Nowrouzi, Somayeh (2017) ***The macroecology of rainforest ants of the Australian Wet Tropics under climate change*****. PhD thesis, James Cook University.**

https://doi.org/10.4225/28/5ac2fba61317f

The macroecology of rainforest ants of the Australian Wet Tropics under climate change

Thesis submitted by

Somayeh Nowrouzi (BE MSc)

July 2017

Myrmecia sp., Carbine Upland rainforest.

For the degree of Doctor of Philosophy

In College of Science and Engineering

James Cook University

Dedication

This thesis is dedicated to my very supportive husband **Kyran** and beautiful daughter **Shalil**,

‘thank you forever’

and to my parents, **Ali** Nowrouzi and **Roudabeh** Alinezhad Monfared, who taught me many useful skills and worked hard their entire life to provide me a better future.

تقدیم به همسرم کایرن و دخترم شلیل که صبورانه همراهم بودند
و
به پدرم علی و مادرم رودابه که تمام زندگی شان را برای موفقیت
فرزندانشان گذاشتند.

Statement of contribution of others

Chapter 2 and Chapter 3 of this thesis are published and under review, respectively, prior to submission of the thesis. This work is co-authored with my supervisors, Prof. Simon Robson, Prof. Alan Andersen and Dr Jeremy VanDerWal, along with other scientists, Dr Sarina Mcfadyan, Dr Kyran Staunton, Dr Alex Bush and Dr Tom Harwood. The experimental design of each chapter was developed in consultation with a combination of the above-mentioned supervisors. While undertaking this research, I was responsible for the project design, obtaining research funding and permits, collecting field and laboratory data, statistical analysis and interpretation, and synthesis and preparation of the manuscripts for submission to peer reviewed journals. The writing of all chapters was led by me, with corrections and contributions from Kyran Staunton and Alan Andersen.

I obtained direct financial support from James Cook University, College of Science and Engineering, National Environmental Research Program of Australian government, the JCU Centre for Tropical Biodiversity and Climate Change, the Wet Tropic Management Authority and Commonwealth Scientific and Industrial Research Organisation of Australia (CSIRO). Prof Stephen Williams played a key role in establishing the thesis project. I received laboratory and field assistance from technicians and students in CSIRO Tropical Ecosystems Research Centre Ant Lab, Darwin, Australia: Jodie Hayward, Magen Pettit, Célénie Christophe, Maxence Plouviez, Antoine Esnouf, Clémence Roldan. I also received field assistance from Centre for Tropical Biodiversity and Climate Change researcher, Arnaud Gourret, and research assistant, Carina Svensson.

CSIRO scientists at Black Mountain Laboratories provided access to mapping and modelling software, GIS, GDMmodeller and Muru, and GIS input layers. Dr Kristen Williams mentored my PhD progress at Black Mountain Laboratories. Dr Nick Nicholls supervised R scripts through the thesis and Dr Simon Ferrier and Dr Karel Mokany provided advice on mapping and modelling approaches.

Achnowledgements

I am grateful to many people for their contributions to the completion of this thesis. I thank my supervisors, Prof Simon Robson, Prof Alan Andersen and Prof Jeremy VanDerWal for their time, support, wealth of knowledge, and guidance throughout the last few years.

I am exceptionally grateful to scientists at CSIRO Land & Water, Darwin, and Black Mountain Laboratories, Canberra, who provided remarkable field, lab and software support and useful advices throughout my thesis. Dr Nick Nicholls gave valuable advices on R software and Dr Kristen Williams, Dr Simon Ferrier and Dr Karel Mokany provided environmental GIS input layers and valuable advices on GIS, GDMmodeller and Muru software. Special thanks go to technicians Jodie Hayward and Magen Pettit, and also intern students at CSIRO Tropical Ecosystems Research Centre Ant Lab, who provided incredible support during all the field and laboratory works. I am also grateful to Dr Ben Hoffmann for his valuable ant knowledge and supportive words to keep me on track throughout my thesis.

I am also appreciative to members of the Centre for Tropical Biodiversity and Climate Change (CTBCC) for their support and contributions. Dr Kyran Staunton proof-read first drafts of all my thesis documents and was always extremely helpful, for which I will always be thankful. Arnaud Gourret, Carina Svensson and all other researchers of CTBCC who shared their knowledge with me will always be thought of fondly.

Of course, my family were integral to my success in completion of this thesis. I am forever indebted to my husband Kyran who supported me incredibly with his love, patience, sense of humour and academic knowledge, my very understanding angel Shalil, and to my loving parents, parents-in law and siblings who have always been there for me. I am also extremely appreciative of the support from my friend, Dr Hamzeh Valavi who helped keep me on track during the first couple of years of this thesis and his words are always memorable after he passed away.

I am grateful for funding from James Cook University, College of Engineering and Science, under an Australian Postgraduate Award from National Environmental Research Program and the Wet Tropics Management Authority. Further thanks go to Queensland National Parks and Wildlife Service for access to the Wet Topics National Parks and receipt of permit no. WITK11729912.

My special thanks go to Prof Alan Andersen, who mentored my research skills, academic writing and professional communications. He played a key role in stabilishing my thesis project and supervised me wisely and completely through the entire thesis. He was always available, even remotely, to answer my questions and guide me through the gaps in my knowledge with his useful comments and suggestions. I am forever indebted for his patience, support and valuable time.

Publications associated with this thesis

Manuscript published

- Nowrouzi, S., Andersen, N. A., Robson, S. K. A., Macfadyen S., Staunton, M.K., VanDerWal, J. Ant diversity and distribution along elevational gradients in the Australian Wet Tropics: the importance of seasonal moisture stability. *PloS one* 11.4 (2016): e0153420. (Chapter 2).

Manuscript under review

- Nowrouzi, S., Andersen, N. A., Bishop, T. R. and Robson, S. K. A. Is thermal limitation the primary driver of elevational distributions? Not for montane rainforest ants in the Australian Wet Tropics. Submitted to *Oecologia* (Chapter 3).

Manuscript in preparation

- Nowrouzi, S., Bush, A. A., Harwood, T., Staunton, K.M., Andersen, N. A., Robson, S. K. A. Generalised Dissimilarity Models and predicting ant compositional turnover in the Australian Wet Tropics across space and time. (Chapter 4).

Thesis abstract

Anthropogenic climate change is altering biological communities, ecosystems and their associated services. Understanding contemporary distribution and diversity patterns and accurately predicting biological responses to climate change is therefore necessary to help assess the nature of future changes and to mitigate associated negative impacts. Predicting responses to climate change is a particular challenge for invertebrates, for which distributions are often poorly known despite representing most of the Earth's species, and being especially sensitive to a changing climate. There is particular concern about the impact of climate change on the biota of tropical mountains, because tropical species often have particularly narrow geographical and thermal ranges and therefore display high levels of short-range endemism. This thesis examines changes in diversity and distribution patterns of the rainforest ants in the Australian Wet Tropics (AWT) under future climate change.

The thesis addresses the question: How will diversity and distribution patterns of rainforest ant communities in the Australian Wet Tropics be affected by future climate change? It has three specific aims. The first is to document spatial variation in rainforest ant' diversity and composition in the AWT, and to identify the role of climate as a driver of this variation. Ants were comprehensively sampled in leaf litter, on the litter surface and on tree trunks at 26 sites across elevational gradients spanning from 100 – 1,300 m within six montane subregions that spanned the latitudinal range of the AWT. A total of 79,853 individual ants were collected, belonging to 296 species from 63 genera. Species richness showed a slight peak at mid elevations, but did not vary significantly with latitude. Species composition varied

substantially among subregions and changed markedly with elevation, with a striking disjunction at the elevation of the orographic cloud layer.

The second aim is to assess the extent to what the distribution of rainforest ant species related to their physiological thermal limits. Maximum thermal limits (CTmax) and body mass of 20 species were examined along one of the elevational gradients. Phylogenic relationship was controlled, which there was no significant signal in the data. Community CTmax did not vary systematically with increasing elevation and there was no correlation between elevation and elevational ranges of species. However, body mass significantly decreased at higher elevations, but there was no significant difference in CTmax of different-sized ants within a species and models indicated that elevation and body mass had limited influences on CTmax. The results of this chapter showed direct contradictions with climatic variability hypothesis, Rapoport's rule or Bergmann's rule, which adds to the uncertainty around this issue for ants.

The third aim is to investigate how projected climate change and associated changes in suitable habitat will affect rainforest ant community composition in the AWT. Compositional dissimilarity of the communities was estimated using Generalised Dissimilarity Modelling, and the models were fitted into future projections of climatic changes, incorporating projected changes in the distribution of rainforest habitat. Rainforest ant community composition was forecast to change markedly under projected climate change, primarily because of predicted changes in rainforest habitat, especially on the inland side of the region. Habitat suitability is predicted to reduce due to projected transformation of rainforest to sclerophyll forest, which will likely shift the community composition completely from the sites that the rainforest will remain intact. This is an additional change to the expected turnover in the rainforest community composition due to changing climate only.

Noteworthy findings of the thesis are the importance of the orographic cloud layer between 600 m and 800 m elevation as a driver of variation in species composition and likelihood of climate change impact on ant species primarily through changes in rainfall via its effects on vegetation structure and therefore thermal microhabitats, than through direct temperature changes. These findings highlight the sensitivity of the cloud layer zone and vegetation structure in the AWT to a changing climate. Therfore, key future directions for predicting ant community responses to climate change are to incorporate changes in the cloud layer and thermal mircohabitats, via changes in rainforest habitat, into compositional dissimilarity modelling.

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Chapter 1 . General Introduction

1.1 Biodiversity patterns and global climate change

Anthropogenic climate change threatens to alter species distribution patterns and subsequently impact biological communities, ecosystems and their associated services (Thomas *et al.*, 2004a; Thomas, 2010; Yates *et al.*, 2010; Gibson-Reinemer *et al.*, 2015; Nadeau *et al.*, 2017). Global warming is transforming the Earth's climate system, resulting in altered rainfall regimes, sea level rise and ocean acidification in addition to increases in temperature (IPCC, 2014). The global average temperature has increased by 0.85°C since 1850, with a notable increase in extreme temperatures and rainfall events in recent years (Coumou *et al.*, 2013; Mekis *et al.*, 2015; Zhang *et al.*, 2015; Wang *et al.*, 2016). In Australia, average temperatures have increased by 0.9°C since 1910 (CSIRO/BoM, 2016). Australia's rainfall has varied greatly, but there is a recent trend of increasing spring and summer monsoonal rainfall across northern regions (CSIRO/BoM, 2016). Temperatures are projected to increase between 1.1 – 6.4°C by the end of this century, globally (Meehl *et al.*, 2007), and it is expected to cause more severe dry seasons in Australia (Suppiah *et al.*, 2007).

Understanding how and why species diversity varies with climate remains an ongoing challenge both for science and for environmental management under climate change. Climate change could surpass habitat destruction as the greatest global threat to biodiversity over the next few decades (Bellard *et al.*, 2012), with species being affected by climate change both temporally and spatially (Thomas, 2010; Bellard *et al.*, 2012). Recent investigations have projected marked biodiversity change under future climate change (Walther, 2003; Hickling *et al.*, 2006; Chen *et al.*, 2011; Menéndez *et al.*, 2014; Welbergen *et al.*, 2015; Lyra *et al.*, 2016). For example, poleward and upward shifts in distribution have been documented as species track changes in climate to remain within climatically suitable environments (Chen *et al.*, 2011; Menéndez *et al.*, 2014). Understanding these contemporary patterns and accurately predicting biological responses to climate change is necessary to assess the nature of changes in future and to mitigate associated negative impacts (Pereira *et al.*, 2010; Parmesan *et al.*, 2011; Mokany *et al.*, 2016b; Brook & Alroy, 2017; Leroux *et al.*, 2017).

To identify the vulnerability of species to the world's changing climate, it is crucial to answer the basic ecological questions of "*Where are species currently distributed?"* and "*What is the role of climate as a driver of species distributions?"*. Investigating the processes and mechanisms behind the patterns associated with latitudinal and elevational gradients is a powerful approach to addressing these questions (Lomolino, 2001; Willig *et al.*, 2003; Kraft *et al.*, 2011; Sunday *et al.*, 2011; Pintor *et al.*, 2015; Caddy-Retalic *et al.*, 2016). Additionally, climate change can impact biodiversity at various levels (Säterberg *et al.*, 2013; Valiente-Banuet *et al.*, 2015). Metabolic, behavioural, or evolutionary mechanisms may drive population responses to altered temperatures, including changes in body size or dispersal and range expansion in pace with the changing environment (Parmesan, 2006; Urban *et al.*, 2012; Reuman *et al.*, 2014). Changing climatic regimes and extreme weather events are predicted to significantly alter species' distributions and subsequently community composition (Thomas, 2010; Jenkins *et al.*, 2011; Huey *et al.*, 2012; Arribas *et al.*, 2017). This is one of the major concerns that has renewed the focus of ecologists to community-level investigations (Binzer *et al.*, 2016; Tayleur *et al.*, 2016; Gruner *et al.*, 2017).

Community-level responses are more complicated compared with those at the species-level, as changing temperature may differentially favour some species while disadvantaging others (Elmendorf *et al.*, 2012). The magnitude or sign of species interactions also may change and consequently disrupt mutualisms, trophic interactions, competitive hierarchies and ultimately species coexistence (Blois *et al.*, 2013; Sorte & White, 2013; Sentis *et al.*, 2014). Forecasting changes in the distribution and composition of biological communities under future climates is also particularly challenging because the distribution of suitable habitat is likely to change.

1.2 Climate change and tropical biodiversity

There is particular concern about the impact of climate change on the biota of tropical regions. Organisms inhabiting lower latitudes may be more physiologically susceptible to climate warming than organisms at higher latitudes, despite the relatively greater increases in temperature anticipated at higher latitudes (Deutsch *et al.*, 2008a; Diamond *et al.*, 2012; Huey *et al.*, 2012). This pattern results from tropical species inhabiting warm environments close to their upper physiological thermal tolerances compared with temperate species (Diamond *et al.*, 2012). Within the tropics, species often have particularly narrow geographical and thermal ranges and display high levels of short-range endemism (Harrison & Noss, 2017).

Sommer *et al.* (2010) found that global temperature increases will increase the capacity for species richness in temperature-limited high-latitude regions, but will decrease this capacity in the warm, tropical and sub-tropical regions of the world where diversity is currently highest. However, increases in the climatic capacity for richness are not necessarily beneficial for diversity. Specialist species adapted to harsh environmental conditions will be vulnerable to increased competition from generalists, and endemics adapted to long-term climatic stability may be especially poorly adapted to survive change, resulting in disproportionate losses of small-ranged species (Sommer *et al.*, 2010; Harrison & Noss, 2017).

On one hand, tropical biodiversity hotspots, with locally cooler and wetter areas than their surroundings (such as mountain tops and gullies), are predicted to be buffered from the greatest change in future climatic conditions and are therefore considered to be climatic refugia (Reside *et al.*, 2013). On the other hand, rapid warming is predicted to make even relatively stable climatic refugia unsuitable for the long-term sustainability of biodiversity, while continuing loss of natural habitat will eliminate even the most climatically stable macro- and microrefugia (Harrison & Noss, 2017). Therefore, it is critical to be cautious and identify microrefugia that facilitate persistence of species both inside and outside of the larger scale macrorefugia. Furthermore, minimizing global warming and anthropogenic habitat destruction must be a key conservation strategy towards mitigating the negative impacts of climate change on the tropical biodiversity hotspots.

1.3 The Australian Wet Tropics: biodiversity and climate change

The Australian Wet Tropics World Heritage Area (hereinafter ‘AWT’) is a mountainous region supporting Australia’s only large expanses of tropical rainforest. With elevational ranges and topographic complexity of a montane region, the AWT has been listed as a World Heritage Area since 1988 due to high levels of biodiversity and endemism (Williams *et al.*, 2003). This bioregion is suggested to be an important future refugium by supporting the persistence of species and lineages through climate cycles (Reside et al., 2013).

High annual rainfall occurs throughout the AWT, with 2,000 – 8,000 mm received in coastal areas, mostly between December to March (Bonell & Callaghan, 2008). During Glacial and Interglacial climatic periods, the upland regions of the AWT consistently received more rainfall than their current levels (Hilbert et al., 2007). Extreme temperatures have been noted to reach from -2°C to 45°C throughout the AWT (Metcalfe & Ford, 2008). Approximately one-third of the Wet Tropics bioregion is higher than 600 m a.s.l. and is therefore characterised by relative cool conditions, with annual mean temperatures below 22 °C (Stork *et al.*, 2009).

Throughout the Wet tropics rainforest types generally change with elevation from complex mesophyll vine forest in fertile lowlands to upland simple notophyll vine forest (Adam, 1992). A temperature rise of 1°C combined with a 10% decrease in precipitation is predicted to decrease the AWT high elevation rainforests by 60% (Hilbert et al. 2001). These forests may also be further threatened by rising the orographic cloud layers which are responsible for up to 60% of the monthly water input of highland rainforests (>1000 m a.s.l.) in the AWT (McJannet et al. 2007).

In the AWT the average maximum temperature has increased by 0.8°C since 1950 and is projected to increase by between 0.5°C and 1.4°C by 2030 and between 1.0 °C and 4.2°C by 2070 (Suppiah *et al.*, 2007). The cloud layer is also predicted to rise from about 600 to 900 m a.s.l. by 2050 (WTMA, 2013). Rainforests that are currently located at the bottom of the cloud layer are therefore likely to experience drier conditions under a future climate and this can be expected to exacerbate biotic changes caused by rising temperatures alone.

Documented shifts in species' distributions along climatic gradients (Parmesan *et al.*, 1999; Thomas *et al.*, 2004a; Shoo *et al.*, 2006; Kitching *et al.*, 2011) provide evidence of biological responses to contemporary climate change in the AWT. Mountain systems such as those found in the AWT represent hotspots of biodiversity and endemism due to the compression of climatic zones over the elevational gradients (Williams *et al.*, 2008a; Welbergen *et al.*, 2015). The rainforests of the AWT are isolated habitats which lack potential for rainforest endemics to shift their latitudinal or elevational ranges (Williams *et al.*, 2008b).

Hilbert *et al.* (2001a) modelled climate change impacts of highland vegetation within the AWT, projecting up to 50% of range lost due to only one degree of warming. Upland species are predicted to experience reductions in suitable habitat as their currently favourable, montane conditions are lost (Williams & Pearson, 1997; Shoo *et al.*, 2005a; Staunton *et al.*, 2014; Costion *et al.*, 2015). Many vertebrate species in the AWT are now considered severely threatened by climate change (Williams *et al.*, 2003) or predicted to significantly reduce in population size (Shoo *et al.*, 2005b).

Williams et al. (2008) suggest that insects of low vagility and high endemicity in the Wet Tropics will be as vulnerable to climate change impacts as regionally endemic vertebrates. Studies within the Wet Tropics of the responses of insects to climate change have been limited to groups of flies (Schizophora) and beetles (Carabidae and Scarabaeidae). Up to 40% of highland schizophoran species are at risk of extinction due to warming between 2 – 3°C, and even greater losses are expected with warming above 3°C (Wilson, 2010). Similarly, 88% of carabid beetle species are projected to show >80% population declines for the most severe emission scenario by the year 2080 (Staunton et al., 2014). A large proportion (88%) of scarabaeid beetle species are predicted to lose more than 50% of their current populations size by 2085 (Aristophanous, 2014).

The AWT contains important climatic refugia. Areas that are locally cooler and wetter than their surroundings (such as shaded gullies) are predicted to be buffered from the greatest change in future climatic conditions (Reside et al., 2013). Upland regions (such as Windsor and Carbine) are expected to shelter vulnerable species of vertebrates (Welbergen et al., 2015). A comprehensive investigation throughout Australia has considered four separate biological groups, vascular plants, mammals, reptiles and amphibians for community-level biodiversity models and measures of change under climate change (Prober *et al.*, 2015). As yet, no prediction has considered the potential changes from community-level responses of insects throughout Australia and specifically in the AWT.

1.4 Ants in the Australian Wet Tropics

Ants are an ideal focal taxon for studying species distributions. They are a highly diverse and ecologically dominant faunal group globally and especially throughout tropical regions (Holldobler & Wilson, 1990; Agosti *et al.*, 2000a; Andersen *et al.*, 2016). Many studies have documented exceptional local ant diversity in tropical rainforests (Bruhl *et al.*, 1998; Majer *et al.*, 2001; Davidson *et al.*, 2003; Kaufmann & Maschwitz, 2006), but there is a poor understanding of geographic patterns of tropical ant diversity and composition.

Ants are highly sensitive to climatic variations. Temperature is a dominant factor influencing ant distributions globally (Andersen, 1995; Dunn *et al.*, 2009; Diamond *et al.*, 2012). Within the tropics, ant diversity declines with increasing latitude (Dunn *et al.*, 2009) and at higher elevations (Bruhl *et al.*, 1999; Jenkins *et al.*, 2011). This is consistent with general metabolic theory that sees energy as a global driver of biological diversity (Brown *et al.*, 2004; Kaspari *et al.*, 2004; McCain & Grytnes, 2010). Ants also display high levels of species compositional turnover with variation in elevation (Bruhl *et al.*, 1999; Robertson, 2002; Sanders, 2002; Botes *et al.*, 2006; Burwell & Nakamura, 2011) indicating that their distributions are likely to be highly sensitive to global temperature change (Hickling *et al.*, 2006; Botkin *et al.*, 2007; Deutsch *et al.*, 2008a).

Invertebrates are rarely considered in biodiversity conservation planning due to inadequate knowledge of their distributional patterns and the high cost of their surveys (Ashcroft *et al.*, 2010). Within the AWT, there have been some local studies of ant communities (King *et al.*, 1998; Van Ingen *et al.*, 2008; Yek *et al.*, 2009), including their interactions with flightless ground beetles along elevational gradients (Staunton, 2013). There have also been some local studies of ant species distributions in subtropical rainforests in Australia (Nakamura *et al.*, 2007; Burwell & Nakamura, 2011) and describing the aboreal ants in Eastern Australia, including the AWT rainforests (Majer *et al.*, 2001).

A major challenge over the coming decades will be predicting species coexistence in communities confronted with ongoing climate change (Araújo & Rahbek, 2006). This prediction, along with predicted habitat destruction impact on diversity (Bellard *et al.*, 2012), requires to account for both direct effects of climate on individual species as well as indirect effects of climate on habitat structure and interactions among species (Bewick *et al.*, 2014). In ant communities, seemingly similar species often coexist locally (Andersen, 2008) and they have long been model systems for the study of local species coexistence (Levins & Culver, 1971). Therefore, they are an ideal taxon to investigate community-level changes in face of climate change, particularly in tropical diversity hotspots.

1.5 New analytical techniques and modelling tools

Ecological models are important tools for improving our understanding of ecological systems and enabling us to project likely outcomes under global climate change scenarios and to develop robust management strategies (Allnutt *et al.*, 2008; Kearney *et al.*, 2010; Mokany *et al.*, 2016a). Species distribution models (SDMs) are the most commonly used tools to project the future changes in biodiversity globally (Elith & Leathwick, 2007; Elith & Leathwick, 2009; Newbold *et al.*, 2009) and in the AWT (Anderson *et al.*, 2012b; Reside *et al.*, 2012; VanDerWal *et al.*, 2013; Aristophanous, 2014; Staunton *et al.*, 2014). SDMs can predict if a species is likely to occur in a general area that is climatically suitable, but they lack the ability to predict if species will occur in any particular community within a specific location. A major challenge in predicting the impacts of climate change on biodiversity is moving beyond species-level models (Fitzpatrick *et al.*, 2015).

Generalised Dissimilarity Models (GDMs) are relatively new biodiversity modelling techniques based on the concept of community-level compositional turnover, and are useful tools for estimating overall shifts in beta diversity in response to environmental changes (Ferrier et al., 2007; Fitzpatrick et al., 2015). This is especially the case when investigating changes in communities with high levels of beta diversity, such as ants, and in the absence of complete species-level distributional data (Fitzpatrick et al., 2011). GDMs can rapidly analyse datasets containing very large numbers of species, regardless of the number of records per species, and extrapolate compositional turnover patterns beyond sampled communities. This technique can also accommodate a variety of measures of geographic or ecological separation as predictors, including organism-specific representations of barriers to dispersal or cost of movement/gene flow through unfavourable habitats (Fitzpatrick *et al.*, 2015).

Unlike some community-based modelling approaches, GDMs do not assume that species will move together as fixed community types when linked to changing climatic variables (Fitzpatrick et al., 2011). Rather, GDMs assume that emergent rates of spatial turnover along environmental gradients under current climatic conditions can act as reliable surrogates for temporal turnover given environmental change in time (i.e. climatic change). This enables GDM analyses to be interrogated in a variety of ways to assist in conservation decision making in the context of climate change.

1.6 Thesis structure

This thesis is the first comprehensive investigation at the community level on changes in diversity and distribution patterns of the rainforest ants in the Australian Wet Tropics under future climate change. The thesis has focused on addressing how diversity and distribution patterns of rainforest ant communities in the Australian Wet Tropics will be affected by future climate change, and includes three specific aims. The first is to document spatial variation in rainforest ant' diversity and composition in the AWT, and to identify the role of climate as a driver of this variation. The second is to assess the extent to what the distribution of rainforest ant species related to their physiological thermal limits. The third is to investigate how projected climate change and associated changes in suitable habitat will affect rainforest ant community composition in the AWT.

A robust understanding of the role of climate as a driver of species distributions is fundamental to any assessment of likely changes under future climates (Shoo *et al.*, 2006). The first data chapter, chapter 2, aims to explore distribution patterns of the diversity and composition of rainforest ants throughout the AWT and to investigate the role of climate as a driver of these patterns. The overall objective of this chapter is to describe variation in ant diversity and composition patterns with latitude and elevation. Ants were comprehensively sampled in leaf litter, on the litter surface and on tree trunks at 26 sites across elevational gradients spanning from 100 – 1,300 m and within six montane subregions throughout the AWT. Compositional changes were investigated across elevational gradients and between the subregions and the dissimilarity of the communities were estimated. A particular focus of the chapter is on the prediction that there is a marked elevational shift in species composition associated with the orographic cloud layer, which is predicted to rise due to climate change.

The second data chapter, Chapter 3, aims to investigate the extent to which the distribution of rainforest ant species is related to their physiological thermal limits. Biological responses to global climate change in general, and climate warming in particular, are inevitably an outcome of an organism's physiology, behaviour, ecology and evolutionary history (Thomas *et al.*, 2004b; Davis *et al.*, 2010; Sunday *et al.*, 2014). Variation in temperature has an adaptive influence on physiological tolerances of ectotherms, and this determines their potential distributions in relation to both latitude (Sunday *et al.*, 2011) and elevation (Ghalambor *et al.*, 2006).

In Chapter 3, Critical Thermal Maximum (CTmax) and body mass of 20 rainforest ant species were measured across an elevational gradient to investigate four questions. First, does CTmax decrease with increasing elevation and decreasing ambient temperature, paralleling the relationship between CTmax and latitude? Second, do species occurring at higher elevations have larger elevational ranges, as predicted by the climatic variability hypothesis and Rapoport’s rule? Third, does body size increase with elevation, as predicted by Bergman’s rule? Finally, do elevational distributions and body size combine to strongly predict a species’ CTmax?

The third data chapter, Chapter 4, addresses the thesis’ primary aim of exploring how projected climate change will affect rainforest ant communities in the AWT, including through changes in suitable habitat. Climate change impacts species not only spatially, but also via temporal changes (Bellard *et al.*, 2012). In case of ectothermic taxa such as ants, numerus studies suggest that species patterns and distributions are related to climate and in particular temperature, precipitation and humidity (Kaspari *et al.*, 2000; Sanders *et al.*, 2003; Dunn *et al.*, 2009; Diamond *et al.*, 2012). It is therefore vital to link distribution of diversity and composition to environmental variables through the time, particularly in face of changing climate. In Chapter 4, composition dissimilarity of the communities were estimated using GDMs. The models were then fitted into future projections of climatic changes and included rainforest habitat changes in the region.

The thesis concludes (Chapter 5) with a general synthesis of the findings from all data chapters, a discussion of their implications for conservation management, and identification of priorities for future research.

Chapter 2 . Ant diversity and distribution along elevation gradients in the Australian Wet Tropics: the importance of seasonal moisture stability

2.1 Abstract

The threat of anthropogenic climate change has seen a renewed focus on understanding contemporary patterns of species distribution. This is especially the case for the biota of tropical mountains, because tropical species often have particularly narrow elevational ranges and there are high levels of short-range endemism. Here we describe geographic patterns of ant diversity and distribution in the World Heritage-listed rainforests of the Australian Wet Tropics (AWT), revealing seasonal moisture stability to be an important environmental correlate of elevational patterns of species composition. We sampled ants in leaf litter, on the litter surface and on tree trunks at 26 sites from six subregions spanning five degrees of latitude and elevation ranges from 100 – 1,300 m. A total of 296 species from 63 genera were recorded. Species richness showed a slight peak at mid elevations, and did not vary significantly with latitude. Species composition varied substantially between subregions, and many species have highly localised distributions. There was very marked species turnover with elevation, with a particularly striking compositional disjunction between 600 m and 800 m at each subregion. This disjunction coincides with a strong environmental threshold of seasonal stability in moisture associated with cloud ‘stripping’. Our study therefore provides further support for climatic stability as a potential mechanism underlying patterns of diversity. The average height of orographic cloud layers is predicted to rise under global warming, and associated shifts in seasonal moisture stability may exacerbate biotic change caused by rising temperature alone.

Key words: biogeography, climate change, orographic cloud, rainforest, species richness, turnover.

2.2 Introduction

Concerns over the impacts of climate change on biodiversity (Bush, 2002; Thomas *et al.*, 2004b; Pereira *et al.*, 2010; Chen *et al.*, 2011; Bellard *et al.*, 2012) have created an urgent imperative for understanding patterns and drivers of species distributions. Our understanding of species distributions is especially limited for invertebrates, which constitute the great majority of species and play dominant roles in energy and nutrient flow in most terrestrial ecosystems (Rosenberg *et al.*, 1986; Wilson, 1988; Brown, 1997). Invertebrates are also likely to be particularly powerful indicators of biodiversity responses to climate change, because of their high sensitivity to temperature and rainfall, and short generation times (Prather *et al.*, 2013).

There is particular concern about the impact of climate change on the biota of tropical mountains. Even though tropical areas are predicted to warm at lower rates than temperate regions, the response to warming may be greater in tropical assemblages (Sheldon & Tewksbury, 2014; Gibson-Reinemer *et al.*, 2015). Compared with temperate regions, tropical species often have narrower elevational ranges because of greater climatic change with elevation and narrower thermal tolerances (Janzen, 1967; Diamond *et al.*, 2012). Tropical species with narrow elevational ranges are likely to be highly sensitive to climate change and high-elevation species are especially vulnerable to a warming climate because of a lack of dispersal options (Laurance *et al.*, 2011; Menéndez *et al.*, 2014; Staunton *et al.*, 2014).

Tropical biodiversity is strongly influenced by climatic stability (Barron, 1995). Regions with stable climates allow the evolution of finer specialisations and adaptations than do areas with variable climates (Pianka, 1966; Graham *et al.*, 2014). As such, climatically stable areas tend to have high species richness and many range-restricted species (Graham *et al.*, 2010). Moisture stability is a key component of climatic stability in tropical regions (McCann, 2000), and has important consequences for biodiversity and ecosystem function (Benzing, 1998; McCann, 2000). Moisture from persistent clouds can provide montane rainforests with moisture stability by buffering against rainfall seasonality (Bruijnzeel, 1990). In a process known as 'cloud-stripping', fog droplets collecting on vegetation can account for the majority of the water input to rainforests during the dry season months (Hutley *et al.*, 1997; McJannet *et al.*, 2007). This enhanced moisture availability is an important factor influencing species' distributions (Olson, 1994; Burwell & Nakamura, 2011).

Historical climatic stability is a major driver of biodiversity patterns in the World-Heritage-listed rainforests of the Australian Wet Tropics (AWT), which occur in association with a coastal chain of mountains ranging up to 1,600 m elevation. The extent of rainforest in the AWT has undergone marked climate-induced contractions and expansions over the past 20,000 years, with only limited areas supporting rainforest throughout this period (Kershaw, 1994). These stable areas have acted as biodiversity refugia (Welbergen *et al.*, 2015) during drier climates and are contemporary centres of diversity and endemism (Graham *et al.*, 2006; Carnaval *et al.*, 2009). The distributions of rainforest species in the AWT are also strongly influenced by the extent of seasonal stability in moisture availability. Rainfall seasonality is a major driver of latitudinal and longitudinal variation in vegetation structure and composition in the AWT (Webb & Tracey, 1994), and is believed to significantly affect bird richness due to dry-season depletions of food resources (Williams & Middleton, 2008). The orographic cloud layer sits at about 600 m elevation (Goosem, 2002; WTMA, 2013), and seasonal moisture stability above this level is significantly higher than below (McJannet *et al.*, 2007). This has important implications for river flows and availability of habitat for plant and animal species that rely on moist conditions (McJannet *et al.*, 2008; Wallace & McJannet, 2012). However, the extent to which the orographic cloud layer drives patterns of biodiversity has been poorly documented.

This chapter describes rainforest ant diversity and distribution in the AWT, with a particular focus on the association between the orographic cloud layer and elevational patterns of diversity and composition. Ants are an ideal focal taxon for studying species distributions. They are a dominant faunal group in tropical rainforests (Hölldobler & Wilson, 1990; Bruhl *et al.*, 1998; Davidson *et al.*, 2003; Kaufmann & Maschwitz, 2006) and are highly sensitive to climatic variation. Temperature is a dominant factor influencing ant distributions globally (Andersen, 1995; Dunn *et al.*, 2009; Diamond *et al.*, 2012). Within the tropics, ant diversity generally declines with increasing latitude (Majer *et al.*, 2001; Dunn *et al.*, 2009; Andersen *et al.*, 2015) and at higher elevations (Bruhl *et al.*, 1999; Jenkins *et al.*, 2011). This is consistent with metabolic theory that sees energy as a global driver of biological diversity (Brown *et al.*, 2004; Kaspari *et al.*, 2004; McCain & Grytnes, 2010). However, tropical ant diversity can be highest at mid rather than low elevations (Longino *et al.*, 2002), as is often the case in other climatic regions (Sanders, 2002; Munyai & Foord, 2012; Bharti H. *et al.*, 2013). This can be explained by the mid-domain effect, where mid elevations are overlap zones for both lowland and highland taxa (Colwell *et al.*, 2004). Ants also display high levels of species turnover with variation in elevation (Bruhl *et al.*, 1999; Robertson, 2002; Sanders, 2002; Botes *et al.*, 2006; Burwell & Nakamura, 2011) indicating that their distributions are likely to be highly sensitive to global temperature change (Hickling *et al.*, 2006; Botkin *et al.*, 2007; Deutsch *et al.*, 2008a; Del Toro *et al.*, 2015).

The overall objective of our study is to describe variation in ant diversity and composition with elevation across the full latitudinal range of rainforests in the AWT. We particularly focus on the hypothesis that there is a marked elevational shift in species composition associated with the orographic cloud layer.

2.3 Methods

2.3.1 Study system

Mean annual rainfall in the AWT varies from about 1,500 to 9,000 mm, with 75-90% occurring between November and April (McDonald & Lane, 2000). Mean temperature declines at a rate of about 1°C for every 200 m increase in elevation (Shoo *et al.*, 2005a). Vegetation in the AWT is dominated by sclerophyll woodlands and open forests, but includes approximately 10,000 km^2 of rainforests, mostly at higher elevation (Hilbert, 2008) (Figure 2.1). Despite their relatively small area, the rainforests are recognised as a major biodiversity hotspot of global significance due to their extraordinary biological richness and biogeographical uniqueness (Williams *et al.*, 2009).

