

1 **Title:** Unifying coral reef states through space and time reveals a changing ecosystem

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34 **Running title:** Coral reef states through space and time

35  
36 **Keywords:** phase shift; ecosystem function; Anthropocene; global change; regime shift;  
37 overfishing; marine protected area; alternative stable state; herbivory; reef resilience

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41 **Statement of authorship:** SJB and VP developed the project with input from MA, RSS,  
42 SAK, NAJG, GJE, RK and MKD; RSS, GJE, NAJG, SKW, RK, RA, LB, DAE, JEAG,  
43 JG, TH, JPM, DM, CLR, JW and MA provided data; JW and JC processed time series  
44 data; SJB analyzed the data, produced the figures and wrote the first draft of the  
45 manuscript. All authors contributed by editing various drafts of the manuscript.

47 **Acknowledgements:** We thank Sandrine Job, Andrew Baird, as well as all data  
48 collectors for their contributions to the paper. We are grateful to Koniambo Nickel SAS  
49 and especially Gregory Marakovich and Andy Wright, who made the data available. This  
50 research is product of the "SCORE-Reef" group funded by the synthesis center CESAB  
51 of the French Foundation for Research on Biodiversity (FRB;  
52 [www.fondationbiodiversite.fr](http://www.fondationbiodiversite.fr)).

53

54 **Biosketch:** Simon Brandl is an Assistant Professor at The University of Texas at Austin  
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56 broadly centered around the ecology of coastal marine ecosystems, with an emphasis on  
57 biogenic reefs and the role of fishes for their functioning.

58

## 59 **ABSTRACT**

60 **Aim:** Ecological state shifts that alter the structure and function of entire ecosystems are  
61 a concerning consequence of human impact. Yet, when, where, and why discrete  
62 ecological states emerge remains difficult to predict and monitor, especially in high-  
63 diversity systems. We sought to quantify state shifts and their drivers through space and  
64 time in the most ecologically-complex marine ecosystem: tropical coral reefs.

65 **Location:** Worldwide

66 **Time period:** 1987 – 2019

67 **Major taxa studied:** Coral reef communities

68 **Methods:** Using a global dataset of 3,375 coral reef surveys, along with thirteen time  
69 series datasets ranging between 1987 and 2019, we applied a novel double-dichotomy  
70 approach to classify coral reefs into four simplified and discrete states based on the  
71 relative contributions of corals *vs.* algae to benthic cover and small-bodied *vs.* large-  
72 bodied fishes to fish standing stock. We then examined state shifts considering a range of  
73 spatial predictors and tested whether states have shifted directionally over time, and the  
74 nature of the most common transitions.

75 **Results:** We show that geographic, environmental, and anthropogenic context  
76 fundamentally shapes coral reef states at the local scale, which explains disparities among  
77 case studies, and stakes out critical baseline expectations for regional management  
78 efforts. We also reveal clear multi-decadal state shifts on coral reefs: over time, systems  
79 dominated by reef-building corals and small-bodied, planktivorous fishes tend to have  
80 been replaced with reefs characterized by algae and larger-bodied fishes.

81 **Main conclusions:** Our results suggest a previously unrecognized transition from  
82 systems that harness external subsidies through small-bodied consumers associated with  
83 structurally-complex live corals, to herbivore-dominated systems with stronger bottom-  
84 up dynamics. Overall, the partitioning of complex reef ecosystems into a small suite of  
85 discrete ecological states suggests that spatial context-dependency, shifting baselines, and

86 changes in reef functioning are crucial considerations for coral reef management in the  
87 21st century.

88

## 89 INTRODUCTION

90 System-wide state shifts that alter the structure and functioning of entire ecosystems are a  
91 concerning consequence of human impact on Earth (Scheffer *et al.*, 2001a). Such state  
92 shifts are commonly characterized by transitions between foundation species that induce  
93 feedback loops among multiple taxa and can lock systems into alternative regimes  
94 (Scheffer *et al.*, 2001b; Knowlton, 2004). Sustained monitoring of multiple taxa is  
95 expensive, highly heterogeneous in its methodology, spatial, and temporal scale, and  
96 inherently incomplete (Magurran *et al.*, 2010), which can make the precise determination  
97 of the causes and effects of state shifts difficult to determine.

98 In this context, tropical coral reefs are particularly challenging. Complex  
99 ecological interactions among countless organisms are a defining feature of coral reefs  
100 (Rowan & Knowlton, 1995; Pozas-Schacre *et al.*, 2021), but these interactions are  
101 increasingly altered by anthropogenic stressors, sometimes resulting in catastrophic  
102 ecosystem collapse (Knowlton & Jackson, 2008). The most notorious state shift on coral  
103 reefs involves transitions from reef-building corals to algae (most commonly, fleshy  
104 macroalgae) (Gardner *et al.*, 2003; Bruno & Selig, 2007; Bruno *et al.*, 2019). Such ‘phase  
105 shifts’ are facilitated by combinations of heat stress, storms, overexploitation, disease,  
106 and nutrient pollution, which harm corals, promote algal growth, reduce grazing, and  
107 shift reefs towards microbial energy pathways (Done, 1992; Haas *et al.*, 2016; Bruno *et*  
108 *al.*, 2019; Reverter *et al.*, 2020). While these shifts in benthic communities have  
109 unequivocally occurred, their frequency, nature, drivers, and reversibility have been  
110 vigorously debated (Bruno *et al.*, 2009, 2019; Alves *et al.*, 2022; Baumann *et al.*, 2022;  
111 Crisp *et al.*, 2022; Tebbett *et al.*, 2023). A valuable knowledge base has resulted from this  
112 discourse, but uncertainties arising from spatial context dependency, unknown baseline  
113 levels of coral dominance, and idiosyncrasies in benthic organismal categorizations limit  
114 our ability to predict when, where, and why shifts in benthic communities occur.

115 Although causal relationships between fish community structure (primarily  
116 herbivorous fishes) and benthic composition (primarily coral cover) have proven tenuous  
117 in large-scale analyses (Russ *et al.*, 2015; Bruno & Valdivia, 2016; Bruno *et al.*, 2019),  
118 numerous links between the benthos and fishes have been documented at local and  
119 regional scales (Stuart-Smith *et al.*, 2018; Wismer *et al.*, 2019). For example, benthic  
120 composition and structural complexity can impose bottom-up effects on fish communities  
121 by providing shelter and prey (Taylor *et al.*, 2018), often disproportionately affecting  
122 small-bodied fishes (Wilson *et al.*, 2010; Alvarez-Filip *et al.*, 2011; Brandl *et al.*, 2016).  
123 Conversely, direct exploitation of reef fishes has led to widespread extirpations of large-  
124 bodied coral reef fish species (Graham *et al.*, 2005; Lefcheck *et al.*, 2021), which can (but

125 not always does) alter the benthic community through reduced top-down herbivore  
126 grazing, bioerosion, and nutrient provision (Bellwood *et al.*, 2011; Rasher *et al.*, 2013;  
127 Shantz *et al.*, 2020). Thus, state shifts on coral reefs may unfold through a variety of top-  
128 down and/or bottom-up mechanisms that necessitate the simultaneous examination of fish  
129 and benthic communities.

