

Reef fish functional composition and metrics reveal spatial differences in three protected islands in the Eastern Pacific

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ABSTRACT: Reef fish assemblages in the Eastern Pacific (EP) represent an interesting system to understand how areas with lower diversity respond to multiple factors and their effect on ecosystem functions and services. Among the multiple approaches that have emerged, the evaluation of functional metrics provides an initial comprehension of these relationships. In this context, to better understand reef fish variability in the EP, we evaluated spatial differences in ecological metrics, the composition of fish assemblages, and their relationship with habitat structure in coral communities at 3 islands in Mexico (Marietas, Isabel, and Cleofas). To include a functional approach, we created a functional entity (FE) matrix using species abundance and 6 categorical functional traits; specifically, we calculated ecological metrics that reflect the representation or under-representation of species in the functions or FEs (redundancy and vulnerability) and the rarity in FEs and species and their relationship with habitat structure. Overall, most of the fish FEs in the EP were represented by 1 species (i.e. high vulnerability and low functional redundancy). Despite the low redundancy recorded in the islands, reef fish performed multiple key functions; however, many functions remained rare. Furthermore, both metrics and fish composition showed high variability among sites and islands, but this variability was only partially explained by a few variables of habitat structure (i.e. rugosity). These results, in combination with the unique characteristics of coral communities in the EP, highlight the need to identify the drivers of fish assemblages and their effect on the ecosystem processes and services in order to implement unique management strategies for each island.

KEY WORDS: Functional ecology · Traits · Habitat structure · Coral reefs

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1. INTRODUCTION

Coral reefs, like many other ecosystems, have undergone extensive degradation and species loss in recent decades (Connell 1997, Wilkinson 2008). Exposure to several environmental factors, both nat-

ural (e.g. hurricanes, El Niño-Southern Oscillation [ENSO] events, storms) and anthropogenic (e.g. illegal/overfishing, tourism, urban development) affect coral reefs and their associated organisms (Bellwood et al. 2006). Reef fish assemblages, which we consider here as organisms within the community that

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are phylogenetically associated (Fauth et al. 1996), are among the most studied assemblages in marine and freshwater ecosystems (Hoegh-Guldberg et al. 2007). Due to their responses to environmental factors, wide distribution, and high diversity, this group is a good indicator to evaluate and monitor changes in ecosystems (Whitfield & Elliott 2002). In addition to being represented by >6000 species, fish present a broad array of biological characteristics and perform multiple functions in ecosystems (Nelson 2016).

High diversity of organisms is often related to the ability of an ecosystem to regulate processes (Balvanera et al. 2006), defined as 'changes in the stocks or flows of materials in an ecosystem, resulting from interactions among organisms and their physical-chemical environment'. These changes can subsequently provide multiple ecosystem services determined as 'an activity or function of an ecosystem that provides benefit (or occasionally disbenefit) to humans' (Mace et al. 2012, p. 19). The relation between biodiversity and ecosystem services requires an understanding of the multiple components involved, including an analysis of the species' functions that contribute to the diversity; this approach refers to the functional ecology of organisms (Villéger et al. 2017).

Functional ecology has become useful to detect changes, and possible implications of changes, in ecosystem functions and processes (Petchey & Gaston 2006). This approach is based on the use of functional traits, which are characteristics of species (morphological, physiological, or behavioral) measured at the individual level that influence the organism's performance (Violle et al. 2007).

In reef fish, as well as in other organisms, the selection of traits represents a fundamental basis for the evaluation of functional ecology (Petchey et al. 2007). Multiple studies have focused on representing the main functions performed by fish: food acquisition, mobility, nutrient budgets, reproduction, and defense against predation (Holmlund & Hammer 1999, Villéger et al. 2017). These functional traits can also reflect the ecosystem processes (e.g. primary productivity and decomposition rates), and services (e.g. biological control, food provisioning, and recreational ecotourism) that individual species provide (Mouillot et al. 2011). These species traits can be used to calculate functional ecology metrics in assemblages through the creation of functional entity (FE) matrices, which constitute a unique combination of traits.

Multiple studies have focused on disentangling the capability of highly diverse ecosystems to withstand the loss of species that maintain the ecosystems' processes and services (Bellwood et al. 2003, Micheli &

Halpern 2005). Metrics such as functional redundancy (FR; multiple species performing each function) or functional vulnerability (FV; only 1 species per function) have highlighted that ecosystems with many species can also have low redundancy and high vulnerability (Mouillot et al. 2013a). Furthermore, the study of organism rarity can reveal that beyond the loss of species, the loss of even a few individuals may threaten essential functions (Mouillot et al. 2013b, Violle et al. 2017). Thus, in addition to reef fish diversity, a combination of functions, key functions, and species rarity or commonness allows us to understand the effect of multiple environmental factors, including current ecosystem threats (Rosenfeld 2002, Bellwood et al. 2004, Loiseau & Gaertner 2015).

Although many reef fish do not depend directly upon live coral, several studies have related the degradation of coral colonies to changes in the composition of fish species in coral reefs (Feary et al. 2007). Reef fish, even those that do not depend on live coral, can be influenced by spatial and temporal variability of multiple environmental factors such as topographic complexity, wave protection, temperature, ENSO events, and protection status (Izzo et al. 2016).

In the current scenario of ecosystem degradation, including the coral communities, and our undeniable dependence on the ecosystem services they provide, detecting and describing how functions of reef fish are performed in assemblages have become particularly valuable. Coral communities from the Eastern Pacific (EP) represent a valuable opportunity to characterize and understand the functional component in assemblages with lower diversity compared to other areas (e.g. Indo-Pacific or Caribbean) that are exposed to highly variable environmental conditions (Reyes-Bonilla 2003, Kulbicki et al. 2013). Therefore, our aim in this study was to evaluate the functional component of reef fish assemblages through multiple functional metrics, as well as species and FE composition, to identify their spatial differences in 3 natural protected areas in the EP and their relationship with habitat structure variables.

