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Local anthropogenic stress does not exacerbate coral bleaching under global climate change

Jack V. Johnson1 | Jaimie T. A. Dick2 | Daniel Pincheira-Donoso1

Abstract
Aim: Rising ocean temperatures are widely recognized as the dominant driver behind the rapid degradation of coral reefs via the process of coral bleaching (the expulsion of photosynthetic endosymbionts, which reveals the coral skeleton). However, bleaching of hard corals is often assumed to be further aggravated by the effect of local-scale stressors from anthropogenic activity, accelerating coral reef decline where these stressors are stronger. Despite the importance of this hypothesis, the interaction between climate change and local stressors for driving coral bleaching has only been investigated in a handful of studies, with no large scale (regional or global) test conducted thus far. We investigate the impact of human population density (HPD) – a proxy for local stressors – in both protected and non-protected marine regions, and their interaction under heat stress as drivers of coral bleaching.

Location: Global.

Time period: 2002–2018.

Major taxa studied: Scleractinia corals.

Methods: Using 9,170 coral reef surveys worldwide, we performed Bayesian modelling to assess the probability of coral bleaching in response to local-scale stressors in interaction with global warming.

Results: Local HPD does not exacerbate coral bleaching, either independently or under thermal stress from climate change. Rather, the relationship between HPD and temperature stress appears weakly antagonistic for coral bleaching, contradicting the expectation that HPD increases sensitivity of corals to bleaching under thermal stress.

Main conclusions: Local HPD does not interact with global warming for degrading coral reefs. However, regional variation in bleaching patterns exists. Consequently, bleaching will continue to occur on most coral reefs globally regardless of local HPD. Thus, it is likely that even isolated, well-protected, coral reefs will continue to decline because of climate warming-induced bleaching. Therefore, tackling the source of global warming remains the most effective way to mitigate coral reef decline via coral bleaching.
1 | INTRODUCTION

The diversity of coral reefs worldwide is undergoing rapid declines caused mainly by coral bleaching – the expulsion of coral endosymbionts (family Symbiodiniaceae) from coral tissue, which reveals the bright white coral skeleton (Boilard et al., 2020; Douglas, 2003; Pitt et al., 2001; Suggett & Smith, 2011; Warner et al., 1999) – triggering cascading effects that threaten the persistence of the exceptional density of marine biodiversity that depends on them (Fisher et al., 2015). Coral bleaching is caused primarily by rising ocean temperatures and marine heatwaves (Hoegh-Guldberg et al., 2007; Hughes, Anderson, et al., 2018; Hughes, Kerry, et al., 2018; Magel et al., 2019; Oliver et al., 2018; Parmesan, 2006). In addition to heat stress, a number of region-specific factors, such as nutrient levels, hypoxia, turbidity and sedimentation, can cause bleaching in reef building hard corals, and sometimes interact with heat stress to increase bleaching (Donovan et al., 2020; Hoegh-Guldberg & Smith, 1989; Ochsenkühn et al., 2017; Suggett & Smith, 2020; Wagner et al., 2010).

Local human population densities (HPDs) are often related to the localized stressors on coral reefs (Nyström et al., 2000), such as turbidity (Wagner et al., 2010), coastal development (Mora, 2008), and sedimentation (Crabbe & Smith, 2002). Local HPD can have other negative impacts on coral reefs and their ecosystem function. For example, reef fish – a critical group for ecosystem function – have reduced biomass in the presence of increased local HPD (Cinner et al., 2013). Anthropogenic activity in coastal regions also alters the natural disturbance regimes exerted onto coral reefs from pulse events (i.e., hurricanes, coral predator outbreaks) into background chronic stress, such as continued eutrophication of reefs, leading to reef degradation over time (Bozec & Mumby, 2015; Nyström et al., 2000). Furthermore, the benthic composition of reefs on uninhabited islands across the Indo-Pacific showed an increase in active reef builders and calcifiers in comparison to human inhabited islands (Smith et al., 2016). Finally, direct anthropogenic exploitation which exerts local stressors onto coral reefs can also induce phase shifts to less productive states (Bozec et al., 2019; Graham et al., 2013; Hughes et al., 2007), especially in regions where inadequate protection and social engagement exist (Cinner et al., 2016). Therefore, it has been assumed that coral reefs isolated from densely populated areas may be less vulnerable to the effects of ocean warming induced coral bleaching, given the reduced impact of local-scale stressors that interact with climate warming (Hughes et al., 2005, 2010; Kavoussi & Keppel, 2018).

