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Social–environmental drivers inform strategic management of coral reefs in the Anthropocene

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Without drastic efforts to reduce carbon emissions and mitigate globalized stressors, tropical coral reefs are in jeopardy. Strategic conservation and management requires identification of the environmental and socioeconomic factors driving the persistence of scleractinian coral assemblages—the foundation species of coral reef ecosystems. Here, we compiled coral abundance data from 2,584 Indo-Pacific reefs to evaluate the influence of 21 climate, social and environmental drivers on the ecology of reef coral assemblages. Higher abundances of framework-building corals were typically associated with: weaker thermal disturbances and longer intervals for potential recovery; slower human population growth; reduced access by human settlements and markets; and less nearby agriculture. We therefore propose a framework of three management strategies (protect, recover or transform) by considering: (1) if reefs were above or below a proposed threshold of >10% cover of the coral taxa important for structural complexity and carbonate production; and (2) reef exposure to severe thermal stress during the 2014–2017 global coral bleaching event. Our findings can guide urgent management efforts for coral reefs, by identifying key threats across multiple scales and strategic policy priorities that might sustain a network of functioning reefs in the Indo-Pacific to avoid ecosystem collapse.

With the increasing intensity of human impacts from globalization and climate change, tropical coral reefs have entered the Anthropocene[1,2] and face unprecedented losses of up to 90% by mid-century[3]. Against a backdrop of globalized anthropogenic stressors, the impacts of climate change can transform coral communities[4] and reduce coral growth rates that are crucial for maintaining reef structure and tracking rising sea levels[5]. Under expectations of continued reef degradation and reassembly in the Anthropocene, urgent actions must be taken to protect and manage the world's remaining coral reefs. Given such concerns about the long-term functional erosion of coral communities, one conservation strategy is to prioritize the protection of reefs that currently maintain key ecological functions, such as reefs with abundant fast-growing and structurally complex corals that can maintain vertical reef growth and net carbonate production[5,6]. However, efforts to identify potentially functioning reefs across large spatial scales are often hindered by a focus on total coral cover—an aggregate metric that can overlook taxon-specific differences in structural complexity and carbonate production[7,8]. To date, global empirical studies of scleractinian coral communities (and their environmental and socioeconomic drivers) are rare, in part due to the absence of large-scale assemblage datasets—a key challenge that must be overcome in modern ecology. Here, we apply a method developed from trait-based approaches to evaluate regional patterns and drivers of Indo-Pacific coral assemblages.

A full list of affiliations appears at the end of the paper.

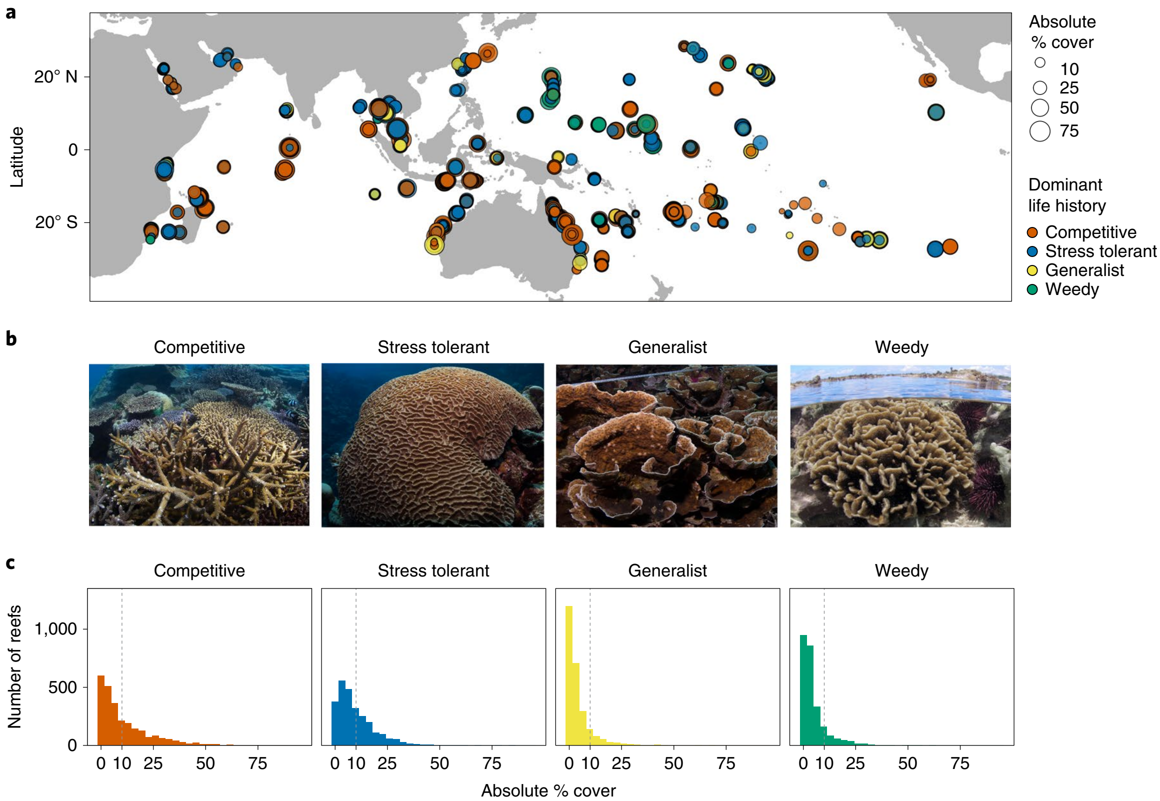

Fig. 1 | Indo-Pacific patterns of reef coral assemblages. a, Percentage cover of corals with four different life histories from 2,584 reef surveys in 44 nations and territories. Colours indicate life histories and circle sizes indicate percentage cover. Circles are semi-transparent; locations with many surveyed reefs are darker than locations with fewer surveyed reefs. **b**, Photos of corals from representative genera with each of the four life histories. From left to right: fast-growing competitive (*Acropora*); slow-growing and long-lived massive stress-tolerant (*Platygyra*); subdominant generalist (*Echinopora*); and fast-growing brooding weedy taxa (*Pavona*). **c**, Distribution of abundance (percentage cover) for each life history. Dotted lines identify 10% cover—a potential threshold for net-positive carbonate production. Maps are shown separately for each life history in Supplementary Fig. 1.

