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Coral reef state influences resilience to acute climate-mediated disturbances

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Abstract

Aim: The aim of this study was to understand the interplay between resistance and recovery on coral reefs, and to investigate dependence on pre- and post-disturbance states, to inform generalizable reef resilience theory across large spatial and temporal scales.

Location: Tropical coral reefs globally.

Time Period: 1966–2017.

Major Taxa Studied: Scleractinian hard corals.

Methods: We conducted a literature search to compile a global data set of total coral cover before and after acute storms, temperature stress and coastal run-off from flooding events. We used meta-regression to identify variables that explained significant variation in disturbance impact, including disturbance type, year, depth and pre-disturbance coral cover. We further investigated the influence of these same variables, as well as post-disturbance coral cover and disturbance impact, on recovery rate. We examined the shape of recovery, assigning qualitatively distinct, ecologically relevant, population growth trajectories: linear, logistic, logarithmic (decelerating) and a second-order quadratic (accelerating).

Results: We analysed 427 disturbance impacts and 117 recovery trajectories. Accelerating and logistic were the most common recovery shapes, underscoring non-linearities and recovery lags. A complex but meaningful relationship between disturbance impact, the state of a reef pre- and post-disturbance, and recovery rate was identified. Fastest recovery rates were predicted for intermediate to large disturbance impacts, but a decline in this rate was predicted when more than ~75% of pre-disturbance cover was lost. We identified a shifting baseline, with declines in both pre- and post-disturbance coral cover over the 50-year study period.

Main Conclusions: We break down the complexities of coral resilience, showing interplay between resistance and recovery, as well as dependence on both pre- and post-disturbance states, alongside documenting a chronic decline in these states. This has implications for predicting coral reef futures and implementing actions to enhance resilience.

KEYWORDS

climate change, coral reef ecology, cyclone, disturbance dynamics, extreme climatic event, marine heatwave, meta-analysis, recovery, resistance, run-off

1 | INTRODUCTION

Understanding the response of natural systems to disturbance is an overarching goal in ecology and a requirement for successful conservation (Morecroft et al., 2012). Coral reefs have long been recognized as dynamic ecosystems that are periodically subjected to disturbances from which they typically recover (Connell, 1997; Dana, 1853; Lamy et al., 2016). However, in recent years, disturbance impacts of previously unobserved magnitude and scale have been observed (Hughes et al., 2018; Souter et al., 2020) and are predicted to worsen (IPCC, 2021).

The resilience of natural systems can be considered as a function of resistance—the capacity of the system to withstand a disturbance, and recovery—the capacity to return to a pre-disturbance state (Hodgson et al., 2015). The concept of resilience has featured heavily in efforts to understand, manage and predict the future of coral reefs in a rapidly changing climate (Hughes et al., 2010; Mumby & Anthony, 2015; O’Leary et al., 2017; Roff & Mumby, 2012; Shaver et al., 2022). High disturbance frequency means shorter windows for recovery (Hughes et al., 2017, 2021), such that the resistance of coral reefs may contribute more to resilience than recovery processes (Darling & Côté, 2018). However, we are still lacking a broadly applicable understanding of the relative roles of, and potential relationships between, impact (resistance) and recovery processes that is grounded in empirical data (Boschetti et al., 2020; Côté & Darling, 2010). We also do not know how these relationships may change with altered disturbance regimes or shifts in the baseline reef state.

Scleractinian corals are the dominant ecosystem engineer in coral reef systems and the impacts of acute disturbance are often clearly measurable by a loss in live coral cover (Connell, 1997; Wild et al., 2011). Cyclones, flooding events and marine heatwaves are linked to the climate and are predicted to increase in frequency and/or intensity (Cheal et al., 2017; Frölicher et al., 2018; Zhang et al., 2013). Various meta-analyses and studies have examined coral cover loss resulting from disturbance (Bruno & Selig, 2007; Claar et al., 2018; Gardner et al., 2005) and recovery following disturbance (Baker et al., 2008; Baumann et al., 2022; Graham et al., 2011; MacNeil et al., 2019; Ortiz et al., 2018). Some of these studies have examined how the dynamics of impact and recovery are influenced by anthropogenic stressors, management, depth, wave exposure, reef geomorphology and geography (Baker et al., 2008; Baumann et al., 2022; Claar et al., 2018; Connell, 1997; Graham et al., 2011; Lamy et al., 2016; Lotze et al., 2011). Potential links between impact and recovery and whether the state of a system at one point in time, for example, the amount of coral pre- or post-disturbance, might influence resilience has received less attention in quantitative syntheses.

While recovery has been investigated in linear frameworks in previous meta-analyses (Baumann et al., 2022; Bruno et al., 2019; Graham et al., 2011), it is clear that recovery is not linear. Various studies have demonstrated recovery lags post-disturbance (Dubois et al., 2019; Gouezo et al., 2020; Ortiz et al., 2018; Warne et al., 2021), which has led to recovery being modelled with logistic or Gompertz models (MacNeil et al., 2019; Mellin et al., 2019;

Thompson & Dolman, 2010; Warne et al., 2021). There are also examples of accelerating rates of recovery, in particular from very low coral cover (e.g. Connell et al., 2004; Edmunds, 2018; Gilmour et al., 2013).

The taxonomic and functional composition of reefs influences these processes (Adjeroud et al., 2009; Johns et al., 2014; Morais et al., 2021; Ortiz et al., 2021; Sandin et al., 2020), but even at a total cover resolution, determining variables that influence the shape of recovery trajectories, and identifying whether these trajectories can be predicted, is highly relevant as research efforts to understand how management and restoration may increase coral resistance and recovery (Johns et al., 2014; Kleypas et al., 2021; Warne et al., 2021).

Here, we compiled a global data set from 50 years of peer-reviewed literature on impact (resistance) and recovery of hard (scleractinian) coral from acute climate-mediated disturbances (short-lived events linked to climate): temperature stress events (heatwaves), storms (cyclones and severe storms) and run-off from flooding events. We assessed the influence of disturbance type and pre-disturbance coral cover on the magnitude of coral reduction following disturbance. We examined both annual recovery rate in the 5-year period following disturbance and recovery trajectory shape over longer time periods. We assessed whether covariates relating to the magnitude of the disturbance or coral cover before and after the disturbance explained variation in recovery rate. We tested for temporal changes in impact and recovery across the 50-year temporal span of the data, as well as several other covariates of interest. This study learns from past disturbances to provide new insight on coral reef resilience as we move to a future of novel disturbance regimes.

