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3 **Social-environmental drivers inform strategic management of coral reefs**
4 **in the Anthropocene**
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136 **Abstract:** Without drastic efforts to reduce carbon emissions and mitigate globalized stressors,
137 tropical coral reefs are in jeopardy. Strategic conservation and management requires identifying
138 the environmental and socioeconomic factors driving the persistence of scleractinian coral
139 assemblages – the foundation species of coral reef ecosystems. Here, we compiled coral
140 abundance data from 2,584 Indo-Pacific reefs to evaluate the influence of 21 climate, social, and
141 environmental drivers on the ecology of reef coral assemblages. Higher abundances of
142 framework-building corals were typically associated with: weaker thermal disturbances with
143 longer intervals for potential recovery; slower human population growth; reduced access by
144 human settlements and markets; and less nearby agriculture. We then propose a framework of
145 three management strategies (*protect*, *recover*, or *transform*) by considering: (i) if reefs were
146 above or below a proposed threshold of >10% cover of coral taxa important for structural
147 complexity and carbonate production, and (ii) reef exposure to severe thermal stress during the
148 2014-2017 global coral bleaching event. Our findings can guide urgent management efforts for
149 coral reefs, by identifying key threats across multiple scales and strategic policy priorities that
150 might sustain a network of functioning reefs in the Indo-Pacific to avoid ecosystem collapse.

151

152 **Two-sentence summary:** Surveys from 2,584 sites across the Indo-Pacific identify key climate,
153 socioeconomic, and environmental drivers associated with hard coral assemblages, the
154 foundation species of tropical coral reefs. This informs a strategic approach to *protect*, *recover*,
155 or *transform* coral reef management.

156

157 **Introduction:** With the increasing intensity of human impacts from globalization and climate
158 change, tropical coral reefs have entered the Anthropocene^{1,2} and face unprecedented losses of
159 up to 90% by mid-century³. Against a backdrop of globalized anthropogenic stressors, the
160 impacts of climate change can transform coral communities⁴ and reduce coral growth rates that
161 are crucial to maintain reef structure and track rising sea levels⁵. Under expectations of continued
162 reef degradation and reassembly in the Anthropocene, urgent actions must be taken to protect
163 and manage the world's remaining coral reefs. Given such concerns about the long-term
164 functional erosion of coral communities, one conservation strategy is to prioritize the protection
165 of reefs that currently maintain key ecological functions, i.e., reefs with abundant fast-growing

166 and structurally-complex corals that can maintain vertical reef growth and net carbonate
167 production^{5,6}. However, efforts to identify potentially functioning reefs across large spatial scales
168 are often hindered by a focus on total coral cover, an aggregate metric that can overlook taxon-
169 specific differences in structural complexity and carbonate production^{7,8}. To date, global
170 empirical studies of scleractinian coral communities – and their environmental and
171 socioeconomic drivers – are rare, in part due to the absence of large-scale assemblage datasets –
172 a key challenge that must be overcome in modern ecology. Here, we apply a method developed
173 from trait-based approaches to evaluate regional patterns and drivers of Indo-Pacific coral
174 assemblages.

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

186 On each reef, we evaluated total coral cover and the abundance of different coral life
187 history types previously developed from a trait-based approach with species characteristics of
188 colony morphology, growth, calcification, and reproduction⁹ (<https://coraltraits.org>). The
189 abundance of different coral taxa can affect key ecological processes for future reef persistence,
190 including the provision of reef structural complexity, carbonate production (the process by which
191 corals and some other organisms lay down carbonate on the reef), and ultimately reef growth (the
192 vertical growth of the reef system resulting from the processes of carbonate production and
193 erosion)^{5,7,8,10}. Fast-growing branching, plating and densely calcifying massive coral taxa that
194 can contribute to these processes are expected to be functionally important, not only by
195 maintaining critical geo-ecological functions that coral reefs provide¹⁰, but might also help reefs

196 track sea level rise⁵, recover from climate disturbances¹¹, and sustain critical habitat for reef fish
197 and fisheries^{12,13}.

198 Here, we adopt a previous classification of four coral life history types to evaluate Indo-
199 Pacific patterns of total coral abundance and the composition of coral assemblages, and their key
200 social-environmental drivers. Specifically, we consider four coral life histories⁹ (Supplementary
201 Table 2): a ‘competitive’ life history describes fast-growing branching and plating corals that can
202 accrete structurally-complex carbonate reef architectures but are disproportionately vulnerable to
203 multiple stressors; a ‘stress-tolerant’ life history describes large, slow-growing and long-lived
204 massive and encrusting corals that can build complex high-carbonate reef structures to maintain
205 coral-dominated, healthy and productive reefs, and often persist on chronically disturbed reefs;
206 by contrast, ‘generalist’ plating or laminar corals may represent a subdominant group of deeper
207 water taxa, while smaller brooding ‘weedy’ corals typically have more fragile, lower-profile
208 colonies that provide less structural complexity and contribute marginally to carbonate
209 production and vertical growth^{10,12,14}. We therefore consider competitive and stress-tolerant life
210 histories as key framework-building species given their ability to build large and structurally
211 complex coral colonies^{8,10,12}. We hypothesize that the abundance of different life histories within
212 a coral assemblage provides a signal of past disturbance histories or environmental conditions^{15–}
213 ¹⁷ that may affect resilience and persistence to future climate impacts¹⁸.

214 Drawing on theoretical and empirical studies of coral reef social-ecological systems^{19,20},
215 we tested the influence of 21 social, climate, and environmental covariates on coral abundance,
216 while controlling for sampling methodologies and biogeography (Supplementary Table 3). These
217 include: (i) climate drivers (the intensity and time since past extreme thermal stress, informed by
218 Degree Heating Weeks, DHW), (ii) social and economic drivers (human population growth,
219 management, agricultural use, national development statistics, the ‘gravity’ of nearby markets
220 and human settlements), (iii) environmental characteristics (depth, habitat type, primary
221 productivity, cyclone wave exposure, and reef connectivity), and (iv) sampling effects and
222 biogeography (survey method, sampling intensity, latitude, and coral faunal province). We fit
223 hierarchical mixed-effects regression models using the 21 covariates to predict the percent cover
224 of total coral cover and the four coral life history types individually. Models were fit in a
225 Bayesian multilevel modelling framework and explain ~25-48% of the observed variation across

226 total cover and the four life histories (Supplementary Table 4). We also fit these models to four
227 common coral genera (*Acropora*, *Porites*, *Montipora*, *Pocillopora*) as a complementary
228 taxonomic analysis.