Evidence for synergisms, defined as increased stress between multiple environmental stressors (Côté et al., 2016; Folt et al., 1999), between local and global stressors for degrading coral reefs and exacerbating bleaching is convoluted. For instance, palaeontological records suggest local stressors synergistically interact with heat stress to exacerbate bleaching for certain coral species (Carilli et al., 2009, 2010). Some coral reefs far removed from human population densities were identified to have increased resilience to thermally induced bleaching (Gilmour et al., 2013; Smith et al., 2008). Yet, for coral cover, Smith et al. (2016) notably found a positive relationship with human population density across Pacific islands, which is in contrast to their findings on active reef builders (which include other calcifying taxa). A recent global-scale study revealed that local scale conditions, in the form of urchin population density and macroalgae cover, are associated with exacerbated levels of coral mortality after marine heatwaves caused by global warming (Donovan et al., 2021). However, it is unclear how urchin density and macroalgae cover are related to local human activities, or even HPD in Donovan et al. (2021).

In opposition to the expectation that both region-specific and global-scale factors operate synergistically to degrade coral reefs (Bozec et al., 2019; Côté et al., 2016; Hughes et al., 2005, 2010), other studies have observed that local-scale stressors have either no effect on coral reef degradation (Bates et al., 2019; Bruno et al., 2019; Bruno & Valdivia, 2016), or even a potentially antagonistic effect (Bates et al., 2019; Bruno et al., 2019; Darling & Côté, 2008; Darling et al., 2010). In relation to bleaching outcomes under local stress, turbidity, which can independently induce bleaching, actually interacts antagonistically with heat to moderate bleaching (Sully & van Woesik, 2020). Furthermore, many isolated coral reef atolls with no human presence continue to experience severe bleaching and subsequent reduction in coral cover because of anthropogenic heating, indicating that refuge from local stressors is not refuge from climate change (Harrison et al., 2019; Hughes et al., 2017; Sheppard et al., 2020). Additionally, refuge from local stress via the implementation of marine protected areas (MPAs) also does not appear to mitigate coral decline under climate change (Bates et al., 2019; Bruno et al., 2018; Selig et al., 2012). Protection from local stressors to increase coral cover results in more sensitive coral species becoming ubiquitous throughout the reef scape, likely resulting in increased bleaching when marine heatwaves occur (Bruno et al., 2019). Given the conflicting nature of evidence regarding the combined effects of local and global stressors on coral reefs and coral bleaching, it is difficult to draw general conclusions about whether multiple stressors exacerbate coral bleaching under global warming.

Such conflicting evidence of how local and global stressors interact for degrading coral reefs highlights the urgent need to determine whether local stressors synergistically interact with heat stress to induce bleaching. Here, we implement a global analysis of over 9,000 coral bleaching surveys spanning the period 2002–2018, to address the relationship between local human population density (HPD), a proxy for local anthropogenic stressors (Bruno & Valdivia, 2016), and heat stress to determine their interaction for predicting coral bleaching.

KEYWORDS
antagonistic, Anthropocene, coral reefs, global warming, human population, marine heatwaves, multiple stressors
METHODS

2.1 | Bleaching data

Bleaching prevalence data for hard coral species (order Scleractinia) were collated from 9,170 Reef Check surveys (http://Reefcheck.org) between 2002–2018 from 3,230 sites across 76 countries (Figure 1, Supporting Information Tables S2, S3). Reef Check data are collected using established protocols to a high standard by citizen scientists, with the reliability reported in Done et al. (2017) who found that the monitoring protocol has high accuracy, showing sampling error <±7% error for cover of benthic components. These data have also been utilized and described in previous macroecological studies (Bruno & Valdivia, 2016; Donovan et al., 2021; Johnson et al., 2021; Sully et al., 2019; Sully & van Woesik, 2020). From Reef Check data, coral bleaching (% of population) along with latitude-longitude geographic coordinates and the date of each survey were collected to allow for spatial extraction for HPD data. The global scale and long-term time frame of bleaching severity data provide a robust dataset to elucidate large spatial scale drivers associated with bleaching and reduce the likelihood of localized anomalous events causing bias.