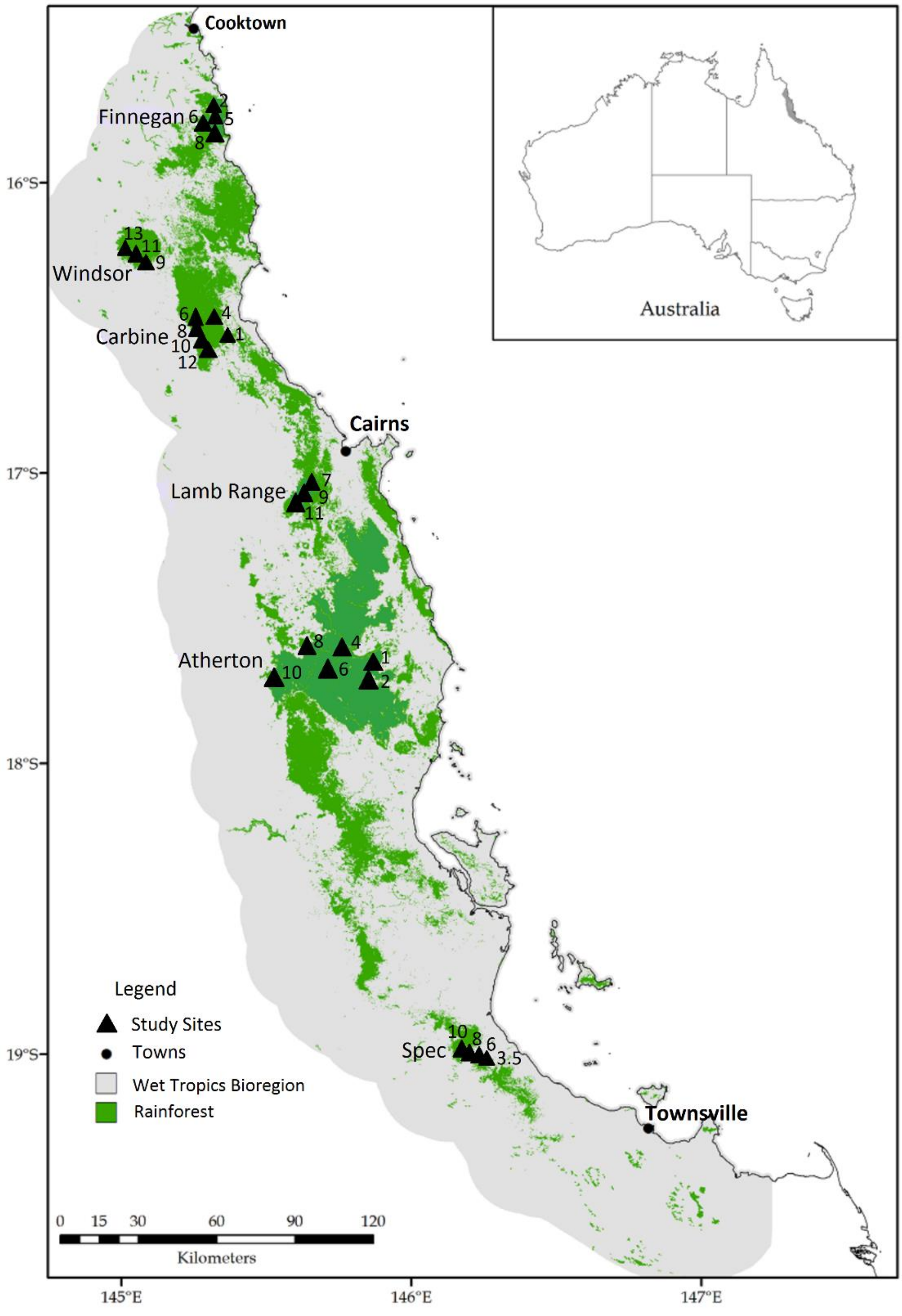

Figure 2.1. Map showing the current extent of rainforest (green shading) in the Australian Wet Tropics bioregion (grey shading), with locations of sampling sites indicated by triangles, with numbers representing elevation ('00 m a.s.l.). Reprinted from Staunton *et al.* (2014) under a CC BY license, with permission from PLOS ONE original copyright (Appendix 1).

The rainforest ant fauna of the AWT has very strong South-East Asian affinities, and contrasts sharply with that of adjacent open sclerophyll habitats, which are dominated by autocthonous, arid-adapted taxa (Taylor, 1972; Andersen, 2000; Van Ingen *et al.*, 2008). The AWT ant fauna includes several South-East Asian-based genera that occur nowhere else in Australia, as well as many others whose distributions elsewhere in Australia are restricted to rainforest patches further south along the eastern coast or west in the monsoonal zone (Reichel & Andersen, 1996; Andersen *et al.*, 2012). A large proportion of the species remain undescribed; for example, a recent revision of the predominantly rainforest genus *Myrmecina* increased the number of described Australian species from 2 to 13 (Shattuck, 2009).

2.3.2 Study sites

Sampling was conducted at 26 long-term sites (Figure 2.1) established by the Centre for Tropical Biodiversity and Climate Change at James Cook University to cover the full latitudinal and elevational range of rainforest in the AWT (Williams *et al.*, 2010b). The sites were distributed across six subregions, ranging from the Finnegan subregion near Cooktown in the north, to Mount Spec near Townsville in the south over a distance of approximately 500 km. This covers the full latitudinal range of Australia's wet tropical rainforests. All sites were located on granite-derived soils except for those in the Atherton subregion where more-fertile basaltic soils are present (McJannet *et al.*, 2008; Parsons & Congdon, 2008). The elevational range of study sites varied among subregions, due to differences in the availability and accessibility of rainforest habitats. Most lowland rainforest in the AWT has been cleared for agriculture, and no lowland sites were available from Mount Windsor or Lamb Range. At Mount Spec, rainforest does not naturally occur below 300 m. Similarly, the different subregions varied markedly in maximum elevation, ranging from 800 m at Mount Finnegan to 1,300 m at Mount Windsor.

The AWT had recently experienced two severe cyclones, cyclone Larry in 2006 (Turton & Dale, 2007) and cyclone Yasi in 2011 (Meteorology, 2015), both of which caused major damage, especially in lowland rainforest (Turton, 2012). At Atherton, sites at 100 and 200 m showed severe cyclone damage, with many broken trunks and fallen trees. A high abundance of the Pioneer Stinging Tree (*Dendrocnide excelsa*) indicated recent, but less severe, cyclone damage at 400 and 600 m.

2.3.3 Ethics statement

Ant samples were collected under Permit no. WITK11729912 from the Queensland Government Department of Environment and Heritage Protection.

2.3.4 Sampling

Ants were sampled at 26 sites distributed along six elevational transects: Finnegan (four sites); Windsor, (three sites); Carbine (six sites); Lamb Range (three sites); Atherton (six sites); and Mount Spec (four sites) (Figure 2.1). Sites were spaced by 200 m elevation along each transect. At each site, sampling was conducted at six plots separated by 200 m along a transect that followed the elevation contour. Only three plots were located at each of the 350 m site at Mount Spec and 100 m site at Atherton due to limited rainforest cover.

Rainforest ants are highly stratified vertically, with distinct faunas associated with litter (cryptic species), the litter surface (epigaeic species) and trees (arboreal species) (Bruhl *et al.*, 1998). Therefore, comprehensive sampling requires a combination of techniques that target these different components of the fauna (Andersen & Majer, 1991; Agosti *et al.*, 2000b). We used bait traps to sample epigaeic and arboreal species, and litter extraction to sample cryptic species. At each plot, 10 bait traps were set on the ground along a line with 5 m intervals, and 10 were set on the closest trees at a height of about 1.5 m. Bait traps were small (1 cm in diameter, 5 cm in length) plastic vials containing a piece of canned tuna. They were set early in the morning, and collected 2 hrs later. We acknowledge that such bait trapping is likely to provide a very limited representation of the specialist arboreal fauna that occurs primarily in the canopy. Leaf litter was collected from two 0.25 m^2 quadrats, one at each end of the 50 m transect at each plot. Samples were sieved to remove large litter fragments, and ants were extracted using Winkler Sacs over a 48-hr period. At Windsor, Carbine, Atherton and Spec, sampling was conducted on three occasions: during two wet seasons (between November and January) of 2011/12 and 2012/3, and one dry season (June to September) of 2012. At Finnegan and Lamb Range, sampling occurred only during the 2011/12 wet season. Additionally, ants were sorted from pitfall samples collected during April 2009 in a previous study across the four main subregions, Windsor, Carbine, Atherton and Spec (Staunton *et al.*, 2014). Pitfall traps were plastic containers, 11.5 cm in diameter and 10 cm depth, protected from rain by a square metal lid (length 26 cm) fixed with wire to a ring of aviary mesh (height 7.8 cm and mesh size 2.5 cm) (Aristophanous, 2010), with propylene glycol as preservative. Three pitfall traps with 15 m spacing were established at every second plot and operated for a month.

For each sampling period, each site had 60 ground bait traps, 60 arboreal bait traps and 12 litter samples, giving a total of 132 samples. The 350 m site at Mount Spec and 100 m site at Atherton were exceptions, with half these numbers of samples. Each site from Windsor, Carbine, Atherton and Spec subregions also had 9 pitfall samples.

2.3.5 Analyses

All ants were sorted to species and where possible named through comparison with identified specimens held in the CSIRO Tropical Ecosystems Research Centre (TERC) in Darwin. Unidentified species were assigned species codes that apply only to this study and highly diverse genera were identified to species group following Andersen (2000). A full set of voucher specimens are deposited in the TERC collection and a duplicate set at the James Cook University ant collection.

We assessed sampling efficiency by creating individual-based rarefaction curves, which plot the number of species against a given number of individuals taken randomly from the observed data (Chao & Jost, 2012; Chao *et al.*, 2013). We then assessed observed species richness as proportion of the Chao 1 estimated total species richness for each subregion. Variation in observed species richness among subregions was tested by one-way ANOVA. We first analysed variation among all six subregions based on the 2011/12 wet season samples. We then analysed variation among sites at Windsor, Carbine, Atherton and Spec based on pooled data across the four sampling periods (three main sampling periods plus pitfall traps). One-way ANOVA followed by Tukey tests for post-hoc pairwise comparisons, were also performed on plot-level data to test for differences in species richness among elevational sites within each subregion (considering the three main sampling periods). Variation in ant species composition among elevations was explored with non-metric multi-dimensional scaling (NMDS) based on Bray-Curtis dissimilarity and using species frequency of occurrence (i.e. the number of samples in which a species occurred, regardless of abundance within a sample) in the 2011/12 wet season samples. ANOSIM (Anderson, 2005) was used to test for differences among sampling strata and subregions. We used cluster analysis (agglomerative clustering) to identify major disjunctions in compositional turnover with elevation.

Analyses were conducted using the R statistical program v3.1.0 packages: the *adehabitat* package for Chao 1 richness estimation and ANOVA analyses, *iNEXT* package for rarefaction curves and the *vegan* package for NMDS and ANOSIM analyses (Clarke, 1993; R Development Core Team, 2013).

2.4 Results

2.4.1 Faunal overview

A total of 79,853 individual ants were collected, belonging to 296 species from 63 genera (Appendix 2). The genera with highest numbers of species were *Pheidole* (40 species), *Strumigenys* (22), *Anonychomyrma* (15) and *Rhytidoponera* (14). The most abundant genera were *Pheidole* (33% of total species records) and *Anonychomyrma* (19%). The most abundant species overall were *Anonychomyrma gilberti* (10% of total species records) and *Pheidole* sp. A2 (*ampla* gp.; 6%) (Appendix 2). The fauna included three introduced species: *Monomorium floricola* (recorded from all subregions), *Tetramorium bicarinatum* (three subregions) and *T. simillimum* (single record only).

Ant species composition varied with sampling method. This variation was systematically related to habitat stratum, following a gradient from Winkler samples to arboreal baits in ordination space (Figure 2.2). Most pitfall samples were positioned between those from Winklers and arboreal baits following the gradient of habitat strata. However, there was a cluster of 6 pitfall samples that formed a clear outlier which can be related to the very low numbers of species recorded in them. These outlier sites were from Atherton, which had a mean of only five species per site compared to 25 species at other subregions. ANOSIM showed that species composition in Winkler samples was significantly ($P<0.01$) different to those from all other methods and that samples from ground and arboreal baits were also significantly different ($P<0.01$).

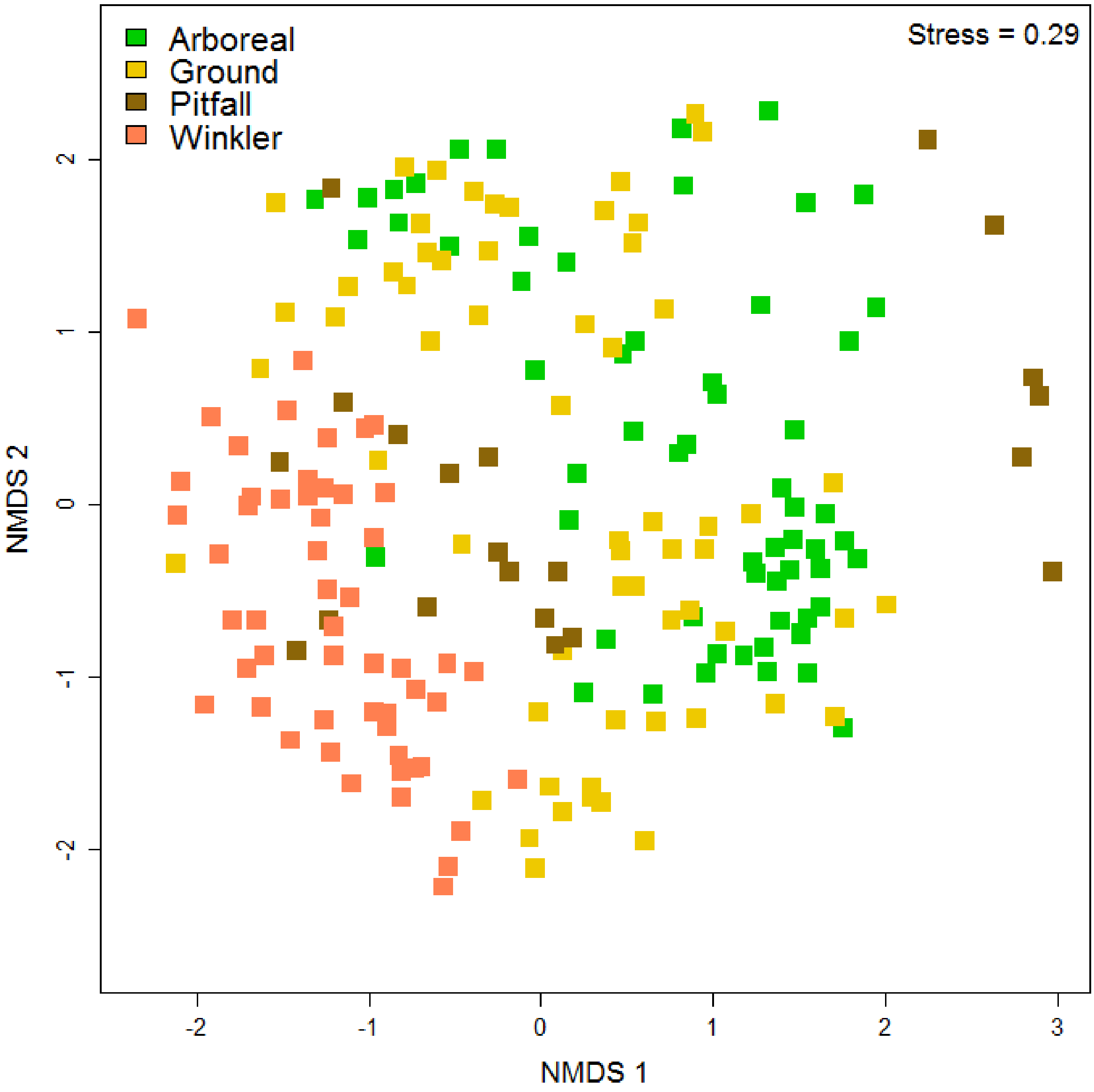

Figure 2.2. NMDS of samples from different techniques, based on species frequencies of occurrence. Each point represents a sample from one site.

Only nine (3%) species occurred in all six subregions: *Rhytidoponera* nr. *victoriae*, *Nylanderia glabrior*, *Carebara* sp. A, *Monomorium floricola*, *Pheidole* sp. A13 (*ampla* gp.), *Solenopsis* sp. A and *Hypoponera* spp. A, B and C. Considering only the 140 native species that occurred in at least three plots (in order to limit sampling artefacts that would arise from consideration of very rare species), 26 (18.6%) were recorded in only one subregion (Table 2.1).

Table 2.1. Ant species occurring in at least three plots that were recorded from single subregions.

Species	Subregions from North to South					
	Finnegan	**Windsor**	**Carbine**	**Lamb Range**	**Atherton**	**Spec**
Heteroponera sp. I (*relicta* gp.)	✓					
Anonychomyrma sp. D (*biconvexa* gp.)		✓				
Myrmecina inaequala		✓				
Leptogenys anitae			✓			
Leptomyrmex dolichoscapus			✓			
Lordomyrma sp. B (*punctiventris* gp.)			✓			
Myrmecina alpina			✓			
Pheidole sp. J2 (Group J)			✓			
Pheidole sp. Q1 (*quadricuspis* gp.)			✓			
Plagiolepis sp. A			✓			
Technomyrmex shattucki			✓			
Heteroponera sp. I (*relicta* gp.)				✓		
Onychomyrmex sp. E				✓		
Pheidole sp. V9 (*variabilis* gp.)				✓		
Strumigenys sp. D (*godeffroyi* gp.)				✓		
Anochetus sp. A (*graeffei* gp.)					✓	
Anonychomyrma sp. O (nitidiceps gp.)					✓	
Pheidole sp. K (Group K)					✓	
Rhytidoponera nr. *scaberrima*					✓	
Anonychomyrma sp. M (biconvexa gp.)						✓
Calyptomyrmex sp. A						✓
Carebara sp. M						✓
Heteroponera sp. K (*relicta* gp.)						✓
Hypoponera sp. O						✓
Leptogenys mjobergi						✓

2.4.2 Species richness

Rarefaction curves indicate that most species occurring in each subregion were recorded, with observed species richness as a proportion of Chao 1 estimated richness ranging from 59% at Windsor to 94% at Finnegan (Figure 2.3). Comparisons of total richness are confounded by variable numbers of sites and sampling periods. There was a weak negative correlation between mean site richness in the 2011/12 wet season samples and latitude ($R^2 = 0.618$, $N = 6$, $P = 0.066$), but ANOVA revealed no significant differences between subregions (Figure 2.4A; $F_{(5, 8)} = 1.463$, $P = 0.248$). There were no significant differences in mean site richness based on pooled data across sampling periods for the four subregions sampled on four occasions (Figure 2.4B; $F_{(3, 6)} = 1.836$, $P = 0.184$). The most extensive elevational gradients were at Carbine and Atherton, and both showed a slight peak in mean plot richness at mid elevations (Figure 2.5). Plot richness declined from mid to high elevation at Spec and there was no significant variation in plot richness at the three high-elevation sites at Windsor. There was no interaction between latitude and elevation (Appendix 3).

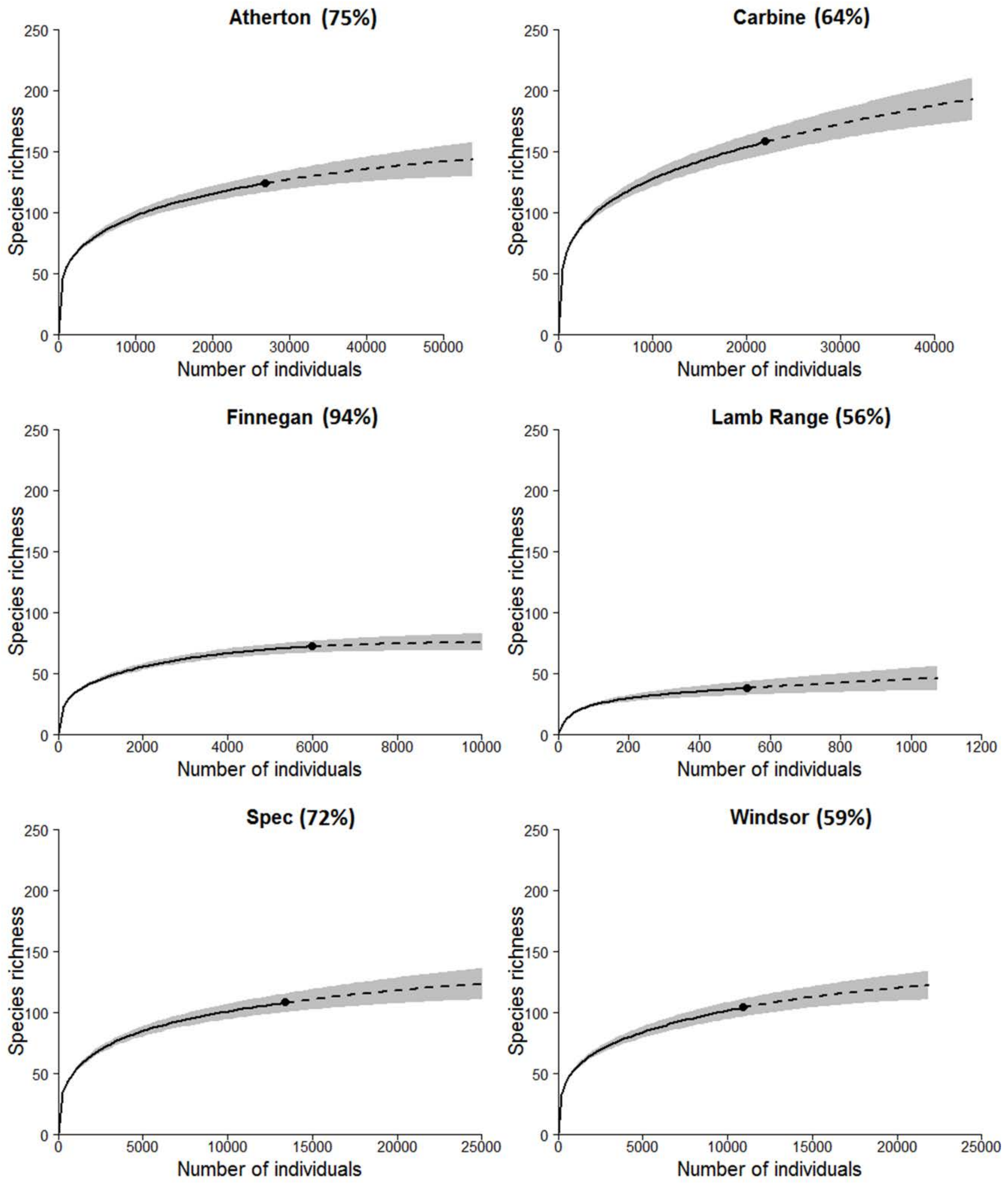

Figure 2.3. Individual-based rarefaction curves (solid) and extrapolation of the curves (dashed) in each of the six subregions based on pooled data across all sampling periods (including the 2009 pitfall trapping) for Spec, Atherton, Carbine and Windsor, and from the 2011/2012 wet season only for Finnegan and Lamb Range. Numbers represent the percentage of observed species richness as proportions of Chao 1 estimated richness. The grey shading represents 95% confidence intervals.

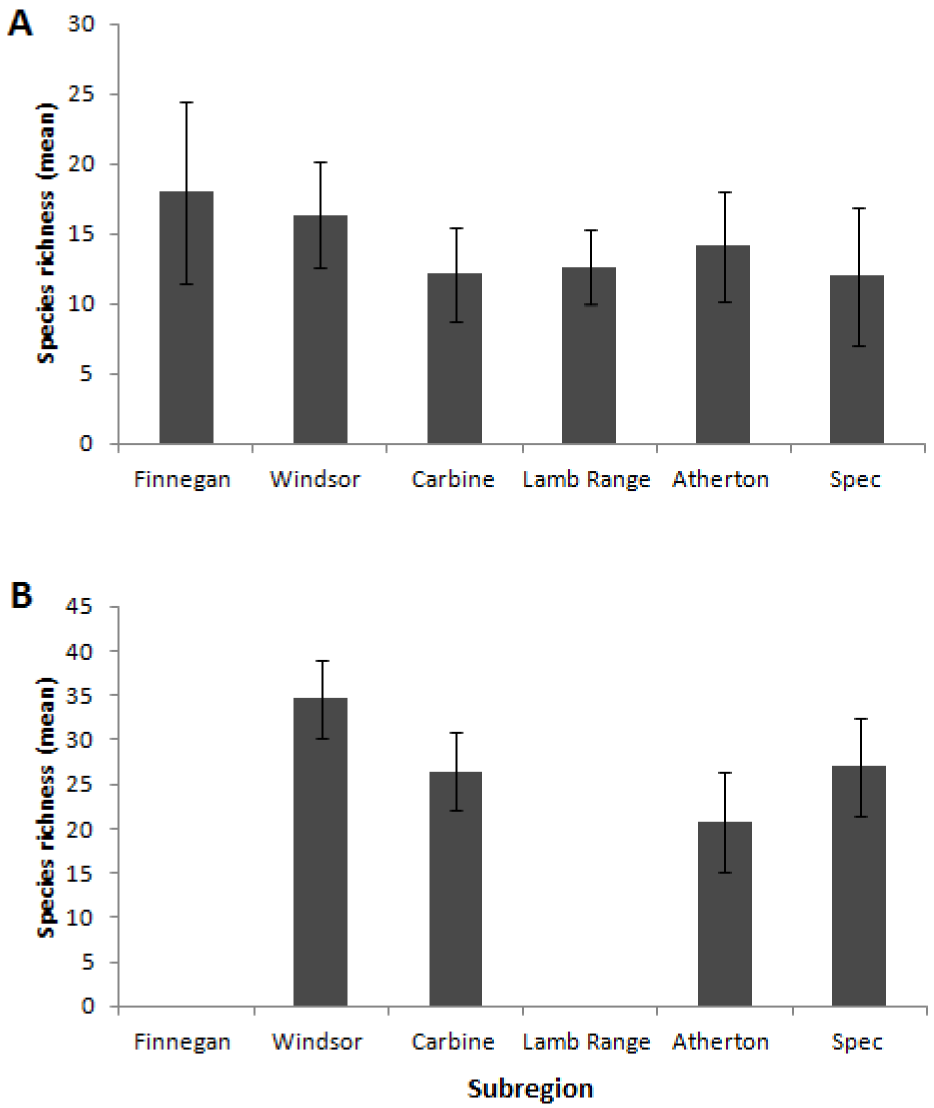

Figure 2.4. Mean site species richness at (**A**) all six subregions, using 2011-2012 wet season data, and (**B**) each of the four main subregions, based on data pooled across all sampling periods. Error bars represent 95% confidence intervals. In both cases there were no statistically significant differences between subregions.

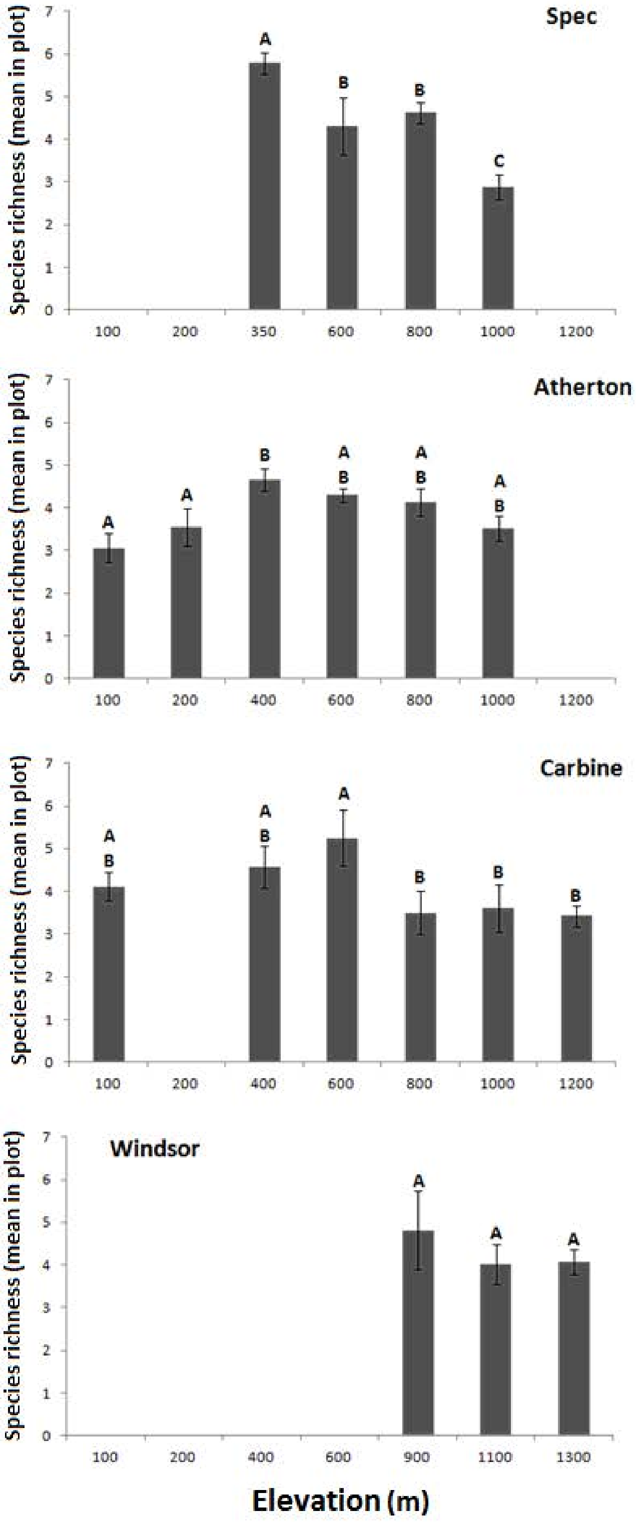

Figure 2.5. Variation in mean plot richness across elevational gradients at Windsor, Carbine, Atherton and Spec, based on data pooled across all sampling periods. Different letters indicate significant differences between elevations within a subregion.

2.4.3 Species composition

NMDS revealed substantial site clustering according to subregion (Figure 2.6A) and ANOSIM showed that many pairs of subregions had significantly dissimilar species composition (Table 2.2). Compositional variation was not systematic with latitude; for example, sites from Spec in the far south were compositionally most similar to those at Windsor and Carbine in the north (Figure 2.6A). For each subregion, plots within a site were tightly clustered in ordination and sites showed systematic variation with elevation (Figure 2.7A-D). In each case, the distributions of a range of ant species were associated with different elevations. At Mount Spec, for example, *Anonychomyrma* sp. A, *Meranoplus hirsutus* and *Tetramorium pacificum* were associated with low elevation, *Anonychomyrma* sp. G and *Pheidole* sp. A15 were associated with mid elevation, and *Anonychomyrma* sp. M, *Pheidole* spp. A11, A2 and A8, and *Rhytidoponera impressa* were associated with high elevation (Figure 2.7D).

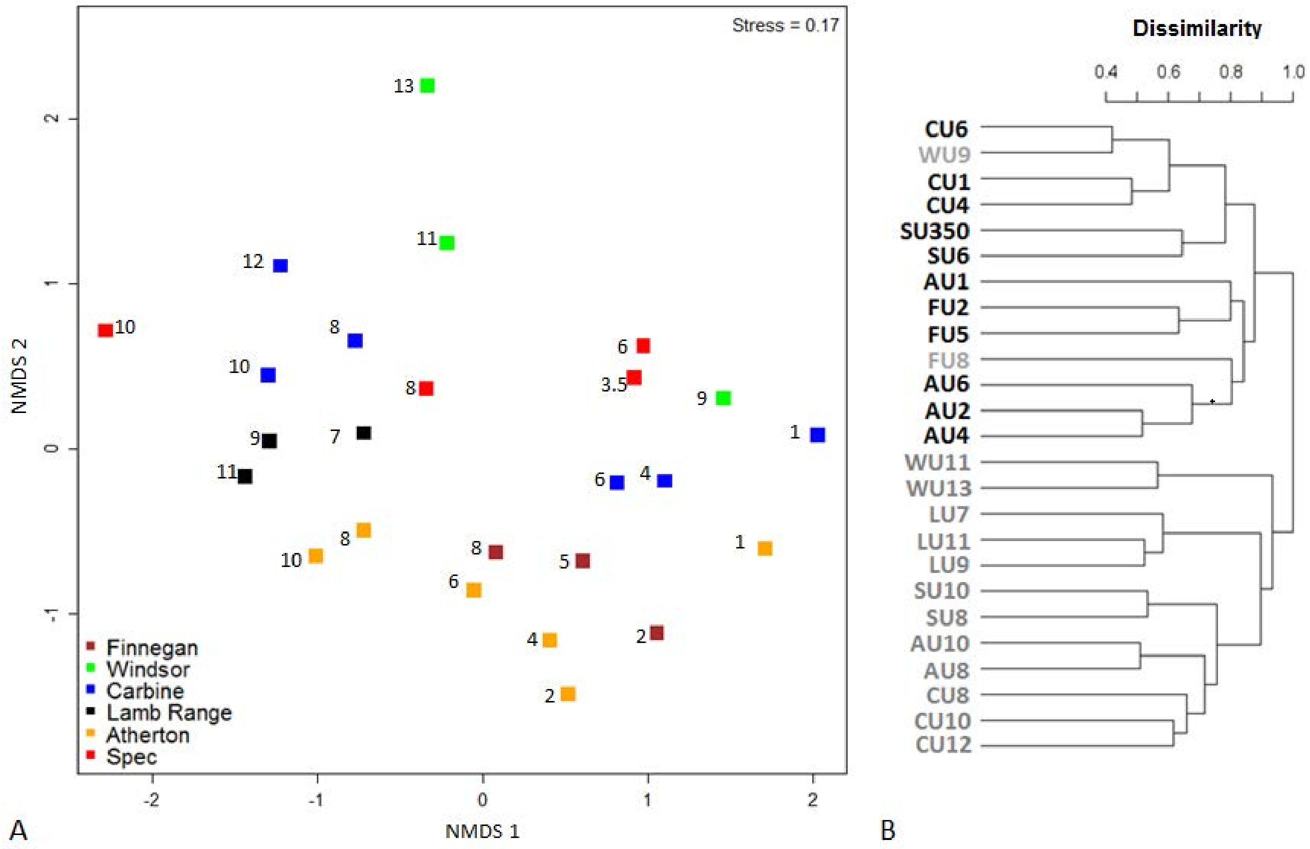

Figure 2.6. (A) NMDS of ant community composition captured from all 26 sites, based on species frequency data from 2011/12 wet season samples. Numbers next to each point represent elevation ('00 m a.s.l.). **(B)** Cluster dendrogram based on dissimilarity in species composition, using the same data. Sites at 600 m or lower elevation are shown in bold. Codes represent mountain names as: AU=Atherton Uplands, CU=Carbine Uplands, FU=Finnegan Uplands, LU=Lamb Range Uplands, SU=Spec Uplands, WU=Windser Uplands.

Table 2.2. ANOSIM results from comparisons of site species composition between each pair of subregions based on species frequency in 2011/2012 wet season samples. Numbers below the diagonal are dissimilarity indices, and those above are P values (P<0.05 in bold).

