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Eastern Tropical Pacific reef fish on the move over the past two decades: Reorganization of taxonomic and functional reef fish diversity

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Abstract

Reef fish communities are shifting their distributions in response to global warming, often migrating toward cooler regions. These migrations can lead to taxonomic and functional reorganizations of communities. While functional diversity metrics are commonly used to detect ecological responses in coral reef fish, few studies have examined spatiotemporal dynamics over broad scales. We analyzed long-term fish survey data conducted in 13 localities within 10 marine protected areas (MPAs) across four subregions of the Eastern Tropical Pacific (ETP), covering the period from 2005 to 2023. Using reef fish abundance data paired with ecological and behavioral trait information, we calculated taxonomic (species richness) and functional diversity (functional richness: FRic, evenness: FEve, dispersion: FDis, and originality: FOri). We evaluated their temporal and spatial variation at the regional scale using generalized linear mixed models (GLMMs) in four subregions and localities within subregions. We assessed the influence of oceanographic and anthropogenic variables on these metrics with the use of GLMMs. We highlighted weak indices variations patterns within subregions. Overall, the ETP region is experiencing stagnation or slight but significant decreases in species richness, FRic, FDis, and FOri, with a stagnation in FEve, indicating subtle shifts in reef fish community structure. Surprisingly, we found that FRic was the only index influenced by oceanographic drivers, and that only FDis index was affected by the anthropogenic variable (fishing pressure). We also found that highly protected MPAs exhibited stagnation or slight increases compared to less protected MPAs. This suggests that reef fish communities might be more impacted by local rather than regional factors. These results highlight the importance of local scale long-term monitoring and functional diversity approaches to perceive signs of ecological change under environmental and human impacts.

Résumé

Les communautés de poissons récifaux changent leurs distributions en réponse au changement climatique, en migrant le plus souvent vers des régions plus froides. Ces migrations peuvent mener à des réorganisations des communautés au niveau taxonomique et fonctionnel. Alors que les indices de diversité fonctionnelle sont couramment utilisés pour détecter des réponses écologique au sein des poissons récifaux, peu d'études ont examiné les dynamiques spatiotemporelles à grandes échelles. Nous avons analysé des données de recensements de poissons à travers 13 localités dans 10 aires marines protégées (AMPs), réparties en quatre sous-régions de l'océan Pacifique Tropical Est (PTE), entre 2005 et 2023. En utilisant des données d'abondance des espèces couplées à des traits écologiques et comportementaux, nous avons calculé plusieurs indices : la richesse spécifique, la richesse fonctionnelle (FRic), la régularité fonctionnelle (FEve), la dispersion fonctionnelle (FDis), et l'originalité fonctionnelle (FOri). Nous avons évalué leurs variations temporelles et spatiales à l'échelle régionale en utilisant des « generalized linear mixed models » (GLMMs) dans les quatre sous-régions et dans les localités au sein de ces sous-régions. Nous avons aussi évalué les effets de variables océanographiques et anthropogéniques sur ces indices à l'aide de GLMMs. Nous avons mis en avant de faibles variations entre les sous-régions et au sein de celles-ci. Dans l'ensemble, l'océan Pacifique Tropical Est montre une stagnation ou une faible baisse de diversité taxonomique et fonctionnelle. Cela indique des variations subtiles dans la structure des communautés de poissons récifaux. A notre surprise, nous avons trouvé que FRic était le seul indice influencé par des variables océanographiques (température, production primaire), et que seul l'indice FDis était influencé par la variable anthropogénique (pression de pêche). Cela suggère que les communautés de poissons récifaux seraient plus impactées par des variables locales plutôt que régionales. Ces résultats mettent en évidence l'importance des larges jeux de données de monitoring à l'échelle locale, couplés avec des approches de diversité fonctionnelle afin de percevoir des signes de changements écologiques résultants des impacts environnementaux

Abbreviation list

DTM	Distance to Markets
ENSO	El Niño Southern Oscillation
ETP	Eastern Tropical Pacific
FDis	Functional dispersion
FEve	Functional evenness
FRic	Functional richness
FOri	Functional originality
GLMM	Generalized linear mixed model
MPA	Marine Protected Area
OISST	Optimum Interpolation Sea Surface Temperature
PP	Primary productivity
Sd(PP)	Standard deviation of PP
Sd(SST)	Standard deviation of SST
Sp Richn	Species richness
SST	Sea surface temperature
UVC	Underwater visual census

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1. Introduction

1.1. Ongoing climate change effects on species distribution

Climate change is displacing biota outside of the native range (e.g., towards higher latitudes or altitudes) (Chen et al., 2011). In every biome, increasing temperatures are forcing species range shifts: the distribution of mountainous trees in the Andes is shifting upslope (Feeley et al., 2011), breeding birds from North America (Hitch & Leberg, 2007), or Finland (Lehikoinen & Virkkala, 2016) are moving northward, North Sea fish are moving northward or towards deeper waters (Perry et al., 2005). At the warmest extreme of the planet tropical reef fish are not the exception (Rummer & Munday, 2017). Tropical reef fish are migrating polewards in Japan (Nakamura et al., 2013), Eastern Atlantic (Kaimuddin et al., 2016), or in Australia (Hobbs, 2010). These shifts reshape communities and diversity. Temperatures 1.5-3.0 °C greater than today's summer averages reduce reef fish growth rates (Munday et al., 2008), swimming ability (Johansen & Jones, 2011), and aerobic functioning (Nilsson et al., 2009; Rummer et al., 2014). Therefore, there is good reason to expect that climate change will continue having significant effects on reef fish populations. In this context of climate change impacts on rocky and coral reef fishes, this study will evaluate the ecological shifts that may occur within communities inside the Eastern Tropical Pacific.

1.2. Different facets of biodiversity

Ecologists are increasingly investigating multiple complementary facets of biodiversity. The taxonomic structure of communities, focused on species richness, and taxonomic evenness (Pielou Index [Pielou, 1969]) (Villéger et al., 2010), may not always reveal clear effects of disturbance (Wan Hussin et al., 2012) or may give wrong indication of ecosystem recovery (Villéger et al., 2010). In fact, these metrics of taxonomic diversity fail to consider species identity and rely on the principle that species are equivalent entities. On the contrary, functional biodiversity metrics recognized that species differ in their ecological role. As an example, we can consider two communities with both two fish species (Figure 1). The first is made up of one moorish idol (*Zanclus cornutus*) and one three-banded butterflyfish (*Chaetodon humeralis*) (Figure 1, assemblage 1). The second is made up of one *Z. cornutus* and one bigeye trevally (*Caranx sexfasciatus*) (Figure 1, assemblage 2). Using species richness, the two assemblages would be similar, each gathering two species. But, if we look at species characteristics the two communities are very different. In the first assemblage, the two species have very similar ecological characteristics: both *Z. cornutus* and *C. humeralis* are rather small (23-25.4 cm), feed on algae and small benthic invertebrates (Fernández-Rivera Melo et al., 2018; Nunes et al., 2020), and both inhabit at the bottom of the water column (Figure 1). However, in the second assemblage, *C. sexfasciatus* has a larger size than *Z. cornutus* (and *C. humeralis*), it's a carnivore species, and it swims at a higher position in the water column (Figure 1). In the second assemblage, species are thus more different in terms of their characteristics, and overall, their ecological role.

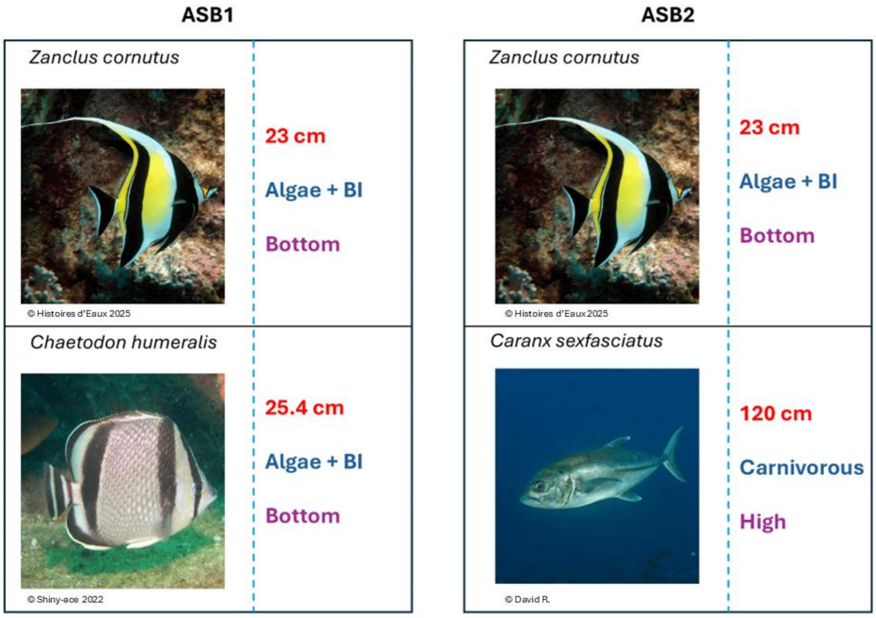


Figure 1. Example of two assemblages (ASB1: assemblage 1, and ASB2: assemblage 2) with two different species in each. Species characteristics in red represent the maximum size, in blue represent the feeding habits, and in purple represent the position (or level) in the water column. BI: benthic invertebrates.

Functional diversity relies on the quantification of traits, which are defined as "any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization" (Violle et al., 2007). When measured at the species-level, traits reflect the way a species uses and potentially impacts its environment. Different fish species in different parts of the world, but occurring in similar environments, therefore, share similar traits (McLean et al., 2021). The potential ecological role of a species can thus be described by studying its functional traits, which situates it within the functioning of the ecosystem (Brandl et al., 2019). The study of communities by looking at species traits is called functional diversity (Díaz & Cabido, 2001; Villéger et al., 2008). More specifically, functional diversity is defined as "the value and the range of those species and organismal traits that influence ecosystem functioning" (Tilman, 2001). Meaning that the more a community gathers species with diversified traits composition, the more it is functionally diverse, with multiple roles attributed to different species.

There is a growing use of functional diversity, and with taxonomic diversity, they together give a multifaceted view of biodiversity which helps to get better conservation measures and assessment of biodiversity (Cadotte et al., 2011). The study of functional diversity has thus gained attraction as an essential tool for understanding the ecological roles of species in ecosystems, including the complex functional roles realized by species inside an ecosystem (Villéger et al., 2010; Mouillot et al., 2013b). Functional diversity enhances ecosystem functions in general (Díaz & Cabido, 2001) like productivity (Tilman et al., 1997; Hooper & Dukes, 2004; Petchey et al., 2004; Hooper et al., 2005), resilience or adaptation (Dukes, 2001; Bellwood et al., 2004), and flux regulation (Waldbusser et al., 2004). Although still discussed (Lipoma et al., 2024), a high functional diversity is expected to provide high ecosystem resilience.

1.3. How to measure functional diversity?

To account for species roles within an ecosystem, it is crucial for functional traits to be carefully selected, meaningful and important for ecosystem functioning (Villéger et al., 2017). The traits need to describe complementary functions of organisms which in turn determine their functional role within the ecosystem. As functional roles can be broad, the traits must be chosen according to what is the goal of the study (like trophic interactions, organism movements, nutrient cycling, or habitat-organism interactions to name a few) (Villéger et al., 2017).

To quantify functional diversity based on species traits, the first approaches gathered species into functional entities: groups of species having the same traits composition. But species responses to ecological processes generally follow a continuous gradient rather than categorical responses. Therefore, grouping species into functional entities can be seen as a loss of information. Species can also be assembled into a functional dendrogram, i.e., a tree in which species are the tips, and branch lengths as well as their proximity on the tree, reflect their functional similarity (Petchey & Gaston, 2002). However, functional dendrograms have been shown to inadequately capture functional similarities and dissimilarities among species (Maire et al., 2015). Another approach to measure functional diversity is to construct a functional space where the axes represent traits or combinations of traits (Villéger et al., 2008). Species in this multidimensional space are placed based on their trait values, meaning that species situated close to each other possess similar traits. The functional space can be built through a principal coordinate analysis (PCoA) if the traits are continuous and categorical, or a principal component analysis (PCA) if all the traits are continuous (Villéger et al., 2008; Laliberté & Legendre, 2010). If we go back to the two assemblages of the previous section: *C. humeralis* and *Z. cornutus* share similar traits so they cluster closely within the functional space (Figure 2), while, *C. sexfasciatus* is very far from the two other species in the functional space (Figure 2), because it has a distinct combination of traits and is estimated to endorse a different role within the community.

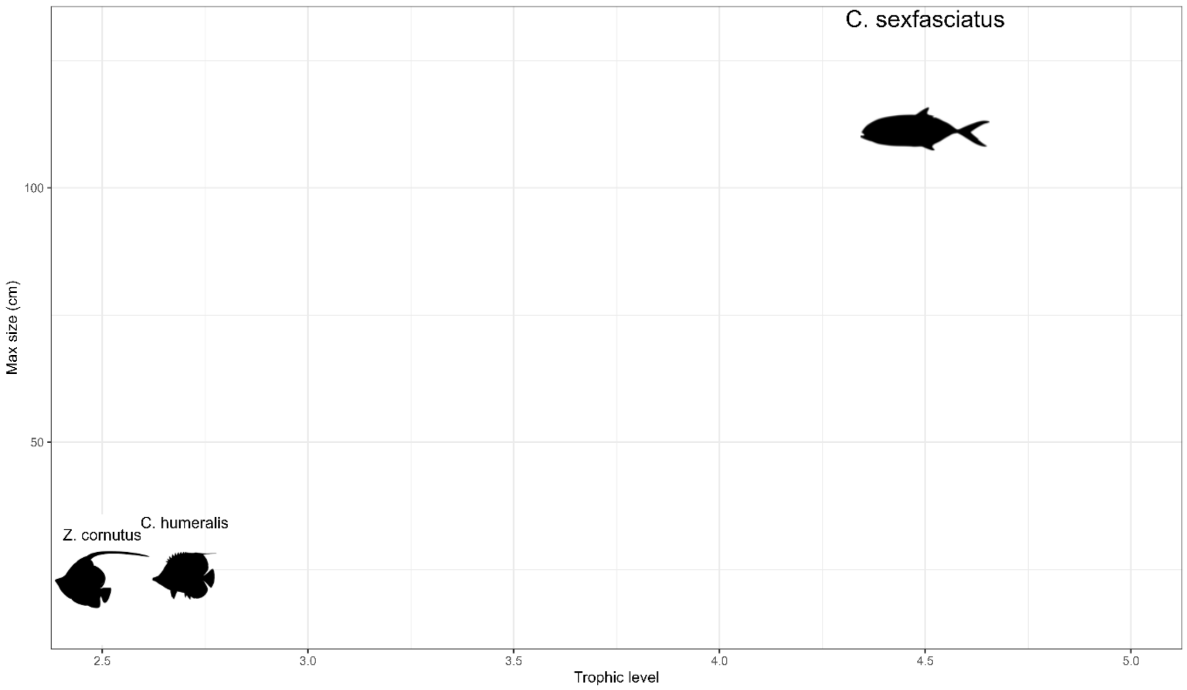


Figure 2. Functional space built on two traits representing each one axis. Each trait (max size (maximum size) and trophic level) is along an axis. Species inside the space are from the first example (Figure 1): Z. cornutus and C. humeralis share similar trait combinations by being both small (23-25cm) and low trophic level (2.5-2.7) species; while C. sexfasciatus gather a more distinct combination of traits, being a large (120cm) and predatory (4.5 trophic level) species.

