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# Contrasting topoclimate, long-term macroclimatic averages, and habitat variables for modelling ant biodiversity at landscape scales

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**Abstract.** 1. Spatial modelling is part of the solution for incorporating insects into conservation policy. Uptake, however, rests on identifying robust environmental predictors. Coarse-grained climate models based on long-term averages and similarly coarse environmental features may not be adequate, especially at regional scales where most planning is done. Here, we test whether topoclimatic variables, which are derived from local-scale climate forcing factors, are more important for structuring ant assemblages.

2. We quantified ant richness and species composition at 86 sites across a large (200 × 300 km) temperate region of southeast Australia, and tested the explanatory power of three groups of environmental variables: (i) topoclimatic variables, (ii) long-term climatic averages modelled from global data, and (iii) habitat features, namely, habitat complexity, soil pH, and soil texture. Generalised Additive and Generalised Dissimilarity Models were used to test predictors.

3. In univariate models, the topoclimatic estimator of maximum temperature (95maxT) explained the largest amount of variance in both richness and compositional turnover (20% and 24% of deviance respectively). The plot for richness indicated a positive but decelerating function of 95maxT. This was consistent for two of three habitat types. Habitat complexity was the most important predictor in cleared habitat (28%).

4. While a topoclimatic variable was a strong predictor of ant biodiversity across the landscape, this was not a 'magic bullet'. Other predictors such as complexity may be more applicable in certain habitat types. We concluded that tailored predictors are needed for landscapes with a mosaic of different land use.

**Key words.** Climate, energy limitation hypothesis, Formicidae, generalised dissimilarity modelling, habitat complexity.

## Introduction

Twenty or so years ago, advocacy for invertebrates in conservation initiatives began to build (e.g. see perspectives of Fry & Lonsdale, 1991; Kremen *et al.*, 1993; Samways, 1993). Although there have been a number of developments in taxonomy, statistical analysis, data compilation, and science communication, there are still impediments to incorporating invertebrates into conservation policy (Cardoso *et al.*, 2011; Leather, 2013). Spatial modelling techniques that allow mapping in previously unsurveyed locations have been proposed as part of the solution (see Cardoso *et al.*, 2011 and refs within). Models can then be used for conservation planning (e.g. Cabeza *et al.*, 2010). However, the reliability of predictive

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mapping relies on the strength of relationships between the variable(s) of interest and climatic, land-use or other variables that are used as predictors.

Predictive mapping also requires that data on predictors exist in the unsurveyed locations and that they are appropriately scaled to reflect genuine conditions experienced across the landscape of interest. Acquiring data meeting both requirements is problematic for invertebrates because most invertebrates perceive and respond to the environment at spatial and temporal scales that are far smaller than the typical scales of human perception (see Virtual Issue: 'Scaling conservation management actions to the fine-grained ecological responses of invertebrates' of *Insect Conservation and Diversity*). Conservation planning strategies using climate variables extracted from widely used and freely available coarse-grained models and future climate simulations using atmosphere–ocean general circulation models (e.g. WorldClim; www.worldclim.org), for instance, may suit many plants and vertebrates (e.g. Lawler *et al.*, 2009; Letten *et al.*, 2013, although see Ashcroft *et al.* in press), whereas they are likely to be ineffective for invertebrates. It is important to note that the issue is not simply 'a scale issue' that can simply be resolved using a climate model with a small grid cell size. It is more that the interpolation method to derive many climate grids is often interpolated from weather stations using only elevation and geographical location (e.g. Bioclim and WorldClim; Houlder *et al.*, 2003; Hijmans *et al.*, 2005).

The argument for which taxa that coarse-scale grids are more appropriate for may be irrelevant because there is increasing recognition that coarse-scale bioclimatic envelope models are of limited use for environmental management as most planning decisions are made within individual regions (Ferrier *et al.*, 2002; Lookingbill & Urban, 2003; Cabeza *et al.*, 2010). Greater emphasis on producing fine-scale models using a broader range of ecologically relevant variables have been called for (Austin & Van Niel, 2011). One method gaining popularity for achieving this in biodiversity modelling is through the use of topoclimate, that is, climate models that consider local climate-forcing factors such as exposure to prevailing winds, slope, and aspect (e.g. Ashcroft *et al.,* 2011; Ashcroft & Gollan, 2012).

Evidence to support the notion that topoclimate is key for understanding invertebrate patterns is mounting. Gollan *et al.* (2013), for example, found that body size of the meat ant, *Iridomyrmex purpureus*, was positively correlated with temperature (conforming to the so-called 'converse Bergmann cline'; Mousseau, 1997), but was not detected using coarse-grained, long-term climatic averages. For butterflies in a mountainous region in central Spain, Illán *et al.* (2010) found that climate models that were modelled using local climate-forcing factors outperformed models based purely on land cover in 72% of occurrence models and 66% of abundance models. Importantly, these studies further support the premise that climate is a crucial environmental parameter for controlling species distributions, especially for ectotherms (Moreno-Rueda & Pizarro, 2007; Aragón *et al.*, 2010).

Another important issue for any modelling lies in the choice of predictor(s). Ultimately, models should be based on an understanding of the environmental processes which control species distribution. Without careful consideration and selection of predictors being tested, there is a risk of detecting spurious correlations with variables that play no part in environmental processes that control species distribution (Austin & Meyers, 1996). This can be challenging for species that have not been studied in detail, where distribution data are absent or sparse, or when collective properties (e.g. species richness) are used. These are the realities of many invertebrate data sets, especially the hyper-diverse groups. In the absence of detailed ecological studies for each and every species and when collective properties are used, ecological theory and principles, and empirical relationships founded in other studies or taxonomic groups can provide clues as to the important predictors and the general shape of the resulting response.

With the prospect of increased climatic variability and increased temperatures in the future (IPCC, 2008), there has been recent interest in these two parameters and the theory underlying hypothesised spatial patterns. For example, at small scales, climate variability can stabilise competition and thus promote diversity by increasing the number of temporal niches available within a fixed space (Chesson, 2000). Contrarily, too much environmental variability can be detrimental to population persistence because of stochastic extinction (Boyce *et al.*, 2006). Others have suggested a unification of these models with richness peaking at intermediate levels of variability (Adler & Drake, 2008). For absolute temperatures, hot temperatures generally mean more species, with studies on ants showing a positive correlation between richness and temperature (Kaspari *et al.*, 2000a,b; Sanders *et al.*, 2007). The positive correlation is hypothesised to be the result of energy limitation, where energy puts constraints on both the density and the number of species that can be supported (Kaspari *et al.*, 2000b).

