

Collapsing ecosystem functions on an inshore coral reef

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27 **Abstract**

28 Ecosystem functions underpin productivity and key services to humans, such as food
29 provision. However, as the severity of environmental stressors intensifies, it is becoming
30 increasingly unclear if, and to what extent, critical functions and services can be sustained.
31 This issue is epitomised on coral reefs, an ecosystem at the forefront of environmental
32 transitions. We provide a functional profile of a coral reef ecosystem, linking time-series data
33 to quantified processes. The data reveal a prolonged collapse of ecosystem functions in this
34 previously resilient system. The results suggest that sediment accumulation in algal turfs has
35 led to a decline in resource yields to herbivorous fishes and a decrease in fish-based
36 ecosystem functions, including a collapse of both fish biomass and productivity.
37 Unfortunately, at present, algal turf sediment accumulation is rarely monitored nor managed
38 in coral reef systems. Our examination of functions through time highlights the value of
39 directly assessing functions, their potential vulnerability, and the capacity of algal turf
40 sediments to overwhelm productive high-diversity coral reef ecosystems.

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42 **Key words:**

43 Algae; Ecosystem management; Ecosystem process; Herbivory; Productivity; Sediment

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49 **Introduction**

50 Ecosystems are characterised by a dynamic suite of functions or processes that
51 maintain equilibrium states (Holling 1973; Scheffer et al. 2001) and sustain the services upon
52 which many people depend (Fu et al. 2013; Liu et al. 2016). Understanding the importance of
53 specific ecosystem processes, and their role in structuring ecosystem functioning, is,
54 therefore, a key focus of ecological research, especially in this era of global climate change
55 (Manning et al. 2018; Bellwood et al. 2019b). Researchers have applied a wide range of
56 functional indicators to understand how ecosystems function and respond to disturbances.
57 These include the abundance or biomass of key taxa (Paine 1969; Banerjee et al. 2018),
58 functional group-based approaches (Steneck and Dethier 1994; Bellwood et al. 2004; Heenan
59 and Williams 2013), as well as traits and associated metrics (e.g. Functional Diversity,
60 Functional Evenness) (Lavorel and Garnier 2002; Mouillot et al. 2013; McWilliam et al.
61 2020). However, while these proxies have provided significant advances in our understanding
62 (McGill et al. 2006; Violle et al. 2007; Bellwood et al. 2019b), they are largely centred
63 around the use of traits that focus on the diversity of species and communities, i.e. ‘pattern
64 traits’ (sensu Volaire et al. 2020). Evidence of how specific ecosystem processes respond to
65 disturbance remains largely unknown (Petchey and Gaston 2006; Mlambo 2014; Bellwood et
66 al. 2019b). This knowledge gap is particularly problematic for managers, especially if the
67 goal is to sustain a desired level of ecosystem functioning despite environmental
68 perturbations.

69 This knowledge gap is compounded by the fact that ecosystem processes are rarely
70 quantified during ecosystem monitoring programs, with the focus generally being on the
71 abundance and diversity of different organisms and their associated traits (Ford et al. 2018;
72 Bellwood et al. 2019b; Volaire et al. 2020). Unfortunately, many ecosystems have already
73 changed due to human-induced environmental stressors, with consequent shifts in our

74 baselines (Hughes et al. 2017; Barlow et al. 2018). This creates a problem: on the one hand
75 we need to understand how ecosystem processes have or have not changed through time, in
76 response to environmental disturbances, yet on the other hand, the data we have is largely
77 restricted to the abundance of organisms rather than direct measurements of specific
78 ecosystem processes. Thus, our ability to examine how the functioning of ecosystems has
79 changed in response to perturbations is limited, with the shifting baseline syndrome
80 potentially compromising our perceptions (Soga and Gaston 2018), unless we can derive
81 estimates of past functions from the data we have at hand.

82 The issues outlined above are epitomised in aquatic ecosystems such as coral reefs,
83 where long-term data on ecosystem processes are scarce. Furthermore, while high-diversity
84 coral reef ecosystems provide services which support millions of people (Teh et al. 2013;
85 Woodhead et al. 2019), they are also at the forefront of environmental change (Hughes et al.
86 2017; Williams et al. 2019). In an effort to understand how this change impacts these
87 ecosystems, functions are often estimated using derived relationships, such as length-weight
88 relationships to estimate fish biomass (Kulbicki et al. 2005; Froese et al. 2014).
89 Unfortunately, the range of functions that can be examined using this approach has been
90 limited by the availability of derived relationships. However, recent advances in functional
91 analysis provide a way forward by enabling us to directly estimate a broader suite of
92 ecosystem functions, such as fish productivity (e.g. Morais and Bellwood 2018; Brandl et al.
93 2019b; Morais et al. 2020b). These functional analyses are based on readily available
94 monitoring data, and permit us to quantify how ecosystem functions may have changed
95 through time in response to perturbations.

96 Here we apply these approaches to examine the impacts of environmental
97 disturbances in a model inshore coral reef system. We use a time-series dataset where key
98 metrics and functionally informative traits are quantified across a decadal timescale. This

99 dataset allows multiple processes, which relate to the core pillars of coral reef ecosystem
100 functioning (Brandl et al. 2019a), to be estimated from abundance data or basic
101 measurements. These estimated functional values complement functions that were measured
102 more directly. In combination, the range of functions include the provision of resources to: a)
103 herbivorous/detritivorous fishes (e.g. algal growth and detrital yields), b)
104 predators/scavengers (i.e. biomass lost through mortality), c) fish stocks (standing biomass)
105 and d) potential yields to humans (e.g. biomass production). As such, we provide a process-
106 based functional evaluation of a coral reef ecosystem incorporating processes ranging from
107 primary production to potential human yields. Importantly, this dataset encompassed a series
108 of major disturbance events, including extreme river runoff events and sedimentation, severe
109 tropical cyclones and repeated coral bleaching events (Goatley et al. 2016; Torda et al. 2018).
110 Our goal is to determine if, and to what extent, coral reef ecosystem processes change when
111 the reef is exposed to cumulative disturbance events.

