

Global patterns of community assembly on coral reefs

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26 draft of the manuscript, and all authors contributed substantially to revisions.

27 **Data accessibility statement.** All data and associated reef images used in this
28 study are freely accessible on [https://espace.library.uq.edu.au/view/](https://espace.library.uq.edu.au/view/UQ:734799)
29 [UQ:734799](https://espace.library.uq.edu.au/view/UQ:734799). R codes to estimate pairwise image comparisons and the modified func-
30 tion to extract spatial data in the presence of missing values are available in the Sup-
31plementary Materials. The script to implement the multivariate latent variable model
32 is also accessible in the Supplementary Materials.

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44 **Abstract**

45 The structure of coral reef communities results from interacting evolutionary, ecological
46 and environmental forces. How these factors interact in structuring these communities
47 at a global scale, and how such effects might vary among biogeographical regions is unclear.
48 We partitioned sources of reef community assemblage patterns by environmental, latent (i.e. unobserved),
49 and random factors on 291 coral reefs distributed across five biogeographical regions. We then
50 estimated how these factors were related to variations in abundance and co-occurrence among
51 16 functional groups. Latent factors better explained the distributions of opportunistic functional
52 groups like algae, whereas environmental factors better explained abundance and co-occurrence of
53 hard corals. Co-occurrence patterns revealed complex interactions between coral and algae groups
54 that were not related to environmental factors but influenced by regional biogeography. Our
55 results show that environmental factors are not the sole drivers of coral reef structure highlighting
56 the importance of assemblage-level interactions and unobserved variables.
58

59 **Introduction**

60 Biological communities are shaped by processes that control the colonization of species
61 from their regional species pool and subsequent interactions at finer spatial scales (Colorado
62 Zuluaga, 2015). These ecological processes operate at diverse spatial, temporal and taxonomic
63 scales resulting in near infinite potential for unique community compositions (Rapacciuolo &
64 Blois, 2019). For example, speciation can influence community assemblage at coarse spatial
65 and temporal scales whereas selection, dispersal and ecological drift can operate across multiple
66 spatial and temporal scales (Vellend, 2010). Understanding global patterns of community
67 assembly requires knowledge of underlying relationships that can be generalised across space
68 and time (Connolly *et al.*, 2017a; McGill, 2019; Rapacciuolo & Blois, 2019). The integration of
69 ecological theories, different sources and types of data, and modern quantitative methods for
70 ecological

71 communities are likely to be important in order to consider the complexity associated
72 with the understanding of multispecies assemblages (Ovaskainen *et al.*, 2017; Vercel-
73 loni *et al.*, 2017; Sequeira *et al.*, 2018; Pearse *et al.*, 2018; Wüest *et al.*, 2019; Brandl
74 *et al.*, 2019; Rapacciuolo & Blois, 2019).

75 A fundamental approach of community assembly patterns is to understand the in-
76 fluence of environmental forces in selecting the most adapted species (Rapacciuolo &
77 Blois, 2019). In particular, the current focus on abiotic drivers of community struc-
78 ture has been reinforced by the unprecedented loss of biodiversity as a result of global
79 changes in climates and habitats (Ceballos *et al.*, 2015). Concurrently, new perspec-
80 tive on species coexistence emphasizes the importance of biotic interactions and other
81 relationships unrelated to the environmental conditions in shaping community struc-
82 ture such as variation in species traits (Kraft *et al.*, 2015; Cadotte & Tucker, 2017;
83 Ovaskainen *et al.*, 2017). Indeed, organisms that share similar ecological traits (or
84 function) tend to be selected in the same ways resulting in positive co-occurrences
85 within an assemblage (Cadotte *et al.*, 2013; Mouillot *et al.*, 2013). These ecological
86 differences among taxa can restrict the transfer from assemblage-level patterns and
87 associated relationships across spatial scales (Yates *et al.*, 2018). Some of these eco-
88 logical traits are themselves correlated with environmental factors (Cadotte & Tucker,
89 2017). Therefore, shifts in an assemblage may be the result of changes in community
90 structuring mechanisms such as lower population growth rates which cannot be esti-
91 mated using presence/absence (i.e. observational) data only; Kraft *et al.* (2015). De-
92 spite current limits to our understanding of how ecological communities are structured,
93 generalizing the effects of environmental pressures at an assembly level is essential for
94 predicting their structural changes across spatial scales (Sequeira *et al.*, 2018; Yates
95 *et al.*, 2018).

96 Coral reefs are being exposed to more and more frequent and intense disturbances
97 (Hoegh-Guldberg, 2014; Hughes *et al.*, 2017; Bellwood *et al.*, 2019b; Hoegh-Guldberg
98 *et al.*, 2019). Recent changes in reef assembly patterns have been largely attributed to
99 changing disturbance regimes including the increased frequency of thermal anomalies
100 (Heron *et al.*, 2016; Hughes *et al.*, 2018), intensity of cyclones (Puotinen *et al.*, 2016),

101 coral diseases (Maynard *et al.*, 2015), predator outbreaks (Kayal *et al.*, 2012), human
102 population pressure (Darling *et al.*, 2019) and over-fishing (Mellin *et al.*, 2016). These
103 pressures can shape coral reef assemblies by selecting against maladapted species (Dar-
104 ling *et al.*, 2013; Mouillot *et al.*, 2013; Kayal *et al.*, 2015) which are filtered out and
105 replaced by generalist species that are typically more stress-tolerant (Darling *et al.*,
106 2012; Kayal *et al.*, 2018). Hard corals in reef communities interact with other benthic
107 groups including competing for space and light (Brown *et al.*, 2018), processes that
108 can shift community dominance away from hard corals in the presence of high levels
109 of environmental pressure (Hughes *et al.*, 2003; Norström *et al.*, 2009). Therefore, un-
110 derstanding disturbance impacts on community assembly patterns in complex ecosys-
111 tems such coral reefs requires accounting for potential interactions among species and
112 environmental regimes (Warton *et al.*, 2015; Fisher *et al.*, 2015).