The functional space is built based on a pool of species whose size is relative to the research question, and functional indices are then computed at the scale of smaller species assemblages within this pool. For instance, while studying the spatio-temporal variation of fish species in the Eastern Tropical Pacific, the functional space is built using all species found throughout the region, while indices are computed, for instance, at the site level. The functional diversity of an assemblage, defined as the distribution of species of the studied assemblage (and their abundance) in the functional space, can be quantified using several complementary indices. Just like taxonomic diversity can not be summed up using one index, gathering measures of species richness, evenness of species abundance, functional diversity can not be summarized into one metric (Villéger et al., 2008; Mouillot et al., 2013b). The different indices can, for example, quantify the richness, the distribution of species abundance, or the center of mass of all the species in the functional space. The functional richness (FRic) of an assemblage, for instance, measures the proportion of the volume of the multidimensional space filled by species present in the studied assemblage and is totally independent of species abundance

(Villéger et al., 2008). It represents the quantity of functional diversity present within the assemblage. The functional evenness (FEve) of an assemblage is defined as the regularity of the distribution of species abundance within the assemblage (Villéger et al., 2008), and represents if the species abundances are spread across the assemblage, or clustered in a few species. This explains if the assemblages are dominated by a species or a group of species located in a specific place within the functional space. The functional dispersion (FDis) of an assemblage is defined as the abundance-weighted mean deviation to the center of gravity of the studied assemblage (Laliberté & Legendre, 2010), and can account for species abundances by shifting the position of the center of gravity toward the abundant species and weighting distances of individual species by their relative abundances (Laliberté & Legendre, 2010). Lastly, functional originality (FOri) of an assemblage is defined as the isolation of species in the functional space, and represents the functional uniqueness of an assemblage, whether or not it gathers species with unique functional roles (Mouillot et al., 2013b). FEve, FDis, and FOri, take species relative abundances into account, meaning that they can be weighted by species individual count, density, or biomass. Those indices, among others, thus explain different facets that are important to compute altogether.

These indices provide a way to characterize the functional niche space used by species communities (Rincón-Díaz et al., 2018), and can operate as early-warning signals as they change steadily along disturbances gradients, reflecting a new repartition of abundances in the functional space (Villéger et al., 2010).

Within a context of rising disturbance severity and frequency, it is necessary to measure functional community structure, in order to forecast the possible loss of species functional roles (Cardinale et al., 2012). Gaining knowledge of how functional diversity changes over time and space provides insights into changes in functional processes under global environmental changes. Specifically, long-term and broad data sets enable us to identify patterns of change, or resilience, that might go undetected.

Descriptors of functional diversity are thus promising to assess how resilient communities are to disturbances (Rincón-Díaz et al., 2018). Because functional diversity is connected to ecosystem functions and the provision of economically significant ecosystem services attributed to coral and rocky reefs, monitoring and measuring the state and trends in the functional diversity of reef fish communities is essential to ecosystem-based management (Micheli et al., 2014). Therefore, in order to direct conservation efforts and ecological resource management, it is imperative to measure and forecast the consequences of disturbance on patterns of biodiversity (Mouillot et al., 2013b).

1.4. Importance of spatiotemporal assessments

In the context of global change, focusing on how functional diversity varies over space and time is crucial for understanding ecosystem functioning and resilience. This has led to a rise in interest in long-term ecological datasets in recent years (Magurran et al., 2010; Dornelas et al., 2025), such as the BioTIme 2.0 database. Ecosystem and biodiversity responses to change recorded in long-term datasets may vary across regions, even when the same sorts of organisms are involved, because the causes of biodiversity variations might vary spatially (Chown et al., 2004). This variability highlights the need to assess temporal biodiversity changes in different regions. With simpler but still highly complex reef communities compared to other tropical regions around the globe, the Eastern Tropical Pacific (ETP) presents a great opportunity to assess how reef fish taxonomic and functional biodiversity has changed regarding regional environmental and anthropogenic pressures.

1.5. Drivers of diversity on coral reefs and in the Eastern Tropical Pacific (ETP)

While coral reefs only cover 0.2% of the ocean surface, they are home to more than 25% of the fish species (Morrison et al., 2019). They offer coastal protection, livelihoods, and food for millions of people around the tropics (Cinner et al., 2016; Woodhead et al., 2019). However, they are particularly threatened by the rise of sea water temperatures (SST), ocean acidification, overfishing, tourism, and coastal development (Jackson et al., 2001; Halpern et al., 2008). The thermal stress resulting from increased SST can lead to breakdown of the coral-algal symbiosis, and ultimately cause bleaching (Baker et al., 2008). Ocean acidification is caused by higher levels of dissolved CO2 in seawater (and thus a decrease in pH), which reduce the availability of carbonate for living organisms when interacting with carbon acid thus decreasing the rate of calcification (growth) of reef-building corals, leading to erosion at higher CO2 concentrations (Hoegh-Guldberg et al., 2007). Primary productivity from phytoplankton is also something influencing the reef ecosystem providing food for many coral reef associated organisms (Yahel et al., 1998; Wild et al., 2008; Genin et al., 2009; Wyatt et al., 2010).

With nearly 40% of the global population living within 100 km of the coast, human density impacts reefs all over the world through direct damage such as dredging, or indirectly through runoff of sediment, pollution, sewage (Wear, 2016), and overfishing (Hughes et al., 2017). For instance, overfishing greatly impacts the coral reef ecosystem by removing larger species due to size-selective harvesting (Genner et al., 2010). Furthermore, many countries with coral reefs have no sewage treatment available; across the Caribbean and Latin America, 86% of wastewater is sent out untreated (UNEP/GPA Coordination Office 2006) which has been shown to impact fish communities (Pastorok & Bilyard, 1985; Reopanichkul et al., 2009; Foo et al., 2021). Those threats have degraded coral reefs all over the tropics with a 14% global loss of reef surface in the last decade (Souter et al., 2021), causing a loss of structural variety, which lowers biomass and species diversity (Graham et al., 2007; Aguilar-Medrano & Calderon-Aguilera, 2016).

The Eastern Tropical Pacific (ETP), having less than 0.5% of the world's coral reefs, is one of the least studied coral reef regions in the world (Souter et al., 2021). Yet, it is home to some endemic species [70 % of species of marine fish are endemic to the region (Robertson & Allen, 2024)], and to a livelihood of millions of people across Central and South Americas (Souter et al., 2021). Such a high endemism in fish species makes it important to monitor those in spatiotemporal assessments, due to a higher risk of species extinction. The average coral cover in the ETP declined from 34.6% in 1998 to 22.8% in 2019 (Souter et al., 2021). This decline was caused by coastal development, eutrophication, and land use practices which have increased in the ETP, suggesting pressures from the degradation of coastal processes (Souter et al., 2021). On top of that, live coral cover as well as the production of carbonate in the ETP is dropping acutely with the warming waters trend (Tortolero-Langarica et al., 2022). The change in these variables erases the tridimensional structure of coral reefs, and with it, the habitats of all the reef-related species, including reef fish (Tortolero-Langarica et al., 2022), leaving places for algae to spread and grow replacing coral cover (Souter et al., 2021). Studies suggest higher rates of sedimentation and eutrophication in the ETP, especially in the Central Mexican Pacific (Martínez-Castillo et al., 2020). Although, the coral communities do not seem impacted by that (Martínez-Castillo et al., 2020), which suggests that reefs that develop under variable water conditions (ENSO, low pH, high seasonal variability) may have greater resistance threshold due to the background and life history of the coral community (Romero-Torres et al., 2020), which can make them future refuges for corals under the current increase in global temperatures and anthropogenic pressures (Martínez-Castillo et al., 2020).

1.6. Objectives and hypotheses

In this context, we investigate the changes in taxonomic and functional diversity of the ETP reef fish over space and time. We focus on five indices to describe the taxonomic and functional composition of communities: species richness, functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), and functional originality (FOri), and focus on 13 localities comprising four geographical subregions (North Continental, North Oceanic, South Continental, and South Oceanic) across the ETP. Specifically, we asked (a) How have the taxonomic and functional facets of diversity changed over time in each geographical subregion within the ETP? Are these changes consistent across localities within a given subregion? (b) What is the relative importance of variation in abiotic factors (sea surface temperature (SST) and primary productivity (PP) and direct human impact (measured as Distance To Markets) in driving these changes?

Specifically, we hypothesized that (a) species richness would decrease at the lower latitudes due to migration towards cooler waters, and that those migrations will be seen in functional indices. More specifically, we expect a decrease over time in functional richness (Clay et al., 2023), which is closely linked to species richness, and in FDis due to increasing relative abundance of similar resistant species. We expect an increase in functional originality due to habitat degradation in coral reefs leading to a loss of functional redundancy (i.e. less species performing the same function) (Brandl et al., 2016),

(b) the continuous climate change on Earth will drive reef fish migration, as the sea surface temperature increases, and the surface waters primary production shifts (due to coral cover and nutrients availability variations), negative effects on fish metabolism are being observed. We expect SST (and sd(SST)) to have a negative effect on every index since higher temperatures impact fish metabolism (Boltaña et al., 2017; Volkoff & Rønnestad, 2020), which could lead to some species reaching their thermal limit. Since reef fish are known to have higher abundance with higher chlorophyll levels in other reef systems (Warmuth et al., 2024), we expect PP to have positive impacts on the metrics. As for distance to market, acting as a fishing pressure proxy (Brewer et al., 2013; Yeager et al., 2017), we predict it to have positive impacts, especially for species richness, FRic, and FDis since fishing activity is targeting bigger-sized fish (usually with high trophic level). These species are the ones generally located at the edges of the functional space. The removal of this type of species thus impacts the former indices. We expect localities and subregions to vary differently depending on their location inside the ETP (latitude, on the center, or at the edges) as species may migrate from warmer areas to colder ones.

2. Methodology

2.1. Study Area

The study area covers the Eastern Tropical Pacific (ETP) (Figure 3). The influence of strong cold (upwelling) currents is delimiting the North and South boundaries of the ETP at 25°N and 3°S. In the Northern area of the ETP, there flows the Californian current southward along the coast from the USA (California State) to Mexico (Baja California) creating a quick transition zone between tropical and temperate ecosystems (biogeographic barrier). In the southern area flows the Humboldt current northward from the coasts of Peru up to the South of Ecuador (also creating a biogeographic barrier). These barriers lead to regional endemism and separate the ETP into three provinces (biogeographic): two continental provinces (Cortez and Panamic), and one province covering the oceanic islands (Robertson & Cramer, 2009).

The ETP is also an isolated region due to physical and biogeographic barriers that are setting it apart from the other marine realms/regions (Robertson & Cramer, 2009). The barrier that separates the ETP and the rest of the Indo-Pacific realm is known as the Eastern Pacific Barrier, a deep ocean that extends 4000 km between Clipperton Atoll (ETP) and the Indo-Pacific islands (Robertson & Cramer, 2009). Another physical barrier is the Isthmus of Panama that separates the ETP and the Atlantic (Caribbean) since its closure three million years ago (Robertson & Cramer, 2009).

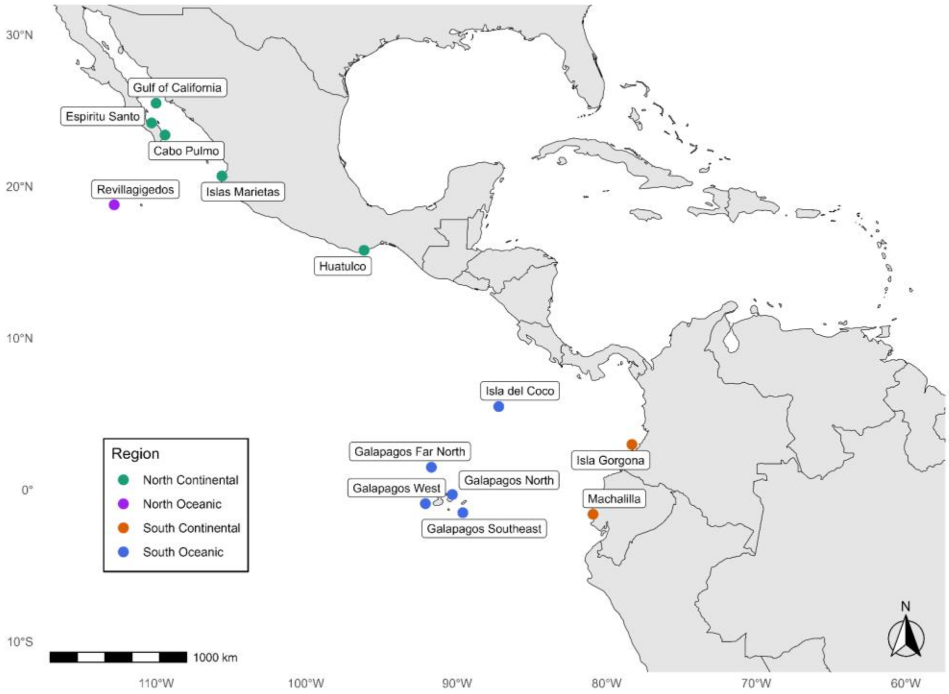


Figure 3. Map of the ETP. Each locality (point) is inside one of the four subregions defined by their location (North or South, and Continental or Oceanic). The colors of each point represent the four subregions. Green for Northern Continental, purple for Northern Oceanic, orange for Southern Continental, and blue for Southern Oceanic. All data provided by the Global Coral Reef Monitoring Network-ETPN.

