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Research

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

H. Gibb, N. J. Sanders, R. R. Dunn, X. Arnan, H. L. Vasconcelos, D. A. Donoso, A. N. Andersen, R. R. Silva, T. R. Bishop, C. Gomez, B. F. Grossman, K. M. Yusah, S. H. Luke, R. Pacheco, J. Pearce-Duvel, J. Retana, M. Tista and C. L. Parr

H. Gibb (<http://orcid.org/0000-0001-7194-0620>) (h.gibb@latrobe.edu.au) and B. F. Grossman, Dept of Ecology, Environment and Evolution, La Trobe Univ, Melbourne 3, VIC, Australia. – N. J. Sanders, Rubenstein School of Environment and Natural Resources, Univ. of Vermont, Burlington, VT, USA. – R. R. Dunn, Dept of Biology, North Carolina State Univ., Raleigh, NC, USA. – X. Arnan, Depo de Botânica, Univ. Federal Pernambuco, Recife, PE, Brazil. – H. L. Vasconcelos and R. Pacheco, Inst. of Biology, Federal Univ. of Uberlândia (UFU), Uberlândia, MG, Brazil. – D. A. Donoso, Univ. de Cuenca, Facultad de Ciencias Agropecuarias, Cuenca, Ecuador. – A. N. Andersen, Charles Darwin Univ., Casuarina, NT, Australia. – R. R. Silva, Coordenação de Ciências da Terra e Ecologia, Museu Paraense Emilio Goeldi, Belém, PA, Brazil. – T. R. Bishop and C. L. Parr, Dept of Earth, Ocean and Ecological Sciences, Univ. of Liverpool, Liverpool, UK. TRB also at: Centre for Invasion Biology, Dept of Zoology and Entomology, Univ. of Pretoria, Pretoria, South Africa. CLP also at: Dept of Animal, Plant and Environmental Sciences, Univ. of Witwatersrand, Wits, South Africa. – C. Gomez, Dept of Environmental Sciences, Univ. of Girona, Girona, Spain. – K. M. Yusah, Inst. for Tropical Biology and Conservation, Univ. Malaysia Sabah, Jalan UMS, Kota Kinabalu, Sabah, Malaysia. – S. H. Luke, School of Biological Sciences, Univ. of East Anglia, Norwich, UK, and Dept of Zoology, Univ. of Cambridge, Cambridge, UK. – J. Pearce-Duvel, Dept of Biology, Univ. of Utah, Salt Lake City, UT, USA. – J. Retana, CREAM, Cerdanyola del Vallès, Catalunya, Spain. – M. Tista, Dept of Tropical Ecology and Animal Biodiversity, Univ. of Vienna, Vienna, Austria.

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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 333 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.



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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, Schmidt-Nielsen 1984, Lomolino and Perault 2007). Larger species are thought to be more susceptible to extinction than are smaller species because they require more resources and take longer to mature (Savage et al. 2004, McCain and King 2014). 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 disturbances which simplify habitats (Gibb and Parr 2013), exposing them to predation and desiccation. 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, Naeem et al. 2012, Dirzo et al. 2014).

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 (Sala et al. 2000, Mantyka-Pringle et al. 2012), 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 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 333 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 (Zelikova et al. 2011, Del Toro et al. 2012), 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 (Weiser and Kaspari 2006, Gibb and Parr 2013). 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 et al. 2013) and ubiquitous animal groups on earth, whether there is evidence of synergistic interactions and whether effects are related to species’ trophic roles.