2 | METHODS

2.1 | Data compilation

Data were identified via electronic literature searches of the peer-reviewed literature on 17 March 2017 and updated on 27 June 2019. Data were extracted from the tables and graphs of publications that met selection criteria (see [Supplementary Information 1](#) for full data selection and extraction details). We focussed on the disturbances most directly linked to climate and considered temperature stress events (marine heatwaves), storms (cyclones and severe storms) and run-off events from high rainfall events resulting in flood plumes onto the study site.

Hard coral cover before, during and after disturbance was extracted. The closest data point prior to the disturbance was assigned as the pre-disturbance coral cover (C_{pre}), while the first measurement following disturbance was assigned as the post-disturbance coral cover (C_{post}). We assigned criteria on the distance between the disturbance and the pre- and post-disturbance measurements ([Supplementary Information 1](#)).

For time series data, all data points following a disturbance were examined as the ‘recovery trajectory’, up until the point where a secondary disturbance (that caused at least ~10% loss of pre-disturbance

cover) occurred. In cases where there were data for different regions, reefs, islands/atolls, sites, reef zones, depths and/or multiple disturbances within a publication or time series, data from these publications were divided into separate 'studies' (Supplementary Information 1). All studies were assigned to an 'ecoregion', 'province' and 'realm' based on their spatial location in Spalding et al.'s (2007) spatial classification system for coastal and shelf waters (Figure S4).

2.2 | Disturbance impact

We conducted mixed-effects meta-regression using the package *metafor* in R (Viechtbauer, 2010) to assess disturbance impact as change in coral cover resulting from disturbance. The response variable (effect size), $\ln RR_i$, was the log response ratio of pre- to post-disturbance percentage coral cover, C , for each study i , such that greater disturbance impacts corresponded to a greater $\ln RR_i$:

$$\text{Impact} = \ln RR_i = \ln \left(\frac{C_{\text{pre}_i} + 0.5}{C_{\text{post}_i} + 0.5} \right)$$

Studies were weighted by the inverse of the sum of the within- and among-study variances to give more weight to studies with more certainty in the impact of disturbance (see Supplementary Information 2).

Using mixed-effects meta-regressions, we individually investigated several covariates (Table 1) that were available across the large

majority of studies as moderators. We examined funnel plots to give an indication of publication bias in the base model.

2.3 | Recovery from disturbance

We investigated recovery from disturbances that resulted in a negative impact with magnitude $\ln RR_i > 0.1$ (which approximately equates to a 10% reduction in the pre-disturbance coral cover). This magnitude of impact may be considered relatively small (e.g. Connell, 1997 defined an ecologically significant decline to be 33% of the pre-disturbance cover), but we wanted to be conservative in retaining studies as we were interested in recovery across a gradient from 'small' to 'large' disturbance impacts.

2.4 | Recovery rate

We first considered an annual linear recovery rate to give an indication of the average speed of recovery. For consistency across studies, we examined an approximate 5-year time window following disturbance and calculated annual recovery rate in this window for each study. Five years was the median length of time series following disturbance (Figure S2). We required at least three data points spanning a time period of more than 4 years, with sampling

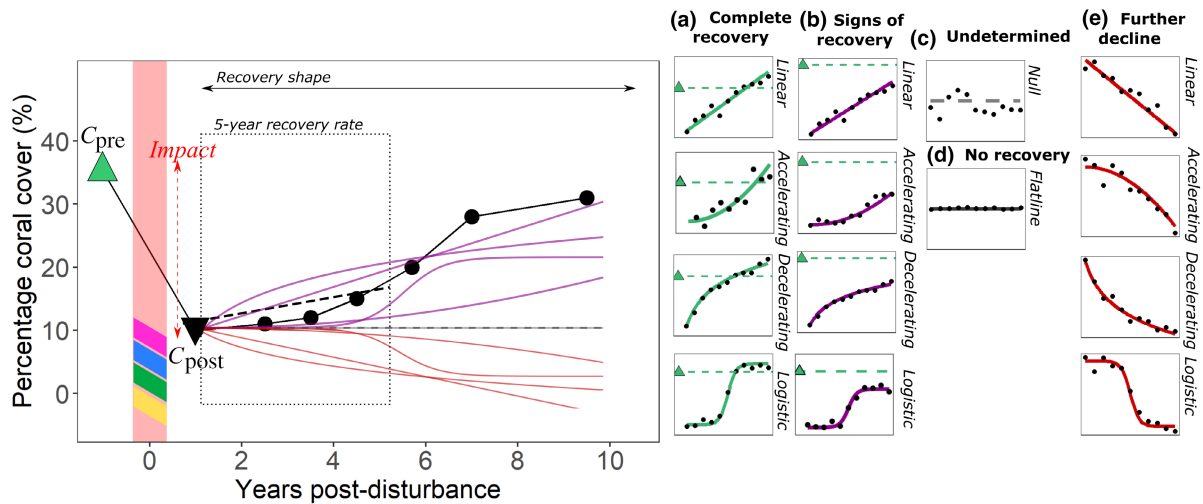


FIGURE 1 Schematic representation of the framework we used to investigate impact and recovery. Black data points are an example of the raw data from a single study that were extracted from any given publication, with the green triangular point representing coral cover pre-disturbance, C_{pre} . The red vertical shading in the left panel represents a disturbance, with coloured stripes indicating four disturbance categories—temperature, storm, run-off or multiple disturbances—which cause a reduction in coral cover to C_{post} (black triangular point). Recovery is analysed from the data points following the disturbance in two ways. First, as an annual recovery rate in the 5-year period following disturbance (black dashed line) by fitting a linear model to these data points. Second, in the recovery shape analysis, different models are fit to all available data points following disturbance and recovery is assigned a shape (linear, accelerating, decelerating, logistic, flatline or null) before being further categorized into one of the five recovery completeness categories shown on the right of the schematic: (a) complete recovery—coral is observed to reach its pre-disturbance coral cover, (b) signs of recovery—a positive trajectory but not reaching pre-disturbance cover in the time period examined, (c) undetermined—no clear pattern in recovery, the null model was the top model, (d) no recovery—the null model was the top model but the linear model had slope and standard error in slope near zero and (e) further decline—the top model had a negative trend. [Correction added on 18 October 2023, after first online publication: figure 1 has been updated in this version.]

having occurred within the 6.5 years following the disturbance (see [Figure 1](#)) else the study was not included.

