Original Research Article

Functional-biogeography of the reef fishes of the islands of the Gulf of California: Integrating functional divergence into marine conservation

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ABSTRACT

The Gulf of California (GC) is a semi-closed sea in the Tropical Eastern Pacific and is recognised as a highly diverse marine ecosystem. Despite this status, this region is still poorly studied in comparison to other marine hotspots. To start filling this gap, we attempt to provide a global overview of reef-fish diversity around the numerous islands of the region. We evaluated species richness, the abundance and biomass, and the functional diversity of the fish assemblages for the major islands of the GC. We first highlight that the southwestern part of the central GC is the hotspot of reef-fishes diversity within the GC, in terms of species richness, functional diversity, and fish abundance. We then found out an important functional divergence between fish assemblages of northern and southern regions. The fish biomass of each region is dominated by different species, characterised by different ecological traits (the opposite of functional convergence). This functional divergence may be explained by an important oceanographic heterogeneity along the latitudinal axis of the GC. The northern part shows larger climate fluctuations while the southern part is more tropical and climatically stable. Such functional divergence is a biodiversity facet to take into account when determining the sites to focus conservation action. In the GC, this criterion allows the importance of some sites to be highlighted to preserve the legacy of the reef-fishes, despite their lower diversity levels.

1. Introduction

Our entrance into a period of decline in biodiversity is widely recognised (Barnosky et al., 2011; Ceballos et al., 2017). To contain this trend there is an urgent need to invest more in conservation policies and to ensure the involvement of all stakeholders to better manage natural resources. To do so, an essential step is to understand and evaluate biodiversity.

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While species richness is an essential parameter, functional diversity or the diversity of ecological traits represented among a suite of species is recognised to better predict ecosystem functioning and services (Bellwood et al., 2004; Mouillot et al., 2011; Naeem et al., 2012; Tilman et al., 1997). In fishes, functional diversity has been shown to highlight new diversity hotspots (Stuart-Smith et al., 2013), to be more sensitive to disturbance (D'agata et al., 2014), and to better evaluate the resilience of assemblages (Micheli and Halpern, 2005; Mouillot et al., 2014). A proliferation of trait-based measures has now followed (Mouillot et al., 2013; Petchey and Gaston, 2002; Schleuter et al., 2010; Villéger et al., 2008) and the term "functional biogeography" was recently coined. Functional biogeography is a new discipline linking the biogeographical patterns of the species with their functional traits (Violle et al., 2014). This new area of research allows the creation of functional maps that go beyond the species richness level, targeting community resilience and biodiversity hotspots. Although this new tool has been used at large scale (D'agata et al., 2016, 2014; Mouillot et al., 2014; Parravicini et al., 2014; Stuart-Smith et al., 2013), there is a need to apply functional biogeography to regional scales to support local conservation efforts.

The Gulf of California (GC, Mexico), also known as the "Sea of Cortés", is among the most biologically rich marine regions on Earth (Roberts et al., 2002). The GC is a dynamic semi-closed marginal sea of the Eastern Pacific (approximately 1000 km long and 150 km wide) with important latitudinal oceanographic and biogeographic variation, e.g. seasonal temperatures, tidal mixing, bathymetry, and geomorphologic diversity (Brusca, 2010; Marinone, 2012; Walker, 1960). One specific aspect of the GC seascape is the presence of a patchwork of ~80 large islands and ~800 islets, designated as a UNESCO World Heritage Site, that includes everything from small emerged rocks to the large 1225 km^2 Tiburon Island (Case et al., 2002). The seas and rocky reefs around all of these islands are essential refuges for the region's littoral and shallow-water biodiversity (Brusca, 2010), which host at least 821 species of bony fishes (Actinopterygii) from which 10% (82 species) are endemic (Hasting et al., 2010). At the same time, the GC is of high economic value for the fishing industry with 70% of the catch in Mexico (Cisneros-Mata, 2010; Díaz-Uribe et al., 2013). Although the human population density is relatively low in the region, it is rapidly increasing and the GC is not exempt from coastal and marine degradation trends (Calderon-Aguilera et al., 2012; Lluch-Cota et al., 2007; Sagarin et al., 2008). Since the mid-1980s there has been a growing awareness of this situation and the Mexican government has established 10 marine protected areas (MPAs) to preserve biodiversity and control the extraction of natural resources (CONANP, 2007; Rife et al., 2013). Unfortunately, successful MPAs are rare in the region (Brusca, 2010; Rife et al., 2013; Torre and Rivera-Melo, 2018). Although the success of an MPA will ultimately depend on active governance, societal involvement, and the consideration of all stakeholders (Mancha-Cisneros et al., 2018; Munguia-vega et al., 2018a; Rife et al., 2013), one step to improve the effectiveness of conservation effort is to identify sites where limited conservation resources could be focused to preserve the natural legacy of the GC. The emerging field of functional biogeography has a clear role in addressing this challenge.

In the marine realm, reef fishes represent a good model for functional and taxonomic analyses, as they are easy to observe, represent a highly diverse vertebrate group, encompass a range of important and diverse ecological roles, and are relatively well known taxonomically and functionally (Froese and Pauly, 2015; Stuart-Smith et al., 2013). The diverse reef fishes play various roles in the maintenance of reefs, which in turn provide important services to human beings as seafood products and for shoreline protection (Micheli et al., 2014; Moberg and Folke, 1999). For example, large herbivores play an important role in sediment removal, bioerosion and algal cover regulation (Steneck et al., 2017), and predator species may play a critical role for fish biomass by ensuring fishery yields (Maire et al., 2018).

In the last decades, some studies have considered reef fishes' functional diversity in a few areas of the GC (Aguilar-Medrano and Calderon-Aguilera, 2016; Alvarez-Filip and Reyes-Bonilla, 2006; Ramírez-Ortiz et al., 2017). However, a global study encompassing the entire GC is still lacking. In the present study, we analysed the functional biogeography of the reef fishes of the main islands in the GC by classifying species according to six categorical traits that describe key facets of their ecology (Guillemot et al., 2011; Mason et al., 2005; Mouillot et al., 2014; Villéger et al., 2008). The goal of the present study was to provide an overview of reef fish diversity throughout the GC, in terms of species number and functional diversity, but also considering fish abundance and biomass. It has been argued that a trait should be considered to be functional when its role in the ecosystem is demonstrated, and the use of the term functional diversity has been debated (Mlambo, 2014). In the present study, we define the functional diversity of assemblages as the diversity of ecological traits characterising each species (Mouillot et al., 2014; Violle et al., 2007).

To achieve our goal, we first identified the hotspots for fish diversity in the GC so that conservation efforts targeted toward them could help to avert the loss of reef fish functional diversity in the GC. As the GC presents a high heterogeneity of oceanographic variables, we investigated how these parameters are related to reef fish diversity. We also studied the relation between fish diversity and fish biomass and abundance, with these latter two representing important ecosystem services (for fishing and recreational diving industries). Finally, based on the high environmental divergence between the northern and central-southern regions (Brusca, 2010; Case et al., 2002), we evaluated the functional divergence among fish assemblages in both regions. We define a functional divergence between assemblages to be when these assemblages are dominated by different species characterised by different functional traits. Conversely, a functional convergence occurs when distinct species compositions share the same functional traits. Such a functional divergence could highlight the importance of some regions, although they are not recognised as diversity hotspots.

