

Climate mediates the effects of disturbance on ant assemblage structure

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Abstract

Many studies have focussed on the impacts of climate change on biological assemblages, yet little is known about how climate interacts with other major anthropogenic influences on biodiversity, such as habitat disturbance. Using a unique global database of 1128 local ant assemblages, we examined whether climate mediates the effects of habitat disturbance on assemblage structure at a global scale. Species richness and evenness were associated positively with temperature, and negatively with disturbance. However, the interaction among temperature, precipitation and disturbance shaped species richness and evenness. The effect was manifested through a failure of species richness to increase substantially with temperature in transformed habitats at low precipitation. At low precipitation levels, evenness increased with temperature in undisturbed sites, peaked at mid temperatures in disturbed sites and remained low in transformed sites. In warmer climates with lower rainfall, the effects of increasing disturbance on species richness and evenness were akin to

decreases in temperature of up to 9 °C. Anthropogenic disturbance and ongoing climate change may interact in complicated ways to shape the structure of assemblages, with hot, arid environments likely to be at greatest risk.

Keywords: assemblage structure, dominance, global warming, probability of interspecific encounter (PIE), species evenness

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

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

However, climate might be expected to mediate the effect of disturbance by, for example, altering the rates of colonisation [10] or the prevalence of competition [15]. Thus, understanding the interaction between climate and disturbance is critical in predicting the outcome for species assemblages under global change. Superficially, the transformation of habitats, for example from native forest to pine plantation, might be expected to respond similarly to a disturbance as biomass is removed in the process (although energy flows are

not necessarily reduced). However, in low biomass systems, such as deserts, where the transformation of habitat results in increased biomass, richness may also increase.

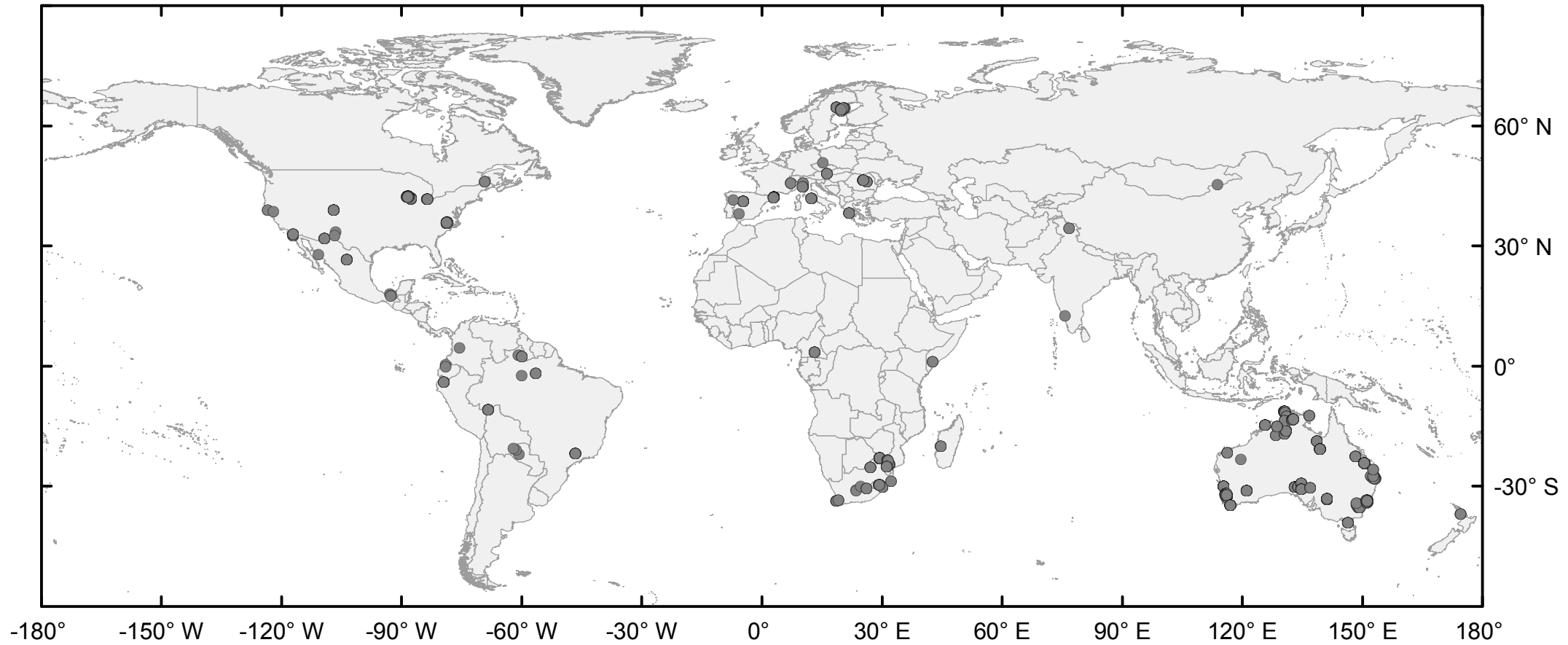
Here, we examine whether contemporary climate mediates the effects of disturbance on ant assemblages around the world. This work is unique in using data from a large set of local assemblages and in examining assemblage evenness in addition to species richness.