Aside from relationships with climate, spatial patterns in diversity have also been linked to habitat characteristics, in particular habitat complexity. Attributed to MacArthur and MacArthur (1961), the habitat heterogeneity hypothesis posits that structurally diverse habitats accommodate more species due to an increasing number of spatial niches. Numerous studies in a range of ecosystems have supported this by showing a positive relationship between diversity and habitat complexity (see review by Kovalenko *et al.*, 2012). This is, however, not always the case for terrestrial invertebrates where soil properties like hardness and texture may be more influential (e.g. Gollan *et al.*, 2009). Links between the soil and invertebrate organisms are also appreciated for conservation (Lal, 1991), and the impacts of soil management on invertebrates are well studied (e.g. Sharley *et al.*, 2008).

In this study we took a correlative approach to investigate the predictive power of temporal climate variability, absolute temperatures, and habitat characteristics on spatial patterns of ant diversity. Ants are an ideal invertebrate study group because they are ubiquitous, ecologically important, and easy to sample. Furthermore, ant richness and community composition can provide insight into key ecological processes and interactions such as nutrient cycling (Andersen & Sparling, 1997) and seed dispersal (Lomov *et al*., 2009). Because many different species can co-exist in the one place, they are the ideal model organisms for testing hypotheses in community ecology and, if strong and robust predictors can be identified, are a good bioindicator group for integrating into conservation policy and planning initiatives. Indeed, ants have been the bioindicator of choice for assessing the progress of ecological restoration and conservation strategies as part of land management more generally (Andersen, 1997; Andersen & Majer, 2004; Majer *et al*., 2007; Gollan *et al*., 2011).

We collected ants at 86 sites across a large (~300 km × 200 km) and topographically complex region in southeast Australia and took advantage of a topoclimatic model that had been derived from temperature data collected at the same sampling sites (Ashcroft & Gollan, 2012). This novel and unique data set allowed consideration of climatic conditions that are closer to what the ants actually experience as compared with the standardised Bureau of Meteorology (BoM) weather stations. Indeed, BoM data for investigating biodiversity–climate relationships have been criticised because: (i) instruments are sheltered in Stephenson screens at a height of 1.5–2 m and so do not reflect the conditions relevant for ground-dwelling fauna, germinating seeds, tender saplings, or ecological processes (Geiger, 1971); and (ii) observations are made on largely flat, unvegetated land and do not reflect the environments (e.g. gorges/forests) that many species actually live in (Geiger, 1971; Suggitt *et al*., 2011). The strength of relationships with topoclimate variables was contrasted against a set of long-term climate data modelled using weather station data, as well as a set of habitat variables, namely: soil pH, soil texture, elevation, and habitat complexity. While we acknowledge that there may be other environmental variables limiting ant distributions such as water table depth (see Tschinkel *et al*., 2012; Baccaro *et al*., 2013), we were constrained by the availability of data for our study area.

## Material and methods

### *Study region and study sites*

Our 86 study sites were spread across the greater Hunter Valley region in New South Wales, Australia (32°31′16″S 150°27′50″E; Fig. 1 inset), and were chosen to coincide with a previous study that developed fine-resolution topoclimatic grids across the wider region (Ashcroft & Gollan, 2012 more detail below). Ashcroft and Gollan (2012) achieved this by placing miniature temperature loggers in a range of vegetation types and aspects in an attempt to capture the widest variation in local climate conditions.

The study area as a whole (~300 km × 200 km) is topographically complex including deep gorges and rugged mountainous terrain particularly in and around

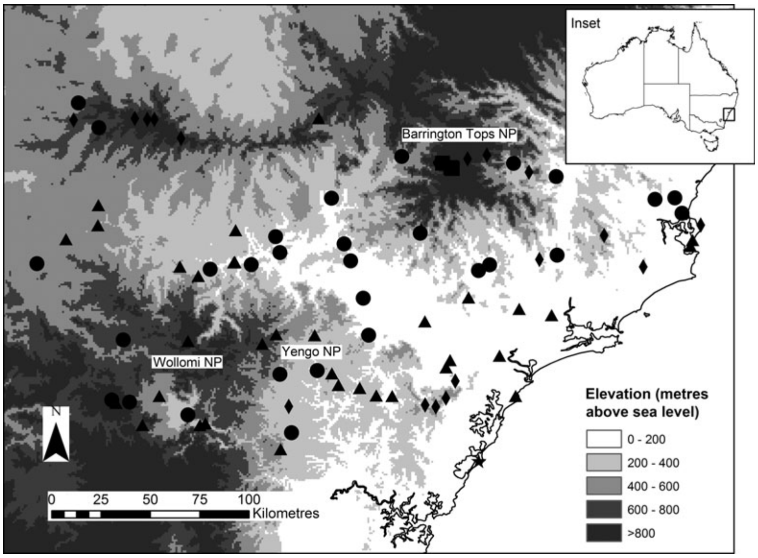

**Fig 1.** Location of the study region in relation to Australia (inset). Larger map shows sites where ants were pitfall trapped in relation to habitat type and elevation. Habitat types (based on maps of broad vegetation types) are as follows: dry sclerophyll forests (triangle, *n* = 34); wet forests (diamond, *n* = 19); cleared habitat (circle, *n* = 29); heathland (star, *n* = 1); and grassy woodland (square, *n* = 3).

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). Mostly on the valley floor and at low elevations, there is a wide range of production land for cattle, cropping, and mining. A wide range of natural ecosystem types are also represented, including coastal forests and heathland, temperate and sub-tropical rainforests, high-elevation peat swamps, and open grassy woodlands (Peake, 2003).

### *Ant diversity*

Ants were sampled using five pitfall traps per site (cylindrical plastic jars, 45 mm diameter, and 105 mm deep). Yet, only four traps were used in analyses due to disturbance of a single trap at several sites. Trapping was conducted in January 2012 (southern hemisphere's midsummer) and chosen to coincide with peak ant activity. Traps at each site were positioned at least 10 m apart along a straight line transect, although traps deviated from a straight line at some sites due to obstructions by trees, boulders, fallen logs, etc. In nearly all cases, the centre trap was within 2 m of where the data logger was positioned (see below). All traps were as follows: (i) one third filled with ethylene glycol as preservative; (ii) placed flush to the ground surface; and (iii) covered by an upturned weigh boat held above the opening of the trap with wooden food skewers. The cover acted to protect the trap from rainwater and debris.

Because of the large number of sites and distances covered, all traps could not be opened on the same day. Traps were subsequently opened in a sequence over a period of 6 days (between 7th and 12th January) and collected in the same sequence between 17th and 22nd January. Thus, all were operating for 10 days. Material was processed at laboratories at the University of Technology, Sydney, where ants were identified to genus, and then to species where possible using relevant keys (Shattuck, 2000; CSIRO, 2013). Species that could not be identified were assigned a morphospecies. All taxonomic assignments are hereafter referred to as 'species' regardless of whether they were assigned to a species or morphospecies. Ant diversity at a site was considered using two collective properties: species richness (the number of different species) and community composition. All specimens were deposited at the Australian Museum, Sydney.

