Habitat disturbance selects against both small and large species across varying climates

H. Gibb[1*], N.J. Sanders[2], R.R. Dunn[3], X. Arnan[4], H.L. Vasconcelos[5], D.A. Donoso[6], A.N. Andersen[7], R.R. Silva[8], T.R. Bishop[9,10], C. Gomez[11], B.F. Grossman[1], K.M. Yusah[12], S.H. Luke[13,14], R. Pacheco[5], J. Pearce-Duvet[15], J. Retana[16], M. Tista[17], & C.L. Parr[9,18]

[1*]Department of Ecology, Environment and Evolution, La Trobe University, Melbourne 3086, Victoria, Australia; h.gibb@latrobe.edu.au; b.grossman@latrobe.edu.au

[2]Center for Macroecology, Evolution, and Climate, University of Copenhagen, Copenhagen Denmark; nathan.sanders@snm.ku.dk

[3]Department of Biology, North Carolina State University, Raleigh, NC 27695, USA; rroberdeaudunn@gmail.com

[4]Departamento de Botânica, Universidade Federal Pernambuco, Av. Prof. Moraes Rego s/no, Cidade Universitária, 50670-901, Recife, PE, Brazil; xavi.arnan@gmail.com

[5]Institute of Biology, Federal University of Uberlândia (UFU), CP 593, 38400-902 Uberlândia, MG, Brazil; heraldo@umuarama.ufu.br; rpneco@yahoo.com.br

[6]Universidad de Cuenca, Facultad de Ciencias Agropecuarias, Ave. 12 de Abril s/n, Cuenca, Ecuador; david_donosov@yahoo.com

[7]CSIRO Land & Water, PMB 44 Winnellie, NT 0822, Australia; alan.andersen@csiro.au

[8]Coordenação de Ciências da Terra e Ecologia, Museu Paraense Emílio Goeldi, Av. Perimetral 1901, 66077-830, Belém, PA, Brazil; rogeriorosas@gmail.com

[9]Department of Earth, Ocean and Ecological Sciences, University of Liverpool, Liverpool, L69 3GP, UK; kate.parr@liverpool.ac.uk; t.r.bishop@liverpool.ac.uk

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

[11]Department of Environmental Sciences, University of Girona, Campus de Montilivi, 17071 – Girona, Spain; crisanto.gomez@udg.edu

[12]Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Jalan UMS, 88400 Kota Kinabalu, Sabah, Malaysia; kalsum.myusah@gmail.com

[13]School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK; sarah.h.luke@gmail.com

[14]Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK.

[15]Department of Biology, University of Utah, 257 S 1400 E, Salt Lake City, UT 84112, USA; jmcolette.pearce@gmail.com

[16]CREAF, Cerdanyola del Vallès, 08193 Catalunya, Spain; javier.retana@uab.es

[17]Department of Tropical Ecology and Animal Biodiversity, University of Vienna, Rennweg 14, Vienna 1030, Austria; melanie.tista@univie.ac.at

[18]Department of Animal, Plant and Environmental Sciences, University of Witwatersrand, Private Bag X3, Wits 2050, South Africa.

Corresponding author: Heloise Gibb, Department of Ecology, Environment and Evolution, La Trobe University, Melbourne, Victoria 3086, Australia; Ph: +61394792278; h.gibb@latrobe.edu.au.

AUTHOR CONTRIBUTIONS

HG coordinated the study, analysed the data and wrote the first draft. HG, NJS, RDD and CLP conceived of and designed the study and helped draft the manuscript. All authors contributed data, revised the article critically and gave final approval of the version to be published.

ABSTRACT

Global extinction drivers, including habitat disturbance and climate change, are thought to affect larger species more than smaller species. However, it is unclear if such drivers interact to affect assemblage body size distributions. We asked how these two key global change drivers differentially affect the interspecific size distributions of ants, one of the most abundant and ubiquitous animal groups on earth. We also asked whether there is evidence of synergistic interactions and whether effects are related to species' trophic roles. We generated a global dataset on ant body size from 331 local ant assemblages collected by the authors across a broad range of climates and in disturbed and undisturbed habitats. We used head length (range: 0.22 – 4.55 mm) as a surrogate of body size and classified species to trophic groups. We used generalized linear models to test whether body size distributions changed with climate and disturbance, independent of species richness. Our analysis yielded three key results: 1) climate and disturbance showed independent associations with body size; 2) assemblages included more small species in warmer climates and fewer large species in wet climates; and 3) both the largest and smallest species were absent from disturbed ecosystems, with predators most affected in both cases. Our results indicate that temperature, precipitation and disturbance have differing effects on the body size distributions of local communities, with no evidence of synergistic interactions. Further, both large and small predators may be vulnerable to global change, particularly through habitat disturbance.

Key words: ants, body size, homogenisation, global change, local assemblage, predators.

INTRODUCTION

The current rate of extinctions, driven by habitat disturbance, climate change and species invasions, is so extensive that it has been dubbed the "sixth mass extinction" (Barnosky, et al. 2011). However, not all species are equally vulnerable to global change-driven extinction. Body size is considered the most important physiological and ecological trait of an animal, and is linked to energy use, abundance and geographic range size (Calder 1984, Lomolino and Perault 2007, Schmidt-Nielsen 1984). Larger species are thought to be more susceptible to extinction than are smaller species because they require more resources and take longer to mature (McCain and King 2014, Savage, et al. 2004). Evidence from a range of sources suggests that declines in assemblage body size through a loss of large species or selection against large body size within a species are a near universal response to ongoing climate change (Gardner, et al. 2011, Sheridan and Bickford 2011, Teplitsky and Millien 2014). Similar body size shrinkage may also result from habitat disturbance (Senior, et al. 2013). However, smaller species might also be vulnerable to global change (Ewers, et al. 2015). Changes in body size could alter species interactions and ecological functions (Sheridan and Bickford 2011), with effects potentially cascading throughout ecosystems (Chown and Gaston 2010, Dirzo, et al. 2014, Naeem 2012).