We assembled a large dataset of the community structure of tropical scleractinian corals from 2,584 Indo-Pacific reefs within 44 nations and territories, spanning 61° of latitude and 219° of longitude (see Methods). Surveys were conducted between 2010 and 2016 following continuous and repeated mass bleaching events including the 1998 El Niño. A 'reef' was defined as a unique sampling location where coral genera and species-level community composition were evaluated on underwater transects using standard monitoring methods. Compared with coral reef locations selected at random, our dataset is representative of most geographies: 78 out of 83 Indo-Pacific marine ecoregions with coral reef habitat are represented with <5% sampling disparity, although there are exceptions of undersampled (Palawan/North Borneo and the Torres Strait Northern Great Barrier Reef) and oversampled ecoregions (Hawaii, Rapa-Pitcairn and Fiji) (Supplementary Table 1).

On each reef, we evaluated total coral cover and the abundance of different coral life-history types previously developed from a trait-based approach with species characteristics of colony morphology, growth, calcification and reproduction[9] (https://coraltraits.org). The abundance of different coral taxa can affect key ecological processes for future reef persistence, including the provision of reef structural complexity, carbonate production (the process by which corals and some other organisms lay down carbonate on the reef), and ultimately reef growth (the vertical growth of the reef system resulting from the processes of carbonate production and erosion)[5,7,8,10]. Fast-growing branching, plating and densely calcifying massive coral taxa that can contribute to these processes are expected to be functionally important by maintaining critical geoecological functions that coral reefs provide[10] and might also help reefs track sea-level rise[5], recover from climate disturbances[11], and sustain critical habitat for reef fish and fisheries[12,13].

Here, we adopt a previous classification of four coral life-history types to evaluate Indo-Pacific patterns of total coral abundance and the composition of coral assemblages, and their key social–environmental drivers. Specifically, we consider four coral life histories[9] (Supplementary Table 2): (1) a 'competitive' life history of fast-growing branching and plating corals that can accrete structurally complex carbonate reef architectures but are disproportionately vulnerable to multiple stressors; (2) a 'stress-tolerant' life history of large, slow-growing and long-lived massive and encrusting corals that can build complex high-carbonate reef structures to maintain coral-dominated, healthy and productive reefs, and often persist on chronically disturbed reefs; (3) in contrast, 'generalist' plating or laminar corals may represent a subdominant group of deeper-water taxa, while; (4) smaller brooding 'weedy' corals typically have more fragile, lower-profile colonies that provide less structural complexity and contribute marginally to carbonate production and vertical growth[10,12,14]. We therefore consider competitive and stress-tolerant life histories to be key framework-building species, given their ability to build large and structurally complex coral colonies[8,10,12]. We hypothesize that the abundance of different life histories within a coral assemblage provides a signal of past disturbance histories or environmental conditions[15–17] that may affect resilience and persistence to future climate impacts[18].

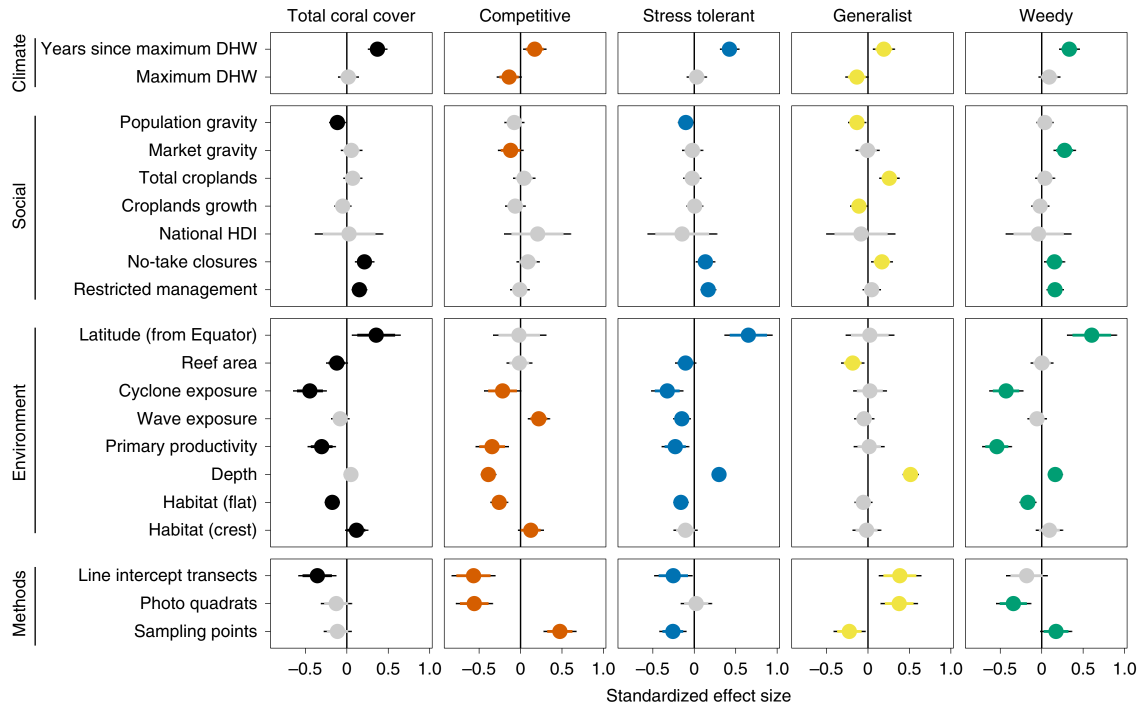

Fig. 2 | Relationship between climate, social, environmental and methodology variables with coral abundance. Response variables are the percentage cover of total hard corals and the four life history types. Standardized effect sizes are Bayesian posterior median values with 95% Bayesian credible intervals (CIs; thin black lines) and 80% CIs (coloured thicker lines). Filled points indicate that the 80% CI does not overlap with zero, whereas grey circles indicate an overlap with zero and a less credible trend. HDI, human development index. For the effects of population gravity on stress-tolerant and generalist corals, which appear to intersect zero, there was a 96.0% (15,362 out of 16,000 posterior samples) and 98.0% (15,670 out of 16,000) probability, respectively, of a negative effect. For market gravity and competitive corals, there was a 90.2% (14,424 out of 16,000 posteriors) probability of a negative effect. Models of four dominant coral genera are shown in Supplementary Fig. 2.

