

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 (α diversity) and composition (β 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 α 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 α diversity increased from 46 species (± 2.47 S.E.) in 2005 to exceed pre-
62 bleaching levels by ~eight species in 2017 (58.5 ± 3.00). Although both reef states supported
63 similar levels of richness prior to bleaching (1994 richness: recovering = 52.1 ± 1.92 ; regime-
64 shifted = 55.3 ± 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 (± 2.80) in 2008 (Figure 1A). Most strikingly, temporal trends in β 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 α and β
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 (β_{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 ± 0.01 on recovering reefs),
93 and β_{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. β_{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 β_{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 β_{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 β_{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 β_{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 β_{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 ≥ 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) α diversity (i.e. species richness), 2) β diversity (i.e. compositional
280 dissimilarity), and 3) species biomass. First, we measured α 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 β diversity metrics. We
290 generated species \times site matrices with mean biomass (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 β diversity using the Bray-Curtis
293 index (β_{BC}) [53] for pairwise comparisons between sites across survey years (temporal) or
294 among sites in each survey year (spatial). β_{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 β_{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 β_{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 β_{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 β_{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 β_{seq} , was used to assess changes in composition between survey years.
309 Third, we quantified temporal trends in spatial β diversity by estimating β_{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 β_{BC} across all pairwise site comparisons in each year. This

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

317 To complement our assessment of temporal β 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 β_{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 β_{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), β_{1994} (M3), and β_{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 (α , β 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 β_{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]. β 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).

351

352 **Acknowledgements**

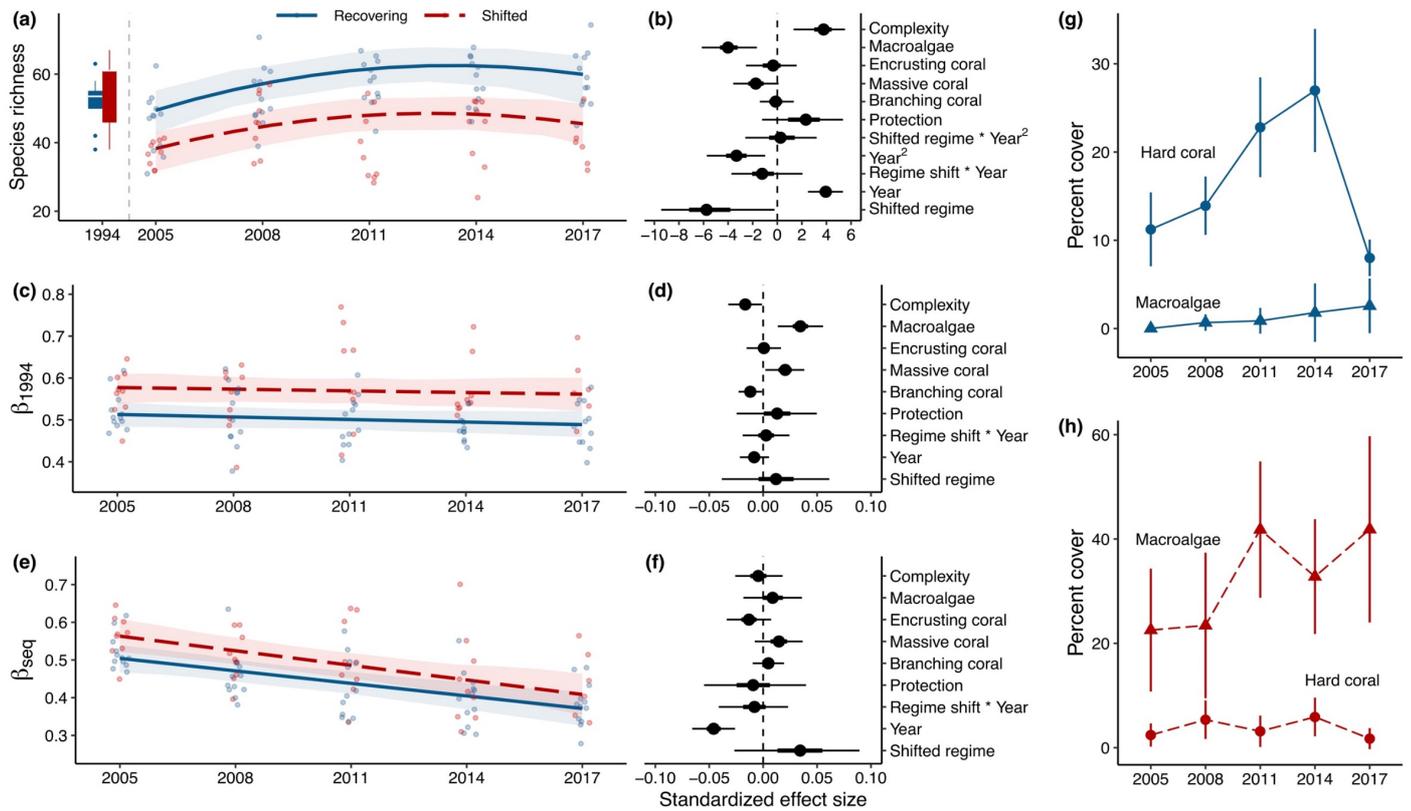
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354 Seychelles Fishing Authority, Nature Seychelles, and Global Vision International for field
355 assistance, and Cameron Freshwater for statistical advice.

