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Remoteness Does Not Enhance Coral Reef Resilience

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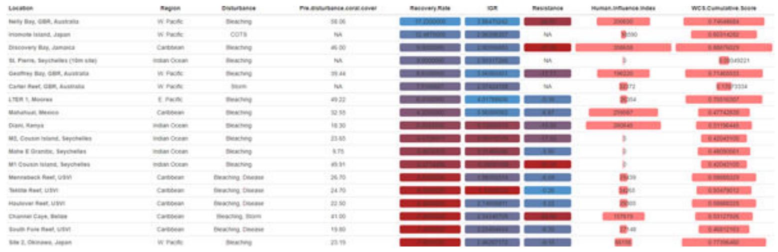
Abstract

Remote coral reefs are thought to be more resilient to climate change due to their isolation from local stressors like fishing and pollution. We tested this hypothesis by measuring the relationship between local human influence and coral community resilience. Surprisingly, we found no relationship between human influence and resistance to disturbance and some evidence that areas with greater human development may recover from disturbance faster than their more isolated counterparts. Our results suggest remote coral reefs are imperiled by climate change, like so many other geographically isolated ecosystems, and are unlikely to serve as effective biodiversity arks. Only drastic and rapid cuts in greenhouse gas emissions will ensure coral survival. Our results also indicate that some reefs close to large human populations were relatively resilient. Focusing research and conservation resources on these more accessible locations has the potential to provide new insights and maximize conservation outcomes.

Graphical Abstract



Location	Region	Disturbance	Pre.disturbance.coral.cover	Recovery.Rate	IGR	Resistance	Human.Influence.Index	WCS.Cumulative.Score
Nelly Bay, GBR, Australia	W. Pacific	Bleaching	58.06	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Iriomote Island, Japan	W. Pacific	COTS	NA	[illegible]	[illegible]	NA	[illegible]	[illegible]
Discovery Bay, Jamaica	Caribbean	Bleaching	46.00	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
St. Pierre, Seychelles (10m site)	Indian Ocean	Bleaching	NA	[illegible]	[illegible]	NA	[illegible]	[illegible]
Geoffrey Bay, GBR, Australia	W. Pacific	Bleaching	39.44	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Carter Reef, GBR, Australia	W. Pacific	Storm	NA	[illegible]	[illegible]	NA	[illegible]	[illegible]
LTER 1, Moorea	E. Pacific	Bleaching	49.22	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Mahahual, Mexico	Caribbean	Bleaching	32.55	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Diani, Kenya	Indian Ocean	Bleaching	16.30	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
M2, Cousin Island, Seychelles	Indian Ocean	Bleaching	23.65	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Mahe E Granitic, Seychelles	Indian Ocean	Bleaching	9.75	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
M1 Cousin Island, Seychelles	Indian Ocean	Bleaching	45.91	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Mennebeck Reef, USVI	Caribbean	Bleaching, Disease	26.70	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Tektite Reef, USVI	Caribbean	Bleaching, Disease	24.70	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Haulover Reef, USVI	Caribbean	Bleaching, Disease	22.50	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Channel Caye, Belize	Caribbean	Bleaching, Storm	41.00	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
South Fore Reef, USVI	Caribbean	Bleaching, Disease	19.80	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Site 2, Okinawa, Japan	W. Pacific	Bleaching	23.19	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Written Summary:Remote coral reefs (with lower human influence) are not more resilient to acute disturbances (e.g., bleaching, storms, and disease) than reefs with higher human influence. Our results suggest that recovery from a disturbance may even be slightly higher on reefs with high

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human influence, likely due to an ecosystem configuration that favors weedy and fast-growing corals.

Keywords

Coral Reefs; Disturbance; Climate Change; Resilience; Recovery; Local Impacts; Global Impacts; Biological Sciences; Ecology

Introduction

Remote ecosystems far from humans are thought to have especially high conservation value due to their biodiversity and relatively intact food webs. If these remote ecosystems remain vibrant, they could serve as biodiversity arks, able to repopulate more degraded locations (Abecasis et al., 2015; Hoegh-Guldberg et al., 2018). For remote areas to repopulate denuded sites, they will have to be more resilient to the onslaught of disturbances associated with global climate change. The absence of localized human impacts in many remote areas has the potential to promote resistance to and recovery from disturbances.

A number of studies have found that localized human impacts can erode resilience, supporting the hypothesis that remote areas away from humans are likely to be more resilient. For example, overfishing and climate change have reduced the resilience of kelp forest ecosystems in Tasmania (Ling et al., 2019), logging has reduced the resilience of tropical forests in the Amazon (de Andrade et al., 2020), and overharvesting has reduced the resilience of salt marshes in the western Atlantic (Altieri et al., 2012). While there is some evidence suggesting that coral reefs isolated from people could be more resilient to disturbance (Bellwood et al., 2006; Donovan et al., 2020, 2021; Sandin et al., 2008; Smith et al., 2016), the strength and generality of this relationship remains unclear.

Here we determined whether isolation increases the resilience of coral communities to disturbances associated with global climate change, including bleaching, storm damage, predator outbreaks, and disease (Bruno et al., 2007; Hughes et al., 2017; Madin et al., 2012; Uthicke et al., 2015). Reef-building corals live near their upper thermal limit. Consequently, decadal ocean warming, short-term marine heatwaves, and increasingly intense hurricanes are causing mass coral bleaching and mortality around the globe. This in turn has led to reductions in living coral cover and reef accretion (Alvarez-Filip et al., 2009; Perry et al., 2018; Perry & Alvarez-Filip, 2019), and a loss in the ecosystem services coral reefs provide to humans such as coastal protection, tourism, and fisheries (Barbier et al., 2011).

Isolated coral reefs tens to hundreds of kilometers from humans offer an important opportunity to determine whether reducing localized human impacts (e.g., fishing and pollution) promotes resilience to anthropogenic climate change. We tested the hypothesis that isolation from humans promotes coral reef resilience to large-scale disturbances. We compiled a global database of 57 peer-reviewed studies that measured coral community resistance to and recovery from acute, large-scale disturbances, including storms, predator outbreaks, bleaching, and disease. Our results suggest that reef remoteness does not enhance resilience to disturbance. Instead, some of the most resilient reefs are close to large human populations. These findings have important implications for reef conservation and management.

