

Ecography

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Diamond, S. E. and Chick, L. D. 2017. Thermal specialist ant species have restricted, equatorial geographic ranges: implications for climate change vulnerability and risk of extinction. – Ecography doi: 10.1111/ecog.03264

Supplementary material

Supplementary material Appendix 1

Methods

Geographic range

We assembled a dataset of global ant species occurrences from three sources comprising published records of global georeferenced ant presence data (Fitzpatrick et al. 2011), AntWeb records (<http://www.antweb.org> last accessed June 2017), and global georeferenced ant thermal tolerance data (Diamond et al. 2012a). To estimate geographic range size, we computed the minimum convex polygon enclosing the occurrence points of each species. We used the *mcp* function from the *adehabitatHR* package in R (Calenge 2006), with a Lambert azimuthal equal-area projection and a 95% interval for the occurrence points to minimize the influence of extreme occurrences (fringe or intermittent populations). Geographic range sizes were expressed in units of km². We also estimated the latitudinal position of the centroid of the geographic range using the *centroid* function from the *geosphere* package in R (Hijmans 2016); this allowed us to explore latitudinal clines in thermal specialism and geographic range size. The number of occurrences for individual species ranged from 12 to 1887, with a median of 204 records. Alternative methods to estimate range size and range parameters based on dynamic alpha hulls (Rabosky et al. 2016) were highly correlated with our minimum convex polygon methods (r_s and 95% CI = 0.90 [0.85,0.93], $P < 0.0001$, $df = 88$), and yielded qualitatively similar results in our analyses of range size and thermal tolerance.

Because of the ambiguity in the geographic range estimation for introduced species, we excluded them from our analyses. These species included *Anoplolepis gracilipes*, *Brachyponera chinensis*, *Linepithema humile*, *Monomorium floricola*, *Monomorium pharaonis*, *Pheidole*

pallidula, *Solenopsis geminata*, *Solenopsis invicta*, *Tetramorium bicarinatum* and *Tetramorium caespitum*.

Thermal tolerance

We supplemented a published global dataset of ant upper and lower thermal tolerances (Diamond et al. 2012a) with additional thermal tolerance data we generated using methods comparable to the global dataset (dynamic temperature ramping protocols were used to assess upper thermal tolerance, CT_{max} , and lower thermal tolerance, CT_{min} , each defined as the temperature at which muscular coordination was lost). The additional thermal tolerance data were aimed at improving replication in the availability of lower thermal tolerances. The original global dataset of Diamond et al. (2012a) had only 9 species for which CT_{min} and suitable occurrence data for estimating range size were available; the new dataset presented here contributes an additional 32 species which meet these criteria (see Table A1).

We restricted our collection of ant upper and lower thermal tolerance data to the growing season at each location. This design reflects both a focus on biological relevance and practical constraints on obtaining thermal tolerance data. Assessing CT_{max} during the warmest part of the year is biologically relevant as these environmental temperatures are likely to be closest to the upper thermal tolerances of ants. In contrast, assessing CT_{min} during the warmest part of the year represents a practical constraint: because many ants move underground for the winter and may be buried under significant snowpack, especially at higher latitudes, we were unable to obtain CT_{min} during the winter season when environmental temperatures are likely to be closest to the lower thermal tolerances of ants. However, there are at least two reasons why the measurement of CT_{min} during the growing season is unlikely to impact our results in a qualitative manner.

Recent work suggests that for a subset of ant species living in the temperate region, seasonal acclimation in upper and lower thermal tolerances is limited (Maysov and Kipyatkov 2009, Stuble et al. 2013, Penick et al. 2017). Further, our experimental design leads to a conservative evaluation of the relationship between thermal tolerance breadth and range size. Lower latitude regions are, in general, more thermally stable year-round, likely making the seasonal timing of assessment of thermal tolerance less important in these areas. Although higher latitude regions are more thermally variable throughout the year, the assessment of CT_{min} during the warmer part of the year should tend to underestimate the thermal tolerance breadth in these locations, as cold tolerance would be expected to be greater (lower CT_{min} values) over winter compared with summer. None of the foregoing is to downplay the importance of overwintering physiology and its relationship with population growth (Boggs and Inouye 2012, Lynch et al. 2014), but simply provides a rationale for how our results are likely to be robust to the seasonal timing of CT_{min} assessment.