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

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.



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

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

Data analysis

All statistical analyses were carried out in the R 3.0.3 statistical environment [19]. We selected two commonly-used metrics to describe assemblage structure: species richness and a measure of species evenness, the Probability of Interspecific Encounter [PIE, 20, 21]. We calculated PIE from Simpson's diversity index ($PIE = 1 - \text{Simpson's diversity index}$) using the *vegan* package [22]. PIE gives the probability that two randomly sampled individuals from an assemblage represent two different species. PIE is equivalent to the slope of an individual-based rarefaction curve measured at its base [23] and ranges from 1.0 when all species are equally abundant in an assemblage to 0 when there is only a single species in an assemblage. PIE is also robust to variation in abundance among assemblages [24] and is a scale-independent metric [18]. Additionally, PIE was strongly and inversely correlated with a measure of dominance (number of individuals of the most abundant species divided by the number of individuals of all species) ($t_{(748)} = -87.0, p < 0.0001, r = -0.95$) and positively correlated with a range of other diversity measures for our dataset, including Shannon's *H* and Pielou's evenness. PIE and species richness were correlated, but the relationship was weak ($r = 0.13$). We henceforth refer to PIE as "species evenness".

We tested the effect of climate (mean annual temperature, mean annual precipitation and temperature range) and disturbance (three levels: disturbed, undisturbed, transformed) on species richness and evenness of ant communities. Additionally, to control for sampling differences, we included the number of trap days and transect length in all models. Because sites were spatially clustered, we used mixed effects models, with clusters of sites separated by $\leq 100\text{km}$ from each other represented by a single random effect to control for potential autocorrelation between localised sites (see Fig. S2 for map of clusters). We also included continent and hemisphere as fixed effects in the models, in order to account for any regional

differences in ant assemblages. For species richness, we used the lme 4 package [25] to fit generalised linear mixed models (GLMMs), specifying a Poisson error distribution. Fitted models for species richness showed evidence of over dispersion, so to control for this we included an observation level random effect [26, 27]. To model the effects of disturbance and climate on species evenness (PIE), we built linear mixed effects models in the lme4 package. Because PIE represents a bounded variable (between 0 and 1), we used a logit transformation [28]. The minimum non-zero value (3.35×10^{-4}) was added to the denominator and the numerator of the logit transform equation to allow transformation of values equal to zero and 1, which would otherwise transform to $-\infty$ and ∞ , respectively. To test for non-linear relationships in the response variables (species richness and evenness), we used Akaike's Information Criterion (AIC) to compare models which included key climatic variables (mean annual temperature, mean annual precipitation) as: 1) linear terms; and 2) second order polynomial terms. Polynomial terms were fitted as orthogonal variables to avoid correlations between the linear and quadratic components in the model [29]. To test for the significance of climate and disturbance effects, we used type III tests based on Wald Chi-square statistics calculated using the car package [30]. We also report both marginal (fixed effects; $R^2_{GLMM(m)}$) and conditional (fixed + random effects; $R^2_{GLMM(c)}$) R^2 values [31]).

