Climate mediates the effects of disturbance on ant assemblage structure

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Short title: *Climate, disturbance and assemblages*

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.

Introduction

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

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

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

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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.

Materials and Methods

Assemblage data

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

Environmental variables: climate and disturbance

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

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: 0.1-28.5ºC),

182   annual precipitation (157-3303 mm), temperature range (9.7-52.2ºC), 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 – Simpson's diversity index) using

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 ≤100km 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

227   package. Because PIE represents a bounded variable (between 0 and 1), we used a logit

228   transformation [28]. The minimum non-zero value (3.35×10^{-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 ∞, 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; $R^2_{GLMM(m)}$ and conditional (fixed + random effects; $R^2_{GLMM(c)}$) 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° to 17°) were excluded,

249   because transformed sites were not represented within that range.

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 ($R^2_{GLMM(m)} = 0.45$; $R^2_{GLMM(c)} = 0.77$). The slope of the positive relationship between

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

10

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 ($R^2_{GLMM(m)} = 0.37$;

284     $R^2_{GLMM(c)} = 0.49$). 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).

Discussion

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

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

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].

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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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.

Data accessibility

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

References

1.	Weiher E., Keddy P. 1999 *Ecological Assembly Rules: Perspectives, advances, retreats*. Cambridge, UK, Cambridge University Press.
2.	Hubbell S.P. 2001 *The Unified Neutral theory of Biodiversity and Biogeography*. Princeton, NJ, Princeton University Press.
3.	Gaston K.J. 2000 Global patterns in biodiversity. *Nature* **405**, 220-227. (10.1038/35012228).
4.	Buckley L.B., Jetz W. 2007 Environmental and historical constraints on global patterns of amphibian richness. *P R Soc B* **274**, 1167-1173. (DOI 10.1098//rspb.2006.0436).
5.	Dunn R.R., Agosti D., Andersen A.N., Arnan X., Bruhl C.A., X. C., Ellison A.M., Fisher B.L., Fitzpatrick M.C., Gibb H., et al. 2009 Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecol Lett* **12**, 324-333.
6.	Grime J.P. 1973 Competitive exclusion in herbaceous vegetation. *Nature* **242**, 344-347.
7.	Dornelas M. 2010 Disturbance and change in biodiversity. *Philos T R Soc B* **365**, 3719-3727. (DOI 10.1098/rstb.2010.0295).
8.	Newbold T., Hudson L.N., Phillips H.R.P., Hill S.L.L., Contu S., Lysenko I., Blandon A., Butchart S.H.M., Booth H.L., Day J., et al. 2014 A global model of the response of tropical and sub-tropical forest biodiversity to anthropogenic pressures. *Proceedings of the Royal Society B: Biological Sciences* **281**.
9.	Graves G.R., Rahbek C. 2005 Source pool geometry and the assembly of continental avifaunas. *P Natl Acad Sci USA* **102**, 7871-7876. (DOI 10.1073/pnas.0500424102).
10.	Harrison S., Cornell H. 2008 Toward a better understanding of the regional causes of local community richness. *Ecol Lett* **11**, 969-979.
11.	Belote R.T., Sanders N.J., Jones R.H. 2009 Disturbance alters local–regional richness relationships in Appalachian forests. *Ecology* **90**, 2940-2947.
12.	Buckley L.B., Davies T.J., Ackerly D.D., Kraft N.J.B., Harrison S.P., Anacker B.L., Cornell H.V., Damschen E.I., Grytnes J.A., Hawkins B.A., et al. 2010 Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *P R Soc B* **277**, 2131-2138. (DOI 10.1098/rspb.2010.0179).
13.	Willig M.R., Kaufman D.M., Stevens R.D. 2003 Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. *Annual Review of Ecology, Evolution and Systematics* **34**, 273-309.
14.	Mackey R.L., Currie D.J. 2000 A re-examination of the expected effects of disturbance on diversity. *Oikos* **88**, 483-493. (DOI 10.1034/j.1600-0706.2000.880303.x).
15.	Lessard J.P., Borregaard M.K., Fordyce J.A., Rahbek C., Weiser M.D., Dunn R.R., Sanders N.J. 2012 Strong influence of regional species pools on continent-wide structuring of local communities. *P R Soc B* **279**, 266-274. (DOI 10.1098/rspb.2011.0552).
16.	Dunn R.R., Sanders N.J., Fitzpatrick M.C., Laurent E., Lessard J.P., Agosti D., Andersen A.N., Bruhl C., Cerda X., Ellison A.M., et al. 2007 Global ant (Hymenoptera: Formicidae) biodiversity and biogeography - a new database and its possibilities. *Myrmecological News* **10**, 77-83.
17.	Hijmans R.J., Cameron S., Parra J. 2004. *WorldClim, Version 12 A square kilometer resolution database of global terrestrial surface climate* **Available at: http://www.worldclim.org/download**.
18.	Chase J.M., Knight T.M. 2013 Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. *Ecol Lett* **16**, 17-26. (Doi 10.1111/Ele.12112).

