Article

Benthic composition changes on coral reefs at global scales

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

The pace and spatial extent of ecosystem transformation is expected to increase in the Anthropocene as the strength of human-mediated stressors intensifies[1–3]. The magnitude of these stressor effects is so large that it has led to suggestions that returning altered ecosystems to configurations of the recent past may be an unattainable goal[4–6]. Instead, the primary goals now are to maintain the functions that sustain these ecosystems, and to secure the services that they deliver to people, even in their highly altered configurations[4–6]. A prerequisite to these goals is an understanding of the variability in the structure of altered ecosystems at a global scale.

These challenges are epitomized by coral reefs, vulnerable ecosystems at the forefront of environmental transformations[7–9]. Climate change is foremost among the stressors modifying these ecosystems, with repeated mass coral bleaching events at global spatial scales[10,11]. It is inevitable that coral reefs of the future will be different and will continue to change. These changing configurations may have far-reaching

consequences for marine biodiversity[12], reef ecosystem functions[13] and the hundreds of millions of people that rely on coral reefs for services[14,15]. Clearly, if we are to manage reefs through these changes, we need to understand their likely composition in the near future. Given the spatial and temporal scope of the stressors currently acting upon coral reefs, this understanding must be at a global scale.

To gain an insight into likely coral reef composition in the near future, and to identify the most pressing future research endeavours, we need to answer two relatively straightforward questions: (1) how is the benthic composition of coral reefs changing at a global scale? and (2) how, and to what extent, do these changes vary among the world's marine realms? In this Article, to explore these questions, we compiled an extensive, global dataset composed of 24,468 observations of mean coral reef benthic composition. These observations spanned 13,802 unique global positioning system (GPS) coordinates and 22 years from 1997 (that is, before the first global mass coral bleaching event[16]) until

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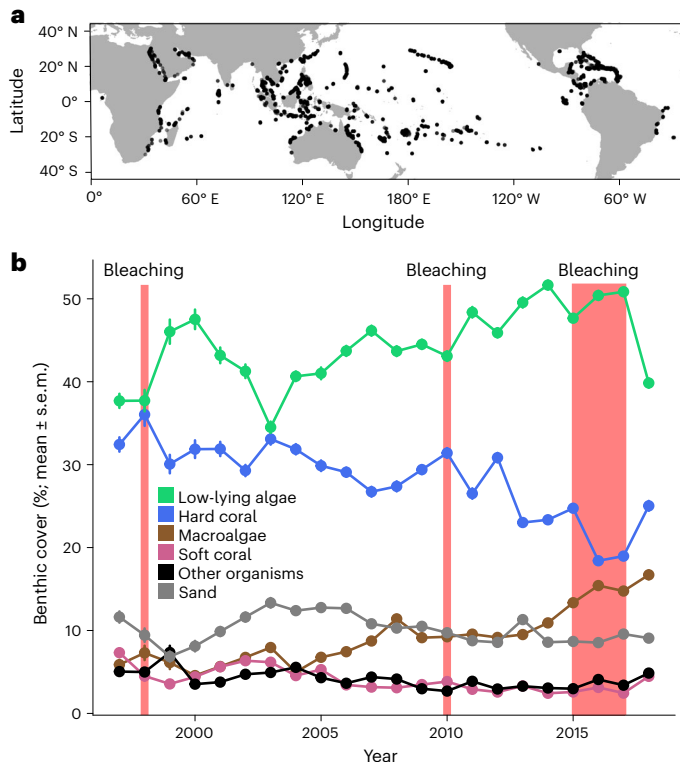
Fig. 1 | Benthic composition of the world's coral reefs. a, World map showing the spatial extent of coral reef benthic composition data ($n = 24{,}468$ data points). **b**, The mean (± s.e.m.) percentage cover of the six benthic categories in the global dataset ($n = 424, 269, 256, 331, 508, 700, 733, 970, 831, 1{,}259, 1{,}196, 1{,}193, 1{,}355, 1{,}239, 1{,}071, 1{,}303, 1{,}787, 1{,}639, 2{,}320, 1{,}914, 1{,}932$ and $1{,}238$ cover observations for each benthic category in each year from 1997 to 2018, respectively). The red vertical lines denote the three global bleaching events (1998, 2010 and 2015–2017) that occurred during this period (based on ref. [16]). Note that this figure represents an initial visualization of the raw data in its entirety; subsequent analyses (Figs. 2–4) explore spatial variability in more detail.

2018 (that is, a year after the most recent global coral bleaching event[16]). They encompassed all major reef regions across 60° of latitude (Fig. 1a).

Results

Reef benthic composition data—a global overview

An initial exploration of the dataset suggests that, from 1997 to 2018, variation in the benthic composition of the world's coral reefs has largely been typified by the dynamics of reef-building scleractinian corals (that is, hard corals) and low-lying algal communities (Fig. 1). Indeed, this initial visualization shows low-lying algal communities largely replacing hard corals on reefs as their cover decreased, especially in the past decade (Fig. 1b). Interestingly, there is also a signal in the data that is potentially related to the three global mass coral bleaching events; in the year following each bleaching event, there was a decrease in hard coral cover and a concomitant increase in low-lying algal cover (Fig. 1b). Overall, from the onset of the first global bleaching event (1998) to the end of the most recent event (2017), the global average (± standard error of the mean (s.e.m.)) of hard coral cover decreased from $36 \pm 1.4\%$ to $19 \pm 0.4\%$, while low-lying algae cover increased from $37.7 \pm 1.3\%$ to $50.8 \pm 0.5\%$, although for the full temporal span of our analysis (1997–2018), the average hard coral cover decreased from $32.4 \pm 0.9\%$ to $25 \pm 0.6\%$, while low-lying algal cover increased from $37.7 \pm 0.9\%$ to $39.8 \pm 0.6\%$ (Fig. 1b). This decrease in coral cover is expected; widespread coral mortality typically follows mass bleaching events[17,18]. However, the increase in low-lying algae has not

been well documented in previous global-scale studies of coral reef change. These low-lying algal communities range from biofilms and crustose coralline algae (CCA) to long sediment-laden algal turfs (for a comprehensive discussion of this continuum of algal groups, and a justification for pooling them in this study, see Supplementary Text 1 and Supplementary Figs. 1–4), and they are poorly captured in most existing coral reef data, frequently being lumped together as 'dead coral', 'pavement' or even 'bare space' (Supplementary Fig. 1). This situation limits our capacity to divide them further and make more informed inferences about how they relate to coral loss (Supplementary Text 1). However, once corals are lost, it is these low-lying algal communities, especially algal turfs and cyanobacteria, that generally fill the vacated space[18,19], with such reef conditions often being perceived as 'degraded' (that is, low coral cover)[20,21].

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

Reef benthic composition among realms

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

Among-realm dynamics of key benthic categories

Given the overwhelming contribution of hard corals, low-lying algal communities and macroalgae to benthic dynamics and associated changes (Figs. 1 and 2), the among-realm variation of these key benthic
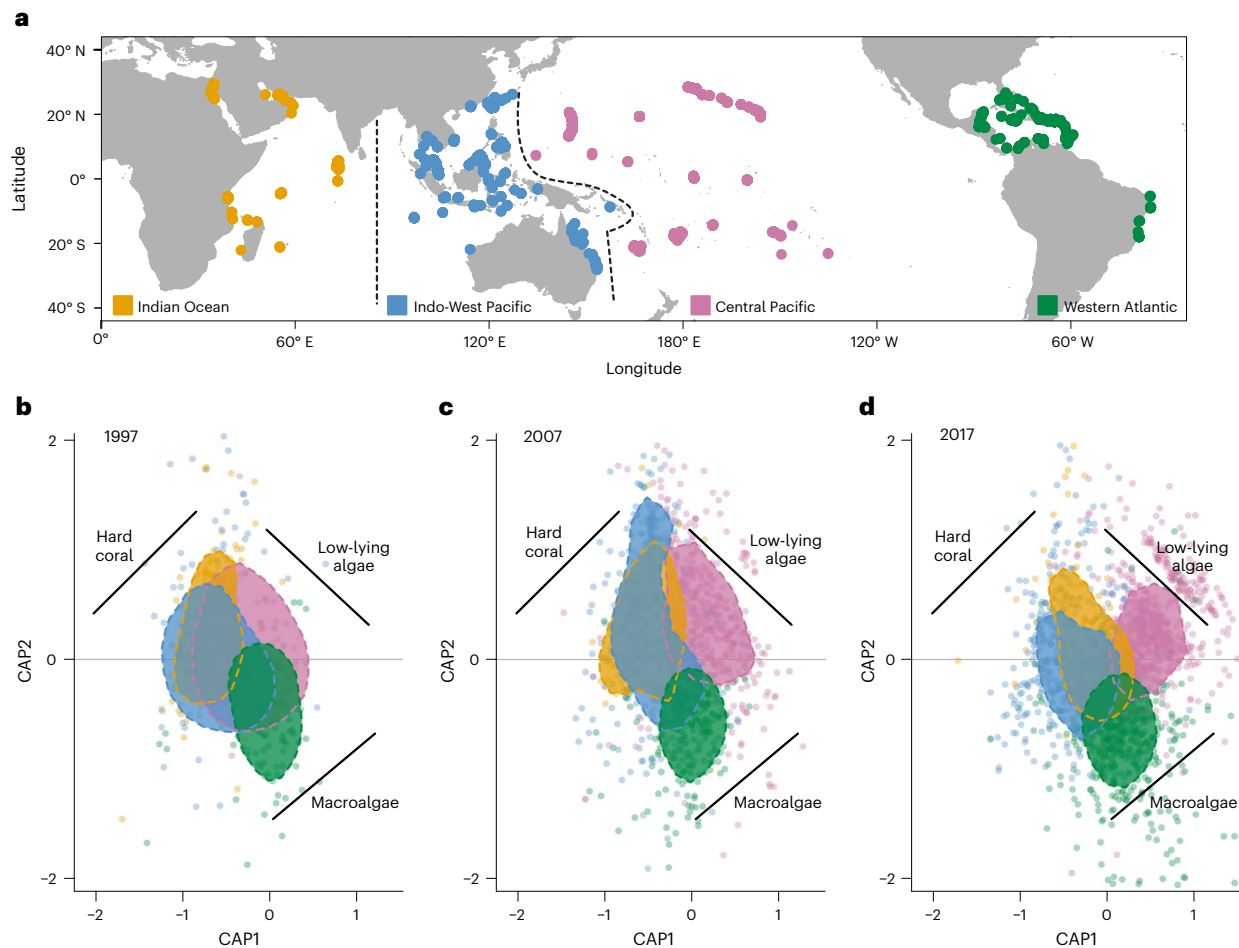
Fig. 2 | Coral reef benthic composition among major realms. a, World map showing the delineation of the major marine realms based on the data from 1997, 2007 and 2017 used in the ordination plots (n = 424, 1,102 and 1,924 benthic composition observations each year, respectively). **b–d,** Multivariate ordination plots based on the Morisita–Horn index and constrained by realm, habitat, year and depth, showing coral reef benthic composition in the four realms in 1997 (**b**), 2007 (**c**) and 2017 (**d**). The coloured polygons (matching the realm colours in **a**) in the ordinations are based on 50% kernel density distributions, denoting where the data points are concentrated in multivariate space. CAP1 and CAP2 refer to constrained analysis of principal coordinates axes 1 and 2, respectively. The lines in **b–d** denote the areas of multivariate space typified by the three major benthic categories, while the area in the bottom left corner of each panel is typified by soft corals, sand and 'other' organisms (for details, see Extended Data Fig. 1). For a version of this figure with full data points, vectors of each benthic component, and vectors of constraining factors (realm, habitat, year and depth) refer to Extended Data Fig. 1. For ordination plots with different start and end years, see Supplementary Figs. 5 and 6 .