356

357 **Author contributions**

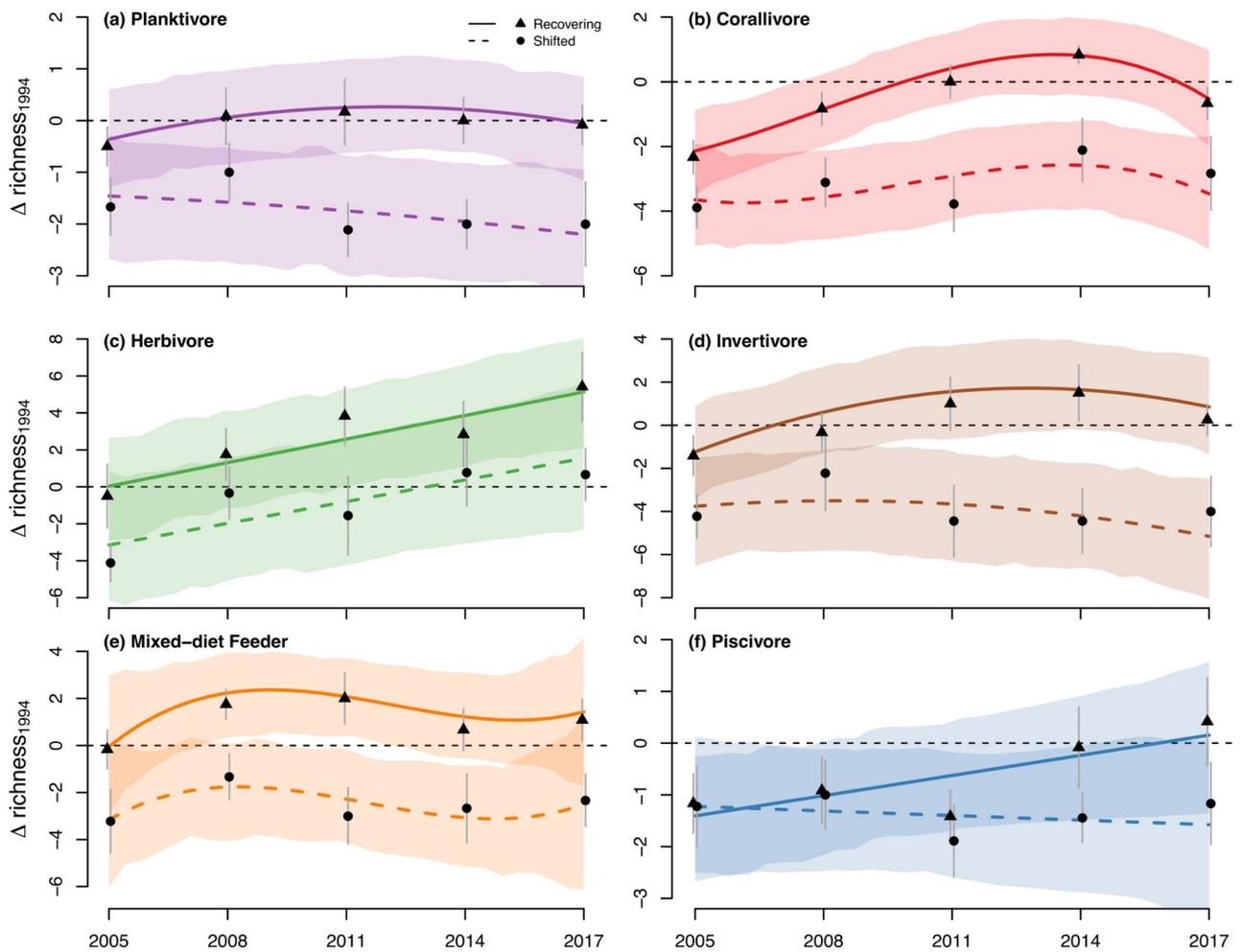
358 NAJG conceived the study. NAJG, SW and SJ conducted ecological surveys. JPWR
359 performed all statistical analyses and led the manuscript writing, with substantial input from
360 SW, SJ and NAJG.

