



RESEARCH ARTICLE

Global patterns and drivers of beta diversity facets of reef fish faunas

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Abstract

Aim: Exploring the relationships between the different facets of beta diversity and both past and current environmental conditions can unveil the processes that have shaped spatial patterns of biodiversity. In the marine realm, large-scale patterns and processes of beta diversity have been less investigated. Our study aimed to investigate the patterns and drivers of multiple facets of beta diversity and its components, contrasting pairs of reef fish assemblages among marine realms.

Location: Tropical reefs.

Taxon: Reef fishes.

Methods: Based on trait data and phylogenetic relationships for 5182 tropical reef fish species, we calculated compositional differences between pairs of reef fish assemblages across the Atlantic, the Tropical Eastern Pacific (TEP) and the Indo-Pacific realms. We also applied a partitioning approach to distinguish between the turnover and nestedness components. We then evaluated the relative importance of several variables related to historical and contemporary environmental conditions in shaping spatial patterns of beta diversity using Constrained Analysis of Principal coordinates (CAP) models.

Results: Both the turnover and the nestedness components contributed to total phylogenetic and taxonomic beta diversity in the TEP and Indo-Pacific realms, while the turnover component was found to be more important in the Atlantic realm. In contrast, total trait beta diversity displayed very low values and was primarily explained by the nestedness component. Taxonomic and phylogenetic differences in the composition of tropical reef fish assemblages were influenced by both historical and contemporary factors or solely by historical variables.

Main conclusions: Our results suggest that past climate changes and historical contingency left an imprint in the present-day composition of tropical reef fish assemblages. The very low levels of trait beta diversity indicate that reef fish assemblages display similar trait composition even among geographically distant assemblages with contrasting evolutionary histories, which may result from environmental filtering or evolutionary convergence, or the combination of both processes.

KEYWORDS

marine realms, nestedness, phylogenetic diversity, taxonomic diversity, trait diversity, tropical reefs, turnover

1 | INTRODUCTION

The search for patterns and processes in biodiversity, as well as its variation throughout space and time, is the holy grail of macroecology (McGill, 2019). Biological diversity is not evenly distributed on Earth, with differences brought up by contemporary environmental gradients (Brown, 2014; Melo et al., 2009; Tittensor et al., 2010), past environmental changes (Leprieur, Descombes, et al., 2016; Pellissier et al., 2014) and the evolutionary history of clades (Miller et al., 2018; Ricklefs & Starck, 1996). Such differences in biodiversity across space can be measured through the number of species inhabiting a given location (alpha diversity) but also by the change in species composition between locations (beta diversity; see Baselga, 2010; Mittelbach & McGill, 2019). The beta diversity can be partitioned into two additive components: (i) the turnover, which represents the replacement of species between assemblages and (ii) the nestedness component, where assemblages with lower species richness are subsets of those with higher species richness (Baselga, 2010). These components can reveal the role of different processes in shaping large-scale patterns of assemblage composition, such as dispersal processes, associated with turnover and selective extinction and colonization, that produce nestedness (Si et al., 2016). Also, this beta diversity based-approach can be applied to delineate biogeographical regions, with the identification of species composition breaks based on species turnover patterns (see Hattab et al., 2015; Mouillot et al., 2013). More generally, exploring the link between beta diversity patterns and contemporary and past environmental conditions may unveil the mechanisms that shape differences in diversity across space (Leprieur et al., 2011; Qian et al., 2020) and time (Hatosy et al., 2013).

Beyond species richness, biodiversity is now widely recognized as constituted by multiple facets, such as functional and phylogenetic diversities (Cavender-Bares et al., 2009). Trait (or functional) diversity corresponds to the breadth of trait values in assemblages and is frequently measured through characteristics related to morphology, ecological requirements and physiology (Villéger et al., 2013; Violle et al., 2007). Phylogenetic diversity, based on branch lengths in a phylogenetic tree, captures the amount of evolutionary history of the clades composing a species assemblage (Cavender-Bares et al., 2009; Webb et al., 2002). Thus, trait and phylogenetic beta diversity measure differences in these facets between two or more assemblages (Leprieur et al., 2012; Villéger et al., 2011). Approaches including such facets can reveal contrasting patterns of biodiversity and the underlying processes (Bender et al., 2013, 2017; Villéger et al., 2012, 2013), which is not possible when using only a taxonomic approach. Furthermore, the study of these facets can unravel the relative influence of historical (e.g. past climate changes) and contemporary (e.g. environmental filtering) processes in shaping

present-day patterns of biodiversity (González-Trujillo et al., 2021; Weinstein et al., 2014), and that within an evolutionary context.

Trait beta diversity patterns may support a niche-based model of community assembly led by filtering of species according to their traits (Siefert et al., 2012; Swenson et al., 2011). While trait dissimilarity is often associated with environmental filtering and geographical distance (Fluck et al., 2020; Siefert et al., 2012; Swenson et al., 2011), taxonomic and phylogenetic dissimilarities are related to historical and biogeographical processes (Dexter et al., 2012). Studies incorporating at least two facets (i.e. taxonomic, phylogenetic, and/or trait) of beta diversity have been developed at different spatial scales and with different taxonomic groups, such as flowering trees (Qian et al., 2020), fishes (Hattab et al., 2015; Leprieur et al., 2011; Loiseau et al., 2017; Villéger et al., 2012), bats (Varzinczak et al., 2018) and birds (Fluck et al., 2020; Meynard et al., 2011). For instance in the Amazon Forest, taxonomic and phylogenetic turnover of passerine assemblages are mainly driven by differences in temperature and geographical distance (Fluck et al., 2020). Geographical and climatic distances also explained taxonomic and phylogenetic beta diversity patterns in regional assemblages of angiosperms in China (Qian et al., 2020). For marine organisms, differences in taxonomic and phylogenetic composition are frequently associated with environmental drivers (e.g. reef heterogeneity, sea surface temperature [SST] and bathymetry), as observed for coastal and reef fishes, starfishes and corals (Arias-González et al., 2008; Hattab et al., 2015; Price, 2002). These studies are mostly conducted at local or regional scales (Arias-González et al., 2008; Becking et al., 2006; Carlos-Júnior et al., 2019; Hattab et al., 2015; Loiseau et al., 2017). Overall, very few studies investigated simultaneously the different facets of beta diversity at the global scale (see Penone et al., 2016), and more particularly considering a partitioning approach to disentangle the effects of species turnover and differences in species richness (see Montaña-Centellas et al., 2021).

