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1 **Title:**

2 Benthic composition changes on coral reefs at global scales

3
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18
19
20
21 **Abstract**

22 Globally, ecosystems are being reconfigured by a range of intensifying human-induced
23 stressors. Coral reefs are at the forefront of this environmental transformation, and if we are
24 to secure their key ecosystem functions and services, it is important to understand the likely
25 configuration of future reefs. However, the composition and trajectory of global coral reef
26 benthic communities is currently unclear. Our global dataset of 24,468 observations spanning
27 22 years (1997-2018), revealed that particularly marked declines in coral cover occurred in
28 the Western Atlantic and Central Pacific. The data also suggests that high macroalgae cover,
29 widely regarded as the major degraded state on coral reefs, is a phenomenon largely restricted
30 to the Western Atlantic. At a global scale, the raw data suggests decreased average (\pm SE)
31 hard coral cover from $36 \pm 1.4\%$ to $19 \pm 0.4\%$ (during a period delineated by the first global
32 coral bleaching event [1998] until the end of the most recent event [2017]) was largely
33 associated with increased low-lying algal cover such as algal turfs and crustose coralline
34 algae. Enhanced understanding of reef change, typified by decreased hard coral cover and
35 increased cover of low-lying algal communities, will be key to managing Anthropocene coral
36 reefs.

37
38 **Main Text**

39 **Introduction**

40 The pace and spatial extent of ecosystem transformation is expected to increase in the
41 Anthropocene as the strength of human-mediated stressors intensifies¹⁻³. The magnitude of
42 these stressor effects is so large that it has led to suggestions that returning altered ecosystems
43 to configurations of the recent past may be an unattainable goal⁴⁻⁶. Instead, the primary goals
44 now are to maintain the functions that sustain these ecosystems, and to secure the services

45 that they deliver to people, even in their highly-altered configurations⁴⁻⁶. A prerequisite to
46 these goals is an understanding of the variability in the structure of altered ecosystems at a
47 global scale.

48 These challenges are epitomised by coral reefs, vulnerable ecosystems at the forefront
49 of environmental transformations⁷⁻⁹. Climate change is foremost among the stressors
50 modifying these ecosystems, with repeated mass coral bleaching events at global spatial
51 scales^{10,11}. It is inevitable that coral reefs of the future will be different and will continue to
52 change. These changing configurations may have far-reaching consequences for marine
53 biodiversity¹², reef ecosystem functions¹³, and for the hundreds of millions of people that
54 rely on coral reefs for services^{14,15}. Clearly, if we are to manage reefs through these changes,
55 we need to understand their likely composition in the near future. Given the spatial and
56 temporal scope of the stressors currently acting upon coral reefs, this understanding must be
57 at a global scale.

58 To gain an insight into likely coral reef composition in the near future, and to identify
59 the most pressing future research endeavours, we need to answer two relatively
60 straightforward questions: 1) how is the benthic composition of coral reefs changing at a
61 global scale? and 2) how, and to what extent, do these changes vary among the world's
62 marine realms? To explore these questions, we compiled an extensive, global, dataset
63 composed of 24,468 observations of mean coral reef benthic composition. These observations
64 spanned 13,802 unique GPS coordinates and 22 years from 1997 (i.e. prior to the first global
65 mass-coral bleaching event¹⁶) until 2018 (i.e. a year after the most recent global coral
66 bleaching event¹⁶). They encompassed all major reef regions across 60° of latitude (Fig. 1a).

67

68 **Results**

69 *Reef benthic composition data – a global overview*

70 An initial exploration of the dataset suggests that, from 1997-2018, variation in the
71 benthic composition of the world's coral reefs has largely been typified by the dynamics of
72 reef building scleractinian corals (i.e. hard corals) and low-lying algal communities (Fig. 1).
73 Indeed, this initial visualisation shows low-lying algal communities largely replacing hard
74 corals on reefs as their cover decreased, especially in the last decade (Fig. 1b). Interestingly,
75 there is also a signal in the data that is potentially related to the three global mass coral
76 bleaching events; in the year following each bleaching event, there was a decrease in hard
77 coral cover and a concomitant increase in low-lying algal cover (Fig. 1b). Overall, from the
78 onset of the first global bleaching event (1998) to the end of the most recent event (2017), the
79 global average (\pm SE) of hard coral cover decreased from $36 \pm 1.4\%$ to $19 \pm 0.4\%$ while low-
80 lying algae cover increased from $37.7 \pm 1.3\%$ to $50.8 \pm 0.5\%$. Although for the full temporal
81 span of our analysis (1997-2018), the average hard coral cover decreased from $32.4 \pm 0.9\%$ to
82 $25 \pm 0.6\%$ while low-lying algal cover increased from $37.7 \pm 0.9\%$ to $39.8 \pm 0.6\%$ (Fig. 1b).
83 This decrease in coral cover is expected; widespread coral mortality typically follows mass
84 bleaching events^{17,18}. However, the increase in low-lying algae has not been well documented
85 in previous global scale studies of coral reef change. These low-lying algal communities
86 range from biofilms and crustose coralline algae (CCA) to long sediment-laden algal turfs
87 (see Supplementary Text 1 and Supplementary Figs 1-4 for a comprehensive discussion of
88 this continuum of algal groups, and a justification for pooling them in this study) and they are
89 poorly captured in most existing coral reef data, frequently being lumped together as 'dead
90 coral', 'pavement', or even 'bare space' (Supplementary Fig. 1). This situation limits our

91 capacity to divide them further and make more informed inferences about how they relate to
92 coral loss (Supplementary Text 1). However, once corals are lost, it is these low-lying algal
93 communities, especially algal turfs and cyanobacteria, that generally fill the vacated space
94 ^{18,19}, with such reef conditions often being perceived as a ‘degraded’ (i.e. low coral cover)
95 ^{20,21}.

96 Beyond hard coral cover and low-lying algal community cover, there is an apparent
97 trend of increasing macroalgae, from an average of $5.9 \pm 0.6\%$ to $16.7 \pm 0.5\%$ cover (across
98 the entire temporal span 1997-2018), at a global scale. This is somewhat intriguing given that
99 high macroalgae cover is widely considered to represent a common degraded condition on
100 coral reefs ^{7,20}. Indeed, given the occurrence of multiple bleaching events during this period,
101 one would expect a stronger signal of increased macroalgae cover in the data. It is also
102 interesting to note that despite a growing focus in the literature on soft corals and other
103 benthic organisms (e.g. sponges and ascidians) ²², these benthic categories have never
104 represented major components of global reef cover, consistently covering just ~5-10% of the
105 benthos, on average (Fig. 1b).

106

107 *Reef benthic composition among realms*

108 While the analyses above provide an overall picture of average global trends, both the
109 composition of reef systems and the nature and intensity of human impacts varies
110 considerably, both geographically and among habitat types. Therefore, we explored how
111 benthic composition varied across four major marine realms (Central Pacific, Indian Ocean,
112 Indo-West Pacific, Western Atlantic). We focused in on three equidistant time points (1997,
113 2007, 2017), while also accounting for the influence of depth and habitat. To do this, we first
114 tested if the four factors (realm, year, depth, habitat) were significantly correlated with the
115 multivariate benthic composition data using a permutational multivariate analysis of variance
116 (PERMANOVA). This analysis suggested that all factors were significantly correlated with
117 the data ($p < 0.001$ in all cases; Supplementary Table 1), although among-realm differences
118 overwhelmingly explained more variation than the other factors (Supplementary Table 1). To
119 visualise these differences, we utilised a multivariate ordination constrained by these four key
120 factors (Fig. 2). This revealed three distinct patterns. Firstly, from 1997 to 2017 the Western
121 Atlantic has occupied an increasingly distinct area of multivariate space compared to the
122 other realms, characterized by a relatively high cover of macroalgae and ‘other’ organisms
123 (Fig. 2b-d; Extended Data Fig. 1). Secondly, the Central Pacific has become increasingly
124 restricted to an area of multivariate space typified by a high relative cover of low-lying algal
125 communities (Fig. 2b-d; Extended Data Fig. 1). Thirdly, despite numerous large-scale
126 disturbances in the 20-year period ^{10,11,23}, reefs in the Indian Ocean and Indo-West Pacific
127 have consistently occupied an area of multivariate space typified by relatively high hard coral
128 cover (Fig. 2; Extended Data Fig. 1). Importantly, these three general inferences were
129 consistent when the data were examined using different start and end points (1998 and 2016,
130 1999 and 2015; Supplementary Figs 5, 6; Supplementary Table 1). Overall, this suggests that
131 there are major differences in benthic compositions across realms.