Materials and Methods

Study selection

To test the hypothesis that reefs isolated from humans are more resilient, we conducted a global meta-analysis based on published monitoring studies that quantified changes in total hard (scleractinian) coral cover due to a documented large-scale acute disturbance including bleaching, storm damage, disease, and *Acanthaster planci* outbreaks (e.g., Edmunds & Gates, 2002; N. A. Graham et al., 2015; Holbrook et al., 2018; McClanahan et al., 2014).

We queried ISI Web of Science using the following search term to build our database:

ISI Web of Science Search Term:

TI= (CORAL) AND TS= ("CORAL COVER") AND TS=(DISTURB* OR COTS OR STORM OR CYCLONE OR HURRICANE OR BLEACHING OR ACIDIFICATION OR EUTROPHICATION OR DISEASE OR RECOVER* OR DECLINE*) AND TS=(YEAR* OR TIME* OR TRAJECTORY)

These studies tracked coral cover over time via diver surveys or video transects. We leveraged previously published coral cover change databases compiled by Graham et al. (2011) and Zhang et al. (2014) and added 134 new observations from 36 additional peer-reviewed studies to this database, resulting in 65 published studies and observations from 182 unique sites and four geographic regions: Caribbean Sea, Indian Ocean, West Pacific, and East Pacific (Table S1).

We included data from peer-reviewed studies in our analysis if they met the following criteria: i) a recorded acute disturbance event, ii) estimated pre-disturbance coral cover, iii) estimated post-disturbance coral cover, and iv) coral cover after a recovery interval. Use of these criteria allowed us to calculate both aspects of resilience (recovery rate and resistance) as defined by Holling (1973) while also maximizing the amount of data we could use. As a result of this approach, we were able to extract data from a maximum of three time points at each site. While more detailed time series were available at some sites, we elected to only retain coral cover data from up to three time points following the above criteria, for the sake of comparison. We included any studies that allowed us to estimate just resistance or just recovery, or both. Fifty-seven studies documented resistance to (impact of) disturbances (based on data from 175 unique reef sites). Twenty studies that documented resistance did so within MPAs (at 57 unique sites). Fifty-six studies documented coral recovery rates based on data from 181 unique reef sites. Twenty-six studies that documented coral recovery rates did so within MPAs (at 65 unique sites). Forty-five studies documented both resistance and recovery (Table S1). We excluded one study in the Arabian Gulf which met our criteria because it was the only study in the region that met the criteria. Notably, data from long-term monitoring programs such as Reef Life Survey or AGRRA were not included in our analysis, as most of these programs did not consistently record acute disturbance events.

Coral taxa specific cover data were only available for 22% of reefs in this study and fish data were only available for 21% of reefs. As a result, the analysis was limited to total coral cover only.

Data Extraction

We extracted coral cover data directly from text or tables when possible. When coral cover data were only included in figures, we determined coral cover values with plot digitization via webplotdigitizer. Coral cover was recorded at three intervals: Pre-disturbance (before the acute disturbance event), Post-disturbance (immediately following the acute disturbance event), and Recovery (coral cover recorded after a post-disturbance recovery interval) (Fig 1).

For each site we also categorized the location (latitude and longitude) depth (min and max, range: 1–30 m), and reef type (fringing reef, barrier reef, rocky reef, back reef, reef crest, atoll, patch reef, and lagoon). When site locations were presented in maps and figures but not detailed in the paper, we used webplotdigitizer (Rohatgi, 2017) to extract approximate coordinates for each site. We excluded reef type, reef zone, and depth from all analyses due to inconsistent reporting and the absence of data.

Estimating Resilience as Resistance and Recovery from Disturbance

Following Graham et al. (2011), we calculated coral resistance to and recovery from disturbance using the following equations. Resistance = (Post-disturbance coral cover – pre-disturbance coral cover) (Fig 1). Recovery = (Coral Cover after recovery interval - Post-disturbance Coral Cover) / Time (years between measurements) (Fig 1). This formula for recovery rate assumes linearity and matches a formula that is often used in the coral literature (N. Graham et al., 2011; Zhang et al., 2014). Negative recovery rates may have indicated continued loss of coral cover following the disturbances, suggesting chronic or compounding stressors or a phase shift from coral to algae. Positive recovery rates indicated the recovery of the ecosystem back to a pre-disturbance coral cover. Negative resistance values represented a loss of coral cover following a disturbance, indicating that the recorded disturbance had a negative effect on ecosystem state. Resistance values near zero indicated a resistant community and positive resistance values represented a gain of coral cover following a disturbance, indicating that the recorded disturbance likely had little to no effect on coral cover or that the post-disturbance coral cover values were recorded following a period of recovery. Alternatively, resistance values near zero may also have been driven by low pre-disturbance coral cover, whereby the already degraded reef appears more resistant simply because there is very little coral cover left to lose. To consider the potential covariate of pre-disturbance coral cover, we calculated relative coral cover (post-disturbance or recovery coral cover / pre-disturbance coral cover at the same site) was also calculated for each site, when possible. Additionally, as recovery trajectories can be non-linear (Gilmour et al., 2013), instantaneous growth rates (IGR) were calculated across the entire recovery interval at each site following Ortiz et al (2018). IGR assume exponential growth during recovery. See supplementary methods for details.

