

Habitat degradation increases functional originality in highly diverse coral reef fish assemblages

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Abstract. As anthropogenic and natural disturbances intensify, there is mounting concern about the loss of functionally important or unique species. Functional redundancy, or the presence of several different species occupying similar functional niches, can provide insurance against diversity loss, but evidence for this effect is rare. Likewise, the ways in which functional redundancy patterns respond to disturbances are poorly known, impeding a thorough understanding of community-level dynamics post disturbance. Here, we use an extensive reduction of hard coral cover following a tropical cyclone to explore the response of a highly diverse reef fish assemblage to habitat degradation. We demonstrate that despite clear trait value-specific susceptibility of fishes to the disturbance, five of six functional indices (including functional richness and evenness) showed no relationship with habitat degradation. In contrast, functional originality, which quantifies the average functional uniqueness of species within an assemblage, increased post disturbance, exhibiting a negative, albeit weak, relationship with decreasing coral cover. The increase in functional originality is simultaneously driven by the loss of functionally similar species in susceptible groups (predominantly small planktivorous and omnivorous species that associate with live coral habitat) and the addition of functionally unique species in groups that benefit from the disturbance (large, non-territorial species feeding on algal turfs, detritus, and invertebrates). Our findings suggest that coral reefs with high coral cover can foster fish assemblages with low functional originality (i.e., high functional redundancy), therefore preventing detectible changes in some of the most commonly applied functional indices post disturbance. However, we caution that the limited resolution of trait-based approaches may mask the loss of functionally unique species and that, with an increase in functional originality, post disturbance assemblages may be less suited to adequately maintain certain ecosystem functions in the face of future disturbances. Thus, there is an urgent need for further exploration of the dynamics between disturbances, functional redundancy, and ecosystem functioning.

Key words: biodiversity; climatic disturbance; coral cover; coral reef fish; Cyclone Ita; functional redundancy; functional richness; functional traits; habitat loss; niche partitioning; response diversity; tropical storm.

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‡ Correction added on 20 February 2017, after first online publication: Coral cover data were collected by Zoe T. Richards, who has therefore been included as a co-author.

INTRODUCTION

Over the last two decades, there has been mounting evidence for a link between biodiversity and ecosystem functioning (Loreau et al. 2003, Duffy 2008, Cardinale et al. 2012, Gamfeldt et al. 2015). In particular, functional diversity (i.e., the diversity of ecological roles performed by species within an ecosystem) has emerged as a crucial component for the sustainability of ecosystems worldwide (Tilman et al. 1997, Petchey and Gaston 2006, Duffy et al. 2016). While functional diversity is highly susceptible to both natural and anthropogenic disturbances (Worm et al. 2006, Cardinale et al. 2012), functional redundancy may act as biological insurance against the loss of diversity following disturbances (Duffy et al. 2001, Rosenfeld 2002, Loreau et al. 2003). Functional redundancy exists when the niches of several species overlap to the degree that a portfolio of functionally equivalent species is present within an ecosystem (Yachi and Loreau 1999). There is preliminary empirical evidence to support the presence of functional redundancy in natural systems (Duffy et al. 2001, Bêche and Statzner 2009, Gallagher et al. 2013, Mouillot et al. 2014); however, outside of controlled experiments (Isbell et al. 2011, Joner et al. 2011, MacDougall et al. 2013), there is little indication for the buffering capacity of functional redundancy, particularly in vertebrate assemblages (Barnum et al. 2013).

Despite the importance of functional diversity and redundancy for our understanding of ecosystems' responses to disturbance, they are inherently difficult to measure. Recently, trait-based approaches, which quantify a species' ecological role using either individually measurable variables (traits), or discrete species-level trait values (which are categorical and commonly extracted from the literature), have emerged as the primary method of evaluating functional assemblage structure (McGill et al. 2006, Petchey and Gaston 2006, Laliberté and Legendre 2010, Mouillot et al. 2014). Both measurable traits and categorical trait values permit the calculation of a series of functional diversity indices, which collectively quantify multiple facets of functional diversity patterns in species assemblages (Box 1; Petchey and Gaston 2006, Mouillot et al. 2013). Among these indices, functional richness (the range of ecological niches occupied by an assemblage) and functional

evenness (the regularity with which these niches are represented) are the most commonly used metrics (Petchey and Gaston 2006). In addition, a suite of supplementary indices has also been proposed, including functional divergence, functional dispersion, functional specialization, and functional originality (Box 1; Mouillot et al. 2013).

As species loss following disturbances is typically nonrandom (Smith and Knapp 2003), a frequently held baseline assumption is that functional diversity indices will decrease in response to disturbance (Mouillot et al. 2013). Empirical support for this hypothesis exists from hoverflies to birds, suggesting that functional richness, evenness, divergence, dispersion, and specialization decrease after disturbance, particularly in the context of habitat degradation (Ernst et al. 2006, Schweiger et al. 2007, Flynn et al. 2009, Bihn et al. 2010). Similarly, functional originality has decreased following anthropogenic disturbance in fish assemblages, resulting in assemblages of functionally similar species (Mouillot et al. 2008, Buisson et al. 2013). Such loss of functional originality following disturbance can occur if species with unique sets of discrete trait values are selectively removed from the assemblage, resulting in smaller pairwise distances among species in functional trait space. However, if high functional redundancy (or at least, similarity) exists within assemblages, the loss of functionally redundant species is likely to increase functional originality (as remaining species become more unique), while stabilizing other indices such as functional richness. Thus, although not commonly considered in this context, functional originality may represent an important indicator of an assemblage's functional redundancy.

Coral reef ecosystems are a focal system for the study of functional redundancy due to their high diversity and vulnerability to human disturbances (Knowlton and Jackson 2008). To date, most reports suggest that functional redundancy is rare in marine consumer assemblages, which instead spread their species across numerous complementary functional entities (Micheli and Halpern 2005, Halpern and Floeter 2008, Brandl and Bellwood 2014a). Coral reef fishes are of particular interest, due to their exceptional diversity, high susceptibility to natural and anthropogenic disturbances, and their performance of critical ecosystem functions such as herbivory or nutrient cycling (Bellwood et al. 2004, Allgeier et al.

Box 1. Definition of terms relating to functional traits, functional diversity, and redundancy. Functional diversity is defined as the sum of all six multidimensional functional diversity indices. Redundancy patterns are defined as the sum of redundancy, complementarity, vulnerability, and over-redundancy. Definitions are aligned with those provided in McGill et al. (2006), Slade et al. (2007), and Mouillot et al. (2013, 2014).

Functional diversity	
Functional richness	Proportional volume of the synthetic niche space encompassed by the outermost vertices of the assemblage
Functional evenness	Biomass-weighted regularity of species in functional niche space along a minimum spanning tree
Functional divergence	Proportion of biomass on the periphery of the synthetic niche space representing species with extreme trait combinations, based on the average distance from the center of the assemblage
Functional dispersion	Biomass-weighted mean distance from the center of the assemblage in the synthetic niche space
Functional specialization	Average distance of species from the center of the synthetic niche space
Functional originality	Average pairwise distance between a species and its nearest-neighbor species in synthetic niche space
Redundancy patterns	
Functional group	All species that are united by a given trait value (e.g., all “planktivores”)
Functional entity	Suite of species characterized by the exact same set of trait values
Functional complementarity	Richness of functional entities within a functional group
Functional redundancy	Average species richness within functional entities of an assemblage or functional group
Functional vulnerability	Proportion of an assemblage’s or functional group’s functional entities with only one species
Functional over-redundancy	Proportion of species within functional entities, which exceed the level of redundancy

2014). Among reef fishes, functional redundancy is known to be limited in two functional groups, large-bodied herbivores and apex predators, which are particularly susceptible to anthropogenic exploitation (Bellwood et al. 2004, Burkepile and Hay 2008, Stallings 2009, Rasher et al. 2013, Brandl and Bellwood 2014a). In contrast, functional redundancy in other common reef fishes, such as butterflyfishes (f. Chaetodontidae) and damselfishes (f. Pomacentridae), is rarely quantified, despite their known susceptibility to natural disturbances that degrade live coral habitat (Wilson et al. 2006, Emslie et al. 2011). However, as opposed to drastic declines in ecosystem functioning following losses of herbivorous fishes and apex predators through anthropogenic exploitation (Friedlander and DeMartini 2002, Bellwood et al. 2004), natural disturbances do not commonly result in drastic shifts in fish functional structure (but see Graham and Nash 2013, Emslie et al. 2014). This stability of reef fish functional structure, despite high trait-specific susceptibility to habitat degradation, may be rooted in the recently identified over-redundancy in these functional groups (i.e., the proportion of species in excess of

the average level of redundancy; Mouillot et al. 2014, Bellwood et al. 2016), but to date, no evidence for links between over-redundancy in fishes and their response to disturbance exists.

