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**Variation in coral rubble cryptofauna is scale-dependent and driven by small-scale habitat characteristics.**

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23 **ABSTRACT**

24 Motile cryptofauna living in dead coral rubble represent some of the greatest biodiversity and  
25 basal energetic resources on tropical coral reefs. Yet, we know relatively little about how and  
26 why coral rubble cryptofauna communities change over space and time. As human impacts  
27 increase the degradation of living hard corals to dead coral rubble on many reefs worldwide,  
28 understanding the communities that will succeed in these degraded environments, and the  
29 factors paramount to their success, becomes increasingly central to coral reef ecology and  
30 conservation. Using a remote and uninhabited oceanic atoll in the Pacific Ocean, we quantified  
31 the natural spatial variability in motile cryptofauna diversity and community structure in coral  
32 rubble across scales (m to km) and tested whether variability at smaller scales could be  
33 explained by gradients in microhabitat. We show that coral rubble cryptofauna communities  
34 are most variable at intra-site scales (m) rather than inter-site scales (100s m) or between reef  
35 zones (km scales). We also show that a substantial amount of variation in cryptofauna density  
36 (55%) and phyla-level community structure (31%) is explained by small-scale habitat  
37 characteristics, specifically the substrate type below the rubble and the variability in macroalgal  
38 cover on individual rubble pieces. Our findings highlight the need to study small-scale  
39 processes that are relevant to motile cryptofauna and their community interactions if we are to  
40 elucidate the structuring forces of these diverse cryptic assemblages on coral reefs.

41

42 **KEYWORDS:**

43 Coral reef, community structure, degraded habitats, spatial variability, microhabitat

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47 **1. INTRODUCTION**

48 Living, growing structures formed by ecosystem engineers like trees and reef-building corals  
49 provide important habitat to a diverse range of organisms (Larsson & Danell 2001, Coker et al.  
50 2014, Kristensen et al. 2015, Stella et al. 2022). After death, the structural artefacts left behind  
51 continue their legacy, sustaining and often enhancing biodiversity across the ecosystem by  
52 creating newly available habitat for generalist species, decomposers, and scavengers (Jonsson  
53 et al. 2005, Enochs & Manzello 2012, Andringa et al. 2019, Saldaña et al. 2023). Historically,  
54 research efforts have focused on the living structures of ecosystem engineers and their  
55 biological and ecological attributes, while their non-living forms have received much less  
56 attention (Barnhill et al. 2023). However, as climate change-induced impacts intensify on land  
57 and in the ocean, ecosystem engineers are suffering mass mortality, and their dead remains are  
58 becoming more prevalent (Anderegg et al. 2013, Hughes et al. 2017, Stavi et al. 2021). To fully  
59 understand how ecosystems are being and will continue to be affected by climate change  
60 requires that we incorporate the ecological role these dead materials play in overall ecosystem  
61 function (Barnhill et al. 2023, Saldaña et al. 2023). This, in part, requires an explicit  
62 understanding of the structure and function of biotic communities that inhabit dead materials  
63 left by ecosystem engineers, and how they contribute to ecosystem processes.

64 Tropical reef-building corals are suffering mass mortality at local and regional scales due to  
65 rising ocean temperatures, which can trigger coral bleaching and disease (Hughes et al. 2018,  
66 Burke et al. 2023). These global impacts are exacerbated by local human stressors like  
67 overfishing and coastal pollution that reduce reef resistance and resilience to ocean warming  
68 (Graham et al. 2015, Gove et al. 2023). After death, coral skeletons can rapidly degrade to form  
69 coral rubble (Morais et al. 2022). While coral rubble is a naturally occurring habitat across the  
70 seascape (Odum & Odum 1955, Rasser & Riegl 2002), human impacts are increasing the  
71 prevalence of coral rubble on many reefs and this is expected to increase in the coming decades

## Variation in coral rubble cryptofauna

72 (Rogers et al. 2014, 2018, Morais et al. 2020, Tebbett et al. 2023). As a result, the role coral  
73 rubble plays in overall reef ecosystem structure and function has become a focus of research in  
74 recent years (Rasser & Riegl 2002, Biondi et al. 2020, Ceccarelli et al. 2020, Kenyon et al.  
75 2020, Masucci et al. 2021, Wolfe et al. 2021).

76 Despite a seemingly barren and featureless appearance, coral rubble forms complex  
77 microhabitats that host a diversity of life including microbes and biofilms, sessile and  
78 encrusting taxa, and motile cryptobenthic fishes and invertebrates (Gischler & Ginsburg 1996,  
79 Enochs 2012, Kramer et al. 2014). Invertebrate motile cryptofauna (hereafter motile  
80 cryptofauna) like crabs, shrimps, molluscs, and polychaetes, comprise the highest density and  
81 diversity of animals directly associated with coral reef substrates (Plaisance et al. 2009). Their  
82 diversity and abundance enable them to perform a wide range of functional roles including  
83 scavenging, predation, cleaning fishes, sediment clearing, bioturbation and parasitism (Keable  
84 1995, Becker & Grutter 2004, Stewart et al. 2006, Pollock et al. 2013). One of their more  
85 influential roles is arguably as a significant basal energetic resource to higher level consumers  
86 (Glynn 2011, Kramer et al. 2013a, 2014, 2017) and they are well represented among the gut  
87 contents of many reef fishes (Randall 1967, Kramer et al. 2015, Casey et al. 2019a).

88 Motile cryptofauna density, biomass and productivity are more than an order of magnitude  
89 greater in dead corals and coral rubble than within live coral colonies (Enochs & Manzello  
90 2012, Fraser et al. 2021, Stella et al. 2022). Due to their disproportionate abundance in coral  
91 rubble and the increasing prevalence of coral rubble on reefs, motile cryptofauna will likely  
92 play an increasingly important role in coral reef food webs and ecosystem functioning (Fraser  
93 et al. 2021, Stella et al. 2022, Wolfe et al. 2023b). This is well supported by modelling  
94 projections that predict an initial increase in secondary productivity of benthic invertebrates on  
95 degraded reefs which may temporarily support reef trophodynamics (Rogers et al. 2014, 2018).  
96 However, despite their ubiquity, motile cryptofauna remain one of the most understudied

97 groups of organisms on coral reefs. Their small size, cryptic nature and the methodological  
98 difficulties involved with quantitative sampling, means they remain poorly described and  
99 underrepresented in ecological studies (Reaka-Kudla 1997, Small et al. 1998, Dennis &  
100 Aldhous 2004, Plaisance et al. 2011). This represents a substantial gap in our understanding of  
101 community organisation for some of the greatest metazoan biodiversity on coral reefs.

102 In many ecosystems, ecological communities are most variable at small spatial scales (cm to  
103 m) driven in part by gradients in microhabitat structure (Underwood & Chapman 1996,  
104 Coleman 2002, Anderson et al. 2005, Harris et al. 2015). For example in woodlands and  
105 rainforests, small-scale features like branch thickness, leaf density (Halaj et al. 2000) and leaf  
106 litter quality (Lassau et al. 2005) drive invertebrate abundance and community structure.  
107 Similarly, the high density, biomass and productivity of motile cryptofauna in coral rubble may  
108 be due to the increased complexity of interstitial spaces (Wolfe et al. 2023a) and the micro-  
109 structural complexity provided by encrusting taxa like macroalgae and turf algae living on the  
110 rubble (Kramer et al. 2013b, Roff et al. 2013, Lavender et al. 2017). However, motile  
111 cryptofauna in coral rubble have typically been described across broader spatial scales (10s m  
112 to km) that compare community structure between reef habitats and depths, and investigations  
113 into their driving forces focused on site-level gradients in wave exposure (Takada et al. 2012,  
114 Masucci et al. 2021) and water quality (Takada et al. 2008). While these studies show  
115 generalisable patterns at broader scales, it remains unclear at what scales motile cryptofauna  
116 are most variable and what role, if any, microhabitat structure plays in dictating these patterns.

117 Here, our overarching aims were to quantify the variability in motile cryptofauna diversity and  
118 community structure (total density, biomass, and community composition at three taxonomic  
119 resolutions) in coral rubble across scales (m to km) and test whether variability at smaller scales  
120 could be explained by gradients in microhabitat. We partitioned community composition into  
121 three taxonomic levels (phyla, order and family) to determine how much variation could be

122 explained by microhabitat factors across these incremental increases in underlying ecological  
123 complexity. We did this at a remote, uninhabited coral reef atoll system that lacks the  
124 confounding effects of direct local human impacts on reef ecosystem structure and function. In  
125 doing so, we provide key insights into the natural variability of motile cryptofauna living in  
126 coral rubble across scales.

127

## 128 **2. MATERIALS AND METHODS**

### 129 **2.1 Study site**

130 Palmyra Atoll National Wildlife Refuge is the northernmost atoll in the Northern Line Islands,  
131 central Pacific. It consists of 12 km<sup>2</sup> of land area and 47.2 km<sup>2</sup> of subtidal reef (Williams et al.  
132 2011). Palmyra has no permanent human population and is part of the Pacific Remote Islands  
133 Marine National Monument and is protected under United States federal law. Palmyra's remote  
134 location and its protected status provides the unique opportunity to study the natural variability  
135 of ecosystems with minimal direct human impacts.

