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

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

## **Abstract**

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.

We quantified ant richness and species composition at 86 sites across a large (200 x 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.

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%).

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.

## **Disciplines**

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1 Title: Contrasting topoclimate, long-term macroclimatic averages and habitat variables for  
2 modelling ant biodiversity at landscape scales

3 Running head: Predictors for modelling

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14

15 **Abstract**

- 16 1. Spatial modelling is part of the solution for incorporating insects into conservation  
17 policy. However, uptake rests on identifying robust environmental predictors. Coarse-  
18 grained climate models based on long-term averages and similarly coarse  
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20 planning is done. Here we test whether topoclimatic variables, which are derived from  
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31 (20% and 24% of deviance, respectively). The plot for richness indicated a positive  
32 but decelerating function of 95maxT. This was consistent for two of three habitat  
33 types. Habitat complexity was the most important predictor in cleared habitat (28%).
- 34 4. While a topoclimatic variable was a strong predictor of ant biodiversity across the  
35 landscape, this was not a ‘magic bullet’. Other predictors such as complexity may be  
36 more applicable in certain habitat types. We concluded that tailored predictors are  
37 needed for landscapes with a mosaic of different land use.

38 **Key words:** climate, energy limitation hypothesis, Formicidae, Generalized Dissimilarity  
39 Modelling, habitat complexity

40

## 41 **Introduction**

42 Twenty or so years ago, advocacy for invertebrates in conservation initiatives began to build  
43 (e.g. see perspectives of Fry & Lonsdale, 1991; Kremen *et al.*, 1993; Samways, 1993).  
44 However, while there have been a number of developments in taxonomy, statistical analysis,  
45 data compilation, and science communication, there are still impediments to incorporating  
46 invertebrates in conservation policy (Leather, 2013; Cardoso *et al.*, 2011). Spatial modelling  
47 techniques that allow mapping in previously unsurveyed locations have been proposed as part  
48 of the solution (see Cardoso *et al.*, 2011 and refs within). Models can then be used for  
49 conservation planning (e.g. Cabeza *et al.*, 2010). However, the reliability of predictive  
50 mapping relies on the strength of relationships between the variable(s) of interest and  
51 climatic, land-use or other variables that are used as predictors.

52 Predictive mapping also requires that data on predictors exist in the unsurveyed  
53 locations and that they are appropriately scaled to reflect genuine conditions experienced  
54 across the landscape of interest. Acquiring data meeting both requirements is problematic for  
55 invertebrates because most invertebrates perceive and respond to the environment at spatial  
56 and temporal scales that are far smaller than the typical scales of human perception (see  
57 Virtual Issue: ‘Scaling conservation management actions to the fine-grained ecological  
58 responses of invertebrates’ of *Insect Conservation and Diversity*). Conservation planning  
59 strategies using climate variables extracted from widely used and freely available coarse-  
60 grained models and future climate-simulations using atmosphere-ocean general circulation  
61 models (e.g. WorldClim; [www.worldclim.org](http://www.worldclim.org)) for instance may suit many plants and  
62 vertebrates (e.g. Lawler *et al.*, 2009 although see Ashcroft *et al.* in press), they are likely to be  
63 ineffective for invertebrates. It is important to note that the issue is not simply ‘a scale issue’  
64 that can simply be resolved by using a climate model with a small grid cell size. It is more  
65 that the interpolation method to derive many climate grids are often interpolated from

66 weather stations using only elevation and geographical location (e.g. Bioclim and  
67 WorldClim; Houlder et al., 2003; Hijmans et al., 2005).

68 The argument for which taxa that coarse-scale grids are more appropriate for may be  
69 irrelevant because there is increasing recognition that coarse-scale bioclimatic envelope  
70 models are of limited use for environmental management as most planning decisions are  
71 made within individual regions (Ferrier *et al.*, 2002; Lookingbill & Urban, 2003; Cabeza *et*  
72 *al.*, 2010). Greater emphasis on producing fine-scale models using a broader range of  
73 ecologically relevant variables have been called for (Austin & Van Niel, 2011). One method  
74 gaining popularity for achieving this in biodiversity modelling is through the use of  
75 topoclimate, that is, climate models that consider local climate forcing factors such as  
76 exposure to prevailing winds, slope and aspect (e.g. Ashcroft *et al.*, in press; Letten *et al.*,  
77 2013; Ashcroft *et al.* 2011).

78 Evidence to support the notion that topoclimate is key for understanding invertebrate  
79 patterns is mounting. Gollan *et al.*, (2013) for example, found that body size of the meat ant,  
80 *Iridomyrmex purpureus*, was positively correlated with temperature (conforming to the so-  
81 called ‘converse Bergmann cline’; Mousseau, 1997), but was not detected using coarse-  
82 grained, long-term climatic averages. For butterflies in a mountainous region in central Spain,  
83 Illán *et al.*, (2010) found that climate models that were modelled using local climate forcing  
84 factors outperformed models based purely on land cover in 72% of occurrence models and  
85 66% of abundance models. Importantly, these studies further support the premise that climate  
86 is a crucial environmental parameter for controlling species distributions, especially for  
87 ectotherms (Moreno-Rueda & Pizarro, 2007; Aragón *et al.*, 2010).