Estimating Isolation Using the Human Influence Index and WCS cumulative impact score

For each site, we measured reef-specific isolation from local human impacts using the Global Human Influence index (HII, referred to as "human influence" in the results and discussion) v2 (1995–2004) database provided by the NASA Socioeconomic Data and Applications Center (WCS and CIESIN, 2005). Human Influence Index (HII) is gridded into 1km^2 cells aggregated from 1995–2004. Global Human Influence (HII) is an integrated product that includes human population density, human land use and infrastructure, and human access (coastlines, roads, railroads, and navigable rivers). These aspects of human communities are known to be predictive of local human impacts in many natural systems including coral reefs (Bruno & Valdivia, 2016; Cinner et al., 2018; Fabricius, 2005; Knowlton & Jackson, 2008; Mora, 2008; Stallings, 2009; Ward-Paige et al., 2010). The sum of human influence (HII) values within a 10, 25, 50, 75, and 100 km radius of each site were calculated using the 'extract' function in the *raster* package in R. The cumulative HII value within a 100km radius or a site was used a proxy for isolation, where lower HII scores indicated more isolation from human impact and HII values of zero indicated no human impact based on HII. The reef-site specific cumulative human pressure index value was also extracted for each site using the metric published by Andrello et al (2021). This metric, henceforth referred to as the WCS cumulative impact score, integrates fishing pressure (through calculations of market gravity (Cinner et al., 2018)), coastal development (using human populations living on coastlines as a proxy), industrial development (indicated by number of nearby ports), tourism (utilizing reef value from Spalding et al. (2017)), and pollution (including sediment and nitrogen delivery to reefs using a sediment plume model) into cumulative impact score with a resolution of ~ 5km. Cumulative impact scores were extracted from the pixels containing each of our reef sites utilizing code modified from Andrello et al (2021). Both HII and WCS cumulative score were included in our models. Both are proxies for human influence but they utilize different methods and metrics with HII focused on populations and land use and the WCS score focused on fishing, tourism, coastal development, and land-based pollution.

Estimating effects of other covariates

Because local human impacts are thought to contribute heavily to reef resilience (Bellwood et al., 2004; Hughes et al., 2010), We also assessed the relative impacts of local stress metrics (distance to shore, travel time to nearest human population, human gravity, and distance to nearest river) as well as protective status (inside or outside MPA). We hypothesized distance from shore and travel time from nearest human population (Maire et al., 2016) as possible proxies for isolation, because increased distance from a human population is likely to decrease its impact on the ecosystem. We included distance to the nearest river in the analysis as distance from a river mouth is considered a proxy for sedimentation and nutrient stress (Golbuu et al., 2011). MPAs are designed to minimize local impacts, especially fishing pressure, thereby potentially enhancing the resilience of a coral reef (Bellwood et al., 2004; Hughes et al., 2010). Geographic coordinates from each reef site in this study were compared to geospatial datasets of shorelines, river mouths, and MPA shape files in order to determine distance from shore, distance from the nearest river, and MPA status (inside or outside MPA). For details on other data extraction and preparation methods, please see the supplementary methods.

Statistical analysis

We identified reefs with anomalously high or low recovery rates, IGR, and/or resistance values to a single acute disturbance event in order to understand the spatial distribution of such reefs and their proximity to human influence. Reefs were identified as high outliers (1.5 IQR above the 3rd quartile for their home region) or low outliers (1.5 IQR below the 1st quartile for their home region). Visual distributions of the regional data can be found in Figure 2 and the results of the outlier test can be found in Table 1. While such instances of high and low resilience to a single disturbance do not consider the context of environmental history at each site, they do highlight the variance in ecosystem scale responses across regions and may provide examples of locations or environmental regimes in which resilience is high (Lester et al., 2020). Such information may be valuable for managers and restoration practitioners.

We used linear models to assess the effect of isolation from human effect (HII) on coral resistance to and recovery from acute disturbance. Because resistance and recovery are hypothesized to be governed by many environmental and anthropogenic factors, we employed a mixed effects modeling approach using the ‘lmer’ function in the *lme4* package in R with Human Influence (HII) as a fixed effect. Our models also included other fixed factors known or believed to influence coral community resilience to acute, large-scale disturbances, including: geographic region, distance from shore, distance from nearest river, MPA status, region, pre-disturbance coral cover, recovery or resistance time, and disturbance type. The parameter “study” (the name of the study from which the data were collected) was set as a random effect as we wanted to account for variations in the data associated with different methods, though we were not interested in differences in recovery rates between each individual study and reef location (Negret et al., 2020). Latitude and longitude of each reef were considered as random effects to account for spatial autocorrelation but including both in any model resulted in overfitting of the data (singular fit). Numerical fixed effects were centered and scaled as a means of standardization using the scale() function in R, following recommendations from Gelman (2008).

Interactions of fixed effects were not included in the models as they resulted in multicollinearity of fixed effects. Multicollinearity of fixed effects were also high when distance to the nearest river was included in the model (co-varied with distance to shore and region). Thus, distance to the nearest river was excluded from the final model. The final models used in each analysis were selected using a top-down modeling approach (Table S2, S3) in which the most complex model was fit and model complexity was gradually reduced until the best fit model was selected (Zuur et al., 2009). We produced two models, one for resistance and one for recovery, and performed a comprehensive model check to assess that the assumptions of each model (collinearity, normality of residuals, homoscedasticity, homogeneity of variance, outliers / influential observations) were met using the “check_model” function in the *Performance* package in *R* (Lüdecke et al., 2021). Models in which assumptions were not satisfactorily met were discarded. Models in which assumptions were met were compared to one another using the “check_performance” function in the *Performance* package in R. This function outputs Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), conditional and marginal R^2, Interclass Correlation Coefficient (ICC), and Root Mean Squared Error (RMSE) as well as a performance score for each model. We selected a 'best fit' model for each analysis based on AIC and BIC scores, as well as ΔAIC following Burnham et al (2011). Models with ΔAIC <7 from the model with the lowest overall AIC score were considered as plausible options. The models selected as overall 'best fit' for both recovery rate and resilience were the models with the lowest AIC and BIC scores, in this case. Details of each candidate model and the model selection pipeline are available in the Supplementary Materials (Table S2, S3). The same modeling pipeline was used for additional models that utilized relative coral cover in calculating both aspects of resilience instead of absolute coral cover. The output of the relative coral cover model is available in Fig S4.

