BIODIVERSITY RESEARCH

Global diversity in light of climate change: the case of ants

Clinton N. Jenkins[1]*, Nathan J. Sanders[2,3], Alan N. Andersen[4], Xavier Arnan[5], Carsten A. Brühl[6], Xim Cerda[7], Aaron M. Ellison[8], Brian L. Fisher[9], Matthew C. Fitzpatrick[10], Nicholas J. Gotelli[11], Aaron D. Gove[12], Benoit Guénard[13], John E. Lattke[14], Jean-Philippe Lessard[2], Terrence P. McGlynn[15], Sean B. Menke[16], Catherine L. Parr[17], Stacy M. Philpott[18], Heraldo L. Vasconcelos[19], Michael D. Weiser[13] and Robert R. Dunn[13]

[1]*Department of Biology, University of Maryland, College Park, MD 20742, USA,* [2]*Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA,* [3]*Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, DK-2100 Copenhagen, Denmark,* [4]*CSIRO Ecosystem Sciences, Tropical Ecosystems Research Centre, PMB 44 Winnellie, NT 0822, Australia,* [5]*Unit of Ecology and Center for Ecological Research and Forestry Applications (CREAF), Autonomous University of Barcelona, E-08193 Bellaterra (Barcelona), Spain,* [6]*Institute for Environmental Sciences, University Koblenz-Landau Fortstrasse 7, 76829 Landau, Germany,* [7]*Estacion Biologica Donana, CSIC, 41092 Sevilla, Spain,* [8]*Harvard University, Harvard Forest, 324 North Main Street, Petersham, MA 01366, USA,* [9]*Department of Entomology, California Academy of Sciences, San Francisco, CA 94118, USA,* [10]*University of Maryland Center for Environmental Science, Appalachian Laboratory, Frostburg, MD 21532, USA,* [11]*Department of Biology, University of Vermont, Burlington, VT 05405, USA,* [12]*Department of Environmental and Agriculture, Curtin University, Perth, WA 6845, Australia,* [13]*Department of Biology, North Carolina State University, Raleigh, NC 27695, USA,* [14]*Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela, Venezuela Maracay 2101-A,* [15]*Department of Biology, California State University Dominguez Hills, Carson, CA 90747, USA,* [16]*Department of Biology, Lake Forest College, Lake Forest, IL 60045, USA,* [17]*Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK,* [18]*Department of Environmental Sciences, University of Toledo, Toledo, OH 43606, USA,* [19]*Instituto de Biologia, Universidade Federal de Uberlândia (UFU), CP 593, Uberlândia, MG 38400-902, Brazil*

*Correspondence: Clinton N. Jenkins, Department of Biology, University of Maryland, 1210 Biology-Psychology Building, College Park, MD, USA.
E-mail: Clinton.Jenkins@gmail.com

ABSTRACT

Aim To use a fine-grained global model of ant diversity to identify the limits of our knowledge of diversity in the context of climate change.

Location Global.

Methods We applied generalized linear modelling to a global database of local ant assemblages to predict the species density of ants globally. Predictors evaluated included simple climate variables, combined temperature × precipitation variables, biogeographic region, elevation, and interactions between select variables. Areas of the planet identified as beyond the reliable prediction ability of the model were those having climatic conditions more extreme than what was represented in the ant database.

Results Temperature was the most important single predictor of ant species density, and a mix of climatic variables, biogeographic region and interactions between climate and region yielded the best overall model. Broadly, geographic patterns of ant diversity match those of other taxa, with high species density in the wet tropics and in some, but not all, parts of the dry tropics. Uncertainty in model predictions appears to derive from the low amount of standardized sampling of ants in Asia, in Africa and in the most extreme (e.g. hottest) climates. Model residuals increase as a function of temperature. This suggests that our understanding of the drivers of ant diversity at high temperatures is incomplete, especially in hot and arid climates. In other words, our ignorance of how ant diversity relates to environment is greatest in those regions where most species occur – hot climates, both wet and dry.

Main conclusions Our results have two important implications. First, temperature is necessary, but not sufficient, to explain fully the patterns of ant diversity. Second, our ability to predict ant diversity is weakest exactly where we need to know the most, the warmest regions of a warming world. This includes significant parts of the tropics and some of the most biologically diverse areas in the world.

Keywords
Aridity, biodiversity, biogeography, Formicidae, species richness, temperature.

A Journal of Conservation Biogeography

Diversity and Distributions

INTRODUCTION

Most pollinators, predators, disease vectors, and pests are insects (Beattie & Ehrlich, 2010), but our understanding of global patterns of insect diversity is still in its infancy (Diniz-Filho *et al.*, 2010). Scientists have yet to examine diversity patterns for most insect taxa but have made major progress in mapping a few focal groups at coarse spatial grains (e.g. countries and 10° grid cells, see Pearson & Cassola, 1992; Eggleton *et al.*, 1994; Foley *et al.*, 2007; Balian *et al.*, 2008; Guénard *et al.*, 2010). A next step is to document and model the patterns of diversity at finer spatial grains, ones at which ecological and evolutionary processes play out. This will be particularly important for understanding how insect diversity, and the services that insects provide, may respond to anthropogenic pressure and a changing climate (e.g. Fitzpatrick *et al.*, 2011). We present here a fine-grained global map for ants, documenting both what we know about global ant diversity and, perhaps more importantly, what we do not know.

