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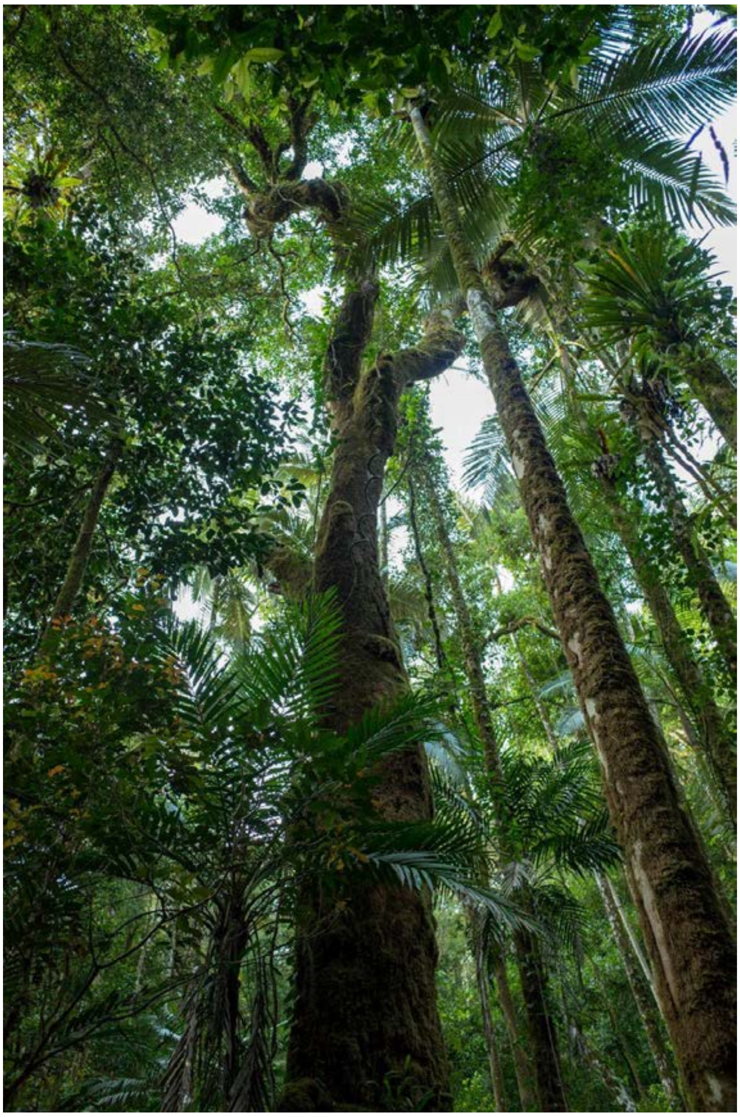
Climatic variability and the vulnerability of rainforest biota to a warming world



"The only lasting truth is change…."
Octavia Butler, Parable of the Sower, 1993

Thesis submitted by
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Cover photo: Tannar Coolhaus, montane rainforest, Mt. Lewis, Australian Wet Tropics.

***Myrmecia mjobergi* – Mt. Lewis National Park.** Photo: Rishab Pillai

Publications Associated with this Thesis

Chapter 2

Leahy, L., Scheffers, B. R., Williams, S. E., and Andersen, A. N. 2020. Diversity and distribution of the dominant ant genus *Anonychomyrma* (Hymenoptera: Formicidae) in the Australian Wet Tropics. Diversity **12**:474.

Chapter 3

Leahy, L., Scheffers, B. R., Andersen, A. N., Hirsch, B. T., and Williams, S. E. 2021. Vertical niche and elevation range size in tropical ants: Implications for climate resilience. *Diversity and Distributions* **27**:485-496.

Chapter 5

Leahy, L., Scheffers, B. R., Williams, S. E., Andersen, A. N. (Accepted) Arboreality drives heat tolerance while elevation drives cold tolerance in tropical rainforest ants. *Ecology*.

Statement of the Contribution of Others

My advisory panel Stephen Williams, Alan Andersen, Brett Scheffers, and Ben Hirsch, provided advice and supervision in various aspects of the thesis. Steve Williams, Alan Andersen, and Brett Scheffers are co-authors of the published articles that constitute chapters two, three, and five, and contributed to the development of all chapters. Ben Hirsch is a co-author on the published article of chapter three.

Brett Scheffers contributed to the collection of data used in chapters two, three, and four. During a post-doctoral position with Stephen Williams, Brett devleoped a survey protocol to survey rainforest ants along the arboreal gradient from ground to canopy. He collected data at multiple trees at elevation sites along the Finnegan, Windsor, and Carbine subregions. I continued this fieldwork using the same survey protocol.

Alan Andersen taught me ant pinning and identification and identified ant samples to morphospecies. Alan also funded and facilitated the CO1 barcoding of *Anonychomyrma* specimens for chapter two.

As my primary supervisor, Steve oversaw the general development and direction of the thesis. Steve, Alan, and Brett contributed to the development of my chapters and provided detailed edits and comments on all drafts. They also provided statistical advice at various points. In addition, Somayeh Nowrouzi (CSIRO) contributed to the thesis by providing data on *Anonychomyrma* distributions for Chapter Two.

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Thesis Abstract

Climatic variability occurs on the scale of millimetres to kilometres and from minutes to millennia. These multiple spatial and temporal scales interact with the traits and geographies of organisms to shape how species respond to climatic change. Currently, the global climate is changing at a faster pace than at any point in the preceding 65 million years. Predicting how species and communities will respond to climate change is an urgent task. This requires a predictive understanding of how biota respond to climatic variability at multiple spatial and temporal scales. This dissertation seeks to advance our knowledge of how climatic variability influences biogeography and climate change vulnerability. I explore this topic using the study system of rainforest ants with a specific focus on vertical (arboreal) and elevational gradients in the Australian Wet Tropics Bioregion.

Climate change vulnerability is the product of a species' climatic sensitivity and exposure. Vulnerability is mediated by response capacity and together these factors drive extinction probability. In this thesis I apply a multiscale climatic framework that takes the assessment of climate change vulnerability in novel directions. This framework posits microscale climatic gradients of vertical tree structure and the transition from day to night as nested and interactive with broader scale climatic gradients of elevation and region. The broad aim was to better predict the responses of species and communities to climate change with an informed understanding of how multiple spatio-temporal climate gradients interact to shape vulnerability.

The two main thesis objectives were: 1) investigate the relationship between vertical climate gradients, ant species' distributions, and community composition, along elevation sites and between subregions of the Australian Wet Tropics, and 2) investigate the physiology and behaviour of ants along microscale (vertical and day-night) and mesoscale (elevation) climate gradients.

I collected and identified ants using vertical survey transects (ground to canopy) along elevation gradients at multiple mountain subregions in the Australian Wet Tropics. Field data was complimented by thermal physiology experiments and the extensive collection of microclimate data. I conducted day and night-time vertical transects at a subset of elevation sites. Through a variety of analytical approaches, I quantified the relationships between climatic gradients and species' distributions (chapters two and three), community composition (chapter four), thermal traits (chapter five), and degree of behavioural or ecological plasticity (chapter six).

I found that lowland canopy species are tolerant of high temperatures (and not thermally sensitive) but are still relatively vulnerable because their upper thermal limits are close to current maximum temperatures. This vulnerability can be offset, however, by behavioural flexibility at the local scale or broad elevation distribution at the regional scale. Ants with the ability to forage further down trees and into the cooler parts of the night have behavioural options to avoid extreme temperatures, while diurnal canopy specialists in the lowlands are most at risk. Vertical habitat use was also associated with the rate of species turnover across elevation. Consistent with theory, ground species that experience low thermal variation have higher rates of species turnover with elevation than arboreal species (that experience high thermal variability). This establishes different starting points for shifting range distributions under climate change. Ground species are more likely to be elevationally restricted and to find it difficult to track their current climates.

These findings have important conservation implications, given that lowland tropical canopies are global hotspots of biodiversity. I strongly suggest that arboreality is an important trait for determining climatic sensitivity and exposure and should be considered in conservation assessments of species' vulnerability to climate change.

My thesis provides a multiscale climatic framework that will improve the assessment of climate change vulnerability in tropical forests. This will be highly applicable in other systems where vertically layered habitat creates microscale climate gradients from kelp forests to coral reefs, and caves to lakes.

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Figure 7.1. Schematic of the links between microscale climate variability, vulnerability, and potential population, species, and community responses to climate change. At the microscale of a tree, vertical (ground to canopy) and temporal (day to night) climatic gradients set up a four-dimensional climatic landscape, along which populations have different (a) thermal sensitivity, (b) exposure, and (c) degree of niche breadth or plasticity. From my findings I predict niche shifts along these gradients at the local scale (d). The climatic variability along the vertical gradient sets up different levels of thermal overlap across elevation (e), and vertical niche breadth is positively associated with elevation range size (f). This will result in different pressures to execute range shifts (g), I predict arboreal species, and species with greater ecological plasticity to exhibit slower range shifts. The underlying degree of thermal overlap across elevation is positively correlated to rates of species turnover, such that arboreal species have higher turnover than ground species (h). The different paces of range shifts as well as the underlying differences in community composition will create different possibilities for novel communities (i). Concepts (a-c), (f), and (h) are matched to results presented in the thesis chapters in Table 1. Concept (e) is directly demonstrated in Scheffers et al. 2017, and Scheffers and Williams 2018. Climate change responses (d), (g), and (i) are predictions based off the findings of the thesis chapters.

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Location of Online Data Associated with this Thesis

Chapter Two – Data available on request from Research Data JCU.

Chapter Three – Leahy, L., Scheffers, B. R., Andersen, A. N., Hirsch, B. T., & Williams, S. E. (2021) Vertical niche and elevation range size in tropical ants: Implications for climate resilience. Diversity and Distributions, **27**, 485-496.

Data for ant collections and microclimate are provided on the Dryad Repository: https://doi.org/10.5061/dryad.9ghx3ffg3

Chapter Four – Data for ant collections as above on Dryad Repository: https://doi.org/10.5061/dryad.9ghx3ffg3

Chapter Five – Leahy, L., Scheffers, B. R., Williams, S. E., Andersen, A. N. (Accepted) Arboreality drives heat tolerance while elevation drives cold tolerance in tropical rainforest ants. Ecology.

Data for thermal tolerance traits are provided on the Dryad Repository: https://doi.org/10.5061/dryad.zpc866t8t

Chapter Six – Data available on request from Research Data JCU.

Chapter One - Introduction

Climate fundamentally shapes biology. Climatic variability occurs on the scale of millimetres to kilometres and from minutes to millennia. These multiple spatial and temporal scales interact with the traits and distributions of organisms to shape how species respond to climatic change. This dissertation seeks to advance our knowledge of how climatic variability influences vulnerability to anthropogenic climate change. I explore this topic using the study system of rainforest ants along spatial and temporal climatic gradients with a specific focus on vertical (arboreal) and elevational gradients in the Australian Wet Tropics Bioregion. This chapter presents the context and theoretical background of the thesis, outlines the structure of the chapters, and establishes a multiscale framework that is applied throughout the research.

Predicting climate change vulnerability

The climate is currently changing faster than at any point in the last 65 million years (Diffenbaugh and Field 2013). This is altering life on earth, from genes to entire ecosystems (Scheffers et al. 2016). The most recent research predicts that up to one third of plant and animal species could suffer extinction by 2070, with extinction risk 2–4 times higher in the tropics (Román-Palacios and Wiens 2020). Forecasting how species will respond to climate change, and where to prioritise management actions, is one of the greatest challenges that ecologists and conservation biologists will face this century (Root and Schneider 2006, Williams et al. 2020). To appropriately manage this threat, we need to understand how climatic variability shapes vulnerability and extinction risk of species (Williams et al. 2008, Williams et al. 2020).

To frame how climatic variability influences vulnerability, we need to look both to the past and to the future (Moritz and Agudo 2013, Nadeau et al. 2017a). Climate change vulnerability is determined by exposure and sensitivity to climate, resilience to extreme climatic events, and ability to adapt to change (Williams et al. 2008, Huey et al. 2012). Historic climatic variability determines a species' intrinsic sensitivity by influencing genetic diversity, propensity for phenotypic plasticity, physiological tolerances, and current geographic distributions (Kingsolver and Huey 1998, Graham et al. 2006, Davison and Chiba 2008, Moussalli et al. 2009, Rodríguez-Trelles et al. 2013, Huang et al. 2015, Otero et al. 2015). These intrinsic factors determine resilience and the capacity to respond to climate change via genetic adaptions or ecological mechanisms (Chown et al. 2010, Moritz and Agudo 2013, McCain and King 2014). Current and future climatic variability determines extrinsic exposure and dictates when and where species will feel the effects of rising global temperatures. Exposure will be strongly influenced by geographic distribution, habitat specialisation, behaviour, and ecology. This leaves species with several options to avoid extinction: move (shift geographic distributions), buffer (mitigate exposure *in situ* through existing behavioural, ecological, or phenotypic plasticity), or adapt (through genetic (physiological) adaptation or via ecological/behavioural niche shifts)(Moritz and Agudo 2013).

Framing vulnerability in these terms allows a system of grouping species into categorical groups which move beyond simple taxonomic lines (McGill et al. 2006). For example, groups of multiple taxa can be classed as thermal specialists or thermal generalists based on measurable physiological traits (i.e., thermal performance curves; (Huey et al. 2012, Sinclair et al. 2016)). Taking a community or multiple-species approach rather than focusing on a single population or species allows generalisation and the identification of patterns and processes that underlie climatic responses (Fitzpatrick et al. 2011, Sunday et al. 2012, Anderson et al. 2013, Sunday et al. 2014, Gibb et al. 2015, Roeder et al. 2021, Williams and de la Fuente 2021). Such groupings also allow conservation managers to streamline vulnerability assessments and effectively concentrate resources (Williams et al. 2020).

The concept of the niche is central to understanding how climate relates to species distributions and ecology. The fundamental niche can be conceptualised as a multidimensional space whose axes collectively capture the limits of the environmental conditions that allow a population to persist at a location or habitat (Hutchinson 1957, Kearney and Porter 2004). The actual niche space that can be occupied by a species is limited by biotic factors such as competition and barriers to dispersal (e.g., configuration of land masses), such that species are found only in a subset of the fundamental niche space known as the realised niche (Soberon and Arroyo-Pena 2017). Ascertaining the climatic constraints to the fundamental niche (i.e., thermal limits) facilitates predictions of species potential geographic ranges and whether increasing temperatures will push environmental conditions outside of a species niche (Thuiller et al. 2005, Kearney and Porter 2009, VanDerWal et al. 2009, Saupe et al. 2015, Qiao et al. 2016).

Climatic gradients

Climatic gradients provide ideal “ecological theatres” to study how climatic variability influences species distributions and traits (sensu Hutchinson 1965). The latitudinal climate gradient from temperate zones to the tropics correlates strongly with the observed gradient in global species diversity (Stevens 1992, Blackburn and Gaston 1996, Mittelbach et al. 2007), although the exact mechanisms underlying these patterns remain somewhat controversial (Gaston 2000, Hillebrand 2004). Elevation provides another strong climate gradient representing a steep shift in abiotic and biotic factors within a geographical location, driving patterns of diversity and community structure (McCain 2009, Williams et al. 2010a, Sanders and Rahbek 2012, Beck et al. 2017, Longino and Branstetter 2019). Elevational gradients are useful systems to identify underlying causes of diversity and trait patterns in relation to climate. Each mountain range represents a replicate gradient, which facilitates the testing of potential mechanisms and provides generality to patterns.

Tropical species tend to have narrow elevational and geographic ranges compared to temperate species; this was observed by Janzen (1967) in relation to elevation range sizes and referred to by Stevens (1989) as Rapoport's rule in relation to the pattern of increasing latitudinal range size towards higher latitudes. In both cases it was proposed that temperate species are adapted to highly seasonal environments, are therefore more tolerant of variation, and thereby achieve broader spatial distributions compared to tropical species that experience low seasonality environments. Many criticisms of the statistical approaches taken to test these patterns by Stevens (1989) and other researchers (Pagel et al. 1991, Rohde et al. 1993) ensued, in addition to much debate concerning the underlying mechanisms of these patterns (Colwell and Hurtt 1994, Gaston et al. 1998). The concept was generalised to be termed the 'climate variability hypothesis' and has received theoretical and empirical support with the main mechanism proposed as follows: species that live in climatically variable environments need to tolerate a broader range of climates (usually regarding temperature tolerance). Correspondingly, these species have larger fundamental niches and consequently can persist over a wider range of environments, thereby achieving broader geographical ranges (Addo-Bediako et al. 2000, Pintor et al. 2015, Gutierrez-Pesquera et al. 2016, Sheldon et al. 2018).

The climate variability hypothesis is intuitive and appealing because it links together climatic exposure, thermal physiology, and dispersal capacity to form a mechanistic basis for explaining patterns of species distributions and community organisation across space and time. In the 21st century this hypothesis also forms a conceptual framework for why tropical species are predicted to be more vulnerable to anthropogenic climate change: climatic stability selects for narrow thermal tolerance range and small range size, both of which will increase sensitivity to climate change (Deutsch et al. 2008, Huey et al. 2009, Wright et al. 2009, Corlett 2011, Sunday et al. 2011, Diamond et al. 2012, Huey et al. 2012). This leads to the key prediction that tropical species are likely to be more vulnerable to climate change than temperate species, and there is mounting evidence that this prediction has proven to be correct (Sinervo et al. 2010, Román-Palacios and Wiens 2020, Williams and de la Fuente 2021).

A focus on large-scale climatic gradients of latitude and elevation has been extremely important for understanding global patterns of biogeography and vulnerability. The next critical step in climate change biology is to move beyond broad generalisations such as tropical versus temperate to focus on finer-resolution models that account for the substantial climatic variation that occurs at local and microclimate scales (Suggitt et al. 2011, Logan et al. 2013, Bennie et al. 2014, Storlie et al. 2014, Pincebourde et al. 2016, Maclean et al. 2017, Nadeau et al. 2017b).

Microclimate

In the last two decades, there has been a renaissance of microclimate research, spurred on by the race to improve the science of forecasting climate change impacts. This is largely due to a unification of thermal physiology and macroecology (Gaston et al. 2009), resulting in a shift in research focus from broad climate gradients to the perspective of how an organism experiences the thermal landscape of their natural environment (Huey 1991, Angilletta 2009). It is at this local scale that the thermal environment is imposing selective pressure on an organism and is thus the arena in which natural selection is occurring (Angilletta 2009). There is accumulating evidence that populations adapt their thermal physiology to microclimatic conditions (Kaspari et al. 2015, Montejo-Kovacevich et al. 2020), and this could explain some of the discrepancies between the correlation of thermal traits and environmental gradients at global scales.

Mapping climate to the scales that are relevant to the organisms under investigation is vital to predicting the impacts of climate change (Storlie et al. 2014, Maclean et al. 2017). Microclimate often diverges from regional climate due to a number of factors including vertical layering, vegetation structure, and topography (Bonebrake and Deutsch 2012, Scheffers et al. 2014). This means that maximum temperatures and temperature variation at a local site can be substantially higher or lower than the climate measurements recorded by a regional weather station (Suggitt et al. 2011). In oceans, deep waters are cold and show little variation (2–3 °C), whereas at the same location, temperature of surface waters can vary by as much as 6 °C over 24h (Pacanowski and Philander 1981). In an intertidal zone along the west coast of North America, within-site temperature variation over a few hundred metres was equivalent to the variation in mean temperature between-sites separated by 14° in latitude (Denny et al. 2011). On an even smaller scale, the surface temperature of a single leaf can vary as much as 4–7 °C (Caillon et al. 2014). Incorporating what is happening at the local scale and how that influences processes and patterns at regional and global scales will provide a much more nuanced understanding of how climatic variation influences biology and climate change responses.

Scaling back down to the perspective of an organism in their immediate thermal landscape also allows an assessment of the role of behaviour and ecological plasticity in mitigating climate exposure. This is particularly critical because range shifts are not going to be possible for all taxa, particularly where habitat loss and fragmentation present additional barriers to dispersal (Northrup et al. 2019), and the rapid pace of climate change will preclude genetic adaptation for many species with longer generation times (Kelly et al. 2012, Kellermann and van Heerwaarden 2019). Many species may need to rely on within-site thermal heterogeneity to mitigate exposure, either moving to thermally buffered microhabitats or by shifting activity to cooler hours of the day (Scheffers et al. 2013, Levy et al. 2019).

Vertical climate gradients

Vertical climate gradients are a key example of local scale climatic variation formed through the vertical layering of habitat structure in the environment. The upper parts of vertical climate gradients are exposed to atmospheric conditions and solar radiation and are therefore generally hotter and more variable, while the lower parts are buffered and are therefore cooler and more climatically stable. Examples of this phenomenon can be found in lake systems, intertidal rock shelves, oceans, caves, the vertical profile of soil, and trees (Hays et al. 2009, Krab et al. 2010, Scheffers et al. 2014, Alahuhta et al. 2017, Kennedy et al. 2017, Stickle et al. 2017, De Frenne et al. 2019, Mammola et al. 2019).

Forest trees provide the most ubiquitous vertical climate gradients in terrestrial systems (De Frenne et al. 2019). The change in climate along a tree can be far steeper than across elevation and latitude: the difference in temperature from the ground to the canopy (approximately four degrees), is equivalent to hundreds of meters in elevation, and hundreds of kilometers of latitude (Scheffers et al. 2013). Thus, arboreal gradients provide an excellent system to study the influence of climatic variation at the local scale and how that interacts with mesoscale and macroscale climatic gradients. Together these climatic gradients determine sensitivity and exposure of organisms to climate change.

Arboreality – the organisation of species along the arboreal gradient – has been proposed as a third biogeographic dimension that can influence patterns of species distribution and community assembly over broader scales (Scheffers et al. 2013). Given the strong gradient in climatic variability, vertical gradients of trees should recapitulate the thermal variation patterns predicted by the climate variability hypothesis (or Janzen's seasonality hypothesis). Arboreal species should be exposed to greater thermal variation, have broader thermal tolerance ranges (i.e., be less thermally sensitive), and therefore obtain broader elevation and geographic range sizes than ground species which are restricted to a stable thermal environment (Scheffers and Williams 2018, Klinges and Scheffers 2021). This should also influence community patterns of turnover across elevation gradients (Fagan et al. 2006, Jankowski et al. 2009). These theoretical predictions have not been tested with empirical data. Such patterns, however, would greatly influence climate change vulnerability through the synergistic impacts on thermal physiology (sensitivity), exposure, and range size.

Diurnal cycles as climatic gradients

Temporal climatic gradients are critical piece of the puzzle when it comes to predicting exposure and response to a changing climate. For an organism, the most predictable form of thermal heterogeneity is the cycle of environmental temperatures between day and night (Aronson et al. 1993). Typical daily activity patterns include, nocturnal (active at night), diurnal (active in the day), cathemeral (active in both day and night), and crepuscular (active during dawn and twilight). Within these active time periods, species may also behaviourally thermoregulate to maintain optimum temperatures (Carroll et al. 2015). Thus temporal activity patterns allow species to anticipate daily temperature fluctuations and concentrate activity into set time periods, preventing exposure to unfavourable temperatures, and reducing the need for costly thermoregulation (Kronfeld-Schor and Dayan 2003).

At the local scale, spatial and temporal thermal gradients interact with each other to create localised thermal environments. For example, spatial microclimatic variation created by sun and shade exposure is a key feature of diurnal environments, but at night this spatial microclimatic variation disappears, and thermal microclimates become more homogenised

(Freiberg 1997). Together small scale spatial and short-term temporal climate gradients set up a multidimensional thermal landscape within which species operate (Bonebrake and Deutsch 2012, Huey et al. 2012). Quantifying the localised thermal landscape in which an organism operates, allows a determination of its exposure and ability to mitigate climate change impacts through behaviour and ecological plasticity.

Study system

The overarching aim of this thesis was to develop a comprehensive understanding of how climatic variability at different scales influences sensitivity and exposure to climate. Meeting this aim will contribute to more general predictions of climate change vulnerability and help identify the potential responses we might expect from species and communities under climate change.

I develop a multiscale framework that posits spatial and temporal climatic scales at macro, meso, and microscales as nested and interactive. For example, arboreal gradients are nested in their position along mountain ranges, which are nested in their latitudinal position on the globe. Temporal climatic variability at different scales underpins each of these spatial scales. Where and when a population is located in this multi-dimensional space determines sensitivity and exposure to climatic variation. I apply this multiscale framework to explore the distribution, community composition, physiology, and behaviour of rainforest ants across spatio-temporal climatic gradients in the Australian Wet Tropics Bioregion.

I narrow the scope of my thesis to specifically investigate the microscale of arboreal gradients formed by rainforest trees and the mesoscale of elevation gradients formed by mountain ranges. These two scales (arboreal and elevation) underly every chapter. In two chapters (chapters two and four) I incorporate the macroscale of regional differences between mountain chains (subregions) of the Australian Wet Tropics. In the final data chapter (chapter six) I add the microscale temporal component of the transition from day to night and look at how that interacts with spatial climatic gradients.

Australian Wet Tropics

The Australian Wet Tropics of north-eastern Queensland is a mountainous region supporting the last large and intact remnant of Australia's tropical rainforests. The region is comprised of a set of mountain ranges running from north to south along the east coast referred to in the literature as distinct subregions (Williams and Pearson 1997, Williams et al. 2010b). The Australian Wet Tropics was listed as a protected World Heritage Area in 1988 for its exceptional biodiversity values based on high rates of endemism, evolutionary significance, and phylogenetic distinctiveness (Williams et al. 2016). It has been described as the second most irreplaceable World Heritage Area in the world (Bertzky et al. 2013).

The current distributional patterns of biodiversity of the Australian Wet Tropics can be largely attributed to historic processes that occurred during climate fluctuations of the late Quaternary (last ~18 Kya) when rainforests contracted and expanded several times (Hopkins et al. 1993, Kershaw 1994, Williams and Pearson 1997, Hugall et al. 2002). As rainforests contracted to wetter uplands, many lowland species became locally extinct (Williams and Pearson 1997). As a result, many vertebrate and invertebrate species that are endemic to the AWT are restricted to elevations above 300 m a.s.l. that have had historically stable climates and consistently supported rainforest throughout this period of high climatic fluctuations (Winter 1997, Yeates et al. 2002, Graham et al. 2006, Williams et al. 2010b, Staunton et al. 2014, Moreau et al. 2015, Ashton et al. 2016, Nowrouzi et al. 2016).

Much like other tropical montane systems around the world, the Australian Wet Tropics is highly vulnerable to climate change (Urban 2018). Recent evidence of dramatic range shifts and declines of bird species in the Australian Wet Tropics (Williams and de la Fuente 2021) have proven accurate the predictions made nearly 20 years ago that climate change would have a catastrophic impacts on the biodiversity of the region (Williams et al. 2003). Upland-specialised species of birds and regional endemics have undergone population declines of 50% between 2000 – 2016 (Williams and de la Fuente 2021). The Australian Wet Tropics therefore provides a unique opportunity to study climate change because we can observe how historic climate fluctuations have shaped biogeographic patterns of today at the same time as contemporary climate warming is already eliciting population responses of the most sensitive and vulnerable species.

Ants

Ants are ideal organisms to investigate the interaction of climatic gradients on traits and biogeography (Dunn et al. 2009, Diamond et al. 2012, Longino et al. 2014, Gibb et al. 2015, Economo et al. 2018, Gibb et al. 2019). Ants are widely distributed across arboreal, elevational, and temporal gradients, and are highly responsive to temperature and moisture (Andersen 1983, Cerdá et al. 1998, Yanoviak and Kaspari 2000, Sanders et al. 2007, Hashimoto et al. 2010, Andrew et al. 2013, Bujan et al. 2016, Bishop et al. 2017, Houadria and Menzel 2020). Arthropods, in general, make up ~46% of Earth’s animal biomass (Bar-On et al. 2018) constituting some 5–10 million species (Ødegaard 2000). Recognised ant species number approximately 15 000 but there are a large number of undescribed species. There have been recent documented declines in abundance and species richness of arthropods connected to climate warming (Resasco et al. 2014, Diamond et al. 2016, Fitzgerald et al. 2021). This is of concern as many arthropods, including ants (Evans et al. 2011, Del Toro et al. 2015) play critical roles in ecosystem function (Seastedt and Crossley Jr 1984, Yang and Gratton 2014, Griffiths et al. 2018).

In the Australian Wet Tropics, previous research found strong community patterns of ants across elevational and regional climatic gradients, with high rates of species turnover, and distinct fauna between each mountain subregion (Burwell and Nakamura 2015, Nowrouzi et al. 2016). Modelling from Nowrouzi et al. (2019) indicated that up to 90% of ant species in the Australian Wet Tropics may lose half of their suitable habitat under the direct (climate) and indirect (changes in rainforest habitat) effects of climate change. However, we need more information on each aspect that will determine climate change vulnerability (Williams et al. 2008). For example, we do not know how ant distributions, physiology, and behaviour will interact with local (e.g., arboreal) and larger scale (e.g., elevation) climate gradients to shape sensitivity and exposure. Further, we have insufficient microclimate data at a relevant scale suitable to small ectotherms such as ants (Storlie et al. 2014).

Therefore, utilising ants in the Australian Wet Tropics Bioregion as a study system for this thesis meets two goals. Firstly, this is a model system for understanding how climatic variability along spatial and temporal climate gradients influences sensitivity and exposure, allowing general findings to be extended to other ecosystems which support localised climatic (particularly vertical) gradients. Secondly, it further investigates climate change vulnerability specifically for ant communities in a topographically complex rainforest environment. This allows specific predictions to be made for ants in the Australian Wet Tropics and advances our understanding of how tropical rainforest invertebrates may respond to climate change more broadly.

Thesis objectives and structure

There were two specific objectives of the thesis:

Objective 1: Investigate the relationship between vertical climate gradients, ant species' distributions, and community composition, along elevation sites and between subregions of the Australian Wet Tropics

Objective 2: Determine how the physiology and behaviour of ants along microscale (vertical and day-night) and mesoscale (elevation) climate gradients influences sensitivity and exposure and predicts response capacity to climate change.

With this information, I can make informed predictions of potential climate change responses of ant species and communities in the Australian Wet Tropics at both local scales (*in situ*) and regional scales (e.g., distribution shifts). The thesis is structured as five data chapters in the format of a series of scientific publications. Objective one is met by chapters two, three, and four. Objective two is met by chapters five and six.

Chapter Two – "Diversity and distribution of the dominant ant genus *Anonychomryma* (Hymenoptera: Formicidae) in the Australian Wet Tropics" (published)

The ant genus *Anonychomyrma*, is a largely undescribed group of dominant arboreal ants in the Australian Wet Tropics. This chapter is an overview of the diversity and distribution of the genus *Anonychomyrma* using a genetic (CO1 barcoding) and morphological approach to delimit species' identities which are then used throughout the subsequent chapters.

Chapter Three – "Vertical niche and elevation range size in tropical ants: implications for climate resilience" (published)

This chapter explores the correlation between the vertical distribution of rainforest ants at the microscale of trees, exposure to temperature variance, and elevation range size. The chapter draws on the niche breadth – range size hypothesis and the climate variability hypothesis as underlying theories for explaining patterns of elevation range size in relation to ant species' vertical niche breadth.

Chapter Four – "Community turnover of ants in the rainforests of the Australian Wet Tropics: elevation and arboreality"

This chapter investigates community composition at three spatial scales of vertical, elevation, and subregions (between mountain ranges). I test Janzen's (climate variability) hypothesis at the microscale. I predict that ground communities, that are accustomed to a stable microclimate, should have higher rates of species turnover over elevation compared to arboreal communities that experience a variable microclimate.

Chapter Five – "Arboreality drives heat tolerance while elevation drives cold tolerance in rainforest ants" (accepted for publication)

This chapter explores how microscale (vertical habitat – referred to as microgeographic) and mesoscale (elevation – referred to as mesogeographic) climatic gradients interact to shape the thermal tolerance traits of rainforest ants and their sensitivity to climate change.

Chapter Six – "The nightshift lowdown: ants take the heat out of tropical rainforest"

This chapter investigates the role of behaviour patterns in mitigating exposure to climate change along the elevation gradient by characterising the foraging activity of ants within the thermal landscape of their local site.

Chapter Seven – "Synthesis and future directions"

I synthesise the findings of the thesis and present a schematic summary figure that draws on key findings from the thesis chapters to outline 1) the relationship between microscale climate gradients (vertical and temporal) and rainforest ants’ sensitivity, exposure, and ecological/behavioural plasticity, 2) how this relationship scales up to influence thermal exposure and species’ distributions over elevation, 3) how this relates to community patterns over elevation, and 4) how each of these (1–3) is linked to a potential climate change response at the population, species, and community level. I then place these findings into the broader context of global climate change and suggest future research directions.

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Chapter Two - Diversity and distribution of the dominant ant genus *Anonychomryma* (Hymenoptera: Formicidae) in the Australian Wet Tropics

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Abstract

Anonychomryma is a dolichoderine ant genus of cool-temperate Gondwanan origin with a current distribution that extends from southern Australia north into the Australasian tropics. Despite its abundance and ecological dominance, little is known of its species diversity and distribution throughout its range. Here, we describe the diversity and distribution of *Anonychomyrma* in the Australian Wet Tropics Bioregion, where only two of the many putative species are described. We hypothesise that the genus in tropical Australia retains a preference for cool wet rainforests reminiscent of the Gondwanan forests that once dominated Australia but now only exist in upland habitats of the Wet Tropics. Our study is based on extensive recent surveys across five subregions and along elevation and vertical (arboreal) gradients. We integrate genetic (CO1) data with morphology to recognise 22 species among our samples, 20 of which appear to be undescribed. As predicted, diversity and endemism were concentrated in uplands above 900 m a.s.l. Distribution modelling of the eight commonest species identified maximum temperature of the warmest month, rainfall seasonality, and rainfall of the wettest month as correlates of distributional patterns across subregions. Our study supports the notion that *Anonychomyrma* has radiated from a southern temperate origin into the tropical zone, with a preference for areas of montane rainforest that have been stably cool and wet over the late Quaternary.

Introduction

The ubiquity, high species richness, and ecological dominance of ants makes them model organisms for understanding spatial patterns of diversity and community assembly (Hölldobler and Wilson 1990). Ant distribution is tightly coupled to climate (Dunn et al. 2009), so that an understanding of ant species distributions across climatic gradients provides clues as to how ectothermic species coped with climatic conditions in the past and provides important insights into how they are likely to respond to a future climate.

Anonychomryma Donisthorpe 1947, is an ecologically dominant ant genus in relatively cool and mesic habitats of Australia and New Guinea, extending north-west into South-East Asia and east to the Solomon Islands (Shattuck 1992). The genus contains 27 described species and a further five subspecies, with most of these from New Guinea (AntWeb 2020, Plowman et al. 2020). The genus is member of an Australian dolichoderine subgroup that is thought to be of Gondwanan origin and that most likely originated in Australia approximately 30 million years ago from an ancestor shared with southern South America through a land connection via Antarctica (Ward et al. 2010). *Anonychomyrma* is particularly common in heathlands, woodlands and open forests of temperate southern Australia ((Fox and Fox 1982, Andersen 1986); in both referenced articles the genus is referred to as the *nitidiceps* group of *Iridomyrmex*) and in rainforest of subtropical and tropical mountains of Queensland and New Guinea (Blüthgen and Stork 2007, Nowrouzi et al. 2016, Plowman et al. 2020). Most species in drier habitats nest in the ground, whereas rainforest species appear to be primarily arboreal.

The Australian Wet Tropics (AWT) Bioregion of north-eastern Australia represents the largest remaining remnant of the Gondwanan mesothermal rainforests that once dominated Australia (Schneider and Moritz 1999). Two species of *Anonychomyrma* have been described from the region. One of these is *A. gilberti* (Forel) (Figure 2.1), a widely distributed species in the region where it is a dominant ant in the rainforest canopy (Blüthgen et al. 2004, Blüthgen and Stork 2007). The second species is *A. malandana* (Forel), which was described from Malanda on the Atherton Tablelands in 1915. Since its original description, we are aware of only one other publication documenting it, where it was commonly recorded on Mt. Windsor (Figure 2.2) and referred to as *Anonychomyrma* sp. D (Nowrouzi et al. 2016). Despite just two described species, the AWT *Anonychomyrma* fauna is highly diverse, with Nowrouzi et al. (2016) reporting 15 species during ant surveys of just four of the thirteen upland subregions.

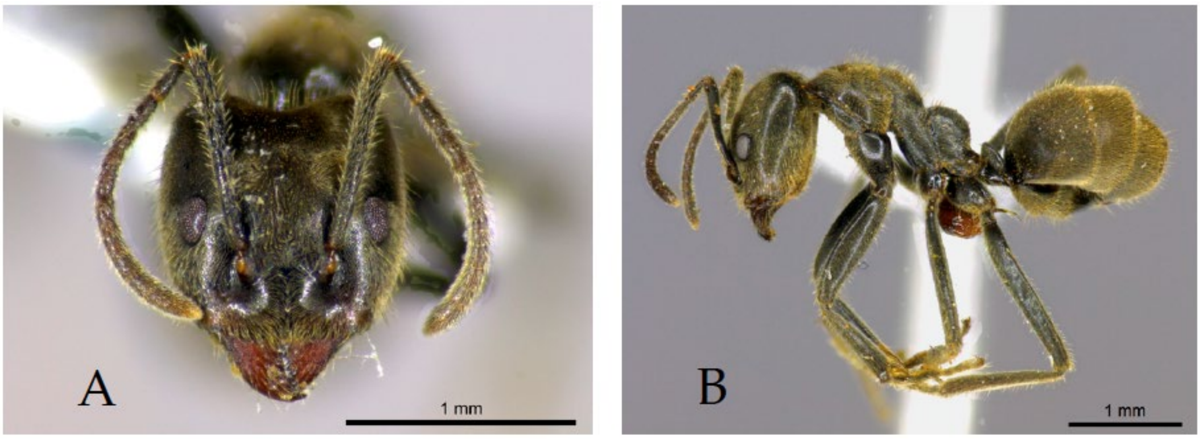


Figure 2.1. *Anonychomyrma gilberti*, showing head (A) and lateral (B) views.

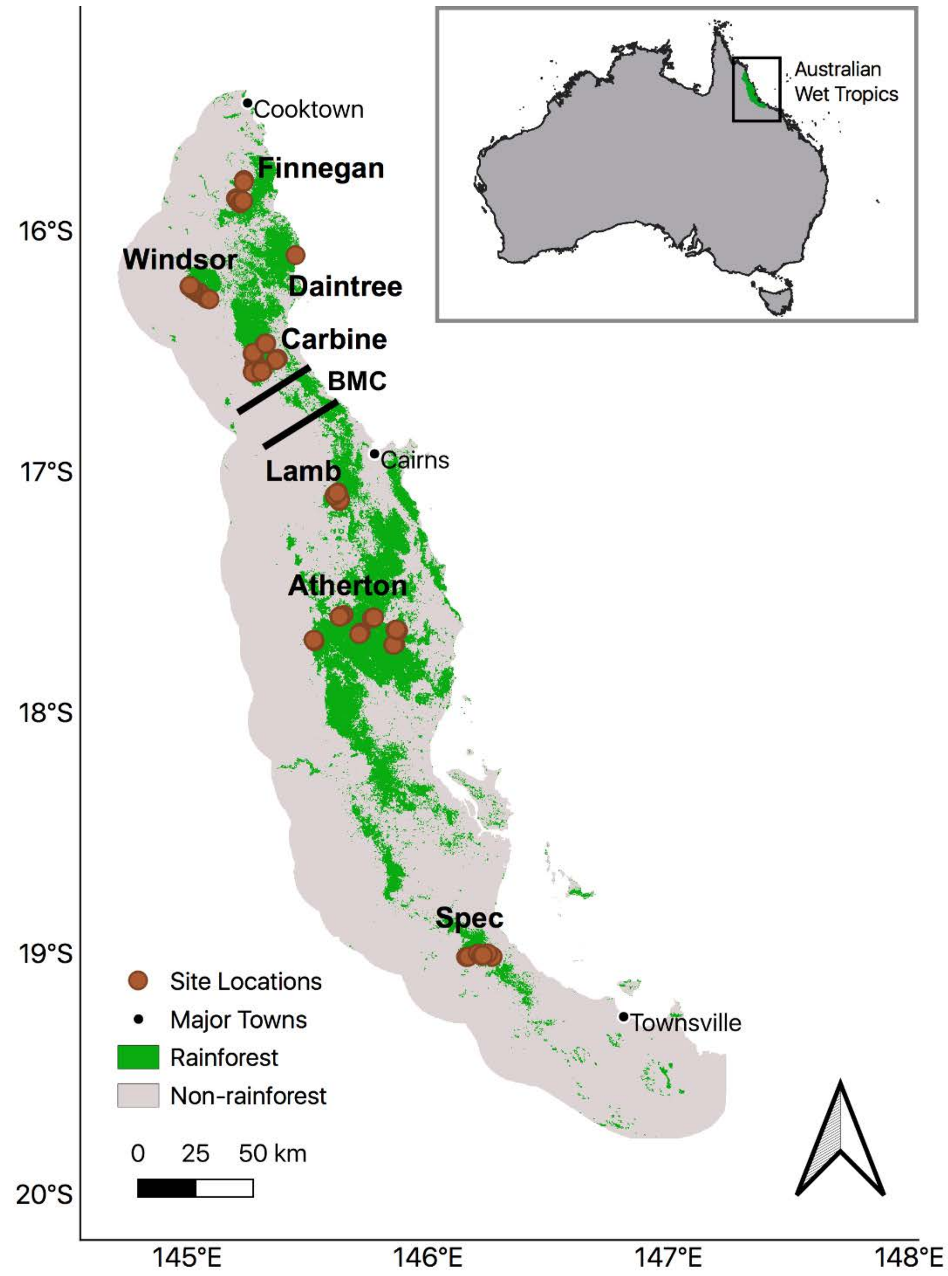


Figure 2.2. Map of the Australian Wet Tropics showing survey site locations for each subregion (naming of subregions follows Williams et al. (1995)). Rainforest distribution is shown in green. BMC is the Black Mountain Corridor and represents a well-known biogeographic barrier for numerous taxa within the AWT.

Both contemporary and historical factors drive the distribution and diversity of species and thereby the geographic structure of biological communities (Carnaval and Moritz 2008, Davies et al. 2011). The biogeography of the AWT is strongly driven by historic processes that occurred during climate fluctuations of the late Quaternary (last ~18 Kya) when rainforests contracted and expanded several times (Hopkins et al. 1993, Kershaw 1994, Williams and Pearson 1997, Hugall et al. 2002). As rainforests contracted to wetter uplands, many lowland species became locally extinct, leading to a substantial loss of species richness in the lowlands (Colwell et al. 2008). As a result, many vertebrate and invertebrate species that are endemic to the AWT are restricted to elevations above 300 m a.s.l. that have had historically stable climates and consistently supported rainforest throughout this period of high climatic fluctuations (Graham et al. 2006). In addition, there is an older biogeographic barrier along the Black Mountain Corridor (BMC), just south of the Carbine uplands (Figure 2.2), that has possibly existed since the Pliocene more than 2.5 Mya ago (Ponniah and Hughes 2004) and did not support rainforest until ~8 Kya ago (Schneider and Moritz 1999, Moritz et al. 2009). There is evidence in multiple taxa of a phylogeographic break across the Black Mountain Corridor that structures phylogenetic diversity at interspecific as well as intraspecific levels (Hugall et al. 2002, Moussalli et al. 2009, Moreau et al. 2015), such that many species have either a northern or southern restricted distribution (Moreau et al. 2015).

Biogeographic patterns in the region are also strongly influenced by contemporary climatic conditions at both regional and local scales. At a regional scale, seasonality of rainfall and temperature varies markedly among subregions (Williams and Middleton 2008). Rainfall seasonality is negatively correlated with the abundance of birds in the AWT, with dry-season severity creating bottlenecks in critical food resources such as insects, fruits and nectar (Williams and Middleton 2008). Similarly, there are marked seasonal fluctuations in the abundance of homopteran insects in the AWT (Frith and Frith 1985), which, through their production of honeydew, provide a particularly important food resource for ants, including *A. gilberti* (Blüthgen and Fiedler 2004). As such, honeydew-reliant ants such as species of

Anonychomyrma might be expected to show strong biogeographic patterns in response to rainfall seasonality.

At a finer geographic scale, temperature and rainfall both vary markedly with elevation. Mean temperature in the AWT declines by approximately 1°C per 200 m increase in elevation (Shoo et al. 2005). Elevations above 600-800 m a.s.l. receive year-round moisture via the orographic cloud layer that creates a misty and cool environment (McJannet et al. 2007). The orographic cloud layer has been linked to a significant change in ant species composition (Nowrouzi et al. 2016). Finally, at a local scale, there are strong microclimatic gradients across vertical space from the ground to the canopy, a general feature of rainforest environments globally (De Frenne et al. 2019). A recent study of ant distributions (including nine species of *Anonychomyrma*) in the AWT found a strong positive correlation between vertical niche breadth, and therefore exposure to microclimatic variation, and elevation range size (Leahy et al. 2021), indicating that vertical microhabitat associations of ants influence climatic niches and distributional patterns along elevation gradients.

Here, we use extensive collections from five mountain ranges to document the AWT *Anonychomyrma* fauna and to investigate patterns of species diversity and distributions across latitude, elevation, and vertical habitat space. Like many other dolichoderine genera (Shattuck 1992), *Anonychomyrma* is morphologically conservative and therefore taxonomically challenging, and so we use an integrated taxonomic approach that includes CO1 gene barcoding (Schlick-Steiner et al. 2006) to inform species boundaries. We identify the key climatic drivers of species distributions and employ species distribution modelling based on climatic niches to compare actual with potential distributions and thus identify factors that may have shaped contemporary subregional patterns of distribution.

Specifically, we address the following questions:

1. How many species of *Anonychomyrma* can be recognised in the AWT?
2. How are the species distributed among subregions and along elevational and vertical gradients?
3. What are the patterns of species richness and endemism?
4. To what extent do species distributions correlate with contemporary climatic variables and reflect historical patterns of rainforest refugia?

We predict that given the Gondwanan origin of *Anonychomyrma* and its prevalence in cool-temperate Australia, most species will have montane distributions in the AWT, with high levels of diversity and endemism in the cool upland regions that have retained stable rainforest vegetation and climate conditions more reminiscent of the Gondwanan rainforest that once dominated the east coast of Australia (Graham et al. 2006). This is the pattern for other faunal lineages of Gondwanan origin such as *Terrisswalkerius* earthworms (Moreau et al. 2015), rainforest possums (Williams et al. 2016), and myobatrachid frogs (Williams et al. 2010). We also expect species distributions to be strongly influenced by the paleogeography of the AWT, with most species having restricted northern or southern distribution across the Black Mountain Corridor (Moritz et al. 2009). Finally, in addition to high temperature we expect rainfall seasonality to be a key driver of species distributions.

Methods

Study region

The Australian Wet Tropics Bioregion is a World Heritage Area in far north-eastern Australia covering approximately 10 000 km^2 (20° to 15° S and 147° to 145° E). Rainfall is highly seasonal, with 75 – 90 % of the annual 2000 – 8000 mm rainfall occurring in the wet season between November and April. Elevations above 1000 m a.s.l. can also receive up to 66% of monthly water input from cloud stripping (McJannet et al. 2007). Rainforests of the AWT harbour a distinctive ant fauna that is highly disjunct from that of surrounding savanna (Taylor 1972, van Ingen et al. 2008). The fauna has strong affinities with that of Indo-

Malayan rainforests, containing many genera that are rainforest specialists and whose Australian distributions are restricted to North Queensland. The fauna notably lacks the arid-adapted taxa such as *Iridomyrmex* and *Melophorus* that dominate ant communities of Australia’s open sclerophyll habitats (Reichel and Andersen 1996). Tropical rain forests are generally regarded as supporting the world’s richest ant faunas (Brühl et al. 1998, Longino et al. 2002), but Australia’s rainforest ant fauna is relatively depauperate (Taylor 1972), in striking contrast to its exceptionally rich savanna fauna (Andersen 2000).

Ant sampling

Collections of *Anonychomyrma* were assembled from three sources. The first was the study of Nowrouzi et al. (2016), which was based on surveys at 26 of the long-term biodiversity monitoring sites established by Stephen E Williams at James Cook University (Williams et al. 2010). These sites are distributed across six subregions, covering the full latitudinal and elevational range of the AWT and representing approximately 94% of the available environmental space in the region (Williams et al. 2016). The subregions span approximately 500 km from north to south and sites were placed approximately every 200 m along the elevation gradient as follows: Finnegan (200, 500, 600, 800 m a.s.l.), Windsor (900, 1100, 1300 m a.s.l.), Carbine (100, 400, 600, 800, 1000, 1200 m a.s.l.), Lamb (700, 900, 1100 m a.s.l.), Atherton (200, 400, 600, 800, 1000 m a.s.l.), and Spec (350, 600, 800, 1000 m a.s.l.) (Figure 2.2). Sampling occurred within six plots at each site separated by a distance of 200 m; only three plots were located at each of the 350 m a.s.l. site at Spec and 100 m a.s.l. site at Atherton due to limited rainforest cover. Each site was sampled using a combination of pitfall trapping, litter extractions and baiting (both on the ground and on trees at a height of 1.5 m). At Windsor, Carbine, Atherton and Spec, sampling was conducted on three occasions from 2011-2013, covering two wet seasons (November - January) and one dry season (June - September). At Finnegan and Lamb sampling occurred only during one wet season. The study also included ants collected in pitfall traps during previous beetle surveys at the Windsor, Carbine, Atherton, and Spec sites (Staunton et al. 2014).

The second source was from Leahy et al. (2021) a study involving additional surveys at 15 of the above sites: at Finnegan (200, 500, 700 m a.s.l.), Windsor (900, 1100, 1300 m a.s.l.), Carbine (100, 600, 1000, 1200 m a.s.l.) and Atherton (200, 400, 600, 800, 1000 m a.s.l.). At each of these sites either two (1 site), three (4 sites), four (4 sites) or five (6 sites) trees were sampled, totalling 60 trees. Trees were at least 50 m apart and were chosen for surveying based on size and climbing accessibility. Trees were sampled using tuna bait traps and accessed using the single-rope climbing technique. At each tree, five bait traps were set on the ground and at every 3 m above ground to the maximum accessible height of the tree, which ranged from 15–27 m. Traps were set in the morning and collected 2–3 hours later. Finnegan, Windsor, and Carbine were surveyed from October – December 2012 and Atherton surveyed from December 2017 – February 2018.

