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Quantifying spatial gradients in coral reef benthic communities using

multivariate dispersion

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coral species

1 Abstract

1 Tropical coral reefs are dynamic, disturbance-driven ecosystems that are heterogeneous across space 2 and time, partly due to gradients in cross-scale human impacts and natural environmental factor. Localised management interventions which strive to maintain the long-term persistence and function 3 4 of coral reefs need to be informed by how and why reef habitats vary. Using the 'multivariate 5 dispersion' metric, a statistical approach to measure ecological community variability, we quantified 6 spatial gradients in coral reef benthic communities around Tutuila Island in American Samoa, central 7 South Pacific. Benthic communities with low, medium, and high dispersion each had distinct and 8 consistent underlying benthic community characteristics. Low dispersion sites were consistently 9 characterised by high hard coral cover, medium dispersion sites were generally dominated by 10 crustose coralline algae, while high dispersion sites were dominated by turf and fleshy coralline algae. Variability in hard coral and turf algal cover explained 42 % of the underlying variation in 11 12 benthic community dispersion across sites, while site-level gradients in human impacts and 13 environmental factors did not correlate well with variations in benthic community dispersion. The 14 metric should be further tested on temporal data to determine whether it can summarise complex 15 community changes in response to and following acute disturbance.

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16 **1. Introduction**

17 Tropical coral reefs are dynamic, disturbance-driven ecosystems that display habitat heterogeneity across space and time (1,2). This heterogeneity is partly driven by gradients in environmental factors 18 19 like surface wave energy, seawater temperature, and differences in nutrient concentrations and 20 primary production (3–6). These broad scale environmental gradients cause variation in habitat 21 condition that, in part, dictate which benthic groups can then compete for space at smaller scales on 22 the reef floor (7,8). Human impacts of varying scale, such as ocean warming, over-harvesting of 23 resources, habitat loss, and nearshore declines in water quality associated with coastal development also drive reef ecosystem patterns and processes (9). These impacts are superimposed over the 24 25 backdrop of natural environmental factors and together shape coral reef benthic community 26 organisation on many contemporary coral reefs (10–12). Localised management interventions which 27 strive to maintain the long term persistence and function of coral reefs need to be informed by how 28 and why coral reef habitats vary (13–15). Attempts to modify reef condition by manipulating 29 manageable human drivers must do so within the natural bounds of the system and what is even 30 achievable given the local environmental context of the reef community (16). An essential step to 31 achieve this is to effectively quantify and characterise coral reef benthic community heterogeneity 32 across gradients in these various driving forces.

33

34 Over the last four decades, multiple stressors on coral reefs have occurred more frequently and at 35 stronger intensities (17), driving global decline in coral cover and habitat complexity (18–20), and 36 changes in ecosystem function (21–23). Some coral reefs typically formed by reef-building 37 scleractinian corals have become dominated by other non-accreting benthic groups (e.g. fleshy 38 macroalgae, soft coral, turf algae, and sponges) (14,15,24–26). In some instances this can lead to 39 'biotic homogenisation', whereby multiple specialist species and groups are replaced by fewer, more generalist species and groups to create more spatially homogenous reef communities (12,27,28). 40 41 Studies documenting such changes in reef communities have often focussed on overall declines in 42 total coral cover, overlooking more taxonomically-resolved changes in community structure (12,29-31). For example, shifts in coral community composition following acute and chronic disturbance can 43

44 occur because of a disproportionate loss of fragile habitat-forming branching, plating and digitate 45 Acropora and Pocillopora coral species, compared to the more resilient massive and encrusting coral forms that offer more limited shelter for reef-associated organisms (32–36). One approach to better 46 47 understand changes in coral communities beyond changes in total cover is to categorise coral species 48 by their life history strategy. These include the 'competitively' dominant fast-growing species, which 49 are more sensitive to disturbance compared with 'stress-tolerant' slower-growing species, the 50 opportunistic 'weedy' corals which quickly recolonise after disturbance, and the 'generalist' group of 51 species that display characteristics of the other three strategies (37). The application of these trait-52 based groups is one method of characterising coral reef composition in the face of their natural 53 heterogeneity and in response to acute and chronic disturbance (35,38). 54 55 Changes in ecological community composition can also be quantified statistically, and although 56 functional diversity indices are commonly used, there is a need to explore other community level 57 metrics. Beta diversity, a measure of biodiversity related to species turnover, can be used to estimate 58 the variability in species composition among sampling units for a given area at a given spatial scale 59 (39). Anderson (40) developed the 'multivariate dispersion' metric, as a measure of beta diversity, 60 which quantifies the variability in ecological communities (in multivariate space) among independent sampling units (Fig. 1). 61 62 63 Figure 1: Analytical pipeline used to quantify benthic community multivariate dispersion (MvD) 64 among observations (in our case 'transects') within each group (in our case 'sites') (STEP 1) and to 65 characterise the underlying benthic community composition of gradients in dispersion in multivariate 66 space (STEP 2).

67

Low multivariate dispersion indicates that community composition is highly consistent between
replicates (e.g. transects) within groups (e.g. sites), whereas high multivariate dispersion is indicative
of more heterogeneous communities, with greater replicate to replicate variability in community

71 structure. Two groups can of course have the same level of multivariate dispersion (e.g., low or high 72 dispersion sites) but for different underlying taxonomic reasons. As such, two groups with similar dispersion levels may overlap or not overlap in multivariate space, indicating that they have similar 73 74 or different underlying communities, respectively (Fig. 1). Previous works have used changes in multivariate dispersion of ecological communities to indicate environmental stress (41,42), capture 75 76 the recovery trajectories of coral reefs following warming events (43), quantify depth and latitudinal 77 gradients in temperate reef fish communities (44), and highlight how temperate reef fish communities 78 respond differently to changes in habitat structure at varying spatial scales (45). Very few studies have applied the multivariate dispersion metric to understand the spatial heterogeneity within and 79 80 across locations on tropical coral reefs, despite the metric having higher sensitivity compared to 81 univariate counterparts in detecting low levels of disturbance (39,43,46). This synthetic data 82 reduction method has the potential to be used more broadly to understand underlying differences in 83 habitat within the whole community and to characterise the differences that may exist within and 84 between reefs.