For vertebrates, maps of diversity are often created by overlaying species range maps (e.g. Jetz & Rahbek, 2001; Rahbek & Graves, 2001; Young *et al.*, 2004; Orme *et al.*, 2005, 2006; Pimm & Jenkins, 2005; Grenyer *et al.*, 2006; Jenkins & Giri, 2008). However, this method is not yet practical for the vast majority of insects. Relatively few insect taxa have had sufficient sampling to produce valid range maps. Even by conservative tallies, only a small fraction of insects have even been described (Hamilton *et al.*, 2010). An exception would be the butterflies, but even for them, maps exist only for some regions (Hawkins, 2010).

An alternative to the range map approach is to take field plot inventories and correlate these estimates of local diversity with environmental variables estimated for the same locations (e.g. Lobo *et al.*, 2004; Kreft & Jetz, 2007; Beck *et al.*, 2011). This statistical modelling approach can be useful both to understand contemporary diversity patterns (e.g. Dunn *et al.*, 2009a) and to predict potential changes in diversity as the environment changes. Additionally, such models can be projected across space and through time (e.g. for current and predicted future climates) to reveal places and environments where our understanding of diversity is limited or where the model performs poorly.

A common assumption when using correlative models is that the relationships between environment and diversity operate in a similar manner in different parts of the world. Such an assumption is likely to be violated, but to what extent and in what ways remains largely unexplored for insects. For example, to our knowledge, relatively few quantitative samples of the diversity of ants exist for Africa. Does this restrict our ability to explore climate–diversity relationships for ants, or are climate–diversity relationships in Africa similar enough to those in other parts of the world that we can assume generality? If evolutionary history has shaped the African ant fauna such that ants in Africa respond differently to the environment than do ants in other areas, then a region-specific model might be necessary (Ricklefs, 2007). Similar logic can apply to a changing climate. Do we understand what happens to diversity in the extreme climates of today, some of which may be rare and unexplored, but which climate models predict will expand greatly in the future?

We focus on these topics using ants, because they are ecologically important, conspicuous and easily sampled in standardized ways. Just as importantly, they are among the most well-known taxa of terrestrial invertebrates and so represent one of the best-case scenarios in terms of our knowledge of terrestrial invertebrates. To assess our ability to understand the current and potential future patterns of ant diversity, we constructed global regression models and maps of one measure of local diversity, ant species density (number of species per 10×10 km grid cell). We did this by correlating extensive field data on local ant assemblages with a suite of environmental variables. We then compared the environmental sample space of the model with the current and predicted future distribution of climates, highlighting specific climatic and geographic gaps in our knowledge of global ant diversity. In the spirit of S.W. Boggs (1949), we produce a map of ignorance for ants. Like Boggs, we argue that understanding the limits of our current knowledge, particularly in the light of future conditions, will reduce our ignorance in the future. We hope that the gaps in knowledge we identify here will be, as Boggs put it, 'a needed stimulus to honest thinking and hard work'.

METHODS

Ant assemblage database

We compiled sampling data for local ant communities from all continents except Antarctica. We present a brief description of the database here, but details appear elsewhere (Dunn *et al.*, 2007, 2009a). The ant community data and associated environmental data for this study are archived in the Harvard Forest Data Archive: http://harvardforest.fas.harvard.edu/data/archive.html, dataset HF-113. The database includes the majority of studies that used standardized methods to sample ants as of January 2010, including additional studies published since Dunn *et al.* (2009a), for a total of 235 published studies. Some studies included multiple sampling events. Studies used in the current analyses met the following criteria: (1) the ground-foraging ant community was sampled using standard (e.g. pitfalls, Winkler litter samples and baits), though not identical, field methods; (2) sampling was not trophically or taxonomically limited (e.g. the study did not focus only on seed-harvesting ants); (3) sampling occurred on continental mainlands or large islands (e.g. Madagascar), but not on small oceanic islands; and (4) study sites were undisturbed or minimally disturbed natural habitats. Measures of diversity apply to ground-foraging ants only and exclude both soil-dwelling and canopy ants missed by the sampling methods considered here (Bestelmeyer *et al.*, 2000; Delabie *et al.*, 2000; Weiser *et al.*, 2010).

