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Fine-grained climate data alters the interpretation of a trait-based cline

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Abstract. Investigating responses to climate often rely on macroclimatic models. This is problematic because of the potential to miss or wrongly attribute relationships. Here we compare the explanatory power of macroclimatic models and near-surface topoclimatic models. Body-size measurements of the ant species, *Iridomyrmex purpureus*, were collected from separate colonies spanning a range of climatic conditions in a large region ($\sim$75,000 km^2) of Australia. Regional regression was used to derive two topoclimatic variables, while ANUCLIM was used to derive macroclimatic variables. Relationships were tested using linear mixed-effect models with Akaike information criterion used as an indication of the relative goodness of fit for each model. Significant trends for both topoclimatic variables with body size were detected but only one of the three macroclimatic variables showed a significant trend. Although the significant macroclimatic variable was correlated with one of the topoclimatic variables, the topoclimatic variable had greater explanatory power. Few studies have considered climatic data accuracy or the effects of inaccurately quantified climatic data on ecological theory. This cannot continue to be ignored. As we show in this study, there is potential for important trends to go undetected and interpretation of results to be completely different.

Key words: Bergmann's Rule; body size; climate change; Formicidae; Hunter Valley; *Iridomyrmex*; topoclimate.

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INTRODUCTION

Temperature related body-size clines have long been of interest since the observation of Carl Bergmann in 1847 who made the observation that closely related animals tend to be smaller in lower latitudes (warmer climates) and get larger with latitude (colder climates); later termed 'Bergmann's Rule' (Blackburn et al. 1999). With a rapidly warming planet (Duarte et al. 2012), interest in this topic is likely to continue as the rule offers potential insights into the effects of shifting climate regimes on development, growth rates, body size, and the potential for animals to adapt through phenotypic plasticity (Forster et al. 2012). Indeed, spatio-temporal shifts in body size should be of interest more broadly, because the trait has cascading effects through ecological communities (Lawton 1990). Every aspect of an animal's life is influenced by body size, including its interactions with the abiotic environment, the rates of its physiological processes, and the outcomes of its interactions with other organisms (Cushman et al. 1993). Problematically, the lack

of temperature information that are at the scale which are relevant for organisms such as terrestrial invertebrates have hampered investigation of climate-related body-sized clines at local and regional scales.

Studies investigating biodiversity-climate relationships typically use observations from the nearest standardised weather station (i.e., Stevenson screens ~1.5–2 m above flat, cleared areas) or estimates based on long-term (~50 year) averages interpolated from those observations (e.g., Baumgärtner and Hartmann 2000, Finch et al. 2008, Kumar and Stohlgren 2009). These renditions of climate are defined as macroclimate as only broad-scale trends are captured (after Stoutjesdijk and Barkman 1992).

Studies exploring relationships between biotic responses and climate—testing Bergmann's rule or otherwise—often rely on correlative evidence between occurrence records and corresponding macroclimatic data (e.g., Harris et al. 2012). However, there has been recent scrutiny over the appropriateness of macroclimatic data and the legitimacy of conclusions that can be subsequently drawn from them. Scherrer et al. (2011) for example postulated that predictions made using macroclimate data that do not account for effects of complex topography and plant cover could be highly inaccurate. They concluded that the use of interpolated weather station data can lead to overestimates when assessing elevation shifts. Thus there is an urgent need to interrogate climatic data because erroneous conclusions could be made or important trends could go undetected. Unfortunately, the accuracy of spatial climatic layers and the effects of systematic errors in these data are rarely considered (Soria-Auza et al. 2010, Storlie et al. 2013).