361 **Figure captions**

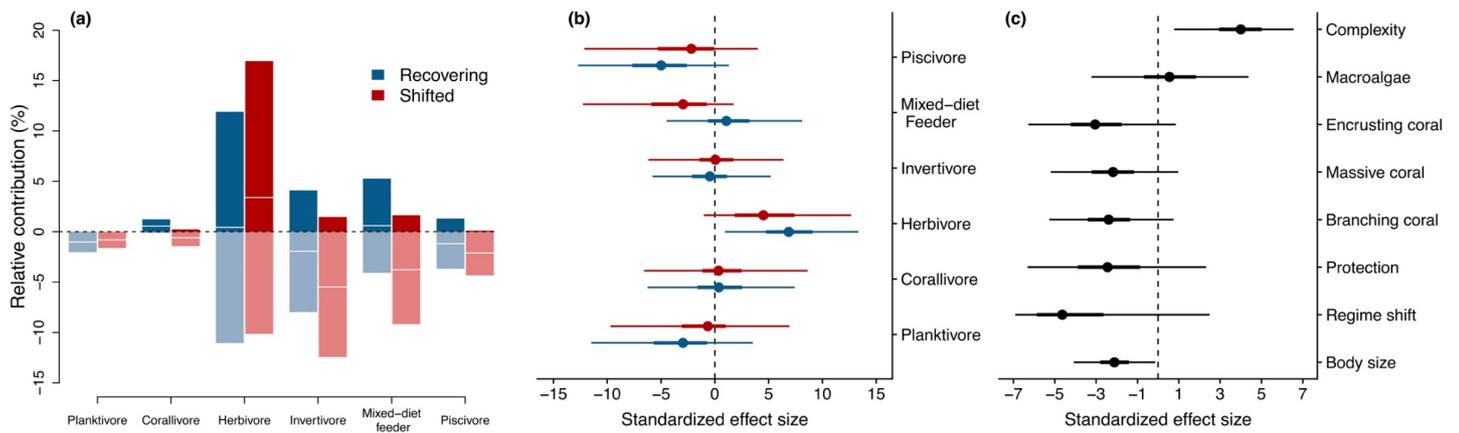


362 **Figure 1. Temporal change in fish assemblage diversity from 2005-2017.** (A) Species
 363 richness with (B) posterior parameter estimates, (C) β_{1994} with (D) posterior parameter
 364 estimates, and (E) β_{seq} with (F) posterior parameter estimates. Temporal trend lines (a,c,e)
 365 were generated 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 (± 2 standard errors). See also Figure S1 which

374 shows β_{spatial} temporal trends, Figure S2 which shows incidence-based and null model-based
 375 β 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 (± 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.