2. MATERIALS AND METHODS

2.1. Study area

This study evaluated the marine portion of 3 natural protected islands from Mexico located in the EP region: Islas Marietas National Park, Isla Isabel National Park, and Isla Cleofas within the Islas Marias Biosphere Reserve (Fig. 1). The area is characterized by

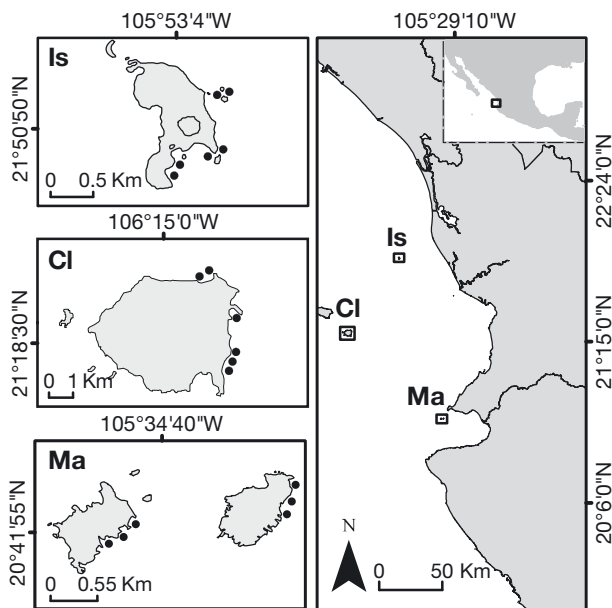


Fig. 1. Study areas across 3 protected islands in the Eastern Pacific (EP) that belong to Mexico: Isla Isabel (Is), Isla Cleofas (Cl), and Isla Marietas (Ma). Filled circles indicate the 6 surveyed sites per island

highly variable and complex ocean circulation (Kessler 2006). Seasonal variation is caused by the convergence of distinct currents and mixing of water masses, providing the area with transitional characteristics due to the influence of the northern California Current water in winter and spring, accompanied by upwelling events, and of tropical surface water in the summer and fall (Lavín et al. 2006). The 3 islands are exposed to a high water dynamism, marked hydroclimatic periodicity, and anthropogenic pressure (Reyes-Bonilla 2003). However, the islands differ in their local conditions, such as area, distance to the mainland coast, coral coverage, and principal sources of anthropogenic pressure (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m635p139_supp.pdf). At each island, we selected 6 sites with rocky reefs and hard coral patches, representing the heterogeneity of the coral communities at the islands (Fig. 1).

2.2. Data collection

The data were obtained through diurnal visual censuses using 25 m belt transects parallel to the coast at depths between 3 and 13 m. Data were collected in the warm season of 2015 (Marietas and Isabel in July; Cleofas in September). During each visit, we recorded reef fish species abundance with a visual census in the belt transect in a 100 m² area (25 × 4 m). To repre-

sent the variables that could define habitat structure in coral communities in the EP, we recorded the percentage cover of the main benthic components and rugosity. The percentage of benthic components was recorded placing 5 quadrants (1 m²) at each 5 m of the 25 m belt transect to estimate the percentage of branching coral, submassive coral, turf, macroalgae, rock, and sand. Rugosity was measured using the chain method, placing a 10 m chain in the transect following the vertical contour of the benthic floor and registering the length of the chain in the transect. We then calculated the rugosity index $C = 1 - d/l$, where d is the distance of the chain in the transect, and l is the total length of the extended chain (Risk 1972). The survey design considered 3 spatial scales: islands (64–194 ha, $n = 3$), sampling sites (500–2500 m², 6 per island), and transects (100 m², 5 per site), with a total sampling effort covering 90 transects.

We used 2 approaches to explore spatial differences in the functional component of fish species and their relationship with habitat structure: (1) changes in functional metrics, and (2) changes in species and FE composition; for both metrics and composition, we also analyzed the linear relationship with habitat structure. Each approach requires an FE matrix, built based on the species abundance matrix and the functional traits matrix, placing each species, according to its traits, into FEs. The reef fish functional traits used in our study reflect the main functions performed by fish (except for reproduction) and have been previously used in the evaluation of reef fish functional ecology (Richardson et al. 2017, Villéger et al. 2017). We included 6 traits: length, diet, aggregation, position in the water column, mobility, and activity period. All traits were divided into categories. The trait information for each species varies, and therefore the selection of the category is based on the best choice from multiple sources; articles that individually evaluate the trait are preferred (i.e. nocturnal and diurnal census to classify reef fish), but not all of the species information is available. Detailed information and a description of the traits and species within FEs are shown in Tables S2 & S3. Valid species names were used according to Fricke et al. (2018), and family arrangements were made in the manner suggested by Nelson et al. (2016).

2.3. Functional ecology metrics

We calculated 6 functional metrics based on the number of species and FEs; the first 2 metrics focus on the representation of fish species within FEs: func-

tional redundancy (FR) refers to several species that can support the same function (i.e. having a unique combination of traits); this metric is calculated as the mean number of species per FE. Functional vulnerability (FV) is inversely related to FR and expresses those functions that are only represented by 1 species; FV is calculated as the percentage of FEs with only 1 species (Mouillot et al. 2014). To evaluate the rarity of reef fish functional facet, we calculated 4 metrics. We defined as 'rare' those FEs or species within FEs that had <1% of the relative abundance from the species or FEs with the highest abundance at each evaluated level (transect, site, or island), and as 'rarest' those FEs or species within FEs that had only 1 individual. The 2 FE rarity metrics evaluate the percentage of rare (% rare FEs) and rarest (% rarest FEs) (Mouillot et al. 2013b). We also included 2 additional novel metrics to represent species rarity within the FEs. These metrics measure the percentage of FEs that are represented by $\geq 50\%$ of rare (% rare species in FEs) or rarest species (% rarest species in FEs). All metrics were calculated at the transect level for statistical analysis and at the island level for the graphical representation of all reef fish species recorded at the islands. Functional and rarity metrics were performed in R (R Core Team 2018). FR and FV metrics were calculated following the script provided at <http://villeger.sebastien.free.fr/Rscripts.html>.