2. Materials and Methods

2.1. Fish data

We first built a species list for 28 islands in the GC considering literature, museums' collections (Del Moral-Flores et al., 2013), and scuba-diving censuses (Munguia-Vega et al. (2015) and other monitoring programmes, see Appendix A), this dataset will be referred to as "Dataset A". Here we termed "islands" to be either isolated islands or archipelagoes composed of various islands separated by less than 10 km (Fig. 1; Appendix B; Table S1). For each island, we determined the species richness ($S_{richness}$), i.e., the number of species of bony fishes (Actinopterygii) referred to as "reef-associated" (Robertson and Allen, 2015). This first dataset combining the three sources of information (literature, museums, and scuba-diving) contained 293 species and had the advantage of considering a wide number of species including rare and cryptic species that are rarely considered in biodiversity assessment (Appendix A). Nevertheless, because the museum data were collected in a very heterogeneous way, it was not possible to accurately control the sampling effort, a potentially important source of variation. To address this problem, we used a second dataset for which we could control the sampling effort. This dataset was referred to as "Dataset B", with only scuba-diving censuses, almost all of which (>95%) were made in the last decade. This dataset considered conspicuous and common species (114 species) recorded during 724 visual censuses from various underwater monitoring efforts in the GC (Appendix A). The length and width of the censuses varied slightly according to the institution conducting the surveys, but the area monitored by census was generally close to 200 m² (average 220 ± 63 m², median $= 180$ m²). For each census, the abundance and the individual size (to the nearest 5 cm) were collected (for schools, the most common size was selected). The fish biomass was estimated with the length-weight relation: $Weight = a*Length^b$, the coefficients a and b being collected from FishBase (Froese and Pauly, 2015). The number of censuses was different between islands (from 12 to 124). Hence, we standardised the sampling effort, randomly selecting 12 censuses per island in bootstrap analyses with 999 iterations. This resample was performed in R (R Development Core Team, 2016).
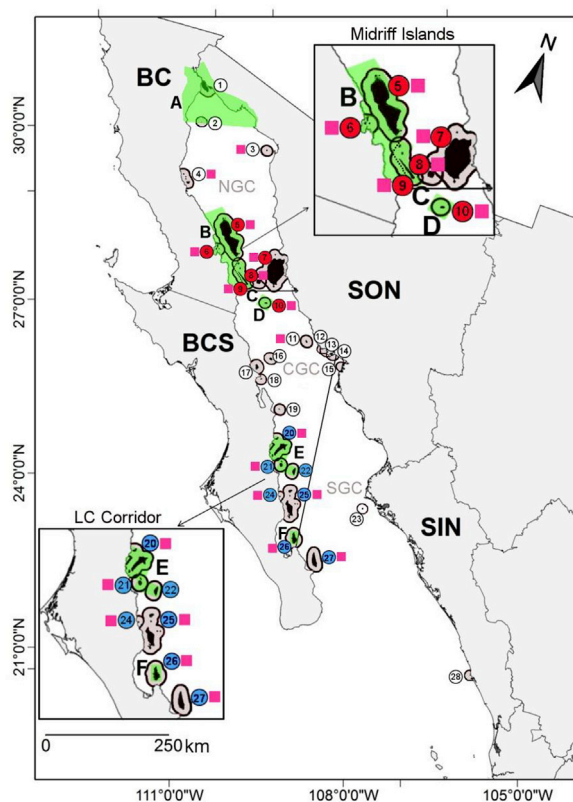

Fig. 1. Distribution of survey locations in the Gulf of California (GC). Each island or archipelago is referred with a number (See Appendix B; table S1 for the names of islands). The areas within marine protected areas (MPAs) are green-lighted: A. Upper Gulf of California and Colorado River Delta Biosphere Reserve, B. Los Angeles Bay, Canal de Ballenas y de Salsipuedes Biosphere Reserve, C. San Lorenzo Archipelago National Park, D. Isla San Pedro Martir Biosphere Reserve, E. Loreto Bay National Park, F. Espiritu Santo Archipelago National Park. The 10 km buffer around each island is grey-lighted. The pinked-squares indicate the islands for which we have scuba-diving monitoring data. The main islands of the Midriff Islands and Loreto-Cerralvo (LC) corridor are red- and blue-lighted, respectively. Zooms represent both regions in more details. The three faunal regions according to Thomson et al. (2000) are indicated: Northern GC (NGC), Central GC (CGC) and Southern GC (SGC). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2.2. Functional information

The functional ecology of each species was determined according to six categorical traits that describe key facets of fish ecology and that are available for a wide range of reef species (Mouillot et al., 2014). 1) Fish size (total length) was coded using six ordered categories: 0–7 cm, 7.1–15 cm, 15.1–30 cm, 30.1–50 cm, 50.1–80 cm, and >80 cm. 2) The mobility, i.e., home range (Guillemot et al., 2011; Mouillot et al., 2014), was coded using four ordered categories: highly site-attached species (mainly territorial and cryptic species), mobile species with a small home range (e.g. Chaetodontidae, Pomacanthidae, non-territorial Pomacentridae, etc.), very mobile species with a large home range (e.g. large Labridae and Acanthuridae, Scaridae, Hae-mulidae, most of the Lutjanidae and Serranidae, etc.), and widely mobile species with a very large home range (species capable of travelling over very long distances, e.g. Carangidae, Belonidae, or very large Lutjanidae and Serranidae, etc.). 3) The period of activity was defined as the period of the day during which foraging activity mainly occurs and was coded using two nominal categories: diurnal and nocturnal. 4) Gregariousness was coded using four ordered categories: solitary (1 individual), living in pairs (2 individuals), and in small-medium (3–50 individuals) or large (>50 individuals) groups. 5) The vertical position of the habitat in the water column was coded using three ordered categories: benthic, bentho-pelagic, and pelagic. 6) Diet was characterised based on the main items consumed by each species, which led to six nominal categories: herbivores-detritivores (i.e., fish feeding on algae and/or undefined organic material), invertivores targeting sessile invertebrates (i.e., corals, sponges, ascidians), invertivores targeting mobile invertebrates (i.e., benthic species such as crustaceans), planktivores (i.e., fish eating small organisms in the water column), piscivores (including fish and cephalopods), and omnivores (i.e., fish for which both vegetal and animal material are important in their diet). We collected the functional data using the online databases "Shorefishes of the Eastern Pacific online information" (Robertson and Allen, 2015) and "FishBase" (Froese and Pauly, 2015), and a series of specialised books (see references in Appendix A). In case of conflict among sources of infor-mation, we followed the "Shorefishes of the Eastern Pacific online information" which is probably the most complete data source for fishes of the Tropical Eastern Pacific (TEP). We also used our own expertise to form a decision.

2.3. Functional trait space and indices

Unique combinations of the six categorical traits represent functional entities (FEs). The $FE_{richness}$, i.e., the number of FEs, was the first variable used to determine the functional diversity within a community. Then, we used the FEs to measure three complementary functional indices proposed by Mouillot et al. (2014) and Parravicini et al. (2014): 1) the functional redun-dancy (FR), or the mean number of species per FE; 2) the functional sensitivity (FS), which estimates the proportion of FEs having only one species; 3) the functional over-redundancy (FOR), or the percentage of FEs having more species than ex-pected from FR (a modification of the initial index which measured the percentage of species in FEs having more species than expected from functional redundancy (Mouillot et al., 2014)).