130 Recent investigations include quantifications of coral reef states across benthic  
131 and fish communities (Cresswell *et al.*, 2017; Donovan *et al.*, 2018; Jouffray *et al.*, 2019)  
132 (including, for instance, herbivore-dominated systems or coral-bacterial mat states), but  
133 global drivers and temporal dynamics of coupled fish-benthic reef states have remained  
134 largely unexplored (Strain *et al.*, 2019). In other words, while there is rich evidence for  
135 univariate state shifts on coral reefs and their proximate drivers –most prominently, from  
136 coral-dominated to macroalgae-dominated (due to climate change (Schutte *et al.*, 2010;  
137 Graham *et al.*, 2015; Crisp *et al.*, 2022)) and from large to small-bodied fishes (due to  
138 overfishing (Graham *et al.*, 2005; Cinner *et al.*, 2016))– system-wide shifts in fish and  
139 benthic communities combined are only documented in isolated case studies, which can  
140 be affected by local variability and temporal mismatches (Jouffray *et al.*, 2015; Donovan  
141 *et al.*, 2018; Bruno *et al.*, 2019; Wismer *et al.*, 2019).

142 A simple, novel approach for addressing this knowledge gap is through a double  
143 dichotomy approach (i.e., an orthogonal arrangement of two axes) (Caprihan *et al.*,  
144 2021), where two opposing configurations of benthic and fish communities combine for  
145 four discrete ecological states, defined by coral vs. algal dominance and fish community  
146 size structure (Fig. 1). Among these simplified reef states, those characterized by high  
147 coral cover and large-bodied fishes are conventionally perceived as ‘healthy,’ while reefs  
148 dominated by algae and small-bodied fishes typically indicate ecosystem degradation  
149 (Graham *et al.*, 2005; Mumby *et al.*, 2021). By integrating producers, habitat providers,  
150 and mobile consumers into a single framework, this approach may yield insights into  
151 system-wide dynamics rarely considered in the context of state shifts on coral reefs.

152 We use a global dataset of coral reef communities (the Reef Life Survey) in  
153 combination with thirteen time series datasets to examine spatial and multidecadal trends  
154 in coral reef states based on the described double-dichotomy. Specifically, we 1) classify  
155 reefs into four discrete states, 2) examine spatial determinants of reef states across a  
156 global dataset, and 3) examine temporal trends in reef states across 13 time series  
157 datasets. The panoramic perspective arising from our framework places all coral reefs  
158 into a unified context to guide management strategies and track our progress towards  
159 conservation targets.

160

## 161 **MATERIALS & METHODS**

162 Our analyses consist of two main parts. First, we use the RLS (Reef Life Survey) dataset  
163 (Edgar & Stuart-Smith, 2014; Edgar *et al.*, 2020) to create a global coral reef state space

164 based on a double-dichotomy approach. This allows us to examine the spatial prevalence  
165 of the obtained reef states and interrogate their potential drivers. Second, we use this  
166 global state space to assign surveys across a compilation of 13 time series datasets of the  
167 benthos, fishes, or both, across 12 broad locations (two datasets from Mo'orea, French  
168 Polynesia) and ranging between 1987 and 2019 to the different reef states, which allows  
169 us to trace changes in reef state assignments over time. Time series ranged in their spatial  
170 and temporal spread from more than 20 years of monitoring at a single site in French  
171 Polynesia, to surveys over shorter time spans at a wide range of reefs across Ningaloo  
172 Reef in Western Australia (Table S1). While we compiled 13 total time-series datasets,  
173 only ten of them were synchronized between fish and benthic surveys to permit analyses  
174 of all four states (with a total of 109 distinct sites across locations). All datasets (RLS and  
175 the time series) consist of diver-based survey protocols for fish (>5cm total length) and  
176 benthic communities. While the RLS database employs a standardized protocol  
177 throughout (Edgar & Stuart-Smith, 2014), time series datasets used variable  
178 implementations of diver-based surveys (Supporting Information).

179 Using the RLS data, we tested whether coral reefs globally split into pre-  
180 conceived states (coral vs. algae-dominated and small fish vs. large fish-dominated). To  
181 do so, we computed the aggregated cover of benthic groups across four coarse categories:  
182 corals (all hard and soft corals across all growth forms, including bleached corals), clean  
183 calcareous substrate (bare structures suitable for coral settlement, including bare rock and  
184 crustose coralline algae [CCA]), algae (all red, green, brown, and calcified macro- and  
185 micro-algae, including rubble and dead coral, which are covered by turf algae and  
186 microorganisms, but not including CCA), and all other categories (e.g., all sessile  
187 invertebrate taxa, sand, seagrass) (Table S2).

188 For fishes, we allocated all surveyed fishes to four size-classes, based on their *in*  
189 *situ* recorded body size: small (S  $\leq$  10 cm TL), medium (M > 10-20 cm), large (L > 20-40  
190 cm), and very large (XL > 40 cm). We then computed the relative contribution of the four  
191 fish size classes to overall biomass using recorded size estimates of fishes in the field and  
192 conversions to weight via length-weight relationships (Kulbicki *et al.*, 2005). For fish  
193 species that did not have species-specific estimates for length-weight relationships, we  
194 used averaged genus or family-level estimates. Since cryptobenthic fishes are not reliably  
195 surveyed by visual methods and generally contribute little to total standing biomass  
196 values (Brandl *et al.*, 2018, 2019), they were not included in this study.

197 Our double-dichotomy approach based on coarse categories undoubtedly  
198 simplifies a complex ecological system. Algae, for instance, are often divided into short,  
199 productive, filamentous turf algae and fleshy, upright macroalgae, with the former often  
200 considered a healthy part of many reefs, while the latter are commonly considered to be a  
201 sign of degradation (Steneck & Dethier, 1994; Bruno *et al.*, 2014). Nevertheless, within  
202 both groups, numerous important and nuanced divisions can be made: for instance, turf

203 algae can be divided into ‘beneficial’ short, productive forms, and ‘detrimental’ long,  
204 sediment-laden mats (Goatley & Bellwood, 2013; Tebbett & Bellwood, 2020), while  
205 macroalgae can include benign species that actively contribute to calcium carbonate  
206 production (e.g., *Halimeda* spp. (Castro-Sanguino *et al.*, 2020)), and harmful, allelopathic  
207 algae that can lead to swift overgrowth of other benthic organisms (Rasher *et al.*, 2011).  
208 However, field surveys rarely monitor these groups with comparable resolution and  
209 accuracy, which renders attempts to synthesize large-scale dynamics across datasets  
210 (such as the second step in the present study) reliant on broader groups that obscure fine-  
211 scale functional variability.

212 Our high-level classifications provide the necessary simplicity to analyze  
213 inherently heterogeneous datasets and rigorously test existing paradigms. Specifically,  
214 rather than tying benthic organisms to a specific role in the degradation of reefs, we build  
215 on characteristics that unite coral and algal categories. Corals are long-lived, mixotrophic  
216 animals with relatively low productivity that provide a rigid (Scleractinia) or semi-rigid  
217 (Octocorallia) reef framework that is likely to persist for years, while turf algae,  
218 macroalgae algae and cyanobacteria represent relatively short-lived and often ephemeral,  
219 autotrophic organisms (macroalgae, turf algae, and cyanobacteria) that contribute little to  
220 reef structural complexity but have high primary productivity. As such, despite pertinent  
221 functional heterogeneity within each group, our birds-eye analysis captures important  
222 system-wide attributes that allow us to interpret past changes and infer future trajectories.  
223 Importantly, our approach provides only one avenue to simplify an inherently complex  
224 system; various other methods, such as trait-based approaches, may offer fruitful  
225 complementary insights to the results presented below.