88 Another important issue for any modelling lies in the choice of predictor(s).  
89 Ultimately, models should be based on an understanding of the environmental processes  
90 which control species distribution. Without careful consideration and selection of predictors

91 being tested, there is a risk of detecting spurious correlations with variables that play no part  
92 in environmental processes that control species distribution (Austin & Meyers, 1996). This  
93 can be challenging for species that have not been studied in detail, where distribution data is  
94 absent or sparse, or when collective properties (e.g. species richness) are used. These are the  
95 realities of many invertebrate datasets, especially the hyper-diverse groups. In the absence of  
96 detailed ecological studies for each and every species and when collective properties are  
97 used, ecological theory and principles, and empirical relationships founded in other studies or  
98 taxonomic groups can provide clues as to the important predictors and the general shape of  
99 the resulting response.

100         With the prospect of increased climatic variability and increased temperatures in the  
101 future (IPCC, 2008), there has been recent interest in these two parameters and the theory  
102 underlying hypothesised spatial patterns. For example, at small scales, climate variability can  
103 stabilize competition and thus promote diversity by increasing the number of temporal niches  
104 available within a fixed space (Chesson, 2000). Contrarily, too much environmental  
105 variability can be detrimental to population persistence because of stochastic extinction  
106 (Boyce *et al.*, 2006). Others have suggested a unification of these models with richness  
107 peaking at intermediate levels of variability (Adler & Drake, 2008). For absolute  
108 temperatures, hot temperatures generally mean more species, with studies on ants showing a  
109 positive correlation between richness and temperature (Sanders *et al.*, 2007, Kaspari *et al.*,  
110 2000a, Kaspari *et al.* 2000b). The positive correlation is hypothesised to be the result of  
111 energy limitation, where energy puts constraints on both the density and the number of  
112 species that can be supported (Kaspari *et al.*, 2000b).

113         Aside from relationships with climate, spatial patterns in diversity have also been  
114 linked to habitat characteristics, in particular habitat complexity. Attributed to MacArthur and  
115 MacArthur (1961), the habitat heterogeneity hypothesis posits that structurally diverse

116 habitats accommodate more species due to an increasing number of spatial niches. Numerous  
117 studies in a range of ecosystems have supported this by showing a positive relationship  
118 between diversity and habitat complexity (see review by Kovalenko *et al.*, 2012). However,  
119 this is not always the case for terrestrial invertebrates where soil properties like hardness and  
120 texture may be more influential (e.g. Gollan *et al.*, 2009). Links between the soil and  
121 invertebrate organisms are also appreciated for conservation (Lal, 1991), and the impacts of  
122 soil management on invertebrates are well studied (e.g. Sharley *et al.*, 2008).

123         In this study we took a correlative approach to investigate the predictive power of  
124 temporal climate variability, absolute temperatures and habitat characteristics on spatial  
125 patterns of ant diversity. Ants are an ideal invertebrate study group because they are  
126 ubiquitous, ecologically important and easy to sample. Furthermore, ant richness and  
127 community composition can provide insight into key ecological processes and interactions  
128 such as nutrient cycling (Andersen & Sparling, 1997) and seed dispersal (Lomov *et al.*,  
129 2009). Because many different species can co-exist in the one place, they are the ideal model  
130 organisms for testing hypotheses in community ecology and, if strong and robust predictors  
131 can be identified, are a good bioindicator group for integrating into conservation policy and  
132 planning initiatives. Indeed, ants have been the bioindicator of choice for assessing the  
133 progress of ecological restoration and conservation strategies as part of land management  
134 more generally (Gollan *et al.*, 2011; Majer *et al.*, 2007; Andersen & Majer, 2004; Andersen,  
135 1997).

136         We collected ants at 86 sites across a large (~300 km × 200 km) and topographically  
137 complex region in southeast Australia and took advantage of a topoclimatic model that had  
138 been derived from temperature data collected at the same sampling sites (Ashcroft & Gollan,  
139 2012). This novel and unique dataset allowed consideration of climatic conditions that are  
140 closer to what the ants actually experience as compared to the standardised Bureau of



141 Meteorology (BoM) weather stations. Indeed, BoM data for investigating biodiversity-  
142 climate relationships have been criticised because: (1) instruments are sheltered in  
143 Stephenson screens at a height of 1.5–2 m and so do not reflect the conditions relevant for  
144 ground dwelling fauna, germinating seeds, tender saplings or ecological processes (Geiger  
145 1971), and (2) observations are made on largely flat, unvegetated land and do not reflect the  
146 environments (e.g. gorges/forests) that many species actually live in (Geiger 1971; Suggitt et  
147 al. 2011). The strength of relationships with topoclimate variables were contrasted against a  
148 set of long-term climate data modelled using weather station data, as well as a set of habitat  
149 variables, namely: soil pH, soil texture, elevation and habitat complexity. While we  
150 acknowledge that there may be other environmental variables limiting ant distributions such  
151 as water table depth (see Baccaro *et al.*, 2013; Tschinkel *et al.*, 2012), we were constrained  
152 by the availability of data for our study area.

