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Strategic conservation and management of coral reefs in the Anthropocene

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Abstract: Without drastic efforts to reduce carbon emissions and mitigate globalized stressors, tropical coral reefs are in jeopardy (1, 2). Strategic conservation and management will require identifying the environmental conditions and socioeconomic characteristics associated with scleractinian coral assemblages – the foundation species of coral reef ecosystems. Here, we compiled coral abundance from 2,584 Indo-Pacific sites to evaluate the influence of 21 climate, social, and environmental drivers on reef coral assemblages. Higher abundances of framework-building corals were typically associated with: weaker past thermal disturbances and longer recovery intervals from past bleaching events; slower human population growth; reduced access to human settlements and markets; and less agricultural use. Given the variability in climate exposure faced by coral reefs (3), we used this information to propose a framework of three management strategies (*protect – recover – transform*) by considering if reefs were, (i) above or below a proposed threshold of >10% cover of coral taxa important for structural complexity and carbonate accretion, and (ii) their exposure to severe thermal stress during the 2014-2017 global coral bleaching events. Based on our dataset, we identify a subset of reefs ($n = 449$, or 17.4%) that meet the criteria for protecting potential ecological refuges, amidst other locations that may ultimately be priorities for recovery actions ($n = 1405$, or 54.4%) or transformation away from reef-dependent livelihoods ($n = 728$, 28.2%). 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.

Main text: With the increasing intensity of human impacts from globalization and climate change, tropical coral reefs have entered a new era of the Anthropocene (1, 4) and face unprecedented losses of up to 90% by mid-century (5). Against a backdrop of globalized anthropogenic stressors, the impacts of climate change can transform coral communities (6) and reduce coral growth rates that are crucial to maintain structure and track rising sea levels (2). Under expectations of continued reef degradation and reassembly in the Anthropocene (4), time is growing short. Given such concerns about the long-term functional erosion of coral communities, one conservation strategy is to prioritize protecting reefs that currently maintain key ecological functions, i.e., reefs with abundant fast-growing and structurally-complex corals that can maintain net carbonate accretion and vertical reef growth (1, 2). However, efforts to

165 identify these potentially functioning reefs across large spatial scales are often hindered by a focus on total coral cover, an aggregate metric that can overlook taxa-specific differences in structural complexity and carbonate accretion (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.

170 We assembled the largest dataset of tropical scleractinian corals from 2,584 Indo-Pacific reefs within 44 nations and territories and spanning 61° of latitude and 219° of longitude (see Methods). Surveys were conducted between 2010 and 2016, during continuous and repeated mass bleaching events, notably following 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 to coral reef locations selected at random, our dataset is representative of most conditions: 78 out of 83 Indo-Pacific marine ecoregions with coral reef habitat are represented with <5% disparity, although there are exceptions of undersampled (Palawan/North Borneo and Torres Strait Northern Great Barrier Reef) and oversampled (Hawaii, Rapa-Pitcairn and Fiji Islands) ecoregions (Table S1).

180 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) (www.coraltraits.org, Table S2). The abundance of different coral taxa can affect key ecological processes for future reef persistence, including the provision of reef structural complexity, carbonate accretion (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 accretion and erosion) (2, 7, 8, 10). Fast-growing, branching, plating and densely calcifying massive coral taxa that can maintain these processes are expected to be functionally important, not only by maintaining critical geo-ecological functions that coral reefs provide, but 190 might also help reefs recover from climate disturbances, track sea level rise (2), and continue to provide critical habitat for reef fisheries (11).

Here, we build on a previous classification of four coral life history types to evaluate Indo-Pacific patterns of total coral abundance and trait-based groups of corals, and their key socio-environmental drivers. Specifically, we consider four coral life histories (9) (Table S2): the
195 ‘competitive’ life history describes fast-growing branching and plating corals that can accrete structurally-complex carbonate reef architectures but are disproportionately vulnerable to multiple stressors; the ‘stress-tolerant’ life history describes 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;
200 by contrast, ‘generalist’ plating or laminar corals may represent a subdominant group of deeper water taxa, while 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, 13). We therefore consider competitive and stress-tolerant life histories as key framework-building species given their ability to build large and
205 structurally complex coral colonies. We hypothesize that the abundance of different life histories within a coral assemblage provides a signal of past disturbance histories or environmental conditions (14–17) that may affect resilience and persistence to future climate impacts (18).

