Determinants of Reef Fish Assemblages in Tropical Oceanic Islands

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ABSTRACT

Diversity patterns are determined by biogeographic, energetic, and anthropogenic factors, yet few studies have combined them into a large-scale framework in order to decouple and compare their relative effects on fish faunas. Using an empirical dataset derived from 1527 underwater visual censuses (UVC) at 18 oceanic islands (five different marine provinces), we determined the relative influence of such factors on reef fish species richness, functional dispersion, density and biomass estimated from each UVC unit. Species richness presented low variation but was high at large island sites. High functional dispersion, density, and biomass were found at islands with large local species pool and distance from nearest reef. Primary productivity positively affected fish richness, density and biomass confirming that more productive areas support larger populations, and higher biomass and richness on oceanic islands. Islands densely populated by humans had lower fish species richness and biomass reflecting anthropogenic effects. Species richness, functional dispersion, and biomass were positively related to distance from the mainland. Overall, species richness and fish density were mainly influenced by biogeographical and energetic factors, whereas functional dispersion and biomass were strongly influenced by anthropogenic factors. Our results extend previous hypotheses for different assemblage metrics estimated from empirical data and confirm the negative impact of humans on fish assemblages, highlighting the need for conservation of oceanic islands.

INTRODUCTION

Efforts to understand the mechanisms responsible for variation in biodiversity over broad spatial scales have produced general hypotheses related to ecological and historical factors, differential speciation and extinction rates, and physiological and energetic constraints (Brown et al. 2004, Mittelbach and Schemske 2015). Although the mechanisms are debated, striking patterns materialize at large scales whereby environmental and biogeographical factors explain the number and density of species in a given area. For instance, in the marine realm, the surface area of coral reef habitats is the strongest predictor of tropical reef fish species richness (Parravicini et al. 2013), whereas the densities of whole fish assemblages are determined mainly by species richness and available energy (Barneche et al. 2016). In addition, anthropogenic drivers have gained considerable importance as predictors of large scale patterns of biodiversity in the last 50 years. Sharks and other large top predators, for instance, have become locally extinct in remote areas under high fishing pressure (Luiz and Edwards 2011), and biodiversity and ecosystem functioning are most commonly negatively affected by human population density (Mora et al. 2011, Sandin et al. 2008). Understanding the mechanisms that control spatial variation in biodiversity may help improve predictions of how species will respond to environmental change and other human impacts, and to design and implement effective conservation strategies (Mellin et al. 2016). As multiple factors affect large-scale patterns of biodiversity, it is important to compare the relative strength of several competing theories in order to understand what drives diversity distributions and to guide global conservation actions.

Biological diversity is too complex to be described by a single parameter. Multiple dimensions of diversity must be assessed and tested against proposed predictions to evaluate the robustness of macroecological and biogeographical hypotheses (e.g., Whittaker et al. 2008). However, hypotheses typically focus on a single biodiversity metric, usually species richness, and uncommonly make use of multiple parameters such as biomass, density of individuals or parameters linked to ecological function, which are key to fully understanding the mechanisms driving global distributions of reef fish assemblages (Kulbicki et al. 2013, Mouillot et al. 2014, Floeter et al. 2018). For instance, knowing the drivers of functional dispersion at the global scale may help predict species responses to environmental change because traits dictate their resource and habitat requirements (Laliberté and Legendre 2010). For reef fishes, using these approaches have revealed the importance of specific functional groups, such as herbivores and top predators, in maintaining ecosystem processes (Mora et al. 2011), such as energy flux in food webs (Barneche et al. 2016), and the resilience of coral reefs (Bellwood et al. 2004).

Oceanic islands are those that have never been connected to a continent (Dawson 2015) and encompass a wide range of topography, size, age, available area, nutrient availability, and isolation, yielding a variety of unique habitats and species assemblages (MacArthur and Wilson 1967, Losos & Schluter 2000, Brown 2014). These factors affect colonization, speciation and extinction rates, making oceanic islands excellent candidates for ecological and evolutionary studies (Dawson 2015, Hachich et al. 2015, Pinheiro et al. 2017). Marine faunas on

oceanic islands are vulnerable to habitat destruction, fragmentation, overfishing and the introduction of invasive species (Jackson et al. 2001, Triantis et al. 2010). Despite this vulnerability, isolated islands still harbor some of the last near-pristine marine habitats on Earth, therefore offering unique opportunities to observe habitats with presumably low or no history of direct anthropogenic disturbance (Sandin et al. 2008, Willians et al. 2015). Therefore, it is crucial to assess the assemblages of these natural laboratories and multiple competing theories under a common integrative approach. In particular, it is important to contrast the predictions combining historical processes with current trends in the species and population distributions of island faunas and their response to human impacts.

Tropical reef fishes are the most diverse marine vertebrate group with over 6,300 species worldwide (Kulbicki et al. 2013), wide geographic distributions (Parravicini et al. 2013), high functional diversity (Mouillot et al. 2014) and high economic value for human populations (Mora et al. 2011). However, little is known about how reef fish assemblages are organized around oceanic islands, or how biogeographic, energetic, and anthropogenic factors may structure these assemblages. During the last decade, several studies have shown that both predatory and herbivorous fish species are present at higher density and biomass on remote islands from the Indo-Pacific (Sandin et al. 2008), Central Pacific (Williams et al. 2015), and Caribbean regions (Newman et al. 2006). Only recently have the fish assemblages at islands of the Tropical Eastern Pacific and Tropical Atlantic been explored (e.g., Luiz et al. 2015, Quimbayo et al. 2017b). To date no large-scale comparisons of fish assemblages from oceanic islands have been made, nor have the factors determining general spatial patterns of species richness, functional dispersion, density of individuals and biomass been assessed.