Reefs harbour remarkable species diversity and ecosystem functions (Bellwood et al., 2017). There are over 6000 fish species inhabiting reefs distributed across the world's oceans (Kulbicki et al., 2013). Reef fish biodiversity peaks in the Indo-Australian Archipelago (IAA) – that hosts more than 2500 species – and varies along environmental gradients of reef area (Bellwood et al., 2005; Parravicini et al., 2013), SST (Barneche et al., 2019) and isolation (Bender et al., 2017; Parravicini et al., 2013). Past environmental changes also left a strong imprint on reef fish biodiversity, shaping past (Pellissier et al., 2014; Siqueira et al., 2020) and current structure of reef fish assemblages (Donati et al., 2019; Leprieur, Colosio, et al., 2016). The trait structure of tropical fish assemblages is redundant (Mouillot et al., 2014), nested and shaped by isolation (Bender et al., 2017) – this set of traits is thought to have a functional role at large (Mouillot et al., 2014) and small spatial scales (Brandl



et al., 2016). Nevertheless, we do not know the level to which differences in trait structure are associated with differences in taxonomic or phylogenetic structure in such assemblages. Also, to date, there are no assessments of the main determinants of beta diversity in the global reef fish fauna (but see Mouillot et al., 2013 for Indo-Pacific coral reef fishes), simultaneously considering three different facets of beta diversity.

In this study, our main aims were: (i) to investigate taxonomic, phylogenetic and trait beta diversity patterns of tropical reef fish assemblages for the three major tropical marine realms (the Atlantic, the Tropical Eastern Pacific [TEP] and the Indo-Pacific), and (ii) to determine the contribution of contemporary and historical factors in explaining those patterns. Given the high levels of trait redundancy found in both marine and freshwater fish faunas (McLean et al., 2021; Mouillot et al., 2014; Villéger et al., 2013), we expect lower levels of trait turnover among assemblages than those observed for the taxonomic and phylogenetic facets of beta diversity respectively. Then, we expect that isolation processes related to plate tectonics and Quaternary climatic changes have left an imprint on the taxonomic and phylogenetic composition of tropical reef fish assemblages, and more especially on the turnover component (see Leprieur, Descombes, et al., 2016; Polanco et al., 2020). For instance areas peripheral to the IAA and the Caribbean region, recognized as marine biodiversity hotspots, should be more dissimilar in their tropical reef fish faunas (e.g. the Red Sea, the Hawaiian Islands, the Eastern Atlantic tropical reefs), as a result of in situ speciation processes and limited recolonization from Quaternary refugia (Bowen et al., 2013; Pellissier et al., 2014).

2 | MATERIALS AND METHODS

2.1 | Reef fish distribution, traits and phylogenetic data

Reef fish species occurrences at 169 tropical sites worldwide were compiled from published works, checklists, monographs and scientific reports (Kulbicki et al., 2013; Parravicini et al., 2013). This data covers 6316 reef fish species distributed in three marine realms (*sensu* Kulbicki et al., 2013): the Atlantic, the TEP and the Indo-Pacific realms. However, we restricted our analysis to 5182 species following the most recent phylogeny published in Siqueira et al. (2020), which covers 82% of reef fish species listed in our distribution database.

Based on species occurrences, we built species' distribution extent maps defined by a convex hull polygon. Due to the presence of multiple polygons with clear extant range discontinuities, the prior convex hull was divided into multiple polygons to avoid disjunctive distribution ranges being merged (Buckley & Jetz, 2008). Then, species composition was extracted from grid cells of $5^\circ \times 5^\circ$ degrees (i.e. ~550 km at the Equator), totalizing 323 cells. This grid size is considered appropriate given the resolution and available geographical information for the reef fish fauna (Parravicini et al., 2014). Analyses

were conducted at the realm scale, namely: the Atlantic, the TEP and the Indo-Pacific realms (*sensu* Kulbicki et al., 2013).

We classified all reef fish species according to six categorical biological and ecological traits defined by Mouillot et al. (2014) which included: (1) Maximum body size (<7 cm, 7.1–15 cm, 15.1–30 cm, 30.1–50 cm, 50.1–80 cm and >80 cm); (2) Trophic group (herbivores-detritivores, planktivores, piscivores, omnivores, macroalgal-herbivores, sessile invertebrates feeders and mobile invertebrates feeders); (3) Mobility (sedentary – including territorial species –, mobile and very mobile); (4) Period of activity (diurnal, nocturnal or both); (5) Schooling (solitary, pairing, small groups of 3–20 individuals, medium groups of 20–50 individuals and large groups – >50 individuals –) and (6) Vertical position in the water column (benthic, benthopelagic and pelagic species). These traits have been previously used to explore the functional biogeography of reef fish assemblages (Bender et al., 2017; Mouillot et al., 2014; Quimbayo et al., 2019).

2.2 | Environmental and historical data

We selected six variables related to contemporary environmental conditions (current reef area, SST, isolation from the nearest reef areas), historical contingency (distance from the biodiversity centre) and past climate changes during the Quaternary (past reef area, isolation from Quaternary coral reef refugia), which we subsequently used for evaluating their importance in explaining beta diversity patterns. Current reef area was estimated from the Coral Reef Millennium Census Project (Andrefouet et al., 2006). Isolation from the nearest reef areas was obtained based on the connectivity between each site to the 10 nearest reef habitats (see Parravicini et al., 2013 for more details). This variable has been previously used as a proxy for connectivity (Bender et al., 2017; Parravicini et al., 2013). The mean SST was extracted from Bio-ORACLE database, from 2002 to 2009, for each cell with a spatial resolution of 5-arcmin (Assis et al., 2018; Tyberghein et al., 2012). The distance from the biodiversity centre was measured in degrees for each marine realm, considering the Caribbean for cells within the Atlantic (Floeter et al., 2008), and the IAA for cells within the Indo-Pacific (Bellwood et al., 2005). These two marine biodiversity hotspots are indeed considered as both centres of accumulation and speciation, resulting from plate tectonics processes that have shaped the configuration of shallow-water habitats through the Cenozoic (see Leprieur, Descombes, et al., 2016; Miller et al., 2018). The distance from the biodiversity centre would therefore reflect the effect of past isolation processes resulting from changes in reef habitat configuration since at least the Miocene (see Leprieur, Descombes, et al., 2016). To evaluate the impact of past climate changes, we used the isolation from Quaternary coral reef refugia, that is the distance required to recolonize a given cell from the nearest refugia over the last three million years after repeated phases of climatic unsuitability (see Pellissier et al., 2014 for more details). We also used the historical reef area availability during the Quaternary, computed as

the average of reef areas available through the coldest periods (see Pellissier et al., 2014 for more details). Both current and past reef areas were log-transformed prior to the analyses. These variables have been widely used in global scale studies of tropical reef fish diversity patterns (Barneche et al., 2019; Bellwood et al., 2005; Bender et al., 2017; Leprieur, Colosio, et al., 2016; Ottimofiore et al., 2017; Parravicini et al., 2014; Quimbayo et al., 2021).