We used the critical thermal tolerance as our thermal performance metric, which defines an ecological death, where an ant, through heat or cold-induced loss of muscular coordination, could not move itself to a thermal refuge in nature (Terblanche et al. 2011). This metric is distinct from the lethal thermal limit, which defines a physiological death. Although it has been suggested that critical thermal limits and lethal thermal limits are underlain by different sub-cellular physiological mechanisms and may be under separate genetic control (Hoffmann et al. 2003), at the whole-organism level, the critical and lethal thermal limits are often positively correlated (Andersen et al. 2015), including in ants (Jumbam et al. 2008).

For each species, we computed the mean upper and lower critical thermal tolerances across their geographic range. In a minority of cases (CT_{max} : $n = 31$; CT_{min} : $n = 7$) where we did

not have replication of thermal tolerance values across the geographic range, we used a single critical thermal tolerance value from near the center of the geographic range (see Table A1). For some ant species, geographic clines in thermal tolerance values are apparent, *i.e.* with increased cold tolerance and decreased heat tolerance at higher latitudes, but this is not true for all ant species (Diamond et al. 2012b). Because we were interested in the species-level relationship between thermal tolerance and range size, we homogenized over intra-specific variation in thermal tolerance in this study.

Like many global-scale studies of thermal physiological traits (Huey et al. 2012), our data are biased towards higher latitudes (CT_{\max} : $n = 10$ tropical, $n = 24$ subtropical, and $n = 57$ temperate; CT_{\min} : $n = 3$ tropical, $n = 11$ subtropical, $n = 27$ temperate; Fig. A1). However, our study does not necessarily rely on evaluating the relationship between range size and tolerance breadth for tropical versus temperate species *per se*. Rather, we are interested in how range size and thermal tolerance breadth are related across a latitudinal cline in temperature.

Evolutionary history

To account for non-independence owing to shared evolutionary history among species, we computed the phylogenetic independent contrasts (PICs) for geographic range and thermal tolerance traits using the *pic* function from the *ape* package in R (Paradis et al. 2004). We used a genus-level ant phylogeny (Moreau and Bell 2013), and interpolated unknown species relationships as terminal polytomies (thermal tolerance breadth and lower thermal tolerance: 19 species; upper thermal tolerance only: 53 species). PICs assume a Brownian motion (random walk) model of trait evolution (Felsenstein 1985), and while other methods including phylogenetic generalized least squares (PGLS) models are more flexible in that they do not

necessarily assume Brownian motion (either by allowing lower phylogenetic signal or different models of trait evolution), we preferred PICs for two reasons. First, by using PICs, we avoided making assumptions regarding the assignment of response and predictor variables among our geographic range and thermal tolerance traits. Second, we avoided making the assumption that the relationship between geographic range and thermal tolerance traits (after phylogenetic correction) was linear (see below).

In addition to examining the correlation between phylogenetically independent contrasts for geographic range and thermal tolerance traits, we also explored phylogenetic signal, or the tendency of closely related species to resemble one another with respect to their trait values, in each of the thermal tolerance traits and range size alone. We used the *phyloSignal* function from the *phylosignal* package in R (Keck et al. 2016), to quantify multiple measures of phylogenetic signal. Two of these measures assume a Brownian motion model of trait evolution: Pagel's λ which ranges from values of 0, indicating no phylogenetic signal (a star phylogeny), to 1, indicating high phylogenetic signal (where the trait distribution across the phylogeny conforms to a model of Brownian trait evolution) (Pagel 1999), and Blomberg's K which ranges from 0 to > 1 , with values greater than one indicating traits are more conserved than expected under a Brownian motion model (Blomberg et al. 2003). Two other measures are based on autocorrelation indices and do not assume a specific model of trait evolution: Moran's I and Abouheif's C_{mean} (Münkemüller et al. 2012).

