UNIVERSIDAD DE COSTA RICA
SISTEMA DE ESTUDIOS DE POSGRADO

DIVERSIDAD FUNCIONAL DE PECES HERBÍVOROS ARRECIFALES EN EL PACÍFICO TROPICAL ORIENTAL

Tesis sometida a la consideración de la Comisión del Programa de Estudios de Posgrado en Biología para optar al grado y título de Maestría Académica en Biología

ANDREA ARRIAGA-MADRIGAL

Ciudad Universitaria Rodrigo Facio, Costa Rica
2023

DEDICATORIA

A mami, que con todo su amor da siempre lo mejor de sí para acompañarme en el camino.

AGRADECIMIENTOS

Agradezco a las personas, asistentes, investigadoras y quienes apoyaron en la logística, en más de seis países diferentes, para que biólogas, biólogos y submarinistas pudieran estar a lo largo de 10 años monitoreando los arrecifes en la región. Agradezco además a sus redes de apoyo que dieron los medios y acompañamiento para realizar este trabajo que asume mucho riesgo y compromiso.

Agradezco muchísimo a las personas docentes que pusieron a mi disposición sus enorme experiencia y conocimiento para darme consejo y guiarme a través de los análisis y retos que surgieron a lo largo del proceso. Entre estas personas están Hannia Vega Bolaños, Karol Ulate, Keilor Rojas, Eduardo Chacón, Cindy Fernández García, Rodney Mora Escalante, Andrea Vincent, Mario Espinoza, Jeffrey Sibaja Cordero y Jorge Cortés. A lo largo de este tiempo, fue también indispensable el aporte de los miembros de mi comité de tesis, quienes hicieron más de lo que correspondía, dando consejo sobre la vida académica y personal.

Agradezco sobre todo a mi famila: mami, papi, tía, Toño, Adrián, Tania, Sofi, Mari, Isma, Mati y Migue, primitxs, tíos y a los que estuvieron antes, que dejaron un legado de amor y valentía. A Dani, Sebas, Ale, Celeste, Luis y mis otras personas “familia no de sangre” les agradezco porque no se han limitado a acompañarme desde lo afectivo sino que han puesto tiempo, apoyo económico, creatividad, trabajo, viajes, paseos y chineos que fueron indispensables para encontrar la motivación y fuerza.

Esta Tesis fue aceptada por la Comisión del Programa de Estudios de Posgrado en Biología de la Universidad de Costa Rica, como requisito parcial para optar al grado y título de Maestría Académica en Biología

Dr. Jorge Cortés Núñez

Representante del Decano

Sistema de Estudios de Posgrado

Dr. Juan José Alvarado Barrientos

Profesor Guía

Dr. Juan Pablo Quimbayo Agreda

Asesor

Marcelo Araya S

Dr. Marcelo Araya Salas

Asesor

Dr. Eric Fuchs Castillo

Director del Programa de Posgrado en Biología

Andrea Arriaga-Madrigal

Sustentante

ÍNDICE

RESUMEN

Los arrecifes de coral brindan servicios ecosistémicos insustituibles para el desarrollo humano. Sin embargo, debido al aumento de la presión antrópica, presentan una gran pérdida de especies y un deterioro de las funciones y servicios ecosistémicos que proveen. En los arrecifes, los peces son el grupo de vertebrados más representativo y, particularmente los herbívoros, cumplen un vínculo clave en el paso de energía de los productores primarios al resto de la red trófica y favorecen el asentamiento de reclutas de corales. Las especies desempeñan diversas funciones y servicios en el ecosistema según sus rasgos morfológicos y de comportamiento. Rasgos que suelen estar moldeados por la combinación de presiones competitivas, gradientes ambientales y condiciones antropicas.

En el presente estudio utilicé censos visuales subacuáticos para estimar la variación de la comunidad de peces herbívoros arrecifales en el Pacífico Tropical Oriental (PTO) en términos de riqueza, densidad y biomasa. Además, recopilé variables abióticas (*i.e.*, temperatura superficial del mar, productividad primaria y geomorfología) y factores humanos (*i.e.*, presión antrópica y tiempo de protección) para examinar su posible efecto sobre la distintividad taxonómica y diversidad funcional, utilizando modelos de regresión bayesianos de efectos mixtos. Para este propósito, calculé tres índices de diversidad funcional: dispersión funcional (FDis), divergencia funcional (FDiv) y uniformidad funcional (FEve), con base en rasgos morfológicos, tróficos y de comportamiento. Finalmente, obtuve la media ponderada de la comunidad (“community weighted mean”) y la incluí en un análisis de factores múltiples (MFA) para describir la distribución de los rasgos funcionales en las diferentes ecorregiones. Así como para cuantificar las similitudes por pares de las ecorregiones según la presencia de los rasgos.

Encontré 25 especies de peces herbívoros distribuidas en 18 grupos funcionales. Los máximos valores observados en una ecorregión fueron: riqueza de 20 especies, biomasa promedio de 85.57 g/m² y densidad de 250 ind/km². Estos valores varían en la región debido a la interacción de condiciones a pequeña y gran escala. Observé que las condiciones ambientales, tanto SST como PP, y presión antrópica, se relacionan con la distintividad taxonómica, FEve y FDiv. FDis no se relacionó con ninguno de los parámetros incluidos. El efecto negativo de la variación de SST en individuos taxonómicamente distintos o con rasgos especializados representa una advertencia temprana del deterioro de los procesos que ellos sostienen. Por otro lado, el efecto positivo de la variación de PP sobre FDiv, FEve y distintividad taxonómica puede implicar que sustenta diversas funciones y procesos, dadas por gran abundancia de rasgos especializados y distintividad taxonómica. En cuanto a la presión antrópica, el estudio confirma su efecto negativo sobre la diversidad funcional porque, aunque se asocia con la presencia de rasgos especializados, deja algunos poco representados. Para las islas oceánicas, la alta distintividad taxonómica podría ser advertencia de mayor vulnerabilidad a las perturbaciones en comparación con áreas costeras.

SUMMARY

Coral reefs provide irreplaceable ecosystems services for human development and due to the increase in human population are showing a great loss of species, consequently affecting the ecosystem functions and services that this habitat offers to human population. Reef fish assemblage is the most representative vertebrate group within the coral reefs. This is a key group that allows the exchange of energy between primary producers and the rest of the trophic network and favor the settlement and prevalence of hard corals. The ecological function of herbivorous fishes depends on morphological and behavioral traits. The assemblage of species and consequently, the functions they perform, are shaped by the combination of competitive pressures, environmental gradients, and anthropogenic factors.

I use underwater visual census to estimate the variation of herbivorous reef fish community in the Eastern Tropical Pacific (ETP) in terms of richness, density, and biomass. I also compile abiotic variables (*i.e.*, SST, PP and geomorphology) and human factors (*i.e.* human gravity and protection time) to examine their possible effect on the taxonomic and functional diversity using mixed effect Bayesian regression models. For that matter I calculate the taxonomic distinctness and three indices of functional diversity: functional dispersion (FDis), functional divergence (FDiv) and functional evenness (FEve), based on morphological, behavioral and dietary traits. Finally, I calculated the community weighted mean (CWM) and include it in a multiple factor analysis (MFA) to assess if the environmental conditions represent a filter for the functional traits and to quantify the pairwise similarities between the ecoregions.

The maximum species richness in an ecoregion reaches up to 20 species, the highest mean biomass is 85.57 g/m² and the maximum density was of 250 ind/km². I found that richness, density and biomass of the herbivore community vary within the region due to the interaction of small and large-scale conditions. Species are distributed in 18 functional groups. I observed that environmental conditions, both SST and PP, as well as anthropic pressure, are related to some of the facets of functional diversity (*i.e.* taxonomic distinctness, FEve and FDiv), except to FDis which was not related to any parameter. The negative effect of SST variation on individuals that are taxonomically distinct or have specialized traits represents an early notification of the deterioration of processes that they sustain. On the other hand, the positive effect of PP variation on FDiv, FEve and taxonomic distinctness may allow to sustain diverse functions and processes, fostered by high abundance of specialized traits and taxonomic diversity. Regarding anthropic pressure, the study confirms a negative effect on diversity because, even if it's associated with the presence of specialized traits, it leaves some traits poorly represented. For oceanic islands, the high taxonomic distinctness could be a warning of greater vulnerability to disturbances compared to coastal areas.

LISTA DE FIGURAS

Functional diversity of herbivorous reef fishes in the Eastern Tropical Pacific

1. Introduction

Coral reefs sustain high levels of biodiversity but, at the same time, are subject to growing natural and anthropogenic pressures (Cortés et al., 2017). These environments provide irreplaceable ecosystems services for human development such as coastal protection, tourism, and fisheries resources (Moberg & Folke, 1999; Woodhead et al., 2019). Due to the increased human population and its constant consumption of resources, coral reefs are suffering a great loss of species which consequently affects the ecosystem functions (Williams & Graham, 2019), and services that these habitats offer to human populations (Woodhead et al., 2019).

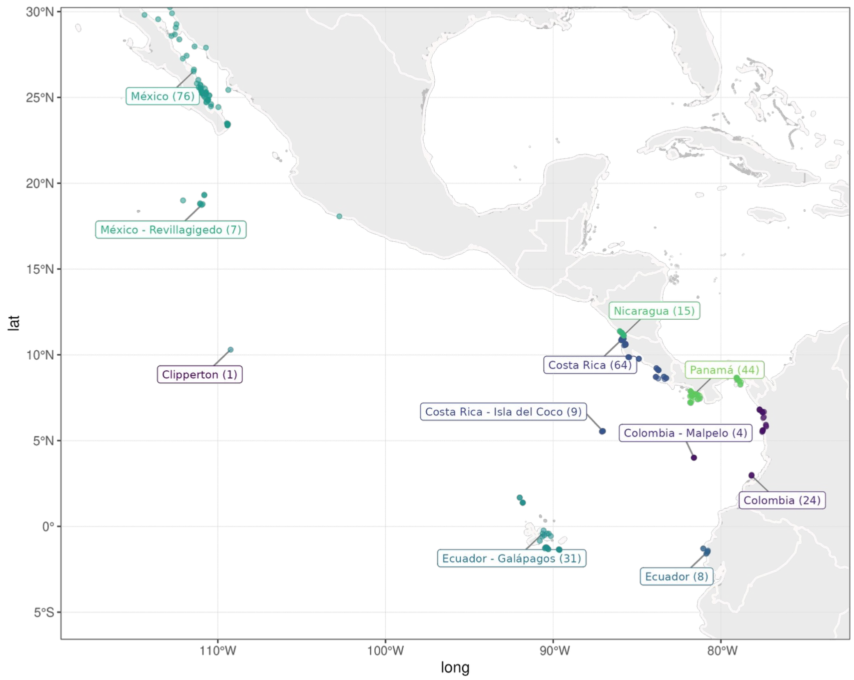


Figure 1. Location of study sites at Eastern Tropical Pacific. Sites were located at rocky and coral reef habitats between 1 and 30 m in depth. Reef fishes were surveyed at all sites through 3899 underwater visual census by scuba diving, which were mostly done between 2006 and 2019. These data were provided by the ETP Node of the Global Coral Reef Monitoring Network (GCRMN).

The reefs in the Eastern Tropical Pacific (ETP) harbor complex, interdependent and diverse communities (Cortés et al., 2017). Although these reefs have been characterized as poorly developed, scattered and with low species richness (Cortés et al., 2017), they maintain irreplaceable economic and biological resources (Moberg & Folke, 1999). For this reason, there is a need to understand the mechanisms that sustain this diversity and how it is modified in the face of adverse conditions.

The reef fish assemblage is the most representative vertebrate group within the coral reefs (Eschmeyer et al., 2010), which perform different ecosystem functions (Choat, 1992). For instance, herbivorous fish (*i.e.* those that feed on turf or filamentous algae and/or undefined organic material, large fleshy algae and/or seagrass) (Mouillot et al., 2014) are a key group that allows the exchange of energy between primary producers and the rest of the trophic network (Burkepile & Hay, 2008). In particular, this species group improve the settlement and prevalence of hard corals (Mumby et al., 2006), since it regulates macroalgae biomass through feeding (Graham & Nash, 2013). Studies have shown that their exclusion from coral reefs could lead to an increase in the accumulation of sediments, affecting the benthic composition (Rasher et al., 2012). Therefore, understanding herbivorous fish can help reveal the factors that affect ecosystem functions in coral reefs (Bellwood et al., 2004).

Studies have shown that the ecological function of herbivorous fish dependend on morphological (Edwards et al., 2013), or behavioral traits (Bellwood & Choat, 1990). For instance, large bodied herbivorous fish, like parrotfishes, can shape the abundance and distribution of coral colonies where they feed (Bonaldo & Bellwood, 2011), which induces different environmental changes than those caused by damselfishes, small bodied fish that maintain small territories (Ceccarelli et al., 2001). Likewise, the impact on recover to coral-dominated states varies depending on the area they prey on (Bonaldo et al., 2012) and according to their mobility and movement patterns (Bellwood et al., 2016; Carpenter, 1986).

The assemblage of species and consequently, the functions they perform are shaped by the combination of competitive pressures, environmental gradients, and anthropogenic factors (Bellwood et al., 2012). Therefore, studies that quantify the functional diversity, integrate the structure of communities, with morphological, physiological, and behavioral traits of each species to understand the performance of their functions (Bellwood et al., 2019; Pombo Ayora et al., 2020; Somerfield et al., 2008). Functional diversity refers to the roles that organisms perform in the ecosystem, in terms of their variety, scope and degree of expression (Naeem et al., 2012). In this way, the factors that shape the herbivorous species composition and the diversity of functions they perform can bring insight into key characteristics of the ecosystems (Hooper et al., 2005; Petchey et al., 2004; Tilman et al., 1997).

To understand the ecological dynamics of herbivorous fish, it is essential to integrate the factors that shape their community. For instance, on a large scale, the main determinant of species richness is latitude (Connell & Irving, 2008; Duffy et al., 2016; Hillebrand, 2004) as it masks patterns associated with solar radiation, temperature, and primary productivity (Floeter et al., 2001; Tuya et al., 2012). These factors allow for hosting greater energy in low latitudes, capable of supporting richer and more diverse communities (Floeter et al., 2005), high speciation and low extinction rates (Siqueira et al., 2016).

Herbivorous fish are usually restricted to warm waters, since the variation of sea surface temperature (SST) represents an environmental filter (Floeter et al., 2005) and the biomass or density of individuals may change in response to this environmental condition. In damselfish of the genera *Stegastes* and *Pomacentrus*, due to an increase in SST, certain metabolic processes generate a decrease in body size (Barneche et al., 2009), representing changes in the biomass. Likewise, fluctuation in primary productivity (PP), using concentration of chlorophyll *a* (chl-*a*) as proxy (Spencer, 1985), represent a change in nutrient availability and changes in benthos composition. For example, in the Great Barrier Reef, a negative relationship has been observed between chl-*a* concentration and coral richness, but positive with macroalgal cover (De´ath & Fabricius, 2010). The possible alteration of the bottom composition due to changes in PP can work as a particularly selective filter in this community due to its close relationship with the benthic environment (Vergés et al., 2014). Other environmental gradients associated with salinity, dissolved oxygen, and pH are also expected to shape the herbivore community (Cornwell et al., 2006; Mouillot et al., 2007).

