

1 **Thermal stress induces persistently altered coral reef fish assemblages**

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15 **Ecological communities are reorganizing in response to warming temperatures,**  
16 **producing unexpected ecosystem configurations [1,2]. For continuous ocean habitats**  
17 **this reorganization is characterized by large-scale species redistribution [3], but for**  
18 **tropical discontinuous habitats such as coral reefs, spatial isolation coupled with strong**  
19 **habitat dependence of fish species [4] imply that turnover and local extinctions are more**  
20 **significant mechanisms [5,6]. In these systems, transient marine heatwaves are causing**  
21 **coral bleaching and profoundly altering habitat structure [7]. Despite severe bleaching**  
22 **events becoming more frequent [8] and projections indicating annual severe bleaching**  
23 **by the 2050s at most reefs [9], long-term effects on the diversity and structure of fish**  
24 **assemblages remain unclear. Using a 23-year time-series of fish and benthic surveys**  
25 **spanning a thermal stress event in Seychelles, we describe and model structural changes**  
26 **and recovery trajectories of fish communities after mass bleaching. Fish assemblages**  
27 **transitioned into previously unseen compositions that persisted over 15 years, which**  
28 **exceeds realized and projected intervals between thermal stress events on coral reefs.**  
29 **After bleaching, fish communities homogenized in time and space, leading to**  
30 **assemblages characterized by exceptional herbivore dominance. Composition changes**  
31 **occurred despite recovery of coral habitat on some reefs, and were most pronounced**  
32 **after macroalgal regime shifts on other reefs. Modification to reef habitats caused by**  
33 **frequent marine heatwaves will lead to persistent changes in fish diversity, community**  
34 **structure and function. Our results indicate that fish communities historically**  
35 **associated with coral reefs will not reestablish following severe coral bleaching,**  
36 **requiring substantial adaptation by managers and resource users.**

37

38 **Keywords: beta diversity, biodiversity, biotic homogenization, bleaching, community**  
39 **structure, coral reef ecology, regime shifts, thermal stress**

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## 41 RESULTS AND DISCUSSION

42 *2,500 limit, currently at 2,344 words.*

43 We investigated the effects of a marine heatwave and associated severe coral bleaching on  
44 the compositional turnover and persistence of fish assemblages. Because reef-associated  
45 fishes are highly dependent on complex coral-dominated habitat [4,10], bleaching-driven  
46 habitat collapse can reduce species richness [11] and homogenize compositions [12] within  
47 1-3 years. Knowledge of long-term changes in fish communities following bleaching will  
48 help to reveal how recurring thermal stress events may lead to permanent changes in these  
49 communities. We focus on Seychelles where, in 1998, a strong El-Ninō coincided with the  
50 Indian Ocean Dipole to cause severe coral bleaching, leading to loss of >90% coral cover and  
51 collapse of habitat structure [13]. Using data collected over 1994-2017, we examined  
52 temporal change in richness ( $\alpha$  diversity) and composition ( $\beta$  diversity) of fish assemblages  
53 following bleaching. Because reefs either underwent regime shifts to macroalgal states or  
54 recovered coral cover and complexity [7] and also experienced severe bleaching in 2016 [8],  
55 our analyses examine compositional turnover on both regime-shifted and recovering reefs,  
56 and document how fish assemblages reorganized between successive mass bleaching events.

57 Biodiversity losses were most severe on regime-shifted reefs, which were dominated  
58 by macroalgae (mean cover >20% from 2005-2017) and remained at low  $\alpha$  diversity levels  
59 throughout the post-bleaching recovery period (Figure 1A,H). In contrast, recovering reefs  
60 steadily increased coral cover to reach pre-bleaching levels by 2014 (mean cover = 27%)  
61 (Fig. 1A,G), and  $\alpha$  diversity increased from 46 species ( $\pm 2.47$  S.E.) in 2005 to exceed pre-  
62 bleaching levels by ~eight species in 2017 ( $58.5 \pm 3.00$ ). Although both reef states supported  
63 similar levels of richness prior to bleaching (1994 richness: recovering =  $52.1 \pm 1.92$ ; regime-  
64 shifted =  $55.3 \pm 3.50$ ) and followed similar temporal trajectories to stabilize richness levels  
65 by 2011, regime-shifted reefs did not recover pre-bleaching richness, reaching a maximum of

66 46 species ( $\pm 2.80$ ) in 2008 (Figure 1A). Most strikingly, temporal trends in  $\beta$  diversity  
67 indicated that fish communities settled into compositions which had not existed before  
68 bleaching. Across all reefs, community compositions were dissimilar to their 1994 baseline  
69 ( $0.37 < \beta_{1994} < 0.77$ ) and did not recover towards pre-bleaching compositions over 2005-2014  
70 ( $year\ mean = -0.01$ , 95% CI = -0.02, 0.00) (Figure 1C,D). Collectively, these  $\alpha$  and  $\beta$   
71 diversity patterns indicate that coral reef fish communities did not return to pre-bleaching  
72 diversity levels over a 16-year recovery window (1998-2014). Persistence of post-bleaching  
73 compositions has been observed for cryptobenthic fish assemblages [14], and we confirm that  
74 such long-term bleaching impacts extend to species spanning multiple trophic levels and  
75 providing important ecosystem services (e.g. fisheries).