85

86 Here we apply and assess the utility of the multivariate dispersion metric to characterise coral reef 87 benthic communities. This is an important first step in determining whether the metric is an effective 88 reef resilience monitoring indicator for synthesising complexities in benthic communities that can 89 inform local management interventions in maintaining the long-term persistence and function of 90 coral reef ecosystems. Using survey data, we quantified the spatial gradients in coral reef benthic 91 community variability across sites around the island of Tutuila in American Samoa, which represent 92 major watersheds along a gradient of reef geomorphologies (steepness and habitat complexity), wave 93 exposures, water quality and human impact. American Samoa has a history of multiple and varied 94 types of disturbance over the past 40 years, including two major coral predator (crown-of-thorns) outbreaks (1976 and 2013), four mass bleaching events (1994, 2002, 2003 and 2017), ten cyclones, 95 96 six extreme low tide events, and a tsunami in 2009 (47). The coral reef communities in American 97 Samoa have shown resiliency for rapid recovery and high tolerance to natural and human-induced 98 stressors (47), providing a suitable study area to understand spatial heterogeneity in response to the

99	various driving factors. Specifically, the study aims were to: (i) quantify patterns of benthic
100	community multivariate dispersion across space (sites); (ii) characterise the underlying benthic
101	community composition of gradients in multivariate dispersion (composition of benthic functional
102	groups and coral communities); (iii) test whether the percentage cover of specific benthic groups or
103	metrics of benthic diversity explains patterns of multivariate dispersion across space; and (iv) test
104	whether gradients in human impacts and environmental factors explain patterns of multivariate
105	dispersion across space.
106	
107	2. Materials and Methods
108	
109	Study area
110	Data were collected around the high volcanic island of Tutuila in American Samoa, an
111	unincorporated United States of America Territory located in the central South Pacific Ocean
112	(14.27°S, 170.13°W) (Fig. 2A). Tutuila Island has a human population of ~56,000, a total land area
113	of ~200 km ² , and a forereef habitat area (the outer reef slope facing the open ocean) of ~49 km ² (48).
114	Surveys were conducted over a 3-week period in November 2016, as part of an inter-agency
115	watershed monitoring project, which aimed to integrate existing coral reef surveys and water quality
116	sampling conducted by local government agencies (49). As part of the project, 28 sites were chosen
117	using ArcMap 10.4 to represent major watershed delineations around Tutuila (Fig. 2C). To ensure
118	comparability, survey sites were located in bays on the forereef habitat at 10 m depth, and
119	approximately 250 m out from any major stream mouth (Fig. 2B). Human population density per
120	major watershed was calculated from the 2010 census of American Samoa using the population
121	counts for places (villages), and each site was categorised into low (\leq 25th percentile), medium (\geq
122	25th and \leq 75th percentile), or high (\geq 75th percentile) human population (50). Sites were categorised
123	into four geographical sectors (North-west, North-east, South-west, South-east), based on
124	biogeographic habitat delineations used by the National Oceanic and Atmospheric Administration's
125	(NOAA) Pacific Reef Assessment and Monitoring Program (51) (Fig. 2C).

126

127 Figure 2. (A) Location of American Samoa in the central South Pacific Ocean (black marker). (B)

128 Example site surveyed using multiple transects (yellow dotted lines), image source: (52). (C) Survey

129 site locations (displayed with black dots) within the four biogeographical sectors around Tutuila

130 Island (delineated by dotted lines), and categories of major watershed delineations based on human

- 131 population density (low, medium, high).
- 132

133 Benthic community digital surveys and post-processing

At each site, surveys were conducted by divers on SCUBA by laying two 100-m transect tapes consecutively along the 10-m depth contour parallel to shore in the direction of the open ocean (Fig. 2B). Benthic community surveys were then conducted along six 25-m sections of this combined 200 m linear distance with 5-m breaks in between each of them: 0-25 m, 30-55 m, 60-85 m, 90-115 m, 120-145 m, 150-175 m. Along each 25-m section, digital images of the benthos were taken ~1 m above the sea floor at 1-m intervals using an Olympus Tough TG-4 camera (n= 26 images taken per transect, n = 156 images per site).

141

142 For each image, five randomly allocated points were overlaid (n = 125 data points per transect, 750 143 data points per site) (53) using Coral Point Count with Excel extensions (CPCe) (54) and the 144 substrate under each point identified as belonging to one of the following ten major categories: hard 145 coral (to genus level and growth forms within genera such as Acropora 'tables', 'staghorn', or 146 'arborescent'); crustose coralline algae (CCA; multiple genera); branching coralline algae; non-147 calcified macroalgae (greater than 2 cm, to genus level if abundant); Halimeda spp. (a common genus 148 of calcifying macroalgae across the Pacific); turf algae (a mixed community of filamentous algae and 149 cyanobacteria less than 2 cm tall, including the 'epilithic algal matrix'); fleshy coralline algae (e.g. 150 shedding-calcareous algae known to overgrow corals like *Peyssonnelia* spp. (55)); other invertebrates 151 (including sponges, and soft coral to genus level if abundant); sand; and rubble (Table S1). This 152 categorisation resulted in 61 minor categories, 41 of which were coral genera and common coral 153 species within the hard coral major category (Table S2). The benthic substrate ratio (BSR) can be