19.   R Development Core Team. 2014 R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing.

20.   Hurlbert S.H. 1971 Nonconcept of species diversity - critique and alternative parameters. *Ecology* **52**, 577-586. (Doi 10.2307/1934145).

21.   Magurran A.E. 2004 *Measuring biological diversity*. Oxford, Blackwell Publishing.

22.   Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Henry M., Stevens H., et al. 2013 vegan: Community Ecology Package. In *R package version 20-8*.

23.   Olszewski T.D. 2004 A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. *Oikos* **104**, 377-387. (DOI 10.1111/j.0030-1299.2004.12519.x).

24.   Gotelli N.J., Graves G.R. 1996 *Null Models in Ecology*. Washington, D.C. , Smithsonian Institution Press.

25.   Bates D., Maechler M., Bolker B., Walker S. 2014 lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-6. http://CRAN.R-project.org/package=lme4.

26.   Zuur A.F., Savaliev A.A., Ieno E.N. 2012 *Zero Inflated Models and Generalized Linear Mixed Models with R*. Newburgh, UK, Highland Statistics.

27.   Laird N.M., Ware J.H. 1982 Random-Effects Models for Longitudinal Data. *Biometrics* **38**, 963-974. (Doi 10.2307/2529876).

28.   Warton D.I., Hui F.K.C. 2011 The arcsine is asinine: the analysis of proportions in ecology. *Ecology* **92**, 3-10. (10.1890/10-0340.1).

29.   Chambers J.M., Hastie, T.J. 1992 *Statistical Models in S*, Wadsworth & Brooks/Cole.

30.   Fox J., Weisberg S. 2011 An {R} Companion to Applied Regression. (Second ed. Thousand Oaks CA, Sage.

31.   Nakagawa S.S., H. 2013 A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol Evol* **4**, 133-142.

32.   Kreft H., Jetz W. 2007 Global patterns and determinants of vascular plant diversity. *P Natl Acad Sci USA* **104**, 5925-5930. (DOI 10.1073/pnas.0608361104).

33.   Kaspari M., Alonso L., O'Donnell S. 2000 Three energy variables predict ant abundance at a geographical scale. *P R Soc B* **267**, 485-489. (DOI 10.1098/rspb.2000.1026).

34.   Syms C., Jones G.P. 2000 Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology* **81**, 2714-2729. (Doi 10.1890/0012-9658(2000)081[2714:Dhsatd]2.0.Co;2).

35.   Gibb H., Parr C.L. 2010 How does habitat complexity affect ant foraging success? A test of functional responses on three continents. *Oecologia* **164**, 1061-1073.

36.   Guo Q. 1994 Slow recovery in desert perennial vegetation following prolonged human disturbance. *J Veg Sci* **15**, 757-762.

37.   Hoffmann B.D., Andersen A.N. 2003 Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecol* **28**, 444-464.

38.   Hughes L. 2000 Biological consequences of global warming: Is the signal already apparent? *Trends Ecol Evol* **15**, 56-61. (Doi 10.1016/S0169-5347(99)01764-4).

39.   Colwell R.K., Brehm G., Cardelus C.L., Gilman A.C., Longino J.T. 2008 Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* **322**, 258-261. (DOI 10.1126/science.1162547).

40.   Sala O.E., Chapin III F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A., et al. 2000 Global biodiversity scenarios for the year 2100. *Science* **287**, 1770-1774.

41.   Jentsch A., Beierkuhnlein C. 2008 Research frontiers in climate change: Effects of extreme meteorological events on ecosystems. *Cr Geosci* **340**, 621-628. (DOI 10.1016/j.crte.2008.07.002).