While our understanding of functional redundancy has greatly benefited from long-term experiments (Isbell et al. 2011, Reich et al. 2012), such experiments are normally limited to artificial assemblages and/or unnatural manipulations. In contrast, despite their phenomenological nature, natural experiments provide valuable opportunities to test predictions about the effect of disturbances on functional diversity and the role of functional redundancy in mediating these effects under natural settings (Bihn et al. 2010, Barnum et al. 2013). In April 2014, Tropical Cyclone Ita directly passed over the reefs around Lizard Island in Australia’s northern Great Barrier Reef, resulting in a substantial and widespread decrease in live coral cover. Thus, as detailed data on fish assemblages predated the disturbance existed (Ceccarelli et al. 2016), the cyclone created an opportunity to explore the functional response of reef fishes to this severe natural disturbance across a gradient of habitat degradation.

Here, we utilize categorical trait values to functionally characterize species, along with in situ estimates of reef fish biomass to explore the effect of habitat degradation (reductions in live coral cover) on the functional structure of reef fish assemblages. We account for the multifaceted nature of functional diversity using six multidimensional functional diversity indices: functional richness, functional evenness, functional divergence, functional dispersion, functional specialization, and functional originality (Box 1; Mouillot et al. 2013). To further inspect redundancy patterns, we also quantify the extent of functional redundancy, complementarity, vulnerability, and over-redundancy within the whole assemblage and within four selected functional groups that showed clear responses to the cyclone (planktivores, omnivores, macro-invertivores, turf/detritivores).

Given available evidence on the response of reef fish assemblages to natural disturbances, we hypothesized: (1) that reef fish species will show trait value-specific susceptibility to the cyclone and, if this is the case, (2) that habitat degradation will result in reductions of functional diversity indices, unless the detrimental effects of habitat degradation are buffered by high functional redundancy within vulnerable functional entities. In the latter case, we predicted an increase in functional originality, as functionally similar species succumb to the disturbance.

METHODS

Fish biomass

We surveyed coral reef fish assemblages at 14 sites around Lizard Island, a granitic mid-shelf island in the northern Great Barrier Reef (14°39.873 S, 145°26.715 E) in September 2011 and in January 2015, 10 months after Tropical Cyclone Ita passed over Lizard Island. At each site, we performed three 50-m belt transects in two depths (3 and 9 m; $n = 6$ transects per site) using two transect widths (50 × 1 m belts for small site-attached damselfish species; 50 × 5 m for all remaining large, mobile fishes). We identified all individuals of diurnal, noncryptic, resident reef fish species to species level and recorded their total length to the nearest centimeter. Subsequently, we calculated relative biomass (kg/1000 m²) for each species at each site using previously published length-weight relationships (Ceccarelli et al. 2016).

Concurrently, we determined live coral cover at each site using line-point intercept transects with the same replication as detailed above. The 14 sites are characterized by different exposure regimes, ranging from lagoonal sites to sites exposed to southeastern trade winds. Biomass data are provided in Data S1 (see Metadata S1 for description).

Functional trait values

We assigned discrete trait values to all species from four different categories, relating to their dietary preferences, habitat association, territoriality, and maximum body size (Table 1). We chose trait categories based on their demonstrable sensitivity to natural disturbances (Wilson et al. 2006, Graham et al. 2011), and their relationship with critical ecosystem processes (e.g., herbivory, nutrient transfer, predation; Mouillot et al. 2014), making trait values both effect and response trait values. Specifically, previous work suggests that small, sedentary, coral-dependent species that feed on small benthic or planktonic invertebrate prey are particularly susceptible to habitat degradation, while large mobile carnivores and herbivores are commonly less affected (Wilson et al. 2006, Graham et al. 2011, Pratchett et al. 2011). The vulnerability of small sedentary species is prevalently linked to their reliance on shelter and food provided by topographically intricate live coral structures, which are frequently destroyed by high-energy disturbances such as cyclones. We performed the trait value assignment using published information (Randall et al. 1997, Allen et al. 2003, Brandl and Bellwood 2014b) and information available on FishBase (www.fishbase.org). Trait values within a given category were mutually exclusive, resulting in a total of 512 possible trait combinations within the entire fish fauna surveyed. Trait assignments are provided in Data S1, and the number of species within each category is given in Appendix S1: Table S1.

Trait value-specific responses

We estimated the response of functional trait values to the disturbance, depth, and exposure to the prevailing trade winds using a redundancy analysis based on biomass data (Appendix S1: Fig. S1). As the analysis showed no effect of depth on fish assemblages, we pooled transects from both depths for subsequent analyses. To permit

Table 1. Functional trait values used to classify fishes based on their dietary preferences, habitat associations, territoriality, and body size.

Category	Trait value	Description
Diet	Plankton	Feeding on planktonic invertebrates
	Omniv	Omnivorous, feeding on a range of food items including plant and animal material
	SessInv	Feeding on sessile invertebrate prey such as corals, sponges, and ascidians
	Algae	Feeding on macroalgal thalli such as <i>Sargassum</i> sp.
	Fish	Feeding on teleost fishes of all sizes
	EAM	Feeding on filamentous algal turfs as well as associated organic matter such as detritus
	InvMac	Feeding on mobile, benthic, macroscopic invertebrates such as echinoids or gastropods
	InvMic	Feeding on mobile, benthic, microscopic invertebrates such as copepods
	Habitat	Coral
Rubble		Associating with loose coral rubble fields
Mangr.		Associating with mangroves and estuaries
Hard		Associating with hard, rocky substratum
Anem.		Associating with anemones
Sand		Associating with sandy habitats
Seagr.		Associating with seagrass beds
Algae		Associating with macroalgal beds such as <i>Sargassum</i> sp.
Territoriality		Territorial
	Non-territorial	Establishing no territories or loose home ranges which are defended only against intraspecific intruders
Size	Small	<150 mm
	Medium	151–300 mm
	Large	301–600 mm
	Very large	>600 mm

Note: Traits were chosen to reflect both response and effect traits (which are indistinguishable in this instance).

predictions about each trait value's likelihood of benefitting or disadvantaging species in the wake of the cyclone, and due to the nature of biomass data (which is often zero-inflated and overdispersed, and therefore difficult to model accurately), we then divided species into "winners" and "losers" (Mouillot et al. 2013). The classification into winners and losers included species not recorded in 2011 at a given site that were present after the disturbance (labeled as winner species), and species that disappeared entirely after the disturbance (labeled as loser species). Only species in which the magnitude of biomass change exceeded 50% of the initial biomass were considered. We then fitted a binary variable to every species, reflecting its performance after the cyclone (1 = winner, 0 = loser), and included each species' trait values as categorical descriptor variables. This resulted in separate data sets for the four categories of discrete trait values (diet, habitat, territoriality, size) and their response to the

disturbances (winner or loser), which included 1586 observations (Data S1). We then ran four Bayesian mixed models (BMMs), for which we fitted the binary variable indicating winning (1) or losing (0) as the response variable, and a given category of trait values (diet, habitat, territoriality, size) and their respective levels (e.g., planktivory, omnivory) as fixed effect. We applied a binomial error distribution and also fitted site (nested within exposure regime) as a random factor (Gelman et al. 2003). As residual variance cannot be estimated in categorical BMMs, we fixed the residual variance to 1 while using uninformative priors on the fixed and random effect parameters (Hadfield 2010). Each BMM was run for 3,000,000 iterations with an initial burn-in phase of 50,000 and a thinning interval of 1000. Based on the model parameters, we then predicted the probability of trait values biomass to increase or decrease following the disturbance and assessed the performance among trait values using mean

predicted posterior distributions and their 95% credible intervals.