76         Regeneration of coral-dominated habitat was somewhat effective in mitigating  
77 bleaching impacts on fish communities, with reefs that recovered (i.e. structurally complex  
78 habitat, dominated by branching corals with negligible macroalgal cover) having fish  
79 compositions most similar to those recorded pre-bleaching (Figure 1B,D). However, coral  
80 community composition is also a strong structuring influence on fish communities after  
81 bleaching [12,14], and the contrasting effects of branching and massive corals on fish  
82 compositions here imply that compositional shifts in coral growth forms are similarly  
83 important. For example, stress-tolerant corals such as massive *Porites* were associated with  
84 lower species richness (Figure 1B) and higher compositional dissimilarity through time  
85 ( $\beta_{1994}$ ) (Figure 1D), possibly because these sites failed to recover pre-bleaching compositions  
86 of dominant branching coral growth forms [15] which provide shelter for abundant and  
87 diverse small-bodied fishes [16,17]. Because several coral growth forms contribute to  
88 seascape-level complexity [18,19], and bleaching impacts were minimized but not reversed  
89 by fast growth of branching corals, our findings confirm that fish communities should not be  
90 expected to fully recover when coral communities reassemble [20,21].

91 Regime-shifted reefs were most dissimilar to their coral-dominated pre-bleaching  
92 baselines (mean  $\beta_{1994} = 0.57 \pm 0.01$  on regime-shifted reefs;  $0.50 \pm 0.01$  on recovering reefs),  
93 and  $\beta_{1994}$  was maximized on reefs with high macroalgal cover and low structural complexity  
94 (Figure 1C,D). Declines in coral cover and flattening of habitat structure likely prevented  
95 coral-associated species from relocating or recruiting to macroalgal reefs, despite these fish  
96 being present on nearby recovering reefs. These patterns build upon previous observations  
97 from Seychelles which have demonstrated that macroalgal overgrowth has resulted in  
98 bottom-heavy fish biomass pyramids and reduced functional diversity [7,21].

99 Fish communities also homogenized in time and space.  $\beta_{seq}$ , a measure of  
100 compositional similarity between sequential survey years, declined from 2005-2017 (*year*  
101 mean = -0.05, 95% CI = -0.066, -0.026) at similar rates for recovering and regime-shifted  
102 reefs (*regime state \* year* mean = -0.01, 95% CI = -0.042, 0.023) (Fig. 1E,F). For recovering  
103 reefs, declines in  $\beta_{seq}$  were mirrored by temporal changes in spatial dissimilarity, whereby  
104  $\beta_{spatial}$  declined from 0.61 to 0.50 to fall below baseline  $\beta_{spatial}$  levels by 2017 (Figure S1A). In  
105 contrast, compositional dissimilarity of regime-shifted reefs remained greater than baseline  
106 levels throughout 2005-2014 (mean  $\beta_{spatial} = 0.57$ ) (Figure S1B). Such high spatial  
107 heterogeneity suggests that habitat associations underlie compositional differences on  
108 regime-shifted reefs, as macroalgal habitat quality can vary substantially among seasons and  
109 years [22,23].

110 We examined how functional groups and species contributed to compositional  
111 differences following bleaching by tracking temporal patterns in functional group richness  
112 (Figure 2). Corallivore and invertivore group richness recovered non-linearly and, by 2014  
113 had reached pre-bleaching levels on recovering reefs but not on regime-shifted reefs (Figure  
114 2B,D). Herbivore richness increased linearly from 2005-2014 on both reef states though,  
115 again, recovering sites consistently supported more species than regime-shifted reefs and

116 exceeded pre-bleaching levels by 2008, whereas regime-shifted reefs maintained pre-  
117 bleaching levels of herbivore richness from 2008-2017 (Figure 2C). Changes in richness of  
118 planktivore, mixed-diet feeding, and piscivore groups were also strongly differentiated by  
119 reef regime, with planktivore, mixed-diet feeder, and piscivore groups consistently less  
120 speciose than 1994 baselines on regime-shifted reefs, but less impacted on recovering reefs  
121 where pre-bleaching richness levels were matched or exceeded throughout 2005-2017 (Fig.  
122 2A,E,F). Regime shifts, therefore, led to a greater loss of functional redundancy (i.e. fewer  
123 species with similar functional roles). This implies that on reefs close to human settlements,  
124 such as Seychelles, the vulnerability of fish functional groups to fishing [24,25] will be  
125 exacerbated by bleaching, with transitions to macroalgal states likely to produce communities  
126 that are functionally depauperate relative to historic coral-dominated states [26]. In contrast,  
127 the functional capacity of fish communities was restored on reefs that resisted regime shifts,  
128 with richness levels of all six dietary groups returning to pre-bleaching baselines on  
129 recovering reefs. For piscivores, which returned to pre-bleaching richness most slowly (by  
130 2014) (Fig. 2F), it is likely that recovery was lagged because these are long-lived species that  
131 depend on reef-associated fishes for food [27] and require temporally stable reef habitats  
132 [28].

133 By comparing species-level biomass estimates of 1994 (pre-bleaching) and 2014  
134 (post-bleaching) fish assemblages, we found that compositional dissimilarity between pre-  
135 and post-bleaching communities was characterized by biomass changes within herbivore,  
136 invertivore and mixed-diet functional feeding groups, and reduced biomass of planktivore,  
137 corallivore and piscivore species (Figures 3, 4). For positive and negative biomass changes  
138 combined, herbivores explained 23.0% and 27.1% of observed  $\beta_{BC}$  at recovering and regime-  
139 shifted reefs, respectively (Figure 3A), and exhibited biomass changes of  $\pm 0-163 \text{ kg ha}^{-1}$   
140 (Figure 4). For herbivore species, the mean biomass difference between 1994 to 2014 was

141 positive at both recovering (mean = 7.14, 95% CIs = 0.60, 13.84) and regime-shifted reefs  
142 (mean = 5.01, 95% CIs = -1.375, 13.248) (Figure 3B), indicating that declines in commonly  
143 observed species were outweighed by gains in newly abundant species (Figure 4). Although  
144 our infrequent visual surveys cannot be used to describe population dynamics, the recovery  
145 period spanned several generations of most species (Table S1) and thus these patterns are  
146 likely due to positive population feedbacks in dominant species that benefited from bleaching  
147 (e.g. herbivores) and slow or failed recovery of species dependent on return of habitat  
148 structure (e.g. planktivores, corallivores). For example, increases in herbivore biomass are  
149 often associated with coral declines [4, 29, 30] and, here, species responses depended on  
150 habitat type, where browsing species associated with macroalgal reefs and scraping species  
151 associated with recovering reefs [31].