2.2 | Human population density data

Local anthropogenic stressors on coral reefs are intrinsically related to the local HPD (Nyström et al., 2000). HPDs within 50 km of surveyed reefs were extracted from the WorldPop database (available at https://www.worldpop.org/) at a 1-km resolution (Lloyd et al., 2019) for each year, temporally associated with the timing of coral bleaching surveys, using the ‘raster’ package (Hijmans et al., 2015) in R 4.0.0 (R Core Team, 2021). The distance of 50 km was selected after preliminary analyses showed negligible differences in model performance between 25, 50 and 100 km distance (Supporting Information Table S1). Therefore, the 50-km distance was used as it represents a regularly used distance for studies investigating human impacts associated with coral reefs (Bruno & Valdivia, 2016; Moberg & Folke, 1999; Mora, 2008), and was found to consistently provide the best fit for models in studies where multiple other distances ranging from 10–500 km were used (Alves et al., 2022; Baumann et al., 2022). HPD represents a proxy of the implied impacts of local scale stressors (Bruno et al., 2019; Cinner et al., 2013; D’agata et al., 2014; Mora, 2008; Nyström et al., 2000; Williams et al., 2008) that have potential to exacerbate coral bleaching.

2.3 | Degree heating weeks data

To assess the interaction between local stressors and thermal stress, we used degree heating weeks (DHW), which are the global standard for determining the likelihood of thermal stress inducing coral bleaching on coral reefs. One DHW represents a 1 °C increase in the local mean climatic temperature for 1 week over the previous 12 weeks. Weekly DHW data were collected from the Coral Reef Temperature Anomaly database (CoRTAD version 6), supplied by the National Oceanic and Atmospheric Administration. These data

FIGURE 1 Global distribution of the Reef Check surveys used in this study. Panels are split into (a) Reef Check surveys that were not within marine protected areas (MPAs) and (b) Reef Check surveys that fell within an MPA.
are highly robust for predicting bleaching (Kayanne, 2017), and are specified at the highest resolution available (~4.6 km at the equator).

2.4  Marine protected areas

Data on marine protected areas (MPAs), defined as a marine area that falls under one of the seven International Union for Conservation of Nature (IUCN) protected area categories, were extracted from the IUCN’s (2016) World Database on Protected Areas using the ‘sp’ package (Pebesma et al., 2021). These data also supply the year of when the current MPA status was implemented for the location where a survey was undertaken. Therefore, reef check surveys that took place before protected status was implemented were not considered an MPA site. All sites were split into MPA sites or non- MPA sites. If data were unavailable, the survey was excluded from the analysis.

2.5  Coral ecoregions

Coral ecoregions of the world (COTW) were extracted from Veron et al. (2015) for each reef check survey. If the reef check survey fell outside the boundary of any coral ecoregion, the survey was excluded from analysis. These ecoregions were extracted to examine spatial variation across coral ecoregions in bleaching responses to local stressors inferred by HPD, as bleaching responses vary spatially (McClanahan et al., 2020; Sully et al., 2019). The taxonomic configuration, dispersal, isolation processes, and patterns of evolutionary history are consistent within these ecoregions and distinct across ecoregions (Spalding et al., 2007; Veron et al., 2015).