226  
227 **Classifying reef states:** Our analytical approach relied on the clustering of reefs into  
228 discrete states. To assign reefs to different states, we ran a fuzzy-clustering analysis based  
229 on c-means (FCM) with two mobile centers (*i.e.*, two state categories, in this case  
230 representing coral *vs.* algae and small *vs.* large fish dominated states) and a fuzziness  
231 exponent of 1.2 for both the benthic and fish data, which we normalized using the Box-  
232 Cox-chord-transformation (De Cáceres *et al.*, 2010). This analysis was chosen based on  
233 its successful application in plant ecology, and its ability to reveal archetypal regimes and  
234 their associated assignment uncertainties (De Cáceres *et al.*, 2010). To visualize the  
235 clustering outputs, we performed a principal components analysis (PCA). The ordination  
236 revealed that the clusters largely corresponded to the expected orthogonal states along  
237 PC1, identifying clusters dominated by coral and algae for the benthic communities, and  
238 clusters dominated by small and medium sized fishes and large fishes for the fish  
239 communities (Fig. 1). We incorporated the uncertainty of state assignments in all  
240 analyses, and tested the sensitivity of our results to pooling turf and macroalgae for the  
241 state assignments (see Supporting Information; Figs. S1, S2). An alternative aggregation

242 scheme for benthic groupings (following the RLS\_coarse category in Table S3) was also  
243 used as a sensitivity analysis, which showed broad agreement in state assignments  
244 between classification schemes (Fig. S3).

245

246 **Modeling reef states across space and conditions:** We calculated the probabilities of  
247 being assigned to each of the four states (coral-large fish, coral-small fish, algae-large  
248 fish, algae-small fish) for each survey by multiplying the respective assignment  
249 probabilities (e.g.,  $P_{coral} \times P_{small\ fish} = P_{coral:small\ fish}$ ). We then examined the geographic  
250 prevalence of state types using a Bayesian model with *Realm* (Eastern Indo-Pacific,  
251 Tropical Eastern Pacific, Tropical Western Atlantic, Western Indo-Pacific, and Central  
252 Indo-Pacific; (Kulbicki *et al.*, 2013)) as a fixed effect using the Dirichlet distribution for  
253 the multinomial response variable (Hijazi & Jernigan, 2009).

254 To examine the potential drivers of reef states globally, we then tested the  
255 predictive power of six environmental and anthropogenic covariates for state  
256 assignments: absolute latitude (in degrees, to incorporate the well-known tendency of  
257 reefs to flourish near the equator), depth (in m), significant wave height as a proxy of  
258 wave exposure (in m, remotely sensed from 2011 to 2019 based on Wavewatch III global  
259 model estimates; (Cheung, 2010)), chlorophyll *a* concentration (in  $\text{mg m}^{-3}$ , remotely  
260 sensed from the Bio-ORACLE (Assis *et al.*, 2018)), human gravity (dimensionless, a  
261 composite metric of human impacts in a given location based on population density and  
262 distance (Cinner *et al.*, 2018)), and fishing restrictions (open or restricted fishing vs. no-  
263 take zones). We parsed the dataset down to surveys for which data across all six  
264 covariates existed, resulting in a total of 3,375 datapoints. We then again ran a Dirichlet  
265 Bayesian regression model with the four state probabilities specified as multinomial  
266 outcomes, and each of the six predictor variables specified as fixed effects. To account  
267 for spatial non-independence within survey sites (i.e., single reefs or reefs in close  
268 vicinity), we specified *Site* as a random effect. Finally, we sought to gauge how the  
269 model outcomes may inform our expectations for reef states under varying conditions. To  
270 do so, we predicted reef states for two hypothetical scenarios (reefs with minimal human  
271 impact at 3° absolute latitude and 20° absolute latitude), obtaining estimated probabilities  
272 for the four state types based on the specified conditions.

273

274 **Modeling reef states through time:** To examine trends in reef states over time we used  
275 the state assignments from the RLS data – a comprehensive, standardized dataset of reef  
276 communities available – as a training algorithm to categorize reefs throughout the time  
277 series datasets. Using the mobile centers obtained from the spatial FCM, we assigned  
278 each datapoint (i.e. year) in the time series datasets to one of the respective states, again  
279 conserving the probability of each assignment to ensure consideration of uncertainty.  
280 Because time series differed vastly in their temporal spread, we standardized them based

281 on their start ( $t = 0$ ) and end ( $t = 1$ ) date, with every intermediate survey year  
282 corresponding to the respective value between 0 and 1 (i.e., the halfway point of each  
283 time series would be 0.5), while accounting for time-series length in the models.

284 Since there was no perfect overlap between the benthic and fish time-series data  
285 (i.e., some datasets contained only fish or only benthic data), we first ran two Bayesian  
286 mixed models with Beta distributions and log-link functions to test the effect of time on  
287 state probabilities in benthic communities and fishes (Fig. S4). For both models, we  
288 specified an interaction effect between chronology (i.e., years in the standardized time  
289 series) and the length of the time series, as well as a random slope for each location (a  
290 spatial descriptor for a suite of reefs), and a random intercept for each site (usually  
291 corresponding to a single or small number of surveyed reefs within a location). We then  
292 combined the surveys that monitored the benthos and fish communities in synchrony at  
293 the same site (ten time series datasets, spanning a total of 109 sites) and ran a Dirichlet  
294 Bayesian mixed model, examining the effect of time on the probability of belonging to  
295 one of the four state types, again specifying a random slope for *Location*, and a random  
296 intercept for each *Site* within a location. Since the length of the time series had only weak  
297 effects on the benthic states and no effects on fish states through time (see Fig. S4), we  
298 omitted time-series length as a predictor due to the demanding nature of the model. To  
299 complement this analysis, we also explored the likelihood of discrete state shifts over  
300 time using Discrete Time Markov Chains (DTMCs). DTMCs are an ideal analytical  
301 framework for analyzing the probability of transitions between discrete states based on a  
302 sequence of categorical events. Their stochastic nature means that only the current state  
303 influences the transition probability, making them well-suited for our analysis of discrete  
304 state shifts (as opposed to the continuous analyses previously). Additional information  
305 about the DTMCs is provided in the Supplementary Text.

306 Finally, to briefly explore hypothesized changes in fish functional structure (from  
307 small-bodied planktivores towards large-bodied herbivores), we examined changes in  
308 biomass through time for fish genera classified as either herbivores (*sensu lato*) or small-  
309 bodied planktivores (Table S4). This was based on previous research that has suggested  
310 negative responses of planktivorous species to loss of coral cover (Brandl *et al.*, 2016)  
311 and increases in herbivores following disturbance (Taylor *et al.*, 2020), alongside  
312 correlations among their respective functional traits (planktivory and small body size,  
313 herbivory and large body size; Floeter *et al.*, 2018). We ran a Bayesian mixed model on  
314 transects as the replicate unit, using a random slope for *Location* and a random intercept  
315 for *Site* within *Location*. We log-transformed biomass estimates (in grams per 100m<sup>2</sup>) to  
316 normalize the data, and ran the model using a Gaussian error distribution. Details on  
317 model specifications are provided in the Supporting Information.



318

## 319 RESULTS

320 **Reef classification:** The PCA of the Reef Life Survey data revealed the predicted  
321 double-dichotomy (Fig. 1). For the benthos, there was a clear distribution of reefs along  
322 the first axis (which explained 47.6% of the total variability) that parsed reefs into  
323 systems dominated by either corals or algae. PC2 split reefs based on the presence of  
324 clean, calcareous substrate and other benthic organisms and substrates. Likewise, the  
325 PCA for fish communities revealed a clear distribution along the first axis (explaining  
326 50.9% of the total variability), with fish biomass being either concentrated in the small  
327 and medium size classes, or large and very large size classes (Fig. 1). Notably, the gravity  
328 of very large fishes was weak on PC1, which correlated with increased uncertainty of  
329 state assignments with high biomass of very large fishes (likely due to the more random  
330 occurrence of these large-bodied species) (Fig. S1). Across the full dataset, reef state  
331 assignments displayed weak correlations between coral-dominated and small fish-  
332 dominated states, and algae-dominated and large fish-dominated states (Pearson  
333 correlation coefficient: 0.084).