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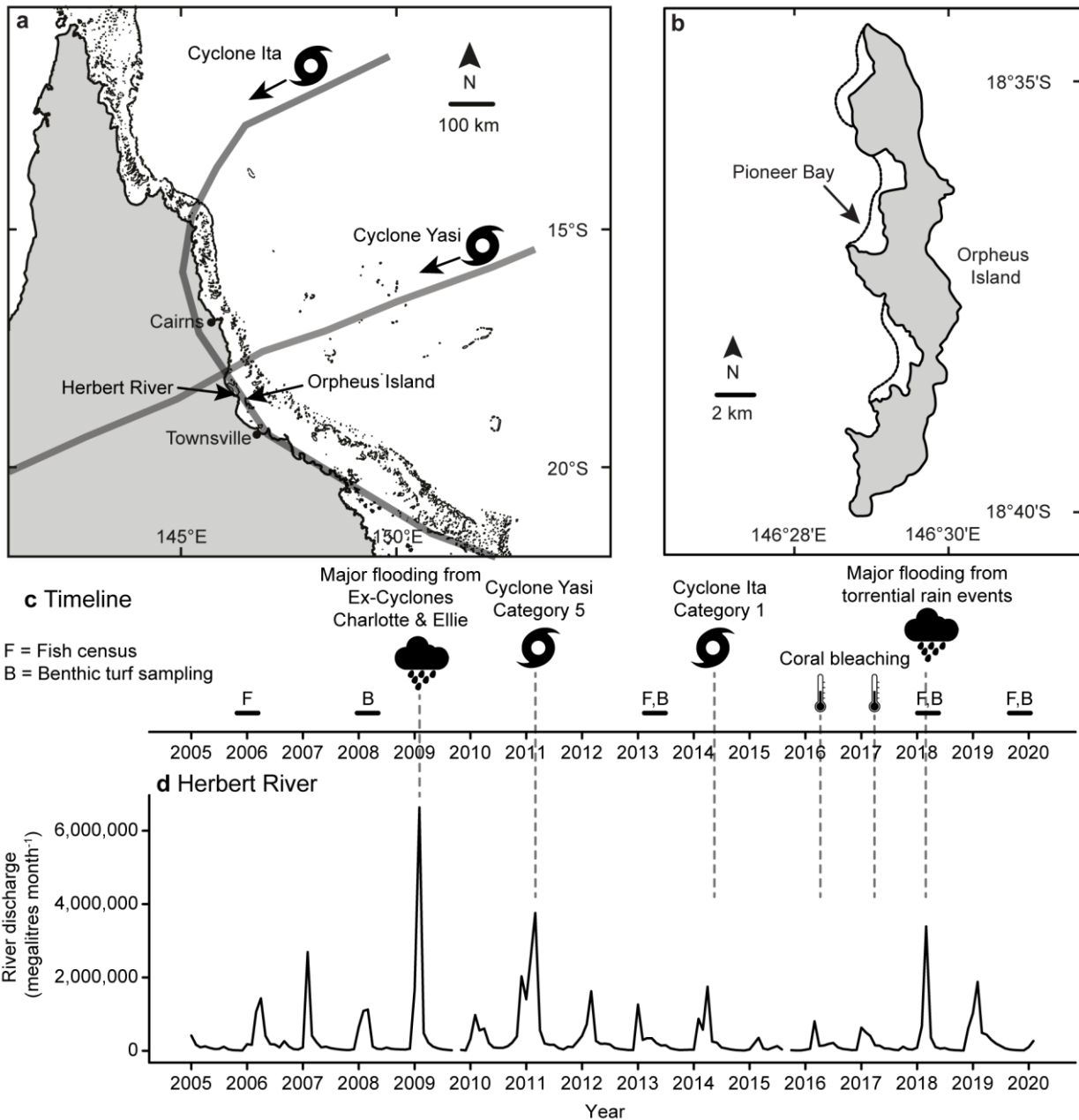
113 **Methods**

114 *Study site and overview*

115 Field data were collected from Pioneer Bay, on the leeward side of Orpheus Island on
116 the inner-shelf of Australia's Great Barrier Reef (GBR), between 2005 and 2019. To examine
117 long-term trends, we collected data in 2018 and 2019 to match data from previous studies at
118 this location (Fox and Bellwood 2007; Bonaldo and Bellwood 2011; Goatley et al. 2016).
119 During this time (2005-2019) Orpheus Island has been subjected to a suite of environmental
120 disturbances, including extreme river runoff events, sedimentation, cyclones and coral
121 bleaching events (Bellwood et al. 2019a; Goatley et al. 2016; Gordon et al. 2016a; Torda et
122 al. 2018) (Figure 1).

123 This study focused on how the functioning of the algal turf community (in terms of its
124 ability to provide nutritional resources to fishes) and the herbivorous fish community (in
125 terms of its trophodynamic functioning) on this coral reef changed over time. Although
126 collected at approximately the same time, the benthic and fish components are examined
127 separately to reveal the production and consumption components of the ecosystem under
128 investigation. These two communities, and the production *vs* consumption processes they
129 support, were selected for examination because in terms of production: a) algal turfs are
130 among the most abundant benthic covering on many coral reefs (Jouffray et al. 2015; Smith
131 et al. 2016; Emslie et al. 2019), b) high algal turf coverage is expected to typify reefs of the
132 future (Bellwood et al. 2019a; Tebbett and Bellwood 2019), and c) algal turf communities act
133 as a reservoir of nutritional resources for fishes (Crossman et al. 2001; Wilson et al. 2003;
134 Kramer et al. 2012). Herbivorous fishes were likewise selected to represent consumption
135 processes because: a) most nominally herbivorous fishes utilise one or more components of
136 algal turf communities as a nutritional resource (Choat et al. 2002; Kelly et al. 2016), b)
137 nominally herbivorous fishes are expected to dominate future reefs with limited coral cover
138 (Pratchett et al. 2018; Robinson et al. 2019a), and c) nominally herbivorous fishes support
139 many fisheries around the world and are likely to continue to do so into the future (Edwards
140 et al. 2014; Bellwood et al. 2018; Robinson et al. 2019b).

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Figure 1 Overview of study location and sampling timeline. a) Map of North Queensland, Australia, showing the location of Orpheus Island relative to the Herbert River as well as the tracks of two relevant cyclones. b) Map of Orpheus Island showing the location of Pioneer Bay where sampling occurred. c) Sampling timeline indicating when benthic algal turf sampling and herbivorous fish censuses occurred relative to major disturbance events. d) The monthly discharge from the Herbert River during the sampling period (Source: Queensland Government 2020).

152 ***Benthic data: algal turfs and benthic production***

153 *Sample collection and processing*

154 We assessed the nature of the algal turf community, and the sediments it contains, on
155 the reef crest in Pioneer Bay in April 2018 and December 2019. This data matched equivalent
156 samples taken in February 2008 (Bonaldo and Bellwood 2011) and April 2013 (Goatley et al.
157 2016). As algal turf sediment loads are remarkably stable over short temporal time scales
158 (days to months) (Gordon et al. 2016a; Tebbett et al. 2018), these sampling time periods are
159 representative of the years in which sampling was conducted. To sample the algal turf
160 communities we used a submersible electronic vacuum sampler (modified after Purcell
161 1996), to collect 6 algal turf particulate samples from two sites (n = 12) on the reef crest (2 –
162 4 m) each year. Suitable sampling surfaces were outside of the territories of farming
163 damselfishes, flat, smooth, free of sediment-retaining pits, macroalgae and encrusting
164 organisms and were covered in algal turfs (following Tebbett et al. 2017a). Sampling areas
165 were delineated using a 58 cm² PVC ring. Within the sampling area, we also quantified algal
166 turf length by measuring the length of 5 haphazardly selected algal turf filaments using the
167 depth probe of vernier callipers (following the methods outlined in Tebbett and Bellwood
168 2019). The collected particulates were then processed to yield: a) particulate volume, b) total
169 dry particulate mass, c) dry inorganic sediment mass, and d) dry organic detrital particulate
170 mass following Tebbett and Bellwood (2020). Particulate processing methods are provided in
171 the supplemental material (see Supplemental Text S1, S2).