Across the 2,584 reefs, total hard coral cover varied from <1% to 100% (median +/- SD, 23.7 +/- 17.0%). Competitive and stress-tolerant corals were the dominant life history on 85.7%
210 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. 1a, b; Fig. S1). It is striking that the majority of reefs were able to achieve dominance by structurally-important corals even following the 1998 mass bleaching event, despite different histories of ongoing bleaching impacts and recovery (19, 20). Notably, these findings are in contrast to contemporary
215 Caribbean reefs where very few reefs are dominated by key reef-building species and instead comprised of weedy taxa with limited functional significance (8, 21). However, Indo-Pacific reefs varied in their absolute abundance of the four types (Fig. 1c), also suggesting the potential for dramatic structural and functional shifts away from expected historical baselines of highly abundant competitive branching and plating corals (22), a warning sign given recent community
220 shifts in the Caribbean (23).

Drawing on theoretical and empirical studies of socio-economic and environmental drivers on coral reefs (24–26), we tested the influence of 21 social, climate, and environmental covariates on coral abundance, while controlling for sampling methodologies and biogeography (Table S3). These include: (i) social drivers (human population growth, management, agricultural use, national development statistics, the ‘gravity’ of nearby markets, and human populations that measure the size and accessibility of the nearest major market and human settlement, respectively), (ii) climate drivers (the intensity and time since past extreme thermal stress, informed by Degree Heating Weeks, DHWs), (iii) environmental characteristics (depth, habitat type, primary productivity, cyclone wave exposure, and reef connectivity), and (iv) sampling effects and biogeography (survey method, sampling intensity, latitude, and coral faunal province). We fit hierarchical mixed-effects regression models using the 21 covariates to predict the percent 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 (Table S4). We also fit these models to four common coral genera (*Acropora*, *Porites*, *Montipora*, *Pocillopora*) as a complementary taxonomic analysis (Fig. S2).

Climate variables describing the frequency and intensity of past thermal stress events strongly affected coral assemblages (Fig. 2). Total hard coral cover and the abundance of all four life histories increased with time since the strongest past thermal disturbance, providing empirical support for the importance of recovery windows for corals (1). These results also highlight the consequences of shrinking recovery windows for coral community structure, and its potential associations with ecosystem function as the abundance of live coral declines (1, 6). Reefs with more extreme past climate disturbances (assessed by maximum DHWs) had fewer competitive and generalist corals (Fig. 2), consistent with expectations that branching and plating corals are extremely vulnerable to temperature anomalies and bleaching (6, 15, 18). Stress-tolerant and weedy corals were less affected by the magnitude of past thermal stress, as suggested by long-term studies in Kenya (15) and Indonesia (7) that have shown these corals can persist through acute disturbances. There was no effect of the magnitude of past thermal stress on patterns of total coral cover, likely because this composite metric overlooks differences in species and trait responses.

Our results also reveal the important role of socioeconomic drivers on some life histories: reefs adjacent to human populations and agricultural use were associated with a lower abundance of stress-tolerant and generalist corals (Fig. 2). The mechanisms underpinning these relationships could include the overexploitation of grazing herbivorous fishes that control macroalgae, declining water quality from agriculture and urban centers that can increase turbidity and nutrients to smother corals and fuel algal overgrowth or disease, or increases in coral disease or mortality from destructive fishing practices, tourism or industrial activities (27, 28). We also observed two positive associations of coral abundance with human use: generalist corals with nearby agricultural land use, and weedy corals with market gravity. In some cases, these relationships may be complex and require further investigation; for example, the abundance of generalists (e.g., deeper-water plating corals) was negatively associated with the expansion of nearby croplands between 2002-2012, but positively associated with a more croplands by 2012 (Fig. 2). Overall, we identify human gravity and agricultural use as key social drivers that can reduce the abundance of structurally-complex corals and increase the abundance of ‘weedier’ corals; drivers that could therefore be locally mitigated 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 (e.g., gear restrictions) were associated with higher total coral cover, and greater abundance of stress-tolerant and weedy corals, but not competitive or generalist corals (Fig. 2). The finding that management did not increase the abundance of all coral life histories may be surprising, because protection from local stressors is often expected to support coral resilience by increasing herbivory and suppressing macroalgae, reducing coral disease, and providing chemical cues that facilitate coral recruitment (29, 30). However, our analyses did not account for reserve age, size, design, or compliance, which could influence these outcomes; for example, older marine protected areas (MPAs) have been shown to reduce the loss of total coral cover (31). Nevertheless, these results are also consistent with our findings that competitive and generalist corals are vulnerable to thermal stress, and with the argument that MPA effects can be swamped by the effect of climate change and bleaching mortality (32), especially for taxa that can be extremely sensitive to bleaching losses (12, 15). Our results also suggest that partial protection is associated with increases in coral abundance similar to fully no-take areas. For corals, any type of management that reduces destructive fishing practices (e.g., dynamite bombing, trawling, or

anchoring) can have benefits for coral survival and growth (28, 33), compared to global studies of reef fish that highlight the importance of compliant, no-take fisheries management (26, 34).

