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Taxonomic and functional richness of fish in temperate and tropical reefs of the Mexican Pacific

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Abstract. Taxonomic and functional diversity patterns of fish in temperate reefs in the Mexican Pacific have not been analyzed in integrative biodiversity studies. Thus, this study compared the taxonomic, phylogenetic, and functional diversity of reef fish in 4 biogeographic provinces: Californian, Cortez, Panamic, and Oceanic Islands. Species checklists were compiled from the literature, museum collections, and monitoring data from 21 sites in marine protected areas (MPAs) and 45 non-protected sites. Based on this data and 6 biological traits (size, mobility, period of activity, gregariousness, position in the water column, and diet), we calculated species richness (*S*), average taxonomic distinctness (Δ+), number of functional entities (*FE*), functional redundancy (*RED*), functional vulnerability (*FV*), and functional volume (*FVol*). We registered 1,045 species; the dominant categories were benthic, highly site-attached, diurnal, solitary, medium-sized, and invertivores. The Cortez province showed the highest *S* and *FE* values, whereas the Californian province presented the lowest values. Notably, *FVol* was >70% across the 4 biogeographic provinces, suggesting that the range of ecological functions and processes was maintained across provinces despite their contrasting biodiversity levels, environmental conditions, and evolutionary histories. A “regional backbone” was identified, consisting of 74 species and 58 *FE* (the fundamental species and shared ecological roles across provinces). At the regional level, low *RED* (<3 species·FE^{-1}) and high *FV* (>55% of *FE*s represented by a single species) were observed. All provinces presented high values of Δ+ (>80%), reflecting the broad range of taxonomic lineages within the region. The MPAs presented higher *S* and *RED* than non-protected sites; however, further research is needed to elucidate the positive effects of protection.

Key words: marine protected areas, marine ecosystems, ichthyofauna, biogeographic patterns, biological traits.

Introduction

Marine and coastal ecosystems worldwide are increasingly threatened by human activities (e.g., fishing, pollution, and habitat fragmentation), as well as by environmental factors associated with climate change (e.g., increasing sea temperatures and rising sea levels), which could result in a loss of species and the functions and services they provide (Halpern et al. 2015, Morzaria-Luna et al. 2018). Understanding how fish diversity varies across biogeographic provinces with distinct environmental conditions and evolutionary histories is crucial for developing effective

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conservation strategies (Stuart-Smith et al. 2013, McLean et al. 2021). These comparisons can help identify regions with unique or vulnerable assemblages that require targeted management efforts (Olivier et al. 2018). In the face of the loss of species, functions, and services, marine protected areas (MPAs) serve as a primary conservation tool to safeguard biodiversity and improve ecosystem resilience (Hernández-Andreu et al. 2024).

Although taxonomic diversity-based studies are common for describing spatial and temporal differences (Mora et al. 2008, Lin et al. 2020, Pham et al. 2023), it has been reported that these studies are not highly sensitive to the effects of disturbances on ecological processes (Mouillot et al. 2013). An alternative is to use trait-based approaches that consider the biological information of each species as an approximation of their role in the ecosystem and assess the loss of species and their functions (Francisco and De la Cueva 2017). Using species presence and their biological traits makes it possible to calculate functional indices and describe spatial patterns such as biodiversity "hotspots" or functionally vulnerable areas at the global level (Mouillot et al. 2014). Moreover, based on a functional diversity analysis, it has been reported that no-take zones inside MPAs were not sufficiently representative to safeguard ecosystem functions in tropical reefs (Hernández-Andreu et al. 2024).

Regional descriptions of the functional patterns of reef fish have been extensively reported given the ample biological information available, the wide variety of functions they perform, and the economic importance of some species (Mouillot et al. 2014, Olivier et al. 2018). Mouillot et al. (2014) analyzed the taxonomic and functional richness of 6,316 tropical reef fish species at a global level, evaluating data from 169 locations. The authors found the highest species richness (S = 3,689 species) in the Central Indo-Pacific region and the lowest richness in the Eastern Atlantic (S = 403 species) and Eastern Tropical Pacific (ETP) (S = 570 species). However, Mouillot et al. (2014) reported that even the later regions with low species richness could be able to maintain the ecological processes necessary to sustain tropical reefs, as they presented similar functional volume values and shared most of the key functions with richer faunas, such as those found in the Central Indo-Pacific. Moreover, these authors reported that even highly diverse systems, such as tropical reefs, could be threatened by species loss, as fish species tended to be disproportionately packed into a few specific functional entities, leaving many functions highly vulnerable.

McLean et al. (2021) analyzed 2,786 fish species. These authors reported a consistent variety of traits (the dominant categories were invertivore diets; demersal, diurnal, and solitary behavior; and small-medium size), including a "backbone" of 21 functional entities common to the 89 studied ecoregions, highlighting the existence of shared ecological roles in shallow reefs worldwide. Even though the authors found more species in tropical reefs than in temperate regions, they reported similar trait compositions among fish assemblages under similar environmental conditions (even when thousands of kilometers separated study sites), despite the assemblages hosting drastically different species from separate evolutionary lineages. These findings suggest that similar trait-based management strategies can be applied to regions with distinct species pools. Therefore, understanding taxonomic, phylogenetic, and functional biodiversity patterns in marine regions is needed to unravel the contributions of species (and their evolutionary lineages and functional entities) to ecosystem processes and to support the development of management strategies that enhance reef resilience.

While studies have been conducted in the Mexican Pacific, a comprehensive comparison of the taxonomic and functional richness of fish across regions is missing. In the ETP, Robertson and Cramer (2009) identified a high number of resident species in the central region of the Panamic province (Panama and Costa Rica) and at the tip of the Baja California Peninsula in the Cortez province. Similarly, Dubuc et al. (2023) reported the highest values of taxonomic and functional richness in the central region of the ETP (based on an analysis of 313 species registered by visual censuses at 122 sites from Mexico to Ecuador), which was positively influenced by sea surface temperature and conservation status and negatively influenced by shelf area and the distance from the mainland. In contrast, Ramírez-Ortiz et al. (2017) found a decreasing biogeographic pattern in the functional richness of fish and macroinvertebrates towards the tropics, with the highest values in the Cortez and Oceanic Islands provinces (compared to the Panamic province), which were associated with habitat heterogeneity and the oceanographic conditions of those regions.

