HIGHLIGHTED STUDENT RESEARCH

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

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

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 (CT_{max}) of insects and their latitudinal ranges, the nature of this relationship across elevation is less clear. Here we investigated the combined relationships between CT_{max}, elevation and ant body mass, given that CT_{max} can also be influenced by body mass, in the World Heritage-listed rainforests of the Australian Wet Tropics. We measured the CT_{max} and body mass of 20 ant species across an elevational gradient from 350 to 1000 m a.s.l. Community CT_{max} 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 CT_{max} and body mass at the community level, there was no significant difference in CT_{max} 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 CT_{max}. 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.

Keywords Body size · Climate change · CT_{max} · Ectotherm · Elevation gradient

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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.

✉ Somayeh Nowrouzi
somayeh.nowrouzi@my.jcu.edu.au

1 Centre for Tropical Biodiversity and Climate Change, College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia

2 CSIRO Land and Water Flagship, Darwin, NT 0822, Australia

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

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

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 (CT_{max}), 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' CT_{max} and its latitudinal distribution. CT_{max} 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 CT_{max} shows little variation across temperature gradients (Araújo et al. 2013; Bishop et al. 2017). Therefore, the generality of this relationship between CT_{max} 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 CT_{max}. 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 CT_{max} 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 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 CT_{max}, 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 CT_{max} decrease with increasing elevation and decreasing ambient temperature, paralleling the relationship between CT_{max} 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' CT_{max}?
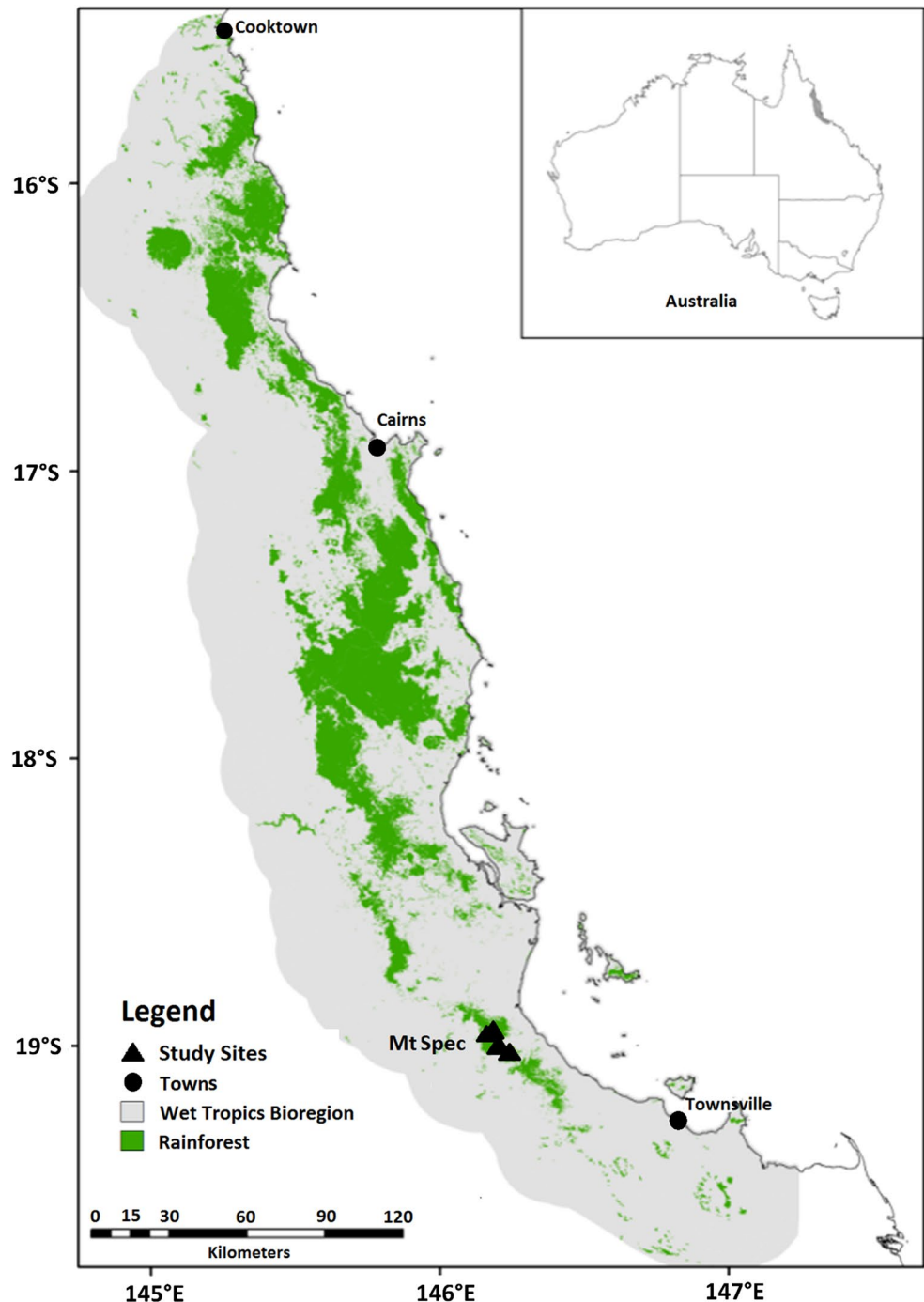
Methods