Multiple 2-way nested ANOVAs based on permutations were performed to assess the spatial variation of species, FEs, functional, and rarity metrics. We used a mixed model with 2 factors [$Y_{ijk} = \mu + Island_i + Sites_j(Island_i) + e_{ijk}$], where Y_{ijk} is the observation of k replicates for $Island_i$ and $Sites_j(Island_i)$; μ is the general mean; $Island_i$ is the island effect (3 levels: Marietas, Isabel and Cleofas; fixed effect); $Sites_j(Island_i)$ is the site effect nested in the island (6 sites per island; random effect); and e_{ijk} is the associated error. All permutational ANOVA designs were performed with Euclidean distance matrices following the criteria of Anderson et al. (2008). The main test and a *posteriori* comparison at the island level were assessed using 9999 permutations of residuals under a reduced model with type III sum of squares. To explore the relationship between metrics and habitat structure variables, we performed multiple regression analyses with a previous best procedure to select the model with the best significant explanatory variables ($p < 0.05$) from all possible combinations. We carried out simple linear regressions for models with 1 variable and multiple linear regressions for those with more variables. The adjusted R^2 is reported for models with 2 or more variables, and the significance of the model

was evaluated with an F -test. In each regression, we tested constant variance and normality; we avoided severe multi-collinearity, verifying that the models had a variance inflation factor (VIF) < 3 and variables were $< 90\%$ correlated.

2.4. Species and FE composition

Permutational multivariate analyses of variance (PERMANOVAs), using the same ANOVA design, were performed to evaluate the spatial variation of species and FE composition. First, data were fourth-root transformed, and then a Bray-Curtis similarity matrix was built. PERMDISP analyses were used to verify the homogeneity of dispersion among islands and sites; differences were visualized with non-metric multidimensional scaling (nMDS). Similarity percentage analyses (SIMPER) were used to estimate the species and FE contributions to the average dissimilarity among islands and sites within each island. SIMPER and nMDS were performed based on the PERMANOVA-described data transformation, resemblance matrix, and design. For a total graphical representation of fish functional components at the island level, we plotted the total species and FE abundance. To explore the relationship between species and FE composition and habitat structure variables, we performed redundancy analysis (RDA) with Hellinger transformation. Variables in models were selected with stepwise (both forward and backward) procedures to select the significant variables ($p < 0.05$). The multi-collinearity was verified with the same procedure of the regressions of the metrics. Statistical significance of the model and axes were tested with 9999 permutations, and we report the adjusted R^2 for models with 2 or more variables. Analyses and graphics were carried out using R (R Core Team 2018), PRIMER v.6 and PERMANOVA+ (Anderson et al. 2008), and SigmaPlot software v. 11.0.

3. RESULTS

3.1. Traits and FE characteristics

Reef fish FEs from the islands presented a higher percentage of some categories within each trait, including diurnal behavior (61%), distribution above the bottom (63%), solitary (59%), either within reef (39%) or sedentary (37%), sizes of 7–15 cm (33%) and 15–30 cm (35%), and with invertivorous (30%) and

piscivorous (28%) diet. Although the species registered in the surveys represented all of the categories (i.e. all of the categories in diet), within traits, we rarely registered fish FEs with diurnal-nocturnal behavior, pelagic distribution, and larger size (see Table S3).

3.2. Functional ecology metrics

A total of 20 943 fish were recorded at the 3 islands in the EP, with the lowest abundance of 5581 at Cleofas, followed by 7642 at Marietas and 7720 at Isabel. We surveyed a total of 80 species (Cleofas: 59, Isabel: 63, Marietas: 58), with 39 species shared among islands and 19 not shared between islands, being exclusively present in only 1 of the islands. These fish species were distributed in a total of 52 FEs for the 3 islands (Cleofas: 41, Isabel: 44, Marietas: 45), with 42 shared and 18 exclusively found at only 1 island (Fig. 2; Table S3). An overview of the functional metrics in the EP islands showed that most of the FEs

were represented by only 1 species (34 FEs); thus, reef fish species had many FEs represented by only 1 species (65%), and only 18 FEs with more than 1 species (Table S3).

From an island perspective, Isabel had the highest total FR (11 FEs with more than 1 species), followed by Cleofas (10) and Marietas (7). The survey of reef fish abundance revealed that the 2 most abundant fish FEs had only 1 species: FE14, with 4525 individuals of *Chromis atrilobata* Gill 1862, and FE15, with 4320 individuals of *Thalassoma lucasanum* (Gill 1862). Moreover, low abundance fish species were also present at the islands, with 4 FEs having only 1 individual per species: FE48 *Caranx melampygus* Cuvier 1833, FE31 *Alphestes immaculatus* Breder 1936, FE33 *Rypticus bicolor* Valenciennes 1846, and FE30 *Sphoeroides lobatus* (Steindachner 1870) (Table S3). Overall, most of the FEs (57% of the total) had fewer than 100 individuals (Fig. 2; Table S3).