One approach to address these issues is to place large numbers of miniature and inexpensive data loggers across different environments to develop fine-grained (<100 m grid cells) topoclimatic models of near-surface conditions (e.g., Ashcroft and Gollan 2012). That is, models that account for a broad range of local-scale climate-forcing factors such as cold air drainage, topographic exposure, and foliage cover. While there are no studies to date that have comprehensively assessed the explanatory power of topoclimatic data derived from data loggers relative to the freely available and widely used

averages of macroclimate (e.g., WorldClim database, www.worldclim.org), there is mounting evidence of the explanatory power of topoclimatic grids relative to other coarse-scale variables such as land cover. Illán et al. (2010) for example found that for butterflies in a mountainous region in central Spain, topoclimatic models outperformed models based purely on land cover in 72% of occurrence models and 66% of abundance models. If topoclimatic data can explain more variation in structural parameters of biodiversity (e.g., species richness and abundance), then they may also be superior in understanding patterns in species traits across the landscape.

For climate-related body-size clines more specifically, a review by Shelomi (2012) pointed out that climate does not vary with latitude evenly across longitudes or altitudes because mountains and valleys will affect regional temperatures. Thus, comparing organism size along points of an isotherm map would be more meaningful than a latitude-only analysis. The critical review of Shelomi (2012) also noted that body size analyses should: examine broader climatic factors; data should represent two- or three-dimensional contour clines rather than latitude- or altitude-only data sets, and that precise habitat temperature readings should be taken in lieu of weather-station data wherever possible. To our knowledge, these recommendations have yet to be achieved in any study of climate-related body size clines. Here we investigated whether the body size of an ecologically dominant Australian ant was better explained by topoclimatic variables compared to similar and often utilized macroclimatic variables. The macroclimate variables were derived from official weather station data. The topoclimatic model on the other hand accounted for local scale climate forcing factors (and thus analogous to three-dimensional contour clines), and was a more accurate representation of the habitat temperatures as they were derived from a network of data loggers across a diversity of habitats in the landscape.