229

230 **Results & Discussion** Across the 2,584 reefs, total hard coral cover varied from <1% to 100%
231 (median \pm SD, 23.7 \pm 17.0%). Competitive and stress-tolerant corals were the dominant life
232 history on 85.7% of reefs (competitive: 42.4%, $n = 1,095$ reefs; stress-tolerant: 43.3%, $n = 1,118$
233 reefs); generalist and weedy taxa dominated only 8.8% and 5.6% of reefs respectively (Figure 1;
234 Supplementary Figure 1). It is striking that the majority of Indo-Pacific reefs remain dominated
235 by structurally-important corals even following the impacts of the 1998 mass coral bleaching
236 event and subsequent bleaching events, and given expectations of different trajectories of regime
237 shifts and recovery following bleaching impacts or human activities^{6,21,22}. Notably, these findings
238 are in contrast to contemporary Caribbean reefs where very few reefs remain dominated by key
239 reef-building species and instead comprised of weedy taxa with limited functional
240 significance^{8,23}. However, Indo-Pacific reefs varied in their absolute abundance of the four types
241 (Figure 1), also suggesting the potential for dramatic structural and functional shifts away from
242 expected historical baselines of highly abundant branching and plating corals²⁴, a warning sign
243 considering recent community shifts in the Caribbean²³.

244

245 *Climate, social and environmental drivers*

246 Climate variables describing the frequency and intensity of past thermal stress events
247 strongly affected coral assemblages. Reefs with more extreme past climate disturbances
248 (assessed by maximum DHW) had fewer competitive and generalist corals, while time since the
249 strongest past thermal disturbance was associated with more hard coral cover and the cover of all
250 four life histories (Figure 2). These results provide some of the first large-scale empirical support
251 for the importance of recovery windows after bleaching in structuring coral assemblages^{25,26}. Our
252 findings are also consistent with expectations that branching and plating corals are vulnerable to
253 temperature anomalies and bleaching^{4,11,15}. Stress-tolerant and weedy corals were less affected
254 by the magnitude of past thermal stress, consistent with long-term studies in Indonesia⁷, the

255 Seychelles¹¹, and Kenya¹⁵ that have shown these coral taxa often persist through acute
256 disturbances and maintain important reef structure^{12,27}. There was no effect of past thermal stress
257 on total coral cover, possibly because this composite metric can overlook important differences
258 in species and trait responses.

259 Our results also reveal the important role of socioeconomic drivers on some life histories:
260 reefs influenced by human populations, markets, and agricultural use were associated with a
261 lower abundance of competitive, stress-tolerant, and generalist corals (Figure 2). The
262 mechanisms underpinning these relationships could include direct mortality from destructive
263 fishing practices²⁸, tourism, or industrial activities²⁹, or indirect effects on coral growth
264 associated with the overexploitation of grazing herbivorous fishes that control macroalgae³⁰ or
265 declining water quality that can increase sediments and nutrients to smother or sicken corals³¹.
266 We also observed two positive associations of coral abundance with human use: generalist corals
267 increased near agricultural land use, and weedy corals increased near larger and more accessible
268 markets. In some cases, these relationships require further investigation; for example, the
269 abundance of generalists (e.g., deeper-water plating corals) was negatively associated with
270 cropland expansion, but positively associated with cropland area. Overall, we identify human
271 gravity and agricultural use as key social drivers that could be locally mitigated (i.e., through
272 behaviour change³²) to promote structurally complex and calcifying reefs that can sustain
273 important ecological functions.

274 Local management actions in the form of no-take reserves or restricted management (e.g.,
275 gear restrictions) were associated with higher total coral cover, and greater abundance of stress-
276 tolerant, generalist, and weedy corals, but not competitive corals (Figure 2). Our findings suggest
277 that management approaches typically associated with marine protected areas (MPAs) and
278 fisheries management can both have benefits for total coral cover and some, but not all, life
279 histories. Notably, local management did not increase the abundance of structurally-important
280 branching and plating competitive corals. This is consistent with expectations that branching and
281 plating corals are often extremely sensitive to extreme heat events and bleaching mortality^{11,14,15},
282 which can swamp any potential benefits of local management^{15,33}. Our analyses did not account
283 for management age, size, design, or compliance, all of which could influence these outcomes;
284 for example, older, larger, well-enforced, and isolated marine protected areas (MPAs) have been

285 shown to increase total coral cover, although mostly through the cover of massive (i.e., stress-
286 tolerant) coral growth forms³⁴. Our results also suggest that partial protection (i.e., gear
287 restrictions) can be associated with similar increases in coral abundance as fully no-take areas.
288 For corals, any type of management that reduces destructive practices can have direct benefits
289 for coral survival and growth²⁸. While protection from local stressors may not increase coral
290 resilience³³, we find that managed sites are associated with a higher abundance of total coral
291 cover and some coral life histories relative to unmanaged sites, even after accounting for climate
292 disturbances and other environmental conditions.

293 Environmental factors such as latitude, reef zonation (i.e., depth and habitat), primary
294 productivity, wave exposure, and cyclone intensity were also strongly associated with coral
295 abundance (Figure 2). Competitive corals were more abundant on reef crests, shallower reefs and
296 on reefs with higher wave exposure, compared to stress-tolerant corals that were more abundant
297 on deeper reefs and reefs with lower wave exposure. Stress-tolerant, weedy and generalist corals
298 were typically associated with higher latitudes, smaller reef areas, and greater depths. Primary
299 productivity and cyclone exposure were associated with fewer competitive, stress-tolerant and
300 weedy corals, likely due to unfavourable conditions for coral growth in areas of eutrophication
301 and high productivity³¹, or hydrodynamic breakage or dislodgement of coral colonies³⁵. These
302 findings suggest that environmental conditions are important in predicting conservation baselines
303 and guiding management investments. For example, restoring or maintaining grazer functions
304 when environmental conditions can support abundant corals and other calcifying organisms³⁶.
305 After controlling for method and sampling effort in the models (Figure 2), our results suggest
306 that future comparative studies would benefit from standardized methods and replication to allow
307 for faster comparative approaches for field-based monitoring³⁷, especially given the urgency of
308 tracking changes to coral assemblages from climate change and bleaching events.

309 The four life histories showed some different responses than common genera
310 (Supplementary Figure 2). For example, life histories were generally more sensitive to climate
311 and social drivers (17 vs. 12 significant relationships for life histories compare to genera,
312 respectively; Figure 2, Supplementary Figure 2). For example, competitive corals had stronger
313 associations with two metrics of climate disturbance (years since maximum DHW and maximum
314 DHW) compared to *Acropora* (a genus classified as competitive). Three of the four life histories

315 showed positive associations with local management (no-take or restricted management)
316 compared to only one genus (*Porites*, a stress-tolerant and weedy genus); *Acropora* was
317 negatively associated with restricted management. Overall, our results suggest that life histories
318 might provide more sensitive signals of disturbance for coral assemblages, perhaps because life
319 history groups integrate morphological and physiological traits that can determine coral
320 responses to disturbance³⁸. However, further comparisons of life history and taxonomic
321 responses, at both regional and local scales, are certainly warranted.

