

Coral species composition drives key ecosystem function on coral reefs

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1 **Title**

2 Coral species composition drives key ecosystem function on coral reefs

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15 **Abstract**

16 Rapid and unprecedented ecological change threatens the functioning and stability of
17 ecosystems. On coral reefs, global climate change and local stressors are reducing and
18 reorganising habitat-forming corals and associated species, with largely unknown
19 implications for critical ecosystem functions such as herbivory. Herbivory mediates coral-
20 algal competition, thereby facilitating ecosystem recovery following disturbance such as
21 coral bleaching events or large storms. However, relationships between coral species
22 composition, the distribution of herbivorous fishes, and the delivery of their functional impact
23 are not well understood. Here, we investigate how herbivorous fish assemblages and delivery
24 of two distinct herbivory processes, grazing and browsing, differ among three taxonomically
25 distinct, replicated coral habitats. While grazing on algal turf assemblages was insensitive to
26 different coral configurations, browsing on the macroalga *Laurencia cf. obtusa* varied
27 considerably among habitats, suggesting that different mechanisms may shape these
28 processes. Variation in browsing among habitats was best predicted by the composition and
29 structural complexity of benthic assemblages (in particular the cover and composition of
30 corals, but not macroalgal cover), and was poorly reflected by visual estimates of browser
31 biomass. Surprisingly, the lowest browsing rates were recorded in the most structurally
32 complex habitat, with the greatest cover of coral (branching *Porites* habitat). While the
33 mechanism for the variation in browsing is not clear, it may be related to scale-dependent
34 effects of habitat structure on visual occlusion inhibiting foraging activity by browsing fishes,
35 or the relative availability of alternate dietary resources. Our results suggest that maintained
36 functionality may vary among distinct and emerging coral reef configurations due to
37 ecological interactions between reef fishes and their environment determining habitat
38 selection.

39

40 **Keywords**

41 *Species composition; ecosystem function; habitat selection; herbivory processes; community*

42 *structure; climate change*

43

44 **Introduction**

45

46 Global climate change and mounting local stressors are degrading ecosystems via species
47 extirpations and introductions, modifying the composition of assemblages and threatening
48 ecological function [1,2]. Non-random species turnover, ordered by the susceptibility of
49 organism traits [3], is increasing the taxonomic and functional similarity of communities [4-
50 6]. These changes can disrupt ecosystem processes, such as habitat provisioning [7,8],
51 primary productivity [9], trophic energy flow [10], nutrient cycling [11,12], and pollination
52 [13]. Whilst evidence exposes a coherent pattern of ecological change across biomes [14],
53 variation exists from the individual to community level in how ecological structure,
54 ecosystem processes, and ongoing disturbance dynamics interact [15,16]. For effective and
55 adaptive local management, better understanding is needed of the extent to which different,
56 and in some cases emerging, species configurations support processes critical to ecological
57 stability [17].

58

59 We focus on coral reefs, one of the most biodiverse but threatened ecosystems [18], to
60 elucidate how the composition of habitat-building species (i.e. corals) influences key
61 ecosystem functions. Climatic changes and local human impacts have reduced populations of
62 corals, resulting in unprecedented loss of coral cover and marked shifts in coral species
63 composition due to differential susceptibilities of corals to thermal stress, severe storms,
64 predation by crown-of-thorns starfish, and poor water quality [19,20]. Typically stress-
65 sensitive, topographically complex branching corals (e.g. Acroporidae) are replaced by more
66 robust, prostrate corals (e.g. Mussidae, Poritidae) following disturbance [20,21]. The
67 composition and cover of coral species are key determinants of the structural complexity of
68 reef habitats [21,22], and can exert considerable influence over the taxonomic and functional

69 structure of reef fish assemblages [6]. However, the capacity of altered coral species
70 configurations to support key ecosystem processes despite on-going disturbance is largely
71 unknown and of growing concern [20,23].

72

73 Herbivory, the consumption of algal material, is dominated by fishes on coral reefs with
74 relatively intact fish assemblages. Herbivory processes can promote coral dominance by
75 reducing the cover and/or biomass of algae, though the amount of herbivory necessary will
76 depend on the extent of substrate available to algae, background nutrient levels that can
77 accelerate algal increase [24], and the effect of anthropogenic ocean warming on corals [25].
78 If herbivory is sufficient, it can mediate competitive interactions with corals [26], mitigate
79 shifts to macroalgal dominance following extensive coral mortality, and facilitate recovery of
80 coral populations [27]. However, the distribution of herbivorous fishes and their rates of
81 herbivory can be highly spatially variable; among regions [28,29], latitudes [30], across the
82 continental shelf [31], with the amount of nutrients entering the system [32], and among reef
83 zones [33,34]. Importantly, rates of herbivory by fishes often vary among sites within reef
84 zones [35,36], with studies relating variation to differences in habitat structural complexity
85 [28], the cover of live coral [29,37], the relative palatability of resident algal communities
86 [34,38], predation pressure, or competition for resources [39]. Where variation in herbivory is
87 driven by the differential composition of benthic reef habitats [35], this may carry
88 implications for the variable functioning of distinct coral species configurations. However,
89 relationships between coral species composition and herbivory processes by fishes at the
90 within-reef scale remain unclear.