The third source was data from additional surveys conducted in 2018–2019. Carbine sites were resampled in February 2018 using the same methodology as Leahy et al. (2021) , and from June-October 2019, but with surveys during both day and night. At each site, five trees (at least 50 m apart) were surveyed once in the daytime and once at night. Day and night surveys of the same trees were not conducted sequentially and were at least a day apart to allow resumption of normal ant activity in the tree in case of disruption. Daytime surveys started at 10:00 hours and night-time surveys at 21:00 hours, and baits were collected three hours later. Ants were also opportunistically hand collected immediately adjacent to baited vials. In addition, a collection was made over five days during the same period at the Daintree Rainforest Observatory (100 m a.s.l.) placing baited vials at 25 - 30m in height at ten trees (accessed by the canopy crane) for one hour and conducting one-hour hand searches on the ground.

Gene barcoding

DNA was extracted from foreleg tissue and sequences obtained for 97 specimens of *Anonychomyrma* collected during the study (Table S2.1). DNA extraction and CO1 sequencing were conducted through the Barcode of Life Data (BOLD) System (for extraction details, see http://ccdb.ca/resources). Each sequenced specimen was assigned a unique identification code that combines the batch within which it was processed and its number within the batch (e.g., ANONC006-20), and all specimens are labelled with their respective BOLD identification numbers in the ant collection held at the CSIRO Tropical Ecosystems Research Centre in Darwin.

DNA sequences were checked and edited in MEGA 7 (Kumar et al. 2016). Sequences were aligned using the UPGMB clustering method in MUSCLE (Edgar 2004), and translated into (invertebrate) proteins to check for stop codons and nuclear paralogues. The aligned sequences were trimmed accordingly, resulting in 657 base pairs. A sequence from the *anceps* complex of *Iridomyrmex* (sp. A, IRIDX092-18 from (Andersen et al. 2020)) was used as an outgroup for rooting the gene tree. Tree inference by maximum likelihood was conducted through the IQTREE web server (http://iqtree.cibiv.univie.ac.at/; (Trifinopoulos et al. 2016)) using ultrafast bootstrap approximation (Minh et al. 2013). IQTREE has been shown to be a robust algorithm for tree inference that compares favourably with other methods (Nguyen et al. 2015). Model selection was inferred using a 3-codon partition file and linked branch lengths with the AutoMRE 'ModelFinder' function to find the best-fit model for tree inference (Chernomor et al. 2016). Trees were viewed and edited in FigTree v1.4.3 (Rambaut 2007) and annotated using Photoshop CS5.1®.

Species delimitation

There is no specific level of CO1 divergence that can be used to define a species, but the level of CO1 variation within ant species is typically 1–3% (Smith et al. 2005). However, some ant species can show substantially higher variation (for example (Smith et al. 2005, Wild 2009)), and in other cases two clear species can show no CO1 differentiation (for example, Schär et al. (2018)). We also note that some ant species from other genera are known to have workers that are virtually identical morphologically, and they can only be separated by detailed morphometric analysis or through reproductive castes (Wagner et al. 2018). When delimiting species, we focused on morphological differentiation between sister (i.e., most closely related) CO1 clades, considering all available samples from the same collections as sequenced specimens. A full set of voucher specimens of recognised species is held at the CSIRO Tropical Ecosystems Research Centre in Darwin and a duplicate set in the James Cook University ant collection.

Patterns of abundance, diversity, and endemism

We used total number of occurrences in survey plots including repeat surveys (n = 525 surveys) across all sites (n = 23) as a measure of abundance. Species were then ranked by abundance to document the species-abundance pattern. We excluded the Daintree subregion from all analyses of diversity as there was only one site sampled. *Anonychomyrma* was not recorded from the Lamb subregion and these sites were also excluded from the analysis. To assess latitudinal diversity patterns, we assessed variation in species richness among subregions by plotting the mean number of species across sites per subregion along with the total number of surveys per subregion. We likewise plotted the number of subregion endemics per subregion. To assess elevation diversity patterns, we investigated differences in species richness among elevations by pooling across the five subregions and plotting the mean number of species across plots per elevation along with the total number of surveys per elevation. To assess the vertical distributions (foraging activity from ground to canopy) of species, we considered only the vertical (arboreal) surveys conducted by Leahy et al. (2021). We selected species for which there were two or more survey records and 10 or more sample records (as there were 5 samples per vertical height band). For each of the resultant eight species, we plotted the number of sample records in a 3-m band divided by the total number of sample records for that species, to provide a relative proportion of occurrence in each 3-m band from ground to canopy.

Species distribution modelling

We used species distribution models to first identify the key climatic drivers of species distributions, and secondly, to map predicted rainforest distributions based on species location records and climate variables in order to identify the potential role of historical factors in shaping contemporary distributions. We included the Daintree subregion in our species records. Species distribution models based on species occurrences and associated climatic data were derived using Maxent, a maximum entropy algorithm, in the program Maxent using default settings (Version 3.4.1, (Phillips et al. 2017)). Ten replicates were used per species model with cross validation and a 1000 iterations (Elith and Leathwick 2009). First, we filtered species for ≥ 5 location points (not counting repeated surveys and counting a record in a survey plot as one occurrence/location point), which resulted in a subset of nine species (van Proosdij et al. 2016). The number of location points ranged from 96 (*A. gilberti*) to six (sp. H). A small number of location points can be a problem for modelling species distributions if those points are widely dispersed across the environmental space (Elith et al. 2006, Wisz et al. 2008). We regressed mean annual temperature against mean annual precipitation to create the environmental space of all survey locations and plotted each species' location points within that plot. Species with low (<25) numbers of points were highly concentrated in environmental space, indicating that the number of location points sufficiently captured each species climatic niche volume (Figure S2.1).

We used the accuCLIM climate variables derived by Storlie et al. (2013) that provide statistically downscaled spatial layers of 250 m^2 resolution for the AWT region that are highly accurate in relation to regional topography and vegetation. We clipped all climate variables to rainforest extent in the AWT as we were interested in predicting the distribution of *Anonychomyrma* species within their primary habitat of rainforest vegetation. We selected nine of the 17 climate variables that were most ecologically relevant (VanDerWal et al. 2009a, Staunton et al. 2014, Nowrouzi et al. 2019). We looked for collinearity in variables by looking at all pairwise interactions between continuous covariates using Pearson's correlation coefficient. Variables with an R^2 value of >0.7 were considered for removal (Dormann et al. 2013). Variance inflation factors were then calculated and any variables that had a value >10 were excluded from further analysis using the package *usdm* in R (Naimi et al. 2014). A final set of five variables was selected, as follows: maximum temperature of the warmest month, temperature seasonality, rainfall of the wettest month, rainfall seasonality, and isothermality (an indicator of temperature variability: mean diurnal temperature range divided by annual temperature range; (Storlie et al. 2013)). All models presented had values for the area under the receiver-operating characteristic curve (AUC) greater than 0.9 and therefore performed adequately (Pearce and Ferrier 2000). We then calculated summed habitat suitability for the rainforest extent by summing all nine species habitat suitability scores across all pixels and standardizing each pixel's value to a summed habitat suitability score between 0–1.

Results

The Anonychomyrma fauna

We recognise 22 species of *Anonychomyrma* (sp. A-C and E-U, along with *A. gilberti* and *A. malandana*) among our samples, nine of which were recorded at a single subregion (Table 2.1). All but one of our recognised species were successfully sequenced. The CO1 tree (Figure 2.3) indicates that species C (Figure 2.4A, B) is the most phylogenetically divergent, with no close relatives (13% - 20% divergence from other species). It is a relatively large, gracile and somewhat polymorphic species with an angular propodeum, and was common at high elevation at Carbine and Windsor. *Anonychomyrma malandana* is also indicated as highly distinctive phylogenetically (>12% divergence from all other species) as well as being highly distinctive morphologically – it is an extremely shiny species with a globose head and very long antennal scapes (Figure 2.4C, D). It is a high-elevation species that was common at Windsor. Species H and sp. G are also phylogenetically distinct (Figure 2.3), both with >11% divergence from all other species. Species H is a small, nondescript species with a biconvex mesosoma and relatively short scapes (Figure 2.5A, B) and is morphologically very similar to several unrelated species (see below); it was recorded at Carbine and Windsor at the highest elevations (1200 m and 1300 m respectively). Species G has a short, prominently rounded propodeum, and its scape and first gastric tergite atypically lack erect hairs (Figure 2.5C, D). These characters are shared by the smaller sp. J (Figure 2.5E, F), but despite their morphological similarity (they were considered conspecific in Nowrouzi et al. (2016)) these species are widely separated in the CO1 tree (Figure 2.3). They have overlapping geographic distributions at Atherton: sp. G was recorded from all five subregions, whereas sp. J was recorded exclusively from Atherton (Table 2.1). Species J is shown as being most closely related to sp. I (Figure 2.6A, B) and sp. S (Figure 2.6C, D; Figure 2.3). Compared with sp. I, sp. S has a substantially larger head with a markedly concave occipital margin, more angular occipital corners, and shorter scapes. Both species were recorded only from Atherton and only from high elevation (800 m and 1000 m: Table 2.1).

Table 2.1. The subregion locations and elevation range (maximum – minimum elevation) and number of survey points of 22 species of *Anonychomyrma* in the Australian Wet Tropics, species are ordered from their north to south subregion distribution, and then by number of survey points. The position of the Black Mountain Corridor, a well-known biogeographic barrier, is indicated. With full elevation range of rainforest habitat is shown in brackets for each subregion.

				Black Mountain Corridor		
Region		North	North	North ↓	South	South
		Finnegan	Windsor	Carbine	Atherton	Spec
Species	No. survey points	(200-800)	(900-1300)	(100-1200)	(100-1000)	(350-1000)
gilberti	96	200-800	900-1300	100-1200	100-1000	350-1000
sp. G	50	200-800	900-1300	100-1200	400-1000	350-800
sp. B	1	200				
sp. C	22		1100-1300	1000-1200		
malandana	13		1100-1300	1200	1000	
sp. E	8		900-1100			
sp. K	7		900-1100	1000	800	800
sp. H	6		1300	1200		
sp. F	1		1100			
sp. Q	1		900			
sp. T	1		1100			
sp. L	1			1200		
sp. P	1			1000		
sp. J	4				200-1000	
sp. O	4				400-800	
sp. I	2				800-1000	
sp. N	1				1000	
sp. R	1				600	
sp. S	1				1000	
sp. U	1				800	
sp. M	11					800-1000
sp. A	10					350-1000

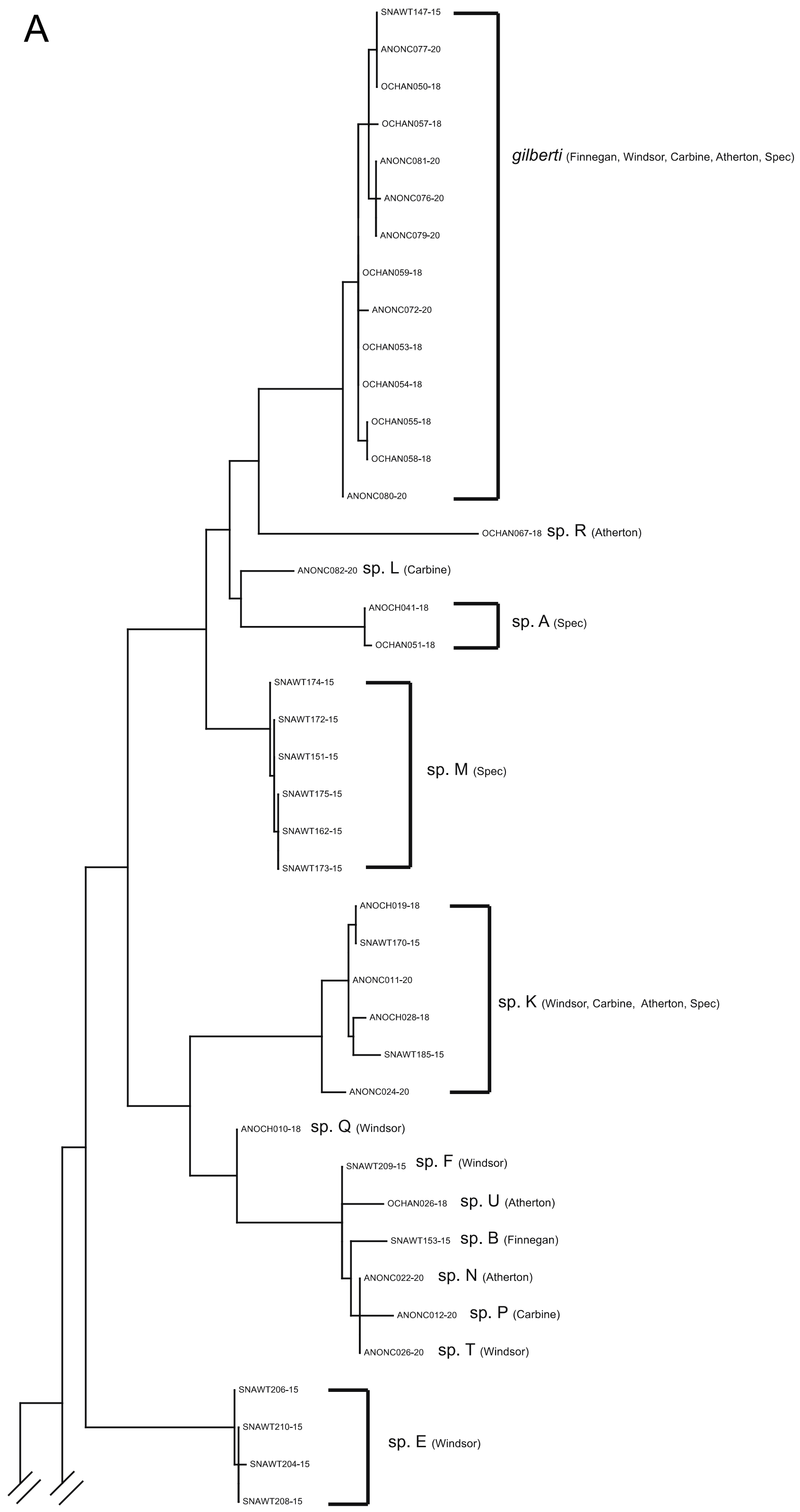


Figure 2.3. (part) Maximum Likelihood CO1 tree of 97 specimens of *Anonychomyrma* from the Australian Wet Tropics, with a specimen of the *anceps* complex of *Iridomyrmex* as an outgroup.

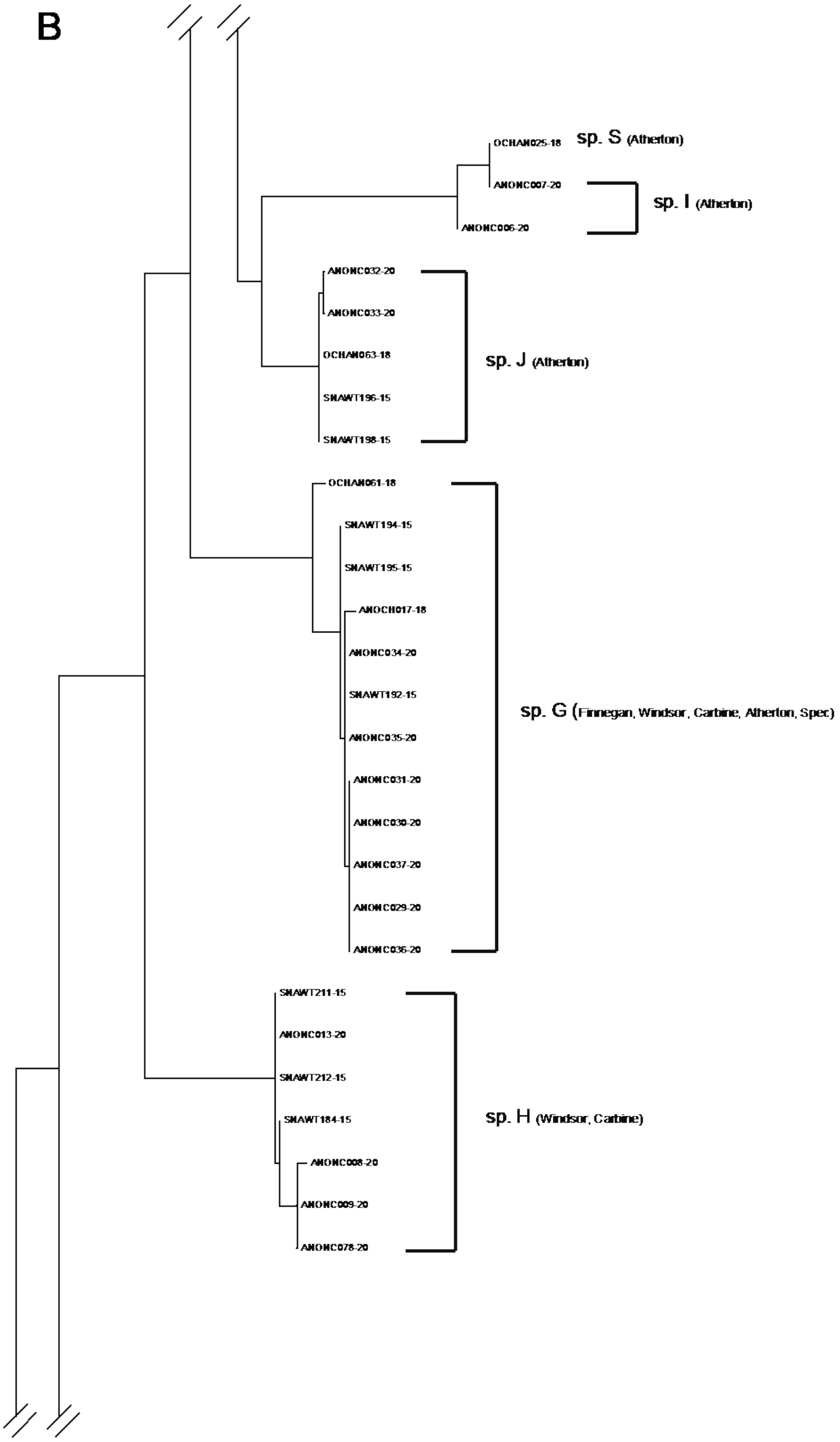
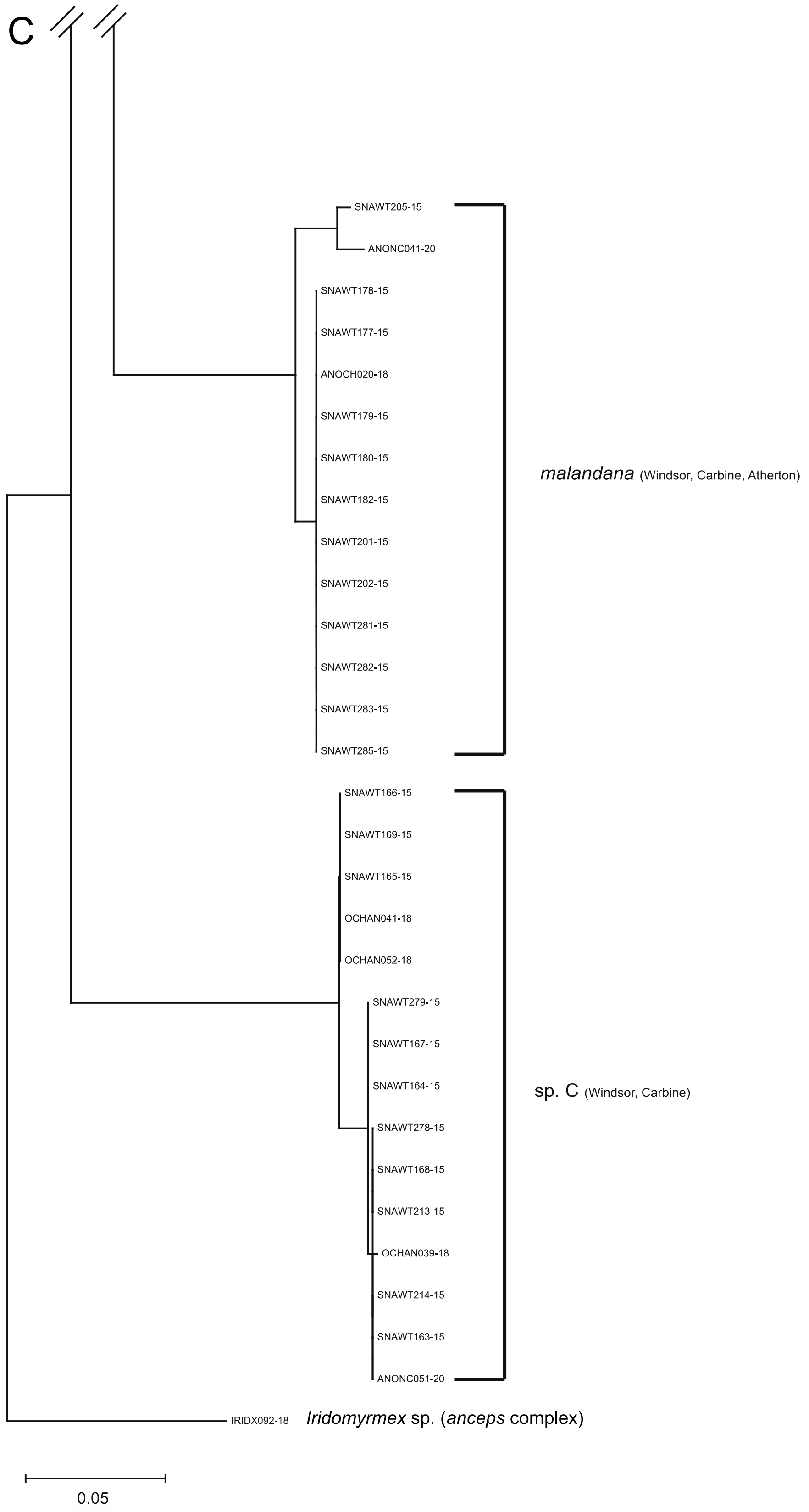


Figure 2.3. Continued.



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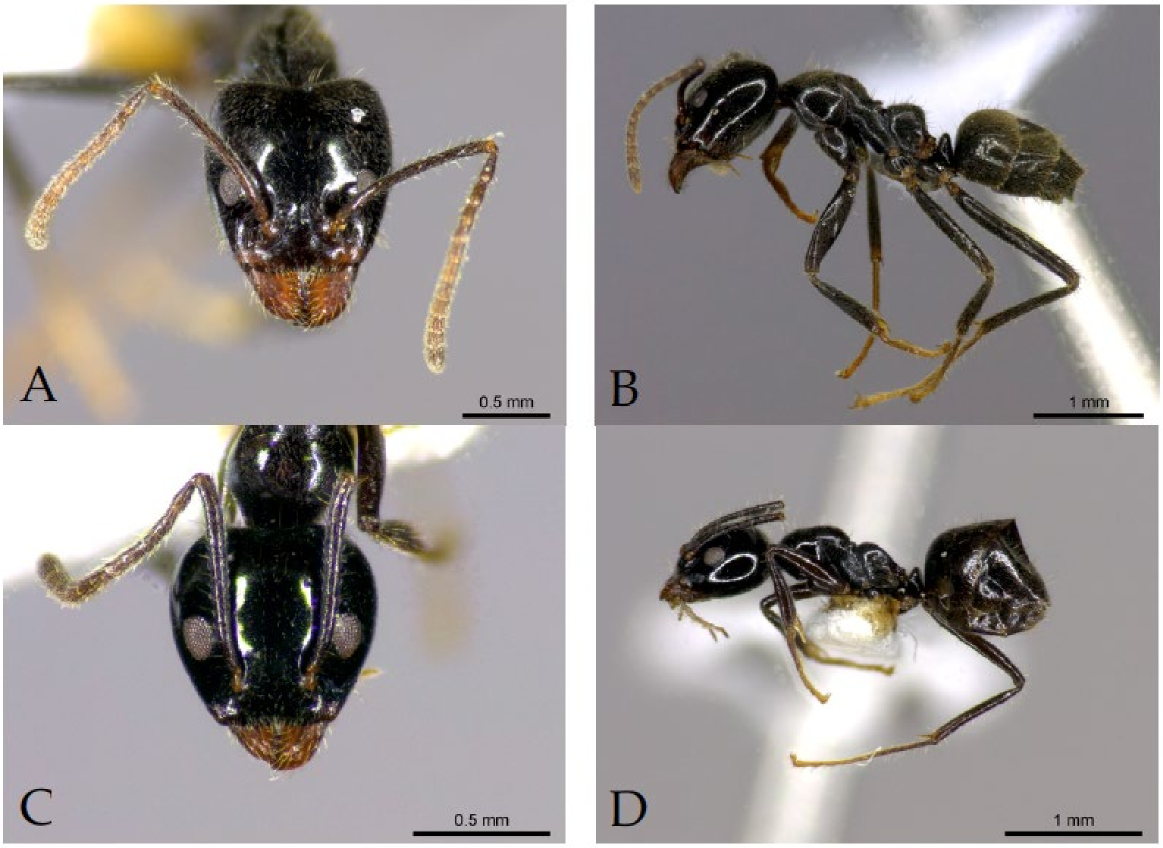

Figure 2.4. Head and lateral views of *Anonychomyrma* sp. C (A, B), *A. malandana* (C, D).

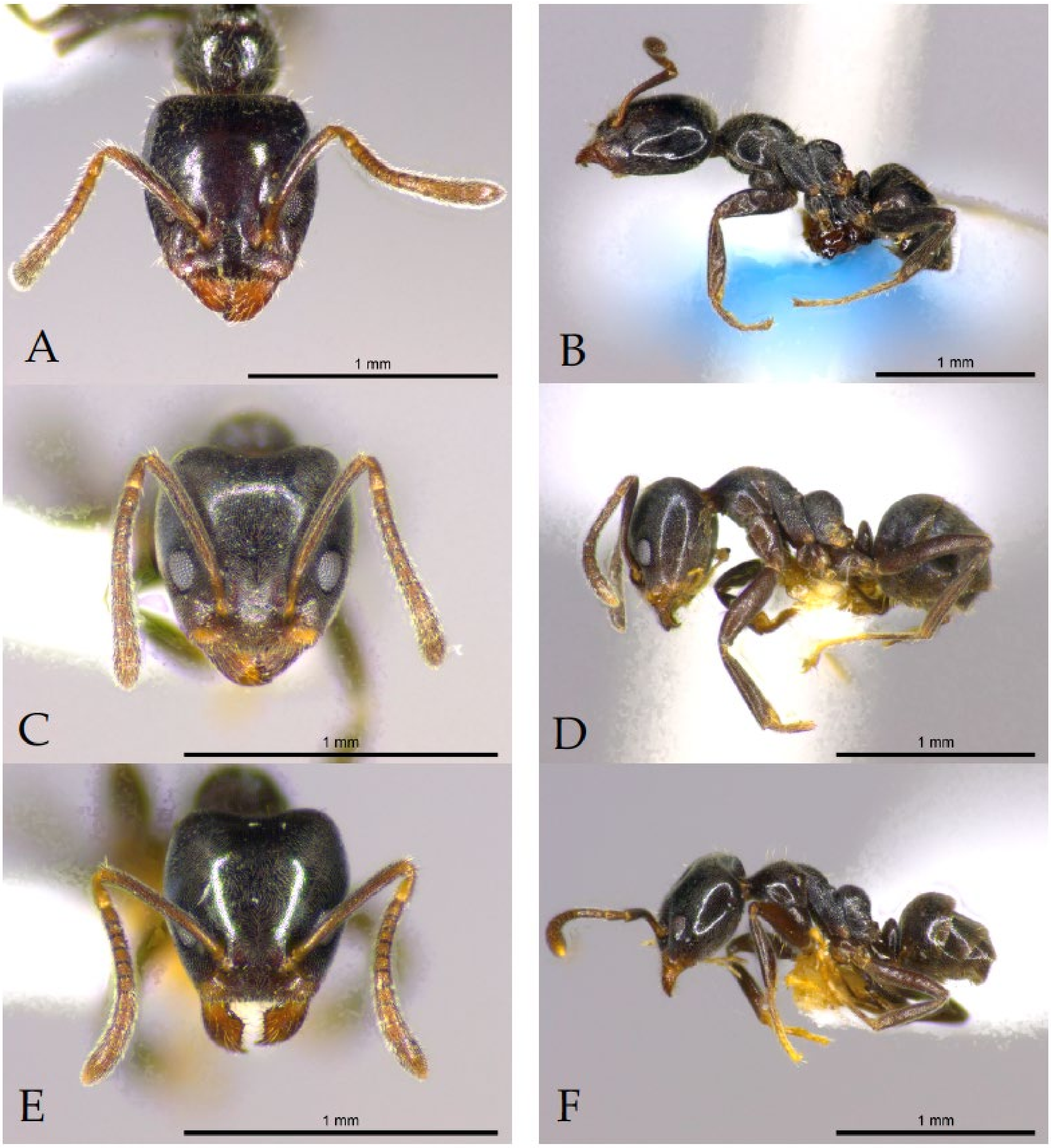

Figure 2.5. Head and lateral views of *Anonychomyrma* sp. H (A, B), sp. G (C, D), and sp. J (E, F).

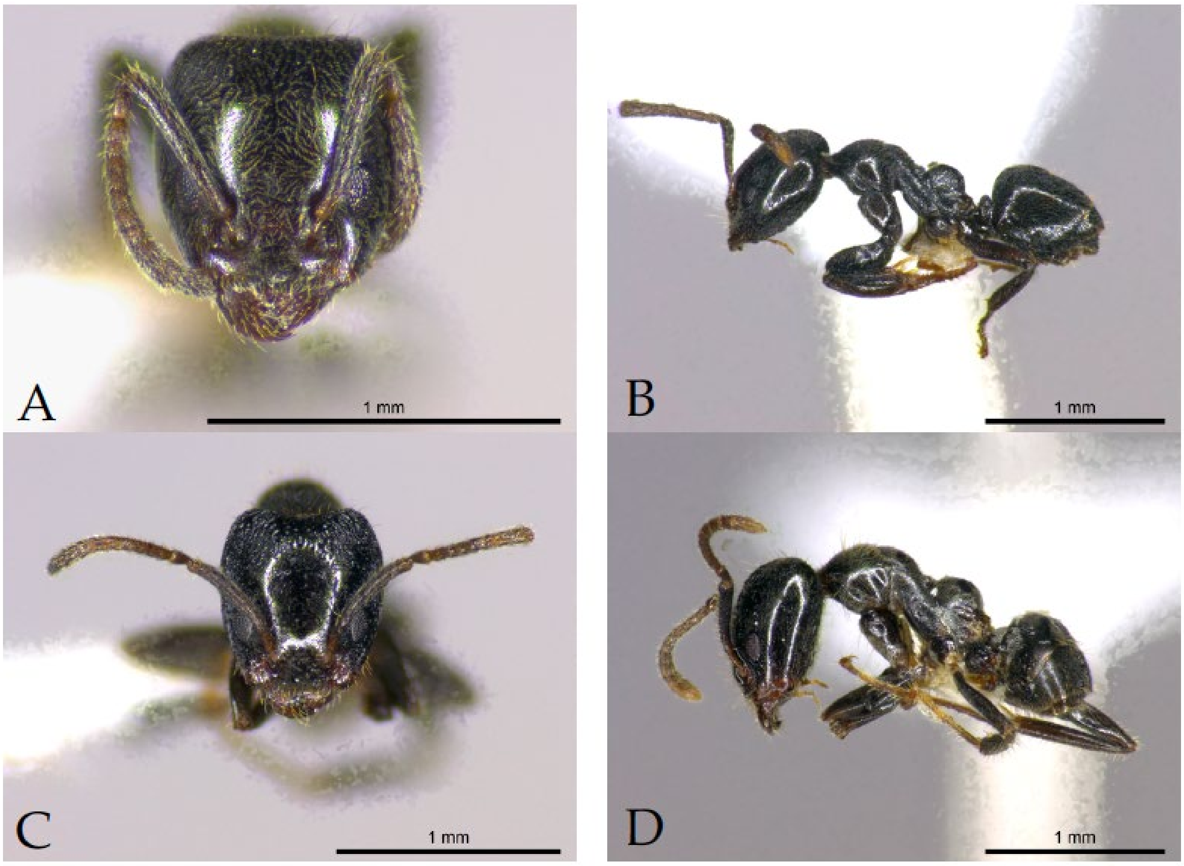

Figure 2.6. Head and lateral views of *Anonychomyrma* sp. I (A, B), sp. S (C, D).

Thirteen of the remaining 14 species form two clades. The first contains *A. gilberti* and species A, L, M and R, which have 6–8% mean CO1 divergence among them (Figure 2.3). *Anonychomyrma gilberti* occurred in all subregions but the other four species were each recorded in a single subregion (Table 2.1). Species A, L and M (Figure 2.7A-F) have the general appearance of *A. gilberti* (Figure 2.1), but without such strongly golden pubescence or deeply V-shaped occipital margin; indeed, sp. L has relatively weak pubescence and rounded occipital corners (Figure 2.7C, D). Species R is morphologically very different to these taxa – it is much smaller, lacks any golden pubescence, has short scapes and the occipital margin is only feebly concave. Despite its location on the CO1 tree, it seems to be more closely allied to members of the second clade spanning sp. P to sp. K (Figure 2.3). Indeed, it seems morphologically indistinguishable from sp. N from Atherton (Figure 2.8A, B). All species within this second clade are similar morphologically, and CO1 divergence among them is often <2%. Compared with sp. N, sp. T (known only from Windsor) has a more conspicuously concave occipital margin and more angular occipital corners, and in sp. P the occipital margin is even more deeply concave. Species U has a narrow head, short scapes and a prominently rounded propodeum. The propodeum is also prominently rounded in sp. F (Figure 2.8C, D), but the head is markedly broader and scapes longer. Species Q has a flattened propodeum and short scapes. Species K (Figure 2.8E, F) has a very similar appearance to that of sp. N (Figure 2.7A, B), but the two taxa are very distinct genetically (11% mean CO1 divergence).

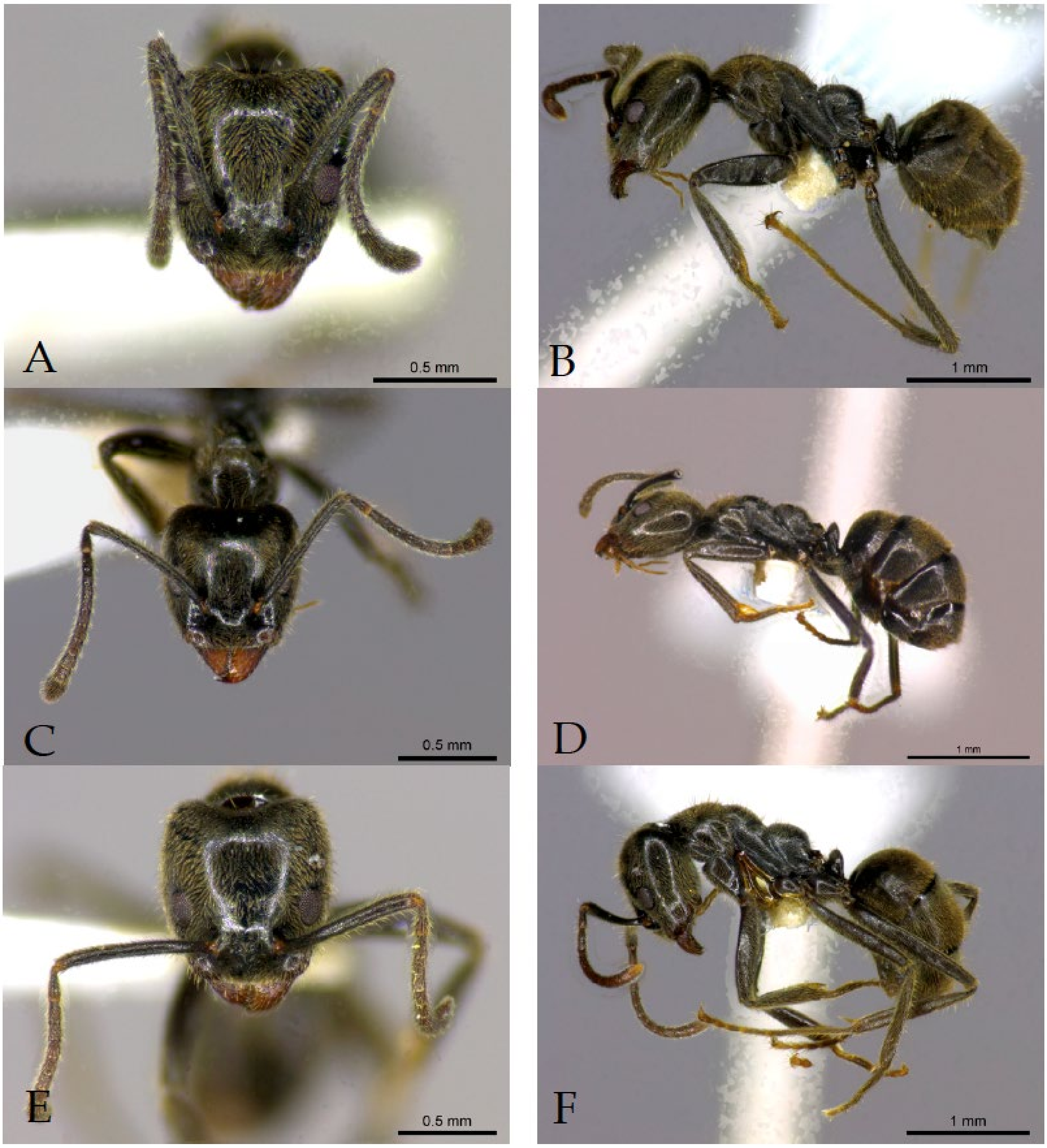

Figure 2.7. Head and lateral views of *Anonychomyrma* sp. A (A, B), sp. L (C, D) and sp. M (E, F), which are all closely related to *A. gilberti* (Figure 2.1).

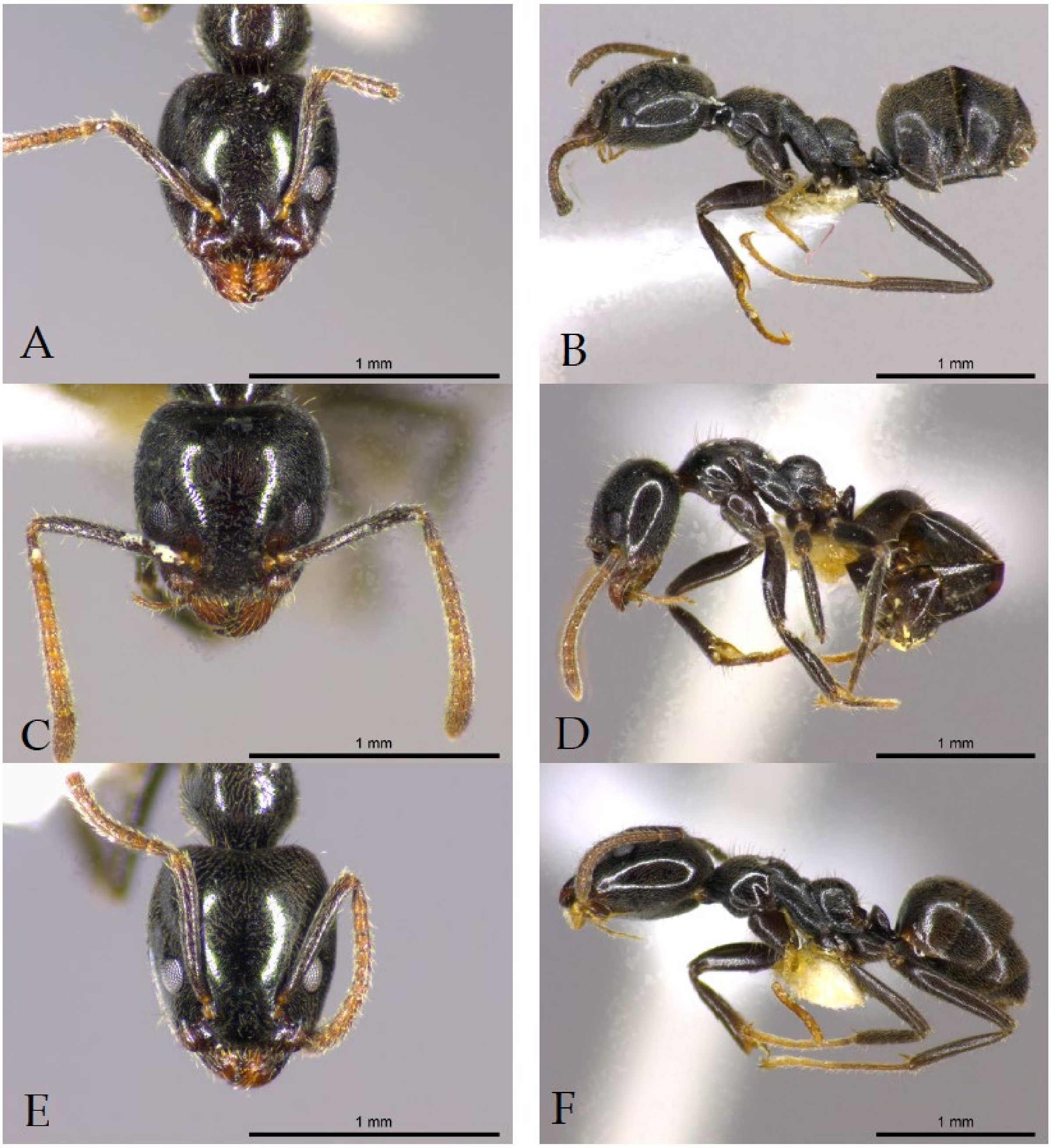

Figure 2.8. Head and lateral views of *Anonychomyrma* sp. N (A, B), sp. F (C, D) and sp. K (E, F).

The final sequenced species is sp. E, which has a biconvex mesosoma, broad head and long scapes (Figure 2.9E, F). It occurred exclusively at Windsor (Table 2.1). The species that was not sequenced, sp. O, is highly distinctive – it is very small, with a narrowly rectangular head and very short scapes (Figure 2.10). It appears to be closely allied to *A. minuta* (Donisthorpe) from New Guinea. It was recorded only at Atherton, at mid elevation (400, 600, and 800 m sites).

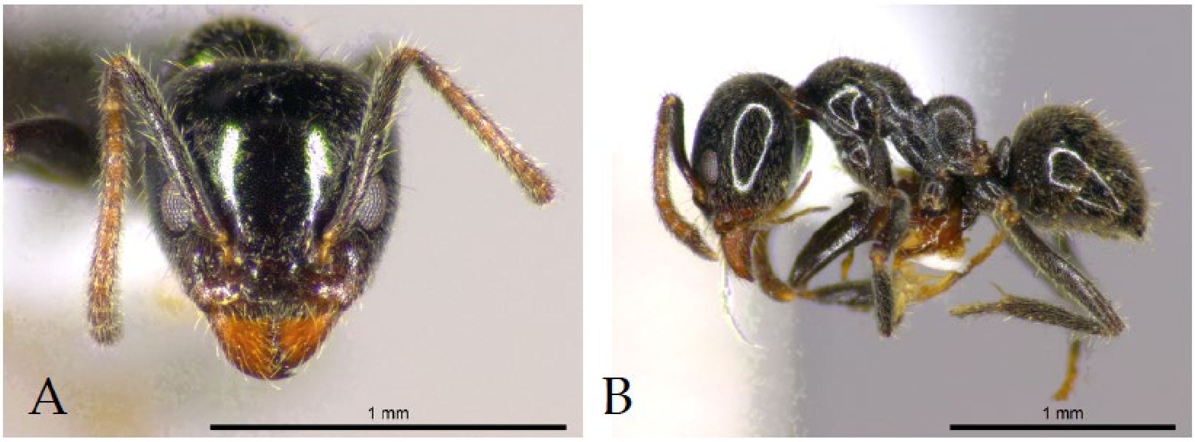

Figure 2.9. Head and lateral views of *Anonychomyrma* sp. E (A, B).

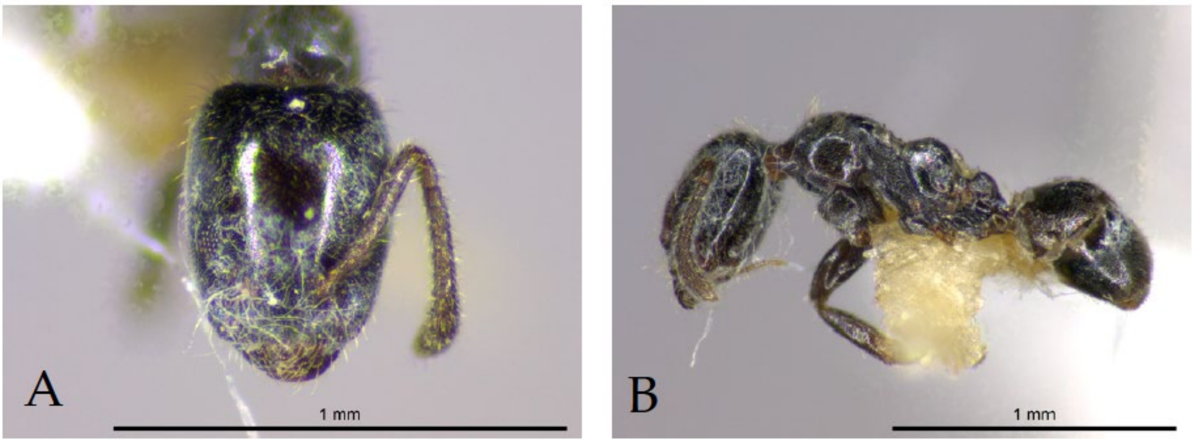

Figure 2.10. Head and lateral views of *Anonychomyrma* sp. O (A, B).

Patterns of abundance, diversity, and endemism

Anonychomyrma gilberti (185 records) and sp. G (73 records) dominated the samples, collectively representing 81.3% of all species records (Figure 2.11). Nine species were recorded in only one survey (Figure 2.11). The number of species within a subregion ranged from zero at Lamb Range to eleven at Atherton. There was no discernible relationship between survey effort and mean number of species per either subregion (Figure 2.12a, b) or elevation (Figure 2.13). Windsor (1100 – 1300 m a.s.l.) had the highest mean species richness per elevational site (5.7 ± 0.7 SE; Figure 2.12a), and the second highest number of subregion endemics with 4 out of its 10 species (Figure 2.12b). Atherton (100 – 1000 m a.s.l.) had the highest number of subregion endemics with seven endemics out of its total of eleven species (Figure 2.12b). Carbine, despite having the greatest elevation range (100 – 1200 m a.s.l.), and the highest survey effort, had similar mean species richness to other low diversity subregions and had only two endemic species out of the eight total species recorded there (Figure 2.12a and Figure 2.12b). Overall, there was high subregion endemism with 16 (72%) species recorded in only one subregion (Table 2.1). However, all four species (*A. gilberti*, *A. malandana*, sp. G and sp. K) that occurred in more than two subregions had distributions spanning the BMC (Table 2.1). Mean number of species increased with elevation peaking at 1100 m a.s.l. and slightly declining again at 1200 and 1300 m a.s.l. (Figure 2.13).

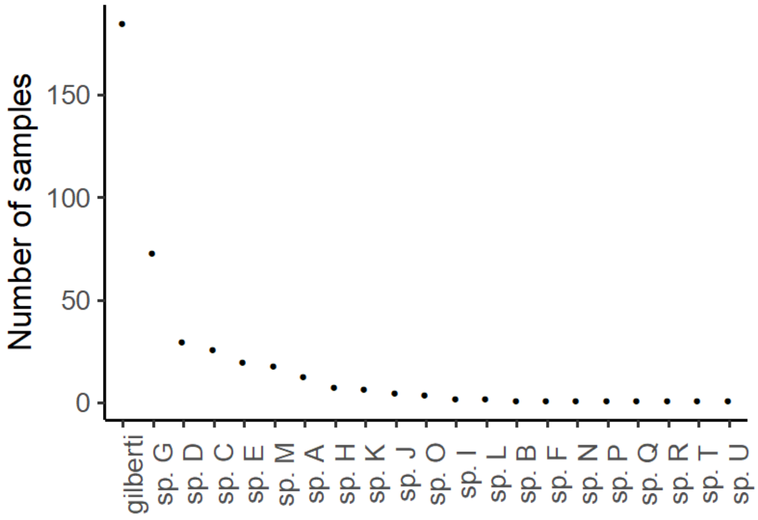

Figure 2.11. Ranked abundance as total number of samples for each species from pooled data for all survey sites across five subregions in the Australian Wet Tropics.