The evaluation of spatial differences in the number of reef fish species showed similar values between

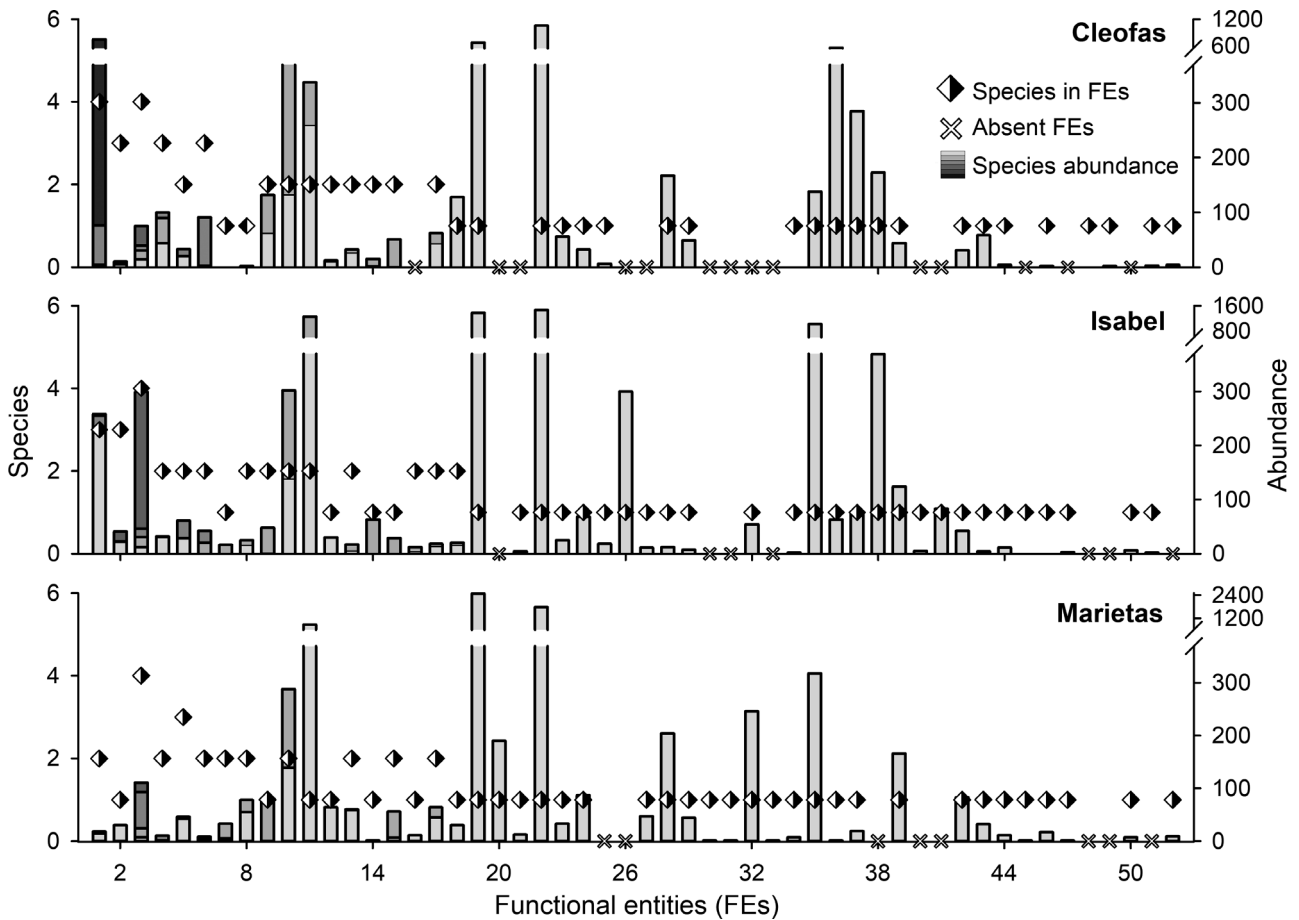


Fig. 2. Functional entities (FEs) for the 3 islands in Eastern Pacific: Cleofas, Isabel, and Marietas. FEs include the number of species and individuals. Shading in bars represents the number of individuals of each species. 'x' shows the absence of the FE on the island. n = 30 transects per island

the islands and no significant differences. However, we found significant differences between sites at each island (Table 1, Fig. 3a). The number of fish FEs evaluated were also similar both in the islands as well as at the sites at each island (Table 1, Fig. 3b). The fish functional metrics (FR and FV) between the islands indicated that in addition to a generalized low FR, there were significant differences in fish FR within the sites of each island (Table 1, Fig. 3c). Moreover, FV was markedly high for all islands but with no significant differences between islands, in contrast to the significant differences at the site level (Table 1, Fig. 3d). Assessment of reef fish functional rarity indicated overall high values for rarity metrics of FEs (Table 1, Fig. 3e,f) and species within FEs (Table 1, Fig. 3g,h). However, all rarity metrics were statistically similar between islands and sites at each island, except for the metric of rare species in FEs, where Cleofas and Marietas were responsible for the differences (Table 1). Regressions showed that among the habitat structure variables (branching and submassive coral, turf, macroalgae, sand, rock, and rugosity), only a few predicted the ecological

metrics (FR, FV, rare FEs, and species in FEs), and the rarest FEs and species in FEs could not be predicted by any habitat structure variable (Table 2). The number of species and FEs were significantly predicted by the percentage of sand cover at the sites. Rugosity was the variable present in more predictive models of the metrics, in combination with turf for FR, branching coral in FV, macroalgae and sand in rare FEs, and rare species in FE, respectively (Table 2).

