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### Global Ecology and Biogeography

DOI:  
[10.1111/geb.13638](https://doi.org/10.1111/geb.13638)

Published: 01/03/2023

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

*Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):*  
Sheppard, C., Williams, G. J., Exton, D., & Keith, S. (2023). Co-occurrence of herbivorous fish functional groups correlates with enhanced coral reef benthic state. *Global Ecology and Biogeography*, 32(3), 435-449. <https://doi.org/10.1111/geb.13638>

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**Co-occurrence of herbivorous fish functional groups correlates with enhanced coral reef benthic state**

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**Funding information**

This work was supported by the Natural Environment Research Council (SAK, grant number NE/S00050X/1 and CES, grant number NE/S007423/1), with CES's studentship through the Envision Doctoral Training Partnership.

**Acknowledgments**

We thank Lisa Bostrom Einarsson, Rachel Gunn, Rucha Karkarey and James Boon for stimulating discussion. CES acknowledges funding by a studentship from the NERC Envision Doctoral Training Partnership (NE/S007423/1).

**Biosketch**

The authors are ecologists interested in how behaviour and species interactions scale up to affect population, community and ecosystem ecology.

**Conflict of interest**

All authors declare that they have no conflicts of interest.

## 28    **Abstract**

29    Aim: Biodiversity loss is impacting essential ecosystem functions and services across the globe. More  
30    recently, our interest in the benefits of biodiversity on ecosystem function has shifted focus from  
31    measurements of species richness to functional diversity and composition. However, the additional  
32    importance of other community characteristics, such as species evenness and co-occurrence, for  
33    diversity-driven ecosystem function is less known. We used herbivorous coral reef fish as a model  
34    system to investigate how co-occurrence of different functional groups, rather than purely  
35    functional diversity, within an assemblage may affect coral reef benthic state.

36    Location: Western Atlantic

37    Time period: 2007 – 2017

38    Major taxa studied: Herbivorous reef fish

39    Methods: We analysed benthic and fish assemblage data from 601 sites across 12 countries in the  
40    Western Atlantic. Using Diversity-Interactions models, we investigated how the composition and  
41    relative abundances of reef fish functional groups correlated with benthic cover and estimates of  
42    coral calcification rates. We used statistical interactions to explore the importance of herbivorous  
43    fish functional group co-occurrence for coral reef benthic state.

44    Results: We found that co-occurrence of herbivorous fish functional groups, as well as functional  
45    diversity, was correlated with reduced algal cover and increased coral accretion. Moreover, pairwise  
46    statistical interactions between functional groups were significantly correlated with improved coral  
47    reef benthic state.

48    Main conclusions: Our results support the idea that functional group co-occurrence, as well as  
49    functional diversity, within herbivorous fish offers additional benefits to coral reef benthic state. We  
50    identify farming damselfish and excavating parrotfish as potential key determinants of coral reef  
51    benthic state, and highlight that co-occurrence of cropping and scraping herbivores may promote  
52    coral accretion. Our findings support the argument that protecting herbivore abundance without  
53    regard to the species and functional groups present is not enough to preserve coral reef health, and  
54    that fine-scale community composition must be considered.

55    Keywords: communities, co-occurrence, coral reefs, ecosystem function, functional groups, reef fish,  
56    relative abundance

## 1. Introduction

Biodiversity loss is driving changes to ecosystem function across biomes (Hooper et al., 2012). Ecosystem function, defined as the fluxes of energy and material within an ecosystem (Bellwood et al., 2019), can be mediated by the identity and composition of species present, and their interactions with their environment (Brandl et al., 2019). Historically, the positive effects of biodiversity on ecosystem function focussed on measures of species richness, likely due to the prominent interest in and irreversibility of species loss (Chapin et al., 2000; Hooper et al., 2012; Kirwan et al., 2007). However, more recently, interest in diversity-driven ecosystem function has shifted towards functional diversity and the composition of functional traits (Bellwood et al., 2019; Cheal et al., 2010; Finn et al., 2013; Grange et al., 2021; Mouillot et al., 2011; Stuart-Smith et al., 2013). When fewer species are present, increased functional diversity improves a community's ability to extract resources from its environment and maintain ecosystem function (Cadotte et al., 2011). Equally, niche partitioning between species allows for better utilisation of an ecosystem's limited resources and increases the probability of positive co-occurrence effects on ecosystem function (Duffy et al., 2017).

Coral reefs are highly diverse, productive ecosystems and provide numerous ecosystem services that benefit human well-being, including food provisioning and cultural importance (MEA, 2005; Woodhead et al., 2019). Like many tropical systems, anthropogenic impacts, such as overfishing, pollution and climate change, are increasingly altering species composition and fundamentally changing ecological processes on coral reefs (Hughes et al., 2017; Mora et al., 2011; Williams & Graham, 2019). Functional diversity within herbivorous reef fish is widely recognised to support healthy coral reef function. Herbivorous fish play a crucial role in maintaining the physical structure and continued accretion of coral reefs (Green & Bellwood, 2009). By removing algal biomass, herbivores support reef-building benthic organisms and help prevent regime shifts to fleshy macroalgal dominated systems (Graham et al., 2015). High functional diversity within the herbivore guild can increase measurements indicative of enhanced reef function, such as total fish biomass (Duffy et al., 2016), standing biomass (Mora et al., 2011) and herbivory rate (Lefcheck et al., 2019). Complementary feeding behaviours between herbivorous reef fish can also lower the abundance of certain algae and increase hard coral cover (Burkepile & Hay, 2008).

Understandably, there is much emphasis on broadly protecting herbivory in order to conserve the functions and services of coral reefs (Adam et al., 2015). However, high functional diversity within herbivorous reef fish (Green & Bellwood, 2009) means that such broad approaches to managing herbivores as a whole fail to appreciate the importance of their fine-scale community composition.

Furthermore, little is known of how functional group evenness and co-occurrence within the herbivore guild influences coral reef state and resilience (Brandl et al., 2019). It is plausible that co-occurrence of different herbivore species, or functional groups, provides additional benefits to coral reef function than their single identities alone. Consequently, any attempt to predict ecosystem function based solely on species richness and community composition may be inaccurate.

We can explore the potential effects of individual versus combinations of herbivores using Diversity-Interactions models. These models quantify the effects of species identity and diversity on ecosystem function, separating the contributions of different species and their statistical interactions (Kirwan et al., 2009). “Interactions” are not necessarily direct biological interactions, and may simply imply that the presence of various species in different relative abundances significantly impacts ecosystem function (Connolly et al., 2013). As such, interaction effects may be understood as the additional effects arising through species co-occurrence. Even so, this approach aids the understanding of how interspecific interactions may affect ecosystem function and allows us to develop more explicit hypotheses for future exploration.

Previous work using Diversity-Interactions models to investigate diversity-driven coral reef function found that species diversity enhanced herbivory rates on coral reefs, yet no additional effect of herbivore species co-occurrence was identified (Lefcheck et al., 2019). However, these analytical approaches were limited to an “average interaction” term rather than separate pairwise interactions (Lefcheck et al., 2019). This modelling approach is analogous to the “evenness model” (Kirwan et al. 2009), which assumes that the strength of any statistical interaction between species is the same for all pairwise combinations. By modelling each pairwise statistical interaction separately, we can explore and identify the pairwise co-occurrences between herbivorous fish functional groups with the greatest potential effects.

Here, we investigate the influence of community composition and co-occurrence of herbivorous fish functional groups using measurements of coral reef benthic state as a proxy for reef function. To achieve this aim, we apply Diversity-Interactions models (Kirwan et al., 2009) to a large-scale dataset spanning 10 years, located across 12 countries in the western Atlantic. Specifically, we use benthic cover and estimates of dynamic processes, hereafter referred to collectively as “benthic metrics”, and relative abundances of reef fish functional groups. Using these results, we discuss the potential importance of functional group co-occurrence within herbivorous reef fish communities to coral reef benthic state.

## 2. Methods

### AGRRA dataset description

In total, our analysis used data from 942 surveys across 601 sites. We analysed benthic and fish abundance data from 16541 transects collected as part of the Atlantic and Gulf Rapid Reef Assessment (AGRRA; Marks, 2018) between 2007 and 2017, bolstered with past estimations of coral calcification rates (González-Barrios & Álvarez-Filip, 2018). The AGRRA dataset consists of a comprehensive set of measurements that quantify multiple components of coral reef ecosystem state and covers a large geographic extent (latitude: 12.0° – 27.3°, longitude: -96.1° – -61.5°; 12 countries, 601 sites) across the western Atlantic (see Supporting Information Figure S1).

AGRRA surveys benthic and fish communities with a focus on ecologically or commercially important reef fish species, alongside measurements of coral reef benthic condition (Marks, 2018). Fish species were recorded along belt transects (30 m x 2 m) and their body size estimated as one of six size categories (0-5 cm; 6-10 cm; 11-20 cm; 21-30 cm; 31-40 cm; > 40 cm). From these size estimates, biomass was calculated using standardised length-to-weight relationships from FishBase (fishbase.org; Froese & Pauly, 2020). Belt transects (10 m x 1 m) were also used to capture coral colonies  $\geq 4$  cm in maximum length, which were identified where possible to the species level (occasionally genera; 2.01 % of observations included in our analysis) and their maximum length and width recorded. Depth was measured at the start and end of each fish transect and an average calculated.

Benthic composition was recorded using 10 m long point intercept transects (PIT) where substrate type was noted every 0.1 m (totalling 100 points). Coral recruits  $\leq 2$  cm in maximum length within a 25 cm x 25 cm square quadrat placed at 2 m intervals along these transects were also recorded, as well as the number of adult and juvenile *Diadema antillarum* (historically important herbivorous urchins on western Atlantic reefs; Bodmer *et al.*, 2015). For each site, geographic coordinates, ecoregion and geographical subregion were available. Sites included in our analysis were spread across 47 subregions and five ecoregions (see Supporting Information Figure S1).

### Calculation of herbivore functional group abundances

Our data included 99 fish taxa. Herbivorous fish are commonly assigned to four main functional groups based on their feeding behaviour: croppers (e.g. surgeonfish: *Acanthuridae*), browsers (e.g. chubs: *Kyphosidae*), scrapers and excavators (e.g. parrotfish: *Labridae*) (Bellwood *et al.*, 2019;

Edwards et al., 2013; Green & Bellwood, 2009; Tebbett et al., 2022). Additionally, the unusual farming behaviour displayed by territorial damselfish often distinguishes these species as a separate functional group (Ceccarelli et al., 2005). Territorial farming damselfish are known to affect species occurrence and subsequent changes to coral reef benthic structure (Ceccarelli, 2007; Ceccarelli et al., 2001). As our main aim is to explore the effects of herbivore co-occurrence on coral reef benthic state, we reason that the distinct behaviours and ecological consequences of this group of herbivores necessitates their inclusion in our analysis as a separate functional group. It must be noted that recent work by Tebbett et al. (2022) examining the functional roles of surgeonfishes classified *Acanthurus chirurgus* and *A. tractus* as sediment suckers rather than croppers. However, sediment suckers are functionally very similar to croppers in relation to their role in algal removal in the Atlantic and were, therefore, grouped alongside *A. coeruleus* as croppers in our study.