2.3 | Data analysis

2.3.1 | Beta diversity patterns

Taxonomic beta diversity was quantified as the dissimilarity between pairs of reef fish assemblages using the Sorensen's dissimilarity index and its turnover and nestedness components (Baselga, 2010, 2012). The turnover component of taxonomic beta diversity quantifies 'true' turnover of species (i.e. species replacement) without the influence of difference in species richness between sites. The nestedness component quantifies the taxonomic beta diversity resulting from nestedness of species between sites. Nestedness between sites occurs when the species of the poorer site are a subset of the species of the richer site (Baselga, 2010). We used this beta diversity partitioning approach instead of other approaches proposed in the literature (e.g. Carvalho et al., 2012) because nestedness was found to be important for explaining beta diversity patterns in tropical reef fish faunas (Mouillot et al., 2013).

To quantify phylogenetic and trait beta diversity, we employed the approaches proposed by Leprieur et al. (2012) and Villéger et al. (2013), respectively, that extend the framework of Baselga (2010, 2012) to phylogenetic and trait information. To quantify trait beta diversity, we first measured trait dissimilarity between species considering a set of six species traits and using the Gower's distance. We then applied a Principal Coordinate Analysis (PCoA) based on the Gower's distance matrix to build a unique functional trait space. We assessed the quality of the trait space using the 'mSD' metric proposed by Maire et al. (2015) and selected the first three PCoA axes to quantify trait beta diversity.

Previous studies showed that three facets (taxonomic, phylogenetic and trait) of beta diversity may be strongly correlated when quantified using classical dissimilarity indices such as the Sorensen's index (e.g. Swenson, 2011). To complement the above-mentioned analyses, we measured phylogenetic and trait beta diversity using the D_{pw} metric (Swenson, 2011; Webb et al., 2008). In contrast to Sorensen's index, the D_{pw} is a basal beta diversity metric, calculated as the average distance between all species in one assemblage and all species in a second assemblage. This index is therefore less influenced by the distances between the nearest neighbour species compared to the Sorensen's index, this latter being considered as a tip-weighted metric of beta diversity when applied to phylogenetic information (Qian et al., 2020; Swenson et al., 2011). Tip-weighted metrics of phylogenetic beta diversity are sensitive to turnover among recently diverged lineages, whereas basal-weighted metrics

of phylogenetic beta diversity are sensitive to turnover deep within the phylogeny (Jin et al., 2015; Swenson, 2011). In addition, the D_{pw} index was found to be less related to taxonomic beta diversity compared to other metrics (see Swenson et al., 2011). To evaluate the degree of congruence between the three beta diversity facets, we performed Spearman's correlation tests.

To explore the spatial variation in the composition of tropical reef fish assemblages, we performed a series of Principal Coordinates Analysis (PCoA) based on the taxonomic, phylogenetic and trait dissimilarity matrices. Then, the ordination results were plotted and mapped using a $5^\circ \times 5^\circ$ cells resolution for each marine realm. The RGB colour of each grid cell corresponds to its position in the plan formed by the two first PCoA axes. Similar grid cells indicate that fish assemblages display similar taxonomic, phylogenetic, or trait composition, while cells with different colours have more dissimilar compositions.

2.3.2 | Drivers of beta diversity

To this set of analyses, only those cells with available data on the isolation from Quaternary coral reef refugia were considered (i.e. 270 grid cells out of 323 cells). Canonical Analysis of Principal coordinates (CAP – Anderson & Willis, 2003) was performed to assess the relative importance of a set of contemporary and historical factors in shaping observed patterns of taxonomic, phylogenetic and trait total beta diversity, as well as their turnover and nestedness components. For each marine realm, we created three different CAP models, considering (i) contemporary factors only (isolation from the nearest reef areas, SST and current reef area), (ii) historical factors only (distance from the biodiversity centre, past reef area and isolation from Quaternary coral reef refugia) and (iii) taking into account all predictors. We then applied a variation partitioning approach to decompose the total variation (or inertia) in compositional dissimilarity into four fractions: (1) uniquely explained by contemporary factors, (2) uniquely explained by historical factors, (3) jointly explained by contemporary and historical factors and (4) unexplained.

All data analyses were performed using the R software version 3.6.1 (R Core Team, 2019) and the following packages: 'ade4' (Dray & Dufour, 2007), 'ape' (Paradis et al., 2004), 'betapart' (Baselga & Orme, 2012), 'cluster' (Maechler et al., 2017), 'dplyr' (Wickham et al., 2015), 'maptools' (Bivand & Lewin-Koh, 2013), 'picante' (Kembel et al., 2010), 'recluster' (Dapporto et al., 2013), 'rgdal' (Bivand et al., 2015) and 'vegan' (Oksanen et al., 2019).

3 | RESULTS

3.1 | Beta diversity patterns

Overall, the turnover and the nestedness components both contributed to total phylogenetic and taxonomic beta diversity in the TEP and Indo-Pacific realms (Figure 1). In contrast, the turnover