91

92 Herbivory processes are diverse, carried out by multiple species that perform complementary,
93 and in some cases functionally overlapping, roles in removing algae from the reef substrate

94 [40,41]. For example, grazing fishes (including algal croppers/detritivores, scrapers, and
95 excavators) feed on surfaces covered by epilithic algal matrices (EAM: a conglomerate of
96 algal turfs, macroalgal propagules, sediment, detritus and microbes; [42]), but have limited
97 capacity to remove large fleshy macroalgae [38]. By feeding on EAM covered surfaces,
98 grazers maintain algal communities in a cropped state, reduce the growth of macroalgal
99 propagules within the EAM, reduce coral-algal competition and thereby facilitate settlement,
100 growth and survival of corals and coralline algae [41]. In contrast, macroalgal browsers
101 typically feed on larger fleshy macroalgae and have the potential to reverse phase shifts by
102 removing macroalgae biomass, facilitating the recovery of coral populations [27,43].
103 Understanding the extent to which different configurations of structurally distinct corals
104 maintain populations of herbivorous fishes and the critical functions they provide, is
105 paramount for the management of ecological integrity yet is largely unknown.

106

107 The primary objective of this study was to investigate how grazing and browsing herbivory
108 processes by reef fishes varied among coral habitats that differed in coral species composition
109 and structural complexity across within-reef scales [22]. Using a combination of *in situ*
110 surveys and transplanted algal assays across three replicated habitats characterised by the
111 predominance of distinct coral taxa (*sensu* [22]), we specifically ask the following questions:
112 1) Do the structure of herbivorous fish assemblages and rates of grazing and browsing vary
113 among reefs characterised by distinct coral habitats? 2) What is the relative influence of coral
114 species composition and structural complexity, and herbivore biomass on these herbivory
115 functions within reefs?

116

117 **Methods**

118

119 *Study sites*

120

121 This study was conducted in April and May 2016 on coral reefs surrounding the continental
122 high islands of the Lizard Island Group, 33 km off the mainland coast of Cape Flattery in the
123 northern Great Barrier Reef (14°41'S, 145°27'E; Fig. S1). Three replicate sites of three
124 taxonomically and structurally distinct coral habitats were selected on shallow (<6 m) reefs,
125 based on surveys completed in September 2015 [22]. These three habitats were characterised
126 by predominant cover of: i) branching *Porites* (mostly *P. cylindrica*); ii) soft coral (mostly
127 *Lobophyton*, *Sarcophyton*, and *Sinularia*); and iii) mixed coral assemblages (mostly staghorn,
128 corymbose and plating *Acropora*, massive and branching *Porites*, *Lobophyton*, *Sarcophyton*)
129 (Fig. S2; Table S2). The study coincided with a large-scale coral-bleaching event at Lizard
130 Island [44], with fish and benthic communities affected across the study sites [6]. At each
131 site, we quantified herbivore fish and benthic assemblages (including extent of coral
132 bleaching), and the consumption of algal turfs and a locally abundant macroalga. All sites
133 (each >250 m x 5 m) were positioned on the leeward side of the islands protected from the
134 prevailing south-east swell, had comparable geomorphology and water clarity [45,46], and
135 were separated by >500 m.

136

137 *Benthic composition and herbivore assemblages*

138

139 Benthic composition was quantified along six 30 m point-intercept transects at each site,
140 recording the substratum immediately under the tape every 25 cm (120 points per transect).
141 Transects were positioned approximately 2.5 m from, and parallel to, the reef-sand interface.
142 Substratum categories were hard (scleractinian) corals identified to genus (or species where
143 possible) and morphology, soft (alcyonacean) corals identified to genus, 'other sessile

144 invertebrates' (mainly clams, sponges, and ascidians), macroalgae identified to genus, 'dead
145 substrata' (dead coral and pavement, covered in EAM), rubble, and sand. For corals directly
146 under surveyed points, the extent of bleaching was assessed *in situ* using the CoralWatch
147 colour reference card estimating coral tissue colour saturation on a 6-point scale (1-2
148 considered 'bleached').

149

150 To account for behavioural plasticity, functional overlap, and uncertainty regarding specific
151 herbivore species particularly across their different life history stages [40,43,47], the
152 abundance and total length (TL; nearest cm) of all nominally herbivorous fishes (i.e.
153 Acanthuridae, Kyphosidae, Pomacanthidae, Scarinae, Siganidae, Pomacentridae; Table S1)
154 were visually censused along the same six 30-m transects used to quantify benthic
155 assemblages. Omnivorous herbivores known to consume algae in addition to zoobenthos and
156 zooplankton were also censused. Fishes >10 cm TL were recorded within a 5-m wide belt
157 while initially deploying the transect tape to minimise disturbance to fish assemblages, and
158 those ≤ 10 cm TL were recorded within a 1-m wide belt on the return swim. Fish abundance
159 estimates were standardised per 150 m² and converted to biomass (kg ha⁻¹) using published
160 species length-weight relationships (Table S1). All surveyed species were categorised into six
161 nominal groups (i.e., macroalgal browsers, croppers/detritivores, scrapers, excavators,
162 farmers, and omnivorous herbivores) based on their diet and feeding behaviour (Table S1).

163

164 *Rates of herbivory*

165

166 To quantify rates of grazing on algal turfs among habitats, we exposed established turf algal
167 communities on terracotta tiles (10 x 10 x 1 cm) with to resident herbivores at each site for
168 seven days. To establish turf algal communities, 79 tiles were deployed at a single shallow

169 reef site (~2 m depth) at Lizard Island, covered with plastic mesh (5 cm square mesh) to
170 exclude feeding by large herbivorous fishes and left *in situ* for six months. After this period,
171 the tiles were collected, and eight haphazardly selected tiles were deployed at each of the nine
172 sites. Six tiles were exposed to local herbivores, and two were placed inside individual
173 exclusion cages (300 x 300 x 300 mm; 12-mm² steel mesh) to determine if observed changes
174 in algal turf height were due to herbivory (cages: at each site. An additional caged tile was
175 included at seven of the nine sites (all sites except one mixed coral site and one soft coral
176 site). The tiles were deployed at each site by securing to individual cement pavers with a
177 galvanized steel nut and bolt through the centre of the tile. The pavers were placed on
178 horizontal surfaces that were free of live coral at each site, with >10 m between adjacent
179 pavers/tiles. Exclusion cages were cleaned of fouling organisms (mostly algae) every two to
180 three days. The initial height of the turf algal community was quantified at nine uniformly
181 spaced points *in situ* using callipers (nearest mm) across the upper surface of the tile
182 immediately after deployment (mean \pm SE = 4.89 mm \pm 0.13; no significant variation among
183 habitats, lme, $F_{2,6}=1.14$, $P=0.38$), and again after seven days.