132

133 *Among-realm dynamics of key benthic categories*

134 Given the overwhelming contribution of hard corals, low-lying algal communities,
135 and macroalgae to benthic dynamics and associated changes (Figs 1, 2), the among-realm

136 variation of these key benthic categories clearly warrants more detailed examination. To do
137 this, we used generalised additive mixed effects models (GAMMs) to specifically focus on
138 the dynamics of hard corals, macroalgae and low-lying algal communities from 1997-2018
139 (Fig. 3; Supplementary Fig. 7). These models revealed a trend of decreasing hard coral cover
140 in the Western Atlantic and Central Pacific, with limited net change in the Indo-West Pacific
141 and Indian Ocean (Fig. 3a; Extended Data Fig. 2a; Supplementary Table 2). In the Western
142 Atlantic, along with coral loss, there has been a significant concomitant non-linear increase in
143 macroalgal coverage (F value = 13.68, $p < 0.001$; Fig. 3b; Extended Data Fig. 2b;
144 Supplementary Table 2). Thus, it is likely that this increase in macroalgae in the Western
145 Atlantic is underpinning the signal of increasing macroalgae cover at a global scale (Fig. 1).
146 This is because, macroalgal cover has remained consistently low in the Indo-West Pacific and
147 Central Pacific (Fig. 3b; Extended Data Fig. 2b), with only a small, but strongly fluctuating,
148 net increase in the Indian Ocean (Fig. 3b; Extended Data Fig. 2b). Unlike in the Western
149 Atlantic, coral loss in the Central Pacific has largely been associated with a concomitant
150 change in the cover of low-lying algal communities (Fig. 3c; Extended Data Fig. 2c;
151 Supplementary Table 2). Given that many reefs in the Indo-West and Central Pacific have
152 been repeatedly subjected to a wide array of stressors, including repetitive mass coral
153 bleaching events and widespread coral mortality^{10,11}, we would have expected a more
154 detectable signal in the data if macroalgae were going to increase in these realms. We
155 conclude, therefore, that the dynamics between hard coral and macroalgae cover differ
156 markedly between the Western Atlantic versus Indo-West, Central Pacific and Indian Ocean
157 realms.

158 It is important to note that these general inferences were found to be robust when the
159 influence of potential confounding factors were explored. Specifically, we performed
160 additional GAMMs to examine if model trajectories differed substantially when: a) the data
161 were pooled at two increasingly coarse spatial resolutions (i.e. to explore if sample size
162 and/or if numerous data points in close proximity were influencing patterns) (Supplementary
163 Figs 8, 9; Supplementary Table 3); b) only a subset of the benthic composition data were
164 used (to explore susceptibility to collection methods) (Supplementary Fig. 10; Supplementary
165 Table 4) and c) variation of the temporal extent (to explore sensitivity to start and end years)
166 (Supplementary Fig. 11; Supplementary Table 5). In all cases the general trajectories of hard
167 coral, macroalgae and low-lying algae cover across realms were maintained, or even
168 strengthened, suggesting that our inferences were robust. Additionally, we explored the
169 dynamics of the other benthic categories that made up the dataset (i.e. soft corals, other
170 organisms and sand) through time and across depths (see Supplementary Fig. 12;
171 Supplementary Table 2). However, as these benthic categories only made up a minor fraction
172 of benthic composition (often less than 5% of average benthic cover) and/or there was limited
173 net change through time (Supplementary Fig. 12), we have not expanded on the discussion of
174 these findings herein.

175

176 *Habitat and depth specific dynamics of key benthic categories*

177 Beyond realm differences, the largest ecological gradients on coral reefs are often
178 cross-habitat or cross-depth gradients²⁴. It is for this reason that these factors were
179 specifically accounted for in our analysis of hard coral, macroalgae and low-lying algae cover
180 trajectories across realms, and the trends presented above are standardized for such effects.
181 However, given the extent of variation that may occur across these gradients, further, detailed
182 analysis was warranted. To do this, we focused on two habitats which were generally most

183 frequently sampled in each of the four realms (Extended Data Fig. 3; Supplementary Fig. 13):
184 the reef crest (0-5 m) and upper reef slope (5-15 m). Based on these habitat subsets, we
185 performed the same analyses as above, to explore benthic trajectories through time across
186 realms.

187 In general, the habitat-specific analyses revealed similar trends to the complete
188 analyses (Figs 3, 4; Supplementary Tables 2, 6). However, there were three more nuanced
189 trends which were particularly notable. Firstly, the extent of hard coral loss in the Central
190 Pacific was far greater on shallow reef crests compared to the upper slope (Fig. 4a, b).
191 Consequently, concomitant increases in the cover of low-lying algae in the Central Pacific
192 were also higher on the crest relative to the slope (Fig. 4e, f). Secondly, in the Western
193 Atlantic, macroalgae cover has increased to a greater extent on the reef crest compared to the
194 upper slope (Fig. 4c, d). Finally, there was a particularly strong signal of coral loss and
195 increased low-lying algal cover in the Indian Ocean on upper reef slopes in the late 1990s
196 (Fig. 4b, f). This strong signal aligns well with the 1998 coral bleaching event in this realm.
197 Taken together, these analyses support the general inferences from the full dataset, but also
198 extend the findings by revealing more nuanced variation of benthic trajectories within
199 specific habitats.

200

201 Discussion

202 The change in coral reef benthic composition is generally associated with the loss of
203 hard scleractinian coral cover^{7,20,25}. In this respect, our results are consistent with previous
204 studies. For example, the long history of declining hard coral cover in the Western Atlantic,
205 especially in the Caribbean, is well established in the literature²⁶⁻²⁸. Our results suggest that
206 the declines documented in earlier studies in this realm^{26,27}, have continued, with the low
207 levels of 10-15% coral cover in our study aligning well with recent reports²⁹. Moreover, the
208 relative stability of hard coral cover during this period (1997-2018) in the Indo-West Pacific
209³⁰ as well as in the Indian Ocean (with the notable exception of the 1998 bleaching event)³¹,
210 has been previously documented, with our levels of 25-30% also aligning well with recent
211 reports from these regions²⁹. Nevertheless, our study differs from these past studies as we
212 separated algal forms and highlight that increasing cover of tall macroalgae is largely
213 restricted to the Western Atlantic, with ramifications for how we perceive coral reef change
214 globally. However, it is important to highlight that our study, along with the previous studies,
215 all represent realm-wide average trends, with changes within specific locations potentially
216 diverging from these trajectories^{27,29}.