334

335 **Global distribution and drivers of reef states:** State assignments displayed  
336 considerable spatial heterogeneity across scales, with all biogeographic realms harboring  
337 reefs across the four states (Fig. 2). Coral reefs in the Tropical Eastern Pacific and  
338 Tropical Western Atlantic were more likely to be in the algae-large fish or algae-small  
339 fish states, while reefs throughout the Western and Eastern Indo-Pacific showed high  
340 probabilities of being in coral-dominated states. Reefs in the Central Indo-Pacific were  
341 most likely to be in the algae-large fish or coral-large fish states.

342 We found strong correlations between the four coral reef states and environmental  
343 and anthropogenic drivers (Fig. 3). Nearer to the equator, reefs were most likely in the  
344 coral-large fish state (mean predicted posterior probability estimate: 29.6% [26.9, 32.3;  
345 lower and upper 95% credible interval]), while reefs at the highest latitudes (20 – 30°  
346 absolute latitude) were most likely to be in the algae-large fish state (33.7% [31.4, 36.2]).  
347 At the shallowest depths, reefs were equally likely to be in either of the four states, but  
348 with increasing depth, state probabilities increased for coral-large fish (36.2%  
349 [29.2,42.9]) and algae-large fish states (32.0% [25.6, 38.7]). In the most oligotrophic  
350 waters (minimum mean chlorophyll *a* values), the four states had similar probabilities,  
351 but at high chlorophyll *a* values, the combined likelihood of reefs to be in an algae  
352 dominated state was >80%. Low wave exposure favored large fish states, while high  
353 wave energy environments had equal probabilities of reef states. Our additional

354 investigation into the sensitivity of our results to the grouping of turf and algae indicated  
355 that high exposure slightly favored coral dominated states (Fig. S5, S6).

356 Even intermediate human impact dramatically decreased the probability of being  
357 in a large fish state, with very low probabilities of both the coral-large fish (2.6% [1.0,  
358 4.5]) and algae-large fish state (7.9% [4.0, 14.5]) at the highest human impact (although  
359 there were only very few observations at the highest human impact values). Both fished  
360 and unfished reefs were most likely to be in either of the two large fish states, but this  
361 probability increased strongly in no-take zones, where the algae-large fish state was the  
362 most likely (34.9% [33.1, 36.7]) and the coral-small fish state was the least likely (17.9  
363 [16.9, 18.9]). Separating turf and macroalgae in the initial classification resulted in higher  
364 assignments of coral-large fish states both inside fished and no-take zones (Fig. S5),  
365 suggesting some ecologically relevant effects of MPAs on the relative prevalence of turf  
366 vs. macroalgae.

367

368 **Temporal trends in reef states:** While our spatial decomposition provides a useful  
369 indication of recent reef states (average survey year = 2013), our global baselines of coral  
370 reefs may have already shifted due to long-standing human impact. Indeed, we detected  
371 substantial changes in reef states over time. For benthic states (twelve datasets), the  
372 likelihood of algal states increased over time (Bayesian parameter estimate: Time = 0.69  
373 [0.22, 1.16]) (Table S1) and showed a clear decrease in the intercept for time series  
374 length, suggesting that longer time series had lower probabilities of being in the algal  
375 state at the beginning (time series length = -0.05 [-0.09, -0.02]) (Fig. S4a). For fishes  
376 (eleven time series datasets), we found a substantial decrease in the likelihood of being in  
377 the small fish state over time (-0.93 [-1.51, -0.34]), which was not markedly affected by  
378 time series length (Fig. S4b). In absolute terms, algal cover increased by 13.9% ( $\pm 2.0\%$   
379 SE) across all sites, while coral cover decreased by 6.5% ( $\pm 1.9\%$  SE). Likewise, the  
380 smallest fishes decreased by 1,191g ( $\pm 363$ g SE) across sites, while the largest fishes  
381 increased by 7,946g ( $\pm 5,180$ g SE). There was no relevant change in total fish biomass  
382 from the beginning to the end of all time series datasets ( $-423$ g  $\pm 1,578$ g SE).

383 Across ten combined time series spanning an average of 12.2 years ( $\pm 6.6$  years  
384 SD), most datasets showed at least one state shift (88.1% out of 109 time series), while  
385 11.9% of sites remained in the same state throughout the observation period. Of sites that  
386 exhibited state shifts, only 21.5% were in the same state at the beginning and the end of  
387 the time series (a dynamic interpretable as disturbance and recovery). This was most  
388 prevalent when the original state was coral-large fish (7.5% of sites), followed by the two  
389 algal regimes (5.4% each), and least likely (3.2%) when reefs were in the coral-small fish  
390 state at the onset of the monitoring period. Accordingly, we also found an increasing  
391 probability of the algae-large fish state over time (45.2% [38.7, 51.5] at the conclusion of  
392 the time series), and a decreasing probability of the coral-small fish state (14.3% [12.0,

393 16.7%]) (Fig. 4). In the DTMCs, discrete shifts were more likely between fish states than  
394 benthic states, more likely to occur within the two algal regimes than the coral regimes,  
395 and least likely to involve diagonal shifts across benthic and fish states simultaneously  
396 (Fig. 5). The most likely state shifts were from small fish to large fish in the algae state  
397 (48.5% [39.7, 57.4]) and from the coral-large fish state to the algae-large fish state  
398 (45.7% [37.8, 53.7]). Finally, reefs were least likely to shift into the coral-small fish state  
399 (average predicted probability: 28.0%).

400

## 401 **DISCUSSION**

402 Predicting where, when, and why coral reefs shift from one ecological state to another,  
403 and whether changes in benthic and fish communities co-occur, remains challenging. By  
404 parsing these highly-complex ecosystems into a small suite of simplified states, we  
405 harness the power of divergent datasets to quantify the prevalence of different reef states  
406 globally, their drivers, and the temporal dynamics of coral reef states over the past few  
407 decades.

408 While all geographic realms harbored all four reef states, their respective  
409 prevalence varied, reflecting documented differences in environmental conditions and  
410 biogeographic history (Roff & Mumby, 2012; McWilliam *et al.*, 2018; Parravicini *et al.*,  
411 2021; Reverter *et al.*, 2022; Tebbett *et al.*, 2023): the Tropical Eastern Pacific –such as  
412 the Galapagos Islands– can be heavily influenced by cold upwelling that favors algal  
413 growth (both turf and macroalgae) and supplies nutrient rich resources to larger-bodied  
414 fishes (Glynn, 2001). In turn, the low probability of the coral-large fish in the Western  
415 Atlantic is likely related to the regional decline of corals, loss of herbivorous fish and  
416 urchins, and overfishing of large-bodied fishes (Jackson *et al.*, 2001; Gardner *et al.*, 2003;  
417 Schutte *et al.*, 2010; Shantz *et al.*, 2020). Notably, separating turf and macroalgae  
418 resulted in an even probability of reef states in the Tropical Atlantic only, suggesting that  
419 correlations between turf and macroalgal prevalence are weaker in the Tropical Atlantic  
420 than elsewhere (Fig. S5, S6). For the Indo-Pacific, state assignments are probably –at  
421 least in part– influenced by spatial clumping in survey distributions (Reverter *et al.*,  
422 2022). Central Indo-Pacific reefs had high probabilities of being dominated by large  
423 fishes (both algae- and coral-dominated). Most surveys were located in Australia, with  
424 comparably low human impact, relatively selective fisheries, and a long-standing  
425 fisheries management system. Conversely, the high probability of coral and small fish  
426 states in the Western Indian Ocean may be influenced by comparatively sparse coverage  
427 of reefs from more impacted regions of the Indian Ocean, such as India, Sri Lanka, or the  
428 Southwest Indian Ocean.