	Finnegan	**Windsor**	**Carbine**	**Lamb Range**	**Atherton**	**Spec**
Finnegan		0.094	0.332	**0.021**	0.096	**0.015**
Windsor	0.444		0.171	0.100	**0.037**	**0.028**
Carbine	0.054	0.167		0.167	0.151	0.137
Lamb Range	0.741	0.097	0.212		**0.012**	0.088
Atherton	0.242	0.414	0.091	0.796		**0.032**
Spec	0.475	0.630	0.175	0.364	0.361	

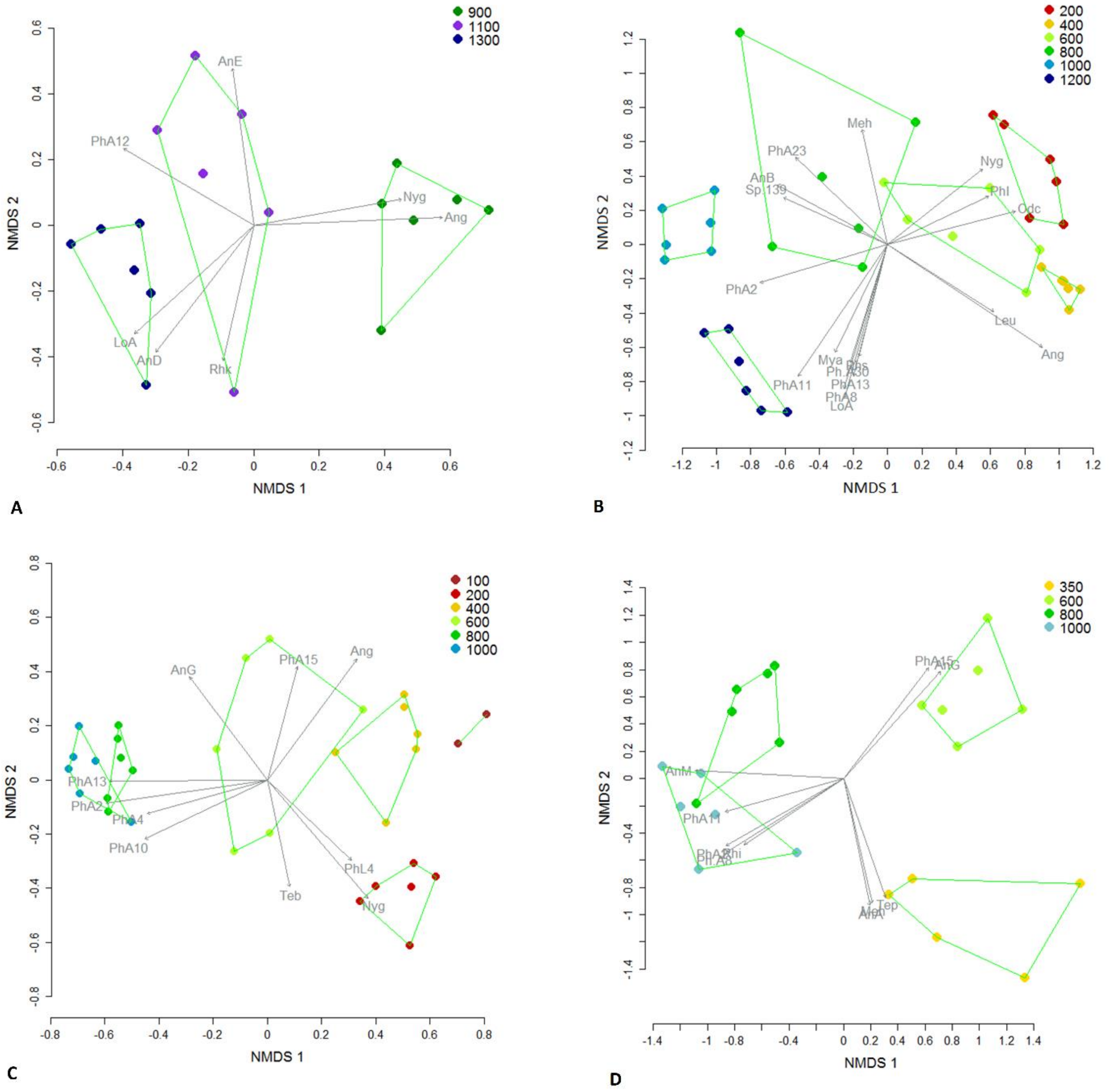

Figure 2.7A-D. NMDS of ant community composition in plots at the four main subregions (A=Windsor, B=Carbine, C=Atherton and D=Spec), based on species frequencies from pooled data across all four sampling periods. Significantly different (P<0.01) communities are shown by convex hulls. Significantly correlated (P<0.01) species are represented by vectors, with vector length proportional to level of significance. Species codes are: Ang=*Anonychomyrma gilberti*, AnA=*Anonychomyrma* sp. A *nr. gilberti*, AnB=*Anonychomyrma* sp. B (*biconvexa* gp.), AnD=*Anonychomyrma* sp. D (*biconvexa* gp.), AnE=*Anonychomyrma* sp. E (*nitidiceps* gp.), AnG= *Anonychomyrma* sp. G (*nitidiceps* gp.), AnM=*Anonychomyrma* sp. M, CaH=*Carebara* sp. H,

CrH=*Crematogaster* sp. H, DiB=*Discothyrea* sp. B, Leu=*Leptomyrmex unicolor*, LoA=*Lordomyrma* sp. A (*punctiventris* gp.), Meh=*Meranoplus hirsutus*, MoB=*Monomorium* sp. B (*nigrius* gp.), Myn=*Myrmecia nigrocincta*, Mya=*Myrmecina alpina*, Nyg= *Nylanderia glabrior*, Odc=*Odontomachus cephalotes*, PhA1=*Pheidole* sp.A1 (*ampla* gp.), PhA2=*Pheidole* sp.A2 (*ampla* gp.), PhA4=*Pheidole* sp.A4 (*ampla* gp.),PhA8=*Pheidole* sp.A8 (*ampla* gp.), PhA10=*Pheidole* sp.A10 (*ampla* gp.), PhA11=*Pheidole* sp.A11 (*ampla* gp.), PhA12=*Pheidole* sp. A12 (*ampla* gp.), PhA13=*Pheidole* sp. A13 (*ampla* gp.), PhA15=*Pheidole* sp.A15 (*ampla* gp.), PhA23=*Pheidole* sp.A23 (*ampla* gp.), Ph.A30=*Pheidole* sp.A30 (*ampla* gp.), PhI=*Pheidole* sp.I1 (*impressiceps* gp.), PhF1=*Pheidole* sp.F1 (Group F), PhL4=*Pheidole* sp.L4 (*longiceps* gp.), PrD=*Prolasius* sp.D, Rhs=*Rhytidoponera scaberrima*, Rhi=*Rhytidoponera impressa*, Rhk=*Rhytidoponera kurandensis*, Rhp=*Rhytidoponera purpurea*, StA=*Stigmacros* sp.A, Sty=*Strumigenys yaleopteura*, Ten=*Technomyrmex nitens*, Teb=*Tetramorium bicarinatum*, Tep=*Tetramorium pacificum*.

NMDS revealed clear elevational zonation of sites even when sites from different mountains were considered together (Figure 2.6A). There was a very marked compositional disjunction between 600 m and 800 m. With only two exceptions (800 m at Finnegan, and 900 m at Windsor), all sites higher than 600 m formed a cluster that was distinct from a cluster containing all lower elevation sites (Figure 2.6A). This disjunction was identified by cluster analysis as the primary division of sites based on ant species composition (Figure 2.6B). Within each of these primary clusters, most sites grouped according to subregion.

2.5 Discussion

The AWT is a major biodiversity hotspot of global significance (Williams *et al.*, 2009) and our study demonstrates that it supports a highly diverse ant fauna with high levels of spatial turnover. Each subregion supported a compositionally distinctive ant fauna, and a substantial proportion (19%) of species were recorded from a single subregion. Some of these species are known to occur elsewhere and so are not locally endemic; for example, *Technomyrmex shattucki* (recorded here only from Carbine) is distributed further south to the Tully region (Bolton, 2007), *Leptogenys anitae* (likewise recorded here only from Carbine) occurs south to southeastern Queensland (Taylor & Brown, 1985), and *Myrmecina inaequala* (recorded here only from Mount Windsor) is likewise very widely distributed (Shattuck, 2009). However, we recorded *Leptomyrmex dolichoscapus* only at Carbine and it appears to be endemic to this area (Smith & Shattuck, 2009). The same is true for *Myrmecina alpina* (Shattuck, 2009). Other species of *Myrmecina* not recorded here also have very localised distributions within the AWT (Shattuck, 2009). This is the case for virtually all other AWT ant genera that have undergone recent taxonomic revision, including *Orectognathus* (Taylor, 1977), *Monomorium* (Heterick, 2001), *Pristomyrmex* (Wang, 2003), *Anochetus* (Shattuck & Slipinska, 2012) and *Teratomyrmex* (Shattuck & O'REILLY, 2013). Such small-range endemism is known for other invertebrate taxa, including flightless insects (Yeates & Monteith, 2008), flightless ground beetles (Staunton, 2013) and dung beetles (Aristophanous, 2014) in the region.

There was high species turnover with elevation at all subregions, as appears to be typical for tropical ants (Smith *et al.*, 2014). However, the rates of turnover in our study are unusually high. For example, we recorded 50 - 65% species dissimilarity per 200 m change in elevation, which is much higher than the 20% in Malaysia (Bruhl *et al.*, 1999). Similarly, our Figure. of 90% species dissimilarity with a 400 m change in elevation shows higher rate than 55% over the same elevational change in Madagascar (Fisher, 1999) and 50% over 500 m in Panama (Olson, 1994). Other invertebrate taxa also have particular high rates of elevational turnover in the AWT. Dung beetles displayed up to 40% species dissimilarity for every 200 m (Aristophanous, 2014), and beetles in general displayed 50% over elevational ranges of 500 m (Yeates & Monteith, 2008). Such high rates of elevational turnover possibly reflect unusually narrow thermal tolerances (Huey et al 2012; Sunday et al 2014).

Species richness showed only weak patterns, in contrast to the high levels of species turnover. Ant species richness typically declines with increasing latitude (Cushman *et al.*, 1993; Dunn *et al.*, 2009), as is the case for biological diversity more generally (Willig *et al.*, 2003; McCain & Grytnes, 2010). We found a trend of declining ant richness with increasing latitude in the AWT, but it was not statistically significant. This supports the results presented by Majer *et al.* (2001), where elevation appears to be stronger predictor than latitude in explaining ants assemblages pattern, but it is not in line with the declining trend of species richness with latitude in the same study, which might be because of the shorter span of latitude in our study. Additionally, temperature is a dominant factor regulating diversity in ant communities (Dunn *et al.*, 2009) and latitudinal gradients are typically gradients in mean temperature. However, although our limited latitudinal gradient spanned 4.8 degrees and 500 km, there was only a relatively slight decrease in mean annual temperature, from 21.3 °C in the north (Finnegan) to 20 °C in the south (Spec). Such a rate of reduction in mean annual temperature is much lower than the global average of 1^{o} C for every 145 km change in latitude at a given elevation (New *et al.*, 2002). Latitudinal variation in diversity in the AWT is also highly confounded by variation in historic climatic stability, with marked spatial variation in the extent to which rainforest in the AWT has persisted over the past 20,000 years (Graham *et al.*, 2010). Such variation is an important driver of diversity and distribution for both vertebrates (Williams *et al.*, 2009; Anderson *et al.*, 2012a) and invertebrates (Yeates & Monteith, 2008).

Previous studies of rainforest ant diversity along elevational gradients have shown either a monotonic decline with increasing elevation (Bruhl *et al.*, 1999; Burwell & Nakamura, 2011), or a hump-shaped pattern featuring a mid-elevation peak (Longino & Colwell, 2011; Longino *et al.*, 2014). These are the two dominant elevational patterns for invertebrates more generally (Rahbek, 2005). A full elevational gradient was represented at two of our subregions (Atherton and Carbine), and in both cases there was a slight peak in plot richness at mid elevations. The declining trend of species richness at Mount Spec could also be a manifestation of a slight mid-range peack with no rainforest (and therefore no data) for lower elevations. The relatively low richness at low elevation at Atherton could possibly be attributed to cyclone damage. Cyclone Larry had a significant impact on the beetle assemblages of affected areas, increasing the proportional representation of open-habitat taxa (Grimbacher & Stork, 2009). However, treefall-gap formation appears to have little influence on litter ants (Patrick *et al.*, 2012). Moreover, relatively low ant richness at lowland sites in the Atherton region was recorded prior to the recent cyclones (Yek *et al.*, 2009) and so does not appear to be an artefact of cyclone impacts. Our results generally suggest that ants species richness and composition patterns are more pronounced across elevation than latitude in the AWT.

Our most noteworthy finding was a striking elevational disjunction in ant species composition across all subregions between 600 and 800 m. This faunistic disjunction corresponds with a major climate/vegetation boundary in the AWT associated with persistent orographic cloud. Rainforest vegetation changes from mesophyll vine forest in the lowlands to complex notophyll vine forest and microphyll vine fern forests on cloud-affected mountains (Hilbert *et al.*, 2001a). Some vertebrate species are known to be restricted to moist mountain tops (Kanowski, 2001; Williams *et al.*, 2006), but the compositional disjunction we have documented for ants represents the clearest known faunistic association with cloud stripping in the region. There were two higher elevation sites that did not conform to the 600 m disjunction in ant species composition: 800 m at Finnegan and 900 m at Windsor. They are the only sites that have a westerly aspect and so are not subject to the moisture-laden, south-easterly winds that are the source of orographic cloud in the region.

Previous studies have shown that biodiversity patterns in the AWT are strongly influenced by regional variation in long-term climatic stability, which has determined the extent to which rainforest in the AWT has persisted over the past 20,000 years (Graham *et al.*, 2010). Stable patches have acted as biodiversity refuges and are now centres of diversity and endemism for a range of taxa (Williams *et al.*, 2009; Anderson *et al.*, 2012a). Rapid turnover of species composition, as a result of short-term climatic changes, may destabilize the ecosystem by loss of co-occurring species (Gibson-Reinemer *et al.*, 2015). Our study is consistent with the notion that climatic stability over contemporary timescales is an important driver of ant biodiversity patterns along elevational gradients in the AWT and provides further support for the importance of climatic stability as a driver of tropical biodiversity patterns.

The average elevation of orographic cloud layers is predicted to rise throughout the world under global warming (Pounds *et al.*, 1999; Rapp & Silman, 2014), and in the AWT it is predicted to rise from about 600 to 900 m by 2050 (WTMA, 2013). Sites that are currently located at the bottom of the cloud layer are therefore likely to experience drier conditions under a future climate and this can be expected to exacerbate biotic change caused by rising temperatures alone. The 600 – 800 m elevation zone is therefore likely to be especially sensitive to a changing climate and represents a priority location to focus efforts for monitoring climate-change impacts in the AWT.

2.6 Acknowledgements

Stephen Williams played a key role in establishing the project. Jodie Hayward, Magen Pettit, Célénie Christophe, Maxence Plouviez, Antoine Esnouf, Clémence Roldan, Carina Svensson and Arnaud Gourret provided valuable field and laboratory assistance, and Nick Nicholls gave valuable advice on R software. We thank them all. SN was supported by a PhD scholarship from the National Environmental Research Program of Australian Government.

Chapter 3 . Is thermal limitation the primary driver of elevational distributions? Not for montane rainforest ants in the Australian Wet Tropics

3.1 Abstract

Terrestrial ectotherms are likely to face increased periods of heat stress given that temperatures are projected to increase over coming decades. Thermal limits are used to measure climatic tolerances that potentially affect ectotherm distribution. While there is a strong relationship between the critical thermal maximum (CTmax) of insects and their latitudinal ranges, the nature of this relationship across elevation is less clear. Here we investigated the combined relationships between CTmax, elevation and ant body mass, given that CTmax can also be influenced by body mass, in the World Heritage-listed rainforests of the Australian Wet Tropics. We measured the CTmax and body mass of 20 ant species across an elevational gradient, 350 - 1,000 m a.s.l.. Community CTmax did not vary systematically with increasing elevation and there was no correlation between elevation and elevational ranges of species. However, body mass significantly decreased at higher elevations. Despite negative correlation between CTmax and body mass of ant communities, there was no significant difference in CTmax of different-sized ants within a species. These findings are not consistent with either the climatic variability hypothesis, Rapoport's rule or Bergmann's rule. Models indicated that elevation and body mass had limited influences on CTmax. Our results suggest that the distribution of most montane ants in the region is not strongly driven by thermal limitation, and climate change will likely impact ant species differently. This is likely to occur primarily through changes in rainfall via its effects on vegetation structure and therefore thermal microhabitats, than through direct temperature changes.

Key words: body size, climate change, critical thermal maximum, ectotherm, elevation gradient.

3.2 Introduction

Ambient temperatures influence the activity, performance and survival of ectotherms as these organisms have a limited capacity to generate heat internally (Huey & Stevenson, 1979). Therefore, differences in temperature regimes across space and time strongly influence the distributions of ectotherms (Huey & Stevenson, 1979; Ghalambor *et al.*, 2006; Sunday *et al.*, 2011). Many ectotherm species, which represent a very large proportion of global species diversity (Wilson, 1992), have distinct elevational and latitudinal limits, as well as clear patterns in daily and seasonal activity (Andersen, 1983; Ghalambor *et al.*, 2006; Sunday *et al.*, 2011). This sensitivity to temperature will also mediate the reorganization of ectotherm distributions and diversity across the globe as temperatures rise following climate change (Deutsch *et al.*, 2008b; Buckley *et al.*, 2012; Hoffmann *et al.*, 2013). Within-site variation in temperature is relatively low in the tropics, and so ectotherms tend to have narrow thermal limits in the tropics (Deutsch *et al.*, 2008b; Clusella-Trullas *et al.*, 2011; Huey *et al.*, 2012). Tropical ectotherms are therefore likely to be especially sensitive to rising temperatures (Diamond *et al.*, 2012).

The physiological thermal tolerance limits of ectotherms are often used to assess the limits of their potential geographic distributions (Bozinovic *et al.*, 2011; Sunday *et al.*, 2012). Critical thermal maximum (CTmax), which measures the maximum operating temperature of an organism, is a commonly used measure of thermal sensitivity (Rezende *et al.*, 2011; Ribeiro *et al.*, 2012; Baudier *et al.*, 2015) and there is often a strong relationship between a species' CTmax and its latitudinal distribution. For example, CTmax declines with increasing latitude (Addo-Bediako *et al.*, 2000; Hoffmann *et al.*, 2013) and along other temperature gradients (Vorhees *et al.*, 2013) – including elevation (Gaston & Chown, 1999; Terblanche *et al.*, 2006).

This is not always the case, however, and in some instances CTmax shows little variation across temperature gradients (Araújo *et al.*, 2013; Bishop *et al.*, 2017). Therefore, the generality of this relationship between CTmax and temperature among different ectotherm groups remains unclear.

Variation in temperature regimes can also influence the range sizes of species, just as it influences the variation in their CTmax. The climatic variability hypothesis states that species occurring at higher elevations have wider thermal tolerances, and larger elevational ranges, because they are adapted to the greater temporal variability in climatic conditions at these locations (Stevens, 1992; Gaston & Chown, 1999). This positive relationship between elevation and the elevational range of species has been called Rapoport's rule (Stevens, 1992). However, the mechanism behind the positive relationship between CTmax and elevational range has recently been questioned (Payne & Smith, 2017), and the relationship does not appear to hold for all ectotherms, especially in less climatically variable regions (Addo-Bediako *et al.*, 2000), such as the tropics.

Finally, the thermal tolerances of species are also strongly related to body size (Atkinson, 1994; Angilletta Jr & Dunham, 2003; Angilletta *et al.*, 2004). As ectotherms decrease in size, their body surface area to volume ratio increase, and their thermal inertia therefore decreases (Angilletta, 2009). Similarly, the body size of widespread species tends to be larger in colder parts of their ranges - Bergmann's Rule, which is also based on the thermoregulatory benefit of being large in a cold environment (Meiri & Dayan, 2003; Olalla-Tárraga *et al.*, 2006). Therefore, we would expect body size to increase with elevation. This implies that body size should correlate positively with thermal tolerance. Indeed, this has been shown for rainforest ants in Brazil (Ribeiro *et al.*, 2012) and Panama (Kaspari *et al.*, 2015). However, in some cases this correlation was not found, such as in some common ant species in North America (Verble-Pearson *et al.*, 2015).

In this study, we investigate the relationships between CTmax, body mass and the elevational distributions of ant (Hymenoptera: Formicidae) species from one of the world's biodiversity hot spots, World Heritage-listed rainforests of the Australian Wet Tropics (AWT). Ants are an ideal focal taxon for studying relationships between thermal tolerances and species distribution patterns. They are a dominant faunal group in tropical rainforests (Hölldobler & Wilson, 1990; Bruhl *et al.*, 1998; Davidson *et al.*, 2003; Kaufmann & Maschwitz, 2006; Griffiths *et al.*, 2017), and temperature is a primary driver of ant distributions globally (Andersen, 1995; Dunn *et al.*, 2009; Diamond *et al.*, 2012). Physiological traits combined with some behavioural and natural history traits can be important predictors of the biogeographical climatic niches of ant species (Arnan & Blüthgen, 2015). There is very high turnover of ant species across elevation in the AWT (Nowrouzi *et al.*, 2016), and this can be expected to be influenced by variation in temperature. We specifically ask four questions. First, does CTmax decrease with increasing elevation and decreasing ambient temperature, paralleling the relationship between CTmax and latitude? Second, do species occurring at higher elevations have larger elevational ranges, as predicted by the climatic variability hypothesis and Rapoport's rule? Third, does body size increase with elevation, as predicted by Bergman's rule? Finally, do elevational distributions and body size combine to strongly predict a species' CTmax?

3.3 Methods

3.3.1 Study sites

Sampling was conducted at four sites along an elevational gradient at Mount Spec, 90 km north of Townsville (Figure 3.1). The four sites were distributed at 350 m, 600 m, 800 m and 1,000 m elevation. All sites were located on granite-derived soils (McJannet *et al.*, 2008; Parsons & Congdon, 2008).

Mean annual rainfall at Mount Spec varies from about 1,200 to 2,500 mm along the elevation gradient (Bureau of Meteorology, 2015), with more rain at higher elevation and 84% occurring between November and April (Lovadi *et al.*, 2012). Mean temperature declines at a rate of about 1 °C for every 200 m increase in elevation (Shoo *et al.*, 2005a), and therefore by about 3° C across our gradient. Vegetation is dominated by sclerophyll woodlands and open forests at low elevation, and the cover of rainforest increases with elevation (Hilbert, 2008). Despite their relatively small area, the rainforests of the AWT are recognized as a major biodiversity hotspot of global significance due to their extraordinary biological richness and biogeographical uniqueness (Williams *et al.*, 2009).

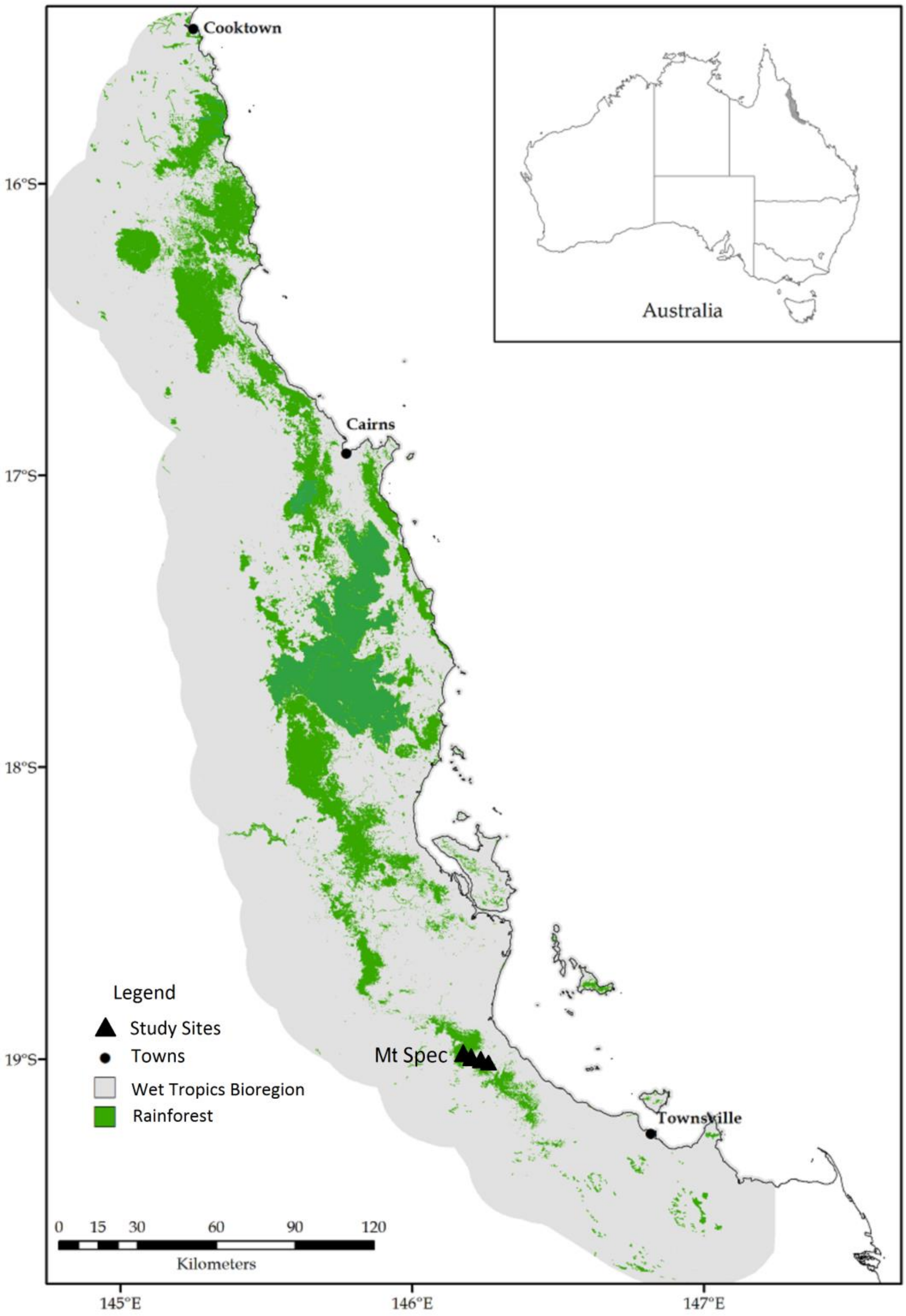

Figure 3.1. Map showing the current extent of rainforest (green shading) in the Australian Wet Tropics bioregion (light shading), with locations of sampling sites indicated by triangles at Mount Spec.

3.3.2 Methodology

CTmax and body mass (as our measure of body size; (Moretti *et al.*, 2017)) were measured for 160 ants representing 20 species and 13 genera (Appendix 4) that were a mix of common and rare species (based on the entire community surveyed by Nowrouzi *et al.* (2016) and provided in Chapter 2; Figure 3.2). Our study species represented 19% of the 108 ant species known to occur at Mount Spec (Nowrouzi *et al.*, 2016). The ants were randomly hand-collected during daytime from rainforest at the four sites, and we consider them to be broadly representative of the species occurring at the sites, based on the rank abundance plot of the data (Figure 3.2). The ants included widely distributed generalist species (species of *Anonychomyrma* and *Rhytidoponera*) as well as more-specialized species with narrow elevational ranges (e.g. species of *Notostigma* and *Myrmecia*) (for classifications of functional groups see Andersen (1995)). All individuals at a site were collected as stray foragers within 30 m of each other to provide a repetitive sample of ants foraging at the time within the local community. However, whether or not conspecifics came from different colonies is unknown, and so some conspecifics of large-sized species may have come from the same colony. We also acknowledge that we did not control for dimorphism in body mass measurements of species (e.g. *Camponotus* or *Pheidole*), which is also the case for the latest protocol for standardized measurements of terrestrial invertebrate functional traits (Moretti *et al.*, 2017).

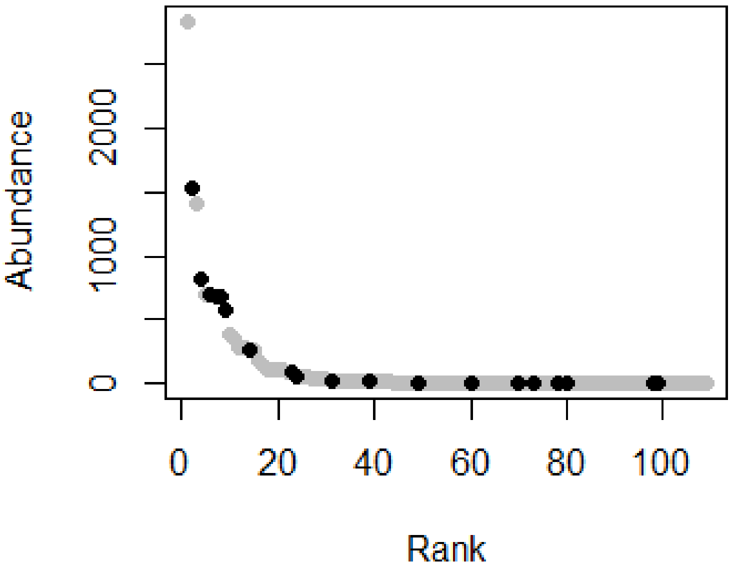

Figure 3.2. Rank abundance plot of the entire ant fauna of Mount Spec based on the comprehensive survey (pitfall traps, Winkler sacs and ground and arboreal baits) across the entire gradient (350 – 1000 m) and time series (2009 – 2013), provided in Chapter 2. Species for which CTmax data was collected are shaded in black. Species for which CTmax data was not collected are shown in grey.

CTmax was measured in the field, with individuals assayed within three hours of collection to reduce the likelihood of acclimation. Individuals were placed into a 1.5-ml microcentrifuge tube plugged with cotton wool. They were assigned to a Thermal-Lock dry heat bath pre-warmed to 25°C (Diamond *et al.*, 2012), and CTmax was recorded by increasing the temperature by 1°C/minute until the knockdown point (when the ant exhibited loss of the righting reflex (Spellerberg, 1972)). All tested individuals were then taken to the lab to confirm identification and measure body mass. Individuals were oven-dried for 24 hrs at 70 °C, using a Blue M Electric drying oven, and body mass was measured using a Satorius semimicrobalance scale with 0.01 mg accuracy. All CTmax experiments were conducted during December 2014 (wet season).

Most ant species could not be confidently assigned to species, and were given codes that follow those used in Nowrouzi *et al.* (2016) and Chapter 2. A complete collection of voucher specimens is deposited in the CSIRO Tropical Ecosystems Research Centre, Darwin, Australia and the James Cook University Entomology Collection.

3.3.3 Data analysis

3.3.3.1 Phylogenetic signal

A genus level, time-calibrated phylogeny from Moreau and Bell (2013) was used to estimate phylogenetic signal in CTmax and body mass. We added species from this study as polytomies onto the original genus phylogeny. We then calculated genus level means in the CTmax and body mass measures and used the original genus level phylogeny to calculate phylogenetic signal. Only one genus, *Nylanderia*, was not present on the original phylogeny; it was inserted as a tip next to its closest sister genus *Paratrechina* (LaPolla *et al.*, 2011). Phylogenetic signal was calculated using Pagel's λ (Pagel, 1999) and Blomberg's K (Blomberg *et al.*, 2003). A likelihood ratio test was used to test for a significant departure of both of these statistics from 0 (no phylogenetic signal). The *phytools* package in R was used to manipulate the phylogeny and perform the phylogenetic signal tests (Revell, 2012). CTmax did not display significant phylogenetic signal (Pagel's λ<0.01, P=1, Blomberg's K=0.698, P=0.474) at the genus level. Similar results were found for body mass (Pagel's λ<0.01, P=1, Blomberg's K=0.684, P=0.523). All the species were therefore treated as independent in our analyses.

3.3.3.2 CTmax and elevation

We calculated mean CTmax values for each species and the community (based on occurrence of species) at each elevation site. We then used one-way ANOVA, followed by a post hoc Tukey test, to assess the differences in mean CTmax among species and site communities at different elevations.

3.3.3.3 Elevation and species elevational ranges

We calculated the elevation midpoint for each species occurring at the sites, based on the dataset provided by Nowrouzi *et al.* (2016) and Chapter 2. We then used a simple linear regression to test correlation between elevation midpoint and elevational ranges of the species tested for CTmax.

3.3.3.4 Body size and elevation

We calculated mean body mass values for each species and the community (based on occurrence of species) at each elevation site. We then used one-way ANOVA, followed by a post hoc Tukey test, to assess the differences in mean body mass among species and site communities at different elevations.

3.3.3.5 CTmax, elevation and body size

We used linear mixed-effect model to model body mass and elevation (which ants were collected from) as explanatory variables for variation in CTmax. To control for variation in species occurrence with elevation, we treated species as a random factor. We considered the effect of two fixed variables, elevation and body mass, in one model and used the ratio of CTmax per mg of body mass as a dependent variable because of potential correlation between body mass and elevation as co-variables. Analyses were conducted using the *adehabitat* and *lme4* packages of R v2.12.1 (R Development Core Team, 2010; Bates *et al.*, 2013).

3.3.4 Data Accessibility

Data for this chapter can be found in the supporting information (Appendix 4).

3.4 Results

3.4.1 CTmax and elevation

Overall mean CTmax was 47.2 (± 0.54) °C, ranging from 37–65 °C among species. CTmax at the community level did not vary systematically with elevation (Figure 3.3; Appendix 5).

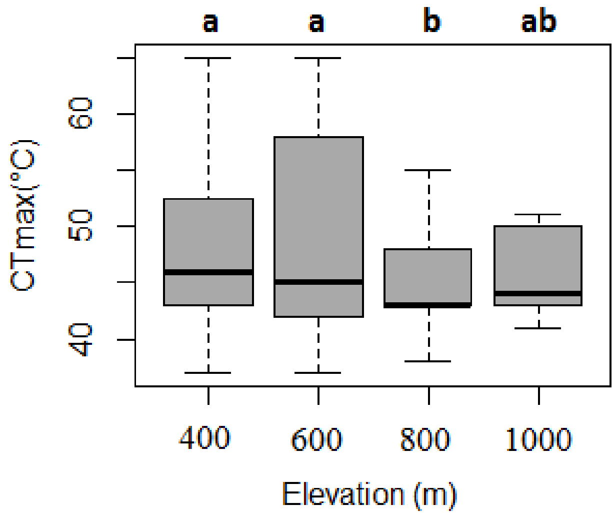

Figure 3.3. Variation in mean CTmax across elevational sites, based on pooled data from all tested species; with 95% confidence intervals. Different letters indicate significant differences between elevational sites.

CTmax was tested for ≥10 individuals for nine species, all of which occurred at multiple elevational sites (Table 3.1). Mean CTmax significantly decreased with increasing elevation for only three of the species (*Myrmecia nigrocincta*, *Rhytidoponera* cf. *victoriae* and *Rhytidoponera impressa*), but showed no significant differences for the others (Figure 3.4; Appendix 6).

Table 3.1. Species list and number of individuals tested for CTmax and body mass from sites at different elevations on Mount Spec. Species with ≥ 10 individuals are highlighted.

Species	Elevational sites (m)				Total
	350	600	800	1000	
Anonychomyrma gilberti	**11**	**2**			**13**
Anonychomyrma* cf.*gilberti	**10**		**2**		**12**
***Anonychomyrma* sp. M**			**5**	**8**	**13**
Camponotus sp.N2 (*novaehollandiae* gp.)		2			2
***Crematogaster* sp. G**	**4**	**6**			**10**
Leptogenys mjobergi	**3**	**10**			**13**
Leptomyrmex rufipes	3				3
Myrmecia nigrocincta	**3**	**12**			**15**
Notostigma carazii	2	3			5
Nylanderia glabrior			4	2	6
Odontomachus cephalotes	6				6
***Pheidole* sp. A2 (*ampla* gp.)**			**3**	**8**	**11**
Pheidole sp. V1 (*variabilis* gp.)		1			1
Polyrhachis argentosa	5				5
Polyrhachis delecta		4	1		5
Rhytidoponera cf. victoriae	**3**	**1**	**9**	**2**	**15**
Rhytidoponera impressa	**4**		**5**	**1**	**10**
Rhytidoponera purpurea		5	1		6
Technomyrmex cheesmanae			2	1	3
Technomyrmex quadricolor				6	6

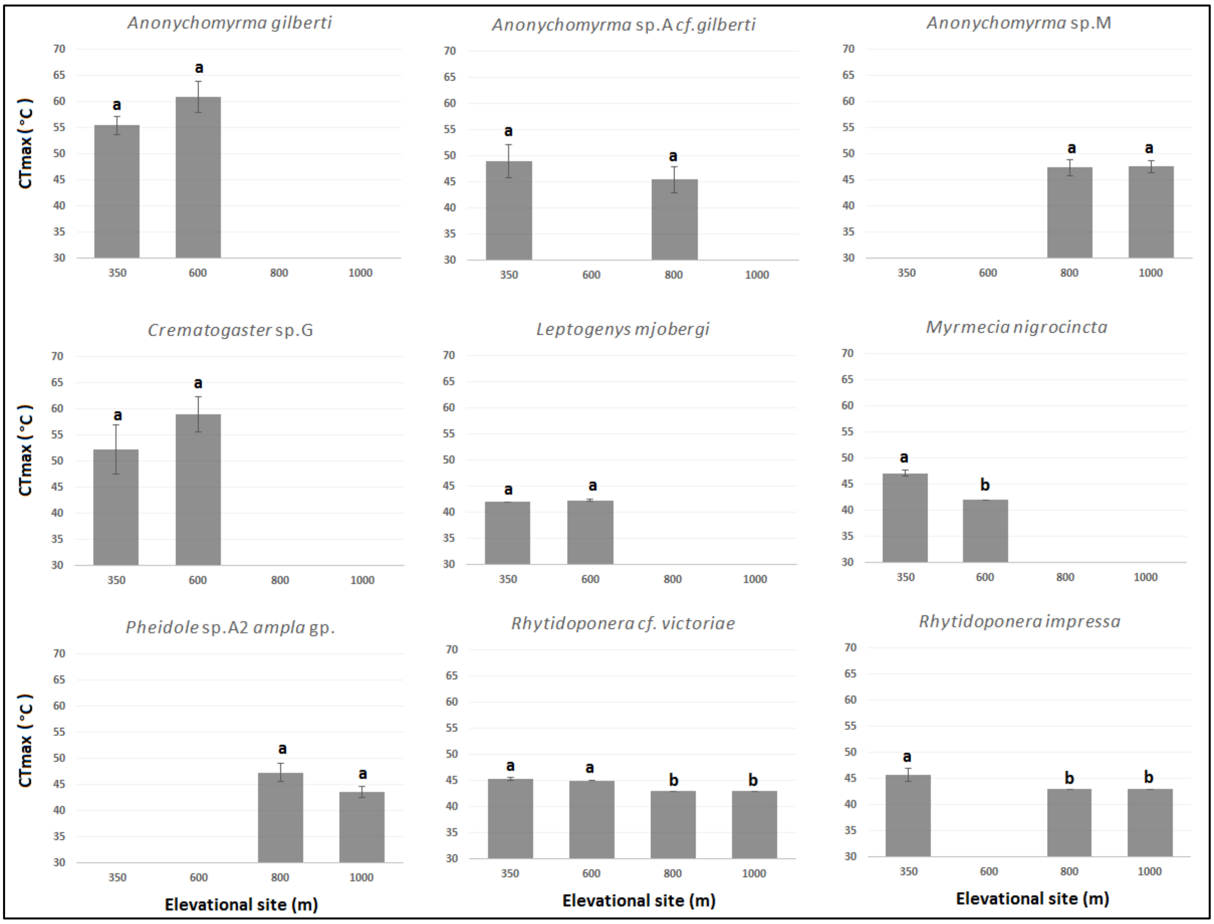

Figure 3.4. Mean CTmax in different elevational sites for each species; based on species tested for ≥10 individuals; with 95% confidence intervals. Different letters indicate significant differences between elevational sites for each species.

