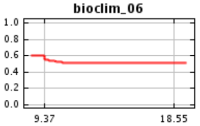
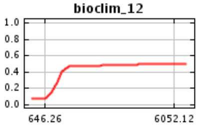
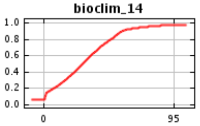
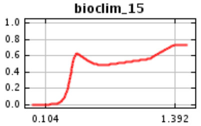
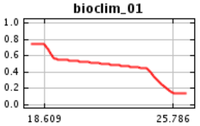
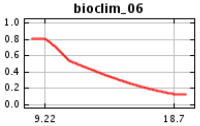
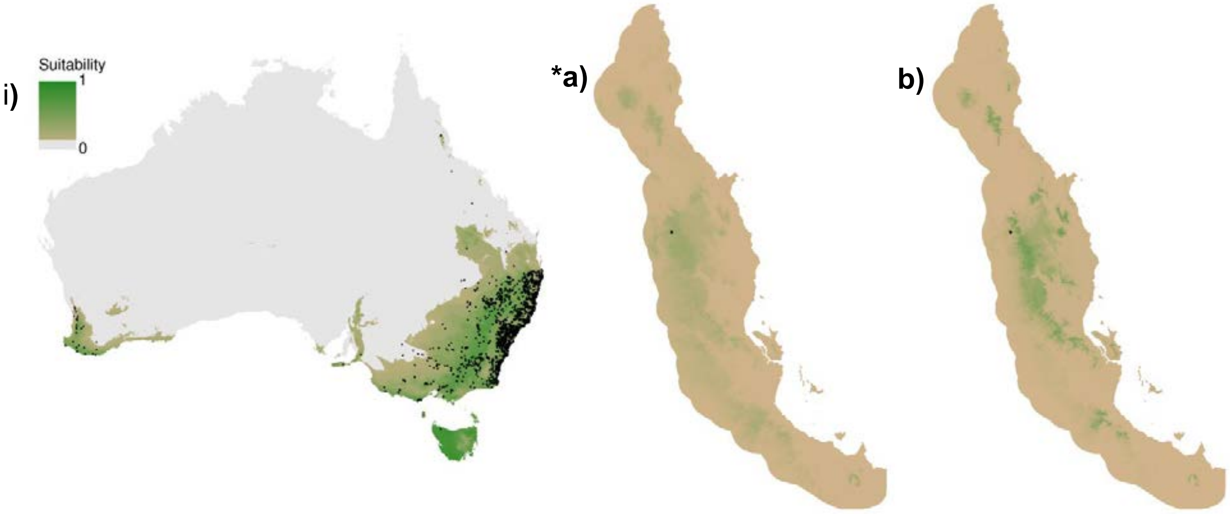
Global data, bias-corrected (a) Ranking: 1 (3.75 stars)			Global data, bias-uncorrected (b) Ranking: 2 (3.5 stars)			Focal data, bias-corrected (c) Ranking:3 (3.5 stars)			Focal data, bias-uncorrected (d) Ranking: 4 (3.25 stars)		
Model AUC	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**
0.71	482	36992	0.73	482	20475	0.77	76	728	0.81	76	20018
Variable	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**
bc15	**41.5**		**bc12**	**56.4**		**bc14**	**55.4**		**bc01**	**28.9**	
bc06	**19.4**		**bc14**	**23.3**		**bc06**	**19.1**		**bc12**	**24.4**	
bc14	**10.4**		**bc15**	**7.7**		**bc01**	**10.4**		**bc06**	**18.2**	
Total	**71.3**		**Total**	**87.4**		**Total**	**84.9**		**Total**	**71.5**	

Figure 3.1.11 Distribution of *Nyctophilus bifax* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Nyctophilus gouldi



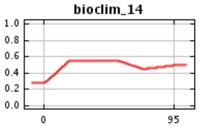
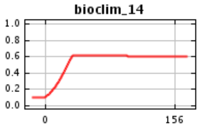
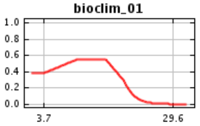
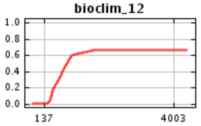
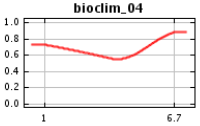
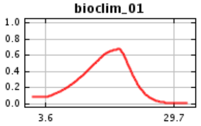
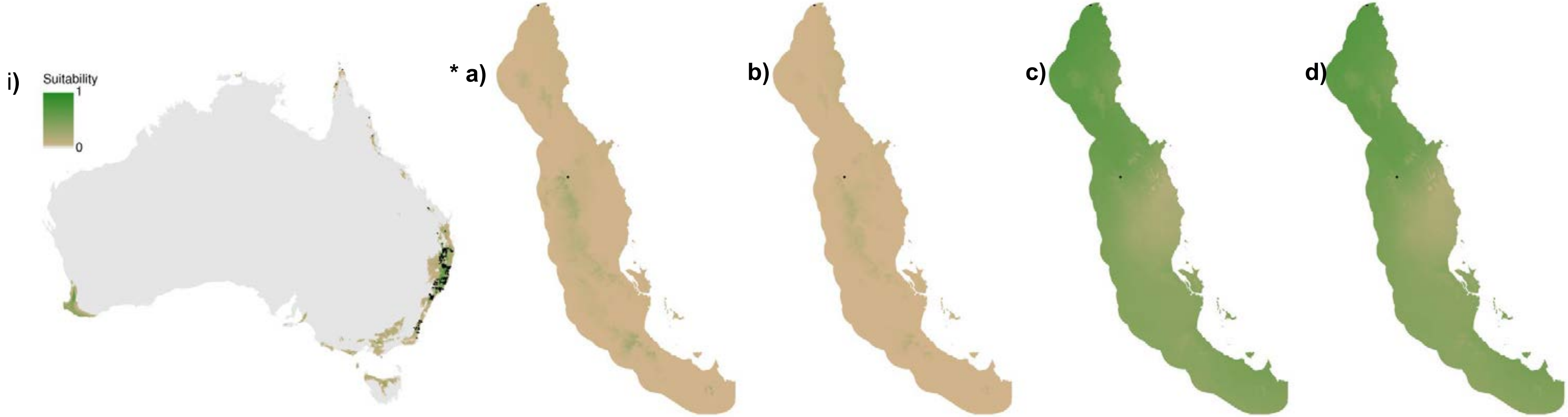
Global data, bias-corrected (a) Ranking: 1 (4.5 stars)			Global data, bias-uncorrected (b) Ranking: 2 (4 stars)			Focal data, bias-corrected (c) Ranking: x (no model)			Focal data, bias-uncorrected (d) Ranking: x (no model)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.96	3606	36992	0.83	3606	20475	0.500	1	728	0.500	1	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc14	**50.2**		**bc14**	**89.2**		-	-	-	-	-	-
bc01	**34.9**		**bc12**	**6.2**		-	-	-	-	-	-
bc04	**4.4**		**bc01**	**2.0**		-	-	-	-	-	-
Total	**89.5**		**Total**	**97.4**		-	-	-	-	-	-

Figure 3.1.12 Distribution of *Nyctophilus gouldi* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Phoniscus papuensis



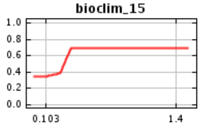
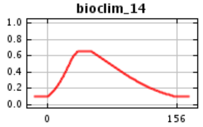
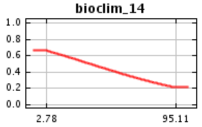
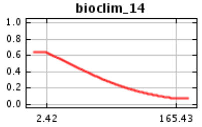
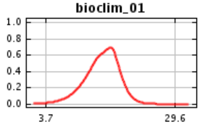
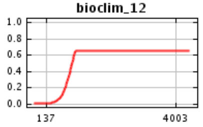
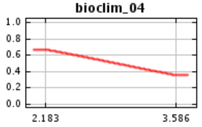
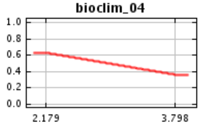
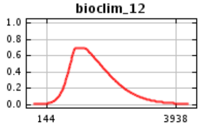
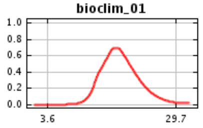
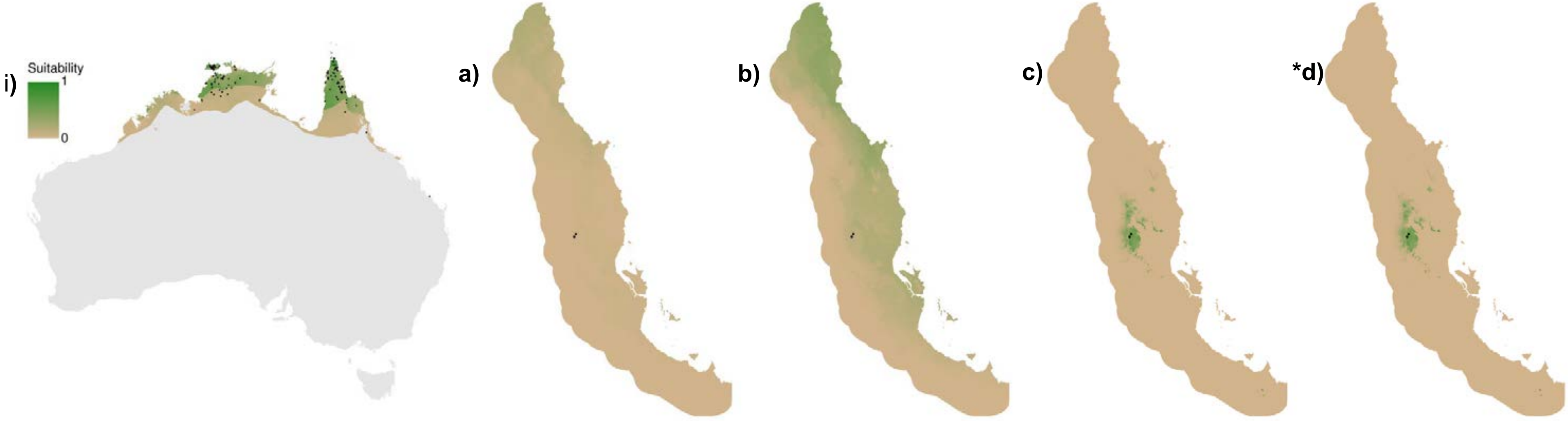
Global data, bias-corrected (a) Ranking: 1 (3.25 stars)			Global data, bias-uncorrected (b) Ranking: 2 (3 stars)			Focal data, bias-corrected (c) Ranking: 3 (2 stars)			Focal data, bias-uncorrected (d) Ranking: 4 (2 stars)		
Model AUC	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**	**Model AUC**	**Occurrence points**	**Background points**
0.79	**447**	**36992**	**0.73**	**447**	**20475**	**0.83**	**2**	**728**	**0.83**	**2**	**20018**
Variable	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**	**Variable**	**% contribution**	**Response curve**
bc15	**22.5**		**bc14**	**43.2**		**bc14**	**55.2**		**bc14**	**73.3**	
bc01	**17.5**		**bc12**	**37.9**		**bc04**	**44.8**		**bc04**	**26.7**	
bc12	**16.7**		**bc01**	**5.7**		-	-	-	-	-	-
Total	**56.7**		**Total**	**86.8**		**Total**	**100**		**Total**	**100**	

Figure 3.1.13 Distribution of *Phoniscus papuensis* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Pipistrellus adamsi



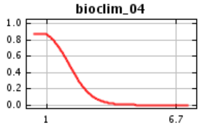
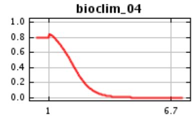
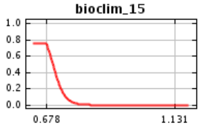
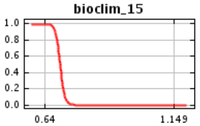
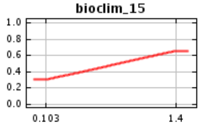
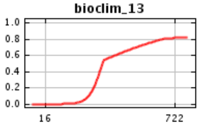
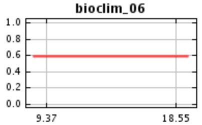
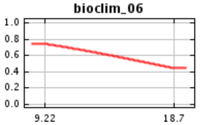
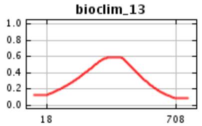
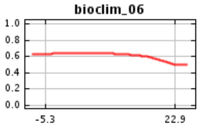
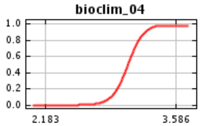
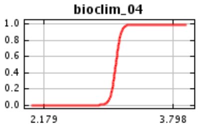
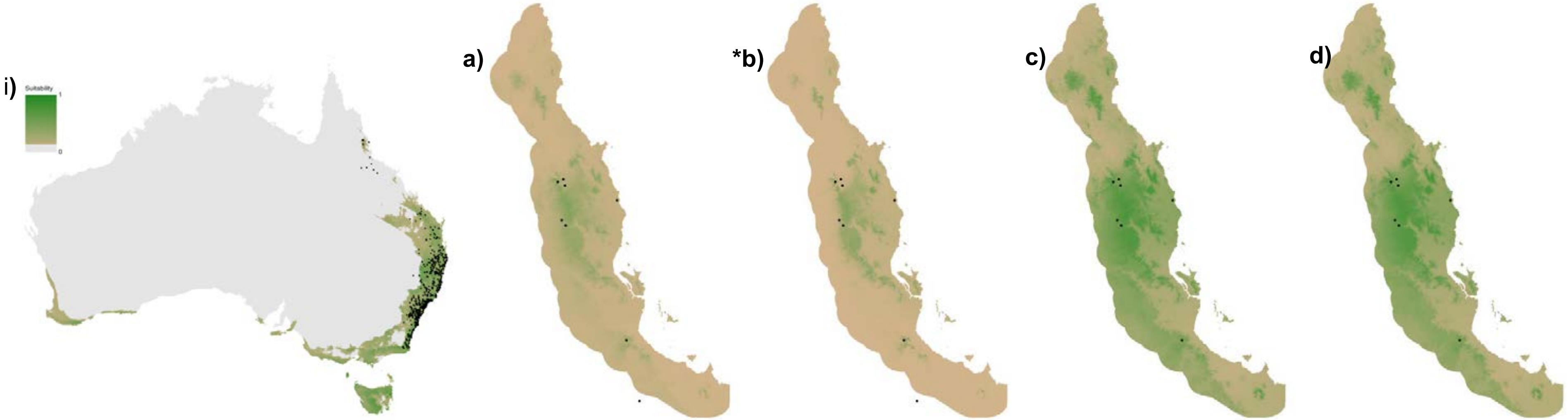
Global data, bias-corrected (a) Ranking: 4 (2.25 stars)			Global data, bias-uncorrected (b) Ranking: 3 (2 stars)			Focal data, bias-corrected (c) Ranking: 2 (3 stars)			Focal data, bias-uncorrected (d) Ranking: 1 (3.25 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.58	235	36992	0.59	235	20475	0.999	2	728	0.999	2	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc04	**40.2**		**bc04**	**51.1**		**bc15**	**72.8**		**bc15**	**65.2**	
bc15	**25.0**		**bc13**	**39.4**		**bc06**	**16.8**		**bc06**	**19.1**	
bc13	**14.4**		**bc06**	**2.1**		**bc04**	**4.5**		**bc04**	**14.7**	
Total	**79.6**		**Total**	**92.6**		**Total**	**94.1**		**Totoal**	**99**	

Figure 3.1.14 Distribution of *Pipistrellus adamsi* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Scoteanax rueppellii



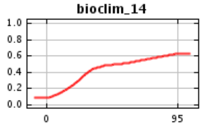
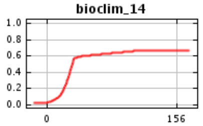
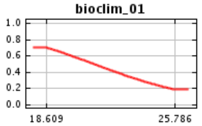
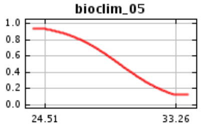
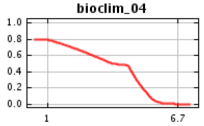
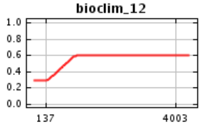
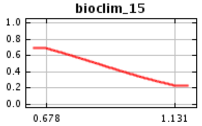
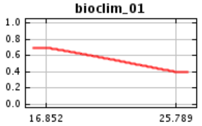
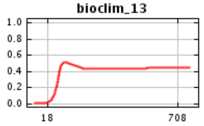
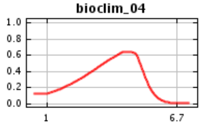
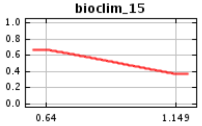
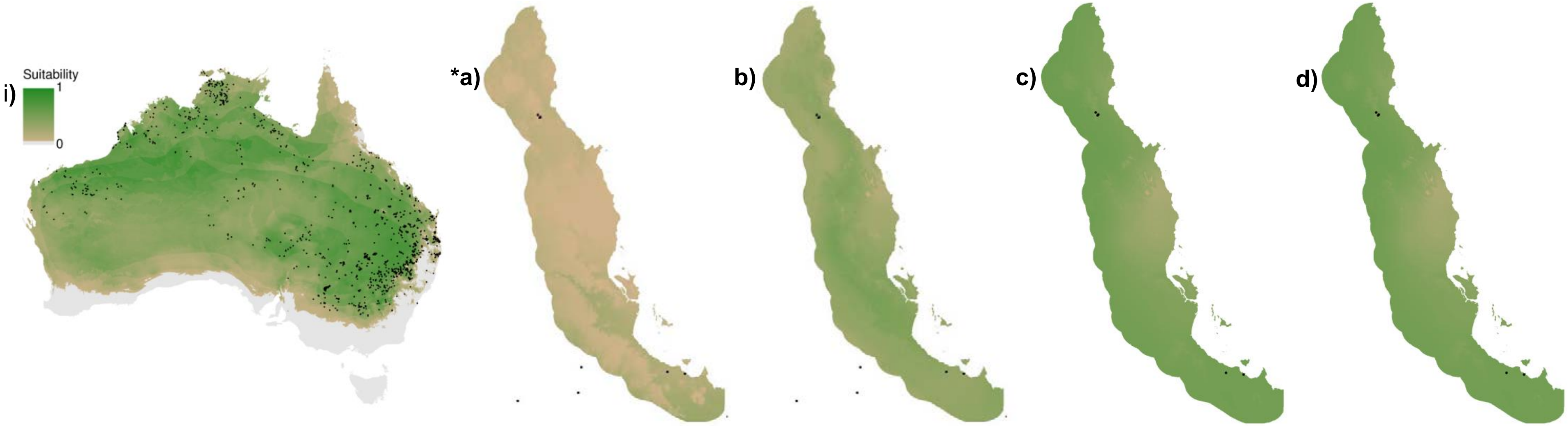
Global data, bias-corrected (a) Ranking: 2 (3.75 stars)			Global data, bias-uncorrected (b) Ranking: 1 (3.75 stars)			Focal data, bias-corrected (c) Ranking: 4 (2.25 stars)			Focal data, bias-uncorrected (d) Ranking: 3 (2.5 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.89	1100	36992	0.86	1100	20475	0.90	8	728	0.89	8	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc14	49.5		bc14	63.2		bc01	68.3		bc05	71.2	
bc04	26.9		bc12	21.6		Bc15	31.7		bc01	18.6	
bc13	12.2		bc04	6.7		-	-	-	bc15	10.2	
Total	88.6		Total	91.5		Total	100		Total	100	

Figure 3.1. 15 Distribution of *Scoteanax rueppellii* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Scotorepens greyii



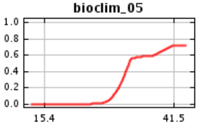
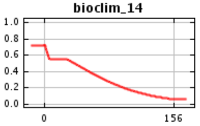
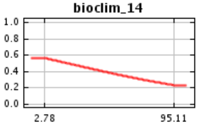
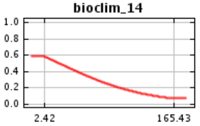
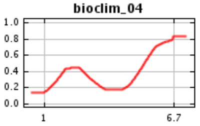
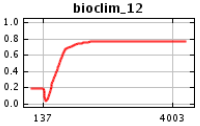
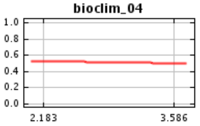
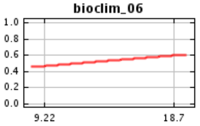
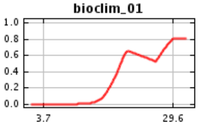
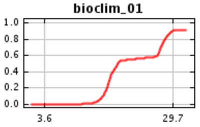
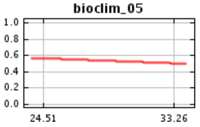
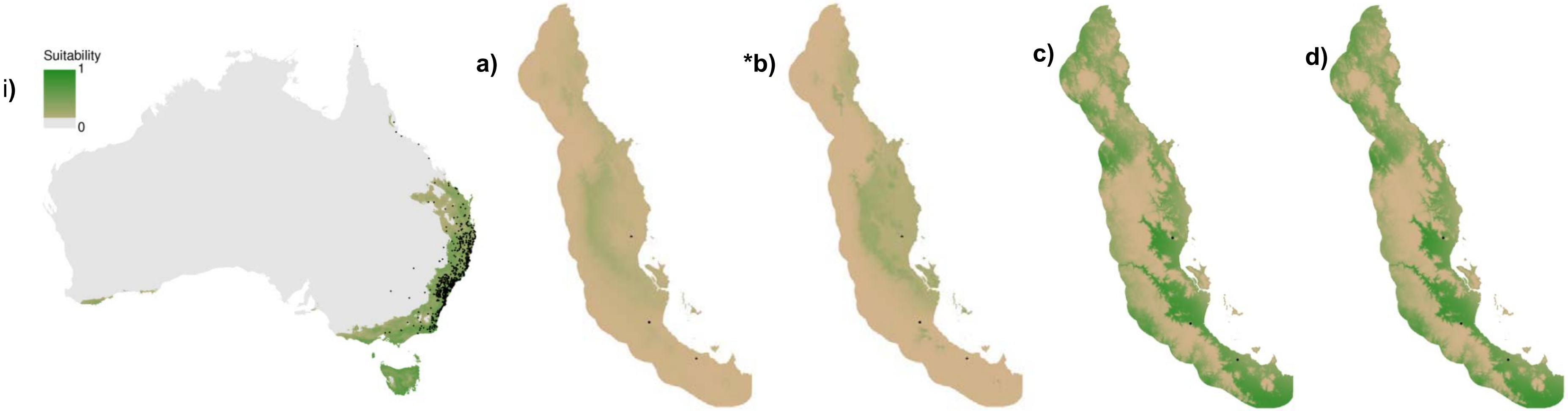
Global data, bias-corrected (a) Ranking: 1 (3 stars)			Global data, bias-uncorrected (b) Ranking 2 (2.75 stars)			Focal data, bias-corrected (c) Ranking: 4 (1.5 star)			Focal data, bias-uncorrected (d) Ranking: 3 (1.75 star)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.53	1533	36992	0.61	1533	20475	0.59	5	728	0.68	5	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc05	75.4		bc14	34.0		bc14	99.4		bc14	90.0	
bc04	10.6		bc12	28.8		bc04	0.6		bc06	9.5	
bc01	5.1		bc01	18.9		-	-	-	bc05	0.5	
Total	91.1		Total	81.7		Total	100		Total	100	

Figure 3.1.16 Distribution of *Scotorepens greyii* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Scotorepens orion



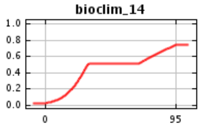
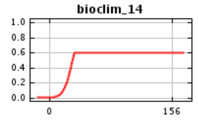
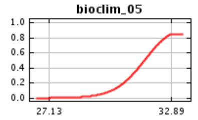
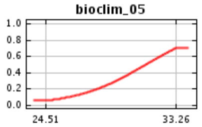
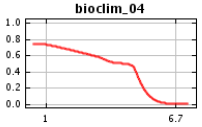
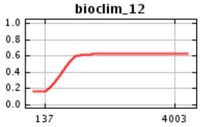
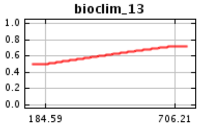
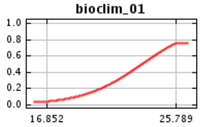
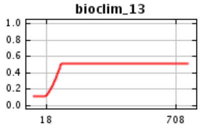
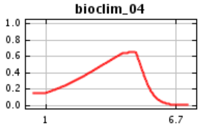
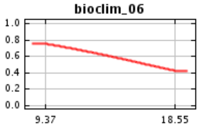
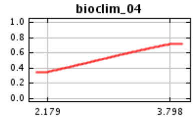
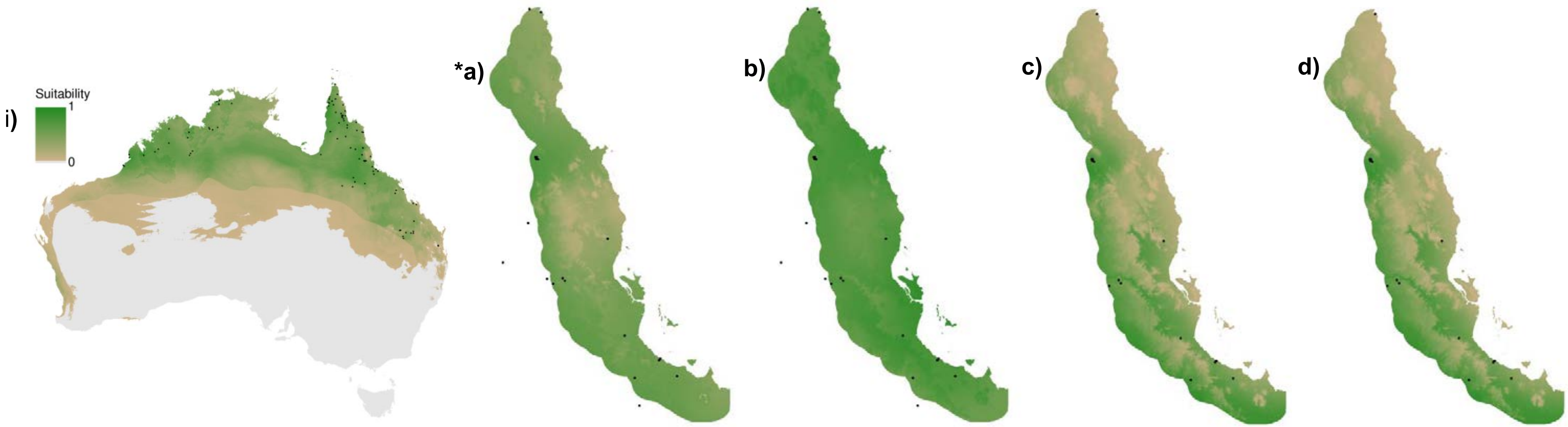
Global data, bias-corrected Ranking: 2 (3.25 stars)			Global data, bias-uncorrected Ranking: 1 (3.25 stars)			Focal data, bias-corrected Ranking: 4 (2.5 stars)			Focal data, bias-uncorrected Ranking: 3 (2.75 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.62	1470	36992	0.54	1470	20475	0.85	3	728	0.85	3	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc14	60.2		bc14	71.0		bc05	97.2		bc05	47.5	
bc04	28.1		bc12	16.5		bc13	2.4		bc01	43.7	
bc13	5.0		bc04	6.8		bc06	0.4		bc04	8.8	
Total	93.3		Total	94.3		Total	100		Total	100	

Figure 3.1.17 Distribution of *Scotorepens orion* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Scotorepens sanborni



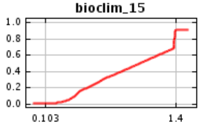
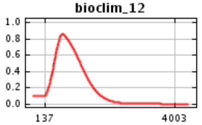
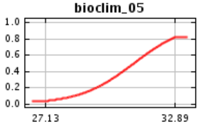
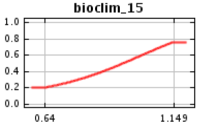
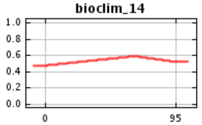
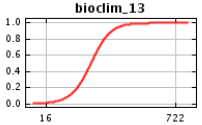
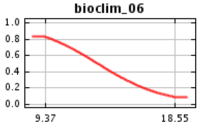
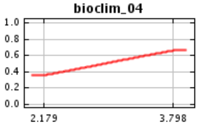
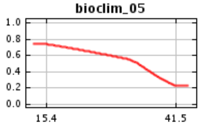
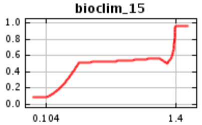
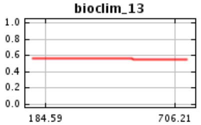
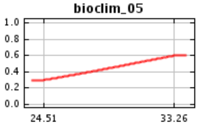
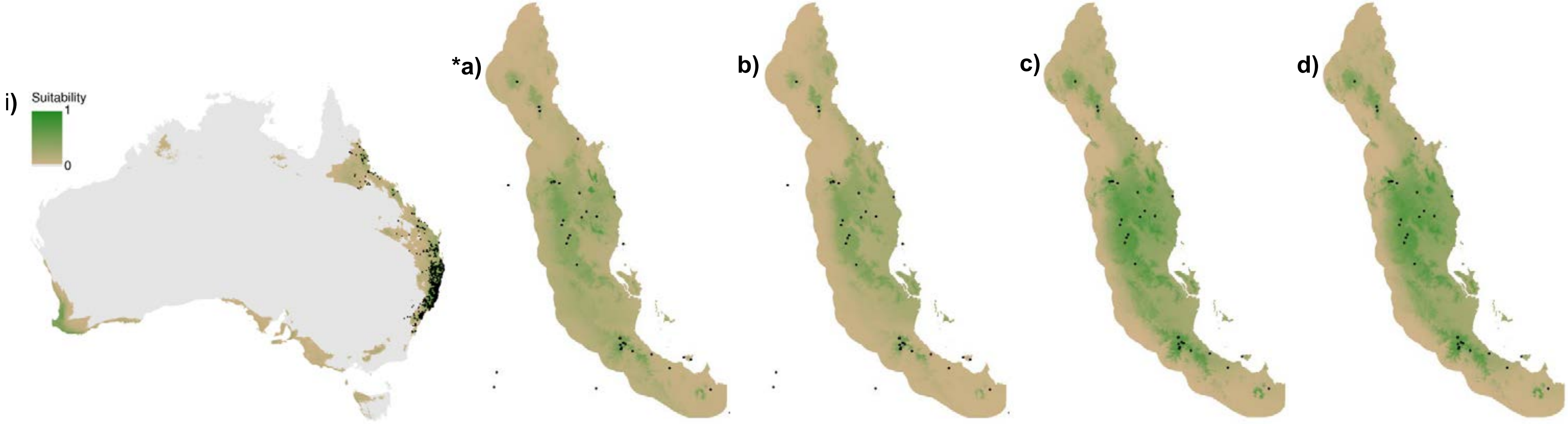
Global data, bias-corrected (a) Ranking: 1 (2.75 stars)			Global data, bias-uncorrected (b) Ranking: 2 (2.25 stars)			Focal data, bias-corrected (c) Ranking: 3 (2.75 stars)			Focal data, bias-uncorrected (d) Ranking: 4 (2.5 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.71	101	36992	0.50	101	20475	0.70	14	728	0.73	14	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc15	58.2		bc12	39.5		bc05	48.2		bc15	75.8	
bc14	21.7		bc13	31.0		bc06	27.3		bc04	16.8	
bc05	5.9		bc15	10.3		bc13	24.5		bc05	7.4	
Total	85.8		Total	80.8		Total	100		Total	100	

Figure 3.1.18 Distribution of *Scotorepens sanborni* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Vespadelus pumulis



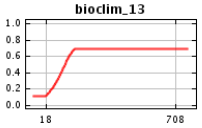
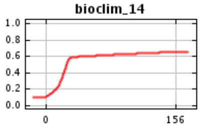
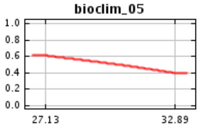
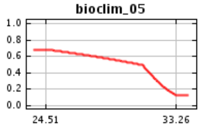
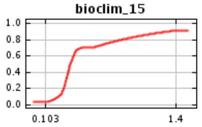
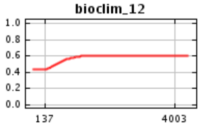
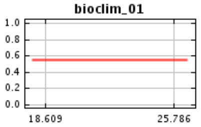
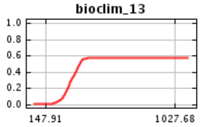
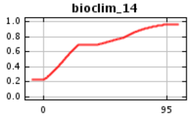
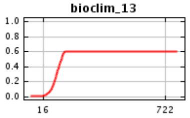
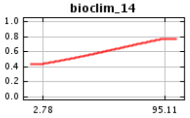
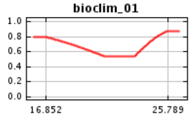
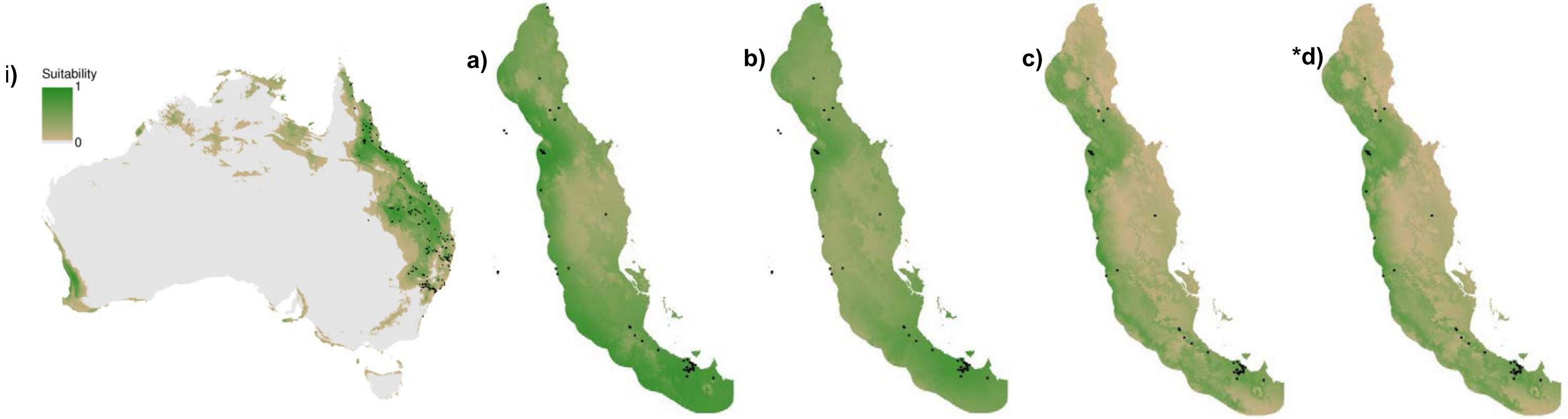
Global data, bias-corrected (a) Ranking: 1 (3.75 stars)			Global data, bias-uncorrected (b) Ranking: 2 (3.75 stars)			Focal data, bias-corrected (c) Ranking: 4 (3.25 stars)			Focal data, bias-uncorrected (d) Ranking: 3 (3.25 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.82	1952	36992	0.83	1952	20475	0.86	35	728	0.87	35	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc13	43.6		bc14	48.4		bc05	40.3		bc05	40.8	
bc15	25.4		bc12	35.3		bc01	16.6		bc13	18.9	
bc14	20.0		bc13	7.8		bc14	13.5		bc01	11.8	
Total	89.0		Total	91.5		Total	70.4		Total	71.5	

Figure 3.1.19 Distribution of *Vespadelus pumulis* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Vespadelus troughtoni



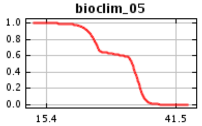
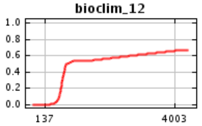
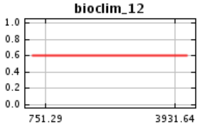
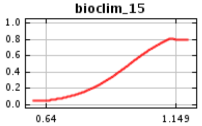
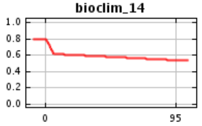
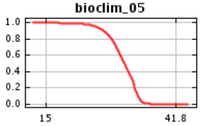
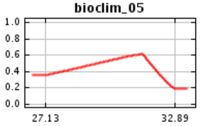
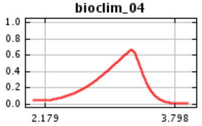
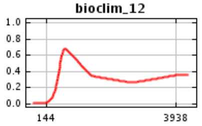
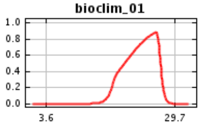
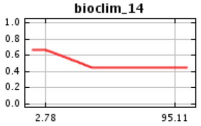
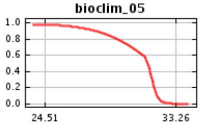
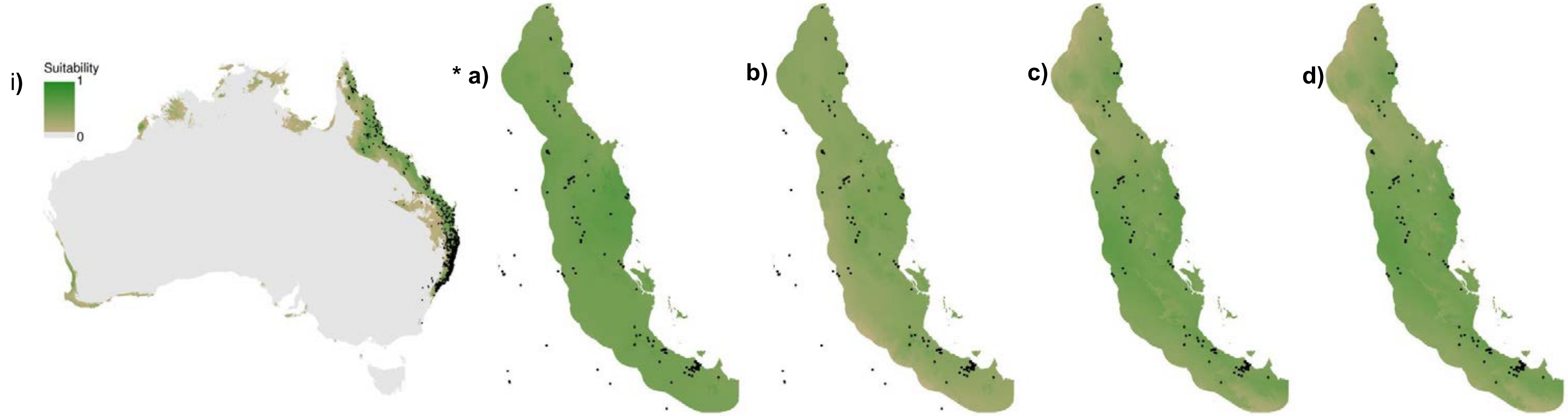
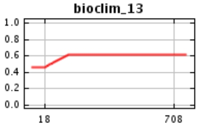
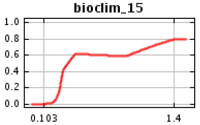
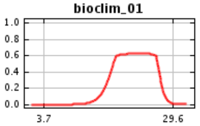
Global data, bias-corrected (a) Ranking: 3 (2.75 stars)			Global data, bias-uncorrected (b) Ranking: 2 (2.75 stars)			Focal data, bias-corrected (c) Ranking: 4 (2.75 stars)			Focal data, bias-uncorrected (d) Ranking: 1 (3 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.79	353	36992	0.83	353	20475	0.84	43	728	0.89	43	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc05	39.1		bc12	49.9		bc12	39.6		bc15	34.8	
bc14	14.8		bc05	22.8		bc05	17.3		bc04	30.8	
bc12	13.6		bc01	12.5		bc14	15.2		bc05	17.5	
Total	67.5		Total	85.2		Total	72.1		Total	83.1	

Figure 3.1.20 Distribution of *Vespadelus troughtoni* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

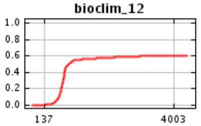
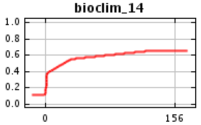
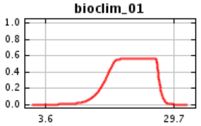
Miniopterus australis



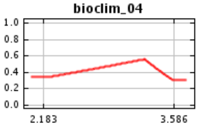
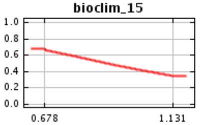
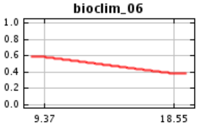
Global data, bias-corrected (a)
Ranking: 1 (4 stars)

Model AUC	Occurrence points	Background points
0.55	2302	36992
Variable	**% contribution**	**Response curve**
bc13	31.4	
bc15	28.8	
bc01	15.4	
Total	**75.6**	

Global data, bias-uncorrected (b)
Ranking: 2 (3.75 stars)

Model AUC	Occurrence points	Background points
0.62	2302	20475
Variable	**% contribution**	**Response curve**
bc12	56.8	
bc14	23.7	
bc01	5.6	
Total	**86.1**	

Focal data, bias-corrected (c)
Ranking: 4 (3.25 stars)

Model AUC	Occurrence points	Background points
0.65	114	728
Variable	**% contribution**	**Response curve**
bc04	31.6	
bc15	28.2	
bc06	13.0	
Total	**72.8**	

Focal data, bias-uncorrected (d)
Ranking: 3 (3.5 stars)

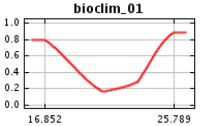
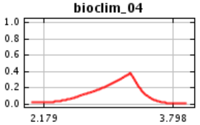
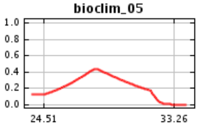
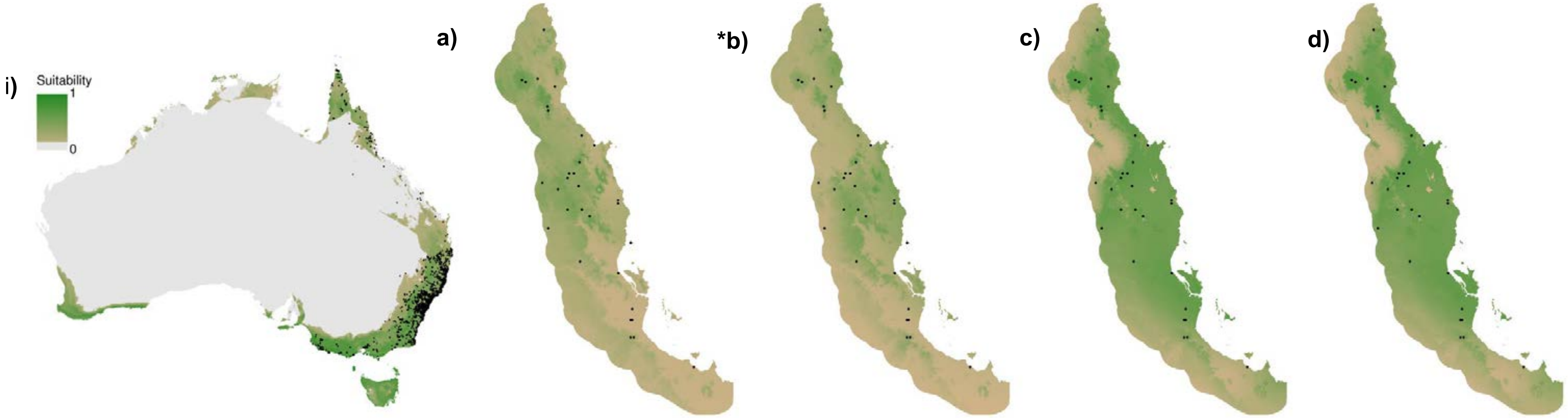
Model AUC	Occurrence points	Background points
0.84	114	20018
Variable	**% contribution**	**Response curve**
bc01	28.6	
bc04	22.0	
bc05	16.7	
Total	**67.3**	

Figure 3.1.21 Distribution of *Miniopterus australis* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Miniopterus orianae oceanensis



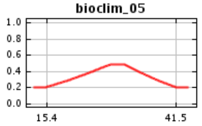
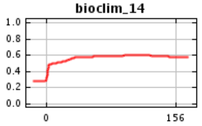
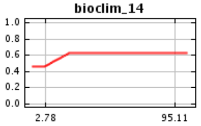
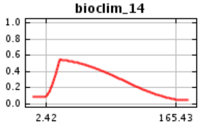
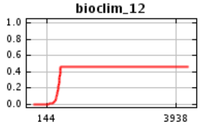
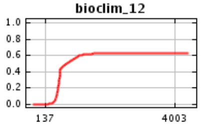
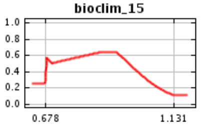
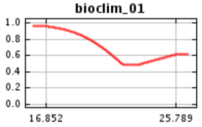
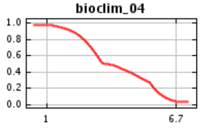
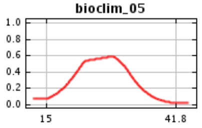
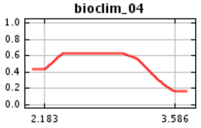
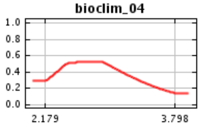
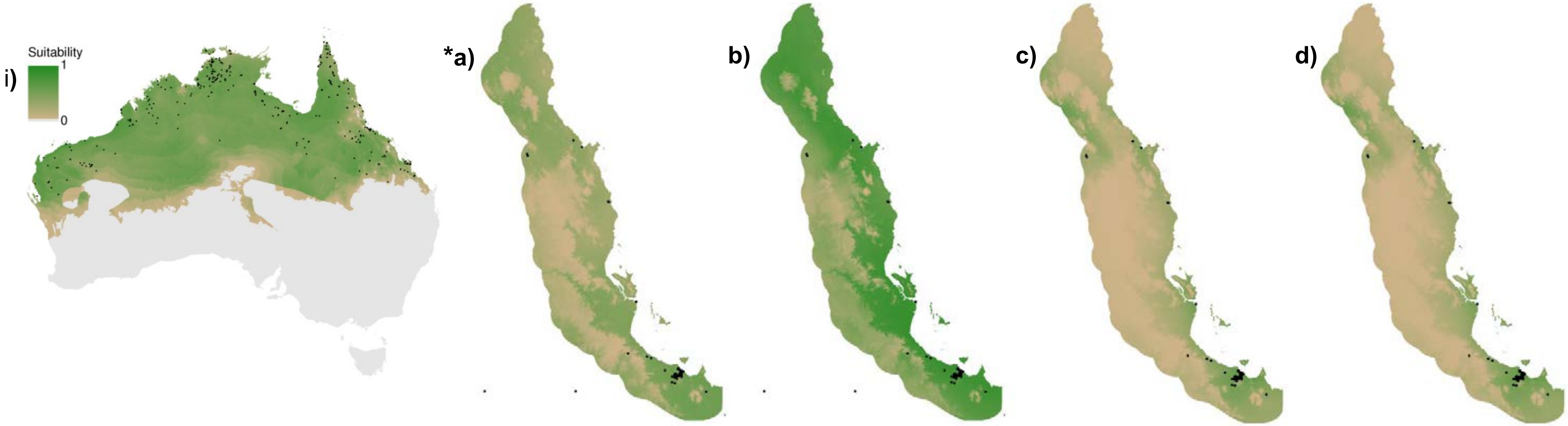
Global data, bias-corrected (a) Ranking: 4 (3.25 stars)			Global data, bias-uncorrected (b) Ranking: 1 (3.5 stars)			Focal data, bias-corrected (c) Ranking: 3 (3.75 stars)			Focal data, bias-uncorrected (d) Ranking 2 (3.75 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.64	2856	36992	0.69	2856	20475	0.78	114	728	0.81	114	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc05	37.9		bc14	52.7		bc14	55.0		bc14	53.2	
bc12	29.7		bc12	31.4		bc15	20.0		bc01	28.9	
bc04	7.9		bc05	11.0		bc04	13.4		bc04	11.8	
Total	75.5		Total	95.1		Total	88.4		Total	93.9	

Figure 3.1.22 Distribution of *Miniopterus orianae oceanensis* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Chaerephon jobensis



