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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-century[3]. Against a backdrop of globalized anthropogenic stressors, the impacts of climate change can transform coral communities[4] and reduce coral growth rates that are crucial to maintain reef structure and track rising sea levels[5]. Under expectations of continued reef degradation and reassembly in the Anthropocene, urgent actions must be taken to protect and manage the world's remaining coral reefs. Given such concerns about the long-term functional erosion of coral communities, one conservation strategy is to prioritize the protection of reefs that currently maintain key ecological functions, 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 – 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 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 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 history types previously developed from a trait-based approach with species characteristics of colony morphology, growth, calcification, and reproduction[9] (https://coraltraits.org). The abundance of different coral taxa can affect key ecological processes for future reef persistence, including the provision of reef structural complexity, carbonate production (the process by which corals and some other organisms lay down carbonate on the reef), and ultimately reef growth (the vertical growth of the reef system resulting from the processes of carbonate production and erosion)[5,7,8,10]. Fast-growing branching, plating and densely calcifying massive coral taxa that can contribute to these processes are expected to be functionally important, not only by maintaining critical geo-ecological functions that coral reefs provide[10], but might also help reefs track sea level rise[5], recover from climate disturbances[11], and sustain critical habitat for reef fish and fisheries[12,13].

Here, we adopt a previous classification of four coral life history types to evaluate Indo-Pacific patterns of total coral abundance and the composition of coral assemblages, and their key social-environmental drivers. Specifically, we consider four coral life histories[9] (Supplementary

Table 2): a ‘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; 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 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 a coral assemblage provides a signal of past disturbance histories or environmental conditions[15–17] that may affect resilience and persistence to future climate impacts[18].

Drawing on theoretical and empirical studies of coral reef social-ecological systems[19,20], we tested the influence of 21 social, climate, and environmental covariates on coral abundance, while controlling for sampling methodologies and biogeography (Supplementary Table 3). These include: (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 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 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 ± SD, 23.7 ± 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 corals[24], a warning sign considering recent community shifts in the Caribbean[23].

Climate, social and environmental drivers

Climate variables describing the frequency and intensity of past thermal stress events strongly affected coral assemblages. Reefs with more extreme past climate disturbances (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 Indonesia[7], the Seychelles[11], and Kenya[15] 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 practices[28], tourism, or industrial activities[29], or indirect effects on coral growth associated with the overexploitation of grazing herbivorous fishes that control macroalgae[30] or declining water quality that can increase sediments and nutrients to smother or sicken corals[31]. We also observed two positive associations of coral abundance with human use: generalist corals increased near agricultural land use, and weedy corals increased near larger and more accessible markets. In some cases, these relationships require further investigation; for example, the abundance of generalists (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 change[32]) to promote structurally complex and calcifying reefs that can sustain important ecological functions.

Local management actions in the form of no-take reserves or restricted management (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 forms[34]. 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 growth[28]. While protection from local stressors may not increase coral resilience[33], 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 productivity[31], or hydrodynamic breakage or dislodgement of coral colonies[35]. These findings suggest that environmental conditions are important in predicting conservation baselines and guiding management investments. For example, restoring or maintaining grazer functions when environmental conditions can support abundant corals and other calcifying organisms[36]. After controlling for method and sampling effort in the models (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 monitoring[37], 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 disturbance[38]. However, further comparisons of life history and taxonomic responses, at both regional and local scales, are certainly warranted.

Management strategies in the Anthropocene

The livelihoods of millions of people in the tropics depend on healthy and productive coral reefs[19,20], yet coral reefs worldwide are imperilled by climate change[3,25]. Between 2014 and 2017, reefs worldwide experienced an unprecedented long, extensive, and damaging El Niño and global 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 mortality[39] (Supplementary Figure 3). Previous studies have identified 10% hard coral cover as a minimum threshold for carbonate production on Caribbean[40] and Indo-Pacific[27,41] reefs. Below this threshold (or 'boundary point'), reefs are more likely to have a neutral or negative carbonate budget and may succumb to reef submergence with rising sea levels[5]. Here, we adapt this threshold by considering only the live cover of competitive and stress-tolerant corals (hereafter, 'framework' corals) since these are two life histories that can build large, structurally-complex colonies to maintain carbonate production and vertical reef growth[10,12,27]. 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 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 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 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 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 quickly as possible following climate impacts. Active management to restore habitat with natural or artificial complexity, coral 'gardening', or human-assisted evolution could be considerations to quickly recover coral cover following climate disturbances[42], although often at high cost but there are options for low-cost, long-term restoration[46]. 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, 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 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 recovery[33]. Thus, addressing global climate change is paramount.

Our dataset describes contemporary coral assemblages within a period of escalating thermal stress, notably following the 1998 bleaching event[26,39]. Patterns of coral bleaching vary spatially[25], and we can make no predictions 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 reef[40], while our dataset consists primarily of planar two-dimensional methods that do not account for the vertical or three-dimensional components of coral colonies[50]. Thus, the 10% threshold should be considered an uncertain, but potentially precautionary, threshold of net carbonate production and reef growth, and a sensitivity analysis considering this threshold at 8% or 12% cover suggests a three-strategy framework is robust to uncertainty around these thresholds (Supplementary Table 5). Future work can help refine these thresholds by considering species-specific contributions to structural complexity and carbonate production, as has been recently developed for Caribbean corals[8].

Conclusions

Facing an Anthropocene future of intensifying climate change and globalized anthropogenic impacts[1,2,39], coral reef conservation must be more strategic by explicitly incorporating climate impacts and ecological functioning into priority actions for conservation and management. Given expectations that coral assemblages will shift towards smaller and simpler morphologies and slower growth rates to jeopardize reef function[4,7,15], our findings highlight the importance of urgently protecting and managing reefs that support assemblages of large, complex branching, plating and massive taxa that build keystone structure on coral reefs[10–12]. Our findings reveal key drivers of coral assemblages, and identify some locations where societies can immediately enact strategic management to protect, recover, or transform coral reefs. Our framework also provides a way to classify management strategies based on relatively simple thresholds of potential ecological function (10% cover of framework corals) and recent exposure to thermal stress (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 emissions. The widespread persistence of functioning coral assemblages requires urgent and effective action to limit warming to 1.5˚C. Our findings suggest there is still time for the strategic conservation and management of the world's last functioning coral reefs, providing some hope for global coral reef ecosystems and the millions of people who depend on them.

Methods

We conducted coral community surveys along 8,209 unique transects from 2,584 reefs throughout the Indian and Pacific Oceans, covering ~277 km of surveyed coral reef. Our dataset provides a contemporary Indo-Pacific snapshot of coral communities between 2010 and 2016; surveys occurred following repeated mass bleaching events (e.g., 1998, 2005, 2010), but were not influenced by widespread mortality during the 2014-2017 global coral bleaching event. Surveyed reefs spanned 61.2 degrees of latitude (32.7°S to 28.5°N) and 219.3 degrees of longitude (35.3°E to 105.4°W), and represented each of the 12 coral faunal provinces described for Indo-Pacific corals[51]. A random subsampling method was used to evaluate the representation of our dataset across Indo-Pacific coral reefs, whereby we compared locations of empirical 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 grid[53]. 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).

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

(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 ± standard deviation, 8.9 ± 5.6 m), though the majority of surveys (98.8%) occurred 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 km was informed by the spatial movement patterns of artisanal coral reef fishing activities as used in a global analysis of global reef fish biomass[19]. We generated a complete-linkage hierarchical cluster dendrogram based on great-circle distances between each point of latitude and longitude, and then used the centroid of each cluster to estimate site-level social, climate and environmental covariates (Supplementary Table 3). This provided a median of 2.0 reefs (+/- 2.83) per site.

(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.

Coral communities and life histories. At each reef, underwater surveys were conducted using one of three standard transect methods: point-intercept transects (n = 1,628 reefs), line-intercept transects (n = 399 reefs) and photo quadrats (n = 557 reefs). We estimated sampling effort as the total number of sampled points during each reef survey. Line-intercept transects were estimated with sampling points every 5 cm, since most studies only estimate the length of corals greater than 3 or 5 cm (T. McClanahan, A. Baird pers. comm). On average, the number of sampling points was 300.0 ± 750.0 (median ± 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 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 classified each coral taxa to a life history type[9]; some species of Pocillopora, Cyphastrea and Leptastrea were reclassified by expert coral taxonomists and ecologists[54]. A representative list of species and their life history types 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, 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 lists[51]. In total, we were able to classify 97.2% of surveyed coral cover to a life history. We then summed coral cover within each of the four life histories on each reef.

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

Analysis of drivers. We first assessed multicollinearity among the different covariates by evaluating variance inflation factors (Supplementary Table 7) and Pearson correlation coefficients between pairwise combinations of covariates (Supplementary Figure 4). 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 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).

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 patterns[51]. 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 1[56]. 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, 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 parameters[57]. We also conducted posterior predictive checks and estimated Bayesian R^2 values for each model to examine goodness of fit[58]. All models were fit with Stan[59] and brms[60]; analyses were conducted in R[61].

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

Strategic portfolios. We developed three management strategies (protect, recover, or transform) based on the potential thermal stress experienced during the 2014-2017 bleaching event, and a reef's previous observed ecological condition. To evaluate potential thermal stress, we estimated the maximum annual Degree Heating Weeks (DHW) between 2014 and 2017 from NOAA's

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 DHW[39], and this range of thresholds also represents the lowest quintile of DHW exposure for the 2,584 reefs during the 2014-2017 global bleaching event (20th quintile = 3.2 DHW). Considerations of different DHW thresholds were highly correlated and identified similar 'no-regrets' locations of limited thermal stress exposure between 2014 and 2017 (Supplementary 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 carbonate production, whereby 10% hard coral cover is a key threshold above which reefs are more likely to maintain a positive carbonate budget and therefore net reef growth[27,40,41]. Additionally, 10% coral cover is suggested to be a threshold for reef fish communities and standing stocks of biomass[62–64], and associated with some thresholds to undesirable algal-dominated states at low levels of herbivore grazing and coral recruitment[65]. As a sensitivity analysis for the 10% coral cover threshold, we considered how 8% and 12% coral cover thresholds would affect the distribution of conservation strategies across the 2,584 reefs (Supplementary Table 5). This sensitivity analysis also helps account for the uncertainty in how two-dimensional planar estimates of percent cover recorded during monitoring may affect three-dimensional processes on coral reefs, like carbonate production[50]. Ultimately, applying 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 competitive and stress-tolerant corals, we predicted coral cover across a range of observed values for five key covariates: population gravity, market gravity, years since maximum DHW, primary productivity, and cyclone exposure. For each covariate combination, we kept all other parameters at their median values for continuous predictors, or their reference value for categorical predictors (habitat: reef slope; method: 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. 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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Author contributions E.S.D. envisioned and led the project, performed all analyses, secured funding for, 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.

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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(values). Results are predicted separately for three management categories: fished, restricted, or no-take reserves.

Supplementary Information for

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

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This PDF file includes:

- Supplementary Acknowledgements
- Supplementary Methods
- Supplementary Figures 1 to 7
- Supplementary Tables 1 to 8

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Supplementary Methods

Description of covariates To evaluate the relative influence of climate, social and environmental drivers on coral communities, we identified a suite of covariates at reef, site and country scales (Table S3). Descriptions, data sources and rationale are provided below for each covariate.

Local population growth. We created a 100 km buffer around each site and estimated local human population sizes in 2000 and 2010 using a global gridded population database from the NASA Socioeconomic Data and Applications Center (SEDAC) at http://sedac.ciesin.columbia.edu/data/collection/groads/maps/gallery/search, and queried from the Marine Socio-Environmental Covariates online platform (MSEC: shiny.sesync.org/apps/msec) (S1). We also estimated annual population growth within each buffer between 2000 and 2010. A 100 km buffer was selected as a reasonable scale of human influences on coral reefs (e.g., fishing, water quality and land use) and to match previous global analyses of reef fishes (19)

Gravity. Drawing on economic geography, 'gravity' is an indicator of potential interactions between human populations and coral communities, which accounts for both the size of human populations and accessibility of coral reefs to nearby human settlements and markets. Gravity metrics were estimated using a density-decay function, where the population estimate of the nearest settlement or market was divided by the squared 'least-cost' travel time (minutes) between the population and the reef site (S2, S3). Here, we estimated two metrics of gravity within 500 km buffers around each site: (i) the gravity of the nearest human settlement, and (ii) the cumulated gravity of provincial capital cities, major population centers, landmark cities, national capitals, and ports. The gravity of the nearest settlement can provide an indicator of the direct impacts of local fishing, coastal development or land-based runoff, while market gravity can evaluate market-driven influences on coral reef fish biomass and fisheries. A 500 km buffer was chosen as the maximum distance any non-market fishing or land use activities could influence coral reefs.

Local management. We determined the local management of each reef at the time of survey as: openly fished with no access restrictions; restricted management, with some active partial restrictions on fishing gear, catch size, species or access; or fully no-take with full restriction on fishing activities within the borders of a no-take marine reserve. We did not assess management age, size or compliance in this study, and future studies of management rules or the capacity to enforce those rules can provide more information on management effectiveness.

Agricultural use. Using a global land cover database resolved to 5 arc-minutes (~10 km; Global Land Cover Facility, http://glcf.umd.edu/data/lc/), we estimated the percent of land area classified as croplands within a 100 km buffer of each site. We estimated the percent cover of croplands within each buffer in 2012, and the change in percent cover of croplands between 2002 and 2012. Our estimates could be improved by accounting for direct links between watershed catchments, ocean currents and tidal flushing, but this was not possible in the current analysis.

National governance. We used the Human Development Index (HDI) (United Nations Development Program, http://hdr.undp.org/en/content/human-development-index-hdi) as a composite indicator of human development, based on national statistics of life expectancy, education, and per capita income. We also estimated national metrics of GDP per capita and a World Bank Index of Voice and Accountability. National indices can provide some estimate of the resources and capital available to natural resource management and conservation, although it can overlook local tenure and governance in some countries.

Past thermal stress. We assessed thermal stress using Coral Temp, a 32-year record of daily gap-free global sea surface temperatures (SSTs) between 1985 and 2017 at a spatial resolution of 0.05 degrees produced by NOAA's Coral Reef Watch (https://coralreefwatch.noaa.gov/). For each year prior to the date of survey, we determined the maximum annual degree heating weeks (DHWs) and extracted the highest annual value during the entire time series as an indication of the strongest past thermal stress event. We also extracted the calendar year that this event occurred and calculated the number of years between the strongest past thermal anomaly and the year of survey. DHWs are a standard metric used to characterize warming thresholds + 1°C above a baseline summer maximum and commonly used to predict coral bleaching and coral disease outbreaks, and can be highly correlated with other metrics of thermal stress (e.g., HotSpots, summer SSTs and warm season variability) (44).