Drawing on theoretical and empirical studies of coral reef social–ecological systems[19,20], we tested the influence of 21 social, climate and environmental covariates on coral abundance, while controlling for sampling methodologies and biogeography (Supplementary Table 3). These include: (1) climate drivers (the intensity and time since past extreme thermal stress, informed by degree heating weeks (DHW)); (2) social and economic drivers (human population growth, management, agricultural use, national development statistics, and the 'gravity' of nearby markets and human settlements); (3) environmental characteristics (depth, habitat type, primary productivity, cyclones, wave exposure and reef connectivity); and (4) sampling effects and biogeography (survey methods, sampling intensity, latitude and coral faunal province). We fit hierarchical mixed-effects regression models using the 21 covariates to predict the percentage cover of total coral cover and the four coral life-history types individually. Models were fit in a Bayesian multilevel modelling framework and explain ~25–48% of the observed variation across total cover and the four life histories (Supplementary Table 4). We also fit these models to four common coral genera (*Acropora*, *Porites*, *Montipora* and *Pocillopora*) as a complementary taxonomic analysis.

Results and discussion

Across the 2,584 reefs, total hard coral cover varied from <1–100% (median ± s.d.: 23.7 ± 17.0%). Competitive and stress-tolerant were the dominant life history types on 85.7% of reefs (competitive: 42.4% (*n* = 1,095 reefs); stress tolerant: 43.3% (*n* = 1,118 reefs)). Generalist and weedy taxa dominated only 8.8 and 5.6% of reefs, respectively (Fig. 1 and Supplementary Fig. 1). It is striking that the majority of Indo-Pacific reefs remain dominated by structurally important corals, even following the impacts of the 1998 mass coral bleaching event and subsequent bleaching events, and given expectations of different trajectories of regime shifts and recovery following bleaching impacts or human activities[6,21,22]. Notably, these findings are in contrast with contemporary Caribbean reefs where very few reefs remain dominated by key reef-building species and are instead comprised of weedy taxa with limited functional significance[8,23]. However, Indo-Pacific reefs varied in their absolute abundance of the four types (Fig. 1), also suggesting the potential for dramatic structural and functional shifts away from expected historical baselines of highly abundant branching and plating corals[24]—a warning sign considering recent community shifts in the Caribbean[23].

Climate, social and environmental drivers. Climate variables describing the frequency and intensity of past thermal stress events strongly affected coral assemblages. Reefs with more extreme past climate disturbances (as assessed by maximum DHW) had fewer competitive and generalist corals, while time since the strongest past thermal disturbance was associated with more hard coral cover and the cover of all four life histories (Fig. 2). These results provide large-scale empirical support for the importance of recovery windows after bleaching in structuring coral assemblages[25,26]. Our findings are also consistent with expectations that branching and plating corals are vulnerable to temperature anomalies and bleaching[4,11,15]. Stress-tolerant and weedy corals were less affected by the magnitude of past thermal stress, consistent with long-term studies in Indonesia[7], the Seychelles[11] and Kenya[15] that have shown that these coral taxa often persist through acute disturbances and maintain important reef structure[12,27]. There was no effect of the magnitude of past thermal stress on total coral cover, possibly because this composite metric can overlook important differences in species and trait responses.

Our results also reveal the important role of socioeconomic drivers on coral life histories: reefs influenced by human populations, markets and agricultural use were associated with a lower abundance of competitive, stress-tolerant and generalist corals (Fig. 2). The mechanisms underpinning these relationships could include direct mortality from destructive fishing practices[28], tourism or industrial activities[29], or indirect effects on coral growth associated with the overexploitation of grazing herbivorous fishes that control macroalgae[30], or declining water quality that can increase sediments and nutrients to smother or sicken corals[31]. We also observed two positive associations of coral abundance with human use: generalist corals increased near agricultural land use, and weedy corals increased near larger and more accessible markets. In some cases, these relationships require further investigation; for example, the abundance of generalists (such as deeper-water plating corals) was negatively associated with cropland expansion, but positively associated with cropland area. Overall, we identified human gravity and agricultural use as key social drivers that could be locally mitigated through behaviour change[32] to promote structurally complex and calcifying reefs that can sustain important ecological functions.

Local management actions in the form of no-take reserves or restricted management (for example, gear restrictions) were associated with higher total coral cover and greater abundance of stress-tolerant, generalist and weedy corals, but not competitive corals (Fig. 2). Our findings suggest that management approaches typically associated with marine protected areas (MPAs) and fisheries management can both have benefits for total coral cover and some, but not all, life histories. Notably, local management did not increase the abundance of structurally important branching and plating competitive corals. This is consistent with expectations that branching and plating corals are often extremely sensitive to extreme heat events and bleaching mortality[11,14,15], which can swamp any potential benefits of local management[15,33]. Our analyses did not account for management age, size, design or compliance, all of which could influence these outcomes; for example, older, larger, well-enforced and isolated MPAs have been shown to increase total coral cover, although mostly through the cover of massive (stress-tolerant) coral growth forms[34]. Our results also suggest that gear restrictions can be associated with similar increases in coral abundance to fully no-take areas. For corals, any type of management that reduces destructive practices can have direct benefits for coral survival and growth[28]. While protection from local stressors may not increase coral resilience[33], we found that managed sites are associated with a higher abundance of total coral cover and some coral life histories relative to unmanaged sites, even after accounting for climate disturbances and other environmental conditions.

