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Deficits in functional trait diversity following recovery on coral reefs

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The disturbance regimes of ecosystems are changing, and prospects for continued recovery remain unclear. New assemblages with altered species composition may be deficient in key functional traits. Alternatively, important traits may be sustained by species that replace those in decline (response diversity). Here, we quantify the recovery and response diversity of coral assemblages using case studies of disturbance in three locations. Despite return trajectories of coral cover, the original assemblages with diverse functional attributes failed to recover at each location. Response diversity and the reassembly of trait space was limited, and varied according to biogeographic differences in the attributes of dominant, rapidly recovering species. The deficits in recovering assemblages identified here suggest that the return of coral cover cannot assure the reassembly of reef trait diversity, and that shortening intervals between disturbances can limit recovery among functionally important species.

1. Introduction

Ecosystems are naturally exposed to pulse disturbances. However, the rate and severity of disturbances is increasing because of human influences, especially anthropogenic climate change [1–3]. The resilience of ecosystems is defined by their ability to withstand these changes, or bounce back from perturbation [4]. Nevertheless, if the frequency and intensity of disturbances is raised, and the survival or recovery of species is compromised, transitions into new configurations of species can occur [5,6], including dramatic regime shifts into alternate ecological states [7,8]. Deficits in recovering assemblages may occur if ecosystems fail to reassemble to their previous configurations of species and functions [9]. The extent and magnitude of this deficit may be determined by how the functions of resistant or rapidly recovering species compare to the original set of functions prior to degradation [10,11].

In many complex systems, ‘redundant’ elements can continue to support critical functions when other components fail. In machines, repeated components can maintain functionality despite mechanical failure [12]. In genomes, duplicate genes can conserve functions after mutation [13]. In economics, diverse industries can protect regions against sector-specific shocks [14]. Similarly, ecological functions can be maintained if declining species are replaced by functionally similar, but less vulnerable species that have a greater tolerance to environmental change, or faster regeneration rates after perturbation [15,16]. This phenomenon (known as ‘response diversity’) is driven by differences in response to environmental change among functionally similar species [8,17–19], and can theoretically reduce potential deficits in ecosystem function following pulse disturbances.

Response diversity has stabilized functions in a range of species assemblages, including plants, sea urchins, seaweed, insects, fishes, birds and microbes [16,18,20–24]. For example, tropical bird species can respond differently to agricultural practices, allowing essential functions such as seed dispersion to be

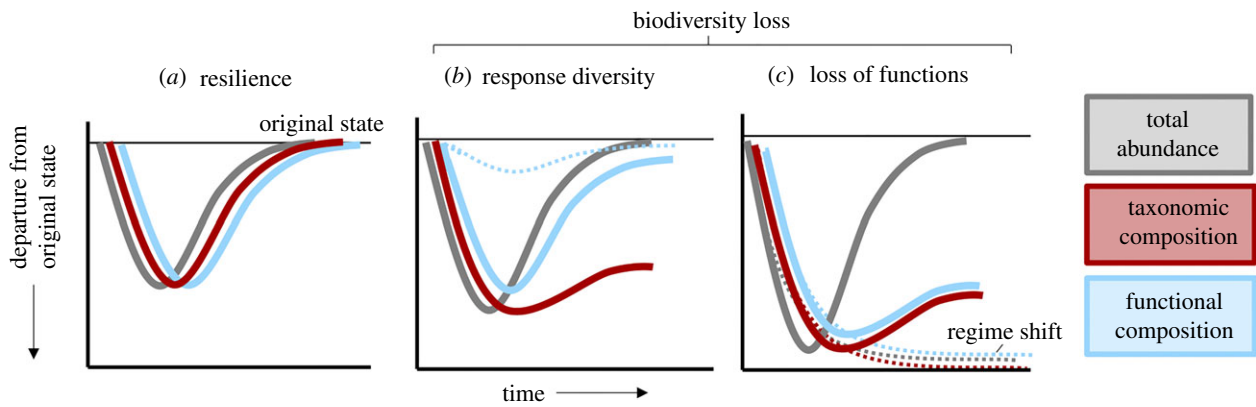


Figure 1. Hypothetical patterns of resilience to disturbance through time. In each scenario, disturbances drive a loss of total abundance and a shift in taxonomic and functional composition caused by different susceptibilities among taxa. (a) The recovery of all parameters to their original state, indicating full resilience. (b) Taxonomic composition fails to recover, yet depleted taxa are replaced by recovering taxa with similar ecological functions, indicating response diversity. The dotted line indicates an alternate scenario where functions are maintained by taxa that survive the disturbance. (c) Following severe disturbance, declining taxa are replaced by a subset of taxa with depleted functions, indicating a deficit. The dotted line indicates a regime shift into an alternate ecological state, where parameters are persistently depleted. Other possible scenarios (e.g. loss of functions despite taxonomic consistency) are not shown.

sustained [16]. Similarly, invasive pollinators may respond positively to land-use changes as native taxa decline, maintaining pollination services [22]. In marine systems, heavily exploited herbivorous fishes can be replaced by high numbers of grazing sea urchins, maintaining herbivory [7]. Despite these examples, response diversity is far from ubiquitous, and many diverse ecosystems have lost unique species with no redundancy, or groups of species with similar responses, ultimately leading to collapsed ecological functions [25,26]. Moreover, the gradual depletion of taxa owing to chronic stressors (e.g. overfishing, land use) can leave ecosystems more vulnerable to collapse if the remaining species show a limited set of tolerances to subsequent disturbances [7,27].