The way in which environmental conditions affect the abundance and diversity of reef organisms is usually related to the magnitude of anthropogenic pressure to which they are exposed (Downs et al., 2005). Human activities negatively affects traits diversity (DeMalach et al., 2021) by limiting the presence of species with vulnerable traits (Shah Esmaeili et al., 2022; Vellend, 2016). Fishing can impact by the selective extraction of large-body herbivorous organisms (Bejarano et al., 2017, 2019; Hawkins & Roberts, 2004; Thiault et al., 2019), consequently affecting their biomass and abundance. Fishing can also impact communities through a top-down cascade effect when extracting large predators, which control mesopredators that consume herbivores (Mumby et al., 2012; Ruppert et al., 2013) , or bottom-up control through coastal eutrophication, that modify the composition of primary producers (Rasher et al., 2012) which herbivores consume (Puk et al., 2016). These anthropic pressures can be partially compensated through management strategies for conservation (Beita-Jiménez et al., 2019). Marine Protected Areas (MPAs), through the regulation of fishing, protect top-down mechanisms (Edwards et al., 2013; Man et al., 1995; Ulate et al., 2018). Furthermore, the positive effect of these actions tend to improve with time of implementation (Arias et al., 2015; Ulate et al., 2018).

The differential pressures of environmental conditions on particular traits can affect the overall species assemblage (Duffy et al., 2016). Several metrics have been proposed to quantify the potential changes in functional traits at the community level. If we assume that the most abundant traits are those that mainly determine ecosystem processes (Grime, 1998), differences in traits values (quantified by the Community Weighted Mean; CWM) can give valuable information regarding possible processes that differ between the conditions in the region. CWM averages the functional traits present weighted by the abundance of species with each trait (Cornwell & Ackerly, 2009; Sonnier et al., 2010; Wright et al., 2004). To assess the diversity of functions that the combination of traits perform in a community, the functional dispersion (FDis) can be used to represent the volume of the functional space of the community. It is calculated as the average distance of each species to the community centroid, weighted by the abundance of each species (Laliberté & Legendre, 2010). Functional evenness (FEve) evaluates the regularity of the points in the functional space and the homogeneity of their abundances (Villéger et al., 2008). The functional divergence (FDiv) represents the divergence of the points from the center of gravity of the functional volume weighted by abundance (Villéger et al., 2008). A community with high divergence can perform a great deal of ecosystem function as a result of a high degree of niche differentiation and more efficient resource use (Mason et al., 2005). The functional diversity of a community could be linked to the degree of relatedness of the species, because taxonomic relationships, usually covary with anatomical and biological features of species (Lee, 2004). Taxonomic distinctness quantifies the phylogenetic relatedness between species in a community (Clarke & Warwick, 1998; Somerfield et al., 2008) and provides different information than species richness (Warwick & Clarke, 1998) or functional diversity (Somerfield et al., 2008). Functional diversity is usually explored at the community level but rarely at the trophic level, which can bring to light more detail information about the processes that structure these groups.

Here, I examined the variation in the taxonomic and functional distribution of the herbivorous fish in the ETP. The variation of taxonomic and functional diversity of herbivorous reef fish assemblages was estimated across the region, and the effect of the biophysical conditions (*i.e.* SST, PP and geomorphology), and human factors (*i.e.* gravity and protection time) on those parameters. Lastly, I evaluated whether there is a differentiated distribution of the functional traits present in the different ecoregions. As the rate at which trait diversity is lost is often greater than the loss of species diversity (Pombo Ayora et al., 2020), this approach may allow earlier assessment of an altered condition of the environment.

I hypothesize that herbivore richness, density and biomass are likely to peak at lower latitudes (Floeter et al., 2005), consistent with patterns observed globally (Fischer, 1960; Pianka, 1966; Rhode, 1992). On the other hand, the relationship between taxonomic distinctness and latitude is usually weak and variable with the bottom depth (Tolimieri & Anderson, 2010), so it is likely that the level of distinctiveness does not respond to a latitudinal gradient. Also, I expect to find greater richness of herbivores in the continental ecoregions compared to the oceanic islands, a pattern observed in other shorefishes (Robertson & Cramer, 2009).

Since the wide SST variation represents an environmental filter for herbivorous species, it is possible that this variable has a negative effect on diversity. Consequently, I expect to observe low FDis, FDiv, FEve and taxonomic distinctness in sites with high variation in SST. Similarly, it is likely that the variation in PP, through pressure for food availability, has a negative relationship with the diversity parameters (*i.e.* low FDiv, FDis, FEve and taxonomic distinctness). Different geomorphologies are likely to vary in taxonomic distinctness, being probably lower on oceanic islands due to its isolation and productivity conditions compared to coastal areas. For this reason, FEve, FDiv and FDis are expected to be lower in oceanic ecoregions than in coastal ones which have probably higher migration rates supporting more uniform trait representation. Human gravity could negatively affect diversity (DeMalach et al., 2021). Therefore I expect it to be negatively related to FEve, FDiv, FDis and taxonomic distinctness because it represents the status of degraded sites (Quimbayo et al., 2019). Is likely to find that sites with longer protection having complex functional structures and larger functional volumes. This would be represented as a positive relationship between protection time and FDis, FDiv and FEve (Quimbayo et al., 2019). The last prediction is that trait values differ by ecoregion. Oceanic islands will probably have different fauna (Cortés et al., 2017) (*i.e*. lower taxonomic distincness) adapted to overcome the barrier of long distances (Kulbicki, 2015; Robertson et al., 2004). As well as the adaptations to the diet and way of feeding of herbivores associated with the composition of the bottom (Poore et al., 2012). Likewise, traits vulnerable to fishing, or eutrophication could be affected due to the degree of anthropic impact (*e.g.*, traits such as diet, body size and way of feeding) (Shah Esmaeili et al., 2022).

2. Methods

Study region

The Eastern Tropical Pacific (ETP; Fig. 1, Supp.mat. Table S1) is a marine region in the western tropical coast of America, from the Gulf of California in Mexico, to Guayaquil in Ecuador, including its oceanic islands (Revillagigedos, Clipperton, Isla del Coco, Malpelo and Galápagos) (Spalding et al., 2007). The ETP is separated from the central Pacific by the East Pacific Barrier (EPB), usually considered the most important barrier to species migration (Grigg & Hey, 1989). To the east, the Isthmus of Panama has separated the ETP from the Caribbean for 3.1 million yr (Coates & Obando, 1996). Despite its high isolation, it has coral reefs and reef-building coral communities (Glynn, 2017). There are two segments composed of muddy and sandy bottoms without reef formations: in the southeast of the Gulf of California the Sinaloan Gap and from the southern part of Mexico to El Salvador the Central American Gap (Robertson & Cramer, 2009). The El Niño-Southern Oscillation (ENSO) phenomenon and the Peruvian coastal upwelling ecosystem (Tarazona & Arntz, 2001) are important determinants of environmental and oceanographic conditions.

Coral reef formations in the ETP are small, poorly developed, scattered (Dana, 1975), without protruding platforms, with a thin structural framework and composed of few predominant species (Glynn, 2001, 2017). The restricted area with coral reefs is due to conditions such as the narrow continental shelf of the region (Glynn et al., 2017), low aragonite saturation state, high pCO_2, and upwelling waters (Manzello et al., 2008), reduced salinities, high turbidity (Dana, 1975), low water exposure events (Baker et al., 2008; Glynn, 2001), harmful algal blooms, recurrent bleaching events (Glynn, 2017), and white band disease (Baker et al., 2008). Communities are composed of tropical fauna, although with influence of temperate regions on its limits (Robertson & Cramer, 2009). For the ETP, about 1,300 species of shallow water fish (<100 m depth) are reported (Cortés et al., 2017), and 611 (47%) are associated with rocky or coral reef habitats. This study covers 284 sites and documented in the censuses 460 species of rocky or coral reef environments (Supp.mat. Table S1).

Visual census data

The herbivorous fish were sampled through 3899 underwater visual census (UVC) which were done between 2006 and 2019 (Fig. 1). On each UVC the species richness, abundance, and body size of the reef fish were estimated. Body size was categorized in seven size classes (*i.e.* <5, 5-10,10-15, 15-20, 20-25, 25-50, >50 cm) (Alvarado et al., 2016) and the average value of the range was calculated to be included in subsequent analyses. The transect area vary between 40 and 500 m^2, and between 1 and 30 m depth (Supp.mat. Table S1). The survey was done visually estimating fish size as total body length by scuba diving. These data were provided by the ETP Node of the Global Coral Reef Monitoring Network (GCRMN; Supp.mat. Table S2). From the recorded fish community, herbivorous fish were selected based on their recorded feeding pattern in Fishbase (Froese & Pauly, 2019). This selection was reviewed by experts, and as a result 25 herbivorous species (eight different families) of the total of 286 registered species was documented (Supp.mat. Table S3, Fig. 2A).

The fish biomass was calculated using an allometric length-weight conversion according to the following equation: $\mathbf{w = a * TL^b}$ (Froese et al., 2011); where **w** is the weight (g), **a** and **b** are specific constants for each species and **TL** is the total length (cm) determined in the size categories on the visual census. Subsequently, the biomass per unit area was estimated by dividing **w** by the area (m^2) of the given transect. I extracted parameters **a** and **b** from FishBase (Froese & Pauly, 2019). In cases where a species was not found in that database, I used the coefficients from a morphologically similar congeneric species (Quimbayo et al., 2021).

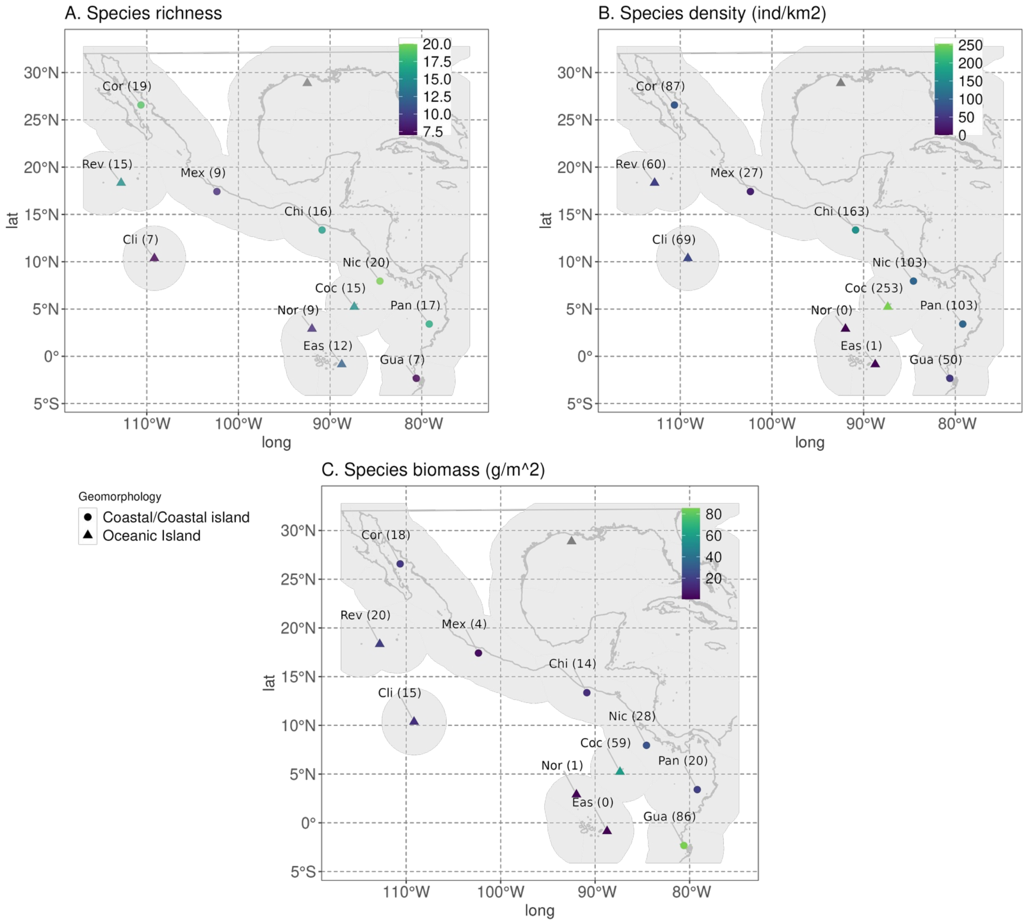


Figure 2. (A) Species richness, (B) mean density (ind/km^2), and (C) mean biomass (g/m^2) of herbivorous fish for each ecoregion in the Eastern Tropical Pacific (bounded in by gray polygons). Cortezian (Cor), Revillagigedos (Rev), Mexican Tropical Pacific (Mex), Chiapas Nicaragua (Chi), Clipperton (Cli), Nicoya (Nic), Isla del Coco (Coc), Panama Bay (Pan), Guayaquil (Gua), Northern Galapagos Islands (Nor), Eastern Galapagos Islands (Eas). The oceanic ecoregions are represented with triangles, and the coastal ones (including coastal islands) with circles, each are colored proportional to the value in parentheses.

Environmental and anthropic pressure characterization

To characterize the environment of the communities, I include the abiotic variables, the degree of anthropic pressure and the level of protection. These were considered because the biophysical variables are key to fish physiological aspects (Floeter et al., 2005). Likewise, given the relative fidelity to the site of the group (Mumby & Wabnitz, 2002), communities are likely to be vulnerable to fishing and habitat destruction and to be affected by the level of protection.

Biophysical conditions

I compiled data of SST and PP (chl-*a* reflectance) from the NASA Ocean Biology Processing Group (2017) (data were collected at 4-km resolution by the NASA Ocean Biogeochemical Model -NOBM- Data Version 2018, which provides monthly mean values for the years 2008 to 2019; https://oceancolor.gsfc.nasa.gov/data/10.5067/AQUA/MODIS/L3M/CHL/2018/). I extracted monthly SST and chl-*a* for the four months prior to each data collection and calculated the range of variation (max – min) (hereafter SST).

Degree of anthropic pressure

Human density has been considered one of the best indicators of anthropic impact, since it has a direct effect on the increase in the exploitation of ecosystems, an increase in disturbances and CO_2 emissions, which causes a degradation of the environment and, in turn a decrease in biodiversity (Forester & Machlist, 1996; Mora, 2008). Given its importance, I used the human population density (number of persons per km^2) for the year 2015 to estimate the effect of human impact on reef fish herbivores communities. The data was estimated on national censuses and population registers with respect to relative spatial distribution population density. This information was obtained from the Center for International Earth Science Information Network (http://www.ciesin.org; (CIESIN, 2018). Additionally, to evaluate the possible effect of anthropic pressure on herbivorous fish communities, I used the gravity index (Cinner et al., 2016). This index assumes that the anthropic pressure increases as the human population in the surrounding settlements increases, but decreases with the distance at which they are located (Cinner et al., 2016). I calculated the average human population density of each settlement around each site in a radius of 10, 50, 100 and 250 km, weighted by the distance from the settlement to the monitoring point. The value of gravity with a radius of 10 km was kept for the analyses, since it preserves most information with the highest Pearson product-moment correlations with the other radius evaluated (r(d.f. =285) ≥ 0.50, $p < 0.001$).

Protection level

To evaluate the effect of the protection level on the herbivory fish biomass and composition, I used the number of years each site has been under protection management as a proxy for protection (Parravicini et al., 2014). As a source of information, I used the World Database on Protected Areas (https://www.iucn.org/theme/protected-areas/our-work/world-database-protected-area; (UNEP-WCMC & IUCN, 2020).

