# **RESEARCH ARTICLE**

# The functional ecology of mangrove fishes across the lsthmus of Panama

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#### Abstract

Aim: Biogeographic history and variation in modern environmental conditions can greatly influence local and regional community structure and, more generally, ecosystem functioning. This is clearly exemplified at the Isthmus of Panama where marine communities and environments from the Caribbean Sea and the Tropical Eastern Pacific Ocean differ despite ancient connections during the Miocene and Pleistocene. Here, we compare the functional (implied from traits) and isotopic structure of mangrove fish communities from those two biogeographic regions, which have been separated by the Isthmus of Panama for ~3 my.

Location: Caribbean and Pacific coasts of Panama (Eastern Pacific and Caribbean Sea). **Methods:** We gathered data on five functional traits (salinity preference, body mass, diet, position in the water column and lifespan) of mangrove fishes from the sampled regions. We also analysed  $\delta^{13}$ C and  $\delta^{15}$ C isotopic values and calculated functional isotopic metrics of the most abundant fish species inhabiting mangroves of these two regions.

Results: The taxonomic composition and functional and trophic diversity differed between the mangrove fish communities of the Caribbean and the Eastern Pacific. Although the species richness of both assemblages was similar, there was very little taxonomic overlap between them: Snooks (Centropomidae) numerically dominated in the Eastern Pacific, whereas grunts (Haemulidae) and snappers (Lutjanidae) dominated in the Caribbean Sea. Functional divergence (FDiv) and isotopic richness (IRic) were higher in the Caribbean than in the Eastern Pacific, indicating differences in the way fishes use mangroves in these areas.

Main conclusions: Taxonomic and functional characteristics of mangrove fish assemblages across biogeographic realms can be strongly influenced by local environmental factors (e.g. tidal regimes, the presence of adjacent coastal ecosystems and productivity), and these can override similarities that recent historical connections of faunas might be expected to produce. All such aspects need to be considered when seeking generalizations about ecosystem functioning.

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#### KEYWORDS

biogeography, Caribbean Sea, Eastern Pacific, functional diversity, isotopic diversity, mangrove fish communities, trait-based ecology

# 1 | INTRODUCTION

Over the last two decades, community ecology has focused on functional traits, which are defined as "any biological attribute of an individual that impacts organism performance and thus fitness" (Violle et al., 2007), bringing a more mechanistic understanding of the organization of biotic communities and ecosystem processes (McGill et al., 2006; Nock et al., 2016; Villéger et al., 2008). Aspects of ecology related to ecosystem productivity and disturbance are being increasingly examined from a functional trait perspective, providing insights into the consequences that the Anthropocene will bring to modern ecosystems (e.g. Moulliot et al., 2013). These insights are clearly more applicable to natural resource management than are those provided by nomenclatural community ecology and are more likely to be understood and used by policymakers. In fish communities, the functional approach has been applied predominantly to coral-reef fish assemblages (Bellwood et al., 2019; Mouillot et al., 2014) and recently applied to other tropical shallow-water fish communities, including mangroves, in the context of functional differences across different biogeographical regions (Hemingson & Bellwood, 2018). Previous research has suggested that biogeography can affect the taxonomic composition but not the functional characteristics of mangrove fish assemblages across regions (Hemingson & Bellwood, 2018; Sheaves, 2012). However, it also has been demonstrated that other environmental factors that vary at local and regional scales may affect the way fish use mangroves and thus the functional trait structure of those communities. Those factors include the tidal regimes, salinity fluctuations, the connectivity with adjacent ecosystems and the geomorphology of the coast (Baker et al., 2015; Castellanos-Galindo & Krumme, 2015; Igulu et al., 2014; Olds et al., 2013; Stuthmann & Castellanos-Galindo, 2020). Moreover, the degree of anthropogenic activity and the level of protection (e.g. existence of protected areas) around mangroves can ultimately affect key fish ecological functions (Goodridge Gaines et al. 2020).

Mangrove forests thrive in tropical and subtropical regions at the land-sea interface, providing a unique habitat for a variety of terrestrial and marine organisms. As nursery areas, mangroves are an essential habitat in the life cycle of many marine species (Laegdsgaard & Johnson, 1995). Many of these species in the Neotropics are main targets for small-scale fisheries (Aburto-Oropeza et al., 2008). In addition, fish inhabiting mangroves provide energetic connections between different ecosystems in the shallow-water coastal habitat mosaic (Nagelkerken, 2009). The way in which these connections operate will depend on the particular environmental and biotic characteristics within mangroves and their adjacent ecosystems (Nagelkerken et al., 2015; Sheaves et al., 2015). For example, the nursery function of mangroves and other shallow-water ecosystems can vary across biogeographical regions with differing environmental conditions and settings (Hemigson & Bellwood, 2018, 2020).

Stable isotope analysis is a well-established tool in ecology to trace the carbon and nitrogen sources of foods used by different organisms. In this way, stable isotopes help to understand aspects of the trophic structure within ecosystems and connections between them. Some of the studies on mangrove food webs have questioned the old paradigm that mangroves fuel adjacent food webs and suggested that secondary consumers in mangroves, such as fish, obtain most of their food from external sources (Igulu et al., 2013). These findings have important implications for understanding the functioning of mangrove ecosystems and adjacent coastal habitats. Several models have been developed to analyse stable isotope data (reviewed by Layman et al., 2012). One approach is to interpret stable isotopes, often of carbon and nitrogen, to quantify community-wide characteristics of trophic diversity (Layman et al., 2007). This approach can be used in conjunction with functional trait community ecology, where organisms are represented in multidimensional spaces, with axes representing functional traits (Mouchet et al., 2010; Villéger et al., 2008). New functional trait metrics that use stable isotope information (Cucherousset & Villéger, 2015) can help in disentangling the role that fish play within mangrove ecosystems. The simultaneous use of functional and trophic diversity metrics can help to understand the processes that shape coastal marine fish communities (Gaidzik et al., 2018), including those inhabiting mangroves.

