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1 **Macroalgae removal on coral reefs: realised ecosystem functions transcend**
2 **biogeographic locations**

3
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29 **Abstract**

30

31 Coral reef ecosystems are at the forefront of biodiversity loss and climate change-mediated
32 transformations. This is expected to have profound consequences for the functioning of these
33 ecosystems. However, assessments of ecosystem function on reefs are often spatially limited,
34 within biogeographic realms, or rely on presumed proxies such as traits. To address these
35 shortcomings and assess the effects of biogeography and fish presence on the critical
36 ecosystem function of macroalgal removal, we used assays of six algal genera across three
37 reef habitats in two biogeographically distinct locations, Little Cayman in the Caribbean and
38 Lizard Island on the Great Barrier Reef (GBR). Patterns of fish feeding, and realised
39 ecosystem function, were strikingly similar between the two geographic locations, despite a
40 3-fold difference in the local diversity of nominally herbivorous fishes, a 2.4-fold difference
41 in the diversity of fishes feeding, and differences in the biogeographic history of the two
42 locations. In both regions a single species dominated the function: a surgeonfish, *Naso*
43 *unicornis*, at the GBR location and, surprisingly, a triggerfish, *Melichthys niger*, at the
44 Caribbean location. Both species, especially *M. niger*, were relatively rare, compared to other
45 nominally herbivorous fishes, in censuses covering more than 14000 m² at each location. Our
46 study provides novel insights into the critical function of macroalgal removal in hyperdiverse
47 coral reef ecosystems, highlighting: a) that function can transcend biogeographic, taxonomic
48 and historical constraints; and b) shortcomings in our assumptions regarding fish presence
49 and realised ecosystem function on coral reefs.

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59 **Introduction**

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61 Coral reefs are the embodiment of marine biodiversity in the tropics, with millions of
62 people directly relying on these ecosystems for basic subsistence (Moberg and Folke 1999;
63 Woodhead et al. 2019). Yet coral reefs are also at the forefront of ecosystem transitions, with
64 the effects of climate change manifesting themselves in a particularly pronounced manner
65 through repetitive, global coral bleaching events (Hughes et al. 2018). Coral reefs are primed
66 to undergo major transitions including substantial losses in biodiversity, and the functional
67 extinction of species (Hughes et al. 2017; Barlow et al. 2018). This is expected to have
68 profound consequences for the functionality of these hyperdiverse tropical ecosystems, and
69 makes understanding the nature and role of critical ecosystem functions on geographically
70 distinct reefs, with different potential resilience, a particularly pragmatic endeavor (D'agata
71 et al. 2016; Bellwood et al. 2019c). This situation raises the question: is the operation of
72 critical ecosystem functions uniform or consistent across biogeographically distinct coral reef
73 locations?

74 Trait-based approaches have recently provided new insights into the potential
75 relationships between diversity, ecosystem functions and redundancy of coral reef taxa at
76 large biogeographic scales (Stuart-Smith et al. 2013; Mouillot et al. 2014; Hemingson and
77 Bellwood 2018; McWilliam et al. 2018). Despite these advances, processes are rarely
78 quantified directly at large scales, reducing the clarity of our understanding (Bellwood et al.
79 2019a; Brandl et al. 2019). Indeed, there is a growing recognition of a mismatch between the
80 insights gleaned from quantifying ecosystem functions or processes directly, vs. assumed
81 functions based on proxies, such as traits, or from the presence of key taxa, especially if there
82 is no demonstrable, causal, relationship between taxa or traits and specific ecosystem
83 processes (Bellwood et al. 2019c). Surprisingly, we even lack a comprehensive understanding
84 of the critical ecosystem function of 'macroalgal removal' (sensu Bellwood et al. 2004) at

85 large biogeographic scales. This is one of the most widely quantified processes on reefs,
86 relying on estimated (fish feeding rates) or realised (mass of algae lost) functional metrics
87 (e.g. Rasher et al. 2013; Longo et al. 2015; Plass-Johnson et al. 2015; Bonaldo et al. 2017;
88 Loffler et al. 2018). Such studies on macroalgal removal have substantially enhanced our
89 understanding of the identity of the key taxa involved and provided information on patterns
90 of redundancy vs. complementarity on reefs (e.g. Bennett and Bellwood 2011; Vergés et al.
91 2012; Rasher et al. 2013; Humphries et al. 2015; Loffler et al. 2015; Longo et al. 2015; Streit
92 et al. 2015). Unfortunately, despite this large body of research, experimental limitations (e.g.
93 the range of habitats and/or algal genera considered) have prevented comparisons across
94 global biogeographic locations. This lack of cross-system comparisons limits our ability to
95 understand the impacts of evolution, biodiversity or biogeography on this critical ecosystem
96 function, and to assess our ability to infer function from presence in key fish species.

97 A wide range of fishes have been identified as key players in macroalgal removal on
98 coral reefs (Lewis and Wainwright 1985; Hoey and Bellwood 2009; Rasher et al. 2013;
99 Loffler et al. 2015). Yet geological and evolutionary history has resulted in a situation where
100 the taxonomic and functional diversity of fishes is not evenly distributed among the world's
101 coral reefs (Kulbicki et al. 2013; Bellwood et al. 2017). This is because the two major realms,
102 the Atlantic and Indo-Pacific, have been largely separated for the last 12 million years
103 (Siqueira et al. 2019b). During this time, the Caribbean, in the Atlantic, has been an area of
104 geographic isolation and species extinction, while the Great Barrier Reef (GBR), in the Indo-
105 Pacific, has been a place of refuge and speciation (Floeter et al. 2008; Bellwood et al. 2017;
106 Siqueira et al. 2019a, 2019b). As a result, few coral reef species are shared between the two
107 locations and the GBR hosts a four-fold higher diversity of fishes compared to the Caribbean
108 (Bellwood et al. 2004; Roff and Mumby 2012). This is expected to have significant flow-on
109 effects for function, with the Caribbean and the GBR considered to be functionally distinct

110 (Bellwood et al. 2004, 2019c; Roff and Mumby 2012; Siqueira et al. 2019a). The Caribbean
111 and the GBR therefore, are particularly amenable to examining variation in the nature of
112 ecosystem functions, as reef systems with highly divergent histories. To-date, no single study
113 assessing the ecosystem function of macroalgal removal has accounted for varying habitats
114 and varying algal assay genera (accounting for niche partitioning) across these two disparate
115 biogeographic localities.