## 153 **Material and Methods**

### 154 *Study region and study sites*

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

161         The study area as a whole (~300 km × 200 km) is topographically complex including  
162 deep gorges and rugged mountainous terrain particularly in and around Barrington Tops,  
163 Wollemi and Yengo National Parks. Low rolling hills with shallow broad valleys skirt the  
164 mountainous areas that eventually meet the relatively flat, surrounding plains and valley  
165 floors. Elevation ranges from sea level to around 1600 m in Barrington Tops National Park

166 (Fig. 1). Mostly on the valley floor and at low elevations, there is a wide range of production  
167 land for cattle, cropping and mining. A wide range of natural ecosystem types are also  
168 represented, including coastal forests and heathland, temperate and sub-tropical rainforests,  
169 high-elevation peat swamps and open grassy woodlands (Peake, 2003).

#### 170 *Ant diversity*

171 Ants were sampled using five pitfall traps per site (cylindrical plastic jars, 45 mm diameter,  
172 and 105 mm deep). However, only four traps were used in analyses due to disturbance of a  
173 single trap at several sites. Trapping was conducted in January 2012 (southern hemisphere's  
174 mid-summer) and chosen to coincide with peak ant activity. Traps at each site were  
175 positioned at least 10 m apart along a straight line transect, although traps deviated from a  
176 straight line at some sites due to obstructions by trees, boulders, fallen logs etc. In nearly all  
177 cases, the centre trap was within 2m of where the data logger was positioned (see below). All  
178 traps were: (1) one-third filled with ethylene glycol as preservative; (2) placed flush to the  
179 ground surface; and (3) covered by an upturned weigh boat held above the opening of the trap  
180 with wooden food skewers. The cover acted to protect the trap from rainwater and debris.

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

190 number of different species) and community composition. All specimens were deposited at  
191 the Australian Museum, Sydney.

### 192 *Topoclimatic variables*

193 The topoclimatic estimators of temperature extremes: (1) 95<sup>th</sup> percentile of maximum  
194 temperature (hereafter ‘95maxT’) and (2) 5<sup>th</sup> percentile of minimum temperature (hereafter  
195 ‘5minT’), were calculated for each of the 86 sites extracted from the models of Ashcroft and  
196 Gollan (2012). In summary, these models using a 25 m resolution raster grids were produced  
197 from temperature recorded by miniature data loggers (DS1923 hygrochron iButtons by  
198 Maxim) at 150 sites for 666 days (between June 2009 and May 2011) across the study region.  
199 A regional regression approach used the local-scale forcing factors: elevation, distance to  
200 coast, canopy cover, latitude, cold-air drainage, and topographic exposure to prevailing winds  
201 as predictors. By utilising percentiles, and since these data were measured at hourly intervals  
202 over a two year period, it can be assumed that the 95maxT and 5minT captured the hottest  
203 and coldest conditions at each site (respectively), even if they did not occur simultaneously or  
204 consecutively. Consistent patterns have since been confirmed with data collection over a  
205 subsequent two year period (M.B.A. & J.R.G., unpublished data). We chose to focus on these  
206 two gradients because they are likely to have more relevancy than quantities such as mean  
207 annual temperature for ecological systems (Pimm, 2009). 95maxT was largely influenced by  
208 canopy cover and exposure. 5minT in contrast, was largely determined by cold air drainage,  
209 which is common under clear skies, low wind and anticyclonic conditions. Full details of the  
210 topoclimatic models and analytical procedures can be found in Ashcroft & Gollan (2012).

211 To calculate variability in each climate parameter, variation was initially partitioned  
212 into three time-scales: (1) intra-seasonal variation; (2) intra-annual variation; and (3) inter-  
213 annual variation. An overall measure of variability for each (hereafter ‘v95maxT’ and

214 ‘v5minT’) was then calculated as the average of the three time-scales. Full details of this  
215 procedure can be found in Ashcroft et al. (2012).

### 216 *Long-term macroclimate variables*

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

### 231 *Habitat attributes*

232 Habitat attributes considered were two soil properties (pH and soil texture), habitat  
233 complexity and elevation. Soil pH was determined at each site from a bulked sample using a  
234 colorimetric pH test kit (Manutec Pty. Ltd.). The bulked sample was the product of  
235 thoroughly mixing the excavated material from the holes dug for the pitfall traps (as  
236 described above). Soil texture using the bulked sample was determined using the protocols of  
237 Department of Environment and Primary Industries Victoria (Anon., 2013). In brief, the  
238 method involves moistening a sample of soil, manipulating the bolus in the palm of the hand

239 and then comparing the feel and behaviour against a texture category. There were 21 ordinal  
240 categories ranging from sand to heavy clay with the order reflecting decreasing amounts of  
241 coarse sand particles and an increasing amount of fine clay particles. The nominal categories  
242 were re-assigned the ordered nominal values to accommodate the regression analyses (see  
243 below).