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175 *Benthic data statistical analysis*

176 We initially analysed traditional metrics related to the condition of the algal turf
177 community (inorganic sediment mass and algal turf length), and a key function (potential
178 algal turf growth; calculation details are provided in Supplemental Text S3). It should be
179 noted that algal turf length and growth provide different insights into the functioning of the
180 system as the former is a static, standing stock, measure (i.e. a measure of how much turf
181 there is), while the latter is a process-based metric, productivity, that provides information on
182 the rate of resource renewal (i.e. how quickly turf is replaced). Data were compared among
183 years using Bayesian generalised linear mixed-effects models (GLMMs) fitted with a Gamma
184 distribution and log-link (sediment mass and turf length) or lognormal distribution (turf
185 growth). In all cases, sampling year was treated as a categorical fixed effect while site was
186 treated as a random effect (to account for any lack of spatial independence). All models were
187 based on weakly informative priors (see Supplemental Table S1 for prior details and chain
188 specifications for each model). Model convergence, fit and assumptions were assessed using
189 trace plots, autocorrelation plots, Rhat plots, posterior predictive checks, effective sample
190 sizes and residual plots. In all cases, the diagnostics suggested that the chains were well
191 mixed and converged on a stable posterior (with all Rhat values less than 1.05) and were
192 uncorrelated (with lag values <0.2). In addition, our effective samples were >1000 , and there
193 were no patterns in the residuals. It should be noted that turf length data were based on the
194 mean turf length in each sediment sampling location in 2008, 2018 and 2019. However, in
195 2013 the nature of the turf length data differed in that it was based on 30 haphazard turf
196 measurements at each of two sites. All analyses of benthic data were performed in the
197 software R (R Core Team 2019), using the *rstan* (Stan Development Team 2018), and
198 *rstanarm* (Goodrich et al. 2018) packages.

199

200 *Benthic algal turf function-space*

201 Algal turf community functions were also calculated for each individual replicate unit
202 (i.e. each algal turf sample) and then plotted in multivariate space to provide an overview of
203 the relative levels of the benthic functions in each sample period. The resultant benthic
204 function-space was based on five functions that were specifically selected as they, a) pertain
205 directly to the ability of the algal turf community to provide nutritional resources to fishes,
206 and b) were able to be quantified ([M = measured directly] or derived [C = calculated]) from
207 the long-term data at hand (a major limitation in studies of this nature). Specifically, these
208 five functions were: potential algal turf growth ([C]; linear growth in mm day^{-1}), algal turf
209 biomass ([C]; g m^{-2}), standing detritus mass ([M]; g m^{-2}), relative detrital mass in particulates
210 ([M]; %), and harpacticoid copepod standing biomass ([C]; μg ash-free dry weight [AFDW]
211 m^{-2}). Algal turf biomass, detrital biomass and copepod biomass were selected as functions as
212 they relate to the storage of nutrients in the system that can be exploited directly and/or
213 inadvertently by herbivorous fishes (Hatcher and Larkum 1983; Purcell and Bellwood 2001;
214 Choat et al. 2002; Kramer et al. 2017). Potential algal turf growth was also selected as a
215 function because this process relates to the speed at which resources are generated for
216 herbivorous fishes to exploit (Russ 2003; Kelly et al. 2017). Relative detrital mass in
217 particulates is a measure of the trade-off nominally herbivorous fishes face when feeding on
218 particulate matter in algal turfs, i.e. the return of nutritious detritus relative to the cost of
219 processing inorganic sediments (Gordon et al. 2016b; Tebbett et al. 2017b). The computed
220 benthic function-space, therefore, focuses on the ability of a critically important compartment
221 of the benthos (i.e. algal turf communities) to directly provide nutritional resources to fish
222 populations (i.e. herbivorous fishes).

223

224 The five benthic functions were directly measured, or calculated from the measured
225 turf traits, during each sampling period (details of these calculations are provided in the
226 Supplemental Material Text S3). After all of the functions were calculated and compiled into
227 a data matrix, we constructed the benthic function-space. Initially, the data matrix was fourth-
228 root transformed and range standardised by columns to ensure each function had an equal
229 weighting in the analysis. Subsequently, a Euclidean distance matrix was calculated. As we
230 wanted to examine how the individual replicate sample units were positioned in
231 multidimensional function-space we formulated a principal co-ordinate analysis from our
232 Euclidean distance matrix and visualised this using 'heatmaps'. Heatmaps were used to
233 visualise the function-space because they focus on where the greatest density of points is
234 located in multidimensional space rather than focusing on the outliers that are used to
235 delineate polygons. To compute the heatmaps, we used the scores of the PCoA to calculate
236 four Kernel Utilization Distributions (KUDs), one for each time period. KUDs are widely
237 used in the field of animal movement as they describe the probability distributions of 'animal
238 detections' in space (Worton 1989). In our context, the 'animal detections', were the
239 individual algal turf sampling units across the multidimensional function-space. Colour
240 gradients were subsequently informed by the bivariate KUDs, with the 'hottest' areas
241 marking areas with the highest density of samples. Please note, this approach highlights areas
242 in multidimensional space with more samples exhibiting the functional characteristics
243 associated with that area, not necessarily more 'function'. Finally, significant differences
244 between the years in terms of position in the function-space were assessed using a
245 permutational multivariate analysis of variance (PERMANOVA). Site identity was also
246 included as a factor to account for the lack of spatial independence. Homogeneity of variance
247 was also examined using permutational multivariate analysis of dispersions (PERMDISPs)
248 (Supplemental Table S2). The benthic function-space was computed in the software R (R

249 Core Team 2019), using the *raster* (Hijmans 2017), *adehabitatHR* (Calenge 2006) and *vegan*
250 (Oksanen et al. 2019) packages. For discussion on the correlation and non independence of
251 the five functions, as well as discussion on uncertainty and interpretation please see the
252 supplemental material (Text S4).

