

Gibb, H. and Sanders, N. and Dunn, R. and Watson, S. and Photakis, M. and Abril, S. and Andersen, A. et al. 2015. Climate mediates the effects of disturbance on ant assemblage structure. *Proceedings of the Royal Society B: Biological Sciences*. 282 (1808): pp. 1-8.

## 1 **Climate mediates the effects of disturbance on ant assemblage structure**

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92

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96 **Abstract**

97 Many studies have focussed on the impacts of climate change on biological assemblages, yet  
98 little is known about how climate interacts with other major anthropogenic influences on  
99 biodiversity, such as habitat disturbance. Using a unique global database of 1128 local ant  
100 assemblages, we examined whether climate mediates the effects of habitat disturbance on  
101 assemblage structure at a global scale. Species richness and evenness were associated  
102 positively with temperature, and negatively with disturbance. However, the interaction  
103 among temperature, precipitation and disturbance shaped species richness and evenness. The  
104 effect was manifested through a failure of species richness to increase substantially with  
105 temperature in transformed habitats at low precipitation. At low precipitation levels,  
106 evenness increased with temperature in undisturbed sites, peaked at mid temperatures in  
107 disturbed sites and remained low in transformed sites. In warmer climates with lower  
108 rainfall, the effects of increasing disturbance on species richness and evenness were akin to  
109 decreases in temperature of up to 9 °C. Anthropogenic disturbance and ongoing climate  
110 change may interact in complicated ways to shape the structure of assemblages, with hot, arid  
111 environments likely to be at greatest risk.

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## 112 **Introduction**

113 Although considerable debate exists about the forces that structure ecological assemblages  
114 [e.g., 1, 2], there is little doubt that, at global scales, climate and disturbance are key drivers.  
115 For instance, numerous studies have demonstrated that species richness at both regional (e.g.,  
116 10 km × 10 km grids) and local (i.e., the scale of local assemblages) scales tracks  
117 contemporary climatic conditions [3-5], and many studies have documented predominantly  
118 negative effects of anthropogenic disturbance on diversity at local scales [6, 7]. Although  
119 anthropogenic disturbance and climate are key drivers of assemblage structure, surprisingly  
120 few studies have addressed their interaction as a driver of biological change. Here, we use  
121 data from a global database of the abundances of ant species from 1128 local assemblages to  
122 determine how assemblage structure changes with climate and disturbance.

123 Global-scale studies of determinants of species richness are most commonly based on  
124 geographic ranges of species, rather than local assemblages, and thus may not consider sets of  
125 species that co-occur and interact with one another [5, 8]. Local assemblages result from  
126 species being filtered from regional species pools at large spatial grains [9, 10], and both  
127 climate and disturbance act as important filters [10, 11], influencing not only which species  
128 are present in assemblages but also their relative abundances and ultimately species evenness  
129 within the assemblage (how evenly individuals are divided among species within an  
130 assemblage).

131 For numerous taxa, global-scale studies of species richness indicate that richness is highest in  
132 warm and stable climates [4, 5, 12], although the extent to which this is true at more local  
133 scales (i.e. the scale of a local community) and for other metrics of diversity is an open  
134 question [13]. Moreover, these patterns might be mediated by landscape-level disturbances

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135 (e.g. fire) or transformation (e.g. establishment of exotic plantations), especially with  
136 increasing human pressures in the most biodiverse regions in the world [8]. An additional  
137 challenge in considering the structure of local assemblages is that whereas at regional scales  
138 diversity data is composed simply of presences and absences, zeros and ones (as a  
139 consequence of the kind of data available, if nothing else), at more local scales the  
140 differences in the relative abundances of taxa become more important in distinguishing  
141 between communities. As a result, it becomes important to consider the drivers not only of  
142 the number of species, but also their relative abundance.

143 Theory predicts that disturbance should lead to either decreases in richness and evenness [14]  
144 through reductions in energy, or increases in richness and evenness (at intermediate levels of  
145 disturbance) due to a trade-off between competitive dominance and colonization [6].

