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Biogeographic, historical and environmental influences on the taxonomic and functional structure of Atlantic reef fish assemblages

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ABSTRACT

Aim To disentangle how historic, biogeographic and environmental factors have shaped the composition of different reef fish assemblages, we analysed assemblage structure from a taxonomic (proportions of species from different families) and functional perspective (diet and body size).

Location Atlantic Ocean.

Methods The distributions of 1629 fish species were compiled for 31 locations across the Atlantic Ocean (39°66' N, 27°50' S). These locations provide a richness gradient ranging from 54 species in St Paul's Rocks to 474 in Cuba. We used cluster analyses to assess how historical and biogeographic factors have shaped the taxonomic and functional structure (i.e. the distribution of species within families, diet and body size groups) of assemblages. We then employed a constrained analysis of principal coordinates (CAP) to test the relative influence of the distance from the biodiversity centre in the Atlantic, sea surface temperature, isolation, coral species richness and area, and coastal length on the observed patterns of assemblage structure.

Results The taxonomic and functional structure of reef fish assemblages across the Atlantic exhibits a biogeographic fingerprint, with a marked discrimination between species-rich biogenic reefs (concentrated primarily in the Caribbean and composed of small species feeding on invertebrates) and poorer peripheral regions dominated by larger species with more diverse diets. The first CAP axis explains 87% of body size distribution in assemblages, showing that the effects of sea surface temperature and coral richness and those of isolation are antagonistic and can be embedded into a single dimension. Environmental factors, such as temperature and habitat complexity, explain the disproportionate number of small species in the Caribbean, whereas in the remaining regions the predominance of large-bodied fish increases with isolation due to high dispersal ability.

Main conclusions We found that historical events, which have shaped the biogeography of reef fishes, and environmental characteristics (coral reefs versus periphery) have both played a role in structuring the taxonomic and functional components of Atlantic fish assemblages.

Keywords

Assemblage structuring, Atlantic Ocean, body size, functional group, reef fish, taxonomic structure.

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INTRODUCTION

Evolutionary history and biogeography play an essential role in the assembly of regional species pools (Whittaker *et al.*, 2001; Bellwood & Wainwright, 2002; Scheiner *et al.*, 2011). While a number of historical processes – speciation, colonization, immigration, extinction – are known to shape regional species pools (Ricklefs, 1987; Hortal *et al.*, 2012), there is major interest in understanding which factors structure the species assemblages at finer scales (Hortal *et al.*, 2012). Ultimately, an understanding of the different processes underpinning the structure of species assemblages can improve the predictions of their trajectories under global change scenarios (Cavender-Bares *et al.*, 2009; Götzenberger *et al.*, 2012). Thus, the question is no longer to determine which process shapes the structure of species assemblages, but to disentangle and assess the relative influence of these different processes at any given scale.

This question is even more challenging because the structure of species assemblages encompasses multiple components (taxonomic, functional, phylogenetic) (Devictor *et al.*, 2010; Mouillot *et al.*, 2011) that may respond differently to each process (Meynard *et al.*, 2011). Most of the research on the structure of marine assemblages has focused on patterns of species richness (e.g. Bellwood & Hughes, 2001), yet there is evidence that the structure of functional traits within assemblages determines ecosystem functioning (Fisher *et al.*, 2010). For instance, body size distribution within fish assemblages drives the structure of trophic interactions (Jennings *et al.*, 2001) and the responses of fish to exploitation (Reynolds *et al.*, 2005). Thus, assessing the functional component of species assemblages and identifying the processes underlying their structure can improve our knowledge of ecosystem functioning under ever-increasing multiple threats (Halpern *et al.*, 2008). The integration of this component into our understanding of

biodiversity patterns has been a major step forward in biogeography (Stevens *et al.*, 2003; Safi *et al.*, 2011; Münkemüller *et al.*, 2012), but there are still few applications to marine assemblages over large scales (but see Bellwood *et al.*, 2002; Halpern & Floeter, 2008).