184

185 To quantify rates of macroalgal browsing, transplanted “bioassays” (hereafter ‘assays’) of the
186 red macroalga *Laurencia* cf. *obtusata* were used. *Laurencia* was selected as it was the most
187 abundant macroalga on reefs surrounding Lizard Island at the time of the study, and
188 *Laurencia* spp are known to be consumed by herbivorous reef fishes on the Great Barrier
189 Reef [48,49]. Thalli of *Laurencia* were collected by hand from a local shallow reef flat and
190 placed in an aquarium (6000 L) with flow-through seawater within 30 mins of collection.
191 Whole thalli of similar size were spun in a salad-spinner for 30 s to remove excess water, and
192 the wet weight recorded (to the nearest 0.1 g). The initial mass (mean \pm SE) of each assay
193 was 45.4 \pm 1.0 g. Six haphazardly selected assays were transplanted to each site between

194 0930-1030 h, with three exposed to resident herbivore assemblages and three placed within
195 adjacent herbivore exclusion cages (300 x 300 x 300 mm) for 24 h. Each caged assay was
196 positioned within 2 m from its paired exposed assay, and adjacent assay pairs were separated
197 by a minimum of 10 m. Assays were deployed with a short (<10 cm) length of PVC-coated
198 wire (2 mm diameter) around the thallus base and attached to a small lead weight. Small
199 plastic tags placed adjacent to assays were used to identify individual thalli. After 24 h assays
200 were collected, spun and re-weighed. This procedure was replicated on three non-consecutive
201 days at each site ($n=9$ exposed assays per site).

202

203 To identify herbivorous fish species removing *Laurencia* biomass, stationary underwater
204 video cameras (GoPro) recorded feeding activity on up to three (mean=2.2 assays)
205 haphazardly selected assays at each site on each day. Each camera was attached to a dive
206 weight (2 kg) and positioned approximately 1 m from each assay, with a scale bar
207 temporarily placed adjacent to each assay at the start of filming to allow calibration of fish
208 sizes on video footage. Filming commenced immediately after assays were deployed and was
209 continuous for 2.2-4.4 h (variable duration due to differences in battery life among cameras).
210 This procedure was replicated on each day of the experiment (3 per site), resulting in $20.5 \pm$
211 1.7 h (mean \pm SE) of video observations for each site (189 h in total). Body-size (TL) and
212 number of bites taken from the *Laurencia* by each species on the video footage were
213 recorded. To account for variation in fish body-size on algal mass removed per bite, mass-
214 standardised bite impact was calculated as the product of the number of bites and the
215 estimated body mass for each individual (following [50]). Bite impact was then standardised
216 per hour to account for varying video lengths (mass-standardised bites h^{-1}).

217

218 *Data analysis*

219

220 Benthic composition and herbivore assemblages

221

222 Variation in the total cover of hard and soft coral, bleached coral (hard and soft), macroalgae,
223 and dead substrata and macroalgae combined among habitats was analysed with linear mixed
224 effects models (lme in *nlme*; fixed factor: habitat, random factor: site), with Tukey's multiple
225 comparisons *post hoc* to identify significant differences (*multcomp*).

226

227 Variation in taxonomic composition of herbivorous fish assemblages among habitats was
228 visualised with non-metric multi-dimensional scaling (nMDS) based on Bray-Curtis
229 similarities of log-transformed biomass data (kg ha^{-1} ; log (x+1)-transformed), and differences
230 assessed with two-factor nested PERMANOVAs (9999 permutations), using habitat (fixed
231 factor) and site (random within habitat), and Monte Carlo pairwise comparisons. Variation in
232 total biomass (kg ha^{-1}) of all herbivores (log-transformed) among habitats was assessed with
233 a linear mixed effects model fitted with Gaussian residual structure (lme in *nlme*; fixed:
234 habitat; random: site). Variation in herbivore species richness (Poisson distribution), total
235 herbivore abundance, and grazer biomass (combined biomass of croppers/detritivores,
236 scrapers, excavators, and omnivorous herbivores; both models using negative binomial
237 distributions) was assessed with generalised mixed models to accommodate non-stable
238 variances and alternative exponential residual distributions (glmer in *lme4*), followed by
239 Tukey's multiple comparisons to identify significant differences among habitats (*multcomp*).
240 Variation in macroalgal browser biomass was assessed using the same fixed and random
241 effects, but with a zero-inflated negative binomial generalized linear mixed effects model
242 (glmmTMB in *glmmTMB*, and multiple comparisons for glmmTMB in [https://cran.r-](https://cran.r-project.org/web/packages/glmmTMB/vignettes/model_evaluation.html#multcomp)
243 [project.org/web/packages/glmmTMB/vignettes/model_evaluation.html#multcomp](https://cran.r-project.org/web/packages/glmmTMB/vignettes/model_evaluation.html#multcomp)).