These three indices are expressed as the following ratios:

$$FR = \frac{S}{FE} \tag{1}$$

$$FS = \frac{FE - \sum_{i=1}^{FE} \min(n_i - 1, \ 1)}{FE} \tag{2}$$

$$FOR = \frac{\sum_{i=1}^{FE} \ \min \ [[\max \ (n_i, \ FR)] - FR, \ 1]}{FE} \tag{3}$$

where S is the total number of species and n_i the number of species represented in the i_{th} FE.

In addition to the number of FEs, we calculated the functional richness ($F_{richness}$) which is the volume enclosing all the FEs (Cornwell et al., 2006; Mouillot et al., 2013; Villéger et al., 2008). The $F_{richness}$ is assessed by computing the pairwise functional distances between species using the Gower distance, which allows different types of variables to be mixed while giving them equal weight (Gower, 1971). A principal coordinate analysis (PCoA) was then performed using this functional distance matrix. We selected the first four PCoA axes to compute the volume. The choice of the number of PCoA axes followed the method of Maire et al. (2015). Euclidean distances between FEs in this four-dimensional space were strongly correlated with initial Gower distances (Mantel test, $r = 0.89$, $P < 0.001$) and showed one of the lowest mean squared deviations from the original data (Appendix B; Figure S1). We used the function "dbFD" and "multidimFD" from the "FD" R packages (Laliberté et al., 2014).

2.4. Functional vulnerability

We defined the vulnerability of the function according to three components: 1) the number of species representing the FE (functional redundancy), 2) the sensitivity to fishing of the species that compose the FE, and 3) the latitudinal distribution of the species composing the FE. The fishing sensitivity was estimated according to a fuzzy logic index considering various life-history characteristics that make fish species more or less sensitive to fishing, with a scale ranging from 0 to 100 (Cheung

et al., 2005). We assessed latitudinal distribution in five range size categories: $0-10°$, $11-20°$, $21-30°$, $31-40°$, and $>40°$. The whole Tropical Eastern Pacific (TEP) has a latitudinal range of $40°$ ($32°$ N to $8°$ S). As we focused on reef fishes (hence coastal fishes), to consider only one dimension (latitude) is a reliable representation of the geographical range of the species because the coast of the TEP is simple, straight, and latitudinally oriented (Mora and Robertson, 2005). The sensitivity to fishing and the latitudinal range were aggregated at the level of FEs by taking the median value of all species belonging to a given FE. We then fitted a two-way ANOVA to determine the relationships of fishing sensitivity and latitudinal range to the functional redundancy.

2.5. Environmental and geographic predictors

We collected 11 environmental variables assumed to influence the distribution of marine shallow-water organisms (Stuart-Smith et al., 2013; Tyberghein et al., 2012). From MODIS Aqua images (https://oceancolor.gsfc.nasa.gov/), we extracted the monthly average (from 2003 to 2016) at a 5 arcmin (c. 9.2 km) spatial resolution for seven variables: (1) colored dissolved organic matter (CDOM, m^{-1}), (2) chlorophyll a (Chl a, mg m^{-3}), (3) photosynthetically active radiation (PAR, Einstein/m^2/day), (4) particulate organic carbon (POC, mg m^{-3}), (5) particulate inorganic carbon (PIC, mol m^{-3}), (6) the minimum and (7) average annual sea surface temperature (SST-min and SST-mean, °C). The other four variables came from NOAA's National Oceanographic Data Centre (NODC): (8) phosphates (PO_4, μmol/l), (9) salinity (S, UPS), (10) silicates (SiO_4, μmol/l) and (11) dissolved oxygen (O, ml/l). These data were collected through oceanographic cruises from 1950 to 2016. A total of 958 hydrographic surveys from 52 cruises were analysed. We only used the data at a depth of $0-10$ m to be coherent with the MODIS Aqua images that provided data for the ocean surface only. Given that the samplings in situ were not systematically or periodically carried out for the entire GC, we interpolated the values using the inverse distance weighting (IDW) routine for a 5 arcmin (c. 9.2 km) spatial resolution. We measured the average for the 11 environmental variables in the 10 km around the coast of each island/archipelago. We used the software ArGis 10.3 (Esri, USA) to extract the data and performed the analysis with the Zonal Statistics tools. To the environmental predictors, we added three geographic predictors: 1) the latitude, 2) the size of the islands (perimeter in km), and 3) the human population (H. pop) living in a buffer of 50 km around each island. The human population data came from the software *Population Explorer* (ForestWalk, USA). The isolation distance has been described as a determinant factor in the structure of fish assemblages for islands (Bender et al., 2017; Quimbayo et al., 2018). However, most of the islands in the GC are very close to the coast (<10 km (Case et al., 2002)), therefore we did not consider the island's isolation as a predictor. Table S2 (Appendix B) summarises the 14 predictors and their range in our dataset.

To the 14 aforementioned predictors we added fish biomass and abundance to build predictive random forest models (Breiman, 2001) of S and $F_{richness}$ (using Dataset B). The full set of censuses was randomly divided into two subsets, one *training* set comprising 70% of the observations and one *test* set with the remaining 30%. We then generated 500 regression trees from a bootstrap sample of the *training* set, for which we fixed the number of predictors randomly chosen at each split to six (the number of total predictors divided by 3, see James et al., 2017). The observations not selected in the bootstrap sample for a tree (the "out-of-bag" sample) were compared to their predictions, in a similar way to cross-validation. The accuracy importance, or mean decrease in accuracy when the predictor variable is randomly permuted, was measured to assess the importance of each predictor variable. To evaluate the model, we compared the model-predicted and actual values within the *test* set by calculating the R^2-adjusted. We finally repeated all the process by simulating 100 pairs of *training* and *test* sets. The analyses were performed in R software with the *randomForest* package (Liaw and Wiener, 2002). Random forests are non-parametric models that are very robust to outliers and high-leverage points because of bootstrapping, and to correlation among predictors because a number of predictors are randomly chosen at each splitting node (Breiman, 2001). Random forest models are also robust to cluster-correlated data (Karpievitch et al., 2009). We used the Moran's I test from the package *ape* (Paradis et al., 2004) to check for Spatial Auto-Correlation (SAC) in the residuals of our models. No significant results were found (Appendix B; Table S3). Random forests can provide very good predictions but the relationship of each variable to the output is more difficult to interpret. To help the understanding of a positive or negative association of each predictor with S and $F_{richness}$, we ran non-parametric Spearman correlations between each predictor and both aspects of fish diversity (S and $F_{richness}$).

We aimed to more specifically determine the relationships of reef fish diversity with fish abundance and biomass (two ecosystem services). To respect parametric conditions (normality and variance homogeneity) we log-transformed the dependent and independent variables. The visualisation of the data did not suggest any relation other than linear. The residuals of the linear models did not reveal any important effects of outliers or high leverage points (using Cook's distance). However, we detected a high SAC value. To solve this issue, we ran mixed effect linear models with the locations as a random variable. The residuals of the mixed effect models did not show any SAC issues (Appendix B; Table S3). We used the function *lme* of the R package *nlme* to run the mixed effect models (Pinheiro et al., 2011).