146 However, climate might be expected to mediate the effect of disturbance by, for example,  
147 altering the rates of colonisation [10] or the prevalence of competition [15]. Thus,  
148 understanding the interaction between climate and disturbance is critical in predicting the  
149 outcome for species assemblages under global change. Superficially, the transformation of  
150 habitats, for example from native forest to pine plantation, might be expected to respond  
151 similarly to a disturbance as biomass is removed in the process (although energy flows are  
152 not necessarily reduced). However, in low biomass systems, such as deserts, where the  
153 transformation of habitat results in increased biomass, richness may also increase.

154 Here, we examine whether contemporary climate mediates the effects of disturbance on ant  
155 assemblages around the world. This work is unique in using data from a large set of local  
156 assemblages and in examining assemblage evenness in addition to species richness.

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## 157 **Materials and Methods**

### 158 *Assemblage data*

159 We compiled species abundance data from local ant assemblages from 1128 sites distributed  
160 throughout the world (Fig. 1). The data used here were largely collected by the authors and  
161 built upon a database originally created by Dunn et al. [5, 16]. Additional studies were added  
162 after searches of the Web of Science and Google Scholar for published data sets on ant  
163 assemblages that included site-specific details of species abundances. Assemblages included  
164 in this analysis met the following criteria: 1) the ground-foraging ant assemblage was  
165 sampled using standardised passive field methods, with all studies including pitfall trapping  
166 and some studies also including Winkler or Berlese funnel sampling (both of which involve  
167 sampling from leaf litter); 2) sampling was not trophically or taxonomically limited (e.g., the  
168 study was not focused on only seed-harvesting ants); and 3) assemblages that included one of  
169 the top five invasive ants (*Anoplolepis gracilipes*, *Linepithema humile*, *Pheidole*  
170 *megacephala*, *Solenopsis invicta* or *Wasmannia auropunctata*) outside their native range  
171 were excluded (55 localities). Assemblages were located in Oceania (54.7%), Europe  
172 (12.1%), North America (17.2%), Africa (11.5%), South America (4.0%) and Asia (0.3%).  
173 Ideally all regions would have been well represented, but studies were scarce in some regions  
174 or did not fit our criteria for inclusion. The main broad habitat types represented were forest  
175 (28%), shrubland (22%), woodland (21%) and grassland (16%).

### 176 *Environmental variables: climate and disturbance*

177 Contemporary environmental variables were obtained from the WorldClim database [17] at a  
178 spatial resolution of 30-arc second resolution (ca. 1 × 1 km) and were extracted using ArcGIS  
179 (ESRI 2010). The 1 km resolution was selected so that the environmental data would

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180 describe the conditions with high specificity for the site at which ants were sampled and the  
181 surrounding environment. We used mean annual temperature (MAT: range: 0.1-28.5°C),  
182 annual precipitation (157-3303 mm), temperature range (9.7-52.2°C), hemisphere, continent,  
183 trap days (range: 2-18360) and transect length (range: 1-1000 m) in our analyses. Sampling  
184 grain and extent can affect the outcome of analyses of diversity metrics [18], so including  
185 details of trap days and total transect length in all analyses accounted for differences in  
186 sampling protocols among studies. When the same site was sampled multiple times, we  
187 summed the data across sampling dates to obtain a species abundance value (i.e., the number  
188 of workers) for each species in that site. MAT and annual precipitation peaked at the equator  
189 and were slightly higher in the southern hemisphere than at equivalent latitudes in the  
190 northern hemisphere (Fig. S1a,b). Temperature range was lowest at the equator and was  
191 slightly greater in the northern hemisphere than in the southern hemisphere (Fig. S1c).

192 We categorized sites into three disturbance categories, based on study site descriptions by the  
193 investigators: 1) undisturbed, i.e., no evidence of recent anthropogenic or natural disturbance;  
194 2) disturbed, including moderate disturbances such as forestry (native tree species), wind, fire  
195 (natural), fire (anthropogenic) and restoration (following clearing or mining); and 3)  
196 transformed, including severe disturbances such as agriculture, cropping, grazing, forestry  
197 (introduced tree species), mining, urban and recreation.