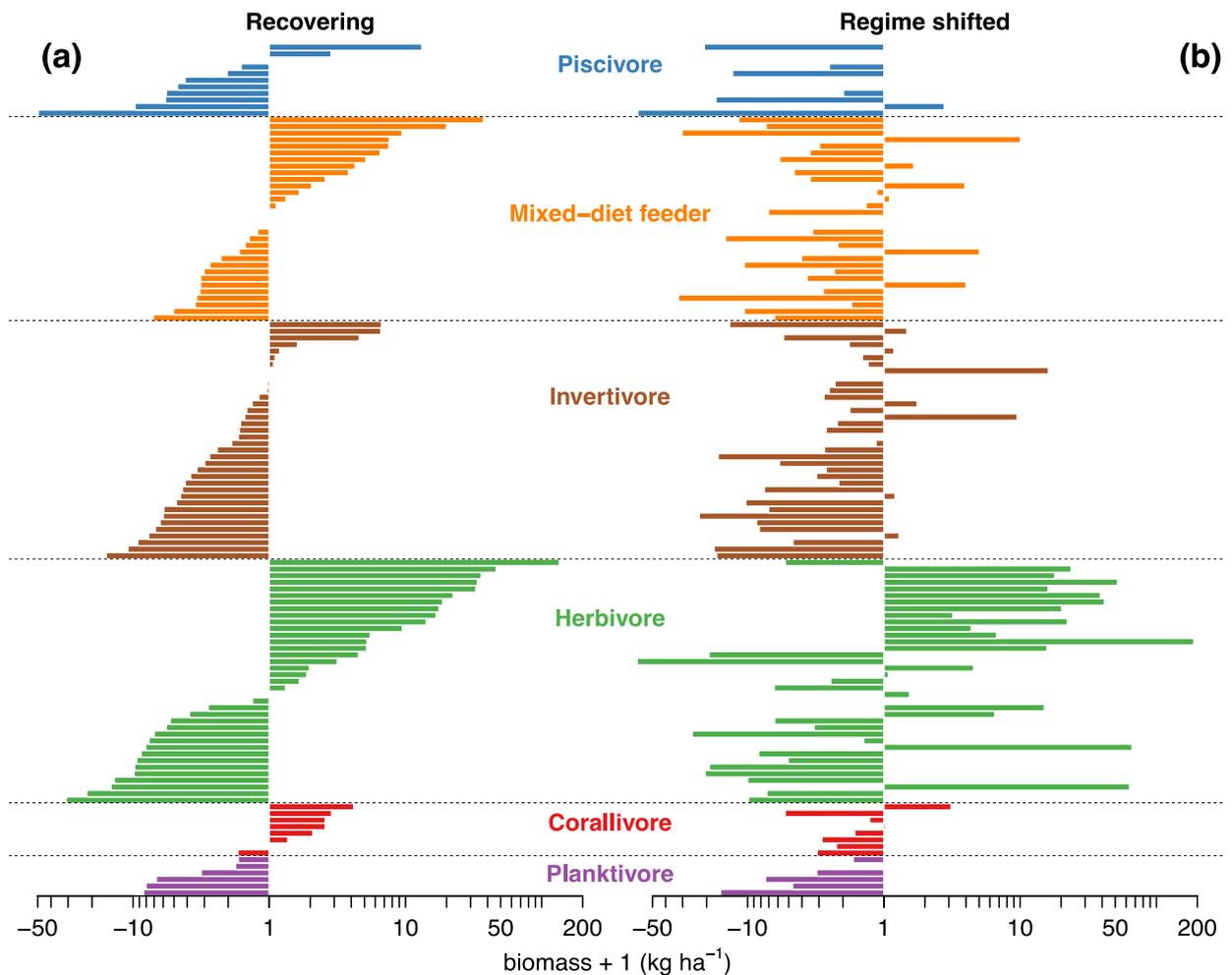


387

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

389 **reefs.** (A) SIMPER analysis of species contributions to β_{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 β_{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 (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.

413

414 **REFERENCES**

415 1. Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001). Catastrophic shifts
416 in ecosystems. *Nature*, 413, 591–596.

417

418 2. Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., *et al.* (2014).
419 Assemblage time series reveal biodiversity change but not systematic loss. *Science*, 344,
420 296–299.

421

422 3. Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., *et al.*
423 (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human
424 well-being. *Science*, 355, eaai9214.

425

426 4. Wilson, S.K., Graham, N.A.J., Pratchett, M.S., Jones, G.P. & Polunin, N.V.C. (2006).
427 Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or
428 resilient? *Glob. Chang. Biol.*, 12, 2220–2234.

429

430 5. Graham, N.A.J., Cinner, J.E., Norström, A.V., and Nyström, M. (2014). Coral reefs as
431 novel ecosystems: embracing new futures. *Current Opinion in Environmental Sustainability*
432 7, 9–14.

433

434 6. Hobbs, R.J., Higgs, E. & Harris, J.A. (2009). Novel ecosystems: implications for
435 conservation and restoration. *Trends Ecol. Evol.*, 24, 599–605.

