Oecologia

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

--Manuscript Draft--

Manuscript Number:	OECO-D-17-00743R3
Full Title:	Is thermal limitation the primary driver of elevational distributions? Not for montane rainforest ants in the Australian Wet Tropics
Article Type:	Highlighted Student Paper - Original Research
Corresponding Author:	Somayeh Nowrouzi James Cook University Townsville, QLD AUSTRALIA
Order of Authors:	Somayeh Nowrouzi
	Alan N. Andersen
	Tom Bishop
	Simon K.A. Robson
Response to Reviewers:	We thank the Handling Editor and Editor in Chief for their time and useful comments. Our responses to each comment are detailed below. Response to the handling editor The comment from the handling editor was: From my perspective, you have done what can be done to respond to the reviewer's critical comments, in an ant fauna for which many physiological characters of the component species remain to be addressed. I recommend the revised paper for acceptance. Thank you. Response to the editor in chief The points raised by the editor in chief were: Some of your figures are boxed, some not: Please use a consistent layout. Boxes are removed from all the figures. The relative size of the labels differs between figures. Again use a consistent layout. We used a consistent layout for all the label sizes. However, considering nine graphs in one figure (Figures 3 and 5) changes the final layout compared with the other single-graph figures. As far as can remember, in some figures the labels of the ticks for the y-axes are horizontal in others these labels are along the axes. We prefer horizontal labels. We have corrected all the y-axes labels to horizontal (see new figures 3, 4 and 5). In one figure you present lines indicating the y-values. Please remove! Lines indicating the y-values have been removed from the figures 3 and 5. Kind regards, Somayeh Nowrouzi
Funding Information:	James Cook University (NERP Postgraduate Scholarship) — Mrs Somayeh Nowrouzi

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

Somayeh Nowrouzi, PhD
James Cook University, Cairns, QLD 4878, Australia
Somayeh.nowrouzi@my.jcu.edu.au

17 February 2018

Dear Prof. Roland A. Brandl,

Thank you very much for your decision regarding the publication of our paper titled '*Is thermal limitation the primary driver of elevational distributions? Not for montane rainforest ants in the Australian Wet Tropics*'.

We are grateful for the comments from the Handling Editor and yourself on our manuscript. We have addressed all the issues raised by you on the figures, attached responses to the comments, and uploaded the new files.

We look forward to seeing our manuscript published in Oecologia.

Somayeh Nowrouzi

OECO-D-17-00743
Is thermal limitation the primary driver of elevational distributions? Not for montane rainforest ants in the Australian Wet Tropics

Responses to Comments

We thank the Handling Editor and Editor in Chief for their time and useful comments. Our responses to each comment are detailed below.

Response to the handling editor
The comment from the handling editor was:

> *From my perspective, you have done what can be done to respond to the reviewer's critical comments, in an ant fauna for which many physiological characters of the component species remain to be addressed. I recommend the revised paper for acceptance.*

Thank you.

Response to the editor in chief
The points raised by the editor in chief were:

> *Some of your figures are boxed, some not: Please use a consistent layout.*

Boxes are removed from all the figures.

> *The relative size of the labels differs between figures. Again use a consistent layout.*

We used a consistent layout for all the label sizes. However, considering nine graphs in one figure (Figures 3 and 5) changes the final layout compared with the other single-graph figures.

> *As far as can remember, in some figures the labels of the ticks for the y-axes are horizontal in others these labels are along the axes. We prefer horizontal labels.*

We have corrected all the y-axes labels to horizontal (see new figures 3, 4 and 5).

> *In one figure you present lines indicating the y-values. Please remove!*

Lines indicating the y-values have been removed from the figures 3 and 5.

Kind regards,

Somayeh Nowrouzi

Title: Is thermal limitation the primary driver of elevational distributions? Not for montane rainforest ants in the Australian Wet Tropics

Short title: Thermal limits of rainforest ants

Nowrouzi, Somayeh[1,2*], Andersen, Alan N. [2,3], Tom, R. Bishop[4], Robson, Simon K. A. [1]

[1] Centre for Tropical Biodiversity & Climate Change, College of Science & Engineering, James Cook University, Townsville, QLD 4811, Australia.

[2] CSIRO Land & Water Flagship, Darwin, NT 0822, Australia.

[3] Charles Darwin University, Research Institute for the Environment and Livelihoods, Darwin, NT 0810, Australia.

[4] Centre for Invasion Biology, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa.

* Corresponding author. E-mail: somayeh.nowrouzi@my.jcu.edu.au; Phone: +61408296060; Orcid ID (http://orcid.org/0000-0002-4143-1507) [1]

Noteworthy findings in our study are contradictions between our results and climatic variability hypothesis, Rapoport's rule or Bergmann's rule, and adds to the uncertainty around this issue for ants.

---

[1] **Author contributions:** S.N., A.N.A., S.K.A.R. conceived the ideas; S.N. collected the data, S.N. and T.R.B. analysed the data; S.N. led the writing, with other authors also contributing.

Abstract

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

Key words: body size, climate change, CTmax, ectotherm, elevation gradient.

Introduction

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

The physiological thermal tolerance limits of ectotherms are often used to assess the limits of their potential geographic distributions (Bozinovic et al. 2011; Sunday et al. 2012). Critical thermal maximum (CTmax), which measures the maximum operating temperature of an organism, is a commonly used measure of thermal sensitivity (Baudier et al. 2015; Rezende et al. 2011; Ribeiro et al. 2012) and there is often a strong relationship between a species' CTmax and its latitudinal distribution. CTmax not only commonly declines with increasing latitude (Addo-Bediako et al. 2000; Hoffmann et al. 2013), but also along other temperature gradients (Vorhees et al. 2013), including elevation (Gaston and Chown 1999; Terblanche et al. 2006). This is not always the case, however, and for some ectatherms CTmax shows little variation across temperature gradients (Araújo et al. 2013; Bishop et al. 2017). Therefore, the generality of this relationship between CTmax and temperature among different ectotherm groups remains unclear.