### *Topoclimatic variables*

The topoclimatic estimators of temperature extremes: (i) 95th percentile of maximum temperature (hereafter, '95maxT') and (ii) 5th percentile of minimum temperature (hereafter, '5minT') were calculated for each of the 86 sites extracted from the models of Ashcroft and Gollan (2012). In summary, these models using 25-m resolution raster grids were produced from temperature recorded by miniature data loggers (DS1923 hygrochron iButtons by Maxim) at 150 sites for 666 days (between June 2009 and May 2011) across the study region. A regional regression approach used the local-scale forcing factors: elevation, distance to coast, canopy cover, latitude, cold-air drainage, and topographic exposure to prevailing winds as predictors. By utilising percentiles, and since these data were measured at hourly intervals over a 2 year period, it can be assumed that the 95maxT and 5minT captured the hottest and coldest conditions at each site (respectively), even if they did not occur simultaneously or consecutively. Consistent patterns have since been confirmed with data collection over a subsequent 2-year period (M. B. Ashcroft & J. R. Gollan, unpub. data). We chose to focus on these two gradients because they are likely to have more relevance than quantities such as mean annual temperature for ecological systems (Pimm, 2009). 95maxT was largely influenced by canopy cover and exposure to the northwest. 5minT in contrast was largely determined by cold air drainage, which is common under clear skies, low wind, and anticyclonic conditions. Full details of the topoclimatic models and analytical procedures can be found in Ashcroft and Gollan (2012).

To calculate variability in each climate parameter, variation was initially partitioned into three timescales: (i) intra-seasonal variation; (ii) intra-annual variation; and (iii) inter-annual variation. An overall measure of variability for each (hereafter, 'v95maxT' and 'v5minT') was then calculated as the average of the three timescales. Full details of this procedure can be found in Ashcroft *et al.* (2012).

### *Long-term macroclimate variables*

The ANUCLIM 6.1 package (Xu & Hutchinson, 2011) was used to estimate five macroclimatic variables corresponding to the geographic location of each site using a digital elevation model (DEM) with a 25-m cell size. ANUCLIM uses decades of monthly mean temperature and rainfall values from official BoM weather stations (30 in the study region) and uses latitude, longitude, and elevation to interpolate climate variables using thin-plate smoothing splines. Hereafter, we refer to these variables as 'macroclimate' because local-scale climate-forcing factors such as aspect, canopy cover, and exposure are not considered, and therefore only broad-scale trends are captured (after Stoutjesdijk & Barkman, 1992). This same method is used to derive the freely available and widely used (as discussed above) variables as part of the WorldClim database (see www.worldclim.org). The variables used for analyses were as follows: mean annual temperature (hereafter, 'BIO1'); mean diurnal range (hereafter, 'BIO2'); maximum temperature of the warmest month (hereafter, 'BIO5'); minimum temperature of the coldest month (hereafter, 'BIO6'); and mean annual rainfall (hereafter, 'BIO12').

### *Habitat attributes*

Habitat attributes considered were two soil properties (pH and soil texture), habitat complexity, and elevation. Soil pH was determined at each site from a bulked sample using a colorimetric pH test kit (Manutec Pty. Ltd., Cavan, South Australia, Australia). The bulked sample was the product of thoroughly mixing the excavated material from the holes dug for the pitfall traps (as described above). Soil texture using the bulked sample was determined using the protocols of Department of Environment and Primary Industries Victoria (Anonymous, 2013). In brief, the method involves moistening a sample of soil, manipulating the bolus in the palm of the hand, and then comparing the feel and behaviour against a texture category. There were 21 ordinal categories ranging from sand to heavy clay with the order reflecting decreasing amounts of coarse sand particles and an increasing amount of fine clay particles. The nominal categories were re-assigned the ordered nominal values to accommodate the regression analyses (see below).

Habitat complexity was determined using a modification of Coops and Catling (1997). Here, eight habitat variables [amount of: rock cover, coarse woody debris, and amount of foliage in six strata (0–25 cm; 25 cm–1 m; 1–2 m; 2–5 m; 5–10 m; and >10 m)] were scored using an ordinal scoring system (0–9), where zero denoted an absence and nine was at maximum. Habitat complexity was then determined by summing the eight individual components.

### *Statistical analyses*

For species richness, we produced a Generalised Additive Model (Hastie & Tibshirani, 1990) using the mgcv package (Wood, 2013) in R (R Development Core Team, 2008) for individual predictors. Each predictor was included as a spline with two degrees of freedom. This allowed for non-linear response shapes, but did not provide enough freedom for complex responses which may lead to over-fitting. GAMs were fitted to data at all 86 sites. We then modelled species richness for individual vegetation communities to assess generalities of relationships (if any). Broad vegetation communities were identified for each site using a state-wide vegetation layer (200 m × 200 m cell size) from the NSW Office of Environment and Heritage (Keith, 2002). Eight categories were initially identified. So there were enough data points for analysis; some of the initial eight were reduced to three by combing some categories. '*Dry sclerophyll forests* (*grassy subformation*)' and '*Dry sclerophyll forests* (*shrubby subformation*)' were combined to the single category '*Dry sclerophyll forests*' ($n = 34$). '*Rainforests*', '*Wet sclerophyll forests* (*Grassy subformation*)', and '*Wet sclerophyll forests* (*Shrubby subformation*)' were combined to the single category '*Wet forests*' ($n = 19$). The category, '*Cleared*' ($n = 29$), was places where the native vegetation community had been removed or severely modified for land use like grazing and other intensive agricultural activities. Heathlands and grassy woodlands were not considered in isolation as there were insufficient data points ($n = 1$ and 3 respectively). Vegetation communities identified using the vegetation layer were field validated at the time traps were collected. The per cent deviance explained and Akaike Information Criterion (AIC) were used to assess the strength of relationships among models. The AIC is essentially a goodness-of-fit measure that provides a way to compare the relative quality of a statistical model. Given a set of candidate models, the 'preferred' model has the smaller AIC value (Akaike, 1973).

Generalised dissimilarity modelling (GDM; Ferrier *et al.*, 2002) was used to analyse spatial patterns of turnover in community composition and to determine the relative explanatory power of each environmental variable. GDM is an extension of matrix regression, but overcomes the two different types of non-linearity commonly encountered in ecological data: (i) The curvilinear relationship between increasing ecological distance and observed compositional dissimilarity between sites; and (ii) the variation in the rate of compositional turnover at different positions along environmental gradients (Ferrier *et al.*, 2007). GDM is thus suited to invertebrate data sets that are notorious for exhibiting high levels of beta diversity (i.e. a sizeable number of sites that share no species with one another).