Following selection of a best fit model, collinearity was checked using the "check_collinearity" function and outliers or influential observations were assessed using the "check_outliers" function in the *Performance* package in *R.* Variance Inflation Factors (VIF) did not exceed 4 for the final models, indicating that issues of collinearity were unlikely to influence the models (Table S4, S5; Hair, 2009). "Check_outliers" uses a composite outlier score that applies multiple outlier detection algorithms including: Z-scores, IQR, Mahalanobis distance, and Cook's Distance. For both models the check_outliers test returned no outliers. Additionally, spatial autocorrelation of model residuals was assessed using a Moran's I test (Cliff, 1973) for each model used in the analysis. In both instances, there was no significant effect of spatial autocorrelation in the models (Table S4, S5). Model fixed effects in which the estimate was greater than the absolute value of the standard error were deemed to significantly impact the response variable (recovery rate or resistance) with the magnitude of the effect represented by the "estimate" value and the direction of the effect given by the sign of the estimate value (positive or negative). Error ranges that did not overlap indicated significant differences between fixed effects. For categorical fixed effects, the model predicted categorical means and 95% confidence intervals were generated using the "ggpredict" function in the *ggeffects* package in R (Lüdecke, 2018). Confidence intervals that do not overlap (Figures S2, S3) represent significant differences between groups.

Results

Globally, coral resilience varied tremendously. After a disturbance, some reefs continued to decline, while others showed no response or even a positive response to a disturbance (resistance: −78.5% to 18.3%, Fig. 2B). Similarly, reefs varied greatly in their rates of recovery ranging from −7.7% to 17% coral cover per year (Fig. 2A) and IGR (−0.09 – 4.01; Fig S5). Certain reefs appear to have been resilient to single acute disturbance events (Table 1; Fig S1). For example, places such as Nelly Bay, GBR; Iriomote Island, Japan; and Carter Reef, GBR recovered rapidly (>9% coral cover per year) following major disturbances (bleaching, sea star outbreak, and storm, respectively). Notably, such "bright spots" can and do often suffer declines following additional acute disturbances or chronic stress (Cinner et al., 2016; Haapkylä et al., 2013). Thus, historical and environmental context is essential when interpreting "bright spots" for management purposes. Other reefs are more fragile and seem to have little capacity to resist and/or recover from disturbance. For example, following bleaching events in Okinawa, the USVI, and Belize, reef sites used in this study failed to recover and instead continued to show coral cover decline 1–2 years after the bleaching event.

Surprisingly, coral resilience was positively associated with local human influence. We found a positive correlation between HII and recovery rate (model coefficient = 0.80 ± 0.42 (SE); Fig 3, Table S6) but not resistance (model coefficient = −0.58 ± 1.90 (SE); Fig 3, Table S7). We also found a slight positive correlation between WCS cumulative stress score and IGR (Fig S6 G). Areas with low human influence index recovered at a rate of 1.28% per year while areas with high human influence index recovered almost 3 times faster (3.69% per year). However, there was no correlation (positive or negative) between WCS cumulative score (the other measure of human influence used in the model) and either linear recovery rate or resistance (Fig 4C, D). Additionally, the recovery models do not differ when relative coral cover is used instead of absolute coral cover. However, in the resistance models that utilize relative coral cover, there is a positive correlation between WCS cumulative score and resistance (Fig S4). Taken together, it is clear that there is not a negative correlation between local human pressure and resilience. This finding rejects the core hypothesis that reefs isolated from human influence are more resilient. Other variables assessed by our models also contributed to variance in resilience.

Additional drivers of recovery

Coral recovery was positively influenced by pre-disturbance coral cover, with reefs that had high coral cover recovering two times faster than reefs with low pre-disturbance cover (on average 2.22% / year vs. 1.13% / year) (Table S6, Fig S2C). Recovery rates did not statistically differ among regions, but on average Caribbean and Indian ocean reefs did not recover from acute disturbance (1.32% / year ± 2.36 (95% CI), 0.51% / year ± 1.38 (95% CI)), while reefs in the East and West Pacific showed slight recovery (2.44% / year ± 2.31 (95% CI), 2.39% / year ± 1.71 (95% CI)) (Table S6, Table S8, Fig S2D). Additionally, sites that experienced co-occurring disturbances, especially co-occurrence of bleaching and disease were least likely to recover and even showed continued declines over time, while the effects of single acute disturbances on recovery did not differ from one another (Table S6, Table S8, Fig S2E). Estimates of coral recovery rate were not correlated with recovery time, travel time to nearest human population, WCS cumulative score, or MPA status (Table S6, Table S8, Fig S2A, S2B, S3A). Overall, human influence index had the greatest positive impact on recovery rate. Notably, even regions with relatively high human influence could still have struggled to recover due to the effect of co-occurring disturbances, especially co-occurrence of bleaching and disease, which had the most significant negative effect on recovery rate.

Additional drivers of Instantaneous Growth Rate (IGR)

Instantaneous growth rate (IGR), a representation of recovery rate assuming exponential growth, was negatively influenced by recovery time, where sites with higher recovery times had two times lower IGR than sites with longer recovery times (Fig S7A) due to the nature of the IGR equation (Supplemental Methods). Estimates of IGR were not correlated with travel time to nearest human population, pre-disturbance coral cover, or HII (Fig S7B, C, F).

Instantaneous Growth Rates (IGR) did not vary by region, disturbance, or MPA status (Fig S7D, E, H).

Additional drivers of resistance

Coral resistance was negatively influenced by pre-disturbance coral cover, where sites with high (80%) pre-disturbance coral cover lost 11 times more coral cover following a disturbance (60% decline in cover) than sites with low (20%) pre-disturbance coral cover (5% decline in cover) (Table S7, Table S9, Fig S2H). Changes in resistance were not correlated with resistance time, travel time to nearest human population, region, disturbance type, WCS cumulative score, HII, or MPA status (Table S7, Table S9, Fig S2F-J, Fig S3B). Thus, the only variable that significantly influenced resistance was pre-disturbance coral cover (large negative effect). Based on the effect sizes of these variables, it is clear that of the drivers considered in this study, pre-disturbance coral cover is the best predictor of coral resistance to disturbance, where reefs with higher coral cover are much less resistant than reefs with lower coral cover. Thus, resistance rates near zero may indicate resistance of a robust coral community or may simply indicate that coral cover did not decrease tremendously following a disturbance because pre-disturbance coral cover was already quite low and prevented a large decrease in cover from being possible. As such, interpretations of resistance values should be considered in the context of past disturbance history and coral cover prior to the disturbance.