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

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

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

Methods

Study sites

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

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

Methodology

CTmax and body mass (as our measure of body size; (Moretti et al. 2017)) were measured for 160 ants representing 20 species and 13 genera (Table 1). The ants were randomly hand-collected during daytime from rainforest at the four sites, in January 2013. Collections were conducted between 8-11 am on two occasions (separated by 2 days) at each site. All individuals at a site were collected as stray foragers within 30 m of each other, and so are likely to have come from independent colonies (although we do not have observations to confirm this). We consider the study species to be broadly representative of the diurnal, epigaeic ant communities at the sites, and this is supported by results from extensive ant sampling between 2009 and 2013 (Nowrouzi et al. 2016). The study species include a strong representation of the most common species at each site, as well as a range of less common and rare species (Fig. S1). They included widely distributed generalist species (species of *Anonychomyrma* and *Rhytidoponera*) as well as more-specialized species with narrow elevational ranges (e.g. species of *Notostigma* and *Myrmecia*). We considered minor workers only for species of polymorphic genera (*Pheidole* and *Camponotus*).

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

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

Data analysis

Phylogenetic signal

A genus level, time-calibrated phylogeny from Moreau and Bell (2013) was used to estimate phylogenetic signal in CTmax and body mass. We calculated genus level means in the CTmax and body mass measures and used the original genus level phylogeny to calculate phylogenetic signal. Only one genus, *Nylanderia*, was not present on the original phylogeny; it was inserted as a tip next to its closest sister genus *Paratrechina* (LaPolla et al. 2011). Phylogenetic signal was calculated using Pagel's λ (Pagel 1999) and Blomberg's K (Blomberg et al. 2003). A likelihood ratio test was used to test for a significant departure of both of these statistics from 0 (no phylogenetic signal). The *phytools* package in R was used to manipulate the phylogeny and perform the phylogenetic signal tests (Revell 2012). CTmax did not display significant phylogenetic signal (Pagel's λ<0.01, P=1, Blomberg's K=0.698, P=0.474) at the genus level. Similar results were found for body mass (Pagel's λ<0.01, P=1, Blomberg's K=0.684, P=0.523). All the species were therefore treated as independent in our analyses. We also inserted species into the original genus-level phylogeny as basal polytomies, and tested for phylogenetic signal at the species level. Again, there was no significant phylogenetic signal in either CTmax (Pagel's λ<0.01, P=1, Blomberg's K=0.728, P=0.078) or body mass (Pagel's λ = 1.17, P=0.18, Blomberg's K=0.762, P=0.091).

CTmax and elevation

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

Elevation and species elevational ranges

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

Body size and elevation

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

CTmax, elevation and body size

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

Data Accessibility

Data for this paper can be found in the Electronic Supplementary Materials (Table S1).

Results

CTmax and elevation

Overall mean CTmax was 47.2 (± 0.54) °C, ranging from 37–65 °C among species. CTmax at the community level did not vary systematically with elevation (Fig. 2A; Table S2).

CTmax was tested for ≥10 individuals for nine species, all of which occurred at multiple elevational sites (Table 1). Mean CTmax significantly decreased with increasing elevation for only three of these species (*Myrmecia nigrocincta*, *Rhytidoponera* cf. *victoriae* and *Rhytidoponera impressa*), but showed no significant differences for the others (Fig. 3; Table S3).

Elevation and species elevational ranges

There was no correlation between elevation midpoint and elevational ranges of species (simple linear regression, $F_{1,18}$=0.057, P=0.814), and species with higher elevation midpoints did not specifically present larger elevational ranges. For example, of the nine species with ≥10 individuals tested, six occurred at high elevation (>800 m); two of these (*Anonychomyrma* sp. M and *Pheidole* sp. A2 (*ampla* gp.)) occurred exclusively at high elevation, whereas the other four (*Anonychomyrma gilberti*, *A.* cf. *gilberti*, *Rhytidoponera* cf. *victoriae* and *R. impressa)* occurred across the full elevation gradient (Fig. 4).

Body mass and elevation

Mean body mass at the community level decreased markedly with increasing elevation (ANOVA, $F_{3,153}$ = 10.86, P < 0.001), with the decline occurring primarily between 600 m and 800 m (Fig. 2(B); Table S4). However, mean body mass decreased with increasing elevation within only three of the nine species with ≥10 individuals tested (*Anonychomyrma* cf. *gilberti*, *Rhytidoponera* cf. *victoriae* and *Rhytidoponera impressa*), and showed no significant variation with elevation within the others (Fig. 5; Table S5). Notably, large (>4 mg) ants were found only at low elevations (350 and 600 m; Fig. 6).

CTmax, elevation and body size

Overall, there was a negative relationship between CTmax and body mass (simple linear regression, $F_{1,155}$=6.93, P = 0.009; Fig. 6). However, this relationship occurred within a species only for *Anonychomyrma gilberti* (Table S6). Results from the linear mixed effect model showed species (the random factor in the model) as the strongest predictor of variation in CTmax (Conditional R^2=0.87; Table S7). Removing the effect of species, only 3.1% of the variation in CTmax (Marginal R^2=0.031; Table S7) was explained by a combination of elevation and body mass.

Discussion

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

Terblanche et al. 2006), and do not support the generality of declining CTmax with decreasing ambient temperature (Addo-Bediako et al. 2000; Hoffmann et al. 2013; Vorhees et al. 2013).