436

- 437 7. Graham, N.A.J., Jennings, S., MacNeil, M.A., Mouillot, D. & Wilson, S.K. (2015).
438 Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, 518,
439 94–97.
440
- 441 8. Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., *et al.*
442 (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene.
443 *Science*, 359, 80–83.
444
- 445 9. van Hooidonk, R., Maynard, J.A. & Planes, S. (2013). Temporary refugia for coral reefs in
446 a warming world. *Nat. Clim. Chang.*, 3, 508.
447
- 448 10. Messmer V, Jones GP, Munday PL, Holbrook SJ, Schmitt RJ, Brooks AJ (2011) Habitat
449 biodiversity as a determinant of fish community structure on coral reefs. *Ecology*, 92, 2285–
450 2298.
451
- 452 11. Halford, A.R. & Caley, M.J. (2009). Towards an understanding of resilience in isolated
453 coral reefs. *Glob. Chang. Biol.*, 15, 3031–3045.
454
- 455 12. Richardson, L.E., Graham, N.A.J., Pratchett, M.S., Eurich, J.G. & Hoey, A.S. (2018).
456 Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Glob. Chang.*
457 *Biol.*, 99, 1134.
458
- 459 13. Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Bijoux, J.P. & Robinson, J.
460 (2006). Dynamic fragility of oceanic coral reef ecosystems. *Proc. Natl. Acad. Sci. USA*, 103,
461 8425–8429.

462

463 14. Bellwood, D.R., Baird, A.H., Depczynski, M., González-Cabello, A., Hoey, A.S.,
464 Lefèvre, C.D., *et al.* (2012). Coral recovery may not herald the return of fishes on damaged
465 coral reefs. *Oecologia*, 170, 567–573.

466

467 15. Wilson, S.K., Graham, N.A.J., Fisher, R., Robinson, J., Nash, K., Chong-Seng, K., *et al.*
468 (2012). Effect of macroalgal expansion and marine protected areas on coral recovery
469 following a climatic disturbance. *Conserv. Biol.*, 26, 995–1004.

470

471 16. Munday, P.L. & Jones, G.P. (1998). The ecological implications of small body size
472 among coral reef fishes. *Ocean Coast. Manag.*, 36, 373–411.

473

474 17. Darling, E.S., Graham, N.A.J., Januchowski-Hartley, F.A., Nash, K.L., Pratchett, M.S. &
475 Wilson, S.K. (2017). Relationships between structural complexity, coral traits, and reef fish
476 assemblages. *Coral Reefs*, 36, 561–575.

477

478 18. Richardson, L.E., Graham, N.A.J. & Hoey, A.S. (2017). Cross-scale habitat structure
479 driven by coral species composition on tropical reefs. *Sci. Rep.*, 7, 7557.

480

481 19. Berumen, M.L. & Pratchett, M.S. (2006). Recovery without resilience: persistent
482 disturbance and long-term shifts in the structure of fish and coral communities at Tiahura
483 Reef, Moorea. *Coral Reefs*, 25, 647–653.

484

- 485 20. Mellin, C., Aaron MacNeil, M., Cheal, A.J., Emslie, M.J. & Julian Caley, M. (2016).
486 Marine protected areas increase resilience among coral reef communities. *Ecol. Lett.*, 19,
487 629–637.
488
- 489 21. Hempson, T.N., Graham, N.A.J., MacNeil, M.A., Hoey, A.S. & Wilson, S.K. (2018).
490 Ecosystem regime shifts disrupt trophic structure. *Ecol. Appl.*, 28, 191–200.
491
- 492 22. Fulton, C.J., Depczynski, M., Holmes, T.H., Noble, M.M., Radford, B., Wernberg, T., *et*
493 *al.* (2014). Sea temperature shapes seasonal fluctuations in seaweed biomass within the
494 Ningaloo coral reef ecosystem. *Limnol. Oceanogr.*, 59, 156–166.
495
- 496 23. Wilson, S.K., Depczynski, M., Fisher, R., Holmes, T.H., Noble, M.M., Radford, B.T., *et*
497 *al.* (2018). Climatic forcing and larval dispersal capabilities shape the replenishment of fishes
498 and their habitat-forming biota on a tropical coral reef. *Ecol. Evol.*, 8, 1918–1928.
499
- 500 24. Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J.E., Bender,
501 M., *et al.* (2014). Functional over-redundancy and high functional vulnerability in global fish
502 faunas on tropical reefs. *Proc. Natl. Acad. Sci. USA*, 111, 13757–13762.
503
- 504 25. D’agata, S., Mouillot, D., Wantiez, L., Friedlander, A.M., Kulbicki, M. & Vigliola, L.
505 (2016). Marine reserves lag behind wilderness in the conservation of key functional roles.
506 *Nat. Commun.*, 7, 12000.
507