322

323 *Management strategies in the Anthropocene*

324 The livelihoods of millions of people in the tropics depend on healthy and productive
325 coral reefs^{19,20}, yet coral reefs worldwide are imperilled by climate change^{3,25}. Between 2014 and
326 2017, reefs worldwide experienced an unprecedented long, extensive, and damaging El Niño and
327 global bleaching event^{26,39}. The 2,584 reefs in our dataset were exposed to thermal stress ranging
328 between 0 to 30.5 annual °C-weeks above summer maxima (i.e., Degree Heating Weeks, DHW)
329 between 2014 and 2017 (Figure 3; Methods). Nearly three-quarters of the surveyed reefs (74.9%,
330 n = 1,935 reefs) were exposed to greater than 4 °C-week DHW, a common threshold for
331 ecologically significant bleaching and mortality³⁹ (Supplementary Figure 3). Previous studies
332 have identified 10% hard coral cover as a minimum threshold for carbonate production on
333 Caribbean⁴⁰ and Indo-Pacific^{27,41} reefs. Below this threshold (or ‘boundary point’), reefs are
334 more likely to have a neutral or negative carbonate budget and may succumb to reef
335 submergence with rising sea levels⁵. Here, we adapt this threshold by considering only the live
336 cover of competitive and stress-tolerant corals (hereafter, ‘framework’ corals) since these are two
337 life histories that can build large, structurally-complex colonies to maintain carbonate production
338 and vertical reef growth^{10,12,27}. Prior to the third global bleaching event between 2014 and 2017,
339 71.8% of reefs (1,856 out of 2,584) maintained a cover of framework corals above 10%,
340 suggesting the majority of reefs could sustain net-positive carbonate budgets prior to their
341 exposure to the 2014-2017 global bleaching event. The abundance of framework corals was
342 independent of the thermal stress experienced in the 2014-2017 bleaching event (Figure 3).
343 Considering these two thresholds of ecologically significant thermal stress (4 DHW) and
344 potential ecological function (10% cover; sensitivity analysis provided in Supplementary Table

345 5), this creates a portfolio of three management strategies: 1) *protect* functioning reefs exposed
346 to less intense and frequent climate disturbance during the 2014-7 bleaching event, 2) *recover*
347 reefs exposed to ecologically significant bleaching stress that were previously above potential
348 functioning thresholds, and 3) on degraded reefs exposed to ecologically significant bleaching
349 stress, *transform* existing management, or ultimately assist societies to transform away from
350 reef-dependent livelihoods (Figure 3).

351 A *protect* strategy was identified for 449 reefs (out of 2,584, or 17.4%), which were
352 exposed to minimal bleaching-level stress (<4 DHW during 2014-2017) and had >10% cover of
353 framework corals (Figure 3; Supplementary Table 5). These reefs were located throughout the
354 Indo-Pacific (Figure 4, Supplementary Table 6) suggesting that it is currently possible to
355 safeguard a regional network of functioning coral reefs^{6,42,43}. The conservation goal for *protect*
356 reefs is to maintain reefs above functioning thresholds, while anticipating the impacts of future
357 bleaching events. Policy actions include dampening the impacts of markets and nearby
358 populations, placing local restrictions on damaging fishing, pollution, or industrial activities
359 within potential refugia from climate change, while addressing the broader context of poverty,
360 market demands, and behavioural norms^{32,44} – and ideally within areas of potential climate
361 refugia^{43,45}. The *recover* strategy was identified for the majority of reefs: 1,407 reefs (out of
362 2,584, or 54.4%) exceeded 10% cover of framework corals but were likely exposed to severe
363 bleaching-level heat stress during 2014-2017 global bleaching event (i.e., >4 DHW). As these
364 reefs had recently maintained 10% cover, mitigating local stressors as described above, alongside
365 targeted investments in coral reef rehabilitation and restoration could help to accelerate natural
366 coral recovery. In this strategy, the goal is to move reefs back above the 10% threshold as
367 quickly as possible following climate impacts. Active management to restore habitat with natural
368 or artificial complexity, coral ‘gardening’, or human-assisted evolution could be considerations
369 to quickly recover coral cover following climate disturbances⁴², although often at high cost but
370 there are options for low-cost, long-term restoration⁴⁶. For the *transform* strategy, we identified
371 728 reefs (or 28.2%) below 10% cover that were likely on a trajectory of net erosion prior to the
372 2014-2017 bleaching event. Here, transformation is needed – either by management to enact new
373 policies that urgently and effectively address drivers to rapidly restore coral cover, or ultimately,
374 by societies who will need to reduce their dependence on coral reef livelihoods facing the loss of
375 functioning coral reefs. Such social transformations could be assisted through long-term

376 investments in livelihoods, education, and adaptive capacity^{47,48}, investments which can also
377 accompany the *protect* and *recover* strategies.

378 We also investigated how combinations of key drivers could affect the predicted cover of
379 framework corals (Figure 5). While certain combinations were predicted to reduce cover below a
380 10% threshold (e.g., high population or market gravity with less recovery time from climate
381 disturbances or with high cyclone exposure, and high gravity with high primary productivity),
382 the majority of parameter space predicted coral cover above 10%. In addition, increasing
383 management restrictions appeared to expand a safe operating space for corals above a 10%
384 threshold. This is hopeful, in that even as the frequency of bleaching events is expected to
385 increase, reducing the impact of local stressors may provide conditions that can sustain some
386 functions on coral reefs. Nevertheless, management through MPAs alone have not been shown to
387 increase climate resistance or recovery³³. Thus, addressing global climate change is paramount.

388 Our dataset describes contemporary coral assemblages within a period of escalating
389 thermal stress, notably following the 1998 bleaching event^{26,39}. Patterns of coral bleaching vary
390 spatially²⁵, and we can make no predictions about which reefs might escape future bleaching
391 events or mortality from our dataset. The long-term persistence of corals within potential climate
392 refuges (i.e., the *protect* strategy) requires a better understanding of future climate conditions and
393 tracking the long-term ecological responses of different reefs^{6,37,45}. Predicting and managing
394 coral reefs through a functional lens, such as through coral life histories, is challenging but
395 necessary^{10,49}. Here, we adapt previous estimates of 10% coral cover as a threshold of net-
396 positive carbonate production. However, this threshold is based on methods that estimate the
397 three-dimensional structure of a reef⁴⁰, while our dataset consists primarily of planar two-
398 dimensional methods that do not account for the vertical or three-dimensional components of
399 coral colonies⁵⁰. Thus, the 10% threshold should be considered an uncertain, but potentially
400 precautionary, threshold of net carbonate production and reef growth, and a sensitivity analysis
401 considering this threshold at 8% or 12% cover suggests a three-strategy framework is robust to
402 uncertainty around these thresholds (Supplementary Table 5). Future work can help refine these
403 thresholds by considering species-specific contributions to structural complexity and carbonate
404 production, as has been recently developed for Caribbean corals⁸.

