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Legacy effects of anthropogenic disturbances modulate dynamics in the world's coral reefs

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Abstract

Rapidly changing conditions alter disturbance patterns, highlighting the need to better understand how the transition from pulse disturbances to more persistent stress will impact ecosystem dynamics. We conducted a global analysis of the impacts of 11 types of disturbances on reef integrity using the rate of change of coral cover as a measure of damage. Then, we evaluated how the magnitude of the damage due to thermal stress, cyclones, and diseases varied among tropical Atlantic and Indo-Pacific reefs and whether the cumulative impact of thermal stress and cyclones was able to modulate the responses of reefs to future events. We found that reef damage largely depends on the condition of a reef before a disturbance, disturbance intensity, and biogeographic region, regardless of the type of disturbance. Changes in coral cover after thermal stress events were largely influenced by the cumulative stress of past disturbances and did not depend on disturbance intensity or initial coral cover, which suggests that an ecological memory is present within coral communities. In contrast, the effect of cyclones (and likely other physical impacts) was primarily modulated by the initial reef condition and did not appear to be influenced by previous impacts. Our findings also underscore that coral reefs can recover if stressful conditions decrease, yet the lack of action to reduce anthropogenic impacts and greenhouse gas emissions continues to trigger reef degradation. We uphold that evidence-based strategies can guide managers to make better decisions to prepare for future disturbances.

KEYWORDS
climate change, cumulative stress, cyclone, ecological memory, initial ecosystem state, thermal stress

1 | INTRODUCTION

Coral reefs are the most biodiverse marine ecosystems in the world and provide key services that support human well-being such as protecting coasts, providing habitats for commercially important species, and producing sediments (Moberg & Folke, 1999). The benefits of these services are intimately linked to the capacity of scleractinian corals to accumulate calcium carbonate and create complex three-dimensional structures (Woodhead et al., 2019). However, coral reefs currently exist in environments dominated by human activities, which has affected natural disturbance regimes. The influence of anthropogenic activities on these regimes has created compound perturbations, which have resulted in the rapid decline of corals in many reefs around the world (Bellwood et al., 2019; Hughes, Kerry, Connolly, et al., 2019; Williams et al., 2019).

There are multiple drivers of coral reef degradation, which inherently vary in intensity, spatial scale damage, and frequency (Nyström & Folke, 2001). Climate change is a major driver of coral loss. For example, elevated thermal stress that manifests as mass bleaching events has resulted in coral cover and reshaped coral assemblages worldwide (Hughes, Kerry, et al., 2018). Climate change also alters the frequency, intensity, and spatial scales of other disturbances (Emanuel, 2021; Hughes, Anderson, et al., 2018). For example, cyclones, which have shaped reef ecosystems over geological time scales (e.g., Medina-Valmaseda et al., 2022), are becoming more severe and frequent, which has contributed to coral decline (Mudge & Bruno, 2021; Wang et al., 2022). As climatic conditions continue to rapidly change, the intensity of thermal stress events and cyclones will increase while the intervals between these events appear to be shrinking (Hughes, Anderson, et al., 2018; Mudge & Bruno, 2021).

However, climate change is not the only threat to the integrity of coral reefs. Many other disturbances have been linked to widespread coral mortality and ecological phase shifts at both local and regional scales such as coral disease, coastal eutrophication, fishing pressure, and crown of thorn starfish outbreaks (Hughes et al., 2010; Vega Thurber et al., 2014; Vercelloni et al., 2017). In the tropical Atlantic, coral disease is a leading driver of the major declines of important reef-building corals with drastic consequences for reef functionality (Alvarez-Filip et al., 2022). At smaller spatial scales, acute disturbances, such as dredging or grounding, physically damage coral colonies while increasing turbidity and sedimentation in the water column with devastating consequences (Erftemeijer et al., 2012). Given the multiple existing threats to reef integrity, it is critical to understand how reef dynamics across large spatial scales are impacted as pulse-like stressors transition into more persistent forms of stress.

In addition to the contemporary environment, the legacy effects of past disturbances shape ecological dynamics, the recovery potential of reefs, and ecosystem resilience (Hughes, Kerry, Connolly, et al., 2019; Peterson, 2002). Commonly, the mounting stress of multiple transient disturbances impairs reef recovery and compromises reef functionality (Bowman et al., 2015; Ortiz et al., 2018). This is the case in the tropical Atlantic region, where many reefs exhibit compositional shifts in coral communities that are characterized by a lack of recovery of key reef-building species and a newfound dominance of opportunistic species, many of which are relatively tolerant to changing environmental conditions (González-Barrios et al., 2021; Molina-Hernández et al., 2020). However, the cumulative stress of past disturbances is also a key determinant of the responses of organisms and ecological communities to stress. This is known as the ecological memory of previous events and can be generated by various biological mechanisms, including acclimatization, adaptation, or even shifts in species composition (Drury & Greer, 2022; Nyström & Folke, 2001). In the Great Barrier Reef, it has been recently shown that the severity of coral bleaching depends on the heat exposure of previous thermal stress events (Hughes, Kerry, Connolly, et al., 2019). It has also been observed that reefs that have been impacted by thermal stress exhibit less bleaching in subsequent thermal stress events (Hughes et al., 2021). This raises the question of whether reef integrity, which is often defined as coral cover, can also be modulated by the cumulative impact of past disturbances. Thus, reefs that have experienced cumulative disturbances may be predisposed to respond more favorably to future disturbance events than reefs that have not.

In a context of rapidly increasing human pressures (Williams et al., 2019), it is critical that we understand the consequences of different forms of stress and how reefs in different ecoregions respond to the cumulative stress of multiple climate-driven disturbances such as coral thermal stress events and cyclones. To gain insights into the effects of disturbances on reef integrity, we first used a quantitative-based approach to conduct a global analysis of the impacts of 11 types of acute disturbances on reef integrity using initial coral cover as a means to gauge the resulting damage. Then for thermal stress and cyclones, the most data extensive disturbances, we evaluated (i) the manner in which the magnitude and extent of the damage caused by these disturbances varied according to the intensity of the disturbance, (ii) whether cumulative stress exerted a legacy effect on reef response, and (iii) whether coral reefs are still capable of recovering in the absence of cumulative stress due to multiple disturbances. To explore these questions, we compiled an extensive global data set composed of studies that measured changes in coral cover after large-scale disturbances, such as storms, predator outbreaks, thermal stress, or disease, and local-scale events such as oil spills or grounding.

2 | METHODS

2.1 | Data collection

We used peer-review and synthesis articles to identify acute disturbances (i.e., short-term stochastic events) that were reported as the main drivers behind changes in coral cover (e.g., Ban et al., 2014; Wilkinson, 1999). We identified 11 types of disturbances that were commonly referred to in the literature and had clear start and end times (Figure 2a; Table S1). The effects of these drivers could thus be evaluated with before and after comparisons (*often referred as Before-After Control-Impact analysis*). Some disturbances had very clear and descriptive names, which were adopted (i.e., *Acanthaster* and cyclones). In addition, others had different origins but similar characteristics or effects and were thus grouped into a single category (i.e., flood events or coastal runoff; Table S1).

To better understand the effects of disturbances, we did not include data of chronic stressors (longer-term underlying sources of stress) or those with unclear temporal delimitations (e.g., coastal development, watershed-based pollution, or fisheries pressure). We then conducted a systematic electronic literature search to identify the primary literature of the effects of these

11 disturbances on coral cover. Our systematic assessment followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses guidelines (Appendix S1). This resulted in a total of 157 documents that identified the disturbance and reported mean coral cover at the reef-site level for at least two well-defined dates (Figure S1). From these documents, we obtained the survey years, type of disturbance, and coral cover estimates (before and after a given disturbance). When available, we also recorded the sample size, variance estimator, depth, and site coordinates of the study. Data were collected from the text, tables, supplementary data, and graphs (in most cases), which were extracted using Web Plot Digitizer (Rohatgi, 2020). This tool has been proven to facilitate accurate and timely data extraction by producing results that show small absolute differences with respect to the true values while exhibiting excellent consistency (Burda et al., 2017). When geographic coordinates were not provided, we obtained them from Google Earth based on the location descriptions in either the maps or text.