Following these common classifications, we grouped herbivorous fish species into five functional groups (croppers, browsers, farmers, scrapers and excavators) based on the literature (Green & Bellwood, 2009; Choat et al., 2012; Adam et al., 2018; Supporting Information Table S1). Parrotfish of the genera *Scarus* and *Sparisoma* that were not identified in Adam et al. (2018) were assigned functional groups guided by the closest related species (See Supporting Information Table S1 for further details: Bellwood & Choat 1990; Bernardi et al., 2000; Choat et al., 2012). Species from the parrotfish genus *Cryptotomus* did not appear in Adam et al. (2018) and were assigned functional groups using dietary data available from Fishbase (Froese & Pauly, 2020; Supporting Information Table S1).

Proportional abundances of each herbivorous functional group, as well as total herbivorous fish biomass, were calculated per transect. We focus on proportional abundance rather than proportional biomass as, in this context, the number of individual fish per functional group is more useful for investigating the importance of co-occurrence. We believe this is justified as it is presence and behaviour of individuals that shape activities at the population level which, in turn, have consequences to community structure and interspecific interactions. Although herbivore biomass is an important determinant of coral reef benthic state (Williams & Polunin, 2001; Williams et al., 2019), when divided into functional groups, proportional biomass can be dramatically skewed by just a few large-bodied individuals, particularly excavating parrotfish (e.g. *Sparisoma viride*; Adam et al., 2018) (per survey; mean number of excavators: 1.80; mean proportional biomass of excavators: 0.24). As such, it seemed more appropriate to use proportional abundance as a measure of community structure to remove this size bias. Total herbivore biomass was, however, included in our analysis as a separate explanatory variable.

186

## 187 **Calculation of benthic metrics**

188 We calculated multiple metrics associated with coral reef benthic state using methods adapted from  
189 Lester et al. (2020). Our benthic metrics were chosen to reflect the core coral reef processes laid out  
190 by Brandl et al. (2019) and focus on measurements relating to algal and coral communities (full  
191 summary in Supporting Information Table S2). These metrics help to identify the most dominant  
192 benthic organism (algae or coral) and rate of coral reef accretion and expansion, offering an  
193 indication of coral reef health and function.

194 Our data included 63 coral taxa. Coral species were classified into four trait-based groups as per  
195 Darling et al. (2012); competitive, weedy, stress-tolerant and generalist. Coral species not identified  
196 in Darling et al. (2012) and those not recorded at the species-level were classified based on genus  
197 and known traits (Madin et al., 2016; Supporting Information Table S3). Grouping corals in this way  
198 allows us to explore the correlation between herbivore and coral community compositions. This is  
199 important as different trait-based groups of coral vary in their contribution to coral reef accretion  
200 and function (Darling et al., 2012; González-Barrios et al., 2021; González-Barrios & Álvarez-Filip,  
201 2018; Green et al., 2008). Coral species richness (total number of coral species) and coral cover ( $\text{m}^2$ )  
202 were computed per transect, as well as the cover of each separate trait-based coral group ( $\text{m}^2$ ). Total  
203 calcification rates ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ ) per transect were calculated by applying mean species-  
204 specific calcification rates (González-Barrios & Álvarez-Filip, 2018) to coral cover estimates. Where  
205 corals were not recorded at the species-level, we applied the average calcification rate across all  
206 species in the genus (González-Barrios & Álvarez-Filip, 2018). Coral taxa with no calcification  
207 estimates available were removed from our analysis ( $<0.0002$  percent area). We used PIT counts to  
208 estimate percentage cover of fleshy and calcareous macroalgae, turf algae and crustose coralline  
209 algae (CCA). Adult and juvenile *Diadema* counts were summed across each PIT to calculate total  
210 *Diadema* population.

211 Fish transects (number of transects per survey:  $n = 10$ ) and corresponding coral transects ( $n = 2$ ) and  
212 benthic PITs ( $n = 6$ ) were grouped into whole surveys to collate data of fish abundance and benthic  
213 cover (Note: some sites were surveyed multiple times;  $n = 194$ ; range: 2 – 5 times). Occasionally, fish  
214 transects within the same survey were not all conducted on the same day due to forces beyond the  
215 control of the surveyors such as interruption by weather events (2.1% of surveys included had fish  
216 transects over multiple days). We considered all transects taken within 14 days of each other as the  
217 same survey, which is a reasonable assumption as shifts in coral, fish and algal assemblages,



particularly after a disturbance (Airoldi, 1998; Wilson et al., 2006), typically take much longer. Average benthic metrics and proportional abundances of herbivorous fish functional groups were calculated for each survey, alongside average depth (range: 1.0 – 24.6 m), total *Diadema* population (individuals/10 m<sup>2</sup>) and total herbivore biomass (g/60m<sup>2</sup>). Preliminary analysis which included *Diadema* abundance as an explanatory variable revealed that their abundance was significantly correlated with metrics of coral reef benthic state. We therefore excluded all surveys where *Diadema* populations were not counted to have *Diadema* abundance in all further analysis. One survey with a *Diadema* abundance greater than 25 standard deviations above the average from across all surveys was also removed from our analysis as this was concluded to be highly unlikely and therefore an error (observed: 168 individuals/10 m<sup>2</sup>, mean: 1.3 individuals/10 m<sup>2</sup>).

## Data analysis

To test the extent to which pairwise statistical interactions between herbivorous fish functional group abundances correlated with metrics of coral reef benthic state, and whether functional groups varied in their correlation with benthic composition, we applied the Diversity-Interactions modelling framework, as presented by Kirwan et al. (2009). The Diversity-Interactions modelling framework offers a suite of linear regression models designed to test biologically meaningful hypotheses about how species and functional group interactions may contribute to ecosystem function (Kirwan et al., 2009). We fit three separate Diversity-Interactions models: null model, species identity model, and full pairwise interactions model (Figure 1). Briefly, the null model assumes no effect of species identity or interactions on ecosystem function. The identity model considers only the effects of species identity on ecosystem function, whereas the pairwise interactions model includes the effects of both species identity and interactions separately.

The null model (Model 1; Figure 1) reflects an ecosystem in which a change in species diversity or relative abundances has no effect on ecosystem function, and is as follows:

$$y = \beta + \alpha M + \varepsilon \quad \text{Equation 1}$$

where  $\alpha$  represents the effect of changing species abundance ( $M$ ) and  $\beta$  is the level of ecosystem function at average  $M$ .

The species identity model (Model 2; Figure 1) assumes that species differ in their individual effects on ecosystem function, but that interactions between species do not affect ecosystem function. In

this instance, the level of ecosystem function of a community can be calculated using the proportional abundance ( $P$ ) of each individual species and the level of ecosystem function when they are the sole species present ( $P = 1$ ). Their individual performance (ecosystem function when  $P = 1$ ) is as follows:

$$y = \sum_{i=1}^s \beta_i P_i + \alpha M + \varepsilon \quad \text{Equation 2}$$

where  $\beta_i$  represents the estimated effect of changing the proportional abundance of species  $i$  ( $P_i$ ) on the level of ecosystem function (its identity effect). We can test whether individual species' identity effects are significantly different by conducting an  $F$  test (or equivalent) between Models 1 and 2.

When species interact to affect ecosystem function, the performance of a community formed of different species can be significantly different from that estimated using separate identity effects alone. These interactions can have a positive (synergistic) or negative (antagonistic) effect. This full pairwise interactions model (Model 3; Figure 1) is as follows:

$$y = \sum_{i=1}^s \beta_i P_i + \alpha M + \sum_{\substack{i,j=1 \\ i < j}}^s \delta_{ij} P_i P_j + \varepsilon \quad \text{Equation 3}$$

where  $\delta_{ij}$  measures the effect of changing relative abundances between species  $i$  and  $j$  on ecosystem function. In this model, the relative abundances of the two species,  $i$  and  $j$ , determines how strongly their interaction correlates with ecosystem function. The sum of all pairwise interaction terms form the net interaction effect, defined as:

$$\sum_{\substack{i,j=1 \\ i < j}}^s \delta_{ij} P_i P_j \quad \text{Equation 4}$$

We can test whether pairwise interactions between species have a significant effect on ecosystem function by conducting an  $F$  test (or equivalent) between models 2 and 3 (Kirwan et al., 2009). When net interaction effects play a significant role in driving ecosystem function, domination by one functional group will reduce interaction effects and subsequently cause ecosystem function to be compromised.

All analyses were conducted in RStudio version 1.4.1717 (RStudio Team, 2021) using the *tidyverse* (Wickham et al., 2019) and *geepack* packages (Halekoh et al., 2006). We fit benthic metrics (dependent variable) against proportional abundances of herbivorous fish functional groups (independent variable) using generalised estimating equations (GEE: *geeglm* function in the *geepack* package; Halekoh et al., 2006). This approach allowed us to control for any spatial correlation between sites within the same subregion (Supporting Information Table S4) by including an exchangeable correlational structure within subregions which provided an estimate of correlation ( $\alpha$ ). GEE are a common approach to analysing correlated non-normal data (Zuur et al., 2009) and can be understood as analogous to generalised mixed models (GLM), in which subregion would be included as a random effect. To resolve the issue of multicollinearity between proportional independent variables that sum to one (i.e. one variable can be predicted from the others), the intercept was removed from Models 2 and 3.

As some study sites were surveyed multiple times ( $n = 194$ ; range: 2 – 5 times), we used a bootstrapping approach to prevent pseudoreplication. For all sites surveyed multiple times, we selected one survey at random and joined these to all single-surveyed sites ( $n = 407$ ) to form a temporary dataset of 601 independent surveys which we then used to fit our three GEE models. Within each iteration, we tested GEE models against each other, as described above, using an analysis of the “Wald statistic” (analogous to  $F$  test), and extracted all test statistics and model coefficients. We repeated this whole process 1000 times with replacement. All benthic metrics were lower-bound at zero and algal percentage cover was upper-bound at 100. Benthic metrics relating to coral (coral richness, calcification rate, coral cover and recruitment) were, therefore, modelled using a Poisson distribution and algal cover was modelled using a binomial distribution (transformed to a 0 to 1 scale). Total herbivore biomass, depth, year and *Diadema* abundance were included in all GEE models as additional fixed effects. Note that not all surveys had data for all benthic and coral metrics; however, we modelled all benthic metrics separately, and did not include surveys that were missing the benthic metric being analysed.