Our modelling approach compared nested models that included: 1) climate (mean annual temperature (MAT, precipitation and temperature range); 2) climate + disturbance; 3) the climate \times disturbance interaction, where only MAT was included in the interaction; and 4) the climate \times disturbance interaction, where both MAT and precipitation were included in the interaction (i.e., MAT \times precipitation \times disturbance). All models included lower level interactions and the main effects MAT, precipitation and temperature range. We used AIC to select the best model. For a subset of the data where we had more detailed information on the type of disturbance ($n = 755$), we also tested models where fire-affected sites were

excluded, because the absence of fire might be considered a disturbance in highly fire-prone biomes. Additionally, we examined models where low latitudes (-17° to 17°) were excluded, because transformed sites were not represented within that range.

Results

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

Best-fit models for climate and disturbance

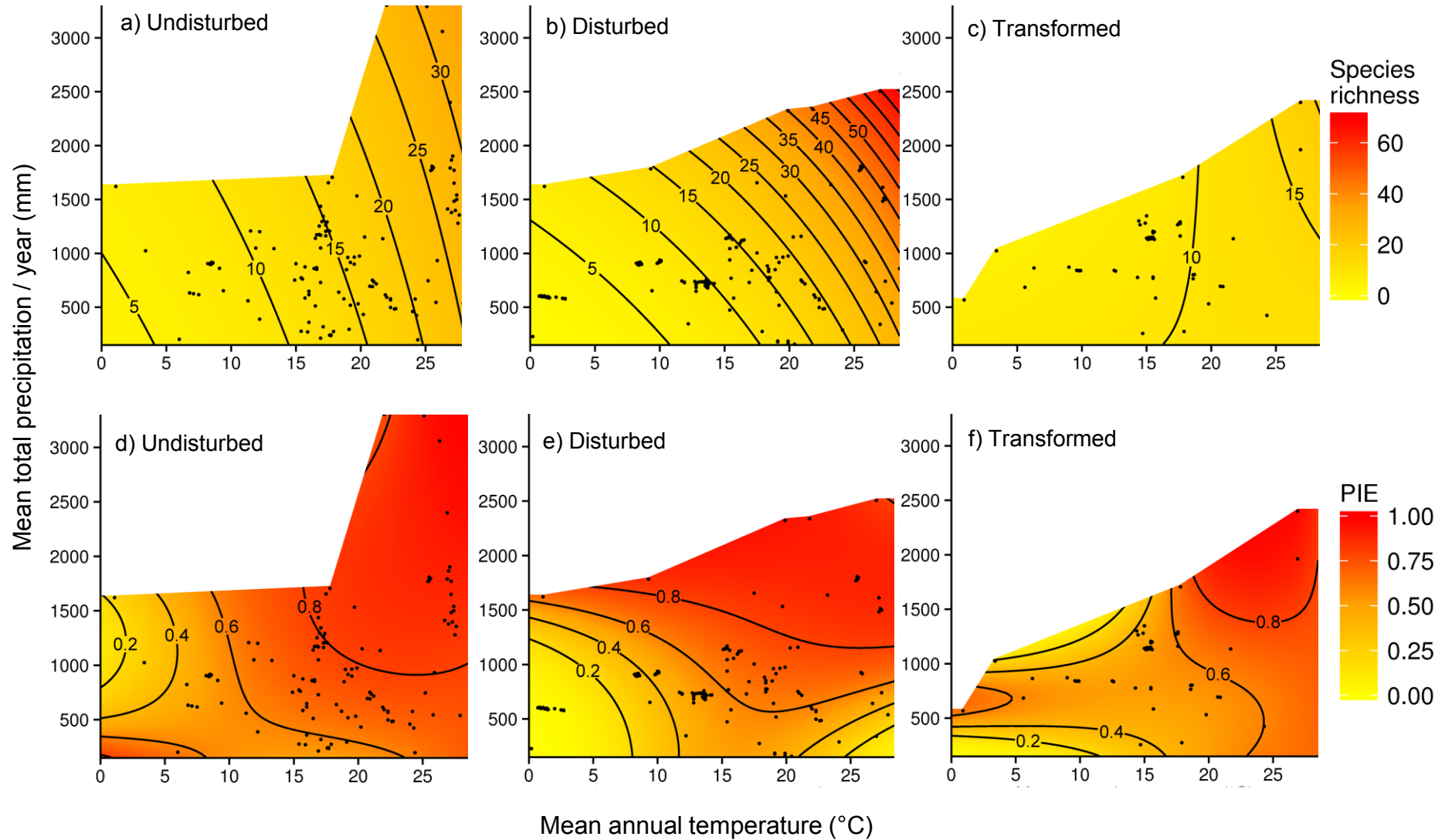
The best-fit models (lowest AIC) for both species richness and species evenness were the most complex models, including the three-way interaction between disturbance, mean annual temperature (MAT) and precipitation (Table 1). Models including the three-way interaction also had the lowest AIC when sites affected by fire or low latitude sites were excluded (Table S1). MAT and precipitation were linear terms in the best-fit model for species richness and polynomial terms in the best-fit model for species evenness. For species richness, the top three models included a three-way interaction between MAT, precipitation and disturbance (with various combinations of polynomial and linear terms). The top eight models for species richness included the MAT×Disturbance interaction, and models without this term differed from the best model by at least 99.5 AIC points. For species evenness, four of the top eight models included the three-way interaction, and seven of the eight models included the MAT×Disturbance term. AIC values for the top model for species evenness were