Functional diversity indices

To evaluate the functional diversity of fish assemblages, we first calculated the pairwise distances between species using Gower's distance metric. Based on the pairwise distances, we used principal coordinate analyses (PCoA) for the construction of synthetic four-dimensional niche spaces within which the species were arranged based on their trait values. Four dimensions were chosen as a trade-off between the extracted information and the computing time. We then used the biomass-weighted fish species as vertices in a four-dimensional hyperspace to calculate six functional diversity indices at each site and time point (Box 1). Following this, we first performed BMMs to assess the change in indices between years across all sites (resulting in $N = 28$). To do so, we fitted year as a fixed effect and site nested within exposure as a random effect. To account for the potential bias arising from the chosen functional classification scheme, we performed a sensitivity analysis by repeating the calculation of functional indices twice with different subsets consisting of three of the four trait categories, and assessing their values at the two time points (Appendix S1: Fig. S2). To further examine whether these changes are related to habitat degradation, we then modeled the relationship between changes in each functional diversity index and live coral cover. To do so, we fitted the change in functional index values (Δ) as the response variable with a Gaussian error distribution, and change in coral cover (Δ % coral cover) and initial coral cover (% coral cover 2011) as fixed effects. Data were scaled and centered before the analysis to yield comparable values for all indices. We used uninformative priors for the fixed effect and the residual variance. Models were run for 3,000,000 iterations with a burn-in of 50,000 and a thinning interval of 100.

Changes in functional redundancy

To disentangle functional redundancy patterns in the response of fish assemblages, we investigated species richness patterns within any given functional entity (i.e., a unique combination of discrete trait values; Mouillot et al. 2014) for both the entire assemblage and a suite of functional groups. From these data, four metrics can be extracted for

any given assemblage (Box 1), describing the assemblage's level of redundancy (i.e., the average species richness per functional entity; Fonseca and Ganade 2001), complementarity (i.e., the number of unique functional entities within a given functional group; Slade et al. 2007), vulnerability (i.e., the proportion of functional entities represented by only one species; Bihn et al. 2010), and over-redundancy (i.e., the proportion of species in excess of the mean level of redundancy; Mouillot et al. 2014). As previously, we first fitted each index (redundancy, complementarity, vulnerability, and over-redundancy) as a response variable with a Gaussian error distribution, while fitting year as a fixed effect and site nested within exposure as a random effect. Complementarity was log-transformed prior to this analysis. We then explored the relationship of each index with coral cover, by fitting the change in each index at each site (Δ) as a response variable, and change in coral cover (Δ % coral cover) and initial coral cover (% coral cover 2011) as fixed effects. Models were run with the same specifications as functional diversity models, again using scaled and centered data to ensure comparability.

Finally, we calculated the same four indices (redundancy, complementarity, vulnerability, and over-redundancy) for four functional groups (planktivores, omnivores, macro-invertivores, and turf-feeders/detritivores). Then, we analyzed all 16 indices using a permutational multivariate analysis of variance (PERMANOVA, 9999 permutations), with coral cover and year (2011 and 2015) fitted as fixed effects, while fitting site as a blocking stratum. To visualize the results, we produced a nonmetric multidimensional scaling ordination based on Euclidean distances of log-transformed indices.

Chain convergence for all BMMs was assessed using chain trace plots. All analyses were performed and visualized using the software R (R Development Core Team 2015) and the packages *ape*, *cluster*, *geometry*, *ggplot2*, *MCMCglmm*, *rcdd*, and *vegan* as well as the modified function *FDchange*.

RESULTS

We found clear trait value-specific responses to Cyclone Ita, with several trait values showing strong deviations from the baseline assumption of no change in biomass (0.5 on the y -axis; Fig. 1;