Primary productivity. Estimates of primary productivity were produced by NOAA Coast Watch (https://coastwatch.pfeg.noaa.gov)and made available by the MSEC online platform (S1). Data were extracted and processed from 8-day composite layers based on satellite measurements of photosynthetically available radiation, sea surface temperatures, and chlorophyll a concentrations; a general mean was estimated for each site between 2003-2013.

Depth. The depth, m, of each survey was identified to the nearest meter by each data provider.

Habitat. We assessed reef habitat as, (i) slope, typically occurring on the ocean side of a reef as it slopes down into deeper waters; (ii) crest, the section that joins the slope and flat, typically associated with higher wave energy; (iii) reef flat, a horizontal habitat that can extend 10s to 100s of meters from the reef to the shore and include lagoon and back reef habitats typically sheltered from wave energy but exposed to high variation in daily tides and temperature. Habitat classifications were provided by each data contributor.

Wave exposure. We estimated the general mean wave energy (kW/m) for each site from NOAA WAVEWATCH III hindcast models, accessed using the MSEC online platform (S1). Wave energy estimates are based on significant wave height, peak period and direction of waves, and the speed and direction of wind using a 31-year dataset (1979-2009) and a 3-hour temporal resolution of measurements.

Cyclones. Disturbances and recovery time associated with tropical cyclones were extracted from a global dataset (1985-2009; S4) For each site, we calculated the maximum annual number of days of potential exposure to extreme cyclone conditions, defined as exposure to gale force winds or higher. We then extracted the highest annual number of extreme cyclone days for each site and recorded the calendar year when each exposure occurred. Our variable of potential recovery time from cyclone influences was the number of years between the maximum cyclone exposure and survey year. Sites with no potential exposure to cyclones through the entire time series (e.g., zero maximum tropical cyclone days, equatorial locations) were recorded as having 30 years of potential recovery time since no cyclone events occurred in the time series.

Habitat connectivity. We extracted the total amount of available reef habitat within a 100 km buffer of each site as the effect of habitat availability or isolation has been identified as a previous driver of regional-scale community assembly for reef corals (S5). We chose 100 km arbitrarily, as previous studies have also shown this scale to have identical results to larger buffers of 200 km and 600 km for reef fish diversity (S5). Estimates were produced from a 500 m gridded global dataset produced by the Reefs at Risk Revisited project of the World Resources Institute and queried from the MSEC online platform (S1).

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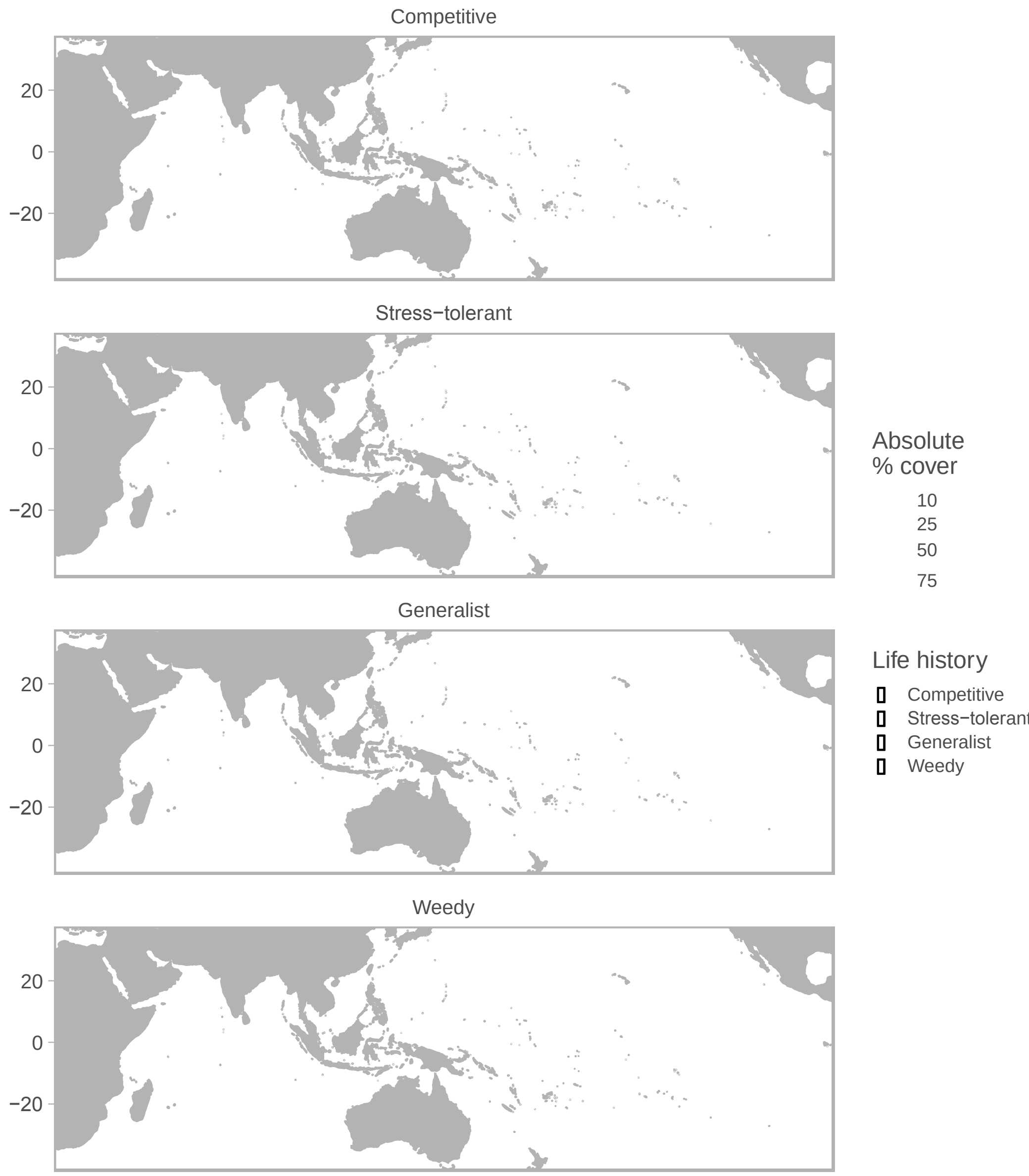
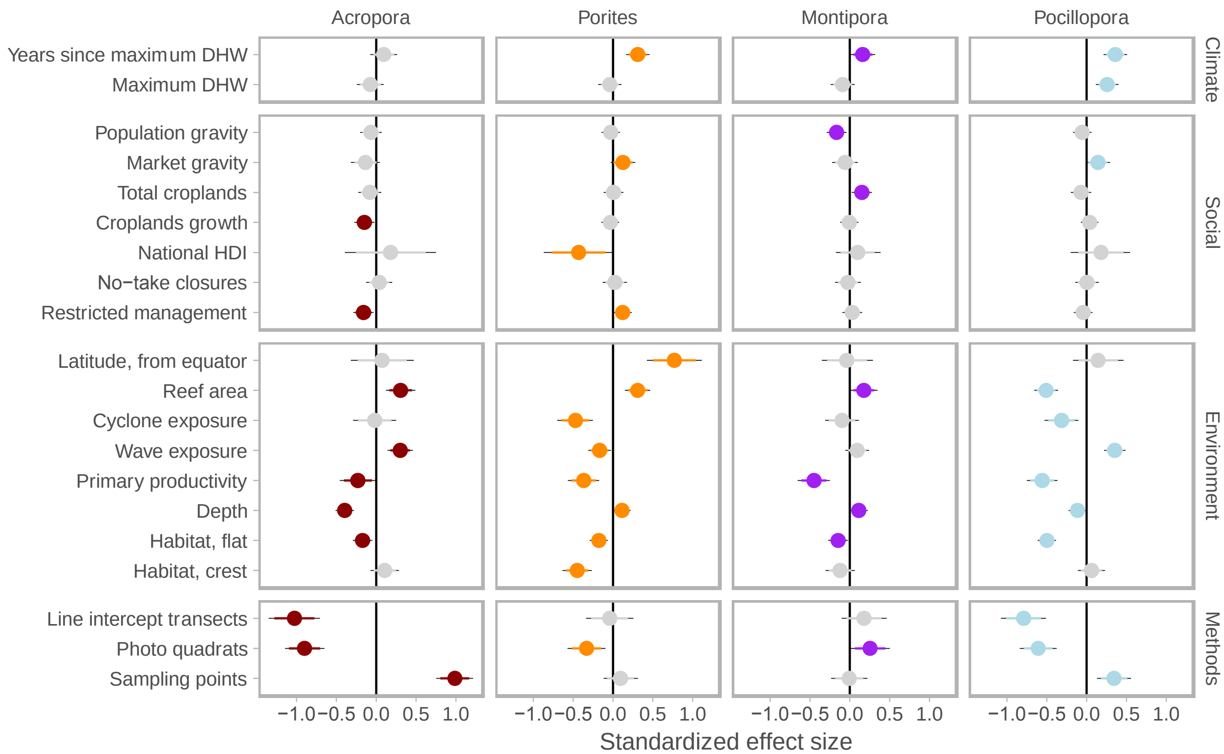
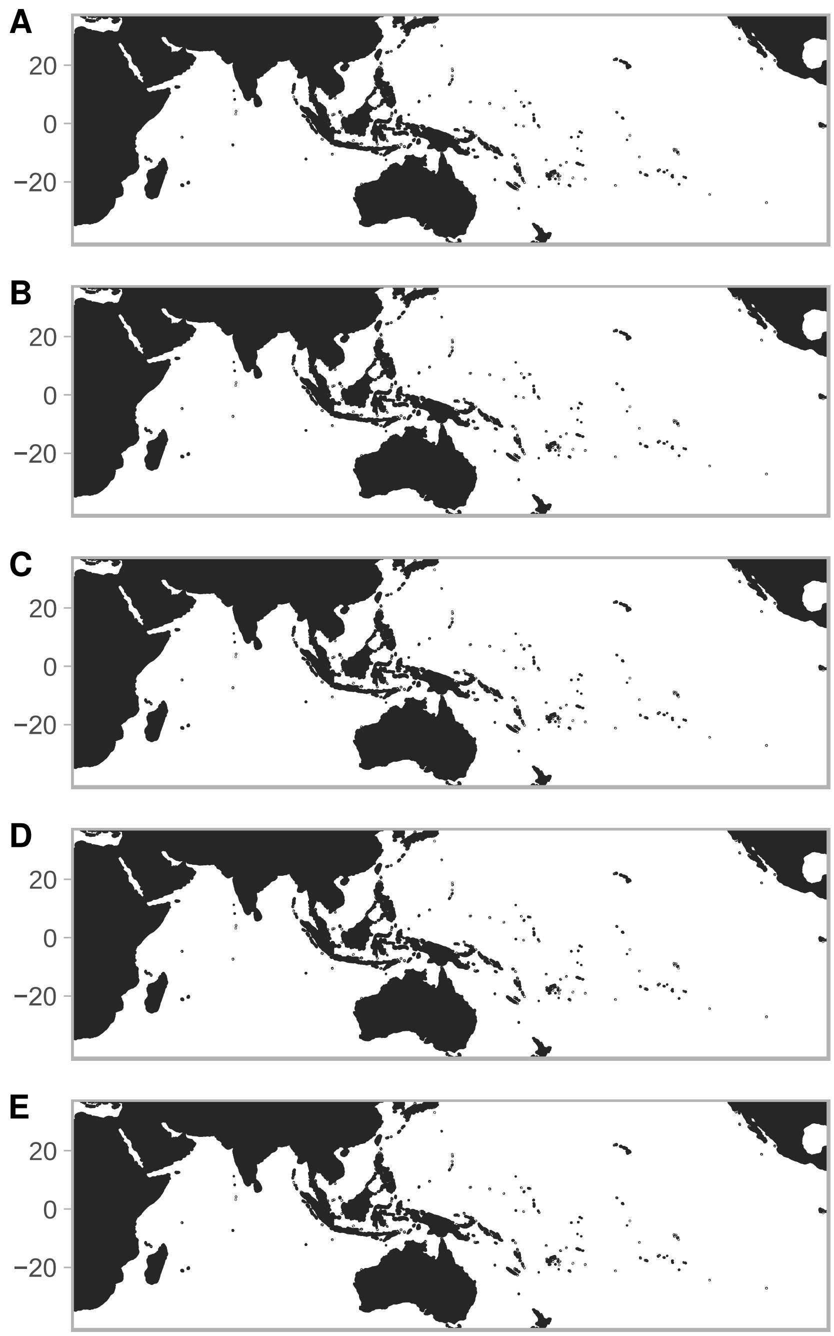


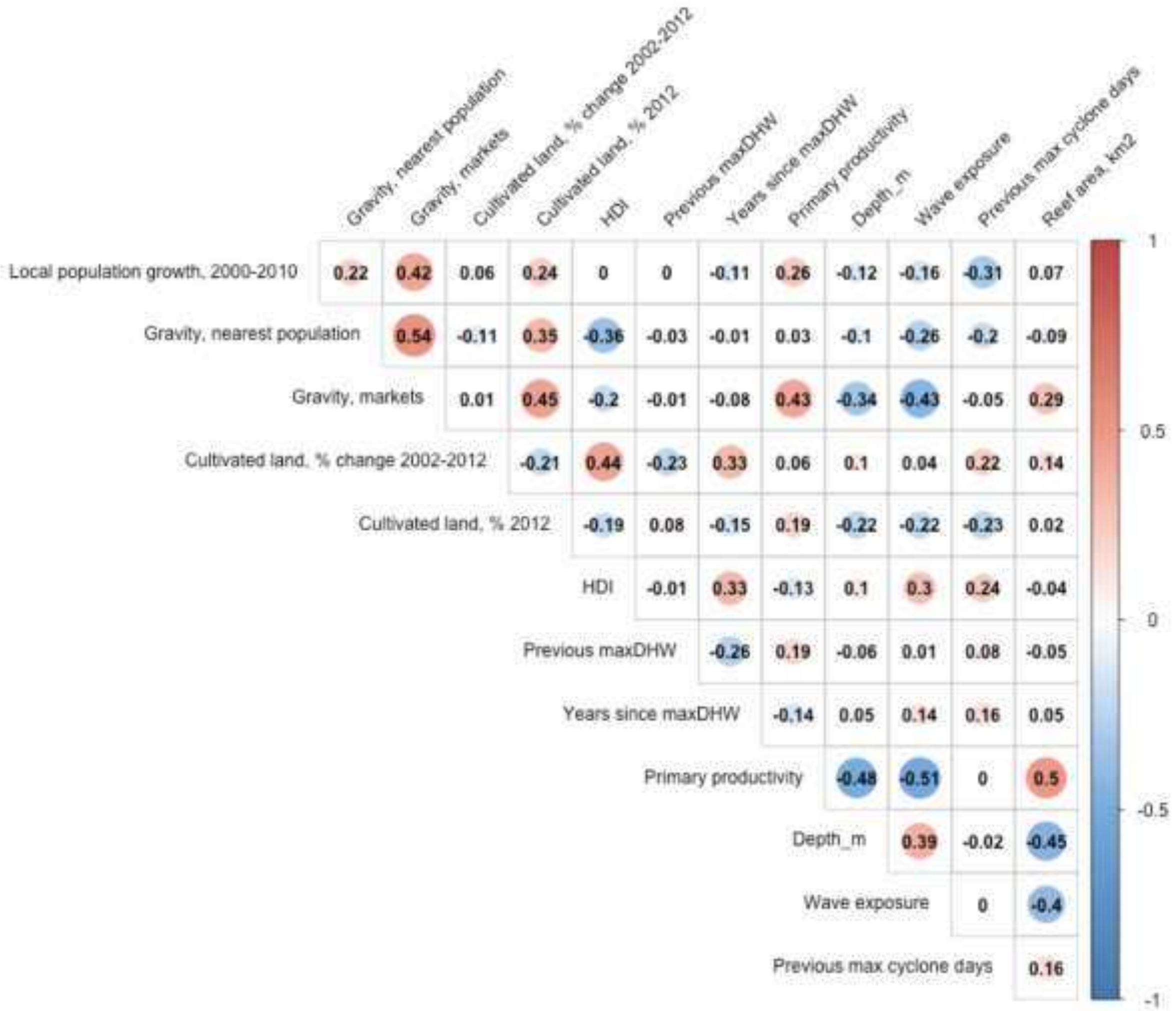
Supplementary Figure 1. Indo-Pacific patterns of reef coral assemblages separated by each life history, based on 2,584 coral reef surveys in 44 nations and territories. Colour indicates life history and circle size indicates percent cover. Points are slightly transparent to show overlapping records.