A GDM was fitted using all predictors, which automatically removed environmental factors not significantly affecting turnover in species composition. A GDM was then produced for significant predictors independently, and the relative fit for each predictor was assessed by examining the percentage deviance explained. Response plots were examined to assess: (i) the total amount of compositional turnover associated with each predictor (as indicated by the maximum height reached on the $y$-axis by each function), and (ii) the rate of compositional turnover, and how this rate varied along each gradient (as indicated by the slope of each function).

Compositional dissimilarity in all GDMs was calculated using the Bray–Curtis measure based on presence–absence data. Three-spline basis functions were used for each predictor. Geographical distance (straight line) between sites was included as a model term using the latitude and longitude for each site. This assessed structuring that was potentially due to spatial autocorrelation. GDMs were produced for the entire data set only as the sample size of each habitat type was too small. GDMs were produced using the gdmfunc.1.1 package (Ferrier & Manion, 2007) in R.

## Results

### *Range in environmental predictors captured*

For variables capturing the warm gradients (i.e. max95T and BIO5) and the long-term average temperature

**Table 1.** The mean ± SD for each environmental predictor within four habitat types and all habitat types combined.

| | Cleared habitat (*n* = 29) | Dry sclerophyll forests (*n* = 34) | Wet forests (*n* = 19) | All habitats combined (*n* = 86*) |
|---|---|---|---|---|
| 95maxT | 43.2 ± 4.4 (32.0–48.5) | 41.2 ± 4.1 (32.7–48.9) | 34.2 ± 3.7 (29.1 –42.8) | 39.0 ± 5.4 (29.1–48.9) |
| 5minT | 7.0 ± 2.6 (1.8–12.8) | 9.0 ± 2.8 (1.9–14.0) | 10.1 ± 3.7 (1.3–15.1) | 8.3 ± 3.5 (0.3–15.1) |
| v95maxT | 6.0 ± 0.1 (3.8–7.4) | 6.0 ± 0.7 (4.0–7.2) | 5.7 ± 0.7 (3.9–6.4) | 5.9 ± 0.7 (3.8–7.4) |
| v5minT | 6.1 ± 0.6 (4.8–7.2) | 5.6 ± 0.8 (4.5–7.9) | 5.1 ± 0.8 (4.0–7.1) | 5.7 ± 0.8 (4.0–7.9) |
| BIO1 | 15.9 ± 1.7 (11.2–17.5) | 15.6 ± 16.2 (11.5–17.7) | 14.0 ± 2.2 (10.3 –17.5) | 15.1 ± 2.1 (9.9–17.7) |
| BIO2 | 12.9 ± 0.1 (11.5–14.1) | 12.4 ± 1.1 (9.2–14.1) | 11.7 ± 10.4 (9.9–13.6) | 12.3 ± 1.2 (9.2–14.1) |
| BIO5 | 28.9 ± 1.7 (24.7–31.0) | 28.2 ± 1.5 (25.2–31.0) | 26.0 ± 1.7 (22.4–28.7) | 27.7 ± 2.2 (22.0–31.0) |
| BIO6 | 2.8 ± 1.6 (−0.5 to 4.7) | 2.8 ± 1.9 (−0.3 to 6.5) | 1.8 ± 2.5 (−1.4 to 5.5) | 2.5 ± 2.1 (−1.4 to 6.5) |
| BIO12 | 811 ± 204 (585–1213) | 835 ± 204 (599–1359) | 1129 ± 270 (703 –1663) | 916 ± 267 (585–1663) |
| Elevation | 302 ± 278 (2–1026) | 345 ± 278 (10–984) | 667 ± 438 (54–1388) | 433 ± 389 (2–1449) |
| Habitat complexity | 13.5 ± 6.8 (3–28) | 25.1 ± 6.5 (6–39) | 30.3 ± 7.0 (18–46) | 22 ± 9 (3–46) |
| Soil pH | 6.3 ± 0.5 (5 –7) | 6.1 ± 0.6 (5–7) | 6.5 ± 0.7 (4.5–8) | 6.3 ± 0.6 (4.5–8.0) |
| Soil texture | 7.7 ± 3.7 (2–15) | 5.8 ± 3.2 (2–11) | 8.0 ± 4.1 (2–16) | 7 ± 4 (2–16) |

The range (minimum–maximum) for each is given in parentheses.

*Four sites not belonging to 'Cleared habitat', 'Dry sclerophyll forests', or 'Wet forests' were included in 'All habitats combined'.

(i.e. BIO1), wet forest (WF) sites tended to be coolest, cleared sites generally warmest, and dry sclerophyll forest (DSF) intermediate. The ranges captured for each variable, however, indicated that some WF sites could be similar or warmer than some cleared sites (Table 1). For variables capturing cool gradients (i.e. 5minT and BIO6), the average 5minT within each habitat type indicated that cleared habitat tended to be coolest, WFs warmest, and DSFs intermediate. In contrast, the average of BIO6 showed that WFs were coolest, whereas cleared habitat and DSFs were similar. This pattern was the same for BIO12 (mean annual rainfall), where WFs were wettest and cleared and DSFs similar (Table 1).

For habitat attributes, WF sites tended to be at highest elevations, whereas cleared and DSF sites were at similar elevation. Averages of habitat complexity indicated that complexity tended to be higher in WFs, lowest in cleared habitat, and intermediate in DSFs, although the range indicated that some cleared habitat (3–28) could be just as complex as WF sites (18–46). While the range in soil pH captured was rather broad (4.5–8.0), the mean was similar across all habitat types (Table 1). The distribution of all environmental variables across all sites is included as (Figs S1–S13).

### *Species richness models using single predictors*

A total of 153 species and 15 016 individuals were collected in the 344 traps (86 sites, 4 traps per site). Species richness at the site-level ranged from 1 to 23 with a mean (±SD) of 11 species per site (±4). The distribution of species richness across all sites is included as (Fig. S14).

Across all habitat types combined and in single-predictor GAMs, '95MaxT' explained the greatest variation in ant species richness (20.3%). This was also the case for DSFs and WFs (18.3% and 38.9% respectively). The variable reflecting the long-term average of the maximum temperature of the warmest month (BIO5) was also a fairly strong predictor, explaining 3.4%, 1.4% and 0.4% less than models for all habitats, WF, and DSFs respectively. For all three models, the partial response plots showed that species richness increased with increasing maximum temperature (as indicated by 95MaxT) before reaching a peak with a slight decline (Fig. 2a–c). The most important single predictor in cleared habitat was 'Habitat complexity', which explained 27.6% of the deviance. Each of the long-term climate variables explained around 9% or less of the deviance in species richness (Table 2). The partial response plot showed increasing richness with increasing values of complexity (Fig. 2d).