The El Niño-Southern Oscillation (ENSO) is the primary source of variability in the oceanographic and meteorologic conditions of the ETP, alternating between El Niño, La Niña, and neutral phases over periods during from 2 to 7 years, with individual events generally lasting approximately a year (Fiedler, 2002). The Humboldt cold current and equatorial upwellings create a cold tongue throughout the equatorial latitude (Fiedler & Lavín, 2017), resulting in colder SST at the lowest latitudes that extend westward. Along the coasts of South Mexico and Guatemala, emerges the eastern Pacific warm pool characterized by temperatures greater than 27,5°C (Fiedler & Lavín, 2017). The ETP is also characterized by spatial differences in terms of surface water salinity. The lowest values can be found in the Gulf of Panama (29–31 psu), due to extreme freshwater input during the summer monsoon rainfall along the Pacific slope of Central America (Amador et al., 2006). Low pH values are characteristic of the ETP, which lowers aragonite saturation values, which thus lowers the calcium carbonate production needed for reef-building corals (Manzello et al., 2008).

The study focuses on 13 locations (Figure 3) surveyed for at least seven years or more and located inside Marine Protected Areas (MPAs). These included the "Reserva de la Biosfera Isla San Pedro Martir" and “Zonas de refugio Puerto Libertad" in the Gulf of California, “Parque Nacional Archipiélago Espíritu Santo” , Cabo Pulmo National Park, Islas Marietas National Park, Revillagigedo National Park in Mexico, Isla de Coco National Park in Costa Rica, Nacional Natural Park Isla Gorgona in Colombia, as well as Machalilla National Park, and the far North, North, South East and Western Galapagos National Park in Ecuador. Each locality was chosen with four criteria: (1) there must be at least five years of sampling, (2) with transects during both dry and rainy seasons, (3) inside National Parks, and (4) at the same isobath. We decided to cluster the localities into four subregions: Northern Continental (Gulf of California, Espíritu Santo, Cabo Pulmo, Islas Marietas, and Huatulco), Northern Oceanic (Revillagigedo Archipelago), Southern Continental (Isla Gorgona, and Machalilla), and Southern Oceanic (Isla del Coco and the four localities within the Galapagos Archipelago) (Figure 3). Comparison will be made among subregions to understand broader spatial patterns, and across localities within those subregions to account for a more local spatial scale.

2.2. Data collection

2.2.1. *In situ* fish biodiversity assessments

Species abundances were retrieved by Underwater Visual Census (UVCs) at 13 different localities across the whole ETP (i.e. Mexico, Costa Rica, Colombia, and Ecuador), from 2005 to 2023. The ETP Node of the Global Coral Reef Monitoring Network (GCRMN-ETPN), which collected the field data, led efforts to compile and homologate all datasets. The GCRMN is a network of scientists and organizations that focus on monitoring the condition of coral reefs around the world. The aim is to provide the best available data on health and conservation status of coral reefs. Data were collected at sites with rocky reefs, coral formations and coral reefs. During UVCs, the surveyor identified at the species or genus level and counted all fish species observed in the water column and on the bottom of belt transects. The area per transects varied between 50 and 250 m2 and all transects were located above the 35 m isobath. As the transects of the UVCs did not cover the same area (from 50m2 up to 250m2), a standardization of the abundance was performed. We ended up with densities (number of species per m2) as abundances.

2.2.2. Compilation of trait data

We characterized all species observed in the UVCs using six morphological and behavioral traits which are linked to key functions supported by reef fish (Villéger et al., 2008; Mouillot et al., 2014; Quimbayo et al., 2021) and that have been used in a handful of studies describing the functional structure of fish assemblages (Parravicini et al., 2021; Quimbayo et al., 2021; Dubuc et al., 2023). We chose six different traits of fish species: (1) body size (length from 3.8 to 333 cm) (numeric and continuous variable), (2) trophic level that ranges from 2, to 5 (quantitative variable), (3) diel activity (qualitative trait with three levels: diurnal, nocturnal, or both), (4) home range (qualitative trait with three levels: sedentary, mobile, and very mobile), (5) level (or position) in the water column (qualitative ordered trait with three levels: bottom, low, high), and (6) group size (qualitative ordered trait with five levels: solitary, pairing, small groups of 3-20 individuals, medium groups of 20-50 individuals, and large groups of >50 individuals). We extracted all trait values from Quimbayo et al. (2021), from FishBase and from the Shorefishes of the Tropical Eastern Pacific online information system (Robertson & Allen, 2024).

2.2.3. Compilation of drivers of fish biodiversity change

Optimum Interpolation Sea Surface Temperature (OISST) with a 1/4° spatial resolution and a daily temporal resolution (Huang et al., 2021) were utilized to calculate a monthly average sea surface temperature (SST). SST was used as the principal driver of fish abundance shift under a warming world. We then calculated a monthly time series of net primary productivity (hereafter referred to as PP) in mgC m^{-2} day^{-1}. PP was based on a 25 km spatial resolution and 8-day temporal resolution model (Ryan-Keogh et al., 2023). PP is used as a proxy of ecosystem productivity and may serve as an indicator of food availability to sustain the warming-induced shifts in metabolic rates (Dillon et al., 2010). Finally, we extracted distance to market (DTM) which refers to “distance to provincial capital (in km) as a standardized metric of market access, as provincial capitals are likely to provide fishers access to national and export markets" (Yeager et al., 2017) to account for the fishing effort (Brewer et al., 2013). We computed the average and standard deviation of SST, and primary productivity for the four-month period prior to the transects periods for each site. Each parameter was extracted with the nearest coordinates associated with each site in the study area using the *extract* function from the *raster* R package version 3.6-32 (Hijmans et al., 2025) and the *st_as_sf* function from the *sf* R package version 1.0-21 (Pebesma, 2018; Pebesma & Bivand, 2023).

2.3. Data analysis

2.3.1. Computation of functional and taxonomic diversity indices

Functional analyses were computed using the R package *mFD* vers 1.0.7 (Magneville et al., 2022). We chose this package for the large number of functional indices it can compute. We computed trait-based distances between species using the Gower distance, which allows for the combination of quantitative and qualitative traits (Gower, 1971). We performed a Principal Coordinates Analysis (PCoA) based on the Gower's distance dissimilarity matrix, leading to functional spaces between two and ten dimensions. The quality of PCoA-based multidimensional spaces was evaluated using the mean absolute deviation (*mad*) between trait-based distances and distances in the functional space (Maire et al., 2015). We retained the first three PCoA axes, which had the lowest *mad* value, to compute the different indices. For the functional space visualizations, we chose to keep only the first and last year of sampling at the locality level. The functional space representations were made using the first two axes (PC1-PC2). The statistical test determining the correlation between the traits and the PCoA axis is done using Kruskal-Wallis' eta2 for categorical traits, and Pearson's r2 for continuous traits.

Five indices were computed: one taxonomic index (species richness), and four different functional indices (FRic, FEve, FDis, and FOri). Species richness is the number of unique reef fish species present at one site, accounting for taxonomic diversity based on occurrences. FRic represents the whole volume occupied by every species at one site. This index is determined only by the occurrences of the peripheral species. The regularity of distribution in the functional space (FEve) is an abundance-based index used to assess shifts in the functional structure and distribution of species. FDis, corresponding to the mean deviation to the center of the whole species assemblage at one site, is weighted by abundances. FOri is also an abundance-based index. It computes the uniqueness of species in the functional space. Together, these five indices give a multifaceted view of reef fish taxonomic and functional structure, and can detect bigger changes, like species gain or loss, and also smaller changes, like abundance shifts and collapses.

2.3.2. Statistical modelling

Generalized linear mixed-effects models (GLMMs) were used for each subregion and locality, for each taxonomic or functional index with *year* as a fixed effect to account for the temporal variation at the locality scale. As a better fitting distribution, a gaussian was used for all indices with the exception of FOri for which a beta distribution was a better fit. The *anova* function from the *stats* R package version 4.1.5 (R Core Team, 2025) was used to assess the fitness of each model. The model used was:

Index ~ year + (1 | site)

This model assumes a linear relationship between the index and year with the sites as a random effect. For each fitted model, we extracted the slope coefficient and its associated p-value to assess the significance of temporal trends. Predicted values and 95% confidence intervals over the years were obtained with the use of the *ggpredict* function from the *ggeffects* package version 2.3.0 (Lüdecke, 2018). All models were computed using the function *glmmTMB* from the R package *glmmTMB* version 1.1.11 (Brooks et al., 2017).

To assess the relative role of different factors influencing diversity, we used GLMM models with the R package glmmTMB (Brooks et al., 2017) as these models estimate fixed and random effects. All predictors were standardized (mean = 0, SD = 1) before fitting the models using the *scale* function in R. This was done for coefficient compatibility and model convergence.

The models used were:

$$\textbf{Index} \sim \textbf{SST + sd SST + PP + sd PP + Dist to market + (1 | locality/site),}$$

with site nested inside locality as random effects (1 | locality/site)). Functions *check_collinearity* and *check_model* from the *performance* package version 0.15.0 (Lüdecke et al., 2021) were used to check that the predictors were not highly correlated, and to check normality of residuals, normality of random effects, and homogeneity of variance. The *simulateResiduals* function from the R package *DHARMa* was used on each model to check for overdispersion, and the distribution of outliers (Hartig et al., 2024). All statistical modelling steps were performed using R statistical software version 4.5.1 (R Core Team, 2025). All graphical visualizations were created using the *ggplot2* R package version 3.5.2 (Wickham et al., 2025).

3. Results

3.1. How has functional diversity changed at the subregional scale?

The trajectories of fish functional diversity over time differed across subregions (Figure 4). Species richness decreased by 22% and 25% respectively in both the North Continental and the South Oceanic subregions, while the two others remained stable (non-significant slope) (Figures 4a). The same subregions showed a significant decrease in FRic, exhibiting the same magnitude (Figures 4b).