244

245 Rates of herbivory

246

247 Variation in the reduction in height of algal turfs, and reduction in biomass of *Laurencia*
248 assays among habitats was assessed with linear mixed effects models with a Gaussian
249 residual structure (with lme in *nlme*). Models included habitat, treatment (exposed vs caged-
250 control), and their interaction (fixed effects), and site (random effects). Day of deployment
251 was included as an additional random effect for the model of the reduction in *Laurencia*
252 biomass. A generalised mixed effects model with a negative binomial distribution was used
253 to assess variation in feeding on *Laurencia* (total mass-standardised bites h⁻¹) due to
254 exponential residual distribution, with habitat (fixed), site, and day of deployment (random).
255 Multiple linear regression and information-theoretic model selection was used to assess the
256 relative influence of centred site-mean environmental variables on the change in exposed
257 assays (assay loss) where significant differences were found among habitats: the first axis of
258 a principal components analysis of benthic composition (accounting for 61.7% variation in
259 benthic composition of transects among habitats); percent cover of dead substrata and
260 macroalgae; and underwater visual census (UVC) estimated biomass of nominal herbivore
261 groups (grazers or browsers). Total coral cover was collinear with the cover of dead substrata
262 and macroalgae so was not included. All variables had a variance inflation factor (VIF) <2,
263 and multi-model inference (including null models) estimated by ranked changes in AICc <2.

264

265 Model assumptions of homogeneity of variance and normality were validated with visual
266 assessment of Pearson residuals, and multicollinearity of explanatory variables in the multiple
267 linear regression analysis was assessed by calculating relative VIF. Where variance was
268 heterogeneous among habitats, a constant covariance structure was fitted (i.e. change in

269 macroalgal weight; percentage cover of macroalgae, bleached coral, and hard and soft coral).
270 All analyses were performed in R (R Core Team 2019), and Primer v6 with
271 PERMANOVA+.

272

273 **Results**

274

275 *Benthic composition and herbivore assemblage structure*

276

277 Total coral cover was significantly higher in branching *Porites* habitats than mixed coral
278 habitats (contrast 16.6%, confidence interval CI: 27.48 | 5.67) and intermediate in soft coral
279 habitats (Fig.1a; Table S3). There was no significant variation in the total cover of bleached
280 coral or macroalgae among habitats (Table S3), the latter being low across all sites (mean:
281 0.3-1.4%) and comprised mainly of *Padina*, *Halimeda*, and *Dictyota*. However, the cover of
282 dead substrata and macroalgae (predominately turf algae) was lower in branching *Porites*-
283 than mixed coral habitats (contrast: 17.2%, CI: 3.09 | 31.36) and intermediate in soft coral
284 habitats (Table S3).

285

286 The taxonomic composition of herbivorous fish assemblages differed significantly between
287 branching *Porites* habitats and soft coral habitats, largely driven by differences in the relative
288 biomass of grazing species, such as the parrotfishes *Chlorurus microrhinos*, *Scarus niger*, *S.*
289 *rivulatus*, and the surgeonfishes *Acanthurus blochii* and *Ctenochaetus striatus*
290 (PERMANOVA, Pseudo- $F=2.47$, $df=2,53$, $P=0.004$, unique permutations=280; pairwise test,
291 $P(\text{MC})=0.004$; Fig. 2). Herbivore assemblages from the mixed coral habitat did not differ
292 from the other two habitats. Variation in herbivore assemblages (species richness, total
293 biomass, biomass of grazers, and browsers) among habitats was inconsistent with the cover

294 of turf and macroalgae described above. Herbivore species richness and total herbivore
295 biomass (kg ha^{-1} ; log-transformed) were significantly greater in mixed coral habitats than soft
296 coral habitats, and intermediate in branching *Porites* habitats (Fig. 1b and c; Tables S3 and
297 S4) as was the biomass of grazers (Table S5). Conversely, the biomass of browsers was
298 significantly greater in branching *Porites* habitats than soft coral habitats (CI: 1.43 | 11.98),
299 and intermediate in mixed coral habitats (Fig. 3; Tables S4 and S5).

300

301 *Rates of herbivory*

302

303 Although the reduction in height of algal turf assays differed among habitats (both caged and
304 exposed), with the greatest reduction in the soft coral habitat and lowest reduction in the
305 branching *Porites* habitat, the difference between caged and exposed tiles (i.e. the reduction
306 in height due to herbivores) was consistent among habitats (Fig. 4a; Table S6). The reduction
307 in algal turf height on tiles exposed to local herbivore assemblages was significantly greater
308 than on caged tiles across all habitats (CI: 0.21 | 1.38).

309

310 The reduction in *Laurencia* biomass was greater in the mixed coral and soft coral habitats
311 than in the branching *Porites* habitats where the change in weight of exposed assays did not
312 differ significantly to caged assays (Fig. 4b; Table S6). Model selection of variables that
313 explained the reduction in mass of *Laurencia* assays yielded two models within $\Delta\text{AICc} < 2$ of
314 the top model (Table S7). The most parsimonious included the cover of dead substrata and
315 macroalgae (relative importance: 1.00) and first axis of the principal component of benthic
316 composition among habitats (PC1; relative importance: 0.53), and was 1.1 times more
317 plausible than the second ranked model (Table S7). Across both top models, dead substrata

318 and macroalgae had a significant (CI: 0.04 | 0.98) and positive effect on assay weight change,
319 whilst PC1 did not have a significant effect (CI: -1.76 | 0.29) (Table S7).

320

321 Total feeding on *Laurencia* assays was significantly lower in the branching *Porites* habitat
322 than mixed coral habitat (CI: 3.32 | 3347.43), and intermediate in the soft coral habitat (Fig.
323 4; Table S6). Analysis of video footage revealed 35 species of reef fishes taking bites from
324 exposed assays across all habitats, with four species accounting for 96% of total mass-
325 standardised bites: *Naso brevirostris* (69%), *Siganus doliatus* (13%), *N. vlamingii* (9%), and
326 *Pomacanthus sexstriatus* (6%). Feeding by each of these species was highly variable among
327 assays and sites, and poorly reflected UVC estimates of fish biomass (Fig. S3). Of these four
328 species, only *P. sexstriatus* was recorded feeding in branching *Porites* habitats.