3.3. Species and FE composition

The abundance and presence of reef fish species varied significantly between islands (pseudo- $F = 5.581$, $p = 0.001$) and sites (pseudo- $F = 3.479$, $p = 0.0001$) as did the FEs between islands (pseudo- $F = 4.543$, $p = 0.0001$) and sites within each island (pseudo- $F = 3.421$, $p = 0.0001$). Subsequent pairwise comparisons at the island level showed that reef fish composition between Cleofas and Isabel had the highest dissimilarity (65%) at the island level

Table 1. Two-way nested ANOVA based on 9999 permutations of residuals under a reduced model. Number of species, functional entities (FEs), and functional and rarity metrics of reef fish species between Eastern Pacific islands (Cleofas, Isabel, and Marietas) and sites within the islands. Values in **bold** are significant ($p < 0.05$)

Metric	Source	df	SS	MS	Pseudo- F	p(perm)
Species	Island	2	0.150	0.075	2.134	0.1473
	Sites (Island)	15	0.527	0.035	3.048	0.001
	Residual	72	0.830	0.011		
FEs	Island	2	0.182	0.091	3.522	0.053
	Sites (Island)	15	0.389	0.026	2.441	0.007
	Residual	72	0.765	0.010		
Functional redundancy	Island	2	0.002	0.083	1.222	0.328
	Sites (Island)	15	0.001	0.001	2.057	0.025
	Residual	72	0.024	0.0003		
Functional vulnerability	Island	2	0.003	0.002	1.637	0.230
	Sites (Island)	15	0.015	0.001	2.535	0.004
	Residual	72	0.028	0.0004		
Rare FEs	Island	2	0.092	0.046	1.785	0.202
	Sites (Island)	15	0.386	0.026	2.256	0.010
	Residual	72	0.821	0.011		
Rarest FEs	Island	2	0.757	0.378	3.096	0.073
	Sites (Island)	15	1.834	0.1223	0.706	0.791
	Residual	72	12.467	0.173		
Rare species in FEs	Island	2	0.032	0.0160	0.539	0.588
	Sites (Island)	15	0.445	0.030	2.056	0.019
	Residual	72	1.041	0.014		
Rarest species in FEs	Island	2	0.342	0.171	4.627	0.031
	Sites (Island)	15	0.554	0.037	0.567	0.886
	Residual	70	4.691	0.065		

(Table 3). The PERMDISP test indicated significant differences in the dispersion at the island level of species ($p = 0.009$), but dispersion in FEs was not significant ($p = 0.286$). Within the sites, species dispersion was significant for Cleofas ($p = 0.0002$), Isabel ($p = 0.0001$), and Marietas ($p = 0.0002$); FE dispersion was also significant for Cleofas ($p = 0.012$), Isabel (0.013), and Marietas ($p = 0.012$). The use of PERMANOVA and PERMDISP analyses, in combination with data visualization with the nMDS plot, allowed us to detect dispersion and location effects between islands and among sites on each island (Fig. S1). The SIMPER procedure showed a great dissimilarity between islands, with >50% of average dissimilarity between the islands, and with many species and FEs that contributed to the cumulative dissimilarity (Table 3). These differences in species, mainly between islands, highlight that Cleofas and Isabel had a greater abundance of piscivorous FEs, including one of the most redundant FEs (FE1: 15–30 cm, small group, piscivorous, between