2.6. Functional divergence between assemblages

Most of the islands considered in the dataset B (12 out of 15) belong to two distinct regions in the GC, i.e., the "Midriff Islands" and the "Loreto-Cerralvo corridor" (LC corridor). The Midriff Islands region is located in the northern GC and comprises six major islands/archipelagoes (5–10 on Fig. 1). The LC corridor region extends from the centre to the southwest part of the GC and comprises seven main islands/archipelagoes (20–22 and 24–27 on Fig. 1). Three islands of the Midriff

Islands are within multi-use MPAs (Fig. 1, Table S1), representing the only cluster of MPAs in the GC, each island being in close proximity to the others (~10−50 km). The LC corridor is also shaped by close neighbouring islands (~20−40 km between each of them, Fig. 1) but the current MPAs of the region are quite far from each other (~110 km, Fig. 1). Hence the set of islands of the LC corridor represent a potential MPA cluster for the southwestern GC. In this study, we compared several aspects of these two patchworks of islands (Midriff Islands vs. LC corridor), in terms of species and functional diversity, but also in considering fish abundance and biomass. To compare the two regions, we performed linear mixed effect models with the locations (island) and census identification as random variables (the censuses were nested within the islands). To consider an equivalent weight of each island, bootstrap analyses were performed considering 12 censuses by islands (with 999 iterations). No parametric violations were observed (normality and variance homogeneity).

We then went further in the comparison by investigating the functional divergence between the two regions. To evaluate functional divergence, we identified "winner" species either in the Midriff Islands or in the LC corridor. We defined a winner as a species that gains importance (has been "favoured") in one region in comparison to the other. This was defined as a species for which its relative biomass was at least 2% higher in one region than in the other (using Dataset B) and for which the difference was statistically supported. Only 17% and 20% of the species represented at least 2% of the biomass in the LC corridor and Midriff Islands, respectively. Hence, even when the 2% threshold value was arbitrarily chosen, we can consider that such an increase in the relative biomass of a species is an important change. To identify winner species, we performed bootstrap analyses with 12 censuses for each island and we determined the relative biomass of each species (the median value of the 999 iterations to decrease the effects of outliers) for each island. We took the average for each species for both regions. We selected the species with a gain of at least 2% in one or another region. We then used the census values to detect whether the difference in relative biomass between the two regions was significant for each selected species. As parametric hypotheses were not respected, we ran permutation t-tests and we gave an equivalent weight to each island by bootstrapping. We then plotted the final selection of winners in the four-dimensional functional space to estimate the functional divergence between both regions. A poor overlap in the functional space would indicate a functional divergence between both assemblages.

2.7. Sensitivity analyses

Previous studies have shown that none of the six variables chosen to create our FEs had a disproportionate importance (Mouillot et al., 2014; Parravicini et al., 2014). However, the lack of information or the resolution of the categorisation of functional traits could lead to a misclassification of the species. To test the robustness of our results, we ran all the analyses using a coarse categorisation of functional traits (Appendix C, Table S1 and Fig. S1).

The censuses were made in the last decade, which can represent a large range in terms of temporal scales. We did not have homogeneity in the years of monitoring, i.e., not all sites were monitored for the same years, so to consider the years as a random effect would not be adequate. A part of the data (76 censuses) came from a cruise made in October−November 2016 and included 12 of the 15 islands of Dataset B. To prove that our results were not due to a year effect, we used this subset to compare the LC corridor's islands to the other islands of the GC (Appendix C; Table S2).

3. Results

The 293 species (Dataset A) are categorised into 132 FEs (Appendix A), giving an average FR of 2.2 species per FE. The distribution of species among FEs is strongly uneven (Fig. 2a). On one hand, the functional over-redundancy (i.e. proportion of FEs with more than two species) represents 22% of the FEs and 58% of the species. On the other hand, 62% of the FEs have only one species (Fig. 2a). The eleven most species-rich FE (5−41 species per FE) represent 37% of the $S_{richness}$ but fill only 2% of the $F_{richness}$ (functional volume) and are mainly represented by poorly mobile, solitary, and benthic species, the majority of these being carnivorous (feeding on vagile invertebrates or fish) (Fig. 2b).

The 109 species representing the eleven most species rich FEs are generally not considered to be particularly sensitive to fishing, 85% have a low or low to moderate sensitivity index. However, one third of these species have a low geographical range, i.e., $\leq 10°$ (Fig. 2a, Appendix A). On the other hand, more than one third (34%) of the single-species FEs (functionally sensitive) are considered to be moderately to very highly sensitive to fishing, but only 2% of them have a 10° (or less) geographical range (Fig. 2a, Appendix A). The two-way ANOVA results support these observations, the interaction of fishing sensitivity and geographical range is significantly related to functional redundancy ($F_{1,128} = 9.9$, $P = 0.002$).