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

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

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

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

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

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

Acknowledgements

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

References

Addo-Bediako A, Chown SL, Gaston KJ (2000) Thermal tolerance, climatic variability and latitude. Proceedings of the Royal Society of London B: Biological Sciences 267:739-745

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

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

Angilletta Jr MJ, Dunham AE (2003) The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. The American Naturalist 162:332-342

Angilletta MJ (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press

Angilletta MJ, Steury TD, Sears MW (2004) Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. Integrative and Comparative Biology 44:498-509

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

Arnan X, Blüthgen N (2015) Using ecophysiological traits to predict climatic and activity niches: lethal temperature and water loss in Mediterranean ants: Using physiology to predict niches. Global Ecology and Biogeography 24:1454-1464. doi: 10.1111/geb.12363

Arnan X, Blüthgen N, Molowny-Horas R, Retana J (2015) Thermal Characterization of European Ant Communities Along Thermal Gradients and Its Implications for Community Resilience to Temperature Variability. Frontiers in Ecology and Evolution 3:138

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

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

Baudier KM, Mudd AE, Erickson SC, O'Donnell S (2015) Microhabitat and body size effects on heat tolerance: implications for responses to climate change (army ants: Formicidae, Ecitoninae). Journal of Animal Ecology 84:1322-1330. doi: 10.1111/1365-2656.12388

Bishop TR, Robertson MP, RENSBURG BJ, Parr CL (2017) Coping with the cold: minimum temperatures and thermal tolerances dominate the ecology of mountain ants. Ecological Entomology 42:105-114

Blomberg SP, Jr TG, Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717-745. doi: 10.1554/0014-3820(2003)057[0717:TFPSIC]2.0.CO;2

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

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

Bruhl CA, Gunsalam G, Linsenmair KE (1998) Stratification of ants (Hymenoptera, Formicidae) in a primary rain forest in Sabah, Borneo. Journal of Tropical Ecology 14:285-297

Buckley LB, Hurlbert AH, Jetz W (2012) Broad-scale ecological implications of ectothermy and endothermy in changing environments. Global Ecology and Biogeography 21:873-885

Bureau of Meteorology (2015) Climate Data Online, vol. 2015

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

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

Costion CM, Simpson L, Pert PL, Carlsen MM, Kress WJ, Crayn D (2015) Will tropical mountaintop plant species survive climate change? Identifying key knowledge gaps using species distribution modelling in Australia. Biological Conservation 191:322-330

Davidson DW, Cook SC, Snelling RR, Chua TH (2003) Explaining the Abundance of Ants in Lowland Tropical Rainforest Canopies. Science 300:969-972. doi: 10.1126/science.1082074

Deutsch CA et al. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences 105:6668-6672

Diamond S et al. (2012) Who likes it hot? A global analysis of the climatic, ecological, and evolutionary eterminants of warming tolerance in ants. Global Change Biology 18:448–456. doi: doi: 10.1111/j.1365-2486.2011.02542.x

Dunn RR et al. (2009) Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. Ecology Letters 12:324-333. doi: 10.1111/j.1461-0248.2009.01291.x

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

Gaston KJ, Chown SL (1999) Elevation and climatic tolerance: a test using dung beetles. Oikos 86:584-590

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

Ghalambor CK, Huey RB, Martin PR, Tewksbury JJ, Wang G (2006) Are mountain passes higher in the tropics? Janzen's hypothesis revisited. Integrative and Comparative Biology 46:5-17. doi: 10.1093/icb/icj003

Griffiths HM et al. (2017) Ants are the major agents of resource removal from tropical rainforests. Journal of Animal Ecology; 00:1–8. doi: 10.1111/1365-2656.12728

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

Hoffmann AA, Chown SL, Clusella-Trullas S (2013) Upper thermal limits in terrestrial ectotherms: how constrained are they? Functional Ecology 27:934-949

Hölldobler B, Wilson EO (1990) The ants. Belknap Press of Harvard University Press, Cambridge

Huey RB, Kearney MR, Krockenberger A, Holtum JA, Jess M, Williams SE (2012) Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philosophical Transactions of the Royal Society of London B: Biological Sciences 367:1665-1679

Huey RB, Pascual M (2009) Partial Thermoregulatory Compensation by a Rapidly Evolving Invasive Species along a Latitudinal Cline. Ecology 90:1715-1720. doi: 10.1890/09-0097.1

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

Kaspari M, Clay NA, Lucas J, Revzen S, Kay A, Yanoviak SP (2016) Thermal adaptation and phosphorus shape thermal performance in an assemblage of rainforest ants. Ecology 97:1038-1047. doi: 10.1890/15-1225.1

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

Kaspari M, Vargo EL (1995) Colony Size as a Buffer Against Seasonality: Bergmann's Rule in Social Insects. The American Naturalist 145:610-632

Kaspari M, Weiser MD (2000) Ant Activity along Moisture Gradients in a Neotropical Forest. Biotropica 32:703-711

Kaufmann E, Maschwitz U (2006) Ant-gardens of tropical Asian rainforests. Die Naturwissenschaften 93:216-227. doi: 10.1007/s00114-005-0081-y

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

Kimura MT (2004) Cold and Heat Tolerance of Drosophilid Flies with Reference to Their Latitudinal Distributions. Oecologia 140:442-449. doi: 10.1007/s00442-004-1605-4

LaPolla JS, Brady SG, Shattuck SO (2011) Monograph of Nylanderia (Hymenoptera: Formicidae) of the World: An introduction to the systematics and biology of the genus. Zootaxa 3110:1-9

Levy RA, Nufio CR (2015) Dispersal potential impacts size clines of grasshoppers across an elevation gradient. Oikos 124:610-619

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

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

Meiri S, Dayan T (2003) On the validity of Bergmann's rule. Journal of Biogeography 30:331-351. doi: 10.1046/j.1365-2699.2003.00837.x

Moreau CS, Bell CD (2013) TESTING THE MUSEUM VERSUS CRADLE TROPICAL BIOLOGICAL DIVERSITY HYPOTHESIS: PHYLOGENY, DIVERSIFICATION, AND ANCESTRAL BIOGEOGRAPHIC RANGE EVOLUTION OF THE ANTS. Evolution 67:2240-2257. doi: 10.1111/evo.12105

Moretti M et al. (2017) Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. Functional Ecology 31:558-567

Nelson AS et al. (2017) Day/night upper thermal limits differ within Ectatomma ruidum ant colonies. Insectes Sociaux. doi: 10.1007/s00040-017-0585-4

Nowrouzi S, Andersen AN, Macfadyen S, Staunton KM, VanDerWal J, Robson SK (2016) Ant diversity and distribution along elevation gradients in the Australian wet tropics: the importance of seasonal moisture stability. PloS one 11:e0153420

Oberg EW, Del Toro I, Pelini SL (2012) Characterization of the thermal tolerances of forest ants of New England. Insectes Sociaux 59:167-174. doi: 10.1007/s00040-011-0201-y