152         The relative infrequency of our fish surveys, focus on adult fish and use of a fixed  
153 species list mean that we cannot disentangle the relative contributions of recruitment, growth  
154 and relocation among habitat types and depths, nor account for potential emergence of new  
155 species. However, it is likely that short-term dispersal among reef habitats [12,32], increased  
156 population growth due to greater food availability [33], and high juvenile survivorship [34]  
157 all contributed to the long-term persistence of these populations. Reef fish populations are  
158 ecologically connected over relatively small scales, as larval dispersal distances are typically  
159 <5 – 15 km and many species are territorial as adults (damselfishes, butterflyfishes) or inhabit  
160 small home ranges (<3 km linear distance) [35]. Additionally, Seychelles reefs are isolated by  
161 deep water dispersal barriers for reef fishes and by limited connectivity to distant continental  
162 reefs (>1,000 km) (Kool & Graham *unpublished data*), meaning that species larval  
163 connectivity or relocation from neighbouring reef systems are unlikely to be responsible for  
164 the majority of compositional changes we observe.

165 Other functional groups made lower overall contributions to  $\beta_{BC}$ , and also tended to  
166 have the greatest degree of species declines. For example, invertivores and mixed-diet  
167 feeders had moderately high dissimilarity contributions (9.4 - 13.9%) that were mostly due to  
168 species declines, particularly on regime-shifted reefs (Figures 3A, 4B). Although  
169 dissimilarity contributions from planktivore and piscivore groups were relatively minor (1.62  
170 – 4.99%), almost every species declined in biomass and group-level posterior means were  
171 negative for both recovering and regime-shifted reefs (Figures 3B, 4). In contrast, corallivore  
172 biomass changes were more closely linked to regime state, with biomass increases explaining  
173 observed  $\beta_{BC}$  at recovering reefs (relative contribution from species with biomass increases =  
174 1.23% and from biomass decreases = 0.13%) but biomass declines explaining observed  $\beta_{BC}$   
175 at regime-shifted reefs (0.23%, 1.43%). Positive responses of highly coral-associated species,  
176 which could also be driven by recruitment as well as growth and relocation, reduced  
177 compositional differences relative to regime-shifted reefs. Such strong effects may be  
178 because corallivore species are highly dependent upon live branching coral for food and  
179 shelter [36].

180 In each analysis, we considered how fishing protection influenced recovery and  
181 change in fish assemblages after bleaching. By enhancing grazing functions [37] and  
182 minimizing stressors on coral populations [38], ecosystem protection of coral reefs is  
183 expected to accelerate recovery towards pre-bleaching conditions. Such effects, however,  
184 depend upon the severity of bleaching, disturbance history, and local anthropogenic stressors.  
185 For example, large-scale and well-enforced protection of the Great Barrier Reef has  
186 shortened recovery times to minor bleaching events by up to ~2.4 years [20] whereas at  
187 Indian Ocean reefs, where 1998 bleaching was severe and protected areas are small and less  
188 effectively enforced, both fished and no-take areas experienced declines in fish richness and  
189 abundance after bleaching [39]. In Seychelles, no-take areas were a poor predictor of



190 bleaching responses of benthic communities [7] and, here, did not improve recovery of fish  
191 community composition after bleaching (Figure 1D,F). Protected reefs did support higher  
192 species richness (Figure 1B) but experienced greater biomass declines (Figure 3C). Although  
193 richness patterns were potentially confounded by high abundances that inflated diversity  
194 estimates in no-take areas, large biomass declines highlight how reef protection, which  
195 promoted pre-bleaching reef fish biomass [27], did not insure fish communities against  
196 habitat collapse.

197         Irrespective of benthic recovery trajectory or ecosystem protection, post-bleaching  
198 assemblages were characterized by a speciose and high biomass herbivore group and low  
199 representation of planktivore, invertivore, and piscivore species. Such communities may be  
200 considered hybrid states, which contain aspects of pre- and post-bleaching configurations but  
201 with altered ecosystem functioning [6]. Concepts of such ‘no-analog’ states have typically  
202 been developed to describe highly-degraded terrestrial ecosystems [6,40], but are equally  
203 relevant for coral reefs where species may have unexpected, differential responses to climate  
204 impacts [5]. For example, one striking effect of the 1998 bleaching event was to raise  
205 herbivore productivity and diversity on both regime-shifted and recovering reefs. Herbivore  
206 populations are expected to increase with algal productivity following rapid declines in coral  
207 cover [41] but, in pristine systems, return to baseline levels once benthic habitat has returned  
208 to a coral-dominated state [42]. However, on fished Seychelles reefs herbivores remained  
209 dominant >10 years after bleaching, with both richness and biomass exceeding pre-bleaching  
210 levels by 2014. Such sustained herbivore productivity may occur due to long-term  
211 availability of diverse algal resources, but also in response to dampening of natural predation  
212 levels when upper trophic levels are overexploited and their recovery from bleaching is slow.  
213 Furthermore, high herbivore survivorship during the first few years after bleaching may have  
214 helped to sustain large herbivore populations over decadal time scales, particularly for long-

215 lived acanthurid and scarid species [27]. Thus, high herbivore productivity may be  
216 characteristic of bleached reefs that are adjacent to human populations, which may help  
217 buffer fisheries from declining predatory fish populations by continuing to provide catches of  
218 low trophic level species [31].