categories clearly warrants more detailed examination. To do this, we used generalized additive mixed-effects models (GAMMs) to specifically focus on the dynamics of hard corals, macroalgae and low-lying algal communities from 1997 to 2018 (Fig. 3 and Supplementary Fig. 7). These models revealed a trend of decreasing hard coral cover in the Western Atlantic and Central Pacific, with limited net change in the Indo-West Pacific and Indian Ocean (Fig. 3a, Extended Data Fig. 2a and Supplementary Table 2). In the Western Atlantic, along with coral loss, there has been a concomitant non-linear increase in macroalgal coverage (F value = 13.68, P < 0.001; Fig. 3b, Extended Data Fig. 2b and Supplementary Table 2). Thus, it is likely that this increase in macroalgae in the Western Atlantic is underpinning the signal of increasing macroalgal cover at a global scale (Fig. 1). This is because macroalgal cover has remained consistently low in the Indo-West Pacific and Central Pacific (Fig. 3b and Extended Data Fig. 2b), with only a small, but strongly fluctuating, net increase in the Indian Ocean (Fig. 3b and Extended Data Fig. 2b). Unlike in the Western Atlantic, coral loss in the Central Pacific has largely been associated with a concomitant change in the cover of low-lying algal communities (Fig. 3c, Extended Data Fig. 2c and Supplementary Table 2). Given that many reefs in the

Indo-West and Central Pacific have been repeatedly subjected to a wide array of stressors, including repetitive mass coral bleaching events and widespread coral mortality[10,11], we would have expected a more detectable signal in the data if macroalgae were going to increase in these realms. We conclude, therefore, that the dynamics between hard coral and macroalgal cover differ markedly between the Western Atlantic versus Indo-West, Central Pacific and Indian Ocean realms.

It is important to note that these general inferences were found to be robust when the influence of potential confounding factors were explored. Specifically, we performed additional GAMMs to examine if model trajectories differed substantially when: (1) the data were pooled at two increasingly coarse spatial resolutions (that is, to explore if sample size and/or if numerous data points in close proximity were influencing patterns) (Supplementary Figs. 8 and 9 and Supplementary Table 3), (2) only a subset of the benthic composition data were used (to explore susceptibility to collection methods) (Supplementary Fig. 10 and Supplementary Table 4) and (3) variation of the temporal extent (to explore sensitivity to start and end years) (Supplementary Fig. 11 and Supplementary Table 5). In all cases, the general trajectories of hard coral, macroalgae and low-lying algae cover

across realms were maintained, or even strengthened, suggesting that our inferences were robust. Additionally, we explored the dynamics of the other benthic categories that made up the dataset (that is, soft corals, other organisms and sand) through time and across depths (Supplementary Fig. 12 and Supplementary Table 2). However, as these benthic categories made up only a minor fraction of benthic composition (often less than 5% of average benthic cover) and/or there was limited net change through time (Supplementary Fig. 12), we have not expanded on the discussion of these findings herein.

## Habitat- and depth-specific dynamics of key benthic categories

Beyond realm differences, the largest ecological gradients on coral reefs are often cross-habitat or cross-depth gradients[24]. It is for this reason that these factors were specifically accounted for in our analysis of hard coral, macroalgae and low-lying algae cover trajectories across realms, and the trends presented above are standardized for such effects. However, given the extent of variation that may occur across these gradients, further detailed analysis was warranted. To do this, we focused on two habitats that were generally the most frequently sampled in each of the four realms (Extended Data Fig. 3 and Supplementary Fig. 13): the reef crest (0–5 m) and upper reef slope (5–15 m). On the basis of these habitat subsets, we performed the same analyses as above, to explore benthic trajectories through time across realms.

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

Discussion

The change in coral reef benthic composition is generally associated with the loss of hard scleractinian coral cover[7,20,25]. In this respect, our results are consistent with previous studies. For example, the long history of declining hard coral cover in the Western Atlantic, especially in the Caribbean, is well established in the literature[26–28]. Our results suggest that the declines documented in earlier studies in this realm[26,27] have continued, with the low levels of 10–15% coral cover in our study aligning well with recent reports[29]. Moreover, the relative stability of hard coral cover during this period (1997–2018) in the Indo-West