On coral reefs, a range of processes depend on the ability of reef-building corals to fix carbon, build skeletons and produce a complex and dynamic reef framework [28,29]. The abundance of corals (usually measured as the combined cover of all coral species) is frequently used to quantify reef condition. However, a focus on coral cover alone can mask important changes to reef composition and diversity. These shifts can have major consequences for the trait composition of assemblages [30–32], potentially affecting ecosystem functions such as carbonate accretion or the provision of habitat structure [33,34]. Analysis of species-level abundances and functional traits over years and decades is, therefore, required to reveal the capacity for response diversity to maintain reef functional composition as vulnerable species decline.

Here, we analyse changes in the total cover and trait diversity of coral assemblages over multiple decades. We focus on three potential scenarios of resilience (figure 1) and quantify the reassembly and response diversity of coral assemblages and their traits in the aftermath of a disturbance. We generate a trait space of coral taxa (table 1), and quantify response diversity by comparing the trait diversity of ‘winners’ (species that increased in abundance after recovery) with that of ‘losers’ (species that decreased after recovery). Our study focuses on case studies of reefs located on the Great Barrier Reef (GBR), Moorea in French Polynesia, and Jamaica. These locations allow for the comparison of reefs which differ markedly in their inherent species richness and functional composition [35].

2. Material and methods

(a) Time series data

Time series data were assembled for individual reefs from three different locations; Lizard Island, GBR (North Reef, 12° S, 145° E), Moorea, French Polynesia (Tiahura Reef, 17° S, 149° W) and Discovery Bay, Jamaica (Rio Bueno, 18° N, 77° W). Case studies were selected to include at least one cycle of disturbance and recovery. For each case study, coral composition was measured over a time-span of a decade or longer. Our analysis primarily focuses at mid-depth sites (7–15 m depth). However, additional censuses were taken in each location at shallow (1–7 m) and deep (15–30 m) sites. On Lizard Island, coral composition was recorded at three depths (1–3, 10 and 18–20 m) at seven time points between 1995 and 2017 [36]. In Moorea, coral composition was quantified at three depths (1–3 m, 8–10 m and 15–30 m) at five dates between 1979 and 2009 [37–39]. In Jamaica, coral composition was censused at three depths (7, 10 and 15–20 m) at 16 time points between 1977 and 2013 [7]. At each census, all hard coral colonies along five replicate 10 m transects were identified to genus level or greater and their intercepts were recorded to the nearest centimetre.

To measure taxonomic and trait composition consistently across these three case studies, including rare species, we pooled taxa into 44 taxonomic categories. Of these 44 taxonomic categories, 28 are genera, five are families and 11 are morphological subgroups for diverse and abundant genera, such as *Acropora* (e.g. staghorn *Acropora*, digitate *Acropora*, tabular *Acropora*), *Pocillopora* (e.g. *Pocillopora damicornis*, other *Pocillopora*) and *Porites* (e.g. branching *Porites*, massive *Porites*) [30]. Of these 44 categories, 30 occurred on Lizard Island, 20 in Moorea and 16 in Jamaica, reflecting in part the overall species richness at these three locations (species richness of reef-building scleractinians at each location ranges from approximately 400 on the GBR, to 180 in Moorea, and 65 in Jamaica).

(b) Coral trait diversity

In order to measure shifts in the functional trait diversity of coral assemblages through time, we used seven traits to measure trait-based dissimilarities among taxa: growth rate, skeletal density, maximum colony size (diameter), corallite width, interstitial branch spacing, colony height and colony surface area (table 1). Raw species-level data on coral growth rates, skeletal densities, colony size, corallite widths and growth forms were gathered from the Coral Traits Database [40]. Species were pooled by their taxonomic category, and average trait values were found

Table 1. Traits used in the analysis, and their functional relevance.

trait	categories used	reef function
growth rate (GR)	in mm yr ⁻¹ : 0–5 (1), 5–10 (2), 10–25 (3), 25–50 (4), 50–200 (5)	carbonate framework accretion; reef regeneration
skeletal density (SD)	in g cm ⁻³ : 0–1.2 (1), 1.2–1.5 (2), 1.5–1.8 (3), 1.8–2.1 (4), 2.1–3 (5)	carbonate framework accretion
corallite width (CW)	in mm: 0–1.5 (1), 1.5–6 (2), 6–12 (3), 12–25 (4); 25–100 (5)	filter feeding; nutrient capture
interstitial branch spacing (IB)	(1–5) based on morphological categories	habitat provision
colony height (CH)	(1–5) based on morphological categories	carbonate framework accretion; habitat provision
surface area to volume ratio (SV)	(1–5) based on morphological categories	primary productivity; nutrient cycling
maximum colony size (CS)	in cm: 0–50 (1), 50–100 (2), 100–200 (3), 200–400 (4), 400–2000 (5)	carbonate framework accretion; habitat provision