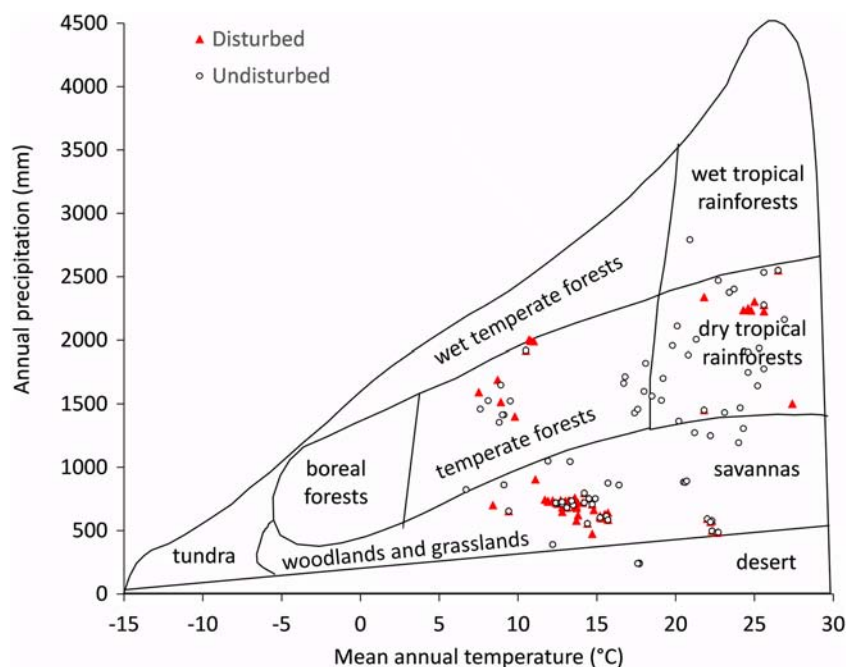


Figure 1. Distribution of the 333 study sites across Whittaker’s biomes.

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, 2009, Gibb et al. 2015a, 2017a, 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, pit-falls 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 *Wasmanina 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 31 disturbed localities at high latitudes were removed from the analyses as there were no undisturbed localities at similarly high latitudes. Further, we excluded seven grazed sites for which we could not be certain of grazing history prior to human management because grazing might have occurred historically and therefore not represent a disturbance. This left 333 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: 0.22–4.55 mm). Head length is a strong correlate of body size for ants (Weiser and Kaspari 2006, Gibb and Parr 2013). For assemblages where head length was not available, but Weber's length (Weber 1938, Parr et al. 2017) ($< \text{http://globalants.org} >$) 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 = $-0.095 + 0.811 \times \log_{10}$ 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, Yates et al. 2014, Gibb et al. 2015b) and are correlated with important traits such as mobility in complex environments, desiccation tolerance and metabolic rate (Hood and Tschinkel 1990, Gillooly et al. 2001, Gibb and Parr 2013). 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. Further, it is unclear to what extent colony size and worker body mass are correlated (Kaspari 2005, Geraghty et al. 2007), so patterns for worker body size may not reflect an underlying colony size response.

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: 6.7–27.4°C), annual precipitation (AP: 237–2791 mm), temperature range (TR: 8–29.6°C) 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 either recent anthropogenic or natural disturbance; and 2) disturbed, including disturbances such as forestry (native tree species or introduced tree species), fire, restoration (following clearing or mining; all sites < 20 yr since restoration), cropping and grazing (intensive grazing by stock or transformed from woodland; sites with

unclear grazing histories prior to human management were excluded). Similarly to Gibb et al. (2015a), we combined 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. The key distinction we make here (i.e. disturbed vs undisturbed) is based on whether biomass was removed or not, hence in some cases we combined natural and anthropogenic disturbances such as fire.

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). 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 as we were interested in the responses of species, rather than individuals). 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 333 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 \pm 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 and Schielzeth 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.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.3dt70>> (Gibb et al. 2017b).