### 136 **2.2 Defining and surveying coral rubble habitats**

137 Nine sites were surveyed around Palmyra in October to November 2022 (Fig. 1). Six of these  
138 sites were located on the wave sheltered backreef and three were on the wave exposed forereef  
139 (the reef slope facing the open ocean). Of the backreef sites, three were located on the open  
140 western terrace, and the remaining three were located on the closed eastern side of the atoll  
141 (Fig. 1). Overall, the nine sites were selected based on two factors: 1) their spatial breadth  
142 across the atoll which, given the concurrent gradients in other benthic communities like corals  
143 (Williams et al. 2011, 2013) should encompass a wide range of cryptofauna communities, and  
144 2) that all these sites contained 'rubble patches', defined here as accumulations of dead coral  
145 rubble  $\geq 1$  m in length and width. During reconnaissance surveys on the backreef, we observed

146 two physically distinct rubble habitat types, likely formed by different physical mechanisms.  
147 Type 1, which we referred to as ‘reef rubble’, were rubble patches interspersed between other  
148 benthic habitats (e.g., live coral) on the coral-dominated reef (Fig. 1). Type 2, which we referred  
149 to as ‘rubble beds’, were featureless mass accumulations of coral rubble that spanned > 1 km  
150 in extent (Fig. 1), similar to rubble flats described at One Tree Reef in the southern Great Barrier  
151 Reef (Shannon et al. 2012). We hypothesised that the smaller ‘reef rubble’ patches were formed  
152 by the physical destruction of corals within close proximity, whereas the larger ‘rubble beds’  
153 were the result of rubble accumulation over greater distances by strong hydrodynamic action.  
154 Once deposited, rubble within rubble beds may undergo further fragmentation through physical  
155 reworking (Shannon et al. 2012). We hypothesised that if reef rubble and rubble beds were  
156 indeed different rubble habitat types, then they may contain different cryptofauna communities.  
157 No rubble beds were located on the forereef, likely due its sloping geomorphology whereby  
158 rubble accumulates as a talus at the foot of the slope at great depths (Scoffin 1993), beyond the  
159 accessible survey limits of this study.

160 Within each rubble habitat type ( $n = 2$  habitat types), a  $0.5 \text{ m}^2$  quadrat was haphazardly placed  
161 over rubble and cryptofauna and rubble characteristic data were collected (described below).  
162 This was repeated twice within each rubble habitat type ( $n = 3$  quadrats) of each reef zone (i.e.  
163  $n = 6$  quadrats per backreef site;  $n = 3$  quadrats per forereef site).

### 164 **2.3 Quantifying coral rubble cryptofauna communities**

165 Within each  $0.5 \text{ m}^2$  quadrat, approximately 1 L of coral rubble was scooped to an average depth  
166 of 5 – 10 cm directly from the rubble patch surface using a plastic beaker. Each scoop of rubble  
167 was immediately placed in double-bagged sealable plastic bags underwater and returned to the  
168 lab for processing. At the lab, each rubble scoop was emptied into a bucket and flushed with  
169 fresh water three times. After each flushing, the water was poured through a 1x1 mm mesh net



## Variation in coral rubble cryptofauna

170 to retrieve cryptofauna individuals. This method was effective in capturing fauna >1 mm, but  
171 excluded fauna <1 mm, meaning the total density and diversity of organisms documented here  
172 is likely underestimated.

173 Using a dissecting microscope, each cryptofauna individual was identified to phylum, order  
174 and family and measured to the nearest 0.1 mm using standard linear measurements (carapace  
175 width for crab-like crustaceans, carapace length for shrimp-like crustaceans, longest distance  
176 of shell length for molluscs diameter for echinoderms with radial symmetry, and length for all  
177 types of worms. Individuals were blotted dry and weighed to the nearest whole mg on an  
178 analytical balance ( $\pm 0.0001\text{mg}$ ). Total cryptofauna density (individuals  $\text{L}^{-1}$ ), biomass, and  
179 community composition were determined for each rubble patch ( $n = 45$  scoops in total).

### 180 **2.3 Quantifying rubble habitat characteristics**

181 Within each  $0.5 \text{ m}^2$  quadrat, eight pieces of rubble were haphazardly collected ( $n = 24 - 48$   
182 pieces per site) and used to estimate the following rubble morphological parameters: (a) length  
183 (longest span in any direction), (b) mean width ( $n = 2 - 3$  measurements per rubble piece), (c)  
184 number of branches (referred to here as ‘branchiness’), and (d) mean branch length. The  
185 substrate type found immediately below the rubble layer (e.g. sand, dead *Halimeda* pellets, or  
186 more rubble) was recorded, and provided an additional rubble habitat characteristic.

187 Of the rubble pieces collected, the cover of sessile organisms growing on each individual piece  
188 of rubble was quantified. Sessile communities can differ between the top and underside of  
189 rubble pieces due largely to differences in light exposure, interstitial sediment, and water  
190 movement (Choi & Ginsburg 1983, Gischler & Ginsburg 1996, Kenyon 2021). We therefore  
191 photographed each rubble piece from both sides using a Olympus TG-6 camera and used these  
192 images to quantify the proportional cover of: encrusting algae (mainly crustose coralline algae  
193 (CCA), *Peysonnelia*), turf algae, macroalgae (including *Dictyota*, *Lobophora* and *Halimeda*),

## Variation in coral rubble cryptofauna

194 sessile invertebrates (including live coral and sponges), and bare surface (if the surface  
195 appeared bare or covered in micro and endolithic algae). We did this using the guides function  
196 in Microsoft Powerpoint. A 66 x 38 grid (in which each grid cell = 0.5 cm) was placed over  
197 each image. The number of cells occupied by each sessile group on both sides of each rubble  
198 piece was counted. The proportion of each sessile group on a rubble piece was calculated by  
199 dividing the total number of grid cells occupied by the sessile group by the total number of grid  
200 cells occupied by the respective rubble piece.

## 201 **2.5 Statistical analyses**

### 202 **2.5.1 Testing for differences in cryptofauna communities on the backreef**

203 We tested for an effect of backreef habitat type (fixed factor, 2 levels: open western terrace and  
204 closed eastern; with site as a random factor nested within backreef habitat type) on cryptofauna  
205 total density, total biomass, richness (calculated using Margalef's index) (univariate responses),  
206 and community composition (multivariate response). We also separately tested for an effect of  
207 rubble habitat type (fixed factor, 2 levels: reef rubble and rubble bed; with site as a random  
208 factor nested within rubble habitat type) on the same community metrics.

209 We used a hierarchical nested permutational analysis of variance (PERMANOVA) (Anderson  
210 2001a) using the PERMANOVA+ (Anderson et al. 2008) add-on for PRIMER-E (version 7.0)  
211 (Clarke & Gorley 2015). Analyses were based on square-root transformed data, a Euclidean  
212 (for total density, total biomass, Margalef's richness) and a Bray-Curtis (for community  
213 composition) similarity matrix, and 9999 permutations of the residuals under a reduced model  
214 (Anderson 2001b). Differences in dispersion amongst groups were tested using PERMDISP in  
215 PRIMER-E (version 7.0) (Clarke & Gorley 2015).

216 There was no effect of backreef habitat type on cryptofauna total density, total biomass,  
217 richness or community composition at each of three taxonomic levels (phylum, order and

218 family) (Table S1, Supplemental Material). Similarly, there was also no effect of rubble habitat  
219 type on any of the measured community metrics. (Table S2, Supplemental Material).  
220 Furthermore, there was no significant dispersal effects amongst groups (Table S3,  
221 Supplemental Material). As a result, data collected on the backreef across both habitat types  
222 and both rubble habitat types were pooled for further analyses.

### 223 **2.5.2 Determining scales of variation in cryptofauna communities**

224 The cryptofauna data were assigned to three hierarchical levels of spatial organisation: ‘reef  
225 zone’ (forereef, backreef) which spanned kilometres, ‘site’ (n = 9) spaced 100s of metres apart,  
226 and ‘quadrat’ spaced metres apart at each site (n = 3 - 6 per site, n = 45 across all sites). To  
227 determine which of these scales (reef zone, inter-site, intra-site) captured the most underlying  
228 variation in total cryptofauna density, total biomass, and richness (univariate responses) and  
229 community composition at three taxonomic resolutions (phylum, order, family) (multivariate  
230 responses), we used variance components analyses. In hierarchical designs such as ours, larger  
231 spatial scales necessarily have fewer degrees of freedom than smaller spatial scales. Therefore,  
232 when estimating individual components of variation, estimates obtained for larger scales  
233 subsequently have lower precision than estimates obtained for smaller scales. Nevertheless,  
234 comparisons of the relative importance of the factors based on estimates of variance  
235 components are rigorous as both analysis of variance (ANOVA) estimators and multivariate  
236 analogues of ANOVA estimators are unbiased, so their accuracy is not affected by sample size  
237 (Searle et al., 1992).