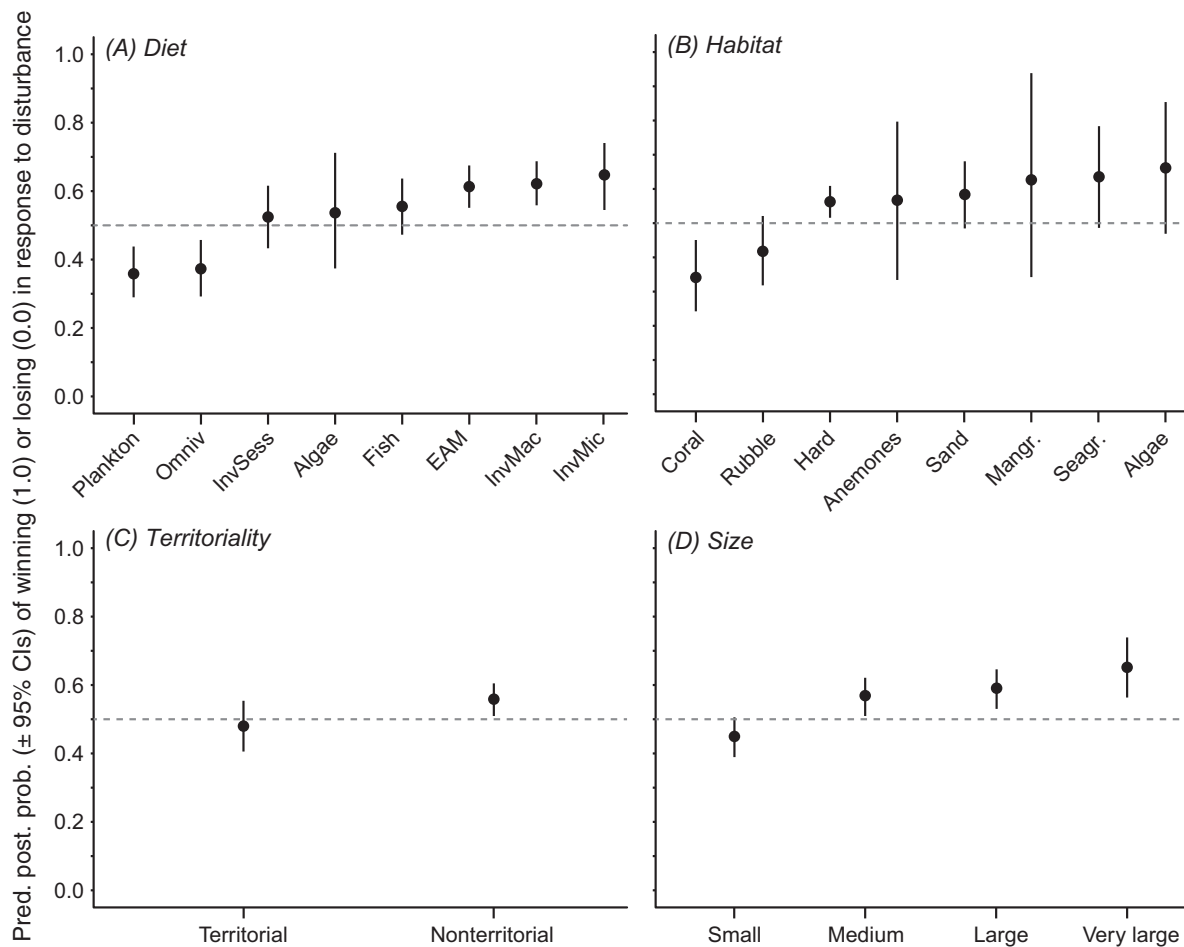


Fig. 1. Predicted posterior probabilities ($\pm 95\%$ credible intervals) from binomial Bayesian mixed models (BMMs), illustrating trait-specific responses in the reef fish assemblage following Cyclone Ita ($n = 1586$). The line originating at 0.5 on the y -axis denotes the value at which a trait was perfectly balanced between winning (increases in biomass exceeding 50% of initial biomass) or losing (decreases in biomass exceeding 50% of initial biomass) after the disturbance. Traits in which the credible intervals do not intercept 0.5 were likely to increase or decrease in biomass after the disturbance. Panels show the four different categories, including diet (A), habitat (B), territoriality (C), and maximum body size (D). “Omniv”, plant and animal material; “InvSess”, sessile invertebrates; “EAM”, epilithic algal matrix; “InvMac”, macroscopic benthic invertebrates; “InvMic”, microscopic benthic invertebrates. “Small” < 150 mm; “Medium” = 151–300 mm; “Large” = 301–600 mm; “Very large” > 600 mm.

Appendix S1: Fig. S1). Among dietary trait values, omnivores and planktivores were most likely to undergo biomass declines after the cyclone, as their parameter estimates were exclusively negative (omnivores: posterior mean estimate [PM] = -0.644 ; lower 95% credible interval [LCI] = -1.084 ; upper 95% credible interval [UCI] = -0.207 ; planktivores: PM = -0.697 ; LCI = -1.095 ; UCI = -0.304). In contrast, there was strong evidence that turf-feeders/detritivores,

macro-invertivores, and micro-invertivores were most likely to increase in biomass (turf-feeders/detritivores: PM = 0.570 ; LCI = 0.253 ; UCI = 0.900 ; micro-invertivores: PM = 0.756 ; LCI = 0.228 ; UCI = 1.297 ; macro-invertivores: PM = 0.614 ; LCI = 0.294 ; UCI = 0.973). The credible intervals of all other dietary trait values intersected 0.5, suggesting no substantial changes in their biomass between 2011 and 2015. In terms of habitat associations, species relying on live coral were

most likely to decline, suggesting substantial declines from 2011 to 2015 (live coral: $PM = -0.817$; $LCI = -1.387$; $UCI = -0.240$). Species relying on loose coral rubble were also negatively affected, but their predicted probability of winning or losing intersected 0.5, providing only weak evidence for biomass changes following the cyclone ($PM = -0.413$; $LCI = -0.896$; $UCI = 0.149$). In contrast, species associated with the underlying rocky reef matrix were likely to increase ($PM = 0.311$; $LCI = 0.075$; $UCI = 0.544$), while all other trait values showed no effects. Non-territorial species were likely to benefit from the disturbance ($PM = 0.292$; $LCI = 0.046$; $UCI = 0.525$), while territoriality had no discernable effect ($PM = -0.100$; $LCI = -0.477$; $UCI = 0.266$). Body size also influenced the chances of change in biomass: There was strong evidence for a decrease in biomass for the smallest fishes ($PM = -0.249$; $LCI = -0.555$; $UCI = 0.028$), while all other size classes consistently increased in biomass (medium size: $PM = 0.344$; $LCI = 0.042$; $UCI = 0.606$; large size: $PM = 0.454$; $LCI = 0.142$; $UCI = 0.731$; very large size: $PM = 0.777$; $LCI = 0.285$; $UCI = 1.241$). This was consistent when using absolute or proportional biomass change (Appendix S1: Figs. S1 and S3).

Despite the clear trait value-specific responses to the cyclone, we found no detectable changes between 2011 and 2015 in five of six functional indices (Fig. 2a). In contrast, functional originality increased in 2015 ($PM = 0.059$; $LCI = 0.035$; $UCI = 0.083$). This effect was supported by the sensitivity analysis, which revealed an increase in functional originality from 2011 to 2015 regardless of the number and identity of trait categories used (Appendix S1: Fig. S2). Relating the changes in functional indices to Δ % coral cover also supported the increase in functional originality (Fig. 2b–g), because functional originality increased slightly as habitat became more degraded ($PM = -0.490$; $LCI = -1.263$; $UCI = 0.269$). Notably, Coconut Beach, which had the highest initial species richness (127 species), was identified as a site where extensive degradation of live coral cover resulted in a substantial decline in functional richness (Fig. 2b), suggesting that at this site, several functionally unique species succumbed to the disturbance (Appendix S1: Table S4). Accordingly, excluding this site from the analyses eliminated a spurious relationship

between functional richness and Δ % coral cover (including Coconut Beach: $PM = 0.336$; $LCI = -0.426$; $UCI = 1.128$; excluding Coconut Beach: $PM = -0.022$; $LCI = -0.682$; $UCI = 0.616$), while substantially strengthening the relationship between functional originality and Δ % coral cover ($PM = -0.716$; $LCI = -1.50$; $UCI = 0.076$). Initial coral cover had no effect on the indices.

Furthermore, we found no changes in the four redundancy indices between 2011 and 2015 when examining the entire assemblage. Likewise, none of the indices exhibited a relationship with Δ % coral cover (Fig. 3), although coral cover negatively affected Δ over-redundancy in 2011, largely due to one outlier (Palfrey Lagoon; Fig. 3e). However, when examining patterns within affected functional groups (planktivores, omnivores, macro-invertivores, turf/detritivores), we detected evidence for a considerable effect of the disturbance (PERMANOVA pseudo- $F = 3.415$; pseudo- $R^2 = 0.115$), although coral cover had little explanatory power (pseudo- $F = 1.169$; pseudo- $R^2 = 0.040$). Specifically, the nMDS ordination suggested high levels of over-redundancy in planktivores and omnivores, as well as high complementarity of planktivores for assemblages in 2011. In contrast, high complementarity and vulnerability of macro-invertivores were characteristic of 2015 (Fig. 4).

DISCUSSION

Our results indicate that on coral reefs, extensive live coral habitat fosters high superficial functional redundancy in reef fishes, which may act as biological insurance against natural disturbances. Based on relatively coarse categorical functional groupings, there appear to be many species performing roles that are highly susceptible to natural disturbances, ensuring the representation of these functional entities despite substantial declines in the biomass of affected species. For example, numerous small-bodied, coral-associated planktivorous fishes perform the transfer of pelagic nutrients to the benthic community (cf. Bellwood et al. 2016). Consequently, even if some of these species disappear in the wake of extensive habitat degradation, high redundancy of planktivorous species may ensure at least the rudimentary representation of their functional role on coral reefs. However, we also