We aimed to establish a comparable annual recovery rate across studies. To achieve this, we fit linear models to the time series following disturbance, with coral cover as the response variable and years since disturbance as the explanatory variable. This allowed us to derive a line-of-best-fit, with the slope representing the recovery rate. In this way we could use all available data points in the temporal window following disturbance, reducing the influence of any one data point in the time series. We extracted the slope (i.e. annual recovery rate as % coral cover year⁻¹) and its standard error from the model statistics for each study. The inverse of the latter was used in subsequent analyses to give a measure of confidence in the slope estimate (studies with fewer data points and more variability yielded higher standard errors). However, we were conscious of possible statistical violations arising from fitting a linear model to a response variable bounded by 0% and 100% (but note that the median maximum coral cover in the 5-year recovery time period was 22.6%). Therefore, we also considered two other approaches to calculating recovery rate (see [Supplementary Information 4](#)) and found similar results ([Figure S12](#)).

Similar to the impact analysis, using mixed-effects meta-regressions, we investigated several covariates that were available across the large majority of studies to understand their influence on recovery rate ([Table 1](#)). Models were weighted by the inverse of the standard error of the slope of the linear models used to obtain recovery rate. We examined funnel plots to assess publication bias in the base model.

2.5 | Covariates

We selected several covariates for which we had a clear associated question and for which the data set was appropriate for making robust conclusions (detailed in [Table 1](#)).

We were particularly interested in understanding potential relationships between impact and recovery, and whether coral cover at a study site before and after a disturbance influenced the recovery rate. We considered the 'state variables' of pre- and post-disturbance coral cover and disturbance impact separately as moderators, but we were also interested in potential interactions

TABLE 1 Covariates considered in meta-analyses for disturbance impact (I) and recovery rate (R). Columns detail the response variable, the name of the covariate, the range of values for continuous variables or the number of factor levels for categorical variables and the question associated with the covariate. C_{pre} is coral cover pre-disturbance and C_{post} is coral cover post-disturbance. Asterisks (*) indicate a variable was square-root transformed to reduce skewness.

Response variable	Covariate (moderator in meta-analysis)	Range/levels in factor (I = impact analysis; R = recovery analysis)	Question/reason for inclusion
I & R	Disturbance type	Temperature, storm, run-off (impact only), multiple	Do different disturbance types have different impact or recovery rates?
I & R	C_{pre}^*	0.5–100% (I) 0.5–79% (R) (Figure S13)	Is the magnitude of the disturbance impact influenced by the pre-disturbance coral cover? Is recovery rate influenced by the pre-disturbance coral cover?
I & R	Depth*	0.5–35m (I & R) (Figure S5)	Does disturbance impact decrease with depth? Is recovery faster in shallow sites?
I & R	Realm	Central Indo-Pacific, Eastern Indo-Pacific, Temperate Northern Pacific, Tropical Atlantic, Tropical Eastern Pacific, Western Indo-Pacific (Figures S4 and S10)	Are there differences in impact or recovery rate between realms?
I & R	Province	22 provinces (I) 13 provinces (R) (Figures S4 and S9)	Are there differences in impact or recovery rate between provinces?
I & R	Latitude (distance from equator)	0.58–28.2° latitude from equator (I) (Figure 2a)	Do disturbance impacts or recovery rates vary with distance from the equator?
I & R	Method	Photoquadrat, phototransect, in situ rapid assessment, in situ transect, in situ quadrat, video transect, aerial survey, manta tow, multiple	Does survey method influence observations of disturbance impact or recovery rate?
R	C_{post}^*	0–62% (R) (Figure S13)	Is recovery rate influenced by the post-disturbance coral cover?
R	C_{post}/C_{pre} (impact measure)		Is recovery rate influenced by both pre- and post-disturbance coral cover, or the interaction which describes disturbance impact?
I & R	Disturbance year	1966–2017 (I) 1966–2014 (Figure 2b,c)	Have disturbance impacts increased over time? Has recovery rate decreased?
C_{pre}	Disturbance year	1966–2017	How has the state of reefs changed over time?
C_{post}	Disturbance year	1966–2017	How has the state of reefs changed over time?

between these variables. We acknowledge some collinearity between these variables (as shown [Table S5](#)), so to account for this, we took an 'all-subsets' approach to the regressions (Kraha et al., 2012) to identify the most parsimonious combination of variables. We used the dredge function in R package *MuMIn* (Barton, 2009) and fit models in the *metafor* package to explore combinations of these predictor variables. Models were fit using 'maximum likelihood' for model selection, and then, the top models were refitted with 'restricted maximum likelihood', following protocol in Zuur et al. (2009). For comparisons between models, we selected a heuristic threshold of $\Delta AIC_c < 2$ and examined all models within this threshold (Anderson & Burnham, 2004).

With a study of this scale and complexity, we also needed to consider random effects to help account for any potential spatial and temporal autocorrelation. We considered different combinations of the geographic groupings (site, ecoregion, province, realm). Following the protocol suggested in Zuur et al. (2009), we selected between different nested combinations of these spatial groupings with the models fit using REML using AIC_c . The best random effect for the impact meta-regressions was determined to be for site nested in ecoregion nested in province ([Table S2](#)). Ecoregion would account for potential spatial autocorrelation of study sites while site would account for potential temporal autocorrelation of multiple studies at the same site. The best random effect for the recovery meta-regressions was determined to be ecoregion ([Table S3](#)). Ecoregion would account for potential spatial autocorrelation of study sites and there were few cases when there was more than one study at a site in the recovery analysis.

2.6 | Temporal changes in impact and recovery rate

We investigated whether there was any trend in the magnitude of disturbance impact, the annual recovery rate or in the pre- or post-disturbance coral covers, over the period from 1966–2017. For impact and recovery rate, we tested this using meta-regressions (as above) with disturbance year as a moderator. For pre- and post-disturbance coral cover as the response variable, we also used meta-regression and weighted these models by the inverse of the error in the mean for these values.