238 For the three univariate responses, we used a hierarchical nested analysis of variance  
239 (ANOVA), with ‘site’ nested in ‘reef zone’. All factors were treated as random. By treating the  
240 factors as random, we tested the significance of variation between levels within each factor.  
241 Assumptions of normality and homogeneity of variance for each metric was tested using a

## Variation in coral rubble cryptofauna

242 Shapiro-Wilk test and Levene's test, respectively. To accommodate the unbalanced design and  
243 to force non-negative variance components, a restricted maximum likelihood estimation model  
244 (REML) was used to calculate the variance components. Variance for each metric is presented  
245 as both absolute variance and as a percent of total variation (termed the 'magnitude of effect'  
246 (Graham & Edwards 2001). This allows for both quantification of total variability attributed to  
247 each spatial scale and the proportion of total variability that occurs between specific scales to  
248 be determined. Levene's test was performed using the *leveneTest* function (car package) and  
249 the Shapiro-Wilk test was performed using the in-built *shapiro.test* function in R 4.2.3.  
250 Hierarchical ANOVAs were performed using *lmer* function (lme4 package) in R 4.2.3 (R Core  
251 Team, 2023).

252 For the multivariate responses, we again used PERMANOVA, with 'site' nested within 'reef  
253 zone', with both factors treated as random. Measures of variability at the three spatial scales,  
254 reef zone (km), inter-site (100s m), and intra-site (quadrat, m), were calculated from the mean  
255 squares of the PERMANOVA, using the multivariate analogue of the ANOVA variance  
256 component estimators and statistical significance tested using 9999 permutations of the raw  
257 data under a reduced model. PERMANOVA variance components are presented as absolute  
258 variance (i.e. the square root of estimates of the variance components) (Anderson et al., 2008)  
259 and as a proportion of total variability within each response variable (Underwood & Chapman,  
260 1996).

261 Given the unbalanced sampling design, where we had a greater number of backreef sites ( $n =$   
262  $6$ ) than forereef sites ( $n = 3$ ), and an uneven number of quadrats at the lowest spatial scale ( $n =$   
263  $6$  per site on backreef;  $n = 3$  per site on forereef), we conducted a sensitivity analysis using a  
264 constrained jackknife approach to determine if our estimates of variation were influenced by  
265 our sampling effort. We randomly subset the data with a smaller number of replicates at the  
266 lowest spatial scale (but ensuring the full complement of levels was retained at the higher

267 scales) to see whether/how this changed the estimates of variance components. We conducted  
268 a traditional leave-one-out jackknife analysis (i.e. dropping only one sample from each  
269 resampled dataset). We also conducted an analysis where we dropped 18 random backreef  
270 samples from each resampled dataset. By dropping these 18 samples, we created datasets where  
271 the sampling effort on the backreef and forereef were equal, i.e.  $n = 3$  quadrats per site. We  
272 performed resampling 10 times, and the analyses were conducted on all community metrics –  
273 density, biomass, richness, and community composition at all three taxonomic levels.

### 274 **2.5.3 Visualising rubble habitat characteristics**

275 To simultaneously visualise the correlation across all rubble habitat characteristics (rubble  
276 morphometrics (rubble length, width, branchiness, branch length), cover of sessile organisms,  
277 and the substrate types below the rubble patches), we used Principal Component Analysis  
278 (PCA). To visualise variability of rubble morphometrics at the site and quadrat scales, we  
279 calculated the coefficient of variation (CoV), a unitless measure calculated as the ratio of the  
280 standard deviation to the mean.

### 281 **2.5.4 Testing for correlations between cryptofauna communities and rubble habitat** 282 **characteristics**

283 To test whether variations in rubble habitat characteristics explained variation in cryptofauna  
284 community composition, we used a permutational distance-based multivariate multiple  
285 regression model (DISTLM) (McArdle & Anderson 2001). DISTLM is used for modelling the  
286 relationship between a resemblance matrix and a single (multivariate regression) or set of  
287 predictor variables (multivariate multiple regression). The technique makes no prior  
288 assumptions about the distribution of the response variable, and therefore normality does not  
289 have to be satisfied (Anderson et al. 2008).

## Variation in coral rubble cryptofauna

290 Models were constructed for three univariate responses using a Euclidean similarity matrix  
291 (cryptofauna total density and total biomass, and Margalef's richness), and three multivariate  
292 responses using a Bray-Curtis similarity matrix (community composition at the phylum, order,  
293 and family taxonomic resolution). Additionally, we constructed univariate models for the four  
294 most abundant taxa (*Gammarida*, *Amphinomidae*, *Eunicidae* and *Anthuridae*) and two others  
295 (*Xanthidae* and *Gnathiidae*) chosen due to their ecological significance to coral reef  
296 trophodynamics (Kramer et al. 2015, Artim et al. 2017, Casey et al. 2019b, Nicholson et al.  
297 2020).

298 Prior to model fitting, the predictor variables were investigated for co-linearity using draftsman  
299 plots and Pearson's ( $r$ ) pairwise correlations. For the rubble morphometrics and sessile  
300 organism cover, each variable's mean value correlated with its respective standard deviation ( $r$   
301  $> 0.7$ ). We chose to retain the standard deviation for each predictor rather than the mean, with  
302 two exceptions: the mean number of branches was retained (we deemed this more reflective of  
303 each individual rubble piece's structural complexity) and mean bare surface cover since its  
304 standard deviation also correlated with the standard deviation of encrusting algae. The  
305 remaining eleven predictors (Table A1, Appendix) were included in the model-fitting process.  
306 Each predictor was log-transformed, normalised (to account for the differences in units and  
307 ranges among the predictors) and fitted conditionally in a step-wise manner to the cryptofauna  
308 community resemblance matrix. Tests were based on 9999 permutations of the residuals under  
309 the reduced model (Anderson 2001a). Model selection was based on Akaike's Information  
310 Criterion (Akaike 1998) with a second-order bias correction applied (AICc) (Hurvich & Tsai  
311 1989) to account for the relatively high number of predictor variables relative to the response  
312 variable replication. Once the optimal model was selected, we further investigated the  
313 underlying relationships between the response and top contributing predictor variables using

314 distance-based redundancy analysis (dbRDA) (McArdle & Anderson 2001) (for the  
315 multivariate models) and boxplots and scatter plots (for the univariate models).

316

### 317 **3. RESULTS**

#### 318 **3.1 Cryptofauna communities in coral rubble (density, biomass, richness, community** 319 **composition)**

320 Across our samples, we identified 2603 individual motile cryptofauna from 6 phyla, 28 orders,  
321 and 57 families (Fig. 2; Table S4 in Supplemental Material)). Mean ( $\pm 1$  standard error) density  
322 of cryptofauna across all quadrats ( $n = 45$ ) was  $58 \pm 5.3$  individuals  $L^{-1}$  (range = 17 – 194  
323 individuals  $L^{-1}$ ), mean biomass was  $1.4 \pm 0.21$  mg (range = 0.03 – 5.01 mg), mean number of  
324 families was  $13 \pm 0.5$  (range 6 – 21), and mean richness was  $3.2 \pm 5.3$  (range 1.3 – 5.1).

325 The Arthropoda (primarily crustaceans) and Annelida (polychaetes) were the most abundant  
326 phyla, representing 47% and 36% of all individuals, respectively (Fig. 2). The most abundant  
327 orders were Amphipoda, Isopoda, Amphinomida and Eunicida, which also contained the most  
328 abundant families *Gammarida*, *Anthuridae*, *Amphinomidae* and *Eunicidae*. The phylum  
329 Mollusca dominated, representing 71% of the total cryptofauna biomass, with the family  
330 *Cypraeidae* (cowries) and order Neogastropoda contributing 48% and 18% to total biomass,  
331 respectively. The second top contributing phylum Echinodermata represented 11% of total  
332 biomass, with the family Holothuriidae (sea cucumbers) representing 9% of total biomass. The  
333 phyla Arthropoda and Annelida encompassed the greatest number of families identified, with  
334 21 and 20 families, respectively.

#### 335 **3.2 Scales of variation in cryptofauna density, biomass, and richness (univariate)**

## Variation in coral rubble cryptofauna

336 Across the intra-site (m), inter-site (100s m) and reef zone (km) scales we examined,  
337 cryptofauna density, biomass and richness were always greatest at the smallest intra-site scale  
338 (Fig. 3, Table S5 in Supplemental Material). Variation in total cryptofauna density was greatest  
339 at intra-site and inter-site scales, representing 51% and 49% of the total variation, respectively  
340 (Fig. 3A). Variability in total cryptofauna biomass was greatest at the intra-site and reef zone  
341 scales, representing 55% and 35% of the total variation, respectively. Variability in total  
342 richness was greatest at the intra- and inter-site scale, representing 64% and 36% of the total  
343 variation, respectively.

344 There was significant variation in total cryptofauna density at the inter-site (100s m) scale  
345 (ANOVA;  $F_{7,44} = 7.07$ ,  $p < 0.001$ ) but not at the reef zone (km) scale (ANOVA;  $F_{1,44} = 0.52$ ,  $p$   
346  $= 0.480$ ). Similarly, there was significant variation in cryptofauna richness at the inter-site (100s  
347 m) scale (ANOVA;  $F_{7,44} = 2.84$ ,  $p = 0.018$ ) but not at the reef zone (km) scale (ANOVA;  $F_{1,44}$   
348  $= 0.26$ ,  $p = 0.613$ ). In contrast, there was significant variation in total cryptofauna biomass at  
349 the reef zone (km) scale (ANOVA;  $F_{1,44} = 6.70$ ,  $p = 0.014$ ) but not at the inter-site (100s m)  
350 scale (ANOVA;  $F_{7,44} = 1.04$ ,  $p = 0.420$ ).

