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# Patterns of reef fish taxonomic and functional diversity in the Eastern Tropical Pacific

**Alexia Dubuc[1,2*], Juan Pablo Quimbayo[3,4*], Juan José Alvarado[5], Tatiana Araya-Arce[5], Andrea Arriaga[5], Arturo Ayala-Bocos[6], Jose Julio Casas-Maldonado[7,8,9], Luis Chasqui[10], Jorge Cortés[5], Amilcar Cupul-Magaña[11], Damien Olivier[12], Manuel Olán-González[12,13], Alberto González-Leiva[14], Andrés López-Pérez[15], Héctor Reyes-Bonilla[12], Franz Smith[16], Fernando Rivera[17], Fabián A. Rodríguez-Zaragoza[18], Jenny Carolina Rodríguez-Villalobos[6,19], Johanna Segovia[20], Fernando A. Zapata[21] and Sonia Bejarano[1]**

[1]Reef Systems Research Group, Leibniz Centre for Tropical Marine Research, Bremen, Germany
[2]Institut Français de Recherche pour l'Exploitation de la MER (IFREMER), LEAD NC, New Caledonia
[3]Centro de Biologia Marinha da Universidade de São Paulo, São Sebastião, SP, Brazil
[4]Department of Evolution, Ecology and Organismal Biology, The Ohio State University, Columbus, OH, USA
[5]Centro de Investigación en Ciencias del Mar y Limnología, Universidad de Costa Rica, San Pedro, San José, Costa Rica
[6]Ecosistemas y Conservación, Proazul Terrestre A.C., La Paz, México
[7]Ministerio de Ambiente de Panamá, Panamá
[8]Universidad Marítima Internacional de Panamá, Panamá
[9]Estación Científica Coiba AIP, Cuidad de Panamá, Avenida Omar Torrijos Herrera Cuidad del Saber, Panama
[10]Instituto de Investigaciones Marinas y Costeras INVEMAR. Santa Marta, Colombia
[11]Centro Universitario de la Costa, Universidad de Guadalajara, Puerto Vallarta, Jalisco, México
[12]Departamento Académico de Ciencias Marinas y Costeras, Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, México
[13]Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Coyoacán, México
[14]Instituto para el Crecimiento Sostenible de la Empresa, San Salvador, El Salvador
[15]Laboratorio de Ecosistemas Costeros/Laboratorio de Arrecifes y Biodiversidad (ARBIOLAB), Universidad Autónoma Metropolitana, Ciudad de México, México
[16]Independent researcher, Puerto Ayora, Galápagos Islands, Ecuador
[17]Instituto NAZCA de Investigaciones Marinas, Quito, Ecuador
[18]Departamento de Ecología Aplicada, CUCBA, Universidad de Guadalajara, Guadalajara, México
[19]Departamento de Pesquerías y Biología Marina, Centro Interdisciplinario de Ciencias Marinas Instituto Politécnico Nacional, La Paz, Baja Califronia Sur, México
[20]Universidad Francisco Gavidia, San Salvador, El Salvador
[21]Departamento de Biología, Universidad del Valle, Cali, Colombia

**Correspondence: Juan Pablo Quimbayo (quimbayo.j.p@gmail.com)**

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A core challenge in ecology is identifying the factors that determine species distribution and functional diversity of species assemblages. Reef fish are the most diverse group of vertebrates, form taxonomically rich and functionally diverse communities and represent a key source of food for humans. We examine regional distribution patterns of reef fish species richness and functional diversity and investigate how these are determined by historical, biogeographic, energetic, and anthropogenic factors.

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We compiled data from 3,312 underwater visual censuses performed at 122 locations comprising rocky and coral reefs along the Eastern Tropical Pacific (ETP). We used generalized linear mixed-effects models (GLMMs) implemented in a Bayesian framework to investigate whether distance from quaternary refugia, distance from mainland, shelf area, primary productivity, sea surface temperature (SST), human population gravity, and conservation status influence reef fish species richness and functional diversity in the ETP. Species richness and functional richness (FRic) peaked towards the center of the ETP and our null model suggests that FRic followed a spatial pattern that would be predicted by species richness. Additionally, functional evenness (FEve) was highest at higher latitudes whereas functional dispersion (FDis) was homogeneous throughout the ETP. Species richness was negatively influenced by shelf area and distance from mainland, but positively influenced by SST and conservation status. FEve was influenced by human population gravity and FDis by shelf area. Reef fish species richness and functional diversity in the ETP exhibited a strong division within the region mainly mediated by SST and human population gravity. Our results also suggest that dominant species within small shelf areas share more common traits than dominant species in large areas. This study uncovers previously unknown regional patterns of reef fish functional diversity and provides new insights into how historical, biogeographic, energetic, and anthropogenic factors influence complementary biodiversity facets.

Keywords: anthropogenic factors, biodiversity, biogeographic factors, energetic factors, functional diversity, reef fish

## Introduction

Understanding the distribution patterns of biodiversity and identifying the factors that explain these patterns is essential for predicting the response of biodiversity to global change (Mora et al. 2003, Ricklefs 2004). Some studies have postulated that species interactions (e.g. mutualism, competition or predation), environmental factors (e.g. primary productivity, temperature), and anthropogenic factors (e.g. human density) shape local species assemblages by progressively filtering species from the regional pool to local communities (Tittensor et al. 2010, Barneche et al. 2019, Longo et al. 2019). Other studies sustain that the glacial-interglacial cycles of the Quaternary period left an imprint on contemporary marine biodiversity whereby refugia (i.e. areas that remained stable over geological time) preserved species from extinction that then recolonized nearby unstable areas more successfully than isolated ones (Pellissier et al. 2014, Leprieur et al. 2016, 2021). These filters should successively influence several components of local and regional communities, such as the number of species and interactions among species (e.g. mutualism, predation, and competition; Cantor et al. 2018). For instance, in terrestrial habitats, plant-herbivore interactions are more intense in the tropics than elsewhere (Freestone et al. 2011). Further, historical predictors that influence surface area and distance from rivers determine species richness and phylogenetic diversity of freshwater fish in the Amazon River (Salgueiro et al. 2022). In marine habitats, reef fish species richness varies with coral area (Luza et al. 2022), energy availability (Parravicini et al. 2013, Barneche et al. 2016), and human impacts that concentrate close to reefs (Cinner et al. 2018). Although these studies provided important insights regarding the factors determining species richness, disentangling the simultaneous influence of these multiple factors on functional diversity remains a central challenge in community ecology.