The reef fish fauna is recognized as one of the most diverse vertebrate assemblages on Earth (Bellwood & Wainwright, 2002), encompassing over 6000 species that occur in all tropical and subtropical biogeographic provinces (Briggs, 1974; Bellwood & Wainwright, 2002; Floeter *et al.*, 2008; Parravicini *et al.*, 2013). This diversity of species and ecological attributes provides ecosystem services to millions of people (Sadovy, 2005). It is thus important to understand the structure of reef fish assemblages, not only taxonomically but also in terms of the functional characteristics that govern how the ecosystem works (Fisher *et al.*, 2010; Mora *et al.*, 2011). Bellwood & Hughes (2001) have already identified remarkably consistent proportions in the taxonomic composition of reef fish and coral assemblages across a richness gradient in the Indo-Pacific Ocean. Furthermore, reef fish traits (e.g. fin shape in Labridae species) showed common assembly rules between regions (the Great Barrier Reef, French Polynesia and the Caribbean) despite differences in species composition (Bellwood *et al.*, 2002). However, relatively little is known about the extent to which these patterns hold in other oceans or with other traits such as diet or body size. More specifically, to the best of our knowledge, no study to date has carried out a comprehensive comparison of the functional structure of reef fish assemblages across a large set of conditions (biogeographic, environmental and historical).

The well-established biogeography and evolutionary history of reef fishes in the Atlantic (Briggs, 1974; Floeter *et al.*, 2008) provides a relevant context for addressing three possible scenarios shaping reef fish assemblages (Fig. 1). Our main goal was to understand the role of historical, biogeographic and environ-

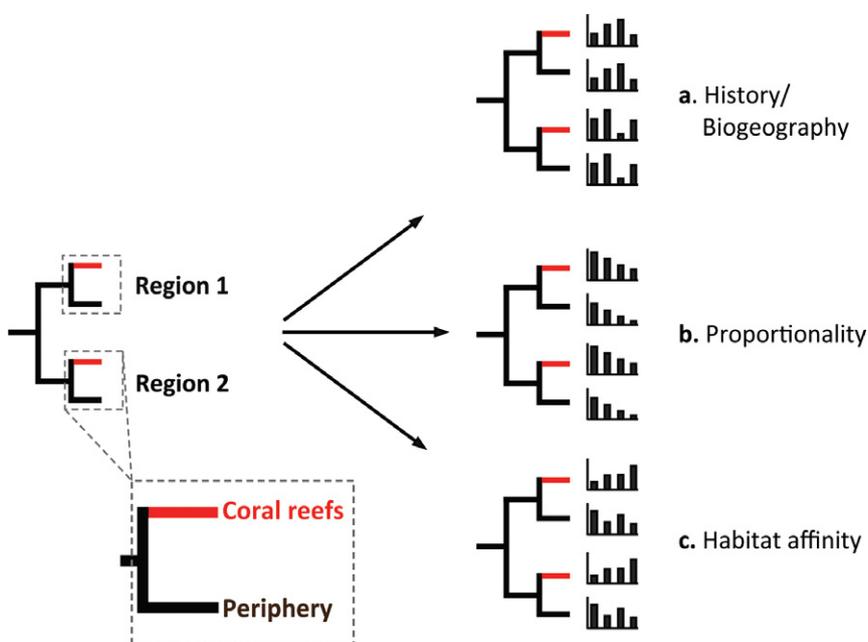
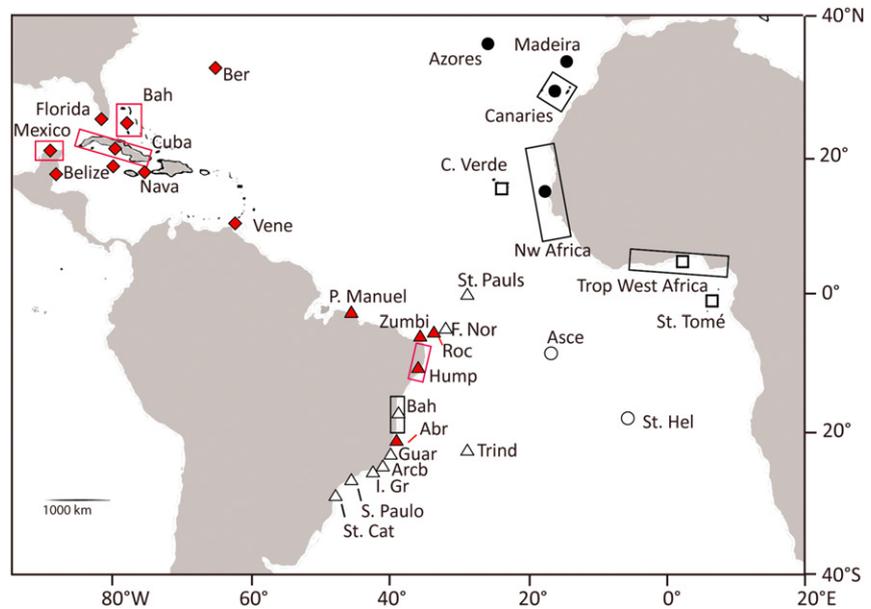