used as a metric of reef condition (56), by calculating the ratio of heavily calcified organisms (hard 154 155 corals, CCA, branching coralline algae, and Halimeda spp.) to less-or-non calcifying (turf algae, non-156 calcified macroalgae, fleshy coralline algae) benthic variables for each survey site. Coral genera and 157 common coral species were classified into four different life-history strategy categories: competitive, 158 opportunistic weedy, stress-tolerant and generalist, which are primarily separated by colony 159 morphology, growth rate and reproductive mode (sensu (37)) (Table S2). Key coral genera were also 160 classified into rapid- and slow-growing categories (35), based on the growth forms 'bushy and 161 tabular', and 'massive and columnar' (Table S2). 162 163 Quantifying human impacts and environmental factors 164 Human impacts and environmental factors collated for each survey site included surface wave 165 energy, dissolved inorganic nitrogen, human population density per major watershed, the proportion 166 of disturbed land in each major watershed, reef steepness, and habitat complexity. Surface wave 167 energy, a key driver of benthic community structure on coral reefs (4,57), was calculated using a 168 wave exposure proxy developed for Tutuila by the National Oceanic and Atmospheric 169 Administration (58), which is an estimate of the mean maximum daily wave power (kW/m) over a 170 10-year period (2002-2012), at 1-km resolution using the NOAA WaveWatch III (WW3) global 171 wave model (<u>http://pacioos.org/metadata/as_noaa_all_wave_avg.html</u>). Dissolved inorganic nitrogen 172 was used as a proxy of 'water quality', due to it often being the most abundant and bioavailable form of nitrogen, and relatively straightforward and economical to analyse (59). Dissolved inorganic 173

174 nitrogen concentrations (in mg L^{-1}) were measured using a SEAL Analytical AA3 HR Nutrient

175 Analyzer (49). Mean, standard deviation, and maximum dissolved inorganic nitrogen were calculated

176 for each survey site using data from samples collected at 26 streams, which were located within

177 major watersheds associated with each survey site. The samples were collected at the same time each

- 178 month over a 12 month period between September 2016 to September 2017 with a few exceptions.
- 179 Two of the survey sites were only sampled twice, and another two sites were not sampled at all due
- 180 to inaccessibility of the stream from land. As each sample represents a snapshot in time, we

181 calculated the 12-month mean, standard deviation, and maximum value for each site to account for 182 any seasonal variations in rainfall and storm events. To try and capture local human impacts to the 183 nearshore reefs, we quantified two proxies: human population density and nearby land use. Human 184 population density per major watershed was calculated from the 2010 census of American Samoa 185 using the population counts for places (villages)

(https://www.census.gov/population/www/cen2010/island_area/as.html). The proportion of disturbed
land to undisturbed land in each major watershed's area was estimated in ArcGIS 10.4 using the
American Samoa Vegetation layer derived from QuickBird satellite imagery (60). The total area of

189 disturbed land was calculated using four categories: quarry/landfill (areas recently bulldozed for

190 quarrying activities or used for solid waste disposal), secondary scrub (an intermediate type of

191 vegetation that occurs when cultivated land is abandoned and allowed to revert to natural forest),

192 urban built-up (impervious urban surfaces such as houses and paved roads), and urban cultivated area

193 (all vegetated areas within a general urban boundary). To quantify site-level habitat complexity, four

194 digital images were taken of the reefscape at the start of each transect at each site, by facing each

195 major cardinal direction (N, E, S, W). Each image was visually and manually scored from 0 to 5,

where 0 = no vertical relief; 1 = low and sparse relief; 2 = low but widespread relief; 3 = moderately

197 complex; 4 = very complex with numerous fissures and caves; 5 = exceptionally complex with

numerous caves and overhangs (61). Site-level reef steepness was also estimated using the same

images, by assigning a value from 1 to 5, where 1 = flat; 2 = gradual slope; $3 = 45^{\circ}$ slope; $4 = 65^{\circ}$

slope; and 5 = vertical wall. These transect level values of habitat complexity and steepness were

201 then used to calculate site-level averages.

202

203 Statistical analyses

204 To quantify variability in community composition (multivariate dispersion) across the six benthic

transects at each site, we used the 'betadisper' function in the vegan package (62) for R (www.r-

206 project.org). The 'betadisper' function runs a distance-based test for the analysis of multivariate

207 homogeneity of group dispersions (variances) (40,46) and calculates the distance of each observation

208 (in this case 'transect', n=6) to its group centroid (in this case 'site', n=28). We used distance to

209	spatial median as our distance measure (the point in the multivariate cloud which minimizes the sum
210	of the distances from each replicate observation to that point) as it is less affected by outliers (63).
211	Calculations of multivariate dispersion were run on a Euclidean similarity matrix for the mean
212	percentage cover of the ten major benthic variables. No transformations were applied to the data to
213	preserve the raw dispersion among transects within each site (40). Patterns of multivariate dispersion
214	were visualised using non-metric multi-dimensional scaling (nMDS) using the metaMDS function in
215	the vegan package (62), again using Euclidean similarity matrices for the major benthic variables.
216	Sites were ranked based on their distance to median (dispersion) values, which were defined as low
217	(\leq 25th percentile), medium (\geq 25th and \leq 75th percentile), or high (\geq 75th percentile) dispersion
218	categories.
219	To investigate which of the benthic characteristics and human impacts and environmental factors
220	(predictor variables) best explained variation in multivariate dispersion at the major benthic category
221	taxonomic resolution (response variable), we used distance-based linear modelling (DISTLM;
222	(64,65). In addition to the benthic variables and human impacts and environmental factors, we
223	calculated a suite of diversity indices on both the mean percentage cover of the major benthic
224	variables and the coral genera data using the DIVERSE function in PRIMER version 7.0.23 (66). The
225	indices calculated for each site were: Margalef's species richness (d); Shannon-Wiener index (H'),
226	which places more emphasis on rare or less abundant variables; Simpson's index (λ), which places
227	more emphasis on the more dominant variables (63), and Pielou's evenness (J), which measures how
228	uniformly spread the total abundance of each variable is within each observation (66). Prior to
229	model-fitting, we tested whether any of the predictor variables were significantly correlated with
230	each other using the 'ggcorrplot' package in R (67), testing the null hypothesis that each pairwise
231	comparison was not correlated (Fig. S1 and Fig. S2). The following predictors significantly
232	correlated: Shannon's diversity index of the major and minor benthic substrate groups correlated with
233	the Simpson's diversity index ($r = 1$), we retained the Shannon diversity index as it emphasizes less
234	abundant species instead of dominant species; Pielou's evenness of benthic groups and Simpson's
235	diversity index of benthic groups ($r = 0.9$), we retained Pielou's evenness of benthic groups; sand and