Statistical analyses

All statistical analyses were performed using R version 3.3.2 (R Core Team 2016). Prior to computing the phylogenetic independent contrasts, we natural log transformed range size to

satisfy the assumptions for this analysis. In the development of independent contrasts, (Felsenstein 1985) assumed the traits were drawn from a multivariate normal distribution, leading to a linear relationship between trait values and subsequently, their contrasts. Non-linearity in the relationships among traits can increase scatter in the relationships between the independent contrasts, leading to incorrect conclusions regarding the nature and strength of the relationship (Quader et al. 2004).

We took the absolute value of the latitudinal position of the geographic range centroid prior to computing the phylogenetic independent contrasts, as we were interested in comparisons of higher versus lower latitude ant species (*i.e.*, their distance from the equator), rather than the precise latitudinal position of the species. Because some of the phylogenetic independent contrasts had a few values of larger magnitude (Fig. 1), we used Spearman's rank correlations to examine the relationship between independent contrasts of geographical range and thermal tolerance attributes (Pearson's parametric correlations can be sensitive to values of large magnitude, though we found very similar results using both types of correlation coefficient in our analyses). We used a similar approach to analyze the relationship between range size and upper and lower thermal tolerances, and between latitudinal position and thermal tolerance breadth. The 95% confidence interval for the rank correlations were obtained using the *CIrho* function from the *mada* package in R (Doebler 2015).

Supporting Results

Correlates of latitudinal position

We found a significant positive correlation between the latitudinal position of the range centroid and range size (r_s and 95% CI = 0.49 [0.21,0.70], $P = 0.0015$, $df = 38$). We likewise

found a significant positive correlation between the latitudinal position of the range centroid and thermal tolerance breadth (r_s and 95% CI = 0.39 [0.089,0.63], $P = 0.013$, $df = 38$). Together these results indicate that ant species with lower latitudinal positions of the center of their range have both smaller geographic ranges and narrower tolerance breadths.

Phylogenetic signal in thermal tolerance traits and range size

In general, we found high phylogenetic signal (consistent with a Brownian model of trait evolution) for thermal tolerance traits (upper and lower thermal tolerance and tolerance breadth), but low phylogenetic signal for range size (Table S2). The limited, but growing literature describing phylogenetic signal in thermal tolerance traits paints a somewhat complex picture, though there does appear to be an emerging trend of high phylogenetic signal in upper thermal tolerance (with some exceptions). *Drosophila* exhibit quite high phylogenetic signal in CT_{max} (Kellermann et al. 2012), as do snails (Marshall et al. 2015) and lizards (Grigg and Buckley 2013). Intertidal crabs also show high phylogenetic signal in upper thermal tolerance, but low signal in lower thermal tolerance (Faria et al. 2017). Rolled-leaf beetles are an exception to this pattern, exhibiting little role for phylogeny in shaping CT_{max} (García-Robledo et al. 2016). Our results for ants further support the case for high phylogenetic signal in CT_{max} . The role of evolutionary history in shaping CT_{min} was less clear, as estimates of the strength of phylogenetic signal appeared to strongly depend on the metric used (Table A2), and Pagel's λ , a robust indicator of phylogenetic signal (Münkemüller et al. 2012), was not significantly different from zero, despite a high estimated value.