In the Mexican Pacific, Olivier et al. (2018) identified similar fish diversity patterns in the Gulf of California by analyzing different data sources and reported greater taxonomic and functional diversity in the southern islands associated with the oceanographic conditions of this region. Although their findings revealed low functional redundancy and high functional vulnerability at the regional level, uneven species distributions between functional entities and spatial differences in fish diversity were reported.

Despite an increase in studies of the Mexican Pacific, analyses of the regional patterns in fish diversity in temperate and tropical reefs, as well as in MPAs and non-protected sites, remain scarce. Thus, we compiled fish species presence data from 66 reefs from different sources (the literature, museum collections, and monitoring programs) to describe the spatial patterns of taxonomic, phylogenetic, and functional richness in 4 biogeographic provinces (Californian, Cortez, Panamic, and Oceanic Islands). We also sought to identify possible ecological factors that influence reef fish fauna, considering the effects of protection by MPAs on species conservation and their ecological functions. Overall, the results of this study help to elucidate common and particular traits and the taxonomic and functional diversity patterns of fish in each biogeographic province of the Mexican Pacific.

MATERIALS AND METHODS

Study area

We compiled information on fish presence in 66 sites (21 MPA sites and 45 non-protected sites) along the Mexican Pacific (Fig. 1). The study region was divided into 4 biogeographic provinces according to the regional classification of Robertson and Cramer (2009), which is based on the geographic distribution of shore fish species (i.e., resident species whose abundance or distributions indicate they exhibit self-sustaining populations in the region; Robertson et al. 2004). The Californian province extends north from 25° N along the Pacific coast of the Baja California Peninsula (Robertson and Cramer 2009). It is influenced by the California Current, which imposes its temperate features (average sea surface temperature [SST] of 16 °C; SAGARPA 2018), and the North Equatorial Current and its tropical features (SST of 29.2–25.6 °C; SAGARPA 2018) (Bernal et al. 2001, Valdez and Díaz 1996).

The Cortez Province covers the Gulf of California and the southern Pacific coast of Baja California Peninsula, reaching north to about 25° N near Magdalena Bay (Robertson and Cramer 2009); the average SST range for the province is 19.8–27.8 °C (Anislado-Tolentino 2008, SAGARPA 2018). The Cortez province is influenced by the North Equatorial Current and North Pacific Gyre (Bernal et al. 2001). Northwest winds generate upwelling events that bring nutrient-rich waters to the euphotic zone and increase primary productivity (Escalante et al. 2013). These oceanographic conditions support a high diversity of marine fauna and a great variety of habitats such as mangroves, coastal lagoons, and rocky and coral reefs (Cruz-García 2009).

The Panamic province extends from 25° N to 4° S off the Gulf of Guayaquil in Ecuador (Robertson and Cramer 2009). The mean SST of this province is 28 °C, and it is influenced

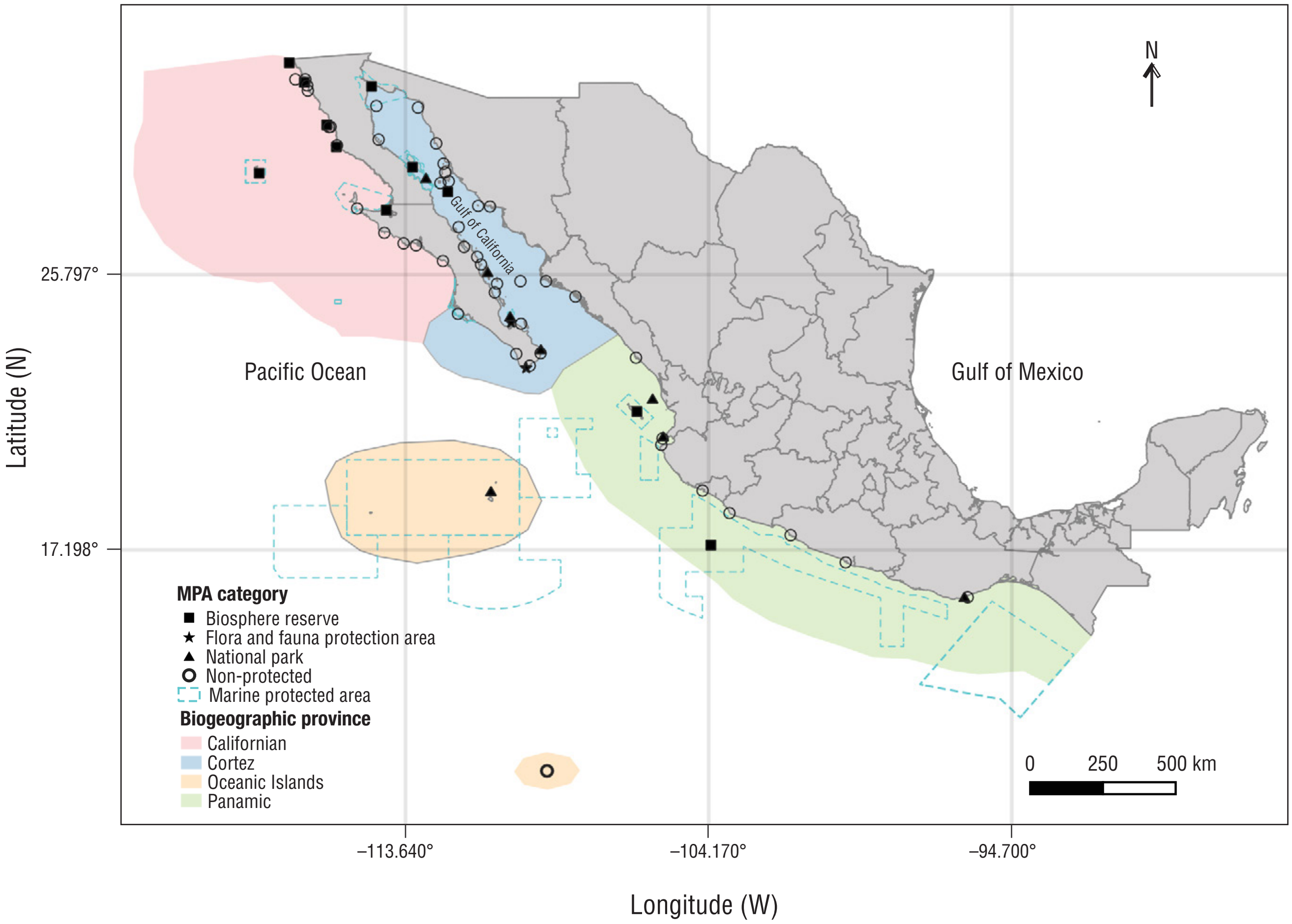

Figure 1. Map of the Mexican Pacific depicting study sites in the Californian (red), Cortez (blue), Panamic (green), and Oceanic Islands (orange) biogeographic provinces. Circles indicate non-protected sites; other markers indicate that study sites are located in marine protected areas (MPAs) (blue dashed line) with distinct protection categories: national parks (triangles), biosphere reserves (squares), and flora and fauna protected areas (stars).