253

254 ***Herbivorous fish assemblage: consumption of benthic production***

255 *Fish censuses*

256 The abundance and community composition of herbivorous fishes (parrotfishes
257 [Labridae], surgeonfishes [Acanthuridae] and rabbitfishes [Siganidae]) were initially
258 quantified on the reef crest in Pioneer Bay in December/January 2005/2006 (Fox and
259 Bellwood 2007) and April 2013 (Goatley et al. 2016). It is important to note that the first-
260 time point for fish (2005) differs to that for benthic algal turfs (2008); however, no major
261 stressors acted upon this system between these sampling periods (Figure 1). In April 2018
262 and December 2019, we repeated the same methods to match this existing data by performing
263 12 non-overlapping censuses across the bay (each year). To minimise diver effects on fishes
264 (Emslie et al. 2018) we used 5-minute timed swims (GPS calibrated length = 46.1 ± 1.1 m
265 [mean \pm SE]), or 45 m tape transects laying the tape as fishes were counted. All censuses
266 were undertaken by two divers on SCUBA. The first diver counted all relevant herbivorous
267 fishes >10 cm total length (TL) in a 5 m wide transect, while the second diver counted all
268 fishes 5-10 cm long in a 1 m wide transect. All fishes were identified to the lowest taxonomic
269 level (generally species) and placed into 5 cm TL size categories (fishes >10 cm TL) or 2.5
270 cm size categories (fishes <10 cm TL). Size data were subsequently used to calculate the
271 biomass of each fish using Bayesian length-weight regression parameters (Froese and Pauly
272 2018).

273 *Herbivorous fish data statistical analysis*

274 Initially, we analysed more traditional monitoring data and a key function (biomass
275 productivity; calculation details are provided in the Supplemental Text S5) related to the
276 herbivorous fish community. Specifically, we examined how the abundance, biomass,
277 biomass production and community composition of herbivorous fishes changed over the 14-
278 year sampling period. Abundance, biomass and biomass production were compared among
279 years (categorical fixed effect) using Bayesian generalised linear models (GLMs) fitted with
280 Gamma distributions and log-links. In all cases, weakly informative priors were used (see
281 Supplemental Table S1 for prior details and chain specifications for each model). Model fit
282 and assumptions were assessed as above.

283 To explore how the community composition of the herbivorous fish species in Pioneer
284 Bay changed among sampling periods, we used a multivariate approach. Specifically, we
285 computed a Bray Curtis similarity matrix for both species abundance and species biomass
286 data, and visualised changes using constrained distance-based redundancy analysis.
287 Significant differences between the years in terms of the position of the communities in
288 multivariate-space were assessed using permutational multivariate analysis of variance
289 (PERMANOVA). Variation in homogeneity was assessed as above (i.e. using a PERMDISP
290 [Supplemental Table S2]). The statistical analyses were performed in the software R (R Core
291 Team 2019), using the *rstan* (Stan Development Team 2018), *rstanarm* (Goodrich et al.
292 2018) and *vegan* (Oksanen et al. 2019) packages.

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297 To understand how changes in the herbivorous fish community may have influenced
298 its functioning, we calculated a function-space based on five functions that specifically
299 pertain to how energy is stored or cycled in fish communities. This function-space was based
300 on individual censuses as the replicate units. The five functions were: standing biomass (g m^{-2})
301 2), rate of biomass production ($\text{g m}^{-2} \text{ day}^{-1}$), consumed biomass ($\text{g m}^{-2} \text{ day}^{-1}$), carbon respired
302 ($\text{g m}^{-2} \text{ day}^{-1}$) and turnover rate (%). These five functions broadly cover the three main aspects
303 of trophodynamics: energy use (carbon respired), assimilation and conversion to biomass
304 (biomass production and standing biomass), and transfer to other trophic levels (consumed
305 biomass and turnover). As for the turf community above, these functions are not necessarily
306 independent (see Supplemental Text S4 for discussion). Indeed, they are likely to be
307 correlated with each other, a feature that is well captured in multivariate analyses. Although
308 these functions are unlikely to capture the full extent of herbivorous fish functioning, they are
309 likely to provide a more detailed understanding of the trophodynamic functioning of this
310 herbivorous fish community when compared to findings based on changes in fish abundances
311 alone (cf. Brandl et al. 2019b; Benkwitt et al. 2020; Morais et al. 2020b). The procedures to
312 obtain standing biomass, biomass production, consumed biomass and turnover all follow
313 Morais et al. (2020b) (full details are provided in the Supplemental Material Text S5).

314 After the functions had been calculated for the herbivorous fish community, the
315 function-space for these fishes was formulated as above for the algal turf community (a
316 PCoA with which we calculated bivariate KUDs and heatmaps). The herbivorous fish
317 function-space was likewise analysed as above, i.e. using a PERMANOVA and PERMDISP
318 (see Supplemental Table S2) and the same software packages.

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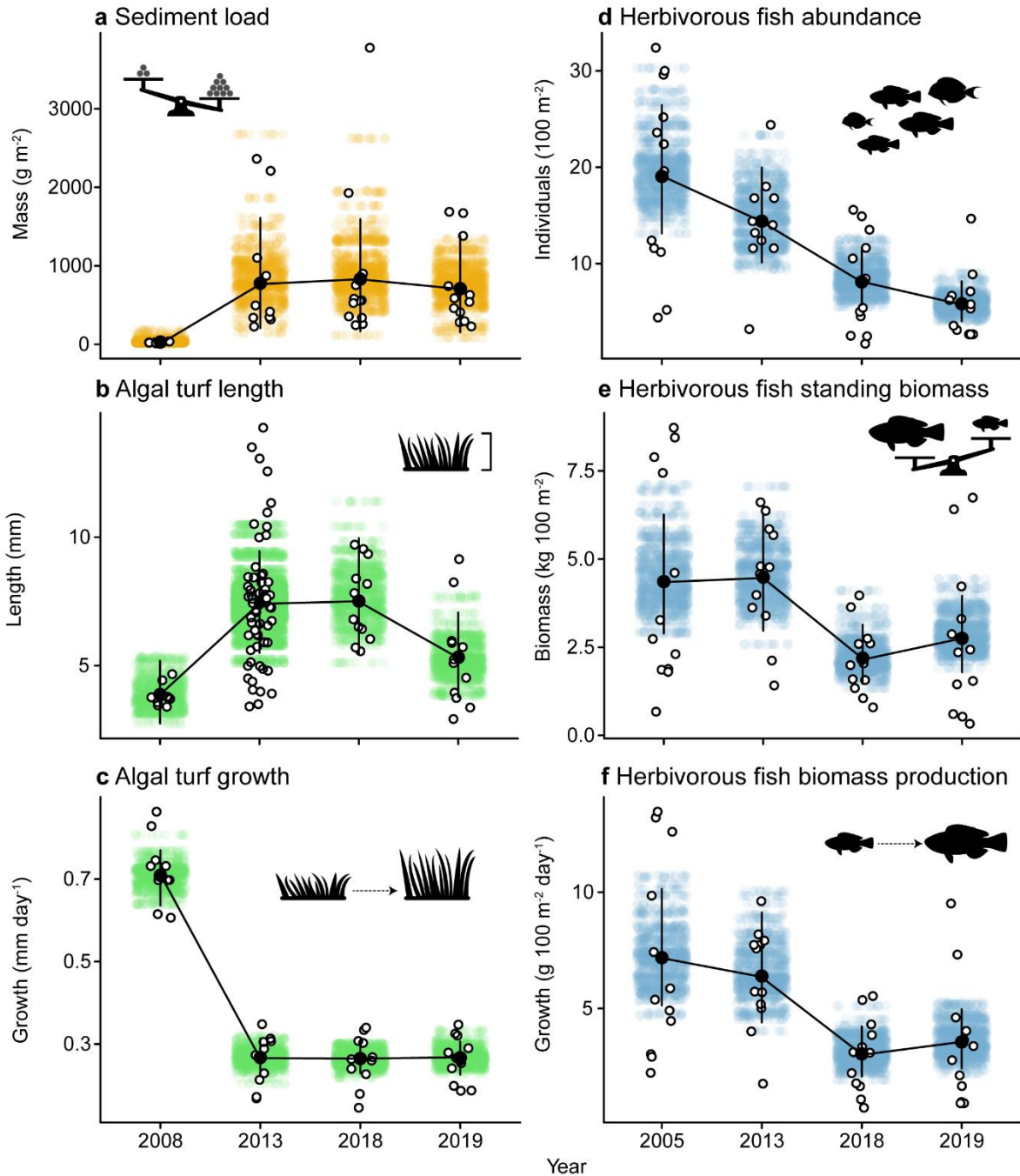
320 **Results**