### 198 *Data analysis*

199 All statistical analyses were carried out in the R 3.0.3 statistical environment [19]. We  
200 selected two commonly-used metrics to describe assemblage structure: species richness and a  
201 measure of species evenness, the Probability of Interspecific Encounter [PIE, 20, 21]. We  
202 calculated PIE from Simpson's diversity index ( $PIE = 1 - \text{Simpson's diversity index}$ ) using



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203 the vegan package [22]. PIE gives the probability that two randomly sampled individuals  
204 from an assemblage represent two different species. PIE is equivalent to the slope of an  
205 individual-based rarefaction curve measured at its base [23] and ranges from 1.0 when all  
206 species are equally abundant in an assemblage to 0 when there is only a single species in an  
207 assemblage. PIE is also robust to variation in abundance among assemblages [24] and is a  
208 scale-independent metric [18]. Additionally, PIE was strongly and inversely correlated with  
209 a measure of dominance (number of individuals of the most abundant species divided by the  
210 number of individuals of all species) ( $t_{(748)} = -87.0, p < 0.0001, r = -0.95$ ) and positively  
211 correlated with a range of other diversity measures for our dataset, including Shannon's H  
212 and Pielou's evenness. PIE and species richness were correlated, but the relationship was  
213 weak ( $r = 0.13$ ). We henceforth refer to PIE as "species evenness".

214 We tested the effect of climate (mean annual temperature, mean annual precipitation and  
215 temperature range) and disturbance (three levels: disturbed, undisturbed, transformed) on  
216 species richness and evenness of ant communities. Additionally, to control for sampling  
217 differences, we included the number of trap days and transect length in all models. Because  
218 sites were spatially clustered, we used mixed effects models, with clusters of sites separated  
219 by  $\leq 100$ km from each other represented by a single random effect to control for potential  
220 autocorrelation between localised sites (see Fig. S2 for map of clusters). We also included  
221 continent and hemisphere as fixed effects in the models, in order to account for any regional  
222 differences in ant assemblages. For species richness, we used the lme 4 package [25] to fit  
223 generalised linear mixed models (GLMMs), specifying a Poisson error distribution. Fitted  
224 models for species richness showed evidence of over dispersion, so to control for this we  
225 included an observation level random effect [26, 27]. To model the effects of disturbance  
226 and climate on species evenness (PIE), we built linear mixed effects models in the lme4

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227 package. Because PIE represents a bounded variable (between 0 and 1), we used a logit  
228 transformation [28]. The minimum non-zero value ( $3.35 \times 10^{-4}$ ) was added to the  
229 denominator and the numerator of the logit transform equation to allow transformation of  
230 values equal to zero and 1, which would otherwise transform to  $-\infty$  and  $\infty$ , respectively. To  
231 test for non-linear relationships in the response variables (species richness and evenness), we  
232 used Akaike's Information Criterion (AIC) to compare models which included key climatic  
233 variables (mean annual temperature, mean annual precipitation) as: 1) linear terms; and 2)  
234 second order polynomial terms. Polynomial terms were fitted as orthogonal variables to  
235 avoid correlations between the linear and quadratic components in the model [29]. To test  
236 for the significance of climate and disturbance effects, we used type III tests based on Wald  
237 Chi-square statistics calculated using the car package [30]. We also report both marginal  
238 (fixed effects;  $R_{GLMM(m)}^2$ ) and conditional (fixed + random effects;  $R_{GLMM(c)}^2$ )  $R^2$  values [31]).

239 Our modelling approach compared nested models that included: 1) climate (mean annual  
240 temperature (MAT, precipitation and temperature range); 2) climate + disturbance; 3) the  
241 climate  $\times$  disturbance interaction, where only MAT was included in the interaction; and 4)  
242 the climate  $\times$  disturbance interaction, where both MAT and precipitation were included in the  
243 interaction (i.e., MAT  $\times$  precipitation  $\times$  disturbance). All models included lower level  
244 interactions and the main effects MAT, precipitation and temperature range. We used AIC to  
245 select the best model. For a subset of the data where we had more detailed information on  
246 the type of disturbance ( $n = 755$ ), we also tested models where fire-affected sites were  
247 excluded, because the absence of fire might be considered a disturbance in highly fire-prone  
248 biomes. Additionally, we examined models where low latitudes ( $-17^\circ$  to  $17^\circ$ ) were excluded,  
249 because transformed sites were not represented within that range.