244 Habitat complexity was determined using a modification of Coops and Catling  
245 (1997). Here, eight habitat variables (amount of: rock cover, coarse woody debris, and  
246 amount of foliage in six strata [0-25cm; 25cm-1m; 1-2m; 2-5m; 5-10m and >10m]) were  
247 scored using an ordinal scoring system (0–9) where zero denoted an absence and nine was at  
248 maximum. Habitat complexity was then determined by summing the eight individual  
249 components.

#### 250 *Statistical analyses*

251 For species richness, we produced a Generalized Additive Model (Hastie &  
252 Tibshirani, 1990) using the mgcv package (Wood, 2013) in R (R Development Core Team  
253 2008) for individual predictors. Each predictor was included as a spline with two degrees of  
254 freedom. This allowed for non-linear response shapes but did not provide enough freedom for  
255 complex responses which may lead to over-fitting. GAMs were fitted to data at all 86 sites.  
256 We then modelled species richness for individual vegetation communities to assess  
257 generalities of relationships (if any). Broad vegetation communities were identified for each  
258 site using a state-wide vegetation layer (200m × 200 m cell size) from the NSW Office of  
259 Environment and Heritage (Keith, 2002). Eight categories were initially identified. So there  
260 were enough data points for analysis some of the initial eight were reduced to three by  
261 combining some categories. ‘*Dry sclerophyll forests (grassy subformation)*’ and ‘*Dry*  
262 *sclerophyll forests (shrubby subformation)*’ were combined to the single category ‘*Dry*  
263 *sclerophyll forests*’ ( $n = 34$ ). ‘*Rainforests*’, ‘*Wet sclerophyll forests (Grassy subformation)*’

264 and ‘*Wet sclerophyll forests (Shrubby subformation)*’ were combined to the single category  
265 ‘*Wet forests*’ ( $n = 19$ ). The category, ‘*Cleared*’ ( $n = 29$ ), were places where the native  
266 vegetation community had been removed or severely modified for land use like grazing and  
267 other intensive agricultural activities. Heathlands and grassy woodlands were not considered  
268 in isolation as there were insufficient data points ( $n = 1$  and  $3$ , respectively). Vegetation  
269 communities identified using the vegetation layer were field validated at the time traps were  
270 collected. The percent deviance explained and Akaike Information Criterion (AIC) were used  
271 to assess the strength of relationships among models. The AIC is essentially a goodness of fit  
272 measure that provides a way to compare the relative quality of a statistical model. Given a set  
273 of candidate models, the ‘preferred’ model has the smaller AIC value (Akaike, 1971).

274         Generalized dissimilarity modelling (GDM; Ferrier *et al.*, 2002) was used to analyse  
275 spatial patterns of turnover in community composition and to determine the relative  
276 explanatory power of each environmental variable. GDM is an extension of matrix regression  
277 but overcomes the two different types of nonlinearity commonly encountered in ecological  
278 data: (1) the curvilinear relationship between increasing ecological distance and observed  
279 compositional dissimilarity between sites; and (2) the variation in the rate of compositional  
280 turnover at different positions along environmental gradients (Ferrier *et al.*, 2007). GDM is  
281 thus suited to invertebrate data sets that are notorious for exhibiting high levels of beta  
282 diversity (i.e. a sizeable number of sites that share no species with one another).

283         A GDM was fitted using all predictors, which automatically removed environmental  
284 factors not significantly affecting turnover in species composition. A GDM was then  
285 produced for significant predictors independently, and the relative fit for each predictor was  
286 assessed by examining the percentage deviance explained. Response plots were examined to  
287 assess: (1) the total amount of compositional turnover associated with each predictor (as  
288 indicated by the maximum height reached on the *y-axis* by each function), and (2) the rate of

289 compositional turnover, and how this rate varied along each gradient (as indicated by the  
290 slope of each function).

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

## 298 **Results**

### 299 *Range in environmental predictors captured*

300         For variables capturing the warm gradients (i.e. max95T and BIO5) and the long term  
301 average temperature (i.e. BIO1), wet forest (WF) sites tended to be coolest, cleared sites  
302 generally warmest and dry sclerophyll forest (DSF) intermediate. However, the ranges  
303 captured for each variable indicated that some WF sites could be similar, or warmer than  
304 some cleared sites (Table 1). For variables capturing cool gradients (i.e. 5minT and BIO6),  
305 the average 5minT within each habitat type indicated cleared habitat tended to be coolest,  
306 WFs warmest, and DSFs intermediate. In contrast, the average of BIO6 showed that WFs  
307 were coolest, while cleared habitat and DSFs were similar. This pattern was the same for  
308 BIO12 (mean annual rainfall), where WFs were wettest and cleared and DSFs similar  
309 (Table 1).