429 Despite geographic differences, there was high heterogeneity of reef states at local  
430 and regional scales, emphasizing the strong spatial context-dependency of reef states  
431 (Schmitt *et al.*, 2019; Crisp *et al.*, 2022). Our results allow us to establish some general,

432 quantitative expectations of reef states based on prevailing conditions, which may help  
433 transcend the idiosyncratic nature of case studies. Algal domination at high latitudes is  
434 likely driven by lower survival, competitiveness, and recruitment of corals in high-  
435 latitude environments due to a temperature, light levels, aragonite saturation state,  
436 grazing pressure, larval supply, and settlement cues (Robinson *et al.*, 2018; Abrego *et al.*,  
437 2021). For coral reef fishes, empirical evidence for latitudinal variability in body size is  
438 somewhat equivocal (Taylor *et al.*, 2019; Audzijonyte *et al.*, 2020), but marine fish  
439 assemblages tend to have fewer small-sized species at high latitudes (Lindsey, 1966;  
440 Coghlan *et al.*, 2024). Similarly, given that reef fish species tend to mainly recruit to  
441 shallow habitats such as lagoons and back reefs (Adams & Ebersole, 2002), the steeply  
442 increasing probability of deeper reefs to be in the large fish states appears intuitive.  
443 Chlorophyll *a* concentrations (which are often indicative of nutrient availability) does not  
444 appear to curtail the abundance of large-bodied fishes (Heenan *et al.*, 2016). However,  
445 the sharp increase of algae-dominated states at high chlorophyll *a* concentrations aligns  
446 with both the reported negative impacts of coastal nutrient input on corals and high cover  
447 of algae in naturally nutrient-rich environments, even where healthy communities of  
448 large-bodied herbivores exist (Burkepile *et al.*, 2013; Wiedenmann *et al.*, 2013).

449 The clear decline of the coral-large fish state at high human impact reflects the  
450 rapid extirpation of large reef fishes near human settlements (Stallings, 2009; Cinner *et al.*,  
451 2016; Lefcheck *et al.*, 2021). In turn, the comparatively high probability of the coral-  
452 small fish state at high anthropogenic impact (despite considerable uncertainty) supports  
453 the notion that local human impact does not inextricably foster algal dominance (Bruno  
454 & Valdivia, 2016). More specifically, although fishing restrictions increase the likelihood  
455 of reefs to be dominated by large fishes, this does not consistently translate to an  
456 increased probability of coral dominance. This finding supports suggestions that no-take  
457 zones may have little detectable influence on the reef benthos (Bruno *et al.*, 2019;  
458 Graham *et al.*, 2020) –in part due to the lack of statistical power and ill-suited metrics to  
459 assess benthic community change (Mumby *et al.*, 2021)– and that fish biomass is more  
460 readily replenished on macroalgal reefs than on coral reefs after disturbance (Hamilton *et al.*,  
461 2022).

462 Our results set important expectations concerning present-day management  
463 targets for coral reefs worldwide (Fig. S7). Coral reefs in ostensibly ‘pristine’ settings (3°  
464 absolute latitude, minimal human impact, minimal chlorophyll *a*, and inside a no take  
465 zone), would indeed have the highest probability of being in the widely considered  
466 ‘healthy’ coral-large fish state, followed by the algae-large fish state. Yet, a reef in these  
467 exact same conditions at 20° absolute latitude (which traverses reefs in the Middle East,  
468 India, Southeast Asia, Hawaii, Mexico, the Caribbean, the East African Coral Coast, the  
469 Southwestern Indian Ocean Islands, Australia’s Ningaloo Reef and Great Barrier Reef, as  
470 well as several Pacific Islands) would most likely be in the algae-large fish state.

471 Collectively, these reef systems form a substantive proportion of the global coral reef  
472 area. Thus, even under ideal present-day conditions with minimal human impact (e.g.,  
473 Ningaloo Reef), many reefs are likely to be in an algal-dominated state with fish biomass  
474 concentrated in the larger size classes.

475 Importantly, several other important predictors were unaccounted for in our  
476 analysis, especially recent bleaching events, seascape configuration, or larval  
477 connectivity (Berkström *et al.*, 2020; Fontoura *et al.*, 2022). Nevertheless, our analyses  
478 provide a non-exhaustive suite of baseline expectations concerning coral reef states  
479 worldwide given their local settings, including the notion that benthic dominance by  
480 algae may be a common and/or natural state on today's coral reefs, even in areas where  
481 present-day local human influence is low.

482

483 **Temporal trends in reef states:** The observed trend towards algal-dominated states over  
484 time supports observations of local coral-algae phase shifts and their—at least regional—  
485 ubiquity. Given the coarse nature of our state classification, we are unable to tease apart  
486 trends within algal states (turf or macroalgae) (Tebbett *et al.*, 2023) or the prevalence and  
487 importance of shifts toward other benthic organisms (Crisp *et al.*, 2022; Reverter *et al.*,  
488 2022). Nevertheless, our results reaffirm that reefs have generally moved from systems  
489 characterized by mixotrophic, structure-building animals to more ephemeral, autotrophic  
490 primary producers.

491 There is little doubt that humans directly reduce fish biomass in the largest size-  
492 classes (Stallings, 2009; Cinner *et al.*, 2016; Shantz *et al.*, 2020; Lefcheck *et al.*, 2021).  
493 Yet, fish communities decreased in the relative representation of small fishes over time.  
494 There are several non-exclusive explanations for this trend. First, the increased  
495 implementation of MPAs over time may bolster fish populations in larger size classes due  
496 to the preferential harvest of large individuals by humans (Edgar *et al.*, 2014; Strain *et*  
497 *al.*, 2019), with a large number of MPAs represented in the time series. Second, baseline  
498 configurations of reefs in our time-series may represent an already depleted fish  
499 community that lacks biomass in the largest size classes, as human impact on reef fish  
500 communities significantly predates the beginning of even the earliest time series. Third,  
501 salient ecological drivers may have caused the general decrease in small fish-dominated  
502 states, related to bottom-up processes mediated by the benthos. In this context, examining  
503 fish and benthic state changes simultaneously provides critical insights.

504 As the primary habitat builders, scleractinian corals provide important fine-scale  
505 structural architecture that increases surface area and shelter availability, which  
506 disproportionately favors small-bodied reef fish species (Almany, 2004). As such, the  
507 concurrent demise of corals and small-bodied fishes is intuitive, and supported by case  
508 studies (Graham *et al.*, 2007; Wilson *et al.*, 2010; Alvarez-Filip *et al.*, 2011). While  
509 larger bodied fishes also benefit from structural complexity on reefs (Rogers *et al.*, 2014),

510 strong size-selectivity of fishes for shelter holes and the sequential erosion of the reef  
511 structure (including rapid disappearance of delicate branching structures and the  
512 persistence of larger, boulder-like structures) suggests that adverse effects of reef  
513 flattening due to coral loss will, at least initially, primarily affect small-bodied animals.