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## 250 **Results**

251 Both species richness and species evenness showed hump-shaped relationships with latitude,  
252 reflecting patterns observed for climatic variables (Fig S3). Species richness of ground-  
253 dwelling ants ranged from 1 to 172 per assemblage, while species evenness, ranged from 0 to  
254 0.98 per assemblage (with 1 being maximally “even”). Both measures peaked at the equator  
255 (Fig S3).

### 256 *Best-fit models for climate and disturbance*

257 The best-fit models (lowest AIC) for both species richness and species evenness were the  
258 most complex models, including the three-way interaction between disturbance, mean annual  
259 temperature (MAT) and precipitation (Table 1). Models including the three-way interaction  
260 also had the lowest AIC when sites affected by fire or low latitude sites were excluded (Table  
261 S1). MAT and precipitation were linear terms in the best-fit model for species richness and  
262 polynomial terms in the best-fit model for species evenness. For species richness, the top  
263 three models included a three-way interaction between MAT, precipitation and disturbance  
264 (with various combinations of polynomial and linear terms). The top eight models for  
265 species richness included the MAT×Disturbance interaction, and models without this term  
266 differed from the best model by at least 99.5 AIC points. For species evenness, four of the  
267 top eight models included the three-way interaction, and seven of the eight models included  
268 the MAT×Disturbance term. AIC values for the top model for species evenness were  
269 considerably lower than those for other models. The three-way models were also the best-fit  
270 models when fire-affected and low latitude sites were excluded (Table S1).

271 For species richness (Table 2, Table S2, Figs. 2a, b, c), the best-fit model was a good fit to  
272 the data ( $R_{GLMM(m)}^2 = 0.45$ ;  $R_{GLMM(c)}^2 = 0.77$ ). The slope of the positive relationship between

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273 temperature and species richness was contingent on both disturbance and precipitation. In  
274 both undisturbed and disturbed sites, species richness increased strongly with temperature,  
275 with precipitation having a stronger effect on species richness in disturbed sites (Figs. 2a, b).  
276 In transformed sites, species richness increased with temperature at a slower rate than in other  
277 disturbance categories. While species richness tended to be higher in disturbed than  
278 undisturbed sites, the effects of habitat transformation on species richness was equivalent to  
279 the effects of substantial declines in mean annual temperature. As example of this effect, at  
280 an annual precipitation of 1000 mm, species richness in transformed habitats with mean  
281 annual temperatures of 20 °C was equivalent to species richness in undisturbed sites at 13 °C  
282 (Fig. 2 a, c).

283 The best model for species evenness was also a strong fit to the data ( $R_{GLMM(m)}^2 = 0.37$ ;  
284  $R_{GLMM(c)}^2 = 0.49$ ). Species evenness generally increased with temperature and precipitation,  
285 with the increase with temperature most pronounced for undisturbed sites (Table 2, Table S2,  
286 Figs. 2 d, e, f). Under low precipitation, species evenness was higher in undisturbed than  
287 disturbed and transformed sites. At high temperatures and low precipitation (less than 1000  
288 mm), predicted species evenness decreased at disturbed sites. At an annual precipitation of  
289 1000 mm, transformed sites with mean annual temperatures of 20 °C had species evenness  
290 equivalent to that found at 15 °C in disturbed sites and 11 °C in undisturbed sites (Figs. 2 d,  
291 e, f).

## 292 **Discussion**

293 Over the range of mean annual temperatures represented in this study (0.1°C to 28.5 °C),  
294 species richness was positively associated with temperature, in agreement with patterns  
295 previously documented for a range of taxa, including plants and mammals [e.g., 32] and ants

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296 [5, 33]. Species evenness was also largely positively associated with temperature, even  
297 though species richness and evenness were not well correlated. In warmer regions, ant  
298 assemblages were both more diverse (as has been well-documented) and more even (which  
299 has not been considered previously).

