

Social-environmental drivers inform strategic 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. Strategic conservation and management requires identifying 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 with longer intervals for potential recovery; slower human population growth; reduced access by human settlements and markets; and less nearby agriculture. We then propose a framework of three management strategies (*protect, recover, or transform*) by considering: (i) if reefs were above or below a proposed threshold of >10% cover of coral taxa important for structural complexity and carbonate production, and (ii) 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.

Introduction: 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-century³. Against a backdrop of globalized anthropogenic stressors, the impacts of climate change can transform coral communities⁴ and reduce coral growth rates that are crucial to maintain reef structure and track rising sea levels⁵. 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, i.e., 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 –
165 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.

We assembled the largest dataset of the community structure of tropical scleractinian
corals from 2,584 Indo-Pacific reefs within 44 nations and territories, spanning 61° of latitude
170 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
175 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 Torres Strait Northern Great Barrier Reef) and oversampled (Hawaii, Rapa-Pitcairn,
and Fiji) ecoregions (Supplementary Table 1).

On each reef, we evaluated total coral cover and the abundance of different coral life
180 history types previously developed from a trait-based approach with species characteristics of
colony morphology, growth, calcification, and reproduction⁹ (<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
185 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, not only by
maintaining critical geo-ecological functions that coral reefs provide¹⁰, but might also help reefs
track sea level rise⁵, recover from climate disturbances¹¹, and sustain critical habitat for reef fish
190 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 histories⁹ (Supplementary

Table 2): a ‘competitive’ life history describes fast-growing branching and plating corals that can
195 accrete structurally-complex carbonate reef architectures but are disproportionately vulnerable to
multiple stressors; a ‘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;
by contrast, ‘generalist’ plating or laminar corals may represent a subdominant group of deeper
200 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^{10,12,14}. We therefore consider competitive and stress-tolerant life
histories as 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
205 a coral assemblage provides a signal of past disturbance histories or environmental conditions<sup>15–
17</sup> that may affect resilience and persistence to future climate impacts¹⁸.

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
210 include: (i) climate drivers (the intensity and time since past extreme thermal stress, informed by
Degree Heating Weeks, DHW), (ii) social and economic drivers (human population growth,
management, agricultural use, national development statistics, the ‘gravity’ of nearby markets
and human settlements), (iii) environmental characteristics (depth, habitat type, primary
productivity, cyclone wave exposure, and reef connectivity), and (iv) sampling effects and
215 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 (Supplementary Table 4). We also fit these models to four
220 common coral genera (*Acropora*, *Porites*, *Montipora*, *Pocillopora*) as a complementary
taxonomic analysis.

Results & Discussion: Across the 2,584 reefs, total hard coral cover varied from <1% to 100% (median \pm SD, 23.7 \pm 17.0%). Competitive and stress-tolerant corals were the dominant life history 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 (Figure 1; Supplementary Figure 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 to contemporary Caribbean reefs where very few reefs remain dominated by key reef-building species and instead comprised of weedy taxa with limited functional significance^{8,23}. However, Indo-Pacific reefs varied in their absolute abundance of the four types (Figure 1), also suggesting the potential for dramatic structural and functional shifts away from expected historical baselines of highly abundant branching and plating corals²⁴, a warning sign considering recent community shifts in the Caribbean²³.