Functional diversity has been recognized as the missing link between the characteristics of an organism – i.e. traits – and its ecological role in nature (McGill et al. 2006, Cadotte et al. 2013, Violle et al. 2014). Most advances in understanding geographic patterns of functional diversity and underlying processes have come from studies of terrestrial communities (Lavorel et al. 2013, Toussaint et al. 2016). Studies in marine ecosystems have demonstrated that reef fish functional diversity depends on species distribution (Mouillot et al. 2014, McLean et al. 2021), whereas coral trait dissimilarities reflect different historical and evolutionary processes in each marine province (McWilliam et al. 2018). A suite of functional diversity indices has been proposed to describe complementary biodiversity facets (Mason et al. 2005, Villéger et al. 2008, Laliberté et al. 2015). Functional richness (FRic), for instance, quantifies the amount of niche space occupied by a given species assemblage (Mason et al. 2005, Villéger et al. 2008). Functional evenness (FEve) quantifies the regularity in the distribution of abundance within the occupied niche space (Mason et al. 2005, Villéger et al. 2008), and functional dispersion (FDis) quantifies the spread of species within the occupied niche space weighted by their relative abundance (Villéger et al. 2008, Laliberté and Legendre 2010). These functional indices respond differently to the various local and regional community assembly mechanisms (Yeager et al. 2017, Tsianou and Kallimanis 2020). Therefore, understanding how biodiversity varies through environmental gradients and in response to human impacts remains a challenge in marine habitats. This is partially due to the magnitude and direction of the relationship between diversity and specific factors, which in turn depend on the metric used. For instance, species richness correlates strongly and positively with mean sea surface temperature (SST), whereas the latter has limited effect on functional diversity (Stuart-Smith et al. 2013, Quimbayo et al. 2019). Further, anthropogenic factors can also influence taxonomic richness and trait composition because of differential vulnerability among communities (Dornelas et al. 2014, Ceretta et al. 2020). Human density and accessibility to fish markets, for instance, can have a negative effect mainly on top predators and large herbivores on coral reefs (Cinner et al. 2016, 2018).

Reef fishes comprise the most speciose group of vertebrates, form functionally diverse assemblages and include functionally



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and economically important species (Kulbicki et al. 2013, Mouillot et al. 2014, Brandl et al. 2019). Globally, reef fish species are distributed heterogeneously because of historical (Pellissier et al. 2014), evolutionary (Siqueira et al. 2016) and biogeographical factors (Parravicini et al. 2013). Such heterogeneity in species distribution influences the functional structure of fish assemblages in the different marine realms (Parravicini et al. 2021, Quimbayo et al. 2021b, Maxwell et al. 2022). For instance, the fish fauna in the Eastern Tropical Pacific (ETP) is divided into three large provinces (i.e. Cortez, Panamic, and Ocean Island, see Robertson and Cramer 2009). The ETP is characterized by high regional endemism and relatively low functional diversity due to the marked isolation of this marine region from others (Briggs and Bowen 2012). Although global assessments have reported species-poor fish fauna in the ETP, the regional species pool encompasses key functions for the maintenance of ecological processes (Mouillot et al. 2014, Maxwell et al. 2022). Knowledge of fish functional diversity in the ETP is, however, under-represented in global assessments of coral reef status and fish biodiversity (Stuart-Smith et al. 2013, Mouillot et al. 2014) and scarce at both regional (Ramírez-Ortiz et al. 2017, Olivier et al. 2018, Quimbayo et al. 2019) and local scales (Quimbayo et al. 2017, Olán-González et al. 2020). We tackle this issue by assembling for the first time an empirical dataset collected through underwater visual censuses (UVCs) in 122 locations conducted by researchers within local monitoring programs throughout the region.

Here we map taxonomic and functional diversity of reef fish throughout the ETP and quantify the role of historical, biogeographic, energetic, and anthropogenic factors driving the observed patterns. We expect that given the peculiarities of the ETP, such as its strong isolation, high regional endemism and strong differences among its provinces (Mora and Robertson 2005a, Zapata and Robertson 2007, Robertson and Cramer 2009), taxonomic and functional diversity would respond differently to factors governing global fish biodiversity (Parravicini et al. 2013, Barneche et al. 2019, Maxwell et al. 2022). Considering the high isolation of the ETP from Quaternary refugia located currently in the Indo-Australian Archipelago (IAA) (Bellwood and Meyer 2009), we expect a negative effect of this historical factor on taxonomic richness and FRic, and a positive effect on FEve and FDis. As higher speciation rates occur in large habitat areas (Losos and Schluter 2000), and reef area is an important driver of reef fish distribution (Parravicini et al. 2013), we expect a positive effect of shelf area on both species richness and FRic. In contrast, we expect high values of FEve and FDis in small areas, because these areas are likely to shelter fewer species with different functions. We also anticipate that SST and primary productivity (PP) would play the strongest roles in driving all biodiversity facets through their effect on metabolism and speciation rates (Barneche et al. 2014, 2016). Specifically, we expect both SST and PP to relate positively with species richness and FRic but negatively with FEve and FDis which are inversely related to species richness. We also expect that the proximity to human populations and open access to fishing would strongly and negatively influence species richness and functional diversity due to the disruptive effect of human impact on fish community structure (Clavel et al. 2011). Lastly, considering the separation of reef fish richness within provinces in the ETP (i.e. Cortez, Panamic, and Ocean Island; Robertson and Cramer 2009), we expect functional indices to also reflect these biogeographic differences.