405

406 *Conclusions*

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

426

427 **Methods**

428 We conducted coral community surveys along 8,209 unique transects from 2,584 reefs
429 throughout the Indian and Pacific Oceans, covering ~277 km of surveyed coral reef. Our dataset
430 provides a contemporary Indo-Pacific snapshot of coral communities between 2010 and 2016;
431 surveys occurred following repeated mass bleaching events (e.g., 1998, 2005, 2010), but were
432 not influenced by widespread mortality during the 2014-2017 global coral bleaching event.
433 Surveyed reefs spanned 61.2 degrees of latitude (32.7°S to 28.5°N) and 219.3 degrees of
434 longitude (35.3°E to 105.4°W), and represented each of the 12 coral faunal provinces described
435 for Indo-Pacific corals⁵¹. A random subsampling method was used to evaluate the representation

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

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

443 (i) Reef ($n = 2,584$). Coral community surveys were conducted at the scale of ‘reefs’,
444 defined as a sampling location (with a unique latitude, longitude and depth) and comprised
445 of replicate transects. Surveys occurred across a range of depths (1 - 40 m; mean \pm standard
446 deviation, 8.9 ± 5.6 m), though the majority of surveys (98.8%) occurred shallower than 20
447 m. Surveys were conducted across a range of reef habitat zones, classified to three major
448 categories: reef flat (including back reefs and lagoons), reef crest, and reef slope (including
449 offshore banks and reef channels).

450 (ii) Site ($n = 967$). Reefs within 4 km of each other were clustered into ‘sites’. The
451 choice of 4 km was informed by the spatial movement patterns of artisanal coral reef fishing
452 activities as used in a global analysis of global reef fish biomass¹⁹. We generated a
453 complete-linkage hierarchical cluster dendrogram based on great-circle distances between
454 each point of latitude and longitude, and then used the centroid of each cluster to estimate
455 site-level social, climate and environmental covariates (Supplementary Table 3). This
456 provided a median of 2.0 reefs (± 2.83) per site.

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

461

462 **Coral communities and life histories.** At each reef, underwater surveys were conducted using
463 one of three standard transect methods: point-intercept transects ($n = 1,628$ reefs), line-intercept
464 transects ($n = 399$ reefs) and photo quadrats ($n = 557$ reefs). We estimated sampling effort as the

465 total number of sampled points during each reef survey. Line-intercept transects were estimated
466 with sampling points every 5 cm, since most studies only estimate the length of corals greater
467 than 3 or 5 cm (T. McClanahan, A. Baird pers. comm). On average, the number of sampling
468 points was 300.0 ± 750.0 (median \pm SD), and effort ranged from 30 to 5,138 sampling points.
469 Method and sampling effort were included as fixed effects in the models to control for their
470 effects.

471 The absolute percent cover of hard corals was evaluated to the taxonomic level of genus or
472 species for each transect. Surveys that identified corals only to broader morphological or life
473 form groups did not meet the criteria for this study. The majority of surveys recorded coral taxa
474 to genus (1,506 reefs out of 2,584, or 58.2%), and the remainder recorded some or all taxa to
475 species level; a small proportion of unidentified corals (0.30% of all surveyed coral cover) were
476 excluded from further analyses. We estimated the total hard coral cover on each transect, and
477 classified each coral taxa to a life history type⁹; some species of *Pocillopora*, *Cyphastrea* and
478 *Leptastrea* were reclassified by expert coral taxonomists and ecologists⁵⁴. A representative list of
479 species and their life history types are provided in Supplementary Table 2, and original trait
480 information is available from the Coral Traits Database (<https://coraltraits.org/>)⁵⁵. Four genera
481 included species with more than one life history classification (*Hydnophora*, *Montipora*,
482 *Pocillopora*, *Porites*), and we distributed coral cover proportional to the number of species
483 within each life history, which was estimated separately for each faunal province based on
484 available species lists⁵¹. In total, we were able to classify 97.2% of surveyed coral cover to a life
485 history. We then summed coral cover within each of the four life histories on each reef.

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

494 **Analysis of drivers.** We first assessed multicollinearity among the different covariates by
495 evaluating variance inflation factors (Supplementary Table 7) and Pearson correlation
496 coefficients between pairwise combinations of covariates (Supplementary Figure 4). This led to
497 the exclusion of four covariates: (i) local population size, (ii) national GDP per capita, (iii)
498 national voice and accountability, and (iv) years since extreme cyclone activity. A final set of 16
499 covariates was included in statistical models, whereby all pairwise correlations were less than 0.7
500 and all variance inflation factors were less than 2.5 indicating that multicollinearity was not a
501 serious concern (Supplementary Table 7, Supplementary Figure 4).

502 To quantify the influence of multi-scale social, human and environmental factors on hard
503 coral assemblages, we modelled the total percent cover of hard corals and the percent cover of
504 each life history as separate responses. We fit mixed-effects Bayesian models of coral cover with
505 hierarchical random effects, where reef was nested within site, and site nested within country; we
506 also included a random effect of coral faunal province to account for regional biogeographic
507 patterns⁵¹. For each response variable, we converted percent coral cover into a proportion
508 response and fit linear models using a Beta regression, which is useful for continuous response
509 data between 0 and 1⁵⁶. We incorporated weakly informative normal priors on the global
510 intercept (mean = 0, standard deviation = 10) and slope parameters (mean = 0, standard deviation
511 = 2), and a Student *t* prior on the Beta dispersion parameter (degrees of freedom = 3, mean = 0,
512 scale = 25). We fit our models with 5,000 iterations across four chains, and discarded the first
513 1,000 iterations of each chain as a warm-up, leaving a posterior sample of 16,000 for each
514 response. We ensured chain convergence by visual inspection (Supplementary Figure 5), and
515 confirmed that Rhat (the potential scale reduction factor) was less than 1.05 and the minimum
516 effective sample size (n_{eff}) was greater than 1000 for all parameters⁵⁷. We also conducted
517 posterior predictive checks and estimated Bayesian R^2 values for each model to examine
518 goodness of fit⁵⁸. All models were fit with Stan⁵⁹ and *brms*⁶⁰; analyses were conducted in R⁶¹.