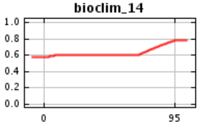
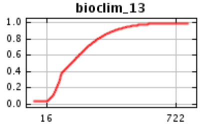
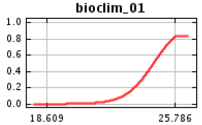
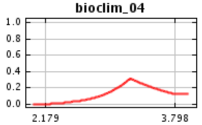
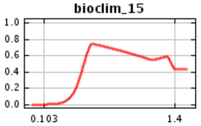
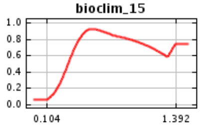
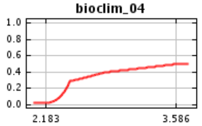
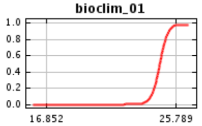
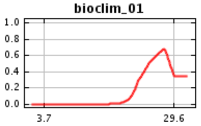
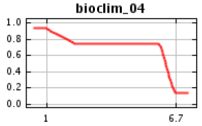
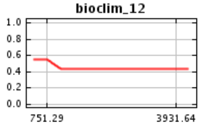
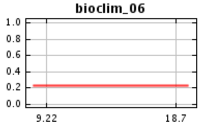
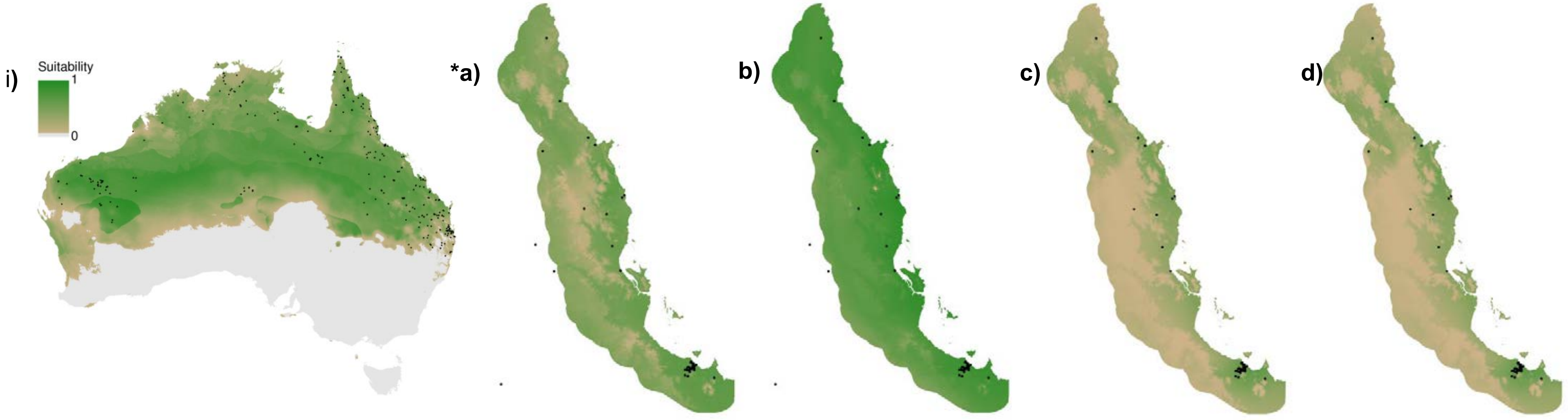
Global data, bias-corrected (a) Ranking: 1 (4.5 stars)			Global data, bias-uncorrected (b) Ranking: 3 (4 stars)			Focal data, bias-corrected (c) Ranking: 4 (3.75 stars)			Focal data, bias-uncorrected (d) Ranking: 2 (3.5 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.89	475	36992	0.86	475	20475	0.96	45	728	0.97	45	20018
Variable	% contr.	Response curve	Variable	% contr.	Response curve	Variable	% contr.	Response curve	Variable	% contr.	Response curve
bc14	50.9		bc13	62.4		bc01	62.3		bc04	23.1	
bc15	34.7		bc15	14.3		bc04	14.5		bc01	21.9	
bc01	9.1		bc04	5.6		bc12	14.3		bc06	19.3	
Total	**94.7**		**Total**	**82.3**		**Total**	**91.1**		**Total**	**64.3**	

Figure 3.1.23 Distribution of *Chaerephon jobensis* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Mormopterus lumsdenae



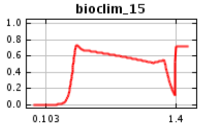
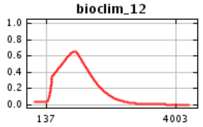
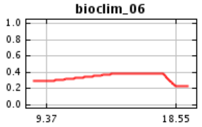
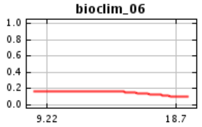
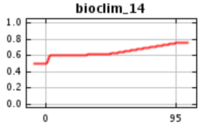
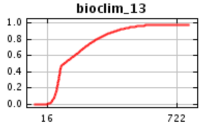
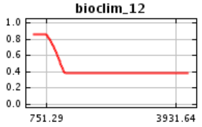
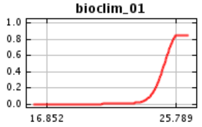
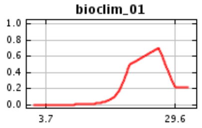
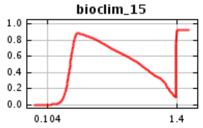
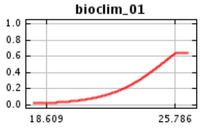
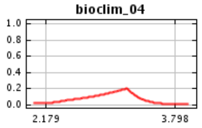
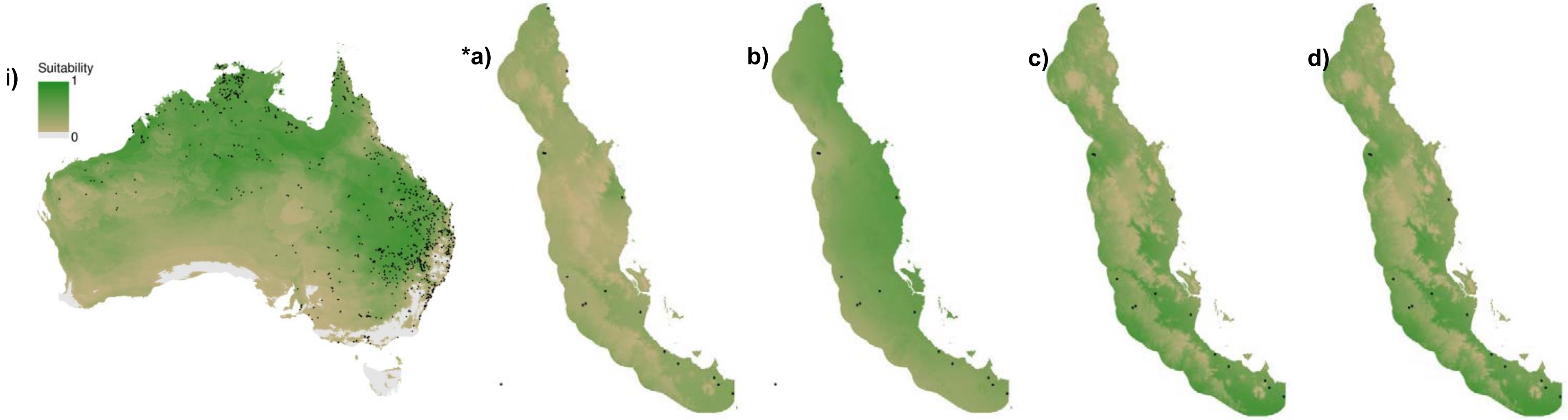
Global data, bias-corrected (a) Ranking: 1 (4 stars)			Global data, bias-uncorrected (b) Ranking: 2 (3.5 stars)			Focal data, bias-corrected (c) Ranking: 4 (3.25 stars)			Focal data, bias-uncorrected (d) Ranking: 3 (3.25 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.88	394	36992	0.85	394	20475	0.93	41	728	0.95	41	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc15	40.5		bc12	31.2		bc06	52.1		bc06	26.4	
bc14	24.1		bc13	26.4		bc12	21.7		bc01	19.8	
bc01	21.7		bc15	16.7		bc01	17.7		bc04	17.6	
Total	**86.3**		**Total**	**74.3**		**Total**	**91.5**		**Total**	**63.8**	

Figure 3.1.24 Distribution of *Mormopterus lumsdenae* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Saccolaimus flaviventris



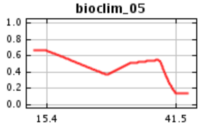
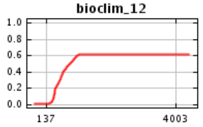
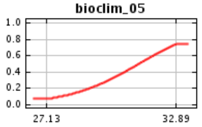
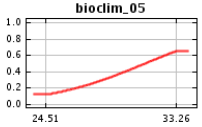
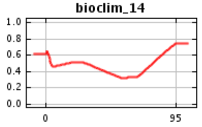
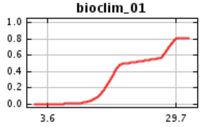
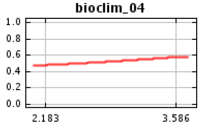
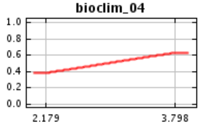
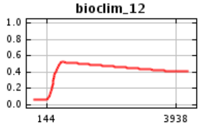
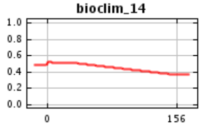
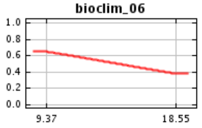
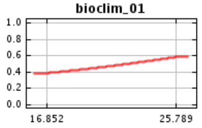
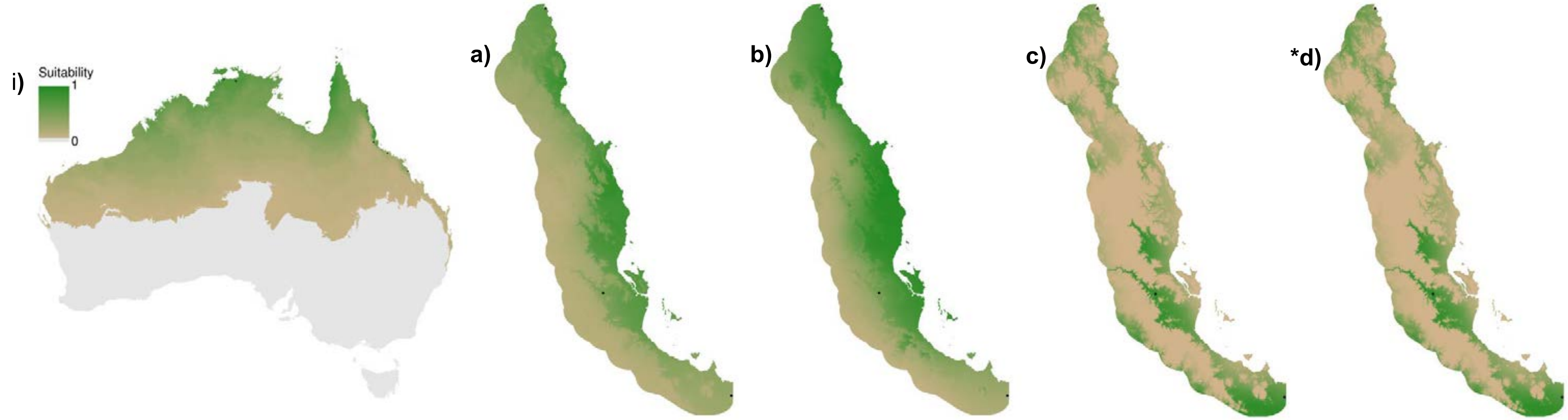
Global data, bias-corrected (a) Ranking: 1 (3.5 stars)			Global data, bias-uncorrected (b) Ranking: 4 (2.5 stars)			Focal data, bias-corrected (c) Ranking: 2 (3 stars)			Focal data, bias-uncorrected (d) Ranking: 3 (3 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.73	1361	36992	0.58	1361	20475	0.68	14	728	0.70	14	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc05	54.9		bc12	62.7		bc05	84.6		bc05	80.0	
bc14	20.4		bc01	13.3		bc04	12.2		bc04	17.0	
bc12	8.9		bc14	20.6		bc06	3.1		bc01	2.3	
Total	84.2		Total	96.6		Total	99.9		Total	99.3	

Figure 3.1.25 Distribution of *Saccolaimus flaviventris* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Saccolaimus saccolaimus



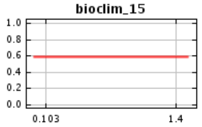
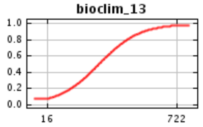
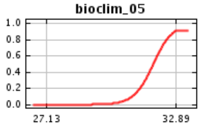
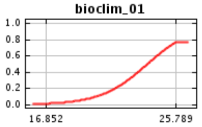
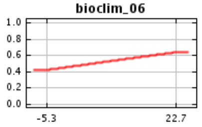
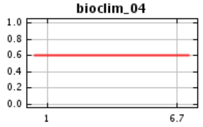
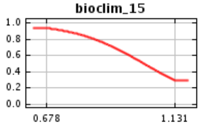
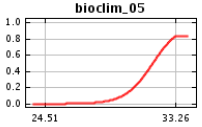
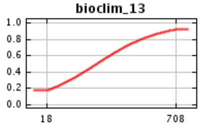
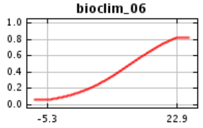
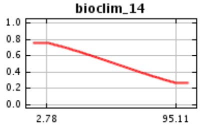
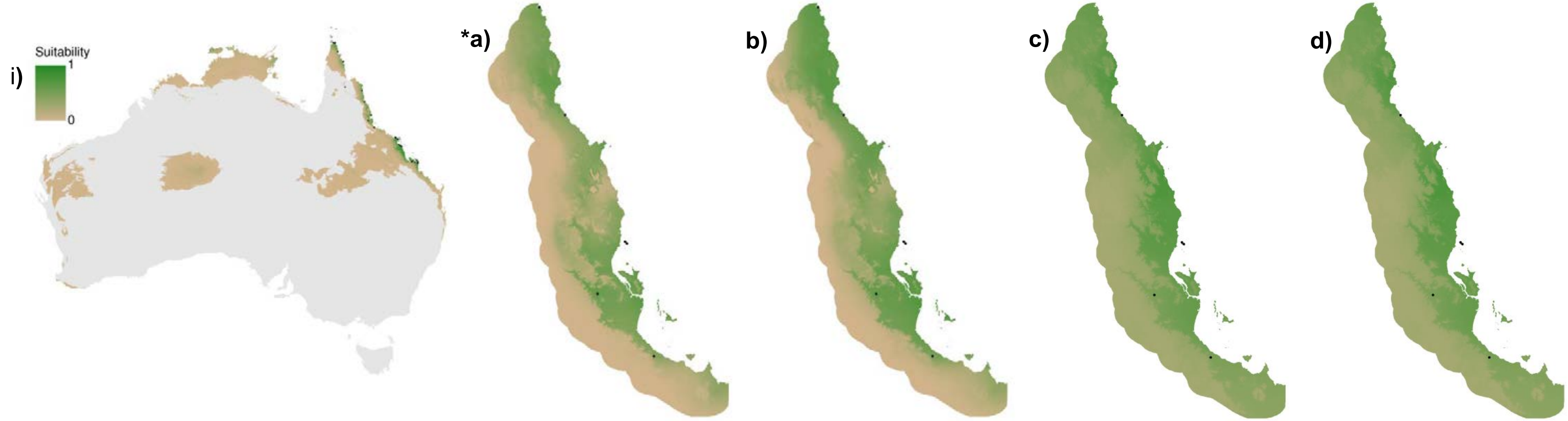
Global data, bias-corrected (a) Ranking: 3 (2.5 stars)			Global data, bias-uncorrected (b) Ranking: 4 (1.75 stars)			Focal data, bias-corrected (c) Ranking: 2 (2.75 stars)			Focal data, bias-uncorrected (d) Ranking: 1 (3 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.68	7	36992	0.55	7	20475	0.90	3	728	0.94	3	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc15	51.0		bc13	78.6		bc05	93.1		bc01	65.9	
bc06	26.8		bc04	19.1		bc15	6.3		bc05	34.1	
bc13	17.7		bc06	2.0		bc14	0.6		-	-	-
Total	95.5		Total	99.7		Total	100		Total	100	

Figure 3.1.26 Distribution of *Saccolaimus saccolaimus* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Taphozous australis



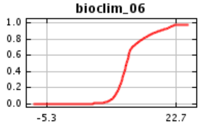
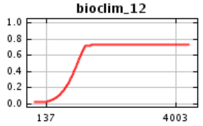
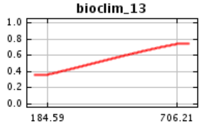
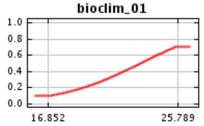
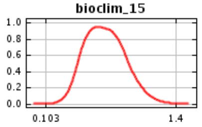
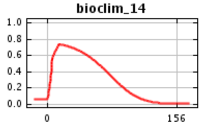
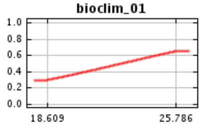
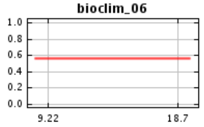
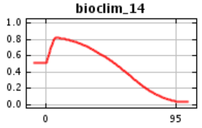
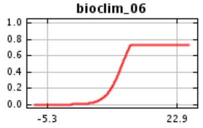
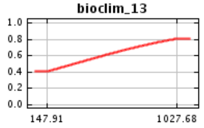
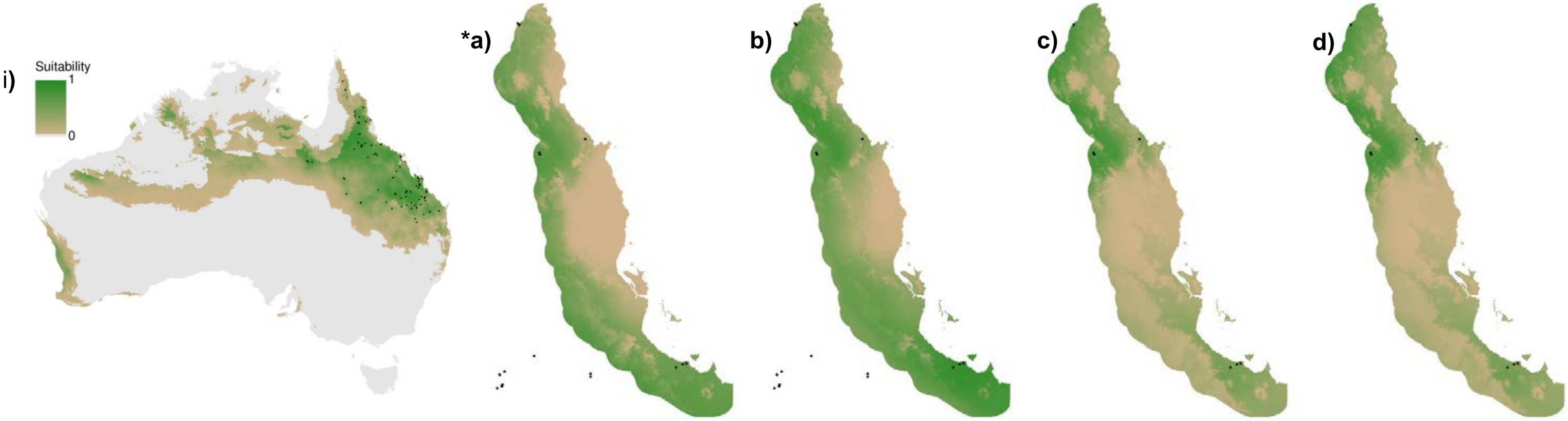
Global data, bias-corrected (a) Ranking: 1 (2.75 stars)			Global data, bias-uncorrected (b) Ranking: 2 (2.5 stars)			Focal data, bias-corrected (c) Ranking: 4 (2 stars)			Focal data, bias-uncorrected (d) Ranking: 3 (2.25 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.88	37	36992	0.84	37	20475	0.82	5	728	0.80	5	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc06	40.8		bc12	54.4		bc13	51.0		bc01	43.4	
bc15	34.8		bc14	20.1		bc01	49.0		bc06	39.7	
bc14	16.7		bc06	15.7		-	-	-	bc13	16.9	
Total	92.3		Total	90.2		Total	100		Total	100	

Figure 3.1.27 Distribution of *Taphozous australis* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Taphozous troughtoni



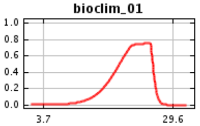
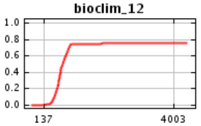
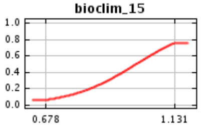
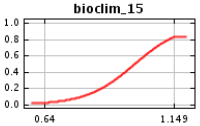
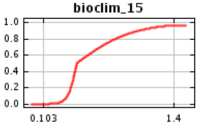
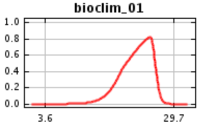
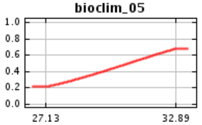
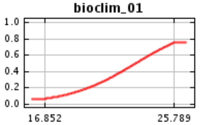
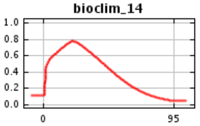
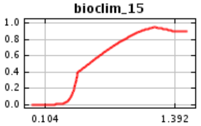
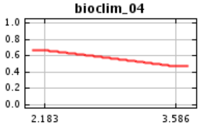
Global data, bias-corrected (a) Ranking: 1 (3 stars)			Global data, bias-uncorrected (b) Ranking: 2 (3 stars)			Focal data, bias-corrected (c) Ranking: 3 (2.75 stars)			Focal data, bias-uncorrected (d) Ranking: 4 (2.25 stars)		
Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points	Model AUC	Occurrence points	Background points
0.72	140	36992	0.79	140	20475	0.87	8	728	0.90	8	20018
Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve	Variable	% contribution	Response curve
bc01	38.1		bc12	42.8		bc15	78.9		bc15	80.8	
bc15	32.1		bc01	18.2		bc05	17.6		bc01	19.2	
bc14	14.2		bc15	14.5		bc04	3.4		-	-	-
Total	84.4		Total	75.5		Total	99.9		Total	100	

Figure 3.1.28 Distribution of *Taphazous troughtoni* (bias-corrected and bias-uncorrected models), and model analyses including accuracy rank, AUC values, and highest ranking climatic variable correlates.

Chapter 4: Winners and losers: the expansion and contraction of Wet Tropics bat species distributions with climate change

Abstract

Climate change will have numerous and profound effects on global biodiversity. For most species, the impact of climate change will be detrimental with few benefitting from environmental changes. Species able to survive and thrive are likely to be highly vagile, generalist species. One of the most common methods used to assess the potential impacts of climate change on species, as discussed in Chapter 3, is Species Distribution Modelling. The information from such models, in its simplest form, can highlight species most vulnerable to climate change and can be used to inform potential mitigation and management strategies to conserve species. Here, species distribution models are used to examine the potential impacts of climate change on echolocating bats in the Wet Tropics World Heritage Area of Australia. This study builds on the work described in previous chapter by projecting future climate conditions onto models built using ‘global’ species information (see Chapter 3) to assess the potential impact of climate change on species’ distributions and richness as a whole. Under a projected high-emissions future climate change scenario (RCP8.5) different species are predicted to react by either expanding or contracting their distributions, or experiencing no change to distribution at all. It is predicted that environmental conditions will become more suitable for almost half of the modelled species (46% survivors or ‘winners’). However, for almost half of all Wet Tropics bat species, conditions are predicted to become less favourable resulting in a contraction of distribution (46% of species). Only 7% of species’ distributions were predicted to experience no change at all. Species movement is predicted to be high with species expanding into upland areas to the centre of the region and contracting out of lowland coastal areas. Predicted future richness was also modelled. Under a lower-emissions scenario (RCP4.5) less contraction of species rich areas will occur in a future with reduced carbon emissions than the amount of contraction expected under a ‘worse case’ scenario (RCP8.5). Swift action to reduce global emissions, and targeted refugia conservation in the region, is therefore required to mitigate some of the predicted future biodiversity loss.

Introduction

The impacts of climate change on species and ecosystems are increasingly being studied (Parmesan & Yohe, 2003; Williams *et al.*, 2003; Hickling *et al.*, 2006; Bellard *et al.*, 2012; Pacifici *et al.*, 2015; Taylor & Kumar, 2016). Global temperature increases of between 2° to 7°C, unpredictable rainfall, rising sea levels, and more frequent extreme events will all have important ramifications for the world's biodiversity (IPCC, 2013). The world is predicted to be entering the 6th mass extinction period (Barnosky *et al.*, 2011). Identifying species likely to go extinct and species that may persist in the face of changing conditions has been problematic, since species differ in their capacities to respond to climate change (Bellard *et al.*, 2012). For example, species that might be expected to persist will be those that are capable of adapting to changes in current locations, or capable of moving to track the changing location of suitable conditions; generally towards the poles or to higher elevations (Parmesan & Yohe, 2003; Bellard *et al.*, 2012). For species incapable of these responses, local, and even global, extinction may be a reality.

Assessed against likely distributional change associated with climate change predictions, species can be broadly categorised into two distinct groups: climate 'winners' or 'losers' (O'Brien & Leichenko, 2003). 'Winners' are species predicted to expand their future distributions with changing environmental conditions (also termed 'expanders' in this study; elsewhere termed 'immigrants' (Reside *et al.*, 2013)). These species will survive the effects of climate change, at least in the time frames over which realistic projections from climatic models can be made. In general, they will do this via either adapting to changes in environmental conditions or shifting their distributions to track favourable conditions (Bellard *et al.*, 2012). 'Losers' are species that are predicted to, or have been demonstrated to, experience a reduction in their range limits, or disappear completely with climate change (also termed 'contractors' in this study; elsewhere termed 'emigrants' (Reside *et al.*, 2013)).

There is much in the global change literature about those species who are climate change 'losers', particularly more recently (e.g. Clucas *et al.*, 2014; McGill *et al.*, 2015; Bateman *et al.*, 2016; Tayleur *et al.*, 2016). The plight of these species, and the potential loss of global biodiversity, emphasises the case for climate change mitigation and species conservation. However, little attention is often paid to those species that will expand their distribution with climate change, even though these species will most likely represent resultant future biodiversity (Somero, 2010). Some studies have indicated expansion of range sizes in a small number of species (e.g. Warren *et al.*, 2013), but in general predictions suggest fewer species will benefit from climate change than will experience negative effects. Given this, expansions in some species' distributions will not 'offset' the large number of contractions. This may consequently reduce biodiversity as a whole if new species do not move into these areas to replace those that have moved out (Warren *et al.*, 2013; McGill *et al.*, 2015). This loss of biodiversity makes identifying 'winners' even more important. Determining areas where a high number of species are likely to persist in the future is key to implementing effective management strategies to reduce biodiversity loss under changing conditions.

The predicted loss of biodiversity associated with climate change will perhaps be most evident in the world's biodiversity 'hotspots' such as the Australasian tropics (Malcolm *et al.*, 2006; Welbergen *et al.*, 2011). Previous studies conducted in the region's Wet Tropics World Heritage Area (henceforth 'Wet Tropics') predict significant declines in biodiversity across the region (Williams *et al.*, 2003; Reside *et al.*, 2013). For example, models for invertebrates, amphibians, reptiles, birds, and many species of mammal (e.g. Williams *et al.*, 2003; Shoo *et al.*, 2006; Isaac *et al.*, 2009; VanDerWal *et al.*, 2009a; Staunton *et al.*, 2014) all predict persisting flora and fauna to move toward upland areas of the region which are generally cooler and more aseasonal (in terms of a stable range of temperatures and amount of rainfall). This movement would leave lowland areas with a reduced richness (e.g. Williams, 2003; Williams *et al.*, 2010a; Reside *et al.*, 2013). However, a significant gap in our knowledge remains.

As mentioned in previous chapters, insectivorous and echolocating bats account for 15% of the region's overall vertebrate diversity and 20% of the region's mammal diversity. This group has, however, been largely omitted from biodiversity studies in the region (Williams, 2006; Welbergen *et al.*, 2011). Recent studies (see Chapters 2 and 3 of this thesis) show that bats are present across the full latitudinal and altitudinal gradient of the Wet Tropics. This may suggest that, should this high diversity persist, bats could have an important role to play in the species composition of future communities.

This chapter presents the first models showing the potential impact of climate change on individual species distributions, and thus patterns of future species diversity, of echolocating bats in the Wet Tropics. The study provides an in-depth look at how the region's biodiversity will respond to two different predicted future climate change scenarios. The models identify species who will be climate change ‘winners’ (the expanders) and losers (contractors), providing an indication of how each bat species will be impacted, and what changes we might see to species’ distribution and regional diversity under different climate change scenarios.

Methods

This chapter continues work conducted on echolocating bats in the Wet Tropics (see Chapter 2 and 3 of this thesis) (Chapter 1, Figure 1.2a and 1.2b). A detailed description of the study area can be found in the introduction and in previous chapters.

Occurrence records used for input into future prediction models were collated from a combination of sources. These include self-collected data points (see Chapter 2 for detail) and occurrence records from historical sources such as museum databases (see Chapter 3 for detail). Species distributions models produced for previous analyses (see Chapter 3 for detailed methodology) were then used to produce predictions of future species’ distributions under different climate change scenarios. Collated data covered 28 species, from all seven families of echolocating bat occurring in Australia (Megadermatidae, Rhinolophidae, Hipposideridae, Verspertilionidae, Miniopteridae, Molossidae, and Emballonuridae) (Churchill, 2008). As discussed in previous chapters, this study focused on echolocating bats. As such, the Pteropodidae, or flying foxes, are not considered in this analysis.

Species distribution models were generated using the Maxent modelling package (Phillips et al., 2006) and calibrated as detailed in Chapter 3. Models were created using bioclimatic variables representing temperature and precipitation data (from 1976 – 2005) and processed using the climates package (VanDerWal *et al.*, 2011a) in R (R Development Core Team, 2011, www.r-project.org). Models were trained with Australia-wide species observations (global), using all Australian bat records as background points at 5km resolution (bias-corrected background), and projected on to Wet Tropics spatial layers at 250m resolution (see Chapter 3 for additional detail). Modelling using wider distribution records (i.e. Australia wide) were found to produce more accurate species distribution models for the majority of species than those using Wet Tropics species records only (see Chapter 3).

Two climate change scenarios were used to produce future projections of bat distribution. Eighteen global circulation models (GCMs) for two Representative Concentration Pathways (RCP) scenarios (RCP4.5 and RCP8.5) were selected to represent a complete spectrum of various possible future climate scenarios, culminating in species distribution models for three time-steps into the future (2035, 2055, and 2085) (Annex 4.1, Table 4.1.1). RCP4.5 represents a lower carbon emissions scenario while RCP8.5 represents a future with high, unregulated carbon emissions, or a 'worst case' scenario (Riahi *et al.*, 2011; Thomson *et al.*, 2011).

Under future climate change species were categorised as either 'expanders' (i.e. those whose distribution increases under future climate change scenarios), or 'contractors' (i.e. species whose distribution decreases under future climate change scenarios), depending on the movement of the species distribution. Species which were predicted to experience no change in their distribution are categorised as exhibiting 'no movement'. Categories of movement were determined by visual assessment of species distribution maps. The proportion of each movement type accounting for overall future species movement was calculated and this movement was then graphically depicted in species turnover maps. These maps explicitly calculate species turnover for each grid cell. To do this the number of species that do not currently exist in a grid cell but are projected to move into a grid cell by 2085 (the expanders) and species that are currently predicted to occur in a grid cell but are projected to no longer occur there by 2085 (the contractors) are determined. Overall species movement is then determined as simply the sum of expanders and contractors. On the species turnover maps, grid cells containing no to minimal species movement are indicated by a gradient of dark to pale red colouring. Areas of moderate to high species movement are indicated by a gradient of yellow to dark green colouring.

Finally, change in overall species richness was modelled. This was achieved by overlaying all 28 species distribution maps and assessing cell occupancy. If a species was found to exist within a cell at each time-step it was given a score of 1, while non-occupancy was given a score of 0. Occupancy records were then summed for all species in each grid cell to produce a cumulative value, used to produce a species richness map for each time-step. Species movement and richness turnover calculations were conducted in R version 3.1.1. using the 'SDMTools' package (VanDerWal *et al.*, 2011b).

Results

Species identification and general trends

Species distribution models for the two different climate change scenarios (RCP4.5 and RCP8.5), across three time-steps into the future (2035, 2055, 2085), were produced for 28 bat species known to inhabit the Wet Tropics (Annex 4.2, Figures 4.2.1 – 4.2.28). Broadly, species were determined to either expand or contract their distributions under either RCP4.5 or RCP8.5, although two species (*Rhinolophus robertsi* and *Saccolaimus saccolaimus)* were predicted to experience no change to their distribution at all. Half of the species models forecasted using scenario RCP4.5 indicated expansions in the extent of suitable climate in the area, and thus an expansion of species' distributions (50%, 14 species) (Table 4.1, 4.2). This was also the case for RCP8.5 projections but with slightly fewer species (46%; 13 species) indicating expansion. Similarly, slightly less than half of the species modelled indicated some contraction with future climate change (RCP4.5: 43%, 12 species; RCP8.5: 46%, 13 species) (Table 4.1, 4.2). Less than 10% of the models under both future scenarios (2 species) showed no change in species' distribution. All changes to distribution were consistent between RCP4.5 and RCP8.5 with one exception; distribution of *Hipposideros semoni* is predicted to expand under an RCP4.5 scenario but contract under an RCP8.5 scenario.

Future distributions

The distribution of the sole representative species from the Megadermatidae family, *Macroderma gigas,* was predicted to remain relatively stable, with only minimal expansion, under future climate change scenarios. Under both RCP4.5 and RCP8.5, the amount of habitat in the Wet Tropics climatically suitable for this species expands slightly in all time-steps to 2085 (Annex 4.2, Figure 4.2.1). Although the extent of suitable areas are predicted to increase for this species, overall distribution is not predicted to change. Areas that are modelled to be most suitable remain in upland parts of the region, particularly to the north (Windsor, Carbine, Lamb, and Atherton Uplands; Chapter 1, Figure 1.2a) with mountain tops and coastal lowland areas being modelled as unsuitable (Annex 4.2, Figure 4.2.1).

Future projections for the two species of the Rhinolophid family indicated different responses to climate change across the modelled time-steps. *Rhinolophus megaphyllus* exhibited small but steady distribution contractions to 2085 under both RCP4.5 and RCP8.5, while *R. robertsi* showed no change in overall distribution under either scenario (Annex 4.2, Figure 4.2.2, Figure 4.2.3).

The three Wet Tropics Hipposiderid species are each predicted to respond differently to climate change. *Hipposideros ater* showed a steady distribution expansion in 2035, 2055, and 2085 under both RCP4.5 and RCP8.5 (Annex 4.2, Figure 4.2.4). The area of habitat climatically suitable for *H. ater* is predicted to expand under future climate change scenarios, primarily in coastal lowland areas throughout the region. In contrast, distribution of *H. diadema* is predicted to contract with future climate change. Unsurprisingly, this contraction is most pronounced in RCP8.5 where suitable climate contracts steadily to 2085, at which time *H. diadema* is predicted to persist predominantly in upland areas (such as the Windsor and Carbine Uplands (Chapter 1, Figure 1.2a)) (Annex 4.2, Figure 4.2.5). Finally, the impact of climate change on the distribution of *H. semoni* differed depending on the modelled scenario. Under RCP4.5 *H. semoni* distribution expands slightly southward with suitable areas for this species in the more southern areas of the region predicted to increase by 2085 (Annex 4.2, Figure 4.2.6). This southerly shift is also seen under RCP8.5, although the size of climatically suitable areas steadily contract over the 2035, 2055, and 2085 time-steps (Annex 4.2, Figure 4.2.6).

The Vespertilionid’s are a highly diverse family of bats and as such, no one pattern was found across species. Of this family, 14 species from nine different genera are modelled to inhabit the Wet Tropics (Annex 4.2, Figure 4.2.7 – 4.2.20). Of these species, 50% (7 species) were predicted to expand their distributions while distributions of the other 50% were found to contract. The only consistency in distribution change identified for this family was that the distributions of both species of Nyctophils (*N. bifax* and *N. gouldi*) were modelled to contract with time under both RCP4.5 and RCP8.5 (Annex 4.2, Figure 4.2.11 and 4.2.12). Predictably, this contraction is more pronounced under RCP8.5 with predicted climatically suitable habitat for *N. bifax* considerably reduced by 2085 while *N. gouldi* is predicted to decline entirely in the Wet Tropics by 2085 under an RCP8.5 scenario (Annex 4.2, Figure 4.2.11 and Figure 4.2.12 respectively).

Distributions of both Wet Tropics Miniopterus species are predicted to contract and reduce their distribution under future scenarios. The current distribution of *M. orianae oceanensis* is more restricted than that of *M. australis* (a common species in the study area (Churchill, 2008; Chapters 2 and 3 of this thesis)) (Annex 4.2, Figure 4.2.21, Figure 4.2.22). Regardless, both species are predicted to respond to climate change in the same way with both distributions contracting across all time-steps under both RCP4.5 and RCP8.5 scenarios (Annex 4.2, Figure 4.2.21, Figure 4.2.22). Again, as expected, there are greater contractions under RCP8.5 than under RCP4.5, with this being more pronounced in the already restricted *M. orianae oceanensis.* By 2085, under RCP8.5, both species are predicted to persist only in upland areas of the region, with *M. orianae oceanensis* being further restricted to upland areas of the Windsor, Carbine, and Atherton Uplands only (Chapter 1, Figure 1.2; Annex 4.2, Figure 4.2.22).

Conversely, both species of Molossid known to inhabit the Wet Tropics showed expansions to their distributions under future scenarios. The amount of climatically suitable habitat for both *Chaerephon jobensis* and *Mormopterus lumsdenae* is predicted to expand across the time-steps to 2085 under both RCP4.5 and RCP8.5 (Annex 4.2, Figure 4.2.23 and 4.2.24). In both scenarios, climatically suitable habitat is predicted to expand from lowland and coastal areas to upland areas of the region. By 2085, under both RCP4.5 and RCP8.5, the majority of the region is predicted to be climatically suitable habitat for these species (Annex 4.2, Figure 4.2.23, Figure 4.2.24).

Finally, species within the Emballonurid family also showed varied predicted patterns of change in distribution under future climate change scenarios (Annex 4.2, Figure 4.2.25 – 4.2.28). For species in the genus *Saccolaimus*, climatically suitability habitat was predicted to expand by 2085 under both RCP4.5 and RCP8.5 scenarios (Annex 4.2, Figure 4.2.25, Figure 4.2.26). This increase, coinciding with a slight expansion in distribution, was most prominent in the more common and more widely distributed *S. flaviventris* (Annex 4.2, Figure 4.2.25). For *S. saccolaimus*, although climate is predicted to become more suitable for this species, overall distribution is not predicted to change, with suitable areas remaining in lowland coastal areas of the region (Annex 4.2, Figure 4.2.26). The two other Wet Tropics species in this family, *Taphozous australis* and *T. troughtoni* showed conflicting responses. Distribution of *T. australis* was predicted to expand through 2035, 2055, and 2085 under both RCP4.5 and RCP8.5 with areas around the Atherton Uplands becoming the most suitable for this species. (Chapter 1, Figure 1.2a; Annex 4.2, Figure 4.2.27). Conversely, distribution of *T. troughtoni* was predicted to contract across the time-steps to 2085 under both RCP4.5 and RCP8.5, with contractions primarily occurring from the lowland areas to the far north of the region (Chapter 1, Figure 1.2a; Annex 4.2, Figure 4.2.28).

Species turnover

Species turnover modelling indicates greater contraction of species than expansion, particularly under RCP8.5 (Figure 4.2). Analysis of species turnover as a whole indicates that species movement with future climate change differs depending on the modelled scenario. Analysis shows that by 2085, under both RCP4.5 and RCP8.5, approximately half of the species are predicted to expand (RCP4.5 = 14 (50%) species, RCP8.5 = 13 (46%) species (Table 4.1, 4.2)). However, the vast majority of this expansion is predicted to occur predominantly toward the centre of the region, accumulating around the Atherton Uplands (Chapter 1, Figure 1.2a; Figure 4.1). This is indicated in Figure 4.1 by green colouration with greater species movement (and thus greater concentration of species diversity) indicated by the darkest green colouring (accumulated around the Atherton Uplands (Chapter 1, Figure 1.2a) with the dark red colouration indicating no movement of species (Figure 4.1). Some expansion is also predicted to occur in the Windsor and Carbine Uplands to the north and the Spec Uplands to the south under RCP8.5 but not under RCP4.5 (Chapter 1, Figure 1.2a; Figure 4.1).

Differences between scenarios in the 2085 species turnover models are most evident when looking at species contractions. For example, under mitigation scenario RCP4.5 less than half (12 (43%)) of species are predicted to experience contractions to their distribution (Table 4.1, 4.2). However, when looking at the species turnover models (Figure 4.1) we see the greatest contraction occurs out of the centre of the region (around the Atherton Uplands) (Chapter 1, Figure 1.2a) as indicated by the dark green colouring (Figure 4.1). Some contraction is also predicted for the Windsor and Carbine Uplands to the north and the Spec Uplands to the south (Chapter 1, Figure 1.2a) indicated by the yellow to light green colouring (Figure 4.1). Predicted expansion combined with species turnover modelling indicates that overall species movement in the region, under RCP4.5, will be minimal. Approximately half of species are predicted to also experience contractions in their distributions by 2085 under RCP8.5 (13 (46%) species) (Table 4.1, 4.2). However, species turnover and movement is much greater and more widespread under RCP8.5 than RCP4.5 (Figure 4.1). Locations that will experience a majority of species 'contracting' (indicated by a gradient of light to dark green colouration on Figure 4.1) are the lowland areas to the north and south of the region. Less contraction is predicted to occur from the lowland area in the centre of the region (indicated by a gradient of pink to yellow colours in Figure 4.1).

Table 4.1 Classification of each of the 28 Wet Tropics bat species under future climate change scenarios RCP4.5 (lower-emissions scenario) and RCP8.5 (high-emissions, 'worst case' scenario). Movement indicates either expansion, contraction, or no change in modelled environmental niche and thus species distribution.

Family	Species	Overall movement RCP4.5	Overall movement RCP8.5
Megadermatidae	*Macroderma gigas*	Expand	Expand
Rhinolophidae	*Rhinolophus megaphyllus*	Contract	Contract
	Rhinolophus robertsi	No movement	No movement
Hipposideridae	*Hipposideros ater*	Expand	Expand
	Hipposideros diadema	Contract	Contract
	Hipposideros semoni	Expand	Contract
Vespertilionidae	*Chalinolobus gouldii*	Expand	Expand
	Chalinolobus nigrogriseus	Contract	Contract
	Murina florium	Contract	Contract
	Myotis macropus	Expand	Expand
	Nyctophilus bifax	Contract	Contract
	Nyctophilus gouldi	Contract	Contract
	Phoniscus papuensis	Expand	Expand
	Pipistrellus adamsi	Expand	Expand
	Scoteanax rueppellii	Contract	Contract
	Scotorepens greyii	Expand	Expand
	Scotorepens orion	Contract	Contract
	Scotorepens sanborni	Expand	Expand
	Vespadelus pumulis	Contract	Contract
	Vespadelus troughtoni	Expand	Expand
Miniopteridae	*Miniopterus australis*	Contract	Contract
	Miniopterus orianae oceanensis	Contract	Contract
Molossidae	*Chaerephon jobensis*	Expand	Expand
	Mormopterus lumsdenae	Expand	Expand
Emballonuridae	*Saccolaimus flaviventris*	Expand	Expand
	Saccolaimus saccolaimus	No movement	No movement
	Taphozous australis	Expand	Expand
	Taphozous troughtoni	Contract	Contract

Table 4.2 Frequency and percentage of modelled overall distribution change of 28 Wet Tropics bat species whose suitable environment is predicted to expand, contract, or remain relatively suitable (no movement), under climate change scenarios RCP4.5 and RCP8.5.

Scenario	Frequency of Expansion	Frequency of Contract	No Movement
RCP4.5	14 (50%)	12 (43%)	2 (7%)
RCP8.5	13 (46%)	13 (46%)	2 (8%)

Species richness

Areas containing high bat species richness across the Wet Tropics are predicted to decline with climate change. The level of this decline differs depending on the climate scenario and time-step. Under scenario RCP4.5, modelling indicates that over time (to 2085) the climate within the Wet Tropics becomes slightly but steadily less suitable, and thus unable to support as high levels of species diversity (Figure 4.2). Areas of currently high biodiversity (e.g. Atherton Uplands) are also seen to contract through 2035, 2055, and 2085 (Chapter 1, Figure 1.2a; Figure 4.2). However, no mass loss of species is evident and only one species (*N. gouldi;* Annex 4.2, Figure 4.2.12) is predicted to become extinct from the region. Generally, areas that are highly species diverse now (e.g. the Atherton Uplands) retain a high diversity relative to other areas in the region in the future. Richness is predicted to contract away from areas with currently low species numbers (e.g. coastal Cairns/Cardwell Lowlands) (Chapter 1, Figure 1.2a; Figure 4.2).

Scenario RCP85 is the highest emissions scenario and indicates considerable environmental change and instability in the future. This scenario is reported by the Intergovernmental Panel on Climate Change (IPCC) as the one we are currently tracking (IPCC, 2013). Modelled time-steps 2035 and 2055 show the majority of upland areas will become less species diverse with time, with diversity reducing in general through the centre of the region (Figure 4.2). Between time-steps 2055 and 2085 significant and rapid diversity shifts from the lowland coastal areas throughout the region are predicted (Figure 4.2). Areas of high diversity persist only in the upland areas of the region, predominantly to the centre (Atherton Uplands) but also including Windsor and Carbine Uplands in the north and the Spec Uplands to the south (Chapter 1, Figure 1.2a; Figure 4.2).

Discussion

This study is the first to investigate the projected impacts of climate change on the bat richness and diversity of the Australian Wet Tropics. With future climate change, conditions will become more suitable for some species while considerably less suitable for others. Surprisingly, half of species' responses predicted by the models (under both RCP4.5 and RCP8.5) indicated the likelihood of an expansion in distribution as a function of an increase in the suitablility of climate in the area. This result was unanticipated and more species were expected to contract their distributions or become locally extinct based on the results of previous similar studies (on other

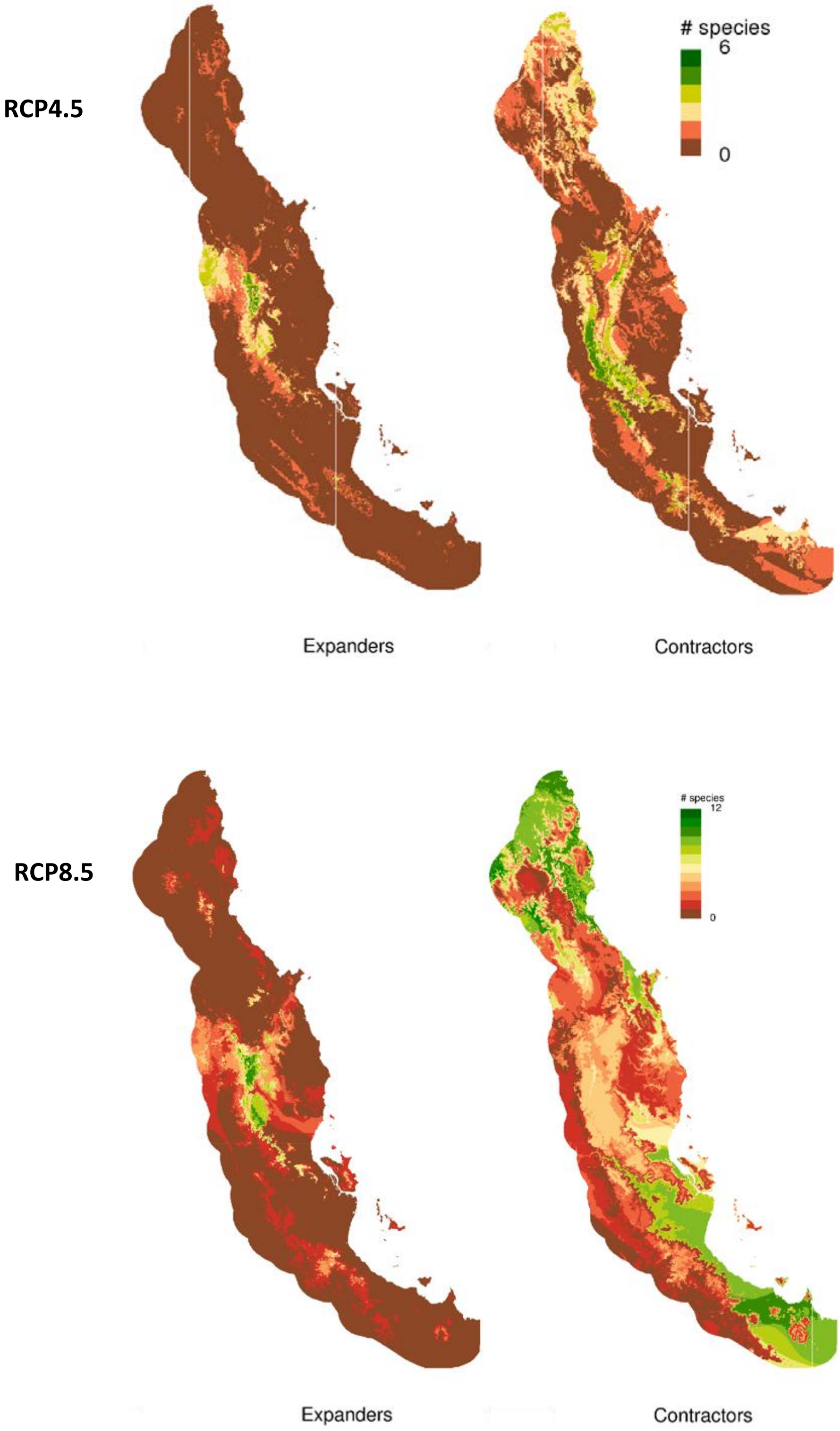


Figure 4.1 Number of species predicted to 'expand' and 'contract' into areas within the Wet Tropics by 2085. Models are calculated by analysing movement of the cumulative total of the modelled distributions of 28 bat species within the Wet Tropics, under climate change scenarios RCP4.5 and RCP8.5. The number of species expanding or contracting their distribution is indicated in a gradient from red (no movement) to dark green (movement).