rubble (r = 0.9), rubble was retained due to the relative importance of rubble with regard to benthic invertebrate diversity (68); and mean correlated with maximum dissolved inorganic nitrogen (r =0.9). We retained maximum dissolved inorganic nitrogen given that maximum exposure to nutrient stress is likely to be more important than mean exposure. The final suite of benthic variables and human impacts and environmental factors included in the models are listed in Table 1.

241

Table 1. Predictor variables, biotic (A) and human impacts and environmental (B), used to try and explain variation in coral reef benthic community multivariate dispersion among sites using distancebased linear modelling (DISTLM). Units and spatial/temporal resolution are shown for each variable and the data sources for the human impacts and environmental factors.

246

247 Models were first built using the benthic characteristics as the predictor variables, and then the model-248 fitting process was repeated using the human impacts and environmental factors as predictors. In each 249 case, the DISTLM models were built from a Euclidean similarity matrix of the site dispersion values. 250 All possible candidate models (i.e. unique combinations of the predictor variables) were computed 251 using the 'best' model selection procedure (63) and ranked using Akaike's Information Criterion (69) 252 with a second-order bias-correction applied (AICc) (70) to account for the relatively small sample size 253 relative to the number of predictor variables. All models within 15% AICc of the top model are reported, and the marginal relationships between each predictor and benthic dispersion were plotted to 254 255 identify the overall directionality of the relationships and Pearson's correlations calculated. All 256 DISTLM analyses were completed using the PERMANOVA+ add-on (63), for PRIMER version 257 7.0.23 (71). Source code available at https://github.com/alicelawrence2021/dispersion.git.

258

259 **3. Results**

260 Intra-island gradients in benthic cover

261 There were clear intra-island gradients in benthic group cover within the four biogeographical sectors

262 (north-east, north-west, south-east, south-west) (Fig. 3A). Mean (\pm SE) hard coral cover peaked in

263 the north-east ($35.6 \pm 7.4 \%$), and was lowest in the south-east ($22.4 \pm 4.9 \%$) (Fig. 3A). Sites in the

264	north-east also had the highest mean cover of branching coralline algae (7.2 \pm 2.4 %), <i>Halimeda</i> spp.
265	$(6.6 \pm 3.4 \%)$, rubble $(2.2 \pm 1.6 \%)$, sand $(4.0 \pm 2.4 \%)$, and turf algae $(14.9 \pm 3.9 \%)$. The mean
266	cover of turf algae was also high in the north-western sites (14.1 \pm 3.8%), and lowest in the south-
267	east (3.8 \pm 0.5 %). Sites in the south-east had the highest mean cover of crustose coralline algae
268	(CCA) and fleshy coralline algae (33.5 \pm 2.0 % and 30.8 \pm 5.5 %, respectively). The highest mean
269	cover of non-calcifying macroalgae was at south-western sites (9.2 \pm 2.8 %), and lowest in the north-
270	west (0.9 \pm 0.5 %). The benthic substrate ratio did not identify any island-wide trends in calcifying to
271	non-calcifying organisms by sector, with the highest ratio in the south-west (2.4 \pm 0.8), and lowest in
272	the south-east (1.9 ± 0.5) (Table S3).
273	

274 Figure 3. (A) Median percentage cover of benthic groups within the four biogeographical sectors 275 north east) (n = 8 sites), north west) (n = 6 sites), south east) (n = 9 sites), south west) (n = 5 sites)). 276 CCA, Crustose Coralline Algae; FCA, Fleshy coralline algae; MA (non-calc), Macroalgae (non-277 calcified); BCA, Branching coralline algae; Halimeda, Halimeda spp.; Other Inverts, Other 278 invertebrates. Black dots represent outliers and boxes show the interquartile range and their middle 279 lines represent median values. (B) Location of the 28 survey sites around Tutuila Island and their 280 associated multivariate dispersion (distance to median) category (low, medium, high), mean 281 maximum daily wave power (kW/m) from 2002-2012, location of villages, and biogeographic sector 282 delineations.

283

284 Gradients in benthic community multivariate dispersion

At the site level, low dispersion sites were characterised as having a higher percentage cover of hard

286 coral (49.9 \pm 1.4 %), compared to medium (20.0 \pm 1.8 %) or high (17.1 \pm 1.8 %) dispersion sites

287 (Fig. 4, 5i). The medium and high dispersion sites had a mixture of benthic substrate groups,

including turf algae, branching coralline algae, macroalgae, sand, and rubble (Fig. 4). The cover of

- turf algae, *Halimeda* spp. and branching coralline algae was highest at high dispersion sites $(17.8 \pm$
- 290 2.0 %, 4.1 ± 0.8 %, and 5.9 ± 1.0 %, respectively) as compared to low dispersion sites (5.4 ± 0.7 %,

291 0.9 ± 0.2 %, and 1.3 ± 0.3 %, respectively). CCA cover was highest at medium dispersion sites (25.3 292 ± 1.3 %), and lowest at high dispersion sites (18.6 ± 2.1 %) (Fig. 5ii). CCA cover exceeded hard 293 coral cover (by between 10 to 28 %) at 7 of the 28 survey sites, 6 of which had medium dispersion 294 (see Fig. S3 for site-level graphs). Overall, the benthic substrate ratio decreased with increasing 295 dispersion (Fig. 5viii), suggesting that low dispersion sites had a higher proportion of calcifying, reef-296 building organisms. However, there was no consistent pattern in benthic community multivariate 297 dispersion within and between the four island sectors (Table S3).

