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

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10

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20

21 **Biosketch**

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

24

25 **Conflict of interest**

26 All authors declare that they have no conflicts of interest.

27

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

57 1. Introduction

58 Biodiversity loss is driving changes to ecosystem function across biomes (Hooper et al., 2012).
59 Ecosystem function, defined as the fluxes of energy and material within an ecosystem (Bellwood et
60 al., 2019), can be mediated by the identity and composition of species present, and their interactions
61 with their environment (Brandl et al., 2019). Historically, the positive effects of biodiversity on
62 ecosystem function focussed on measures of species richness, likely due to the prominent interest in
63 and irreversibility of species loss (Chapin et al., 2000; Hooper et al., 2012; Kirwan et al., 2007).
64 However, more recently, interest in diversity-driven ecosystem function has shifted towards
65 functional diversity and the composition of functional traits (Bellwood et al., 2019; Cheal et al., 2010;
66 Finn et al., 2013; Grange et al., 2021; Mouillot et al., 2011; Stuart-Smith et al., 2013). When fewer
67 species are present, increased functional diversity improves a community's ability to extract
68 resources from its environment and maintain ecosystem function (Cadotte et al., 2011). Equally,
69 niche partitioning between species allows for better utilisation of an ecosystem's limited resources
70 and increases the probability of positive co-occurrence effects on ecosystem function (Duffy et al.,
71 2017).

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

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

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

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

104 Previous work using Diversity-Interactions models to investigate diversity-driven coral reef function
105 found that species diversity enhanced herbivory rates on coral reefs, yet no additional effect of
106 herbivore species co-occurrence was identified (Lefcheck et al., 2019). However, these analytical
107 approaches were limited to an “average interaction” term rather than separate pairwise interactions
108 (Lefcheck et al., 2019). This modelling approach is analogous to the “evenness model” (Kirwan et al.
109 2009), which assumes that the strength of any statistical interaction between species is the same for
110 all pairwise combinations. By modelling each pairwise statistical interaction separately, we can
111 explore and identify the pairwise co-occurrences between herbivorous fish functional groups with
112 the greatest potential effects.

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

121

122 2. Methods

123 AGRRA dataset description

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

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

141 Benthic composition was recorded using 10 m long point intercept transects (PIT) where substrate
142 type was noted every 0.1 m (totalling 100 points). Coral recruits ≤ 2 cm in maximum length within a
143 25 cm x 25 cm square quadrat placed at 2 m intervals along these transects were also recorded, as
144 well as the number of adult and juvenile *Diadema antillarum* (historically important herbivorous
145 urchins on western Atlantic reefs; Bodmer *et al.*, 2015). For each site, geographic coordinates,
146 ecoregion and geographical subregion were available. Sites included in our analysis were spread
147 across 47 subregions and five ecoregions (see Supporting Information Figure S1).

148

149 Calculation of herbivore functional group abundances

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

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

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

173 Proportional abundances of each herbivorous functional group, as well as total herbivorous fish
174 biomass, were calculated per transect. We focus on proportional abundance rather than
175 proportional biomass as, in this context, the number of individual fish per functional group is more
176 useful for investigating the importance of co-occurrence. We believe this is justified as it is presence
177 and behaviour of individuals that shape activities at the population level which, in turn, have
178 consequences to community structure and interspecific interactions. Although herbivore biomass is
179 an important determinant of coral reef benthic state (Williams & Polunin, 2001; Williams et al.,
180 2019), when divided into functional groups, proportional biomass can be dramatically skewed by just
181 a few large-bodied individuals, particularly excavating parrotfish (e.g. *Sparisoma viride*; Adam et al.,
182 2018) (per survey; mean number of excavators: 1.80; mean proportional biomass of excavators:
183 0.24). As such, it seemed more appropriate to use proportional abundance as a measure of
184 community structure to remove this size bias. Total herbivore biomass was, however, included in our
185 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 (m²)
202 were computed per transect, as well as the cover of each separate trait-based coral group (m²). Total
203 calcification rates (kg CaCO₃ m⁻² 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,

218 particularly after a disturbance (Airoldi, 1998; Wilson et al., 2006), typically take much longer.
219 Average benthic metrics and proportional abundances of herbivorous fish functional groups were
220 calculated for each survey, alongside average depth (range: 1.0 – 24.6 m), total *Diadema* population
221 (individuals/10 m²) and total herbivore biomass (g/60m²). Preliminary analysis which included
222 *Diadema* abundance as an explanatory variable revealed that their abundance was significantly
223 correlated with metrics of coral reef benthic state. We therefore excluded all surveys where
224 *Diadema* populations were not counted to have *Diadema* abundance in all further analysis. One
225 survey with a *Diadema* abundance greater than 25 standard deviations above the average from
226 across all surveys was also removed from our analysis as this was concluded to be highly unlikely and
227 therefore an error (observed: 168 individuals/10 m², mean: 1.3 individuals/10 m²).

228

229 **Data analysis**

230 To test the extent to which pairwise statistical interactions between herbivorous fish functional
231 group abundances correlated with metrics of coral reef benthic state, and whether functional groups
232 varied in their correlation with benthic composition, we applied the Diversity-Interactions modelling
233 framework, as presented by Kirwan et al. (2009). The Diversity-Interactions modelling framework
234 offers a suite of linear regression models designed to test biologically meaningful hypotheses about
235 how species and functional group interactions may contribute to ecosystem function (Kirwan et al.,
236 2009). We fit three separate Diversity-Interactions models: null model, species identity model, and
237 full pairwise interactions model (Figure 1). Briefly, the null model assumes no effect of species
238 identity or interactions on ecosystem function. The identity model considers only the effects of
239 species identity on ecosystem function, whereas the pairwise interactions model includes the effects
240 of both species identity and interactions separately.