Discussion

We found that isolation from local human influence did not measurably affect coral community resilience to large-scale disturbances such as bleaching, disease, storms, and predator outbreaks. The absence of greater resilience on isolated reefs suggests that they are just as susceptible to degradation caused by climate change. Therefore, we cannot expect isolated areas to act as biodiversity arks able to rescue degraded sites. The conservation of isolated areas, while valuable for many other reasons (Edgar et al., 2014; Turner & Corlett, 1996), is therefore unlikely to be sufficient in promoting thriving coral reefs elsewhere unless we are able to also rapidly reduce greenhouse gas emissions to mitigate the impacts of global climate change.

Why might recovery be higher in areas with higher human influence?

The mechanisms underlying the observed positive association between the human influence index and recovery rate, and WCS cumulative score and IGR are unclear. One possible explanation is that reefs with a large human footprint could be more resilient to disturbance due to past selection for resilient genotypes or species in response to local impacts. Nearly all the world’s reefs are transitioning (or have fully transitioned) towards dominance by weedy or stress-tolerant taxa (Darling et al., 2013; Van Woesik et al., 2011). These selective processes could have progressed further on reefs with intense human impacts, many of which have been present for decades or even centuries (Jackson, 1997; Pandolfi et al., 2003). Côté and Darling (2010) predicted that the co-tolerance (among-species) of sensitivity to local human impacts and larger-scale disturbances combined with selection for traits related to resilience should lead to the pattern we observed. The protection paradox, where protected areas exhibit lower resilience due to the retention of relatively vulnerable taxa or genotypes, is based on this idea (and lower resilience in manged areas where local stressors are effectively mitigated — aka the protection paradox sensu Bates et al., 2019). Specifically, areas near humans dominated by weedy and/or stress-tolerant species may show high resilience to disturbance, while isolated areas that have yet to shift into a more stress-tolerant community may still have low tolerance to disturbance and recover more slowly. Shifts in species composition may similarly explain why we see some reefs with high recovery rates but low resistance and other reefs with low recovery and high resistance (Table 1). Reefs dominated by stress-tolerant species are likely to be more resistant while reefs dominated by competitive species and weedy species are likely to recover faster from acute disturbances (Darling et al., 2013). It is also notable that recovery of coral cover does not always lead to recovery of function, as shifts toward weedy and non-framework building species often result in increased cover but low functionality (González-Barrios et al., 2021).

Where does coral reef conservation go from here?

A small fraction of reefs appear to be especially resilient (i.e. they have relatively high recovery rates or IGR) to single, acute large-scale disturbances despite high human influence (Table 1, Fig 4A, C). These sites deserve additional research focus because they could offer insight into what mechanisms underlie resilience. However, resilience to a single acute disturbance may not translate to a trajectory of continued resilience in the face of additional acute and chronic stressors. Sites with a history of high resilience may also be resilient in the future and be key to the supply of tolerant species or genotypes needed to repopulate degraded sites. This may be a silver lining because resilient reefs near human populations may be more cost-effective to study and manage than isolated reefs and thus may prove to be a prudent area of focus for limited conservation dollars. While our study identified sites that have demonstrated resilience to acute disturbance events, we do not account for long-term disturbance history and growth trajectories at each site, two additional factors that will be important in management decision making.

The lack of resilience in areas with little human influence shown here, combined with the lack of resilience afforded locally by MPAs (Bruno et al., 2019; N. Graham et al., 2011) points to the importance of drastically reducing emission of carbon dioxide, methane, and black carbon in the near term to slow global climate change. While MPAs have been shown effective at reducing local stressors or increases herbivore and predator abundances (Bonaldo et al., 2017; Strain et al., 2019), they cannot stop climate change and other large-scale disturbances, nor have they proven particularly effective at improving coral resilience (Hargreaves-Allen et al., 2017; Harvey et al., 2018; Strain et al., 2019). Coral reef scientists, managers, conservationists, and island states have (for decades) been strongly advocating for reductions in greenhouse gas emissions. In 2015, the International Coral Reef Society called on “all nations to take the action necessary, within the next 12 years, to keep global warming to a maximum of 1.5°C” (Hoegh-Guldberg et al., 2015). However, the world is currently not on track to reduce emissions to levels agreed upon through the Paris Agreement, where nations pledged to pursue emission reductions that hold the global average temperature to ‘well below 2°C … and to pursue … 1.5°C’ that of pre-industrial levels (Anderson et al., 2020). Without this drawdown, we will see dramatic changes to both remote and human dependent coral reef ecosystems and a loss of ecosystem services provided by coral reefs to the human communities that depend on them (Donner & Potere, 2007). This includes a loss or reduction of food, income, and coastal protection coral reefs provide to over 500 million people worldwide (Wilkinson, 2008).

Combating the threats of climate change involves embracing a multitude of potential solutions that could mitigate global coral decline and aid in reef adaptation. Climate change legislation at a global scale is likely the fastest route to mitigation and allowing populations to adapt. Yet the glacial pace of actual emissions reduction action has us looking for alternative solutions. Stop gap methods that can be enacted quickly include restoration (Boström-Einarsson et al., 2020), genetic engineering and assisted evolution (Cleves et al., 2018; van Oppen et al., 2015), and reducing fishing pressure and local human impacts (McClanahan et al., 2006; Selig & Bruno, 2010). Many governments (e.g., in the U.S. and Australia) and NGOs are promoting an approach based on protection measures that aim to reduce impacts from fishing, pollution, and other human activities. The thinking behind such “managed resilience” is that local stressors interact additively or synergistically with ocean heating and other aspects of climate change. Therefore, local mitigation should make coral communities more resilient to large-scale disturbances, including mass-bleaching, disease outbreaks, and storm impacts. Although this solution avoids the difficult issue of greenhouse gas mitigation, a growing body of evidence indicates it is not effective (Bruno et al., 2019; Carassou et al., 2013; Côté & Darling, 2010; N. A. Graham et al., 2015).