Environmental factors such as latitude, reef zonation (depth and habitat), primary
285 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
on reefs with higher wave exposure, compared to 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 deeper depths. Primary
290 productivity and cyclone exposure were associated with a decrease in the abundance of
competitive, stress-tolerant and weedy corals, likely associated with unfavourable conditions for
coral growth in areas of eutrophication and high productivity (35), or hydrodynamic breakage or
dislodgement of coral colonies (36). These findings suggest that environmental conditions are
important in predicting conservation baselines and guiding management investments, such as
295 restoring or maintaining grazer functions when environmental conditions can support corals and
other calcifying organisms (37). 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,
especially given the urgency of tracking changes to coral assemblages worldwide (38).

300 The livelihoods of millions of people in the tropics depend on healthy and productive
coral reefs (39), yet coral reefs worldwide are imperilled by climate change (1, 5, 6, 32).
Previous studies have identified 10% hard coral cover as a minimum threshold for carbonate
accretion on Caribbean (40) and Indo-Pacific (41, 42) reefs, where reefs around this threshold (or
'boundary point') are more likely to have a neutral carbonate budget and may succumb to reef
305 submergence with rising sea levels (2). Here, we adapt this threshold as the live cover of
competitive and stress-tolerant corals (hereafter, 'framework' corals) as these are two life
histories that can build large, structurally-complex colonies to maintain carbonate production and
vertical reef growth (10, 41). Prior to 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% (Fig.
310 3a), suggesting the majority of reefs could sustain potential function. We then assessed the
exposure to potential bleaching-level thermal stress for the 2,584 reefs in our dataset during the

third global bleaching event. Between 2014 and 2017, reefs were exposed to variable maximum thermal stress, ranging between 0 to 30.5 DHWs annually (Fig 3a; Methods); nearly three-quarters of the surveyed reefs (74.9%, n = 1935 reefs) were exposed to >4 DHWs, a common
315 threshold for potential bleaching and mortality (43) (see also Fig. S3). Coral abundance, as related to potential thresholds of function (10%; but see sensitivity analysis in Table S5), was independent of the thermal stress experienced in the 2014-2017 bleaching event. This creates the potential for three strategic types of management: 1) *protect* functioning reefs exposed to less intense and frequent climate disturbances, 2) *recover* reefs exposed to potential bleaching-level
320 stress but above a potential functioning threshold before bleaching, and 3) on degraded reefs exposed to potential bleaching-level thermal stress, assist societies to *transform* away from reef-dependent livelihoods (Fig. 3a).

A *protect* strategy was identified for 449 reefs (out of 2,584, or 17.4%), which were exposed to minimal bleaching-level stress (<4 DHWs during 2014-2017) and had >10% cover of
325 framework corals (Fig. 3a; Table S5). These reefs were located throughout the Indo-Pacific (Fig. 3b, Fig. S4, Table S6) suggesting that it is currently possible to safeguard a regional network of functioning coral reefs (3). The conservation goal for *protect* reefs is to maintain reefs above functioning thresholds ideally through future potential bleaching events, i.e., through policies that can dampen the market and population impacts of nearby populations, or through
330 management that can include restrictions on fishing, development, tourism, pollution and run-off (4, 27, 45, 46). The *recover* strategy comprised the majority of surveyed reefs: 1407 reefs (out of 2584, or 54.4%) exceeded 10% cover of framework corals, but were likely exposed to severe bleaching-level heat stress during 2014-2017 El Niño (i.e., >4 DHWs). As these reefs had recently maintained 10% cover, mitigating local stressors as described above alongside targeted
335 investments in coral reef rehabilitation and restoration could help to accelerate natural coral recovery. For the *transform* strategy, we identified 728 reefs (or 28.2%) below 10% cover that were likely on a trajectory of net erosion prior to the 2014-2017 bleaching event. Here, societies may ultimately need to transform away from dependence on coral reef livelihoods, which could be assisted with long-term social investments in livelihoods, education, and adaptive capacity;
340 investments which can also accompany the *protect* and *recover* strategies (39, 44).