113 To address this shortfall in our understanding of coral reef assembly patterns across
114 spatial and taxonomic scales, we partitioned reef benthic community structure based
115 on three potential sources of variation; (1) environmental factors composed of three
116 major reef disturbance types: human population density, cyclone exposure and coral
117 bleaching; (2) latent factors related to sources not accounted for by responses to the
118 environmental factors such as biotic interactions or missing environmental informa-
119 tion, and (3) random factors at the reef level. The structure of coral reef community
120 assemblies was estimated from half million of images from the regions of the west-
121 ern Atlantic Ocean, eastern Australia, central Indian Ocean, central Pacific Ocean and
122 Southeast Asia (González-Rivero *et al.*, 2019). Images were automatically annotated
123 using machine learning image analysis (González-Rivero *et al.*, 2020) and character-
124 ized using up to 16 benthic coral reef functional groups. We hypothesize that the en-
125 vironmental factors will be the primary drivers of reef assembly patterns, as quantified
126 by our expectation that they would explain a higher proportion of variation in com-
127 munity assembly patterns. This hypothesis is consistent with earlier studies that found
128 environmental factors are strong drivers of benthic distributions (Darling *et al.*, 2013;
129 Mouillot *et al.*, 2013; Darling *et al.*, 2019). We also hypothesize that the latent factors
130 would capture biotic interactions among benthic functional groups, namely the direct

131 interactions between algae and hard corals (Hughes *et al.*, 2003; Brown *et al.*, 2018).
132 This approach allows us to explore sources of community assembly patterns across
133 broad spatial scales creating new insights on regional variation in structuring fine-scale
134 benthic coral reefs assemblies.

135 **Methods**

136 **Data processing.** Compositional data were collected across kilometers of coral
137 fore-reef slopes from the Atlantic, Australia, Indian Ocean, Pacific and Southeast (SE)
138 Asia (González-Rivero *et al.*, 2019; González-Rivero *et al.*, 2020) and used to assess
139 assembly patterns of benthic flora and fauna within coral reefs at the regional scale
140 (Fig. 1). Surveys were conducted over the period September 2012 - May 2016, with
141 surveys occurring prior to any regional mass coral bleaching events of 2014-2017.
142 They were conducted on reef slopes between 8 to 12 meters depth using dive propulsion
143 vehicles fitted with cameras that acquired 1 x 1 m² high-definition, downward-facing
144 reef images every three seconds along two kilometer long transects (González-Rivero
145 *et al.*, 2014). A convolutional neural network was used to automatically classify benthic
146 categories and estimate their relative abundances per geo-referenced image (González-
147 Rivero *et al.*, 2020). The protocol involved manual annotation of hundreds images by
148 experts in coral reef species identification using the CoralNet platform (Beijbom *et al.*,
149 2015). For each image, 100 randomly placed points were manually assigned a benthic
150 category to train the machine learning algorithm and find the optimal neural network
151 parameterisation that minimized model errors (González-Rivero *et al.*, 2016; González-
152 Rivero *et al.*, 2020). Abundances of benthic categories on the remaining images were
153 then automatically estimated based on 50 random points per image deriving propor-
154 tions of different benthic categories per m². This method was applied independently to
155 each biogeographical region using different target categories. Benthic categories were
156 chosen for their functional relevance to regional coral reefs and their ability to be reli-
157 ably identified from images (González-Rivero *et al.*, 2016). A total of ~ 447,000, 1 x
158 1 m² reef images, were automatically annotated by the machine learning algorithm.

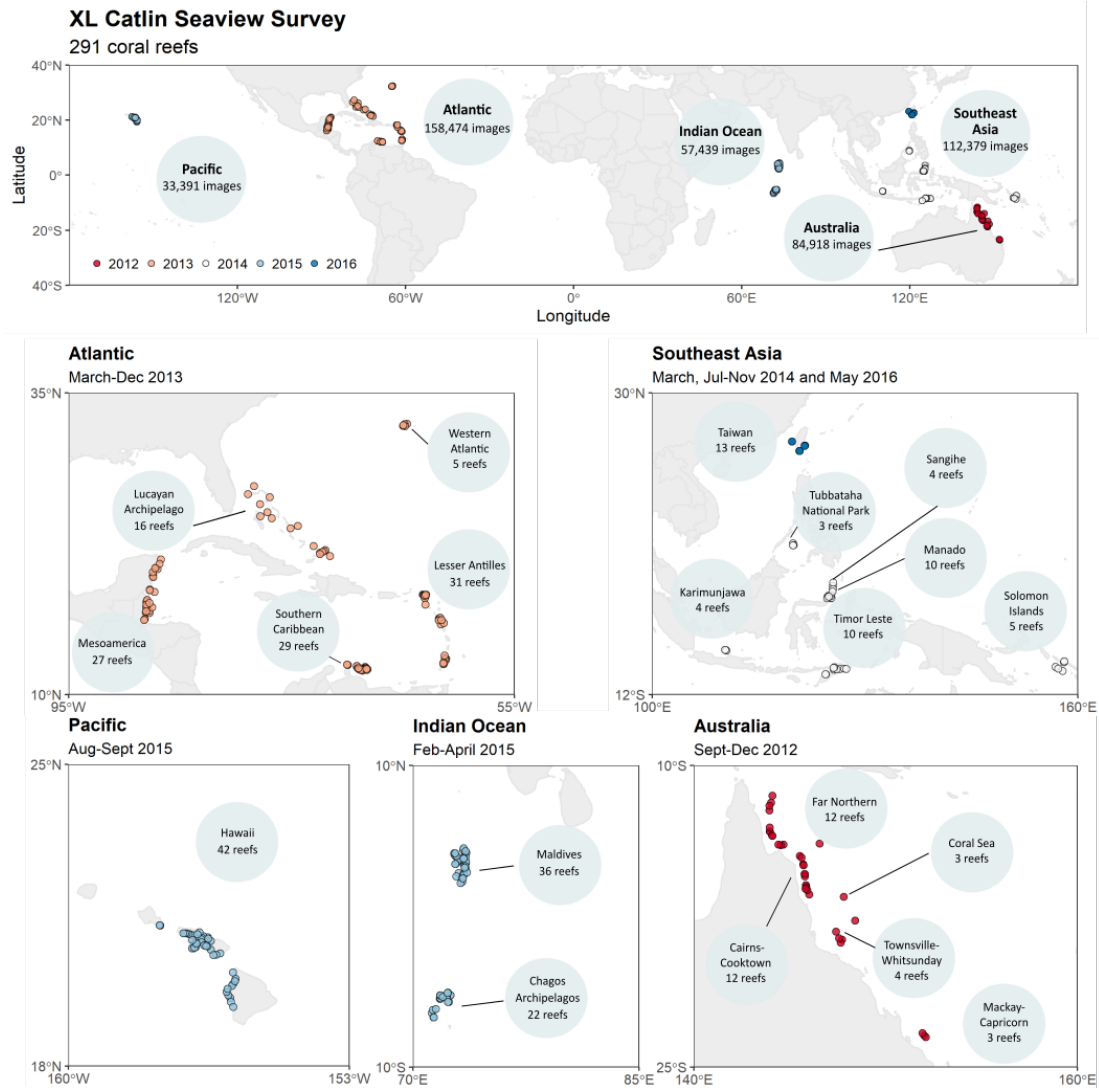


Figure 1: Locations of the surveyed coral reefs at the global scale (top map) and within the five biogeographical regions (bottom maps). Data are accessible through the following open access repository: <https://espace.library.uq.edu.au/view/UQ:734799>, (González-Rivero *et al.*, 2019).