Pacific[30] as well as in the Indian Ocean (with the notable exception of the 1998 bleaching event)[31], has been previously documented, with our levels of 25–30% also aligning well with recent reports from these regions[29]. Nevertheless, our study differs from these past studies as we separated algal forms and highlight that increasing cover of tall macroalgae is largely restricted to the Western Atlantic, with ramifications for how we perceive coral reef change globally. However, it is important to highlight that our study, along with the previous studies,
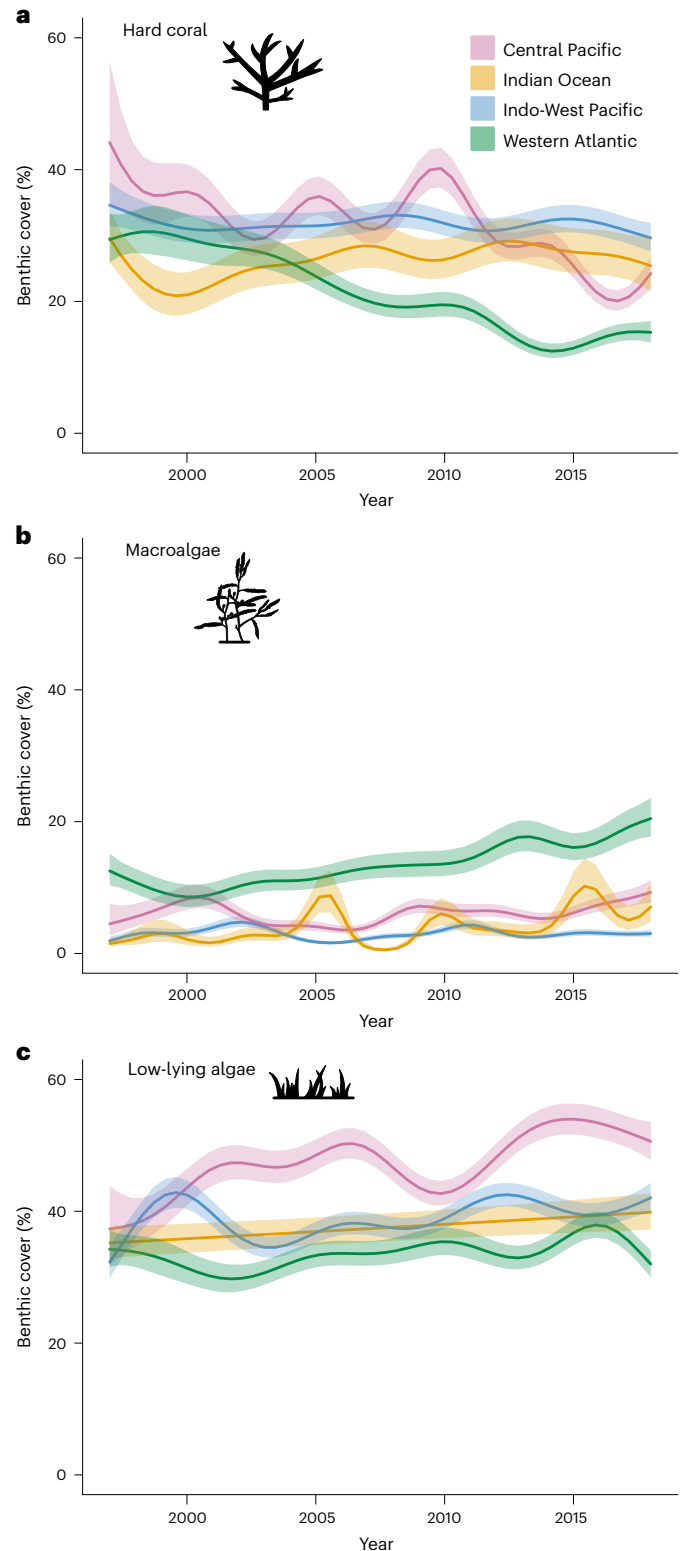
Fig. 3 | Hard coral, macroalgal and low-lying algal community dynamics in major marine realms. a–c, The benthic cover of hard corals (**a**), macroalgae (**b**) and low-lying algal communities (**c**) on coral reefs in the Western Atlantic (*n* = 5,071 cover observations for each benthic category), Indo-West Pacific (*n* = 8,382 cover observations for each benthic category), Central Pacific (*n* = 8,786 cover observations for each benthic category) and Indian Ocean (*n* = 1,713 cover observations for each benthic category). Solid lines denote the mean fit from GAMMs, while shaded areas denote the 95% confidence intervals. All predictions are based on the mean depth across data (8.77 m). For plots with varying *y*-axis ranges that allow patterns to be seen more clearly, see Extended Data Fig. 2. Note that the trends at the very start and end of the time series should be interpreted with caution.
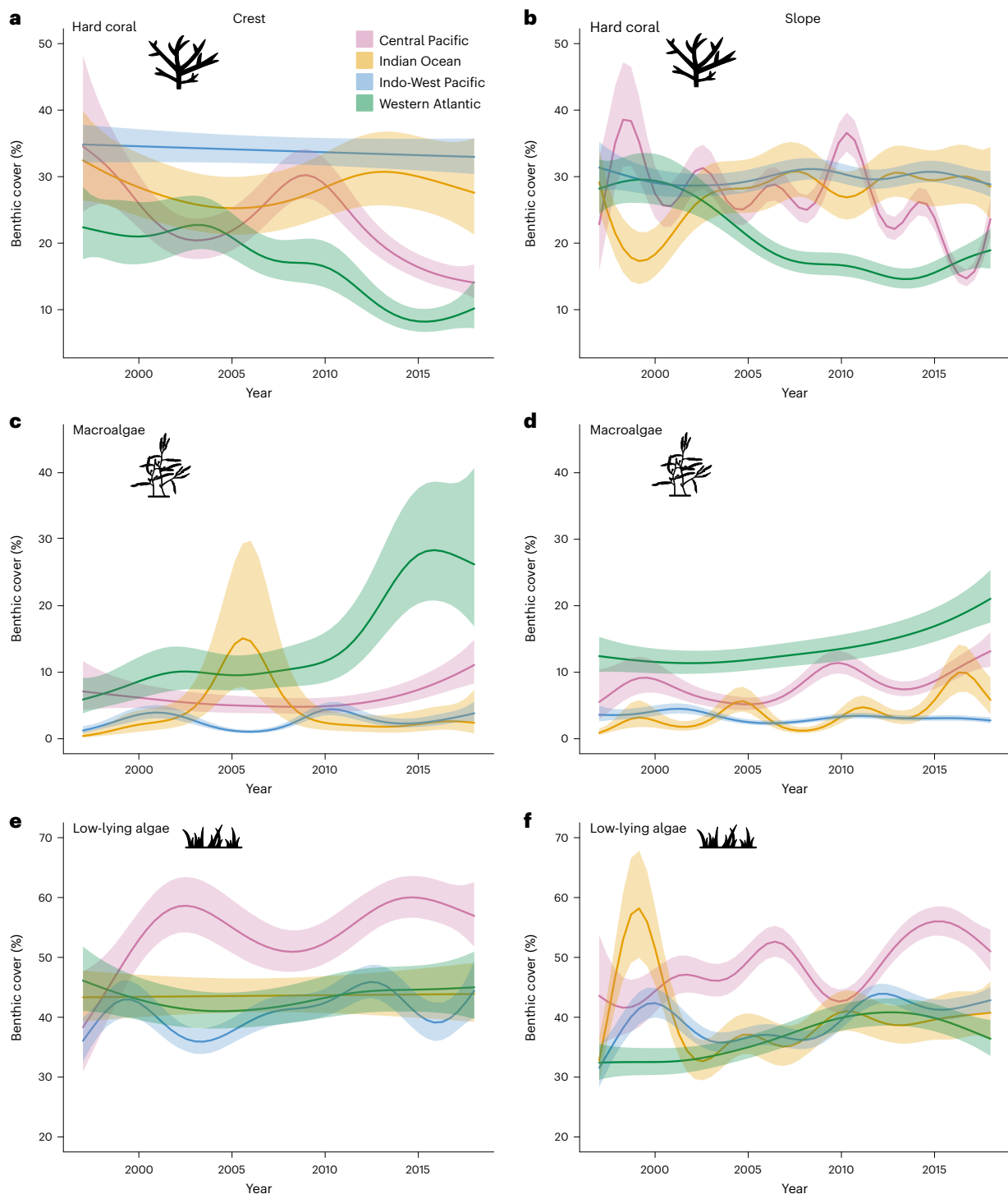
Fig. 4 | Hard coral, macroalgal and low-lying algal community dynamics in key habitats across marine realms. a–f, The benthic cover of hard corals (**a** and **b**), macroalgae (**c** and **d**) and low-lying algal communities (**e** and **f**) on reef crest (0–5 m) and slope (5–15 m) habitats in the Western Atlantic (n = 533 and 2,090 cover observations for each benthic category in each habitat, respectively), Indian Ocean (n = 326 and 1,046 cover observations for each benthic category in each habitat, respectively), Indo-West Pacific (n = 2,219 and 4,791 cover observations for each benthic category in each habitat, respectively) and Central Pacific (n = 1,372 and 4,147 cover observations for each benthic category in each habitat, respectively). Solid lines denote the mean fit from GAMMs, while the shaded areas denote the 95% confidence intervals. Note that the y-axis ranges differ across benthic categories to better illustrate among-realm variability.

represents realm-wide average trends, with changes within specific locations potentially diverging from these trajectories[27,29].

Importantly, we also explored how benthic trajectories varied in reef crest and slope habitats within realms. In doing so, we revealed that the trajectories were quite consistent across these two habitats,

but that there were some key differences in the magnitude of benthic change. Such differences probably relate to a range of abiotic (for example, light levels and wave exposure) and biotic (for example, herbivory and competition) factors that may vary across habitats (that is, at a scale of tens of metres). Unfortunately, we were only able

to explore benthic trajectories in reef crest and slope habitats owing to the relative paucity of benthic data from other habitats (Extended Data Fig. 3). While the only habitat/depth-related restriction we placed on the inclusion of data in our study was that it had to be collected at depths shallower than 30 m, most data (76%) came from reef crest and slope habitats (Extended Data Fig. 3). By contrast, just 7% of data were derived from reef flat habitats (Extended Data Fig. 3), despite this habitat generally being the most expansive (by areal extent) on coral reefs[32]. Interestingly, the same patterns have recently been described for research on reef fishes[32], suggesting that, as a whole, research on reefs is focused on a subset of habitats, potentially resulting in an incomplete understanding of how they function[33].

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

Nevertheless, given a situation of relatively low, and in some cases decreasing, hard coral cover on reefs in recent decades, we might ask: what benthic category is replacing corals? This is where our study differs from many previous studies, particularly those at a similar spatial scale, as we specifically endeavoured to separate large (that is, taller than approximately >2 cm) macroalgae from low-lying algal forms (for example, CCAs and turfs). Previous global data compilations have largely focused on 'algae' cover, with the constituent algal groups (tall macroalgae, turf algae, CCA and so on) often being unclear[22,29]. Indeed, it is exactly this lack of resolution from past studies that hinders the inclusion of more specific categories herein, and why our division of algal categories was limited to macroalgae versus low-lying algae (for a discussion about problems with the historical quantification of low-lying algae in coral reef monitoring, see Supplementary Text 1). However, this division between macroalgae and low-lying algae was sufficient to reveal that, while 'algae' may be increasing on many reefs globally[29], in most cases this is not tall macroalgae but rather low-lying algae, such as turfs. Moreover, increases in macroalgal cover are largely restricted to Western Atlantic reefs (Figs. 2–4 and Extended Data Fig. 5). This has important implications for our understanding of changing coral reefs.

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

Marked differences in biodiversity and functional diversity between the Indo-West Pacific and the Western Atlantic[20,36] stem from their fundamentally distinct biogeographical histories[38,39]. For instance, these realms differ more than three- and seven-fold in their diversity of fishes and scleractinian corals, respectively[20]. Importantly, these disparities could explain some of the variation in benthic composition trajectories between the Indo-West Pacific and the Western Atlantic. Many fast-growing *Acropora* coral growth forms, which drive early coral recovery on Indo-West Pacific reefs[20,40], as well as functional groups of key herbivorous fishes that may be key in controlling macroalgae proliferation (for example, crevice cleaning surgeonfishes/rabbitfishes and browsing rabbitfishes/nasine surgeonfishes)[36,41], are completely lacking in the Western Atlantic. This potentially predisposes Atlantic reefs to much higher macroalgal cover following coral loss. Consequently, the modern-day configurations of both fish and benthic communities on reefs in each realm could ultimately be rooted in historical biogeography, with the influence of these drivers being concatenated in the 'realm' factor in our analyses.

