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Authors for correspondence:

Dominique G. Maucieri

e-mail: dominiquemaucieri@uvic.ca

Julia K. Baum

e-mail: baum@uvic.ca

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Tipping points and interactive effects of chronic human disturbance and acute heat stress on coral diversity

Dominique G. Maucieri¹, Samuel Starko^{1,2} and Julia K. Baum^{1,3}

¹Department of Biological Sciences, University of Victoria, Victoria, British Columbia, Canada V8P 5C2

²UWA Oceans Institute, School of Biological Sciences, University of Western Australia, Crawley, Western Australia, Australia

³Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, HI, 96744, USA

DGM, 0000-0003-1849-2472; SS, 0000-0002-9604-9188; JKB, 0000-0002-9827-1612

Multiple anthropogenic stressors co-occur ubiquitously in natural ecosystems. However, multiple stressor studies often produce conflicting results, potentially because the nature and direction of stressor interactions depends upon the strength of the underlying stressors. Here, we first examine how coral α - and β -diversities vary across sites spanning a gradient of chronic local anthropogenic stress before and after a prolonged marine heatwave. Developing a multiple stressor framework that encompasses non-discrete stressors, we then examine interactions between the continuous and discrete stressors. We provide evidence of additive effects, antagonistic interactions (with heatwave-driven turnover in coral community composition diminishing as the continuous stressor increased), and tipping points (at which the response of coral Hill-richness to stressors changed from additive to near synergistic). We show that community-level responses to multiple stressors can vary, and even change qualitatively, with stressor intensity, underscoring the importance of examining complex, but realistic continuous stressors to understand stressor interactions and their ecological impacts.

1. Introduction

Multiple anthropogenic stressors are a feature of almost all modern ecosystems, with global climate change typically superimposed on systems already exposed to chronic local human stressors, such as habitat degradation, invasive species, overharvesting and pollution [1–3]. Biological responses to multiple stressors may simply be additive, equalling the sum of each stressor's individual effect. Often however, outcomes are more complex, with antagonistic interactions between stressors leading to smaller responses than expected, and synergistic interactions between stressors resulting in amplified responses [4,5]. Understanding such complex stressor interactions is essential given their capacity to drive (otherwise unpredictable) shifts in species abundances, biodiversity and community composition [6–8], any of which can lead to changes in ecosystem productivity and function [4,9]. Although an increasing number of studies have examined biological responses to multiple stressors over the past two decades [4,10–13], results are often inconsistent within marine [6,14], freshwater [15] and terrestrial systems [16], with studies variously reporting synergistic, antagonistic or other stressor effects. Most studies have, however, treated the stressors as being either present or absent (e.g. protected area versus unprotected area) [6,8,12], ignoring the reality that most stressors are continuous, and ecological communities exist on stressor gradients. Here, we propose that contrasting findings in past studies may arise because of variation in stressor intensity and the presence of 'tipping points' [17,18], or critical values in either stressor, beyond which the nature of interactions may change. Given that the role of tipping points and/or nonlinearities in the strength and direction of stressor interactions remains unclear,

examining continuous stressors could help to advance understanding of complex stressor interactions and multiple stressor impacts on ecosystem diversity and dynamics.

Several recent studies have noted that regression-based approaches may be better suited for multiple stressor analyses, rather than approaches that simply combine binary responses, recognizing that the strength of stressors can affect responses [19–22]. Using process-based models of a seagrass system with combinations of stressor treatment levels, Turschwell *et al.* [11] found that the strength and type of stressor interaction depended upon the magnitude of the stressor effects (along with when the interaction was quantified relative to equilibrium conditions, and consumer presence); they advised that additional studies of stressor magnitude are needed [11]. Regression-based approaches, such as that by King *et al.* [22], have also been used to examine how stressor interaction types differ with the experimental context of the study, namely the intensity and duration of stressors, and to examine nonlinear relationships to approach generalities within multiple stressor interactions [22]. Despite this progress, observational studies of how biological responses to multiple stressors vary across stressor gradients in natural ecosystems remain limited.

Interacting stressors could have significant consequences for the biodiversity of future ecosystems [9,23]: α -diversity metrics are commonly used to assess if multiple stressors have impacted the number of species (richness) or their relative abundances (evenness) in communities [24,25]; β -diversity (variation in community composition across sites), in turn, can be used to measure how stressors alter community composition, whether sampling areas are becoming more or less similar with ongoing anthropogenic change [26], and how biodiversity varies spatially [25]. Understanding changes in, and conserving, both α - and β -diversities in the presence of multiple stressors will be important for maintaining ecosystem functions, as stability in functions depends on both of these critical facets of biodiversity [9].