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 (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 (Figure 2). These results provide some of the first 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 Indonesia⁷, the Seychelles¹¹, and Kenya¹⁵ that have shown these coral taxa often persist through acute disturbances and maintain important reef structure^{12,27}. There was no effect 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 some life histories: reefs influenced by human populations, markets, and agricultural use were associated with a lower abundance of competitive, stress-tolerant, and generalist corals (Figure 2). The mechanisms underpinning these relationships could include direct mortality from destructive fishing practices²⁸, tourism, or industrial activities²⁹, or indirect effects on coral growth associated with the overexploitation of grazing herbivorous fishes that control macroalgae³⁰ or declining water quality that can increase sediments and nutrients to smother or sicken corals³¹. 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 (e.g., deeper-water plating corals) was negatively associated with cropland expansion, but positively associated with cropland area. Overall, we identify human gravity and agricultural use as key social drivers that could be locally mitigated (i.e., through behaviour change³²) 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, generalist, and weedy corals, but not competitive corals (Figure 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 marine protected areas (MPAs) have been shown to increase total coral cover, although mostly through the cover of massive (i.e., stress-tolerant) coral growth forms³⁴. Our results also suggest that partial protection (i.e., gear restrictions) can be associated with similar increases in coral abundance as fully no-take areas. For corals, any type of management that reduces destructive practices can have direct benefits for coral survival and growth²⁸. While protection from local stressors may not increase coral

resilience³³, we find 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, reef zonation (i.e., depth and habitat), primary productivity, wave exposure, and cyclone intensity were also strongly associated with coral abundance (Figure 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 greater depths. Primary productivity and cyclone exposure were associated with fewer competitive, stress-tolerant and weedy corals, likely due to unfavourable conditions for coral growth in areas of eutrophication and high productivity³¹, or hydrodynamic breakage or dislodgement of coral colonies³⁵. 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 organisms³⁶. After controlling for method and sampling effort in the models (Figure 2), our results suggest that future comparative studies would benefit from standardized methods and replication to allow for faster comparative approaches for field-based monitoring³⁷, especially given the urgency of tracking changes to coral assemblages from climate change and bleaching events.

The four life histories showed some different responses than common genera (Supplementary Figure 2). For example, life histories were generally more sensitive to climate and social drivers (17 vs. 12 significant relationships for life histories compare to genera, respectively; Figure 2, Supplementary Figure 2). For example, competitive corals had stronger associations with two metrics of climate disturbance (years since maximum DHW and maximum DHW) compared to *Acropora* (a genus classified as competitive). Three of the four life histories showed positive associations with local management (no-take or restricted management) compared to only one genus (*Porites*, a stress-tolerant and weedy genus); *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 disturbance³⁸. However, further comparisons of life history and taxonomic responses, at both regional and local scales, are certainly warranted.

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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 bleaching event^{26,39}. The 2,584 reefs in our dataset were exposed to thermal stress ranging between 0 to 30.5 annual °C-weeks above summer maxima (i.e., Degree Heating Weeks, DHW) between 2014 and 2017 (Figure 3; Methods). Nearly three-quarters of the surveyed reefs (74.9%, n = 1,935 reefs) were exposed to greater than 4 °C-week DHW, a common threshold for ecologically significant bleaching and mortality³⁹ (Supplementary Figure 3). Previous studies have identified 10% hard coral cover as a minimum threshold for carbonate production on Caribbean⁴⁰ 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 levels⁵. 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}. 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%, suggesting the majority of reefs could sustain net-positive carbonate budgets prior to 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 (Figure 3). Considering these two thresholds of ecologically significant thermal stress (4 DHW) 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 2014-7 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

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stress, *transform* existing management, or ultimately assist societies to transform away from reef-dependent livelihoods (Figure 3).

A *protect* strategy was identified for 449 reefs (out of 2,584, or 17.4%), which were
345 exposed to minimal bleaching-level stress (<4 DHW during 2014-2017) and had >10% cover of
framework corals (Figure 3; Supplementary Table 5). These reefs were located throughout the
Indo-Pacific (Figure 4, 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
350 bleaching events. Policy actions include dampening the impacts of markets and nearby
populations, placing local restrictions on damaging fishing, pollution, or industrial activities
within potential refugia from climate change, 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
355 2,584, or 54.4%) exceeded 10% cover of framework corals but were likely exposed to severe
bleaching-level heat stress during 2014-2017 global bleaching event (i.e., >4 DHW). 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 natural
coral recovery. In this strategy, the goal is to move reefs back above the 10% threshold as
360 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 disturbances⁴², although often at high cost but
there are options for low-cost, long-term restoration⁴⁶. 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
365 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 which can also
370 accompany the *protect* and *recover* strategies.