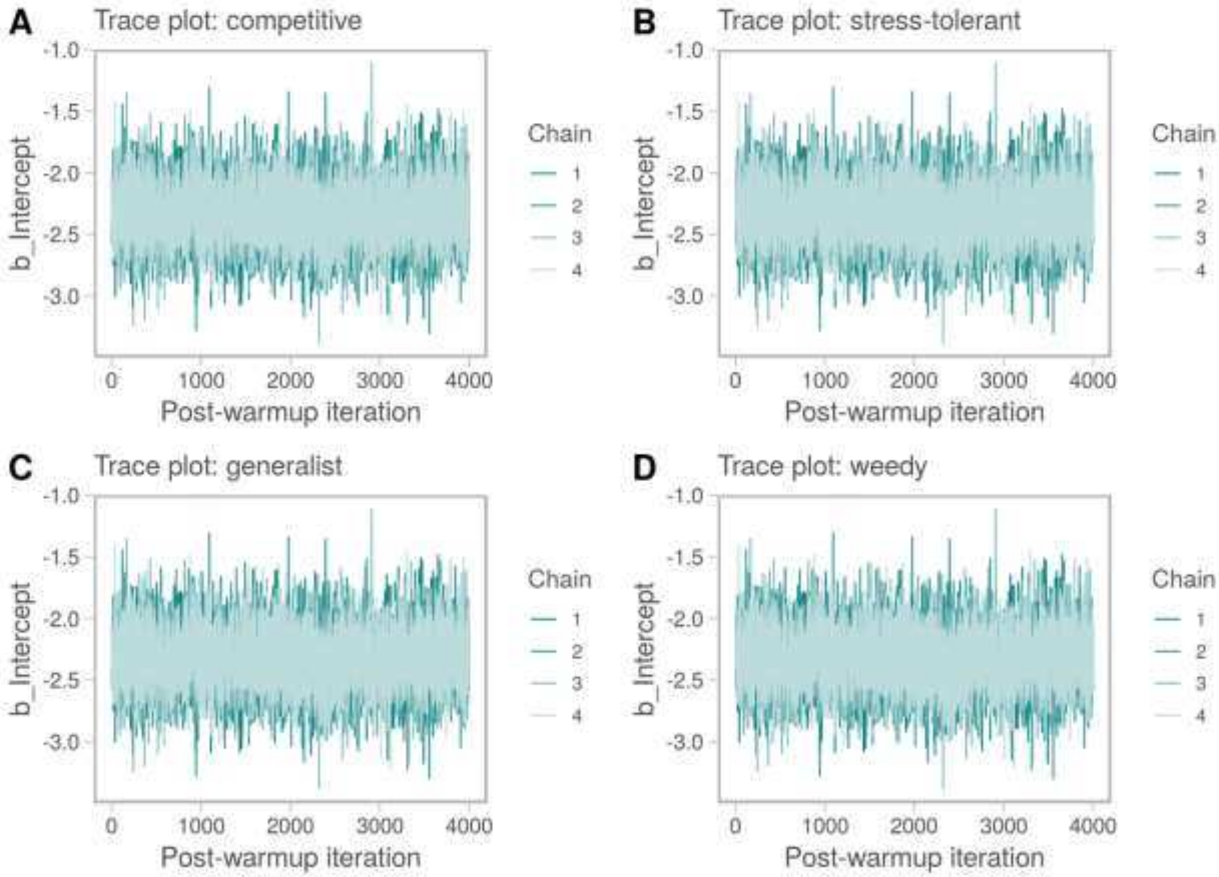
Supplementary Figure 2. Relationship between climate, social, environment and methodology variables for four common coral genera. Standardized effect sizes are Bayesian posterior median values with 95% Bayesian credible intervals (CI; thin black lines) and 80% credible intervals (coloured thicker lines) for 4 chains of 4,000 iterations each. Coloured points indicate the 80% CI does not overlap with zero while grey circles indicate an overlap with zero and a less credible trend. DHW indicates Degree Heating Weeks; HDI indicates the national statistic of Human Development Index.



Supplementary Figure 3. Locations of reefs with a 'protect' strategy using different thresholds of degree heating weeks (DHWs) during the 2014-2017 global bleaching event. (A) DHW < 2.0; (B) DHW < 2.5. (C) DHW < 3.0. (D) DHW < 3.5. (E) DHW < 4.0. The maps identify a similar geography of reefs exposed to relatively limited DHWs and coral cover of competitive and stress-tolerant corals > 10%.



Supplementary Figure 4. Correlation plot among continuous social, climate and environment drivers. After accounting for multicollinearity, all correlation coefficients are less than 0.55, and variance inflation factors are less than 2.5, indicating multicollinearity between covariates is not an issue in the full model set of drivers (see Extended Data Table 1 for detailed description of drivers, and Extended Data Table 2 for analysis of variance inflation factors).



Supplementary Figure 5. Trace plots of Bayesian models for coral life histories. Mixing is shown for the Intercept parameter b across four chains of 5,000 iterations each, where the first 1,000 iterations of each chain were discarded as warm up iterations.

Supplementary Table 1. Comparison of random and empirical sampling of coral communities. Randomly sampled points were selected from 500 m grid of coral reef distribution in the Indo-Pacific, compared to the number of randomly selected points from the empirical dataset (n = 2,584 reefs), and summarized by ecoregion. Relative undersampling for an ecoregion is indicated by negative level of sampling, and positive values indicate relative oversampling.

Ecoregion	Randomly sampled site counts	Empirically sampled site counts	Percentage of randomly sampled reefs	Percentage of empirically sampled reefs	Level of sampling (%)
Palawan/North Borneo	184	0	7.1%	0.0%	-7.1%
Torres Strait Northern GBR	195	37	7.5%	1.4%	-6.1%
Eastern Philippines	116	1	4.5%	0.0%	-4.4%
Banda Sea	114	0	4.4%	0.0%	-4.4%
Northern and Central Red Sea	89	18	3.4%	0.7%	-2.7%
Solomon Archipelago	87	20	3.3%	0.8%	-2.6%
Sulawesi Sea/Makassar Strait	87	20	3.3%	0.8%	-2.6%
Solomon Sea	66	0	2.5%	0.0%	-2.5%
South China Sea Oceanic Islands	53	2	2.0%	0.1%	-2.0%
Tuamotus	53	4	2.0%	0.2%	-1.9%
Southern Red Sea	58	12	2.2%	0.5%	-1.8%
Sunda Shelf/Java Sea	67	34	2.6%	1.3%	-1.3%
Bismarck Sea	54	24	2.1%	0.9%	-1.1%
Halmahera	26	0	1.0%	0.0%	-1.0%
Vanuatu	31	6	1.2%	0.2%	-1.0%
Papua	33	8	1.3%	0.3%	-1.0%
Bonaparte Coast	23	0	0.9%	0.0%	-0.9%
Southeast Papua New Guinea	23	0	0.9%	0.0%	-0.9%
Arabian (Persian) Gulf	28	6	1.1%	0.2%	-0.8%
East African Coral Coast	70	48	2.7%	1.9%	-0.8%
Andaman and Nicobar Islands	31	10	1.2%	0.4%	-0.8%
Coral Sea	16	0	0.6%	0.0%	-0.6%
Gilbert/Ellis Islands	46	30	1.8%	1.2%	-0.6%
Arnhem Coast to Gulf of Carpentaria	15	0	0.6%	0.0%	-0.6%
Western Sumatra	39	24	1.5%	0.9%	-0.6%
Gulf of Aden	12	0	0.5%	0.0%	-0.5%
Northern Monsoon Current Coast	12	0	0.5%	0.0%	-0.5%
Gulf of Tonkin	10	0	0.4%	0.0%	-0.4%
Northeast Sulawesi	9	0	0.3%	0.0%	-0.3%
Arafura Sea	7	0	0.3%	0.0%	-0.3%
Southern Java	7	0	0.3%	0.0%	-0.3%
South India and Sri Lanka	6	0	0.2%	0.0%	-0.2%
East Caroline Islands	60	55	2.3%	2.1%	-0.2%
Cargados Carajos/Tromelin Island	4	0	0.2%	0.0%	-0.2%
Central Kuroshio Current	4	0	0.2%	0.0%	-0.2%
Houtman	4	0	0.2%	0.0%	-0.2%
Western India	4	0	0.2%	0.0%	-0.2%
Northern Bay of Bengal	3	0	0.1%	0.0%	-0.1%
Southern Vietnam	3	0	0.1%	0.0%	-0.1%
Bight of Sofala/Swamp Coast	5	2	0.2%	0.1%	-0.1%
Southeast Madagascar	2	0	0.1%	0.0%	-0.1%
Western Arabian Sea	2	0	0.1%	0.0%	-0.1%
Malacca Strait	14	12	0.5%	0.5%	-0.1%
Gulf of Papua	1	0	0.0%	0.0%	0.0%

Leeuwin	1	0	0.0%	0.0%	0.0%
Southern Cook/Austral Islands	3	2	0.1%	0.1%	0.0%
Mascarene Islands	5	4	0.2%	0.2%	0.0%
East China Sea	4	4	0.2%	0.2%	0.0%
Southern China	6	6	0.2%	0.2%	0.0%
Maldives	64	64	2.5%	2.5%	0.0%
Western and Northern Madagascar	69	69	2.7%	2.7%	0.0%
Marquesas	0	1	0.0%	0.0%	0.0%
Society Islands	7	8	0.3%	0.3%	0.0%
Seychelles	20	21	0.8%	0.8%	0.0%
West Caroline Islands	18	20	0.7%	0.8%	0.1%
New Caledonia	86	88	3.3%	3.4%	0.1%
Manning-Hawkesbury	0	3	0.0%	0.1%	0.1%
Gulf of Oman	2	6	0.1%	0.2%	0.2%
Chagos	32	36	1.2%	1.4%	0.2%
South Kuroshio	22	27	0.8%	1.0%	0.2%
Shark Bay	4	13	0.2%	0.5%	0.3%
Ningaloo	2	14	0.1%	0.5%	0.5%
Tweed-Moreton	1	14	0.0%	0.5%	0.5%
Gulf of Thailand	5	19	0.2%	0.7%	0.5%
Phoenix/Tokelau/Northern Cook Islands	8	23	0.3%	0.9%	0.6%
Delagoa	1	24	0.0%	0.9%	0.9%
Clipperton	0	28	0.0%	1.1%	1.1%
Andaman Sea Coral Coast	14	43	0.5%	1.7%	1.1%
Cocos-Keeling/Christmas Island	3	37	0.1%	1.4%	1.3%
Marshall Islands	47	84	1.8%	3.3%	1.4%
Easter Island	0	40	0.0%	1.5%	1.5%
Revillagigedos	0	42	0.0%	1.6%	1.6%
Lord Howe and Norfolk Islands	1	45	0.0%	1.7%	1.7%
Central and Southern Great Barrier Reef	184	236	7.1%	9.1%	2.1%
Tonga Islands	17	71	0.7%	2.7%	2.1%
Samoa Islands	9	69	0.3%	2.7%	2.3%
Exmouth to Broome	14	94	0.5%	3.6%	3.1%
Line Islands	10	92	0.4%	3.6%	3.2%
Mariana Islands	5	95	0.2%	3.7%	3.5%
Lesser Sunda	41	168	1.6%	6.5%	4.9%
Hawaii	50	193	1.9%	7.5%	5.5%
Rapa-Pitcairn	1	152	0.0%	5.9%	5.8%
Fiji Islands	71	256	2.7%	9.9%	7.2%
Grand Total	2600	2584	100.0%	100.0%	0.0% (average)

Supplementary Table 2. List of scleractinian species identified to four life history 'types'. Classifications were based on published species traits including colony growth form, growth rate, maximum size and reproduction to derive species-level classifications (4) and updated by genera-level classifications informed by expert opinion (18).