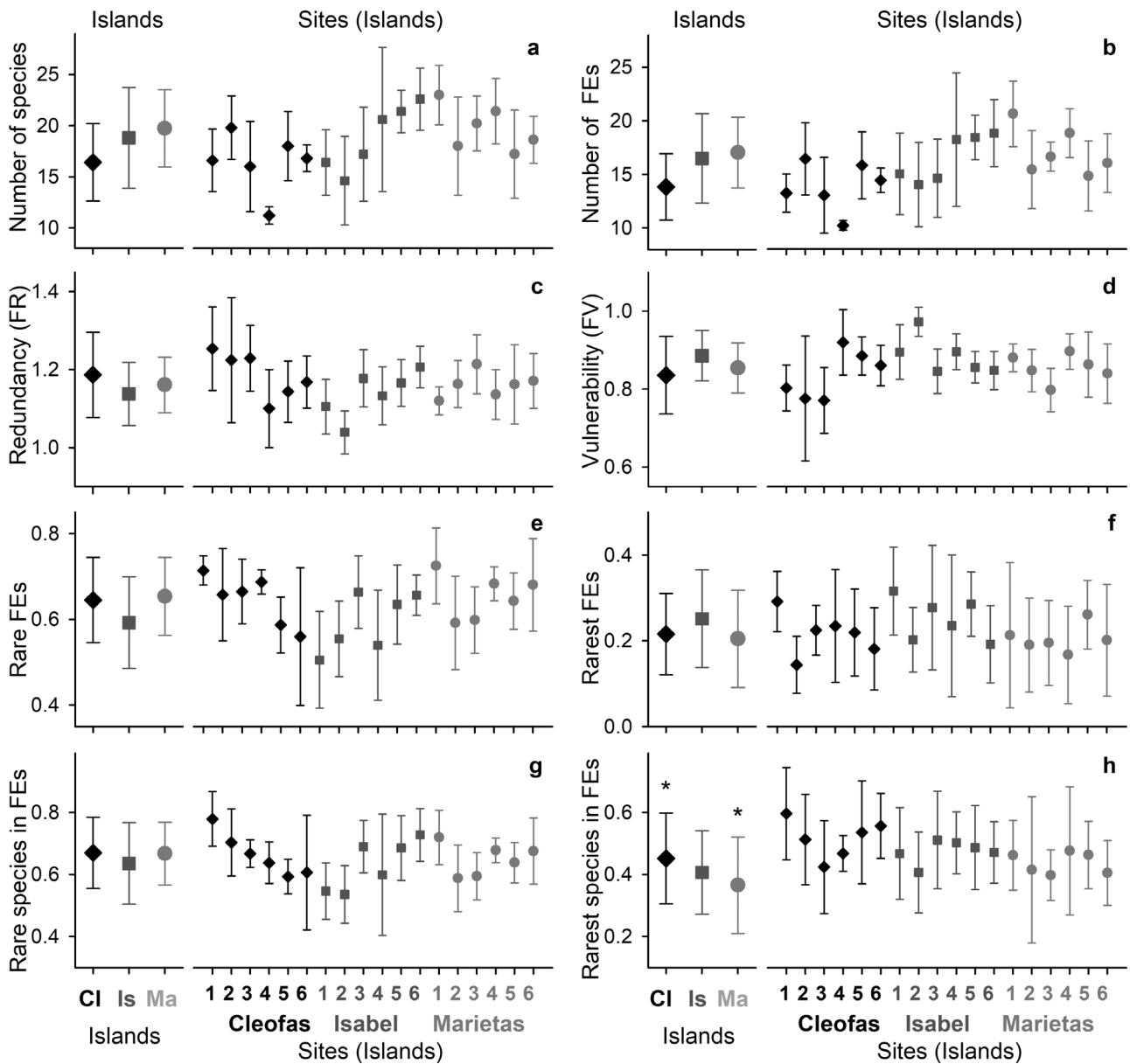


Fig. 3. Reef fish metrics at the 3 islands (means \pm 1 SE): Cleofas (diamond), Isabel (square), and Marietas (circle). Differences in (a) number of species, (b) number of functional entities (FEs), (c) functional redundancy (FR), (d) functional vulnerability (FV), (e) rare FEs, (f) rarest FEs, (g) rare species in FEs, (h) rarest species in FEs. Asterisks at the island level of the rarest species in FEs indicate significant differences in an *a posteriori* comparison ($p = 0.016$)

reef, above the bottom, and nocturnal, with 5 species), that was very abundant in Cleofas and Isabel. The 2 most abundant reef fish FEs present in the islands (FE19, *C. atrilobata*; FE22, *T. lucasanum*), had twice the abundance in Marietas compared to the other 2 islands. Within the FEs with greater contribution to the overall dissimilarity, we found the 2 distinctive species (*T. lucasanum*, *C. atrilobata*) and FEs (FE12, FE53) with the highest abundances (Table 2). SIMPER among sites of each island

showed that there is an average dissimilarity of species and FEs between islands higher than 40%, with abundant species contributing to the dissimilarity, like the species and FEs at the site level (Table S4). The predictive models from the RDA results suggest that species composition was influenced by the percentage of macroalgae and rock, although despite being significant, the regression values remained low; moreover, FE composition was only significantly predicted by macroalgae cover (Table 2).

Table 2. Results of linear regression models for fish ecological metrics, species, and functional entity (FE) composition with variables of habitat structure in 3 islands in the Eastern Pacific. Only the models of the significant variables selected with the best subset procedure are shown. For models with ≥ 2 variables, adjusted R^2 values are reported; Values in **bold** are significant ($p < 0.05$); NA: not applicable

Factor	Model	R^2	F	p
Metrics				
Num. of species	Sand	0.323	7.646	0.014
Num. of FEs	Sand	0.353	8.727	0.009
Functional redundancy	Turf+Rugosity	0.389	6.407	0.010
Functional vulnerability	Branching+Rugosity	0.351	5.590	0.015
Rare FE	Macroalgae+Rugosity	0.225	3.474	0.058
Rarest FE	No significant model	NA	NA	NA
Rare species in FE	Sand+Macroalgae+Rugosity	0.560	8.198	0.002
Rarest species in FE	No significant model	NA	NA	NA
Composition				
Species	Macroalgae+Rock	0.106	1.996	0.006
FEs	Macroalgae	0.462	1.926	0.043

4. DISCUSSION

A few studies have addressed the functional component in the evaluation of fish communities from the EP (Alvarez-Filip & Reyes Bonilla 2006, Aguilar-Medrano & Calderon-Aguilera 2016, Ramírez-Ortiz et al. 2017). However, these analyses are often conducted with multiple methods and sometimes lack homogenization; therefore, the results of such studies often reveal multiple outcomes in a single area. For example, in the Eastern Tropical Pacific, Aguilar-Medrano & Calderon-Aguilera (2016) evaluated trophic and functional groups using morphometric measures and trophic guilds as functional traits, and their results showed a high FR, with only 19 functional groups among fish. In contrast, our results for the islands in the same area demonstrate a higher number of FEs (52) and thus a correspondingly lower FR. A low FR is also a characteristic common to other marine assemblages besides reef fish, even in highly diverse ecosystems (Micheli & Halpern 2005). These striking differences in FR could be due to the selection of functional traits; therefore, the results found in each study would be highly dependent on the selection of traits, the function that they represent, the number of selected traits, and even the number of categories within each one (Villéger et al. 2017). It is essential to consider the limitations in comparing functional metrics with other studies in order to maintain the homogeneity in their evaluation. Hence, the selection of traits, and the creation of large trait data-

bases remain a core step in the evaluation of functional ecology (Petchey et al. 2007, Violle et al. 2007).

The aim of measuring traits in reef fish, including the semi-qualitative measurements used in this study, is to reflect the main functions performed by fish; however, using multiple morphological traits can be redundant, and to some extent, the traits may refer to only 1 function (e.g. food acquisition) (Villéger et al. 2017). Nonetheless, despite the selection of different traits or methods, high vulnerability has been reported in multiple studies, including ours, indicating a functional vulnerability in reef fish worldwide (Mouillot et al. 2014).

Mora et al. (2011) evaluated the vulnerability of reef ecosystems based on multiple ecological descriptors, including functional richness, and the effect of human influence on this vulnerability. They found that areas with greater diversity are also the most vulnerable mainly due to human impact. Although the Eastern Pacific has less uninhabited reef areas, future predictions of population growth (especially in coastal areas) reveal that fish communities, even in these currently minimally impacted sites, will be threatened in the future; thus, in combination with the distance from the coast, illegal fishing or tourism pressure, such as observed especially in Marietas, could also influence functional and ecosystem vulnerability.

Further, many ecosystems have relatively few abundant species, while most species are present in low abundance (Magurran 2004). The rarity of reef fish has previously been observed both locally and regionally, with many rare species supporting essential yet unusual functions that represent central components of coral reef ecosystems (Mouillot et al. 2013b). Therefore, rarity metrics, including those used in this study (e.g. the rarity of species within a given FE) reveals another facet of vulnerability, and further analysis should focus on the implications regarding this commonness or rarity within ecosystems (Violle et al. 2017).