Recent theory and empirical evidence support the “protection paradox”; the idea that when effective, local protection could make reefs less resilient (Bates et al., 2019; Bruno et al., 2019). In some cases, pursuing these solutions may be valuable as a portfolio approach to conservation, but in others, these quick fixes distract from the primary management lever needed to resolve the problem (Nguyen & Bosch, 2013). The rapid protection of large swaths of isolated areas in hopes that protecting these locations may serve as biodiversity arks has become a popular idea (McCauley et al., 2013). Yet, our finding that coral on remote reefs is no more resilient than corals with high human impact suggests that this protection may not alone afford the coral reef resilience in the future.

Conclusion

Coral reefs are already experiencing massive declines from global climate change. It is therefore imperative that we double down on our commitment to an expedient transformation of industries, infrastructure, and energy systems which is needed to ensure the survival and services of coral reefs and many other ecosystems. Achieving such emission reductions will require international cooperation, enhanced polycentric governance, and building the capacity of civil society and the private sector to take mitigation actions. With our developing realization that the reduction of local stressors will not be enough to promote resilience, combined with advances in technology and interdisciplinary creativity, we are increasingly capable of confronting climate change and protecting the future of nature and people.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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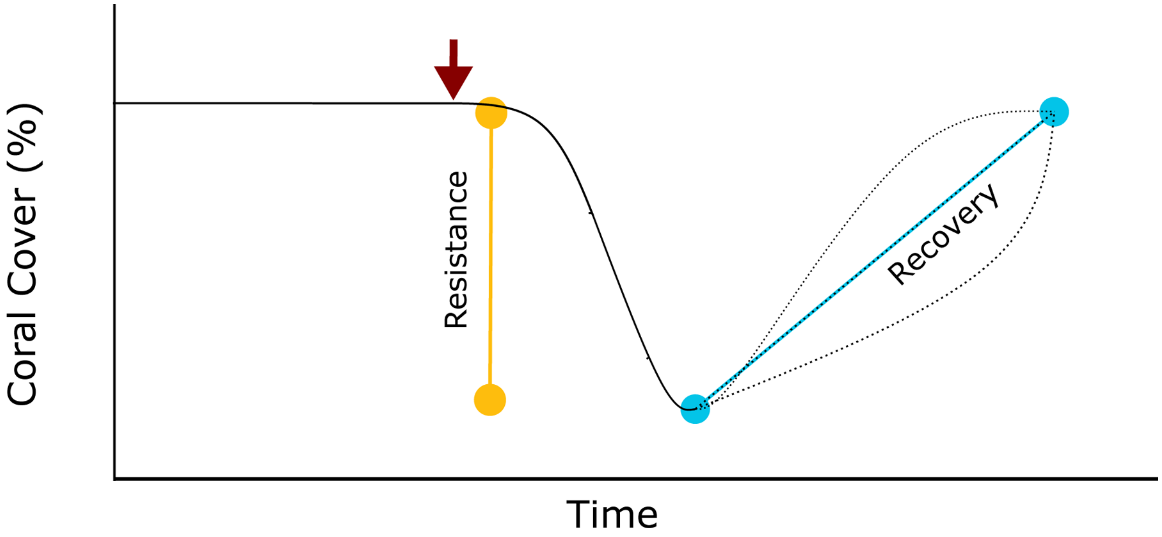


Fig 1:

Conceptual diagram of resistance to and recovery from an acute disturbance. Resistance is defined as post-disturbance coral cover – pre-disturbance coral cover and recovery is defined as: (coral cover after a recovery interval – post-disturbance coral cover) / Time between measurements. Recovery trajectories may vary. Represented here are exponential, linear, and logarithmic trajectories.

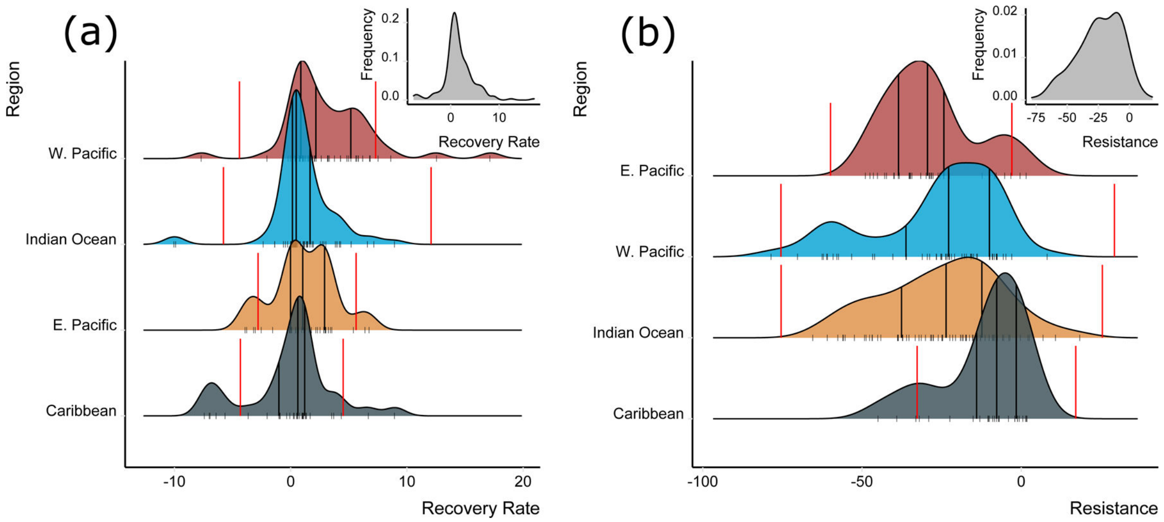
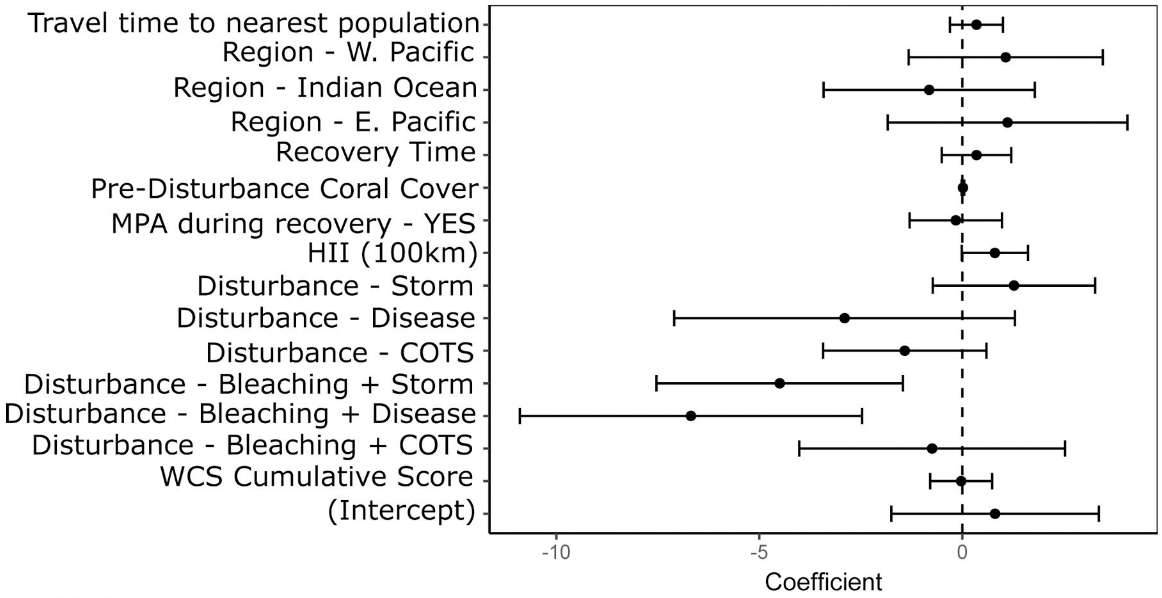