2.7 | Recovery trajectory shape

Assuming initial recovery was linear was useful as it allowed us to compare recovery across all studies in terms of the average annual recovery rate and to investigate this as a continuous response variable. Our second approach to analysing recovery considered recovery 'shape' to investigate a range of possible non-linear recovery trajectories. We investigated a set of qualitatively distinct, ecologically relevant, population growth trajectories by fitting five models—null, linear, logarithmic (decelerating), a simple second-order quadratic (accelerating) and logistic ([Figure 1](#), [Figure S6](#))—to the longest time series of data available following disturbance for each study individually. Coral cover was the response variable and

years since disturbance was the predictor variable. The null model was distinguished from a sixth 'flatline' recovery trajectory category if there was limited variation around the slope of the linear model fit to the same data ([Supplementary Information 3](#)). At least four data points were required in the recovery trajectory, the trajectory was required to span more than 4 years, and the trajectory needed to start within 1.5 years of the disturbance; otherwise, the study was not included in this analysis. We selected the model that best represented the recovery shape by modifying code in Thiault et al. (2017) (for another possible approach see Vercelloni et al., 2019), that is, based on 'relative likelihood', which is proportional to the probability that the model minimizes the (estimated) information loss. Relative likelihood was based on Akaike information criterion (AIC), though we also investigated AIC corrected for small sample sizes (AIC_c) and Bayesian information criterion (BIC; Anderson & Burnham, 2002; [Supplementary Information 3](#)).

We further classified the recoveries into five categories of recovery 'completeness' through reference to the pre-disturbance coral cover: (a) complete recovery, (b) signs of recovery, (c) undetermined, (d) no recovery and (e) further decline ([Figure 1](#)). Complete recovery was only classified in the case when the final data point in the study was equal to or greater than 90% of the pre-disturbance cover. If a study had a positive trajectory but it did not reach this level, or there was no pre-disturbance measurement available, then it was classified as 'signs of recovery'.

3 | RESULTS

Our database spans 54 degrees of latitude from 26°S to 28°N ([Figure 2a](#)) with studies from 1966 to 2017. A list of the data sources can be found in [Appendix 1](#).

3.1 | Disturbance impact

The average magnitude of disturbance impact, as measured with the log response ratio of coral cover pre- to post-disturbance, $\ln RR$, was 0.73 (± 0.24); 95% CI, which can be interpreted as disturbances on average reducing pre-disturbance coral cover by 62.3%. As expected, there was large heterogeneity in this response ($Q_T = 333,317$, $df = 426$, $p < 0.001$), indicating high variability between studies, and including cases when coral cover was higher post- than pre-disturbance ([Table S4](#)). Run-off and multiple disturbances, on average, had a greater impact than temperature and storm disturbances ($Q_M = 22.8$, $df = 3$, $p < 0.001$, [Figure 3](#), [Table S4](#)), although noting that the first two disturbances have less samples.

Greater disturbance impacts tended to be measured when pre-disturbance coral cover was higher $\ln RR = 0.12 (\pm 0.05) \times \sqrt{C_{pre}} + 0.08 (\pm 0.37)$, 95% CI, ([Table S4](#)). We did not detect a significant difference in disturbance impact with site depth, or across different survey methods ([Table S4](#)). No differences between realms or with latitude were detected ([Table S4](#)). We tested for province as a fixed effect

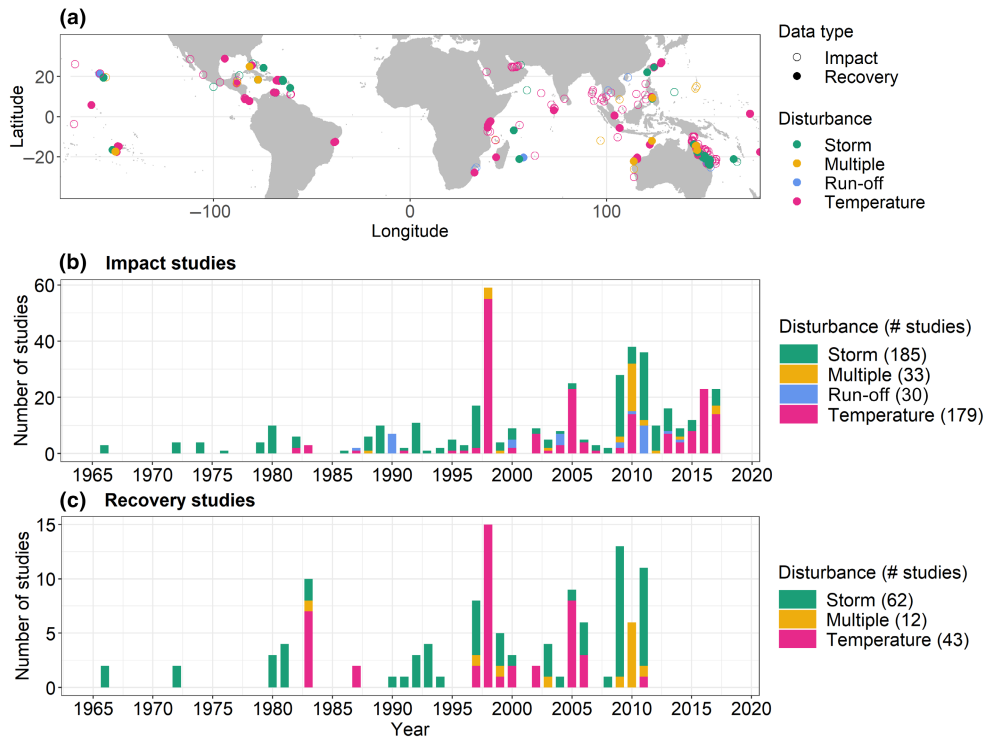


FIGURE 2 Distribution of studies: (a) Spatial distribution of studies showing study location with colour indicating the category of disturbance. Open circles show locations with impact data and closed circles show locations with recovery data. Temporal distribution of disturbances included in (b) impact and (c) recovery rate analyses. The number of studies available for analysis is given in the legend in brackets.