310         For habitat attributes, WF sites tended to be at highest elevations, while cleared and  
311 DSF sites were at similar elevation. Averages of habitat complexity indicated that complexity  
312 tended to be higher in WFs, lowest in cleared habitat, and intermediate in DSFs, though the  
313 range indicated that some cleared habitat (3 to 28) could be just as complex as WF sites (18

314 to 46). While the range in soil pH captured was rather broad (4.5 to 8.0), the mean was  
315 similar across all habitat types (Table 1). The distribution of all environmental variables  
316 across all sites is included as Supplementary material (S1 Figures 1–13).

### 317 *Species richness models using single predictors*

318 A total of 153 species and 15 016 individuals were collected in the 344 traps (86 sites, 4 traps  
319 per site). Species richness at the site-level ranged from 1 to 23 with a mean ( $\pm$  SD) of 11  
320 species per site ( $\pm$  4). The distribution of species richness across all sites is included as  
321 Supplementary material (S1 Figures 14).

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

### 334 *Community composition*

335 Two local climate predictors (‘v95maxT’ and ‘5minT’) and two long term climate predictors  
336 (BIO6 and BIO12) did not significantly affect turnover in species composition and so were  
337 not considered further. The GDM the remaining 10 remaining predictors explained 29.5% of  
338 the deviance in observed species turnover. Fitted functions for individual predictor variables



339 showed their relative importance and shape of the response surface (Fig. 3a-j). Comparison of  
340 the maximum heights reached (i.e. *y-axis* range) by each function indicated that ‘95maxT’  
341 was the most important single variable (Fig. 3e). This variable in isolation also explained the  
342 greatest percentage of the deviance in observed species turnover (24.4%). The variable  
343 explaining the second highest deviance was BIO5 (16.5%) and the response in turnover  
344 revealed that it was not as important as 95maxT. The fitted functions indicated some  
345 importance of ‘Habitat complexity’ (Fig. 3b) and ‘Elevation’ (Fig. 3f) to spatial turnover.

## 346 **Discussion**

347         Across a large region comprising different land-use and vegetation types, our results  
348 clearly showed that maximum temperature is an important parameter for explaining spatial  
349 patterns of ant diversity. In-conjunction with topoclimatic models derived using local-scale  
350 climate forcing factors (e.g. Ashcroft & Gollan, 2012) or freely available long-term climatic  
351 data (e.g. [www.worldclim.org](http://www.worldclim.org)), the predictive models that are needed for incorporating ants  
352 into conservation planning and policy are conceivable. The finding that warmer sites had  
353 more ant species than cooler sites agrees with other studies examining environmental factors  
354 shaping ant assemblages at local (e.g. Sanders *et al.*, 2007) and global scales (Kaspari *et al.*,  
355 2000a) and thus we are confident that our results are not spurious.

356         Across all habitat types, and in two of the three single habitat types, ant species  
357 richness increased with maximum temperature before reaching a peak and then decreasing.  
358 For compositional turnover, maximum temperature also had the greatest total effect. While  
359 studies on plants and zooplankton have shown that climate variability plays an important role  
360 in controlling richness gradients (e.g. Letten *et al.*, 2013; Shurin *et al.*, 2010), for ants at least,  
361 we found little justification for its attention when modelling diversity. While community  
362 dynamics and spatial patterns driven by climatic variability seem plausible for explaining  
363 patterns in diversity, our results, along with studies with similar objectives (e.g. Kaspari *et*

364 *al.*, 2000b), indicate that it is questionable as to whether the predictions about variability hold  
365 for terrestrial invertebrates. For these organisms, absolute temperatures may be more  
366 important than variability because it is the available amount of energy that puts constraints on  
367 both the density and the number of species that can be supported (Kaspari *et al.*, 2000b).  
368 Indeed, energy availability has long been considered a fundamental constraint to species  
369 richness (Hutchinson, 1959, Connell & Orias, 1964, although see Currie *et al.*, 2004).

370 In general, ants are described as ‘thermophiles’ because of their aversion towards cool  
371 moist conditions (Hölldobler & Wilson, 1990). So perhaps it is no surprise that maximum  
372 temperature was the most important variable for explaining patterns of ant diversity. The  
373 aversion for cool moist conditions was clear in our analysis of species richness in wet forests  
374 where maximum temperature explained almost twice the deviance (38.9%) in both dry  
375 sclerophyll forest (18.3%) and all habitats combined (20.3%). In all three cases, species  
376 richness increased with increasing temperature (Fig. 2a-c). The peak of the response varied  
377 between ~38°C and 42°C when all habitat types were combined, which could well represent  
378 the tipping point where energy starts to constrain the number of species that can be supported.  
379 Whether these values are applicable to other regions or for other invertebrate groups requires  
380 more research. Further evidence for such a tipping point could provide vital clues as to the  
381 landscape effects of global warming. With rising global temperatures predicted in the future  
382 (IPCC, 2008), a redistribution of diversity is a real potential, where the cooler areas (which  
383 tend to be species poor) become susceptible to invasion of new species under warmer  
384 conditions (Bertelsmeier *et al.*, 2013; Roura-Pascual *et al.*, 2009).