Elucidating the factors governing stressor interactions is a particularly high priority for coral reefs, given that they are the most biologically diverse marine ecosystems and almost all are impacted by multiple intense stressors [27,28]. Climate change-intensified marine heatwaves are triggering mass coral bleaching and mortality events, which pose an imminent threat to coral reef persistence [29,30]. On most reefs, global climate change is overlaid on chronic local anthropogenic stressors, ranging from coastal development and pollution (e.g. from agricultural nutrients and waste runoff) to overfishing [3,14,20,31]. Communities of co-occurring coral species encompass species with distinct life-history strategies—broadly classified as stress-tolerant, competitive, weedy and generalist [32], within which species tend to have similar stressor sensitivities—that fulfil various ecological functions. Mechanistically, thermal stress from marine heatwaves triggers a physiological response, disrupting the obligate symbiosis between corals and their dinoflagellate endosymbionts (family Symbiodiniaceae) [33,34] with consequences for coral energy acquisition. Local anthropogenic stress in the form of water pollution can also cause a physiological response, with the ratio between nitrate and phosphate in the water affecting levels of coral oxidative stress [35,36]. By contrast, local stress in the form of coastal development (e.g. dredging) and destructive fishing practices causes physical damage. Beyond different mechanisms by

which stressors impact organisms, understanding stressor interactions is further challenged by the different spatial scales over which stressors operate [37–39]. However, it is crucial to understand how stressors affect multiple spatial scales, as local protection provides management options that could be directly implemented to protect ecosystems if we understand how and what will be the most effective.

To advance understanding of community responses and stressor interactions when non-discrete stressors are considered, we used a natural ecosystem experiment, examining how coral α - and β -diversities varied across a gradient of chronic anthropogenic stress before and after an extreme marine heatwave. In order to test if the strength and direction of stressor interactions depend on the underlying values of a given stressor, we expanded upon the multiple stressor framework of Côté *et al.* [12] and Folt *et al.* [40] for responses to two discrete stressors to include possible responses for systems where the strength of one response varies across a continuous gradient (figure 1; electronic supplementary material, Methods). We hypothesized that both the underlying local anthropogenic stress and the heatwave would lead to consistent reductions in coral α -diversity, the former owing to physical damage and poor water quality causing poor growth conditions, and the latter through physiological effects that lead to coral bleaching and mortality. Additionally, we hypothesized that both stressors would homogenize the coral communities, owing to the loss of rare species, as has been previously been recorded in other reef communities during heat stress events [41,42]. Finally, we hypothesized that the stressors would interact antagonistically, because the initial stressor would eliminate sensitive coral species leaving a more stress-tolerant community to the second stressor, and that the strength of this relationship would depend on the intensity of stressors being experienced.

2. Methods

(a) Study site and design

Data for this study were collected in the context of an ecosystem-scale natural experiment in which localized chronic anthropogenic stress on an atoll created a spatial gradient of stress that was overlaid by a marine heatwave. Specifically, we collected coral diversity data from 17 shallow forereef sites on Kiritimati, (also known as Christmas Island; Republic of Kiribati; electronic supplementary material, figure S1), a large atoll (150 km perimeter) in the central equatorial Pacific. Surveyed sites are part of a long-term monitoring programme [43], and span a significant gradient of local stress owing to the concentration of Kiritimati's local population (approx. 6500 people [44]) and infrastructure on the northwest side of the atoll. Data were collected on six expeditions between 2013 and 2017; not all sites were surveyed in each expedition (mean = 10.2 sites expedition⁻¹) owing to weather and timing constraints (electronic supplementary material, table S1, figure S1). At each site, transects were laid following the 10–12 m isobath and benthic photo quadrats of 1 m² were taken at 20–35 randomly selected locations along the transects.

Local anthropogenic stress within Kiritimati's reef environment has been previously quantified with an integrated measure that encompasses the nearby human population and local fishing pressure for each site [43,45,46]. Human population on the atoll serves as an accurate proxy for the local stressors of dredging, sewage runoff and pollution, which are probably