217 Importantly, we also explored how benthic trajectories varied within reef crest and
218 slope habitats within realms. In doing so, we revealed that the trajectories were quite
219 consistent across these two habitats, but that there were some key differences in the
220 magnitude of benthic change. Such differences likely relate to a range of abiotic (e.g. light
221 levels, wave exposure) and biotic (e.g. herbivory, competition) factors that may vary across
222 habitats (i.e. at a scale of 10s of metres). Unfortunately, we were only able to explore benthic
223 trajectories in reef crest and slope habitats due to the relative paucity of benthic data from
224 other habitats (Extended Data Fig. 3). While the only habitat/depth related restriction we
225 placed on the inclusion of data in our study was that it had to be collected at depths shallower
226 than 30 m, most data (76%) came from reef crest and slope habitats (Extended Data Fig. 3).
227 By contrast, just 7% of data were derived from reef flat habitats (Extended Data Fig. 3),
228 despite this habitat generally being the most expansive (by areal extent) on coral reefs³².

229 Interestingly, the same patterns have recently been described for research on reef fishes ³²,
230 suggesting that, as a whole, research on reefs is focused on a subset of habitats, potentially
231 resulting in an incomplete understanding of how they function ³³.

232 Furthermore, most benthic composition data on coral reefs were collected after the
233 global 1998 coral bleaching event (Extended Data Fig. 4), which means that large scale
234 monitoring efforts often began on systems which were already disturbed. Indeed, it is for this
235 reason that our timeseries only focused on data from 1997 onwards. It could be that the
236 relatively stable levels of hard coral cover documented in some regions (i.e. the Indo-West
237 Pacific and Indian Ocean) in recent years may not reflect historical baselines that may have
238 been higher preceding the initial global mass bleaching event ^{20,30,34}. Unfortunately, benthic
239 composition data is exceedingly sparse in earlier years ^{29,34} (Extended Data Fig. 4), making it
240 hard to discern the full extent of reef benthic community change.

241 Nevertheless, given a situation of relatively low, and in some cases decreasing, hard
242 coral cover on reefs in recent decades, we might ask: what benthic category is replacing
243 corals? This is where our study differs from many previous studies, particularly those at a
244 similar spatial scale, as we specifically endeavoured to separate large (i.e. $\sim >2$ cm tall)
245 macroalgae from low-lying algal forms (e.g. CCAs and turfs). Previous global data
246 compilations have largely focused on ‘algae’ cover, with the constituent algal groups (tall
247 macroalgae, turf algae, CCA etc) often being unclear ^{22,29}. Indeed, it is exactly this lack of
248 resolution from past studies that hinders the inclusion of more specific categories herein, and
249 why our division of algal categories was limited to macroalgae versus low-lying algae (see
250 Supplementary Text 1 for a discussion about problems with the historical quantification of
251 low-lying algae in coral reef monitoring). However, this division between macroalgae and
252 low-lying algae was sufficient to reveal that while ‘algae’ may be increasing on many reefs
253 globally ²⁹, in most cases this is not tall macroalgae but rather low-lying algae, such as turfs.
254 Moreover, increases in macroalgae cover are largely restricted to Western Atlantic reefs (Figs
255 2, 3, 4 and Extended Data Fig. 5). This has important implications for our understanding of
256 changing coral reefs.

257 Much of our understanding about coral reef decline is based on reefs in the Western
258 Atlantic realm ^{20,28,35}. However, our analyses strongly support the hypothesis that the Western
259 Atlantic is functioning in a fundamentally different manner to other coral reef realms, and
260 calls into question the extent to which insights gleaned there can inform our understanding of
261 ongoing change in other realms (see ^{25,36,37}). It has previously been highlighted that many top-
262 down (e.g. herbivory) and bottom-up (e.g. macroalgal growth rate) factors, as well as
263 anthropogenic stressors (e.g. fishing pressure, relative accessibility of reefs [but see
264 Supplementary Text 2; Supplementary Fig. 14]) can, and probably do, differ fundamentally
265 between reefs in the Western Atlantic versus Indo-West Pacific, with implications for their
266 respective resilience to perturbations ³⁶. Deciphering how these various explanatory variables
267 are potentially linked to differences in benthic composition across realms could thus be a
268 worthwhile future research endeavour. However, it is important to note that any resulting
269 correlations from these analyses could be spurious, or proximal, as the ultimate drivers may
270 largely be related to differences in historical biogeography among realms.

271 Marked differences in biodiversity and functional diversity between the Indo-West
272 Pacific and the Western Atlantic ^{20,36} stem from their fundamentally distinct biogeographical
273 histories ^{38,39}. For instance, these realms differ more than 3-fold and 7-fold in their diversity
274 of fishes and scleractinian corals, respectively ²⁰. Importantly, these disparities could explain
275 some of the variation in benthic composition trajectories between the Indo-West Pacific and

276 the Western Atlantic. Many fast-growing *Acropora* coral growth forms, which drive early
277 coral recovery on Indo-West Pacific reefs^{20,40}, as well as functional groups of key
278 herbivorous fishes that may be key in controlling macroalgae proliferation (e.g. crevice
279 cleaning surgeonfishes/rabbitfishes and browsing rabbitfishes/nasine surgeonfishes)^{36,41}, are
280 completely lacking in the Western Atlantic. This potentially pre-disposes Atlantic reefs to
281 much higher macroalgal cover following coral loss. Consequently, the modern-day
282 configurations of both fish and benthic communities on reefs in each realm could ultimately
283 be rooted in historical biogeography, with the influence of these drivers being concatenated in
284 the ‘realm’ factor in our analyses.

285 Outside the Western Atlantic, coral loss and reef change are largely independent of
286 macroalgal cover. In this respect, the Central Pacific could represent a harbinger of future
287 reefs in the Indo-West Pacific realm as it has experienced a substantial degree of coral loss
288 over recent decades; potentially mirroring what could happen on Indo-West Pacific reefs
289 going forward^{7,10}. Central Pacific and Indo-West Pacific reefs may respond to disturbance in
290 a broadly similar manner, as they share critical functional groups of hard corals^{20,40} and
291 herbivorous fishes^{36,41}, yielding similar response diversity and resilience mechanisms,
292 especially when compared to the Western Atlantic^{20,36,40,41}. As a result, concepts derived
293 from Central Pacific reefs may provide a more meaningful insight into the future of Indo-
294 West Pacific reefs when compared to those from Western Atlantic reefs.

295 Given a situation where macroalgae may not be the major benthic category replacing
296 corals on Indo-Pacific reefs, it is critical to consider what the functional implications of more
297 extensive low-lying algal cover may be. To do this, we first need to recognize that these low-
298 lying algal communities are by no means homogenous. They exist on a continuum ranging
299 from biofilms and CCAs, through sparse algal turfs and CCAs, to long sediment-laden algal
300 turfs (for a full discussion see Supplementary Text 1; Supplementary Figs 2-4). Where the
301 state of low-lying algal communities falls along this continuum may have a variety of
302 implications for future reefs and how they function. These include core ecosystem processes
303 such as coral recruitment, herbivory/productivity and calcification¹³. For example, a benthic
304 condition typified by low-lying algal communities composed of high CCA and/or short well-
305 cropped algal turf cover is not resistant to the return of corals via recruitment after a
306 disturbance^{18,42-44}. By contrast, long sediment-laden algal turfs, can inhibit coral settlement,
307 growth and, as a consequence, the recovery of coral cover^{42,43}, mirroring reef states typified
308 by high macroalgal cover^{42,44,45}. Management actions that aim to maintain low-lying benthic
309 communities typified by CCA and short algal turfs may thus be beneficial, until climate
310 change is addressed and/or corals adapt, to facilitate the return of corals to reefs via
311 recruitment.