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, 600, 800 and 1000 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 1200–2500 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).

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 (colour figure online)

Methodology

CT_{max} 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 and 11 a.m. 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

Table 1 Species list and number of individuals tested for CT_{max} and body mass from sites at different elevations on Mount Spec

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

Species with ≥ 10 individuals are highlighted in bold

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*).

CT_{max} was measured in the field, with individuals assayed within 3 h 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-Lok dry heat bath pre-warmed to 25 °C (Diamond et al. 2012), and CT_{max} was recorded by increasing the temperature by 1 °C/min 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 h 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 CT_{max} 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 CT_{max} and body mass. We calculated genus level means in the CT_{max} 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 (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). CT_{max} did not display significant phylogenetic signal (Pagel's < 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 < 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 CT_{max} (Pagel's < 0.01, $P = 1$, Blomberg's $K = 0.728$, $P = 0.078$) or body mass (Pagel's $= 1.17$, $P = 0.18$, Blomberg's $K = 0.762$, $P = 0.091$).

CT_{max} and elevation

We calculated mean CT_{max} 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 CT_{max} 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 CT_{max}.

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.

CT$_{max}$, 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 CT$_{max}$. 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 CT$_{max}$ 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

CT$_{max}$ and elevation

Overall mean CT$_{max}$ was 47.2 ($\pm$ 0.54) °C, ranging from 37 to 65 °C among species. CT$_{max}$ at the community level did not vary systematically with elevation (Fig. 2a; Table S2).

CT$_{max}$ was tested for $\geq$ 10 individuals for nine species, all of which occurred at multiple elevational sites (Table 1). Mean CT$_{max}$ 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 $\geq$ 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. 2b; Table S4). However, mean body mass decreased with increasing elevation within only three of the nine species with $\geq$ 10 individuals tested (*Anonychomyrma* cf. *gilberti*, *Rhytidoponera* cf. *victoriae* and *R. 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).

CT$_{max}$, elevation and body size

Overall, there was a negative relationship between CT$_{max}$ 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 *A. gilberti* (Table S6). Results from the linear mixed effect model showed species (the random factor in the model) as the strongest predictor of variation