We also investigated how combinations of key drivers could affect the predicted cover of framework corals (Figure 5). While certain combinations were predicted to reduce cover below a 10% threshold (e.g., 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 have not been shown to increase climate resistance or recovery³³. 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 spatially²⁵, and we can make no predictions about which reefs might escape future bleaching events or mortality from our dataset. 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^{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 reef⁴⁰, while our dataset consists primarily of planar two-dimensional methods that do not account for the vertical or three-dimensional components of coral colonies⁵⁰. 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 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 corals⁸.

Conclusions

400 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
405 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<sup>10–
12</sup>. 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
410 simple thresholds of potential ecological function (10% cover of framework corals) and recent
exposure to thermal stress (4 DHW); 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
415 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.

420 **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 (e.g., 1998, 2005, 2010), but were
425 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 corals⁵¹. A random subsampling method was used to evaluate the representation
of our dataset across Indo-Pacific coral reefs, whereby we compared locations of empirical

430 surveys to the global distribution of coral reefs by generating 2600 randomly selected Indo-Pacific coral reef sites using the R package *dismo*⁵² from a 500 m resolution tropical coral reef grid⁵³. Comparing our empirical surveys ($n = 2,584$ reefs) to the randomly generated reefs allowed us to estimate ecoregions with relative undersampling or oversampling (Supplementary Table 1).

435 Climate, social and environmental covariates were organized at three spatial scales¹⁹:

(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 shallower than 20
440 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 km was informed by the spatial movement patterns of artisanal coral reef fishing activities as used in a global analysis of global reef fish biomass¹⁹. We generated a
445 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 reefs (± 2.83) per site.

450 (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 France, the United Kingdom, and the United States were informed by their respective country.

455 **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
460 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), and 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.

The absolute percent cover of hard corals was evaluated to the taxonomic level of genus or
465 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 (1,506 reefs out of 2,584, or 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
470 classified each coral taxa to a life history type⁹; some species of *Pocillopora*, *Cyphastrea* and
Leptastrea were reclassified by expert coral taxonomists and ecologists⁵⁴. A representative list of
species and their life history types are 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*,
475 *Pocillopora*, *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 lists⁵¹. 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
480 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
485 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 Figure 4). This led to
490 the exclusion of four covariates: (i) local population size, (ii) national GDP per capita, (iii)
national voice and accountability, and (iv) years since extreme cyclone activity. A final set of 16
covariates was 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 (Supplementary Table 7, Supplementary Figure 4).

495 To quantify the influence of multi-scale social, human and environmental factors on hard
coral assemblages, we modelled the total percent cover of hard corals and the percent 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 nested within country; we
also included a random effect of coral faunal province to account for regional biogeographic
500 patterns⁵¹. 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 continuous response
data between 0 and 1⁵⁶. We incorporated weakly informative normal priors on the global
intercept (mean = 0, standard deviation = 10) and slope parameters (mean = 0, standard deviation
= 2), and a Student t prior on the Beta dispersion parameter (degrees of freedom = 3, mean = 0,
505 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 Figure 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 1000 for all parameters⁵⁷. We also conducted
510 posterior predictive checks and estimated Bayesian R^2 values for each model to examine
goodness of fit⁵⁸. All models were fit with Stan⁵⁹ and *brms*⁶⁰; analyses were conducted in R⁶¹.

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.

515 **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 Degree Heating Weeks (DHW) between 2014 and 2017 from NOAA's

520 CoralTemp dataset (Coral Reef Watch version 3.1; see Drivers section). Ecologically significant
bleaching and mortality can occur at different thresholds of thermal stress, likely between 2 and
4 DHW³⁹, 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 DHW).
525 Considerations of different DHW thresholds were highly correlated and identified similar ‘no-
regrets’ locations of limited thermal stress exposure between 2014 and 2017 (Supplementary
Figure 3).