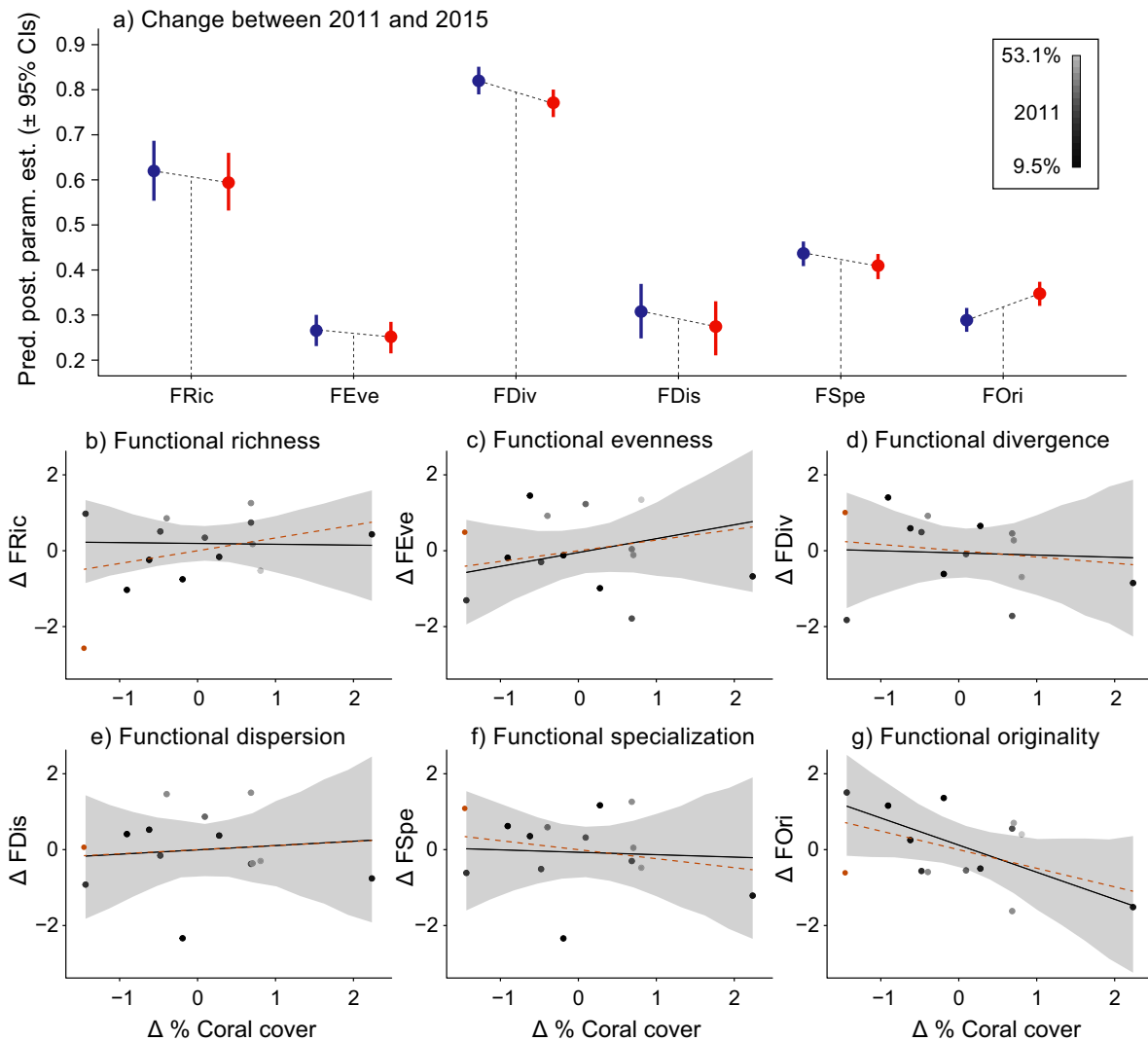


Fig. 2. Changes in functional diversity indices between years (a) and in relation to changes in % coral cover (b–g). (a) Between 2011 and 2015, only functional originality showed a considerable change, increasing in the year after the disturbance. (b–g) The change in functional originality appears to be related to changes in coral cover, as the two variables exhibit a weak negative relationship. Dots represent superimposed raw values (colored by their initial coral cover values), while the solid line and shaded area represent the predicted model fit. Coconut Beach (tan dot) was excluded from the analysis, as it was identified as the only site where a strong decline in coral cover resulted in a sharp decrease in functional richness, suggesting that at this site, many functionally unique species were lost. Tan, dashed lines represent the predicted model fit when Coconut Beach is included. All data were scaled and centered prior to analyses to permit comparability among indices.

show that continuing habitat degradation can erode functional redundancy by reducing the number of species that perform the same role, suggesting that the capacity to which these functions are performed may be diminished. Similarly, habitat degradation may also lead to a

reduction of the variety of roles performed within a functional group (less complementarity, i.e., the complete loss of a planktivorous functional entity). Such attrition of the system's buffering capacity and the variety of closely related functions that are performed may not be

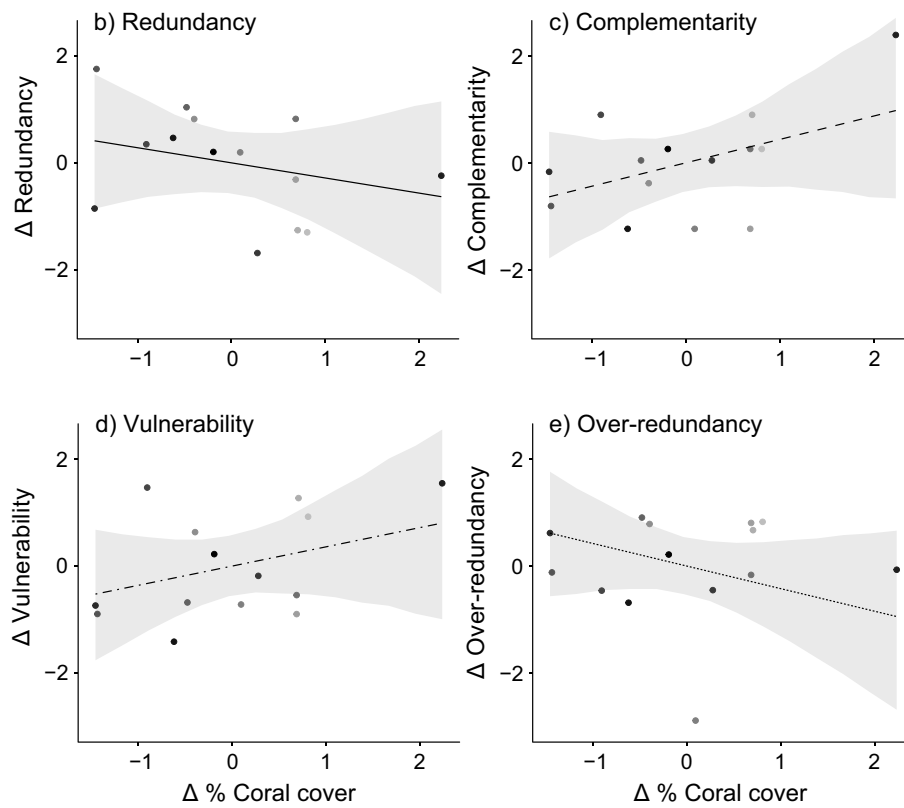
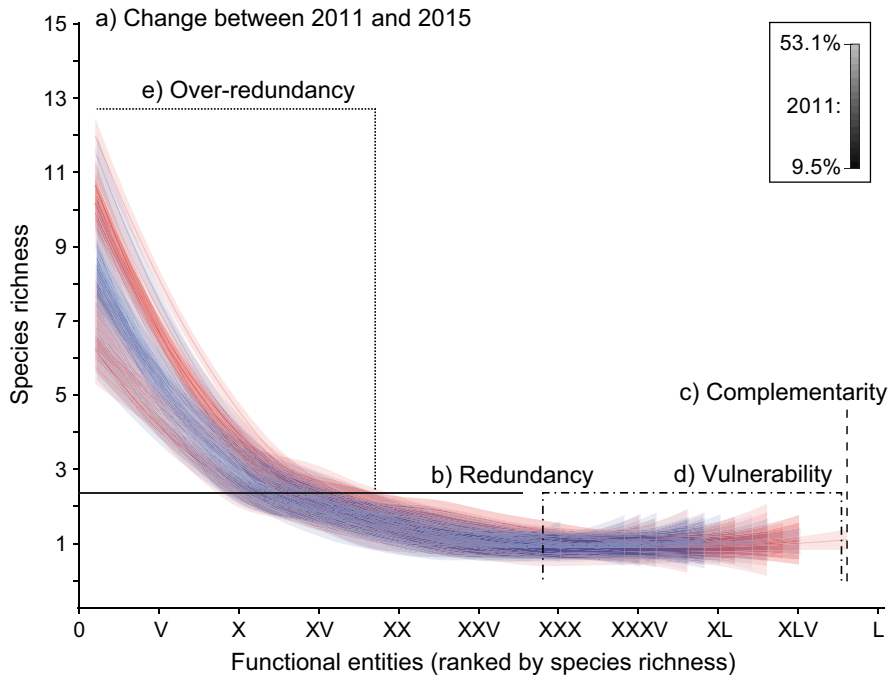