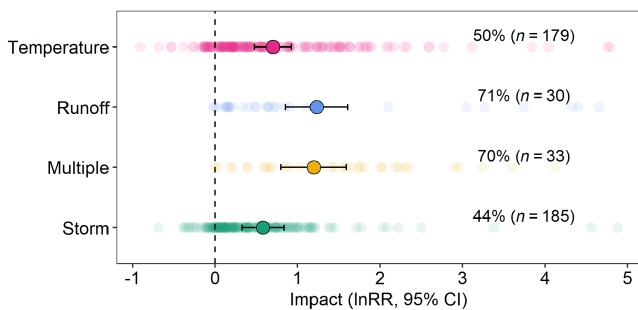


FIGURE 3 The weighted mean impact ($\pm 95\%$ CI), as log response ratio $\ln RR$ for each disturbance type, as determined from meta-regression. Shaded points are the raw $\ln RR_i$ for each study. The dashed line indicates where pre-disturbance coral cover is equal to post-disturbance coral cover, that is, no measured impact of disturbance. Impacts increase along the x-axis. For example, a $\ln RR$ of 1 means there was $\exp(1) = 2.72$ times more coral cover pre-disturbance compared to post-disturbance, that is, a 64% reduction of the pre-disturbance cover occurred. Text showing percentages indicate the mean reduction in pre-disturbance coral cover, followed by the number of studies in each disturbance category in brackets.

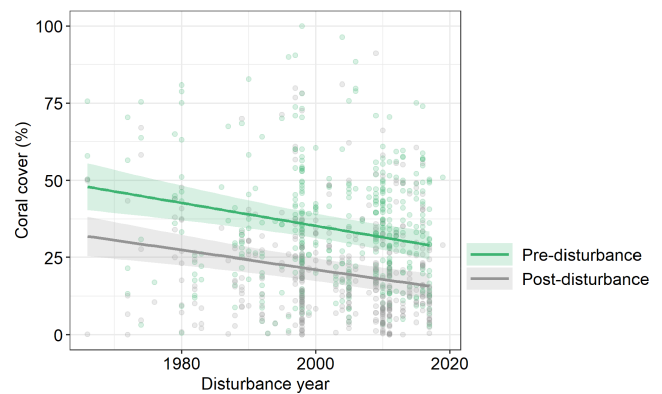


FIGURE 4 Relationship between disturbance year (1966–2017) and the pre- and post-disturbance coral cover.

coral cover $C_{\text{post}} = -0.32 (\pm 0.14) \times \text{Year} + 652 (\pm 282)$, 95% CI, were found to decline significantly across the time period (Table S4, Figure 4).

Funnel plots are provided in Figure S8 as a way to investigate publication bias. As expected, given it was more probable that a study would be published for large or drastic impact or recoveries, there was some indication of publication bias influencing the distribution of studies, but to an acceptable extent given the nature of the data set. We also expected more studies in more recent years, due to an increase in funding and monitoring programmes for coral reefs. Higher counts of studies in certain years (Figure 2b,c) can be partly

and found significant differences in impact in different provinces (see Figure S9).

No significant trend in the magnitude of disturbance impact was detected across the temporal period 1966 to 2017 (Table S4). However, both pre-disturbance cover $C_{\text{pre}} = 0.37 (\pm 0.17) \times \text{Year} + 781 (\pm 344)$, 95% CI, and post-disturbance

explained by the occurrence of three pan-tropical El Niño events causing mass coral bleaching in 1998, 2010 and 2016 (Hughes et al., 2018). Understandably, the last event has not yet accumulated as much literature as the former two at the time of the present study.

3.2 | Recovery rate

The mean annual recovery rate in the 5-year window following disturbance was 1.41% coral cover year⁻¹ (±0.63, 95% CI) and there was significant heterogeneity in this effect ($Q_T=822.5$, $df=109$, $p<0.001$; Table S4). 81% of the 110 studies had positive slopes and the remaining 19% had negative slopes (Figures S11 and S17).

The variables disturbance type, depth, disturbance year, latitude and method did not explain significant heterogeneity in the annual recovery rate (see all model statistics in Table S4). Individually, pre-disturbance cover did not explain significant heterogeneity either, while post-disturbance cover and the ratio of pre- to post-disturbance cover (i.e. impact, Figure 5b) were found to explain significant heterogeneity (Table S4). Faster recovery rates were correlated with lower post-disturbance coral cover ($\text{rate} = 0.27 (\pm 0.24) \times \sqrt{C_{\text{post}}} + 2.45 (\pm 1.09)$, 95% CI, Table S4). However, as we had the hypothesis that the state variables may interact to help explain recovery rate we also examined pre- and post-disturbance coral cover in an all-subsets approach to determine the combination of these variables that best explained recovery rate. Two top models within 2 ΔAICc were identified, and just one according to AIC (Table 2). The top model included coral cover pre- and post-disturbance, and the magnitude of the impact (modelled as $\left(\frac{C_{\text{post}}}{C_{\text{pre}}}\right)$) (Table 3). This combination of moderator variables explained significant heterogeneity ($Q_M=21.0$, $df=3$, $p<0.001$), but there remained significant residual heterogeneity ($Q_E=707.8$, $df=106$, $p<0.001$), indicating that other factors are also important. The next top model, in which recovery rate was predicted by disturbance impact, also explained

significant heterogeneity, but less than the combination of variables in the top model ($Q_M=14.4$, $df=1$, $p<0.001$, Table 2).

The top model revealed a parabolic-shaped relationship between post-disturbance coral cover and recovery rate, which depended on both the pre-disturbance coral cover and the size of the disturbance impact (Figure 5a, Table 3). Fastest recovery was predicted to occur when approximately two-thirds to three-quarters of the pre-disturbance cover was lost. If more than this was lost, recovery rate became constrained, resulting in slower recovery rates (Figure 5a). In other words, the fastest recovery was predicted for intermediate to large disturbance impacts, not for small disturbance impacts nor for very large impacts that removed most of the pre-disturbance cover. The second top model (Figure 5b) did not detect this second component and rather predicted faster recovery for greater disturbance impact.

Our analyses also revealed that both province and realm explained significant heterogeneity in recovery rate, indicating recovery rate varied geographically (Table S4, Figures S9 and S10). Of note was that the Tropical Atlantic realm was found to have the slowest recovery rates. At the ecoregion resolution, fastest rates were in South East Polynesia, the Tropical Southwestern Pacific, the Western Indian Ocean and the Northeast Australian Shelf, alongside some others that had very small sample sizes. Slowest recoveries were found in the Tropical Northwestern Atlantic and Hawaii ecoregions.