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Table A1. Geographic range size (km²), number of occurrence records used in the estimation of range size, and upper and lower thermal tolerance (CT_{max}, CT_{min}, °C) of ant species. The ID column is for comparison with Figure A1, which shows the geographic position of the range centroid of each species.

| ID | Species | Range size | Number of occurrence records | CT _{max} | CT _{min} |
|----|-----------------------------------|-------------|------------------------------|-------------------|-------------------|
| 1 | <i>Acromyrmex versicolor</i> | 611533.60 | 34 | 41.00 | NA |
| 2 | <i>Aphaenogaster carolinensis</i> | 667312.27 | 137 | 43.04 | 7.01 |
| 3 | <i>Aphaenogaster floridana</i> | 300710.82 | 48 | 44.93 | 6.89 |
| 4 | <i>Aphaenogaster fulva</i> | 1959424.86 | 226 | 43.45 | 6.11 |
| 5 | <i>Aphaenogaster lamellidens</i> | 1565672.48 | 109 | 42.86 | 6.59 |
| 6 | <i>Aphaenogaster occidentalis</i> | 2037332.09 | 640 | 43.99* | NA |
| 7 | <i>Aphaenogaster picea</i> | 2025171.27 | 312 | 40.59 | 1.50 |
| 8 | <i>Aphaenogaster rudis</i> | 2358271.20 | 695 | 42.48 | 4.39 |
| 9 | <i>Aphaenogaster senilis</i> | 265552.88 | 41 | 46.00* | NA |
| 10 | <i>Atta cephalotes</i> | 11519939.60 | 548 | 49.50* | NA |
| 11 | <i>Atta sexdens</i> | 9584740.65 | 81 | 44.00* | NA |
| 12 | <i>Brachymyrmex depilis</i> | 11161707.16 | 458 | 42.93 | 3.65 |
| 13 | <i>Camponotus americanus</i> | 2396264.64 | 280 | 42.99 | 6.99 |
| 14 | <i>Camponotus castaneus</i> | 2345166.12 | 227 | 41.91 | 7.68 |
| 15 | <i>Camponotus chromaiodes</i> | 1453948.03 | 197 | 42.54 | 6.14 |
| 16 | <i>Camponotus cruentatus</i> | 428324.99 | 48 | 48.00* | NA |
| 17 | <i>Camponotus foreli</i> | 235307.96 | 18 | 48.00* | NA |
| 18 | <i>Camponotus herculeanus</i> | 13541842.50 | 614 | 42.75 | NA |
| 19 | <i>Camponotus nearcticus</i> | 6690662.39 | 440 | 41.51 | 4.08 |
| 20 | <i>Camponotus novaeboracensis</i> | 3939715.49 | 100 | 40.00 | NA |
| 21 | <i>Camponotus pennsylvanicus</i> | 5054684.69 | 905 | 41.83 | 5.09 |
| 22 | <i>Camponotus subbarbatus</i> | 1343666.26 | 179 | 41.67 | 5.05 |
| 23 | <i>Camponotus sylvaticus</i> | 140563.28 | 22 | 46.00* | NA |
| 24 | <i>Camponotus vicinus</i> | 3867976.52 | 1204 | 45.90* | NA |
| 25 | <i>Cataglyphis bombycina</i> | 5994397.31 | 27 | 53.60* | NA |
| 26 | <i>Cataglyphis iberica</i> | 145969.46 | 14 | 52.00* | NA |
| 27 | <i>Crematogaster californica</i> | 376167.92 | 63 | 48.47* | NA |
| 28 | <i>Crematogaster coarctata</i> | 542564.46 | 210 | 48.13* | NA |
| 29 | <i>Crematogaster inflata</i> | 19432.62 | 18 | 47.75 | NA |
| 30 | <i>Crematogaster lineolata</i> | 3882035.26 | 586 | 45.35 | 6.52 |
| 31 | <i>Dolichoderus cuspidatus</i> | 41285.29 | 17 | 45.50 | NA |
| 32 | <i>Dorymyrmex bureni</i> | 431122.88 | 81 | 46.40 | 7.69 |
| 33 | <i>Dorymyrmex insanus</i> | 4744051.41 | 437 | 47.60* | NA |
| 34 | <i>Eciton burchellii</i> | 4397006.75 | 341 | 46.60* | NA |
| 35 | <i>Forelius mccooki</i> | 3634058.53 | 166 | 50.95* | NA |
| 36 | <i>Formica aserva</i> | 6007343.27 | 450 | 40.00 | NA |
| 37 | <i>Formica moki</i> | 595624.15 | 181 | 46.79* | NA |