351

### 352 **3.3 Scales of variation in cryptofauna community composition (multivariate)**

353 At all three taxonomic resolutions, cryptofauna community variability decreased as scale  
354 increased. Variability was greatest at the intra-site scale (quadrat, m), and then decreased at the  
355 inter-site scale (100s m), and then again at the reef zone scale (km) (Fig. 3B). Variability at the  
356 intra-site scale also increased as taxonomic resolution increased (from phylum, to order to  
357 family), while the proportion of variability at the inter-site and reef zone scale was unaffected  
358 by taxonomic resolution (Fig. 3B). There was significant variation in community composition



359 at both the reef zone and inter-site scale at all three taxonomic resolutions (Table S6 in  
360 Supplemental Material).

361 Patterns of univariate and multivariate variation across the three spatial scales remained the  
362 same following our jackknife analyses, reinforcing that the largest portion of variation was  
363 always found at the smallest spatial scale despite our unbalanced sampling design. As expected,  
364 the largest spatial scale (reef zone, km) had the least precision for estimating variance  
365 components (Table S7, Supplemental Material). While in this study it was logistically  
366 necessary to have only two levels at the largest spatial scale (km), future studies could aim to  
367 increase this (reducing the number of lower-level replicates, if necessary) to improve the  
368 precision of variance components estimates across spatial scales ranging kilometres.

### 369 **3.4 Summary of rubble habitat characteristics**

370 Across our samples, mean ( $\pm 1$  standard error) rubble length was  $7.1 \pm 3.4$  cm, and mean rubble  
371 thickness was  $2.3 \pm 1.4$  cm. The mean number of branches was  $1.0 \pm 1.2$ , and mean branch  
372 length was  $0.9 \pm 1.4$  cm (Fig. 4). Encrusting algae was the most dominant sessile organism  
373 living on rubble, with a mean cover of  $52.7 \pm 30.8$  %, followed by bare surface ( $39.2 \pm 30.9$   
374 %). Three substrate types were recorded below the sampled rubble. The most common was  
375 more rubble (found under 62% of quadrats), followed by sand at three out of the six backreef  
376 sites (27% of quadrats), and *Halimeda* sediment was found predominantly at forereef sites  
377 (11% of quadrats) (Fig. 4).

378 There were correlations among the rubble habitat characteristics (Fig. 4). Sandy substrates  
379 strongly correlated with bare surface cover on rubble, whilst rubble substrates strongly  
380 correlated with encrusting algae on rubble. Rubble morphological characteristics were  
381 uncorrelated or had weak correlations with substrate type and algal cover. Some sites had low  
382 intra-site variability in rubble morphological characteristics, whereas others were much more

383 variable. For example, the southwest backreef (site: PS, Fig. 1) was consistently characterised  
384 by sandy substrates and rubble pieces with a higher percentage of bare surface cover (Fig. 4,  
385 note the low overall dispersion among replicates). In contrast some sites, like the northwest  
386 backreef (site: TG, Fig. 1), showed high intra-site variability in rubble habitat characteristics,  
387 and were characterised by rubble substrates and rubble pieces with a higher percentage of  
388 encrusting algae (Fig. 4).

### 389 **3.5 Correlations between cryptofauna communities and rubble habitat characteristics**

390 Substrate type below the rubble, variability in macroalgae and turf algae cover, variability in  
391 rubble thickness, and the average number of rubble branches together explained 54.8 % of the  
392 total variation in cryptofauna density (Table 1). Of these five predictors, substrate type and  
393 variability in macroalgae cover were the top performing predictors, explaining 21.7% and  
394 17.6% of the total variation in cryptofauna density, respectively. Cryptofauna density was  
395 greatest over sandy substrates (compared to rubble or *Halimeda* sediment substrates) and  
396 showed a positive trend with variability in macroalgal cover (Fig. 5A, B). In contrast, rubble  
397 habitat characteristics did not explain as much of the variation in cryptofauna biomass (9.3 %  
398 variation explained) or cryptofauna richness (17.4 % variation explained) (Table 1).

399 Substrate type, variability in rubble length and variability in turf algae cover best explained  
400 variations in cryptofauna community composition (Fig. 5B). At the phylum level, these three  
401 predictors explained 31.4% of the total variation in cryptofauna community composition, with  
402 substrate type explaining the most variation (22.3%) (Table 1). As taxonomic resolution  
403 increased model performance decreased, with rubble habitat characteristics explaining just  
404 12.7% and 5.4% of the cryptofauna community composition at the order and family level,  
405 respectively (Table 1).

## Variation in coral rubble cryptofauna

406 Variations in rubble habitat characteristics correlated with variations in the density of the four  
407 most abundant cryptofauna organisms in our samples (Table 1). Variability in rubble length  
408 and substrate type explained 22% of the total variation in *Gammarida* (Arthropoda) density,  
409 while substrate type and variability in macroalgae cover explained 33% of the total variation in  
410 *Anthuridae* (Arthropoda) density. Similarly, substrate type, variability in macroalgae cover and  
411 variability in rubble length explained 36% of the total variation in *Amphinomidae* (Annelida)  
412 density (Table 1). Both *Anthuridae* and *Amphinomidae* were best predicted by substrate type  
413 (20.8 and 23%, respectively), with the density of both groups greatest over sandy substrates  
414 (Fig. 5C, D). Variability in turf algae cover and various rubble morphometrics including  
415 variability rubble thickness, mean number of branches and variability in length, explained 30%  
416 of the total variation in *Eunicidae* (Annelida) density. However, no single predictor explained  
417 more than 12% of the total variation and two explained less than 5% (Table 1). As such, these  
418 relationships were not explored further. Variations in *Xanthidae* (crab) density were best  
419 explained by the cover of bare substrate on rubble, variability in turf algae cover, encrusting  
420 algae cover and macroalgae cover, together explaining 47% of the total variation in *Xanthidae*  
421 density (Table 1). The cover of bare substrate on rubble alone explained 23.9%; *Xanthidae*  
422 density decreased as the cover of bare substrate on the rubble increased (Fig. 5E). Finally,  
423 rubble habitat characteristics did not explain any appreciable variation in *Gnathiidae* density  
424 (Table 1).

425

## 426 **4. DISCUSSION**

427 Coral rubble cryptofauna represent an abundant basal energetic resource that support higher  
428 trophic level consumers and overall coral reef biodiversity (Kramer et al. 2016, Wolfe et al.  
429 2021, Stella et al. 2022). Yet, we know relatively little about how and why coral rubble  
430 cryptofauna communities change over space and time. Here we show that coral rubble

431 cryptofauna communities are most variable at intra-site scales (m) rather than inter-site scales  
432 (100s m) or between reef zones (km scales). We also show that a substantial amount of variation  
433 in cryptofauna density and phyla-level community composition is explained by small-scale  
434 habitat characteristics, including the substrate type below the rubble and the variability in  
435 macroalgal cover on individual rubble pieces. Our findings highlight the need to study small-  
436 scale processes that are relevant to individual cryptofauna organisms and their community  
437 interactions if we are to elucidate the structuring forces of these diverse cryptic assemblages on  
438 coral reefs.

#### 439 **4.1 Scales of variation in cryptofauna communities in coral rubble**

440 Across the intra-site (m), inter-site (100s m) and between reef zone (km) scales we examined,  
441 all cryptofauna community parameters measured were most variable at the smallest intra-site  
442 scale. This is congruent with benthic invertebrate assemblages in other ecological systems. For  
443 example, in temperate systems, benthic invertebrates inhabiting kelp holdfasts are most  
444 variable at metre scales, from holdfast to holdfast (Anderson et al. 2005), while in the deep sea,  
445 infaunal communities change substantially more with differences in sediment depth layers than  
446 with differences associated to larger geographical or bathymetrical scales (Ingels & Vanreusel  
447 2013). Similarly, invertebrate assemblages on temperate rocky shores are most variable at  
448 centimetre to metre scales (Underwood & Chapman 1996, Benedetti-Cecchi 2001, Fraschetti  
449 et al. 2005). On tropical coral reefs, other benthic groups also tend to show the greatest  
450 variability at smaller spatial scales. For example, algal turf assemblages are most variable at  
451 centimetre scales rather than at metre or kilometre scales (Harris et al. 2015). Understanding  
452 the primary spatial scales at which organisms interact with one another and their environment  
453 is an essential basis to identifying the processes that dictate community structure (Underwood  
454 & Chapman 1996). These commonalities across trophic levels and ecological systems suggest

## Variation in coral rubble cryptofauna

455 that small-scale processes contribute a substantial amount to driving benthic community  
456 organisation in the marine environment (Coleman 2002, Fraschetti et al. 2005).

457 Beyond the intra-site scale, the univariate responses of cryptofauna communities (overall  
458 density, biomass, and richness) showed different patterns of variation across spatial scales.