Many studies covered multiple years (i.e., time series), and in some cases, the same time series included the effects of different disturbances. Therefore, we decided to use the term *risk-sets*, which is defined as a specific period in the times series that includes information of coral cover from before and after a disturbance. *Risk-sets* formed the sampling units of our analyses. When a secondary disturbance occurred within one time series, a new risk-set was created with well-defined pre- and post-disturbance coral cover. For studies with long-term time series that included multiple disturbance events, we defined the before values as the data points closest to the impacts of the disturbances for each risk-set.

We removed the risk-sets from the analyses that contained (a) initial coral cover estimates below 5%, (b) unreliable sample sizes, or (c) multiple disturbances within the same period. We did not consider time series that had initial live coral cover values below 5% because these low coverage values could not be related to any previous disturbance. Furthermore, coral communities with cover values below 5% are likely representative of non-accretional habitats or alternative states (e.g., hard grounds, seagrasses, or gorgonian fields; see Perry et al., 2013) and are therefore not representative of the objectives of this study. To ensure adequate and reliable representation of a study area, we also did not consider risk-sets with less than three replicates per survey period (Hill & Wilkinson, 2004). Given that it was not possible to separate the effects of multiple disturbances that occurred within the same period (e.g., a bleaching event and a cyclone), we also did not consider risk-sets that met this third criterion.

A total of 1000 time series and 1609 *risk-sets* from 136 studies (for a full list of references, see Appendix S2) remained in our database after evaluating the three criteria. In 90% of risk-sets, 3 years or less had elapsed between the starting and end points of a disturbance. The data set is publicly available in a DRYAD repository (González-Barrios et al., 2023).

2.2 | Intensity indicators

We used the intensity of each thermal stress and cyclone event in our database to evaluate the manner and extent to which the magnitude of thermal stress and cyclone damage varied according to disturbance intensity.

To evaluate thermal stress intensity, we used degree heating weeks (DHW), which has been widely used to evaluate heat stress in reef systems (Eakin et al., 2010; Hughes, Anderson, et al., 2018). We obtained DHW values from the NOAA Coral Reef Watch product (CRW, V 3.1) and estimated the thermal stress intensity for each risk-set (see Appendix S1, Supporting Methods 1 for details). We classified the DHW data for 484 risk-sets containing thermal stress events using the Liu et al. (2014) system to evaluate the relationship between the DHW values and the severity of coral bleaching. The following three categories were employed: (1) low intensity indicative of possible bleaching (DHW < 4°C-weeks), (2) medium intensity associated with significant bleaching (DHW between 4°C and 8°C-weeks), and (3) high intensity associated with widespread bleaching and significant mortality (DHW > 8°C-weeks).

Cyclone data were also obtained from IBTrACS v. 04 (Knapp et al., 2010) and subsequently classified using the Saffir–Simpson Hurricane Wind Scale (Table S2). We identified the highest intensity of each cyclone that passed within a radius of 100 km of each site in 617 risk-sets containing cyclone events (see Appendix S1, Supporting Methods 1 for details). In 25 risk-sets, we were not able to identify a cyclone that passed within 100 km of the site in question. In these cases, the studies reported that the site had been affected by a cyclone. In light of this information, we expanded the radius to 200 km and were able to identify the cyclone in question for those risk-sets. For 11 of these risk-sets, no cyclone was identified within the 200-km radius of the site, and therefore these risk-sets were not considered in the analyses, as this distance is far greater than the distances employed in other studies (Gardner et al., 2005).

2.3 | Data analysis

For the pre- and post-disturbance data, we estimated the change in coral cover after a disturbance as the change in the annual rate of absolute coral cover $\frac{(V_f - V_i)}{t}$, where V_i and V_f are coral cover before and after the disturbance, respectively, and t is the time elapsed between measurements. This metric provides a transparent, directly interpretable measure of coral cover change and matches a formula often used in the coral literature to assess the resistance and recovery of coral communities (e.g., Baumann et al., 2021; Graham et al., 2011). We used the closest coral cover survey available after the impact of a disturbance to represent the damage as accurately as possible and avoid including confounding effects from other disturbances or coral recovery. Then, we used generalized linear mixed-effects models to estimate the severity of the impact of 11 disturbance types on coral cover.

For the generalized linear mixed-effects models, we used reef-site nested within latitude (in bins of 1°) as a random effect given that each site could have more than one risk-set (i.e., a time series with more than one disturbance with well-defined pre- and post-coral cover), to account for temporal correlations within each site, and because has been demonstrated that latitude is an important predictor of ecosystem change (Chaudhary et al., 2021). In addition, we weighted the models by incorporating the sources of two variables that could influence their robustness. First, we considered the number of years from the time of a disturbance impact to the post-disturbance survey of coral cover (i.e., the sooner the reef was surveyed after a disturbance, the more credible the data). Second, we considered the sampling effort (e.g., number of transects) as a measure of the representativeness of a site. The larger the sample size (i.e., more replicas), the more reliable the data (e.g., Côté et al., 2005). We multiplied the number of years elapsed since the disturbance by the sample size and obtained the natural logarithm of the product, which was used as a weighting factor to account for the potential effects of time and effort in our analysis. Model assumptions were validated with residual plots. All analyses were conducted in R (R Team, 2020) with the *lmer* function from the "*lme4*" package (Bates, Mächler, et al., 2015). The predicted categorical estimates and confidence intervals of the models were calculated using the *ggpredict* function from the "*ggeffects*" package in R (Lüdecke, 2018).

Calculating *p*-values in mixed models is ambiguous due to the null distribution not being *t*-distributed (Bates, Kliegl, et al., 2015), and thus *p*-values are not a good measure of evidence of a model or hypothesis (American Statistical Association, 2016). For this reason, changes in coral cover within disturbances were assessed using model coefficients and the 95% CIs around the coefficients. If the 95% CIs do not overlap with zero, the result is significant (Bates, Kliegl, et al., 2015). To illustrate the differences among the effects of disturbances on reefs, we plotted the estimated slopes with their confidence intervals at 95% confidence of the annual rate of change in absolute coral cover as a response variable for each disturbance.

2.4 | Global effect of disturbances on coral cover

Global-level models were constructed with the 11 types of disturbances as explanatory variables (i.e., fixed factors). Here, tropical depressions and storms were gathered into one category as "storms," and category 4 and 5 cyclones were grouped as "major cyclones." Thermal stress was classified into three DHW categories (see Intensity indicators section for details). Thus, we obtained 17 disturbance categories which were included in the analysis.

Given that the change in coral cover is often dependent on the initial coral cover (Baumann et al., 2021), we used this variable as a covariate in the model (i.e., survey before disturbance). Reefs with ~20% coral cover are considered proper models to investigate the thresholds of coral reef resilience after disturbances (Bozec & Mumby, 2015). In our study, this coral cover percentage was the average of our post-disturbance data. We then measured how disturbances affected reefs that exhibited either less or more than 20% initial coral cover (Appendix S3; Equation S1). In the models, *Acanthaster* spp. and high coral cover were used as arbitrary categorical variable references.

Furthermore, we contrasted the severity of thermal stress events, cyclones, and disease outbreaks among the two major reef regions: the Indo-Pacific and tropical Atlantic. We focused on these disturbances because they have resulted in global declines in coral cover and are comparable between regions (Harvell et al., 2007; Hughes, Anderson, et al., 2018; Precht et al., 2020). Disturbances resulting from direct human impacts, such as oil spills, ship activity, and grounding, were not considered in this comparison, as their impacts on reef integrity are largely related to the specific conditions of the event and not the biogeographic region in which they occurred. We also did not include disturbances (i.e., tsunamis, low tides, flood events, and plankton blooms) with low sample sizes ($n < 10$ risk-sets) for both regions in this analysis. Given the reduced sample sizes in some categories, tropical depressions and tropical storms were grouped as "storms" (maximum sustained winds of 15–64 knots). All cyclones were classified as "cyclones" (> 64 knots), and thermal stress events were classified into one of two DHW groups (<4°C-DHW or ≥4°C-DHW; Appendix S3; Equation S2).

2.5 | Thermal stress and cyclone intensity

We used a subset from our database to explore the effects of thermal stress (i.e., DHW) and cyclone intensity (i.e., maximum sustained winds). We contrasted their effects using the initial coral cover and depth (m) of each reef site at the global level in 562 risk-sets included in the subset. Bleaching and cyclones accounted for the disturbances in 158 and 404 of these risk-sets, respectively, while the regions of the Indo-Pacific and tropical Atlantic accounted for 276 and 286 of these risk-sets, respectively. For this analysis, all predictors were used as continuous covariates in the generalized linear mixed-effects models (Appendix S3; Equations S3 and S4).