### *Community composition*

Two local climate predictors ('v95maxT' and '5minT') and two long-term climate predictors (BIO6 and BIO12) did not significantly affect turnover in species composition and so were not considered further. The GDM of the 10 remaining predictors explained 29.5% of the deviance in observed species turnover. Fitted functions for individual predictor variables showed their relative importance and shape of the response surface (Fig. 3a–j). Comparison of the maximum heights reached (i.e. *y*-axis range) by each function indicated that '95maxT' was the most important single variable (Fig. 3e). This variable in isolation also explained the greatest percentage of the deviance in observed species turnover (24.4%). The variable explaining the second highest deviance was BIO5 (16.5%) and the response in turnover revealed that it was not as important as 95maxT. The fitted functions indicated some importance of 'Habitat complexity' (Fig. 3b) and 'Elevation' (Fig. 3f) to spatial turnover.

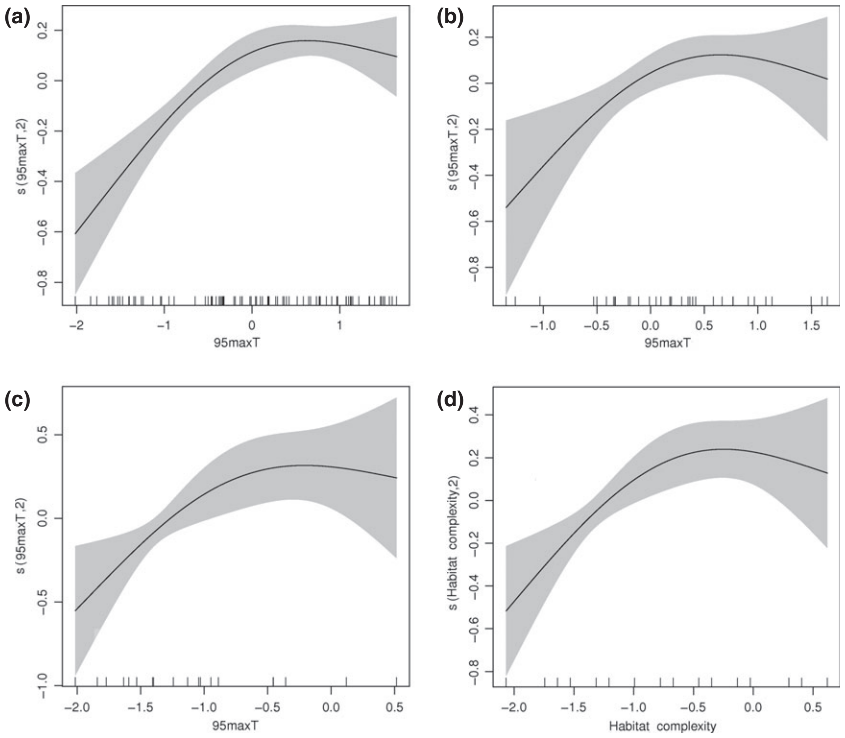

**Fig 2.** Partial response plots (with 95% confidence intervals) of predictors that explained the largest percentage of deviance in ant species richness. Panels a, b, c, and d show responses in ‘All habitats types combined ($n$ = 86)’, ‘Dry sclerophyll forests’ ($n$ = 34), ‘Wet forests ($n$ = 19)’, and ‘Cleared habitat ($n$ = 29)’ respectively. The deviance explained for all predictors in single-parameter models are shown in Table 1.

## Discussion

Across a large region comprising different land use and vegetation types, our results clearly showed that maximum temperature is an important parameter for explaining spatial patterns of ant diversity. In conjunction with topoclimatic models derived using local-scale climate-forcing factors (e.g. Ashcroft & Gollan, 2012) or freely available long-term climatic data (e.g. www.worldclim.org), the predictive models that are needed for incorporating ants into conservation planning and policy are conceivable. The finding that warmer sites had more ant species than cooler sites agrees with other studies examining environmental factors shaping ant assemblages at local (e.g. Sanders *et al.*, 2007) and global scales (Kaspari *et al.*, 2000a) and thus we are confident that our results are not spurious.

Across all habitat types, and in two of the three single-habitat types, ant species richness increased with maximum temperature before reaching a peak and then decreasing. For compositional turnover, maximum temperature also had the greatest total effect. While studies on plants and zooplankton have shown that climate variability plays an important role in controlling richness gradients (e.g. Shurin *et al.*, 2010; Letten *et al.*, 2013), for ants at least, we found little justification for its attention when modelling diversity. While community dynamics and spatial patterns driven by climatic variability seem plausible for explaining patterns in diversity, our results, along with studies with similar objectives (e.g. Kaspari *et al.*, 2000b), indicate that it is questionable as to whether the predictions about variability hold for terrestrial invertebrates. For these organisms, absolute temperatures may be more important than variability because it is the available amount of energy that puts constraints on both the density and the number of species that can be supported (Kaspari *et al.*, 2000b). Indeed, energy availability has long been considered a fundamental constraint to species richness (Hutchinson, 1959; Connell & Orias, 1964; although see Currie, 1991).

In general, ants are described as ‘thermophiles’ because of their aversion towards cool moist conditions (Hölldobler & Wilson, 1990). So perhaps it is no surprise that maximum temperature was the most important variable for explaining patterns of ant diversity. The aversion for cool moist conditions was clear in our analysis of species richness in wet forests where maximum temperature explained almost twice the deviance (38.9%) in both dry sclerophyll forest (18.3%) and all habitats combined (20.3%). In all three cases, species richness increased with increasing temperature (Fig. 2a–c). The peak of the response varied between ~38 and 42 °C when all habitat

**Table 2.** Per cent deviance explained in ant species richness and community composition.

| Species richness | | | | | Community composition |
|---|---|---|---|---|---|
| Predictor variable | Cleared habitat ($n$ = 29) | Dry sclerophyll forests ($n$ = 34) | Wet forests ($n$ = 19) | All habitats combined ($n$ = 86*) | All habitats combined ($n$ = 86*) |
| Geographic distance | 4.4 (177) | 1.2 (207) | 4.1 (109) | 8.8 (509) | 1.4 |
| 95maxT | 4.2 (174) | 18.3 (196) | 38.9 (97) | 20.3 (489) | 24.4 |
| v95maxT | 6.1 (174) | 1.8 (204) | 1.1 (107) | 2.0 (518) | Not selected |
| 5minT | 2.3 (176) | 1.9 (204) | 1.0 (107) | 5.4 (513) | Not selected |
| v5minT | 9.3 (172) | 3.3 (204) | 10.6 (105) | 6.5 (511) | 7.8 |
| Soil pH | 20.8 (166) | 17.6 (196) | 0.8 (108) | 1.3 (519) | 0.7 |
| Soil texture | 9.9 (172) | 13.8 (194) | 21.9 (104) | 4.1 (515) | 0.1 |
| Habitat complexity | 27.6 (163) | 0.3 (205) | 6.8 (106) | 7.6 (509) | 4.3 |
| Elevation | 13.3 (170) | 13.0 (199) | 16.2 (103) | 10.5 (505) | 10.3 |
| BIO1 | 18.8 (167) | 9.6 (200) | 16.2 (103) | 7.4 (510) | 8.5 |
| BIO2 | 0.9 (176) | 10.6 (199) | 8.4 (105) | 10.0 (505) | 5.2 |
| BIO5 | 14.1 (170) | 17.9 (196) | 37.3 (98) | 16.9 (494) | 16.5 |
| BIO6 | 11.2 (171) | 9.4 (200) | 8.3 (105) | 6.8 (510) | Not selected |
| BIO12 | 5.3 (174) | 9.75 (200) | 22.9 (102) | 16.0 (496) | Not selected |

For species richness, the deviance explained is for single-predictor models fitted with a Generalised Additive Model using a spline with two degrees of freedom. Akaike Information Criterion is shown in parentheses. Partial response plots for the predictor explaining the greatest deviance in each model are shown in Fig. 2 (panels a–d). For community composition, a Generalised Dissimilarity Model revealed that 10 of the 14 predictors were important. Partial responses for all 10 are shown in Fig. 3 (panels a–j).