459 Variation in cryptofauna density and richness were both significant at the inter-site scale (100s  
460 m) but not at the reef zone scale (km). However, variance components for cryptofauna density

461 were almost equivalent at the intra-site (m) and inter-site scales. This suggests that quantifying  
462 processes acting at metres to 100s of metres should capture a large proportion of variation in

463 cryptofauna density in coral rubble. In contrast though, variance components for cryptofauna  
464 richness at the intra-site scale was almost double that at the inter-site scale, suggesting that

465 processes acting at the metre scale or smaller influence the diversity of cryptofauna organisms.  
466 Variation in cryptofauna biomass was significant at the reef zone scale (km) and at the intra-

467 site scale (m), but not significant at the inter-site scale (100s m). Further, the majority of  
468 variance components were divided between the reef zone scale (km) and intra-site scale (m).

469 This suggests that broad-scale (km scale) processes may have direct influences on small-scale  
470 processes that in turn structure cryptofauna biomass in coral rubble.

471 In contrast to univariate responses (cryptofauna density, biomass and richness), the multivariate  
472 community responses showed consistent patterns of variation across spatial scales. Cryptofauna

473 community composition was significantly different across inter-site and reef zone scales,  
474 suggesting that small-scale (m) to larger-scale (km) processes dictate community structure.

475 Variance components at the intra-site scale increased with increasing taxonomic resolution, a  
476 similar finding observed for benthic invertebrates in temperate kelp holdfasts (Anderson et al.

477 2005) and temperate soft sediments (Vanderklift et al. 1996, Olsgard et al. 1998), and reflects  
478 the increased ecological information gained via lower-level taxonomic resolution. At the inter-

479 site scale, differences in variance components across taxonomic resolutions were marginal.

## Variation in coral rubble cryptofauna

480 Similarly at the reef zone scale, phylum-level community composition had the greatest variance  
481 components, with marginal differences between order- and family-level variance components.  
482 This suggests that processes acting at kilometres and 100s of metres structure cryptofauna  
483 communities at a broad taxonomic level (phylum in this case) with not much change in  
484 community variance with increasing taxonomic resolution.

485 While these findings are novel for cryptofauna communities inhabiting rubble on tropical coral  
486 reefs, the diversity of the sampled assemblages in this study (57 families from six phyla) is  
487 comparably much lower than studies from Australia where greater than 122 families occur at  
488 individual study sites (Stella et al. 2022, Wolfe et al. 2023b). Due to its remoteness and size,  
489 island biogeography theory may explain the lower species richness found at Palmyra Atoll  
490 compared to Australia (Maragos & Williams, 2011), however there are methodological  
491 limitations within this study that may have influenced this as well. While we identified most  
492 organisms to family, some individuals were grouped at the phylum level (e.g. Ribbon worms:  
493 Nemertea), while others were grouped at the order level (e.g. the gastropod Mollusca:  
494 Neogastropoda, Littorinimorpha). Furthermore, the density and biomass of coral rubble  
495 cryptofauna can be dominated by Harpacticoid copepods that are <1 mm in size (Fraser et al.  
496 2021, Wolfe et al. 2023a) and that would have been missed by our sampling approach.  
497 Therefore, it is likely the abundance and biodiversity of motile cryptofauna we describe here is  
498 underestimated. Despite this, the diversity of cryptofauna (57 families) is impressive  
499 considering that of the two most frequently studied marine organisms at Palmyra Atoll – hard  
500 corals and non-cryptic reef-associated fish – there are only 26 families and 31 families recorded  
501 respectively (Williams et al. 2008, Caselle & Carlsen unpubl. data). This finding underscores  
502 the significance of cryptofauna as a source of biodiversity on Palmyra’s coral reefs, and the  
503 need for further study into their functional importance.

## 504 **4.2 Association of cryptofauna with rubble habitat characteristics**

## Variation in coral rubble cryptofauna

505 The substrate type below the sampled rubble best explained variation in cryptofauna density,  
506 including variation in the two most abundant organisms - annelids *Amphinomidae* and  
507 arthropods *Anthuridae*. In particular, we found sandy substrates below coral rubble supported  
508 increased cryptofauna density compared to either more rubble substrate or *Halimeda* sediment  
509 (the calcium carbonate pellets left by the calcifying macroalga *Halimeda*). While sandy habitats  
510 on coral reefs have comparably low rates of community production (Brock & Smith 1983,  
511 Johnstone et al. 1990, Kramer et al. 2014), here we demonstrate that sandy substrates covered  
512 by coral rubble can support diverse cryptofauna communities.

513 The rubble pieces are likely providing structurally complex, habitable substrate and algal and  
514 other organic matter food resources (Klumpp et al. 1988, Enochs & Manzello 2012, Takada et  
515 al. 2012, 2014). Also sand, while not a structurally complex habitat, does retain algal and  
516 detrital resources (Johnstone et al. 1990, Kramer et al. 2014). A high proportion of the  
517 organisms found within dead coral substrates are deposit feeders and omnivores (Enochs 2012,  
518 Kramer et al. 2017). Across the three substrate types we recorded, sand may act as the best sink  
519 for organic matter from the overlaying rubble. This may explain the increased densities of  
520 *Amphinomidae* and *Anthuridae* we observed living in rubble that overlaid a sandy substrate.  
521 *Amphinomidae* are an omnivorous group of polychaetes with a preference for colonising  
522 environments with accumulations of decaying organic matter (Fauchald & Jumars 1979,  
523 Cosentino & Giacobbe 2011, Schulze et al. 2017). *Anthuridae* are anecdotally suggested to be  
524 detritivores, carnivores, browsers or filter feeders (Poore & Bruce 2012), and so too may benefit  
525 from the increased food resources likely found in sandy substrates. Whilst dead *Halimeda*  
526 sediments could potentially perform the same trapping function of organic matter as sand, at  
527 Palmyra Atoll this substrate type is typically characteristic of the forereef zone. Strong surge  
528 may frequently stir up and redeposit this sediment (Williams et al. 2011), thus reducing its  
529 ability to retain organic content. The arrangement of rubble overlaying sand may represent a

## Variation in coral rubble cryptofauna

530 'sweet spot' to rubble cryptofauna. It marries the habitat-provisioning of rubble and its  
531 relatively extensive surface area colonised by a variety of algal and encrusting taxa that  
532 promotes detrital resources, with the retainment ability of sand, providing a food-rich  
533 environment to fauna inhabiting rubble.

534 Variation in motile cryptofauna community composition at the phylum level was also best  
535 explained by the substrate type below the sampled rubble. Increasing taxonomic resolution  
536 (from phyla to family) resulted in a substantial reduction in the explanatory power of rubble  
537 habitat characteristics. This is not surprising given that the strength of community-environment  
538 relationships often differ depending on the taxonomic resolution of the community data (Lu et  
539 al. 2016). For example at a coarse taxonomic resolution, variations in benthic invertebrate  
540 communities in temperate fjords closely reflect gradients in anthropogenic pollution, whereas  
541 the same communities viewed at the species-level correlate more with small-scale habitat  
542 characteristics like sediment grain size (Warwick 1988a b). From the perspective of these tiny  
543 organisms, the rubble characteristics measured here may represent broad-scale habitat features  
544 that allow phyla-level taxa with similar traits to occupy the same niche space. However, perhaps  
545 to understand community organisation of coral rubble motile cryptofauna at a finer taxonomic  
546 resolution requires an appreciation of other small-scale processes, like organism dispersal  
547 capabilities, competition, predation or finer-scale habitat characteristics like the availability and  
548 quality of organic matter (Pacala & Levin 1997, Harris et al. 2015, Lu et al. 2016).

549 Variability in macroalgal cover was the second-best predictor of cryptofauna density in coral  
550 rubble at Palmyra. This is consistent with coral rubble cryptofauna in Australia, where  
551 macroalgal cover on rubble had a direct positive influence on total cryptofauna density (Wolfe  
552 et al. 2023b). The physical structure of macroalgae enhances occupiable space available to  
553 small benthic fauna through an increase in micro-habitat complexity that provides refuge from  
554 fish predation and may enhance nutritional resource availability to herbivorous cryptofauna



## Variation in coral rubble cryptofauna

555 (Stoner 1985, Roff et al. 2013, Ape et al. 2018). Furthermore, macroalgae may reduce water  
556 flow, increasing the deposition of sediment (Gibbons & Griffiths 1986) rich in detritus and  
557 other particulate organic matter that act as a food source to cryptofauna (Takada et al. 2012).  
558 In contrast, variability in rubble thickness and the average number of branches accounted for  
559 little variation in cryptofauna density. These findings imply that micro-complexity gained from  
560 sessile organisms growing on rubble is more beneficial to cryptofauna than the structural  
561 complexity of the rubble itself. However, rubble structural complexity may indirectly affect  
562 cryptofauna density because branchier rubble pieces tend to have higher macroalgal overgrowth  
563 (Wolfe et al. 2021). While we found that the variation in rubble crab, *Xanthidae*, density was  
564 not well explained by variations in algal cover on rubble, their density was negatively  
565 associated with increasing bare surface cover on rubble. *Xanthidae* are omnivores with a  
566 preference for algae, ranging from crustose coralline algae to turf algae (Knudsen 1960,  
567 Skilleter & Anderson 1986, Kyomo 1999), suggesting their densities may be regulated in some  
568 way by the abundance of sessile organisms growing on rubble.