2.6 | Cumulative impacts of climate-driven disturbances and recovery potential

The existence of multiple time series in our database with information for multiple impacts allowed us to also explore the temporal dynamics of coral cover in three different scenarios. First, we examined the cumulative effect of multiple disturbances of the same type (i.e., cyclones or thermal stress) in reef sites. Second, we tested for evidence of coral recovery in sites free of disturbance for at least 4 years. Lastly, we estimated the change in coral cover in reef sites that were not impacted by any disturbance throughout the time series (i.e., free of disturbance for 4–14 years). For this, we considered the studies that reported that no imminent damage to the site occurred within the given period due to disturbances. The time series used for each of these scenarios were independent and were only used in one scenario.

To evaluate cumulative effects, we only selected time series with cumulative impacts for the same type of disturbance (i.e., cyclones or thermal stress). We focused on those disturbances because they occur globally and their intensity and frequency have increased due to climate change (Hughes et al., 2021; Mudge & Bruno, 2021). In addition, these disturbances allowed for a robust sample size of multiple impacts. We tested the cumulative impacts of individual disturbances (cyclones or thermal stress) to recognize the footprint of each disturbance instead of the signature of a combination of multiple disturbances (e.g., Vercelloni et al., 2020). When another type of disturbance was present between two cyclone or thermal stress events, they were not considered in the time series for this analysis.

A total of 169 time series were used to assess the cumulative effect of multiple impacts. For each time series, we classified the impacts as being the first, second, or third event of the same type that impacted the site. To control the intrinsic variation in the capacity to respond to disturbances among reef sites, we restricted our analysis using the same time series (i.e., reef sites) for the first and second impacts ($n=169$; Appendix S3; Equation S5). We must note that due to the lack of consecutive impacts after two cumulative impacts, we obtained a lower sample size for the third impact ($n=40$); however, this is a subgroup of time series linked to the first and second impacts. We restricted our analyses to three impacts to retain statistical power and control assumptions given the low sample size of time series with more than three impacts ($n=12$), which might be related to the decreasing probability of subsequent disturbances impacting the same reef especially when the intensity of climate-driven disturbance events becomes severe (Cheung et al., 2021). Furthermore, we also compared cumulative effects using only the subsets of the time series that contained three impacts of the same disturbance type ($n=40$) to explore whether this smaller data set exhibited the same trend. The time intervals between the impacts of one disturbance and another ranged from 0 to 23 years. However, 99.7% and 91.8% of the data showed time intervals between disturbances of 0–10 years and 0–5 years, respectively.

We also fitted generalized linear mixed-effects models using the annual rate of change in absolute coral cover each time a disturbance impacted a reef to investigate cumulative impacts at regional (i.e., Indo-Pacific and tropical Atlantic) and global levels (Appendix S3; Equation S6). We also investigated the dynamics of pre- and post-coral cover associated with each of the three disturbance events at global and regional levels (Appendix S3; Equations S7 and S8). Furthermore, to gain insights into the legacy effects of individual climate-driven disturbances, we explored cyclone intensity (i.e., maximum sustained winds) and thermal stress (i.e., DHW) for each disturbance (Appendix S3; Equations S9 and S10). Here, we restricted our analysis to two impacts because of the low sample size of the third impact, which increased the uncertainty of the model. We further restricted the effect of cyclones by excluding storms with intensities <34 knots.

We also fitted generalized linear models to investigate the recovery potential of reefs following cyclones or coral bleaching events due to thermal stress. We estimated the change in coral cover after a disturbance as the annual rate of absolute change in coral cover $\frac{(V_{\text{recovery}} - V_{\text{post}})}{t}$, where V_{post} is the coral cover obtained from post-disturbance survey data, V_{recovery} is the coral cover peak reported in the time series after the disturbance, and t is the time elapsed between measurements (Graham et al., 2011). We used thermal stress and cyclones given that we were interested in investigating the recovery potential after climate-driven disturbances and because each group showed a robust sample size when we gathered the disturbances into major groups (thermal stress = 62, cyclones = 22). We used time series that included data for at least 3 years post-disturbance to retain sites that were in recovery regimes (Graham et al., 2011). Finally, we used a subset of reefs without registered impacts in the time series ($n=42$) as a control model to evaluate reef trends in the absence of disturbance (Appendix S3; Equation S11). Using this framework, we were able to evaluate the potential trends of coral reefs in recovery regimes. This analysis was conducted using the *glm* function in R (R Team, 2020).

3 | RESULTS

Our global analysis comprised 1000 reef sites (unique coordinates) and included 1609 pre- and post-disturbance surveys (i.e., *risk-sets*) spanning more than 55 years from 1965 to 2021 and 11 disturbance types across all major reef regions (Table S1; Figure 2a; Figure S2). Nearly 70% of the risk-sets showed a decrease in coral cover, while 29% of the risk-sets showed an increase in cover. The coral cover of only 2.4% of risk-sets remained unchanged after a disturbance. Cyclones and thermal stress events, which were the disturbance types that were best represented within the database, comprised 38.37% and 34.43% of the risk-sets, respectively. Seven of the 11 disturbances were found in multiple regions (Figure 2a), and 4 disturbances showed limited representation. For example, *Acanthaster* spp. and plankton blooms were only reported for Indo-Pacific and eastern tropical Pacific reefs, while tsunamis and dredging were only reported in the Indo-Pacific (Figure 2a). Thermal stress and cyclone events were the only disturbance types with worldwide representation.

Overall, we observed that the distribution of coral cover data before a disturbance was consistently higher compared to the distribution of coral cover data after a disturbance (Figure 1). However, the initial condition and magnitude of change before and after a disturbance were markedly different among regions (Figure 1). The median coral cover for the tropical Atlantic and Indo-Pacific regions decreased from 16.9% to 14.2% and 32.4% to 20.53%, respectively, after disturbance events (Figure 1a). Within the four Indo-Pacific realms with available information, a more consistent pattern was observed. The median coral cover decreased from 39.1% to 25.4% in the western Indo-Pacific, from 28.6% to 21.7% in the Tropical Eastern Pacific, from 29.3% to

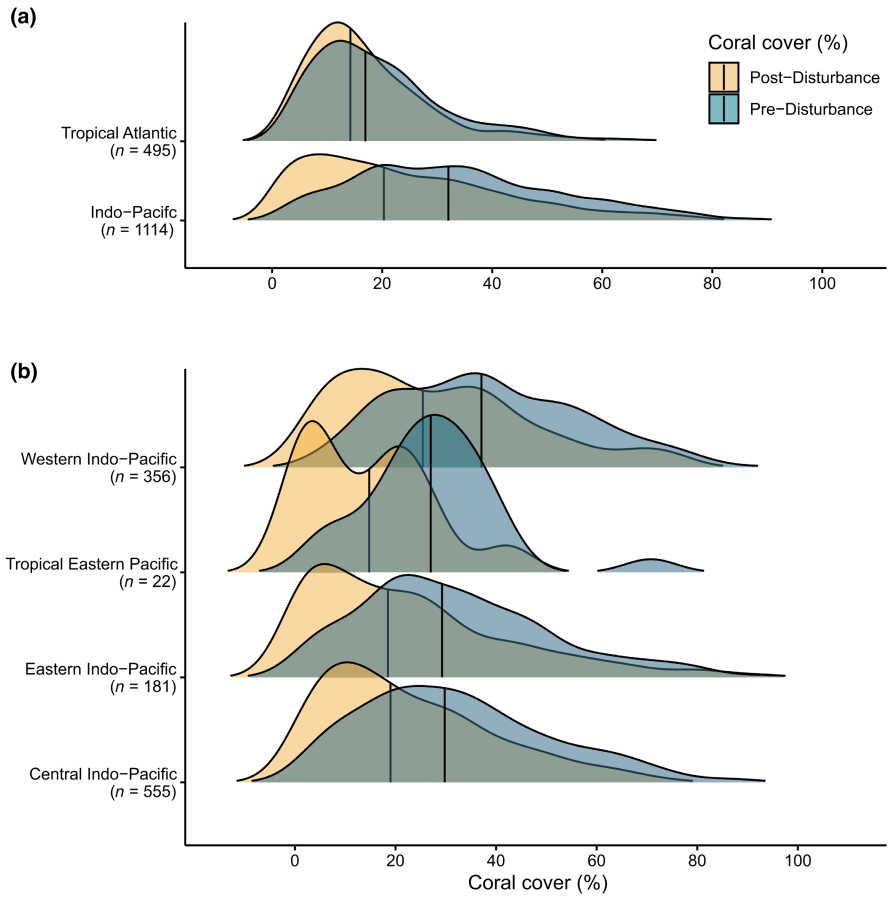

FIGURE 1 Pre- and post-coral cover in the tropical Atlantic and Indo-Pacific regions. Plot density represents coral cover pre-disturbance (blue) and post-disturbance (orange). (a) Plot density of the coral cover (%) in the Tropical Atlantic and Indo-Pacific reefs. Vertical black lines represent the median of each pre- and post-disturbance period. (b) Plot density of the coral cover (%) for four Indo-Pacific realms (according to Spalding et al., 2007).