Results

Climate and disturbance acted independently to determine body size (Fig. 2a, b, c), i.e. there were no significant climate \times disturbance interactions (Fig. 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 (Fig. 2b, 3b), while the larger ant species in an assemblage were (on average) smaller where it was wetter (Fig. 2c, 3c). The median body size of ants declined as precipitation and temperature increased (Fig. 2b, c). Analysis of among-species (interspecific) variation in body size confirmed that it was lower in disturbed ecosystems and declined with increasing precipitation (Supplementary material Appendix 2 Table A2). There were no effects of hemisphere or the temperature \times precipitation or temperature \times precipitation \times disturbance interactions on body size, suggesting that none of these factors affected the distribution of ant body sizes (Fig. 2d, g, i). 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 ($R^2_{GLMM(m)} = 0.53$; $R^2_{GLMM(c)} = 0.85$) and was lowest for the largest ant species ($R^2_{GLMM(m)} = 0.31$; $R^2_{GLMM(c)} = 0.61$). 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 ($\chi^2_{(1)} = 0.86$, $p = 0.031$)

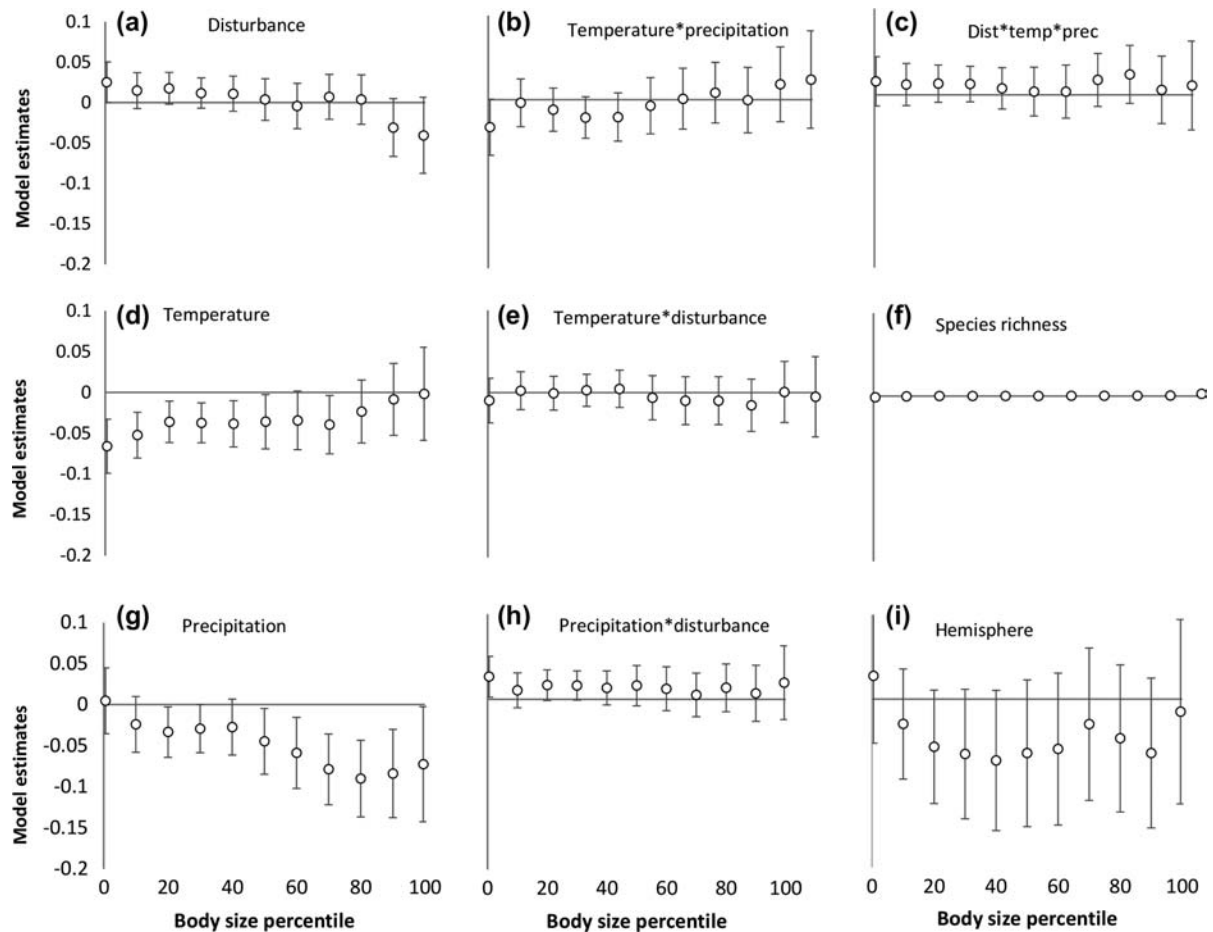