298

Figure 4. Variation in benthic group cover among multivariate dispersion categories (low, medium, 299 300 high). Relative similarity in site-level (n=6 transects per site) multivariate dispersion of benthic 301 communities across 28 sites around Tutuila Island, American Samoa. NMDS was constructed from 302 all six transect replicates at each survey site, using Euclidean dissimilarities of non-transformed mean 303 percentage cover estimates of all major benthic categories (stress value: 0.18). The correlation 304 between each benthic variable and the first two ordination axes are overlaid as a bi-plot, with the 305 length of each vector line proportional to the strength of the correlation. CCA = crustose coralline 306 algae; FCA = fleshy coralline algae; BCA = branching coralline algae; OtherInverts = other 307 invertebrates.

308

309 Figure 5. Variation in mean percentage cover of the main benthic substrate categories within each 310 multivariate dispersion category; (i) low, (ii) medium, (iii) high. The ratio of mean percentage cover 311 of heavily calcified organisms to less-or-non calcifying within each multivariate dispersion category 312 is shown in plot (iv) Benthic Substrate Ratio (BSR). Boxplots are overlaid with transect replicate data 313 for each survey site, black dots represent outliers and boxes show the interquartile range and their 314 middle lines represent median values. CORAL = hard coral; CCA = crustose coralline algae; BCA = 315 branching coralline algae; HALI = Halimeda spp.; TURF = turf algae; MA = macroalgae; FCA = 316 fleshy coralline algae.

317

318 Gradients in hard coral community multivariate dispersion

319	The corals that best discriminated amongst the high-medium-low dispersion categories were
320	Montipora, Pavona, Acropora branching and corymbose growth forms, and Porites rus (Fig. 6A, see
321	Fig. S4 for site-level graphs). Low dispersion sites were dominated by the encrusting coral
322	Montipora grisea (Fig. 6B), where mean cover (23.8 \pm 1.5 %) was 16.5 % higher than at medium
323	dispersion sites (7.3 \pm 0.7 %), and 19 % higher than at high dispersion sites (4.7 \pm 1.1 %). The cover
324	of <i>Pavona</i> and all <i>Acropora</i> growth forms were also highest at low dispersion sites ($6.1 \pm 0.7\%$ and
325	8.1 ± 0.7 %, respectively) (Fig. 6B). <i>Pocillopora</i> corals were present in similar abundances at both
326	low and medium dispersion sites (1.2 \pm 0.2 %, and 0.8 \pm 0.1 %, respectively), and the cover of
327	Isopora and Porites rus corals were highest at medium dispersion sites (4.7 \pm 1.2 % and 6.4 \pm 0.9 %,
328	respectively) (Fig. 6B). The mean percentage cover of coral at high dispersion sites was relatively
329	low (18.5 \pm 15.0 %), with the communities dominated by <i>Montipora, Pavona</i> , and <i>Porites rus</i> (4.7 \pm
330	1.1% , $1.0 \pm 0.2 \%$, and $5.2 \pm 1.0 \%$, respectively). (Fig. 6B).

331

332 Figure 6. Variation in percentage cover of corals that best discriminated amongst the different 333 multivariate dispersion categories (low, medium, high). (A) Relative similarity in site-level (n=6 334 transects per site) multivariate dispersion of benthic communities across 28 sites around Tutuila 335 Island, American Samoa. NMDS plot on the basis of all six transect replicates at each survey site, 336 using Bray-Curtis dissimilarities of non-transformed mean percentage cover estimates of all coral 337 genera categories (stress value: 0.28). The correlation between each benthic variable and the first two 338 ordination axes are overlaid as a bi-plot, with the length of each vector line proportional to the 339 strength of the correlation. (B) Median percentage cover of six coral genera within each benthic 340 dispersion category (i) low; (ii) medium; and (iii) high. Boxplots are overlaid with transect replicate 341 data for each survey site, black dots represent outliers and boxes show the interquartile range and 342 their middle lines represent median values.

343

There were also clear patterns in the cover of hard corals with different life history strategies across
dispersion categories (Fig. 7). The cover of rapid-growing corals was higher at low dispersion sites

346 $(33.0 \pm 5.0 \%)$ compared to high dispersion sites $(4.2 \pm 3.5 \%)$ (Fig. 7). The cover of slow-growing 347 corals was higher at medium and high dispersion sites $(4.8 \pm 4.5 \% \text{ and } 4.8 \pm 6.5 \%, \text{ respectively})$ 348 compared to low dispersion sites $(3.5 \pm 5.2 \%)$. The mean cover of generalist, competitive, and 349 stress-tolerant corals was highest at low dispersion sites $(22.0 \pm 7.5 \%, 7.0 \pm 12.2 \%, 6.0 \pm 4.3 \%)$ 350 respectively), and all three groups decreased in cover with increasing dispersion (Fig. 7). Medium 351 dispersion sites had the highest cover of opportunistic weedy coral species (such as *Porites rus* and 352 *Pocillopora* corals) (8.0 \pm 8.2 %), followed by high (4.0 \pm 0.4 %), and then low dispersion sites (2.5 353 ± 4.2 %) (Fig. 7).