Fig. 2 Variation in mean CT$_{max}$ (**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
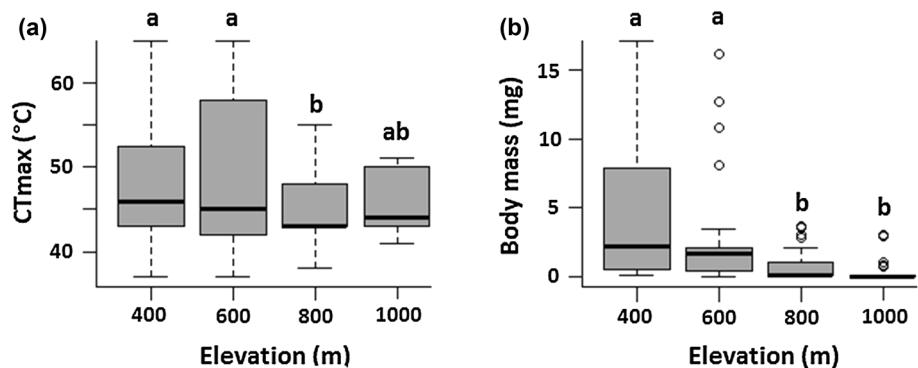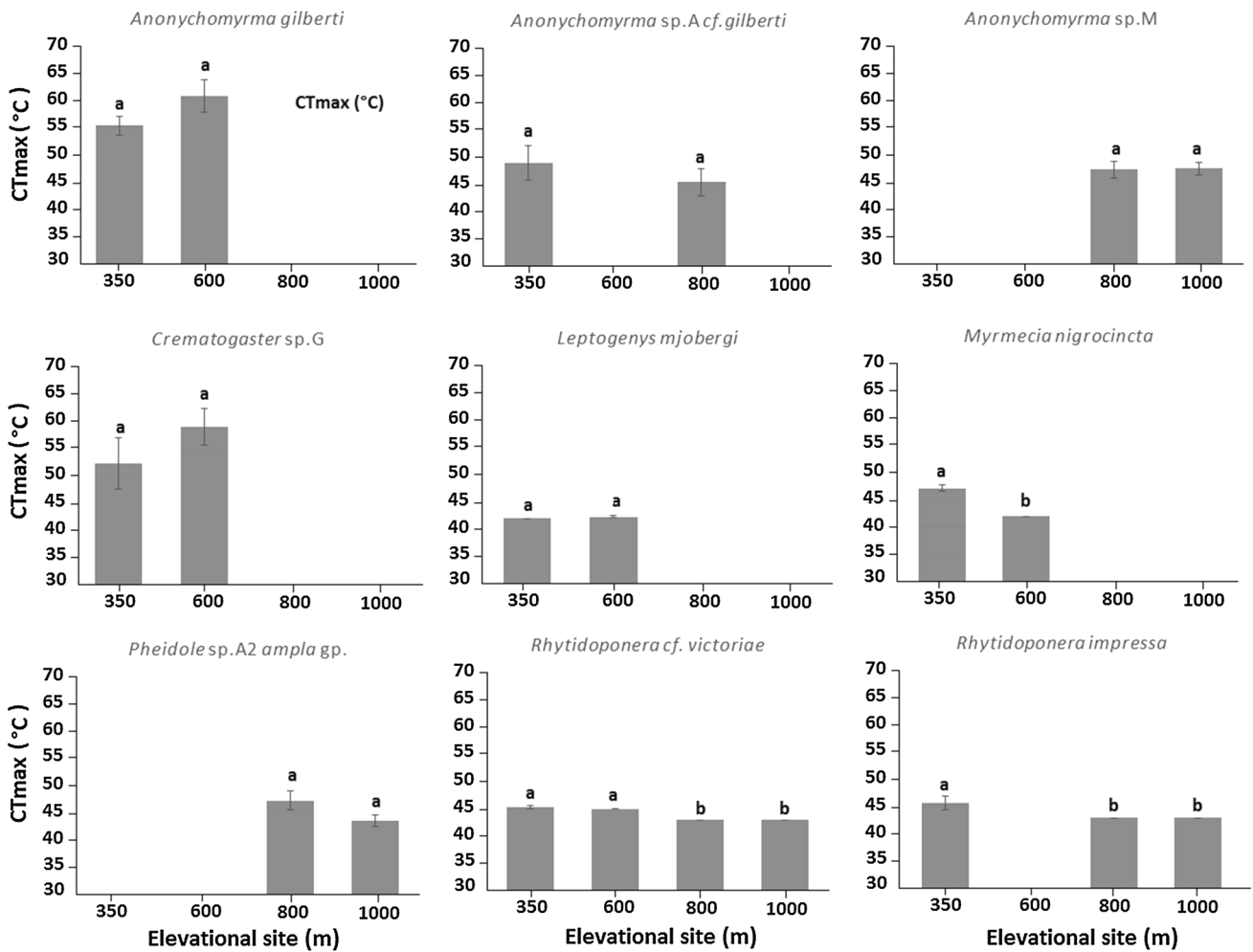
Fig. 3 Mean CT_{max} in different elevational sites for each species tested for ≥ 10 individuals; with 95% confidence intervals. Different letters indicate significant differences between elevational sites for each species
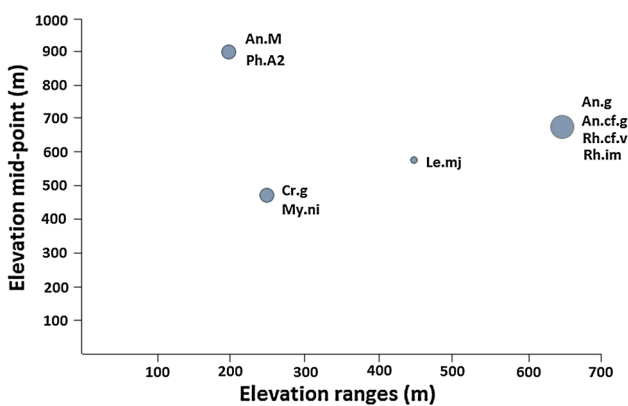