18.5% in the eastern Indo-Pacific, and from 29.8% to 19.0% in the central Indo-Pacific (Figure 1b).

3.1 | Global impacts on coral cover

Our findings show that most of the disturbances resulted in a significant reduction of coral cover regardless of the spatial extension of the disturbance (Figure 2b). However, there was an apparent difference in the reduction in coral cover that appeared to depend on initial coral cover or type of disturbance. Overall, reefs with >20% initial coral cover showed higher reductions in cover (mean annual rate of change = −18.50, CI = 20.35, −16.64) than reefs with low initial coral cover (<20%; −4.01, CI = −6.58, −1.45; Figure 1b). Reefs with high initial coral cover showed negative and significant (i.e., not intercepted by the zero line) change for all disturbance types, whereas reefs with low initial coral cover exhibited consistently lower losses of coral cover (many not significant). Severe disturbances, such as ship activity, major cyclones, and intense thermal stress events, resulted in the greatest changes in coral cover when comparing low and high coral treatments (Figure 2b). Overall, the most severe disturbances were ship activity (−24.71, CI = −30.45, −18.97), plankton blooms (−15.50, CI = −19.83, −11.17), and thermal stress (−18.50, CI = −20.35, −16.64) in the high coral cover treatment, although it should be noted that the sample sizes for ship activity and plankton blooms were relatively small (Figure 2b).

A detailed comparison of widespread disturbances revealed that thermal stress events, cyclones, and diseases had different effects on Indo-Pacific and tropical Atlantic reefs (Figure 3). Diseases had a greater impact on the loss of coral cover in the tropical Atlantic, whereas disease did not significantly affect the rates of coral cover loss in the Indo-Pacific. On the contrary, the impacts of tropical storms and cyclones were considerably more severe in Indo-Pacific reefs when compared to those of the tropical Atlantic (Figure 3). The effect of tropical storms was not significant for the tropical Atlantic. The greater degree of change in coral cover detected in the Indo-Pacific after a tropical cyclone when compared to that of the tropical Atlantic may be related to the fact that coral cover tended to be higher in this region prior to disturbance (Figure 3).

Thermal stress that caused coral bleaching was the only disturbance that resulted in significant coral cover declines in both major regions. Interestingly, no evident difference between the effects of

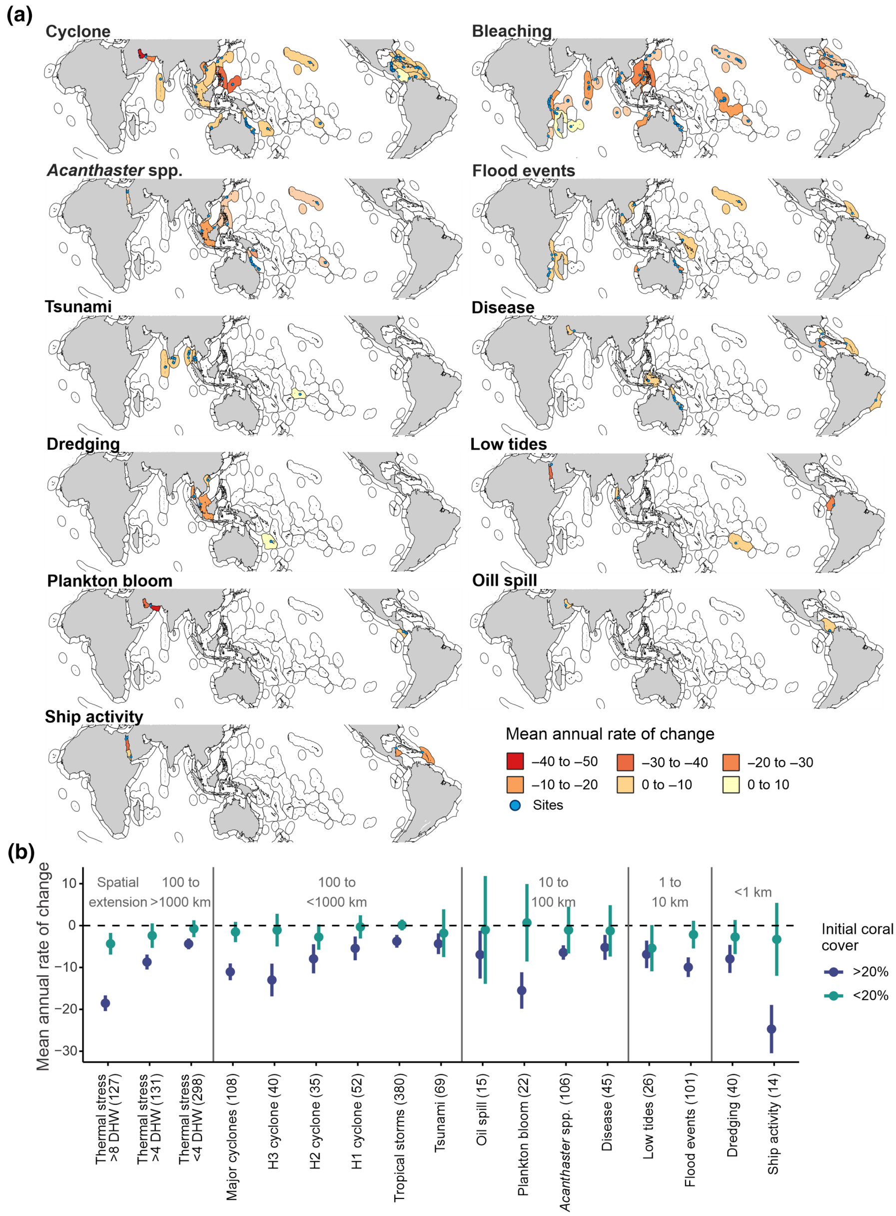

FIGURE 2 Worldwide changes in coral cover in 1609 risk-sets associated with 11 disturbance types. (a) Colors indicate the average change in coral cover (%) associated with disturbances at the ecoregion level (according to Spalding et al., 2007). (b) Predicted values of the annual rate of change in absolute coral cover among disturbances at the global level. Effect sizes are the mixed models in which dots represent the average slope of the risk-sets used in the analysis within each disturbance type and the lines represent the 95% CIs. The purple and blue lines represent reefs with high (>20%) and low (<20%) initial coral cover, respectively. The slopes are significantly different from zero if their 95% CIs do not overlap with the vertical dashed line centered on zero. Disturbances are organized as the spatial extension of damage (in grey) from left (major extension) to right (minor extension). Tropical depressions (wind below 34 knots) and tropical storms (wind between 34 and 64 knots) were grouped as "Tropical storms." Cyclones were grouped by category: Category H1 (wind ≤64 and >83 knots), Category H2 (wind greater ≤83 and >96 kn), and Category H3 (wind ≤96 and >113 knots), with Category 4 (wind ≤ to 113 and <137 knots) and Category 5 (wind ≤137 knots) being grouped together as "Major Cyclones." We classified the DHW data for the 484 risk-sets using the system proposed by Liu et al. (2014) to visualize the relationship between the DHW values and the severity of coral thermal stress. The Liu et al. (2014) classification system is as follows: (1) low intensity indicative of possible thermal stress (DHW > 4°C-weeks), (2) medium intensity associated with significant thermal stress (DHW between 4 and 8°C-weeks), and (3) high intensity associated with widespread thermal stress and significant mortality (DHW < 8°C-weeks). The sample size used for each disturbance in the mixed model is shown in brackets in panel B.