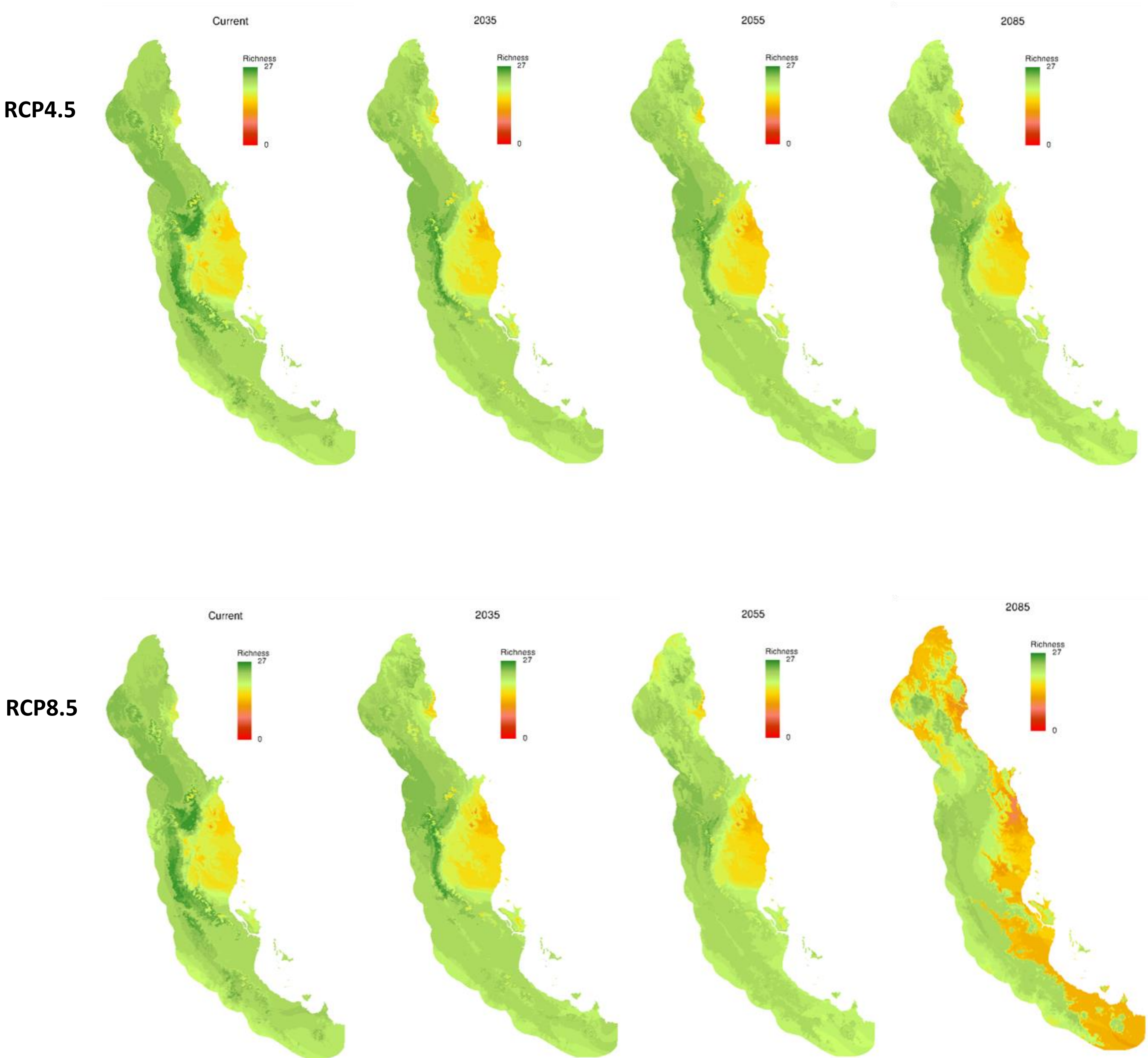


Figure 4.2 Model of regional species richness, calculated by the cumulative total of the modelled distributions of 28 bat species within the Wet Tropics, under climate change scenarios RCP4.5 and RCP8.5. Richness is indicated in a gradient from red (less rich) to dark green (most rich).

taxa including birds, non-volant mammals, amphibians, and species of invertebrate) conducted in the region (Shoo *et al.*, 2005; Issac, 2008; Welbergen *et al.*, 2011; Staunton *et al.*, 2014). For example, Vespertilionidae is the most diverse family of bats in the region incorporating half of all bats (14 (50%) species) modelled in this study. Half of these species (7 (50%) species) would be consider climate change 'winners' based on the predicted distribution expansions shown in this study while half would be considered 'losers' based on the predicted distribution contractions. Family and individual species distribution changes are discussed below in detail.

The higher than expected proportion of species predicted to be climate change 'winners' may be attributed to the highly vagile nature of insectivorous bats. The high mobility of bats may mean a reduced vulnerability to climate change as high mobility may allow species to better track changes in preferred conditions by moving to more suitable environments more readily (Bellard *et al.*, 2012; Schloss *et al.*, 2012). However, species may not be able to avoid the impacts of climate change, or harsher than modelled climate change, indefinitely. This is evident by the greater and more widespread contraction of species' distributions by 2085 under RCP8.5 despite modelling indicating that the number of species contracting is the same as in 2085 under RCP4.5.

Interestingly, outcomes from both climate change scenarios (RCP4.5 and RCP8.5) were modelled to have the same broad effect. For example, if a species range was predicted to contract under RCP4.5 then it also contracted under RCP8.5. Although, as expected, in most cases contraction of species' distributions was greater under the 'worst case' RCP8.5 scenario. The one exception to this was *H. semoni*, with this species potential distribution predicted to expand under RCP4.5 to 2085 but contract under RCP8.5 across the same time period. This may be due to differences in the environmental conditions modelled to occur in each climate change scenario. *Hippodieros semoni* is a northern Australian species, primarily restricted to Far North Queensland and Cape York Peninsula (Churchill, 2008). A previous study (see Chapter 3 of this thesis) has shown that this species inhabits areas with warm and relatively stable temperatures and low rainfall. The lower-emissions scenario (RCP4.5) is predicted to provide these conditions (increased temperatures and lower rainfall), increasing climatically suitable habitat throughout the region (Sun *et al.*, 2013). However, conditions provided under the high-emissions scenario (RCP8.5) reduce the occurrence of these conditions, thus negatively impacting species' distributions.

Although both future climate change scenarios were found to have broadly similar effects on the distribution of individual species (i.e. if a species distribution expanded under RCP4.5 it also expanded under RCP8.5), there appears to be no consistent trend of impact across the different families of bat. The distribution of the sole representative species from the Megadermatidae family, *Macroderma gigas,* was predicted to expand slightly but remain relatively stable. Rhinolophidae, Hipposideridae, and Emballonuridae species inhabiting the Wet Tropics indicated different responses to climate change across the modelled time-steps.

Differences in species responses to predicted climate, even within families, may be attributable to aspects of ecology. For example, the two species of the Rhinolophidae family indicated different responses to climate change across the modelled time-steps. *Rhinolophus megaphyllus* exhibited steady declines to 2085 under both RCP4.5 and RCP8.5, while *R. robertsi* showed no substantial change in overall distribution under either scenario. This is not unexpected, as the two species have very different current distributions and are known to respond to different climatic conditions (*R. megaphyllus* distribution is driven primarily by precipitation variables while *R. robertsi* is driven by precipitation and temperature seasonality (See Chapter 3 for details)). The influence of temperature on one species and not the other may explain the difference in modelled response to future climate change.

Within the large and highly diverse Vespertilionid family, no one pattern was found between species. Of this family, 14 species from nine genera were modelled. Half of these were predicted to expand their distributions while half were predicted to contract. For three species (*N. bifax, S. rueppellii, V. pumulis)* change to distribution appears minimal under RCP4.5. These have been categorised as overall contractions as areas of modelled suitability become more condensed and lowland areas of the region are modelled to become climatically less suitable for these species by 2085. The only consistency between species in how distributions might change was between the two species of Nyctophius (*N. bifax* and *N. gouldi*) with the extent of the distributions of both being predicted to contract under RCP4.5 and RCP8.5. Predictably, this contraction is more pronounced under RCP8.5. For both species, outcomes under this scenario are negative, with areas of climate suitable for *N. bifax* predicted to considerably reduce by 2085 and *N. gouldi* predicted to decline to regional extinction in the Wet Tropics by 2085 under an RCP8.5 scenario.

In contrast to the above families of bat, distributions of related species in the two remaining families (Miniopteridae and Molossidae) exhibit similar trends in future distributions. For example, the distributions of both species of Miniopterus are predicted to contract while both Molossidae species will experience expansions to their distributions. This congruence might again be explained by the variables known to drive their distributions with precipitation variables identified as being the primary influence (see Chapter 3 for detail).

As demonstrated, there is considerable current and predicted future variation within bat families and across individual species. Investigating overall species turnover allows us to look at changes to the region's richness and bat biodiversity as a whole in greater detail. This provides us with more refined information on the effects of climate change. Overall movement of individual species within the Wet Tropics was found to accumulate around the upland areas to the centre of the region. Species turnover maps reflect this with range expansion primarily occurring in the Atherton Uplands. Most distribution contraction was found to occur in lowland areas to the centre of the region and along the western border. This may indicate species movement toward cooler, more stable rainforested areas of the region.

A variety of species inhabiting the Wet Tropics have been predicted to respond to climate change in similar ways as the species in this study. Herpetofauna, and microhylid frogs in particular, are predicted to be the most vulnerable Wet Tropics species to the impacts of climate change (Shoo & Williams, 2004; Isaac *et al.*, 2009; Welbergen *et al.*, 2011). Increasing temperatures may already have reduced microhylid frog distributions in the region with persistence of these species into the future predicted to be restricted to mountaintops (Shoo & Williams, 2004). At least 74% of Wet Tropics bird species are predicted to be threatened by mid-range climate warming with some 30 species likely to become critically endangered, particular those already confined to upland areas (Shoo *et al.*, 2005; Anderson, 2011). A 'reshuffling' of bird assemblages has been predicted as a consequence of climate change as lowland species expand into cooler, more upland areas with increasing temperatures (Anderson, 2011).

With diversity predicted to become concentrated in these small mountainous areas, other factors not taken into consideration in this study may affect species distribution and persistence in addition to environmental suitability. For example, species predicted to experience significant range reduction in 2035 and 2055 may have exhausted their 'adaptation potential' (i.e. their ability to modify an aspect of their life whether behaviour or location to cope with changing conditions to their niche) by 2085. Species already restricted to high elevation, mountainous areas will be unable to move to higher elevations to further track preferred environmental conditions. Similarly, increased intraspecific and interspecific competition for food sources or roosting sites could result in an reduction in fitness or breeding ability (Bellard *et al.*, 2012). Thus, although the area of climatically suitable habitat for a species to inhabit is predicted to expand, overall conditions may become less favourable with time. This hypothesis is supported by the species richness modelling in this study which predicts that, overall, areas of high biodiversity in the region will reduce and contract under worst case scenario modelling. However, additional study would be required to determine the effect of such factors as competition or a species 'adaptation potential' on future species' distributions.

All modelling conducted in this study (individual species, species turnover, and regional biodiversity) indicate that areas of high biodiversity will remain only in upland areas to the centre of the region. The Atherton, Windsor, and Carbine Uplands in particular remain species rich. These areas, particularly the Atherton Uplands, have been predicted to become important refuge for regional biodiversity under future climate change scenarios (Reside *et al.*, 2013). Reside and colleagues highlight that there is 'likely no place on the continent that will not experience catastrophic increases in local temperatures in the next 75 years' (Reside *et al.*, 2013). They report that coastal areas in particularly will see the greatest temperature increases in the future meaning more upland, cooler areas will become refugia for much of the region's diversity (Reside *et al.*, 2013). The results of this study add support to Reside *et al's* findings by showing that under the high-emission scenario RCP8.5, bat species distributions are seen to dramatically contract out of the lowland coastal areas of the region and expand into the centre of the region, particularly to the areas identified as priority refugia.

Implications

Modelling shows that under a lower-emission mitigation scenario (RCP4.5) areas in the Wet Tropics become more suitable for over half of the species present. However, biodiversity contraction and loss is still implicated albeit to a lesser degree and occurring more slowly than predicted under RCP 8.5. This is evidence in support of the case for immediate and effective mitigation action. Indeed, the call for strong and immediate mitigation has been made numerous times. For example, Warren *et al* (2013) determined that loss of biodiversity could be reduced by 60% if global emissions were to peak in 2016. This reduction may have been achievable in 2013 when this study was published, but with global emissions continuing to increase each year this is now unobtainable (IPCC, 2013). If the world were able to ensure emissions peaked by 2030, a mitigation in species loss of 40% could be achieved (Warren *et al*, 2013). This highlights how crucial significant and swift action to reduce global carbon emissions is if we are to have any hope of saving the world's biodiversity. Timely mitigation may also slow the rate of biodiversity movement and loss, allowing more time to effectively manage species and refugia areas. Only rapid and strong action will ensure these species, and the region's biodiversity as a whole, can be spared the negative effects of unmitigated human induced climate change.

Annex 4.1

Table 4.1.1 The 18 Global Climate Models (GCMs) used in producing future species distribution models of 28 bat species. Climate change scenarios RCP4.5 and RCP8.5 were mapped for years 2035, 2055, and 2085.

Global Climate Change model	Abbreviation
Coupled Global Climate Model (CGCM3)	cccma-cgcm31
MIROC3.2 (hires)	ccsr-micro32hi
MIRCO3.3 (medres)	ccsr-micro32med
CNRM-CM3	csiro-mk30
CSIRO Mark 3.0	gfdl-cm20
CM2.0 – AOGCM	gfdl-cm21
CM2.1 – AOGCM	giss-modeleh
GISS ModelE-H	giss-modeler
GISS ModelE-R	iap-fgoals10g
FGOALS1.0_g	inm-cm30
INMCM3.0	inm-cm4
IPSL-CM4	ipsl-cm4
ECHAM5/MPI-OM	mpi-echam5
MRI-CGCM2.3.2	mri-cgcm232a
Community Climate System Model – version 3.0 (CCSM3)	ncar-ccsm30
Parallel Climate Model (PCM)	ncar-pcm1
HadCM3	ukmo0hadcm3
Hadley Centre Global Environmental Model – version 1 (HadGEM1)	ukmo-hadgem1

Annex 4.2

Macroderma gigas

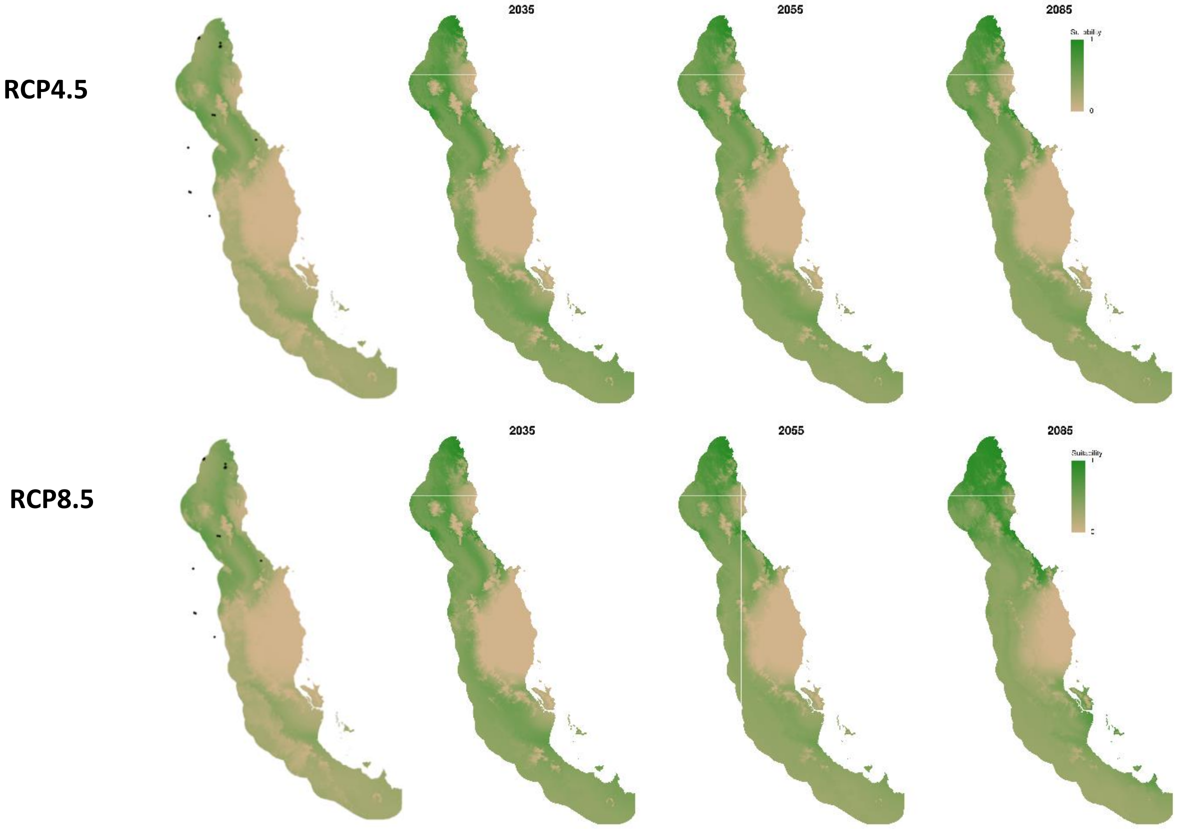


Figure 4.2.1 Current and predicted future distribution of *Macroderma gigas* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Rhinolophus megaphyllus

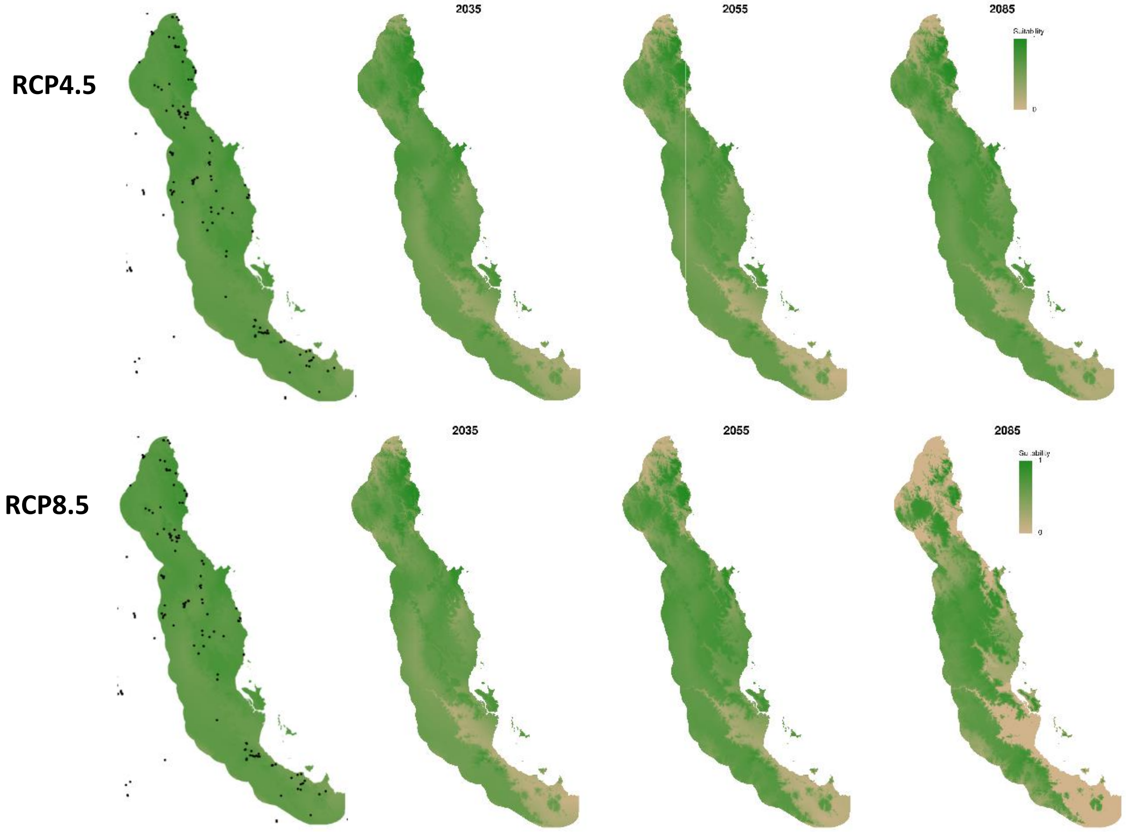


Figure 4.2.2 Current and predicted future distribution of *Rhinolophus megaphyllus* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Rhinolophus robertsi

Figure 4.2.3 Current and predicted future distribution of *Rhinolophus robertsi* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Hipposideros ater

Figure 4.2.4 Current and predicted future distribution of *Hipposideros ater* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Hipposideros diadema

Figure 4.2.5 Current and predicted future distribution of *Hipposideros didama* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Hipposideros semoni

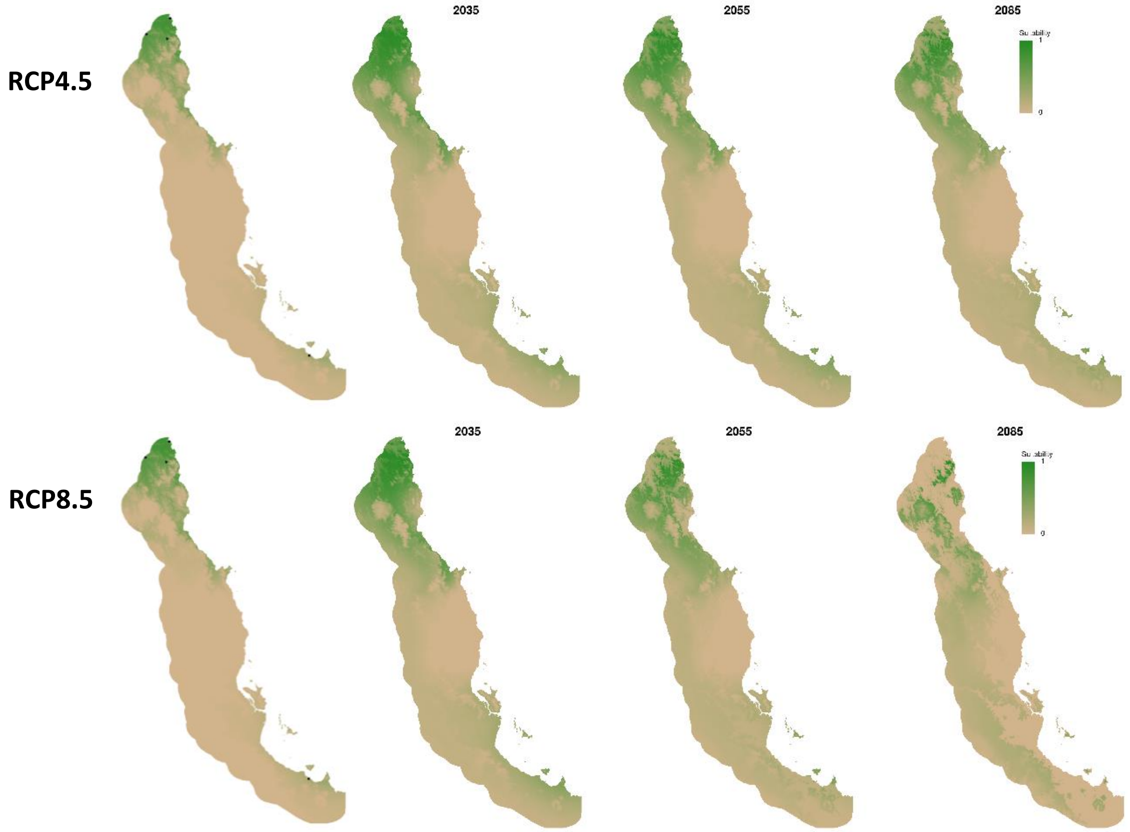


Figure 4.2.6 Current and predicted future distribution of *Hipposideros semoni* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Chalinolobus gouldi

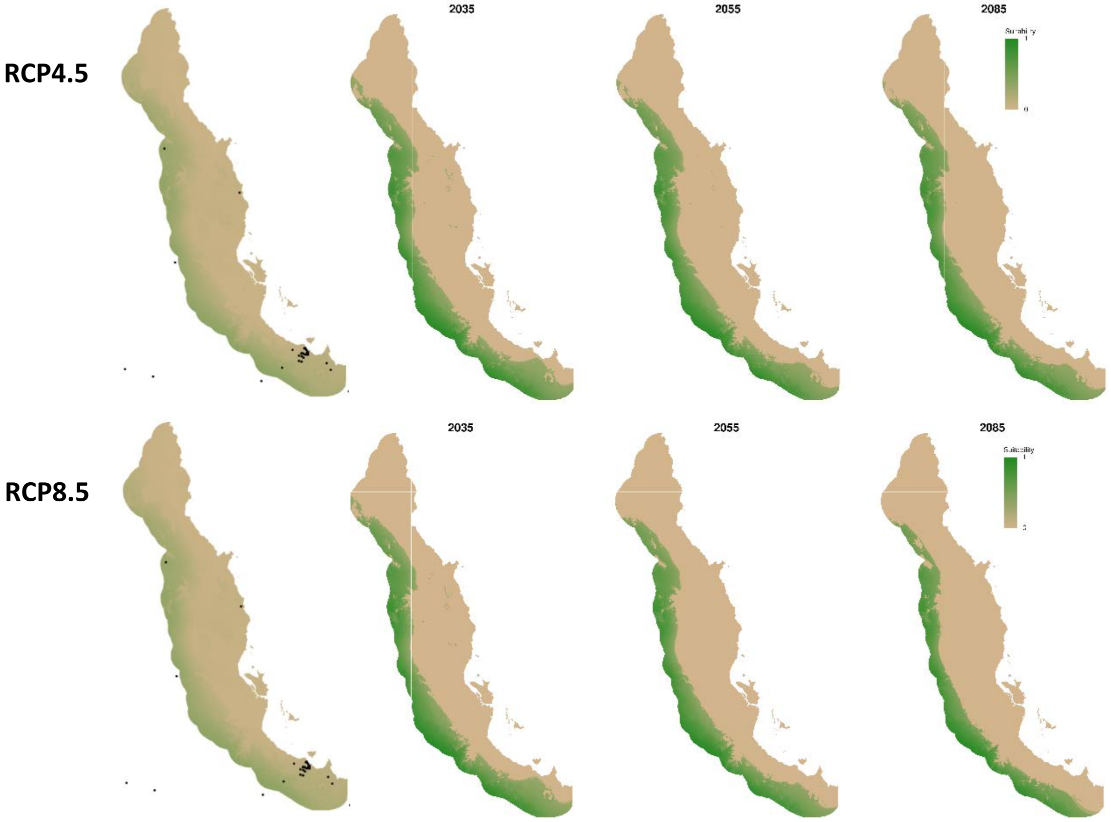


Figure 4.2.7 Current and predicted future distribution of *Chalinolobus gouldii* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Chalinolobus nigrogriseus

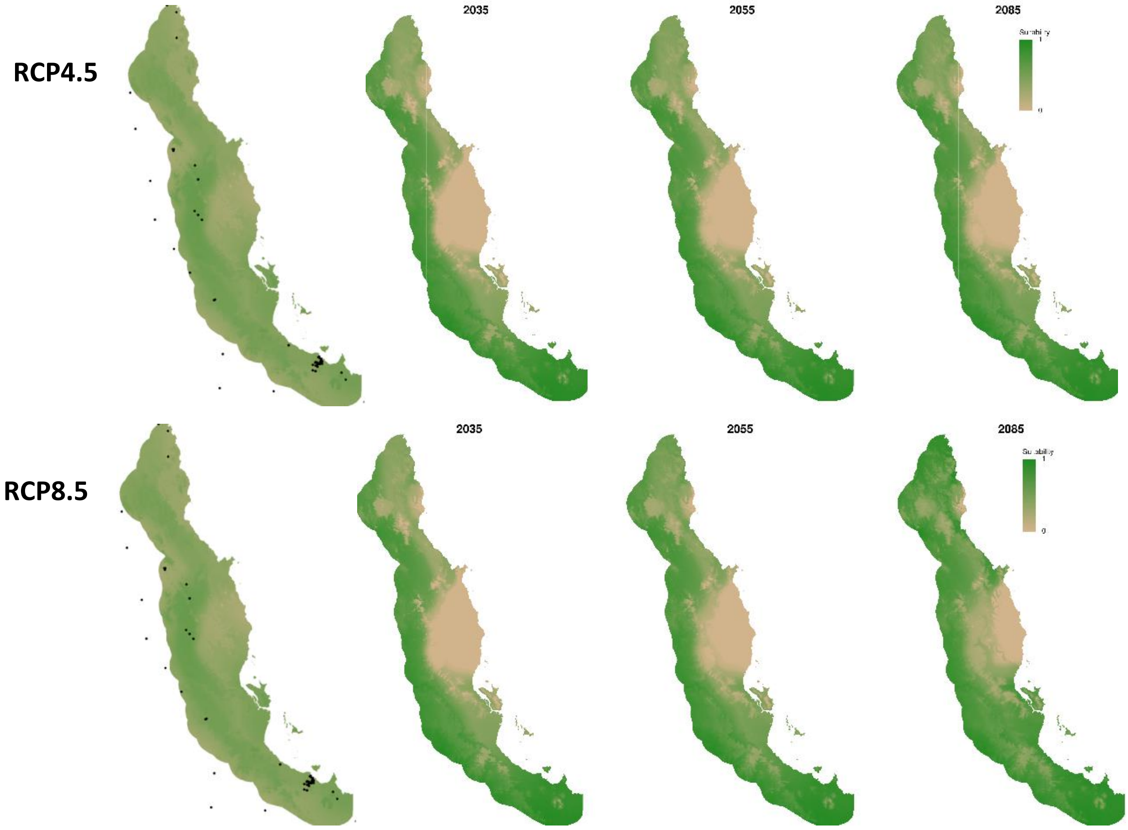


Figure 4.2.8 Current and predicted future distribution of *Chalinolobus nigrogriseus* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Murina florium

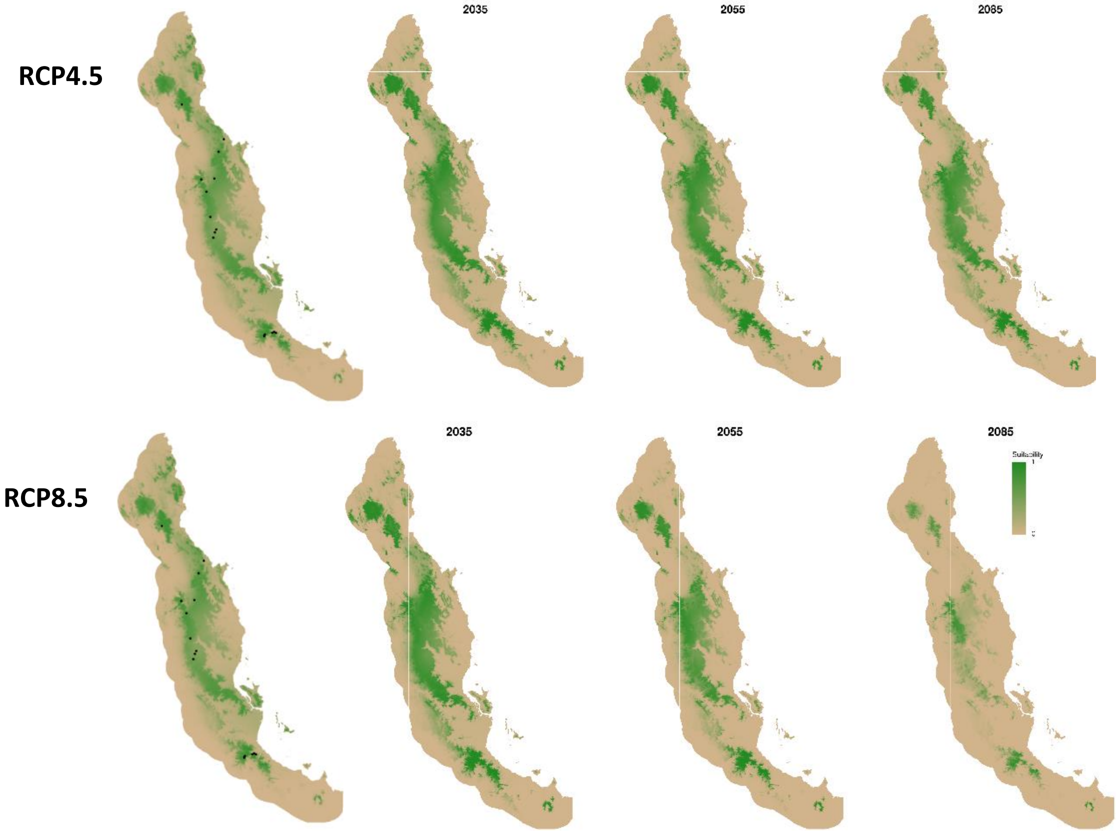


Figure 4.2.9 Current and predicted future distribution of *Murina florium* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Myotis macropus

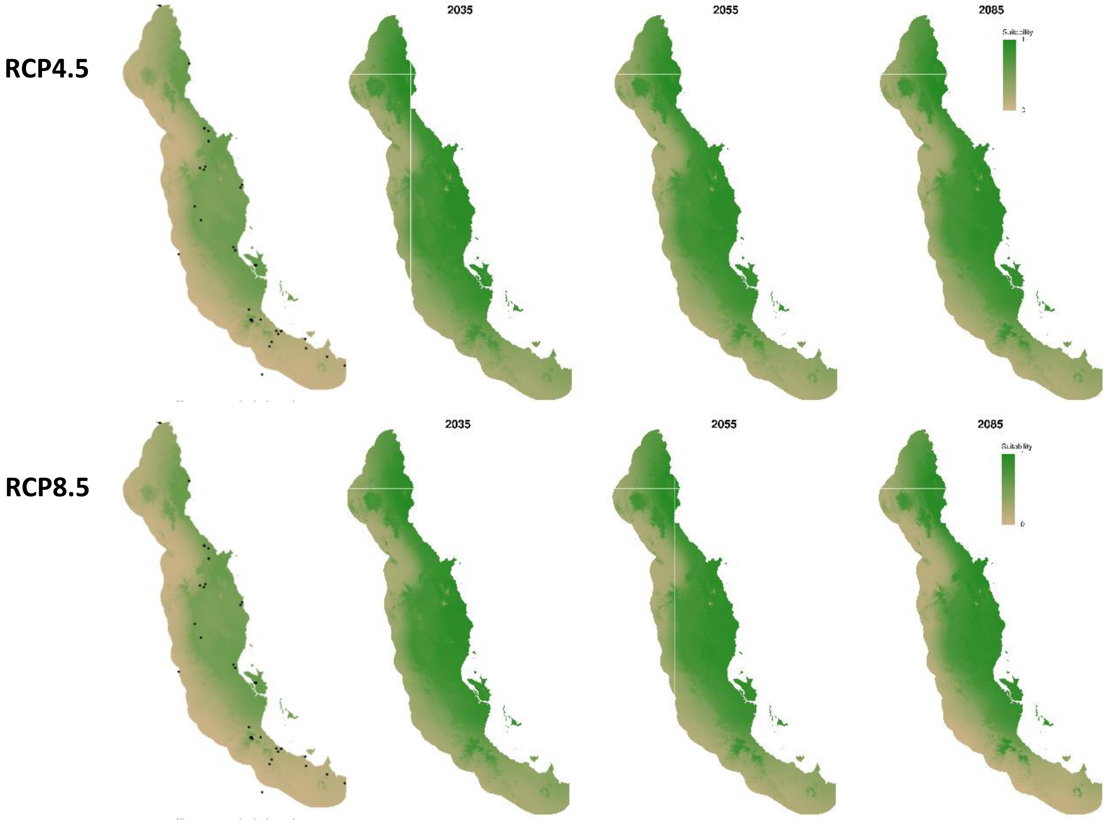


Figure 4.2.10 Current and predicted future distribution of *Myotis macropus* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Nyctophilus bifax

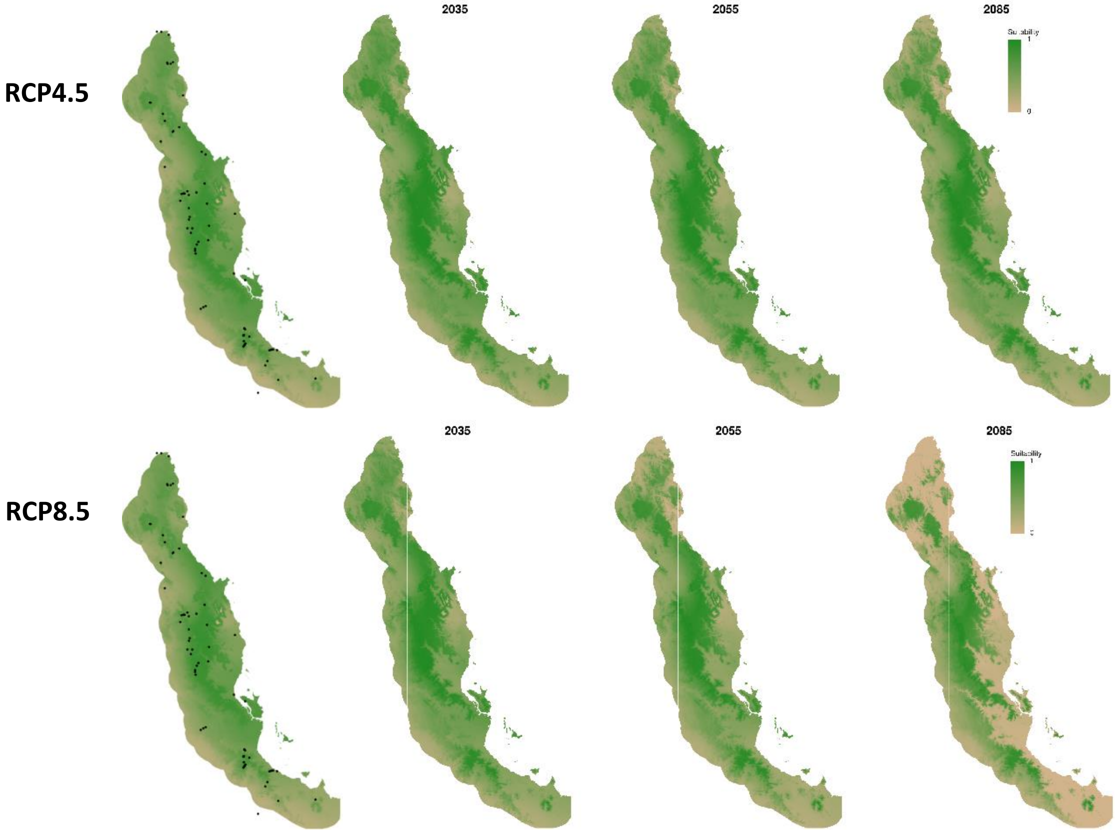


Figure 4.2.11 Current and predicted future distribution of *Nyctophilus bifax* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Nyctophilus gouldi

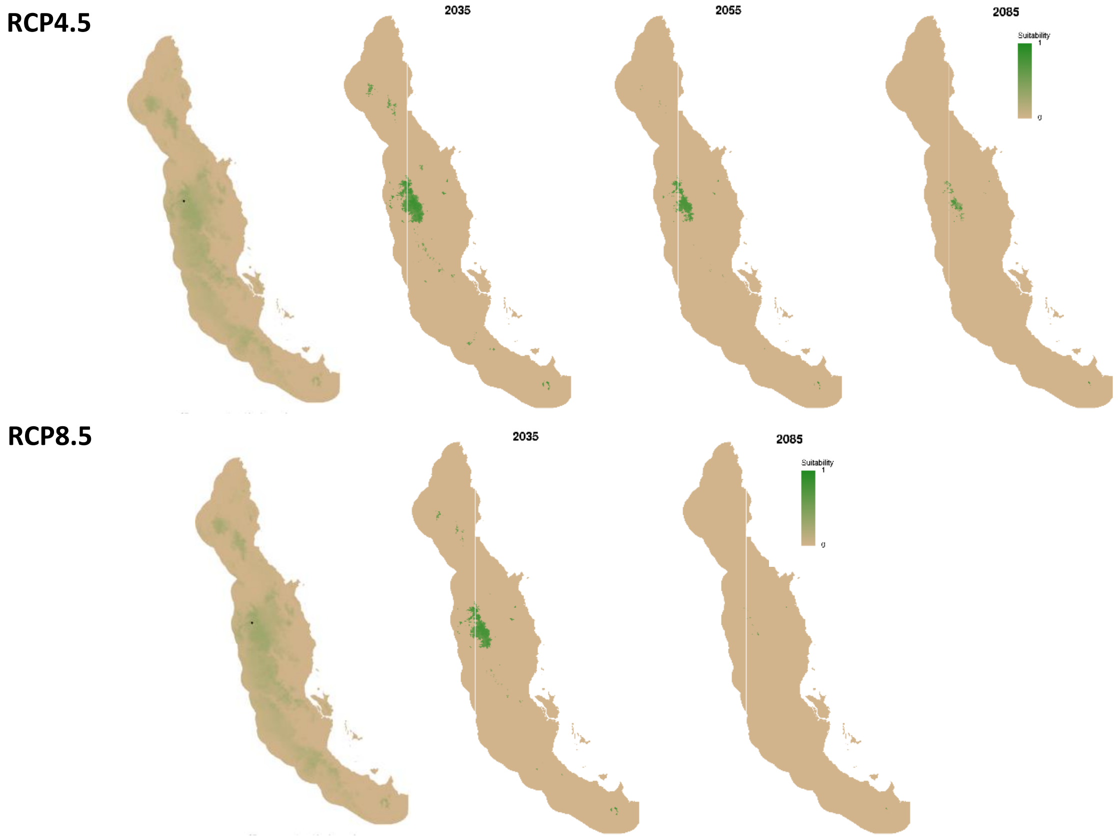


Figure 4.2.12 Current and predicted future distribution of *Nyctophilus gouldi* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Phoniscus papuensis

Figure 4.2.13 Current and predicted future distribution of *Phoniscus papuensis* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Pipistrellus adamsi

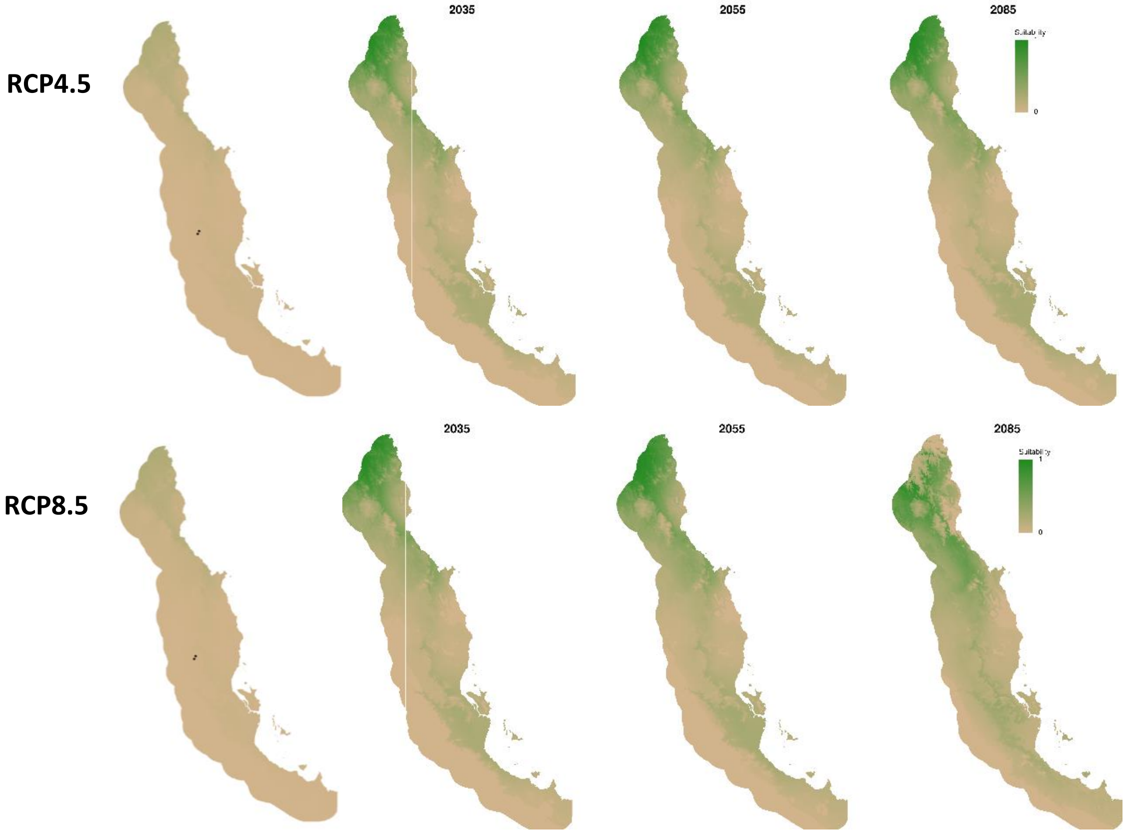


Figure 4.2.14 Current and predicted future distribution of *Pipistrellus adamsi* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Scoteanax rueppellii

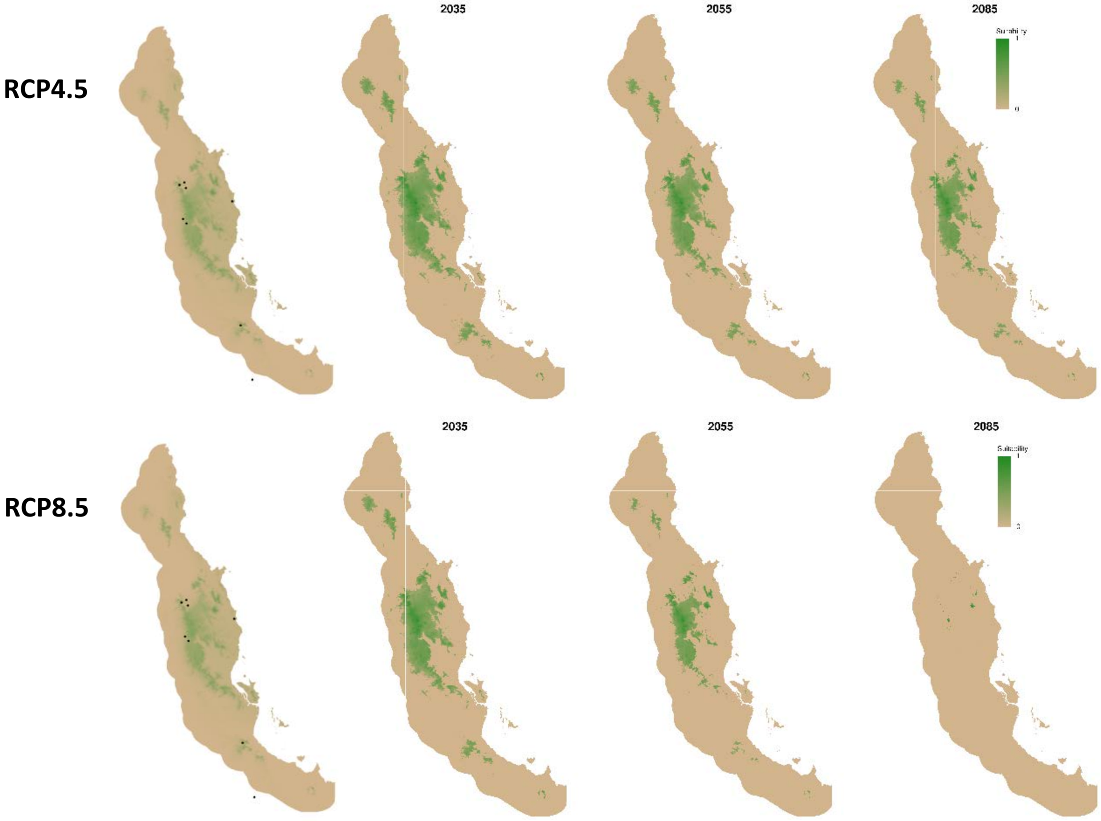


Figure 4.2.15 Current and predicted future distribution of *Scoteanax rueppellii* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Scotorepens greyii

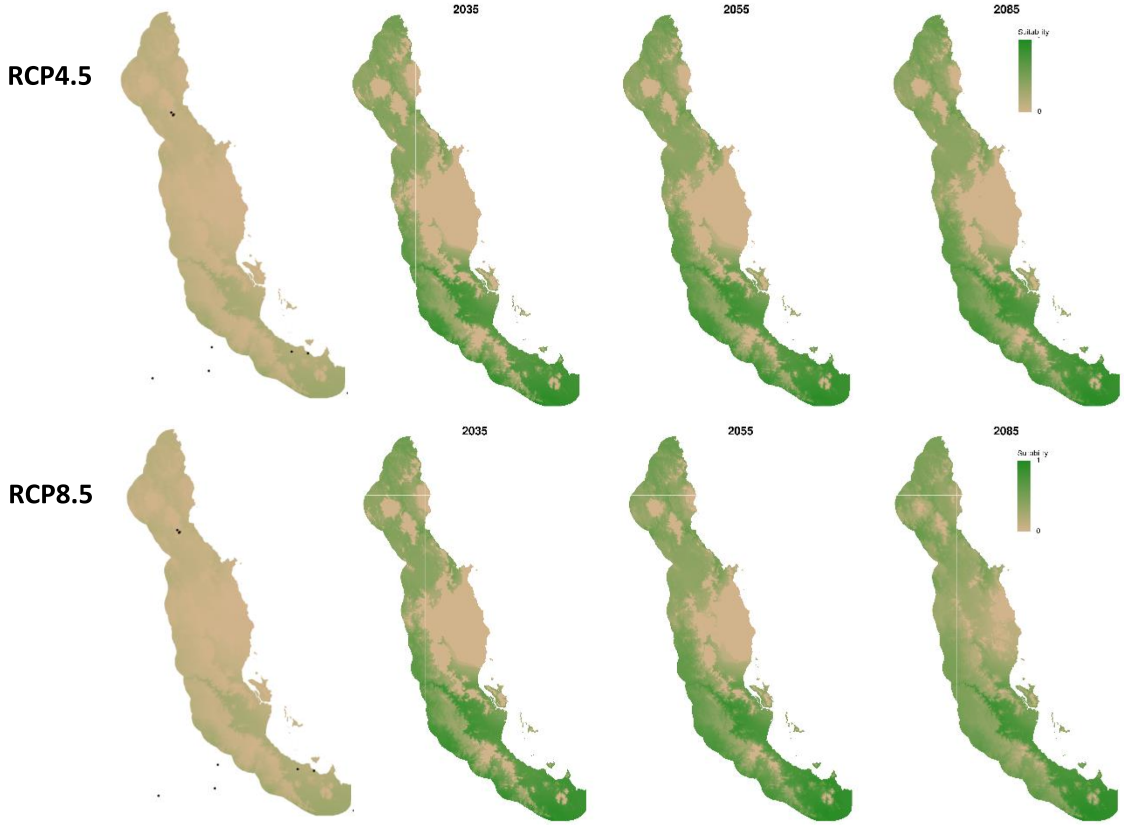


Figure 4.2.16 Current and predicted future distribution of *Scotorepens greyii*i in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Scotorepens orion