## Material and methods

### Study area

This study focused on the ETP (Fig. 1), one of the most isolated marine regions in the world due to different biogeographic and physical barriers that separate it from others (Robertson and Cramer 2009). The ETP is disconnected from the Indo-Pacific by more than 4000 km of deep open ocean that separates Clipperton Atoll, the westernmost area within the ETP, from the Central Pacific and Indo-Pacific islands (Robertson and Cramer 2009, Kulbicki et al. 2013). This stretch of deep ocean is known as the Eastern Pacific Barrier (Grigg and Hey 1992, Robertson and Cramer 2009). Further, the closure of the Isthmus of Panama approximately three million years ago, isolated the ETP from the Atlantic, promoting allopatric speciation processes (Briggs and Bowen 2012, O' Dea et al. 2016). Lastly, the ETP is strongly influenced by the California current in the north and the Humboldt current in the south, which delimit the tropical and subtropical fish faunas within this region (Robertson and Cramer 2009). These barriers favor high regional endemism (ca 79 % of the fish fauna) and divide the province in two continental provinces (i.e. Cortez and Panamic), and one oceanic province encompassing the five ocean islands (i.e. Revillagigedos, Clipperton, Cocos, Malpelo, and Galápagos) (Robertson and Cramer 2009).

The ETP has marked oceanographic conditions strongly influenced by low-latitude trade winds, a shallow thermocline and interannual climate variations associated with the El Niño-Southern Oscillation (ENSO) (Fiedler and Lavín 2017). Further, this region is characterized by low surface pH values that directly influence the development of coral communities (Fiedler and Lavín 2017). These oceanographic conditions create a distinct environment with incipient coral reef development where live coral cover has progressively declined from 34.6% in 1998 to 22.4% in 2016 (Reyes-Bonilla et al. 2021). Lastly, the ETP has 41 Marine Protected Areas with different levels of protection (Supporting information) and spanning a total area of about 180 335 km$^2$ (Alvarado et al. 2017).

### Dataset

We compiled reef fish data from 3,312 UVCs conducted at 296 sites within 122 locations comprising both rocky and coral reefs along of the ETP between 2004 and 2020 (Supporting information). The ETP Node of the Global Coral Reef Monitoring Network led efforts to compile and



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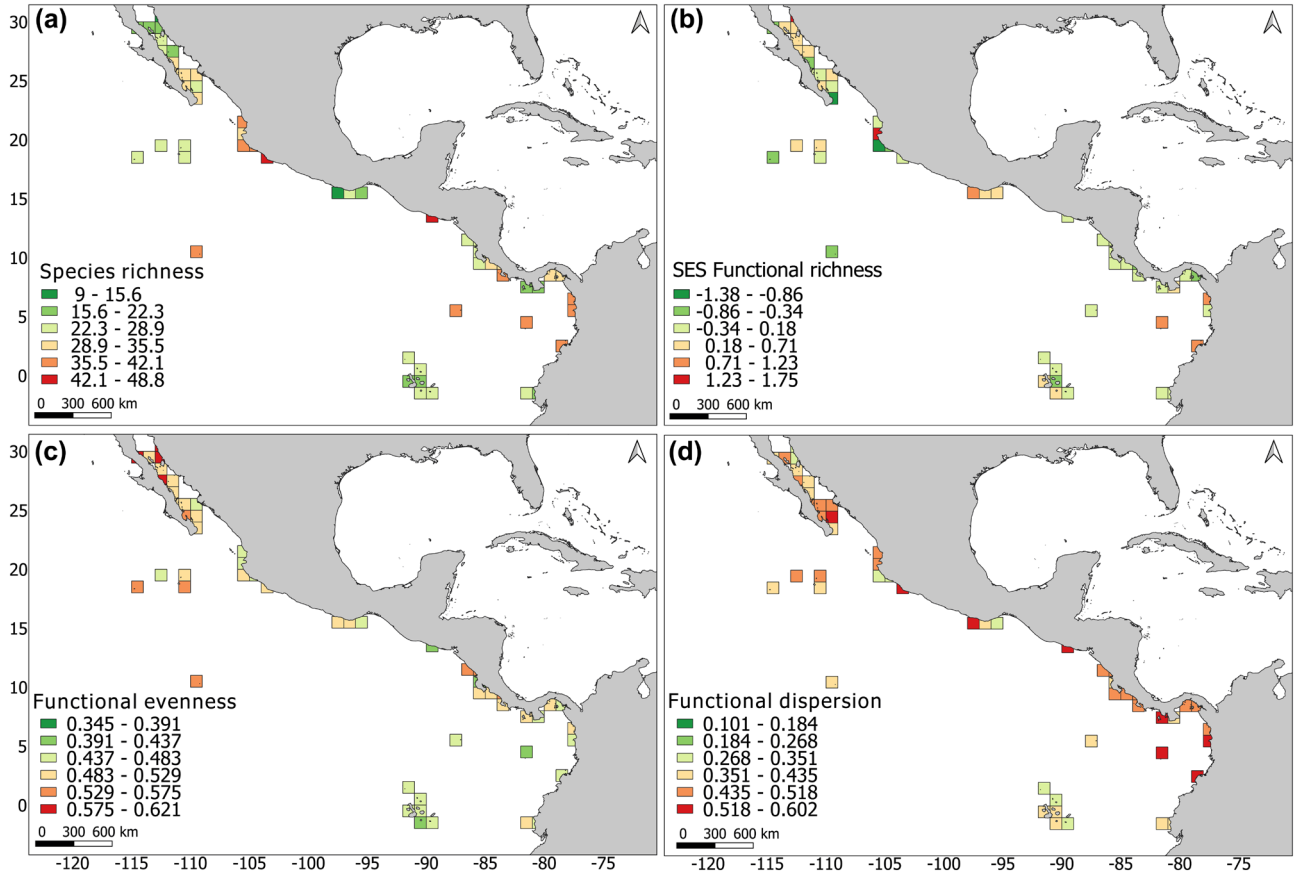