low-intensity thermal stress events (<4 DHW) and high-intensity thermal stress events (>4 DHW) was present in the tropical Atlantic (Figure 3). This is probably due to the high variability associated with the low sample size of high thermal stress events in this region ($n = 9$) and the fact that there are no data for sites with more than 7.3 DHW. On the contrary, a clear difference in the effects of low and high

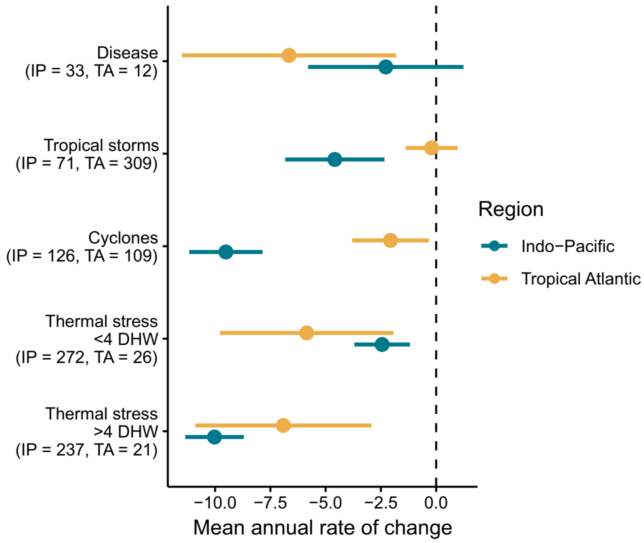

FIGURE 3 Predicted annual rates of change of absolute coral cover due to disturbances at the regional level. Effect sizes are the mixed models in which dots represent the average slope of the risk-sets used in the analysis within each disturbance and lines represent the 95% CIs for the Indo-Pacific (blue) and tropical Atlantic (orange). The slopes are significantly different from zero if their 95% CIs do not overlap with the vertical dashed line centered on zero. Disturbances are organized as the spatial extension of damage from top (minor extension) to bottom (major extension). The sample size used for each disturbance in the mixed model is shown in brackets. IP, Indo-Pacific; TA, tropical Atlantic.

thermal stress events on coral cover decline was evident in the Indo-Pacific, with low-intensity thermal stress resulting in relatively minor losses in coral cover (10.0%–3.6%).

A detailed analysis of the relationship between the rates of change in coral cover and the intensity of thermal stress and cyclones using intensity, initial coral cover, and depth as continuous variables revealed a clear relationship between increases in coral cover loss and increases in event intensity (Figure 4). In the case of thermal stress, the number of DHW had a greater effect on changes in coral cover than initial coral cover or depth (Figure 4a–d). However, initial coral cover was the main predictor of change after a cyclone, with cyclone intensity (maximum sustained wind) contributing to a lesser degree to the observed trend. This suggests that thermal stress events have more severe effects on coral cover than cyclones, even in reefs with low initial coral cover. Depth was not a significant predictor in either the cyclone or thermal stress analyses, yet shallow reefs tended to be more susceptible to cyclone damage than deeper reefs (Figure 4e–h).

3.2 | Cumulative impacts of climate-driven disturbances

Overall, the cumulative effects of past disturbances consistently indicated that the first impact produced the most notable declines in coral cover, which gradually decreased with the second and third impacts (Figure 5a). The greatest decrease from pre- to post-disturbance coral cover occurred after the first impact, while coral cover remained fairly stable following the second and third impacts (Figure 5b). Although the pattern is consistent for both major regions, reefs in the tropical Atlantic showed markedly lower declines after the first impact when compared with the substantial changes observed in the Indo-Pacific after the first impact (Figure 5c). This is likely because the tropical Atlantic exhibited considerably lower levels of coral cover at any given time (before or after disturbances) compared to those of the Indo-Pacific and showed a slight tendency of coral cover decline even though acute events did not appear to drastically reduce coral cover (Figure 5d). Furthermore, when we only focused on the time series containing three impacts ($n=40$), we found that the same overall pattern was observed (Figure S3). Similarly, when we tested for relative changes (instead of absolute changes; see methods for details) we found that the same overall trend depicted in (Figure 5; Figure S4).

The coral cover patterns of Tropical Atlantic reefs are in part explained by the data included in the analysis given that most data sets began in the late 1990s (Figure S2) when most Tropical Atlantic reefs were already impaired. Furthermore, the cumulative effects in tropical Atlantic reefs were mainly explained by the cumulative effect of cyclones and storms, as we only have one reef with two consecutive impacts due to thermal stress events in our data set for that region. Conversely, the cumulative effect in Indo-Pacific reefs tended to be based on the relatively greater sample sizes for both the thermal stress and cyclone events, although sites were only impacted twice by cyclones (Table S3).

The relationship between the annual rate of change of thermal stress and cyclone intensity was explored using the first and second consecutive impacts. For thermal stress (bleaching), we found marked differences in coral responses when comparing the changes in coral cover after the first and second impacts (Figure 6a,c). For the first impact, we found a negative and steep relationship between the intensity of the thermal stress event and the annual rate of coral cover loss. However, the second event resulted in considerably less and non-significant damage, regardless of high thermal stress (Figure 6a,c) and despite the intensity of thermal stress events being fairly similar during the first and second events for the majority of sites and at times being even higher during the second event (Figure S6). When evaluating cyclone events, we observed a very similar negative relationship to that of thermal stress between wind intensity and coral cover loss during the first and second events (Figure 6b,d), and cyclone intensity (wind speed) was similar between the first and second impacts in most cases (Figure S6). Furthermore, we did not find considerable differences in the trends when estimating changes with a relative rate of change (Figure S5).

Our analyses also revealed that coral cover can recover in the absence of recurrent disturbances (Figure 7). We found that coral cover increased in nearly 80% of reef sites impacted by cyclones and bleaching events, albeit at different rates. Reef sites impacted by cyclones increased in coral cover by 2.82% (CI = 1.86, 3.78) per year, while reefs impacted by bleaching events increased by 1.30%