3.4.2 Elevation and species elevational ranges

There was no correlation between elevation midpoint and elevational ranges of species (simple linear regression, $F_{1,18}$=0.057, P=0.814), and species with higher elevation midpoints did not specifically present larger elevational ranges. For example, of the nine species with ≥10 individuals tested, six occurred at high elevation (>800 m); two of these (*Anonychomyrma* sp. M and *Pheidole* sp. A2 (*ampla* gp.)) occurred exclusively at high elevation, whereas the other four (*Anonychomyrma gilberti*, *A.* cf. *gilberti*, *Rhytidoponera* cf. *victoriae* and *R. impressa)* occurred across the full elevation gradient (Figure 3.5).

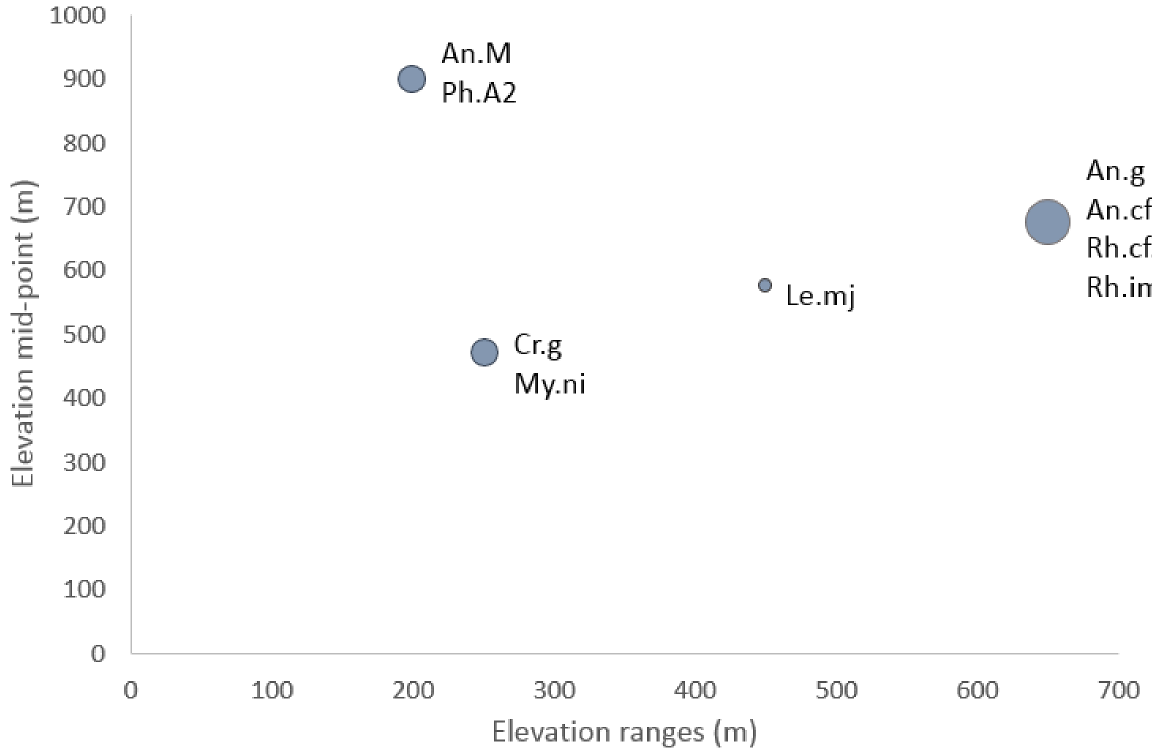

Figure 3.5. Mid elevation point and elevational ranges for each species with ≥10 individuals tested. Larger points represent higher number of species overlapped. Abbreviations are species names as: An.g= *Anonychomyrma gilberti*, An.cf.g= *Anonychomyrma* cf.*gilberti*, An.M= *Anonychomyrma* sp. M, Cr.G= *Crematogaster* sp. G, Le.mj= *Leptogenys mjobergi*, My.ni= *Myrmecia nigrocincta*, Ph.A2= *Pheidole* sp. A2 (*ampla* gp.), Rh.cf.v= *Rhytidoponera cf. victoriae* and Rh.im= *Rhytidoponera impressa*.

3.4.3 Body mass and elevation

Mean body mass at the community level decreased markedly with increasing elevation (ANOVA, $F_{3,153} = 10.86$, $P < 0.001$), with the decline occurring primarily between 600 m and 800 m (Figure 3.6; Appendix 7). However, mean body mass decreased with increasing elevation within only three of the nine species with ≥10 individuals tested (*Anonychomyrma* cf. *gilberti*, *Rhytidoponera* cf. *victoriae* and *Rhytidoponera impressa*), and showed no significant variation with elevation within the others (Figure 3.7; Appendix 8). Notably, large (>4 mg) ants were found only at low elevations (350 and 600 m; Figure 3.8).

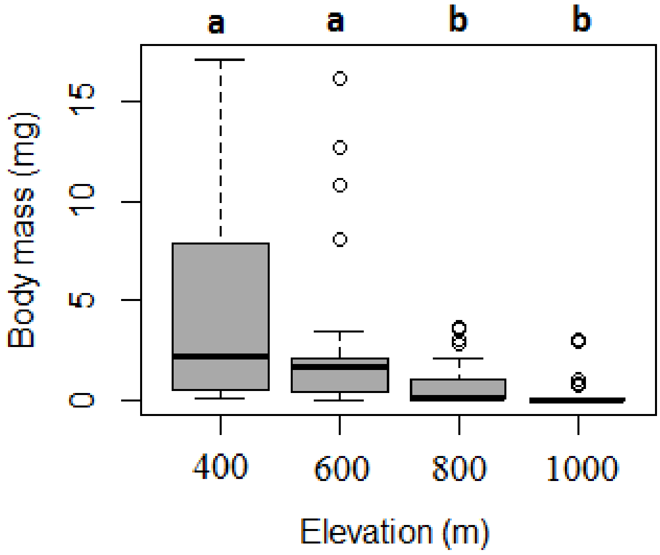

Figure 3.6. Variation in mean body mass across elevational sites, based on pooled data from all tested species; (with 95% confidence intervals). Different letters indicate significant differences between elevational sites.

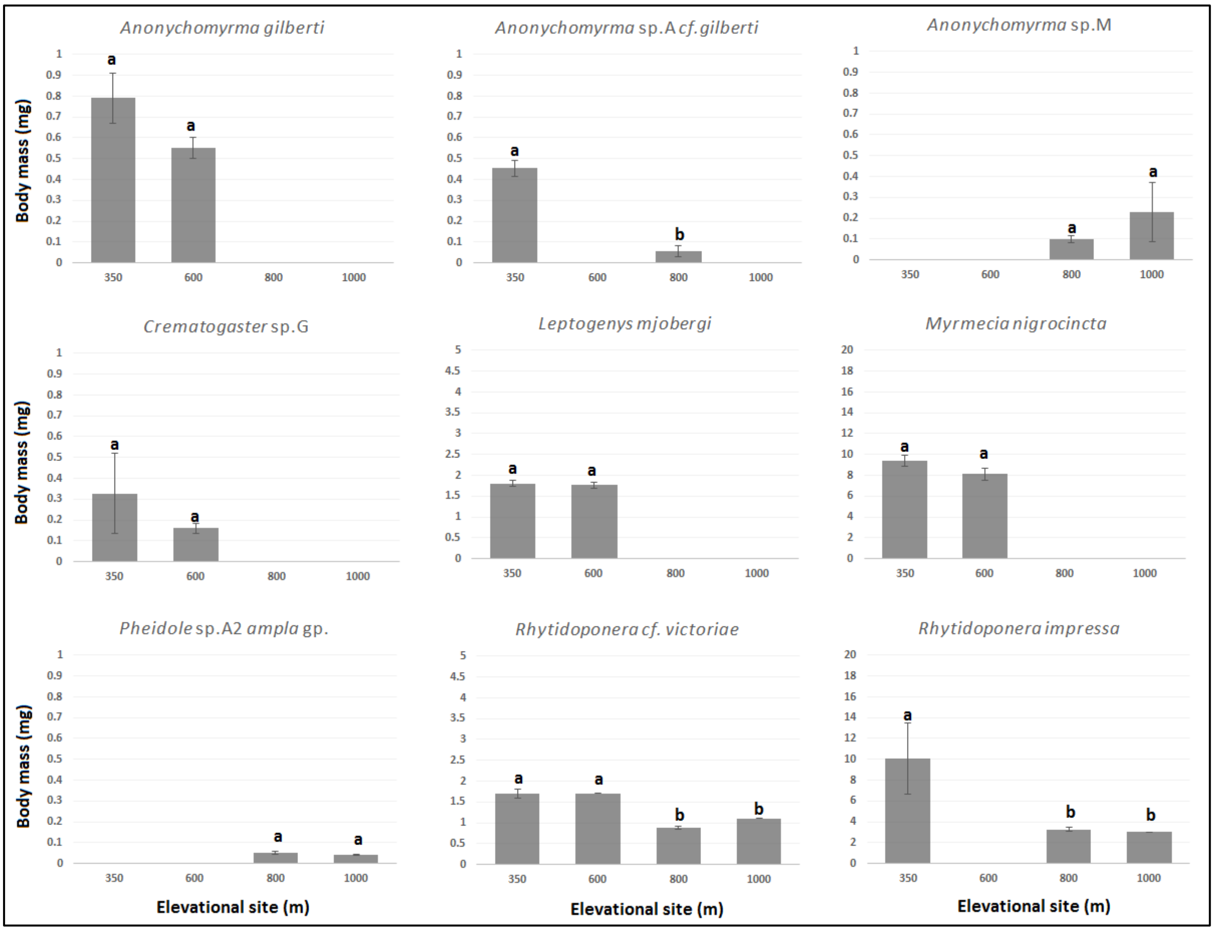

Figure 3.7. Mean body mass (with 95% confidence intervals) in different elevational sites for each species with ≥10 individuals tested. Different letters indicate significant differences between elevational sites for each species.

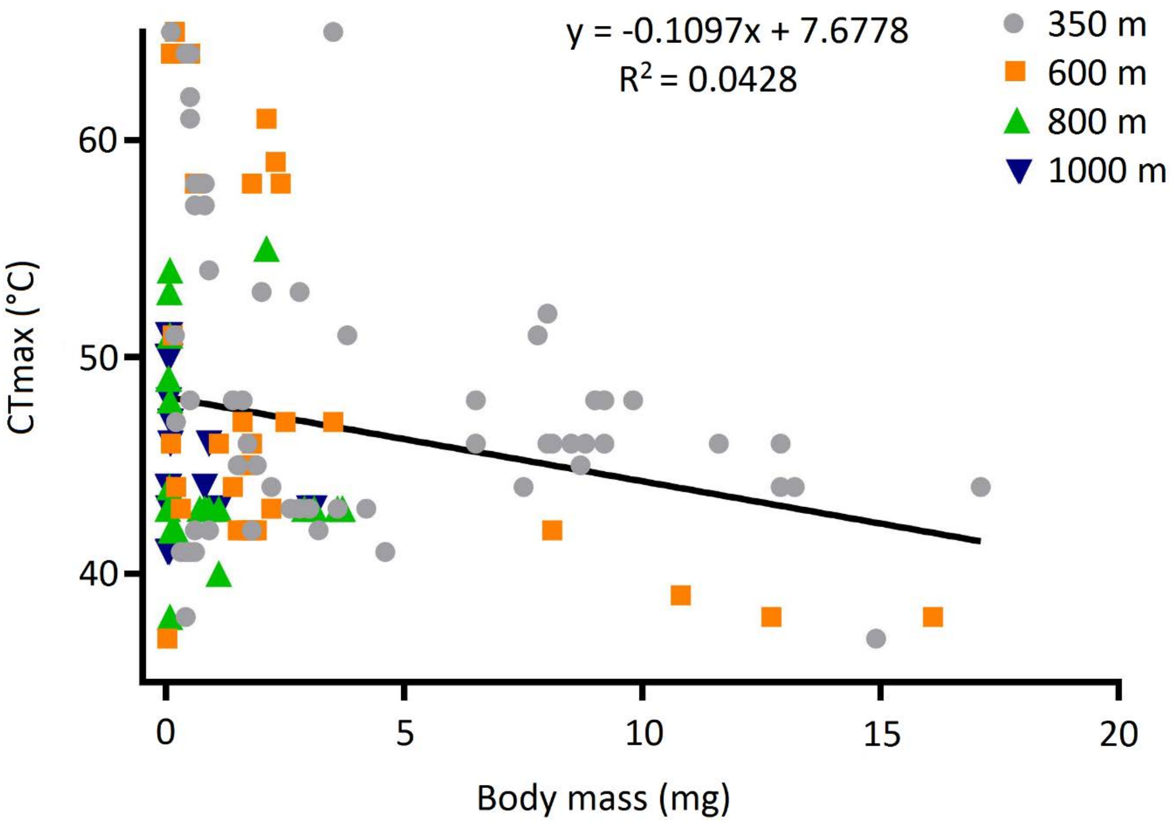

Figure 3.8. CTmax variation in relation to body mass changes, based on pooled data from all the species of all the elevation sites, with simple linear regression line.

3.4.4 CTmax, elevation and body size

Overall, there was a negative relationship between CTmax and body mass (simple linear regression, $F_{1,155}$=6.93, P = 0.009; Figure 3.8). However, this relationship occurred within a species only for *Anonychomyrma gilberti* (Appendix 9). Results from the linear mixed effect model showed species (the random factor in the model) as the strongest predictor of variation in CTmax (Conditional R^2=0.87; Appendix 10). Removing the effect of species, only 3.1% of the variation in CTmax (Marginal R^2=0.031; Appendix 10) was explained by a combination of elevation and body mass.

3.5 Discussion

Our study investigated the relationships between CTmax, body mass and elevational distribution of rainforest ant species in the Australian Wet Tropics, as a basis for understanding their potential responses to climate change. We first questioned if CTmax decreases with increasing elevation, paralleling the common pattern of declining CTmax of species with increasing latitude. We found this negative relationship for only three of the nine species tested, and it did not hold at the community level. Bishop *et al.* (2017) also found no significant change in CTmax across an elevation gradient for ants in South Africa. Our findings are not consistent with studies of CTmax variation across elevational gradients in other insect groups (Gaston & Chown, 1999; Terblanche *et al.*, 2006), and do not support the generality of declining CTmax with decreasing ambient temperature (Addo-Bediako *et al.*, 2000; Hoffmann *et al.*, 2013; Vorhees *et al.*, 2013).

The median CTmax of 45 °C for rainforest ants in our study slightly exceeds that of ants globally as estimated in a world-wide survey, 43.3 °C (Diamond *et al.*, 2012). This may be explained by the tropical location of our study system, which experiences warmer than average conditions globally. The CTmax range of 37-65 °C among our species is also wider than the range for Panamanian rainforest ants, 41-56 °C (Kaspari *et al.*, 2016); this can be explained by the AWT's location at higher latitudes, following the thermal adaptation prediction that the hotter location creates broader CT ranges (Kaspari *et al.*, 2016).

Our second question was if the climatic variability hypothesis and Rapoport's rule apply to our study fauna. Higher-elevation species did not tend to occur across broader elevational ranges. Subsequently, Rapoport's rule also did not apply to ant species in the AWT. The contrary finding by Sanders (2002) that Rapoport's rule applies to ants from North America can be explained by the lower climatic variability within the tropics compared with temperate regions. Arnan *et al.* (2015) similarly showed that temperature variability and species thermal breadth are related in (temperate) ants of western Europe.

Our third question was if body size increases with increasing elevation, following Bergmann's rule. For individual species we found either no relationship between body size and elevation, or that body size actually decreased with increasing elevation. At the community level, there was a very strong decrease in mean body size with increasing elevation. Such a pattern is in direct contradiction of Bergmann's rule, but has previously been reported for ants (Geraghty *et al.*, 2007) and other insects (Brehm & Fiedler, 2004; Eweleit & Reinhold, 2014; Levy & Nufio, 2015). It has been suggested that Bergmann's rule might apply to colony size rather than body size in ants across altitude (Kaspari & Vargo, 1995), but an analysis of colony size was beyond the scope of our study.

Finally, we questioned if a combination of elevational distribution and body size would be a strong predictor of a species' CTmax. We found a negative correlation between body mass and CTmax at the community level, which conforms with studies of North American ants (Verble-Pearson *et al.*, 2015) but contrasts with findings from ant communities elsewhere in the tropics (Ribeiro *et al.*, 2012; Kaspari *et al.*, 2015). However, we found that the combination of elevational distribution and body mass explained only 3.1% of the variation in CTmax, and species was by far the best predictor. One explanation for the poor predictive power of elevational distribution and body mass over species CTmax is foraging plasticity. For example, ant species may preferentially forage in microhabitats (Kaspari & Weiser, 2000; Baudier *et al.*, 2015), or during different times of the day (Christian & Morton, 1992; Stuble *et al.*, 2013), that best match their thermal requirements. This can include switching from diurnal to nocturnal activity (Nelson *et al.*, 2017). Given the variation among species in both thermal tolerance and foraging behaviour, climate change is likely to have highly species-specific impacts (Oberg *et al.*, 2012), which can also include reduction in foraging efficiency (Andrew *et al.*, 2013).

The fact that elevation was such a poor predictor of variation in CTmax suggests that the distribution of most montane ants in the Australian Wet Tropics is not strongly driven by thermal limitation. This is in line with studies on *Drosophila*, which have found a poor association between CTmax and latitude (Kimura, 2004; Kellermann *et al.*, 2012). The positive correlation between CTmax and environmental temperature seems to be strong in dry environments (Stratman & Markow, 1998), whereas in wet regions there is often a negative correlation between precipitation and CTmax (Kellermann *et al.*, 2012). In wet regions, precipitation might act through its influence on canopy cover, which in turn influences the diversity of thermal microclimates (Pincebourde *et al.*, 2012) and therefore the capacity for behavioural thermo-regulation rather than requiring thermal adaptation (Huey & Pascual, 2009). It is possible that CTmax is more responsive to maximum rather than mean temperature, as appears to be the case for *Drosophila* (Kellermann *et al.*, 2012) and Mediterranean ants (Cerdá *et al.*, 1998).

In conclusion, our findings point to complex interactions between ambient temperature, vegetation, ant physiology and ant behaviour under future climates (Wiescher *et al.*, 2012). A temperature rise of 1°C combined with a 10% decrease in precipitation is predicted to decrease the extent of montane elevation rainforests in the AWT by 60% (Hilbert et al. 2001). This is predicted to reduce suitable habitat for montane species (Williams & Pearson, 1997; Shoo *et al.*, 2005a; Staunton *et al.*, 2014; Costion *et al.*, 2015). In the AWT, climate change is likely to affect ants more through changes in rainfall, including rainfall seasonality, through its effects on vegetation structure and therefore thermal microhabitats, than through direct changes in temperature.

3.6 Acknowledgements

Dr Kyran Staunton provided valuable comments on the manuscript, which we are grateful for. SN was supported by a PhD scholarship from the National Environmental Research Program of Australian Government.

Chapter 4 . Climate-change impacts on rainforest ant communities: reduction in habitat suitability and compositional change in the Australian Wet Tropics

4.1 Abstract

Understanding how species' diversity and distribution respond to climate change has become a major focus of ecology and conservation biology. Forecasting changes in the distribution and composition of biological communities under future climates is particularly challenging, because (1) component species are likely to show variable responses to climate change, and (2) the distribution of suitable habitat is also likely to change. Major gaps in our knowledge of geographic distributions of many taxonomic groups, especially in highly diverse tropical regions, limits the applicability of commonly used species-level modelling approaches to predict future diversity patterns. Community modelling approaches provide important tools for projecting future scenarios in the absence of comprehensive species-level distributional data, as is typically the case for invertebrates. Here we used an information theoretic approach combined with Generalised Dissimilarity Modelling to assess influences of environmental variables on compositional turnover, and to predict future changes in the ecological environments of rainforest ant communities in the World Heritage-listed Australian Wet Tropics. We estimated diversity patterns from 5,204 species occurrence records across six mountains in the Australian Wet Tropics (AWT) and correlated levels of dissimilarity between communities using environmental variables. We created a model that calculated the effective area of similar ecological environments (SEE) for the communities throughout the region, using their compositional dissimilarity. We then projected the changes in the effective area of SEE under two future climate projections, for three different times: 2035, 2055 and 2085. We found that temperature and habitat disturbance from cyclones had the greatest influence on ant species turnover. Therefore, forecast increases in temperatures and extreme cyclonic events are predicted to significantly affect ant communities in the AWT. Our models indicated that rainforest ant communities will be under pressure due to loss of effective area of SEE under both climate change scenarios. The drier inland side of the AWT will be at highest risk of reduction in area of SEE, and therefore major compositional change, due to substantial changes in rainforest vegetation in addition to the direct effects of a changing climate.

Key words: biogeography, climate change, composition turnover, ecological environments, GDMs, habitat, rainforest.

4.2 Introduction

Anthropogenic climate change and associated extreme weather events are predicted to significantly alter species' distributions and subsequently the composition of biological communities (Thomas, 2010; Jenkins *et al.*, 2011; Huey *et al.*, 2012; Arribas *et al.*, 2017). At the species level, rising temperatures might cause metabolic, behavioural, or evolutionary change, or drive dispersal to climatically suitable areas (Parmesan, 2006; Urban *et al.*, 2012; Reuman *et al.*, 2014). Community-level responses are more complicated, as changing temperature may differentially favour the vital rates or demographic attributes of some species while penalizing others (Elmendorf *et al.*, 2012). The magnitude or sign of species interactions also may change and consequently disrupt mutualisms, trophic interactions, competitive hierarchies and ultimately species coexistence (Blois *et al.*, 2013; Sorte & White, 2013; Sentis *et al.*, 2014). Therefore, forecasting changes in the distribution and composition of biological communities under future climates can be extremely challenging.

Tropical forests are the most biodiverse of all terrestrial habitats (Bradshaw *et al.*, 2009), and while deforestation rates have recently declined, forests remain severely threatened by anthropogenic climate change (Hérault & Gourlet-Fleury, 2016; Lyra et al., 2016). The combination of high diversity and limited information in species distributions make the applicability of species-level modelling approaches particularly limited for the tropics (Elith & Leathwick, 2009). This is especially the case for invertebrates, which, as ectotherms, are sensitive to climate change (Deutsch *et al.*, 2008b; Sheldon *et al.*, 2011; Sheldon & Tewksbury, 2014).

Even when environmental correlates of species occurrences are well known, stacked species distribution models (SDMs) have a poor record of predicting changes in community composition (Pellissier *et al.*, 2013; D'Amen *et al.*, 2015). One reason for this is that SDMs can predict if a species might occur in a general area that is climatically suitable, but they are not able to predict if they will occur in any particular community within that area, given that any community has only a fraction of the regional species pool. Therefore, commonly used species-level modelling approaches (Elith & Leathwick, 2009) have a limited role in predicting how the diversity and composition of whole ecosystems will change under future climates.

One approach to predicting responses of biological communities to climate change is to use Generalised Dissimilarity Modelling (GDM), a nonlinear extension of premutational matrix regression that models pairwise biological dissimilarity between sites as a nonlinear function of pairwise site difference in environmental and geographic variables (Ferrier *et al.*, 2007; Ferrier *et al.*, 2012; Brown *et al.*, 2014; Fitzpatrick *et al.*, 2015). GDM extrapolates patterns of compositional turnover beyond sampled communities, and is particularly well suited to communities with high levels of beta diversity. It can accommodate almost any measure of geographic or ecological separation as a predictor, including organism-specific representations of barriers to dispersal, or cost of movement/gene flow through unfavourable habitat (Fitzpatrick *et al.*, 2015). GDM can also rapidly analyse datasets containing very large numbers of species, regardless of the number of records per species. Unlike some community-based modelling approaches, GDM does not assume that species will move together as fixed community types when linked to changing climatic variables (Fitzpatrick *et al.*, 2011). Rather, GDM assumes that emergent rates of spatial turnover along environmental gradients under current climatic conditions can act as reliable surrogates for temporal turnover given environmental change in time (i.e. climatic change). These strengths enable GDM analyses to be interrogated in a variety of ways to assist in conservation decision making.

Recent investigations have projected marked biodiversity change under future climate change (Walther, 2003; Hickling *et al.*, 2006; Chen *et al.*, 2011; Menéndez *et al.*, 2014; Welbergen *et al.*, 2015; Lyra *et al.*, 2016). For example, poleward and upward shifts in distribution has been documented as species attempt to track changes in climate to remain within climatically suitable environments (Chen *et al.*, 2011; Menéndez *et al.*, 2014). A reduction in climatically suitable area leads to contractions in distribution resulting in decreases in population size and ultimately decreases in species richness, as species become locally extinct (Fordham *et al.*, 2012; Urban *et al.*, 2012).

In this study, we use GDM to investigate compositional turnover of rainforest ant communities under future climates in the Australian Wet Tropics (AWT). The novelty of our study is the inclusion of vegetation change in our predictions of ant community change through reductions in areas of ecological environments, including biome shifts from rainforest to open sclerophyll forest.

The rainforests of the Australian Wet Tropics (AWT) are highly threatened by future climatic changes (Hilbert *et al.*, 2001b; Ostendorf *et al.*, 2001; Thomas *et al.*, 2004b; Suppiah *et al.*, 2007). These rainforests are predicted to decrease in extent by 60% with a temperature rise of 1 °C combined with a 10% decrease in precipitation (Hilbert *et al.*, 2001b). Future projections show significant decreases in core distributional area of all 65 endemic vertebrates (Williams *et al.*, 2003) and population size of 74% of rainforest birds (Shoo et al., 2005b). The insects of the AWT are also highly threatened by climate change, with predictions of the extinction of a large proportion (40%) of schizophoran flies (Wilson, 2010) and 88% reduction in populations size of flightless ground beetles (Staunton *et al.*, 2014).

Ants are an ecologically dominant faunal group, mediating many key ecological processes, such as nutrient cycling, plant growth and reproduction (Greenslade & Greenslade, 1984; Andersen & Sparling, 1997), and so changes in ant communities can potentially have large ecological consequences (Fitzpatrick et al., 2011). They are one of the most comprehensively studied ectothermic groups (Jenkins et al., 2011), and their patterns of diversity and composition are strongly related to climatic variables such as temperature, precipitation and humidity (Kaspari *et al.*, 2000; Sanders *et al.*, 2003; Dunn *et al.*, 2009; Diamond *et al.*, 2012). Ants are highly diverse in AWT rainforests (Andersen & Majer, 2000) and a lack of implicit species-specific information makes their individual species modelling impractical.

Our study addresses two key questions. First, which environmental variables best explain patterns of ant species turnover in rainforests of the AWT? Second, how are patterns of species diversity and composition likely to change under projected climate change? Our specific aims are to: (1) identify environmental variables that are most correlated with compositional dissimilarity in rainforest ant communities throughout the AWT, using both a Generalised Dissimilarity Model (GDM) and an information theoretic approach; (2) use the GDM to forecast changes in the area of climate-based Similar Ecological Environments (SEEs) for different community types; and (3) refine climatically-based SEEs to include changes in rainforest condition, in order to forecast ant community changes caused by a combination of direct (climate) and indirect (habitat) effects. Our study will allow the identification of areas in the AWT that are likely to be most sensitive to climate-change impacts, and are therefore priorities for conservation management.

4.3 Methods

4.3.1 Study sites and compositional data

Mean annual rainfall in the AWT varies from about 1,500 to 9,000 mm, with 75-90% occurring between November and April (McDonald & Lane, 2000). Within the region, mean temperature declines at a rate of about 1°C for every 200 m increase in elevation (Shoo *et al.*, 2005a). This study was confined to rainforest and covered a range of structural rainforest types from complex mesophyll vine forest in the fertile lowlands to upland simple notophyll vine forest (Adam, 1992; Hilbert, 2008). Despite their relatively small area, the rainforests are recognized as a major biodiversity hotspot of global significance due to their extraordinary biological richness and biogeographical uniqueness (Williams et al., 2009).

We used a data-set of 5,204 occurrence records of 296 ant species, including leaf litter ants, ground doweling and arboreal ants (sampled using bait traps, litter extractions and pitfall trapping) from 150 sites that cover the full latitudinal and elevational range of rainforest in the AWT (Nowrouzi *et al.*, 2016). The sites were distributed across six mountains, ranging from the Finnegan uplands in the north, to Mount Spec in the south, over a distance of approximately 500 km. All sites were located on granite-derived soils except for those in the Atherton subregion where more-fertile basaltic soils are present (McJannet et al., 2008; Parsons & Congdon, 2008). The elevational range of study sites varied among subregions, due to differences in the availability and accessibility of rainforest habitats. Sampling transects were separated by 200 m elevation from the lowland rainforests to the upland following the elevation contour, with six sites separated by 200 m along each transect. Only three sites were located at each of the 350 m elevation transect at Mount Spec and 100 m elevation transect at Atherton due to limited rainforest cover.

4.3.2 Ethics statement

Ant samples were collected under Permit no. WITK11729912 from the Queensland Government Department of Environment and Heritage Protection.

4.3.3 Environmental variables, habitat condition and climate projections

We generated a comprehensive set of environmental variables including bioclimatic variables (BC01- BC35), soil and topographic layers, along with information on litter depth, canopy cover and disturbance. Bioclimatic data were used to represent the baseline climate, defined as a 30-year average from 1976 to 2005. These data were derived using the ANUCLIM 6.0 software (Xu & Hutchinson, 2013) at a 9-second resolution, approximately 250 m grids (Hutchinson *et al.*, 2009). Soil properties were sourced from the Soil and Landscape Grid of Australia, which were based on estimated values from 0-5 cm depth and derived from the National Soil Attribute Map as composite products (http://www.clw.csiro.au/aclep/soilandlandscapegrid) as well as from the Commonwealth Scientific and Industrial Research Organisation (CSIRO) and the Terrestrial Ecosystem Research Network (TERN), created using terrain analysis techniques developed by Gallant (2000), http://www.asris.csiro.au/arcgis/rest/services/TERN. Litter depth, canopy cover and habitat disturbance (tree falls and cyclone damage) were measured during sampling at the sites (see Staunton et al. (2014)).

To include the indirect effects of habitat condition on the community changes, vegetation data were extracted from the National Vegetation Information System broad vegetation subgroups (Australian Government Department of the Environmental Water Resources, 2007). Analyses of future changes in rainforest vegetation were based on a method of habitat condition assessment that integrates remotely sensed rainforest vegetation layers and available field-based reference data to assign each 250 x 250 m cell a habitat condition value (*h*) ranging from 0 (totally unsuitable for rainforest species) to 1 (capable of supporting the maximum number of species) (Harwood *et al.*, 2016). A previous analysis has assigned habitat condition values to AWT rainforest ranging from 0.001 to 0.715 (maximum values are restricted to forests of previous climates), with higher values occurring in mountain ranges (Figure 4.1).

Future projections of climatic data were extracted from 30-year averages of bioclimatic layers within three different times, 2035, 2055 and 2085. These layers were applied as splined deltas over the 9-second resolution environmental layers. We used the Australian Climate Futures Tool (http://www.climatechangeinaustralia.gov.au/en/climate-projections/climate-futures-tool/), which has been built on Climate Futures Framework (Clarke et al., 2011; Whetton et al., 2012) to select the climatic models. This tool includes projections from global and regional climate models based on simulations performed for the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (Pachauri et al., 2014). We selected two out of 15 Global Climate Models (GCMs) that best reproduced Australian average (1961-1990) patterns of temperature and rainfall (Suppiah et al., 2007): (1) ‘mild’ (Model for Interdisciplinary Research on Climate (MIROC) -H; ~125 km resolution), and (2) ‘harsh’ (Geophysical Fluid Dynamics Laboratory (GFDL) 2.0; ~ 300 km resolution), under the greenhouse gas concentration RCP8.5 scenario. Future projections of rainforest condition were also extracted from SDMs of projected rainforest vegetation layers that were derived using the ANUCLIM 6.0 software (Xu & Hutchinson, 2013) at a 9-second resolution and 250 m grids (Hutchinson *et al.*, 2009), provided by eResearch Centre, James Cook University, Australia.

4.3.4 Analyses

Environmental predictors of compositional dissimilarity. We first selected 17 out of 39 environmental variables using Pearson correlation coefficients to exclude highly correlated variables in the data set (the threshold was > 0.75 correlations; Appendix 11). We then assessed which environmental variables best explained dissimilarity of ant communities across the sample sites using the variable selection strategy detailed in Williams *et al.* (2010a) and Generalised Dissimilarity Model (GDM) (Ferrier *et al.*, 2007). This strategy ranks the variables based on their 'explained deviance' in the model. To increase the certainty of our variable selection, we also assessed them by using an information theoretic approach (Burnham & Anderson, 2002). This approach fits multivariate Generalised Linear Models (GLMs) for species composition, developed by Wang *et al.* (2012), using the nine selected predictors. We used a model averaging technique that quantifies relative importance (likelihood) of all possible models that can be generated using the combinations of selected predictor variables (2^9 = 512 models in this study case), based on a modified Akaike Information Criterion (AICc). We then evaluated the standardised effect size of each predictor variable by calculating the differences between observed summed Akaike weight and mean summed Akaike weight derived from 999 null datasets, divided by the standard deviation of summed Akaike weights of null datasets. The calculations were all executed using the *mglmn R* package developed by Katabuchi and Nakamura (2015). When using the information theory, we did not directly include geographic distance as a variable because of correlation between climatic variables (e.g. temperature) and geographic location (e.g. latitude and elevation). However, excluding geographic distance did not change the impact of other variables in the model, and so we included it as a driver of composition turnover in the model as suggested by Williams *et al.* (2010a).

Compositional change under future climates. A GDM was fitted using ant species presence-absence data and environmental variables to infer potential changes in composition as a function of projected changes in climate. The model assumes that the amount of change in species composition expected for any location as a result of climatic change will be equivalent to the compositional dissimilarity currently observed between that location and another location with a current climate matching that projected for the first location (Ferrier *et al.*, 2007; Ferrier *et al.*, 2012). This creates a matrix of predicted compositional dissimilarities between pairwise locations (150 sites in our model) using the Sørensen index. Cross-validation was used to test the predictive accuracy of the GDM (Roberts *et al.*, 2017).

Future predictions of the community's compositional change were obtained by transforming future climate layers using the model fitted to the current climate data (see process below). Analyses were conducted using the *ecodist* and *GDM* R packages (R Development Core Team, 2010; Manion *et al.*, 2015). To visualise the predicted changes, multidimensional scaling was applied in a Geographic Information System (GIS) mapping software.