Olalla-Tárraga MÁ, Rodríguez MÁ, Hawkins BA (2006) Broad-scale patterns of body size in squamate reptiles of Europe and North America. Journal of Biogeography 33:781-793. doi: 10.1111/j.1365-2699.2006.01435.x

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

Parsons SA, Congdon RA (2008) Plant litter decomposition and nutrient cycling in north Queensland tropical rain-forest communities of differing successional status. Journal of Tropical Ecology 24:317-327

Payne NL, Smith JA (2017) An alternative explanation for global trends in thermal tolerance. Ecology Letters 20:70-77. doi: 10.1111/ele.12707

Pincebourde S, Woods HA, Fox C (2012) Climate uncertainty on leaf surfaces: the biophysics of leaf microclimates and their consequences for leaf-dwelling organisms. Functional Ecology 26:844-853. doi: 10.1111/j.1365-2435.2012.02013.x

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, URL http://www.R-project.org

Revell LJ (2012) phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217-223. doi: 10.1111/j.2041-210X.2011.00169.x

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

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

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

Shoo L, Williams S, Hero J (2005) Climate warming and the rainforest birds of the Australian Wet Tropics: Using abundance data as a sensitive predictor of change in total population size. Biological Conservation 125:335-343. doi: 10.1016/j.biocon.2005.04.003

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

Staunton KM, Robson SKA, Burwell CJ, Reside AE, Williams SE (2014) Projected distributions and diversity of flightless ground beetles within the Australian Wet Tropics and their environmental correlates. PLoS ONE 9 (2) 1-16

Stevens GC (1992) The Elevational Gradient in Altitudinal Range: An Extension of Rapoport's Latitudinal Rule to Altitude. The American Naturalist 140:893-911

Stratman R, Markow TA (1998) Resistance to thermal stress in desert Drosophila. Functional Ecology 12:965-970. doi: 10.1046/j.1365-2435.1998.00270.x

Stuble KL, Pelini SL, Diamond SE, Fowler DA, Dunn RR, Sanders NJ (2013) Foraging by forest ants under experimental climatic warming: a test at two sites. Ecology and evolution 3:482-491. doi: 10.1002/ece3.473

Sunday JM, Bates AE, Dulvy NK (2011) Global analysis of thermal tolerance and latitude in ectotherms. Proceedings.Biological sciences / The Royal Society 278:1823-1830. doi: 10.1098/rspb.2010.1295

Sunday JM, Bates AE, Dulvy NK (2012) Thermal tolerance and the global redistribution of animals. Nature Climate Change 2:686-690

Terblanche JS, Klok CJ, Krafsur ES, Chown SL (2006) Phenotypic plasticity and geographic variation in thermal tolerance and water loss of the tsetse Glossina pallidipes (Diptera: Glossinidae): implications for distribution modelling. The American journal of tropical medicine and hygiene 74:786-794

Verble-Pearson RM, Gifford ME, Yanoviak SP (2015) Variation in thermal tolerance of North American ants. Journal of thermal biology 48:65-68

Vorhees AS, Gray EM, Bradley TJ (2013) Thermal resistance and performance correlate with climate in populations of a widespread mosquito. Physiological and Biochemical Zoology 86:73-81

Wiescher PT, Pearce-Duvet JM, Feener DH (2012) Assembling an ant community: species functional traits reflect environmental filtering. Oecologia 169:1063-1074

Williams SE, Pearson RG (1997) Historical rainforest contractions, localized extinctions and patterns of vertebrate endemism in the rainforests of Australia's wet tropics. Proceedings of the Royal Society of London Series B 264:709-716

Williams SE, Williams YM, VanDerWal J, Isaac JL, Shoo LP, Johnson CN (2009) Colloquium Papers: Ecological specialization and population size in a biodiversity hotspot: How rare species avoid extinction. Proceedings of the National Academy of Sciences 106:19737-19741. doi: 10.1073/pnas.0901640106

Wilson EO (1992) The Diversity of Life. Harvard University Press, Harvard

Table 1. Species list and number of individuals tested for CTmax and body mass from sites at different elevations on Mount Spec. Species with ≥ 10 individuals are highlighted.

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

Figure legends

Fig.1 Map showing the current extent of rainforest (green/dark shading) in the Australian Wet Tropics bioregion (light shading), with locations of sampling sites at Mount Spec indicated by triangles.

Fig.2 Variation in mean CTmax (A) and body mass (B) across elevational sites, based on pooled data from all tested species; with 95% confidence intervals. Different letters indicate significant differences between elevational sites.

Fig.3 Mean CTmax in different elevational sites for each species tested for ≥10 individuals; with 95% confidence intervals. Different letters indicate significant differences between elevational sites for each species.

Fig.4 Mid elevation point and elevational ranges for each species with ≥10 individuals tested. Larger points represent higher number of species overlapped. Abbreviations are species names as: An.g= *Anonychomyrma gilberti*, An.cf.g= *Anonychomyrma* cf.*gilberti*, An.M= *Anonychomyrma* sp. M, Cr.G= *Crematogaster* sp. G, Le.mj= *Leptogenys mjobergi*, My.ni= *Myrmecia nigrocincta*, Ph.A2= *Pheidole* sp. A2 (*ampla* gp.), Rh.cf.v= *Rhytidoponera cf. victoriae* and Rh.im= *Rhytidoponera impressa*.

Fig.5 Mean body mass (with 95% confidence intervals) in different elevational sites for each species with ≥10 individuals tested. Different letters indicate significant differences between elevational sites for each species.

Fig.6 CTmax variation in relation to body mass changes, based on pooled data from all the species of all the elevation sites, with simple linear regression line. Colour version of the figure is available online.