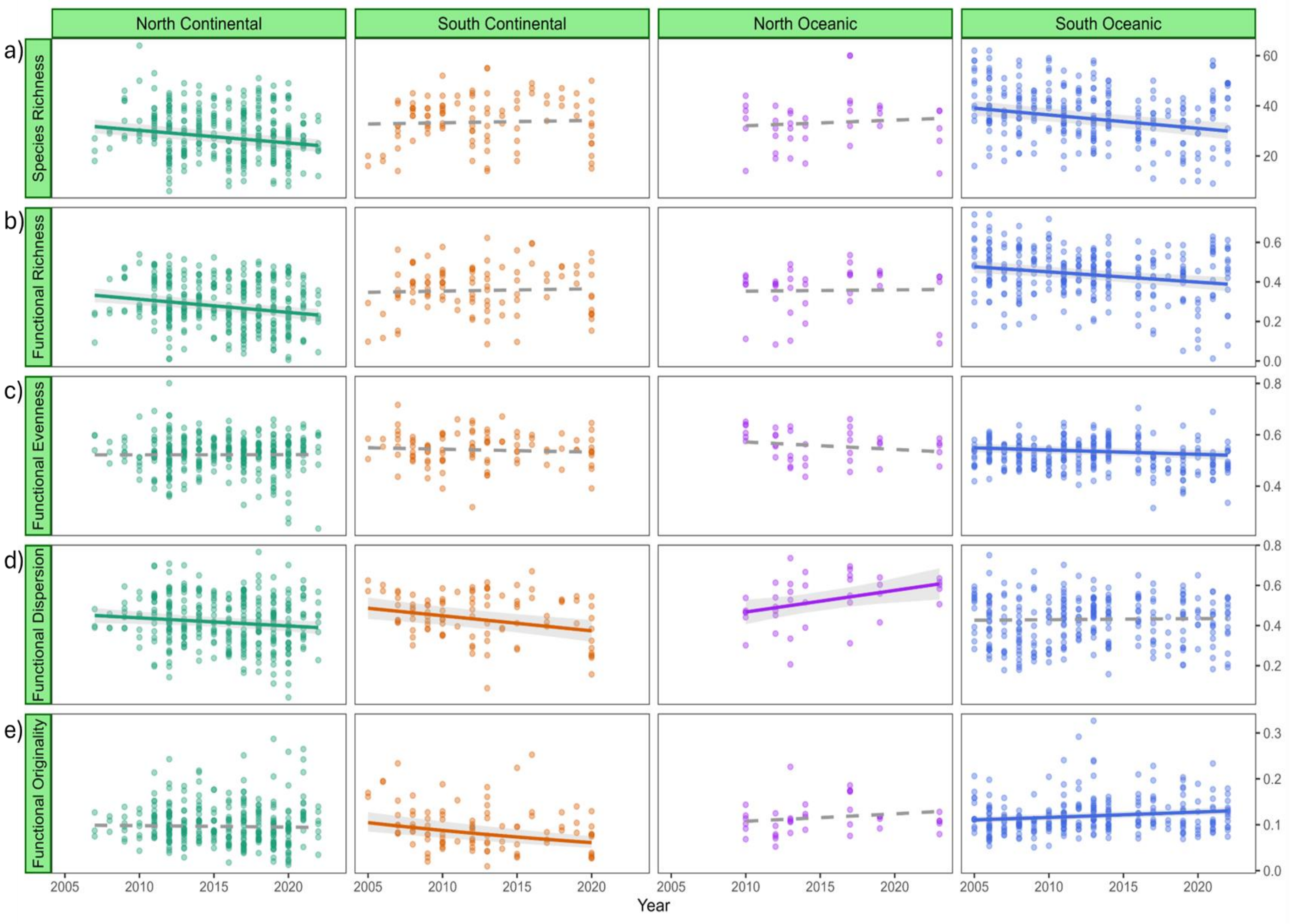


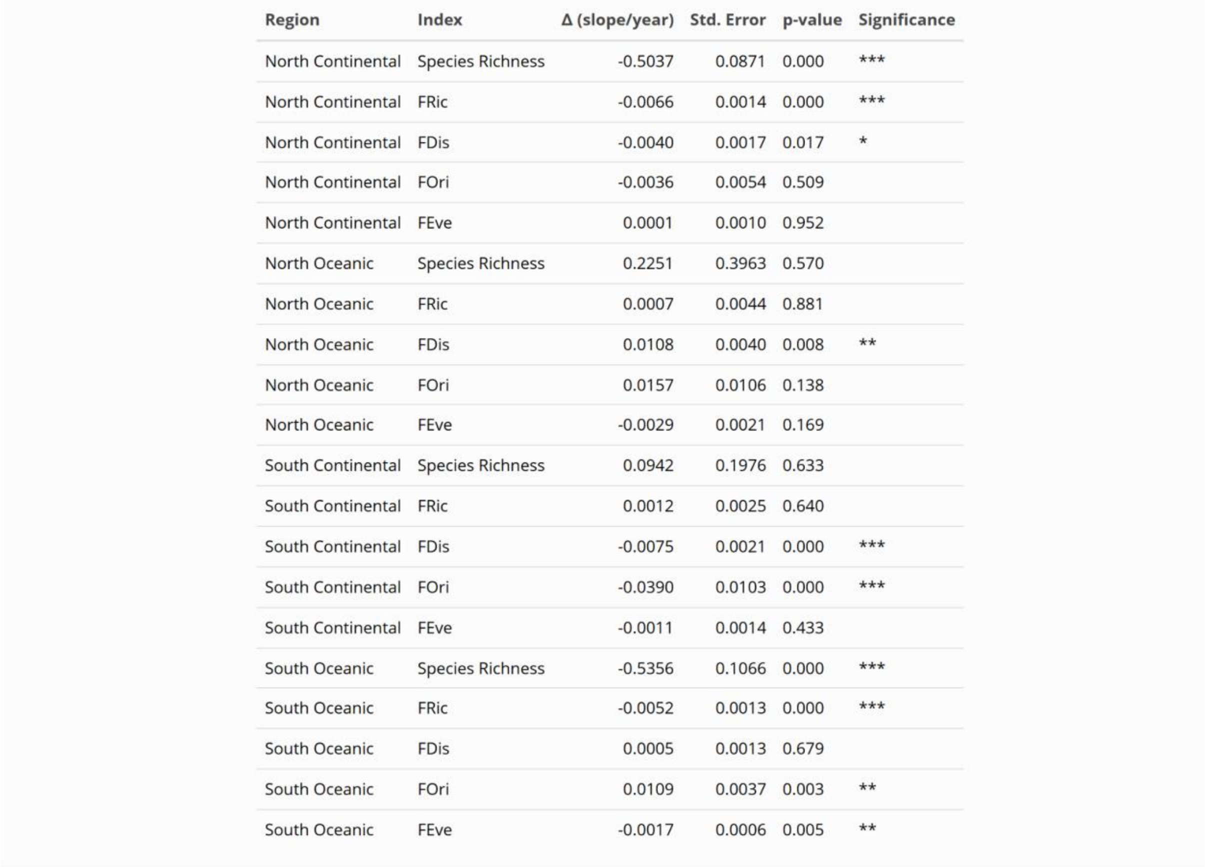
Figure 4. Taxonomic and functional indices over time for each subregion. (a) Species richness, (b) functional richness, (c) functional evenness, (d) functional dispersion, (e) functional originality. Each point represents a site inside the subregion. Models (GLMMs) are shown with a colored line when the variation is significant ($p < 0.05$), and with a grey dashed line when the variation is not significant.

In terms of functional evenness, the majority of subregions remained stable with no significant trends. Only the South Oceanic subregion showed a drop in FEve (Figures 4c). This decrease is slight in magnitude with a 5% drop.

The two continental subregions experienced a drop in FDis: a slight drop in the North (-13%), and a bigger drop in the South (-23%) (Table 1). The South Oceanic remained stable, while the North Oceanic showed an increase (+30%) (Figures 4d).

FOri has changed significantly inside the two southern subregions (Figures 4e). For the South Continental, FOri halved, while an 18% increase took place in the South Oceanic subregion. We must take into account that FOri values are very low (~0.1) which impacts the percentage magnitude of change.

Table 1. Statistical values of the GLMM models to account for the change at the subregional scale. Significance: 0.05 < *, < 0.01 <**, < 0.001 < ***. P-values are reported with three digits after the decimal point. Δ (slope/year) represents the model's variation per year. FRic: functional richness; FEve: functional evenness; FDis: functional dispersion; FOri: functional originality.



Region	Index	Δ (slope/year)	Std. Error	p-value	Significance
North Continental	Species Richness	-0.5037	0.0871	0.000	***
North Continental	FRic	-0.0066	0.0014	0.000	***
North Continental	FDis	-0.0040	0.0017	0.017	*
North Continental	FOri	-0.0036	0.0054	0.509	
North Continental	FEve	0.0001	0.0010	0.952	
North Oceanic	Species Richness	0.2251	0.3963	0.570	
North Oceanic	FRic	0.0007	0.0044	0.881	
North Oceanic	FDis	0.0108	0.0040	0.008	**
North Oceanic	FOri	0.0157	0.0106	0.138	
North Oceanic	FEve	-0.0029	0.0021	0.169	
South Continental	Species Richness	0.0942	0.1976	0.633	
South Continental	FRic	0.0012	0.0025	0.640	
South Continental	FDis	-0.0075	0.0021	0.000	***
South Continental	FOri	-0.0390	0.0103	0.000	***
South Continental	FEve	-0.0011	0.0014	0.433	
South Oceanic	Species Richness	-0.5356	0.1066	0.000	***
South Oceanic	FRic	-0.0052	0.0013	0.000	***
South Oceanic	FDis	0.0005	0.0013	0.679	
South Oceanic	FOri	0.0109	0.0037	0.003	**
South Oceanic	FEve	-0.0017	0.0006	0.005	**

3.2. How have taxonomic and functional diversity changed in localities?

When comparing the temporal trajectories of fish diversity across localities, some patterns within subregions can be highlighted, although it is not consistent across subregions. Species richness remained stable or decreased slightly in North Continental localities species richness with the steepest decrease in Espiritu Santo (-42%, Figure 5, Table 2). Localities from the Oceanic subregions follow the same trend with either no changes (Revillagigedo, Galapagos Far North, Galapagos Southeast), or slight decrease (-18% at Isla del Coco, -33% at Galápagos North) (Figure 5, Table 2). The South Continental exhibits variations between its two localities: Machalilla recorded a decrease of 33% in the number of species and Isla Gorgona a 53% increase (Figure 5, Table 2).

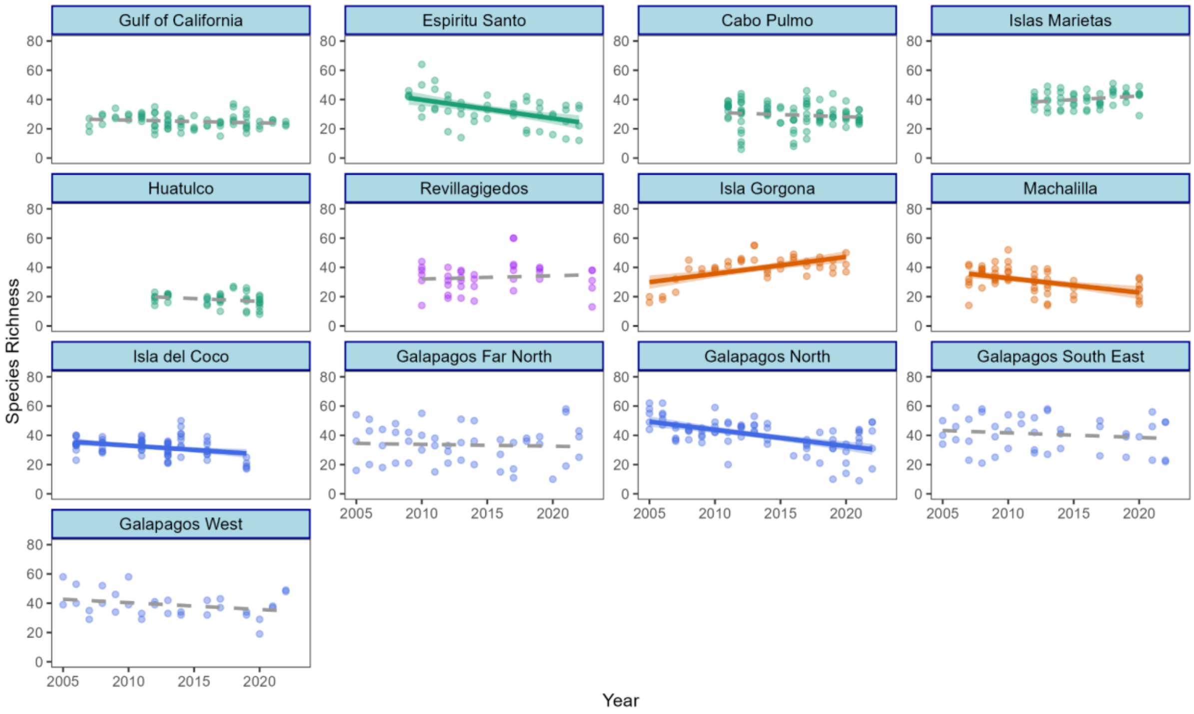


Figure 5. Species richness (number of species) over time for the 13 localities. Each point represents a site inside the locality. The subregions in which the localities are located are shown with the points in the color correspondent (green: North Continental, purple: North Oceanic, orange: South Continental, blue: South Oceanic). Models (GLMMs) are shown with a line colored in the subregional color when the variation is significant ($p < 0.05$), and grey when the model is not significant.

Functional richness varied differently across the ETP (Figure 6). FRic is following the same trend as species richness as they both are highly correlated. Inside the North Continental, North Oceanic, and South Oceanic, localities stayed constant (Gulf of California, Cabo Pulmo, Revillagigedo, Isla del Coco, Galapagos Far North, Galapagos Southeast), decreased (-43% at Espiritu Santo, -43% at Huatulco, -36% at Galapagos North, and -22% at Galapagos West). The only locality to slightly increase (+14%) in these three subregions was Islas Marietas (Figure 6, Table 2). Isla Gorgona and Machalilla showed the same pattern for FRic as species richness, meaning that the former locality increased (+73%) and the latter decreased (-40%) (Figure 6, Table 2).

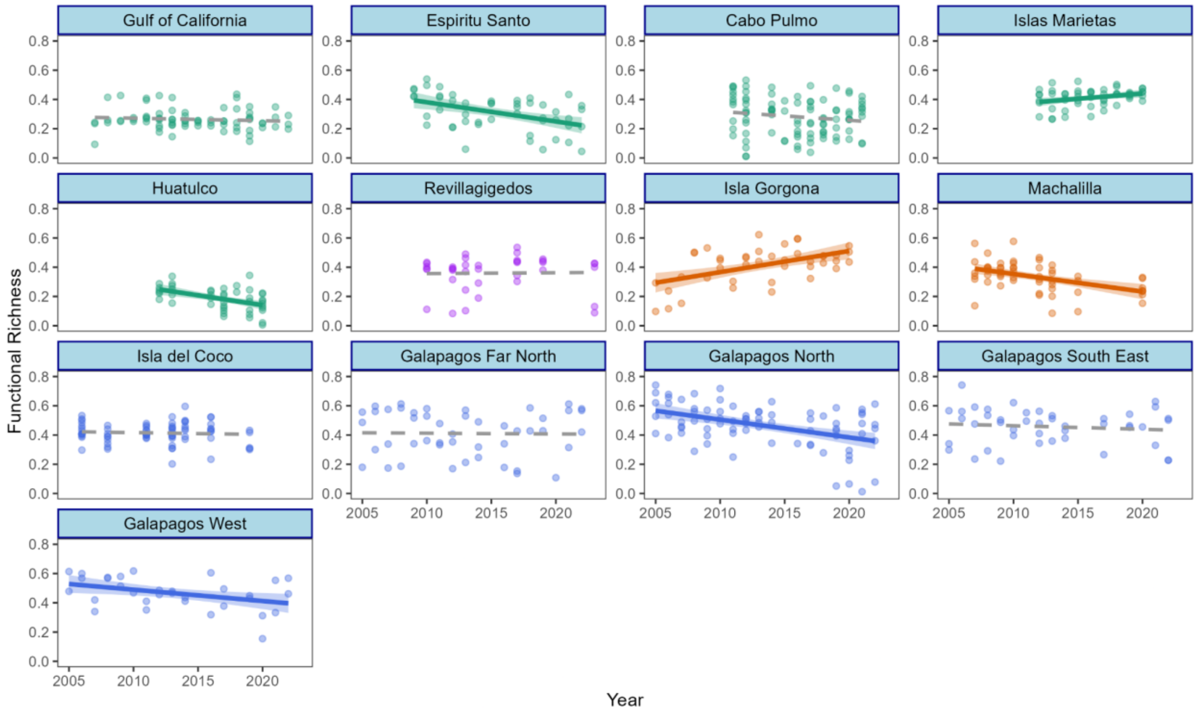


Figure 6. Functional richness (volume of all the species inside the functional space) over time for the 13 localities. Each point represents a site inside the locality. The colors represent the subregions in which the localities are located (green: North Continental, purple: North Oceanic, orange: South Continental, blue: South Oceanic). Models (GLMMs) are shown with a line. Subregional colors are used when the model is significant ($p < 0.05$), and grey dashed lines when the model is not.

Functional evenness has not changed during the study period for each locality (Figure 7). Galapagos North is the only exception with a very slight 7% decrease (Table 2).