for each category. Trait values were subsequently placed into numerical groups between 1 and 5 to account for limitations in the precision of the data. Data coverage was mostly good across groups, however, some gaps remained. To facilitate the infilling of missing data, numerical (1–5) values were allocated based on shared phylogeny (molecular family) and morphology (growth form). Species growth form ('growth form typical' in the coral trait database) and *in situ* morphological measurements [35] were used to score taxa for colony height, surface area to volume ratio, and branch spacing (where non-branching taxa were given the lowest score for branch spacing). A multidimensional coral trait space was generated using a principal coordinate analysis (PCoA) based on a Gower distance matrix between each of the 44 taxonomic groups.

Trait diversity was quantified across locations and time intervals using an abundance-weighted metric of species dispersion in trait space; functional dispersion (FDis) [41]. These parameters measure the distances of each taxon from the mean coordinates of the assemblage, weighted by abundance (community-weighted means; CWM), thereby providing an estimation of the diversity of traits, and the degree to which abundance is distributed evenly among different sets of traits. Large values indicate that the predominant species occupy broad areas of trait space, representing a functionally diverse community. Low values indicate that the most abundant taxa are concentrated into a single area of trait space, suggesting a community dominated by functionally similar species [42]. Trait diversity calculations were conducted for each location using the 'FD' package in R, and trait-based differences were based on the Euclidean distance matrix of PCoA coordinates in the combined trait space [41]. To calculate trait diversity, four PCoA dimensions were used to minimize deviations between Euclidean and Gower distances and thus maximize the quality of the trait space [43], although different numbers of dimensions had little impact on the results (electronic supplementary material, figure S1a). Furthermore, to test how arbitrary variations in the trait-based analyses influenced our results, we conducted a sensitivity analysis by repeating our calculations using different numbers and combinations of traits to construct four-dimensional trait space (electronic supplementary material, figure S1b).

(c) Resilience and response diversity

We focused on three hypothetical scenarios of resilience. First, a highly resilient assemblage could recover to its original taxonomic and functional trait composition (figure 1a). Second, a subset of taxa could fail to recover, yet their traits or functions could be restored by different taxa that survive, or rapidly recover (response

diversity, figure 1b). Lastly, a deficit could be generated if a subset of taxa fail to recover, and their traits or functions are not restored by others (figure 1c). To test these scenarios in reef communities, we considered the extent to which the total abundance and trait diversity of corals changed across three time intervals: (1) pre-disturbance, (2) immediately following disturbance, and (3) after recovery. Pre-disturbance assemblages are not considered to be pristine or climax assemblages, but are simply the mature assemblages encountered during the earliest surveys at each site. The recovering assemblages were defined as assemblages that had regained most or all of their original coral cover prior to disturbance.

Response diversity is defined as differences in response to disturbance among taxa that contribute to the same ecosystem functions [17]. Unlike previous metrics of response diversity which measure different responses within functional groups [44], we quantified response diversity continuously in trait space using two tests. The first test measured the degree to which the trait space of losers (taxa that decreased in abundance after recovery) was replaced by the trait space of winners (taxa that increased after recovery). Under this test, high response diversity can occur when winners and losers each occupy broad and similar areas of trait space (measured using FDis and CWM, respectively). These patterns of response diversity were compared to null expectations using 1000 random permutations of observed losses and gains in abundance across trait space [18]. The second test quantified associations between changes in the abundance of taxa and changes in the abundance of their closest neighbours in trait space. A negative association (measured using Spearman's rank correlation coefficients) demonstrates high response diversity because large losses of abundance in taxa would coincide with large increases in abundance in functionally similar neighbours. A test of the relationship between the trait dissimilarity of all pairs of taxa and their differences in response to disturbance was also undertaken.

3. Results

In the decades following major disturbances, the trait-based functional composition of coral assemblages failed to fully recover at each location in the analysis, even where coral cover returned to pre-disturbance levels (figure 2). Disturbances such as storms, outbreaks of predatory starfish and mass bleaching because of heat extremes, initially drove rapid declines in coral cover (time points 1 and 2, figure 2a), which were followed by periods of recovery that varied in