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

$$243 \quad y = \beta + \alpha M + \varepsilon \quad \text{Equation 1}$$

244 where α represents the effect of changing species abundance (M) and β is the level of ecosystem
245 function at average M .

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

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

$$252 \quad y = \sum_{i=1}^s \beta_i P_i + \alpha M + \varepsilon \quad \text{Equation 2}$$

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

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

$$260 \quad y = \sum_{i=1}^s \beta_i P_i + \alpha M + \sum_{\substack{i,j=1 \\ i < j}}^s \delta_{ij} P_i P_j + \varepsilon \quad \text{Equation 3}$$

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

$$266 \quad \sum_{\substack{i,j=1 \\ i < j}}^s \delta_{ij} P_i P_j \quad \text{Equation 4}$$

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

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

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

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

305 disputed and can give rise to errors (Wang et al., 2015). Model choice and correlation structure can
306 therefore be guided by the data (Wang et al., 2015). As the premise of our study is based around the
307 statistical tests between models, use of the QIC here was deemed inappropriate. Mean and standard
308 deviation of all model summary statistics and statistical tests between models can be found in Table
309 1 and Supplementary Table S5.

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

319

320 **3. Results**

321 **Functional group co-occurrence**

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

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

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

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

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

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

359

360 **Comparison of functional group identity effects**

361 The correlation between herbivore functional groups and benthic metrics (their identity effects)
362 were significantly different from each other, with the exception of calcareous macroalgal cover and
363 competitive coral cover (Table 1, Test 1). Across our study sites, the cover of calcareous macroalgae
364 and competitive corals was low (mean: 5.78% and 0.40 m², respectively) reducing the likelihood that
365 relationships would be detectable in the data.

366 Reefs dominated by one herbivore functional group ($P > 0.2$) were predicted to have lower levels of
367 all coral-related benthic metrics (richness, recruitment, cover and calcification rate), with the
368 exception of farmer- or scraper-dominated reefs, which were predicted to have higher coral
369 recruitment (Figure 2). In particular, coral richness, total coral cover and calcification rate were
370 predicted to be substantially lower on reefs dominated by excavators. Higher coral calcification rate
371 was predicted on reefs where scrapers were relatively abundant (up to a point; $P_{\text{Farmers}} = 0.31$ and
372 $P_{\text{Scrapers}} = 0.44$; Figure 2), whereas coral richness was predicted to be higher when browsers were
373 more abundant (up to a point; $P_{\text{Browsers}} = 0.36$). Coral recruitment rate was predicted to be higher on
374 reefs dominated by farmers or scrapers (Figure 2). Overall, metrics of coral reef benthic state were
375 lower on reefs where one functional group were less abundant ($P < 0.1$) or absent (Figure 2).

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

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

391

392 **4. Discussion**

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

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

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

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

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

439

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

441 By modelling each pairwise interaction separately, the full pairwise interactions model (Model 3) can
442 be used to identify functional group pairings that are most correlated with coral reef benthic state.
443 Statistical interactions between scrapers and croppers were correlated with a moderate increase in
444 CCA cover and coral-related measures (coral richness, coral cover and calcification rate). Scraping
445 herbivores, such as smaller parrotfish species (e.g. *Scarus vetula*; *Labridae*; Adam et al., 2018), are
446 widely recognised to facilitate the settlement and growth of CCA and corals by limiting the
447 establishment and growth of macro- and turf algae (Hoey and Bellwood, 2008; Green and Bellwood,
448 2009; Smith et al. 2010). Croppers (e.g. surgeonfish *Acanthurus coeruleus*; Acanthuridae; Green &
449 Bellwood, 2009) and browsers also play an important role in controlling algal abundance by
450 consuming algae, which competes with CCA and coral recruits for space and shades adult corals
451 (Barott et al., 2012; Green & Bellwood, 2009; Smith et al., 2010). Our results suggest that, in addition
452 to their individual benefits to coral reef benthic state, the co-occurrence of scrapers and croppers
453 may further support CCA growth and indirectly benefit coral diversity and growth. As such, we would
454 predict reefs higher in proportional abundance of both scrapers and croppers to demonstrate a
455 more favourable benthic state, in which algal cover is well-maintained and corals are the dominant
456 benthic organism.

457

458 **Evidence in support of excavating and farming herbivores as key determinants of coral reef** 459 **benthic state**

460 Herbivorous fish functional groups varied significantly to each other in their correlation with coral
461 reef benthic state (Table 1; Test 1). It is well established that herbivore functional groups perform
462 alternative roles within coral reef communities (Burkepile & Hay, 2010; Daniela M. Ceccarelli et al.,
463 2005; Edwards et al., 2013), yet few studies have quantified and compared these effects. Here, we
464 quantify the correlation between herbivore functional groups and benthic cover, from which we can
465 begin to infer which groups may have the greatest impact on aspects of coral reef benthic state.

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

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

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

505 Coral reefs relatively abundant in farming damselfish ($P_{farmers} > 0.2$) were predicted to have lower
506 macroalgal cover and higher CCA cover, whilst turf algal cover remained reasonably unchanged
507 (Figure 2). Concurrently, total coral cover and coral recruitment were predicted to rise (up to a
508 point). Upon closer inspection of coral cover, we found that increasing abundance of farming
509 damselfish was correlated with a disproportionate expansion of non-framework, weedy species of
510 coral (e.g. *Porites astreoides*; Darling et al 2012; Green et al 2008) (Supporting Information Figure
511 S3). Weedy coral species have relatively low calcification rates compared with other trait-based
512 groups (e.g. weedy: *Porites astreoides*: 5.78 kg CaCO₃m⁻²year⁻¹; competitive: *Acropora cervicornis*:
513 19.28 kg CaCO₃m⁻²year⁻¹; González-Barrios & Álvarez-Filip, 2018), which may explain why calcification
514 rate was not predicted to increase alongside coral cover with increasing abundance of farmers
515 (Figure 2).