A key challenge for our understanding of the impacts of global change drivers such as habitat disturbance and climate change on biodiversity is that they likely do not act in isolation (Brook, et al. 2008, Hof, et al. 2011). Interactions among these drivers are poorly studied (Mantyka-Pringle, et al. 2012, Sala, et al. 2000), but understanding whether they act independently, additively, or synergistically is critical to facilitate accurate forecasts of the effects of global change on biodiversity and the functions it provides (Gibb, et al. 2015a). In particular, if the drivers act synergistically then
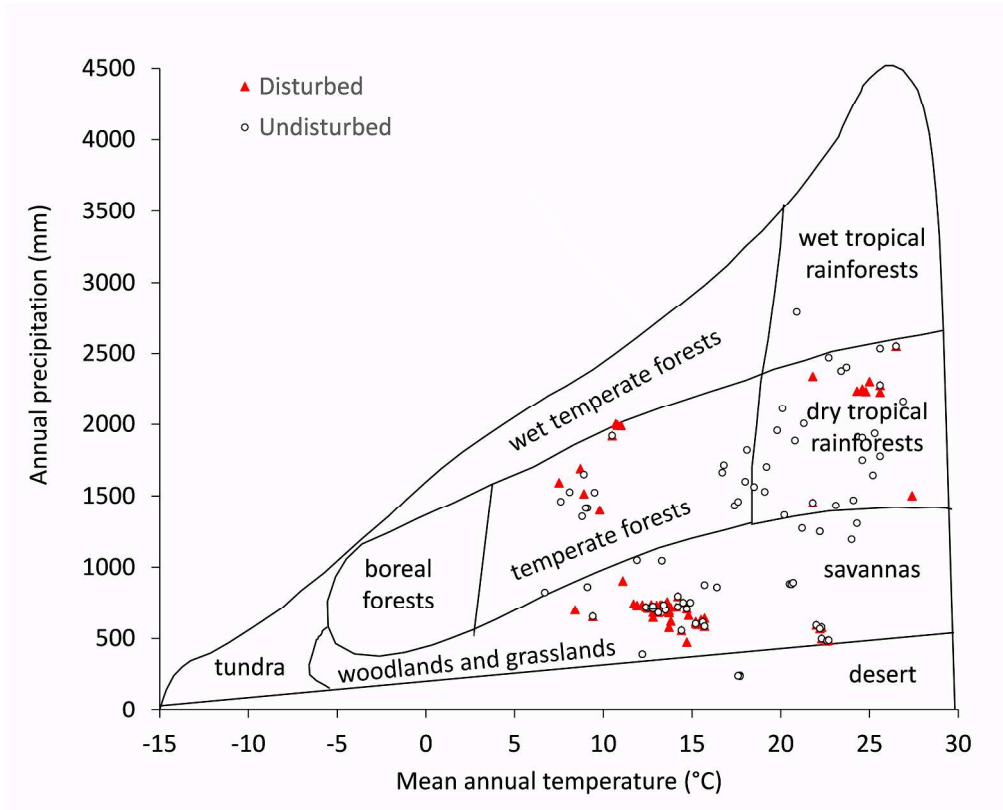
Figure 1: Distribution of the 331 study sites across Whittaker's
biomes. 793x640mm (96 x 96 DPI)

ecological change under a changing climate might be substantially greater than currently predicted. However, no global-scale studies have investigated the potential for multiple global change drivers to act synergistically on biodiversity (Brook, et al. 2008) through the loss of species, based on body size.

Here, we present the first global test of the combined and interactive effects of climate and habitat disturbance on body sizes of more than 2000 ant species from 331 local assemblages from all the world's major biomes (except tundra) (Fig. 1). We focus on ants because they are ubiquitous and abundant, range in body size over nearly three orders of magnitude (from 0.75 mm to nearly 40 mm in length), and provide or mediate many key ecosystem functions and processes (Del Toro, et al. 2012, Zelikova, et al. 2011), both in natural ecosystems and in those dominated by humans (Penick, et al. 2015). We constructed a global dataset of local assemblages and morphological measures (Parr, et al. 2017) (http://globalants.org) including head length, previously shown to be a strong correlate of body size (Gibb and Parr 2013, Weiser and Kaspari 2006). Previous analyses showed that disturbance and climate interact to shape species richness and evenness (Gibb, et al. 2015a), but it is unclear what role species traits may have in driving global patterns. We use this unique dataset to ask how these two key global change drivers differentially affect the interspecific size distributions of one of the most abundant (King 2013) and ubiquitous animal groups on earth, whether there is evidence of synergistic interactions and whether effects are related to species' trophic roles.