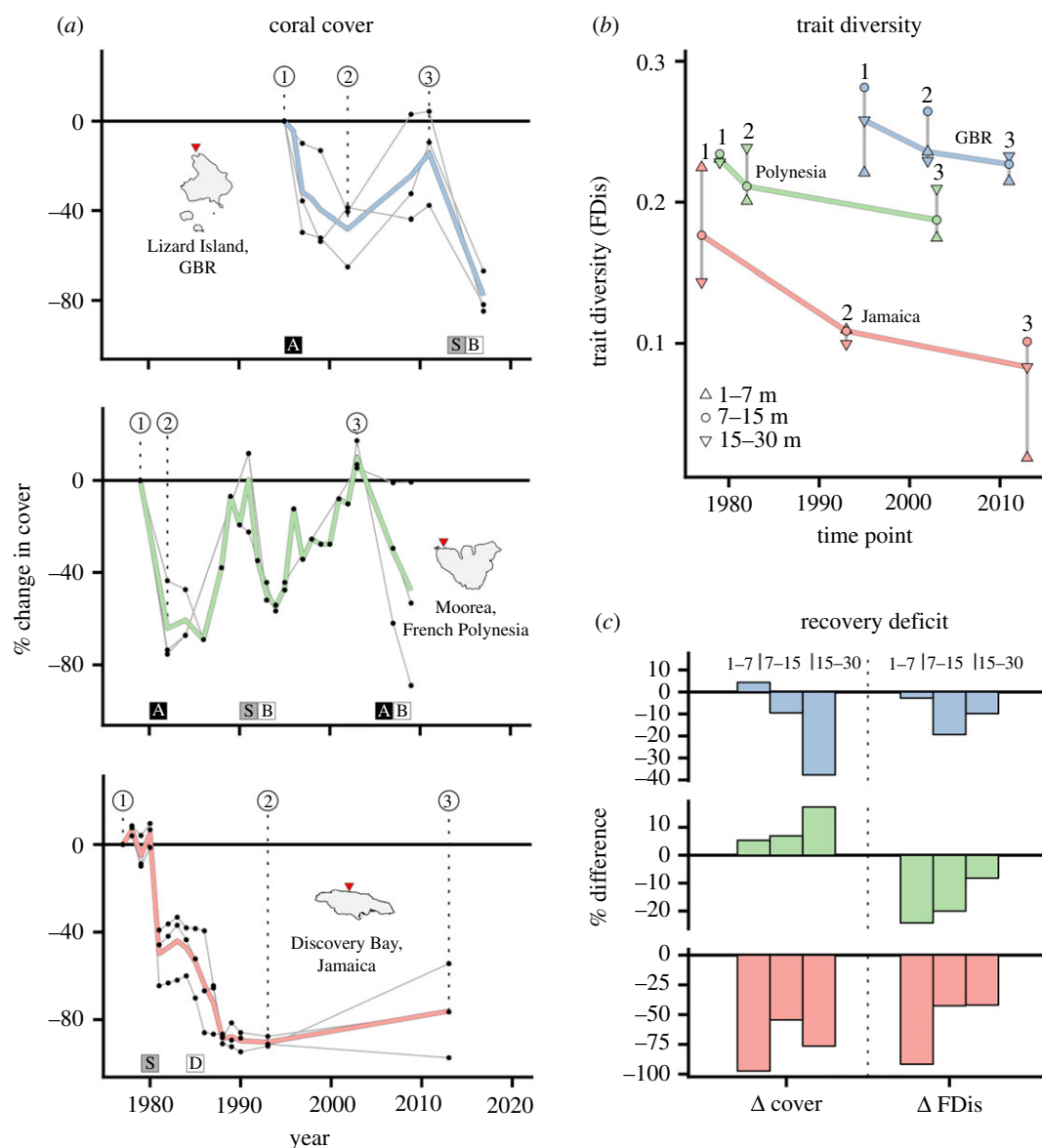


Figure 2. Disturbance–recovery cycles and loss of coral trait diversity. (a) Changes in coral cover on repeatedly surveyed reefs. Coloured lines are the mean trendline for three depths, which are shown individually in grey. Timing of original surveys varies between locations; Jamaica: 1977; Moorea: 1980; Lizard Island: 1995. Numbers indicate (1) pre-disturbance, (2) disturbed, and (3) recovering assemblages. Boxes indicate the timing of major disturbance events (B, bleaching; A, *A. planci* outbreak; S, storms; D, *Diadema* die-off). (b) Shifts in abundance-weighted trait diversity (FDIs) at three depths between (1) pre-disturbance, (2) disturbed, and (3) recovering assemblages. Coloured lines connect median trait diversity across depths through time. Vertical grey lines show the differences in trait diversity between depths at each time point. (c) The percentage difference in coral cover and trait diversity between pre-disturbance and recovering reefs (assemblages 1 and 3) at three depths. Negative values indicate a deficit. Positive values indicate a gain.

duration across different locations. Following disturbances on Lizard Island and Moorea, coral cover at most sites bounced back to over 90% of its original level within 10 years (time points 2 and 3, figure 2a). By contrast, recovery of coral cover was incomplete in Jamaica, where a hurricane in 1980 reduced cover on most reefs to approximately 5% of its original level for at least 8 years, followed by a subsequent partial recovery of coral cover 20 years later (figure 2a). Despite return trajectories of coral cover, trait diversity in each location declined following disturbance (time points 1–2, figure 2b), and continued to decline during recovery (time points 2–3, figure 2b). Consequently, comparisons with the pre-disturbance assemblages reveal substantial deficits in the trait dispersion of recovering assemblages (figure 2c).