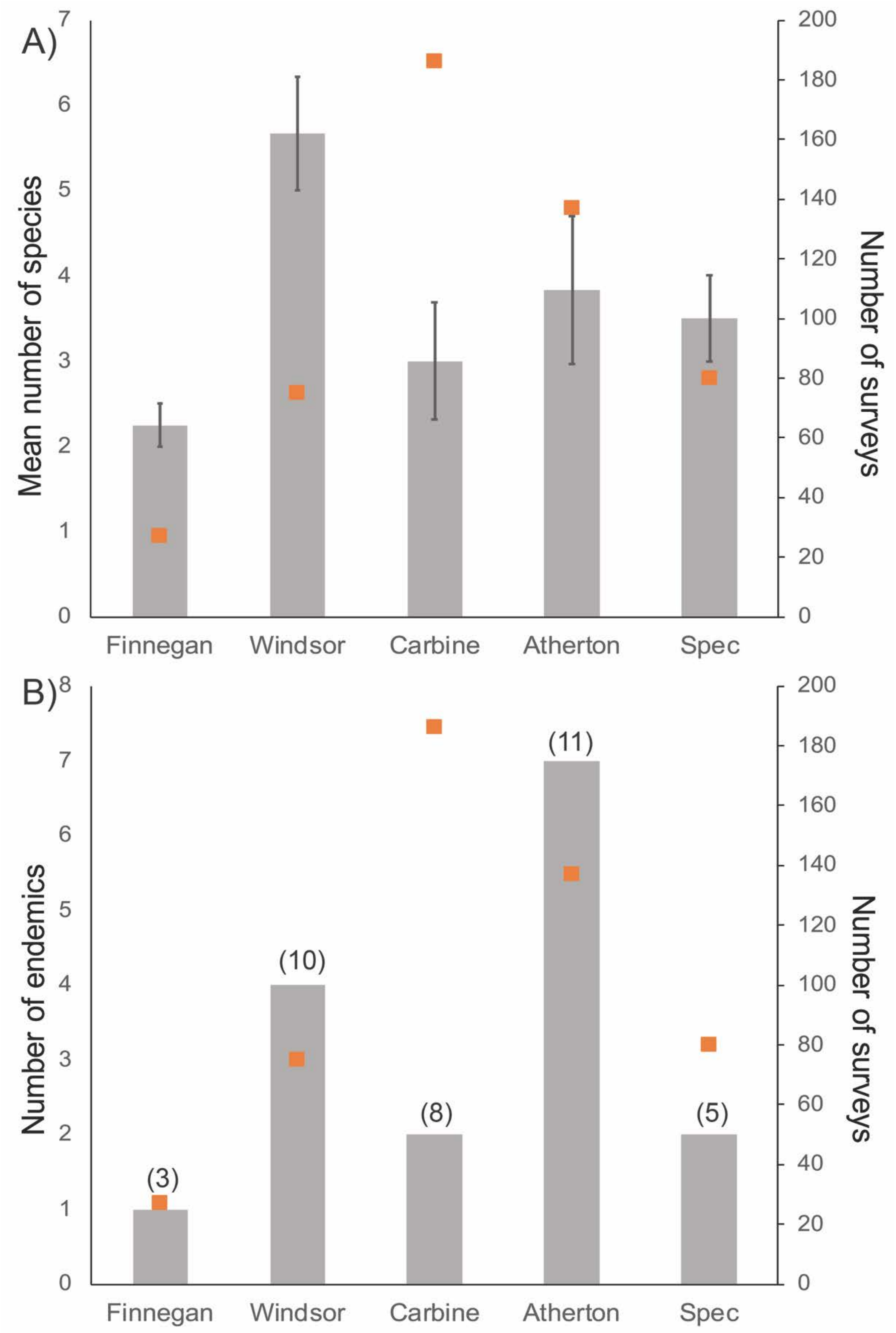

Figure 2.12. Variation in diversity and endemism among subregions. Subregions labelled from left to right along the north to south latitudinal gradient. A) Mean (± SE) number of *Anonychomyrma* species per elevational site as grey bars and number of surveys per

subregion as orange symbols, B) Number of subregion endemics per subregion, in brackets, total species richness per subregion, and number of surveys per subregion as orange symbols.

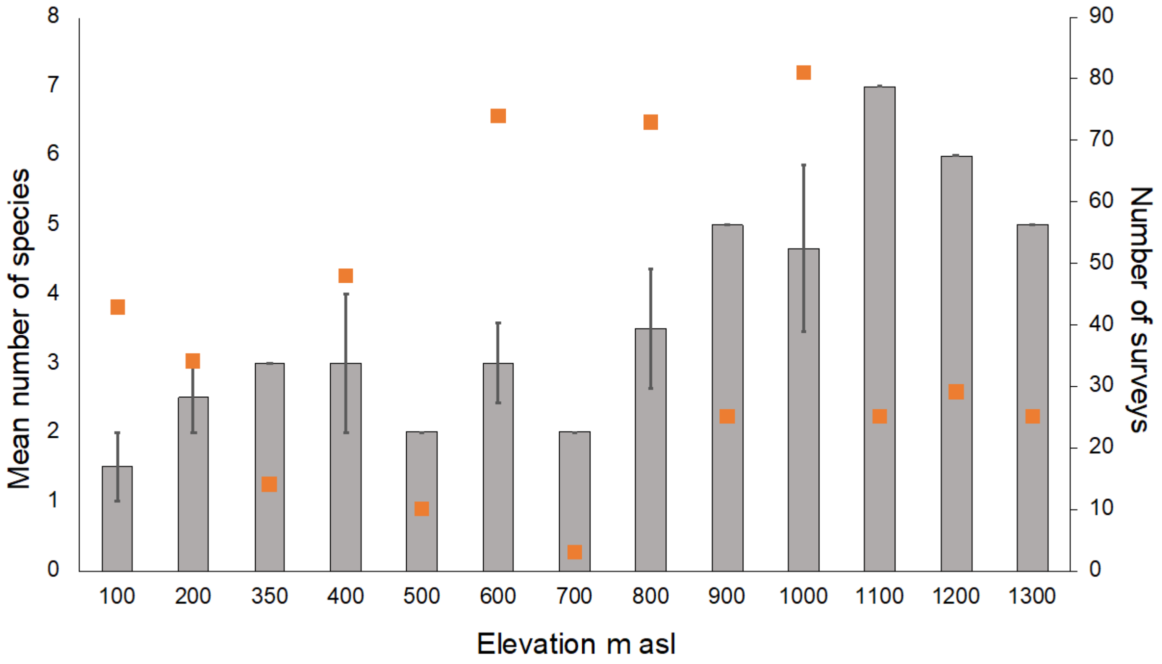

Figure 2.13. Diversity across elevation, pooling across five subregions. Mean number of *Anonychomyrma* species (± SE) per elevation as gray bars and number of surveys per elevation as orange symbols.

All eight species recorded during vertical (tree) surveys nested arboreally (L. Leahy pers. obs), with most species foraging high into the canopy. However, there was variation in the way different species used the vertical gradient (Figure 2.14). Three species, *A. gilberti*, *A. malandana* and sp. G foraged on the ground as well as arboreally. The two most commonly sampled species, *A. gilberti* and sp. G, were most evenly distributed in their foraging along the vertical gradient, with relatively equal foraging from ground to canopy. These two species were also the most geographically and elevationally widespread species (Table 2.1). *Anonychomyrma malandana* and sp. C also showed relatively even foraging across the vertical gradient. The less commonly sampled species showed increasing foraging concentration in the upper parts of the tree from the subcanopy (9 – 12 m) up to the high canopy (18 – 27 m; Figure 2.14).

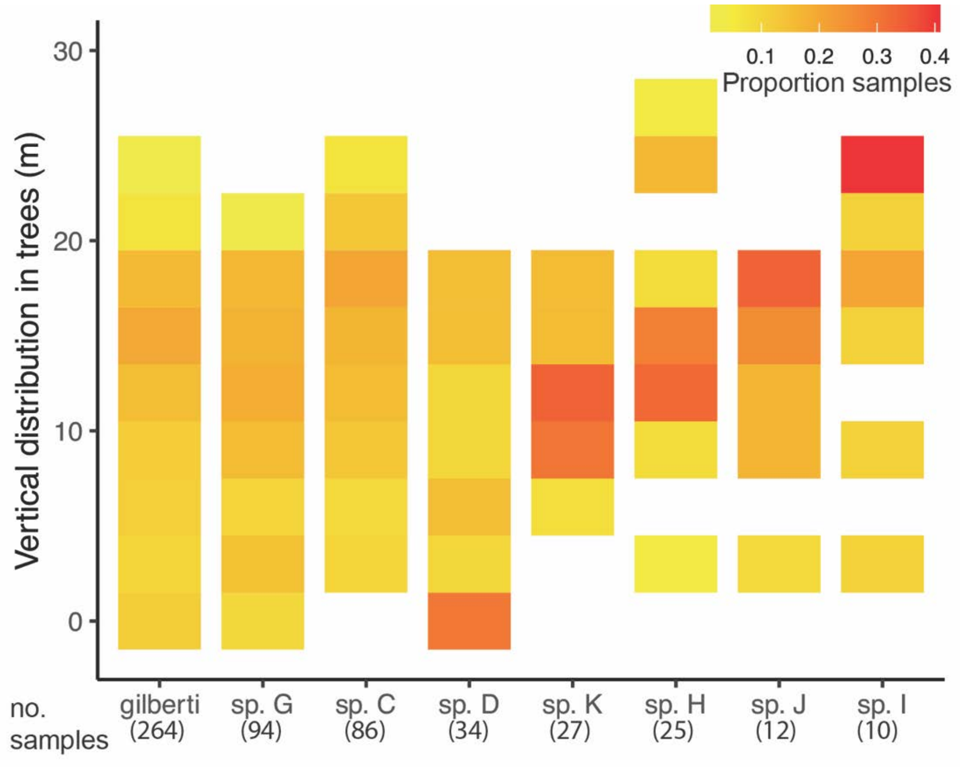

Figure 2.14. Vertical distribution of *Anonychomyrma* species sampled in 105 surveys (out of 525 total surveys) from ground to canopy at 15 elevation sites at four subregions in the AWT. Pooled occurrence data from four subregions across the Australian Wet Tropics, with species ordered by number of survey occurrences from left to right. Each tile represents a three-metre vertical band, coloured by proportion of total sample occurrence for each species. Numbers beneath species labels are total number of samples occurrences for that species (total samples = 3745). The maximum potential tree survey height for each species (based off occurrence in each surveyed tree) is: *gilberti* = 27 m, sp. G = 27 m, sp. C = 24 m, *malandana* = 24 m, sp. K = 24 m, sp. H = 27 m, sp. J = 21 m, sp. I = 24 m. Red represents high proportion of samples and yellow represents low proportion of samples.

Species distribution modelling

Maximum temperature of the warmest month was the most important predictor for seven species and the second most important predictor for the other two species modelled (Table 2.2). For all species there was a negative relationship between maximum temperature of the warmest month and predicted habitat suitability, but the temperature at which habitat suitability declined (ranging from 26°C for the high-elevation restricted sp. H to 34°C for the widespread *A. gilberti* and sp. G) and the rate of decline differed substantially (Figure S2.2). Rainfall of the wettest month was the second most important predictor variable for *A. gilberti*, sp. E, *A. malandana*, and sp. K, being strongly negatively related to habitat suitability in all cases (Table 2.2, Figure S2.3). Rainfall seasonality was also important in models, but generally ranked as the second or third most important variable, except for two Spec endemics, sp. A and sp. M, for which rainfall seasonality was the most important predictor. These two Spec endemic species had a positive relationship between rainfall seasonality and habitat suitability, whereas all other species had higher habitat suitability at intermediate levels of rainfall seasonality or had a negative relationship with rainfall seasonality (Figure S2.4).

Table 2.2: Species distribution model outputs for nine species showing the three highest ranking environmental variables and their permutation importance in the model. AUC = area under the curve, a value between 0–1 indicating model performance, higher AUC scores indicate better model fit. *n* = number of unique survey location points for each species.

Species	*n*	AUC	Variable	Permutation importance
gilberti	96	0.798	**Max T hottest month**	31.2
			Rain wettest month	21.8
			Rain seasonality	22.6
sp. G	50	0.754	**Max T hottest month**	64.4
			Rain seasonality	12.3
			Rain wettest month	11.4
sp. C	22	0.971	**Max T hottest month**	95.7
			Isothermality	3
			Rain wettest month	0.7
malandana	13	0.958	**Max T hottest month**	82.6
			Rain wettest month	14.7
			Rain seasonality	2.4
sp. M	11	0.992	**Rain seasonality**	48.9
			Max T hottest month	39.4
			Rain wettest month	10.5
sp. E	10	0.948	**Max T hottest month**	72
			Rain wettest month	13.5
			Isothermality	11.9
sp. A	8	0.971	**Rain seasonality**	73.4
			Max T hottest month	23.7
			Temp seasonality	2.8
sp. K	7	0.892	**Max T hottest month**	95.9
			Rain wettest month	2.1
			Isothermality	1.3
sp. H	6	0.99	**Max T hottest month**	98.7
			Rain seasonality	1.1
			Isothermality	0.2

Distribution modelling predicted that six out of nine species modelled have potential distributions limited to high elevations in either the north (Windsor and Carbine) or far south (Spec) (Figure 2.15). Summed rainforest habitat suitability (summing each grid cell for suitability for the nine modelled species) was highest at high elevation (Figure 2.15a), which is consistent with the occurrence of highest species richness (Figure 2.13). Species-specific habitat suitability generally matched surveyed occurrences, suggesting that actual distributions are close to the potential distributions based on climatic niches (Figure 2.15). However, our models indicated that highly suitable (≥ 0.75 probability of occurrence) environments occurred in the southern region for sp. C, sp. E, and sp. H, despite these species being recorded only in the northern subregions in our study. None of the species modelled had a potential distribution restricted to the centre (Atherton or Lamb) or to the northern lowlands (Figure 2.15 b-j). However, it must be noted that many of the species that were not sufficiently common for modelling were recorded from Atherton, and one species (sp. B) with one record was recorded only at Finnegan at 200 m a.s.l. (Table 2.1). Models predicted *A. gilberti* and sp. G to have the greatest potential geographic range, followed by sp. K (Figure 2.15, Table 2.2). Distribution maps show there is a high probability that these three species occur in other rainforest subregions in the AWT not surveyed here, including Bartle Frere, Bellenden Ker, Lamb, and Kirrama (Figure 2.15; for map of all AWT subregions see (Williams and Pearson 1997)).

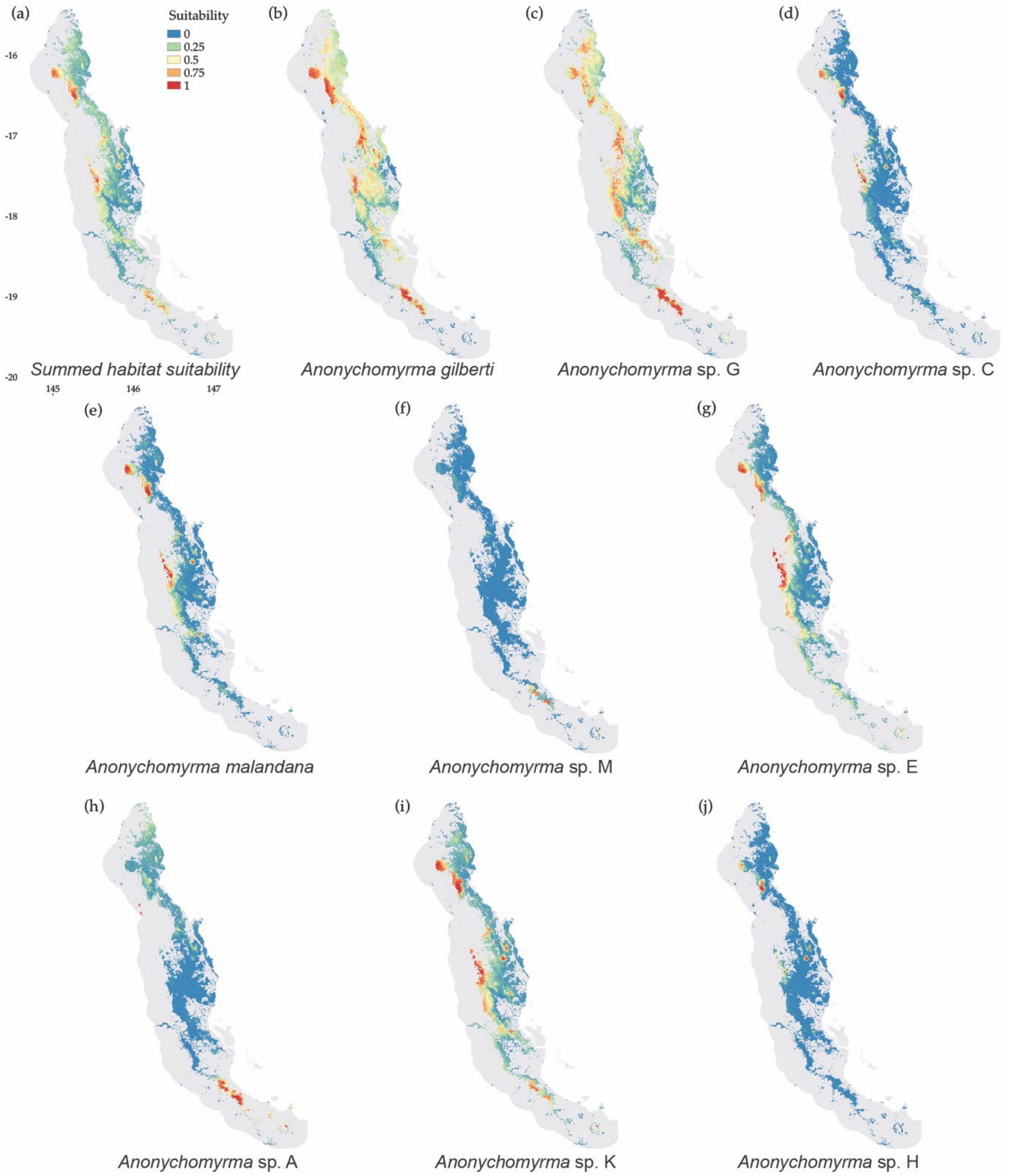

Figure 2.15. (a) Summed rainforest habitat suitability across all species in a grid cell based on the Maxent species distribution model for each species. (b) – (j) Modelled rainforest distributions for nine species of *Anonychomyrma* showing habitat suitability in the AWT bioregion. In all figures, blue is low habitat suitability and red is high habitat suitability, grey background is outline of the AWT region.

Discussion

The Australian Wet Tropics hosts a diverse *Anonychomyrma* fauna whose species show strong geographic patterning. Our genetic and morphological analysis delimited 22 species from our samples, far more than previously recorded in the region. Only two of the species appear to be described. One of these, *A. gilberti* is an ecologically dominant ant in rainforest canopies throughout the region (Blüthgen and Stork 2007, Nowrouzi et al. 2016). The other is *A. malandana*, which was originally described from Malanda on the Atherton Uplands but in our samples was recorded in Windsor and Carbine as well (Figure 2.2). Our samples were from a restricted range of sites in the region and many of our species are known from just one or a few records, which suggests that many additional species likely occur in the AWT.

The distribution and diversity of *Anonychomyrma* within the AWT suggests that this Gondwanan genus has retained a preference for cooler climates. This is evidenced by the concentration of species at elevations above 900 m a.s.l., with only three of the 22 species being recorded at elevation below 300 m a.s.l. The uplands of Windsor and Atherton are centres of particularly high diversity and endemism. Species distribution models also supported this pattern, with summed habitat suitability revealing upland areas of long-term rainforest stability are highly suitable (for AWT map of paleo-geological habitat stability see (Graham et al. 2006)). Such a preference for high elevation is in contrast to the distributional patterns of most other ant taxa in the AWT, and more broadly across the tropics, where ant diversity peaks at low to mid-elevations and drops dramatically at high elevations (Longino et al. 2014, Burwell and Nakamura 2015, Nowrouzi et al. 2016, Longino and Branstetter 2019). A similar distributional pattern for *Anonychomyrma* occurs in Papua New Guinea, where six of eight species surveyed were restricted to high elevation (≥ 900 m a.s.l.) (Plowman et al. 2020). Similarly, in neotropical sites of Central America, several lineages of ants that have a north American temperate climate origin, such as *Temnothorax* (Prebus 2017), are restricted to montane rainforests (Longino and Branstetter 2019).

All eight species surveyed for vertical distribution were strongly arboreal, often foraging from the understorey up into the high canopy. Only a few species were recorded also foraging on the ground. This suggests that arboreality is a strong trait in the tropical clades of *Anonychomyrma* in Australia. Many of the species were noted to nest arboreally in trunk cavities (L. Leahy pers. obs). The two most abundant species (*A. gilberti* and sp. G) had the broadest vertical ranges and had the broadest geographic and elevation ranges, occurring in all subregions and at all elevations. Species with foraging restricted to the canopy tended to have more restricted subregional and elevational distributions. These findings are consistent with the general pattern for AWT ants that vertical niche breadth is positively related to elevation range size (Leahy et al. 2021). This pattern also follows the general macroecological rule that locally common species tend to be widely distributed (Gaston et al. 1997).

Species distribution modelling of nine species strongly supported maximum temperature during the warmest month as an important predictor of distribution, indicating that high temperature is an important factor limiting species distributions. The two most abundant species (*A. gilberti* and sp. G) were more tolerant of higher maximum temperatures, occurring in all sub-regions and across the full elevation range. In our modelling the estimated maximum temperature at which predicted habitat suitability declines is based on a downscaled climatic layer specific to the AWT and is therefore more accurate than a climate layer based on the limited coverage of weather stations in the region (Storlie et al. 2013, Storlie et al. 2014). However, it is important to note that climate circulation models do not account for vertical climatic gradients, whereby the canopy can experience temperatures several degrees warmer than the forest floor (Scheffers et al. 2013, De Frenne et al. 2019). This is an important consideration because the diminutive stature of ants places them close to surface temperatures, which can be far hotter under direct solar radiation, particularly in the canopy (Kaspari et al. 2015). Therefore, given the arboreal habits of *Anoncyhomryma*, maximum temperature exposure is likely to be much higher than the predicted estimates from our species distribution models.

For several species, there was a negative relationship between habitat suitability and rainfall of the wettest month and rainfall seasonality. This could explain the relative depauperate species representation in the uplands of Carbine, where elevations above 1000 m have high rainfall seasonality (Williams and Middleton 2008) and very high rainfall during the wet season. Windsor in comparison, which had the highest species richness, sits in the rain shadow of Carbine and therefore has less rainfall with less seasonality (Williams and Middleton 2008). Similarly, Atherton, also with high species richness and endemism, has relatively low seasonality of both rainfall and temperature. Spec in the extreme south of the AWT had low species richness and may be too dry for most species as its dry seasons are substantially more severe than in the other subregions (Williams and Middleton 2008). Rainfall seasonality is a strong driver of insect abundance throughout the tropics (Janzen and Schoener 1968, Lowman and D 1982, Frith and Frith 1985), including in the AWT (Williams and Middleton 2008). High rainfall seasonality is likely to limit ant distributions through its effect on food availability, particularly honeydew from homopteran insects.

A number of our distribution models predicted species to occur in subregions that were not sampled in this study. Of particular note, although we did not record any *Anonychomyrma* species in the Lamb subregion, several species were predicted to occur there based on availability of suitable habitat. The absence of *Anonychomyrma* at Lamb was therefore likely to be at least partly an artifact of low sampling intensity. Other subregions that had high predicted suitability but were not sampled here include Bartle Frere and Bellenden-Ker. These are the two highest mountain ranges in the Australian Wet Tropics and have not been systematically sampled for ants. They are centres of diversity and subregion endemism for several Wet Tropics species, including the Gondwanan plant species *Eucryphia wilkei,* which is endemic to elevations above 1500 m on Bartle Frere, and whose congeners occur only in Tasmania and Chile (Forster and Hyland 1997, Williams et al. 2010). It is highly likely that the tops of these two mountains harbour additional species of *Anoncyhomyrma*.

There was limited evidence of a biogeographic barrier across the Black Mountain Corridor. Four out of six species that occurred in more than one subregion had distributions north and south of the BMC. Invertebrate taxa such as dung beetles (Aristophanous 2014), earthworms (Moreau et al. 2015), flightless insects (Yeates et al. 2002) and Schizophoran flies (Wilson et al. 2007), that show a biogeographic divide between northern and southern distributions, all have limited dispersal ability compared to ants with winged queens (such as occurs in *Anonychomyrma*), which can be dispersed by wind over long distances, including across biogeographic barriers (e.g. Levins et al. (1973)).

Conclusions

The biogeographic pattern of *Anonychomyrma* in the AWT supports the hypothesis that this genus has a Gondwanan origin and has radiated from a Australian southern temperate distribution into the tropics (Ward et al. 2010). *Anonychomyrma* has persisted and diversified in rainforest areas of cool climate with only a few species reaching into the hotter lowland environments and spreading across multiple subregions (Pianka 1966, Williams and Pearson 1997, VanDerWal et al. 2009b). This mirrors the distributional pattern of the genus in Papua

New Guinea (Plowman et al. 2020) and we would expect a similar pattern to occur in other parts of the genera's tropical range.

Tropical species restricted to upland habitats with a limited geographic range are considered highly vulnerable to anthropogenic climate change (Williams et al. 2003, Williams et al. 2008). The arboreal foraging habits of *Anonychomryma* may provide some options to behaviourally regulate climate exposure given the strong thermal gradient along trees (Huey et al. 2012, Scheffers et al. 2017a, Scheffers et al. 2017b). However, the increasingly warm and more seasonal climate that is forecasted for the Australian Wet Tropics (Williams et al. 2016), along with significant predicted shifts of habitat from rainforest to drier vegetation types (Nowrouzi et al. 2019), places these Gondwanan mountain-top relics under increasing threat.

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Chapter Three - Vertical niche and elevation range size in tropical ants: implications for climate resilience.

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Abstract

Aim: We propose that forest trees create a vertical dimension for ecological niche variation that generates different regimes of climatic exposure, which in turn drives species elevation distributions. We test this hypothesis by statistically modelling the vertical and elevation distributions and microclimate exposure of rainforest ants.

Location: Wet Tropics Bioregion, Australia

Methods: We conducted 60 ground-to-canopy surveys to determine the vertical (tree) and elevation distributions, and microclimate exposure of ants (101 species) at 15 sites along four mountain ranges. We statistically modelled elevation range size as a function of ant species' vertical niche breadth and exposure to temperature variance for 55 species found at two or more trees.

Results: We found a significant positive association between vertical niche and elevation range of ant species. Temperature variance increased with vertical height along the arboreal gradient and ant species exposure to temperature variance explained some of the variation in elevation range size.

Main conclusions: We demonstrate that arboreal ants have broader elevation ranges than ground-dwelling ants and are likely to have increased resilience to climatic variance. The capacity of species to expand their niche by climbing trees could influence their ability to persist over broader elevation ranges. We propose that wherever vertical layering exists - from oceans to forest ecosystems - vertical niche breadth is a potential mechanism driving macrogeographic distribution patterns and resilience to climate change.

Keywords: biogeography, canopy, climate change, climate resilience, vertical niche, range size, temperature gradient, rainforest, ants

Introduction

A key focus of biogeography has been to explain how and why environmental gradients, such as elevation and latitude, shape global biodiversity patterns (Addo-Bediako et al. 2000, Gaston 2000). Within forests, the architecture of trees adds a third environmental gradient with a strong climatic component that could also drive biogeographic patterns (Scheffers et al. 2013, Ashton et al. 2016). Forest species occupy different vertical layers, creating microgeographic patterns in biodiversity at the local or microscale (Sheldon et al. 2018, Oliveira and Scheffers 2019). We pose the question: could the way animals utilise vertical forest structure influence species' distribution patterns at the landscape scale? We investigate this question by exploring the relationship between vertical niche and elevation range size distributions amongst ant species in a tropical forest bioregion. Understanding this relationship between microgeographic patterns in vertical niche use and macrogeographic species' distributions is important in the context of a changing climate (Williams et al. 2008). The association between vertical niche use and elevation range size could indicate potential adaptive responses of species to climate change, including capacity for shifting elevation distributions or vertical movement within the forest strata (Thuiller et al. 2005, Moritz and Agudo 2013, Nadeau et al. 2017).

The ecological niche is a central concept for understanding the spatial structuring of biodiversity (Pulliam 2000). The niche can be conceptualised as a multidimensional space whose axes collectively capture the potential resources a species can use and the environmental conditions under which they can persist (Hutchinson 1957, Kearney and Porter 2004). The niche breadth-range size hypothesis proposes that greater breadth along one or more niche axes should allow a species to occur under a greater range of local conditions and therefore be distributed over a larger geographic area (Slatyer et al. 2013, Kennedy et al. 2017). The complex structure of forests creates a vertical dimension of niche space, including a vertical climate gradient, and increases the diversity of food and nest resources (Blüthgen et al. 2003, Scheffers et al. 2013). As species gain access to the arboreal space, niche breadth should expand along several possible niche axes relating to climatic tolerance and food and nest resources (Kaspari et al. 2016). Species with greater vertical niche breadth should have broader distributions across geographic space than do vertically restricted species (Scheffers et al. 2017b, Scheffers and Williams 2018).

In tropical forests, the vertical climate gradient is ubiquitous and orders of magnitude steeper than climatic gradients associated with elevation or latitude (Scheffers et al. 2013). As such, vertical niche breadth should have a strong association with climatic tolerance (Kaspari et al. 2015). Importantly, not only does the mean temperature change from ground to canopy but temperature variability increases as well - canopy species are exposed to higher temperature variability than those living on the ground (Scheffers and Williams 2018). Thermal adaptation to these microhabitats should result in broad thermal tolerance for arboreal species, and subsequently a broader elevation/geographic distribution, and narrow thermal tolerance for ground species resulting in a more restricted distribution (Calosi et al. 2010, Kaspari et al. 2015, Pintanel et al. 2019). This proposed mechanism is captured by the climate variability hypothesis, which proposes that species exposed to variable climates evolve generalised thermal physiology, allowing those species to traverse climatic gradients along latitude and elevation, resulting in a wider geographic distribution than thermal specialists from stable climates (Janzen 1967, Addo-Bediako et al. 2000, Calosi et al. 2010, Pintor et al. 2015).

Here we test the hypothesis that vertical niche use is positively associated with elevation range and propose exposure to temperature variance as the key underlying mechanism. We test this relationship using the rainforest ant fauna of the Australian Wet Tropics Bioregion.

Ants are an excellent study system for testing scaling rules in biogeography as they fill multiple niches in the rainforest environment and occupy space along both vertical and elevation gradients (Blüthgen et al. 2003, Longino et al. 2019). Ant distribution is strongly related to temperature – temperature requirements for brood development and adult foraging success are both important drivers of ant distributions (Kipyatkov and Lopatina 2015, Penick et al. 2017). Here we focus on foraging niche breadth of adult workers rather than the nest sites of colonies. The persistence of a colony at a site will be contingent on both nest success and foraging success but nests can be buffered from external temperature variation, through either nest construction (Jones and Oldroyd 2006) or social thermal regulation (Villalta et al. 2020), whereas foragers must cope with thermal extremes (Jayatilaka et al. 2011).

The framework for our study is represented in Fig. 3.1. First, we test the premise that arboreality increases exposure to climate variability by examining how mean temperature and temperature variance change along the vertical gradient from ground to canopy. Second, we incorporate vertical niche breadth (how much ground-arboreal space is utilised) into a statistical model of species’ elevation distributions. Along this continuous vertical gradient, we propose three main vertical niche positions: primarily ground-dwelling, semi-arboreal (active in both ground and arboreal habitats), and primarily arboreal. Thirdly, we investigate species’ exposure to temperature variance (derived from microclimate temperature loggers) along the vertical gradient as an explanatory mechanism for elevation range patterns.

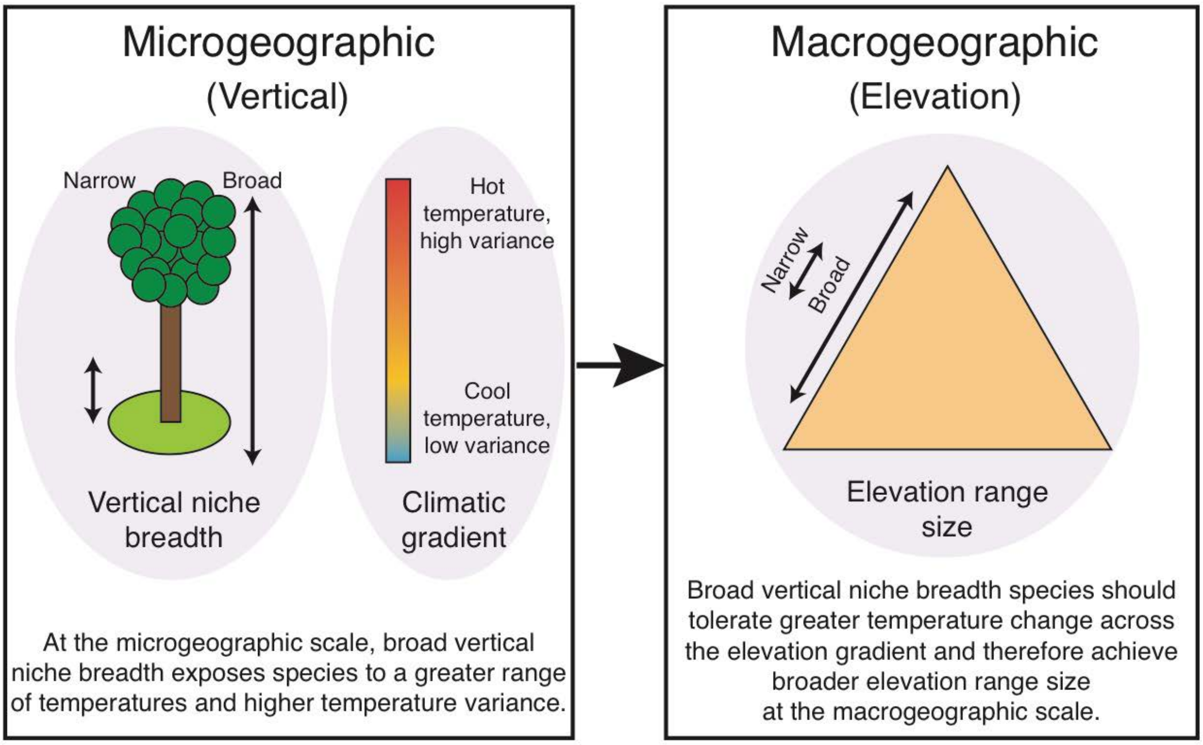

Figure 3.1. Schematic representation of key hypothesis that the microgeographic vertical climate gradient could influence macrogeographic patterns of ant species distribution across elevation. Trees represent a vertical dimension of temperature variance that ant species will be differentially exposed to depending on their vertical foraging niche breadth. We hypothesise that vertical niche breadth will predict elevation range size.

In our models we focus on a subset of factors that we have measured and expect to influence elevation range size. We expect that our measured variables (vertical niche breadth and temperature variance exposure) will impose a limit on species' elevation ranges, creating an upper bound which species cannot exceed. Species will also fall below this upper bound, not reaching their potential elevation range due to unmeasured factors not included in the model, such as interspecific competition (Thomson et al. 1996, Cade et al. 1999, Machac et al. 2011). Such a relationship is expressed as a wedge-shape distribution of points that is bounded by an upper limit (Cade et al. 1999, VanDerWal et al. 2009a) and we are interested in modelling the slope of this upper limit as well as the mean value. We use quantile regression to model these portions of the response distribution, and we expect a stronger rate of change in elevation range size with our explanatory variables at the upper bound of the response distribution than at the mean of the response distribution (Cade and Noon 2003). Finally, we discuss the importance of vertical niche characteristics and elevation distribution patterns in the context of tropical forest species and climate change.

Methods

Study sites

This study was conducted across the Australian Wet Tropics (AWT) Bioregion, Queensland, at long-term monitoring sites (Williams et al. 1995, Williams et al. 2010a). Elevational gradients were sampled in four mountain ranges that represent four of six main sub-regions within the AWT, running from north to south: Mt. Finnegan, Mt. Windsor, Mt. Carbine, and Atherton Range. For more details on sub-regions and a map of elevation sites see Nowrouzi et al. (2016). Rainforest habitat ranged from complex mesophyll vine forests in the lowlands to simple notophyll vine forests in the uplands. Rainfall in the AWT is highly seasonal with 75-90% of the 2000-8000 mm per year falling during the wet season from November to April. In addition, elevations above 1000 m a.s.l. can receive up to 66% of monthly water input from cloud stripping (McJannet et al. 2007). The number of elevation sites sampled for each sub-region varied depending on the availability of rainforest habitat: Finnegan (200, 500, 700 m a.s.l.), Windsor (900, 1100, 1300 m a.s.l.), Carbine (100, 600, 1000, 1200 m a.s.l.) and Atherton (200, 400, 600, 800, 1000 m a.s.l.), which summed to 15 elevation sampling sites.

Sampling

At each elevation site per subregion, we sampled an average of 4 trees per site, at six sites 5 trees were sampled (see Appendix Table S3.1). Trees were sampled using bait traps comprised of plastic vials (1 cm in diameter, 5 cm in length) containing canned tuna in oil, attached to the tree. At each tree, 5 bait traps were set on the ground and every three metres above ground level up to the maximum accessible height of the tree. Survey height ranged from 15 - 27 m, depending on the height of the tree and accessibility (Appendix Table S3.1). Traps were set in the morning and collected 2 - 3 hours later. This design does not sample cryptic ant fauna in the leaf litter, and results in a bias for dominant ant species that recruit large numbers to baits (Agosti et al. 2000). We deemed this an acceptable limitation to the study design, as the primary aim was to document relative patterns for ant species along environmental gradients rather than to document total community diversity. The canopy was accessed using the single-rope climbing technique. At each site, sampled trees were at least 50 m apart and were chosen based on size and climbing accessibility. Finnegan, Windsor, and Carbine Uplands were surveyed from October – December 2012 and Atherton Uplands surveyed from December to February of 2017-2018. Ants were sorted to species and where possible named. Unnamed species were given codes following Nowrouzi et al. (2016). Voucher specimens were deposited in the CSIRO TERC collection in Darwin, Australia.

Microclimate monitoring

We recorded microclimate temperature across the vertical and elevation gradient at the Atherton Uplands. Thermochron data loggers were deployed to record temperature for 43 days in the wet season from Dec 2017-Jan 2018 at Atherton Uplands. A thermochron data logger was placed every 3 m in height from ground to the highest point of the tree at one tree per elevation site along the Atherton Uplands gradient. Thermochrons were shielded from sun exposure and rain, and recorded temperature every 30 minutes. Temperatures recorded between daytime hours of 0800 and 1700 hours, matching the time of our ant sampling, were used in analyses to quantify mean temperature and temperature variance along vertical and elevation gradients, and to derive an exposure to temperature variance value for each species based on that species' occurrence along vertical and elevation gradients.

Analysis

Quantifying temperature change along vertical and elevation gradients

We quantified the change in mean temperature and temperature variance along vertical and elevation gradients using linear regression models. We derived two climate models using linear regression: mean temperature as a function of vertical height and elevation, and temperature variance as a function of vertical height and elevation.

Exploring patterns of vertical niche foraging

We wished to explore how ant species use the vertical gradient for foraging. We classed species into three vertical niche positions using an arboreal score based on their occurrence in tree or ground vials. This was calculated as the proportion of arboreal vials occupied divided by the proportion of vials occupied in total (i.e., arboreal plus ground). Ant species with arboreal scores of <10% were classified as ground-dwelling, between 10% and 90% semi-arboreal, and >90% arboreal. We visualised niche position in relation to vertical niche breadth and the modal value of vertical height (subsequently referred to vertical height mode) using violin plots.

Relationship between vertical niche breadth and elevation range size

Our first aim was to examine the association between vertical niche breadth and elevation range size. We defined vertical niche breadth as the minimum to maximum vertical height of a species recorded across the study area and elevation range as the difference between the minimum and maximum elevation point of the species across the study area. Single records of species are problematic in distributional studies because it is difficult to determine if these species are genuinely geographically rare or simply have a low probability of detection

(Longino and Colwell 1997, Coddington et al. 2009). We therefore considered only 55 species found at two or more trees. We were interested to know if the relationship between vertical niche breadth and elevation range size varies among genera with very different ecological traits (including body size), and so we also ran separate models for the most speciose genera *Pheidole* (Myrmicinae; 19 species) and *Anonychomyrma* (Dolichoderinae; 9 species).

Relationship between exposure to temperature variability and elevation range size

Our second aim was to test whether exposure to temperature variability along the vertical gradient could be an underlying mechanism influencing elevation range. Species with wide elevation ranges will inevitably be exposed to greater temperature ranges, leading to a positive relationship between a species overall temperature range and its' elevation range (Pintor et al. 2015). However, our hypothesis was that a species ability to cope with temperature variability at a given point in its range – due to its vertical niche – should influence that species capacity to distribute over elevation. As such, we derived a location-specific estimate of exposure to temperature variability for each species as the most variable occurrence point where each species was recorded along the vertical and elevation gradients. We used our fitted temperature variance model derived from the Atherton Uplands data loggers to estimate a variance value for each vertical height increment and elevation band at the remaining three sub-regions (Finnegan Uplands, Windsor Uplands, and Carbine Uplands). We then obtained a temperature variance value for each ant capture record based on its vertical height in the tree and the elevation of its occurrence. From this set of values, we defined temperature variance exposure as the temperature variation at the single most variable point for each species (Pintor et al. 2015).

Testing for sampling artefacts and confounding factors

We took into account a potentially confounding effect of a positive abundance-range size relationship as an artefact of common species being sampled at more sites (Gaston et al. 1997), which could still be the case after removing singletons from the study. We included a measure of local abundance for each ant species as a covariate in our vertical niche breadth-range size model and exposure to temperature variance-range size model. Abundance was calculated as the mean proportion of trees occupied at sites where that species was present.

We considered that ant body size could influence an ant's ability to forage over greater distances and therefore play a role in determining vertical niche breadth and range size. As well, body size can alter an ant's thermal exposure – larger ants walk slightly higher above the surface boundary layer and therefore experience cooler operative temperatures than small ants (Kaspari et al. 2015). We had body mass measurements for 22 of our study species from a separate thermal tolerance project in the Carbine Uplands (L. Leahy, unpublished data), and in preliminary analyses we modelled elevation range size as a function of body mass and then modelled vertical niche breadth as a function of body mass as separate models using only these 22 species (see Appendix Table S3.2). Body mass did not have a significant effect on either elevation range size or vertical niche breadth for these 22 species (Appendix Table S3.2) and was therefore not included in further analyses.

We ran several tests to explore how our sampling design may have affected our calculation of vertical niche breadth, exposure to temperature variance, and elevation range size. We tested whether differences in survey height of trees affected our calculation of vertical niche breadth and found a very weak relationship (Appendix Table S3.3). Likewise, differences in survey height of trees had a very weak relationship with exposure to temperature variance (Appendix Table S3.3). We investigated if there was a consistent trend in tree height across elevation, as this could influence the relationship between vertical niche breadth and elevation range size (for survey tree heights see Appendix Table S3.1) but found no trend in vertical tree height with elevation (Appendix Table S3.4). Finally, we tested whether differences in maximum elevation and total elevation range of each of the four mountains affected our calculation of elevation range size and found no substantial relationship (Appendix Table S3.5).

Statistical models

We used generalised linear models (GLM) with a gamma distribution and a log link function to model the change in the mean of the response variable – elevation range – as a function of the predictors – vertical niche breadth and mean local abundance. In a separate model we modelled elevation range as a function of exposure to temperature variation and mean local abundance. A gamma distribution with a log link function was chosen because the response variable, elevation range, was positive and highly right skewed rather than following a Gaussian distribution. Predictor variables were scaled to obtain standardised beta coefficients and we took the log of local abundance. Variance inflation was checked and there was no evidence of collinearity between the covariates in either model. Each model was run with interactions between the covariates and as an additive model. Model performance was evaluated using Akaike information criterion (AIC_c) values (Appendix Table S3.6); the most parsimonious and best performing models are reported. To model the upper bound of the relationship between elevation range and the explanatory variables we used quantile regression. Thus, we modelled two parts of the relationship: both the mean (0.5 quantile) and upper limit (0.9 quantile) for each model. Quantile regression was performed using the R package quantreg ver. 5.51 (Koenker 2019); for more information on quantile regression see Cade et al. (1999) and Cade and Noon (2003). To assess the performance of each model, including quantile regressions, we used a pseudo R^2 measure that was estimated using equations of Nagelkerke (1991) and the package rcompanion ver. 2.3.0 (Mangiafico 2019).

This measure permits comparison of all regression models used, as it is not limited to simple linear regressions. All analyses were performed in R ver. 3.5.1 (http://www.R-project.org).

Results

Mean temperature increased with vertical height and decreased with elevation in the linear model (LM, $F_{2, 32} = 148.7$, $p < 0.001$, Adjusted $R^2 = 0.9$; Table 3.1, Fig. 3.2a and 3.2b). Variance in temperature increased with vertical height but not with elevation (LM, $F_{2, 32} = 28.8$, $p < 0.001$, Adjusted $R^2 = 0.62$; Table 3.1, Fig. 3.2c and 3.2d). Recorded daytime temperatures ranged from 16–38 °C across the elevation gradient over the two months of temperature sensor deployment during the wet season. The degree of temperature variance varied markedly with vertical position (Fig. 3.2d). Median temperature variance over the period of sensor deployment was 3.13 °C on the ground compared to 12.9 °C in the high canopy at 24 m (Fig. 3.2d). Temperature variance increased sharply from ground to 3 m, gently increased in the understorey and sub-canopy, between 3 m and 18 m, before sharply increasing in the high canopy between 21 and 24 m (Fig. 3.2d). The increasing temperature variance with vertical height was driven by increasing maximum temperatures, while minimum temperatures remained relatively static as shown in Fig. 3.2b by the outlying maximum temperature points that fall on the upper side of the boxplots.

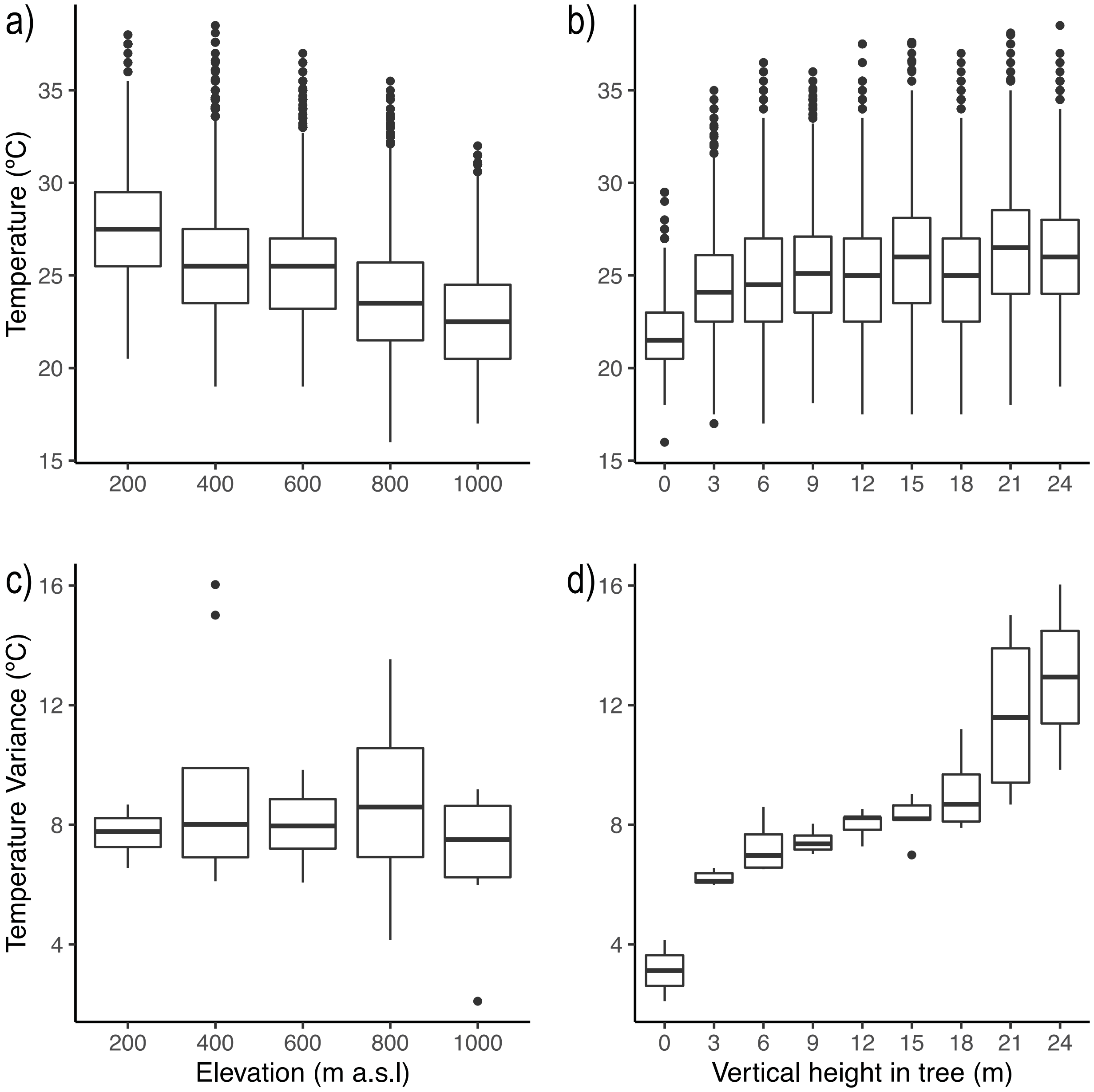

Figure 3.2. Temperature recorded every half hour over a) elevation and b) vertical height (in the tree) and mean temperature variance for period of deployment for c) elevation and d) vertical height from data loggers placed every three metres into trees at five elevation sites (200, 400, 600, 800, 1000 m a.s.l.) and set to record temperature every half hour for 43 days at Atherton Uplands during Wet Season 2017-2018. All data from daytime hours between 0800 and 1700 hours. Box plots show the median (central band), 25th and 75th percentiles (bottom and top of boxes) and 1.5 times the interquartile range above or below the 25th and 75th percentiles (whiskers) and points show outliers above or below this.

A total of 11, 770 individual ants from 101 species from 30 genera were collected at the 60 trees across the 15 elevation sites and four sub-regions. Forty-six species were recorded only once at one tree and therefore excluded from analysis. Semi-arboreal ant species foraged over the greatest extent of the tree with an average vertical niche breadth of 19.6 ± 2.1 m; however, they were generally concentrated in the lower sections of the tree (vertical height mode averaged 4.8 ± 1.6 m, Fig. 3.3b). Some ground-dwelling ants made very occasional forays into the arboreal zone, but average vertical niche breadth was only 4.2 ± 1.6 m (Fig. 3.3a and b). The average vertical niche breadth of arboreal specialists was 11.5 ± 1.3 m (Fig. 3.3a), and they tended to be concentrated in the upper parts of the tree and canopy (vertical height mode averaged 14.0 ± 1.0 m, Fig. 3.3b).