METHODS

Study region

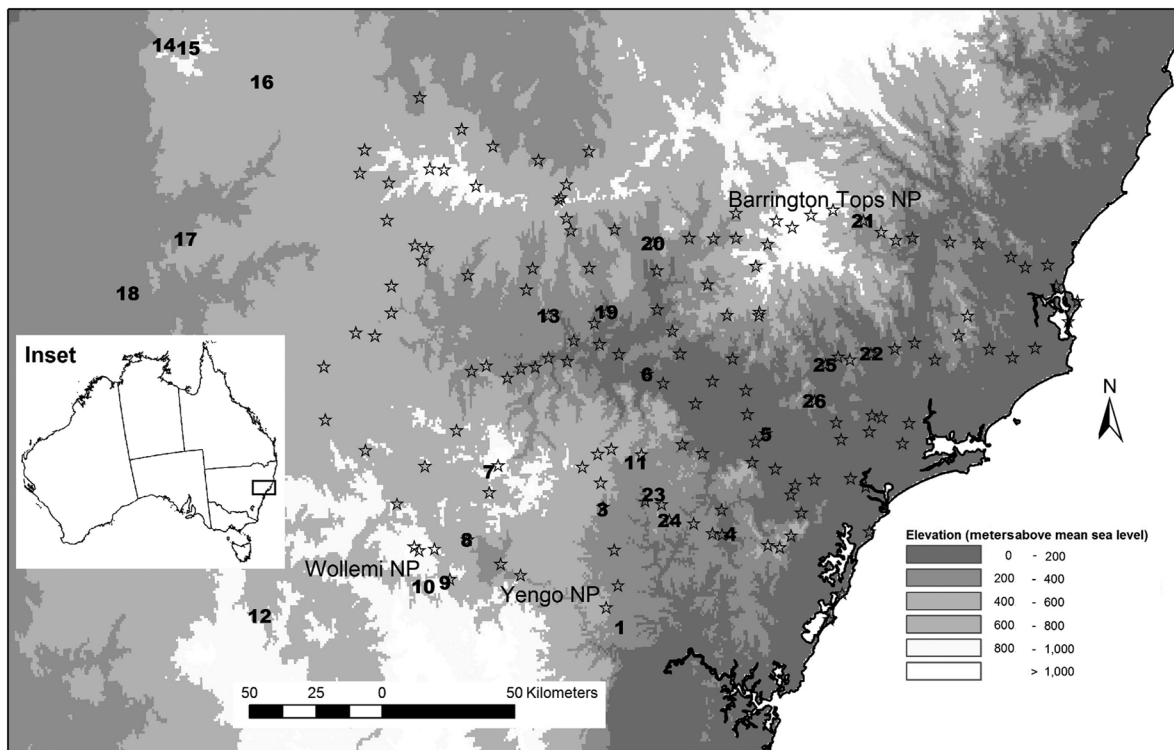Our study was conducted in the greater

Fig. 1. Location of study area in New South Wales, Australia (inset) and the 26 colonies where *Iridomyrmex purpureus* were collected for body size measurements. Numbering of colonies (1–26) is for illustrative and reference purposes only. Open stars show position of iButton data loggers used to produce the topoclimatic model in Ashcroft and Gollan (2012). NP = National Park.

Hunter Valley region, approximately 100 km north of Sydney, NSW, Australia (31.4–33.4° S, 149.4–152.6° E; Fig. 1 inset). This large study area (~375 km by 200 km) is topographically complex including deep gorges and rugged mountainous terrain particularly in and around Barrington Tops, Wollemi and Yengo National Parks. Low rolling hills with shallow broad valleys skirt the mountainous areas that eventually meet the relatively flat, surrounding plains and valley floors. Elevation ranges from sea level to around 1600 m in Barrington Tops National Park (Fig. 1). There is a mix of land use in the region spanning natural wilderness in the national parks, to intensive agriculture and mining mostly on the valley floor.

Study species

We used the endemic Australian ant species, *Iridomyrmex purpureus* (Smith 1858) as a model organism. This species is found throughout all of mainland Australia, thus spanning an east to west range of approximately 4000 km (or ~40° of longitude) and 3000 km north to south (or ~20° of latitude). *Iridomyrmex purpureus* is considered ecologically 'dominant' because they are highly abundant in their community, active and aggressive, and thus superior at interference and exploitation competition (Greenslade 1976). This dark red ant with a faintly iridescent purple to blue sheen builds large (~2 m radius), mound-shaped nests. Nests are conspicuous, not only due to size, but they are also covered in small pebbles, giving rise to the common name 'gravel ants'. *Iridomyrmex purpureus* has a monomorphic (single-sized) worker caste and so are ideal subjects for investigating patterns of intraspecific variation in body size. Moreover, specimens are easily collected as they are a fairly common species across the study area (*personal observation*). Established colonies can be made up of thousands to tens of thousands of individuals

(CSIRO 2013). Individuals are relatively large (~6 mm long) and thus easily handled, and their mounds are easily sighted from a distance.

Body size

Worker ants were collected at random from the surface of active mounds (total 26 nests across the study region) between 14th and 26th May 2011 (Fig. 1). Selection of individual mounds was not done a priori and so first involved their initial sighting from a moving vehicle. Whether individual ants were then sampled from a mound depended on its proximity to a previously cited mound. *Iridomyrmex purpureus* is known to create super-colonies of many small nests that are connected together, reaching as large as 650 m in length (CSIRO 2013). To avoid sampling individuals from the same colony, we ensured that the minimum distance between sampled mounds was larger than 650 m. In selecting individual mounds for sampling, we also attempted to ensure that a wide range of climatic and environmental conditions were surveyed. This included a range of elevations, modified and unmodified habitat and distance to coast.