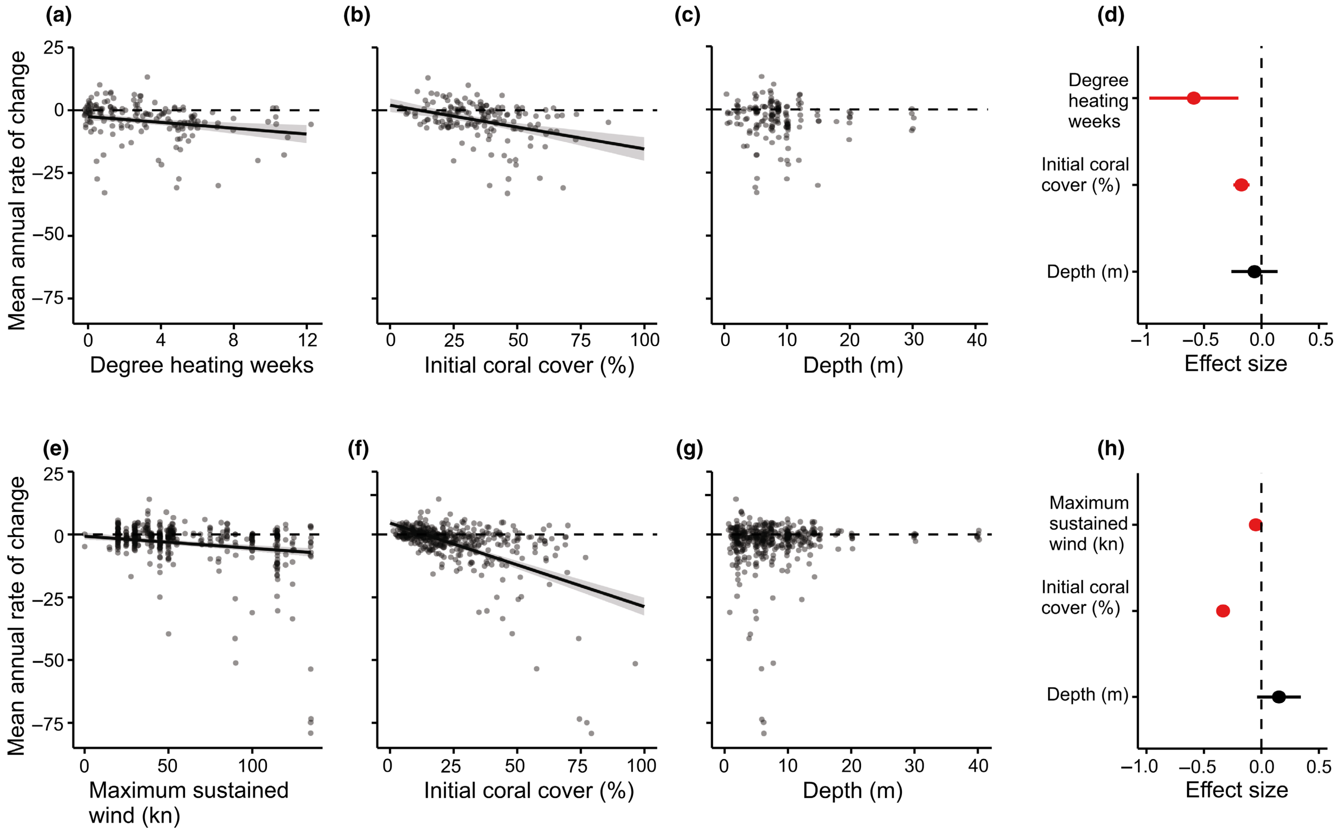

FIGURE 4 Predicted values of the annual rate of change of absolute coral cover due to the intensity of thermal stress and cyclone events. Changes in coral cover (%) in reef sites driven by thermal stress events with the indicators of (a) degree heating weeks, (b) initial coral cover (%), and (c) depth (m). Changes in coral cover (%) in reef sites driven by cyclone events with the indicators of (e) maximum sustained wind (kn), (f) initial coral cover (%), and (g) depth (m). Dots represent risk-sets within time series, and the lines represent the mixed models fitted by the changes in coral cover. Effect sizes of the regression model for (d) degree heating weeks (DHW) and (h) maximum sustained wind (kn), in which points represent the mean of the general linear mixed model used in the analysis and lines represent the 95% CIs. Red and black slopes indicate significant and non-significant effects, respectively. Slopes are significantly different if their 95% CIs do not overlap.

(0.73, 1.87) per year. Furthermore, we showed that in the absence of any acute disturbance, reefs exhibited significant increases in coral cover but at relatively low rates (0.83%, CI = 0.15, 1.50).

4 | DISCUSSION

Coral reefs are highly dynamic ecosystems. Our findings show that the effects of disturbances largely depend on the condition of the system before the impact, disturbance severity, cumulative effect of previous impacts, and biogeographic region, with the latter reflecting differences among life-history traits of geographically distinct coral assemblages, such as those between the Tropical Atlantic and Indo-Pacific reefs (e.g., McWilliam et al., 2020). Reefs with higher initial coral cover underwent the most severe losses in coral cover, regardless of the disturbance type. Despite the numerous sources of stress, both natural and anthropogenic, our findings confirm that thermal stress is the leading driver of change in coral reefs, as it causes high coral cover declines that do not depend on the previous condition of a reef and because thermal stress can occur over very large spatial scales. However, we have also shown that losses in coral cover after a bleaching event are modulated by the cumulative stress of previous impacts, regardless of the bleaching intensity or initial coral cover, which suggests that previous events of thermal stress determine to some degree the response of reef systems to future events of the same type. On the contrary, the effect of a cyclone (and likely other physical impacts) is primarily modulated by the initial condition of a reef. Moreover, the system does not seem to develop a predisposition to better adapt to future disturbance events in the short term (Cheal et al., 2017). Lastly, our findings show that in the absence of disturbance, almost 80% of coral reefs were capable of recovery.

Pre-disturbance coral cover was strongly related to the ability of a reef to resist disturbance, with reefs with lower levels of coral cover tending to be more resistant than reefs with higher levels of coral cover (Guest et al., 2012; Mudge & Bruno, 2021; Figure 1). This was confirmed by the observed differences in coral cover trends between the Indo-Pacific and tropical Atlantic. In the Indo-Pacific, initial coral cover was considerably higher (mean ± standard deviation; 32.4 ± 18.81% versus 16.9 ± 12.61% in the tropical Atlantic; Figure 1) and consequently was considerably more affected by thermal stress events and cyclones, although not by diseases, which

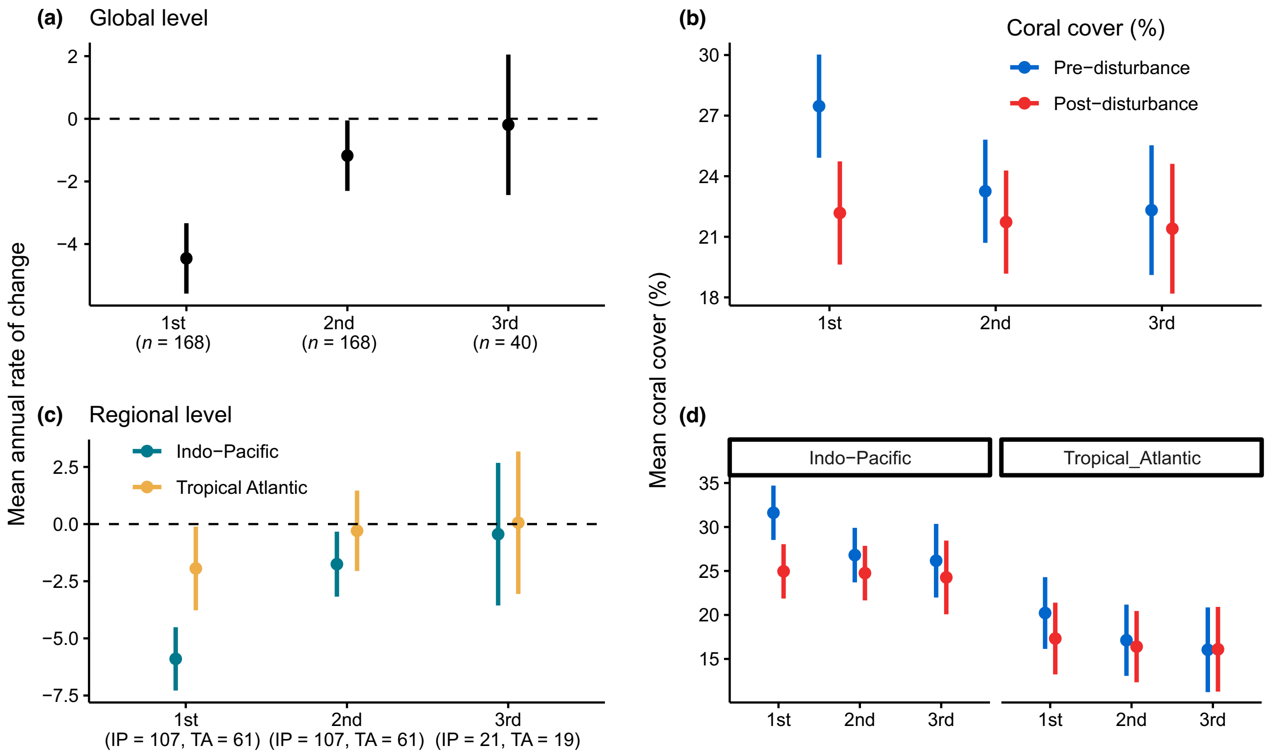

FIGURE 5 Coral reef responses to the cumulative stress of past climate-driven disturbances at global and regional levels. Changes in coral cover following cumulative past climate disturbances (cyclones and thermal stress) at global (a) and regional (c) levels. Associated changes in pre- and post-disturbance coral cover at global (b) and regional (d) levels. Effect sizes are the mixed models in which dots represent the average slope of the risk-sets used in the analysis and lines represent the 95% CIs. The slopes are significantly different from zero if their 95% CIs do not overlap with the vertical dashed line centered on zero. The vertical axes in (b) and (d) each have their own scale. The sample sizes used in the mixed models in (a; same in b) and (c; same in d) are shown in brackets. IP, Indo-Pacific; TA, tropical Atlantic.

are more pervasive in the tropical Atlantic region (Figure 3; Alvarez-Filip et al., 2022). Furthermore, the cumulative effect analysis revealed consecutive losses in coral cover in the Indo-Pacific after the first and second impacts of climate-driven disturbances, which were not observed in the reefs of the tropical Atlantic (Figure 5c). This trend is likely due to two circumstances. First, most of our data for the tropical Atlantic were collected beginning in the late 1990s (Figure S1) when most reefs were already severely degraded (Jackson et al., 2014). Therefore, there was already little left in this region to be affected by disturbance. Second, regimes of chronic and acute disturbances in many sites have resulted in non-random losses of coral species, and many of these impaired systems are now dominated by opportunistic species (González-Barrios & Alvarez-Filip, 2018; Green et al., 2008). Although these species are more likely to resist stressful conditions, they also tend to lock ecosystems into low functional states (González-Barrios et al., 2021; McWilliam et al., 2020; Molina-Hernández et al., 2020). Overall, our findings suggest that tropical Atlantic reefs are not more resistant than those in the Indo-Pacific but rather are more degraded and thus have less coral cover to lose.