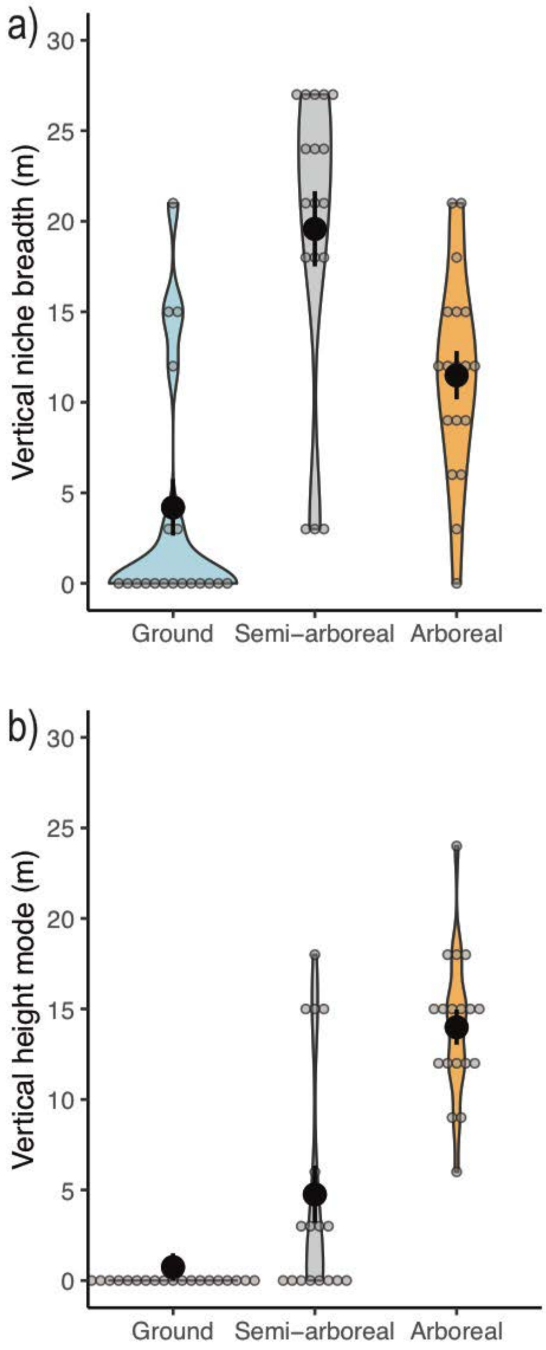

Figure 3.3. a) Vertical niche position and vertical niche breadth and b) Vertical niche position and vertical height mode for 55 ant species based on their vertical distributions from ground to canopy at elevation sites along four mountain ranges in the Australian Wet Tropics Bioregion. Black dots and whiskers show mean ± se, grey points are each species vertical niche breadth and vertical height mode respectively, coloured violins represent kernel probability density of the data for each point on the y axis.

The vertical niche breadth model that included local abundance explained some variation in the elevational range of the ant species (GLM, Pseudo $R^2 = 0.26$, Table 3.1). Vertical niche breadth had a positive association with elevation range size, and the model predicted 1.5 times (95% CI: 1.25 – 1.75) increase in elevation range for every one-metre increase in vertical niche breadth (Table 3.1 and Fig. 3.4). In the same model, local abundance had a weak but negative relationship with elevation range size (GLM, 0.76 times decrease, 95% CI: 0.64 – 0.92, Table 3.1 and Fig. 3.5). At the 0.9 quantile of the relationship between vertical niche breadth and elevation range size (including local abundance as a covariate), more variation in elevation range size was explained than when we modelled the mean of the relationship (Quantile regression, 0.9 quantile, Pseudo $R^2 = 0.38$, Table 3.1 and Fig. 3.3). In Figure 3.4, the distribution of data points (species) are bounded by the upper limit (0.9 quantile) of species' elevation range with a large scatter of points below the upper limit, creating a wedge-shaped distribution of data points. The slope of the relationship between vertical niche breadth and elevation range at the 0.9 quantile was similar to the slope of the relationship at the mean; the model predicted a 1.32 times (95% CI: 1.2 – 1.81) increase in elevation range with every one metre increase in vertical niche breadth (Table 3.1 and Fig. 3.4). There was no relationship between local abundance and elevation range size at the 0.9 quantile (Quantile regression, 0.96 times decrease, 95% CI: 0.6 – 1.06, Table 3.1). A similar pattern was found when the two dominant genera were considered as separate models; *Pheidole* (GLM, *n = 19 species*, Pseudo $R^2 = 0.3$, 1.44 times increase in elevation range for every one metre increase in vertical niche breadth, 95%: 1.13 – 1.87) and *Anonychomyrma* (GLM, *n = 9 species*, Pseudo $R^2 = 0.58$, 1.95 times increase 95% CI:1.3 – 2.8) both showed a positive association between vertical niche breadth and elevation range size but no relationship between local abundance and elevation range size (Fig. 3.4, Table 3.1).

Table 3.1. Linear models for mean temperature and temperature variance across vertical tree height and elevation from temperature data loggers deployed in Atherton Uplands, Wet Tropics Bioregion, Australia. Generalised linear models (GLM) for elevation range as a function of vertical niche breadth and exposure to temperature variability as separate models, including local abundance as a covariate. Each model is presented for the mean (using GLM) and 0.9 quantile (using quantile regression) for 55 ant species surveyed across four mountains in the Wet Tropics Bioregion, Australia. Vertical niche breadth model also presented for the mean (GLM) as separate models for two of the common ant genera in the study area *Pheidole* (n = 19 species) of the Myrmicinae subfamily and *Anonychomyrma* (n = 9 species) of the Dolichoderine subfamily. For all models, coefficients and lower and upper 95% confidence intervals are presented and the Adjusted R^2 or Nagelkerke Pseudo R^2.

Temperature regression models	**Est. coef.**	**Lower CI**	**Upper CI**	**Adj. R^2**
Mean Temp ~ Elevation +Vertical height				0.9
Intercept	27.056	26.4	27.7	
Elevation	-0.005*	-0.006	-0.004	
Vertical height	0.124*	0.09	0.16	
Temp variance ~ Elevation + Vertical height				0.62
Intercept	4.84	3.08	6.6	
Elevation	0.00	-0.002	0.002	
Vertical height	0.3*	0.22	0.38	
Vertical niche breadth models: **All species**	**Est. coef.**	**Lower CI**	**Upper CI**	**Pseudo R^2**
GLM all species: *Elevation range ~ Vertical niche breadth + local abundance*				0.26
Intercept	472	407	552	
Vertical niche breadth	1.5*	1.25	1.75	
Local abundance	0.76*	0.64	0.92	
0.9 quantile regression all species: *Elevation range ~ Vertical niche breadth + local abundance*				0.4
Intercept	837	728	935	
Vertical niche breadth	1.32*	1.2	1.81	
Local abundance	0.96	0.6	1.06	
Vertical niche breadth models: ***Anonychomyrma* and *Pheidole***	**Est. coef**	**Lower CI**	**Upper CI**	**Pseudo R^2**

***GLM Pheidole*:** *Elevation range ~ Vertical niche breadth + local abundance*				0.3
Intercept	413	328	531	
Vertical niche breadth	1.44*	1.13	1.87	
Local abundance	0.8	0.62	1.04	
GLM Anonychomyrma: *Elevation range ~ Vertical niche breadth + local abundance*				0.58
Intercept	435	304	654	
Vertical niche breadth	1.95*	1.3	2.8	
Local abundance	0.78	0.51	1.17	
Exposure temp. variance models				
GLM all species: *Elevation range ~ Exp. Temp. variability + local abundance*				0.17
Intercept	483	414	568	
Exposure temperature variability	1.35*	1.15	1.6	
Local abundance	0.83	0.7	1.0	
0.9 quantile regression all species: *Elevation range ~ Exp. temp. variability + local abundance*				0.35
Intercept	888	780	953	
Exposure temperature variability	1.34*	1.15	1.56	
Local abundance	0.99	0.64	1.1	

*** = significance p < 0.05**

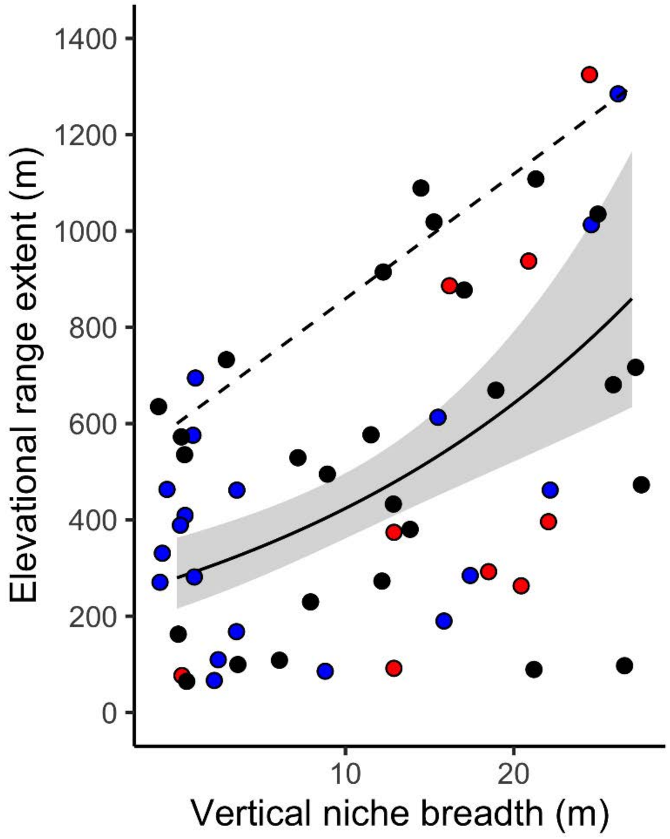

Figure 3.4. Vertical niche breadth (m) of ant species (n = 55) and elevation range extent (m), based on ant species vertical distributions from ground to canopy and occurrence across elevation along four mountains in the Australian Wet Tropics. Solid line fitted from the GLM model (Table 3.1) with a gamma distribution and log-link function and 95% confidence intervals, dotted line fitted from 0.9 quantile regression model (Table 3.1). Coloured circles show two common ant genera in the study area, blue = *Pheidole* (Subfamily: Mrymicinae, n = 19), and red = *Anonychomyrma* (Subfamily: Dolichoderinae, n = 9), black = all other genera.

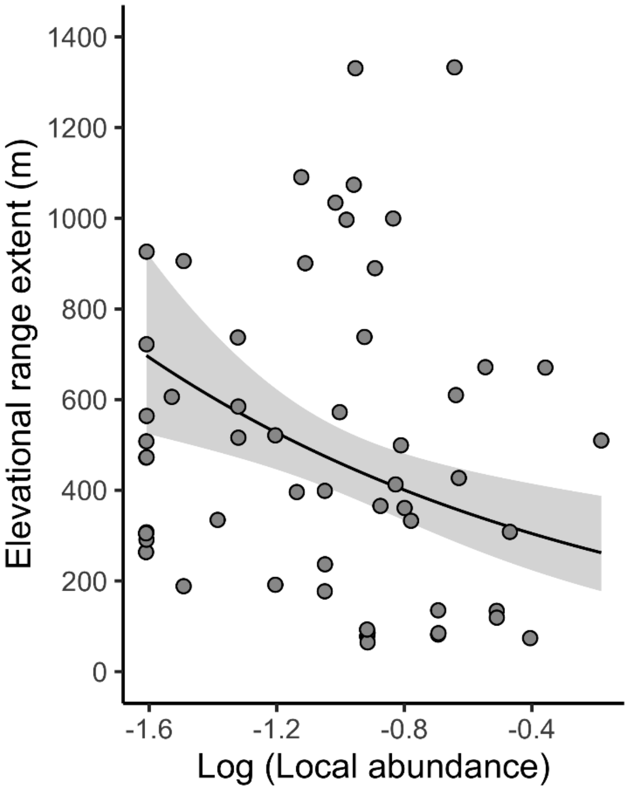

Figure 3.5. Log of mean local abundance for ant species (n = 55) and elevation range extent (m) based on occurrence of ant species across elevation along four mountains in the Australian Wet Tropics. Lines fitted from the model (Table 3.1) with a gamma distribution and log-link function and 95% confidence intervals.

There was a positive association between exposure to temperature variance (calculated from temperature sensors and each species' location records) and elevation range size, however there was some variation left unexplained by the model. The mean model explained less variation in elevation range size compared to the 0.9 quantile model (GLM: Pseudo R^2 = 0.17 compared to 0.9 quantile model: Pseudo R^2 = 0.35; Table 3.1, Fig. 3.6). For the mean model, there was 1.35 times (95% CI: 1.15 – 1.6) predicted increase in elevation range with increasing temperature variance exposure. The effect size was almost identical (1.34 times; 95% CI: 1.15 – 1.56) for the 0.9 quantile model. Notably, the eleven species with the greatest elevation range size (> 800m elevation range size) were all exposed to high degree of temperature variance (Fig. 3.6). In the exposure to temperature variance model, there was a very weak negative relationship between local abundance and elevation range at the mean of the relationship (0.83, 95% CI: 0.7 – 1.0) and no effect of local abundance on elevation range at the 0.9 quantile (0.99, 95% CI: 0.64– 1.1) (Table 3.1).

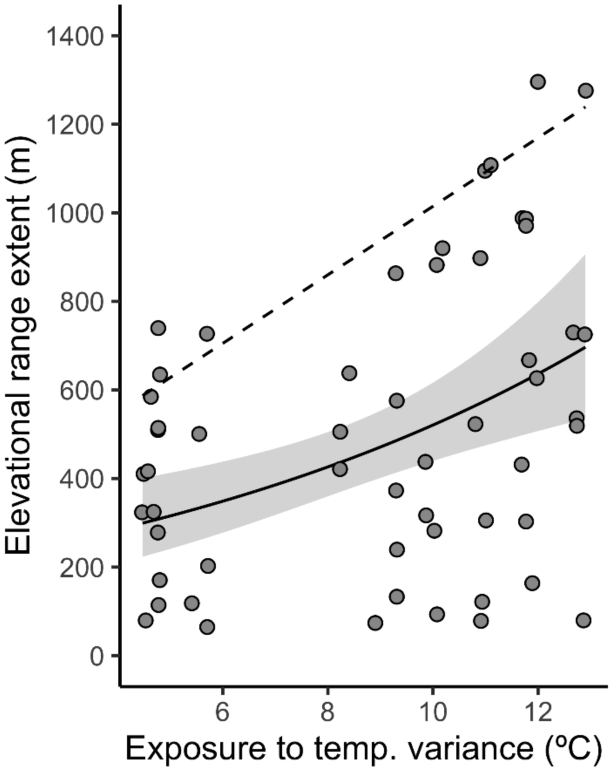

Figure 3.6. Exposure to temperature variability (℃) for ant species (n = 55) and elevation range extent (m), derived from temperature sensor deployment, and ant species vertical distributions from ground to canopy and occurrence across elevation along four mountains in the Australian Wet Tropics. Lines fitted from the model (Table 3.1) with a gamma distribution and log-link function and 95% confidence intervals, dotted line fitted from 0.9 quantile regression model.

Discussion

We found that ant species using more of the vertical tree space tend to have broader elevation ranges. Ant species with the broadest vertical niche foraged from the ground up to the high canopy, and vertical niche breadth was positively associated with elevation range. This pattern was consistent when considering all species (n = 55 species) and two contrasting genera (*Pheidole* and *Anonychomyrma*) separately. Local abundance was weakly and negatively correlated with elevation range size, a pattern that is not consistent with the widely reported positive abundance-range size relationship often found for vertebrate taxa (Gaston et al. 1997). Arboreal species were exposed to far higher levels of climatic variation than were ground-restricted ants. There was support for the hypothesis that exposure to temperature variability influences the relationship between a species' vertical niche use and elevation range. Overall, our results suggest that the ecological flexibility to forage in ground and canopy habitats in combination with climate variability exposure are factors determining the capacity of species to occur across broader climatic and geographic gradients (Kennedy et al. 2017).

The differences in elevation range size were not explained by differences in species abundances, which is a commonly confounding factor (Brown 1984, Gaston et al. 1997). Indeed, contrary to expectations we found a (weakly) negative association between local abundance and range size for ant species. One would expect that locally dominant and abundant ants would also be the most widespread over geographic space (Gaston et al. 1997), but we found the opposite pattern. Although small range size is often associated with being locally rare, the opposite can be true in locations where strong extinction filtering has occurred (Johnson 1998). Species with restricted ranges can persist through high local abundance (Johnson 1998). This appears to be the case for vertebrates in the Australian Wet Tropics Bioregion where repeated habitat contractions have filtered species assemblages leading to a negative relationship between local abundance and range size (Williams et al. 2006, Williams et al. 2009).

Our quantile regression modelling showed that vertical niche breadth and exposure to temperature variance imposed an upper bound on elevation range. Other factors we have not measured, including climatic variability over an annual cycle (Chan et al. 2016), temporal foraging activity (Levy et al. 2019), interspecific competition (Andersen 2008), dispersal ability (Scheffers et al. 2017b), and the distribution of nest sites and food resources (Yanoviak and Kaspari 2000), also potentially influence exposure to climatic variance and therefore elevation range size.

Species varied widely in their use of the vertical gradient. Semi-arboreal ant species had the greatest vertical niche breadth, whereas arboreal specialists were concentrated in the higher parts of the tree. The ability of semi-arboreal species to forage at multiple vertical layers allows them to exploit the full temperature gradient along with a potentially wider range of food resources (Yanoviak and Kaspari 2000). Some of our arboreal specialists were restricted to specific microhabitats such as epiphytes, and so would be buffered from temperature variability, inhabiting a climatically stable environment similar to ground-restricted ants (Blüthgen et al. 2004, Scheffers et al. 2014). Others forage along branches and trunks and would be exposed to high climate variability (Blüthgen et al. 2004, Stark et al. 2017). Therefore, microclimate exposure will differ between species depending on both vertical niche and foraging microhabitat. Mammola et al. (2019) report a similar pattern in cave spiders: deep cave specialists were adapted to low climate variability and had narrow elevation ranges compared to non-specialised cave spiders that were exposed to more variable climates associated with cave openings.

We considered that body size could influence the ability of an ant to forage over the vertical gradient, yet for 22 of our study species we found no relationship between body mass and vertical niche breadth or body mass and elevation range size. The two most speciose genera in the study are quite different in their morphology and ecology; the tiny *Pheidole* in our study had a mean body mass of 0.07 mg, compared with 0.24 mg for *Anonychomyrma*. Yet both genera showed the same pattern to the total species model whereby broad vertical niche breadth was positively correlated with elevation range size. This indicates that there is a general ecological – and possibly climatic – advantage to behavioural flexibility along the microgeographic gradient, allowing species to become more widespread along the macrogeographic (elevation) gradient.

Many of the ant species recorded in our study area were highly restricted in either vertical niche breadth or elevation range. Species with a narrow niche breadth and distribution could be vulnerable to climate change due to the synergistic effects of restricted elevation range size, sensitivity to climate variation, and limited ability to compensate behaviourally through vertical movement (Thuiller et al. 2005, Williams et al. 2008, Huey et al. 2009). Semi-arboreal generalist species with a broader vertical niche and elevation range have more options (Scheffers et al. 2017b), having the capacity to shift their vertical position to compensate for broader scale shifts in the climate-environment or shift their geographic distribution further up the mountain as the lowland climate warms. Recent research found a positive correlation between verticality and resilience to climatic instability for several vertebrate taxa in the Australian Wet Tropics, where arboreal species dominated in areas with historically unstable climates (Scheffers et al. 2017b). A similar pattern might be expected in tropical invertebrates, as species distribution and persistence in space and time are generally tightly coupled to climate and temperature (Davison and Chiba 2008, Bonebrake and Deutsch 2012, Burwell and Nakamura 2015). The pattern for ants that we have presented here provides further support to the idea that arboreality is an important trait for assessing relative vulnerability to climate change in rainforest biomes (Scheffers and Williams 2018). Arboreality may have provided species with the tools to overcome climatic instability in the past and could provide resilience to future climate change (Thuiller et al. 2005, Davison and Chiba 2008, Nadeau et al. 2017, Scheffers et al. 2017b). Our findings can be applied more broadly to vertically layered systems such as freshwater lakes (Kennedy et al. 2017), oceans (Hays et al. 2009) and caves (Mammola et al. 2019), where vertical niche is associated with climatic exposure and is therefore a potential mechanism driving macrogeographic patterns and resilience to climate change.

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Chapter Four - Community turnover of ants in the rainforests of the Australian Wet Tropics: elevation and arboreality

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Abstract

Climatic conditions in tropical forests vary markedly across vertical space, such that ground-active species experience low climatic variation while arboreal species are exposed to highly variable climates. Along mountain gradients, thermally variable microhabitats will create bands of overlapping thermal conditions between each elevational zone, reducing the role of elevation as a climatic barrier for arboreal species, while low thermal variability microhabitats will form non-overlapping thermal bands, reinforcing elevation as a barrier for ground-dwelling species. We predicted, therefore, that ground communities accustomed to a stable microclimate should be more elevationally restricted and consequently have higher rates of species turnover over elevation compared to arboreal communities whose microclimate is variable. We sampled ground-active and arboreal ants along elevation gradients at four mountain subregions in the Australian Wet Tropics Bioregion. We assessed community composition at three spatial scales (regional, elevation, vertical), and then calculated beta diversity (species turnover) over elevation for ground and arboreal communities, using null modelling procedures to compare different sized species pools. On average, the ground community showed higher turnover and exhibited an elevational distance-decay pattern, while the arboreal community had lower turnover with no relationship between turnover rate and elevational distance. Ground ants are elevationally restricted and have high rates of turnover across elevation, which could make those communities more vulnerable to global warming. Vertical climate gradients are ubiquitous in tropical forests, creating a microgeography of environmental variation that influences patterns of community composition.

Introduction

A key goal of ecology is to predict how environmental variation influences different processes across levels of ecological organisation. Thermal variation can have profound impacts across different biological scales, strongly influencing individual physiology and species distributions up to the organisation and structure of communities through space and time (Huey and Hertz 1984, Holt et al. 2004, Nadeau et al. 2017, Oliveira et al. 2020). Janzen's seasonality hypothesis (1967: *American Naturalist*) linked these biological and climatic scales into a simple framework. Janzen observed that for thermally stable environments such as the tropics, there is little thermal overlap between different elevational bands across mountains, whereas in thermally variable environments, such as the highly seasonal temperate zone, there is a large degree of thermal overlap across mountains.

The implication was that tropical species adapted to a narrow range of temperatures will encounter physiological barriers to dispersal along mountain gradients and consequently have restricted elevational distributions compared to temperate species (Ghalambor et al. 2006, Sheldon et al. 2018). These predictions can then be scaled up to the community level: differences in degree of thermal overlap between elevation bands should explicitly create non-random heterogeneity in species composition along elevation gradients. This should create the conditions for a high rate of species turnover (beta diversity) across tropical mountains (Fagan et al. 2006, Jankowski et al. 2009, Archibald et al. 2013, Zagmajster et al. 2014).

Although Janzen's original hypothesis compared differences in seasonality across latitude, there is mounting evidence the same principles can be applied at smaller geographic (microgeographic) scales. The strongest examples of this have come from forests, where the vertical structure of a tree creates a strong gradient of climatic variability (Scheffers et al.

2013, Scheffers and Williams 2018, Leahy et al. 2021a). As such, arboreal fauna generally experience a hotter, drier, and more climatically variable environment than ground-dwelling fauna (Scheffers et al. 2017a, Leahy et al. 2021a). Due to this inherent difference in thermal variability, soil, and leaf-litter temperatures (stable environment) form distinct thermal profiles from one elevation band to the next, but canopy temperatures (variable environment) overlap across elevation (Scheffers and Williams 2018, Klinges and Scheffers 2021). Thus, arboreal species are exposed to more similar temperatures across elevation gradients, and this could reduce the barriers to dispersal over mountains compared to elevationally restricted ground-dwelling species (Sheldon et al. 2018).

In support of this hypothesis, Leahy et al. (2021a) (Chapter 3) demonstrated a positive relationship between ant distributions across vertical tree gradients, exposure to thermal variation, and elevation range size. Additionally, ground-dwelling ant species have narrower thermal tolerance ranges compared to arboreal- or canopy-based ant species (Baudier et al. 2015, Kaspari et al. 2015, Leahy et al. 2021b). This provides compelling evidence that vertical gradients influence both exposure and sensitivity to thermal variation and could, therefore, influence a species capacity to traverse broader climatic gradients such as elevation. In cave systems, Mammola et al. (2019) also extended Janzen’s hypothesis, finding that horizontal gradients of thermal variability within caves select for contrasting thermal tolerance ranges of cave spiders and was correlated with the elevational range size of different species. Therefore, thermal variation at the microscale appears to influence thermal traits and patterns of species distributions across broader climatic gradients and we would predict that influence to extend to patterns of community turnover along these gradients.

The theoretical framework for understanding community patterns based on this hypothesis is outlined in Figure 4.1. We explore community composition across the three spatial scales of region (between subregions/mountain ranges), elevation, and verticality, and apply Janzen's hypothesis at the microgeographic scale, by exploring how thermal variation along vertical (tree) gradients influences community patterns along elevation using rainforest ants in the Australian Wet Tropics Bioregion. We predict that ground ant communities should have higher compositional change between elevational sites and a faster rate of species turnover than arboreal ant communities (Fagan et al. 2006, Davison and Chiba 2008, Oliveira and Scheffers 2019, Antoniazzi et al. 2020). Therefore, ground ant communities should follow an elevational distance-decay pattern, whereby sites that are closer together along the elevational gradient are more similar to each other in species composition but become increasingly dissimilar with further elevational distance.

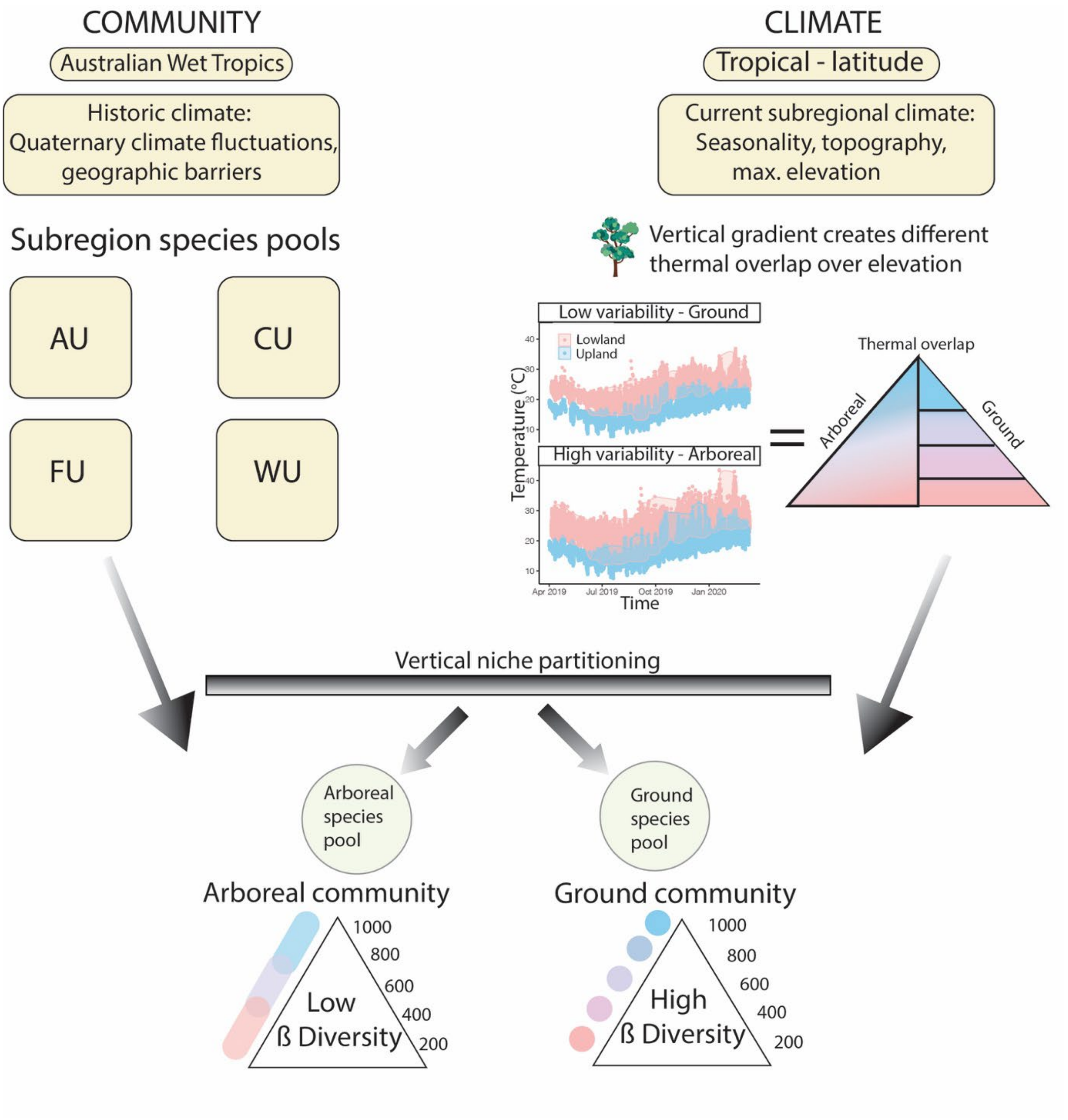

Figure 4.1. Schematic representation of the factors leading to the proposed hypothesis that vertical niche is associated with rates of species turnover over elevation. Both climate and the regional community influence rates of species turnover. At the regional scale, species composition in the Australian Wet Tropics has been influenced by long-term geological and biogeographic factors. The tropical latitude creates the broad climate conditions of the region. The community of each subregion is likely influenced by historic climate events, geographic barriers to dispersal. At the subregion scale of each mountain range (AU = Atherton, CU =

Carbine, FU = Finnegan, WU = Windsor), the contemporary climate is influenced by differences in temperature and precipitation seasonality, topographic features, and mountain height, that each vary amongst the subregions. The vertical climate gradient creates differences in thermal variability through time (temperature data collected in ground and arboreal habitats at lowland and upland elevation sites at between April 2019–April 2020 in Atherton and Carbine Uplands), such that there is greater overlap of thermal conditions across elevation in arboreal than ground habitats. The subregion species pool is further partitioned into vertical niche positions of ground and arboreal, creating two separate communities. Thermal overlap combines with dispersal and creates different probabilities of species encountering unfamiliar climates as they move up mountains. This drives different rates of species turnover over elevation. Note that biotic factors and stochastic events are also likely to play a role in determining species turnover rates.

Beta diversity is a powerful tool for quantifying changes in community composition and can be used to compare rates of change between distinct communities, such as, in this case, ground and arboreal rainforest ants (Fitzpatrick et al. 2013, Socolar et al. 2016). Beta diversity is the ratio between gamma diversity, representing the regional species pool, and alpha diversity, representing the mean local species diversity at a set of sites/units (Whittaker 1960). Beta diversity can be partitioned into two components: turnover (species replacement) and nestedness (the directional loss or gain of species over a gradient) (Baselga 2010, Ulrich and Almeida-Neto 2012). Here we extract the species turnover component of beta diversity to explicitly examine species replacement across elevation.

Ant beta diversity has generally been assessed for either ground or arboreal communities separately along elevation (Longino and Colwell 2011, Bishop et al. 2015, Nowrouzi et al. 2016, Plowman et al. 2020) and latitude (Majer et al. 2001). We utilise the same sampling methodology (baiting) in ground and arboreal habitats, thereby facilitating a direct comparison of beta diversity for each community across the same geographic extent (Antoniazzi et al. 2020). We account for the potentially confounding effects of comparing two different sized communities (ground and arboreal) by using null modelling procedures (Chase and Myers 2011, Kraft et al. 2011, Ashton et al. 2016).

In an initial analysis we investigate overall patterns of community composition across the three spatial scales of vertical, elevation, and subregion (between mountain ranges) to understand which climatic gradients are most pertinent in driving community structure across the region. We then assess species composition along the vertical gradient specifically, to explore how species partition the vertical gradient and whether ground and arboreal communities are compositionally distinct. From this standpoint, we then compare patterns of beta diversity and elevational distance-decay for ground and arboreal communities separately across the elevation gradient. We discuss the implications of our findings for predicting community-wide responses to climate change.

Methods

Study sites and sampling

Study sites, ant sampling design, and protocol outlined in Chapter Three and published in Leahy et al. (2021a).

Analysis

Species diversity and community composition

Firstly, we investigated the effect of subregional, elevational, and vertical gradients on community structure to establish which of these climatic gradients explained the most variation in community composition. We used a PERMANOVA (using ‘adonis2’: all multivariate analysis used package *vegan* ver. 2.5 (Oksanen 2013)) with vertical height (0–27 m), elevation, and subregion (four subregions) as fixed factors and 999 permutations. In this specific analysis the “sites” are the concatenation of subregion, elevation, and vertical height (every three metres) with 101 species collected across the region. As we had an unbalanced design due to the different elevational extents of each subregion, we tested the marginal effects of each factor rather than using sequentially added terms (McArdle and Anderson 2001). We created a dissimilarity matrix using a species-by-site table with species abundances calculated as the proportion of trees occupied at each site and the Bray-Curtis dissimilarity index. We removed one site (AU, 1000 m a.s.l., 15 m) as this was identified as an outlier and removal substantially improved convergence of the model. We used the percentage of explained variance (partial R^2) to compare effect sizes between the three factors. Multivariate dispersion was evaluated for each explanatory factor separately (using ‘betadisper’) and elevation sites were found to have different dispersion. However, given the strong difference between centroid means (visualisation using nMDS), our model results were considered satisfactory. Community composition was then visualised with an ordination plot following non-metric multidimensional scaling (using ‘metaMDS’) with k = 3 dimensions and 999 permutations. The correlation of subregion, elevation, and vertical height, with nMDS axes was visualised with boxplots. To ease visualisation in these boxplots, the ground and arboreal strata were classed as categorical with 0m = ground, and 3–27m = arboreal on the x-axis.

Vertical strata

Secondly, we investigated whether the ant community is partitioned into distinct vertical strata at the local scale. A distinct disjuncture in species composition between ground and arboreal habitats in this analysis provides an evidential basis for classing ground and arboreal species as distinct communities. We pooled all data from each subregion, elevation site, and individual tree plots and constructed a species-site matrix with species presence-absence and each 3 m in vertical height (sampling points) as sites. In this specific analysis, pooling data across sites allowed us to investigate the vertical gradient in isolation without the overarching effect of elevation, as we predicted elevation would have a strong effect of community composition. We then performed an ordination using non-metric multidimensional scaling (‘metaMDS’) using the jaccard dissimilarity index (appropriate for presence-absence), and k = 2 dimensions with 999 permutations and plotted the results to visualise whether there was separation between ground and arboreal vertical heights.

Beta diversity

To compare beta diversity for ground and arboreal communities, we assigned species to each vertical community based off 90% frequency of occurrence in samples in their respective vertical habitat. We classed species based on their occurrence in tree or ground vials. For each species, we first summed the number of vials a species occurred in at every three-metre vertical sampling point (0 m, 3m… 27m). We then pooled arboreal vial occurrences together (i.e., number of vials occurred in at 3 m + 6 m + 9 m…27 m) and divided this number by the total number of arboreal vials deployed across the study (i.e., number of vials deployed at 3 m + 6 m + 9 m… 27 m). We then divided the number of ground (0 m) vial occurrences by the number of ground vials deployed across the study. This standardised frequency of occurrence in a stratum by survey effort. We then calculated an arboreal occurrence score as the proportion of arboreal vials occupied divided by the proportion of vials occupied in total (i.e., arboreal plus ground). Ant species with arboreal scores of <=10% were classified as ground-dwelling and the rest as arboreal. This is a more accurate division of the niche difference for this analysis than using the raw presence-absence data as many species (particularly arboreal species) had occasional vagrants in the other vertical strata (e.g., primarily arboreal species with some records on the ground, or ground species with occasional records in trees (Leahy et al. 2021a)).

We calculated pairwise beta diversity metrics for each community (ground and arboreal) through pairwise comparisons (n = 44) between each set of elevation sites within each subregion. We partitioned beta diversity into three metrics following the methods of Baselga (2010); *total compositional change* ($ß_{sor}$), which is the Sørensen dissimilarity index, *turnover* ($ß_{sim}$), which is compositional change due to species replacement, and *nestedness* ($ß_{sne}$), which is the difference between $ß_{sor}$ and $ß_{sim}$ and represents the compositional change due to directional species loss or gain. We used species presence-absence data and calculated the metrics using 'beta.pair' function of package *BETAPART* ver. 1.5.2 in R (Baselga and Orme 2012). We then extracted the species turnover ($ß_{sim}$) component for downstream analyses, as this was required for our specific research question. To determine whether mean species turnover values (across all pairwise elevation sites) differed for ground and arboreal communities, we used Wilcoxon rank sum tests.

Elevational distance-decay

To test for a distance-decay pattern in species turnover over elevational distance for ground and arboreal communities respectively, we used generalised linear models (GLM). Under Janzen's (climate variability) hypothesis, we would expect species turnover to be a function of interaction between vertical niche (ground or arboreal) and elevational distance. Specifically, the intercept and slope of the relationship between ground community turnover and elevational distance should be higher and stronger than for the arboreal community. We modelled the response variable (species turnover) as a function of vertical niche and elevational distance using a Beta family distribution and logit-link function using package *glmmTMB* (Brooks et al. 2017). Not to be confused with beta diversity, the Beta family is commonly used distribution in generalised linear models to model response values ranging between 0–1 (Ferrari and Cribari-Neto 2004, Zeileis et al. 2010). Elevational distance was calculated as the difference between pairwise sites, for example, 200 m in elevational distance could be 400 m a.s.l. – 200 m a.s.l. or 1100 m a.s.l. – 1300 m a.s.l. and so on. For the elevational models the patterns within each subregion were similar (Appendix Figure S4.1), and in early model exploration, including subregion as a random effect did not account for any additional variance. Therefore, species turnover values were pooled across subregions in subsequent models. Models with linear, log10, quadratic, and cubic functions of distance were compared using Akaike information criteria (AIC) and the best performing model was reported (AIC model comparisons: Appendix Table S4.1). Model diagnostics were checked using the package *DHARMa* (Hartig 2021).

Monte-carlo simulation

For the generalised linear models, the response variable was not independent (because beta diversity values are obtained from pairwise comparisons of site-species compositions), violating the assumptions of the model. We therefore obtained adjusted pseudo p-values to test the significance of each coefficient by constructing a custom monte-carlo simulation using a mantel-test approach. The rows and columns of the beta diversity matrix were shuffled 5000 times maintaining subregion identity and vertical category and then combined and modelled as above to obtain a test statistic (Chi-squared). Pseudo p-values were then derived by calculating the number of times the randomised test statistic was equal to or greater than the observed test statistic divided by 4999.

Null modelling of beta diversity

Due to the implicit relationship between regional (gamma), local (alpha) and beta diversity, it can be problematic to compare beta diversity for biogeographic regions or taxonomic groups which have different sized regional species pools (Chase and Myers 2011, Kraft et al. 2011). In this case, we are comparing beta diversity of two groups based on their habitat niches, but the same issues apply. Beta diversity can increase with an increasing gamma diversity (Kraft et al. 2011), this is because, in larger regional species pool, a smaller fraction of species in the species pool can potentially gain membership in any given local community, thereby probabilistically increasing species turnover (Chase and Myers 2011). To establish whether differences in species turnover across elevation for ground and arboreal communities still held once we accounted for the potential influence of the size of each communities species pool, we used a null modelling procedure (Chase and Myers 2011). We randomised species occurrences across sites and explored whether the relationship between species turnover and distance deviated from what we would expect given random assortment of species across sites. For elevational distance, a null distribution of species turnover values was generated using a 1000 random community assemblage matrices using the ‘c0’ algorithm (using ‘null.model’ and ‘simulate’ in package *vegan*). This algorithm is appropriate for testing null expectations of species turnover patterns as it randomly shuffles species occurrence across sites, maintaining individual species frequencies across sites but randomises site species richness (Jonsson 2001). Standardised effect sizes were calculated using the observed species turnover values and the mean and standard deviation of the 1000 null assemblages as follows:

$$SES = \frac{observed - mean(null)}{SD(null)}$$

SES values less than 0 are smaller than expected by random chance, while values greater than 0 are larger than expected by random chance. We were interested in the magnitude of departure from random expectation and how that changed over elevational distance. Models were constructed as above for observed species turnover. However, the response variable was gaussian (normal distribution) and therefore we used ordinary least squares (OLS) regression models. It was not necessary to obtain pseudo p-values for the null models (as above for the monte-carlo simulation) because the underlying beta diversity values were already randomised.

Results

Community composition

Elevation was the strongest factor explaining ant community composition. A total of 11, 770 individual ants from 101 species from 30 genera were collected at the 60 trees across the 15 elevation sites and four sub-regions. For the effect of subregion, elevation, and vertical height on community composition we found that more variation in species composition was explained by elevation (28%) than either subregion (9%) or verticality (7%) (Table 4.1). Subregions were delineated in the nMDS plot, particularly Atherton, while there was less differentiation in species composition between Carbine and Windsor (Figure 4.2). Each nMDS axis correlated well with one of the climatic gradient axes (Figure 4.3a–c). All combinations of each axis with each climate gradient are presented in Appendix Figure S4.2. Both subregion and elevation showed a systematic trend with nMDS1 and 2 because different subregions contain different elevational extents. Arboreal and ground communities separated clearly along nMDS axis 3 (Figure 4.3c).

Table 4.1. The results of analysis of ant species composition using a PERMANOVA with a Bray-Curtis distance matrix to model the marginal effect of subregion, elevation, and vertical height on ant community composition in the Australian Wet Tropics Bioregion.

Variable	df	Pseudo-F	% Explained variance	p-value
Subregion	2	4.4	9	0.001
Elevation	10	13.6	28	0.001
Vertical	9	3.4	7	0.001
Residuals	99	18.6	39	

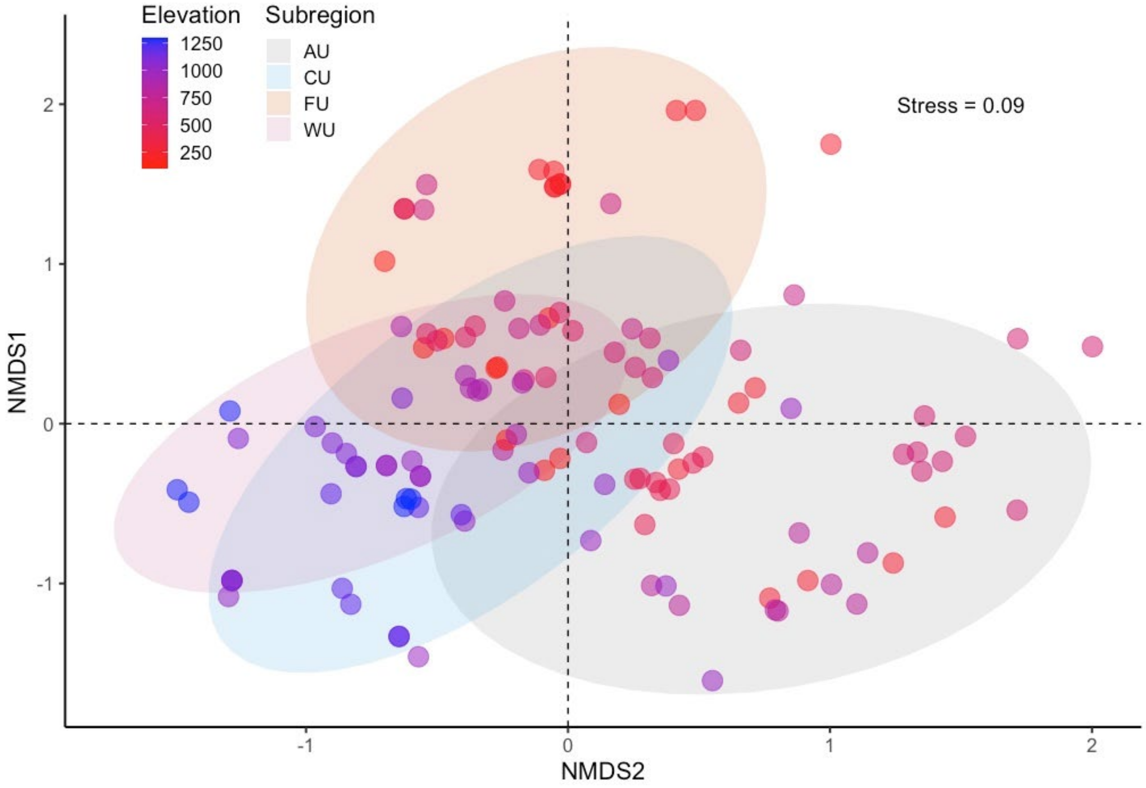

Figure 4.2. Ant species composition (101 species) at vertical height, elevation, and subregion from vertical tree surveys at 15 elevation sites at four subregions in the Australian Wet

Tropics Bioregion. Ordination of sites represented through a nMDS with Bray-Curtis dissimilarity for species frequency of occurrence. Points are sites (subregion, elevation, vertical height), coloured by elevation and ellipses show species groupings for each subregion, vertical height is not indicated by symbols or colours in this model to allow easier interpretation of elevation and regional patterns. AU = Atherton Uplands, CU = Carbine Uplands, FU = Finnegan Uplands, WU = Windsor Uplands.

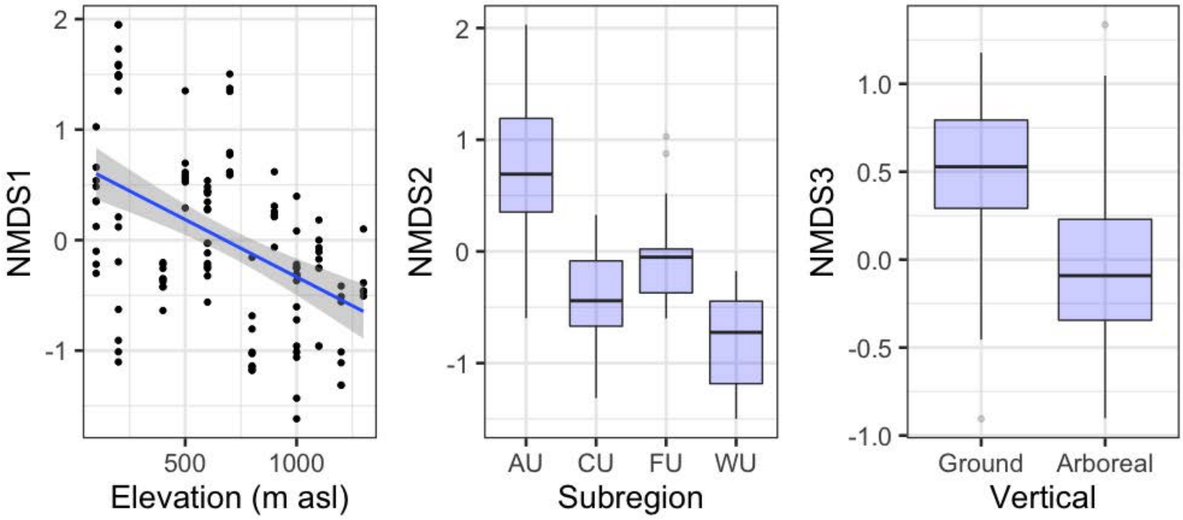

Figure 4.3. Visual representation of the correlation among spatial climate gradients (environmental variables) and extracted axes 1–3 from nMDS fit represented in Figure 4.2. All combinations of environmental variables and nMDS axes are presented in Appendix S1, Figure S4.2. Vertical height (0–27m), re-classified in this figure on the x-axis as ground and arboreal to allow for easier interpretation.

Vertical strata

The ground ant community was very different to the arboreal community. When we pooled data across sites and looked specifically at the influence of vertical height on composition there was strong evidence of vertical partitioning with ground (0 m) and arboreal (3–27 m) species clearly demarcated as separate groups of species in the nMDS ordination in Figure

4.4. As such, we were confident in our classification of ground and arboreal species as distinct communities in downstream analyses.

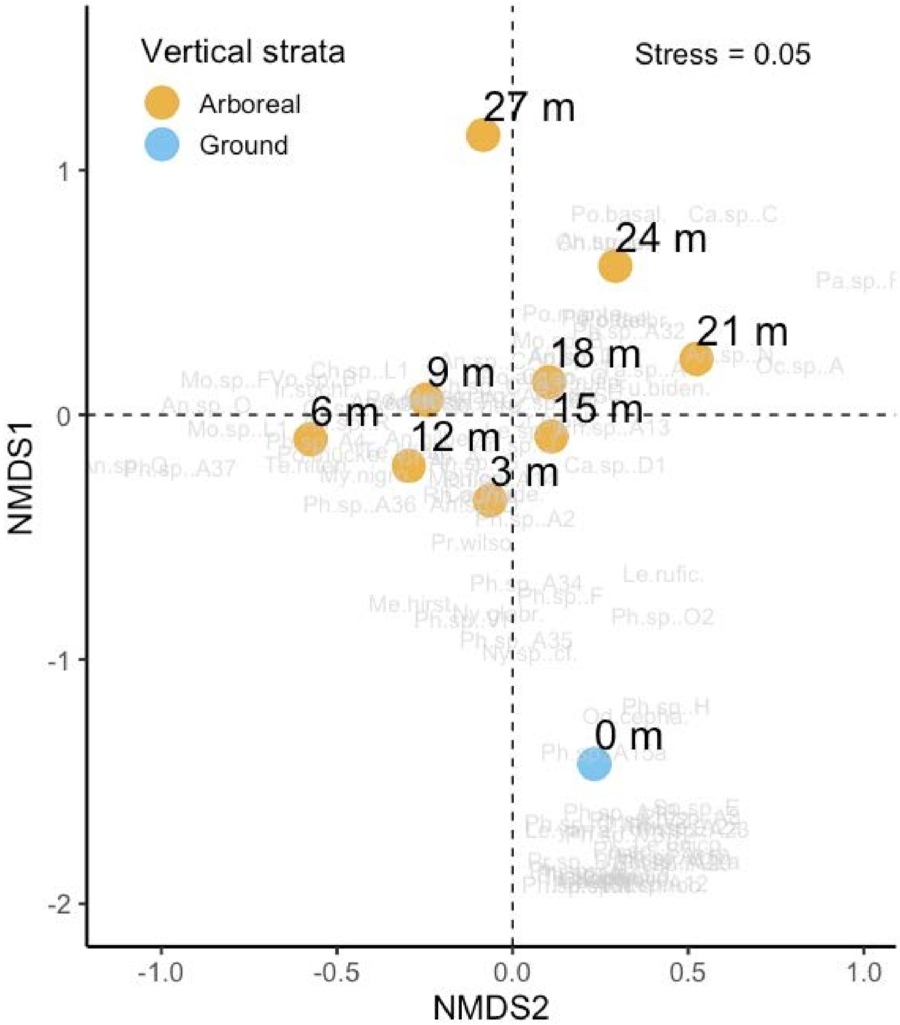

Figure 4.4 Ant species composition (101 species) along vertical height for surveys pooled together from 60 trees sampled at 15 elevation sites along four subregions in the Australian Wet Tropics Bioregion. Ordination of sites calculated with a nMDS with Jaccard dissimilarity based off species presence-absence at each height. Abbreviated species names in grey.