Visual model validation was conducted following methods outlined by Zuur et al. (2009). We plotted all explanatory variables against the appropriate residuals, Pearson residuals (Poisson distributed variables) or deviance residuals (binomial distributed variables), to check that no patterns were observed (See online code). Unlike GLM, GEEs are not based on the maximum likelihood theory and therefore statistics derived under this theory, such as Akaike’s information criterion, may not be applied to GEE. The quasi-likelihood information criterion (QIC) (Pan, 2001) was introduced as an alternative method of model selection in a GEE setting, however these methods are commonly

disputed and can give rise to errors (Wang et al., 2015). Model choice and correlation structure can therefore be guided by the data (Wang et al., 2015). As the premise of our study is based around the statistical tests between models, use of the QIC here was deemed inappropriate. Mean and standard deviation of all model summary statistics and statistical tests between models can be found in Table 1 and Supplementary Table S5.

Mean coefficients from the full pairwise interaction models (Model 3) were used to predict benthic metrics on hypothetical reefs along a scale of varying herbivorous fish community composition. Each functional group was set along a scale of proportional abundance from 0 to 1, with all other functional groups kept equal to each other. For example, when the proportional abundance of functional group  $i$  was 0.5, all other functional group proportional abundances were 0.125 (see Figure 1). As a community of five distinct groups, maximum evenness between functional groups was reached when the proportional abundances ( $P$ ) of all functional groups was 0.2. For calculations of predicted values, we set total herbivore biomass, depth, year and *Diadema* abundance across all surveys to the mean.

### 3. Results

#### Functional group co-occurrence

Coral richness, total coral cover and calcification rate were predicted to be higher on reefs where herbivorous fish functional groups had the same relative abundance ( $P = 0.2$ ; maximum evenness) compared with when a single functional group was present ( $P_i = 1$ ) (Figure 2). The model also predicted moderate levels of fleshy and calcareous macroalgal, turf algal and CCA cover under these circumstances (Figure 2; see Table 2 for percentages and predicted maximums of all benthic metrics).

Statistical interactions between the proportional abundances of herbivore functional groups were significantly correlated with improved coral reef benthic state (Table 1; Test 2). In addition, when separated into functional group identity (identity effects) and functional group co-occurrence (interaction effects) (see Figure 1), predicted benthic metrics were largely made up of the contribution of functional group co-occurrence (Figure 3). Due to the nature of proportional abundances, it is difficult to interpret the size of the interaction effects, as increasing the proportion of one functional group inevitably changes the proportion of others. Therefore, we focus on the

direction of correlation between functional group co-occurrence and benthic state; whether it is positive (synergistic) or negative (antagonistic).

Net interaction effects (the sum of all pairwise interaction effects; Equation 4) were consistently positively correlated with fleshy macroalgal cover, coral richness, total coral cover and coral calcification rate (Figure 3). Net interaction effects were positively correlated with coral recruitment except in communities dominated by farmers ( $P_{farmers} > 0.67$ ), where correlation was negative (Figure 3). Net interaction effects were positively correlated with calcareous macroalgal cover except when communities were dominated by croppers ( $P_{croppers} > 0.57$ ), where correlation was negative. Similarly, net interaction effects were positively correlated with CCA cover, however, when browsers were more abundant ( $P_{browsers} > 0.26$ ), or where croppers were rare ( $P_{croppers} < 0.14$ ), the correlation between net interaction effects and CCA cover was negative.

In some cases, pairwise statistical interactions between herbivorous fish functional groups were significantly correlated with algal metrics: excavators and scrapers, and excavators and browsers with reduced turf algal cover (Supporting Information Table S5); croppers and scrapers with increased CCA cover. No singular pairwise functional group statistical interaction was significantly correlated with calcareous macroalgal cover (Supporting Information Table S5), even though the correlation with the net interaction effect was significant (Table 1; Test 2).

Not all pairwise statistical interactions between herbivore functional groups were significantly correlated with coral-related benthic metrics (coral richness, calcification rate, total coral cover), however those that were showed a positive correlation (13 out of 40; Supporting Information Table S5). The majority of these significant correlations involved excavators (9 out of 13; Supporting Information Table S5). Other significant pairwise statistical interactions between croppers and scrapers were correlated with increased coral richness, coral cover, and coral calcification rate, and browsers and scrapers were correlated with increased coral richness.

### **Comparison of functional group identity effects**

The correlation between herbivore functional groups and benthic metrics (their identity effects) were significantly different from each other, with the exception of calcareous macroalgal cover and competitive coral cover (Table 1, Test 1). Across our study sites, the cover of calcareous macroalgae and competitive corals was low (mean: 5.78% and 0.40 m<sup>2</sup>, respectively) reducing the likelihood that relationships would be detectable in the data.

Reefs dominated by one herbivore functional group ( $P > 0.2$ ) were predicted to have lower levels of all coral-related benthic metrics (richness, recruitment, cover and calcification rate), with the exception of farmer- or scraper-dominated reefs, which were predicted to have higher coral recruitment (Figure 2). In particular, coral richness, total coral cover and calcification rate were predicted to be substantially lower on reefs dominated by excavators. Higher coral calcification rate was predicted on reefs where scrapers were relatively abundant (up to a point;  $P_{\text{Farmers}} = 0.31$  and  $P_{\text{Scrapers}} = 0.44$ ; Figure 2), whereas coral richness was predicted to be higher when browsers were more abundant (up to a point;  $P_{\text{Browsers}} = 0.36$ ). Coral recruitment rate was predicted to be higher on reefs dominated by farmers or scrapers (Figure 2). Overall, metrics of coral reef benthic state were lower on reefs where one functional group were less abundant ( $P < 0.1$ ) or absent (Figure 2).

Extremely high turf algal cover ( $P_{\text{Excavators}} = 0.5$ ; Turf cover = 51%) and low macroalgal cover were predicted on reefs dominated by excavators (Figure 2). In contrast, reefs dominated by browsers had higher macroalgal cover and lower turf algal cover (Figure 2). Lower macroalgal cover and higher CCA cover were predicted on reefs where farmers were more common. Lower CCA cover was predicted on reefs dominated by scrapers and excavators (Figure 2). The correlation between CCA cover, and both croppers and browsers, was less clear and nonlinear.

Total coral cover was predicted to be higher on reefs where farmers and scrapers were relatively abundant (Figure 2). However, this correlation was inconsistent when observing coral cover of trait-based groups separately. Weedy coral cover was predicted to be higher when farmers were relatively abundant (Supporting Information Figure S2), whereas stress-tolerant coral cover was predicted to be greater with increasing abundance of browsers (Supporting Information Figure S2). Competitive coral cover was predicted to be higher when functional groups had the same relative abundance in a community ( $P = 0.2$ ; Supporting Information Figure S2) and with increasing abundance of browsers. Generalist coral cover was predicted to be substantially greater on reefs with increasing abundance of scrapers (Supporting Information Figure S2).

#### 4. Discussion

Using data collected across 12 countries within the western Atlantic, we found strong correlations between herbivorous fish functional diversity and improved coral reef benthic state. These correlations were mostly driven by the co-occurrence of fish functional group proportional abundances.

Statistical interactions between functional groups were significantly correlated with reduced turf algal cover and increased calcareous macroalgal and CCA cover, as well as increased coral cover and coral calcification rate (Table 1; Test 2). However, no such correlation was found with coral recruitment. Calcareous macroalgae (e.g. *Halimeda spp.*) and CCA play an important role in reef-building by binding sediment and contributing to calcium carbonate production, assisting the growth of coral reefs (Birrell et al., 2008). In contrast, when relieved from grazing pressure, turf algae can form dense mats which smother coral, leading to mortality and a decline in coral reef accretion (Birrell et al., 2008). Our findings support previous consensus that co-occurrence of herbivorous fish functional groups could be an important mediator of reef function by controlling turf algal cover (Adam et al., 2015; Burkepile & Hay, 2008; Duffy et al., 2016; Green & Bellwood, 2009; Holbrook et al., 2016; Lefcheck et al., 2019). As such, co-occurrence of functional groups may promote reef accretion indirectly by mediating competition with algae, rather than through a direct benefit to coral recruitment and settlement.

Fleshy macroalgal cover was not significantly correlated with statistical interactions between functional group proportional abundances. This finding is reasonable to expect given that, of the five functional groups investigated, only browsers (e.g. chubs; Kyphosidae; Green & Bellwood, 2009) directly affect fleshy macroalgae through consumption (Green & Bellwood, 2009). However, correlations between different functional groups and fleshy macroalgal cover did significantly differ. Herbivorous fish functional groups vary widely in their preferred diet and feeding behaviours (Green & Bellwood, 2009; Kelly et al., 2016). Therefore, it can be expected that the composition of algal assemblages will affect the community composition of herbivorous fish through a bottom-up effect. For example, as browsing herbivores are the only functional group that rely on macroalgae as a dietary resource (Green & Bellwood, 2009), we would expect their proportional abundance to be higher on reefs with greater macroalgal cover, as we observed (Figure 2).

The general assumption is that herbivore abundance and diversity benefits coral reefs by controlling the abundance of algae (Adam et al., 2015; Holbrook et al., 2016). With increased functional diversity and niche partitioning, a community is better able to fully utilise the limited resources from its environment, helping to maintain ecosystem function (Cadotte et al., 2011). Although we must acknowledge bottom-up effects of algal assemblages on herbivore community composition, it seems reasonable to expect that co-occurrence of herbivore functional groups improves algal control on coral reefs by increasing the dietary breadth and resource utilisation of herbivorous fish as a whole. Here, we demonstrate significant correlation between herbivorous fish functional group co-occurrence, reduced algal cover and increased coral accretion. Our results support the expectation

that functional diversity within the herbivore guild enhances coral reef benthic state, and suggests that co-occurrence of functional groups could have an important positive effect on wider coral reef function. This would infer that the identity and abundances of herbivorous fish functional groups alone are not enough to accurately predict coral reef benthic state. Both the identity model (Model 2) and full pairwise interaction model (Model 3) made similar predictions of coral reef benthic state when all functional groups had similar relative abundance (Figures 2 and S2). However, when the proportional abundance of one functional group increased, predictions between models were no longer comparable. This inconsistency supports the idea that detailing patterns of herbivorous reef fish co-occurrence may allow us to predict coral reef benthic state more accurately.