Reef slope assemblages at mid-depth sites (7–15 m) in each location showed consistent declines in trait diversity following the return of coral cover (figure 2b,c). At Lizard Island, despite

reaching 90% of its original coral cover, trait diversity at mid-depths was depleted by 19% of its original level (figure 2c). Similarly in Moorea, coral cover in 2007 exceeded the original level measured in 1979 (7% absolute gain), yet the original trait diversity at mid-depths was diminished by 20%. In Jamaica, coral cover at mid-depth sites in 2013 returned to 46% of the original level measured in 1977, and the original trait diversity of assemblages was diminished by 43%. Deficits in trait diversity following recovery were generally similar among depths (figure 2b). Shallow and deep sites showed considerable losses of trait diversity in recovering assemblages in Moorea and Jamaica, despite the return of coral cover in Moorea (figure 2c). Exceptions occurred on Lizard island, where low-diversity shallow assemblages were initially dominated by a single taxon (tabular *Acropora*) which recovered following disturbance. Patterns of lower trait diversity in recovering assemblages were consistent when different

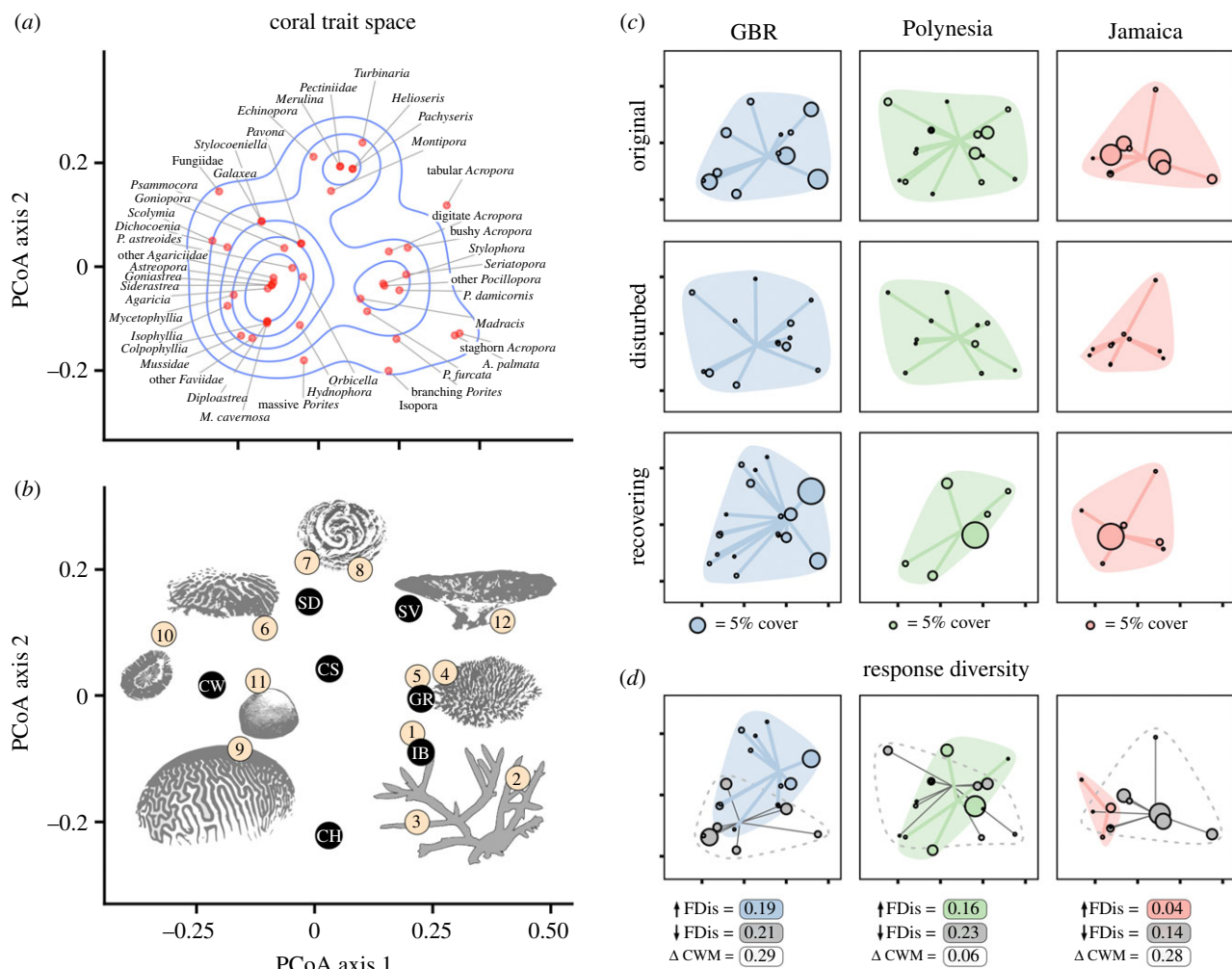


Figure 3. Shifts in abundance in coral trait space in three locations. (a) Coral trait space showing the positions of 44 taxonomic groups pooled across the three locations. Blue contour lines indicate the presence of distinct clusters of taxa. (b) Centroids of 12 morphological types in trait space: (1) complex-branching, (2) stag-horn, (3) columnar, (4) corymbose, (5) digitate, (6) encrusting, (7) upright-encrusting, (8) laminar, (9) massive, (10) solitary, (11) submassive, and (12) tabular. Letters indicate seven vectors used to generate the trait space (table 1). (c) Abundances of taxa in trait space, comparing original, disturbed and recovering assemblages on reef slopes. The sizes of points indicate the abundance of each taxon at each time interval. Lines connect each taxon to the abundance-weighted means of trait space. (d) Changes in abundance in trait space following disturbance and recovery (between time points 1 and 3). The sizes of points indicate the increase (coloured) or decrease (grey) in abundance. Lines connect each taxon to the mean coordinates of winners and losers, weighted by the increase or decrease in abundance, respectively.