516 The relationship between farming damselfish and coral reef health remains unclear (Green &
517 Bellwood, 2009). Territories of farming damselfish may provide refuge for CCA and coral recruits, as
518 their aggressive territorial behaviour drives away corallivores and excavating herbivores (Bellwood &
519 Choat, 1990; Sammarco, 1983). On the other hand, farming damselfish can indirectly harm coral
520 communities by cultivating turf algae, leading to a reduction of available space for recruits and
521 mortality of adult corals (Sammarco & Williams, 1982). Farming damselfish require areas of hard
522 substratum on which to grow their turf algal farms (Ceccarelli et al., 2001, 2005) and their
523 abundance is often strongly associated with live coral cover (Komyakova et al., 2019; Pratchett et al.,
524 2012; Wilson et al., 2008). Given this reliance, we would expect a positive correlation between
525 proportional abundance of farmers and greater coral cover, as our results show. However, as the

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

535

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

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

557

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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810 [87458-6](https://doi.org/https://doi.org/10.1007/978-0-387-87458-6)

811

812 **Data availability statement**

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

815 **Tables**

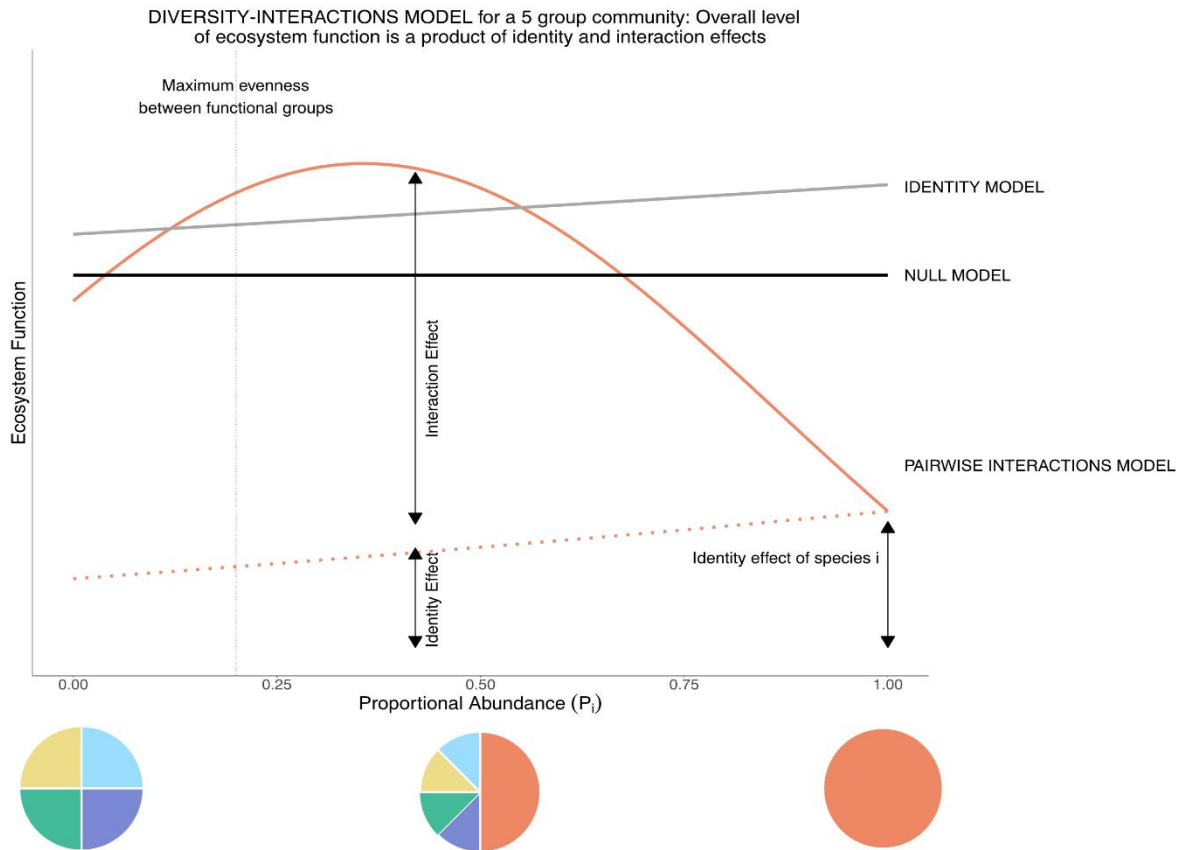
816 **Table 1:** Comparison of Diversity-Interactions models using analysis of the Wald statistic (analogous
 817 to *F* test). Test 1 (Model 1: Null model vs Model 2: Identity model) tests whether herbivore
 818 functional groups differ significantly in their association with coral reef benthic state. Test 2 (Model
 819 2: Identity model vs Model 3: Full pairwise interactions model) tests whether interactions between
 820 herbivore functional groups are significantly associated with coral reef benthic state. Values
 821 represent the mean \pm standard deviation of 1000 bootstrapped iterations. Percentage refers to the
 822 percentage of bootstrapped iterations with p -values ≤ 0.05 . Significant results are shown in bold and
 823 indicate that functional groups differ in their association with benthic state (Test 1) and that
 824 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> | % |
| Coral Richness | 24.94 \pm 4.10 | 0.00 \pm 0.00 | 100 | 45.38 \pm 9.59 | 0.00 \pm 0.00 | 100 |
| Total Coral Cover | 64.25 \pm 15.76 | 0.00 \pm 0.00 | 100 | 69.89 \pm 21.15 | 0.00 \pm 0.00 | 100 |
| Coral Calcification Rate | 39.25 \pm 7.88 | 0.00 \pm 0.00 | 100 | 52.16 \pm 13.48 | 0.00 \pm 0.00 | 100 |
| Coral Recruitment | 43.66 \pm 11.81 | 0.00 \pm 0.00 | 100 | 11.50 \pm 5.84 | 0.43 \pm 0.29 | 11.4 |
| Competitive Coral Cover | 3.71 \pm 1.05 | 0.46 \pm 0.14 | 0 | 27.46 \pm 9.25 | 0.03 \pm 0.07 | 85.3 |
| Weedy Coral Cover | 54.60 \pm 15.56 | 0.00 \pm 0.00 | 100 | 25.94 \pm 10.75 | 0.05 \pm 0.09 | 73.9 |
| Stress-tolerant Coral Cover | 36.43 \pm 5.39 | 0.00 \pm 0.00 | 100 | 82.01 \pm 34.61 | 0.00 \pm 0.00 | 100 |
| Generalist Coral Cover | 51.39 \pm 9.88 | 0.00 \pm 0.00 | 100 | 65.75 \pm 15.63 | 0.00 \pm 0.00 | 100 |
| Fleshy Macroalgal Cover | 42.63 \pm 7.47 | 0.00 \pm 0.00 | 100 | 18.85 \pm 5.92 | 0.10 \pm 0.13 | 48.3 |
| Calcareous Macroalgal Cover | 6.09 \pm 1.78 | 0.23 \pm 0.13 | 4.1 | 22.23 \pm 5.03 | 0.03 \pm 0.04 | 78.8 |
| Turf Algal Cover | 17.88 \pm 5.20 | 0.01 \pm 0.01 | 99.3 | 25.26 \pm 5.6. | 0.02 \pm 0.03 | 92 |
| CCA Cover | 11.80 \pm 2.50 | 0.03 \pm 0.03 | 83.6 | 36.06 \pm 14.11 | 0.01 \pm 0.04 | 91.1 |