considerably lower than those for other models. The three-way models were also the best-fit models when fire-affected and low latitude sites were excluded (Table S1).

For species richness (Table 2, Table S2, Figs. 2a, b, c), the best-fit model was a good fit to the data ($R^2_{GLMM(m)} = 0.45$; $R^2_{GLMM(c)} = 0.77$). The slope of the positive relationship between temperature and species richness was contingent on both disturbance and precipitation. In both undisturbed and disturbed sites, species richness increased strongly with temperature, with precipitation having a stronger effect on species richness in disturbed sites (Figs. 2a, b). In transformed sites, species richness increased with temperature at a slower rate than in other disturbance categories. While species richness tended to be higher in disturbed than undisturbed sites, the effects of habitat transformation on species richness was equivalent to the effects of substantial declines in mean annual temperature. As example of this effect, at an annual precipitation of 1000 mm, species richness in transformed habitats with mean annual temperatures of 20 °C was equivalent to species richness in undisturbed sites at 13 °C (Fig. 2 a, c).

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

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



Discussion

Over the range of mean annual temperatures represented in this study (0.1°C to 28.5 °C), species richness was positively associated with temperature, in agreement with patterns previously documented for a range of taxa, including plants and mammals [e.g., 32] and ants [5, 33]. Species evenness was also largely positively associated with temperature, even though species richness and evenness were not well correlated. In warmer regions, ant assemblages were both more diverse (as has been well-documented) and more even (which has not been considered previously).

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

Critically, our study reveals that precipitation plays a key role in mediating the relationships among richness, evenness, disturbance and temperature. At higher precipitation, our models showed that, although evenness is lower in disturbed and transformed sites, and richness is lower in transformed sites, both richness and evenness exhibit a similar relationship to temperature as undisturbed sites (i.e. increase with increasing temperature). This is likely due

to increasing habitat complexity and resource availability [34, 35]. There is, however, a strikingly different scenario in arid habitats: here evenness in disturbed and transformed sites remains low, regardless of temperature. In other words, under low precipitation, undisturbed habitats support the highest species evenness, particularly at higher temperatures, suggesting that the costs of disturbance are greater in warmer, low productivity sites. A similar effect occurs for species richness in transformed sites. The effects of disturbance in hot arid environments such as shrublands, deserts and savannas might be particularly acute if recovery after disturbance is slower [e.g., 36]. However, previous studies suggest that ant assemblages in arid environments recover rapidly following disturbance because changes in habitat structure are small [37]. Collectively, these findings highlight that the biota in low productivity environments can be highly sensitive to disturbance. Given the dominance of pastoralism in these regions, it is likely these disturbances may have a more immediate and longer-lasting local legacy than climate change.