Individual ants were collected by hand from the surface of mounds (~20) and immediately placed in 95% alcohol for transport. In the laboratory, heads were removed from eight individuals (chosen from the larger sample at random) at each site (total 208 heads) and glued on linear strips of card paper. The heads were examined using a dissecting microscope (Leica M205A) and maximum head widths (to 0.001) were measured using the Leica Application Suite V3.8. For each measurement, the head was positioned so that the plane of the face was parallel to the lens of microscope. We used head width as a measure of body size as it has been considered a standard and accurate measure of overall body size (Hölldobler and Wilson 1990).

Climate data

Macroclimatic variables.—A hand-held GPS (Garmin eTrex) was used to record the latitude and longitude of each of the 26 colonies. The ANUCLIM 6.1 package (Xu and Hutchinson 2011) was then used to estimate three bioclimatic variables corresponding to the geographic location of each nest using a digital elevation model (DEM) with a 25-m cell size. A similar method is used to derive the freely available and widely used (as discussed above) macroclimatic variables of WorldClim (see www.worldclim.org). The two temperature variables (BIO1 = mean annual temperature and BIO5 = maximum temperature of the warmest month), were chosen because they could be aligned with two hypotheses relating to body size clines in ectotherms. The first was the seasonality hypothesis, which predicts that body size should increase with temperature. Because season length increases with temperature, this allows longer growth periods and therefore bigger individuals (Chown and Gaston 1999). The combination of temperature and moisture has also led to the desiccation resistance hypothesis, where body size is expected to increase with aridity because the reduction in surface area-to-volume ratio in larger animals increases the ability to withstand desiccation (Stillwell et al. 2007). Therefore the third variable based on precipitation (BIO12 = mean annual precipitation) was also selected. We acknowledge here that our justification for using these three variables is a simplistic way of testing the above hypotheses and a thorough investigation might consider other macroclimatic variables and/or combinations of variables. Moreover, there are other hypotheses on body size patterns for ectotherms (e.g., Table 1 in Entling et al. 2010) and so we make no claims for completeness. However, we note that the main purpose of this work was to examine the relative performance of topoclimatic variables over macroclimatic variables, the latter of which are commonly used for testing body-size clines (e.g., Harris et al. 2012).

Topoclimatic variables.—For estimates of temperature and humidity that are hypothesised to be closer to what our model organism experienced, the fine-grain (25-m grid cell size) topoclimatic model published in Ashcroft and Gollan (2012) were used. These models were derived using a range of local-scale climate-forcing factors (e.g., topographic exposure, susceptibility to cold air drainage and % foliage cover). In brief, the data used to produce the models were collected from 127 iButton data loggers (DS1923 by Maxim) that recorded hourly temperature and humidity data between 1 June 2009 and 28 May 2010. Each data logger was housed in a plastic container with holes to allow air flow. Within the container, the logger was

Table 1. Correlation coefficients (r) between all pairs of predictor variables and output summaries of linear mixed-effect models of ant body size and predictor variables. Plots for each relationship are shown in Fig. 2. AIC, Akaike information criterion.

Variable	BIO1	BIO5	BIO12	Elevation	5thminH	P	AIC
BIO1						0.318	−524.735
BIO5	0.62					0.325	−524.703
BIO12	0.05	−0.56				0.030	−528.532
Elevation	−0.96	−0.44	−0.16			0.178	−525.571
5thminH	0.30	−0.48	0.79	−0.46		0.002	−533.099
95thmaxT	0.20	0.76	−0.78	−0.07	−0.79	0.018	−529.425

held in fine plastic gauze that was suspended approximately 5 cm above the ground surface using a plastic cable tie. Loggers were placed in a diversity of habitats and positioned across the entire study area (see Fig. 1 for locations and Ashcroft and Gollan [2012] for full details) to cover a broad range of environmental factors including distance to coast (ranging between 200 m and 224 km), elevation (ranging between 2 m and 1428 m), and remotely sensed foliage cover (ranging between 0 and 100%).

For temperature, we used the 95th percentile of maximum daily temperature gradient ("95thmaxT" hereafter). For humidity, we used the 5th percentile of minimum daily humidity gradient ("5thminH" hereafter). These variables capture the hottest and driest conditions at each site, even if they do not occur simultaneously or consecutively.