Environmental factors, such as latitude, depth and habitat, primary productivity, wave exposure and cyclone intensity, were also strongly associated with coral abundance (Fig. 2). Competitive corals were more abundant on reef crests, shallower reefs and reefs with higher wave exposure, compared with stress-tolerant corals that were more abundant on deeper reefs and reefs with lower wave exposure. Stress-tolerant, weedy and generalist corals were typically associated with higher latitudes, smaller reef areas and greater depths. Primary productivity and cyclone exposure were associated with fewer competitive, stress-tolerant and weedy corals, probably due to unfavourable conditions for coral growth in areas of eutrophication and high productivity[31], or hydrodynamic breakage or dislodgement of coral colonies[35]. These findings suggest that environmental conditions are important in predicting conservation baselines and guiding management investments (for example, restoring or maintaining grazer functions when environmental conditions can support abundant corals and other calcifying organisms[36]). After controlling for method and sampling effort in the models (Fig. 2), our results suggest that future comparative studies would benefit from standardized methods and replication to allow for faster comparative approaches for field-based monitoring[37], especially given the urgency of tracking changes to coral assemblages as a result of climate change and bleaching events.

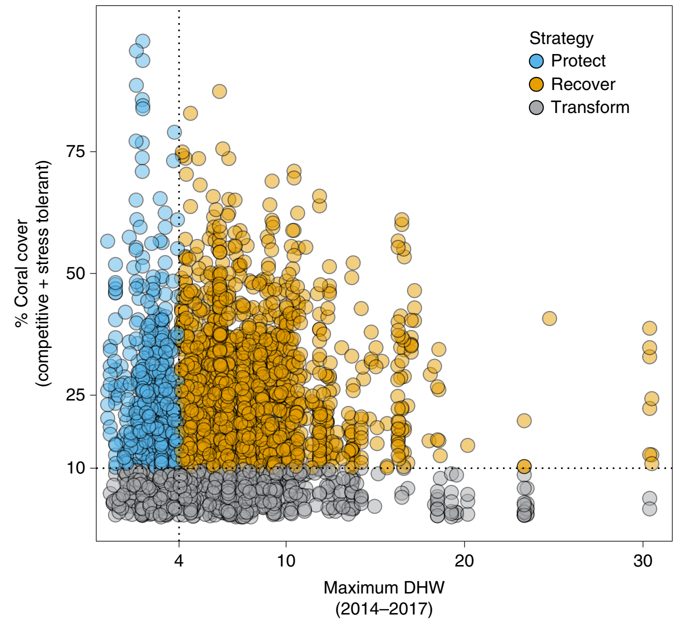

Fig. 3 | Strategic management portfolio of protect, recover and transform for Indo-Pacific coral reefs. The 2,584 reefs varied in their ecological conditions (assessed as the combined cover of stress-tolerant and competitive corals) and exposure to maximum annual DHW during the 2014–2017 third global coral bleaching event. A protect strategy (blue dots) is suggested for 449 reefs (out of 2,584 (17.4%)) that were associated with limited exposure to recent bleaching-level thermal stress (DHW < 4 °C-weeks) and maintained coral cover above 10%. A recover strategy could be prioritized for reefs that have recently maintained cover above 10% but were exposed to severe potential bleaching stress in 2014–2017 (orange dots; $n = 1{,}407$ (54.5%)). For coral cover below net-positive carbonate budgets (<10% hard coral cover), societies may ultimately need to transform away from reef-dependent livelihoods (grey dots; $n = 728$ (28.2%)).

The four life histories showed some different responses compared with common genera (Supplementary Fig. 2); they were generally more sensitive to climate and social drivers (17 versus 12 significant relationships for the life histories compared with common genera, respectively; Fig. 2 and Supplementary Fig. 2). For example, competitive corals had stronger associations with two metrics of climate disturbance (years since maximum DHW and maximum DHW) compared with *Acropora* (a genus classified as competitive); three of the four life histories showed positive associations with local management (no-take or restricted management) compared with only one genus (*Porites*—a stress-tolerant and weedy genus); and *Acropora* was negatively associated with restricted management. Overall, our results suggest that life histories might provide more sensitive signals of disturbance for coral assemblages, perhaps because life-history groups integrate morphological and physiological traits that can determine coral responses to disturbance[38]. However, further comparisons of life-history and taxonomic responses—at both regional and local scales—are certainly warranted.

Management strategies in the Anthropocene. The livelihoods of millions of people in the tropics depend on healthy and productive coral reefs[19,20], yet coral reefs worldwide are imperilled by climate change[3,25]. Between 2014 and 2017, reefs worldwide experienced an unprecedented long, extensive and damaging El Niño and global