Life history	Species
Competitive	Acropora abrolhosensis, Acropora abrotanoides, Acropora aculeus, Acropora acuminata, Acropora anthocercis, Acropora aspera, Acropora austera, Acropora azurea, Acropora carduus, Acropora caroliniana, Acropora cerealis, Acropora chesterfieldensis, Acropora clathrata, Acropora corymbose, Acropora cytherea, Acropora digitate, Acropora digitifera, Acropora divaricata, Acropora donei, Acropora echinata, Acropora elseyi, Acropora eurystoma, Acropora florida, Acropora gemmifera, Acropora glauca, Acropora globiceps, Acropora grandis, Acropora granulosa, Acropora hispidose, Acropora horrida, Acropora humilis, Acropora hyacinthus, Acropora intermedia, Acropora japonica, Acropora kimbeensis, Acropora latistella, Acropora listeri, Acropora lokani, Acropora longicyathus, Acropora loripes, Acropora lutkeni, Acropora microclados, Acropora microphthalma, Acropora millepora, Acropora monticulosa, Acropora muricata, Acropora nana, Acropora nasuta, Acropora natalensis, Acropora palmerae, Acropora paniculata, Acropora papillare, Acropora pectinata, Acropora polystoma, Acropora pulchra, Acropora retusa, Acropora robusta, Acropora roseni, Acropora rudis, Acropora samoensis, Acropora sarmentosa, Acropora secale, Acropora selago, Acropora solitaryensis, Acropora speciosa, Acropora spicifera, Acropora striata, Acropora subglabra, Acropora subulata, Acropora tenuis, Acropora tortuosa, Acropora valenciennesi, Acropora valida, Acropora vaughani, Acropora verweyi, Acropora willisae, Acropora yongei, Hydnophora rigida, Isopora crateriformis, Isopora cuneata, Isopora elizabethensis, Isopora palifera, Montipora capitata, Montipora digitata, Montipora hispida, Montipora incrassata, Montipora mollis, Montipora samarensis, Montipora spongodes, Montipora spumosa, Montipora stellata, Montipora turgescens, Montipora undata
Generalist	Cycloseris explanulata, Cyphastrea agassizi, Cyphastrea chalcidicum, Cyphastrea decadia, Cyphastrea japonica, Cyphastrea microphthalma, Cyphastrea ocellina, Cyphastrea serailia, Echinopora gemmacea, Echinopora hirsutissima, Echinopora horrida, Echinopora lamellosa, Echinopora mammiformis, Echinopora pacificus, Hydnophora exesa, Hydnophora microconos, Isopora cuneata, Isopora palifera, Leptastrea bewickensis, Leptastrea inaequalis, Leptastrea pruinosa, Leptastrea purpurea, Leptastrea transversa, Merulina ampliata, Merulina scabricula, Montipora aequituberculata, Montipora australiensis, Montipora calcarea, Montipora corbettensis, Montipora crassituberculata, Montipora danae, Montipora florida, Montipora foliosa, Montipora foveolata, Montipora grisea, Montipora hoffmeisteri, Montipora informis, Montipora lobulata, Montipora mactanensis, Montipora monasteriata, Montipora nodosa, Montipora orientalis, Montipora peltiformis, Montipora tuberculosa, Montipora turtlensis, Montipora verrucosa, Mycedium elephantotus, Mycedium mancaoi, Oxypora glabra, Oxypora lacera, Pachyseris rugosa, Pachyseris speciosa, Pavona bipartita, Pavona cactus, Pavona chiriquensis, Pavona clavus, Pavona decussata, Pavona duerdeni, Pavona explanulata, Pavona frondifera, Pavona maldivensis, Pavona minuta, Pavona varians, Pavona venosa, Pectinia alcicornis, Pectinia lactuca, Pectinia paeonia, Pocillopora aliciae, Pocillopora grandis, Pocillopora ligulata, Pocillopora meandrina, Pocillopora verrucosa, Pocillopora woodjonesi, Podabacia crustacea, Podabacia motuporensis, Psammocora contigua, Psammocora digitata, Psammocora haimiana, Psammocora nierstraszi, Psammocora profundacella, Psammocora stellata, Turbinaria bifrons, Turbinaria frondens, Turbinaria heronensis, Turbinaria mesenterina, Turbinaria patula, Turbinaria peltata, Turbinaria radicalis, Turbinaria reniformis, Turbinaria stellulata
Stress-tolerant	Acanthastrea echinata, Acanthastrea hemprichii, Acanthastrea pachysepta, Alveopora allingi, Alveopora tizardi, Astrea annuligera, Astrea curta, Astreopora cucullata, Astreopora listeri, Astreopora myriophthalma, Astreopora ocellata, Astreopora randalli, Astreopora scabra, Australogyra zelli, Bernardpora stutchburyi, Blastomussa wellsi, Caulastraea furcata, Coelastrea aspera, Coelastrea palauensis, Coeloseris mayeri, Coscinaraea columna, Coscinaraea exesa, Coscinaraea monile, Ctenactis albitentaculata, Cycloseris mokai, Danafungia horrida, Diploastrea heliopora, Dipsastrea amicorum, Dipsastrea danai, Dipsastrea faviaformis, Dipsastrea favus, Dipsastrea laxa, Dipsastrea lizardensis, Dipsastrea matthaii, Dipsastrea maxima, Dipsastrea pallida, Dipsastrea rotumana, Dipsastrea rotundata, Dipsastrea speciosa, Dipsastrea veroni, Dipsastrea vietnamensis, Echinophyllia aspera, Echinophyllia echinata, Echinophyllia echinoporoides, Echinophyllia orpheensis, Euphyllia ancora, Euphyllia divisa, Euphyllia glabrescens, Favites abdita, Favites chinensis, Favites complanata, Favites flexuosa, Favites

	halicora, Favites magnistellata, Favites pentagona, Favites valenciennesi, Favites vasta, Fungia fungites, Galaxea astreata, Galaxea fascicularis, Galaxea horrescens, Gardineroseris planulata, Goniastrea edwardsi, Goniastrea favulus, Goniastrea minuta, Goniastrea pectinata, Goniastrea retiformis, Goniastrea stelligera, Goniopora djiboutiensis, Goniopora fruticosa, Goniopora lobata, Goniopora pedunculata, Goniopora somaliensis, Goniopora tenuidens, Halomitra pileus, Herpolitha limax, Homophyllia bowerbanki, Leptoria irregularis, Leptoria phrygia, Leptoseris explanata, Leptoseris foliosa, Leptoseris hawaiiensis, Leptoseris incrustans, Leptoseris mycetoseroides, Leptoseris papyracea, Leptoseris scabra, Leptoseris solida, Leptoseris yabei, Lithophyllon concinna, Lithophyllon repanda, Lithophyllon scabra, Lithophyllon undulatum, Lobactis scutaria, Lobophyllia agaricia, Lobophyllia corymbosa, Lobophyllia hataii, Lobophyllia hemprichii, Lobophyllia radians, Lobophyllia recta, Lobophyllia robusta, Lobophyllia vitiensis, Micromussa amakusensis, Micromussa lordhowensis, Micromussa regularis, Montipora caliculata, Montipora efflorescens, Montipora flabellata, Montipora floweri, Montipora meandrina, Montipora millepora, Montipora patula, Montipora venosa, Oulophyllia crispa, Paragoniastrea australensis, Paragoniastrea russelli, Paramontastrea annuligera, Paramontastrea serageldini, Physogyra lichtensteini, Platygyra contorta, Platygyra daedalea, Platygyra lamellina, Platygyra pini, Platygyra sinensis, Platygyra verweyi, Platygyra yaeyamaensis, Plerogyra sinuosa, Plesiastrea versipora, Pleuractis granulosa, Pleuractis paumotensis, Porites annae, Porites arnaudi, Porites australiensis, Porites brighami, Porites evermanni, Porites gabonensis, Porites lichen, Porites lobata, Porites lutea, Porites mayeri, Porites monticulosa, Porites myrmidonensis, Porites profundus, Porites randalli, Porites sillimaniani, Porites stephensoni, Stylocoeniella armata, Stylocoeniella guentheri
Weedy	Pocillopora damicornis, Porites attenuata, Porites compressa, Porites cylindrica, Porites heronensis, Porites nigrescens, Porites rus, Porites vaughani, Seriatopora caliendrum, Seriatopora hystrix, Seriatopora stellata, Stylophora pistillata

Supplementary Table 3. Summary of human, climate and environmental covariates.

Covariate	Description	Scale	Rationale
Local population growth	Population growth was estimated as the change in population density between 2000 and 2010 within a 100 km buffer	Site	Population growth can increase the influence of local human populations on coral reefs through increases in fishing, pollution and coastal development
Gravity of nearest human settlement	The population of the nearest human settlement divided by the squared travel time between the reef site and the settlement	Site	Gravity' is an indicator of human use and fishing pressure related to the size and accessibility of coral reefs to nearby human settlements and markets. In a global study, Cinner et al. (2016) identified market gravity as the strongest determinant of reef fish biomass
Market gravity	The population of a major market divided by the squared travel time between a reef site and market This value was summed for all major markets within 500 km of the site	Site	
Management	Whether the reef is open access (fished), restricted (some gear or access restrictions) or no-take (full restriction on fishing with high compliance)	Reef	No-take marine reserves or other management restrictions can limit the direct and indirect effects of fishing on coral communities
Cultivated land	Percent of land area classified as croplands with a 100 km buffer -- two variables calculated: total % cover in 2012, and change in % cover between 2002 and 2012	Site	Land conversion to agriculture or crops can increase the flow of sediments, nutrients and pesticides to reefs, which can directly affect coral growth and mortality, or can disrupt coral-algae competitive dynamics
Human Development Index (HDI)	A composite statistic of life expectancy, education, and per capita income Higher HDIs are scored when the lifespan is higher, the education level is higher, and the GDP per capita is higher	Country	Countries with higher HDI scores may have greater social and financial resources to operationalize natural resource management. Although this metric does not account for some lower-HDI countries with strong customary management of natural resources
GDP per capita	Average GDP per capita in 2014, current prices USD	Country	National financial assets can inform the resources that a country can use to assist in the governance of coral reef resources and mitigation or adaptation of human threats.
Voice and accountability	World Bank index that describes the extent to which a country's citizens are able to participate in selecting their government, as well as freedom of expression, freedom of association, and a free media	Country	If citizens can make decisions that can mitigate local impacts through policy mechanisms, we hypothesize that nations with stronger national or state governance might better mitigate human influences on coral reefs
Past magnitude of thermal exposure	Highest maximum annual Degree Heating Week (DHWs) in all years between 1985 and year of survey	Site	Degree Heating Weeks (DHWs) can characterize extreme thermal stress that can directly affect coral assemblages through mortality. The number of years between disturbances is an indicator of potential recovery time for coral assemblages
Years since maximum thermal stress	The number of years between maximum past DHW and year of survey	Reef	
Primary productivity	Average ocean productivity between 2003 and 2013 in mg C /m2/ day estimated from satellite measurements of photosynthetically available radiation, sea surface temperatures, and chlorophyll a concentrations	Site	Primary productivity can influence coral growth, community assembly patterns, and recovery from disturbances

Depth, m	Depth of the ecological survey, meters	Reef	Depth influences light scatter for reef growth, local temperature and patterns of community assembly. Depth may also influence exposure to coral bleaching (cooler waters) or to cyclones and waves
Habitat	Reef flat (includes lagoon and back reef habitats), reef slope or reef crest	Reef	Habitat is a strong determinant of coral reef community structure by moderating temperature variability and wave exposure
Wave exposure	Mean wave energy (kW/m) calculated from hindcast WAVEWATCH III data (1979-2009)	Site	Wave energy can moderate coral communities in their tolerance to physical disturbance
Cyclone days	The maximum number of days in a single year of potential exposure to extreme cyclone conditions, during a time series from 1985 to one year prior to the survey Extreme cyclone conditions are defined as exposure to a minimum threshold of gale force winds or higher	Site	Tropical cyclone waves can severely damage coral reefs and alter community structure or in some instances provide beneficial cooling from high SSTs. The amount of exposure can inform cyclone damage or potential cooling, and years since cyclones can inform potential recovery
Years since maximum cyclone	Number of years between maximum exposure to extreme cyclone conditions and year of survey	Reef	
Connectivity to other reefs	Reef area (km2) within a 100 km buffer of each site	Site	Habitat area available to coral reefs has been associated with higher biodiversity of reef fish and coral assemblages at regional scales
Method	Whether the survey used a point intercept transect, line intercept transect or photo quadrat method	Site	Methodological differences may account for sampling noise associated with the dataset
Total sampling points	Total number of sampling points for the survey, which integrates transect length, number of transect replicates and sampling intensity	Site	Sampling effort is expected to be an important influence on coral abundance and diversity recorded on each survey
Latitude	Latitude of ecological survey	Site	Latitude is correlated with solar radiation, temperature, and aragonite saturation, and can serve as a proxy for environmental gradients of substrate type, wave energy, salinity and water quality
Faunal province	Biogeographic faunal province of survey, based on co-occurrence of multiple species boundaries	Site	Indo-Pacific corals can be characterized within 11 distinct faunal provinces evaluated from the co-occurrence of multiple species' range limits

Supplementary Table 4. Bayesian R^2 values from Bayesian applied regression models fit with Stan models for (a) total coral cover and life histories and (b) common coral genera. Bayesian R^2 is an estimate of the proportion of variance explained by a model, and estimated as the expected predicted variance divided by the expected predicted variance plus error variance (Gelman et al. unpublished, http://www.stat.columbia.edu/~gelman/research/published/bayes_R2_v3.pdf)

	Bayesian R^2	**Error**
(a) Total cover and life history		
Total coral cover	0.482	0.014
Competitive	0.403	0.017
Stress tolerant	0.404	0.018
Generalist	0.253	0.022
Weedy	0.372	0.023
(b) Genus		
Acropora	0.414	0.020
Porites	0.351	0.026
Montipora	0.295	0.033
Pocillopora	0.306	0.027

Supplementary Table 5. Sensitivity analysis comparing the three management strategies (protect – recover – transform) across different thresholds of ecological condition related to net-positive carbonate production. Analyses in the main text use a 10% threshold of live cover of competitive and stress-tolerant corals. Here, we show the distribution of reefs (total out of 2584, N; and percent, %) using an 8% or 12% threshold of coral cover.

	10% cover		8% cover		12% cover	
	N reefs	% of reefs	N reefs	% of reefs	N reefs	% of reefs
Protect	449	17.38	490	18.96	408	15.79
Recover	1407	54.45	1522	58.90	1305	50.50
Transform	728	28.17	572	22.14	871	33.71

Supplementary Table 6. Location of 449 reefs with a '*protect'* strategy, identified by country, site, dominance of coral community (with a 10% cover threshold) and thermal stress <4 DHW during the 2014-2017 global coral bleaching event. These reefs are located within 25 nations (including overseas territories) and under the governing jurisdiction of 22 countries.