Figure 1. Geographic distribution of (a) species richness, (b) Starndardized Effect Size functional richness (SES.FRic), (c) functional eveness (FEve), and (d) functional dispersion (FDis) of reef fish assemblages throughout the Eastern Tropical Pacific.

homologate all datasets. Given that sites located less than 10 km apart from one another were considered contiguous, we opted for grouping them into unique locations using a buffer area of < 10 km. This process resulted in 122 unique locations and enabled us to obtain a better spatial representation of fish assemblages at the 10-km scale. However, insular sites were considered separate from mainland sites even when they were less than 10 km apart. The total area surveyed per location varied between 320 and 74 000 $m^2$. During UVCs, the surveyor identified and counted all actinopterygian fish species observed in the water column and on the bottom of belt transects (Brock 1954). The area per transect varied between 40 and 250 $m^2$ (Supporting information) and all transects were located above the 35 m isobath.

## Fish traits

We characterized all species observed in the UVCs using six morphological and behavioral traits related to fish life-history strategies and ecosystem functions (Mouillot et al. 2014, Quimbayo et al. 2021a). These traits were: 1) mean body size (numeric and continuous variable directly calculated from the dataset by averaging the estimated size of all individuals observed per species), 2) trophic level (quantitative variable ranging from 1 to 5 according to the main food items consumed by the species), 3) position in the water column (qualitative ordered trait with three levels: bottom, low, and high), 4) group size (qualitative ordered trait with five levels: solitary, pairing, small group of 3–20 individuals, medium group of 20–50 individuals, and large group > 50 individuals), 5) diel activity (qualitative trait with three levels: diurnal, night, or both), 6) home range (qualitative trait with three levels: sedentary, mobile within-reef, and very mobile among reefs). These traits have been successfully used to describe the functional structure of reef fish assemblages at different scales (Mouillot et al. 2014, Parravicini et al. 2021, Quimbayo et al. 2021a, b). We extracted all trait values from Quimbayo et al. (2021a) and from online repositories, such as FishBase (Froese and Pauly 2021) and the Shorefishes of the Tropical Eastern Pacific online information system (Robertson and Allen 2015).

## Taxonomic and functional diversity indices

Based on the UVCs compiled, we calculated species richness and three functional diversity indices (i.e. FRic, FEve, and FDis) (Mason et al. 2005, Villéger et al. 2008, Laliberté and Legendre 2010). These functional indices were estimated based



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on the topology of a multidimensional space, obtained by ordering all species according to their trait values (Mason et al. 2005, Villéger et al. 2008, Laliberté and Legendre 2010). To this end, we performed a Principal Coordinates Analysis (PCoA) based on the Gower's distance dissimilarity matrix, which allows for the combination of qualitative and quantitative trait values (Podani and Schmera 2006). We retained the first four PCoA axes, which accounted for more than 79% of the total data variance. Therefore, we built a 4D space where pairwise distances between species were congruent with their initial trait-based Gower distances (Maire et al. 2015).

### Explanatory factors

We compiled historical, biogeographic, energetic, and anthropogenic factors to examine their influence on the reef fish species richness and functional diversity in the ETP. As a historical factor, we considered 1) the isolation from Quaternary refugia quantified as the distance (degrees) from each site to the closest Quaternary refugia reported by Pellissier et al. (2014). As biogeographic factors, we considered 2) shelf area and 3) distance from mainland, as energetic factors we included 4) mean SST and 5) PP, and as anthropogenic factors we considered 6) conservation status and 7) human population gravity index. Shelf area (degrees$^2$) was defined as the area of continental shelf over the ~ 35 m isobath (i.e. set by the deepest limit of our fish surveys) calculated across a circular buffer of 5 km radius around the centroid of each site. The gridded bathymetry layer was downloaded from the General Bathymetric Chart of the Oceans at 15 arc-second resolution (GEBCO 2021). Distance from mainland (degrees) corresponds to the closest distance from the centroid of each location or site to the mainland coastline and was calculated from the mainland coastline vector downloaded from Natural Earth at 1:10 m resolution (Patterson and Kelso 2021). Mean SST (°C) was extracted from MODIS Aqua Global Level 3 Mapped SST at 4 km resolution (NASA 2020). PP rates were modelled at a 5 arcmin resolution from 2000 to 2014 for surface layers and extracted from the BioOracle database (Tyberghein et al. 2012). Conservation status corresponds to a category assigned per location indicating the level of protection and size of the marine protected area if present. Four categories were defined: 1) non-protected area when the location afforded no protection, 2) medium-size managed area when the location was inside a marine protected area of less than 5000 m$^2$ belonging to IUCN categories IV (habitat/species management area) or VI (protected area with sustainable use of natural resources), 3) medium-size highly protected area when the location was inside a marine protected area of less than 5000 m$^2$ belonging to IUCN categories Ia (strict nature reserve) or II (national park) and 4) large-size highly protected area when the location was inside a marine protected area of more than 5000 m$^2$ classified as IUCN categories Ia or II. The human population gravity index corresponds to a measure of potential human impact considering the relation between human population density and travel time to the nearest reef (Cinner et al. 2018).