Figure 2.

Regional trends in A.) Coral Recovery Rate (% / Year) and B.) Coral Resistance (%) to acute disturbance. Inset figures represent global trends. Black vertical lines represent Q1, Median, and Q3 values by basin. Points outside of the red lines (1.5*IQR outside of quartiles) are outliers. Tick marks on X-axes represent raw data. While there are no clear differences in recovery and resistance across ocean basins, these plots detail the variability of responses observed on a global scale.

(a) Recovery Rate



(b) Resistance

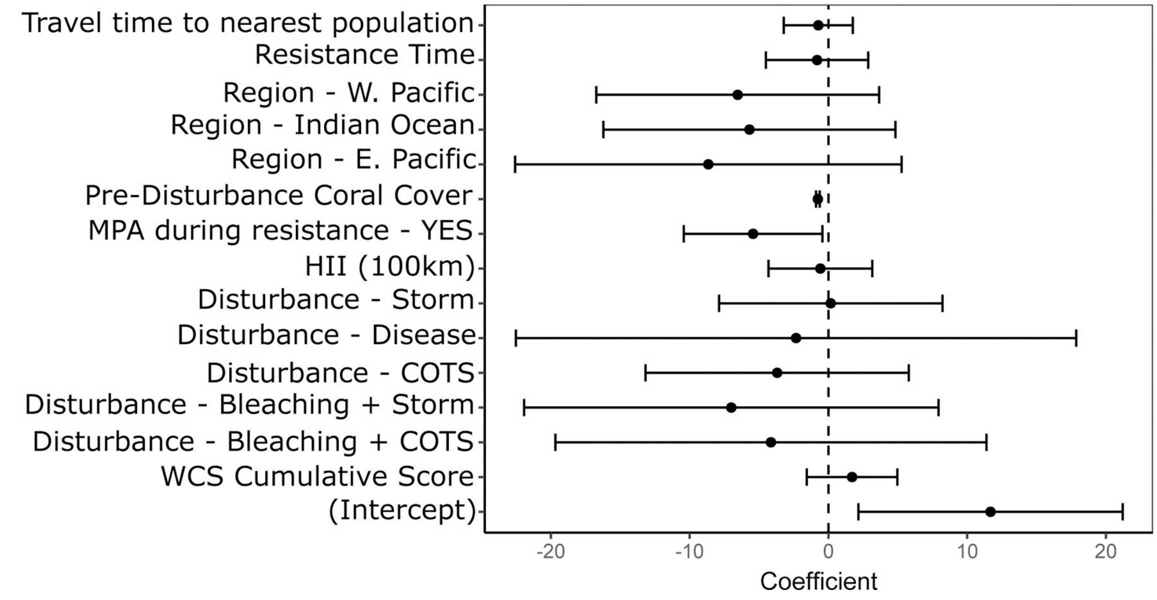


Fig 3.

Linear mixed effect model coefficient plots for A.) Recovery rate and B.) Resistance. Error bars are ± 1 S.E.