2.6  Data analysis

Monte Carlo Markov Chain generalized linear mixed models (MCMCglmm) from the R package ‘MCMCglmm’ (Hadfield, 2021) were used to assess the relationship between bleaching prevalence and local HPD, for MPA only sites, and non- MPA sites. Models were run separately by whether or not sites fell within MPAs as protection does not always reflect the level of protection enforced (Strain et al., 2019). Thus, comparing models allows us to identify whether there is an effect of protection in conjunction with local HPD. These models were implemented on a global scale and for each ecoregion (Veron et al., 2015). The global scale models included the random effects of ecoregions, where posterior variance was examined to identify global effects. Ecoregion models included a minimum sample size of 30 surveys, as regions with fewer than 30 surveys did not converge. All models ran with a minimum of 100,000 iterations, 40,000 burn-ins, and a thinning interval of 10. All models were specified with a Poisson family function as data were Poisson distributed and overdispersed (residual deviance exceeded degrees of freedom), which the Poisson family function in MCMCglmm accounts for (Hadfield, 2021). Flat normal priors were used for the fixed effects, while inverse-Wishart priors were used for the random effects. Convergence of all models was visually assessed from trace plots. All models had a minimum effective sample size of 1,000. Results are considered significant when the 95% credible interval coefficient does not cross zero (Hadfield, 2021).

3  RESULTS

Overall, local HPD did not increase the probability of coral bleaching, either independently or when under thermal stress (Figure 2). Rather, the interaction between DHW and local human population shows a slight reduction in the probability of coral bleaching. These results indicate local stressors do not drive coral bleaching independently or when under thermal stress from climate change.

Regional variance in bleaching patterns in the models was apparent (Figure 3, Supporting Information Figures S5 and S6). For example, in the Brazil ecoregion, local stressors strongly predicted bleaching. Within the Belize and West Caribbean ecoregion, coral bleaching probability appears slightly reduced in response to local stressors (Figure 3c).

Within the Pacific Ocean, the Fiji ecoregion showed an increase in bleaching probability in response to local stressors independently and a slight, but not significant, increase when under thermal stress (Figure 3a). Within the Sunda Shelf, Southeast Asia ecoregion, local stressors strongly increased the probability of coral bleaching independently (Figure 3b). However, the interaction between local stressors and thermal stress did not increase the probability of bleaching within this region (Figure 3c).

4  DISCUSSION

Our findings show that coral bleaching is not globally exacerbated by local stressors, either independently, or synergistically under thermal stress from anthropogenic warming (Figure 2). Rather, a weakly antagonistic relationship between local stressors and thermal stress is revealed by our analyses. This weakly antagonistic relationship may exist because of cosensitivity (sensitivity to multiple disturbances) and cotolerance (tolerance of multiple disturbances) of coral species (Bruno et al., 2019). Sites where localized pressures are reduced to promote increased coral cover are more likely dominated by fast growing branching acroporid corals, which are more sensitive to disturbance. Thus, when a disturbance event occurs (e.g., marine heatwave), the impact of coral bleaching is far more prevalent. Alternatively, the antagonistic relationship may exist because the impacts of global warming eclipse the impacts of local stressors (Baumann et al., 2022; Bruno et al., 2019; Bruno & Valdivia, 2016; Hughes et al., 2017). Our results also show regional variation affects the response of coral bleaching to local stressors, both independently and under thermal stress (Figure 3, Supporting Information Figures S5 and S6). This regional variation is succinctly highlighted...
by the contrast in bleaching probabilities from local stressors between adjacent ecoregions, such as the Gulf of Thailand and Sunda Shelf (Figure 3 and Supporting Information Figure S6). Therefore, while our study is the first to show there is no global effect of local stressors exacerbating coral bleaching, we also highlight how the consideration of regional variation is critical for predicting the effects of how anthropogenic heating will interact with local stressors exerted on coral reefs.