Functional traits and indices of functional diversity

All fish species observed through UVCs were classified into six functional traits (morphological -a-, behavioral -b, c, d, e-, and diet traits -f-; Supp.mat. Table S3) defined by Mouillot et al. (2014), Bejarano et al. (2019), and Quimbayo et al. (2021): (a) the log of maximum body size; (b) home range (sedentary, mobile, and wide-ranging); (c) feeding territoriality (yes or no); (d) schooling (solitary, in pairs, small groups from 3 to 20 individuals, medium groups from 20 to 50 individuals, or large groups of more than 50 individuals); (e) trophic-functional group (brushers, grazer/croppers/concealed surface, grazer/croppers/sand suckers, grazer/croppers/open surface, grazer/scrapers, grazer/excavators, browsers, shearer) (Bellwood et al., 2019); (f) trophic group of primary consumers (herbivores-detritivores, macroalgae and seagrasses or omnivores) (Mouillot et al., 2014; Quimbayo et al., 2021). In the case of trophic-functional group the criteria of experts was used to categorize the species according to the classification criteria of Bellwood et al., (2019).

Considering all fish species traits, I built a Gower dissimilarity matrix with the daisy function of the cluster R package (Maechler et al., 2021), which allows including categorical and numerical variables as species traits (Gower, 1971). From this matrix, I performed a Principal Coordinate Analysis (PCoA) (Gower, 1966) with the cmdscale function of the stats package (R Core Team, 2020). This technique allows the generation of new uncorrelated dimensions that can be use to calculate the diversity indices (Villéger et al., 2008) according to the contribution of the traits to these dimensions.

I used three indices of functional diversity to evaluate multiple functional traits considering the abundance of the species: FDis, FDiv and FEve. The indices were computed with a customized version of the multidimFD function described in Mouillot et al. (2013). In addition, I calculated taxonomic distinctness (Dstar) using the taxondive function from the vegan package (Oksanen et al., 2020).

Functional diversity analysis

The sample coverage is a measure of the number of species of the community that are represented in the sample taken (Chao & Jost, 2012), to have a sampling quality standard. I only included in the analysis sites with sample coverage (Chao & Jost, 2012) greater than 0.95. The value was calculated using the iNEXT function of the iNEXT package (Hsieh et al., 2022). Due to the large differences in the total area surveyed per site, I selected a sample of each site of standard size to perform the diversity calculations. I randomly selected combinations of transects that added a similar value (henceforth called “target area”), allowing a margin of variation (henceforth called “buffer”). I define the target area and buffer with the best performance as those optimizing the following parameters: (a) a higher proportion of sampled area; (b) a higher number of transects; (c) making use of the larger number of sites and localities and (d) lower transect overrepresentation. Transect overrepresentation is an index that quantifies how balanced is the representation of each transect across several transect samples, in which high values represent unbalance representation of transects. Those combinations with high overrepresentation were excluded so that the most represented transects are found no more than twice as often as the least represented transects.

Based on these criteria, I used a target area of 300 m² with a buffer of 45 m² (Supp.mat. Table S1). Considering these selection parameters, 265 sites were retained, after removing sites with low sample coverage. We applied a bootstrap subsampling routine in order to account for the uncertainty in selecting different (random) combinations of transects for calculating diversity indices. For each site the routine produce 100 combinations of transects that reached the target area, with a variable number of transects. Each combination of transects appears only once, but a given transect could be included in several combinations. I calculated functional indices FDis, FDiv, FEve and taxonomic distinctness (Dstar) for each combination of transects and averaged them to obtain a single value for the site. This procedure was iterated 100 times. The presence of each trait was weighted by the biomass of the individuals. Weighted biomass makes it possible to observe both the presence of the traits and to approximate the magnitude in which it is expressed given the size of the individuals (Pombo Ayora et al., 2020).

Subsequently, the combinations of transects with less than four species, the minimum required for estimating diversity indices, were excluded. Some sites had very low species richness, so many of their transects were left out of the analysis. This variation in richness between sites means that the proportion of random transects that were excluded varies significantly among sites. Hence, I estimated the sites with the highest proportion of samples excluded and excluded the same proportion from all sites. This correction is made so that there is no over-representation of the richest sites and under-representation of those with few species. Hence, to avoid having sites with a low number of species artificially select those transects with higher diversity, the same proportion of lowest species number combinations were excluded from all sites.

It is important to mention that I was unable to estimate the diversity indices for three ecoregions (Mexican Tropical Pacific, Guayaquil and Northern Galapagos Islands; Fig. 3), given that the transects at those sites did not met at least one of the following conditions: (1) the sample coverage was less than 0.95, (2) the sampled areas could not be combined to generate a value within the range of the target area (300 ± 45 m^2; described below), in some cases because they had a smaller total area or because the area of the transects exceeded the range of target areas, or (3) did not have the number of herbivorous species necessary to calculate the functional indices (at least 4).

Statistical analysis

I evaluated the effect of biophysical and anthropic parameters on the functional diversity indices and taxonomic distinctness. Since the biophysical variables of SST and primary productivity (*i.e.,* the concentration of chl-*a;* PP) have a temporal resolution at the month level and the rest of the parameters have a value per site, I assigned to the combination the average range of variation of temperature and PP of the transects, weighted by the area that each date contributed.

I evaluate the collinearity between the environmental factors, as well as the collinearity between the functional diversity indices using the cor function of stats package (R Core Team, 2020). The predictors were plotted to observe relationships between them (Fig. S1). I conducted three regression models for each index FDis, FEve, FDiv and taxonomic distinctness. The first with all the environmental and anthropic variables (*i.e.* range of variation of SST and PP, geomorphology, gravity, and protection time). The second only with the anthropic variables (*i.e.* gravity and years of protection) and the third only with the environmental variables (*i.e.* range of variation of SST, PP and the categorical variable geomorphology). The models were grouped according to the type of predictor, prioritizing the computational capacity in the number of iterations instead of using all of them in the same model with fewer repetitions given the computational requirements of the process. All models included site as a random factor (varying intercept) to control pseudoreplication. I performed the analysis using mixed effect Bayesian regression in the brms R package (Bürkner, 2017). Continuous predictors were transformed to unit variance and zero-centered to control for differences in magnitude and measurement between them, and to improve model mixing. A beta distribution was used as link function for all models. One effect was considered significant when the posterior high-density interval (95% credibility) does not intersect zero. Bayesian leave-one-out information criterion (LOOIC) (Vehtari et al., 2017) was used to compare the fit of all models to the data. Since neither model was substantially better, model averaging was performed to calculate parameter estimates weighted by LOOIC weights (*i.e.* the relative support of each model).

The models were run in two chains of 50,000 iterations, in which the first half

(25,000) were used as 'warm-up'. I evaluate model convergence with the potential scale reduction factor (kept below 1.05 for all parameter estimates), where values less than 1.05 were considered to have adequate convergence. The effective sample size was kept above 300 for all parameters (Vehtari et al., 2021).

Finally, to assess whether certain environmental conditions represent a filter for some traits in the different ecoregions, the community weighted mean (CWM) of the functional traits was calculated. CWM allows knowing the dominant traits in a community (Ricotta & Moretti, 2011). If we assume that the most abundant traits are those that more strongly influence ecosystem processes (Grime, 1998), CWM differences can give valuable information regarding possible processes that differ between ecoregions. For this estimation, the data were then standardized using the Hellinger method (Legendre & Gallagher, 2001) and a multiple factor analysis (MFA) was performed using the MFA R function (Le et al., 2008). The first two dimensions of the MFA were used to quantify the pairwise similarities of the ecoregion sites, using the space_similarity function from the R package PhenotypeSpace (Araya Salas & Odom, 2022). The proportional overlap was used to quantify the similarity. That is, the overlapped area between each pair of ecoregions divided by the combined area of the two ecoregions (Araya Salas & Odom, 2022). All analysis and graphics were implemented in the R platform version 4.2.1 (R Core Team, 2020)

3. Results

Distribution patterns of species richness, density, and biomass of herbivorous fishes

I found 25 herbivorous fishes belonging to eight families (Supp.mat. Table S3). The maximum richness found in an ecoregion is 20 species, the mean biomass reaches up to 85.57 g/m² as density's maximum value was 250 ind/km² (Fig. 2). Nicoya and Cortezian ecoregions were the richest with 20 and 19 species, followed by Panama Bight (17), Chiapas-Nicaragua (16), Revillagigedos and Isla del Coco (15), Eastern Galapagos Islands (12), Northern Galapagos Islands and Mexican Tropical Pacific (9), Clipperton and

Guayaquil (7) (Fig. 2A). The species are distributed in 18 functional groups. Functional diversity indices showed a similar distribution in all ecoregions and different geomorphologies (Fig. 3).

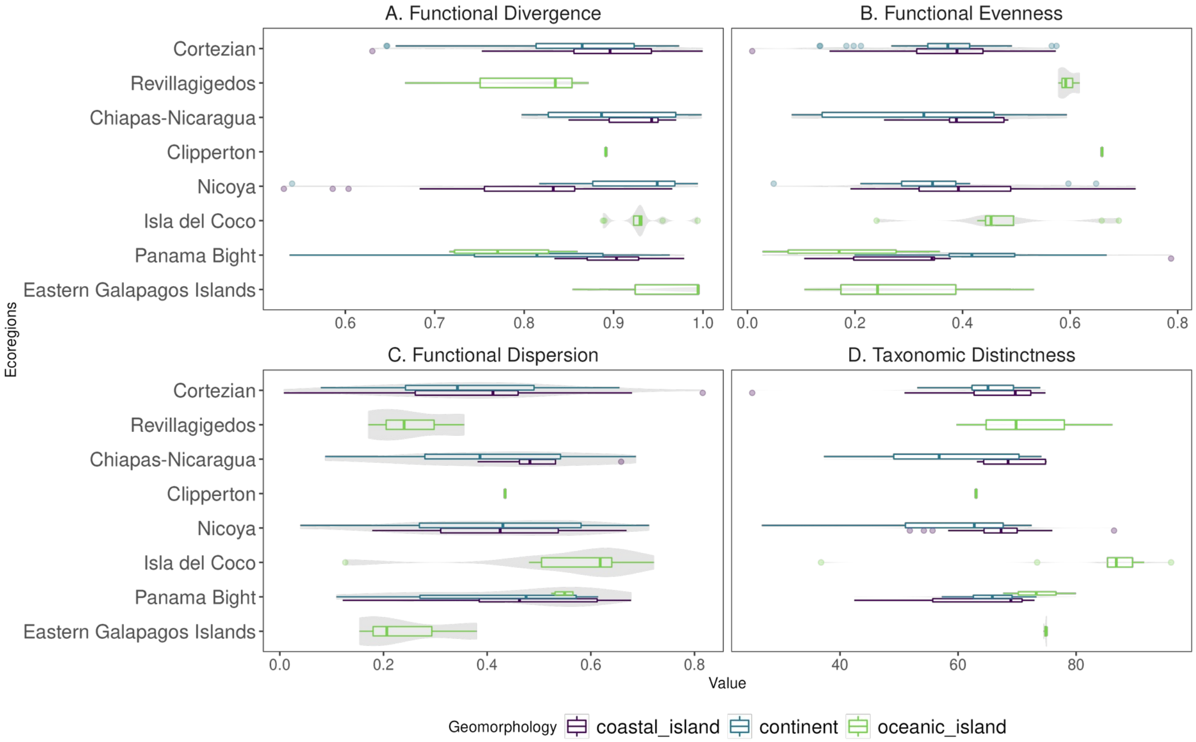


Figure 3. Indices of functional diversity and taxonomic distinctness, of the herbivorous fish communities in the Eastern Tropical Pacific, according to their ecoregion (sorted by latitude). The colored box plots represent the different geomorphologies.

Effect of environmental and anthropic variables on diversity

Collinearity was tested between predictors and was 0.5 or less in all cases (Fig. 4A) and less than 0.46 between diversity indices and taxonomic distinctness (Fig. 4B). SST negatively influence FDiv and taxonomic distinctness (Figs. 5B and 5D). PP has a positive effect on FDiv, FEve and taxonomic distinctness (Figs. 5B, 5C and 5D). Taxonomic distinctness is higher in oceanic islands compared to coastal sites (Fig. 5D). Human gravity is a positive driver for FDiv, but its effect is negative on FEve (Figs. 5B and 5C). I did not observe any effect of the abiotic and anthropic variables on FDis and protection time was not significant for any response variable (Fig. 5).

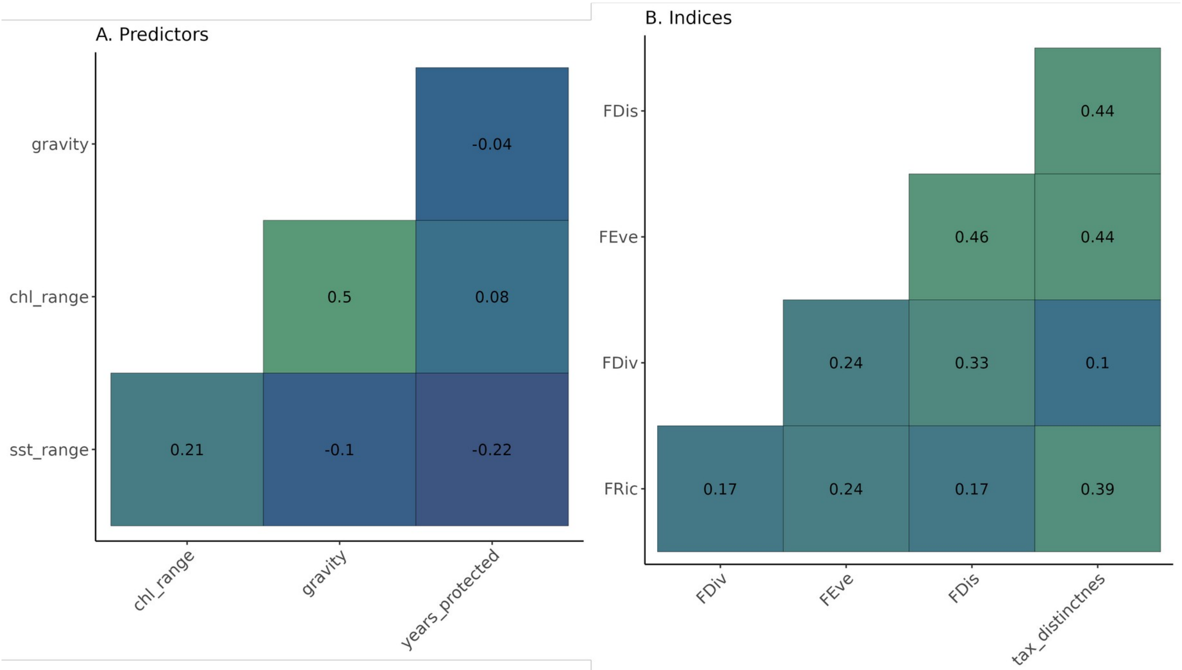


Figure 4: Maximum collinearity observed in 100 transect combinations of herbivorous reef fishes in the Eastern Tropical Pacific. A. Collinearity between environmental predictors and B. Collinearity between indices of functional diversity and taxonomic distinctness.