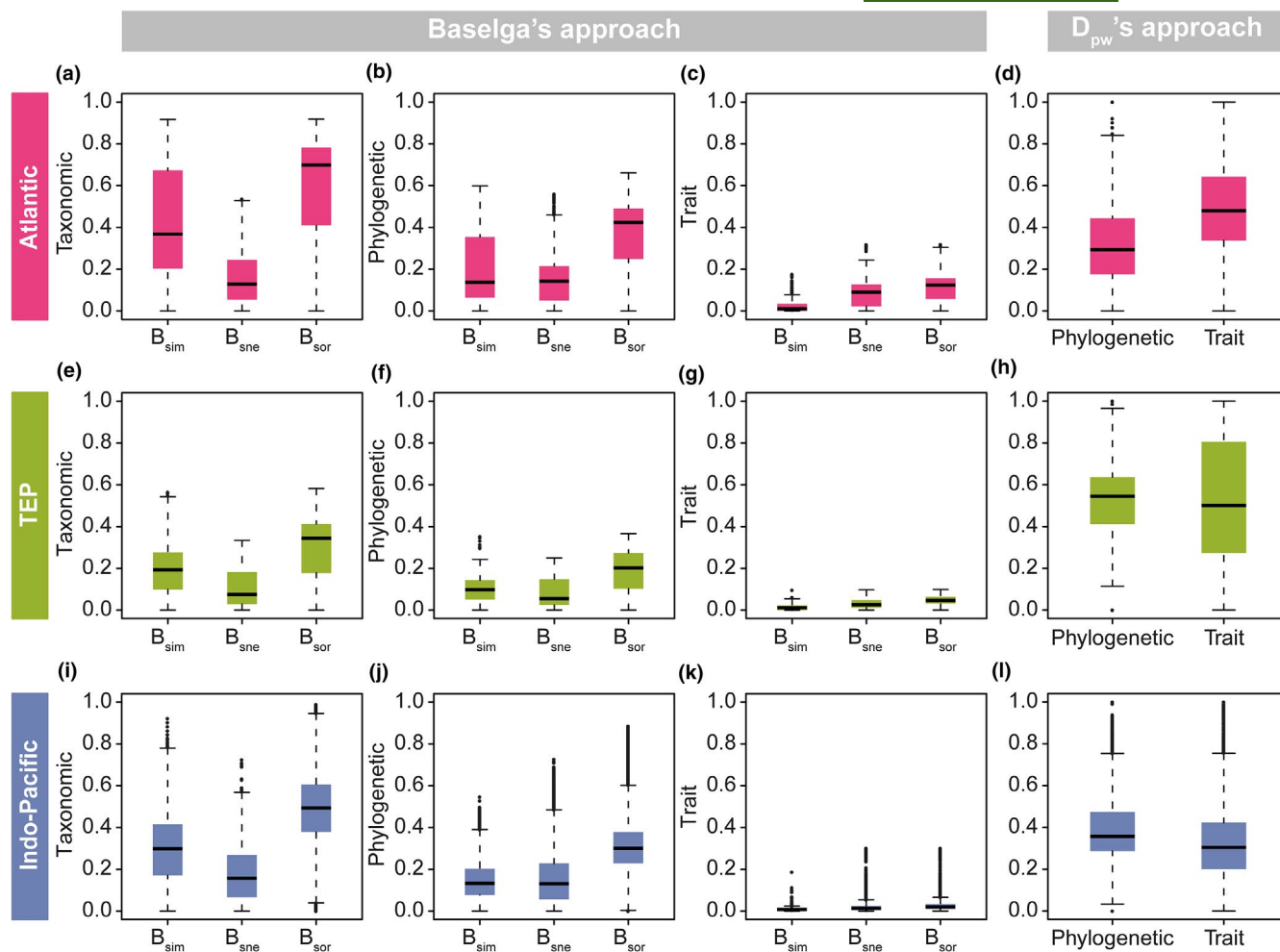


FIGURE 1 Boxplots illustrating the distribution of pair-wise dissimilarity values between reef fish assemblages of the Atlantic, the Tropical Eastern Pacific (TEP), and the Indo-Pacific marine realms. The first three columns correspond to the Sorensen's dissimilarity index (B_{sor}) and its turnover (B_{sim}) and nestedness (B_{sne}) components (Baselga's approach) calculated for each beta diversity facet (taxonomic, phylogenetic and trait), while the last column corresponds to the standardized (between 0 and 1) phylogenetic and functional-derived D_{pw} values (D_{pw} 's approach).

component contributed more to total phylogenetic and taxonomic beta diversity in the Atlantic realm (Figure 1). When considering trait information, total beta diversity showed very low values (mean = 0.03–0.12 and \pm SD = 0.02–0.07; Figure 1) compared to the taxonomic and phylogenetic facets of beta diversity. In addition, the nestedness component primarily contributed to total trait beta diversity (mean = 0.02–0.09 and \pm SD = 0.03–0.07; Figure 1).

In the Atlantic realm, taxonomic and phylogenetic beta diversity and their turnover components showed similar patterns, with clear compositional breaks between the Eastern and Western Atlantic regions, and the Caribbean (Figure 2a,b; Figure S1a,b). When considering trait beta diversity and its turnover component, these compositional differences were found to be less important (Figure 2c; Figure S1c). In the TEP, total taxonomic and phylogenetic beta diversity, along with their turnover components, showed a strong latitudinal gradient (Figure 2d,e; Figures S1d,e), with large compositional differences between the northern and southern regions (Figure 2d,e), as well as between the TEP islands and the coastal

areas. When considering trait beta diversity and its turnover component, these compositional differences are less marked, especially between the Galápagos Islands and the southern coastal areas (Figure 2f; Figure S1f). In the Atlantic realm, the contribution of nestedness to different beta diversity facets appears in the Caribbean, along the Brazilian coast, in Mid-Atlantic islands and Western Africa (Figure S2a–c). In the TEP, similar nestedness values appear in the central region (Figure S2d–f).

In the Indo-Pacific realm, total taxonomic and phylogenetic beta diversity showed a marked longitudinal gradient with the identification of three compositional breaks separating three regions: the Western Indian, the Central Indo-Pacific and the Central Pacific including the Hawaiian Archipelago (Figure S3a,b). A similar result is found when considering the turnover component only (Figures 3a,b), which also revealed a more marked latitudinal gradient in both the taxonomic and phylogenetic composition of reef assemblages (Figure 3a,b). In contrast, considering total trait beta diversity and its turnover component displayed a striking homogeneous spatial