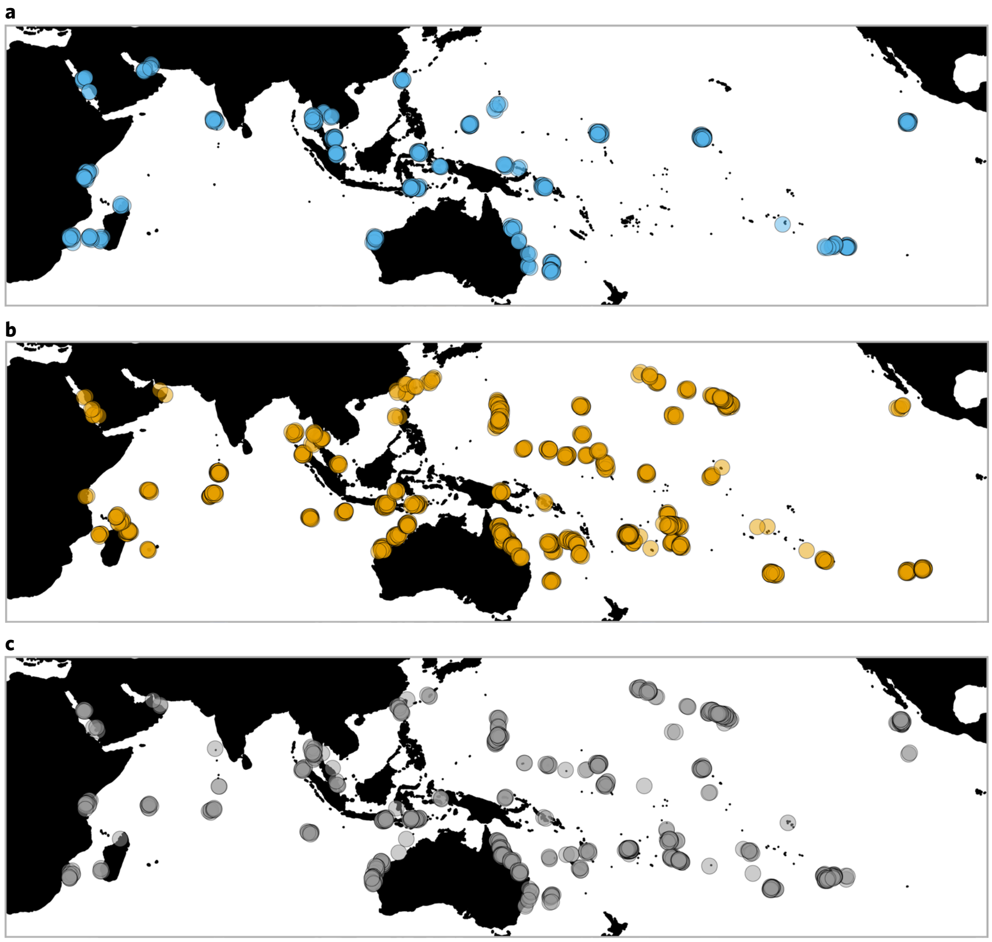

Fig. 4 | Indo-Pacific map of management strategies. a–c, Three management strategies of protect (**a**), recover (**b**) and transform (**c**) are distributed across reefs throughout the Indo-Pacific suggesting that there remain opportunities to sustain a network of functioning reefs while supporting coral recovery or social transformations for the majority of reefs.

bleaching event[26,39]. The 2,584 reefs in our dataset were exposed to thermal stress between 0 and 30.5 annual °C-weeks above summer maxima between 2014 and 2017 (Fig. 3 and Methods). Nearly three-quarters of the surveyed reefs (74.9%; $n=1,935$ reefs) were exposed to DHW of >4 °C-weeks—a common threshold for ecologically significant bleaching and mortality[39] (Supplementary Fig. 3). Previous studies have identified 10% hard coral cover as a minimum threshold for carbonate production on Caribbean[40] and Indo-Pacific[27,41] reefs. Below this threshold (or 'boundary point'), reefs are more likely to have a neutral or negative carbonate budget and may succumb to reef submergence with rising sea levels[5]. Here, we adapt this threshold by considering only the live cover of competitive and stress-tolerant corals (hereafter, 'framework' corals) since these are two life histories that can build large, structurally complex colonies to maintain carbonate production and vertical reef growth[10,12,27]. Before the third global bleaching event between 2014 and 2017, 71.8% of reefs (1,856 out of 2,584) maintained a cover of framework corals above 10%, suggesting that the majority of reefs could sustain net-positive carbonate budgets before their exposure to the 2014–2017 global bleaching event. The abundance of framework corals was independent of the thermal stress experienced in the 2014–2017 bleaching event (Fig. 3). Considering these two thresholds of ecologically significant thermal stress (DHW: >4 °C-weeks) and potential ecological function (10% cover; sensitivity analysis provided in Supplementary Table 5), this creates a portfolio of three management strategies: (1) protect functioning reefs exposed to less intense and frequent climate disturbance during the 2014–2017 bleaching event; (2) recover reefs exposed to ecologically significant bleaching stress that were previously above potential functioning thresholds; and (3) on degraded reefs exposed to ecologically significant bleaching stress, transform existing management, or ultimately assist societies to transform away from reef-dependent livelihoods (Fig. 3).

A protect strategy was identified for 449 reefs (out of 2,584 (17.4%)) that were exposed to minimal bleaching-level stress (DHW < 4 °C-weeks during 2014–2017) and had >10% cover of framework corals (Fig. 3 and Supplementary Table 5). These reefs were located throughout the Indo-Pacific (Fig. 4 and Supplementary Table 6), suggesting that it is currently possible to safeguard a regional network of functioning coral reefs[6,42,43]. The conservation goal for 'protect' reefs is to maintain reefs above functioning thresholds, while anticipating the impacts of future bleaching events. Policy actions include dampening the impacts of markets and nearby populations and placing local restrictions on damaging fishing, pollution or industrial activities while addressing the broader context of poverty, market demands and behavioural norms[32,44]—and ideally within areas of potential climate refugia[43,45]. The recover strategy was identified for the majority of reefs: 1,407 reefs (out of 2,584 (54.4%)) exceeded 10% cover of framework corals but were probably exposed to severe bleaching-level heat stress during the 2014–2017 global bleaching event (DHW > 4 °C-weeks). As these reefs had recently maintained 10% cover, mitigating local stressors as described above, alongside targeted investments in coral reef rehabilitation and restoration, could help to accelerate