385 The exception to the maximum temperature gradient being important for predicting  
386 ant biodiversity was in cleared habitat (Table 2). A poor relationship is perhaps intuitive as all  
387 cleared habitats would be expected to be warm relative to forests that have canopies that may  
388 cause greater spatial variation in thermal conditions. However, some cleared sites

389 experienced conditions that were just as cool (in terms of 95maxT at least) as for wet forest  
390 and dry sclerophyll forest (Table 1 and Figure 1–13 in S1). Hence, we did not simply capture  
391 a portion of the overall temperature gradient in cleared habitat. Since the temperatures range  
392 was just as wide as the gradient for wet forest and dry sclerophyll forest, it is reasonable to  
393 conclude that any one predictor may not hold across all types of habitat types. The  
394 implication of this for predictive mapping is that tailored predictors are needed for modelling  
395 within particular habitat types.

396         The results of our study also highlight that it is more desirable to have more proximal  
397 and direct predictors (*sensu* Austin, 2002) of temperature rather than reliance on proxies such  
398 as elevation to explain ecological trends. Elevation is often used to infer temperature  
399 gradients when climatic data have not been measured or are otherwise unavailable (e.g.  
400 Gilbert, 2010). The relationship between long-term (50 years) mean annual temperature (as  
401 derived by BioClim; [www.worldclim.org](http://www.worldclim.org); Hijmans *et al.*, 2005) and elevation at our 86 study  
402 sites was almost a perfect correlation ( $R^2 = 0.987$ ). As our results showed, elevation (and its  
403 equivalent at the scale of our study, mean annual temperature) was a relatively poor predictor  
404 of ant diversity compared to maximum temperatures (Table 2). Thus, the purported  
405 importance of climatic means for controlling diversity gradients at broad scales (Francis &  
406 Currie, 2003), did not hold at the regional scale of our analysis. A possible reason for this is  
407 that we used contemporary climate data which is more biologically meaningful than long-  
408 term averages. If macroclimatic data are used to establish relationships between climatic  
409 parameters and diversity, there is the very real possibility of a ‘mix-match’ between the  
410 temporal scale of the climatic observations and the biological processes operating.  
411 Invertebrates, including ants, generally have short-lives with rapid turnover and so it is  
412 plausible that community dynamics are more closely tied to climatic conditions in the lead up  
413 to when they are collected or observed, rather than averages of long-term conditions. Even at

414 broad geographic scales this source of error could well hold. This is not to say that long-term  
415 macroclimatic averages are not informative. Indeed, BIO5 (maximum temperature of the  
416 warmest month) was the second strongest predictor for richness. But our results did show that  
417 models using small and inexpensive *in-situ* data loggers can explain more deviance and be a  
418 better fit than long term climatic averages. Whether this improvement is warranted will  
419 depend on the needs of the individual study.

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608

Table 1 The mean  $\pm$  SD for each environmental predictor within four habitat types and all habitat types combined. The range (minimum – maximum) for each are given in parentheses.

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

<sup>†</sup>Four sites not belonging to ‘Cleared habitat’, ‘Dry sclerophyll forests’, or ‘Wet forests’ were included in ‘All habitats combined’.

Table 2. Percent deviance explained in ant species richness and community composition. For species richness, the deviance explained is for single predictor models fitted with a Generalized 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 Figure 2 (panels a–d). For community composition, a Generalized Dissimilarity Model revealed that 10 of the 14 predictors were important. Partial responses for all 10 are shown in Figure 3 (panels a–j).

Predictor variable	Species richness			Community composition	
	Cleared habitat (n=29)	Dry sclerophyll forests (n=34)	Wet forests (n=19)	All habitats combined (n=86 <sup>†</sup> )	All habitats combined (n=86 <sup>†</sup> )
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