### Minimal sampling area

Considering the unequal sampling effort and variation in transect area across locations, we identified the location with minimal sampling area (MSA) (i.e. 320 m$^2$, Supporting information). Once the MSA was defined, we selected the same MSA in all other locations. As several combinations of UVCs could be assembled to compose each MSA per location, we repeated this procedure 1000 times to produce a distribution of estimated species richness and functional indices. This procedure is analogous to using sample-based rarefaction curves thus allowing for comparisons among locations, while controlling for the difference in sample size based on the MSA (Gotelli and Colwell 2001, Magurran and McGill 2011). This method has previously been used to compare fish assemblages from oceanic (Quimbayo et al. 2019) and continental islands (Silva et al 2023).

### Null model

To test whether the observed functional richness differed from the expected distribution given the species richness observed across provinces within the ETP, we used a null model based on the regional randomization of species composition (Villéger et al. 2008, Oliveira et al. 2016). To build the null model, we generated 999 randomized assemblages per province (i.e. Cortez, Panamic and Ocean Island). Species were drawn from the regional species pool reported in the ETP, while holding the species richness estimated in each MSA selection constant. We then shuffled the species names in the trait matrix to obtain random estimates of functional richness. We quantified the Standardized Effect Size Functional Richness (SES.FRic) as the difference between observed and random functional richness using the following equation: (FRic (observed) – mean of null FRic distribution)/standard deviation (SD) of the null FRic distribution). The SES.FRic indicates the number of SDs by which the observed FRic deviates from the mean expected FRic derived from the null models. Positive SES.FRic values indicate that FRic is greater than would be expected by chance (functional overdispersion), whereas negative values indicate that FRic is lower than expected by chance (functional clustering). Observed FRic values outside the 95% confidence interval can thus be considered different from the null model (Gotelli 2000).

### Data analysis

Prior to running the statistical analysis, we scaled all predictors to a mean of zero and a standard deviation of one to facilitate the direct comparison among effect sizes. We then checked for strong collinearity among our seven predictors using the Pearson's correlation coefficient and taking an absolute value of $r = 0.70$ as a threshold (Dormann et al. 2013). Additionally, we calculated the variance inflation factor using the *vif* R (www.r-project.org) function from the 'car' package (Fox and Weisberg 2019) to verify that the predictors



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included in our models were not collinear, considering a value of three as a cut-off. As no collinearity was observed among our predictors (Supporting information), all predictors were included in our initial models.

To quantify the relative importance of historical, biogeographic, energetic, and anthropogenic factors on species richness and functional diversity, we considered these predictors as fixed factors in generalized linear mixed-effects models (GLMMs) implemented under a Bayesian framework. A Gaussian distribution (using the log link function) was specified for models fitted to species richness and SES.FRic, whereas FEve and FDis were modeled using a Beta distribution adequate for values between 0 and 1. Our models have a hierarchical structure where locations are nested within countries and countries nested within biogeographical provinces (i.e. Cortez, Panamic and Ocean Island, Robertson and Cramer 2009). Thus, we considered country and biogeographical province as random factors. We did not include depth as a random factor in our models because this information is averaged during the procedure applied to control for the MSA in each location. Four Markov Chain Monte Carlo simulations were run simultaneously, each with 100 000 iterations and 25 000 warm-up iterations. We achieved convergence on all four chains (rhat = 1.00 for all coefficient estimates). We considered the effect size significant when the 95% credible interval of the estimated posterior distribution of the parameters did not include 0. We also used Bayesian $R^2$ to estimate the amount of variation explained by each model (Gelman et al. 2019). All models exhibited $R^2 > 0.50$. Posterior predictive checks are provided in the Supporting information. All Bayesian procedures were fitted using functions implemented in the package 'brms' (Bürkner 2017). Based on the model residuals controlling for the effects of country (nested within biogeographical province) and geographical coordinates per location, we estimated Moran's I test using the Moran.I R (www.r-project.org) function from the 'ape' package (Paradis and Schliep 2019). We did not observe spatial autocorrelation ($p = 0.07$), which suggests that a hierarchical structure was adequate to account for the spatial structure of our sampling design. All analyses and figures were implemented using the R environment ver. 4.0.2. (www.r-project.org).

## Results

Species richness estimated within the MSA (i.e. 320 $m^2$) ranged between 9 and 49 species with an average of 26.51 ± 7.53 (mean ± S.D.). Species richness hotspots were observed in the Central Mexican shelf, El Salvador and between Panama and Colombia (Fig. 1a). SES.FRic ranged between −1.38 and 1.75, with an average of −0.06 ± 0.50 (Fig. 1b). The SES.FRic results indicate that all FRic values are within the 95% confidence intervals, therefore FRic values are well-explained by the patterns of species richness, without evidence for functional overdispersion or clustering (Supporting information). FEve ranged between 0.34 and 0.62 with an average of 0.50 ± 0.05, peaked in the Gulf of California and Clipperton and had moderate values in Panama and Ecuador (Fig. 1c). FDis ranged between 0.09 and 0.60 with an average of 0.43 ± 0.10 and was homogeneously distributed throughout the ETP (Fig. 1d).