To define the pressure of climate change on a community at a location, the GDM was used to calculate the effective area of similar ecological environments (SEE). SEE is a measure of the total area of land with an environment similar to that of a particular location, and therefore suitable for the community. Using this model, we transformed a set of raster maps of environmental predictors into units of ecological distance (ΔE), which is logarithmically related to compositional similarity ($s_{ij} = e^{-\Delta E_{ij}}$) (Allnutt *et al.*, 2008; Ferrier *et al.*, 2012). The result is a stack of nine transformed environmental predictor layers. This produces a stack of transformed predictors for each time point. We then used the transformed grid stacks to examine the predicted compositional similarity (s_{ij}) between two points (*i,j*) in space and projected the models through different times (Allnutt *et al.*, 2008). The model enabled us to calculate the change in area of SEE (***C**$_i$*) for ant communities, according to the equation below:

$$C_i = \frac{\sum_{j=1}^{j=n} s_{ij}^{future}}{\sum_{j=1}^{j=n} s_{ij}^{current}} \qquad [1]$$

The basic GDM analysis does not consider changes in communities due to changes in vegetation. To incorporate vegetation change, we overlapped the layers of rainforest habitat condition (Harwood et al 2016; Figure 4.2) and the GDMs (based on transformed grids, which are logarithmically related to compositional similarity) and calculated the effective area of ecologically similar habitat from an ant community perspective, ***A**$_i$*, for each rainforest cell, as specified in the equation:

$$A_i = \sum_{j=1}^{n} s_{ij} h_j \qquad [2]$$

To indicate the direct impact of climate change on the ant communities without considering changes in rainforest habitat, we overlapped the layers of rainforest habitat condition and the transformed GDMs according to future climate projections and calculated the proportional reduction in SEE within the current condition of rainforest habitat using the equation:

$$C_i = \frac{A^{\text{future climate}}}{A^{\text{current climate and habitat}}} \qquad [3]$$

To indicate the overall impact of climate change on ant communities, considering its direct impact combined with indirect effects through changes in rainforest habitat, we overlapped the projected rainforest habitat condition layers and the transformed GDMs according to future climate projections and calculated the proportional reduction in SEE within the 'changing rainforest' using the equation:

$$C_i = \frac{A^{\text{future climate and habitat}}}{A^{\text{current climate and habitat}}} \qquad [4]$$

Similarly, we calculated the proportion of species retained in the entire rainforest of the region as $P_i = [A^{\text{future climate \& habitat change}} / A^{\text{current}}]^z$ (using z, the exponent of the species-area curve, which is typically 0.25 (Allnutt *et al.*, 2008) and therefore estimate regional species loss. Calculations and projections were conducted using the Windows GDMmodeller software and the results were mapped in GIS mapping software.

4.4 Results

4.4.1 Environmental predictors of compositional dissimilarity

Nine out of 17 candidate explanatory variables (Appendix 12) were selected as best explaining the turnover in species composition of ant communities using both GDM and information theoretic approaches. The GDM accounted for 25.8% of the deviance in observed turnover, and indicated that environmental and geographical distances both played important roles in explaining compositional dissimilarity (see the sum of the fitted coefficients for each environmental predictor, Table 4.1). We acknowledge that the GDM had a high intercept (0.896; see cross-validation of the GDM model in Figure 4.2), which reflects the many singletons in the data and, therefore, high proportion of site pairs with complete turnover.

Additionally, low deviance of the model points to difficulty of assessing a large dataset collected using a comprehensive combination of sampling methods to represent ant species from different strata in the rainforest as a community. The largest amount of spatial patterning in the GDM was observed along the gradient of Bulk Density of Soil (BDW), followed by Mean Temperature of Coldest Quarter (MTCQ), Mean Temperature of Warmest Quarter (MTWQ), geographic distance and Temperature Seasonality (TS) (Table 4.1). The information theoretic approach also revealed that spatial patterning of compositional dissimilarity was likely explained by Isothermality, TS, MTWQ, MTCQ, Precipitation of Wettest Period (PWP), BDW, Available Water Capacity of Soil (AWC), litter depth and habitat disturbance (Table 4.2). In contrast with the GDM, the highest effect sizes (>20) were achieved by MTWQ and MTCQ when using the information theory (Table 4.2).

Table 4.1. Sum of the coefficients based on the GDM results, ranking the relative strength of the environmental variables contributing to dissimilarity of ant species composition.

Variable		**Coefficient**
Geographic	Geographic Distance	0.47
Climatic	Isothermality	0.15
	Temperature Seasonality (TS)	0.41
	Mean Temperature of Warmest Quarter (MTWQ)	**0.52**
	Mean Temperature of Coldest Quarter (MTCQ)	**0.66**
	Precipitation of Wettest Period (PWP)	0.16
Soil	Bulk Density (Whole Earth product) of Soil (BDW)	**0.73**
	Available Water Capacity of Soil (AWC)	0.20
Site context	Litter Depth	0.05
	Habitat Disturbance	0.19
	Model explanation	25.78

Table 4.2. Summary results of the information theoretic approach for identifying predictors of ant species composition, showing (a) summed Akaike weights from observed data, (b) mean summed Akaike weights from randomised data, (c) standard deviation (SD) of summed Akaike weights, standardised effect size ((a-b)/c), and P values calculated from 999 null models generated by permutation. TS = Temperature Seasonality; MTWQ = Mean Temperature of Warmest Quarter; MTCQ = Mean Temperature of Coldest Quarter; PWP = Precipitation of Wettest Period; BDW = Bulk Density of Soil; AWC = Available Water Capacity of Soil.

Environmental variable	(a) Summed Akaike weight (observed)	(b) Mean summed Akaike weight (null models)	(c) SD of summed Akaike weight (null models)	Standardised effect size	*P* value
Isothermality	0.44	0.33	0.02	4.8	0.000
TS	0.52	0.33	0.02	11.2	0.000
MTWQ	0.59	0.33	0.01	**23.2**	0.000
MTCQ	0.59	0.33	0.01	**21.2**	0.000
PWP	0.57	0.34	0.02	11.4	0.000
BDW	0.50	0.33	0.02	9.4	0.000
AWC	0.51	0.33	0.02	8.2	0.000
Litter Depth	0.46	0.33	0.02	6.5	0.000
Habitat Disturbance	0.58	0.33	0.02	**14.9**	0.000

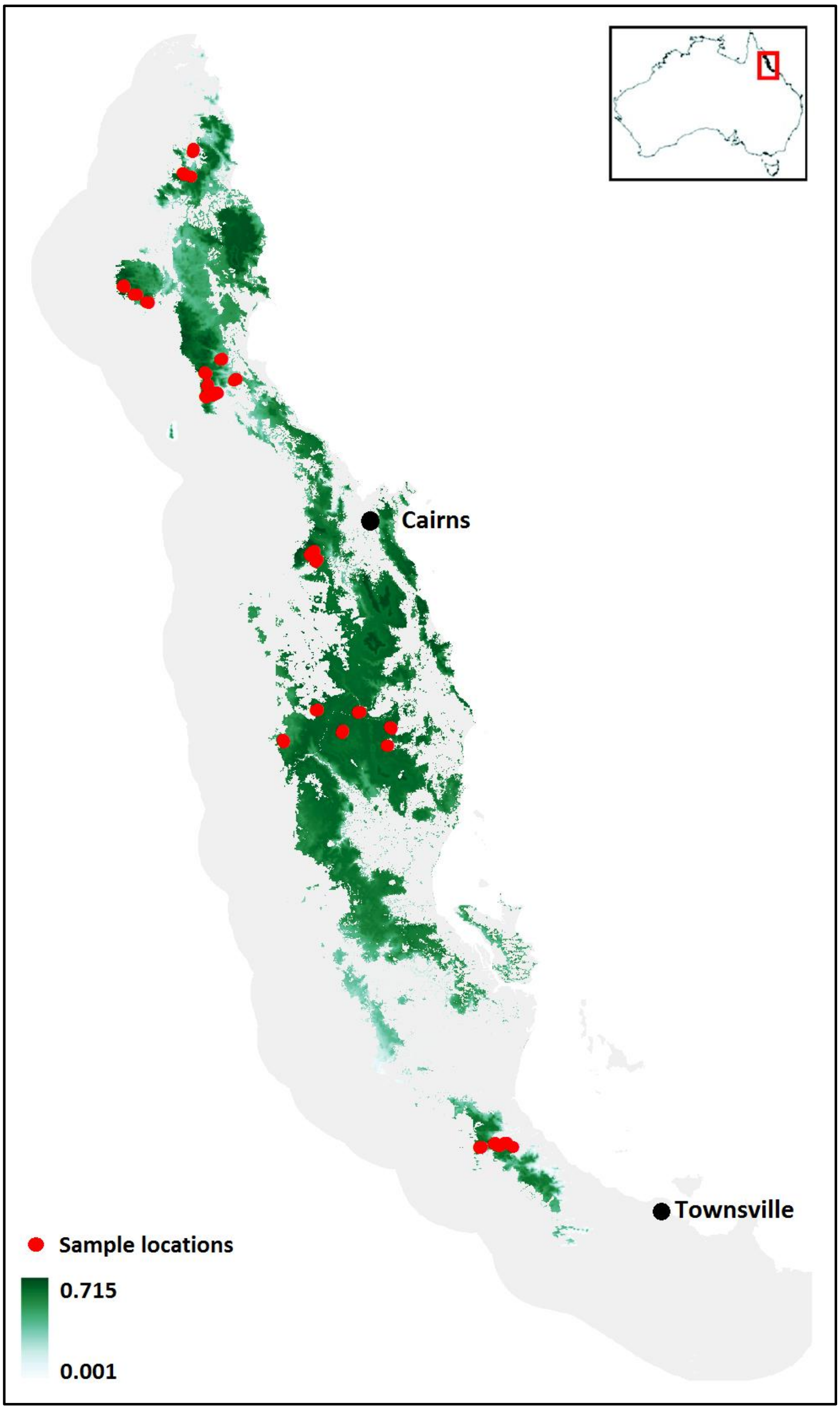

Figure 4.1. Current habitat condition of the rainforest and sample locations in the AWT. Darker colour represents higher-condition habitats in terms of capacity to support the maximum number of plant species. Sample sites are overlapped within each sample location.

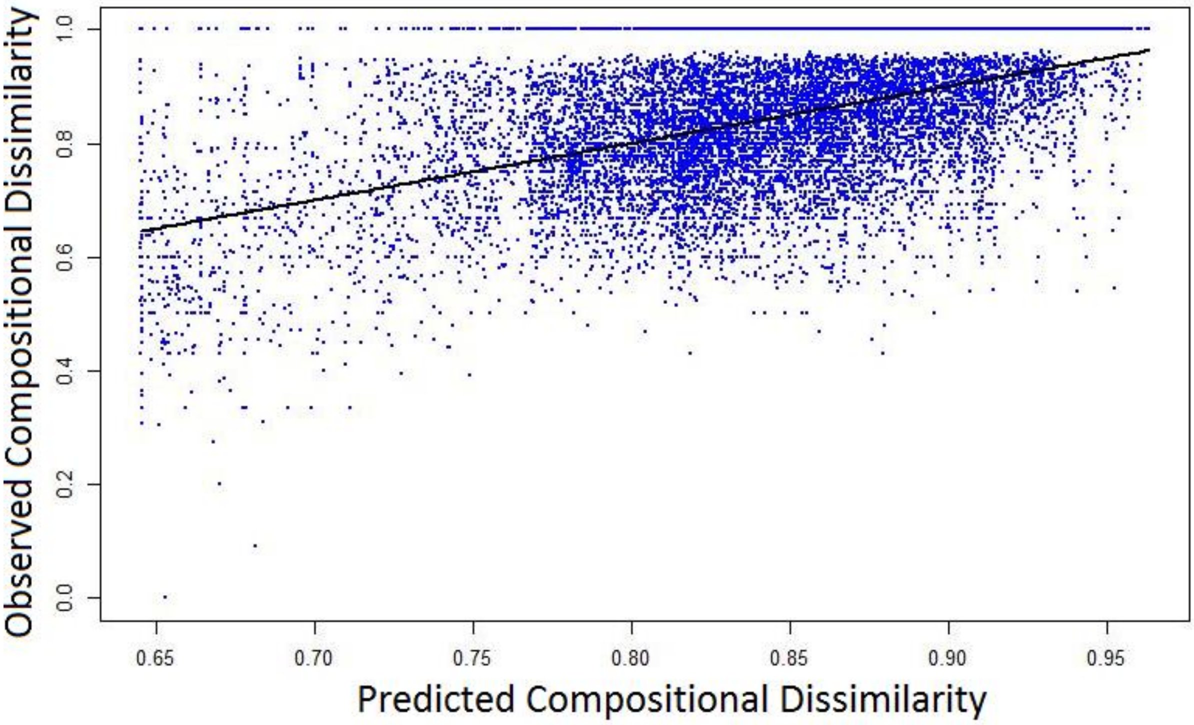

Figure 4.2. Cross-validation of the GDM. The observed response is Sørensen dissimilarity. Both axes are based on proportional dissimilarities.

4.4.2 Compositional change under future climates

Direct effects of climate. Under a mild climate model (MIROC), the GDM predicts that the current-condition rainforest habitat would lose more than 50% of the SEE throughout the AWT in 2085 (Figure 4.3). The C values >1 (calculated using equation 3) indicated an increase in the area of SEE for most of these communities in the region in years 2035 and 2055 (Figure 4.3). The higher values of C in the coastal zone compared with the inland side of the region indicated the higher chance of increasing the area of SEE for the coastal zone communities. In contrast, under a harsh climate model (GFDL), there was no increase in the area of SEE for at least 50% of the communities in the region, and the coastal zone communities were buffered from losing their area of SEE only in the near future (Figure 4.4). In this scenario, there was a gradual decline in the effective area of SEE for the communities towards year 2085 (Figure 4.4). Therefore, the rainforest ant communities within more than half of the region were expected to experience compositional change even under a mild change in climatic environments in future.

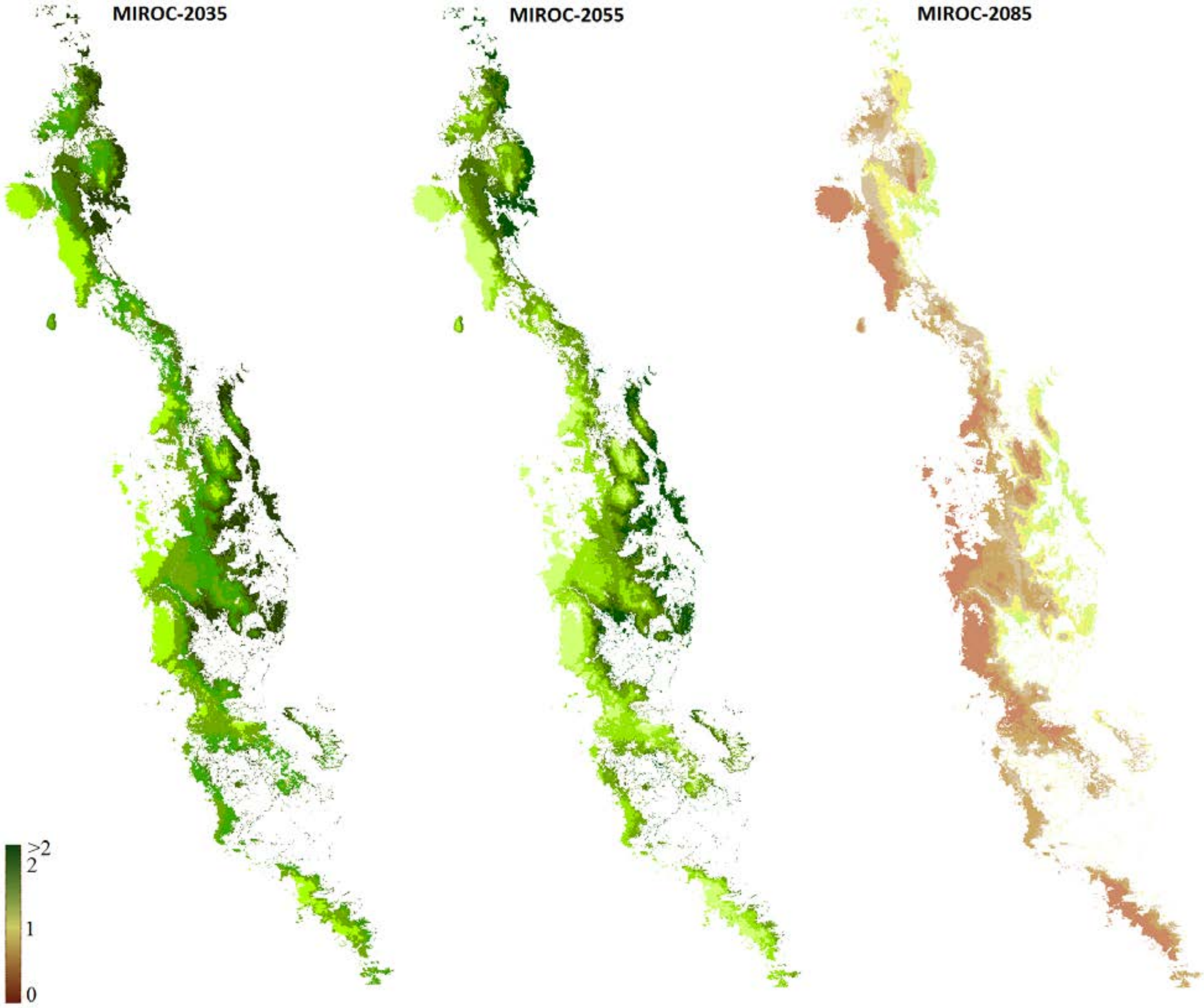

Figure 4.3. Effective area of SEE (C value; equation 3) for predicted ant species composition in the AWT under predicted climate change only; based on MIROC model within three different times, 2035, 2055 and 2085 (30 years averaged each period; under RCP8.5 scenario). C value =1, no change, C value <1, decrease and >1, increase in area of SEE.

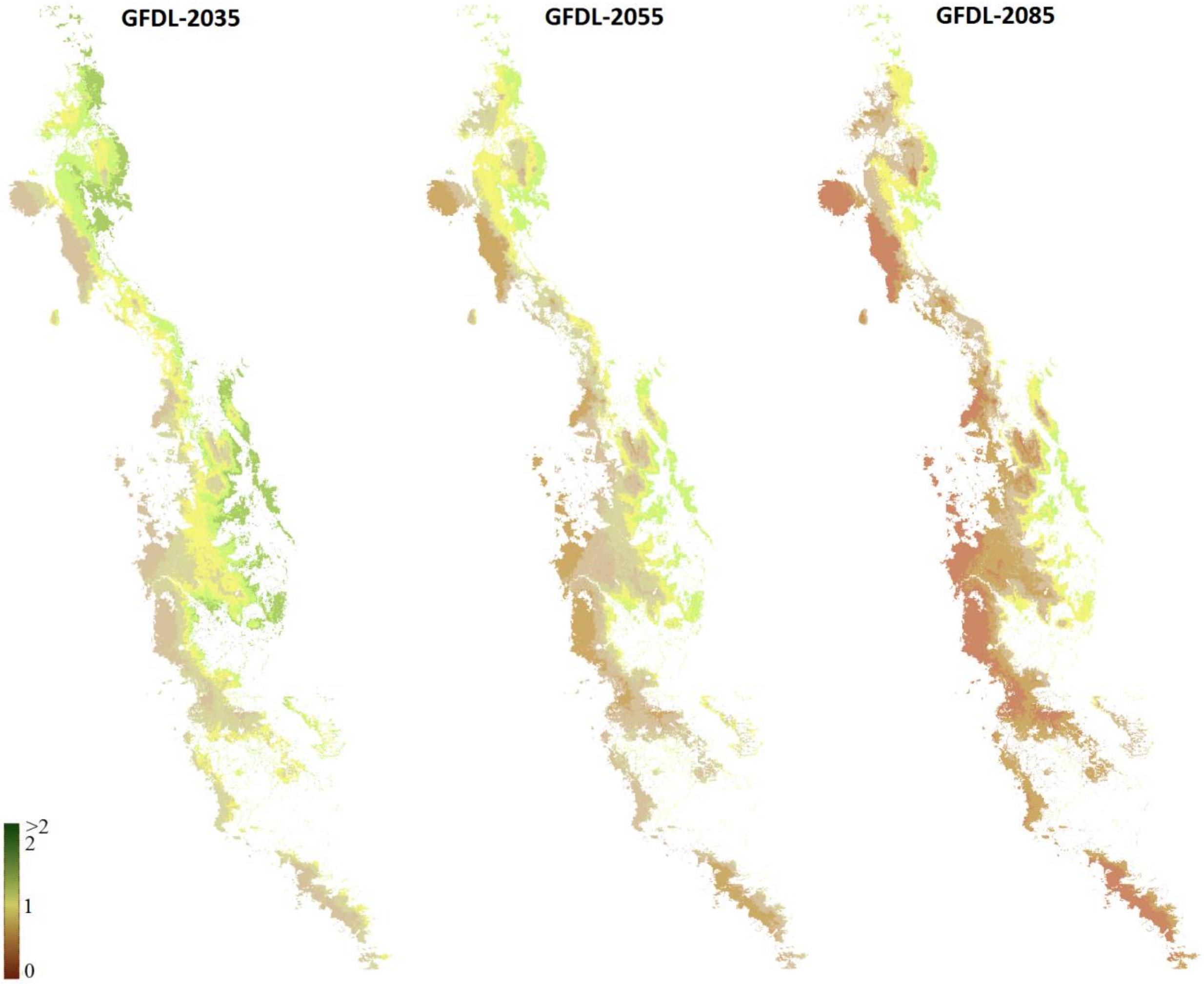

Figure 4.4. Effective area of SEE (C value; equation 3) for predicted ant communities' composition in the AWT under predicted climate change only; based on GFDL model within three different times, 2035, 2055 and 2085 (30 years averaged each period; under RCP8.5 scenario). C value =1, no change, C value <1, decrease and >1, increase in area of SEE.

Direct effects of climate combined with indirect effects of rainforest change. Under a combined mild climate model and associated change in rainforest habitat, ant communities showed a faster rate of decline in their SEE towards 2085, and were not buffered from losing their SEE in any part of the region in future (Figure 4.5). The new C values (calculated using equation 4), were less than 1 for most of the region even in near future (Figure 4.5). The area of SEE decreased even more dramatically under a combined harsh climate model and associated change in rainforest habitat (Figure 4.6). All rainforest ant communities in the AWT were predicted to be at risk of losing their area of SEE, with 90% loss for the communities located in more than half of the region in year 2085 (Figure 4.6). Despite the expected dramatic overall changes in species composition under both climate-change scenarios, species loss (using the calculated *P* values), even with changing condition of the rainforest habitat, was only 3% under GFDL.

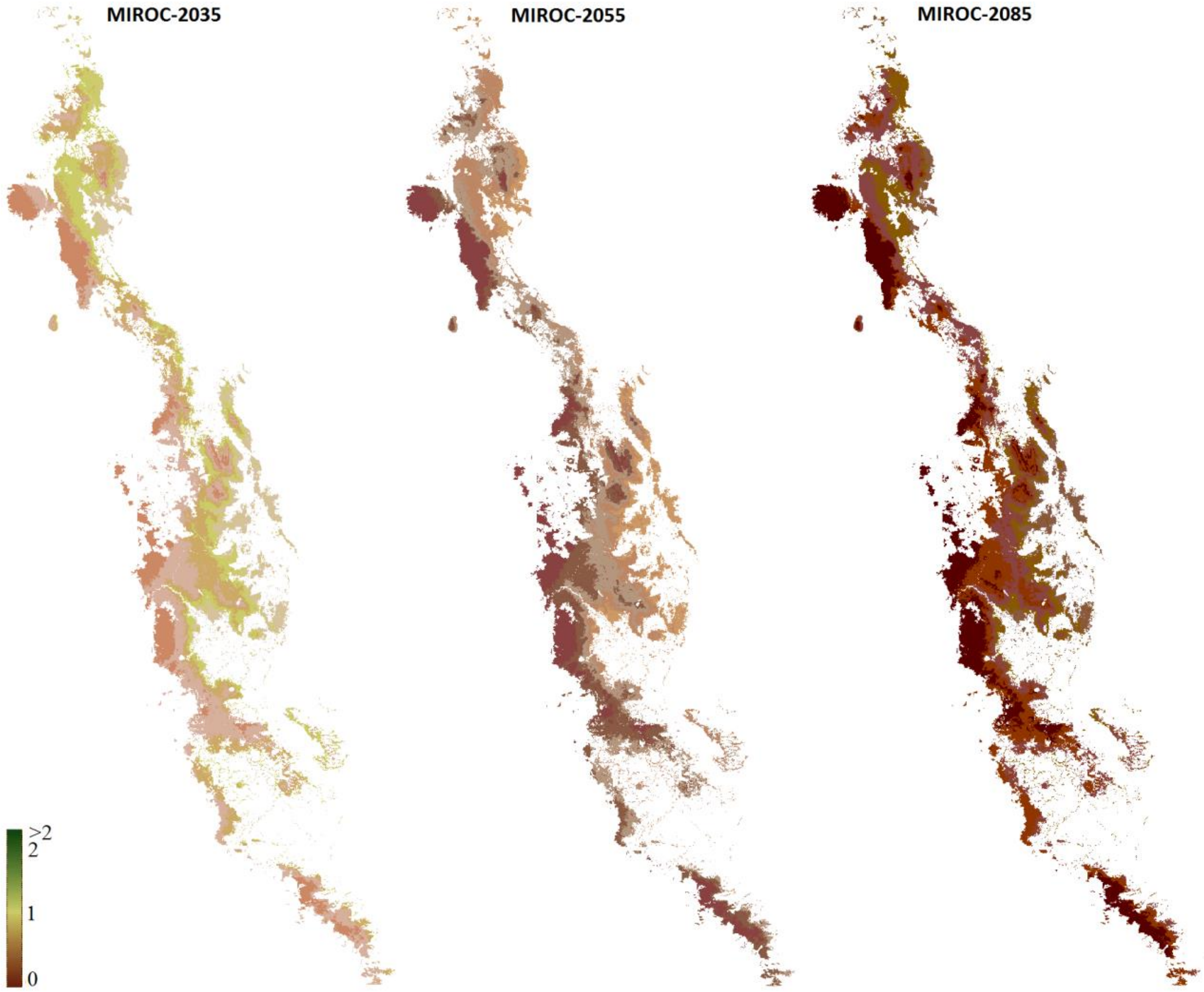

Figure 4.5. Effective area of SEE (C value; equation 4) for predicted ant communities' composition in the AWT under predicted climate and habitat changes; based on MIROC model within three different times, 2035, 2055 and 2085 (30 years averaged each period; under RCP8.5 scenario). C value =1, no change, C value <1, decrease and >1, increase in area of SEE.

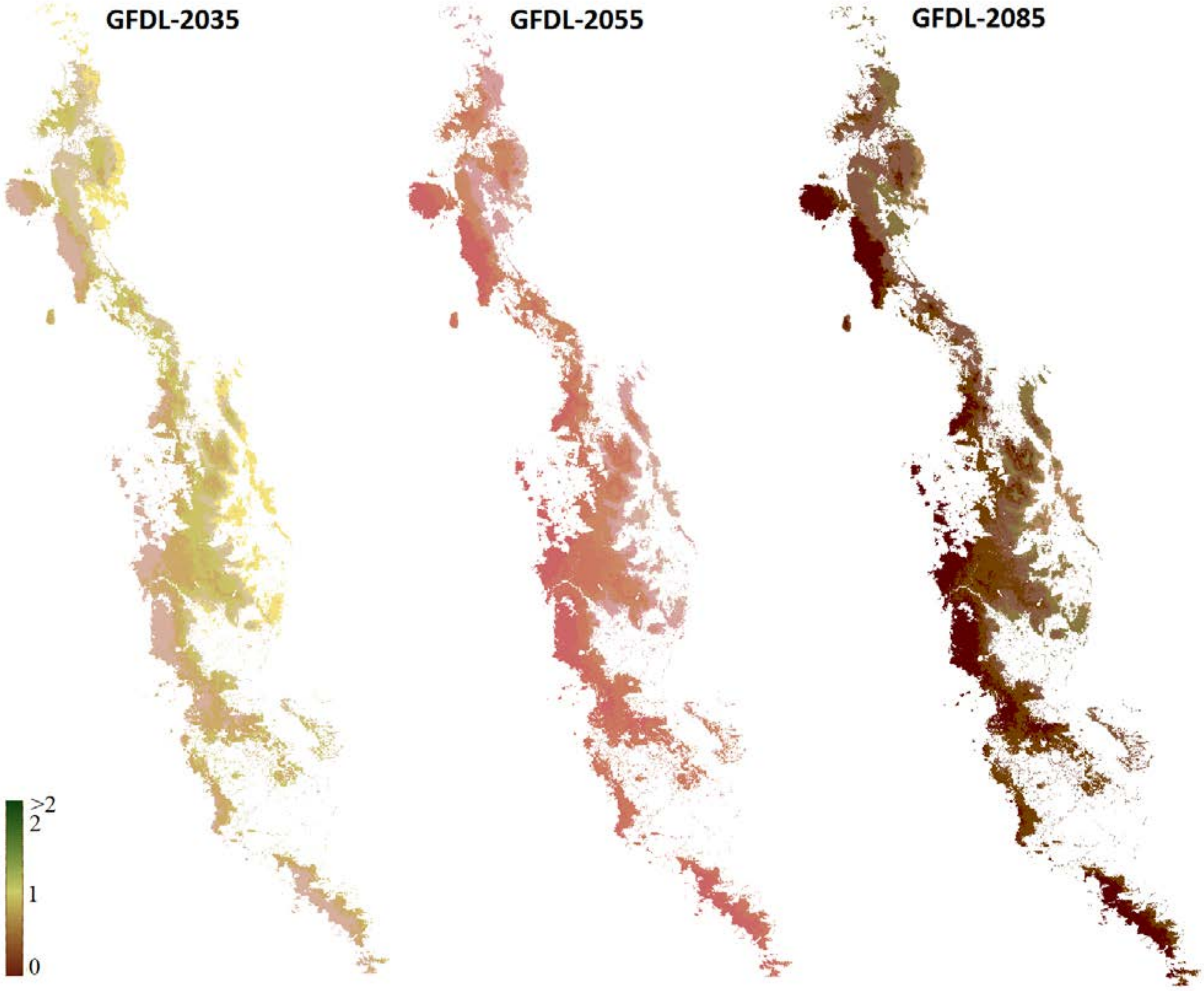

Figure 4.6. Effective area of SEE (C value; equation 4) for predicted ant communities' composition in the AWT under predicted climate and habitat changes; based on GFDL model within three different times, 2035, 2055 and 2085 (30 years averaged each period; under RCP8.5 scenario). C value =1, no change, C value <1, decrease and >1, increase in area of SEE.

4.5 Discussion

Our study represents the first analysis of climate change impacts on ant communities using macroecological models to evaluate the context of spatial and temporal changes. Both GDM and the Information Theoretic approaches indicated that temperature is the most important climatic driver of rainforest ant species compositional change in either cold or warm periods of the year in the AWT. Temperature has been identified as primary driver of ant species diversity patterns at both global (Dunn *et al.*, 2009) and regional (Diamond *et al.*, 2012; Bishop *et al.*, 2014) scales.

After temperature, habitat disturbance, had the second highest effect on community composition dissimilarities according to the information theory models, and it significantly contributed to the spatial pattering in the GDM model. A common effect of habitat disturbance is simplification of habitat structure (Hoffmann & Andersen, 2003; Gibb & Parr, 2013), and so disturbance can have especially strong effects in complex habitats like tropical rainforest. Climate change is predicted to increase the frequency of extreme weather events, including cyclones, which are the major agent of disturbance in the AWT.

Rainforest ant communities are expected to be buffered from the effects of climate change in the near future, but only if rainforest vegetation remains unchanged. However, even without considering vegetation change, marked change in ant species composition is still expected to occur in 2085 due to direct impact of climate change. The noteworthy finding of this study is the combined impact of climate change on the communities through reduction in area of their ecological environments due to changes in habitat condition. Recent comprehensive combined modelling across the entire continent of Australia, using the vascular plant models and a few climate change projections, suggested such environmental stress could lead to turnover as soon as 2030, and be highly significant and widespread by 2070 (Ferrier *et al.*, 2012). We also predict that changes in ant communities will likely occur not only due to rising temperature, but also largely because of the decline in availability of their suitable habitat under changing climate. However, the usual warning signs for loss of species by increasing temperature (Laurance *et al.*, 2011; Welbergen *et al.*, 2015) is less likely to be raised for this relatively heat resistant group, but significant turnover in species compositions are expected due to reduction in area of their ecological environments and a corresponding change in species coexistence and interactions.

The coastal zone of the AWT will likely be buffered in the near future under climate change due to its close proximity to the ocean, which has a moderating influence on temperatures (Dowdy *et al.*, 2015). In contrast, the inland side of the AWT will be at higher risk of marked reduction in the effective area of SEE for the communities under climate change. This greater and faster rate of reduction pattern in the inland side persisted through time, even when the condition of the rainforest habitat remained unchanged. When accounting for predicted climate change and associated habitat changes in future, ant communities in the inland side of the AWT will lose almost all of their effective area of SEE, even under a mild climate projection. This may completely shift the rainforest community compositions to sclerophyll fauna in the inland side of the AWT. Our findings are consistent with widespread predictions of more severe dry conditions for drier regions under rising temperature (Hughes, 2003; Suppiah *et al.*, 2007; Reside *et al.*, 2013; Welbergen *et al.*, 2015).

Shifts in rainforest habitat may have additional effects on the communities through restriction for their ability to disperse to the places which are best suited. There are some major uplands and mountain peaks of the AWT, including Windsor, Carbine and Atherton uplands, located in the inland side, that have been investigated as refugia over the past Glacial and Interglacial periods (Reside et al., 2013). Compared with their surroundings, these areas are at higher risk of habitat change and subsequently species composition turnover in future. In the past climatic periods, the upland regions of the AWT have consistently received more rainfall than present (Hilbert et al., 2007). Areas that are locally cooler and wetter than their surroundings (such as shaded gullies) are predicted to be buffered from the greatest change in future climatic conditions and are therefore considered to be climatic refugia (Reside et al., 2013). Similarly, upland regions (such as Windsor and Carbine; see Figures 2.1 and 4. 1) are expected to shelter vulnerable species of vertebrates (Welbergen et al., 2015). As yet, no prediction has considered the potential changes from losing effective area of similar ecological environments and expected turnover in communities within these refugia.

Upland species are predicted to experience reductions in suitable habitat as their currently favourable, montane conditions are lost (Williams & Pearson, 1997; Shoo *et al.*, 2005a; Costion *et al.*, 2015). Our findings of higher risk of reduction in area of ecological environments for upland rainforest communities in the region suggest that these areas will not act as refugia for in situ species that currently rely on that cool, stable upland habitat. This is not consistent with the predictions that montane regions might act as refugia for nearby lowland species (Reside et al., 2013).

We also found that soil bulk density, between all the considered variables, had highest contribution to the GDM model. But, changes in bulk density have been indicated as indirect impact of climate change on soil ecosystem, via plant community changes (Kardol *et al.*, 2010). Increasing temperature may lead to increase in bulk density and hence making soil more sensitive to climate change stresses (Allen *et al.*, 2011). Predicted changes in rainforest habitat mainly due to changes in rainfall and temperature is likely to affect soil ecosystem functioning, which is critical for ant communities (Parr *et al.*, 2016; Sanabria *et al.*, 2016). However, we did not have a projected BDW layer available for the AWT in future, but this effect in our models was compensated for by our consideration of rainforest habitat suitability. Future models in the region could improve by investigating the changes in BDW under climate change and its impact on ant communities.

This study demonstrated that ants in the Australian Wet Tropics are likely to be as severely impacted under climate change as other well-studied groups such as mammals (Williams & Pearson, 1997), birds (Shoo *et al.*, 2005a), dragonflies (Bush *et al.*, 2014), reptiles and frogs (Schneider *et al.*, 1998; Schneider & Moritz, 1999). Ants are too diverse to be evaluated case by case and our community-level approach identified the major gradients of turnover and where the resulting changes are likely to be greatest. However, the low proportion of species loss might be explained by foraging plasticity, as it was the case for poor power of geographical distribution over thermal limits of montane ants in the region (Chapter 3). For example, ant species may preferentially forage in microhabitats (Kaspari & Weiser, 2000; Baudier *et al.*, 2015), or during different times of the day (Stuble *et al.*, 2013), that best match their thermal requirements. Given the variation among species in both thermal tolerance and foraging behaviour, climate change is likely to have highly species-specific impacts (Oberg *et al.*, 2012). Ultimately, the disjunction in community composition at the orographic cloud layer elevation across six uplands in the AWT, revealed in Chapter 2, suggests temperature increases in future may accelerate the decline in habitat suitability by change in precipitation and subsequently rainforest habitat, particularly at the cloud layer elevation. Within the AWT, inevitably the taxa most threatened are isolated in pockets of cloud forest, and monitoring the breadth of biodiversity at this transition zone should be a priority for detecting the impacts of climate-change in the region.

4.6 Acknowledgements

We are grateful for the help from Kristen Williams and Simon Ferrier in exchanging ideas for the GDM analyses and Karel Mokany and Jeremy VanDerWal in providing environmental layers.