Figure 2. Estimates and confidence intervals from models testing the effects of climate and disturbance on head length by body size percentile and for minimum and maximum body size (placed at the 1st and 99th percentile, respectively) ($n = 333$). Estimates represent the effect size for the difference 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.

(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, the susceptibility of species to particular global change drivers depends on their traits. We showed that climate and habitat disturbance (biomass removal) act independently, differentially affecting 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. Contrasting relationships between species traits and different elements of climate will be important to consider when predicting species responses to changes in climate. Although we could not test for this, within-species variation in response to climate (Ohlberger 2013, Caruso et al. 2014) 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

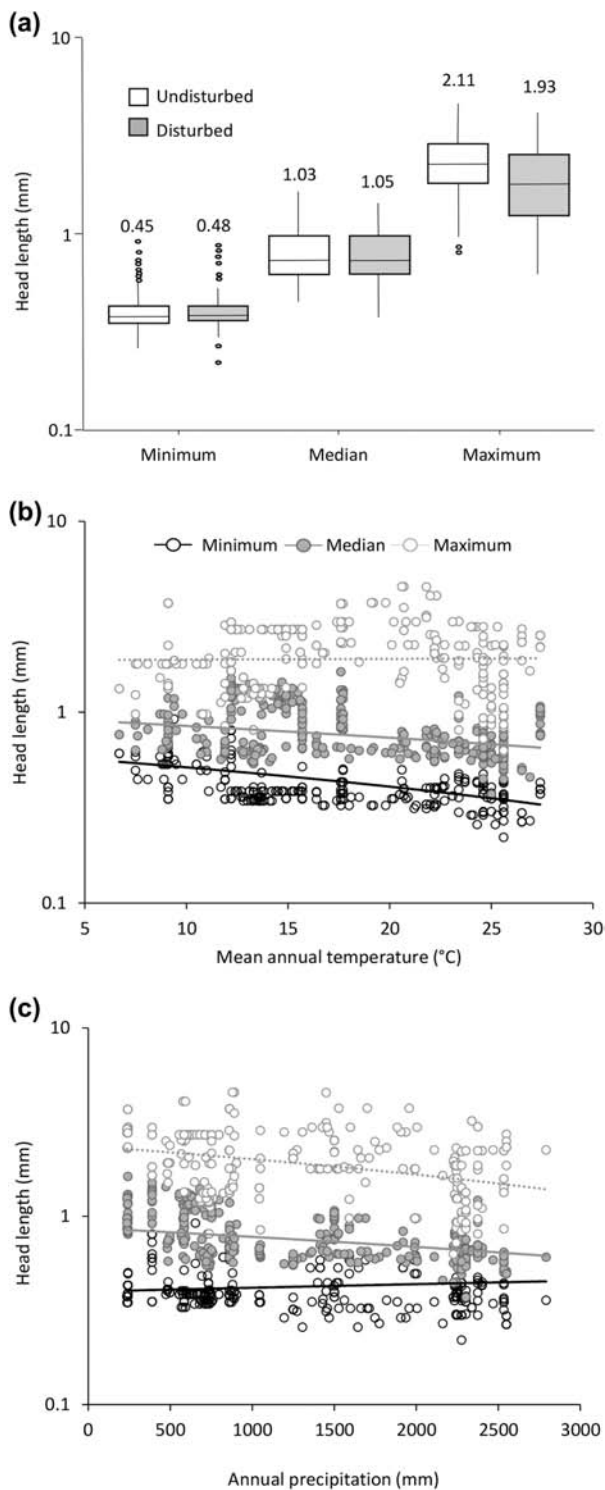


Figure 3. Minimum, median and maximum head length ($n=333$) plotted against: (a) disturbance; (b) mean annual temperature; and (c) annual precipitation for ant assemblages examined in this study. (a) Shows predicted means above box plots of the raw data for disturbance, with the central line representing 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 \log_{10} scale.