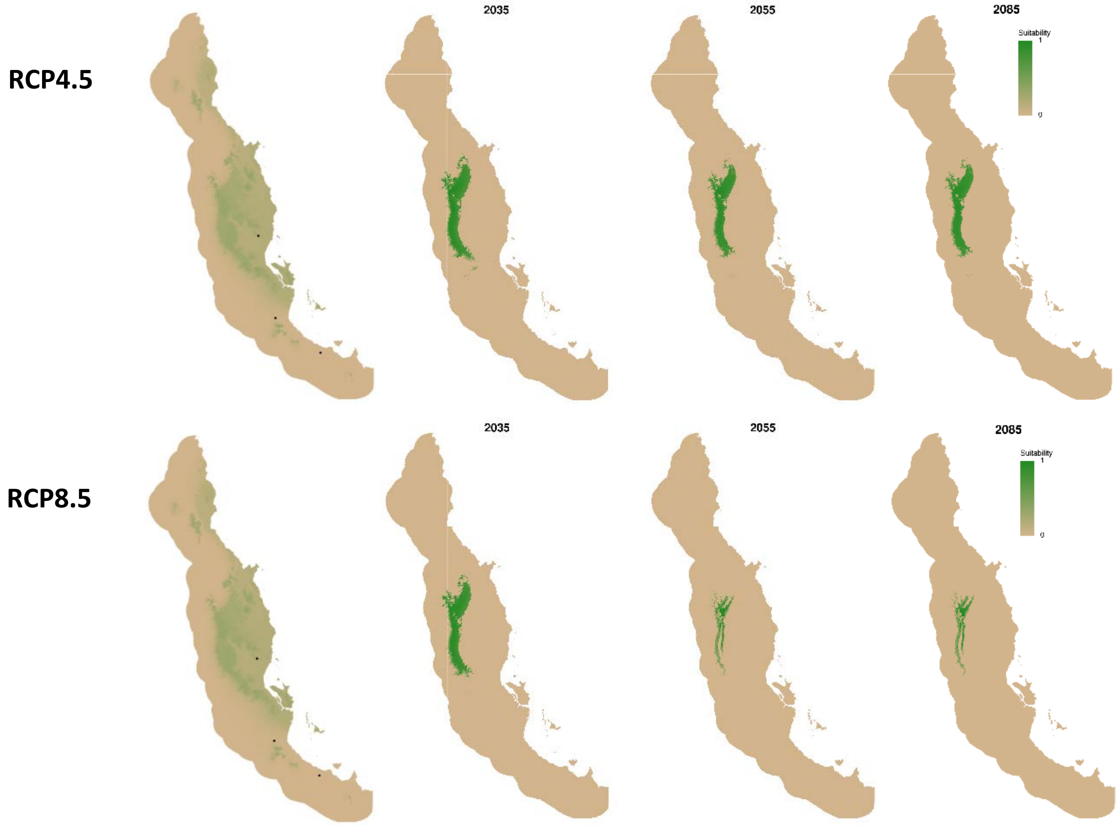


Figure 4.2.17 Current and predicted future distribution of *Scotorepens orion* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Scotorepens sanborni

Figure 4.2.18 Current and predicted future distribution of *Scotorepens sanborni* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Vespadelus pumulis

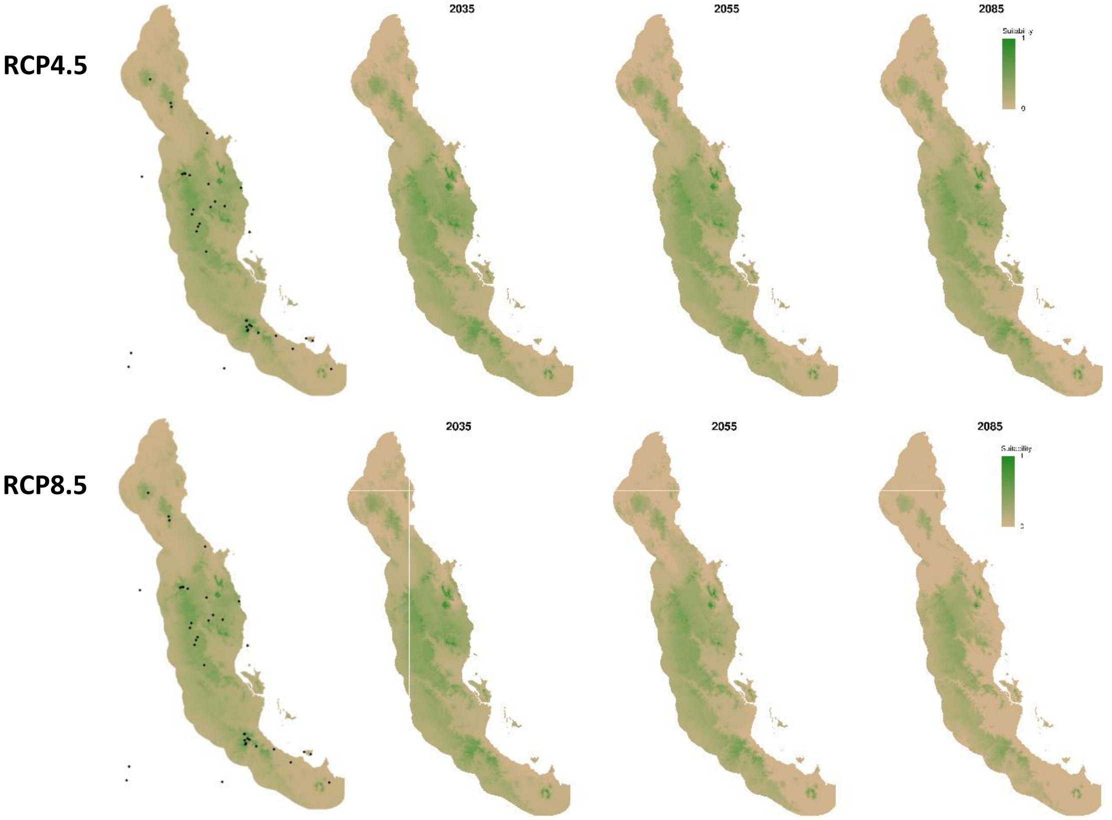


Figure 4.2.19 Current and predicted future distribution of *Vespadelus pumulis* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Vespadelus troughtoni

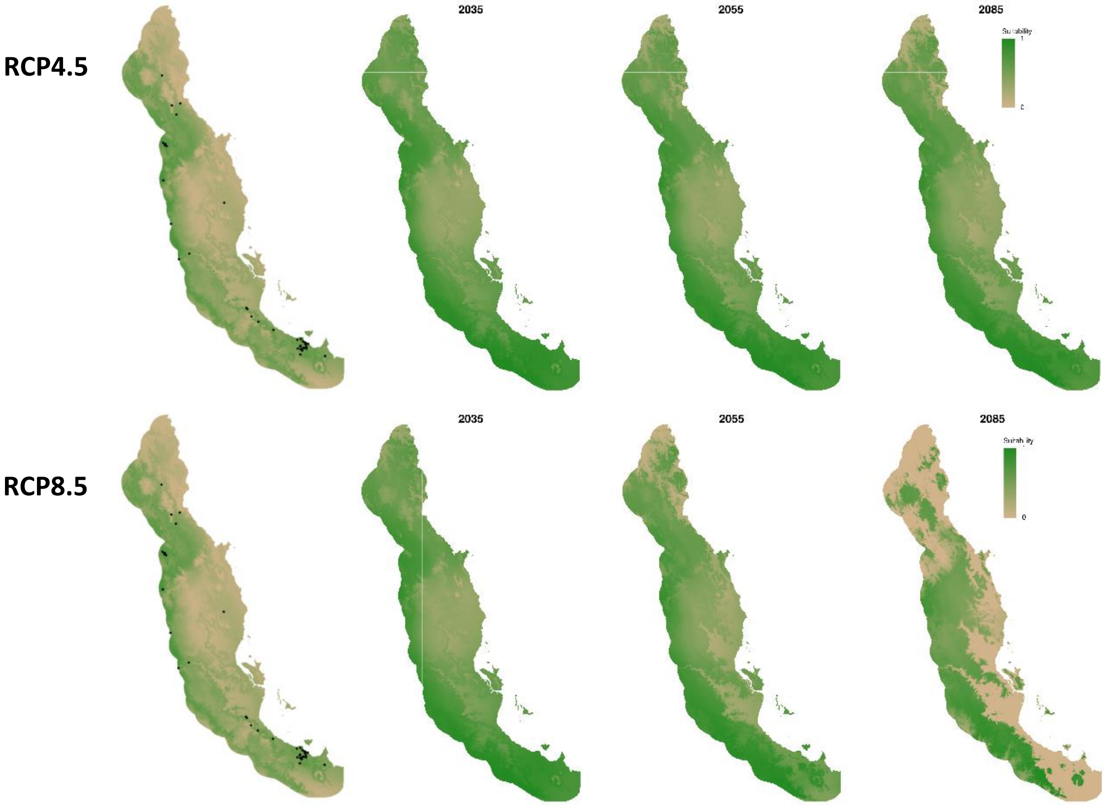


Figure 4.2.20 Current and predicted future distribution of *Vespadelus troughtoni* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Miniopterus australis

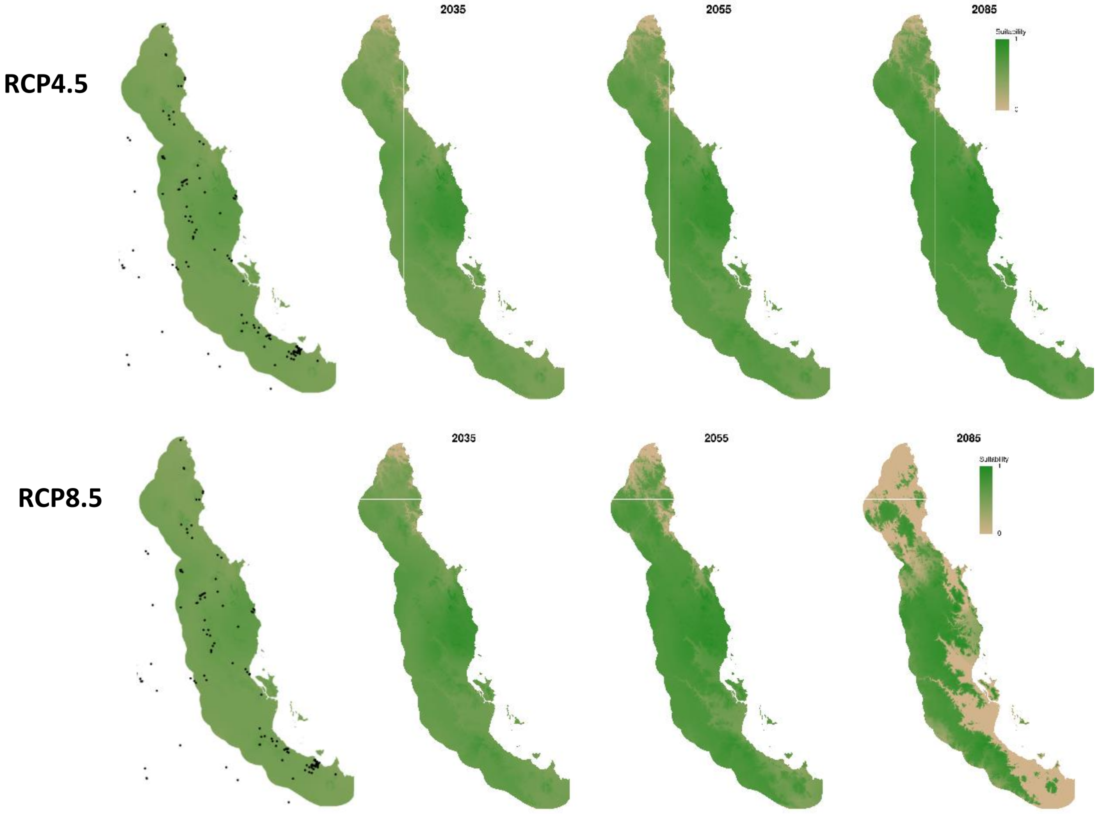


Figure 4.2.21 Current and predicted future distribution of *Miniopterus australis* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Miniopterus orianae oceanensis

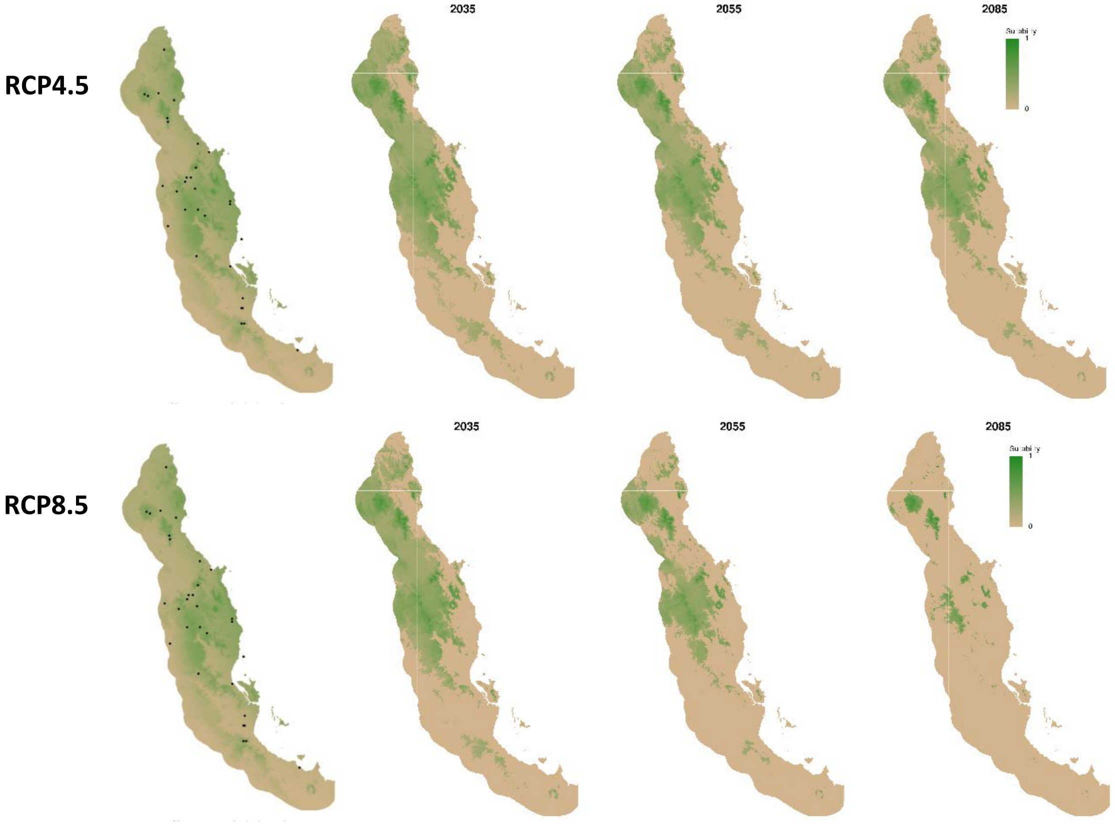


Figure 4.2.22 Current and predicted future distribution of *Miniopterus* orianae oceanensis in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Chaerephon jobensis

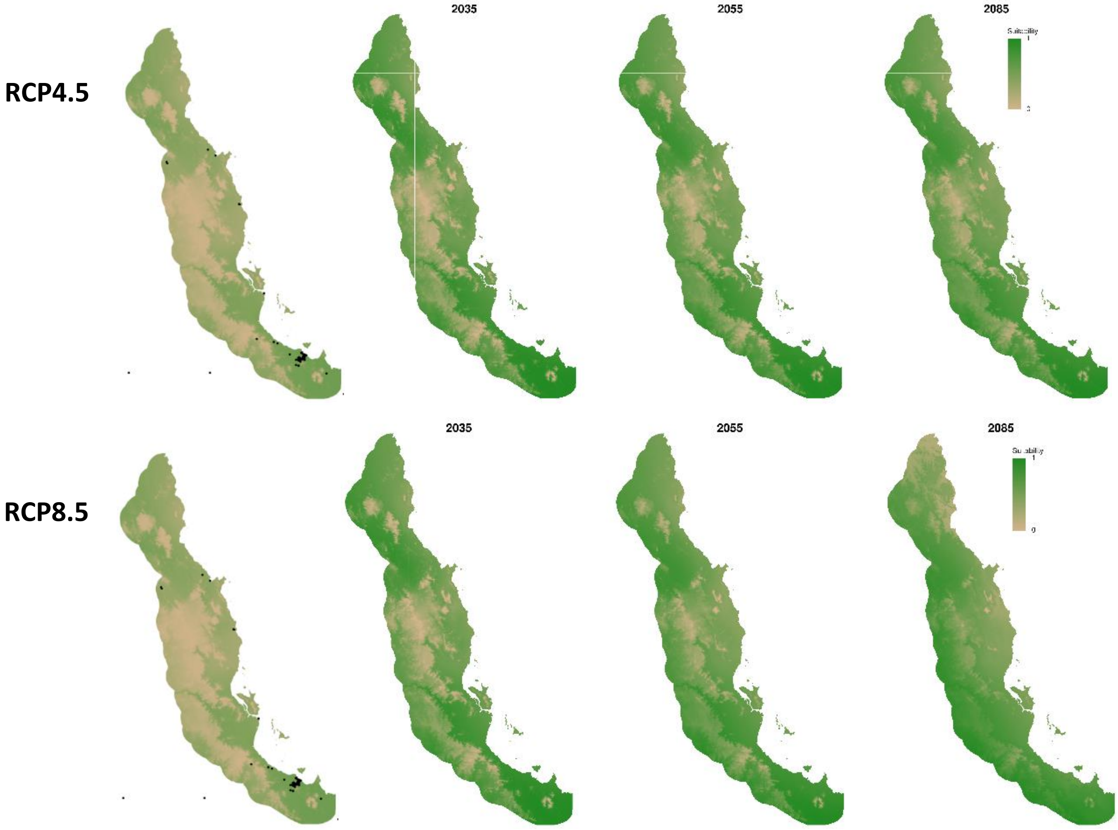


Figure 4.2.23 Current and predicted future distribution of *Chaerephon jobensis* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Mormopterus lumsdenae

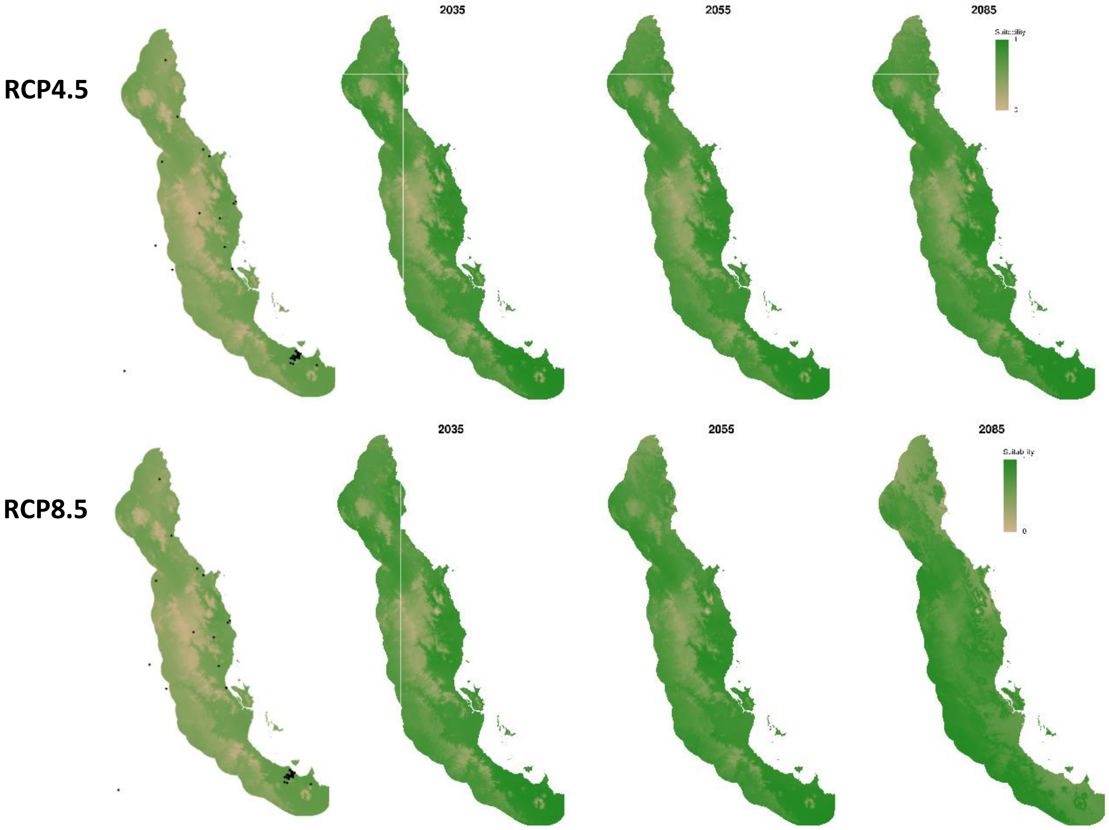


Figure 4.2.24 Current and predicted future distribution of *Mormopterus lumsdenae* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Saccolaimus flaviventris

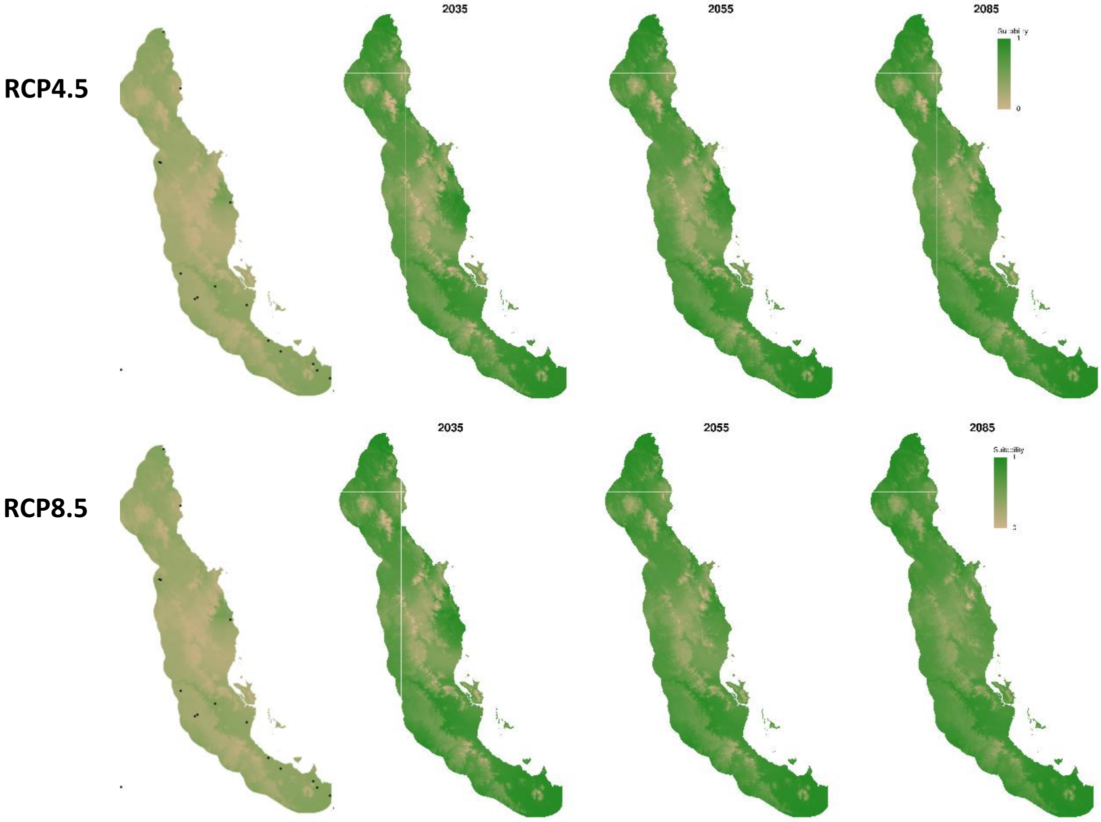


Figure 4.2.25 Current and predicted future distribution of *Saccolaimus flaviventris* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Saccolaimus saccolaimus

Figure 4.2.26 Current and predicted future distribution of *Saccolaimus flaviventris* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Taphozous australis

Figure 4.2.27 Current and predicted future distribution of *Taphozous australis* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios.

Taphozous troughtoni

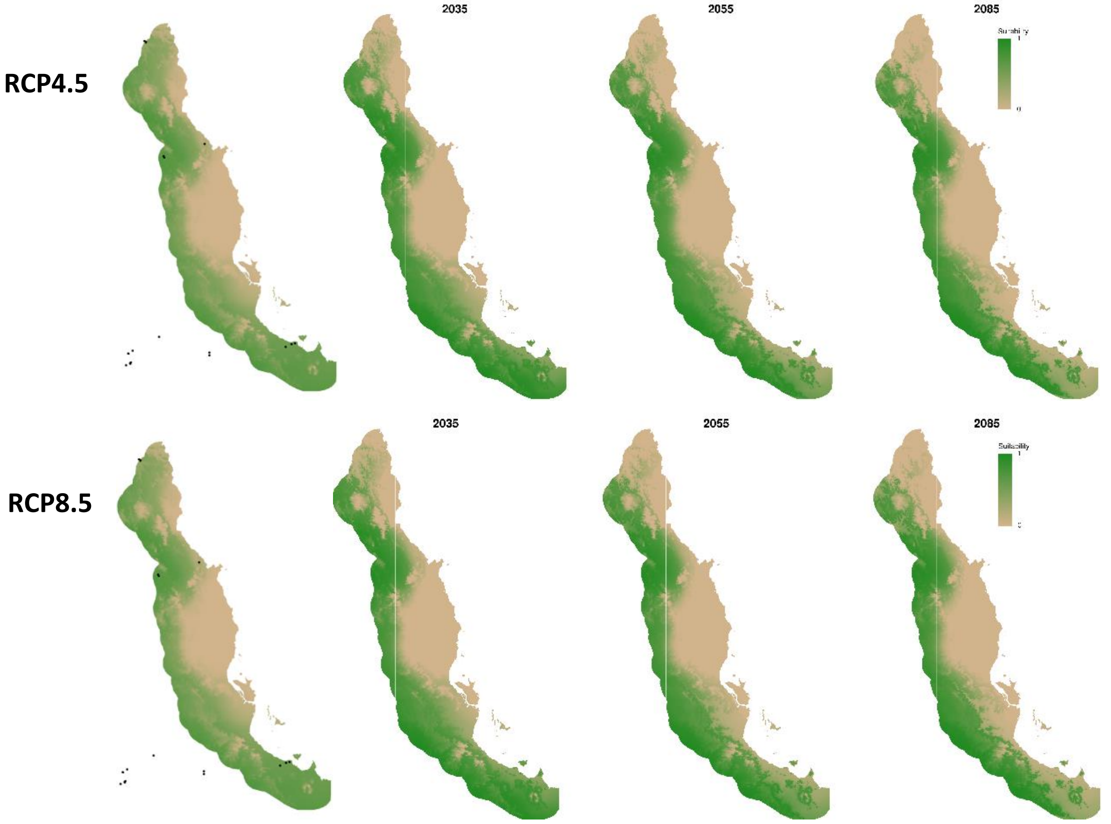


Figure 4.2.28 Current and predicted future distribution of *Taphozous troughtoni* in the Wet Tropics in 2035, 2055, and 2085 under RCP4.5 and RCP8.5 climate change scenarios

Chapter 5: General Discussion

Summary of major findings

This thesis presents the first detailed species distribution models for 28 species of echolocating bat known to inhabit the Wet Tropics World Heritage Area. Species' distributions were modelled using climatic variables and precipitation (water availability) was found to primarily determine probability of species' occurrence. This information was used to produce SDMs predicting how species' distributions will alter under various potential future climate change conditions. Modelling predicts that climatic conditions will become more suitable for almost half of the study species. However, conditions are predicted to become less favourable for almost half of the study species resulting in contractions in distributions. These results, and the corresponding thesis chapter in which they are presented, are discussed in further detail below.

Chapter 2 of this thesis, '*Climate, not elevation, drives bat species' distributions in the Australian Wet Tropics World Heritage Area'* investigated patterns of bat species richness and community composition in the Wet Tropics rainforests. This chapter tested whether bat distribution patterns are driven by elevation, latitude, climatic variables, or some combination of all of these variables. No evidence of a relationship between richness and any climatic variables, nor between richness and elevation or latitude alone was found in this study. Total species richness was similar across all subregions and neither a peak in richness at mid-elevation, nor a monotonic decline in richness with elevation, was evident. The lack of a defined richness pattern is a contrast to other similar studies conducted globally. In other regions bats tend to exhibit various distribution patterns depending on latitude. Generally, richness is found to decrease with increasing elevation in the tropics and peak at mid-elevations in temperate zones (McCain, 2007). This was well demonstrated by a recent study conducted by Herkt and colleagues looking at bat distribution patterns at a fine scale across the entire African continent (Herkt et al., 2016). They found that within tropical areas of the continent, predicted richness peaked near the base of mountains but for the more dry, temperate areas richness peaked further upslope or at mid-elevations (Herkt et al., 2016).

While regional richness patterns were not found, further analysis indicated that patterns in individual species' probability of occurrences are primarily driven by temperature seasonality, with precipitation and subregion variables also being influential. This supports the results of other bat studies conducted in other tropical regions. For example, Stevens (2013) found seasonality to be an important predictor of bat diversity in the Atlantic Forest of South America. Steven's found that seasonality was related to changes in bat abundance commenting that it may be too 'energetically costly' for some species to occur in areas of high seasonality. Measures of temperature and precipitation were also found to explain the majority of variation in bat diversity in a Norwegian study (Michaelsen, 2016) and in Australia, modelling conducted by Milne and colleagues showed that amount of annual rainfall was significant in determining bat occurrence and distribution in the Northern Territory (Milne et al., 2006). Interestingly, a study conducted in South Africa found that the occurrence of bat species in their study sites was linked with water availability and temperature, as was found in this Wet Tropics study (Weier et al., 2017). However, Weier and colleagues were able to link the correlation between distribution and water availability and temperature with the mid-elevational peaks in richness in more temperate areas and a linear decrease with increasing altitude in wetter areas. Making this link may have been possible due to the habitat diversity in their study area allowing them to compare and contrast temperate and tropical gradients; something which was not possible in this study.

Chapter 2 concludes that climatic variables (temperature and precipitation) coupled with site specific factors drive species' distributions in each subregion. This subregional effect could result from differences in the structural complexities of forest types and fine scale aspects of the environment, such as appropriate roosting sites, associated with the different mountain gradients sampled (e.g. Speakman & Thomas, 2003; Rebelo *et al.,* 2010; Presley et al., 2012). Chapter 2 represents one of the first detailed descriptions of the richness and community composition patterns of echolocating bats in the rainforest habitats of the focal, tropical, region. With the impending threat of climate change, greater understanding of the links between species' distributions, richness and assemblage, and the environmental factors driving them in particular study regions, is crucial to predicting responses of species and ecological communities to climate change.

Chapter 3 of this thesis, '*Improved understanding of local biodiversity using global information: a case study of bats in the Australian Wet Tropics*' builds on work conducted in Chapter 2 and sought to build the greater understanding called for above. Species' distribution models (SDMs; also known as ecological niche models) were used to assess the suitability of different environments for the 28 study species. These models were produced using four different model parameters based on different levels of species occurrence data (global vs local) and background information (bias corrected vs bias-uncorrected backgrounds) to determine which would provide the most accurate distribution models. SDMs generally performed best when models were produced using global species occurrence data in combination with background layers that accounted for any sampling bias.

Collated, these models provide information on the region's species richness overall. Rainforested areas to the centre of the region, and particularly the Atherton Uplands, were found to be the most species rich while lowland coastal regions were generally found to be the most species poor. Overall, precipitation variables were found to be the most important correlate to predicted species' distribution for all families and the majority of modelled species within each family. In terms of distribution, the majority of bat species diversity is demonstrated to be clustered around lowland coastal areas and mid-elevation mountain ranges, particularly around the Atherton Uplands to the centre of the region.

Chapter 3 highlights the importance of correctly selecting model inputs when producing species distributions models confirming the results of other similar studies (e.g. Araújo & Guisan, 2006; Merow et al., 2013; Mainali et al., 2015; Singer et al., 2016). Restricting the extent of occurrence data used was found to place significant limitations on the resulting model outputs. Others have demonstrated that this ultimately leads to more conservative, and potentially less usful, outputs (Thuiller et al., 2004; Phillips et al., 2009; Kramer-Schadt et al., 2013). As well as providing more accurate SDMs, the use of global information in this type of modelling provides a more accurate basis for future climate modelling. Including information on the full climatic and environmental range of a species distribution strengthens climate modelling by detailing environmental conditions where a species currently occurs or not. The results of this study demonstrate that models built using focal region observations may misrepresent the distribution of a species and thus bias projections onto novel environments such as that of a changing climate. This knowledge will be important for future studies producing these kinds of models, regardless of species or regional focus, as model accuracy becomes increasingly important and greater reliance is placed on techniques like SDMs to predict and inform mitigation of diversity losses due to global climate change.

Determining where species are, and why, is an important first step towards understanding how bat biodiversity in the Wet Tropics will be affected by global climate change. This study represents the first broad characterisation of the distributions of all bats species known, or predicted, to inhabit the Wet Tropics. This study is also the first to characterise bat species richness in the region in detail through the use of species' distribution modelling. This will allow finer scale conservation efforts in the near term, but also, importantly, provides the basis for projecting species' distributions onto future climate scenarios.

Chapter 4 of this this thesis, '*Winners and losers: the expansion and contraction of Wet Tropics bat species' distributions with climate change*' provides an in-depth look at how the region's biodiversity will respond to different predicted future climate change scenarios. It also provides an indication of how each of the bat species inhabiting the Wet Tropics will be impacted, and what changes we might see to species distribution.

This study builds on previous studies conducted in the region, and the chapters reported on above, to determine how Wet Tropics bat species, and bat diversity as a whole, will be affected by climate change. Not surprisingly, different species are predicted to react to future climate change in various ways (potentially contracting or expanding their range, or experiencing no change at all). Modelling of potential future distributions of individual species indicates that future climatic conditions may become more suitable for almost half of the species of bat in the Wet Tropics. This result was unanticipated and more species were expected to contract their distributions or become locally extinct based on the results of previous similar studies (on other taxa including birds, non-volant mammals, amphibians, and species of invertebrate) conducted in the region (Shoo et al., 2005; Issac, 2008; Welbergen et al., 2011; Staunton et al., 2014). However, for a large proportion of species conditions are modelled to worsen and distribution is predicted to contract. For example, At least 74% of Wet Tropics bird species are predicted to be threatened by mid-range climate warming with some 30 species likely to become critically endangered, particular those already confined to upland areas (Shoo et al., 2005; Anderson, 2011). In some cases, range contractions are considerable, placing the species close to local extinction. This is already being demonstrated with increasing temperatures already attributed to reductions in microhylid frog distributions in the region (Shoo & Williams, 2004). Persistence of these species into the future is predicted to be restricted to mountaintops (Shoo & Williams, 2004). A closer look at species turnover indicates a many species 'expand' into the Atherton upland region, with the majority of species 'contracting' out of the lowland areas to the north and south of the region. Indeed, the Atherton Uplands have been predicted to become important refuge for regional biodiversity under future climate change scenarios (Reside et al., 2013). For biodiversity in the region as a whole, 'worst case scenario' modelling (RCP8.5), which corresponds with the future we are currently tracking, indicates high diversity loss in the lowland coastal areas throughout the region. This models show areas of high diversity persisting only in the high elevation mountainous areas.

In the face of global climate change, effective conservation of species will depend on adequate knowledge of species to be conserved. Knowledge of echolocating bats in general is limited, but information regarding individual species distributions and the mechanisms driving them is poor. This thesis contributes to filling this knowledge gap. The chapters presented within represent the first detailed description of the richness and assemblage patterns of echolocating bats in the focal, tropical, region. This thesis also represents the first predictions of the impact climate change will have on bat biodiversity in the Wet Tropics. It provides an in-depth look at how the region's biodiversity will respond to different predicted future climate change scenarios. It also provides an indication of how each of the bat species inhabiting the Wet Tropics will be impacted, and what changes we might see to species distribution. Importantly, this study adds crucial information to ongoing studies regarding the impacts of climate change, both in the study region and globally, helping to strength such work and increasing success of climate change mitigation and species conservation efforts. Modelling indicates that lower emissions could result in a lower amount of biodiversity loss. Therefore, swift action to reduce global emissions, and targeted refugia conservation in the region, may mitigate some of the predicted biodiversity loss.

International context

The research presented within this thesis does not wholly reach consensus with any one study but rather supports aspects of some studies while disputing others. For example, a study conducted in South Africa also surveyed bats along a mountain gradient (Linden *et al.*, 2014). Conversely to this research they found a clear relationship between species richness and elevation with diversity decreasing with increasing altitude. Linden and colleagues also found no relationship between elevation and community composition, as was in this Wet Tropics study, suggesting that changes in diversity are likely correlated with other factors like climate or vegetation type rather than elevation itself, (Linden *et al.*, 2014). They recommended that as species richness was found to decrease with increasing elevation conservation efforts should not ignore these lower altitudes. In the Wet Tropics, however, modelling of the potential effects of climate change on bat diversity showed that bat diversity contracts away from lowland areas indicating that conversation efforts should be focused on areas of higher elevation. The results of this study may differ from that of Linden *et al* due to the differences in the elevational gradient sampled; this study samples truly low-elevation areas (from 100m a.s.l) while the South African elevational gradient spans 900m to 1800m a.s.l. (Linden *et al.*, 2014). Conservation recommendations could be refined and 'future proofed' in this South African region through the production of future climate models, as presented in this study.

The impacts of climate change on 28 European bat species was investigated by Rebelo, Tarroso and Jones (Rebelo *et al.,* 2010). Using presence-only modelling techniques similar to those used in this study, they found that future climate change would cause rapid shifts northward coupled with reductions to species' ranges and a general decline in bat presence across Europe. Species inhabiting colder, more northern areas were particularly vulnerable to climate change with local extinctions predicted to be likely by the end of the century (Rebelo *et al.,* 2010). A study c onducted in China has demonstrated that climate change has already begun to impact bat species' distributions. Using long-term survey records for 17 species, Wu determined that distribution have been shifting northward over the last 50 years, likely due to temperature increases attributed to climate change (Wu, 2015). Species that exhibited northward range shifts were found to be insectivorous species typical of tropical and subtropical rainforest (Wu, 2015).

Studies looking at the potential impacts of climate change on bats and their distributions are currently limited for tropical regions. A review on the impacts of climate change on bats generally indicates that bats inhabiting tropical areas are affected by temperature changes and are likely to be most at risk from extreme weather events and rising temperatures that climate change will bring about (Sherwin *et al.,* 2013). This study lends evidence to this hypothesis by detailing potential species range contractions with future climate change and highlighting areas of potential high conservation value for protection in the future. Similar studies are urgently needed for other tropical regions in order to better protect and conserve the world's diversity hotspots.

Additional findings and future directions

During the course of this research other notable results were recorded, although in many cases the expansion of these was outside the scope of this study. These additional results therefor represent areas that may provide future study opportunities, or which require study in greater detail than what was possible during this research.

As reported, research into elevational trends in the distribution of Wet Tropics bat species (presented in Chapter 2) indicated there was no effect of elevation on observed bat richness. This chapter discussed the possibility that this result was due to richness potentially being too coarse a measure of diversity to garner an accurate result. It was discussed that richness, as expressed by a simple count, may fail to address changes in species identities across sites thus providing little insight in how individual species occurrences might change across gradients.

Thus, further analysis incorporated consideration of individual species identities and was able to reveal significant relationships between community-level patterns in species' probability of occurrence. This analysis determined that the probability of species occurrence is driven by temperature seasonality, with precipitation and subregion variables also being influential. Chapter 3 expanded on the above results by producing SDM's for individual species. These models incorporated more information from the region but again highlighted that species' distributions are primarily driven by precipitation, or water availability.

The results of Chapter 2 also suggest that site specific factors, such as physical habitat suitability, forest structure, and roost or prey availability, within and across subregions, may be important for determining species' distributions. With the impending threat of climate change, greater understanding of the links between species' distributions, richness and assemblage, and the environmental factors driving them in particular study regions, is crucial to predicting responses of species and ecological communities to climate change. Further, more detailed study could include aspects of microclimate (roosts, etc.), species physiological tolerances and/or genetic variability, and species interactions and completion, including with prey. All of this information would help further refine our knowledge on bat diversity and responses to climate change.

Research presented in Chapter 2 also commented that traditional bat surveying techniques, specifically the use of trapping and/or echolocation monitoring only, may be appropriate for local studies, or studies targeting specific species. However, it was determined that such methods used in isolation may have limited application for determining species whole-range distributions. It was found that richness detected during in-field surveys using acoustic echolocation detection methods did not detect nearly the species diversity predicted to be in the area by the SDMs (Chapter 3). Given that SDMs are based on actual occurrence records, all be it in large numbers, and across more wide spread geographical area than the study sites, there is no reason to assume that the predicted richness is inflated. The bias in the type of habitat surveyed is acknowledged with field surveys conducted in Chapter 2 being focused on those species utilising rainforest habitats, while SDMs presented in Chapter 3 were based on species occurrence records collected from the entire region. Notwithstanding, this study suggests that traditional bat surveying methods may provide excellent small scale knowledge about species in their local habitats, or about the ecology of a species in general. However, results suggest that for studies wishing to investigate species biodiversity across a large geographic range, and into the future under various conditions, it is important to use all information available (global information). Local information alone may not be enough to determine widespread trends or predict future responses. However, further study is required into the limitation of using traditional bat surveying methods only before this conclusion can be confirmed.

Finally, both appendices included in this thesis provide opportunity to extend the work of this thesis. Appendix 1 was originally intended to be a stand-alone chapter. However, technical issues meant that the results of this experiment were more limited than planned. Repeating this experiment with a more powerful, measurable, ultrasonic pulse source could provide more accurate data. This would help to statistically confirm observed trends discussed within Appendix 1. Confirming these trends would allow for calibration and qualification of studies of echolocating bats in tropical rainforest environments such as the Australia Wet Tropics World Heritage Area.

Appendix 2 provides the first description of a bat community along a single elevational gradient in Papua New Guinea. A similar number of species were positively identified from the Huon Peninsula gradient (11 species) as in the Wet Tropics (10 species) during initial surveys (Chapter 2). However, during the Wet Tropics surveys an additional five potentially unique species, which could not be identified fully, were also recorded while in Papua New Guinea another 11 potentially unique species were detected. This indicates that the Huon Peninsula gradient is likely to have a much greater overall species diversity than present in the Wet Tropics. The preliminary results of surveys conducted in Papua New Guinea indicate that there is a correlation between species richness and elevation with richness peaking at low elevations. No such correlation was found in the Wet Tropics. Expanding the preliminary work conducted in Papua New Guinea, in a similar vain to Chapters 2, 3, and 4 would greatly add to the results of both the Wet Tropics and the Papua New Guinea studies. Replicating the Huon Peninsula surveys along other elevational gradients in Papua New Guinea and analysing this data as in Chapter 2-4 of this thesis would allow for species' distributions trends and movements as a result of climate change to be modelled across Australasian rainforests. This may provide additional information on general distribution trends but also more specifically how species may shift their latitudinal distributions with climate change, and how communities may change with the potential influx of species from other latitudes and regions. Indeed, a recent study predicted, that with climate change, Papua New Guinea will become one of the most extensive remaining forests systems (Underwood *et al.*, 2014). This suggests that preserving biodiversity in this region, particular Australasian specific diversity that may be displaced from or move to northern Australia, will become increasingly important.

Mitigating biodiversity loss in the face of a changing climate

Climate change is perhaps the greatest environmental and ecological disaster of our time. A continuing increase of CO_2 emissions in the atmosphere since pre-industrial times has put the world on a path to extreme global change. This 'Anthropocene' age will be characterised by rising sea levels and temperatures, unpredictable rainfall, and an increase in extreme events such as severe storms or devastating wild fires all of which significantly threaten the earth's biodiversity (Steffen *et al.*, 2011). Indeed, we are now predicted to be entering the earth's sixth period of mass biodiversity extinctions (Barnosky *et al.*, 2011). The IPCC 5th assessment report (see thesis introduction) makes it very clear that continued emissions of GHG, at the levels they are currently being emitted, will cause further warming increasing the negative effects on the earth (IPCC, 2013). A 'tipping point' will soon be reached where these impacts are deleterious and irreversible.

As reported in Chapter 4 of this thesis, multiple RCP scenarios were used in this research to predict the impacts of climate change on these species, as well as how climate change mitigation efforts may alter this future reality. The RCP8.5 scenario modelled in this research is presented by the IPCC as the 'worst case future' scenario. This climate change scenario most closely represents the current global emissions trajectory. No higher scenario than RCP8.5 has been devised as the effects of radiative forcing higher than that represented in RCP8.5 would be catastrophic, and possibly unimaginable (IPCC, 2013). Therefore, it is of critical importance that the world heads warnings provided by the scientific community and begins to implement effective mitigation strategies. Species adaptation to new environmental conditions will only be possible to a limited degree if RCP8.5 is actually realised.

Understanding what drives species' distributions is an important first step in mitigating biodiversity loss. Many studies have documented the effects of climate change on species' distributions and richness for a large variety of flora and fauna. Generally, these changes are recorded as being 'upward' or 'poleward' with species moving higher in elevation or latitudinal ranges in order to find more suitable conditions. This study adds to that literature and represents the first predictions of the impact global climate change will have on bat biodiversity in the Wet Tropics. This study provides an in-depth look at how the region's biodiversity will respond to different predicted future climate change scenarios.

With future climate change, different species will be affected in different ways, with conditions becoming more suitable for some while considerably less suitable for others. In general, 46% (14 species) of the models (both RCP4.5 and RCP8.5) indicated expansions in the amount of suitable climatic niche and thus species' distributions. However, species turnover maps indicate that the most climatically suitable areas will be concentrated in mid to high elevation areas located predominantly through the centre of the region. With diversity predicted to concentrate in these limited, mountainous areas, other factors not taken into consideration in this study (such as competition, adaptation potential, etc.) may affect species' distribution and persistence more so than environmental suitability alone. For example, species already restricted to high elevation, mountainous areas will be unable to move to higher elevations to further track preferred environmental conditions potentially resulting in local or regional extinction in a worst-case scenario. Similarly, increased intraspecific and interspecific competition for limited food sources or roosting sites could result in an reduction in fitness or breeding ability resulting in limited adaptation potential (Bellard *et al.*, 2012). Support for this hypothesis is indicated when models of the region's species richness as a whole are taken into consideration. Species richness is modelled to become steadily less suitable under scenario RCP4.5, however, no mass loss of species was evident from areas that don't already have low species richness. Biodiversity modelling under lower-emissions scenario RCP4.5 still indicates biodiversity loss, but to a lesser degree and occurring more slowly. However, when richness is modelled using 'worst case scenario' RCP8.5, conditions for biodiversity are seen to worsen in the long term, with areas of high biodiversity persisting in isolated, mountainous areas of the Wet Tropics only.

This study adds crucial information to ongoing research on the impacts of climate change, helping to strengthen such work and potentially increasing the success of any conservation efforts. By determining where species currently exist, and predicting how they are likely to be impacted by climate change, scientists and conservation managers alike are armed with the basic information needed to help preserve some of world's biodiversity. By developing future species distributions models we can help demonstrate that all is not lost; through reducing emissions and slowing the rate of warming some of these losses can be avoided. Timely implementation of dramatic and effective mitigation measures may halt or reduce biodiversity loss allowing more time to effectively manage species and refugia areas. Only rapid and substantial action will ensure biodiversity as a whole can be spared the effects of anthropogenic climate change. It is not too late to act in order to save our biodiversity.