We also investigated how combinations of key drivers could affect the predicted cover of framework corals (Fig. 3c). While certain driver combinations were predicted to reduce cover below a 10% threshold (e.g., low recovery time from climate disturbances with high population or market gravity, or with high cyclone exposure; at levels of high gravity and high primary productivity; Fig. 3c), the majority of parameter space predicted coral cover above 10%. 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 coral reefs (6). Our results show that while addressing global climate change is paramount, other factors such as recovery time from bleaching events, low to medium levels of net primary productivity (e.g., through improving water quality) or dampening the effects of nearby populations and markets should help to maintain the cover of framework corals above 10% (Fig. 3c) at a minimum, and ideally sustain reefs at higher levels of coral cover.

Our dataset describes contemporary coral assemblages within a period of escalating thermal stress, notably following the 1998 bleaching event. However, patterns of coral bleaching vary spatially (1), and we can make no predictions about which reefs might escape future bleaching events or mortality. The long-term persistence of corals within potential climate refuges (i.e., the *protect* strategy) requires a better understanding of future climate conditions and tracking the long-term ecological responses of different reefs (38, 45). Predicting and managing coral reefs through a functional lens is challenging but necessary (10, 46). 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 of primarily planar two-dimensional methods that do not account for the vertical or three-dimensional components of complex colonies (47). Thus, the 10% threshold based on planar methods should be considered an uncertain, but potentially precautionary, threshold of net carbonate accretion. A sensitivity analysis considering this threshold at 8% or 12% cover finds similar distributions of reefs across the three strategies (Table S5), suggesting a three-strategy framework is robust to uncertainty around thresholds of functionality. Future work can help refine these thresholds by considering species-specific contributions to complexity and carbonate production, as has been recently developed for Caribbean corals (8).

Facing an Anthropocene future of intensifying climate change and globalized anthropogenic impacts, coral reef conservation can be more strategic by explicitly incorporating climate impacts and ecological functioning into priority actions (4). Given expectations that coral assemblages will shift towards smaller and simpler morphologies and slower growth rates to jeopardize reef function (6, 7, 15), our findings highlight the importance of urgently protecting and managing reefs that support diverse assemblages of large, complex branching, plating and massive taxa (10). Our findings reveal key drivers of coral assemblages, and identify some locations where societies can immediately enact strategic actions of *protect*, *recover*, or *transform*. Our framework also provides a way to classify reefs for management based on two simple thresholds of their potential ecological function and recent exposure to thermal stress; 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 1.5-2°C (1, 5, 6). 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.

390 **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 during repeated mass bleaching events (e.g., 1998, 2005, 2010), but were not influenced by widespread mortality during the 2014-2017 global coral bleaching event. Surveys spanned 61 degrees of latitude (32.7°S to 28.5°N) and 219.4 degrees of longitude (35.3°E to 105.4°W) and represented each of the 12 coral faunal provinces described for Indo-Pacific corals (48). A random subsampling method was used to evaluate the representation of our dataset across Indo-Pacific coral reefs, whereby we compared locations of empirical surveys to the global distribution of coral reefs by generating 2600 randomly selected Indo-Pacific coral reef

sites using the ‘dismo’ package (49) from a 500 m resolution tropical coral reef grid (50). Comparing our empirical surveys ($n = 2,584$ reefs) to the randomly generated reefs allowed us to estimate ecoregions with relative undersampling or oversampling (Table S1).

Climate, social and environmental covariates were organized at three spatial scales,
405 following the methods of (26):

(i) 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 \pm standard deviation, 8.9 ± 5.6 m), though the majority of surveys (98.8%) occurred at depths
410 shallower than 20 m. Surveys were conducted across a range of reef habitat zones, classified to three major categories: reef flat (including back reefs and lagoons), reef crest, and reef slope (including offshore banks and reef channels).

(ii) Site ($n = 967$). Reefs within 4 km of each other were clustered into “sites”. The choice of 4 was informed by the spatial movement patterns of artisanal coral reef fishing
415 activities as used in a global analysis of global reef fish biomass (26). We generated a complete-linkage hierarchical cluster dendrogram based on great-circle distances between each point of latitude and longitude. This provided a median of 2.0 reefs (± 2.83) per site. We then used the centroid of each cluster to estimate site-level social, climate and environmental covariates (Table S3).