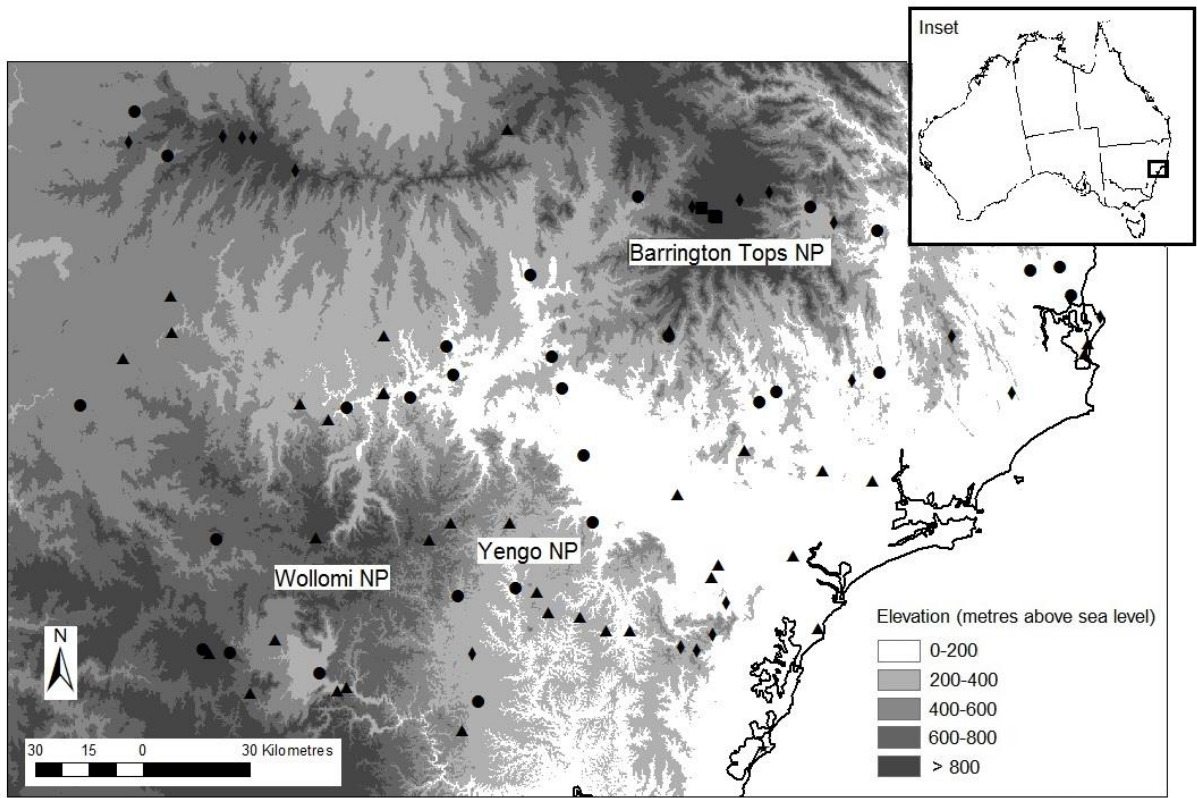
<sup>†</sup>Four sites not belonging to ‘Cleared habitat’, ‘Dry sclerophyll forests’, or ‘Wet forests’ were included in ‘All habitats combined’.

613 Figure legends

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

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

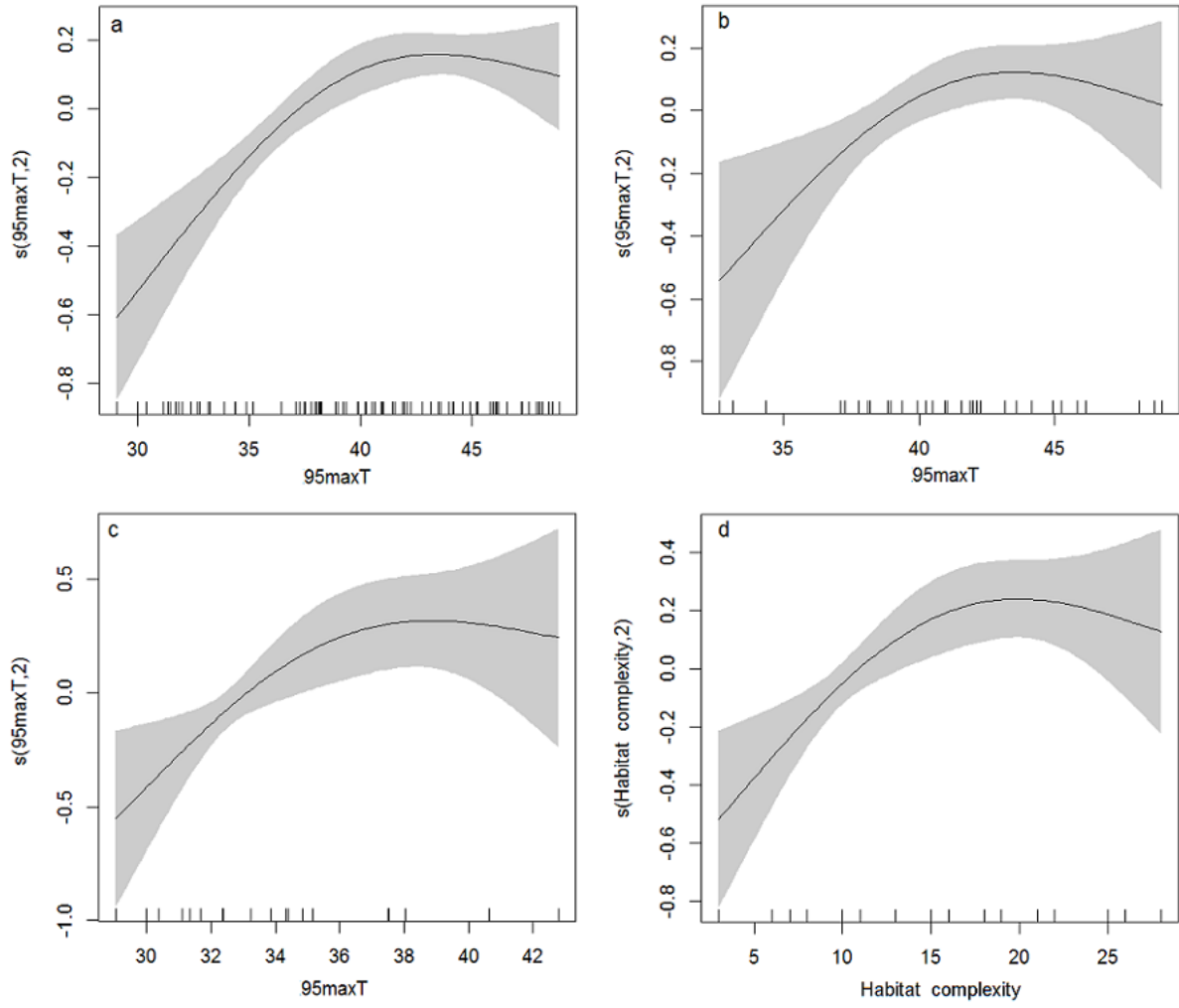
624 Fig. 3. Generalised Dissimilarity Model showing fitted functions of individual predictors  
625 (panels a–j) to ant communities from 86 sites in southeast NSW, Australia (Fig. 1).  
626 Percentage deviance explained for a given predictor is shown in Table 1.