METHODS

Assemblage data

The data used here built upon a database of net species richness and abundance for assemblages, expanded upon to include species traits (Dunn, et al. 2007, Dunn, et al. 2009, Gibb, et al. 2015a,

Gibb, et al. in press, Parr, et al. 2017). For this study, we used data from 371 localities around the world, collected between 1996 and 2012 in 21 separate studies (Fig. 1). All studies met the following criteria: 1) the ground-foraging ant assemblage was sampled using baits, hand collecting, litter sampling, pitfalls or mixed methods; 2) a minimum of three species were sampled and measured; 3) sampling was not trophically or taxonomically limited (e.g., the study was not focused on only seed-harvesting ants); and 4) assemblages that included one of the top five invasive ants (*Anoplolepis gracilipes*, *Linepithema humile*, *Pheidole megacephala*, *Solenopsis invicta* or *Wasmannia auropunctata*) outside their native range were excluded. Invaded assemblages were excluded as invasive species alter ant species composition (Holway, et al. 2002), which might lead to changes in body size distributions. We used only presence-absence data in this study. Assemblages were located in Oceania (23%), Europe (29%), North America (12%), Africa (13%), South America (7%) and Asia (16%). Data from 40 disturbed localities at high latitudes were removed from the analyses as there were no undisturbed localities at similarly high latitudes, leaving 331 assemblages for analysis.

Body size data

Body size data for each species or morphospecies in each assemblage were available for up to six individuals for species with monomorphic workers and up to ten individuals for species with polymorphic workers. Means of these values were used for each species and we do not consider intraspecific variation in body size here. For dimorphic workers, soldiers were relatively rare in the dataset and were not measured. Head length (the maximum longitudinal length from the most anterior part of the clypeus to the posterior cephalic margin, in full face view) was used as a measure of ant body size (Parr, et al. 2017) (range: 0.22 mm – 4.55 mm). Head length is a strong correlate of

body size for ants (Gibb and Parr 2013, Weiser and Kaspari 2006). For assemblages where head length was not available, but Weber's length (Parr, et al. 2017, Weber 1938) (http://globalants.org) was (16% of species across all assemblages), head length was estimated from the relationship between Weber's length and head length, calculated from our data (n = 1539 species or morphospecies with both measures, $R^2 = 0.93$, $\log_{10}$ head length = -0.095+0.811*$\log_{10}$ Weber's length). For some assemblages (5% of localities), body size had not been measured, but body size measures for the same species collected in the same country were used. Assemblage body size was considered in terms of interspecific variance, size of the largest and smallest species and in terms of body size percentiles (across species), as detailed in the data analysis section.

Although colony size is also considered a critical measure of body size in colonial organisms, such as ants (Kaspari 2005), morphological measures of ant body size have previously been shown to respond to disturbance and climate gradients (Cushman, et al. 1993, Gibb, et al. 2015b, Yates, et al. 2014) and are correlated with important traits such as mobility in complex environments, desiccation tolerance and metabolic rate (Gibb and Parr 2013, Gillooly, et al. 2001, Hood and Tschinkel 1990). Colony size would be another useful measure of ant 'body size', but we consider head length to be a key phenotypic trait of ants that interacts with the environment to determine organism success, similarly to non-eusocial organisms.

Environmental variables: climate, disturbance and covariates

Contemporary environmental variables were obtained from the WorldClim database (Hijmans, et al. 2004) at a spatial resolution of 30-arc second resolution (ca. 1 × 1 km) and were extracted using ArcGIS (ESRI 2010). The 1 km resolution was selected so that the environmental data would describe the conditions with high specificity for the site at which ants were sampled and the

surrounding environment. We used mean annual temperature (MAT: range: 6.7-27.4ºC), annual

precipitation (AP: 237-2791 mm), temperature range (TR: 8-29.6ºC) and precipitation variability

(PV: 9-104). Initial data exploration showed that most climate variables were strongly correlated (AP

– MAT: $r = 0.57$, $p < 0.0001$; AP – TR: $r = -0.86$, $p < 0.0001$; MAT – TR: $r = -0.81$, $p < 0.0001$),

although PV was not strongly correlated with any other climate variables ($r > 0.05$, $p > 0.3$).

Preliminary analyses showed that inclusion of PV did not improve the fit of models. We considered

it important to retain AP as an indicator of productivity due to water availability.   Although the

biological implications of MAT and TR differ (MAT is expected to affect a species' metabolic rate,

while TR is expected to affect a species' ability to withstand variable climates), we elected to include

MAT instead of TR because hypotheses describing body size responses to temperature are more

commonly based on MAT.

We categorized sites into two disturbance categories, based on study site descriptions by the

investigators: 1) undisturbed, i.e., no evidence of recent anthropogenic or natural disturbance; and 2)

disturbed, including disturbances such as forestry (native tree species), wind, fire (natural), fire

(anthropogenic), restoration (following clearing or mining), agriculture, cropping, grazing, forestry

(introduced tree species), mining, urban and recreation. Similarly to Gibb, et al. (2015a), we lumped

disturbance types because the dataset included a large variety of disturbances, which were often

restricted to individual studies, so analysis by disturbance type was not possible.

Hemisphere, trap type (baits, hand collecting, litter sampling, pitfalls, mixed), species richness and

data source (the study from which the data were obtained; random factor) were used as covariates in

our analyses. Hemisphere was included in analyses as it has previously been shown to be important

in determining ant community responses to climate (Dunn, et al. 2009). Species richness was

included to account for the possibility that the number of species at a site might affect the range of body size values through a sampling effect. Data source was included to account for differences in sampling effort and trap layout among studies. Latitude and elevation were excluded from analysis as they were correlated with mean annual temperature and MAT was considered to provide a more mechanistic explanation of determinants of body size.