#### **Co-occurrence of croppers and scrapers correlated with increased coral reef accretion**

By modelling each pairwise interaction separately, the full pairwise interactions model (Model 3) can be used to identify functional group pairings that are most correlated with coral reef benthic state. Statistical interactions between scrapers and croppers were correlated with a moderate increase in CCA cover and coral-related measures (coral richness, coral cover and calcification rate). Scraping herbivores, such as smaller parrotfish species (e.g. *Scarus vetula*; *Labridae*; Adam et al., 2018), are widely recognised to facilitate the settlement and growth of CCA and corals by limiting the establishment and growth of macro- and turf algae (Hoey and Bellwood, 2008; Green and Bellwood, 2009; Smith et al. 2010). Croppers (e.g. surgeonfish *Acanthurus coeruleus*; *Acanthuridae*; Green & Bellwood, 2009) and browsers also play an important role in controlling algal abundance by consuming algae, which competes with CCA and coral recruits for space and shades adult corals (Barott et al., 2012; Green & Bellwood, 2009; Smith et al., 2010). Our results suggest that, in addition to their individual benefits to coral reef benthic state, the co-occurrence of scrapers and croppers may further support CCA growth and indirectly benefit coral diversity and growth. As such, we would predict reefs higher in proportional abundance of both scrapers and croppers to demonstrate a more favourable benthic state, in which algal cover is well-maintained and corals are the dominant benthic organism.

#### **Evidence in support of excavating and farming herbivores as key determinants of coral reef benthic state**



Herbivorous fish functional groups varied significantly to each other in their correlation with coral reef benthic state (Table 1; Test 1). It is well established that herbivore functional groups perform alternative roles within coral reef communities (Burkepile & Hay, 2010; Daniela M. Ceccarelli et al., 2005; Edwards et al., 2013), yet few studies have quantified and compared these effects. Here, we quantify the correlation between herbivore functional groups and benthic cover, from which we can begin to infer which groups may have the greatest impact on aspects of coral reef benthic state.

We found that coral reef benthic state was particularly strongly correlated with the abundance of excavating herbivores. Coral cover and calcification rates were predicted to be higher on reefs that had a proportional abundance of excavators within a narrow window ( $P_{Excavators} > 0.1$  and  $< 0.2$ ; Figure 2). Large excavating herbivores, such as larger-bodied parrotfish (e.g. *Scarus coelestinus*; Adam et al., 2018), play a key role in bioerosion on coral reefs, clearing space for the settlement of CCA and corals by removing both dead and live corals through their intense feeding behaviours (Adam et al., 2018; Bellwood & Choat, 1990; McCauley et al., 2014). The direction (positive or negative) and strength of the effects of large parrotfish on coral reefs is based partly on their abundance (McCauley et al., 2014). The intermediate disturbance hypothesis suggests that diversity and ecosystem function is maximised when ecological disturbance is present at an intermediate level (Connell, 1978). We would therefore expect excavating herbivores to be of maximum benefit to coral richness and coral cover when at intermediate proportional abundance (as observed here and in previous studies; Figure 2).

Turf algae, on the other hand, which can outcompete corals for space (Barott et al., 2012; Birrell et al., 2008), thrive on reefs that are subject to frequent disturbance and are often the first species to colonise a disturbed area (Done et al., 2007; Gove et al., 2015; McManus & Polsenberg, 2004). With increasing abundance of excavators, we would expect the greater ecological disturbance caused by their feeding behaviours to result in expanding turf algal cover (as observed here; Figure 2), leading to an overgrowth of corals and reduction of coral reef state. In accordance with the intermediate disturbance hypothesis, we found that higher coral richness and coral cover was predicted on reefs that held an intermediate proportional abundance of excavating herbivores (Figure 2). In addition, turf algal cover was predicted to expand rapidly on reefs with increasing proportional abundance of excavators. However, it is worth noting that this rapid expansion of turf algal cover stems from proportional abundances of excavators beyond what we observed in our empirical data. Our findings support the notion that excavating herbivores are key determinants of coral reef benthic state (Adam et al., 2018; Bellwood & Choat, 1990; McCauley et al., 2014), but that their benefits may not be universal and instead depend on their abundance (McCauley et al., 2014).

All statistical interactions between the proportional abundance of excavators and other functional groups were significantly correlated with increased coral cover and coral calcification rate. Additionally, statistical interactions between browsers and excavators, and scrapers and excavators were significantly correlated with reduced turf algal cover. As the proportional abundance of excavators increases, we would expect these pairwise interaction effects to become stronger (up to a point;  $P_{Excavators} = 0.6$ ) and would anticipate an associated decline in turf algal cover and increase in coral cover. However, turf algal cover was predicted to increase sharply on reefs with a proportional abundance of excavators above maximum functional group evenness ( $P > 0.2$ ), whilst coral cover and calcification rate were predicted to decline. Although our results suggest that co-occurrence of excavators and other functional groups is correlated with improved turf algal control, and subsequent increase in coral growth, functional group co-occurrence may not be enough to buffer the negative impacts of disturbance by high-level excavating feeding behaviours.

Coral reefs relatively abundant in farming damselfish ( $P_{farmers} > 0.2$ ) were predicted to have lower macroalgal cover and higher CCA cover, whilst turf algal cover remained reasonably unchanged (Figure 2). Concurrently, total coral cover and coral recruitment were predicted to rise (up to a point). Upon closer inspection of coral cover, we found that increasing abundance of farming damselfish was correlated with a disproportionate expansion of non-framework, weedy species of coral (e.g. *Porites astreoides*; Darling et al 2012; Green et al 2008) (Supporting Information Figure S3). Weedy coral species have relatively low calcification rates compared with other trait-based groups (e.g. weedy: *Porites astreoides*: 5.78 kg CaCO<sub>3</sub>m<sup>-2</sup>year<sup>-1</sup>; competitive: *Acropora cervicornis*: 19.28 kg CaCO<sub>3</sub>m<sup>-2</sup>year<sup>-1</sup>; González-Barrios & Álvarez-Filip, 2018), which may explain why calcification rate was not predicted to increase alongside coral cover with increasing abundance of farmers (Figure 2).

The relationship between farming damselfish and coral reef health remains unclear (Green & Bellwood, 2009). Territories of farming damselfish may provide refuge for CCA and coral recruits, as their aggressive territorial behaviour drives away corallivores and excavating herbivores (Bellwood & Choat, 1990; Sammarco, 1983). On the other hand, farming damselfish can indirectly harm coral communities by cultivating turf algae, leading to a reduction of available space for recruits and mortality of adult corals (Sammarco & Williams, 1982). Farming damselfish require areas of hard substratum on which to grow their turf algal farms (Ceccarelli et al., 2001, 2005) and their abundance is often strongly associated with live coral cover (Komyakova et al., 2019; Pratchett et al., 2012; Wilson et al., 2008). Given this reliance, we would expect a positive correlation between proportional abundance of farmers and greater coral cover, as our results show. However, as the

abundance of farming damselfish continued to rise ( $P_{farmers} > 0.5$ ; Figure 2), predicted coral cover and coral calcification rate declined despite an increase in CCA cover and coral recruitment (Figure 2). These findings support the idea that territorial farming damselfish may benefit coral by protecting coral recruits when at an intermediate abundance, yet negatively impact reef accretion when populations grow. These negative impacts of rising proportional abundance of farmers may be due to their intensive farming behaviour (Hata & Kato, 2004) or simply through lack of functional diversity within the herbivore guild as a whole. Further investigation is required to fully disentangle the relationship between farming damselfish, benthic state and coral health and identify a possible threshold between the benefits and costs of territorial behaviour on coral reef ecosystem state.

### **Practical implications – the impact of selective fishing**

Selective fishing of predators and larger herbivorous species is shifting the composition of herbivorous fish communities, causing a disproportionate reduction of certain functional groups and reducing herbivore diversity (Edwards et al., 2013; Heenan et al., 2016). Large excavating parrotfish are particularly vulnerable to high fishing pressure and are declining across the Caribbean (Adam et al., 2015; Shantz et al., 2020). Despite their intense feeding behaviours, these species play an important role in continued coral accretion by clearing space for the settlement of CCA and corals (Bellwood & Choat, 1990; McCauley et al., 2014; Adam et al., 2018; Figure 2), and their decline may come at significant cost to coral reef function (Green & Bellwood, 2009). On the other hand, small farming damselfish are subject to a low fishing pressure and are becoming increasingly abundant worldwide (Edwards et al., 2013; Vermeij et al., 2015). Although our results give support for the potential benefits of farming damselfish on coral recruitment (Figure 2), their aggressive territorial defence indirectly promotes algal growth by excluding other reef herbivores, leading to both recruit and adult coral mortality (Sammarco & Williams, 1982). Our analysis also predicted an expansion of weedy coral cover on reefs with rising populations of farmers, suggesting that farming damselfish may influence coral composition by disproportionately promoting the growth of non-framework, weedy coral species. The abundance of weedy coral species is increasing across the Caribbean and is thought to be contributing to the reduction in coral reef function (Alvarez-Filip et al., 2011; González-Barrios & Álvarez-Filip, 2018; Green et al., 2008). The proliferation of damselfish populations as a result of selective fishing of predators and larger herbivores could explain this shift towards weedy coral species and subsequent decline in coral reef function.

## 558 **Conclusion**

559 Our results demonstrate a positive correlation between functional diversity of herbivorous reef fish  
560 and increasing coral richness, total coral cover and reef calcification rate (Table 1; Test 2).  
561 Furthermore, by modelling pairwise statistical interactions, we found that functional group co-  
562 occurrence positively correlates with improved coral reef benthic state. Using these results, we  
563 explored the potential role that herbivore functional diversity and functional group co-occurrence  
564 may play in determining the dominant benthic organisms on tropical coral reefs. We highlight  
565 excavating and farming herbivorous fish as potential key determinants of coral reef benthic state,  
566 predicting that their benefits may be greatest when at intermediate abundances. Using Diversity-  
567 Interactions models, we highlight the importance of managing for a diverse herbivorous fish  
568 assemblage and co-occurrence of functional groups to promote coral reef persistence.

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## Data availability statement

All data analysed in this study are available from the sources cited. We provide code associated with this study at an open source repository (<https://github.com/cesheppard/cooccurrence-benthos>).