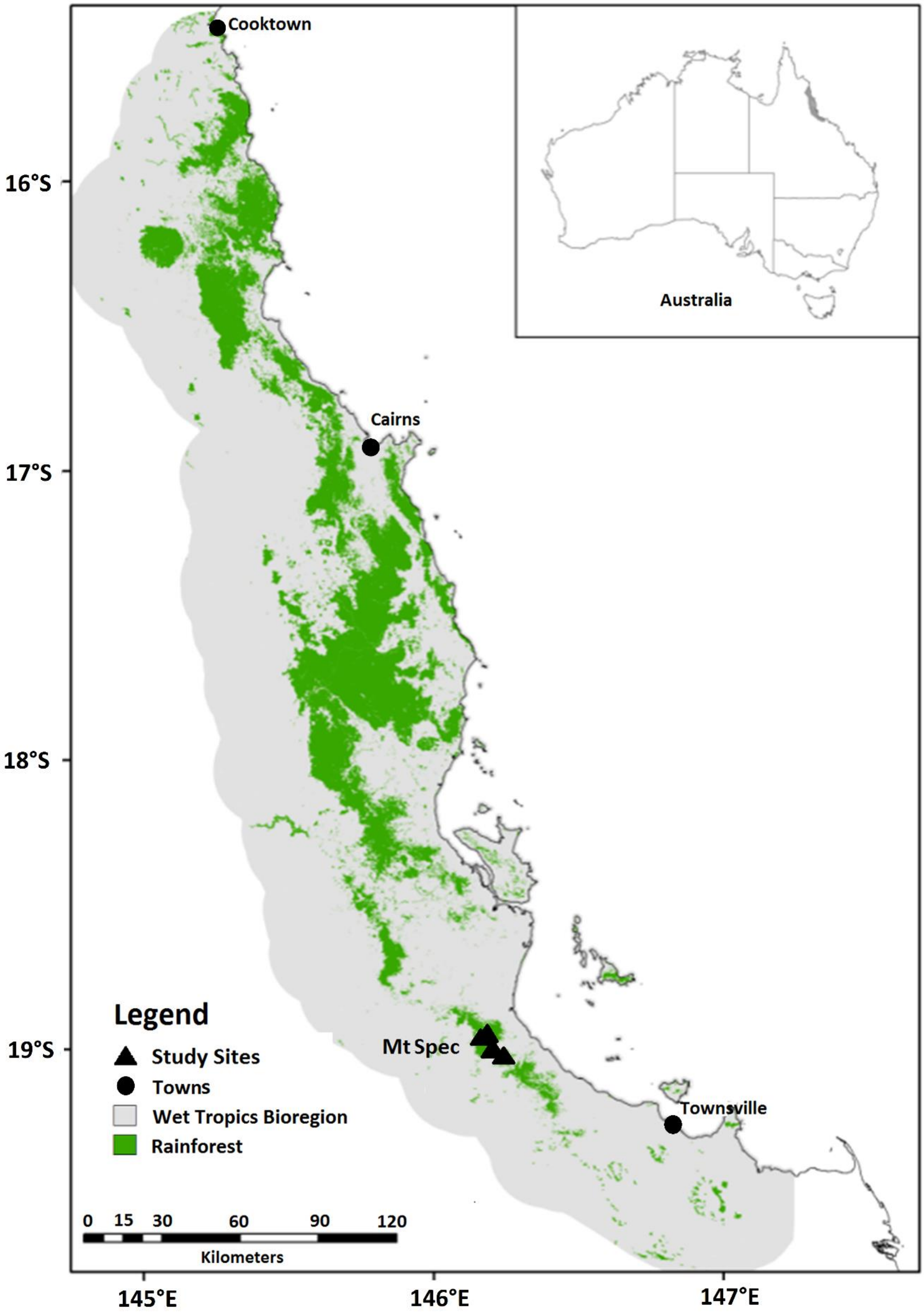

Cooktown
Australia
Cairns
Townsville
Mt Spec
Legend
Study Sites
Towns
Wet Tropics Bioregion
Rainforest
0 15 30 60 90 120
Kilometers
16°S
17°S
18°S
19°S
145°E
146°E
147°E

Fig.1

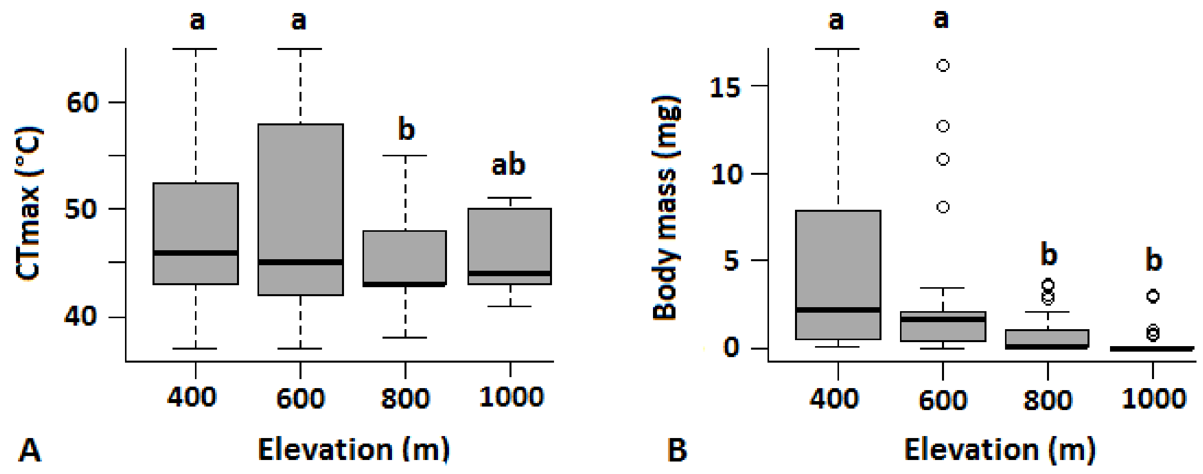

a
a
b
ab
60
50
40
CTmax (°C)
400
600
800
1000
A
Elevation (m)
a
a
b
b
15
10
5
0
Body mass (mg)
400
600
800
1000
B
Elevation (m)