In addition to evaluating metrics, we observed spatial changes in the species and FE composition of reef fish among the islands in the EP. Ramírez-Ortiz et al. (2017) evaluated at a larger scale where the Mexican Province showed higher functional diversity, suggesting that these differences in functional diversity

Table 3. Summary of similarity percentage analysis with 9999 permutations of residuals under a reduced model. Species and functional entities (FEs) average abundance percentage contribution (av. cont.) and cumulative contribution (cum. cont.) to the dissimilarity (diss.) between islands: Cleofas (Cl), Isabel (Is), and Marietas (Ma). Full species names and details of FEs are given in Table S3 in the Supplement

Species	Average abundance		Av. Cont.	Cum. Cont.	FEs	Average abundance		Av. Cont.	Cum. Cont.
Av. Diss 63.37	Cl	Is			Av. Diss 55.94	Cl	Is		
<i>C. atrilobata</i>	22.67	45.83	4.34	4.34	FE19	22.67	45.83	5.78	5.78
<i>L. viridis</i>	22.37	0.00	4.30	8.64	FE35	4.60	33.87	5.63	11.42
<i>P. punctatus</i>	4.60	33.87	4.24	12.88	FE28	2.60	26.43	5.21	16.62
<i>A. troschelii</i>	2.60	26.43	3.94	16.82	FE1	29.07	9.13	4.82	21.45
<i>T. lucasanum</i>	35.23	48.87	3.42	20.24	FE22	35.23	48.87	4.57	26.01
<i>S. flavilatus</i>	5.57	0.40	3.37	23.61	FE10	13.17	10.07	4.18	30.20
<i>S. acapulcoensis</i>	8.67	15.50	3.32	26.93	FE37	5.77	12.30	4.01	34.20
<i>H. dispilus</i>	8.73	5.43	3.10	30.03	FE39	14.23	15.90	3.73	37.93
<i>A. xanthopterus</i>	5.77	12.30	3.01	33.04					
<i>L. argentiventris</i>	0.03	7.83	2.84	35.88					
<i>M. dorsalis</i>	1.47	4.13	2.80	38.68					
Av. Diss 63.37	Cl	Ma			Av. Diss 55.94	Cl	Ma		
<i>C. atrilobata</i>	22.67	82.33	5.29	5.29	FE19	22.67	82.33	6.74	6.74
<i>L. viridis</i>	22.37	0.00	4.31	9.60	FE1	29.07	1.47	5.37	12.11
<i>S. acapulcoensis</i>	8.67	28.90	3.90	13.50	FE32	0.00	8.20	4.95	17.05
<i>O. steindachneri</i>	0.00	8.20	3.87	17.37	FE39	1.47	5.53	4.10	21.15
<i>M. dorsalis</i>	1.47	5.53	3.22	20.59	FE37	5.77	0.00	4.07	25.23
<i>A. xanthopterus</i>	5.77	0.00	3.20	23.79	FE10	4.40	2.67	3.77	29.00
<i>H. dispilus</i>	8.73	4.97	3.05	26.84	FE22	35.23	59.30	3.76	32.76
<i>T. lucasanum</i>	35.23	59.30	2.96	29.80	FE35	4.60	10.60	3.75	36.51
<i>P. punctatus</i>	4.60	10.60	2.94	32.74	FE6	3.03	0.27	3.39	39.90
<i>H. chierchiaie</i>	4.43	4.63	2.73	35.47					
<i>S. rubroviolaceus</i>	2.93	0.17	2.67	38.14					
Av. Diss 63.37	Is	Ma			Av. Diss 55.94	Is	Ma		
<i>C. atrilobata</i>	45.83	82.33	5.42	5.42	FE19	45.83	82.33	6.91	6.91
<i>S. flavilatus</i>	0.40	6.80	4.51	9.93	FE28	26.43	0.00	5.29	12.20
<i>A. troschelii</i>	26.43	0.00	4.20	14.13	FE35	33.87	10.60	4.97	17.17
<i>P. punctatus</i>	33.87	10.60	3.91	18.04	FE37	12.30	0.00	4.52	21.69
<i>S. verres</i>	8.43	0.60	3.78	21.81	FE32	1.80	8.20	4.23	25.92
<i>A. xanthopterus</i>	12.30	0.00	3.57	25.38	FE11	15.90	35.70	3.85	29.77
<i>O. steindachneri</i>	1.80	8.20	3.31	28.69	FE1	9.13	1.47	3.78	33.55
<i>S. acapulcoensis</i>	15.50	28.90	3.12	31.81	FE22	48.87	59.30	3.68	37.24
<i>H. dispilus</i>	5.43	4.97	2.94	34.75					
<i>T. lucasanum</i>	48.87	59.30	2.89	37.64					

could be the result of local perturbations of specific groups (e.g. piscivorous fish) that have modified the assemblage structure through their effects on other organisms in the trophic web. At a smaller spatial scale in the EP (e.g. localities or islands), changes in species composition were observed between islands (including Isabel and Marietas) and even among the sites within each island (Galván-Villa 2015). These results are consistent with the considerable variability in metrics and composition of reef fish despite the closeness between the islands and sites.

Multiple factors could be responsible for these differences, including large-scale oceanographic conditions shared between the islands and local character-

istics that could have a strong influence on these differences (Friedlander et al. 2003, Izzo et al. 2016, Richardson et al. 2017). At a much smaller scale, differences among the sites at each island could reflect the heterogeneity of the island due to environmental factors (e.g. depth, benthic components, vertical complexity) representing the island's heterogeneity. Many studies relate these composition changes to multiple factors, especially those related to habitat protection (Friedlander et al. 2003, Fulton & Bellwood 2004); however, few studies have addressed the relation of each factor with reef fish functional metrics and composition. Identifying the specific effects of factors on the functional component is cur-

rently one of the main challenges in the study of functional ecology (Villéger et al. 2017).