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

Given a situation where macroalgae may not be the major benthic category replacing corals on Indo-Pacific reefs, it is critical to consider what the functional implications of more extensive low-lying algal cover may be. To do this, we first need to recognize that these low-lying algal communities are by no means homogeneous. They exist on a continuum ranging from biofilms and CCAs, through sparse algal turfs and CCAs, to long sediment-laden algal turfs (for a full discussion, see Supplementary Text 1 and Supplementary Figs. 2–4). Where the state of low-lying algal communities falls along this continuum may have a variety of implications for future reefs and how they function. These include core ecosystem processes such as coral recruitment, herbivory/productivity and calcification[13]. For example, a benthic condition typified by low-lying algal communities composed of high CCA and/or short well-cropped algal turf cover is not resistant to the return of corals via recruitment after a disturbance[18,42–44]. By contrast, long sediment-laden algal turfs can inhibit coral settlement, growth and, as a consequence, the recovery of coral cover[42,43], mirroring reef states typified by high macroalgal cover[42,44,45]. Management actions that aim to maintain low-lying benthic communities typified by CCA and short algal turfs may thus be beneficial, until climate change is addressed and/or corals adapt, to facilitate the return of corals to reefs via recruitment.

In addition to being a more favourable benthic state for coral recruitment, coral reefs typified by a high cover of low-lying algal communities may also benefit the provision of some other key services. For example, fisheries catches in many reef locations are already heavily composed of fishes that derive their nutrition from components of low-lying algal communities[46,47]. Indeed, compared with macroalgae, low-lying algal communities generally provide a broader range of nutritious resources (for example, algal turfs, detritus and biofilms) that are fed on by a wider diversity of fishes[48]. Therefore, maintaining highly productive, short algal turf communities may be important in sustaining fisheries catches in some areas, although this is inherently linked to the quantity of sediments in low-lying algae[49]. Moreover, a decrease

in coral cover and coral-derived calcification in the future[50] may mean that the role of CCA in calcification and reef building also becomes more important. In this respect, the reef-building capacity of CCA is increasingly being recognized[33], with the suggestion that the substratum formed by CCA may be resistant to future climate change[51,52]. If the outlook for reefs is typified by high coverage of low-lying algal communities it may, therefore, be possible to maintain some key ecosystem functions within this configuration.

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

Methods

Benthic composition dataset compilation

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

On the basis of an initial examination of available data, and the manner in which previous studies and monitoring schemes had categorized the benthos, we selected six benthic categories to represent benthic composition: hard corals (generally considered scleractinian corals), soft corals (generally considered corals from the order Alcyonacea), macroalgae (generally considered algae approximately >20 mm in height[37,54] (Supplementary Fig. 3)), a low-lying algal community category (analogous to the 'crustose corralline algae, algal turf and bare space' category often used in past studies), which included algal turf/CCA/rubble/cyanobacteria/dead coral/bare substratum/rock (as benthic composition data rarely discriminated among these different benthic categories, a single category was used following refs. [18,55–57] to maximize data retention; for an extensive discussion on this, see Supplementary Text 1), other biotic organisms (for example, other biotic organisms that are found on reefs but are often not major constituents such as sponges, ascidians, seagrass and bivalves) and sand/sediment. It is critical to note that in all cases, we ensured the 'other' category did not comprise benthic categories often classed as 'abiotic' but are almost always covered in a constituent of the low-lying algal category (for example, algal turfs, CCA and cyanobacteria)[19,58–60]. Likewise, we ensured that all data had specifically monitored for 'other' biotic benthic components such as sponges and ascidians to ensure these were not erroneously included as constituents of the low-lying algal category. With these six benthic categories we were able to capture 100% of the coral reef benthic community composition (that is, we did not focus on just a subset of the biotic benthic community). We relied on these major divisions to maximize the resolution in the dataset, while minimizing the amount of data that had to be excluded because it was collected at a coarser resolution. Indeed, given the varied nature in how the benthos has been categorized globally (as discussed in Supplementary Text 1), this relatively coarse categorization scheme helped with our endeavour to standardize benthic categories to the best of our ability given the available data. However, important additional insights can be realized if future work prioritizes a finer-resolution categorization of the benthos. We recommend that a standardized global scheme for categorizing the benthos (with careful consideration of how various low-lying algal groups are classified) would substantially improve the utility of coral reef monitoring programmes.

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

To complement the data from these databases and to ensure that our dataset was as comprehensive as possible, we then undertook an extensive formal search of the literature for available data. Our search and filtering process was based on preferred reporting items for systematic reviews and meta-analyses protocols[61], and a flow diagram outlining each step is provided in the supplementary material (Supplementary Fig. 15). This was achieved using the search engine Google Scholar and the search terms 'coral reef' AND benthic AND percent AND (transect OR quadrat). This search yielded 14,900 total results on 20 May 2020 (not including patents or citations). Note that, in contrast to searches in databases such as Web of Science and Scopus, these search terms take advantage of Google Scholar's default setting to search within the full text of documents. Therefore, for example, the use of terms such as 'transect' do not limit the papers returned to methods papers containing this term in the title, abstract or keywords of documents.

We evaluated these 14,900 documents on the basis of their title and abstract for any potentially relevant documents. This process identified a subset of 1,748 potentially relevant documents for further investigation. Each of these documents was then examined in detail and the suitability of their data for inclusion in our dataset was assessed against a set of criteria. Acceptance criteria were as follows: (1) sampling was conducted on a coral reef system within our definition of a coral reef (that is, ±30° of latitude from the Equator and 0–30 m water depth), (2) the document contained benthic community composition data at sufficiently fine resolution to fit into our six benthic categories in a form that we could extract (that is, raw data, tables or from figures), with no missing data/benthic categories, (3) the data were pooled at the scale of the sampling site or a finer spatial scale (that is, data across individual sampling sites were not pooled and presented together), (4) the data presented in the manuscript had not already been included in our database from another source, (5) sufficient detail was presented in the document that outlined the sampling location, depth, time and methods used and (6) there was no clear selection of study sites to meet predefined criteria (for example, if a study specifically selected for 'high coral cover' sites, it was not included).

We relied on the criteria above to ensure that: (1) the ecosystem sampled was consistent across data, (2) the data covered the entire coral reef benthos, (3) among-site level variation was not averaged out, (4) we did not include the same data twice, (5) we had sufficient information on the sampling to explain any patterns in benthic

community composition and (6) any potential sampling biases associated with focused site selection were minimized. On this later point, it should be noted that coral reef research in general often focuses on coral-dominated rather than algae-dominated habitats[22,62], with the habitats most frequently sampled by coral reef researchers (that is, slope and crest; Extended Data Fig. 3) often having the highest coral cover[32]. This means that, in most coral reef research, a decline rather than recovery in coral cover is likely to be documented (also see ref. [62]). After this second extensive filtering process, we were left with a subset of 83 studies that contained relevant data for our dataset (for a full list of references, see Supplementary Text 3). The vast majority of documents (1,449) simply did not contain the necessary data (that is, most only reported 'coral cover' or 'algae cover' rather than complete benthic community composition).

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

Database cleaning and checking

With the compiled database at hand, we undertook a quality-control procedure to check the data. To do this, we manually checked each data point. Specifically, we ensured that (1) the six benthic categories were standardized (that is, they added up to 100%), (2) the latitude and longitude data were accurate (we checked this by examining each individual set of coordinates in Google Earth), (3) each data point had a corresponding depth (in metres) and year sampled value, (4) the method used to collect each data point was categorized (line intercept transect, point intercept transect, chain intercept transect, photo quadrats along a transect, in situ quadrats or analysis of individual frames from a video; it is important to note that the vast majority of data were derived from one of two planar point-based methods (point intercept transect or photo quadrats along a transect with subsequent examination using points)) (Supplementary Fig. 16), (5) the habitat sampled was categorized as either reef flat, lagoon, slope, back reef, crest or submerged reef (where this information was not presented we placed the data point into a category based on its depth and satellite imagery in Google Earth) and (6) the location of each data point was also designated into a category within three increasingly fine spatial scales: biogeographic realm ($n = 6$), ecoregion ($n = 20$) and geographic unit ($n = 113$) (Supplementary Fig. 17 and Supplementary Table 7). Realm and ecoregion classifications were based on the schemes presented in refs. [64,65], while the geographic unit level was primarily based on the country from where the data were sourced; however, where data were from large countries, remote territories or clustered island groups, we used more informative, finer-scale categorization within the country level (Supplementary Fig. 17 and Supplementary Table 7). Following this final quality control procedure, our time series dataset contained 24,674 unique data points representing mean coral reef benthic community composition spread across more than 40 years of sampling (1977–2018).

Data analyses

All statistical analyses and data handling were performed in the software R (ref. [66]). Initially, we filtered our data to retain data from 1997 to 2018. Even though our dataset spanned 1977–2018, there were very few data points before 1997 (only 0.83% of all data in the dataset were from

the 20 year period from 1977 to 1996 (Extended Data Fig. 4)), making any inferences based on this early data difficult. It is important to note that all analyses described below are focused on examining if there had been change in the cover of benthic categories over this multidecadal timespan (that is, long-term, continuous change). Therefore, we were not studying change from the perspective of 'regime shifts' or 'phase shifts' nor assessing for 'alternative stable states'. Given that these topics are still debated in the literature (for example, refs. [67,68]) and/or their definitions can be unclear[62], they are outside of the scope of the present study.