825

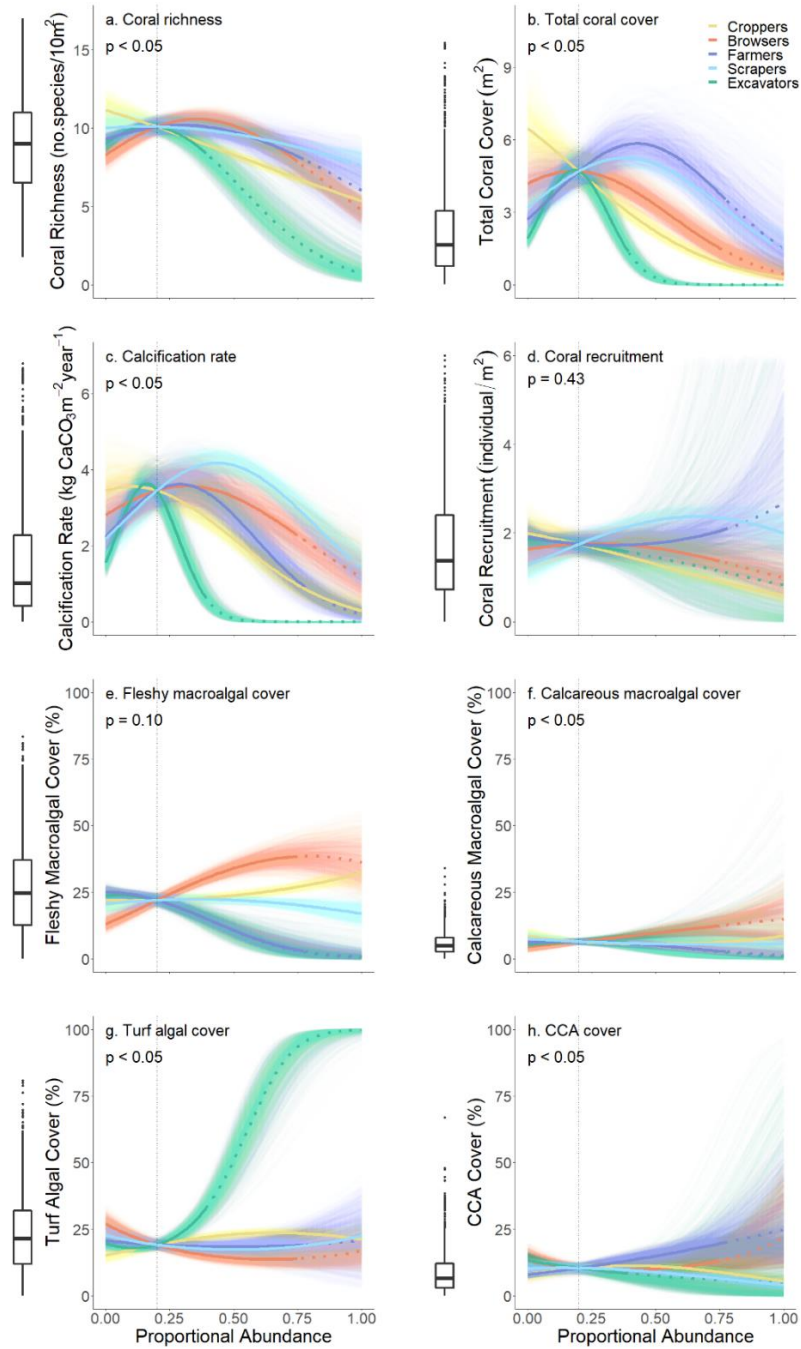
Table 2: Predicted maximums, percentages and break downs of metrics of coral reef benthic state.