329

330 **Discussion**

331

332 Shifts in the composition of habitat-forming species and consequences for the function of
333 ecosystems pose new challenges for conservation as the composition of assemblages that rely
334 on habitats for food and shelter reorganise [7,51]. Focusing on coral reefs, we show that the
335 taxonomic and functional composition of herbivorous fish assemblages, and rates of
336 browsing, but not grazing, differed among taxonomically distinct coral habitats. Browsing on
337 the red macroalga *Laurencia* was greatest in soft coral and mixed coral habitats, and lowest in
338 branching *Porites* habitats. These differences in the consumption of *Laurencia* were best
339 predicted by variation in both the composition and cover of benthic assemblages, with the
340 highest rates of removal in habitats with the lowest coral cover, lowest structural complexity,
341 and highest cover of dead substrata and macroalgae. Interestingly, rates of browsing on
342 *Laurencia* were poorly reflected by visual estimates of the biomass of browsing fishes,

343 despite browsing fishes being recorded in all three habitats. In contrast to browsing rates,
344 grazing on algal turfs did not differ among habitats. This contrast highlights that different
345 environmental mechanisms, such as those determined by the influence of differential habitat
346 characteristics on foraging behaviour, may shape the functional impact of key species and
347 functional groups such that shifts in species configurations under mounting disturbances may
348 have varied consequences for maintained ecosystem function [7,8].

349

350 Observed variation in rates of browsing among habitats was best predicted by the cover and
351 composition of benthic communities, indicating that particular habitat characteristics may
352 influence foraging behaviour and/or habitat selection by browsing reef fishes. The cover of
353 live coral and structural complexity of reef habitats typically have positive effects on the
354 abundance, biomass, and diversity of herbivorous fish communities [33,52], and rates of
355 herbivory [35,36]. In contrast, however, we found that browsing on *Laurencia* was greater in
356 habitats with lower coral cover that had lower structural complexity, and higher cover of dead
357 substrata and macroalgae (e.g. mostly mixed coral habitats, largely characterised by massive
358 and branching *Porites*, *Sarcophyton*, *Lobophyton*). Conversely, whilst branching *Porites*
359 habitats were the most structurally complex [22], had the highest coral cover, and the greatest
360 observed biomass of browsing fishes among habitats, no significant reduction in *Laurencia*
361 biomass was detected over a 24 h period. The negative relationship between the cover of
362 structurally complex corals (and conversely the positive relationship with the cover of dead
363 substrata and macroalgae) and browsing rates may be related to increased levels of visual
364 occlusion during feeding in high-relief habitats and hence greater risk of foraging [53,54].
365 Studies show the physical topography of structurally complex habitats can inhibit access to
366 algal resources at fine scales (i.e. between coral branches [55]), and can alter the foraging
367 behaviour of fishes by reducing their visual fields and thereby enhancing perceived predation

368 risk [53]. Such findings reflect patterns of habitat use in other terrestrial and aquatic systems
369 where foraging species favour open over structurally complex habitats due to the enhanced
370 ability to detect approaching predators (e.g. African savannahs: [56,57]; temperate intertidal
371 rocky shores and mudflats: [58]; alpine forests: [59]; European grasslands: [60]; temperate
372 arable areas: [61]). Indeed, evidence shows that visual obstruction can increase vigilant
373 predator-scanning behaviour at the cost of time spent foraging in various taxa [57,60].
374 Moreover, perceived predation risk can also be mediated by body-size with larger prey less
375 susceptible to predation [56]. Of the four main species recorded feeding on *Laurencia* in our
376 study, only *Pomacanthus sexstriatus* was observed feeding within the structurally complex
377 branching *Porites* habitat, despite *Naso brevirostris* and *Siganus doliatus* being recorded in
378 visual surveys of that habitat. *P. sexstriatus* was the largest-bodied species observed (mean
379 biomass \pm SE: 670 g \pm 77; other species mean biomass 195-539 g), potentially reducing
380 predation risk and enabling less discriminant foraging activity.

381
382 The positive relationship between browsing and the cover of dead substrata and macroalgae
383 (which was highly collinear with the cover of live coral), also suggests that habitat condition
384 may influence the foraging behaviour of herbivore fishes. Indeed, feeding rates by
385 herbivorous reef fishes can be higher in degraded areas, or often lower topographic
386 complexity [37]. By feeding where food resources are more abundant, animals may maximise
387 net energy gain by reducing energetic costs of movement [62,63], and risk of predation
388 associated with moving larger distances between resource patches [64]. In our study,
389 differential browsing rates may relate to the differential availability of algal dietary resources
390 [35,39] following the bleaching event that caused coral loss and increased the cover of turf
391 algae (Fig. 1a; [6]) at our study sites (between 52.4-71.4% cover of dead substrata). Browsing
392 on *Laurencia* was greatest in mixed coral habitats that also had the highest cover of dead

393 substrata and macroalgae as a result of the bleaching (due to loss of mainly *Acropora* and soft
394 coral taxa; [6]), and highest biomass and diversity of herbivorous fish. Increased cover of
395 algae (predominately turf communities) following large-scale bleaching-induced coral
396 mortality and subsequent increases in the abundance and/or biomass of herbivorous fishes
397 (e.g. [65]), has led to suggestions that herbivorous fish populations may be food limited in
398 areas of high coral cover [66]. However, this relationship may not hold at very low levels of
399 macroalgal cover [34], such as those observed in the present study (mean: 0.3-1.4% cover).