42.   Gibb H., Parr C.L. 2013 Does structural complexity determine the morphology of assemblages? An experimental test on three continents. *Plos One* **8**, e64005. (10.1371/journal.pone.0064005).

43.   Tews J., Brose U., Grimm V., Tielbörger K., Wichmann M.C., Schwager M., Jeltsch F. 2003 Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *J Biogeogr* **31**, 79-92.

44.   IPCC. 2013 Summary for Policymakers. Working Group I Contribution to the IPCC Fifth Assessment Report. Climate Change 2013: The Physical Science Basis.

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.
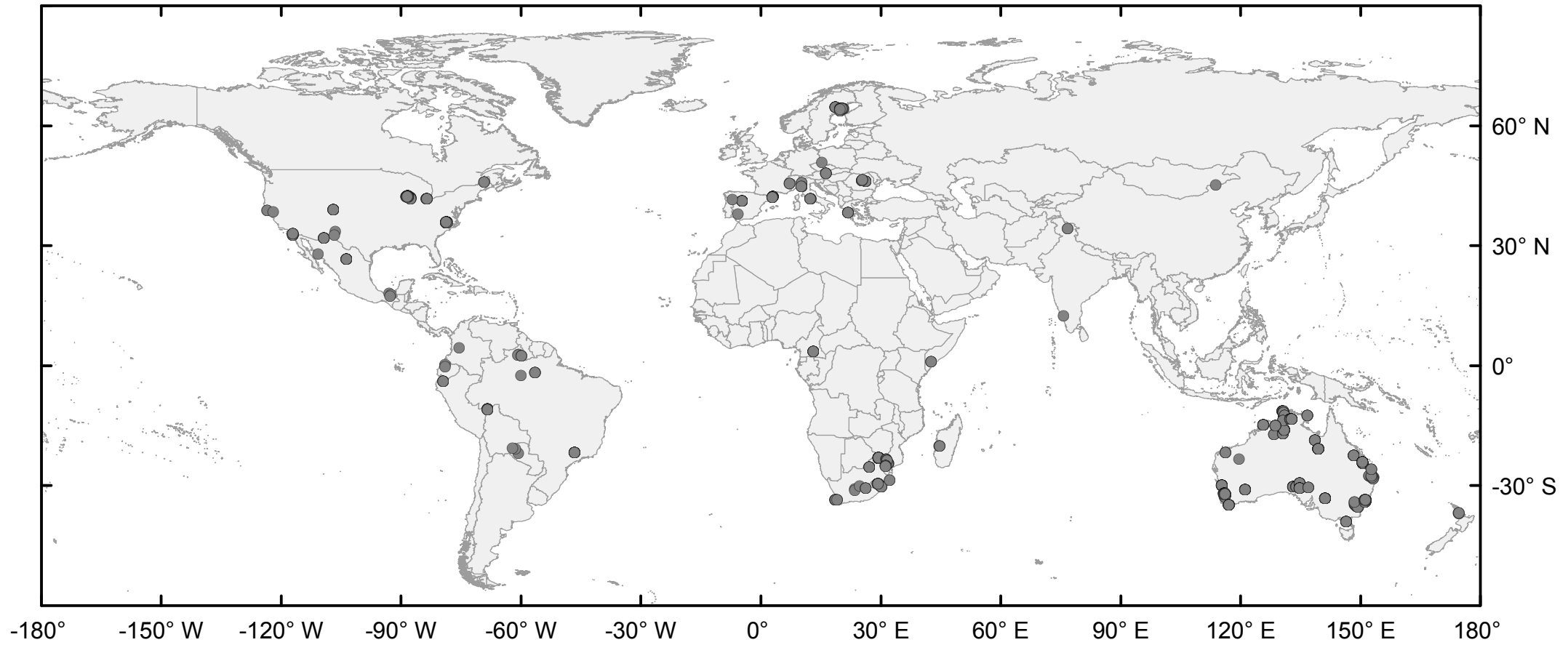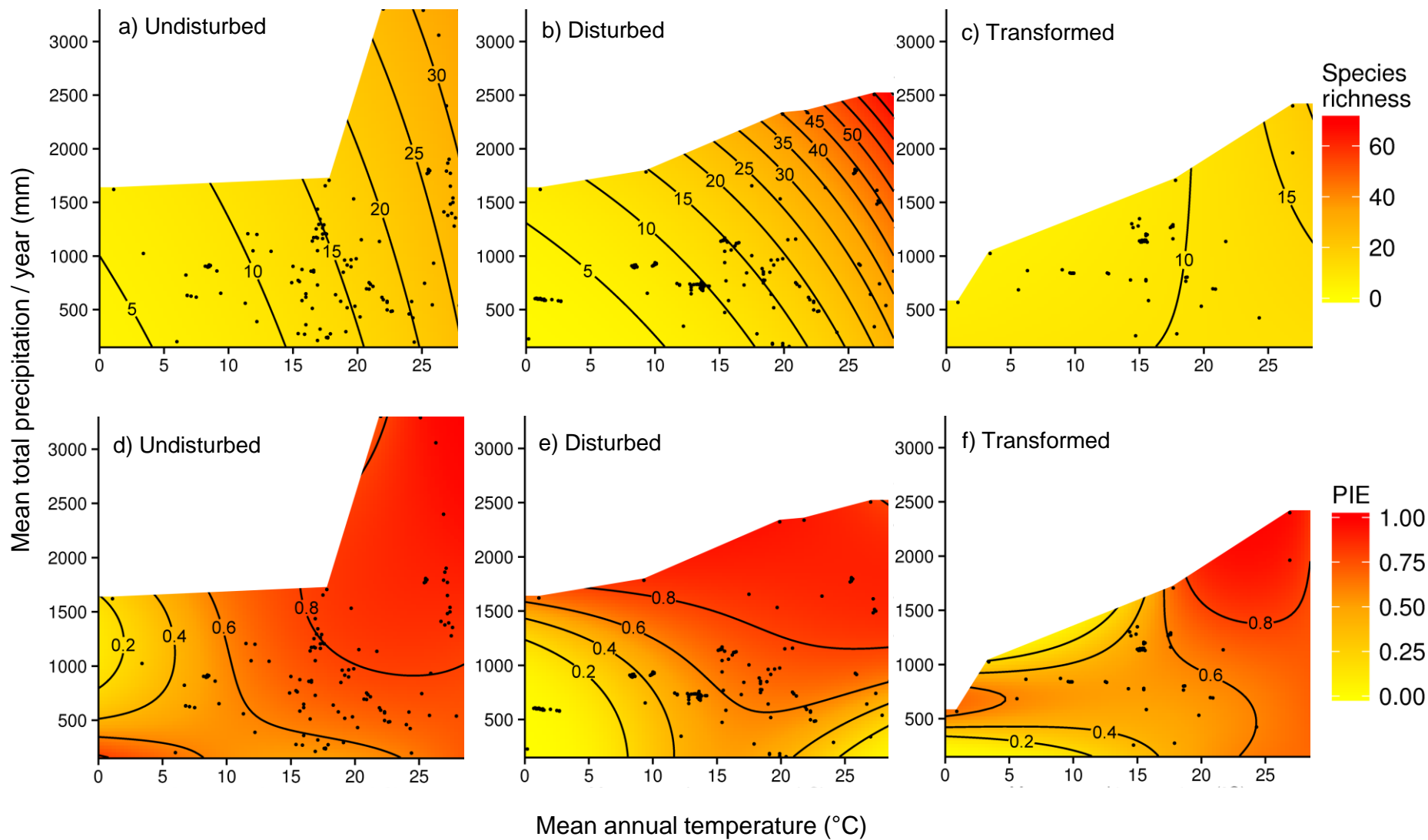
Fig. 1