*Four sites not belonging to 'Cleared habitat', 'Dry sclerophyll forests', or 'Wet forests' were included in 'All habitats combined'.

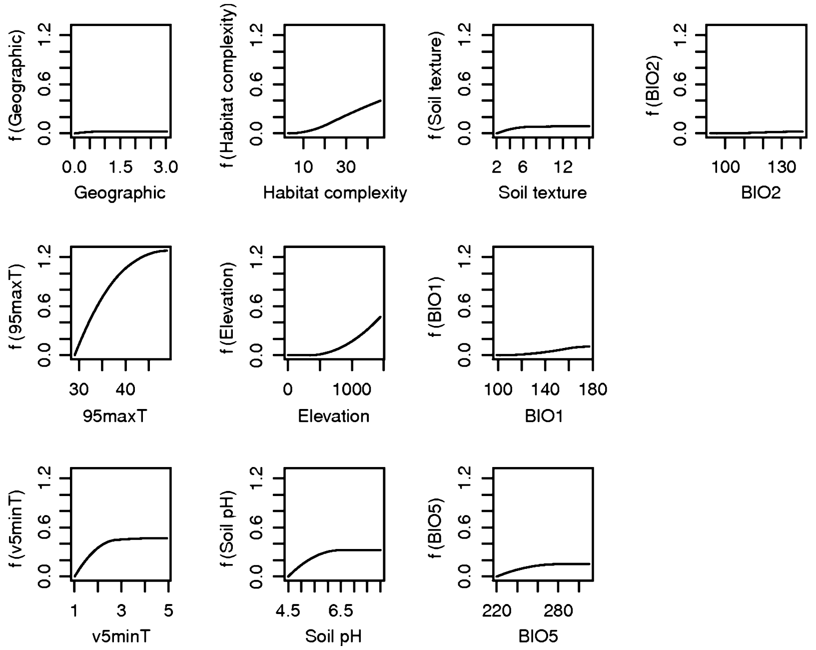

**Fig 3.** Generalised Dissimilarity Model showing fitted functions of individual predictors (panels a–j) to ant communities from 86 sites in southeast NSW, Australia (Fig. 1). Percentage deviance explained for a given predictor is shown in Table 1.

types were combined, which could well represent the tipping point where energy starts to constrain the number of species that can be supported. Whether these values are applicable to other regions or for other invertebrate groups requires more research. Further evidence for such a tipping point could provide vital clues as to the landscape effects of global warming. With rising global temperatures predicted in the future (IPCC, 2008), a redistribution of diversity is a real potential, where the cooler areas (which tend to be species poor) become susceptible to invasion of new species under warmer conditions (Roura-Pascual *et al.*, 2009; Bertelsmeier *et al.*, 2013).

The exception to the maximum temperature gradient being important for predicting ant biodiversity was in cleared habitat (Table 2). A poor relationship is perhaps intuitive as all cleared habitats would be expected to be warm relative to forests that have canopies that may cause greater spatial variation in thermal conditions. Some cleared sites, however, experienced conditions that were just as cool (in terms of 95maxT at least) as for wet forest and dry sclerophyll forest (Table 1; Figs S1–S13). Hence, we did not simply capture a portion of the overall temperature gradient in cleared habitat. As the temperature range was just as wide as the gradient for wet forest and dry sclerophyll forest, it is reasonable to conclude that any one predictor may not hold across all types of habitat types. The implication of this for predictive mapping is that tailored predictors are needed for modelling within particular habitat types.

The results of our study also highlight that it is more desirable to have more proximal and direct predictors (*sensu* Austin, 2002) of temperature rather than reliance on proxies such as elevation to explain ecological trends. Elevation is often used to infer temperature gradients when climatic data have not been measured or are otherwise unavailable (e.g. Gilbert, 2010). The relationship between long-term (50 years) mean annual temperature (as derived by BioClim; www.worldclim.org; Hijmans *et al.*, 2005) and elevation at our 86 study sites was almost a perfect correlation ($R^2 = 0.987$). As our results showed, elevation (and its equivalent at the scale of our study, mean annual temperature) was a relatively poor predictor of ant diversity compared with maximum temperatures (Table 2). Thus, the purported importance of climatic means for controlling diversity gradients at broad scales (Francis & Currie, 2003) did not hold at the regional scale of our analysis. A possible reason for this is that we used contemporary climate data which are more biologically meaningful than long-term averages. If macroclimatic data are used to establish relationships between climatic parameters and diversity, there is the very real possibility of a ‘mis-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 community dynamics are more closely tied to climatic conditions in the lead up to when they are collected or observed, rather than averages of long-term conditions. Even at broad geographic scales this source of error could well hold. This is not to say that long-term macroclimatic averages are not informative. Indeed, BIO5 (maximum temperature of the warmest month) was the second strongest predictor for richness. But our results did show that models using small and inexpensive *in situ* data loggers can explain more deviance and be a better fit than long-term climatic averages. Whether this improvement is warranted will depend on the needs of the individual study.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12081:

**Figure S1.** Distribution of 95maxT across the three major habitat types (cleared = cleared habitat, DSF = dry sclerophyll forest, and WF = wet forest).

**Figure S2.** Distribution of 5minT across the three major habitat types (cleared = cleared habitat, DSF = dry sclerophyll forest, and WF = wet forest).

**Figure S3.** Distribution of v95maxT across the three major habitat types (cleared = cleared habitat, DSF = dry sclerophyll forest, and WF = wet forest).

**Figure S4**. Distribution of v5minT across the three major habitat types (cleared = cleared habitat, DSF = dry sclerophyll forest, and WF = wet forest).

**Figure S5.** Distribution of BIO1 across the three major habitat types (cleared = cleared habitat, DSF = dry sclerophyll forest, and WF = wet forest).

**Figure S6.** Distribution of BIO5 across the three major habitat types (cleared = cleared habitat, DSF = dry sclerophyll forest, and WF = wet forest).