Patterns of beta diversity over elevation

Ant communities on the ground changed with elevation much more than arboreal communities. Once divided into ground and arboreal communities based on 90% frequency of occurrence for each species in each respective habitat, there were 65 arboreal and 36 ground species across the four subregions. The ground community had higher average turnover rates than the arboreal community when comparing all pairwise values ($ß_{sim}$ – Wilcoxon: W = 114.5, p = 0.003 Figure 4.5). In addition, ground and arboreal ant communities showed markedly different patterns of species turnover with elevational distance (Figure 4.6). For elevational models there was a significant interaction (pseudo p-value = 0.034) between elevational distance and vertical niche indicating the two communities exhibited different elevational distance-decay patterns (Table 4.2). This trend persisted in standardised null models (interaction: p-value = 0.06, Table 4.2), indicating that our results were unlikely to be due to random sampling effects of two different sized species pools (Figure 4.7). The arboreal community showed no relationship with elevational distance (Figure 4.6). Whereas the ground community showed a strong positive and logarithmic relationship with elevational distance, a classic distance-decay pattern (Table 4.2, Figure 4.6). Over elevational distance, the ground species composition was more similar than expected by chance, but very quickly after ~ 400 m elevational difference became less similar than expected by chance (Figure 4.7).

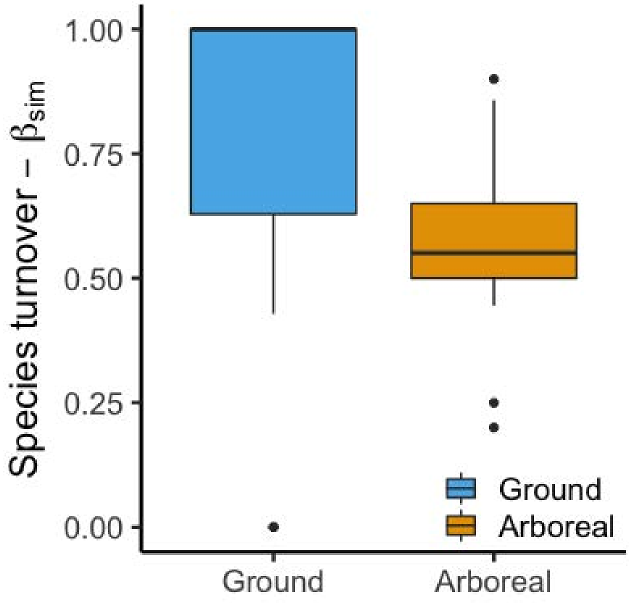

Figure 4.5. Species turnover ($ß_{sim}$ component of beta diversity) for pairwise site comparisons between elevation sites within each mountain range of four subregions. Showing the distribution of beta diversity values for ground and arboreal communities. On the y-axis, 0 represents low turnover and 1 represents high turnover. Boxplots show median (central band), 25th and 75th percentiles (bottom and top of boxes) and 1.5 times the interquartile range above or below the 25th and 75th percentiles (whiskers) and points show outliers above or below this.

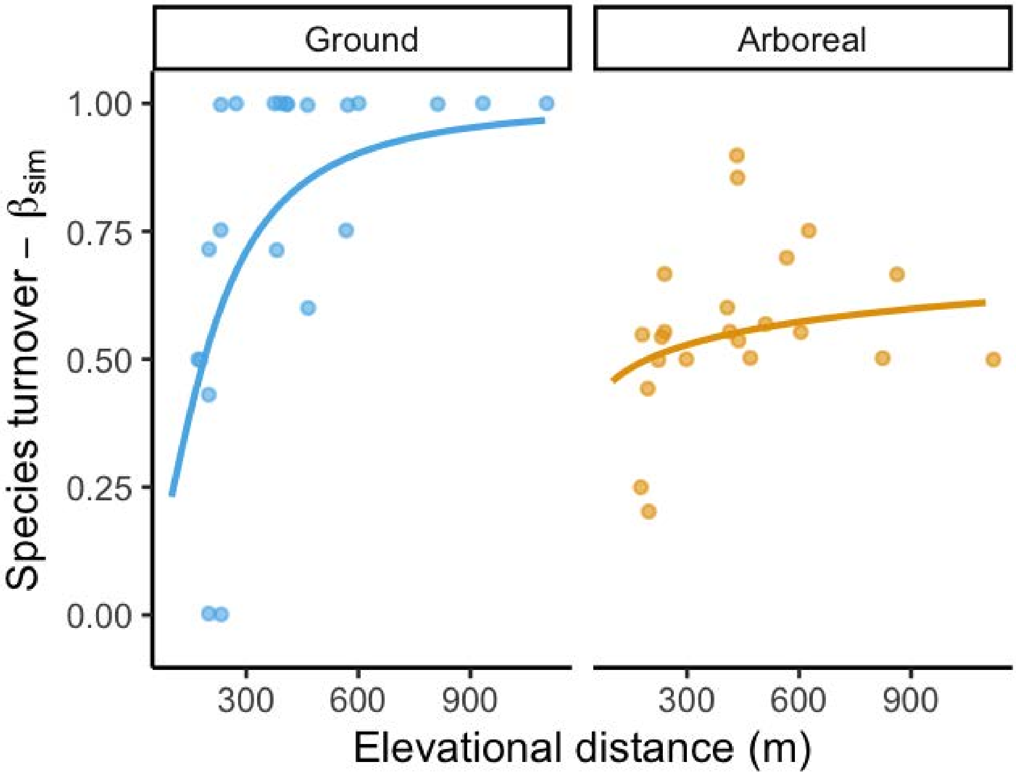

Figure 4.6. Observed ant species turnover with increasing elevational distance in the Australian Wet Tropics for ground and arboreal ant communities. Showing species turnover component of beta diversity ($ß_{sim}$). Points are pairwise comparisons of species composition between elevation sites within each mountain range from four mountain subregions shown here together (see Appendix S4.1 for individual subregion patterns). Lines are model fits from models presented in Table 4.2. On the y-axis, 0 represents low turnover and 1 represents high turnover.

Table 4.2. Model summaries for the relationship between species turnover as a function of elevational distance and vertical community and their interaction. Observed turnover ($ß_{sim}$ – generalised linear model) and standardised turnover (SES $ß_{sim}$ – linear model) models shown. Significance (pseudo p-values) of estimated coefficients in observed model calculated through custom monte-carlo simulation. Standardised turnover response values calculated using a null modelling procedure that shuffled species occurrences in sites. Variation

explained by model indicated by Pseudo R^2 for observed model and Adjusted R^2 for standardised model. Note, coefficient estimates and standard errors (SE) for the observed ß$_{sim}$ models are on the logit scale.

Models	GLM - Observed ß$_{sim}$		LM - SES ß$_{sim}$	
Pseudo/Adjusted R^2	0.48		0.19	
	Coef. ± SE	Pseudo p-value	Coef. ± SE	p-value
Estimates				
Vertical community – Ground	1.14 ± 0.35	0.999	0.35 ± 0.33	0.294
log10(elevational distance)	0.14 ± 0.25	0.002	0.16 ± 0.24	0.507
Vertical:log10(elevational distance)	0.9 ± 0.34	0.034	0.65 ± 0.34	0.061

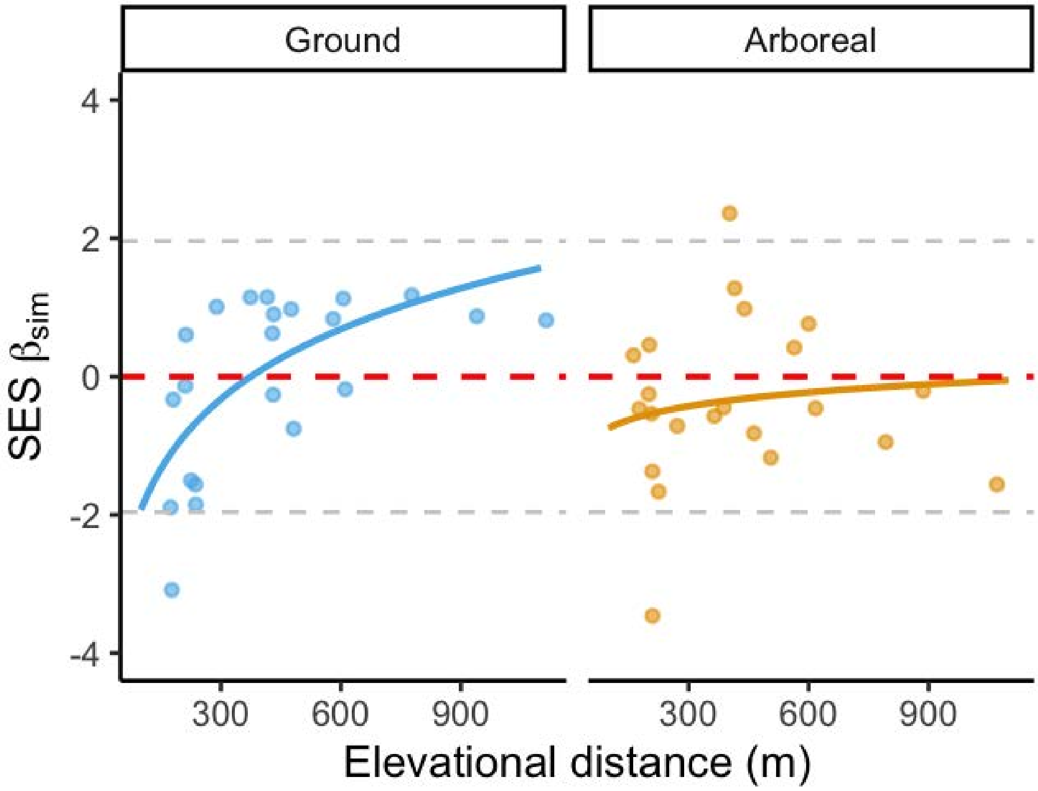

Figure 4.7. Standardised models of ant species turnover with increasing elevational distance pooled from four mountain subregions in the Australian Wet Tropics. Showing species turnover component of beta diversity ($ß_{sim}$). Points are pairwise comparisons of species composition between elevation sites within each mountain range from four mountain subregions shown here together. Lines are model fits from models presented in Table 4.2. Red dotted lines at 0 indicate random expectation, where points below the line indicate less than expected by random chance and above the line indicate more than expected by random chance. The grey dotted lines indicate significance threshold ($\alpha = 0.05$) of ± 1.96 SES.

Discussion

We investigated ant community composition across three spatial gradients of regional diversity along a series of mountain ranges, differing elevations, and the vertical gradient created by trees. We then assessed whether rates of species turnover over elevation were different for ground or arboreal communities at four replicate elevation gradients across the region. Overall, elevation was the strongest driver of community patterns but compositional change across elevation was different for ground and arboreal communities. Ground communities had far higher rates of species turnover over elevation compared to arboreal communities.

Scheffers and Williams (2018) downscaled conception of Janzen’s hypothesis proposed that ground communities experience stable thermal environments, and consequently there is low thermal overlap across elevation, and ground species should be restricted to their elevational band creating strong patterns of beta diversity across mountains. Arboreal species on the other hand are exposed to greater climatic variation and should obtain broader elevational distributions and have lower rates of species turnover over elevation (Jankowski et al. 2009, Scheffers and Williams 2018, Klinges and Scheffers 2021). Consistent with this hypothesis, we found that the relationship between elevational distance and species turnover strongly depended on which vertical community was under consideration. This result was consistent for the elevation gradients at each of the four subregions suggesting that this was a widespread pattern for ant fauna of the Australian Wet Tropics. The average rate of species turnover between any pairwise set of elevation sites was 36% higher for the ground community (mean ßsim = 0.771 ± 0.07 SE) than the arboreal community (mean ßsim = 0.564 ± 0.03 SE). Further, the ground community showed a classic distance-decay pattern whereby species composition was similar between short distances but became rapidly dissimilar with increasing elevational distance, whereas there was no relationship between arboreal species turnover and elevational distance.

The patterns of ground and arboreal species turnover were not simply explained by random chance effects due to differences in the size of each community. In our models of species turnover, gamma or ‘regional’ diversity was the species present at each respective subregion divided into ground or arboreal communities. Differences in the size of our two species pools (ground and arboreal) could influence our observed beta diversity values creating seemingly different patterns of turnover that are simply due to stochastic effects of sample size (Chase and Myers 2011, Kraft et al. 2011). Our null modelling approach used a well-established procedure (Qian et al. 2013, Stegen et al. 2013, Bishop et al. 2015, Xu et al. 2015, Ashton et al. 2016), which attempts to remove the effect of the size of the regional species pool by testing whether our observed beta diversity values for ground and arboreal communities are smaller or larger than expected under a stochastic model of community assembly (i.e., indistinguishable from a random community arrangement across elevation, given our gamma and alpha values). We found a similar pattern in our null models to our observed beta diversity models indicating that our results are unlikely to be due to stochastic sampling effects.

One caveat of our study was that we sampled only a specific subset of the whole ant fauna attracted to baited vials or easily captured by hand. While our methodology allowed the same sampling technique to be applied in ground and arboreal habitats, which was important for our comparative study, it is unlikely to capture the full extent of ant fauna. Therefore, a key caveat of our work is that these patterns could be distinct to bait attracted ants. We would encourage further investigation of these patterns, both in other biogeographic regions and with a full complement of the ant fauna, to explore the generality of the results reported here.

At the macroscale, the composition of a regional species fauna is strongly influenced by both historical biogeography and contemporary climatic gradients (Cornell and Lawton 1992, Williams et al. 2002, Graham et al. 2006). We found distinct compositional patterns between our four subregion locations. Windsor and Carbine subregions were similar in composition, but Finnegan and Atherton had distinct subsets of species. This is commonly reported in the Australian Wet Tropics Bioregion, with a similar pattern displayed in birds and small mammals (Williams and Pearson 1997, Williams et al. 2002). There is an historic biogeographic barrier along the Black Mountain Corridor, just south of the Carbine uplands, that did not support rainforest until ~8 Kya (Schneider and Moritz 1999, Moritz et al. 2009). This separates Windsor, Carbine, and Finnegan in the north and Atherton in the south. As well, Carbine and Windsor both support upland environments and have similar contemporary climatic conditions including high rainfall seasonality, while Finnegan is a smaller mountain range reaching only a maximum of ~800 m a.s.l. (Williams and Middleton 2008). These regional historic and contemporary climatic factors likely drive the composition of each subregional mountain range as outlined in our research framework in Figure 4.1.

Despite these distinct subregional differences, elevation explained more of the variation in regional scale community composition than subregion identity. As in many other studies, this signifies the importance of elevational temperature gradients to ant community assemblage (Bruhl et al. 1999, Sanders et al. 2007, Burwell and Nakamura 2015, Longino and Branstetter 2019). Critically, once we removed the effect of elevation, we also found a very strong effect of the vertical habitat on community assemblage. There was a distinct disjuncture in species composition between ground and arboreal habitats, indicating that the arboreal community starts at just three metres above the ground (Beaulieu et al. 2010). In other words, the set of species that frequent the shrub layer and lower trunk (at three metres in height) are more similar to the set of species that live 18 m above them in the high canopy than they are to set of species that the that dwell in the leaf litter a mere three metres below them. Therefore, while there are a number of species which traverse both ground and arboreal zones (referred to as semi-arboreal species in Leahy et al. (2021a)) in this region, the ant fauna can be clearly demarcated into ground and arboreal habitat niches as separate communities.

Few studies have investigated whether rates of species turnover over elevation varies depending on vertical habitat. Our results are consistent with a study that compared turnover across elevation for terrestrial and canopy mites. Fagan et al. (2006) found that terrestrial (ground) mites had distinct elevational preferences and high species turnover, while canopy mite species had no distinct elevational preferences and low turnover. The authors suggest this may indicate that canopy mites are tolerant of a wider range of environmental conditions (Fagan et al. 2006). At a more localised scale of horizontal turnover across sites over a short distance, Antoniazzi et al. (2020) reported a similar pattern for neotropical ants, whereby there was a horizontal distance-decay pattern for ground but not canopy ant species, while Basham et al. (2019) reported the opposite pattern, finding higher turnover of canopy-dwelling and understorey amphibians than terrestrial amphibians. The factors controlling species turnover at localised scales are likely to be different to the dynamics which shape community composition along broader climatic gradients such as elevation. At the local scale rainforest trees can act like islands for some taxa (frogs; Basham et al. 2019), restricting horizontal dispersal, while for cursorial taxa such as ants, tree lianas can act as super highway facilitating horizontal movement (Adams et al. 2017) . These examples from localised studies, however, indicate that vertical gradients are likely to be playing a role in determining community structure and distance-decay patterns at multiple spatial scales (Antão et al. 2019).

Vertical niche determines both the exposure (Leahy et al. 2021a) and tolerance (Kaspari et al. 2015, Kaspari et al. 2016) to climatic variability and this in turn will influence biogeographic patterns of community composition through its effect on thermal traits and dispersal capacity. Rainforest canopy ants have broader tolerance ranges than ground restricted ants fitting this expectation (Kaspari et al. 2015, Bujan et al. 2020, Leahy et al. 2021b). A broader thermal tolerance range should allow species to achieve broader geographical distributions (Brown 1984, Slatyer et al. 2013, Leahy et al. 2021a). Whether vertical niche specifically influences dispersal capacity of rainforest ants is unclear and it remains difficult to obtain precise data on dispersal distance in ants. However, using turnover rates as a proxy for dispersal distance, we find an elevational distance-decay relationship in ground ants but not arboreal ants. This would indicate that for ground-based species, newly dispersing young queens either can’t disperse as far as arboreal species, or that upon arrival in a climatically different site along the elevation gradient, the environmental conditions are incompatible resulting in failure to establish a colony (Machac et al. 2011).

This has important implications for the resilience of communities to climate change (Williams et al. 2008). Vertical climate gradients may select for certain traits which inherently prime species to be more or less resilient to climatic variation that in turn drive the responses of whole communities to anthropogenic climate change. Arboreality has been associated with greater resilience to climatic variance over environmental gradients and longer geological time scales (Davison and Chiba 2008, Oliveira and Scheffers 2019). For example, arboreality (vertical movement) in vertebrates (mammals, birds, frogs, and reptiles) was positively correlated with dispersal potential and these communities were disproportionately represented in historically and contemporarily unstable environments in the Australian Wet Tropics Bioregion (Scheffers et al. 2017b).

Different patterns of species turnover over elevation will have significant implications for species undergoing range shifts under climate change. On average, ground-based species might find it more difficult to shift range further up mountain ranges in response to rising temperatures than their arboreal counterparts (Colwell et al. 2008, Perez et al. 2016). Additionally, high species turnover (i.e., ground community) is likely to be associated with increased chance of encountering novel interspecific interactions as species move upwards in elevation. In conclusion, individual species responses to climate change are likely to interact with extant community composition patterns creating diverse possibilities for the formation of novel communities in ground and arboreal habitats.

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Chapter Five - Arboreality drives heat tolerance while elevation drives cold tolerance in tropical rainforest ants.

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Abstract

Determining how species thermal limits correlate with climate is important for understanding biogeographic patterns and assessing vulnerability to climate change. Such analyses need to consider thermal gradients at multiple spatial scales. Here we relate thermal traits of rainforest ants to microclimate conditions from ground to canopy (microgeographic scale) along an elevation gradient (mesogeographic scale) and calculate warming tolerance in the Australian Wet Tropics Bioregion. We test the thermal adaptation and thermal niche asymmetry hypotheses to explain interspecific patterns of thermal tolerance at these two spatial scales. We tested CT_{min}, CT_{max}, and calculated CT_{range} using ramping assays for 71 colonies of 40 ant species collected from terrestrial and arboreal habitats at lowland and upland elevation sites and recorded microclimatic conditions for one year. Within sites, arboreal ants were exposed to hotter microclimates and on average had a 4.2°C (95% CI: 2.7 – 5.6°C) higher CT_{max}, and 5.2°C (95% CI: 3.5 – 7°C) broader CT_{range} than ground-dwelling ants. This pattern was consistent across the elevation gradient, whether it be the hotter lowlands or the cooler uplands. Across elevation, upland ants had significantly lower CT_{min} than lowland ants, whereas the change in CT_{max} was less pronounced, and CT_{range} did not change over elevation. Differential exposure to microclimates, due to localised niche preferences, drives divergence in CT_{max} while environmental temperatures along the elevation gradient drive divergence in CT_{min}. Our results suggest that both processes of thermal adaptation and thermal niche asymmetry are at play depending on the spatial scale of observation, and we discuss potential mechanisms underlying these patterns. Despite the broad thermal tolerance range of arboreal rainforest ants, lowland arboreal ants had the lowest warming tolerance and may be most vulnerable to climate change.

Introduction

Determining how species thermal limits correlate with prevailing climatic conditions is important for understanding biogeographic patterns and assessing potential vulnerability to climate change. Thermal tolerances have typically been studied in relation to a single climatic gradient, at either macrogeographic (e.g. latitude; Addo-Bediako et al. 2000, Araújo et al. 2013), mesogeographic (e.g. elevation; Nowrouzi et al. 2018, Bishop et al. 2017) or microgeographic (e.g. microhabitat; Baudier et al. 2015, Kaspari et al. 2015) scales. However, climatic variance is a complex multi-scale phenomenon, where each of the above spatial scales are nested like Russian dolls such that the thermal exposure of a population is contingent on the microclimatic variation from local to regional scales as in Figure 5.1 (Bonebrake and Deutsch 2012, Muñoz et al. 2014, Klinges and Scheffers 2020). Assessments of vulnerability to future climate change therefore need to account for the multi-scale nature of climatic variation (Bonebrake and Deutsch 2012).

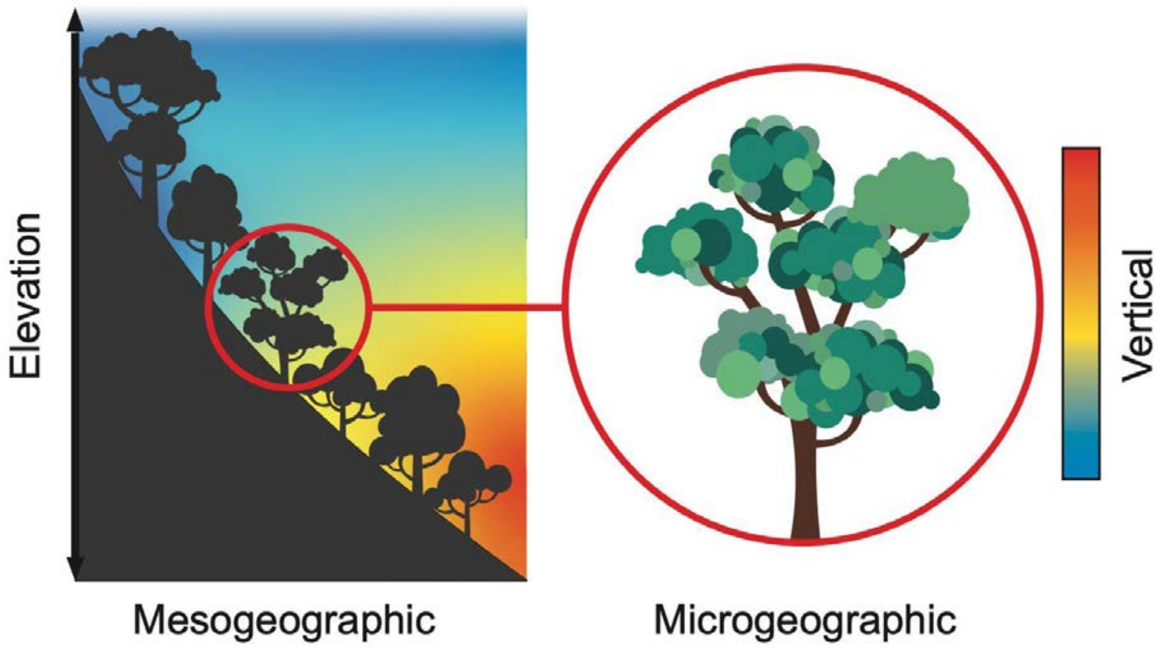

Figure 5.1. Trees create a microgeographic climate gradient in average temperature, the degree to which temperatures fluctuate, and moisture, from ground to canopy that is then nested in its position at the mesogeographic climate gradient of elevation. This in turn is nested in the macrogeographic latitudinal gradient.

The vertical layering of vegetation within terrestrial habitats creates a climate gradient at the microgeographic scale (Scheffers et al. 2013, Leahy et al. 2021). In tropical rainforests, where mean temperatures are relatively stable throughout the year, arboreality along the vertical climate gradient represents a key source of spatial thermal variation for forest-dwelling biota (Scheffers et al. 2013). Forest trees provide a gradient from ground to canopy in increasing temperature, vapor pressure deficit (VPD – the drying power of the air), and temperature variance (Scheffers et al. 2013, Leahy et al. 2021). The microgeographic vertical climate gradient is nested in its position in geographic climatic gradients of elevation and latitude (Scheffers et al. 2013, Montejo-Kovacevich et al. 2020). Further, vertical climate gradients create selection pressures for particular traits that in turn influence species distributions and biogeographic patterns at broader geographic scales (Scheffers et al. 2017, Oliveira and Scheffers 2019).

A population's geographical position within these nested climatic gradients should determine their physiological tolerances, according to the thermal adaptation hypothesis (sensu Kaspari et al. 2015). The hypothesis states that an organism should be physiologically adapted to its environment, which could occur via short-term phenotypic plasticity (Bujan et al. 2020b), longer-term thermal acclimation (Sørensen et al. 2016), or genetic adaptation (Martin et al. 2019). The hypothesis predicts that the thermal limits of a population should correlate with minimum and maximum temperatures of the thermal environment to which it is exposed (Janzen 1967), because it is physiologically costly to maintain thermal limits that are broader than needed (Angilletta 2009). As a result, populations experiencing stable environments with little thermal variation should become climatic specialists with a narrow thermal tolerance range, whereas those experiencing greater thermal variation should have a broad thermal tolerance range (Janzen 1967, Huey and Hertz 1984). Under this hypothesis, thermal exposure along a climatic gradient and the process of environmental filtering are key drivers of thermal niche differences in biological communities (Angilletta 2009).

Cold tolerance has repeatedly been shown to vary widely among species and to be strongly correlated with thermal variation along gradients of elevation and latitude (Araújo et al. 2013). However, this is often not the case for heat tolerance (Addo-Bediako et al. 2000, Araújo et al. 2013, Hoffmann et al. 2013, Diamond and Chick 2018, Bujan et al. 2020a). In a large study, for example, the thermal limits of 239 terrestrial species from a wide range of taxa were sampled at different latitudinal points across the globe, Sunday et al. (2011) found that whereas cold tolerance declined at 2.4°C for every 10 degrees in latitude, heat tolerance declined at only 0.3°C. This pattern in thermal tolerance variability has been referred to as the thermal niche asymmetry hypothesis (sensu, Herrando-Pérez et al. 2020).

Variation in heat tolerance among species has been better explained by phylogenetic relatedness than geographic or climatic variation along environmental gradients for diverse taxa from ants to frogs (Diamond and Chick 2018, Pintanel et al. 2019). This suggests an evolutionary mechanism underlying thermal niche asymmetry whereby heat tolerance is a constrained trait while cold tolerance is more labile (Araújo et al. 2013, Hoffmann et al. 2013). Behavioural thermoregulation, however, could result in a similar asymmetrical pattern because it can dampen the need for physiological adaption at one end of the thermal tolerance range (Muñoz and Bodensteiner 2019). In *Anolis* lizards for example, cold tolerance evolved faster than heat tolerance because thermoregulation more effectively shielded the lizards from hot temperatures, but they could not escape the physiological selection provided by cold temperatures (Muñoz et al. 2014). Thermal niche asymmetry has critical implications for biodiversity conservation in a changing climate, particularly if heat tolerance is phylogenetically conserved, as this could significantly limit species capacity to respond to warming temperatures (Hoffmann et al. 2013).

Ants are model organisms for investigating thermal ecology and are an ecologically dominant faunal group in tropical rainforests. Across latitude and elevation, ants conform to the thermal niche asymmetry hypothesis, wherein cold tolerance tracks geographic climate gradients, but heat tolerance does not (Bishop et al. 2017, Diamond and Chick 2018, Nowrouzi et al. 2018). However, ants appear to fully conform to the thermal adaptation hypothesis across vertical climate gradients: subterranean ants have lower heat tolerance than understorey ants, which in turn have lower heat tolerance than canopy ants (Baudier et al. 2015, Kaspari et al. 2015).

Here we address variation in thermal tolerance and its relationship with thermal exposure by using a multi-scale approach to explore how microgeographic (vertical microhabitat) and mesogeographic (elevation) climatic gradients interact to shape the thermal tolerances of rainforest ants. We test the extent to which cold tolerance (hereafter, CT_{min}), heat tolerance (hereafter, CT_{max}), and thermal tolerance range (hereafter, CT_{range}) correlate with climate conditions along vertical (micro) and elevation (meso) gradients. We focus on whether CT_{max} is strongly correlated with maximum temperature exposure (thermal adaptation hypothesis) or is relatively uniform (thermal asymmetry hypothesis). We also test for the strength of phylogenetic signal in thermal limits using a genus-level phylogeny; high levels of phylogenetic signal for CT_{max} would indicate phylogenetic conservatism in upper thermal limits (Wiens and Graham 2005). Finally, we apply a nested multi-scale thermal framework and use microclimate data to calculate contemporary warming tolerances and to estimate warming tolerances under 1.5 °C and 2 °C increases above current temperatures for ants in each vertical microhabitat at low and high elevation.

Methods

Study sites

Field and experimental work took place in the Australian Wet Tropics (AWT) bioregion, Queensland. Ants were sampled for thermal experiments along the Mt. Lewis/Carbine Tablelands (hereafter, Carbine) elevation gradient at Mossman Gorge (Lowland, 100 m a.s.l.; -16.470, 145.320) and Mt. Lewis National Park (Upland, 1200 m a.s.l.; -16.510, 145.270) as well as the Daintree Rainforest Observatory (Lowland, 100 m a.s.l.; -16.103, 145.448). Carbine is a contiguous rainforest area that runs from sea level to 1200 m a.s.l. over a distance of 10 km, and the Daintree Rainforest Observatory is located in a 1200 km^2 area of lowland rainforest ~ 40 km to the north. Rainfall in the AWT is highly seasonal, with 75-90% of the 2000 – 8000 mm per year falling during the wet season from November to April (WTMA 2013). All field work and thermal experiments took place during the dry season from August to October 2019.

Measuring microclimate

We recorded ambient temperature at 30 min intervals using HOBO Pro v2 (U23-001) temperature data loggers over the vertical habitat and elevation gradient of Carbine. Loggers were placed at ground (~ 0.5 m) and arboreal (~ 20 m) microhabitats for one year from March 2019 – March 2020 at the same 100 m a.s.l. and 1200 m a.s.l. Carbine sites for ant sampling.

Ant sampling

The aim of sampling was to collect as many individuals and species as possible from ground and arboreal habitats to test and characterise the thermal limits of a wide range of species.

Live ants were sampled from the two Carbine sites using a combination of baiting with tuna in plastic vials (1 cm in diameter, 5 cm in length) and active hand collection using soft forceps and an aspirator. We avoided baiting with sugar or carbohydrate baits as ants can exhibit short-term thermal plasticity in CT_{max} in response to sugar ingestion (Bujan and Kaspari 2017). Five trees – at least 50 m apart – were surveyed once in each site. Using the single-rope climbing technique, for each tree at every 3 m point from the ground to the highest part of the tree, we set five baited vials that were attached using tape and thumbtacks to the trunk, branches, and available epiphytes. Baited vials were set at 10:00 hr and collected three hours later. During deployment and collection of vials, ants were opportunistically hand collected when observed. Ants were also opportunistically hand collected immediately adjacent to baited vials. The Daintree Rainforest Observatory canopy crane and surrounding forest was used to collect additional lowland species at only ground and canopy heights (not every 3 m as above) over five days in October between 10:00 hr and 16:00 hr. From the canopy crane, we sampled 10 trees that were ~10 m apart. Here we only visited heights of 25–30 m and placed three baited vials on small branches and the trunk and were collected after 1 hr. This was followed by beating of leaves and branches of each tree adjacent to baited vials to collect additional ants. Hand collections were then conducted on the ground and around logs and rocks for 1 hr.

Across all sites, we considered all individuals of a species from a single tree to be from the same colony and ants from separate trees as from different colonies. Multiple colonies of each species were collected where possible. We tested 20 species represented by one colony and the remaining 20 species by 2–5 colonies (mean ± SE: 1.85 ± 0.17). We aimed to test five individual worker ants from each colony. In some cases, there were more or less than five individuals available to test. Overall, the mean number tested per colony was 4.8 ± 0.3 SE. For the polymorphic genera *Pheidole* and *Camponotus* we tested minor workers only.

Following thermal tolerance experiments (see below) ants were placed in ethanol and returned to the lab to confirm species identification and to measure body mass. Between 3–5 (mean ± SE: 4.1 ± 0.1) workers of each tested colony were oven dried for 24 hrs at 70 °C using a Blue M Electric drying oven, and dry weight body mass was measured using a Satorius semi-microbalance scale with 0.01 mg accuracy. Voucher specimens were deposited in the ant collection held at CSIRO's Tropical Ecosystems Research Centre in Darwin, Australia.

Thermal tolerance experiments

The primary aim of our thermal experiments was to ascertain whether patterns of thermal tolerance observed in multiple species of wild ants match the predictions of either thermal adaptation or thermal asymmetry. Common-garden experiments would be required to establish whether patterns in the wild are a result of genetic adaptation or phenotypic plasticity (Sørensen et al. 2016), and this is not practical for assessing many ant species in the one study. We took measures to limit sources of variation from any potential seasonal or daily thermal trait plasticity. Ants from different sites were tested within a three-month period of one year during the dry season when the weather is more stable, and ants within sites were tested within a period of seven to ten days. In addition, ants were tested for thermal tolerance as soon as possible after collection to avoid experimental acclimation. Average time between collection in the field and beginning testing was 3 hrs 22 min (± SD 2 hrs) and the maximum time was 8 hrs and 47 min.

To measure thermal limits, we used a custom digital dry bath with 20 individual wells set into an insulated aluminium block above a Peltier plate that was programmed to heat and cool at a set rate. Each single ant was placed in a 1.5 ml microcentrifuge vial capped with a firm piece of foam to prevent it from hiding in the lid space above the thermal block. We tested several species at one time and individual workers of different species were randomly placed in one of the 20 well positions to prevent any systematic biases. We reserved one random well position for a temperature test vial without an ant, which had a microcentrifuge vial with a thermocouple wire inserted and capped with firm foam. This ensured we were recording the temperature that an ant would experience inside the vial. Following Kaspari et al. (2015), we used a protocol that ramped temperatures down to CT_{min}, allowed ants to recover, and then ramped upwards to CT_{max}. Kaspari et al. (2015) did not find any evidence that ramping down before ramping upwards systematically biases the final estimate of CT_{max}. We placed ants in the thermal block for 15 min at 20 °C to allow the resumption of normal behaviours. To test CT_{min} we ramped temperature down at 0.5 °C per minute. This ramping rate was chosen as a careful balance between a slow ramping rate that is more likely to be experienced in nature and a faster ramping rate that avoids the potentially confounding effect of desiccation associated with long experimental times (Rezende et al. 2011). On ramping down, the ants were checked at 15 °C, 12 °C, and then every 1 °C until there was loss of muscle coordination or absence of any movement after flicking the vial, indicating CT_{min} (Lutterschmidt and Hutchison 1997). Upon reaching CT_{min} ants were removed from the experiment and left to acclimate back to room temperature. Once all ants were removed, they were left for 15 min, after which they were checked for survival and normal movement. Ants that did not recover were replaced by a worker from the same colony for the CT_{max} assay (15 out of 380 ants tested, 4% of tests). Ants were then acclimated for another 15 min at 20 °C in the thermal block before temperature was ramped up. Temperature was raised 0.5 °C per minute and ants were checked at every 2 °C increment between 30–40 °C and then every 1 °C from 40 °C until CT_{max} was reached. CT_{max} was determined as above for CT_{min} and ants were checked for recovery after 15 min. Ants that did not recover from CT_{max} were excluded from the analysis as they had reached a lethal rather than critical thermal limit. We calculated

CT_{range} (CT_{max} – CT_{min}) for individuals which recovered from both CT_{min} and CT_{max} assays. Excluding failed tests, we analysed the test results for 40 species for each thermal trait with 355 individuals of 74 colonies for CT_{min}, 277 individuals of 73 colonies for CT_{max}, and 269 individuals of 73 colonies for CT_{range}.

We acknowledge the experimental issues surrounding testing thermal limits for insects, particularly that ramping rate can affect the final outcome of the experiment and faster ramping rates have been criticised for not representing the conditions likely to be experienced by insects in nature (Rezende et al. 2011). We chose a methodology and ramping rate suitable for logistical constraints related to doing thermal tolerance experiments in the field (Bishop et al. 2017). Our estimates are standardised and suitable for addressing ecological hypotheses in the context of thermal limits within our study area and taxa. However, we advise caution when comparing the numerical values of our thermal limits to other studies of ants that have used different methodologies (Rezende et al. 2011).

Statistical analysis

Thermal tolerance

Ant species were classed as arboreal or ground based on location of capture, nest observations, literature, and expert opinion. We calculated average CT_{min}, CT_{max}, and CT_{range} values for each colony of each ant species and modelled each of the three traits individually using linear mixed effects models with each trait as the response variable, vertical niche and elevation site as fixed effects, and species as a random effect. Each response variable fitted a gaussian distribution. For each colony, we then calculated mean body mass of individual worker ants to include as a fixed effect in the models, as ant body mass might influence thermal traits (Kaspari et al. 2015). Variance inflation was checked and there was no evidence of collinearity among factors in any model. We assessed whether higher order terms (interactions between fixed effects) significantly improved model fit via likelihood ratio tests using ANOVA and found they did not (Appendix Table S5.1). We then compared models with and without body mass using the same method and found better model fit without body mass (Appendix Table S5.1). We therefore excluded body mass from our subsequent analysis. Linear mixed effects models were performed using the package *nlme* (Pinheiro et al. 2020) with degrees of freedom calculated as outlined in Pinheiro and Bates (2006). Final hypothesis testing was done via likelihood ratio tests using ANOVA by comparing the full model to a null model with no fixed effects. We calculated marginal (R_m^2, fixed effects) and conditional (R_c^2, random effects) R^2 values (Nakagawa and Schielzeth 2013).

In total, thermal limits were tested for 74 colonies from 40 ant species, 32 species from the lowland sites (100 m a.s.l.), and eight species from the upland site (1200 m a.s.l.). We tested 19 arboreal and 13 ground species at the lowland sites, and four arboreal and four ground species at the upland site. Given these differences we used a null simulation modelling approach to test whether differences in thermal tolerance limits between sites were due to an uneven sample size and did not find this to be the case (Appendix Section S5.1).

Relationships between thermal tolerances and temperature exposure

We compared the magnitude of thermal trait differences of ant species to the magnitude of temperature differences between ground and arboreal habitats and between elevation sites. Our approach compared the estimated marginal means from the thermal trait model to the microclimate model. First, we took the model of CT_{min} and CT_{max} that included elevation site and vertical niche as predictors and extracted the estimated marginal means (also known as least-squares means). Second, we constructed linear regression models with daily maximum and minimum temperatures (from ambient microclimate data loggers) as a function of elevation and vertical niche — using only temperatures from the months, August – October

2019, when thermal experiments took place — and extracted the estimated marginal means from those models. We then compared the magnitude of difference —using extracted estimated marginal means/effect size — in ambient temperature to the magnitude in difference of ants' CT limits at the microgeographic scale (between ground and arboreal habitats) and at the mesogeographic scale (between lowland and upland sites).

Assessing the effect of phylogeny

To assess whether thermal trait variation among ants is closely associated with shared ancestry, we tested for phylogenetic signal in thermal traits using a genus-level, time-calibrated phylogeny from Moreau and Bell (2013). We chose to use a genus-level phylogeny as the phylogenetic relationships of species within our study area are not well resolved. Details on pruning and construction of the genus-level phylogeny provided in Appendix Section S5.2. We calculated genus-level means of CT_{min}, CT_{max}, and CT_{range} and calculated Pagel's λ (Pagel 1999) and Blomberg's K to test for phylogenetic signal using function 'phylosig' in *phytools* (Blomberg et al. 2003, Revell 2012). We acknowledge that we may lack sufficient statistical power to calculate Blomberg's K given that Blomberg *et al.* (2003) states that 21 tips should be a minimum to calculate phylogenetic signal and here we use 18 tips (genera). We assigned genera to vertical niche as three categories either primarily arboreal, primarily ground, or mixed (i.e., both ground and arboreal species well represented), reflecting their known foraging and nesting habits based on literature records and consultation with experts. We then tested for differences in genus thermal limits between the three vertical microhabitats while accounting for phylogenetic relatedness using a phylogenetic ANOVA using the function 'phylANOVA' implemented in *phytools* (Revell 2012).

We had more confidence in using a genus-level phylogeny to assess the effect of shared ancestry on thermal traits given the lack of a well-constructed species-level phylogeny for ants in Australian Wet Tropics. However, for completeness we also constructed a species-level phylogeny by adding soft polytomies (unresolved nodes) to the tips of each genus to represent our species and used phylogenetic generalised least squares to model each thermal trait as a function of elevation and vertical microhabitat while accounting for phylogeny, for details and results of this analysis see Appendix Section S5.3 and Appendix Table S5.2.

Warming tolerance

Using our microclimate 2019–2020 temperature recordings, for each ant species we calculated habitat and site specific contemporary warming tolerance and projected warming tolerance under 1.5 ºC and 2 ºC temperature increases (Masson-Delmotte et al. 2018). Warming tolerance was calculated as each species CT_{max} subtracted from the maximum annual microclimate temperature (taken from one-year deployment of in-situ microclimate HOBO loggers), specific to that species microhabitat and elevation site, plus 1.5 and 2 ºC respectively using our 2019-2020 climate data as a baseline. A negative thermal tolerance indicates that the environmental temperature has surpassed a species' CT_{max} and should cause physiological failure and/or death (Huey et al. 2012). We used one-way ANOVA and Tukey's HSD to test for difference between each microhabitat and elevation site.

Results

Thermal tolerance

Overall, arboreal species had significantly lower CT_{min}, higher CT_{max} and broader CT_{range} than ground species and this pattern was consistent at both lowland and upland sites (Table 5.1, Figure 5.2a–c). Mean CT_{max} of arboreal ants was 4.2 °C (95% CI: 2.7 – 5.6 °C) higher and thermal tolerance range was 5.3 °C (95% CI: 3.5 – 7.0 °C) wider than for ground dwelling ants (Table 5.2, Figure 5.2b, c). Mean CT_{min} of arboreal ants was 1 °C (95% CI: -1.9 – -0.2 °C) lower on average than for ground ants; however, although the difference was significant based on p-value, the confidence intervals showed the effect size to be very close to 0 – a confidence interval passing 0 would indicate no change. Comparing across elevation, and pooling across vertical habitat, upland ants had a mean CT_{min} 3.9 °C (95% CI: -5.0 – -2.7 °C) lower when compared to lowland ants (Table 5.1, Figure 5.2a). Mean CT_{max} was 2.3 °C (95% CI: -4.2 – -0.3 °C) lower in upland ants compared to lowland ants, although the confidence intervals were close to 0 indicating the change in CT_{max} may be relatively minor across elevation (Table 5.1, Figure 5.2b). There was no significant difference in CT_{range} between upland and lowland ants (Table 5.1, Figure 5.2c).

Table 5.1. Linear mixed effects model results modelling colony CT_{min}, CT_{max}, and CT_{range} with elevation site and vertical habitat as fixed effects and species as a random factor, for 74 (CT_{min}) and 73 (CT_{max}, CT_{range}) colonies of 40 ant species in the Australian Wet Tropics.

Thermal trait	R_m^2	R_c^2	Estimate (°C)	95% CI	t-value	P-value
CT_{min}	0.48	0.7				<0.001
Elevation: *Lowland - Upland*			-3.9	-5.0 – -2.7	-6.77	<0.001
Vertical habitat*: Ground - Arboreal*			-1.0	-1.9 – -0.2	-2.38	0.022
CT_{max}	0.42	0.60				<0.001
Elevation: *Lowland - Upland*			-2.3	-4.2 – -0.3	-2.34	0.025
Vertical habitat: *Ground - Arboreal*			4.2	2.7 – 5.6	5.7	<0.001
CT_{range}	0.41	0.54				<0.001
Elevation: *Lowland - Upland*			1.5	-0.8 – 3.8	1.31	0.198
Vertical habitat: *Ground - Arboreal*			5.3	3.5 – 7.0	6.06	<0.001

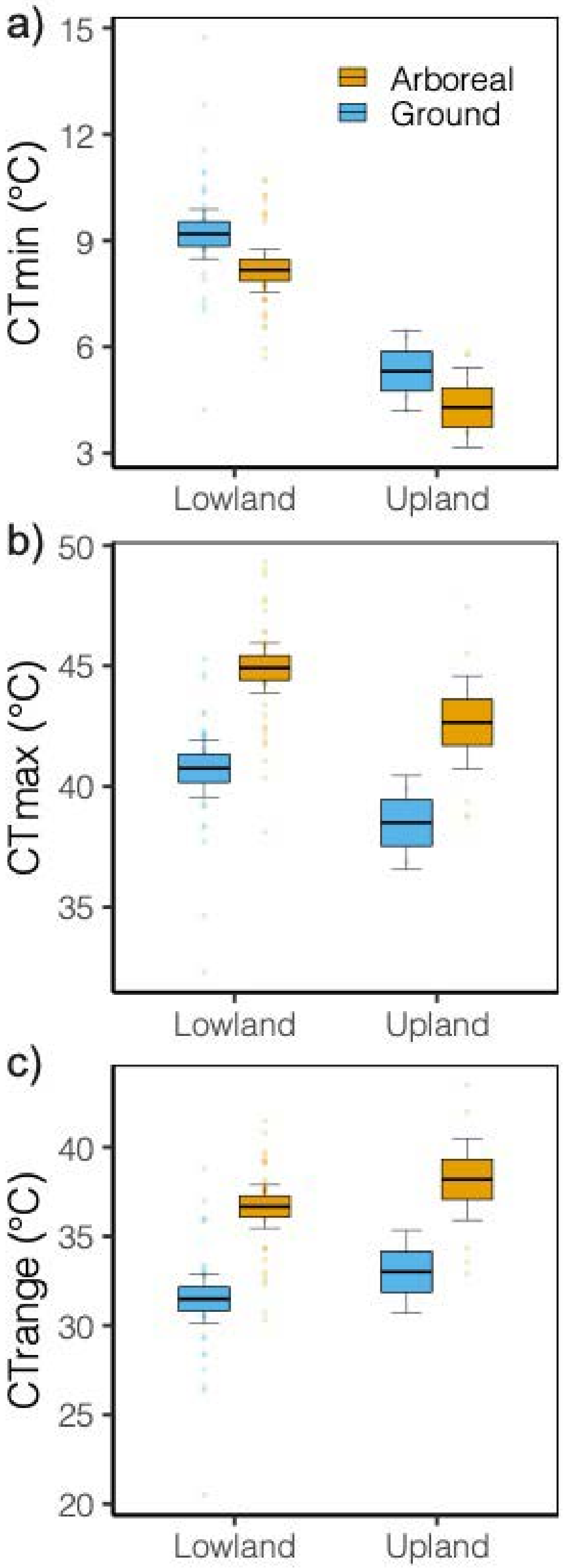

Figure 5.2. Thermal limits a) CT_{min}, b) CT_{max}, c) CT_{range} for ant species from ground or arboreal vertical habitats and lowland (100 m a.s.l.) or upland (1200 m a.s.l.) sites. Thermal limits from 74 (CT_{min}) and 73 (CT_{max} and CT_{range}) colonies of 40 ant species in the Australian

Wet Tropics. Box is mean ± SE and whiskers 95% confidence intervals using estimated marginal means from the respective linear mixed effects models (see Table 5.1), semi-transparent points are raw data of colony thermal limits.

Relationships between thermal tolerances and temperature exposure

At the microgeographic scale, the differences in ant species CT_{min} and CT_{max} matched the differences in absolute minimum and maximum microclimate temperature (Figure 5.3a, b). Averaging across elevation, minimum temperatures did not vary between ground and arboreal habitats (T_{min}: -0.08 °C, 95% CI: -0.5 – 0.3 °C), and, likewise, the change in CT_{min} between microhabitats was relatively small (Table 5.1, Figure 5.3b). In contrast, canopy maximums averaged 1.9 °C (95% CI: 1.2 – 2.5 °C) higher than ground maximums and the CT_{max} of arboreal species averaged 4.2 °C (95% CI: 2.7 – 5.6 °C) warmer than the CT_{max} of ground species. At the mesogeographic scale and averaging across microhabitat, minimum temperatures were, on average, 4.4 °C (95% CI: -4.8 – -4.0 °C) lower in upland compared with lowland sites, and this was matched by a similar average difference in ant species CT_{min} (Table 5.1, Figure 5.3b). Maximum temperature change across elevation, averaging over microhabitat, was approximately four times stronger than the change in CT_{max} (Figure 5.3b). Maximum temperatures were far hotter in lowland than upland sites, averaging 9 °C (95% CI: 8.4 – 9.7 °C) higher in the lowlands than the uplands, but the equivalent change in average CT_{max} between elevation was 2.3 °C (95% CI: 0.3 – 4.2 °C).