The formation of the Isthmus of Panama changed profoundly the terrestrial and marine biotas at regional and global scales (Leigh et al., 2014). In the marine realm, the closure of the isthmus promoted an extreme differentiation of environmental conditions between the Eastern Pacific and the Caribbean Sea. Among the most notable features arising from this separation that likely have effects on mangrove and other coastal ecosystems are the differences in productivity between basins (e.g. the Pacific side of Panama being more productive than the oligotrophic Caribbean Sea) and strong differences in tidal regimes between both Panamanian coasts (i.e. regularly macrotidal in the Pacific and irregularly microtidal in the Caribbean) that produce variation in temporal and spatial patterns of inundation of mangroves. In addition, mangrove trees on the Pacific coast are tall (> 10 m) compared with their stunted equivalents on the Caribbean coast (D'Croz, 1993). Variation in these and other conditions have profound implications for the type of shallow-water habitats that currently dominate the Caribbean and Pacific coasts in Panama. Here, we use metrics based on stable isotope and functional trait analyses to compare two mangrove fish communities from different biogeographical marine regions separated by the Isthmus of Panama (i.e. the Caribbean Sea vs the Eastern Pacific). We hypothesize that, despite these two regions being isolated only recently in geologic terms (< 3 mya; Lessios, 2008; O'Dea et al., 2016), the large

current contrasts in the environmental characteristics under which mangroves exist in these two regions will influence the functional trait and trophic structures of these fish communities.

# 2 | MATERIALS AND METHODS

#### 2.1 | Study area

Sampling took place in the Eastern Pacific and Caribbean coasts of Panama in Central America (Figure 1). Panama experiences a dry (January–April) and wet (May–December) season, as a result of the shifting Tropical Convergence Zone (Ogden et al., 2013). The formation process of the Isthmus of Panama in the Miocene and Pliocene (Montes et al., 2015; O´Dea et al., 2016) has shaped Panama's terrestrial and marine biogeography. The previously connected marine biotas in the Atlantic and Pacific oceans have followed distinct evolutionary trajectories following the completion of this process about 3mya (Lessios, 2008; O'Dea et al., 2016). Shallow-water habitats, including mangroves, have formed under the different environmental conditions on both sides of the isthmus (Leigh et al., 2014). These contrasting conditions within mangroves provide a natural experimental ground for this study.

Sampling in the Eastern Pacific took place in the large mangrove system of the Gulf of Montijo (7.767°N, -81.116°W), which is typical of mangrove systems on that coast of Panama and contiguous countries. This estuarine system contains 12.7% of the mangroves on the Pacific coast of Panama (Recio et al., 2016). It has well-developed

mangrove forests that often reach up to 30 m tree height and are dominated by the red mangrove *Rhizophora mangle* (Gross et al., 2014). The gulf has a regular, year-round, semidiurnal tidal regime with amplitudes of ~4 m. These result in twice-daily exposure of all the substrate in all the mangrove areas in the study area during low tides. Discharge of freshwater through various rivers that empty into the gulf and the seasonal rainfall leads to strong fluctuations in salinities (8 – 34 practical salinity units (psu); Vega et al., 2004). Compared with the situation in the Caribbean, coral reefs and seagrass beds represent minor habitats in the Tropical Eastern Pacific and the great majority of reef areas are rocky reefs. The nearest coral and rocky reefs and seagrass beds are tens of kilometres from the mangrove forests of the study site.

In the Caribbean Sea, sampling took place in the Archipelago de Bocas del Toro (9.350°N, -82.250°W), inside the Chiriqui Lagoon on the western Caribbean coast of Panama. The fringing mangrove forests there, with trees that rarely exceed 15 m in height and usually are only several metres high, are also dominated by *R. mangle* (Guzman et al., 2005) and account for >30% of the mangroves on the Panamanian Caribbean coast (Recio et al., 2016). This type of mangrove system is common on the Caribbean coast of Panama and throughout the wider Caribbean region. This area, like most of the Caribbean, has a seasonally varying mixture of diurnal and semidiurnal tides, and mangroves there normally are permanently inundated because tidal amplitudes usually are less than 50 cm. Both coral reefs and seagrass beds are present within a few metres of the outer edge of the mangrove fringe at the Caribbean site, again a situation typical in many parts of the Caribbean. Despite high annual precipitation



FIGURE 1 (a) Study site indicating the sampled localities (shaded areas) in the Caribbean Sea (Bocas del Toro) and the Eastern Pacific (Golf of Montijo) in Panama. Arrows indicating location of sampling points; (b) drone photograph of a sampling site in the Caribbean showing permanently inundated mangroves; and (c) drone photograph of mangroves in the Gulf of Montijo showing mangroves and mudflats exposed at low tide

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(> 3000 mm), salinities at Bocas del Toro fluctuate much less than at the Gulf of Montijo (i.e. between 24 and 36 psu; Smithsonian Tropical Research Institute, 2016). Environmental parameters, tidal ranges and precipitation at both sampling locations are summarized in Table 1. Environmental parameter values obtained during the present study correspond to longer-term values at the respective locations in the Caribbean Sea (Graniero et al., 2016; Smithsonian Tropical Research Institute, 2016) and the Eastern Pacific (Vega et al., 2004).