300 Climate clearly regulated the effects of disturbance on both species richness and evenness,  
301 suggesting that there may be implications for predicting how climate change will affect local  
302 assemblages. Climate filters species into assemblages [15], so extreme climates act to exclude  
303 species from assemblages; our results suggest that disturbance and habitat transformation  
304 have the same filtering effect, with predictably greater effects from transformation in low  
305 precipitation environments. The negative effects of disturbance seen in transformed sites  
306 may occur because disturbance both reduces biomass and simplifies habitats [34], resulting in  
307 an outcome similar to the effects of aridity on assemblages. However, in warm climates,  
308 species richness tended to be higher in disturbed than in undisturbed habitats. This might be  
309 a result of increased habitat heterogeneity or the dynamic of colonisers and competitively  
310 dominant species predicted by the intermediate disturbance hypothesis [6].

311 Critically, our study reveals that precipitation plays a key role in mediating the relationships  
312 among richness, evenness, disturbance and temperature. At higher precipitation, our models  
313 showed that, although evenness is lower in disturbed and transformed sites, and richness is  
314 lower in transformed sites, both richness and evenness exhibit a similar relationship to  
315 temperature as undisturbed sites (i.e. increase with increasing temperature). This is likely due  
316 to increasing habitat complexity and resource availability [34, 35]. There is, however, a  
317 strikingly different scenario in arid habitats: here evenness in disturbed and transformed sites  
318 remains low, regardless of temperature. In other words, under low precipitation, undisturbed  
319 habitats support the highest species evenness, particularly at higher temperatures, suggesting

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320 that the costs of disturbance are greater in warmer, low productivity sites. A similar effect  
321 occurs for species richness in transformed sites. The effects of disturbance in hot arid  
322 environments such as shrublands, deserts and savannas might be particularly acute if  
323 recovery after disturbance is slower [e.g., 36]. However, previous studies suggest that ant  
324 assemblages in arid environments recover rapidly following disturbance because changes in  
325 habitat structure are small [37]. Collectively, these findings highlight that the biota in low  
326 productivity environments can be highly sensitive to disturbance. Given the dominance of  
327 pastoralism in these regions, it is likely these disturbances may have a more immediate and  
328 longer-lasting local legacy than climate change.

### 329 *Conclusions*

330 Our results suggest that, at global scales, with increasing temperature, assemblages become  
331 more species rich, with a greater evenness (and reduced dominance by single species).  
332 However, extrapolating from these findings to predict responses to climate change may be  
333 overambitious. The manner in which assemblage structure changes in response to  
334 temperature depends on the local species pool and the ability of colonising species to disperse  
335 rapidly enough to track temperature change [38]. At the predicted extreme climates, it is  
336 unclear whether species with suitable tolerances exist in the regional species pool. It is  
337 therefore possible that temperature increases will lead to increasing dominance and reduced  
338 diversity close to the equator (the 'edge' of the species pool, where species experience the  
339 highest temperatures) [39] and in assemblages to which dispersal is limited. Moreover while  
340 our data also indicate the critical role precipitation plays in shaping assemblage structure,  
341 predictions for changes in rainfall regimes and understanding of how biota might respond are  
342 even more uncertain than those for temperature [40].

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343 Climate change is predicted to increase the frequency of extreme weather events, such as  
344 drought, heatwaves and heavy rainfall, which can either act directly as disturbances to  
345 ecosystems or increase the severity of other disturbances (e.g., fire) [41]. A common effect  
346 of habitat disturbances is simplification of habitat structure [34, 42], and habitat complexity is  
347 positively associated with species richness and evenness [43]. The predicted increase in  
348 extreme events due to climate change therefore has the potential to be a significant driver of  
349 change in assemblage structure. Our data suggest that the effects of disturbance on  
350 assemblage structure could be equivalent to the effects of changes in mean annual  
351 temperature up to 9°C (Fig. 2), which is much greater than temperature increase predictions  
352 for the next 100 years of up to 4.8 °C in the most extreme scenarios [44]. However while our  
353 data suggest that climate change would result in more species-rich and even assemblages  
354 (assuming species are available to colonise sites), we argue that severe disturbance is likely to  
355 pose a more immediate and pressing threat to ecosystems by decreasing diversity and  
356 promoting dominance by disturbance specialists.