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

522 **Strategic portfolios.** We developed three management strategies (*protect*, *recover*, or *transform*)
523 based on the potential thermal stress experienced during the 2014-2017 bleaching event, and a

524 reef's previous observed ecological condition. To evaluate potential thermal stress, we estimated
525 the maximum annual Degree Heating Weeks (DHW) between 2014 and 2017 from NOAA's
526 CoralTemp dataset (Coral Reef Watch version 3.1; see Drivers section). Ecologically significant
527 bleaching and mortality can occur at different thresholds of thermal stress, likely between 2 and
528 4 DHW³⁹, and this range of thresholds also represents the lowest quintile of DHW exposure for
529 the 2,584 reefs during the 2014-2017 global bleaching event (20th quintile = 3.2 DHW).
530 Considerations of different DHW thresholds were highly correlated and identified similar 'no-
531 regrets' locations of limited thermal stress exposure between 2014 and 2017 (Supplementary
532 Figure 3).

533 For ecological condition, we assessed whether each reef had the potential for a net positive
534 carbonate budget prior to the 2014-2017 bleaching event based on a reference point of 10%
535 cover of competitive and stress tolerant corals. We assumed that this threshold represents a
536 potential tipping point (i.e. unstable equilibrium, or boundary point) for reef growth and
537 carbonate production, whereby 10% hard coral cover is a key threshold above which reefs are
538 more likely to maintain a positive carbonate budget and therefore net reef growth^{27,40,41}.
539 Additionally, 10% coral cover is suggested to be a threshold for reef fish communities and
540 standing stocks of biomass⁶²⁻⁶⁴, and associated with some thresholds to undesirable algal-
541 dominated states at low levels of herbivore grazing and coral recruitment⁶⁵. As a sensitivity
542 analysis for the 10% coral cover threshold, we considered how 8% and 12% coral cover
543 thresholds would affect the distribution of conservation strategies across the 2,584 reefs
544 (Supplementary Table 5). This sensitivity analysis also helps account for the uncertainty in how
545 two-dimensional planar estimates of percent cover recorded during monitoring may affect three-
546 dimensional processes on coral reefs, like carbonate production⁵⁰. Ultimately, applying
547 thresholds of recent extreme heat and reef led to the proposed framework of three management
548 strategies: *protect*, *recover* and *transform*, which we mapped across the Indo-Pacific based on
549 the surveyed locations in our dataset.

550 We also investigated how combinations of key drivers differentiated reefs below or above
551 10% cover of competitive and stress-tolerant corals. Using the Bayesian hierarchical models for
552 competitive and stress-tolerant corals, we predicted coral cover across a range of observed values
553 for five key covariates: population gravity, market gravity, years since maximum DHW, primary

554 productivity, and cyclone exposure. For each covariate combination, we kept all other
555 parameters at their median values for continuous predictors, or their reference value for
556 categorical predictors (habitat: reef slope; method: PIT); we then summed the median predicted
557 cover of competitive and stress-tolerant corals from 10,000 posterior samples for an estimate of
558 combined cover. We repeated this approach with each level of management: fished, restricted
559 management, and no-take management.

560

561 **Data availability** All R code is available on <https://github.com/esdarling/IndoPacific-corals>. To
562 access primary data, interested parties can contact data contributors. Contact information and the
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564

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577

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582

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584

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730 **Figure captions**

731 **Figure 1.** Indo-Pacific patterns of reef coral assemblages. (a) Percent cover of four coral life
732 histories from 2,584 reef surveys in 44 nations and territories; colour indicates life history and
733 circle size indicates percent cover. Circles are semi-transparent; locations with many surveyed
734 reefs are darker than locations with fewer surveyed reefs. (b) Example of life histories with a
735 representative genus, from left to right: fast-growing competitive (*Acropora*); slow-growing and
736 long-lived massive stress-tolerant (*Platygyra*); sub-dominant generalists (*Echinopora*); fast-
737 growing brooding weedy taxa (*Pavona*). (c) Distribution of abundance (percent cover) for each
738 life history; dotted line identifies 10% cover, a potential threshold for net-positive carbonate
739 production. Maps are shown separately for each life history in Supplementary Figure 1.

740

741 **Figure 2.** Relationship between climate, social, environment and methodology variables with
742 total coral cover and life history type. Standardized effect sizes are Bayesian posterior median
743 values with 95% Bayesian credible intervals (CI; thin black lines) and 80% credible intervals
744 (coloured thicker lines); filled points indicate the 80% CI does not overlap with zero and grey
745 circles indicate an overlap with zero and a less credible trend. DHW indicates Degree Heating
746 Weeks; HDI is Human Development Index. For the effects of population gravity on stress-
747 tolerant and weedy corals which can appear to intersect zero, there was a 96.0% (15,362 out of
748 16,000 posterior samples) and 98.0% (15,670 out of 16,000) probability, respectively, of a
749 negative effect; for market gravity and competitive corals, there was a 90.2% (14,424 out of
750 16,000 posteriors) probability of a negative effect. Models of four dominant coral genera are
751 shown in Supplementary Figure 2.

752

753 **Figure 3.** Strategic management portfolio of *protect*, *recover*, and *transform* for Indo-Pacific
754 coral reefs. The 2,584 reefs varied in their ecological condition (assessed at the combined cover
755 of stress tolerant and competitive corals) and exposure to maximum annual DHW during the
756 2014-2017 Third Global Coral Bleaching Event. A protect strategy (blue dots) is suggested for
757 449 reefs (out of 2,584, or 17.4%) that were associated with limited exposure to recent
758 bleaching-level thermal stress (<4 DHW) and maintained coral cover above 10%. A recover
759 strategy could be prioritized for reefs that have recently maintained cover above 10% but were

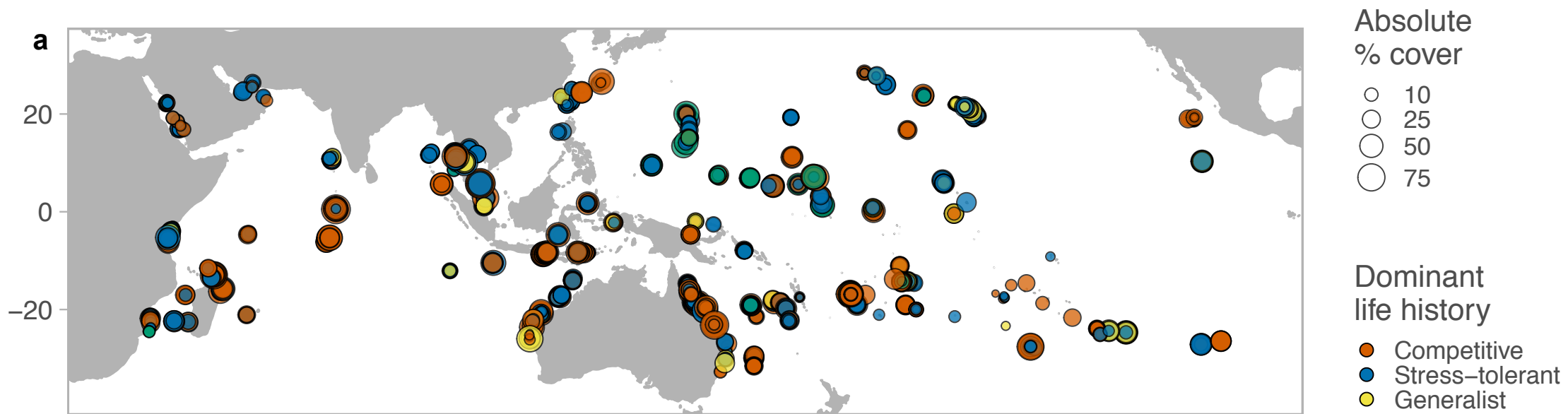
760 exposed to severe potential bleaching stress in 2014-2017 (orange dots; $n = 1407$, or 54.5%). As
761 coral cover falls below potential net-positive carbonate budgets (i.e., <10% hard coral cover), a
762 transformation is needed for existing management or ultimately, the dependence of societies on
763 reef-dependent livelihoods (grey dots; $n = 728$, or 28.2%).