#### 2.2 Sampling

Fish collection was carried out monthly at both locations in the Eastern Pacific and the Caribbean Sea from November 2016 to February 2017. Nine different sampling stations were sampled at each location on three consecutive sampling days, covering three stations per day (see details and georeferenced coordinates in Supplement S1). Fish sampling methods varied between the two locations, due to differences in effects of tidal variation on inundation of the mangrove systems. At the Pacific coast, block nets (dimensions: 13 m x 2.5 m; 15 mm stretched mesh size) were set in small intertidal mangrove creeks during ebb tide so that fish migrating in the creeks at high tide were captured on their way out at low tide (see details about the method in Castellanos-Galindo & Krumme, 2014). Clove oil, an effective fish anaesthetic (Robertson & Smith-Vaniz, 2010), was used to facilitate fish capture when creeks were not fully drained at ebb tide. At the Caribbean coast, mangrove stands located ~1 m from the main fringe area were selected and encircled with a net (dimensions: 13 m x 1.5 m; 15 mm stretched mesh size) to capture fish in the surrounded area. The net was smaller in height at the Caribbean coast than at the Pacific, due to the lower water level. Clove oil was also used to facilitate fish capture in the encircled area. On both coasts, clove oil in the ratio of 1:9 (clove oil:alcohol) was spread from the nozzle of a plastic bottle until the first signs of disoriented fishes were observed at each sampling occasion. Normally, <100 ml was needed for each sampling event. Samples were initially processed at the Smithsonian Tropical Research Institute marine laboratory at Bocas del Toro. All fish were identified, measured (standard length in cm), weighted (in g) and frozen prior to further analysis.

#### 2.3 Data analyses

# 2.3.1 | Conventional functional characteristics of fish assemblages

Fish were categorized based on five relevant ecological traits: (1) "salinity preference," which included the categories marine, marinebrackish and freshwater; (2) "diet," categorizing fish as invertivores, macro-carnivores, planktivores and herbivores; (3) "position in the water" encompassing the three categories pelagic, benthopelagic (living on the bottom and in the water column) and demersal (living only on the bottom); (4) "body mass," consisting of four levels of ordered body mass <50, 51-100, 101-300 and >300 g; and (5) "lifespan" that included four ranges <5, 5-10, 10.1-15 and >15 years. These four traits have all ecological relevance and determine to a great extent the functional niche of fishes within mangroves (see Moulliot et al., 2014). For example, body size is a fundamental trait that determines organism's energy needs and potential impact on the ecosystem. Likewise, position in the water column determines which type of prey an organism may access to and also can be indicative of the connectivity or energy transfer with adjacent ecosystems. Information for the first three and the last trait (1-3 and 5) was compiled from the online database FishBase (Froese & Pauly, 2019) and online fish guides for the region (Robertson & Allen, 2015; Robertson & van Tassell, 2015). "Body mass" was derived from the actual biomasses of fishes collected in this study. This set of categories within each of the five functional traits led to a number of unique combinations of species trait values equivalent to those termed "functional entities" (FEs) by Mouillot et al. (2014) and Villéger et al. (2011).

Based on the trait combinations in different FEs identified here, we created a multidimensional Euclidean space that included both Pacific and Caribbean assemblages. That multidimensional functional space was produced by principal coordinate analysis (PCoA) based on a dissimilarity matrix. We chose four dimensions for the PCoA, as indicated by analysis of the plot (Supplement S2) produced using the quality\_func\_space function (Maire et al., 2015), and to keep the framework to a manageable size. The chosen FE-based approach reveals links between functional diversity and ecosystem processes, as the redundant species in the community are expected to have similar ecological roles and therefore similar trait information.

Based on the arrangement of the FEs in the computed space, three functional diversity indices-FDIs [functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv)]-were estimated following the framework proposed by Mouchet et al. (2010).

- 1. Functional richness (FRic). This describes the total extent of multidimensional space occupied by the FEs. This index tends to zero when FEs are located in the same part of the functional space and maximizes when they are dispersed around the edges of the space (Villéger et al., 2008). While FRic describes how much of the functional space is filled up by the assemblage, the FEve and Div indices explain how the space is filled (Schleuter et al., 2010).
- 2. Functional evenness (FEve) quantifies the regularity in the distribution of FEs by accounting for their weight along the shortest tree that links all of them. Low FEve values indicate that the FEs are located in a small region of the functional space, whereas high values indicate that they are evenly dispersed in the space (Villéger et al., 2008).
- 3. Functional divergence (FDiv) represents how FEs and their abundance are distributed in the functional space. Low FDiv values indicate that all FEs are close to the centre of gravity, while a value near 1 suggests that FEs are situated on the edges of the space.

TABLE 1 Environmental conditions of sampling areas at both sampling localities in the lsthmus of Panama

Archipelago de Bocas del Toro (Caribbean Sea)	Gulf of Montijo (Tropical Eastern Pacific)
32.54 ± 1.47	26.50 ± 3.04
28.40 ± 1.27	$28.95 \pm 0.34$
$8.15\pm0.07$	7.81 ± 0.14
$6.66 \pm 1.31$	$5.25\pm0.94$
3658 ± 467	3114 ± 329
0.24	~4
	Archipelago de Bocas del Toro (Caribbean Sea) $32.54 \pm 1.47$ $28.40 \pm 1.27$ $8.15 \pm 0.07$ $6.66 \pm 1.31$ $3658 \pm 467$ $0.24$

<sup>a</sup>Values are means with standard deviation of measurements taken close to fish sampling points in December 2016, January and February 2017 at high tide

<sup>b</sup>Precipitation values are mean (± SD) for Western Panama (Valiela et al., 2012) and for Bocas del Toro (Smithsonian Tropical Research Institute, 2016) from 2004 to 2011.

The higher the value of *FDiv*, the greater is the number of niches that can be differentiated in the multidimensional space (Laliberté & Legendre, 2010; Mouillot et al., 2014).

*FRic*, *FDiv* and *FEve* were quantified using the *multidimFD* function (Maire et al., 2015; Mouillot et al., 2013; Villéger et al., 2008) in R (R Core Team, 2019). This function accounts for variation in species abundances in the community by integrating the relative catch mass per species as percentage of the overall catch mass obtained for each fish assemblage (Pacific or Caribbean) in the final calculation of the indices.