116 To capture and directly quantify the function of macroalgae removal, we conducted a
117 series of macroalgal assays encompassing six macroalgal genera, across three distinct reef
118 habitats at two locations: one on the GBR and the other in the Caribbean. Due to the
119 divergent evolutionary histories of the GBR and Caribbean, one might expect a far higher
120 number of macroalgae-feeding species at the high-diversity GBR location, resulting in a
121 wider range of algal genera being targeted and a higher rate of the ecosystem process (i.e.
122 algal removal) (*sensu* Hector and Bagchi 2007; Lefcheck et al. 2015). By contrast, in the
123 lower diversity Caribbean location one might expect: a) reduced levels of the process in
124 question, or b) the process to operate at a similar level, given that they are ecologically
125 similar ecosystems (*sensu* Cody and Diamond 1975). If the latter is the case: a) the lower
126 taxonomic diversity would suggest that fewer species would maintain this function, or that b)
127 the same number of species could maintain the function, as a result of behavioural flexibility
128 in this lower-diversity assemblage. These various alternatives will have implications for reef
129 resilience in the face of changing ecosystem configurations. The aim of this study, therefore,
130 is to quantify the magnitude of this key ecosystem process in the two systems and to examine
131 the nature of its delivery in terms of the number and identity of the species involved.

132 133 **Methods**

134
135 This study was conducted in June 2007 at Snap Shot and Sailfin reefs off Little
136 Cayman Island, in the Caribbean and in January 2008 at Bird Islet and South Island in the

137 Lizard Island Group, GBR (Fig. S1). All four reefs are located within marine management
138 areas that limit fishing. At each reef, three habitats were examined, the reef slope (10–14 m
139 depth), reef crest (2–4 m depth) and back reef (2–4 m depth) and within each habitat, three
140 sites at least 30 m apart. Different habitats were used to encompass the breadth of
141 herbivorous fish feeding activity on reefs in both biogeographic locations.

142 To assess macroalgal removal rates across locations, a series of macroalgal transplant
143 assays were used, consisting of six different macroalgal genera (*Acanthophora*, *Galaxaura*,
144 *Halimeda*, *Laurencia*, *Sargassum*, *Turbinaria*), encompassing a range of taxonomic and
145 functional groups. Species within each macroalgal genus were selected with similar growth
146 forms to facilitate direct comparisons between biogeographic locations. Macroalgal thalli
147 were collected by hand from adjacent shallow water habitats (primarily reef flat and shallow
148 back reef/lagoonal areas) and transferred to recirculating seawater aquaria until they were
149 used in the feeding trials. All algae were used within three days of collection.

150 For algal assays, each thallus was spun in a salad spinner for 30 s to remove excess
151 water, and the wet mass of the thallus recorded (see Table S2 for initial masses). Macroalgae
152 were offered to reflect their usual growth form to assess selectivity of genera (rather than
153 assessing preference by offering ‘equal-sized’ specimens, (see Mantyka and Bellwood 2007)).
154 The macroalgae were attached separately to coral rubble with a rubber band and deployed
155 haphazardly together within a 1 m² area at each site. After 8 h on the reef (~0900-1700 to
156 encompass most herbivorous fish feeding activity), the macroalgae assays were collected,
157 spun and reweighed (as above) to determine the mass of algae lost (details of handling
158 controls are in the supporting information). The deployment procedure was replicated across
159 three days in each site, reef and habitat (n = 54 in each biogeographic location).

160 To identify the fish species feeding on the macroalgal assays, stationary underwater
161 digital video cameras (Sony DCR-SR100 HDD cameras in Ikelite housings) were used to

162 record feeding activity. A camera mounted on a concrete block was positioned approximately
163 2 m from one of the three macroalgal assays in each reef within each habitat. Filming
164 commenced immediately after the assays were deployed (a small bar was placed adjacent to
165 the assays for ~10 s to allow calibration of fish sizes on the footage) and was continuous for 8
166 h (~0900 – 1700 h), apart from a 2 – 4 min interval after 4 h to change batteries. This
167 procedure was replicated three times within each habitat in each reef (a total of 144 h of total
168 video in each biogeographic location). All video footage was viewed, recording the number
169 of bites on each macroalgal genus, the fish species and size (total length to the nearest cm).
170 Fish biomass was estimated using Bayesian length-weight regression parameters (Froese and
171 Pauly 2018), and a biomass-standardised bite impact (the product of biomass and number of
172 bites following Bellwood et al. 2006a) was calculated to account for body size related
173 variation in bite size.