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## 361 **Authors' contribution**

362 HG coordinated the study. HG, NJS, RDD and CLP conceived of and designed the study and  
363 helped draft the manuscript. SW and HG analysed the data. All authors except SW  
364 contributed data. All authors revised the article critically and gave final approval of the  
365 version to be published.

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366 **Data accessibility**

367 Data can be accessed through the Dryad database: doi:10.5061/dryad.r36n0.



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## Figure legends

**Figure 1:** World map (Plate Carrée projection) showing the 1128 independent study locations (open circles) from which we obtained data on ant assemblages from pitfall trapping. Note that many of the studies used evaluated multiple independent locations in relatively close proximity, so appear as a single point.

**Figure 2:** Contour plots showing model predictions for relationships with mean annual temperature and precipitation for species richness at: a) undisturbed sites; b) disturbed sites; and c) transformed sites; and for PIE at: d) undisturbed sites; e) disturbed sites; and f) transformed sites. Data are plotted only to the environmental space of each dataset.

Fig. 1

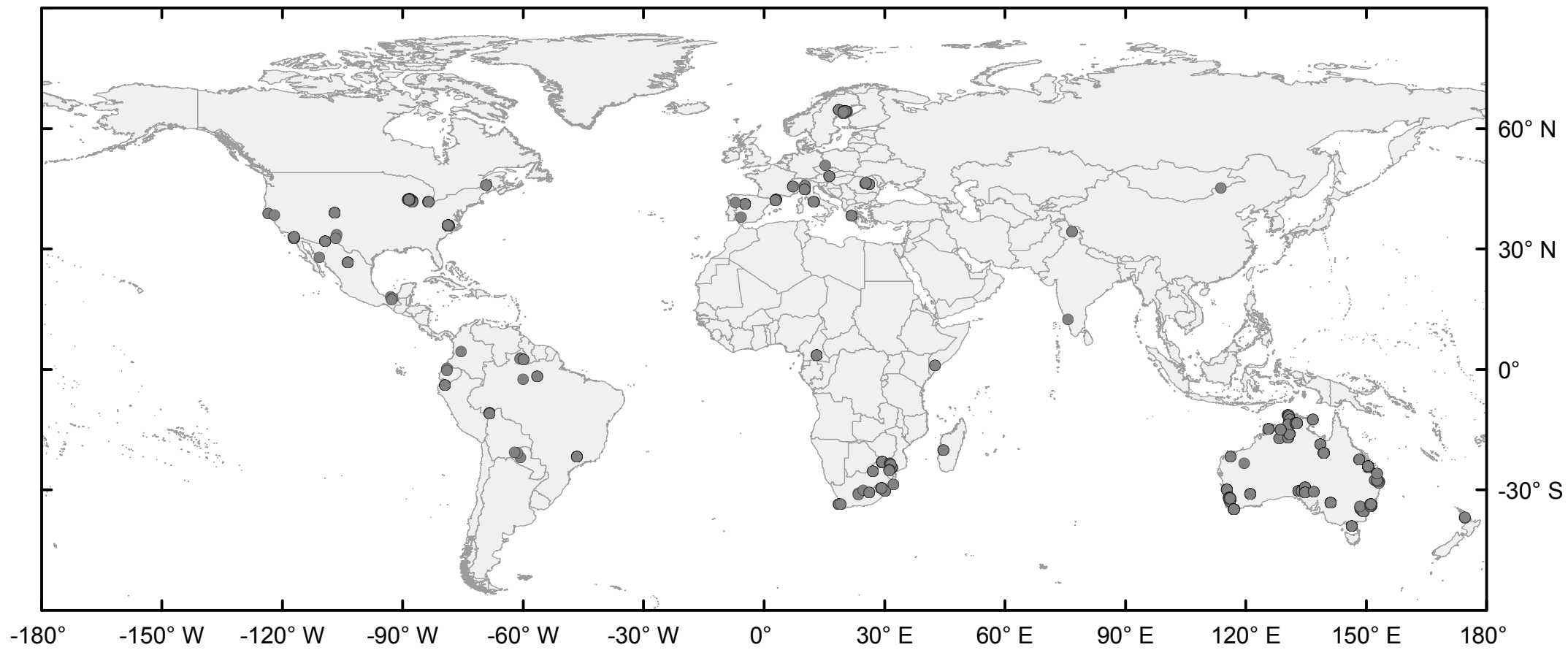
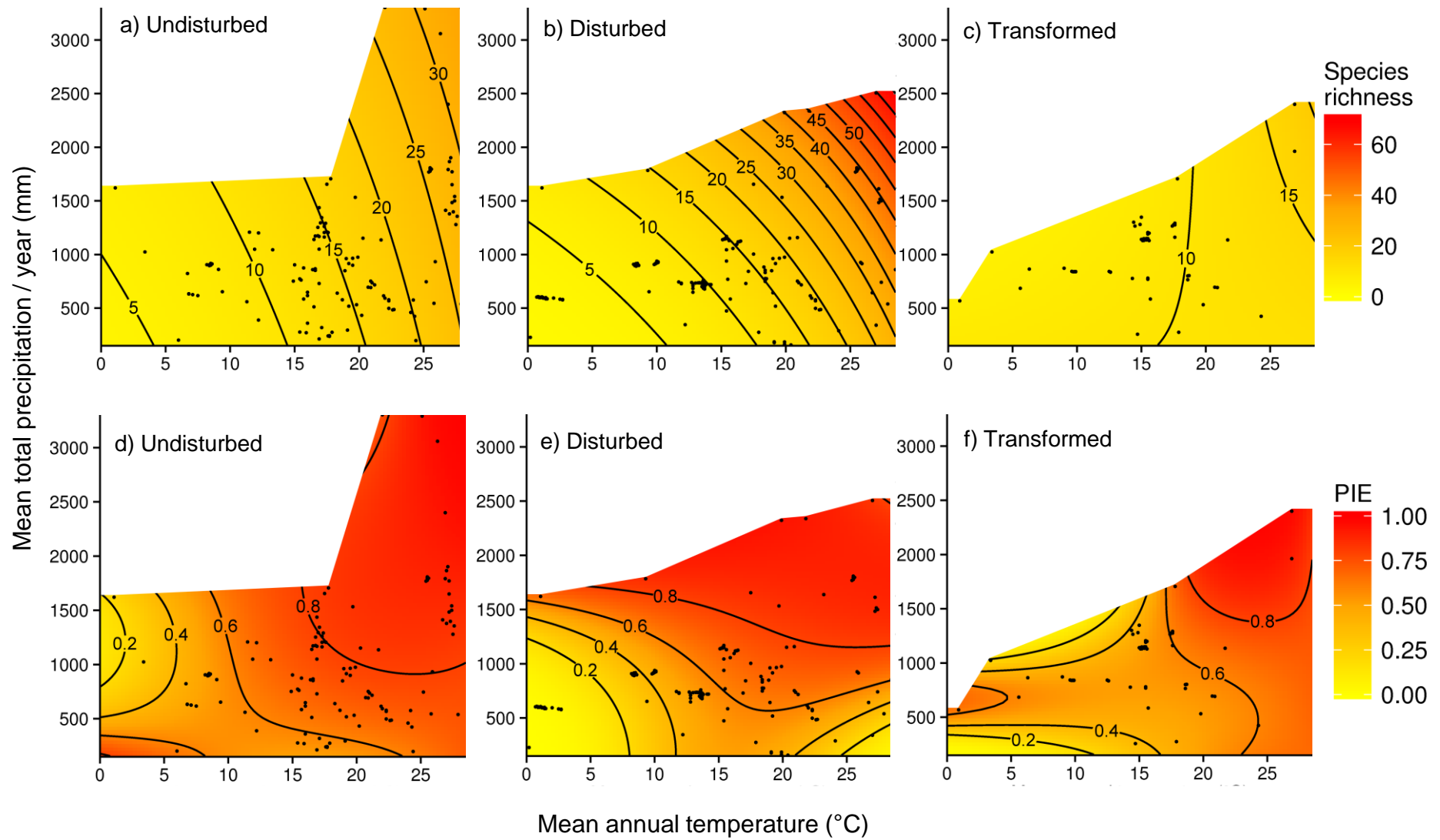