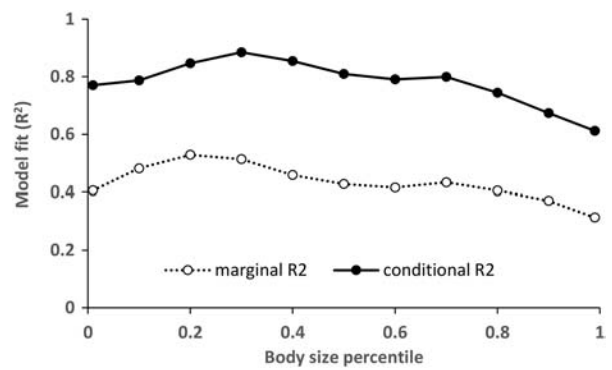


Figure 4. Model fits (marginal (R^2_m) and conditional (R^2_c) R-square) from general linear mixed models testing the effect of mean annual temperature, annual precipitation, disturbance and their interactions on the body size of ant assemblages ($n=333$).

pattern. Independent of the mechanism, our findings highlight the importance of simultaneously considering the impacts of multiple climatic variables on functional traits.

The negative temperature–size relationship observed in this study is consistent with Bergmann’s rule, which states that the smallest species and individuals tend to occur at low latitudes (in warm climates) (Bergmann 1847). Although this pattern is common for endotherms (Meiri and Dayan 2003), its validity for ectotherms such as insects is less clear. Previous studies suggest that taxon, scale and methodology are important in determining whether Bergmann’s rule is detected in insects (Shelomi 2012). For ants, the relationship between the body size of workers and latitude or elevation has been examined in several previous studies, with four showing a negative size–temperature relationship (intraspecific: Heinze and Oberstadt 1999, Heinze et al. 2003, Bernadou et al. 2016) (interspecific: Cushman et al. 1993), three showing no pattern (interspecific: Gomez and Espadaler 2000, Geraghty et al. 2007, myrmecochores only: Gomez and Espadaler 2013), and one showing the converse relationship (intraspecific: Diniz and Fowler 1998). Studies examining the colony size of ants and other social insects have been similarly inconsistent (intraspecific: Bernadou et al. 2016, interspecific: Kaspari and Vargo 1995, Porter and Hawkins 2001, Geraghty et al. 2007). However, it is notable that those operating at the largest spatial and taxonomic scales (Cushman et al. 1993, Kaspari and Vargo 1995 and this study) are consistent in showing a negative temperature–size relationship among species. A range of adaptive and non-adaptive hypotheses explaining temperature–size relationships exist for insects, including greater resistance to starvation in more seasonal environments (Heinze et al. 2003), reduced oxygen availability at high temperatures (Atkinson 1996) and maturation at smaller sizes resulting from elevated metabolic rates at higher temperatures (Gillooly et al. 2001). By examining body size in percentiles, we show that the size–temperature relationship is strongest for the smallest species. This suggests that a mechanism, such as the starvation resistance hypothesis, that limits how small individuals can be at low

temperatures, rather than how large they can be at high temperatures, may be at play.

Several hypotheses might explain why the largest ants were larger 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 with decreasing body size (Remmert 1981, Hood and Tschinkel 1990, Chown and Gaston 2010). 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 by physically obstructing movement, favoring reduced body size (Kaspari and Weiser 2000, Gibb and Parr 2013). 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 (biomass removal) 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 (McKinney 2006, Clavel et al. 2010). 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 (Robinson and Redford 1986, Chown and Gaston 2010).