Grouping of ecoregions according to their functional traits

The multiple factor analysis (MFA) of the community weighted mean (CWM) explained totaled 100% of variance, with 43.35% on the first axis, 17.53% on the second, and 12.06% on the third (Fig. 6). When comparing between ecoregions, the functional traits that represent most of the variance for the first dimension are home range, territoriality, schooling and diet (Fig. S4). A relationship between omnivorous diet, sedentary home range and territoriality was also found (Fig. 6). Likewise, larger species are usually non-territorial (Fig. 6).

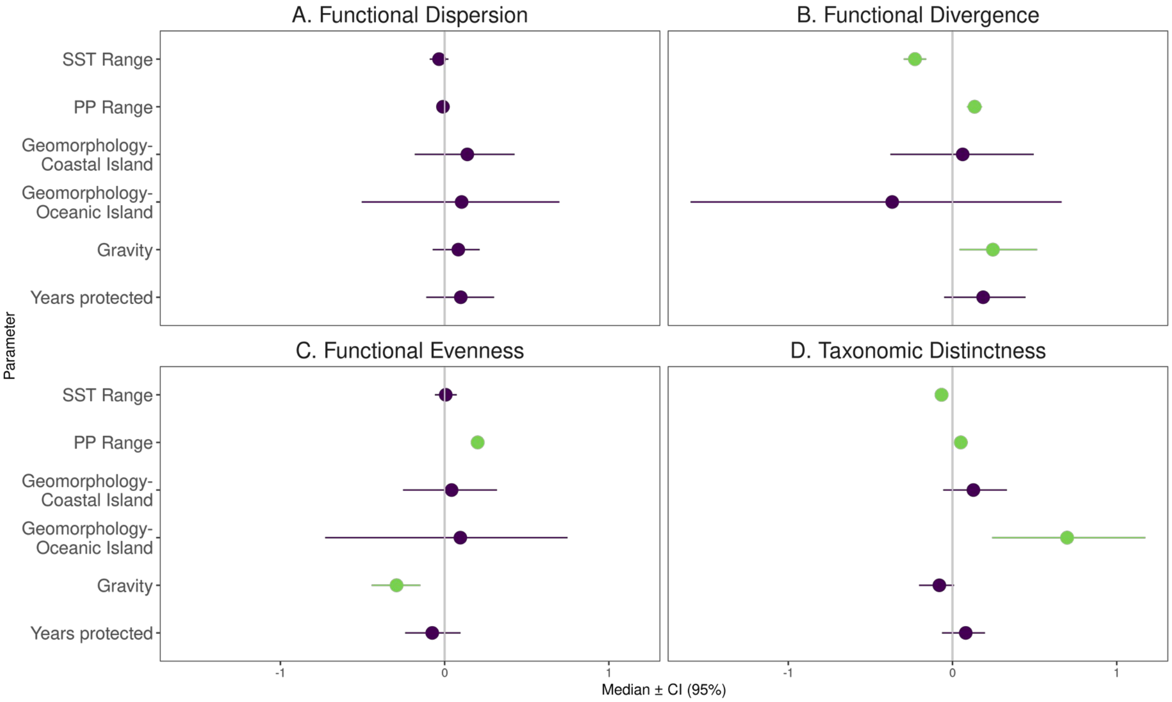


Figure 5: Effect (median ± 95% credibility interval; CI) of environmental conditions: sea surface temperature variation range (SST Range), primary productivity variation range (PP Range), geomorphology and anthropogenic conditions: years of protection (Years protected) and human gravity (Gravity) on the indices of functional diversity and taxonomic distinctness of herbivorous reef fish communities in the Eastern Tropical Pacific. Significant variables in green.

Most of the ecoregions overlap in the MFA of the functional traits (Fig. 7). The most similar ecoregions are the three Central American ones (Fig. 8): Chiapas-Nicaragua and Nicoya with 0.81 overlapping area, Chiapas-Nicaragua and Panama Bight with 0.65, and Nicoya and Panama Bight with 0.64 (Fig. 8). Cortezian is most similar to Panama, Chiapas-Nicaragua, Nicoya and Revillagigedos (overlapping areas are 0.42, 0.41, 0.37 and 0.23 respectively). Revillagigedos overlaps with Panama Bight, Chiapas-Nicaragua, Cortezian, Nicoya and Isla del Coco (overlapping areas of 0.36, 0.26, 0.23, 0.22 and 0.01 respectively) (Fig. 8). Isla del Coco overlap to a small extent with Nicoya, Chiapas-Nicaragua, Panama Bight and Revillagigedos (overlapping areas are 0.13, 0.11, 0.06 and 0.01, respectively). Guayaquil overlaps in a smaller area with Cortezian, Nicoya, Chiapas-Nicaragua, Panama Bight and Eastern Galapagos Islands (overlapping areas are 0.25, 0.20, 0.18, 0.17 and 0.02, respectively). Eastern Galapagos Islands have a small overlap with Guayaquil (0.02) and with Cortezian (0.01) (Fig. 8).

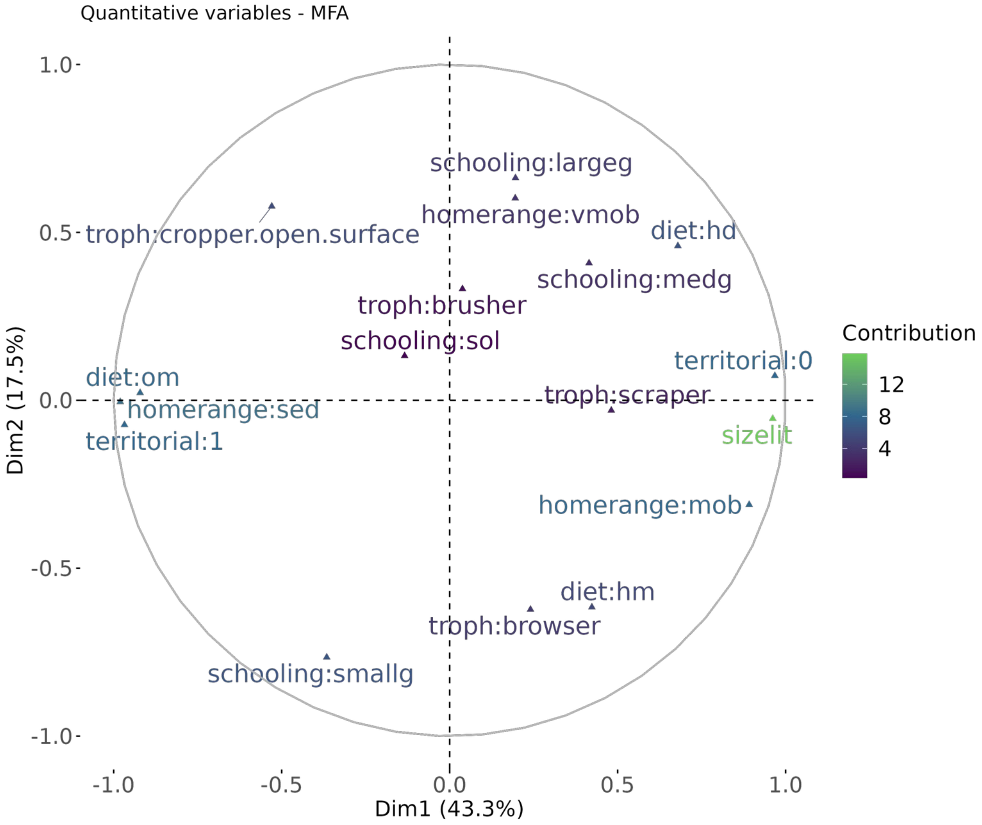


Figure 6. Contribution of each trait to the Multiple Factor Analysis for the community weighted mean (CWM) values of functional traits of herbivorous reef fishes in the Eastern Tropical Pacific. Maximum body size reported in literature with a logarithmic transformation (sizelit); home range: sedentary (sed), mobile (mob), and very mobile (vmob); feeding territoriality: yes (1) or no (0); schooling: solitary (sol), small groups (smallg), medium groups (medg), or large groups (largeg); trophic group: brushers (brusher), grazer croppers in open surface (cropper.open.surface), grazer scrapers (scraper), browsers (browser); trophic group of primary consumers (diet): herbivores-detritivores (hd), macroalgae and seagrasses (hm) or omnivores (om).

4. Discussion

The mechanisms to choose protection and management strategies to protect ecosystem functions and values, usually recognize diversity in terms of species richness, sometimes considering their abundances or biomass (Darling et al., 2019). However, high species richness should not be understood as an insurance for diversity in all cases (Parravicini et al., 2014). For instance, in coral reefs with a high species richness at the Central Indo-Pacific, one-third of the functions are performed by only one species (Mouillot et al., 2014). These vulnerable functions can disappear in the face of disturbances that affect the species that perform them (Hooper et al., 2005). For this reason, observing how functions change, as an indicator of diversity, provide information on the robustness of key processes in groups such as herbivores, associated with various ecosystem services. The approach I used, from the trophic group point of view, has rarely been evaluated and improve the understanding of the dynamics in which they are involved. By using a data set that encompasses a wide latitudinal gradient and most of the sites with significant reef development in the region, we can get an idea of the community trends over the past decade.

Distribution patterns of species richness, density, and biomass of herbivorous fishes

I found that herbivores represent 9% of the surveyed fish community. The ecoregions that presented the greatest herbivores richness (Nicoya and Cortezian) accounted for 7% (20 of the 289 total species). The high species richness observed in the Nicoya and Cortezian ecoregions is consistent with previous reports (Cortés et al., 2017; Robertson & Cramer, 2009). This trend responds to the fact that the Panama region was the last to have migration of Caribbean species prior to the emergence of the Central American isthmus that separated both oceans (Robertson & Cramer, 2009). This process is usually responsible for the high species richness and affinity that marine faunas have in this geographical space (Dana, 1975). This historical process, in conjunction with oceanographic conditions such as the present upwelling zone and the great discharge of rivers (Glynn, 2001), can be related to the productivity and richness of herbivores observed. In this Nicoya's region endemism is high in worldwide comparisons (Miloslavich et al., 2011) and provides a high number of endemic species for the ETP (Robertson, 2009).

Although herbivore species richness tends to decrease with latitude globally (Floeter et al., 2005), the results follow this pattern only in the continental ecoregions (Fig. 2B).

Two ecoregions deviate from this pattern, the Galapagos ecoregion with very few species and the Cortezian ecoregion with the highest richness. This can be because the Cortezian ecoregion encompasses different reef fish faunas. In the south, the sites have tropical fauna, while in the interior of the Gulf of California are organisms transitioning to subtropical zones (Robertson & Cramer, 2009). The differences on the pattern between these two ecoregions could be a combination of multiple conditions associated with the type of environment such as connectivity, structural complexity and algae palatability (Puk et al., 2016). Supporting the predictions, the oceanic islands and Guayaquil (represented by Gorgona) have less species richness than the continental regions (Robertson & Cramer, 2009).

Isla del Coco has more than twice the herbivorous density and biomass of the rest (Fig. 2B), a pattern that could be associated with having a high level of protection and no fishing access (Alvarado et al., 2016; Fourriére et al., 2017). The fish communities of Isla del Coco are subject to a high top-down control since it has a high abundance of top predators (Alvarado et al., 2016), which may be generating a positive cascading effect for herbivores. Finally, Guayaquil (Gorgona), despite presenting the lowest values of richness and density, has the highest average biomass (Fig. 2). This relationship may be associated with the fact that the biomass of browsers and large excavators may benefit from the geomorphologies of low islands (carbonate) and atoll geomorphologies (Heenan et al., 2016). Associated with the fact that the presence of the lagoon habitat, generating a structural complexity that allows shelter for large body size organisms (Heenan et al., 2016).

Effect of environmental variables on diversity

The ETP has been considered as one of the three poorest regions in terms of tropical reef fishes diversity in global comparisons and with low functional redundancy with 2.8 species for each combination of functional traits (Mouillot et al., 2014). However, the low number of species probably, as in the richer regions, encompasses the key functional space to sustain the development of tropical reefs (Mouillot et al., 2014). The herbivore community usually has low functional redundancy due to their close dependence on the substrate (Bender et al., 2017) and the ETP behaves in a concordant way. The 25 species perform 18 different functions on the reef (in average 1.4 species with each combination of traits). I observed that environmental conditions, both SST and PP, as well as anthropic pressure, are related to some of the facets of functional diversity (*i.e.* taxonomic distinctness, FEve and FDiv), except to FDis which was not related to any parameter. This suggests that, regardless of the fact that the volume of the functional space (represented by FDis) does not vary significantly depending on the predictors, there are differences in the other dimensions of functional diversity. In other words, the distribution of the functions within that volume and the abundance in which each one is represented, show differences in the functional diversity of the herbivore community. This demonstrates the importance of evaluating the different facets of functional diversity beyond counting species and functions as a gross measure.

There is evidence that temperature limits the distribution of herbivorous fish (Heenan et al., 2016), through physiological mechanisms associated with feeding and digestion (Floeter et al., 2005) in the ETP (Robertson & Cramer, 2009). Several factors have been proposed to explain the association of the herbivorous fish communitiy with warm temperatures (above 20°C) according to Floeter et al. (2005): (1) The time of evolution of the group, (2) availability of food due to seasonal variation, (3) qualities of the available algae, or (4) adaptations of behavior, phylogeny and biogeography to consume the algae abundant but with low energy content. The availability of food and shelter is related to changes in SST as well. Canopy biomass production of some canopy-forming genera in the Indo-Pacific and Red Sea is sensitive to both mean SST and annual SST variation range (Fulton et al., 2019). For example, *Laurencia* spp. and *Lobophora* spp. grow in intermediate SST values and *Sargassum* spp. decrease towards extreme values (Fulton et al., 2019).

In the ETP the negative effect of SST variation on functional divergence indicates that in sites where SST varies widely, the most abundant functional groups are around the mean values of the distribution and the least abundant are those with specialized traits (Mason et al., 2005). In the same way, when the variation in SST is wide, species are taxonomically alike. This suggests that temperature works as an environmental filter according to the niche filtering hypothesis (Zobel, 1997) compacting the traits of herbivorous species in a similar environment. In environments dominated by macroalgae (not turf) grazing might depend more on changes in temperature than on algae composition, but this requires further experimental investigation (Robinson et al., 2018). This trend is of great relevance because the increase in ecological trait divergence may favor the shift from the coral-dominated to the algae-dominated habitat (Pombo Ayora et al., 2020).

PP in terms of chl-*a* was the predictor related to the variation of most indices, and behaves in the opposite direction to temperature. When the variation in PP increases, the most different functional traits are more abundant (high FDiv) and the species differ taxonomically (high taxonomic distinctness). At the same time, the abundance and distribution of functional groups are more uniform (high FEve), which usually implies that all the functional entities present are represented in a similar way, as in environments with low disturbance (Mouillot et al., 2013). Some rapid changes in chl-*a* are linked to nutrient inputs associated with favorable upwelling winds (Carr & Kearns, 2003; T. B. Smith, 2005), La Niña effect, thermocline shoaling (T. B. Smith et al., 2010) and eutrophication (J. E. Smith et al., 2005). In the ETP, some of the seasonal upwelling zones are found in the Gulfs of Tehuantepec, Papagayo, Panama (Kessler et al., 2003; Xie et al., 2005) and the Peruvian coastal upwelling ecosystem (Tarazona & Arntz, 2001). Increased nutrients may result in increased growth of macroalgae (Littler et al., 1991; Schaffelke & Klumpp, 1998; T. B. Smith et al., 2010). This increase represents greater food availability, suggesting that the herbivore community could benefit (Glynn, 2004).

