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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Abstract

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

43

Introduction

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

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

4

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

6

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 m^2 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 nice

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-mm^2 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 ± SE = 4.89 mm ± 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. *obtusa* 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 ± SE) of each assay

193 was 45.4 ± 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 ±

211 1.7 h (mean ± 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-

243   project.org/web/packages/glmmTMB/vignettes/model_evaluation.html#multcomp).

245   Rates of herbivory

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.

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(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

13

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 ΔAICc<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

14

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 ± SE: 670 g ± 77; other species mean biomass 195-539 g), potentially reducing

380 predation risk and enabling less discriminant foraging activity.

381

382 The positive relatitionship 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, of 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 browing 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   negative 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

488

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490

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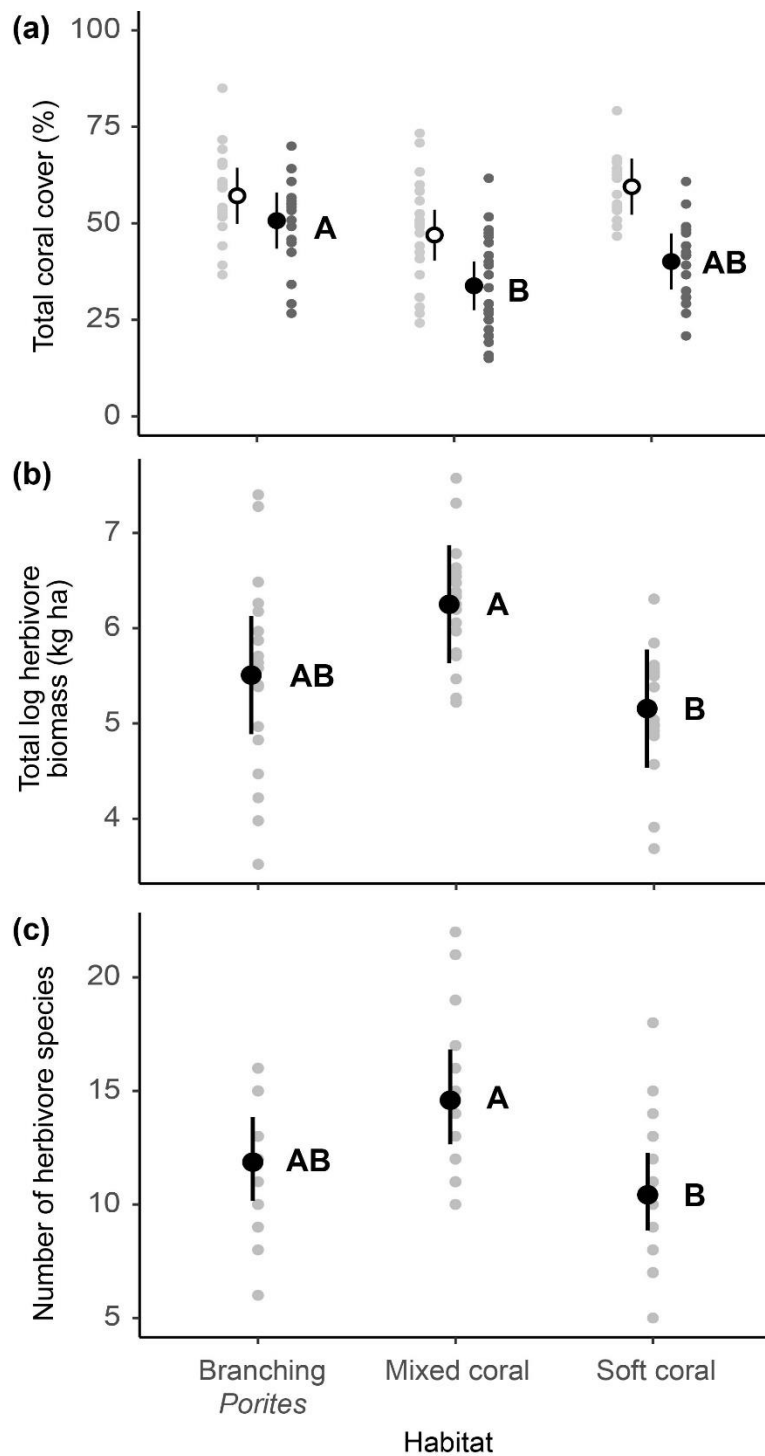
Fig. 1 Among-habitat variation (fitted values ± 95% confidence intervals) in, (a) total coral

cover (hard and soft coral) in September 2015 (white; [6]), and April 2016 (black); (b) total

herbivore biomass (log-transformed, kg ha^{-1}); (c) number of herbivore species. Partial residuals

in grey; contrasting letters indicate significant differences among habitats (Tukey, $P<0.05$).