3.3 | Recovery shape

The top predictive models for 5-year recovery rate indicated non-linear drivers of recovery (Figure 5) and the recovery shape analysis allowed us to further investigate these non-linearities. One hundred and seventeen recovery trajectories were examined. AIC and BIC selected a similar set of 'best shapes', whereas the AICc selection

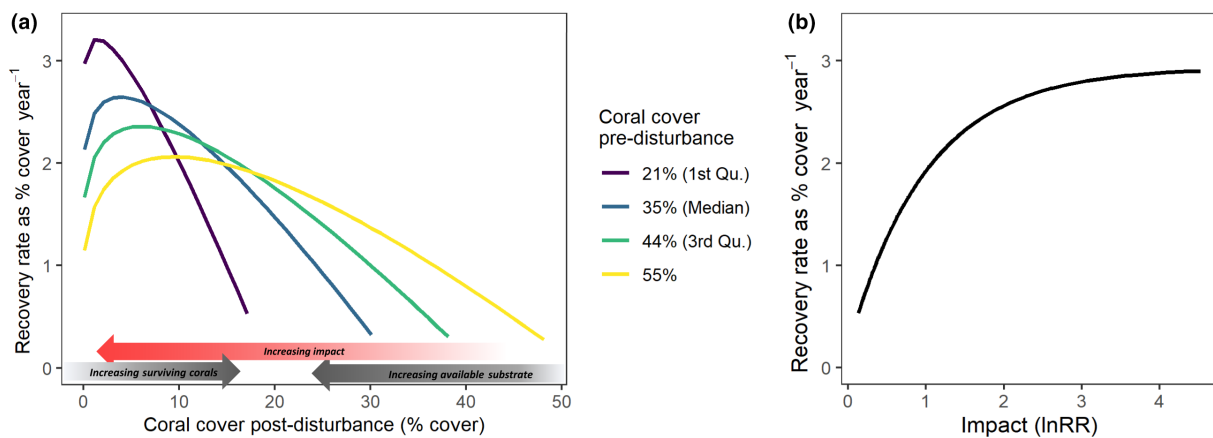


FIGURE 5 Predicted 5-year recovery rate from (a) the top model, as a relationship with pre- and post-disturbance coral cover, and (b) the next top model, shown as a relationship with disturbance impact. In (a), different colours indicate predictions for different values of pre-disturbance coral cover (1st quartile, median, 3rd quartile and a high value of 55% cover). The arrows along the x-axis are to aid interpretation of potential mechanisms causing the shape of the relationship: There are generally larger impacts as you move from right to left along the x-axis (red arrow) which creates more substrate available for coral growth and settlement; conversely, there are more surviving corals as you move from left to right along the x-axis as post-disturbance coral cover is higher (see Section 4 for further interpretation).

TABLE 2 Top three of a total eight variable combinations compared in the all-subsets analysis, detailing delta AICc, weighted AICc, AIC, weighted AIC and degrees of freedom. Bold text indicated the model was within 2 AICc/AIC. C_{pre} is coral cover pre-disturbance and C_{post} is coral cover post-disturbance. The full table is provided in Table S6.

Model	$\Delta AICc$	$\omega AICc$	ΔAIC	ωAIC	df
rate ~ Intercept + sqrt(C_{post}) + $\left(\frac{C_{post}}{C_{pre}}\right)$ + sqrt(C_{pre})	0.00	0.53	0.00	0.58	7
rate ~ Intercept + $\left(\frac{C_{post}}{C_{pre}}\right)$	1.71	0.23	2.23	0.19	5
rate ~ Intercept + $\left(\frac{C_{post}}{C_{pre}}\right)$ + sqrt(C_{pre})	2.50	0.15	2.78	0.15	6

TABLE 3 Model estimates and statistics for the top annual recovery rate models fit with REML.

Variable	Estimate	95% CI	p-value
Model 1: rate ~ Intercept + sqrt(C_{post}) + $\left(\frac{C_{post}}{C_{pre}}\right)$ + sqrt(C_{pre}) + 1 Ecoregion (Figure 5a)			
Intercept	6.06	2.69	<0.0001
sqrt(C_{post})	0.73	0.64	0.02
$\left(\frac{C_{post}}{C_{pre}}\right)$	-6.66	3.52	0.0002
sqrt(C_{pre})	-0.68	0.54	0.012
Model 2: rate ~ Intercept + $\left(\frac{C_{post}}{C_{pre}}\right)$ + 1 Ecoregion (Figure 5b)			
Intercept	2.93	0.97	<0.0001
$\left(\frac{C_{post}}{C_{pre}}\right)$	-2.74	1.41	<0.0001

resulted in more null and flatline models, though the proportions of the other shapes were comparable (Figure S18). Visual inspection of the model fits to the data indicated that the AIC fits were reasonable (Figure S18) and so AIC was used for classification. All recovery categories were observed at least once (Figure 6). Positive trajectories were found in 72.6% of studies (43.6% complete recovery, 29.0% showing signs of recovery), negative trajectories in 17.9%, no recovery in 7.7% and in 1.7% of studies recovery was undetermined (Figure 6a). The most common recovery shapes observed were logistic (24.8%) and accelerating (27.4%), both which imply a slower recovery rate immediately following disturbance that will increase over time. The proportion of each recovery type was different for each of the disturbance types, with, for example, decelerating shapes more common for temperature disturbances than for other disturbances (Figure 6c).

4 | DISCUSSION

We compiled a global data set of coral cover dynamics surrounding acute climate-mediated disturbance, which allowed investigation of general patterns in resistance and recovery and the interplay between these components of resilience. We identified a relationship between impact, recovery and pre- and post-disturbance reef state, which indicated that fast recovery rates were likely for intermediate

to large disturbance impacts, whereas recovery rate declined for very large disturbance impacts. This showed that the state of a coral system pre- and post-disturbance influences the recovery rate in complex but potentially predictable ways. Despite not detecting a change in the average disturbance impact over time, we found long-term temporal declines in the pre- and post-disturbance states in terms of coral cover. Non-linearities in recovery trajectories, with slower recovery closer to the disturbance (52% of studies had either accelerating or logistic recovery shapes), in combination with predictions of increasing disturbance frequency (Hughes et al., 2018), mean that even if fast recovery is possible, full recovery may be unlikely to occur before a secondary disturbance. The database included cases of full and relatively rapid recovery following large losses in coral cover (e.g. Connell et al., 2004; Edmunds, 2018; Gilmour et al., 2013) and 44% of studies were classified as realizing complete recovery to pre-disturbance cover, demonstrating that corals can exhibit strong recovery from acute disturbances, at least according to the 'total coral cover' metric. However, this was by no means ubiquitous, as in 27% of studies, no recovery or negative trajectories were observed.