Fig. 2

Table S2: Estimates, standard errors and test statistics for analyses of best models for species richness (Z-statistics) and species evenness (t-statistic). For species evenness, P indicates a polynomial term; L indicates a linear term.

Source	Estimate	Std Err	Test statistic
Species richness			
(Intercept)	3.25	0.28	11.68
MAT	1.20	0.13	9.08
Precipitation	0.51	0.12	4.34
Disturbance - Transformed	-0.39	0.05	-7.73
Disturbance - Undisturbed	-0.04	0.04	-0.84
Temperature range	0.55	0.12	4.70
Hemisphere - South	-0.37	0.25	-1.47
Continent - Eurasia	-0.55	0.31	-1.76
Continent - North America	-0.63	0.32	-1.95
Continent - Oceania	0.10	0.19	0.52
Continent - South America	0.29	0.24	1.19
Transect length	-0.02	0.02	-0.96
Pitfall days	0.03	0.02	1.57
MAT*Precipitation	-0.23	0.20	-1.18
MAT*Disturbance - Transformed	-0.74	0.12	-6.32
MAT*Disturbance - Undisturbed	-0.34	0.11	-3.18
Precipitation*Disturbance - Transformed	-0.57	0.13	-4.39
Precipitation*Disturbance - Undisturbed	-0.35	0.11	-3.04
MAT*Precipitation*Disturbance - Transformed	0.58	0.27	2.19
MAT*Precipitation*Disturbance - Undisturbed	0.14	0.21	0.68
Species evenness			
(Intercept)	0.49	0.54	0.92
poly(MAT, 2)(L)	18.69	4.67	4.01
poly(MAT, 2)(P)	-20.71	4.01	-5.16
poly(Precipitation, 2)(L)	26.71	5.13	5.20
poly(Precipitation, 2)(P)	0.33	5.47	0.06
Disturbance - Transformed	-0.34	0.40	-0.87
Disturbance - Undisturbed	0.58	0.14	4.17
Temperature range	0.94	0.27	3.48
Hemisphere - South	0.09	0.54	0.17
Continent - Eurasia	-0.19	0.61	-0.32
Continent - North America	-0.06	0.63	-0.10
Continent - Oceania	0.41	0.30	1.39
Continent - South America	0.42	0.42	0.99
Transect length	-0.08	0.07	-1.14
Pitfall days	0.12	0.07	1.76
poly(MAT, 2)(L)*poly(Precipitation, 2)(L)	-97.55	139.10	-0.70
poly(MAT, 2)(P)*poly(Precipitation, 2)(L)	352.00	129.80	2.71
poly(MAT, 2)(L)*poly(Precipitation, 2)(P)	-305.70	209.20	-1.46
poly(MAT, 2)(P)*poly(Precipitation, 2)(P)	-142.00	175.70	-0.81
poly(MAT, 2)(L)*Disturbance - Transformed	15.52	23.76	0.65
poly(MAT, 2)(P)*Disturbance - Transformed	9.70	17.31	0.56
poly(MAT, 2)(L)*Disturbance - Undisturbed	-1.81	4.95	-0.37
poly(MAT, 2)(P)*Disturbance - Undisturbed	15.28	5.07	3.01
poly(Precipitation, 2)(L)*Disturbance - Transformed	-44.23	21.21	-2.09
poly(Precipitation, 2)(P)*Disturbance - Transformed	-25.37	31.04	-0.82
poly(Precipitation, 2)(L)*Disturbance - Undisturbed	-17.60	5.61	-3.14
poly(Precipitation, 2)(P)*Disturbance - Undisturbed	-1.00	6.61	-0.15
poly(MAT, 2)(L)*poly(Precipitation, 2)(L)*Disturbance - Transformed	1800.00	1312.00	1.37
poly(MAT, 2)(P)*poly(Precipitation, 2)(L)*Disturbance - Transformed	1425.00	899.60	-1.58
poly(MAT, 2)(L)*poly(Precipitation, 2)(P)*Disturbance - Transformed	1999.00	1783.00	1.12
poly(MAT, 2)(P)*poly(Precipitation, 2)(P)*Disturbance - Transformed	-852.40	1245.00	-0.68
poly(MAT, 2)(L)*poly(Precipitation, 2)(L)*Disturbance - Undisturbed	279.20	165.90	1.68
poly(MAT, 2)(P)*poly(Precipitation, 2)(L)*Disturbance - Undisturbed	-458.40	157.90	-2.90
poly(MAT, 2)(L)*poly(Precipitation, 2)(P)*Disturbance - Undisturbed	123.60	260.70	0.47
poly(MAT, 2)(P)*poly(Precipitation, 2)(P)*Disturbance - Undisturbed	393.50	219.50	1.79

Table 1: Change in Akaike's information criterion (ΔAIC) 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 2nd order polynomial terms (poly) were included for precipitation and temperature range.

Model	df	Species richness		Species evenness	
		Δ AIC	Rank	Δ 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