3.1. Hotspot identification

Dataset A (records from museums, literature, and underwater censuses) highlights that four islands stand out for their species and functional diversity (20: Carmen, 25: San José, 26: Espiritu Santo and 27: Cerralvo; Fig. 3a−c). These four islands are found in the Loreto-Cerralvo corridor region (LC corridor). Dataset B (underwater censuses, controlled sampling efforts) strengthens our first observation because the fish communities around the six islands of the LC corridor are more diverse than around other islands of the GC (Fig. 3a−c). The fish density (individuals 100 m^{-2}) is also higher in the LC corridor than in the other islands (Fig. 3d). Finally, four islands of the LC corridor have a fish biomass (g 100 m^{-2}) well above the median for the GC, against a single island for the Midriff Islands region (Fig. 3d). The linear mixed-effect models confirm that the LC corridor has
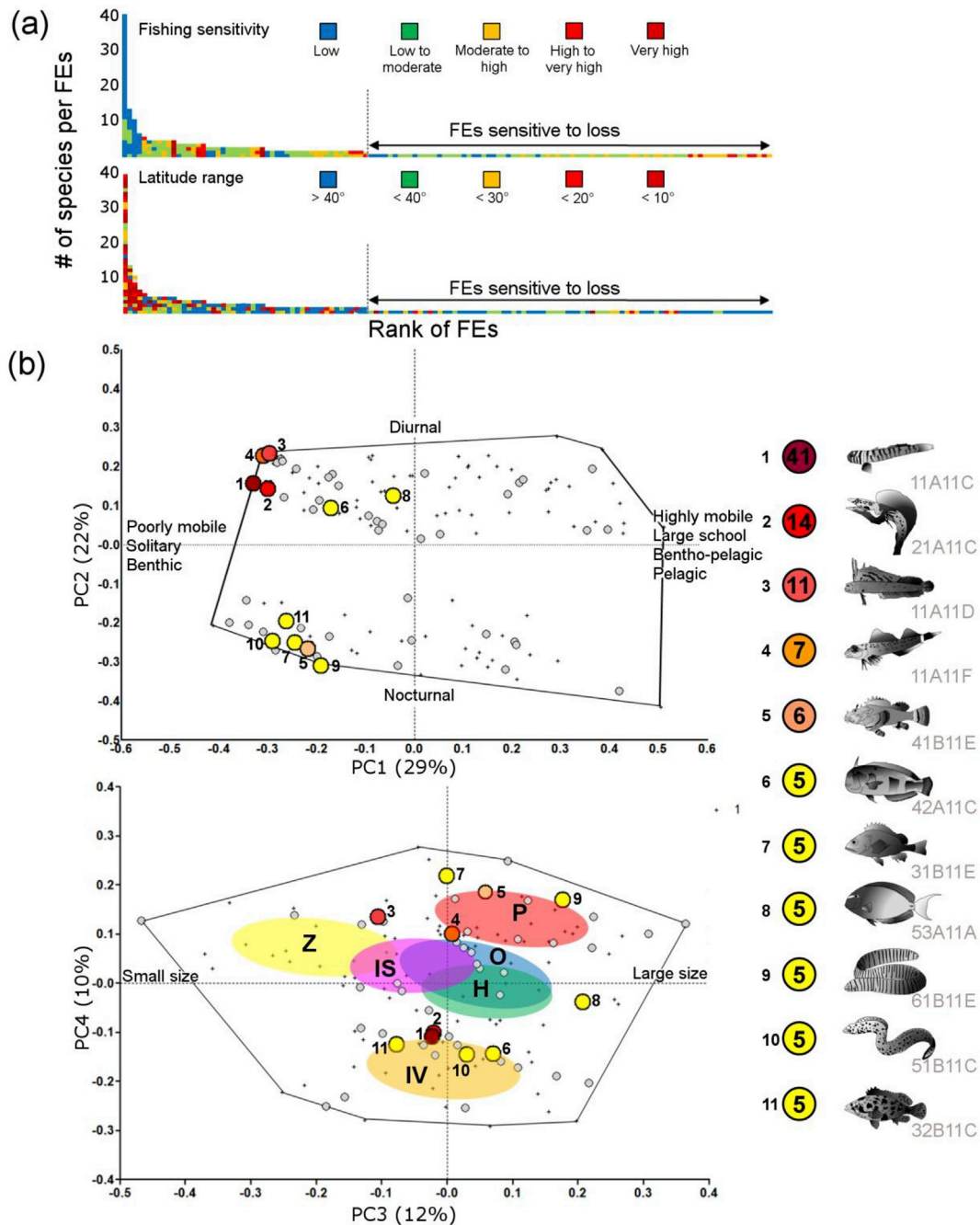
Fig. 2. (a) Ranking of the functional entities (FEs) according to their number of species. The doubled arrows indicate the proportion of FE having only one species. Each species within each FE is first color-coded according to its fishing sensitivity (Cheung Index), then according to its geographical distribution (latitude range). (b) Functional space according to the first four axes of the PCoA. The 11 most species-rich FE are represented by color-coded circles and are numbered. The circle color refers to the number of species inside the FEs (the exact number is indicated in the colored-circles). The combination of the FE is indicated for each of these 11 FEs (see Methods for interpretation). The crosses inside the convex hull represent single-species FEs while the grey circles represent FEs with 2—4 species. The ecological meaning of the functional volume is indicated: mobility, gregariousness, period of activity and water column position separate better the FEs along PC1 and PC2 while the size and trophic group do along PC3 and PC4. The standard ellipse areas for each trophic group are represented. P: piscivores, IV: invertivores vagile, IS: invertivores sessile, Z: zooplanktivores, O: omnivores and H: herbivores. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

higher species richness, functional diversity, and fish abundance than the other islands (Appendix B; Table S4). However, no significant difference was found in biomass (Appendix B; Table S4). Our observations are robust to the coarse categorisation (Appendix C; Table S1). The results are also confirmed when considering only the data for 2016, except for fish abundance (although a strong positive trend in favour of the LC corridor islands is observed; Appendix C; Table S2).
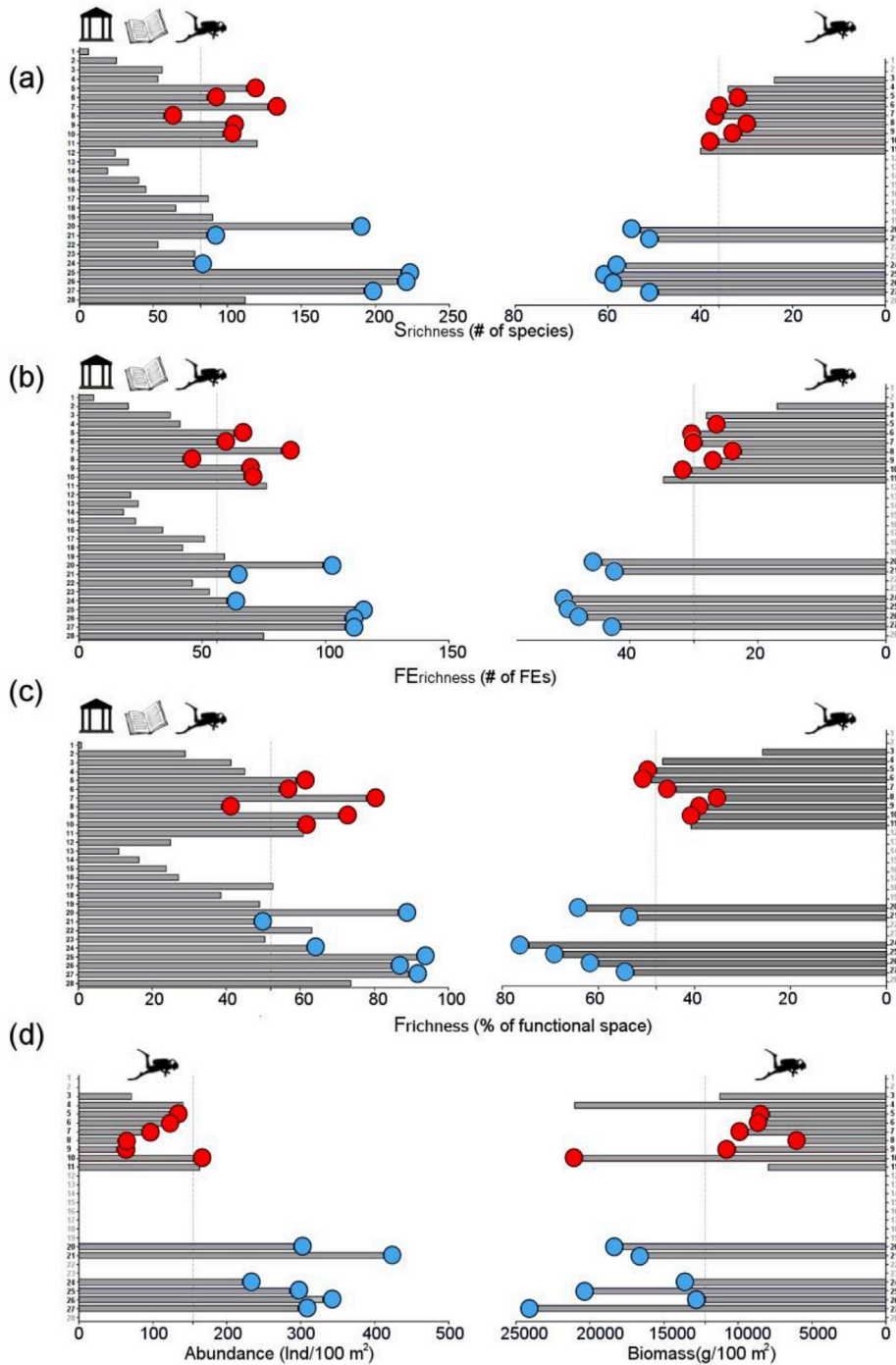
Fig. 3. Diversity of the reef-fishes assemblages in the islands surveyed, ordered according to their latitude. The numbers are the same than in Fig. 1 (See Appendix B; table S1 for the names of islands). (a) Species richness, (b) Functional Entities richness, (c) Functional richness and (d) fish abundance and biomass. The dashed line represents the median value for each variable. For a-c, the left part of the figure corresponds to the data considering various sources of information (museums' collections, literature and scuba-diving monitoring). Data were available for 28 islands. The right-part corresponds to the only scuba-diving data after bootstrap resampling. The data were available for 15 islands. The islands of the Midriff Islands and Loreto-Cerralvo corridor are color-lighted in red and blue respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.2. Predictive models