Fig. 3. Redundancy patterns of the examined reef fish assemblages before (blue) and after (red) Cyclone Ita (a) and in relation to changes in % coral cover (b–e). (a) Functional entities ranked by their species richness (y -axis) are denoted in roman numerals on the x -axis. A LOESS smoother ($\pm 95\%$ CIs) provided curves for each of the 14 sites before and after the cyclone ($n = 28$). The overlap between pre- and postcyclone assemblages suggests that assemblage-level redundancy showed no changes after the cyclone. Redundancy indices and the measures they pertain to are highlighted. (b–e) There was no tangible relationship between the change in functional redundancy indices and changes in coral cover. Dots represent superimposed raw values (colored by their initial coral cover values), while lines and shaded ribbons represent the predicted model fit ($\pm 95\%$ CIs). Line types are consistent with the description of indices in (a). All data were scaled and centered prior to analyses to permit comparability among indices.

detectable if standard community-level functional diversity indices (such as functional richness or evenness) are used, as these indices will indicate no change based on the continuous representation of a given functional role. Therefore, we stress the need to carefully and comprehensively monitor the functional structure of species assemblages beyond traditional metrics,

as repeated disturbances may ultimately result in unheralded losses of functional diversity and ecosystem functioning (Fig. 5). We suggest that controlled experiments that expand on our exploratory results are needed to determine causality in the dynamics between habitat degradation, functional redundancy, and ecosystem functioning in the wake of disturbances.

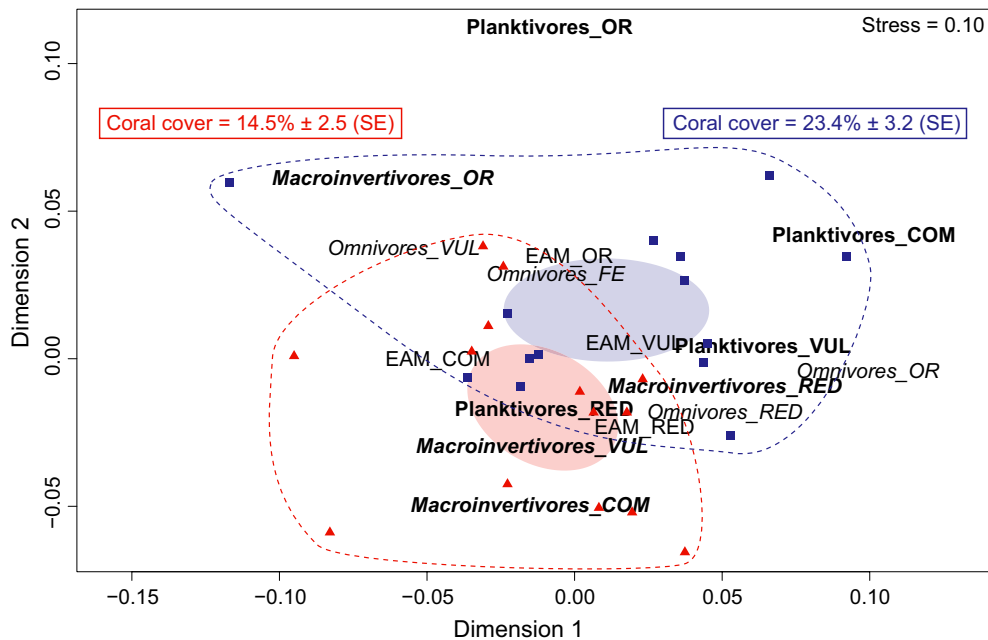


Fig. 4. Nonmetric multidimensional scaling ordination of combined redundancy indices (redundancy, complementarity, vulnerability, and over-redundancy) for four trophic groups (planktivores, omnivores, macroinvertivores, turf/detritivores). Blue squares and ellipses mark the 14 sites in 2014, while red triangles and ellipses mark the sites in 2015. Index values in the upper right periphery (planktivore over-redundancy, planktivore complementarity, and omnivore over-redundancy) are characteristic for sites in 2011, while high macro-invertivore vulnerability and complementarity are characteristic for sites in 2015. These results support the hypothesis that the habitat loss-induced increase in originality is driven by decreases in over-redundancy and complementarity in susceptible groups and the addition of novel functional entities in nonsusceptible groups. Shaded ellipses represent the standard deviation of the weighted average of each group.