219         As low-latitude ecosystems that operate near their thermal limits [43], coral reefs are  
220 more likely to reorganize and suffer local extinctions than receive temperature driven non-  
221 native species. Thus, the diversity patterns documented here suggest that climate-driven  
222 compositional changes on coral reefs will be particularly unique, and driven indirectly by  
223 changes in physical habitat structure rather than directly by the effects of changes in  
224 temperature on species distributions, for example in sub-tropical coastal [44] and temperate  
225 shelf [45] ecosystems. The implications for future coral reef ecosystems are stark, given that  
226 coral reef fish communities did not return to pre-bleaching diversity levels over a 16-year  
227 recovery window (1998-2014) which was bounded by two climate-driven mass coral  
228 bleaching events (1998, 2016). With over 60% of reefs projected to experience annual  
229 bleaching-level thermal stress by ~2050 [9] and bleaching recovery windows only ~six years  
230 by 2016 [8], we conclude that realized and projected increases in the frequency of thermal  
231 stress events on coral reefs will cause persistent changes in fish diversity and community  
232 structure. These changes will alter the functions and ecosystem services historically provided  
233 by reef fishes, such as grazing rates [26] and the species accessible to fisheries [31]. This  
234 poses a challenge for management and reef dependent communities to adapt to these alters  
235 reef fish configurations.

236

237

## 238 **EXPERIMENTAL PROCEDURES**

239

240 **Study sites**

241 Six surveys of 21 Seychelles reef sites were conducted from 1994-2017 (one in each of the  
242 years 1994, 2005, 2008, 2011, 2014, 2017). Surveys were spatially stratified to encompass  
243 carbonate, patch, and granitic habitat types (n = 7 per habitat) in both fished (12) and  
244 protected (9) areas. All 21 sites were surveyed in each year, except 2017, when 18 sites were  
245 surveyed.

246

247 **Fish and benthic survey data**

248 Fish and benthic community surveys were conducted at each site in each year using point  
249 counts of 7 m radius. Within each point count area, one diver (NAJG or SJ) estimated  
250 individual body lengths for any diurnally active reef-associated fish on a list of 129 species  
251 and estimated to be  $\geq 8$  cm total length. Individual sizes (total length to nearest cm) were  
252 converted to biomass using published length ~ weight relationships [46]. Each species was  
253 assigned to one of six functional feeding groups (planktivore, corallivore, herbivore,  
254 invertivore, mixed-diet feeder, piscivore) based on published dietary information [46] and  
255 assigned an estimated average age to first maturity based on life history information [47]  
256 (Table S1). Following fish surveys, one diver (SW or SJ) performed visual assessments of  
257 benthic habitat composition within the point count area. Benthic composition was recorded as  
258 the percent cover (%) of macroalgae, sand, rubble and rock substrate, and three  
259 morphological types of hard coral (branching, massive, encrusting). Structural complexity  
260 was assessed on a 6-point scale ranging from flattened sites with no vertical relief (0) up to  
261 highly complex sites characterized by overhangs and caves (5) [48]. These visual cover and  
262 complexity estimates correlate closely with line transect methods and commonly-used  
263 rugosity metrics [49]. For each survey year, benthic habitat observations were averaged

264 across replicates to give site-level estimates of the percent cover of macroalgae, branching,  
265 massive, and encrusting corals, and structural complexity.

266

267 Fish and benthic point count surveys were repeated for 8 (2011, 2014, 2017) or 16  
268 (1994, 2005, 2008) replicates per site. Because species richness estimates depend on the area  
269 sampled, we ensured that temporal comparisons were valid by only analyzing data from the  
270 first 8 replicates in 1994, 2005 and 2008. By conducting surveys from a fixed species list, at  
271 similar depths, and repeating locations in space and time with equal effort (8 survey  
272 replicates per site), we minimize issues of sample incompleteness that might bias diversity  
273 estimates through a failure to detect rare species [50]. Although we did not census all resident  
274 fish species, our species list incorporates taxa that are commonly observed on Seychelles  
275 reefs [51].

276

### 277 **Temporal trends in diversity and community composition**

278 Bleaching-induced shifts in community composition were assessed by examining temporal  
279 change in 1)  $\alpha$  diversity (i.e. species richness), 2)  $\beta$  diversity (i.e. compositional  
280 dissimilarity), and 3) species biomass. First, we measured  $\alpha$  diversity by tallying the total  
281 number of species observed at each site in each year, for the full community and each  
282 functional group. Temporal richness patterns among functional groups were assessed relative  
283 to pre-bleaching assemblages where, by estimating the difference between observed richness  
284 and 1994 richness for each site in 2005-2017, we examined how different functional groups  
285 responded to bleaching and subsequent habitat changes, and how those groups contributed to  
286 overall richness patterns. Although sampling effort was standardized across the time series,  
287 richness estimates may have been sensitive to spatial and temporal variation in abundances  
288 [52].

289 Shifts in community composition were described with  $\beta$  diversity metrics. We  
290 generated species  $\times$  site matrices with mean biomass ( $\text{kg ha}^{-1}$ ) estimates, that were averaged  
291 across replicates at each site in each year ( $n = 6$  community matrices, each with dimensions  
292  $129$  species  $\times$   $21$  sites). From these matrices, we calculated  $\beta$  diversity using the Bray-Curtis  
293 index ( $\beta_{BC}$ ) [53] for pairwise comparisons between sites across survey years (temporal) or  
294 among sites in each survey year (spatial).  $\beta_{BC}$  is bounded by  $0$  (perfect similarity) and  $1$   
295 (perfect dissimilarity), and quantifies biomass ( $x$ ) differences of each species  $i$  at site  $k$   
296 between years  $a$  and  $b$ , relative to overall biomass:

$$297 \quad \beta_{BC} = \frac{\sum_i (x_{ika} - x_{ikb})}{\sum_i (x_{ia} + x_{ib})} \quad (1)$$