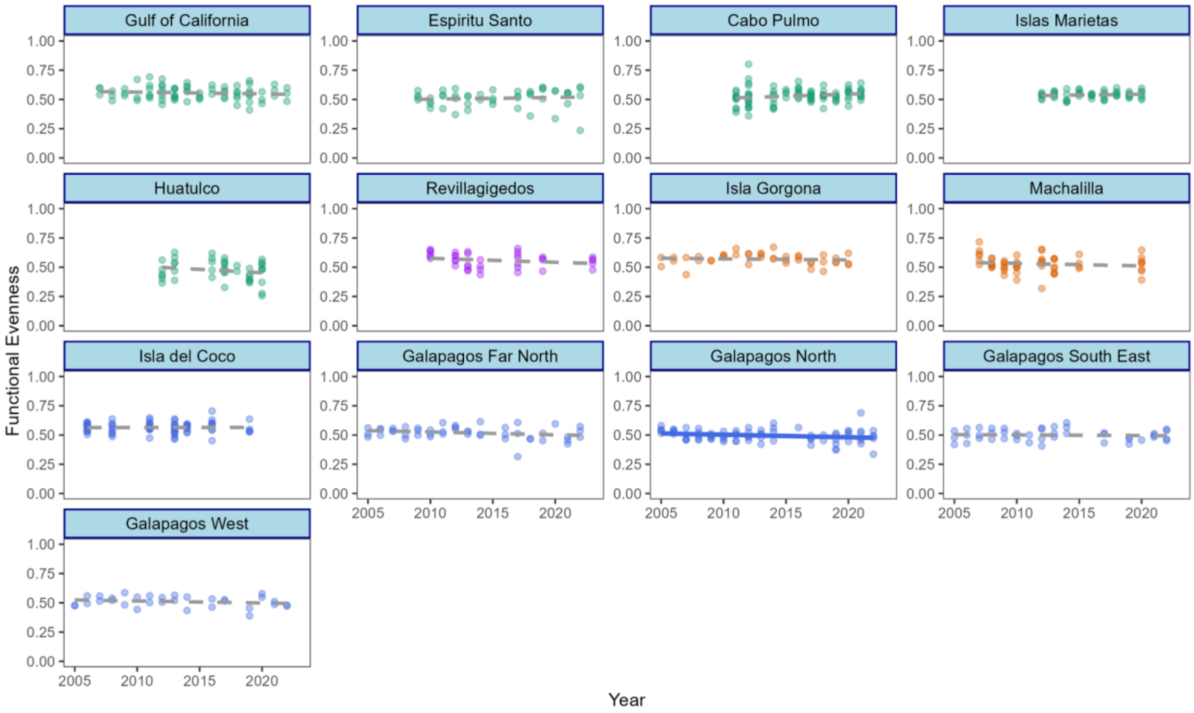


Figure 7. Functional evenness (evenness of distribution of species inside the functional space) over time for the 13 localities. Each point represents a site inside the locality. The colors represent the subregions in which the localities are located (green: North Continental, purple: North Oceanic, orange: South Continental, blue: South Oceanic). Models (GLMMs) are shown with a line. Subregional colors are used when the model is significant ($p < 0.05$), and grey dashed lines when the model is not.

The majority of the localities have not recorded any change concerning FDis (Figure 8). Nine localities across the ETP either stagnated or decreased slightly in FDis. Which is the case for all the North Continental localities (except Huatulco with a 39% decrease), and all the Galapagos Archipelago (Figure 8, Table 2), although Galapagos West experienced a 22% decrease. The North Oceanic (composed only by Revillagigedo), and Isla del Coco are the two localities that increased moderately in FDis with +23% and +29% respectively (Figure 8, Table 2). Huatulco and Machalilla, both Continental localities (North and South respectively), exhibit bigger decreases with 40% (Figure 8, Table 2).

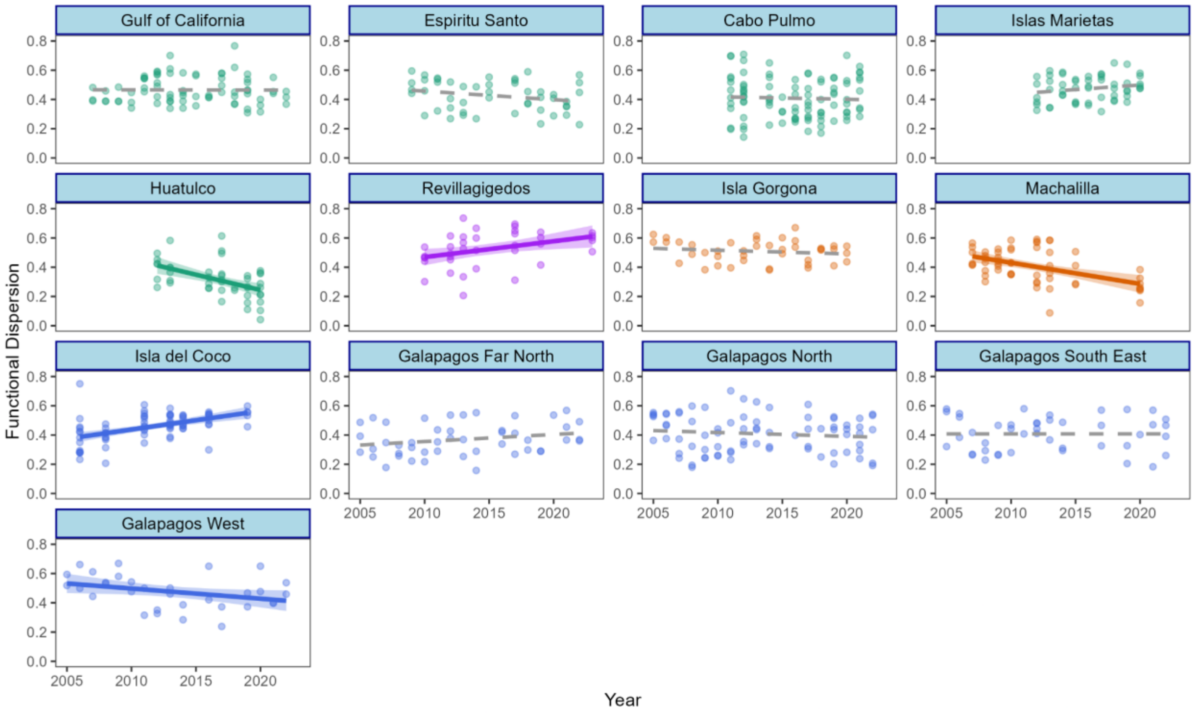


Figure 8. Functional dispersion (the weighted deviation to center of gravity of species in the assemblage) over time for the 13 localities. Each point represents a site inside the locality. The colors represent the subregions in which the localities are located (green: North Continental, purple: North Oceanic, orange: South Continental, blue: South Oceanic). Models (GLMMs) are shown with a line. Subregional colors are used when the model is significant ($p < 0.05$), and grey dashed lines when the model is not.

Concerning functional originality, each locality follows a pattern at the subregional scale. All localities in North Continental stay stable. The locality in North Oceanic (Revillagigedos) is also stable. Both localities in the South Continental slightly decreased in FOri (-38% for Isla Gorgona and -50% for Machalilla). And all localities in the South Oceanic stagnate except Isla del Coco with a 58% increase (Figure 9, Table 2).

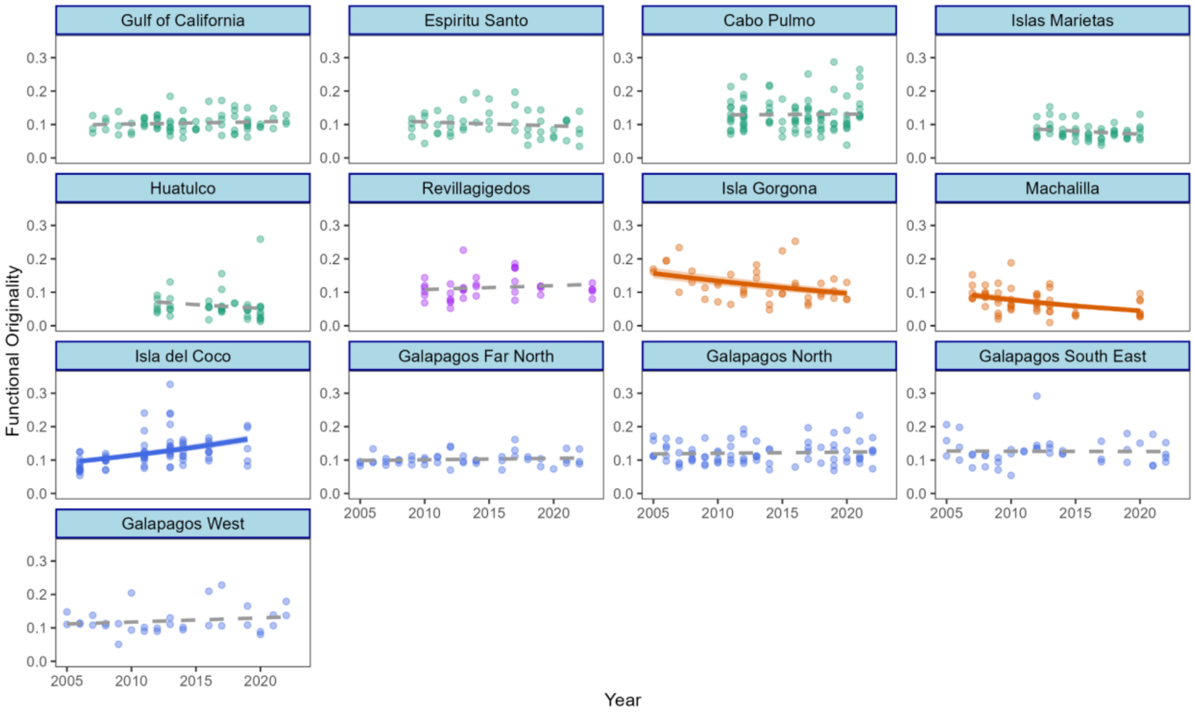
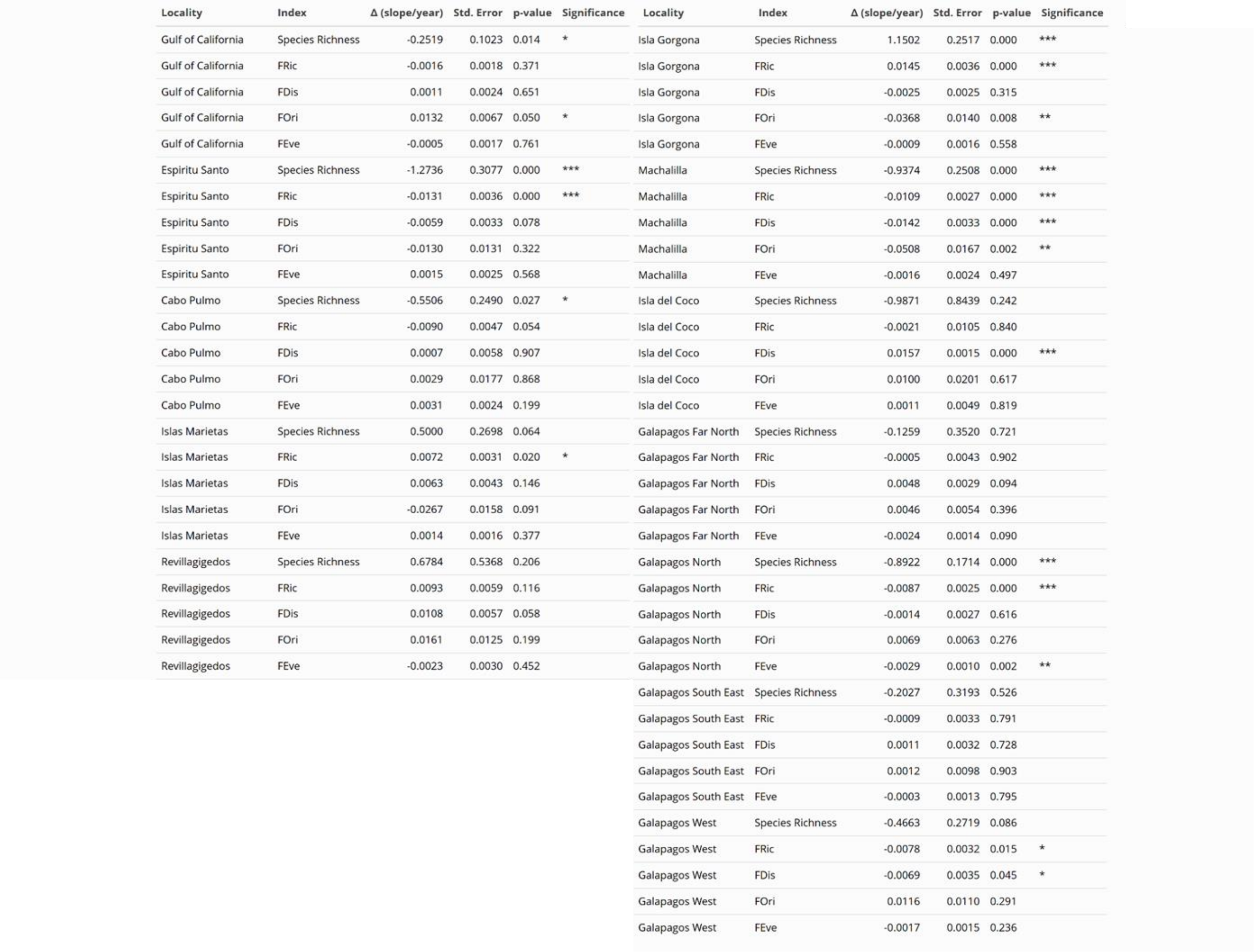


Figure 9. Functional originality (the isolation of a species in the functional space) over time for the 13 localities. Each point represents a site inside the locality. The colors represent the subregions in which the localities are located (green: North Continental, purple: North Oceanic, orange: South Continental, blue: South Oceanic). Models (GLMMs) are shown with a line. Subregional colors are used when the model is significant ($p < 0.05$), and grey dashed lines when the model is not.

Table 2. Statistical values of the GLMM models to account for the change at the subregional scale. Significance: 0.05< * < 0.01 < ** <0.001 < ***. P-values are reported with three digits after the decimal point. Δ (slope/year) represents the model's variation per year. FRic: functional richness; FEve: functional evenness; FDis: functional dispersion; FOri: functional originality.