To understand the variation in body size (fish total length) between the two fish assemblages, violin plots were constructed using the information from the sampling campaigns and information from the literature on the maximum body size attained by each species found (Robertson & Allen, 2015; Robertson & Tassell, 2015). Using the ratio of mean total length to maximum total length of each fish species, it was possible to compare the overall use of mangrove habitats by small- vs. large-sized individuals in each assemblage.

#### 2.4 | Isotopic functional diversity

#### 2.4.1 | Stable isotope sample processing

For the stable isotope analyses, we used the species with highest biomass and numerical abundance in each study system. Based on the species contribution to the total weight of the community, eight species from the Pacific assemblage and five species from the Caribbean assemblage were chosen and used for such analysis (see Data Analysis, below). Whenever possible, 10 individuals of the same size were selected from each species. For stable isotope analysis, a muscle sample, free of inorganic carbon, was taken directly under the dorsal fin of the fish. For individuals <5 cm TL, the whole organism was taken and treated with hydrochloric acid to remove inorganic carbon prior to analysis. This difference in treatment of small and large individuals followed the assumption that while muscle samples of larger individuals provide a good estimation of the isotopic value (Schielke & Post, 2010), by only introducing minor variability in  $\delta^{13}$ C, smaller organisms should be ground whole, to avoid bias introduced in nitrogen isotope values that arises when only muscle plugs are used (Schielke & Post, 2010). All samples were dried at 60 °C for at least 48 hours, ground to a fine powder with mortar and pestle, and stored at room temperature in clean vials until further analysis. Stable isotope ratios of  $^{13}$ C/ $^{12}$ C and  $^{15}$ N/ $^{14}$ N were measured at the Leibniz Centre for Tropical Marine Research in Bremen (Germany) with a mass spectrometer (Delta plus Analyser) coupled to an elemental analyser (Flash EA 1112, Thermo Finnigan). The standard used for carbon ratios was Pee Dee Belemnite (PDB), while atmospheric nitrogen was used as a standard for nitrogen ratios. Stable isotope ratios were expressed in delta ( $\delta$ ) notation in units per mil (‰) based on the formula

 $\delta^{15}$ N or  $\delta^{15}$ C =  $[(R_{sample}/R_{standard})] - 1 \times 1000,$ 

where *R* was  ${}^{12}C/{}^{13}C$  or  ${}^{15}N/{}^{14}N$ .

# 2.5 | Isotopic functional characteristics of fish assemblages

To determine the dominant species for stable isotope analysis, the relative biomass of each species within the distinct assemblages was calculated based on the total catch biomass. Our sampling method likely underestimated the biomass of abundant small pelagic fishes that escaped through the nets at both localities [i.e. the engraulid *Anchoa walkeri* Baldwin and Chang, 1970 in the Pacific and the clupeid *Jenkinsia stolifera* (Jordan and Gilbert, 1884) in the Caribbean; personal observations]. We therefore used estimates from similar mangrove fish studies in both regions, where small pelagic biomass quantification has previously been carried out (*see* Castellanos-Galindo & Krumme, 2013; Vaslet et al., 2010) to derive a rough estimate of their relative abundance in our study areas.

Following Cucherousset and Villéger (2015), the fish  $\delta^{15}$ N values from both regions were transformed to trophic positions (TP) using the approach of Quevedo et al. (2009) to allow for crossecosystem comparisons (Pacific vs Caribbean). TPs were calculated -WILEY- Diversity and Distributions

using a two-end-member-mixing model of Post (2002), incorporating isotopic values of snail and mussel species as the benthic and pelagic baselines for the two mangrove systems.  $\delta$   $^{13}C$  values were not transformed, as the baselines had similar  $\delta$   $^{13}C$  values, enabling a direct comparison between raw  $\delta$   $^{13}C$  fish values. The TPs and  $\delta^{13}C$  values of both assemblages were pooled before scaling.

The choice of the isotopic FDIs (*isotopic richness*, *isotopic diver*gence and *isotopic evenness*) followed the framework of Mouchet et al. (2010) and paralleled the three functional diversity indices described above. In addition, one extra index (*isotopic uniqueness*) was chosen to describe the trophic structure of the communities. These four isotopic FDIs were proposed by Coucherousset and Villéger (2015) and are adapted from the functional diversity indices developed by Villéger et al. (2008). The calculated indices are the following:

- 1. Isotopic richness (IRic) describes the extent of the area of the isotopic space ( $\delta^{13}$ C  $\delta^{15}$ N) occupied by the species in the communities (Coucherousset & Villéger, 2015; Layman et al., 2007).
- 2. *Isotopic divergence (IDiv)* estimates the distribution of the species in the isotopic space, as with the *FDiv*.
- Isotopic evenness (IEve) tends towards zero when most of the species are located within a small part of the isotopic space and approaches one when the species are evenly distributed over the space.
- 4. *Isotopic uniqueness (IUni)* reflects the average closeness (distance to the nearest neighbour) of organisms in the isotopic space. *IUni* equals zero when communities consist of pairs of species with similar diets or when the major weight belongs to organisms that are isotopically similar. The value tends to 1 when most organisms are isolated in the isotopic space.

All the isotopic indices are unitless, with values between zero and 1, and are mathematically independent of the number of organisms used in the calculation. They also take species abundance into account. For the quantification of the isotopic diversity indices *IRic*, *IDiv*, *IEve* and *IUni*, the script "Si\_Div" (Cucherousset & Villéger, 2015) was used in R (R Core Team, 2019). In order to assess the potential for differences in the indices between oceans, we performed Monte Carlo simulations with 10<sup>4</sup> iterations and calculated z-scores, following Gajdzik et al. (2018).