298 We used  $\beta_{BC}$  to quantify temporal shifts in community composition in three ways.  
299 First, we quantified compositional turnover relative to pre-bleaching compositions by  
300 expressing  $\beta_{BC}$  as the site-level difference in species biomass between each survey year and  
301  $1994$ , thus giving estimates for each of the  $21$  sites ( $k$ ) in each post-bleaching survey year  
302 (e.g.  $\beta_{k,2014}$  = pairwise comparison between  $k_{2014}$  and  $k_{1994}$ ). This approach, hereafter  $\beta_{1994}$ ,  
303 enabled us to measure the dissimilarity between pre and post-bleaching communities, and to  
304 assess the degree of recovery to pre-bleaching community compositions. Second, we  
305 quantified turnover between survey years by expressing  $\beta_{BC}$  as the site-level difference in  
306 species biomass between successive survey years, thus giving estimates at  $21$  sites for five  
307 temporal comparisons (e.g.  $\beta_{k,2014}$  = pairwise comparison between  $k_{2014}$  and  $k_{2011}$ ). This  
308 approach, hereafter  $\beta_{seq}$ , was used to assess changes in composition between survey years.  
309 Third, we quantified temporal trends in spatial  $\beta$  diversity by estimating  $\beta_{BC}$  for pairwise site  
310 combinations among either recovering or regime-shifted reefs, separately for each survey  
311 year (e.g.  $\beta_{1,2\_2014}$  = pairwise comparison between recovering sites  $1$  and  $2$  in  $2014$ ). Site-level  
312 dissimilarity values were the mean  $\beta_{BC}$  across all pairwise site comparisons in each year. This

313 approach, hereafter  $\beta_{\text{spatial}}$ , enabled us to assess changes in spatial similarity of community  
314 compositions through time, separately for recovering and shifted reefs. Null and alternative  $\beta$   
315 metrics indicated that temporal  $\beta$  diversity patterns were robust to potential sampling biases  
316 and richness gradients (Supplementary Methods).

317 To complement our assessment of temporal  $\beta$  diversity trends, we sought to identify  
318 which functional groups and species accounted for compositional differences between pre-  
319 and post-bleaching assemblages. We defined pre- and post-bleaching assemblages as those  
320 surveyed in 1994 and 2014, respectively, thereby incorporating potential reorganization of  
321 fish communities following the 1998 bleaching event while excluding any additional impacts  
322 of the 2016 bleaching event. For  $\beta_{\text{BC}}$  values generated by pairwise comparison of sites in  
323 1994 and 2014, we measured each species' contribution to compositional dissimilarity with a  
324 SIMilarity PERcentage analysis (SIMPER) [54]. The percentage contribution to  $\beta_{\text{BC}}$  was the  
325 absolute difference in biomass between 1994 and 2014 for each species  $i$  at each site  $k$ ,  $x_{ik,1994}$   
326  $- x_{ik,2014}$ . Compositional shifts were reported by summing SIMPER percentages across  
327 functional groups, grouping species by the direction of biomass change (increased vs.  
328 decreased), for either recovering or regime-shifted reefs. Finally, we characterized species-  
329 level biomass changes by calculating the difference in biomass of each species before  
330 bleaching (1994) and after recovery (2014) in each reef regime.

331

### 332 **Statistical modelling**

333 We utilized Bayesian hierarchical models to compare temporal changes in fish community  
334 composition between recovering and regime-shifted reefs. For diversity metrics, models were  
335 fitted to predict variation in overall species richness (Model 1, M1), functional group richness  
336 (M2 fitted separately to 6 functional groups),  $\beta_{1994}$  (M3), and  $\beta_{\text{seq}}$  (M4) (Tables S2, S3). After  
337 identifying appropriate temporal structures, we hypothesized that site-specific benthic

338 recovery rates and fishery access would predict temporal change in overall fish community  
339 diversity. Diversity models ( $\alpha$ ,  $\beta$  metrics) were fitted with management status (no-take or  
340 fished), branching coral, encrusting coral, massive coral and macroalgae (% cover), and  
341 structural complexity as explanatory covariates. For species-level biomass differences  
342 between 1994 and 2014, we modelled the same fixed effects used in diversity models, and as  
343 well as mean observed species size (cm; fixed term) and functional feeding group (random  
344 terms for recovering and regime-shifted reefs) (M5). Model fitting procedures are described  
345 in full in the Supplementary Methods. Temporal trends in  $\beta_{\text{spatial}}$ , which were pairwise site  
346 comparisons and thus not independent samples, were visualized but not modelled.  
347 All analyses were conducted in R [55].  $\beta$  metrics were estimated using *beta.temp* function in  
348 *betapart* [56], SIMPER analyses were run in *vegan* [57], and Bayesian hierarchical models  
349 were implemented in Stan using *rethinking* [58] following [59]. We archive our R code and  
350 model outputs at an open source repository ([github.com/jpwrobinson/beta-bleaching](https://github.com/jpwrobinson/beta-bleaching)).