Chapter 5 . General Discussion

5.1. Aims and major findings

Understanding the mechanisms behind biodiversity patterns is fundamental to ecology and conservation science (Gaston, 2000). It is especially important to understand the role of climate as a driver of species distributions and community composition, in order to predict likely changes under future climates. Forecasting the impacts of climate change on biological communities is particularly challenging, because (1) there is often a limited understanding of climatic drivers of species distributions, (2) component species are likely to show variable responses to climate change, and (3) the distribution of suitable habitat is likely to change. The primary objective of this thesis is to understand how the diversity and distribution of rainforest ant communities in the Australian Wet Tropics is likely to respond to future climate change.

The first aim of the thesis was to investigate how the diversity and composition of rainforest ants is distributed throughout the AWT, and how important is climate as a driver of this distribution (Chapter 2). In particular, it tested the prediction that there is a marked elevational shift in species composition associated with the orographic cloud layer, which provides seasonal moisture stability and is expected to rise under climate change. Species richness had a slight peak at mid elevations, but did not vary significantly with latitude. Species composition varied substantially among subregions and with elevation. As predicted, there was a particularly striking compositional disjunction between 600 m and 800 m in each subregion, which coincides with the orographic cloud layer.

The second aim of the thesis was to investigate the extent to which the distribution of rainforest ant species is related to their physiological thermal limits (Chapter 3). It first questioned if there was a decreasing pattern in Critical Thermal Maximum (CTmax) with increasing elevation, paralleling the relationship between CTmax and latitude. Elevational distribution of rainforest ants was not systematically related to their CTmax. It was then questioned if species at higher elevations have larger elevational ranges, following climatic variability hypothesis and Rapoport's rule. The results were in direct contradictions with these rules. The third question was if body size increases with increasing elevation, following Bergmann's rule. Body mass, as surrogate of body size, declined significantly with increasing elevation. However, there was a negative correlation between CTmax and body mass of ant communities, but no significant difference in CTmax of different-sized ants within a species. Ultimately, the chapter questioned if a combination of elevational distribution and body size would be a strong predictor of a species' CTmax, but this was shown not to be the case.

The third aim of the thesis was to explore how projected climate change will affect rainforest ant communities in the AWT, including through changes in suitable habitat (Chapter 4). The environmental variables that best correlated with dissimilarity in community composition were identified and used to project changes in ecological environments through climatic changes and reduction in habitat suitability. Temperature and habitat disturbance (mainly cyclone damage) were found to have the highest effect sizes on ant community compositional dissimilarity. Projections suggested that the coastal zone of the AWT was likely to be buffered from changes in diversity and composition in the near future by its close proximity to the ocean. In contrast, ant species composition is predicted to change markedly with the risk of a complete shift from rainforest to sclerophyll fauna in inland areas due to a drier climate and, most importantly, reductions in availability of suitable rainforest habitat.

5.2. Implications of the findings

This thesis demonstrates that the AWT, a major biodiversity hotspot of global significance (Williams *et al.*, 2009), supports a highly diverse rainforest ant fauna (discovered in Chapter 2) with a high level of spatial turnover that is strongly related to climate. This makes the fauna especially sensitive to climate change. The finding of major disjunction in community composition (Chapter 2) at the level of the orographic cloud layer (between 600 m and 800 m elevation) is particularly noteworthy, because this layer is predicted to rise by about 300 m by 2050 (WTMA, 2013). The 600 – 800 m elevation zone is therefore likely to be especially sensitive to a changing climate, with sites that are currently located at the bottom of the cloud layer highly likely to experience drier conditions in addition to rising temperatures.This zone represents a priority location to focus efforts for monitoring climate-change impacts in the AWT.

The direct contradictions between the results of Chapter3 and climatic variability hypothesis and also both Rapoport’s and Bergmann’s rules, that apply to many other taxa, adds to the uncertenity around this issue for ants. The explanation for the poor predictive power of elevational distribution and body mass over species CTmax could be foraging plasticity that best match their thermal requirements. Ant species may preferentially forage in microhabitats (Kaspari & Weiser, 2000; Baudier *et al.*, 2015), or during different times of the day (Christian & Morton, 1992; Stuble *et al.*, 2013), which can include switching from diurnal to nocturnal activity (Nelson *et al.*, 2017). Therfore, climate change is likely to have highly species-specific impacts on ants, including reduction in their foraging efficiency (Andrew *et al.*, 2013).

The projected rapid change associated with reduction in availability of suitable habitats for the communities under climate change, particularly in inland side (Chapter 4), is consequently expected to turnover species composition. Reduction in suitability of the habitat for most rainforest ant species will occur due to projected transformation of rainforest to sclerophyll habitat under climate change. Consequently, this will likely increase the dissimilarity of the community composition from the sites that the rainforest will remain intact, which is an additional change to the expected turnover in the rainforest community composition due to changing climate only.

Shifts in rainforest habitat may also have additional effects on the ant communities through restrictions for their ability to get to the places which are best suited. This may negatively impact upland species, as their habitats might not act as refugia for in situ species that currently rely on that cool, stable upland habitat. These findings highlight the importance of rainforest habitat in the persistence of diversity in the region and the synergic impact of climate change on communities' composition also through changes in habitat suitability. Ultimately, the non-coastal side of the AWT, with greater risk of change in future, may be considered a conservation priority in decision making for the region.

5.3. Future research

This thesis has contributed fundamentally to community-level studies in the AWT and has provided valuable information for further community-based investigations, particularly in rainforest habitats. The extensive systematic sampling of this study over a few seasons (Nov. 2012 - Jan. 2013) not only gave valuable insights into the diversity of the AWT, but also produced a large scale standardised survey of ants in the region. This baseline data-set can be used to monitor changes in distribution and composition of species in future and have fundamental contributions to further studies on rainforest communities at both regional and global scales.

Diversity patterns investigated in Chapter 1 across six rainforest uplands gave accurate comparisons to those in other rainforest regions. Investigating the CTmax and body mass of a large number of species out of a diverse community pool indicates reliability of patterns revealed in Chapter 3 results. Such a fundamental knowledge in understanding insects' biological responses contributes new information to entomological science, which often has not been investigated. Furthermore, other community-based studies can benefit from using the methods created in Chapter 4.

The results of this thesis can be beneficial for further studies on biological communities' diversity and distribution patterns from two main points of view, 1) under climatic changes and 2) under a combined climate and associated habitat changes. However, there is still much to investigate regarding the diversity and distribution of biological communities, particularly within rainforest habitats and under the future climate change. Chapter 4 results will be beneficial to many researchers by providing a much needed straightforward first-step towards spatial representations of community distributions derived from Generalised

Dissimilarity Models (GDMs). The community-base model of a diverse taxon, such as ants, not only can be used to monitor diversity at the community level but also to further investigate communities in the region. Furthermore, the extensive presence/absence data-set strengthened the results obtained from the GDMs in this study. The newly developed mix of habitat change along with climate change impacts on a community was the most beneficial outcome of this chapter and the thesis.

There are limitations in every study, which leads into the identification of future research priorities. The large data-set of this study could have been improved by measuring environmental variables at the regional scale parallel with the surveys sampling. Such data could have been used to correlate the distribution patterns of the species in Chapter 2 and provide a better understanding of the drivers behind those patterns. Further studies could potentially investigate the precise nature of the orographic cloud layer shifts throughout the AWT. Such work could further investigate the links between moisture stability and community composition disjunctions in montane rainforests revealed by this thesis. Furthermore, investigations on the impact of orographic cloud layer shifts in montane rainforest diversity across the world can identify the generality of the moisture stability impact on persistence of the rainforest communities through time.

The direct contradictions between Chapter 3 results and some global rules, along with possibility of applying some of the rules to other aspects of ant community, such as colony size, reflected the need for further investigations for this diverse insect taxon. However, not controlling for dimorphism in some species also reflected the difficulty of taxonomic identification in the field for a diverse insect taxon, when being time limited to test alive specimens for physiological purposes. Subsequently, increasing the sampling effort by increasing the number of species and individuals of known species could increase the strength of the conclusions in Chapter 3. Additional investigations regarding the ecophysiological influences on species' distributional patterns could also be beneficial in understanding the mechanisms behind those patterns. For example, researchers may further test the contradictions between the ecological rules, such as Bergmann's rule and Rappoport's rule, and the link between species elevational ranges to their thermal limits in tropical ants elsewhere. Investigating species interactions will also assist to clarify the ecophysiological influences on the diversity and distribution patterns of a community and to increase the accuracy of the predictions produced by community-based models.

Chapter 4 could be improved by incorporating predicted changes in cloud layer elevation into the expected community composition changes and also produce quantitative comparisons of different scenarios between different locations in the region. These additional information however were out of the scope of this thesis. Similar to all types of modeling tools, GDM might also have some limitations when predicting across time, which could have influenced the small proportion of species loss estimated in Chapter 4. Additionally, the GDMs created in this thesis did not consider species interactions or adaptations and also ant/plant interactions when the ant community is altered in future models, which can influence the predictions obtained. Therefore, extensive attention to appropriate dispersal and adaptation scenarios for species is valuable to accurately estimate species redistributions in future models of communities.

References

Adam, P. (1992) *Australian Rainforest*. Oxford University Press, Melbourne.

Addo-Bediako, A., Chown, S.L. & Gaston, K.J. (2000) Thermal tolerance, climatic variability and latitude. *Proceedings of the Royal Society of London B: Biological Sciences*, **267**, 739-745.

Agosti, D., Majer, J., Alonso, L. & Schultz, T. (eds.) (2000a) *Sampling ground-dwelling ants: Case studies from the world's rainforests*. Curtin University of Technology, Perth.

Agosti, D., Majer, J.D., Alonso, L.E. & Schultz, T.R. (eds.) (2000b) *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington.

Allen, D.E., Singh, B.P. & Dalal, R.C. (2011) Soil health indicators under climate change: A review of current knowledge. *Soil Health and Climate Change*, pp. 25-45. Springer.

Allnutt, T.F., Ferrier, S., Manion, G., Powell, G.V., Ricketts, T.H., Fisher, B.L., Harper, G.J., Irwin, M.E., Kremen, C. & Labat, J.N. (2008) A method for quantifying biodiversity loss and its application to a 50-year record of deforestation across Madagascar. *Conservation Letters*, **1**, 173-181.

Andersen, A.N. (1983) Species diversity and temporal distribution of ants in the semi-arid mallee region of northwestern Victoria. *Australian Journal of Ecology*, **8**, 127-137.

Andersen, A.N. (1995) A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography*, **22**, 15-29.

Andersen, A.N. (2000) *The Ants of Northern Australia: a guide to the monsoonal fauna*. CSIRO Publishing, Collingwood.

Andersen, A.N. (2008) Not enough niches: non-equilibrial processes promoting species coexistence in diverse ant communities. *Austral Ecology*, **33**, 211-220.

Andersen, A.N. & Majer, J.D. (1991) The structure and biogeography of rainforest ant communities in the Kimberley region of northwestern Australia. *Kimberley Rainforests* (ed. by N.L. Mckenzie, R.B. Johnston and P.G. Kendrick), pp. 333-346. Surrey Beatty & Sons, Chipping Norton, Australia.

Andersen, A.N. & Sparling, G.P. (1997) Ants as indicators of restoration success: relationship with soil microbial biomass in the Australian seasonal tropics. *Restoration Ecology*, **5**, 109-114.

Andersen, A.N. & Majer, J.D. (2000) The Australian rain forest ant fauna: A biogeographic overview. *Sampling ground dwelling ants: Case studies from the world's rainforests* (ed. by D. Agosti, J. Majer, L. Alonso and T. Schultz), pp. 51-58. Curtin University of Technology, Perth.

Andersen, A.N., Del Toro, I. & Parr, C.L. (2015) Savanna ant species richness is maintained along a bioclimatic gradient of increasing latitude and decreasing rainfall in northern Australia. *Journal of Biogeography*, **42**, 2313-2322.

Andersen, A.N., Hoffmann, B.D. & Oberprieler, S. (2016) Diversity and biogeography of a species-rich ant fauna of the Australian seasonal tropics. *Insect Science*,

Andersen, A.N., Houadria, M., Berman, M. & van der Geest, M. (2012) Rainforest ants of the Tiwi Islands: a remarkable centre of endemism in Australia's monsoonal tropics. *Insectes Sociaux*, **59**, 433-441.

Anderson, A.S., Reside, A.E., VanDerWal, J.J., Shoo, L.P., Pearson, R.G. & Williams, S.E. (2012a) Immigrants and refugees: the importance of dispersal in mediating biotic attrition under climate change. *Global Change Biology*, **18**, 2126-2134.

Anderson, A.S., Reside, A.E., VanDerWal, J.J., Shoo, L.P., Pearson, R.G. & Williams, S.E. (2012b) Immigrants and refugees: the importance of dispersal in mediating biotic attrition under climate change.

Anderson, M.J. (2005) *PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance*. Department of Statistics, University of Auckland, Auckland.

Andrew, N.R., Hart, R.A., Jung, M.-P., Hemmings, Z. & Terblanche, J.S. (2013) Can temperate insects take the heat? A case study of the physiological and behavioural responses in a common ant, Iridomyrmex purpureus (Formicidae), with potential climate change. *Journal of Insect Physiology*, **59**, 870-880.

Angilletta Jr, M.J. & Dunham, A.E. (2003) The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. *The American Naturalist*, **162**, 332-342.

Angilletta, M.J. (2009) *Thermal adaptation: a theoretical and empirical synthesis*. Oxford University Press.

Angilletta, M.J., Steury, T.D. & Sears, M.W. (2004) Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, **44**, 498-509.

Araújo, M., Ferri-Yáñez, F., Bozinovic, F., Marquet, P., Valladares, F. & Chown, S. (2013) Heat freezes niche evolution. *Ecology Letters*, **16**, 1206-1219.

Araújo, M.B. & Rahbek, C. (2006) How does climate change affect biodiversity? *Science*, **313**, 1396-1397.

Aristophanous, M. (2010) Does your preservative preserve? A comparison of the efficacy of some pitfall trap solutions in preserving the internal reproductive organs of dung beetles. *ZooKeys*, **34**, 1-16.

Aristophanous, M. (2014) Understanding patterns of endemic dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) biodiversity in the Australian Wet Tropics rainforest: Implications of climate change. *James Cook University, Townsville, QLD, Australia*,

Arnan, X. & Blüthgen, N. (2015) Using ecophysiological traits to predict climatic and activity niches: lethal temperature and water loss in Mediterranean ants: Using physiology to predict niches. *Global Ecology and Biogeography*, **24**, 1454-1464.

Arnan, X., Blüthgen, N., Molowny-Horas, R. & Retana, J. (2015) Thermal characterization of European ant communities along thermal gradients and its implications for community resilience to temperature variability. *Frontiers in Ecology and Evolution*, **3**, 138.

Arribas, P., Abellán, P., Velasco, J., Millán, A. & Sánchez-Fernández, D. (2017) Conservation of insects in the face of global climate change. *Global Climate Change and Terrestrial Invertebrates*, 349-367.

Ashcroft, M.B., Gollan, J.R., Faith, D.P., Carter, G.A., Lassau, S.A., Ginn, S.G., Bulbert, M.W. & Cassis, G. (2010) Using Generalised Dissimilarity Models and many small samples to improve the efficiency of regional and landscape scale invertebrate sampling. *Ecological Informatics*, **5**, 124-132.

Atkinson, D. (1994) Temperature and organism size: a biological law for ectotherms? *Advances in ecological research*, **25**, 1-1.

Australian Government Department of the Environmental Water Resources (2007) Australian Government, C. (*Ed.*), Metadata: Australia- present major vegetation subgroups- NVIS Stage 1, version 3.1, Albers.

Barron, E.J. (1995) Tropical climate stability and implications for the distribution of life. *Effects of past global change on life. National Academy Press Studies in Geophysics, Washington, DC*, 108-117.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2013) lme4: Linear mixed-effects models using Eigen and S4. *R package version*, **1**

Baudier, K.M., Mudd, A.E., Erickson, S.C. & O'Donnell, S. (2015) Microhabitat and body size effects on heat tolerance: implications for responses to climate change (army ants: Formicidae, Ecitoninae). *Journal of Animal Ecology*, **84**, 1322-1330.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365-377.

Benzing, D.H. (1998) Vulnerabilities of tropical forests to climate change: the significance of resident epiphytes. *Potential Impacts of Climate Change on Tropical Forest Ecosystems*, pp. 379-400. Springer.

Bewick, S., Stuble, K.L., Lessard, J.P., Dunn, R.R., Adler, F.R. & Sanders, N.J. (2014) Predicting future coexistence in a North American ant community. *Ecology and evolution*, **4**, 1804-1819.

Bharti H., Sharma Y. P., Bharti M. & Pfeiffer M. (2013) Ant species richness, endemicity and functional groups, along an elevational gradient in the Himalayas. *Asian Myrmecology*, **5** 79-101.

Binzer, A., Guill, C., Rall, B.C. & Brose, U. (2016) Interactive effects of warming, eutrophication and size structure: impacts on biodiversity and food-web structure. *Global change biology*, **22**, 220-227.

Bishop, T.R., Robertson, M.P., Rensburg, B.J. & Parr, C.L. (2014) Elevation–diversity patterns through space and time: ant communities of the Maloti-Drakensberg Mountains of southern Africa. *Journal of Biogeography*,

Bishop, T.R., Robertson, M.P., RENSBURG, B.J. & Parr, C.L. (2017) Coping with the cold: minimum temperatures and thermal tolerances dominate the ecology of mountain ants. *Ecological Entomology*, **42**, 105-114.

Blois, J.L., Zarnetske, P.L., Fitzpatrick, M.C. & Finnegan, S. (2013) Climate change and the past, present, and future of biotic interactions. *Science*, **341**, 499-504.

Blomberg, S.P., Jr, T.G. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**, 717-745.

Bolton, B. (2007) Taxonomy of the dolichoderine ant genus Technomyrmex Mayr (Hymenoptera: Formicidae) based on the worker caste. *Contributions of the American Entomological Institute.*

Bonell, M. & Callaghan, J. (2008) The synoptic meteorology of high rainfalls and the storm run-off response in the Wet Tropics. *Living in a Dynamic Tropical Forest Landscape* (ed. by N. Stork and S. Turton), pp. 23-46. Blackwell Publishing, Oxford.

Botes, A., McGeoch, M.A., Robertson, H.G., Niekerk, A., Davids, H.P. & Chown, S.L. (2006) Ants, altitude and change in the northern Cape Floristic Region. *Journal of Biogeography*, **33**, 71-90.

Botkin, D.B., Saxe, H., Araujo, M.B., Betts, R., Bradshaw, R.H., Cedhagen, T., Chesson, P., Dawson, T.P., Etterson, J.R. & Faith, D.P. (2007) Forecasting the effects of global warming on biodiversity. *BioScience*, **57**, 227-236.

Bozinovic, F., Calosi, P. & Spicer, J.I. (2011) Physiological correlates of geographic range in animals. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 155-179.

Bradshaw, C.J., Sodhi, N.S. & Brook, B.W. (2009) Tropical turmoil: a biodiversity tragedy in progress. *Frontiers in Ecology and the Environment*, **7**, 79-87.

Brehm, G. & Fiedler, K. (2004) Bergmann's rule does not apply to geometrid moths along an elevational gradient in an Andean montane rain forest. *Global Ecology and Biogeography*, **13**, 7-14.

Brook, B.W. & Alroy, J. (2017) Pattern, process, inference and prediction in extinction biology. *Biology Letters*, **13**, 20160828.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771-1789.

Brown, J.L., Cameron, A., Yoder, A.D. & Vences, M. (2014) A necessarily complex model to explain the biogeography of the amphibians and reptiles of Madagascar. *Nature communications*, **5.**

Brown, K.S.J. (1997) Diversity, disturbance, and sustainable use of Neotropical forests: insects as indicators for conservation monitoring. *Journal of Insect Conservation*, **1**, 25-42.

Bruhl, C.A., Gunsalam, G. & Linsenmair, K.E. (1998) Stratification of ants (Hymenoptera, Formicidae) in a primary rain forest in Sabah, Borneo. *Journal of Tropical Ecology*, **14**, 285-297.

Bruhl, C.A., Mohamed, M. & Linsenmair, K.E. (1999) Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology*, **15**, 265-277.

Bruijnzeel, L.A. (1990) *Hydrology of moist tropical forests and effects of conversion: a state of knowledge review*. Faculty of Earth Sciences, Free University, Amsterdam.

Buckley, L.B., Hurlbert, A.H. & Jetz, W. (2012) Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, **21**, 873-885.

Bureau of Meteorology (2015) *Climate Data Online*. Available at: http://www.bom.gov.au/jsp/ncc/climate_averages/rainfall/ (accessed 8/12/ 2015).

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multi-model inference: a practical information-theoretic approach*. Springer Verlag, New York.

Burwell, C.J. & Nakamura, A. (2011) Distribution of ant species along an alitutdinal transect in continuous rainforest in subtropical Queensland, Australia. *Memoirs of the Queensland Museum | Nature*, **55**, 391-412.

Bush, A.A., Nipperess, D.A., Duursma, D.E., Theischinger, G., Turak, E. & Hughes, L. (2014) Continental-scale assessment of risk to the Australian Odonata from climate change. *PloS one*, **9**, e88958.

Bush, M.B. (2002) Distributional change and conservation on the Andean flank: a palaeoecological perspective. *Global Ecology and Biogeography*, **11**, 463-473.

Caddy-Retalic, S., Andersen, A.N., Aspinwall, M.J., Breed, M.F., Byrne, M., Christmas, M.J., Dong, N., Evans, B.J., Fordham, D.A. & Guerin, G.R. (2016) Bioclimatic transect networks: Powerful observatories of ecological change. *Ecology and Evolution*,

Carnaval, A.C., Hickerson, M.J., Haddad, C.F., Rodrigues, M.T. & Moritz, C. (2009) Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. *Science*, **323**, 785-789.

Cerdá, X., Retana, J. & Manzaneda, A. (1998) The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. *Oecologia*, **117**, 404-412.

Chao, A. & Jost, L. (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, **93**, 2533-2547.

Chao, A., Wang, Y. & Jost, L. (2013) Entropy and the species accumulation curve: a novel entropy estimator via discovery rates of new species. *Methods in Ecology and Evolution*, **4**, 1091-1100.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024-1026.

Christian, K.A. & Morton, S.R. (1992) Extreme thermophilia in a central Australian ant, Melophorus bagoti. *Physiological Zoology*, **65**, 885-905.

Clarke, J., Whetton, P. & Hennessy, K. (2011) Providing application-specific climate projections datasets: CSIROs climate futures framework. *Proceedings of MODSIM, international congress on modelling and simulation, modelling and simulation society of Australia and New Zealand* (ed by, pp. 12-16.

Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117-143.

Clusella-Trullas, S., Blackburn, T.M. & Chown, S.L. (2011) Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *The American Naturalist*, **177**, 738-751.

Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004) The Mid-domain effect and species richness patterns: What have we learned so far? *The American Naturalist*, **163**, E1-E23.

Costion, C.M., Simpson, L., Pert, P.L., Carlsen, M.M., Kress, W.J. & Crayn, D. (2015) Will tropical mountaintop plant species survive climate change? Identifying key knowledge gaps using species distribution modelling in Australia. *Biological Conservation*, **191**, 322-330.

Coumou, D., Robinson, A. & Rahmstorf, S. (2013) Global increase in record-breaking monthly-mean temperatures. *Climatic Change*, 1-12.

CSIRO/BoM (2016) State of the Climate - 2016. Available at: http://www.bom.gov.au/state-of-the-climate/ (accessed 15/10/ 2016).

Cushman, J.H., Lawton, J.H. & Manly, B.F.J. (1993) Latitudinal patterns in European ant assemblages: Variation in species richness and body size. *Oecologia*, **95**, 30-37.

D'Amen, M., Pradervand, J.N. & Guisan, A. (2015) Predicting richness and composition in mountain insect communities at high resolution: a new test of the SESAM framework. *Global Ecology and Biogeography*, **24**, 1443-1453.

Davidson, D.W., Cook, S.C., Snelling, R.R. & Chua, T.H. (2003) Explaining the abundance of ants in lowland tropical rainforest canopies. *Science*, **300**, 969-972.

Davis, C.C., Willis, C.G., Primack, R.B. & Miller-Rushing, A.J. (2010) The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 3201-3213.

Del Toro, I., Silva, R.R., Ellison, A.M. & Andersen, A. (2015) Predicted impacts of climatic change on ant functional diversity and distributions in eastern North American forests. *Diversity and Distributions*, **21**, 781-791.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Cameron, K.G., Haak, D.C. & Martin, P.R. (2008a) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 6668-6672.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. & Martin, P.R. (2008b) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, **105**, 6668-6672.

Diamond, S., Sorger, D.M., Hulcr, J., Pelini, S.L., Del Toros, I., Hirsch, C., Oberg, E. & Dunn, R.R. (2012) Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Global Change Biology*, **18**, 448–456.

Dowdy, A., Abbs, D. & Bhend, J. (2015) East coast cluster report, climate change in Australia projections for Australia's Natural Resource Management Regions: Cluster Reports, eds. Ekström, M. et al. In. CSIRO and Bureau of Meteorology, Australia

Dunn, R.R., Agosti, D., Andersen, A.N., Arnan, X., Bruhl, C.A., Cerdá, X., Ellison, A.M., Fisher, B.L., Fitzpatrick, M.C., Gibb, H., Gotelli, N.J., Gove, A.D., Guenard, B., Janda, M., Kaspari, M., Laurent, E.J., Lessard, J.-P., Longino, J.T., Majer, J.D., Menke, S.B., McGlynn, T.P., Parr, C.L., Philpott, S.M., Pfeiffer, M., Retana, J., Suarez, A.V., Vasconcelos, H.L., Weiser, M.D. & Sanders, N.J. (2009) Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecology Letters*, **12**, 324-333.

Elith, J. & Leathwick, J. (2007) Predicting species distributions from museum and herbarium records using multiresponse models fitted with multivariate adaptive regression splines. *Diversity and Distributions*, **13**, 265-275.

Elith, J. & Leathwick, J.R. (2009) Species Distribution Models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677-697.

Elmendorf, S.C., Henry, G.H., Hollister, R.D., Björk, R.G., Bjorkman, A.D., Callaghan, T.V., Collier, L.S., Cooper, E.J., Cornelissen, J.H. & Day, T.A. (2012) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology letters*, **15**, 164-175.

Eweleit, L. & Reinhold, K. (2014) Body size and elevation: do Bergmann's and Rensch's rule apply in the polytypic bushcricket Poecilimon veluchianus? *Ecological Entomology*, **39**, 133-136.

Ferrier, S., Harwood, T. & Williams, K. (2012) Using generalised dissimilarity modelling to assess potential impacts of climate change on biodiversity composition in Australia, and on the representativeness of the National Reserve System. *CSIRO Climate Adaptation Flagship Working Paper No. 13E, Canberra, Australia*,

Ferrier, S., Manion, G., Elith, J. & Richardson, K. (2007) Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, **13**, 252-264.

Fisher, B.L. (1999) Ant diversity patterns along an elevational gradient in the Reserve Naturelle Integrale d'Andohahela, Madagascar. *Fieldiana Zoology*, **94**, 129-147.

Fitzpatrick, M.C., Keller, S.R. & Vellend, M. (2015) Ecological genomics meets community-level modelling of biodiversity: mapping the genomic landscape of current and future environmental adaptation. *Ecology Letters*, **18**, 1-16.

Fitzpatrick, M.C., Sanders, N.J., Ferrier, S., Longino, J.T., Weiser, M.D. & Dunn, R. (2011) Forecasting the future of biodiversity: a test of single- and multi-species models for ants in North America. *Ecography*, **34**, 836-847.

Fordham, D.A., Resit Akçakaya, H., Araújo, M.B., Elith, J., Keith, D.A., Pearson, R., Auld, T.D., Mellin, C., Morgan, J.W. & Regan, T.J. (2012) Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? *Global Change Biology*, **18**, 1357-1371.

Gallant, J.C. (2000) *Terrain analysis: principles and applications*. John Wiley & Sons.

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220-227.

Gaston, K.J. & Chown, S.L. (1999) Elevation and climatic tolerance: a test using dung beetles. *Oikos*, **86**, 584-590.

Geraghty, M.J., Dunn, R. & Sanders, N.J. (2007) Body size, colony size, and range size in ants (Hymenoptera: Formicidae): are patterns along elevational and latitudinal gradients consistent with Bergmann's rule. *Myrmecological News*, **10**, 51-58.

Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J. & Wang, G. (2006) Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology*, **46**, 5-17.

Gibb, H. & Parr, C.L. (2013) Does structural complexity determine the morphology of assemblages? An experimental test on three continents. *PloS one*, **8**, e64005.

Gibson-Reinemer, D.K., Sheldon, K.S. & Rahel, F.J. (2015) Climate change creates rapid species turnover in montane communities. *Ecology and Evolution*, **5**, 2340-2347.

Goosem, S. (2002) Update of Original Wet Tropics of Queensland Nomination Dossier. In, p. 98. Wet Tropics Management Authority, Australian Government, Queensland, Australia.

Graham, C.H., Moritz, C. & Williams, S.E. (2006) Habitat history improves prediction of biodiversity in rainforest fauna. *Proceedings of the National Academy of Sciences*, **103**, 632-636.

Graham, C.H., VanDerWal, J., Phillips, S.J., Moritz, C. & Williams, S.E. (2010) Dynamic refugia and species persistence: tracking spatial shifts in habitat through time. *Ecography*, **33**, 1062-1069.

Graham, C.H., Carnaval, A.C., Cadena, C.D., Zamudio, K.R., Roberts, T.E., Parra, J.L., McCain, C.M., Bowie, R.C., Moritz, C. & Baines, S.B. (2014) The origin and maintenance of montane diversity: integrating evolutionary and ecological processes. *Ecography*, **37**, 711-719.

Greenslade, J. & Greenslade, P. (1984) Invertebrates and environmental assessment. *Environment and Planning*, **3**, 13-15.

Griffiths, H.M., Ashton, L.A., Walker, A.E., Hasan, F., Evans, T.A., Eggleton, P. & Parr, C.L. (2017) Ants are the major agents of resource removal from tropical rainforests. *Journal of Animal Ecology; 00*, 1–8.

Grimbacher, P.S. & Stork, N.E. (2009) Seasonality of a diverse beetle assemblage inhabiting lowland tropical rain forest in Australia. *Biotropica*, **41**, 328-337.

Gruner, D.S., Bracken, M.E., Berger, S.A., Eriksson, B.K., Gamfeldt, L., Matthiessen, B., Moorthi, S., Sommer, U. & Hillebrand, H. (2017) Effects of experimental warming on biodiversity depend on ecosystem type and local species composition. *Oikos*, **126**, 8-17.

Harrison, S. & Noss, R. (2017) Endemism hotspots are linked to stable climatic refugia. *Annals of Botany*, mcw248.

Harwood, T.D., Donohue, R.J., Williams, K.J., Ferrier, S., McVicar, T.R., Newell, G., White, M. & Anderson, B. (2016) Habitat Condition Assessment System: a new way to assess the condition of natural habitats for terrestrial biodiversity across whole regions using remote sensing data. *Methods in Ecology and Evolution*, **7**, 1050-1059.

Hérault, B. & Gourlet-Fleury, S. (2016) Will tropical rainforests survive climate change? *Climate Change and Agriculture Worldwide*, pp. 183-196. Springer.

Heterick, B.E. (2001) Revision of the Australian ants of the genus Monomorium (Hymenoptera: Formicidae). *Invertebrate Systematics*, **15**, 353-459.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450-455.

Hilbert, D.W. (2008) The Dynamic forest landscape of the Australian Wet Tropics: present, past and future. *Living in a Dynamic Tropical Forest Landscape* (ed. by N. Stork and S. Turton), pp. 107-122. Blackwell Publishing, Oxford.

Hilbert, D.W., Ostendorf, B. & Hopkins, M.S. (2001a) Sensitivity of tropical forests to climate change in the humid tropics of north Queensland. *Austral Ecology*, **26**, 590-603.

Hilbert, D.W., Ostendorf, B. & Hopkins, M.S. (2001b) Sensitivity of tropical forests to climate change in the humid tropics of north Queensland.

Hilbert, D.W., Graham, A. & Hopkins, M.S. (2007) Glacial and interglacial refugia within a long-term rainforest refugium: The Wet Tropics Bioregion of NE Queensland, Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **251**, 104-118.

Hoffmann, A.A., Chown, S.L. & Clusella-Trullas, S. (2013) Upper thermal limits in terrestrial ectotherms: how constrained are they? *Functional Ecology*, **27**, 934-949.

Hoffmann, B.D. & Andersen, A.N. (2003) Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology*, **28**, 444-464.

Holldobler, B. & Wilson, E.O. (1990) *The Ants*. Springer-Verlag, Berlin.

Hölldobler, B. & Wilson, E.O. (1990) *The ants*. Belknap Press of Harvard University Press, Cambridge.

Huey, R.B. & Stevenson, R. (1979) Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *American Zoologist*, **19**, 357-366.

Huey, R.B. & Pascual, M. (2009) Partial Thermoregulatory Compensation by a Rapidly Evolving Invasive Species along a Latitudinal Cline. *Ecology*, **90**, 1715-1720.

Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A., Jess, M. & Williams, S.E. (2012) Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **367**, 1665-1679.

Hughes, L. (2003) Climate change and Australia: trends, projections and impacts. *Austral Ecology*, **28**, 423-443.

Hutchinson, M., Stein, J. & Stein, J. (2009) GEODATA 9 second digital elevation model (DEM-9S) version 3. *Online at http://www. ga. gov. au*.

Hutley, L.B., Doley, D., Yates, D.J. & Boonsaner, A. (1997) Water balance of an Australian subtropical rainforest at altitude: The ecological and physiological significance of intercepted cloud and fog. *Australian Journal of Botany*, **45**, 311-329.

IPCC (2014) *Climate Change 2013: The Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.

Janzen, D.H. (1967) Why mountain passes are higher in the tropics. *The American Naturalist*, **101**, 233-249.

Jenkins, C.N., Sanders, N.J., Andersen, A.N., Arnan, X., Brühl, C.A., Cerda, X., Ellison, A.M., Fisher, B.L., Fitzpatrick, M.C., Gotelli, N.J., Gove, A.D., Guénard, B., Lattke, J.E., Lessard, J.-P., McGlynn, T.P., Menke, S.B., Parr, C.L., Philpott, S.M., Vasconcelos, H.L., Weiser, M.D. & Dunn, R.R. (2011) Global diversity in light of climate change: the case of ants. *Diversity and Distributions*, **17**, 652-662.

Kanowski, J. (2001) Effects of elevated CO_2 on the foliar chemistry of seedlings of two rainforest trees from north-east Australia: Implications for folivorous marsupials. *Austral Ecology*, **26**, 165-172.

Kardol, P., Cregger, M.A., Campany, C.E. & Classen, A.T. (2010) Soil ecosystem functioning under climate change: plant species and community effects. *Ecology*, **91**, 767-781.

Kaspari, M. & Vargo, E.L. (1995) Colony size as a buffer against seasonality: Bergmann's Rule in social insects. *The American Naturalist*, **145**, 610-632.

Kaspari, M. & Weiser, M.D. (2000) Ant activity along moisture gradients in a neotropical forest. *Biotropica*, **32**, 703-711.

Kaspari, M., Alonso, L. & O'Donnellkwd, S. (2000) Three energy variables predict ant abundance at a geographical scale. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **267**, 485-489.

Kaspari, M., Ward, P.S. & Yuan, M. (2004) Energy gradients and the geographic distribution of local ant diversity. *Oecologia*, **140**, 407-413.

Kaspari, M., Clay, N.A., Lucas, J., Yanoviak, S.P. & Kay, A. (2015) Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. *Global change biology*, **21**, 1092-1102.

Kaspari, M., Clay, N.A., Lucas, J., Revzen, S., Kay, A. & Yanoviak, S.P. (2016) Thermal adaptation and phosphorus shape thermal performance in an assemblage of rainforest ants. *Ecology*, **97**, 1038-1047.

Katabuchi, M. & Nakamura, A. (2015) mglmn: Model averaging for multivariate GLM with null models. R package version 0.0.2. In:

Kaufmann, E. & Maschwitz, U. (2006) Ant-gardens of tropical Asian rainforests. *Die Naturwissenschaften*, **93**, 216-227.

Kearney, M.R., Wintle, B.A. & Porter, W.P. (2010) Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters*, **3**, 203-213.