To control for marked taxonomic differences in the two assemblages, and for interspecific variation, isotopic values of species of the family Haemulidae from both assemblages were compared separately for their *IRic* values and isotopic similarity and nestedness. Isotopic similarity and nestedness are both quantified using *IRic. Isotopic similarity* is defined as the ratio between the volume of the two-dimensional isotopic space shared and the volume of the union of the spaces. *Isotopic nestedness* is the ratio between the volume shared and the volume of the smallest occupied isotopic space (Cucherousset & Villéger, 2015). The Caribbean assemblage included three haemulids, Haemulon flavonlineatum, H. carbonarium and H. plumierii, while the Pacific assemblage included two haemulids, Pomadasys branickii and Rhencus macracanthus. Our isotopic analysis only incorporated the most abundant species of each assemblage, and therefore, only two species in the Caribbean [H. flavolineatum (n = 10) and H. plumerii, (n = 10)] and one in the Pacific

(*R. macracanthus*, n = 9) were considered. A bootstrapping procedure was performed (1000 iterations) to control for any effects of the higher sample sizes in the Caribbean. *IRic* for these species is presented as mean (+ SD).

## 3 | RESULTS

## 3.1 | Taxonomic and ecological diversity

The Caribbean and Eastern Pacific mangrove fish communities had comparable taxonomic richness. The Caribbean mangrove fish assemblage included 26 species in 19 families, while the assemblage from the Eastern Pacific comprised 25 species in 18 families. However, in taxonomic terms the composition of the two assemblages was very different: only five (15.6%) of 32 families and one (2.4%) of 42 genera were common to both assemblages (Figure 2, Supplement S3).

Fish assemblages in the Eastern Pacific were dominated numerically by estuarine species (snooks—Centropomidae; croakers—Sciaenidae; marine mojarras—Gerreidae; and white-eye fish—Anablepidae), which represented 20% of the species and 78% of the numbers of individuals found there. In contrast, fish assemblages in the Caribbean were dominated by reef-associated marine species (snappers—Lutjanidae; grunts—Haemulidae; and parrotfishes— Scarinae; Figure 2; Supplement S3), which represented 23% of the species and 63% of the numbers of individuals found there. In fact, only three species in the Caribbean assemblage are regularly found in brackish conditions, whereas in the Eastern Pacific, all species encountered regularly occur in brackish conditions and four of them even in freshwater.

The body weight of 65% of all the species found in the Caribbean was <50 g, and only 19% of the species had individual weights >100 g. In the Eastern Pacific, only 36% of the species had individuals weighing <50g and the same percentage was represented by species with individuals with weights >100 g. The same pattern was observed when comparing individual total lengths (i.e. larger fish sizes in the Eastern Pacific; Figure 3). The range of maximum body sizes (derived from the literature) was also greater in the Eastern Pacific with some species reaching >100 cm in total length (TL). In the Caribbean, the maximum known body size attained by any species was <70 cm TL (Figure 3, Supplement S3). The estimated lifespan characteristics were more diverse in the Caribbean fish assemblage due to the presence of both small, short-lived cryptobenthic fishes (e.g. the gobiid *Coryphopterus dicrus*) and long-lived species (e.g. the scorpaenid *Scorpaena plumieri*). The two



assemblages also differed in terms of patterns of habitat usage: 85% of the Caribbean species were demersal, with only one pelagic species and three benthopelagic species. In contrast, in the Eastern Pacific only 56% of the species were classified as demersal with the remaining species being either pelagic (n = 4) or benthopelagic (n = 7). While all 26 species in the Caribbean assemblage are common inhabitants of coral reefs, and most are also known from seagrass beds, only seven of the 25 species in the Pacific assemblage are known to associate with reefs (Supplement S3). Fish trophic groups in the Caribbean assemblage were more evenly distributed with 54% of 26 species considered carnivores (invertivore or macrocarnivore) and the remaining species being either omnivore (23%), herbivore (15%) or planktivore (8%). In the Eastern Pacific, 80% of the 25 species were carnivores (invertivore or macrocarnivore), only one species was a herbivore, three were omnivores, and one was planktivore.

#### 3.2 | Functional composition and diversity

The Caribbean and Pacific mangrove fish assemblages were grouped in 22 and 24 FEs, respectively (Figure 4a). In the Pacific assemblage, 23 of the FEs consisted of only one species, and one FE included two species. In the Caribbean, 19 FEs contained a single species, two FEs consisted of two species, and one FE included three species. The slightly higher number of FEs in the Eastern Pacific reflects the more diverse salinity preferences and larger range of body sizes of this fish assemblage compared with the one in the Caribbean Sea (Figure 3).



FIGURE 3 Violin plots of (a) the distribution of fish body sizes and maximum body sizes (total length) within Caribbean and Eastern Pacific mangrovefish assemblages and (b) the ratio of mean total length of collected specimens to maximum known total length for fish species in the Caribbean and Eastern Pacific. Dots in (b) are scaled to the relative biomass of each species within the assemblage

Not surprisingly, given the marked taxonomic and functional characteristic differences between the two assemblages described above, they occupied different areas of the functional space (Figure 4c-f). First, the area of such multidimensional space (PC1-PC2 and PC3-PC4) occupied by the Eastern Pacific assemblage was larger, which translated into a higher functional richness in that assemblage (*FRic*—Pacific=0.344, vs Caribbean=0.280; Figure 4b). In both assemblages, the FEs are concentrated towards the borders of the space rather than in the centre of gravity, with the Caribbean assemblage showing a slightly higher functional diversity than the Pacific assemblage (*FDiv*—Caribbean =0.847, Pacific =0.785; Figure 4b-d). However, the FEs in the Pacific are distributed slightly

more regularly in the space (FEve=0.385) than the Caribbean equivalent (*FEve*=0.299) (Figure 2).