Fig. 2



**Table 1:** Change in Akaike’s information criterion ( $\Delta$ AIC) and model rank for all models predicting the effect of climate (mean annual temperature and total annual precipitation) and disturbance on species richness and evenness (n = 1123). All models included lower level interactions, temperature range, transect length, pitfall days, hemisphere and continent. Both linear and 2<sup>nd</sup> order polynomial terms (poly) were included for precipitation and temperature range.

Model	df	<i>Species richness</i>		<i>Species evenness</i>	
		$\Delta$ AIC	Rank	$\Delta$ AIC	Rank
Temp. x Prec. x Disturbance	22	0.0	1	234.6	6
Temp.(poly) x Prec. x Disturbance	28	3.0	2	137.5	3
Temp. x Prec.(poly) x Disturbance	28	3.2	3	174.5	4
Prec.(poly) x Temp.(poly) x Disturbance	37	6.3	4	0.0	1
Temp.(poly) x Prec.(poly) + Temp.(poly) x Disturbance	25	6.8	5	133.4	2
Temp. x Prec.(poly) + Temp. x Disturbance	20	10.4	6	254.5	7
Temp.(poly) x Prec. + Temp.(poly) x Disturbance	22	10.5	7	176.3	5
Temp. x Prec. + Temp. x Disturbance	18	13.4	8	273.1	9
Temp. x Prec.(poly) + Disturbance	18	99.5	9	312.8	12
Temp. x Prec. + Disturbance	16	102.6	10	331.0	18
Temp.(poly) x Prec.(poly) + Disturbance	21	103.1	11	261.8	8
Temp.(poly) x Prec. + Disturbance	18	106.4	12	303.3	11
Temp. + Prec.	13	168.4	13	344.3	22
Temp. + Prec.(poly)	14	168.7	14	336.7	19
Temp. x Prec.	14	169.8	15	346.0	23
Temp.(poly) + Prec.	14	170.3	16	327.8	16
Temp. x Prec.(poly)	16	170.4	17	327.2	15
Temp.(poly) + Prec.(poly)	15	170.6	18	320.1	14
Temp.(poly) x Prec.(poly)	19	172.7	19	276.6	10
Temp.(poly) x Prec.	16	172.9	20	319.0	13
Temp.	4	194.4	21	342.2	20
Temp.(poly)	5	195.4	22	329.8	17
Prec.	4	242.1	23	349.4	24
Precipitation(poly)	5	243.8	24	342.3	21

**Table 2:** Test statistic and significance for best fit models testing the effect of climate and disturbance on diversity indices. † p < 0.10; \* p < 0.05; \*\* p < 0.01 \*\*\* p < 0.001.

Response	Species Richness			Evenness	
	df	$\chi^2$		$\chi^2$	
Mean annual temperature (MAT)	2	72.0	***	28.5	***
Precipitation	2	5.8	*	18.6	***
Disturbance	2	79.2	***	29.0	***
Temperature range	1	22.1	***	12.1	***
Hemisphere	1	2.2		0.0	
Continent	4	8.9		2.5	
Transect length	1	0.9		1.3	
Pitfall days	1	2.5		3.1	
MAT*Precipitation	4	0.4		3.6	
MAT*Disturbance	4	58.5	***	101.2	***
Precipitation*Disturbance	4	17.2	***	11.7	*
MAT*Precipitation*Disturbance	8	4.8		20.7	**