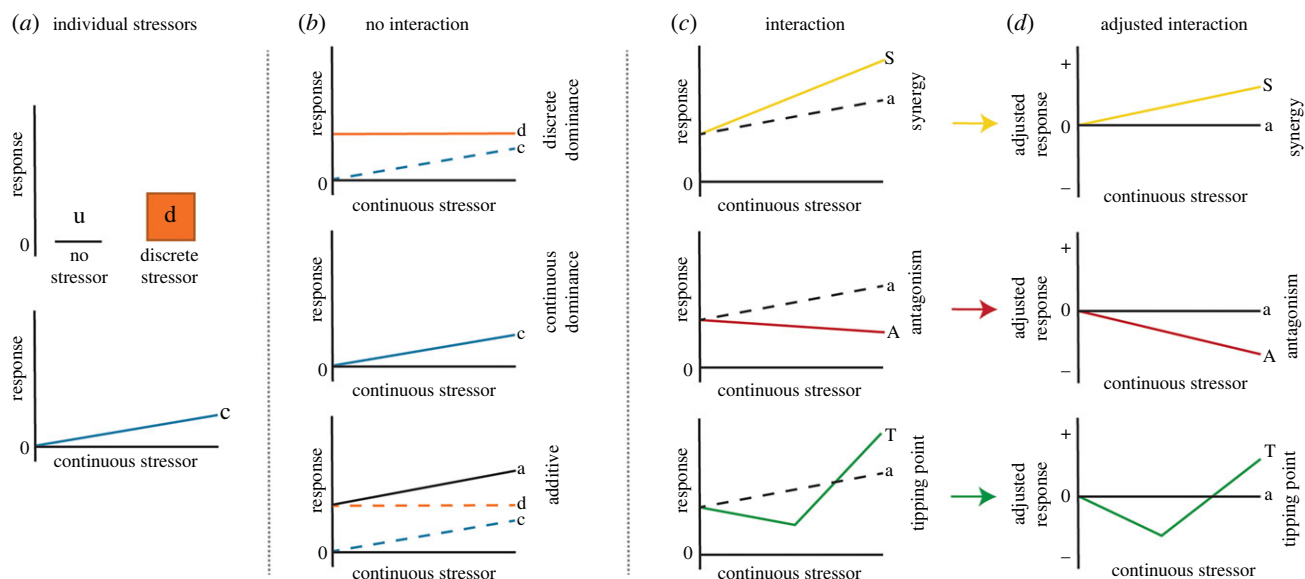


Figure 1. Models of potential responses to multiple ecosystem stressors when the individual stressors are a combination of discrete and continuous. (a) Two individual stressors, one a **discrete stressor** (**d**; orange bar) and one a **continuous stressor** (**c**; blue line), acting separately in a biological system elicit individual responses (a change owing to the stressor that can be quantified), here in the same direction. (b) When there is no interaction between the stressors, their combined effect on the biological response could be equal to the effect of one of the two stressors (i.e. dominance effect), or to the sum of the two stressors (i.e. additive effect). Dominance of the discrete stressor (orange line) will elicit a constant response across the continuous stressor (dashed blue line), whereas when the continuous stressor is dominant (blue line) the response will increase with it. An **additive effect** (**a**; black line) will show the same trends over the continuous gradient as those seen for the individual continuous stressor, but the response will be shifted upwards by the magnitude of the discrete stressor ($a = c + d$; black line = blue line + orange line). (c) Interactions between the two stressors can produce a **synergistic response** (**S**; yellow line), in which the response observed across the continuous stressor is larger than the additive effects (dashed black line) of both stressors; an **antagonistic response** (**A**; red line) when the response observed across the continuous stressor is smaller than the additive effects (dashed black line) of both stressors; or a **tipping point response** (**T**; green line), when there is a point along the continuous stressor, where there is a shift from one type of response to another. The tipping point response shown here is a shift from antagonism to synergy around the center of continuous stressor. (d) When the response is adjusted so that the additive response is seen as the baseline (black line), synergistic responses produce a positive response (yellow line), antagonistic responses produce a negative response (red line) and tipping point responses (green line) can show both negative and positive responses, depending on the value of the continuous stressor.

the primary local stressors for corals [43,47]. We applied a square root transformation for all examinations of local anthropogenic stress, to account for the right skew in the data. For visual purposes, our sites were then grouped into five anthropogenic stress categories (very low, low, medium, high and very high) based on clear breakpoints in this continuous measure, as in Magel *et al.* [46] and Claar *et al.* [47]. Additionally, we extracted site-level maximum net primary productivity (NPP; $\text{mg C m}^{-2} \text{d}^{-1}$) data from the Marine Socio-Environmental Covariates, an open source data product that uses satellite-derived measures of photosynthetically available radiation, sea surface temperature and chlorophyll-*a* concentrations from the National Oceanic and Atmospheric Administration CoastWatch to calculate maximum NPP over a 2.5-arcmin grid [48].

To date, the 2015/2016 El Niño event was the longest and most intense of any El Niño event on record, leading to the highest cumulative heat stress inflicted on any coral reef to date [49]. This marine heatwave caused Kiritimati's reefs to experience continuous heat stress between May 2015 and April 2016, peaking at approximately 25°C-weeks 'degree heating weeks' (DHW), and culminating in a loss of 89% of the atoll's coral cover [43]. Heat stress was consistent across the shallow forereef sites surveyed for this study, with DHW magnitudes during the 2015/2016 El Niño event differing by only 1°C (range: 24.3–25.3°C) around the atoll [49].

(b) Data processing

We analysed benthic community composition in CoralNet [50], by randomly overlaying 100 points onto each of $n = 1731$ quadrat images (electronic supplementary material, table S1), and

identifying the substrate below each point to the lowest possible taxonomic classification. We determined per cent cover for each of 24 individual coral taxonomic groups by dividing the number of points for each taxonomic group by the total number of useable points in each quadrat: reef building, hard corals (order Scleractinia) were identified to genus or species ($n = 19$ taxonomic groups), soft corals (order Alcyonacea) were identified as one of four genera, and all free-living hard corals were grouped at the family level (family Fungiidae; electronic supplementary material, table S2). Unusable points included shadows, transect and quadrat hardware or unclear points where accurate identification was not possible; quadrats with greater than 10% unusable points were removed from analysis (seven quadrats: 0.4%).

Quadrats were classified as 'before' the heatwave if they were sampled between July 2013 and May 2015, and 'after' if they were sampled in November 2016 or July 2017. To ensure an accurate coral cover baseline was represented in our analysis, all sampling before the heatwave was examined to ensure there were no large fluctuations in total coral cover between years. For subsequent analyses, if a site was sampled multiple times before or after the heatwave, one sampling year was randomly selected so that each site was only sampled once before and once after the heatwave (electronic supplementary material, table S1).