Province	Nation	Site	% Cover of competitive and stress-tolerant corals	Dominant life history	Maximum DHW, 2014-2017
Africa-India	France, Iles Eparses	Europa4	56.15	Competitive	2.46
Africa-India	France, Iles Eparses	Europa2	49.28	Stresstolerant	2.55
Africa-India	France, Iles Eparses	Europa5	48.00	Stresstolerant	2.54
Africa-India	France, Iles Eparses	Europa6	46.71	Stresstolerant	2.54
Africa-India	France, Iles Eparses	Europa3	45.54	Competitive	2.54
Africa-India	France, Iles Eparses	Europa7	33.69	Stresstolerant	2.68
Africa-India	France, Iles Eparses	Europa1	25.91	Stresstolerant	2.54
Africa-India	India	Black Tangs_Deep	40.45	Stresstolerant	3.04
Africa-India	India	Lighthouse_Deep	36.23	Stresstolerant	3.04
Africa-India	India	Black Tangs_Shallow	31.27	Stresstolerant	3.04
Africa-India	India	Lighthouse_Shallow	27.91	Competitive	3.04
Africa-India	India	Cave_Shallow	21.14	Stresstolerant	3.68
Africa-India	India	Japanese Garden_Shallow	18.45	Stresstolerant	2.79
Africa-India	India	Japanese Garden_Deep	18.20	Stresstolerant	2.79
Africa-India	India	Cave_Deep	16.55	Stresstolerant	3.68
Africa-India	India	The Groove_Deep	15.38	Stresstolerant	3.05
Africa-India	India	The Groove_Shallow	14.30	Stresstolerant	3.05
Africa-India	India	Potato Patch_Shallow	10.78	Stresstolerant	3.68
Africa-India	Kenya	Kibuyuni B	29.85	Stresstolerant	2.60
Africa-India	Kenya	Changai	29.79	Stresstolerant	2.60
Africa-India	Kenya	Mradi 2	26.01	Stresstolerant	1.10
Africa-India	Kenya	Mtangata 2	23.47	Stresstolerant	1.77
Africa-India	Kenya	Chale Mwaromba 1	23.40	Stresstolerant	1.61
Africa-India	Kenya	Kibuyuni A	22.64	Stresstolerant	2.60
Africa-India	Kenya	Kanamai 2	19.70	Stresstolerant	1.07
Africa-India	Kenya	Mtangata 1	17.54	Stresstolerant	1.77
Africa-India	Kenya	Msumarini 1	17.44	Stresstolerant	1.06
Africa-India	Kenya	Mwaepe 1	16.66	Stresstolerant	1.61
Africa-India	Kenya	Mombasa 1	16.03	Stresstolerant	1.26
Africa-India	Kenya	Mradi 1	15.40	Stresstolerant	1.10
Africa-India	Kenya	Mvuleni Mecca 1	14.41	Stresstolerant	1.61
Africa-India	Kenya	Vipingo 1	14.20	Stresstolerant	1.29
Africa-India	Kenya	Msumarini 2	12.58	Stresstolerant	1.06
Africa-India	Kenya	Vanga	12.54	Stresstolerant	3.51
Africa-India	Kenya	Malindi 2	11.88	Stresstolerant	2.54
Africa-India	Kenya	Mombasa 2	10.15	Stresstolerant	1.26
Africa-India	Madagascar	Frere 2	79.00	Competitive	3.74
Africa-India	Madagascar	Soeur 1	61.04	Competitive	3.91
Africa-India	Madagascar	South Tsarajabina	55.10	Competitive	3.91
Africa-India	Madagascar	Smahasaha ext	51.20	Competitive	1.46
Africa-India	Madagascar	Frere 1	45.21	Stresstolerant	3.91
Africa-India	Madagascar	Coco_Salary ext	44.87	Stresstolerant	1.76
Africa-India	Madagascar	Wmahasaha ND	20.01	Stresstolerant	1.46
Africa-India	Madagascar	Anjokojoko ext	19.59	Competitive	1.76
Africa-India	Madagascar	Ravenome ND	10.58	Stresstolerant	1.31
Africa-India	Mozambique	Bazaruto_2mileReef	42.03	Competitive	2.64

Africa-India	Mozambique	Pomene_Trojan	35.03	Competitive	0.15
Africa-India	Mozambique	Bazaruto_Lighthouse1	34.84	Competitive	2.10
Africa-India	Mozambique	Bazaruto_5mileReef	33.79	Competitive	2.78
Africa-India	Mozambique	Mahangate_Africa_Bank	30.94	Competitive	0.75
Africa-India	Mozambique	SAN SEBASTIAN_Lighthouse	28.75	Competitive	0.95
Africa-India	Mozambique	Bazaruto_North_SailfishBay	26.61	Competitive	2.49
Africa-India	Mozambique	Magaruque_Baluba	21.55	Stresstolerant	2.29
Africa-India	Mozambique	Bazaruto_25mileReef	21.42	Stresstolerant	1.96
Africa-India	Mozambique	Bazaruto_SailfishBay	20.88	Competitive	2.49
Africa-India	Mozambique	Bazaruto_Queenies	18.20	Stresstolerant	1.96
Africa-India	Mozambique	Pomene_Rappies	15.70	Competitive	0.78
Africa-India	Mozambique	SAN SEBASTIAN_Bump	13.92	Stresstolerant	1.26
Africa-India	Mozambique	Masinga_Masinga1	12.88	Stresstolerant	0.97
Africa-India	Mozambique	Bazaruto_Lighthouse2	11.11	Stresstolerant	2.10
Africa-India	Tanzania	Makome North 1	59.50	Stresstolerant	1.82
Africa-India	Tanzania	Dambwe 1	40.16	Stresstolerant	2.50
Africa-India	Tanzania	Maziwe S 1	37.43	Stresstolerant	2.17
Africa-India	Tanzania	Taa 1	35.60	Stresstolerant	1.67
Africa-India	Tanzania	Makome South 1	27.66	Stresstolerant	1.82
Africa-India	Tanzania	Makome temp 1	26.76	Stresstolerant	2.17
Africa-India	Tanzania	Chanjale 1	22.81	Stresstolerant	1.67
Africa-India	Tanzania	Maziwe N 1	17.36	Stresstolerant	2.17
Africa-India	Tanzania	Makome 1	14.25	Stresstolerant	1.82
Australian	Australia	Cape Farquhar	61.07	Competitive	1.63
Australian	Australia	Knuckle Reef	57.45	Competitive	1.21
Australian	Australia	Turquoise	39.98	Competitive	3.09
Australian	Australia	Hardy Reef 3	39.31	Competitive	2.26
Australian	Australia	Pelican	38.44	Competitive	2.86
Australian	Australia	M3	37.80	Competitive	3.92
Australian	Australia	GK9	36.91	Competitive	3.92
Australian	Australia	Knuckle Reef 2	35.94	Competitive	1.21
Australian	Australia	Middleton8_3m	34.88	Competitive	3.39
Australian	Australia	Flinders Reef	34.01	Competitive	3.63
Australian	Australia	Bruboodjoo	30.70	Competitive	3.35
Australian	Australia	Middleton6_4m	30.42	Competitive	3.23
Australian	Australia	Middleton9_4m	30.42	Competitive	2.97
Australian	Australia	Inner Gneering Shoals	28.20	Stresstolerant	2.10
Australian	Australia	M4	27.80	Competitive	3.92
Australian	Australia	Middleton4_1m	26.68	Competitive	2.97
Australian	Australia	Stevens Hole_2m	26.50	Competitive	1.73
Australian	Australia	Winderabandi	23.99	Competitive	3.00
Australian	Australia	Middleton9_10m	23.88	Competitive	2.97
Australian	Australia	Little Black Reef	23.38	Competitive	2.07
Australian	Australia	North Bay_2m	22.80	Competitive	1.94
Australian	Australia	Mudjimba	22.42	Stresstolerant	1.79
Australian	Australia	Net Reef	22.07	Competitive	1.11
Australian	Australia	Middleton6_10m	20.55	Stresstolerant	3.23
Australian	Australia	Erscotts_3m	19.83	Competitive	1.73
Australian	Australia	Middleton7_4m	19.27	Competitive	2.97
Australian	Australia	Middleton7_10m	19.15	Stresstolerant	2.97
Australian	Australia	Bundera	19.01	Competitive	2.99
Australian	Australia	Stevens Hole_8m	18.97	Competitive	1.73
Australian	Australia	North Bay_8m	18.63	Competitive	1.94
Australian	Australia	Oyster Stacks 1	18.23	Competitive	3.09

Australian	Australia	Middleton8_9m	18.10	Stresstolerant	3.39
Australian	Australia	Osprey	18.07	Competitive	3.12
Australian	Australia	Potholes_8m	18.03	Competitive	1.73
Australian	Australia	Nth Passage South_8m	17.80	Competitive	1.94
Australian	Australia	Stevens Hole_3m	17.63	Competitive	1.73
Australian	Australia	Bait Reef 2	17.57	Stresstolerant	3.24
Australian	Australia	Fairey Reef 2	17.28	Stresstolerant	1.31
Australian	Australia	Coral Bay	17.21	Competitive	2.71
Australian	Australia	Erscott_8m	16.75	Competitive	1.73
Australian	Australia	Lefroy Bay	16.31	Competitive	3.00
Australian	Australia	South West Solitary Island	16.10	Stresstolerant	3.01
Australian	Australia	South Solitary Island	15.98	Competitive	3.23
Australian	Australia	North Passage_3m	15.87	Competitive	1.94
Australian	Australia	Fairey Reef	15.78	Stresstolerant	1.31
Australian	Australia	Mid2_20	15.47	Stresstolerant	2.14
Australian	Australia	North Solitary Island	15.38	Stresstolerant	2.62
Australian	Australia	North West Solitary Island	15.25	Stresstolerant	3.19
Australian	Australia	Nth Passage South_2m	15.23	Competitive	1.94
Australian	Australia	Pot Holes_2m	15.20	Competitive	1.73
Australian	Australia	Middleton5_10m	12.55	Stresstolerant	3.00
Australian	Australia	Turquoise Bay 1	12.28	Stresstolerant	3.09
Australian	Papua New Guinea	Ahus Fished 1_3m	16.09	Stresstolerant	3.93
Australian	Papua New Guinea	Nusa	15.94	Stresstolerant	3.67
Australian	Papua New Guinea	Ahus Tambu 2_7m	15.71	Competitive	3.78
Australian	Papua New Guinea	Ahus Tambu 1_3m	14.95	Stresstolerant	3.78
Australian	Papua New Guinea	Mongol	13.87	Stresstolerant	3.67
Australian	Papua New Guinea	Ahus Fished 2_3m	12.75	Stresstolerant	3.93
Australian	Papua New Guinea	Ahus Tambu 2_3m	11.38	Competitive	3.78
Australian	Papua New Guinea	Ahus Tambu 1_7m	10.85	Stresstolerant	3.78
Australian	Solomon Islands	KOL06	36.93	Competitive	3.30
Australian	Solomon Islands	KOL07	29.20	Stresstolerant	3.30
Australian	Solomon Islands	KOL04	27.47	Stresstolerant	3.46
Australian	Solomon Islands	KOL18	26.33	Competitive	3.19
Australian	Solomon Islands	KOL09	24.67	Stresstolerant	3.39
Australian	Solomon Islands	KOL08	22.27	Stresstolerant	3.39
Australian	Solomon Islands	KOL05	19.67	Stresstolerant	3.46
Australian	Solomon Islands	KOL10	19.33	Stresstolerant	3.99
Australian	Solomon Islands	KOL20	15.27	Stresstolerant	3.19
Australian	Solomon Islands	KOL17	14.33	Stresstolerant	3.19
Australian	Solomon Islands	KOL01	14.27	Stresstolerant	3.37
Australian	Solomon Islands	KOL19	14.00	Stresstolerant	3.19
Australian	Solomon Islands	KOL03	12.67	Stresstolerant	3.64
Australian	Solomon Islands	KOL11	12.67	Stresstolerant	3.99
Australian	Solomon Islands	KOL16	12.00	Stresstolerant	3.84
Eastern Pacific	France, Clipperton Island	Clipperton.14_10m	49.37	Stresstolerant	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.4_20m	48.78	Stresstolerant	3.05
Eastern Pacific	France, Clipperton Island	Clipperton.5_20m	40.69	Stresstolerant	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.9_20m	40.46	Stresstolerant	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.13_20m	37.75	Stresstolerant	3.05
Eastern Pacific	France, Clipperton Island	Clipperton.9_10m	36.80	Competitive	3.04

Eastern Pacific	France, Clipperton Island	Clipperton.6_20m	33.69	Stresstolerant	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.7_10m	33.14	Stresstolerant	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.13_10m	29.90	Competitive	3.05
Eastern Pacific	France, Clipperton Island	Clipperton.10_10m	28.80	Stresstolerant	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.1_20m	28.53	Stresstolerant	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.10_20m	26.97	Stresstolerant	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.14_20m	26.88	Stresstolerant	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.3_10m	25.28	Stresstolerant	3.05
Eastern Pacific	France, Clipperton Island	Clipperton.6_10m	23.44	Competitive	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.12_10m	22.03	Stresstolerant	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.8_10m	21.67	Competitive	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.5_10m	20.66	Competitive	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.11_10m	19.66	Stresstolerant	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.4_10m	18.56	Competitive	3.05
Eastern Pacific	France, Clipperton Island	Clipperton.3_20m	17.31	Stresstolerant	3.05
Eastern Pacific	France, Clipperton Island	Clipperton.2_20m	15.91	Stresstolerant	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.2_10m	14.86	Stresstolerant	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.8_20m	14.49	Stresstolerant	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.11_20m	12.57	Stresstolerant	3.04
Eastern Pacific	France, Clipperton Island	Clipperton.12_20m	10.79	Stresstolerant	3.04
Fiji-Caroline Islands	Federated States of Micronesia	YAP-17	46.15	Stresstolerant	2.62
Fiji-Caroline Islands	Federated States of Micronesia	YAP-11	38.33	Stresstolerant	3.09
Fiji-Caroline Islands	Federated States of Micronesia	YAP-2	36.56	Stresstolerant	2.62
Fiji-Caroline Islands	Federated States of Micronesia	YAP-3	35.02	Stresstolerant	2.76
Fiji-Caroline Islands	Federated States of Micronesia	YAP-20	34.67	Stresstolerant	3.09
Fiji-Caroline Islands	Federated States of Micronesia	YAP-1	29.91	Competitive	2.92
Fiji-Caroline Islands	Federated States of Micronesia	YAP-12	29.54	Stresstolerant	2.62
Fiji-Caroline Islands	Federated States of Micronesia	YAP-10	29.27	Stresstolerant	2.94