For ecological condition, we assessed whether each reef had the potential for a net positive
carbonate budget prior to 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 (i.e. unstable equilibrium, or boundary point) for reef growth and
530 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 biomass⁶²⁻⁶⁴, and associated with some thresholds to undesirable algal-
dominated states at low levels of herbivore grazing and coral recruitment⁶⁵. As a sensitivity
535 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 percent cover recorded during monitoring may affect three-
dimensional processes on coral reefs, like carbonate production⁵⁰. Ultimately, applying
540 thresholds of recent extreme heat and reef 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 reefs below or above
10% cover of competitive and stress-tolerant corals. Using the Bayesian hierarchical models for
545 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

550 categorical predictors (habitat: reef slope; method: PIT); 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 with each level of management: fished, restricted management, and no-take management.

Data availability: All R code is available on <https://github.com/esdarling/IndoPacific-corals>.
555 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

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References

- 580 1. Norström, A. V. *et al.* Guiding coral reef futures in the Anthropocene. *Front. Ecol. Environ.* **14**, 490–498 (2016).
2. Williams, G. J. *et al.* Coral reef ecology in the Anthropocene. *Funct. Ecol.* **33**, 1014–1022 (2019).
3. Frieler, K. *et al.* Limiting global warming to 2 °C is unlikely to save most coral reefs. *Nat.*
585 *Clim. Change* **3**, 165–170 (2013).
4. Hughes, T. P. *et al.* Global warming transforms coral reef assemblages. *Nature* **556**, 492–496 (2018).
5. Perry, C. T. *et al.* Loss of coral reef growth capacity to track future increases in sea level. *Nature* **558**, 396–400 (2018).
- 590 6. Guest, J. R. *et al.* A framework for identifying and characterising coral reef “oases” against a backdrop of degradation. *J. Appl. Ecol.* **55**, 2865–2875 (2018).
7. Denis, V., Ribas-Deulofeu, L., Sturaro, N., Kuo, C.-Y. & Chen, C. A. A functional approach to the structural complexity of coral assemblages based on colony morphological features. *Sci. Rep.* **7**, (2017).
- 595 8. González-Barrios, F. J. & Álvarez-Filip, L. A framework for measuring coral species-specific contribution to reef functioning in the Caribbean. *Ecol. Indic.* **95**, 877–886 (2018).
9. Darling, E. S., Alvarez-Filip, L., Oliver, T. A., McClanahan, T. R. & Côté, I. M. Evaluating life-history strategies of reef corals from species traits. *Ecol. Lett.* **15**, 1378–1386 (2012).
10. Perry, C. T. & Alvarez-Filip, L. Changing geo-ecological functions of coral reefs in the
600 Anthropocene. *Funct. Ecol.* **33**, 976–988 (2019).