## 3.3 | Isotopic diversity

The structural arrangement of the communities in the isotopic space was different between the Pacific and Caribbean assemblages. Eastern Pacific fishes displayed lower scaled  $\delta^{13}$ C with smaller dispersions (standard deviations), compared with their Caribbean counterparts in the lower right sector. This indicates the use of different and more limited primary resources in the Pacific assemblage.

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FIGURE 4 (a) Number of fish species and functional entities (FE) found in mangroves at both sides of the Isthmus of Panama and (b) calculated functional diversity indices (functional richness, FRic; functional diversity, FDiv; and functional evenness, FEve). Functional space occupied by Pacific (c, e) and Caribbean (d, f) fish assemblages in PC1-PC2 and PC3-PC4 axes from a principal component analysis on functional traits. Vertical bars on axes mark minimum and maximum values. The coloured convex polygon is a projection of the multidimensional space in 2D. Filled points are vertices in the multidimensional space, and crosses illustrate the position in space of points belonging to the other-ocean assemblage

Eastern Pacific (a) (b) 30 25 20 15 10 5 0 FE Species



0 2

10%

0.4

C

10%

0.4

0.2

0

 $\cap$ C

0.2



As with scaled  $\delta^{13}$ C, dispersions of scaled TPs were smaller in the Pacific than in the Caribbean assemblage (Figure 5).

The larger area of the isotopic space occupied by the Caribbean assemblage (IRic=0.221) indicates a higher trophic diversity, compared with the Pacific assemblage (IRic=0.078) (Figure 6a). In both communities, species and their weight, indicated as point size, were distributed around the borders of the occupied space, rather than

towards the centre of gravity (occupied by only one species in the Caribbean and two in the Pacific), resulting in high values for IDiv in both assemblages (Pacific=0.92; Caribbean=0.893; Figure 6b). The weight along the shortest tree linking all species of the assemblages was distributed regularly in both assemblages, leading also to similar values of IEve (Pacific=0.669 vs Caribbean=0.665, Figure 6c). However, overall species redundancy was higher in the

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**FIGURE** 5 Scaled fish  $\delta^{13}$ C values and trophic position, transformed based on  $\delta^{15}$ N values using two-end-member-mixing model from the dominant assemblages in the Caribbean Sea (blue) and the Eastern Pacific (green). Fish species differentiated by shape according to the position in the water column with benthopelagic (circle), demersal (triangle) and pelagic (square). Values shown as means ( $\pm$  SD)

Pacific assemblage, where species formed pairs with similar trophic preferences (Figure 6e). In the Caribbean assemblage, species were more isolated from one another (*IUni* =0.509 Pacific vs 0.635 for Caribbean). However, while no significant differences (p > 0.05 in all cases) were found between regions in any of these four indices (Figure 6), this may be due to the high intraspecific dispersion of carbon and nitrogen isotope values observed among Caribbean species (Figure 5).

To control as much as possible for effects of the very different taxonomic composition of the two assemblages and the potential interspecific variability, species of Haemulidae from both locations were compared. Isotopic richness (*IRic*) of *R. macracanthus* (0.027) was markedly smaller than *IRic* of either Caribbean member of the same family: *H. flavolineatum* (0.066) and *H. plumierii* (0.227). Isotopic nestedness and similarity of *R. macracanthus* to *H. flavolineatum* (Figure 7a) and *H. plumierii* (Figure 7b) were zero in all cases. Resource use of the two Caribbean grunts was more extensive compared with the Pacific grunt, based on the extension of scaled  $\delta^{13}$ C values (Figure 7). Similar patterns can be found for scaled TP, with *R. macracanthus* in the Eastern Pacific occupying <0.2 of the scaled TP axis and the Caribbean species each occupying >0.6 of that axis space (Figure 7a,b). Overall, the grunts mirror the pattern, detected in the whole assemblage (Figures 5 and 6), namely the higher IRic and greater intraspecific variation (SD) among Caribbean species. The isotopic space occupied by *H. flavolineatum* and *H. plumierii* overlaps on both axis (isotopic similarity =0.051; isotopic

FIGURE 6 Scaled and weighted  $\delta^{13}$ C index values for two fish assemblages (see Methods for details). Mean values (± SD) of the mangrove fish assemblage in the Eastern Pacific (left, green) and Caribbean Sea (right, blue). Isotopic richness (a) is presented as a coloured area, while the filled points represent the position of organisms in the multidimensional space and their size corresponds to the relative biomass of the species. (b) Isotopic divergence is illustrated in relation to the centre of gravity of the vertices (central diamond in both assemblages) and the distances of species from it (dashed lines). (c) Isotopic evenness is illustrated with a minimum spanning tree linking all points in the multidimensional space. (d) Isotopic uniqueness is symbolized with all the distances to the nearest organism (black arrows). Isotopic diversity indices (e-h) show 50%, 75% and 95% confidence intervals from dark to light colours, respectively. Modal values are indicated by a black dot



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(g) Isotopic Eveness





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FIGURE 7 Scaled, transformed  $\delta^{13}$ C values for congeneric mangrove fishes in two oceans. (a) *Rhencus macracanthus* (Eastern Pacific, green) and *Haemulon flavolineatum* (Caribbean, red) in comparison and (b) *Rhencus macracanthus* (Eastern Pacific, green) and *Haemulon plumierii* (Caribbean, orange) and (c) *Haemulon flavolineatum* (Caribbean, red) and *Haemulon plumierii* (Caribbean, orange). Values are of individuals of the species

nestedness =0.217), indicating that those two species have similar, although not identical, feeding strategies. These results indicate a different use of primary resources by confamilial species in the different oceans.

mangrove systems in the Caribbean and the Pacific are reflected in their effects on fish assemblages that inhabit them (Lefebvre & Poulin, 1997).