Data analysis

Analyses were conducted in the R 3.03 statistical environment (R Development Core Team 2014). We tested the effect of a model consisting of the predictors climate (MAT and AP), disturbance (two levels: disturbed and undisturbed), their interactions and the covariates hemisphere, trap type and data source (random) on assemblage body size using general linear mixed models in the package nlme (Pinheiro, et al. 2013). The response variables were body size measures for each assemblage based on species presences (not weighted for abundance). All body size measures were $\log_{10}$-transformed because body size was left-skewed. We tested the ability of our model to predict the following body size variables, obtained for each of the 331 assemblages: 1) interspecific variance; 2) maximum and minimum body size (the largest and smallest species in the assemblage); and 3) body size percentiles (10th, 20th, 30th, 40th, 50th, 60th, 70th, 80th and 90th percentiles). We used body size percentiles in order to identify the component of the assemblage most affected by climate and disturbance. Variance in body size in disturbed and undisturbed habitats was similar (e.g., mean ± variance for the 50th percentile (median) was 0.802 ± 0.059 mm for disturbed habitats and 0.831 ± 0.064 mm for undisturbed habitats).

Preliminary analyses suggested that model selection could not identify a clear best model, so we retained the full model for all analyses. We report both marginal (fixed effects; $R^2_{GLMM(m)}$) and

conditional (fixed + random effects; $R^2_{GLMM(c)}$) R^2 values (Nakagawa 2013), calculated using the package MuMIn (Barton 2011). We used plots of estimates of model terms with confidence intervals to show effect size and significance of responses for each body size percentile and minimum and maximum head lengths (Fig. 2). We used a χ^2 test to determine whether the trophic function (Supplementary material Appendix 1, Table A1) of the smallest (minimum) and largest (maximum) ants differed between disturbed and undisturbed habitats.