420 (iii) Country ($n = 36$). Reefs and sites were identified within geopolitical countries to evaluate national-level covariates (GDP per capita, voice and accountability in governance, and Human Development Index). Overseas territories within the jurisdiction of the United States, United Kingdom and France were informed by their respective country.

425 **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 as having sampling points every 5 cm, since most studies only estimate the length of corals

430 greater than 3 or 5 cm (T. McClanahan, A. Baird pers. comm). On average, the number of
sampling points was 300.0 ± 750.0 (median \pm SD), although effort ranged from 30 to 5,138
sampling points. Method and sampling effort were included as fixed effects in the models to
control for their effects.

435 The absolute percent 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 (e.g., branching, massive corals) did not meet the criteria for this study. The
majority of surveys recorded coral taxa to genus (1506 reefs out of 2584, or 58.2%), and the
remainder recorded some or all taxa to species level; a small proportion of corals that remained
unidentified from species or genus surveys (0.30% of all surveyed coral cover) were excluded
440 from further analyses. We estimated the total hard coral cover on each transect, and classified
each coral taxa to a life history type following the classification presented in (9); some species of
Pocillopora, *Cyphastrea* and *Leptastrea* were reclassified by expert coral taxonomists and
ecologists following the methods of (14). A representative list of species and their life history
types are provided in Table S2, and original trait information is available from the Coral Traits
445 Database (<https://coraltraits.org/>) (51). For genera-level monitoring that included species across
more than one life history classification (*Hydnophora*, *Montipora*, *Pocillopora*, *Porites*), we
distributed coral cover of each genus proportional to the number of species within each life
history, which was estimated separately for each faunal province based on available species lists.
In total, we were able to classify 97.2% of surveyed coral cover to a life history, and then
450 summed coral cover for 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 (Table S3). These covariates included: the frequency
and intensity of thermal stress since 1982 as indicators of ocean warming and bleaching, local
455 human population growth, market and settlement gravity (a function of human population size
and accessibility to reefs), management, nearby agricultural use, national 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 Information.

460 **Analysis of drivers.** We first assessed multicollinearity among the different covariates by
evaluating variance inflation factors (Table S7) and Pearson correlation coefficients between
each pairwise combination of covariates (Fig. S5). This led to the exclusion of four covariates:
(i) local population size, (ii) national GDP per capita, (iii) national voice and accountability, and
(iv) years since maximum annual extreme cyclone days. A final set of 16 covariates was
465 included in statistical models, whereby all pairwise correlations were less than 0.7 and all
variance inflation factors were less than 2.5 indicating that multicollinearity was not a serious
concern (Table S7, Fig. S5).

To quantify the multi-scale social, human and environmental factors on hard coral
assemblages, we modelled total percent cover of hard corals and the percent cover of each life
470 history as separate responses. We fit mixed-effects Bayesian models of coral cover that represent
spatial organization as hierarchical random effects, where reef was nested within site, and site
nested within country; we also included a random effect of coral faunal province to account for
regional biogeographic patterns (48). For each response variable, we converted percent coral
cover into a proportion response and fit linear models using a Beta regression, which is useful for
475 continuous response data between 0 and 1 (52). We incorporated weakly informative priors:
Normal (mean 0, standard deviation 10) on the global intercept, Normal (mean 0, standard
deviation 2) on slope parameters, and Student t (degrees of freedom 3, mean of 0, scale of 25) on
the beta dispersion parameter. 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; in total, the posterior sample was
480 16,000 for each model. We ensured chain convergence by visual inspection (Fig. S6), and
ensuring that Rhat (the potential scale reduction factor) was less than 1.05 and the minimum
effective sample size (n_{eff}) was > 1000 for all parameters (53). We also conducted posterior
predictive checks and estimated Bayesian R^2 values for each model as an indication of the
proportion of variance explained (54). We fit models with Stan (55), *brms* (56) and *R* 3.5.2 (57).

485 We applied the same modelling approach to the percent cover of four dominant coral
genera: *Acropora*, *Porites*, *Montipora*, and *Pocillopora*, in order to provide a comparison
between life history and taxonomic responses (Fig. S2).