Fig.2

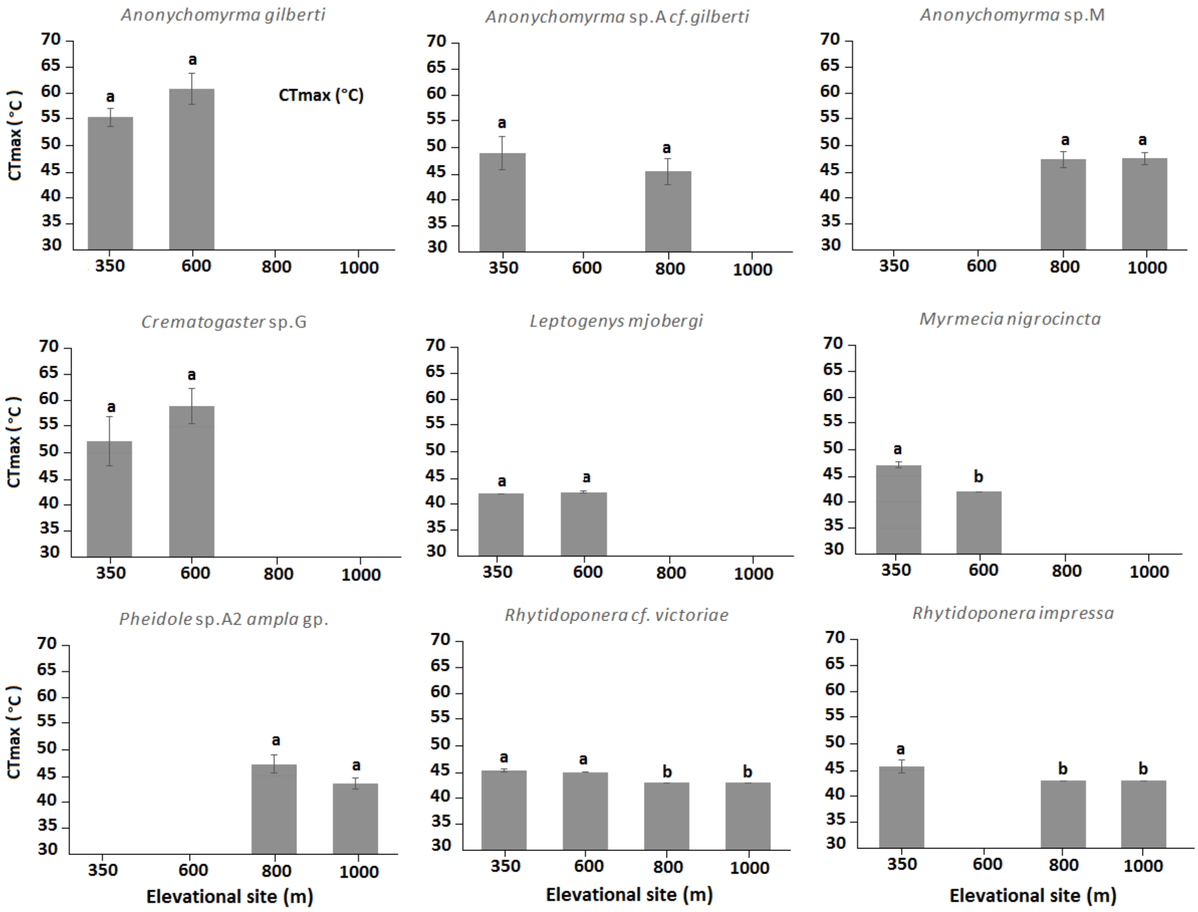

Anonychomyrma gilberti
CTmax (°C)
a
a
CTmax (°C)
Anonychomyrma sp.A cf. gilberti
a
a
Anonychomyrma sp.M
a
a
Crematogaster sp.G
a
a
Leptogenys mjobergi
a
a
Myrmecia nigrocincta
a
b
Pheidole sp.A2 ampla gp.
a
a
Rhytidoponera cf. victoriae
a
a
b
b
Rhytidoponera impressa
a
b
b
70
65
60
55
50
45
40
35
30
350
600
800
1000
Elevational site (m)