by the confluence of 2 marine currents in the central Mexican Pacific, the Costa Rican Coastal Current and California Current, which merge to contribute to the formation of the North Equatorial Current (Lara-Lara 2008). This province is also influenced by northwest winds, which increase the presence of gyres and eddies, thus favoring primary productivity near the coast for most of the year (Pérez-de-Silva 2023). In addition, the upwelling zone of the Gulf of Tehuantepec, which is induced by Tehuano winds, is considered one of the most productive zones in the study region (Lara-Lara 2008).

Finally, the Robertson and Cramer (2009) classification considers oceanic islands as an independent biogeographic province relative to mainland areas, as the Oceanic Islands province hosts relatively smaller ichthyofauna, distinct functional groups, and a greater number of transpacific and endemic species. This biogeographic province is comprised of 5 islands (from north to south): Revillagigedo, Clipperton, Cocos, Malpelo, and Galapagos. In the present study, we only considered the islands of Revillagigedo and Clipperton (CONANP 2004, Ricart et al. 2016). These islands present the same average SST (28 °C), as they are mainly influenced by the North Equatorial Current and, in the case of the Revillagigedo Archipelago, by the California Current, making the area a transition zone due to the convergence of 2 water masses (CONANP 2004, Velasco-Lozano et al. 2020).

Species checklist and biological traits

We compiled a species checklist of conspicuous bony fish (Teleostei) in the Mexican Pacific from 21 sites in MPAs and 45 non-protected sites. Data sources included published literature (scientific articles [e.g., Olivier et al. 2018], reports [e.g., Del Moral-Flores et al. 2013], and MPA management programs [e.g., CONANP 2004]), museum collections (e.g., Del Moral-Flores et al. 2016), and diurnal monitoring efforts (e.g., Mascareñas-Osorio et al. 2018) (Supplementary Material 1). Using different data sources has the advantage of including rare, nocturnal, and cryptic species that usually are not considered in biodiversity analyses (Olivier et al. 2018). We excluded fish species with maximum sizes of <5 cm and minimum depths of >70 m, organisms that were not identified at the species level, and species with particular life cycles (e.g., Anguilliformes). We did not consider areas with fewer than 10 registered species; non-protected sites encompassed reefs on the continental shelf, islands, or archipelagos separated by less than 10 km and located outside of the protection polygon of an MPA, whereas the protected reefs included all sites within a protection polygon.

We characterized all species using 6 biological traits that reflected key aspects of fish ecology (Mouillot et al. 2014). Biological information was compiled from the online repository FishBase (Froese and Pauly 2024) and included categories grouped into traits that have been used in previous studies at the global (Mouillot et al. 2014) and regional (Olivier et al. 2018, Ramírez-Ortiz et al. 2022) levels: (a) maximum fish size (5–7 cm, 7.1–15 cm, 15.1–30 cm, 30.1–50 cm, 50.1–80 cm, or >80 cm), (b) mobility (highly site-attached, mobile within-reef, mobile among reefs, or very mobile with very large home ranges), (c) period of activity (diurnal or nocturnal), (d) gregariousness (solitary, pairing, small group of 3–50 individuals, or large group >50 individuals), (e) position in the water column (benthic, bentho-pelagic, or pelagic), and (f) diet (herbivores-detritivores, invertivores targeting sessile invertebrates, invertivores targeting mobile invertebrates, planktivorous, piscivores, or omnivores). Based on species presence and biological trait information, we calculated the relative frequency of each category in the biogeographic provinces. We repeated this process for an additional subset of common species for all provinces, which we considered to be the regional backbone (McLean et al. 2021). The relative frequency of each category was represented in histograms using the packages ‘tidyverse’ (Wickham and Wickham 2017), ‘ggplot2’ (Wickham 2016), and ‘gridExtra’ (Auguie 2017) in R v. 4.3.3 (R Core Team 2024).

Biogeographic patterns in the taxonomic, phylogenetic, and functional diversity of reef fish

To describe regional patterns in fish diversity in temperate and tropical reefs, we used various ecological indicators to assess distinct diversity components. For taxonomic diversity, we considered species richness (*S*), which is the number of species in a community at a given time; high values of this indicator reflect high diversity (Halffter et al. 2005).

For phylogenetic diversity, we used the average taxonomic distinctness index (Δ+), which measures the mean distance (according to the Linnaean classification tree) between each pair of species within a study site (Clarke and Warwick 1998). To calculate Δ+, we used 6 hierarchical levels (species, genus, family, order, subclass, and class) and Eq. (1):

$$\Delta^{+} = \frac{\left[\sum \sum_{i<j} w_{ij}\right]}{\left[\frac{S(S-1)}{2}\right]} \;, \tag{1}$$

where w_{ij} is the taxonomic distance between each pair of species, and S is the total number of species. Low values of this index show that the species present in a certain site share a close evolutionary origin (i.e., low phylogenetic distance between species; Clarke and Gorley 2001).