Locality	Index	Δ (slope/year)	Std. Error	p-value	Significance
Gulf of California	Species Richness	-0.2519	0.1023	0.014	*
Gulf of California	FRic	-0.0016	0.0018	0.371	
Gulf of California	FDis	0.0011	0.0024	0.651	
Gulf of California	FOri	0.0132	0.0067	0.050	*
Gulf of California	FEve	-0.0005	0.0017	0.761	
Espiritu Santo	Species Richness	-1.2736	0.3077	0.000	***
Espiritu Santo	FRic	-0.0131	0.0036	0.000	***
Espiritu Santo	FDis	-0.0059	0.0033	0.078	
Espiritu Santo	FOri	-0.0130	0.0131	0.322	
Espiritu Santo	FEve	0.0015	0.0025	0.568	
Cabo Pulmo	Species Richness	-0.5506	0.2490	0.027	*
Cabo Pulmo	FRic	-0.0090	0.0047	0.054	
Cabo Pulmo	FDis	0.0007	0.0058	0.907	
Cabo Pulmo	FOri	0.0029	0.0177	0.868	
Cabo Pulmo	FEve	0.0031	0.0024	0.199	
Islas Marietas	Species Richness	0.5000	0.2698	0.064	
Islas Marietas	FRic	0.0072	0.0031	0.020	*
Islas Marietas	FDis	0.0063	0.0043	0.146	
Islas Marietas	FOri	-0.0267	0.0158	0.091	
Islas Marietas	FEve	0.0014	0.0016	0.377	
Revillagigedos	Species Richness	0.6784	0.5368	0.206	
Revillagigedos	FRic	0.0093	0.0059	0.116	
Revillagigedos	FDis	0.0108	0.0057	0.058	
Revillagigedos	FOri	0.0161	0.0125	0.199	
Revillagigedos	FEve	-0.0023	0.0030	0.452	
Isla Gorgona	Species Richness	1.1502	0.2517	0.000	***
Isla Gorgona	FRic	0.0145	0.0036	0.000	***
Isla Gorgona	FDis	-0.0025	0.0025	0.315	
Isla Gorgona	FOri	-0.0368	0.0140	0.008	**
Isla Gorgona	FEve	-0.0009	0.0016	0.558	
Machalilla	Species Richness	-0.9374	0.2508	0.000	***
Machalilla	FRic	-0.0109	0.0027	0.000	***
Machalilla	FDis	-0.0142	0.0033	0.000	***
Machalilla	FOri	-0.0508	0.0167	0.002	**
Machalilla	FEve	-0.0016	0.0024	0.497	
Isla del Coco	Species Richness	-0.9871	0.8439	0.242	
Isla del Coco	FRic	-0.0021	0.0105	0.840	
Isla del Coco	FDis	0.0157	0.0015	0.000	***
Isla del Coco	FOri	0.0100	0.0201	0.617	
Isla del Coco	FEve	0.0011	0.0049	0.819	
Galapagos Far North	Species Richness	-0.1259	0.3520	0.721	
Galapagos Far North	FRic	-0.0005	0.0043	0.902	
Galapagos Far North	FDis	0.0048	0.0029	0.094	
Galapagos Far North	FOri	0.0046	0.0054	0.396	
Galapagos Far North	FEve	-0.0024	0.0014	0.090	
Galapagos North	Species Richness	-0.8922	0.1714	0.000	***
Galapagos North	FRic	-0.0087	0.0025	0.000	***
Galapagos North	FDis	-0.0014	0.0027	0.616	
Galapagos North	FOri	0.0069	0.0063	0.276	
Galapagos North	FEve	-0.0029	0.0010	0.002	**
Galapagos South East	Species Richness	-0.2027	0.3193	0.526	
Galapagos South East	FRic	-0.0009	0.0033	0.791	
Galapagos South East	FDis	0.0011	0.0032	0.728	
Galapagos South East	FOri	0.0012	0.0098	0.903	
Galapagos South East	FEve	-0.0003	0.0013	0.795	
Galapagos West	Species Richness	-0.4663	0.2719	0.086	
Galapagos West	FRic	-0.0078	0.0032	0.015	*
Galapagos West	FDis	-0.0069	0.0035	0.045	*
Galapagos West	FOri	0.0116	0.0110	0.291	
Galapagos West	FEve	-0.0017	0.0015	0.236	

3.3. What is the role of climate change and fishing in driving these changes?

FRic is impacted positively by SST (0.007 ± 0.003, p = 0.032), SST sd (0.02 ± 0.007, p = 0.008), and PP (0.0001 ± 0.00004, p = 0.004), and negatively by PP sd (-0.00013 ± 0.00006, p = 0.02) (Figure 10). FDis is impacted positively by DTM (0.0002 ± 0.00006, p = 0.013). No significant effect is observed for species richness, FEve, and FOri with the predictors used

(Figure 10). Although not significant, species richness shows a positive trend with PP (2.23 ± 1.2, p = 0.06) and sd(SST) (0.639 ± 0.364, p = 0.007) (Figure 10).

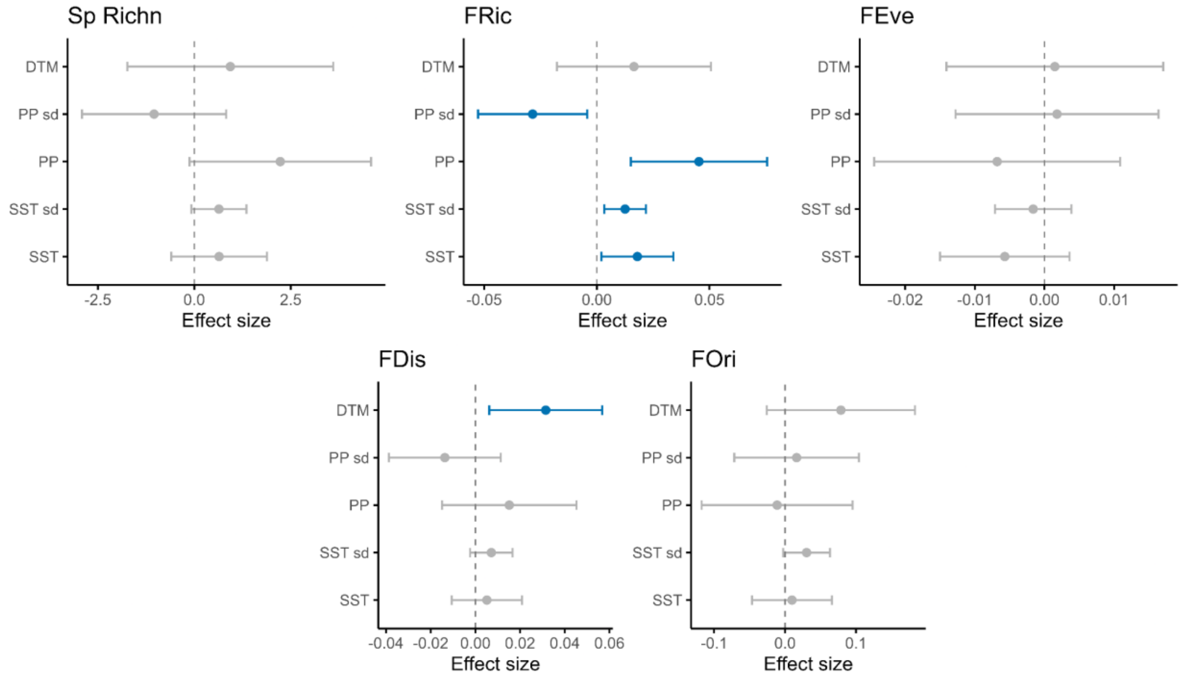


Figure 10. Effects of oceanographic and anthropogenic predictors on ETP reef fish taxonomic and functional diversity metrics. Oceanographic predictors: SST: sea surface temperature and PP: primary productivity, and their respective standard deviation, anthropogenic predictors: DTM: distance to market. Points represent mean estimates; lines represent 95% confidence intervals. Blue lines represent parameters with a significant effect on the metric.

3.4. Traits within the multidimensional space

Species positions inside the PCA space along PC1 are mostly informative regarding the species values of the home range, size group, and level water with an eta2 of 0.5 or above (Figure 4). A weaker influence of diel activity is also noticeable with an eta2 of 0.232. Diel activity, and trophic level are the only two traits to have a high correlation in the PC2 dimension (eta2 and r2 above 0.5), home range, size group, and body size present a weaker correlation (eta2 and r2 between 0.102 and 0.182). All the traits are thus significantly related to either PC1, PC2, or both (Figure 11).

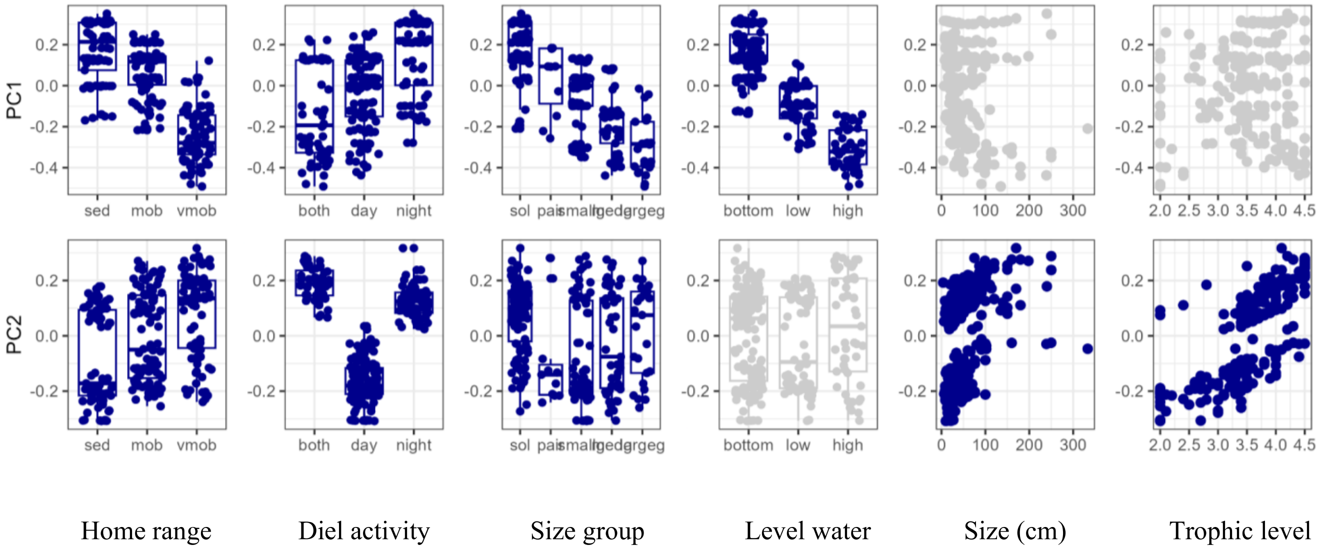
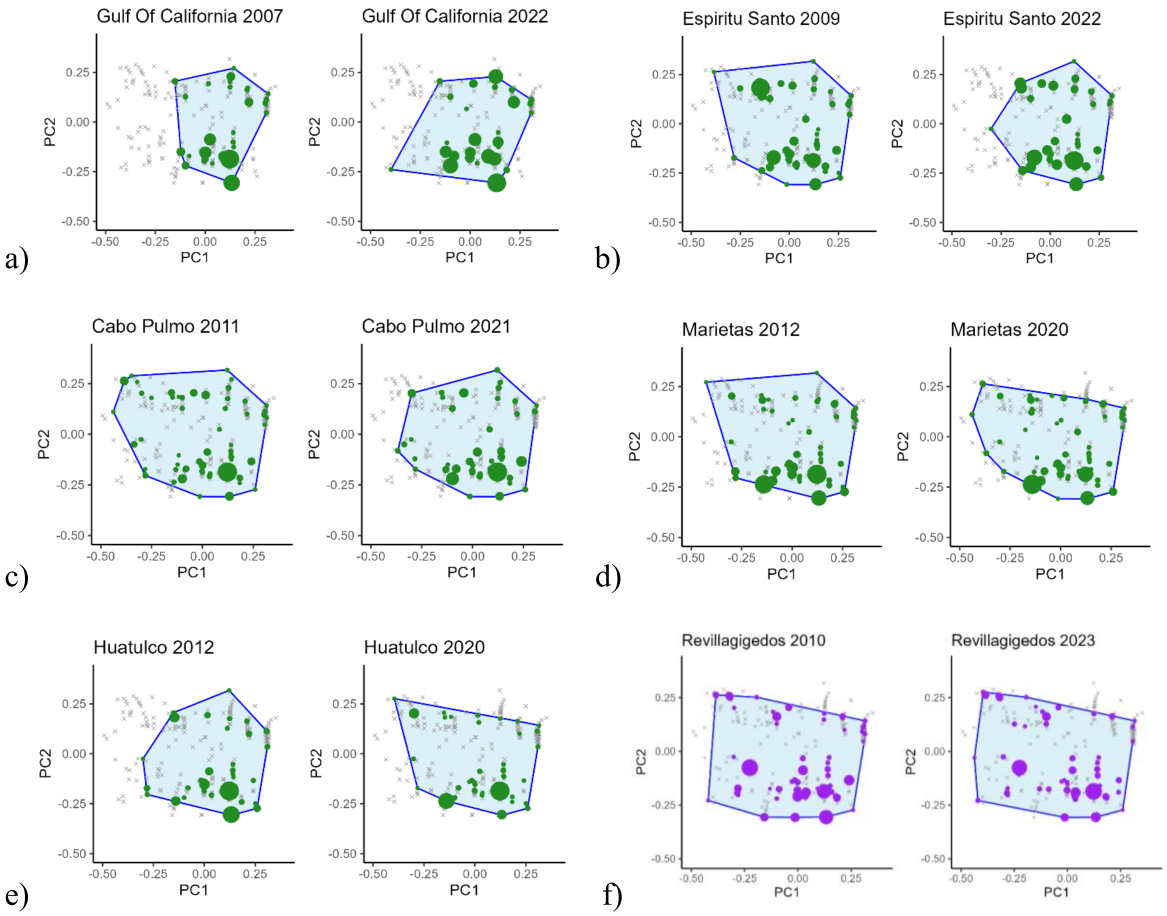
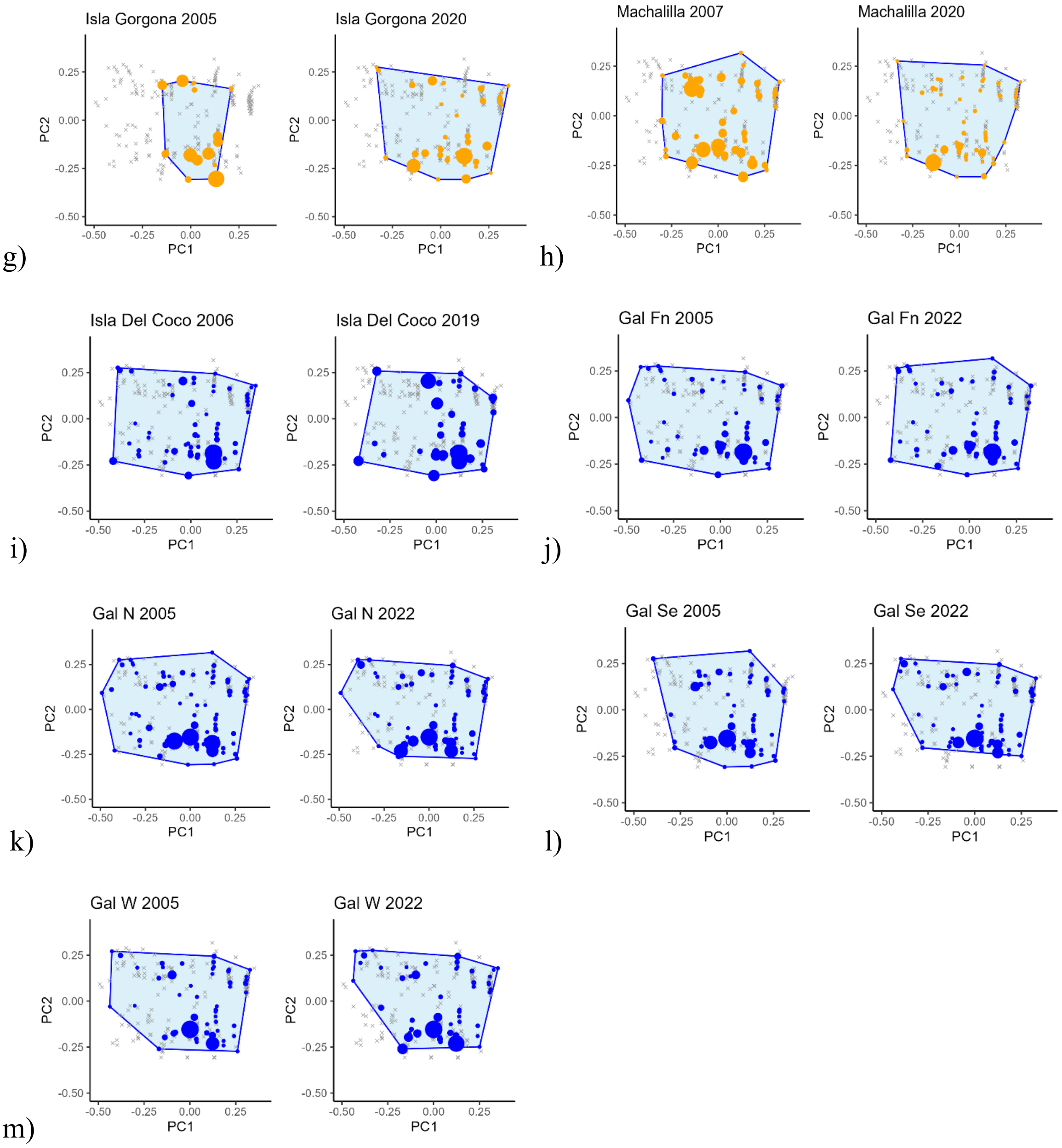