Although reef fish can also be influenced by spatial and temporal variability of multiple environmental factors, the response is dependent on the degree of association with these variables (Feary et al. 2007). For example, fish with a corallivorous diet would be most vulnerable to changes in coral cover because they feed directly on the coral (Cole et al. 2008). In reef fish from EP islands, structural complexity was among the best predictor of ecological metrics (Reyes-Bonilla 2003). Richardson et al. (2017) also observed the relationship with functional metrics, structural complexity, and other benthic elements for reef fish in the Great Barrier Reef. However, as in this study, not all benthic variables explained the ecological metrics, and only part of the variability was explained by the variables (<40%). Structural complexity in coral reefs is commonly related to the presence of organisms such as branching coral colonies or sponges that provide tridimensional structures (Alvarez-Filip et al. 2011); nonetheless, other structural elements such as geological features and rocky substrates could also provide these structures (Kleypas et al. 2001), especially in areas with low coral cover like the EP (Hernández-Zulueta et al. 2017). Therefore, the unique habitat characteristics of the coral communities in the islands of the EP, and the differences in the degree of association with benthic components could also explain the weak relationship with structural complexity variables. In addition to habitat structure variables, fish communities in the EP could be also be correlated to multiple other factors that need further evaluation (i.e. anthropogenic pressure) and to ecological theories, including the theory of island biogeography (Jacquet et al. 2017).

Beyond detecting spatial changes, the functional ecology of reef fish, and explicitly their traits, can also give us a deeper understanding of fish functions and their implications for an ecosystem (Richardson et al. 2017). Reef fish from the EP, despite not being as taxonomically diverse compared to other sites (Kulbicki et al. 2013, Mouillot et al. 2013a), displayed all the categories of the evaluated traits. Mobility is one of the most commonly evaluated traits, since it determines the distribution of species and is involved in multiple ecosystem processes. The most common mobility category found among reef fish in the EP islands was sedentary, or with narrow movement; this characteristic could contribute to internal nutrient cycling and maintenance of biodiversity through interactions (Sale 1991). Otherwise, greater mobility

could contribute to increased nutrient export (Lundberg & Moberg 2003).

Fish diet is an essential trait in the evaluation of functional ecology since it can identify the presence of fish that perform key processes in coral reef ecosystems, such as food web controllers, including macro-algae and piscivorous feeders (Plass-Johnson et al. 2015). In reef fish, one of the most studied processes is the control of food webs, particularly herbivory, i.e. the feeding activity upon algae by key species that regulate their overgrowth that competes for space with live coral (Cheal et al. 2010). Comparing the traits found between the islands, Cleofas had many FEs with key traits (e.g. macro-algae diet, medium size). Other studies have considered these key traits as useful after acute disturbance events, where coral reef sites with a strong representation of FEs with key traits, in combination with other resistance factors, could withstand disturbance (Grimsditch & Salm 2006).

The most distant islands, Isabel and Cleofas, were characterized by piscivorous fish, and the high biomass of piscivorous fish and high vulnerability may reflect the pristine state of sites; however, further and exhaustive analyses of piscivorous fish need to be considered to reveal current states of and threats to fish assemblages (Quimbayo et al. 2017). Conversely, Marietas, the island closest to the coast, had marked differences in FE composition, with low abundance and redundancy of herbivorous and piscivorous reef fish and high abundances of *Thalassoma lucasanum* and *Chromis atrilobata*. Contrary to the relation of fish assemblages with structural complexity and live coral cover (Friedlander et al. 2003), previous studies have related the presence of *T. lucasanum* to the availability of food supply in areas with benthic algae and small crustaceans (Giraldo et al. 2001). Interestingly, *C. atrilobata*, an active plankton feeder (including eggs of *T. lucasanum*), has been observed with increased food supply (Hobson 1965). Seasonal upwelling events that occur in the area could enhance nutrient and food availability (López-Sandoval et al. 2009). Further temporal variation of fish assemblages would also be useful to detect temporal variability, both at seasonal (e.g. hydroclimatic periods) and interannual scales (e.g. ENSO events), especially for areas like the EP with large variability of oceanographic factors. In addition to variability, it is also fundamental to combine multiple methods that allow researchers to include as many species as possible that contribute to the ecosystem functions, especially those

overlooked or underestimated, such as nocturnal or cryptic fish (Spence 2017, Brandl et al. 2018).

Overall, the present study shows that despite the low ecological redundancy present in the 3 islands, we also found many functions, suggesting that reef fish in the EP could perform crucial multiple ecosystem processes (e.g. food web control, participation in nutrient cycling), even with a lower diversity compared to the Indo-Pacific or Caribbean (Mouillot et al. 2014). However, like other ecosystems, many of the functions remain vulnerable and rare (Violle et al. 2017). Complementary to these results, the islands had specific functional fish FEs and a marked dissimilarity among fish species and FE composition, with the most considerable differences found between Cleofas and Marietas.

These unique characteristics define each island and highlight the importance of specific protection for the 3 islands and the sites within each one, especially those experiencing constant anthropogenic pressure. Of the 3 islands, Marietas has characteristics such as significant anthropogenic impacts (tourism, illegal fishing, and closeness to coast) combined with high vulnerability, rarity, and absence of crucial functions, that could compromise the maintenance of the ecosystem. On the other hand, Isabel and Cleofas provide a better understanding of how the maintenance and management of these areas and their functions (including critical functions in coral reefs) could be translated into ecosystem processes and services. In addition to fish assemblage variability, the weak relationship with few variables emphasizes the need to identify the drivers of coral ecosystems (Hughes et al. 2017), especially in coral communities with high variability and unique conditions such as EP islands. Our results support the usefulness of including multiple approaches in the evaluation of communities (e.g. functions, key functions, rarity or commonness, as well as other components of assemblage structure), especially given the multiple threats that these ecosystems have faced in recent decades (Rosenfeld 2002).

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