354

Figure 7. Variation in cover of corals with different life-history strategies among multivariate dispersion categories (low, medium, high). Summary boxplots showing median percentage cover of life history categories within each benthic dispersion category (i) low; (ii) medium; and (iii) high. Boxplots are overlaid with transect replicate data for each survey site, black dots represent outliers and boxes show the interquartile range and their middle lines represent median values.

360

361 **Ecological drivers of multivariate dispersion among sites**

362 Variations in hard coral and turf algae cover (top performing model) explained 41.5 % of the

363 underlying variation in benthic community multivariate dispersion across the 28 sites (Table 2).

364

365 Table 2. Distance-based linear modelling (DistLM) results testing for relationships between benthic 366 community multivariate dispersion across sites (n=28) and underlying benthic community 367 characteristics. All possible candidate models were run (unique combinations of the predictor 368 variables) and models were ranked using Aikaike's Information Criterion with a second-order-bias-369 correction applied (AICc). All models within 15% AICc of the top-performing model are reported. 370 Proportion (prop.) (%), overall variation in multivariate dispersion explained by the candidate model 371 (individual contribution of each predictor to the overall model performance is shown in parentheses 372 for each predictor within each candidate model); RSS, Residual Sum of Squares.

374	Benthic community multivariate dispersion was negatively correlated with hard coral cover, and
375	positively correlated with turf algae cover (Fig. 8). Variations in coral genera diversity, benthic
376	substrate group diversity, and macroalgae explained 45.5 % of the underlying variation, and the cover
377	of turf algae and fleshy coralline algae explained 39.5 % of the variation in benthic community
378	dispersion. Benthic dispersion positively correlated with mean cover of turf algae and benthic
379	substrate group diversity (Fig. 8). Conversely, benthic dispersion was negatively correlated with hard
380	coral cover and coral genera diversity (Fig. 8).
381	
382	Figure 8. Correlations between benthic community multivariate dispersion (site-level, n=28, mean
383	distance to median) and underlying benthic community characteristics, selected from DISTLM model
384	results. R = Pearson correlation coefficient, p = p -value.
385	
386	Correlations between benthic community multivariate dispersion and human impacts and
387	environmental factors
387 388	environmental factors Overall, the variation in site-level benthic community multivariate dispersion were not well explained
387 388 389	environmental factors Overall, the variation in site-level benthic community multivariate dispersion were not well explained by the human impacts and environmental factors we quantified. Variations in benthic habitat
387 388 389 390	environmental factors Overall, the variation in site-level benthic community multivariate dispersion were not well explained by the human impacts and environmental factors we quantified. Variations in benthic habitat complexity, reef steepness, and population density (top three performing models) explained only 10.2
387 388 389 390 391	environmental factors Overall, the variation in site-level benthic community multivariate dispersion were not well explained by the human impacts and environmental factors we quantified. Variations in benthic habitat complexity, reef steepness, and population density (top three performing models) explained only 10.2 %, 7.4 %, and 7.3 % of the overall variability in benthic community multivariate dispersion,
 387 388 389 390 391 392 	environmental factors Overall, the variation in site-level benthic community multivariate dispersion were not well explained by the human impacts and environmental factors we quantified. Variations in benthic habitat complexity, reef steepness, and population density (top three performing models) explained only 10.2 %, 7.4 %, and 7.3 % of the overall variability in benthic community multivariate dispersion, respectively (Table 3). The combination of benthic habitat complexity with reef steepness explained
 387 388 389 390 391 392 393 	environmental factors Overall, the variation in site-level benthic community multivariate dispersion were not well explained by the human impacts and environmental factors we quantified. Variations in benthic habitat complexity, reef steepness, and population density (top three performing models) explained only 10.2 %, 7.4 %, and 7.3 % of the overall variability in benthic community multivariate dispersion, respectively (Table 3). The combination of benthic habitat complexity with reef steepness explained 14.7% of the variation in multivariate dispersion across sites. Similarly, the combination of benthic
 387 388 389 390 391 392 393 394 	environmental factors Overall, the variation in site-level benthic community multivariate dispersion were not well explained by the human impacts and environmental factors we quantified. Variations in benthic habitat complexity, reef steepness, and population density (top three performing models) explained only 10.2 %, 7.4 %, and 7.3 % of the overall variability in benthic community multivariate dispersion, respectively (Table 3). The combination of benthic habitat complexity with reef steepness explained 14.7% of the variation in multivariate dispersion across sites. Similarly, the combination of benthic habitat complexity with population density, and with mean wave power explained 13.6 % and 11.9 %
 387 388 389 390 391 392 393 394 395 	environmental factors Overall, the variation in site-level benthic community multivariate dispersion were not well explained by the human impacts and environmental factors we quantified. Variations in benthic habitat complexity, reef steepness, and population density (top three performing models) explained only 10.2 %, 7.4 %, and 7.3 % of the overall variability in benthic community multivariate dispersion, respectively (Table 3). The combination of benthic habitat complexity with reef steepness explained 14.7% of the variation in multivariate dispersion across sites. Similarly, the combination of benthic habitat complexity with population density, and with mean wave power explained 13.6 % and 11.9 %
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 387 388 389 390 391 392 393 394 395 396 397 	environmental factors Overall, the variation in site-level benthic community multivariate dispersion were not well explained by the human impacts and environmental factors we quantified. Variations in benthic habitat complexity, reef steepness, and population density (top three performing models) explained only 10.2 %, 7.4 %, and 7.3 % of the overall variability in benthic community multivariate dispersion, respectively (Table 3). The combination of benthic habitat complexity with reef steepness explained 14.7% of the variation in multivariate dispersion across sites. Similarly, the combination of benthic habitat complexity with population density, and with mean wave power explained 13.6 % and 11.9 % of the variation in multivariate dispersion, respectively. Benthic community multivariate dispersion was negatively correlated with habitat complexity, there were weak positive correlations between benthic dispersion and reef steepness, and with human population density (Fig. S5). Dissolved
 387 388 389 390 391 392 393 394 395 396 397 398 	environmental factors Overall, the variation in site-level benthic community multivariate dispersion were not well explained by the human impacts and environmental factors we quantified. Variations in benthic habitat complexity, reef steepness, and population density (top three performing models) explained only 10.2 %, 7.4 %, and 7.3 % of the overall variability in benthic community multivariate dispersion, respectively (Table 3). The combination of benthic habitat complexity with reef steepness explained 14.7% of the variation in multivariate dispersion across sites. Similarly, the combination of benthic habitat complexity with population density, and with mean wave power explained 13.6 % and 11.9 % of the variation in multivariate dispersion, respectively. Benthic community multivariate dispersion was negatively correlated with habitat complexity, there were weak positive correlations between benthic dispersion and reef steepness, and with human population density (Fig. S5). Dissolved inorganic nitrate and disturbed land only explained 0.0003 % and 1.15 % of the overall variation in
 387 388 389 390 391 392 393 394 395 396 397 398 399 	environmental factors Overall, the variation in site-level benthic community multivariate dispersion were not well explained by the human impacts and environmental factors we quantified. Variations in benthic habitat complexity, reef steepness, and population density (top three performing models) explained only 10.2 %, 7.4 %, and 7.3 % of the overall variability in benthic community multivariate dispersion, respectively (Table 3). The combination of benthic habitat complexity with reef steepness explained 14.7% of the variation in multivariate dispersion across sites. Similarly, the combination of benthic habitat complexity with population density, and with mean wave power explained 13.6 % and 11.9 % of the variation in multivariate dispersion, respectively. Benthic community multivariate dispersion was negatively correlated with habitat complexity, there were weak positive correlations between benthic dispersion and reef steepness, and with human population density (Fig. S5). Dissolved inorganic nitrate and disturbed land only explained 0.0003 % and 1.15 % of the overall variation in multivariate dispersion, respectively.