174 The nominal herbivorous fish community in the vicinity of the assay deployment sites
175 was also characterized in each location (see ESM table S3). This was achieved by counting
176 nominally herbivorous fishes >10 cm total length (TL) on SCUBA along 5 m wide transects
177 and all fishes <10 cm TL on 1 m wide transects, during ten-minute timed swims. All relevant
178 fishes from the benthos to the water surface were recorded during swims (size stratified
179 censuses permitted full water column quantification, other methods such as traditional belt
180 transects targeting more demersal fishes may be more limited in this regard). All fishes were
181 placed into TL size categories (2.5 cm classes for fishes <10 cm, 5 cm classes for fishes >10
182 cm TL). Fish biomass was subsequently estimated using Bayesian length-weight regression
183 parameters and/or published length-weight regression parameters (Froese and Pauly 2018).
184 For biomass estimates all fish size classes were considered. For total abundance estimates
185 only fishes >10 cm TL were considered as fishes in smaller size classes have limited
186 functional impacts on macroalgae but contribute disproportionately to abundance estimates

187 (following Bellwood et al. 2019c). Four timed swims were performed in each habitat at each
188 reef, with each swim covering approximately 117 ± 27 m (mean \pm SE). Full details of the
189 methods are given in (Bellwood and Wainwright 2001; Wismer et al. 2009).

190

191 *Statistical analysis*

192 A series of linear and generalised linear mixed effects models (LMEs and GLMMs)
193 were used to examine herbivorous fish feeding rates and genera-specific macroalgal removal
194 rates between biogeographic locations. Herbivorous fish feeding rate was examined using
195 both absolute bites and biomass-standardised bites per hour. In both cases bite rates were
196 standardised by the initial algal mass offered in each assay, separately for each genus, thus
197 accounting for differences in algal assay mass. Macroalgal removal was also considered as a
198 response variable in the models in two ways: absolute and relative loss of mass, to examine
199 the function rate and also to account for differences in the initial mass.

200 In all cases both LMEs as well as GLMMs fitted with a Beta (proportional data) and
201 Gamma, lognormal, or log-transformed distribution were considered. A small constant
202 (0.001) was added across the data in the case of Gamma and lognormal models to allow them
203 to be fitted, due to the presence of zeroes. Final models were selected based on the residual
204 plots and the fit of the model to the data (Table S5). In all models, algal genera,
205 biogeographic location and habitat were fitted as fixed effects with all two-way interactions.
206 Reef and algal assay identity nested within reef were fitted as random effects to account for
207 any lack of independence especially between algae within the same arrays. Full models with
208 all two-way interactions were initially fitted, followed by subsequent model simplification
209 based on six relevant models in each case. Selection of the most parsimonious model was
210 based on the corrected Akaike Information Criterion (AICc) (Table S4). Model assumptions
211 and fits were assessed using residual plots. To examine within-level differences, comparisons

212 between biogeographic locations for each algal genera were performed using pairwise means
213 comparisons. All statistical analysis was performed in the software R (R Core Team 2018),
214 using the *lme4* (Bates et al. 2015), *glmmTMB* (Brooks et al. 2017), *MuMIn* (Barton 2018),
215 *bipartite* (Dormann 2008) and *emmeans* (Lenth 2019) packages.

216

217 **Results**

218 Estimated ecosystem function (biomass-standardised bite rate) was dominated by a
219 single species at each location (Fig. 1). The surgeonfish, *Naso unicornis*, and the triggerfish,
220 *Melichthys niger*, accounted for 82.5% and 62% of the biomass-standardised bites delivered
221 to algal assays at Lizard Island and Little Cayman, respectively, while only accounting for
222 4.7% and 2.7% of the total abundance (14.5% and 2.2% of total biomass), of species recorded
223 feeding in the vicinity, respectively (Fig. 1). The biomass-standardised bites of *N. unicornis*
224 were largely delivered on *Sargassum* (94.1% of bites), while *M. niger* predominantly fed on
225 *Galaxaura* (79.7% of bites) (Figs 1e, f, S2). Collectively, the top three species at each
226 location accounted for more than 93% of all biomass-standardised bites delivered in both
227 cases (Fig. 1). Despite this marked similarity in patterns, there was a substantial difference in
228 the diversity of fish species recorded biting the assays. Fish feeding richness was more than
229 2.4-fold higher in the GBR location compared to the Caribbean location (Fig. 1), reflecting
230 the diversity of nominally herbivorous fishes detected in the vicinity (3-fold higher on the
231 GBR) (Table S3).

232 Despite marked differences in the taxonomic richness of fishes recorded feeding on
233 the macroalgal assays, this did not appear to translate to higher overall estimates of
234 ecosystem function for either absolute bite rate, or biomass-standardised bite rate (Figs 2, S3)
235 per gram of algae offered. Furthermore, it did not appear to result in a greater breadth of
236 feeding across algal genera, with all genera being fed on to varying extents across both

237 biogeographic locations. For both absolute and biomass-standardised bite rates per gram of
238 algae offered, the models suggested that the interaction between location and algal genera
239 was influential (Table S4). However, only *Sargassum* and *Acanthophora* received
240 significantly higher absolute bite rate on the GBR relative to the Caribbean ($p < 0.01$ and
241 < 0.05 respectively; Tables S5, S6). Furthermore, in terms of biomass-standardised bite rates,
242 significant differences were limited to higher rates on the GBR on *Sargassum* ($p < 0.01$; Table
243 S5, S6) and *Turbinaria* ($p < 0.01$; Tables S5, S6). For the majority of algal genera, there were
244 negligible differences in feeding rates between biogeographic locations with no statistically
245 significant differences detected (Figs 2, S3; Tables S5, S6).

246 The results of realised ecosystem function (macroalgae removed) were remarkably
247 similar to those for estimated ecosystem function (fish feeding rate) (Figs 3, S4). For the
248 majority of algal genera, there were negligible differences in terms of both percentage of
249 mass removed and absolute mass removed (Figs 3, S4), with no statistically significant
250 differences detected in most cases (Figs 3, S4; Tables S5, S6). The only significant
251 differences between the Caribbean and GBR was a higher absolute loss of *Sargassum* and
252 *Halimeda* ($p < 0.001$ and < 0.05 respectively; Tables S5, S6) on the GBR. Therefore, despite
253 the use of two different metrics to quantify algal loss, with one accounting for differences in
254 initial algal mass and the other focusing on a measure of the process (algal removal rates),
255 both metrics largely converged on similar results: limited between-location differences.