569 With the ever-increasing degradation of living hard corals to dead coral rubble on many reefs  
570 (Williams & Graham 2019), understanding the communities that will succeed in these  
571 environments, and the factors paramount to their success, becomes increasingly central to coral  
572 reef ecology and conservation. Motile cryptic fauna represent a significant source of coral reef  
573 biodiversity and basal energetic resources to higher level consumers, and therefore  
574 understanding their role in future coral reef functioning and reef trophodynamics deserves  
575 attention. The overall findings here suggest that cryptofauna communities are primarily  
576 structured by small-scale processes. Habitat characteristics like the substrate type below rubble  
577 and sessile organisms growing on rubble may explain broad community metrics, like density  
578 and phyla-level community composition, suggesting a link with habitat complexity and food  
579 availability. Future research is needed to explicitly quantify these parameters and their effects

580 in structuring motile cryptofauna communities, and how ever-changing environmental  
581 conditions on contemporary reefs may impact the structure and function of these diverse cryptic  
582 assemblages.

583

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594

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## 846 TABLES

847 **Table 1.** Summary results of a distance-based permutational multivariate multiple regression  
848 model (DISTLM) for associations of cryptofauna community composition and rubble habitat  
849 characteristics at Palmyra Atoll, central Pacific. The optimal predictors of variation in  
850 community composition, along with the proportion of variability they explained (% variability)  
851 are shown.

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Variation in coral rubble cryptofauna

Predictor	AICc	Pseudo-F	P value	% Variability	% Total
<b>Total density</b>					
Substrate type	307.48	5.836	0.008	21.7	
Standard deviation macroalgal cover	298.56	11.857	0.002	17.6	
Standard deviation rubble thickness	295.15	5.651	0.022	7.5	
Average number of branches	293.76	3.691	0.060	4.6	54.8
<b>Total biomass</b>					
Standard deviation encrusting algae cover	29.398	4.424	0.040	9.3	9.3
<b>Richness</b>					
Standard deviation rubble thickness	-32.16	9.045	0.004	17.4	17.4
<b>Community composition (Phylum)</b>					
Substrate type	272.57	3.933	p < 0.001	22.3	
Standard deviation rubble length	272.22	2.654	0.038	4.8	
Standard deviation turf algal cover	272.17	2.430	0.061	4.3	31.4
<b>Community composition (Order)</b>					
Standard deviation turf algal cover	318.22	3.218	0.002	7.0	
Standard deviation rubble length	317.65	2.757	0.005	5.7	12.7
<b>Community composition (Family)</b>					
Standard deviation turf algal cover	340.4	2.457	0.004	5.4	5.4
<b>Gammarida density</b>					
Standard deviation rubble length	40.03	6.768	0.013	13.6	

Variation in coral rubble cryptofauna

Substrate type	39.705	2.429	0.104	9.2	22.8
<b><i>Amphinomidae</i> density</b>					
Substrate type	49.842	5.508	0.008	20.8	
Standard deviation macroalgal cover	45.021	7.152	0.018	11.8	
Standard deviation rubble length	44.361	2.947	0.097	4.6	37.2
<b><i>Anthuridae</i> density</b>					
Substrate type	26.558	6.263	0.006	23.0	
Standard deviation macroalgal cover	21.76	7.127	0.010	11.4	34.4
<b><i>Eunicidae</i> density</b>					
Standard deviation turf algal cover	39.421	5.068	0.024	10.5	
Standard deviation rubble thickness	35.268	6.477	0.016	12.0	
Average number of branches	35.112	2.410	0.138	4.3	
Standard deviation rubble length	34.558	2.846	0.099	4.9	31.7
<b><i>Xanthidae</i> density</b>					
Average bare surface cover	-30.694	13.483	p < 0.001	23.9	
Standard deviation turf algal cover	-34.812	6.438	0.015	10.1	
Standard deviation encrusting algae cover	-38.731	6.196	0.018	8.7	
Standard deviation macroalgal cover	-40.439	3.958	0.052	5.2	47.9
<b><i>Gnathiidae</i> density</b>					
Standard deviation rubble thickness	-19.063	2.217	0.143	4.9	4.9

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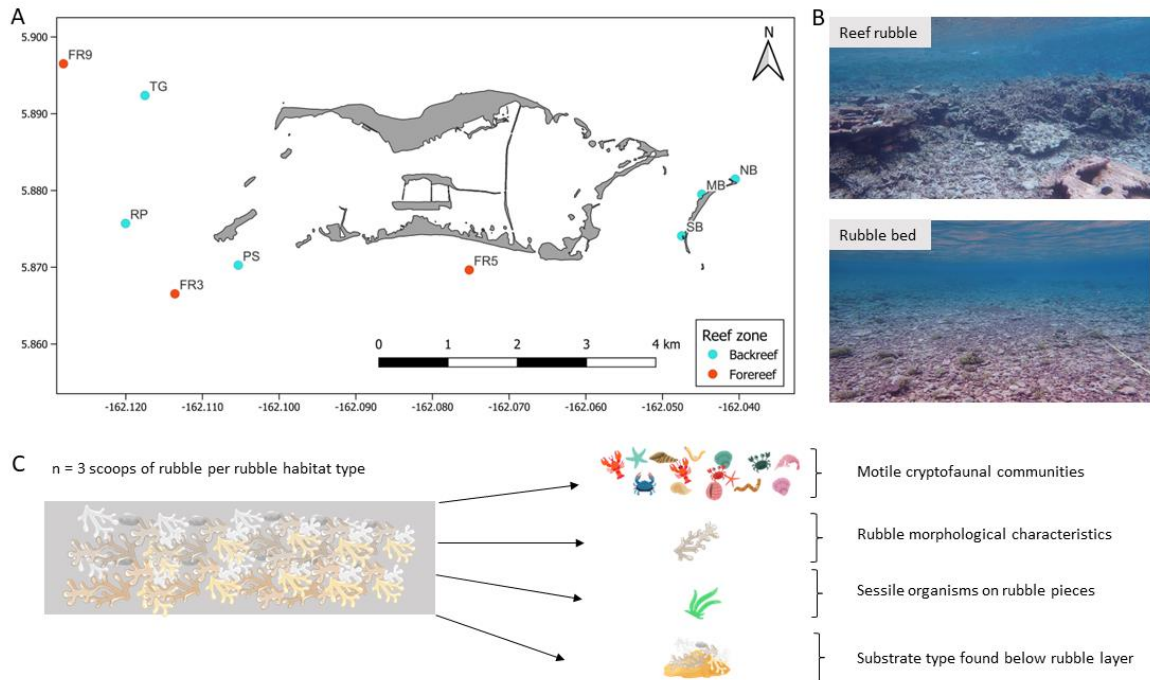
# Variation in coral rubble cryptofauna

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## 858 FIGURES

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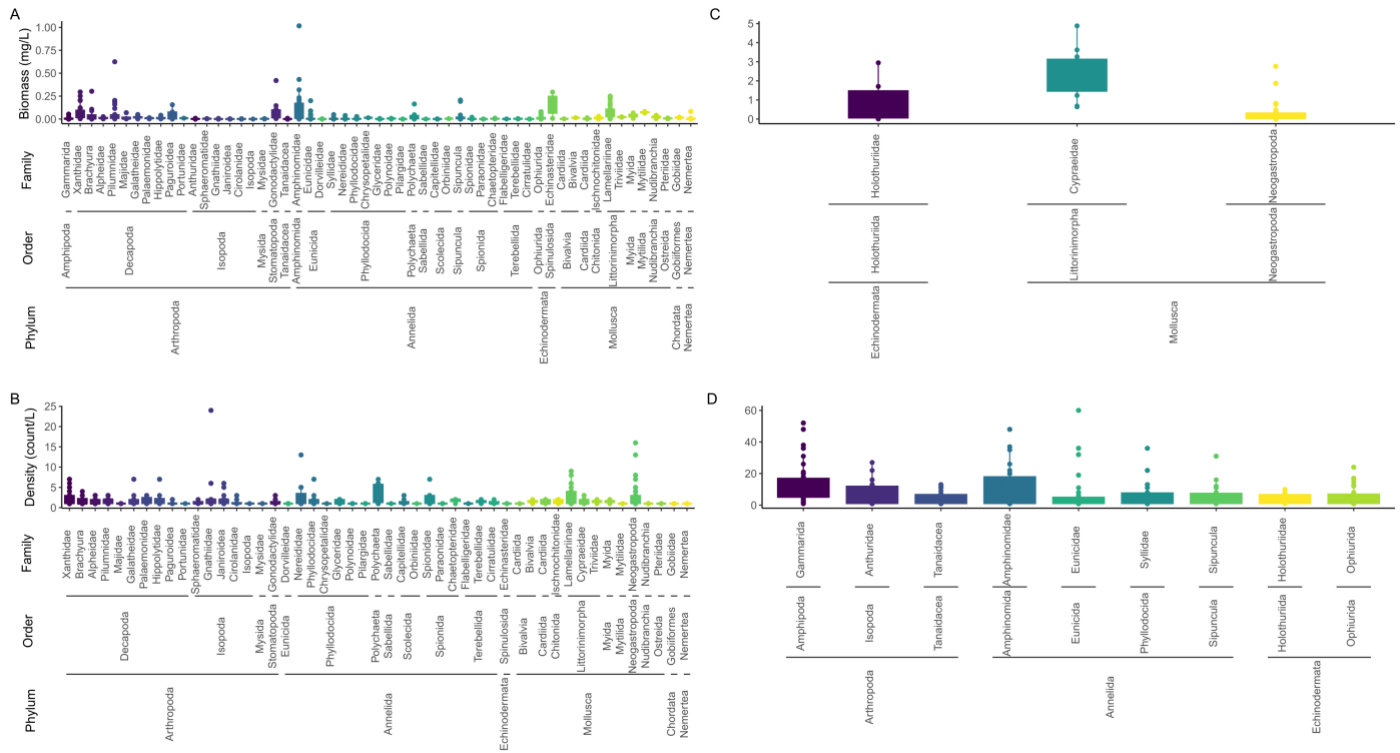
862 **Figure 1.** A) Location of survey sites ( $n = 9$ ) around Palmyra Atoll, central Pacific. B) Two  
863 distinct rubble habitats were identified within reef zones ( $n = 2$  for backreef;  $n = 1$  for forereef).  
864 C) Coral rubble collected within quadrats ( $n = 3$ ) from each rubble habitat per site to  
865 characterise rubble cryptofauna communities and rubble habitat features.