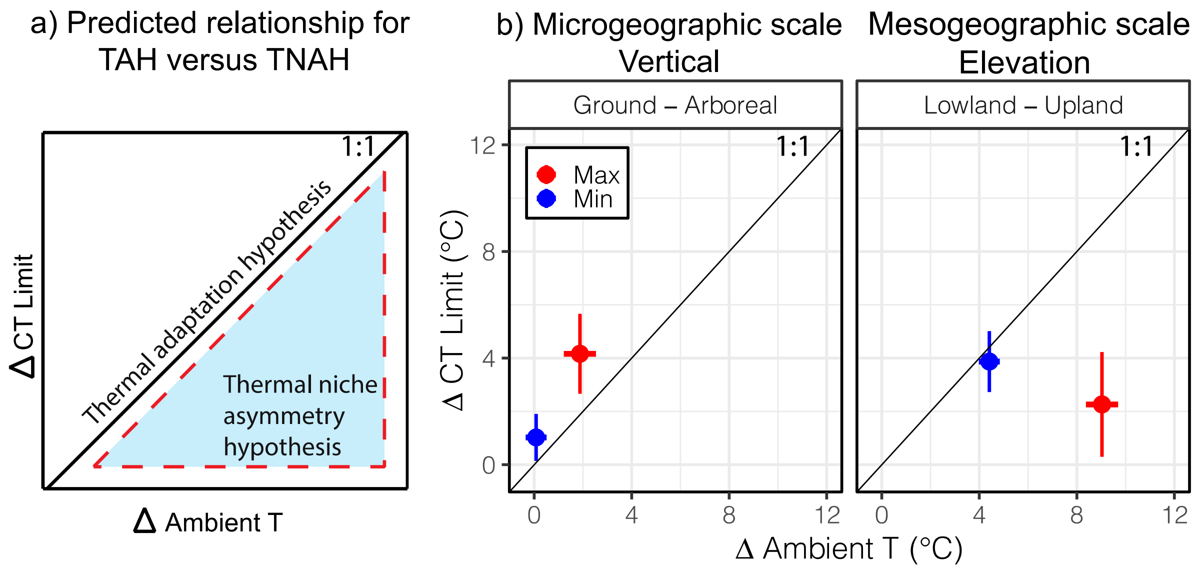

Figure 5.3. Relationships between changes in exposure temperature (Ambient T) and critical thermal limits (Max and Min) at the microgeographic scale of ground to arboreal (vertical) the mesogeographic scale lowland to upland (elevation). Thermal limits for 74 (CT_{min}) and 73 (CT_{max}) colonies of 40 ant species in the Australian Wet Tropics. The 1:1 line conforms to the thermal adaptation hypothesis (TAH), that states that thermal limits should correlate tightly with environmental temperature exposure, the area below that line conforms to the thermal niche asymmetry hypothesis (TNAH), that states that while CT_{min} closely tracks climatic gradients, CT_{max} does not, and therefore heat tolerance is similar between populations across environmental gradients.

Assessing the effect of phylogeny

We did not find a strong phylogenetic signal in CT_{min} across genera (Pagel's $\lambda = 0.61$, $p = 0.14$, Blomberg's $K = 0.75$, $p = 0.08$), but there was some indication of phylogenetic signal in CT_{max} (Pagel's $\lambda = 1$, $p = 0.09$, Blomberg's $K = 0.89$, $p = 0.03$) and CT_{range} (Pagel's $\lambda = 1.0$, $p = 0.04$, Blomberg's $K = 0.98$, $p = 0.02$). Accounting for phylogenetic relatedness, there was no significant difference in the mean CT_{min} of genera between vertical habitats (phylANOVA; $F_{2, 16} = 1.6$, $p = 0.32$), but there was a significant difference in the mean CT_{max} of genera between vertical habitats (phylANOVA; $F_{2, 16} = 11.9$, $p = 0.004$) (Figure 5.4). Mean genus CT_{max} differed between ground and arboreal genera ($t = 4.85$, $p = 0.01$) and mixed and ground genera ($t = 2.8$, $p = 0.06$), but not between mixed and arboreal genera ($t = 1.33$, $p = 0.14$). At the species-level, the same pattern between thermal traits, vertical habitat and elevation was found after accounting for phylogeny (Appendix Table S5.2).

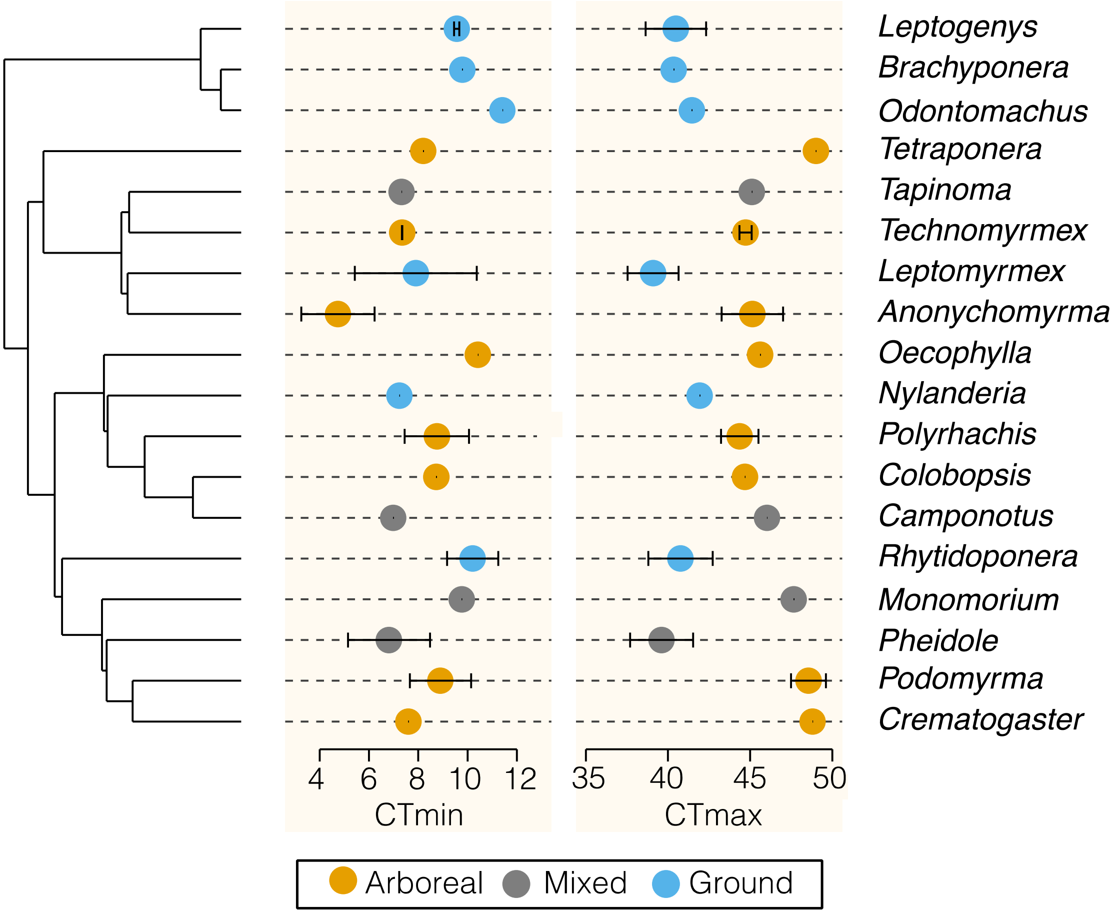

Figure 5.4. Phylogenetic relationships between the 18 genera and the genus level means for critical thermal minimum (CT_{min}) and critical thermal maximum (CT_{max}). Dots indicate mean thermal limit (i.e., averaged across species belonging to that genera). Error bars are ± SD. Colours of dots indicate the vertical habitat niche of the genus specifically for the Australian Wet Tropics, yellow = arboreal nesting, blue = ground/terrestrial nesting, and grey = mixed.

Warming tolerance

The warming tolerance of ants was significantly related to microhabitat and elevation ($F_{3, 36}$ = 32.64, $p < 0.001$). Lowland arboreal ants had the lowest warming tolerance of 1.9 ± 2.3 °C (mean ± SD throughout) under 2019–2020 temperatures (Figure 5.5). With a 1.5 °C increase, 47% of lowland arboreal ants tested here had negative warming tolerances, and with a 2 °C increase this rose to 58%. Lowland ground ants had marginally higher warming tolerances compared to lowland arboreal ants (Tukey's HSD: ground versus arboreal, $p = 0.09$) at 3.9 ± 2.0 °C. However, with 2 °C additional warming, warming tolerance of lowland ground ants narrowed to 1.9 ± 2.0 °C (Figure 5.5). Upland ants had greater warming tolerances than lowland ants (upland arboreal:10.8 ± 3.7 °C and upland ground: 11.9 ± 1.2 °C; Figure 5.5) and upland ground and arboreal species were not significantly different in warming tolerance (Tukey's HSD: ground versus arboreal, $p = 0.9$). Under 1.5 and 2 °C warming, the lower limit of warming tolerance for upland ant species was still above 5 °C (Figure 5.5).

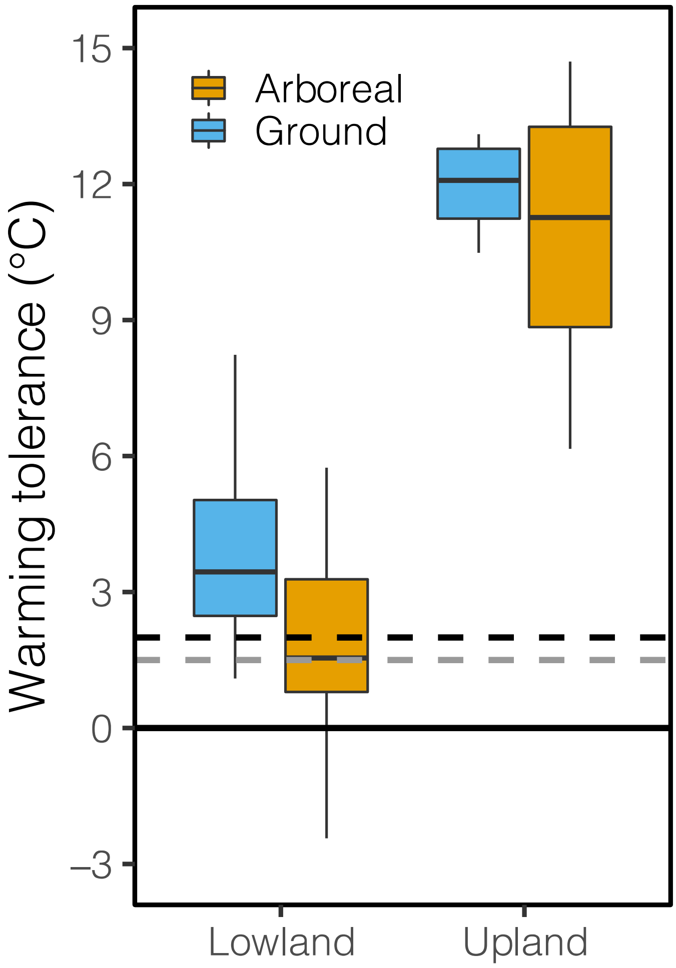

Figure 5.5. Current day 2019–2020 warming tolerances for Australian Wet Tropics ants in ground and arboreal microhabitats at lowland (100 m a.s.l.) and upland (1200 m a.s.l.) sites along the Carbine Uplands range. Box plots show the median (central band), 25th and 75th percentiles (bottom and top of boxes) and 1.5 times the interquartile range above or below the percentiles (whiskers) for 40 ant species. Warming tolerances were calculated from the maximum annual microclimate temperature for that microhabitat and site recorded for the year of March 2019 – March 2020 subtracted from each species mean CT_{max} values. The solid black line at 0 °C represents a potentially lethal threshold if an ant were exposed to that temperature; grey and black dotted lines represent the potentially lethal threshold at 1.5 °C and 2 °C warming from current day temperatures respectively.

Discussion

Our study uses a multi-scale approach to explore how microgeographic (vertical microhabitat) and mesogeographic (elevation) climatic gradients interact to shape the thermal tolerances of rainforest ants, addressing variation in thermal tolerance and its relationship with thermal exposure. We found that rainforest ants have CT_{min} and CT_{max} that match closely to thermal exposure along vertical gradients at the microgeographic scale as predicted by the thermal adaptation hypothesis. However, at the mesogeographic scale there is clear thermal niche asymmetry, whereby CT_{min} tracks declining minimum temperatures across elevation while CT_{max} remains relatively constant. There was stronger phylogenetic signal at the genus level in CT_{max} than $CT_{min.}$ Thus, both processes of thermal adaptation and thermal niche asymmetry are at play depending on the spatial scale of observation. Critically, we found that arboreal ants in the hot lowland canopy have very low warming tolerances (to projected increases in temperature), potentially placing them at risk of climate change. Arboreal ants living at the top of the mountain, however, have higher warming tolerance while ground ants in both habitats are somewhat buffered from high temperatures.

Tree canopies are hotter, drier, and more variable compared with the forest floor (Scheffers et al. 2013, Leahy et al. 2021) and we found that rainforest ants have matched their thermal tolerance limits to these conditions. We found arboreal ants to have a broader thermal tolerance range and the capacity to withstand temperatures on average 4.2 °C (95% CI: 2.7 – 5.6 °C) hotter compared to ground-dwelling species. We do not know the exact mechanism underlying this pattern – if ant populations were genetically adapted to their local habitats, whether they were expressing a short-term physiological response to recent thermal conditions, or whether they were exhibiting longer-term acclimation to conditions the colony has experienced since its inception (Sinclair et al. 2012, Sørensen et al. 2016, Martin et al.

2019). Our findings, however, meet the theoretical expectations of the thermal adaptation hypothesis and are in accordance with other studies (Baudier et al. 2015, Kaspari et al. 2015, Bujan et al. 2020a), suggesting that differences in ant thermal traits due to vertical microhabitat may be generalised across different biogeographic regions.

Our results are also consistent with the thermal niche asymmetry hypothesis. We found that upland ants had CT_{min} on average 3.9 °C lower than that of lowland ants and were therefore suited to cooler minimum air temperatures. In contrast, the change in CT_{max} over elevation was smaller than the marked decline in maximum air temperatures over elevation, regardless of microhabitat association — a pattern also shown for ground-dwelling ants along another mountain range in the Australian Wet Tropics (Nowrouzi et al. 2018) and along elevational gradients in other biomes (Bishop et al. 2017, Bujan et al. 2020a). In addition, we found evidence for genus-level phylogenetic signal in CT_{max} but not for CT_{min}, which is consistent with several ant thermal physiology studies (Diamond and Chick 2018, Bujan et al. 2020a) and could indicate a phylogenetic association for the thermal niche asymmetry pattern. We also established that CT_{max} is strongly driven by vertical microhabitat association at the genus level.

The key question arising from our results is why upland ants do not have lower CT_{max} if maintaining broad thermal limits is costly, or conversely, why do lowland ants (particularly, canopy ants) not have even higher CT_{max}, given the maximum temperatures we recorded in their microhabitat? This is important given that we found such low warming tolerance in relation to climate change for lowland arboreal ant species. One biogeographic explanation for phylogenetic conservatism in heat tolerance is that many taxa, including ants (Moreau and Bell 2013), likely originated and diversified from the tropical equatorial zone. Such taxa would have the upper limits of their fundamental niche set to a warm tropical climate, while their cold tolerance reflects intense selection for cooler climates as taxa have moved into higher latitudes and elevations (Araújo et al. 2013). As well, there may be a hard set upper limit to heat tolerance because the proteins involved in ameliorating the effects of high temperatures on bodily function are ancient and highly conserved across the tree of life (Araújo et al. 2013, Hoffmann et al. 2013).

On the other hand, behavioural thermoregulation is likely to play an important role in setting thermal limits, especially if it is operating to buffer ants from extreme high temperatures (Buckley et al. 2015). As colonial organisms, ants have their “reproductive organs”, the queens, and their workers variously thermally buffered from heat or cold in nests ranging from very sheltered nests in the soil (most species), to deep inside arboreal cavities of large old trees (e.g. *Anonychomyrma*), up to small exposed twigs in the canopy (e.g. *Tetraponera*) (Hölldobler and Wilson 1990, Leahy et al. 2020). Foraging ants can also draw on a range of foraging behaviours to mitigate exposure to undesirable temperatures such as avoiding superheated sunspots during foraging (Spicer et al. 2017), shifting foraging height with time of day, and flexibility in diel activity (Yusah et al. 2018). This type of behavioural mitigation of high temperatures will weaken selective pressure on physiological heat tolerance but not necessarily cold tolerance and in general, these processes will be highly species specific and strongly related to nesting and foraging ecology (Huey et al. 2012, Buckley et al. 2015, Muñoz and Bodensteiner 2019).

It is likely that a combination of evolutionary, physiological, and behavioural factors are operating to determine thermal limits in these rainforest ants (Huey et al. 2012). Overall, our results suggest that lowland arboreal ants are more vulnerable to climate change than are ground-dwelling species. Arboreal ants had broad thermal tolerances ranges, indicating that these species are likely to be thermal generalists and therefore relatively less sensitive to temperature exposure close to their upper thermal limits (for reasons see Huey et al. 2012). Based on our findings, however, some arboreal species could have theoretically passed their critical thermal limits on the hottest days of 2019–2020. Under a 2 °C warming scenario from this baseline, 58% of lowland arboreal ants in the Australian Wet Tropics could experience temperatures beyond their CT_{max} limits. In addition, our maximum temperatures were based on microclimate air temperatures, but the surface temperatures that foraging ants experience in the canopy can be up to 8 °C hotter than ambient air temperature in the sun (Kaspari et al. 2015). Therefore, although the types of behavioural buffering discussed above could limit exposure to some degree, even the most heat-tolerant lowland canopy ants in this study could be at increasing risk. An important caveat is that our thermal tests took place in the cooler dry season and temperate forest ants have been known to shift their upper thermal limit with season (Bujan et al. 2020b). We do not know if tropical forest ants undergo seasonal plasticity, and this should be an area for further investigation.

Although there were greater warming tolerances in both ground and arboreal ants in the cooler upland rainforest, heatwaves could still place upland ants at risk. Our models showed upland ground species had upper thermal limits of 38.6 °C (95% CI: 36.6 – 40.5 °C) and arboreal species of 42.6 °C (95% CI: 40.7 – 44.6 °C). These limits are far above typical upland temperatures. Yet in November 2018, a record-breaking 7-day heat wave occurred with maximum temperatures between 35–39°C at 1600 m a.s.l. on Mt. Bartle Frere, which is 400 m higher in elevation than our upland sites (pers. comm. Chris Roach, QPWS). Wet Tropics montane ants are also likely to be significantly affected by drying out of upland rainforests predicted with climate change (Nowrouzi et al. 2019). The orographic cloud layer is predicted to shift from 600 m a.s.l. to around 900 m a.s.l. by 2050 (WTMA 2013, Nowrouzi et al. 2019). This will likely interact with the vertical gradient in vapor pressure deficit and the distribution of thermal traits, including desiccation resistance in the community, resulting in differential impacts on ground and canopy species of the upland rainforest.

Conclusion

Investigating thermal ecology from a multiscale perspective is essential to capture the nested nature of climatic gradients. Our study found that arboreality drives divergence among ant species in CT_{max} and elevation drives divergence in CT_{min}. In the rainforests of a warming world, microhabitat niche will be a critical determinant of climate change vulnerability, influencing both thermal exposure and thermal sensitivity. Based on our findings, we conclude that lowland canopy ants may be most vulnerable to projected global warming in coming decades. If heat tolerance is evolutionary constrained, rapid genetic adaptation is unlikely, particularly given the long generation times of some ant species (Hölldobler and Wilson 1990, Araújo et al. 2013). If behavioural thermoregulation buffers lowland arboreal ants from extreme temperatures, this may only go so far before foraging productivity and hence fitness is affected. In addition, while beneficial in the short term, if behavioural buffering is setting the brakes on physiological adaptation, the result could be reduced adaptive capacity in the longer term (Buckley et al. 2015, Muñoz and Bodensteiner 2019).

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Chapter Six - The nightshift lowdown: ants take the heat out of tropical rainforest.

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Abstract

Tropical species are thought to be especially vulnerable to climate change because they are not physiologically adapted to high temperature variation and don’t cope well with temperature extremes. However, such vulnerability can be reduced by behavioural responses that avoid high temperatures, such as foraging in cooler microhabitats or during cooler parts of the day. In tropical rainforests, species are potentially active over two thermal niche dimensions, one spatial (from ground to canopy) and the other temporal (day to night). The advantages of selective foraging when and where it is cooler will vary along elevation gradients. Here we investigate the spatiotemporal activity and thermal ecology of rainforest ants along an elevation gradient in the Australian Wet Tropics Bioregion. Along temporal and vertical thermal gradients at different elevation sites we: a) quantify thermal exposure (degree of thermal overlap along local thermal gradients, and the relationship between surface temperatures and air temperature), b) document ant activity patterns, and c) characterise the proportion of specialist versus generalist foraging strategies in vertical space and time. We then test the thermal limits of selected species at a lowland and upland site and incorporate activity niches, thermal exposure, and thermal traits to make predictions of the buffering potential of selective foraging. Regardless of elevation, we found that a high proportion of species have the capacity to be active where (on or near the ground) and/or when (at night) it is cooler. Such species had scope to buffer temperatures that are close to their upper thermal limits. Our results indicate that rainforest ants have more potential to buffer temperature exposure than previously considered, thereby reducing the impacts of global warming on their populations. Species that are canopy specialists and obligately diurnal do not have such buffering potential and are therefore likely to be most at risk. This is likely to apply more broadly to lowland ectothermic canopy specialists with obligate daytime activity, which represent a large proportion of tropical rainforest biodiversity.

Introduction

Tropical rainforest species are predicted to be especially vulnerable to climate change because they are considered to be more thermally sensitive and generally have limited elevational and geographic ranges (Huey et al. 2009). The rapid pace of climatic warming limits the capacity of many species to shift their ranges and there is low potential for evolutionary adaptation (Stillman 2003, Moritz and Agudo 2013). However, the effects of rising temperatures can be potentially mitigated by *in situ* behavioural responses that allow populations to exploit local thermal variability while remaining within their current ranges (Williams et al. 2008, Kearney et al. 2009, Sunday et al. 2014).

Spatial and temporal thermal gradients interact with each other to create climatic variability at the microscale, and localised thermal environments are nested within broader scale climatic gradients of elevation and latitude (Potter et al. 2013). For example, microclimatic variation created by sun and shade exposure is a key feature of diurnal environments, but at night this microclimatic variation disappears, and thermal microclimates become more homogenised (Freiberg 1997). Species therefore exist in a multidimensional thermal landscape within which their ecology and behaviour determine thermal exposure and their physiology determines their persistence under those conditions (Bonebrake and Deutsch 2012, Huey et al. 2012). These factors will combine to determine vulnerability to global warming (Williams et al. 2008).

In forests there are two localised thermal gradients along which species can be active, one relating to vertical space from ground to canopy (Leahy et al. 2021a), and the other to the time of day (Kronfeld-Schor and Dayan 2003, Yusah et al. 2018). These localised thermal gradients represent spatial and temporal niche axes that populations can exploit for maintaining optimal thermal exposure (Kronfeld-Schor and Dayan 2003, Holt 2009). Species exhibit different activity patterns along each niche axis, ranging from generalist to specialist (Gaston 2019). For example, true lemurs (*Eulemur* group) are generally cathemeral (active both day and night) with more or less diurnal activity depending on season, diet, group size, and level of anthropogenic disturbance (Donati et al. 2016). Flexibility can also be triggered by various environmental or biological cues; for example, amphibians in Panama shift downward from the canopy in the dry season and up again in the wet season when the canopy is more humid (Basham and Scheffers 2020). Different niche strategies may have evolved for a wide range of reasons including maximising resource acquisition, avoiding predation and competition, as well as for thermal optimisation (Holt 2009, Huey et al. 2012). Whatever the case, in a warming world, generalist species could utilise this existing behavioural flexibility along spatio-temporal thermal gradients to buffer unfavourable temperatures (Levy et al. 2019). On the other hand, specialised species that are restricted to the hotter parts of the environment, will have less behavioural buffering capacity and therefore may be more vulnerable (Huey et al. 2012, McCain and King 2014).

In tropical forests, mountainous topography creates elevational climatic gradients in which localised thermal gradients are nested. Along these elevational gradients, the benefits and costs of different spatiotemporal activity patterns are likely to change in tandem with both climatic and biotic changes (Machac et al. 2011, Bishop et al. 2015, Lasmar et al. 2021). Species may wish to buffer hot temperatures in the lowlands and cold temperatures in the uplands, leading to elevation-specific patterns of spatiotemporal movement (Bennie et al. 2014). In particular, we might expect more specialisation towards the warmer daytime temperatures and/or the canopy in cooler upland environments (Scheffers et al. 2013).

Rainforest ants are excellent organisms for investigating spatiotemporal patterns of foraging activity in relation to thermal ecology as they are widely dispersed along vertical, temporal, and elevational gradients (Yanoviak and Kaspari 2000, Hashimoto et al. 2010, Houadria et al. 2015). Many ant species are flexible in their diel activity patterns (Whitford 1978, Heatwole and Muir 1991, Houadria et al. 2015, Yusah et al. 2018) as well as across vertical strata (Brühl et al. 1998, Vasconcelos and Vilhena 2006, Leahy et al. 2021a). There have been several studies of spatiotemporal activity patterns in relation to niche partitioning (Kaspari and Weiser 2000, Blüthgen et al. 2004, Gaston 2019), but not from the perspective of thermal ecology.

Accurately characterising thermal exposure is essential to understanding species behaviour in localised thermal landscapes and how they might avoid temperatures close to their thermal limits (Suggitt et al. 2011, Potter et al. 2013, Storlie et al. 2014, Woods et al. 2015). At the local scale, ant thermal limits are strongly related to microclimate; canopy species tend to tolerate hotter temperatures than do ground or subterranean species (Baudier et al. 2015, Kaspari et al. 2015) and obligate nocturnal species can withstand colder temperatures than diurnal species (Garcia-Robledo et al. 2018). However, we have a limited understanding of how much thermal overlap there is along vertical, temporal, and elevation gradients. In addition, the diminutive stature of ants means that their operative temperature – the temperature that an organism perceives in the environment independent of any physiological thermoregulation (Angilletta 2009) – is strongly influenced by the surface temperatures on which they walk rather than simply by ambient air temperature (Kaspari et al. 2015). In the hot canopy of lowland tropical rainforests, for example, surface temperatures can reach up to eight degrees higher than air temperature, potentially exposing ants to far higher temperatures than in the surrounding air (Storlie et al. 2014, Kaspari et al. 2015). We also have little understanding of how surface temperatures decouple from ambient air temperature along vertical, temporal and elevation gradients.

Here we focus on the question: to what extent might flexibility in activity along spatiotemporal axes of verticality and time of day confer resilience to climate change? We use a multiscale approach to investigate the foraging activity and thermal ecology of rainforest ants along vertical, temporal, and elevational gradients in the Australian Wet Tropics Bioregion to: (1) quantify the thermal environment, considering microclimatic air temperature, and foraging-surface temperature, and patterns of their decoupling along each thermal gradient; (2) characterise species activity along each thermal gradient in order to identify the proportion of species with specialised or generalised activity niches; and (3) incorporate activity niches, thermal exposure, and thermal traits to predict how flexibility in activity along these gradients could buffer species from rising temperatures. We then discuss the implications of our findings for predicting climate change vulnerability in ants and rainforest fauna more generally.

Methods

Study sites

Ants were sampled at three elevation sites along the Mt. Lewis/Carbine (hereafter, Carbine) elevation gradient at a lowland 100 m a.s.l. (Mossman Gorge; -16.470, 145.320), and two upland sites, 1000 m a.s.l. and 1200 m a.s.l. (Mt. Lewis National Park; -16.510, 145.270). We sampled 1000 m a.s.l. sites in February 2018, and 100 and 1200 m a.s.l. sites from August – October 2019 (Leahy et al. 2021b). At all sites, sampling was conducted only in the absence of rain. The ant fauna at these sites has been previously described in Nowrouzi (2016), Leahy et al. (2020), and Leahy et al. (2021a).

Ant surveys

At each elevation site, we established five plots – at least 50 m apart – and for sampling selected the largest tree per plot (20–30 m total height) that was considered safe to climb.

Ants were sampled in both day and night surveys with a combination of tuna baits and hand collection in ground and arboreal strata. Using the single-rope climbing technique, for each tree at every 3 m point from the ground to the highest part of the tree, we set five baited vials (~1cm by 5cm), that were attached using tape and thumbtacks to the trunk, branches, and available epiphytes. Ground baits were placed on the leaf litter or close to logs or other ground substrate. Baits were collected after three hours. During deployment and collection of baits, over a period of approximately one hour in each stratum, foraging ants were opportunistically hand collected using soft forceps and an aspirator. Day surveys began at 10:00 hr and night surveys began at 20:00 hr. Day and night surveys of the same trees were not conducted sequentially and were at least a day apart to allow resumption of normal ant activity in the tree. We note that our sampling of ground-foraging ants targets epigaeic species and is largely ineffectual for the cryptobiotic fauna. Data from day surveys were previously used in Leahy et al. (2021b), data from night surveys has not been previously reported. All voucher specimens were deposited in the ant collection held at CSIRO’s Tropical Ecosystems Research Centre in Darwin, Australia.

Measuring activity temperatures and ambient microclimate

Quantification of the thermal environment was conducted at the 100 m a.s.l. and 1200 m a.s.l. sites as these represented the hot and cold extremes of the elevation gradient. For each ant occurrence we took both air and surface temperature. Air temperature was taken with a HOBO Pro v2 (U23-002) Temperature/Relative humidity data logger attached to the surveyor’s climbing harness by a short rope so as to not be influenced by the body temperature of the climber. This logger was set to record temperature every 1 minute from start to finish of the survey. Surface temperature was recorded using a handheld infrared temperature gun at every baited vial deployed every three metres from ground to canopy at each tree surveyed. Thus, for every ant capture in a baited vial we have a matched surface temperature and air temperature for that specific location and time of day.

To characterise the longer-term microclimate conditions of our vertical habitats and elevation sites, we recorded temperature at 30-minute intervals using HOBO Pro v2 (U23-002) Temperature/Relative humidity data loggers placed at ground (~ 0.5 m) and arboreal (~ 20 m) habitats for two years from March 2019 – March 2021 at the 100 m a.s.l. and 1200 m a.s.l. sites. Data loggers were hung freely underneath a wide funnel (30 cm radius) to allow air flow while ensuring protection from extreme sun exposure which can degrade the equipment over long time periods and cause misleading spikes in temperature recordings.

Thermal tolerance experiments

To determine the thermal limits of ant species, we again chose the lowland 100 m a.s.l. and upland 1200 m a.s.l. sites that represented the extremes of the elevation gradient. Following collection of live ants during surveys, ants were tested for CT_{min} and CT_{max} using ramping assays in the field. For both day and night surveys, thermal tolerance tests were conducted as soon as possible after field collection to avoid experimental acclimation. Details of testing protocol in Leahy et al. (2021b), Chapter 5.

Data analysis

Quantifying thermal overlap

We aimed to quantify how much temperatures overlapped between each combination of the vertical and temporal dimensions at the lowland and upland elevation site. For each elevation site and for each of the four-way combinations of ground, canopy, day, night (e.g., ground day – ground night, etc) we calculated a thermal overlap value as the overlap of two kernel density distributions using the function ‘overlap’ in the *overlapping* package (Pastore 2018). Kernel density distributions consisted of recorded temperature values from the two years of continuous microclimate recordings. Low thermal overlap would indicate that ant species are exposed to very different thermal conditions. We then plotted the density distributions using function ‘geom_density_ridges’ from the *ggridges* package (Wilke 2021).

Decoupling of surface and air temperature

To quantify how surface temperature decoupled from ambient microclimate temperature with vertical height for daytime and night-time sampling periods at each elevation site, we calculated the difference between surface temperature and ambient temperature. Positive values indicate that surface temperatures were warmer than surrounding air temperature and *vice versa* for negative values. To ensure consistency in measurements across the vertical gradient we used only surface temperatures taken from the trunk of the tree surveyed, from the ground (at the very base of the tree) and every three metres in vertical height as outlined above. This resulted in 520 paired surface and air temperature values. We modelled the temperature difference as a function of vertical height (continuous variable), day or night (categorical), and elevation site (categorical), and their interactions as a linear mixed effects model with date and time as a random effect to account for different weather conditions on the days of sampling. Best performing model was selected using ‘stepAIC’ function (*MASS* package). Linear mixed effects models were performed using the package *nlme* (Pinheiro et al. 2020) with degrees of freedom calculated as outlined in Pinheiro and Bates (2006). Final hypothesis testing was done via likelihood ratio tests using ANOVA by comparing the full model to a null model with no fixed effects. We calculated marginal (R_{m}^2, fixed effects) and conditional (R_{c}^2, random effects) R^2 values (Nakagawa and Schielzeth 2013).

Ant community composition and activity niches

For these analyses we pooled data from baited samples and hand collections. We also pooled arboreal samples into one zone from 3m to the height of highest vial deployment in each tree based on vertical stratification analysis conducted in Chapter Four. Under this designation, the amount of time spent conducting hand collections was equal in ground and arboreal strata, but there was a difference in the number of baited vials deployed in ground and arboreal strata because 5 vials were deployed every 3m band of the tree resulting in 5 vials in ground and >25 vials in arboreal depending on height of tree. Therefore, we standardised each species occurrence by total survey effort in each vertical stratum by calculating occurrences in sample vials as a proportion of total vials deployed.

To explore patterns of community composition in vertical space (ground vs arboreal) and time (day vs night) and at each elevation site, we used multivariate ordination of relative frequency data from all species collected (n = 63 species), based on Bray-Curtis dissimilarity. For each elevation, we tested the effect of vertical habitat (ground vs arboreal), time (day vs night), and their interaction on species composition using a PERMANOVA (using ‘adonis’ from *vegan* ver. 2.5; Oksanen *et al.* 2020) with “vertical habitat” and “day-night” as fixed factors and with “plot” as a random block factor and 999 permutations. Placing survey plot as a block factor accounted for our nested survey design and allowed the spatial variation in community structure created by turnover between individual plots to be accounted for in the model. We then standardised the data using the Wisconsin double standardization, which standardises the values in each row and column by the totals for that row and column respectively, thereby allowing easier computation and revealing more-subtle patterns of species composition (Legendre and Gallagher 2001). We tested for homogeneity of multivariate dispersions for our fixed factors using ‘betadisper’ in *vegan* ver 2.5 (Oksanen et al. 2020). Note that PERMANOVA with a balanced design, as in our models, is relatively robust to non-homogeneity of multivariate dispersions (Anderson and Walsh 2013). We used the percentage of explained variance (partial R^2) to compare effect sizes between elevation sites.

To explore species-specific patterns of foraging activity in each elevation site, we selected the 28 species with ≥ 4 total occurrences (100 m a.s.l., n = 13 species, 1000 m a.s.l., n = 10 species, 1200 m a.s.l., n = 8 species). This cut-off value was chosen to allow for the potential for a species to have been recorded in both strata and each time period (Houadria et al. 2015). To describe the overall foraging activity, we combined each species occurrences along vertical and temporal niche axes and then calculated a proportion of activity for each species in each of the four niche categories: canopy day, ground day, canopy night, ground night. Following Houadria *et al.* (2015), for each species we calculated the proportion of foraging activity in each elevation site by taking the mean plot-level relative frequency (taking the mean across the five plots sampled per site) for each of the categories (e.g., canopy day) divided by the summed total frequency across the four categories for that species. For graphical representation of species-specific foraging activity, night category values were multiplied by -1 to place temporal foraging activity on a -1 (purely nocturnal) to +1 (purely diurnal) scale and vertical category values represented within night and day in paired colours.

To statistically test for generalisation/specialisation we modelled specialisation on each niche axis (vertical and temporal) separately to simplify interpretation of the results. We tested specialisation using paired Wilcoxon signed-rank tests for species with three or more plot occurrences (8 species, 7 species, and 5 species at 100, 1000, 1200 m a.s.l., respectively). Here, ‘specialised’ indicates a significant difference in activity in one category e.g., significantly more activity in ground or significantly more foraging at night. A non-significant Wilcoxon test indicated ‘generalised’ foraging (i.e., foraging distribution not specialised). We used species plot-level relative frequency in day versus night, or ground versus canopy respectively, divided by the summed plot total frequency, as the independent variable, and day versus night or ground versus canopy as the dependent variable.

Activity niche, thermal exposure, and thermal limits

Our final question was whether spatiotemporal patterns of foraging activity provide options for buffering temperature exposure in relation to microclimate conditions and each species thermal tolerance limits. To explore the relationship between species activity, temperature exposure, and thermal tolerance we selected the two sites at the extremes of the elevation gradient, 100 m a.s.l., and 1200 m a.s.l., where we had collected data on microclimate and thermal tolerance. At these sites we selected species for which we had both thermal tolerance data and ≥ 8 recorded sample occurrences (no species for this analysis occurred in both lowland and upland sites), to better capture the thermal exposure of that population. We used the surface temperatures recorded for each species capture as their field foraging activity temperatures, we used the long-term microclimate data (ground and canopy) as the species ambient microclimate, and we used each species CT_{min} and CT_{max} as their thermal tolerance limits.

Results

Quantifying thermal overlap

In the lowlands, temperatures overlap less between ground and arboreal habitats and between day and night than they do in the uplands (Figure 6.1). At both lowland and upland sites there was a greater degree of thermal overlap between ground and canopy at night (92% and 93% for lowland and upland respectively) than in the day (62% and 80%) and the thermal overlap between day and night-time temperatures was greater on the ground (56% and 70%) compared to in the canopy (31% and 64%).

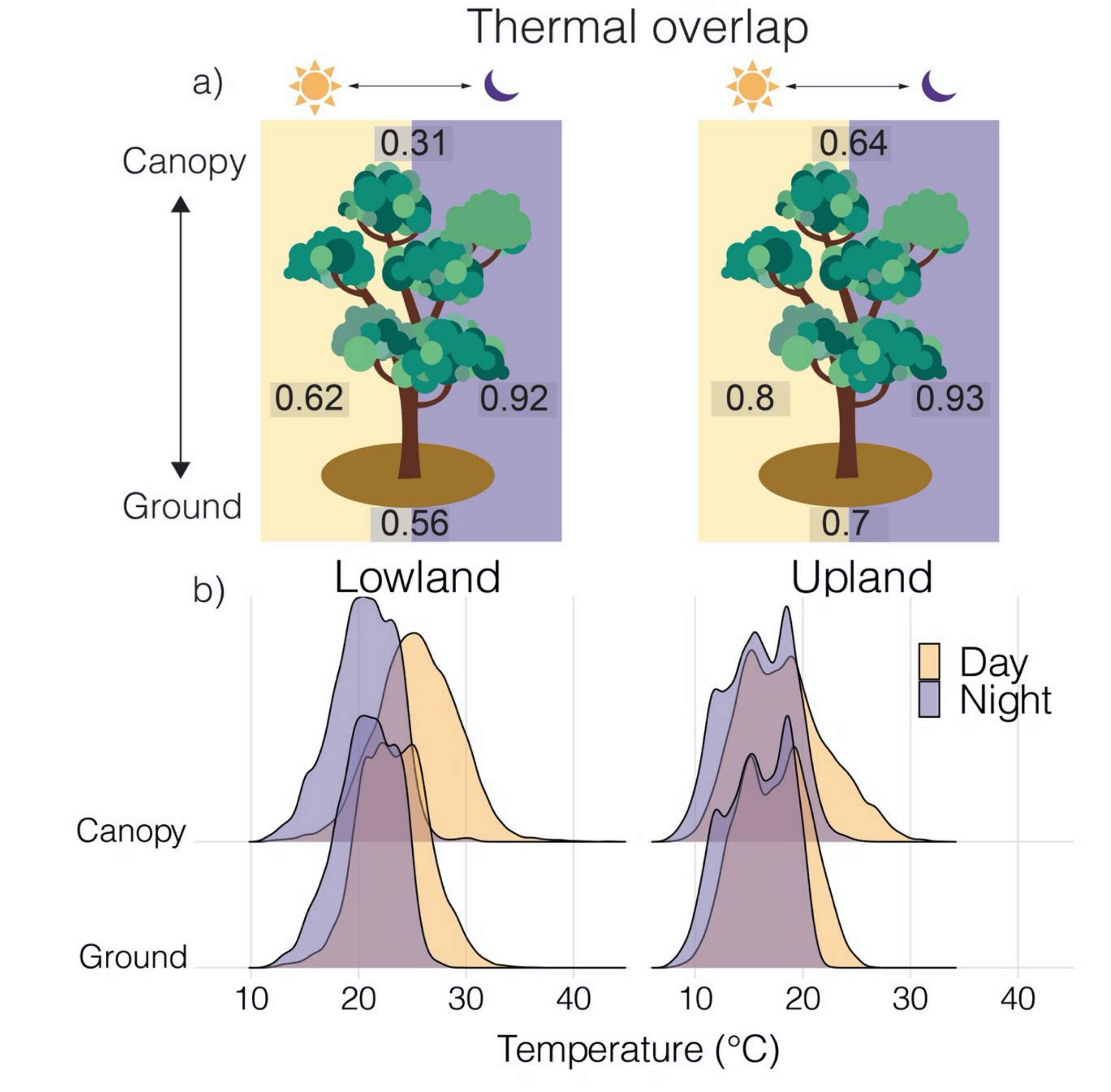

Figure 6.1. Thermal overlap along thermal niche dimensions of vertical (ground and canopy), time-period (day and night) and their different combinations at a lowland (100 m a.s.l.) and upland (1200 m a.s.l.) rainforest site in the Australian Wet Tropics Bioregion. Showing a) thermal overlap values from b) kernel density distributions (y-axis) of microclimate air temperature recorded every half hour in each vertical position and elevation site for two years (March 2019-March 2021).

Decoupling of surface and air temperature

Surface temperatures were much lower (as much as 10 °C) than air temperature on the ground, but this difference declined with increasing vertical height and was reversed after about 15 m vertical height in the lowland site and 5 m in the upland site. (Figure 6.2). Surface temperatures were >5 °C higher than air temperature at the top of trees in the upland site. This vertical effect was significantly stronger in the daytime (LME: interaction, time-period*height, $F_{1–147}$, p = 0.002) than in the night-time, particularly in the uplands, where night-time surface temperatures along the vertical gradient were not different to air temperature (LME: interaction, elevation site*time-period, $F_{1–147}$, p = 0.005). Model results reported in Appendix Table S6.1.

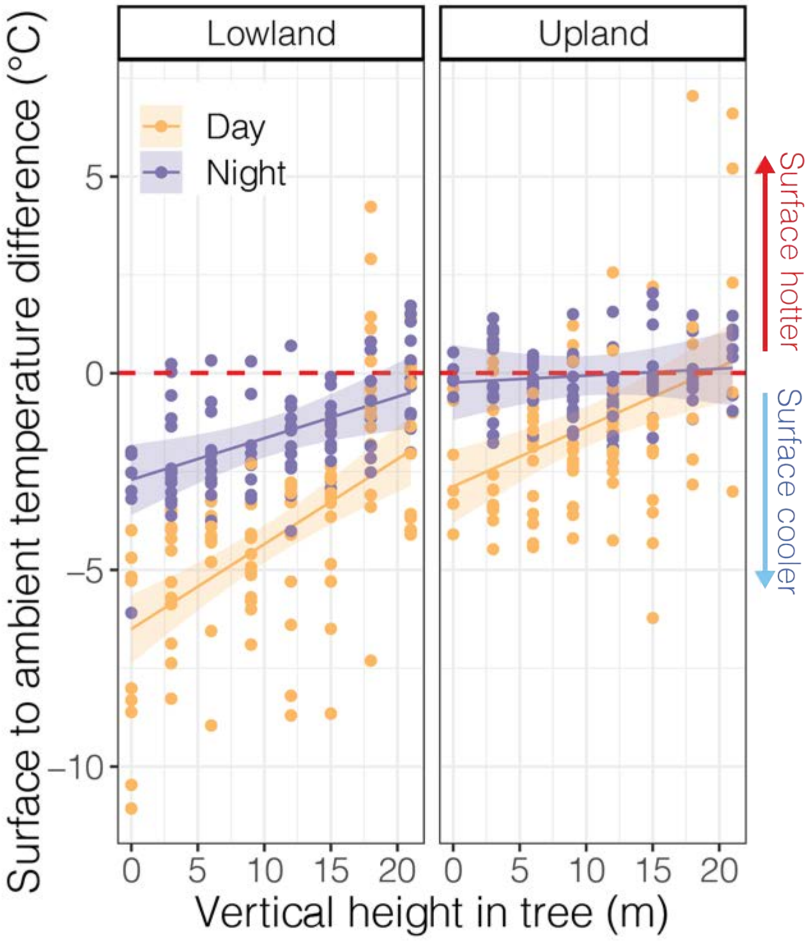

Figure 6.2. Decoupling of tree trunk surface temperatures from ambient air temperature along vertical tree gradient in day and night at lowland (100 m a.s.l.) and upland (1200 m a.s.l.) elevation sites in the Australian Wet Tropics Bioregion. Negative points indicate surface temperatures cooler than air temperature and positive points indicate surface temperatures hotter than air temperature and red dotted line at 0 represents surface and air temperature equivalency. Fitted lines and 95% confidence intervals from linear mixed effects model.

Spatio-temporal variation in ant species composition

There were different species in ground and arboreal habitats at all elevations, but there was not much difference in species composition between day and night, particularly at the two higher elevations (Table 6.1, Figure 6.3a-c). There was no interactive effect of vertical habitat and time-period on species composition at any elevation. Vertical habitat (independent of time) explained 17% (pseudo-$F_{(1)} = 3.96$, $p = 0.001$) of variation in species composition in the lowlands (100 m a.s.l.), 15% (pseudo-$F_{(1)} = 2.71$, $p = 0.001$) at 1000 m a.s.l. and 20% (pseudo-$F_{(1)} = 4.29$, $p = 0.001$) at 1200 m a.s.l. (Table 6.1). Time-period (independent of vertical habitat) explained 10% (pseudo-$F_{(1)} = 2.27$, $p = 0.007$) of variation in species composition in the lowlands, 7% at 1000 m a.s.l. (pseudo-$F_{(1)} =1.46$, $p = 0.07$). and 9% (pseudo-$F_{(1)} =1.83$, $p = 0.05$) at 1200 m a.s.l. (Table 6.1).

Table 6.1. The effect of vertical habitat and time-period on community composition of ants along an elevation gradient in the Australian Wet Tropics Bioregion. Results of PERMANOVA based on species relative frequency in ground and arboreal surveys conducted in day and night. With “Vertical habitat” and “Time-period” and their interaction as fixed factors and “plot” as a random block factor and using Bray-Curtis dissimilarity. Significance threshold: $p < 0.05$.

Elevation (m a.s.l.)	**Vertical** (df = 1)			**Time-period** (df =1)			**Vertical:Time-period** (df = 1)			**Residuals** (df)
	Pseudo F	*p*	% Explained variance	Pseudo F	*p*	% Explained variance	Pseudo F	*p*	% Explained variance	% Explained variance
100	3.96	0.001	17	2.27	0.007	10	1.22	0.187	5	0.68 (16)
1000	3.10	0.001	15	1.46	0.07	7	1.02	0.304	5	0.73 (15)
1200	4.29	0.001	20	1.83	0.05	9	1.0	0.443	5	0.66 (14)

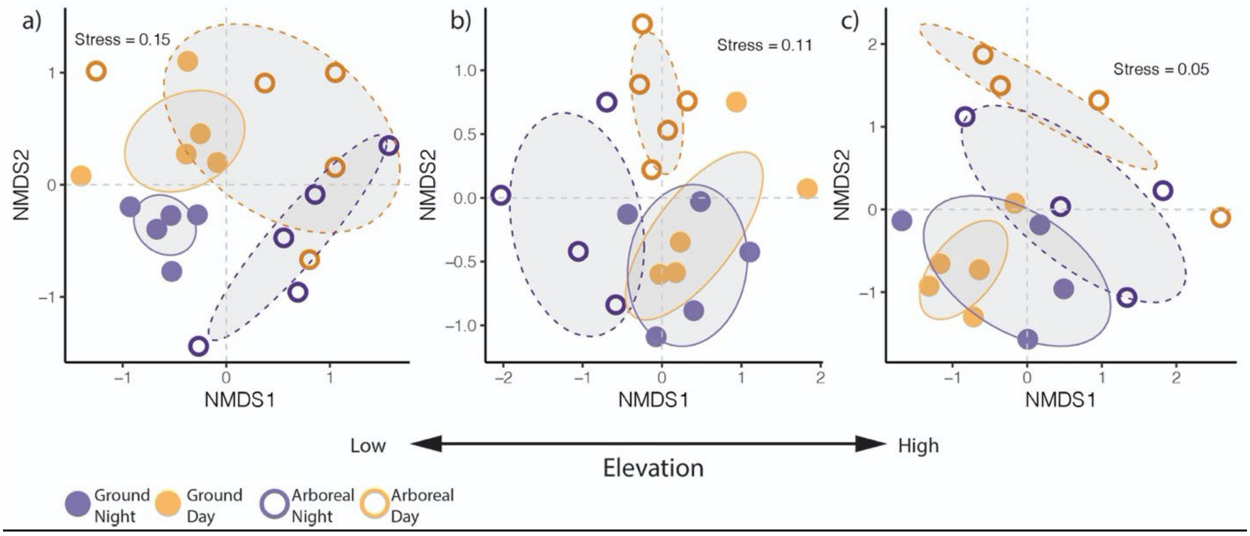

Figure 6.3. Spatio-temporal ant community structure showing nMDS ordinations of ant species composition in ground and arboreal habitats in day and night-time surveys at three elevations along the Carbine range in the Australian Wet Tropics Bioregion. A) 100 m a.s.l. (n = 42 species), B) 1000 m a.s.l. (n =19 species) C) 1200 m a.s.l. (n = 18 species). Polygons show grouping of surveys/sites where further separation between polygons represents greater differences in species composition.

Vertical and temporal foraging activity of common species

The majority of common species analysed were captured in both day and night samples: 77%, 60%, and 87.5% at the 100, 1000, and 1200 m a.s.l. sites, respectively (Figure 6.4). Most (60% and 62% respectively) of the common species were also recorded in both ground and canopy habitats at the 100 (60%) and 1000 m a.s.l. (62%) sites (Figure 6.4a–b). However, at 1200 m a.s.l., about half the species were recorded only on the ground or in the canopy (Figure 6.4c).

For those species with sufficient plot occurrences for statistical testing, there was a greater degree of specialisation in vertical habitat than temporal activity. At 100 m a.s.l., three species (*Camponotus* sp. N1, *Nylanderia glabrior*, and *Rhytidoponera spoliata*) showed a statistically significant level of nocturnal specialisation and one species (*Anonychomyrma gilberti*) of diurnal specialisation (Table 6.2, Figure 6.4a). At 1000 m a.s.l., there was one nocturnal (*Camponotus* sp. N3) and one diurnal (*Anonychomyrma* sp. C) specialist species (Table 6.2, Figure 6.4b), while only one species (*Pheidole* sp. A5) showed marginally significant daytime activity at 1200 m a.s.l. (Table 6.2, Figure 6.4c). In general, ground specialisation predominated over canopy specialisation. At 100 m a.s.l., seven of the eight species were ground specialists, and none were canopy specialists (Table 6.2, Figure 6.4a). There were two ground and one canopy specialist at 1000 m a.s.l. (Table 6.2, Figure 6.4b) and three ground specialists and one species that showed marginally significant canopy specialisation at 1200 m a.s.l. (Table 6.2, Figure 6.4c).