To examine variation in benthic composition, we initially utilized multivariate analyses. Specifically, we explored how the composition of all six benthic categories varied across the four realms with most of the data (Central Pacific, Indian Ocean, Indo-West Pacific and Western Atlantic; Extended Data Fig. 4) in 1997, 2007 and 2017. We based our analysis on these 3 years as 1997 represented the earliest year in our retained dataset, while 2007 and 2017 were equidistantly spaced apart, and covered most of the temporal scope in our dataset (for analysis and ordination plots based on different start and end years (1998 and 2016, 1999 and 2015) using the same methods as outlined here, refer to Supplementary Figs. 5 and 6 and Supplementary Table 1). A 10 year period was chosen to limit any influence of temporal autocorrelation. On the basis of these 3 years of data, we then calculated a dissimilarity matrix based on the Morisita–Horn index (as this is robust when sample sizes differ[69]). We then explored if the key variables of habitat, depth, year and realm were correlated with the multivariate space using a permutational multivariate analysis of variance (package: vegan[70]). To visualize the results, we then produced a constrained analysis of principal coordinates ordination plot (package: vegan[70]), which was constrained by the key variables that were correlated with the multivariate benthic composition data. It should be noted that, to ensure the axes were directly comparable, the multivariate analysis was conducted as one analysis (that is, all 3 years together) and only the results were plotted separately by year. To aid interpretation, we then calculated 50% kernel density estimates for each realm in each year (package: adehabitatHR[71]). Calculating kernel density estimates is a technique that has been popularized in the field of animal movement to describe the probability of animal detections in a space and to delineate core areas[72]. Kernel density techniques are superior to convex hulls for visualizing patterns in multivariate spaces as they are not as sensitive to outlying data points[73]. Therefore, in our case, the 50% kernels indicate the core areas of the ordinations occupied by the individual sampling locations from each realm in each year.

On the basis of the ordinations, the specific examination of the temporal dynamics of each benthic category in the Western Atlantic, Indo-West Pacific, Indian Ocean and Central Pacific was warranted, especially given the history of comparing these realms in the coral reef literature (for example, refs. [20,36,40,41].). To do this, we utilized separate GAMMs (package: mgcv[74]) to examine temporal variation in the proportional cover of the six benthic categories separately in the four realms. We treated time (year sampled) as a continuous fixed effect with separate splines for each realm. In addition, to account for depth-related patterns, we fitted depth as a continuous fixed effect with separate splines for each realm. In all cases, we used thin plate splines for the fixed effects. We also fitted habitat and geographic unit as random effects using random effects smoothers. Method and ecoregion were not included in the models as they had a high level (>0.8) of concurvity with the other factors already included. For all models, we utilized a tweedie distribution with a log link function. A tweedie distribution was superior to a betabinomial distribution here owing to the nature of the data in all cases (that is, the data contained a large number of exact zeroes and the non-zero observations were continuous and positively skewed (and with very few observations at the upper bounds of the proportional dataset—that is, close to 100% cover)).

After fitting the GAMMs, we checked that a sufficient number of knots were used by checking if k and edf were close to each other, while considering the values of the k-index and simulated P value in gam.check[74]. In all cases, we initially relied on the default level of knots in each model ($k = 10$). However, where our knot checking procedure suggested that this was too restrictive, we increased k until it was indicated that enough knots had been used (the maximum value of k in any model was 15). In addition, we examined the residuals of both models for temporal autocorrelation. No meaningful patterns of temporal autocorrelation were detected. We also assessed the residuals of both models for spatial autocorrelation using variograms (package: gstat[75]), and compared these with variograms of the residuals from models containing only the fixed effects structure as well as variograms of the raw data (Supplementary Figs. 18–26). For all variograms we accounted for potential among-year differences by only comparing point pairs from within the same year, and we examined for patterns across multiple directional axes (that is, north–south; north-east–south-west; east–west; south-east–north-west). In all cases, our models accounted for spatial correlation and there were no clear patterns of concern (that is, increasing variance with increasing distance) in the residuals. We also examined model residuals using simulation-based model-checking (package: DHARMa[76]) and standard residual plots. In all cases, this indicated that the fit was satisfactory.

In addition to the GAMMs, which examined benthic trends in the entire dataset, we also specifically examined how hard coral, macroalgae and low-lying algal cover differed through time and among realms, separately, for the two most frequently sampled habitats (the crest (0–5 m) and the slope (5–15 m); only the upper slope was considered as data for deeper regions were relatively sparse for the Indian Ocean and Indo-West Pacific; Extended Data Fig. 3 and Supplementary Fig. 13). We specifically performed this comparison because cross-habitat and cross-depth gradients represent some of the strongest ecological gradients on coral reefs[24], and because treating habitat as a random effect (as in the original analysis) would not allow us to detect interactions between habitat and time or realm. Therefore, by comparing benthic trends among realms in the same habitats across narrow depth ranges, we could eliminate any results that might have been artefacts of differential representation of habitat types through time or among realms, and to detect whether there were differences in temporal trends or among-realm differences among habitat types. For each GAMM, we treated time (year sampled) as a continuous fixed effect with separate splines for each realm and geographic unit as a random effect using random effects smoothers. In all cases, we relied on the same model distributions and model validation procedures, as above. Additional packages used for graphical representation of the data included emmeans[77], tidyverse[78], sf[79], rnaturalearth[80], ggtern[81] and patchwork[82].

Sensitivity analyses

To ensure our GAMM results and associated inferences were robust, we undertook a suite of sensitivity analyses to explore if the results were being influenced by other confounding factors. These factors were (1) sampling effort/influential but spatially clustered data points, which may arise from methods such as numerous replicate samples in close proximity but with limited sampling effort for each replicate; (2) variation in the methods used to collect benthic cover data; and (3) the length of the time series examined, especially in terms of the first and last year given the timing of global bleaching events (that is, in 1998 and 2015–2017). Owing to the number of different GAMMs these sensitivity analyses entailed, we focused on the dynamics of the three primary benthic categories (hard corals, macroalgae and low-lying algal communities) that underpinned our main results and inferences.

To explore the influence of the first potential confounding factor (that is, influential data points/variation in sampling effort), we clustered the data (that is, re-calculated mean benthic cover of each benthic category) at two different spatial resolutions within the same habitats and year sampled: (1) the nearest 0.01° latitude and longitude and nearest 3 m depth ($n = 21,025$ data points) and (2) the nearest 0.1° latitude and longitude and nearest 3 m depth ($n = 13,837$ data points). In both cases we also recorded the number of individual data points that were used to calculate the new means in each grid cell. With these two spatially clustered datasets at hand, we then constructed new GAMMs using the same model structure, distributions and validation procedures as for the full GAMMs in the original analyses, above. To explore how robust the results were to sampling effort (that is, the number of data points underlying each mean calculated), we performed the above analyses twice, with and without weighting each mean by the number of points used to calculate it. By comparing the output of each set of analyses we could then determine how influential sample size was to our observations (if sample size was influential, one would expect results to diverge markedly).

To ensure our inferences were not biased by variation in sampling methods in the dataset, we produced a subset of benthic data that was collected using only a planar point-count approach (that is, point intercept transects or photo quadrats along a transect (where points are subsequently generated to estimate benthic cover)). We then constructed GAMMs using the same model structure as the full GAMMs in the original analyses. In addition, to ensure the temporal span of the data was not influencing the nature of our inferences, especially given that our first year (1997) in our time series was before the first global coral bleaching event, while the last year (2018) was after the latest global bleaching event had subsided, we re-fitted our GAMMs on three different subsets of the data with differing first and last years (1998–2017, 1999–2016 and 2000–2015). In all cases, we used the same model structure as the original analysis. For all GAMMs examining sensitivity to method or temporal factors, we relied on the same model distributions and model validation procedures as above for the original analyses. Furthermore, for all sensitivity analyses we used the same R packages as for the original analyses.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

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

Code availability

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

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Acknowledgements

Author contributions

S.B.T., S.R.C. and D.R.B. conceived the study; S.B.T. compiled the data; S.B.T. and S.R.C. conducted the analyses; S.B.T., S.R.C. and D.R.B. interpreted the analyses; S.B.T. drafted the initial version of the manuscript; S.B.T., S.R.C. and D.R.B. contributed to editing and revising the manuscript, approved the submitted version and agree to be personally accountable for their contributions.

Competing interests

The authors have no competing interests to declare.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41559-022-01937-2.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41559-022-01937-2.