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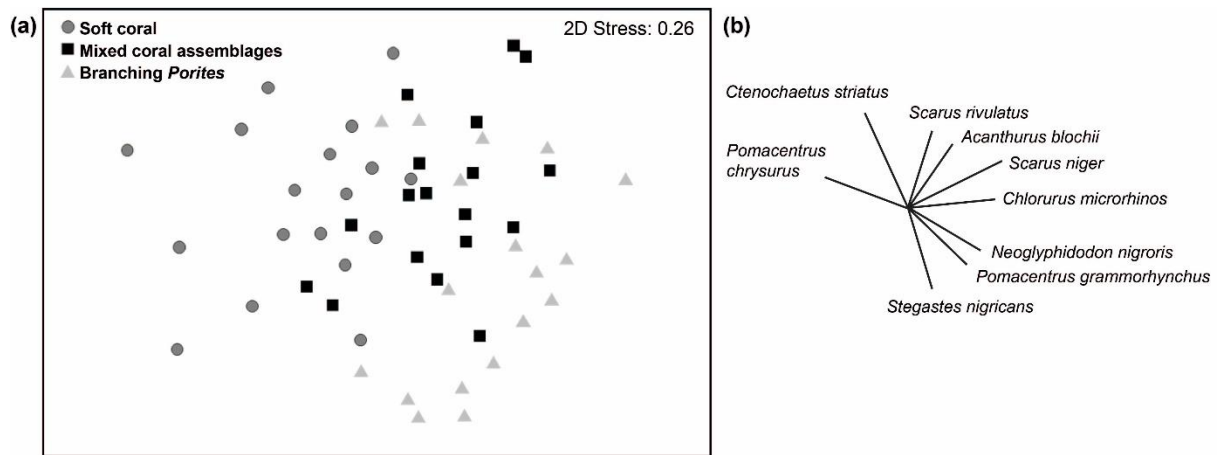
Fig. 2 Non-metric multidimensional scaling analysis showing variation in taxonomic composition of herbivorous fishes among surveyed coral habitats, using transect-level log (x+1) transformed data (a). The relative contribution of species to the observed variation in composition (>0.5 Pearson correlation) (b).
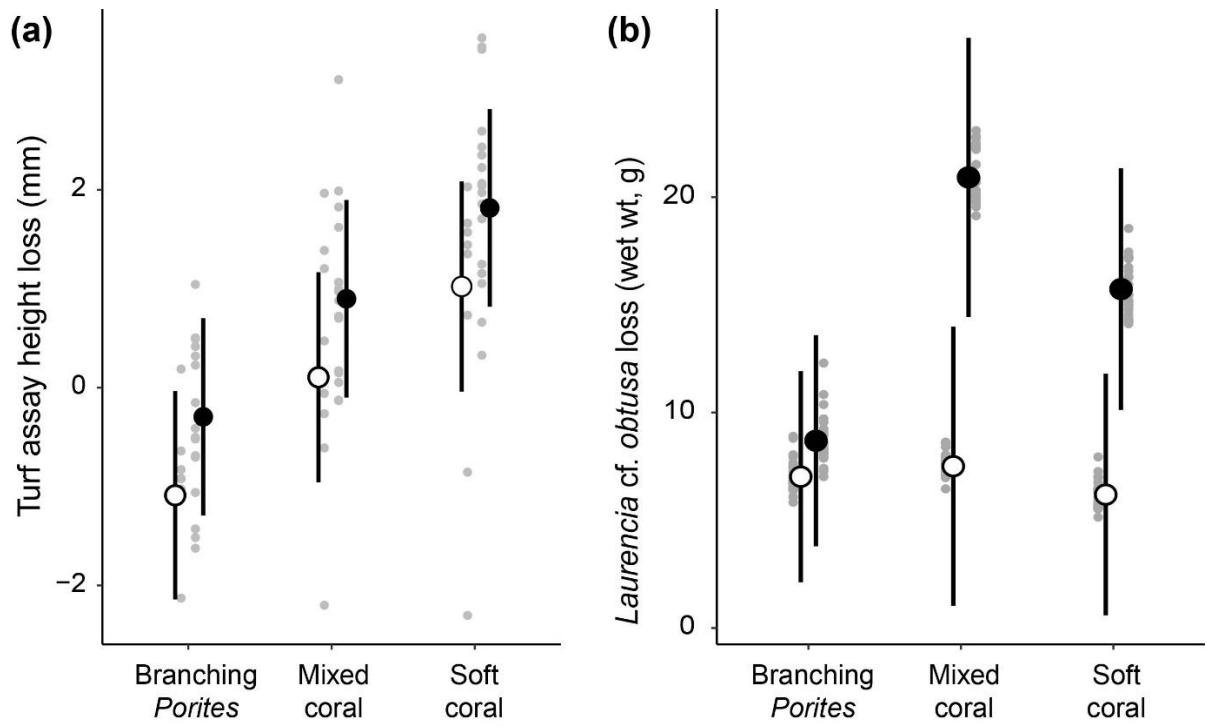
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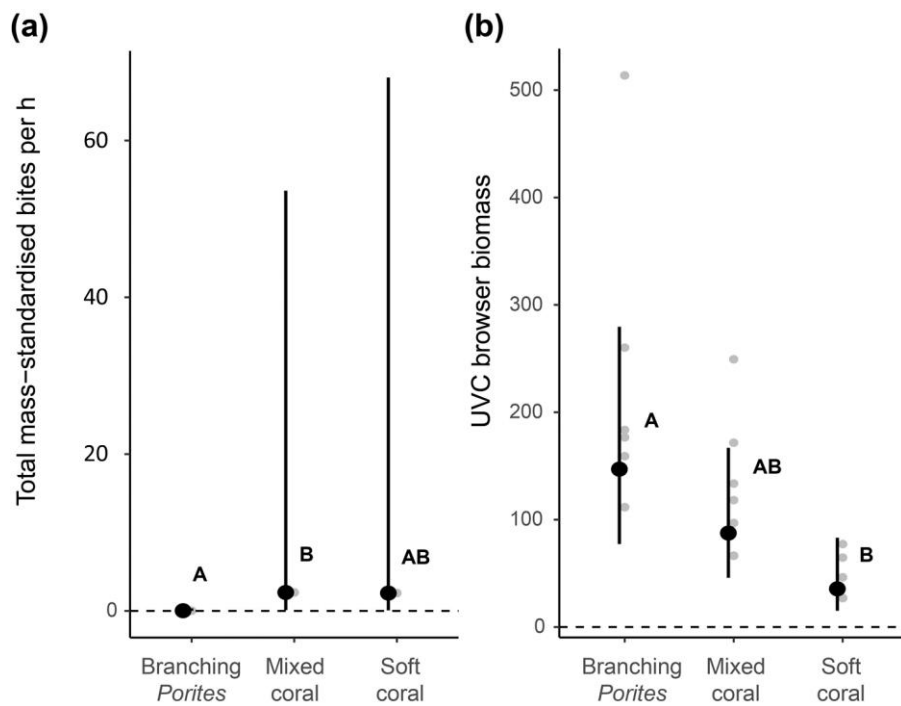
Fig. 3 Among-habitat variation (fitted values ± 95% confidence intervals) in: (a) feeding rates on *Laurencia* assays by all species; (b) visual biomass estimate of all nominal browsers (kg ha^{-1}). Contrasting letters indicate significant differences among habitats (Tukey, $P<0.05$).

720

Fig. 4 Among-habitat variation (fitted values ± 95% confidence intervals) in assay loss of: (a) turf algae (mean turf height (mm); (b) *Laurencia* (wet weight, g); caged assays (white), exposed assays (black); partial residuals (grey).