RESULTS

Climate and disturbance acted independently to determine body size (Figs. 2a,b,c), i.e., there were no significant climate×disturbance interactions (Figs. 2e,f,g) (confidence intervals for model estimates all crossed zero). Disturbance was associated with larger minimum body size (marginally non-significant) and smaller maximum body size across species in a local assemblage, but had no effect on ants of intermediate sizes (Fig. 2a, 3a). The effects of disturbance were thus greatest at the extremes of body size (Fig. 2a). Different elements of climate acted differently on body size: the smaller ant species in an assemblage were (on average) smaller in the hottest climates (Figs. 2b, 3b), while the larger ant species in an assemblage were (on average) smaller where it was wetter (Figs. 2c, 3c). The median body size of ants declined as precipitation and temperature increased (Figs. 2b, c). Analysis of among-species (interspecific) variation in body size confirmed that it was lower in disturbed ecosystems and declined with increasing precipitation ($F_{(1,308)} = 17.4$, $p < 0.002$, Supplementary material Appendix 2, Table A2). There were no effects of hemisphere or the temperature×precipitation or temperature×precipitation×disturbance interactions on body size, suggesting that none of these factors affected the distribution of ant body sizes (Figs. 2d,g, i).
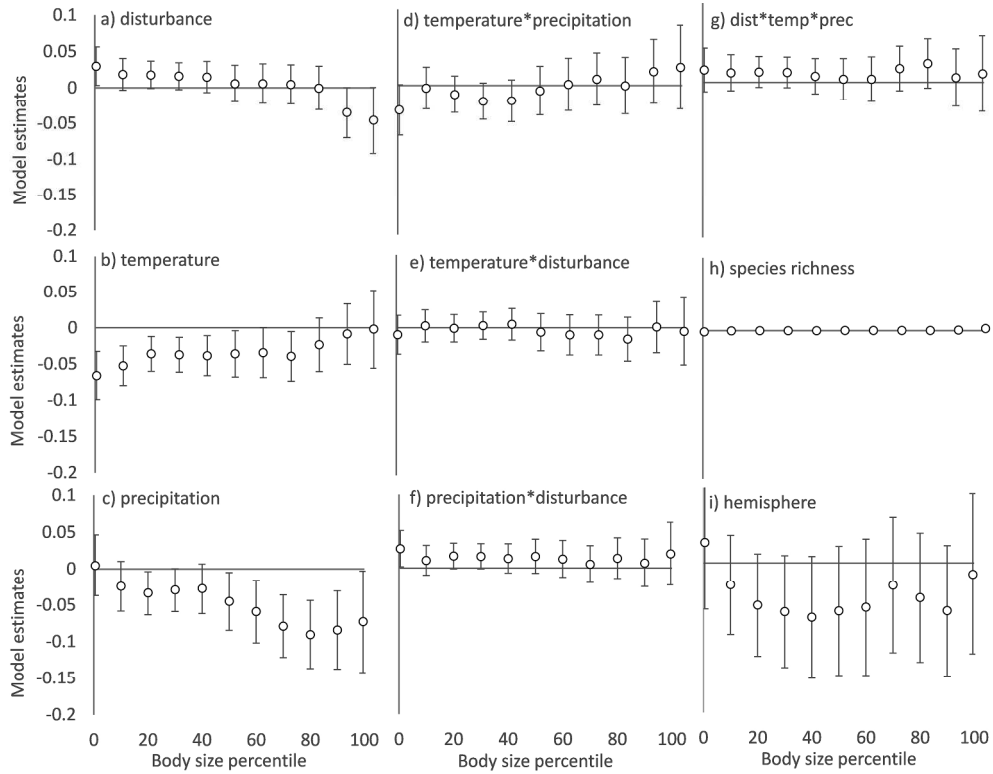
Figure 2: Estimates and confidence intervals from models testing the effects of climate and disturbance on head length by body size percentile and for minimum and maximum body size (placed at the 1st and 99th percentile, respectively) (n = 331). Estimates represent the effect size for the difference between the body size of species in disturbed and undisturbed habitats, with estimates > 0 indicating that species are larger in disturbed sites and estimates < 0 indicating that species are larger in undisturbed sites. Effects are significant where confidence intervals do not cross the line at zero.
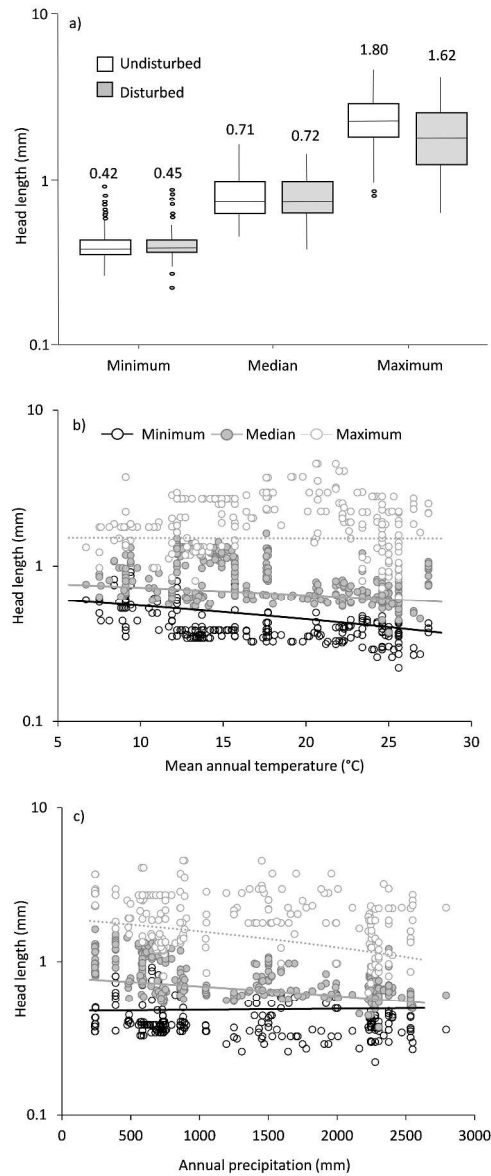
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Figure 3: Minimum, median and maximum head length (n = 331) plotted against: a) disturbance; b) mean annual temperature; and c) annual precipitation for ant assemblages examined in this study. a) shows predicted means above box plots of the raw data for disturbance, with the central line representing the median, boxes including the third and first quartiles, whiskers showing maxima and minima and circles representing suspected outliers. b) and c) show raw data (circles) and model predictions (lines); Y-axes are presented on a log10 scale.
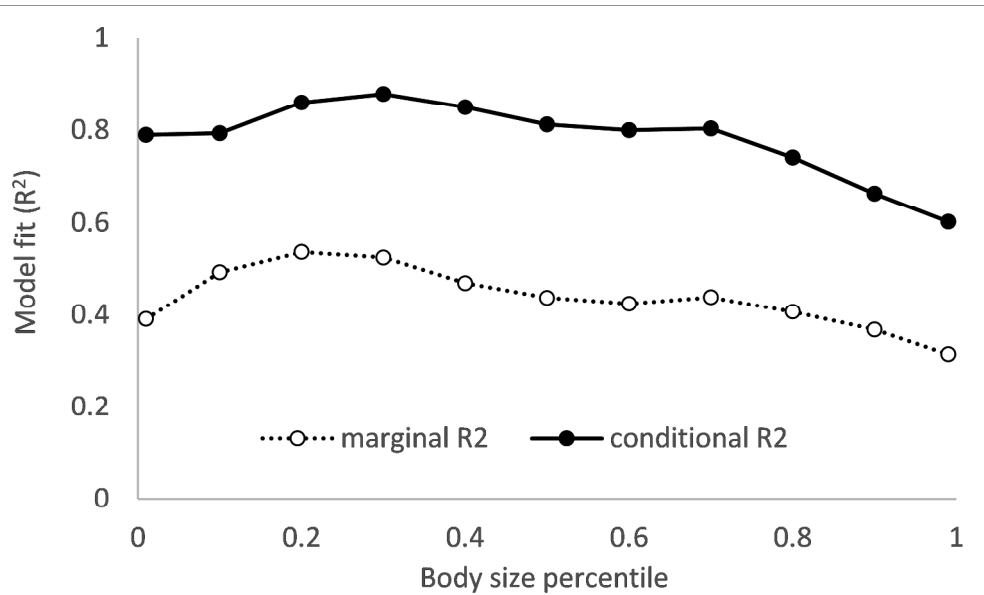
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Figure 4: Model fits (Marginal (R2m) and conditional (R2c) R-square) from general linear mixed models testing the effect of mean annual temperature, annual precipitation, disturbance and their interactions on the body size of ant assemblages (n = 331).

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Further, species richness also had no significant effect on ant body size, indicating that these findings were not the result of a sampling effect (Fig. 2h).