256 In all models, the interactions between habitat and both biogeographic location and
257 algal genera were influential (Table S4). As expected, there were some nuanced differences
258 in the response variables (feeding rates and removal rates) among different habitats across
259 algal genera and between biogeographic locations (Figs S3, S4). However, in most cases,
260 especially for feeding rates and absolute removal rates, the similarity between biogeographic
261 locations was marked (Figs S3, S4).

263

266

267 **Discussion**

268 Overall, the Caribbean and GBR exhibit a four-fold difference in the diversity of reef
269 fishes as a result of markedly different biogeographic histories (Kulbicki et al. 2013;
270 Bellwood et al. 2017; Hemingson and Bellwood 2018). The taxonomic and functional
271 composition of the herbivorous fish assemblage is, likewise, strikingly different (Bellwood et
272 al. 2004; Roff and Mumby 2012; Siqueira et al. 2019a). This is mirrored across reefs at our
273 two locations, Little Cayman and Lizard Island, where there was a 3-fold difference in the
274 richness of nominally herbivorous fishes. Despite expectations that such differences might
275 yield increased ‘functionality’ at Lizard Island, we found no consistent between-location
276 differences in macroalgal removal. Indeed, in the face of a 2.4-fold difference in the richness
277 of fishes recorded feeding on the assays, we revealed marked similarities in the extent of
278 algal consumption, in terms of both estimated (bites delivered) and realised (mass removed)
279 ecosystem function. Furthermore, regardless of the location and regional diversity, a single
280 species dominated the process, with more than 93% of biomass-standardised bites being
281 delivered by just three species in each location. Despite biogeographic, taxonomic and
282 historical constraints, there were remarkable similarities in the delivery of ecosystem process
283 in these two biogeographic locations. When it comes to the process of macroalgal removal on
284 coral reefs, it appears that the delivery of this function may transcend biodiversity,
285 biogeographic locations, and evolutionary history.

286 While a similar number of species contributed to >90% of mass-standardised bites at
287 both locations, there was evidence of greater behavioural flexibility in the less species rich
288 Caribbean location. At our GBR location, *Naso unicornis*, a specialist macroalgal feeder
289 (Choat et al. 2002; Hoey and Bellwood 2009) dominated; however, the omnivorous
290 triggerfish, *Melichthys niger* (Kavanagh and Olney 2006; Mendes et al. 2019), was the

291 dominant species at our Caribbean location. The identification of *M. niger*, in this context
292 was particularly surprising (but see Randall 1967; Mendes et al. 2019). To-date, evidence
293 from the Caribbean generally suggests that the sparisomatine parrotfishes dominate
294 macroalgal removal (Sparisomatina; Bellwood et al. 2019b; Siqueira et al. 2019b) with
295 secondary roles attributed to *Acanthurus* surgeonfishes (e.g. Lewis and Wainwright 1985;
296 Burkepile and Hay 2008; Catano et al. 2016; Shantz et al. 2017; Topor et al. 2019). While
297 four different species of *Sparisoma* were recorded feeding on assays, collectively making up
298 40% (abundance) and 46% (biomass) of the nominal herbivorous fish community in the
299 general vicinity, they contributed less than 3.3% of estimated ecosystem function (biomass-
300 standardised bites delivered).

301 Our results differed from expectations based on previous herbivory studies in the
302 Caribbean which may be due to location-specific variation in herbivore communities and/or
303 methodological differences. Many previous Caribbean studies used the seagrass *Thalassia* in
304 bio-assays (e.g. Hay 1984; Lewis and Wainwright 1985; Catano et al. 2016), whereas we
305 used a representative range of macroalgal targets (with no seagrass). The clear preference of
306 *M. niger* for feeding on *Galaxaura* (79.7% of all biomass-standardised bites delivered by *M.*
307 *niger* where on *Galaxaura*) suggests that if this genus of macroalgae was not included in
308 algal assays much of the feeding activity of *M. niger* would not be recorded. Indeed, studies
309 from Brazilian reefs that share identical or sister-species to those found on Caribbean reef
310 systems, have shown that a diversity of fishes are involved in macroalgae removal, with the
311 fishes responsible being dependent on the identity of the algae used in assays (Longo et al.
312 2015; Mendes et al. 2015).

313 Although macroalgal removal is perhaps the single best-studied function on reef
314 systems (Bellwood et al. 2019c) and the Caribbean is one of the most frequently studied coral
315 reef regions, the identification of *M. niger* as the principle macroalgal remover came as a

316 surprise. Interestingly, our findings were remarkably similar to those found on the GBR
317 where the batfish *Platax pinnatus* (Bellwood et al. 2006a) and the rabbitfish *Siganus*
318 *canaliculatus* (Fox and Bellwood 2008), were identified as the key macroalgal removers of
319 large (>2 m) *Sargassum* thalli and small <50 cm *Sargassum* fronds, respectively. The former
320 was previously known as an invertivore and the latter had not been previously recorded at the
321 study area. Collectively, this series of results highlight the inherent flexibility of fishes
322 involved in the process of macroalgae removal. However, while the identity of the fishes
323 involved in the process can differ fundamentally in different circumstances, the process itself,
324 macroalgae removal, appears to be relatively conserved, supporting calls for a more direct
325 process-based assessment of coral reef functioning (Bellwood et al. 2019a; 2019c).