Strategic portfolios. We developed three conservation strategies (*protect*, *recover* and
transform) based on the potential thermal stress during the 2014-2017 bleaching event, and each

490 reef's previous observed ecological condition. To evaluate the potential thermal stress
experienced by the 2,584 reefs during the Third Global Bleaching Event, we estimated the
maximum annual Degree Heating Weeks (DHWs) between 2014 and 2017 from two global
satellite products: NOAA's CoralTemp dataset (Coral Reef Watch version 3; see Drivers section)
and NOAA's Coral Reef Watch version 2 (<https://coralreefwatch.noaa.gov>). There was generally
495 strong agreement in maximum annual DHWs experienced by each reef between the two datasets
(Pearson correlation, $r = 0.68$). Here, we use DHWs derived from the CoralTemp version 3
product, which provides more accurate SSTs although the climatologies to interpret bleaching-
level stress DHW thresholds remain in development (W. Skirving, pers. comm). Potential
bleaching-level thermal stress can occur at different thresholds, likely between 2 and 4 DHWs,
500 and this range of thresholds also represents the lowest quintile of DHW exposure for the 2,584
reefs during the 2014-2017 El Niño (0-20th quintile: 0 - 3.2 DHW). Considerations of different
thresholds were highly correlated and identified similar 'no-regrets' locations of limited thermal
stress exposure between 2014 and 2017 (Fig. S3).

For ecological condition, we assessed whether each reef had the potential for a net positive
505 carbonate budget prior to the 2014-2017 bleaching event based on 10% cover of competitive and
stress tolerant corals. We assumed that this threshold represents a potential tipping point (i.e.
unstable equilibrium, or boundary point) for reef growth and carbonate accretion, 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 (40–42). Additionally, 10% coral cover is
510 suggested to be a threshold for reef fish communities and standing stocks of biomass (58–60),
and also associated with some thresholds to undesirable algal-dominated states at low levels of
herbivore grazing and coral recruitment (61). As a sensitivity analysis for the 10% coral cover
threshold, we also considered how 8% and 12% coral cover thresholds would affect the
distribution of conservation strategies across the 2,584 reefs (Table S5). This sensitivity analysis
515 helps account for the uncertainty in how two-dimensional planar estimates of percent cover
recorded during monitoring may affect three-dimensional processes on coral reefs, like carbonate
production (47). Ultimately, applying thresholds of recent potential bleaching-level stress and
reef condition (percent cover of competitive and stress tolerant corals) led to the proposed
framework of three management strategies: *protect*, *recover* and *transform*, which we mapped
520 across the Indo-Pacific based on the surveys in our dataset (Fig. 3, Fig. S4).

We also investigated how combinations of key drivers differentiated between reefs below or above 10% cover of competitive and stress-tolerant corals (Fig. 3C). 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 and 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 (management: fished; habitat: reef slope; method: PIT); we then added the median predicted cover of competitive and stress-tolerant corals from 10,000 posterior samples for an estimate of combined cover.

Data availability Data available on request from the authors.

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

Competing interests The authors declare no competing interests.

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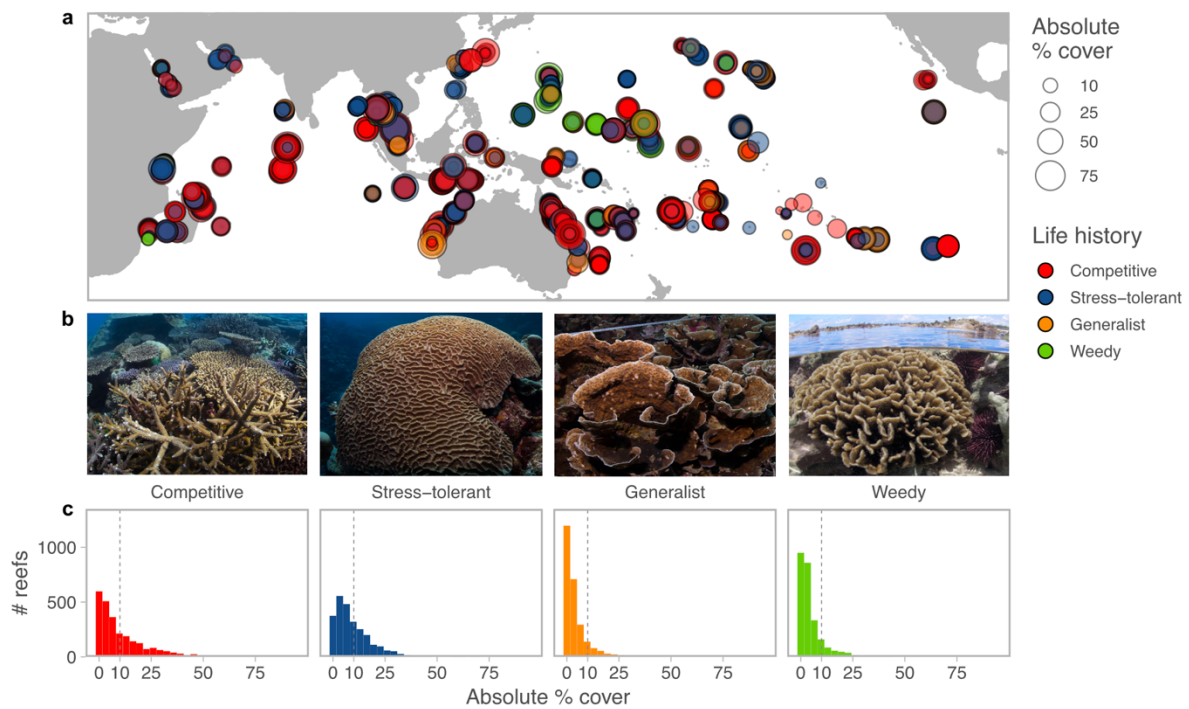