Measures of the fit of the model testing the effects of climate, disturbance and their interactions on ant body size revealed that model fit was lower for species with large body size (Fig. 4). This was true for marginal ($R^2_{GLMM(m)}$) and conditional ($R^2_{GLMM(c)}$) R^2 measures, representing model fit for fixed only and fixed + random factors, respectively. Model fit peaked for ant species in the 20th percentile for size ($R^2_{GLMM(m)} = 0.54$; $R^2_{GLMM(c)} = 0.86$) and was lowest for the largest ant species ($R^2_{GLMM(m)} = 0.29$; $R^2_{GLMM(c)} = 0.63$). Low model fit for larger ants suggests that unmeasured biotic or abiotic factors become increasingly important in determining the body size of larger species.

In disturbed ecosystems, the smallest species were less likely to be specialist predators ($\chi^2_{(1)} = 0.86$, p = 0.021) than in undisturbed ecosystems, while the largest species were less likely to be generalist predators ($\chi^2_{(1)} = 0.86$, p = 0.031) (Supplementary material Appendix 1, Table A1). Generalists that also acted as predators replaced the small specialist predators in disturbed ecosystems ($\chi^2_{(1)} = 0.95$, p = 0.003), but no specific trophic group replaced the large generalist predators.

DISCUSSION

The effects of global change are not consistent among species. Rather, some traits of species make them more or less susceptible to particular global change drivers. Here, we show that climate and habitat disturbance acted independently, and differentially affected small- and large-bodied species. In more than 300 local assemblages consisting of more than 2000 species, the smallest species were smaller at high temperatures, while the largest species were smaller under high precipitation. Importantly, disturbance was associated with a loss of the extremes of body size, homogenizing body

size distributions, i.e., both the largest and smallest species may be more prone to local extinction when habitats are altered. Body size is associated with a range of fundamental properties of organisms, and we showed that disturbance was most likely to result in the loss of both large and small predators. Changes in body size distributions are therefore likely to be associated with changes in the trophic function of assemblages, with the potential for these effects to cascade through ecosystems.

Climate was an important correlate of body size, but different elements of climate acted differently on the extremes of body size: the smallest species were, on average, smaller in the hottest climates, while the largest species were, on average, smaller where it was wetter. Such a result posits a novel prediction for the effects of climate change on biodiversity: increasing temperatures may select for species with certain traits, while altered precipitation regimes affect another suite of species with a different suite of traits. Although we could not test for this, within-species variation in response to climate (e.g., Caruso, et al. 2014, Ohlberger 2013) may also have played a role in the observed patterns. An obvious extension of our work would be to understand the ecological, behavioural, physiological and evolutionary mechanisms that led to this pattern. Independent of the mechanism, our findings highlight the importance of simultaneously considering the impacts of multiple climatic variables on functional traits.

The smallest species and individuals may occur in climates with high temperatures because the metabolic limitations associated with small body size (Gillooly, et al. 2001) make it difficult for very small animals to persist in cooler climates. For larger ants, several hypotheses might explain larger body size where it is drier (Fig. 2c). First, desiccation tolerance correlates strongly and positively with body size in insects as surface area to volume ratio increases, while cuticle thickness decreases

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with decreasing body size (Chown and Gaston 2010, Hood and Tschinkel 1990, Remmert 1981). Second, drier environments are likely to be less productive, resulting in a less reliable food base that might favor larger, more starvation-resistant species (starvation resistance hypothesis: (Cushman, et al. 1993, Kaspari and Vargo 1995)). Third, more complex habitats in wetter environments might limit the mobility of larger species, favoring reduced body size (e.g., Gibb and Parr 2013, Kaspari and Weiser 2000). Changes in precipitation associated with global warming will vary with region (Trenberth 2011). This means that precipitation-related selective pressures on body size will also differ.

A key finding of this global-scale study was that disturbance was associated with the smallest species in a local assemblage being larger but the largest species smaller (Fig. 2a), similar to the "island effect" (Lomolino 2005). The net result of disturbance was therefore a homogenisation of body size distributions within local communities. This is unlikely to be a result of selection within species as the disturbances examined were short-term. Homogenisation occurred through the loss of both the largest and smallest species from disturbed sites. Species richness was not a predictor of body size, so the reduction in the range of body sizes occupied in disturbed sites was not simply a result of fewer species being present. Such homogenisation may have remained undetected in previous studies because they have focused on the mean body size of species within a local assemblage, rather than considering body size distributions. Importantly, the homogenisation detected in our study is not the result of dominance of disturbed sites by invasive species because we excluded sites with invasive ant species. The homogenisation of body size demonstrated here is therefore independent of the homogenisation of composition commonly reported as a result of global change (Clavel, et al. 2010, McKinney 2006). We thus suggest that homogenisation in body size distributions is a further

consequence of global change in the Anthropocene (Dirzo, et al. 2014); this homogenisation may well be more general than any trend toward larger or smaller species per se. Homogenisation of body size will have broad-reaching consequences for ecosystem function because body size is closely tied to many functional traits, including desiccation resistance, population density and trophic roles (Chown and Gaston 2010, Robinson and Redford 1986).

For disturbance to act differently on the extremes of body size, selective pressures must depend on body size. Small species might be expected to be most affected by changes in microclimate (Chen, et al. 1999, Hardwick, et al. 2015) and microhabitat (Gibb and Parr 2013) and reduced food reliability in disturbed habitats (Ewers, et al. 2015). Some disturbance agents, such as wildfires (Arnan, et al. 2013), can lead to increases in ant body size because only the biggest species persist in simplified post-disturbance habitats. In contrast, other disturbance agents, such as logging, have been linked with reduced body size in ants, possibly because larger ants are more vulnerable to vertebrate predation, which increases after disturbance (Senior, et al. 2013). Alternatively, life history traits of larger species may increase their vulnerability to disturbance (Purvis, et al. 2000, Savage, et al. 2004). While the net effect of increasing disturbance is likely to be a homogenisation of body size, the cumulative effects of global change may lead to greater declines in large species (Fig. 5) as assemblages pass through the filters of increasing temperature (favoring small body size), increasing disturbance (homogenising body size within assemblages) and changes in precipitation (higher rainfall is associated with smaller maximum body sizes).