400

401 While visual census estimates show macroalgal browsing herbivores are present in each of
402 the studied habitats, browser biomass was a poor predictor of browsing rates. This is
403 consistent with previous studies of herbivorous coral reef fishes [36,50] and processes in
404 other systems (e.g. the decomposition of dung by invertebrates: [67]; pollination by bees:
405 [13]) in which abundance shows little relation to their functional impact. The discrepancy
406 between observed browser presence and function in our study may also reflect the high
407 mobility and opportunistic foraging behaviour of roving herbivores [68], or the diver-
408 sive behaviours of some fishes [69]. The utility of using the density or biomass of
409 browsing herbivores as a proxy for macroalgal removal may be further hindered by the
410 plasticity and opportunistic diets among herbivorous fishes [47], and a potential bias in the
411 literature classifying browsers as those species known to feed on large fleshy brown
412 macroalgae versus those that consume other fleshy macroalgae [48].

413

414 In contrast to browsing, there were no detectable differences in grazing on the algal turf
415 assays among habitats. This provides further evidence of a disconnect between the observed
416 density and realised impact of functional groups of herbivorous fishes. Despite no detectable
417 differences in grazing rates, among habitat differences in herbivore assemblages were largely

418 driven by differences in the biomass of grazing species. The lack of among-habitat variation
419 in grazing may be related to the high diversity of fishes that feed on algal-turf covered
420 substrata [41], and their response diversity to changes in benthic composition [70]. Similarly,
421 the lack of observed differences may be due to grazing herbivores preferentially targeting
422 sparse and short early-successional turfs and avoiding later successional dense turf
423 assemblages [71]. Feeding rates and foraging behaviours of grazing coral reef fish species
424 have been shown to vary with the condition and structure of reef habitats and algal
425 communities, however responses tend to be species specific [37]. The among-habitat
426 variation in the changes in the turf height on caged tiles was interesting as, despite feeding by
427 large herbivorous fishes being excluded, there was a decline in height in soft coral habitat and
428 increase in branching *Porites* habitat which may be related to grazing by small invertebrates
429 and/or differences in algal productivity [72]. Similarly, negative values of turf height loss for
430 both caged and exposed assays in branching *Porites* habitats may be due to high algal
431 productivity in that habitat, warranting further investigation.

432

433 Our results provide new evidence of the variable influence of the composition and cover of
434 habitat-building corals on two key functions on coral reefs—grazing and browsing—based on
435 comparisons among three taxonomically distinct coral habitats. While the use of *Laurencia*
436 has provided valuable information on the variable browsing behaviour among habitats,
437 previous studies have shown rates of macroalgal browsing can be dependent on the
438 macroalgae used due to feeding preferences of local herbivore assemblages [48,49].
439 Therefore, further investigation using other commonly occurring macroalgae may offer
440 insight into behavioural variation among habitats of a broader suite of herbivores. Similarly,
441 herbivory processes can vary with depth, exposure, and reef zonation [33,73,74]. Our study
442 compared relatively small experimental assay units among habitats within in a sheltered

443 lagoon environment. Therefore, further study across a wider range of environmental
444 gradients, reef zones, across additional coral species configurations, and across broader
445 spatial scales is now needed. Our study coincided with a large-scale bleaching event [44],
446 resulting in rapid coral loss and changes in reef fish assemblage structure among our study
447 sites [6], and likely affected the foraging behaviour of a range of reef fish species including
448 herbivores [15,65,75]. Although the present study provides clear evidence of how herbivory
449 processes can vary with coral species composition, it was carried out in the context of this
450 disturbance. Disturbance dynamics are complex [15,70], and it is likely that fish assemblages
451 are in transition with changes in coral cover. Further research into the spatio-temporal
452 variation in foraging behaviour of individuals and functional groups across such disturbances
453 would improve our understanding of how changing reef configurations interact with climate
454 change impacts to influence critical ecological functions [15,16].

455

456 Understanding causal links between habitat species composition and ecosystem function is of
457 growing concern in this era of unprecedented and rapid ecological change [5,7,9]. In
458 particular, elucidating how the increasing modification of ecological communities affects
459 ecosystem processes is central to our capacity to anticipate whether new species
460 configurations will continue to provide goods and services as required by societies that
461 depend on them [14,17,23]. On coral reefs, whether herbivores can compensate for increased
462 algal production as coral cover decreases, and maintain critical rates of algal consumption
463 will be fundamental to the persistence of reconfigured coral-dominated systems [66]. Our
464 results show that herbivore assemblage structure varied among the studied habitats, however
465 did not reflect the observed variation in herbivory rates. While grazing was insensitive to
466 variation in coral composition, browsing varied considerably, indicating that different
467 mechanisms determined by specific habitat characteristics may be shaping these key

468 processes. While the precise mechanisms are not known, variation in browsing was best
469 predicted by the composition and cover of benthic communities, and conversely the cover of
470 dead substrata and macroalgae, characteristics that underscore the structural complexity of
471 reef habitats and which may have influenced differential foraging behaviour. With ongoing
472 degradation of coral reefs and the homogenization of both coral and fish assemblages [6,20],
473 these results suggest that, within reefs, key ecosystem functions will likely vary among
474 altered coral configurations, according to the differential vulnerability of corals to
475 disturbances and ecological interactions between reef fishes and their environment [15]. More
476 generally, our results emphasise the role of differential habitat characteristics and provide
477 explicit support for assigning greater concern to the composition and structure—as well as
478 cover—of habitat-building species in assessments and management of ecosystem function
479 [7,23].