326 Our observations bring to the fore the dangers of attributing functional importance to
327 species based solely on their presence, abundance, biomass and assumed trophic roles, an
328 observation that has been raised repeatedly for more than three decades (Steneck 1983; Hoey
329 and Bellwood 2009, 2010b; Bellwood et al. 2019c; Streit et al. 2019). Once again, despite
330 relatively diverse nominal herbivorous fish assemblages in both localities, the key functional
331 taxa involved in macroalgal removal were relatively rare (especially *M. niger*), even using
332 methods specifically designed to minimise diver effects (Dickens et al. 2011; Emslie et al.
333 2018). Unfortunately, as Steneck (1983) originally highlighted, such methods are designed to
334 describe and quantify fish distribution patterns, not processes. Unlike sessile reef organisms,
335 such as corals, our assumptions regarding the spatial delivery of functions by fishes can be
336 overwhelmed by their inherent behavioural flexibility (Bellwood et al. 2006b, 2019c; Rasher
337 et al. 2017).

338 So, how useful are functional studies that apply functions to fishes based on their
339 presence? Recent functional inferences from trait-based studies have suggested that despite
340 large regional variation in taxonomic richness, functional redundancy and vulnerability,

341 functions may be maintained across biogeographic realms on reefs (Mouillot et al. 2014;
342 Hemingson and Bellwood 2018; McWilliam et al. 2018). Unfortunately, such studies do not
343 quantify functions directly. Instead, they rely on inferences from traits and ‘trait-space’. How
344 such inferences translate to specific functions is currently unclear (Bellwood et al. 2019c).
345 Our more direct approach herein, builds on these trait-based approaches (Mouillot et al. 2014;
346 Siqueira et al. 2019a) by providing detailed, quantitative measures of one function across two
347 vastly different biogeographic locations. Interestingly, despite the inherent problems with,
348 and assumptions in, trait-based approaches, our study supports their general inference (that
349 function can be conserved across biogeographic locations), at least for the process of
350 macroalgal removal. Other functions require further assessment.

351 If a difference in the function of macroalgae removal exists between
352 biogeographically distinct coral reefs, it should have been reasonably pronounced between
353 the two locations examined herein. Indeed, the Caribbean as a whole, represents a
354 depauperate system as a result of extinctions and the loss of herbivorous taxa over
355 evolutionary timescales (Bellwood et al. 2017; Siqueira et al. 2019a, 2019b). For example,
356 fossil evidence suggest that the Caribbean contained nasine surgeonfish in the Neogene and
357 probably also siganids (Bellwood et al. 2017; Siqueira et al. 2019a, 2019b). Given the loss of
358 these key taxa, and a limited trait-space, one might reasonably expect some degree of
359 functional constraint in today’s Caribbean reef fish assemblages. It is therefore quite
360 remarkable that we found no major, consistent, differences in the magnitude of macroalgal
361 removal between our two biogeographically distinct locations.

362 The removal of macroalgae is just one component of the broader ecosystem function
363 of herbivory and is often performed by a narrow range of fish species which together
364 represent a ‘secondary line of defense’ against the establishment and overgrowth of
365 macroalgae (reviewed in Puk et al. 2016). The full suite of herbivory processes on coral reefs

366 encapsulates a wider range of species involved in the cropping of algal turfs (Robinson et al.
367 2019), removal of algal turf sediments (Tebbett and Bellwood 2019), maintenance of
368 microtopographic refuges (Brandl et al. 2014) and bioerosion (Perry and Harborne 2016).
369 This full suite of herbivore activities collectively play an important role in limiting the
370 overgrowth, development and/or establishment of macroalgae (Hughes et al. 2007; Dell et al.
371 2016; Loffler and Hoey 2019). As such, directly quantifying and comparing other facets of
372 herbivory across distinctly different global reef locations may offer other rich insights into
373 coral reef functioning.

374 Importantly, our study provides direct evidence, through quantification of macroalgae
375 removal across a number of different algal genera and locations that estimating or attributing
376 primary roles of macroalgal removal based on the abundance of resident herbivores or status
377 quo of other reef systems may be incorrect. This further highlights the need to consider the
378 context of the reef in question when implementing management approaches that aim to
379 conserve ecosystem functioning and resilience (Bellwood et al. 2019c). It is likely that
380 investigation of the nuanced differences in fish species selectivity for different algal genera
381 (see Longo et al. 2015; Mantyka and Bellwood 2007; Mendes et al. 2015) across different
382 reef systems would offer further surprises, as was the case with *M. niger* in the current study.
383 Many macroalgae are chemically defended and rich in structural carbohydrates (Hay and
384 Fenical 1988; Rasher et al. 2013), representing significant digestive challenges (Choat and
385 Clements 1998). This paves the way for evolutionary niche diversification of fish-related
386 macroalgal palatability across locations which may be significant and differ even within-
387 species with broad distributions.

388 Similarly, different fish species may play distinct roles in macroalgae removal among
389 reef habitats (e.g. Hoey and Bellwood 2010a; Loffler et al. 2015; Longo et al. 2015). As reef
390 zonation is a major structuring force on coral reefs (Bellwood et al. 2018; Hay et al. 1983;

391 Lewis and Wainwright 1985; Russ 1984), we accounted for habitat-level variability in our
392 models to capture the process of macroalgae removal more holistically across our study
393 locations. However, in doing so, we have not specifically explored habitat level variability
394 beyond noting that there are differences among habitats (Figs S3, S4).

395 It should be noted that this experiment, while biogeographically broad, was only
396 conducted at a single location in each region and over a relatively short temporal scale. As
397 such this limits the strength of regional-scale inferences in the present study, especially as
398 previous evidence suggests different species may dominate algal removal in different
399 locations or at different times (Steneck 1983; Bennett and Bellwood 2011; Lefèvre and
400 Bellwood 2011; Vergés et al. 2012; Loffler et al. 2015; Longo et al. 2015; Topor et al. 2019).
401 Nonetheless, our aim was to investigate variation in herbivory across very distinct locations
402 to identify whether this important ecosystem process was delivered in a similar fashion. If
403 we are to move forward in our quest to quantify dynamic processes on coral reefs (see Brandl
404 et al. 2019), we must recognise that ground-truthing our assumptions at such broad spatial
405 scales is a necessary step towards asking the right questions using the most appropriate
406 metrics in the first place. This study is a first step in examining realised functions across
407 globally distinct locations without relying on proxies of functions, such as traits, that often
408 have only weak correlative links to functions (Bellwood et al. 2019c).