**Figure S7.** Distribution of BIO6 across the three major habitat types (cleared = cleared habitat, DSF = dry sclerophyll forest, and WF = wet forest).

**Figure S8.** Distribution of BIO12 across the three major habitat types (cleared = cleared habitat, DSF = dry sclerophyll forest, and WF = wet forest).

**Figure S9.** Distribution of BIO2 across the three major habitat types (cleared = cleared habitat, DSF = dry sclerophyll forest, and WF = wet forest).

**Figure S10.** Distribution of habitat complexity across the three major habitat types (cleared = cleared habitat, DSF = dry sclerophyll forest, and WF = wet forest).

**Figure S11.** Distribution of elevation across the three major habitat types (cleared = cleared habitat, DSF = dry sclerophyll forest, and WF = wet forest).

**Figure S12.** Distribution of soil pH across the three major habitat types (cleared = cleared habitat, DSF = dry sclerophyll forest, and WF = wet forest).

**Figure S13.** Distribution of soil texture class across the three major habitat types (cleared = cleared habitat, DSF = dry sclerophyll forest, and WF = wet forest).

**Figure S14.** Distribution of ant species richness across the three major habitat types (cleared = cleared habitat, DSF = dry sclerophyll forest, and WF = wet forest).

## References

Adler, P.B. & Drake, J.M. (2008) Environmental variation, stochastic extinction, and competitive coexistence. *American Naturalist*, **172**, 186–195.

Akaike, H. (1973) Information theory as an extension of the maximum likelihood principle. *Second International Symposium on Information Theory* (ed. by B.N. Petrov and F. Csaki), pp. 267–281, Akademiai Kiado, Budapest, Hungary.

Andersen, A.N. (1997) Using ants as bioindicators: multi-scale issues in ant community ecology. *Conservation Ecology*, **1**, 8.

Andersen, A.N. & Majer, J.D. (2004) Ants show the way down under: invertebrates as bioindicators in land management. *Frontiers in Ecology and the Environment*, **2**, 291–298.

Andersen, A.N. & Sparling, G.P. (1997) Ants as indicators of restoration success: relationship with soil microbial biomass in the Australian seasonal tropics. *Restoration Ecology*, **5**, 109–114.

Anonymous (2013) Soil Texture. Department of Environment and Primary Industries Victoria. < http://vro.dpi.vic.gov.au/dpi/vro/vrosite.nsf/pages/soilhealth_texture > 3rd April 2011.

Aragón, P., Lobo, J.M., Olalla-Tárraga, M.Á. & Rodríguez, M.Á. (2010) The contribution of contemporary climate to ectothermic and endothermic vertebrate distributions in a glacial refuge. *Global Ecology and Biogeography*, **19**, 40–49.

Ashcroft, M.B., Cavanagh, R., Eldridge, M. & Gollan, J.R. (In Press) Testing the ability of topoclimatic grids of extreme temperatures to explain the distribution of the endangered brush-tailed rock-wallaby (*Petrogale penicillata*). *Journal of Biogeography*, doi:10.1111/jbi.12298.

Ashcroft, M.B., French, K.O. & Chisholm, L.A. (2011) An evaluation of environmental factors affecting species distributions. *Ecological Modelling*, **222**, 524–531.

Ashcroft, M.B. & Gollan, J.R. (2012) Fine-resolution (25 m) topoclimatic grids of near-surface (5 cm) extreme temperatures and humidities across various habitats in a large (200 × 300 km) and diverse region. *International Journal of Climatology*, **32**, 2134–2148.

Ashcroft, M.B., Gollan, J.R., Warton, D.I. & Ramp, D. (2012) A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Global Change Biology*, **18**, 1866–1879.

Austin, M. (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling*, **157**, 101–118.

Austin, M. & Meyers, J.A. (1996) Current approaches to modelling the environmental niche of eucalypts: implication for management of forest biodiversity. *Forest Ecology and Management*, **85**, 95–106.

Austin, M.P. & Van Niel, K.P. (2011) Improving species distribution models for climate change studies: variable selection and scale. *Journal of Biogeography*, **38**, 1–8.

Baccaro, F.B., Rocha, I.F., del Aguila, B.E.G., Schietti, J., Emilio, T., do Veiga Pinto, J.L.P., Lima, A.P. & Magnusson, W.E. (2013) Changes in ground-dwelling ant functional diversity are correlated with water-table level in an Amazonian Terra Firme Forest. *Biotropica*, **45**, 755–763.

Bertelsmeier, C., Luque, G.M. & Courchamp, F. (2013) Increase in quantity and quality of suitable areas for invasive species as climate changes. *Conservation Biology*, **27**, 1458–1467.

Boyce, M.S., Haridas, C.V., Lee, C.T.; NCEAS Stochastic Demography Working Group. (2006) Demography in an increasingly variable world. *Trends in Ecology and Evolution*, **21**, 141–148.

Cabeza, M., Arponen, A., Jäättelä, L., Kujala, H., Van Teeffelen, A. & Hanski, I. (2010) Conservation planning with insects at three different spatial scales. *Ecography*, **33**, 54–63.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343–366.

Connell, J. & Orias, E. (1964) The ecological regulation of species diversity. *The American Naturalist*, **98**, 399–414.

Coops, N.C. & Catling, P.C. (1997) Predicting the complexity of habitat in forests from airborne videography for wildlife management. *International Journal of Remote Sensing*, **18**, 2677–2682.

Cardoso, P., Erwin, T.L., Borges, P.A.V. & New, T.R. (2011) The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation*, **144**, 2647–2655.

CSIRO (2013) Ants Down Under. < http://anic.ento.csiro.au/ants > 19th April 2013.

Currie, D.J. (1991) Energy and large-scale patterns of animal-and plant-species richness. *The American Naturalist*, **137**, 27–49.

Ferrier, S., Drielsma, M., Manion, G. & Watson, G. (2002) Extended statistical approaches to modelling spatial pattern in biodiversity in north-east New South Wales: II. Community level modelling. *Biodiversity and Conservation*, **11**, 2309–2338.

Ferrier, S. & Manion, G. (2007) gdmfunc.1.1. < http://www.biomaps.net.au/gdm/ > 12th October 2011.

Ferrier, S., Manion, G., Elith, J. & Richardson, K. (2007) Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, **13**, 252–264.

Francis, A.P. & Currie, D.J. (2003) A globally consistent richness–climate relationship for angiosperms. *The American Naturalist*, **161**, 523–536.

Fry, R. & Lonsdale, D. (eds) (1991) *Habitat Conservation for Insects - A Neglected Green Issue*. The Amateur Entomologists' Society, Middlesex, UK.

Geiger, R. (1971) *The Climate Near the Ground*, j edn. Harvard University Press, Cambridge, UK.