351

### 352 **Acknowledgements**

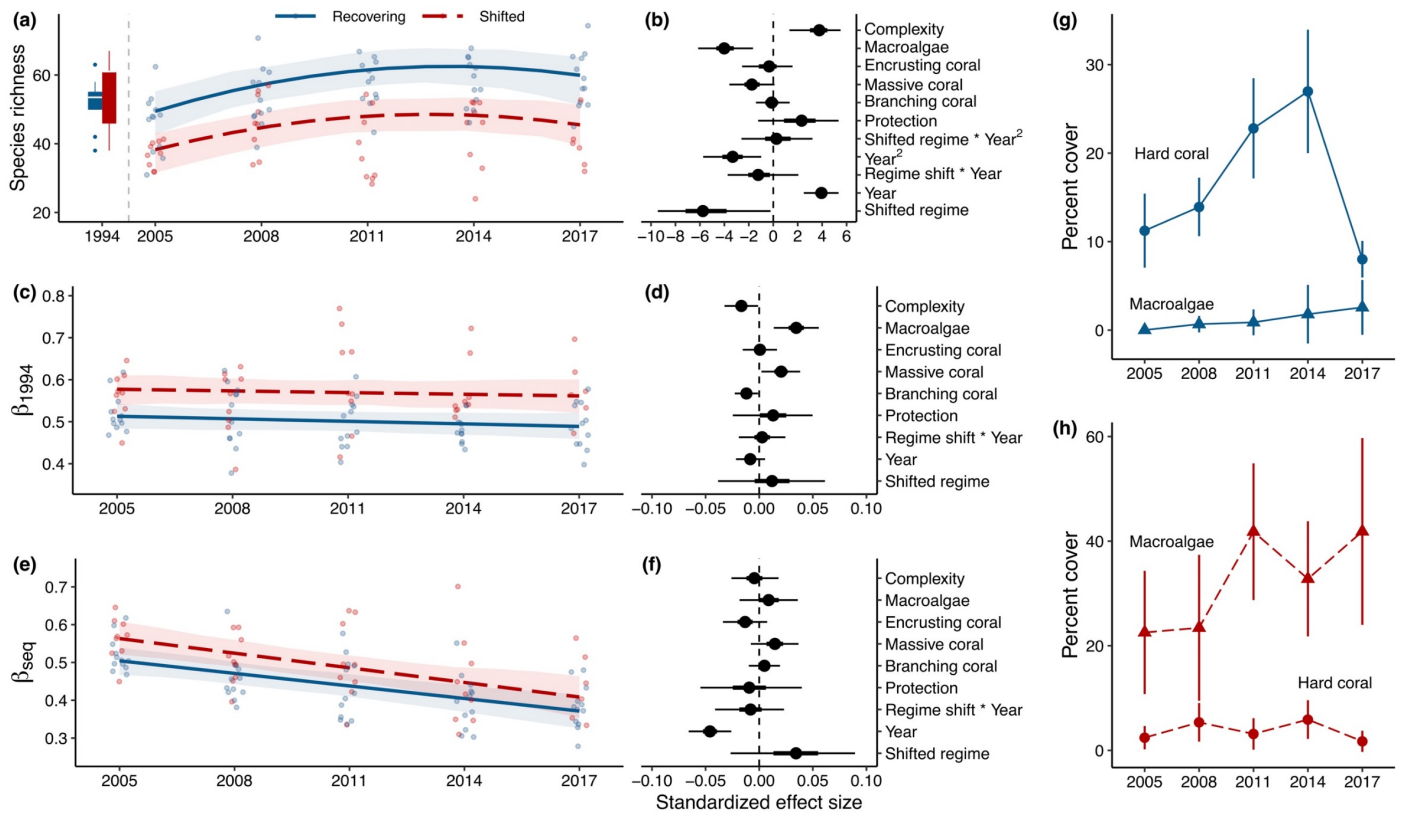
353 This research was supported by the Royal Society (CH160077, UF140691). We thank  
354 Seychelles Fishing Authority, Nature Seychelles, and Global Vision International for field  
355 assistance, and Cameron Freshwater for statistical advice.

356

### 357 **Author contributions**

358 NAJG conceived the study. NAJG, SW and SJ conducted ecological surveys. JPWR  
359 performed all statistical analyses and led the manuscript writing, with substantial input from  
360 SW, SJ and NAJG.