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Appendix 1: Distance of acoustic detection of ultrasonic sound in tropical rainforests

Abstract

Detection of echolocating bats via acoustic monitoring is a commonly used technique in studies exploring the ecology of such species. However, our understanding of the manner in which echolocation calls travel through different habitats is limited. This study, conducted at the Daintree Rainforest Observatory in Northern Australia, sought to investigate the way ultrasonic echolocation pulses, similar to those emitted by bats during navigation and foraging, travelled through the rainforest canopy. How far pulses travel, and how well different pulse types (Constant frequency (CF), Frequency modulated (FM)) can be detected were measured from varying positions within the rainforest canopy. A vertical array of six bat detector units were erected at heights of 0m, 4m, 10m, 20m, 30m, and 40m from the ground. An artificial ultrasonic source (chirp board, or 'electronic bat') was used to emit constant frequency and frequency modulated pulses from varying heights within and above the canopy. Bat calls occurring naturally within the canopy were also recorded. Equipment issues during the study resulted in a severely limited sample size being obtained. Due to this small sample size statistical analysis was limited and no statistically significant results were found. However, some congruence was noted between results of graphical models and best-fit statistical modelling and naturally occurring calls and prior expectations based on the literature. Simulated ultrasonic pulses were found to weaken quickly with increasing distance between the source and detector, with pulses generally not traveling more than 15m in distance. Simulated ultrasonic pulses were found to travel further above and below the canopy, while detectability was reduced to almost zero within the canopy itself. Constant frequency (CF) type pulses appear to have a slightly better probability of detection below the canopy than FM type pulses. These results were consistent with trends found in naturally occurring bat calls. Calls of two dominant species (*Rhinolophus megaphyllus* (CF) and *Miniopterus australis* (FM)) showed greatest detection above and below the canopy with few calls being detected within the canopy itself. Calls of the CF species (e.g. *R. megaphyllus)* were more often detected below the canopy than calls of the FM species. The results of this study suggest a negative association between probability of detection, distance and vegetative clutter. This study, taking into consideration its currently limited form, could provide the basis of future work highlighting the importance of tailoring detection techniques for the sample habitat to ensure appropriate survey designs are implemented.

Introduction

Acoustic monitoring is often the most effective technique for surveying animal populations, especially those with loud, species specific calls like birds or frogs (Shoo & Williams, 2004; Williams *et al.*, 2010a; Adams *et al.*, 2012). Acoustic surveying techniques have been particularly invaluable to ornithologists conducting bird surveys in forested environments where the cryptic nature of many birds, coupled with the difficulty of seeing birds easily, present challenges for accurate surveys (Anderson *et al.*, 2011). The high mobility of birds may also present difficulties for visual surveys. Therefore, it is often best to use a combination of both acoustic and visual surveys to get the most accurate sample (Anderson *et al.*, 2011). Bats are similar to birds in that that are highly mobile, often highly cryptic species. Bats are nocturnal and are difficult to identify to species when sighted in the environment. Therefore, in order to study bat populations, other methods, such as acoustic monitoring, need to be employed. Before beginning such a study it is crucial to have some understanding of how sound travels through the study ecosystem in order to accurately relate acoustic monitoring data to animal populations or behaviours.

Acoustic monitoring is an increasingly common technique used for monitoring populations of echolocating bas. Such species have the ability to produce ultrasonic echolocation calls as they navigate and forage through their environment. Often, call characteristics are species specific, making acoustic monitoring a viable option for conducting surveys (de Oliveira, 1998). Broadly, there are two main echolocation call types, along a continuum of call types, that species can emit: constant frequency (CF) or frequency modulated (FM) type calls (Fenton, 2003). Frequency modulated type calls consist of a series of pulses, with each pulse ‘sweeping’ through several different frequencies. Each pulse is generally of a short duration and present different shape and frequency characteristics depending on the species. In comparison, constant frequency type calls are flat calls of generally one frequency with a longer duration than FM calls (Fenton, 2003). In most cases, each species has a distinct call shape and call frequency allowing different species to be identified. However, monitoring of bat populations through acoustics does present some challenges. As echolocation calls exist primarily within the ultrasound, monitoring cannot be conducted aurally but must be done using specialised equipment.

Multiple studies have been conducted comparing the accuracy of different models of ultrasonic detector (e.g. (Fenton *et al.*, 2001; Skowronski & Fenton, 2009; Adams *et al.*, 2012). AnaBat (Titley Scientific, Ballina, Australia) is a commonly used system for acoustic monitoring in bats studies, particularly in Australia. There has been some debate about the capabilities of AnaBat, mostly with regard to its zero-crossing rather than full spectrum analysis, which only provides a measure of the dominant harmonic of the call (Fenton, 2000; Corben & Fellers, 2001; Adams *et al.*, 2012). This means that information about species specific call harmonics is not available (Skowronski & Fenton, 2009). In some environments, or for studies targeting specific species where harmonics are important for detection, this is a real problem. However, AnaBat capabilities and unique features, which include its ability to detect a much greater range of frequencies than other available detectors, are well suited to non-targeted monitoring of bat communities. However, to be confident that AnaBat is a useful tool for certain studies, it must first be calibrated, and general assumptions must be recognised (Hayes, 2000; Adams *et al.*, 2012). This includes calibration of individual units to ensure detection settings such as sensitivity are consistent across detectors. This helps to ensure that each unit has the same chance of detecting an animal as another (Larson & Hayes, 2000). Appropriate detector calibration for efficient monitoring studies should also include some kind of calibration for the study environment.

In order to conduct an efficient monitoring study, some knowledge of what species are likely to be detected within the environment, and how calls will actually be detected within that habitat, should first be obtained. This crucial part of setting up a monitoring study is often neglected. Few studies have looked at detector calibration in terms of calibration between differing habitats (Weller & Zabel, 2002; Patriquin *et al.*, 2003; Fischer *et al.*, 2009). Elegant experiments conducted by Holderied and colleagues (2005, 2006) linked flight behaviour with origin and intensity of echolocation calls of bats flying through a gorge. By using an array of acoustic detectors, the authors were able to calculate the range, or traveling distance, of echolocation calls (Holderied *et al.*, 2005). Another study investigated the echolocation behaviour of bats flying along a hedgerow, through an experiment involving an array of detectors and a 3D laser scan of the hedgerow environment (Holderied *et al.*, 2006). The study put forward evidence for ‘acoustic focusing’ of bats as they move through their environment, involving adjustment of their call design and duration to focus in on nearby obstacles. The effect of clutter, foliation, habitat structure, and environmental conditions on detection of echolocation calls has also been considered (Griffin, 1971; Barclay *et al.*, 1999; Broders *et al.*, 2004). These studies generally analyse differences in detectability using naturally occurring bat calls, meaning results could potentially be biased by natural variation in the way individual calls are detected.

This study sought to investigate the way that simulated ultrasonic pulses travel through a rainforest environment. Whether different types of echolocation calls travel through the habitat differently, and how this relates to naturally occurring calls, was also investigated. This study utilised AnaBat as a means of detection, with the aim of allowing us to assess common (but rarely tested) assumptions about the effectiveness of the AnaBat system for detecting bats in cluttered habitats such as rainforest. Unfortunate equipment issues during the study resulted in a severely limited sample size being obtained. However, some congruence was noted between results of graphical models and best-fit statistical modelling and naturally occurring calls and prior expectations based on the literature. Therefore, despite the lack of statistical significance, trends observed during this study are presented herein, although conclusions must be interpreted with the lack of statistical significance in mind.

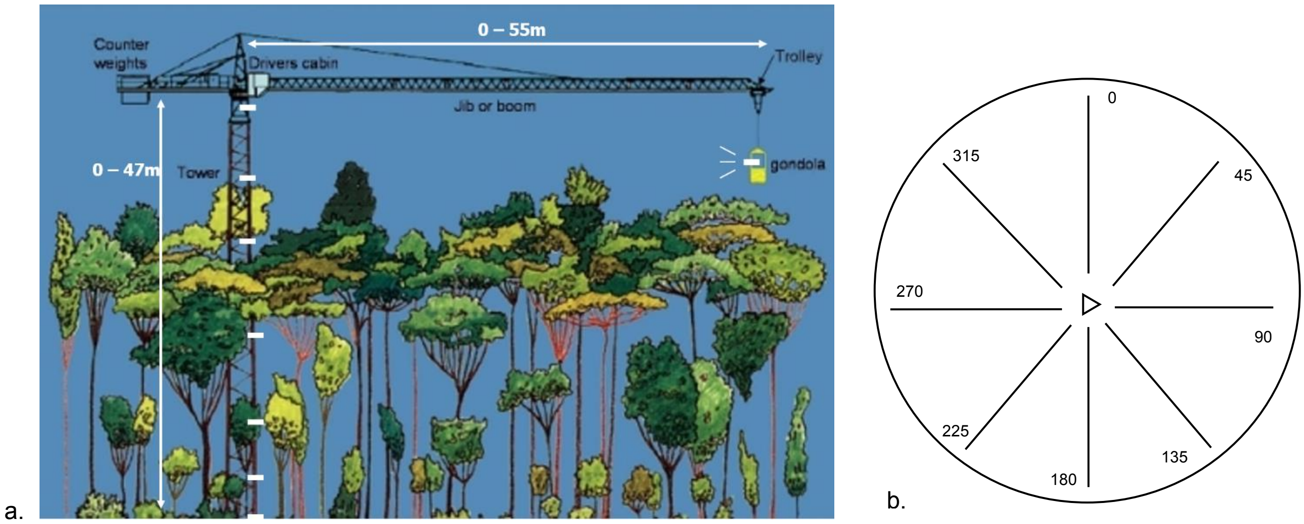
Methods

Study site

The study was conducted at the Daintree Rainforest Observatory (DRO) research facility, located in the Wet Tropics World Heritage Area, far north Queensland (16°06'S, 145°26'E). The research facility sits on 20 hectares of lowland tropical rainforest (40m above sea level). The vegetation of the area is dominated by complex mesophyll vine forest, with the area under the cranes' arc being characterised as having an irregular canopy with an indistinct subcanopy (here 'canopy' is referred to as the section of forest containing the majority of tree crowns, primarily located between 5 and 15 meters above forest floor). The forest structure of this site is not atypical of that found throughout lowland Wet Tropics. The experiment was conducted using a Liebherr 91EC Tower crane (45m tall with a 55m jib) which services approximately a 1 hectare rainforest plot. Access to the canopy is via a gondola suspended from the jib, allowing 3D access to the forest plot.

Experimental design

An ultrasonic testing grid, within the rainforest canopy, was created. A single vertical array of ultrasonic detectors, designed to detect echolocation calls of bats, was placed on the crane tower at standardised heights: 0m (ground), 4m, 10m, 20m, 30m, and 40m above the ground (Figure 1a). In this experiment, AnaBat SD1 CF bat detector units (Titley Electronics, Ballina, Australia) were used to detect ultrasonic calls. An electronic chirp board (Titley Electronics) was used to simulate echolocation calls within the canopy. Two types of ultrasonic signals were emitted, one a constant frequency (CF) 40 kHz pulse, similar to calls of Rhinolophidae and Hipposideridae species. The other a frequency modulated pulse (FM) which swept in range from approximately 40 to 80 kHz. This frequency modulated signal emulated calls similar to the majority of species likely to be detected in the Wet Tropics (Crome & Richards, 1988; Churchill, 1998).



Appendix 1, Figure 1a Configuration of the vertical and horizontal distances of the DRO canopy crane plot (forest picture taken from the DRO website (not to scale) www.jcu.edu.au/canopycrane); Figure 1b Degrees of the cranes circumference surveyed.

The experiment commenced at dusk, allowing pulse detection to occur under conditions similar to naturally occurring calls. Pulses were emitted from up to 48 points within the 3D forest plot, where access via the crane’s gondola was possible. Sound emittance was orientated towards the microphone of the detectors. Points were chosen at random and represented an intersection of one vertical height (0m, 4m, 10m, 20m, 30m, 40m) and a horizontal distance from the crane tower (5m, 10m, 15m, 20m, 25m, 30m, 35m, 40m) (Figure 1a). Each of the two types of pulses were emitted for one minute at each of the 48 points. Type of pulse, time of emittance, and the vertical and horizontal point was recorded. At each point, a measure of distance between the pulse source and the nearest vegetative obstacle was taken using a laser range finder, and a measure of relative density of that obstacle was approximated. A measure of forest clutter was taken from the Daintree Rainforest Observatory database on tree height, position and diameter at breast height (DBH). This measure was taken to include all obstacles in-between the source and the detector, at each vertical height, including tree height and approximate crown size.

The experiment was repeated over eight nights on various degrees of the crane's circumference: 0°, 45°, 90° 180°, 135°, 225°, 270° and 315° (Figure 1b). Each night's radius was chosen at random to account for any vegetative or environmental bias. In addition to the ultrasound experiment, detectors were left in place for the remainder of each night (until dawn) and set to record naturally occurring bat calls within the 3D forest plot.

Analysis

Resulting AnaBat files were analysed to determine whether pulses were detected (AnalookW version 0.3.7.23, Corben, 2009). Recording times of detected pulses were compared with original emittance times. For each intersecting horizontal and vertical point a score of either 1, for calls that were detected, or 0 for calls not detected, was recorded. Based on these scores, probability of detection at each vertical and horizontal distance was then calculated. Exact confidence limits were also calculated using an iterative method adapted from Thompson 2006 (cited in Jones *et al* 2011). Naturally occurring bat calls were analysed using AnalookW and identified to species, where possible, by comparison of sonogram against recorded release calls from known species, and with the aid of previously published call libraries (Crome & Richards, 1988; Reinhold *et al.*, 2001; Milne, 2002; Pennay *et al.*, 2004; Inkster, 2008; Robson *et al.*, 2012). Calls of the dominate FM and CF emitting bats were further analysed for trends in vertical stratification and foraging habits.

Generalised Linear Mixed Models (GLMMs) were used to investigate the relationship between detectability of the simulated ultrasound and environmental variables (R Development Core Team, 2011, www.r-project.org). CF and FM pulses were modelled separately. First, variables were assessed for collinearity. Spearman rank pairwise correlation matrices were produced and examined, with correlations between variables of greater than ±0.5 being eliminated (Booth *et al*. 1994). Variance inflation factors (VIF's) of the remaining variables were computed to determine the extent of any remaining correlation. Variables with a VIF of above 1.5 were also eliminated (Booth *et al.*, 1994).

Remaining variables were then added to the GLMM and fit by the Laplace approximation using the glmer function in R package lme4 (version 0.999375-42, Bates *et al.*, 2015). The variable 'date' was specified as a random factor in order to account for any nightly variation in the environment. Best-fit models were selected using Akaike Information Criterion (AIC) calculated through the MuMIn package in R (version 1.7.2, Barton, 2012). MuMIn performs automated model selection through repeated analysis of random combinations of variables specified within the global model. The best supported model was represented by the lowest AICc value. Akaike weights were also calculated to determine the probability of each model having the best fit, through identification of the 95% confidence set of models (Zuur, 2009). Akaike weights (*wi*) were produced, with values above 0.5 considered good (Ritchie *et al.*, 2009). Best-fit models were then analysed (using the glmer function) and importance of each variable and its significance was calculated (z and Pr(>|z|) values are reported). Filled contour plots (S-Plus) were used to visualise the relationship between probability of detection and the vertical and horizontal points, as well as vegetation density measures. Finally, differences between naturally occurring calls of two dominant species, representing each of the two pulse types, were analysed using Fisher's exact test of independence (R Development Core Team, 2011, www.r-project.org).

Results

Analysis

A total of 332 points, of a possible 384 (6 vertical x 8 horizontal points x 8 radiuses) were accessible within the canopy. Other proposed points were found to be obstructed and unreachable. Due to much lower than anticipated signal strength, analysis of emitted pulses was capped at 20 horizontal metres from the detectors, as pulses were never detected beyond this. Thus, the number of test points was reduced to 148 of which only 17 points produced detectable pulses. Graphical and statistical analysis was carried out, however, the very small sample size resulting from the experiment greatly reduced the impact of these analyses and returned large standard errors of some model variables.

Model environment

CF (40kHz) pulse

The probability of the detection of a CF ultrasonic pulse was indicated by the (statistically non-significant) model to be potentially influenced by the distance between the source and the detector. Detected calls were only detected at the height that they were emitted at. When preparing the variables for entry into the model, high levels of collinearity were found between the estimate of density of closest obstacle (DeNO) and distance to nearest obstacle (DiNO). As a result, DeNO was removed from further analysis. Remaining variables entered into the model included horizontal distance of the pulse source (SH) vertical height of the pulse source (SV), distance to nearest obstacle from the source (DiNO) and date of the experiment (specified as a random factor to account for nightly environmental factors such as temperature or precipitation). The best supported model predicting detectability of CF (40kHz) pulses (although statistically non-significant) included only horizontal distance of the pulse source (SH) (AICc = 54.66) (Table 1.). Two other models were supported (candidate set contained models within 2 ΔAICc of the best model, although again statistically non-significant) however these models were all nested within the top model (Table 1). The results are consistent with a negative correlation between probability of detection of a CF ultrasonic pulse and distance between the source and the detector (*r* = -3.81) (Table 1), however, as stated, all variables were found to be non-significant (Pr(>|z|) = >0.05) (Table 2).

Appendix 1, Table 1 Best supported models, using Akaike's information criteria, for probability of detection of CF pulse. The best supported model contained only SH (distance variable), with all similarly suitable models being nested within the first.

Model	Integer	SH	SV	DiNO	df	logLik	AICc	delta	weight
1	18.55	-3.81			3	-24.24	54.66	0	0.50
2	19.3	-4.05	0.02		4	-23.92	56.13	1.47	0.24
3	18.46	-3.79		-0.07	4	-24.24	56.77	2.11	0.17

Appendix 1, Table 2 Significance values (Z and Pr(>|z|) for all model supported variables for probability of detection of CF pulse. All models, and variables within, are non-significant (*P* = >0.05).

Model term	Estimate	Std. Error	Z value	Pr(>|z|)
Model 1 SH	-3.80	410.18	-0.01	0.99
Model 2 SH	-4.04	689.62	-0.01	0.99
SV	0.02	0.02	0.84	0.40
Model 3 SH	-3.79	433.90	-0.01	0.99
DiNO	-0.07	1489.63	0.00	1.00

FM pulse

The probability that a FM ultrasonic pulse will be detected was indicated to be potentially influenced by the distance between the source and the detector. Detected calls were only ever detected at the height that they were emitted at. Again, when tested, high levels of collinearity were found between the estimate of density of the closest obstacle (DeNO) and distance to nearest obstacle (DiNO) and therefore DeNO was removed from further analysis. Remaining variables included horizontal distance of the pulse source (SH), vertical height of the pulse source (SV), distance to nearest obstacle from the source (DiNO), and date of the experiment (specified as a random factor). These were entered into the model. The best supported model (statistically non-significant) predicting detectability of FM pulses included horizontal distance of the pulse source (SH) and distance to nearest obstacle (DiNO) (AICc = 64.18) (Table 3). One other model was supported (candidate set contained models within 2 ΔAICc of the best model, although again statistically non-significant) however this model was nested within the top model (Table 3). The results are consistent with a negative correlation between probability of detection of a FM ultrasonic pulse and distance between the source and the detector (*r* = - 18.31) (Table 3); however, as stated, all variables were found to be non-significant (Pr(>|z|) = >0.05) (Table 2).

Appendix 1, Table 3 Best supported models, using Akaike's Information Criterion, for probability of detection of FM pulse. The best supported model contained variables SH (distance variable) and DiNo (vegetation measure), with a similarly suitable model, nested within the first, also being recognised.

Model	Intercept	DiNo	SH	SV	df	logLik	AICc	delta	weight
1	91.04	15.18	-18.31		4	-27.95	64.18	0.00	0.58
2	91.59	15.36	-18.49	0.02	5	-27.71	65.85	1.67	0.25

Appendix 1, Table 4 Significance values (Z and Pr(>|z|) for all model supported variables for probability of detection of FM pulse. All models, and variables within, are non-significant (*P* = >0.05).

Model term	Estimate	Std. Error	Z value	Pr(>|z|)
Model 1 DiNO	-18.31	7034.41	0.00	0.99
SH	15.18	5862.01	0.00	0.99
Model 2 DiNo	15.36	5865.00	0.00	0.99
SH	-18.49	7039.00	0.00	0.99
SV	0.02	0.02	0.72	0.47

Probability of detection

Results of the graphical density plots are consistent with the best supported model for each pulse type. The density plots indicate that both types of ultrasonic pulse are detectable in similar ways. Both show intuitive patterns of detection with probability of detection being highest above and below the canopy (generally above 20 meters and below 5 meters in height), rather than within it (generally between 5 – 15 meters above forest floor), and declining with distance from the detector (Figure 2 and 3) (Annex 1, Table 1).

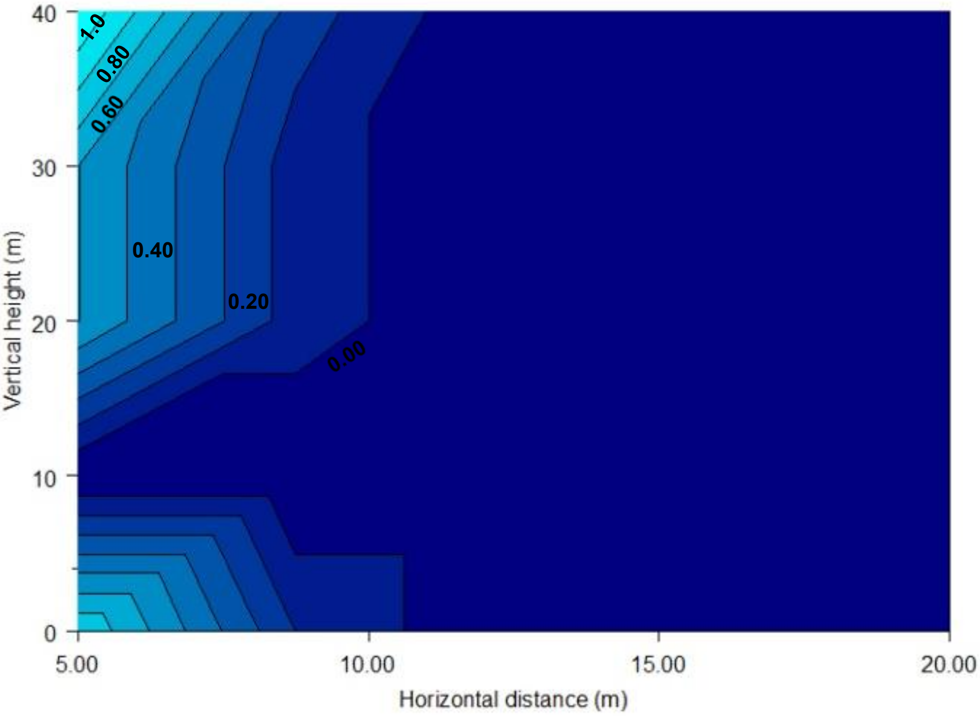
For both the CF and FM pulse types, probability of detection was greatest at around 4m in height (Figure 4) (Annex 1, Table 1). Detection was possible until around 10m in height, at which time detection was close to zero until approximately 15m in height (Figure 2 and 3). Probability of detection then gradually increased with height above the canopy (above 20 meters). Each of the pulse types exhibited slight differences in their detectability (Figure 2 and 3). FM pulses were detected across greater distances than CF 40hKz calls. In the case of FM chirps, detection was not recorded at greater than 13m from the detector, with detection of the CF 40kHz pulses ceasing after 10m. CF 40kHz pulses are detected equally as well above the canopy as below it, while the FM pulses exhibit slightly better detection above the canopy than below it, but with detection distances being shorter above the canopy.

Vegetation characteristics

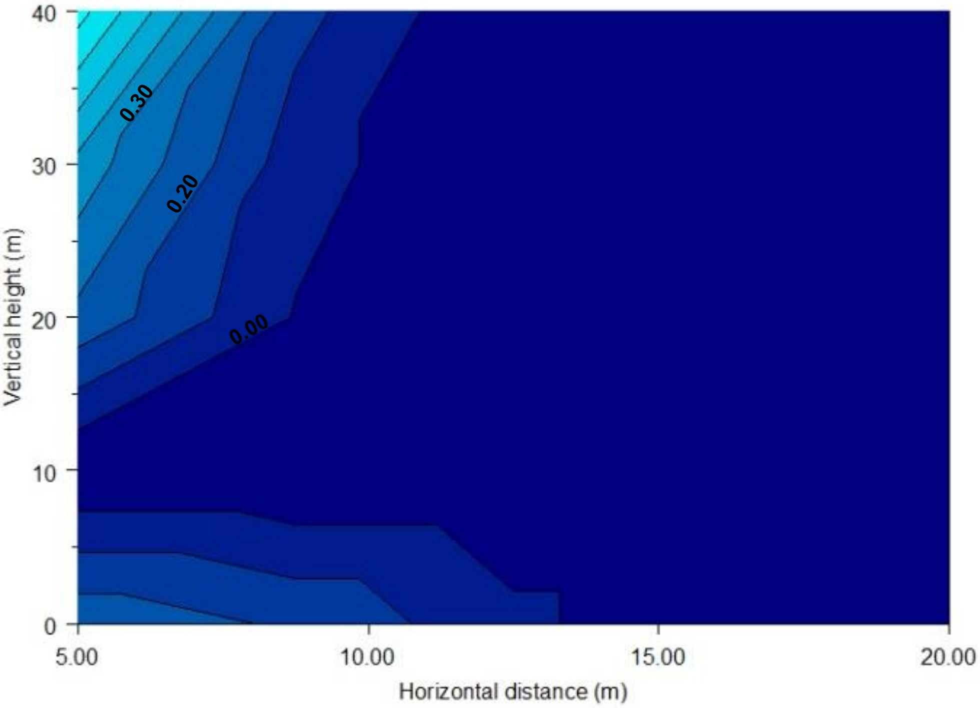
Vegetation density was greatest around 10m in height, with density increasing with distance from the crane tower (Figure 5). The majority of foliage was found to be below 15m in height, with only a few individual trees greater than 30m (Figure 5 and 6). The highest measured vertical point, 40m, was entirely above the canopy. This reflects trends in the probability of detection of the ultrasonic pulses (Figure 2 and 3).

Naturally occurring calls

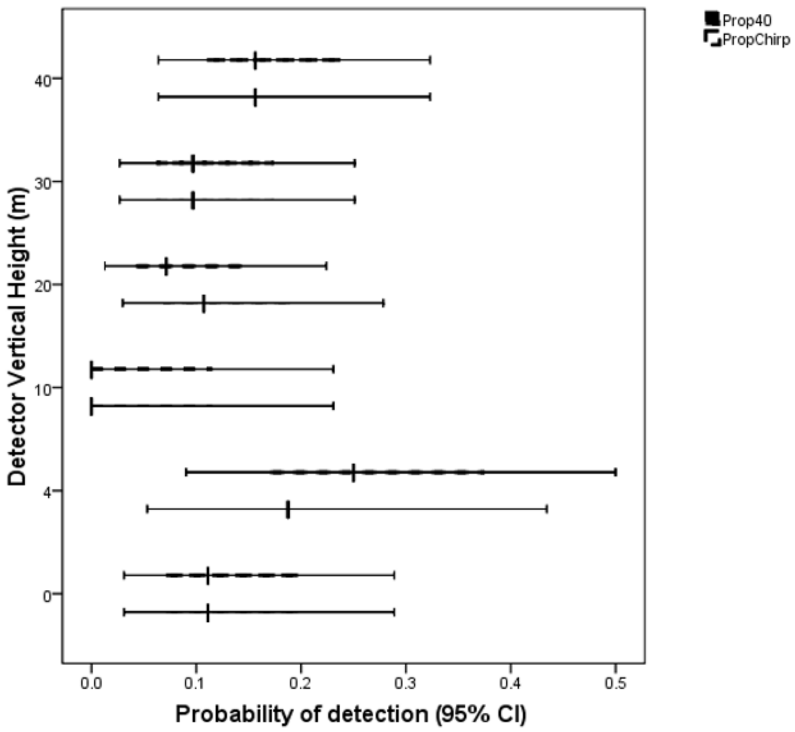
The height distributions of calls emitted by *Rhinolophus megaphyllus* (CF) and *Miniopterus australis* (FM) were found to differ significantly (when analysed using Fisher's exact = $p < 0.01$). The majority of *R. megaphyllus* calls were recorded on detectors located below the canopy (87% at 20m or less), with the majority (60%) being recorded by the detector placed at ground level (0m) (Figure 6). *Miniopterus australis* was recorded at all heights but 4m, with the majority of calls being recorded at detectors above the canopy (20 meters and above) (66%) (Figure 6).



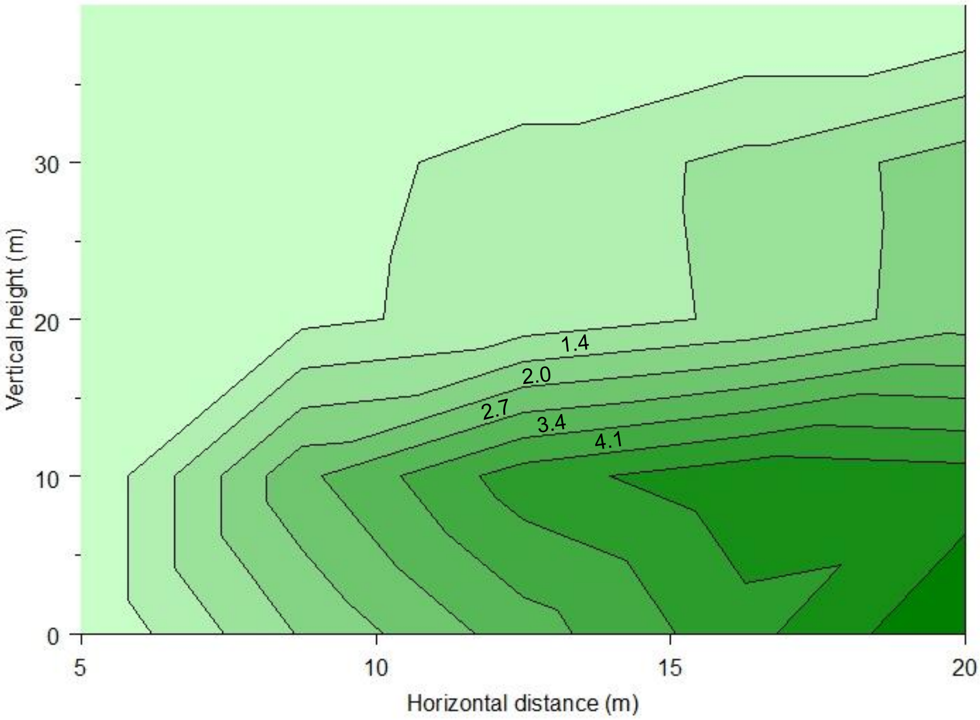
Appendix 1, Figure 2 Probability of detecting a 40kHz CF pulse at various heights and distances throughout the canopy.



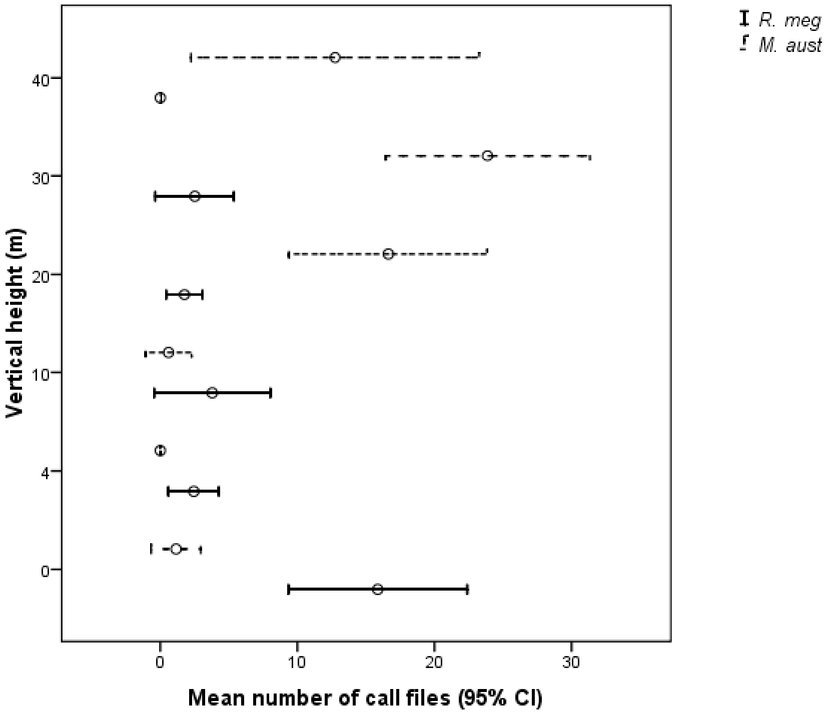
Appendix 1, Figure 3 Probability of detecting a FM pulse at various heights and distances throughout the canopy.



Appendix 1, Figure 4 Error bar plot showing mean probability of detection at each of the vertical heights, with 95% confidence intervals.



Appendix 1, Figure 5 Contour plot showing vegetation density at the DRO canopy crane plot, measured as the distance to the nearest obstacle. Vegetation density is highest around 10m in height.



Appendix 1, Figure 6 Mean number of calls (with 95% confidence intervals) detected for two dominant species *Rhinolophus megaphyllus* (CF) and *Miniopterus australis* (FM) at each of the test heights.

Discussion

Analysis

Probability of detection declined rapidly with increasing distance between the detector array and the source. Although the experiment was repeated in 5m increments over 40 horizontal meters, pulses were never detected beyond 15m from the detectors, with only 17 pulses being positively detected during the experiment. This resulted in a small sample size available for analysis and almost certainly contributed to the lack of significance of any of the best-fit models and variables. It is acknowledged that the limited sample size, and statistical non-significant of the best-fit modelling, means that substantial limitations exist in this study. However, best fit models and available data suggest interesting trends about the way ultrasound may travel through a rainforest environment. We discuss these trends further here but suggest our discussion be interpreted with caution and serve as the basis for potential future research.

As well as the limited detection distance, simulated artificial ultrasonic pulses were only ever detected at the same height as the source, suggesting that pulses are very concentrated and unidirectional. We could not compare the strength of the simulated ultrasonic pulse used in this experiment with that of any particular species of bat. However, as different bat species have calls varying in strength and intensity, we may assume that the intensity of the ultrasonic pulse is somewhere in the realm of naturally occurring calls.

Probability of detection

Best-fit modelling for each of the simulated pulse types (FM or CF pulse types) did not result in identifying a significant model or model variable. Although not statistically significant, the model did suggest that, unsurprisingly, probability of detection may be negatively correlated with distance between the source and the detector. The models suggest that both types of ultrasonic pulse are detectable in similar ways. Results of a graphical analysis of detection probabilities (Figure 2, 3, and 4) support the best-fit models. However, graphs indicate that FM chirps may be slightly better detected across greater distances than CF 40 kHz pulses, with an increase in detection probability above the canopy (above 20 meters). The suggested difference in detection of the two kinds of call types may be due to their physical structure. Frequency modulated type calls offer the bat a finer resolution of 'vision' as the intensity is spread out amongst multiple frequencies (Fenton, 1995). This may also mean that FM chirps may allow the call to be better detected by the AnaBat system, as there is a broader range of frequencies that could be detected, or more opportunity to detect part of the call. Previous studies have indicated that AnaBat may detect certain frequencies better than others, so having a wide frequency sweep may increase the probability of the call being detected (Adams *et al.*, 2012).

Graphical analysis of probability of detection shows the signal of the CF 40 kHz pulse appearing stronger initially, but probability of detection drops off quickly (Figure 2). As calls of this type are generally very limited in frequency band their signal is more concentrated and often more intense which would result in a greater probability of detection over short distances (Fenton, 1995). In this experiment, probability of detection of CF pulse was found to decline quickly with increasing distance, when graphed on a contour plot. It is likely that as there is only one frequency, once this frequency is disrupted the signal may be undetectable by AnaBat. A measure of vegetative clutter came out in the best-fit model as likely to have some influence on probability of detection. This is consistent with our contour plots (Figures 2, 3, and 5) which show probability of detection declined with increasing vegetative clutter. Although vegetative clutter was not a statistically significant variable in the best-fit models, its suggested influence on probability of detection more than likely reflect natural conditions. Also, species with CF type calls are more likely to forage within cluttered environments than their FM type call counterparts so their call would not be required to travel over much distance due to frequent obstacles presented by high amounts of clutter (Clague, 2004; Schnitzler & Kalko, 2005; Lacki *et al.,* 2007). This is supported by the recording of naturally occurring bat calls, discussed further below.

Vegetation characteristics

The best-fit model suggested that vegetative clutter may have some effect on probability of detection, although again, values were not statistically significant. Regardless, it was anticipated that clutter would have some effect on detectability (Patriquin *et al.*, 2003; Fischer *et al.*, 2009). This effect of clutter was observed when data was visualised using density contour plots. Probability of detection was found to rapidly decrease, to zero probability of detection, where the forest structure became its thickest. In the experimental forest plot, the canopy reached maximum thickness around 10m in height, where ultrasonic signals ceased to be detected (Appendix 1, Annex 1, Table 1.1). Contour plots show that probability of detection was greatest below the canopy (below 5 meters from ground lever), with only slightly better probability of detection above the canopy (above 20 meters) than within it (5 – 15 meters). The reduction in detection distance above the canopy could theoretically be explained by environmental variables, such as wind, having a greater effect on calls above the canopy than below it, although quantifying this was outside the scope of this study.

Naturally occurring calls

Statistical analysis of naturally occurring calls showed a significant difference in the detection of two common species, consistent with strong spatial segregation. *Rhinolophus megaphyllus* were recorded at all detector heights except 40m, with calls predominantly recorded below the canopy (0 – 10 meters above ground level). *Miniopterus australis* calls were mostly detected above the canopy (20m and higher), with detectability being highly limited below the thickest part of the canopy (0 – 10 meters above ground level). This is consistent with what is known about species behaviour and morphology. Species such as *R. megaphyllus* are better adapted to foraging within cluttered environments such as canopy understories (Abbott *et al.*, 2012). However, their morphology does not exclude them from foraging in open areas. Conversely, fast flying, less manoeuvrable species such as *M. australis* are restricted to foraging in relatively open areas, as their speed and wing span do not allow easy foraging in cluttered areas (Rhodes, 2002). This is reflected in trends seen in detection of naturally occurring calls with *R. megaphyllus* calls being detected more often, at a greater range of heights, than those of *M. australis* where calls were predominantly detected above the canopy. Above canopy surveying has been quite limited to date due to the logistical limitations of accessing this environment. The results of this study do align with the results of other studies that have sampled bats above canopies. Marques and colleagues investigated patterns in bat use of vertical space in a Brazilian tropical rainforest (Marques *et al.,* 2016). They found that majority of species were primarily detected immediately below the canopy while ‘open space’ species concentrated their activity above the canopy (Marques *et al.,* 2016). Other studies have also found clear vertical stratification below and above the canopy (e.g. Muller *et al.,* 2013; Kennedy *et al.,* 2014) and two-thirds of all bat activity recorded in an old growth Redwood forest in America was recorded above the canopy (Kennedy *et al.,* 2014).

We are unable to calculate the decline in detection with distance of naturally occurring calls as the experimental set up did not allow us to account for at which horizontal distance the bat was present when making the call. We are only able to say at which height a naturally occurring call was detected. Based on the highly directional results of the pulse experiment, we could assume that if a bat call was detected on a detector placed at 10m in height then the bat was flying approximately at 10m height within the forest structure. None the less, patterns in the way naturally occurring calls are detected reflect those identified for experimental pulses. The CF type calls of *R. megaphyllus* and the FM type calls of *M. australis* were recorded at relatively the same positions within the canopy (species behaviours taken into consideration) as the corresponding experimental pulses type. This, along with the obvious obstacle that vegetation may present to detection, lends support to the suggested, although non-significant, results of this study.

Designing effective monitoring studies

This study provides us with rudimentary information which could be useful for setting up acoustic monitoring surveys for echolocating bats within tropical rainforest environments. Based on the inferred results of this study it is suggested that non-targeted studies conducted in tropical rainforests should be mindful of detector placement within their study site. Ultrasound detection was found to decline quickly, especially in areas of high vegetative clutter. The preliminary results presented here suggest that elevating detectors into the canopy could result in less detection than detectors placed under or above the canopy, due to the occurrence of dense vegetative clutter within rainforest canopies. The simulated pulses used in this study were found to only be detectable over short distances. This could indicate that AnaBat detection in cluttered environments may be limited, although further study would be needed to confirm this conclusion.

Based on the preliminary findings of this study it is suggested that if surveys are to be targeted at a particular species or group of species, it is important to take species behaviours into consideration when designing the survey. If, for example, monitoring was being focused on the endangered Rhinolophidae species *Rhinolophus robertsi* (CF type call), a more effective study could be conducted by taking species traits into account. We know that this species is a slow flying, highly manoeuvrable species that forages in closed, cluttered environments under the rainforest canopy (Clague, 2004). The preliminary results of this study suggest that in order to design a survey for targeting this species it would be best to concentrate detection efforts in the first 10m of the forest height. Also, our interpretation suggests that calls would be better detected at distances closer to the detector. Therefore, to increase the chances of detecting this rare species, multiple detectors within the environment may be most effective.

For general surveys in tropical rainforests, with no specific species targeted, preliminary data suggests that detectors be placed below the canopy, but have microphones angled towards the canopy in order to detect any bats flying above. Where possible, multiple detectors could be used within a single survey to allow for the limited distances that detectable sound is predicted to travel (Fischer *et al.*, 2009; Law *et al.*, 2015). Detectors could also be orientated toward areas of the least amount of clutter to increase the probability of detection. Supplementing static surveying using passive detectors with active transects in nearby open areas (such as road ways or forest tracks) may also help to increase probability of detection especially for species who preference open-space as opposed to the closed-canopy environment of tropical rainforest ((Fischer *et al.*, 2009; Law *et al.*, 2015). Although, the efficiency and additional value of mobile detectors over stationary ones has recently been questioned (Tonos *et al.*, 2014). Active surveying in such a way could allow monitoring to detect the greatest range of species and help to gain the most accurate picture of species presence at the surveying site.

Although the limited sample size recorded in this experiment means that the interpretation of results must be viewed with extreme caution, it is felt that observed and discussed trends do reflect real patterns. Patterns of vertical stratification of vegetative clutter within the rainforest canopy are real and evident. It can be reasonably assumed that vegetative clutter will have some effect on probability of ultrasonic detection. The results of this experiment lend support to this hypothesis, if not statistically confirming this correlation. Similarly, quantifiable patterns of detectability observed in naturally occurring bat calls also lend support to the conclusions presented here. Repeating the experiment with a more powerful, measurable, ultrasonic pulse source would help to statistically confirm the trends discussed herein. Confirming these trends would be greatly beneficial to calibrating and qualifying studies of echolocating bats worldwide, but particular in highly cluttered tropical rainforest environments.

Appendix 1: Annex 1

Appendix 1, Table 1.1 Frequency of pulse detection as a function of pulse type, vertical source height and horizontal detector distance, expressed as probability of detection.

Height from ground	Canopy Zone	**Frequency Modulated Pulse** Horizontal distance from source				**Constant Frequency Pulse** Horizontal distance from source			
		5m	10m	15m	20m	5m	10m	15m	20m
40m	Above	0.63	-	-	-	0.63	-	-	-
30m	Above	0.38	-	-	-	0.38	-	-	-
20m	Top of Canopy	0.25	-	-	-	0.38	-	-	-
10m	Within Canopy	-	-	-	-	-	-	-	-
4m	Below	0.67	-	-	-	0.50	-	-	-
0m	Below	0.25	0.17	-	-	0.50	-	-	-

Bats of the YUS Conservation Area Papua New Guinea

Simon KA Robson[1],

Tamara E Inkster[1] &

Andrew K Krockenberger[2]

[1]Centre for Tropical Biodiversity & Climate Change
[2]Centre for Tropical Environmental & Sustainability Science

School of Marine & Tropical Biology
James Cook University, Australia

Table of Contents

Executive Summary

This project provides the first description of bat community structure across a complete altitudinal gradient in Papua New Guinea (from sea-level to 3000m), assembles the largest reference collection of echolocation calls for Papua New Guinean bats (22 species, a valuable tool for species inventory work), and provides species accounts for all 22 microchiropteran (& 4 megachiropteran) bats captured in the YUS Conservation Area.

Microchiropteran bat communities vary across altitudinal gradients, with greatest species abundance at lowland sites, and greatest individual abundance at mid-altitude sites. Despite the reduction in species with increasing elevation there is still a significant number of potential high-altitude species (6) occurring at or above 3000m.

Acoustic monitoring techniques proved to be a cost and labour effective method of surveying bat communities, revealing twice the number of microbats with only one half the surveying effort of traditional capture techniques.

When implemented in concert, traditional survey techniques based on captures (using mist nets and harp traps) and more recently developed techniques (acoustic monitoring) significantly advance our understanding of the bat fauna of the YUS Conservation Area, the Huon Peninsula and Papua New Guinea, resulting in 22 new species-specific echolocation call types for YUS and the Huon Peninsula, 2 new species records for the Huon Peninsula and 5 altitudinal range extensions for Papua New Guinea. Species accumulation curves indicate that the total number of bat species detected in the YUS Conservation Area will increase with greater sampling effort.

Extensive baseline faunal surveys such as those conducted here provide critically important starting points for long term monitoring of community changes on a local, national and global scale. The reference collection of bat calls in concert with additional acoustic surveys provides a valuable opportunity for effective and efficient ongoing monitoring of bat communities in the region, and highlights the value of the YUS Conservation Area for answering questions of changes in community structure of a global significance.

Introduction and rationale

Large scale studies of the composition of communities are becoming increasingly important for assessing the patterns and process underlying global changes in biological communities (Walther et al (2002), Parmesan & Yohe (2003), Root et al (2003), Dunn et al (2009), Pounds et al (2006)).

Studies of attitudinal patterns of community structure are particularly important for assessing the impacts of global changes such as climate change. The changes in community structure with altitude as a function of changing local environmental characteristics such as temperature and precipitation are thought to provide suitable predictive models for more widespread global changes environmental changes. Numerous taxa such as terrestrial insects (Hodkinson 2005), ants (Kaspari Et al 2004) and amphibians (Pounds et al 1999) have been examined in this context, but bats remain poorly represented despite their significant contribution to diversity (they comprise approx: 20% of all mammal species). In part, this reflects the difficulties of sampling small and cryptic nocturnal flying animals.

The island of Papua New Guinea contains a rich mammal fauna that itself comprises approximately 8% of the world's bat fauna (Bonacorso 1998). With its diverse biological and geographical systems, Papua New Guinea represents an ideal environment in which to describe the relationships between bat community structure and altitude. Records of bats are typically nested within larger mammal fauna studies (e.g. Wright *et al*, (1998), Helgen (2007), Aplin and Opiang (2011) and although some recent bat surveys have targeted particular regions or locations (e.g. Muller Ranges, Western Highlands (Armstrong & Aplin 2011), western PNG (Leary & Pennay (2011) no study has as yet examined bat community structure across a complete altitudinal gradient from sea-level to the highest relevant elevation of the region.

The recent development of acoustic survey techniques for bats has significantly improved our ability to survey and monitor bat communities. Ultrasound recording methods such as that used by the AnaBat® system allow extremely efficient and often remote sensing of bat communities based on the detection of species or taxon-specific echolocation calls produced by foraging bats. Again, the bat fauna of PNG is ideally suited for implementing such an approach.

This report details **Result 5: Carbon and climate field science associated with the YUS conservation area, Task 3.2: YUS climate and biodiversity transect, altitudinal survey of the "micro-bat" (*Microchiropteran)* fauna**.

The project achieved the following outcomes:

1. Provided the first descriptions of the community structure of bats in the Huon Peninsula and the first descriptions of how bat community structure varies across an altitudinal gradient in Papua New Guinea, using the YUS conservation area as a study system,
2. Accumulated the largest reference collection of echolocation calls of microchiropterans of PNG and highlighted the role of acoustic monitoring as an additional and important survey technique for bats, &
3. Provided species accounts of those bats detected in the YUS conservation area as a guide for future studies of bats in the region and in Papua New Guinea.

Methodology

Survey effort

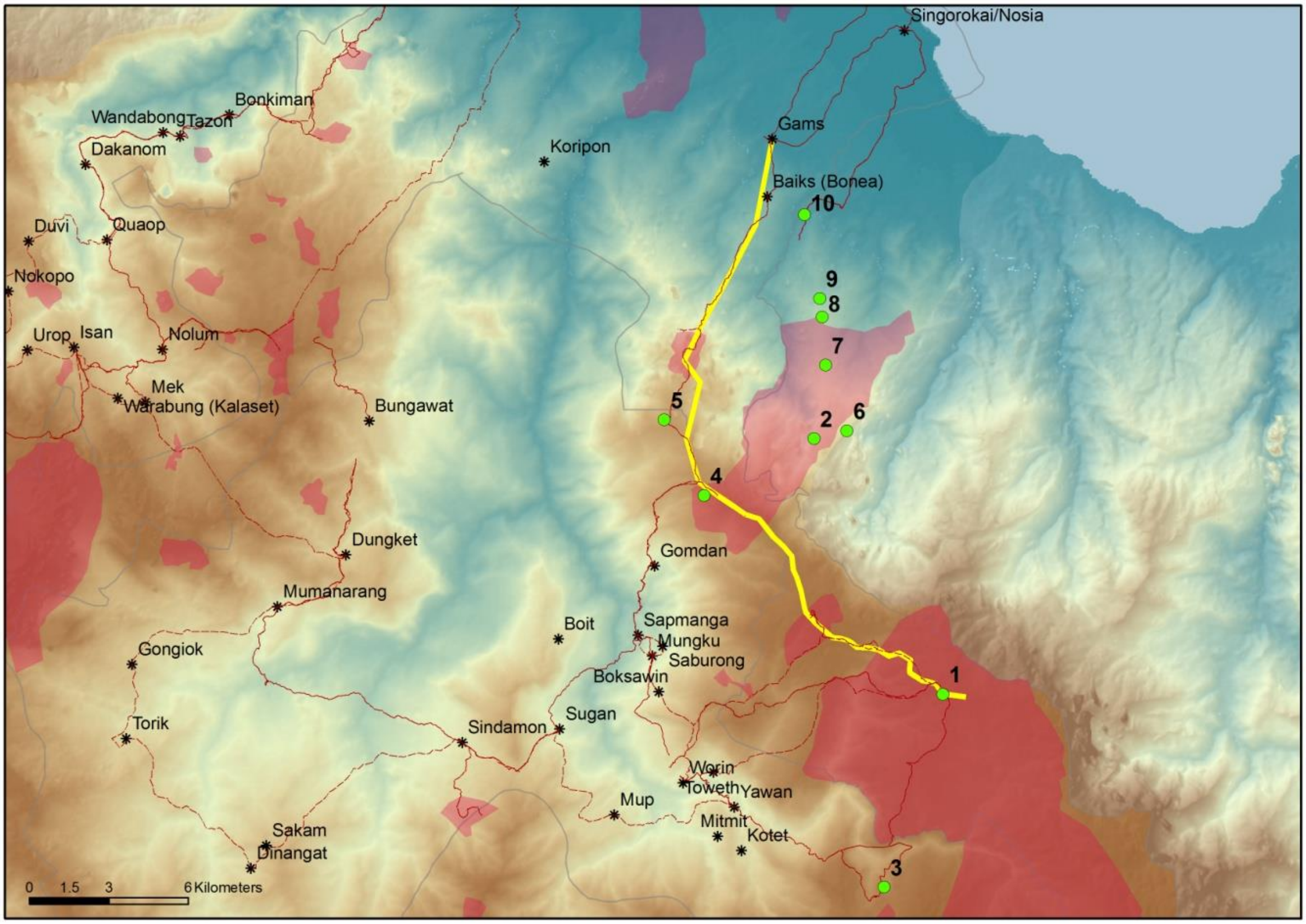
Bat presence and activity was monitored at 11 distinct elevations along the YUS transect, Huon Peninsula, spanning from sea level to 3000m elevation, during two visits to the YUS transect in July 2010 and June/July 2011 (Figure 1). Together, these two trips represent a total of 240 and 103 trap and acoustic recording (AnaBat) nights respectively (Table 1).