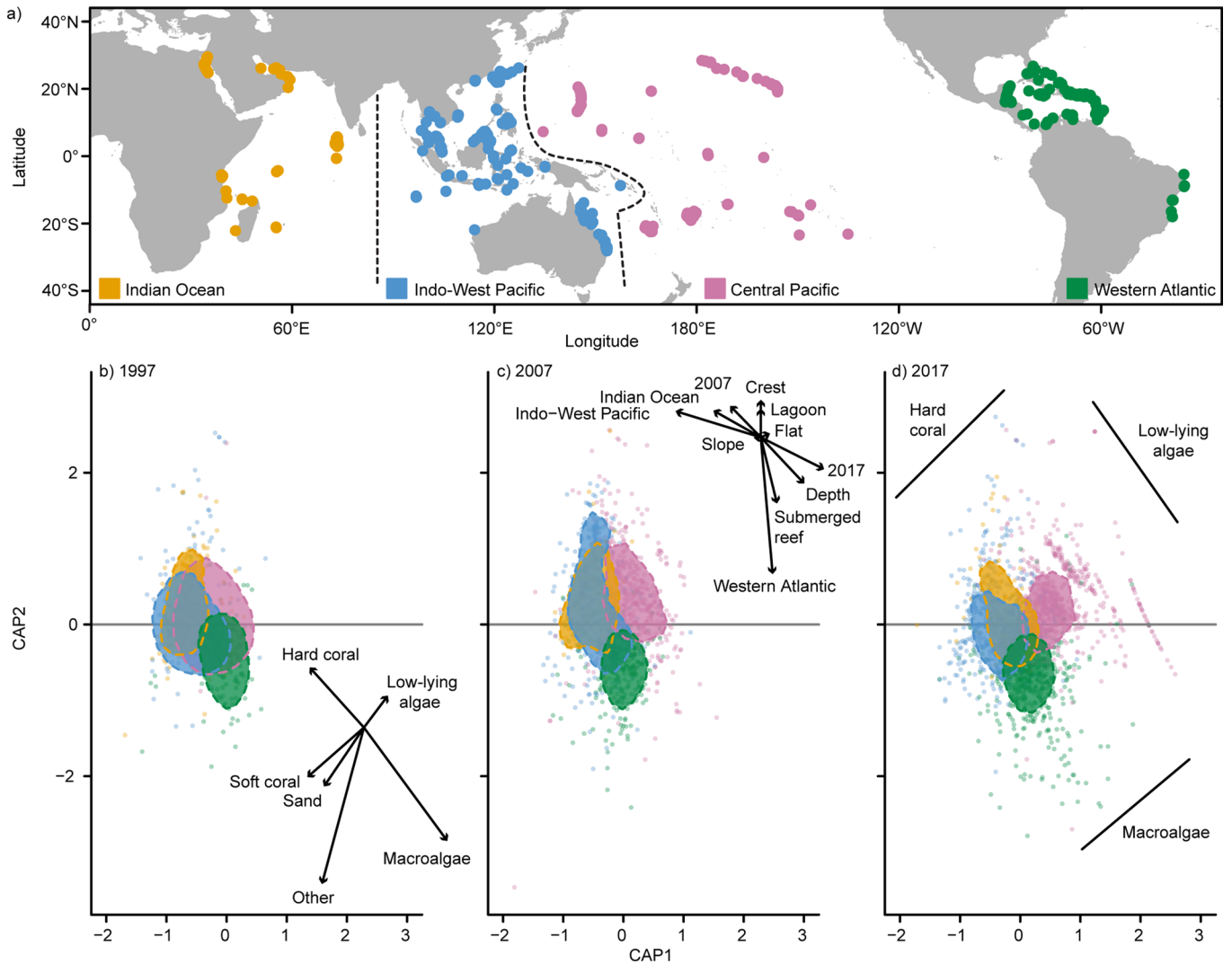**Correspondence and requests for materials** should be addressed to Sterling B. Tebbett.

Peer review information *Nature Ecology & Evolution* thanks Lorenzo Alvarez-Filip, Florian Roth and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

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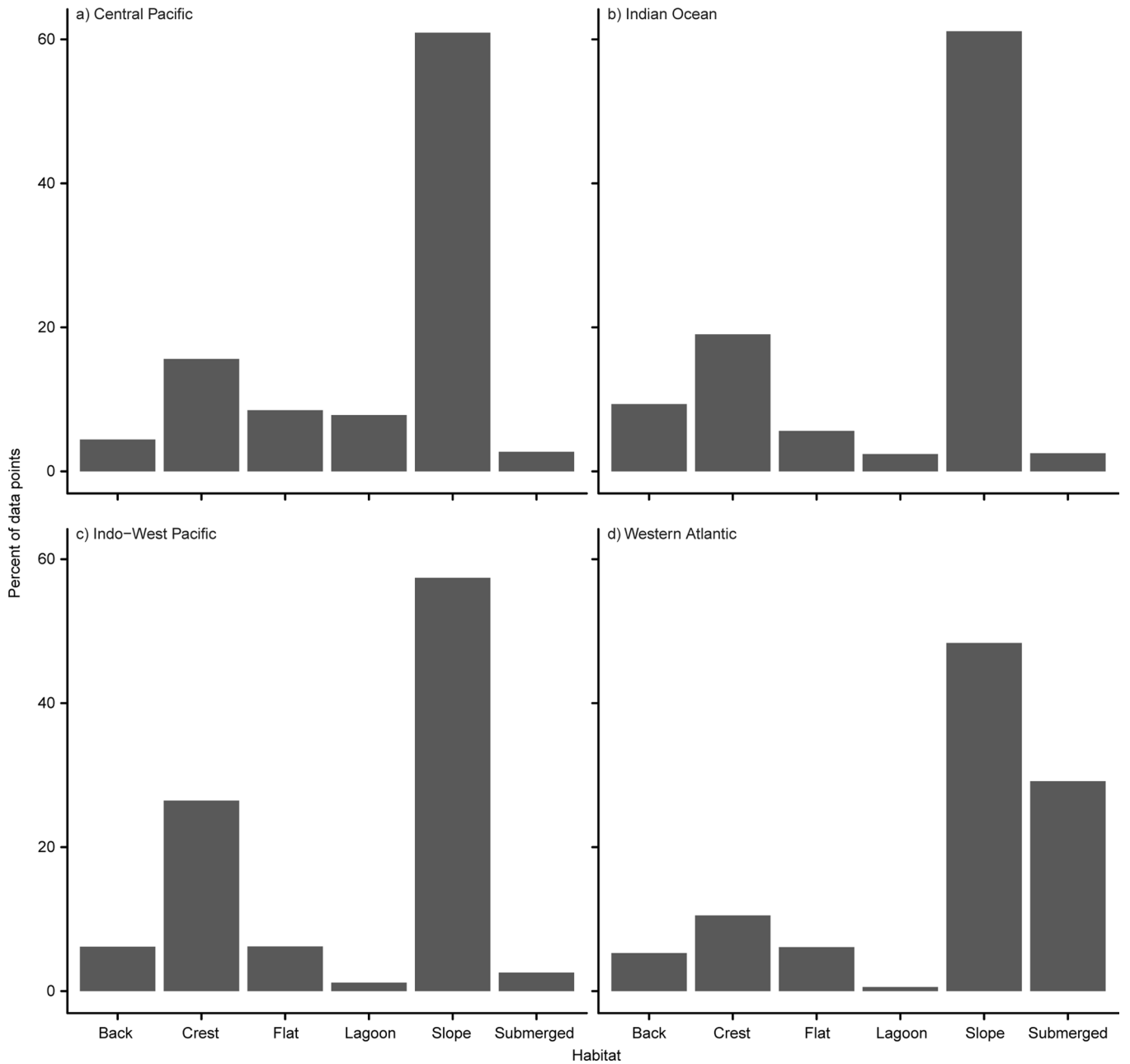**Extended Data Fig. 1 | Coral reef benthic composition among major realms.**
a) World map showing the delineation of the major marine realms based on the data from 1997, 2007 and 2017 used in the ordination plots (b–d). Multivariate ordination plots based on the Morisita–Horn index and constrained by realm, habitat, year and depth, showing coral reef benthic composition in the four realms in b) 1997, c) 2007, and d) 2017. The coloured polygons (matching the realm colours in [a]) in the ordinations are based on 50% kernel density distributions, denoting where the data points are concentrated in multivariate space. Note the vectors in b) show the relationship between the benthic categories and how they influence the benthic composition data points in the ordination plots. The vectors in c) show how the constraining factors correlate with multivariate space (note the strongest correlations are driven by differences across realms). The lines in d) denote the areas of multivariate space typified by the three major benthic categories.
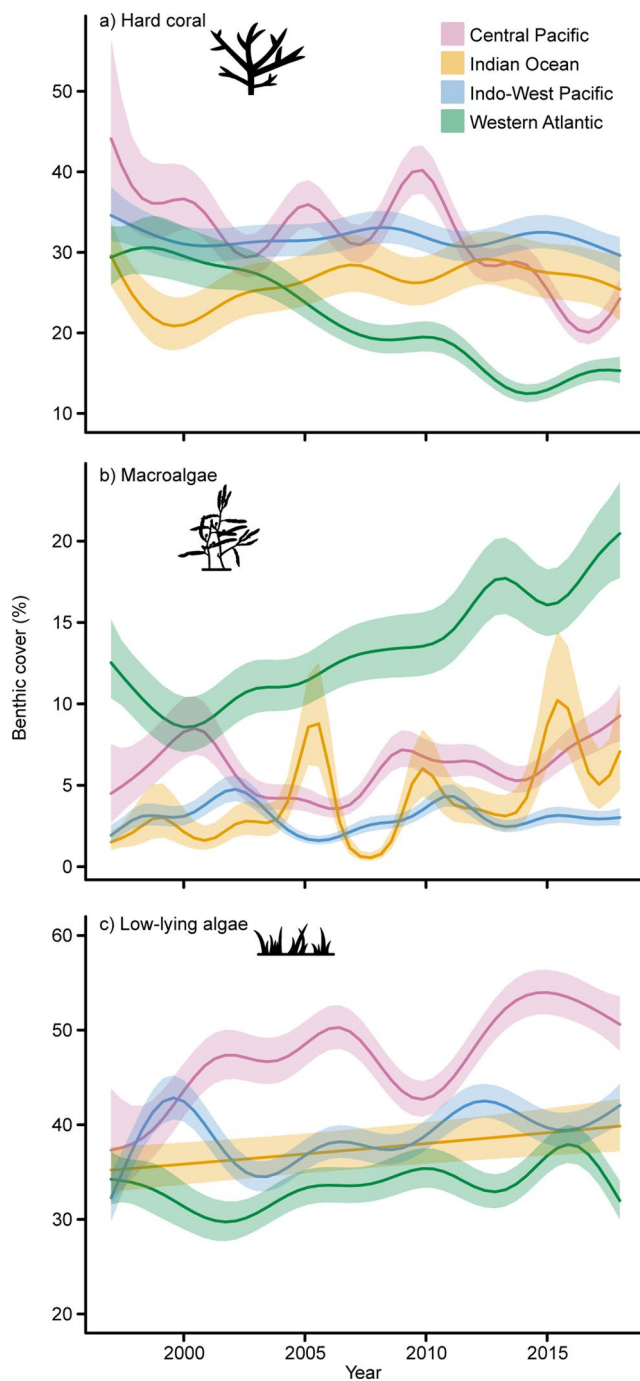
Extended Data Fig. 2 | Hard coral, macroalgal and low-lying algal community dynamics in major marine realms with varying y-axis ranges. The benthic cover of a) hard corals, b) macroalgae and c) low-lying algal communities on coral reefs in the Western Atlantic (n = 5071 cover observations for each benthic category), Indo-West Pacific (n = 8382 cover observations for each benthic category), Central Pacific (n = cover 8786 observations for each benthic category) and Indian Ocean (n = 1713 cover observations for each benthic category). Solid lines denote the mean fit from generalised additive mixed effects models, while the shaded areas denote the 95% confidence intervals.