11. Wilson, S. K., Robinson, J. P. W., Chong-Seng, K., Robinson, J. & Graham, N. A. J. Boom and bust of keystone structure on coral reefs. *Coral Reefs* (2019). doi:10.1007/s00338-019-01818-4
12. Darling, E. S. *et al.* Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs* **36**, 561–575 (2017).
- 605
13. Robinson, J. P. W. *et al.* Productive instability of coral reef fisheries after climate-driven regime shifts. *Nat. Ecol. Evol.* **3**, 183–190 (2019).
14. Alvarez-Filip, L., Carricart-Ganivet, J. P., Horta-Puga, G. & Iglesias-Prieto, R. Shifts in coral-assemblage composition do not ensure persistence of reef functionality. *Sci. Rep.* **3**, 3486 (2013).
- 610
15. Darling, E. S., McClanahan, T. R. & Côté, I. M. Life histories predict coral community disassembly under multiple stressors. *Glob. Change Biol.* **19**, 1930–1940 (2013).
16. Graham, N. A. J., Chong-Seng, K. M., Huchery, C., Januchowski-Hartley, F. A. & Nash, K. L. Coral reef community composition in the context of disturbance history on the Great Barrier Reef, Australia. *PLoS ONE* **9**, e101204 (2014).
- 615
17. Sommer, B., Harrison, P. L., Beger, M. & Pandolfi, J. M. Trait-mediated environmental filtering drives assembly at biogeographic transition zones. *Ecology* **95**, 1000–1009 (2014).
18. Kayal, M. *et al.* Predicting coral community recovery using multi-species population dynamics models. *Ecol. Lett.* **21**, 1790–1799 (2018).
- 620
19. Cinner, J. E. *et al.* Bright spots among the world’s coral reefs. *Nature* **535**, 416–419 (2016).
20. Kittinger, J. N., Finkbeiner, E. M., Glazier, E. W. & Crowder, L. B. Human dimensions of coral reef social-ecological systems. *Ecol. Soc.* **17**, 17 (2012).

21. Gilmour, J. P., Smith, L. D., Heyward, A. J., Baird, A. H. & Pratchett, M. S. Recovery of an isolated coral reef system following severe disturbance. *Science* **340**, 69–71 (2013).
- 625 22. Graham, N. A. J., Jennings, S., MacNeil, M. A., Mouillot, D. & Wilson, S. K. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* **518**, 94–97 (2015).
23. Green, D. H., Edmunds, P. J. & Carpenter, R. C. Increasing relative abundance of *Porites astreoides* on Caribbean reefs mediated by an overall decline in coral cover. *Mar. Ecol. Prog. Ser.* **359**, 1–10 (2008).
- 630 24. Montaggioni, L. F. History of Indo-Pacific coral reef systems since the last glaciation: Development patterns and controlling factors. *Earth-Sci. Rev.* **71**, 1–75 (2005).
25. Hughes, T. P. *et al.* Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* **359**, 80–83 (2018).
- 635 26. Claar, D. C., Szostek, L., McDevitt-Irwin, J. M., Schanze, J. J. & Baum, J. K. Global patterns and impacts of El Niño events on coral reefs: A meta-analysis. *PLOS ONE* **13**, e0190957 (2018).
27. Januchowski-Hartley, F. A., Graham, N. A. J., Wilson, S. K., Jennings, S. & Perry, C. T. Drivers and predictions of coral reef carbonate budget trajectories. *Proc. R. Soc. B Biol. Sci.* **284**, 20162533 (2017).
- 640 28. McManus, J. W., Reyes, B. R. & Nañola, C. L. Effects of some destructive fishing methods on coral cover and potential rates of recovery. *Environ. Manage.* **21**, 69–78 (1997).
29. Pollock, F. J. *et al.* Sediment and turbidity associated with offshore dredging increase coral disease prevalence on nearby reefs. *PLoS ONE* **9**, e102498 (2014).