(c) α -diversity analysis

To assess α -diversity, we used Hill diversity metrics (as outlined by Roswell *et al.* [24]), which provide a method of quantifying richness and evenness at sites using means of species' rarity (i.e. arithmetic, geometric and harmonic means) that scale

rarity differently [51,52]. Hill diversity is widely considered to be the preferred method of measuring α -diversity, as it does so without separating the number of species from their relative abundances, acknowledging that relative abundances cannot be fully eliminated and are not fully independent of species occurrences [24]. Hill diversity recognizes that the three most widely used types of diversity, species richness, Shannon diversity and Simpson diversity are three cases of the same general equation, which differ only in how rare species are scaled. The Hill diversity equation uses a parameter ' ℓ ' to scale rarity (equation (2.1)), where D is the diversity of S number of species, with p_i being the proportion of individuals in species i , and r_i being the rarity of species i :

$$D = \left(\sum_{i=1}^S p_i (r_i)^\ell \right)^{1/\ell} \quad (2.1)$$

Hill-richness calculates rarity using the arithmetic mean, thus giving high leverage to rare species. By contrast, Hill-Simpson diversity calculates rarity using the harmonic mean and thus uses a reciprocal scale, which shifts leverage to common species, while Hill-Shannon diversity, which calculates rarity using the geometric mean, is an intermediate between the first two [24,52].

To ensure equal sampling effort across our 17 sites, we used coverage-based methods from the 'iNEXT' package [53] to either interpolate or extrapolate samples at each site. This equalizes samples by ensuring equal coverage among all sites, and is believed to give more robust results than other methods (e.g. traditional sample rarefaction; [24]) which do not account for the underlying distribution of the species abundances from the sampled community. Coverage-based equalization ensures that the diversity of each sampling unit is not biased by sampling effort or sampling size, by accounting for the amount of sampling that was conducted and the communities' species abundance distributions [24]. We equalized samples at 90% coverage because this level allowed us to maximize the use of the quadrat data, while requiring extrapolation of very few data points. We then determined Hill diversity for each site, at each time point (before or after the heatwave), when q is equal to 0, 1 and 2 which relates to Hill-richness, Hill-Shannon and Hill-Simpson, respectively [24]. We tested the sensitivity of this coverage level by also conducting our analyses at 85% and 95% coverage and comparing the conclusions and trends, and found that our results were robust to these different levels (electronic supplementary material, Methods and Results, figures S2–S6).

As initial examination revealed nonlinear relationships among α -diversity metrics and local anthropogenic stress, we performed three polynomial regressions, with each type of Hill diversity as response variable, using a Gaussian distribution in the 'glimmTMB' package [54]. Each model included marine heatwave period (before or after the heatwave), local anthropogenic stress (linear and quadratic relationships), and an interaction between heatwave period and local anthropogenic stress as fixed effects, with site as a random effect to account for non-independence among sites measured over time. Additionally, NPP was included and excluded (electronic supplementary material, Results, table S3) as a covariate in models for each α -diversity metric. Model assumptions were checked using the 'DHARMA' package [55].

(d) β -diversity analysis

We examined β -diversity as site-level dissimilarities in coral community composition across the local anthropogenic stressor gradient and owing to the heatwave, as well as the interaction between the stressors. We quantified β -diversity using Bray–Curtis dissimilarity [56], because this takes into account relative abundances and excludes joint absences [57]. There is currently no framework to apply coverage-based sampling to β -diversity

analyses, so instead we standardized site-level community composition by quadrat number, averaging the cover of each coral taxon across 25 randomly selected quadrats for each site in each timepoint, and removing sites with fewer than 25 quadrats from analyses ($n = 3$; electronic supplementary material, table S1). We visualized the Bray–Curtis dissimilarities in community composition across sites and timepoints using a distance-based redundancy analysis (dbRDN; 'vegan' package) [58]. Then to statistically quantify differences in community composition, we performed a PERMANOVA with 1000 iterations to compare the centroids of each time point (before and after the heatwave) and local anthropogenic stress, including interactions to assess if coral community composition was more, or less, impacted by the heatwave when exposed to varying degrees of local anthropogenic stress. We also assessed β -diversity using multiple regressions on distance matrices [59], as a sensitivity analysis, to ensure that observed differences in β -diversity were not merely a function of the distance between sites, by testing the effect of distance between sites and difference in local human disturbance on β -diversity (electronic supplementary material, Methods and Results, figure S7).

(e) Mixed multiple stressor analysis

We then used our coral biodiversity data to investigate biological responses to multiple stressors at the ecosystem scale, with the system providing a 'natural experiment' that allowed us to empirically assess the relationship between two anthropogenic stressors, one of which was discrete (i.e. acute marine heatwave) and one of which was continuous (i.e. chronic local anthropogenic stress). Our biological responses of interest were the three measures of α -diversity, and β -diversity. For each of these response types, we calculated the adjusted response of each sample (i.e. a single site in a single expedition) to the two stressors (as detailed in the electronic supplementary material, Methods). To assess if there were statistically significant inflection points in the relationship between the two stressors (i.e. the adjusted combined response) along the range of the continuous stressor, we then performed breakpoint analyses (structural change test, 'sctest') for each of the response types, using the 'strucchange' package [60]. A linear model was run on each relationship, or segment of relationship (if there is at least one significant breakpoint along the range of the continuous stressor), to determine the nature of the relationship (additive, synergistic, antagonistic or a combination with a tipping point) between stressors.