In this study, we examined the relative influence of a set of biogeographic, energetic, and anthropogenic factors on the structure of reef fish assemblages from highly isolated oceanic islands from five marine provinces (Tropical Eastern Pacific-North, Tropical Eastern Pacific-South, Southwestern Atlantic, Central Atlantic, and Tropical Eastern Atlantic) using a dataset of 1527 underwater visual censuses. More specifically, we tested the following hypotheses: H1- Island biogeographic factors such as area and total species pool are positively related to species richness, functional dispersion, density and biomass, whereas isolation from nearby reefs (i.e., another island) is negatively related to these metrics because of its known effects on speciation, extinction and colonization rates (Losos & Schluter 2000, MacArthur and Wilson 1967, Pinheiro et al. 2017); the known effects of island area and isolation on reef fish population size (Kulbicki et al. 2015) may affect species density and biomass across islands, unless these effects are counterbalanced by anthropogenic factors such as fishing (Fig 1A; Cinner et al. 2016). H2: All metrics (species richness, functional dispersion, density, and biomass) are high in locations with high energy availability (primary productivity) and high temperature, because warmer and more productive areas will support large individuals, large populations and high diversification rates (Brown et al. 2004, Barneche et al. 2016; Fig 1B). H3 - Islands with low human density, high protection levels and isolation from the mainland (i.e., isolated from humans) will have high fish species richness, functional dispersion, density

of individuals and biomass because these are near pristine marine habitats (Sandin et al. 2008, Williams et al. 2015, Cinner et al. 2016, Fig. 1C).

METHODS

Study region

Our study comprised 18 tropical oceanic islands from the Pacific and Atlantic oceans located between latitude 19ºN and 22ºS (Fig. 2). These fall within two marine biogeographic provinces in the Eastern Pacific and three in the Atlantic (Fig. 2) classified according to endemism, diversity and species composition (Robertson and Cramer 2009, Kulbicki et al. 2013). Most islands in our study have volcanic origin with low reef development (Hachich et al. 2015, Cortés et al. 2017), with the exception of Clipperton and Rocas Atoll, which were formed by biogenic processes (e.g., Kikuchi and Leão 1997, Cortés et al. 2017). We considered individual oceanic islands to be those with independent isobaths (up to 50 m), and in some cases those with strong upwelling gradients dividing reef fish faunas (specifically in the Galápagos archipelago, where the fish fauna is subdivided into a central and a southern subgroup; Witman et al. 2010).

Fish surveys

We obtained data on fish assemblages from 1527 Underwater Visual Censuses (UVCs), performed at 96 sites at 18 oceanic islands (from five marine provinces) between 2006 and 2016 (Supplementary material Appendix 1, Table A1). The sampling consisted of visually identifying, counting and estimating the size (total length in cm) of all actinopterygian fish species observed both in the water column and on the bottom of belt transects (Brock 1954). The area per transect varied between 40 and 250 m^2 among islands (see Data Analysis; Supplementary material Appendix 1, Table A1). Transect depth varied between 5 and 25 m (97% of UVCs, only 3% were deeper than 30 m). We estimated the weight of each individual fish using the allometric length-weight conversion W = a x TL^b, where W is the fish weight (grams), parameters *a* and *b* are species-specific constants, and TL is the visually estimated total length in cm. Specific length-weight parameters were obtained for nearly all species from FishBase (Froese and Pauly 2016). In cases where species-specific coefficients were not available, we used coefficients of congeneric species that were phylogenetically close or morphologically similar.

Fish traits and assemblage functional index

We classified all fish species according to six different life-history traits using functional properties defined by Mouillot et al. (2014), which included: maximum body size (total length grouped into size classes <7 cm, 8–15 cm, 16–30 cm, 31–50 cm, 51–80 cm or >80 cm); mobility (sedentary, territorial species, mobile and very mobile organisms); period of activity (diurnal, nocturnal, or both); gregariousness (solitary, pairing, small groups of 3–20 individuals, medium groups of 20–50 individuals or large groups >50 individuals); position in the water

column (benthic, benthopelagic, or pelagic species); and finally, trophic group, which included herbivores-detritivores (feed upon turf and filamentous algae and/or detritus), macroalgae-feeders (feed on large fleshy algae and/or seagrass), sessile invertebrate feeders (corals, sponges, ascidians), mobile invertebrate feeders (benthic prey, such as crabs and mobile mollusks), planktivores (feed on small organism in the water column), piscivores (feed on fish and cephalopods) or omnivores (feed on algae, detritus and animal material) as trophic groups. These functional traits have been successfully used to describe functional aspects of reef fish assemblages and vulnerability (e.g. D'agata et al. 2016, Bender et al. 2017). We used Functional Dispersion (FDis) as our measure of functional diversity since this measure quantifies the functional variation of reef fish assemblages by combining the relative abundance of species and functional traits (Laliberté and Legendre 2010). To estimate FDis, we transformed all life-history traits except trophic group into ordinal variables prior to computing a Gower's distance dissimilarity matrix (Mouillot et al. 2014). FDis is calculated as the average distance of individual assemblages to the group weighted centroid in a multivariate functional trait space and is independent of species richness (Laliberté and Legendre 2010). This metric was estimated using the function *dbFD* from the 'FD' R package (Laliberté et al. 2015).