764

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

770

771 **Figure 5.** Combinations of key social and environmental drivers that differentiate between reefs
772 below (red) and above 10% cover of framework corals (yellow to blue gradient), based on model
773 predictions (see Methods). Coral cover refers to the combined cover of competitive and stress-
774 tolerant corals; gravity estimates are reported as $\log(\text{values})$. Results are predicted separately for
775 three management categories: fished, restricted, or no-take reserves.

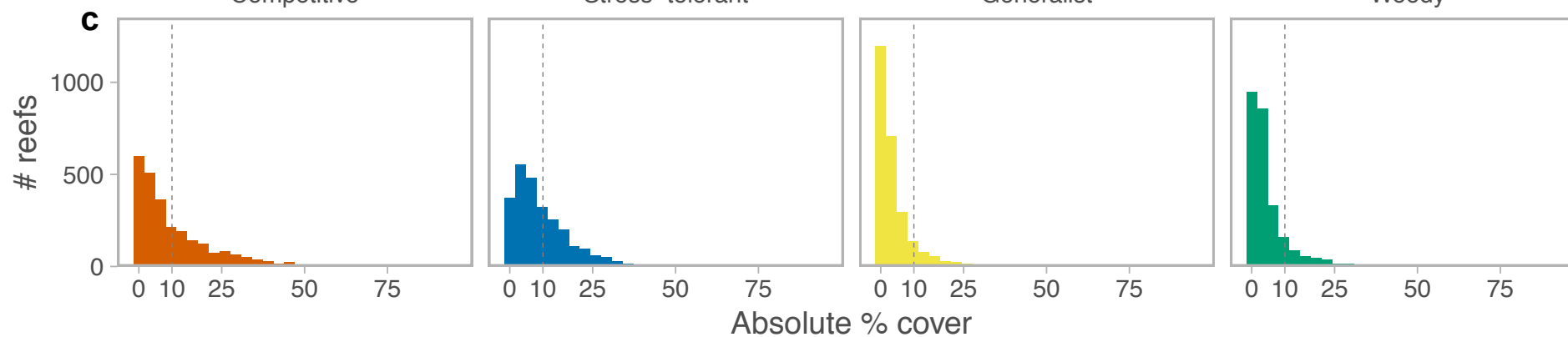


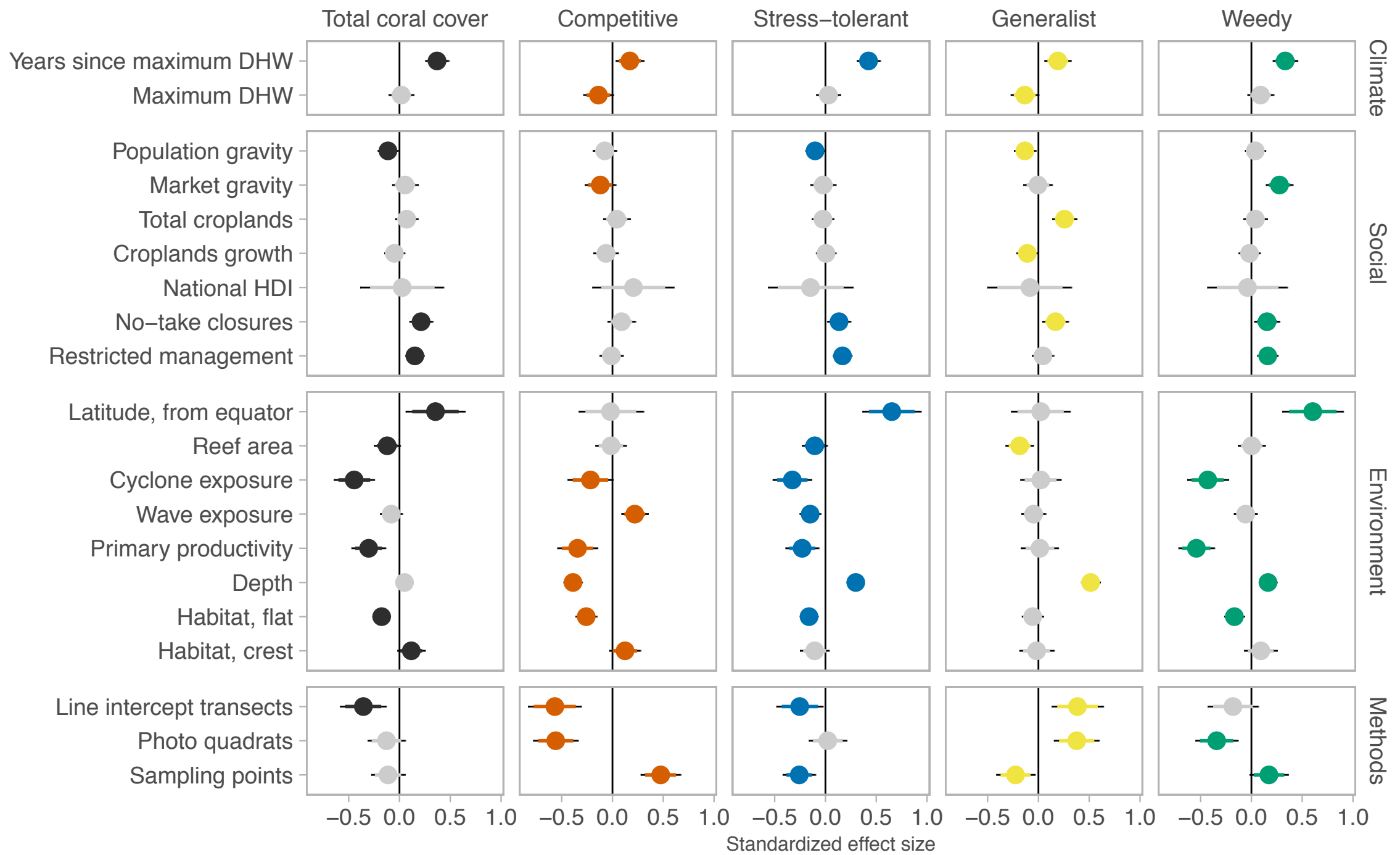
Competitive

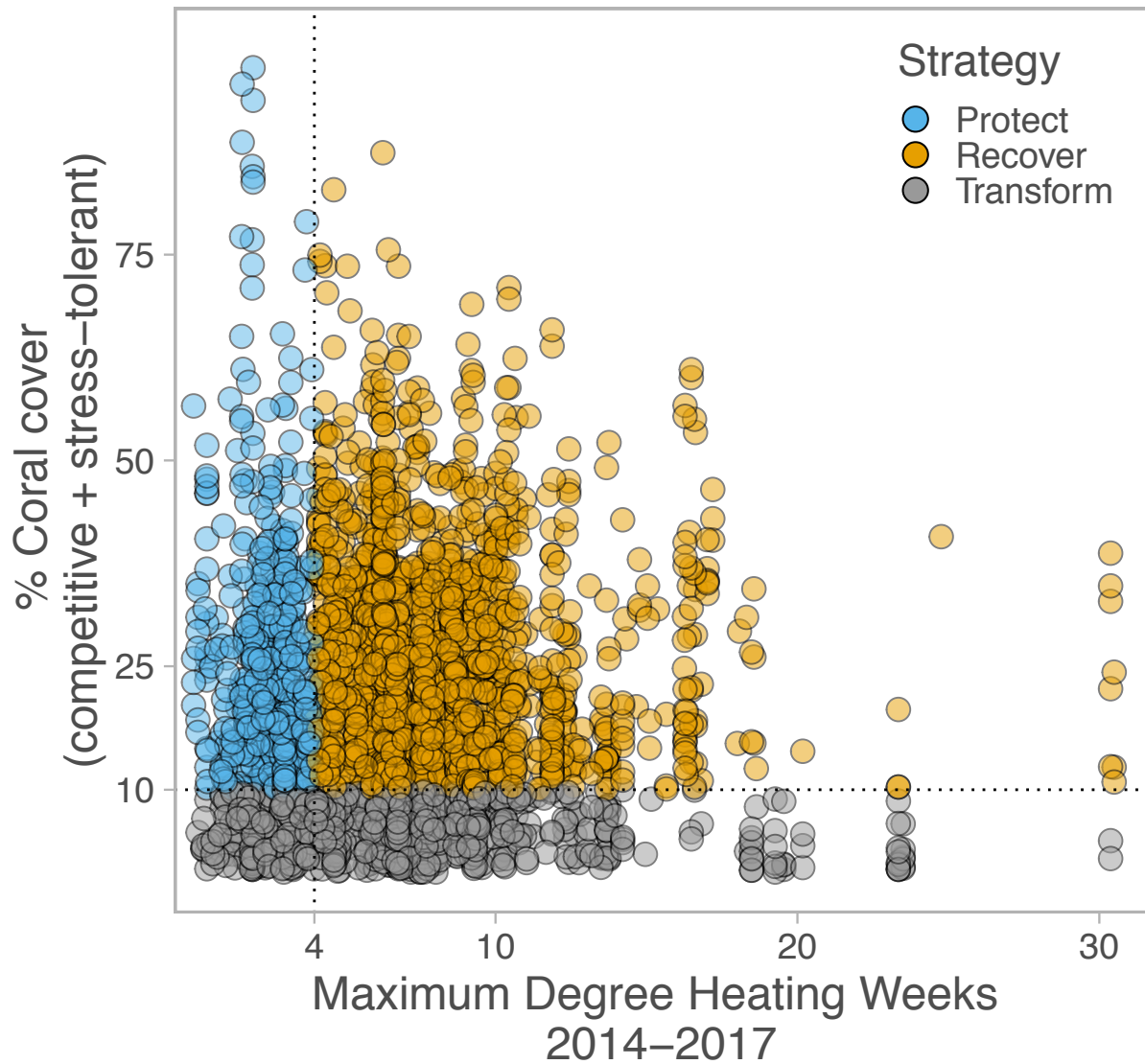