| 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 |



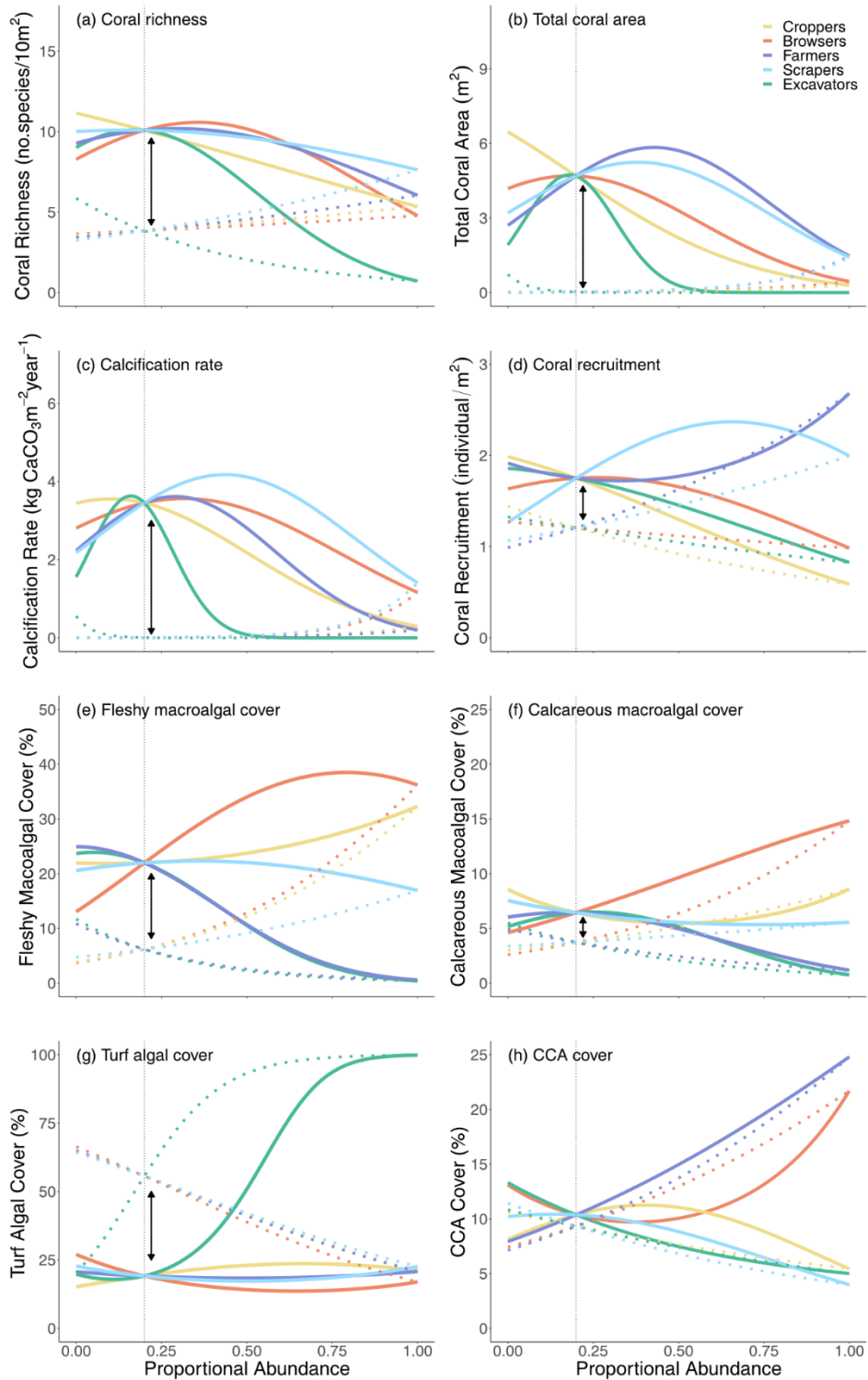
829

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



834

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



844

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

848

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 auofrenatum</i> ; <i>Sp chrysopterum</i> ; <i>Sp rubripinne</i> ; <i>Kyphosidae (not identified to species level)</i> <i>Sparisoma atomarium*</i> ; <i>Sp radians*</i> (<i>Sp chrysopterum</i>) | Adam et al. 2018; Green & Bellwood 2009; www.fishbase.org 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 ¹ ; 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 ²) of all coral colonies ≥ 4 cm across a standardized transect (10m ²) |
| Competitive/weedy/stress-tolerant/generalist coral cover | Total cover (m ²) of all coral colonies ≥ 4 cm classified as competitive/weedy/stress-tolerant/generalist, according to Darling et al. (2012), across a standardized transect (10m ²) |
| Coral calcification rate | Total calcification rate (kg CaCO ₃ m ² year ⁻¹) 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 ²) |
| Fleshy/Calcareous macroalgal/Turf algal/CCA cover | Percentage algal cover estimated from benthic point counts |