312 In addition to being a more favourable benthic state for coral recruitment, coral reefs
313 typified by a high cover of low-lying algal communities may also benefit the provision of
314 some other key services. For example, fisheries catches in many reef locations are already
315 heavily composed of fishes that derive their nutrition from components of low-lying algal
316 communities^{46,47}. Indeed, compared to macroalgae, low-lying algal communities generally
317 provide a broader range of nutritious resources (e.g. algal turfs, detritus, biofilms) that are fed
318 on by a wider diversity of fishes⁴⁸. Therefore, maintaining highly productive short algal turf
319 communities may be important in sustaining fisheries catches in some areas, although this is
320 inherently linked to the quantity of sediments in low-lying algae⁴⁹. Moreover, a decrease in
321 coral cover and coral derived calcification in the future⁵⁰, may mean that the role of CCA in
322 calcification and reef building also becomes more important. In this respect, the reef building
323 capacity of CCA is increasingly being recognised³³, with the suggestion that the substratum

324 formed by CCA may be resistant to future climate change ^{51,52}. If the outlook for reefs is
325 typified by high coverage of low-lying algal and CCA communities it may, therefore, be
326 possible to maintain some key ecosystem functions within this configuration.

327 Overall, the trajectories reported herein carry substantial implications for our
328 understanding of changes on coral reefs at global scales and for the differing, realm-
329 dependent, compositions that may arise in the near future. Western Atlantic coral reefs are
330 clearly typified by relatively high macroalgal cover, with the main axes of change in this
331 realm being one between hard corals and macroalgae (Extended Data Fig. 5). However, in the
332 other realms, coral reef benthic composition rarely falls along this coral-macroalgae axis of
333 change, nor is macroalgae a major benthic category. Instead, for at least two decades, from
334 1997 to 2018, most reefs have had high cover of low-lying algal communities with the
335 majority of benthic dynamics involving fluctuations in hard coral versus low-lying algae.
336 Variation in hard coral and low-lying algae cover is likely to remain a critical axis of change
337 for most future coral reefs.

338

339 **Methods**

340 *Benthic composition dataset compilation*

341 To examine how benthic composition varied across coral reefs globally we compiled
342 an extensive dataset of benthic cover over the past four decades (1977-2018). This dataset
343 consisted of over 24,000 individual benthic composition data points (derived from both
344 smaller scale timeseries and one-off studies). These data were derived from multiple coral
345 reef monitoring databases and by systematically sorting through 14,900 past studies. We
346 limited our definition of coral reefs to locations between $\pm 30^\circ$ of latitude from the Equator
347 (following ⁵³) and from 0 – 30 m water depth. The individual observations in our dataset were
348 mean benthic community composition, which was the finest resolution of data that could be
349 reliably sourced. Means were based on data with the same latitude, longitude, depth and
350 habitat within the same year.

351 Based on an initial examination of available data, and the manner in which previous
352 studies and monitoring schemes had categorised the benthos, we selected six benthic
353 categories to represent benthic composition: hard coral (i.e. Scleractinian corals), soft corals
354 (generally considered corals from the order Alcyonacea), macroalgae (generally considered
355 algae $> \sim 20$ mm in height ^{37,54} [Supplementary Fig. 3]), a low-lying algal community category
356 (analogous to the ‘CTB’ category often used in past studies) which included algal
357 turf/crustose coralline algae[CCA]/rubble/cyanobacteria/dead coral/bare substratum/rock (as
358 benthic composition data rarely discriminated among these different benthic categories a
359 single category was used following ^{18,55–57} to maximise data retention; see Supplementary
360 Text 1 for an extensive discussion on this), other biotic organisms (e.g. other biotic organisms
361 that are found on reefs but are often not major constituents such as sponges, ascidians,
362 seagrass, bivalves), and sand/sediment. It is critical to note that in all cases, we ensured the
363 ‘other’ category did not comprise benthic categories often classed as ‘abiotic’ but are almost
364 always covered in a constituent of the low-lying algal category (e.g. algal turfs, CCA,
365 cyanobacteria) ^{19,58–60}. Likewise, we ensured that all data had specifically monitored for
366 ‘other’ biotic benthic components such as sponges and ascidians to ensure these were not
367 erroneously included as constituents of the low-lying algal category. With these six benthic
368 categories we were able to capture 100% of the coral reef benthic community composition
369 (i.e. we did not just focus on a subset of the biotic benthic community). We relied on these

370 major divisions to maximise the resolution in the dataset, while minimising the amount of
371 data that had to be excluded because it was collected at a coarser resolution. Indeed, given the
372 varied nature in how the benthos has been categorised globally (as discussed in
373 Supplementary Text 1) this relatively coarse categorisation scheme helped with our
374 endeavour to standardise benthic categories, to the best of our ability given the available data.
375 However, important additional insights can be realised if future work prioritises a finer
376 resolution categorisation of the benthos. We recommend that a standardised global scheme
377 for categorising the benthos (with careful consideration of how various low-lying algal
378 groups are classified) would substantially improve the utility of coral reef monitoring
379 programs.

380 Initially, we compiled benthic composition data from six major publicly available
381 monitoring databases: Caribbean Coastal Marine Productivity (CARICOMP), Moorea Coral
382 Reef Long Term Ecological Research, National Oceanic and Atmospheric Administration
383 (NOAA), Reef Check, Reef Check Australia and Reef Life Survey (see Supplementary Text
384 3, 4 for a full list of data sources and links). Where necessary, these data were pooled into the
385 relevant benthic composition categories, and means were calculated (i.e. based on data with
386 the same GPS coordinates, at the same depth, in the same habitat and year sampled). In all
387 cases, spurious data categories (e.g. transect tape, mobile fauna and unclassified) were
388 excluded from calculations as they did not represent sessile benthic substrata. Data from these
389 databases were also excluded if the metadata (namely depth, latitude, longitude, and sampling
390 year) were missing or spurious.

391 To complement the data from these databases and to ensure that our dataset was as
392 comprehensive as possible, we then undertook an extensive formal search of the literature for
393 available data. Our search and filtering process was based on PRISMA protocols ⁶¹, and a
394 flow diagram outlining each step is provided in the supplementary material (Supplementary
395 Fig. 15). This was achieved using the search engine GoogleScholar and the search terms:
396 “coral reef” AND benthic AND percent AND (transect OR quadrat). This search yielded
397 14,900 total results on the 20th of May 2020 (not including patents or citations). Note that, in
398 contrast to searches in databases such as Web of Science and Scopus, these search terms take
399 advantage of Google Scholar’s default setting to search within the full text of documents.
400 Therefore, for example, the use of terms such as ‘transect’ do not limit the papers returned to
401 methods papers containing this term in the title, abstract or keywords of documents.

402 We evaluated these 14,900 documents based on their title and abstract for any
403 potentially relevant documents. This process identified a subset of 1,748 potentially relevant
404 documents for further investigation. Each of these documents were then examined in detail
405 and the suitability of their data for inclusion in our dataset was assessed against a set of
406 criteria. Acceptance criteria were: a) sampling was conducted on a coral reef system within
407 our definition of a coral reef (i.e. $\pm 30^\circ$ of latitude from the Equator and 0 – 30 m water
408 depth), b) the document contained benthic community composition data at sufficiently fine
409 resolution to fit into our six benthic categories in a form that we could extract (i.e. raw data,
410 tables or from figures), with no missing data/benthic categories, c) the data were pooled at the
411 scale of the sampling site or a finer spatial scale (i.e. data across individual sampling sites
412 were not pooled and presented together), d) the data presented in the manuscript had not
413 already been included in our database from another source, e) sufficient detail was presented
414 in the document that outlined the sampling location, depth, time and methods used, and f)
415 there was no clear selection of study sites to meet pre-defined criteria (e.g. if a study
416 specifically selected for ‘high coral cover’ sites it was not included).