Our analysis procedure retained between 2-3 axes to compute FDis, and criticism could emerge concerning the underrepresentation of the number of retained functional axes. We agree that higher dimensionality (i.e., more axes) would produce better quality of functional spaces, and four axes have been successfully used with data and traits similar to ours (e.g., Mouillot et al. 2014; D'agata et al. 2016). Maire et al. (2015) showed, however, that the gain of functional representation from three to seven dimensions is low (considering our type of traits) despite its high computation effort. Moreover, the average quality of the functional space found here was higher than was estimated in another global study (0.60 in Stuart-Smith et al. 2013), and thus we are confident in the robustness of our functional index.

Assemblage metrics and drivers

We examined the effect of several biogeographic factors expected to determine fish assemblages. We estimated reef area as the surface area of the shallow shelf area between 0 and 50 m depth (based upon Gridded Bathymetric Data GEBCO 30 arc-second grid;
http://www.gebco.net/data_and_products/gridded_bathymetry_data/ gebco_30_second_grid/), the local species pool (Lpool: Kulbicki et al. 2013), and distances from the nearest reef (DReef: orthodromic distance between islands or reefs). Area serves as a proxy for habitat size and diversity, DReef represents current isolation from nearby reefs (i.e., sources of recruits). Lpool describes the reef fish checklist (i.e., all reported species within each island), a proxy for the influence of evolutionary factors on fish assemblages in oceanic islands.

Concerning the energetic factors hypothesized to predict species composition of fish assemblages, we compiled annual mean Sea Surface Temperature (SST) and Primary Productivity (PP), the later estimated from mean

surface chlorophyll *a* values for each island. Both variables were estimated from satellite data averaged between 2002 and 2009 from BIO-oracle (Tyberghein et al. 2012). Anthropogenic factors included human density (HumD: human population divided by the land surface area of the island), environmental protection status (Prot: category as defined by the International Union for Conservation of Nature, IUCN), and distance from the mainland (DistM: orthodromic distance between each island and the nearest continent). DistM was considered as an anthropogenic factor because the distance from nearby mainland dictates restricted access to the island by human populations, whereas DReef better represents isolation from major sources of fish colonists. The IUCN environmental protection status categories include Wilderness area (level 4; high conservation status), National park (level 3), Natural monument and natural feature (level 2), and habitat/species management area (level 1; low conservation status; World database on protected areas, available at http://www.protectedplanet.net; see Supplementary material Appendix 1, Table A2, last access July/2015).

We also minimized multicollinearity in our models by excluding highly correlated variables (with $|r| > 0.70$; Supplementary material Appendix 1 Fig. A1) because as suggested by a previous study (Dormann et al. 2007), model results below this correlation threshold are not strongly affected by multicollinearity problems. Surface area and human population density had borderline correlation values ($r = 0.71$, Supplementary material Appendix 1, Figure A1), but we opted to keep both due to their importance as biogeographical and contemporary factors. Prior to the statistical analysis, we log $(x+1)$ transformed surface area, distance from the nearest reef, distance from the mainland, and human density to improve assumptions of linear models. Then, all selected predictors were scaled to mean zero and unity standard deviation so that all estimated parameters were at the same scale and could be directly compared as an effect size.

Data analysis

As the number of UVCs and transect dimensions varied among oceanic islands (Supplementary material Appendix 1, Table A1), we produced a set of simulations to standardize the sampling effort per island. First, we identified the oceanic island with the smallest sampled area in our dataset (Clipperton with 1250 m^2 surveyed; Supplementary material Appendix 1, Table A1), and then restricted the sampled area in all other oceanic islands to this area limit, defined as the Minimal Sampled Area (MSA). For each oceanic island, we then randomly sub-sampled individual UVCs from different locations until reaching the MSA. As multiple combinations of UVCs could be used to compose each MSA per island, we repeated this procedure 999 times to produce a distribution of estimates of species richness (SR), functional dispersion (FDis), density of individuals (DE) and biomass (BS) for each UVCs.

At each simulation step, we modeled the four response variables calculated for each selected UVC against predictors with Linear Mixed-effect Models (LMM), using the islands as the random effect (random intercept model). This modeling technique is useful for controlling variability linked to the clustering of multiple sampling

units (UVCs) within oceanic islands. To quantify the relative importance of each predictor, we estimated a recently developed R^2 statistic for LMM based on the F-statistic for a Wald test for fixed effects and the corresponding estimated denominator degrees of freedom (Jaeger et al. 2017). This method is useful since the global R^2 can be used in model selection procedures, semi-partial R^2 can be computed for individual fixed-effect predictors so that they can be used as relative effect sizes, and it strictly corresponds to the conventional R^2 for linear and generalized linear models (Jaeger et al. 2017). We summed semi-partial R^2 values from predictors of the same group to estimate the relative support for biogeographic, energetic, and anthropogenic hypotheses.