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 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 (Gardner et al. 2011, Dirzo et al. 2014), so it is critical that we identify any important unmeasured limitations for species with large body size. Colony size (worker number) is another important measure of the body size of ants and other social insects, but we were unable to examine this here. The relationship between worker number and worker body mass is unclear and worker number is not related to temperature (Kaspari 2005, Geraghty et al. 2007), but worker number could be important in determining responses to disturbance or rainfall and would be a worthy focus of future studies.

Ants are neither the smallest, nor the largest of taxa, but all animal body designs have size limits, determined by mechanical or thermodynamic functional design constraints (Blackburn and Gaston 1994). Our finding that the extremes of body size were most affected suggests that the constraints that limit the absolute maximum and minimum size of an animal type are exacerbated under stress and that homogenization of body size in response to stress or disturbance might also be expected in other taxa. Frequency, intensity, severity, scale and source are all likely to be important in determining the outcome of disturbances and, while our dataset was insufficient to investigate the role of these factors, we highlight their significance for future studies.

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

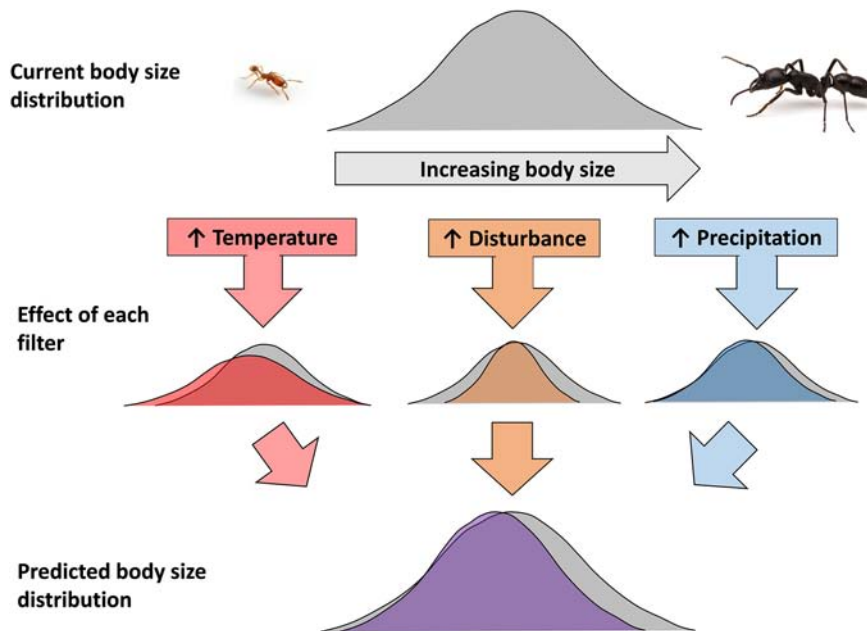


Figure 5. Schematic representation of the cumulative change in body size distributions from the current body size distribution (grey) that is predicted to result when ant assemblages pass through filters of increasing temperature (red: favoring small body size), disturbance (orange: homogenising body 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.

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 (Davies et al. 2004, Brook et al. 2008). Predators have previously been identified as particularly vulnerable to global change (Senior et al. 2013, Jellyman et al. 2014, Ewers et al. 2015), 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, while the largest ants were smaller in areas with high rainfall. This qualifies previous research focusing on endotherms that suggests that a decrease in body size may be a universal response to higher temperatures associated with climate change (Sheridan and Bickford 2011, Dirzo et al. 2014). 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, Senior et al. 2013, Ewers et al. 2015). Our results demonstrate that both large and small predators decline in response to disturbance and are therefore vulnerable to ongoing global change.

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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.

Permits – Appropriate ethics and licences were obtained for all specimens collected.

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Supplementary material (Appendix ECOG-03244 at < www.ecogeography.org/appendix/ecog-03244 >). Appendix 1–2.