401 Table 3. Distance-based linear modelling (DistLM) results testing for relationships between benthic 402 community multivariate dispersion across sites (n=28) and human impacts and environmental factors. 403 All possible candidate models were run (unique combinations of the predictor variables) and models 404 were ranked using Aikaike's Information Criterion with a second-order-bias-correction applied 405 (AICc). All models within 15% AICc of the top-performing model are reported. Proportion (%), overall 406 variation in multivariate dispersion explained by the candidate model (individual contribution of each 407 predictor to the overall model performance is shown in parentheses for each predictor within each 408 candidate model); RSS, Residual Sum of Squares.

409

410 **4. Discussion**

411 Using multivariate dispersion, we quantified spatial gradients in coral reef benthic community 412 variability around the circumference of American Samoa in the central South Pacific and investigated 413 whether different dispersion levels (low, medium, high) had commonalties in their underlying 414 benthic community characteristics (Fig. 1). We found that variability in hard coral and turf algae 415 cover explained most of the underlying variation in benthic community dispersion across sites. Low 416 dispersion sites were consistently characterised by high coral cover, dominated by encrusting corals, 417 and a diverse assemblage of rapid-growing branching and corymbose coral genera in low 418 abundances. Medium dispersion sites were generally dominated by CCA, and coral genera with 419 opportunistic life history strategies, while high dispersion sites were dominated by turf algae, and 420 fleshy coralline algae. There was higher cover of calcifying organisms at low dispersion sites, which 421 decreased as dispersion increased. Variations in benthic community dispersion were not well 422 explained by gradients in the human impacts and environmental factors modelled here (< 15% total 423 variation explained), suggesting that smaller-scale biological processes may be more important in 424 driving these patterns.

425

Low dispersion sites around our study island were consistently dominated by high coral cover rather
than macroalgae, turf algae or soft corals that often characterise more homogenous benthic
communities on coral reefs subjected to chronic and acute disturbance (24,72). Sites with low

429 dispersion were dominated by the encrusting hard coral Montipora grisea, which has rapid-growing, 430 stress-tolerant and competitive life history traits (37). Low dispersion sites were also characterised by 431 a high diversity of other predominantly rapid-growing coral genera all co-occurring in relatively low 432 abundances, including tabulate Acropora corals, and other branching corals such as Pocillopora and 433 Porites cylindrica. Although rapid-growing corals with branching and corymbose growth forms tend 434 to be susceptible to thermal stress (32,34,73), and are selectively fed on by coral predators such as 435 crown-of-thorns starfish (74), they are competitively dominant corals that can propagate through 436 fragmentation following acute physical disturbance from storms and persistent high wave energy 437 (4,33,75). Low dispersion sites also had the highest cover of Pavona corals, which have slow-438 growing and stress-tolerant life history strategies (37). It is unclear why low dispersion sites were 439 characterised by a diverse mix of rapid-growing and stress-tolerant coral genera. One hypothesis is 440 that low dispersion sites may be indicative of locations that have experienced both acute and chronic 441 disturbances, and may represent areas with environmental conditions that naturally create spatially 442 heterogenous habitats and diverse and resilient coral communities. Further temporal studies are 443 required to better understand the interactions between different disturbance events and community 444 dynamics at these low dispersion sites.