409 While it should be noted that the algal species were not identical between
410 biogeographic locations and that they were presented in experimental arrays, we did use
411 identical genera and techniques at both locations, and in both cases the response of fishes was
412 rapid, i.e. they started feeding soon after deployment. While total function rates were broadly
413 similar between locations, some differences between systems were still evident, especially
414 that of *Sargassum* removal rates. These differences appear to be due to the impact of *N.*
415 *unicornis*, a specialist *Sargassum* feeder (Choat et al. 2002; Hoey and Bellwood 2009),

416 and/or the use of larger *Sargassum* thalli at our GBR location (Hoey 2010). However, by
417 using multiple metrics to quantify macroalgae removal we were able to assess removal rates
418 and account for differences in initial algal mass between locations. If these metrics had
419 diverged substantially in their conclusions, then this would have made the interpretation of
420 results more complex and less relevant in a global context. However, the different metrics
421 largely converged on similar results in terms of macroalgae removal between biogeographic
422 locations. Indeed, the similarity in patterns for the bulk of macroalgal removal, including the
423 role of just a small group of species, was remarkable considering the striking biogeographic,
424 evolutionary and taxonomic differences between the locations.

425 Our data suggest that ecosystem function can transcend biogeographic locations and
426 associated taxonomic, historic and functional constraints on coral reefs. In both our GBR and
427 Caribbean locations, a limited range of species fed disproportionately on the macroalgal
428 assays. As coral reefs continue to be ravaged by anthropogenic stressors, especially climate
429 change, and as they transition towards new lower-diversity configurations (Hughes et al.
430 2017; Bellwood et al. 2019a), our results offer some cautious optimism that functions may be
431 sustained. This study also provides a comparative framework for directly quantifying
432 processes on coral reefs at a global scale, as opposed to relying on traits or proxies that are
433 easier to measure (see Bellwood et al. 2019c). This framework revealed surprising results,
434 even though macroalgal removal is perhaps the single best-studied function on coral reefs.
435 Our study highlighted: a) the importance of key species in supporting critical functions on
436 coral reefs, and b) in this example, the limited role of biogeography and biodiversity in
437 shaping the magnitude of ecosystem functions in high-diversity ecosystems.

438

439

440

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448

449 **Conflict of interest statement**

450 On behalf of all authors, the corresponding author states that there is no conflict of interest.

451

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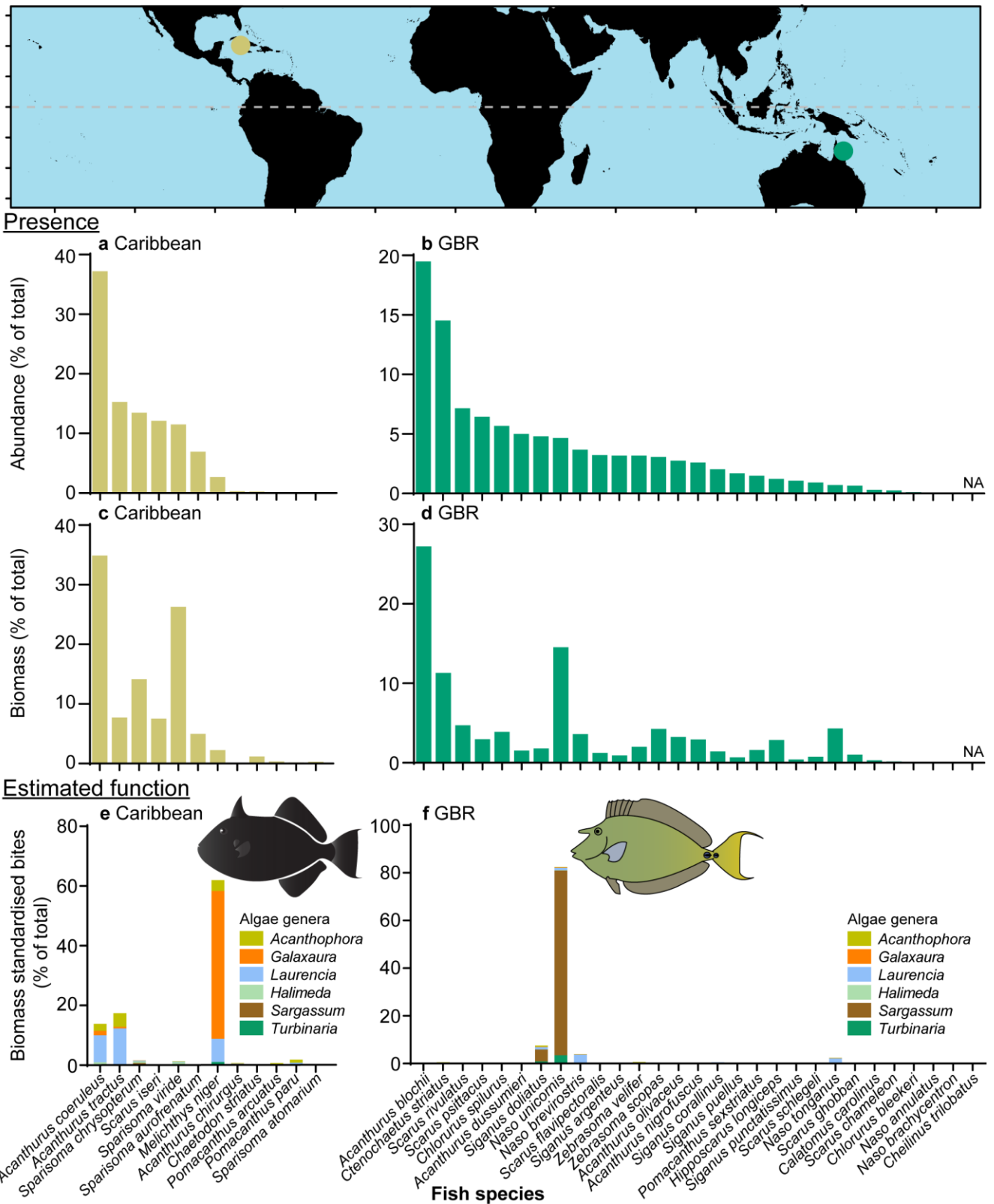
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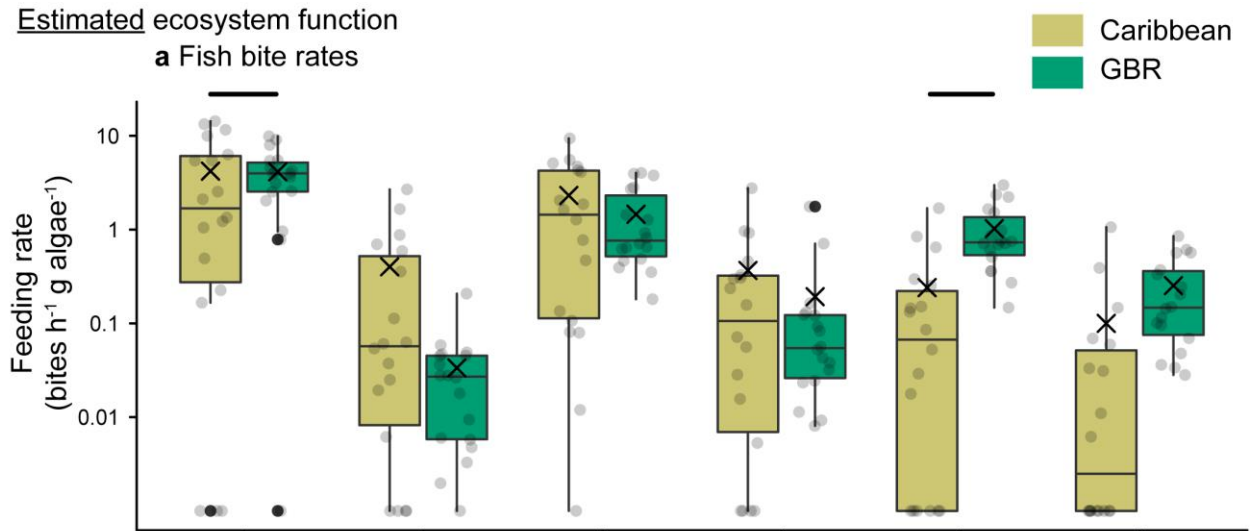
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668 **Fig. 1** The contribution of fish species recorded feeding on the assays to **a, b** total abundance