321 By examining the nature of the algal turfs (i.e. sediment loads and algal turf length)
322 we revealed a fundamental change in the condition of the algal turf community at Orpheus
323 Island (Figure 2a, b, c). Indeed, the mass of inorganic sediments bound within the turfs
324 appears to have increased 2181% (462% - 6870% [95% credibility intervals]) between 2008
325 and 2019 (Figure 2a; Supplemental Table S3). Concomitantly, algal turf length increased by
326 38% (9% - 224%) from 2008 to 2019 (Figure 2b; Supplemental Table S3). Such marked
327 changes in the sediment load and length of algal turfs clearly had an impact on potential turf
328 growth which had declined by 62% (54% - 68%) in 2019 relative to 2005 (Figure 2c;
329 Supplemental Table S3). Essentially, a marked phase-shift in the condition of the turfs
330 occurred, from short productive algal turfs to long sediment-laden algal turfs.

331 The herbivorous fish community exhibited similar changes with an overall decrease in
332 abundance of nearly 70% (51% - 82%) from 2005 to 2019 (Figure 2d; Supplemental Table
333 S3) and a similar decline in herbivorous fish standing biomass (Figure 2e; Supplemental
334 Table S3). However, unlike abundance which declined steadily (Figure 2d), biomass
335 remained relatively stable from 2005 to 2013, before declining by nearly 50% (16% - 71%) in
336 2018, and remaining 37% (-1% - 63%) below 2005 levels in 2019 (Figure 2e; Supplemental
337 Table S3). Furthermore, it appears that the ability of the herbivorous fish community to
338 replace biomass also collapsed as biomass production rates declined by 50% (19% - 70%)
339 from 2005 - 2019 (Figure 2f; Supplemental Table S3). Overall, from 2005 to 2019 70% of the
340 individual fish and 37% of the herbivorous fish biomass was lost from this coral reef system,
341 while the capacity to produce new biomass was reduced by 50%. Analysis of the community
342 composition of herbivorous fishes (weighted by both abundance and biomass) revealed that
343 the declines occurred across all species and that the herbivorous fish communities in 2018

344 and 2019 appeared to represent a depauperate version of that present in 2005 (Supplemental
345 Figure S1; Table S4).

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347

348 **Figure 2** Changes in the algal turf and herbivorous fish communities on the reef crest in
349 Pioneer Bay, Orpheus Island. There was a marked shift in the algal turf community in terms

350 of (a) sediment load, (b) length and (c) potential growth. Similarly, there were concomitant
351 changes in the herbivorous fish community (parrotfishes, rabbitfishes and surgeonfishes),
352 with decreases in abundance (d), standing biomass (e) and growth rate (f). The black points
353 and range bars indicate the predicted mean and 95% credibility intervals from Bayesian
354 generalised linear mixed-effects models (a, b, c) and generalised linear models (d, e, f), the
355 coloured points are 100 randomly selected model fits from the posterior distribution and open
356 circles are the raw data points.

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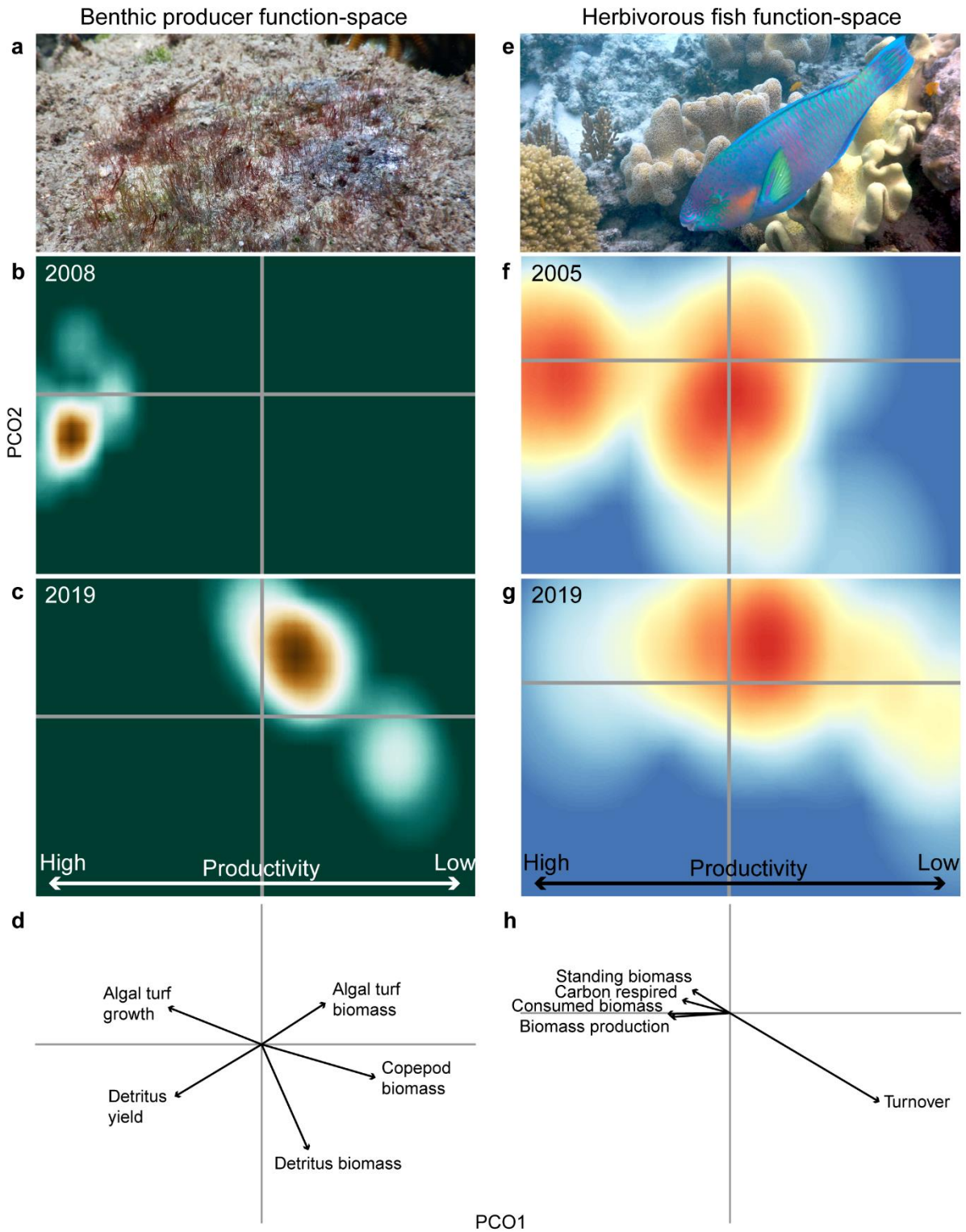
358 It is clear that the algal turf and herbivorous fish communities changed substantially
359 across the study period with flow-on effects on ecosystem functions. Our calculated function-
360 spaces reveal the strength of multiple functions, simultaneously, and provide a broad
361 overview of how the functional configuration of the two communities changed through time.