Regional variation of bleaching responses to local stressors is unsurprising considering spatial variation in bleaching patterns (McClanahan et al., 2020; Sully et al., 2019). These spatial variations exist as a result of numerous factors, including local species composition (and pre-disturbance cover), which is strongly influenced by disturbance history (Selig et al., 2012; Stuart-Smith et al., 2018; Zhang et al., 2014), the biogeography and evolutionary history of regions (Osman et al., 2018), environmental conditions, such as turbidity (Cacciapaglia & Woesik, 2016; Sully & van Woesik, 2020), and connectivity between ecosystems (Johnson et al., 2021). Here, we highlight that local stressors incurred from local HPD may result in exacerbated bleaching severity in certain regions of the world, such as the Sunda Shelf (Figure 3). However, owing to the dynamic relationship of anthropogenic exploitation of coral reef environments, along with complex environmental and organismal networks which drive bleaching, the relationships between local stressors resulting from human activity and bleaching responses are difficult to discern (Suggett & Smith, 2020). For example, local stressors have little effect on the bleaching probability in Bahamas and Florida Keys, and actually interact with heat stress to moderate bleaching (Supporting Information Figure S6). This region experiences higher turbidity caused by anthropogenic activity in this area (Cacciapaglia & Woesik, 2016). Yet turbidity within a moderate range buffers coral bleaching from thermal stress (Sully & van Woesik, 2020), likely explaining the reduced probability of bleaching identified in relation to local stressors. Therefore, the complexity of the relationship between local stressors and coral bleaching means that responses can be highly variable across local and regional spatial scales (McClanahan et al., 2020; Osman et al., 2018; Storfazzii et al., 2020; Sully et al., 2019; Wagner et al., 2010; Wall et al., 2015).

Further considerations for driving the spatial variation in bleaching responses to local stressors include the disparity in reef resilience and resistance to bleaching across biogeographic regions, such as reduced resilience to stressors in the Caribbean compared to the Indo-Pacific (Johnson et al., 2022; McWilliam et al., 2018; Roff & Mumby, 2012). The reduced resilience to stressors may result in regional exacerbation of global and local stressors in the former region (Figure 3). Furthermore, the effects of local stressors are highly divergent over various spatial scales in response to socio-economic (Hughes et al., 2017) and social-environmental factors (Darling et al., 2019), likely contributing to differences in bleaching responses. However, as HPDs, along with levels of protection from MPAs, were used in this study, factors such as the type of exploitation (i.e., fisheries, tourism) are not discernible here. Moreover, MPAs in certain regions of the world are not enforced effectively (Mora et al., 2006); therefore, the inferred adequate protection may not exist within some of the sites analysed in the MPA models. However, the global scale patterns of local stressors driving bleaching independently and under thermal stress suggests MPAs have a minimal role in mitigating climate change regardless (Figure 4; Bruno et al., 2018, 2019; Selig & Bruno, 2010; Selig et al., 2012).

The incongruence between local stressors driving coral bleaching globally suggests that local and global scale stressors do not always act synergistically on coral reefs, with accumulating evidence suggesting antagonistic interactions are more common (Bates et al., 2019; Bruno et al., 2019; Bruno & Valdivia, 2016; Darling & Côté, 2008; Darling et al., 2010), and likely vary regionally (Figure 3). Therefore, when predicting the effects of anthropogenic heating on coral reefs, localized conditions, such as regional bleaching patterns, resistance and resilience of reefs, and levels of exploitation need...
This incongruence also suggests protection from local stressors in the form of MPAs will have a minimal effect in most coral reef regions for buffering the impacts of anthropogenic heat-shock (Bruno et al., 2018, 2019; Selig & Bruno, 2010; Selig et al., 2012). Furthermore, isolated reefs far from human settlements are also unlikely to be refugia from climate change, and thus will continue to experience climate change-induced bleaching (Cerutti et al., 2020; Harrison et al., 2019). However, as local conditions are a driver of increased coral mortality after marine heatwaves, local scale action to mitigate region-specific local stress will be beneficial in reducing coral mortality (Donovan et al., 2021). Nevertheless, the most effective way to mitigate the decline of reef building corals driven by anthropogenic heating is to limit the extent of global temperature rise (Hughes, Anderson, et al., 2018; Hughes et al., 2017).

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**CONFLICT OF INTEREST**

There are no conflicts.

**DATA AVAILABILITY STATEMENT**

All data and code used in this study are available on our GitHub page at https://github.com/JackVJohnson/Bleaching_local_stressors.
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**BIOSKETCH**

Jack V. Johnson is interested in macroecological patterns, especially focusing on the combined effects of multiple stressors across spatial scales.

**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of the article at the publisher’s website.

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