Fig.3

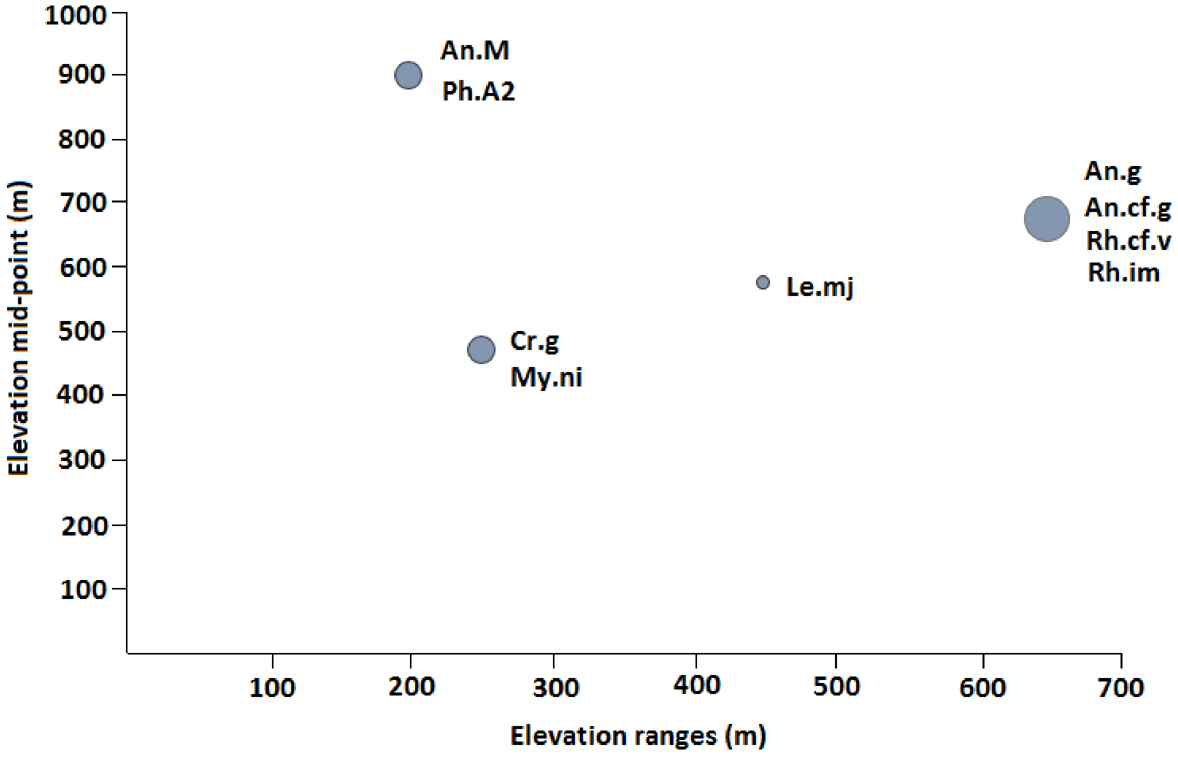
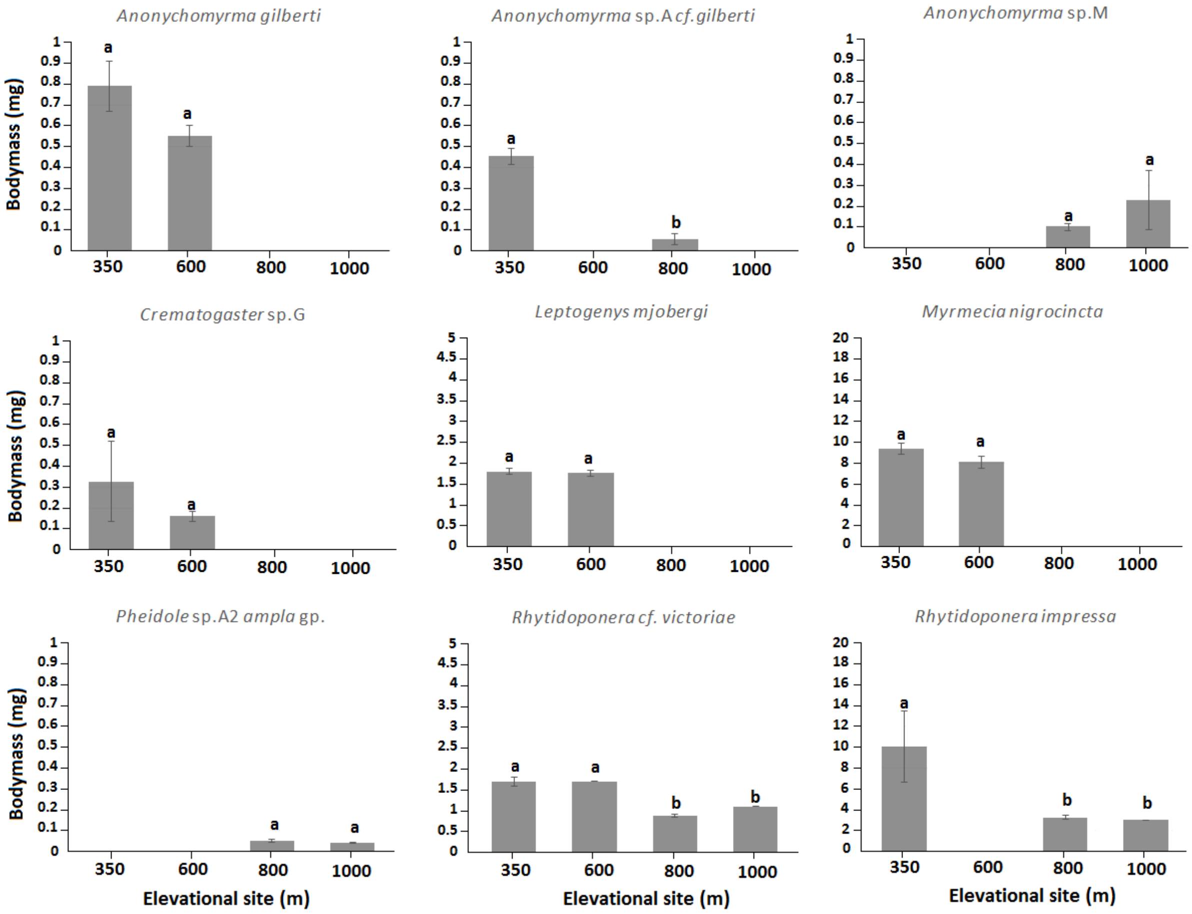

1000
900
800
700
600
500
400
300
200
100
Elevation mid-point (m)
100
200
300
400
500
600
700
Elevation ranges (m)
An.M
Ph.A2
An.g
An.cf.g
Rh.cf.v
Rh.im
Le.mj
Cr.g
My.ni

Fig.4



Anonychomyrma gilberti

Anonychomyrma sp.A *cf.gilberti*

Anonychomyrma sp.M

Crematogaster sp.G

Leptogenys mjobergi

Myrmecia nigrocincta

Pheidole sp.A2 *ampla* gp.