514 This, in turn, may change ecosystem functioning on reefs. In fact, we found a  
515 mean 41.1% decrease in the biomass of small-bodied planktivores (from 362.1g per  
516 100m<sup>2</sup> [234.9, 566.6] to 213.4g per 100m<sup>2</sup> [138.5, 326.7]) throughout our time series,  
517 suggesting that the increasing rarity of the coral-small fish state coincides with a loss of  
518 small-bodied fishes that harness pelagic energy (Fig. S8). These fishes frequently occur  
519 in high numbers, feed on planktonic resources that arrive on reefs as external subsidies,  
520 and sustain a variety of piscivorous predators (Hamner *et al.*, 1988; Morais & Bellwood,  
521 2019; Skinner *et al.*, 2021). Thus, the loss of small-bodied, high-turnover species that  
522 depend on coral for shelter may compromise coral reef food webs worldwide.

523 The simultaneous rise of large-bodied fishes in algal dominated states may, in  
524 turn, reflect a bottom-up, resource-mediated effect expressed through increased  
525 abundances of large-bodied herbivores and omnivores (rather than predators that depend  
526 on small-bodied fishes for food). There is increasing recognition that mobile herbivores  
527 actively track their dietary resources (Tootell & Steele, 2016), and wide availability of  
528 endolithic and epilithic resources following coral mortality may boost the abundance,  
529 biomass, and growth of large-bodied herbivores in the short- and medium-term  
530 (Robinson *et al.*, 2019; Graham *et al.*, 2020; Taylor *et al.*, 2020) to sustain productive  
531 fisheries (Robinson *et al.*, 2019). However, our results also show that algae-dominated  
532 states show frequent transitions between small and large-fish dominated states, which  
533 suggests more seasonal, ephemeral, and volatile producer-consumer dynamics than reefs  
534 in the coral-large fish state. Accordingly, there was a weaker overall trend of increasing  
535 herbivore biomass throughout our time series (Fig. S8), from 2,652g [1,738, 4,056] to  
536 3,226g [2,102, 5,057] (21.6% mean increase).

537

538 **Coral reef states in the 21<sup>st</sup> century.** While there is strong consensus that coral reefs  
539 have changed dramatically, the nature of changes, their significance, and our ability to  
540 counteract these dynamics through protection or restoration continue to be debated. Our  
541 results help to move this debate forward. First, pristine reef conditions on modern reefs  
542 are often thought to be characterized by high coral cover and large-bodied fishes  
543 (McClanahan *et al.*, 2007; Sandin *et al.*, 2008). Although high human impact often pivots  
544 reefs out of the coral-large fish state, the reverse is not inexorably the case: even reefs in  
545 relatively pristine conditions can have high probabilities of being dominated by algae,  
546 small fishes, or both. Thus, baselines for coral reef management need to be precisely  
547 defined with respect to local conditions. Second, while our results support the positive  
548 effect of MPAs for large fish species, the most fragile reef state in recent decades appears

549 to be dominated by corals and small-bodied fishes. Neither are likely to benefit directly  
550 from MPAs that are designed solely for protecting fisheries species, but may benefit from  
551 other restrictions that, for instance, reduce anchoring damage. Thus, well-designed and  
552 enforced MPAs can bestow a variety of ecological benefits on coral reef ecosystems, but  
553 case-by-case evaluations of their design and utility in the face of the costs they can  
554 impose on local stakeholders are critical (Bruno *et al.*, 2019).

555 Finally, the revealed temporal state shifts suggest critical shifts in coral reef  
556 functioning. While reefs in the coral-small fish state are likely to obtain and recycle  
557 energy and nutrients through external subsidies and internal cycling mechanisms (Brandl  
558 *et al.*, 2019; Skinner *et al.*, 2021), reefs dominated by algae and large-bodied herbivores  
559 exhibit direct paths from benthic primary producers to large-bodied fishes (Hempson *et*  
560 *al.*, 2018). Both high-turnover, small-bodied fishes and herbivorous fishes have played  
561 critical roles in the rise of modern coral reefs, their productivity, and their capacity to  
562 sustain coral reef fisheries (Brandl *et al.*, 2019; Lin *et al.*, 2019; Morais *et al.*, 2020;  
563 Siqueira *et al.*, 2023). Yet, the dominance of the algae-herbivore pathway –whether it is  
564 turf or macroalgae– may fundamentally reshape energetic pathways on coral reefs. Such  
565 systems can offer lucrative, nutritionally rich, and potentially resilient fisheries to coastal  
566 communities (Robinson *et al.*, 2019; Wilson *et al.*, 2022), but our results also suggest that  
567 they are less stable (given their frequent transitions between small and large fish  
568 communities). Given this, alongside compromised processes such as reef accretion or  
569 diminished aesthetic appeal, systems in algal states may fail to provide several important  
570 services to society. Determining how to manage such systems, and whether it is feasible  
571 or advisable to restore reef states dominated by corals and small-bodied fishes will be a  
572 critical challenge in the 21<sup>st</sup> century.

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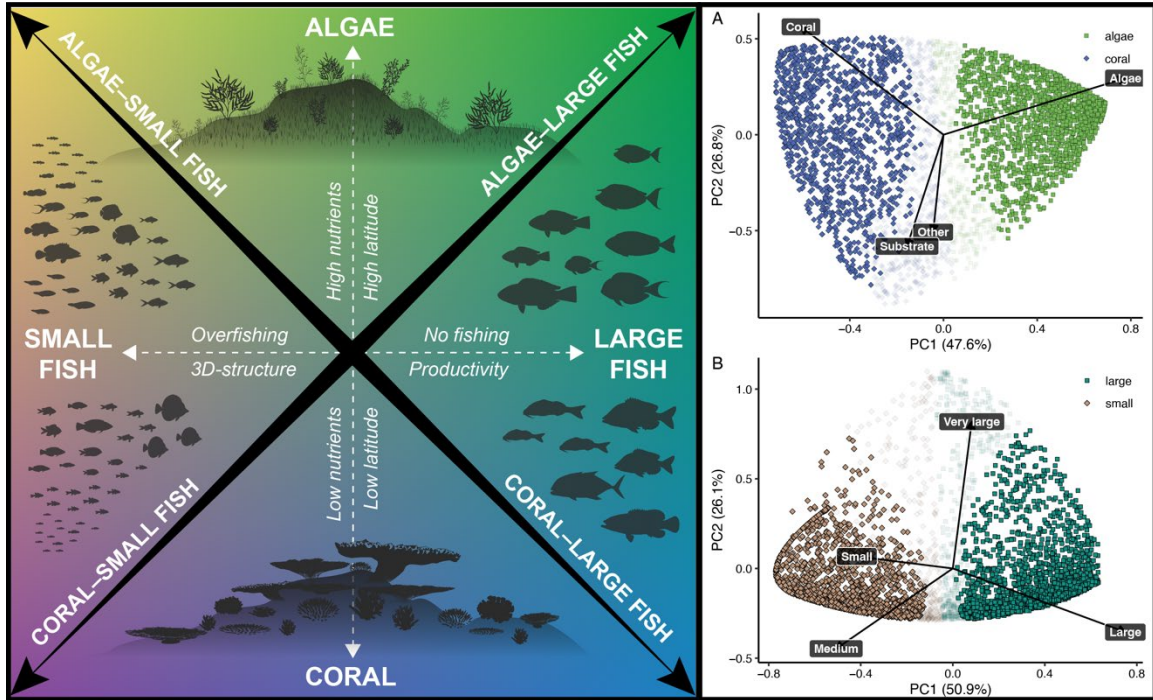
836 **DATA AVAILABILITY:** All data and code are available on [Figshare](#) (doi:  
837 10.6084/m9.figshare.24264109.v1)

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839 **CONFLICT OF INTEREST:** The authors declare no conflict of interest.