628

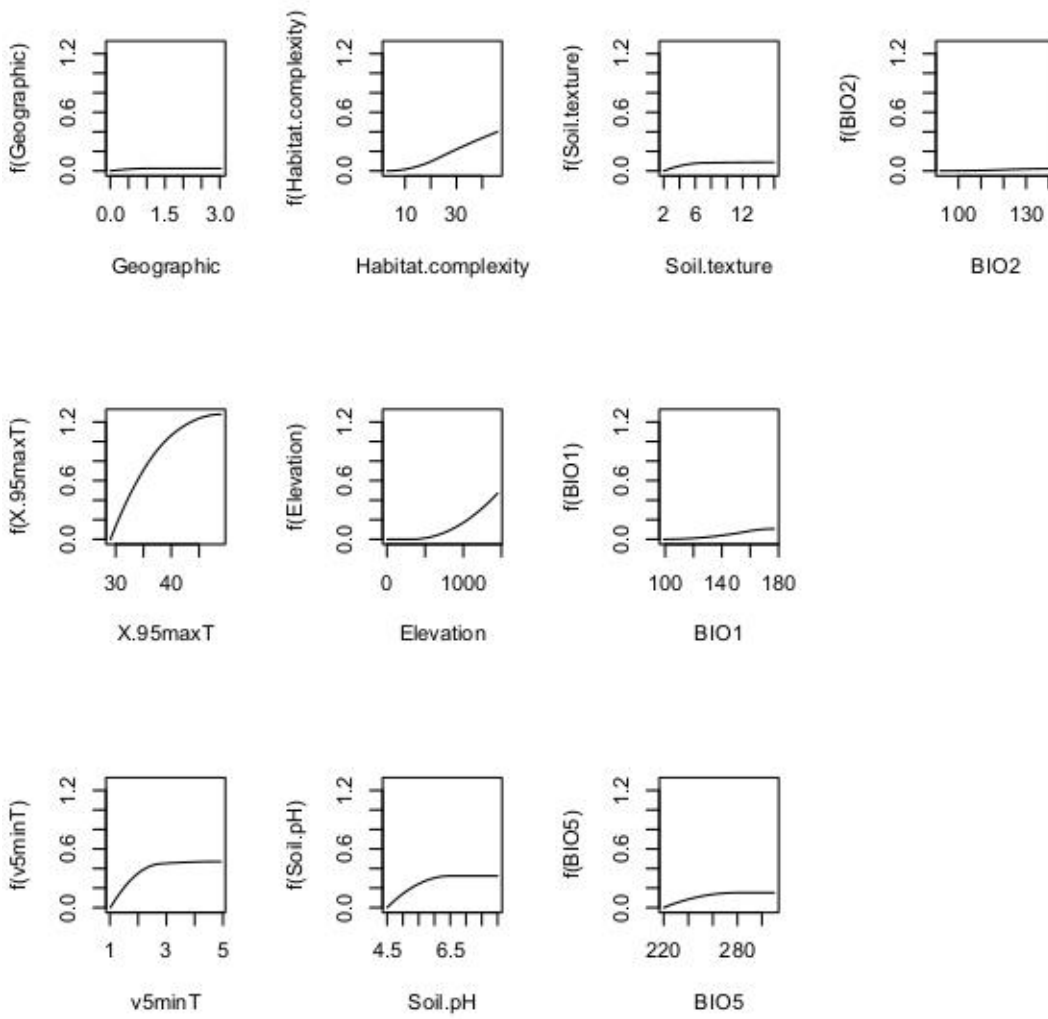
629 Figure 1





630

631 Figure 2



632

633 Figure 3