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Climate mediates the effects of disturbance on ant assemblage structure

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Many studies have focused 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 medium 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.

1. 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. 10×10 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 geographical 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 are 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 colonization [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.

2. Material and methods

(a) Assemblage data

We compiled species abundance data from local ant assemblages from 1128 sites distributed throughout the world (figure 1).

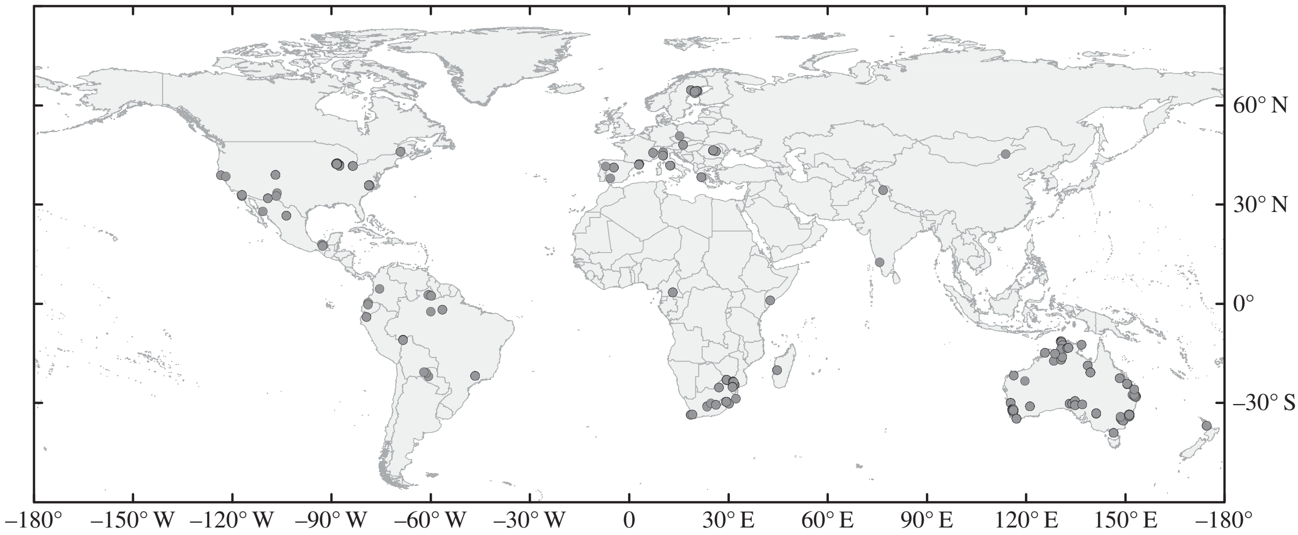

Figure 1. World map (plate carrée projection) showing the 1128 independent study locations (circles) from which we obtained data on ant assemblages from pitfall trapping. Note that many of the studies used evaluated multiple independent locations in relatively close proximity, so appear as a single point.

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 datasets 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 standardized 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%).

(b) Environmental variables: climate and disturbance

Contemporary environmental variables were obtained from the WorldClim database [17] at a spatial resolution of 30-arcsecond resolution (approx. 1×1 km) and were extracted using ArcGIS (ESRI, Redlands, CA; 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: 2–18 360) 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 (electronic supplementary material, figure S1*a*,*b*). Temperature range was lowest at the equator and was slightly greater in the Northern Hemisphere than in the Southern Hemisphere (electronic supplementary material, figure S1*c*).

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.

(c) Data analysis

All statistical analyses were carried out in the R v. 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 − 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 (MAT, mean annual precipitation and temperature range) and disturbance (three levels: disturbed, undisturbed and 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 no more than 100 km from each other represented by a single random effect to control for potential autocorrelation between localized sites (see electronic supplementary material, figure 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 lme4 package [25] to fit generalized linear mixed models, 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 nonlinear relationships in the response variables (species richness and evenness), we used Akaike's information criterion (AIC) to compare models that included key climatic variables (MAT and 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 χ^2 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 (MAT; precipitation and temperature range); (2) climate + disturbance; (3) the climate × disturbance interaction, where only MAT was included in the interaction; and (4) the climate × disturbance interaction, where both MAT and precipitation were included in the interaction (i.e. MAT × precipitation × 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.

3. Results

Both species richness and species evenness showed hump-shaped relationships with latitude, reflecting patterns observed for climatic variables (electronic supplementary material, figure 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 (electronic supplementary material, figure S3).

(a) 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, 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 (electronic supplementary material, 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 (electronic supplementary material, table S1).

For species richness (table 2 and figure 2*a–c*; electronic supplementary material, table S2), 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 (figure 2*a*,*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 MAT. As example of this effect, at an annual precipitation of 1000 mm, species richness in transformed habitats with MATs of 20°C was equivalent to species richness in undisturbed sites at 13°C (figure 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 and figure 2*d–f*; electronic supplementary material, table S2). 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 MATs of 20°C had species evenness equivalent to that found at 15°C in disturbed sites and 11°C in undisturbed sites (figure 2*d–f*).