362 Firstly, the benthic function-space revealed a clear temporal shift in the ability of the
363 algal turf community to provide nutritional resources to herbivorous fishes. The community
364 occupied significantly different areas of function-space in 2013, 2018 and 2019 relative to
365 2008 (Figure 3; Supplemental Figure S2; Table S4). Indeed, in 2008 the composition of the
366 benthic functions were characteristic of a high-productivity system that could readily provide
367 nutritional resources to herbivorous fishes (i.e. high algal turf growth rates and a high
368 proportion of organic detritus relative to inorganic sediments in the turfs) (Figure 3).

369 However, by 2013 the growth of algal turfs had reduced, while the standing biomass of algal
370 turfs, copepods and detritus had increased, leading to an alternative functional configuration
371 in 2018/2019. This new functional configuration represents an algal turf community that has
372 a high standing biomass of nutritional resources (abundant algal turf, detritus, copepods), but
373 a limited ability to replace these resources (e.g. reduced algal growth rates). This new

374 configuration also poses a challenge for detritivorous fishes due to low relative yields of
375 detritus. Ultimately, the new functional composition represents a relatively high biomass-low
376 productivity benthic algal turf community.

377 Reflecting changes in the ecosystem-level functioning of the benthic algal turf
378 community, the functioning of the herbivorous fish community also changed substantially
379 (Figure 3), eventually occupying a significantly different area of function-space in 2019
380 compared to 2005 (Supplemental Table S4). In 2005, the herbivorous fish community
381 occupied an area of function-space that was typified by high standing biomass, and high
382 relative rates of biomass production, biomass consumption and energy use (i.e. a high-
383 productivity position) (Figure 3). However, over time the functioning of the herbivorous fish
384 community shifted into an area of function-space that was characterised by higher relative
385 rates of turnover but low standing biomass, biomass production, biomass consumption and
386 energy use (Figure 3). These shifts mirror the benthic algal turf community. Together, these
387 results reveal a fundamental shift over time from a high productivity/high consumption state
388 to an alternate low-productivity functional configuration.



389

390 **Figure 3** Function-spaces of the benthic algal turf community and the herbivorous fish
 391 community. The benthic function-space is a multivariate space that provides an overview of
 392 the ability of the algal turf community to provide nutritional resources to herbivorous fishes
 393 from 2008-2019 (b, c) based on 5 specific functions (d). The herbivorous fish function-space

394 is a multivariate space that examines the trophodynamic functioning of the herbivorous fish
395 assemblage from 2005-2019 (f, g) based on 5 specific functions (h). The occupation of the
396 function-space is represented as a heat map based on kernel utilisation densities (note brown
397 areas [b, c] and red areas [f, g] indicate more samples with that particular combination of
398 function levels, not necessarily more ‘functions’ per se). See Supplemental Figure S2 for
399 function-spaces from 2013 and 2018 and see Supplemental Figure S3 for specific levels of
400 each individual function. Photographs of a benthic algal turf community (a) and the
401 herbivorous parrotfish *Scarus rivulatus* (g) (Photographs: SB Tebbett).

402

403 **Discussion**

404 Coral reef ecosystems have been subjected to an increasing range and intensity of
405 stressors which have led to extensive changes in the communities that inhabit these
406 ecosystems and, presumably, to the functions that operate within the ecosystem (Kennedy et
407 al. 2013; Hughes et al. 2017; Bruno et al. 2019; Williams et al. 2019; Vercelloni et al. 2020).
408 However, changes in ecosystem functioning are often only inferred from proxies; rarely are
409 they informed by estimates of, or data on, the processes themselves (Ford et al. 2018;
410 Bellwood et al. 2019b). By directly calculating key processes, we revealed a collapse in the
411 abundance and biomass of herbivorous fishes, and in algal turf production as the turfs shifted
412 towards a long sediment-laden state. In addition to patterns based on traditional metrics, we
413 were able to examine and track ecosystem functions (i.e. the relative composition and
414 strength of multiple functions). In doing so, we revealed that the functional status of both the
415 algal turf community and the herbivorous fish community shifted, fundamentally, towards an
416 alternate low-productivity configuration. Such marked shifts in the status of these

417 components of coral reef food webs are concerning as they suggest that the ability of this
418 ecosystem to sustain key services may be compromised.

419 To understand the mechanistic basis of changes and shifts in key functions, we need
420 to consider both the nature of the communities involved, and the context of the ecosystem in
421 question. In doing so, it is important to note that the substantial declines in herbivorous fish
422 abundance and biomass that we documented almost certainly occurred independent of fishing
423 effects (see Morais et al. 2020a). Our study site is part of a relatively well-enforced no-take
424 zone within the Great Barrier Reef Marine Park, with less poaching than in other no-take
425 areas nearby (Bergseth et al. 2017). Furthermore, in contrast to most other tropical regions,
426 herbivorous fishes are rarely targeted on the Great Barrier Reef (Rizzari et al. 2014; Casey et
427 al. 2017). The limited role of fishing-pressure was emphasised by the overall pattern of
428 declining abundance and biomass across all herbivorous fish species examined (Figure S1),
429 rather than impacts on specific species (e.g. selective fishing pressure [Russ and Alcala 1989;
430 Hamilton et al. 2016; Morais et al. 2020a]). Together, these impacts highlight that the system
431 responded with limited response diversity and that there was a generalised impact on fish
432 herbivory.