480

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488

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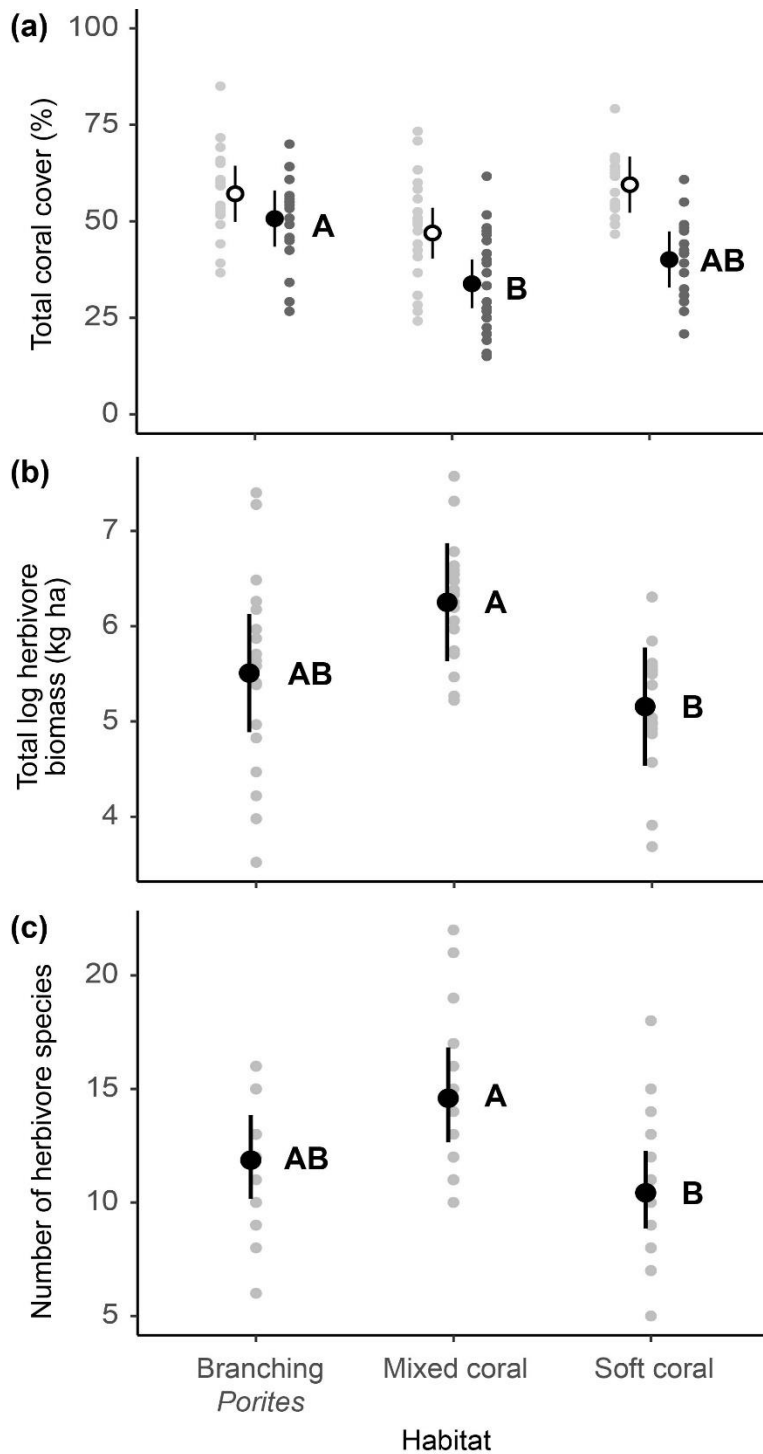
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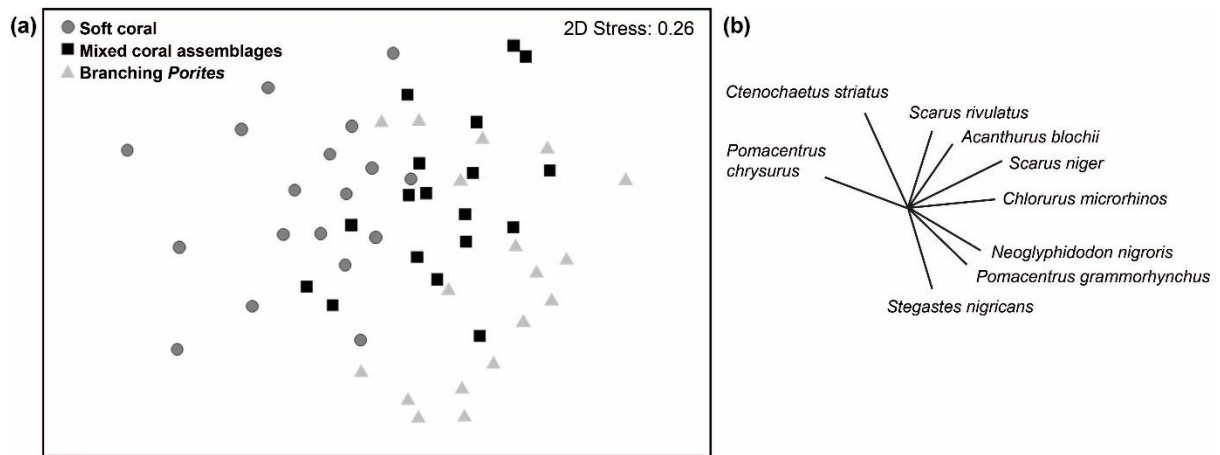
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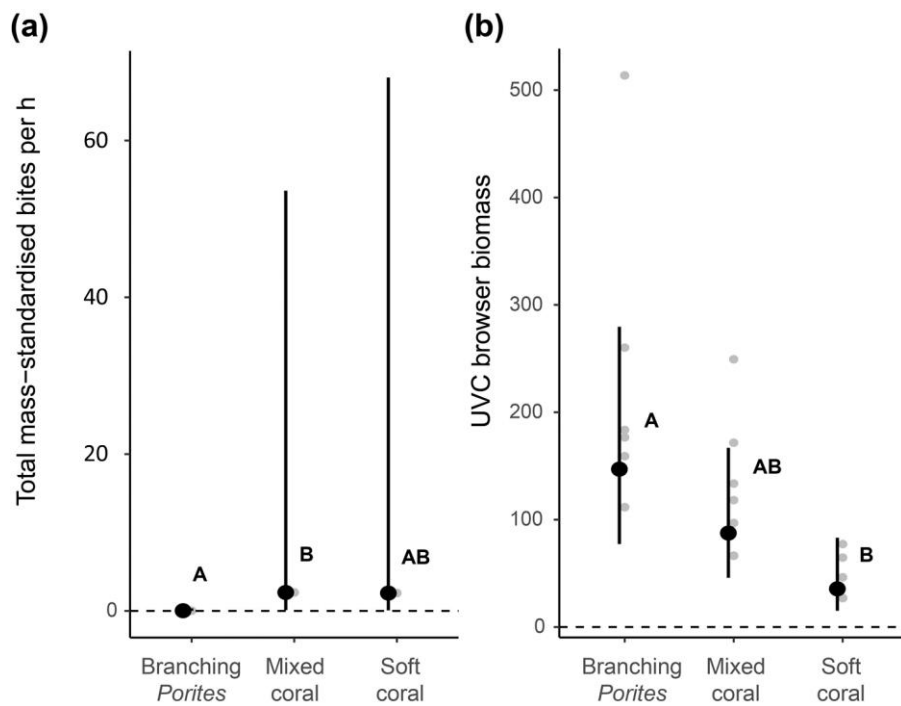
706 **Fig. 1** Among-habitat variation (fitted values \pm 95% confidence intervals) in, (a) total coral
 707 cover (hard and soft coral) in September 2015 (white; [6]), and April 2016 (black); (b) total
 708 herbivore biomass (log-transformed, kg ha⁻¹); (c) number of herbivore species. Partial residuals
 709 in grey; contrasting letters indicate significant differences among habitats (Tukey, $P < 0.05$).