3. Results

(a) Impacts of multiple stressors on coral α - and β -diversities

Coral α -diversity, regardless of the measure (Hill-richness, Hill-Shannon, Hill-Simpson), was significantly influenced by both local anthropogenic stress and the heatwave (table 1 and figure 2; electronic supplementary material, tables S3–S5.). The relationships between each of the Hill diversity metrics and local anthropogenic stress were unimodal, both before and after the heatwave, with coral diversity increasing to a maximum at intermediate stress and declining thereafter (figure 2 and table 1). The marine heatwave negatively impacted α -diversity, with greater losses in Hill-Shannon (mean loss = 4.31 ± 0.46 s.e.m.) and Hill-Simpson (mean loss = 4.46 ± 0.48 s.e.m.) diversity than in Hill-richness (mean loss = 3.40 ± 0.68 s.e.m.; figure 2 and table 1; electronic supplementary material, table S4). Notably, for Hill-richness,

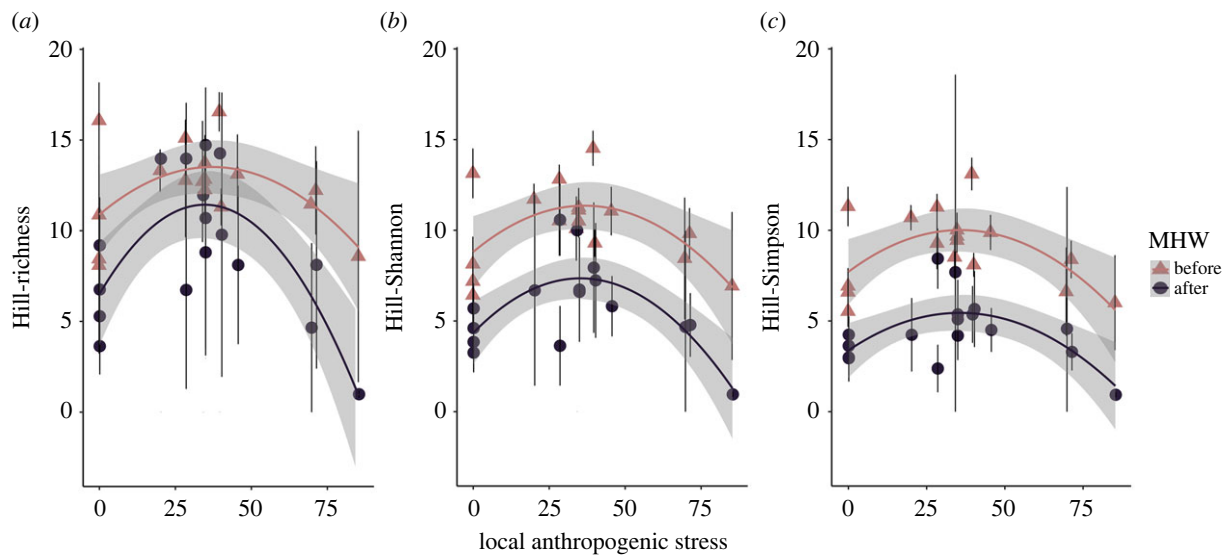


Figure 2. Relationships between coral diversity (assessed via (a) Hill-richness, (b) Hill-Shannon, and (c) Hill-Simpson) and chronic local anthropogenic stress (quantified as a relative index), before and after a prolonged marine heatwave (MHW). Vertical bars represent 95% confidence limits for each site, and grey shading is the standard error for the polynomial lines.

Table 1. Parameter estimates for fixed effects from polynomial regression models describing the factors influencing Hill-richness, Hill-Shannon and Hill-Simpson diversity. (Note: LAS, local anthropogenic stress; MHW, before or after the heatwave; 1° poly, first-order polynomial, the linear term; 2° poly, second-order polynomial, the quadratic term; NPP, max net primary productivity. Italic values indicate statistical significance ($\alpha = 0.05$; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

model	LAS—1° poly	LAS—2° poly	MHW	LAS—1° poly : MHW	LAS—2° poly : MHW	NPP
Hill-richness	2.25	<i>-7.56*</i>	<i>-3.40***</i>	-3.38	<i>-9.27**</i>	-0.013
Hill-Shannon	1.31	<i>-7.65***</i>	<i>-4.31***</i>	-1.13	-2.19	-0.010
Hill-Simpson	0.33	<i>-7.33***</i>	<i>-4.46***</i>	-0.033	0.72	-0.0071

coral losses from the heatwave depended on the strength of the underlying local anthropogenic stress (table 1). Sites exposed to either very low or very high levels of local stress tended to experience greater losses in richness owing to the heatwave than those at intermediate stress levels (figure 2; electronic supplementary material, table S4). By contrast, there was no interaction between the impact of the local stress gradient and the marine heatwave on Hill-Shannon and Hill-Simpson diversity (figure 2; electronic supplementary material, table S4).