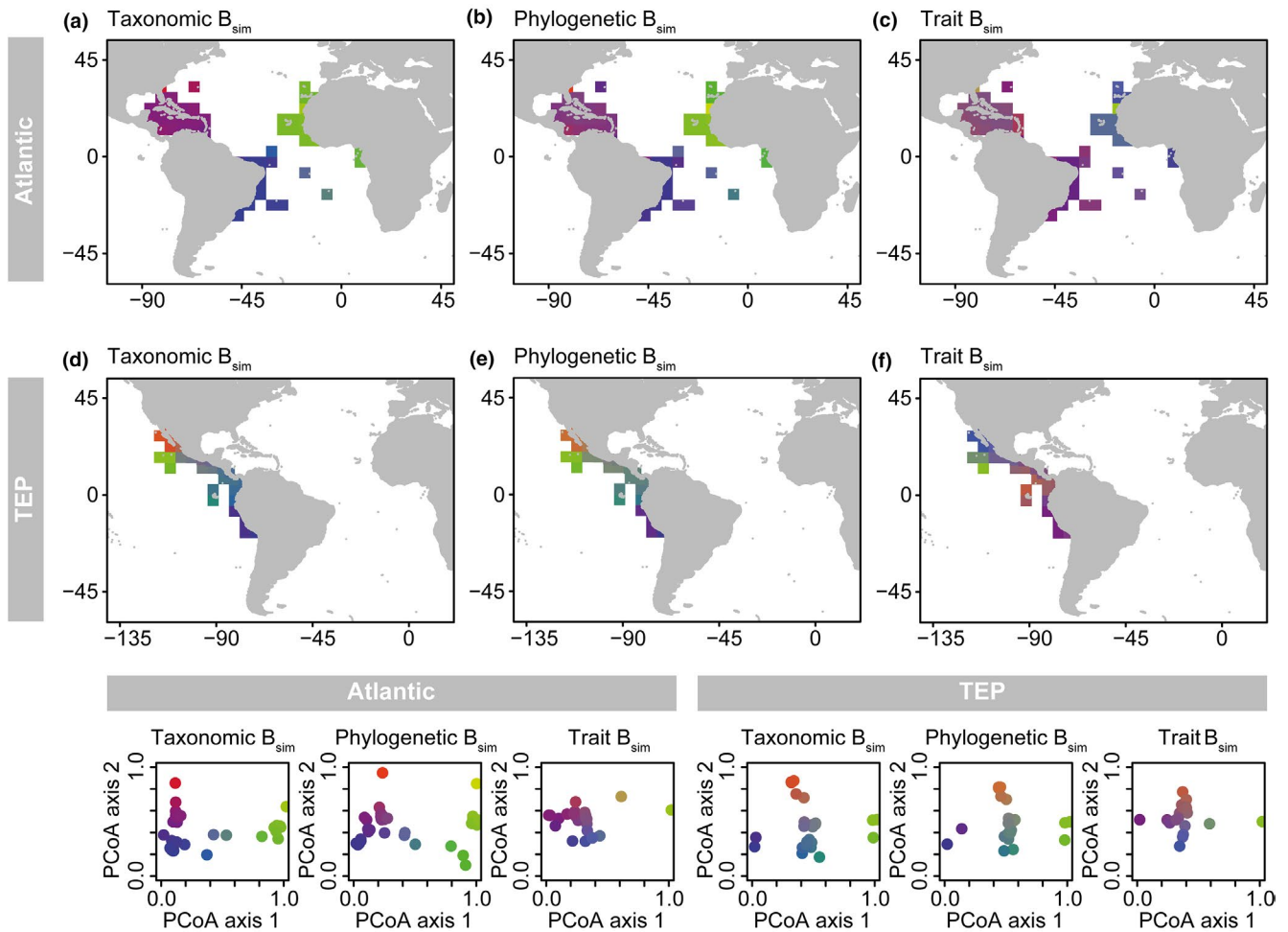


FIGURE 2 Spatial patterns of reef fish beta diversity for (a–c) the Atlantic and (d–f) the Tropical Eastern Pacific (TEP) inferred from the two-first axes of a principal coordinate analysis (PCoA) and based on (a, d) taxonomic turnover (taxonomic B_{sim}), (b, e) phylogenetic turnover (phylogenetic B_{sim}), and (c, f) trait turnover (trait B_{sim}). The original values on the first and second PCoA axis were standardized between 0 and 1. The colour gradient corresponds to the gradient of dissimilarity between pairs of grid cells, where similar colours indicate a lower difference in species composition. At the bottom, the ordination of each cell in the plan formed by the two-first axes of the PCoA is shown.

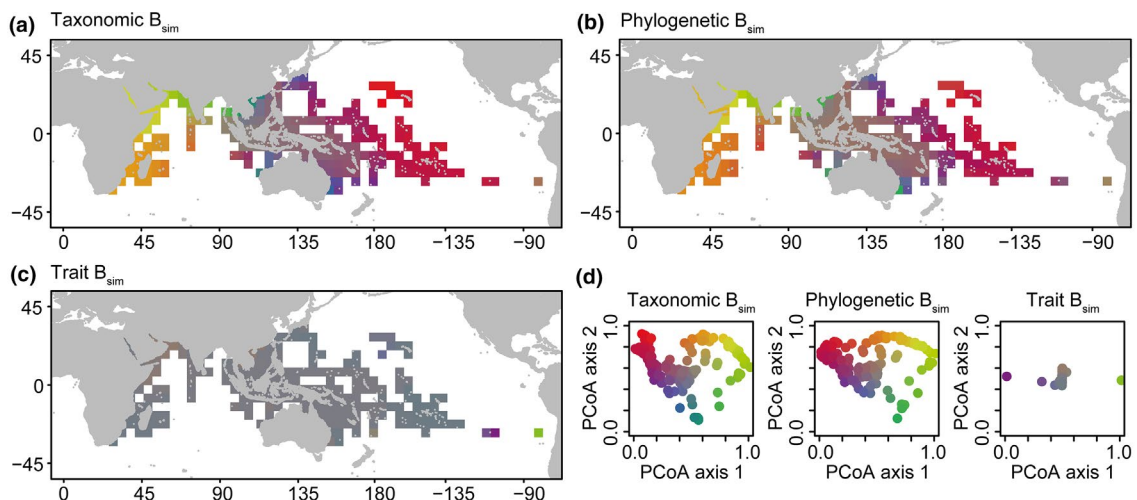


FIGURE 3 Spatial patterns of reef fish beta diversity for the Indo-Pacific inferred from the two-first axes of a principal coordinate analysis (PCoA) and based on (a) taxonomic turnover (taxonomic B_{sim}), (b) phylogenetic turnover (phylogenetic B_{sim}), and (c) trait turnover (trait B_{sim}). The original values on the first and second PCoA axis were standardized between 0 and 1. The colour gradient corresponds to the gradient of dissimilarity between pairs of grid cells, where similar colours indicate a lower difference in species composition. At (d) the ordination of each cell in the plan formed by the two-first axes of the PCoA is shown.