## Tables

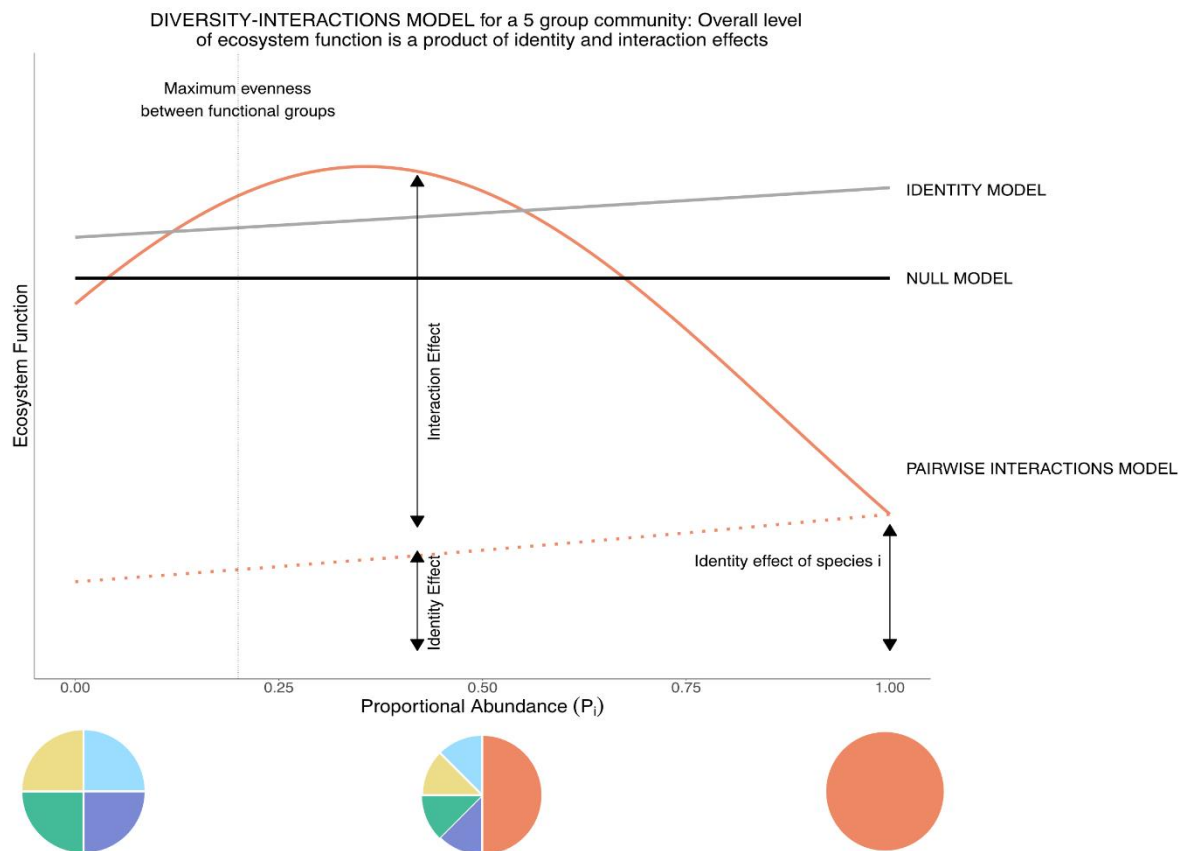
**Table 1:** Comparison of Diversity-Interactions models using analysis of the Wald statistic (analogous to *F* test). Test 1 (Model 1: Null model vs Model 2: Identity model) tests whether herbivore functional groups differ significantly in their association with coral reef benthic state. Test 2 (Model 2: Identity model vs Model 3: Full pairwise interactions model) tests whether interactions between herbivore functional groups are significantly associated with coral reef benthic state. Values represent the mean  $\pm$  standard deviation of 1000 bootstrapped iterations. Percentage refers to the percentage of bootstrapped iterations with *p*-values  $\leq 0.05$ . Significant results are shown in bold and indicate that functional groups differ in their association with benthic state (Test 1) and that interactions between functional groups are associated with benthic state (Test 2).

	Test 1: Model 1 vs Model 2			Test 2: Model 2 vs Model 3		
	Wald	<i>p</i>	%	Wald	<i>p</i>	%
<b>Coral Richness</b>	24.94 $\pm$ 4.10	<b>0.00 <math>\pm</math> 0.00</b>	<b>100</b>	45.38 $\pm$ 9.59	<b>0.00 <math>\pm</math> 0.00</b>	<b>100</b>
<b>Total Coral Cover</b>	64.25 $\pm$ 15.76	<b>0.00 <math>\pm</math> 0.00</b>	<b>100</b>	69.89 $\pm$ 21.15	<b>0.00 <math>\pm</math> 0.00</b>	<b>100</b>
<b>Coral Calcification Rate</b>	39.25 $\pm$ 7.88	<b>0.00 <math>\pm</math> 0.00</b>	<b>100</b>	52.16 $\pm$ 13.48	<b>0.00 <math>\pm</math> 0.00</b>	<b>100</b>
<b>Coral Recruitment</b>	43.66 $\pm$ 11.81	<b>0.00 <math>\pm</math> 0.00</b>	<b>100</b>	11.50 $\pm$ 5.84	0.43 $\pm$ 0.29	11.4
<b>Competitive Coral Cover</b>	3.71 $\pm$ 1.05	0.46 $\pm$ 0.14	0	27.46 $\pm$ 9.25	<b>0.03 <math>\pm</math> 0.07</b>	<b>85.3</b>
<b>Weedy Coral Cover</b>	54.60 $\pm$ 15.56	<b>0.00 <math>\pm</math> 0.00</b>	<b>100</b>	25.94 $\pm$ 10.75	<b>0.05 <math>\pm</math> 0.09</b>	<b>73.9</b>
<b>Stress-tolerant Coral Cover</b>	36.43 $\pm$ 5.39	<b>0.00 <math>\pm</math> 0.00</b>	<b>100</b>	82.01 $\pm$ 34.61	<b>0.00 <math>\pm</math> 0.00</b>	<b>100</b>
<b>Generalist Coral Cover</b>	51.39 $\pm$ 9.88	<b>0.00 <math>\pm</math> 0.00</b>	<b>100</b>	65.75 $\pm$ 15.63	<b>0.00 <math>\pm</math> 0.00</b>	<b>100</b>
<b>Fleshy Macroalgal Cover</b>	42.63 $\pm$ 7.47	<b>0.00 <math>\pm</math> 0.00</b>	<b>100</b>	18.85 $\pm$ 5.92	0.10 $\pm$ 0.13	48.3
<b>Calcareous Macroalgal Cover</b>	6.09 $\pm$ 1.78	0.23 $\pm$ 0.13	4.1	22.23 $\pm$ 5.03	<b>0.03 <math>\pm</math> 0.04</b>	<b>78.8</b>
<b>Turf Algal Cover</b>	17.88 $\pm$ 5.20	<b>0.01 <math>\pm</math> 0.01</b>	<b>99.3</b>	25.26 $\pm$ 5.6.	<b>0.02 <math>\pm</math> 0.03</b>	<b>92</b>
<b>CCA Cover</b>	11.80 $\pm$ 2.50	<b>0.03 <math>\pm</math> 0.03</b>	<b>83.6</b>	36.06 $\pm$ 14.11	<b>0.01 <math>\pm</math> 0.04</b>	<b>91.1</b>

826 **Table 2:** Predicted maximums, percentages and break downs of metrics of coral reef benthic state.

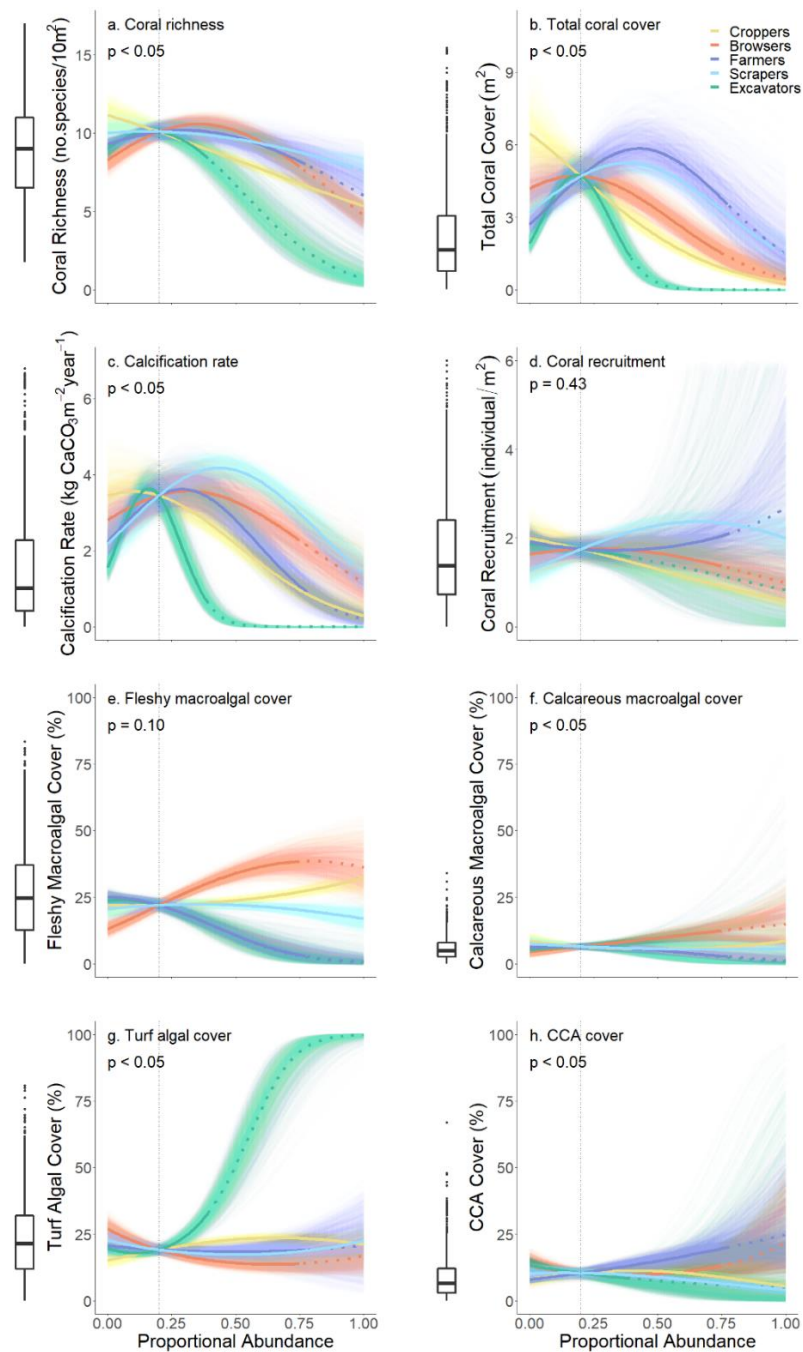
Response	Predicted maximum	Predicted response at maximum functional group evenness ( $P = 0.2$ )	% of predicted maximum at $P = 0.2$	% of predicted response composed of interaction effects at $P = 0.2$
Coral Richness	11.15	10.09	90.47	61.85
Total Coral Cover	6.46	4.69	72.56	99.44
Coral Calcification Rate	4.17	3.45	82.68	99.77
Coral Recruitment	2.68	1.75	65.28	31.03
Fleshy Macroalgal Cover	38.49	21.97	57.09	71.94
Calcareous Macroalgal Cover	14.83	6.43	43.39	42.09
Turf Algal Cover	99.87	19.13	19.16	65.62
CCA Cover	24.80	10.37	41.82	10.12