Regarding β -diversity, the local anthropogenic stressor (PERMANOVA, $F = 3.42$, $p < 0.01$) and the heatwave (PERMANOVA, $F = 14.1$, $p < 0.01$) each had a significant influence on coral community composition (figure 3). Further, as hypothesized, there was a significant interaction between the effect of the marine heatwave and local anthropogenic stress (PERMANOVA, $F = 4.49$, $p < 0.01$; figure 3), such that the sites that had already been exposed to high stress levels, from the local stressors, experienced less turnover in composition during the heatwave (figure 3).

(b) Multiple stressor relationships: interactions and tipping points

We detected synergistic, antagonistic, and additive interactions between stressors depending on the diversity metric considered, and for some metrics the strength and type of interaction varied significantly depending on the underlying strength of local anthropogenic stress, as hypothesized

(figure 4). For Hill-richness, we identified a tipping point at moderate levels of local stress (sctest, $F = 11.7$, $p < 0.05$), below which stressors interacted additively (lm slope and intercept both $p > 0.05$), and above which the response tended towards synergy (slope lm, $t = 2.67$, $p < 0.05$), with sites exhibiting larger adjusted responses to the combined stressors than predicted under the additive model (figure 4a). Examination of this relationship showed that the adjusted response increased with the local stress but was not significantly synergistic, as the confidence intervals still overlapped the x -axis (figure 4a). Applying the methodology presented in the electronic supplementary material, Methods to Hill-Shannon and Hill-Simpson (the two diversity metrics with no significant interactions between the stressors), we determined these relationships to be additive, given non-significant slopes and intercepts (lm, $p > 0.05$) and the lack of significant inflection points (sctest, $p > 0.05$; figure 4b,c). Finally, we found a significant negative relationship between the adjusted response of coral community turnover along the range of the local stress (lm, $t = -4.41$, $p < 0.001$; figure 4d), indicating increasing antagonism with increased stress. There was no significant tipping point along the range of the local stress when considering community composition (sctest, $p > 0.05$; figure 4d).

4. Discussion

Overall, our study shows that community responses to multiple stressors in natural ecosystems can depend strongly

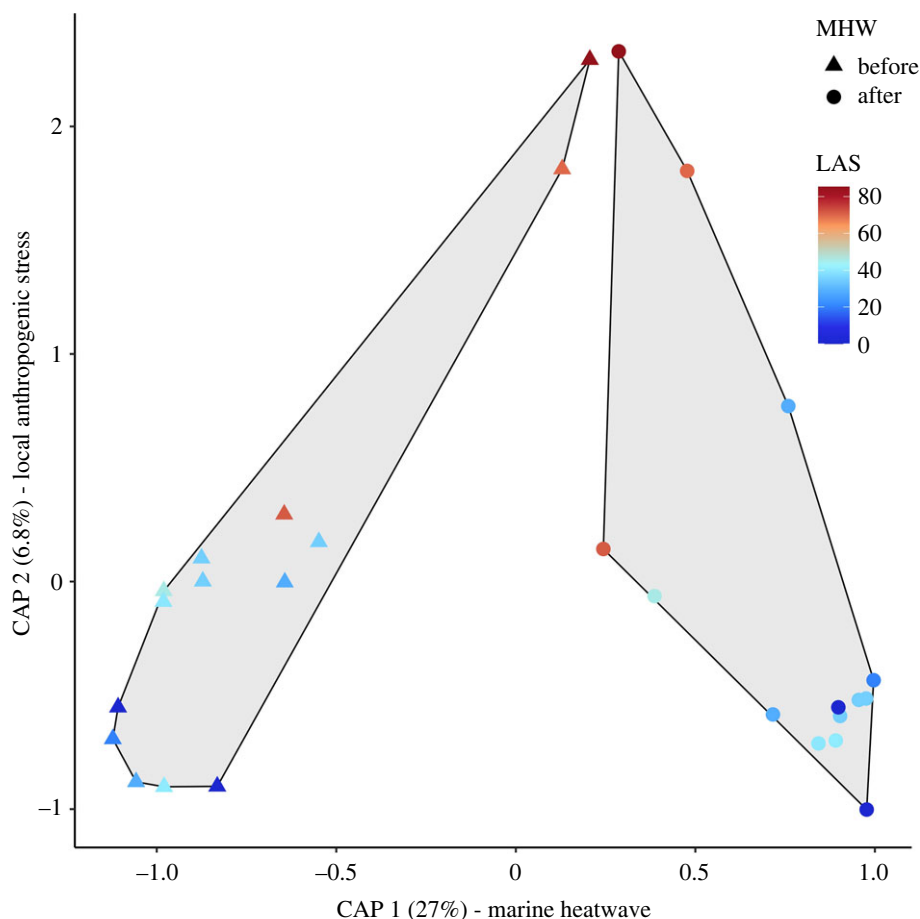


Figure 3. Influence of a global acute (marine heatwave (MHW)) and a local continuous anthropogenic (coastal development, fishing, pollution) stressor on coral community composition. Site-level coral community composition (dbRDA), before (triangles) and after (circles) a prolonged MHW, with sites coloured by intensity of underlying chronic local anthropogenic stress (LAS). Grey hulls group time blocks together.