combinations of traits were used to construct trait space (electronic supplementary material, figure S1b). Similar trait deficit patterns occurred when any one of the seven traits were removed from the analysis, and a large number of recovering sites remain deficient even when considerably fewer traits are included, demonstrating that these observations are robust to the number and type of traits used (electronic supplementary material, figure S1b).

Shifts in abundance across trait space between original and recovering assemblage have generally favoured a subset of taxonomic groups with limited trait diversity. In coral trait space, taxa are positioned continuously according to seven key traits, falling into clusters that correspond to broad morphological types (figure 3a,b). Reef slope assemblages were originally composed of abundant species with diverse functional attributes, including, massive, staghorn, and tabular corals on Lizard Island, bushy, digitate and non-attached corals in Moorea, and staghorn, digitate and submassive or platey corals in Jamaica. However, the following disturbance and return trajectories of coral cover, the abundance-weighted means shifted towards a subset of species (figure 3c), which

are good colonists, characterized by high rates of recruitment and growth (e.g. tabular *Acropora* on Lizard Island, *Pocillopora* in Moorea and *Agaricia* in Jamaica). Crucially, these early successional taxa represent different areas of trait space in each of these three locations, causing the three recovering assemblages to be dominated by distinct subsets of traits (figure 3c).

Changes in absolute abundances between original and recovering assemblages reveal taxa which are 'winners' and 'losers' (figure 3d). The lack of overlap between winners and losers in trait space reveals the limited capacity for response diversity in all locations, because taxa in many areas of trait space have declined with no alternate responses by functionally similar species (isolated grey points in figure 3d). On Lizard Island, winners and losers each occupied broad areas of trait space (shaded and dotted areas in figure 3d). However, the centroids of winners and losers, weighted by the gain or loss of cover, respectively, were distinct (grey and coloured lines in figure 3d, Δ CWM > 96% of random permutations), reflecting different functional attributes of taxa with large losses versus gains in abundance. By contrast, in Moorea, weighted centroids of winners and losers were similar