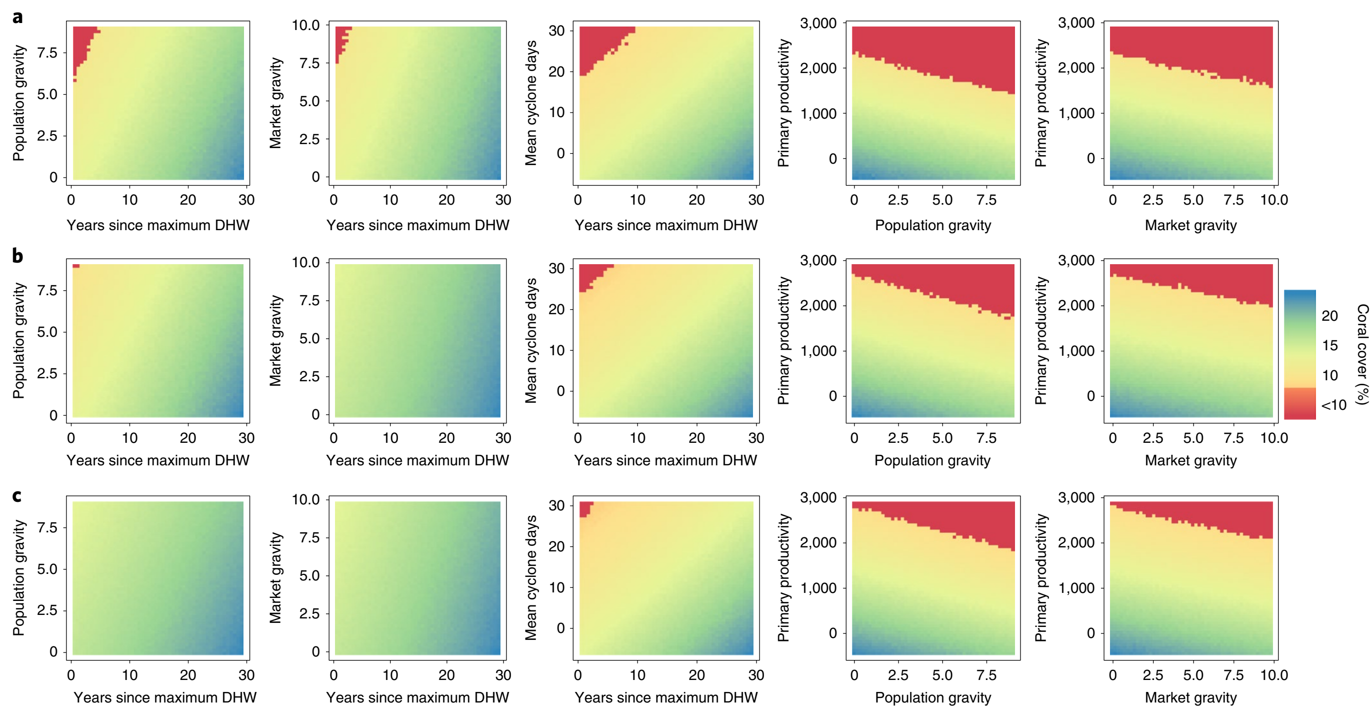

Fig. 5 | Combinations of key social and environmental drivers that differentiate between reefs below and above 10% cover of framework corals. Red indicates reefs below 10% cover of framework corals, whereas the yellow to blue gradient indicates those above it. Coral cover refers to the combined cover of competitive and stress-tolerant corals. Gravity estimates are reported as log[values] with original units of human population min^{-2}. Units of primary productivity are $mg\,C\,m^{-2}\,d^{-1}$; units of cyclone days are the mean maximum days of exposure to gale force winds (or stronger) per year. The results were predicted separately for three management categories (fished (**a**), restricted (**b**) and no-take reserves (**c**)), and are based on model predictions (see Methods).

natural coral recovery. In this strategy, the goal is to move reefs back above the 10% threshold as quickly as possible following climate impacts. Active management to restore habitat with natural or artificial complexity, coral 'gardening' or human-assisted evolution could be considerations to quickly recover coral cover following climate disturbances[42]. This is often at high cost, but there are options for low-cost, long-term restoration[46]. For the transform strategy, we identified 728 reefs (28.2%) below 10% cover that were probably on a trajectory of net erosion before the 2014–2017 bleaching event. Here, transformation is needed—either by management to enact new policies that urgently and effectively address drivers to rapidly restore coral cover or, ultimately, by societies who will need to reduce their dependence on coral reef livelihoods facing the loss of functioning coral reefs. Such social transformations could be assisted through long-term investments in livelihoods, education and adaptive capacity[47,48]—investments that can also accompany the protect and recover strategies.

We also investigated how combinations of key drivers could affect the predicted cover of framework corals (Fig. 5). While certain combinations were predicted to reduce cover below a 10% threshold (for example, high population or market gravity with less recovery time from climate disturbances or with high cyclone exposure, and high gravity with high primary productivity), the majority of parameter space predicted coral cover above 10%. In addition, increasing management restrictions appeared to expand a safe operating space for corals above a 10% threshold. This is hopeful, in that even as the frequency of bleaching events is expected to increase, reducing the impact of local stressors may provide conditions that can sustain some functions on coral reefs. Nevertheless, management through MPAs alone has not been shown to increase climate resistance or recovery[33]. Thus, addressing global climate change is paramount.

Our dataset describes contemporary coral assemblages within a period of escalating thermal stress, notably following the 1998 bleaching event[26,39]. Patterns of coral bleaching vary spatially[25], and we can make no predictions from our dataset about which reefs might escape future bleaching events or mortality. The long-term persistence of corals within potential climate refuges requires a better understanding of future climate conditions and tracking of the long-term ecological responses of different reefs[6,37,45]. Predicting and managing coral reefs through a functional lens, such as through coral life histories, is challenging but necessary[10,49]. Here, we adapt previous estimates of 10% coral cover as a threshold of net-positive carbonate production. However, this threshold is based on methods that estimate the three-dimensional structure of a reef[40], while our dataset consists primarily of planar two-dimensional methods that do not account for the vertical or three-dimensional components of coral colonies[50]. Thus, the 10% threshold should be considered an uncertain, but potentially precautionary, threshold of net carbonate production and reef growth, and a sensitivity analysis considering this threshold at 8 or 12% cover suggests that a three-strategy framework is robust to uncertainty around these thresholds (Supplementary Table 5). Future work can help refine these thresholds by considering species-specific contributions to structural complexity and carbonate production, as has been recently developed for Caribbean corals[8].

Conclusions

Facing an Anthropocene future of intensifying climate change and globalized anthropogenic impacts[1,2,39], coral reef conservation must be more strategic by explicitly incorporating climate impacts and ecological functioning into priority actions for conservation and management. Given expectations that coral assemblages will shift towards smaller and simpler morphologies and slower growth rates to jeopardize reef function[4,7,15], our findings highlight the importance of urgently protecting and managing reefs that support assemblages of large, complex branching, plating and massive taxa that build keystone structure on coral reefs[10–12]. Our findings reveal key drivers of coral assemblages, and identify some locations where societies can immediately enact strategic management to protect, recover or transform coral reefs. Our framework also provides a way to classify management strategies based on relatively simple thresholds of potential ecological function (10% cover of framework corals) and recent exposure to thermal stress (DHW > 4 °C-weeks)—thresholds that have the potential to be incorporated into measurable indicators of global action under the Convention on Biological Diversity's Post-2020 Strategic Plan that will include a revised target for coral reefs. Local management alone—no matter how strategic—does not alleviate the urgent need for global efforts to control carbon emissions. The widespread persistence of functioning coral assemblages requires urgent and effective action to limit warming to 1.5 °C. Our findings suggest there is still time for the strategic conservation and management of the world's last functioning coral reefs, providing some hope for global coral reef ecosystems and the millions of people who depend on them.