We converted sample point data to a gridded map with 10×10 km (100 km^2) cells, matching the resolution of the environmental data used in the model. If two or more sites were < 10 km apart, we combined those data and assigned a central coordinate and total species richness to the combined sites. Species richness for a set of combined sites was calculated by combining their cumulative species lists. When site-level species lists were unavailable, we used the study only if all sites were within 10 km of one another. The final database had 358 records suitable for analysis (Fig. 1). As we counted the number of species per 100-km^2 grid cell, this measure of diversity is most appropriately termed species density (Simpson, 1964; Gotelli & Colwell, 2001). One might think of it as the species richness of a single grid cell. Analyses were also carried out for 1- and 5-km grains, and those results and discussion are available online as Supporting Information.

Species diversity estimates can be sensitive to the extent of field sampling, and a weak but statistically significant correlation does exist between the number of samples and species density ($R^2 = 0.053$; $P < 0.001$; one outlier with 20,000 samples excluded). To minimize potential bias because of insufficient sampling while still maintaining the bulk of the data, we excluded records having fewer than 20 total samples (e.g. pitfalls, litter samples and baits at a location). While more advanced selection methods exist for choosing well-sampled sites (see Lobo *et al.*, 2004), current data cannot yet support such methods. We also examined the correlation between the area sampled in the field and species density. However, there was no correlation for the 278 records with information on sample area ($R^2 < 0.01$, $P > 0.4$).

Environmental correlates

A suite of climatic variables are known to be correlated with ant diversity (Kaspari *et al.*, 2003, 2004; Sanders *et al.*, 2007; Dunn *et al.*, 2009a,b; Vasconcelos *et al.*, 2010; Weiser *et al.*, 2010) and are among the few environmental variables for which there are global, future predictions. As such, they are our main focus. For contemporary climate, we evaluated 12

variables from the WorldClim data set (Hijmans *et al.*, 2005): mean annual temperature, mean temperatures of the coldest month, coldest quarter, warmest month and warmest quarter, the annual temperature range, temperature seasonality, mean annual precipitation, mean precipitation of the driest month, driest quarter, wettest month and wettest quarter.

Previous meta-analyses of both vertebrates and invertebrates have found that variables measuring energy and water availability – and the interaction between them – are strong predictors of species diversity (Hawkins *et al.*, 2003a). We evaluated temperature–precipitation interactions using three variables: (1) a simple interaction term of mean annual temperature multiplied by precipitation; (2) potential evapotranspiration (PET); and (3) an aridity index. The PET and aridity data are from Trabucco & Zomer (2009) who used the WorldClim data plus estimates of solar radiation to model PET, and the aridity index is equal to mean annual precipitation divided by PET. To our knowledge, the recently developed aridity and PET data sets have not been used previously for diversity modelling.

Data on predicted climate in 2050 are from the study by Ramirez & Jarvis (2008) using climate scenario SRES A2a. We chose three climate models (CGCM3.1-T47, BCCR-BCM2 and GISS-AOM) that represent a range of future predictions but emphasize that our intent is to illustrate potential futures, not judge one model as better than another. We recognize that other climate models yield predictions that differ in their specifics, particularly with regard to precipitation, although all such models predict net global warming and warming to some extent in all biomes (IPCC, 2007).

Species density, and its correlation with environmental variables, may vary among geographic regions because of historic reasons such as glaciation or evolutionary history (Gaston, 1996; Chown *et al.*, 2004; Ricklefs *et al.*, 2004; Dunn *et al.*, 2009a,b). We evaluated continent and biogeographic realm (Olson *et al.*, 2001; WWF, 2008), and the interactions between environmental variables and these geographic regions, as potential predictors. Although ant diversity was previously
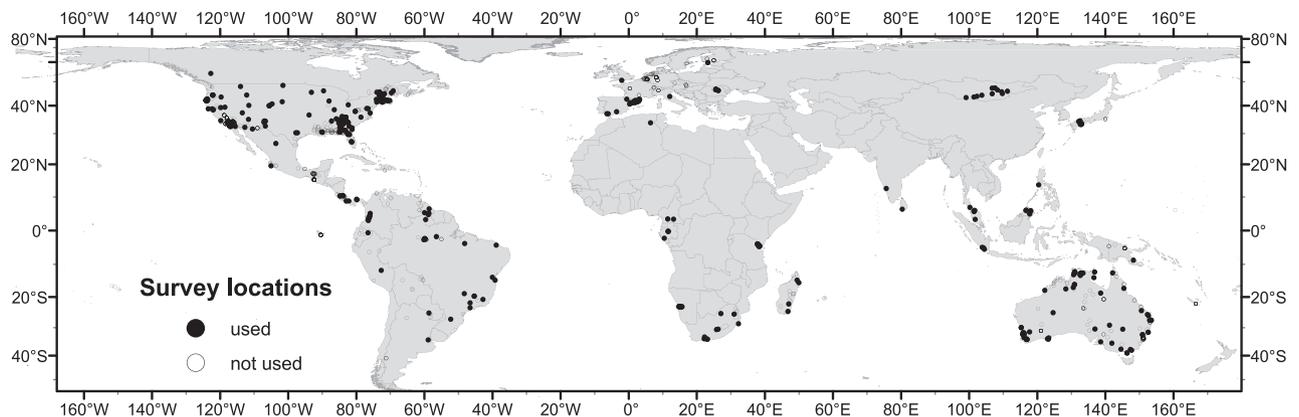
Figure 1 Map of standardized survey locations included in the ant assemblage database, both those used in the 10-km grain analyses (filled circles) and those excluded as unsuitable for our analyses (open circles). Map uses an equal area projection.

shown to be higher in the Southern Hemisphere, even after accounting for climate (Dunn *et al.*, 2009a), we used continents and biogeographic realms here to allow for the possibility of regional effects above and beyond those captured simply by Hemisphere.