Gilbert, L. (2010) Altitudinal patterns of tick and host abundance: a potential role for climate change in regulating tick--borne diseases? *Oikos*, **162**, 217–225.

Gollan, J.R., Ashcroft, M.B., Cassis, G., Donnelly, A.P. & Lassau, S.L. (2009) Testing common habitat based surrogates in a semiarid rangeland. *Biodiversity and Conservation*, **18**, 1147–1159.

Gollan, J.R., Ashcroft, M.B. & Ramp, D. (2013) Fine-grained climate data alters the interpretation of a trait-based cline. *Ecosphere*, **4**, art154.

Gollan, J.R., Lobry de Bruyn, L., Reid, N., Smith, D. & Wilkie, L. (2011) Can ants be used as ecological indicators of restoration progress in dynamic environments? A case-study in a revegetated riparian zone. *Ecological Indicators*, **11**, 1517–1525.

Hastie, T.J. & Tibshirani, R.J. (1990) *Generalized Additive Models*. Chapman and Hall, London, UK.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hölldobler, B. & Wilson, E.O. (1990) *The Ants*. Belknap, Cambridge, Massachusetts.

Houlder, D., Hutchinson, M., Nix, H. & McMahon, J. (2003) *ANUCLIM 5.1 User's Guide*. Australian National University, Canberra, Australian Capital Territory.

Hutchinson, G. (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *The American Naturalist*, **93**, 145–159.

Illán, J.G., Gutie′rrez, D. & Wilson, R.J. (2010) The contributions of topoclimate and land cover to species distributions and abundance: fine-resolution tests for a mountain butterfly fauna. *Global Ecology and Biogeography*, **19**, 159–173.

IPCC (2008) Climate Change and Water. Intergovernmental Panel on Climate Change Technical Paper VI, IPCC Secretariat, Geneva, Switzerland.

Kaspari, M., Alonso, L. & O'Donnell, S. (2000a) Three energy variables predict ant abundance at a geographical scale. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 485–489.

Kaspari, M., O'Donnell, S. & Kercher, J.R. (2000b) Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. *The American Naturalist*, **155**, 280–293.

Keith, D. (2002) *A Compilation Map of Native Vegetation for New South Wales*. NSW National Parks and Wildlife Service, Hurstville, New South Wales.

Kovalenko, K.E., Thomaz, S.M. & Warfe, D.M. (2012) Habitat complexity: approaches and future directions. *Hydrobiologia*, **685**, 1–17.

Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F. & Sanjayan, M.A. (1993) Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology*, **7**, 796–808.

Lal, R. (1991) Soil conservation and biodiversity. *The Biodiversity of Microorganisms and Invertebrates: Its Role in Sustainable Agriculture*. (ed. by D.L. Hawkesworth), pp. 89–103. CAB International, Wallingford, UK.

Lawler, J.J., Shafer, S.L., White, D., Kareiva, P., Maurer, E.P., Blaustein, A.R. & Bartlein, P.J. (2009) Projected climate-induced faunal change in the western hemisphere. *Ecology*, **90**, 588–597.

Leather, S.R. (2013) Institutional vertebratism hampers insect conservation generally; not just saproxylic beetle conservation. *Animal Conservation*, **16**, 379–380.

Letten, A.D., Ashcroft, M.B., Keith, D.A., Gollan, J.R. & Ramp, D. (2013) The importance of temporal climate variability for spatial patterns in plant diversity. *Ecography*, **36**, 1341–1349.

Lomov, B., Keith, D.A. & Hochuli, D.F. (2009) Linking ecological function to species composition in ecological restoration: seed removal by ants in recreated woodland. *Austral Ecology*, **34**, 751–760.

Lookingbill, T.R. & Urban, D.L. (2003) Spatial estimation of air temperature differences for landscape-scale studies in montane environments. *Agricultural and Forest Meteorology*, **114**, 141–151.

MacArthur, R.H. & MacArthur, H.J. (1961) On bird species diversity. *Ecology*, **42**, 594–598.

Majer, J.D., Orabi, G. & Bisevac, L. (2007) Ants (Hymenoptera: Formicidae) pass the bioindicator scorecard. *Myrmecological News*, **10**, 69–76.

Moreno-Rueda, G. & Pizarro, M. (2007) The relative influence of climate, environmental heterogeneity, and human population on the distribution of vertebrate species richness in south-eastern Spain. *Acta Oecologia*, **32**, 50–58.

Mousseau, T.A. (1997) Ectotherms follow the converse to Bergmann's rule. *Evolution*, **51**, 630–632.

Peake, T. (2003) *Hunter Bushland Resources Kit*. Hunter Catchment Management Trust, Tocal, New South Wales.

Pimm, S.L. (2009) Climate disruption and biodiversity. *Current Biology*, **19**, R595–R601.

R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org> 1st March 2012.

Roura-Pascual, N., Brotons, L., Peterson, A.T. & Thuiller, W. (2009) Consensual predictions of potential distributional areas for invasive species: a case study of Argentine ants in the Iberian Peninsula. *Biological Invasions*, **11**, 1017–1031.

Samways, M.J. (1993) Insects in biodiversity conservation. *Biodiversity and Conservation*, **2**, 258–282.

Sanders, N.J., Lessard, J., Fitzpatrick, M.C. & Dunn, R.R. (2007) Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography*, **16**, 640–649.

Sharley, D.J., Hovmann, A.A. & Thomson, L.J. (2008) The effects of soil tillage on beneficial invertebrates within the vineyard. *Agricultural and Forest Entomology*, **10**, 233–243.

Shattuck, S. (2000) *Australian Ants their Biology and Identification*. CSIRO Entomology, Collingwood, Victoria.

Shurin, J.B., Winder, M., Adrian, R., Keller, W.B., Paterson, A.M., Paterson, M.J., Pinel-Alloul, B., Rusak, J.A. & Yan, N.D. (2010) Environmental stability and lake zooplankton diversity – contrasting effects of chemical and thermal variability. *Ecology Letters*, **13**, 453–463.

Stoutjesdijk, P. & Barkman, J.J. (1992) *Microclimate, Vegetation and Fauna*. Opulus Press AB, Knivsta, Sweden.

Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B. & Thomas, C.D. (2011) Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos*, **120**, 1–8.

Tschinkel, W.R., Murdock, T., King, J.R. & Kwapich, C. (2012) Ant distribution in relation to ground water in north Florida pine flatwoods. *Journal of Insect Science*, **12**, 114.

Wood, S. (2013) Mixed GAM Computation Vehicle with GCV/AIC/REML smoothness estimation. <http://stat.ethz.ch/R-manual/R-patched/library/mgcv/html/00Index.html> 1st October 2013.

Xu, T. & Hutchinson, M. (2011). ANUCLIM 6.1 user's guide. <http://fennerschool.anu.edu.au/research/software-datasets/anuclim> 1st March 2012.

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