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|----|----------------------------------|-------------|------|--------|--------|
| 38 | <i>Formica neogagates</i> | 6464916.93 | 631 | 40.00 | NA |
| 39 | <i>Formica obscuripes</i> | 3344630.92 | 753 | 41.58 | NA |
| 40 | <i>Formica pallidefulva</i> | 4372067.55 | 418 | 45.61 | 6.21 |
| 41 | <i>Formica pergandei</i> | 3713739.76 | 73 | 40.00 | NA |
| 42 | <i>Formica podzolica</i> | 3427241.75 | 302 | 41.63 | NA |
| 43 | <i>Formica polycтена</i> | 40081.51 | 634 | 46.80* | NA |
| 44 | <i>Formica subsericea</i> | 4825034.89 | 672 | 42.68 | 4.76 |
| 45 | <i>Iridomyrmex rufoniger</i> | 5860176.20 | 646 | 50.00* | NA |
| 46 | <i>Lasius alienus</i> | 26843694.00 | 1408 | 41.24 | 3.30 |
| 47 | <i>Lasius fallax</i> | 2669247.13 | 112 | 39.75 | NA |
| 48 | <i>Lasius nearcticus</i> | 3866971.65 | 186 | 36.61 | 0.89 |
| 49 | <i>Lasius neoniger</i> | 7402325.28 | 981 | 38.34 | 1.84 |
| 50 | <i>Liometopum luctuosum</i> | 2007500.23 | 242 | 48.09* | NA |
| 51 | <i>Melophorus bagoti</i> | 682876.21 | 13 | 56.70 | 13.80 |
| 52 | <i>Messor bouvieri</i> | 514509.19 | 48 | 44.00* | NA |
| 53 | <i>Messor capitatus</i> | 489883.19 | 36 | 44.00* | NA |
| 54 | <i>Monomorium minimum</i> | 5707660.57 | 608 | 44.88 | 4.75 |
| 55 | <i>Myrmecina americana</i> | 5203518.38 | 437 | 42.33 | 5.04 |
| 56 | <i>Myrmecocystus depilis</i> | 319663.67 | 41 | 46.70 | 11.60* |
| 57 | <i>Myrmecocystus mimicus</i> | 2063868.51 | 110 | 48.05 | 11.20* |
| 58 | <i>Myrmecocystus navajo</i> | 914291.79 | 39 | 43.70* | NA |
| 59 | <i>Myrmecocystus romainei</i> | 1133440.44 | 60 | 45.53 | 10.20 |
| 60 | <i>Myrmica americana</i> | 4101784.65 | 366 | 38.00 | NA |
| 61 | <i>Myrmica punctiventris</i> | 2016902.93 | 324 | 41.77 | 4.73 |
| 62 | <i>Nylanderia faisonensis</i> | 1305773.33 | 204 | 42.41 | 4.55 |
| 63 | <i>Ochetellus flavipes</i> | 1734781.80 | 33 | 44.70* | 11.20* |
| 64 | <i>Pheidole dentata</i> | 3216589.53 | 253 | 45.04 | 7.65 |
| 65 | <i>Pheidole noda</i> | 332426.29 | 33 | 39.40 | NA |
| 66 | <i>Pheidole tenuinodis</i> | 74157.38 | 12 | 42.90* | 8.50* |
| 67 | <i>Plagiolepis pygmaea</i> | 4857697.94 | 94 | 40.00* | NA |
| 68 | <i>Pogonomyrmex barbatus</i> | 5337132.38 | 853 | 46.50 | NA |
| 69 | <i>Pogonomyrmex californicus</i> | 1834358.17 | 778 | 52.32 | 4.66* |
| 70 | <i>Pogonomyrmex desertorum</i> | 706415.77 | 214 | 53.30* | NA |
| 71 | <i>Pogonomyrmex rugosus</i> | 3355565.74 | 993 | 52.69 | 4.77* |
| 72 | <i>Pogonomyrmex subnitidus</i> | 546243.04 | 93 | 49.00* | NA |
| 73 | <i>Polyrhachis bihamata</i> | 2450990.98 | 15 | 45.00 | NA |
| 74 | <i>Prenolepis imparis</i> | 7831666.82 | 799 | 38.89 | 0.97 |
| 75 | <i>Pristomyrmex punctatus</i> | 2616938.61 | 83 | 41.73 | NA |
| 76 | <i>Proceratium silaceum</i> | 2005561.80 | 82 | 40.00 | NA |
| 77 | <i>Rhytidoponera convexa</i> | 1737304.79 | 53 | 48.00* | NA |
| 78 | <i>Solenopsis aurea</i> | 1240226.99 | 86 | 42.70* | NA |
| 79 | <i>Solenopsis molesta</i> | 7723133.92 | 1004 | 42.41 | 4.81 |
| 80 | <i>Solenopsis xyloni</i> | 6847754.81 | 326 | 44.95 | NA |
| 81 | <i>Stenamma impar</i> | 1753594.56 | 95 | 40.64 | 2.81 |