Using data from the Shuttle Radar Topography Mission (Rabus *et al.*, 2003), we evaluated elevation as a potential predictor variable, because it might capture additional variation in climate missed by climate models. The interpolation methods used to produce the WorldClim data do consider elevation, but the approach is imperfect (Daly, 2006). However, elevation contributed little explanatory power in the models and was not included in the final analyses.

Model fitting and evaluation

We used generalized linear modelling in JMP 8.0 (SAS, 2008) using the log-link function and a Poisson distribution with species density as the response variable. There were 17 potential predictor variables (12 climate variables, 3 temperature × precipitation variables, continent and biogeographic realm) plus the interactions between geographic region and environmental variables. We compared candidate models using both log-likelihood and Akaike's Information Criterion with the small sample size correction (AICc) (Burnham & Anderson, 2002). Adjusted R^2's were calculated from a comparison of model predictions with the sample data. We mapped model predictions globally by applying the models to environmental data layers using ArcGIS 9.3 (ESRI, Redlands, CA, US). Areas with climates beyond the range sampled by the ant assemblage database were excluded from predictions. For models with a climate–geography interaction variable, areas were excluded within each geographic region using the interacting climate variable based only on the ant samples within that region.

RESULTS

Environmental predictors

Mean annual temperature accounted for more than a third of the variation in ant species density globally and was the best single predictor (41% decrease in AICc, adjusted $R^2 = 0.36$, Table 1). Addition of the precipitation in the wettest quarter of the year, followed by biogeographic realm, improved the model substantially (56% decrease in AICc, adjusted $R^2 = 0.51$, Table 1). The incorporation of the interaction between precipitation and biogeographic realm also improved the model (66.6% decrease in AICc, adjusted $R^2 = 0.67$, Table 1). Additional variables improved model performance only marginally but complicated model interpretation. Plots of the predicted versus observed species density for each model are presented in the Supporting Information. Model predictors and rankings for 1- and 5-km grains are presented in the Supporting Information, but in general, the results were similar to those for 10-km grains.

Table 1 General linear models of global species density of ants at a 10-km grain.

Variables	R^2*	AICc	ΔAICc (-%)	ΔLog likelihood	DF
MAT + Precip + Realm + Precip × Realm	0.67	5472	−10901 (66.6%)	5463	12
MAT + Precip + Realm	0.51	7205	−9168 (56.0%)	4591	7
MAT + Precip	0.37	9383	−6990 (42.7%)	3497	2
MAT	0.36	9663	−6710 (41.0%)	3356	1
Intercept only	–	16373	–	–	0

The percent change for ΔAICc represents the percent decline in the AICc value relative to that of the intercept only model.
MAT, mean annual temperature; Precip, precipitation in the wettest quarter of the year; Realm, biogeographic realm.
*For GLZ models, this is sometimes referred to as a pseudo-R^2.

At very high temperatures, the relationship between species density and temperature is extremely variable. In our limited sampling of the hottest (> 27 °C mean annual temperature) and/or most arid areas (< 500 aridity index), species density varies from 0 to 145 species (Table S3). In the simplest model that using mean annual temperature only, the model residuals increase with temperature with the regression line having a slope of *c.* 0.2 (Fig. 2a). Reassuringly, the best-performing model has smaller residuals and less increase in those residuals with temperature (slope = ∼0.1, Fig. 2b). Nevertheless, the residuals still increase with temperature across the temperatures sampled. It is possible that this trend would extend to even warmer climates, beyond those where we currently have data.

Climatic limits

Many of the world's biomes are represented by well-described, quantitative samples of ants, but the distribution among biomes is biased (Fig. 3). The relatively cold tundra and taiga biomes, the wettest temperate forests and the hottest subtropical deserts have few or no quantitative samples (Fig. 3). To some extent, we knew that these climatic regions were underrepresented (Dunn *et al.*, 2007), but we explore them here in more detail, particularly in the context of their present and future distribution.