433 This lack of a fishing effect is particularly interesting as one of the most widely held
434 paradigms in coral reef ecology is that overfishing of herbivorous fishes results in reduced
435 grazing pressure on the benthos and therefore increased algal coverage and coral collapse
436 (reviewed in Bellwood et al. 2004; Bruno et al. 2019). However, based on the available
437 evidence, and considering the context of the stressors impacting our system, the most
438 parsimonious explanation for the changes we have documented appears to be a sediment-
439 driven bottom-up collapse of trophic interactions in this coral reef system (cf. Russ et al.
440 2015, 2018). Indeed, the >2100% increase in accumulated sediments from 2008 to 2019 is
441 notable and may be a result of the acute river runoff events that have impacted this system,

442 particularly in 2009 (Figure 1; see Supplemental Text S6 for further discussion on the source
443 of sediments). It should also be noted that cyclones can directly impact reef fishes in the short
444 term (Cheal et al. 2017; Khan et al. 2017) and this may also have been a contributing factor to
445 the documented population declines. However, such cyclone impacts represent an acute
446 disturbance that does not match the chronic, protracted declines in herbivore populations
447 documented herein, leaving increased sediment loads alone as the most parsimonious
448 explanation.

449 Sediment accumulation in algal turfs has previously been causally linked to the
450 development of longer algal turfs (Goatley and Bellwood 2013; Fong et al. 2018), marked
451 decreases in algal turf productivity (Clausing et al. 2014; Tebbett et al. 2018), and declines in
452 herbivorous fish feeding activity (Goatley and Bellwood 2012; Tebbett et al. 2017b). This
453 latter point is particularly important as sediments appear to represent a bottom-up control on a
454 top-down force (herbivorous fishes feeding), that may facilitate the development of longer
455 algal turfs and enhanced sediment trapping in a positive-feedback (reviewed in Tebbett and
456 Bellwood 2019). Importantly, such a positive-feedback may compromise a variety of key
457 ecological services including the settlement of corals (Speare et al. 2019; Ricardo et al.
458 2017), reductions in algal removal rates (Goatley et al. 2016) and shifts in bioerosion patterns
459 (Hutchings et al. 2005). Consistent with this prior evidence, we revealed the extent to which
460 increasing sediment accumulation also correlates with declines in algal turf growth (Figure
461 2c) and shifts in the functional configuration of the algal turf community (Figure 3). Top-
462 down control of turfs by herbivorous fishes is also possible (Smith et al. 2010; Tebbett et al.
463 2017c; Fong et al. 2018; McAndrews et al. 2019), however, as fish abundances were slow to
464 change and biomass changes were delayed, the most parsimonious explanation, in this case,
465 appears to be bottom-up (although in all cases the top-down and bottom-up effects are clearly
466 linked). As the dynamics of herbivorous fish communities are tightly linked to their food

467 supply (Russ et al. 2015; Tootell and Steele 2016; Graham et al. 2018; Taylor et al. 2020), it
468 is logical to conclude that a sediment-driven collapse in resource yields represents the most
469 plausible mechanism for the marked declines in herbivorous fish biomass and biomass
470 production documented in this system. It is likely that the strengthening of positive feedbacks
471 by sediments (see Tebbett and Bellwood 2019) has maintained the long sediment-laden algal
472 turf state in this system since 2013; this may reflect some degree of hysteresis (Goatley et al.
473 2016; Hughes et al. 2017).

474 Declines in the ability of coral reefs to sustain key functions and services also have
475 clear implications for people. Notably, from a human perspective, reefs are often valued for
476 their high productivity, which underpins fisheries and in turn supports the people that depend
477 on these systems (Teh et al. 2013; Lau et al. 2019). Our results suggest that if people were
478 relying on herbivorous fishes for food provision in this system, as they do in many areas of
479 the world (Edwards et al. 2014; Robinson et al. 2019b; Wenger et al. 2020), then these people
480 would be confronted with a herbivorous fish stock 37% smaller in 2019 relative to 2005.
481 Furthermore, the extraction of fisheries resources requires biomass to be produced and
482 replenished (Allen 1971; Hilborn and Walters 1992). As such, the rate of production of new
483 biomass provides a more relevant metric for assessing the sustainability of this critical
484 ecosystem service than standing biomass (Morais et al. 2020a, 2020b). It is sobering to note
485 that the observed declines in herbivorous fish biomass production exceed those seen in
486 standing biomass, with decreases in the order of 50% or more between 2005 and 2019
487 (Figure 2f). Furthermore, beyond compromising potential fisheries productivity, this loss of
488 herbivorous fishes is also likely to compromise other key services, such as the perceived
489 aesthetic value of the reef, due to the loss of large colourful fishes that people find attractive
490 (Woodhead et al. 2019; Bellwood et al. 2020). Clearly, the magnitude of the changes
491 documented may have serious implications for the sustained provision of services to humans.

492 Importantly, a clear discrepancy between herbivorous fish abundance and biomass
493 declines appeared to exist in this system (Figure 2d, e) and this is likely to be the result of a
494 storage effect (e.g. Morais et al. 2020b). Essentially, the discrepancy reflects a change in the
495 size structure of the herbivorous fish community, with relatively more larger fishes in 2013
496 compared to 2005 (Supplemental Figure S4). The aging of fishes already present in this
497 community appears to have sustained standing biomass levels up to 2013, thus masking
498 background declines in abundance. However, beyond 2013 the apparent limited recruitment
499 of new fishes into the system and eventual loss of the larger cohorts overwhelmed the
500 buffering capacity of this storage effect.

501 Importantly, the change in herbivore size structure also suggests that the recruits of
502 these herbivorous fishes were disproportionately impacted by the increased algal turf
503 sediment loads compared to adults. Unfortunately, how algal turf sediments impact
504 recruit/juvenile herbivorous reef fishes is currently unclear. However, we do know that
505 parrotfishes (the main herbivorous fishes in this system) recruit to coral reefs at a smaller size
506 than most other reef fishes and form a close association with algal turfs (often lying on or
507 within the algal turf canopy, especially in damselfish territories or in short, well-grazed turfs;
508 both of which contain low sediment loads) (Bellwood & Choat 1989). As such, any alteration
509 of algal turfs by sediments could impact parrotfish recruits directly and certainly warrants
510 further investigation. Furthermore, previous studies have revealed a second mechanism by
511 which sediments may impact juvenile parrotfishes. Specifically, high sedimentation may
512 impact the juvenile habitat (namely branching corals) of some parrotfish species, with flow-
513 on consequences for adult populations (DeMartini et al. 2013; Hamilton et al. 2017).
514 Regardless of the exact mechanisms, the documented population declines represent a delayed
515 response to disturbance, which is unlikely to be detected during immediate post-disturbance
516 monitoring (cf. Bellwood et al. 2006).