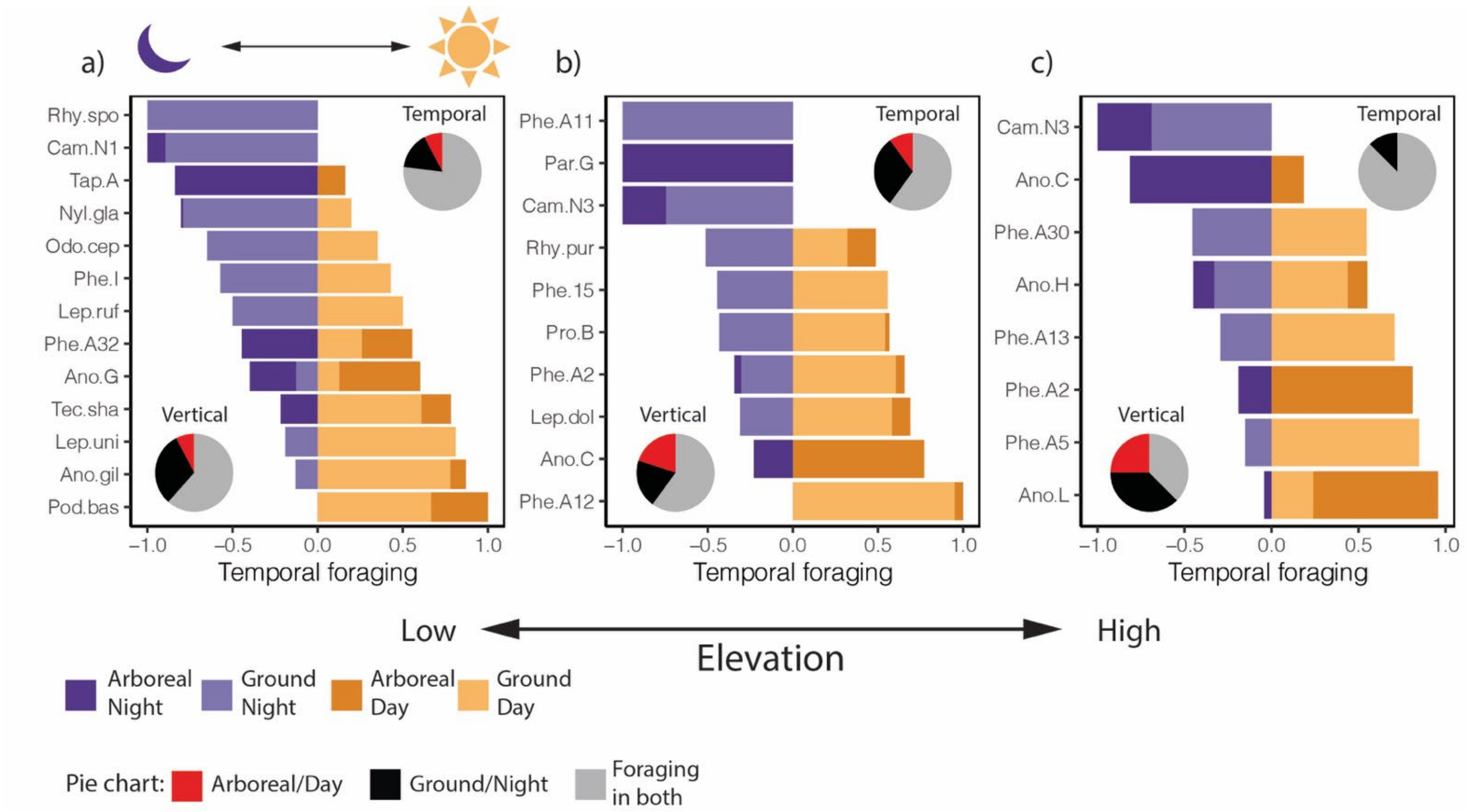

Figure 6.4. Temporal and vertical activity of ants based on species relative frequencies in surveys conducted in ground and arboreal habitats in the day or night along an elevation gradient in the Australian Wet Tropics Bioregion. Showing common species with four or more occurrences at a) 100 m a.s.l. b) 1000 m a.s.l. c) 1200 m a.s.l. Bar charts show activity frequency, where negative values indicate night-time activity and positive values indicate daytime activity. Within each bar, dark colours indicate arboreal activity, and light colours indicate ground activity. Pie charts show temporal and vertical separately and are representing the proportion of species with activity recorded in both niche categories and activity only recorded in one niche category. Abbreviated names are first three letters of genus and species. Full species names are shown in Table 6.2.

Table 6.2. Species nesting (based on literature and visual confirmation of nests), number of plot and sample occurrences, relative frequency of occurrence in arboreal and ground during daytime and night-time, and specialisation along temporal and vertical niche axes, thermal tolerance (n = 1–3 colonies/species), and body mass (n = 3–5 workers/colony). Showing species with four or more sample occurrences. Specialisation indicated by significant Wilcoxon test denoted with symbols († P < 0.1, * P < 0.05, ** P < 0.01), 'generalised' indicates a non-significant result (i.e., activity not specialised, therefore generalised), '–' indicates not enough data for test (<3 plot occurrences).

Site	Species				Activity						Physiological traits	
		Nesting	Plot (n)	Sample (n)	Arboreal Day	Arboreal Night	Ground Day	Ground Night	Temporal specialisation	Vertical specialisation	Mean CT_{min} ± SD (ºC)	Mean CT_{max} ± SD (ºC)
100	*Anonychomyrma gilberti*	Arboreal	4	12	0.09	0.00	0.78	0.13	Day *	Ground *	6.6 ± 1.36	43.43 ± 2.78
	Anonychomyrma sp. G	Arboreal	2	38	0.48	0.27	0.13	0.13	–	–	6.58 ± 1.17	45.97 ± 1.51
	Camponotus sp. N1	Arboreal	5	11	0.00	0.11	0.00	0.89	Night *	Ground *	6.8 ± 0.41	41.87 ± 2.88
	Leptomyrmex ruficeps	Ground	2	4	0.00	0.00	0.50	0.50	–	–	6.15 ± 2.27	38 ± 5.13
	Leptomyrmex unicolor	Ground	4	5	0.00	0.00	0.81	0.19	Day †	Ground *	10.4 ± 0.76	41.6
	Nylanderia glabrior	Mixed	5	11	0.00	0.01	0.20	0.79	Night *	Ground *	7.23 ± 0.7	41.93 ± 2.4
	Odontomachus cephalotes	Ground	5	9	0.00	0.00	0.35	0.65	Generalised	Ground *	11.86 ± 1.23	41.45 ± 1.45
	Pheidole sp. A32	Unknown	3	21	0.29	0.45	0.26	0.00	Generalised	Generalised	8.27 ± 1.02	42.03 ± 1.52
	Pheidole sp. I	Ground	3	5	0.00	0.00	0.43	0.57	Generalised	Ground †	8.74 ±1.1	40.49 ± 2.52
	Podomyrma basalis	Arboreal	2	4	0.33	0.00	0.67	0.00	–	–	9.78 ± 1.8	49.3 ± 3.25
	Rhytidoponera spoliata	Ground	4	4	0.00	0.00	0.00	1.00	Night *	Ground *	6.41 ± 0.88	42.49 ± 0.83
	Tapinoma sp. A	Arboreal	2	6	0.16	0.84	0.00	0.00	–	–	7.32 ± 2.01	45.1 ± 0.14
	Technomyrmex shattucki	Arboreal	2	11	0.17	0.22	0.61	0.00	–	–	7.19 ± 1.04	44.48 ± 1.83

1000	*Anonychomyrma* sp. C	Arboreal	5	25	0.77	0.23	0.00	0.00	Day *	Arboreal *	-	-
	Camponotus sp. N3	Unknown	4	6	0.00	0.26	0.00	0.74	Night *	Generalised	-	-
	Leptomyrmex dolichoscapus	Ground	4	9	0.11	0.00	0.58	0.31	Generalised	Ground *	-	-
	Paraparatrechina sp. G	Unknown	1	6	0.00	1.00	0.00	0.00	–	–	-	-
	Pheidole sp. A11	Ground	2	4	0.00	0.00	0.00	1.00	–	–	-	-
	Pheidole sp. A12	Ground	1	4	0.05	0.00	0.95	0.00	–	–	-	-
	Pheidole sp. A15	Ground	3	4	0.00	0.00	0.56	0.44	Generalised	Ground †	-	-
	Pheidole sp. A2	Unknown	4	22	0.05	0.04	0.60	0.30	Generalised	Generalised	-	-
	Prolasius sp. B	Unknown	3	5	0.03	0.00	0.54	0.43	Generalised	Generalised	-	-
	Rhytidoponera purpurea	Ground	3	7	0.17	0.00	0.32	0.51	Generalised	Generalised	-	-
1200	*Anonychomyrma* sp. C	Arboreal	1	9	0.19	0.81	0.00	0.00	–	–	n/a	n/a
	Anonychomyrma sp. H	Arboreal	3	26	0.11	0.12	0.44	0.33	Generalised	Generalised	3.84 ± 1.14	47.44 ± 2.62
	Anonychomyrma sp. L	Arboreal	1	23	0.72	0.04	0.24	0.00	–	–	3.61 ± 0.2	42.48 ± 1.12
	Camponotus sp. N3	Unknown	2	8	0.00	0.31	0.00	0.69	–	–	4.01 ± 0.78	40.76 ± 0.52
	Pheidole sp. A13	Ground	4	8	0.00	0.00	0.71	0.29	Generalised	Ground *	5.72 ± 0.93	39.48 ± 1.14
	Pheidole sp. A2	Unknown	3	11	0.81	0.19	0.00	0.00	Generalised	Arboreal †	5.47 ± 0.79	38.9 ± 0.93
	Pheidole sp. A30	Ground	5	10	0.00	0.00	0.55	0.45	Generalised	Ground *	4.2 ± 0.19	36.86 ± 0.4
	Pheidole sp. A5	Ground	4	8	0.00	0.00	0.85	0.15	Day †	Ground *	5.18 ± 0.29	37.87 ± 1.1

Activity, climatic exposure, and thermal tolerance

For most of the common ant species, flexible spatiotemporal foraging provided options for buffering exposure to dangerously high temperatures. At the lowland site, CT_{min} of the common species ranged from 7–12 °C, and CT_{max} from about 42–46 °C (Figure 6.5). In the upland site these figures were 4–6 °C and 37–48 °C respectively (Figure 6.6). The two species with the lowest CT_{max} (37–38 °C) – *Pheidole* sp. A30 and *Pheidole* sp. A5 – were both upland ground specialists (Table 6.2; Figure 6.6f–g). Maximum air temperatures were generally at least five to ten degrees below CT_{max} for species in the upland site (Figure 6.6), but they reached or exceeded the CT_{max} of six out of seven species at the lowland site (Figure 6.5).

The surface temperatures at which ants were active were generally below maximum air temperatures at both lowland and upland sites. At both lowland (Figure 6.5) and upland (Figure 6.6) sites, our recorded minimum field active (surface) temperatures were very similar to the longer-term minimum microclimate temperatures, whereas maximum field-active temperatures tended to be 2–5 °C lower than maximum microclimatic temperatures. In all cases, field active temperatures were well within the range of a species' CT limits (Figure 6.5 and 6.6). The six species where maximum air temperatures exceeded CT_{max} were all able to buffer such maximum temperatures through spatiotemporal selection: one was a ground specialist (*Odontomachus cephalotes*; Table 6.2, Figure 6.5f), one a nocturnal specialist (*Camponotus* sp. N1; Table 6.2, Figure 6.5c), and the other four were generalists with flexibility to be active closer to the ground or at night (Figure 6.5a, d, e, g).

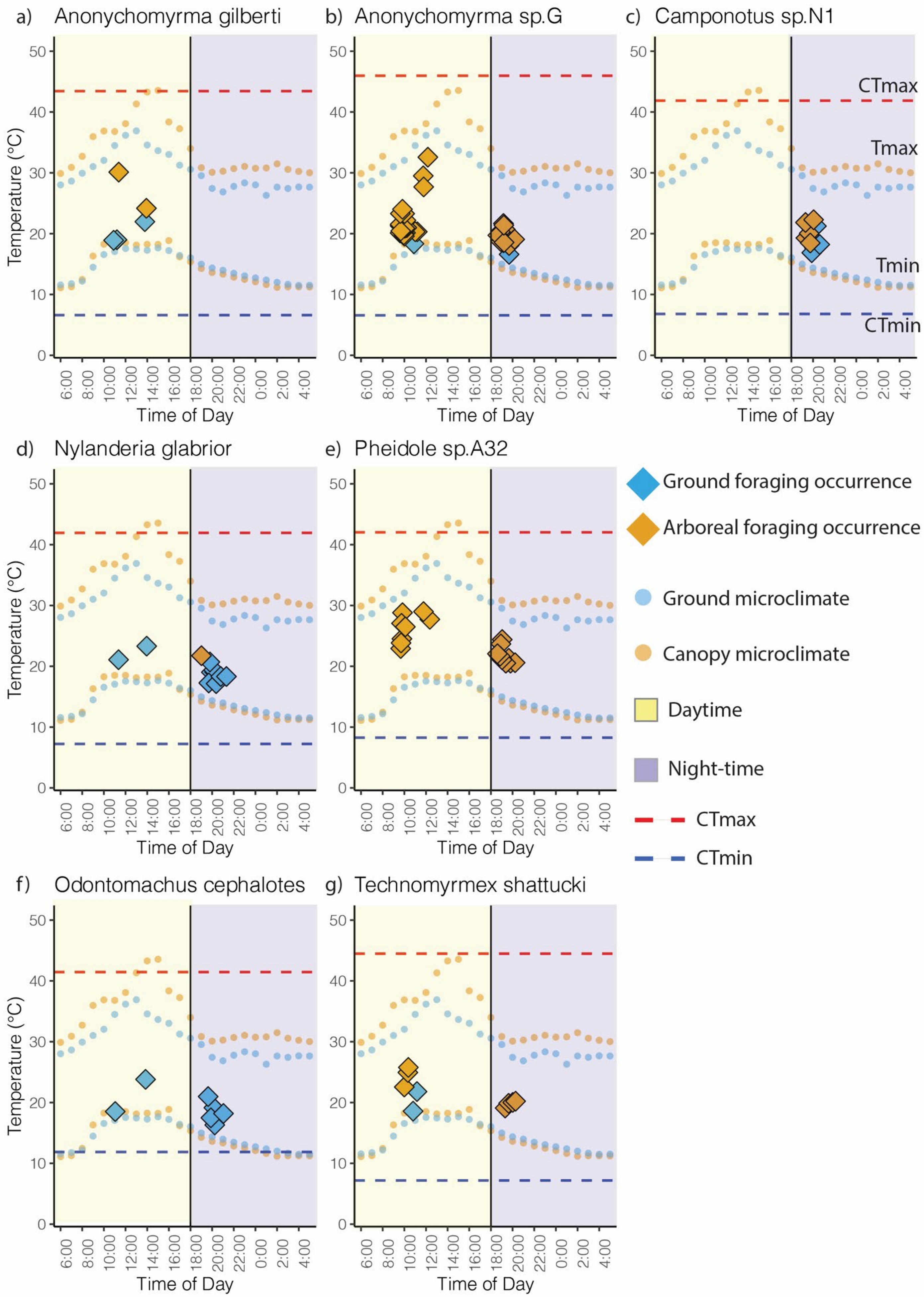
a) Anonychomyrma gilberti
b) Anonychomyrma sp.G
c) Camponotus sp.N1
d) Nylanderia glabrior
e) Pheidole sp.A32
f) Odontomachus cephalotes
g) Technomyrmex shattucki
Temperature (°C)
0
10
20
30
40
50
Time of Day
6:00
8:00
10:00
12:00
14:00
16:00
18:00
20:00
22:00
0:00
2:00
4:00
CTmax
Tmax
Tmin
CTmin
Ground foraging occurrence
Arboreal foraging occurrence
Ground microclimate
Canopy microclimate
Daytime
Night-time
CTmax
CTmin

Figure 6.5. Field active surface temperatures and times of day of each ant species occurrence (diamonds) in lowland (100 m a.s.l.) rainforest in relation to two years of microclimate monitoring (circles) and each species thermal tolerance limits (dashed lines). Showing common species with eight or more survey occurrences. Microclimate temperatures show average minimum and maximum ambient temperature recorded in that vertical habitat and hour of the day from two years of recording between 2019 – 2021. Ant surveys conducted along vertical (ground to canopy) and in day (10:00 – 16:00 hrs) and night (19:00 – 22:30 hrs) time periods over ten days in the dry season at 100 m a.s.l. lowland rainforest site in the Australian Wet Tropics Bioregion.

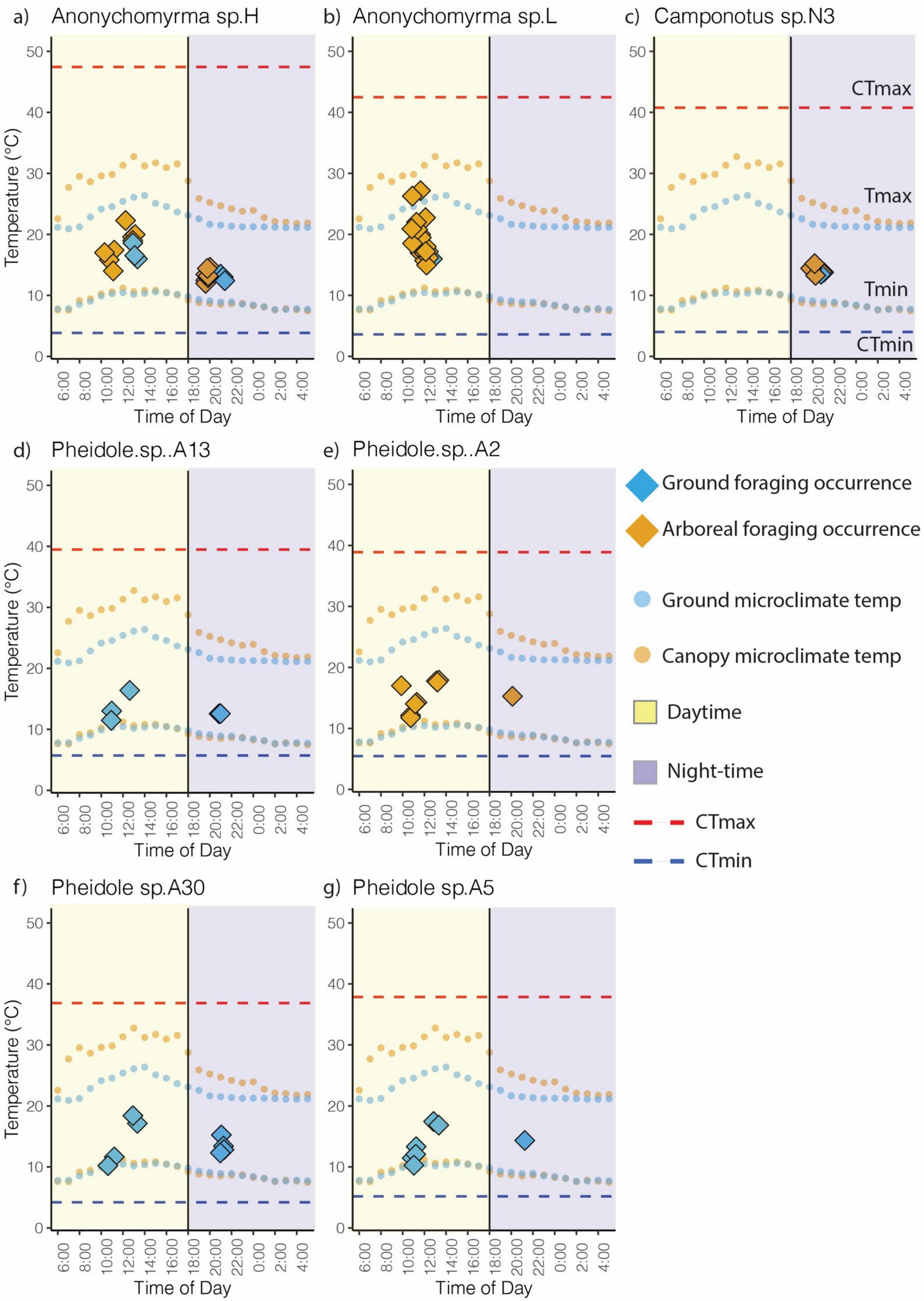
a) Anonychomyrma sp.H
b) Anonychomyrma sp.L
c) Camponotus sp.N3
d) Pheidole.sp..A13
e) Pheidole.sp..A2
f) Pheidole sp.A30
g) Pheidole sp.A5
Temperature (°C)
Time of Day
0
10
20
30
40
50
6:00
8:00
10:00
12:00
14:00
16:00
18:00
20:00
22:00
0:00
2:00
4:00
CTmax
Tmax
Tmin
CTmin
Ground foraging occurrence
Arboreal foraging occurrence
Ground microclimate temp
Canopy microclimate temp
Daytime
Night-time
CTmax
CTmin

Figure 6.6. Field active surface temperatures and times of day of each ant species occurrence (diamonds) in upland rainforest (1200 m a.s.l.) in relation to two years of microclimate monitoring (circles) and each species thermal tolerance limits (dashed lines). Showing common species with eight or more survey occurrences. Microclimate temperatures show average minimum and maximum ambient temperature recorded in that vertical habitat and hour of the day from two years of recording between 2019 – 2021. Ant surveys conducted along vertical (ground to canopy) and in day (10:00 – 16:00 hrs) and night (19:00 – 22:30 hrs) time periods over ten days in the dry season at 1200 m a.s.l. upland rainforest site in the Australian Wet Tropics Bioregion.

Discussion

We investigated the activity and thermal ecology of rainforest ants along local thermal gradients of vertical tree structure and between day and night over the larger-scale climatic gradient of elevation. We aimed to quantify the thermal landscape to which ants are exposed at the local site scale and to describe the relative frequencies of generalist versus specialist species along these gradients to determine the capacity for rainforest ants to buffer climate change *in situ* through shifts in the location and timing of activity. We found that a high proportion of species at all elevations have the capacity to be active in the cooler hours of the night and towards the (cooler) ground, thus buffering the effects of extreme air temperatures.

We found relatively little day to night differentiation in ant activity. Day and night communities were very similar at the highest elevation sites, as revealed by both multivariate analyses, which modelled all species, and the activity niche analyses, which considered common species only. The only exceptions were obligately nocturnal species of *Camponotus*. Species that currently forage in the cooler parts of the environment, such as the ground and at night are buffered from temperature extremes. Here, we show that in addition, species that are active both day and night and/or across vertical space can avoid undesirable temperatures by selecting suitable thermal environments (Sunday et al. 2014, Levy et al. 2019).

Flexible temporal activity in ants – where species are active both day and night or switch seasonally between day and night – has been reported in a wide range of ecosystems; temperate forests and grasslands (Fellers 1989, Albrecht and Gotelli 2001, Stuble et al. 2013, Żmihorski and Ślipinski 2016), semi-arid zones of south-America and Australia (Briese and Macauley 1980, Andersen 1983, Bestelmeyer 2000), desert (Whitford 1978, Heatwole and Muir 1991), neotropical and paleotropical rainforests (Yamane et al. 1996, Kaspari and Weiser 2000, Blüthgen et al. 2004, Hashimoto et al. 2010, Tanaka et al. 2010, Houadria et al. 2015, Yusah et al. 2018, Grevé et al. 2019), and Mediterranean grasslands (Cros et al. 1997, Cerdá et al. 1998a, Cerdá et al. 1998b, Retana and Cerdá 2000). This wide geographic spread indicates that flexible temporal activity may be a common feature of ant ecology, but what influences the adoption of these different temporal strategies across environmental gradients has not been investigated in detail.

It is notable that we found no diurnal specialisation in the upland ants given that ants are generally limited by cold temperatures (Dunn et al. 2009). There was, however, a high degree of thermal overlap in daytime and night-time temperatures in the uplands, indicating that overall thermal exposure may be similar regardless of activity schedule. In addition, two years of microclimate temperature recordings indicated that average minimum temperatures rarely get below ~8ºC, which reflects the fact that our highest upland site was only 1200 m a.s.l.. The diel flexibility we found in many ant species may confer benefits by increasing the time window of food acquisition in the low productivity environment of the uplands where resources are generally expected to be scarcer (Lasmar et al. 2021). Bishop et al. (2015) found that specialised trait combinations were lost from ant assemblages at high elevation sites such that ants tended to become dietary generalists with no preference for open or closed habitats. Relatively low interspecific competition as a result of low species richness might also be a factor contributing to low niche specialisation (Camarota et al. 2016).

In general, we found stronger vertical stratification than temporal differentiation at each site along the elevation gradient. Vertical habitat preference is a highly conserved trait in many ant lineages (Wilson and Hölldobler 2005, Lucky et al. 2013, Moreau and Bell 2013), and therefore we were not surprised that vertical stratification influenced species composition and thermal niches (see also, Leahy et al. Accepted). Our results are similar to Kaspari and Weiser's (2000) study of lowland neotropical ants that found little differentiation between daytime and night-time communities but strong differentiation in vertical microhabitat preference. However, we found ground specialisation was more common than arboreal specialisation as many arboreally nesting ants were active on the ground. As for previous studies of Australian Wet Tropics ants (Leahy et al. 2020, Leahy et al. 2021a), vertical stratification was lower than reported in south-east Asia or the Neotropics: Brühl et al. (1998) found that 75% of species belonged to either ground or arboreal strata in Sabah, Malaysia, while Yanoviak and Kaspari (2000) reported no overlap in species between ground and canopy habitats in Panama.

The widespread flexibility in activity that we found for both vertical and temporal niches along the elevation gradient has important implications for resilience to global warming. A recent global analysis of climate change responses of mammals noted that obligate diurnal and obligate nocturnal species are more than twice as likely to have responded to climate change than mammals with flexible activity times indicating that behavioural flexibility is delaying the effects of climate change for these species (McCain and King 2014). Our prediction would be that those ants that can buffer climate change through flexibility in activity times may lag in their responses to climate change compared to ants with specialisation along thermal gradients. In addition, the field active temperatures (surface temperatures) we recorded during our surveys were well below species upper thermal limits, indicating that there may be a buffer between current operative temperatures and maximum lethal temperatures which could be further widened through behavioural flexibility. An important caveat is that our thermal tests took place in the cooler dry season and temperate forest ants have been known to shift their upper thermal limit with season (Bujan et al. 2020). We do not know if tropical forest ants undergo seasonal plasticity, and this should be an area for further investigation."

An important caveat to this finding was that we did not survey at every hour of the day, and we do not have longer-term data on field active temperatures that ants might experience over a full year. Therefore, ants might be active at hotter temperatures than we have recorded here. We were able, however, to quantify the relationship between surface temperatures (that represent potential operative temperatures of small ectotherms (Kaspari et al. 2015, Spicer et al. 2017)) and ambient air temperatures. Surface temperatures can be very different to, and significantly decoupled from, microclimate air temperatures. During the day in the lowlands, ground and understorey surface temperatures can be up to 11ºC cooler than air temperatures, but in the canopy surface temperatures can reach 4–5ºC hotter than air temperatures. This strong decoupling was much less apparent in the uplands and at night, indicating a complex relationship between time, space, and thermal exposure of small ectotherms.

Combining this more nuanced understanding of thermal exposure with our findings on activity niche flexibility makes it clear that specialised canopy species with an obligate diurnal activity pattern that occur in lowlands have the highest level of thermal exposure and the least capacity for behavioural buffering. Interestingly, we found very few ant species that fit that description, which is consistent with the finding of Bluthgen et al. (2004) that most canopy ants in the lowland Australian Wet Tropics were foraging in both day and night. It suggests that this type of unique specialisation may have been selected against in rainforest ants (Williams et al. 2009).

In conclusion, those species with specialised traits that restrict their activity and distribution to the hottest part of the rainforest thermal landscape are most vulnerable to global warming (Colwell et al. 2008, Corlett 2011, Diamond et al. 2012). There is extraordinary invertebrate biodiversity in the canopies of lowland tropical rainforest (Novotný and Basset 2000, Basset et al. 2003, Ozanne et al. 2003, Basset et al. 2012), but the extent of spatiotemporal specialisation is poorly known. Our findings also have important implications for non-mobile organisms, particularly canopy specialists such as vascular epiphytes, which do not have the capacity to use flexible activity for buffering extreme temperatures.

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Chapter Seven - Synthesis and future directions

Anthropogenic climate change is fundamentally altering the trajectory of life on earth. From the expression of genes to the redistribution of biodiversity, a profusion of case studies has demonstrated the observable impacts of climate change across the globe (Deutsch et al. 2008, Sinervo et al. 2010, Chen et al. 2011, Diamond et al. 2016, Scheffers et al. 2016, Pecl et al. 2017, Rabaiotti and Woodroffe 2019, Román-Palacios and Wiens 2020, Bonachela et al. 2021, Klinges and Scheffers 2021, Mamantov et al. 2021, Roeder et al. 2021, Williams and de la Fuente 2021). Many more articles have made dire future predictions (Williams et al. 2003, Thomas et al. 2004, Corlett 2011, Sunday et al. 2012, Nowrouzi et al. 2019). Identifying and prioritising vulnerable species and communities is an urgent task (Williams et al. 2020). This calls for a predictive understanding of how climate relates to biology across spatial and temporal scales and at different levels of biological organisation.

Vulnerability is the product of sensitivity and exposure to climate change (Williams et al. 2008). Ecological plasticity and behaviour can reduce vulnerability by providing *in situ* options for avoiding unfavourable climates (Sunday et al. 2014). In addition, some populations and species have capacity for phenotypic plasticity or rapid genetic evolution to adapt to increased temperatures (Chown et al. 2010, Hoffmann and Sgro 2011). Vulnerable species that cannot ecologically or genetically adapt *in situ* will need to shift their distribution to track their climatic envelope. Those species that cannot execute one of these options will be increasingly impacted. These differential impacts and responses will alter community composition resulting in new combinations of species (novel communities), with the potential to shift whole ecosystems into alternative states (Pecl et al. 2017, Bonachela et al. 2021).

This thesis explores climatic variability at multiple spatial and temporal scales and how these interact to influence vulnerability in a changing climate. The first objective, met by chapters two, three, and four was to investigate the relationship between vertical climate gradients and species' distributions and community composition along elevation. The second objective, met by chapters five and six, was to determine how physiology and behaviour along microscale, (vertical and temporal) and mesoscale (elevation) climate gradients influence sensitivity and exposure and determines response capacity to climate change. Here, I synthesise the findings of this thesis through a schematic summary presented in Figure 7.1. Concepts in the schematic are linked to specific chapter results in Table 7.1. Drawing on each part of the schematic I outline the key conclusions and predictions from the thesis and present future research directions.

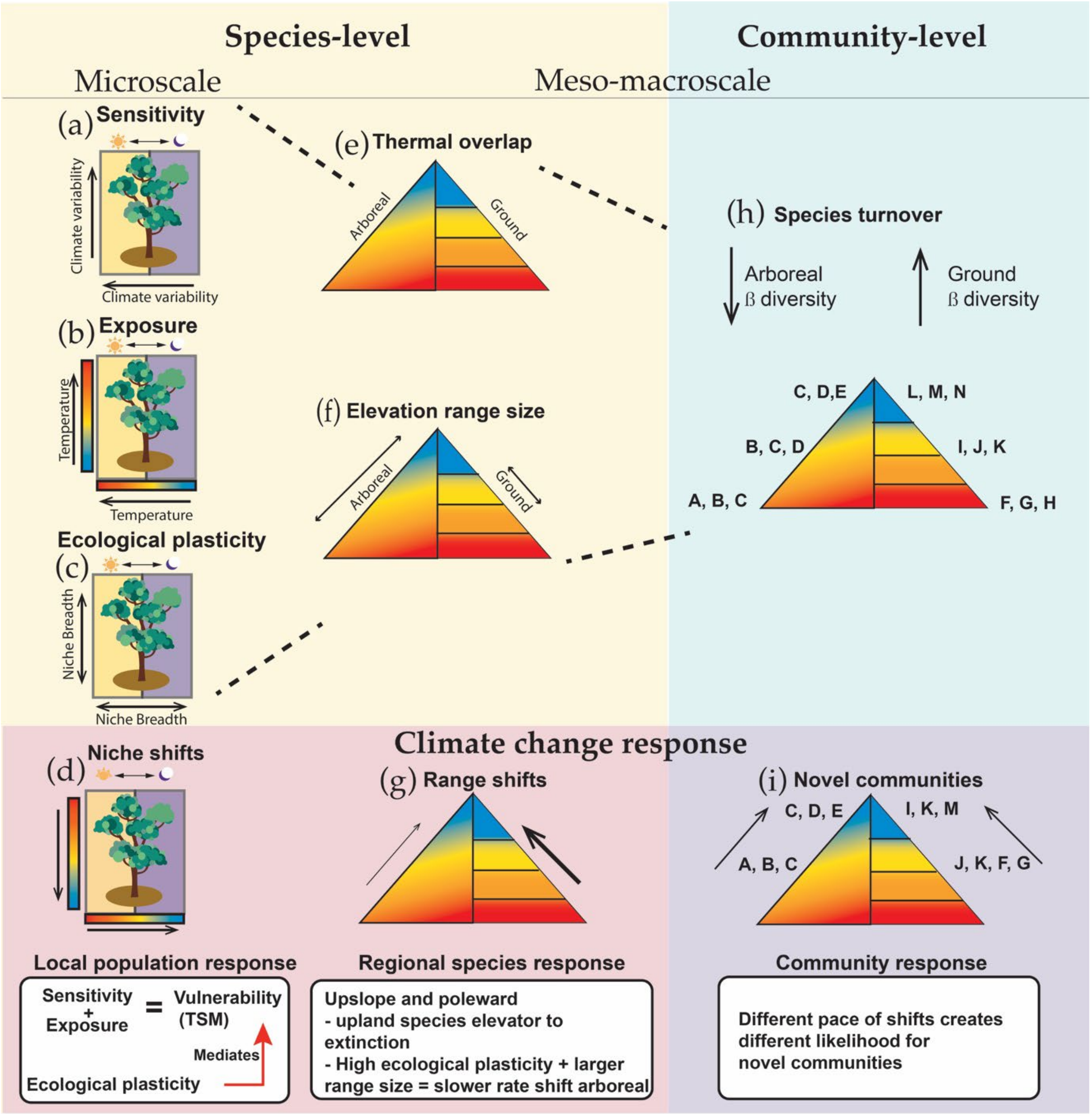

Figure 7.1. Schematic of the links between microscale climate variability, vulnerability, and potential population, species, and community responses to climate change. At the microscale of a tree, vertical (ground to canopy) and temporal (day to night) climatic gradients set up a four-dimensional climatic landscape, along which populations have different (a) thermal sensitivity, (b) exposure, and (c) degree of niche breadth or plasticity. From my findings I predict niche shifts along these gradients at the local scale (d). The climatic variability along the vertical gradient sets up different levels of thermal overlap across elevation (e), and

vertical niche breadth is positively associated with elevation range size (f). This will result in different pressures to execute range shifts (g), I predict arboreal species, and species with greater ecological plasticity to exhibit slower range shifts indicated by the fainter arrow (g). The underlying degree of thermal overlap across elevation (e) is positively correlated to rates of species turnover, such that ground species have higher turnover than arboreal species (h). Hypothetical ant species indicated by letters (h, i). The different paces of range shifts as well as the underlying differences in community composition will create different possibilities for novel communities (i). Concepts (a-c), (f), and (h) are matched to results presented in the thesis chapters in Table 7.1. Concept (e) is directly demonstrated in Scheffers et al. 2017, and Scheffers and Williams 2018. Climate change responses (d), (g), and (i) are predictions based off the findings of the thesis chapters.

Table 7.1. Results presented in thesis chapters to support concepts presented in Figure 7.1. Description and summary of findings presented throughout thesis synthesis.

Concept	Chapter result reference	Summary
(a) Sensitivity	Chapter 5: Figure 5.2., Table 5.1.	Ground ants in both lowlands and uplands have lower CT_{max} and narrower thermal tolerance range than arboreal ants.
(b) Exposure	Chapter 5: Figure 5.5	Lowland arboreal, followed by lowland ground species, are currently exposed to temperatures that are close to exceeding CT_{max}. Upland ants have high CT_{max} relative to current thermal exposure.
(c) Niche breadth (Ecological plasticity)	Chapter 3: Figure 3.3, Chapter 6: Figure 6.4, Table 6.2	Semi-arboreal species have the broadest vertical niche breadth. The majority of ants in lowland and upland sites exhibited ecological

		plasticity along vertical and temporal dimensions.
(f) Elevation range size	Chapter 3: Figure 3.4, Table 3.1	There was a positive relationship between vertical niche breadth and elevation range size.
(h) Species turnover	Chapter 4: Figure 4.5, Figure 4.6, Table 4.2	Ground species have higher rates of species turnover and exhibit a distance-decay relationship with elevational distance. Arboreal species have lower rates of species turnover and do not exhibit a relationship with elevational distance.

Climatically restricted species at greatest risk

Overall, my results strongly suggest that species that are restricted in their climatic niche and range are most vulnerable to climate change (Huey et al. 2009, Perez et al. 2016). Climatic variability occurs at multiple spatial and temporal scales creating a multidimensional climatic space. Species occupy some part of this multidimensional climate space (niche hypervolume) where they can persist and increase within the bounds of their physiological limits (Holt 2009, Soberon and Arroyo-Pena 2017). This concept can be applied at two spatial scales. At the microscale (local within-site) relating to the localised ecological or thermal niche, and meso-macroscales (regional, across elevation and latitude) which relates to species distributions and range size. At the local site scale, I focused on two microclimate gradients which form a multi-dimensional climatic space, the vertical climate gradient, and the transition from day to night.

I found that vertical gradients influence thermal sensitivity through a correlative relationship with thermal limits at the individual and colony level. Ground-dwelling ant species experience stable climates and have lower heat tolerance and a narrower thermal tolerance range than arboreal species that experience high climatic variability (Figure 7.1a). This was the case for ant species in the hot lowland and cool upland rainforest, but thermal sensitivity only tells part of the story. Arboreal species, and particularly lowland canopy species, are exposed to, and are operating at, surface and ambient air temperatures that are very close to their upper thermal limits (Figure 7.1b). On average, canopy species have smaller thermal safety margins (warming tolerance) than ground species. Due to the invariance of heat tolerance across the elevation range, upland arboreal species have broader thermal safety margins as they are not yet experiencing temperatures close to their upper thermal limits.

I have demonstrated that climate exposure can be effectively mitigated through behaviour in both space and time. Ant species with a wide niche breadth along vertical and temporal gradients occupied more of the available climatic space and therefore would have greater response capacity (Figure 7.1c). In a pivotal study comparing the incidence of North American ant genera across a 20-yr period, Roeder et al. (2021) reported a general trend that species with lower CT_{max} had decreased, but, at the same time, species with low and high CT_{max} had increased during this time-period. In other words, some species that are intolerant of high temperatures had also done well in the past twenty years. This indicates that thermal limits are informative, but not entirely sufficient to predict population changes under climate change. My approach here demonstrates the utility of examining both physiology and behaviour and collecting microclimate measurements at an appropriate spatial and temporal scale relevant to the fitness an organism in its thermal environment.

At the local scale I predict that species with the ability to shift activity into cooler parts of their niche space will do so (Figure 7.1d). This may manifest through changes in foraging location during the hottest parts of the day, shifting to more nocturnal activity, or seasonal shifts in vertical foraging. The species that are being exposed to novel temperatures, without these options (e.g., diurnal, canopy-specialists), will be impacted first, with potential reductions in resource acquisition and therefore colony fitness. Further, I found evidence of phylogenetic signal in upper thermal limits which supports previous suggestions that heat tolerance might be evolutionary constrained (Araújo et al. 2013), reducing the potential for thermal adaptation as a possible escape from rising temperatures. Impacted groups of species, that do not have *in situ* response options, may lose the warmer end (lower elevation, lower latitude distribution) of their ranges and therefore initiate range shifts.

At the regional scale, I predict that range restricted species will be more vulnerable. Narrow range species may have to undergo entire range shifts to keep pace with climate change. Species with a broader range extent may be more resilient but could experience range contractions and changes in abundance distributions. I found positive correlative relationships between vertical climate gradients at the local scale and biogeographic patterns over elevation. I demonstrated that the degree to which ants utilise the spatial climate gradient from ground to canopy, as well as exposure to higher temporal variation in arboreal habitats, is positively associated with elevational range extent (Figure 7.1e). This suggests that species that are restricted in climate space at the local scale are also restricted in climate space across their distributional ranges.

In general, arboreal ant species are therefore more likely to have broader elevation ranges than ground species in the Australian Wet Tropics. For arboreal species, climate tracking may manifest as changes in local abundance distribution (i.e., increases in abundance in mid and upland range), rather than localised extinctions and complete shifts in range (Figure 7.1f). The lower elevation generalist species, that can maintain the warmer end of their distributional ranges through *in situ* buffering, may even undergo range expansions as cooler environments become accessible.

Integrating my findings at the local site scale and considering potential regional responses, I would therefore predict that climatically restricted species (diurnal canopy-specialists and ground-dwelling species) may initiate regional scale climate tracking. These shifts will be upslope and in the Australian Wet Tropics, southward towards cooler climates. Upland specialists, such as the many species of *Anonychomyrma* in the Australian Wet Tropics (Chapter Two), may initially benefit from temperature increases (as they have high upper thermal limits) but in the long-term could have their ranges increasingly contract to smaller areas of the mountain tops, placing these species under pressure (Urban 2018). In conclusion, I expect different rates of climate tracking and range shifts based on vertical niches linked to thermal variability exposure and niche breadth at the local scale (Figure 7.1g).

Ecological plasticity and resilience

The logical conclusion of this series of predictions is that ecological plasticity is an important factor in buffering climate change impacts. In general, *in situ* responses are the best option for a population, because they prevent the loss of populations at the hotter end of species ranges and do not require a shift in distribution (Moritz and Agudo 2013, McCain and King 2014). A recent meta-review highlighted the importance of niche shifts over dispersal. Román-Palacios and Wiens (2020) reported that of 538 species of plants and animals from across the globe, 44% have experienced recent localised extinctions. Based on past rates of dispersal, 57–70% of these species would not disperse fast enough to avoid further extinction. Once the authors included the potential for *in situ* niche shifts, however, the predicted extinction rate dropped to ~16–30% by 2070.

Behavioural thermoregulation, as a form of ecological plasticity, can provide immediate and short-term resilience by buffering unfavourable temperatures (Huey 1991, Andrew et al. 2013, Otero et al. 2015). Despite rainforests being traditionally perceived as relatively homogeneous thermal landscapes, there is in fact high thermal heterogeneity at local scales that could be exploited for this purpose (Caillon et al. 2014, Scheffers et al. 2017). It has been highlighted that thermoregulation can prevent selection on thermal traits, thereby impeding genetic adaptation on thermal traits that may provide species with longer-term resilience to global warming (Buckley et al. 2015, Muñoz and Bodensteiner 2019). Whether physiological adaptation is a viable option, however, remains a subject of considerable debate (Hoffmann et al. 2003, Bridle and Vines 2007, Hoffmann and Sgro 2011, Kelly et al. 2012, Merilä and Hendry 2014).

Ecological plasticity that leads to complete transitions in microhabitat use and activity schedules can provide longer-term resilience (Moritz and Agudo 2013, Levy et al. 2019, Bonebrake et al. 2020). There are several examples in the paleoecological record where large-scale environmental changes may have pushed species to expand into new ecological niche space through either climatic pressures or in response to changes in the biotic milieu (Voigt and Lewanzik 2011). One example is the ‘nocturnal bottleneck hypothesis’ which proposes that small mammals were largely nocturnal in the Mesozoic to avoid competition or predation from diurnally active dinosaurs (Gerkema et al. 2013). Following the K/T event and the large-scale extinction of the dinosaurs, these early mammals underwent considerable radiation: Rodentia, for example, subsequently evolved diurnality through secondary evolution at least seven times (Roll et al. 2006). Temporal switching may become a notable response under climate change (Levy et al. 2019), with several authors recently developing frameworks to understand the implications for metabolic rates, water balance, and thermoregulation (Bonebrake et al. 2020). Temporal and microhabitat shifts are likely to have significant implications for biotic interactions and this has yet to be thoroughly investigated.

For most species, being active in multiple time periods is challenging, particularly if the requisite eye adaptations for both diurnal and nocturnal light levels have not evolved (Gaston 2019). In many ant species, however, I found ample evidence of flexible activity schedules, which would strongly predispose ants to ecological adaptation to climate change. The vertical distribution of activity, likewise, showed a high degree of flexibility, generally in the direction of arboreal species foraging close to, or on the ground.

Assessing activity and niche breadth along multiple spatial and temporal gradients, allows a more complete picture of the existing propensity for ecological shifts. From my results, I suggest that there is great potential for ecological plasticity to provide resilience to climate change within local sites, and I recommend further investigation of this potential in other taxa and systems.

Community patterns under a changing climate

From studying the past, we know that dramatic changes in climate precipitate reshuffling of species' associations such that past ecological communities are compositionally unlike the modern communities of today (Jackson and Overpeck 2000, Williams and Jackson 2007). Community responses to climatic change constitute the individualistic responses of populations and species, as well the underlying structure and assemblage dynamics of the constituent community (Bonachela et al. 2021). I found community structuring across the Australian Wet Tropics region such that each mountain subregion contains unique ant species assemblages (chapter two and four). I also found that ant species have different degrees of vulnerability and response capacity based on my assessment of exposure, sensitivity, and niche breadth. Consequently, not all species will be responding in tandem, creating conditions for the formation of novel communities (Caddy-Retalic et al. 2019, Nowrouzi et al. 2019).

In my community analyses, I proposed a correlative link between thermal variability at the local scale (vertical gradient; Figure 7.1a), thermal niche breadth (species' thermal tolerance range), the degree of thermal overlap across elevation (Figure 7.1e), and the rate and magnitude of community turnover between elevation sites (Figure 7.1h). The arboreal microclimate overlaps to a greater degree across elevation (due to high variability) than the ground microclimate, and as predicted by theory (Janzen 1967, Scheffers and Williams 2018) I found higher rates of species turnover in the ground community compared to the arboreal community.

This sets up an interesting dynamic regarding community reshuffling under climate change. We can imagine a scenario where ground species have high thermal sensitivity and initiate range shifts, but, because of the higher rate of species turnover over elevation, there is more likelihood of encountering novel species as they disperse to climatically suitable sites (Figure 7.1i). Arboreal species may be slower to initiate full range shifts, and in addition, the lower rate of species turnover over elevation means they are more likely to encounter species with which they are already familiar as they move up the mountain (Figure 7.1i). I propose that the underlying differences in the thermal niches of species and the different pace of range shifts will interact with extant community composition patterns creating diverse possibilities for the formation of novel communities.

Conclusions and future directions

Past exposure to climatic variability primes species to cope with future climate change (Nadeau et al. 2017, Buckley and Kingsolver 2021). For this reason, species from the climatically stable tropics have been identified as a globally vulnerable group (Huey et al. 2009, Perez et al. 2016). Here I have demonstrated that a consideration of local and regional climates provides a more nuanced picture of global impact. I developed a framework that integrates spatial and temporal climate gradients as nested and interactive. Species occur at the intersection of latitude (macro), elevation (meso), and local-vertical (vertical) gradients that then determines sensitivity, by dictating the degree of past climatic variability, and exposure to current and future climates. Together this forms the basis of vulnerability that is then mediated by the capacity of populations and species to respond.

For ants in the Australian Wet Tropics, I propose that vertically and elevationally restricted species are most at risk, but that ecological plasticity will provide resilience by allowing options for *in situ* responses. Given the current and predicted levels of exposure, I suggest that canopy-restricted diurnal specialists of the lowland rainforest are most at risk, despite having broad thermal tolerance. Interestingly, I did not find many examples of such a trait combination within the community studied here, which could possibly indicate selection against this specific niche. Regionally, ground-dwelling species may face climatic barriers when executing climate tracking as they have, on average, smaller elevation ranges and higher rates of species turnover across elevation.

Tropical rainforest canopies are hotspots of biodiversity (Ozanne et al. 2003). Globally, canopies are estimated to contain between two and six million invertebrate species while approximately 10% of vascular plants are epiphytic canopy dwellers (Ødegaard 2000, Novotny et al. 2002, Ozanne et al. 2003). Many of these species may be at considerable risk under climate change, particular in extensive lowland rainforests, such as the Amazon basin where climate tracking is not possible (Corlett 2011). My major finding is that *in situ* plasticity is key to mitigating climate change effects and this should be a priority of future research. The climatic complexity of rainforest canopies may provide options for vertical, horizontal, and temporal shifts in location and activity. However, the ecology of many rainforest invertebrates, let alone their taxonomy, has been vastly understudied, particular regarding temporal and microhabitat activity.

There are several limitations and caveats of the thesis that are important to address. Firstly, the thesis largely focused on the activity and thermal biology of worker ants and did not delve into nesting ecology or the thermal sensitivity of other ontogenetic stages (both can influence vulnerability (Sinclair et al. 2016)). I regard this as a worthwhile trade-off, however, as it allowed the collection of data on multiple species and entailed a detailed focus on workers. Workers represent the main source of resource acquisition and thereby determine colony fitness (Hölldobler and Wilson 1990).

Secondly, ants are a thermophilic group and are therefore less likely to be impacted by global warming compared to highly sensitive taxa, for example, microhylid frogs, epiphytic ferns, or the endemic ringtail possums of the Australian Wet Tropics (Williams et al. 2003). In addition, their remarkable ecological versatility along spatio-temporal climate gradients provides additional resilience that might not be available to more climatically specialised species. My findings in this thesis regarding vulnerability of ants could therefore be considered a conservative assessment when generalised to other taxa.

Finally, the research refers substantially to climatic gradients, however, mostly temperature and thermal components of physiological traits were measured and analysed. I acknowledge that other aspects of climate are likely highly important for predicting climate change impacts, particularly relative humidity (vapor pressure deficit) at the local scale and precipitation seasonality at the regional scale (Bonebrake and Mastrandrea 2010, McCain and Colwell 2011). For small ectotherms, such as ants, desiccation risk is an important functional trait and has been linked to distribution and activity (Kaspari and Weiser 2000, Bujan et al. 2016). Further, some models have predicted changes in precipitation will result in significant drying out of rainforests and shifts to open sclerophyll and even savannah in some parts of the Australian Wet Tropics by the end of this century (Reside et al. 2013, Nowrouzi et al. 2019). These changes in habitat type will act synergistically with the direct impacts of global warming and are likely to contribute to localised extinctions of some ant species (Nowrouzi et al. 2019).