### 4 | DISCUSSION

The larger number of FEs and generally higher FDI values (i.e. functional richness and evenness) in the mangrove fish assemblage of the Eastern Pacific than in the Caribbean Sea indicate that these taxonomically very different assemblages likely make use of these habitats in different ways. Similarly, the differences in the isotopic FDIs, although not statistically significant, provide some indication of differences in the feeding strategies of mangrove fishes in these two regions. Moreover, the comparison of isotopic FDIs among confamilial haemulids in both regions revealed patterns similar to those observed at the community level. Mangrove fishes in the Caribbean exhibit larger isotopic niches, as reflected by higher dispersion in their carbon and nitrogen isotopic values (Figure 5) and trophic positions (Stuthmann & Castellanos-Galindo, 2020), as well as higher values in some of the isotopic FDIs (Figure 6a-h). The two complementary approaches (functional trait diversity and isotopic diversity) indicate that fishes use mangroves in different ways depending on the environmental setting in which mangroves exist. Two factors could play fundamental roles here: (1) habitat availability, as determined by influences of the tidal regime on the depth and extent of inundated areas, and on the size of individual fish able to use mangrove habitats, and (2) the characteristics of the habitat mosaic within which the mangroves exist. A more diverse habitat mosaic, such as that in the Caribbean, with seagrass beds and coral reefs immediately adjacent to the mangroves, potentially could provide larger feeding niche for fishes known to regularly associate with all three habitats. It is therefore not surprising that such large biological and environmental differences between

# 4.1 | Taxonomic and functional composition and diversity

The fish assemblage in the Eastern Pacific comprised slightly more FEs than the Caribbean assemblage (24 vs 22), with many entities also being only represented by one species. In the Eastern Pacific, the fish community includes a higher proportion of brackish-tolerant species than does the Caribbean community, where the fish community is predominantly composed of marine species. This difference reflects the disparities in the environmental conditions within mangrove systems in these two ocean basins; that is, mangroves in the Eastern Pacific usually occur in estuaries and bays with abundant freshwater discharge and distinctly reduced salinities, whereas in many parts of the Caribbean mangroves occur on coastal fringes in near-marine environments. In the Eastern Pacific, where fish in the mangrove assemblage were also larger in size and had predominantly benthopelagic and pelagic habitats (see Figure 3; Supplement S3), the larger tidal amplitudes (~4 m) may allow larger and more mobile fishes to access relatively large mangrove areas at high tide and use pelagic and benthopelagic resources such as smaller fishes, shrimp or swimming crabs brought into the mangroves by the strong tidal flux. Tides also determine the activity patterns of potential prey for fishes within the mangroves (Pülmanns et al., 2018). In contrast, in the microtidal Caribbean site, water depth at the outer edge of the mangrove was ~1.5 m, becoming shallower further in a relatively small mangrove area behind that fringe. This characteristic of the Caribbean mangrove system may restrict habitat availability to smaller-bodied fishes with demersal habits that can readily access these very shallow waters that are not subject to frequent tidal surges that influence the types of resources available. A permanently

inundated shallow-water habitat mosaic in the Caribbean also implies that feeding resources from seagrasses of coral reefs are also available to mangrove fishes in that region. In fact, evidence suggests that mangroves in the Caribbean are not important feeding areas for fishes in comparison with seagrasses (Verweij et al., 2006). The pronounced environmental differences found between the Caribbean and Eastern Pacific mangrove seascapes could therefore play a strong role in determining the different functional characteristics of the fish assemblages inhabiting mangroves in those two regions. In addition, strong variation in the degree to which contiguous ancillary habitats are available in the two systems influences not only the taxonomic composition of the two fish assemblages but also their reliance on mangroves for resources. The mangrove fish assemblages found in these two localities in Panama are representative of such assemblages in each biogeographical region. The dominant fish species and families found in the Bocas del Toro mangroves are the same as those found in other non-estuarine, microtidal mangrove systems that interface with coral reefs and seagrass beds of the Greater Caribbean (e.g. in the Bahamas, Belize, Curaçao, Florida; Nagelkerken, 2007). Similarly, the fish assemblage composition and the dominance of some families in the Gulf of Montijo is equivalent to that found in another macrotidal mangrove in the Eastern Pacific (Castellanos-Galindo et al., 2013), a region with few coral reefs or areas of seagrass.

Median (measured) and maximum (literature values) total lengths of the fish captured in this study tended to be higher in the Eastern Pacific fish assemblage than those in the Caribbean fish assemblage (Figure 3a). This pattern may be simply a reflection of generally larger body sizes of fishes in the Eastern Pacific compared with the fish body sizes in the Caribbean Sea (see Barneche et al., 2019). In contrast, the average ratio of mean total length to maximum total length among the collected specimens did not appear to differ between the two assemblages (Figure 3b), indicating that very similar numbers of species in both regions have relatively small individuals (ratio <0.5 in Figure 3b) inhabiting mangroves.

A number of studies examining fish FDI have used trait information derived from the literature or online sources (e.g. FishBase). A fundamental trait determining ecosystem function is body size. Because mangroves are regarded as nurseries, using maximum body size data (e.g. Henriques et al., 2017) may well mask differences in the functional structure of fish communities in these nursery habitats. As our results indicate, the standard practice of using maximum known body size in fish functional structure studies may miss important aspects of the variation found in body sizes between and within ecosystems that could help to understand fauna/habitat functional relationships (Bellwood et al., 2019).