To calculate functional indices, we classified each species into a functional entity (*FE*) based on a combination of the categories of the 6 biological traits, which was represented by an alphanumeric code indicating the possible ecological role played by each species in the ecosystem (Villéger et al. 2017). Using this information and species presence data, we calculated 4 indices: number of *FE*s, functional redundancy (*RED*), functional vulnerability (*FV*), and functional volume

(*FVol*). (1) Number of *FE*s: the number of unique combinations of the categories considered for the biological traits (Mouillot et al. 2014). High values of *FE* indicate that a wide variety of functions are represented within the assemblage (Quimbayo et al. 2017). (2) *RED*: the mean number of species per *FE* (Mouillot et al. 2014). Low values of this index suggest a reduced potential for functional compensation in the event of species loss (Micheli and Halpern 2005). (3) *FV*: the percentage of *FE*s represented only by one species (Mouillot et al. 2014). This index was calculated with Eq. (2):

$$FV = \frac{FE - \sum_{i=1}^{FE} min(n_i - 1, 1)}{FE} \quad , \qquad (2)$$

where S is the total number of species, and n_i is the number of species represented in the ith *FE*. High *FV* values indicate a high risk of losing functions in the event of species loss, as most *FE*s are represented only by one species (Mouillot et al. 2014). (4) *FVol*: the volume covered by a set of species proportional to the functional space defined by the outermost vertices of the total assemblage. In the present study, *FVol* represents the distribution of *FE*s in a particular province. High *FVol* values indicate the presence of highly extreme functions within the assemblage, similar to the total registered across the entire study region (Mouillot et al. 2013, 2014).

To calculate *FVol*, we employed a principal coordinates analysis (PCoA) based on a Gower distance dissimilarity matrix, which allows for comparing different types of variables while assigning them equal weight (Gower 1971). We selected the first 5 PCoA axes, which accounted for more than 70% of the total data variance. This created a 5D space for the biogeographic provinces and regional backbone, where pairwise distances between species were congruent with their initial trait-based Gower distances (Mouillot et al. 2021). These distances represent coordinates and were used to estimate *FVol* according to the convex hull volume model of Cornwell et al. (2006), in which the outermost vertices (*FE*s with more extreme traits) define the convex hull (Villéger et al. 2008). The amount of space that the provinces and regional backbone assemblages encompassed in proportion to the total volume of the Mexican Pacific were calculated to determine *FVol* using the packages 'elbow' (Casajus 2024), 'mFD' (Magneville et al. 2022), 'geometry' (Habel et al. 2023), 'vegan' (Oksanen et al. 2022), and 'tidyverse' (Wickham and Wickham 2017) in R v. 4.3.3 (R Core Team 2024).

Finally, *S*, *FE*, and *FVol* of the fish assemblages in each province and the regional backbone were plotted to visualize spatial differences using the packages 'ggplot2' (Wickham et al. 2016) and 'gridExtra' (Auguie 2017). The ecological indicators for each site were illustrated in maps with QGIS v. 3.34.0 to describe regional patterns. Classes or intervals of *S*, Δ+, *FE*, *RED*, and *FV* values were determined using Sturges' rule.

Results

Species checklist and biological traits

We registered 1,045 conspicuous fish species in 66 temperate and tropical reefs in the Mexican Pacific (Supplementary Material 1), representing 450 genera, 148 families, and 42 orders (Supplementary Material 2). The most represented family was Serranidae (64 species and 16 genera), followed by Gobiidae (47 species and 29 genera) and Carangidae (47 species and 16 genera).

Despite the presence of distinct species between provinces, all biological trait categories were present (Fig. 2). Their relative proportions remained similar within the study region, where the most frequent biological trait categories were: benthic (Fig. 2a), highly site-attached species (Fig. 2b), diurnal (Fig. 2c), solitary (Fig. 2d), medium-sized (15–30 cm; Fig. 2e), invertivores, and piscivores (Fig. 2f). These biological trait categories were dominant in the 4 biogeographic provinces and in the regional backbone.

Biogeographic patterns in the taxonomic, phylogenetic, and functional diversity of reef fish

The Cortez province presented the highest fish diversity values (911 species, 382 *FE*s, and *FVol* = 96%), followed by the Panamic (465 species, 265 *FE*s, and *FVol* = 80%) and Oceanic Islands (393 species, 233 *FE*s, and *FVol* = 77%) provinces. The lowest values were observed in the Californian province (314 species, 196 *FE*s, and *FVol* = 73%). In comparison, the regional backbone was comprised of 74 species (30% of the total species richness registered in the study area) and 58 *FE*s, covering 38% of the total regional volume (Fig. 3). These results indicate that the range of "functions" (*FVol*) was similar between biogeographic provinces despite the differences in *S* and *FE* values. Moreover, through the regional backbone description, we identified the fundamental species and, thus, the *FE*s necessary to maintain reef processes in the Mexican Pacific.

Regarding the protection level, in sites within MPAs, 898 species and 323 *FE*s were registered, while in non-protected sites, a total of 829 species were registered and grouped into 362 *FE*s (Table 1; Fig. 4a, b); thus, *RED* was higher in MPA sites (2.78 species·FE^{-1}) than in non-protected sites (2.29 species·FE^{-1}). At the regional scale, for most sites, we registered low mean *RED* values (2.4 species·FE^{-1}; Fig. 4c) and high *FV* values (55% of the *FE*s were represented only by one species; Fig. 4d) due to the high percentage of species concentrated in a relatively small subset of *FE*s. High *RED* values (~1.64–1.96) and medium *FV* values (~60–80%) were mainly observed in MPAs (e.g., Revillagigedo National Park and Islas Marias Biosphere Reserve) than in non-protected sites, which presented low *RED* values (~1–1.64) and high *FV* values (>80%). Finally, high Δ+ values (>97%; Fig. 4e) were observed in the 4 biogeographic provinces, indicating