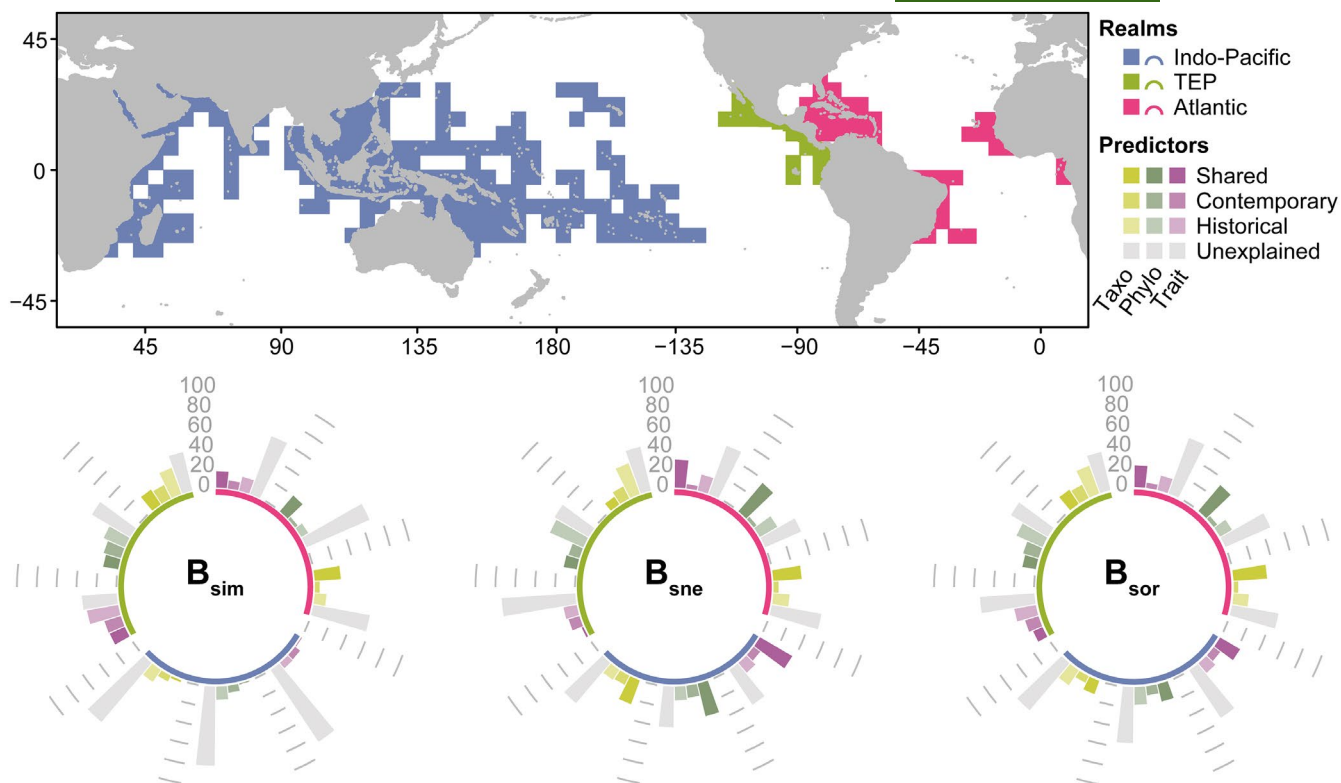


FIGURE 4 Results from Canonical Analysis of Principal coordinates (CAP) in the Atlantic, the Tropical Eastern Pacific (TEP), and the Indo-Pacific marine realms. Circular barplots show the percentage of explained inertia shared between contemporary predictors and historical predictors and unique to contemporary (isolation from the nearest reef areas, sea surface temperature and current reef area) or historical (distance from the biodiversity centre, past reef area and isolation from Quaternary coral reef refugia) predictors, and the percentage of unexplained inertia. Results are shown for each beta diversity facet (taxonomic, phylogenetic and trait) and for total (B_{sor}) beta diversity and its turnover (B_{sim}) and nestedness (B_{sne}) components.

pattern, with weak differences in trait composition across the Indo-Pacific (Figure 3c; Figure S3c). This similarity in trait composition of reef fish assemblages is supported by the nestedness contribution to trait beta diversity across the Indo-Pacific realm (Figure S4c). For taxonomic and phylogenetic beta diversity, the nestedness component had similar values mainly in the Central Indo-Pacific region (Figure S4a,b).

Correlation analyses revealed that the three facets of beta diversity, as measured using a dissimilarity-based approach, were all strongly correlated (Figure 5; Figures S8 and S9). However, the level of correlation between trait beta diversity and taxonomic and phylogenetic beta diversity, respectively, is found to be lower, and more particularly in the Indo-Pacific (Figure 5g–i).

3.2 | Drivers of beta diversity

According to the CAP models, total beta diversity and its turnover and nestedness components were explained by the combination of historical (distance from the biodiversity centre, past reef area and isolation from the Quaternary coral reef refugia) and contemporary (isolation from the nearest reef areas, SST and current reef area) variables (shared inertia), or solely by historical variables (Figure 4).

However, there is a large proportion of unexplained inertia in the CAP models performed for the total beta diversity (~39%–61%), the turnover (~35%–87%) and nestedness (39%–74%) components. For example for the Indo-Pacific realm, the historical and contemporary variables altogether explained up to ~40% of total beta diversity (for both phylogenetic and trait beta diversity), and up to 1% when considering the turnover component only. In the Atlantic and TEP realms, the historical and contemporary variables altogether explained up to 60% of the turnover component. However, the unique contribution of historical variables was found to be greatest in the TEP than in the other realms, and this whatever the beta diversity facet and the beta diversity component considered (Figure 4).

3.3 | Phylogenetic and trait beta diversity considering the D_{pw} metric

The phylogenetic and trait-derived D_{pw} indices both showed a weak correlation with the total taxonomic beta diversity, as measured by the Sorensen's index, and the turnover and the nestedness components (Figures S10, S11 and S12). In the Atlantic realm, the phylogenetic-derived D_{pw} index showed similar values among cells belonging to the Brazilian coast and the Caribbean, with differences