517 The findings outlined above also have implications for our understanding of how
518 coral reef functioning responds to disturbances, as these findings contrast markedly with prior
519 results from other coral reefs. Indeed, it is generally accepted that following disturbances,
520 especially coral bleaching events, the abundance, biomass and productivity of herbivorous
521 fishes will increase as a result of an increasing food supply (i.e. higher algal turf cover) (Russ
522 et al. 2015; Cheal et al. 2017; Pratchett et al. 2018; Robinson et al. 2019b, 2019a). Increased
523 algal resources are also expected to enhance the somatic growth of herbivores (Morais et al.
524 2020b; Taylor et al. 2020). This has provided a glimmer of hope that herbivorous fish
525 assemblages can sustain high fishing pressure on Anthropocene reefs (Robinson et al. 2019b;
526 Morais et al. 2020a). However, in our study system, despite a general increase in algal turf
527 cover over the last 15 years (Supplemental Text S7; Figure S5), there has been a prolonged
528 decline in herbivorous fishes (Figure 2d) and a marked shift in the trophodynamic
529 functioning of the herbivorous fish community (Figure 3). These results highlight how the
530 different types of disturbance exert their effects. Most studies report a decrease in coral cover
531 without evaluating the responses of the non-coral benthos in detail (Russ et al. 2015;
532 Robinson et al. 2019a; Morais et al. 2020b). By contrast, we show a decline in benthic algal
533 turf condition that occurred with only limited hard coral loss (and presumably a limited loss
534 of structural complexity associated with hard corals, although this was not assessed)
535 (Supplemental Text S7; Figure S5). Our results, therefore, pertain to changing algal turfs, not
536 coral loss.

537 Our data suggests that if the quality of nutritional resources is compromised by
538 sediments, then this could overwhelm any potential short-term benefits that increased
539 resource abundance might offer herbivorous fishes. Sediment accumulation in algal turfs
540 could be the ‘Achilles-heel’ to sustaining productive herbivorous fish assemblages and may
541 explain the declining yields of fisheries on other sediment-impacted coral reefs (Orlando and

542 Yee 2017; Delevaux et al. 2018; Wenger et al. 2020). Importantly, this sediment
543 accumulation would not have been detected by evaluating patterns of benthic cover alone, be
544 it coral or algal turf cover. Moreover, it is unlikely that traditional fisheries management tools
545 such as marine protected areas would provide much resilience against the documented
546 productivity loss, as sediments can transcend the boundaries of these areas (Bégin et al. 2016;
547 Wenger et al. 2016; Suchley and Alvarez-filip 2018). Management of sediment impacts
548 requires an approach that addresses both marine and terrestrial drivers of change (Brodie et
549 al. 2012; Bartley et al. 2014; Oleson et al. 2017; Comeros-Raynal et al. 2019; Wenger et al.
550 2020).

551 Although based on just one reef system on the Great Barrier Reef, our findings may
552 have a broad application to coral reefs around the world, as a large proportion of the world's
553 coral reefs occur in close vicinity to land (Burke et al. 2011; Maire et al. 2016). These
554 nearshore coral reefs, and the herbivorous fishes that occupy them, are heavily relied upon by
555 subsistence fisheries (Edwards et al. 2014; Wenger et al. 2020). However, they are also at
556 particularly high risk of sediment accumulation. Indeed, evidence suggests that more than
557 50% of the world's coral reefs are at risk of increased terrestrial sediment inputs (Burke et al.
558 2011), with far-reaching impacts (reviewed in Fabricius 2005; Bainbridge et al. 2018; Magris
559 and Ban 2019). Unfortunately, there are currently no monitoring programs on any reef system
560 globally that assess the amount of sediments accumulated in algal turfs (reviewed in Tebbett
561 and Bellwood 2019), nor many of the other critical hydrodynamic and geological parameters
562 associated with these sediments (Elliff et al. 2019). Without such quantitative baseline
563 information, our ability to evaluate systems may be compromised by shifting baselines (Soga
564 and Gaston 2018).

565 Even on the highly managed and monitored GBR, our study site is the only location
566 where algal turf sediments have been sampled repeatedly over time. Indeed, this study site is

567 one of only four inner-shelf reefs on which turf sediments have been quantified (with total
568 sediment loads approximately comparable in all cases [Tebbett and Bellwood 2019]). As
569 such, we cannot quantitatively determine how widespread the problem of turf-bound
570 sediments and their flow-on effects for critical ecosystem processes is likely to be (reviewed
571 in Tebbett and Bellwood 2019). However, there do appear to be clear critical thresholds.
572 Growing evidence suggests that when turf-bound sediment loads exceed approximately 100 g
573 m⁻² the growth of algal turfs slows markedly (Tebbett and Bellwood 2020) and the feeding
574 activities of some nominally herbivorous fishes are impacted (Tebbett et al. 2017b). In
575 addition, sediment loads of approximately 250-500 g m⁻² can correlate strongly with the
576 absence of key fish species (Tebbett et al. 2020). This suggests that if sediment loads exceed
577 these levels (approximately half the levels reported herein during 2013, 2018 and 2019) the
578 functioning of the reef community is likely to be directly impacted by sediments. It should be
579 noted, however, that further long-term, spatially replicated work, is required to confirm these
580 threshold levels. Clearly, the lack of monitoring of turf-bound sediments represents a
581 significant knowledge gap that may stymie our endeavours to secure and sustain the key
582 ecosystem services that reefs provide (Hughes et al. 2017).

583 Overall, our study emphasises the importance of functional evaluations in
584 understanding how disturbances shape ecosystems. We highlight how turf-bound sediments
585 potentially disrupt the functioning of coral reefs through core trophic interactions. Our
586 results, as well as other lines of evidence (Ricardo et al. 2017; Fong et al. 2018; McAndrews
587 et al. 2019; Speare et al. 2019; Evans et al. 2020; Tebbett et al. 2020), suggest that turf-bound
588 sediments pose a considerable risk to ecosystem processes on coral reefs. Unfortunately,
589 increasing accumulation of such turf-bound sediments is likely to be prevalent on many coral
590 reefs globally, although often cryptic and unmonitored. As the strength of connections
591 between people, the land, and marine ecosystems grow, the impacts of sediment are likely to

592 increase. Our study provides a functional understanding of how the impacts of these
593 sediments could reverberate up through the food chain and affect both critical ecosystem
594 functions and human populations that rely on coral reefs.

595

596 **Acknowledgements**

597 We thank: R.J. Fox, R.M. Bonaldo, M.J. Kramer and Z. Loffler for their pioneering research
598 that inspired this manuscript; Reef Check Australia and their volunteers for the provision of
599 benthic cover data; F.X. Latrille, A. Oakley-Cogan, M. Mihalitsis and the Orpheus Island
600 Research Station staff for field support; three anonymous reviewers for constructive and
601 insightful comments; and the Australian Research Council (DRB: CE140100020 and
602 FL190100062), the Orpheus Island Research Station Morris Family Trust (SBT), and an
603 Australian Government Research Training Program Scholarship (SBT) for financial support.

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