Extended Data Fig. 3 | Relative frequency distribution of the benthic composition data among habitats. Frequency distribution of benthic composition data (1997–2018) across habitats in the a) Central Pacific, b) Indian Ocean, c) Indo-West Pacific and d) Western Atlantic.
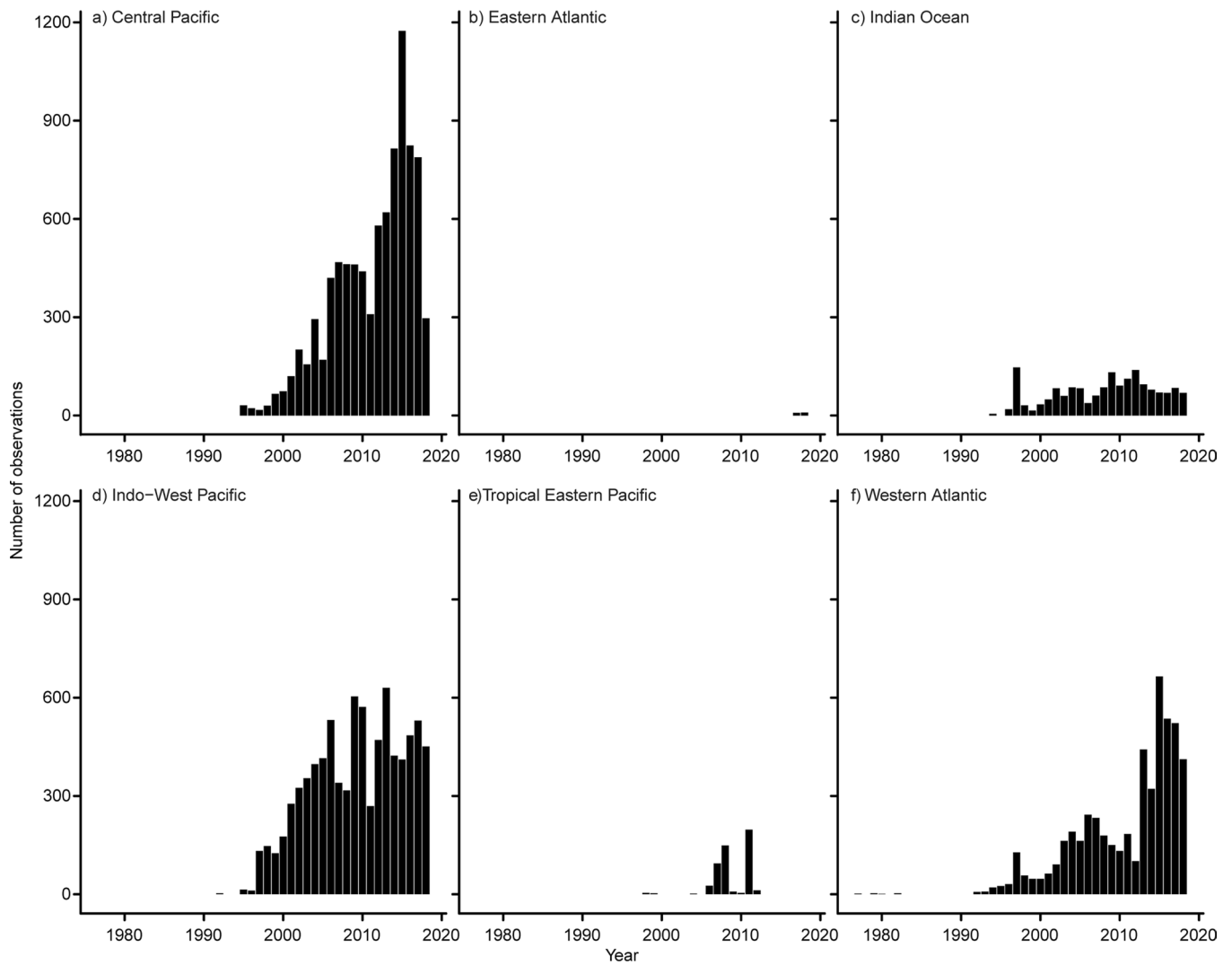
Extended Data Fig. 4 | Frequency histogram of the benthic composition data among realms through time. The number of benthic composition observations in the dataset in each year in the a) Central Pacific, b) Eastern Atlantic, c) Indian Ocean, d) Indo-West Pacific, e) Tropical Eastern Pacific, and f) Western Atlantic.
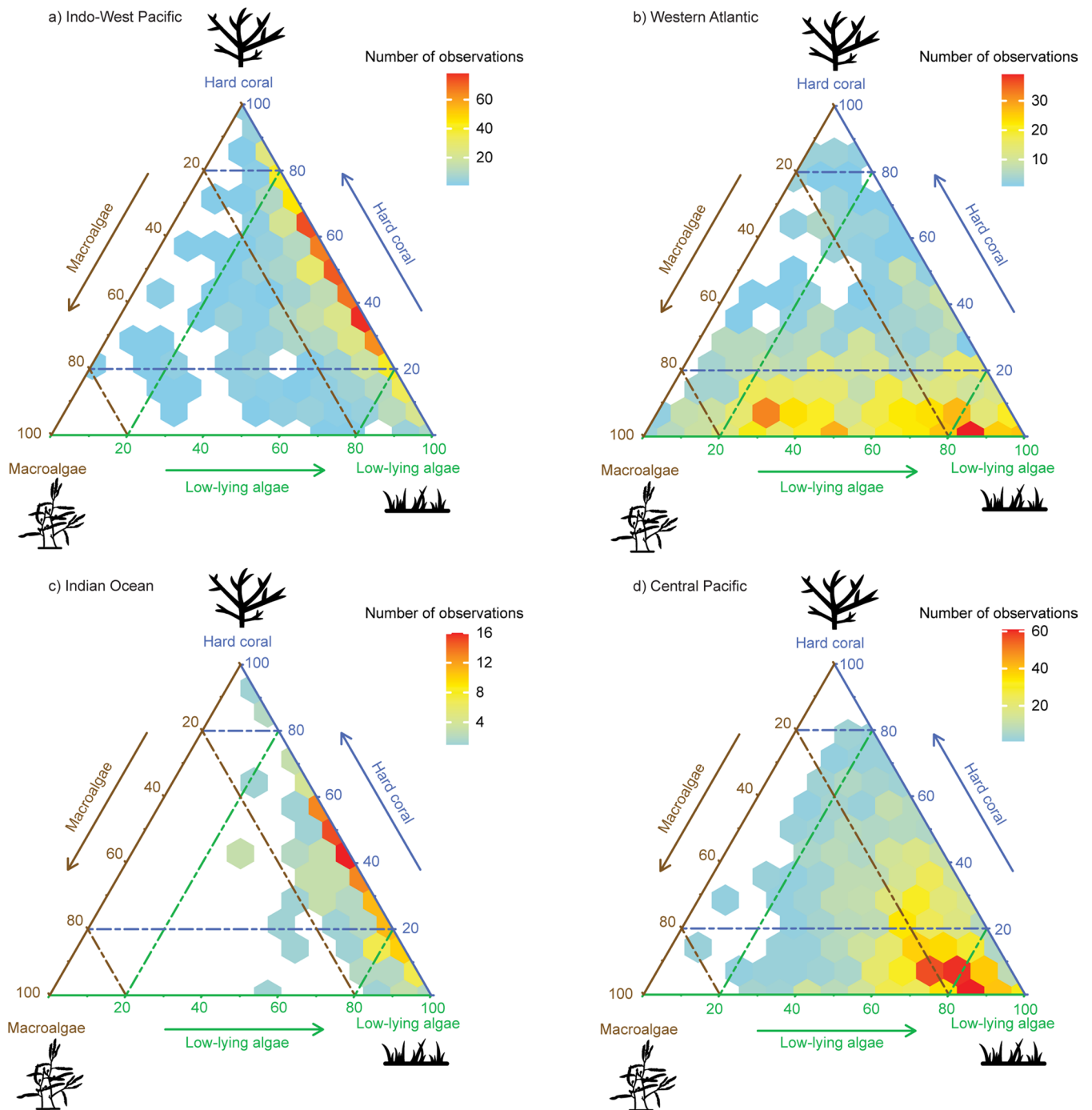
Extended Data Fig. 5 | The cover of hard corals, macroalgae and low-lying algal communities on the world's coral reefs. Ternery plots of hard coral, macroalgae and low-lying algal community cover on the world's coral reefs in 2017/2018 in the a) Indo-West Pacific, b) Western Atlantic, c) Indian Ocean, and d) Central Pacific. Colouring of the hexagons corresponds to the number of data points that fall within each hexagon.