Statistical analysis

So that all predictor variables were directly comparable, all were standardised to a mean of zero and standard deviation of one. Correlations among all pairs of variables were first examined and their strengths assessed using the correlation coefficient (r). All 208 head measurements were then used to construct a linear mixed-effect model (using the residual maximum likelihood method) for each climatic variable. Mixed models are appropriate for representing clustered and therefore dependent data (Fox 2002). Site was treated as a random effect and body size and climatic variables were fixed. A linear line of best fit was fitted where trends were significant ($P <$ 0.05). Akaike information criterion (AIC) was used as an indication of the relative goodness of fit for each model. All analyses were conducted using the nlmn package in R (R Development Core Team 2008). We note here that non-linear

functions using GAMs were also fitted, but these were not selected over linear models.

RESULTS

Range of conditions sampled and correlations among predictor variables

The elevation where colonies were sampled ranged from 64 to 900 m above mean sea level (site 5 and 10, respectively; Fig. 1). In terms of the range of climatic conditions experienced by the 26 colonies, BIO1 ranged from 11.9°C at site 10 to 17.6°C at site 5. These two sites corresponded with the highest and lowest elevations and reflected the strong correlation between these two variables (r = −0.964; Table 1). The coolest 95thmaxT was 39.5°C at site 21, while the hottest temperature was 49.1°C at site 18. This was in contrast to the coolest and hottest sites identified by BIO5, which ranged from 25.7°C at site 10 to 31.7°C (site 14). Unlike the macroclimatic variable; BIO1, the 95thmaxT was not strongly correlated with elevation (r = −0.073).

The least amount of average annual rainfall was at site 18 (BIO12 = 574 mm), while the highest was at site 26 (BIO12 = 1082 mm). The humidity gradient derived from the topoclimate grid also indicated that site 18 was the driest (5thminH = 12.42%) although humidity was greatest at site 21 (5thminH = 37.34%). BIO12 and 5thminH were moderately and positively correlated as were BIO1 with BIO5, and BIO5 with 95thmaxT. Moderate, but negative correlations were also apparent between BIO12 and 95thmaxT, and 5thminH and 95thmaxT (Table 1).

Models of body size fitted with climatic variables

The smallest body size was 1.574 mm at site 26 and the largest was 2.134 mm at site 15. The

smallest and largest mean ($\pm$ SE) body sizes were also found at these two sites (1.709 ± 0.010 and 2.082 ± 0.044, respectively). Only one of the macroclimatic variables (BIO_{12}) showed a significant trend with body size (Table 1) and examination of the corresponding bi-plot showed a negative relationship (Fig. 2C). There were significant trends for both topoclimatic variables with body size (Table 1), but the direction of the relationship was different for each model. Body size increased with increasing temperature but, and in common with $BIO_{12,}$ decreased with increasing humidity (Fig. 2E–F). Comparison of AIC for models fitted with BIO_{12} and 5thminH showed that the latter was a better fit (-528.532 and -533.099, respectively; Table 1).

DISCUSSION

Our results showed that topoclimatic variables, which are hypothesised to better-reflect the climatic conditions that species are actually experiencing, explained more variation in the body size of the ant, *Iridomyrmex purpureus*, than did macroclimatic variables modelled using long-term averages from official meteorology stations. The main implication is that when relying on macroclimatic averages for understanding climate-related body size clines, there is a potential for important trends to go undetected and interpretation of results to be completely different. For example, if we had simply relied on mean annual temperature (BIO_1) or maximum temperature of the warmest month (BIO_5), then a trend with body size would not have been detected—as was the case in a study by Harris et al. (2012). When using topoclimate variables, we found significant trends between body size and temperature (95thmaxT) and humidity (5thminH). This highlights that not only is it desirable to have more proximal and direct predictors (sensu Austin 2002) such as topoclimate to explain the ecological trends, but it may indeed be necessary to avoid erroneous conclusions. Without the backing of empirical data but from a critical review of studies of body-size clines of insects, Shelomi (2012) noted that precise habitat temperature readings should be taken in lieu of weather-station data wherever possible. Our results are supportive of this recommendation in studies of climate-related