852

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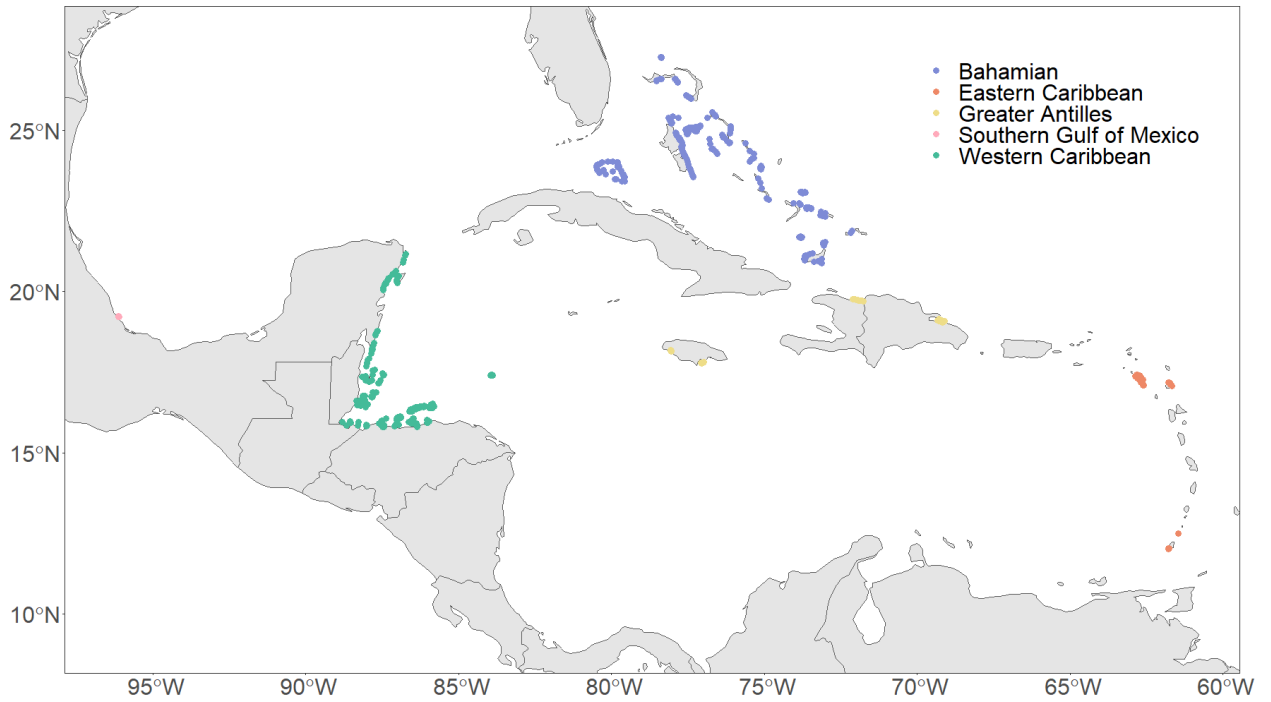
Table S3: Trait-based groupings of coral species not identified in Darling et al. (2012). Classification was made based on genus, phylogeny and known traits (coraltraits.org).

| Species | Coral Group ⁸⁵⁵ |
|--------------------------------|----------------------------|
| <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 (α). Values represent the mean \pm standard deviation of 1000 bootstrapped iterations.
 857 Percentage refers to the percentage of bootstrapped iterations with p-values ≤ 0.05 . Significant results shown in bold.