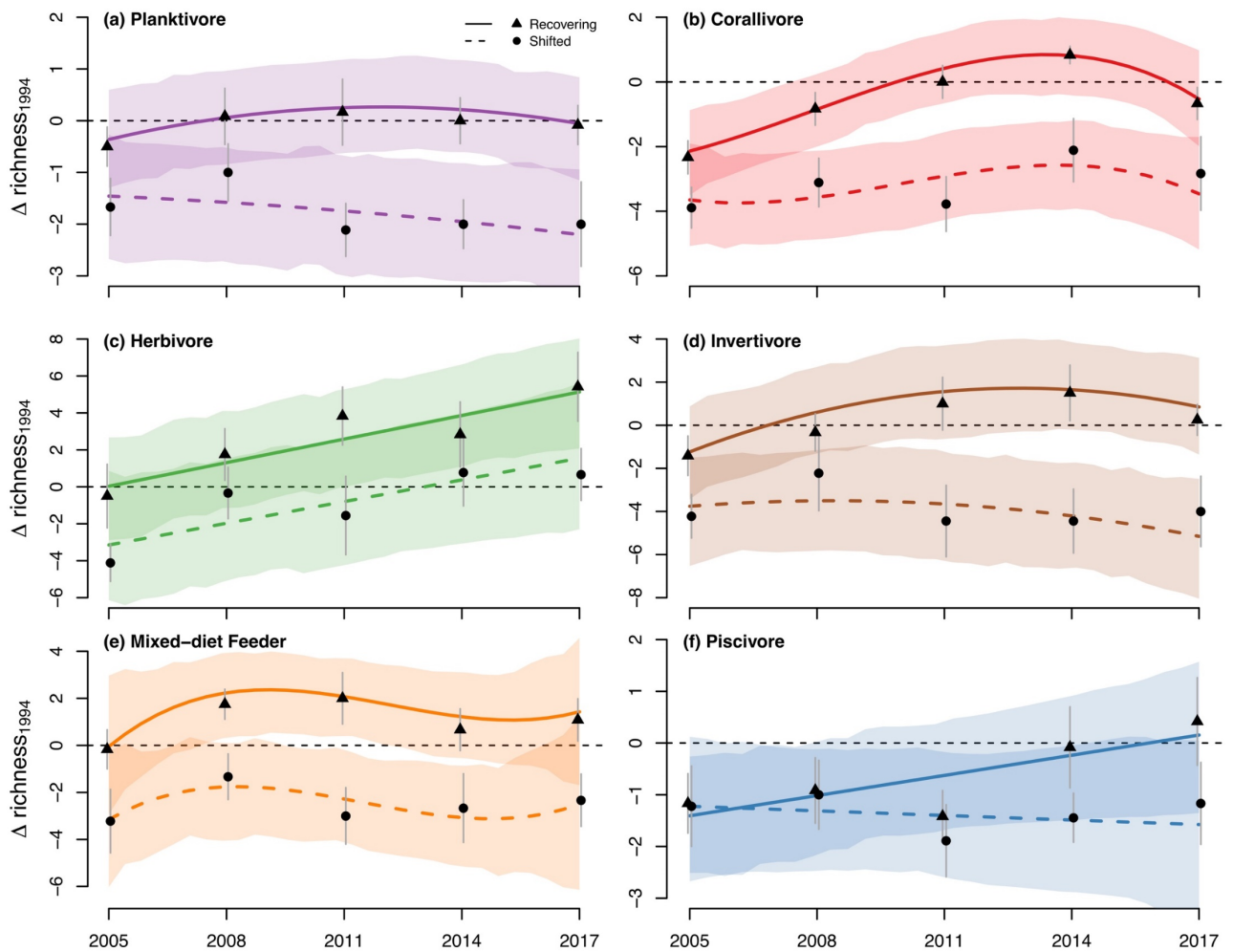
361 **Figure captions**



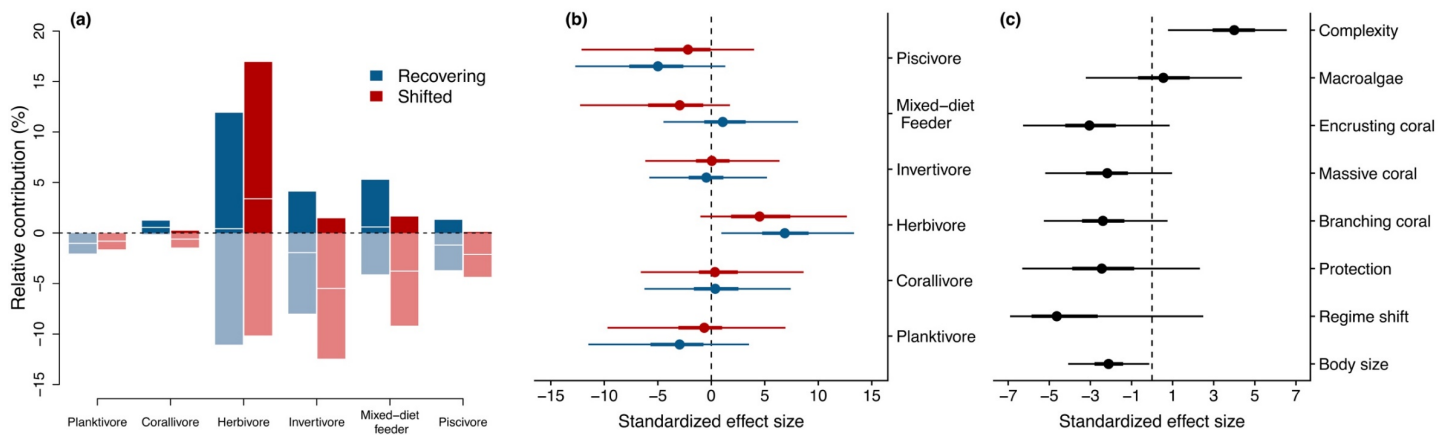
362 **Figure 1. Temporal change in fish assemblage diversity from 2005-2017.** (A) Species  
 363 richness with (B) posterior parameter estimates, (C)  $\beta_{1994}$  with (D) posterior parameter  
 364 estimates, and (E)  $\beta_{seq}$  with (F) posterior parameter estimates. Temporal trend lines (a,c,e)  
 365 were generated from mean posterior predictions through time, conditioned on mean post-  
 366 bleaching benthic cover and complexity for recovering (blue solid line) and regime-shifted  
 367 (red dashed line) sites, with 95% highest posterior density intervals. Observed site-level  
 368 values are displayed as points jittered for each survey year, and baseline 1994 species  
 369 richness included as boxplots in (a). Posterior parameter estimates indicate mean (point),  
 370 95% (thick line) and 50% (thin line) credible intervals generated from a posterior distribution  
 371 of 1,000 samples for each explanatory covariate. (G-H) Temporal change in cover of hard  
 372 coral (blue) and macroalgae (red) on recovering (G) and regime-shifted (H) reefs, with points  
 373 indicating site-level mean percent cover ( $\pm 2$  standard errors). See also Figure S1 which



374 shows  $\beta_{\text{spatial}}$  temporal trends, Figure S2 which shows incidence-based and null model-based  
 375  $\beta$  estimates, and Tables S2 and S3 which show Bayesian model structures and priors.  
 376



377  
 378 **Figure 2. Change in species richness in each year relative to 1994 for functional feeding**  
 379 **groups.** Panels show (A) planktivores, (B) corallivores, (C) herbivores, (D) invertivores, (E)  
 380 mixed-diet feeders, and (F) piscivores. Lines are mean posterior predictions over time  
 381 generated from top-ranked linear or non-linear temporal models for recovering (solid) and  
 382 regime-shifted reefs (dashed), shaded with 95% highest posterior density intervals and  
 383 overlaid with mean observed richness change ( $\pm 2$  standard errors). See also Table S1 which  
 384 shows species in functional feeding groups and average age to maturity, and Tables S2-S4  
 385 which show Bayesian model structures, priors, and model selection on temporal structures.