Survey effort, and species accumulation, across elevations was estimated using the program EstimateS Version 8.2 (Colwell, 2006), a re-sampling program that provides diversity estimates and their confidence limits based on the sampling effort performed during the study.

Acoustic monitoring

Data was collected using ultrasonic acoustic detectors (AnaBat SD1®, Titley Electronics, Ballina, Australia) and examined using AnalookW software (version 3.7w). Surveying was conducted for a period of four nights at elevations 2350m, 2050m, 1150m, 750m, and 350m, three nights at 1550m and 3000m, and one

Figure 1. Survey sites within the YUS conservation area, Papua New Guinea



night each at 2800m, 2550m, 950m and sea level (Table 1).

Detectors were set to record passively from pre-dusk to post-dawn each night. Detectors were moved within the surveying area in order to maximise detection potential, and placed in areas most likely to obtain calls such as flyways or orientated towards open areas.

Calls were identified to species using reference calls collected during this survey (see Section 3.3 & 4). This involved determining whether the call was of constant frequency (flat calls with little variability in frequency) or frequency modulated (sloping calls often with high variability in frequency) type. The characteristic frequency, the flattest, and often longest part of each pulse, was then determined. Additional call characteristics, such as droops or up and down sweeps, which may be species specific, were also noted. Additional species were identified using other call libraries developed for Papua New Guinea (Armstrong and Aplin, 2011; Leary and Pennay, 2011). Calls that could not be confidently identified to species were assigned a code name detailing their shape (cf,fm or sfm) and characteristic frequency.

Monitoring via mist nests and harp traps

Mist nets and harp traps were used in addition to Anabat ultrasound detectors. Four 5-bank harp traps and four mist nets were used at each elevation. Trapping was conducted in conjunction with passive recording. Traps were erected before dusk each night, and were left open for a minimum of five hours. Trap positions were moved every night in order to avoid any trapping bias from trap-familiar animals. Morphological parameters were taken in order to identify individuals to species. Data recorded included sex, reproductive condition, forearm (FA), ear (E), tail (TL) and tibia (TB) length, weight (W), the width between outer canine (OCW), and details of age (adult or juvenile) and reproductive condition. The most informative parameters (sex, age, forearm length, and weight) are presented in each species account. These have been compared with morphological measurement recorded by Flannery (1995) and Bonaccorso (1998).

Reference calls were recorded for each

Table 1. Location, duration & type of bats sampling in YUS

Start date	Camp	Lat.	Elev. (m)	# nights	# harp traps & nets	# Ana Bats	Total trap nights	Total AnaBat nights	# AnaBat files
22 June 2010	Wasaunon	-06.09530 146.91556	3000	3	8	2	24	6	730
25 June 2010	Camp 13 (YD)	-06.00788 146.87122	2800	1	8	2	8	2	77
28 June 2011	Plot Y3	-06.16436 146.89419	2550	1	8	1	8	1	0
22 June 2011	Camp 12	-06.02756 146.83376	2350	4	8	4	32	16	42
26 June 2011	Camp 11	-06.00138 146.82063	2050	4	8	4	32	16	439
02 June 2011	Saburong	-06.00505 146.88272	1550	3	8	4	24	12	317
05 July 2011	Camp 950m	-05.98282 146.87534	1150	4	8	4	32	16	825
09 July 2011	Camp 950m	-05.96624 146.87498	950	1	8	1	8	1	69
12 July 2011	Camp 950m	-05.95932 146.87431	750	4	8	4	32	16	1028
13 July 2011	Camp 6	-05.93076 146.86761	250	4	8	4	32	16	265
17 July 2011	Singorokai	-05.86768 146.91211	9	1	8	1	8	1	4
TOTAL			**11**	**30**	**88**	**31**	**240**	**103**	**3796**

Microbats of YUS

A total of 11 microbat species from 5 microchiropteran subfamilies were captured and identified during this study (Table 2). When compared to predicted bat presence based on the details provided by Flannery (1996) and Bonaccorso (1998), these captures represent at least 50% of the microbat species likely to be present. However it is worth noting that this study also detected another potential 11 species based on unique echolocation calls (se Section 3.3 & 3.4). If these currently unidentified species are already represented in the lists provided by previous studies of PNG bats, then the total number of species detected in this study (22) exceeds the total predicted species pool. An additional four species of megabat (58 individuals) were also captured during the survey. Species accounts of these species can be found at the end of this document.

Examination of species accumulation curves using both capture and acoustic recording techniques suggest that further sampling will be rewarded with the detection of more species. The species accumulation curve (Figure 2) has yet to reach an asymptote and hence the current best estimate of the number of 21± 5 species (mean ± 95% confidence limits) is likely to be an underestimate of total species numbers.

The relationship between the number of microchiropteran species (determined by both methods) and altitude is shown in Figure 3. The highest abundance of species occurs at lowland sites (200 m), a similar pattern to that found in other bat studies. The confidence limits around the estimates of the number of species at each elevation are quite variable, and further survey efforts are required to improve these estimates. It is worth noting that this study alone provided new altitude records for 5 (45%) of the 11 species captured and identified.

The relationship between the number of microbat individuals captured and altitude is shown in Figure 4. The highest abundance of individuals occurs at mid-altitude sites (1150 m), which is surprising given the highest species abundance at lower-elevation sites and the strong relationship typically found between species and individual abundance.

The patterns of abundance shown here may reflect some inequalities in the sampling effort across the entire altitudinal gradient. The 900m site for example, has relatively low numbers of species and individuals (Fig. 3, 4) but unfortunately the sampling effort at this site was much lower than at its neighbours (Table 1).

Table 2. Microbats predicted to be within YUS

Family	Genus species	Common name	Flannery (1996)	Bonaccorso (1998)	Dabek (2001, 2003)	This study
Emballonuridae	Emballonura beccarii	Beccari's Sheath-tailed bat	x	x		
	Emballonura nigrescens	Lesser Sheath- tailed bat	x			
	Saccolaimus spp.	Naked-rumped Sheath-tailed bat		x		
Molossidae	Chaerephon jobensis	Northern Mastiff bat	x	x		
	Mormopterus beccarii	Beccari's Mastiff bat	x	x		
	Otomops secundus	Mantled Mastiff bat	x			
Hipposideridae	Aselliscus tricusidatus	Trident Horseshoe bat			x	x
	Hipposideros ater	Dusky Horseshoe bat		x		
	Hipposideros calcaratus	Spurred Horseshoe bat	x	x	x	
	Hipposideros cervinus	Fawn Horseshoe bat	x	x	x	x
	Hipposideros diadema	Diadem Horseshoe bat	x	x		x
	Hipposideros maggietaylorae	Maggie Taylor's Horseshoe bat	x	x		x
	Hipposideros muscinu	Fly river Horseshoe bat	x			
	Hipposideros semoni	Greater wart-nosed Horseshoe bat		x		

Rhinolophidae	Rhinolophus euryotis	New Guinea Horseshoe bat	x	x	x	x
	Rhinolophus megaphyllus	Eastern Horseshoe bat	x	x		x
Vespertilionidae	Kerivoula muscina	Fly River Trumpet-eared bat				x
	Miniopterus	Little Bent-winged bat	x	x		
	Miniopterus australis	Small Melanesian Bent-winged bat		x		
	Miniopterus magnater	Western Bent-winged bat	x	x		
	Miniopterus medius	Javan Bent-winged bat		x		
	Miniopterus propitristis	Large Melanesian Bent-winged bat	x	x		
	Miniopterus schreibersii	Common Bent-winged bat	x	x		
	Murina florium	Insectivorous Tube-nose bat	x	x		x
	Myotis adversus	Large Footed Mouse-eared bat	x			
	Nyctophilus	Small Eared Nyctophilus		x	x	x
	Nyctophilus microtis	Greater Nyctophilus	x	x		
	Philetor brachypterus	Rohu's bat	x	x		
	Pipistrellus angulatus	New Guinea Pipistrelle		x		x
	Pipistrellus collinus	Mountain Pipistrelle	x	x		x
	Pipistrellus papuanus	Papuan Pipistrelle	x	x	x	
		TOTAL	22	18	6	11

Figure 2. Estimated number of microbat species within YUS

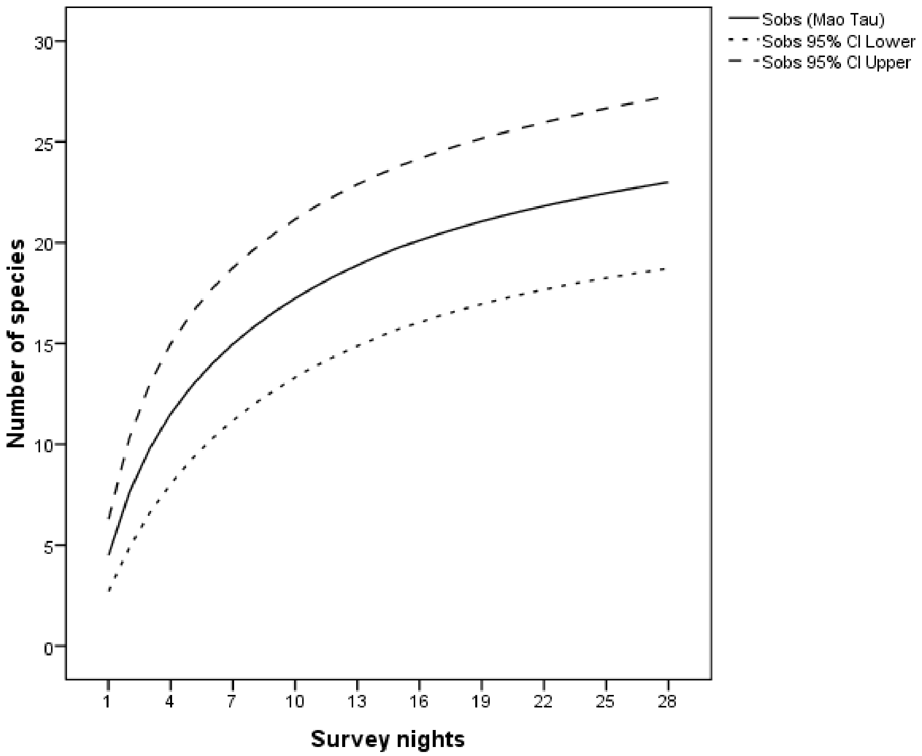


Figure 3. Microbat species and altitude within YUS

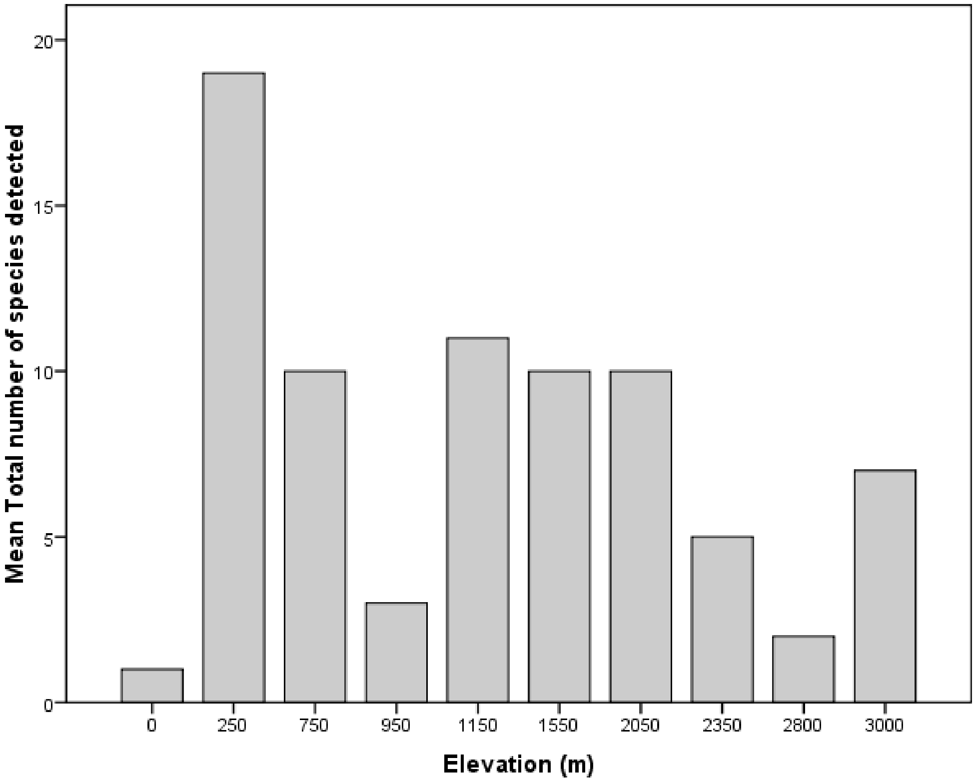


Figure 4. Microbat individuals and altitude within YUS

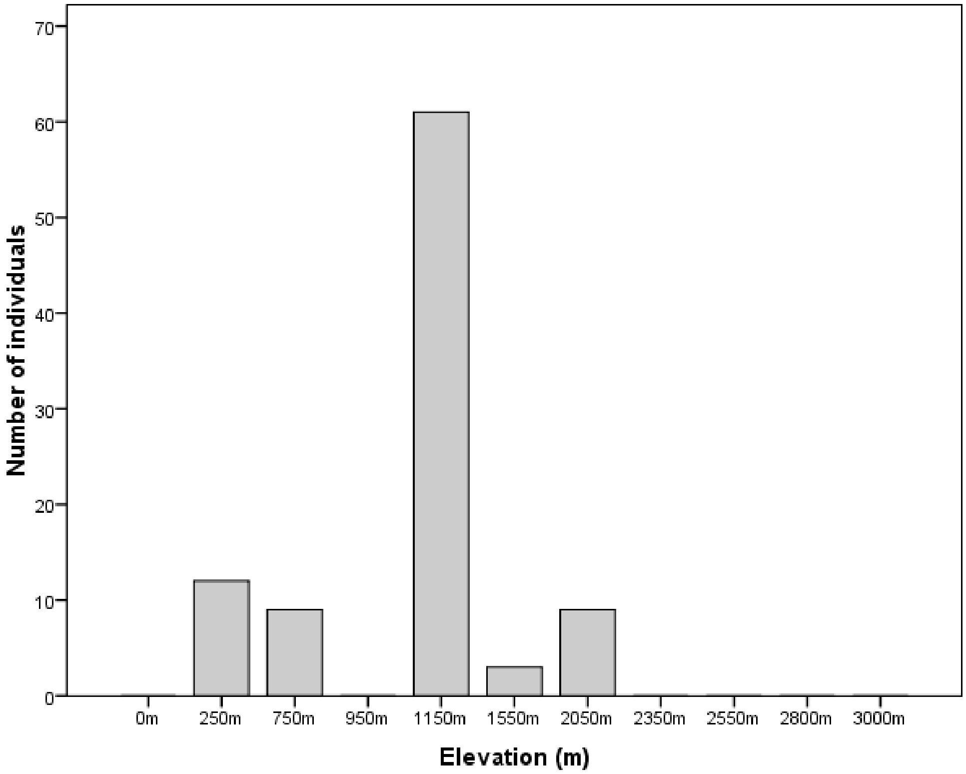
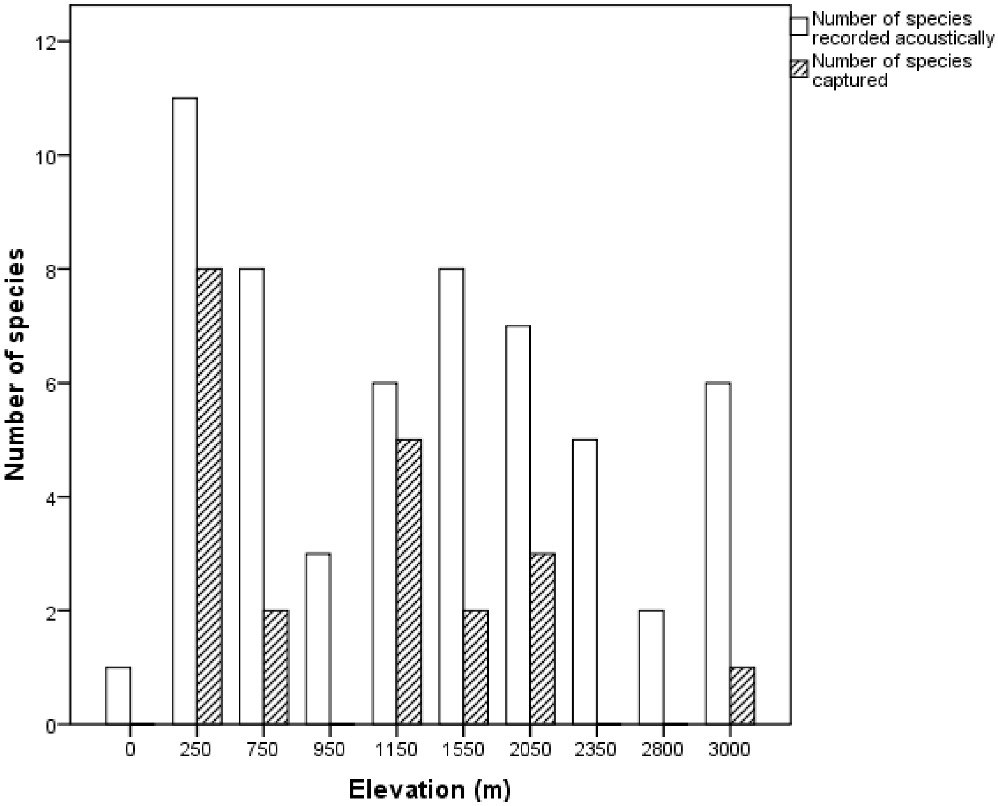


Figure 5. Microbats, altitude and survey method



The role of acoustic monitoring in bat surveys

Acoustic monitoring provides a valuable addition to the standard 'capture method' approach to surveying bats, providing evidence of a greater diversity of bats and over a greater altitudinal range than that provided by capture methods alone (Figure 5).

Traditional capture methods (harp traps and mist nets) captured a total of 96 individuals from 9 different species and 5 families (Figure 5). The majority of individuals were trapped at 1150m elevation (61 individuals) while the majority of species were caught around 250m (8 species). Acoustic monitoring techniques recorded 18, 254 sound files of which 3,792 contained bat calls. From these files 21 distinct bat species were recognised, of which 11 could be assigned to individual bat species from 5 families. The majority of individuals were detected at 1150m elevation, while the majority of species were detected at 250 m (11 species). Acoustic surveys therefore detected a greater number of microchiropteran species than traditional capture methods, even though the total number of acoustic-sampling nights was less than half that of the total number of capture nights (Table 1). And although both methods indicate higher numbers of species at lower elevations, acoustic methods are clearly more capable of detecting bats at higher elevations than capture methods alone (and with less sampling effort). The ability to accurately sample bats at higher elevations is particularly important, given that high altitude species are more likely to suffer the effects of rising temperature due to global climate warming. Capture techniques for example identified only 6 microchiropteran species at or above 1550 m, compared to 28 for acoustic methods.

The ability of acoustic surveys to quickly detect new species is also evident when comparing the two species accumulation curves for acoustic and capture surveys. Species accumulation curves are predicted to increase with greater sampling effort and currently predict a total number of microchiropteran species of 16 ± 7) (Figure 6). Species accumulation curves based on capture data only, while yet to asymptote, suggest a much lower total species number (8 ± 5) (Figure 7).

The value of adding acoustic surveys to bat monitoring efforts are further illustrated in Table 3. Although many species were both physically captured and detected acoustically, over half of the 22 species found at YUS (12 species, 55%) could only be identified by detecting their echolocation calls. And while some of these species may be quite rare as they were detected at only single elevations (sfm22 and cf35 for example), others such as smf45 and smf42 were detected across almost the entire elevation gradient. Future studies determining the species identity of these currently unknown calls would be highly valuable.

In conclusion, acoustic monitoring represents a valuable addition to traditional bat survey techniques, and together with capture methods represents an effective method of surveying bats across all elevations. Acoustic methods appear particularly suitable for detecting bats at higher elevations which much less effort than capture methods such as harp traps and mist nets, but capture methods are also required to provide the species identities to the calls detected through acoustic surveys. Together they provide a powerful method for surveying bats. Great value could be added through future studies in the YUS area designed to provide the missing species identities to the 11 species currently only known from their echolocation calls.

Figure 6. Species accumulation with acoustic surveys

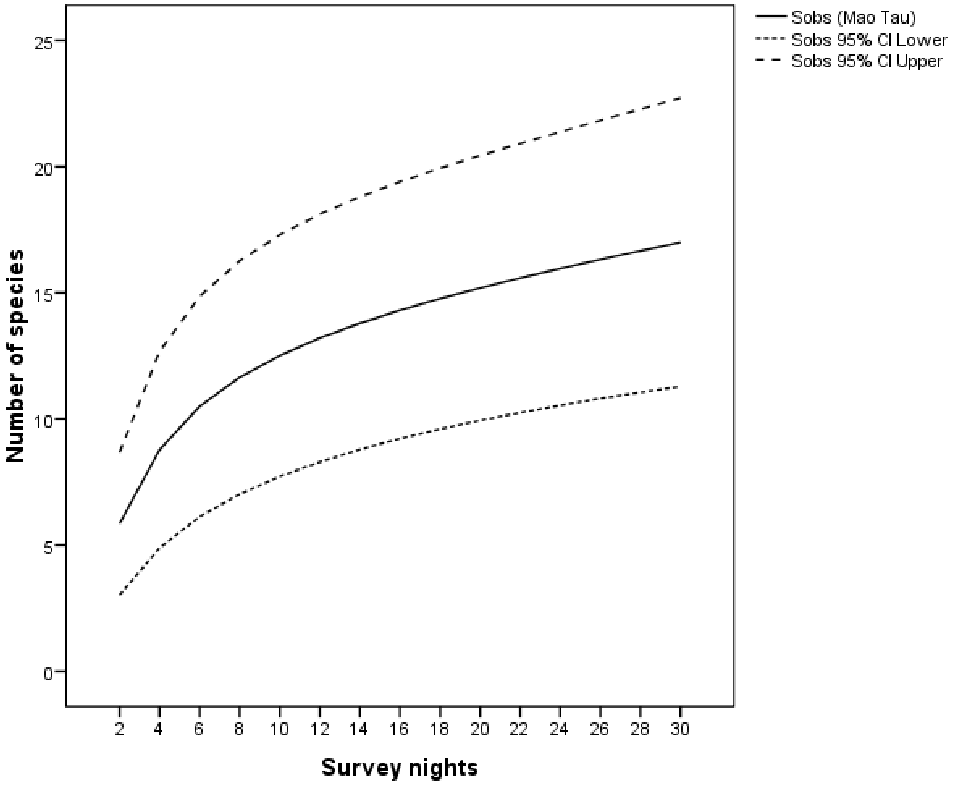


Figure 7. Species accumulation with capture surveys

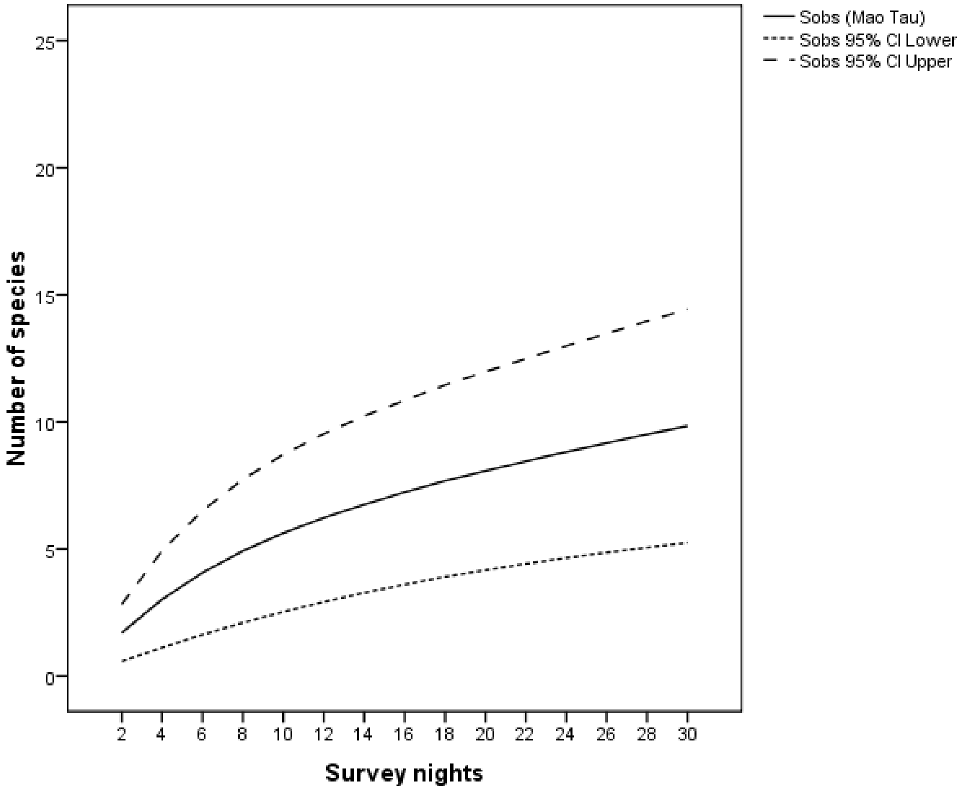
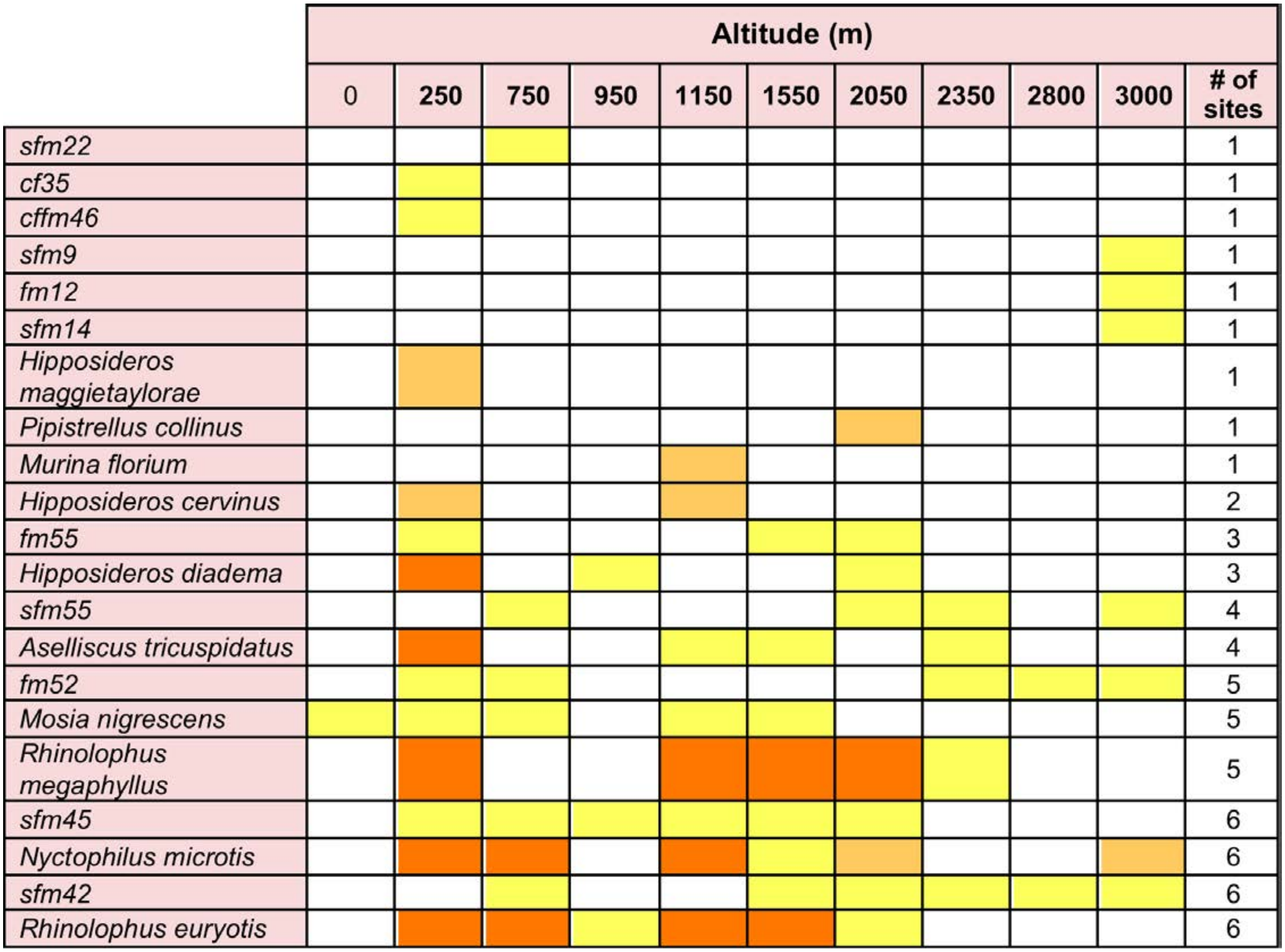


Table 3. Microbats of YUS and the survey methods used to detect them (🟨 = detected acoustically, 🟧 =captured in harp



	Altitude (m)										
	0	250	750	950	1150	1550	2050	2350	2800	3000	# of sites
sfm22			🟨								1
cf35		🟨									1
cffm46		🟨									1
sfm9										🟨	1
fm12										🟨	1
sfm14										🟨	1
Hipposideros maggietaylorae		🟧									1
Pipistrellus collinus							🟧				1
Murina florium					🟧						1
Hipposideros cervinus		🟧			🟧						2
fm55		🟨				🟨	🟨				3
Hipposideros diadema		🟥		🟨			🟨				3
sfm55			🟨				🟨	🟨		🟨	4
Aselliscus tricuspidatus		🟥			🟨	🟨		🟨			4
fm52		🟨	🟨					🟨	🟨	🟨	5
Mosia nigrescens	🟨	🟨	🟨		🟨	🟨					5
Rhinolophus megaphyllus		🟥			🟥	🟥	🟥	🟨			5
sfm45		🟨	🟨	🟨	🟨	🟨	🟨				6
Nyctophilus microtis		🟥	🟥		🟥	🟨	🟧			🟧	6
sfm42			🟨			🟨	🟨	🟨	🟨	🟨	6
Rhinolophus euryotis		🟥	🟥	🟨	🟥	🟥	🟨				6

Species accounts

Species accounts are provided for each of the 22 microchiropteran and 4 megachiropteran species recorded in the YUS conservation area

Accounts include species descriptions and photographs where available, details of altitudional records and an example of the echolcation calls if relevant.

These descriptions facilitate embedding the results of this study into previous research into the bats of PNG, and provide a greater understanding of within- and between-species variability in echolocation calls, a key component of furture bat survey work on the region,

To highlight the contributions of this study, all accounts indicate whether the findings of this study represent new location records for the Huon Peninsula, new altitude records for PNG, new echolcation calls for the Huon Peninsula or new echolcation calls for PNG.

Aselliscus tricuspidatus
Trident Leaf-nosed Bat

The smallest of the Hipposideridae found in Papua New Guinea, where two subspecies are known to occur. *Aselliscus tricuspidatus novaguinea* occurs on the mainland, while *A. tricuspidatus koopmani* occurs on small islands to the north east (Bonaccorso, 1998).

A total of 62 files containing calls from this species were recorded during the course of this survey, with one individual being captured. Capture was made in a harp trap, at 250m elevation.

This species was also acoustically detected at 250m, 1150m and 1550m elevation. Previous studies have recorded this species from sea level up to 900m in elevation (Flannery, 1995; Bonaccorso, 1998; Dabek, 2001, 2003). This survey significantly extends the known altitudinal range of this species in Papua New Guinea.

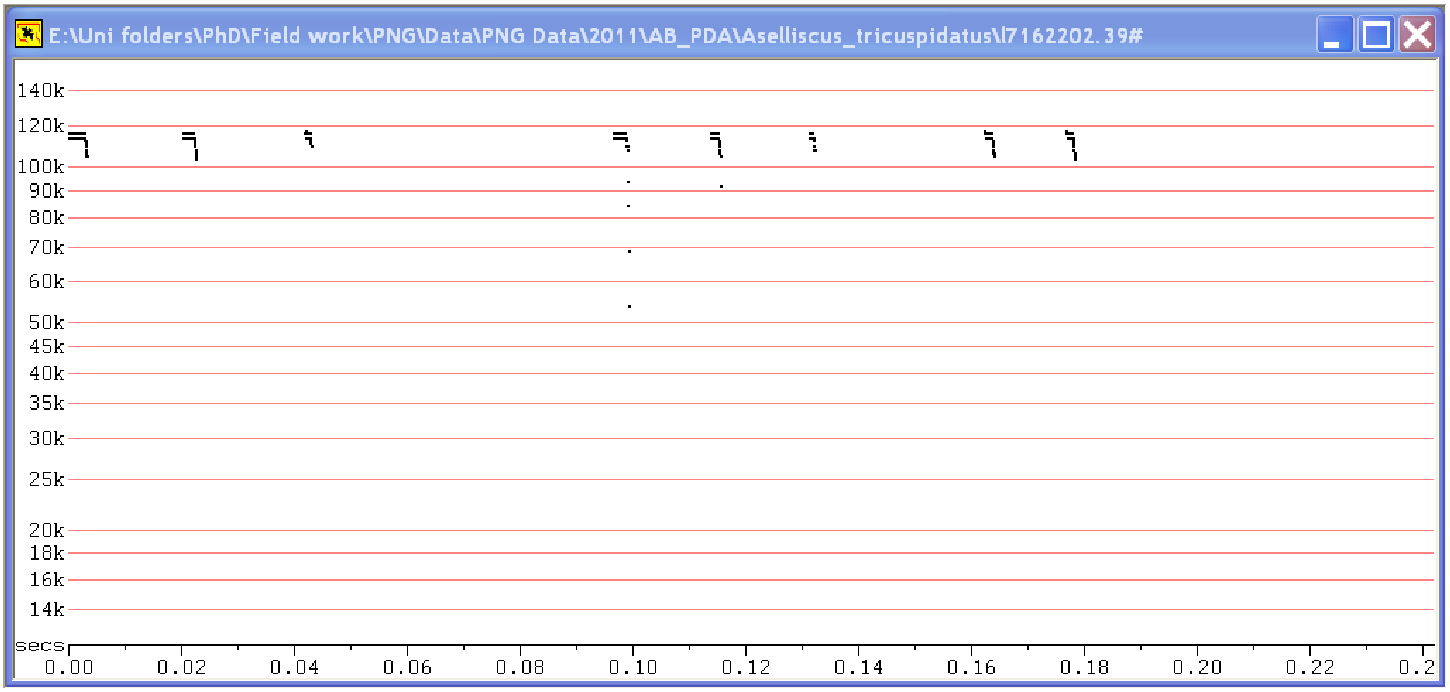
A distinctive characteristic of this species is the three projections on the top ridge of the nose leaf. Fur was bicoloured with brownish tips over a paler base. Fur around the muzzle had a slight yellowish hue, extending into the ventrum fur. Morphological parameters recorded were in accordance with previous records.

Hipposideridae

New record for Huon Peninsula

New call for Huon Peninsula

Five reference calls were collected from this species during handling and upon release. The call is of a constant frequency and relatively short duration



		Aselliscus triscuspidatus											
		Flannery (1995)				**Bonaccorso (1998)**				**This study**			
FA	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	41.30	40.00	42.00	4	-	39.40	41.90	5	-	-	-	0
	F	42.00	41.00	43.00	3	-	40.10	43.60	12	42.8	-	-	1
	J	-	-	-	-	-	-	-	-	-	-	-	-
WT	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	3.80	3.00	4.10	4	-	3.50	-	1	-	-	-	0
	F	5.00	4.00	7.00	3	-	-	4.00	1	4.5	-	-	1
	J	-	-	-	-	-	-	-	-	-	-	-	0

typical of *Hipposideros*. The characteristic frequency is around 115kHz with each pulse ending with a long down sweeping tail dropping around 5kHz in frequency. The call is displayed below as an uncompressed file in F7 magnification. This species call was also detailed by Leary and Pennay (2011). Calls recorded during this survey match the shape of the ones recorded by Leary and Pennay, but are of a slightly higher frequency (115kHz vs. 112kHz).

Aselliscus triscuspidatus				
Elevation (m asl)	**Flannery (1995)**	**Bonaccorso (1998)**	**Dabek (2001, 2003)**	**This study**
3000m				
2800m				
2500m				
2350m				X
2050m				
1550m				X
1150m				X
950m			X (900m)	
750m		X (600m)	X	
250m	X (360m)	X	X	X
0m	X	X		

Hipposideros cervinus
Fawn Leaf-nosed Bat

Hipposideridae

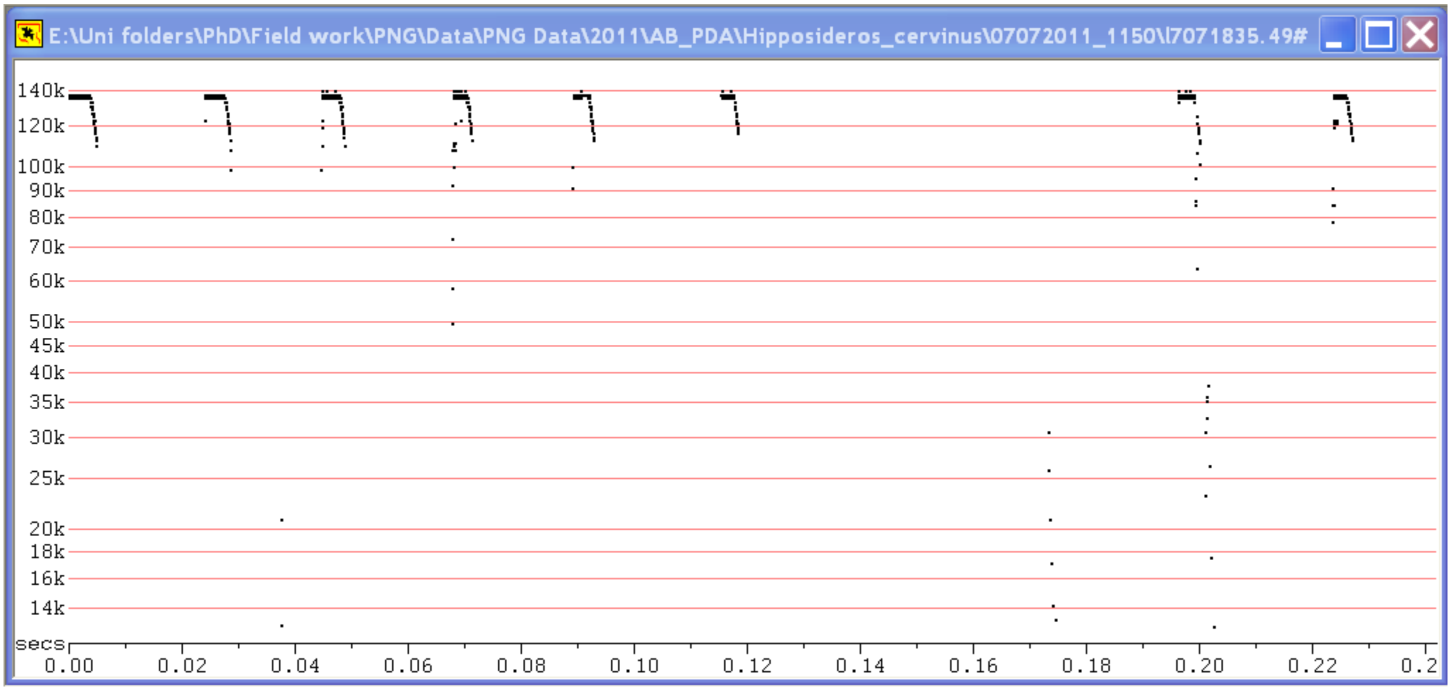
New call for Huon Peninsula

A small leaf nosed bat. Four subspecies exist but only one of these, *H. c. cervinus*, is present in Papua New Guinea (Bonaccorso, 1998).

This species was not acoustically detected during passive surveying. Eight individuals were captured during this survey using harp traps. Individuals were captured at 250m and 1150m elevation. Previous studies have recorded this species from sea level up to 1400m in elevation (Flannery, 1995; Bonaccorso, 1998; Dabek, 2001, 2003).

This species has a simple nose leaf structure without central projections. It has a raised ridge at the top of the nose leaf, and two tiny lateral leaflets to the side of the horseshoe. This species ears are small and funnel like, rounding to an outward pointing tip. Fur is bicoloured with brownish tips over a paler base, with ventrum fur only slightly paler than the dorsum. Morphological parameters recorded were in accordance with previous records

Reference calls were collected from all eight individuals during handling and upon release. A total of 21 call files were recorded. The call is of a constant frequency and relatively short duration typical of Hipposideros. The characteristic frequency is around 135kHz with each pulse ending with a long down sweeping tail dropping around 20kHz in frequency. The call is displayed below as an uncompressed file in F7 magnification. This species call was also detailed by Leary and Pennay (2011). Calls recorded during this survey matched the ones recorded by Leary and



E:\Uni folders\PhD\Field work\PNG\Data\PNG Data\2011\AB_PDA\Hipposideros_cervinus\07072011_1150\l7071835.49#

		Hipposideros cervinus											
		Flannery (1995)				**Bonaccorso (1998)**				**This study**			
FA	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	48.90	48.70	49.00	2	-	44.30	49.20	17	46.59	-	-	1
	F	49.00	-	-	1	-	46.40	50.70	20	48.06	46.30	48.80	7
	J	-	-	-	-	-	44.80	-	1	-	-	-	0
WT	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	9.40	8.80	9.90	2	-	6.00	10.00	26	7.5	-	-	1
	F	13.00	-	-	1	-	7.00	9.80	19	10.0	7.0	17.0	7
	J	-	-	-		-	-	-	-	-	-	-	0

Pennay, who also recorded lower harmonics. Calls recorded for this species from Papua New Guinea are of a considerably higher frequency than those recorded in Australia (120kHz) (Churchill, 2008).

Hipposideros cervinus				
Elevation (m asl)	**Flannery (1995)**	**Bonaccorso (1998)**	**Dabek (2001, 2003)**	**This study**
3000m				
2800m				
2500m				
2350m				
2050m				
1550m				
1150m	X (1360m)	X (1400m)		X
950m	X	X	X (900m)	
750m	X	X	X	
250m	X	X	X	X
0m	X	X		

Hipposideros diadema
Diadem Leaf-nosed Bat

The largest Hipposideros in Papua New Guinea. Four subspecies exist, though *H. diadema griseus* is the only on to occur on the mainland (Bonaccorso, 1998).

A total of 67 files containing calls from this species were recorded during passive acoustic surveying, with only two individuals being captured. Both were captured in mist nets set at 250m elevation. This species was also acoustically detected at 250m, 950m and 2050m elevation. Previous studies have recorded this species from sea level up to 1300m in elevation (Flannery, 1995; Bonaccorso, 1998). This survey extends the known Altitudinal range of this species in Papua New Guinea.

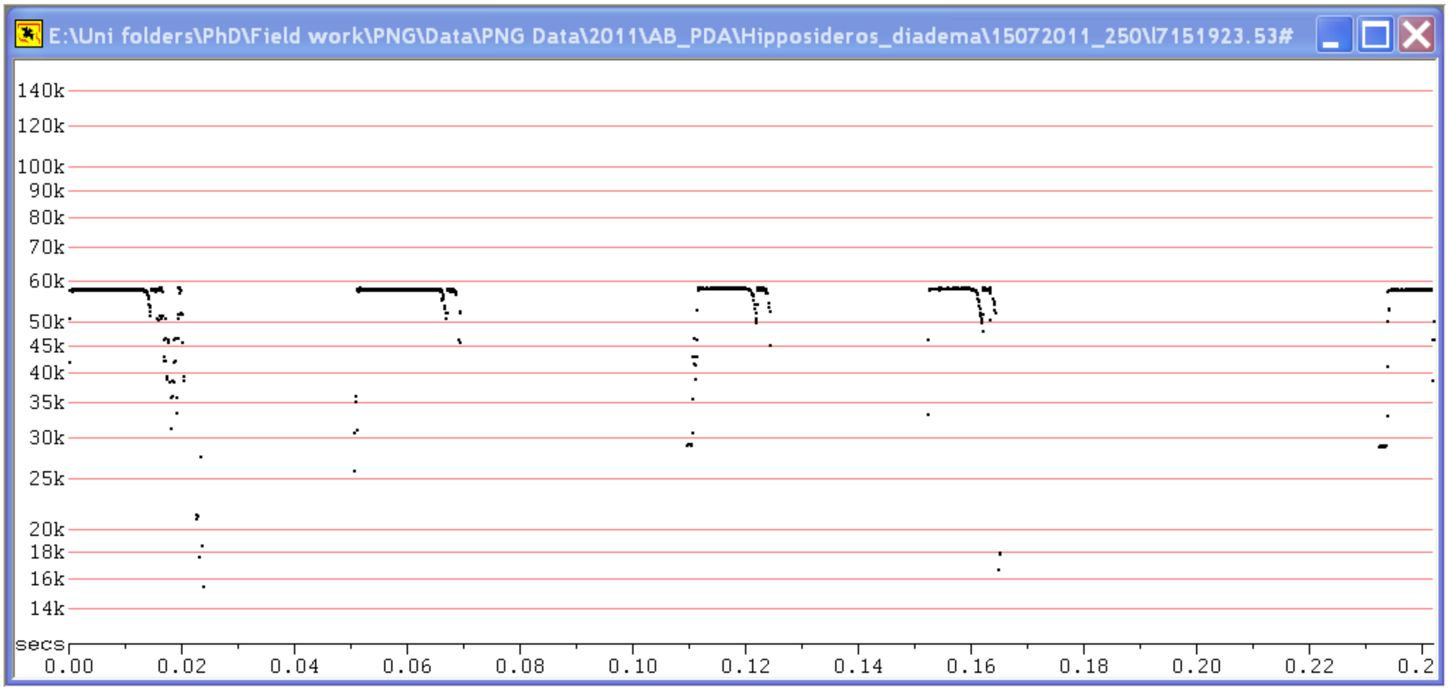
This species is easily recognisable by its considerable size. Fur is mottled grey and white in colouration with distinctive dark strips on the head and back. Forearm parameters recorded were in accordance with records made by Flannery (1995) and Bonacorsso (1998), however maximum weight was slightly higher than previously recorded.