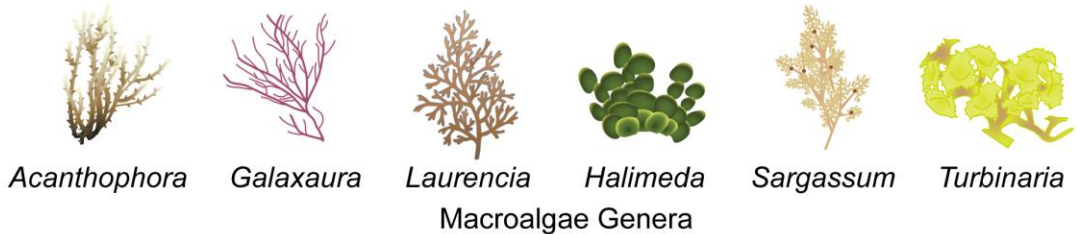
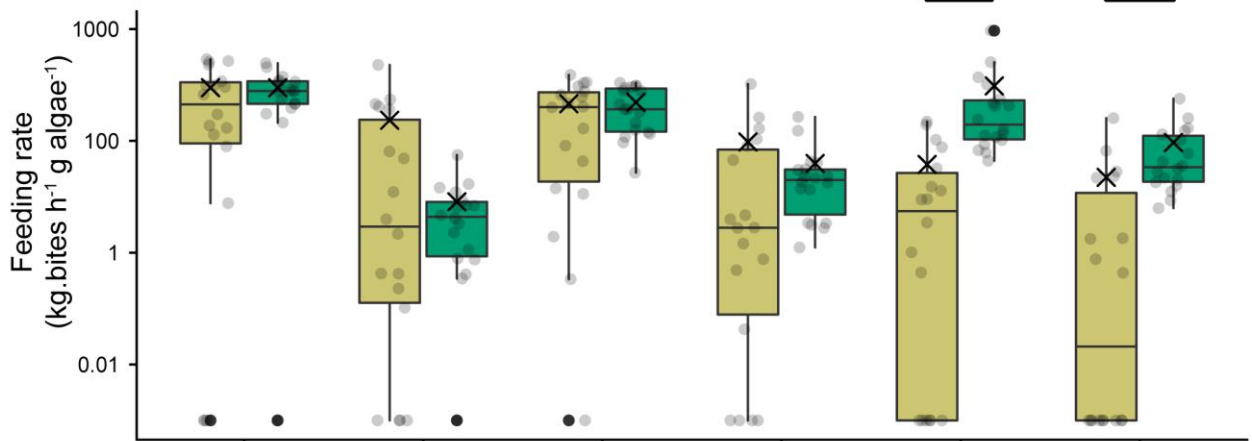
669 (based on individuals >10 cm) and **c, d** biomass (based on all fish size classes) in the vicinity