Methods

We conducted coral community surveys along 8,209 unique transects from 2,584 reefs throughout the Indian and Pacific Oceans, covering ~277 km of surveyed coral reef. Our dataset provides a contemporary Indo-Pacific snapshot of coral communities between 2010 and 2016; surveys occurred following repeated mass bleaching events (for example, 1998, 2005 and 2010), but were not influenced by widespread mortality during the 2014–2017 global coral bleaching event. Surveyed reefs spanned 61.2 degrees of latitude (32.7° S to 28.5° N) and 219.3 degrees of longitude (35.3° E to 105.4° W), and represented each of the 12 coral faunal provinces described for Indo-Pacific corals[51]. A random subsampling method was used to evaluate the representation of our dataset across Indo-Pacific coral reefs, whereby we compared the locations of empirical surveys with the global distribution of coral reefs by generating 2,600 randomly selected Indo-Pacific coral reef sites using the R package dismo[52] from a 500-m-resolution tropical coral reef grid[53]. Comparing our empirical surveys (n = 2,584 reefs) with the randomly generated reefs allowed us to estimate ecoregions with relative undersampling or oversampling (Supplementary Table 1).

Climate, social and environmental covariates were organized at three spatial scales[19]:

(1) Reef (n = 2,584). Coral community surveys were conducted at the scale of 'reefs', defined as a sampling location (with a unique latitude, longitude and depth) and comprised of replicate transects. Surveys occurred across a range of depths (1–40 m; mean ± s.d.: 8.9 ± 5.6 m), although the majority of surveys (98.8%) occurred shallower than 20 m. Surveys were conducted across a range of reef habitat zones, classified into three major categories: reef flat (including back reefs and lagoons), reef crest and reef slope (including offshore banks and reef channels).

(2) Site (n = 967). Reefs within 4 km of each other were clustered into 'sites'. The choice of 4 km was informed by the spatial movement patterns of artisanal coral reef fishing activities, as used in a global analysis of reef fish biomass[19]. We generated a complete-linkage hierarchical cluster dendrogram based on great-circle distances between each point of latitude and longitude, and then used the centroid of each cluster to estimate site-level social, climate and environmental covariates (Supplementary Table 3). This provided a median of 2.0 ± 2.83 reefs per site.

(3) Country (n = 36). Reefs and sites were identified within geopolitical countries to evaluate national-level covariates (gross domestic product per capita, voice and accountability in governance, and the human development index). Overseas territories within the jurisdiction of France, the United Kingdom and the United States were informed by their respective country.

Coral communities and life histories. At each reef, underwater surveys were conducted using one of three standard transect methods: point-intercept transects (n = 1,628 reefs), line-intercept transects (n = 399 reefs) and photo quadrats (n = 557 reefs). We estimated sampling effort as the total number of sampled points during each reef survey. Line-intercept transects were estimated with sampling points every 5 cm, since most studies only estimate the length of corals greater than 3 or 5 cm (T. McClanahan and A. Baird; personal communication). On average, the number of sampling points was 300.0 ± 750.0 (median ± s.d.), and effort ranged from 30–5,138 sampling points. Method and sampling effort were included as fixed effects in the models to control for their effects.

The absolute percentage cover of hard corals was evaluated to the taxonomic level of genus or species for each transect. Surveys that identified corals only to broader morphological or life-form groups did not meet the criteria for this study. The majority of surveys recorded coral taxa to genus level (1,506 reefs out of 2,584 (58.2%)), and the remainder recorded some or all taxa to species level. A small proportion of unidentified corals (0.30% of all surveyed coral cover) were excluded from further analyses. We estimated the total hard coral cover on each transect, and classified each coral taxon to a life-history type[9]; some species of *Pocillopora*, *Cyphastrea* and *Leptastrea* were reclassified by expert coral taxonomists and ecologists[54]. A representative list of species and their life-history types is provided in Supplementary Table 2, and original trait information is available from the Coral Traits Database (https://coraltraits.org/)[55]. Four genera included species with more than one life-history classification (*Hydnophora*, *Montipora*, *Pocillopora* and *Porites*), and we distributed coral cover proportional to the number of species within each life history, which was estimated separately for each faunal province based on available species lists[51]. In total, we were able to classify 97.2% of surveyed coral cover to a life history. We then summed coral cover within each of the four life histories on each reef.

Climate, social and environmental drivers. To evaluate the relative influence of climate, social and environmental drivers on total hard coral cover and coral assemblages, we identified a suite of covariates at reef, site and country scales (Supplementary Table 3). These covariates included: the frequency and intensity of thermal stress since 1982; local human population growth; market and population gravity (a function of human population size and accessibility to reefs); local management; nearby agricultural use; a country's human development index; primary productivity; depth; reef habitat; wave exposure; cyclone history; and habitat connectivity. A full description of covariates, data sources and rationale can be found in the Supplementary Methods.

Analysis of drivers. We first assessed multicollinearity among the different covariates by evaluating variance inflation factors (Supplementary Table 7) and Pearson correlation coefficients between pairwise combinations of covariates (Supplementary Fig. 4). This led to the exclusion of four covariates: (1) local population size; (2) national gross domestic product per capita; (3) national voice and accountability; and (4) years since extreme cyclone activity. A final set of 16 covariates was included in the statistical models, whereby all pairwise correlations were <0.7 and all variance inflation factors were <2.5, indicating that multicollinearity was not a serious concern (Supplementary Table 7 and Supplementary Fig. 4).

To quantify the influence of multiscale social, human and environmental factors on hard coral assemblages, we modelled the total percentage cover of hard corals and the percentage cover of each life history as separate responses. We fit mixed-effects Bayesian models of coral cover with hierarchical random effects, where reef was nested within site, and site was nested within country; we also included a random effect of coral faunal province to account for regional biogeographic patterns[51]. For each response variable, we converted the percentage coral cover into a proportion response and fit linear models using a beta regression, which is useful for continuous response data between 0 and 1 (ref. [56]). We incorporated weakly informative normal priors on the global intercept (mean = 0; s.d. = 10) and slope parameters (mean = 0; s.d. = 2), and a Student's t prior on the beta dispersion parameter (d.f. = 3; mean = 0; scale = 25). We fit our models with 5,000 iterations across four chains, and discarded the first 1,000 iterations of each chain as a warm-up, leaving a posterior sample of 16,000 for each response. We ensured chain convergence by visual inspection (Supplementary Fig. 5), and confirmed that Rhat (the potential scale-reduction factor) was less than 1.05 and the minimum effective sample size (n_{eff}) was greater than 1,000 for all of the parameters[57]. We also conducted posterior predictive checks and estimated Bayesian R^2 values (that is, the variance of the predicted values divided by the variance of the predicted values plus the variance of the errors) for each model to examine goodness of fit[58]. All models were fit with Stan[59] and brms[60]; analyses were conducted in R[61].