body size clines. While our study is the first to assess the utility of a topoclimatic model where data was drawn from a purposely-built iButton array at a landscape scale (see Ashcroft and Gollan 2012), we are not the first to highlight the potential for misinterpretation and inaccurate prediction due to the use of weather station data (e.g., Scherrer et al. 2011, Graae et al. 2012, Storlie et al. 2013). Therefore we are confident that our results are not spurious.

It should be noted that the size of the study area may influence the shape of relationships. For example, at a larger spatial extent (e.g., at a global scale or in our example, across the full latitudinal extent of *I. purpureus*' distribution) the temperature variables derived from the macro-climate model may detect significant trends. Non-linear clines such as sawtooth, stepwise, hump- and U-shape patterns are also possible, which can be due to marked physiological changes in species at a point along a cline (see Fig. 1 in Shelomi 2012). We cannot rule out these possibilities in our study, but we do note that trends identified by the topoclimatic variables may have also detected stronger trends over broader environmental ranges. Even if trends are detected at a larger spatial extent, it would be valid to question the realness of the relationship. Criticisms of using macroclimatic data for understanding biodiversity-climate relationships have been directed to those studies that use latitude as a surrogate of climatic parameters. Graae et al. (2012) highlighted that when using latitudinal gradients, a number of co-varying factors make it difficult to disentangle the true impact of changing temperatures compared to other latitudinal factors such as precipitation, irradiation, photoperiod and land-use changes. Latitudinal studies may also fail to detect significant trends (e.g., Andrew and Hughes 2008) due to these same potentially confounding factors (Shelomi 2012). Generating climate data using the topoclimatic models can account for some of these co-varying factors, and thus provide a more genuine rendition of conditions in the actual habitats that are occupied and used by species. Furthermore, when using elevation transects to represent a climate gradient, the same co-varying factors can make it just as problematic to identify genuine temperature gradients. Accounting for local-scale climate
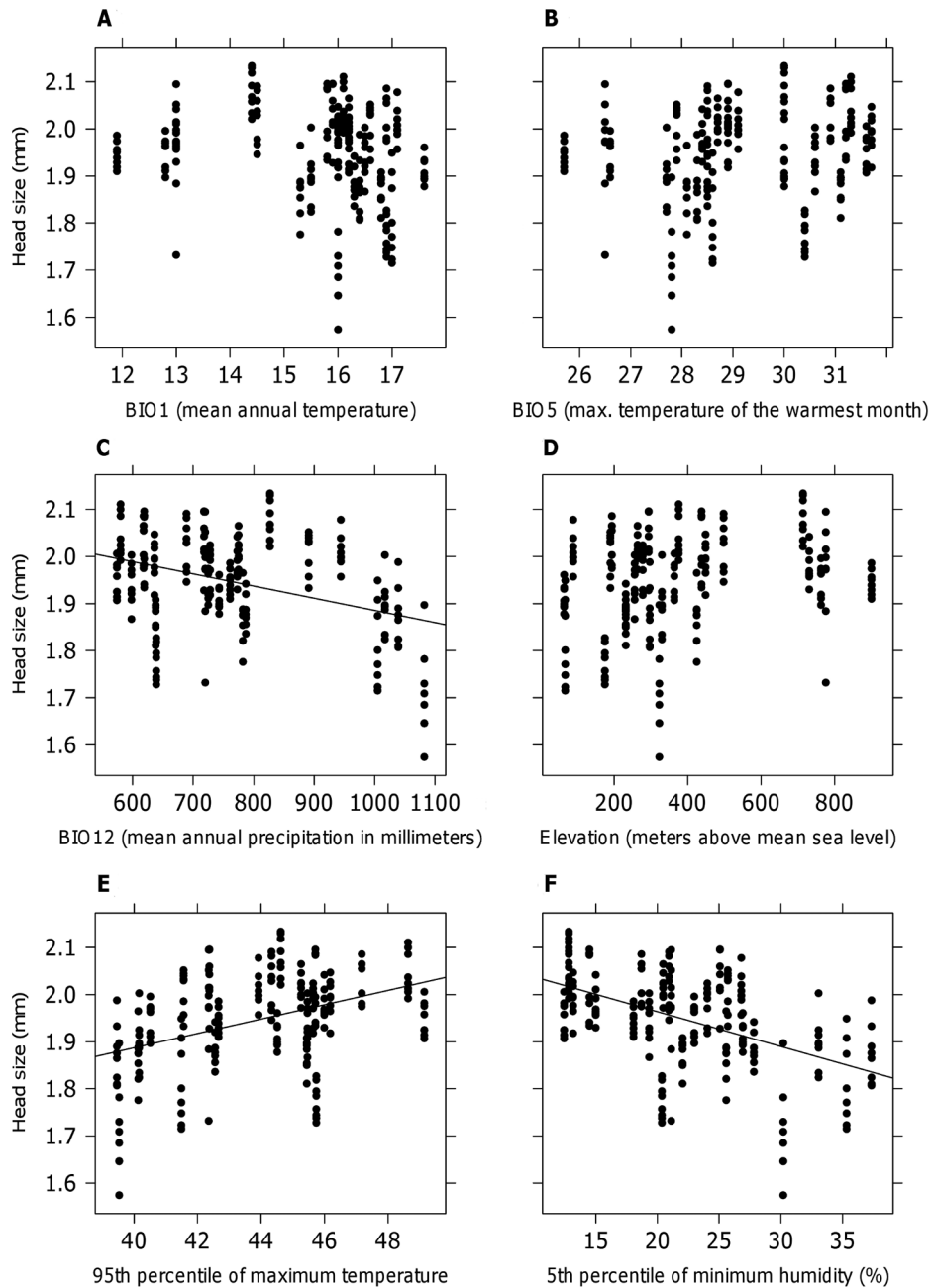
Fig. 2. Relationship between maximum body size of *Iridomyrmex purpureus* (eight individuals collected at 26 sites; n = 208) and five climatic variables (A–C and E–F). Elevation (D) was also included as it is often used as a surrogate of temperature. Plots are of raw data with the lines of best fit shown only for those models that were significant ($P < 0.05$; see Table 1). Temperatures are in °C.