Different historical, biogeographic, energetic, and anthropogenic factors influenced fish species richness and functional diversity indices in the ETP (Fig. 2). Species richness was positively influenced by conservation status and SST [(0.01:0.12) and (0.13:0.38); 95% CI respectively], but negatively affected by shelf area and distance from mainland [(−0.39: −015) and (−0.19: −0.01), respectively; Fig. 2a]. None of the historical, energetic or anthropogenic factors influenced SES.FRic (Fig. 2b). Human population gravity favored high levels of FEve [0.01:0.09] (Fig. 2c). Lastly, FDis was negatively influenced by shelf area [FDis: (−0.20: −0.03); Fig. 2d].

## Discussion

Our understanding of the association between taxonomic and functional diversity across different gradients remains incomplete (Edie et al. 2018, Schumm et al. 2019). This is partially due to our limited knowledge on how functional diversity responds to environmental change. We evaluated how historical, biogeographic, energetic, and anthropogenic factors influence multiple facets of reef fish biodiversity in the most isolated tropical marine region of the world. The simultaneous assessment of species richness, SES.FRic, FEve, and FDis, highlighted differences in geographic patterns of fish biodiversity throughout the ETP, and discrepancies in the relative importance of the factors that explain these patterns. We find that species richness, SES.FRic, FEve, and FDis differ in distribution throughout the ETP, with certain biodiversity facets peaking in the center of the region. The location of some of these hotpots is consistent with results reported by Mora and Robertson (2005a). Interestingly, FEve increased with human population gravity index, suggesting that human impact promotes the functional homogenization of reef fish assemblages in the ETP. This result can be associated with a reduction of specific species traits, such as large body size and high trophic levels. Lastly, our results indicate that FDis decreased with shelf area. This likely reflects that species with high abundances in small areas share more common traits than do abundant species in large areas. We provide the first map of multiple facets of taxonomic and functional reef fish diversity in the ETP and new insights on the factors that shape these biodiversity patterns.

### Regional patterns of reef fish species richness and functional diversity

FRic did not deviate from the mean expected values derived from the null model, indicating that variation in FRic was directly related to variation in species richness. Species



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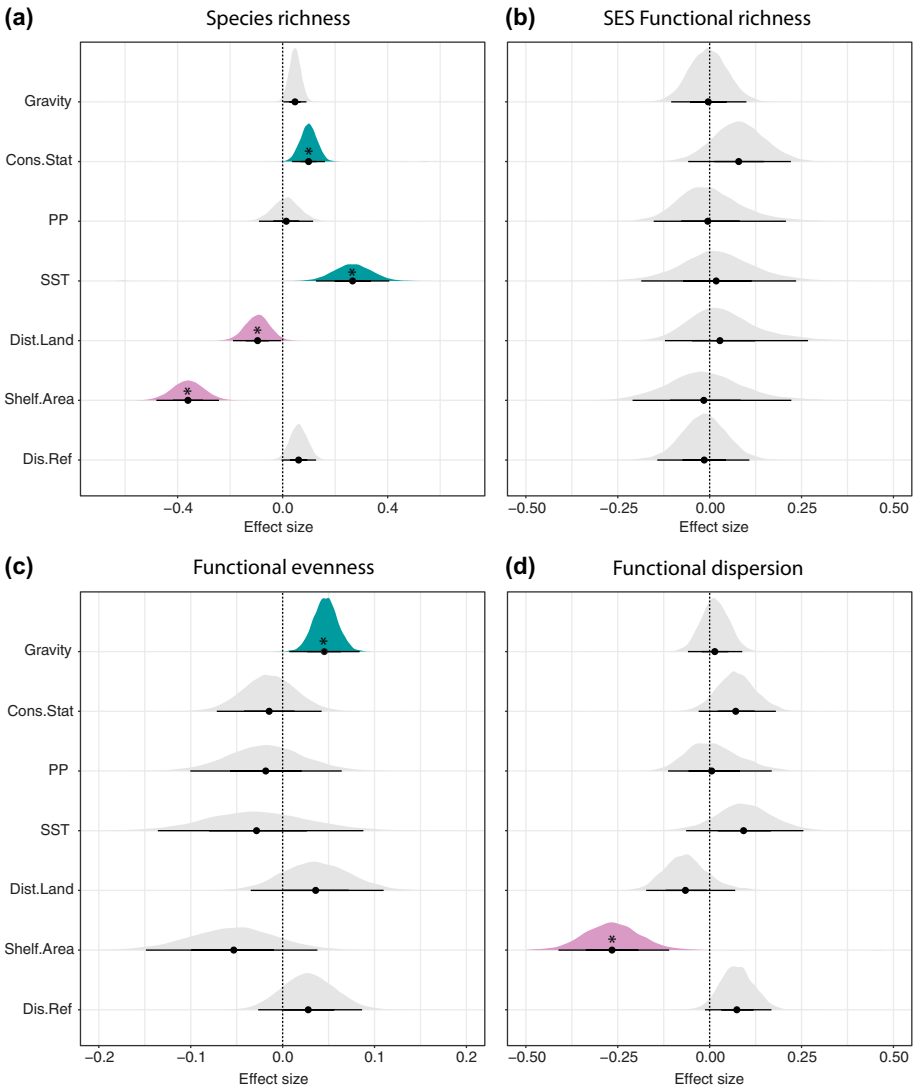


Figure 2. Effect of historical (Dis.Ref: distance from Quaternary refugia), biogeographic (Shelf.Area and Dist.Land: distance from the mainland), energetic (SST: sea surface temperature and PP: primary productivity), and anthropogenic (Con.Stat: Conservation status and Gravity: human population gravity) predictors on ETP reef fish diversity. Values are standardized as positive (blue) or negative (purple) effect sizes. Points represent mean parameter estimates, lines represent 95% credible intervals, and density plots represent the distribution of the effect sizes per factor. Asterisks denote factors that had a 95% credible interval of the posterior distribution not overlapping with zero.