Fig. 4 Mid-elevation point and elevational ranges for each species with ≥ 10 individuals tested. Larger points represent higher number of species overlapped. Abbreviations are species names as: An.g = *Anonychomyrma gilberti*, An.cf.g = *Anonychomyrma* cf.*gilberti*, An.M = *Anonychomyrma* sp. M, Cr.G = *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*

in CT_{max} (conditional $R^2 = 0.87$; Table S7). Removing the effect of species, only 3.1% of the variation in CT_{max} (marginal $R^2 = 0.031$; Table S7) was explained by a combination of elevation and body mass.

Discussion

Our study investigated the relationships between CT_{max}, 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 CT_{max} decreases with increasing elevation, paralleling the common pattern of declining CT_{max} 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 CT_{max} for ants across an elevation gradient in
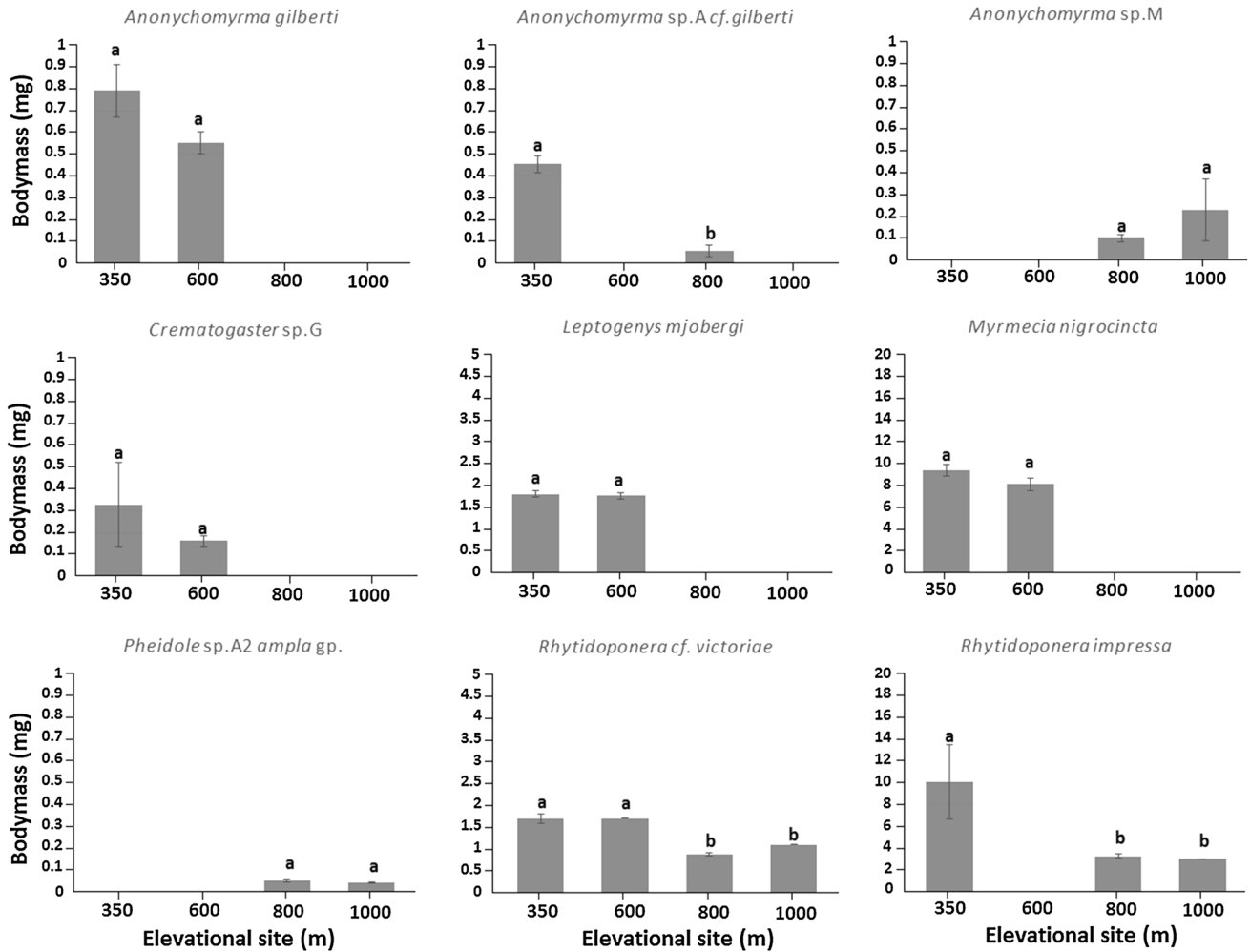
Fig. 5 Mean body mass (with 95% confidence intervals) in different elevational sites for each species with ≥ 10 individuals tested. Different letters indicate significant differences between elevational sites for each species
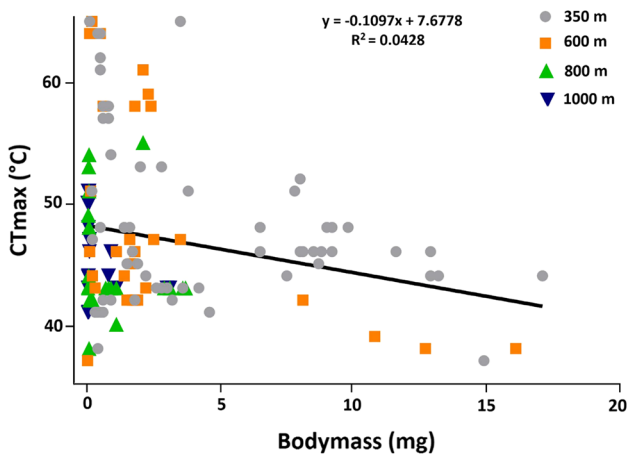

Fig. 6 CT_{max} variation in relation to body mass changes, based on pooled data from all the species of all the elevation sites, with simple linear regression line. Colour version of the figure is available online

South Africa. Our findings are not consistent with studies of CT_{max} variation across elevational gradients in other insect groups (Gaston and Chown 1999; Terblanche et al. 2006), and do not support the generality of declining CT_{max} with decreasing ambient temperature (Addo-Bediako et al. 2000; Hoffmann et al. 2013; Vorhees et al. 2013).

The median CT_{max} of 45 °C for rainforest ants in our study slightly exceeds that of ants globally as estimated in a worldwide 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 CT_{max} 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' CT_{max}. We found a negative correlation between body mass and CT_{max} 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 CT_{max}, 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 CT_{max} 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 CT_{max} and latitude (Kellermann et al. 2012; Kimura 2004). The positive correlation between CT_{max} 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 CT_{max} (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 CT_{max} 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.

Author contribution statement SN, ANA, SKAR conceived the ideas; SN collected the data; SN and TRB analysed the data; SN led the writing, with other authors also contributing.

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