Despite high variation in the impact and recovery of corals to disturbance, we identified a significant parabolic relationship between pre- and post-disturbance coral cover and 5-year recovery rate. The relationship between the state variables and recovery rate expands on previous work. Connell (1997) investigated both whether higher coral cover before disturbance influenced recovery, and if

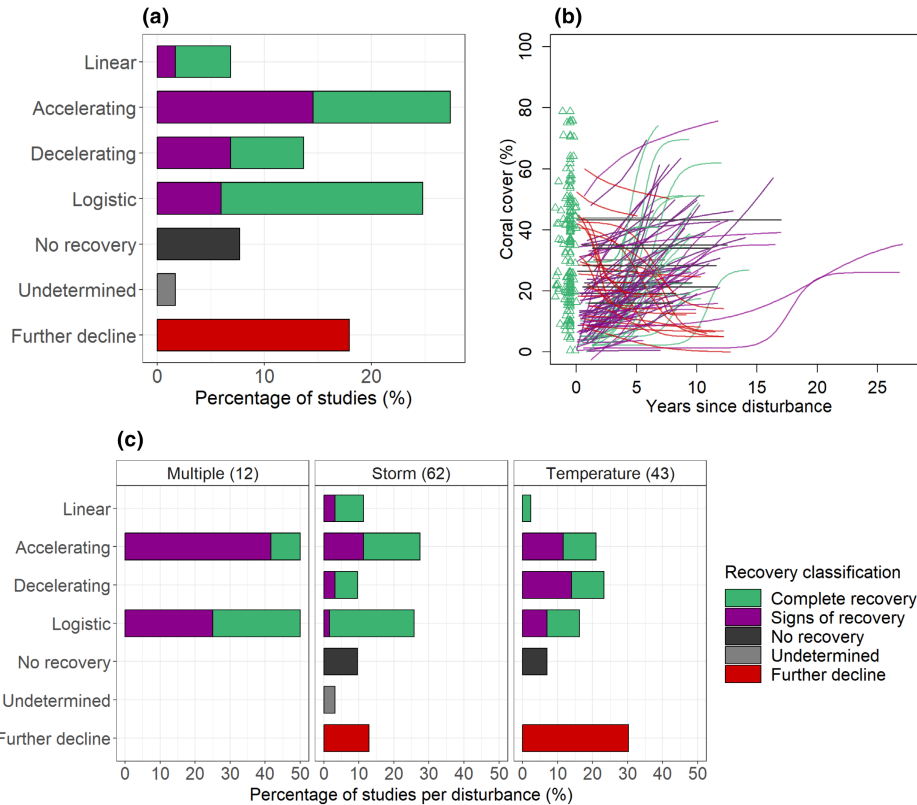


FIGURE 6 Coral recovery shape classifications. (a) Percentage of studies classified to each 'recovery shape category' based on AIC selection criteria. All shapes with negative trajectories are grouped under 'further decline'. Bars are broken into the 'recovery completeness categories' as shown by different colours (refer Figure 1). (b) Visualization of best fit recovery trajectory shape predicted across the span of available recovery data for each study. The pre-disturbance data points are shown by green triangular points. (c) Same as in (a) but divided into the three disturbance types for which recovery data were available. Numbers in brackets give sample size for each disturbance type.

greater loss of coral was associated with slower recovery, but did not find evidence to support these hypotheses. Zhang et al. (2014) and Baumann et al. (2022) found that coral recovery was positively influenced by pre-disturbance coral cover, with reefs that had high pre-disturbance coral cover recovering faster than those with lower cover. Graham et al. (2011) showed a relationship between recovery rate and post-disturbance coral cover that is similar to that of the present study, with highest recovery rates for intermediate levels of post-disturbance coral cover. The modelled relationship in our study provided greater insight on this theory, showing recovery rate can be influenced by pre- and post-disturbance coral cover, and the relationship between these two variables which defines the disturbance impact magnitude.

One interpretation of the relationship between the state variables and recovery rate is that two opposing demographic mechanisms are at play: growth and reproductive potential of locally surviving corals, and space limitation. We suggest the first is the controlling mechanism when disturbance impact is relatively high, creating free space for potentially high recovery rates with limited competition for space. In such cases, even slight increases in the number of surviving corals can result in greater potential for local growth and reproduction (Gilmour et al., 2013). Of course, larvae supply from surrounding undisturbed reefs will also influence this

rate, but in general, recruitment-driven recovery would be lagged compared to recovery as a result of the growth of surviving colonies (Gouezo et al., 2020), but see Edmunds (2018). We suggest the second mechanism, space limitation (Connell, 1978; Hughes & Jackson, 1985), becomes the greater control on recovery rate when coral cover post-disturbance remains high relative to pre-disturbance cover, and there is competition and limited space in the benthic community for fast growth or settlement or corals, despite there being generally more coral survivors that can grow and reproduce. In this sense, we suggest pre-disturbance coral cover is acting as a coarse proxy for the carrying capacity of the system, though this would be highly influenced by the recent disturbance history. The median pre-disturbance coral cover (35%) could be considered lower than we would expect for space limitation to be taking strong effect, but this is not an uncommon average coral cover for reefs (Gudka et al., 2023; Osborne et al., 2011). Nonetheless, more targeted studies are needed to identify the mechanisms underlying the relationship between recovery rate and the reef state pre- and post-disturbance.

Recovery lags were common, as indicated by logistic and accelerating recovery shapes being the most common, but not ubiquitous, as the decelerating and linear shape were also observed. The presence of recovery lags is supported by previous findings (Gouezo

et al., 2020; Mellin et al., 2016; Ortiz et al., 2018; Wilkinson, 1999) and the use of Gompertz models for modelling coral recovery (MacNeil et al., 2019; Mellin et al., 2019; Thompson & Dolman, 2010). Warne et al. (2021), who identified a 'two-phase' recovery pattern in 60% of severely disturbed reefs on the Great Barrier Reef, suggested that corals may be recovering more slowly for 3–4 years after major disturbance. Ortiz et al. (2021) suggest one explanation for this is that tabular colonies reach a size after several years that then triggers fast increases in cover due to their morphology. Recruitment limitation can also explain recovery lags (Gilmour et al., 2013; Holbrook et al., 2018).