- 645 30. Dixon, D. L., Abrego, D. & Hay, M. E. Chemically mediated behavior of recruiting corals and fishes: A tipping point that may limit reef recovery. *Science* **345**, 892–897 (2014).
31. Costa, O. S., Leão, Z. M. A. N., Nimmo, M. & Attrill, M. J. Nutrifcation impacts on coral reefs from northern Bahia, Brazil. in *Island, Ocean and Deep-Sea Biology* (eds. Jones, M. B., Azevedo, J. M. N., Neto, A. I., Costa, A. C. & Martins, A. M. F.) 307–315 (Springer
650 Netherlands, 2000). doi:10.1007/978-94-017-1982-7_28
32. Cinner, J. How behavioral science can help conservation. *Science* **362**, 889–890 (2018).
33. Bruno, J. F., Côté, I. M. & Toth, L. T. Climate change, coral loss, and the curious case of the parrotfish paradigm: why don't marine protected areas improve reef resilience? *Annu. Rev. Mar. Sci.* **11**, 307–334 (2019).
- 655 34. Strain, E. M. A. *et al.* A global assessment of the direct and indirect benefits of marine protected areas for coral reef conservation. *Divers. Distrib.* **25**, 9–20 (2019).
35. Madin, J. S. & Connolly, S. R. Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature* **444**, 477–480 (2006).
36. Robinson, J. P. W. *et al.* Environmental conditions and herbivore biomass determine coral
660 reef benthic community composition: implications for quantitative baselines. *Coral Reefs* **37**, 1157–1168 (2018).
37. Edmunds, P. *et al.* Why more comparative approaches are required in time-series analyses of coral reef ecosystems. *Mar. Ecol. Prog. Ser.* **608**, 297–306 (2019).
38. Zawada, K. J. A., Madin, J. S., Baird, A. H., Bridge, T. C. L. & Dornelas, M. Morphological
665 traits can track coral reef responses to the Anthropocene. *Funct. Ecol.* **33**, 962–975 (2019).
39. Skirving, W. J. *et al.* The relentless march of mass coral bleaching: a global perspective of changing heat stress. *Coral Reefs* (2019). doi:10.1007/s00338-019-01799-4

40. Perry, C. T. *et al.* Caribbean-wide decline in carbonate production threatens coral reef growth. *Nat. Commun.* **4**, 1402 (2013).
- 670 41. Perry, C. T. *et al.* Remote coral reefs can sustain high growth potential and may match future sea-level trends. *Sci. Rep.* **5**, 18289 (2016).
42. Harvey, B. J., Nash, K. L., Blanchard, J. L. & Edwards, D. P. Ecosystem-based management of coral reefs under climate change. *Ecol. Evol.* (2018). doi:10.1002/ece3.4146
43. Beyer, H. L. *et al.* Risk-sensitive planning for conserving coral reefs under rapid climate change. *Conserv. Lett.* e12587 (2018). doi:10.1111/conl.12587
- 675 44. Hughes, T. P. *et al.* Coral reefs in the Anthropocene. *Nature* **546**, 82–90 (2017).
45. van Hooidonk, R. *et al.* Local-scale projections of coral reef futures and implications of the Paris Agreement. *Sci. Rep.* **6**, 39666 (2016).
46. Fox, H. E. *et al.* Rebuilding coral reefs: success (and failure) 16 years after low-cost, low- tech restoration. *Restor. Ecol.* rec.12935 (2019). doi:10.1111/rec.12935
- 680 47. Cinner, J. E. *et al.* Building adaptive capacity to climate change in tropical coastal communities. *Nat. Clim. Change* **8**, 117–123 (2018).
48. Sen, A. The ends and means of sustainability. *J. Hum. Dev. Capab.* **14**, 6–20 (2013).
49. Bellwood, D. R., Streit, R. P., Brandl, S. J. & Tebbett, S. B. The meaning of the term ‘function’ in ecology: a coral reef perspective. *Funct. Ecol.* **33**, 948–961 (2019).
- 685 50. Goatley, C. H. R. & Bellwood, D. R. The roles of dimensionality, canopies and complexity in ecosystem monitoring. *PLoS ONE* **6**, e27307 (2011).
51. Keith, S. A., Baird, A. H., Hughes, T. P., Madin, J. S. & Connolly, S. R. Faunal breaks and species composition of Indo-Pacific corals: the role of plate tectonics, environment and habitat distribution. *Proc. R. Soc. B Biol. Sci.* **280**, 20130818 (2013).
- 690