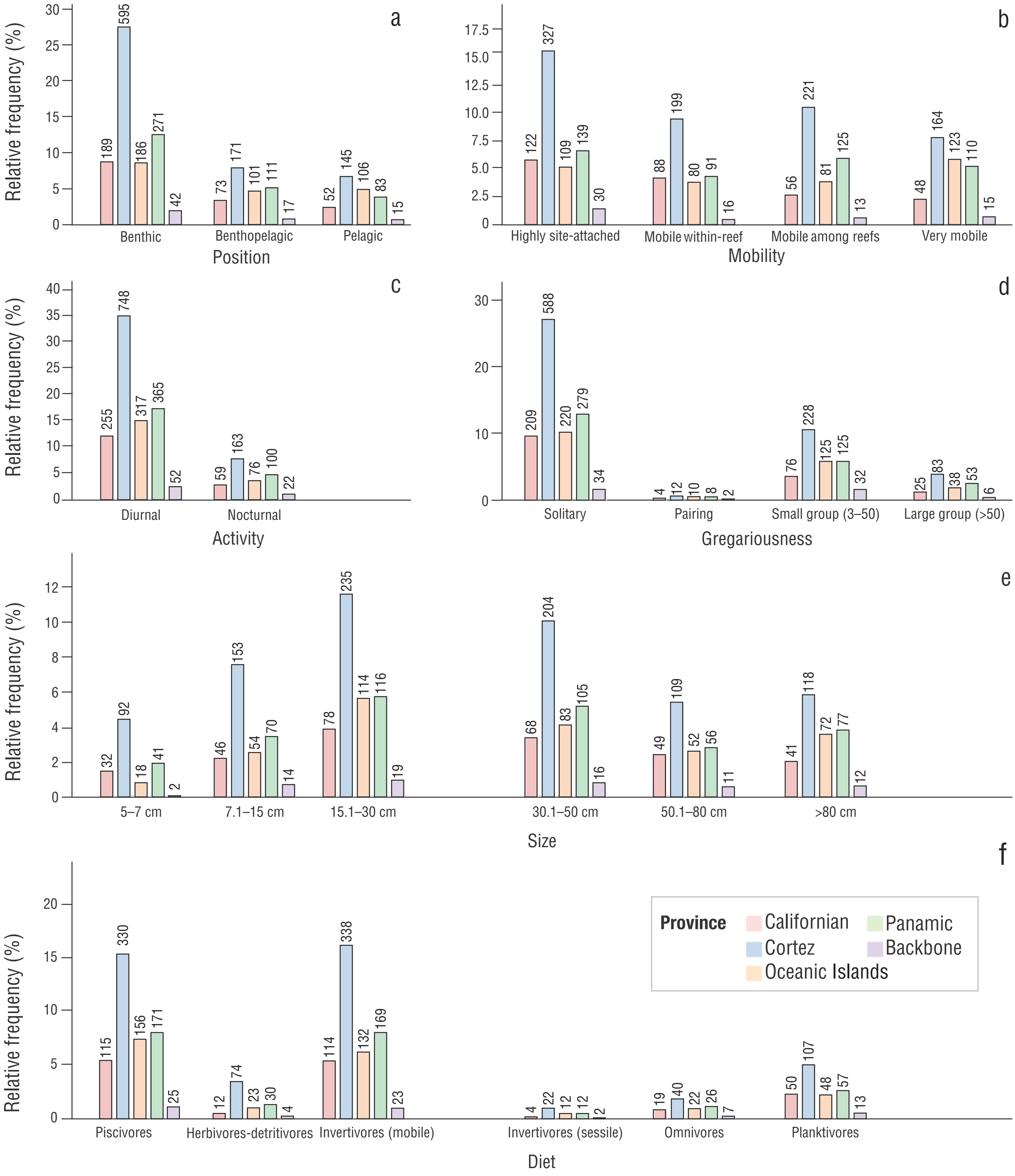

Figure 2. Relative frequency histograms showing the number of species per categories within the considered biological traits: position in the water column (**a**), mobility (**b**), period of activity (**c**), gregariousness (**d**), maximum size (**e**), and diet (**f**). Different columns represent different biogeographic provinces (Californian [red], Cortez [blue], Panamic [green], and Oceanic Islands [orange]) and the regional backbone (purple).

high phylogenetic distance (i.e., distant evolutionary origin) between the species within the study region.

Discussion

Species checklist and biological traits

We reported higher values of species richness (1,045 species) in the Mexican Pacific compared to the reports of previous global studies, which have registered <580 species for the ETP (Mouillot et al. 2014, McLean et al. 2021). Despite the high fish species richness reported in this study, we found that the Mexican Pacific presented lower richness than the Central Indo-Pacific (3,689 species) and Central Pacific (2,911 species), which have been recognized as biodiversity hotspots for reef fish fauna (Mouillot et al. 2014).

Regionally, Dubuc et al. (2023) reported a total of 313 species for the Mexican Pacific, which is less than the value reported in the present study (1,045 species). This difference could be associated with our compilation of information from different sources (scientific articles, reports, MPA management programs, monitoring data, and museum collections), as well as the incorporation of data from temperate reefs of the Californian province, which allowed us to generate a more comprehensive assessment of fish diversity in the different reef habitats of the Mexican Pacific.

Our analysis revealed that the most frequent biological trait categories (benthic, highly site-attached, diurnal, solitary, medium-sized, and invertivores specialized in mobile invertebrates or piscivores) across the 4 biogeographic provinces and regional backbone are among the most common for reef fish, which aligns with global (McLean et al. 2021) and regional (islands located in the central Mexican Pacific; Morales-de-Anda et al. 2020) reports. The high frequency of these categories could be associated with the dominance of families, such as Serranidae and Gobiidae, that exhibit these functional characteristics (Morales-de-Anda et al. 2020, McLean et al. 2021). To evaluate a wider variety of categories within the considered biological traits, future regional analyses should focus on describing functional diversity across different habitats (e.g., pelagic habitats, mangroves, and estuaries). Regarding diet, invertivores specialized in mobile invertebrates were the dominant category. Still, we also found a high frequency of piscivores, which have been reported to be indicators of good conservation status, as most species are commercially important (Quimbayo et al. 2017, Morales-de-Anda et al. 2020). However, we found that MPAs hosted a similar number of piscivores (105 species) as non-protected sites (116 species). Thus, subsequent analysis should consider other ecological indicators (abundance, size, and biomass) to determine if MPA protection positively affects this trophic group at the regional level. Additionally, the high frequency of the diurnal biological trait category could be associated with the period of the day during which most data have been collected. Even though our data encompass different sources, which could help reduce information bias (compared to other studies based on one data collection method), future sampling efforts should focus on describing nocturnal assemblages to provide a more accurate description of this trait.