richness and hence FRic peaked in the Central Mexican shelf, El Salvador and between Panama and Colombia supporting previous studies that examined reef fish assemblages at the regional scale (Mora and Robertson 2005b). According to Mora and Robertson (2005a) there are two explanations for this species richness pattern. The first one is that these locations represent 'centers of origin' because they have high habitat variation that favors high speciation rates. The second is that these locations may represent 'centers of accumulation' which receive fish fauna from several other subregions in the ETP (Robertson et al. 2004, Lavín et al. 2006). For instance, locations in the Central Mexican shelf may have received fish species transported by the currents of the Gulf of California and Costa Rica, which can favor larval recruitment and movement of adults (Lavín et al. 2006). Further, warm water incursions during ENSO in the Central Mexican shelf can also favor the arrival of tropical fish species, therefore increasing species richness. It is also noteworthy that several fish species have narrow distribution ranges within the ETP (Mora and Robertson 2005a), which contributes to the division of fish fauna into provinces (Robertson and Cramer 2009), and, therefore, favors the emergence of several biodiversity peaks along the ETP. The high correlation between species richness and FRic further suggests that higher species richness in those locations contributes to the addition of unique combinations of traits (Mouillot et al. 2014). As selected traits are related to ecological functions, this implies that increases or declines in species richness are associated with the addition or loss of unique ecological functions (Mouillot et al. 2014).



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The geographic distribution of FEve throughout the ETP followed a pattern opposite to species richness. This is consistent with global biodiversity patterns of marine bivalves and terrestrial birds which indicate that FEve peaks towards higher latitudes (Schumm et al. 2019). This inverse relationship between FEve and species richness may be associated to the distribution of species among functional groups being highly skewed in the tropics. In other words, certain functional entities (i.e. groups of species with identical trait combinations) contain many abundant species whereas other functional entities are comprised by many rare species. This reduces the regularity in the distribution of abundance and favors an increased overlap among functional entities in the functional space (Mason et al. 2005, Mouillot et al. 2013). Specifically, the high FEve observed in the Gulf of California can be associated with low connectivity among species in the north and south (Soria et al. 2014, Munguia-Vega et al. 2018), favoring a reduction in species richness but an increase in the FEve. The low FEve values observed in Ecuador can be associated to the combined effect of the Humboldt current and the poor reef development in this area. These factors likely restrict the tropical species richness while favoring subtropical species with distinct traits, thus resulting in high FEve. The geographic variability of FDis suggests that species that are relatively abundant throughout the ETP exhibit similar traits. This conduces to FDis being more homogenously distributed through the region compared to other taxonomic and functional diversity facets. A similarly homogeneous FDis pattern was observed in the intertidal environment communities (e.g. microbenthic algae and invertebrates) of the Southeastern Pacific, where species with high abundance shared similar traits (Valdivia et al. 2017). Geographic variability in FDis could also be explained by evolutionary time and diversification rates linked to the evolutionary history of the region (Mora and Robertson 2005b), which was not explored here.

### Factors that influence reef fish species richness and functional diversity in the Eastern Tropical Pacific

Variability in species richness was mostly explained by the combined effect of shelf area, distance from mainland, SST, and conservation status partially supporting our initial hypotheses. The positive relationship between species richness and SST, can be explained by the fact that temperature strongly influences metabolic and mutation rates typically leading to high species richness (Barneche et al. 2014). Furthermore, the positive effect of conservation status on species richness suggests that protected areas in the ETP appear to preserve species richness (Edgar et al. 2011, Friedlander et al. 2019). Because of the high dependence of FRic on species richness, this is particularly important as changes in species richness could in turn affect ecosystem functioning over large scales, even in species-rich locations, as redundancy appears to be relatively low (Mouillot et al. 2014). The unexpected negative relationship between shelf area and species richness could be explained by the limited development of coral reefs in the region, in association with the narrow continental shelf where reefs are exposed to drastic environmental changes (Cortés 1997). On the other hand, the negative effect of distance from mainland on species richness supports Island Biogeography Theory (MacArthur and Wilson 1967), according to which species richness decreases as distance from mainland increases. Distance from Quaternary refugia had no effect on species richness probably due to the high level of isolation of the ETP from other marine regions. This degree of isolation favors high local and regional endemism. Multiple lines of evidence support that species colonize isolated regions form peripheral areas, which can create biodiversity hotspots. Indeed, these regions can give rise to endemic species that thrive within their new home but do not disperse further (Bowen et al. 2013, Cowman et al. 2017). Our results showed that species richness was unrelated to PP. This result differs from previous studies across oceanic islands within the ETP (Quimbayo et al. 2019) and throughout the entire ETP (Mora and Robertson 2005b), both of which highlighted PP as an important factor shaping fish diversity. We propose two plausible explanations for the lack of an effect in our case. First, in our study the locations with highest species richness are not influenced directly by strong upwelling systems as are oceanic islands. In oceanic islands exposed to strong upwelling systems (e.g. Galápagos Islands) the bathymetric profile favors the vertical transport of nutrient-rich waters and promotes high species richness and abundance (Gove et al. 2016). Second, previous studies focused on the entire local species pool reported in checklists (Mora and Robertson 2005b), whereas our study focused on a subset of species captured through UVCs, thus some effects may not be detected.

The lack of an effect of any of the historical, biogeographic, energetic, and anthropogenic factors on SES.FRic confirmed that the patterns of FRic did not strongly deviate from null expectations. Thus, this result indicates that deterministic processes *per se* do not adequately explain the spatial distribution of FRic throughout the ETP.