- 508 26. Nash, K. L., Graham, N. A. J., Jennings, S., Wilson, S. K. & Bellwood, D.R. (2016).
509 Herbivore cross-scale redundancy supports response diversity and promotes coral reef
510 resilience. *J. Appl. Ecol.*, 53, 646–655.
511
- 512 27. Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Robinson, J., Bijoux, J.P.,
513 *et al.* (2007). Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries,
514 and ecosystems. *Conserv. Biol.*, 21, 1291–1300.
515
- 516 28. Karkarey, R., Kelkar, N., Lobo, A.S., Alcoverro, T. & Arthur, R. (2014). Long-lived
517 groupers require structurally stable reefs in the face of repeated climate change disturbances.
518 *Coral Reefs*, 33, 289–302.
519
- 520 29. Cheal, A.J., Wilson, S.K., Emslie, M.J., Dolman, A.M. & Sweatman, H. (2008).
521 Responses of reef fish communities to coral declines on the Great Barrier Reef. *Mar. Ecol.*
522 *Prog. Ser.*, 372, 211–223.
523
- 524 30. Pratchett, M.S., Hoey, A.S., Wilson, S.K., Messmer, V. & Graham, N.A.J. (2011).
525 Changes in biodiversity and functioning of reef fish assemblages following coral bleaching
526 and coral loss. *Diversity*, 3, 424–452.
527
- 528 31. Robinson, J.P.W., Wilson, S.K., Robinson, J., Lucas, J., Assan, C., Gerry, C., Govinden,
529 R., Jennings, S., Graham, N.A.J. (2018). Productive instability of coral reef fisheries after
530 climate-driven regime shifts. *Nat. Ecol. Evol.*, DOI: 10.1038/s41559-018-0715-z
531

- 532 32. Garpe, K.C., Yahya, S.A.S., Lindahl, U. & Ohman, M.C. (2006). Long-term effects of the
533 1998 coral bleaching event on reef fish assemblages. *Mar. Ecol. Prog. Ser.*, 315, 237–247.
534
- 535 33. Russ, G.R., Questel, S.-L.A., Rizzari, J.R. & Alcala, A.C. (2015). The parrotfish–coral
536 relationship: refuting the ubiquity of a prevailing paradigm. *Mar. Biol.*, 162, 2029–2045.
537
- 538 34. Jones, G.P., McCormick, M.I., Srinivasan, M. & Eagle, J.V. (2004). Coral decline
539 threatens fish biodiversity in marine reserves. *Proc. Natl. Acad. Sci. USA*, 101, 8251–8253.
540
- 541 35. Green, A.L., Maypa, A.P., Almany, G.R., Rhodes, K.L., Weeks, R., Abesamis, R.A., *et*
542 *al.* (2015). Larval dispersal and movement patterns of coral reef fishes, and implications for
543 marine reserve network design. *Biol. Rev.*, 90, 1215–1247.
544
- 545 36. Cole AJ, Pratchett MS, Jones GP (2008) Diversity and functional importance of coral-
546 feeding fishes on tropical coral reefs. *Fish Fish.*, 9, 286–307.
547
- 548 37. Williams, I.D., White, D.J., Sparks, R.T., Lino, K.C., Zamzow, J.P., Kelly, E.L.A., *et al.*
549 (2016). Responses of herbivorous fishes and benthos to 6 years of protection at the Kahekili
550 Herbivore Fisheries Management Area, Maui. *PLoS One*, 11, e0159100.
551
- 552 38. Selig, E.R., Casey, K.S. & Bruno, J.F. (2012). Temperature-driven coral decline: the role
553 of marine protected areas. *Glob. Chang. Biol.*, 18, 1561–1750.
554