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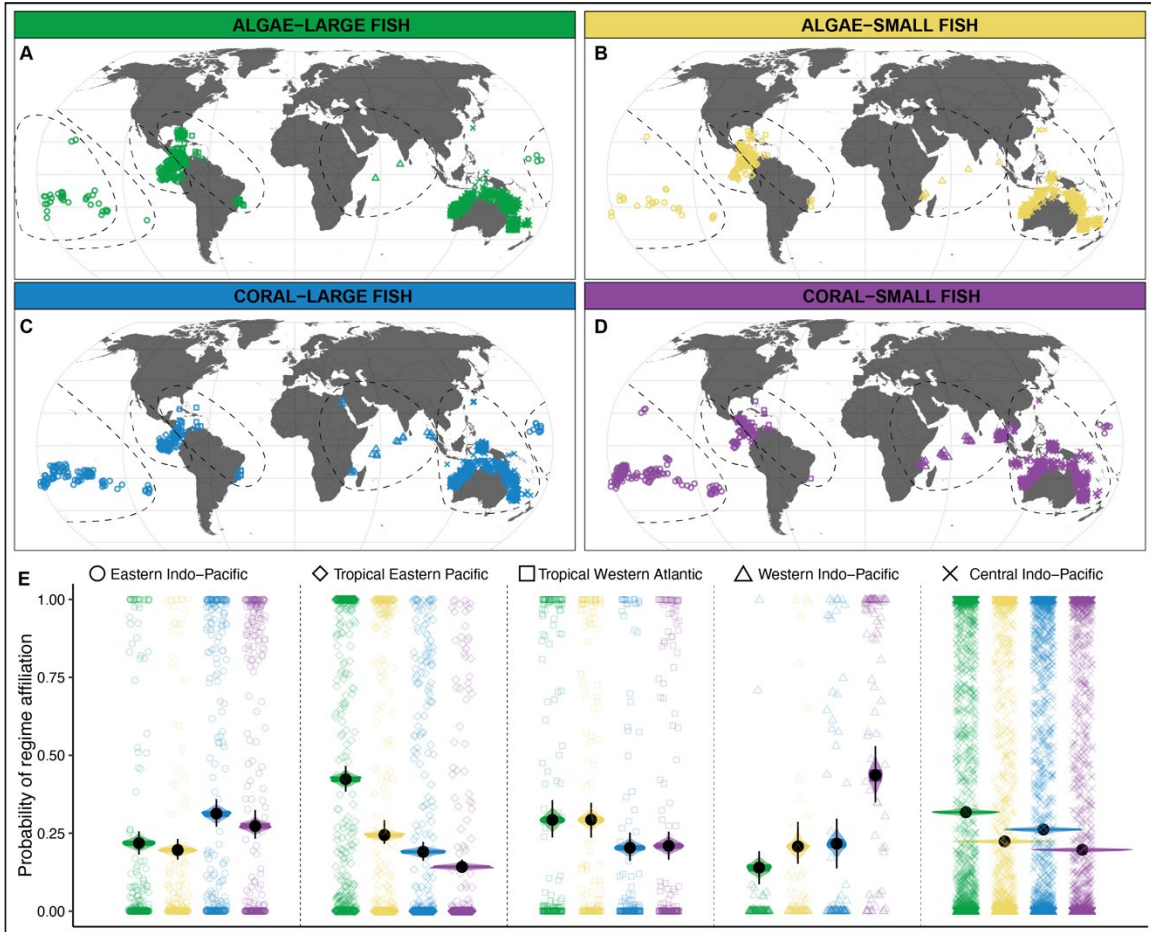
841 **FIGURES**



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**Figure 1. A double dichotomy approach to identifying coral reef states based on benthic and fish communities.**

Using the proportional composition of benthic cover and fish size classes, reefs can be divided into state-dyads dominated by coral vs. algae (y-axis) and small- vs. large-bodied fishes (x-axis). This creates four distinct states along the four diagonal axes (black arrows), denoted as: coral–large fish, algae–large fish, algae–small fish, and coral–small fish. Known and hypothesized key drivers that cause shifts toward each state are provided in white italics. (A) and (B): Ordination plots displaying the spread of RLS surveys in the first two dimensions for the benthos (A) and fishes (B). Colors denote classifications obtained from the fuzzy-clustering method, while positioning in multivariate space is based on the relative contributions of the four categories for benthic and fish communities, respectively. Variance explained by the first two PC axes is provided in parentheses. Points with low opacity denote surveys for which state assignments were <95% confident.

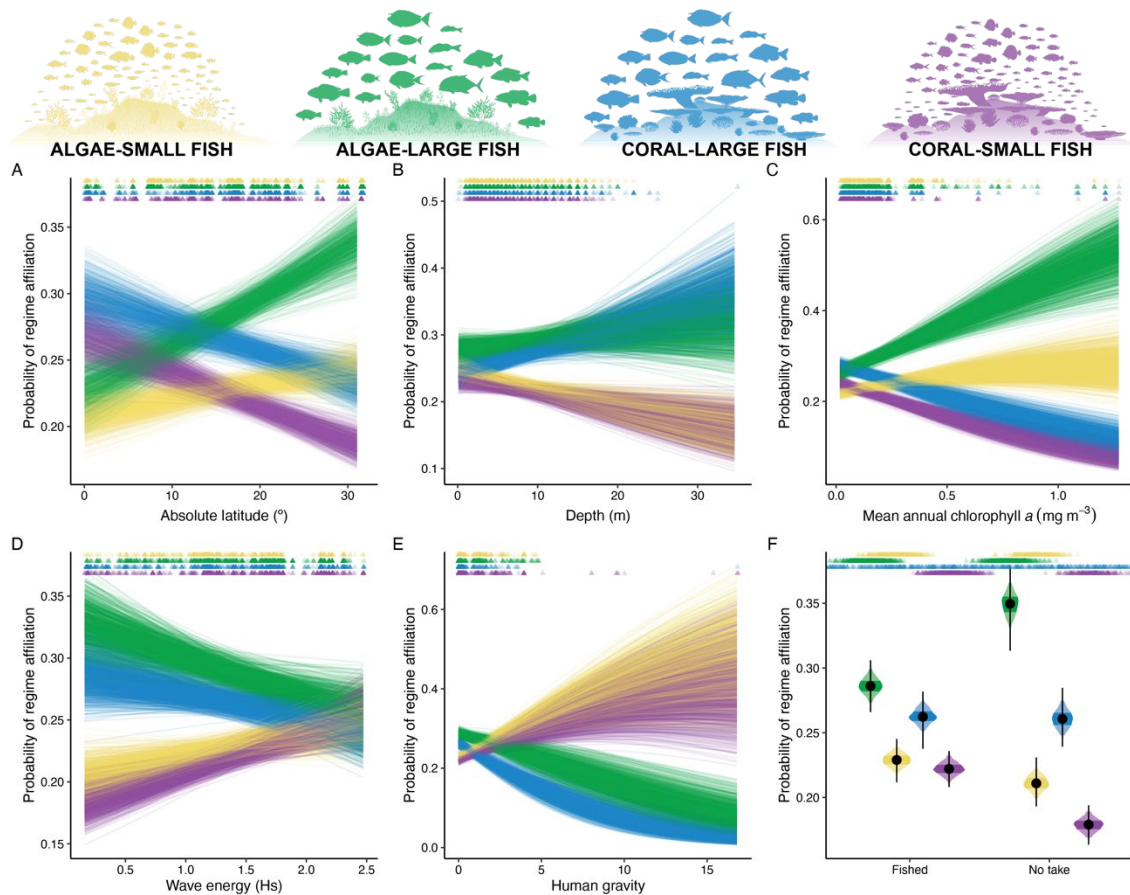


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**Figure 2. Biogeographic patterns in coral reef states.**

The four states are ubiquitous at a global scale, resulting in limited discernable differences among biogeographic realms (A to D). Yet, probabilities of being in the four respective states varied substantially across five biogeographic realms (E). Points in A-D represent individual surveys and are jittered for display purposes. Slab and caterpillar plots in E) represent the distribution of 1,000 fitted draws from the Bayesian posterior, marking the mean predicted value (black circle), its 50% and 95% confidence intervals (shaded slabs), and full range of predictions (black line and lightest shading), and with colors matching the four state colors. Points at the extremes of the y-axis (0 and 1) indicate very high probabilities in their state assignment.