417 We relied on the criteria above to ensure that: a) the ecosystem sampled was
418 consistent across data, b) the data covered the entire coral reef benthos, c) among-site level
419 variation was not averaged out, d) we did not include the same data twice, e) we had
420 sufficient information on the sampling to explain any patterns in benthic community
421 composition, and f) any potential sampling biases associated with focused site selection were
422 minimised. On this later point, it should be noted that coral reef research in general often
423 focuses on coral-dominated rather than algae-dominated habitats ^{22,62}, with the habitats most
424 frequently sampled by coral reef researchers (i.e. slope and crest; Extended Data Fig. 3) often
425 having the highest coral cover ³². This means that in most coral reef research a decline rather
426 than recovery in coral cover is likely to be documented (also see ⁶²). After this second
427 extensive filtering process we were left with a subset of 83 studies that contained relevant
428 data for our dataset (see Supplementary Text 3 for a full list of references). The vast majority
429 of documents (1,449) simply did not contain the necessary data (i.e. most only reported ‘coral
430 cover’ or ‘algae cover’ rather than complete benthic community composition).

431 From each relevant document we then extracted data on the benthic cover (mean
432 percent/proportion) of each of our six benthic categories at the level of individual sites (i.e.
433 unique GPS coordinates, at the same depth, in the same habitat and sampling year). In most
434 cases these data were sourced from raw data files, or tables in the main document. However,
435 in some cases, it was necessary to extract the relevant data from figures in the document
436 using WebPlotDigitizer ⁶³. In addition, we also extracted information on the location of each
437 study (latitude and longitude), the depth of each habitat (where a range was given the median
438 depth was used), the method used to quantify the benthos, the year sampling was conducted,
439 and the habitat which was sampled.

440

441 ***Database cleaning and checking***

442 With the compiled database at hand, we undertook a quality control procedure to
443 check the data. To do this we manually checked each data point. Specifically, we ensured a)
444 the six benthic categories were standardised (i.e. they added up to 100%), b) the latitude and
445 longitude data were accurate (we checked this by examining each individual set of
446 coordinates in Google Earth), c) each data point had a corresponding depth (in meters) and
447 year sampled value, d) the method used to collect each data point was categorised (line
448 intercept transect, point intercept transect, chain intercept transect, photo quadrats along a
449 transect, in-situ quadrats, or analysis of individual frames from a video; it is important to note
450 that the vast majority of data were derived from one of two planar point-based methods [point
451 intercept transect or photo-quadrats along a transect with subsequent examination using
452 points]) (Supplementary Fig. 16), e) the habitat sampled was categorised as either reef flat,
453 lagoon, slope, back reef, crest, or submerged reef (where this information was not presented
454 we placed the datapoint into a category based on its depth and satellite imagery in Google
455 Earth), and f) the location of each datapoint was also designated into a category within three
456 increasingly fine spatial scales: biogeographic realm (n = 6), ecoregion (n = 20) and
457 geographic unit (n = 113) (Supplementary Fig. 17; Supplementary Table 7). Realm and
458 ecoregion classifications were based on the schemes presented in ^{64,65} while the geographic
459 unit level was primarily based on the country from where the data were sourced, however,
460 where data were from large countries, remote territories or clustered island groups we used
461 more informative, finer scale categorisation within the country level (Supplementary Fig. 17;
462 Supplementary Table 7). Following this final quality control procedure our timeseries dataset

463 contained 24,674 unique datapoints representing mean coral reef benthic community
464 composition spread across more than 40 years of sampling (1977 – 2018).

465

466 *Data analyses*

467 All statistical analyses and data handling were performed in the software R ⁶⁶.
468 Initially, we filtered our data to retain data from 1997-2018. Even though our dataset spanned
469 1977-2018 there was very little data prior to 1997 (only 0.83% of all data in the dataset were
470 from the 20-year period from 1977-1996 [Extended Data Fig. 4]) making any inferences
471 based on this early data difficult. It is important to note that all analyses described below are
472 focused on examining if there had been change in the cover of benthic categories over this
473 multidecadal timespan (i.e. long-term, continuous change). Therefore, we were not studying
474 change from the perspective of ‘regime shifts’ or ‘phase shifts’ nor assessing for ‘alternative
475 stable states’. Given that these topics are still debated in the literature (e.g. ^{67,68}) and/or their
476 definitions can be unclear ⁶², they are outside of the scope of the present study.

477 To examine variation in benthic composition we initially utilised multivariate
478 analyses. Specifically, we explored how the composition of all six benthic categories varied
479 across the four realms with most of the data (Central Pacific, Indian Ocean, Indo-West
480 Pacific and Western Atlantic; Extended Data Fig. 4) in 1997, 2007, and 2017. We based our
481 analysis on these three years as 1997 represented the earliest year in our retained dataset,
482 while 2007 and 2017 were equidistantly spaced apart, and covered most of the temporal
483 scope in our dataset (refer to Supplementary Figs 5, 6 and Supplementary Table 1 for analysis
484 and ordination plots based on different start and end years [1998 and 2016, 1999 and 2015]
485 using the same methods as outlined here). A ten-year period was chosen to limit any
486 influence of temporal autocorrelation. Based on these three years of data, we then calculated
487 a dissimilarity matrix based on the Morisita-Horn index (as it is robust when sample sizes
488 differ ⁶⁹). We then explored if the key variables of habitat, depth, year and realm were
489 significantly correlated with the multivariate space using a permutational multivariate
490 analysis of variance (PERMANOVA) (package: *vegan* ⁷⁰). To visualise the results, we then
491 produced a CAP ordination plot (package: *vegan* ⁷⁰) which was constrained by the key
492 variables that were significantly correlated with the multivariate benthic composition data. It
493 should be noted that to ensure the axes were directly comparable, the multivariate analysis
494 was conducted as one analysis (i.e. all three years together) and only the results were plotted
495 separately by year. To aid interpretation we then calculated 50% kernel density estimates for
496 each realm in each year (package: *adehabitatHR* ⁷¹). Calculating kernel density estimates is a
497 technique that has been popularised in the field of animal movement to describe the
498 probability of animal detections in a space and to delineate core areas ⁷². Kernel density
499 techniques are superior to convex hulls for visualising patterns in multivariate spaces as they
500 are not as sensitive to outlying data points ⁷³. Therefore, in our case, the 50% kernels indicate
501 the core areas of the ordinations occupied by the individual sampling locations from each
502 realm in each year.

503 Based on the ordinations, the specific examination of the temporal dynamics of each
504 benthic category in the Western Atlantic, Indo-West Pacific, Indian Ocean and Central
505 Pacific was warranted, especially given the history of comparing these realms in the coral
506 reef literature (e.g. ^{20,36,40,41}). To do this, we utilised separate generalised additive mixed
507 effects models GAMMs (package: *mgcv* ⁷⁴) to examine temporal variation in the proportional
508 cover of the six benthic categories, separately, in the four realms. We treated time (year

509 sampled) as a continuous fixed effect with separate splines for each realm. In addition, to
510 account for depth-related patterns, we fitted depth as a continuous fixed effect with separate
511 splines for each realm. In all cases, we used thin plate splines for the fixed effects. We also
512 fitted habitat and geographic unit as random effects using random effects smoothers. Method
513 and ecoregion were not included in the models as they had a high level (>0.8) of concurrency
514 with the other factors already included. For both models we utilised a tweedie distribution
515 with a log link function. A tweedie distribution was superior to a betabinomial distribution
516 here due to the nature of the data in all cases (i.e. the data contained a large number of exact
517 zeroes and the nonzero observations were continuous and positively skewed [and with very
518 few observations at the upper bounds of the proportional dataset – i.e. close to 1 or 100%
519 cover]).