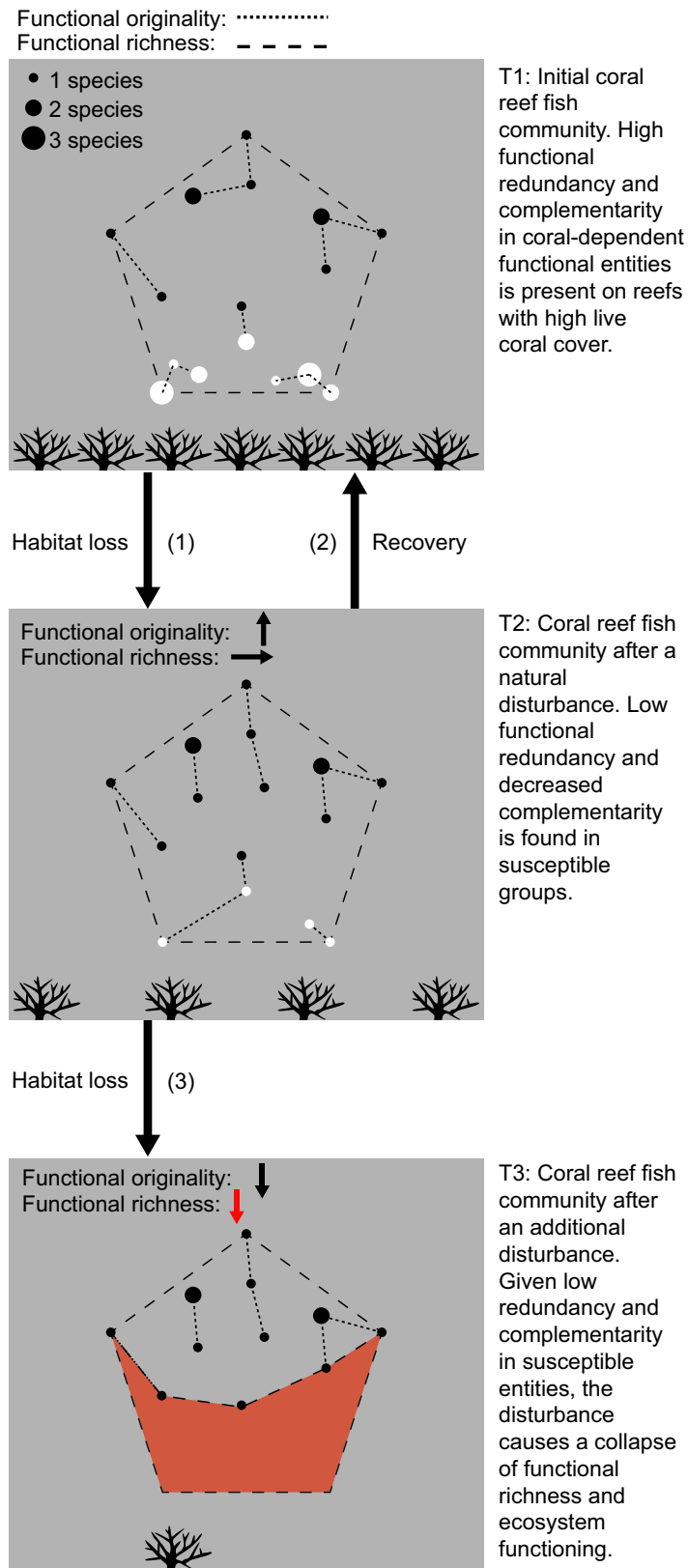


Fig. 5. Conceptual, schematic synthesis of the coupled dynamics between habitat degradation, functional originality, and functional richness. In a high-diversity system containing habitat-dependent (white dots) and habitat-independent species (black dots), extensive habitat coverage fosters high functional redundancy (based on coarse categorical traits) and complementarity in habitat-dependent functional entities, resulting in low functional originality, as pairwise distance is zero (overlying species) or small (complementary species; T1). As the available habitat decreases (1), both redundancy and complementarity in habitat-dependent entities decrease as available resources diminish, resulting in longer pairwise distances and higher functional originality (T2; see Appendix S1: Fig. S4). If habitat recovers (2), redundancy can be restored, recreating the buffering capacity of the community. However, if habitat availability continues to decline due to consecutive disturbances (3), functional richness collapses due to the previous attrition of redundancy, potentially resulting in a critical loss of ecosystem functioning (T3). In this case, functional originality is also likely to decrease, as pairwise distances are reduced (Buisson et al. 2013, Mouillot et al. 2008).

Functional diversity dynamics following habitat degradation

The stability of five functional diversity indices in the face of extensive habitat degradation is surprising given the demonstrated trait value-specific susceptibility to the disturbance. For instance, the estimates predicted from the Bayesian posterior parameters suggest that planktivorous species have approximately a 50% chance (0.498) of losing more than half their initial biomass as coral cover decreases. Given the location of many planktivorous entities at the periphery of the synthetic functional space (Appendix S1: Fig. S4), one might expect a reduction of functional richness following the disturbance due to the loss of planktivorous fishes. In contrast, the severe reduction of coral habitat following Cyclone Ita resulted only

in subtle changes, namely an increase in functional originality (i.e., a decrease in functional redundancy). Specifically, using (untransformed) Bayesian posterior parameter estimates (PM = -0.004; LCI = -0.008; UCI < 0.001), we show that a drop in coral cover of 20.83 percentage points (the highest loss that occurred in this study; Table 2) results in an increase of 0.122 in the functional originality index value. Given the drastic difference between complete originality (no redundant species, functional originality = 1.0) and complete redundancy (all species functionally equivalent, functional originality = 0.0) in a system that harbors up to 127 species per assemblage (Appendix S1: Table S4), an increase of 0.157 represents a substantial structural change, especially considering the high degree of inertia

Table 2. Changes in coral cover and functional redundancy across the 14 sites in 2011 and 2015.

Site	% Coral 2011	% Coral 2015	Δ % Coral	F Ori 2011	F Ori 2015	Δ F Ori
BB	16.333	5.833	-10.500	0.281	0.401	0.120
BL	53.167	39.167	-14.000	0.269	0.339	0.070
BV	13.667	23.000	9.333	0.336	0.327	-0.008
CO	31.333	10.500	-20.833	0.315	0.347	0.032
GR	12.333	5.667	-6.667	0.325	0.362	0.037
LT1	33.833	17.500	-16.333	0.221	0.332	0.111
LT3	29.833	9.167	-20.667	0.235	0.361	0.126
MB	25.500	12.667	-12.833	0.279	0.313	0.034
NR	12.500	9.167	-3.333	0.281	0.364	0.084
PL	35.167	27.000	-8.167	0.285	0.319	0.035
PP	22.500	10.333	-12.167	0.336	0.369	0.033
RE	9.500	6.167	-3.333	0.319	0.306	-0.013
SG	18.333	15.167	-3.167	0.282	0.372	0.090
WM	13.333	11.000	-2.333	0.269	0.346	0.077

Note: % coral, % coral cover; F Ori, functional originality; BB, Bommie Bay; BL, Blue Lagoon; BV, Big Vicki's; CO, Coconut Beach; GR, Granite; LT1, LTMP1; LT3, LTMP3; MB, Monkey's Butt; NR, North Reef; PL, Palfrey Lagoon; PP, Pigeon Point; RE, Resort; SG, Steve's Gully; WM, Washing Machine.

induced by species that are unaffected by habitat degradation and the range of functional originality in assemblages investigated herein (0.22 to 0.40). Thus, our findings clearly differ from previous studies on disturbance-induced shifts in functional indices, which suggest that disturbances deplete and homogenize assemblages through the extinction of functionally unique species (Mouillot et al. 2008, Flynn et al. 2009, Bihn et al. 2010, Buisson et al. 2013). In our study, this was only found at one site, Coconut Beach, where functional richness declined sharply in response to extensive habitat degradation. We suggest that the different response of coral reef fish assemblages to habitat degradation is rooted in the nature of coral reef systems, where the characteristic habitat type (live coral) provides enough niche space for the coexistence of a highly diverse, but functionally unbalanced assemblage of organisms (Mouillot et al. 2014, Bellwood et al. 2016). Consequently, provided the disturbance affects species in which functional overlap is extensive, most functional niches may still be occupied in the wake of the disturbance.

While no support for a decrease in redundancy patterns was found in the entire assemblage, the group-specific analyses suggest that the increases in functional originality were due to the loss of redundant species in some groups and the addition of functionally unique species in others. For instance, planktivore functional over-redundancy and complementarity both declined, increasing nearest-neighbor distances in functional space as functionally similar species were eliminated. The loss of planktivores appears to be driven by their reliance on coral colonies for shelter (Wilson et al. 2006, Graham et al. 2011). As the surrounding habitat is degraded, resources such as shelter become limiting, resulting in a decrease in functional over-redundancy (i.e., competition increases among species with the same set of trait values) and complementarity (i.e., a smaller array of different resources is available, limiting the number of unique functional entities). This appears similar to the loss of functionally similar tropical bird species in densely packed areas of niche space following habitat degradation (Bregman et al. 2015). Conversely, macro-invertivore species appeared to benefit from the cyclone. There were substantial increases in functional complementarity of macro-invertivores,

as novel and original trait combinations were introduced to the assemblage. This suggests that habitat degradation permitted the exploitation of novel resources by fishes that feed on macro-invertebrates. Notably, the introduced unique functional entities are generally represented by single species, potentially increasing the vulnerability of post disturbance assemblages to future disturbances (cf. Fig. 4).