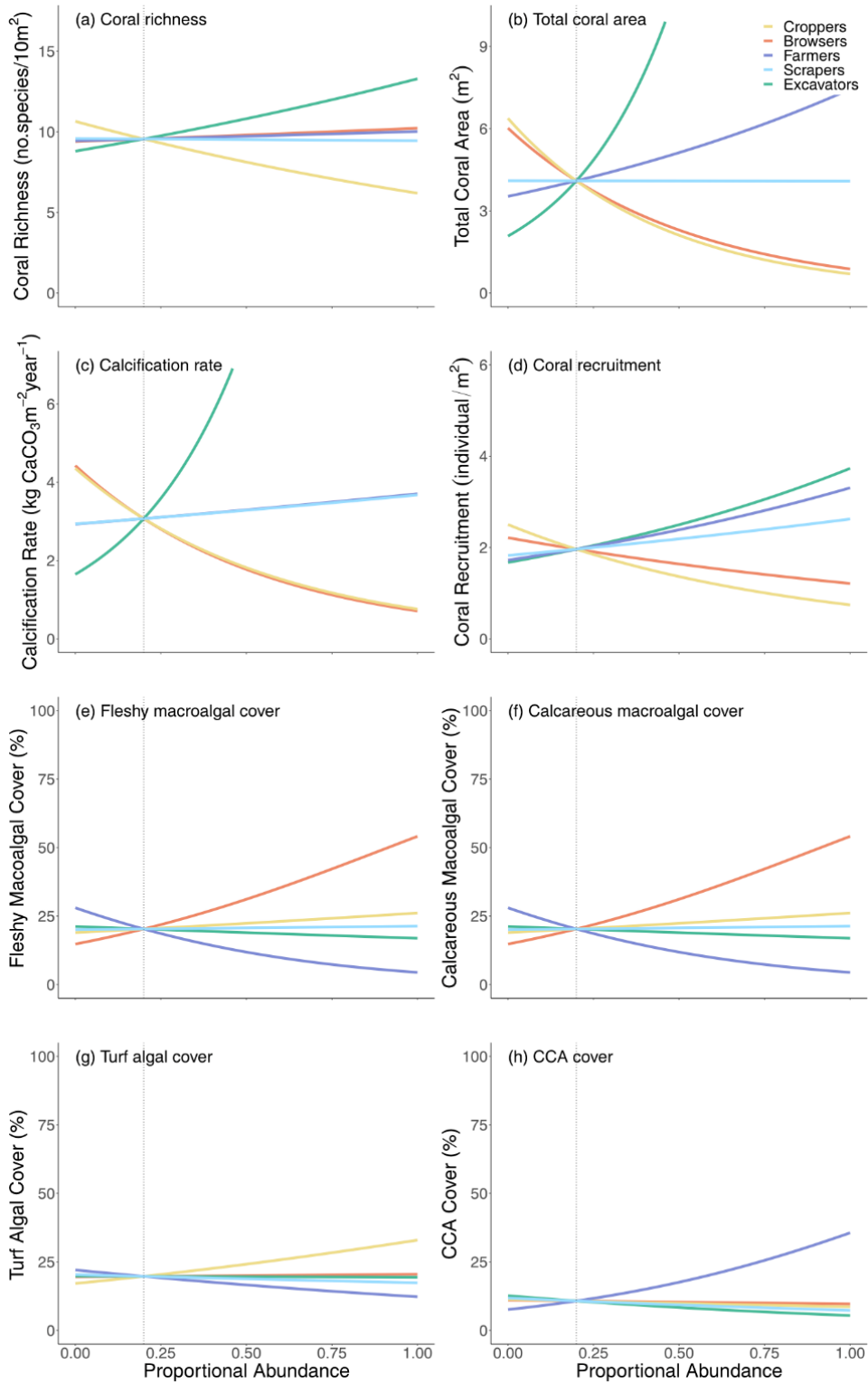
| Metric | Model 1 | | | | Model 2 | | | | Model 3 | | | |
|-----------------------------|-----------------|-----------------|-----------------------------------|-------------|-----------------|-----------------|-----------------------------------|-------------|-----------------|-----------------|-----------------------------------|-------------|
| | 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 | 0.02 \pm 0.01 | 94.7 | 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 | 0.01 \pm 0.02 | 92 | 0.18 \pm 0.02 | 0.07 \pm 0.01 | 0.02 \pm 0.02 | 82.7 | 0.17 \pm 0.02 | 0.06 \pm 0.01 | 0.01 \pm 0.03 | 95.5 |
| 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 | 0.04 \pm 0.02 | 63.3 | 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 | 0.00 \pm 0.00 | 100 | 0.32 \pm 0.02 | 0.11 \pm 0.01 | 0.01 \pm 0.00 | 100 | 0.34 \pm 0.02 | 0.14 \pm 0.01 | 0.02 \pm 0.01 | 99.2 |
| 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 ≤ 0.05 . Significant results shown in bold. **Please see Supplementary_Table_5.xlsx**