Characterization of community assembly. Coral reef communities were characterized at the reef scale using up to 16 functional groups that were based on broad morphological traits (Table 1). These functional groups ensured consistent comparisons across biogeographical regions, by assuming similar functions. The influences of the data aggregation into functional groups were tested through a case study using data from the Atlantic region. In this region, lower species diversity enabled the coral reef benthic communities to be sampled at the finest taxonomic level allowable (genera in most cases), giving us the opportunity to test the effects of the functional grouping on the estimation of assembly patterns (See *Case Study* in Supplementary Material, SM).

Table 1: Description of the functional group and their presence in the Atlantic (Atl), Australia (Aus), Indian Ocean (Ind), Pacific (Pac) and SE Asia (Asia) regions.

| Functional group | Benthic group | Morphological traits | Region |
|-----------------------|---------------|--|------------------------|
| ACR_BRA | hard coral | branching and hispidose <i>Acropora</i> spp. | Atl, Aus, Ind and Asia |
| ACR_TCD | hard coral | table, corymbose and digitate <i>Acropora</i> spp. | Aus, Ind and Asia |
| BRA_nACR | hard coral | branching non- <i>Acropora</i> spp. | All |
| ELS | hard coral | encrusting, laminar and submassive | Atl and Pac |
| FLP | hard coral | foliose, laminar and plate | All |
| FREE | hard coral | free living | Ind and Asia |
| MSE | hard coral | massive, submassive and encrusting | All |
| MSEM | hard coral | massive, submassive and encrusting mendioid | All |
| NON_HERM | hard coral | non-hermatypic | Atl, Ind and Asia |
| GORG | soft coral | mixed fragile soft corals | Atl, Aus, Ind and Asia |
| OTH-SF | soft coral | encrusting and erect | Atl, Aus, Ind and Asia |
| SPONG | other | sponges (excl. cryptic sponges) | Atl, Ind, Pac and Asia |
| CCA | algae | crustose coralline algae | All |
| EAM | algae | epilithic algal matrix (< 1 cm in height, i.e. Turf algae) | All |
| MACRO | algae | upright macroalgae (> 1 cm in height) and cyanobacteria mats | All |
| NON_COLONIZABLE, Sedi | other | sand, terrigenous sediments and unconsolidated rubble | All |

Reef community assemblies were estimated by reef and region using a sampling design approach (SM1). The relative proportions of functional groups per image were used to estimate Spearman rank pairwise-correlation values within each transect. Based on these correlation values we determine the minimum number of images needed to ensure that the functional group abundances were representative at the transect scale. Indeed, community assembly patterns at the image level do not represent the scale at which the coral reef communities typically aggregate. A lack of consideration for spatial properties of benthic organisms can hinder the detection of spatial and temporal changes and lead to erroneous statistical conclusions (Perkins *et al.*, 2019). Here, we assumed that community assemblies at the transect level were relatively homogeneous

for the purpose of the study. A total of 291 reef assemblages across five biogeographical regions were obtained using this approach. At the regional scale, the Atlantic was the most surveyed region with 108 reefs, followed by the Indian Ocean (58 reefs), SE Asia (49 reefs), Australia (34 reefs) and the Pacific (42 reefs). When more than one transect per reef was available, the average of the minimum number of images across transects was used to obtain coral reef community assemblages at the reef scale. In the Pacific, community assemblages at the transect scale were used in the analysis because the main Hawaiian islands are composed of fringing reefs that are not distinguishable from each other. The proportions of each functional group per reef were then transformed into counts by multiplying these values by 50 as per the machine learning image analysis (González-Rivero *et al.*, 2020).

Environmental factors of community assembly. Environmental pressures were characterized using three global datasets. For every surveyed reef location, metrics for human population density (Doxsey-Whitfield *et al.*, 2015), historical exposure to damaging cyclones (Carrigan & Puotinen, 2011) and coral bleaching occurrences (Donner *et al.*, 2017) were extracted (SM2). Each raster layer was reprojected and resampled to facilitate the integration with reef community data and their associated spatial extent. For reef locations with missing values of environmental pressures, the closest known values from neighboring reef areas were used. These environmental pressures were chosen for consideration as they are assumed to be strong drivers of reef community structure (Nyström *et al.*, 2000; Hughes *et al.*, 2003) and are available at the global scale. For example, a high level of cyclone exposure reduces the abundance of branching corals and increases the presence of coral rubble (i.e. unconsolidated assemblage) (Cheal *et al.*, 2017). In this study, "Cyclone exposure" was defined as the average number of days of exposure to cyclonic conditions (i.e. gale force winds of at least 63 km/hr) between 1985-2009. The tracks of cyclones were derived from climate historical records (Knapp *et al.*, 2010) and cyclonic conditions reconstructed for each cyclone that followed the above conditions. These data were then combined into a grid with a 50 km spatial resolution and predicted for each day

between 1985-2009 (Carrigan & Puotinen, 2011). Human population densities, which can impact coral reef ecosystem functioning (Mora *et al.*, 2011), were estimated as the number of people per square kilometer from a gridded map that partitioned records from the 2010 round of censuses into cells of ~ 1 km resolution. This approach produces a comparable metric between countries by removing the variety in country size and shape (Doxsey-Whitfield *et al.*, 2015). "Bleaching occurrence" was defined as the maximum probability of coral bleaching based on observations from 1987 to 2010. Yearly bleaching probabilities were spatially interpolated at a 5 km spatial resolution from a logistic model using coral bleaching presence-only data. Where available, published coral bleaching reports with at least 10% coral bleaching were used, for a given year. In years when no reports were published, positive Degree Heating Week values from NOAA Coral Reef Watch (Eakin *et al.*, 2010) were used as a proxy for the presence of bleaching.