Figure 11. Relation between traits and PCoA axes, made using the *mFD* package. The color blue means that the trait (x axis) is significant along the corresponding PC (dimension) (y axis). The grey color means that the trait is not significant along the axis. Each point represents a species position in the functional space. Meaning of terms: 'sed' (sedentary), 'mob' (mobile), 'vmob' (very mobile), 'sol' (solitary), 'smallg' (small group), 'medg' (medium group), 'largeg' (large group).

3.5. Localities functional spaces

Overall, there were no major changes in the functional space between the first and last year of survey for most localities, although some differences are worth mentioning. The Figure 13 may help to visualize the contents of the functional space and the changes occurring inside of it. The Gulf of California experienced an increase in functional richness due to the presence of one species (low PC1, low PC2 values) in 2022 (Figure 12a). Espiritu Santo and Cabo Pulmo functional spaces did not change drastically in relative abundances and changed slightly in the volume (Figure 12b and c). This volume decrease is especially noticeable in Espiritu Santo where species with low PC1 values vanished. Islas Marietas did not change either in relative abundances or in species position with the exception of a few species (Figure 12d). Huatulco saw its functional space diminish at the top, but expand at low PC1 high PC2 values by only a few species (Figure 12e). Isla Gorgona is the only locality where an expansion of the species volume is observed. The abundances did shift to become more uneven (Figure 12g). On the other hand, the volume in Machalilla functional space stayed constant, but abundances shifted toward an assemblage dominated by one species (Figure 12h). Isla del Coco experienced a change in the relative species abundances with every species gaining dominance (Figure 12i). Revillagigedo and the Galapagos Far North and West localities did not experience any major changes concerning the species volume and relative abundance (Figure 12f, j, and m). In the Galapagos North and Southeast, there was no abundance shift between 2005 and 2022, but there was a loss of the lowest PC2-values species along the PC1 axis (Figure 12k and l).





g)

h)

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l)

m)

Figure 12. Functional spaces for the first and last year of sampling for each locality. (a) Gulf of California. (b) Espiritu Santo. (c) Cabo Pulmo. (d) Islas Marietas. (e) Huatulco. (f) Revillagigedo. (g) Isla Gorgona. (h) Machalilla. (i) Isla del Coco. (j) Galapagos Far North. (k) Galapagos North. (l) Galapagos Southeast. (m) Galapagos West. The blue polygon represents the volume occupied by the species (FRic). Dots represent each species and their relative abundance. Colors represent the subregions in which each locality belongs: North Continental in green, North Oceanic in purple, South Continental in orange, and South Oceanic in blue.

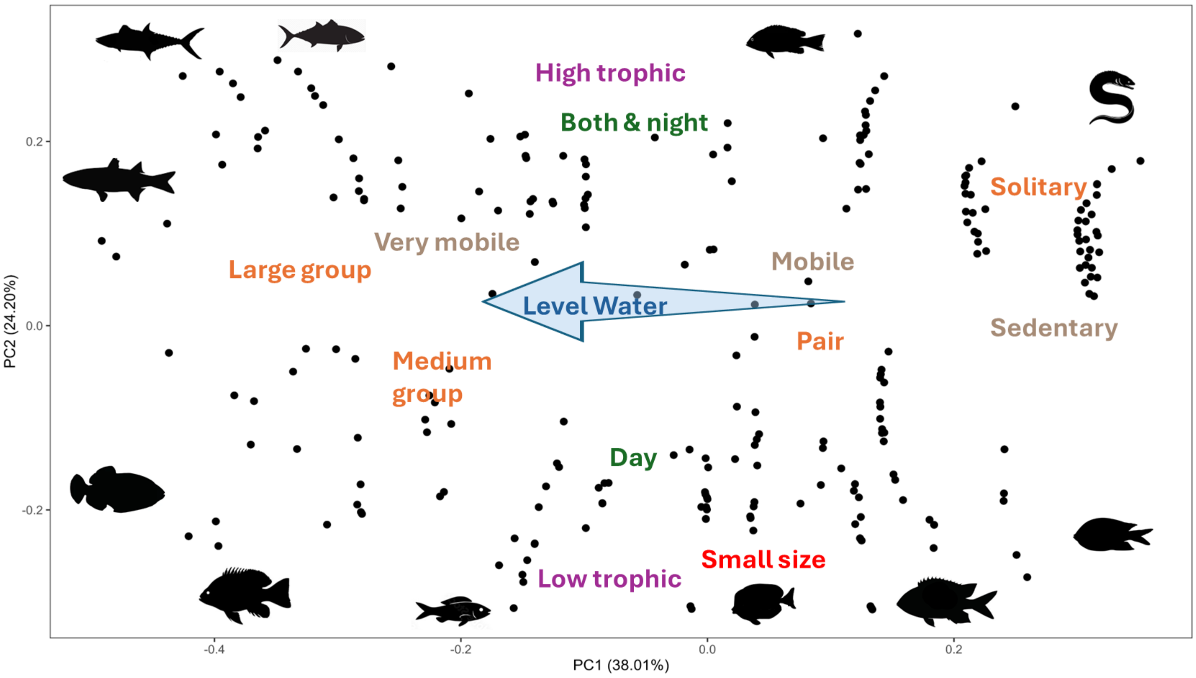

Figure 13. Functional space representing each trait and each species. With each trait: home range in beige, diel activity in green, size group in orange, level water in blue, body size in red; and trophic level in purple. Fish silhouettes represent the vertex species. The level water arrow means that the trait increases toward the low PC1 (from bottom to high).

4. Discussion

Contrary to our expectations, the results demonstrate that taxonomic and functional diversity of ETP reef fish vary differently over time with no consistency across every subregion (Figure 4). These slight variations were also not homogeneous across localities in a given subregion with some localities experiencing stagnation, a decline, or an increase in taxonomic and functional diversity. But as hypothesized, the southernmost locality (Machalilla - 1° S) experienced the most drastic changes in the entire region. The drivers used in this study were unable to formally explain the causes of the spatiotemporal variations for the species richness and functional indices, with only FRic and FDis being significantly impacted. We reveal that even with global warming, and ENSO events, reef fish functional and taxonomic structures in the ETP are not showing any drastic deterioration at large scales on the basis of traits used.

4.1. Spatial trends of diversity across the ETP

Species and functional richness values are highly correlated (Pearson's R = 0.86). They both have higher values in the low latitudes localities with an increasing trend between Gulf of California and Islas Marietas, and in the Galapagos Archipelago where it can reach more than 60 species and more than 0.7 for FRic at site level. On the contrary, localities with the least number of species (and thus FRic) are Huatulco (mean of 20 species and FRic of 0.2 per site) and Gulf of California (mean of 25 species, and FRic of 0.25 per site) (Figures 5 and 6). This is in agreement with previous studies that found peaks of reef fish species richness near Islas Marietas and Isla Gorgona, and lowest amount of reef fish species in the Gulf of California and in the Huatulco area (Mora & Robertson, 2005; Dubuc et al., 2023). López Pérez & López García, 2008 found that Huatulco National Park was poor in coral species. This low number of coral species and low coral cover in Huatulco explain that the lowest reef fish species richness values are found in this locality as it is something that was found by (Komyakova et al., 2013) in the great barrier reef. On the contrary, the high species and functional richness in the Galapagos Islands differ from these studies which found lower values than in this study (McKinley et al., 2022). FEve is the only metric that does not vary in each locality, with only a very slight decrease in Galapagos North (Slopes, Table 2). The overall regularity of species abundances within the functional space is constant between 0.5 and 0.7 everywhere in the ETP even under climate-driven changes, ENSO, or human impact such as fishing or tourism. This is in line with previous research (Dubuc et al., 2023) which found similar functional evenness (FEve) values, varying from 0.34 to 0.62 between distinct sites in the ETP. However, our data contrasts with part of this study, as they found a peak in FEve at higher latitudes (Gulf of California), that we did not observe. On average, functional dispersion (FDis) did not vary much spatially, localities exhibiting a FDis between 0.3 and 0.5, with lower values at Huatulco. This is in accordance with Dubuc et al., 2023 who, with the analysis of more than 100 different sites, also found values ranging between 0.1 and 0.6. Functional originality (FOri) was also constant at the spatial scale with an average value of 0.1, indicating that the uniqueness of reef fish assemblages is low and does not vary with latitude gradients.

4.2. Overall trends at the subregional scale

Although taxonomic and functional diversity did not change drastically over time at the subregional scale, those changes are still significant. The North Continental subregion experienced a loss of species richness and FRic. This is coupled with a decrease in FDis indicating that species functional strategies are narrowing in terms of relative abundances.

Reef fish species in the North Oceanic, represented by Revillagigedo, appear to be increasing in FDis. This indicates that the ecological strategies of this community have become more varied over time (Laliberté & Legendre, 2010). It is worth noting that spatial representation in this region is much lower.

The communities of reef fish in the South Continental subregion have decreased in both FDis and FOri, suggesting species to be less unique and less dispersed in the functional space. Both decreases point to assemblages in which species are more clustered in terms of relative abundances. By looking at the functional space of localities within this subregion, we observe that a few species tend to dominate the entire community in weight (Figure 12g & h).

The structure of South Oceanic reef fish is becoming more unique (FOri). In this subregion, there were also slight but significant decreases in species richness, FRic, and FEve, which might result from the loss of reef fish species forming the functional space volume. Located in the lower latitudes (between 0 and 6° N), the South Oceanic subregion is where we expected the greater displacement of species caused by the increase in water temperature. Our results indicate that all functional and species richness indices decreased, the only one increasing was originality, which is consistent with our initial predictions.

We also noticed that the four subregions studied did not exhibit spatial differences as they have more or less the same values for each index considered. Overall, this indicates a potential regional buffering, given they encompass distinct localities and sites, as suggested by (Jarzyna & Jetz, 2018) who reported a tendency for regional scale to mitigate the variations in functional and taxonomic diversity. No major changes and no specific patterns in taxonomic and functional diversity are emerging at the subregional scale. The reef fish communities are not experiencing drastic declines at large scales, which suggests that more localized variation may be occurring.

4.3. Overall trends at the locality scale

If we zoom closer, at the locality scale, we can observe patterns within subregions. Localities tend to have the same tendencies inside a subregion, with for most subregions, a tendency for taxonomic and functional diversity to either stagnate or slightly decrease. It is the case for all North Continental localities (with the exception of a slight increase in FRic at Islas Marietas), and all the Galapagos Archipelago (South Oceanic without Isla del Coco). This relates to the functional space variations between the first and last year recorded for the locality scale where no major shift can be observed (Figure 12). One species (*Lutjanus novemfasciatus,* corresponding to the highest PC2 value) that was present at Islas Marietas and Huatulco in 2012 disappeared in 2020. This species is very mobile, night active, solitary, benthic, big, and predatory. The same species also disappeared from Machalilla, Galapagos North, and Southeast. This could suggest that *L. novemfasciatus* experienced a decline throughout the ETP.

Gulf of California and Cabo Pulmo did not experience any changes in taxonomic or functional diversity during the study period. This result is concordant with Amador-Castro et al., 2021 who found that rocky reef species have maintained their number (species richness) and abundance between 2007 and 2017 at the Reserva de la Biosfera Isla San Pedro Martir (Gulf of California). For Cabo Pulmo, this stagnation is due this MPA success as a no-take zone in maintaining reef fish species richness and abundance (Ramírez-Ortiz et al., 2022). In Espiritu Santo, a loss of both taxonomic and functional richness is observed. This is a pattern also reported by Ramírez-Ortiz et al., 2022, likely due to the status of this locality as a multi-use MPA. Islas Marietas is increasing in FRic, possibly due to the active coral reefs restoration which has contributed to increase the branching corals cover area (Rodríguez-Troncoso et al., 2023), which in return promote species and traits richness (Cáceres et al., 2020). This FRic increase, although significant when gathering the site level, is not observed when looking at the locality functional spaces (Figure 12d). We could argue that there are some changes (*L. novemfasciatus* disappearing, and some species appearing along low PC1 values), but these remain rather small and driven only by a very few number of species which is not enough to be considered a functional structural shift. The decreases of FRic and FDis at Huatulco did not translate into locality scale functional shifts with both 2010 and 2020 multidimensional space having the same species and abundance structure with the exception of a very few species (Figure 12e).