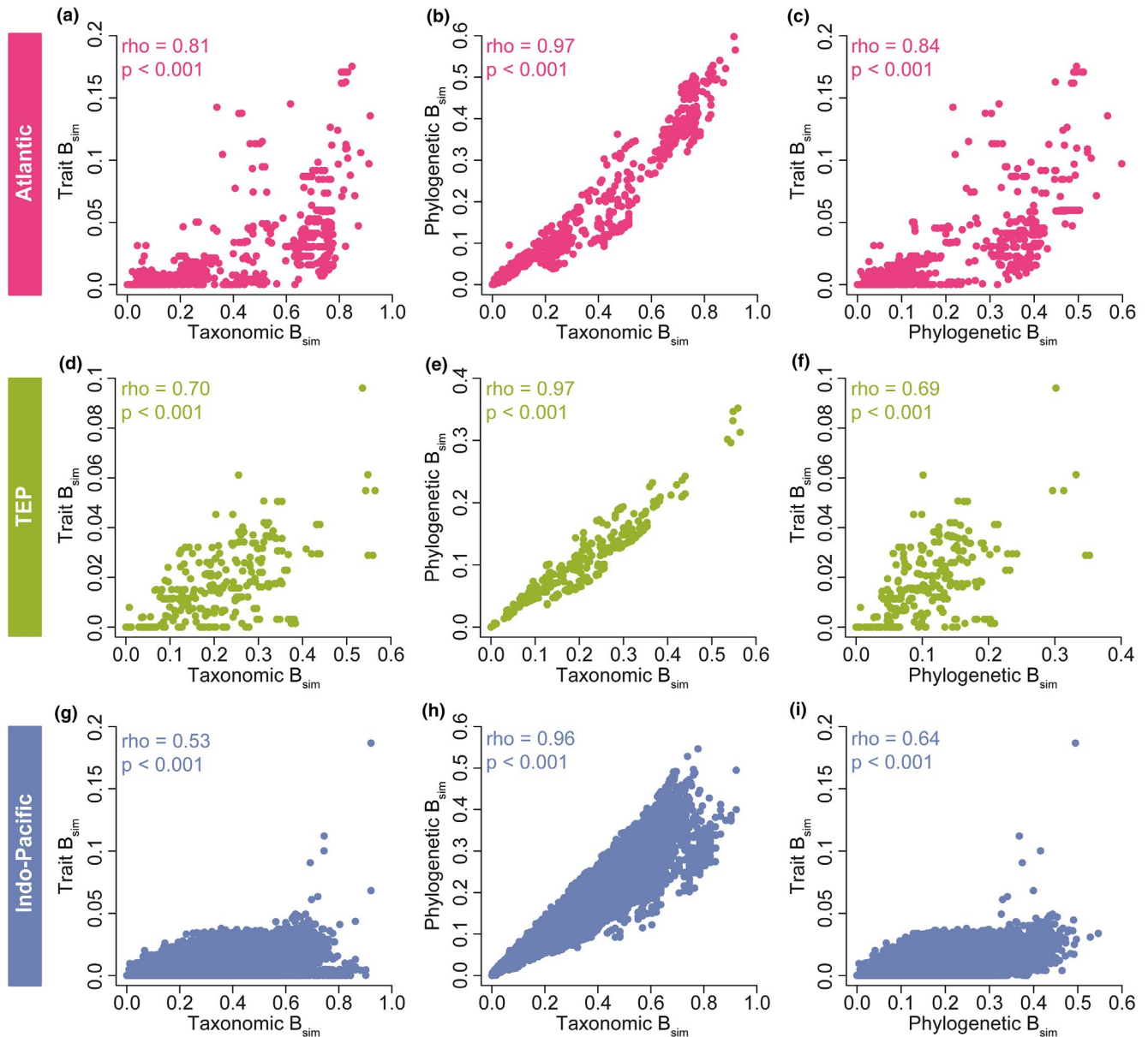


FIGURE 5 Results of Spearman's correlation tests between (a, d, g) taxonomic and trait turnover, (b, e, h) taxonomic and phylogenetic turnover, and (c, f, i) phylogenetic and trait turnover across the Atlantic, the Tropical Eastern Pacific (TEP) and the Indo-Pacific marine realms.

depicted between the Eastern Atlantic, the Western Atlantic and oceanic islands (Figure S5a). In contrast, reef fish assemblages of the Western and Eastern Atlantic and the Western Atlantic displayed similar trait composition according to the trait-derived D_{pw} (Figure S5b). In the TEP realm, reef fish assemblages of the Galápagos Islands and those of coastal areas did not show strong differences in their phylogenetic and trait composition, according to the phylogenetic and trait-derived D_{pw} indices respectively (Figure S5c,d). In the Indo-Pacific realm, the phylogenetic-derived D_{pw} index revealed a longitudinal gradient of phylogenetic beta diversity, but with a less clear distinction between the Western Indian, the Central Indo-Pacific and the Central Pacific regions (Figure S6a), as observed using the tip-weighted Sorensen's index and its turnover component

(Figure 3b). However, in contrast to the tip-weighted phylogenetic beta diversity metrics, the basal-weighted D_{pw} metric revealed a marked difference in the phylogenetic composition of reef assemblages of Hawaii within the Central Pacific region (Figure S6a). Then, the trait-derived D_{pw} index revealed a homogeneous spatial pattern of trait beta diversity (Figure S6b), as similarly observed using the tip-weighted Sorensen's index and its turnover component (Figure 3c).

Overall, across marine realms, spatial patterns of phylogenetic and trait D_{pw} were partly explained solely by contemporary (1.5%–15.8%) or historical variables (1.5%–15.7%; Figure S7). As well as observed for total beta diversity, there is a high contribution of unexplained inertia in CAP models performed to phylogenetic and trait D_{pw} (~68%–97%; Figure S7).



4 | DISCUSSION

Our study is the first effort to evaluate multiple facets (taxonomic, phylogenetic and trait) and components (turnover and nestedness) of beta diversity in the global tropical reef fish fauna, and to explore the relative importance of contemporary and historical variables in shaping the observed spatial patterns across regions.

4.1 | Beta diversity patterns

Whatever the approaches used (Baselga's approach or the D_{pw} index), trait beta diversity was found to be less related to taxonomic and phylogenetic beta diversity, respectively, with very low values, even between assemblages with contrasting species (and lineage) composition. This implies that the majority of traits are shared among tropical reef fish assemblages globally, as recently suggested by McLean et al. (2021) who identified a common backbone of species traits in the global reef fish fauna. Our finding is also not completely unexpected since the trait space filled by reef fish faunas is very similar across biogeographical regions (Mouillot et al., 2014). Furthermore, within regions, the trait composition of species-poor reef fish assemblages was found to be strongly nested within the trait composition of species-rich ones (Bender et al., 2017), which explain the weak turnover of traits among tropical reef fish assemblages (see Figure 1). Overall, the high level of trait similarity between tropical reef fish assemblages is probably the result of evolutionary convergence, where independent lineages display similar traits (and occupy similar ecological niches), or environmental filtering or both processes (Mazel et al., 2017; Rincon-Sandoval et al., 2020).

Large-scale patterns of phylogenetic beta diversity in tropical reef fishes can be related to the evolutionary history of clades in each marine realm (Bellwood et al., 2015; Cowman & Bellwood, 2013; Floeter et al., 2018; Siqueira et al., 2019). The use of tip-weighted metrics of phylogenetic beta diversity, and more especially the turnover component, revealed a high level of spatial congruence between the taxonomic and phylogenetic components of beta diversity. This suggests that the taxonomic composition of tropical reef fish assemblages varies in space due to a spatial turnover among recently diverged lineages (see Qian et al., 2021 for Angiosperms). This finding is consistent with the study of Leprieur, Descombes, et al. (2016) and Leprieur, Colosio, et al. (2016), who showed an overall pattern of clustering in the phylogenetic structure of tropical reef fish assemblages for three conspicuous tropical reef fish families (i.e. Labridae, Pomacentridae and Chaetodontidae), and more particularly when considering the nearest neighbour species in the phylogenies. According to this latter study, tropical reef fish assemblages tend to be composed of more phylogenetically close neighbour species than expected by chance, as a result of recent speciation events, such as those caused by the fragmentation of reef habitats during the climatic oscillations of the Pliocene (5.3 Mya). In contrast,

the use of a basal-weighted metric of phylogenetic beta diversity (D_{pw}) revealed a weak level of spatial congruence between the taxonomic and phylogenetic components of beta diversity (Figure S10e). This suggests that the present-day taxonomic composition of tropical reef fish assemblages does not bear the signature of ancient divergence events, which in contrast have shaped the composition of regional pools of tropical reef fishes globally (Cowman & Bellwood, 2013; Leprieur, Descombes, et al., 2016; Gaboriau et al., 2019). For example, in the Indo-Pacific realm, reef fish assemblages showed weak differences in their lineage composition according to the ' D_{pw} ' metric (Figure S6a), and more particularly in the Western Indian and the Central Indo-Pacific regions, which could be explained by plate tectonic events with the colonization of old lineages from the central Tethys to the IAA (Leprieur, Descombes, et al., 2016). The only exception is the unique tropical reef fish fauna of Hawaii (see Figure S6a), which is composed of both recent and ancient endemic lineages as a result of long-term isolation (Cowman et al., 2017; Gaboriau et al., 2018). Overall, this finding emphasizes the importance of using both tip-weighted and basal-weighted metrics of phylogenetic beta diversity to evaluate the extent to which the evolutionary history of clades left an imprint on contemporary diversity patterns (see also McFadden et al., 2019; Qian et al., 2020, 2021).