For each biogeographical region, environmental pressures were categorized as "high" or "low" based on the median values of their distribution (SM2). The raster (Hijmans *et al.*, 2015) and gdistance (Etten, 2017) packages for these analyses in R statistical Software (R Core Team, 2019).

Modelling community assembly patterns. Coral reef assembly patterns were partitioned using a multivariate latent variable model (Warton *et al.*, 2015; Hui, 2016). Community assembly patterns were characterized as relative counts for each reef i , and functional group j . Counts were modelled using a negative binomial distribution (**NB**) parameterized with a mean parameter (μ_{ij}) and an over-dispersion parameter (ϕ_j) specific to the functional group. These parameters were linked to linear factors via a log-link. The linear factors account for three different sources of assembly patterns (Eq. 1).

$$\begin{aligned}
y_{ij} &\sim \mathbf{NB}(\mu_{ij}, \phi_j) \\
\log(\mu_{ij}) &= \theta_i + x_i^T \beta_j + z_i^T \lambda_j
\end{aligned}
\tag{1}$$

233 The environmental factors, $x_i^T \beta_j$, are composed of three environmental predictors
 234 and an intercept β_{j_0} that accounts for differences in functional group abundance (Eq. 2).
 235 These factors were used to estimate community assemblage patterns due to similarities
 236 in responses to environmental pressures.

$$x_i^T \beta_j = \beta_{j_0} + \beta_{j_1} \text{Cyclone}_i + \beta_{j_2} \text{Bleaching}_i + \beta_{j_3} \text{HumanDensity}_i
\tag{2}$$

237 The latent factors, $z_i^T \lambda_j$, were used to estimate the residual patterns in community
 238 assembly that were not accounted for by responses to environmental factors (Letten
 239 *et al.*, 2015). These factors are composed of two correlated latent variables z_i^T formu-
 240 lated as random parameters and loading factors λ_j (Eq. 3). Other sources of variation
 241 such as biotic interactions (e.g. competition), missing predictors and other influential
 242 drivers not related to the major environmental pressures (i.e. latent) were captured
 243 within this component (Warton *et al.*, 2015). In addition, the reef-level intercepts (θ_i)
 244 are modelled as a random effect.

$$z_i^T \lambda_j = z_{i_1} \lambda_{j_1} + z_{i_2} \lambda_{j_2}
\tag{3}$$

245 The joint hierarchical structure of this multivariate model is the key to exploring the
 246 sources of variation in the abundance and co-occurrence of several functional groups

247 that make up coral reefs communities across biogeographical regions (Warton *et al.*,
 248 2015; Hui, 2016; Ovaskainen *et al.*, 2017). Co-occurrences were parameterized using
 249 multivariate normal distributions with mean equal to 0 and covariance $c_0\mathbf{I}$ (Eq. 4).

$$\begin{aligned}
 z_{i_1}, z_{i_2} &\sim \mathcal{N}(0, \mathbf{I}) \\
 \beta_{j_0}, \beta_{j_1}, \beta_{j_2}, \beta_{j_3}, \theta_i, \lambda_{j_1}, \lambda_{j_2} &\sim \mathcal{N}(0, c_0\mathbf{I}) \\
 \phi &\sim \mathcal{U}(0, 10) \\
 c_0 &= 10
 \end{aligned} \tag{4}$$

250 The model was implemented for each biogeographical region independently be-
 251 cause all functional groups were not present in all regions. The R package Boral (Hui,
 252 2016) was used to implement the model. Posterior distributions were based on 1,400
 253 iterations derived from Markov Chain Monte Carlo (MCMC) simulations of length
 254 90,000 with the first 3,000 discarded as the burn-in period and a thinning rate of 50
 255 iterations. Diagnostic checks of the MCMC were performed visually using trace and
 256 density-plots of parameters.

257 Model selection and assessment results are presented in SM3. The best model for-
 258 mulation was selected from 12 different models using the Deviance Information Crite-
 259 ria (Figures SM3–1 to –4). Spatial correlations between community assemblies were
 260 tested using Euclidean distances and the exponential correlation structure on the latent
 261 factors. Model validation was assessed by examining Bayesian posterior predictive
 262 distributions of the response variables. Posterior predictive distributions preserve the
 263 same structure than the data (Gelman *et al.*, 1996), which allowed us to assess model
 264 fit for each functional group between regions. The discrepancy distributions were es-
 265 timated from the differences between posterior predictive distributions and observed
 266 counts for each MCMC simulation (Figures SM3–5 to –8). These distributions were
 267 used to compute posterior predictive p-values and root mean squared errors (RMSE,
 268 Tables SM3–1 to –4). These assessments can be compared to cross-correlation ap-
 269 proaches typically used for model validation with the added benefit of being able to be

270 implemented directly from model outputs. Model goodness-of-fit was also diagnosed
271 by plotting observed values against discrepancy distributions, overall predicted versus
272 observed data and model residual distributions per functional group.

273 **Sources of community assemblage patterns.** Variance decomposition was
274 used to partition sources of variation in the abundance of each functional group across
275 regions. This approach uses the total variance associated with parameter estimates
276 from the linear predictors (Eq. 1) and assigns a percentage of variability based on their
277 proportions (Hui, 2016). If the variation in functional composition of communities is
278 mainly associated with variation in environmental factors, this suggests that specific en-
279 vironmental requirements are needed in order for those functional groups to be present
280 on a reef.

281 Interactions between functional groups were explored using the residual correla-
282 tion from the covariance matrix. We interpreted these correlations as evidence of co-
283 occurrence related to interactions not accounted for by responses to the environmental
284 factors we examined. Interactions due to shared responses to environmental factors
285 were estimated by calculating the covariance between model estimates of environmen-
286 tal factors. Co-occurrence is expressed in terms of significant correlations varying
287 between -1 and 1 where 95% credible intervals of their posterior distributions did not
288 include zero. The R package Boral was used to partition these sources of interactions
289 (Hui, 2016).