Taxonomic groups on the oceanic islands of the ETP are more distant from each other compared to those on the mainland, as reported before (Robertson & Cramer, 2009). In isolated areas, diversity is usually given by organisms that colonize, adapting and evolving as new species but that does not usually migrate expanding their range of distribution (Bowen et al., 2013; Cowman et al., 2017; Mazzei et al., 2021; Pinheiro et al., 2017). As in these environments migration is limited, speciation remains as the predominant mechanism (Pinheiro et al., 2017). Differences associated with traits such as the ability to swim great distances, have a non-specific diet (Luiz et al., 2012), body size, home range and mobility (Robertson et al., 2004) are usually determining factors in the prevalence of species (Bender et al., 2017). The high taxonomic distinctness due to the isolation of oceanic islands may be linked to a low functional redundancy, which would represent a greater vulnerability to disturbances that drastically change the functions represented (Bender et al., 2017).

Human density has been a driver that negatively affects diversity, density and biomass of reef fish assemblages (McClanahan & Muthiga, 2017) through stressors such as fishing, coastal development, and land use (Mora et al., 2011). Human activities represent a pressure on certain functional traits, favoring, in this case, that the biomass is concentrated in the traits at the extremes values (high FDiv) but leaving some traits poorly represented (low FEve). The negative relationship between anthropic impact and FEve was previously studied (Mouillot et al., 2013). Changes in FDiv are considered early indicators of a disturbed community because they show changes in the early stages (Mouillot et al., 2013). This index decreases in communities exposed to pressures because specialist species decrease in abundance earlier as they are more vulnerable to disturbances (Mouillot et al., 2013) and has been related to sites with low disturbances (Villéger et al., 2010), different from our results where human gravity is a positive driver for FDiv.

Although protection over time can buffer the loss of diversity by compensating for the mechanisms that make a community vulnerable (Mouillot et al., 2013; Parravicini et al., 2013), it is not always possible to observe their results on the diversity parameters (Mora et al., 2011). One possible reason is that the effectiveness of the protection is determined by small-scale conditions associated with the social and politic/economic aspects (Alvarado et al., 2017; Arias et al., 2015). Likewise, the effect of protection on the chain reaction of predators-mesopredators-herbivores is in a dynamism that can conceal temporal patterns (Ruppert et al., 2013) outside the scope of the study. In addition to the environmental variables considered in this study, it is convenient to include in future research the structural complexity of the reefs, since it can be related to the diversity of functions (Richardson et al., 2017) and describe the small scale environmental conditions in as much detail as possible (Laughlin & Messier, 2015).

Grouping of ecoregions according to their functional traits

Given the threats caused by climate change, modifications are expected in the capacity of reefs to host the diversity that sustains key ecosystem processes and services (Fulton et al., 2019). Knowing the relationships between environmental conditions and the distribution of morphological or behavioral traits, provides information to predict which populations and to what extent the changes may occur. The CWM analysis is based on the premise that the species found in greater abundance are those that mainly determine the processes in the ecosystem (Grime, 1998; Mokany et al., 2008). Each trait perceives pressures by different mechanisms, so that the most abundant traits in the different ecoregions can dilute similarities in the pressures they perceive (Ricotta & Moretti, 2011) and in the resistance to future changes. By indicating the predominant traits in a community, it gives an idea about the functions that could be presented.

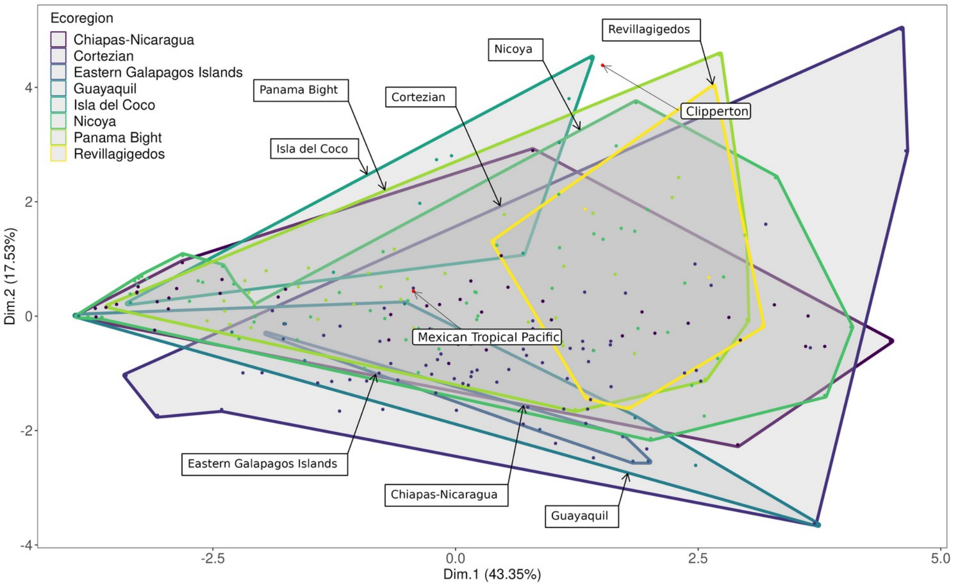
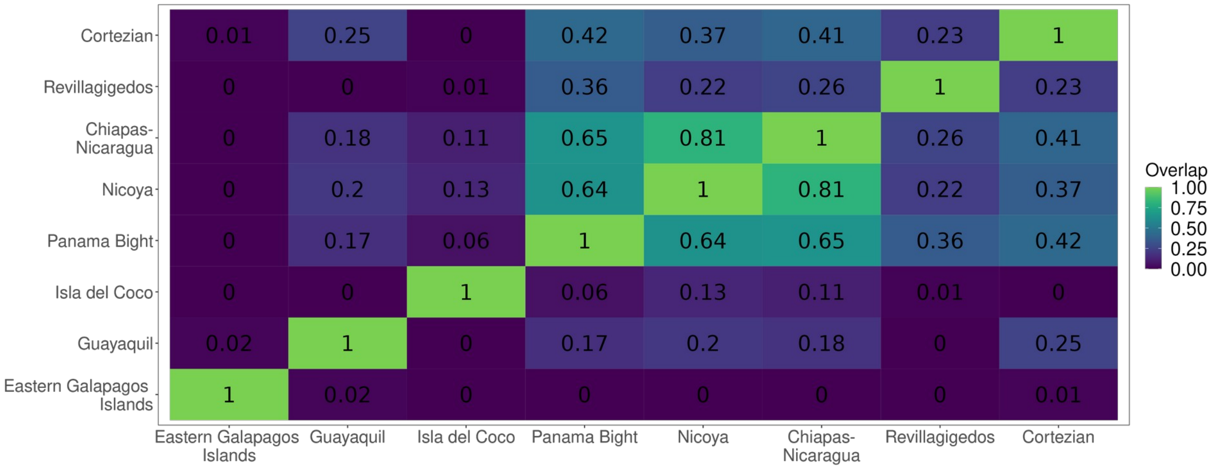


Figure 7. Distribution of the CWM-MFA Individuals (Dim1 and Dim2) of each site (dots) according to ecoregions (convex hull). Ecoregions with only one site are represented by the labeled red dots.

The functional traits with the CWM most variation in our study are home range, territoriality, and schooling, which could be suggesting a pattern, like that previously reported, associated with access to fishing. In the study made by Edwards et al. (2013) the biomass of most herbivores (*i.e.* scraper/excavators, browsers and grazer/detritivores) that are mobile, with schooling and non-territorial, was about half at fished sites, but abundance did not change. Conversely, both biomass and abundance of territorial damselfish (sedentary, small-body size, and territorial) were significantly greater at sites accessible to fishing (Edwards et al., 2013). So that species with these traits can benefit in places with fishing pressure (Dulvy et al., 2004) and could be generating differences in our region. If this pattern reflects an advantage over sites where there is low competition due to fishing, could be evaluated in future studies.



	Eastern Galapagos Islands	Guayaquil	Isla del Coco	Panama Bight	Nicoya	Chiapas-Nicaragua	Revillagigedos	Cortezian
Cortezian	0.01	0.25	0	0.42	0.37	0.41	0.23	1
Revillagigedos	0	0	0.01	0.36	0.22	0.26	1	0.23
Chiapas-Nicaragua	0	0.18	0.11	0.65	0.81	1	0.26	0.41
Nicoya	0	0.2	0.13	0.64	1	0.81	0.22	0.37
Panama Bight	0	0.17	0.06	1	0.64	0.65	0.36	0.42
Isla del Coco	0	0	1	0.06	0.13	0.11	0.01	0
Guayaquil	0.02	1	0	0.17	0.2	0.18	0	0.25
Eastern Galapagos Islands	1	0.02	0	0	0	0	0	0.01

Figure 8. Proportional overlap between the ecoregions (sorted by latitude). Described by the first two dimensions of the MFA from the CWM of each site.

The differences given by home range and territoriality reflect a selection in terms of mobility patterns. Species' movement determine how they perform their functions, such as herbivory or other ecological services (Owen Smith et al., 2010). Those with greater mobility (*i.e.* non-territorial and with a wider home range), responsible for transporting nutrients and energy over long distances, are increasingly limited. This may respond to the fact that in tropical fish the home range has been characterized as being small (Floeter et al., 2013). There is also a relationship between home range and body size. In some cases up to 76% of the variability in the home range data can be explained by the body mass of the fish (Nash et al., 2013; Welsh et al., 2013). So given this relation, if there is an increasing selection for smaller body sizes, home range may be reduced. This trend must be considered because the greater the range of spatial scales in which herbivores operate, there may be better recovery to a state dominated by corals in the face of disturbances caused by temperature (Nash et al., 2016).

The diet and feeding group can be determined by the availability of food, which is the result of the amount of energy available in the environment, as well as by the interspecific competition. Herbivores, regardless of their main source of nutrients (*i.e.*

detritus, macroalgae and seagrasses or omnivores), are adapted to take advantage of low energy content resources (Hay, 1991). It has been observed that this group tends to be more abundant at lower latitudes (Floeter et al., 2013) and the number of species and relative importance tend to decrease at high latitudes. This is probably associated with the type of algae predominant at lower latitudes (*i.e.* highly productive and diverse mats of small algae) (Harmelin Vivien, 2002). Our results stress the need to improve knowledge of the mechanisms that link environmental pressures with affected traits (McLean et al., 2019) at a local scale (Anthony et al., 2017; Muscarella & Uriarte, 2016). Knowing that diet is one of the traits that varies in ecoregions, probably linked to food availability, it is essential to monitor changes in benthic composition at a local level to improve predictions about changes in the herbivore community.

The large overlap in the distribution of functional traits of herbivores in the Chiapas-Nicaragua, Nicoya and Panama Bight regions results from the sum of environmental filters (*e.g.* food availability, temperature) and competition relationships in the community (Cadotte & Tucker, 2017; Zobel, 1997). This pattern is consistent with the entire fish community that has high affinity and endemism in these regions (Miloslavich et al., 2011). The peak of species richness is found in this area, due to the result of historical processes due to the shorter isolation time with the Caribbean Sea (Robertson & Cramer, 2009).

The traits in the insular regions have the lowest percentage of overlap in the ETP, which results from the characteristic distinctiveness of oceanic island reef fishes (Cortés et al., 2017). The regions with traits that resemble Revillagigedos the most, are located from Mexico to Panama. The most related to Isla del Coco are the surrounding regions on the Central American coast (Chiapas-Nicaragua, Nicoya and Panama). In Guayaquil (represented by Gorgona) the non-endemic resident reef fishes in previous works have been grouped by similarity to the oceanic islands of the ETP (Robertson & Cramer, 2009). This affinity is hardly reflected in our results with the functional traits of the herbivore community (Guayaquil - Gorgona and Galápagos overlap only by 0.02). Finally, the two ecoregions at the southern limit of the ETP (Guayaquil and Galapagos) have a small overlap with Cortezian. The Gorgona-Cortezian affinity suggests a similar feature selection at the edges of the region, probably associated with similar oceanographic conditions with temperature influences closer to subtropical environments (Robertson & Cramer, 2009).

5. Conclusions

Richness, density and biomass of the herbivore community vary within the region due to the interaction of small and large-scale conditions. The negative effect of SST variation on individuals that are taxonomically distinct or have specialized traits represents an early notification of the deterioration of processes that they sustain. On the other hand, the positive effect of PP variation may allow to sustain diverse functions and processes, fostered by high abundance of specialized traits and taxonomic diversity. Regarding anthropic pressure, the study confirms a negative effect on diversity because, even if it’s associated with the presence of specialized traits, it leaves some traits poorly represented. Anthropic pressure may also be related to the variation of home range, territoriality, and schooling in the ecoregions, but this needs to be evaluated in future research. For oceanic islands, the high taxonomic distinctness could be a warning of greater vulnerability to disturbances compared to coastal areas.

Functional diversity assessments can provide an early and detailed approximation of the functions that a community performs. It is important to periodically reassess the baseline of the species traits at the local level, as they may change as a result of interspecific pressures or small-scale conditions (Werner & Peacor, 2003). One of the main challenges on conducting regional collaborations is to compensate for the differences between sampling efforts. Our approach of selecting area-equivalent subsamples in multiple iterations manages to overcome uneven sampling making the most out of the data, but limits the computation of multiple predictors at once, due to hardware limitations. Finally, including non-fish herbivores, such as sea urchins, into future research is determinant to continue the understanding of primary consumer processes (McClanahan &

Muthiga, 2017). Our results warn about the vulnerability of the group in the ETP and underscore the importance of increasing conservation efforts with a focus on groups with specific functional traits. In order to optimize the protection of those who perform essential functions for the prevalence of reefs and their services.

6. References

Alvarado, J. J., Aburto-Oropeza, O., Abad, R., Barraza, E., Brandt, M., Cantera, J., Estrada, P., Gaymer, C. F., Guzmán-Mora, A. G., Herlan, J. J., & Maté, J. L. (2017). Coral reef conservation in the Eastern Tropical Pacific. In P. W. Glynn, D. P. Manzello, & I. C. Enochs (Eds.), *Coral Reefs of the Eastern Pacific: Persistence and Loss in a Dynamic Environment. Coral Reefs of the World 8.* (pp. 565–591). Springer Science+Business Media. https://doi.org/10.1007/978-94-017-7499-4

Alvarado, J. J., Beita-Jiménez, A., Mena, S., Fernández-García, C., Guzman-Mora, A. G., & Cortés, J. (2016). Ecosistemas coralinos del Parque Nacional Isla del Coco, Costa Rica: Estructura y comparación 1987-2014. *Revista de Biología Tropical*, *64*(1), 153. https://doi.org/10.15517/rbt.v64i1.23423

Anthony, K., Bay, L. K., Costanza, R., Firn, J., Gunn, J., Harrison, P., Heyward, A., Lundgren, P., Mead, D., Moore, T., Mumby, P. J., Oppen, M. J. H. V., Robertson, J., Runge, M. C., Suggett, D. J., Schaffelke, B., Wachenfeld, D., & Walshe, T. (2017). New interventions are needed to save coral reefs. *Nature Ecology & Evolution*, *1*(October), 1420–1422. https://doi.org/10.1038/s41559-017-0313-5

Araya Salas, M., & Odom, K. (2022). *PhenotypeSpace: And R package to quantify and compare phenotypic trait spaces*.