The non-sampled climates represent *c.* 34% of the planet's land area (dark grey in Fig. 4). With no empirical ant data to compare with the model predictions, we have no rigorous way to evaluate predictions for such climates, and so we excluded them from our results. The area occupied by these non-sampled climates, and future no-analogue climates, is expected to expand greatly in the future (red in Fig. 4). No-analogue climates are those with a mean annual temperature or precipitation beyond what occurs globally today. Considering the CGCM3.1-T47 climate model as an example, 49% of the planet's land area has, or will have in the future, a climate for
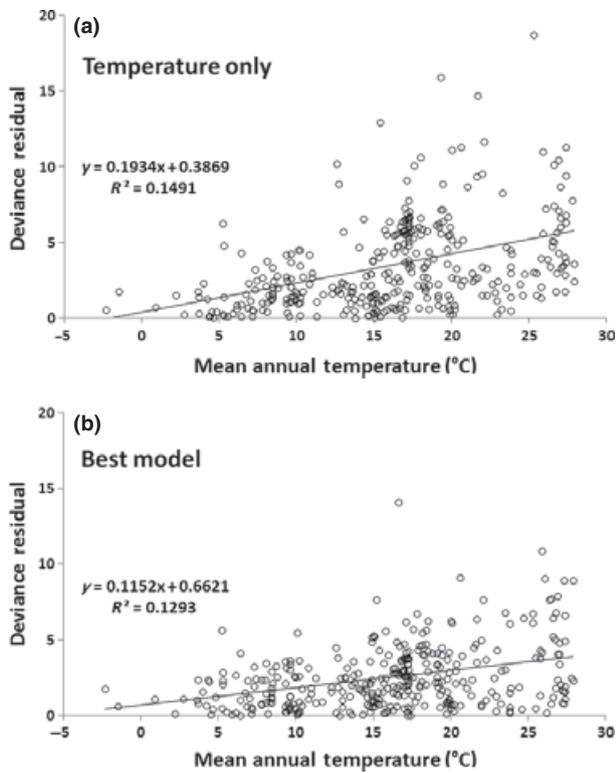
Figure 2 Plots of the absolute values of model deviance residuals versus mean annual temperature. Lines are simple linear regressions. Model residuals tend to increase with mean annual temperature, suggesting a decline in model performance with rising temperature. The decline is most pronounced in the simplest model using only temperature (a). The best-performing model (b) generally has smaller residuals and a slower increase in those residuals with temperature, as indicated by a lower slope of the regression line. One point with a residual of 27.8 is not shown in the temperature only model (a).

which we have insufficient data to model ant diversity. Expansion of these non-sampled climates will be almost entirely within the tropics (Fig. 4). That expansion is mostly because of climates becoming hotter, although some areas also become too dry or too wet to model. Other axes of climate, such as seasonality, will also undoubtedly change. For results using other climate models, see Supporting Information.

Geographic patterns

Applying the best-performing model globally indicates that ground-foraging ants follow some broad patterns of diversity described for other taxa, with higher diversity in the tropics and lower diversity at higher latitudes (Fig. 5). Areas predicted to have relatively low species density include much of North America, Europe and temperate Asia. Areas predicted to have notably high species densities include the Amazon, Congolese and West African forests, scattered localities in eastern Africa and parts of Madagascar, India and south-east Asia. However, many of the areas predicted to have high species densities are in climatic regions poorly represented in the sample data.

DISCUSSION

We find that ant diversity, at least qualitatively, tracks that of other terrestrial plants and animals, with high diversity in the wet tropics and low diversity in the cold and dry subarctic. Importantly, our models highlight what we know in the light of climate change, but even more importantly, what we do not know about current or future distributions of ant diversity.

Two climate variables plus an effect of biogeographic realm accounted for most of the variation in ant species density. The correlation with climate is expected, as many previous studies have documented links between climate and diversity both for ants (e.g. Kaspari *et al.*, 2000, 2003; Dunn *et al.*, 2009a; Vasconcelos *et al.*, 2010) and for other taxa (e.g. Hawkins *et al.*, 2003a; Kreft & Jetz, 2007). The importance of biogeographic realm in the models, particularly the interaction between biogeographic realm and precipitation, suggests that climate–diversity relationships for ants vary by region. Even though biogeographic divisions have been derived largely using plants and vertebrates, it appears that they still help explain diversity patterns for ants. In line with previous work (Dunn *et al.*, 2009a), the biogeographic regions in the Southern Hemisphere tended to be more diverse. Just as for other taxa such as birds (Hawkins *et al.*, 2003b), global models to explain ant diversity need to account explicitly for geography, and by extension evolutionary history, not just the current local environment. This task becomes more difficult as one considers not just the present but also the future.

Our primary focus, though, was not the specific correlates of diversity, but rather the limits posed when predicting diversity of ants both geographically and across time. Our results highlight specific climates (Fig. 3) and geographic areas (Fig. 4) that myrmecologists have yet to sample systematically for ants. These regions tend to be extreme climates (very hot or cold, very wet or dry), where ants might not always be diverse but may still be very important from the perspective of their ecological roles (Wardle *et al.*, 2011).