At each simulation step, we retained parameter estimates (i.e., beta coefficients from LMM, the full model R^2 and semi-partial R^2 values) and then used their mean and standard deviation over all 999 steps as a measure of their effect on each response variable. The overall simulation procedure based on UVC units is analogous to sample-based rarefaction curves as it enables comparison between the effect of each factor on reef fish assemblage metrics while controlling for differences in sample size based on the MSA (e.g., Gotelli and Colwell 2001). We considered a given predictor to have a significant effect only if its 95% confidence interval did not overlap zero, which is similar to procedures adopted in ordinary hypothesis testing. We therefore reported mean and standard errors of model coefficients, full model R^2 values, and semi-partial R^2 values as a relative effect size over all simulations. We did not observe spatial autocorrelation in our analysis as measured by Moran's I index (Supplementary material Appendix 1, Fig. A2), calculated using the function *Moran.I* from the 'ape' package (Paradis et al. 2004). All statistical analyses were performed in the R environment, version 3.2.4 (R Core Team 2016).

RESULTS

Species richness showed little differences among the five provinces (Fig. 2A). Galápagos-Central (GALC) and St Paul's Rocks (SPR) yielded the highest and the lowest values of species richness, respectively (Supplementary material Appendix 1, Table A3). Functional dispersion varied among regions (Fig. 2B), with the highest values in the Tropical Eastern Pacific-North (TEPN) and Tropical Eastern Pacific-South (TEPS), and the lowest values in the Tropical Eastern Atlantic (TEA; Fig. 2B; Supplementary material Appendix 1, Table A3). In contrast, density of individuals varied widely among islands. The highest densities were recorded near the Equator (Malpelo, St Paul's Rocks, Rocas Atoll, Príncipe and São Tomé Fig. 2C), and the lowest densities were observed at high latitudes or on the most isolated islands (e.g. Clipperton; Supplementary material Appendix 1, Table A3). The highest biomass values were observed in the TEPS (Fig. 2D; e.g., Galápagos-South, Malpelo, and Cocos; Supplementary material Appendix 1, Table A3). Fish biomass in the Atlantic Ocean was much lower than in the Tropical Eastern Pacific (Fig. 2D), although some islands including St Paul's Rocks, Martin Vaz, Ascension and Trindade had values greater than 480 g/m^2 (Supplementary material Appendix 1, Table A3). Trophic and size structure showed little variation relative to species richness but varied widely among islands relative to density of individuals and biomass (Supplementary material Appendix 1, Fig. A3).

Our results indicated that each assemblage metric was influenced by a different set of biogeographic, energetic, and anthropogenic factors (Fig. 3). For instance, species richness was positively related to surface area, distance from the nearest reef, primary productivity, distance from the mainland and protection level (Fig. 3A), with most variation being explained by biogeographic and energetic factors (Table 1). In contrast, species richness was negatively correlated with sea surface temperature and human population density (Fig. 3A), though these factors explained a low proportion of variance (Table 1). Functional dispersion was positively related to distance from the nearest reef, local species pool, and distance from the mainland (Fig. 3B), but most variance was explained by related to biogeographic and, to a greater extent, anthropogenic factors (Table 1). Density of individuals was lower in large oceanic islands, as well as those distant from the mainland and with higher levels of protection (Fig. 3C). In contrast, islands distant from nearby reefs, with a larger local species pool and high primary production had high densities of individuals (Fig. 3C). Fish density was positively linked to human population density, though the significance of this predictor varied widely across simulations, indicating that this effect is not consistent and is constrained by the set of chosen UVCs. Energetic (via primary productivity) and biogeographic factors (via area and distance from nearest reefs), explained most of the variation in fish density (Table 1). Fish biomass was high on islands far from the mainland and far from the nearest adjacent reef, with high primary productivity and with high local pool, and was negatively affected by human density and surface area (Fig. 3D). Energetic and anthropogenic factors explained major differences fish biomass between oceanic islands (Table 1).

DISCUSSION

We quantified the relative strengths of three main groups of predictors explaining reef fish assemblages across tropical oceanic islands using four complementary response metrics (fish species richness, functional dispersion, density of individuals and biomass). By using a large data set from isolated oceanic islands and applying an integrative analytical framework for comparing fish assemblage metrics, we confirmed several of our predictions and uncovered several unexpected results concerning the effects of biogeographical, energetic, and anthropogenic factors on fish faunas.

All islands, except the Galápagos, had low variation in species richness (SR) and functional dispersion (FDis), and stable proportions of species richness per trophic group and size classes across islands (Supplementary material Appendix 1, Fig. A3). This low variation could be the result of similar features across oceanic islands, such as high isolation levels (>200 km from mainland), volcanic origins, underdeveloped coral formations, and distance from major biodiversity centers of marine organisms (Indo-Pacific for Tropical Eastern Pacific and Caribbean for Southwestern Atlantic and Tropical Eastern Atlantic). Indeed, isolated oceanic islands are known to support poor fish faunas, though some exhibit high functional diversity (Robertson 2001, Quimbayo et al. 2017b). The Galápagos archipelago is an exception; despite its isolation, the large surface area, the high diversity of benthic habitats (Edgar et al. 2011), and the seasonal upwelling events support high species richness and

functional diversity in this archipelago (Stuart-Smith et al. 2013). Moreover, the Galápagos islands represent a stepping stone for marine fauna between the coastal Tropical Eastern Pacific and the Central Pacific, which could explain the high proportion of non-specialized species previously reported in these islands (Edgar et al. 2011). In contrast, the low functional dispersion values observed in all Tropical Eastern Atlantic islands reflect the low species richness in this province and a homogenization of fish faunas throughout their extent (Kulbicki et al. 2013). This result could suggest high functional redundancy (i.e., many species performing the same ecological function), and a high vulnerability of such ecosystems, since the loss of any given species may imply the loss of a unique ecosystem function (Mouillot et al. 2014).