290 **Results**

291 **Structure of community assembly across regions** A total of 8 functional
292 groups were common to all five regions, with a maximum of 15 groups occurring in
293 the Indian Ocean and SE Asia regions and a minimum of 10 groups occurring in the
294 Pacific (Table 1). The most abundant functional group was the "epilithic algal ma-
295 trix" (EAM) with similar proportions across regions, varying between 51.4% \pm 11.2%
296 Standard Deviation (SD) and 65.6% \pm 13.4% SD (Fig. 2). Hard corals were the sec-
297 ond most abundant group with total coverage estimated as ranging between 18.8% to

298 26.5% in all regions with the exception of the Atlantic. For the Atlantic region, hard
299 corals were estimated to be less than 7.5% with assemblages mostly dominated by
300 macroalgae (MACRO, 11.6% \pm 8.6% SD) and mixed fragile soft corals (GORG, 6.3%
301 \pm 5.7% SD) followed by EAM and sediments. Massive, submassive and encrusting
302 (MSE) forms of hard corals were the most abundant in the Indian Ocean (9.1% \pm 6.4%
303 SD) and SE Asia (7.0% \pm 4.2% SD) and branching non-*Acropora* (BRA_nACR) in the
304 Pacific (9.4% \pm 12.3% SD) and Australia (5.7% \pm 3.1% SD) (Fig. 2). Encrusting and
305 erect forms of soft corals (OTHER-SF) were abundant in Australia (7.4% \pm 5.0% SD)
306 and SE Asia (7.8% \pm 9.9% SD).

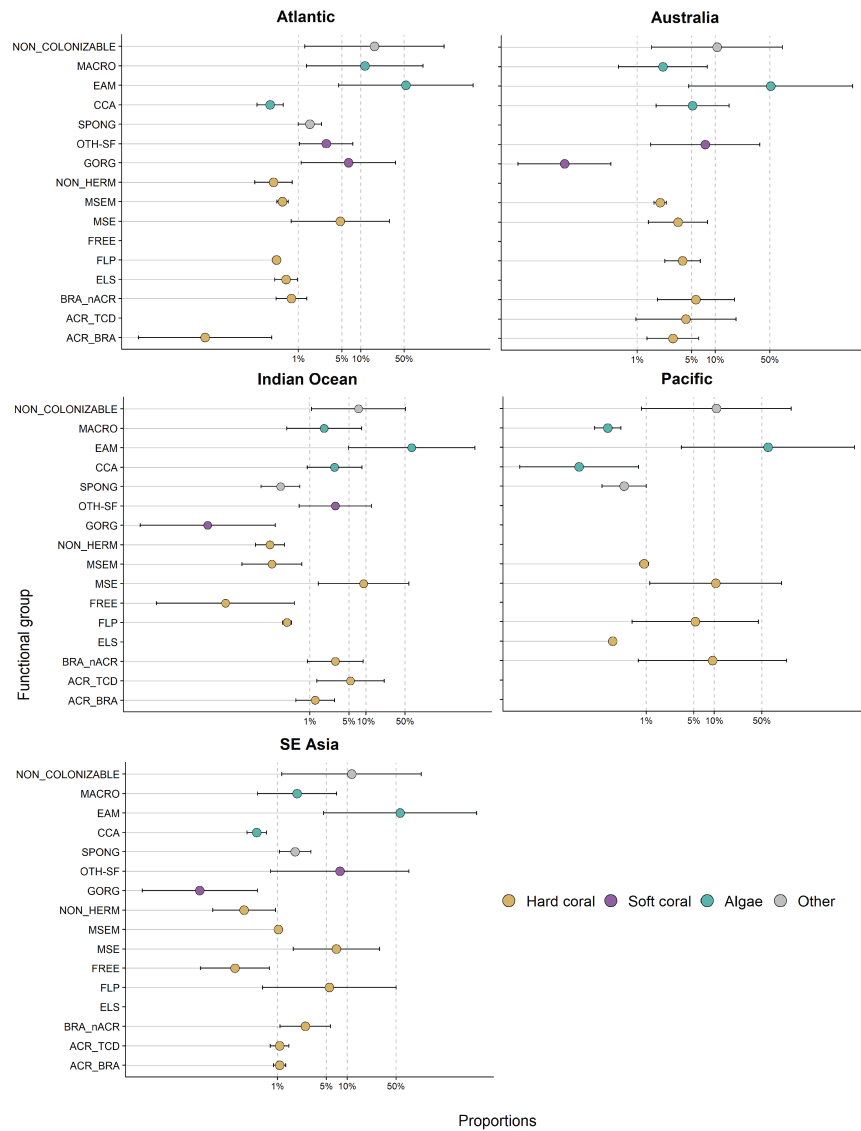


Figure 2: Proportions of the 16 coral reef functional groups by benthic group and region. Dots show the mean proportions in percentage and error bars denote the standard errors. Missing dots show an absence of observations for specific functional group per region. Proportions were log-transformed for visualisations.

Environmental factors of community assembly. Human population density was low in Australia with a median value close to zero (Fig. 3a, Fig. SM2-2). Cyclone exposure was absent on surveyed reefs of the Indian Ocean and Pacific (Figs. SM2-3 and -4) whereas SE Asia showed the greatest exposure to cyclones specifically

in the Taiwan sub-region with an average of 17.4 ± 1.1 days of exposure to cyclonic conditions (Fig. 3b). The median values of coral bleaching probability were close to zero for the Pacific and SE Asia, reaching 20% in Australia and greater than 50% in the Atlantic and, close to 1 in the Indian Ocean (Fig. 3c).

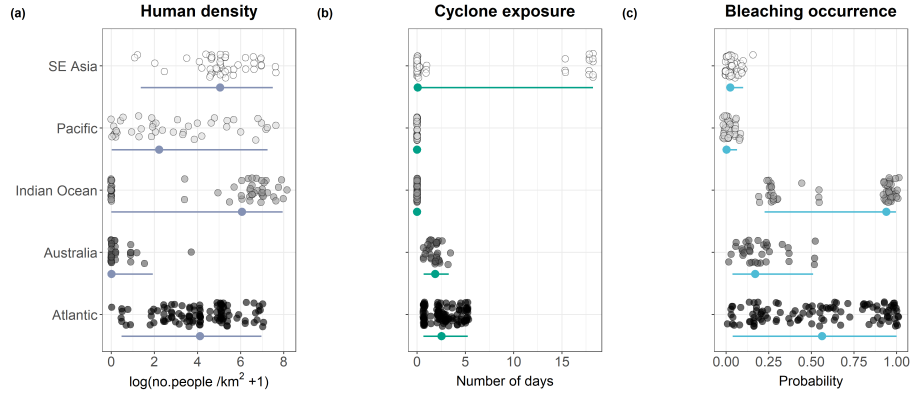


Figure 3: Distributions of environmental pressures for the five biogeographical regions. The grey dots represent the individual coral reefs within regions, slightly jittered for better visualisation. The coloured dots show the median values that were used as cut-offs to define the low and high environmental pressure levels. The coloured lines delimit 95% of the data distribution.