The climates predicted to expand most, though, under the climate models considered here, are the hot climates, both wet and dry. The fact that temperature is positively correlated with ant species density naively suggests that as hot places get hotter, species density should increase. Global models, though, can hide locally important phenomena. For one, species do not track climate perfectly, particularly among biogeographic regions. Even if there are many species that could live in a climate, they might not be able to colonize the regions with that climate. Just as significantly in hot regions, factors other than temperature alone limit diversity. Some of the hottest places on the planet, such as the Sahara, actually have very low ant diversity. It is at this high end of the temperature gradient, where diversity can be extremely high or extremely low, that we reach the limits of our current knowledge. Simply put, we do not yet know enough about ants in extremely hot climates around the world to understand fully the impact of further warming on these underexplored assemblages.
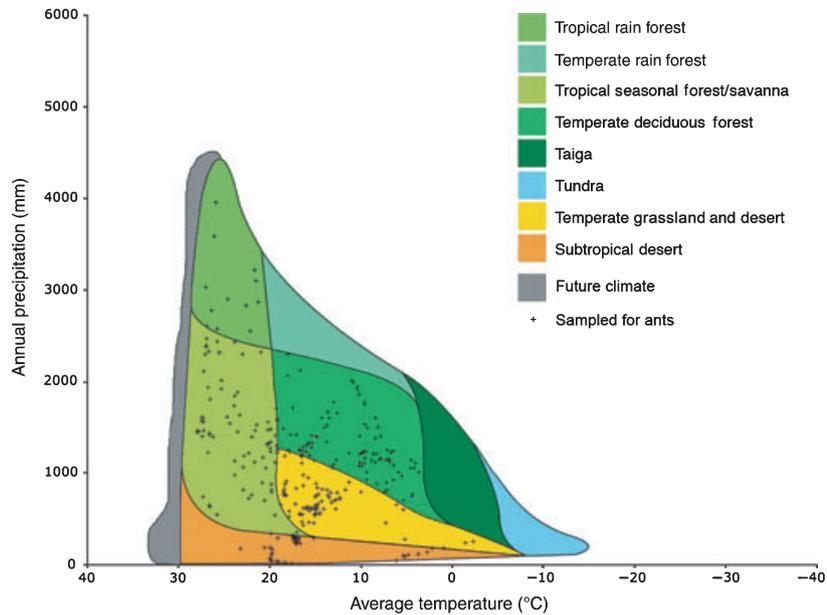
Figure 3 Classic Whittaker plot (Whittaker, 1975) of biomes. Sites from the ant assemblage database are plotted at their corresponding temperature/precipitation coordinate, showing the uneven sampling of the climate space. Very dry and very hot climates have particularly sparse sampling. Climates predicted to occur in the future (2050) but beyond current biomes appear in grey.
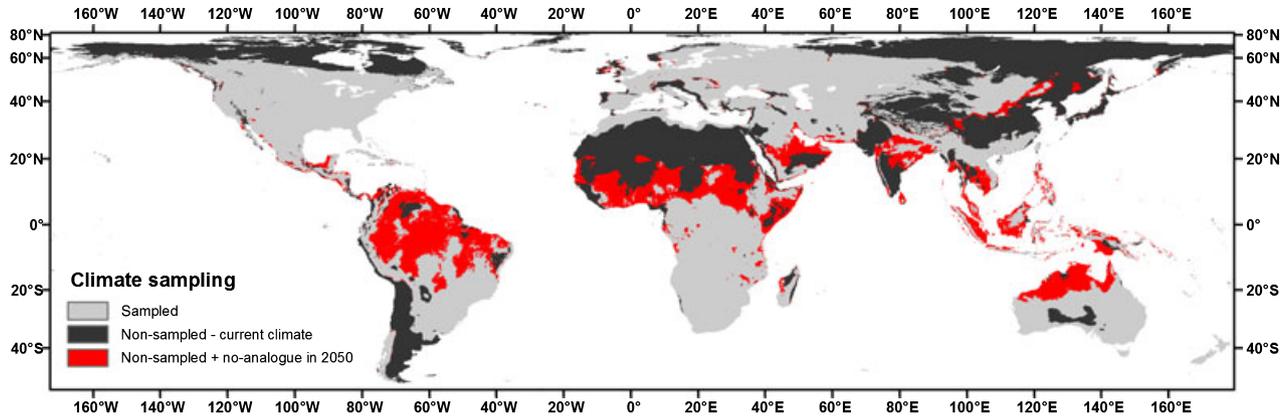
Figure 4 Distribution of climates that have not been adequately sampled for ants, shown under contemporary climate (dark grey, 34% of land area) and the expansion of these non-sampled climates, plus the emergence of no-analogue climates, projected for 2050 (red, 15% of land area). Together these areas cover 49% of the planet's surface and are indicative of our ignorance of the future world. Map uses an equal area projection.