Biogeographic patterns in the taxonomic, phylogenetic, and functional diversity of reef fish

By comparing reef fish diversity across 4 biogeographic provinces, we found the highest values of *S*, *FE*, and *FVol* in the Cortez province, followed by the Panamic, Oceanic Islands, and Californian provinces. The high fish diversity in the Cortez province could be due to the isolation of the Gulf of California from the Pacific Ocean since the formation of Baja California Peninsula, which has favored high speciation rates (Bernal et al. 2001, Mora and Robertson 2005, Robertson and Cramer 2009). The isolation, along with habitat heterogeneity in terms of substrate (rocky reefs and coral communities) and water-column characteristics due to the influence of Tropical Surface Water, California Current Water, and Gulf of California Water, have previously been reported as key factors within the Cortez province (Lavín and Marinone 2003). These factors influence the transport and settlement of fish larvae from other areas, contributing to the high taxonomic and functional diversity due to the convergence of tropical and temperate fish faunas (Ramírez-Ortiz et al. 2017). Additionally, this province hosts the majority of the MPAs analyzed in this study (9), which have been established to conserve biodiversity and ecological functions (SEMARNAT-CONANP 2018, Dubuc et al. 2023). The management of these MPAs and the high sampling effort in these areas to evaluate their effectiveness may have positively influenced the high fish diversity values recorded in the Cortez province.

Compared to the Cortez province, the Panamic province exhibited lower values of *S*, *FE*, and *FVol*, possibly due to its more stable oceanographic conditions throughout the year, as well as its less diverse habitats, such as sandy beaches and coral reefs dominated by *Pocillopora*, which has not been found to affect fish diversity within the ETP (Glynn 2004, Ramírez-Ortiz et al. 2017, Olán-González et al. 2020). In contrast, the Oceanic Islands province, which exhibited intermediate fish diversity values, has been considered a transition zone due to the confluence of the North Equatorial and California Currents, which favor environmental variability and, thus, the presence of multiple species with different biogeographic affinities (Velasco-Lozano et al. 2020). Nonetheless, the distance of these insular territories from the coast (>1,000 km) introduces bias into the sampling efforts in this province. The fact that the Revillagigedo National Park and Islas Marias Biosphere Reserve exhibited some of the highest fish diversity values within the study region may encourage the continuation of management efforts in these areas to promote the protection of key ecological functions in these provinces (CONANP 2004).

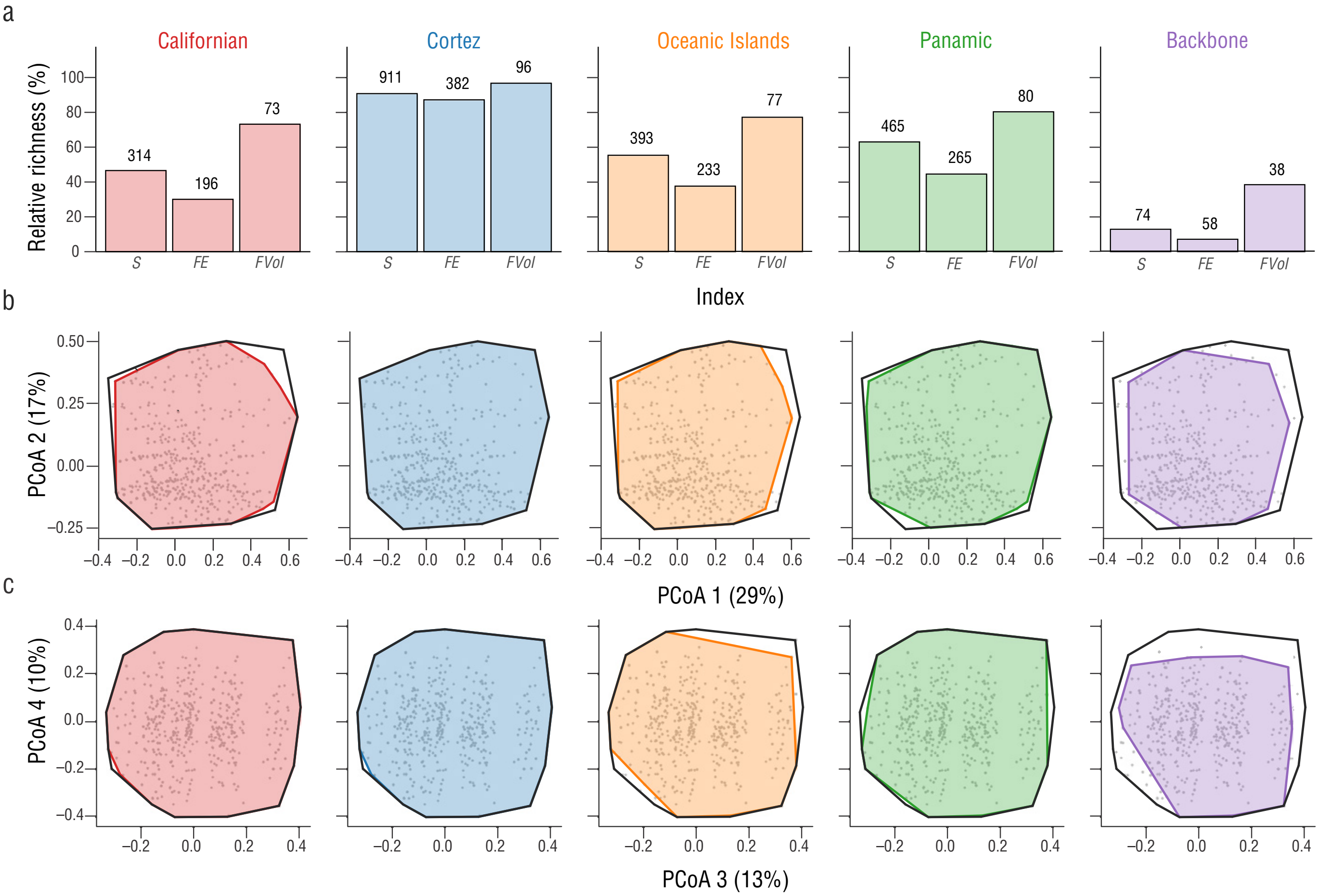

Figure 3. Taxonomic and functional indices calculated for the ichthyofauna across the 4 biogeographic provinces and the regional backbone: histograms of species richness (*S*), number of functional entities (*FE*), and percentage of the occupied functional volume (*FVol*; values are displayed at the top of each bar) (**a**). Functional space occupied by the fish assemblages in each province and the regional backbone (colored polygon) in comparison with the total FVol of the study region (black-line polygon) for axes 1 and 2 (**b**). Axes 3 and 4 of the PCoA (**c**). Gray markers indicate species distribution within the functional space.