The random forest models are good predictive models for $S_{richness}$ in the GC, whereas they give a more moderate result for $F_{richness}$ (Fig. 4ab). Fish abundance and biomass are better predictors for the distribution of S and $F_{richness}$ in the GC than environmental and geographic variables (Fig. 4ab). When fish abundance and biomass are not considered, the models lose 5% in prediction (Fig. 4ab). Among environmental and geographical predictors, the temperature, the PAR, and human population density are positively associated with fish diversity, while the other variables show a negative relationship (Fig. 4ab). However, the size of the island does not seem to have a positive or negative effect, showing a very low Spearman correlation coefficient (Fig. 4ab). Although environmental and geographical variables are relatively good predictors of S and $F_{richness}$ (R^2 of 0.71 and 0.58, respectively), they have a poor predictive power for the fish abundance and biomass (R^2 of 0.33 and 0.03, respectively). Finally, linear mixed models show that fish abundance and biomass have a strong linear relationship with reef fish diversity in the GC (Fig. 4cd; Appendix B; Table S5).

3.3. Functional divergence

The LC corridor and Midriff Islands regions have ten and six species, respectively, that we considered to be winners (gain of at least 2% in relative biomass and which is statistically supported; Appendix B; Table S6). The winners of both regions show a poor overlapping in the four-dimension functional space (Fig. 5a). In the Midriff Islands, large solitary benthic invertivores such as triggerfish, wrasse, or sea bream are favoured (13−15, Fig. 5ab) while this not true for the LC corridor. On the other
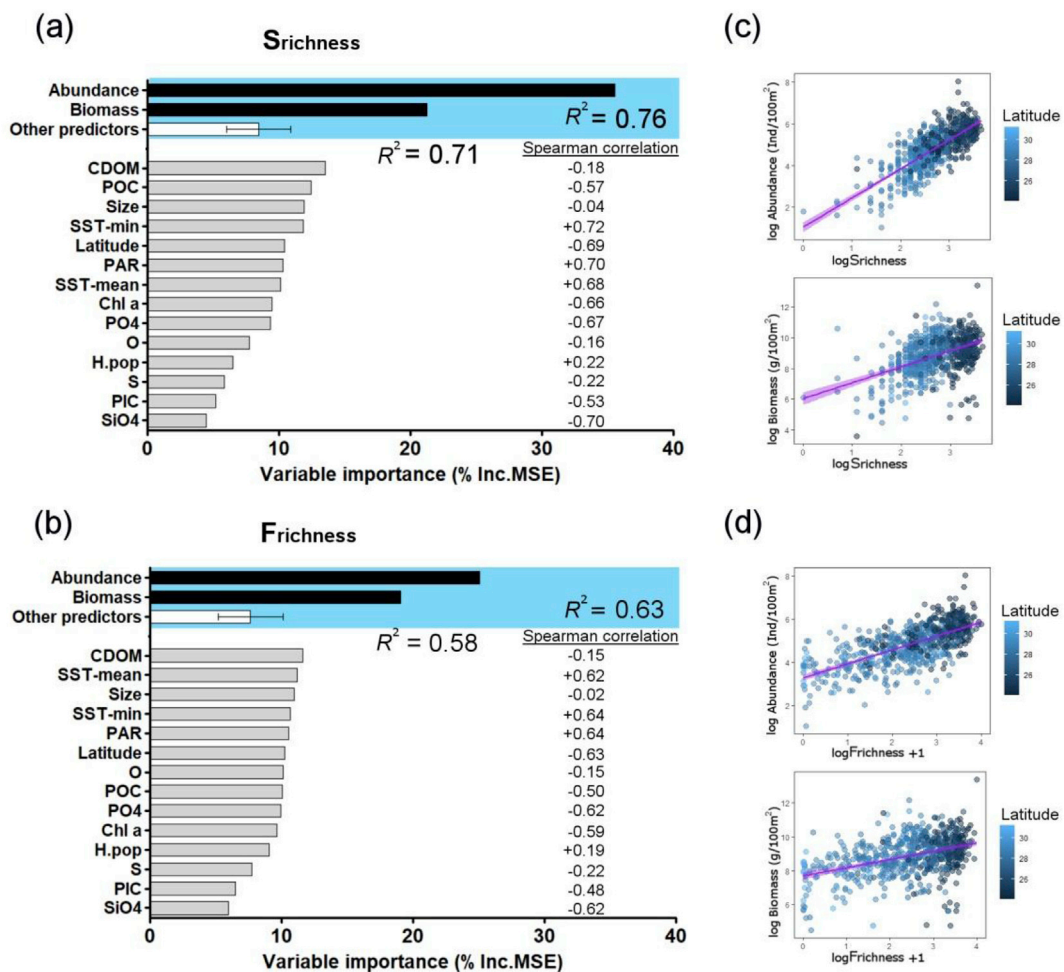

