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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 identification of the environmental and socioeconomic factors driving the persistence of scleractinian coral assemblages—the foundation species of coral reef ecosystems. Here, we compiled coral abundance data from 2,584 Indo-Pacific reefs to evaluate the influence of 21 climate, social and environmental drivers on the ecology of reef coral assemblages. Higher abundances of framework-building corals were typically associated with: weaker thermal disturbances and longer intervals for potential recovery; slower human population growth; reduced access by human settlements and markets; and less nearby agriculture. We therefore propose a framework of three management strategies (protect, recover or transform) by considering: (1) if reefs were above or below a proposed threshold of >10% cover of the coral taxa important for structural complexity and carbonate production; and (2) reef exposure to severe thermal stress during the 2014–2017 global coral bleaching event. Our findings can guide urgent management efforts for coral reefs, by identifying key threats across multiple scales and strategic policy priorities that might sustain a network of functioning reefs in the Indo-Pacific to avoid ecosystem collapse.

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.

Competing interests The authors declare no competing interests.

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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.

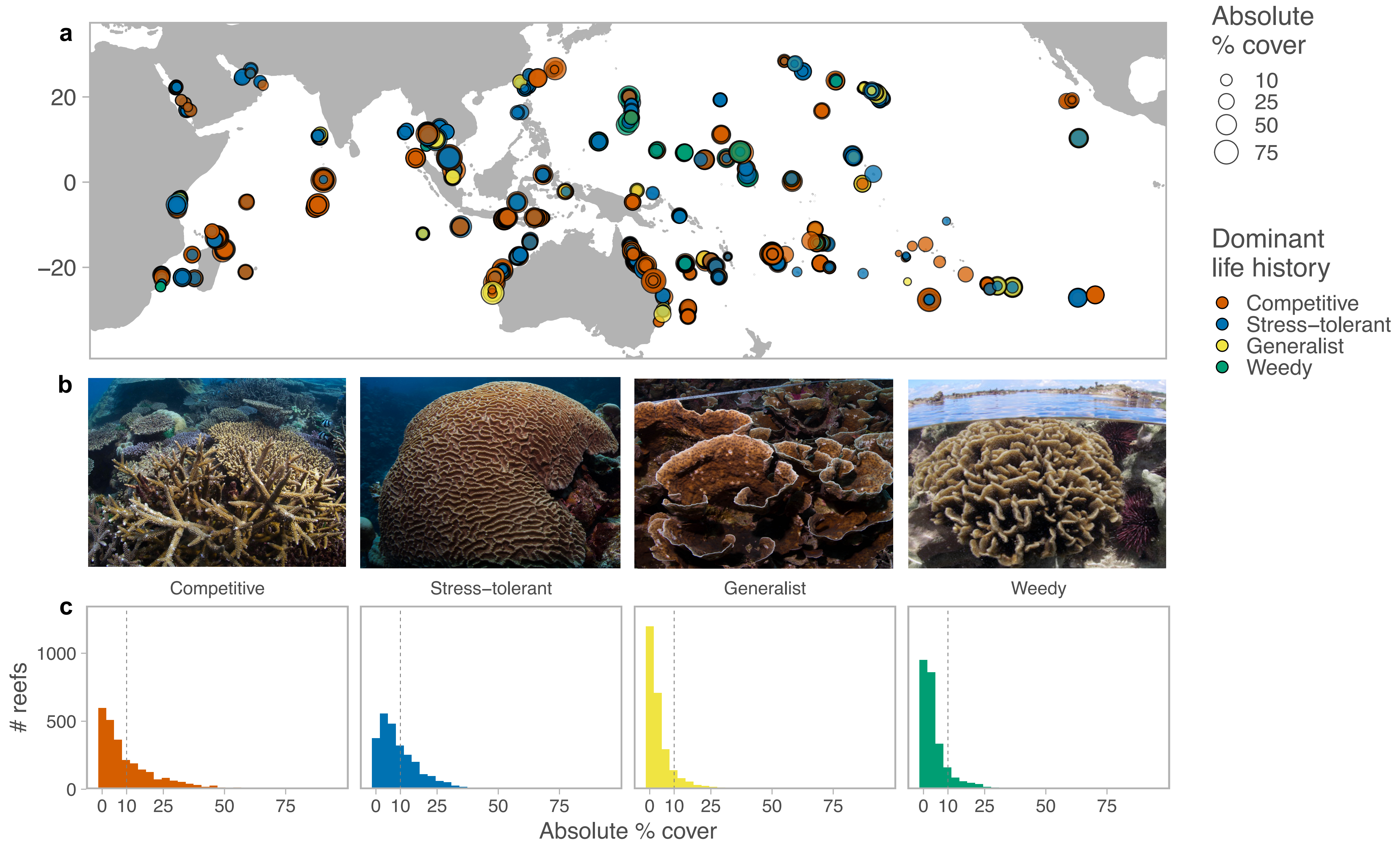
Figure 2. Relationship between climate, social, environment and methodology variables with total coral cover and life history type. Standardized effect sizes are Bayesian posterior median values with 95% Bayesian credible intervals (CI; thin black lines) and 80% credible intervals (coloured thicker lines); 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.