Community assembly patterns. The multivariate models performed in similar ways across the biogeographical regions (SM3). Model parameters for the first latent factor (LV1) showed positive and negative means across functional groups and regions and variable uncertainties in model estimates. The second latent factor (LV2) and environmental factors were often close to zero with smaller credible intervals (Figs. SM3–10 to –14). The effect of environmental pressures was not consistent across regions. However, validation diagnostics show that the models provided satisfactory fits to the data. The posterior predictive p-values were close to 0.5 indicating good model fit, excepted for one or two functional groups per region, (p-values ~ 0.80 , Tables SM3–1 to –4). The RMSE values were largest for the epilithical algae (EAM) and non-colonizable (e.g. sediments, rubble and sand) groups; noting that observed EAM values were also consistently outside the discrepancy distributions (Figs. SM3–5 to –9).

328 **Sources of community assemblage patterns.** Within the Atlantic, Pacific
 329 and Indian Ocean regions, variance decomposition of functional groups was mainly as-
 330 sociated with variation in the latent factors (Fig. 4a). Variation in the presence of func-
 331 tional groups was comparable between Australia and SE Asia, but were not related
 332 to any particular factor (variance $\sim 50\%$). Among functional groups across regions
 333 (Fig. 4b), the sources of occurrence of fragile corals such as ACR_BRA, BRA_nACR,
 334 and also gorgonians (GORG) were related to the environmental factors; whereas al-
 335 gal groups such as MACRO, EAM and CCA were associated with the latent factors.
 336 The Atlantic displayed the highest variability among functional groups for both envi-
 337 ronmental and latent factors suggesting that cyclone exposure was strongly associated
 338 with the occurrence of hard corals and gorgonians associated with human density and
 339 bleaching occurrence (Fig. SM4–1).

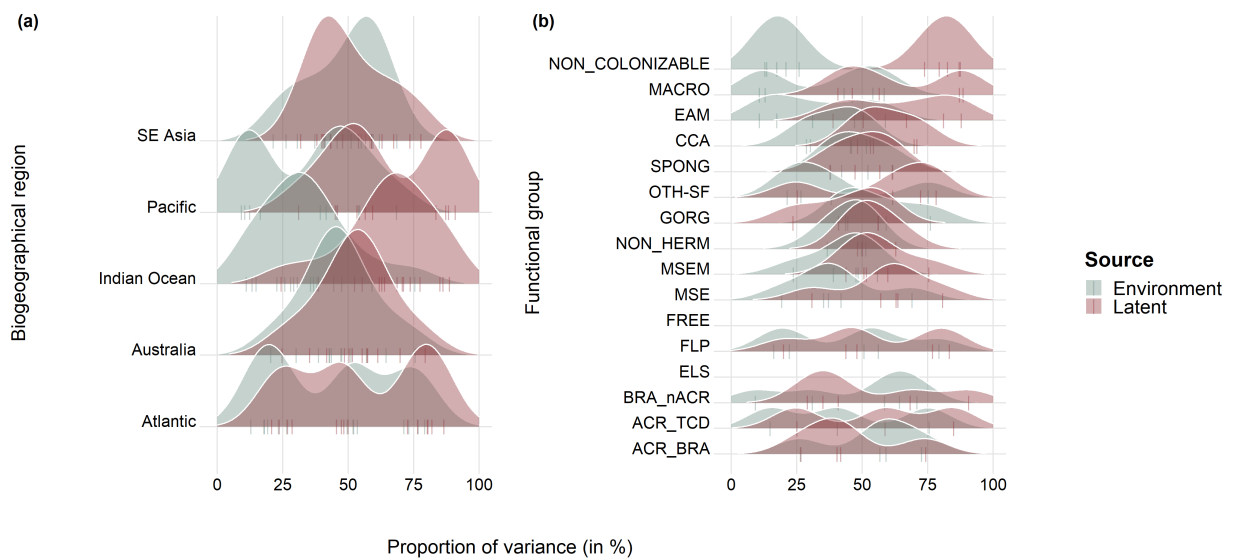


Figure 4: Partitioning of variance by source and region (a) and functional group (b). The bars show variance values used to produce the distributions. Two functional groups are missing in panel B because they were present in only two biogeographical regions precluding estimation of their distributions.

340 Ecological interactions were associated with the latent and environmental factors in
 341 all regions except for Australia and the Pacific, which had no significant co-occurrences
 342 related to latent and environmental factors, respectively (Fig. 5 and Figs. SM4–2 and

343 –5). The co-occurrence patterns related to the latent factor in the Atlantic revealed
 344 strong positive correlations between fragile (GORG) and encrusting and erect (OTH-
 345 SF) octocorals and massive hard corals (MSE and MSEM) and negative correlations
 346 with macroalgae (MACRO). Branching and hispidose *Acropora* spp. (ACR_BRA) and
 347 epilithic algal matrix (EAM) were also positively correlated with massive hard corals
 348 (MSE and MSEM). In the Indian Ocean, the major *Acropora* groups (ACR_BRA and
 349 ACR_TCD) were positively correlated with each other and were negatively correlated
 350 with coralline algae (CCA) and other branching non-*Acropora* species (BRA_nACR).
 351 In SE Asia, MSE corals were positively correlated with EAM. Co-occurrence patterns
 352 related to shared environmental responses were positively related between BRA_nACR
 353 and ACR_TCD in Australia, both being negatively correlated to EAM. Two indepen-
 354 dent patterns were revealed in the Atlantic with positive correlations between branching
 355 non-*Acropora* spp. and foliose, laminar and plate (BRA_nACR and FLP, respectively)
 356 corals and BRA_nACR-MSE and negative correlations between GORG and soft sed-
 357 iments (Sedi). In the Indian Ocean, octocorals (OTH-SF and GORG) responded in a
 358 similar way to environmental responses and were negatively correlated with EAM. Two
 359 additional patterns were found in SE Asia, where MSE and FLP corals were positively
 360 correlated with one another and negatively correlated with FREE and Sedi. The sec-
 361 ond pattern was a positive correlation between GORG and EAM, both of which were
 362 negatively correlated with OTH-SF.