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Last updated by author(s): Oct 4, 2022

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	The dataset was handled in the software R (version: 4.0.2) using the tidyverse (version: 1.3.1) package. Where necessary, data were extracted from graphs using WebPlotDigitizer (versions: 4.3 and 4.4). The geographic location of data points were also examined in Google Earth (version: 7.3)
Data analysis	All data analysis was conducted in the software R (version: 4.0.2) using the mgcv (version: 1.8-31), vegan (version: 2.5-6), emmeans (version: 1.5.1), DHARMa (version: 0.3.3.0), gstat (version: 2.0-7), tidyverse (version: 1.3.1), sf (version: 1.0-0), rnaturalearth (version: 0.1.0), ggtern (version: 3.3.0), adehabitatHR (version: 0.4.18), and patchwork (version: 1.1.1) packages. Code supporting the findings of this study is publicly available on figshare (https://doi.org/10.6084/m9.figshare.21267924.v1).

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

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All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

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Ecological, evolutionary & environmental sciences study design

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Study description	In this study we wanted to gain an insight into likely coral reef configurations of the near future, and to identify the most pressing future research endeavours. Specifically we focused on two relatively straightforward questions: 1) how is the benthic composition of coral reefs changing at a global scale? and 2) how, and to what extent, do these changes vary among major marine realms? To explore these questions, we compiled an extensive, global, dataset composed of 24,468 site-level observations of coral reef benthic composition (mean proportional cover of 6 benthic categories).
Research sample	The individual data points in our dataset were mean site level (i.e. a unique latitude and longitude) benthic community composition data. Mean site level data were used as this was the finest resolution of data that could be reliably sourced. Based on an initial examination of available data we settled on six benthic categories to represent benthic composition: hard coral (i.e. Scleractinian corals), soft corals (generally considered corals from the order Alcyonacea), macroalgae (generally considered algae >~20 mm in height), algal turf/crustose coralline algae[CCA]/rubble/dead coral/bare substratum/rock (data rarely discriminated among these different benthic categories, therefore, to maximise data retention a single category was used), other (e.g. sponges, ascidians, seagrass, bivalves), and sand/sediment. With these six benthic categories we were able to capture 100% of the coral reef benthic community composition (i.e. we did not just focus on a subset of the biotic benthic community). We relied on these major divisions to maximise the resolution in the dataset, while minimising the amount of data that had to be excluded because it was collected at a course resolution.
Sampling strategy	No statistical methods were used to predetermine sample size. We sourced all data from publicly availably databases and previous literature. Specifically, we compiled benthic composition data from six major publicly available monitoring databases: Reef Check, Reef Check Australia, Reef Life Survey, Caribbean Coastal Marine Productivity (CARICOMP), Moorea Coral Reef Long Term Ecological Research and the National Oceanic and Atmospheric Administration (NOAA). To complement the data from these databases and to ensure that our dataset was comprehensive, we then undertook an extensive formal search of the literature for available data. Our search and filtering process was based on PRISMA protocols, and a flow diagram outlining each step is provided in the supplementary material (Supplementary Figure 15). This was achieved using the search engine GoogleScholar and the search terms: "coral reef" AND benthic AND percent AND (transect OR quadrat). This search yielded 14,900 total results on the 20th of May 2020 (not including patents or citations).
Data collection	Data sourced from the six publicly available databases were pooled into the relevant benthic composition categories, and site level means were calculated, where necessary. In all cases, spurious data categories (e.g. transect tape, mobile fauna and unclassified) were excluded from calculations as they did not represent sessile benthic substrata. Data from these databases was also excluded if the metadata (namely depth, latitude, longitude, and sampling year) were missing or spurious.
	We evaluated the 14,900 documents based on their title and abstract for any potentially relevant documents. This process identified a subset of 1,748 potentially relevant documents for further investigation. Each of these documents were then examined in detail and the suitability of their data for inclusion in our dataset was assessed against a set of criteria. Acceptance criteria were: a) sampling was conducted on a coral reef system within our definition of a coral reef (i.e. ±30° of latitude from the Equator and 0 – 30 m water depth), b) the document contained benthic community composition data at sufficiently fine resolution to fit into our six benthic categories in a form that we could extract (i.e. raw data, tables or from figures), with no missing data/benthic categories, c) the data were pooled at the scale of the sampling site or a finer spatial scale (i.e. data across individual sampling sites were not pooled and presented together), d) the data presented in the manuscript had not already been included in our database from another source, e) sufficient detail was presented in the document that outlined the sampling location, depth, time and methods used, and f) there was no clear selection of study sites to meet pre-defined criteria (e.g. if a study specifically selected for 'high coral cover' sites it was not included).
	We relied on the criteria above to ensure that: a) the ecosystem sampled was consistent across data, b) the data covered the entire coral reef benthos, c) among-site level variation was not averaged out, d) we did not double up data points, e) we had sufficient information on the sampling to explain any patterns in benthic community composition, and f) any potential sampling biases associated with focused site selection were minimised. After this second extensive filtering process we were left with a subset of 83 studies that contained relevant data for our dataset (see Supplementary Text 3 for a full list of references). The vast majority of documents (1,449) simply did not contain the necessary data (i.e. most only reported 'coral cover' or 'algae cover' rather than complete benthic community composition).
	From each relevant document we then extracted data on the benthic cover (mean percent) of each of our six benthic categories at the level of individual sites (i.e. unique GPS coordinates, at the same depth, in the same habitat and sampling year). In most cases these data were sourced from raw data files, or tables in the main document. However, in some cases, it was necessary to extract the relevant data from figures in the document using WebPlotDigitizer. In addition, we also extracted information on the location of each study (latitude and longitude), the depth of each habitat (where a range was given the median depth was used), the method used to quantify the benthos, the year sampling was conducted, and the habitat which was sampled.
	Once all benthic composition data had been compiled together, we undertook a quality control procedure to check the data contained within our dataset. To do this we manually checked each data point. Specifically, we ensured a) the six benthic categories

were standardised (i.e. the proportional data added up to 1), b) the latitude and longitude data were accurate (we checked this by examining each individual set of coordinates in Google Earth), c) each data point had a corresponding depth (in meters) and year sampled value, d) the method used to collect each data point was categorised (line intercept transect, point intercept transect, chain intercept transect, photo quadrats along a transect, in-situ quadrats, or analysis of individual frames from a video; it is important to note that the vast majority of data were derived from one of two planar point-based methods [point intercept transect or photo-quadrats along a transect with subsequent examination using points]) (Supplementary Figure 16), e) the habitat sampled was categorised as either reef flat, lagoon, slope, back reef, crest, or submerged reef (where this information was not presented we placed the data point into a category based on its depth and satellite imagery in Google Earth), and f) the location of each data point was also designated into a category within three increasingly fine spatial scales: biogeographic realm (n = 6), ecoregion (n = 20) and geographic unit (n = 113) (Supplementary Figure 17; Supplementary Table 7). Realm and ecoregion classifications were based on the schemes presented in Kulbicki et al. (2013) and Spalding et al. (2007) while the geographic unit level was primarily based on the country from where the data were sourced, however, where data were from large countries, remote territories or clustered island groups more informative, finer scale categorisation was used within the country level (Supplementary Figure 17; Supplementary Table 7). Following this final quality control procedure our timeseries dataset contained 24,674 unique datapoints representing mean coral reef benthic community composition spread across more than 40 years of sampling (1977 – 2018).

Timing and spatial scale	The dataset analysed (24,468 observations) spanned 22 years from 1997 (i.e. immediately prior to the first global mass-coral bleaching event) until 2018 (i.e. a year after the most recent global coral bleaching event). 1997 was chosen as the starting year based on data availability as well as the onset of the first global coral bleaching event in 1998 which marked a change in the status quo for the world's reefs. Sensitivity analyses of how variation in the first and last year in the time series could have shaped inferences was also conducted. The observations encompassed 13,802 sites (unique GPS coordinates) across all major coral reef regions between ±30° of latitude from the Equator and from 0 – 30 m water depth.
Data exclusions	Although our dataset spanned 1977-2018 there were very few data points prior to 1997 (only 0.83% of all data in the dataset was from the 20 year period from 1977-1996) making any inferences based on this early data difficult. As a result we did not include data prior to 1997 in our analysis.
Reproducibility	No experiments were conducted in the current study.
Randomization	This is not relevant as no experiments were conducted that require randomisation. Our dataset was based on the quantification of a natural phenomenon. When compiling our dataset we specifically ensured all underlying data had been collected in a random manner, and specifically excluded data from studies that had 'selected' sites for a specific reason (e.g. high coral cover).
Blinding	As no experiments were conducted, and we were documenting a natural phenomenon, blinding was not possible.

Did the study involve field work? ☐ Yes ☒ No

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☒	Palaeontology and archaeology
☒	Animals and other organisms
☒	Human research participants
☒	Clinical data
☒	Dual use research of concern

Methods

n/a	Involved in the study
☒	ChIP-seq
☒	Flow cytometry
☒	MRI-based neuroimaging