The strength and novelty of this thesis was to develop a framework to assess how climatic variability along multiple spatial and temporal gradients influences vulnerability. This framework can be readily applied to other systems in which vertical climate gradients are formed by three-dimensional habitat structure. Further investigation of ecological plasticity and the potential for niche shifts should be a research priority. Finally, I strongly suggest that verticality, the third biogeographic dimension (Scheffers et al. 2013), should be included as a variable in global climate change models. As I have demonstrated here, it is a critical axis of climatic niche space that strongly determines both vulnerability and response capacity and thereby influences the trajectory of biological communities in a changing world.

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Appendices

Appendix S2: Supplementary material for Chapter Two.

Table S2.1. Collection locations of specimens from the *Anonychomyrma* group that were CO1-barcoded for this study.

Species code	BOLD code	Region	Elevation (m)
gilberti	ANONC 072-20	Carbine	400
	ANONC 076-20	Carbine	400
	ANONC 077-20	Carbine	300
	ANONC 079-20	Carbine	100
	ANONC 080-20	Daintree	100
	ANONC 081-20	Carbine	500
	OCHAN 050-18	Windsor	900
	OCHAN 053-18	Atherton	400
	OCHAN 054-18	Atherton	400
	OCHAN 055-18	Atherton	200
	OCHAN 057-18	Finnegan	700
	OCHAN 058-18	Atherton	200
	OCHAN 059-18	Atherton	400
	SNAWT 147-15	Carbine	100
sp. A	ANOCH 041-18	Spec	600
	OCHAN 051-18	Spec	800
sp. B	SNAWT 153-15	Finnegan	200
sp. C	ANONC 051-20	Carbine	1200
	OCHAN 039-18	Carbine	1200
	OCHAN 041-18	Carbine	1000
	OCHAN 052-18	Carbine	1000
	SNAWT 163-15	Windsor	1100
	SNAWT 164-15	Windsor	1300
	SNAWT 165-15	Carbine	1000
	SNAWT 166-15	Carbine	1000
	SNAWT 167-15	Windsor	1100
	SNAWT 168-15	Windsor	1300
	SNAWT 169-15	Carbine	1000
	SNAWT 213-15	Windsor	1100
	SNAWT 214-15	Windsor	1300
	SNAWT 278-15	Windsor	1100
	SNAWT 279-15	Windsor	1100
malandana	ANOCH 020-18	Windsor	1300
	ANONC 041-20	Carbine	700
	SNAWT 177-15	Windsor	1100
	SNAWT 178-15	Windsor	1100

	SNAWT 179-15	Windsor	1100
	SNAWT 180-15	Windsor	1300
	SNAWT 182-15	Windsor	1300
	SNAWT 201-15	Windsor	1100
	SNAWT 202-15	Windsor	1300
	SNAWT 205-15	Atherton	1000
	SNAWT 281-15	Windsor	1100
	SNAWT 282-15	Windsor	1300
	SNAWT 283-15	Windsor	1300
	SNAWT 285-15	Windsor	1100
sp. E	SNAWT 204-15	Windsor	900
	SNAWT 206-15	Windsor	900
	SNAWT 208-15	Windsor	1100
	SNAWT 210-15	Windsor	1100
sp. F	SNAWT 209-15	Windsor	1100
sp. G	ANOCH 017-18	Finnegan	800
	ANONC 029-20	Atherton	200
	ANONC 030-20	Atherton	200
	ANONC 031-20	Atherton	200
	ANONC 034-20	Carbine	200
	ANONC 035-20	Carbine	200
	ANONC 036-20	Carbine	300
	ANONC 037-20	Carbine	300
	OCHAN 061-18	Windsor	900
	SNAWT 192-15	Carbine	600
	SNAWT 194-15	Finnegan	700
	SNAWT 195-15	Finnegan	700
sp. H	ANONC 008-20	Carbine	1200
	ANONC 009-20	Carbine	1200
	ANONC 013-20	Windsor	1300
	SNAWT 184-15	Windsor	1300
	SNAWT 211-15	Windsor	1300
	SNAWT 212-15	Windsor	1300
sp. I	ANONC 006-20	Atherton	800
	ANONC 007-20	Atherton	1000
sp. J	ANONC 032-20	Atherton	1000
	ANONC 033-20	Atherton	1000
	OCHAN 063-18	Atherton	1000
	SNAWT 196-15	Atherton	800
	SNAWT 198-15	Atherton	1000
sp. K	ANOCH 028-18	Spec	800
	ANONC 011-20	Carbine	1000
	ANONC 024-20	Atherton	800
	SNAWT 170-15	Windsor	1100
	SNAWT 185-15	Carbine	1000
	ANOCH 019-18	Windsor	1100
sp. L	ANONC 082-20	Carbine	400
sp. M	SNAWT 151-15	Spec	800

	SNAWT 162-15	Spec	1000
	SNAWT 172-15	Spec	800
	SNAWT 173-15	Spec	800
	SNAWT 174-15	Spec	1000
	SNAWT 175-15	Spec	800
sp. N	ANONC 022-20	Atherton	1000
sp. P	ANONC 012-20	Carbine	1000
sp. Q	ANOCH 010-18	Windsor	900
sp. R	OCHAN 067-18	Atherton	600
sp. S	OCHAN 025-18	Atherton	1000
sp. T	ANONC 026-20	Windsor	1100
sp. U	OCHAN 026-18	Atherton	800

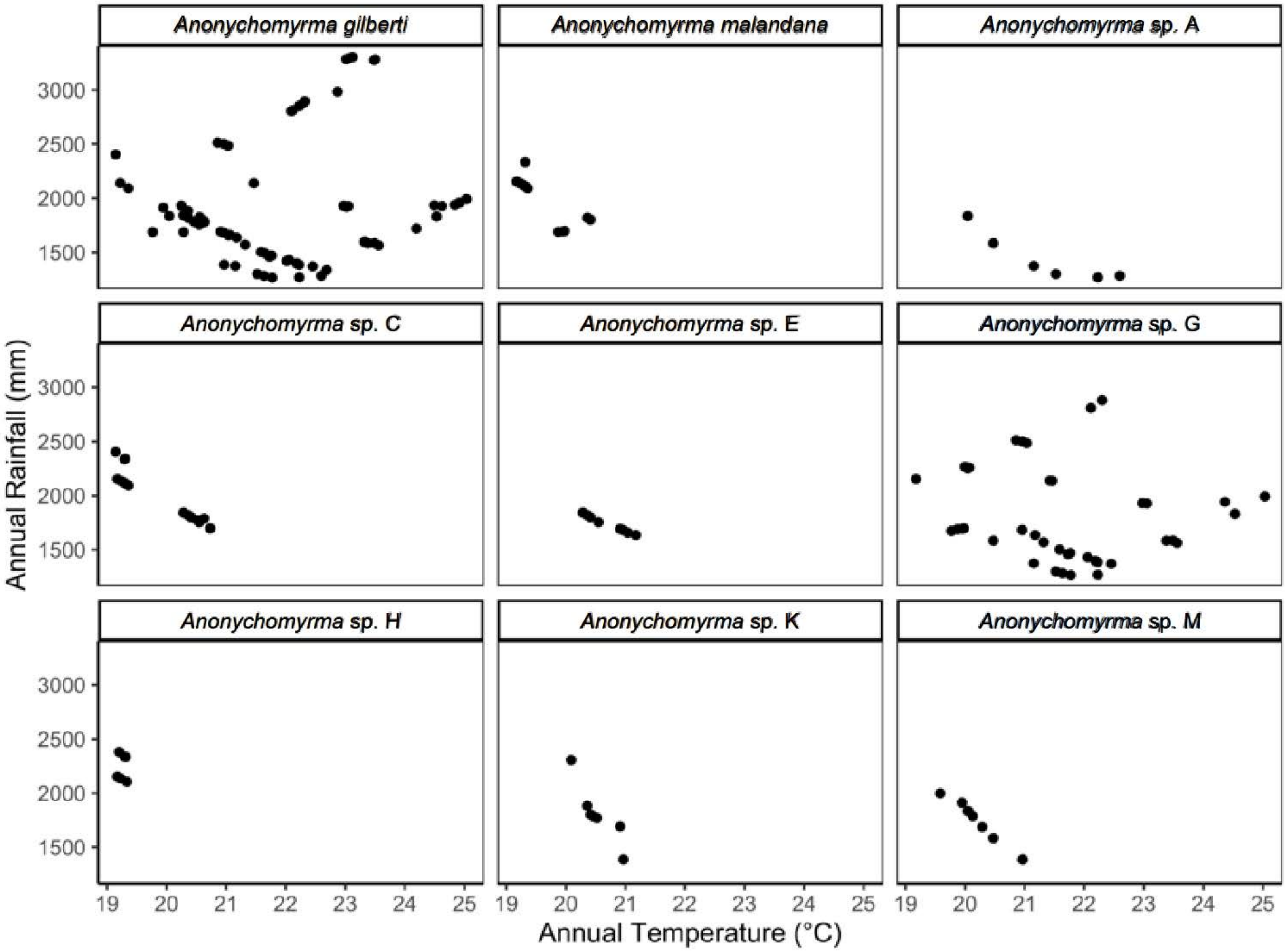
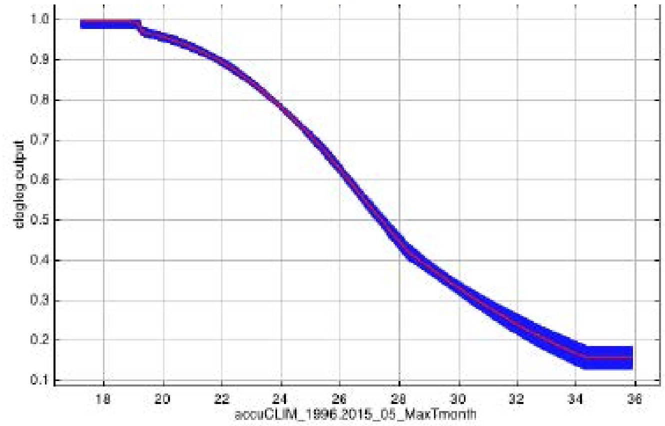


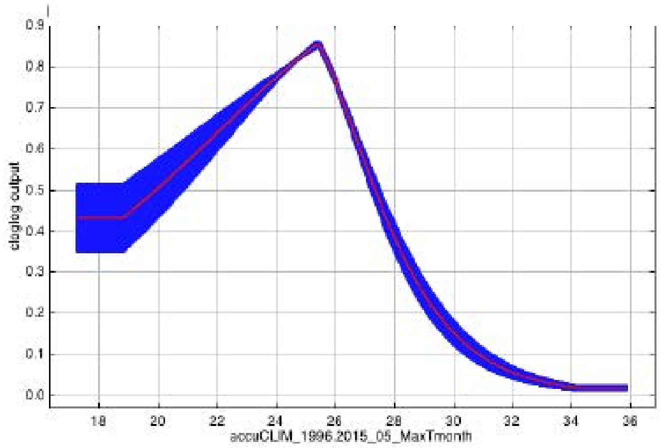
Figure S2.1. Environmental space occupied by nine species used in species distribution modelling based on our sampling across the AWT, annual rainfall and temperature from accuCLIM layers.

Species responses to
accuCLIM 1996-2015_05: Maximum temperature of the warmest month

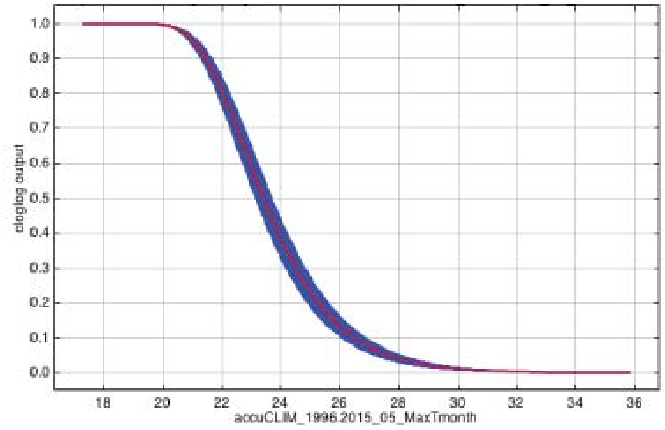
Anonychomyrma gilberti



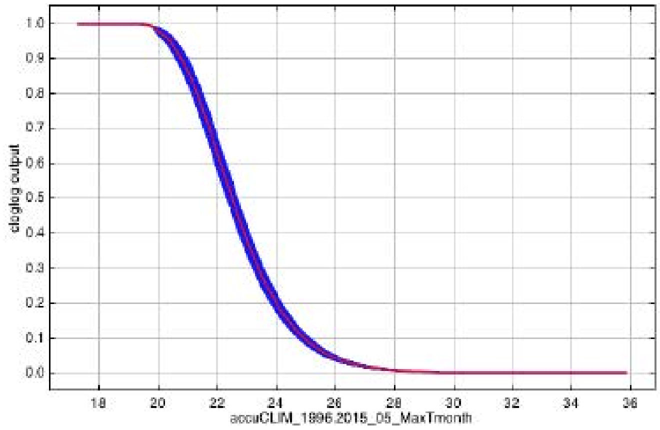
Anonychomyrma sp. G



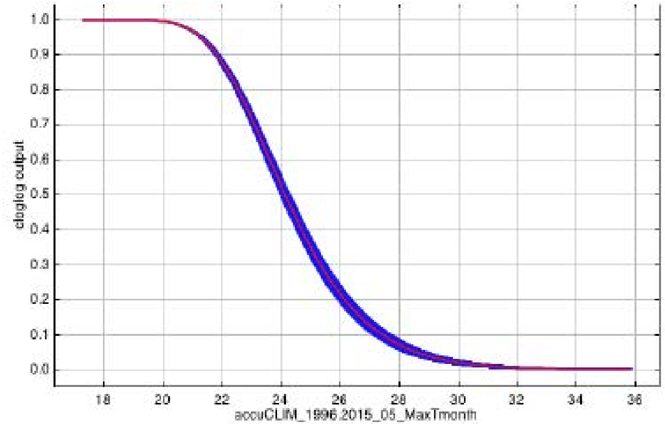
Anonychomyrma malandana



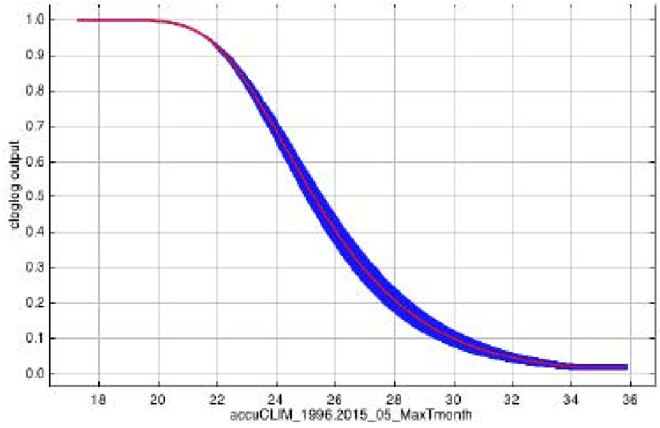
Anonychomyrma sp. C



Anonychomyrma sp. M



Anonychomyrma sp. E



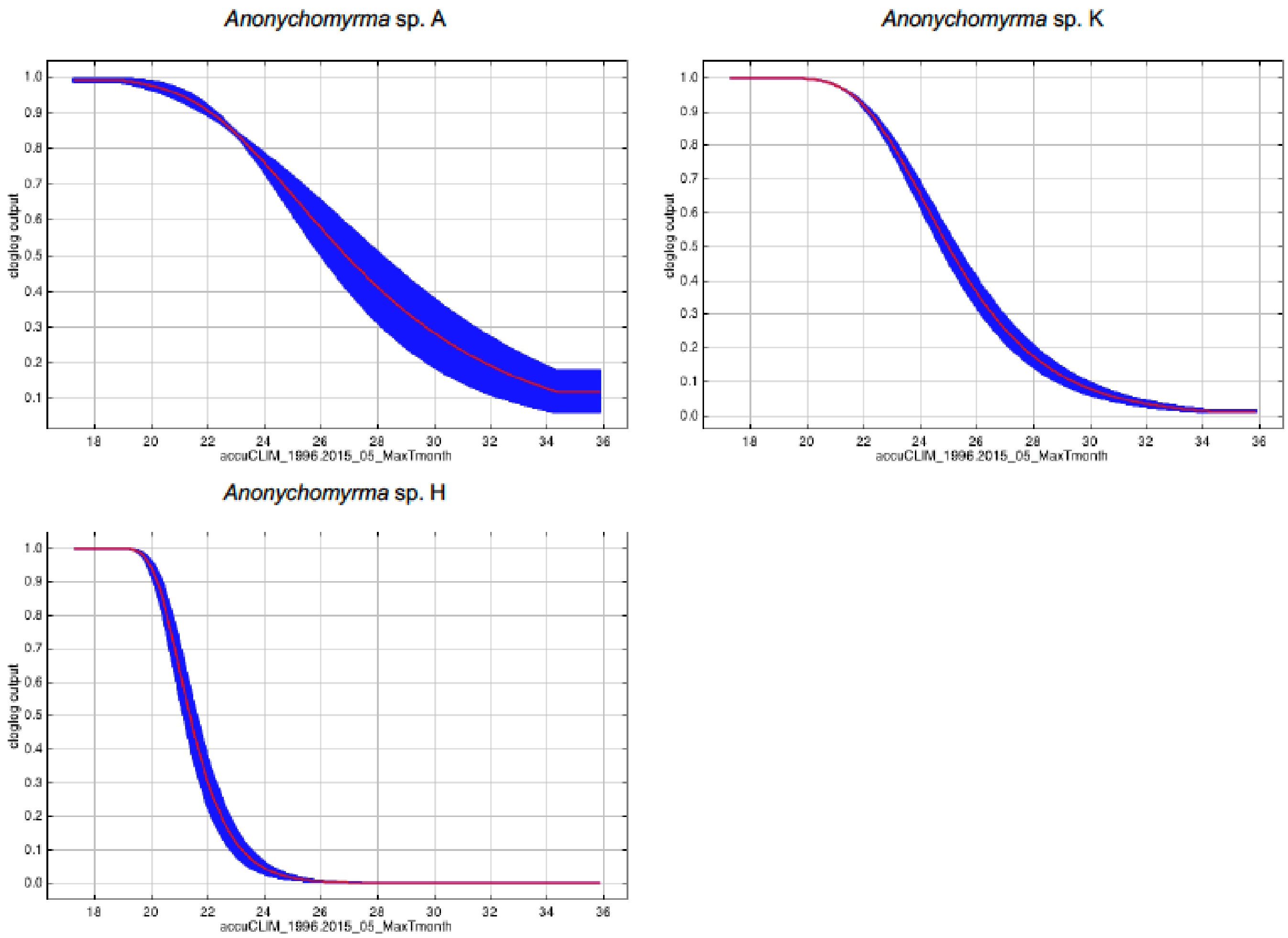
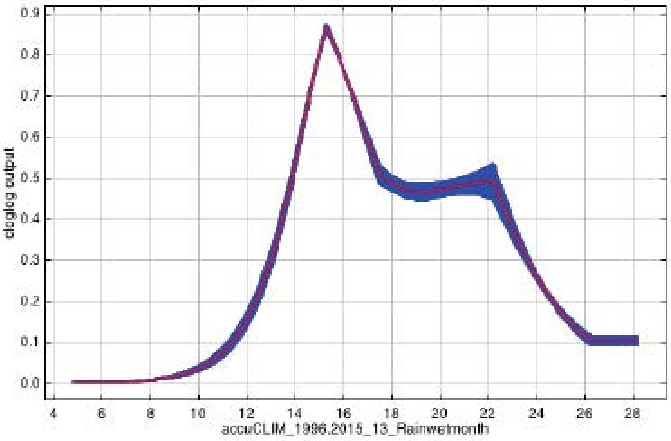
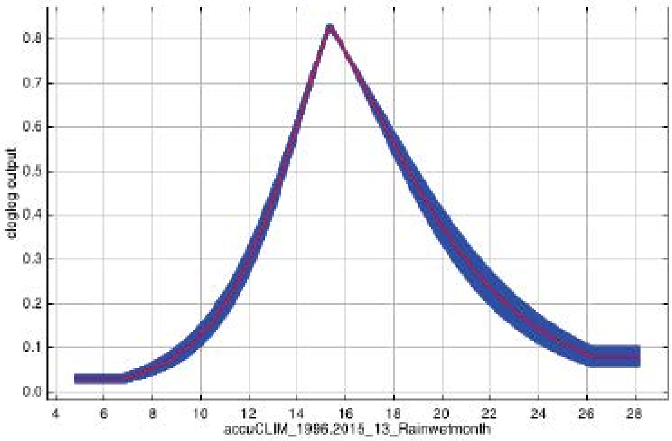
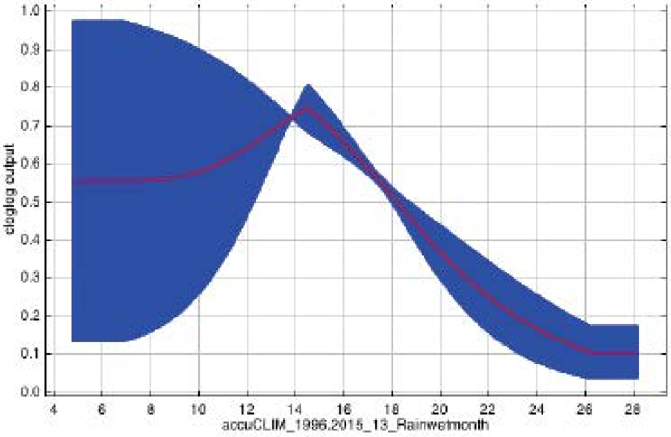


Figure S2.2. Species distribution modelling response curves showing *Anonychomyrma* species responses to accuCLIM 1996-2015 Variable 05: Maximum temperature of the warmest month. Included are those species that this variable ranked in the top three variables in regard to permutation importance. Response is the cloglog output from Maxent which gives an estimate between 0-1 of probability of presence for that species. Plots show modeled probability of presence based off a model using only Maximum temperature of the warmest month.

Species responses to accuCLIM 1996-2015_13: Rainfall of the wettest month


Anonychomyrma gilberti


Anonychomyrma sp. G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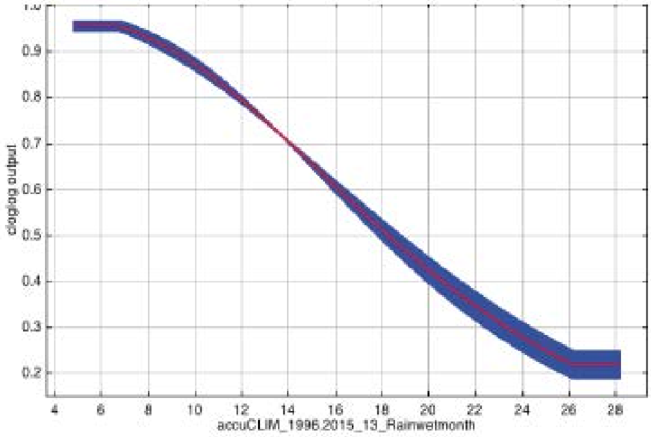
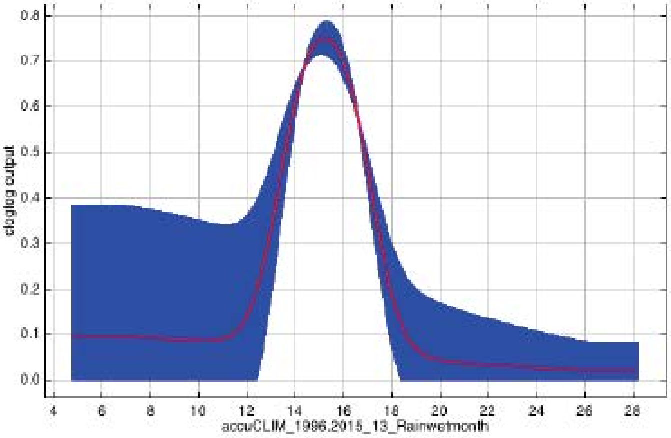

Anonychomyrma malandana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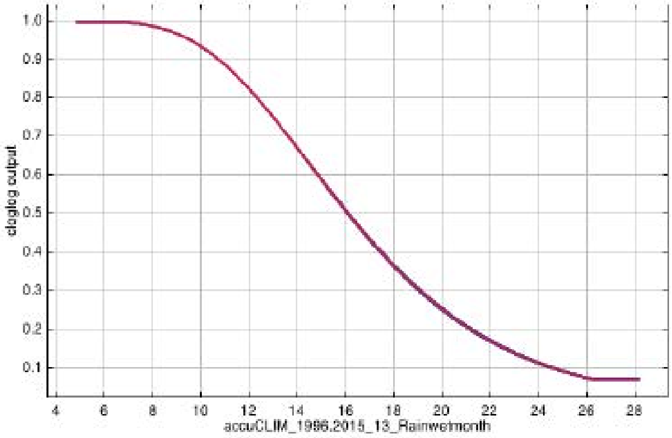
Anonychomyrma sp. E

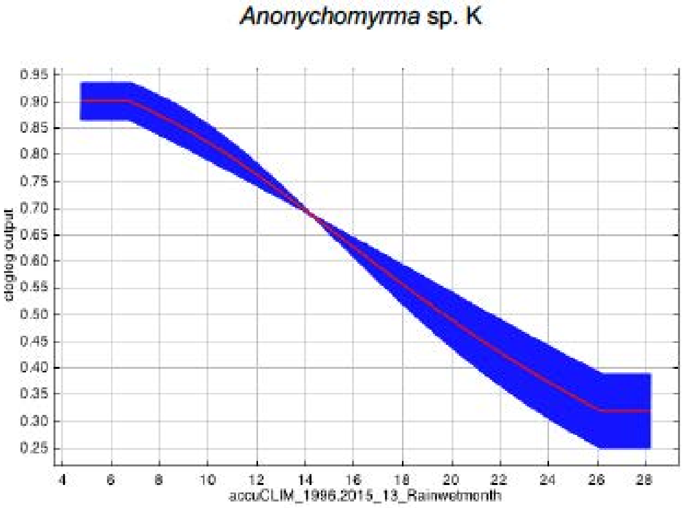

Figure S2.3. Species distribution modelling response curves showing *Anonychomyrma* species responses to accuCLIM 1996-2015 Variable 13: Rainfall of the wettest month. Included are those species that this variable ranked in the top three variables in regard to permutation importance. Response is the cloglog output from Maxent, which gives an estimate between 0-1 of probability of presence for that species. Plots show modeled probability of presence based off a model using only Rainfall of the wettest month.

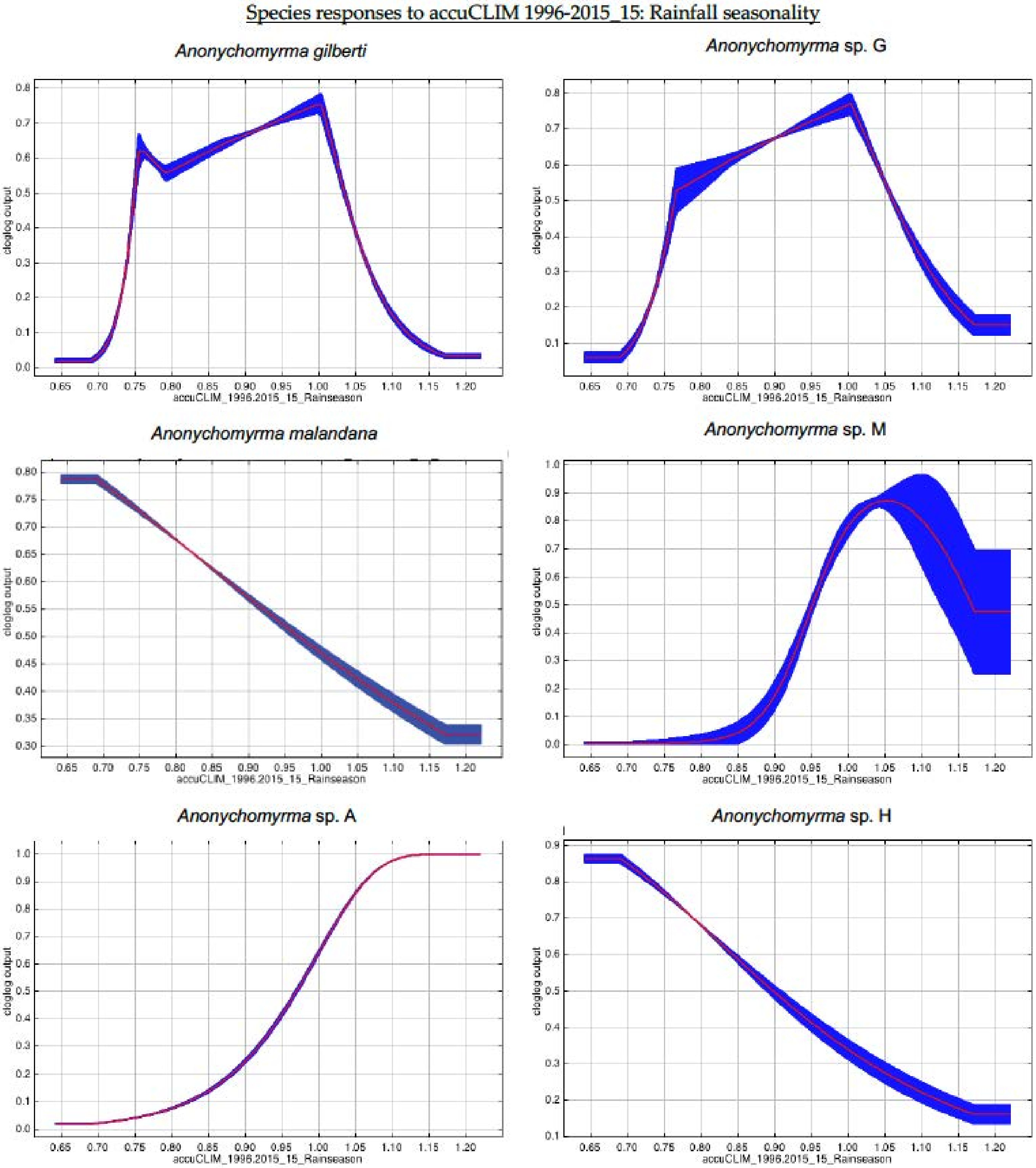

Figure S2.4. Species distribution modelling response curves showing *Anonychomyrma* species responses to accuCLIM 1996-2015 Variable 15: Rainfall seasonality. Included are those species that this variable ranked in the top three variables in regard to permutation importance. Response is the cloglog output from MaxEnt which gives an estimate between 0-1 of probability of presence for that species. Plots show modeled probability of presence based off a model using only Rainfall seasonality.

Appendix S3: Supplementary material for Chapter Three.

Table S3.1. Survey design for sampling ants and microclimate along vertical tree transects, showing elevation sites, number of trees sampled, and the vertical survey height for each tree for 60 trees at 15 elevation sites at four mountain ranges in the Australian Wet Tropics Bioregion.

Mountain	Elevation	Tree number	Maximum survey height (m)
Atherton	200	1	18
		2	15
		3	18
		4	15
		5	18
	400	1	15
		2	21
		3	18
		4	24
		5	21
	600	1	24
		2	27
		3	21
		4	15
		5	27
	800	1	18
		2	21
		3	15
		4	24
		5	27
	1000	1	21
		2	18
		3	21
		4	21
		5	27
Carbine	100	1	27
		2	18
		3	15
		4	21
		5	15
	600	1	15
		2	15
		3	15
	1000	1	18
		2	15
		3	24
	1200	1	15
		2	18
		3	18
Finnegan	200	1	18
		2	27
	500	1	18
		2	21
		3	18
		4	12
	700	1	21

		2	18
		3	18
Windsor	900	1	18
		2	15
		3	15
		4	15
	1100	1	18
		2	18
		3	24
		4	18
	1300	1	15
		2	12
		3	15
		4	15

Table S3.2. Linear model of vertical niche breadth as a function of log body mass. Generalised linear model with a gamma distribution and log-link function of elevation range size as a function of log body mass. Models include data from 22 of our study species for which body mass measurements were taken during a thermal tolerance project in the Carbine Uplands (Leahy L, unpublished data). Mean species body mass was calculated from 3 - 5 workers of each species. Ants were oven dried for 24 hours at 70 °C and weighed with a Satorius semi-microbalance scale with 0.01-mg accuracy.

Model	Est. coef (95% CI)	p-value	Adjusted R-squared/Pseudo R-squared
LM: Vertical niche breadth ~ log(body mass)			0.00
Intercept	16.2 (11.6 - 20.8)		
Log(body mass)	0.31 (-4.4 - 5)	0.89	
GLM: Elevation range size ~ log(body mass)			0.06
Intercept	578 (445 - 770)		
Log(body mass)	1.2 (0.9 - 1.6)	0.22	

Table S3.3. As survey height varied with tree height across the 60 trees surveyed, we wished to examine whether the maximum survey height at which each ant species was recorded influenced our calculation of that species vertical niche breadth and exposure to temperature variance. Presented is a generalised linear model with a gamma distribution and log-link function of vertical niche breadth and exposure to temperature variance as a function of maximum vertical survey height for 55 ant species. Surveys were conducted at 15 elevation sites across four mountains in the Wet Tropics Bioregion, Australia.

Model	Est. coef (95% CI)	p-value	Pseudo R-squared
GLM: Vertical niche breadth ~ Species maximum survey height			0.13
Intercept	2.47 (0.9 – 7)		
Species max. survey height	1.08 (1.03 – 1.1)	0.00	
GLM: Exposure to temp variance ~ Species maximum survey height			0.12
Intercept	3.96 (2.4 – 6.8)		
Species max. survey height	1.03 (1.01 – 1.06)	0.00	

Table S3.4. Linear model of mean vertical survey height as a function of elevation to examine if there is a consistent trend in vertical survey height with elevation for 60 surveyed trees across 15 elevation sites across four mountains in the Wet Tropics Bioregion, Australia.

Model	Est. coef (95% CI)	p-value	Adjusted R-squared
LM: Mean vertical survey height ~ Elevation			0.01
Intercept	20.78		
Elevation	0.00	0.168	

Table S3.5. Four mountain ranges were surveyed for ants in the Wet Tropics Bioregion, Australia, to investigate the relationship between vertical niche breadth and elevation range size. The mountain ranges varied in total range and maximum elevation from 700 m a.s.l. to 1, 300 m a.s.l. We wished to examine whether maximum elevation point and total range which a species could theoretically be surveyed at – given its presence on one or more mountain ranges – influenced our calculation of that species elevation range size. Presented is a generalised linear model with a gamma distribution and log-link function of elevation range size as a function of each species maximum theoretical elevation point and maximum theoretical elevation range, given their recorded presence on each of the four mountains. Note that although each model had a significant predictor, the estimated coefficients show no change in the response variable with each predictor respectively.

Model	Est. coef (95% CI)	p-value	Pseudo R-squared
GLM: Elevation range size ~ Species theoretical maximum elevation point			0.11
Intercept	96 (33.4 – 301)		
Species theoretical max elev.	1.0 (1.0 – 1.0)	0.01	
GLM: Elevation range size ~ Species theoretical maximum elevation range			0.23
Intercept	118 (64.7 – 225)		
Species theoretical max elev.	1.0 (1.0 – 1.0)	0.00	

Table S3.6. Model performance based on AICc values for interactive and additive models for elevation range as a function of vertical niche breadth and elevation range as a function of exposure to temperature variance for 55 ant species in the Wet Tropics Bioregion of Australia.

Models	df	AICc	Δ AICc
Vertical niche breadth			
Elevation range ~ vertical niche breadth + local abundance	4	773.3	0.7
*Elevation range ~ vertical niche breadth * local abundance*	5	774	
Exposure to temperature variance			
Elevation range ~ Exposure to temp variance + local abundance	4	779.7	1.5
*Elevation range ~ Exposure to temp variance * local abundance*	5	778.2	

Appendix S4: Supplementary material for Chapter Four.

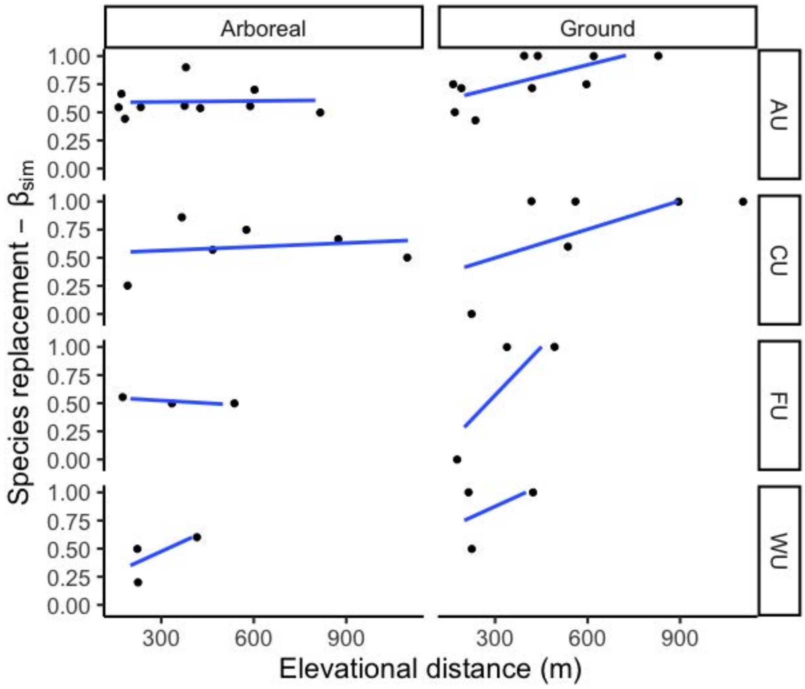

Figure S4.1. Species turnover in ant species with elevational distance within each subregion in the Australian Wet Tropics Bioregion. Turnover ($ß_{sim}$) is calculated between pairwise sites of different elevations within each subregion. Patterns are similar within each subregion, therefore we chose to pool the four subregions for the main models.

Table S4.1. Model selection based on AIC for observed beta diversity ($ß_{sim}$ – species turnover) as a function of the interaction between elevational distance and vertical niche and geographical distance and vertical niche. Elevational and geographic distance were centred and scaled. Top performing model is highlighted in bold. Where AIC values were within 2 units of each other the simplest model (lower degrees of freedom) was chosen. df = degrees of freedom, AIC = Akaike information criteria.

Models	df	AIC
Elevational model – $ß_{sim}$		
$ß_{sim}$ ~ vertical niche *elevational dist	5	-63.93
$ß_{sim}$ ~ vertical niche*log10(elevational dist)	**5**	**-69.03**
$ß_{sim}$ ~ vertical niche*(elevational dist)^2	7	-66.95
$ß_{sim}$ ~ vertical niche*(elevational dist)^3	9	-66.48

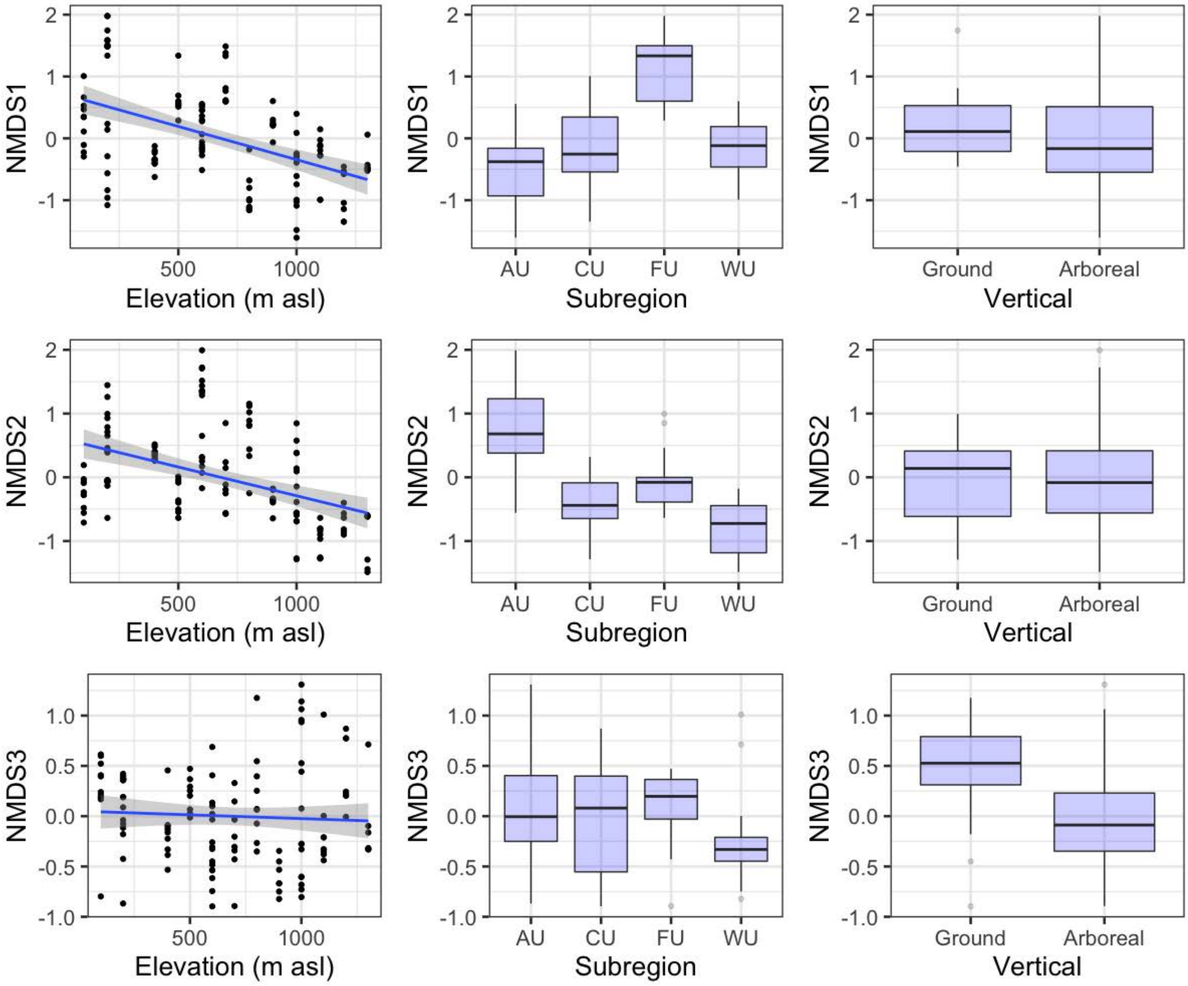

Figure S4.2. Visual representation of the correlation among spatial gradients (Elevation, Subregion, and Vertical habitat) and extracted axes 1–3 from nMDS fit represented in Figure 4.2. and Table 4.1. All combinations presented. Vertical height (0–27m), re-classified in this figure on the x-axis as ground and arboreal to allow for easier interpretation.

Appendix S5: Supplementary material for Chapter Five.

Table S5.1. Model selection based on AICc for linear mixed effects models, modelling ant CT_{min}, (74 colonies) CT_{max}, and CT_{range} (73 colonies) as a function of vertical niche (ground and arboreal) elevation site (lowland and upland) and mean colony body mass for 40 species of ants in the Australian Wet Tropics Bioregion. Species identity included as a random effect. Best performing models highlighted in bold.

Response	Fixed effects	Random Effects	df	AICc
CT_{min}	**Vertical + Elevation**	Species	**5**	**268.4**
	Vertical * Elevation	“	6	270.8
	Vertical * Elevation * log(Bodymass)	“	10	274.7
CT_{max}	**Vertical + Elevation**	Species	**5**	**347.5**
	Vertical * Elevation	“	6	349.8
	Vertical * Elevation * log(Bodymass)	“	10	353.3
CT_{range}	**Vertical + Elevation**	Species	**5**	**377.7**
	Vertical * Elevation	“	6	380.1
	Vertical * Elevation * log(Bodymass)	“	10	382.7

Section S5.1. Testing the effect of sample size on thermal trait differences between sites

There was a discrepancy between the numbers of ant species assayed in lowland and upland sites due to a relatively low abundance and species richness of ants at high elevation (for species richness metrics for Carbine see Nowrouzi *et al.* (2016)). We used a null modelling approach to test the possibility that differences in thermal tolerance limits between sites were due to an uneven sample size. For each CT trait, we created a null model by combining all colonies average CT limit values from all sites and then randomly selecting the same number of colonies ($n = 11$) as that found at the upland site. This process was repeated 1000 times to obtain a distribution of expected mean colony CT limit values from the total species pool. We then repeated this process using only the pool of ant colonies tested at the upland site to obtain a distribution of observed colony CT limit values. We compared the distribution of the null model and the distribution of the observed values using a Welch two sample T-Test. The difference in thermal traits between lowland and upland sites was not due to unequal sample size between the elevation sites, as was confirmed by the null model (Welch two sample T-Test, CT_{min}: $t = 144.6$, $df = 1460$, $p < 0.00$, CT_{max}: $t = 49.8$, $df = 1998$, $p < 0.00$, CT_{range}: $t = -20$, $df = 1964$, $p < 0.00$).

References

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

Section S5.2. Construction of genus-level ant phylogeny

To assess whether thermal trait variation among ants is closely associated with shared ancestry, we tested for phylogenetic signal in thermal traits using a genus-level, time-calibrated phylogeny from Moreau and Bell (2013). We chose to use a genus-level phylogeny for the main analysis as the phylogenetic relationships of species within our study area are not well resolved. We pruned the tree to the 18 genera included in our study using ‘drop.tip’ from *ape* ver 5.3 (Paradis and Schliep 2019), and inserted three additional genera using ‘bind.tip’ from *phytools* (Revell 2012): *Brachyponera* as a sister genus to its closest related genus on the tree, *Odontomachus* (Schmidt and Shattuck 2014); *Colobopsis* as sister to *Camponotus* (Ward et al. 2016); and *Nylanderia* as sister to *Paratrechina* (LaPolla et al. 2011).

References

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

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

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Ward, P. S., B. B. Blaimer, and B. L. Fisher. 2016. A revised phylogenetic classification of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of the genera Colobopsis and Dinomyrmex. Zootaxa **4072**:343-357.

Section S5.3. Assessing the effect of phylogeny on thermal traits at the species level.

To construct a species-level phylogenetic tree for the ant species in our study we used the Moreau and Bell (2013) time-calibrated phylogeny which includes several representative species of each genus worldwide, but these were not the species from our study area, therefore it was necessary to add the our study species into the tree as soft polytomies. First, we pruned the tree to the 18 genera included in our study using ‘drop.tip’ from *ape* ver 5.3 (Paradis and Schliep 2019), and inserted three additional genera using ‘bind.tip’ from *phytools* (Revell 2012): *Brachyponera* (subfamily Ponerine) as a sister genus to its closest related genus on the tree, *Odontomachus* (Schmidt and Shattuck 2014); *Colobopsis* as sister to *Camponotus* (Ward et al. 2016); and *Nylanderia* as sister to *Paratrechina* (LaPolla et al. 2011). We then added species onto the tree as sister to the representative species for each genera again using ‘bind.tip’ from *phytools (Revell 2012)*. We gave the new tips the same branch length as the sister species thus creating soft polytomies at each genus node and thereby retaining an ultrametric tree. We removed the species that were not from our study using ‘drop.tip’ as above. We then used a phylogenetic generalised linear models (PGLS) using the function ‘pgls’ in *caper* ver 1.0.1. (Orme et al. 2013), which fits a linear model while taking into account the phylogenetic non-independence between data points. We fitted three PGLS models, one for each thermal trait (CT_{min}, CT_{max}, and CT_{range}), with the trait as the response variable and elevation (lowland or upland) and vertical habitat (arboreal or ground) as categorical predictor variables. Models did not include higher order interactions. In each model we controlled for phylogenetic signal in the data using maximum likelihood to find the optimal value of Pagel’s λ for our phylogenetic structure.

References

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Orme, D., R. Freckleton, G. Thomas, T. Petzoldt, S. Fritz, and N. Isaac. 2013. The caper package: comparative analysis of phylogenetics and evolution in R. R package version **5**:1-36.

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Ward, P. S., B. B. Blaimer, and B. L. Fisher. 2016. A revised phylogenetic classification of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of the genera Colobopsis and Dinomyrmex. Zootaxa **4072**:343-357.

Table S5.2. Phylogenetic generalised linear model (PGLS) results modelling CT_{min}, CT_{max}, and CT_{range} with elevation site and vertical habitat as predictor variables while accounting for phylogenetic non-independence between data points. For 40 ant species in the Australian Wet Tropics.

Thermal trait	Estimate (°C)	Std. Error	*t*-value	*p* (>|t|)
CT_{min} ($F_{(2, 37)} = 21.6$, $p < 0.001$, Adj $R^2 = 0.5$, $\lambda = 0.52$)				
Elevation: *Lowland - Upland*	-3.18	0.48	-6.56	**<0.001**
Vertical habitat: *Ground - Arboreal*	0.44	0.43	1.01	0.3
CT_{max} ($F_{(2, 37)} = 10.7$, $p = 0.001$, Adj $R^2 = 0.33$, $\lambda = 0.6$)				
Elevation: *Lowland - Upland*	-1.44	0.90	-1.60	0.12
Vertical habitat:*Ground - Arboreal*	3.38	0.81	4.16	**0.001**
CT_{range} ($F_{(2, 37)} = 25.1$, $p < 0.001$, Adj $R^2 = 0.55$, $\lambda = 0$)				
Elevation: *Lowland - Upland*	1.74	1.02	1.70	0.1

Vertical habitat: *Ground* - *Arboreal*	5.81	0.83	6.99	**<0.001**

Appendix S6: Supplementary material for Chapter Six.

Table S6.1. Decoupling of ambient and surface temperature as a function of elevation site, time-period (day or night), and vertical height (continuous variable 0–27m). Results of linear mixed effects model presented with elevation, time-period, and vertical as fixed effects, and date-time as a random effect. Model with all two-way interactions was the best performing model. n = 520.

	R_m^2	**R_c^2**	**Likelihood Ratio**	**P-value**
Model	0.56	0.86	137.2	<0.0001
Random effect (Date-Time)	Std.dev. Intercept = 1.4	Std.dev. Residual = 0.97		
Fixed Effects			**F-value**	**p-value**
Elevation site			85.3	<0.0001
Time-period			65.9	<0.0001
Vertical height			45.2	<0.0001
Elevation site:Time-period			8.0	0.0052
Elevation site:Vertical height			4.3	0.0391
Time-period:Vertical height			10.5	0.0015