In addition to reef condition, we have shown that cumulative effects and the disturbance type determine the trajectory of coral cover following future impacts. For thermal stress, we found that the greatest losses in coral cover occurred during the first impact, while no significant changes in coral cover were observed after the second impact regardless of the intensity of the subsequent events (Figure 6a). Our findings are consistent with recent reports that coral communities can acclimatize to increasing levels of thermal stress (Hughes et al., 2021; Hughes, Kerry, Connolly, et al., 2019), which can be explained by the potential ability of corals to enhance their thermal tolerance through multiple mechanisms (Coles et al., 2018; Drury, 2019). For example, shifts in gene expression enable corals to acclimate to thermal stress (Drury & Greer, 2022; Thomas & Palumbi, 2017). Such acclimatization processes can be anticipated at community scales or even regions, such as in the eastern tropical Pacific, in which reefs have been shown to be highly resilient after encountering acute thermal stress (Romero-Torres et al., 2020). However, these acclimatization processes may vary among reef zones (Tebbett et al., 2022) and there is growing uncertainty regarding whether corals will resist or acclimatize to the impacts of thermal stress given a lengthening of warm periods and a shortening of the intervals between them (Li & Donner, 2022). Moreover, reefs that experience more infrequent bleaching events are more susceptible to coral loss (Guest et al., 2018). As such, it is likely that the ecological memory of past disturbances in ecological systems fades over time (Hughes et al., 2021; Peterson, 2002).

The lack of significant losses after the second or third impacts of thermal stress (Figures 5and 6) can also arouse by shifts in species

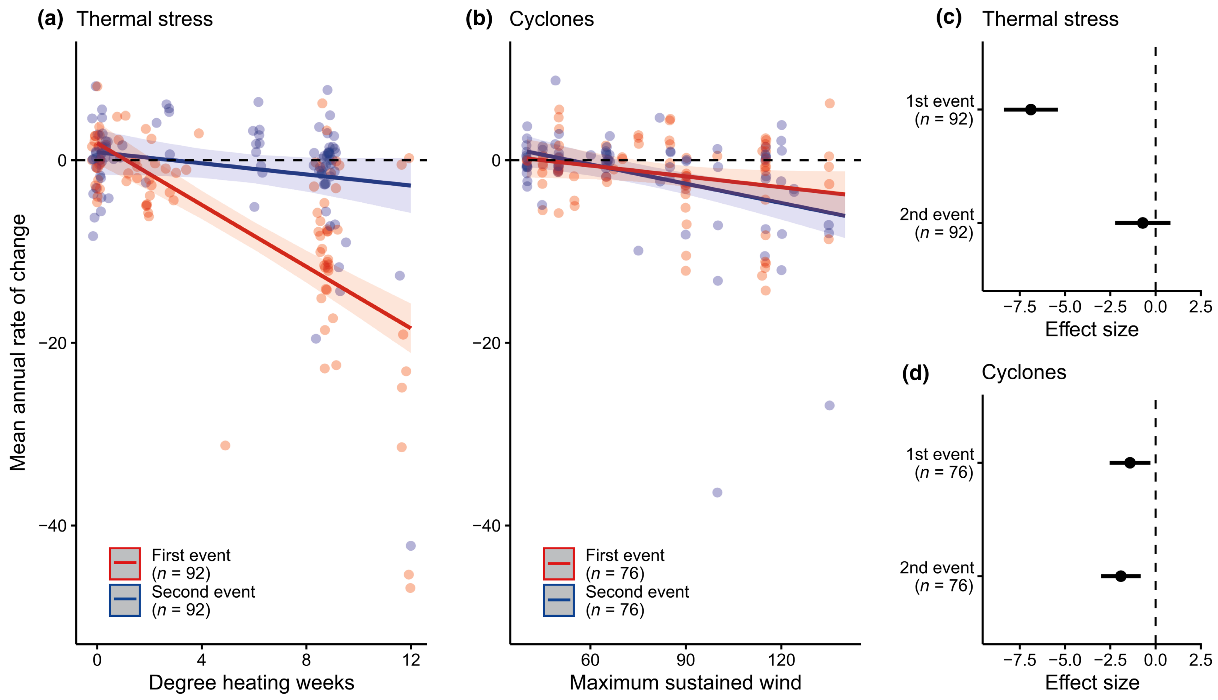

FIGURE 6 Coral reef responses due to cumulative thermal stress and cyclone events. Changes in coral cover (%) driven by (a) thermal stress in the form of degree heating weeks (DHW) and (b) cyclones in the form of maximum sustained winds (kn). The dots in (a) and (b) represent risk-sets within time series, and the lines represent the mixed models fitted by the changes in coral cover due to the first (red) and second (blue) impacts with 95% coefficient intervals (shading). Effect sizes associated with the first and second impacts of (c) thermal stress and (d) cyclones are the mixed models in which dots represent the average slope of the risk-sets used in the analysis and the lines represent the 95% CIs. The slopes are significantly different from zero if their 95% CIs do not overlap with the vertical dashed line centered on zero. The sample size used in the mixed models is shown in brackets.

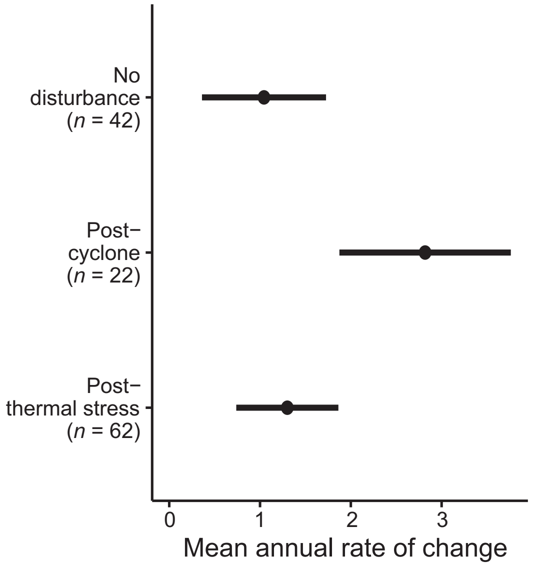

FIGURE 7 Predicted values of the mean annual recovery rate after thermal stress and cyclone events and in the absence of disturbance. Effect sizes are the generalized linear model in which dots represent the average slopes of the risk-sets used in the analysis and lines represent the 95% CIs. The slopes are significantly different from zero if their 95% CIs do not overlap with the vertical dashed line centered on zero. The sample size is shown in brackets.

composition, with some species being capable of resisting and adapting to more extreme disturbances while species with limited abilities to escape warming are compromised (González-Barrios et al., 2021; McWilliam et al., 2020). Although species reshuffling after thermal stress might buffer coral cover losses in the short term, an increase in the frequency and intensity of thermal stress events will likely increase the intrinsic vulnerability of reefs and possibly lead to local extirpations (Sunday et al., 2015). Moreover, if shifts in species composition are determined by the replacement of reef-building coral species by generalist forms, some ecological processes, including calcium carbonate deposition and the provision of architecturally complex structures, will be disrupted in the novel ecological communities and consequently compromise ecosystem functioning (Alvarez-Filip et al., 2013; Hughes, Kerry, et al., 2018; McWilliam et al., 2020). Furthermore, coral species that are vulnerable due to thermal stress can exhibit altered metabolic processes and physiological functioning that affect their ability to accumulate calcium carbonate (Carricart-Ganivet et al., 2012) and reproductive output (Baird & Marshall, 2002), which can dampen coral recruitment and compromise recovery processes in reef systems (Cheung et al., 2021; Hughes, Kerry, Baird, et al., 2019).