#### 4.2 | Isotopic functional diversity (IFD)

Isotopic diversity is based on the stable isotope values obtained from fish and therefore provides a direct measure of the trophic structure of a community. Mangrove carbon generally shows depleted Diversity and Distributions –WILEY

 $\delta^{13}\text{C}$  values relative to values from sea grasses and coral reefs (de la Moriniere et al., 2003). In the Caribbean, the presence and close proximity of coral reefs and seagrass beds to the mangroves support the development of an assemblage of fishes that commonly use and feed in all those habitats. This characteristic is reflected in the higher isotopic richness of the Caribbean fish assemblage. This observation is supported by the isotopic uniqueness values, suggesting a higher species similarity (i.e. redundancy) in the Eastern Pacific assemblage in terms of trophic behaviour. The greater availability of different food sources from three major ecosystems in close proximity to each other in the Caribbean has led to a lower species redundancy, as indicated by higher isotopic uniqueness in the fish assemblage there. Lower isotopic richness of the Eastern Pacific assemblage indicates the use of a smaller range of food sources. Both tidally limited access to mangrove areas and the general absence of corals and seagrasses within reachable distances may contribute to this. Compared with the Caribbean fish community, isotopic redundancy and richness were higher in the Pacific. We suggest that the failure of isotopic FDIs to show statistically significant differences between the two fish communities is due to high intraspecific variability in isotopic values among Caribbean fish species (Figure 5). This effect of higher variability in isotopic niches between these two fish communities was demonstrated by Stuthmann and Castellanos-Galindo (2020) using a Bayesian method that calculates a niche width metric (sensu Layman et al., 2007). Our comparison of IRic, isotopic similarity and nestedness of species of the shared family Haemulidae from both coasts detected a similar pattern (Figure 7).

Recent regional- and global-scale analyses have found taxonomic differences in mangrove fish assemblages that could be largely explained by the biogeographic history of marine regions (Hemingson & Bellwood, 2018; Sheaves, 2012). These studies have also suggested that these taxonomic differences do not necessarily translate into differences in the functional structure of such fish communities between biogeographical regions. Our results with mangrove fish faunas separated relatively recently (in geologic terms) by a major biogeographic barrier, the Isthmus of Panama, do not support such findings. The large-tree mangrove forests in the macrotidal, brackish Eastern Pacific coast of Panama are physiographically very different from the small-tree mangrove systems encountered in the microtidal marine Caribbean coast of the country. In addition, those two mangrove systems differ strongly in terms of the availability of adjacent alternative habitats (coral reefs and seagrass beds) known to be used by fishes found in tropical West Atlantic mangroves. These pronounced environmental differences influence both the taxonomic and functional structure of mangrove fish communities in these two biogeographical regions.

More general, global comparisons of the functional structure of estuarine fishes have found that both biogeography and environmental factors determine the trait structure of fish assemblages. For example, the global meta-analysis of Henriques et al. (2017) found that the tidal amplitude in mangrove estuaries was positively correlated with fish body size. Ancient biogeographical connections of faunas also play a role, with mangrove fish assemblages -WILEY- Diversity and Distributions

of macrotidal areas in both the Eastern Pacific (Colombia) and Western Atlantic (Brazil) being similar in terms of their taxonomic composition (Castellanos-Galindo & Krumme, 2015). The taxonomic and functional composition of the mangrove fish assemblage of the Panamanian Pacific coast examined here resembles those of assemblages in macrotidal areas in Colombia and Brazil. At all these sites, estuarine fish families are dominant. In contrast, the microtidal Caribbean mangrove fish assemblage in our study is dominated by marine species of typical reef fish families, demonstrating the strong influence that habitats such as coral reefs and seagrasses play in determining faunal composition in this tightly interconnected habitat mosaic. Our study at the Isthmus of Panama has shown that faunal taxonomic and functional signals from ancient biogeographical connections can be almost completely overridden by the current coastal environmental conditions (tidal regime and habitat configuration). These results are applicable to other non-estuarine mangrove systems in the Greater Caribbean Sea where corals and seagrasses occur in close proximity to mangroves. Likewise, meso- and macrotidal estuarine mangrove areas of the Eastern Pacific that lack adjacent coral reefs and seagrass beds contain the same set of estuarine fish families found on the Panamanian Pacific coast. Fish-mangrove relationships are therefore highly context-dependent (Bradley et al., 2020; Hemingson & Bellwood, 2020), indicating that the potential for ecological equivalence of such ecosystems across biogeographical regions with disparate coastal environmental conditions needs to be carefully evaluated with empirical studies.

# 5 | CONCLUSIONS

Among fishes living on coral reefs, the functional space filled by their assemblages is very similar in different biogeographical regions (Mouillot et al., 2014). In contrast, the functional spaces filled by the mangrove fish assemblages in the Eastern Pacific and the Caribbean Sea examined in here are clearly different. Coral reef and mangrove ecosystems differ in various characteristics. Unlike many mangroves, shallow coastal coral reefs are permanently inundated wherever they occur. Coral reefs also normally survive in a narrower range of environmental conditions, requiring relatively low turbidity and relatively high salinities. In contrast, mangroves occur in intertidal areas where environmental conditions can vary dramatically during tidal cycles. Mangroves develop differently depending on the coastal environmental and geomorphological setting (Twilley et al., 2018) and may vary greatly in terms of the availability of contiguous ancillary habitats used by mangrove fishes. A greater variety of types of mangrove systems (e.g. estuarine vs non-estuarine, macrotidal vs microtidal, with and without ancillary habitats) implies that the functional structure of these ecosystems could well be more variable than that of coral reefs. The example of mangrove fish faunas from very different settings assessed in the present study reflects how ecosystem function can change according to this variation, variability that may

be seriously reduced or even absent in other shallow coastal ecosystems in the tropics.

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#### CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

#### PEER REVIEW

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#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in Figshare (Functional traits: https://doi.org/10.6084/m9.figsh are.19222509.v1 and Stable isotopes: https://doi.org/10.6084/m9.figshare.19222329.v1

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#### BIOSKETCH

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Author contributions: GAC-G, DRR and LES conceived the ideas and designed methodology; LES and GAC-G collected the data; LES and GAC-G analysed the data; GAC-G and LES led the writing of the manuscript; and DRR contributed to the discussion and writing of the paper. All authors contributed critically to the drafts and gave final approval for publication.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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