Corroborating our expectations, we consistently observed positive influences of surface area on species richness (MacArthur and Wilson, 1967), and of local species pool on functional dispersion, however the positive effect of distance from nearest reef on functional dispersion was unexpected. High dispersion and colonization due to high regional species pools (i.e. within marine province) would support the arrival of distinct functional groups (represented by at least a single species) even in highly isolated islands (e.g., Galápagos). Indeed, recent findings have shown that reef fish fauna are nested subsets of their regional pools due to colonization processes (Bender et al. 2017), and the arrival of a single species of a different functional group is all that is needed to fulfill the functional space of fish assemblages (Mouillot et al. 2014). Yet, new colonists reaching isolated islands could change their ecological function and occupy empty functional niches, hence explaining the high functional dispersion on isolated islands from species-rich provinces. This hypothesis, however, warrants further evaluation.

Contrary to our hypotheses, the density of individuals and biomass of reef fishes were lower at large islands but increased with isolation (i.e., DReef) and the size of the local species pool. According to our first hypothesis, we would expect larger densities and biomasses on large islands, in part because large islands should have more habitat diversity and reef area, hence supporting large populations and large individuals (Kulbicki et al. 2015). This unexpected result could be related to the high influence of fishing and other human disturbances on large islands (Cinner et al. 2016, Maire et al. 2016). On the other hand, this result could be due to the fact that oceanic islands act as oases in the open sea, attracting large predators and pelagic schooling fish in their search for food, cleaning services and/or refuge, with widely roaming species aggregating along with resident reef species (Gove et al. 2016, Quimbayo et al. 2017a). Some studies support the high proportion of large-bodied species (better colonizers) in large and isolated islands (Luiz et al. 2012). These larger species are usually more concentrate (abundance and biomass per unit area) around small isolated islands. Moreover, fish assemblages inhabiting oceanic islands usually comprise species with wide geographic ranges and a combination of traits (e.g., large body size, long pelagic larval duration, high swimming capacity, and plastic diets) that favors colonization and dispersal processes (Luiz et al. 2012, Kulbicki et al. 2015).

Primary productivity was a key energetic factor, confirming that productive areas support large diversity, population densities (Brown et al. 2014), and high fish biomass (Gove et al. 2016). This is due to the "Island

Mass Effect" (Gove et al. 2016), which induces high plankton concentrations around oceanic islands, as well as high densities of benthic species processing dead plankton and fecal material. This planktonic production may therefore boost the species richness, density, and biomass of planktivores, detritivores, and benthic invertivores, all important functional groups detected in our analysis. Islands from the Tropical Eastern Atlantic province had unexpectedly lower biomass despite higher primary productivity, which is a counterbalance caused by the intense fishing activities (Maia et al. 2018). This is consistent with previous findings showing that the so-called "dark spot" localities (such as Tropical Eastern Atlantic islands) have lower biomass than expected for natural conditions in part due to human disturbances (Cinner et al. 2016).

Large predators and herbivores comprise a large proportion of fish faunas on oceanic islands and are a primary target of reef fisheries (Sandin et al. 2008), leading us to conclude that the low species richness and biomass found in densely populated islands results from anthropogenic pressures. Studies in the Indo-Pacific (Sandin et al. 2008), and the Caribbean (Newman et al. 2006) have reported a pronounced decline in fish biomass linked to accessibility from the nearest human settlement and a short distance between source and market, since fish assemblages closer to human population centers are more disturbed than isolated ones or protected populations (D'agata et al. 2016, Maire et al. 2016). The high species richness and biomass we observed on isolated islands with minimal human impacts (e.g., Roca Partida, Clipperton, Cocos, Malpelo, Galápagos, and Ascension) corroborate the mechanism of human pressure as an important driver of reef fish assemblages in oceanic islands.

Our results show that islands with high protection levels contain high local species richness, but unexpected low fish density. This is congruent with top-down effects of the presence of top-predators controlling primary and small consumers such as planktivores and invertebrate feeders (Sandin et al. 2008), which compose the bulk of overfished assemblages (Lamb and Johnson 2010). In contrast, our findings show that islands distant from humans have high values of species richness, functional dispersion and biomass. The world's seas are largely unprotected (Sandin et al. 2008) and the creation and enforcement of marine "No Take" areas is key to preventing the depletion of marine fish stocks and fish extinctions/extirpations in marine environments (Mellin et al. 2016). Some ecological functions (e.g., herbivory) are performed by a restricted number of species on oceanic islands (Bender et al. 2017, Quimbayo et al. 2017b), thus the loss of a single or a few species would remove potentially important functions for the entire island. These results support the idea that anthropogenic impacts clearly extend beyond reducing the biomass of target species, implying negative effects of fisheries at the community (Lamb and Johnson 2010, Edgar et al. 2011) and ecosystem levels (Jackson et al. 2001). Additionally, our reported assemblage metrics along with results from other isolated islands studies with minimal anthropogenic impacts (e.g., Palmyra, Kingman, Chagos, Cocos, Malpelo remote New Caledonian islands) could be used as baselines for future comparative studies on reef fish assemblages from remote regions.