We applied the same modelling approach to the percentage cover of four dominant coral genera (*Acropora*, *Porites*, *Montipora* and *Pocillopora*), to provide a comparison between life history and taxonomic responses.

Strategic portfolios. We developed three management strategies (protect, recover or transform) based on the potential thermal stress experienced during the 2014–2017 bleaching event, and a reef's previous observed ecological condition. To evaluate potential thermal stress, we estimated the maximum annual DHW between 2014 and 2017 from the National Oceanic and Atmospheric Administration's CoralTemp dataset (Coral Reef Watch version 3.1; see Supplementary Methods). Ecologically significant bleaching and mortality can occur at different thresholds of thermal stress (probably DHW = 2–4 °C-weeks[39]), and this range of thresholds also represents the lowest quintile of DHW exposure for the 2,584 reefs during the 2014–2017 global bleaching event (20th quintile = 3.2 °C-weeks DHW). Considerations of different DHW thresholds were highly correlated and identified similar 'no-regrets' locations of limited thermal stress exposure between 2014 and 2017 (Supplementary Fig. 3).

For ecological conditions, we assessed whether each reef had the potential for a net-positive carbonate budget before the 2014–2017 bleaching event, based on a reference point of 10% cover of competitive and stress-tolerant corals. We assumed that this threshold represents a potential tipping point for reef growth and carbonate production, whereby 10% hard coral cover is a key threshold above which reefs are more likely to maintain a positive carbonate budget and therefore net reef growth[27,40,41]. Additionally, 10% coral cover is suggested to be a threshold for reef fish communities and standing stocks of biomass[62–64], and is associated with some thresholds to undesirable algal-dominated states at low levels of herbivore grazing and coral recruitment[65]. As a sensitivity analysis for the 10% coral cover threshold, we considered how 8% and 12% coral cover thresholds would affect the distribution of conservation strategies across the 2,584 reefs (Supplementary Table 5). This sensitivity analysis also helps account for the uncertainty in how two-dimensional planar estimates of percentage cover recorded during monitoring may affect three-dimensional processes on coral reefs, such as carbonate production[50]. Ultimately, applying thresholds of recent extreme heat and reef condition led to the proposed framework of three management strategies (protect, recover and transform), which we mapped across the Indo-Pacific based on the surveyed locations in our dataset.

We also investigated how combinations of key drivers differentiated between reefs below or above 10% cover of competitive and stress-tolerant corals. Using the Bayesian hierarchical models for competitive and stress-tolerant corals, we predicted coral cover across a range of observed values for five key covariates: population gravity; market gravity; years since maximum DHW; primary productivity; and cyclone exposure. For each covariate combination, we kept all other parameters at their median values for continuous predictors, or their reference value for categorical predictors (habitat: reef slope; method: point intercept transect). We then summed the median predicted cover of competitive and stress-tolerant corals from 10,000 posterior samples for an estimate of combined cover. We repeated this approach for each level of management.

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

Data availability
Data are available on request or directly from the data contributors. Contact details and information on the geographies covered by each data contributor are provided in Supplementary Table 8.

Code availability
All R code is available from https://github.com/esdarling/IndoPacific-corals.

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Author contributions

E.S.D. envisioned and led the project, performed all of the analyses, secured funding and wrote the manuscript. T.R.M., J.M., G.G.G., N.A.J.G., F.J.-H., J.E.C., C.M., C.C.H., M.-J.F., M. Krkosek and D.M. contributed to the conceptual ideas, design, analysis, design and writing. All other authors contributed data, and edited and approved the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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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	Not applicable, see fieldwork below.
Data analysis	All code is available on the public GitHub repository, https://github.com/esdarling/IndoPacific-corals

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/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

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

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Data available on request or directly from the data contributors. Contact information and the geographies covered by each data contributor are provided in Supplementary Table 8

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	A regional study of coral communities in the Indo-Pacific
Research sample	Scleractinian coral communities with corals identified to genus or species, using standard transect-based methods that report live percent cover by taxa
Sampling strategy	Sampling strategies were determined by each data collector and often involved replicate transects stratified by depth
Data collection	Individual data collectors recorded the data using line intercept, point intercept or photo quadrat transect methods
Timing and spatial scale	Data were collected between 2010 and 2016; sites collected after 2014 reported no influence of the 2014-2017 bleaching event, as noted by the original data collectors
Data exclusions	None
Reproducibility	All original raw data are stored with their corresponding R code to compile into a regional dataset
Randomization	Not relevant, our dataset compiled all available data without randomization. A random sampling comparison was used to consider oversampling or undersampling by (1) ecoregions and (2) coral faunal provinces
Blinding	Blinding was not relevant to this study.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Field conditions were determined by individual data collectors, and required conditions of temperature, wind, rain and waves that allowed for the identified and recording of benthic coral reef communities along transects.
Location	2,584 reefs in the Indian and Pacific Oceans (see Map - Fig 1 in manuscript)
Access and import/export	All data collectors were responsible for obtaining the necessary permissions and permits required for underwater observations of coral reef benthic communities.
Disturbance	Any disturbance to coral communities was minimized by experienced surveyors using proper buoyancy control to avoid disturbing live coral colonies and other organisms.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology
☐	☒	Animals and other organisms
☒	☐	Human research participants
☒	☐	Clinical data

Methods

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

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	NA
Wild animals	Invertebrate coral communities were sampled non-destructively using standard underwater observation protocols along transect lines, and recorded by experienced scientific divers.

Field-collected samples	NA
Ethics oversight	NA - invertebrates only

Note that full information on the approval of the study protocol must also be provided in the manuscript.