520 After fitting the GAMMs, we checked that a sufficient number of knots were used by
521 checking if k and edf were close to each other, while considering the values of the k -index
522 and simulated p value in `gam.check`⁷⁴. In all cases, we initially relied on the default level of
523 knots in each model ($k = 10$). However, where our knot checking procedure suggested that
524 this was too restrictive, we increased k until it was indicated that enough knots had been used
525 (the maximum value of k in any model was 15). In addition, we examined the residuals of
526 both models for temporal autocorrelation. No meaningful patterns of temporal autocorrelation
527 were detected. We also assessed the residuals of both models for spatial autocorrelation using
528 variograms (package: `gstat`⁷⁵), and compared these to variograms of the residuals from
529 models containing only the fixed effects structure as well as variograms of the raw data
530 (Supplementary Figs 18-26). For all variograms we accounted for potential among year
531 differences by only comparing point pairs from within the same year and we examined for
532 patterns across multiple directional axes (i.e. North – South; North-East – South-West; East –
533 West; South-East – North-West). In all cases our models accounted for spatial correlation and
534 there were no clear patterns of concern (i.e. increasing variance with increasing distance) in
535 the residuals. We also examined model residuals using simulation-based model-checking
536 (package: `DHARMA`⁷⁶) and standard residual plots. In all cases this indicated that the fit was
537 satisfactory.

538 In addition to the GAMMs which examined benthic trends in the entire dataset, we
539 also specifically examined how hard coral, macroalgae and low-lying algal cover differed
540 through time and among realms, separately, for the two most frequently sampled habitats (the
541 crest [0-5 m] and the slope [5-15 m]; only the upper slope was considered as data for deeper
542 regions were relatively sparse for the Indian Ocean and Indo-West Pacific; Extended Data
543 Fig. 3; Supplementary Fig. 13). We specifically performed this comparison because cross-
544 habitat and cross-depth gradients represent some of the strongest ecological gradients on
545 coral reefs²⁴, and because treating habitat as a random effect (as in the original analysis)
546 would not allow us to detect interactions between habitat and time or realm. Therefore, by
547 comparing benthic trends among realms in the same habitats across narrow depth ranges, we
548 could eliminate any results that might have been artefacts of differential representation of
549 habitat types through time or among realms, and to detect whether there were differences in
550 temporal trends or among-realm differences among habitat types. For each GAMM we
551 treated time (year sampled) as a continuous fixed effect with separate splines for each realm
552 and geographic unit as a random effect using random effects smoothers. In all cases, we
553 relied on the same model distributions, and model validation procedures, as above.
554 Additional packages used for graphical representation of the data included `emmeans`⁷⁷,
555 `tidyverse`⁷⁸, `sf`⁷⁹, `rnaturalearth`⁸⁰, `ggtern`⁸¹, and `patchwork`⁸².

556

557 *Sensitivity analyses*

558 To ensure our GAMM results and associated inferences were robust we undertook a
559 suite of sensitivity analyses to explore if the results were being influenced by other
560 confounding factors. These factors were: a) sampling effort/influential but spatially clustered
561 data points, which may arise from methods such as numerous replicate samples in close
562 proximity but with limited sampling effort for each replicate, b) variation in the methods used
563 to collect benthic cover data, and c) the length of the time series examined, especially in
564 terms of the first and last year given the timing of global bleaching events (i.e. in 1998 and
565 2015-2017). Due to the number of different GAMMs these sensitivity analyses entailed, we
566 focused on the dynamics of the three primary benthic categories (hard corals, macroalgae and
567 low-lying algal communities) which underpinned our main results and inferences.

568 To explore the influence of the first potential confounding factor (i.e. influential data
569 points/variation in sampling effort) we clustered the data (i.e. recalculated mean benthic
570 cover of each benthic category) at two different spatial resolutions within the same habitats
571 and year sampled: a) the nearest 0.01° latitude and longitude and nearest 3 m depth ($n =$
572 $21,025$ data points) and b) the nearest 0.1° latitude and longitude and nearest 3 m depth ($n =$
573 $13,837$ data points). In both cases we also recorded the number of individual data points
574 which were used to calculate the new means in each grid cell. With these two spatially
575 clustered datasets at hand, we then constructed new GAMMs using the same model structure,
576 distributions and validation procedures as for the full GAMMs in the original analyses,
577 above. To explore how robust the results were to sampling effort (i.e. the number of data
578 points underlying each mean calculated) we performed the above analyses twice, with and
579 without weighting each mean by the number of points used to calculate it. By comparing the
580 output of each set of analyses we could then determine how influential sample size was to our
581 observations (if sample size was influential, one would expect results to diverge markedly).

582 To ensure our inferences were not biased by variation in sampling methods in the
583 dataset we produced a subset of benthic data which was collected using only a planar point-
584 count approach (i.e. point intercept transects or photo quadrats along a transect [where points
585 are subsequently generated to estimate benthic cover]). We then constructed GAMMs using
586 the same model structure as the full GAMMs in the original analyses. In addition, to ensure
587 the temporal span of the data was not influencing the nature of our inferences, especially
588 given that our first year (1997) in our timeseries was prior to the first global coral bleaching
589 event, while the last year (2018) was after the latest global bleaching event had subsided, we
590 refitted our GAMMs on three different subsets of the data with differing first and last years
591 (1998-2017, 1999-2016 and 2000-2015). In all cases we used the same model structure as the
592 original analysis. For all GAMMs examining sensitivity to method or temporal factors, we
593 relied on the same model distributions, and model validation procedures, as above for the
594 original analyses. Furthermore, for all sensitivity analyses we used the same R packages as
595 for the original analyses.

596

597 **Data Availability**

598 All data used in this study were attained from publicly available databases and previous
599 literature. The sources of all data and links to databases are provided at the appropriate
600 section in the manuscript, in Supplementary Text 3, and are publicly available on figshare
601 (<https://doi.org/10.6084/m9.figshare.21267924.v1>). The derived data from published studies
602 is also publicly available on figshare (<https://doi.org/10.6084/m9.figshare.21267924.v1>).

603 **Code Availability**

604 Code supporting the findings of this study is publicly available on figshare
605 (<https://doi.org/10.6084/m9.figshare.21267924.v1>).

606

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614

615 **Author Contributions Statement**

616 SBT, SRC, and DRB conceived the study; SBT compiled the data; SBT and SRC conducted
617 the analyses; SBT, SRC, and DRB interpreted the analyses; SBT drafted the initial version of
618 the manuscript; SBT, SRC, and DRB contributed to editing and revising the manuscript,
619 approved the submitted version and agree to be personally accountable for their
620 contributions.