forcing factors can generate more realistic renditions of climate for these studies as well, thereby providing confidence that significant trends are not spurious ones (Scherrer et al. 2011).

It could be argued that it is not completely fair to compare macroclimatic variables with those measured by iButtons at the ground level because they are completely different meteoro-

logical quantities. It is not surprising, for example, that the relative differences in the climatic values experienced at our study sites were large. For example, the coolest 95thmaxT derived by the topoclimatic model was 39.5°C (site 21), while the hottest temperature was 49.1°C at site 18. The coolest and hottest temperatures identified by the macroclimatic model ranged from 25.7°C and 31.7°C (site 10 and 14, respectively). These differences can be partly explained due to the fact that conditions measured at the ground level are different to those measured at 1.5 m above the ground by official Bureau of Meteorology weather stations (Geiger 1971). But as demonstrated by our results, studies attempting to understand biodiversity-climate relationships need to account for such large differences otherwise there is potential to miss trends and give erroneous conclusions. While larger and more mobile terrestrial animals (i.e., vertebrates) may experience temperatures over their spatial and temporal ranges that more closely matches the human-measured ambient temperatures (or macroclimate); ground living insects do not. Macroclimate may be suited for large and mobile terrestrial animals, but not for small, relatively immobile ones like insects.

Accounting for the difference between thermal conditions measured by official weather station data and those experienced by the organism, however, is not an easy task. Microhabitats where insects live can vary in unpredictable ways along a geographic range (Shelomi 2012) and where they can be predicted with some certainty, the relative difference is not consistent. For instance, recent work on topoclimatic models of landscape temperatures has shown that moisture plays a key role in dampening climate extremes and reducing variability (Ashcroft and Gollan 2013). The relative difference between temperatures measured by weather stations and those at the ground level are not as large on cloudy days, nor are they as large for winter maximum temperatures (Geiger 1971). The differences may be even bigger in snow covered landscapes where winter snow protection decouples the soil surface temperature from that at 2 m height (Körner 2003). When studying biodiversity-climate relationships, it is important to question whether this decoupling of the ground microclimate from the air temperature is signif-

icant compared to the large-scale climatic variation (Graae et al. 2012). If it is, then climate in habitats where species live may need to be measured in-situ.

In further consideration of the validity of our comparison, it is also worthy to note that variables derived by the macroclimatic model are long-term (1950–2000) averages while the variables derived by the topoclimate model were based on extreme conditions and based on only one year of data. The fact that the extreme topoclimatic variables explained more of the variation in body size than did data reflecting long-term climatic averages does, however, align with a growing number of studies showing that it is the extremes that matter ecologically (Pimm 2009). Averages miss the specific detail of extreme events (e.g., the peak temperature during heat waves) and it is this detail that matters (Pimm 2009). We champion, along with others (e.g., Thompson et al. 2013), for greater emphasis on extremes in biodiversity-climate studies.

In addition to extreme variables, it may also be more ecologically relevant to use recent climate data rather than long-term (30–50 years) averages of macroclimate. If macroclimatic data are used to establish relationships between climatic parameters and ecological processes, there is the very real possibility of a 'mix-match' between the temporal scale of the climatic observations and the biological processes operating. Invertebrates, including ants, generally have short-lives with rapid turnover and so it is plausible that body size is more closely tied to climatic conditions in the lead up to when they are collected or observed, rather than the long-term conditions. Indeed, body-size clines can vary over time, which is especially relevant for quickly evolving organisms such as insects (Shelomi 2012). Ontogenetic development is also very much linked to temperature and body size (Gillooly et al. 2002) and so this offers a further explanation for our results.

While our study is only correlative, we do feel that the trends in body size we detected are genuine as they support others who have shown evidence for the seasonality hypothesis (where body size increases with temperature driven by longer seasons; Chown and Klok 2003), as well as the desiccation resistance hypothesis (where

declining moisture plays a key role along with variation in temperature to produce larger bodies under dry and warm conditions; Stillwell et al. 2007). Indeed, our finding that body size increases with temperature has been referred to as 'converse Bergmann clines' and has been shown for a variety of insect species and their constituent parts (reviewed by Mousseau 1997, Blanckenhorn and Hellriegel 2002, Shelomi 2012).

It makes intuitive sense to use climate information that better reflects what species are actually experiencing (i.e., direct and proximal predictors; Austin 2002) rather than coarse-scale interpolations that only capture the general macroclimatic trends. Our results are yet another piece of evidence that the climate data and the methods to model it can influence outcomes (Soria-Auza et al. 2010, Storlie et al. 2013). The implementation of commonly employed macroclimatic layers represents a major weakness in understanding patterns across the landscape if they are applied at inappropriately fine scales (Daly 2006). The use of topoclimatic predictors is one way the weakness can be addressed, although it may also be possible to use other methods such as indirect estimates based on plant communities (Lenoir et al. 2013). Future challenges are in building topoclimatic models using remote sensing and to predict future climatic conditions. The latter is a significant one because the very properties that are responsible for driving local-scale scale conditions are themselves not necessarily enduring.

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