Fig. 4. The accuracy importance of the predictor variables for each of the random forest models for (a) Species richness ($S_{richness}$) and (b) Functional richness ($F_{richness}$). Models were run twice: 1) Considering fish biomass and abundance as predictors (in blue-shaded). The mean (±SD) importance of the environmental and geographic predictors is indicated. 2) Not considering fish biomass and abundance, the importance of all other predictors being individually indicated. The correlations (Spearman coefficient) of each environmental and geographic predictors with S and $F_{richness}$ are showed. (c and d) Linear regressions models illustrating more specifically the relationships of S and $F_{richness}$ with fish abundance and biomass are presented. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)
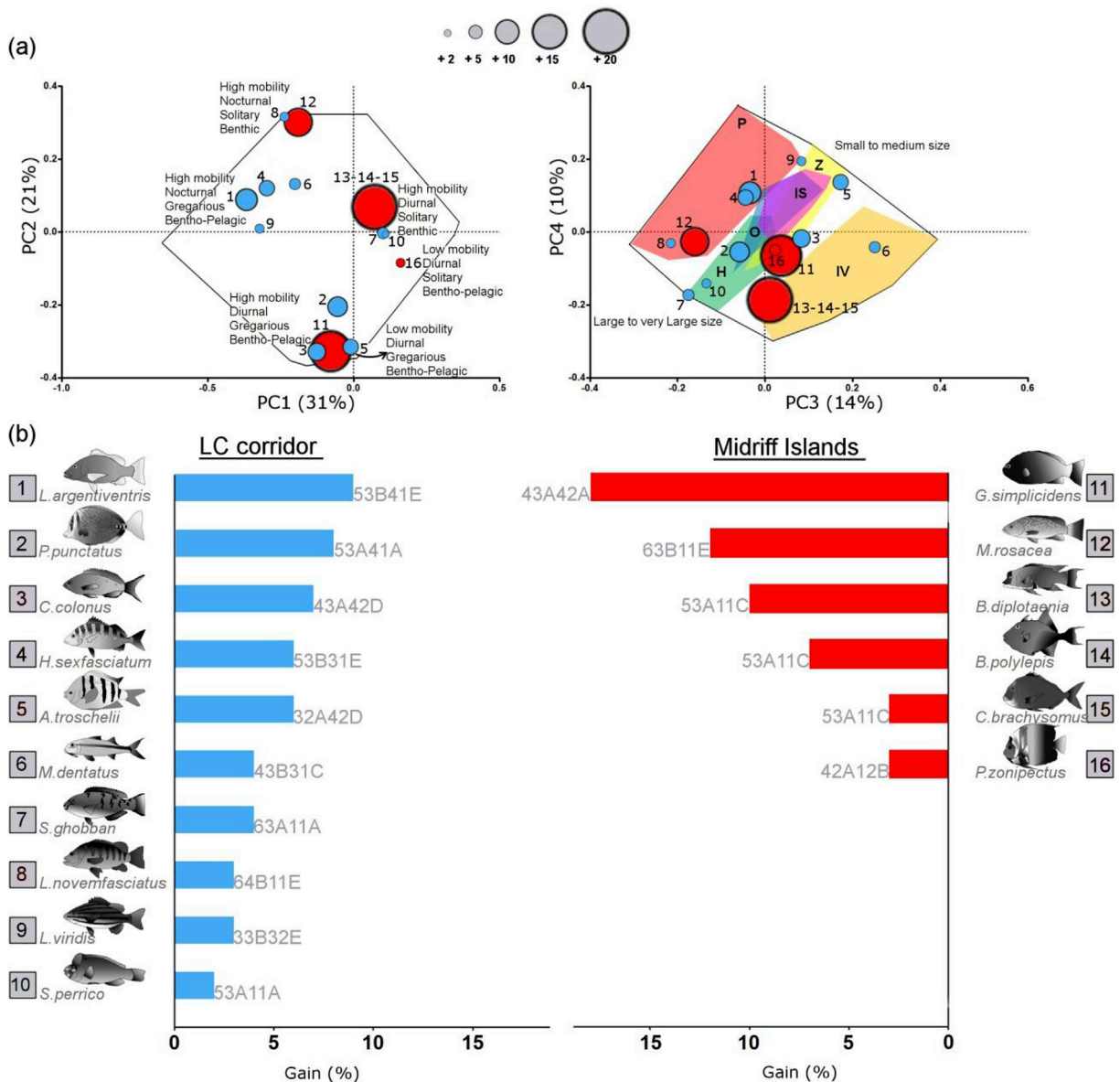
Fig. 5. (a) Functional space (first four PCoA axes) of the conspicuous species in the Gulf of California. Species categorised as "winner species" in the Midriff Islands and LC corridor regions are highlighted in red and blue circles respectively. The size of the circle is proportional to the gain of the species. The ecological meaning of the functional volume is indicated. The convex hulls for each trophic group are represented along PC3 and PC4. P: piscivores, IV: invertivores vagile, IS: invertivores sessile, Z: zooplanktivores, O: omnivores and H: herbivores. Each species in the functional space is numbered according to codes provided in (b). (b) List of the winner species in the Midriff Islands (red) and LC corridor (blue). For each species, the gain in relative biomass in comparison to the other region is indicated. The detail of the functional entity (combinations) is showed for each species (see Methods for their understanding). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

hand, large solitary herbivores (parrotfishes; 7 and 10, Fig. 5ab) and highly gregarious zooplanktivores (damselfishes and serranids; 3 and 5 Fig. 5ab) are favoured in the LC corridor while not in the Midriff Islands. Furthermore, the piscivores are dominated by highly gregarious species such snappers and grunts in the LC corridor (1, 4, and 9; Fig. 5ab), while they are dominated by the solitary grouper *Mycteroperca rosacea* in the Midriff Islands (11; Fig. 5ab). More generally, the winner species of the Midriff Islands are dominated by large predators (piscivores or vagile invertivores represent 4 of the six species). The winners of the LC corridor are more heterogeneous in their trophic strategy, with 50% being predators, 30% herbivores and 20% zooplanktivores. Finally, it is important to note that two winners of the Midriff Islands are endemic to the GC, i.e., *G. simplicidens* and M. *rosacea*, this latter being highly sensitive to fishing (Appendix A). A coarse categorisation of the species did not change our conclusion and confirm a poor functional overlapping among the winners of both regions (Appendix C; Figure S1).

4. Discussion

4.1. Functional redundancy and vulnerability

Functional redundancy is thought to act as a buffer against the loss of diversity following disturbances (Bellwood et al., 2003; Micheli and Halpern, 2005). However, as shown in other studies considering "ecological-trait" combinations (Guillemot et al., 2011; Micheli et al., 2014; Micheli and Halpern, 2005; Mouillot et al., 2014; Parravicini et al., 2014), we observed a low functional redundancy in the islands' reef fish assemblages in the GC. A large number of FEs are represented by a single-species, while some FEs are over-represented. A topic of concern is that one third of the single-species FEs are moderate to highly sensitive to fishing pressure. Hence, as shown in the Caribbean coral reefs (Micheli et al., 2014), fishing has the potential to broadly impact functional diversity in the GC. On the other hand, the species rich FEs are generally represented by species having a low sensitivity to fishing pressure, but with a low geographical range (Fig. 2a) which may make them more vulnerable to other disturbances. The species redundancy of these FEs may buffer them (at least to some extent) against such disturbances. However, this over-redundancy could be over-estimated by the use of coarse traits that fail to capture ecological differences among closely related species (Brandl and Bellwood, 2013). Further investigations targeting this set of species could shed light on their true level of functional redundancy. Some single-species FEs are sensitive to fishing and have a limited geographical range, which makes them particularly vulnerable. Among them, we found endemic species of the GC, such as the sea chub *Girella simplicidens* which represent a functional key species for the Midriff Islands in the northern GC (Fig. 5). Another key species for the Midriff Islands is the grouper *M. rosacea*, an endemic species of the GC that is highly sensitive to fishing pressure and that belongs to an FE with only two species (with the snapper *Hoplopagrus guentherii*). Our analyses added a new dimension of biodiversity and highlighted vulnerable species that may make large contributions to the functioning of reefs and that could be explicitly targeted by conservation efforts to increase ecosystem resilience.