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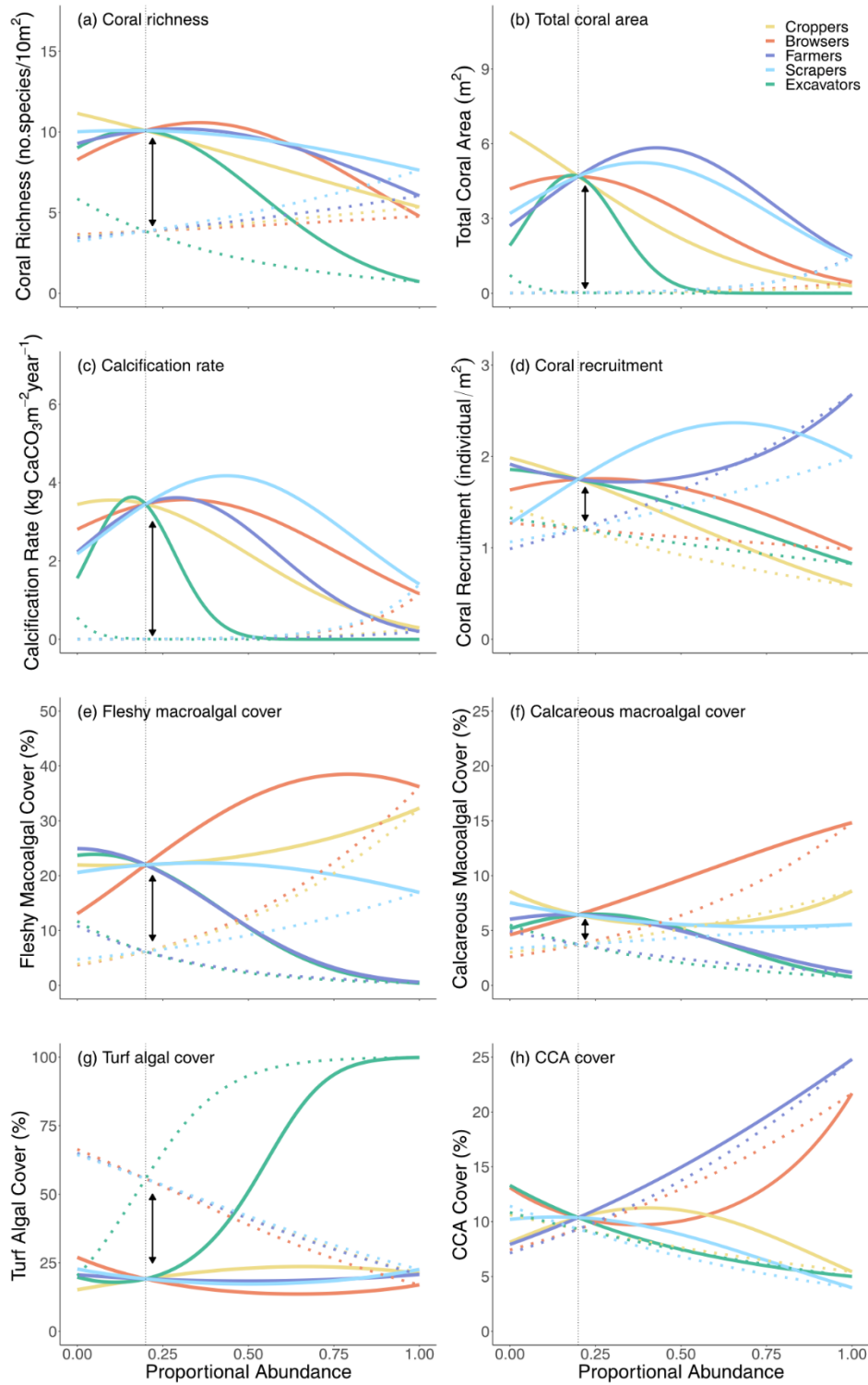


**Figure 1:** Illustration of the Diversity-Interactions modelling approach of an ecosystem function ( $y$ ) in a community of five functional groups. For the pairwise interactions model (Model 3), overall ecosystem function is a product of identity and interaction effects. Coloured pie charts illustrate the changing proportional abundance of five functional groups.





**Figure 2:** Predicted coral reef benthic state using results from 1000 iterations of bootstrapped pairwise interaction models (Model 3). Thicker lines represent mean predicted values. Dotted segments represent predictions extrapolated from empirical data (i.e. no survey in our analysis had proportional abundance of excavators > 0.39). Vertical dotted lines represent maximum evenness between functional groups ( $P = 0.2$ ). p-values represent analysis of Wald statistic between Models 2 and 3, which tests the significance of statistical interactions between functional groups (Table 1; Test 2). Note: coral recruitment y-axis has been limited for ease of viewing. Boxplots represent the spread of raw data by survey and have been limited to correspond with predicted values (see Supporting Information Figure S4 for full boxplots).



**Figure 3:** Mean predicted metrics of coral reef benthic state using results from pairwise interactions models (Model 3), separated into net identity (dotted lines) and net interaction effects (**black arrows**). Vertical dotted lines represent maximum evenness between functional groups ( $P = 0.2$ ).

849 **Table S1:** Classification of fish species into herbivore functional groups: croppers, browsers, farmers, scrapers and excavators.

Functional Group	Family	Species	Reference
Cropper	Surgeonfish (Acanthuridae); Parrotfish (Labridae)	<i>Acanthurus chirurgus</i> ; <i>A. coeruleus</i> ; <i>A. tractus</i> ; <i>Scarus coeruleus</i>	Adam et al. 2018; Green & Bellwood 2009
Browser	Chubs (Kyphosidae); Parrotfish (Labridae)	<i>Cryptotomus roseus</i> ; <i>Sp. aurofrenatum</i> ; <i>Sp. chrysopteron</i> ; <i>Sp. rubripinne</i> ; <i>Kyphosidae</i> (not identified to species level) <i>Sparisoma atomarium</i> *; <i>Sp. radians</i> * ( <i>Sp. chrysopteron</i> )	Adam et al. 2018; Green & Bellwood 2009; <a href="http://www.fishbase.org">www.fishbase.org</a> Bellwood and Choat 1990; Bernardi et al. 2000
Farmer	Territorial Damselfish (Pomacentridae)	<i>Microspathodon chrysurus</i> ; <i>Stegastes planifrons</i>	Green & Bellwood 2009
Scraper	Parrotfish (Labridae)	<i>S. taeniopterus</i> ; <i>S. vetula</i> <i>S. iseri</i> * ( <i>S. vetula</i> )	Adam et al. 2018; Green & Bellwood 2009 Choat et al. 2012
Excavator	Parrotfish (Labridae)	<i>S. coelestinus</i> ; <i>S. guacamaia</i> ; <i>Sp. viride</i>	Adam et al. 2018 <sup>1</sup> ; Green & Bellwood 2009

850 \* Parrotfish of the genera *Scarus* and *Sparisoma* that were not identified in Adam et al. (2018) were grouped guided by their closest related species, given in parenthesis

851 **Table S2:** Metrics of coral reef benthic state

Benthic Metric	Description
Coral species richness	The number of coral species encountered on each survey/site
Total coral cover	Total cover (m <sup>2</sup> ) of all coral colonies ≥ 4 cm across a standardized transect (10m <sup>2</sup> )
Competitive/weedy/stress-tolerant/generalist coral cover	Total cover (m <sup>2</sup> ) of all coral colonies ≥ 4 cm classified as competitive/weedy/stress-tolerant/generalist, according to Darling et al. (2012), across a standardized transect (10m <sup>2</sup> )
Coral calcification rate	Total calcification rate (kg CaCO <sub>3</sub> m <sup>2</sup> year <sup>1</sup> ) per transect, calculated using mean species-specific calcification rates (González-Barrios and Álvarez-Filip, 2018) and coral area estimates
Coral recruitment density	Count of all hard coral colonies less than 2cm in diameter (individuals/m <sup>2</sup> )
Fleshy/Calcareous macroalgal/Turf algal/CCA cover	Percentage algal cover estimated from benthic point counts

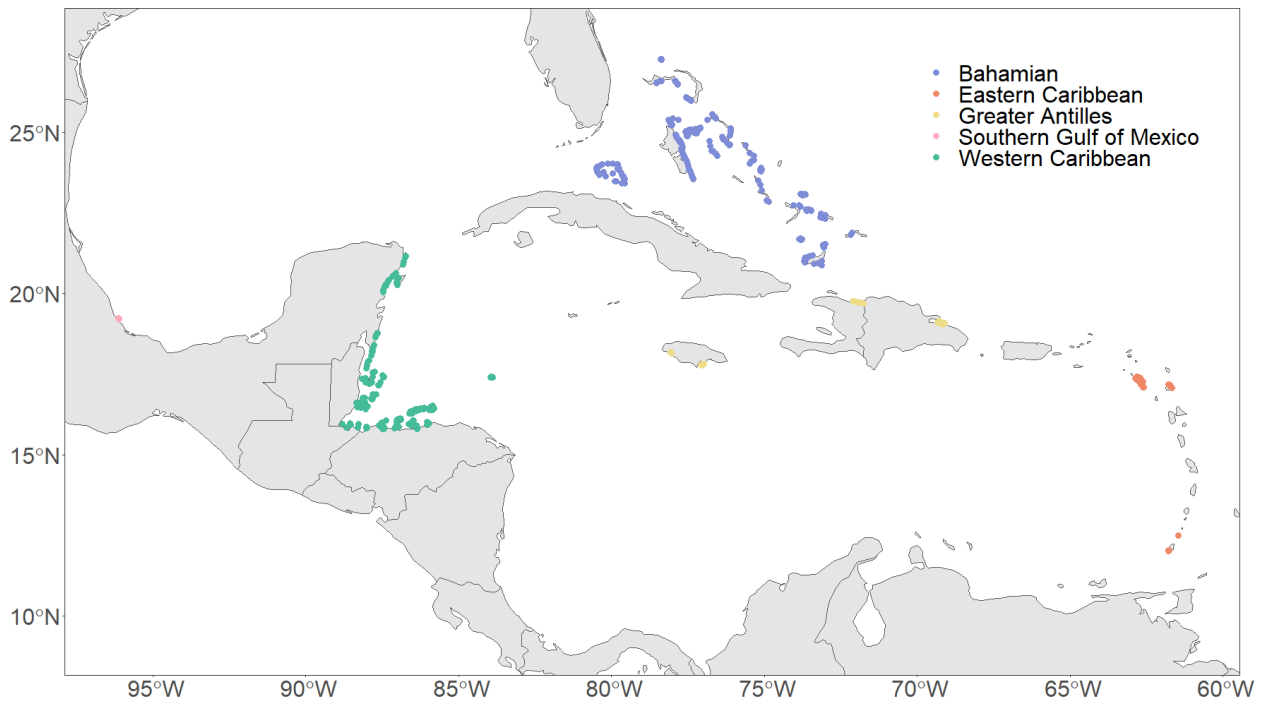
853 **Table S3:** Trait-based groupings of coral species not identified in Darling et al. (2012). Classification  
854 was made based on genus, phylogeny and known traits (coraltraits.org).