Arias, A., Cinner, J. E., Jones, R. E., & Pressey, R. L. (2015). Levels and drivers of fishers' compliance with marine protected areas. *Ecology and Society*, *20*(4). https://doi.org/10.5751/ES-07999-200419

Baker, A. C., Glynn, P. W., & Riegl, B. (2008). Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science*, *80*(4), 435–471. https://doi.org/10.1016/j.ecss.2008.09.003

Barneche, D. R., Floeter, S. R., Ceccarelli, D. M., Frensel, D. M. B., Dinslaken, D. F., Mário, H. F. S., & Ferreira, C. E. L. (2009). Feeding macroecology of territorial damselfishes (Perciformes: Pomacentridae). *Marine Biology*, *156*(3), 289–299. https://doi.org/10.1007/s00227-008-1083-z

Beita-Jiménez, A., Alvarado, J. J., Mena, S., & Guzmán-Mora, A. G. (2019). Benefits of protection on reef fish assemblages in a human impacted region in Costa Rica. *Ocean and Coastal Management*, *169*(December 2018), 165–170. https://doi.org/10.1016/j.ocecoaman.2018.12.023

Bejarano, S., Jouffray, J. B., Chollett, I., Allen, R., Roff, G., Marshell, A., Steneck, R. S., Ferse, S. C. A., & Mumby, P. J. (2017). The shape of success in a turbulent world: Wave exposure filtering of coral reef herbivory. *Functional Ecology*, *31*(6), 1312–1324. https://doi.org/10.1111/1365-2435.12828

Bejarano, S., Pardede, S., Campbell, S. J., Hoey, A. S., & Ferse, S. C. A. (2019). Herbivorous fish rise as a destructive fishing practice falls in an Indonesian marine national park. *Ecological Applications*, *29*(8). https://doi.org/10.1002/eap.1981

Bellwood, D. R., & Choat, J. H. (1990). A functional analysis of grazing in parrotfishes (family Scaridae): The ecological implications. *Environmental Biology of Fishes*, *28*(1–4), 189–214. https://doi.org/10.1007/BF00751035

Bellwood, D. R., Goatley, C. H. R., Khan, J. A., & Tebbett, S. B. (2016). Site fidelity and homing in juvenile rabbitfishes (Siganidae). *Coral Reefs*, *35*(4), 1151–1155. https://doi.org/10.1007/s00338-016-1466-4

Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, *429*(6994), 827–833. https://doi.org/10.1038/nature02691

Bellwood, D. R., Renema, W., & Rosen, B. R. (2012). Biodiversity hotspots, evolution and coral reef biogeography: A review. In *Biotic Evolution and Environmental Change in Southeast Asia* (pp. 216–245). https://doi.org/10.1017/cbo9780511735882.011

Bellwood, D. R., Streit, R. P., Brandl, S. J., & Tebbett, S. B. (2019). The meaning of the term 'function' in ecology: A coral reef perspective. *Functional Ecology*, *33*(6), 948–961. https://doi.org/10.1111/1365-2435.13265

Bender, M. G., Leprieur, F., Mouillot, D., Kulbicki, M., Parravicini, V., Pie, M. R., Barneche, D. R., Oliveira-Santos, L. G. R., & Floeter, S. R. (2017). Isolation drives taxonomic and functional nestedness in tropical reef fish faunas. *Ecography*, *40*(3), 425–435. https://doi.org/10.1111/ecog.02293

Bonaldo, R. M., & Bellwood, D. R. (2011). Parrotfish predation on massive *Porites* on the Great Barrier Reef. *Coral Reefs*, *30*(1), 259–269. https://doi.org/10.1007/s00338-010-0669-3

Bonaldo, R. M., Welsh, J. Q., & Bellwood, D. R. (2012). Spatial and temporal variation in coral predation by parrotfishes on the GBR: Evidence from an inshore reef. *Coral Reefs*, *31*(1), 263–272. https://doi.org/10.1007/s00338-011-0846-z

Bowen, B. W., Rocha, L. A., Toonen, R. J., & Karl, S. A. (2013). The origins of tropical marine biodiversity. *Trends in Ecology and Evolution*, *28*(6), 359–366. https://doi.org/10.1016/j.tree.2013.01.018

Burkepile, D. E., & Hay, M. E. (2008). Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(42), 16201–16206. https://doi.org/10.1073/pnas.0801946105

Bürkner, P.-C. (2017). *Stan, brms: An R Package for Bayesian Multilevel Models Using* (pp. 1–28). Journal of Statistical Software. https://doi.org/doi:10.18637/jss.v080.i01

Cadotte, M. W., & Tucker, C. M. (2017). Should environmental filtering be abandoned ? *Trends in Ecology & Evolution*, *32*(6), 429–437. https://doi.org/10.1016/j.tree.2017.03.004

Carpenter, R. C. (1986). Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs*, *56*(4), 345–364. https://doi.org/10.2307/1942551

Carr, M. E., & Kearns, E. J. (2003). Production regimes in four Eastern Boundary Current systems. *Deep-Sea Research Part II: Topical Studies in Oceanography*, *50*(22–26), 3199–3221. https://doi.org/10.1016/j.dsr2.2003.07.015

Ceccarelli, D. M., Jones, G. P., & McCook, L. J. (2001). Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. *Oceanography and Marine Biology: An Annual Review*, *39*(April 2014), 355–389. https://doi.org/10.1201/b12588

Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation: Standardizing samples by completeness rather than size. *Ecology*, *93*(12), 2533–2547. https://doi.org/10.1890/11-1952.1

Choat, J. H. (1992). The biology of herbivorous fishes on coral reefs. In P. F. Sale (Ed.), *The Ecology of Fishes on Coral Reefs* (pp. 120–155). Academic Press, INC.

CIESIN, C. U. (2018). *Gridded population of the world, version 4 (GPWv4) 2015. Columbia University, NY: Center for International Earth Science Information Network.* https://doi.org/10.7927/H45Q4T5F

Cinner, J. E., Huchery, C., MacNeil, M. A., Graham, N. A. J., McClanahan, T. R., Maina, J., Maire, E., Kittinger, J. N., Hicks, C. C., Mora, C., Allison, E. H., D'Agata, S., Hoey, A., Feary, D. A., Crowder, L., Williams, I. D., Kulbicki, M., Vigliola, L., Wantiez, L., … Mouillot, D. (2016). Bright spots among the world’s coral reefs. *Nature*, *535*, 416–419.

Clarke, K. R., & Warwick, R. M. (1998). A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology*, *35*, 523–531. https://doi.org/10.1046/j.1365-2664.1998.3540523.x

Coates, A. G., & Obando, J. A. (1996). The geological evolution of the Central American Isthmus. In J. B. C. Jackson, A. F. Budd, & A. G. Coates (Eds.), *Evolution and Environment in Tropical America* (pp. 21–56). The University of Chicago Press. https://cir.nii.ac.jp/crid/1571417124880570752.bib?lang=en

Connell, S. D., & Irving, A. D. (2008). Integrating ecology with biogeography using landscape characteristics: A case study of subtidal habitat across continental Australia. *Journal of Biogeography*, *35*(9), 1608–1621. https://doi.org/doi:10.1111/j.1365-2699.2008.01903.x

Cornwell, W. K., & Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, *79*(1), 109–126. https://doi.org/10.1890/07-1134.1

Cornwell, W. K., Schwilk, D. W., & Ackerly, D. D. (2006). A trait-based test for habitat filtering: Convex hull volume. *Ecology*, *87*(6), 1465–1471. https://doi.org/10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2

Cortés, J., Enochs, I. C., Sibaja Cordero, J., Hernández, L., Alvarado, J. J., Breedy, O., Cruz Barraza, J. A., Esquivel Garrote, O., Fernández García, C., Hermosillo, A., Kaiser, K. L., Medina Rosas, P., Morales Ramírez, Á., Pacheco, C., Pérez Matus, A., Reyes Bonilla, H., Riosmena Rodríguez, R., Sánchez Noguera, C., Wieters, E. A., & Zapata, F. A. (2017). Marine biodiversity of Eastern Tropical Pacific coral reefs. In

P. W. Glynn, D. P. Manzello, & I. C. Enochs (Eds.), *Coral Reefs of the Eastern Pacific: Persistence and Loss in a Dynamic Environment. Coral Reefs of the World 8.* (pp. 203–250). Springer Science+Business Media. https://doi.org/10.1007/978-94-017-7499-4

Cowman, P. F., Parravicini, V., Kulbicki, M., & Floeter, S. R. (2017). The biogeography of tropical reef fishes: Endemism and provinciality through time. *Biological Reviews*, *92*(4), 2112–2130. https://doi.org/10.1111/brv.12323

Dana, T. F. (1975). Development of contemporary Eastern Pacific coral reefs. *Marine Biology*, *33*(4), 355–374. https://doi.org/10.1007/BF00390574

Darling, E. S., McClanahan, T. R., Maina, J., & Gurney, G. G. (2019). *Social-environmental drivers inform strategic management of coral reefs in the Anthropocene*. https://doi.org/10.1038/s41559-019-0953-8

De´ath, G., & Fabricius, K. (2010). Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. *Ecological Applications*, *20*(3), 840–850. https://doi.org/10.1890/08-2023.1

DeMalach, N., Ke, P., & Fukami, T. (2021). The effects of ecological selection on species diversity and trait distribution: Predictions and an empirical test. *Ecology*, *0*(0), 1–9. https://doi.org/10.1002/ecy.3567

Downs, C. A., Woodley, C. M., Richmond, R. H., Lanning, L. L., & Owen, R. (2005). Shifting the paradigm of coral-reef health assessment. *Marine Pollution Bulletin*, *51*, 486–494. https://doi.org/10.1016/j.marpolbul.2005.06.028

Duffy, J. E., Lefcheck, J. S., Stuart-Smith, R. D., Navarrete, S. A., & Edgar, G. J. (2016). Biodiversity enhances reef fish biomass and resistance to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(22), 6230–6235. https://doi.org/10.1073/pnas.1524465113

Dulvy, N. K., Polunin, N. V. C., Mill, A. C., & Graham, N. A. J. (2004). Size structural change in lightly exploited coral reef fish communities: Evidence for weak indirect effects. *Canadian Journal of Fisheries and Aquatic Sciences*, *61*(3), 466–475. https://doi.org/10.1139/f03-169

Edwards, C. B., Friedlander, A. M., Green, A. G., Hardt, M. J., Sala, E., Sweatman, H. P., Williams, I. D., Zgliczynski, B. J., Sandin, S. A., & Smith, J. E. (2013). Global assessment of the status of coral reef herbivorous fishes: Evidence for fishing effects. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1774), 7–11. https://doi.org/10.1098/rspb.2013.1835

Eschmeyer, W. N., Fricke, R., Fong, J. D., & Polack, D. A. (2010). Marine fish diversity: History of knowledge and discovery (Pisces). *Zootaxa*, *2525*, 19–50. https://doi.org/10.11646/zootaxa.2525.1.2

Fischer, A. G. (1960). Latitudinal variations in organic diversity. *Evolution*, *14*, 64–81. https://doi.org/10.2307/2405923

Floeter, S. R., Behrens, M. D., Ferreira, C. E. L., Paddack, M. J., & Horn, M. H. (2005). Geographical gradients of marine herbivorous fishes: Patterns and processes. *Marine Biology*, *147*(6), 1435–1447. https://doi.org/10.1007/s00227-005-0027-0

Floeter, S. R., Ferreira, C. E. L., Dominici-Arosemena, A., & Zalmon, I. R. (2013). Latitudinal gradients in Atlantic reef fish communities: Trophic structure and spatial use patterns. *Investigational New Drugs*, *31*(2), 390–398. https://doi.org/10.1111/j.1095-8649.2004.00428.x

Floeter, S. R., Guimarães, R. Z. P., Rocha, L. A., Ferreira, C. E. L., Rangel, C. A., & Gasparini, J. L. (2001). Geographic variation in reef-fish assemblages along the Brazilian coast. *Global Ecology and Biogeography*, *10*(4), 423–431. https://doi.org/10.1046/j.1466-822X.2001.00245.x

Forester, D. J., & Machlist, G. E. (1996). Modeling human factors that affect the loss of biodiversity. *Conservation Biology*, *10*(4), 1253–1263. https://doi.org/10.1046/j.1523-1739.1996.10041253.x

Fourriére, M., Alvarado, J. J., Ayala Bocos, A., & Cortés, J. (2017). Updated checklist and analysis of completeness of the marine fish fauna of Isla del Coco, Pacific of Costa Rica. *Marine Biodiversity*, *47*(3), 813–821. https://doi.org/10.1007/s12526-016-0501-6

Froese, R., & Pauly, D. (2019). *FishBase*. www.fishbase.org

Froese, R., Tsikliras, A. C., & Stergiou, K. I. (2011). Editorial note on weight-length relations of fishes. *Acta Ichthyologica et Piscatoria*, *41*(4), 261–263. https://doi.org/10.3750/AIP2011.41.4.01

Fulton, C. J., Abesamis, R. A., Berkström, C., Depczynski, M., Graham, N. A. J., Holmes, T. H., Kulbicki, M., Noble, M. M., Radford, B. T., Tano, S., Tinkler, P., Wernberg, T., & Wilson, S. K. (2019). Form and function of tropical macroalgal reefs in the Anthropocene. *Functional Ecology*, *33*(6), 989–999. https://doi.org/10.1111/1365-2435.13282

Glynn, P. W. (2001). Eastern Pacific coral reef ecosystems. In K. B. Seeliger U. (Ed.), *Coastal Marine Ecosystems of Latin America* (vol 144, pp. 282–305). Springer. https://doi.org/10.1007/978-3-662-04482-7_20

Glynn, P. W. (2004). High complexity food webs in low-diversity eastern Pacific reef-coral communities. *Ecosystems*, *7*(4), 358–367. https://doi.org/10.1007/s10021-004-0184-x

Glynn, P. W. (2017). History of eastern pacific coral reef research. In P. W. Glynn, D. P. Manzello, & I. C. Enochs (Eds.), *Coral Reefs of the Eastern Pacific: Persistence and Loss in a Dynamic Environment. Coral Reefs of the World 8.* (pp. 1–37).