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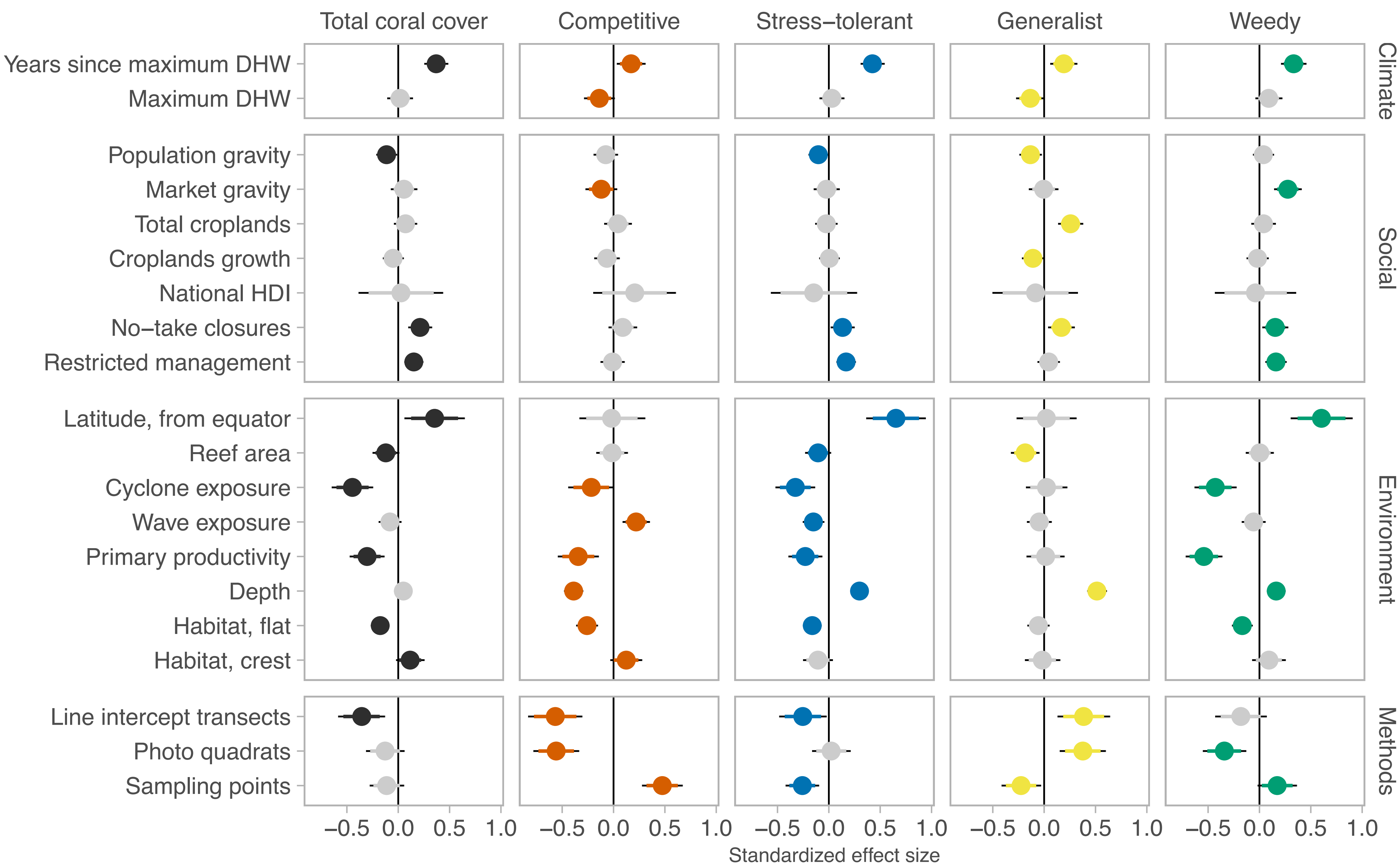
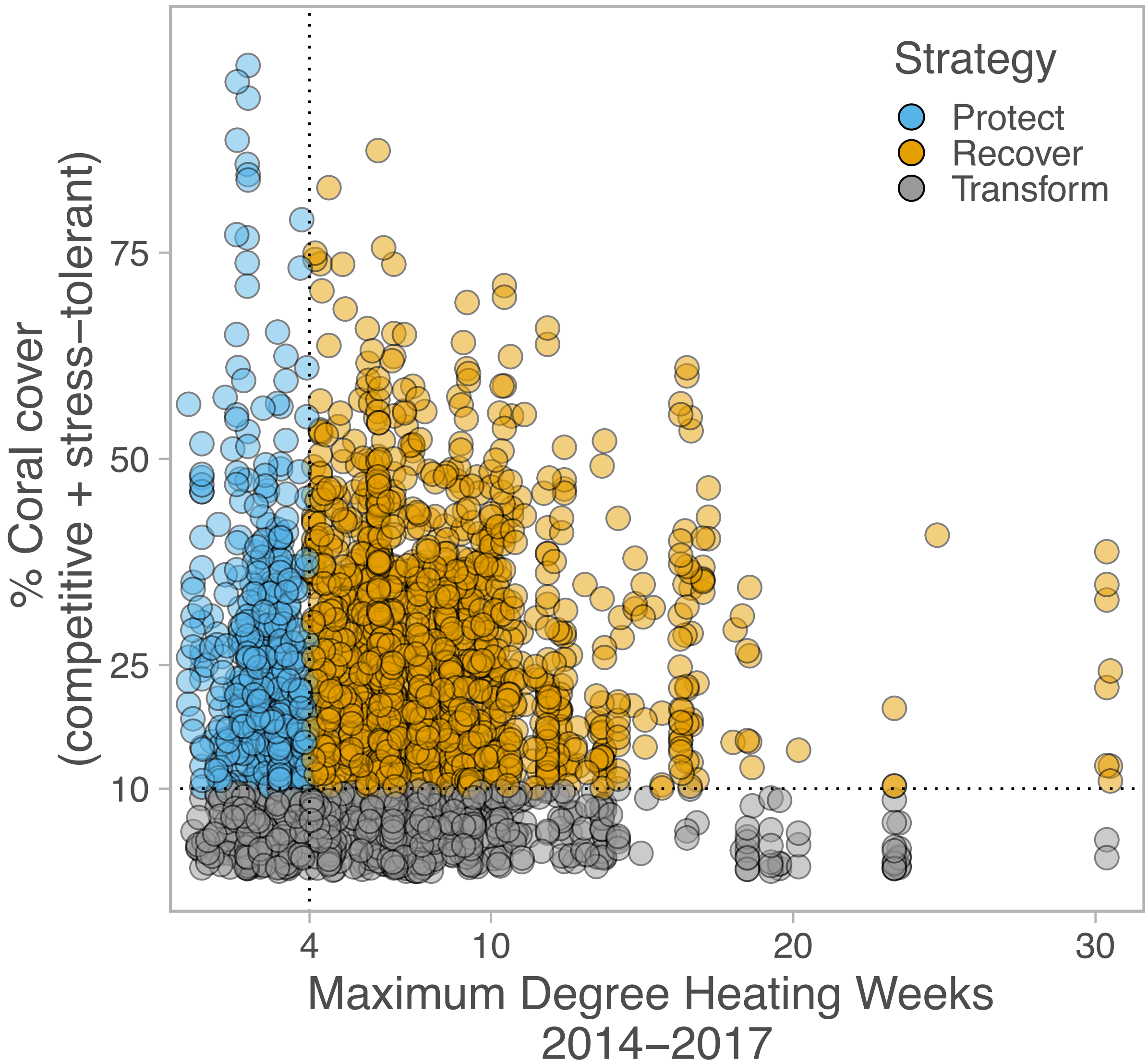