We see three challenges to improving the ability to understand diversity in the hot, expanding climates. First, as we have mentioned, the hottest conditions are poorly sampled, likely contributing to the uncertainty of model predictions within these climates. We need systematic samples of ants in hot climates of all types. Moreover, because climate–diversity relationships vary among biogeographic regions, we need samples from similar climates in all biogeographic regions. Second, the influence of precipitation appears to differ between regions and is dependent on temperature, resulting in complex effects that are difficult to capture in a global model. A few

previous studies of ant diversity have suggested that precipitation is more influential at high temperatures than at low temperatures (Marsh, 1986; Heatwole, 1996; Pfeiffer et al., 2003). The handful of studies from the very hottest studied ant communities (Table S3) do suggest a tendency for drier places to have fewer species (top of Table S3), whereas warm but slightly wetter areas tend to have many more species (bottom of Table S3). Further discussion of some of the best studies of ants in the hottest and most arid parts of the world is available in the online Supporting Information. These studies lead us to conclude that the relationship between precipitation and
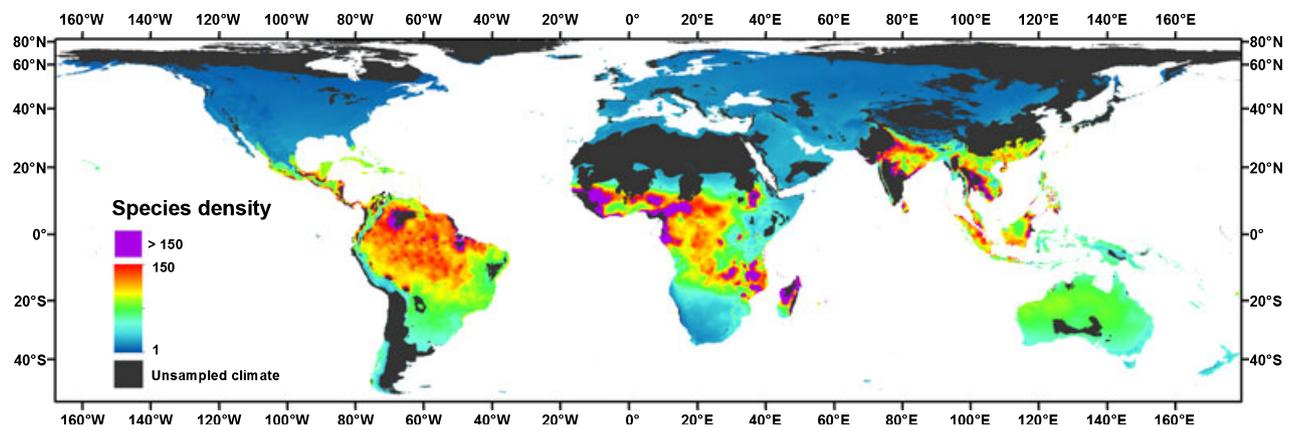
Figure 5 Species density of ants predicted at a 10-km grain using the best-performing model, which includes mean annual temperature, precipitation in the wettest quarter of the year, biogeographic realm and the interaction between precipitation and realm (see Table 1 for details of all models). Dark grey areas are non-sampled climates as described in Fig. 4. Map uses an equal area projection.

diversity in the hottest regions needs more study, as do the traits of species in such regions not just to deal with heat, but also to deal with desiccation.

A third challenge when considering ants in a warmer world is that regions may differ in the extent to which their species are able to adapt to hotter conditions (Morton & Davidson, 1988; Morton & James, 1988; Andersen, 1997). If climatic niches are more conserved in some lineages than in others (Machac *et al.*, 2011), those lineages might more often fail to evolve the traits necessary to adapt to drastic climate changes than would species in lineages with more evolutionarily labile climatic niches (Wiens *et al.*, 2006, 2010; Algar *et al.*, 2009). In other words, faunas in some warm areas may be intrinsically better able to adapt evolutionarily to further warming of their

climate than are faunas in other areas. Whether such biogeographic differences in adaptability exist, because of history or lineage effects, is important. It could mean that particular faunas may be disproportionately likely to thrive in a warmer future, possibly contributing invasive and introduced species.