Fiji-Caroline Islands	Federated States of Micronesia	YAP-18	27.10	Stresstolerant	2.92
Fiji-Caroline Islands	Federated States of Micronesia	YAP-8	25.86	Stresstolerant	2.77
Fiji-Caroline Islands	Federated States of Micronesia	YAP-9	23.52	Stresstolerant	2.77
Fiji-Caroline Islands	Federated States of Micronesia	YAP-6	23.47	Stresstolerant	2.62
Fiji-Caroline Islands	Federated States of Micronesia	YAP-13	22.08	Stresstolerant	3.11
Fiji-Caroline Islands	Federated States of Micronesia	YAP-14	21.36	Stresstolerant	2.94
Fiji-Caroline Islands	Federated States of Micronesia	YAP-19	20.57	Stresstolerant	3.09
Fiji-Caroline Islands	Federated States of Micronesia	YAP-5	20.43	Stresstolerant	2.77
Fiji-Caroline Islands	Federated States of Micronesia	YAP-4	19.24	Stresstolerant	2.76
Fiji-Caroline Islands	Federated States of Micronesia	YAP-16	14.23	Stresstolerant	2.62
Fiji-Caroline Islands	Federated States of Micronesia	YAP-15	10.52	Stresstolerant	2.62
Fiji-Caroline Islands	Federated States of Micronesia	YAP-7	10.10	Stresstolerant	2.61
Fiji-Caroline Islands	Marshall Islands	Arn6n	73.13	Competitive	3.69
Fiji-Caroline Islands	Marshall Islands	Majuro_12a	65.38	Competitive	2.94
Fiji-Caroline Islands	Marshall Islands	Maj06	62.44	Competitive	3.22
Fiji-Caroline Islands	Marshall Islands	Majuro_13a	59.47	Competitive	3.22
Fiji-Caroline Islands	Marshall Islands	Majuro_12b	56.72	Competitive	2.94
Fiji-Caroline Islands	Marshall Islands	Majuro_13b	52.23	Stresstolerant	3.22
Fiji-Caroline Islands	Marshall Islands	Arn9n	48.43	Stresstolerant	3.67
Fiji-Caroline Islands	Marshall Islands	Majuro_6a	45.72	Competitive	3.24
Fiji-Caroline Islands	Marshall Islands	Majuro_6b	42.74	Competitive	3.24
Fiji-Caroline Islands	Marshall Islands	Majuro_3a	41.48	Stresstolerant	2.94
Fiji-Caroline Islands	Marshall Islands	Majuro_5b	41.14	Competitive	3.24
Fiji-Caroline Islands	Marshall Islands	MAJ-13	36.94	Competitive	3.58
Fiji-Caroline Islands	Marshall Islands	Arn11n	35.29	Stresstolerant	3.34
Fiji-Caroline Islands	Marshall Islands	Maj09	33.84	Competitive	3.24
Fiji-Caroline Islands	Marshall Islands	Majuro_3b	33.31	Stresstolerant	2.94
Fiji-Caroline Islands	Marshall Islands	Majuro_10b	32.24	Stresstolerant	3.31

Fiji-Caroline Islands	Marshall Islands	Majuro_10a	32.00	Stresstolerant	3.31
Fiji-Caroline Islands	Marshall Islands	Majuro_7a	26.92	Competitive	2.96
Fiji-Caroline Islands	Marshall Islands	MAJ-8	26.30	Competitive	3.76
Fiji-Caroline Islands	Marshall Islands	Maj03	26.20	Competitive	3.24
Fiji-Caroline Islands	Marshall Islands	Majuro_9a	25.99	Competitive	3.56
Fiji-Caroline Islands	Marshall Islands	Majuro_2a	25.72	Competitive	3.76
Fiji-Caroline Islands	Marshall Islands	Arn13n	25.23	Competitive	3.47
Fiji-Caroline Islands	Marshall Islands	Majuro_7b	23.60	Stresstolerant	2.96
Fiji-Caroline Islands	Marshall Islands	Maj05	23.12	Competitive	3.31
Fiji-Caroline Islands	Marshall Islands	Arn1n	22.01	Stresstolerant	3.69
Fiji-Caroline Islands	Marshall Islands	Arn7n	21.87	Stresstolerant	3.69
Fiji-Caroline Islands	Marshall Islands	Majuro_5a	19.90	Competitive	3.24
Fiji-Caroline Islands	Marshall Islands	Maj01	19.76	Competitive	3.72
Fiji-Caroline Islands	Marshall Islands	MAJ-11	18.55	Competitive	3.72
Fiji-Caroline Islands	Marshall Islands	Arn8n	15.62	Competitive	3.84
Fiji-Caroline Islands	Marshall Islands	MAJ-9	12.97	Stresstolerant	3.31
Fiji-Caroline Islands	Marshall Islands	Majuro_2b	12.67	Competitive	3.76
Fiji-Caroline Islands	Marshall Islands	Majuro_8a	10.53	Stresstolerant	3.24
Fiji-Caroline Islands	Marshall Islands	MAJ-7	10.43	Stresstolerant	3.08
Fiji-Caroline Islands	United States, Northern Mariana Islands	TIN-01	18.72	Stresstolerant	3.59
Fiji-Caroline Islands	United States, Northern Mariana Islands	GUA-07	16.43	Stresstolerant	3.52
Fiji-Caroline Islands	United States, Northern Mariana Islands	SAI-05	13.23	Stresstolerant	3.98
Fiji-Caroline Islands	United States, Northern Mariana Islands	AGU-02	12.45	Stresstolerant	3.87
Fiji-Caroline Islands	United States, Northern Mariana Islands	GUA-09	11.97	Stresstolerant	3.66
Hawaii-Line Islands	United States, Minor Outlying Islands	KIN-16	47.54	Stresstolerant	1.71

Hawaii-Line Islands	United States, Minor Outlying Islands	KIN-13	40.49	Competitive	1.71
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_North Barren	38.73	Competitive	2.18
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_RT6	36.77	Competitive	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_RT10	34.29	Competitive	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_PAL-30-P-B	34.11	Competitive	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PAL-19	32.95	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	KIN-10	31.91	Stresstolerant	1.70
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_RT4	31.49	Competitive	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_SIOFR3_10	30.13	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	KIN-11	29.66	Stresstolerant	1.71
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_RT13	29.11	Competitive	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	KIN-23	29.03	Stresstolerant	1.71
Hawaii-Line Islands	United States, Minor Outlying Islands	KIN-17	28.11	Stresstolerant	1.71
Hawaii-Line Islands	United States, Minor Outlying Islands	PAL-26	27.75	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	KIN-04	27.74	Competitive	1.70
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_RT1_Western Terrace Snorkel Buoy	27.63	Competitive	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PAL-09	27.45	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_RT7	26.94	Competitive	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_RT25	26.85	Competitive	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_Tortugonas	24.92	Competitive	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_WTIP7_20	24.70	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_Penguin Spit Inner	23.19	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PAL-10	22.62	Stresstolerant	2.18
Hawaii-Line Islands	United States, Minor Outlying Islands	PALF2_5	20.32	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PAL-17	20.20	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_WTIP8_20	19.81	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_FR9_10	19.46	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_SIOFR3_20	18.29	Stresstolerant	2.32

Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_DRT2	17.58	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PAL-25	17.49	Stresstolerant	2.18
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_G-Banger	17.32	Competitive	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_FR7_10	17.04	Stresstolerant	2.17
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_PALF22_20	16.64	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_SIO_FR5	16.31	Competitive	2.17
Hawaii-Line Islands	United States, Minor Outlying Islands	KIN-21	16.27	Competitive	1.71
Hawaii-Line Islands	United States, Minor Outlying Islands	PALF25_10	16.13	Stresstolerant	2.18
Hawaii-Line Islands	United States, Minor Outlying Islands	PALF25_5	15.55	Competitive	2.18
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_PALF22_10	15.15	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_Uvic_Holei&Bird_5	15.11	Stresstolerant	2.17
Hawaii-Line Islands	United States, Minor Outlying Islands	KIN-05	15.00	Stresstolerant	1.71
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_PALFR9_20	14.72	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_PALF14_5	14.57	Stresstolerant	2.17
Hawaii-Line Islands	United States, Minor Outlying Islands	PALF25_20	14.56	Stresstolerant	2.18
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_SIOFR5_10	14.12	Stresstolerant	2.17
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_Uvic_Paradise_10	14.00	Competitive	2.17
Hawaii-Line Islands	United States, Minor Outlying Islands	PAL-12	13.98	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PALF2_20	13.90	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_FR7_20	13.39	Stresstolerant	2.17
Hawaii-Line Islands	United States, Minor Outlying Islands	KIN-07	13.17	Stresstolerant	1.71
Hawaii-Line Islands	United States, Minor Outlying Islands	PAL-02	12.59	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PAL-05	12.49	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PAL-11	12.19	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PALF2_10	11.62	Competitive	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_PALF17_20	11.42	Stresstolerant	2.17
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_SIOFR5_20	11.00	Stresstolerant	2.17
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_ETIP1_20	10.85	Stresstolerant	2.18

Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_RT23	10.65	Competitive	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PAL-21	10.62	Competitive	2.17
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_Uvic_Paradise_20	10.39	Stresstolerant	2.17
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_DRT1	10.27	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_PALF17_5	10.24	Competitive	2.17
Hawaii-Line Islands	United States, Minor Outlying Islands	KIN-12	10.14	Stresstolerant	1.71
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_PALF22_5	10.13	Stresstolerant	2.32
Hawaii-Line Islands	United States, Minor Outlying Islands	PANWR_PALF14_20	10.04	Stresstolerant	2.17
Indonesia	Indonesia	Bahoi_S	56.62	Competitive	0.00
Indonesia	Indonesia	Waybalun A	56.33	Competitive	3.06
Indonesia	Indonesia	Kinabuhutan_S	42.04	Competitive	0.99
Indonesia	Indonesia	Watowati A	39.83	Competitive	2.44
Indonesia	Indonesia	Pulau Mas A	39.50	Competitive	2.84
Indonesia	Indonesia	Kalinaun_S	34.18	Stresstolerant	0.15
Indonesia	Indonesia	Pele	33.56	Competitive	1.24
Indonesia	Indonesia	Desa Balaweling A	31.53	Stresstolerant	2.57
Indonesia	Indonesia	Maen_S	30.95	Competitive	0.15
Indonesia	Indonesia	Eco Resort	29.88	Competitive	1.79
Indonesia	Indonesia	Maliambao_S	29.22	Competitive	0.14
Indonesia	Indonesia	Pele North	27.33	Competitive	1.27
Indonesia	Indonesia	Watowati B	27.27	Stresstolerant	2.44
Indonesia	Indonesia	Pulisan_S	27.19	Competitive	0.15
Indonesia	Indonesia	Mubune_S	25.94	Competitive	0.00
Indonesia	Indonesia	Hurung A	25.03	Competitive	2.78
Indonesia	Indonesia	Lihunu_S	24.98	Stresstolerant	0.59
Indonesia	Indonesia	WAAF	24.10	Competitive	1.13
Indonesia	Indonesia	Adonara A	21.53	Stresstolerant	3.72
Indonesia	Indonesia	Tambun_S	20.97	Competitive	0.99
Indonesia	Indonesia	Koten B	20.54	Stresstolerant	2.70
Indonesia	Indonesia	Munte_S	20.26	Competitive	0.00
Indonesia	Indonesia	Latto A	19.50	Stresstolerant	2.89
Indonesia	Indonesia	Aerbanua_S	19.48	Stresstolerant	1.68
Indonesia	Indonesia	Karang Le A	19.47	Competitive	3.21
Indonesia	Indonesia	Tanah Putih_S	18.48	Stresstolerant	0.14
Indonesia	Indonesia	4317	17.54	Stresstolerant	1.82
Indonesia	Indonesia	Karang Le B	17.24	Stresstolerant	3.21
Indonesia	Indonesia	Tarabitan_S	16.97	Stresstolerant	0.14
Indonesia	Indonesia	Batu Payung A	15.87	Stresstolerant	2.91
Indonesia	Indonesia	Koli Dateng A	15.87	Stresstolerant	2.36
Indonesia	Indonesia	Mausamang A	13.33	Stresstolerant	3.11
Indonesia	Indonesia	Mademang A	11.43	Stresstolerant	3.52
Indonesia	Indonesia	Waybalun B	11.36	Competitive	3.06
Indonesia	Indonesia	Talise_S	11.31	Stresstolerant	0.99
Indonesia	Indonesia	Mausamang B	10.52	Competitive	3.11
Indonesia	Indonesia	Koten A	10.50	Stresstolerant	2.70
Indonesia	Indonesia	Tanjung Ikara B	10.40	Stresstolerant	2.96
Indonesia	Malaysia	Paku Besar Island_6m	97.71	Competitive	1.97
Indonesia	Malaysia	Pinang Island_10m	95.72	Stresstolerant	1.61

Indonesia	Malaysia	Lima Island_6m	93.74	Competitive	1.97
Indonesia	Malaysia	Pinang Island_6m	88.65	Stresstolerant	1.61
Indonesia	Malaysia	Ekor Tebu Island_10m	85.72	Stresstolerant	1.94
Indonesia	Malaysia	Lima Island_10m	84.46	Stresstolerant	1.97
Indonesia	Malaysia	Paku Besar Island_10m	83.81	Competitive	1.97
Indonesia	Malaysia	Kerengga Besar Island_10m	76.81	Stresstolerant	1.94
Indonesia	Malaysia	Ekor Tebu Island_6m	73.77	Competitive	1.94
Indonesia	Malaysia	Kerengga Besar Island_6m	70.94	Stresstolerant	1.94
Indonesia	Malaysia	Pasir Cina_Left_3m	53.30	Stresstolerant	1.96
Indonesia	Malaysia	Pasir Cina_Right_3m	51.51	Competitive	1.96
Indonesia	Malaysia	Pasir Akar_10m	48.29	Competitive	1.61
Indonesia	Malaysia	Ekor Tebu_3m	47.41	Competitive	1.94
Indonesia	Malaysia	Chagar Hutang_Left_3m	42.97	Competitive	2.44
Indonesia	Malaysia	Pasir Akar_3m	39.83	Competitive	1.61
Indonesia	Malaysia	Chagar Hutang_Right_3m	38.08	Competitive	2.44
Indonesia	Malaysia	Pasir Cina_Left_10m	30.93	Competitive	1.96
Indonesia	Malaysia	Karah Island_10m	30.28	Competitive	1.96
Indonesia	Malaysia	Karah Island_3m	28.53	Competitive	1.96
Indonesia	Malaysia	Ekor Tebu_10m	26.43	Competitive	1.94
Indonesia	Malaysia	Lima Island_3m	25.91	Competitive	1.97
Indonesia	Malaysia	Pasir Cina_Right_10m	25.64	Stresstolerant	1.96
Indonesia	Malaysia	Teluk Dalam_3m	22.22	Stresstolerant	2.44
Indonesia	Malaysia	Teluk Dalam_10m	18.94	Stresstolerant	2.44
Indonesia	Singapore	Pulau Hantu	34.68	Stresstolerant	2.87
Indonesia	Singapore	Kusu	29.78	Stresstolerant	2.90
Indonesia	Singapore	Raffles	25.93	Stresstolerant	3.01
Indonesia	Singapore	TPT	22.10	Stresstolerant	2.99
Indonesia	Singapore	Kusu Island	16.90	Stresstolerant	2.90
Indonesia	Singapore	Pulau Hantu	14.88	Stresstolerant	2.99
Indonesia	Singapore	Sisters Island	14.09	Stresstolerant	2.90
Indonesia	Singapore	TPL	12.38	Stresstolerant	2.99
Indonesia	Singapore	Semakau	11.14	Stresstolerant	2.99
Japan-Vietnam	Taiwan	Houbihu	29.98	Stresstolerant	3.15
Japan-Vietnam	Taiwan	Outlet	24.23	Stresstolerant	3.15
Japan-Vietnam	Taiwan	Leidashih	15.45	Stresstolerant	3.15
Japan-Vietnam	Taiwan	Sangjiaowan	13.14	Stresstolerant	3.10
Japan-Vietnam	Taiwan	Jialeshuei	10.22	Stresstolerant	2.70
Japan-Vietnam	Taiwan	Tanzihwan	10.03	Stresstolerant	3.15
Persian Gulf	Oman	Coral Garden	31.97	Stresstolerant	0.38
Persian Gulf	Oman	Rashid West	11.00	Stresstolerant	1.06
Persian Gulf	United Arab Emirates	Saadiyat	27.06	Stresstolerant	0.76
Persian Gulf	United Arab Emirates	Ras Ghanadah	23.04	Stresstolerant	0.00
Persian Gulf	United Arab Emirates	Dhabiya West	14.79	Stresstolerant	0.46
Persian Gulf	United Arab Emirates	Dibba Rock	12.21	Competitive	0.91
Persian Gulf	United Arab Emirates	Dhabiya East	11.00	Stresstolerant	0.46
Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU01_10m	51.84	Competitive	0.44

Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU09_20m	48.12	Competitive	0.44
Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU04_10m	47.71	Competitive	0.44
Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU08_20m	46.84	Competitive	0.44
Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU07_10m	46.03	Competitive	0.44
Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU08_10m	46.00	Competitive	0.44
Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU09_10m	40.48	Stresstolerant	0.44
Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU07_20m	36.80	Competitive	0.44
Polynesia	British Overseas Territory, Pitcairn Islands	Henderson.HE13_10m	32.62	Stresstolerant	2.03
Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU04_20m	30.19	Competitive	0.44
Polynesia	British Overseas Territory, Pitcairn Islands	Henderson.HE12_10m	27.47	Stresstolerant	0.95
Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU06_10m	26.80	Competitive	0.44
Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU03_20m	26.00	Competitive	0.44
Polynesia	British Overseas Territory, Pitcairn Islands	Henderson.HE13_20m	25.86	Stresstolerant	2.03
Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU03_10m	24.40	Competitive	0.44
Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU06_20m	23.32	Competitive	0.44
Polynesia	British Overseas Territory, Pitcairn Islands	Henderson.HE11_20m	22.23	Competitive	1.54
Polynesia	British Overseas Territory, Pitcairn Islands	Henderson.HE11_10m	21.09	Stresstolerant	1.54
Polynesia	British Overseas Territory, Pitcairn Islands	Henderson.HE01_20m	16.83	Competitive	0.95

Polynesia	British Overseas Territory, Pitcairn Islands	Pitcairn.PI14_30m	15.97	Stresstolerant	1.95
Polynesia	British Overseas Territory, Pitcairn Islands	Pitcairn.PI08_20m	15.63	Competitive	1.95
Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU05_20m	15.00	Competitive	0.44
Polynesia	British Overseas Territory, Pitcairn Islands	Henderson.HE07_10m	12.99	Stresstolerant	0.95
Polynesia	British Overseas Territory, Pitcairn Islands	Pitcairn.PI13_30m	12.96	Competitive	1.95
Polynesia	British Overseas Territory, Pitcairn Islands	Henderson.HE10_10m	12.92	Competitive	1.54
Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU01_20m	12.72	Competitive	0.44
Polynesia	British Overseas Territory, Pitcairn Islands	Henderson.HE10_20m	10.75	Competitive	1.54
Polynesia	British Overseas Territory, Pitcairn Islands	Henderson.HE06_20m	10.37	Competitive	1.56
Polynesia	British Overseas Territory, Pitcairn Islands	Ducie.DU11_10m	10.20	Stresstolerant	0.44
Polynesia	France, French Polynesia	nengo	18.96	Competitive	3.02
Red Sea	Saudi Arabia	Horseshoe_10m	20.84	Stresstolerant	3.38
Red Sea	Saudi Arabia	Abu Madafi_10m	20.17	Stresstolerant	1.73
Red Sea	Saudi Arabia	Palace Reef_1m	19.62	Competitive	3.94
Red Sea	Saudi Arabia	Shi'b D'auqa_10m	18.46	Stresstolerant	2.56
Red Sea	Saudi Arabia	Shib Nazar_10m	18.44	Stresstolerant	2.19
Red Sea	Saudi Arabia	Shi'b D'auqa_2m	18.16	Competitive	2.56
Red Sea	Saudi Arabia	Abu Madafi_1m	18.07	Competitive	1.73
Red Sea	Saudi Arabia	Horseshoe_1m	17.74	Competitive	3.38
Red Sea	Saudi Arabia	Palace Reef_10m	17.31	Stresstolerant	3.94
Red Sea	Saudi Arabia	Abu Roma_10m	16.43	Competitive	3.31
Red Sea	Saudi Arabia	Abu Roma_1m	14.26	Competitive	3.31
Unclustered	Myanmar	136	77.18	Competitive	1.59
Unclustered	Myanmar	11	65.07	Competitive	1.59
Unclustered	Myanmar	149	55.32	Competitive	1.59
Unclustered	Myanmar	9	54.81	Competitive	1.59
Unclustered	Myanmar	10	46.90	Competitive	1.59
Unclustered	Myanmar	21	44.33	Stresstolerant	2.24
Unclustered	Myanmar	12	36.56	Competitive	1.59
Unclustered	Myanmar	143	36.16	Stresstolerant	2.30
Unclustered	Myanmar	18	33.66	Stresstolerant	2.17
Unclustered	Myanmar	6	31.44	Stresstolerant	2.50
Unclustered	Myanmar	7	29.22	Stresstolerant	3.61
Unclustered	Myanmar	28	27.71	Stresstolerant	3.44
Unclustered	Myanmar	144	25.76	Stresstolerant	2.19

Unclustered	Myanmar	130	24.74	Stresstolerant	2.30
Unclustered	Myanmar	16	21.39	Stresstolerant	2.17
Unclustered	Myanmar	148	21.34	Stresstolerant	1.59
Unclustered	Myanmar	17	20.60	Stresstolerant	2.32
Unclustered	Myanmar	129	18.54	Stresstolerant	2.30
Unclustered	Myanmar	127	18.10	Competitive	2.76
Unclustered	Myanmar	150	17.22	Stresstolerant	3.63
Unclustered	Myanmar	137	11.67	Stresstolerant	3.02
Unclustered	Myanmar	13	11.13	Stresstolerant	3.02
Unclustered	Thailand	Ko Khrok (West)	34.31	Stresstolerant	3.55
Unclustered	Thailand	Ko Yak (South)	23.33	Stresstolerant	3.91
Unclustered	Thailand	Ko thong Lang (West)	22.36	Stresstolerant	3.91
Unclustered	Thailand	South of Ko Lan (Ao Nuan)	21.94	Stresstolerant	3.46
Unclustered	Thailand	Ko Thain (West)	21.05	Stresstolerant	3.91
Unclustered	Thailand	Ko Sak (Northwest)	16.58	Stresstolerant	3.55

Supplementary Table 7. Variance inflation factor (VIF) scores for continuous covariates.

Covariate	Starting VIF	Ending VIF
Local population growth, 2000-2010	1.40	1.24
Gravity – nearest settlement	1.15	1.06
Gravity - market	1.35	1.25
Cultivated land, % change 2002-2012	1.37	1.34
Cultivated land, % 2012	1.32	1.12
GDP per capita	7.15	X
Voice and accountability	2.72	X
HDI	5.75	1.54
Past maximum DHW	1.36	1.25
Years since Maximum DHW	1.39	1.32
Primary productivity	1.96	1.52
Depth	1.41	1.37
Wave exposure	1.83	1.79
Maximum cyclone days	2.10	1.19
Years since max cyclone	2.59	X
Reef area, km^2	1.72	1.44

Supplementary Table 8. Data sources, countries and contact information for the data contributed to this study. Sources are ordered by the number of sites contributed to this survey.