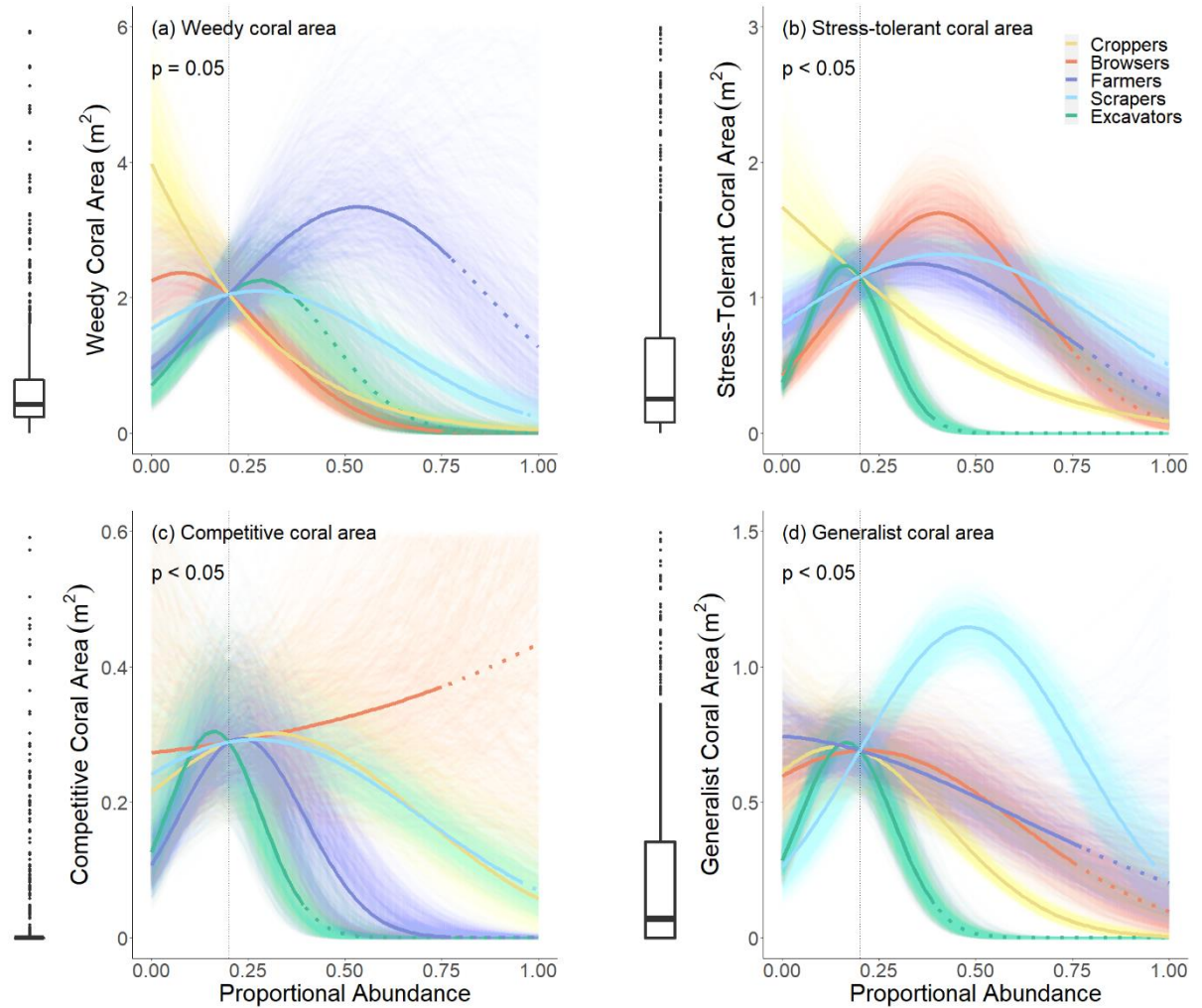
863

864 **Figure S1:** Map of Atlantic and Gulf Rapid Reef Assessment (AGRRA) survey sites included in our
 865 analysis. Colour groups depict five ecoregions.



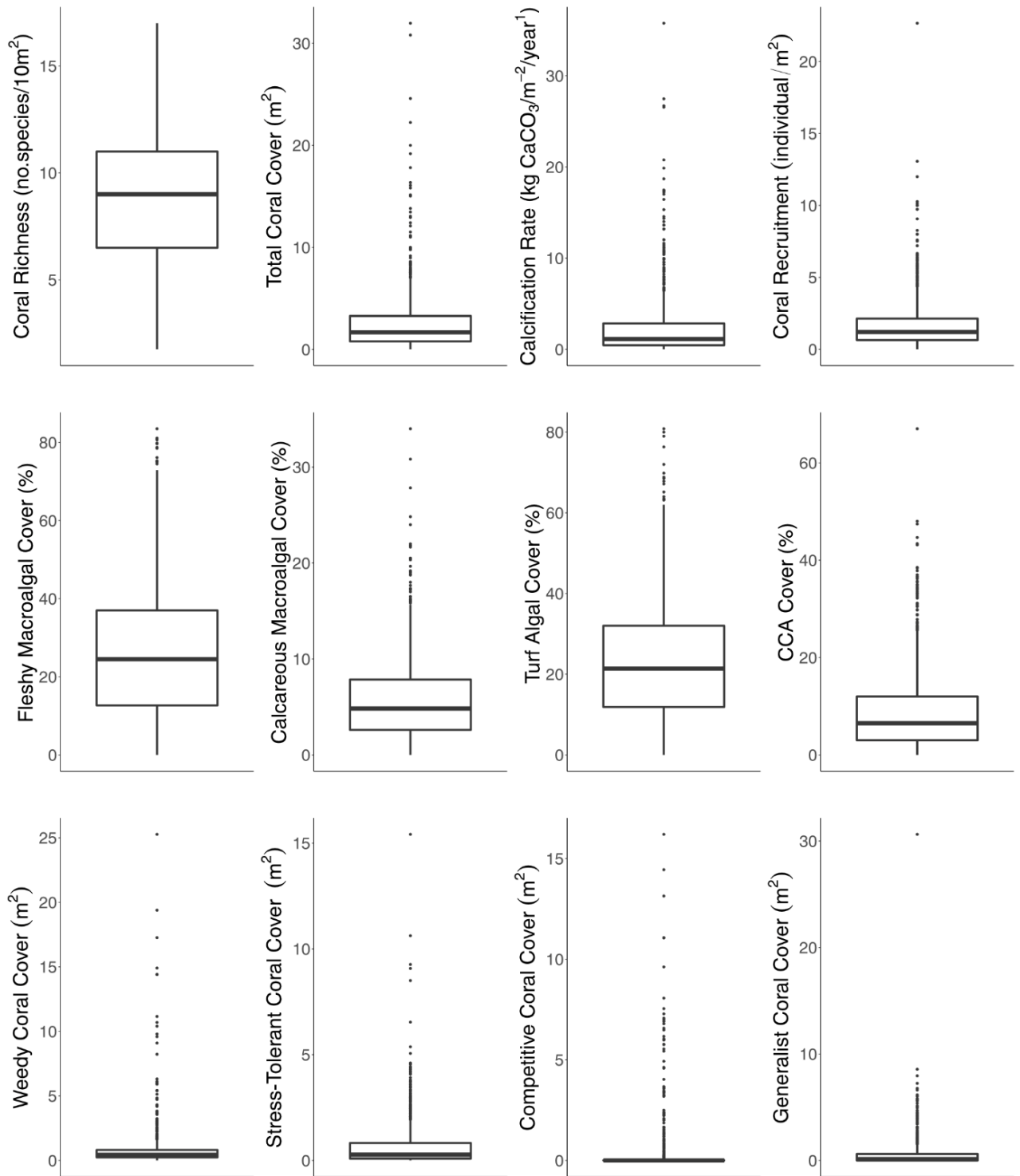
866

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



870

871 **Figure S3:** Predicted metrics of coral cover separated into trait-based groups, using results from
 872 1000 iterations of bootstrapped pairwise interaction models. Thicker lines represent mean predicted
 873 coral cover. Dotted segments represent predictions that are extrapolated from empirical data.
 874 Vertical dotted lines represent maximum evenness between functional groups ($P = 0.2$). p-values
 875 correspond to analysis of Wald statistic between the identity model (Model 2) and pairwise
 876 interaction model (Model 3) (Table 1; Test 2). Boxplots represent the spread of raw metrics of coral
 877 cover by survey and have also been limited to correspond with predicted values for ease of viewing
 878 (see Figure S4 for full boxplots).



879

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

881