Some of our findings (e.g., the negative effect of Sea Surface Temperature on species richness) contradicted our initial hypotheses (Fig. 1). Firstly, we acknowledge that the UVC dataset from five biogeographical provinces

was constructed based on multiple individual initiatives, therefore differences in sampling procedures (mainly related to sampling area, effort, and fish observation) may have occurred while censusing reef fish. Our simulation based on all assemblage metrics and the MSA, which is equivalent to a sample-based rarefaction procedure for species richness (Gotelli and Cowell 2001), was fully developed to cope with such limitations while incorporating most of the dataset rather than excluding UVCs, localities, and/or islands. The robustness of such a procedure should hold even for metrics like functional dispersion, fish density and biomass, and indeed the detected effects are overall conservative across simulations (but see Results). Second, some drivers often interact producing contrasting but interesting results, especially those concerning anthropogenic drivers (e.g., Cinner et al. 2016). Interactions among predictors have not been considered here due to the challenge in evaluating their interactive effects based on observational studies, but remain an avenue for further research.

Past environmental changes are key drivers of global reef fish diversity (Pellissier et al. 2014), however there is little evidence of their influence in highly isolated tropical oceanic islands. Tropical islands in the Atlantic harbor higher richness and endemism than temperate ones (Hachich et al. 2015), which is related to low climate variability during the Pleistocene and higher net diversification rates (Siqueira et al. 2016). As the islands considered here are within tropical latitudes (19°N–22°S), past temperature changes have been less important in the development of these fish faunas. On the other hand, past sea level oscillations strongly dictate island area, isolation and connectivity by promoting fissions and fusions when shallow marine habitats and seamounts predominate over the sea landscape (Pinheiro et al. 2017). However, as the oceanic islands considered here are highly isolated from their past refugia (i.e., Indo-West Pacific) and there are few stepping stones (i.e., seamounts), colonization from past refugia would have a minor effect on these reef fish assemblages. Despite we did not directly include the effect of island age, it would play a role on total richness (Hachich et al. 2015) and functional dispersion. Instead, the effect of island age on fish density and biomass would be of minor importance (if any) because these two metrics mostly depend upon energetic factors (e.g., primary productivity, Table 1). Yet, we acknowledge that the local species pool metric is highly dependent upon the evolutionary history of each island (presumably age and past connectivity) and it was directly included in our analysis. Although further studies using phylogenies will certainly be useful in deciphering the role of evolutionary factors on oceanic islands, we provided herein important results and insights to the macroecology and biogeography of oceanic islands.

We observed that the variation in fish assemblage metrics estimated from field censuses are mainly explained by a combination of biogeographic, energetic and anthropogenic factors, as usually found in regional studies of reef fish diversity (Kulbicki et al. 2013, Parravicini et al. 2013, Mouillot et al. 2014). This study agrees with others showing that island size, isolation, and the size of the local pool are key determinants of local terrestrial (McArthur and Wilson 1967, Whittaker et al. 2008) and aquatic (Hachich et al. 2015, Pinheiro et al. 2017) assemblages. We extend this by showing that traditional predictors can even explain reef fish density and biomass across large spatial extents. Interestingly, whereas fish species richness and density of individuals are

mainly influenced by biogeographical and energetic factors, functional dispersion and biomass are strongly influenced by the anthropogenic factors evaluated here. These results suggest that the relative effects of drivers vary between different metrics of the fish assemblage structure and highlight the importance of considering a complete set of ecological, biogeographical and anthropogenic factors when attempting to explain large-scale patterns in reef fish assemblages. More importantly, our results suggest that knowledge of multiple facets of biodiversity (i.e., species richness, biomass, density, beta diversity, functional and phylogenetic diversity; Mora et al. 2011, Kulbicki et al. 2013, 2015, Mouillot et al. 2014, Floeter et al. 2018) is required to guide long-term conservation actions around oceanic islands.

CONCLUSIONS

Our study focused on determining and quantifying the relative strength of different factors explaining species richness, functional dispersion, density of individuals and biomass of reef fish assemblages for a wide range of oceanic islands. We found that biogeographic factors determine some assemblage metrics, but the direction of these effects varied, probably due to external factors such as fishing and other human disturbances. Our study extends findings from Island Biogeography Theory beyond species richness to include other descriptors of fish assemblages, such as functional dispersion, density and biomass. Finally, our results suggest that oceanic islands with high levels of anthropogenic pressure not only support low density of individuals and biomass, but also functional dispersion. The degree of isolation from humans and protection level of oceanic islands are thus important in maintaining diverse fish assemblages at oceanic islands.