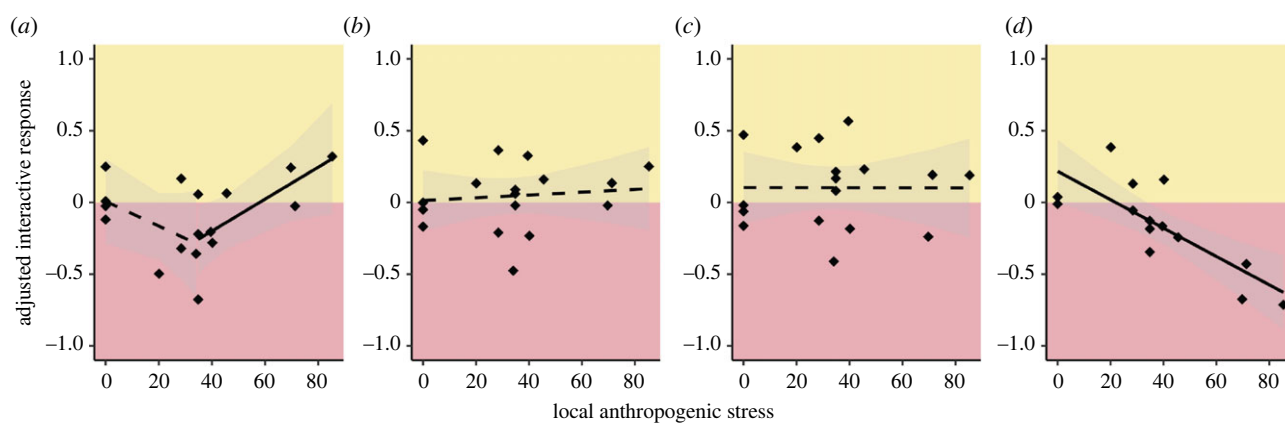


Figure 4. Application of the mixed multiple stressor model, showing coral diversity responses to a combination of discrete and continuous anthropogenic stressors. Adjusted interactive responses are the biological responses to the stressors, relative to a baseline additive response (along the zero line, as in figure 1). The area above the zero line in the plots (pale yellow) indicates where a synergistic response would fall, while the area below the zero line (pink) indicates where an antagonistic response would fall. Responses shown are: (a) Hill-richness, (b) Hill-Shannon, (c) Hill-Simpson, (d) Bray–Curtis community composition, after the heatwave, over the local anthropogenic stressor gradient, with (a) exhibiting a tipping point interaction, (b,c) showing no interaction, and (d) showing an antagonistic interaction between the stressors. Significant slopes, indicative of an interaction between the stressors are solid black lines, non-significant slopes, indicative of no interaction, are dashed. Light grey shading shows standard error.

on, and even change qualitatively with, the strength of the stressors to which they are exposed. We found evidence of stressor tipping points, with the combined impacts of a prolonged marine heatwave and chronic underlying local anthropogenic stressor on the Hill-richness of a coral community transitioning from additive towards synergistic as the

latter stress intensified, as well as an antagonistic interaction for coral community composition that intensified as local anthropogenic stress increased. These community-level findings build from, and are in accordance with, recent studies that examined physiological and population responses to stressor intensities using controlled experiments [22],

statistical and process-based models [11,61], and found that the nature and direction of multiple stressor interactions can vary with stressor intensity and the type of biological response. Tipping points in stressor effects, as we found, may explain why some studies report antagonistic responses to multiple stressors, and others (even within the same ecosystem and with the same stressors) report additive or synergistic responses [6,7,15]; the identification of such critical levels of stress could be important for conservation. The expanded multiple stressor framework we used may not only help resolve conflicting conclusions within the literature by considering the amount of stress being experienced, but also help to unify understanding of multiple stressors relationships.

Our analysis of coral communities subjected to multiple stressors illustrates complex stressor relationships and shows how examining multiple stressors on a continuous gradient can increase understanding of responses to stressors in ecological communities.

(a) Outcome 1: responses to multiple stressors can depend on stressor intensity and include tipping points

The presence of a tipping point in the response of coral richness to both stressors demonstrates that the type of relationship between stressors can vary with the strength of a given stressor [62,63]. Hill-richness exhibited an additive response at low local stressor levels, but after a tipping point at an intermediate stressor level, the response tended towards synergy. Determining the mechanism underlying this community-level tipping point is more challenging than in organismal studies, such as in King *et al.*, in which compensatory plant responses initially increased photosynthetic efficiency but at a tipping point became exhausted, yielding a qualitatively different response [22]. In our system, coral richness increased between low and medium levels of local anthropogenic stress, as predominant species at the lowest stress level (e.g. *Montipora* spp. and large tabulate *Acropora* corals) were outcompeted by a number of more stress-tolerant coral species; within this range of local stress, the heatwave reduced diversity only in an additive manner. Above the tipping point, however, at high levels of local anthropogenic stress where physical coral damage and high sedimentation rates had already reduced coral abundances [64–67], we suggest that the heatwave's amplified effect stemmed from the elimination of multiple, already rare coral taxa. This emergence of a community-level synergism aligns with Vinebrook *et al.*'s [4] proposal that species co-tolerances to stressors could be dynamic [4], but to our knowledge has not previously been shown in field studies. Tipping points illustrate that only examining one stressor intensity will not necessarily be indicative of effects at other stressor intensities, and particularly where stressors become more detrimental through emergent synergistic responses, should be important foci for ecosystem management [62,63].