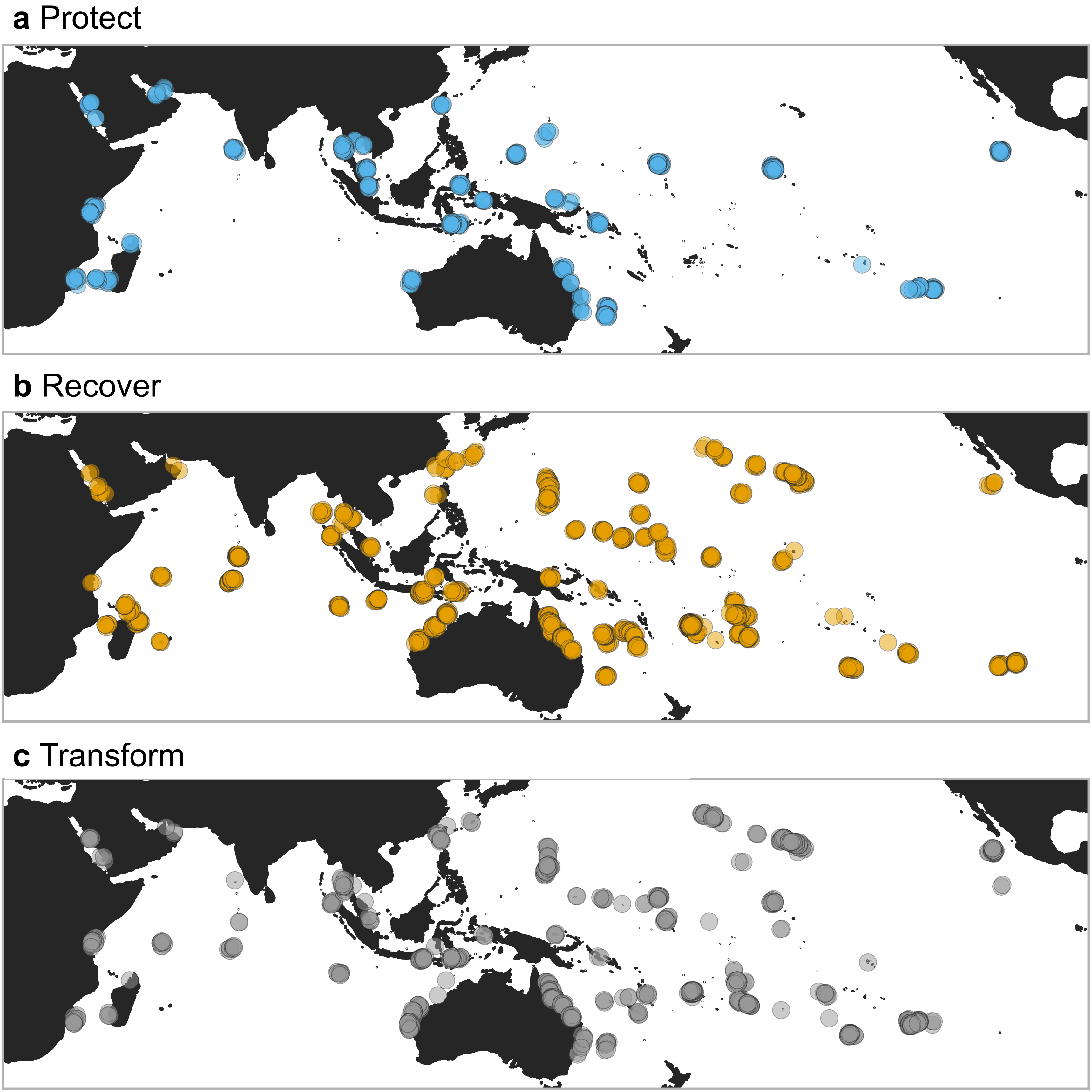
10
25
50
75
Absolute % cover

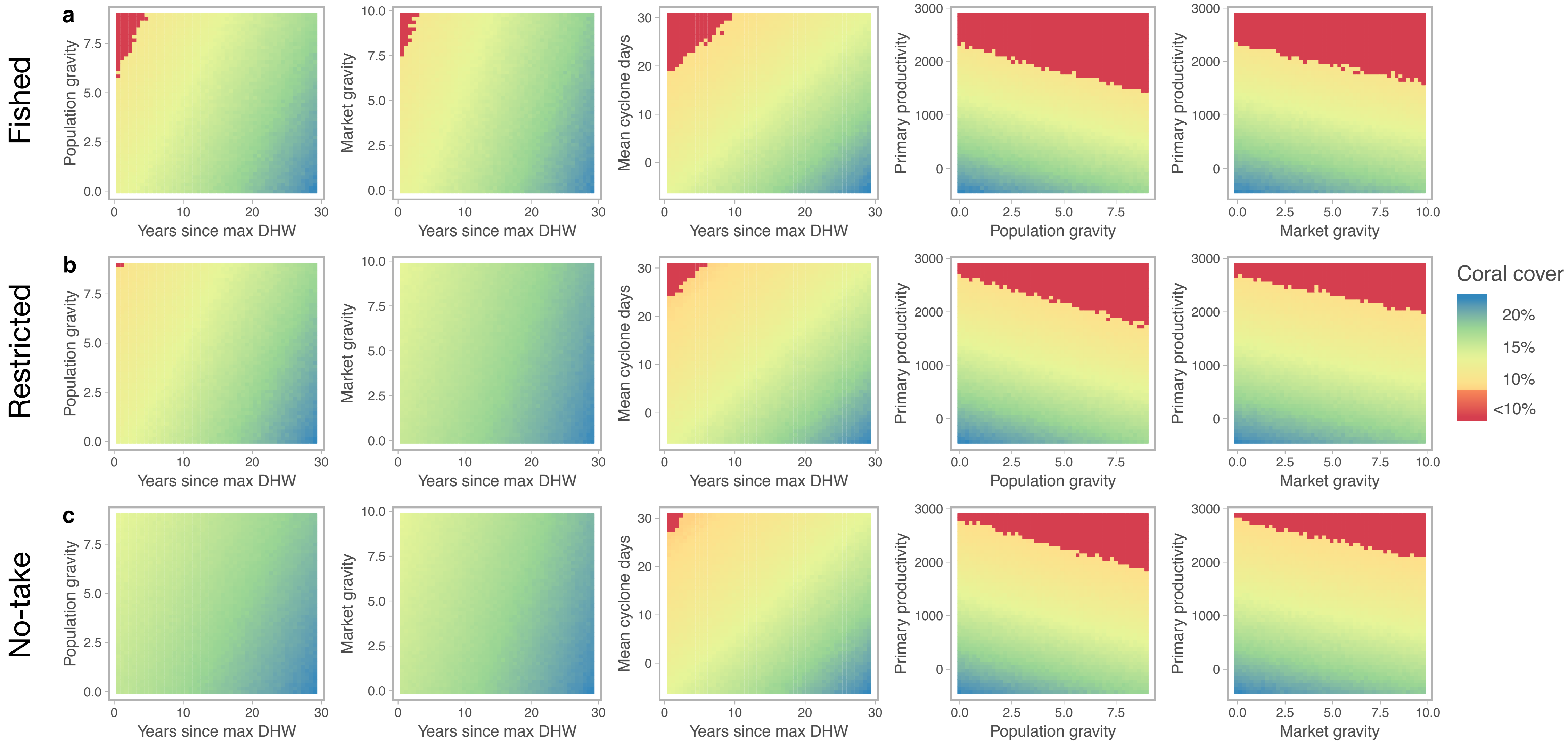


Total coral cover
Competitive
Stress–tolerant
Generalist
Weedy
Years since maximum DHW
Maximum DHW
Population gravity
Market gravity
Total croplands
Croplands growth
National HDI
No–take closures
Restricted management
Latitude, from equator
Reef area
Cyclone exposure
Wave exposure
Primary productivity
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%