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Biosketch:

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Figure Legends

Figure 1. Hypothetical relationships between Species Richness (SR), Functional Dispersion (FDis), Density of individuals (DE), and fish Biomass (BS) and all biogeographic, energetic, and anthropogenic factors considered in this study.
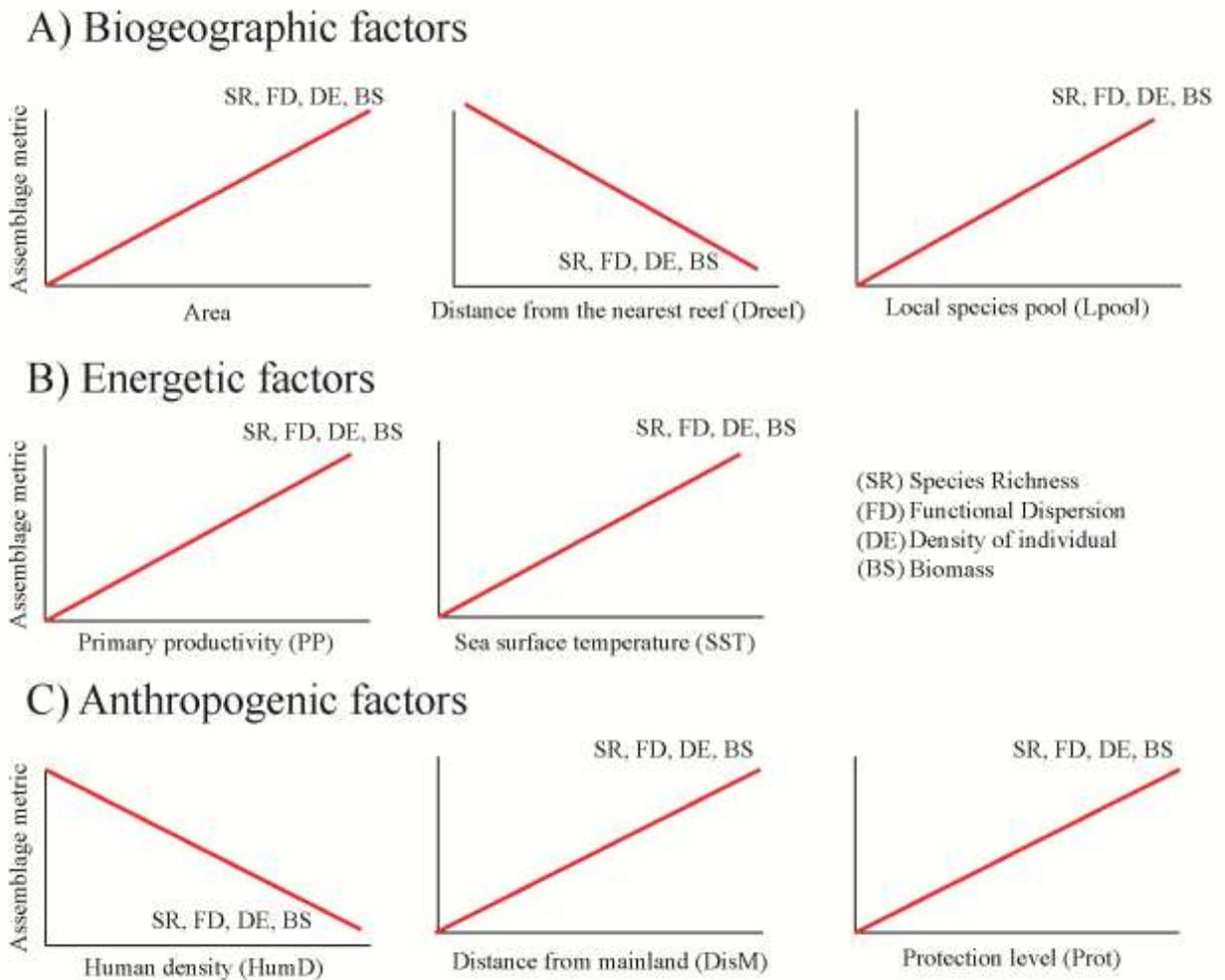
Figure 2. Variation in reef fish assemblage metrics at oceanic islands in the Tropical Eastern Pacific and Atlantic Ocean. (A) Species richness; (B) Functional dispersion; (C) Density of individuals; (D) Biomass. Each color represents a marine province. Circles are proportional to metric values.
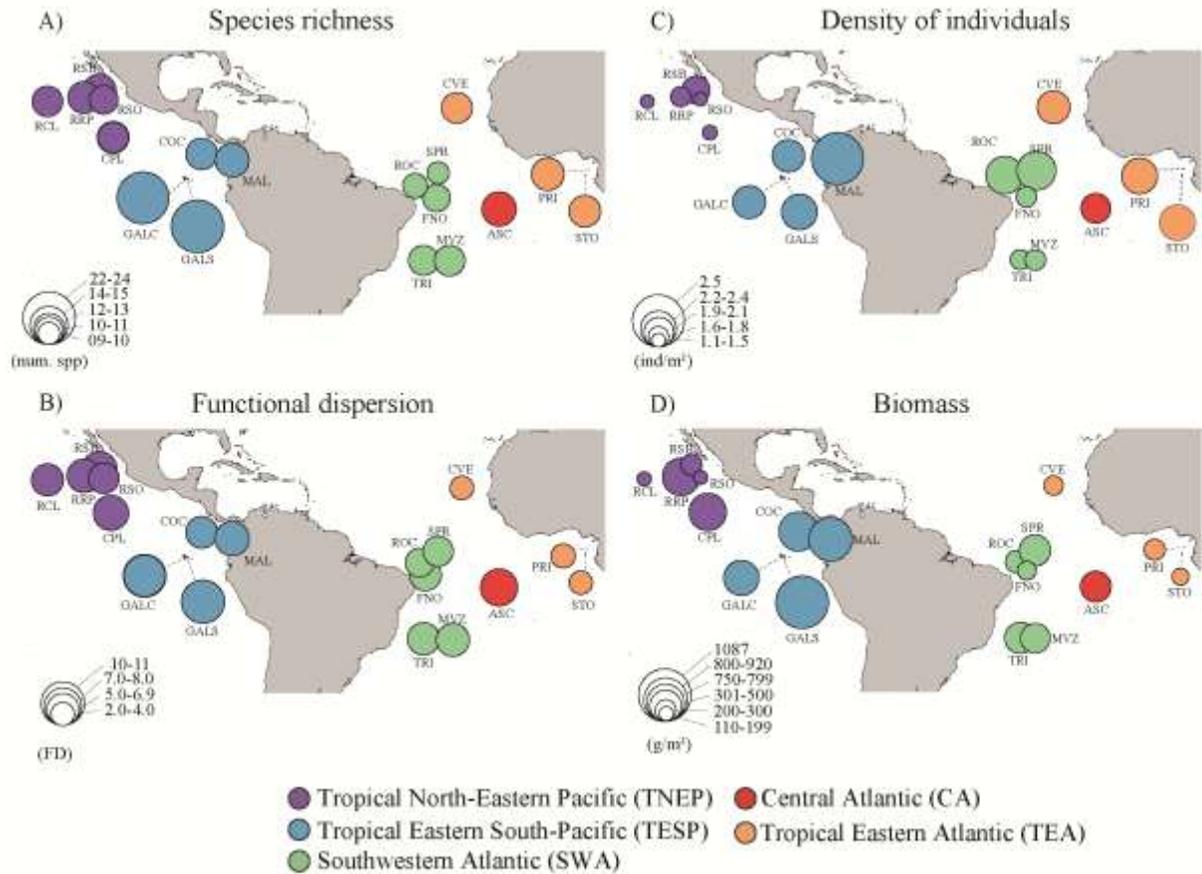
Figure 3. Mean effects of biogeographic (Area, DReef=Distance from the nearest reef, Lpool= Local species pool), energetic (PP= Primary Productivity, SST= Sea Surface Temperature), and anthropogenic (HumD= Human Density, DistM= Distance from the mainland, Prot= Protection level) factors on reef fish assemblages from oceanic islands of the Tropical Eastern Pacific and the Atlantic Ocean. Simulation outputs for (A) species richness, (B) functional dispersion, (C) density of individuals, and (D) biomass. Values have been standardized as effect sizes, circles represent mean parameter estimates and red lines represent 95% confidence intervals. Gray circles indicate significant mean values (i.e., different from zero).
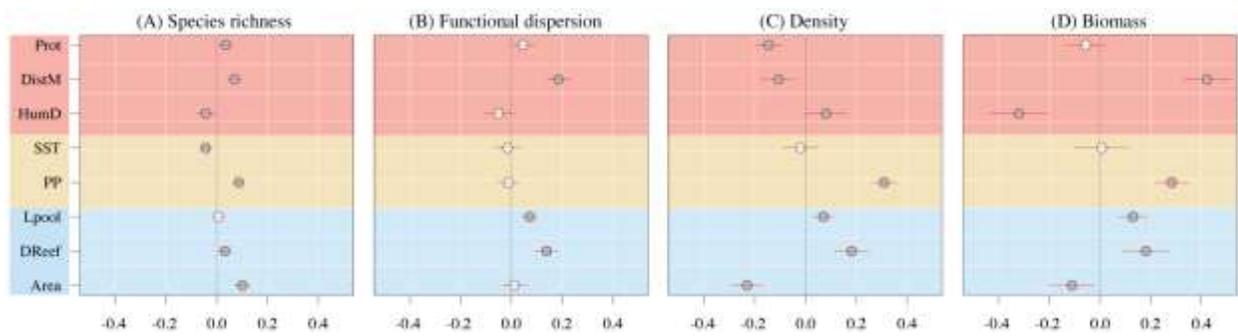
Table Legends