Source	Countries	Sites	Name	Contact
National Geographic Pristine Seas	Chile, France, Mexico, Mozambique, Niue, United Kingdom	431	Alan Friedlander	friedlan@hawaii.edu
NOAA Coral Reef Ecosystem Pacific	Samoa, United States	328	Bernardo Vargas-Angel	bernardo.vargasangel@noaa.gov
Jupiter	Fiji, Solomon Islands	276	Stacy Jupiter	sjupiter@wcs.org
Lamb	Australia, Indonesia, Myanmar, Thailand	179	Joleah Lamb	joleah.lamb@uci.edu
Graham	Australia, Maldives, Seychelles, Chagos	159	Nick Graham	nick.graham@jcu.edu.au
WCS Indonesia	Indonesia	152	Shinta Pardede	spardede@wcs.org
Houk	Marshall Islands, Micronesia, United States	97	Peter Houk	peterhouk@gmail.com
Western Australia Department of Parks and Wildlife	Australia	91	Shaun Wilson	shaun.wilson@dbca.wa.gov.au
Bridge	Australia, Maldives	78	Tom Bridge	thomas.bridge@jcu.edu.au
Richards	Australia, Marshall Islands, Micronesia	76	Zoe Richards	Zoe.Richards@curtin.edu.au
Franklin	United States	61	Erik Franklin	erik.franklin@hawaii.edu
Donner	Kiribati, Marshall Islands	54	Simon Donner	simon.donner@ubc.ca
WWF-US and WWF-Indonesia	Indonesia	54	Estradiveri	estradivari@wwf.id
Williams	United States	51	Gareth Williams	g.j.williams@bangor.ac.uk
WCS Madagascar	Madagascar	49	Ravaka Ranaivoson	rranaivoson@wcs.org
WCS Kenya	Kenya, Tanzania	48	Tim McClanahan	tmcclanahan@wcs.org
Pratchett	Australia	45	Morgan Pratchett	morgan.pratchett@jcu.edu.au
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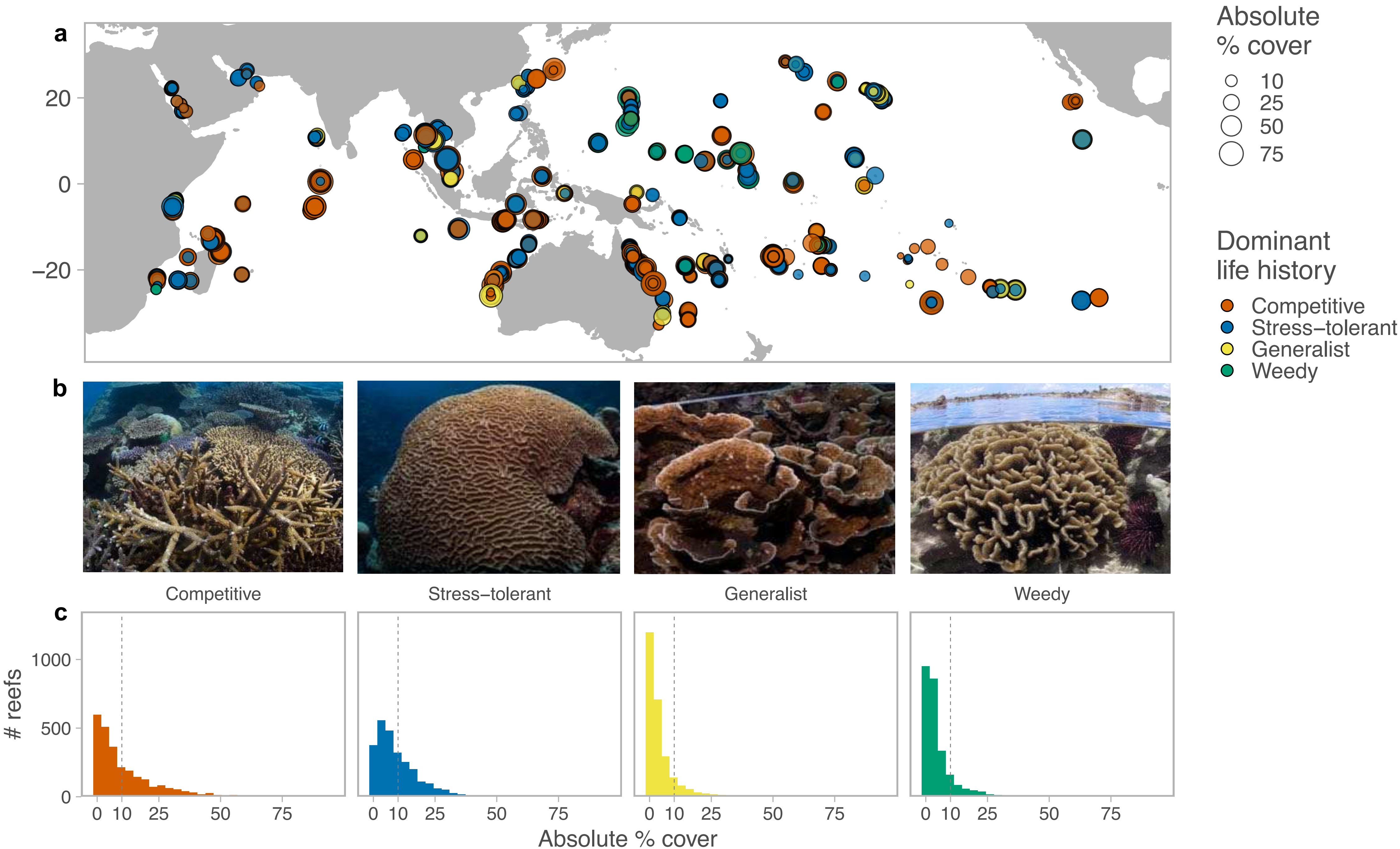
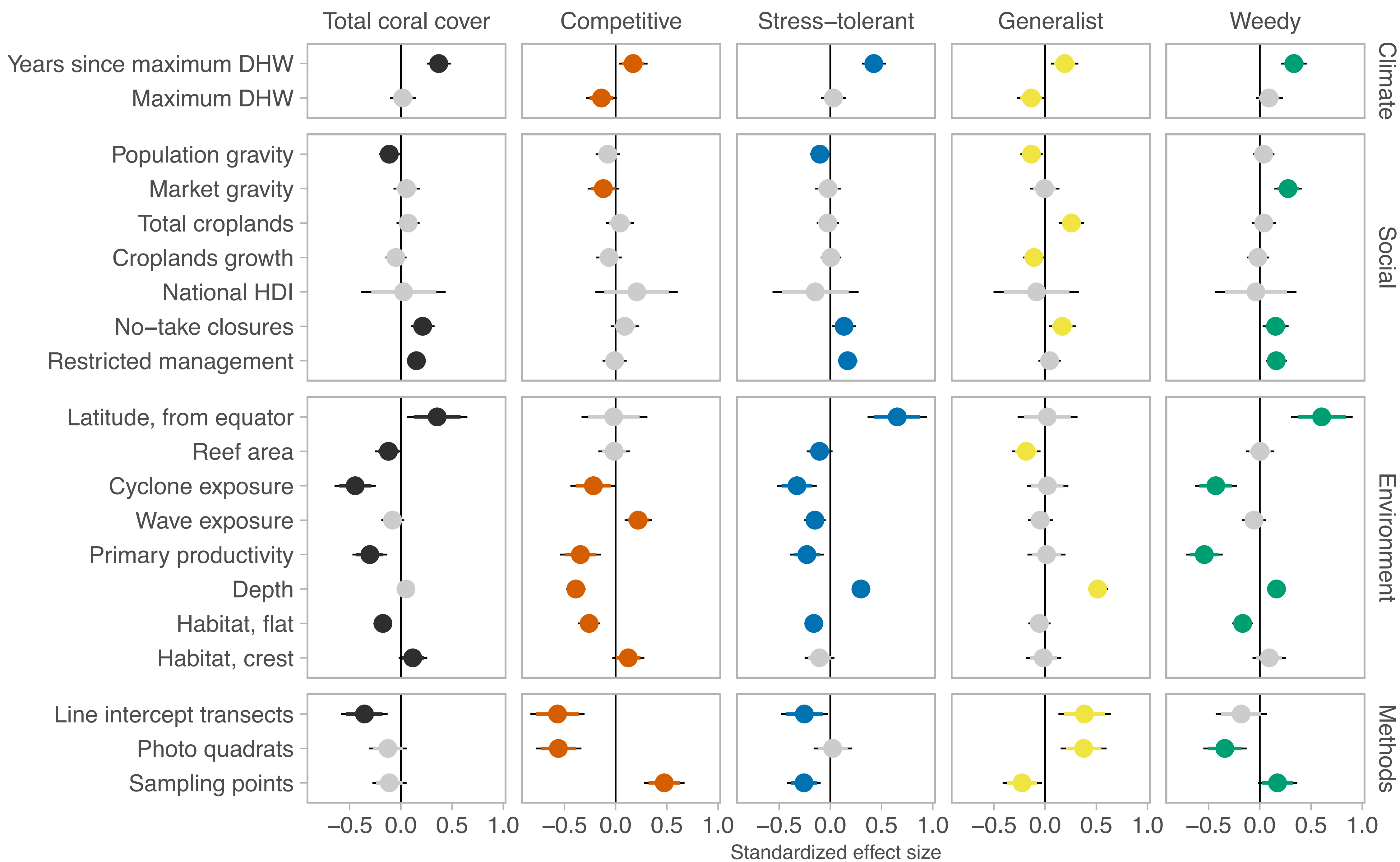
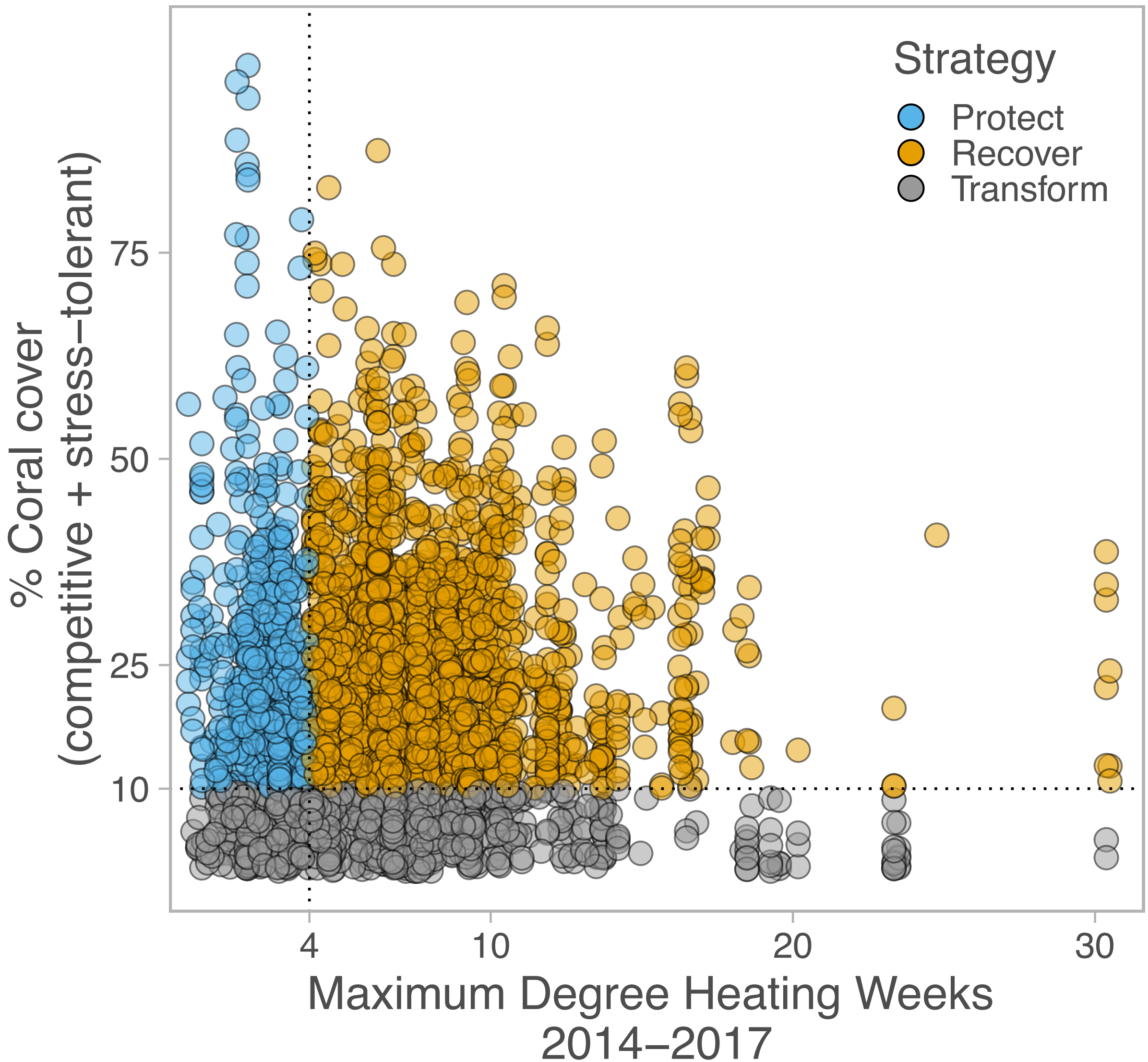
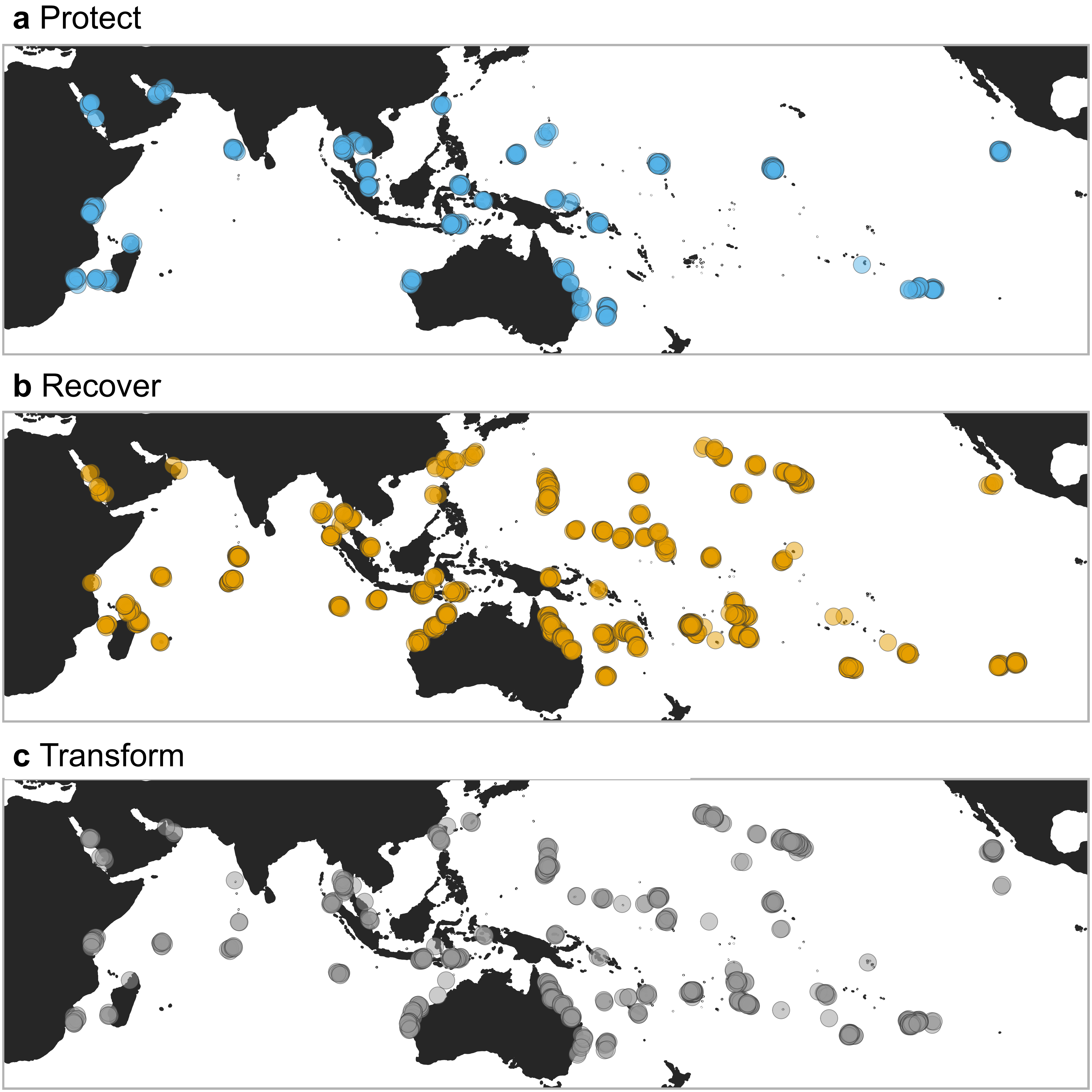

a
20
0
−20
Absolute
% cover
10
25
50
75
Dominant
life history
Competitive
Stress−tolerant
Generalist
Weedy
b
Competitive
Stress−tolerant
Generalist
Weedy
c
reefs
1000
500
0
0 10 25 50 75
Absolute % cover



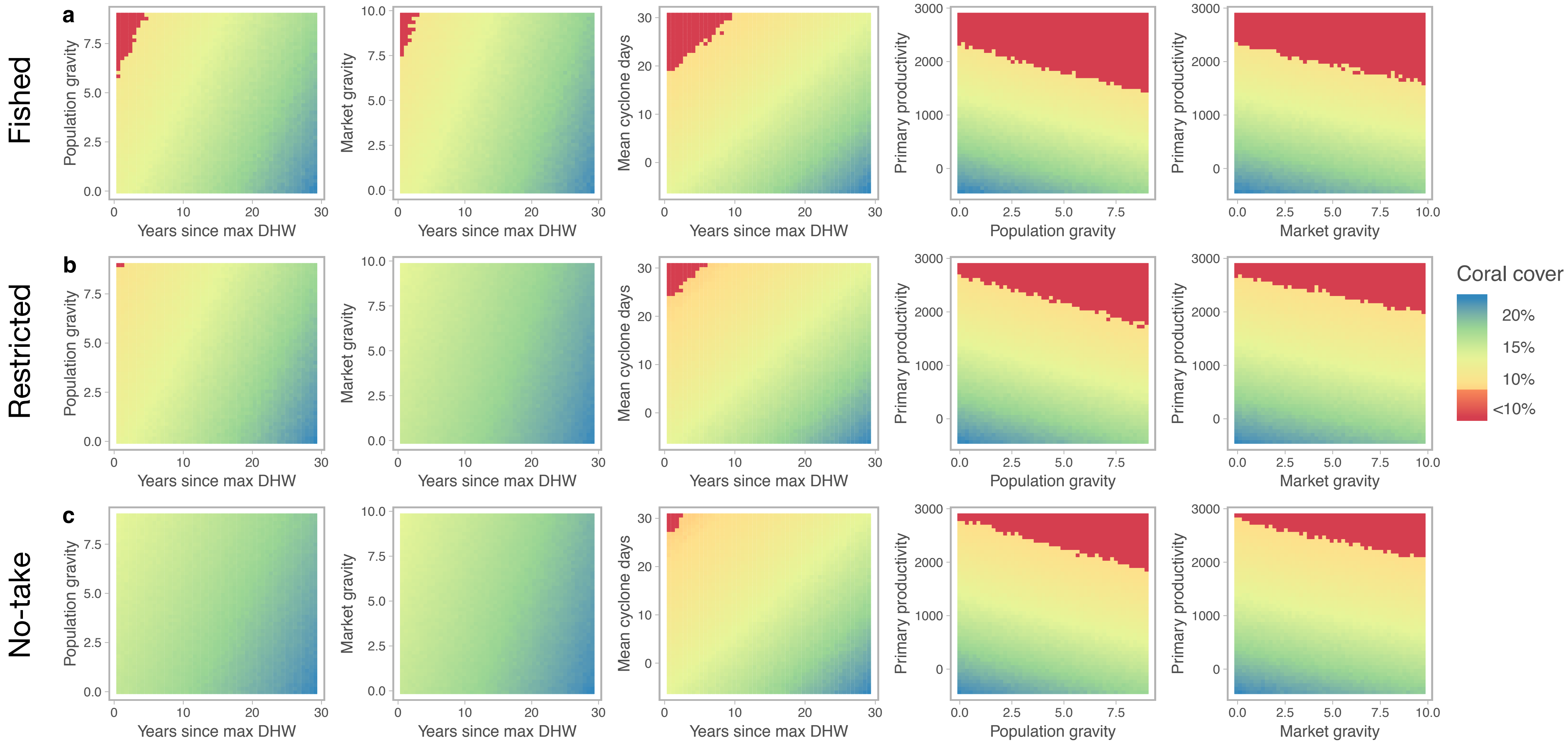
Total coral cover
Competitive
Stress–tolerant
Generalist
Weedy
Years since maximum DHW
Maximum DHW
Population gravity
Market gravity
Total croplands
Croplands growth
National HDI
No–take closures
Restricted management
Latitude, from equator
Reef area
Cyclone exposure
Wave exposure
Primary productivity
Depth
Habitat, flat
Habitat, crest
Line intercept transects
Photo quadrats
Sampling points
Climate
Social
Environment
Methods
–0.5 0.0 0.5 1.0
Standardized effect size



Strategy
Protect
Recover
Transform
% Coral cover
(competitive + stress–tolerant)
75
50
25
10
4
10
20
30
Maximum Degree Heating Weeks
2014–2017



a Protect
b Recover
c Transform



a
b
c
Fished
Restricted
No-take
Population gravity
Market gravity
Mean cyclone days
Primary productivity
Years since max DHW
Population gravity
Market gravity
Coral cover
20%
15%
10%
<10%