Contrary to what was observed with multiple thermal stress events, changes in coral cover following the cumulative impact of tropical cyclones (and potentially other physical disturbances) hardly reflected any potential mechanisms of acclimatization or adaptation within reefs. This might be explained by the fact that the effects of cyclones on coral communities largely depend on the life-history traits, biophysical features, and initial cover of the coral assemblages prior to disturbance (Guest et al., 2012; Madin & Connolly, 2006; Figure 6; Figure S5). Although our database did not allow us to consider the identity of species and their susceptibility to disturbance, ample evidence has shown that morpho-functional traits and life-history strategies are related to the ways in which coral species respond to disturbance (González-Barrios et al., 2021). These factors are particularly relevant for our findings in the tropical Atlantic, in which the effects of cyclones were relatively small (Figure 3). Most of our data from this region were representative of times in which most reefs had already undergone several ecological and structural changes (Alvarez-Filip et al., 2011), and some of the most fragile species, such as the branching acroporids, already exhibited very low abundance values across the region (Cramer et al., 2020; Estrada-Saldívar et al., 2020). Thus, the tropical Atlantic reefs included in our analysis are most likely largely represented by shifted coral assemblages that are defined by low-coral cover and dominated by low-relief species (Cramer et al., 2021; González-Barrios et al., 2021), which are less susceptible to physical damage. On the contrary, the Indo-Pacific reefs were composed of a wide variety of branching, tabular, and digitate morphologies, which are prone to breakage (McWilliam et al., 2018). Consequently, the high coral cover of those reefs tends to be in greater danger of decline due to breakage after the passing of a tropical cyclone when compared to the danger present in tropical Atlantic corals (Figure 3).

Coral disease outbreaks are also a primary driver of coral decline across many reef sites worldwide (Harvell et al., 2007). Similarly, to thermal stress events, disease outbreaks can occur over large spatial scales and are often associated with widespread coral mortality that can rapidly and drastically reduce populations over short periods of time (Alvarez-Filip et al., 2022; Van Woesik & Randall, 2017). Our findings show that in the tropical Atlantic, the impact of disease outbreaks is a significant driver of coral cover decline, which is comparable to the effect of major bleaching events (Figure 3). This is consistent with a large body of evidence that has highlighted that the tropical Atlantic is a hotspot of coral diseases (Weil, 2004), which are linked to the major ecological and structural changes occurring in this region (Alvarez-Filip et al., 2022; Aronson & Precht, 2001). In the Indo-Pacific, the consequences of coral disease outbreaks are less evident, which may be due to the high variability observed among studies of the effects of disease outbreaks (Figure 3). Historically, the Indo-Pacific region has had fewer reports of disease, which could be due to the expansiveness of the area. Nonetheless, certain diseases have also been observed in epizootic proportions that greatly affect coral cover (Bruckner, 2016). At present, the role of disease as a significant driver of reef degradation is not prominent in the Indo-Pacific; however, these events require greater consideration given the strong links between anthropogenic stress and disease susceptibility, which will likely result in increases in the prevalence and severity of coral diseases worldwide (Maynard et al., 2015). This is particularly important given the strong connection between the frequency and intensity of disease outbreaks and the rapidly increasing frequency of human-induced pressures such as rising sea temperatures, decreased water quality, and nutrient enrichment (Bruno & Selig, 2007; Vega Thurber et al., 2014). Indeed, it is necessary to note that management actions that reduce anthropogenic stress are also likely to reduce the prevalence and severity of coral disease (Maynard et al., 2015).

Our findings show that coral reefs are still able to recover in the absence of disturbance (Figure 7). Although we did not compare recovery processes in different regions (given the low sample size), the evidence suggests that the coral reefs of the Indo-Pacific have a much greater potential to recover than those in the tropical Atlantic (Graham et al., 2011; Souter et al., 2021), which can be explained by various processes. Marked recovery following disturbances, even to pre-disturbance levels of coral cover, has been observed in the Indo-Pacific (Adjeroud et al., 2018; AIMS, 2022; Gilmour et al., 2013; Souter et al., 2021). In contrast, tropical Atlantic coral recovery has been only reported in a few areas and is influenced by management strategies (Steneck et al., 2019). In part, this is due to the higher recruitment rates of the Indo-Pacific compared to those of the tropical Atlantic, which promote recovery and are driven by the diversity of coral morphologies in the region that promote the recovery of key functions (Roff, 2021). In contrast, the lack of recruitment of key reef framework corals in the tropical Atlantic may partially explain the functional lockdown that has been observed in the coral reefs of the region (González-Barrios et al., 2021; Roff, 2021). Reef recovery can also drive species reconfigurations within reefs, which may either positively or negatively affect reef functionality. For example, in many reefs worldwide, reef recovery has been driven by low-relief opportunistic species and other foliose or digitate corals, which can contribute to the three-dimensional complexity of the reef at fine scales (González-Barrios et al., 2021; Speare et al., 2019). Ultimately, coral recovery following disturbance events will depend on the adaptive capacity of coral communities to disturbances. This is particularly relevant for temperature-induced bleaching events. Although there is still some degree of uncertainty as to how corals will respond to increasing heat stress levels, the lengthening of warm periods and shortening of the intervals between them will likely diminish the capacity of corals to recover from previous impacts. For example, as marine heatwaves become more frequent and intense, larger colonies and the most fecund corals are likely to become increasingly vulnerable, which may reduce the capacity of coral reefs to recover after stressful events (Speare et al., 2019).

Reversing reef degradation will require a reduction in human pressure, yet the lack of action to reduce anthropogenic impacts and the failure of immediate global action regarding greenhouse gas emissions will exacerbate reef degradation and erode resilience. In light of this, understanding the relative importance of various risks is necessary to properly guide reef management efforts. Our findings contribute to the broader understanding of how disturbance shapes coral reef ecosystems and allow for management actions to be adequately prioritized to mitigate severely stressful events. If the signs or precursors of rapid ecological change can be reliably detected, managers may be able to take early preventative action (Ban et al., 2014). Furthermore, we expect our findings to aid reef managers in making financial assessments and decisions regarding where and how to invest scarce resources to ensure that coral reefs are restored and protected (Secaira Fajardo et al., 2019). In this context, a clear message from our study is that special attention should be allocated to reefs with the highest live coral cover, as these are likely to be more vulnerable to disturbance. For example, ensuring that these reefs, which are often referred to as reef oases, are well managed (e.g., inside functional marine protected areas) should be a conservation priority, as local conditions can increase the capacity to resist and recover from coral bleaching in response to widespread thermal stress (Donovan et al., 2021). This is particularly relevant given the growing spatial mismatch between the scales of potential threats and planned responses (Good & Bahr, 2021). In addition, risk financing and insurance are becoming increasingly relevant (Schelske et al., 2021), as these tools are critical when absorbing financial losses in the wake of disasters and natural catastrophes. Thus, notable opportunities for restoration may lie in risk financing associated with risk reduction services for reefs (Reguero et al., 2019). Finally, the integration of multiple properties of contemporary disturbances, such as their spatial extension, frequency, intensity, and cumulative effects, into our perceptions of coral reef dynamics is the key to improving our understanding of how legacy impacts transform coral reefs worldwide.

AUTHOR CONTRIBUTIONS

Conceptualization, Funding acquisition, and Project administration: F. Javier González-Barrios and Lorenzo Álvarez-Filip. Contributed new reagents/analytic tools: F. Javier González-Barrios and Lorenzo Álvarez-Filip. Data curation: F. Javier González-Barrios, Nuria Estrada-Saldívar, and Esmeralda Pérez-Cervantes; Formal analysis: F. Javier González-Barrios, Nuria Estrada-Saldívar, Lorenzo Álvarez-Filip, and Esmeralda Pérez-Cervantes. Write original draft: F. Javier González-Barrios, Lorenzo Álvarez-Filip, Nuria Estrada-Saldívar, and Esmeralda Pérez-Cervantes. Review and editing: F. Javier González-Barrios, Lorenzo Álvarez-Filip, Nuria Estrada-Saldívar, Fernando Secaira-Fajardo, and Esmeralda Pérez-Cervantes.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in a DRYAD repository at https://doi.org/10.5061/dryad.z8w9ghxhm.

DATA SOURCES

The references of all the studies included in the analysis can be found in the Supporting information in section Appendix S2.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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