We did not find significant differences in recovery rate between the disturbance types, which we expected given recovery processes are known to vary between disturbances (Bellwood et al., 2006; Gardner et al., 2005; Graham et al., 2006, 2015). However, not being able to directly control for disturbance intensity across studies likely limited our capacity to detect differences between disturbance types. Other meta-analyses (Baumann et al., 2022; Graham et al., 2011; Vercelloni et al., 2019) have not found strong differences either. We did find that recovery from temperature disturbances was more commonly classified as the decelerating shape, indicating recovery slowing over time. One explanation for this could be that new coral recruits settle on corals that died from temperature stress, and then, these dead coral structures later break down or topple (Schuhmacher et al., 2005). Another contributing mechanism may be the prolonged impacts of temperature stress events on the physiology and reproductive potential of the remaining corals (Ainsworth et al., 2016; Suggett & Smith, 2020; Van Woessik et al., 2022).

We were limited to examining total coral cover in the present study, but the taxonomic and functional composition undoubtedly influenced the observed dynamics in total coral cover, as shown by previous studies (Adjeroud et al., 2009; Johns et al., 2014; Morais et al., 2021; Ortiz et al., 2021; Sandin et al., 2020; Vercelloni et al., 2019). For example, a shift in coral composition could explain some cases of fast recovery from large impacts, as the freeing up of space may allow 'weedy' coral species to grow quickly (Darling et al., 2013). The data set contained various instances where recovery took the coral cover to much higher values than the pre-disturbance cover. This type of overshoot has also been observed following recent disturbances on the Great Barrier Reef (Emslie, 2021). Demographic taxonomic and functional type analyses are needed to understand what processes are driving this (Edmunds et al., 2014; Edmunds & Riegl, 2020). Recovery of total coral may belie community reassembly or occur over different time periods (Gouezo et al., 2019; Johns et al., 2014). Greater disturbance impacts were correlated with higher pre-disturbance coral cover, which has also been found in previous meta-analyses (Baumann et al., 2022; Zhang et al., 2014). Coral community composition could also be a driver of this, for example, plating acroporids can achieve high coral cover but are also sensitive to disturbances. A shift in community composition resulting from past disturbance may also influence future resilience through changed recruitment patterns (Roff, 2021).

Increasing evidence suggests that the ability of reefs to recover from disturbances is decreasing due to a combination of the legacy effects of previous disturbances and the cumulative effects of chronic pressures (Bruno & Selig, 2007; Côté et al., 2016; Mellin et al., 2019; Ortiz et al., 2018; Osborne et al., 2017). Other work has shown that coral assemblages can exhibit environmental 'memory' which may increase their resistance to subsequent disturbances (Brown et al., 2015; Hackerott et al., 2021; Hughes et al., 2019; Lachs et al., 2023), but not indefinitely (Ainsworth et al., 2016). We did not find a significant temporal trend in disturbance impact magnitude or recovery rate across the 50 years examined; however, both pre- and post-disturbance coral covers declined through time. This speaks to either a chronic decline (Bruno & Selig, 2007) or a disturbance frequency that means recovery cannot occur completely before a secondary disturbance. These declines also represent a shifting baseline (Gudka et al., 2023) with consequences for the resilience to future disturbances.

The 5-year mean linear recovery rate we calculated, 1.41% coral cover year⁻¹, was comparable to rates found in Baumann et al.'s (2022) meta-analysis but lower than averages for other reef systems (Gilmour et al., 2013; Graham et al., 2011; Holbrook et al., 2018; Thompson & Dolman, 2010). We only considered the 5-year period following disturbance, and given non-linear recovery patterns shown in the recovery shape analysis and previous studies, this is generally the period of slowest recovery. We found that geographical groupings from Spalding et al. (2007) explained some variation in this rate (Figures S9 and S10). For example, recovery rates were slowest in the Tropical Atlantic realm. Roff (2021) and Roff and Mumby (2012) explore some of the mechanisms behind reefs in this region having lower resilience compared to the Indo-Pacific reefs, including species composition and diversity, macroalgae, recruitment and growth, nutrient levels and herbivory. We also included cases of decline in our calculation of the average rate. We individually examined the studies showing further decline after disturbance (7.7% of studies did not show any sign of recovery, and 17.9% showed further decline). Each decline could generally be explained by one or more of: additional stressors or disturbances (Gardner et al., 2005), recruitment limitation (e.g. Holbrook et al., 2018; Hughes & Tanner, 2000), a shift in the coral assemblage (Adjeroud et al., 2009; Johns et al., 2014), a phase shift (e.g. to algae; Mumby et al., 2013) or a more general backdrop of chronic decline.

It is challenging to draw strong conclusions regarding coral resistance, or the relative roles of resistance and recovery, without consistent quantification of disturbance intensity. However, the large variation in impact and recovery dynamics included in this data set shows that both have been important. Perfect resistance would mean no disturbance impacts and there would be no need for recovery. Perfect recovery would mean resistance was less important (although depending on recovery time and disturbance frequency). Yet such cases are rare, and therefore, reef resilience as investigated in the study period here, 1966–2017, has been a combination of resistance and recovery processes (also see Baumann et al., 2022). Fastest recovery was predicted for cases of intermediate to high

disturbance impact, which could be interpreted as faster recovery compensating for weaker resistance, but further work including quantification of disturbance intensity and disturbance history is needed to disentangle such relationships.

This study has provided a quantitative summary of the knowledge base of 50 years of research on disturbance dynamics in coral reefs in the context of a future characterized by novel disturbance regimes. We learned from past disturbances while recognizing that resilience to disturbance is changing as disturbance regimes change, which may shift the balance between resistance and recovery (Ainsworth et al., 2016; Côté & Darling, 2010). We showed that the base state of coral reef systems is changing, a shifting baseline with consequences for resilience to future disturbances due to the relationships identified between impact, recovery and the pre- and post-disturbance reef state. Updating this analysis as more data emerge over the next decade in relation to recent global bleaching events will be important to better understand how disturbance dynamics are changing as the disturbances change drastically in frequency, intensity, duration and spatial extent.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available as Table S1 at <https://doi.org/10.5061/dryad.rfj6q57gz>. These data were derived from the resources available in the public domain with references detailed in Appendix 1.

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