Kellermann, V., Overgaard, J., Hoffmann, A.A., Fløjgaard, C., Svenning, J.-C. & Loeschcke, V. (2012) Upper thermal limits of Drosophila are linked to species distributions and strongly constrained phylogenetically. *Proceedings of the National Academy of Sciences*, **109**, 16228-16233.

Kershaw, A. (1994) Pleistocene vegetation of the humid tropics of northeastern Queensland, Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **109**, 399-412.

Kimura, M.T. (2004) Cold and Heat Tolerance of Drosophilid Flies with Reference to Their Latitudinal Distributions. *Oecologia*, **140**, 442-449.

King, J.R., Andersen, A.N. & Cutter, A.D. (1998) Ants as bioindicators of habitat disturbance: validation of the functional group model for Australia's humid tropics. *Biodiversity and Conservation*, **7**, 1627-1638.

Kitching, R.L., Putland, D., Ashton, L.A., Laidlaw, M.J., Boulter, S.L., Christensen, H. & Lambkin, C.L. (2011) Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project. *Memoirs of the Queensland Museum | Nature*, **55**, 235-250.

Kraft, N.J.B., Comita, L.S., Chase, J.M., Sanders, N.J., Swenson, N.G., Crist, T.O., Stegen, J.C., Vellend, M., Boyle, B., Anderson, M.J., Cornell, H.V., Davies, K.F., Freestone, A.L., Inouye, B.D., Harrison, S.P. & Myers, J.A. (2011) Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science*, **333**, 1755-1758.

LaPolla, J.S., Brady, S.G. & Shattuck, S.O. (2011) Monograph of Nylanderia (Hymenoptera: Formicidae) of the World: An introduction to the systematics and biology of the genus. *Zootaxa*, **3110**, 1-9.

Laurance, W.F., Useche, C.D., Shoo, L.P., Herzog, S.K., Kessler, M., Escobar, F., Brehm, G., Axmacher, J.C., Chen, I.C., Gámez, L.A., Hietz, P., Fiedler, K., Pyrcz, T., Wolf, J., Merkord, C.L., Cardelus, C., Marshall, A.R., Ah-Peng, C., Aplet, G.H., del Coro Arizmendi, M., Baker, W.J., Barone, J., Brühl, C.A., Bussmann, R.W., Cicuzza, D., Eilu, G., Favila, M.E., Hemp, A., Hemp, C., Homeier, J., Hurtado, J., Jankowski, J., Kattán, G., Kluge, J., Krömer, T., Lees, D.C., Lehnert, M., Longino, J.T., Lovett, J., Martin, P.H., Patterson, B.D., Pearson, R.G., Peh, K.S.H., Richardson, B., Richardson, M., Samways, M.J., Senbeta, F., Smith, T.B., Utteridge, T.M.A., Watkins, J.E., Wilson, R., Williams, S.E. & Thomas, C.D. (2011) Global warming, elevational ranges and the vulnerability of tropical biota. *Biological Conservation*, **144**, 548-557.

Leroux, S.J., Albert, C.H., Lafuite, A.S., Rayfield, B., Wang, S. & Gravel, D. (2017) Structural uncertainty in models projecting the consequences of habitat loss and fragmentation on biodiversity. *Ecography*, **40**, 36-47.

Levins, R. & Culver, D. (1971) Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences*, **68**, 1246-1248.

Levy, R.A. & Nufio, C.R. (2015) Dispersal potential impacts size clines of grasshoppers across an elevation gradient. *Oikos*, **124**, 610-619.

Lomolino, M.V. (2001) Elevation gradients of species-density: Historical and prospective views. *Global Ecology and Biogeography*, **10**, 3-13.

Longino, J.T. & Colwell, R.K. (2011) Density compensation, species composition, and richness of ants on a neotropical elevational gradient. *Ecosphere*, **2**, art29.

Longino, J.T., Coddington, J. & Colwell, R.K. (2002) The ant fauna of a tropical rain forest: Estimating species richness three different ways. *Ecology*, **83**, 689-702.

Longino, J.T., Branstetter, M.G. & Colwell, R.K. (2014) How ants drop out: Ant abundance on tropical Mountains. *PloS one*, **9**, e104030.

Lovadi, I., Cairns, A. & Congdon, R. (2012) A comparison of three protocols for sampling epiphytic bryophytes in tropical montane rainforest. *Tropical Bryology*, **34**, 93-98.

Lyra, A., Imbach, P., Rodriguez, D., Chou, S.C., Georgiou, S. & Garofolo, L. (2016) Projections of climate change impacts on central America tropical rainforest. *Climatic Change*, 1-13.

Majer, J.D., Kitching, R.L., Heterick, B.E., Hurley, K. & Brennan, K.E.C. (2001) North-south patterns within arboreal ant assemblages from rain forests in eastern Australia. *Biotropica*, **33**, 643-661.

Manion, G., Lisk, M., Ferrier, S., Nieto-Lugilde, D. & Fitzpatrick, M.C. (2015) *gdm: Functions for Generalized Dissimilarity Modeling. R package version 1.1.4.* Available at: http://CRAN.R-project.org/package=gdm (accessed

McCain, C.M. & Grytnes, J.-A. (2010) Elevational gradients in species richness. *eLS*. John Wiley & Sons, Ltd.

McCann, K.S. (2000) The diversity–stability debate. *Nature*, **405**, 228-233.

McDonald, T.E. & Lane, M.B. (2000) *Securing the Wet Tropics?* The Federation Press, Sydney, Australia.

McJannet, D., Wallace, J. & Reddell, P. (2007) Precipitation interception in Australian tropical rainforests: II. Altitudinal gradients of cloud interception, stemflow, throughfall and interception. *Hydrological Processes*, **21**, 1703-1718.

McJannet, D., Wallace, J., Fitch, P., Disher, M. & Reddell, P. (2008) Hydrological processes in the tropical rainforests of Australia. *Living in a Dynamic Tropical Forest Landscape* (ed. by N. Stork and S. Turton), pp. 197-209. Blackwell Publishing, Oxford.

Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J. & Zhao, Z.C. (2007) Global Climate Projections *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the*

Intergovernmental Panel on Climate Change (ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Meiri, S. & Dayan, T. (2003) On the validity of Bergmann's rule. *Journal of Biogeography*, **30**, 331-351.

Mekis, É., Vincent, L.A., Shephard, M.W. & Zhang, X. (2015) Observed trends in severe weather conditions based on humidex, wind chill, and heavy rainfall events in Canada for 1953-2012. *Atmosphere-Ocean*, **53**, 383-397.

Menéndez, R., González-Megías, A., Jay-Robert, P. & Marquéz-Ferrando, R. (2014) Climate change and elevational range shifts: evidence from dung beetles in two European mountain ranges. *Global Ecology and Biogeography*, **23**, 646–657.

Metcalfe, D.J. & Ford, A.J. (2008) Floristics and plant biodiversity of the rainforests of the Wet Tropics. *Living in a Dynamic Tropical Forest Landscape* (ed. by N. Stork and S. Turton), pp. 123-132. Blackwell Publishing, Oxford.

Meteorology, A.B.o. (2015) *Severe Tropical Cyclone Yasi*. Available at: http://www.bom.gov.au/cyclone/history/yasi.shtml (accessed 15 Jan 2015).

Mokany, K., Ferrier, S., Connolly, S.R., Dunstan, P.K., Fulton, E.A., Harfoot, M.B., Harwood, T.D., Richardson, A.J., Roxburgh, S.H. & Scharlemann, J.P. (2016a) Integrating modelling of biodiversity composition and ecosystem function. *Oikos*, **125**, 10-19.

Moreau, C.S. & Bell, C.D. (2013) Testing the museum versus cradle tropical biological diversity hypothesis: Phylogeny, diversification, and ancestral biogeographic range evolution of the ants. *Evolution*, **67**, 2240-2257.

Moretti, M., Dias, A.T., de Bello, F., Altermatt, F., Chown, S.L., Azcarate, F.M., Bell, J.R., Fournier10, B., Hedde11, M. & Hortal12, J. (2017) Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*, **31**, 558-567.

Munyai, T.C. & Foord, S.H. (2012) Ants on a mountain: spatial, environmental and habitat associations along an altitudinal transect in a centre of endemism. *Journal of Insect Conservation*, **16**, 677-695.

Nadeau, C.P., Urban, M.C. & Bridle, J.R. (2017) Coarse climate change projections for species living in a fine-scaled world. *Global change biology*, **23**, 12-24.

Nakamura, A., Catterall, C.P., House, A.P.N., Kitching, R.L. & Burwell, C.J. (2007) The use of ants and other soil and litter arthropods as bio-indicators of the impacts of rainforest clearing and subsequent land use. *Journal of Insect Conservation*,

Nelson, A.S., Scott, T., Barczyk, M., McGlynn, T.P., Avalos, A., Clifton, E., Das, A., Figueiredo, A., Figueroa, L.L., Janowiecki, M., Pahlke, S., Rana, J.D. & O'Donnell, S. (2017) Day/night upper thermal limits differ within Ectatomma ruidum ant colonies. *Insectes Sociaux*,

New, M., Lister, D., Hulme, M. & Makin, I. (2002) A high-resolution data set of surface climate over global land areas. *Climate research*, **21**, 1-25.

Newbold, T., Gilbert, F., Zalat, S., El-Gabbas, A. & Reader, T. (2009) Climate-based models of spatial patterns of species richness in Egypt's butterfly and mammal fauna. *Journal of Biogeography*, **36**, 2085-2095.

Nowrouzi, S., Andersen, A.N., Macfadyen, S., Staunton, K.M., VanDerWal, J. & Robson, S.K. (2016) Ant diversity and distribution along elevation gradients in the Australian Wet Tropics: The importance of seasonal moisture stability. *PloS one*, **11**, e0153420.

Oberg, E.W., Del Toro, I. & Pelini, S.L. (2012) Characterization of the thermal tolerances of forest ants of New England. *Insectes Sociaux*, **59**, 167-174.

Olalla-Tárraga, M.Á., Rodríguez, M.Á. & Hawkins, B.A. (2006) Broad-scale patterns of body size in squamate reptiles of Europe and North America. *Journal of Biogeography*, **33**, 781-793.

Olson, D.M. (1994) The distribution of leaf litter invertebrates along a neotropical altitudinal gradient. *Journal of Tropical Ecology*, **10**, 129-150.

Ostendorf, B., Hilbert, D.W. & Hopkins, M.S. (2001) The effect of climate change on tropical rainforest vegetation pattern.

Pachauri, R.K., Allen, M., Barros, V., Broome, J., Cramer, W., Christ, R., Church, J., Clarke, L., Dahe, Q. & Dasgupta, P. (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.

Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877-884.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology and Systematics*, **37**, 637-669.

Parmesan, C., Duarte, C., Poloczanska, E., Richardson, A.J. & Singer, M.C. (2011) Overstretching attribution. *Nature Clim. Change*, **1**, 2-4.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579-583.

Parr, C.L., Eggleton, P., Davies, A.B., Evans, T.A. & Holdsworth, S. (2016) Suppression of savanna ants alters invertebrate composition and influences key ecosystem processes. *Ecology*, **97**, 1611-1617.

Parsons, S.A. & Congdon, R.A. (2008) Plant litter decomposition and nutirent cycling in north Queensland tropical rain-forest communities of differing successional status. *Journal of Tropical Ecology*, **24**, 317-327.

Patrick, M., Fowler, D., Dunn, R.R. & Sanders, N.J. (2012) Effects of treefall gap disturbances on ant assemblages in a Tropical Montane Cloud Forest. *Biotropica*, **44**, 472-478.

Payne, N.L. & Smith, J.A. (2017) An alternative explanation for global trends in thermal tolerance. *Ecology Letters*, **20**, 70-77.

Pellissier, L., Espíndola, A., Pradervand, J.N., Dubuis, A., Pottier, J., Ferrier, S. & Guisan, A. (2013) A probabilistic approach to niche-based community models for spatial forecasts of assemblage properties and their uncertainties. *Journal of Biogeography*, **40**, 1939-1946.

Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guénette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R. & Walpole, M. (2010) Scenarios for global biodiversity in the 21st century. *Science*, **330**, 1496-1501.

Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *The American Naturalist*, **100**, 33-46.

Pincebourde, S., Woods, H.A. & Fox, C. (2012) Climate uncertainty on leaf surfaces: the biophysics of leaf microclimates and their consequences for leaf-dwelling organisms. *Functional Ecology*, **26**, 844-853.

Pintor, A.F.V., Schwarzkopf, L. & Krockenberger, A.K. (2015) Rapoport's Rule: do climatic variability gradients shape range extent?

Pounds, J.A., Fogden, M.P.L. & Campbell, J.H. (1999) Biological response to climate change on a tropical mountain. *Nature*, **398**, 611-615.

Prather, C.M., Pelini, S.L., Laws, A., Rivest, E., Woltz, M., Bloch, C.P., Del Toro, I., Ho, C.-K., Kominoski, J., Newbold, T.A.S., Parsons, S. & Joern, A. (2013) Invertebrates, ecosystem services and climate change. *Biological reviews of the Cambridge Philosophical Society*, **88**, 327-348.

Prober, S., Williams, K., Harwood, T., Doerr, V., Jeanneret, T., Manion, G. & Ferrier, S. (2015) Helping Biodiversity Adapt: Supporting climate-adaptation planning using a community-level modelling approach. In. CSIRO Land and Water Flagship, Canberra. Available at: www. AdaptNRM. org ISBN

R Development Core Team (2010) *R: A language and environment for statistical computing. R Foundation for Statistical Computing*.

R Development Core Team (2013) *R: A language and environment for statistical computing. R Foundation for Statistical Computing*.

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, **8**, 224-239.

Rapp, J.M. & Silman, M.R. (2014) Epiphyte response to drought and experimental warming in an Andean cloud forest. *F1000Research*, **3**

Reichel, H. & Andersen, A.N. (1996) The rainforest ant fauna of Australia's Northern Territory. *Australian Journal of Zoology*, **44**, 81-95.

Reside, A.E., VanDerWal, J. & Kutt, A.S. (2012) Projected changes in distributions of Australian tropical savanna birds under climate change using three dispersal scenarios. *Ecology and Evolution*, 213-225.

Reside, A.E., VanDerWal, J., Phillips, B.L., Shoo, L.P., Rosauer, D.F., Anderson, B.J., Welbergen, J.A., Moritz, C., Ferrier, S., Harwood, T.D., Williams, K.J., Mackey, B., Hugh, S., Williams, Y.M. & Williams, S.E. (2013) Climate change refugia for terrestrial biodiversity: Defining areas that promote species persistence and ecosystem resilience in the face of global climate change. In, p. 216. National Climate Change Adaptation Research Facility, Gold Coast.

Reuman, D.C., Holt, R.D. & Yvon-Durocher, G. (2014) A metabolic perspective on competition and body size reductions with warming. *Journal of Animal Ecology*, **83**, 59-69.

Revell, L.J. (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**, 217-223.

Rezende, E.L., Tejedo, M. & Santos, M. (2011) Estimating the adaptive potential of critical thermal limits: methodological problems and evolutionary implications. *Functional Ecology*, **25**, 111-121.

Ribeiro, P.L., Camacho, A. & Navas, C.A. (2012) Considerations for assessing maximum critical temperatures in small ectothermic animals: insights from leaf-cutting ants. *PLoS One*, **7**, e32083.

Roberts, D.R., Bahn, V., Ciuti, S., Boyce, M.S., Elith, J., Guillera-Arroita, G., Hauenstein, S., Lahoz-Monfort, J.J., Schröder, B. & Thuiller, W. (2017) Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography*,

Robertson, H.G. (2002) Comparison of leaf litter ant communities in woodlands, lowland forests and montane forests of north-eastern Tanzania. *Biodiversity and Conservation*, **11**, 1637-1652.

Rosenberg, D.M., Danks, H.V. & Lehmkuhl, D.M. (1986) Importance of insects in environmental impact assessment. *Environmental Management*, **10**, 773-783.

Sanabria, C., Dubs, F., Lavelle, P., Fonte, S.J. & Barot, S. (2016) Influence of regions, land uses and soil properties on termite and ant communities in agricultural landscapes of the Colombian Llanos. *European Journal of Soil Biology*, **74**, 81-92.

Sanders, N.J. (2002) Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. *Ecography*, **25**, 25-32.

Sanders, N.J., Moss, J. & Wagner, D. (2003) Patterns of ant species richness along elevational gradients in an arid ecosystem. *Global Ecology and Biogeography*, **12**, 93-102.

Säterberg, T., Sellman, S. & Ebenman, B. (2013) High frequency of functional extinctions in ecological networks. *Nature*, **499**, 468-470.

Schneider, C. & Moritz, C. (1999) Rainforest refugia and evolution in Australia's Wet Tropics. *Proceedings: Biological Sciences*, **266**, 191-196.

Schneider, C.J., Cunningham, M. & Moritz, C. (1998) Comparative phylogeography and the history of endemic vertebrates in the Wet Tropics rainforests of Australia. *Molecular Ecology*, **7**, 487-498.

Sentis, A., Hemptinne, J.L. & Brodeur, J. (2014) Towards a mechanistic understanding of temperature and enrichment effects on species interaction strength, omnivory and food-web structure. *Ecology letters*, **17**, 785-793.

Shattuck, S. & O'REILLY, A. (2013) Revision of the Australian endemic ant genera Pseudonotoncus and Teratomyrmex (Hymenoptera: Formicidae: Formicinae). *Zootaxa*, **3669**, 287-301.

Shattuck, S.O. (2009) A revision the Australian species of the ant genus Myrmecina (Hymenoptera: Formicidae). *Zootaxa*, 1-21.

Shattuck, S.O. & Slipinska, E. (2012) Revision of the Australian species of the ant genus Anochetus (Hymenoptera: Formicidae). *Zootaxa*, **3426**, 1-28.

Sheldon, K.S. & Tewksbury, J.J. (2014) The impact of seasonality in temperature on thermal tolerance and elevational range size. *Ecology*, **95**, 2134-2143.

Sheldon, K.S., Yang, S. & Tewksbury, J.J. (2011) Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure. *Ecology Letters*, **14**, 1191-1200.

Shoo, L., Williams, S. & Hero, J. (2005a) Climate warming and the rainforest birds of the Australian Wet Tropics: Using abundance data as a sensitive predictor of change in total population size. *Biological Conservation*, **125**, 335-343.

Shoo, L.P., Williams, S.E. & Hero, J.-M. (2005b) Potential decoupling of trends in distribution area and population size of species with climate change. *Global Change Biology*, **11**, 1469-1476.

Shoo, L.P., Williams, S.E. & Hero, J.M. (2006) Detecting climate change induced range shifts: Where and how should we be looking? *Austral Ecology*, **31**, 22-29.

Smith, D.J. & Shattuck, S. (2009) Six new, unusually small ants of the genus Leptomyrmex (Hymenoptera: Formicidae). *Zootaxa*, **2142**, 57-68.

Smith, M.A., Hallwachs, W. & Janzen, D.H. (2014) Diversity and phylogenetic community structure of ants along a Costa Rican elevational gradient. *Ecography*, **37**, 720-731.

Sommer, J.H., Kreft, H., Kier, G., Jetz, W., Mutke, J. & Barthlott, W. (2010) Projected impacts of climate change on regional capacities for global plant species richness. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20100120.

Sorte, C.J. & White, J.W. (2013) Competitive and demographic leverage points of community shifts under climate warming. *Proceedings of the Royal Society of London B: Biological Sciences*, **280**, 20130572.

Spellerberg, I.F. (1972) Temperature tolerances of southeast Australian reptiles examined in relation to reptile thermoregulatory behaviour and distribution. *Oecologia*, **9**, 23-46.

Staunton, K.M. (2013) The vulnerability of flightless ground beetles (Carabidae) to climate change in the Australian tropical rainforest. *James Cook University, Townsville, QLD, Australia*,

Staunton, K.M., Robson, S.K.A., Burwell, C.J., Reside, A.E. & Williams, S.E. (2014) Projected distributions and diversity of flightless ground beetles within the Australian Wet Tropics and their environmental correlates. *PLoS ONE* **9 (2)** 1-16.

Stevens, G.C. (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *The American Naturalist*, **140**, 893-911.

Stork, N.E., Goosem, S. & Turton, S.M. (2009) Australian rainforests in a global context. *Living in a Dynamic Tropical Forest Landscape* (ed. by N.E. Stork and S.M. Turton), pp. 4-21. Wiley-Blackwell., Hoboken.

Stratman, R. & Markow, T.A. (1998) Resistance to thermal stress in desert Drosophila. *Functional Ecology*, **12**, 965-970.

Stuble, K.L., Pelini, S.L., Diamond, S.E., Fowler, D.A., Dunn, R.R. & Sanders, N.J. (2013) Foraging by forest ants under experimental climatic warming: a test at two sites. *Ecology and evolution*, **3**, 482-491.

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2011) Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings.Biological sciences / The Royal Society*, **278**, 1823-1830.

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, **2**, 686-690.

Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T. & Huey, R.B. (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences*, **111**, 5610-5615.

Suppiah, R., Macadam, I. & Whetton, P.H. (2007) Climate change projections for the tropical rainforest region of North Queensland. Unpublished report to the Marine and Tropical Sciences Research Facility. In, p. 38. Reef and Rainforest Research Centre Limited, Cairns.

Tayleur, C.M., Devictor, V., Gaüzère, P., Jonzén, N., Smith, H.G. & Lindström, Å. (2016) Regional variation in climate change winners and losers highlights the rapid loss of cold-dwelling species. *Diversity and Distributions*,

Taylor, R. (1977) New ants of the Australian genus Orectognathus, with a key to the known species (Hymenoptera: Formicidae). *Australian Journal of Zoology*, **25**, 581-612.

Taylor, R.W. (1972) *Biogeography of insects in New Guinea and Cape York Peninsula*. Australian National University Press, Canberra.

Taylor, R.W. & Brown, D. (1985) Hymenoptera: Formicoidea. In: D. W. Walton (Ed) Zoological Catalogue of Australia. 2. Hymenoptera: Formicoidea, Vespoidea and Specoidea. 1-149.

Terblanche, J.S., Klok, C.J., Krafsur, E.S. & Chown, S.L. (2006) Phenotypic plasticity and geographic variation in thermal tolerance and water loss of the tsetse Glossina pallidipes (Diptera: Glossinidae): implications for distribution modelling. *The American journal of tropical medicine and hygiene*, **74**, 786-794.

Thomas, C.D. (2010) Climate, climate change and range boundaries. *Diversity and Distributions*, **16**, 488-495.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004a) Extinction risk from climate change. *Nature*, **427**, 145-148.

Thomas, D.C., Cameron, A., Green, R.E. & Bakkenes, M. (2004b) Extinction risk from climate change. *Nature*, **427**, 145.

Turton, M.S. & Dale, A. (2007) A preliminary assessment of the environmental impacts of Cyclone Larry on the forest landscapes of northeast Queensland, with reference to responses to natural resource management issues in the aftermath. In. Australian Bureau of Meteorology Australia.

Turton, S.M. (2012) Securing landscape resilience to tropical cyclones in Australia's Wet Tropics under a changing climate: Lessons from cyclones Larry (and Yasi). *Geographical Research*, **50**, 15-30.

Urban, M.C., Tewksbury, J.J. & Sheldon, K.S. (2012) On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society of London B: Biological Sciences*, **279**, 2072-2080.

Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., García, M.B., García, D., Gómez, J.M. & Jordano, P. (2015) Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology*, **29**, 299-307.

Van Ingen, L.T., Campos, R.I. & Andersen, A.N. (2008) Ant community structure along an extended rain forest–savanna gradient in tropical Australia. *Journal of Tropical Ecology*, **24**, 445-455.

VanDerWal, J., Murphy, H.T., Kutt, A.S., Perkins, G.C., Bateman, B.L., Perry, J.J. & Reside, A.E. (2013) Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature Climate Change*, **3**, 239-243.

Verble-Pearson, R.M., Gifford, M.E. & Yanoviak, S.P. (2015) Variation in thermal tolerance of North American ants. *Journal of thermal biology*, **48**, 65-68.

Vorhees, A.S., Gray, E.M. & Bradley, T.J. (2013) Thermal resistance and performance correlate with climate in populations of a widespread mosquito. *Physiological and Biochemical Zoology*, **86**, 73-81.

Wallace, J. & McJannet, D. (2012) Climate change impacts on the water balance of coastal and montane rainforests in northern Queensland, Australia. *Journal of hydrology*, **475**, 84-96.

Walther, G.-R. (2003) Plants in a warmer world. *Perspectives in plant ecology, evolution and systematics*, **6**, 169-185.

Wang, L., Qian, Y., Zhang, Y., Zhao, C., Leung, L.R., Huang, A. & Xiao, C. (2016) Observed variability of summer precipitation pattern and extreme events in East China associated with variations of the East Asian summer monsoon. *International Journal of Climatology*, **36**, 2942-2957.

Wang, M. (2003) A monographic revision of the ant genus Pristomyrmex (Hymenoptera: Formicidae). *Bulletin of the Museum of Comparative Zoology*, **157**, 383-542.

Wang, Y., Naumann, U., Wright, S.T. & Warton, D.I. (2012) mvabund– an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution*, **3**, 471-474.

Webb, L. & Tracey, J. (1994) The rainforests of northern Australia. *Australian Vegetation. Cambridge University Press, Cambridge*, 87-130.

Welbergen, J., Meade, J., Storlie, C., VanDerWal, J., Dalziell, A., Hodgson, L., Larson, J., Krockenberger, A. & Williams, S. (2015) Climate change and the impacts of extreme events on Australia's Wet Tropics biodiversity. In, p. 81. Tropical Ecosystems Hub, NERP, Australia.

Whetton, P., Hennessy, K., Clarke, J., McInnes, K. & Kent, D. (2012) Use of Representative Climate Futures in impact and adaptation assessment. *Climatic Change*, **115**, 433-442.

Wiescher, P.T., Pearce-Duvet, J.M. & Feener, D.H. (2012) Assembling an ant community: species functional traits reflect environmental filtering. *Oecologia*, **169**, 1063-1074.

Williams, K., Ferrier, S., Rosauer, D., Yeates, D., Manion, G., Harwood, T., Stein, J., Faith, D., Laity, T. & Whalen, A. (2010a) Harnessing continent-wide biodiversity datasets for prioritising national conservation investment. *A report prepared for the Department of Sustainability, Environment, Water, Population and Communities, Australian Government, Canberra, by CSIRO Ecosystem Sciences: Canberra)–systhesis report*, **105**

Williams, S.E. & Pearson, R.G. (1997) Historical rainforest contractions, localized extinctions and patterns of vertebrate endemism in the rainforests of Australia's wet tropics. *Proceedings of the Royal Society of London Series B*, **264**, 709-716.

Williams, S.E. & Middleton, J. (2008) Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: implications for global climate change. *Diversity and Distributions*, **14**, 69-77.

Williams, S.E., Bolitho, E.E. & Fox, S. (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society of London. Series B*, 1887-1892.

Williams, S.E., Isaac, J.L. & Shoo, L.P. (2008a) The impact of climate change on the biodiversity and ecosystem functions of the Wet Tropics. *Living in a Dynamic Tropical Forest Landscape* (ed. by N. Stork and S. Turton), pp. 282-294. Blackwell Publishing, Oxford.

Williams, S.E., Isaac, J.L., Graham, C. & Moritz, C. (2008b) Towards an understanding of vertebrate biodiversity in the Australian Wet Tropics. *Living in a Dynamic Tropical Forest Landscape* (ed. by N. Stork and S. Turton), pp. 133-149. Blackwell Publishing, Oxford.

Williams, S.E., Shoo, L.P., Henriod, R. & Pearson, R.G. (2010b) Elevational gradients in species abundance, assemblage structure and energy use of rainforest birds in the Australian Wet Tropics bioregion. *Austral Ecology*, **35**, 650-664.

Williams, S.E., Williams, Y.M., VanDerWal, J., Isaac, J.L., Shoo, L.P. & Johnson, C.N. (2009) Colloquium Papers: Ecological specialization and population size in a biodiversity hotspot: How rare species avoid extinction. *Proceedings of the National Academy of Sciences*, **106**, 19737-19741.

Williams, Y.M., Williams, S.E., Alford, R.A., Waycott, M. & Johnson, C.N. (2006) Niche breadth and geographical range: ecological compensation for geographical rarity in rainforest frogs. *Biology Letters*, **2**, 532-535.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 273-309.

Wilson, E.O. (1988) *Biodiversity*. National Academy Press, Washinton, D. C.

Wilson, E.O. (1992) *The Diversity of Life*. Harvard University Press, Harvard.

Wilson, R.D. (2010) *The Potential Impact of Climate Change on the Schizophoran Flies of Australia's Wet Tropics Rainforests*. James Cook University, Townsville: PhD Thesis. .

WTMA (2013) Annual Report and State of the Wet Tropics Report. In, p. 90. Wet Tropics Management Authority, Australian Government Cairns, Queensland.

Xu, T. & Hutchinson, M.F. (2013) New developments and applications in the ANUCLIM spatial climatic and bioclimatic modelling package. *Environmental Modelling & Software*, **40**, 267-279.

Yates, C.J., Elith, J., Latimer, A.M., Le Maitre, D., Midgley, G.F., Schurr, F.M. & West, A.G. (2010) Projecting climate change impacts on species distributions in megadiverse South African Cape and Southwest Australian Floristic Regions: Opportunities and challenges. *Austral Ecology*, **35**, 374-391.

Yeates, D.K. & Monteith, G.B.M. (2008) The invertebrate fauna of the Wet Tropics: diversity,endemism and relationships. *Living in a Dynamic Tropical Forest Landscape* (ed. by N. Stork and S. Turton), pp. 178-191. Blackwell Publishing, Oxford.

Yek, S.H., Williams, S.E., Burwell, C.J., Robson, S.K.A. & Crozier, R.H. (2009) Ground dwelling ants as surrogates for establishing conservation priorities in the Australian Wet Tropics. *Journal of Insect Science*, **12**, 1-12.

Zhang, D.-D., Yan, D.-H., Wang, Y.-C., Lu, F. & Wu, D. (2015) Changes in extreme precipitation in the Huang-Huai-Hai River basin of China during 1960-2010. *Theoretical and Applied Climatology*, **120**, 195-209.

Appendices

Appendix 1. Permission from the copyright holder to publish Figure 2.1.

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Appendix 2. Ant species and their frequency of occurrence in the six subregions.

	Finnegan	Windsor	Carbine	Lamb Range	Atherton	Spec	Total
Aenictinae							**6**
Aenictus aratus						1	1
A. nesiotis			1				1
A. prolixus			1		3		4
Amblyoponinae							**47**
Amblyopone australis		1					1
Amblyopone sp. A		1					1
Onychomyrmex hedleyi	1	2	11	1	10		25
Onychomyrmex sp. B			1				1
Onychomyrmex sp. C		4	1				5
Onychomyrmex sp. D			1				1
Onychomyrmex sp. E				3			3
Onychomyrmex sp. F						2	2
Prionopelta robynmae			1	6	1		8
Cerapachyinae							**18**
Cerapachys nr. *adamus*		2					2
C. nr. *binodis*			1				1
Cerapachys sp. A (*turneri* gp.)			1				1
Cerapachys sp. B (*turneri* gp.)				2	1		3
Cerapachys sp. C (*turneri* gp.)					1		1
Cerapachys sp. D (*turneri* gp.)		1					1
Sphinctomyrmex steinheili			1		2		3

	Finnegan	Windsor	Carbine	Lamb Range	Atherton	Spec	Total
Sphinctomyrmex sp. B			1				1
Sphinctomyrmex sp. C	2		1				3
Sphinctomyrmex sp. D	1		1				2
Dolichoderinae							**1,080**
Iridomyrmex nr. *anceps*					2		2
I. mayri		8					8
I. suchieri		7			1		8
Leptomyrmex dolichoscapus			18				18
L. ruficeps		4	3		4	2	13
L. unicolor	2	6	39				47
Tapinoma melanocephalum	4						4
Tapinoma sp. A	1		1			1	3
Technomyrmex cheesmanae						3	3
T. difficilis			3		1	2	6
T. nitens	3	13	11		4	3	34
T. quadricolor	4		5	3	6	8	26
T. shattucki			7				7
T. sophiae						1	1
Turneria bidentata			1				1
Anonychomyrma gilberti	17	81	227		108	48	481
A. nr.*gilberti*			23			56	79
Anonychomyrma sp. B (*biconvexa* gp.)		6	17			14	37
Anonychomyrma sp. C (*biconvexa* gp.)		17	4				21
Anonychomyrma sp. D (*biconvexa* gp.)		35					35

	Finnegan	Windsor	Carbine	Lamb Range	Atherton	Spec	Total
Anonychomyrma sp. E (*nitidiceps* gp.)		34			11	3	48
Anonychomyrma sp. G (*nitidiceps* gp.)	7	2	45		36	57	147
Anonychomyrma sp. H (nitidiceps gp.)			1				1
Anonychomyrma sp. J (nitidiceps gp.)		1					1
Anonychomyrma sp. K (biconvexa gp.)							0
Anonychomyrma sp. L (nitidiceps gp.)	1		1				2
Anonychomyrma sp. M (biconvexa gp.)						40	40
Anonychomyrma sp. N (nitidiceps gp.)			1				1
Anonychomyrma sp. O (nitidiceps gp.)					3		3
Anonychomyrma sp. P (biconvexa gp.)						3	3
Ectatomminae							**574**
Rhytidoponera chnoopyx			8	5	3		16
R. impressa	1		3	2	1	33	40
R. kurandensis	1	23	11		1		36
R. laticeps			1		4	6	11
R. metallica						1	1
R. purpurea	26	22	34		97	16	195
R. scaberrima	2	1	9		5		17
R. nr. *scaberrima*					3		3
R. spoliata			5				5
R. nr. *victoriae*	22	20	27	21	34	84	208
Rhytidoponera sp. C	2				13	4	19
Rhytidoponera sp. F (*araneoides* gp.)			3		4	9	16
Rhytidoponera sp. G *(araneoides gp.)*	3				2		5

	Finnegan	Windsor	Carbine	Lamb Range	Atherton	Spec	Total
Rhytidoponera sp. H					2		2
Formicinae							**395**
Camponotus confusus	1		3		4		8
C. thadeus	2						2
C. vitreus			1		1		2
Camponotus sp. A (*aureopilus* gp.)			1				1
Camponotus sp. B (*macrocephalus* gp.)			1				1
Camponotus sp. D1 (*discors* gp.)						1	1
Camponotus sp. N1 (*novaehollandiae* gp.)			2				2
Camponotus sp. N2 (*novaehollandiae* gp.)		4				2	6
Camponotus sp. S1 (*subnitidus* gp.)						1	1
Notostigma carazii		1			1	10	12
Nylanderia glabrior	27	16	48	5	114	31	241
Nylanderia sp. B					2		2
Nylanderia sp. C		1					1
Oecophylla smaragdina	8				29		37
Paraparatrechina sp. A (*minutula* gp.)		2	2		1	8	13
Paraparatrechina sp. B (*minutula* gp.)			1				1
Paraparatrechina sp. C (*minutula* gp.)		1				1	2
Paraparatrechina sp. D		2	2				4
Plagiolepis sp. A			3				3
Plagiolepis sp. B			1				1

	Finnegan	**Windsor**	**Carbine**	**Lamb Range**	**Atherton**	**Spec**	**Total**
Polyrhachis argentosa	2						2
P. delecta	1					1	2
P. flavibasis		1					1
P. monteithi			1				1
P. rufifemur		1					1
Prolasius sp. B (*nitidissimus* gp.)	1			7	4		12
Prolasius sp. C (*nitidissimus* gp.)			3		1	4	8
Prolasius sp. D (*convexus* gp.)		20	1				21
Stigmacros sp. A (*pusilla* gp.)		2					2
Stigmacros sp. B (*pusilla* gp.)		2					2
Stigmacros sp. C (*aciculata* gp.)						1	1
Stigmacros sp. D (*pusilla* gp.)		1					1
Heteroponerinae							**103**
Heteroponera sp. A (*imbellis* gp.)	2	8	26		5	5	46
Heteroponera nr. *relicta*					4		4
Heteroponera nr. *trachypyx*			1		1		2
Heteroponera relicta		1	32				33
Heteroponera rhodopygea	5	1					6
Heteroponera ?ecarinata			1				1
Heteroponera pendergrasti				4			4
Heteroponera darlingtonorum						7	7
Myrmeciinae							**4**
Myrmecia nigrocincta		1			1	2	4