Most of the sites in the Californian province exhibited low values of *S*, *FE*, and *FVol*, despite being considered an upwelling zone with high primary productivity (Castro-Aguirre et al. 1993, Valdez and Díaz 1996) and the presence of 6 MPAs. Previous studies have reported that reef fish taxonomic and functional diversity is strongly influenced by temperature changes, with diversity increasing towards the equator, as more species coexist in the tropics than in temperate areas (Tittensor et al. 2010, Dubuc et al. 2023). In this study, we observed this pattern of higher fish diversity in the tropical provinces, possibly due to limited species dispersal into the Californian province in contrast to the others. However, this condition might change in the near future, as extreme heat events could promote the colonization of kelp forests and rocky reefs by widely distributed and generalist species (Robertson and Cramer 2009, Dubuc et al. 2023).

Despite the differences in *S* and *FE*, the fish assemblages in each biogeographic province occupied similar volumes (>70%) within the total functional space. This is consistent with the results of McLean et al. (2021), who reported a range of functions shared between tropical and temperate regions worldwide, despite differences in species presence, environmental conditions, and evolutionary history across ecoregions. In this context, we identified 74 species and 58 *FE*s as the regional backbone, which represent the fundamental species and shared ecological roles across provinces that contribute to maintaining reef processes in the Mexican Pacific. This consistency across the study region presents an opportunity to propose trait-based approaches that could improve management outcomes in reefs under similar environmental conditions (McLean et al. 2021). Additionally, it is important to identify specific traits present in reefs with good conservation status in order to determine local priorities for trait-based management.

Regarding conservation status, we reported that although the number of non-protected study sites was higher, the MPAs exhibited greater total species richness (898 species) but

Table 1. Number of sites in non-protected zones in marine protected areas (MPAs) within the 4 biogeographic provinces according to the Robertson and Cramer (2009) classification. Additional rows show species richness (*S*) and functional entities (*FE*s) in non-protected sites and MPAs.

Biogeographic province	Non-protected sites (number of sites)	Marine protected areas (number of sites)
Californian	12	6
Cortez	24	9
Panamic	8	5
Oceanic Islands	1	1
Index		
S	829	898
Number of *FE*s	362	323

lower *FE* values (323 *FE*s) compared to the non-protected sites (829 species; 362 *FE*s). This result may indicate a positive effect of protection by MPAs, not only by increasing taxonomic diversity but also by increasing functional redundancy. However, further analysis is needed to determine whether this result can be attributed to the positive effect of reef conservation status, as influenced by the level of protection and size of the MPA (Dubuc et al. 2023), or whether MPAs, as reported in a global study (Hernández-Andreu et al. 2024), are effective for conserving species despite not always adequately protecting functions.

At regional level, we reported low average values of *RED* (2.48 species$\cdot FE^{-1}$) and high *FV* values (55% of the *FE*s were represented by only one species), which were similar to the values reported for the ETP (*RED* = 2.8; *FV* = 54%; Mouillot et al. 2014). The observed pattern of low *RED* and high *FV* has been previously registered as a global phenomenon and associated with the uneven distribution of species among *FE*s (Mouillot et al. 2014). In our study, species were disproportionately concentrated into a small set of *FE*s (61% of the species were grouped into 21% of the *FE*s), leaving most *FE*s to be represented by a single species and resulting in limited potential for functional compensation in the event of species loss (Micheli and Halpern 2005). This aligns with the results of Parravicini et al. (2014), who reported that, although *RED* is important for maintaining ecosystem processes, functions dependent on few species are especially sensitive, and their loss could jeopardize the maintenance of specific processes over time. It is worth mentioning that the results of indicators based on the relationship between the number of species and *FE*s (e.g., *RED* and *FV*) should be interpreted with caution, as they can change depending on the number of categories and biological traits considered (Ladds et al. 2018). Moreover, trait-based approaches group species based on trait similarities. However, these approaches produce approximations, as each species contributes uniquely to ecosystems, and its loss could notably impact ecosystem processes in ways that are not yet predictable (Eisenhauer et al. 2023).

Finally, we recorded high values of $\Delta+$ in all study sites, indicating that the species presented a wide range of taxonomic lineages while the provinces exhibited high evolutionary diversity. These results could be attributed to the biogeographic isolation of the ETP due to the formation of the Isthmus of Panama, which favored the independent evolution of species within this region (Mora and Robertson 2005, Robertson and Cramer 2009). Nonetheless, future analyses should focus on testing the relationship between latitude, species richness, and speciation rates across marine fish in the ETP.

CONCLUSIONS

We reported higher values of species richness in the Mexican Pacific (1,045 species) compared to those of previous studies, likely because the data in the present study were obtained from diverse sources. The dominant biological trait categories of the fish species observed in the present study (benthic, highly site-attached, diurnal, solitary, medium-sized, and invertivores specialized in mobile invertebrates) align with those reported in global and regional studies. The Cortez province exhibited the highest values of species richness, number of *FE*s, and *FVol*, which could be associated with its geographic isolation, habitat heterogeneity, and water-column conditions. In contrast, the Californian province showed lower diversity, possibly due to limited species dispersal within this region. Despite differences in *S* and the number of *FE*s, the fish assemblages in each province occupied more than 70% of the total functional space, which is consistent with global studies that have reported a range of functions shared between tropical and temperate regions despite variations in environmental