670 of algal deployment sites at Little Cayman (Caribbean) and Lizard Island (Great Barrier
671 Reef), respectively. **e, f** The contribution of fish species, in terms of total biomass
672 standardised bites on macroalgal assays, across six macroalgae genera, at Little Cayman
673 (Caribbean) and Lizard Island (Great Barrier Reef), respectively (for more details see Fig.
674 S2). Percent bites from 144 h of video recording in each realm. Note the large contribution of
675 a single species in each case. Furthermore, note the far larger diversity of fishes feeding on
676 assays in the GBR (29 spp.) relative to the Caribbean (12 spp.), yet their small overall
677 contribution to the total function. NA indicates no abundance data for this species.
678

Estimated ecosystem function
a Fish bite rates



b Fish biomass-standardised bite rates



679

680 **Figure 2** Differences in estimated ecosystem function. **a** fish feeding rates, and **b** biomass

681 standardised feeding rates between Little Cayman (Caribbean) and Lizard Island (Great

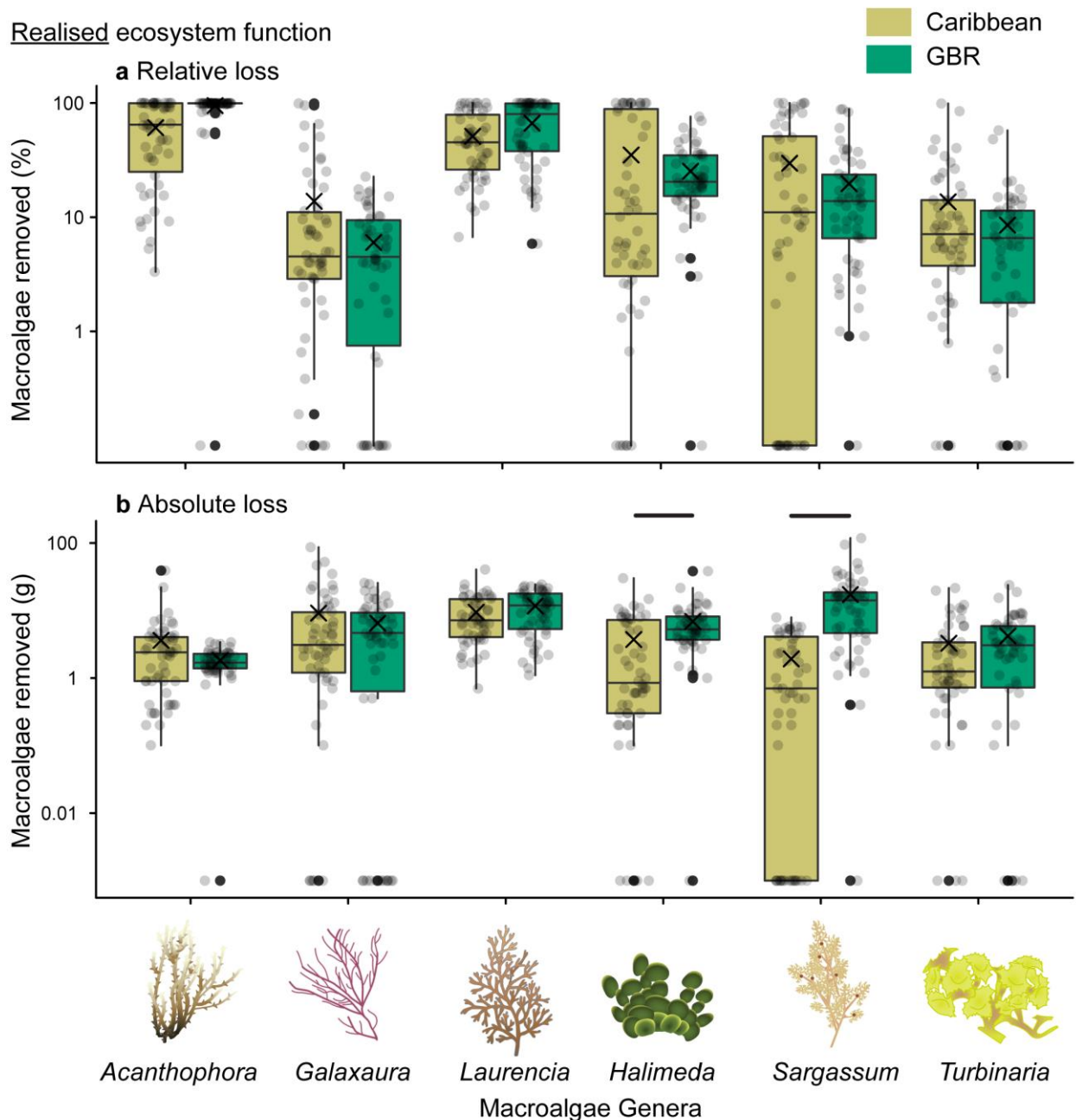
682 Barrier Reef; GBR) for each algal genus offered in the algal assays. Boxplots show the

683 median and 25% quantiles, black dots are outliers, grey dots are raw data points, and crosses

684 are the means. Note that both y axis are on a \log_{10} scale. Black lines above boxplots indicate

685 significant differences ($\alpha < 0.05$).

686



687

688 **Figure 3** Differences in realised ecosystem function. **a** percentage of algae removed, and **b**

689 absolute biomass of algae removed between Little Cayman (Caribbean) and Lizard Island

690 (Great Barrier Reef; GBR) for each algal genus offered in the algal assays. Boxplots show the

691 median and 25% quantiles, black dots are outliers, grey dots are raw data points, and crosses

692 are the means. Note that both y axis are on a \log_{10} scale. Black lines above boxplots indicate

693 significant differences ($\alpha < 0.05$).