Fig. 1. Indo-Pacific patterns of reef coral assemblages. (A) Percent cover of four coral life
695 histories from 2,584 reef surveys in 44 nations and territories; colour indicates life history and
circle size indicates percent cover. Circles are semi-transparent; locations with many surveyed
reefs are darker than locations with fewer surveyed reefs. (B) Example of life histories, from left
to right: fast-growing competitive; slow-growing and long-lived massive stress-tolerant; sub-
dominant generalists; fast-growing brooding weedy taxa. (C) Distribution of abundance (percent
700 cover) for each life history; dotted line identifies 10% cover, a potential threshold for net-
positive carbonate production. Maps are shown separately for each life history in Fig. S1.

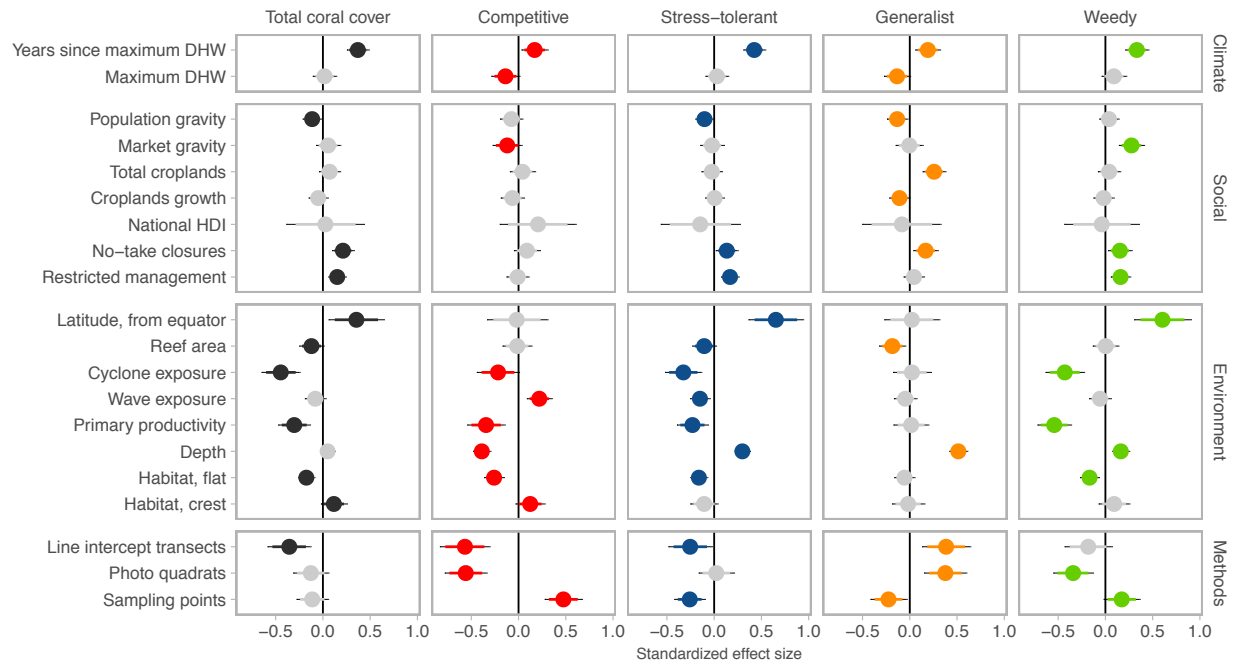


Fig. 2. Relationship between climate, social, environment and methodology variables with total coral cover and life history type. Standardized effect sizes are Bayesian posterior median values with 95% Bayesian credible intervals (CI; thin black lines) and 80% credible intervals (coloured thicker lines); filled points indicate the 80% CI does not overlap with zero and open circles indicate an overlap with zero and a less credible trend. DHW indicates Degree Heating Weeks; HDI indicates the national statistic Human Development Index. For the effects of population gravity on stress-tolerant and weedy corals which can 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 dominant coral genera are shown in Fig. S2.