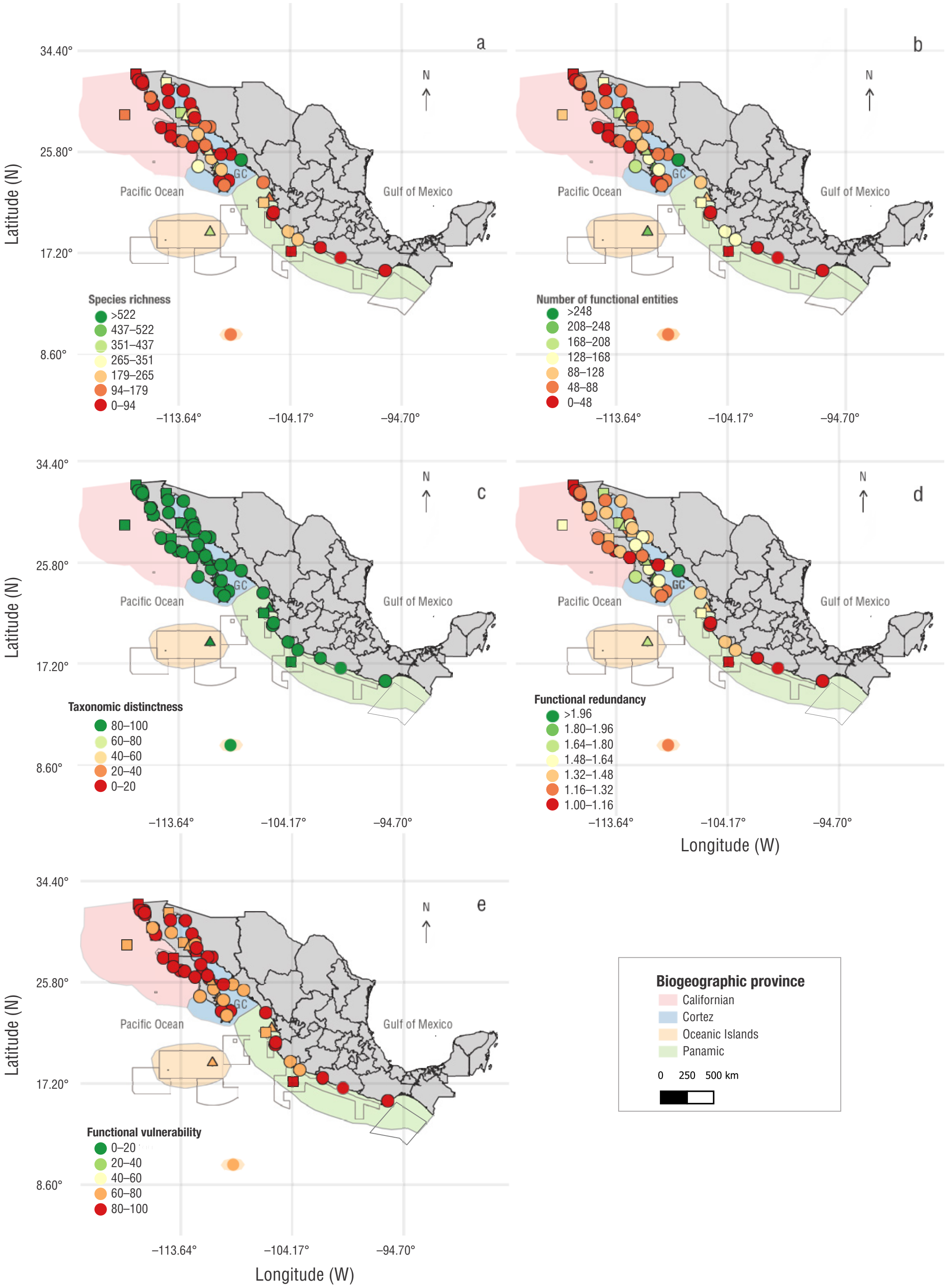

Figure 4. Geospatial representation of the ecological indicators calculated with the information of fish species presence and biological traits: species richness (*S*: total number of species per site) (**a**), number of functional entities (*FE*: number of species groups with unique combination of categories for the biological traits) (**b**), average taxonomic distinctness (Δ+: distance between each pair of species according to the Linnaean classification tree) (**c**), functional redundancy (*RED*: average number of species per functional entity) (**d**), and functional vulnerability (*FV*: percentage of functional entities [*FE*s] with only one species) for the 4 biogeographic provinces (colored polygons) within the Mexican Pacific (**e**). Markers per site indicate the interval scale for each ecological indicator: low (red), medium (yellow and orange), and high (green) values. Gray lines show the protection polygons of marine protection areas (MPAs). Circles indicate non-protected sites; other markers indicate that study sites are located in MPAs with distinct protection categories: national parks (triangles), biosphere reserves (squares), and flora and fauna protected areas (stars).

conditions and evolutionary history. This result, in addition to the identification of the regional backbone, which represents the fundamental species and common ecological roles shared across provinces, presents an opportunity to propose trait-based approaches that could improve management outcomes in reefs under similar environmental conditions. Marine protected areas exhibited higher values of *S* and *RED* than non-protected sites, but further analysis is needed to assess the positive effects of MPA protection. At the regional level, we reported low *RED* and high *FV*, which confirms the uneven distribution of species among *FE*s that has been reported globally. Finally, high Δ+ values indicated that the provinces hosted a wide range of taxonomic lineages among the fish species present, possibly due to the biogeographic isolation imposed by the formation of the Isthmus of Panama.

DECLARATIONS

Supplementary Material

The supplementary material for this work can be downloaded from: https://github.com/lecofym/mexpacfish/blob/main/Data/Supplementary%20Material%201.xlsx and https://github.com/lecofym/mexpacfish/blob/main/Data/Supplementary%20Material%202.xlsx.

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Conflict of interest

The authors declare they have no conflict of interest.

Author contributions

Conceptualization: GRO; Data curation: RTG, EDLS, MVL; Formal analysis: RTG, EDLS, GRO; Funding acquisition: GRO, RBL, JL, LMC; Investigation: GRO, RTG, EDLS, RBL, JL, LMC; Methodology: RTG, EDLS, MVL; Project administration: GRO, RBL, JL, LMC; Resources: GRO, RBL, JL, LMC; Supervision: GRO; Validation: GRO, MVL; Visualization: RTG, EDLS, MVL; Writing – original draft: RTG, EDLS, GRO; Writing – review & editing: RTG, EDLS, GRO, MVL, LMC, RBL, JL.

Data availability

The data for this study are available from: https://github.com/lecofym/mexpacfish.

Ethical approvals and permits for studies involving animals

Field surveys at marine protected areas were conducted with all necessary permits approved by the *Comisión Nacional de Áreas Naturales Protegidas*.

Use of AI tools

The authors did not employ any AI tools in this work.

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