4. Discussion

Over the range of MATs represented in this study (0.1–28.5°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

Table 1. Change in Akaike's information criterion (ΔAIC) and model rank for all models predicting the effect of climate (MAT 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 second-order polynomial terms (poly) were included for precipitation and temperature range.

		species richness		species evenness	
model	d.f.	ΔAIC	rank	ΔAIC	rank
temp. × prec. × disturbance	22	0.0	1	234.6	6
temp. (poly) × prec. × disturbance	28	3.0	2	137.5	3
temp. × prec. (poly) × disturbance	28	3.2	3	174.5	4
prec. (poly) × temp. (poly) × disturbance	37	6.3	4	0.0	1
temp. (poly) × prec. (poly) + temp. (poly) × disturbance	25	6.8	5	133.4	2
temp. × prec. (poly) + temp. × disturbance	20	10.4	6	254.5	7
temp. (poly) × prec. + temp. (poly) × disturbance	22	10.5	7	176.3	5
temp. × prec. + temp. × disturbance	18	13.4	8	273.1	9
temp. × prec. (poly) + disturbance	18	99.5	9	312.8	12
temp. × prec. + disturbance	16	102.6	10	331.0	18
temp. (poly) × prec. (poly) + disturbance	21	103.1	11	261.8	8
temp. (poly) × 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. × prec.	14	169.8	15	346.0	23
temp. (poly) + prec.	14	170.3	16	327.8	16
temp. × prec. (poly)	16	170.4	17	327.2	15
temp. (poly) + prec. (poly)	15	170.6	18	320.1	14
temp. (poly) × prec. (poly)	19	172.7	19	276.6	10
temp. (poly) × 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
prec. (poly)	5	243.8	24	342.3	21

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 relationship with temperature similar to that observed in undisturbed sites (i.e. increase with increasing temperature). This is likely to be 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 savannahs 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 that these disturbances may have a more immediate and longer-lasting local legacy than climate change.

5. Conclusion

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 over-ambitious. The manner in which assemblage structure changes in response to temperature depends on the local species pool and the ability of

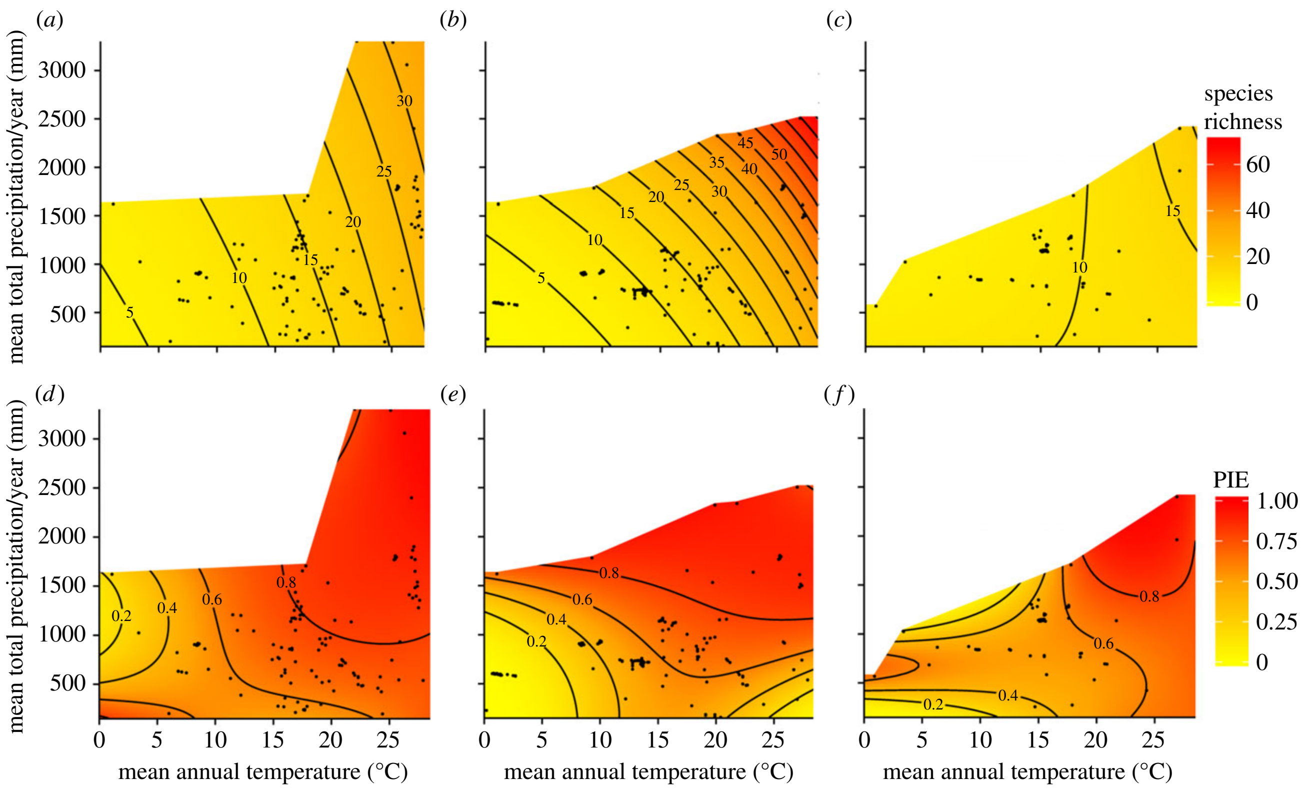

Figure 2. Contour plots showing model predictions for relationships with MAT and precipitation for species richness at (*a*) undisturbed sites, (*b*) disturbed sites and (*c*) transformed sites, and for PIE at (*d*) undisturbed sites, (*e*) disturbed sites and (*f*) transformed sites. Data are plotted only to the environmental space of each dataset. (Online version in colour.)

Table 2. Test statistic and significance for best-fit models testing the effect of climate and disturbance on diversity indices.

response	d.f.	species richness χ^2	evenness χ^2
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**

$^{\dagger}p < 0.10$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

colonizing 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 MAT of up to 9°C (figure 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 colonize 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.

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

Authors' contributions. H.G. coordinated the study. H.G., N.J.S., R.R.D. and C.L.P. conceived of and designed the study and helped draft the manuscript. S.W. and H.G. analysed the data. All authors except S.W. contributed data. All authors revised the article critically and gave final approval of the version to be published.

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