In coral reef communities, few studies have examined the effects of both local anthropogenic impacts and heatwaves [43], but those that have variously reported synergistic, antagonistic and additive effects [68–70]. For example, past studies on Kenyan reefs examining coral cover as the response reported no co-tolerance between a heat stress event and local

anthropogenic stress [5,71], whereas a study in the Philippines showed that locations which were more affected by local anthropogenic stress provided a refuge for corals during a heatwave [72], presumably owing to co-tolerance. Although these differences may be a result of different ecological communities, they could also indicate that each study examined differing intensities of stressors, if there are general tipping points in these ecosystems. Further studies are needed to better elucidate the mechanisms underlying such tipping points in these, and other, ecological communities.

(b) Outcome 2: responses to multiple stressors can diminish with stressor intensity through increasingly antagonistic interactions

We also found that multiple stressors had an increasingly antagonistic effect on community composition as the continuous stressor intensified. Greater losses in coral richness at sites experiencing higher local stress, combined with losses in their already low coral abundance may have resulted in the antagonistic interaction between the heatwave and the local stress on coral community composition because the most intensely stressed sites had limited additional capacity for change. By contrast, coral communities at sites with very low levels of anthropogenic stressors underwent massive coral losses owing to the heatwave and shifts from competitive to more stress-tolerant corals. A previous study on coral microbiomes also found an antagonistic interaction between local anthropogenic stress and heat stress on β -diversity, for the microbiome of *Porites lobata* [73,74], suggesting that the maximum responses of the microbiome occurred with either stressor individually. Overall, the effects of multiple stressors on β -diversity (a complex and multi-faceted diversity measure) are not well studied, but given the potential for different biological responses along stressor gradients illustrated by our results, complex responses are important to consider and investigate, as they could have large implications on survival or for the conservation of communities.

When discrete stressors are examined, the presence and strength of an interactive relationship may be tested for [6,8,12], but these are implicitly assumed to be static, regardless of stressor intensity. However, with different stressor intensities, there may be many different strengths of interactive responses, which if examined could increase our ecological understanding of how increases in stress may affect ecosystems. If the same trends occur with synergisms, where increases in stressor intensity increase the strength of the synergetic response, as seen by Turschwell *et al.* [11] and King *et al.* [22], this could have substantial negative impacts on communities. This is potentially concerning if such synergisms emerge or strengthen with increasing temperature stress, given future climate change predictions.

(c) Outcome 3: responses to multiple stressors may be additive and independent of stressor intensity

In contrast to the responses of coral richness and community composition to multiple stressors in our system, neither Shannon diversity nor Simpson diversity differed from the expected additive response. As the strength of the continuous stressor increased, there was a proportional increase in the response to multiple stressors, showing that the type of

diversity metric and scale examined will influence the types of community responses to increases in continuous stressors. Previous studies have also found additive effects of local anthropogenic stressors and heatwaves on related measures of coral diversity, including coral reefs in Karimunjawa National Park, Indonesia [75] and on the Great Barrier Reef [69], suggesting that increased protection of coral communities from anthropogenic stressors did not influence how heatwaves impacted coral diversity. Additionally, our multiple stressor framework allowed for non-interactive relationships between stressors to be examined further. As there was no interaction between stressors for both Shannon and Simpson diversity metrics from the models, in theory, the response could also have been dominance between the stressors. However, our models enabled us to distinguish between dominance and additive responses based on slope and intercepts within the models, thus we determined that the response was additive (shown by a non-significant slope and intercept) rather than dominance (which would have shown either a significant slope or intercept; figure 1b).

5. Conclusion

Our empirical application of an expansion on the multiple stressor theory to allow for a continuous stressor illustrates that, even within a single system, there can be differences in the types of relationships between stressors, depending on the response being examined and the strength of underlying stressors. To account for the continuous nature of stressors in nature and how the intensity of stressors may affect stressor responses [11,22], we expanded from the multiple stressor framework of [12,40] to examine how the combined effects of a discrete and a continuous stressor affect ecosystems, including a novel examination of tipping points within multiple stressor interactions. In doing so, we enable future ecological studies to explicitly incorporate stressors measured along a continuous gradient, and to determine if the relationships between their stressors are antagonistic, synergistic or additive. Future studies could also expand

upon this framework by examining multiplicative models, including environmental covariates, developing methods for predicting thresholds where stressor relationships change, accounting for the temporal dynamics of stressors [76], or further considering trait-based and functional ecology. Our study provides context and a foundation for predicting the future composition and function of ecosystems experiencing multiple stressors, which are critical if we are to better manage ecosystems through intensifying climate change and human industrialization [3,77].

Data accessibility. All data, as well as the code for figures and data analyses are publicly available through GitHub (https://github.com/baumlab/Maucieri_et al_2023_ProcRoyB) and archived through Zenodo (<https://doi.org/10.5281/zenodo.7719304>) [78].

The data are provided in the electronic supplementary material [79].

Authors' contributions. D.G.M.: conceptualization, data curation, formal analysis, visualization, writing—original draft, writing—review and editing; S.S.: formal analysis, writing—review and editing; J.K.B.: conceptualization, data curation, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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