Rhytidoponera cf. victoriae

Rhytidoponera impressa

Fig.5

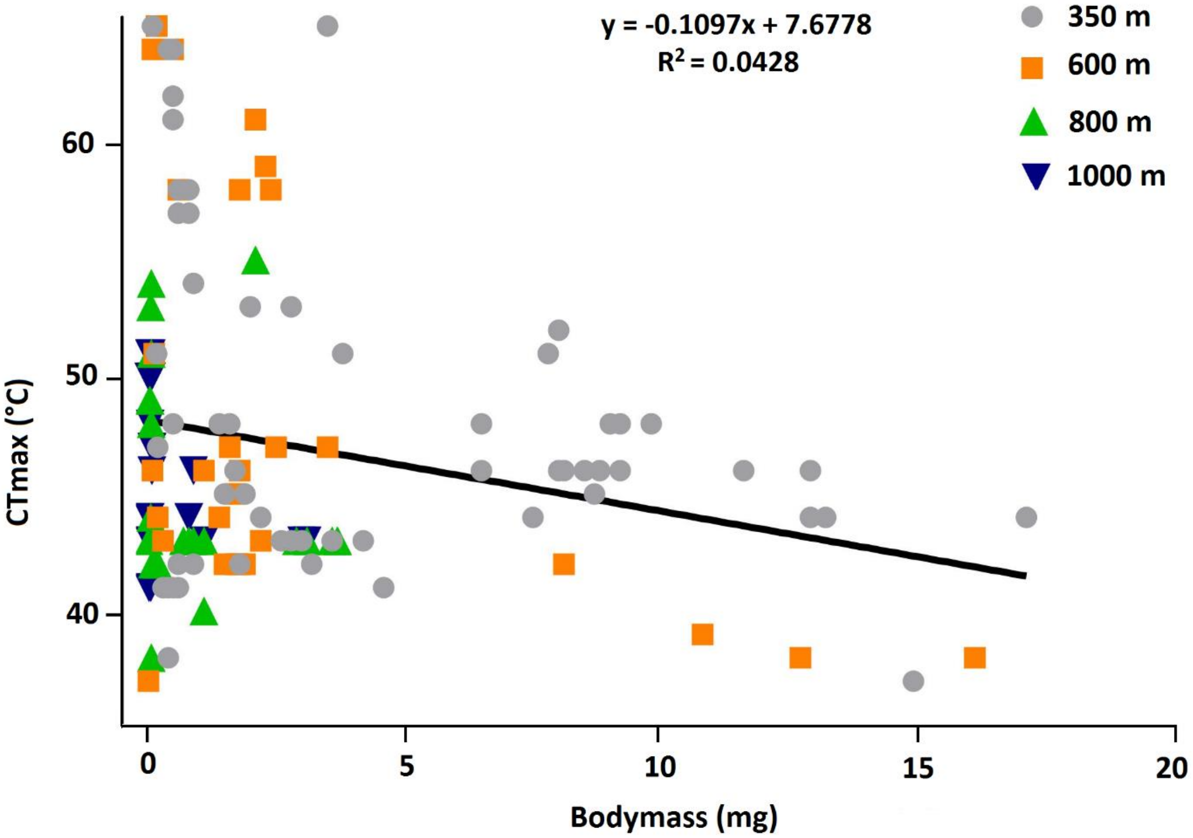

y = -0.1097x + 7.6778
R^2 = 0.0428
350 m
600 m
800 m
1000 m
CTmax (°C)
60
50
40
0
5
10
15
20
Bodymass (mg)

Fig.6

SPRINGER NATURE

Change of authorship request form

Please read the important information on page 4 before you begin

This form should be used by authors to request any change in authorship. Please fully complete all sections. Use black ink and block capitals and provide each author's full name with the given name first followed by the family name.

Section 1 Please provide the current title of manuscript

Manuscript ID no. OECO-D-17-00743R1

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

Section 2 Please provide the current authorship, in the order shown on your manuscript.

	First name(s)	Family name	ORCID or SCOPUS id, if available
1st author	Somayeh	Nowrouzi	http://orcid.org/0000-0002-4143-1507
2nd author	Alan N.	Andersen	
3rd author	Simon K.A.	Robson	
4th author			
5th author			
6th author			
7th author			

Please use an additional sheet if there are more than 7 authors.

Section 3: Please provide a justification for change. Please use this section to explain your reasons for changing the authorship of your manuscript. Please refer to the journal policy pages for more information about authorship. Please explain why omitted authors were not originally included on the submitted manuscript.

Based on Ocologia reviewer's report and the Handling Editor's comments on our manuscript, received on the 12 Sep, we took the revising approach by following the suggested changes in the comments. After seeking advice from another scientist, Tom Bishop, who had familiarity with the reviewer's suggested additional analysis, we asked for his opinion on the entire manuscript. His contribution in further analyses and re-shaping the manuscript, which we believe has improved the manuscript substantially, we decided that his contribution is significant enough to include him as co-author.

Change of authorship request form

Section 4 Proposed new authorship. Please provide your new authorship list in the order you would like it to appear on the manuscript.

	First name(s)	Family name (this name will appear in full on the final publication and will be searchable in various abstract and indexing databases)
1st author	Somayeh	Nowrouzi
2nd author	Alan N.	Andersen
3rd author	Tom R.	Bishop
4th author	Simon K.A.	Robson
5th author		
6th author		
7th author		

Please use an additional sheet if there are more than 7 authors.

Section 5 Author contribution, Acknowledgement and Disclosures. Please use this section to provide revised Author Contribution, Acknowledgement and/or Disclosures of your manuscript, ensuring you state what contribution any new authors made and, if appropriate acknowledge any contributors who have been removed as authors. Please ensure these are updated in your manuscript.

New Disclosures (potential conflicts of interest, funding, acknowledgements):

New Author Contributions statement:

Tom R. Bishop has contributed in analysing the data and re-writing the manuscript.

New Acknowledgement Section:

State 'Not applicable' if there are no new authors.

Section 6 Declaration of agreement. *All* authors, unchanged, new and removed *must* sign this declaration.

*** please delete as appropriate. Delete all of the bold if you were on the original authorship list and are remaining as an author**

	First name	Family name		Signature	Affiliated institute	Date
1st author	Somayeh	Nowrouzi	I agree to the proposed new authorship shown in section 4.		James Cook University	11/11/2017
2nd author	Alan N.	Andersen	I agree to the proposed new authorship shown in section 4.		Charles Darwin University	12/11/2017
3rd author	Tom R.	Bishop	I agree to the proposed new authorship shown in section 4 **and the addition of my name to the authorship list.**	T.Bishop	University of Pretoria	13/11/2017
4th authors	Simon K.A.	Robson	I agree to the proposed new authorship shown in section 4.		James Cook University	14/11/2017

Change of authorship request form

Please use an additional sheet if there are more than 7 authors. * please delete as appropriate. Delete all of the bold if you were on the original authorship list and are remaining.

Important information. Please read.

- Please return this form, fully completed, to the editorial office. We will consider the information you have provided to decide whether to approve the proposed change in authorship. We may choose to contact your institution for more information or undertake a further investigation, if appropriate, before making a final decision.
- Please note, we cannot investigate or mediate any authorship disputes. If you are unable to obtained agreement from all authors (included those who you wish to be removed) you must refer the matter to your institution(s) for investigation. Please inform us if you need to do this.
- If you are not able to return a fully completed form within **30 days** of the date that it was sent to the author requesting the change, we may have to reject your manuscript. We cannot publish manuscripts where authorship has not been agreed by all authors (including those who have been removed).
- Incomplete forms will be rejected.