710

711 **Fig. 2** Non-metric multidimensional scaling analysis showing variation in taxonomic
 712 composition of herbivorous fishes among surveyed coral habitats, using transect-level log
 713 (x+1) transformed data (a). The relative contribution of species to the observed variation in
 714 composition (>0.5 Pearson correlation) (b).

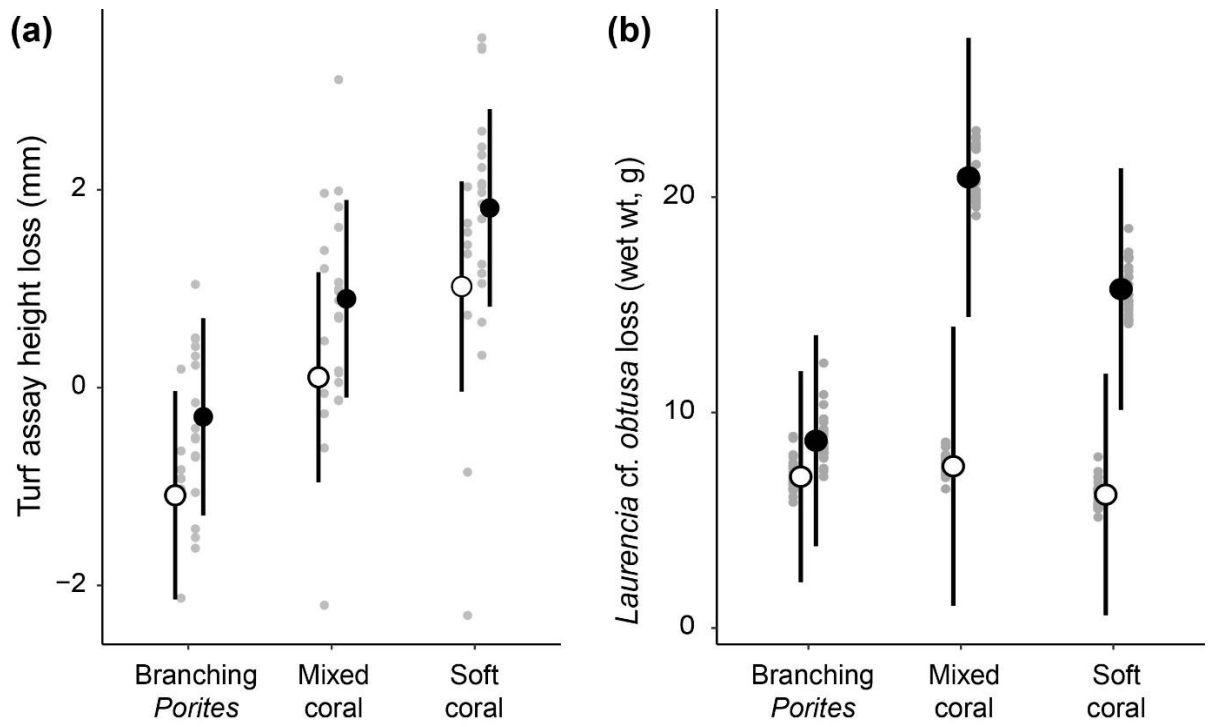
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717 **Fig. 3** Among-habitat variation (fitted values \pm 95% confidence intervals) in: (a) feeding rates
 718 on *Laurencia* assays by all species; (b) visual biomass estimate of all nominal browsers (kg ha^{-1}).
 719 Contrasting letters indicate significant differences among habitats (Tukey, $P < 0.05$).

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722 **Fig. 4** Among-habitat variation (fitted values \pm 95% confidence intervals) in assay loss of: (a)

723 turf algae (mean turf height (mm)); (b) *Laurencia* (wet weight, g); caged assays (white), exposed

724 assays (black); partial residuals (grey).