445

446 Benthic community dispersion increased as the cover of non-reef building organisms, such as turf 447 algae, fleshy coralline algae, and non-calcifying macroalgae increased, and as overall habitat 448 structural complexity decreased. Unlike low dispersion sites that consistently had the same 449 underlying benthic community characteristics (Fig. 1Biii), the benthic communities creating either 450 medium or high dispersion were highly variable (Fig. 1Bii). Medium dispersion sites had the highest 451 mean cover of crustose coralline algae (CCA), which rapidly colonise bare substrate following 452 disturbance (47) stabilising the reef (76,77), and providing substrate for coral settlement and growth 453 (47,78). Medium dispersion sites also had the highest cover of opportunistic weedy corals, including 454 Porites rus, which have brooding reproduction and high population turnover (79) that rapidly 455 colonise newly available space following acute disturbance (80). Long-term monitoring surveys in

456 American Samoa have shown a general decline in the cover of Acropora corals and a widespread 457 increase in cover of Porites rus because of disturbances (Birkeland C, pers. comm., March 2024), 458 which could indicate that medium dispersion sites at this location are characteristic of benthic 459 communities in recovery following acute disturbance. With increased frequency and magnitude of 460 acute disturbances, systems may tend to shift towards earlier successional states (81), which are 461 characterised by simple low ecosystem complexity composed of early colonisers that are quick to 462 respond and react to the change in environmental conditions (13). The high cover of turf algae and 463 fleshy coralline algae at high dispersion sites suggests these sites are dominated by organisms that 464 have colonised newly available space following acute disturbance (82,83), and environmental 465 conditions may not be as favourable as medium dispersion sites.

466

467 Over the last decade, fleshy coralline algae or peyssonnelid algal crusts (PAC) have become spatially 468 dominant across shallow reefs in the Caribbean (84), likely due to their ability to overgrow hard 469 corals (84) and inhibit coral settlement (85). In the absence of sufficient herbivorous fish to maintain 470 cropped algal turfs, sediment can accumulate, which inhibits coral settlement and recruitment, and 471 may provide suitable conditions for fleshy macroalgae to dominate the benthic community (86,87). 472 High dispersion sites had the lowest cover of hard coral, and of the corals present, the highest cover 473 of the large, slow-growing stress-tolerant Porites massive corals. Massive and encrusting coral 474 growth forms such as massive *Porites* and faviids are less susceptible to acute stressors such as coral 475 bleaching (34,73), and can dominate the reef when faster-growing Acropora species are unable to 476 recover due to repeated disturbance (88). One hypothesis is that high dispersion sites are in areas with 477 unfavourable environmental conditions and ongoing chronic stress (e.g. human or abiotic), which 478 could contribute to a slower than expected recovery (two-phase recovery) following acute 479 disturbances (89). Massive and encrusting coral growth forms can be more tolerant to variable and 480 chronic stressors (90–92), although there are exceptions to this generalisation (93).

481

482 Across our study sites, underlying variation in benthic community dispersion was only weakly

483 explained by concurrent gradients in three human impacts and environmental factors: benthic habitat

484 complexity, reef steepness, and human population density. As habitat structural complexity 485 increased, benthic dispersion values decreased. Habitat complexity is driven by the underlying 486 benthic community and at sites with lower dispersion, we saw an increase in coral types that generate 487 higher structural complexity (e.g. tabulate, branching and corymbose corals). There was a weak 488 positive correlation between human population density and benthic community dispersion, where 489 sites close to the highest human population densities around Tutuila had the highest dispersion, 490 relatively low coral cover and habitat structural complexity, and high cover of turf and macroalgae. 491 These drivers only explained a small proportion of the variation in multivariate dispersion, yet many 492 studies have found links between local human impacts and a reduction in reef resilience. For example 493 a decrease in habitat complexity and an increase in fleshy algae cover from overfishing (14,86), 494 nutrient and wastewater pollution (15,94), and from coastal development (95). Additionally, we did 495 not find any associations between variation in benthic community dispersion and surface wave 496 energy, dissolved inorganic nitrogen (water quality proxy), or the proportion of disturbed land in the 497 watershed. Potential explanations are scale mis-matches between the spatial resolution of our human 498 impacts and environmental factors and benthic community dispersion, or that benthic dispersion is 499 being driven by smaller scale biological driving forces, such as competition, predation and 500 reproduction.

501

502 In conclusion, multivariate dispersion (a univariate metric) was able to capture and synthesise 503 complex underlying multivariate gradients in coral reef benthic community characteristics across our 504 study sites in American Samoa. In particular, the metric helped to highlight key differences in coral 505 assemblages and their life history strategies among dispersion categories. Similar community 506 gradients for the other benthic groups (e.g. macroalgae) might be revealed by increasing their 507 taxonomic resolution. The utility of multivariate dispersion as a response metric could be further 508 tested on temporal benthic community data, to test whether it effectively captures shifts in 509 successional states and community recovery following disturbance, and the impacts of gradients in 510 local human disturbance across broader spatial scales. Multivariate dispersion could be used as a

511	synthetic data reduction method for monitoring coral reef benthic communities and has the potential
512	to be used more broadly to understand community differences across other trophic levels that may
513	exist within and between reefs.
514	
515	Declarations
516	Ethics
517	This article does not present research with ethical considerations.
518	Data Accessibility
519	The dataset supporting this article can be found on GitHub at: Source code available at
520	https://github.com/alicelawrence2021/dispersion.git . If and when the paper is accepted, the dataset
521	will be uploaded onto the Dryad Digital Repository and be referenced with an official DOI in the
522	reference section.
523	Declaration of AI use
524	We have not used AI-assisted technologies in creating this article.
525	Authors' Contributions
526	A.K.L.: Project conception and design, planning and acquisition of data, formal analysis, writing-
527	original draft, writing-review and editing; G.J.W.: Project conception and design, formal analysis,
528	writing-review and editing; A.H.: Project conception and design, formal analysis, writing-review and
529	editing. The primary author agrees to be accountable for all aspects of the work in ensuring that
530	questions related to the accuracy or integrity of any part of the work are appropriately investigated
531	and resolved.
532	Competing Interests
533	We have no competing interests.
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