Hipposideridae

New altitudinal record for PNG

New call for Huon Peninsula

A total of 72 reference call files were recorded from two individuals during handling and upon release. The call is of a constant frequency and of slightly longer duration than is typical of Hipposideros. The characteristic frequency is around 58kHz with pulses sometimes ending with a down sweeping tail dropping around 8kHz in frequency. The call is displayed below as an uncompressed file in F7 magnification. This species call was also detailed by Leary and Pennay



		Hipposideros diadema											
		Flannery (1995)				**Bonaccorso (1998)**				**This study**			
FA	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	77.70	75.40	81.20	5	-	75.40	81.20	16	-	-	-	0
	F	81.10	77.90	82.20	2	-	72.60	82.20	6	80.95	79.90	82.0	2
	J	-	-	-	-	-	71.80	72.70	2	-	-	-	0
WT	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	36.50	33.50	42.50	5	-	33.50	42.50	14	-	-	-	0
	F	38.80	34.05	43.00	2	-	34.50	43.00	5	45.25	41.5	49.0	2
	J	-	-	-	-	-	26.70	27.80	2	-	-	-	0

(2011). Calls recorded during this survey were similar in frequency to those recorded by Churchill (2008) and Leary and Pennay but were of the much flatter shape

Hipposideros diadema			
Elevation (m asl)	**Flannery (1995)**	**Bonaccorso (1998)**	**This study**
3000m			
2800m			
2500m			
2350m			
2050m			X
1550m			
1150m	X (1210m)	X (1300m)	
950m	X	X	X
750m	X	X	
250m	X	X	X
0m	X (50m)	X	

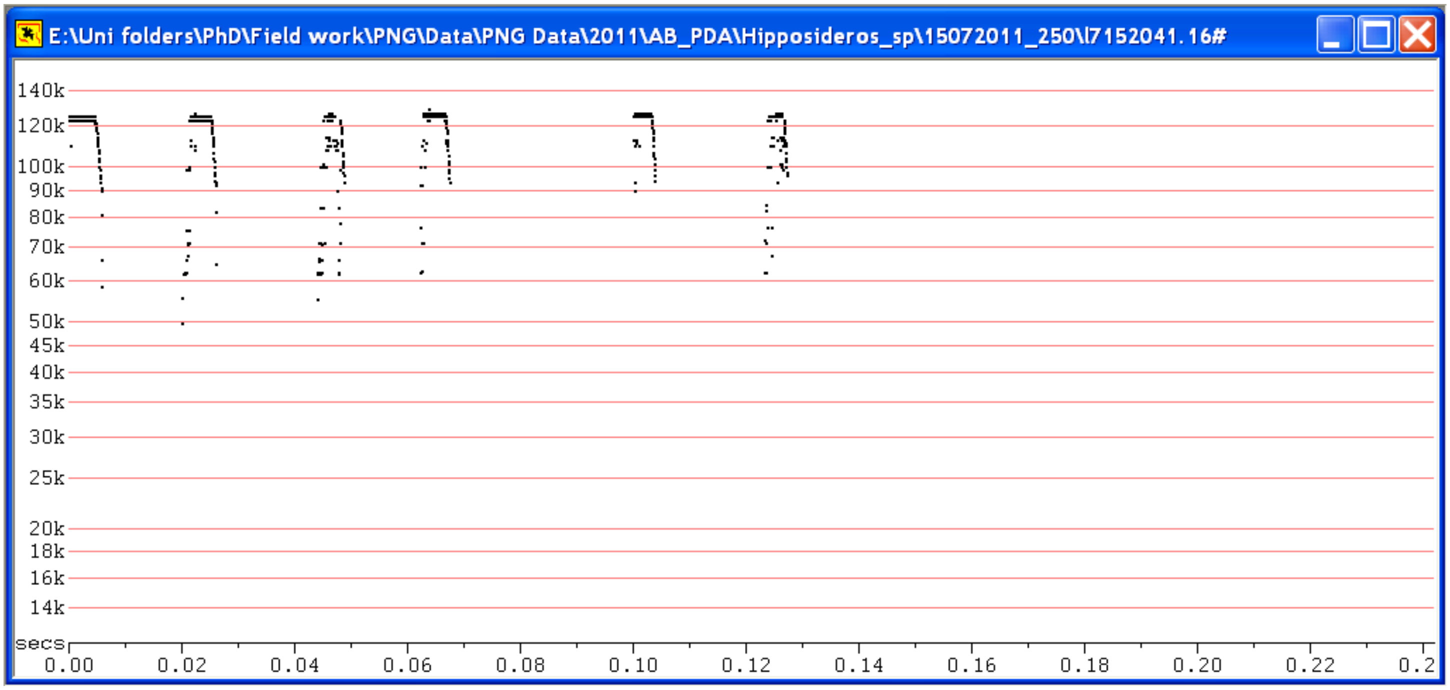
Hipposideros maggietaylorae
Maggie Taylor's Leaf-Nosed Bat

Hipposideridae

New call for Huon Peninsula

This species is endemic to Papua New Guinea, where two subspecies exist. *Hipposideros maggietaylorae erroris* occurs on the mainland, while *H. m. maggietaylorae* occurs on the Bismarck Archipelago (Bonaccorso, 1998). This species was not acoustically detected during passive surveying, and only one individual was captured. Capture was made in a harp trap erected at 250m elevation. Previous studies have recorded this species from sea level up to 360m in elevation (Flannery, 1995; Bonaccorso, 1998).

Nose leaf is of simple structure with no projections or lateral leaflets. Fur of the individual captured was long and woolly with a mottled grey brown colour with a yellowish tinge. Fur on the head was a darker brown with an orangish tinge. In field identification of this species was problematic with some identifying characteristics matching more so to *Hipposideros calcartus*. Bonaccorso (1998) lists the presence of four tail vertebrae as an identifying characteristic of this species. However, this individual was found to have five tail vertebrae as detailed for *H. calcartus.* In addition, ear size and shape matches that of *H. calcartus,* while the ribbing on the outer margin of the inner ear matches that of *H. maggietaylorae* (Bonacorsso, 1998). Positive identification of this species was eventually confirmed based on its



		Hipposideros maggietaylorae											
		Flannery (1995)				**Bonaccorso (1998)**				**This study**			
FA	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	54.00	53.00	56.00	3	-	52.50	58.20	23	-	-	-	0
	F	56.50	55.70	57.00	2	-	52.50	58.50	27	57.9	-	-	1
	J	-	-	-	-	-	52.20	57.20	2	-	-	-	0
WT	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	15.80	14.50	17.00	2	-	14.50	20.00	11	-	-	-	0
	F	19.30	18.00	20.50	2	-	13.00	23.40	10	16.0	-	-	1
	J	-	-	-	-	-	-	-	-	-	-	-	0

echolocation call, with the reference call recorded upon release of the individual matching one positively identified as *H. maggietaylorae* by Leary and Pennay (2011). Forearm parameters recorded were in accordance with records made by Flannery (1995) and Bonacorsso (1998), however weight was slightly lower than previously recorded.

A total of 7 reference call files were recorded during handling and upon release. The call is of a constant frequency and of short duration as is typical of Hipposideros. The characteristic frequency is around 121kHz, with pulses ending with a long down sweeping tail dropping around 30kHz in frequency. The call is displayed below as an uncompressed file in F7 magnification. Calls recorded during this survey matched the ones recorded by Leary and Pennay (2011).

Hipposideros maggietaylorae			
Elevation (m asl)	**Flannery (1995)**	**Bonaccorso (1998)**	**This study**
3000m			
2800m			
2500m			
2350m			
2050m			
1550m			
1150m			
950m			
750m			
250m	X (360m)	X (300m)	X
0m	X	X	

Rhinolophus euryotis
New Guinea Horseshoe Bat

Rhinolophidae

New altitudinal record for PNG

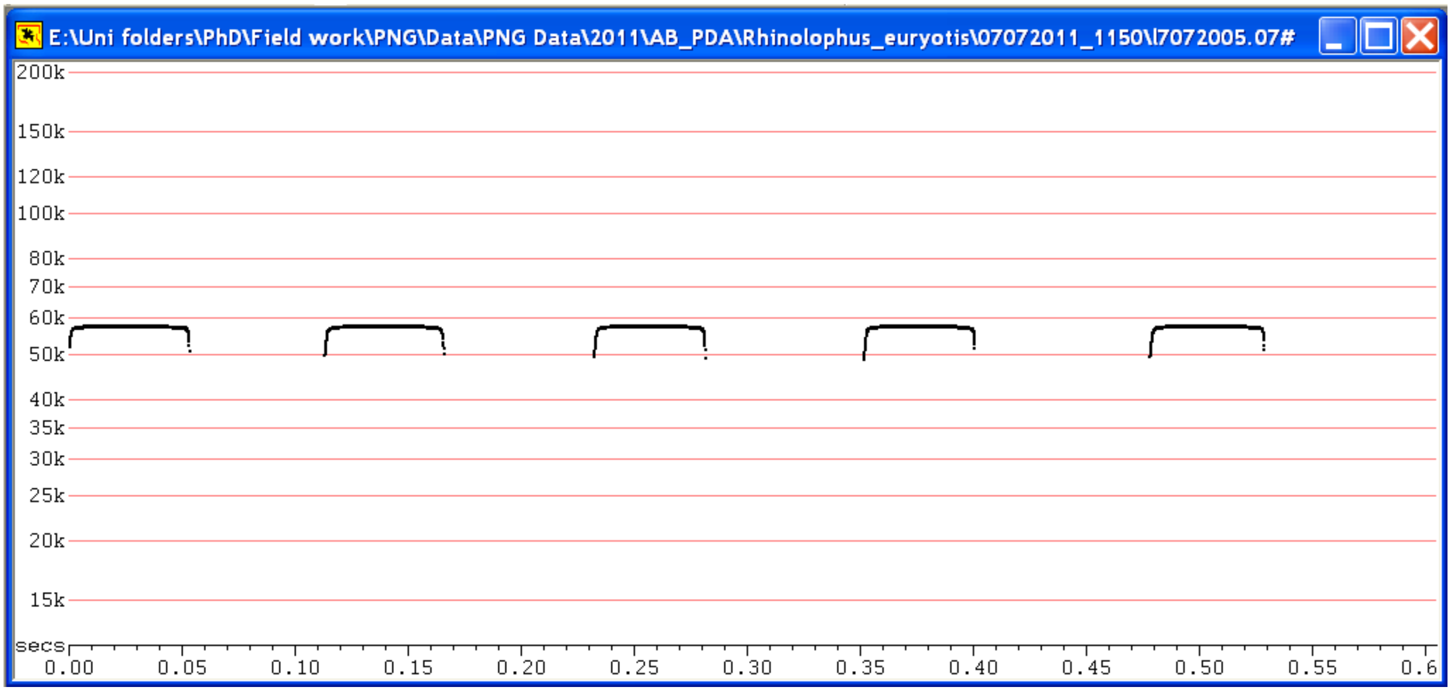
New call for Huon Peninsula

The largest Rhinolophid in Papua New Guinea, where only one of the five subspecies occurs (Bonaccorso, 1998).

This species was the most commonly detected during the survey. A total of 1842 files containing calls from this species were recorded during passive acoustic surveying. A total of 60 individuals were trapped, with eight of these being captured in mist nets. Individuals were captured between 250m and 1550m elevation. This species was also acoustically detected at 250m, 750m, 950m, 1150m, 1550m and 2050m elevation. Previous studies have recorded this species from sea level up to 1800m in elevation (Flannery, 1995; Bonaccorso, 1998; Dabek, 2001, 2003). This survey extends the known Altitudinal range of this species in Papua New Guinea.

Nose leaf is of a complex structure with the hairy, rounded tip of the lancet rising above the top of the head. A distinctive white stripe runs down the centre of the nose lead to the lip. Fur is bicoloured with medium brown tips over a lighter grey brown base. Forearm parameters recorded were in accordance with records made by Flannery (1995) and Bonacorsso (1998), however maximum female weight was slightly higher than previously recorded.

A total of 296 reference call files were recorded from 60 individuals during handling and upon release.



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		Rhinolophus euryotis											
		Flannery (1995)				**Bonaccorso (1998)**				**This study**			
FA	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	-	-	-	-	-	50.00	58.50	33	56.97	51.47	59.96	12
	F	56.70	53.90	59.10	4	-	53.00	58.00	22	56.98	54.81	59.3	48
	J	-	-	-	-	-	-	-	-	-	-	-	0
WT	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	-	-	-	-	-	14.20	19.30	8	18.04	16.5	20	12
	F	16.60	16.00	17.00	4	-	17.80	21.50	4	18.52	15	27.5	48
	J	-	-	-	-	-	-	-	-	-	-	-	0

The call is of a constant frequency of moderate duration typical of Rhinolophids. The characteristic frequency is around 58kHz with pulses beginning and ending with a down sweeping tail dropping around 8kHz in frequency. Although the call of this species is similar in shape and frequency to that of *Hipposideros diadema* their calls can be separated due to the longer pulse duration and the presence of a downwards sweep at the beginning of *R. euryotis* calls. The call is displayed below as an uncompressed file in F6 magnification. This species call was also detailed by Leary and Pennay (2011). Calls recorded during this survey matched the ones recorded by Leary and Pennay (2011).

Rhinolophus euryotis				
Elevation (m asl)	**Flannery (1995)**	**Bonaccorso (1998)**	**Dabek (2001, 2003)**	**This study**
3000m				
2800m				
2500m				
2350m				
2050m				X
1550m	X (1720m)	X (1800m)		X
1150m	X	X		X
950m	X	X	X (900m)	X
750m	X	X	X	X
250m	X	X	X	X
0m	X (165m)	X		

Rhinolophus megaphyllus
Eastern Horseshoe Bat

The smallest Rhinolophid in Papua New Guinea. Three of the five subspecies occur in Papua New Guinea, though only *R. megaphyllus fallax* occurs on the mainland (Bonaccorso, 1998).

A total of 320 files containing calls from this species were recorded during passive acoustic surveying. A total of 13 individuals were captured during this survey, with all of these being captured in harp traps. Individuals were captured between 250m and 2050m elevation. This species was also acoustically detected at 250m, 1150m, 1550m, 2050m, and 2350m elevation. Previous studies have recorded this species from sea level up to 1600m in elevation (Flannery, 1995; Bonaccorso, 1998). This survey extends the known altitudinal range of this species in Papua New Guinea.

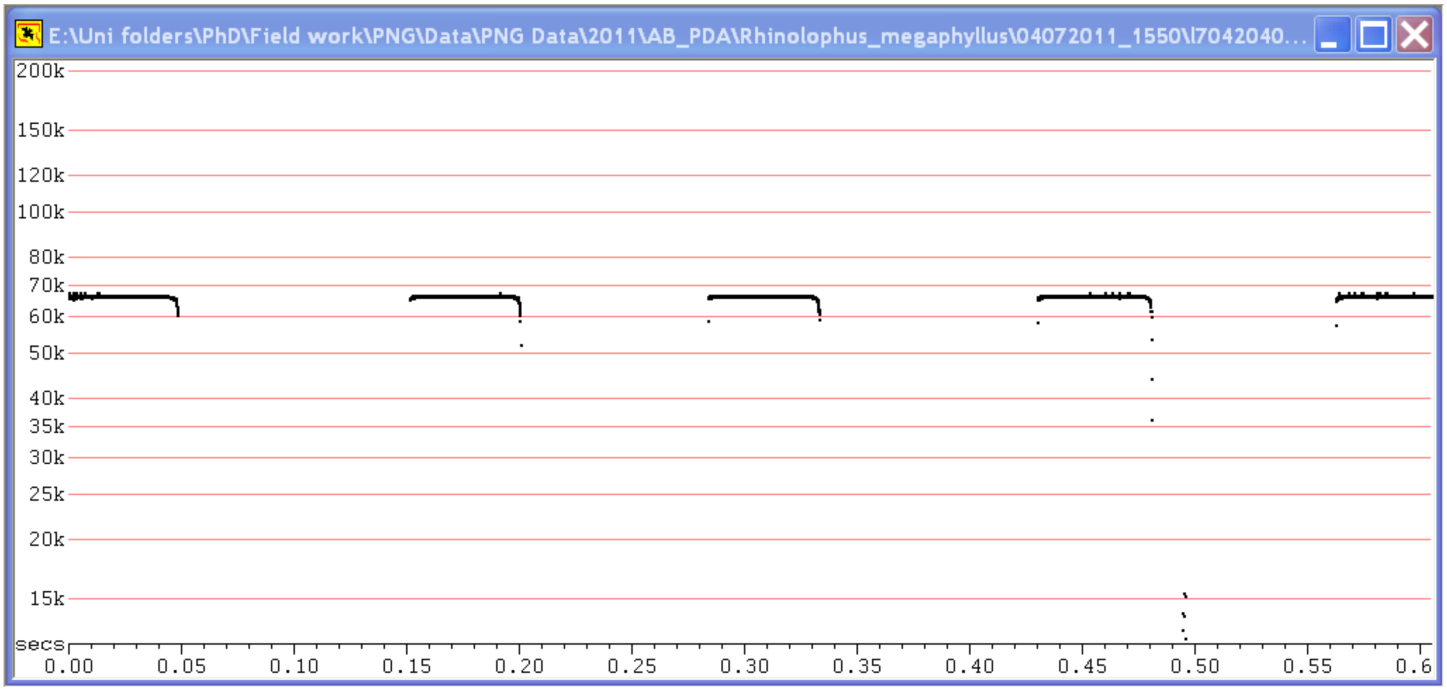
Nose leaf is of a complex structure with a long, narrow, hairless tip. In all individuals captured, the nose leaf had a distinctive yellowish colour. Fur is mottled brown grey all over. Forearm parameters and weights were slightly higher than previously recorded (Flannery, 1995; Bonacorsso, 1998).

Rhinolophidae

New altitudinal record for PNG

New call for Huon Peninsula

A total of 120 reference call files were recorded from 13 individuals during handling and upon release. The call is of a constant frequency of moderate duration typical of Rhinolophids. The characteristic frequency is



		Rhinolophus megaphyllus											
		Flannery (1995)				**Bonaccorso (1998)**				**This study**			
FA	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	49.10	-	-	1	-	43.00	49.00	2	48.44	46.04	49.68	3
	F	48.70	-	-	1	-	45.60	47.70	4	49.82	46.47	59.80	10
	J	-	-	-	-	-	-	-	-	-	-	-	0
WT	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	9.00	-	-	1	-	9.00	-	1	10.33	10	11.00	3
	F	10.50	-	-	1	-	12.00	-	1	10.42	8	12.00	10
	J	-	-	-	-	-				-	-	-	0

around 68kHz with pulses often ending with a down sweeping tail dropping around 8kHz in frequency. The call is displayed below as an uncompressed file in F6 magnification (Figure 19). Calls recorded during this survey matched the ones recorded in Papua New Guinea by Leary and Pennay (2011), and those recorded in Australia (Churchill, 2008).

Rhinolophus megaphyllus			
Elevation (m asl)	**Flannery (1995)**	**Bonaccorso (1998)**	**This study**
3000m			
2800m			
2500m			
2350m			X
2050m			X
1550m		X (1600m)	X
1150m		X	X
950m		X	
750m		X	
250m	X (260 – 360m)	X	X
0m		X	

Pipistrellus collinus
Mountain Pipistrelle

Vespertilionidae

New record for Huon Peninsula

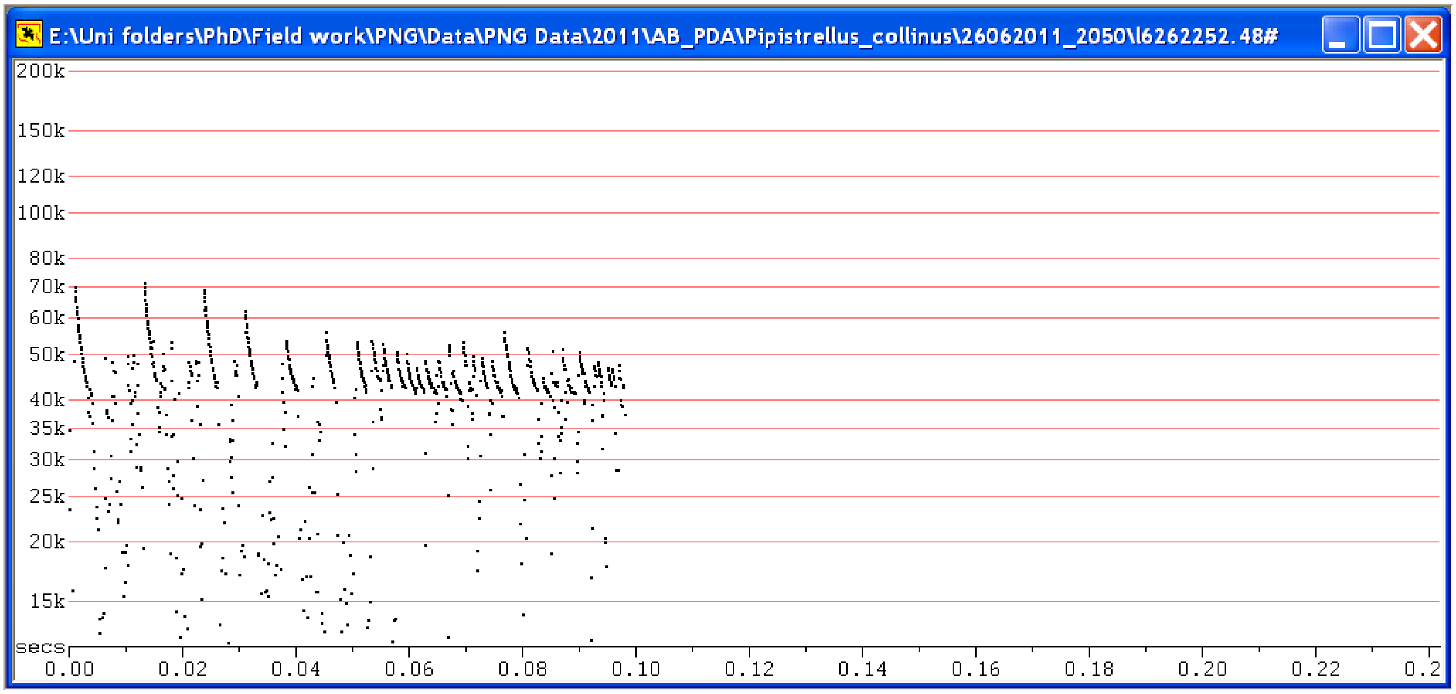
New call for Huon Peninsula

This monotypic species is the largest Pipistrellus in Papua New Guinea (Bonaccorso, 1998).

This species was not conclusively detected during passive acoustic surveying. Only one individual was captured during this survey. To our knowledge, this is the first record of this species for the Huon Peninsula. Capture was made in a harp trap, at 2050m elevation. Previous studies have recorded this species from sea level up to 2950m in elevation (Flannery, 1995; Bonaccorso, 1998).

Fur of the individual captured was bicoloured with light brown tips over a darker base. Dorsum fur was found to be slightly darker than that of the ventrum. The muzzle and ears were relatively hairless, and light brown in colour. The eye is small but conspicuous. Ears are triangular and funnel shaped, with a long slightly inward curved tragus. Morphological parameters recorded were in accordance with previous records (Flannery, 1995; Bonacorsso, 1998).

Five reference call files were collected from this species upon release. The call is frequency modulated, with steep linear pulses ending with a slight curve, and a characteristic frequency around 40kHz. Pulses show upsweeps of between 10kHz and 30 kHz. The call is displayed below as a compressed file in F7 magnification.



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		Pipistrellus collinus											
		Flannery (1995)				**Bonaccorso (1998)**				**This study**			
FA	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	37.20	35.50	38.00	5	-	34.00	38.00	24	-	-	-	0
	F	37.30	36.00	37.80	11	-	33.00	38.50	19	35.58			1
	J	-	-	-	-	-	-	-	-	-	-	-	0
WT	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	5.50	5.10	5.80	5	-	4.30	7.10	19	-	-	-	0
	F	6.40	5.90	6.90	11	-	4.30	8.50	18	5.6			1
	J	-	-	-	-	-	-	-	-	-	-	-	0

Pipistrellus collinus			
Elevation (m asl)	**Flannery (1995)**	**Bonaccorso (1998)**	**This study**
3000m			
2800m	X (2950m)	X	
2500m	X	X	
2350m	X	X	
2050m	X (2950m)	X	X
1550m	X (1770m)	X	
1150m		X	
950m		X	
750m		X	
250m			
0m			

Murina florium
Insectivorous Tube-nosed Bat

Vespertilionidae

New call for Huon Peninsula

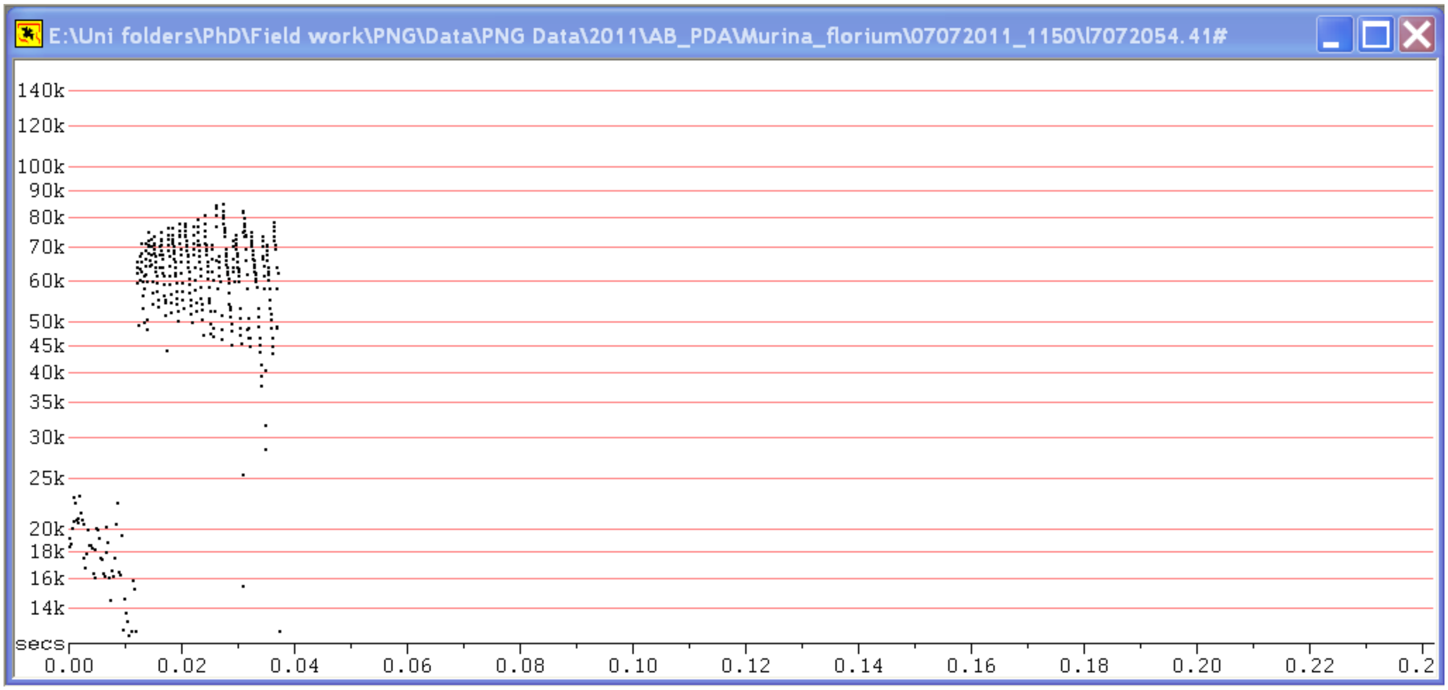
New call for PNG

Also known commonly as the Flores Murine bat, this species is the only representative of this subfamily (Murininae) present in Papua New Guinea (Bonaccorso, 1998).

This species was not conclusively detected during passive acoustic surveying. Only one individual was captured during this survey. Capture was made in a mist net erected at 1150m elevation. Previous studies have recorded this species from 400m up to 2800m in elevation (Flannery, 1995; Bonaccorso, 1998).

This species is easily distinguished by its tubular nostrils. Fur of the individual captured was thick and woolly with a mottled dark brown to golden brown colour, with silver flecks. Dorsum fur was found to be slightly darker than that of the ventrum. Morphological parameters recorded were in accordance with previous records (Flannery, 1995; Bonacorsso, 1998; Dabek, 2001, 2003).

Only two reference call files could be collected from this species upon its release. The call is frequency modulated, with steep linear pulses of highly variable frequencies and a characteristic frequency of around 50kHz. Pulses are clumped closely together. The call is displayed below as a compressed file in F7 magnification. Calls recorded during this survey are similar to those recorded for this species in Australia, though are of a slightly higher frequency (Churchill, 2008).



		Murina florium											
		Flannery (1995)				**Bonaccorso (1998)**				**This study**			
FA	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	33.20	-	-	1	-	33.00	36.20	4	-	-	-	0
	F	35.00	-	-		-	33.00	35.70	8	35.07			1
	J	-	-	-	-	-	-	-	-	-	-	-	0
WT	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	6.20	-	-	1	-	6.00	6.90	3	-	-	-	0
	F	4.25	-	-	1	-	4.30	8.80	5	8.5			1
	J	-	-	-	-	-	-	-	-	-	-	-	0

Murina florium				
Elevation (m asl)	**Flannery (1995)**	**Bonaccorso (1998)**	**Dabek (2001, 2003)**	**This study**
3000m				
2800m		X		
2500m		X	X (2600m)	
2350m		X	X (2300m)	
2050m	X (1720m)	X		
1550m	X	X		X
1150m	X	X		
950m	X	X	X (900m)	
750m	X (700m)	X (400m)	X	
250m			X	
0m				

Nyctophilus microtis *Papuan Big-Eared bat*

Vespertilionidae

New record for Huon Peninsula

New altitudinal record for PNG

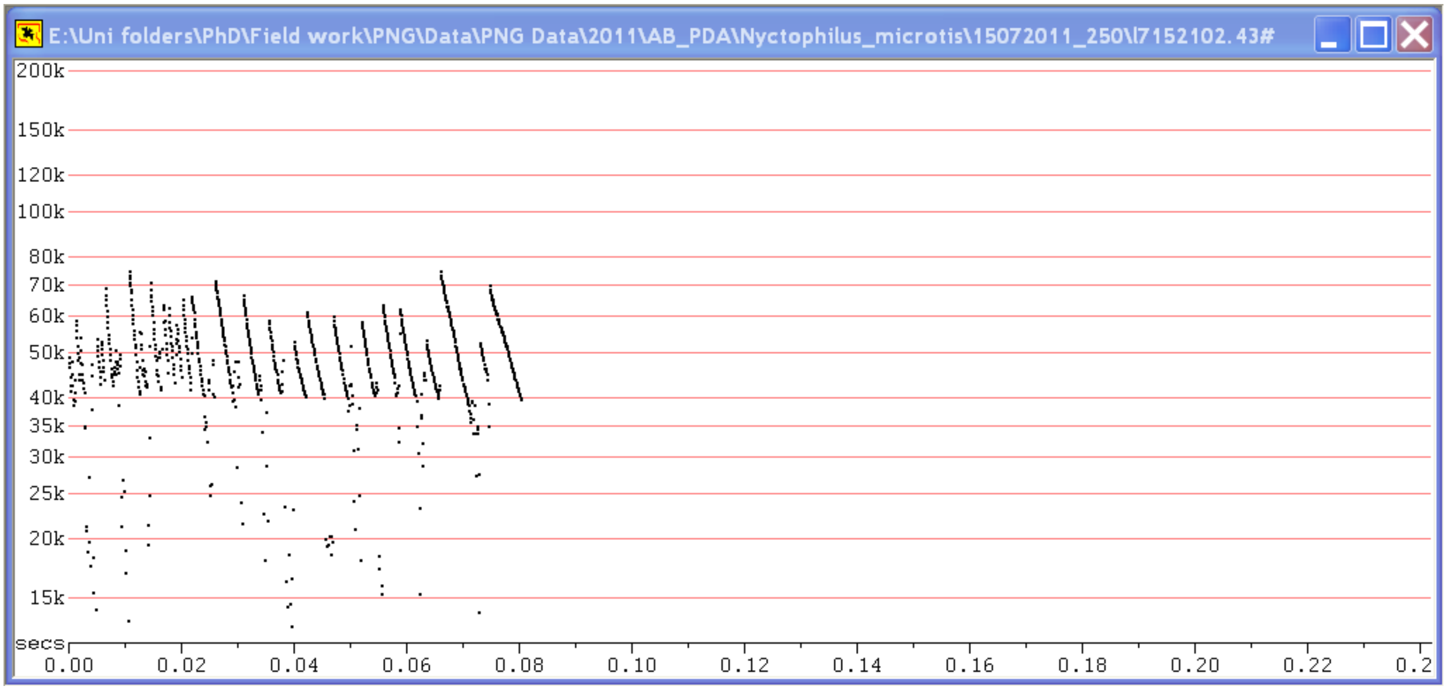
New call Huon Peninsula

New call for PNG

This species is endemic to Papua New Guinea (Bonaccorso, 1998). This species is also commonly known as the Small eared Nyctophilus (Flannery, 1995).

A total of 91 files containing calls from this species were recorded during passive surveying, and seven individuals were captured. Four individuals were caught using harp traps while three were captured in mist nets. Captures were made between 250m and 3000m elevation. This species was also acoustically detected at 250m, 750m, 1150m, and 1550m elevation. Previous studies have recorded this species from sea level up to 2600m in elevation (Flannery, 1995; Bonaccorso, 1998). This survey extends the known altitudinal range of this species in Papua New Guinea.

Distinctive features of this genus are the presence of large folded ears joined by a membrane above the head, and a squarish muzzle with simple nose leaf defined by a prominent upper ridge. The ear of *N. microtis* is slightly narrower and more tapered than other species, and is lightly haired. The tragus is long and almost rectangular in shape, narrowing only slightly



		Nyctophilus microtis											
		Flannery (1995)				**Bonaccorso (1998)**				**This study**			
FA	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	39.00	38.30	39.80	4	-	37.00	40.10	16	39.96	39.05	40.95	5
	F	38.00	-	-	1	-	38.00	40.90	11	41.55	41.5	41.6	2
	J	-	-	-	-	-	-	-	-	-	-	-	0
WT	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	6.70	6.00	8.00	4	-	5.80	9.50	9	7.99	7.4	9	5
	F	7.50	-	-	1	-	6.00	8.00	5	9.5	8.5	10.5	2
	J	-	-	-	-	-	-	-	-	-	-	-	0

at the tip. Fur is bicoloured with a dark base under medium brown tips, with the ventrum being slightly paler. Morphological parameters recorded for males were in accordance with previous records, though females captured during this survey were found to be slightly larger in forearm and weight (Flannery, 1995; Bonacorsso, 1998) .

A total of 10 reference call files were collected from seven individuals upon release. The call is frequency modulated, with linear pulses of highly variable frequencies and a characteristic frequency of around 40kHz. Pulses have a slight leftwards lean to them, but no curve is present. The call is displayed below as a compressed file in F7 magnification.

Nyctophilus microtis				
Elevation (m asl)	**Flannery (1995)**	**Bonaccorso (1998)**	**Dabek (2001, 2003)**	**This study**
3000m				X
2800m				
2500m				
2350m				
2050m	X (2600m)			X
1550m	X			X
1150m	X	X (1450m)	X (1280m)	X
950m	X	X		
750m	X	X		X
250m	X (200m)	X		X
0m		X		

Kerivoula muscina
Fly River Woolly bat

Vespertilionidae

New record for Huon Peninsula

This species is endemic to Papua New Guinea (Bonaccorso, 1998). This species is also commonly known as the Fly River Trumpet-eared bat (Flannery, 1995).

Two individuals were captured during this survey. Both individuals were caught using harp traps erected at 300m. Previous studies have recorded this species from sea level up to 1600m in elevation (Flannery, 1995; Bonaccorso, 1998).

This species is easily distinguished by its small size and distinctive orange glands located on the forehead on either side of the nose. The ear is broad and funnel like, and is lightly haired. The tragus is long and points at the tip, with a slight inwards curve in towards the head. Fur is bicoloured with a dark base under light orangey brown tips, with the ventrum being slightly greyer. Morphological measurements are in accordance with previous records (Flannery, 1995; Bonacorsso, 1998).

A reference call could not be obtained from this species, most likely because *Kerivoula* produce very low intensity calls.

		Kerivoula muscina											
		Flannery (1995)				**Bonaccorso (1998)**				**This study**			
FA	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	32.40	31.80	33.00	3	-	32.00	33.00	5	33.50	33.50	33.50	1
	F	34.20	-	-	1	-	32.40	36.00	7	35.30	35.30	35.30	1
	J	-	-	-	-	-	-	-	-	-	-	-	0
WT	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	4.70	4.00	5.40	2	-	4.00	5.00	3	4.50	4.50	4.50	1
	F	5.10	-	-	1	-	-	5.00	2	5.00	5.00	5.00	1
	J	-	-	-	-	-	-	-	-	-	-	-	0

Kerivoula muscina			
Elevation (m asl)	**Flannery (1995)**	**Bonaccorso (1998)**	**This study**
3000m			
2800m			
2500m			
2350m			
2050m			
1550m	X (1600m)	X (1600m)	
1150m	X	X	
950m	X	X	
750m	X	X	
250m	X	X	
0m	X (20m)	X	X

Mosia nigrescens
Lesser Sheath-tailed Bat

The smallest of the emballonurids found in Papua New Guinea where two of its three subspecies occur (Bonaccorso, 1998). *Mosia nigrescens papuana* occurs on the mainland, while *M. n. solomonis* is only found on islands to the north east.

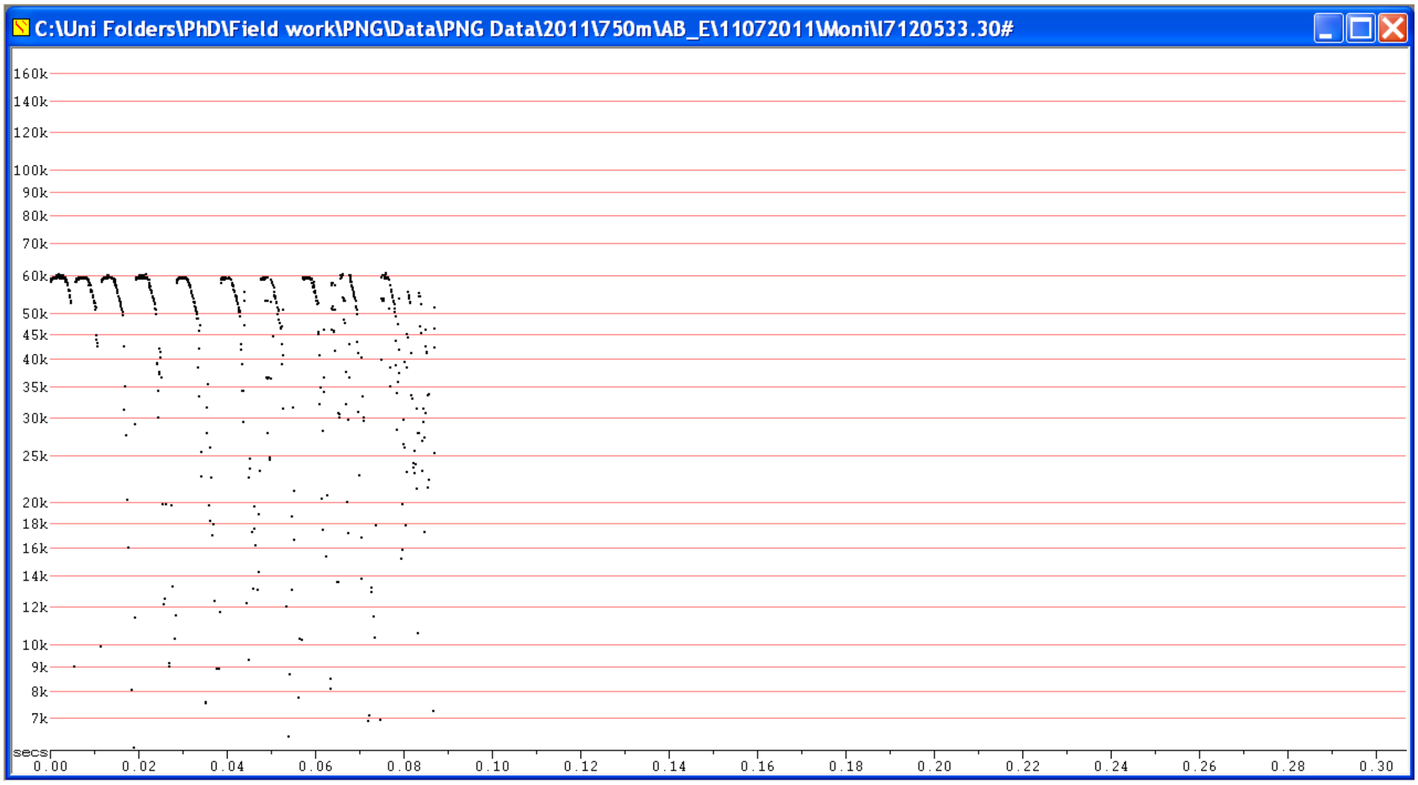
Presence determined by positive identification of echolocation calls recorded during passive acoustic monitoring, based on calls characterised by Armstrong and Aplin (2011), and Leary and Pennay (2011). A total of 136 files containing calls from this species were recorded during passive surveying. No individuals were captured. This species was detected at 0m, 250m, and 750m. Previous studies have recorded this species from sea level up to 1600m in elevation (Bonaccorso, 1998; Armstrong and Aplin; Leary and Pennay, 2011).

The call is frequency modulated, consisting of short linear pulses followed by a steep decrease in frequency around 10 kHz. Characteristic frequency is approximately 60kHz. The call is displayed below as a compressed file in F7 magnification.

Emballonuridae

New call for Huon Peninsula

Mosia nigricens				
Elevat. (m asl)	**Armstrong and Aplin (2011)**	**Leary and Pennay (2011)**	**Bonaccorso (1998)**	**This study**
3000m				
2800m				
2500m				
2350m				
2050m				
1550m	X (1600m)		X (1600)	X
1150m			X	X
950m			X	
750m	X (500m)		X	X
250m		X (270m)	X	X
0m			X	X



cf35

Microchiroptera

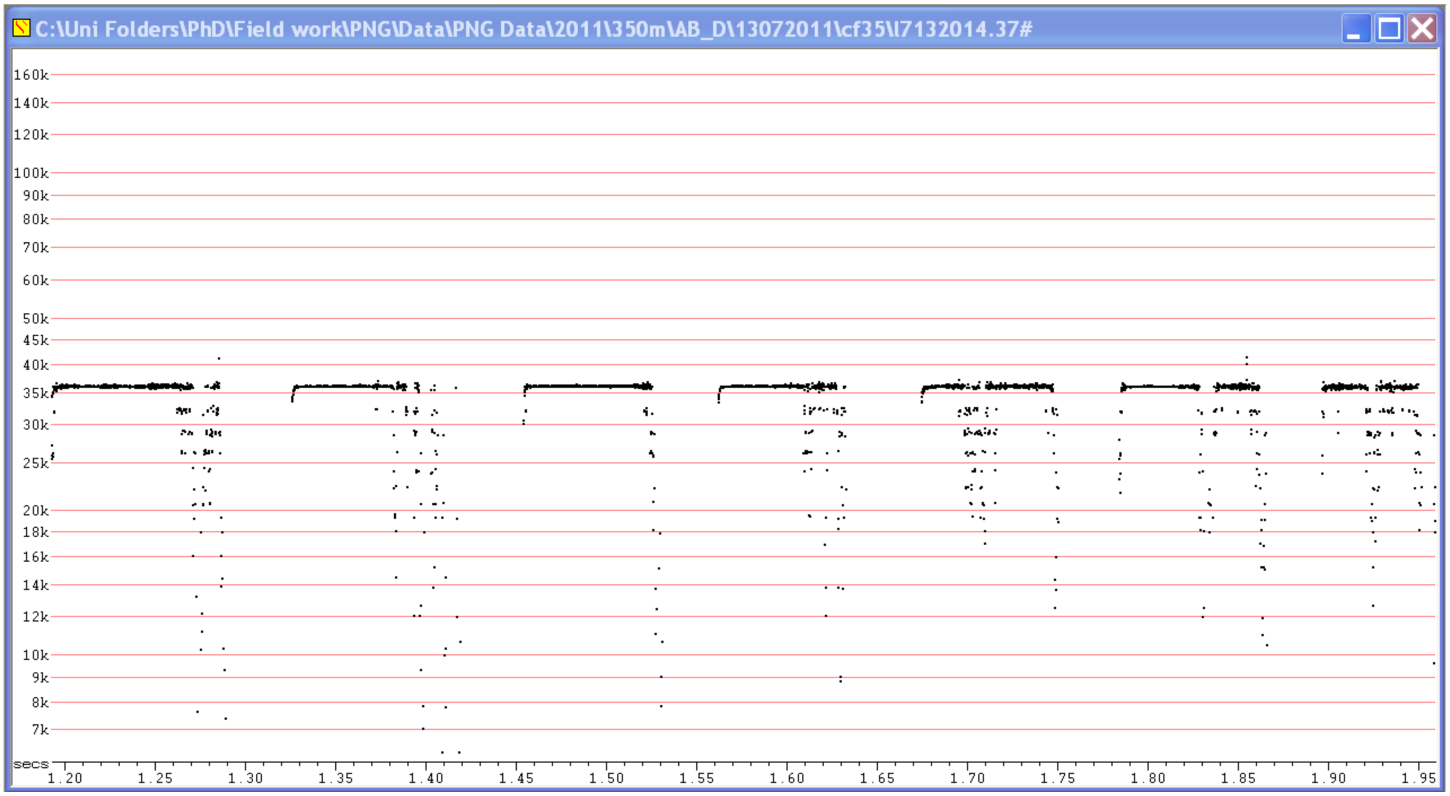
New call for Huon Peninsula

New call for PNG

Only one file containing calls of this species were recorded during this survey. Calls were collected at 250m elevation . No individuals emitting calls of this frequency were captured during this survey, and calls could not be matched to any species identified in other existing call libraries. Therefore, positive identification to species could not be made. This species was thus assigned a species code of cf35, detailing its constant frequency shape (cf) and characteristic frequency.

The call is of a constant frequency of moderate duration typical of Rhinolophids. The characteristic frequency is around 35kHz with pulses often beginning with a down sweeping tail dropping very slightly in frequency. The call is displayed below as an uncompressed file in F6 magnification.

cf35	
Elevation (m als)	**Detected**
3000m	
2800m	
2500m	
2350m	
2050m	
1550m	
1150m	
950m	
750m	
250m	X
0m	



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cfm46

Microchiroptera

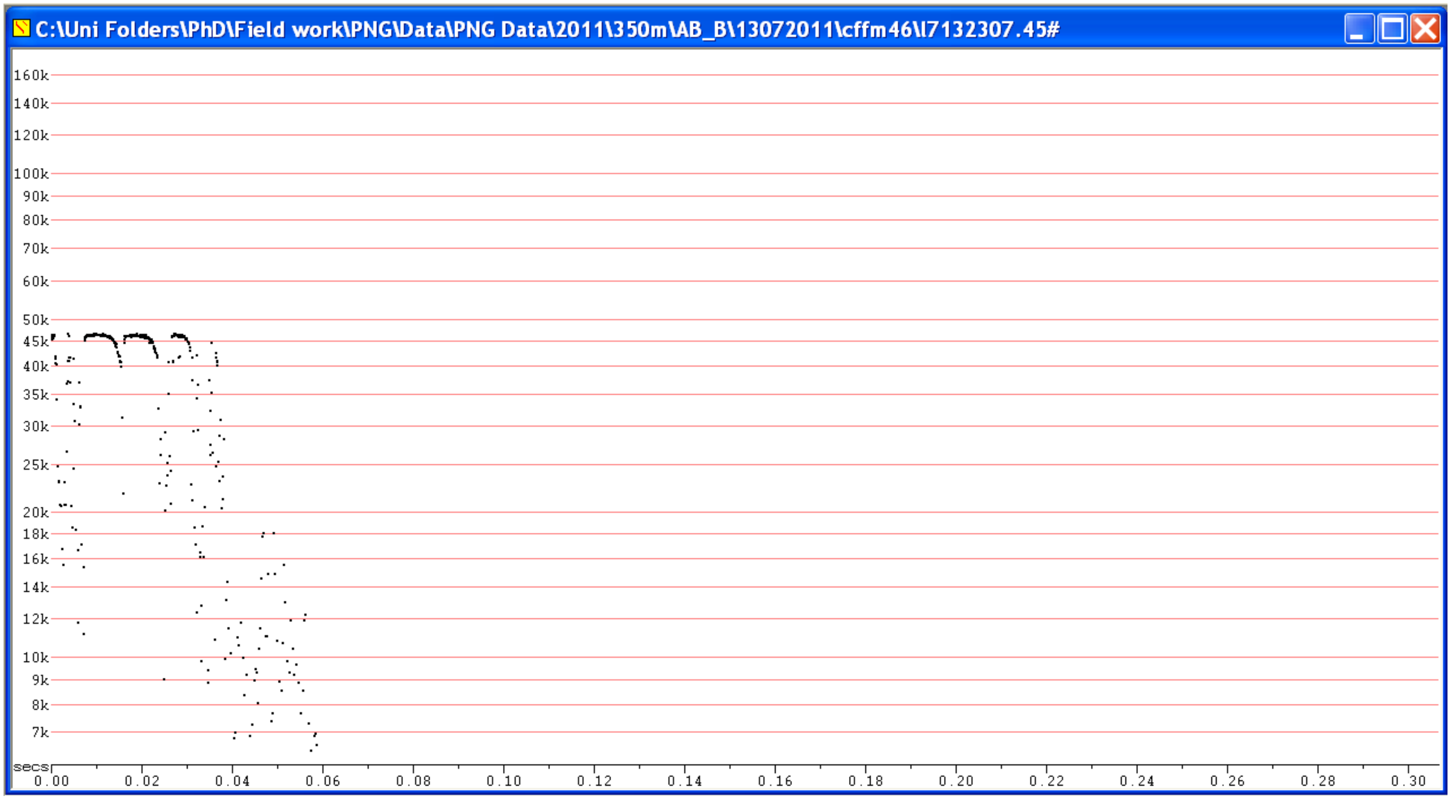
New call for Huon Peninsula

New call for PNG

Only 4 files containing calls of this species, all at 250m, were recorded, none of which could assigned to any species captured during this survey or matched to species identified in other call libraries. This species was thus assigned a species code of cffm46, detailing its almost constant frequency shape but frequency modulated nature (cffm) and characteristic frequency.