From functional diversity patterns to ecosystem functioning

The stability of functional diversity indices in the face of extensive habitat degradation appears to be a double-edged sword for ecosystem functioning on coral reefs. Reef fishes maintain numerous critical ecological processes, and their functional structure has been intensively studied. Such studies have revealed that several important groups (e.g., herbivores) have limited functional redundancy (Burkepile and Hay 2008, Rasher et al. 2013, Brandl and Bellwood 2014a), resulting in dramatic declines of ecosystem functioning under sustained anthropogenic pressures such as overfishing (Bellwood et al. 2004). In contrast, the taxonomic diversity of fish assemblages is widely assumed to be relatively resilient to natural disturbances (cyclones, coral bleaching, *Acanthaster planci* outbreaks; Wilson et al. 2009, Pratchett et al. 2011). In this context, the identified assemblage-level stability of functional diversity, despite clear trait-specific vulnerability to reductions in live coral cover, is encouraging and suggests that functional redundancy can provide some biological insurance against natural disturbances (Bellwood et al. 2016). In fact, the simultaneous decrease in functional over-redundancy and the emergence of novel functional entities as a consequence of live coral-habitat degradation support the notion that disturbances may contribute to the maintenance of high diversity in systems such as tropical coral reefs or rain forests (Connell 1978). It also indicates that natural disturbances may be intricately bound to processes relating to trait assembly, biodiversity patterns, and ecosystem functioning (Cardinale and Palmer 2002, Cardinale et al. 2005).

However, there are three important caveats, which require a careful interpretation of redundancy on coral reefs with regard to sustained

ecosystem functioning. The first limitation relates to the general presence of functional redundancy in ecosystems (Rosenfeld 2002, Loreau 2004). The use of discrete functional trait values represents, at best, a coarse categorical approximation of organisms' ecological role based on biological knowledge of the respective species (McGill et al. 2006). In reality, outside a scenario of neutral assemblage theory, perfect redundancy is unlikely to exist in nature, as functionally equivalent species would be unable to coexist in a stable Lotka–Volterra equilibrium if competition for resources is present (Loreau 2004). Furthermore, the level of redundancy intuitively decreases with the number of traits chosen to categorize an assemblage (i.e., the addition of more axes in an N-dimensional hypervolume; Rosenfeld 2002, Brandl and Bellwood 2014a, 2016). Thus, although our evaluation is insensitive to a further reduction of functional traits (Appendix S1: Fig. S2), it is likely that redundancy will diminish and complementarity will increase, if more traits are added or if measures of individual variability and realized niche spaces are employed. Previous research has demonstrated that decreased diversity of groups with high superficial redundancy can severely compromise the efficacy of resource utilization within a system (Cardinale et al. 2002). Furthermore, environmental, spatial, and temporal variation may necessitate the presence of apparent functional redundancy within an assemblage to ensure ecosystem functioning (Duffy et al. 2001, Isbell et al. 2011, Aguilera and Navarrete 2012). Therefore, we posit that the availability of diverse live coral habitat may foster fish assemblages with finely partitioned functional niches, rather than a host of functionally redundant species, but that such subtle niche partitioning is not currently detectible. Thus, although the continuous representation of most functional entities following habitat degradation is potentially reassuring, more detailed research is needed to understand how the loss of live coral affects the strength of ecosystem processes, especially in the context of ecosystem multifunctionality (Lefcheck et al. 2015b) or the performance of single traits (Butterfield and Suding 2013). In other words, the occupation of a functional niche after a severe disturbance, especially if this niche is characterized using coarse functional groupings based on our limited ability to perceive

ecological complexity, does not ensure an adequate preservation of ecosystem functioning, as fine-scale niche partitioning, biomass-mediated performance, and ecological synergisms may modify ecosystem functioning on a level that is far removed from the presence or absence of a functional entity.

Secondly, we caution that our results only provide a snapshot of long-term dynamics in a highly diverse and complex system and that the applied functional diversity indices are prone to inherent mathematical limitations when applied to high-diversity assemblages (Lefcheck et al. 2015a). For example, species richness increased at eight of the 14 surveyed sites, contrary to the inherent expectations of the effects of disturbances on coral reefs (Mouillot et al. 2013). Notably, this trend may be an artefact of our increased capacity to detect species on reefs that have undergone substantial loss of coral cover using planar surveys (Goatley and Bellwood 2011), or the consequence of longer-term trends in species abundances. Analytically, the somewhat arbitrary selection of categorical traits that are not explicitly measured and the computation of functional indices from these traits can lead to convergence in estimates for indices such as functional richness (Lefcheck et al. 2015a), especially when traits are inherently correlated (as commonly found in nature). Thus, detecting changes in functional indices in highly diverse communities may not be possible using commonly applied trait-based frameworks. Therefore, it will be necessary to exercise extreme caution in the interpretation of functional indices when assessing the response of diverse communities to disturbances. Recently proposed ways of measuring functional redundancy are likely to be helpful in this context (Ricotta et al. 2016).

The third and final proviso relates to the long-lasting impacts of habitat degradation (Gardner et al. 2005) and the predicted intensification and increased frequency of natural disturbances due to human-mediated changes in large-scale climatic patterns (Emanuel 2005, Byrnes et al. 2011). The re-establishment of habitat forming organisms such as branching corals is subject to inherently slow and variable ecological processes such as growth and recruitment (Fenner 1991, Halford et al. 2004, Gardner et al. 2005). Consequently, the restoration of reef fish communities that feature high superficial functional redundancy through

the recovery of live coral habitat will take time, even in short-lived species with high turnover (Bellwood et al. 2006). Yet, the intervals for coral recovery may grow shorter, without enough time to provide the redundancy necessary to bolster functional diversity against future disturbance. This is especially concerning if future disturbances affect not only the amount of live corals, but also the functional structure of the underlying habitat (Madin et al. 2008, Emslie et al. 2014). In such scenarios, biological insurance will be gradually eroded within those functional groups susceptible to habitat degradation, resulting in a loss of functional complementarity. This, in turn, will isolate species at the periphery of functional niche space and may eventually lead to the collapse of functional richness, with potentially catastrophic consequences for ecosystem functioning (Reich et al. 2012, MacDougall et al. 2013, Fig. 5).

Although there is limited information regarding the ecological role of small-bodied, territorial fishes with tight links to the benthos, recent research has demonstrated that many of these species can profoundly affect their surroundings (Ceccarelli 2007, Casey et al. 2014, 2015, Chase et al. 2014). For example, species of damselfishes that establish small territories over coral rubble or within live coral outcrops (e.g., *Stegastes* spp.) are known to act as ecosystem engineers with the ability to alter benthic community composition (Ceccarelli 2007), and have been specifically linked to coral disease and survival (Casey et al. 2014, 2015). Similarly, small planktivorous and omnivorous damselfishes in the genera *Dascyllus* and *Chromis*, for instance, have been shown to perform several actions that may be directly linked to the performance of their coral hosts. By feeding on zooplankton in the water column, these fishes contribute substantially to the transfer of nutrients from pelagic to benthic systems, potentially enhancing coral growth rate and nutrient uptake (Holbrook et al. 2008). In addition, “sleep-swimming” by *D. marginatus*, *D. aruanus*, and *C. viridis* has been demonstrated to promote aeration of coral tissues, therefore influencing coral growth and survival (Goldshmid et al. 2004), and *D. reticulatus* and *C. caeruleus* have been shown to supplement their planktonic diet by feeding on coral parasites within their host colony, thus potentially enhancing coral

health (Zikova et al. 2011). These examples illustrate the potential importance of small coral reef fishes for benthic community dynamics and also illustrate the high potential for functional niche partitioning among these species. Thus, it seems probable that the loss of species with supposedly high functional overlap will disrupt important ecological links between fishes and the benthic community after a series of disturbance events.

Overall, our results demonstrate that the degradation of primary habitat does not necessarily result in grave losses of functional diversity. Instead, we show that on coral reefs, the only detectable effect of live coral cover reduction is an increase in functional originality, as superficially redundant species are removed and novel, functionally unique species enter the pool. We suggest that the dynamics between habitat availability, species’ functional uniqueness, and their effect on ecosystem functioning should be further explored and that functional originality may serve as an important indicator of subtle changes in assemblages’ functional structure after disturbances.

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