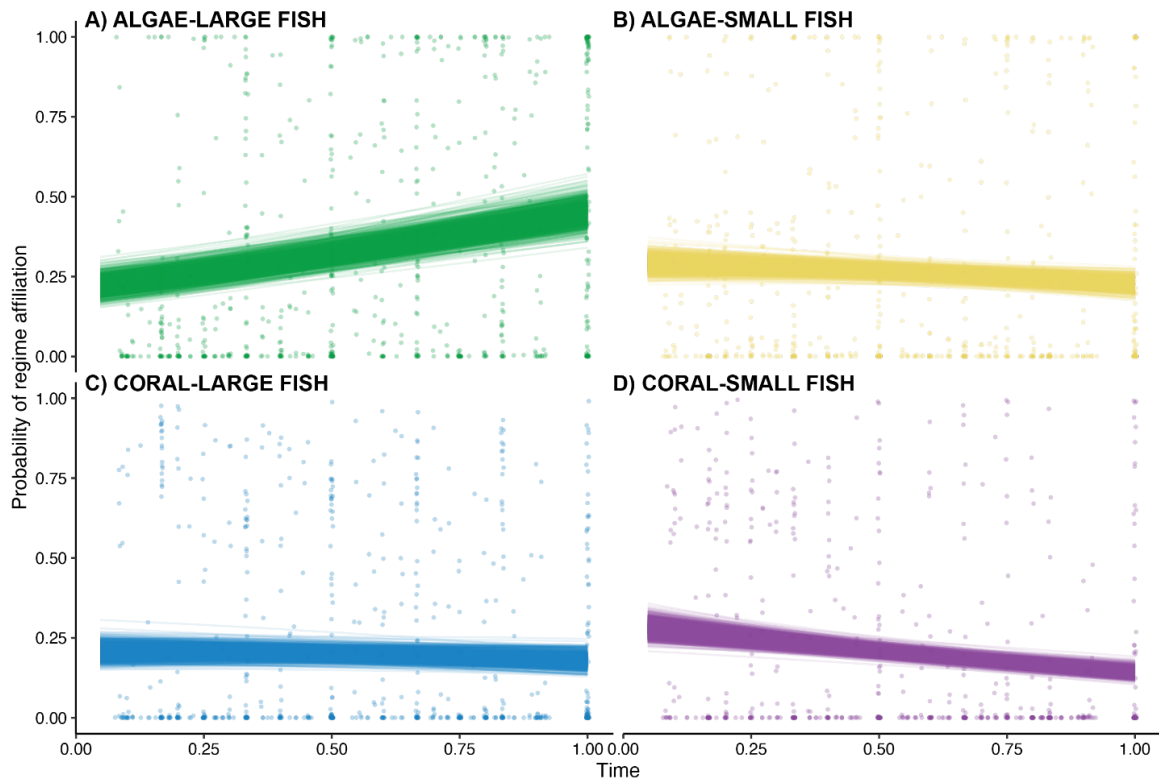




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**Figure 3. Relationships between six explanatory variables and the probability of reefs falling into one of the four states.**

Lines show posterior predicted fits ( $n = 1,000$ ) from the Bayesian regression model for each state type (green = algae-large fish; yellow = algae-small fish; blue = coral-large fish; purple = coral-small fish), with all other predictors held at their median. Points at the top of the plots represent the raw state assignments along each subpanel's x-axis. Slab intervals in F) mark the mean predicted values (black dot), its 50% and 95% CIs (darker shades), and full prediction range (black line and lightest shade).

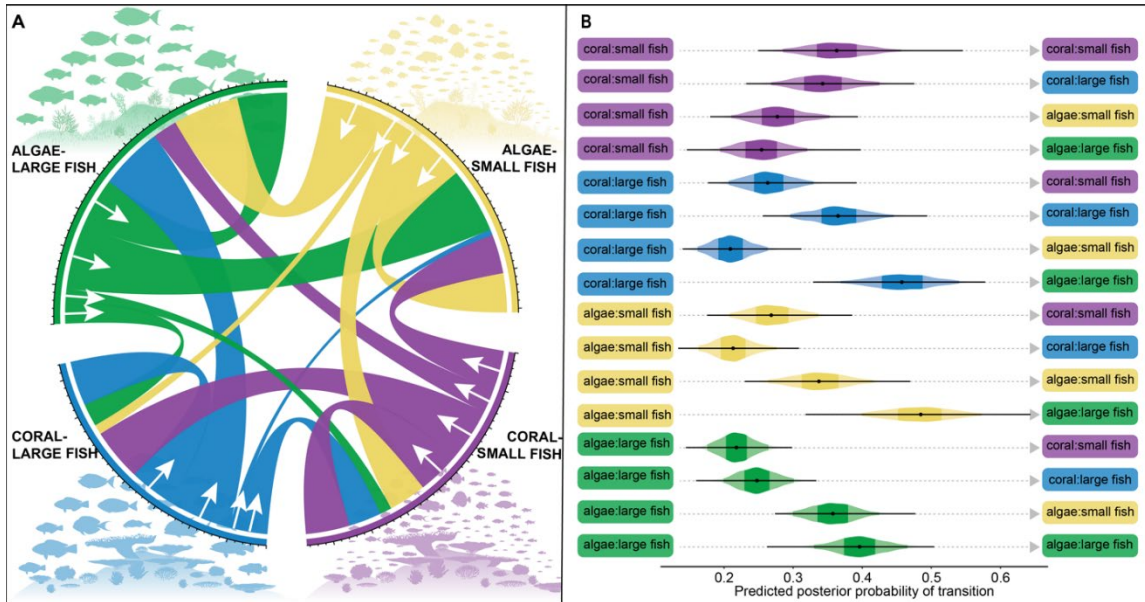


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887 **Figure 4. Temporal trends in coral reef states, as obtained from ten timeseries.**

888 The four plots show the probabilities of state assignments (y-axis) for each state across  
 889 the standardized length of time series (from  $t_0$  at the beginning to  $t_1$  at the conclusion of  
 890 the time series; x-axis). Lines represent 1,000 predicted draws from the Bayesian  
 891 posterior, while points represent the raw probabilities of state assignments obtained from  
 892 the fuzzy-clustering analysis.



**Figure 5. Estimated probability of state shifts between coral reef states across the investigated time series.**

A) Cord diagram highlighting the state change probabilities between the four state types. B) Predicted posterior probabilities of state changes from 1,000 random draws based on the Bayesian mixed model. Labels on the left of the y-axis highlight the original state, while labels on the right denote the state shift (including hysteresis, if the state is the same as the one to the left). Slab intervals in F) mark the mean predicted values (black dot), its 50% and 95% CIs (darker shades), and full prediction range (black line and lightest shade).

## SUPPORTING INFORMATION

Information about datasets, data analyses, additional results, figures, and tables are found in the Supplemental Information.