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|----|-------------------------------------|-------------|------|--------|--------|
| 82 | <i>Stenamma schmittii</i> | 635712.85 | 66 | 40.36 | 3.13 |
| 83 | <i>Strumigenys rostrata</i> | 954831.73 | 46 | 39.50 | NA |
| 84 | <i>Tapinoma nigerrimum</i> | 795080.99 | 17 | 42.00* | NA |
| 85 | <i>Tapinoma sessile</i> | 8550904.85 | 1887 | 44.03 | 5.42 |
| 86 | <i>Temnothorax curvispinosus</i> | 2189890.28 | 349 | 44.86 | 4.45 |
| 87 | <i>Temnothorax longispinosus</i> | 1370757.00 | 271 | 43.40 | 4.01 |
| 88 | <i>Temnothorax nevadensis</i> | 1504870.62 | 302 | 47.83* | NA |
| 89 | <i>Temnothorax pergandei</i> | 5359361.68 | 243 | 46.75 | NA |
| 90 | <i>Tetramorium sericeiventre</i> | 14095138.54 | 395 | 47.90* | 11.60* |
| 91 | <i>Trachymyrmex septentrionalis</i> | 2091637.33 | 123 | 41.23 | NA |

* Tolerances estimated from the center of the geographic range, rather than from multiple populations throughout the species geographic range

Table A2. Phylogenetic signal in thermal tolerance traits and range size. Four indices of phylogenetic signal and their associated p-values are reported: Abouheif's C_{mean} , Moran's I , Blomberg's K and Pagel's λ . Phylogenetic signal was calculated on the dataset where all values of thermal tolerance traits and range size were available ($n = 41$); results were similar using the larger dataset ($n = 91$) for CT_{max} and range size.

| Trait | Phylogenetic signal index | Phylogenetic signal | P value |
|-------------------|---------------------------|---------------------|-----------|
| CT_{min} | C_{mean} | 0.208 | 0.013 |
| | I | 0.275 | 0.006 |
| | K | 0.0923 | 0.001 |
| | λ | 0.910 | 0.0763 |
| CT_{max} | C_{mean} | 0.249 | 0.004 |
| | I | 0.364 | 0.003 |
| | K | 0.146 | 0.001 |
| | λ | 0.944 | 0.001 |
| Tolerance breadth | C_{mean} | 0.370 | 0.005 |
| | I | 0.538 | 0.001 |
| | K | 0.213 | 0.001 |
| | λ | 0.942 | 0.001 |
| Range size | C_{mean} | 0.0244 | 0.276 |
| | I | 0.0872 | 0.110 |
| | K | 0.0322 | 0.136 |
| | λ | 0 | 1 |