- 555 39. Graham, N.A.J., McClanahan, T.R., MacNeil, M.A., Wilson, S.K., Polunin, N.V.C.,
556 Jennings, S., *et al.* (2008). Climate warming, marine protected areas and the ocean-scale
557 integrity of coral reef ecosystems. *PLoS One*, 3, e3039.
- 558
- 559 40. Williams, J.W. & Jackson, S.T. (2007). Novel climates, no-analog communities, and
560 ecological surprises. *Front. Ecol. Environ.*, 5, 475–482.
- 561
- 562 41. Rogers, A., Blanchard, J.L. & Mumby, P.J. (2017). Fisheries productivity under
563 progressive coral reef degradation. *J. Appl. Ecol.*, 55, 1041–1049.
- 564
- 565 42. Gilmour, J.P., Smith, L.D., Heyward, A.J., Baird, A.H. & Pratchett, M.S. (2013).
566 Recovery of an isolated coral reef system following severe disturbance. *Science*, 340, 69–71.
- 567
- 568 43. Rummer, J.L., Couturier, C.S., Stecyk, J.A.W., Gardiner, N.M., Kinch, J.P., Nilsson,
569 G.E., *et al.* (2014). Life on the edge: thermal optima for aerobic scope of equatorial reef
570 fishes are close to current day temperatures. *Glob. Chang. Biol.*, 20, 1055–1066.
- 571
- 572 44. Wernberg, T., Bennett, S., Babcock, R.C., de Bettignies, T., Cure, K., Depczynski, M., *et*
573 *al.* (2016). Climate-driven regime shift of a temperate marine ecosystem. *Science*, 353, 169–
574 172.
- 575
- 576 45. Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R.B., Aschan, M.M. &
577 Dolgov, A.V. (2015). Recent warming leads to a rapid borealization of fish communities in
578 the Arctic. *Nat. Clim. Chang.*, 5, 673–677.
- 579

- 580 46. Froese, R. & Pauly, D. (2018). *FishBase* (www.fishbase.org).
- 581
- 582 47. Thorson, J.T., Munch, S.B., Cope, J.M. & Gao, J. (2017). Predicting life history
583 parameters for all fishes worldwide. *Ecol. Appl.*, 27, 2262–2276.
- 584
- 585 48. Polunin, N.V.C. & Roberts, C.M. (1993). Greater biomass and value of target coral-reef
586 fishes in two small Caribbean marine reserves. *Mar. Ecol. Prog. Ser.*, 100, 167–167.
- 587
- 588 49. Wilson, S.K., Graham, N.A.J. & Polunin, N.V.C. (2007). Appraisal of visual assessments
589 of habitat complexity and benthic composition on coral reefs. *Mar. Biol.*, 151, 1069–1076.
- 590
- 591 50. Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.-J. (2005). A new statistical approach
592 for assessing similarity of species composition with incidence and abundance data. *Ecol.*
593 *Lett.*, 8, 148–159.
- 594
- 595 51. Chong-Seng, K.M., Mannering, T.D., Pratchett, M.S., Bellwood, D.R. & Graham, N.A.J.
596 (2012). The influence of coral reef benthic condition on associated fish assemblages. *PLoS*
597 *One*, 7, e42167.
- 598
- 599 52. Gotelli, N.J. & Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in
600 the measurement and comparison of species richness. *Ecol. Lett.*, 4, 379–391.
- 601
- 602 53. Bray, J.R. & Curtis, J.T. (1957). An ordination of the upland forest communities of
603 southern Wisconsin. *Ecol. Monogr.*, 27, 325-349.
- 604

605 54. Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community
606 structure. *Austral Ecol.*, 18, 117–143.
607

608 55. R Development Core Team (2018). R: A language and environment for statistical
609 computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0,
610 <http://www.R-project.org>.
611

612 56. Baselga, A. & Orme, C.D.L. (2012). betapart: an R package for the study of beta
613 diversity. *Methods Ecol. Evol.*, 3, 808–812.
614

615 57. Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D.,
616 *et al.* (2017). vegan: Community Ecology Package. *R package*, Version 2.4-4.
617

618 58. McElreath, R. (2017). Rethinking: statistical Rethinking book package. *R package*
619 *version*, 1.
620

621 59. Freshwater, C., Trudel, M., Beacham, T.D., Gauthier, S., Johnson, S.C., Neville, C.-E., *et*
622 *al.* (2018). Individual variation, population-specific behaviours, and stochastic processes
623 shape marine migration phenologies. *J. Anim. Ecol.*, doi: 10.1111/1365-2656.12852
624
625