52. Hijmans, Robert J., Phillips, S. & Elith, J. *dismo: Species Distribution Modeling*. R package version 1.1-4. (2017). Available at: <https://CRAN.R-project.org/package=dismo>.
53. Burke, L. M., Reytar, K., Spalding, M. & Perry, A. *Reefs at Risk Revisited*. (World Resources Institute, 2011).
- 695 54. Zinke, J. *et al.* Gradients of disturbance and environmental conditions shape coral community structure for south-eastern Indian Ocean reefs. *Divers. Distrib.* **24**, 605–620 (2018).
55. Madin, J. S. *et al.* The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Sci. Data* **3**, 160017 (2016).
- 700 56. Ferrari, S. & Cribari-Neto, F. Beta regression for modelling rates and proportions. *J. Appl. Stat.* **31**, 799–815 (2004).
57. Gelman, A. *et al.* *Bayesian Data Analysis*. (Chapman and Hall/CRC, 2013).
58. Gelman, A., Goodrich, B., Gabry, J. & Ali, I. R-squared for Bayesian regression models. (2017). Available at:
- 705 http://www.stat.columbia.edu/~gelman/research/unpublished/bayes_R2.pdf.
59. Stan Development Team. *Stan Modeling Language Users Guide and Reference Manual, Version 2.18.0*. (2018).
60. Bürkner, P.-C. brms: An R Package for Bayesian Multilevel Models Using Stan. *J. Stat. Softw.* **80**, 1–28 (2017).
- 710 61. R Core Team. *R: A Language and Environment for Statistical Computing*. (R Foundation for Statistical Computing, Vienna, Austria., 2018).

62. Lamy, T., Galzin, R., Kulbicki, M., Lison de Loma, T. & Claudet, J. Three decades of recurrent declines and recoveries in corals belie ongoing change in fish assemblages. *Coral Reefs* **35**, 293–302 (2016).
- 715 63. Beldade, R., Mills, S. C., Claudet, J. & Côté, I. M. More coral, more fish? Contrasting snapshots from a remote Pacific atoll. *PeerJ* **3**, e745 (2015).
64. Harborne, A. R. *et al.* Modelling and mapping regional-scale patterns of fishing impact and fish stocks to support coral-reef management in Micronesia. *Divers. Distrib.* **24**, 1729–1743 (2018).
- 720 65. Mumby, P. J. Embracing a world of subtlety and nuance on coral reefs. *Coral Reefs* **36**, 1003–1011 (2017).

Figure captions

Figure 1. Indo-Pacific patterns of reef coral assemblages. (a) Percent cover of four coral life 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 with a representative genus, from left to right: fast-growing competitive (*Acropora*); slow-growing and long-lived massive stress-tolerant (*Platygyra*); sub-dominant generalists (*Echinopora*); fast-growing brooding weedy taxa (*Pavona*). (c) Distribution of abundance (percent 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 Supplementary Figure 1.

Figure 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 grey circles indicate an overlap with zero and a less credible trend. DHW indicates Degree Heating Weeks; HDI is 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 four dominant coral genera are shown in Supplementary Figure 2.

Figure 3. Strategic management portfolio of *protect*, *recover*, and *transform* for Indo-Pacific coral reefs. The 2,584 reefs varied in their ecological condition (assessed at 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, or 17.4%) that were associated with limited exposure to recent bleaching-level thermal stress (<4 DHW) 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; $n = 1407$, or 54.5%). As coral cover falls below potential net-positive carbonate budgets (i.e., <10% hard coral cover), a transformation is needed for existing management or ultimately, the dependence of societies on reef-dependent livelihoods (grey dots; $n = 728$, or 28.2%).

Figure 4. Three management strategies of a) *protect*, b) *recover*, and c) *transform* are distributed throughout the Indo-Pacific, suggesting there remain opportunities to sustain a network of functioning reefs, while supporting coral recovery or social transformations for the majority of reefs. Strategies are not restricted by geography and distributed across reefs in the Indo-Pacific region.

Figure 5. Combinations of key social and environmental 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 $\log(\text{values})$. Results are predicted separately for three management categories: fished, restricted, or no-take reserves.