The call consists of a series of very flat pulses, with a characteristic frequency of around 46kHz, ending in a down sweep of around 5kHz. The call is displayed below as a compressed file in F7 magnification. Armstrong and Aplin (2011) collected similar shaped calls of a slightly lower frequency which they coded as 43 *i.fFM.d Emballonura sp.*. They commented that there appears to be high variation in characteristic frequencies of this call type across PNG, and that this may be due to high variability in calls among individuals of a single species, or may be multiple similar species (Armstrong and Aplin, 2011).

cfm46	
Elevation (m asl)	**Detected**
3000m	
2800m	
2500m	
2350m	
2050m	
1550m	
1150m	
950m	
750m	
250m	X
0m	



fm12

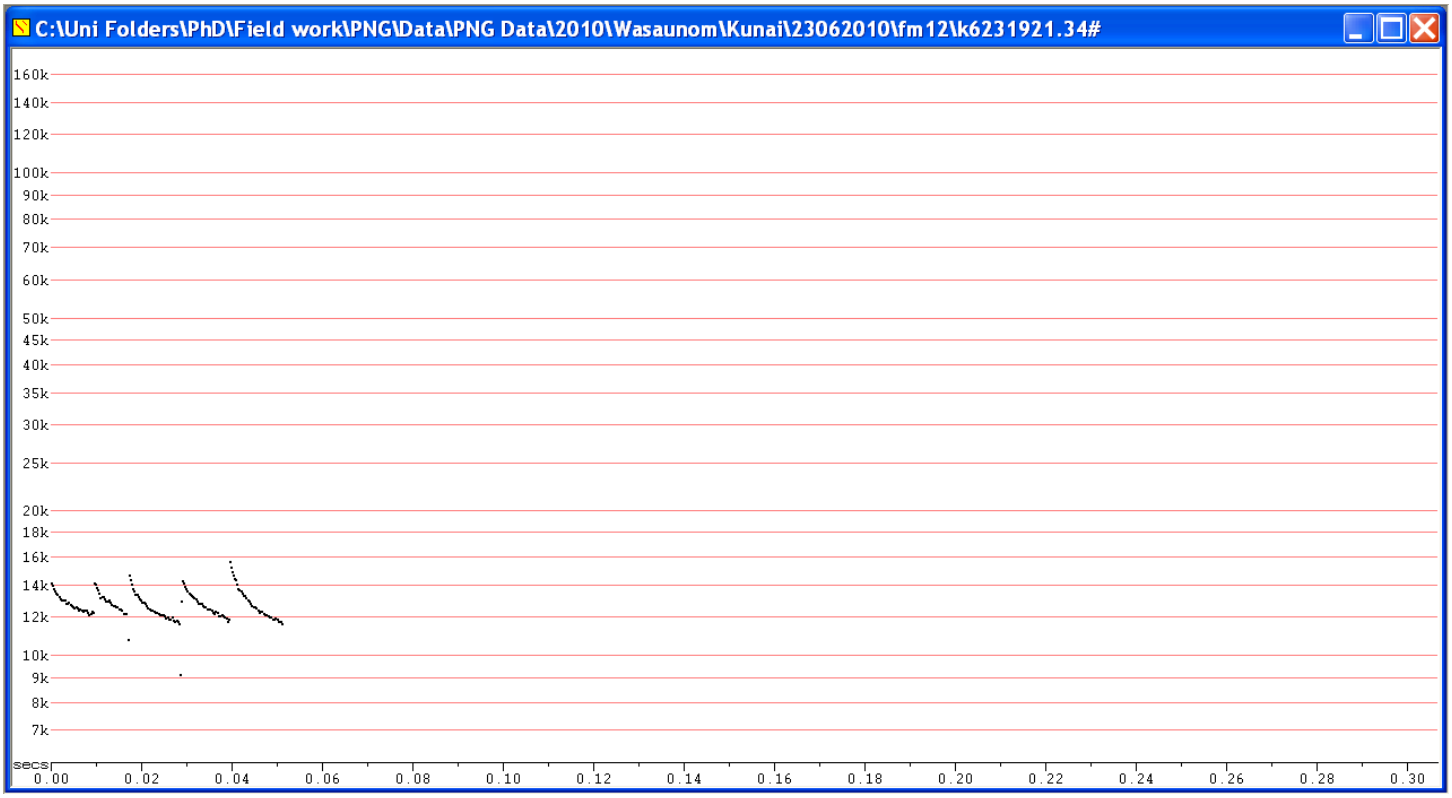
Microchiroptera

New call for Huon Peninsula
New call for PNG

A total of 150 files containing calls of this species were recorded during this survey. Calls were collected at 3000m elevation, from detectors places in open kunai areas around Wasaunon camp. No individuals emitting calls of this frequency were captured during this survey, and calls could not be matched to any species identified in other existing call libraries. Therefore, positive identification to species could not be made. This species was thus assigned a species code of fm12, detailing its frequency modulated shape (fm) and characteristic frequency.

The call consists of a series of leftward curving pulses with a characteristic frequency of around 12kHz, with an upwards sweep of around 2kHz. The call is displayed below as a compressed file in F7 magnification.

fm12	
Elevation (m asl)	**Detected**
3000m	X
2800m	
2500m	
2350m	
2050m	
1550m	
1150m	
950m	
750m	
250m	
0m	



fm52

A total of 12 files containing calls of this species were recorded at 250m, 750m, 2350m, and 3000m. Calls could not be assigned to any species captured during this survey or in existing call libraries: . this species was thus assigned a species code of fm52, detailing its frequency modulated shape (fm) and characteristic frequency. The call consists of a series of curving pulses, ending in a slight downward droop, with a characteristic frequency of around 52kHz . Pulses vary only slightly in frequency with upwards sweeps ranging between 7kHz and 20kHz. The call is displayed below as a compressed file in F7 magnification.

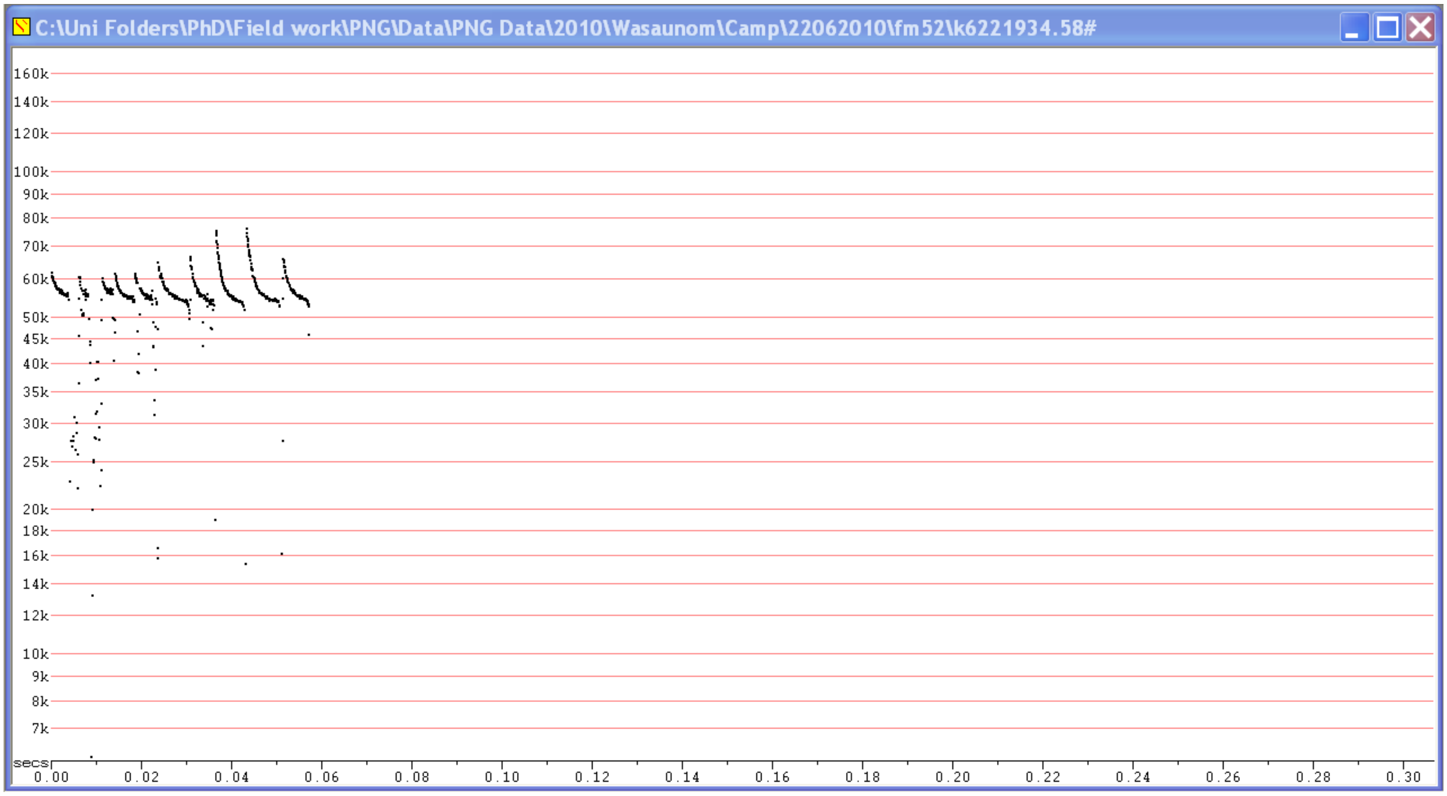
Armstrong and Aplin (2011) collected calls with a similar terminal droop, though with much steeper pulses, which they coded as 53*st.cFM.d.* They commented that pulses with this characteristic droop are likely to be from a species of *Miniopterus* or less likely a species of vespertilionid (Armstrong and Aplin, 2011).

Microchiroptera

New call for Huon Peninsula

New call for PNG

fm52	
Elevation (m asl)	**Detected**
3000m	X
2800m	
2500m	
2350m	X
2050m	
1550m	
1150m	
950m	
750m	X
250m	X
0m	



fm55

Microchiroptera

New call for Huon Peninsula

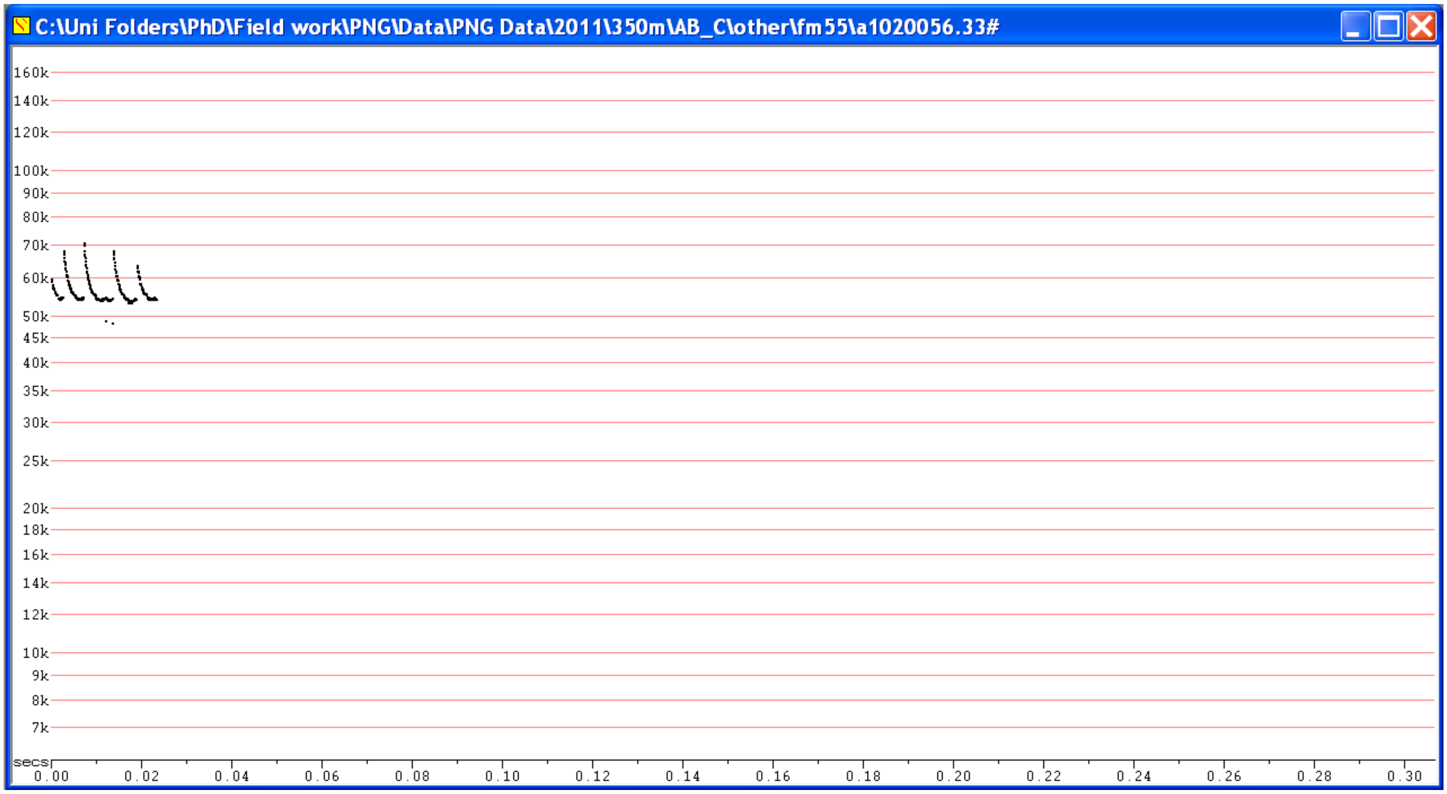
New call for PNG

A total of 25 files containing calls of this species were recorded during this survey. Calls were collected at 250m, 1550m, and 2050m. No individuals emitting calls of this frequency could be confidently assigned to any species captured during this survey, and calls could not be matched to any species identified in other existing call libraries. Therefore, positive identification to species could not be made. This species was thus assigned a species code of fm55, detailing its frequency modulated shape (fm) and characteristic frequency.

The call consists of a series of slightly leftwards leaning curved pulses, with upwards sweeps ranging between 5kHz and 15kHz, and a characteristic frequency of around 52kHz. The call is displayed below as a compressed file in F7 magnification.

It is possible that these calls may be made by the same species as calls coded fm52 as the call shapes and characteristic frequencies are similar (see 3.5.9). However, due to the lack of the distinctive terminal droop, this could not be confidently confirmed.

fm55	
Elevation (m asl)	**Detected**
3000m	
2800m	
2500m	
2350m	
2050m	X
1550m	X
1150m	
950m	
750m	
250m	X
0m	



sfm9

Microchiroptera

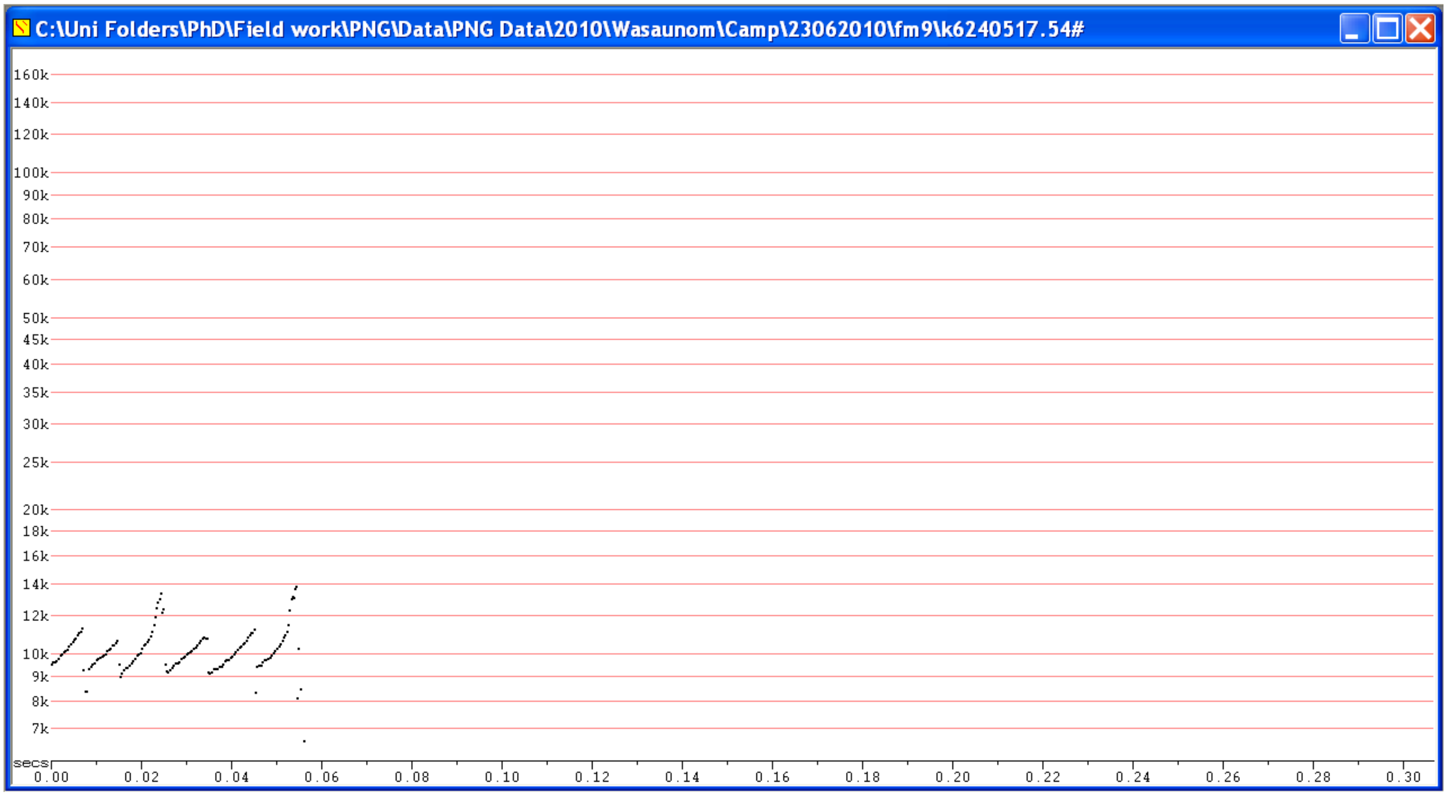
New call for Huon Peninsula

New call for PNG

Only two files containing calls of this species were recorded during this survey. Calls were collected at 3000m elevation, from detectors places in open areas around Wasaunon camp. No individuals emitting calls of this frequency were captured during this survey, and calls could not be matched to any species identified in other existing call libraries. This species was thus assigned a species code of sfm9, detailing its steep frequency modulated shape (sfm) and characteristic frequency. The upward frequency sweep of the call is very unusual for bats, and further observations are required to confirm the identity of this high frequency sound.

The call consists of a series of linear pulses with a characteristic frequency of around 9kHz. Pulses have a slight rightwards lean to them, with an upwards sweep of around 2kHz. The call is displayed as a compressed file in F7 magnification,

sfm9	
Elevation (m asl)	**Detected**
3000m	X
2800m	
2500m	
2350m	
2050m	
1550m	
1150m	
950m	
750m	
250m	
0m	



sfm14

Microchiroptera

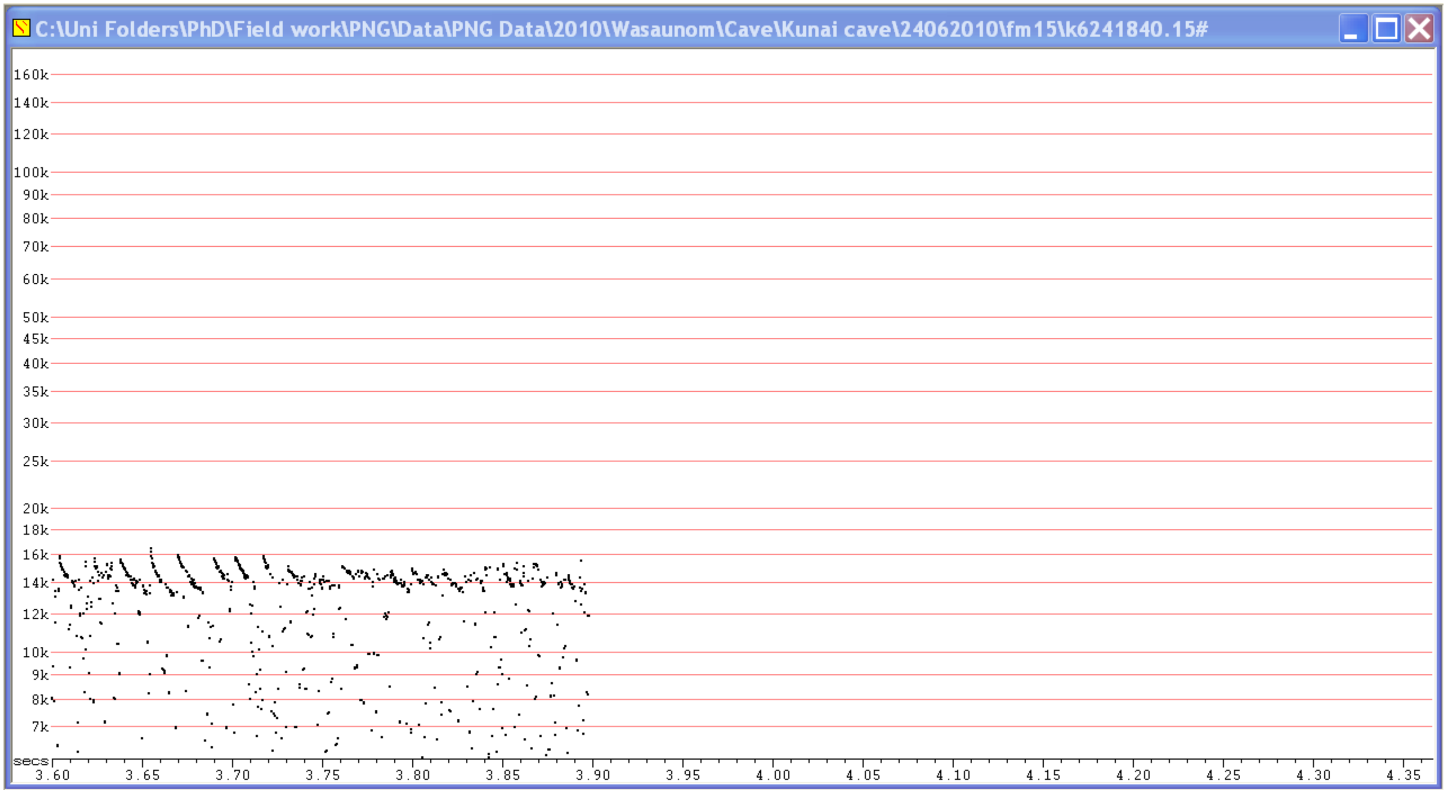
New call for Huon Peninsula

New call for PNG

Only four files containing calls of this species were recorded during this survey. Calls were collected at 3000m elevation, from detectors places in open areas around Wasaunon camp. No individuals emitting calls of this frequency were captured during this survey, and calls could not be matched to any species identified in other existing call libraries. This species was thus assigned a species code of sfm14, detailing its steep frequency modulated shape (sfm) and characteristic frequency.

The call consists of a series of leftward curving pulses with a characteristic frequency of around 14kHz, with an upwards sweep of around 2kHz. This call is similar in shape to unidentified call coded fm12, but at a slightly higher frequency. The call is displayed below as a compressed file in F6 magnification.

sfm14	
Elevation (m asl)	**Detected**
3000m	X
2800m	
2500m	
2350m	
2050m	
1550m	
1150m	
950m	
750m	
250m	
0m	



sfm22

Microchiroptera

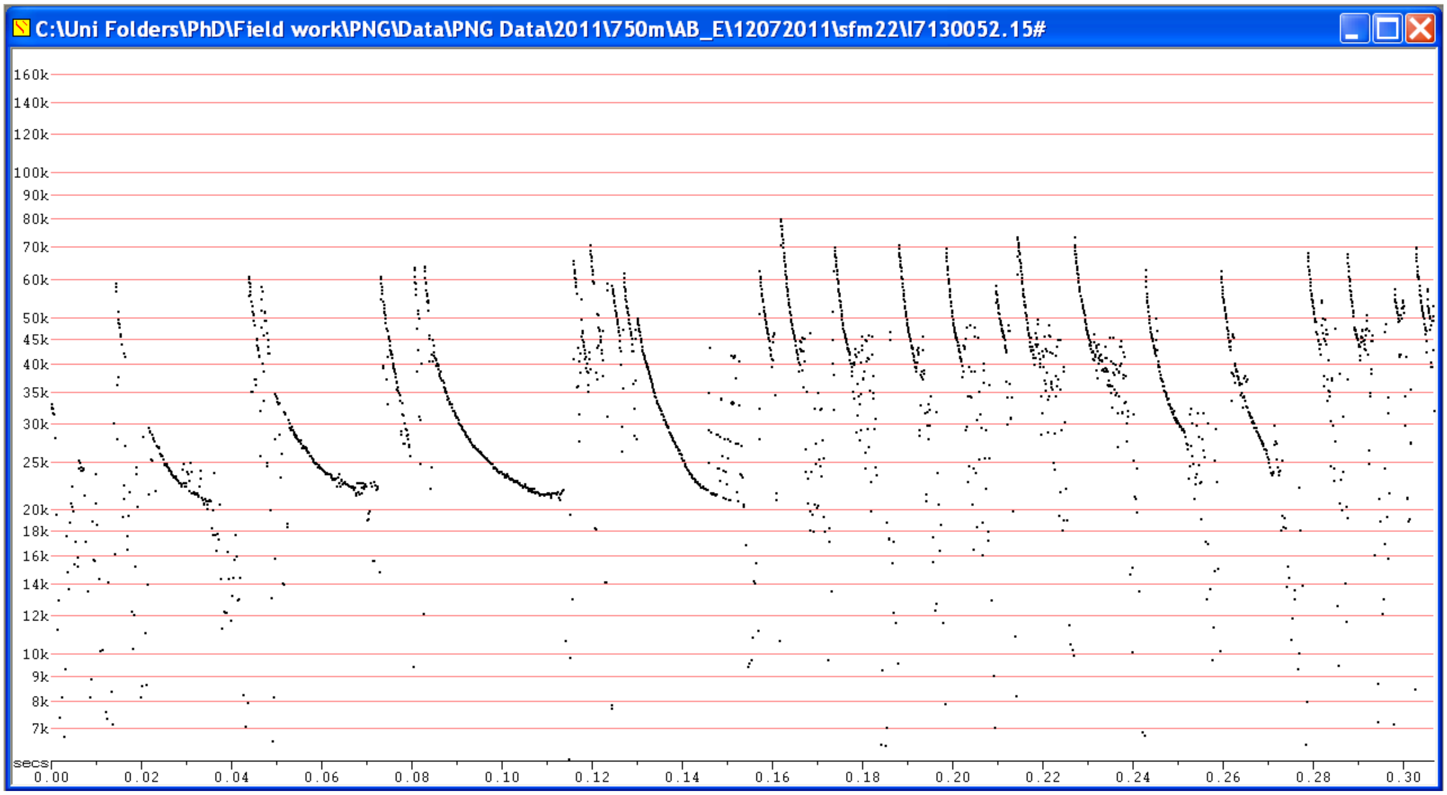
New call for Huon Peninsula

New call for PNG

A total of 47 files containing calls of this species were recorded during this survey. Calls were collected at 250m and 750m elevation. No individuals emitting calls of this frequency were captured during this survey, and calls could not be matched to any species identified in other existing call libraries. This species was assigned a species code of sfm22, detailing its steep frequency modulated shape (sfm) and characteristic frequency.

The call consists of a series of linear pulses of highly variable frequencies ending in a slight curve with a characteristic frequency of around 22kHz. Pulses have a slight leftwards lean with upwards sweeps of between 10kHz and 25kHz. The call is displayed below as a compressed file in F7 magnification.

sfm22	
Elevation (m asl)	**Detected**
3000m	
2800m	
2500m	
2350m	
2050m	
1550m	
1150m	
950m	
750m	X
250m	X
0m	



sfm42

Microchiroptera

New call for Huon Peninsula

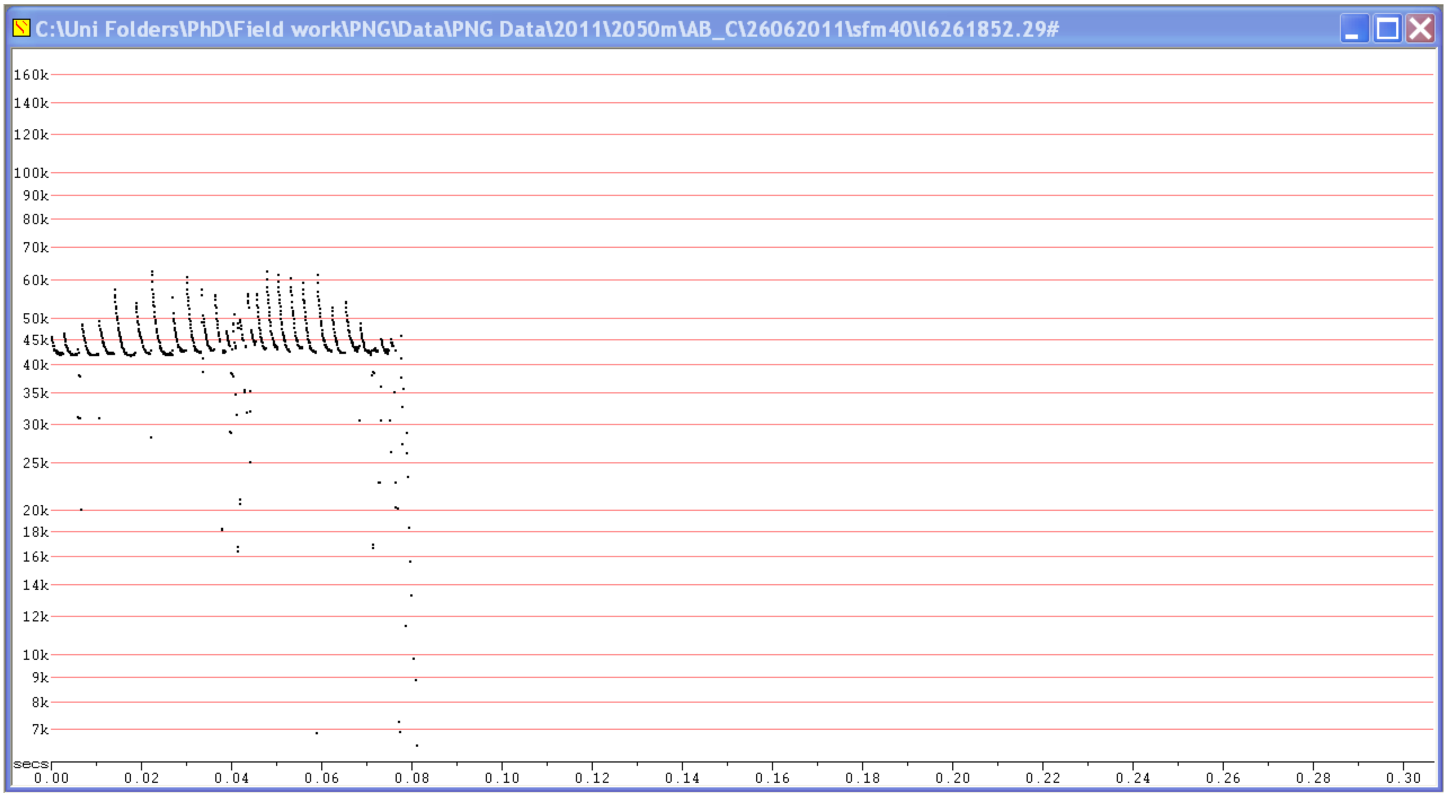
New call for PNG

A total of 925 files containing these calls were recorded, at 750m, 1550m, 2050m, 2350m, 2800m, and 3000m elevation. Calls could not be assigned to a captured species or to call libraries and was assigned a species code of sfm42.

The call consists of a series of linear pulses of highly variable frequencies ending in a slight curve, with a characteristic frequency of around 42kHz. Pulses have upwards sweeps of between 5kHz and 20kHz. The call is displayed below as a compressed file in F7 magnification.

These calls may be attributed to *P. collinus* or *N. microtis,* however release calls from these species had much steeper pulses of greater variability in frequency, with no bottom curve. Armstrong and Aplin (2011) collected similar shaped unidentified calls of a slightly higher frequency which they coded *44st.cFM*. and suggested that may be *Pipistrellus angulatus*, or a species of vespertilionid or *Miniopterus.*

sfm42	
Elevation (m asl)	**Detected**
3000m	X
2800m	X
2500m	
2350m	X
2050m	X
1550m	X
1150m	
950m	
750m	X
250m	
0m	



sfm45

Microchiroptera

New call for Huon Peninsula

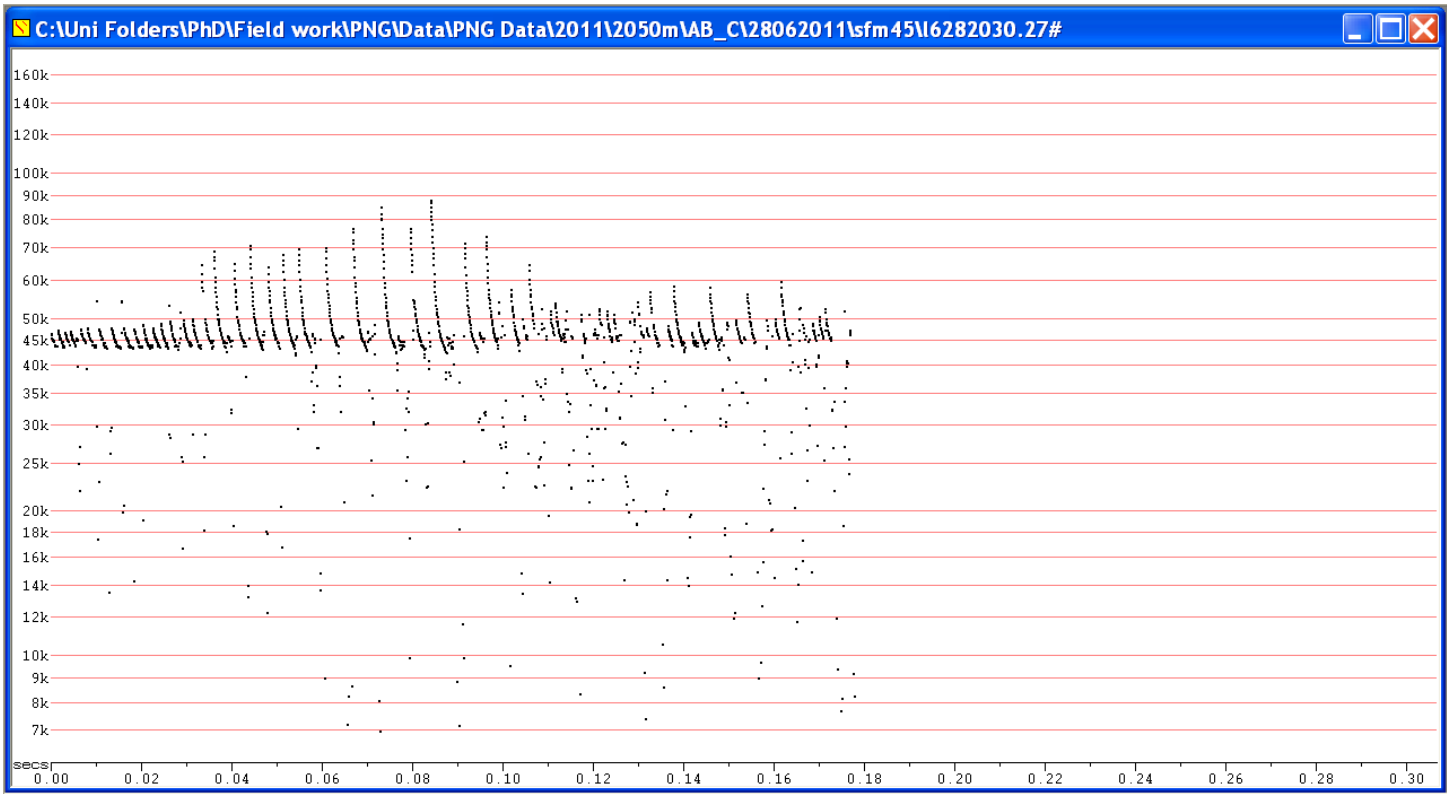
New call for PNG

A total of 48 files containing calls of this species were recorded at 250m, 750m, 950m, 1150m, and 2050m. Calls did not match any species captured or existing call libraries, and were assigned a species code of sfm45, detailing its steep frequency modulated shape (sfm) and characteristic frequency.

The call consists of a series of linear pulses of highly variable frequencies ending in a slight curve, with a characteristic frequency of around 45kHz. Pulses have upwards sweeps of between 2kHz and 40kHz. The call is displayed below as a compressed file in F7 magnification.

It is possible that these calls may be attributed to *P. collinus* captured during this study, as the call shapes and characteristic frequencies are similar. However, calls collected from *P. collinus* upon release had a slightly lower characteristic frequency at 40kHz.

sfm45	
Elevation (m asl)	**Detected**
3000m	
2800m	
2500m	
2350m	
2050m	X
1550m	
1150m	X
950m	X
750m	X
250m	X
0m	



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sfm55

A total of 55 files containing calls of this species were recorded at 250m, 750m, 2050m, 2350m, and 3000m.

Calls could not be assigned to any species captured during this survey or to existing call libraries; this call was therefore assigned a species code of sfm55.

The call consists of a series of linear pulses ending in a slight downward droop, with a characteristic frequency of around 55kHz. Pulses have an upwards sweep of around 15kHz. The call is displayed below as a compressed file in F7 magnification.

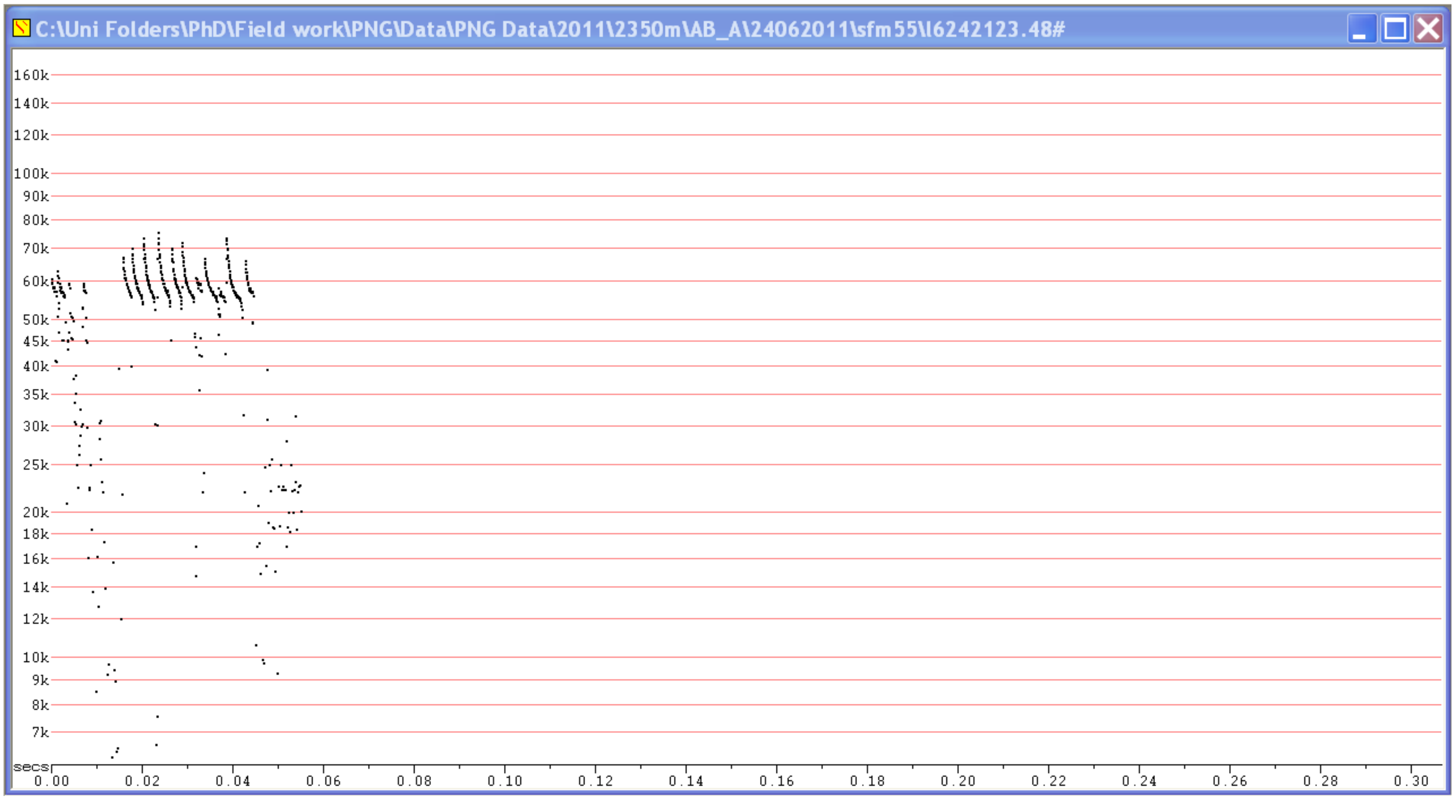
Calls may be made by fm52 as the terminal droop is similar, sfm55 pulses are much steeper than those of fm52. Armstrong and Aplin (2011) collected calls with a similar unidentified calls (53*st.cFM.d)* they suggested might be are likely to be from a species of *Miniopterus* (or less likely a species of vespertilionid) based on pulses with this characteristic droop

Microchiroptera

New call for Huon Peninsula

New call for PNG

sfm55	
Elevation (m asl)	**Detected**
3000m	X
2800m	
2500m	
2350m	X
2050m	X
1550m	
1150m	
950m	
750m	X
250m	X
0m	



Macroglossus minimus nanus
Least Blossom Bat

Pteropodidae

New altitude record for PNG

Representing the blossom bats, a group of bats whose long snouts and tongues are specialised for eating nectar and pollen, the least blossom bat is the smallest of the blossom bats found in New Guinea (Bonaccorso, 1998). Two subspecies occur in the region with *M. minimus nanus* being found on the mainland, and *M. minimus microtis* found on small islands to the east of Papua New Guinea.

Three individuals were caught during this survey. All were trapped using mist nets at 1550m elevation, however, previous studies have recorded this species from sea level up to 1280m in elevation (Flannery, 1995; Bonaccorso, 1998; Dabek, 2001, 2003). This survey extends the known altitudinal range of this species.

The fur of all individuals caught was bicoloured being whitish at the base and light brown at the tips, with a whitish underbelly. Superficially similar to *Syconycteris australis*, *M. minimus* can be distinguished by its much quieter temperament. Maximum forearm length of the two females, and weight of all individuals recorded during this survey was higher than previously recorded.

		Macroglossus minimus nanus											
		Flannery (1995)				**Bonaccorso (1998)**				**This study**			
FA	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	40.30	38.70	42.40	8	-	37.50	43.40	18	43.37	-	-	1
	F	40.10	37.40	43.20	9	-	37.20	43.20	16	44.69	44.47	44.91	2
	J	-	-	-	-	-	37.40	40.80	5	-	-	-	0
WT	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	16.80	14.00	18.50	6	-	14.10	21.30	14	35.75	-	-	1
	F	18.10	14.50	21.00	7	-	14.50	21.00	14	24.5	24.5	-	2
	J	-	-	-	-	-	11.140	15.00	6	-	-	-	0

Macroglossus minimus				
Elevation (m asl)	**Flannery (1995)**	**Bonaccorso (1998)**	**Dabek (2001, 2003)**	**This study**
3000m				
2800m				
2500m				
2350m				
2050m				
1550m				X
1150m		X (1200m)	X (1280m)	
950m	X (1000m)	X		
750m	X	X		
250m	X	X		
0m	X	X		

Nyctimene albiventer
Common Tube-nosed Bat

A member of the genus *Nyctimene*, the tube nosed fruit bats, which are characterised by their tubular like nostrils. This subfamily is endemic to the Indo-Australian region (Bonaccorso, 1998).

Three individuals were caught during this survey. All three were trapped using mist nets. Captures were made between 250m and 1150m elevation. Previous studies have recorded this species from sea level up to 1860m in elevation (Flannery, 1995; Bonaccorso, 1998; Dabek, 2001, 2003).

For all individuals trapped during this study, the dorsum fur was found to be bicoloured, with dark brown tips and a whitish base, while ventrum fur was whitish. A distinctive characteristic of this species is the presence of a thin, dark stripe in the middle of the back extending from the shoulder blades to the base of the tail. Morphological parameters recorded from trapped individuals were in accordance with previous records, with the exception of a juvenile record added by this study.

		Nyctimine albiventer											
		Flannery (1995)				**Bonaccorso (1998)**				**This study**			
FA	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	53.60	49.40	56.50	7	-	49.00	58.30	38	58.0	-	-	1
	F	57.40	-	-	1	-	51.00	58.80	33	59.82	-	-	1
	J	-	-	-	-	-	-	-	-	56.8	-	-	1
WT	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	29.70	27.0	33.0	7	-	20.00	38.00	30	33	-	-	1
	F	32.0			1	-	22.00	35.00	11	33	-	-	1
	J	-	-	-	-	-	-	-	-	34	-	-	1

Nyctimine albiventer				
Elevation (m asl)	**Flannery (1995)**	**Bonaccorso (1998)**	**Dabek (2001, 2003)**	**This study**
3000m				
2800m				
2500m				
2350m				
2050m				
1550m	X (1860m)	X (1700m)		
1150m	X	X		X
950m	X	X	X (900m)	
750m	X	X	X	X
250m	X	X	X	X
0m	X	X		

Paranyctimene raptor
Green Tube-nosed Bat

Pteropodidae

New altitude record for PNG

A member of the genus *Nyctimene*, the tube nosed fruit bats, which are characterised by their tubular like nostrils. This species is endemic to Papua New Guinea (Bonaccorso, 1998).

Thirteen individuals were caught during this survey. All were trapped using mist nets. Captures were made between 250m and 1550m elevation.

Previous studies have recorded this species from sea level up to 1350m in elevation (Flannery, 1995; Bonaccorso, 1998). This survey extends the known altitudinal range of this species.

A distinctive characteristic of this species is a yellowish green tinge to wing and ear membranes, often with yellow spotting on edges. This was evident in all individuals trapped during this study. Dorsum fur was generally bicoloured, with brown tips and a paler brown base, with ventrum fur being paler then the dorsum. Maximum forearm length and weight recording during this survey was slightly higher than previously recorded. A juvenile record was also added by this study.

		Paranyctimine raptor											
		Flannery (1995)				**Bonaccorso (1998)**				**This study**			
FA	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	50.20	48.20	53.30	7	-	47.00	58.00	36	51.71	48.86	52.6	6
	F	51.60	49.80	54.40	3	-	47.00	56.00	27	53.96	52.20	59.19	6
	J	-	-	-	-	-	-	-	-	55	-	-	1
WT	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	24.50	21.80	33.0	7	-	18.00	33.00	26	26.25	25.00	27.00	6
	F	25.70	24.30	26.80	3	-	18.00	30.00	19	29.91	25.00	35.00	6
	J	-	-	-	-	-	-	-	-	24.5	-	-	1

Paranyctimine raptor			
Elevation (m asl)	**Flannery (1995)**	**Bonaccorso (1998)**	**This study**
3000m			
2800m			
2500m			
2350m			
2050m			
1550m			
1150m	X (1350m)	X (1200m)	X
950m	X	X	
750m	X	X	X
250m	X	X	X
0m	X	X	

Syconycteris australis
Common Blossom Bat

Pteropodidae

This species has been broken up into seven subspecies, four of which occur in Papua New Guinea (Bonaccorso, 1998). *Syconycteris australis papuan* is likely to be the species found on the Huon Peninsula.

Of the 39 individuals caught during this survey, only one was captured in a harp trap, with the rest being trapped using mist nets. One female, captured at 300m elevation was caught with young attached. Captures were made between 250m and 2050m elevation. Previous studies have recorded this species from sea level up to 3000m in elevation (Flannery, 1995; Bonaccorso, 1998; Dabek, 2001, 2003).

The fur of all individuals caught was bicoloured, being whitish at the base and light brown at the tips, with a whitish underbelly. Superficially similar to *M. minimus. S. australis* can be distinguished by its raucous temperament. Morphological parameters recorded from trapped individuals were in accordance with previous records.

		Syconyteris australis											
		Flannery (1995)				**Bonaccorso (1998)**				**This study**			
FA	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	42.70	39.90	44.60	31	-	39.00	46.20	73	44.14	41.19	52.59	18
	F	42.00	38.60	44.00	20	-	38.00	48.00	44	43.67	41.5	46.0	12
	J	-	-	-	-	-	40.20	43.10	6	42.20	39.94	43.73	9
WT	Sex	Mean	Min	Max	N	Mean	Min	Max	N	Mean	Min	Max	N
	M	17.10	15.00	20.20	31	-	14.50	23.50	84	19.48	14.5	22.25	18
	F	17.60	13.30	23.00	20	-	13.00	23.00	43	19.31	16.0	24.0	12
	J	-	-	-	-	-	12.80	19.60	6	17.38	15.0	20.0	9

Syconycteris australis				
Elevation (m asl)	**Flannery (1995)**	**Bonaccorso (1998)**	**Dabek (2001, 2003)**	**This study**
3000m	X	X		
2800m	X	X		
2500m	X	X	X (2600m)	
2350m	X	X	X	
2050m	X	X	X	X
1550m	X	X	X (1800m)	X
1150m	X	X	X (1280m)	X
950m	x	X	X (900m)	X
750m	X	X	X	X
250m	X	X	X	X
0m	X	X		

Acknowledgements

We gratefully acknowledge the funding provided by Conservation International which supported this project and we especially thank Jonah of Boksawin, Keston of Gormdan, Mala of Worin, and Robin of Ninea for their assistance with, and enthusiasm for, our bat work. We also thank their respective villages for allowing us to work and stay on their land.

April Reside provided invaluable field assistance and moral support during our time on the transect and provided all of the photographs. Thanks April!

Special thanks to Mark Ziembicki, Gabriel Porolak, Bruce Beehler, Trond Larsen, Jen Mandeville, Suzanne Tomassi, Ben Freeman, and Alexandra Class for their help during fieldwork.

We have to acknowledge the existence of Hungapor Hill and local remedies for dealing with muscle cramps.

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