4.2. Predictive models

We highlight that fish abundance and biomass were better predictors of S and $F_{richness}$ than environmental and geographical variables. Although environmental and geographical variables still provide a good predictive model for S and $F_{richness}$ (Fig. 4ab), they failed to predict fish biomass and abundance within islands. Other environmental variables, such as reef geomorphology, could be a better predictor as has been recently suggested for the GC (Aburto-Oropeza et al., 2015). Our result shows a linear relationship of fish abundance and biomass to fish diversity (S and F richness) which supports the idea that biodiversity effects on productivity are strong (Duffy et al., 2017; Maire et al., 2018) and play a major role in sustaining the productivity of marine ecosystems and benefits for human populations (Micheli et al., 2014). The SST is the environmental predictor that is more related to diversity across many taxa (Bosch et al., 2018; Tittensor et al., 2010) and is an important environmental predictor for both S and $F_{richness}$ in the islands of the GC. The temperature decreases northwards in winter, which limits the survival of some tropical fishes (Thomson et al., 2000; Thomson and Gilligan, 2002). The latitude is also an important (negative) predictor. The GC is a "cul-de-sac" therefore impeding direct connection with adjacent water in the northern GC (Thomson et al., 2000). The bathymetry of the Midriff Islands region, which represents the limit between the central and northern GC, constitutes one of the most notable features of the GC. This region is shaped by a series of deep basins and sills, which restrict the current circulation and so the exchanges between the northern and central GC (Hernández-Ayón et al., 2013). The primary productivity positively affects fish richness in the tropical Oceanic islands (Quimbayo et al., 2018). It is however not the case in the island of the GC. The waters of the northern part are more nutrient-rich than the central and southern parts (Lluch-Cota et al., 2007; Ulate et al., 2016). As the islands of the central-southern GC have more diversified reef fish assemblages, all environmental predictors related to water primary productivity have a negative relationship with our reef fish diversity indices. This pattern, however, is not true for all marine taxa. The sessile-invertebrate fauna shows a decrease in species richness and densities southward (Ulate et al., 2016), many of the sessile invertebrates are filter feeders and would benefit from the nutrient-rich waters in the northern GC. Although the size of the island is identified as an important predictor in the random forests models for both S and $F_{richness}$, it is not possible to identify a clear positive or negative relationship, the Spearman coefficient being very low (Fig. 4ab). In the GC, the two biggest islands (Angel de la Guarda and Tiburón; 5 and 7, Fig. 1) are within the northern GC and are less diversified than the hotspots identified in the southwestern GC. On the other hand, the LC Corridor (where we found the islands with the highest reef fish diversity in the GC) hosts four of the largest islands in the GC (20, 25–27, Fig. 1). Finally, a very small island (Habana Island; 24 on Fig. 1) shows one of the highest diversity levels in the GC. We only studied conspicuous species, so consideration of other taxa could help us to understand the relationship between the size of the islands and the diversity of marine faunas they host. However, previous studies on cryptic reef fish assemblages showed a low relationship between the size of the islands and their $S_{richness}$ in the GC (Thomson and Gilligan, 2002). Although the size of the islands can positively affect the $S_{richness}$ in the tropical Oceanic islands (Quimbayo et al., 2018), this relationship seems more complex for the islands of the GC. The human population density was not considered as an important predictor in the random forest models for both S and $F_{richness}$ but shows a positive correlation with both indices. This indicates that some hotspots of diversity are in close proximity to notable human population density, such as the islands of Espiritu Santo and Cerralvo (26 and 27, Fig. 1). Because of the well-known negative impact of high human population density on reef fish diversity (D'agata et al., 2014), this proximity calls for effective governance to preserve these highly diverse islands.

4.3. The diversity hotspots in the Gulf of California

We identified the islands of the LC corridor to be host to the highest diversity in terms of species richness, functional diversity, and fish abundance (Fig. 3a–d). Although the fish biomass levels were also well above the median value for the GC for most of the LC corridor's islands, no significant results were found (Fig. 3d). Our results agree with previous assessments that identified the central and southern GC biogeographic regions as hosting a larger number of bony fishes (531 and 741 species, respectively) compared to the northern GC region (356 species) (Hasting et al., 2010; Walker, 1960), and confirm that these trends are true for multiple aspects of functional diversity.

The LC corridor region hosts two MPAs, the Loreto Bay National Park and the Espiritu Santo Archipelago National Park which enclose four of the seven main islands/archipelagoes of the region (Fig. 1). These two MPAs are however quite far from each other (>100 km) and larval dispersion study for a typical reef fish revealed a poor direct connection between both areas (Munguia-Vega et al., 2018b). Although more information about connectivity, social factors or economic feasibility are needed, we think our study could contribute to the improvement of the conservation efforts dedicated to this highly diverse area.

4.4. Functional divergence, an additional overlooked factor

The fish biomass in the LC corridor and Midriff Islands regions is dominated by different species characterised by different ecological-trait (functional divergence). This observation suggests that both regions are complementary to each other (as opposed to showing convergence) and that MPAs that include both clusters will more comprehensively preserve the functional diversity of reef fishes in the GC. Some functions are "favoured" or more represented in one region than in the other. The most striking example is the presence of large solitary invertivores in the winner species of the Midriff Islands, while this profile of FE is totally absent among the winners of the LC corridor. The piscivores are also dominated by the solitary grouper *M. rosacea* (this species is able to form large aggregations during the spawning period, (Erisman et al., 2007)) in the Midriff Islands region while the LC corridor favours other FEs such as large solitary herbivores or highly gregarious zooplanktivores and piscivores. In conclusion, an MPA cluster including the Midriff Islands should better preserve some functions, while the protection of additional functions would be more efficient within an LC corridor MPA cluster.

Endemism is also an important factor to consider when identifying areas to protect. Thirty-three reef fish species of our dataset (Dataset A) are considered to be endemic to the GC (Robertson and Allen, 2015). Most of these are cryptic or not common and it is therefore not possible with our dataset to quantify without sampling bias which island or region hosts the endemic species. However, two endemic species are conspicuous (Dataset B), i.e., *G. simplicidens* and *M. rosacea*. These two species are more represented in the Midriff Islands, supporting the importance of this region in maintaining GC diversity.

The functional divergence between northern and southern regions may be explained by the high gradient of oceanographic variables along the GC. In addition, several reef fish winner species of the Midriff Islands are invertivores which could be explained by a higher abundance of prey. However, no spatial structure has been recently found for vagile invertebrates in the GC (Ulate et al., 2016). Although the reasons why some FEs are more represented in one or other of the regions deserves future investigations, our results support the creation of two complementary MPA clusters in the northern and central-southern GC, respectively. Each of these MPA clusters will bring added value for the conservation of the functional role of reef fishes within the GC.

5. Conclusion

The GC hosts a vast variety of life and is dotted with strings of islands registered on the UNESCO World Natural Heritage list in 2005. In a globally changing world and due to increasing local threats, it is of great importance to adopt an efficient conservation policy to preserve the legacy of this biologically rich area. Identifying biodiversity hotspots is a way to concentrate the conservation efforts on areas that can serve as sanctuary sites for the region. Through our functional biogeography study of reef fishes, we provide an overview of the GC that evaluates which islands or archipelagoes represent an important part of the reef fish biodiversity in the GC, both taxonomically and functionally but also considering fish abundance and biomass. We identified the region called the Loreto-Cerralvo corridor to be hosting the majority of the reef fish diversity in the GC, and we argue for an increase in conservation efforts to protect this rich region. However, the GC is not a homogenous inner sea and presents important oceanographic divergence along its latitudinal axis. This heterogeneity translates into a functional divergence between fish assemblages of the northern and southern GC, each zone favouring different ecological trait combinations (FEs). The consideration of this new axis of functional divergence supports the establishment of two distinct complementary MPA clusters to offer an effective protection for reef fish biodiversity in the GC.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2018.e00506.

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