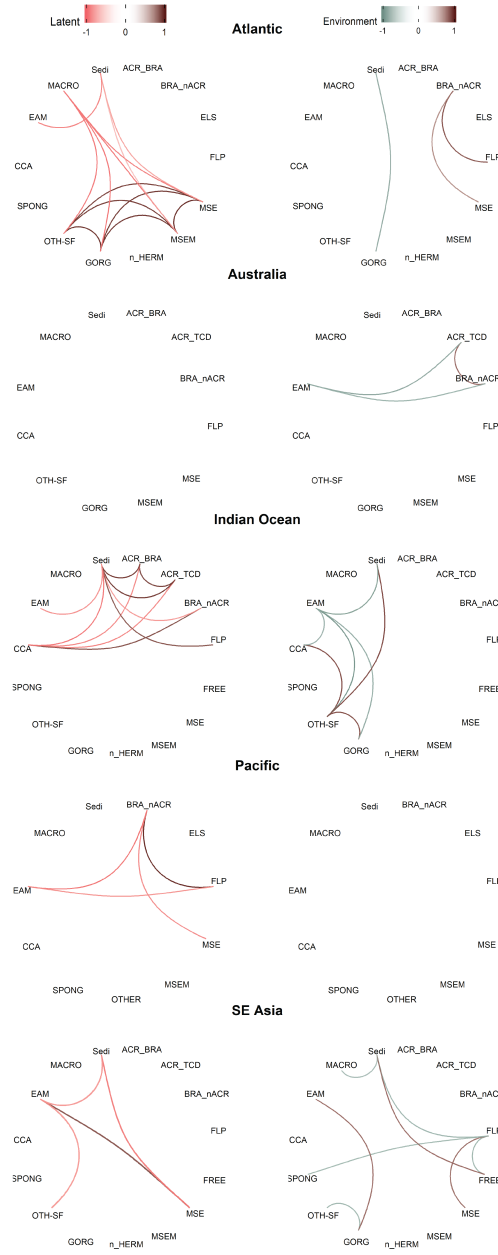


Figure 5: Significant interactions between functional groups (whose 95% credible intervals did not contain zero), by source with latent (red) and environmental (green) factors, and region. For example a red line going from MACRO to MSE in the Atlantic region means that a negative co-occurrence between macroalgae and massive hard corals was estimated. Empty networks denote an absence of significant correlations. See (Table 1) for descriptions of functional groups.

363 Discussion

364 Using a global dataset with unprecedented high taxonomic and spatial resolution, we
365 evaluated the importance of environmental pressures versus latent factors on coral reef
366 benthic communities. Importantly, our approach allowed us to detect strong commu-
367 nity assembly patterns (coral-algae, coral-coral) not associated to environmental forces
368 as important sources of community structure variability at a regional scale. The esti-
369 mation of community assembly patterns in marine ecosystems, including tropical coral
370 reefs, has contributed to a better understanding of the size and membership of regional
371 species pools (Plaisance *et al.*, 2011; Knowlton *et al.*, 2010; Caley *et al.*, 2014; Fisher
372 *et al.*, 2015), the development and application of theoretical models for predicting
373 global patterns of community assembly (Bellwood *et al.*, 2005; Dornelas *et al.*, 2006;
374 Connolly *et al.*, 2017a), and how the behavior of biodiversity indices affects of our abil-
375 ity to quantify community structure and diversity (Loiseau & Gaertner, 2015; Connolly
376 *et al.*, 2017a). Research interest in reef community assembly is shifting towards a bet-
377 ter understanding of ecosystem function and associated drivers versus species identity
378 in coral reef structure in order to maintain its functionalities in a changing environment
379 (Darling *et al.*, 2012; Mouillot *et al.*, 2013; Bellwood *et al.*, 2019b; Brandl *et al.*, 2019).
380 The approach and findings associated to the present study open new opportunities for
381 reaching this goal.

382 **Community assembly across functional groups.** As expected, environ-
383 mental factors drove the abundance of the branching hard corals and the co-existence
384 of different forms of hard corals because of their similar environmental requirements
385 (Done *et al.*, 1983). The percentage of observed variation in functional groups by re-
386 gion explained by the environmental factors varied between 16.9-50.5% which is in
387 the range of other global studies (Darling *et al.*, 2019). The novelty of this study is
388 that we were able to explore sources of variability after accounting for environmental
389 predictors. Complex algae-corals and corals-corals interactions were detected within
390 the latent components including the Atlantic and Indian Ocean regions. Several forms

391 of interactions between these groups have been observed, such as coral-macroalgae
 392 competition. Our findings of correlations among functional groups may not be solely
 393 attributable to biotic interaction and may also be related to environmental predictors not
 394 accounted for in this study (Warton *et al.*, 2015; Dormann *et al.*, 2018). The broad spa-
 395 tial scale of our study challenged the choice of environmental factors and levels of data
 396 aggregation into ecological groups. The combination of the three global datasets that
 397 were used to explain reef community structure was not relevant for all the regions. For
 398 example, the reefs surveyed in the Pacific were not exposed to cyclonic conditions and
 399 bleaching before September 2015 along with minimal cyclone exposure in the Indian
 400 Ocean. Also, the range of values was narrow for bleaching occurrence in the Indian
 401 Ocean and SE Asia and human population in Australia which impeded statistical detec-
 402 tion of their effects on reef community structure. These variable patterns of occurrence
 403 were reflected in the large uncertainties estimated by the model for some environmental
 404 factors in some locations. Using continuous values of these variables maybe more in-
 405 tuitive than their categorization into the low and high environmental pressure levels as
 406 done here. However, the almost half million observations used to estimate reef assem-
 407 blies ensured a broad range of combinations of responses of these communities for a
 408 similar level of environmental pressure. The functional groupings used here was based
 409 on broad morphological forms only, and therefore, does not consider life traits such as
 410 reproduction mode, growth rate and heat-stress tolerance that may be important in driv-
 411 ing the structure of hard coral communities in response to disturbances (Darling *et al.*,
 412 2012). Currently, however, challenges associated with the development of coral reef
 413 trait-based data (Madin *et al.*, 2016) and the high diversity of coral reefs (Brandl *et al.*,
 414 2019) impede the integration of different types of data other than abundances into com-
 415 munity assembly approaches as compared to for example terrestrial plants (HilleRis-
 416 Lambers *et al.*, 2012) or macroorganisms (Aguilar-Trigueros *et al.*, 2017). Despite this
 417 limitation, the application of the model and associated analyses using data at a finer tax-
 418 onomic scale for the Atlantic region shows that functional grouping are able to capture
 419 the main trends (i.e. case study). The assembly patterns found are in agreement with
 420 some of the long established observations by ecologists about bioregional differences

421 in community structuring, for example, the predominance of gorgonians in the Atlantic
422 at surveyed depths and other soft coral types in the Pacific (Spalding *et al.*, 2001). Our
423 approach here, therefore, is arguably a reasonable method to improve estimations of
424 patterns of reef community assembly at a relatively fine taxonomic resolution, parti-
425 tion their variability into different sources, and gain knowledge about their potential
426 drivers.