Species	Coral Group <sup>855</sup>
<i>Orbicella faveolata</i>	Generalist
<i>Orbicella franksi</i>	Generalist
<i>Orbicella</i> sp.	Generalist
<i>Cladocora arbuscula</i>	Stress-tolerant
<i>Dichocoenia stellaris</i>	Stress-tolerant
<i>Dichocoenia stokesii</i>	Stress-tolerant
<i>Oculina diffusa</i>	Stress-tolerant
<i>Oculina varicosa</i>	Stress-tolerant
<i>Oculina</i> sp.	Stress-tolerant
<i>Orbicella annularis</i>	Stress-tolerant
<i>Pseudodiploria clivosa</i>	Stress-tolerant
<i>Pseudodiploria strigosa</i>	Stress-tolerant
<i>Pseudodiploria</i> sp.	Stress-tolerant
<i>Solenastrea bournoni</i>	Stress-tolerant
<i>Solenastrea hyades</i>	Stress-tolerant
<i>Solenastrea</i> sp.	Stress-tolerant
<i>Helioseris cucullata</i>	Weedy
<i>Mussa angulosa</i>	Weedy
<i>Scolymia cubensis</i>	Weedy
<i>Scolymia lacera</i>	Weedy
<i>Scolymia wellsii</i>	Weedy
<i>Scolymia</i> sp.	Weedy

856 **Table S4:** Spatial correlation between sites within the same subregion ( $\alpha$ ). Values represent the mean  $\pm$  standard deviation of 1000 bootstrapped iterations.  
857 Percentage refers to the percentage of bootstrapped iterations with p-values  $\leq 0.05$ . Significant results shown in bold.

Metric	Model 1				Model 2				Model 3			
	Alpha	SE	<i>p</i>	%	Alpha	SE	<i>p</i>	%	Alpha	SE	<i>p</i>	%
Coral Richness	0.14 $\pm$ 0.01	0.07 $\pm$ 0.00	0.06 $\pm$ 0.01	27	0.12 $\pm$ 0.01	0.07 $\pm$ 0.00	0.08 $\pm$ 0.02	0	0.10 $\pm$ 0.01	0.07 $\pm$ 0.01	0.17 $\pm$ 0.03	0
Total Coral Cover	0.08 $\pm$ 0.01	0.05 $\pm$ 0.01	0.10 $\pm$ 0.05	18.6	0.08 $\pm$ 0.01	0.06 $\pm$ 0.00	0.19 $\pm$ 0.04	0	0.08 $\pm$ 0.01	0.05 $\pm$ 0.00	0.11 $\pm$ 0.04	3.2
Coral Calcification Rate	0.03 $\pm$ 0.01	0.04 $\pm$ 0.01	0.45 $\pm$ 0.09	0	0.03 $\pm$ 0.01	0.04 $\pm$ 0.01	0.48 $\pm$ 0.10	0	0.05 $\pm$ 0.01	0.04 $\pm$ 0.01	0.27 $\pm$ 0.10	0.3
Coral Recruitment	0.13 $\pm$ 0.01	0.06 $\pm$ 0.00	<b>0.02 <math>\pm</math> 0.01</b>	<b>94.7</b>	0.09 $\pm$ 0.01	0.05 $\pm$ 0.01	0.07 $\pm$ 0.03	30.7	0.09 $\pm$ 0.01	0.06 $\pm$ 0.01	0.11 $\pm$ 0.04	8.9
Competitive Coral Cover	0.03 $\pm$ 0.00	0.05 $\pm$ 0.01	0.53 $\pm$ 0.08	0	0.03 $\pm$ 0.00	0.06 $\pm$ 0.01	0.64 $\pm$ 0.08	0	0.01 $\pm$ 0.01	0.75 $\pm$ 2.09	0.89 $\pm$ 0.09	0
Weedy Coral Cover	0.15 $\pm$ 0.02	0.05 $\pm$ 0.01	<b>0.01 <math>\pm</math> 0.02</b>	<b>92</b>	0.18 $\pm$ 0.02	0.07 $\pm$ 0.01	<b>0.02 <math>\pm</math> 0.02</b>	<b>82.7</b>	0.17 $\pm$ 0.02	0.06 $\pm$ 0.01	<b>0.01 <math>\pm</math> 0.03</b>	<b>95.5</b>
Stress-tolerant Coral Cover	0.04 $\pm$ 0.01	0.03 $\pm$ 0.00	0.15 $\pm$ 0.05	0.5	0.03 $\pm$ 0.01	0.03 $\pm$ 0.00	0.29 $\pm$ 0.07	0	0.03 $\pm$ 0.01	0.03 $\pm$ 0.00	0.29 $\pm$ 0.10	0
Generalist Coral Cover	0.00 $\pm$ 0.01	0.01 $\pm$ 0.00	0.67 $\pm$ 0.21	0	0.00 $\pm$ 0.01	0.02 $\pm$ 0.00	0.75 $\pm$ 0.18	0	0.02 $\pm$ 0.01	0.07 $\pm$ 0.07	0.72 $\pm$ 0.12	0
Fleshy Macroalgal Cover	0.47 $\pm$ 0.01	0.27 $\pm$ 0.01	0.08 $\pm$ 0.01	0	0.39 $\pm$ 0.01	0.22 $\pm$ 0.01	0.07 $\pm$ 0.01	0.8	0.43 $\pm$ 0.02	0.24 $\pm$ 0.01	0.07 $\pm$ 0.01	2.1
Calcareous Macroalgal Cover	0.13 $\pm$ 0.01	0.06 $\pm$ 0.00	<b>0.04 <math>\pm</math> 0.02</b>	<b>63.3</b>	0.13 $\pm$ 0.01	0.07 $\pm$ 0.01	0.07 $\pm$ 0.02	24.5	0.14 $\pm$ 0.01	0.08 $\pm$ 0.01	0.07 $\pm$ 0.02	20.3
Turf Algal Cover	0.30 $\pm$ 0.02	0.10 $\pm$ 0.01	<b>0.00 <math>\pm</math> 0.00</b>	<b>100</b>	0.32 $\pm$ 0.02	0.11 $\pm$ 0.01	<b>0.01 <math>\pm</math> 0.00</b>	<b>100</b>	0.34 $\pm$ 0.02	0.14 $\pm$ 0.01	<b>0.02 <math>\pm</math> 0.01</b>	<b>99.2</b>
CCA Cover	0.21 $\pm$ 0.02	0.10 $\pm$ 0.01	0.05 $\pm$ 0.02	53.5	0.23 $\pm$ 0.02	0.13 $\pm$ 0.01	0.07 $\pm$ 0.03	27.6	0.25 $\pm$ 0.02	0.15 $\pm$ 0.01	0.11 $\pm$ 0.03	2

859 **Table S5:** Coefficients for all three Diversity-Interactions models for all metrics of coral reef benthic  
860 state. Note: values are raw and therefore log-transformed. Values represent the mean  $\pm$  standard  
861 deviation of bootstrapped iterations. Percentage refers to the percentage of bootstrapped iterations  
862 with p-values  $\leq 0.05$ . Significant results shown in bold. **Please see Supplementary\_Table\_5.xlsx**