Conclusions

Our results suggest that, at global scales, with increasing temperature, assemblages become more species rich, with a greater evenness (and reduced dominance by single species). However, extrapolating from these findings to predict responses to climate change may be overambitious. The manner in which assemblage structure changes in response to temperature depends on the local species pool and the ability of colonising species to disperse rapidly enough to track temperature change [38]. At the predicted extreme climates, it is unclear whether species with suitable tolerances exist in the regional species pool. It is therefore possible that temperature increases will lead to increasing dominance and reduced diversity close to the equator (the ‘edge’ of the species pool, where species experience the highest temperatures) [39] and in assemblages to which dispersal is limited. Moreover while

our data also indicate the critical role precipitation plays in shaping assemblage structure, predictions for changes in rainfall regimes and understanding of how biota might respond are even more uncertain than those for temperature [40].

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

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Authors' contribution

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

Data accessibility

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

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Fig. S1: Variation in climate and disturbance with latitude: a) mean annual temperature and disturbance; b) precipitation; and c) temperature range

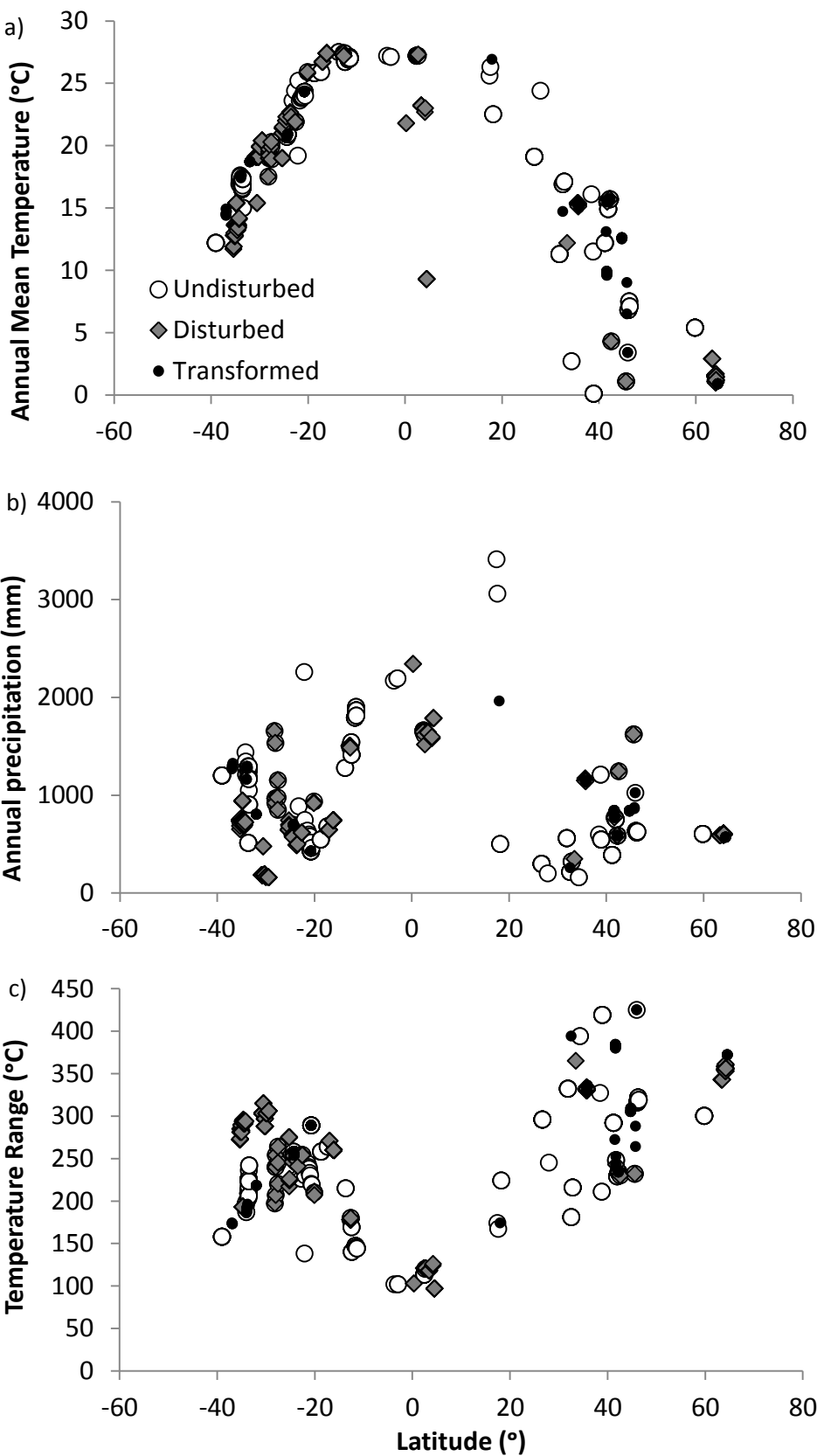


Fig. S2: World map showing the spatial clusters and the number of sites within each cluster used in the analysis of ant assemblages. We used 53 clusters containing between 1 and 80 sites for the 1128 independent study locations.