427 **Community assembly across regions.** The structure of community assem-
428 blies across five biogeographical regions were estimated in a consistent manner and
429 spanned a broad range of environmental gradients, biodiversity, historical factors, and
430 phylogeny. Comparing these communities in this way allows for a space-for-time sub-
431 stitution in understanding the main drivers of community assembly patterns. In our
432 study, drivers of community assembly were different across regions. Reef structures in
433 the Indian Ocean and Pacific were mostly driven by the latent factors only, equal contri-
434 butions of latent and environmental factors in SE Asia and Australia, or had no distinct
435 pattern in the Atlantic. This is likely to be due to the comparatively less impacted state
436 of Indian Ocean and Pacific allowing latent factors to present, compared to the highly
437 impacted state of the Caribbean where communities have been strongly pushed in one
438 direction by environmental pressures, or other underlying factors (Roff & Mumby,
439 2012). Broadly, the finding that the Atlantic is the one region no longer dominated by
440 coral is an indication that the drivers that govern the assembly of such ecosystems are
441 likely to be different compared to the Indo-Pacific. However, additional investigations
442 would be needed to understand if these similarities in responses to different drivers are
443 associated with broad spatio-temporal scales processes such the evolutionary history of
444 oceanic basins (Veron, 2000), disturbance regimes, or other common drivers that con-
445 tributed to shape the community assembly in the same ways (Roff & Mumby, 2012;
446 Darling *et al.*, 2019). Our findings also suggest that assumption of similar mechanisms
447 of community assembly drivers across regions is potentially problematic. Challenges
448 associated with regional variability were previously mentioned in some key papers that
449 compared reef assemblies between the Indian Ocean and Pacific (Bellwood & Hughes,

2001), the Caribbean and the Indo-Pacific (Roff & Mumby, 2012) and across the Pacific region (Smith *et al.*, 2016).

Most global analyses of coral reefs integrate measurements from different surveys with distinct sampling methodologies which is useful in order to improve spatial predictions when data are sparse (Peterson *et al.*, 2018). However, data integration influences estimation of abundance in rare species (Perkins *et al.*, 2016) and habitat structures (Griffin *et al.*, 2017) and ultimately impacts estimation of spatio-temporal changes (Perkins *et al.*, 2019) and drivers of reef community structure (Darling *et al.*, 2019). While these aspects were controlled in our analyses, differences in sampling intensity, from a minimum of 34 reefs surveyed in Australia to 108 reefs in the Atlantic, may have contributed to hinder detection of common drivers of community assembly across regions. The size of single coral reef differed greatly between regions complicated further the application of the method across regions. It is also possible that patterns of reef community assembly operate at spatial scales finer than the region. This specific finding reveals the importance of considering for regional variability in the establishment of global management strategies because similar actions may lead to different outcomes depending on the geographical location (Brandl *et al.*, 2019).

The joint hierarchical modelling approach. The spatial mismatch between environmental impacts and management interventions is important to address in order to protect coral reefs from further climate change (Bellwood *et al.*, 2019b). Environmental drivers tend to have the best predictability at sub-regional to global scales, while corresponding ecological responses have their highest predictability at fine scales (Eakin *et al.*, 2019). New techniques that use the rapid acquisition of images which are then analysed using artificial intelligence have huge potential to help bridge this gap (González-Rivero *et al.*, 2020). However, additional challenges appear when dealing with big data including the use of traditional analytical methods (Wüest *et al.*, 2019). To date, only Brown & Hamilton (2018) used a joint hierarchical modelling approach to estimate the impacts of pollution on benthic reef communities in the Solomon Islands. These authors were able to predict compositional turnover across a gradient of

479 turbidity by introducing latent variables in their model. Here, we used latent variables
480 to account for interactions between functional groups that were not captured by the
481 environmental factors. This approach can be compared to the use of correlation struc-
482 tures that capture the residual spatial variability not accounted by model predictors.
483 Latent variables have the benefits of being estimated by a model and allow to reduce
484 the number of model parameters to be estimated (Warton *et al.*, 2015; Connolly *et al.*,
485 2017b; Brown & Hamilton, 2018). This approach creates new opportunities to predict
486 abundance and co-occurrence across many coral reef communities and understand the
487 effects of different evolutionary, ecological, and environmental forces, at management
488 scales.

489 **Conclusions.** While global strategies for the conservation of coral reefs are crit-
490 ically important for curbing further declines (Hughes *et al.*, 2017; Bellwood *et al.*,
491 2019a; Hoegh-Guldberg *et al.*, 2019), the knowledge gaps associated with broad spatial
492 scale estimation of patterns of reef community assembly may challenge the practical
493 application of these strategies (Brandl *et al.*, 2019). Here, we have used a global coral
494 reef datasets to partition sources of reef community structure and predict assembly pat-
495 terns across 16 functional groups, from half million of 1 x 1 m² images to entire bio-
496 geographical regions. We estimated a small contribution of our environmental factors
497 which potentially highlights relevance and spatial mismatches between these drivers
498 and reef assembly responses. Accounting for the evolutionary and biogeographical
499 context of the changes observed on reef assemblies is important but challenging in
500 terms of characterization and quantification. However, focusing on the variation not
501 accounted for by responses to environmental factors, we predict complex interactions
502 at the assembly-level influenced by regional biogeography. Environmental factors may
503 not be the unique drivers of coral reef structure in which the contributions of diverse
504 functional groups could also play a role in structuring coral reef ecosystems. That is,
505 focusing on a few key functional groups instead of species diversity per se may con-
506 tinue to impede a more complete understanding of patterns of community assembly on
507 coral reefs across space and time. Recent improvements in collection and integration of

different data types across taxonomic, ecological traits and spatial resolutions (Wüest *et al.*, 2019), unified model-based methods (Warton *et al.*, 2015; Hui, 2016; Ovaskainen *et al.*, 2017) and new concepts of ecosystem functioning (Kraft *et al.*, 2015; Brandl *et al.*, 2019; Rapacciolo & Blois, 2019) are promising to guide the development of future quests on the origins of coral reef biodiversity.

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