Springer Science+Business Media. https://doi.org/doi.org/10.1007/978-94-017-7499-4_1

Glynn, P. W., Alvarado, J. J., Banks, S., Cortés, J., Feingold, J. S., Jiménez, C., Maragos, J. E., Martínez, P., Maté, J. L., Moanga, D. A., Navarrete, S. A., Reyes Bonilla, H., Riegl, B., Rivera, F., Vargas Ángel, B., Wieters, E. A., & Zapata, F. A. (2017). Eastern Pacific coral reef provinces, coral community structure and composition: An overview. In P. W. Glynn, D. P. Manzello, & I. C. Enochs (Eds.), *Coral Reefs of the Eastern Pacific: Persistence and Loss in a Dynamic Environment. Coral Reefs of the World 8.* (pp. 107–176). Springer Science+Business Media. https://doi.org/10.1007/978-94-017-7499-4

Gower, J. C. (1966). Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika*, *53*(3/4), 325. https://doi.org/10.2307/2333639

Gower, J. C. (1971). A General coefficient of similarity and some of its properties. *International Biometric*, *27*(4), 857–871. https://doi.org/10.2307/2528823

Graham, N. A. J., & Nash, K. L. N. (2013). The importance of structural complexity in coral reef ecosystems. *Coral Reefs*, *32*(2), 315–326. https://doi.org/10.1007/s00338-012-0984-y

Grigg, R. W., & Hey, R. (1989). Paleoceanography of the Tropical Eastern Pacific Ocean. *Science*, *255*, 172–178. https://doi.org/10.1126/science.255.5041.172

Grime, J. P. (1998). Benefits of plant diversity to ecosystems immediate filter and founder effects. *Journal of Ecology*, *86*, 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Harmelin Vivien, M. L. (2002). Energetics and fish diversity on coral reels. In P. F. . Sale (Ed.), *Coral reef fishes: Dynamics and diversity in a complex ecosystem* (pp. 265–274). Elsevier Science. https://doi.org/10.1016/B978-012615185-5/50016-5

Hawkins, J. P., & Roberts, C. M. (2004). Effects of fishing on sex-changing Caribbean parrotfishes. *Biological Conservation*, *115*(2), 213–226. https://doi.org/10.1016/S0006-3207(03)00119-8

Hay, M. E. (1991). Fish-Seaweed Interactions on coral reefs: Effects of herbivorous fishes and adaptations of their prey. *The Ecology of Fishes on Coral Reefs*, 96–119. https://doi.org/10.1016/b978-0-08-092551-6.50010-6

Heenan, A., Hoey, A. S., Williams, G. J., & Williams, I. D. (2016). Natural bounds on herbivorous coral reef fishes. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1843). https://doi.org/10.1098/rspb.2016.1716

Hillebrand, H. (2004). Strength, slope and variability of marine latitudinal gradients. *Marine Ecology Progress Series*, *273*(1992), 251–267. https://doi.org/10.3354/meps273251

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J., Lodge, D., Loreau, M., Naeem, S., Schmid, B., SetaLa, H., Symstad, A., Vandermeer, J., & Wardle, D. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, *75*(1), 3–35. https://doi.org/10.1890/04-0922

Hsieh, T. C., Ma, K. H., & Chao, A. (2022). *iNext: Interpolation and Extrapolation for Species Diversity* (pp. 1–19). CRAN. http://chao.stat.nthu.edu.tw/wordpress/software_download/

Kessler, W. S., Johnson, G. C., & Moore, D. W. (2003). Sverdrup and nonlinear dynamics of the Pacific equatorial currents. *Journal of Physical Oceanography*, *33*(5), 994–1008. https://doi.org/10.1175/1520-0485(2003)033<0994:SANDOT>2.0.CO;2

Kulbicki, M. (2015). Increase in pelagic larval duration and geographical range for reef fish along an oceanic gradient. *Vie et Milieu*, *65*(1), 1–9.

https://www.researchgate.net/publication/282067219_Increase_in_pelagic_larval_duration_and_geographical_range_for_reef_fish_along_an_oceanic_gradient

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*(1), 299–305. https://doi.org/10.1890/08-2244.1

Laughlin, D. C., & Messier, J. (2015). Fitness of multidimensional phenotypes in dynamic adaptive landscapes. *Trends in Ecology and Evolution*, *30*(8), 487–496. https://doi.org/10.1016/j.tree.2015.06.003

Le, S., Josse, J., & Husson, F. (2008). *FactoMineR: An R Package for Multivariate Analysis* (pp. 1–18). Journal of Statistical Software. https://doi.org/10.18637/jss.v025.i01

Lee, M. S. Y. (2004). Molecularisation of taxonomy. *Invertebrate Systematics*, *18*(1), 1–6. https://doi.org/10.1071/IS03021

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*(2), 271–280. https://doi.org/10.1007/s004420100716

Littler, M. M., Littler, D. S., & Titlyanov, E. A. (1991). Comparisons of N- and P-limited productivity between high granitic islands versus low carbonate atolls in the Seychelles Archipelago: A test of the relative-dominance paradigm. *Coral Reefs*, *10*(4), 199–209. https://doi.org/10.1007/BF00336775

Luiz, O. J., Madin, J. S., Robertson, D. R., Rocha, L. A., Wirtz, P., & Floeter, S. R. (2012). Ecological traits influencing range expansion across large oceanic dispersal barriers: Insights from tropical Atlantic reef fishes Ecological traits influencing range expansion across large oceanic dispersal barriers: Insights from tropical Atlantic ree.

Proceedings of the Royal Society B: Biological Sciences, *279*, 1033–1040. https://doi.org/10.1098/rspb.2011.1525

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., & Hornik, K. (2021). *cluster: Cluster Analysis Basics and Extensions*. https://cran.r-project.org/package=cluster

Man, A., Law, R., & Polunin, N. V. C. (1995). Role of marine reserves in recruitment to reef fisheries: A metapopulation model. *Biological Conservation*, *71*(2), 197–204. https://doi.org/10.1016/0006-3207(94)00047-T

Manzello, D. P., Kleypas, J. A., Budd, D. A., Eakin, C. M., Glynn, P. W., & Langdon, C. (2008). Poorly cemented coral reefs of the eastern tropical Pacific: Possible insights into reef development in a high-CO2 world. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(30), 10450–10455. https://doi.org/10.1073/pnas.0712167105

Mason, N. W. H., Mouillot, D., Lee, W. G., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos*, *111*(1), 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

Mazzei, E. F., Pinheiro, H. T., Simon, T., Moura, R. L., Macieira, R. M., Pimentel, C. R., Teixeira, J. B., Floeter, S. R., Ferreira, C. E. L., Ghisolfi, R. D., Francini-Filho, R. B., Quimbayo, J. P., Rocha, L. A., Gasparini, J. L., & Joyeux, J. C. (2021). Mechanisms of dispersal and establishment drive a stepping stone community assembly on seamounts and oceanic islands. *Marine Biology*, *168*(7). https://doi.org/10.1007/s00227-021-03919-7

McClanahan, T. R., & Muthiga, N. A. (2017). Environmental variability indicates a climate-adaptive center under threat in northern Mozambique coral reefs. *Ecosphere*, *8*(5). https://doi.org/10.1002/ecs2.1812

McLean, M., Auber, A., Graham, N. A. J., Houk, P., Villéger, S., Violle, C., Thuiller, W., Wilson, S. K., & Mouillot, D. (2019). Trait structure and redundancy determine sensitivity to disturbance in marine fish communities. *Global Change Biology*, *25*(10), 3424–3437. https://doi.org/10.1111/gcb.14662

Miloslavich, P., Klein, E., Díaz, J. M., Hernández, C. E., Bigatti, G., Campos, L., Artigas, F., Castillo, J., Penchaszadeh, P. E., Neill, P. E., Carranza, A., Retana, M. V., Díaz de Astarloa, J. M., Lewis, M., Yorio, P., Piriz, M. L., Rodríguez, D., Yoneshigue-Valentin, Y., Gamboa, L., & Alberto, M. (2011). Marine biodiversity in the Atlantic and Pacific coasts of south America: Knowledge and gaps. *PLoS ONE*, *6*(1). https://doi.org/10.1371/ journal.pone.0014631

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics*, *29*(2), 215–233. https://doi.org/10.1016/S0921-8009(99)00009-9

Mokany, K., Ash, J., & Roxburgh, S. (2008). Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, *96*(5), 884–893. https://doi.org/10.1111/j.1365-2745.2008.01395.x

Mora, C. (2008). A clear human footprint in the coral reefs of the Caribbean. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1636), 767–773. https://doi.org/10.1098/rspb.2007.1472

Mora, C., Aburto-Oropeza, O., Ayala-Bocos, A., Ayotte, P. M., Banks, S., Bauman, A. G., Beger, M., Bessudo, S., Booth, D. J., Brokovich, E., Brooks, A. J., Chabanet, P., Cinner, J. E., Cortés, J., Cruz-Motta, J. J., Cupul-Magaña, A., DeMartini, E. E., Edgar, G. J., Feary, D. A., … Zapata, F. A. (2011). Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. *PLoS Biology*, *9*(4). https://doi.org/10.1371/journal.pbio.1000606

Mouillot, D., Dumay, O., & Tomasini, J. A. (2007). Limiting similarity, niche filtering and functional diversity in coastal lagoon fish communities. *Estuarine, Coastal and Shelf Science*, *71*(3–4), 443–456. https://doi.org/10.1016/j.ecss.2006.08.022

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, *28*(3), 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J. E., Bender, M. G., Chabanet, P., Floeter, S. R., Friedlander, A. M., Vigliola, L., & Bellwood, D. R. (2014). Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(38), 13757–13762. https://doi.org/10.1073/pnas.1317625111

Mumby, P. J., Dahlgren, C. P., Harborne, A. R., Kappel, C. V., Micheli, F., Brumbaugh, D. R., Holmes, K. E., Mendes, J. M., Broad, K., Sanchirico, J. N., Buch, K., Box, S., Stoffle, R. W., & Gill, A. B. (2006). Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*, *311*(5757), 98–101. https://doi.org/10.1126/science.1121129

Mumby, P. J., Steneck, R. S., Edwards, A. J., Ferrari, R., Coleman, R., Harborne, A. R., & Gibson, J. P. (2012). Fishing down a Caribbean food web relaxes trophic cascades. *Marine Ecology Progress Series*, *445*, 13–24. https://doi.org/10.3354/meps09450

Mumby, P. J., & Wabnitz, C. C. C. (2002). Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species. *Environmental Biology of Fishes*, *63*(3), 265–279. https://doi.org/10.1023/A:1014359403167

Muscarella, R., & Uriarte, M. (2016). Do community-weighted mean functional traits reflect optimal strategies? *Proceedings of the Royal Society B: Biological Sciences*, *283*(1827). https://doi.org/10.1098/rspb.2015.2434

Naeem, S., Duffy, J. E., & Zavaleta, E. (2012). The functions of biological diversity in an age of extinction. *Science*, *336*(6087), 1401–1406. https://doi.org/10.1126/science.1215855

Nash, K. L. N., Graham, N. A. J., & Bellwood, D. R. (2013). Fish foraging patterns, vulnerability to fishing, and implications for the management of ecosystem function across scales. *Ecological Applications*, *23*(7), 1632–1644. https://doi.org/10.1890/12-2031.1

Nash, K. L. N., Graham, N. A. J., Jennings, S., Wilson, S. K., & Bellwood, D. R. (2016). Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. *Journal of Applied Ecology*, *53*(3), 646–655. https://doi.org/10.1111/1365-2664.12430

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O’Hara, R. B., L. Simpson, G., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). *vegan: Community Ecology Package*. https://cran.r-project.org/package=vegan

Owen Smith, N., Fryxell, J. M., & Merrill, E. H. (2010). Foraging theory upscaled: The behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2267–2278. https://doi.org/10.1098/rstb.2010.0095

Parravicini, V., Kulbicki, M., Bellwood, D. R., Friedlander, A. M., Arias-Gonzalez, J. E., Chabanet, P., Floeter, S. R., Myers, R., Vigliola, L., D’Agata, S., & Mouillot, D.

(2013). Global patterns and predictors of tropical reef fish species richness. *Ecography*, *36*(12), 1254–1262. https://doi.org/10.1111/j.1600-0587.2013.00291.x

Parravicini, V., Villéger, S., McClanahan, T. R., Arias-González, J. E., Bellwood, D. R., Belmaker, J., Chabanet, P., Floeter, S. R., Friedlander, A. M., Guilhaumon, F., Vigliola, L., Kulbicki, M., & Mouillot, D. (2014). Global mismatch between species richness and vulnerability of reef fish assemblages. *Ecology Letters*, *17*(9), 1101–1110. https://doi.org/10.1111/ele.12316

Petchey, O. L., Hector, A., & Gaston, K. J. (2004). How do different measures of functional diversity perform? *Ecology*, *85*(3), 847–857. https://doi.org/10.1890/03-0226

Pianka, E. R. . (1966). Latitudinal gradients in species diversity: A review of concepts. *The American Society of Naturalists*, *100*(910), 33–46. https://doi.org/10.1086/282398

Pinheiro, H. T., Bernardi, G., Simon, T., Joyeux, J. C., Macieira, R. M., Gasparini, J. L., Rocha, C., & Rocha, L. A. (2017). Island biogeography of marine organisms. *Nature*, *549*(7670), 82–85. https://doi.org/10.1038/nature23680

Pombo Ayora, L., Coker, D. J., Carvalho, S., Short, G., & Berumen, M. L. (2020). Morphological and ecological trait diversity reveal sensitivity of herbivorous fish assemblages to coral reef benthic conditions. *Marine Environmental Research*, *162*(August), 105102. https://doi.org/10.1016/j.marenvres.2020.105102

Poore, A. G. B., Campbell, A. H., Coleman, R. A., Edgar, G. J., Jormalainen, V., Reynolds, P. L., Sotka, E. E., Stachowicz, J. J., Taylor, R. B., Vanderklift, M. A., & Emmett Duffy, J. (2012). Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letters*, *15*(8), 912–922. https://doi.org/10.1111/j.1461-0248.2012.01804.x

Puk, L. D., Ferse, S. C. A., & Wild, C. (2016). Patterns and trends in coral reef macroalgae browsing: A review of browsing herbivorous fishes of the Indo-Pacific. *Reviews in*

Fish Biology and Fisheries, *26*(1), 53–70. https://doi.org/10.1007/s11160-015-9412-z

Quimbayo, J. P., Dias, M. S., Kulbicki, M., Mendes, T. C., Lamb, R. W., Johnson, A. F., Aburto-Oropeza, O., Alvarado, J. J., Bocos, A. A., Ferreira, C. E. L., Garcia, E., Luiz, O. J., Mascareñas-Osorio, I., Pinheiro, H. T., Rodriguez-Zaragoza, F., Salas, E., Zapata, F. A., & Floeter, S. R. (2019). Determinants of reef fish assemblages in tropical oceanic islands. *Ecography*, *42*(1), 77–87. https://doi.org/10.1111/ecog.03506

Quimbayo, J. P., Silva, F. C., Mendes, T. C., Ferrari, D. S., Danielski, S. L., Bender, M. G., Parravicini, V., Kulbicki, M., & Floeter, S. R. (2021). Life-history traits, geographical range, and conservation aspects of reef fishes from the Atlantic and Eastern Pacific. *Ecology*, *102*(5), 1–40. https://doi.org/10.1002/ecy.3298

R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. https://www.r-project.org/

Rasher, D. B., Engel, S., Bonito, V., Fraser, G. J., Montoya, J. P., & Hay, M. E. (2012). Effects of herbivory, nutrients, and reef protection on algal proliferation and coral growth on a tropical reef. *Oecologia*, *169*(1), 187–198. https://doi.org/10.1007/s00442-011-2174-y

Rhode, K. (1992). Latitudinal gradients in species diversity: The search for the primary cause. *Nordic Society Oikos*, *65*(3), 514–527. https://doi.org/10.2307/3545569

Richardson, L. E., Graham, N. A. J., Pratchett, M. S., & Hoey, A. S. (2017). Structural complexity mediates functional structure of reef fish assemblages among coral habitats. *Environmental Biology of Fishes*, *100*(3), 193–207. https://doi.org/10.1007/s10641-016-0571-0