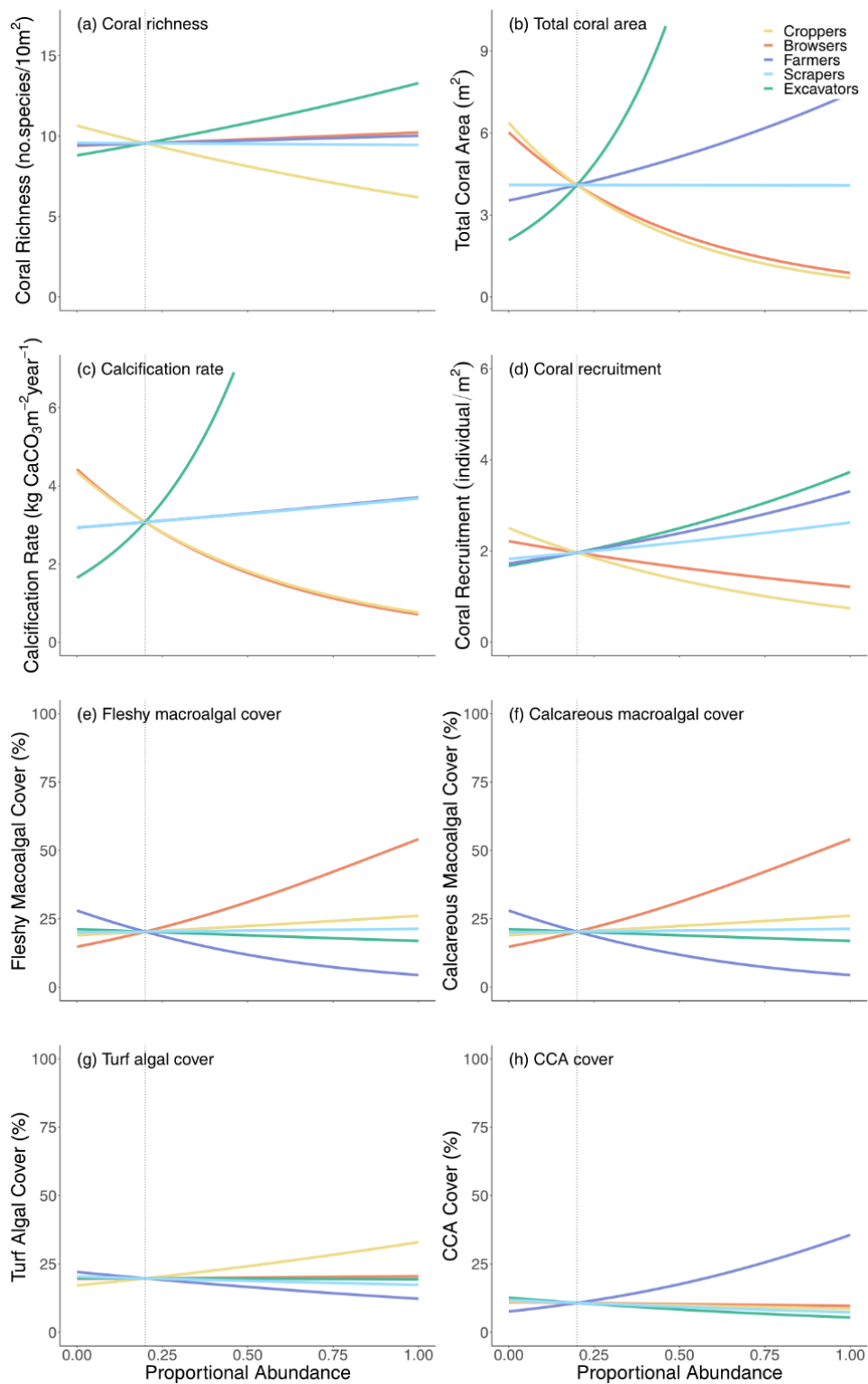


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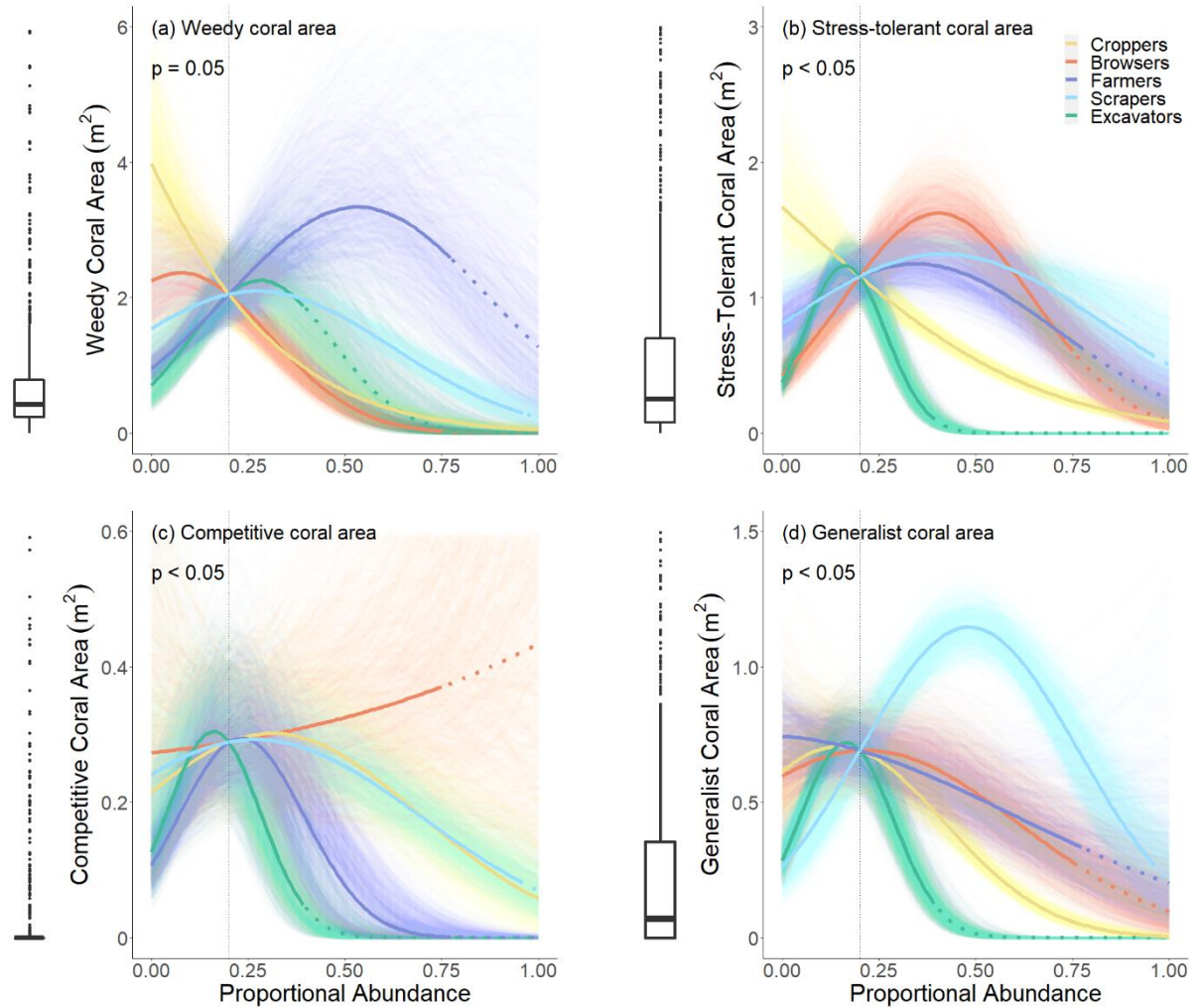
864 **Figure S1:** Map of Atlantic and Gulf Rapid Reef Assessment (AGRRA) survey sites included in our

865 analysis. Colour groups depict five ecoregions.

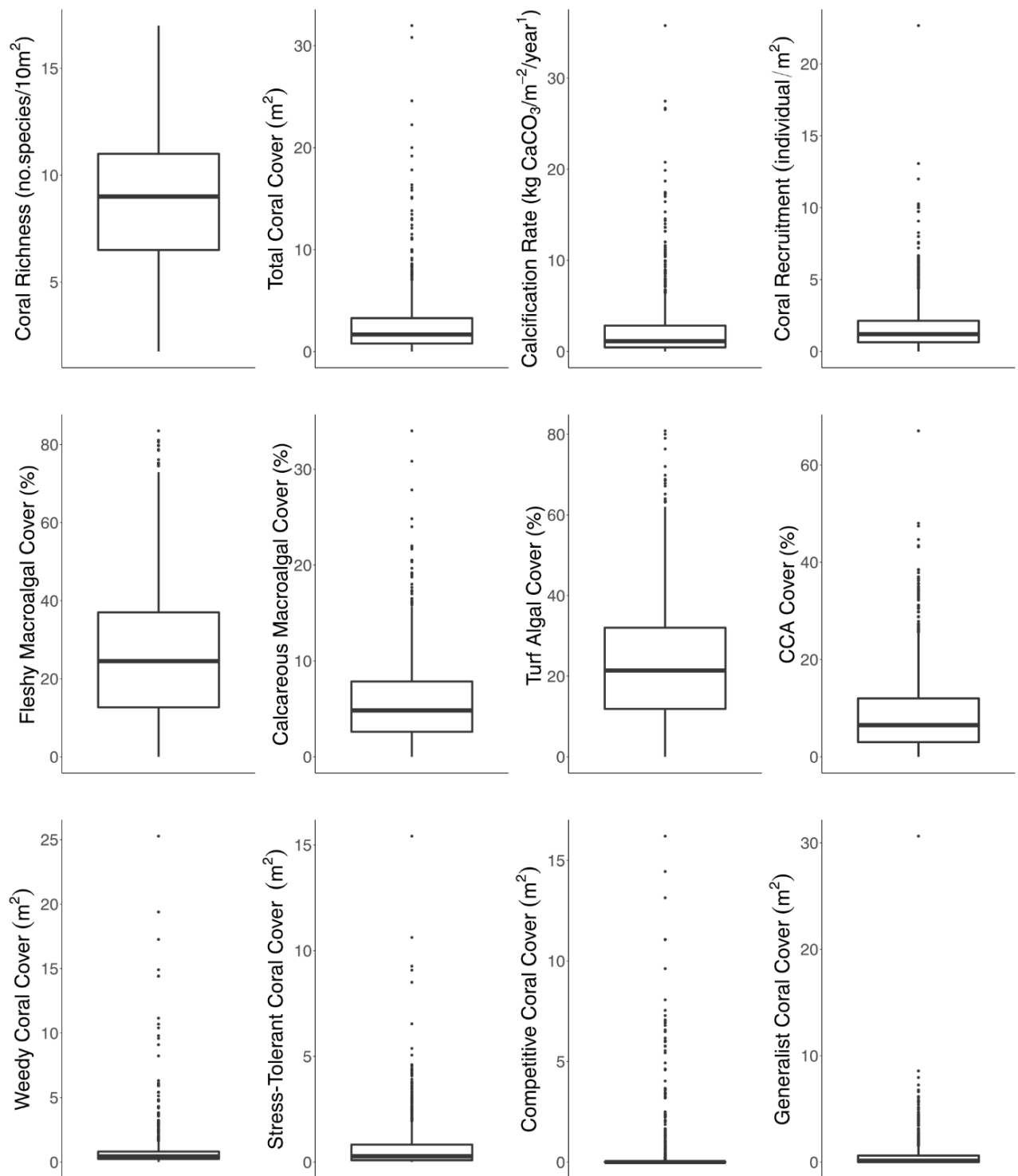




**Figure S2:** Mean predicted metrics of coral reef benthic state using results from identity model (Model 2). Vertical dotted lines represent maximum evenness between functional groups ( $P = 0.2$ ). Note: y-axes have been limited to correspond with Figure 2 for ease of comparison.



**Figure S3:** Predicted metrics of coral cover separated into trait-based groups, using results from 1000 iterations of bootstrapped pairwise interaction models. Thicker lines represent mean predicted coral cover. Dotted segments represent predictions that are extrapolated from empirical data. Vertical dotted lines represent maximum evenness between functional groups ( $P = 0.2$ ). p-values correspond to analysis of Wald statistic between the identity model (Model 2) and pairwise interaction model (Model 3) (Table 1; Test 2). Boxplots represent the spread of raw metrics of coral cover by survey and have also been limited to correspond with predicted values for ease of viewing (see Figure S4 for full boxplots).



**Figure S4:** Full boxplots of raw measurements of coral reef benthos by survey in our analysis.