Even more difficult than modelling ant diversity in expanding climates will be trying to understand the fate of places predicted to have no-analogue climates. These will tend to be hotter than any existing climates, as was shown in the context of a traditional Whittaker biome plot (Fig. 3). While our model suggests that ever warmer sites will tend to have ever more species, as we have discussed the uncertainty increases at higher temperatures. In addition, an aridity threshold appears to exist beyond which species density
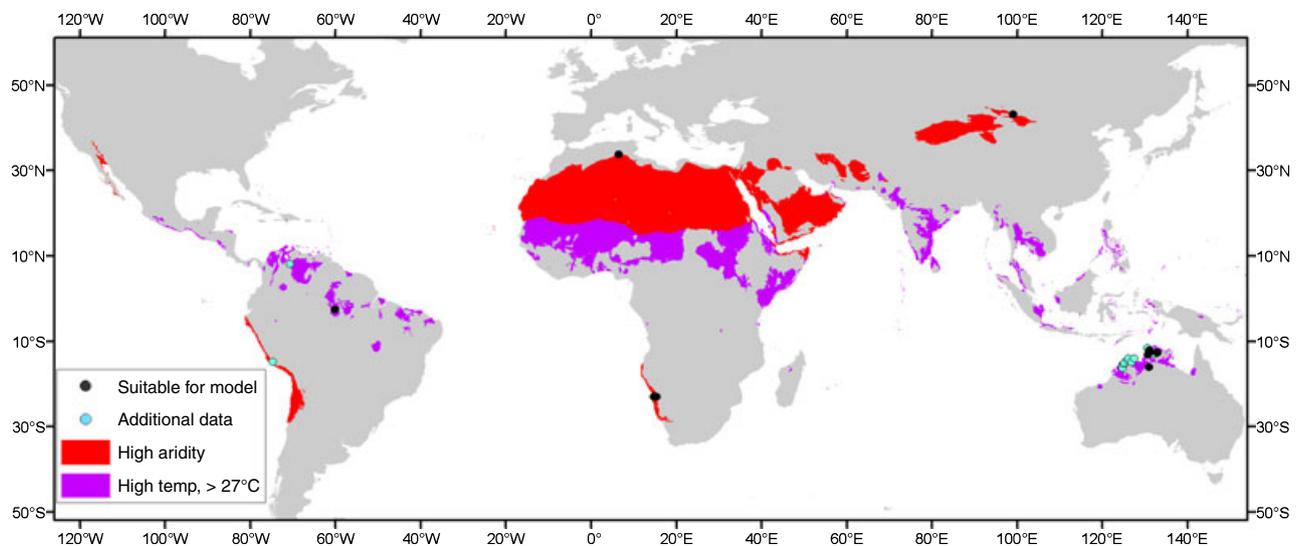
Figure 6 Map of areas of extreme aridity (< 500 on aridity index, Trabucco & Zomer, 2009) and areas that are extremely hot (> 27 °C mean annual temperature) but not necessarily arid. Points marked on the map indicate all sites in the ant assemblage database that are in arid and/or hot areas, including those used for modelling (black dots) and those that did not meet our criteria for use in modelling (blue dots).

sharply decreases. The known hot and extremely arid sites actually have very few or even just one or two species (Table S3), although studies from such conditions are too few to have much influence in models. We also emphasize that our definition of no-analogue here is a conservative one. Climates may also be no-analogue for variables not in the model, such as the variability of precipitation and temperature (e.g. Williams *et al.*, 2007).

In brief, warmer tends to mean more species, but not always, and in those places most similar to the expanding climates of the future, models perform the worst. This poorer performance may relate to the way that precipitation influences diversity at higher temperatures, but as yet our global sampling of ant diversity in the warm climates is insufficient to model the relationship confidently.

Our results provide a measure of what we do and do not know. They also provide a road map for future research. The hottest regions mapped in Fig. 6 have conditions most like those that will be expanding around us, and so they may prove disproportionately interesting for future study. Having good samples from these regions, and studies of the physiological tolerances of species in them, could tell us much about the future shape of regional ant faunas. Some of these areas have been studied, just not from an ecological perspective. Records of individual species exist, such as in systematic revisions, but there is no information on their abundance, life histories or ecology, largely because almost no one goes to do community ecology in places where there is not a community to study or a sparse one. Many of these areas are also physically harsh, making for exceptionally difficult fieldwork. However, verifying that an area has few or no species, and knowing why, is valuable information, particularly as the geographic coverage of such conditions grows.

The future expansion of today's extreme environments, and the likely emergence of no-analogue climates, is new territory for biodiversity (Williams *et al.*, 2007; Fitzpatrick & Hargrove, 2009). Where and how fast these climates develop will likely have major implications for animal and plant life (Loarie *et al.*, 2009). The limits of our current knowledge of ants coincide with these expanding climates of the future. The best strategy is perhaps to focus more of our efforts in the climates similar to those predicted to expand in the future, even if they are uncomfortable to visit, as they will expand whether we study them or not.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Distribution of survey locations in the ant assemblage database for the 1- and 5-km grains of analysis.

Figure S2 Species density of ants predicted at the 1- and 5-km grains using the best-performing model.

Figure S3 Plots of predicted versus observed species density for each of the 10-km grain models.

Figure S4 Distribution of climates that have not been adequately sampled for ants, shown under contemporary climate and the expansion of the non-sampled and no-analogue climates projected for 2050 for two climate models (GISS-AOM and BCCR-BCM2) using greenhouse gas emissions scenario A2a.

Table S1 Models of global species density of ants at 1- and 5-km grains.

Table S2 Pearson correlations between predictions of species density at different grains.

Table S3 Attributes of sampled hot and arid sites.

Appendix S1 Methods and results for the 1- and 5-km grains of analysis.

Appendix S2 Discussion of existing studies about ants in extremely hot and arid places.

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BIOSKETCH

Clinton N. Jenkins is a Research Scientist at the University of Maryland, College Park. His research programme focuses on biodiversity and its conservation, with a focus on Brazil, the western Amazon, and assessment of the global protected area system.

Editor: Núria Roura-Pascual