621

622 **Competing Interests Statement**

623 The authors have no competing interests to declare.

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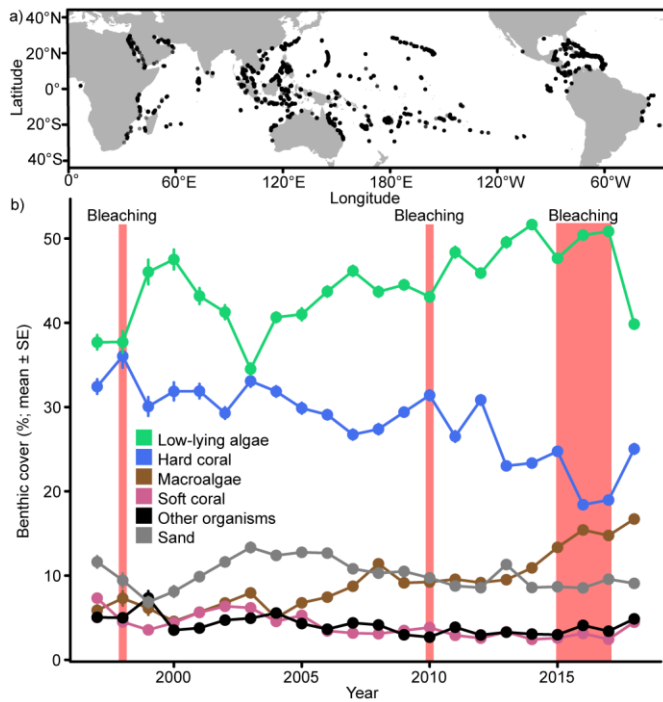
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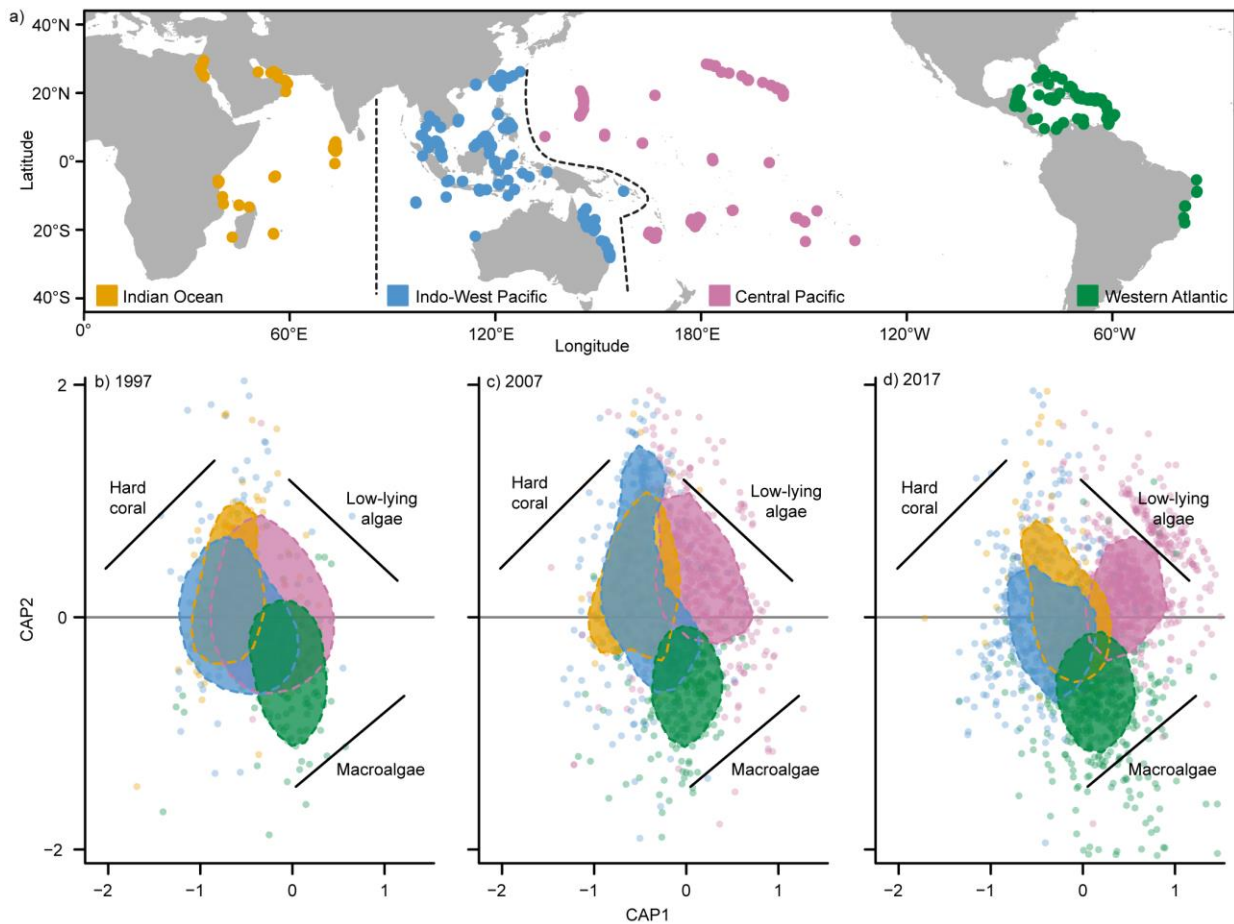
636 **Figure Legends/Captions**



637

638 **Figure 1 Benthic composition of the world's coral reefs.** a) World map showing the spatial
 639 extent of coral reef benthic composition data (n = 24,468 data points). b) The mean (\pm SE)
 640 percent cover of the six benthic categories in the global dataset (n = 424, 269, 256, 331, 508,
 641 700, 733, 970, 831, 1259, 1196, 1193, 1355, 1239, 1071, 1303, 1787, 1639, 2320, 1914,
 642 1932, 1238 cover observations for each benthic category in each year from 1997-2018,
 643 respectively). The red vertical lines denote the three global bleaching events (1998, 2010 and
 644 2015-2017) that occurred during this period (based on ¹⁶). Note that this figure represents an
 645 initial visualisation of the raw data in its entirety; subsequent analyses (Figs 2, 3, 4) explore
 646 spatial variability in more detail.

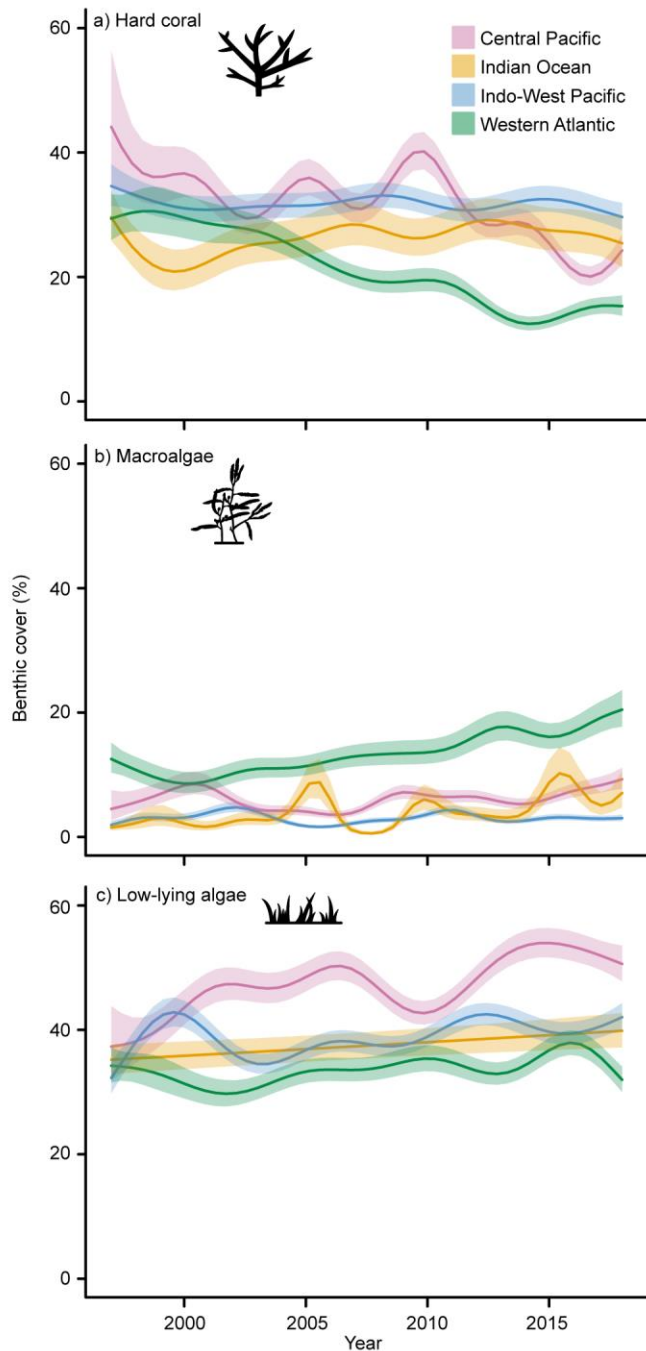
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649 **Figure 2 Coral reef benthic composition among major realms.** a) World map showing the
 650 delineation of the major marine realms based on the data from 1997, 2007 and 2017 used in
 651 the ordination plots (n = 424, 1102, 1924 benthic composition observations each year,
 652 respectively). Multivariate ordination plots based on the Morisita-Horn index and constrained
 653 by realm, habitat, year and depth, showing coral reef benthic composition in the four realms
 654 in b) 1997, c) 2007, and d) 2017. The coloured polygons (matching the realm colours in [a])
 655 in the ordinations are based on 50% kernel density distributions, denoting where the data
 656 points are concentrated in multivariate space. The lines in b-d) denote the areas of
 657 multivariate space typified by the three major benthic categories, while the area in the bottom
 658 left corner of each panel is typified by soft corals, sand and 'other' organisms (see Extended
 659 Data Fig. 1 for details). For a version of this figure with full data points, vectors of each
 660 benthic component, and vectors of constraining factors (realm, habitat, year, and depth) refer
 661 to Extended Data Fig. 1. See Supplementary Figs 5, 6 for ordination plots with different start
 662 and end years.