The importance of body size relative to other traits in determining responses to climate and disturbance might also vary with body size. The capacity of climate and disturbance to predict body size was lower for species with large body size (Fig. 4), suggesting that unmeasured biotic or abiotic
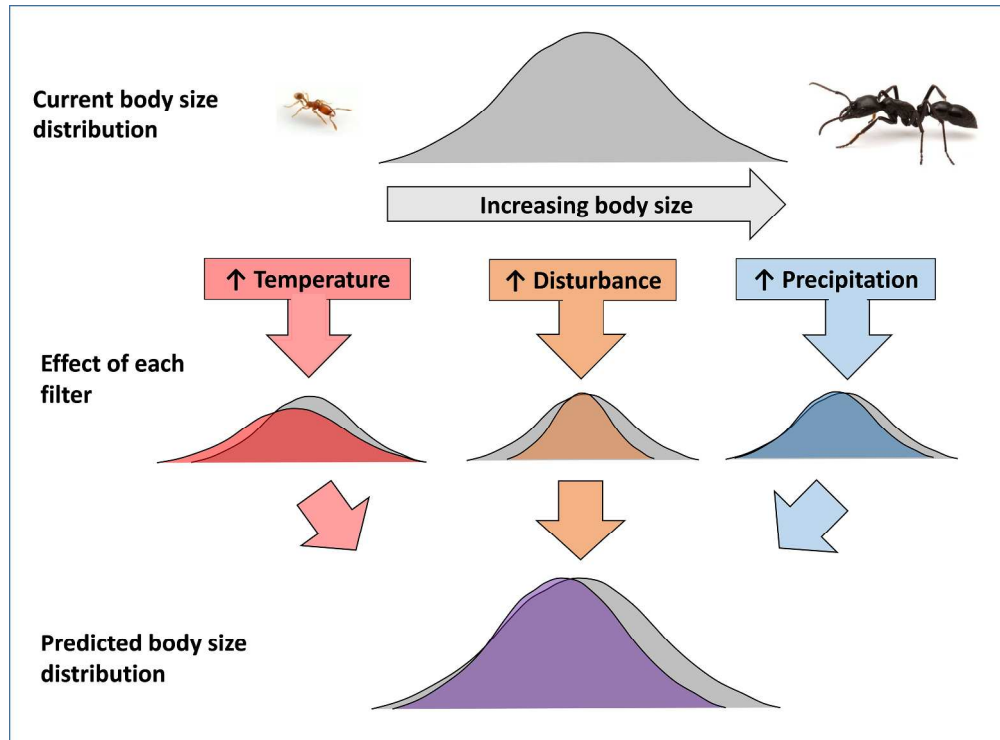
Figure 5: Schematic representation of the cumulative change in body size distributions from the current body size distribution (grey) that is predicted to result when ant assemblages pass through filters of increasing temperature (red: favoring small body size), disturbance (orange: homogenising body size within assemblages) and precipitation (blue: smaller maximum body size is associated with wetter climates). The net effect of global change is likely to be homogenisation of body sizes (purple), with stronger effects on larger species. Photo credit: Alex Wild.

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factors become increasingly important in determining the body size of larger species. A loss of larger species is commonly considered a universal effect of global change (Dirzo, et al. 2014, Gardner, et al. 2011), so it is critical that we identify any important unmeasured limitations for species with large body size.

Importantly, there are likely to be cascading effects of non-random extinctions based on body size in ants. For instance, in disturbed ecosystems, the smallest and largest species were less likely to be specialist or generalist predators, respectively, than in undisturbed ecosystems. Generalists that also acted as predators replaced the small specialist predators in disturbed ecosystems, but no trophic groups replaced the large generalist predators. Changes in body size distributions of the assemblage were thus largely due to the loss of both small and large predators and replacement by more generalized species. It is not surprising that specialist predators were lost: dietary specialization is associated with increased extinction risk because it limits the ability of species to respond to changes in food availability (Brook, et al. 2008, Davies, et al. 2004). Predators have previously been identified as particularly vulnerable to global change (Ewers, et al. 2015, Jellyman, et al. 2014, Senior, et al. 2013), and the loss of top predators has been associated with cascading effects on ecosystems (Borrvall and Ebenman 2006).

Conclusions

In conclusion, our global analysis yielded three key points. First, although numerous studies have documented how body size is related to temperature, our results demonstrate that habitat disturbance and precipitation have independent effects of similar magnitude. Second, the smallest ants are smaller at higher temperatures, and larger body size may be a casualty of climate change only in cold areas where rainfall also increases. This qualifies previous research focusing on endotherms that

suggests that a decrease in body size may be a universal response to climate change (Dirzo, et al. 2014, Sheridan and Bickford 2011). Third, large predators are especially vulnerable to changing climate and disturbance, with often dramatic consequences for the rest of the ecosystem (Borrvall and Ebenman 2006, Ewers, et al. 2015, Senior, et al. 2013). Our results demonstrate that both large and small predators are vulnerable to ongoing global change.