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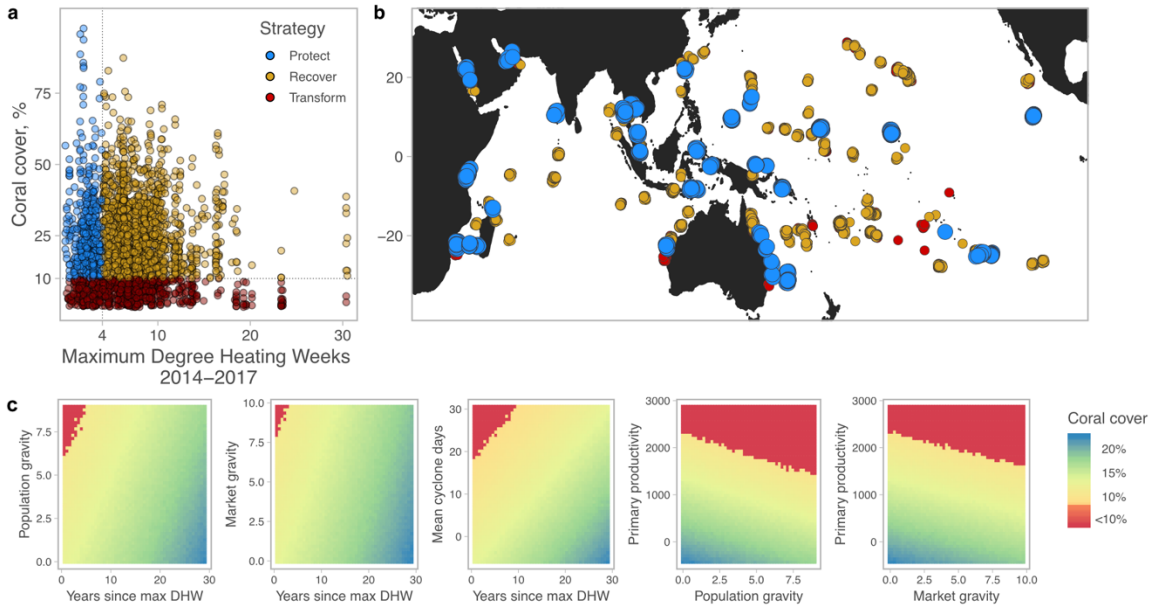


Fig. 3. Strategic management approaches of *protect* – *recover* – *transform* across Indo-Pacific coral reefs. (A) The 2,584 reefs varied in their exposure to maximum annual DHWs during the 2014-2017 Third Global Coral Bleaching Event. Reefs previously above a 10% threshold of framework corals (combined cover of stress tolerant and competitive corals, associated with net positive carbonate budgets), and with limited exposure to potential bleaching-level thermal stress (<4 DHWs, see Fig. S4) may be potential refuges of ecological function to *protect* (blue dots, $n = 449$, or 17.4%). *Recovery* could be a priority for reefs that have recently maintained cover above 10% but were then exposed to severe potential bleaching stress in 2014-2017 (>4 DHWs, orange dots; $n = 1407$, or 54.5%). Societies may ultimately need to *transform* away from reef-dependent livelihoods as coral cover falls below potential accretion thresholds (<10% hard coral cover, dark red dots; $n = 728$, or 28.2%). (B) The three management strategies are distributed throughout the Indo-Pacific (Fig. S4, Table S6), suggesting there remain opportunities to sustain a network of functioning reefs while supporting coral recovery or social transformations for the majority of reefs. (C) Combinations of key drivers that differentiate between reefs below (red) and above 10% cover of framework corals (yellow to blue gradient), based on model predictions (see Methods). Coral cover refers to the combined cover of competitive and stress-tolerant corals; gravity estimates are reported as $\log(\text{values})$.