Table 1. Mean semi-partial R^2 values for each biogeographic, energetic and anthropogenic factors considered in the Linear Mixed-effect Models. Mean values (± Standard Deviation) are shown as percentages, and the sum of individual values per group of predictors is shown in bold.

Factor	Species richness	Functional dispersion	Density of individuals	Biomass
Biogeographic	**4.99**	**4.68**	**10.59**	**2.53**
Area	4.38 (±1.34)	0.14 (± 0.21)	6.14 (±1.68)	0.54 (± 0.40)
Dist. from nearest reef	0.53 (±0.38)	3.18 (± 1.13)	3.56 (± 0.31)	1.12 (± 0.57)
Local Pool	0.08 (±0.11)	1.36 (± 1.55)	0.89 (± 0.48)	0.87 (± 0.39)
Energetic	**6.07**	**0.31**	**15.97**	**4.59**
Prim. Productivity	5.34 (± 1.38)	0.16 (± 0.22)	15.81 (± 2.25)	4.50 (± 1.07)
Sea Surface Temp.	0.73 (± 0.38)	0.15 (± 0.21)	0.16 (± 0.21)	0.09 (± 0.11)
Anthropogenic	**3.39**	**6.41**	**4.93**	**7.96**
Human Density	0.60 (± 0.45)	0.41 (± 0.42)	0.63 (± 0.52)	2.26 (± 0.85)
Dist. from Mainland	2.00 (±0.73)	5.44 (± 1.37)	1.35 (± 0.85)	5.49 (± 1.18)
Protection level	0.79 (± 0.54)	0.56 (± 0.49)	2.95 (± 1.10)	0.21 (± 0.23)