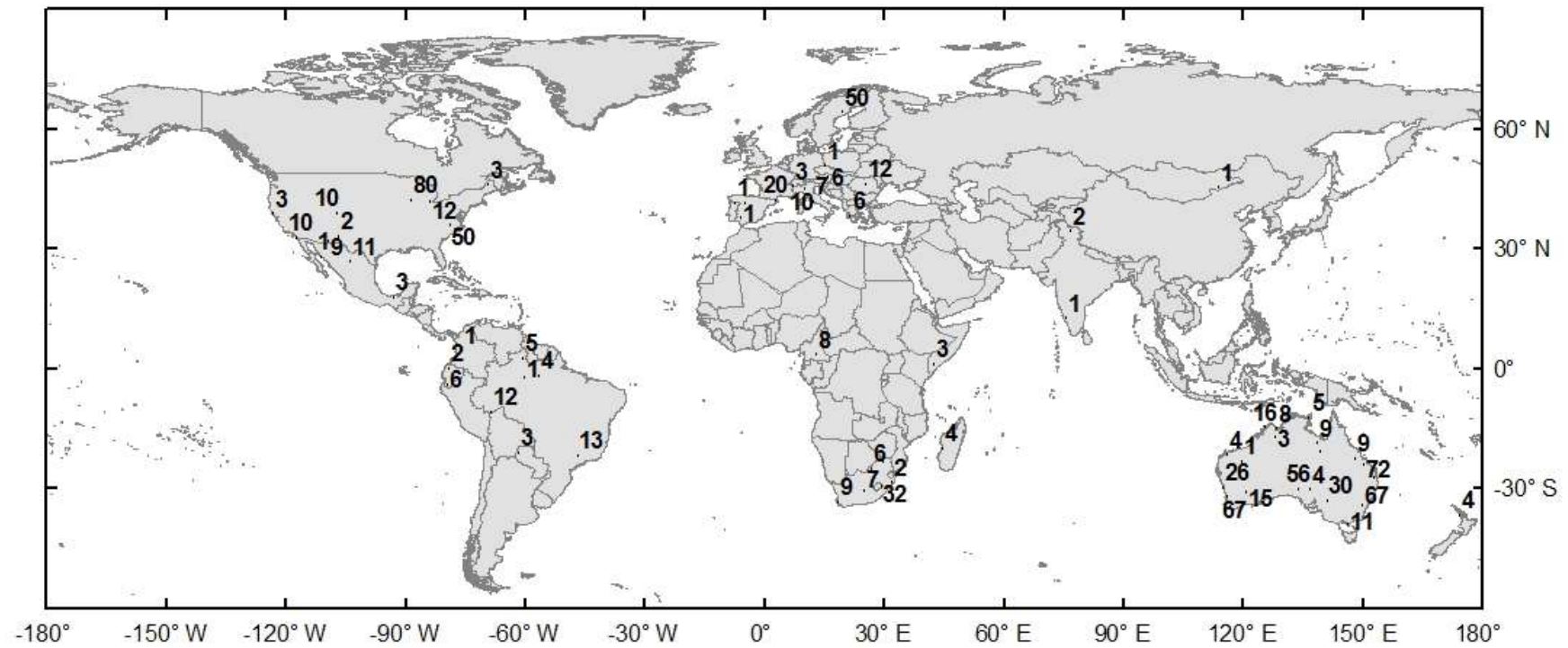


Fig. S3: Relationship between measures of assemblage structure and latitude for: a) species richness; and b) species evenness (PIE).

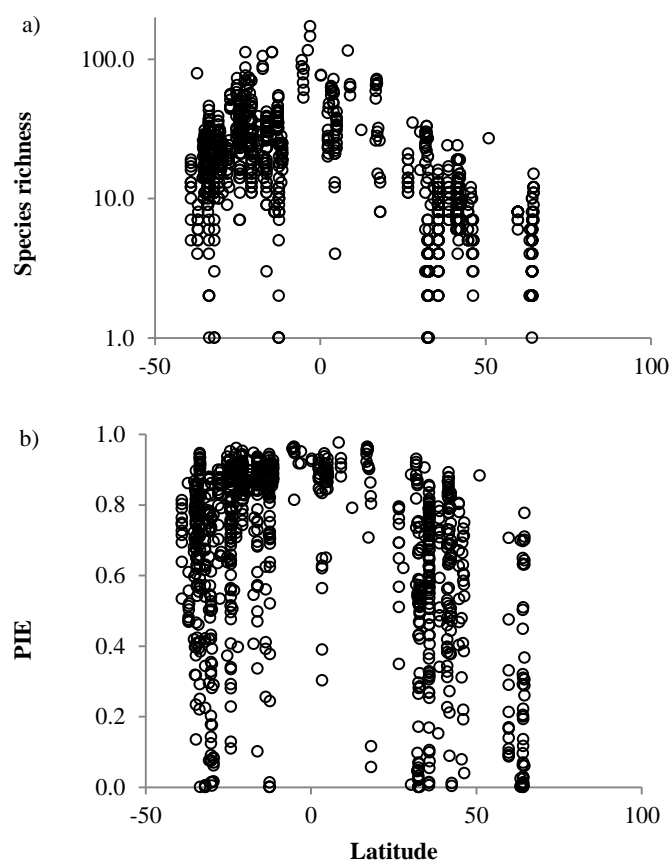


Table S1: Change in Akaike's information criterion (ΔAIC) from the best model for models predicting the effect of: (1) climate (MAT, precipitation and temperature range); (2) climate + disturbance; (3) climate \times disturbance (where only MAT is included in the climate term of the interaction); and (4) climate \times disturbance (where MAT \times precipitation are included in the climate term of the interaction) on residuals of species richness and evenness (PIE) for all data (n = 755), excluding low latitudes ($< 17^\circ$) (n = 620) and excluding fire as a disturbance (n = 681). All models included lower level interactions and the main effects MAT, precipitation and temperature range.

Model	All data		Low latitudes excluded		Fire excluded	
	Species richness	PIE	Species richness	PIE	Species richness	PIE
Climate	168.5	163.2	109.6	164.2	91.9	145.1
Climate + Disturbance	131.9	165.6	39.2	160.9	25.7	140.9
Climate (MAT) \times Disturbance	41.1	119.8	10.1	126.5	23.9	124.6
Climate (MAT \times Precipitation) \times Disturbance	0.0	0.0	0.0	0.0	0.0	0.0

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
<i>Species richness</i>			
(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
<i>Species evenness</i>			
(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