ACKNOWLEDGEMENTS:

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Supplementary material

Appendix S1. Trophic groups

Table A1: Allocation of ant genera to the trophic groups: predator, specialist predator (feeding on only a few taxa), predator + generalist, generalist forager, sugar feeder, sugar feeder + generalist, seed harvester and seed harvester + generalist.

Subfamily	Genus	Diet	Source
Amblyoponinae	*Amblyopone*	Specialist predator	Shattuck (1999)
Dolichoderinae	*Dolichoderus*	Sugar feeder + generalist	Shattuck (1999)
	Iridomyrmex	Sugar feeder + generalist	Shattuck (1999)
	Ochetellus	Generalist forager	Shattuck (1999)
	Tapinoma	Generalist forager	Shattuck (1999)
Dorylinae	*Dorylus*	Specialist predator	Schöning et al. (2005)
Ectatomminae	*Ectatomma*	Predator + generalist	Lachaud (1990)
	Gnamptogenys	Predator + generalist[1]	Delabie et al. (2000)
	Rhytidoponera	Predator + generalist	Shattuck (1999)
Formicinae	*Acropyga*	Sugar feeder	Johnson et al. (2001)
	Brachymyrmex	Sugar feeder + generalist	MacGown et al. (2007)
	Camponotus	Sugar feeder + generalist	Gibb (2012)
	Echinopla	Sugar feeder + generalist	Based on related genera
	Formica	Sugar feeder + generalist	Gibb & Johansson (2010)
	Lasius	Sugar feeder + generalist[2]	Offenberg (2001)
	Lepisiota	Generalist forager	Brown (2000)
	Melophorus	Seed harvester + generalist	Shattuck (1999)
	Notoncus	Generalist forager	Brown (2000)
	Paraparatrechina	Generalist forager	Shattuck (1999)
	Nylanderia	Generalist forager	La Polla et al. (2011)
	Plagiolepis	Sugar feeder + generalist	Shattuck (1999)
	Polyrhachis	Sugar feeder + generalist	Gibb (2012)
	Pseudolasius	Sugar feeder + generalist	Pfeiffer et al. (2013)
Myrmeciinae	*Myrmecia*	Predator + generalist	Shattuck (1999)
Myrmicinae	*Aphaenogaster*	Seed harvester + generalist	Brown (2000)
	Cardiocondyla	Seed harvester + generalist	Shattuck (1999)
	Carebara	Specialist predator	Shattuck (1999)
	Cephalotes	Sugar feeder + generalist	Hu et al. (2013)
	Crematogaster	Sugar feeder + generalist	Shattuck (1999)
	Leptothorax	Generalist forager	Brown (2000)

Subfamily	Genus	Diet	Source
	Lophomyrmex	Generalist forager	Rigato (1994)
	Mayriella	Seed harvester	Andersen (1991)
	Meranoplus	Seed harvester	Shattuck (1999)
	Messor	Seed harvester	Cerda & Retana (1994)
	Monomorium	Generalist forager	Brown (2000)
	Myrmica	Predator + generalist	Brown (2000)
	Myrmicaria	Predator + generalist	Wriedt et al. (2008)
	Ocymyrmex	Generalist forager	Marsh (1985)
	Oxyopomyrmex	Seed harvester	Hölldobler & Wilson (1990)
	Pheidole	Seed harvester + generalist	Shattuck (1999)
	Solenopsis	Generalist forager	Shattuck (1999)
	Strumigenys	Specialist predator	Hölldobler & Wilson (1990)
	Temnothorax	Sugar feeder + generalist	Fiedler et al. (2007)
	Tetramorium	Seed harvester + generalist	Shattuck (1999)
Paraponerinae	*Paraponera*	Sugar feeder + generalist	Young & Hermann (1980)
Ponerinae	*Anochetus*	Predator	Shattuck (1999)
	Cryptopone	Predator	Brown (2000)
	Hypoponera	Generalist forager	Shattuck (1999)
	Leptogenys	Specialist predator	Steghaus-Kovac & Maschwitz (1993)
	Odontomachus	Predator	Shattuck (1999)
	Odontoponera	Predator	Brown (2000)
	Pachycondyla	Predator	Brown (2000)
	Plectroctena	Predator	Hölldobler & Wilson (1990)
	Ponera	Predator	Brown (2000)
	Streblognathus	Specialist predator	Brown (2000)
Proceratiinae	*Discothyrea*	Specialist predator	Brown (1957)

[1]Also includes some specialist predators; [2]Social parasite;

Appendix S2. Variance model

Table A2: Degrees of freedom, F-statistic and p-values for the linear mixed model testing how head length variance is affected by climate (MAT and AP) and disturbance and their interactions and the covariates trap type, hemisphere, species richness, with data source as a random factor. R^2marginal = 0.25; R^2conditional (including random effects) = 0.53.

	df	F-value	p-value
(Intercept)	1,308	281.6	<0.001
Disturbance	1,308	17.4	**<0.001**
Mean annual temperature (MAT)	1,308	0.3	0.562
Annual precipitation (AP)	1,308	9.3	**0.002**
Trap type	4,308	1.2	0.318
Hemisphere	1,18	2.9	0.104
Species richness	1,308	2.2	0.141
MAT*AP	1,308	1.2	0.267
Disturbance*MAT	1,308	0.0	0.962
Disturbance*AP	1,308	0.6	0.425
Disturbance*MAT*AP	1,308	0.5	0.471