Stress-tolerant

Generalist

Weedy



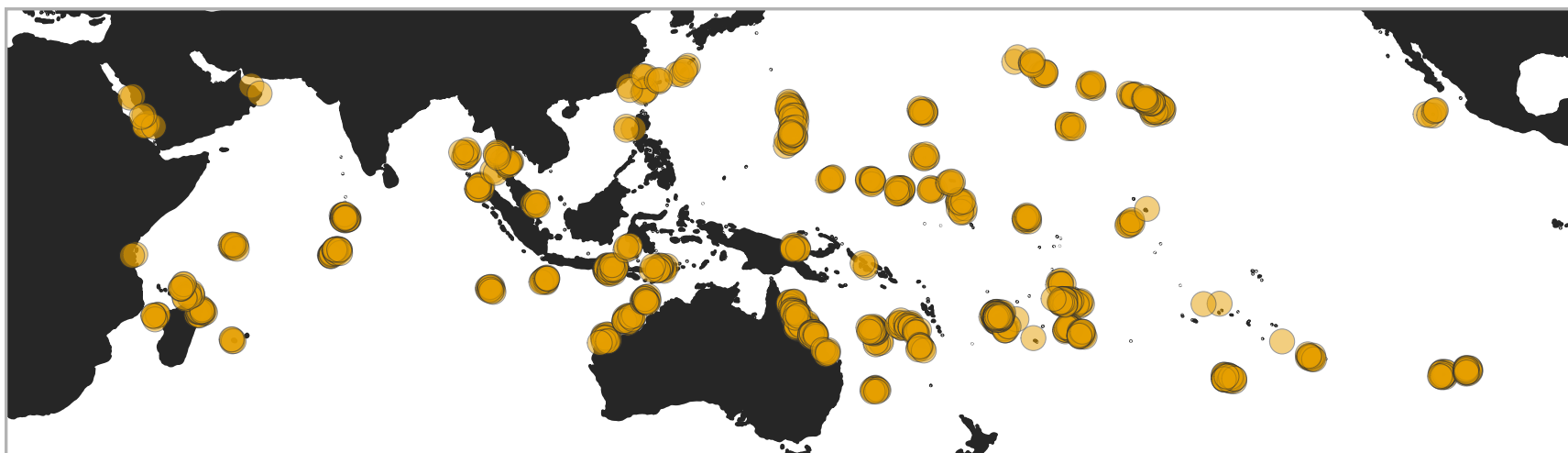




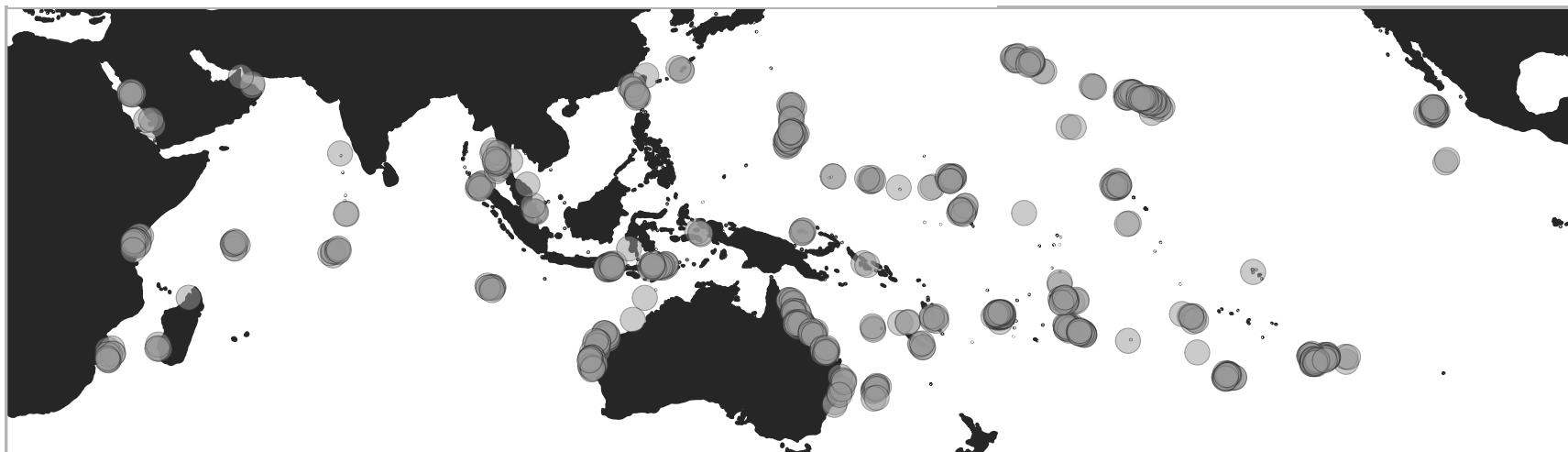
a Protect



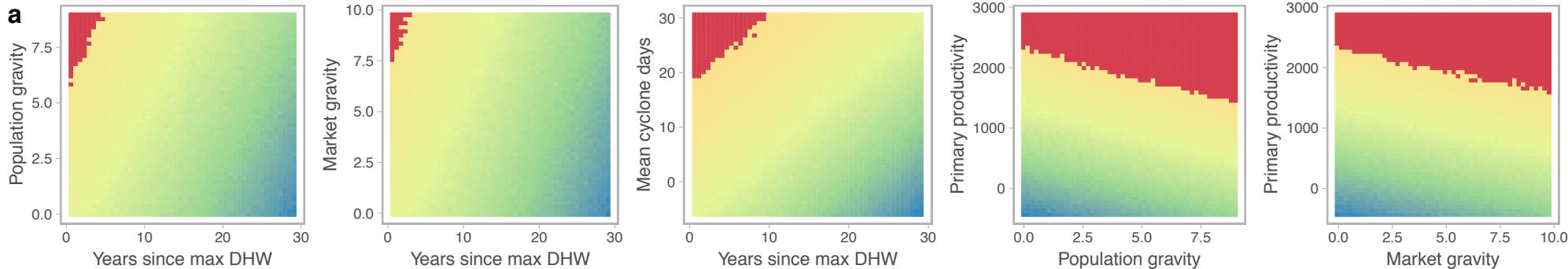
b Recover



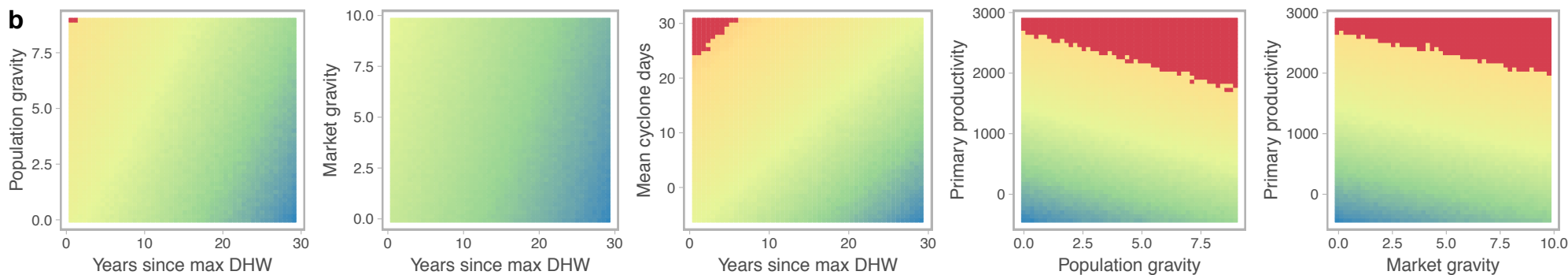
c Transform



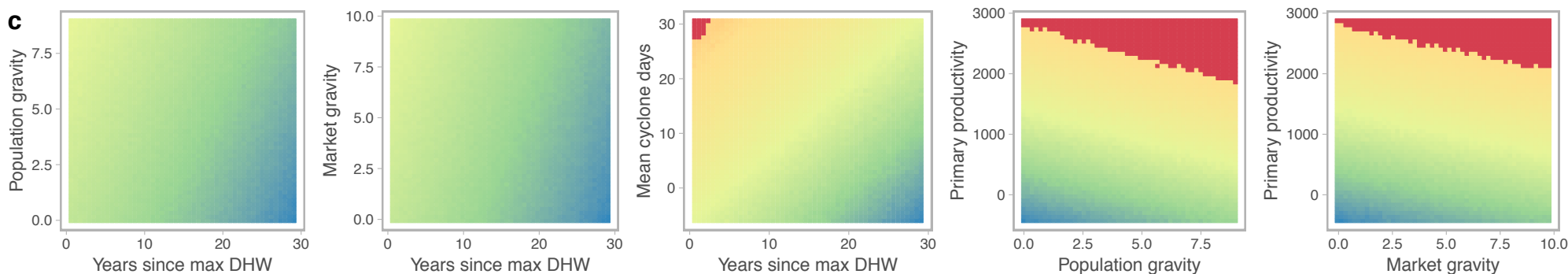
Fished



Restricted



No-take



Coral cover