Even though, when aggregating sites together, we observe an increase in FDis with ecological strategies becoming more varied at Revillagigedo, the locality scale functional spaces show no clear variations between 2010 and 2023 either in species positions, or in abundance distribution (Figure 12f). This suggests that the increase in FDis is occurring at the site scale rather than at the locality scale. This increase indicates a slight shift promoting a wider range of functional niches in terms of species relative abundance. The Revillagigedo National Park is an MPA (Marine Protected Area) where fishing is totally prohibited, which might explain this pattern. In such conditions, a wider range of functional niches can be maintained. In this case, we would assume that larger species or species high in the food web have more weight as functional niches, which are heavily targeted species by the fishing industry (Pauly et al., 1998; Sala & Knowlton, 2006).

Examining the South Continental localities, a great number of species spread to Isla Gorgona expanding the functional space volume occupied by the reef fish communities resulting in an increase in FRic. The distribution of abundance stayed constant with the exception of *Chromis atrilobata* appearing as a predominant species (Figure 12g). Machalilla did not change in species distribution (Figure 12h). In fact, it has recorded the same shift as Isla Gorgona with *C. atrilobata* becoming a dominant species. Unlike what occurred at Isla Gorgona, this species was the only dominant species in 2020 at Machalilla, indicating a shift in abundance toward a sedentary, diurnal, small sized species swimming in surface waters among 20 to 50 peers and eating on small invertebrates and zooplanktons. The predominance of *C. atrilobata* led to a loss of FDis recorded in this locality (Figure 8), and in the South Continental subregion (Figure 4). The different patterns within the South Continental subregion could be due to the different factors acting at the local scale. The Isla Gorgona Natural Park has undergone three management plans during the study time (2004-2010, 2007-2011, 2012-2017) (Alvarado et al., 2017), which may help the reef system to recover and thrive. On the other hand, the Machalilla National Park is impacted by the Humboldt Current, the cold water that the current brings, and by illegal trawling pressures coupled with careless anchoring (Alvarado et al., 2017), damaging the small area of coral reefs that the marine reserve holds. As an uninhabited coastal island, Isla Gorgona is also thought to suffer less from anthropogenic activities than Machalilla which is located at the direct coast of Ecuador. *C. atrilobata* being abundant is not surprising as it is one of the most abundant species in the ETP but its large predominance is something unusual (Myers et al., 2011).

Isla del Coco reflects a decrease in species richness, while increasing in FDis and FOri. The communities in 2006 were largely dominated by two reef fish species (*Thalassoma lucasanum* and *Stegastes arcifrons*) (Figure 12i). But in 2019, these species, alongside others, have lost abundance from 78 and 62 individuals per m2 to 1.2 and 0.97 individuals per m2 for *T. lucasanum* and *S. arcifrons* respectively. This suggests a decline in abundance for species located near the center of abundance which led to a shift in the weighted center of this assemblage suggesting that species exhibit more functional niches based on relative abundances (increasing FDis). As a no-take and uninhabited zone, Isla del Coco exhibits an increase in functional diversity coupled with a decrease in species richness. This decline may be caused by the illegal fishing that is quite high in this National Park (González-Andrés et al., 2020).

The Galapagos remaining localities show either stagnation or a slight decrease in the taxonomic and functional indices. Northern Galapagos is losing species richness and FEve and western Galapagos also seems to decrease according to species richness, FDis. The coefficients of these variation trends, although significant, are still weak (Slopes, Table 2). The functional spaces show no variations whatsoever when considering species position and relative abundance for Galapagos Far North and West while a loss of diurnal, low trophic, small vertex species (low PC2) occurred in Galapagos North and Southeast. That change in species presence can be linked to the decrease in species richness and FRic going on in Galapagos North, although Galapagos Southeast showed no trend in all indices used when aggregating sites. The decrease in FRic in Galapagos West can be seen using the functional spaces as this decrease is likely due to the disappearance of one species (low PC1) that was the only one occupying its functional niche. The slight decreases in functional and taxonomic diversity in some of the localities in the Galapagos may be due to the Galapagos Marine Reserve as survey sites were both located in no-take zones and inside the multi-usage zones.

Although not usually used in this context, functional originality may represent an indicator of functional redundancy (Brandl et al., 2016) as assemblages with low FOri values indicate that multiple species and abundance support the same traits. This could explain the slight variations recorded in the results as communities with low functional originality, as redundancy, may act as a community buffer against environmental changes (McLean et al., 2019).

No-take zones MPAs, such as the ones in Cabo Pulmo, Revillagigedo, Isla Gorgona, and Isla del Coco, were more resilient and stable in terms of the biodiversity indices used in this study compared to multi-usage MPAs which authorize commercial, artisanal, and sport fishing. This stability in biodiversity indices in no-take zones suggests that highly protected areas are more effective in conserving reef fish species over time. This finding underpin the argument for solid conservation measures, particularly in hotspots and ecologically vulnerable marine environments.

4.4. Effects of drivers

None of the predictors tested here has had an effect on species richness at the spatiotemporal scale (Figure 10). This contrasts with previous research that found positive interaction between species richness and temperature at the spatial scale in the ETP (Parravicini et al., 2013; Dubuc et al., 2023), and negative interaction between the same metrics at the temporal scale in the lowest latitudes (Chaudhary et al., 2021). This could be the results of the spatial scale buffering the negative interaction of the temporal scale or inversely. We expected PP to have a positive impact on species richness as higher primary productivity promotes reef fish number and biomass in other reef systems on the globe (Quimbayo et al., 2019; Warmuth et al., 2024), but it appears that it is not the case in our spatiotemporal study although a non-significant positive trend can still be highlighted. As well as a non-significant positive trend between species richness and sd (SST) which could suggest that wider temperature range may support more species due to the fact that different ecological niches could coexist.

FRic is the index that was the most impacted by the chosen predictors. The positive effect of PP was expected due to higher chlorophyll concentration linked with higher reef species richness and biomass (Quimbayo et al., 2019), which increases FRic (correlation species richness - FRic). Although the negative effect of sd(PP) can be a bit surprising, it suggests that reef fish species located at the vertices of the functional space volume do not tolerate wide PP variation ranges. SST and its standard deviation also had a positive impact on the breadth of functional niches. This effect could be interpreted as a greater impact on FRic at the spatial scale than at the temporal scale as FRic is thought to increase with temperature at the spatial scale in the ETP (Dubuc et al., 2023). Variations of SST (sd(SST)) having a positive impact is also a finding that contradicts our initial hypotheses. Just like species richness, the positive impact of sd(SST) on FRic could indicate that more ecological niches may coexist due to temperature ranges supporting more species that have different thermal preferences.

FEve did not vary at any localities with the exception of a very slight, but still significant, decrease at Galapagos North (Table 1). The lack of spatial and temporal variation of FEve explains why none of the variables have had an effect on this metric.

FDis is only affected by one variable: DTM. This expected positive effect suggests that reef fish communities located farther from the fishing market access tend to have broader functional niches, with a greater diversity of strategies represented according to species relative abundances. Conversely, the closer reef fish communities are to the fishing market access, the narrower their functional niches tend to be, with fewer functional strategies dominating in terms of species relative abundances. The idea that FDis decreases with the fishing activity is in accordance with scientific knowledge (Mouillot et al., 2013b; Rincón-Díaz et al., 2021). As the fishing industry targets principally large-bodied fish which are most of the time piscivorous or carnivorous ones with the highest trophic levels (Myers & Worm, 2003; Olden et al., 2007; Genner et al., 2010; Tsikliras & Polymeros, 2014), these are traits located at the periphery of the functional space. These peripheral traits are thus threatened or even removed from the communities and from the functional space, leaving the communities with a functional structure based on low trophic and small species. DTM is only a spatial variable, with no temporal dimension, which indicates that, at the ETP scale, the fishing market is an important contributor to decline in FDis. There is no evidence that FDis is varying positively or negatively with the other drivers.

FOri did not change regarding any of the variables used. The functional originality of the overall communities of reef fish in the ETP is not explained by either SST, PP, or DTM. The lack of drastic spatiotemporal variation probably explains that the drivers did not have an effect on this index.

4.5. Stability of reef fish communities in the ETP

The near stability that ETP reef fish exhibit concerning both taxonomic and functional structure could be partly explained by the resilience and recovery of coral and rocky reefs under high environmental changes such as ENSO (Romero-Torres et al., 2020). Habitats degradation and loss is one of the principal causes of reef fish population decline (Pratchett et al., 2014). Although our data encompasses different types of reef, sites with coral cover typically diminish in coral cover after a bleaching event but tend to recover over 10-15 year cycles without showing any consistent increase or decrease (Romero-Torres et al., 2020). Far from the bleaching and huge mortality rates that follow unusual temperature extremes elsewhere on coral reefs, frequent El Niño events in the ETP have not created regional oceanographic conditions in which coral reefs can no longer live (Romero-Torres et al., 2020). This stability in reef fish communities in the ETP has been demonstrated by Glynn et al., 2014, who identified a pattern of recovery post El Niño events in coral cover and a stability in reef fish species richness and density at Uva Island (Panama).

Reef fish across the tropics are thought to live near their upper thermal limit. Even with the more optimist climate scenarios, temperatures would be too elevated for most reef fish to live at their optimal capacity, or even to survive. This is particularly the case for equatorial reef fishes which have narrower temperature ranges (Rummer et al., 2014). The localities sampled in this study are unique in terms of their oceanographic conditions. All the most southern, equatorial localities (Galapagos, Machalilla, and Isla Gorgona) are located in upwelling zones (Romero-Torres et al., 2017), meaning that the temperature ranges at these localities are wider than the one in non-upwelling zones. Furthermore, Mora & Ospína, 2001 have found that 15 reef fish from the ETP (Isla Gorgona) have a thermal upper limit ranging from 34.7°C for the lowest to 40.8°C. These temperatures are still above the highest sea surface water temperature ever recorded inside the localities in this study which was 32.2°C during the 2015 El Niño event in the Gulf of California (OISST, Huang et al., 2021). If reef fish are migrating due to climate change, it is not observed in the taxonomic and functional diversity indices analyzed in this study.

What drives the subtle variations of taxonomic and functional metrics in the ETP are thus thought to be local factors acting at site level in analogy to what have been found in more temperate areas (Sgarlatta et al., 2023). These local factors could be human density, pollution, wastewater discharges, tourism, fishing as anthropogenic activities (Souter et al., 2021), reef cover, or bottom rugosity and tridimensional structure (Alvarez-Filip et al., 2011). It is also important to highlight that taxonomic and functional diversity trends appear to be influenced by the level of protection inside MPAs with no-take zones (Cabo Pulmo, Revillagigedo, Isla del Coco, parts of the Galapagos) showing slight increases or stagnation in reef fish biodiversity.

5. Conclusions

Here, we assessed the spatiotemporal changes of the ETP reef fish taxonomic and functional diversity at the subregional and locality scale. Overall, we detected no major changes going on during the last two decades within the ETP. However, the absence of drastic large-scale variation is not an indication of no change at all within the reef fish communities. The slight significant declines of some indices characterizing the diversity of reef fish communities act as a warning message. The locality scale showed more variations across the ETP with no clear pattern within or between subregions, but with a slight downward trend in taxonomic and functional. The way reef fish taxonomic and functional structures varied during the last two decades suggests that small scale settings and dynamics may be more important in driving the changes. We also found that no-take zones (Cabo Pulmo, Revillagigedo, Isla Gorgona, and Isla del Coco) exhibited stagnation or slight increases in both taxonomic and functional indices. This finding further encourages the importance to create such zones when designing MPAs. Although it is important to know and understand that this multifaceted view provided by both diversities analyzed in this study is still a simplification of a phenomenon as complex as biodiversity. Reef fish might be able to live and survive under today's ETP regional oceanographic conditions, but the increase of temperatures, the decrease of oxygen concentrations, and the acidification are thought to continue in the next decades impacting directly (migration, reduction of performance abilities), or indirectly (hard bottom structure shifts and collapses) marine organisms.

6. Limits and perspectives

By narrowing the scope further, we could be able to detect some more drastic changes going on at reef level. The way we aggregate transects into sites, into localities, and into subregions has an impact by hiding smaller scale dynamics that can be occurring right now.

An accurate knowledge of fish diet is also an important aspect that needs to be utilized. As reef fish abundance shifts toward herbivore species (Cheal et al., 2008), such traits could be of importance to characterize if similar changes in abundance are occurring in the ETP. Intraspecific traits should also be taken into account to assess more in depth functional diversity changes as individuals of the same species (e.g. juveniles and adults) do not belong to the same traits categories (Palacio et al., 2025).

It is also worth mentioning that oxygen levels greatly impact fish metabolic rates and thus survival, even though reef fish are thought to be more tolerant to hypoxia than temperate fish (Hughes et al., 2020). The deoxygenation impact on reef fish will likely come from avoidance of hypoxic areas, or reduce metabolic rates (Hughes et al., 2020). The following studies should take that into account when assessing reef fish dynamics. We also used surface temperature as a driver of water temperature, but an in-situ sampling of water physicochemical properties would be more accurate.

The different levels of protection and MPAs usages are important to be taken into account as more protected areas would tend to exhibit greater and steady biodiversity. This study encompassed several MPAs which varied in terms of their usages and legal protection. An in-depth analysis of the effect that these have on reef organisms is something to look for in the near future for countries and organizations to create and promote new MPAs or to thoughtfully improve the ones already active.

Long spatiotemporal monitoring datasets are much needed at this moment to understand the global biodiversity crisis. Few research take both spatial and temporal aspects together to assess functional diversity of reef fish assemblages. It is of importance to understand how the structures of communities change at multiple locations, as a pattern occurring at one place may not occur at another. Some key sites and localities in Central America (Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica mainland, and Panama) and additional time series should be added in future studies to fully grasp the spatiotemporal patterns in both taxonomic and functional diversity occurring in the ETP. Although using multiple transect surface areas to survey fish is a common practice in coral reefs (Halford & Thompson, 1994; Mapstone & Ayling, 1998; Sandin et al., 2008), a standardized transect area would also help to better understand the ecological communities as rare species, which are less observed in smaller covered areas, endorse crucial roles for ecosystem functioning (Mouillot et al., 2013a; Leitão et al., 2016).

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