4.2 | Comparison among realms

In the Atlantic Ocean, spatial patterns of taxonomic and phylogenetic turnover are in line with current biogeographical regions (Floeter et al., 2008; Kulbicki et al., 2013), splitting this realm into Western and Eastern reef fish faunas. The observed patterns of taxonomic and phylogenetic turnover in the Atlantic support the role of geographical barriers to dispersal (i.e. the Mid-Atlantic Barrier, the Amazon and Orinoco rivers outflow and the Benguela Current), which were found to promote allopatric and/or parapatric speciation (Floeter et al., 2008; Luiz et al., 2012). The observed latitudinal gradient of taxonomic and phylogenetic turnover in the TEP can be explained by range size differences among closely related species (Mora & Robertson, 2005). Then, differences in the tropical reef fish faunas of oceanic islands relative to the coastal areas of the TEP, can be explained by the recent colonization of some species originating from the Indo-Pacific region (Robertson et al., 2004; Robertson & Cramer, 2009). Compared to the Atlantic and the TEP realms, the Indo-Pacific remained largely connected over evolutionary time, especially in the IAA where more extensive shallow-water habitats have been available since the Miocene (Cowman et al., 2017; Cowman & Bellwood, 2013). This connection may explain the low levels of taxonomic and phylogenetic turnover in the Central Indo-Pacific region. Also, this greater connectivity among reefs could explain the importance of nestedness to beta diversity patterns detected for conspicuous reef fish families (Chaetodontidae, Labridae and Pomacentridae) in this region (Leprieur, Descombes, et al., 2016; Mouillot et al., 2013). In contrast, the Hawaiian Archipelago and the

very isolated islands of Desventuradas Islands and Easter Island are characterized by more dissimilar reef fish faunas within the Central Pacific region, which could be related to high levels of endemism resulting from long-term isolation from the IAA (Allen, 2008; Dyer & Westneat, 2010; Kulbicki et al., 2013).

4.3 | Drivers of beta diversity

Our results suggest that historical contingency and past climate changes may partially explain the variation in reef fish beta diversity across tropical oceans. For instance the TEP is characterized by a strong isolation from other realms (Cowman et al., 2017; Robertson & Cramer, 2009), this realm having been connected with the Northwestern Atlantic until the closure of the Isthmus of Panama, approximately 3.1 million years ago (Coates & Obando, 1996). This event ceased reef fish dispersal between Atlantic and TEP faunas, deeply shaping the biogeography of such regions (Cowman et al., 2017; Floeter et al., 2008; Robertson & Cramer, 2009). In the Atlantic, the Caribbean hosts the greatest reef fish biodiversity in the Atlantic realm (Floeter et al., 2008; Polanco et al., 2020). The distance from the Caribbean largely influenced not only the functional (Bender et al., 2017) but also the taxonomic and phylogenetic structure of reef fish assemblages (Bender et al., 2013, 2017; Leprieur, Colosio, et al., 2016; Leprieur, Descombes, et al., 2016; Pinheiro et al., 2018). During the cold Quaternary periods, only limited areas of the Caribbean were suitable for coral reefs, limiting the refugia available to reef fish assemblages (Cowman & Bellwood, 2013; Pellissier et al., 2014). Distant from the Caribbean, extensive shallow-water areas of the IAA have served as a refuge to species during critical times (Bellwood et al., 2017). Today, areas close to the IAA have the greater reef fish diversity, highlighting the importance of stable reef areas for the maintenance of reef biodiversity over time (Pellissier et al., 2014). Together, these events shaped the regional species pool, which in its turn, is expected to influence beta diversity patterns at broad environmental gradients (Valdujo et al., 2013; Wiens & Donoghue, 2004).

Despite the importance of historical and contemporary factors in shaping current beta diversity patterns, it is important to highlight the high percentage of unexplained inertia, which suggests that observed dissimilarities in taxonomic, phylogenetic and trait reef fish composition could also be explained by other processes, such as dispersal limitation. Indeed, it is worth noting that we did not explicitly consider the influence of dispersal processes associated to plate tectonics, which were found to be major drivers of tropical reef fish diversity worldwide (Leprieur, Descombes, et al., 2016; Polanco et al., 2020). Indeed, the isolation from the biodiversity centres that we used as a proxy for the influence of plate tectonics does not integrate the impact of soft and hard barriers to dispersal as well as stepping stones processes. The integration of more developed dispersal-related variables in correlative approaches of beta diversity is challenging and merits future prospects.

4.4 | Potential limitations and perspectives

According to our expectations, we found that both historical and contemporary variables were important in shaping the current patterns of beta diversity across marine realms. However, a high unexplained inertia was found when performing CAP analyses, which imply that other processes (e.g. dispersal limitation) may be important in shaping beta diversity patterns in tropical reef fishes. Our findings could be potentially influenced by the spatial resolution adopted (i.e. reef fish assemblages), and it would be therefore important to explore to what extent a smaller resolution (e.g. community level based, for instance on underwater visual census data) may change our perception of patterns and processes shaping of beta diversity. Furthermore, we used a set of categorical traits expected to reflect the 'functional' role of species in tropical reefs, but analyses based on additional or more refined traits, with a strong functional significance (i.e. reflecting the role of tropical reef fishes in various ecosystem functions), are needed.

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CONFLICT OF INTEREST

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data used to perform phylogenetic analyses of our study were from Siqueira et al. (2020) and are available at the James Cook University's Tropical Data Hub repository (<https://doi.org/10.25903/5e9659dbca234>). Also, the remaining data and code have been deposited on Dryad Digital Repository (<https://doi.org/10.5061/dryad.4xgxd25bw>).

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BIOSKETCH

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Authors' contributions: Melina F. Maxwell, Mariana G. Bender and Fabien Leprieur conceived the ideas. Melina F. Maxwell and Fabien Leprieur analysed the data. All authors contributed to the writing and commented on the final draft.

SUPPORTING INFORMATION

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