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# Variation in coral rubble cryptofauna



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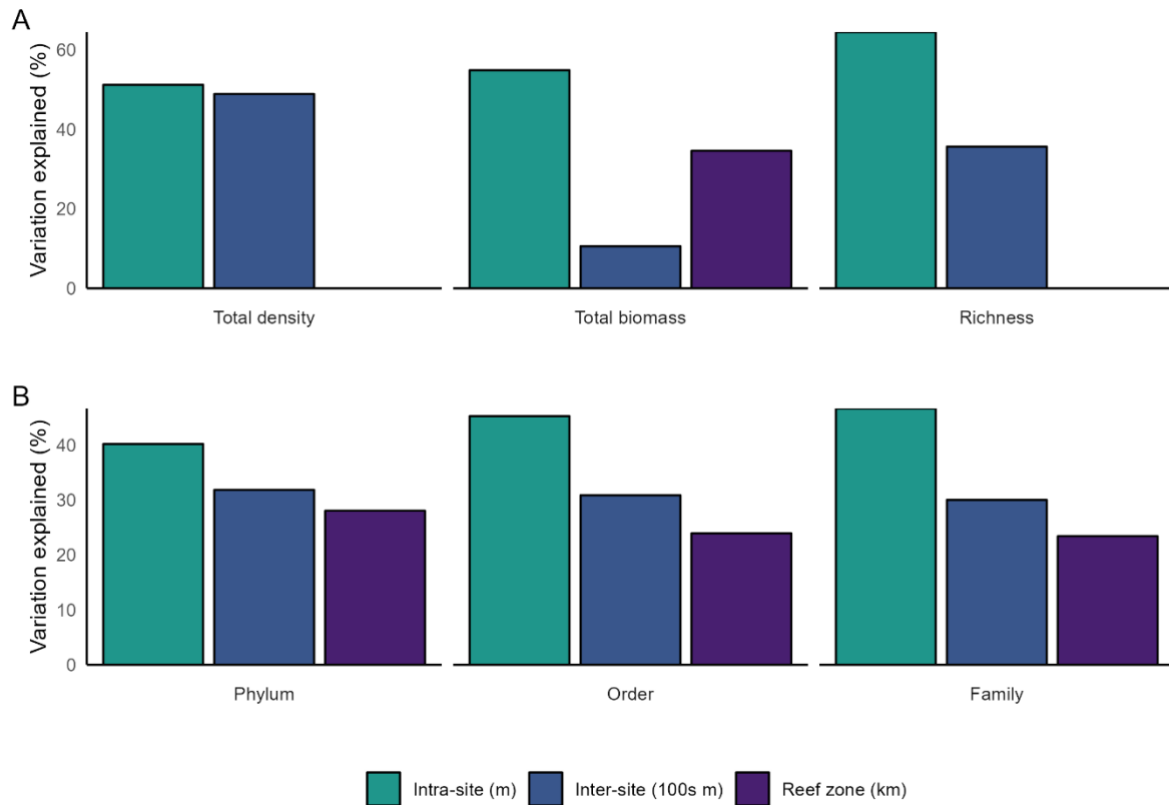
869 **Figure 2.** Biomass (A) and density (B) of motile cryptofauna living in coral rubble (n = 45  
 870 quadrats, n = 9 sites, n = 2 reef zones) at Palmyra Atoll, central Pacific. Those groups showing  
 871 the highest values for both biomass and density are shown in C and D, respectively to better  
 872 highlight the within-family variability.

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## Variation in coral rubble cryptofauna



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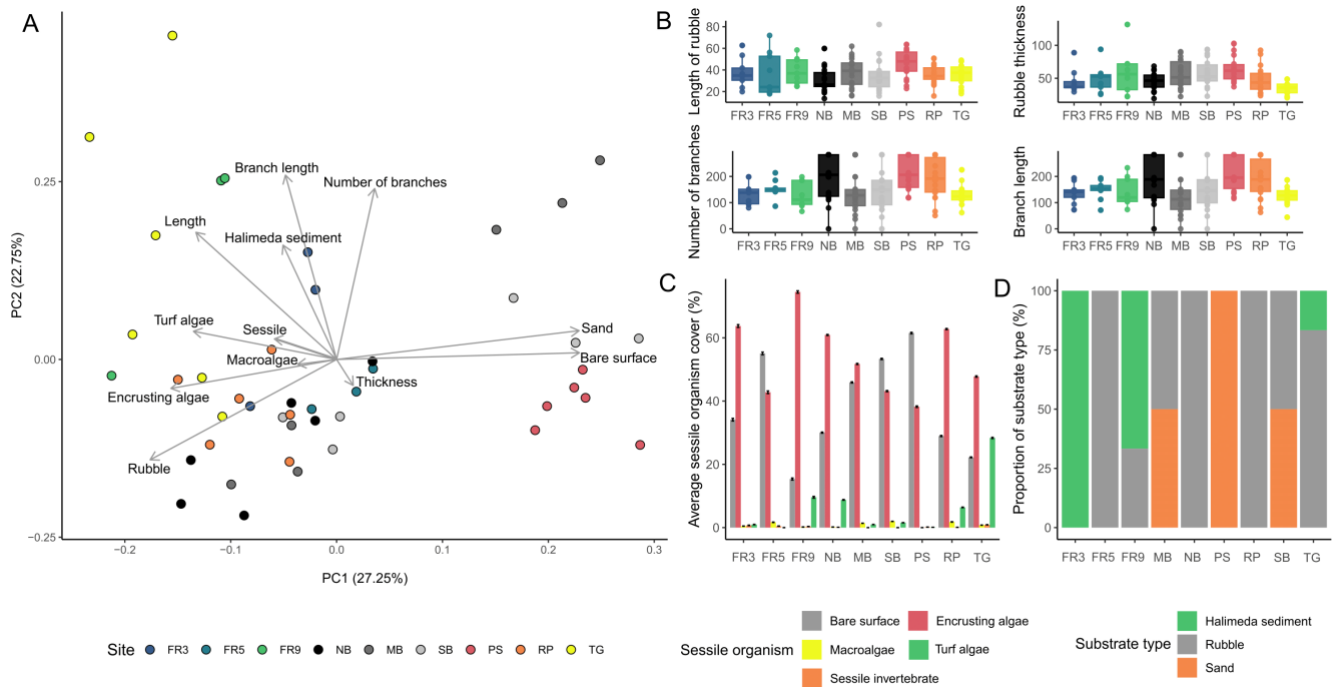
877 **Figure 3.** A) Percentage of total variation in cryptofauna total density, total biomass, and  
878 richness (univariate responses) explained by each spatial scale. B) Percentage of total variation  
879 in cryptofauna community composition (multivariate response) at three taxonomic resolutions  
880 explained by each spatial scale. Variance components in A are derived from nested ANOVA,  
881 and variance components in B are derived from PERMANOVA.