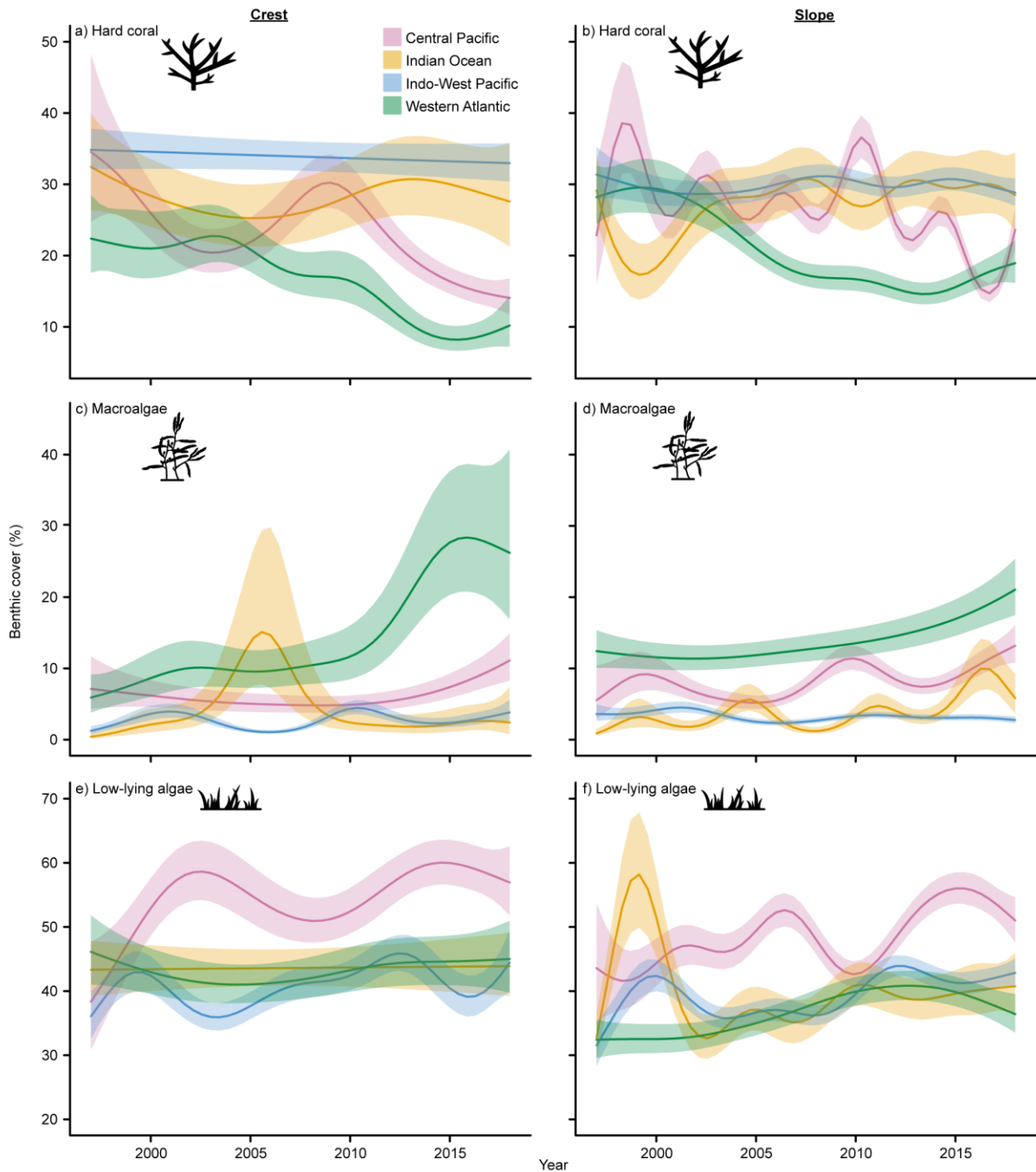
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664

665 **Figure 3 Hard coral, macroalgal and low-lying algal community dynamics in major**
 666 **marine realms.** The benthic cover of a) hard corals, b) macroalgae and c) low-lying algal
 667 communities on coral reefs in the Western Atlantic (n = 5071 cover observations for each
 668 benthic category), Indo-West Pacific (n = 8382 cover observations for each benthic category),
 669 Central Pacific (n = 8786 cover observations for each benthic category) and Indian Ocean (n
 670 = 1713 cover observations for each benthic category). Solid lines denote the mean fit from
 671 generalised additive mixed effects models, while shaded areas denote the 95% confidence
 672 intervals. All predictions are based on the mean depth across data (8.77 m). See Extended
 673 Data Fig. 2 for plots with varying y-axis ranges which allow patterns to be seen more clearly.
 674 Note that interpretation of the trends at the very start and end of the timeseries should be
 675 made with caution.

676



677

678 **Figure 4 Hard coral, macroalgal and low-lying algal community dynamics in key**
 679 **habitats across marine realms.** The benthic cover of a, b) hard corals, c, d) macroalgae and
 680 e, f) low-lying algal communities on reef crest (0-5 m) and slope (5-15 m) habitats in the
 681 Western Atlantic (n = 533 and 2090 cover observations for each benthic category in each
 682 habitat, respectively), Indian Ocean (n = 326 and 1046 cover observations for each benthic
 683 category in each habitat, respectively), Indo-West Pacific (n = 2219 and 4791 cover
 684 observations for each benthic category in each habitat, respectively) and Central Pacific (n =
 685 1372 and 4147 cover observations for each benthic category in each habitat, respectively).
 686 Solid lines denote the mean fit from generalised additive mixed effects models, while the
 687 shaded areas denote the 95% confidence intervals. Note that the y-axis ranges differ across
 688 benthic categories to better illustrate among-realm variability.

689

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