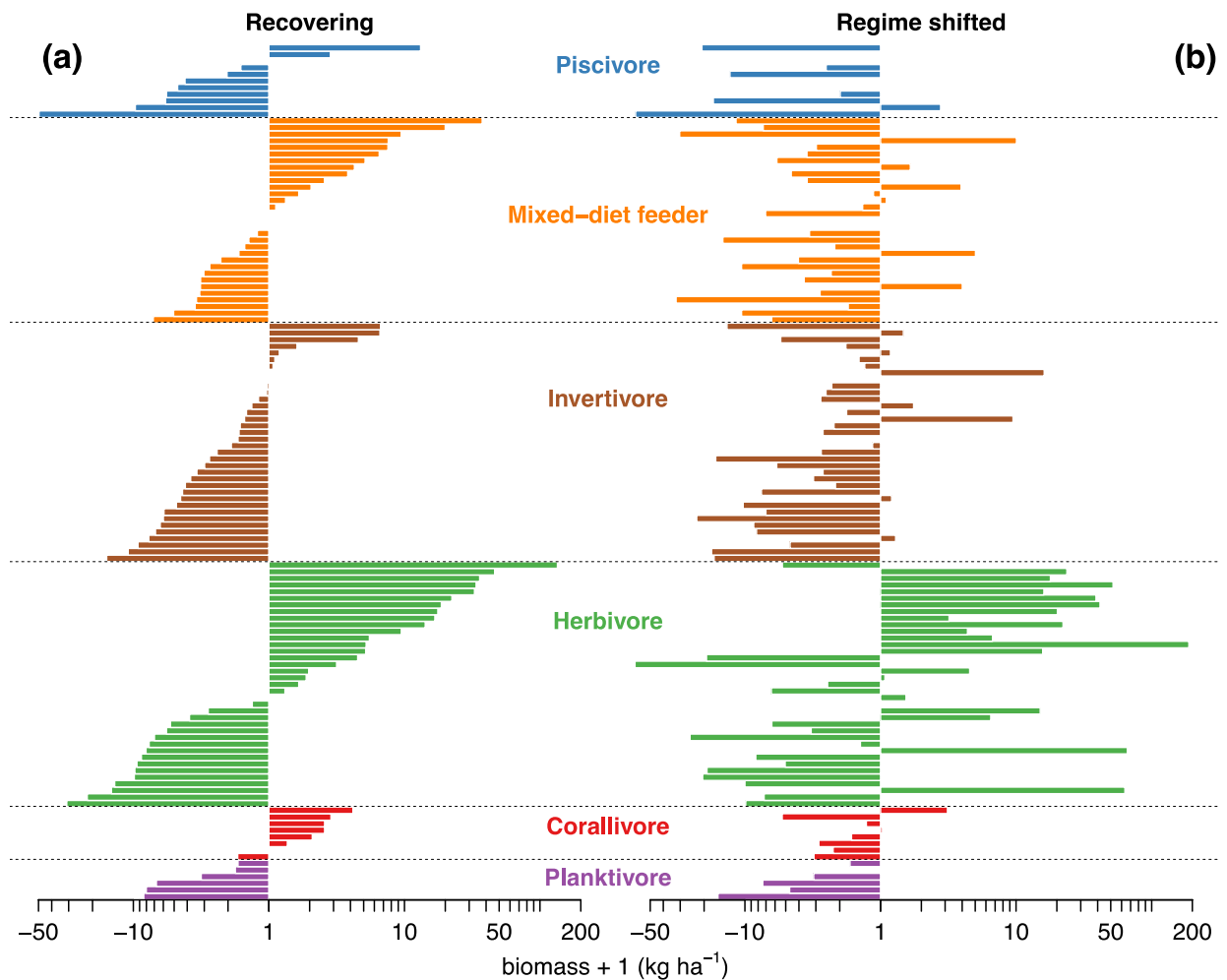


387

### 388 **Figure 3. Biomass composition of fish assemblages on recovering and regime-shifted**

389 **reefs.** (A) SIMPER analysis of species contributions to  $\beta_{BC}$  dissimilarity between 1994 and  
 390 2014 for recovering (blue) and regime-shifted (red) sites. Bars are species-level contributions  
 391 summed by functional feeding group for species that increased (positive  $y$  values, solid color)  
 392 or decreased (negative  $y$ , shaded color) in biomass from 1994 to 2014, where overall  $\beta_{BC}$  was  
 393 0.53 at recovering sites and 0.60 at regime-shifted sites. White lines indicate net change in  
 394 biomass. (B-C) Bayesian model predictions of species-level biomass change from 1994 to  
 395 2014 showing (B) the predicted change in biomass by functional group and (C) effect of  
 396 fixed explanatory covariates on biomass change. Posterior parameter estimates indicate mean  
 397 (point), 95% (thick line) and 50% (thin line) credible intervals, of 1,000 samples of the  
 398 posterior distribution for each functional feeding group on recovering (red) and regime-  
 399 shifted reefs (blue), and each fixed explanatory covariate (black). See also Tables S2 and S3  
 400 for Bayesian model structures and priors.

401



402 **Figure 4. Change in species biomass between pre- and post-bleaching fish assemblages**  
 403 **on recovering and regime-shifted reefs.** Bars are the mean biomass difference ( $\text{kg ha}^{-1}$ )  
 404 from 1994 to 2014 for each species, on a  $\log_{10}$  scale and colored by functional feeding group.  
 405 Bars directed right indicate that biomass increased from 1994 to 2014 and bars directed left  
 406 indicate that biomass decreased from 1994 to 2014. (A) Recovering reef species are ordered  
 407 by biomass change, descending from the largest increase (bars directed right) to the largest  
 408 decrease (bars directed left). (B) Regime-shifted reef species, ordered to correspond with  
 409 species order on recovering reefs. Missing bars indicate species that were not observed in a  
 410 given year and reef state. Across all reefs, three species were not observed in either 1994 or  
 411 2014 (*Diagramma pictum*, *Epinephelus tukula*, *Lethrinus rubrioperculatus*). See also Figures  
 412 S3 and S4 for species names and relative biomass changes on each reef habitat type.

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