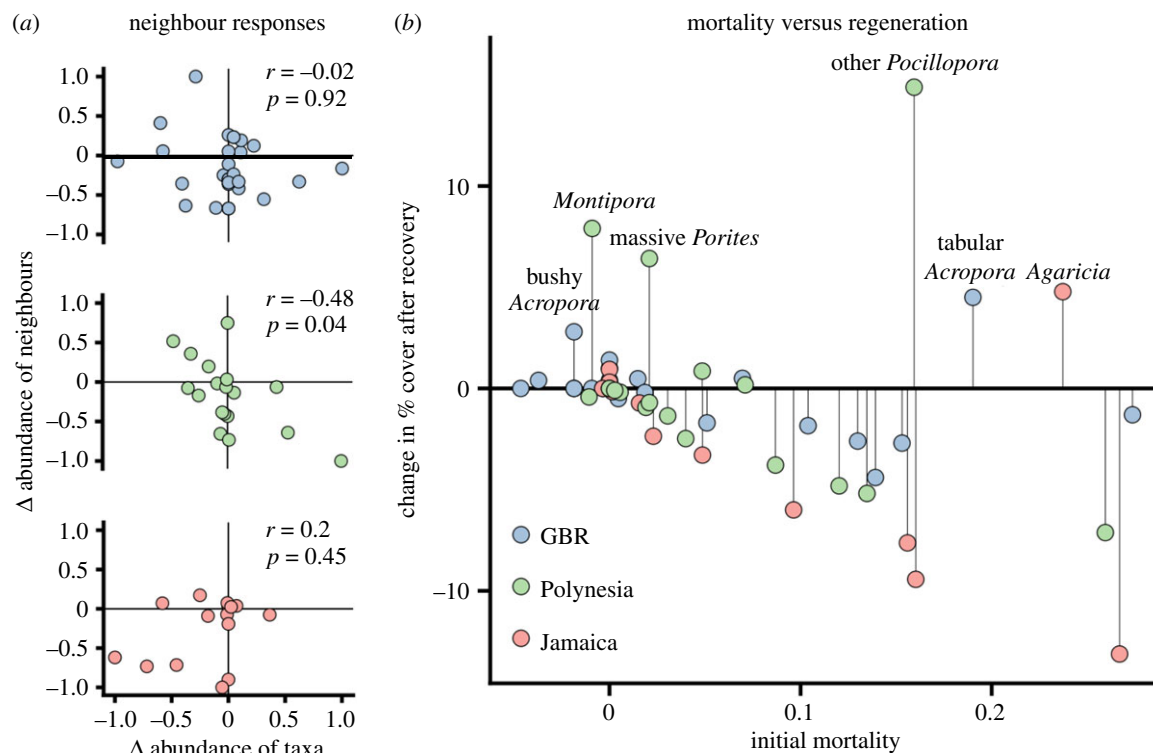


Figure 4. Response diversity driven by differential survival and regeneration among taxa. (a) Response diversity shown by changes in the abundance of taxa after recovery in relation to changes in the abundance of their closest neighbours in trait space. Shifts in neighbour abundance for each taxon are calculated as the summed loss or gain in abundance of the four closest neighbours (scaled between 0 and 1 in each location). Labels show Spearman's rank correlation coefficients. (b) Changes in the abundance of taxa after recovery in relation to susceptibility to the initial disturbance. Change in cover between original and recovering assemblages (time points 1 and 3) is shown on the y-axis. On the x-axis, initial mortality is quantified as the decrease in cover relative to the total assemblage decrease. Labels are included for taxa with large increases in abundance following recovery.

(Δ CWM < 95% of random permutations), indicating higher response diversity compared to Lizard Island. However, response diversity in Moorea did not occur across all areas of trait space, and consequently distinct sets of traits were lost without replacement (figure 3d). Response diversity was the least pronounced in Jamaica, where winners were concentrated into highly localized areas of trait space (figure 3d), and the weighted trait means of winners were distinct from losers (Δ CWM > 79% of random permutations).

Analysis of shifts in abundances within small groups of neighbouring taxa in trait space support these patterns of response diversity (figure 4a and electronic supplementary material, figure S2). Simultaneous increases in abundance among trait space neighbours did not occur at any location (upper right panels, figure 4a). Instances where taxa showed alternate responses to their closest neighbours (upper left and lower right panels, figure 4a) occurred primarily in Moorea ($r = -0.48$), to a lesser degree on Lizard Island ($r = -0.02$), and to a far smaller extent in Jamaica ($r = 0.2$). There was a tendency in all locations for groups of neighbouring taxa to show simultaneous declines (lower left panels, figure 4a), suggesting that response diversity was to some extent limited at each site, and particularly low in Jamaica. This trend is supported by the lack of a strong relationship between trait dissimilarity and difference in response to disturbance at any site (electronic supplementary material, figure S2). Consequently, while response diversity did occur to some extent among corals in our analysis, it did not occur comprehensively, forcing widespread depletions in trait space.

Increases in per cent cover in taxa relative to pre-disturbance levels can occur by two mechanisms. The first is by

having greater levels of resistance, allowing taxa to maintain high abundances throughout recurrent disturbances, requiring minimal colony or population growth. The second is through greater rebound potential following large declines, either through high rates of larval dispersal and colonization, or rapid regrowth from remnant coral tissue. Some 'winner' taxa in our analysis demonstrated limited mortality during the disturbance (figure 4b), and their increases may be attributed to higher survival (e.g. *Montipora* and *Porites* on Moorea and bushy *Acropora* at Lizard Island). Nevertheless, the greatest decadal increases in abundance occurred in taxa that were highly susceptible to the initial disturbance (e.g. tabular *Acropora* on Lizard Island, *Pocillopora* on Moorea, and *Agaricia* in Jamaica, figure 4b). Each of these taxa underwent severe declines followed by substantial recoveries, leading to increases in abundances that can be attributed primarily to larval colonization and growth. In Jamaica especially, survival was very low among all taxa during the decline trajectory, and the prominence of 'winner' taxa was almost entirely reliant on larval recruitment. The high reliance on recruitment for maintaining coral populations in Jamaica, and to a lesser extent on Lizard Island and Moorea, has led to the depletion of many areas of trait space where other taxa have not recovered, but continued to decline owing to limited recruitment and regrowth (figure 3).

4. Discussion

Recovering coral assemblages in this analysis have shown limited resilience to disturbance, demonstrated by long-

term (decadal) shifts in total abundance and trait diversity. Resilience is determined by the capacity of ecosystems to resist, or rapidly recover from pulse disturbances [4,8]. Moreover, a distinction can be made between assemblages that regain their original composition despite recurrent disturbances (figure 1a), versus those that maintain functional traits despite shifts in species composition (figure 1b). Neither signatures of resilience occurred in our analysis. Despite return trajectories in coral cover, recovering assemblages at both Indo-Pacific and Caribbean reef sites regained a limited subset of their original trait composition observed decades ago, generating deficits in trait diversity of between 19% and 43% on all mid-depth sites (figure 1c). These results indicate an inability of these reefs to return to a functionally diverse state, despite extended periods since major disturbance events.

Reefs in all regions are changing rapidly as coral communities reassemble into new configurations following chronic and pulse disturbances [7,45–47]. Long-term trajectories in community composition are increasingly affected by mass bleaching, disease, predator outbreaks and recruitment failure [3,7,36,48]. The loss of functional attributes under recurrent disturbances is determined by response diversity; the degree to which persistent taxa replace the functions of declining, vulnerable taxa. Response diversity can occur if taxa are similar in many respects, but differ in a fundamental attribute [15], such as susceptibility (e.g. stress tolerance, physical robustness) or rebound potential (e.g. fecundity, dispersal, recruitment, growth). For example, differences in thermal tolerance among seaweeds allow warm-adapted taxa to replace cool-adapted taxa [24], differences in mobility and site-fidelity in reef fishes make certain taxa more resistant to storms and bleaching [21,49], and differences in dietary preference among consumers can alter species susceptibility to prey loss [44], in each case potentially maintaining critical functions.