	Finnegan	Windsor	Carbine	Lamb Range	Atherton	Spec	Total
Myrmicinae							**2,613**
Anillomyrma sp. B			1				1
Anillomyrma sp. C			1				1
Calyptomyrmex sp. A						6	6
Cardiocondyla atalanta		1					1
C. nr. *wroughtoni*		1					1
Cardiocondyla sp. A (*emeryi* gp.)	1						1
Carebara sp. A	6	7	22	6	8	11	60
Carebara sp. C			2				2
Carebara sp. D		1				1	2
Carebara sp. E						2	2
Carebara sp. F		2					2
Carebara sp. G			2				2
Carebara sp. H		1	2				3
Carebara sp. I		1	8			5	14
Carebara sp. J			2				2
Carebara sp. L						2	2
Carebara sp. M						3	3
Carebara sp. N						1	1
Carebara sp. O						1	1
Colobstruma biconvexa						2	2
Crematogaster sp. A			7		13	1	21
Crematogaster sp. B			1				1
Crematogaster sp. C					1		1

	Finnegan	**Windsor**	**Carbine**	**Lamb Range**	**Atherton**	**Spec**	**Total**
Crematogaster sp. D			1				1
Crematogaster sp. E					2		2
Crematogaster sp. F			1				1
Crematogaster sp. G	5		9		1	33	48
Crematogaster sp. H			4		12	3	19
Crematogaster sp. I	1			1			2
Eurhopalothrix australis		1	1		3	4	9
Lordomyrma sp. A (*punctiventris* gp.)		14	18	1	1		34
Lordomyrma sp. B (*punctiventris* gp.)			3				3
Lordomyrma sp. E (*punctiventris* gp.)		1					1
Lordomyrma sp. F (*punctiventris* gp.)			4				4
Mayriella abstinens			2		2	2	6
M. spinosior	1						1
Meranoplus beatoni			1				1
M. hirsutus	1	27	60		29	3	120
Monomorium dracula			1				1
M. floricola	4	2	4	1	5	6	22
M. petiolatum			1		13		14
M. pharaonis						1	1
M. sydneyense		1					1
M. turneri					2		2
Monomorium sp. A (*albipes complex*)					1		1
Monomorium sp. B (*nigrius* gp.)	1	3			1		5
Monomorium sp. C (*rubriceps* gp.)			1		95		96
Monomorium sp. D (*albipes complex*)					1		1

	Finnegan	Windsor	Carbine	Lamb Range	Atherton	Spec	Total
Monomorium sp. E (nr. *petiolatum*)					1		1
Monomorium sp. H (*leae* gp.)	2	2				3	7
Myrmecina alpina			9				9
M. nr. *alpina*		1					1
M. difficulta		1	1				2
M. inaequala		8					8
M. mjobergi			1				1
M. pumilla				1			1
M. silvarugosa	1						1
Myrmecina sp. A	1						1
Myrmecina sp. B			2				2
Opistopsis linnaei						1	1
Orectognathus nanus						2	2
O. robustus		1	1		9	2	13
*O.*nr. *satan*		1					1
Pheidole sp. A1 (*ampla* gp.)		21			1		22
Pheidole sp. A10 (*ampla* gp.)			27		50	14	91
Pheidole sp. A11 (*ampla* gp.)		9	57		1	7	74
Pheidole sp. A12 (*ampla* gp.)		85	23				108
Pheidole sp. A13 (*ampla* gp.)	1	15	61	18	121	21	237
Pheidole sp. A14 (*ampla* gp.)		6	4	2	7	7	26
Pheidole sp. A15 (*ampla* gp.)	6	12	13		12	6	49
Pheidole sp. A16 (*ampla* gp.)			1				1
Pheidole sp. A2 (*ampla* gp.)		5	116	9	110	64	304
Pheidole sp. A20 (*ampla* gp.)	2	3					5

	Finnegan	**Windsor**	**Carbine**	**Lamb Range**	**Atherton**	**Spec**	**Total**
Pheidole sp. A23 (*ampla* gp.)			24			7	31
Pheidole sp. A24 (*ampla* gp.)				3	4	2	9
Pheidole sp. A25 (*ampla* gp.)			1	1	14	5	21
Pheidole sp. A26 (*ampla* gp.)					3		3
Pheidole sp. A3 (*ampla* gp.)			9				9
Pheidole sp. A30 (*ampla* gp.)		2	13		1	3	19
Pheidole sp. A4 (*ampla* gp.)		2	7		42	5	56
Pheidole sp. A5 (*ampla* gp.)		1	6	4	3		14
Pheidole sp. A6 (*ampla* gp.)		1	7				8
Pheidole sp. A7 (*ampla* gp.)		5	2		3	3	13
Pheidole sp. A8 (*ampla* gp.)		4	55	4	3	65	131
Pheidole sp. A9 (*ampla* gp.)					4	7	11
Pheidole sp. B	1						1
Pheidole sp. E1 (Group E)					2		2
Pheidole sp. F1 (Group F)	18	1	28		12	3	62
Pheidole sp. F2 (Group F)						3	3
Pheidole sp. ?*impressiceps*	6	1	21				28
Pheidole sp. J1 (Group J)			1				1
Pheidole sp. J2 (Group J)			3				3
Pheidole sp. K (Group K)					4		4
Pheidole sp. L1 (*lonifera* gp.)	5	6	6		12		29
Pheidole sp. L2 (*onifera* gp.)					2		2
Pheidole sp. L4 (*onifera* gp.)	2		14		11		27
Pheidole sp. L5 (*onifera* gp.)	1		7				8
Pheidole sp. Q1 (*quadricuspis* gp.)	2	1	28		14		45

	Finnegan	**Windsor**	**Carbine**	**Lamb Range**	**Atherton**	**Spec**	**Total**
Pheidole sp. V1 (*variabilis* gp.)	2	12	23		5	40	82
Pheidole sp. V2 (*variabilis* gp.)	8	5	1		55		69
Pheidole sp. V4 (*variabilis* gp.)	21	12	12		7		52
Pheidole sp. V6 (*variabilis* gp.)						5	5
Pheidole sp. V9 (*variabilis* gp.)				5			5
Pheidologeton affinis	12	2	10		7	2	33
Podomyrma nr. grossestriata			2				2
P. mjobergi					1	1	2
P. muckeli			1				1
Podomyrma sp. B						2	2
Podomyrma sp. C		1					1
Podomyrma sp. D		1			2		3
Pristomyrmex foveolatus	1		2		1		4
Pristomyrmex nr. foveolatus						1	1
Pristomyrmex wilsoni			2				2
Rhopalothrix sp. A						1	1
Rhoptromyrmex sp. A	4		2		2		8
Solenopsis sp. A	1	22	7	1	3	3	37
Solenopsis sp. B		4	6				10
Solenopsis sp. C	1		1				2
Solenopsis sp. D	5	4	1				10
Solenopsis sp. E		6				1	7
Strumigenys cingatrix	1	1	3	3		3	11
S. deuteras						3	3
S. nr. *deuteras*		1			2		3

	Finnegan	**Windsor**	**Carbine**	**Lamb Range**	**Atherton**	**Spec**	**Total**
S. emdeni			1				1
S. nr. *emmae*	1						1
S. enanna			1				1
S. friedae		1			1		2
S. guttulata					1	1	2
S. harpyia	10	8	14		13	5	50
*S.*nr. *harpyia*			1				1
S. juxta		2				1	3
*S.*nr. *jugis*						1	1
S. minteras						1	1
S. orthanetes		8	4	1	1	1	15
S. paranetes		14	11	2	3	19	49
S. philiporum			3	1	3		7
S. semicompta	2						2
*S.*nr. *snellingi*	1						1
S. yaleopteura					1		1
Strumigenys sp. A			1	4			5
Strumigenys sp. C (*godeffroyi* gp.)				2			2
Strumigenys sp. D (*godeffroyi* gp.)				6			6
Tetramorium bicarinatum			5	4	13		22
T. ornatum	4				1		5
T. pacificum	2		4		3	10	19
T. simillimum			1				1
T. strictum			4		1	8	13
Tetramorium sp. C					1	1	2

	Finnegan	Windsor	Carbine	Lamb Range	Atherton	Spec	Total
Tetramorium sp. F (*strictum* gp.)					1		1
Tetramorium sp. G (*pacificum* gp.)	1		1				2
Tetramorium sp. H (*pacificum* gp.)			1				1
Vollenhovia sp. A					1		1
Vollenhovia sp. B						1	1
Vombisidris sp.A	1						1
unidentified *Stenamminie* sp. A					1		1
Ponerinae							**302**
Anochetus nr. *graeffei*					5		5
Hypoponera sp. A	1	35	18	9	18	19	100
Hypoponera sp. B	1	2	2	8	4	3	20
Hypoponera sp. C	3	13	5	7	2	2	32
Hypoponera sp. G			1				1
Hypoponera sp. H		2					2
Hypoponera sp. J			1				1
Hypoponera sp. K		2					2
Hypoponera sp. L	1				1	1	3
Hypoponera sp. M						1	1
Hypoponera sp. N			1		1		2
Hypoponera sp. O						3	3
Leptogenys anitae			3				3
*L.*nr.*anitae*					1		1
L. longensis					1		1
L. mjobergi						6	6

	Finnegan	**Windsor**	**Carbine**	**Lamb Range**	**Atherton**	**Spec**	**Total**
*L.*nr.*mjobergi*		2	5	1	2		10
L. sjostedti			1			1	2
Leptogenys sp. C (*diminuta* gp.)			1				1
Mesoponera australis				1		1	2
Myopias tenuis			1		2		3
Odontomachus cephalotes	8		42		8	2	60
Ponera sp. A		2					2
Ponera sp. B		2					2
Pseudoneoponera sp. B (*oculata* gp.)					3		3
Pseudoneoponera sp. A (*porcata* gp.)			2		2		4
Pseudoneoponera sp. C (*porcata* gp)						2	2
Brachyponera croceicornis	2		13		10		25
Cryptopone sp. A		2					2
Platythyrea sp. A (*parallela* gp.)			1				1
Proceratiinae							**5**
Discothyrea sp. A					1		1
Discothyrea sp. B		1				1	2
Discothyrea sp. C			1				1
Proceratium sp. A			1				1

Appendix 3. Correlation between ant species richness and latitude, elevation and inetraction of these two factors, based on pooled raw data from the six subregions.

	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	27.986	12.958	2.160	0.033	*
Latitude	0.613	0.748	0.819	0.415	

	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	18.693	1.770	10.560	0.000	***
Elevation	-0.002	0.002	-0.810	0.420	

	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	37.241	40.824	0.912	0.364	
Latitude	1.052	2.375	0.443	0.659	
Elevation	-0.008	0.051	-0.158	0.875	
Latitude : Elevation	-0.001	0.003	-0.112	0.911	

Appendix 4. Complete record of ant species tested for CTmax and body mass in the study.

Mt	Site	Elevation	Genera	Species	CTmax (°C)	Body mass (mg)
SU	SU350	350	*Myrmecia*	*Myrmecia nigrocincta*	48	9.20
SU	SU350	350	*Myrmecia*	*Myrmecia nigrocincta*	46	6.50
SU	SU350	350	*Myrmecia*	*Myrmecia nigrocincta*	46	8.10
SU	SU350	350	*Myrmecia*	*Myrmecia nigrocincta*	46	8.80
SU	SU350	350	*Myrmecia*	*Myrmecia nigrocincta*	48	9.80
SU	SU350	350	*Myrmecia*	*Myrmecia nigrocincta*	46	11.60
SU	SU350	350	*Polyrhachis*	*Polyrhachis argentosa*	51	3.80
SU	SU350	350	*Polyrhachis*	*Polyrhachis argentosa*	44	2.20
SU	SU350	350	*Polyrhachis*	*Polyrhachis argentosa*	53	2.80
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma sp. A cf.gilberti*	41	0.60
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma sp. A cf.gilberti*	41	0.50
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma sp. A cf.gilberti*	41	0.30
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma gilberti*	48	1.40

Mt	Site	Elevation	Genera	Species	CTmax (°C)	Body mass (mg)
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma gilberti*	48	1.60
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma sp. A cf.gilberti*	38	0.40
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma sp. A cf.gilberti*	41	0.40
SU	SU350	350	*Leptomyrmex*	*Leptomyrmex rufipes*	44	7.50
SU	SU350	350	*Leptogenys*	*Leptogenys mjobergi*	42	1.80
SU	SU350	350	*Rhytidoponera*	*Rhytidoponera impressa*	44	17.10
SU	SU350	350	*Odontomachus*	*Odontomachus cephalotes*	43	4.20
SU	SU350	350	*Odontomachus*	*Odontomachus cephalotes*	42	3.20
SU	SU350	350	*Odontomachus*	*Odontomachus cephalotes*	43	3.60
SU	SU350	350	*Odontomachus*	*Odontomachus cephalotes*	43	2.80
SU	SU350	350	*Odontomachus*	*Odontomachus cephalotes*	43	2.60
SU	SU350	350	*Odontomachus*	*Odontomachus cephalotes*	43	3.60
SU	SU350	350	*Notostigma*	*Notostigma carazii*	37	14.90
SU	SU350	350	*Myrmecia*	*Myrmecia nigrocincta*	44	12.90

Mt	Site	Elevation	Genera	Species	CTmax (°C)	Body mass (mg)
SU	SU350	350	*Myrmecia*	*Myrmecia nigrocincta*	48	9.00
SU	SU350	350	*Polyrhachis*	*Polyrhachis argentosa*	53	2.00
SU	SU350	350	*Rhytidoponera*	*Rhytidoponera impressa*	45	8.70
SU	SU350	350	*Crematogaster*	*Crematogaster sp. G*	51	0.18
SU	SU350	350	*Crematogaster*	*Crematogaster sp. G*	51	0.13
SU	SU350	350	*Crematogaster*	*Crematogaster sp. G*	42	0.90
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma sp. A cf.gilberti*	42	0.60
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma gilberti*	48	0.50
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma sp. A cf.gilberti*	47	0.20
SU	SU350	350	*Leptomyrmex*	*Leptomyrmex rufipes*	41	4.60
SU	SU350	350	*Leptomyrmex*	*Leptomyrmex rufipes*	43	3.00
SU	SU350	350	*Myrmecia*	*Myrmecia nigrocincta*	46	12.90
SU	SU350	350	*Rhytidoponera*	*Rhytidoponera impressa*	46	8.00
SU	SU350	350	*Rhytidoponera*	*Rhytidoponera impressa*	48	6.50

Mt	Site	Elevation	Genera	Species	CTmax (°C)	Body mass (mg)
SU	SU350	350	*Crematogaster*	*Crematogaster sp. G*	65	0.10
SU	SU350	350	*Rhytidoponera*	*Rhytidoponera cf. victoriae*	46	1.70
SU	SU350	350	*Polyrhachis*	*Polyrhachis argentosa*	65	3.50
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma gilberti*	57	0.60
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma gilberti*	57	0.80
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma gilberti*	61	0.50
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma gilberti*	57	0.60
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma gilberti*	54	0.90
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma gilberti*	58	0.60
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma gilberti*	64	0.40
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma gilberti*	58	0.80
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma sp. A cf.gilberti*	64	0.50
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma sp. A cf.gilberti*	64	0.40
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma sp. A cf.gilberti*	62	0.50

Mt	Site	Elevation	Genera	Species	CTmax (°C)	Body mass (mg)
SU	SU350	350	*Anonychomyrma*	*Anonychomyrma sp. A cf.gilberti*	58	0.60
SU	SU350	350	*Myrmecia*	*Myrmecia nigrocincta*	51	7.80
SU	SU350	350	*Myrmecia*	*Myrmecia nigrocincta*	52	8.00
SU	SU350	350	*Myrmecia*	*Myrmecia nigrocincta*	46	9.20
SU	SU350	350	*Myrmecia*	*Myrmecia nigrocincta*	46	8.50
SU	SU350	350	*Notostigma*	*Notostigma carazii*	44	13.20
SU	SU350	350	*Rhytidoponera*	*Rhytidoponera cf. victoriae*	45	1.50
SU	SU350	350	*Rhytidoponera*	*Rhytidoponera cf. victoriae*	45	1.90
SU	SU6	600	*Leptogenys*	*Leptogenys mjobergi*	42	1.50
SU	SU6	600	*Leptogenys*	*Leptogenys mjobergi*	42	1.80
SU	SU6	600	*Leptogenys*	*Leptogenys mjobergi*	42	1.90
SU	SU6	600	*Leptogenys*	*Leptogenys mjobergi*	42	1.70
SU	SU6	600	*Leptogenys*	*Leptogenys mjobergi*	42	1.80
SU	SU6	600	*Leptogenys*	*Leptogenys mjobergi*	42	1.90

Mt	Site	Elevation	Genera	Species	CTmax (°C)	Body mass (mg)
SU	SU6	600	*Leptogenys*	*Leptogenys mjobergi*	42	1.90
SU	SU6	600	*Leptogenys*	*Leptogenys mjobergi*	42	1.50
SU	SU6	600	*Crematogaster*	*Crematogaster sp. G*	46	0.10
SU	SU6	600	*Crematogaster*	*Crematogaster sp. G*	51	0.13
SU	SU6	600	*Pheidole*	*Pheidole sp. V1 variabilis gp.*	37	0.02
SU	SU6	600	*Polyrhachis*	*Polyrhachis delecta*	58	2.40
SU	SU6	600	*Polyrhachis*	*Polyrhachis delecta*	58	1.80
SU	SU6	600	*Polyrhachis*	*Polyrhachis delecta*	61	2.10
SU	SU6	600	*Rhytidoponera*	*Rhytidoponera purpurea*	47	1.60
SU	SU6	600	*Rhytidoponera*	*Rhytidoponera purpurea*	47	3.50
SU	SU6	600	*Rhytidoponera*	*Rhytidoponera purpurea*	46	1.10
SU	SU6	600	*Rhytidoponera*	*Rhytidoponera purpurea*	47	2.50
SU	SU6	600	*Rhytidoponera*	*Rhytidoponera purpurea*	46	1.80
SU	SU6	600	*Notostigma*	*Notostigma carazii*	39	10.80

Mt	**Site**	**Elevation**	**Genera**	**Species**	**CTmax (°C)**	**Body mass (mg)**
SU	SU6	600	*Notostigma*	*Notostigma carazii*	38	12.70
SU	SU6	600	*Notostigma*	*Notostigma carazii*	38	16.10
SU	SU6	600	*Leptogenys*	*Leptogenys mjobergi*	43	2.20
SU	SU6	600	*Crematogaster*	*Crematogaster sp. G*	64	0.25
SU	SU6	600	*Crematogaster*	*Crematogaster sp. G*	65	0.18
SU	SU6	600	*Polyrhachis*	*Polyrhachis delecta*	59	2.30
SU	SU6	600	*Crematogaster*	*Crematogaster sp. G*	64	0.20
SU	SU6	600	*Crematogaster*	*Crematogaster sp. G*	64	0.10
SU	SU6	600	*Rhytidoponera*	*Rhytidoponera cf. victoriae*	45	1.70
SU	SU6	600	*Leptogenys*	*Leptogenys mjobergi*	44	1.40
SU	SU6	600	*Myrmecia*	*Myrmecia nigrocincta*	42	8.10
SU	SU6	600	*Anonychomyrma*	*Anonychomyrma gilberti*	64	0.50
SU	SU6	600	*Anonychomyrma*	*Anonychomyrma gilberti*	58	0.60
SU	SU6	600	*Camponotus*	*Camponotus sp. N2 novaehollandiae gp.*	44	0.20

Mt	Site	Elevation	Genera	Species	CTmax (°C)	Body mass (mg)
SU	SU6	600	*Camponotus*	*Camponotus sp. N2 novaehollandiae gp.*	43	0.30
SU	SU8	800	*Rhytidoponera*	*Rhytidoponera cf. victoriae*	40	1.10
SU	SU8	800	*Nylanderia*	*Nylanderia glabrior*	38	0.08
SU	SU8	800	*Nylanderia*	*Nylanderia glabrior*	38	0.08
SU	SU8	800	*Nylanderia*	*Nylanderia glabrior*	38	0.07
SU	SU8	800	*Anonychomyrma*	*Anonychomyrma sp. M*	48	0.08
SU	SU8	800	*Nylanderia*	*Nylanderia glabrior*	38	0.07
SU	SU8	800	*Pheidole*	*Pheidole sp. A2 ampla gp.*	44	0.06
SU	SU8	800	*Pheidole*	*Pheidole sp. A2 ampla gp.*	49	0.05
SU	SU8	800	*Rhytidoponera*	*Rhytidoponera impressa*	43	2.90
SU	SU8	800	*Rhytidoponera*	*Rhytidoponera impressa*	43	3.10
SU	SU8	800	*Rhytidoponera*	*Rhytidoponera impressa*	43	3.70
SU	SU8	800	*Rhytidoponera*	*Rhytidoponera impressa*	43	3.60
SU	SU8	800	*Rhytidoponera*	*Rhytidoponera cf. victoriae*	43	0.80

Mt	Site	Elevation	Genera	Species	CTmax (°C)	Body mass (mg)
SU	SU8	800	*Rhytidoponera*	*Rhytidoponera cf. victoriae*	43	0.80
SU	SU8	800	*Rhytidoponera*	*Rhytidoponera cf. victoriae*	43	0.90
SU	SU8	800	*Rhytidoponera*	*Rhytidoponera cf. victoriae*	43	0.90
SU	SU8	800	*Rhytidoponera*	*Rhytidoponera cf. victoriae*	43	1.10
SU	SU8	800	*Rhytidoponera*	*Rhytidoponera cf. victoriae*	43	0.90
SU	SU8	800	*Polyrhachis*	*Polyrhachis delecta*	55	2.10
SU	SU8	800	*Rhytidoponera*	*Rhytidoponera cf. victoriae*	43	0.70
SU	SU8	800	*Anonychomyrma*	*Anonychomyrma sp. M*	44	0.09
SU	SU8	800	*Anonychomyrma*	*Anonychomyrma sp. M*	48	0.09
SU	SU8	800	*Anonychomyrma*	*Anonychomyrma sp. M*	42	0.10
SU	SU8	800	*Anonychomyrma*	*Anonychomyrma sp. M*	42	0.20
SU	SU8	800	*Technomyrmex*	*Technomyrmex cheesmanae*	51	0.08
SU	SU8	800	*Anonychomyrma*	*Anonychomyrma sp. M*	53	0.06
SU	SU8	800	*Anonychomyrma*	*Anonychomyrma sp. M*	48	0.09

Mt	**Site**	**Elevation**	**Genera**	**Species**	**CTmax (°C)**	**Body mass (mg)**
SU	SU8	800	*Pheidole*	*Pheidole sp. A2 ampla gp.*	49	0.04
SU	SU8	800	*Rhytidoponera*	*Rhytidoponera impressa*	43	3.10
SU	SU8	800	*Rhytidoponera*	*Rhytidoponera purpurea*	43	3.70
SU	SU8	800	*Rhytidoponera*	*Rhytidoponera cf. victoriae*	43	0.90
SU	SU8	800	*Anonychomyrma*	*Anonychomyrma sp. M*	54	0.08
SU	SU8	800	*Technomyrmex*	*Technomyrmex cheesmanae*	44	0.08
SU	SU8	800	*Anonychomyrma*	*Anonychomyrma sp. A cf.gilberti*	43	0.03
SU	SU10	1000	*Technomyrmex*	*Technomyrmex quadricolor*	50	0.03
SU	SU10	1000	*Technomyrmex*	*Technomyrmex quadricolor*	48	0.05
SU	SU10	1000	*Technomyrmex*	*Technomyrmex quadricolor*	51	0.04
SU	SU10	1000	*Technomyrmex*	*Technomyrmex quadricolor*	44	0.05
SU	SU10	1000	*Technomyrmex*	*Technomyrmex quadricolor*	51	0.04
SU	SU10	1000	*Rhytidoponera*	*Rhytidoponera impressa*	43	3.00
SU	SU10	1000	*Rhytidoponera*	*Rhytidoponera cf. victoriae*	43	1.10

Mt	**Site**	**Elevation**	**Genera**	**Species**	**CTmax (°C)**	**Body mass (mg)**
SU	SU10	1000	*Nylanderia*	*Nylanderia glabrior*	46	0.90
SU	SU10	1000	*Anonychomyrma*	*Anonychomyrma sp. M*	44	0.80
SU	SU10	1000	*Anonychomyrma*	*Anonychomyrma sp. M*	47	0.09
SU	SU10	1000	*Anonychomyrma*	*Anonychomyrma sp. M*	47	0.09
SU	SU10	1000	*Anonychomyrma*	*Anonychomyrma sp. M*	50	0.08
SU	SU10	1000	*Anonychomyrma*	*Anonychomyrma sp. M*	50	0.08
SU	SU10	1000	*Nylanderia*	*Nylanderia glabrior*	46	0.09
SU	SU10	1000	*Pheidole*	*Pheidole sp. A2 ampla gp.*	43	0.05
SU	SU10	1000	*Pheidole*	*Pheidole sp. A2 ampla gp.*	44	0.03
SU	SU10	1000	*Pheidole*	*Pheidole sp. A2 ampla gp.*	41	0.03
SU	SU10	1000	*Pheidole*	*Pheidole sp. A2 ampla gp.*	50	0.03
SU	SU10	1000	*Pheidole*	*Pheidole sp. A2 ampla gp.*	43	0.04
SU	SU10	1000	*Pheidole*	*Pheidole sp. A2 ampla gp.*	43	0.04
SU	SU10	1000	*Rhytidoponera*	*Rhytidoponera cf. victoriae*	43	3.10

Mt	**Site**	**Elevation**	**Genera**	**Species**	**CTmax (°C)**	**Body mass (mg)**
SU	SU10	1000	*Technomyrmex*	*Technomyrmex quadricolor*	51	0.07
SU	SU10	1000	*Technomyrmex*	*Technomyrmex cheesmanae*	41	0.04
SU	SU10	1000	*Pheidole*	*Pheidole sp. A2 ampla gp.*	44	0.05
SU	SU10	1000	*Pheidole*	*Pheidole sp. A2 ampla gp.*	41	0.06

Appendix 5. Results from post-hoc Tukey tests comparing mean CTmax among elevational sites, based on pooled data from all the species at each site.

Elevational sites	df	t value	Pr(>|t|)	
350 & 600	96	-0.166	0.998	
350 & 800	95	-2.991	0.017	*
350 & 1000	86	-1.808	0.270	
600 & 800	67	-2.498	0.043	*
600 & 1000	58	-1.499	0.437	
800 & 1000	57	0.794	0.855	

Signif. code: ‘*’ 0.05

Appendix 6. Results from post-hoc Tukey tests comparing variation in mean CTmax within sppecies across elevational sites.

Species	**Elevational sites**	**df**	**t value**	**Pr(>|t|)**	
Anonychomyrma gilberti	350 & 600	11	1.357	0.202	
Anonychomyrma sp.A *cf.gilberti*	350 & 800	10	-0.540	0.601	
Anonychomyrma sp.M	800 & 1000	11	0.155	0.880	
Crematogaster sp.G	350 & 600	8	0.572	0.585	
Leptogenys mjobergi	350 & 600	11	0.424	0.682	
Myrmecia nigrocincta	350 & 600	13	-2.227	**0.046**	*
Pheidole sp.A2 *ampla* gp.	800 & 1000	9	-1.929	0.086	.
Rhytidoponera cf. victoriae	350 & 600	13	-0.310	0.988	
	350 & 800		-4.297	**0.007**	**
	350 & 1000		-2.171	**0.017**	*
	600 & 800		-2.378	**0.037**	*
	600 & 1000		-1.519	**0.047**	*
	800 & 1000		0.340	0.985	
Rhytidoponera impressa	350 & 800	8	-5.175	**0.005**	**
	350 & 1000		-3.273	**0.038**	*
	800 & 1000		0.000	1.000	

Signif. codes: ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Appendix 7. Results of post-hoc Tukey tests comparing on mean body mass across elevational sites**.**

Elevational sites	**df**	**t value**	**Pr(>|t|)**
350 & 600	96	-2.296	0.102
350 & 800	95	-4.551	0.000
350 & 1000	86	-4.738	0.000
600 & 800	67	-1.980	0.044
600 & 1000	58	-2.028	0.021
800 & 1000	57	-0.604	0.9299

Appendix 8. Results of post-hoc Tukey tests comparing mean body mass of each species across elevational sites.

Species	**Elevational sites**	**df**	**t value**	**Pr(>|t|)**	
Anonychomyrma gilberti	350 & 600	11	-0.856	0.410	
Anonychomyrma sp.A *cf.gilberti*	350 & 800	10	-3.143	**0.011**	*
Anonychomyrma sp.M	800 & 1000	11	0.140	0.919	
Crematogaster sp.G	350 & 600	8	0.596	0.570	
Leptogenys mjobergi	350 & 600	11	-0.158	0.878	
Myrmecia nigrocincta	350 & 600	13	-0.647	0.530	*
Pheidole sp.A2 *ampla* gp.	800 & 1000	9	-1.176	0.270	.
Rhytidoponera cf. victoriae	350 & 600	13	0.000	1.000	
	350 & 800		-8.090	**< 0.001**	***
	350 & 1000		-3.503	**0.023**	*
	600 & 800		-5.117	**0.002**	**
	600 & 1000		-2.860	**0.064**	.
	800 & 1000		1.279	0.580	
Rhytidoponera impressa	350 & 800	8	-8.603	**< 0.001**	***
	350 & 1000		-5.783	**0.002**	**
	800 & 1000		-0.361	0.930	

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Appendix 9. Results of linear regressions of CTmax and body mass for each specieswith ≥10 individuals tested.

	Estimate	Std. Error	t value	Pr(>|t|)	
Anonychomyrma gilberti					
(Intercept)	64.514	2.652	24.328	0.000	***
Body mass	-10.886	3.194	-3.408	**0.006**	**
Anonychomyrma sp.A *cf.gilberti*					
(Intercept)	43.035	8.227	5.231	0.000	***
Body mass	13.038	18.242	0.715	0.491	
Anonychomyrma sp.M					
(Intercept)	48.529	1.284	37.801	0.000	***
Body mass	-7.187	5.311	-1.353	0.203	
Crematogaster sp.G					
(Intercept)	60.430	3.690	16.380	0.000	***
Body mass	-18.180	11.440	-1.590	0.151	
Leptogenys mjobergi					
(Intercept)	43.249	1.639	26.390	0.000	***
Body mass	-0.554	0.922	-0.600	0.563	
Myrmecia nigrocincta					
(Intercept)	50.276	3.520	14.283	0.000	***
Body mass	-0.375	0.371	-1.011	0.332	
Pheidole sp.A2 *ampla* gp.					
(Intercept)	47.261	4.185	11.292	0.000	***
Body mass	-60.145	93.168	-0.646	0.535	

	Estimate	Std. Error	t value	Pr(>|t|)	
Rhytidoponera cf. victoriae					
(Intercept)	42.403	0.816	51.972	<2e-16	***
Body mass	0.783	0.578	1.354	0.199	
Rhytidoponera impressa					
(Intercept)	43.266	0.931	46.486	0.000	***
Body mass	0.140	0.127	1.101	0.303	

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘ ’ 1

Appendix 10. Linear mixed effect model of CTmax ratio per mg body mass across elevation, considering the effect of species as random factor.

Scaled residuals:

Min	1Q	Median	3Q	Max
-2.869	-0.298	-0.042	0.146	6.093

Random effects:

Groups	Name	Variance	Std.Dev.
Species	(Intercept)	188835	434.6
Residual	30488	174.6	

Number of obs: 157, groups: Species, 20

Fixed effects:

	Estimate	Std. Error	t value
(Intercept)	123.201	120.571	1.022
Elevation	0.343	0.114	3.016

Correlation of Fixed Effects:

Elevation	-0.574

R2 marginal	R2 conditional	R2 LMER	Adj.R2 LMER
0.031	0.865	0.707	0.707

Appendix 11. Pearson correlation coefficients (bottom left triangle) and P values (top right triangle) of the 17 environmental predictor variables.

	Isothermality	Temperature Seasonality	Mean Temperature of Warmest Quarter	Mean Temperature of Coldest Quarter	Precipitation of Wettest Period	Precipitation Seasonality	Annual Mean Radiation	Annual Mean Moisture Index	Precipitation-Evaporation Ratio	Topographic Wetness Index	Historical Rainforest Shift	Aspect	Slope	Available Water Capacity of Soil	Bulk Density of Soil	Soli Clay Layer	Soil Density
Isothermality		0.000	0.001	0.000	0.407	0.024	0.025	0.051	0.653	0.079	0.000	0.008	0.001	0.645	0.011	0.804	0.259
Temperature Seasonality	0.55		0.000	0.000	0.508	0.309	0.329	0.000	0.817	0.441	0.055	0.147	0.000	0.639	0.004	0.122	0.026
Mean Temperature of Warmest Quarter	-0.05	-0.29		0.000	0.780	0.002	0.032	0.000	0.002	0.014	0.571	0.002	0.809	0.044	0.000	0.000	0.000
Mean Temperature of Coldest Quarter	-0.28	-0.66	0.91		0.947	0.003	0.210	0.000	0.019	0.024	0.688	0.086	0.161	0.174	0.000	0.000	0.000
Precipitation of Wettest Period	0.04	0.06	0.02	-0.01		0.000	0.000	0.000	0.000	0.097	0.000	0.845	0.030	0.357	0.280	0.000	0.000
Precipitation Seasonality	-0.41	-0.08	0.26	0.24	-0.52		0.000	0.000	0.000	0.046	0.000	0.000	0.042	0.132	0.000	0.000	0.000
Annual Mean Radiation	-0.13	0.08	0.18	0.10	-0.60	0.70		0.000	0.000	0.149	0.000	0.000	0.075	0.264	0.001	0.000	0.000
Annual Mean Moisture Index	0.33	0.33	-0.46	-0.51	0.73	-0.87	-0.69		0.000	0.310	0.000	0.016	0.100	0.056	0.000	0.000	0.000
Precipitation-Evaporation Ratio	0.04	-0.02	-0.26	-0.19	0.89	-0.77	-0.73	0.89		0.187	0.000	0.067	0.003	0.035	0.000	0.000	0.000
Topographic Wetness Index	0.12	-0.06	0.20	0.19	0.14	-0.16	-0.12	0.08	0.11		0.019	0.608	0.006	0.000	0.018	0.269	0.011
Historical Rainforest Shift	0.67	0.16	0.05	-0.03	0.35	-0.84	-0.55	0.63	0.48	0.19		0.002	0.444	0.307	0.800	0.000	0.001
Aspect	0.09	-0.12	-0.25	-0.14	-0.02	-0.30	-0.46	0.20	0.15	0.04	0.25		0.153	0.990	0.017	0.000	0.037
Slope	0.13	0.30	0.02	-0.12	-0.18	0.17	0.15	-0.14	-0.24	-0.23	-0.06	-0.12		0.000	0.894	0.000	0.001
Available Water Capacity of Soil	-0.01	-0.04	-0.17	-0.11	0.08	-0.12	0.09	0.16	0.17	0.31	-0.08	0.00	-0.47		0.115	0.000	0.000
Bulk Density of Soil	-0.05	-0.24	0.89	0.80	-0.09	0.32	0.27	-0.51	-0.34	0.19	-0.02	-0.20	0.01	-0.13		0.000	0.000
Soli Clay Layer	0.25	0.13	-0.58	-0.51	0.49	-0.80	-0.59	0.85	0.76	0.09	0.48	0.34	-0.29	0.40	-0.60		0.000
Soil Density	0.15	0.18	-0.70	-0.63	0.43	-0.59	-0.39	0.76	0.66	0.21	0.27	0.17	-0.27	0.49	-0.72	0.83	

Appendix 12. Pearson correlation coefficients (bottom left triangle) and P values (top right triangle) of the nine predictor variables selected by the models.

	TS	**MTWQ.**	**MTCQ.**	**PWP**	**BDW**	**AWC**	**Isothermality**	**LitterDepth**	**Disturbance**
Temperature seasonality - TS		0.002	0.577	0.656	0.256	0.116	0.000	0.009	0.045
Mean Temperature of Warmest Quarter - MTWQ.	-0.26		0.000	0.476	0.859	0.000	0.001	0.000	0.000
Mean Temperature of Coldest Quarter - MTCQ.	-0.05	0.78		0.780	0.002	0.587	0.000	0.001	0.000
Precipitation of Wettest Period - PWP	0.04	0.06	0.02		0.845	0.016	0.023	0.000	0.000
Bulk Density of Soil - BDW	0.09	0.01	-0.25	-0.02		0.099	0.010	0.107	0.370
Available Water Capacity of Soil - AWC	0.13	-0.29	-0.05	-0.20	-0.14		0.644	0.000	0.110
Isothermality	0.55	0.04	-0.28	0.04	-0.05	-0.01		0.000	0.000
LitterDepth	-0.22	-0.34	-0.28	-0.43	-0.13	0.34	0.74		0.000
Disturbance	0.17	0.31	0.52	0.54	-0.07	-0.13	-0.69	-0.58	