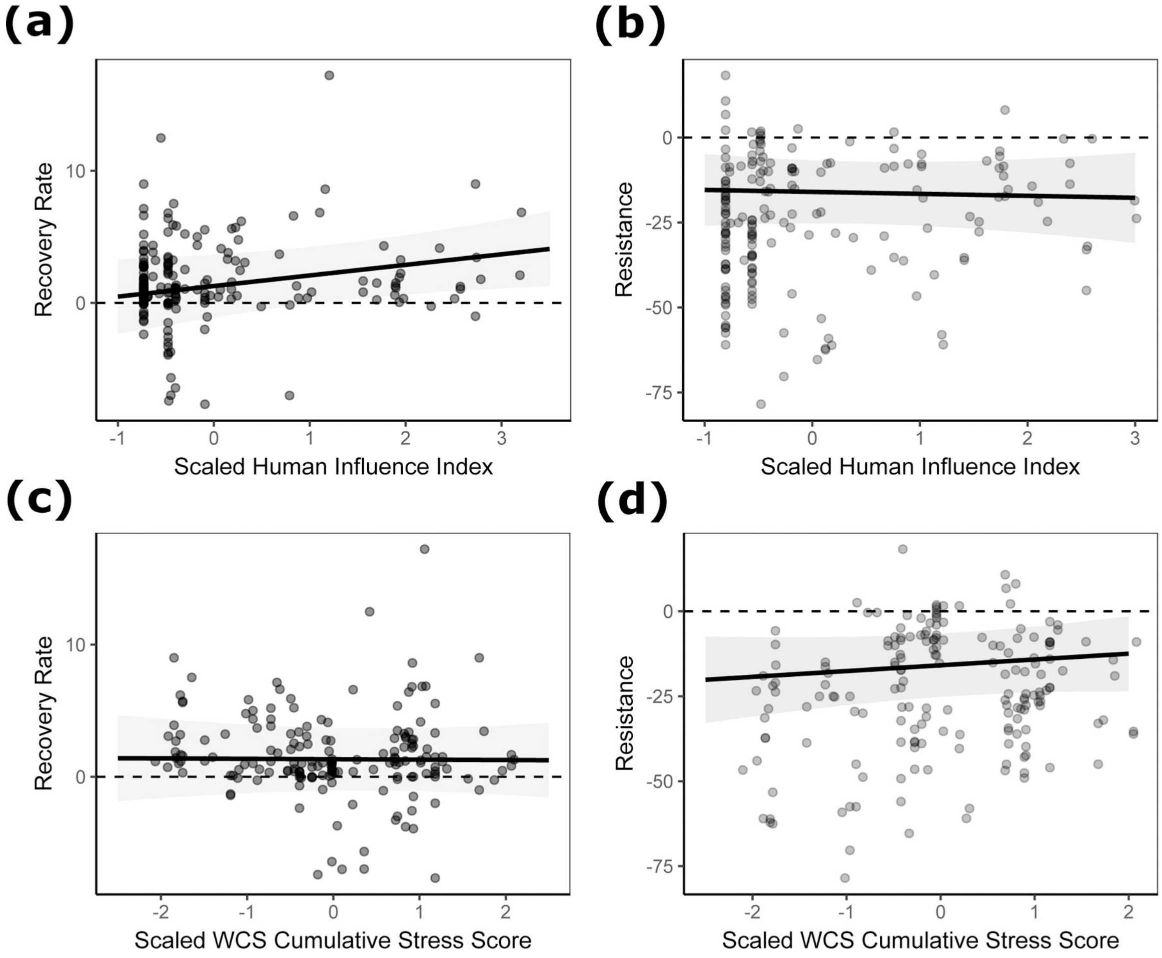


Figure 4.

Relationship between two metrics of human influence and resilience. Correlations between Human Influence Index (HII) and A.) Recovery rate (% / Year) and B.) Resistance (%). Correlations between WCS cumulative local stress score and A.) Recovery rate (% / Year) and B.) Resistance (%).

Table 1.

Examples of resilience to single acute disturbance events. Locations that showed resilience (or lack thereof) to a single disturbance based on coral cover recovery rate (% cover / year), instantaneous growth rate (IGR) over the recovery interval, or resistance. Reefs that were resilient have blue or grey recovery rates or IGR and were positive outliers (1.5 IQR above the 3rd quantile for their home region). Reefs that were not resilient have bright red recovery, IGR, or resistance values and were negative outliers (1.5 IQR below the 1st quantile for their home region). Note that there were no positive outliers for resistance (Fig 2). N/A indicates a lack of necessary data to calculate resistance for a specific reef. Human Influence Index (HII) values are human influence index within a 100km radius of each site. WCS cumulative score reflects the reef-site specific cumulative human pressure index value for each site as extracted from the metric published by Andrello et al (2021). Higher HII and WCS cumulative scores indicate greater human influence (lower “remoteness”).

Location	**Region**	**Disturbance**	**Pre-disturbance coral cover**	**Recovery Rate**	**IGR**	**Resistance**	**Human Influence Index**	**WCS Cumulative Score**
Nelly Bay, GBR, Australia	W. Pacific	Bleaching	58.06	17.22	3.98	−26.67	200650	0.75
Iriomote Island, Japan	W. Pacific	COTS	NA	12.49	2.96	NA	18590	0.60
Discovery Bay, Jamaica	Caribbean	Bleaching	46.00	9.00	2.90	−33.00	358658	0.89
St. Pierre, Seychelles (10 m site)	Indian Ocean	Bleaching	NA	9.00	2.95	NA	0	0.09
Geoffrey Bay, GBR, Australia	W. Pacific	Bleaching	39.44	8.61	3.57	−17.77	196220	0.71
Carter Reef, GBR, Australia	W. Pacific	Storm	NA	7.52	2.37	NA	32372	0.14
LTER 1, Mo’orea	E. Pacific	Bleaching	49.22	6.41	4.02	−5.16	26354	0.71
Mahahual, Mexico	Caribbean	Bleaching	32.55	4.32	3.56	−6.87	259587	0.48
Diani, Kenya	Indian Ocean	Bleaching	18.30	0.33	0.13	−15.30	280845	0.51
M2, Cousin Island, Seychelles	Indian Ocean	Bleaching	23.65	−0.67	0.06	−17.33	0	0.42
Mahe E. Granitic, Seychelles	Indian Ocean	Bleaching	9.75	−0.96	0.11	−5.90	0	0.48
M1, Cousin Island, Seychelles	Indian Ocean	Bleaching	49.91	−2.37	−0.09	−33.20	0	0.42
Mennebeck Reef, USVI	Caribbean	Bleaching, Disease	26.70	−5.66	1.98	−6.09	29439	0.59
Tektite Reef, USVI	Caribbean	Bleaching, Disease	24.70	−5.42	−1.44	−0.26	34265	0.50
Haulover Reef, USVI	Caribbean	Bleaching, Disease	22.50	−5.98	2.75	−5.22	29305	0.59
Channel Caye, Belize	Caribbean	Bleaching, Storm	41.00	−7.00	2.34	−29.00	157619	0.53

Location	**Region**	**Disturbance**	**Pre-disturbance coral cover**	**Recovery Rate**	**IGR**	**Resistance**	**Human Influence Index**	**WCS Cumulative Score**
South Fore Reef, USVI	Caribbean	Bleaching, Disease	19.80	−7.40	2.25	−8.30	27148	0.47
Site 2, Okinawa, Japan	W. Pacific	Bleaching	23.19	−7.66	2.46	−9.15	56156	0.77