Ricotta, C., & Moretti, M. (2011). CWM and Rao’s quadratic diversity: A unified framework for functional ecology. *Oecologia*, *167*(1), 181–188. https://doi.org/10.1007/s00442-011-1965-5

Robertson, D. R. (2009). Shorefishes of the Tropical Eastern Pacific Online Information System. In *Smithsonian Contributions to the Marine Sciences* (Issue 38, pp. 197–208). www.%0Astri.org/sftep

Robertson, D. R., & Cramer, K. L. (2009). Shore fishes and biogeographic subdivisions of the Tropical Eastern Pacific. *Marine Ecology Progress Series*, *380*(Ekman 1953), 1–17. https://doi.org/10.3354/meps07925

Robertson, D. R., Grove, J. S., & McCosker, J. E. (2004). Tropical transpacific shore fishes. *Pacific Science*, *58*(4), 507–565. https://doi.org/10.1353/psc.2004.0041

Robinson, J. P. W., Williams, I. D., Yeager, L. A., McPherson, J. M., Clark, J., Oliver, T. A., & Baum, J. K. (2018). Environmental conditions and herbivore biomass determine coral reef benthic community composition: Implications for quantitative baselines. *Coral Reefs*, *37*(4), 1157–1168. https://doi.org/10.1007/s00338-018-01737-w

Ruppert, J. L. W., Travers, M. J., Smith, L. L., Fortin, M. J., & Meekan, M. G. (2013). Caught in the middle: Combined impacts of shark removal and coral loss on the fish communities of coral reefs. *PLoS ONE*, *8*(9). https://doi.org/10.1371/journal.pone.0074648

Schaffelke, B., & Klumpp, D. W. (1998). Short-term nutrient pulses enhance growth and photosynthesis of the coral reef macroalga *Sargassum baccularia. Marine Ecology Progress Series*, *170*, 95–105. https://doi.org/10.3354/meps170095

Shah Esmaeili, Y., Corte, G. N., Checon, H. H., Bilatto, C. G., Lefcheck, J. S., Cecilia Zacagnini Amaral, A., & Turra, A. (2022). Revealing the drivers of taxonomic and functional diversity of nearshore fish assemblages: Implications for conservation priorities. *Diversity and Distributions*, *28*(8), 1597–1609. https://doi.org/10.1111/ddi.13453

Siqueira, A. C., Oliveira-Santos, L. G. R., Cowmanc, P. F., & Floeter, S. R. (2016). Evolutionary processes underlying reef fish latitudinal differences in biodiversity. *Global Ecology and Biogeography*, *25*(12), 1466–1476. http://dx.doi.org/10.1111/geb.12506

Smith, J. E., Runcie, J. W., & Smith, C. M. (2005). Characterization of a large-scale ephemeral bloom of the green alga *Cladophora sericea* on the coral reefs of West Maui, Hawai'i. *Marine Ecology Progress Series*, *302*, 77–91. https://doi.org/10.3354/meps302077

Smith, T. B. (2005). *The dynamics of coral reef algae in an upwelling system* [PhD Thesis, University of Miami]. https://doi.org/10.2307/40217738

Smith, T. B., Fong, P., Kennison, R., & Smith, J. (2010). Spatial refuges and associational defenses promote harmful blooms of the alga *Caulerpa sertularioides* onto coral reefs. *Oecologia*, *164*(4), 1039–1048. https://doi.org/10.1007/s00442-010-1698-x

Somerfield, P. J., Clarke, K. R., Warwick, R. M., & Dulvy, N. K. (2008). Average functional distinctness as a measure of the composition of assemblages. *ICES Journal of Marine Science*, *65*(8), 1462–1468. https://doi.org/10.1093/icesjms/fsn118

Sonnier, G., Shipley, B., & Navas, M. L. (2010). Quantifying relationships between traits and explicitly measured gradients of stress and disturbance in early successional plant communities. *Journal of Vegetation Science, 21*(6), 1014–1024. https://doi.org/10.1111/j.1654-1103.2010.01210.x

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C. A., & Robertson, J. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience*, *57*(7), 573–583. https://doi.org/10.1641/b570707

Spencer, C. P. (1985). The use of plant micro-nutrient and chlorophyll records as indices of eutrophication in inshore waters. *Netherlands Journal of Sea Research*, *19*(3–4), 269–275. https://doi.org/10.1016/0077-7579(85)90033-X

Tarazona, J., & Arntz, W. (2001). The Peruvian Coastal Upwelling System. In U. Seeliger & B. Kjerfve (Eds.), *Coastal marine ecosystems of Latin America* (Vol. 144, pp. 229–244). Springer Berlin. https://doi.org/10.1007/978-3-662-04482-7_17

Thiault, L., Kernaléguen, L., Osenberg, C. W., Lison de Loma, T., Chancerelle, Y., Siu, G., & Claudet, J. (2019). Ecological evaluation of a marine protected area network: A progressive-change BACIPS approach. *Ecosphere*, *10*(2). https://doi.org/10.1002/ecs2.2576

Tilman, D., Knops, J., Wedin, D., Reich, P. B., Ritchie, M., & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, *277*(5330), 1300–1302. https://doi.org/10.1126/science.277.5330.1300

Tolimieri, N., & Anderson, M. J. (2010). Taxonomic distinctness of demersal fishes of the california current: Moving beyond simple measures of diversity for marine ecosystem-based management. In *PLoS ONE* (Vol. 5, Issue 5). https://doi.org/10.1371/journal.pone.0010653

Tuya, F., Cacabelos, E., Duarte, P., Jacinto, D., Castro, J. J., Silva, T., Bertocci, I., Franco, J. N., Arenas, F., Coca, J., & Wernberg, T. (2012). Patterns of landscape and assemblage structure along a latitudinal gradient in ocean climate. *Marine Ecology Progress Series*, *466*, 9–19. https://doi.org/10.3354/meps09941

Ulate, K., Alcoverro, T., Arthur, R., Aburto-Oropeza, O., Sánchez, C., & Huato-Soberanis, L. (2018). Conventional MPAs are not as effective as community co-managed areas in conserving top-down control in the Gulf of California. *Biological Conservation*, *228*(May), 100–109. https://doi.org/10.1016/j.biocon.2018.09.033

UNEP-WCMC & IUCN. (2020). *Protected Planet: The World Database on Protected Areas (WDPA)/The Global Database on Protected Areas Management Effectiveness (GD-PAME)] [On-line]*. https://www.protectedplanet.net/en

Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, *27*(5), 1413–1432. https://doi.org/10.1007/s11222-016-9696-4

Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., & Bürkner, P. C. (2021). Rank-normalization, folding, and localization: An improved (formula presented) for assessing convergence of MCMC (with Discussion). *Bayesian Analysis*, *16*(2), 667–718. https://doi.org/10.1214/20-BA1221

Vellend, M. (2016). The Theory of Ecological Communities. In *Monographs in Population Biology* (Vol. 57). Princeton University Press. https://doi.org/10.1515/9781400883790

Vergés, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., Heck, K. L., Booth, D. J., Coleman, M. A., Feary, D. A., Figueira, W., Langlois, T., Marzinelli, E. M., Mizerek, T., Mumby, P. J., Nakamura, Y., Roughan, M., van Sebille, E., Gupta, A. S., … Wilson, S. K. (2014). The tropicalization of temperate marine ecosystems: Climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1789). https://doi.org/10.1098/rspb.2014.0846

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*(8), 2290–2301. https://doi.org/10.1890/07-1206.1

Villéger, S., Miranda, J. R., Hernández, D. F., & Mouillot, D. (2010). Contrasting changes in taxonomie vs. Functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, *20*(6), 1512–1522. https://doi.org/10.1890/09-1310.1

Warwick, R. M., & Clarke, K. R. (1998). Taxonomic distinctness and environmental assessment. *Journal of Applied Ecology*, *35*, 532–543. https://doi.org/10.1046/j.1365-2664.1998.3540532.x

Welsh, J. Q., Goatley, C. H. R., & Bellwood, D. R. (2013). The ontogeny of home ranges: Evidence from coral reef fishes. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1773), 1–7. https://doi.org/10.1098/rspb.2013.2066

Werner, E. E., & Peacor, S. D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, *84*(5), 1083–1100. https://doi.org/10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2

Williams, G. J., & Graham, N. A. J. (2019). Rethinking coral reef functional futures. *Functional Ecology*, *33*(6), 942–947. https://doi.org/10.1111/1365-2435.13374

Woodhead, A. J., Hicks, C. C., Norström, A. V., Williams, G. J., & Graham, N. A. J. (2019). Coral reef ecosystem services in the Anthropocene. *Functional Ecology*, *33*(6), 1023–1034. https://doi.org/10.1111/1365-2435.13331

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornellssen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827. https://doi.org/10.1038/nature02403

Xie, S. P., Xu, H., Kessler, W. S., & Nonaka, M. (2005). Air-sea interaction over the eastern Pacific warm pool: Gaps winds, thermocline dome, and atmospheric convection. *Journal of Climate*, *18*(1), 5–20. https://doi.org/10.1175/JCLI-3249.1

Zobel, M. (1997). The relative role of species pools in determining plant species richness: An alternative explanation of species coexistence? *Trends in Ecology and Evolution*, *12*(7), 266–269. https://doi.org/10.1016/S0169-5347(97)01096-3

Anexos

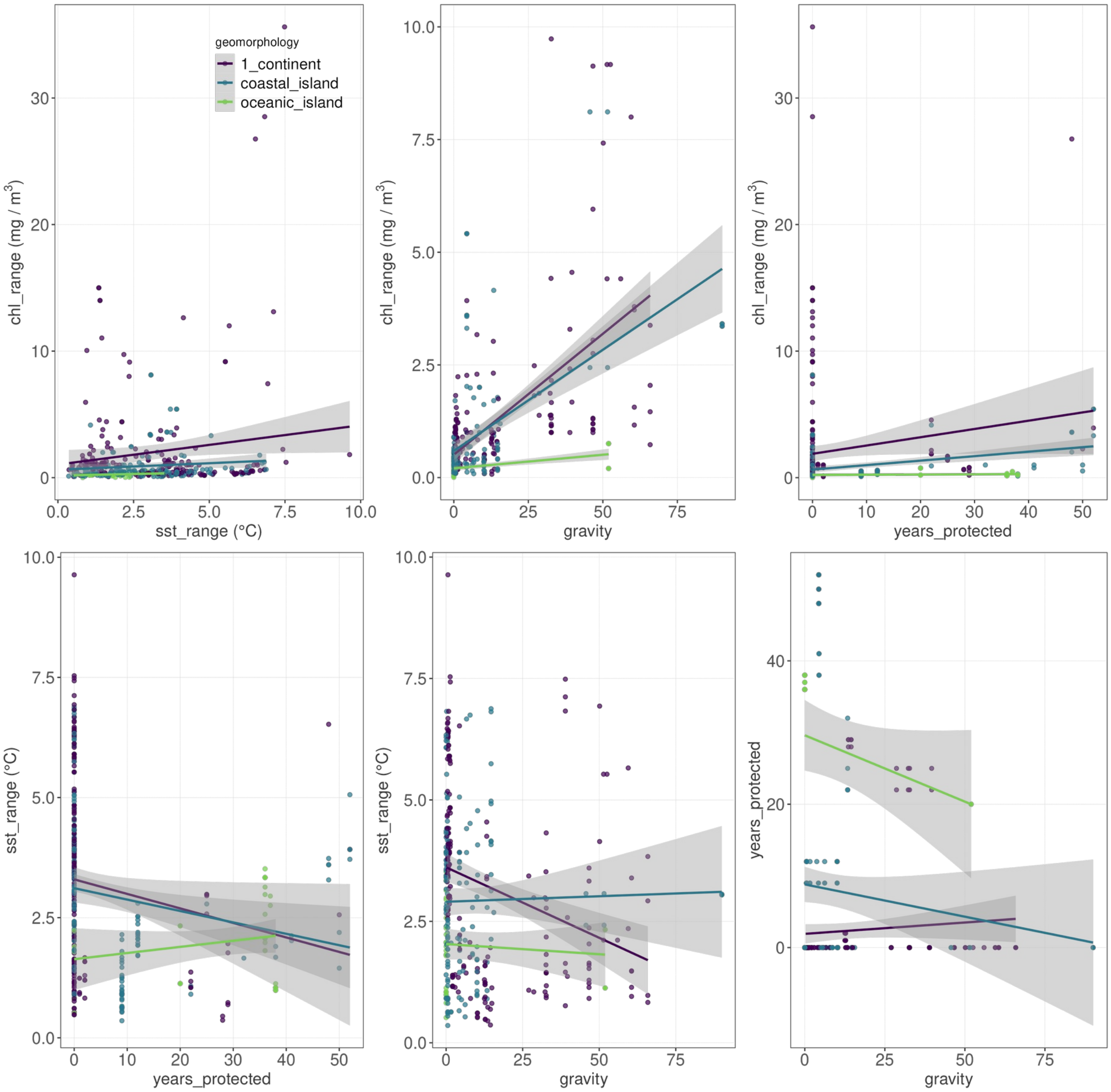
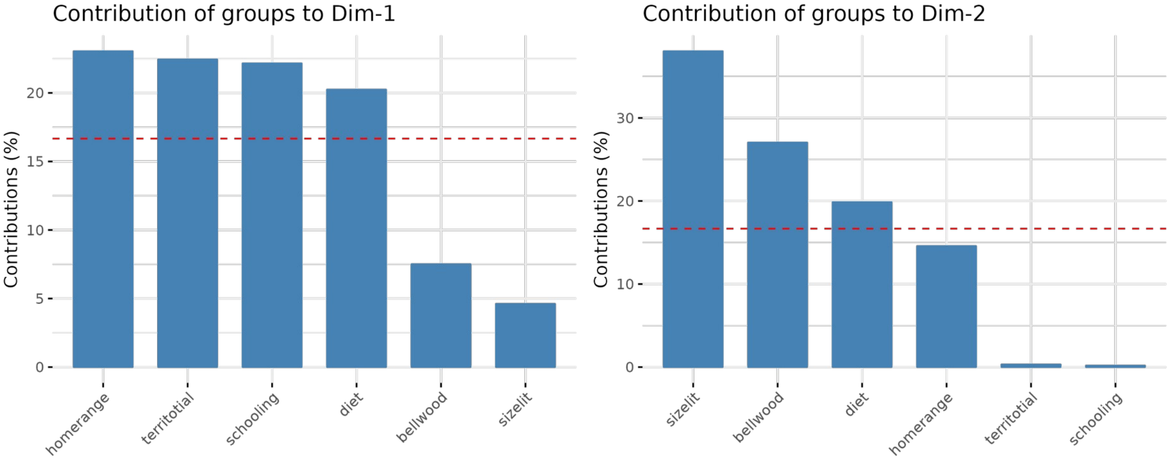


Figure S1. Relations between the biophysical and anthropic variables included in the research as predictors.



Contribution of groups to Dim-1

Contribution of groups to Dim-2

Figure S2. Contribution of each functional trait to the variation in the first two dimensions of the Multiple Factor Analysis for the community weighted mean (CWM) of herbivorous reef fishes in the Eastern Tropical Pacific. (A) Contribution of each functional trait to the first dimention. (B) Contribution of each functional trait to the first dimention. The traits are Maximumbody size reported in literature with a logarithmic transformation (sizelit); home range, feeding territoriality, schooling, trophic-functional group and diet.