FEve integrates information about the distribution of abundance throughout multidimensional trait spaces and it is fundamental to understand how changes in community composition could impact ecosystem functioning (Mason et al. 2005). We observed an increase in FEve with increasing human population gravity. This result could indicate that anthropogenic disturbances (e.g. fishing) are responsible for the removal and/or decline in abundance of certain species with specific traits, such as top predators or large-bodied fish (Ceretta et al. 2020, Giglio et al. 2020), leading to the homogenization of fish assemblages. In homogenized assemblages, abundance appears more evenly distributed among a smaller number of species, as observed in polar regions (Schumm et al. 2019). This hypothesis is also supported by the negative relationship between FRic and FEve in the Atlantic Ocean (Halpern and Floeter 2008), emphasizing that the loss of unique trait combinations may increase FEve. Therefore, this could suggest that human impacts are responsible for the loss of unique



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ecological functions in an impacted niche (Mouillot et al. 2013). An alternative explanation could be that human population gravity is associated with isolation, with isolated areas being usually exposed to very low anthropogenic impact (Cinner et al. 2018). Although isolation had no effect on FEve, it was positively correlated with fish abundance and biomass in remote islands of the ETP (Quimbayo et al. 2019). Further, migration of reef fish into remote areas within the ETP (e.g. oceanic islands) could be limited to some species with small body sizes and short pelagic larval duration, and could imply that speciation becomes the dominant mechanism originating biodiversity (Pinheiro et al. 2017, Mazzei et al. 2021). Speciation in remote areas may thus result in the origin of species that have more similar traits compared to species inhabiting other areas through a combination of colonization and speciation processes. This could explain the observed high levels of FEve in highly isolated areas. Consequently, the observed relationship between human population gravity and FEve may be driven more by the isolation of some locations than by the direct impact of anthropogenic actions, such as pollution and fishing. Future research should aim to determine whether areas under relatively high anthropogenic pressure have experienced changes in species and trait composition over time or will in the near future.

In line with our expectations, FDis decreased with increasing shelf area. This likely reflects that species with high relative abundance have more traits in common in small areas than dominant species within large areas. Some trait combinations are indeed favored over others on isolated reefs, for example large body sizes favor higher dispersal capacities whereas generalist diets favor higher colonization rates (Luiz et al. 2012, Parravicini et al. 2021). FDis was highly variable on nearshore reefs, yet unrelated to the predictors considered here. This suggests that other environmental variables, fine-spatial-scale habitat characteristics, or biotic mechanisms (Yeager et al. 2017) not included in this study might play an important role in shaping the spatial patterns of FDis and merit further attention.

## Conclusion

The use of a multifaceted approach considering taxonomic and functional diversity indices allowed us to assess spatial biodiversity patterns in the ETP and test the applicability of long-debated hypotheses underpinning these patterns. Historical, biogeographic, energetic, and anthropogenic factors were key predictors of biodiversity patterns at coarse scales. However, anthropogenic factors, such as human population gravity and conservation status, also influence present-day fish assemblages at finer spatial scales. Investigating the geographic distribution of any diversity metric in isolation provides an incomplete picture of the regional biodiversity patterns, as certain metrics are poor surrogates of one another. Therefore, we join other studies (Stuart-Smith et al. 2013, Maxwell et al. 2022) in encouraging integrative approaches when studying biodiversity patterns. These findings point out several challenges for biodiversity conservation identifying priority areas for preservation and offering the first empirical baseline of reef fish functional diversity in the region.

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### Author contributions

**Alexia Dubuc**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Resources (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Juan Pablo Quimbayo**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Resources (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Juan José Alvarado**: Data curation (supporting); Resources (supporting); Writing – review and editing (supporting). **Tatiana Araya-Arce**: Data curation (supporting); Validation (supporting); Writing – review and editing (supporting). **Andrea Arriaga**: Data curation (supporting); Validation (supporting); Writing – review and editing (supporting). **Arturo Ayala-Bocos**: Resources (supporting); Writing – review and editing (supporting). **Jose Julio Casas-Maldonado**: Resources (supporting); Writing – review and editing (supporting). **Luis Chasqui**: Data curation (supporting); Resources (supporting); Writing – review and editing (supporting). **Jorge Cortés**: Resources (supporting); Writing – review and editing (supporting). **Amilcar Cupul-Magaña**: Resources (supporting); Writing – review and editing (supporting). **Damien Olivier**: Formal analysis (supporting); Methodology (supporting); Validation (supporting); Writing – review and editing



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(supporting). **Manuel Olán-González**: Data curation (supporting); Writing – review and editing (supporting). **Alberto González-Leiva**: Resources (supporting). **Andrés López-Pérez**: Resources (supporting); Writing – review and editing (supporting). **Héctor Reyes-Bonilla**: Resources (supporting); Writing – review and editing (supporting). **Franz Smith**: Data curation (equal); Methodology (supporting); Resources (supporting); Writing – review and editing (supporting). **Fernando Rivera**: Resources (supporting); Writing – review and editing (supporting). **Fabián A. Rodríguez-Zaragoza**: Investigation (supporting); Resources (supporting); Writing – review and editing (supporting). **Jenny Carolina Rodríguez-Villalobos**: Resources (supporting); Writing – review and editing (supporting). **Johanna Segovia**: Resources (supporting); Writing – review and editing (supporting). **Fernando A. Zapata**: Data curation (supporting); Investigation (supporting); Methodology (supporting); Resources (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Sonia Bejarano**: Conceptualization (equal); Funding acquisition (lead); Investigation (equal); Project administration (lead); Resources (supporting); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (equal).

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### Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.41ns1rnhn (Quimbayo et al. 2023).

### Supporting information

The Supporting information associated with this article is available with the online version.

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