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## Variation in coral rubble cryptofauna



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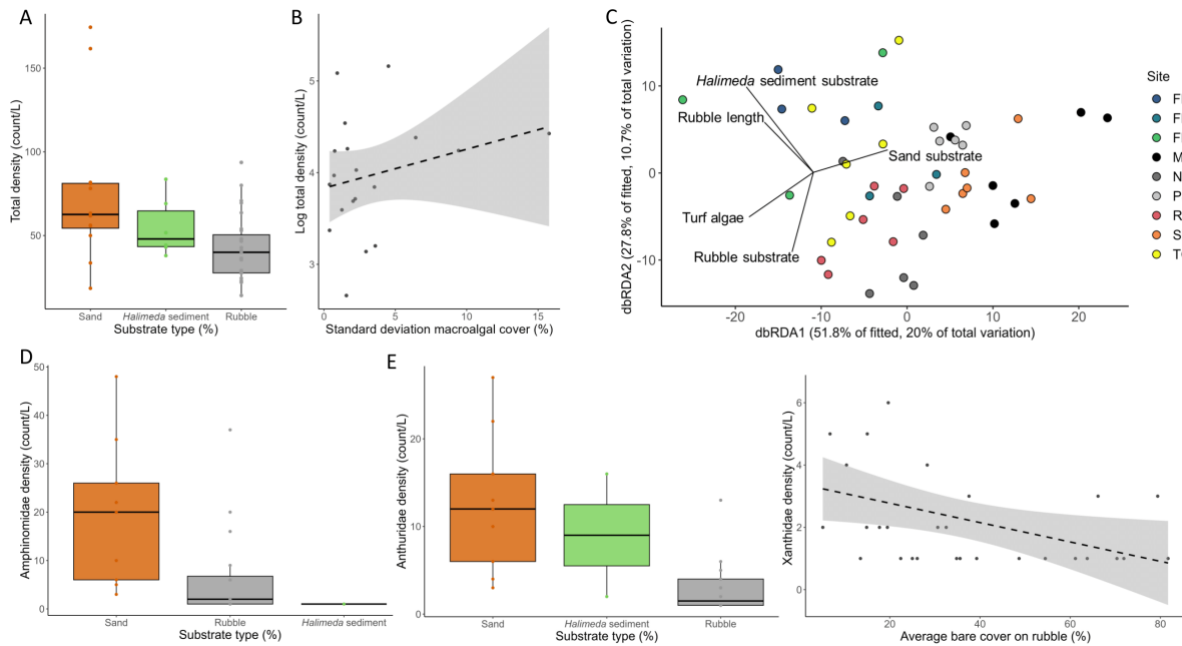
886 **Figure 4.** A) Principal components analysis (PCA) of rubble characteristics sampled from nine  
 887 sites across Palmyra Atoll, central Pacific. B) Box (median and 50% quantile) and whisker  
 888 (95% quantile) plots of the coefficient of variation (CoV) of rubble morphometrics across sites.  
 889 Each point represents the mean from each quadrat (n = 8 rubble pieces per quadrat, n = 360  
 890 rubble pieces for all sites). C) Mean percentage cover of sessile organisms on rubble across  
 891 sites. D) Substrate type found below each scooped rubble sample, expressed as a proportion of  
 892 the total quadrats scooped at each site (n = 3 - 6 quadrats per site, n = 45 quadrats for all sites).  
 893 For location of sites around Palmyra see Fig. 1.

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## Variation in coral rubble cryptofauna



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898 **Figure 5.** A) Variation of total cryptofauna density for each substrate type. Each point  
 899 represents total cryptofauna density from an individual quadrat. B) Relationship between total  
 900 density of cryptofauna and variability in macroalgal cover. Each point represents total  
 901 cryptofauna density in an individual quadrat, and the corresponding variability of macroalgal  
 902 cover on rubble pieces collected in that quadrat. C) Similarity in cryptofauna community phyla  
 903 across sites at Palmyra Atoll and their proximate environmental drivers. The direction of the  
 904 environmental vector lines indicates the relationship of each variable to the site groupings in  
 905 multivariate space. The length of each vector line is proportional to the strength of the variance  
 906 explained by that variable. D) Variation of *Amphinomidae* density measured for each substrate  
 907 type. Each point represents the density of *Amphinomidae* from an individual quadrat. E)  
 908 Variation of *Anthuridae* density measured for each substrate type. Each point represents the  
 909 density of *Anthuridae* from an individual quadrat. F) Relationship between *Xanthidae* density  
 910 with average bare surface cover on rubble. Each point represents the density of *Xanthidae* crabs  
 911 in an individual quadrat, and the corresponding average bare surface cover on rubble pieces  
 912 collected in that respective quadrat.

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## 915 APPENDICES

916 Table A 1 Eleven predictors used to model cryptofauna community structure and rubble habitat  
 917 characteristics. Reef zones include forereef (FR) and backreef (BR) Substrate types include  
 918 *Halimeda* (calcifying alga) sediments (HS), Rubble (R), Sand (S). SD, standard deviation.

Reef Zone	Mean number of branches	SDbranch length (cm)	SDlength (cm)	SDthick (cm)	SDturf algae (%)	SDmacroalgae (%)	SDsessile invert (%)	SDencrusting algae (%)	Mean bare area (%)	Substrate

Variation in coral rubble cryptofauna

FR	FR3	0.96	1.23	4.59	1.65	0.00	1.61	0.00	30.28	35.93	HS
FR	FR3	0.79	1.70	2.91	2.04	0.00	4.22	0.00	38.42	31.74	HS
FR	FR3	0.75	1.04	2.02	1.25	5.92	0.00	10.21	24.36	34.70	R
FR	FR5	0.58	1.31	2.79	0.87	0.00	1.12	4.71	28.82	61.92	R
FR	FR5	0.71	1.15	2.63	1.39	0.00	8.68	0.00	32.47	45.79	R
FR	FR5	1.04	1.00	3.76	2.24	0.00	1.85	0.00	28.84	57.48	R
FR	FR9	0.96	2.21	3.86	0.57	3.06	0.43	0.00	24.61	23.00	HS
FR	FR9	1.25	1.58	3.37	2.45	24.78	0.00	0.00	33.11	18.22	HS
FR	FR9	0.71	1.37	2.89	1.12	20.38	1.63	3.74	24.46	4.85	R
BR	MB	0.38	0.66	3.00	1.33	0.53	5.99	0.00	12.04	21.07	R
BR	MB	0.46	0.99	2.60	1.71	0.00	6.84	0.00	22.10	34.84	R
BR	MB	0.67	1.26	1.43	1.17	0.00	1.18	0.00	18.38	34.42	R
BR	MB	1.46	1.05	3.85	1.07	9.90	0.00	0.00	24.59	53.27	S
BR	MB	1.79	1.41	1.85	0.95	6.00	5.84	0.00	21.72	61.89	S
BR	MB	2.21	1.20	2.82	1.42	0.00	2.68	0.00	21.20	69.98	S
BR	NB	0.67	1.00	2.89	1.28	2.74	0.00	0.00	26.82	42.86	R
BR	NB	0.79	1.13	2.30	1.48	5.29	0.00	0.93	20.99	37.09	R
BR	NB	1.08	1.24	2.34	1.02	2.12	0.00	2.01	21.80	58.34	R
BR	NB	0.25	0.55	1.06	0.70	10.38	0.00	0.00	19.25	19.41	R
BR	NB	0.17	1.57	2.15	0.67	23.02	2.35	0.00	23.33	14.37	R
BR	NB	0.21	0.57	1.38	1.03	20.68	1.25	0.00	18.44	8.13	R
BR	PS	0.63	0.94	1.76	1.18	0.00	0.00	0.00	36.05	51.87	S
BR	PS	0.38	0.79	2.86	1.49	0.00	0.00	0.41	31.19	50.44	S
BR	PS	0.25	0.65	2.61	1.77	0.00	0.00	0.00	33.91	74.75	S
BR	PS	0.63	1.16	2.39	1.85	0.00	0.00	0.00	38.44	60.13	S
BR	PS	0.50	1.70	2.79	1.81	1.66	0.00	0.00	38.17	59.94	S
BR	PS	0.54	1.01	3.36	2.10	1.36	0.00	4.08	23.00	71.94	S
BR	RP	0.92	1.38	2.93	1.09	5.11	0.00	1.26	25.03	37.70	R
BR	RP	0.33	0.94	3.23	1.18	17.06	0.00	0.57	21.42	21.19	R
BR	RP	0.79	1.30	2.58	1.46	8.71	0.00	0.00	22.07	14.54	R
BR	RP	0.58	0.98	2.31	1.15	15.24	0.00	0.00	32.06	31.38	R
BR	RP	0.83	1.79	2.40	1.62	19.33	19.12	0.00	25.15	27.10	R
BR	RP	0.46	1.84	3.01	1.40	12.10	16.82	0.00	28.52	41.81	R
BR	SB	0.63	1.11	2.49	1.85	12.36	9.52	0.00	19.69	36.71	R
BR	SB	0.58	1.22	2.17	1.37	0.00	2.55	0.00	25.93	48.36	R
BR	SB	0.46	0.80	2.29	1.08	0.00	9.34	0.00	16.59	49.17	R
BR	SB	0.96	1.11	2.11	1.37	1.83	0.44	0.00	19.50	76.66	S
BR	SB	0.79	1.42	2.95	1.50	4.81	3.02	0.00	31.18	63.83	S
BR	SB	1.46	0.98	1.77	1.28	0.00	2.55	0.00	33.58	45.27	S
BR	TG	0.75	1.30	2.52	0.82	13.71	0.00	3.40	22.52	21.64	R
BR	TG	0.58	0.80	2.15	0.98	26.50	0.00	0.00	24.34	20.38	R
BR	TG	0.83	1.41	2.36	0.78	21.79	0.00	7.75	28.35	21.10	R
BR	TG	1.04	2.03	4.53	0.82	19.60	0.23	2.07	19.61	28.67	R
BR	TG	1.13	2.60	6.13	0.83	24.77	0.90	0.14	28.70	23.62	R
BR	TG	2.08	1.76	4.31	0.91	1.88	12.71	2.94	26.36	17.87	HS

## Variation in coral rubble cryptofauna

920

921