In corals, response diversity can arise from various sources, including differences in recruitment rate [50], biomechanical stability [51] and bleaching tolerance [48]. As climate change progresses, differences in thermal tolerance among photosynthetic symbionts (*Symbiodinium*) may be a valuable source of response diversity, allowing some species or populations of corals to survive severe bouts of heat stress while others decline [52,53]. Although corals in our analysis exhibited different responses to disturbance such as bleaching and hurricanes, limitations to response diversity are demonstrated by the distinctiveness of winners and losers in multidimensional trait space, reflecting differences in the contribution of taxa to a range of potential functions (table 1). This lack of response diversity is likely to be common in systems where traits linked with functions are also linked with species susceptibility to disturbance ('effect' and 'response' traits; [54]). Moreover, low response diversity has also been observed in systems with lower diversity (e.g. modified grasslands, [26]), and systems with a high severity of anthropogenic disturbance (e.g. tropical forests, [16]).

After severe disturbance events in which even tolerant taxa die, the maintenance of functions depends on rapidly recovering taxa which often occupy limited portions of trait space [55]. These regenerative taxa are important, because many ecosystems are naturally subjected to pulse disturbances. However, critical ecosystem functions are provided by larger and more long-lived taxa that can take many decades or centuries to rebuild populations once they are depleted. In terrestrial landscapes, for example, loss of large, long-lived trees can lead to

depleted states that are functionally compromised for decades or longer because of the limited capacity of these taxa to recruit and recover following elevated mortality [56]. Low levels of survival among corals in this analysis have led to limited response diversity, and has favoured taxa with smaller, shorter and simpler morphologies, with moderate-to-fast growth rates, and 'weedy' life-history traits, such as high size-specific fecundity [57], and high rates of mortality and recruitment [50,58]. Such taxa are often more susceptible to storms [59], mass bleaching [48] and predator outbreaks [36], potentially limiting response diversity during future successive disturbance events.

Despite limitations to response diversity in our analysis, the close proximity of some winners and losers in localized areas of trait space demonstrates that alternate responses by functionally similar taxa can maintain a small subset of traits that would have otherwise been lost. Smaller subsets of traits may be sufficient to restore some functions (e.g. those related to morphological complexity and fast growth on the GBR, figure 1b). Nevertheless, ecological functions that are reliant on high trait diversity, including the suppression of algal competition [60], coral productivity [61] and reef-building [28], are potentially deficient in most recovering assemblages. This emerging dynamic highlights the need to identify specific functions that are most important for reefs and test for the species and traits supporting them [29,62], so that their capacity to be maintained following shifts in the composition can be evaluated (e.g. [63,64]).

Patterns of response diversity and subsequent trajectories in functional trait composition are likely to have been influenced by the biogeographically distinctive pools of species across each of our locations [35]. For example, the high abundance of tabular and bushy corals in the Indo-Pacific has favoured shifts towards key areas of trait space that remain depleted in the Caribbean, where many of these groups are lacking. In the case of French Polynesia, major losses and gains in abundance occurred in broadly similar areas of trait space, a pattern that resembles moderate response diversity observed in grasslands [18]. Consequently, despite substantial losses, functional diversity remains relatively high in the Indo-Pacific (figure 2b), possibly reflecting the greater capacity of high-diversity assemblages to provide insurance (through response diversity) against ongoing degradation and loss. Nevertheless, major subsequent disturbances have now occurred at both of these Indo-Pacific sites (figure 2a), highlighting the diminishing return times between reef disturbance events [3], which may further limit the stabilizing influence of response diversity on coral reefs.

5. Conclusion

Climate change is altering the disturbance regimes of ecosystems, with forecasted increases in temperature extremes, droughts, intense precipitation, and storms [2]. On coral reefs, the increasing severity of mass bleaching events can limit survival among even the most tolerant taxa, and the increasing frequency of bleaching can limit their potential for recovery [3,30]. Abrupt transitions in ecosystems are increasingly common [5], leading to long-term alterations to the functional trait composition of assemblages [65], and deficits in the performance and functioning of recovering assemblages [9,10]. In this study, we show that despite the

apparent recovery in coral communities, reefs in different regions are already depleted following recovery from disturbances, mostly favouring rapid colonizers with more transient or unstable dynamics. The potential for response diversity in these depleted assemblages will dictate the traits and functions that persist as new disturbance regimes emerge.

Data accessibility. Data is available from the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.kh189321w> [66].

Authors' contributions. M.M. and T.P.H. conceived the study. M.S.P. and T.P.H. collected abundance data. M.M., M.O.H. and T.P.H. collated trait data. M.M., M.S.P. and M.O.H. analysed data. M.M. wrote the paper with input from all authors.

Competing interests. We declare we have no competing interests.

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