Figure 1 Scenarios on the role of history, biogeography and environmental factors in the distribution of fish richness within groups (taxonomic-, trophic- or size-based) across the Atlantic Ocean. In scenario (a), history and biogeography shape the proportions of fish richness within groups. The structure of assemblages is similar within regions independent of habitat (coral reefs or periphery habitats). Under scenario (b), proportions of fish richness within groups are remarkably similar across regions and habitats. In scenario (c), habitat affinity (coral reef versus periphery) shapes the distribution of fish richness within groups independently of regions (see the Introduction for a complete explanation of the hypotheses). Red branches represent biogenic reefs and black ones peripheral reefs.

Figure 2 Thirty-one Atlantic locations where presence–absence data were collected for fish species. Symbols indicate regions within the Atlantic Province (*sensu* Floeter *et al.*, 2008): ◆, north-western Atlantic; △, south-western Atlantic; ○, Ascension and St Helena; ●, north-eastern Atlantic; □, tropical eastern Atlantic. Red symbols represent locations where biogenic reefs predominate.



mental factors in the assembly patterns of three components of reef fish biodiversity: families, trophic groups and body-size categories. We propose three scenarios (Fig. 1) in which history, biogeography and environment may have shaped the distribution of species richness within a given group (taxonomic, trophic or size-based). First, the structure of fish assemblages (the proportions of species within a group) differs between regions, reflecting the large influence of evolutionary history and biogeography (Fig. 1a). Second, structures are remarkably similar across fish assemblages in different regions, despite various histories and environments (Fig. 1b). This scenario follows the pattern described by Bellwood & Hughes (2001) for both coral and reef fish families across the Indo-Pacific. Under the third scenario, habitat affinity (coral reef versus periphery) dictates the structure of fish assemblages, despite different evolutionary histories across biogeographic regions (Fig. 1c). Fish assemblages differ substantially across Atlantic locations, ranging from poor assemblages in isolated rocky reefs to species-rich assemblages in coral reefs located in the Caribbean. Coral reefs offer a range of habitats in warm tropical shallow waters that have remained stable over geological time; hence they are considered the main drivers of diversification in reef fishes (Cowman & Bellwood, 2011). The shift from coral reefs to non-coral peripheral environments may thus have a deep influence on the structure of reef fish assemblages, changing the prevalence of certain families and functional groups. For instance, differences in the body size structure of assemblages can be related to size-dependent dispersal or ecological filtering as resources decrease towards poor environments; whereas increased richness of fish species feeding on relatively low-quality food in the tropics (Harmelin-Vivien, 2002; Floeter *et al.*, 2004) could lead to differences in the trophic structure of assemblages. We tested these different scenarios by compiling the distribution of fish species within families, body size

categories and trophic groups across the Atlantic and by examining the potential effect, if any, of historical, biogeographic and environmental factors on these structures.

METHODS

Dataset

We analysed the most comprehensive dataset on the distribution of Atlantic reef fishes to date (Floeter *et al.*, 2008; Halpern & Floeter, 2008), which was based on the occurrence records from species checklists of 31 locations throughout the Atlantic Ocean (Fig. 2). Selected locations refer to the best checklists available for well-documented reefs. The entire dataset includes records of 1629 species from 465 genera and 69 families. 'Reef fishes' were defined as a group that includes any shallow (< 100 m) tropical or subtropical benthic or benthopelagic fish species that consistently associates with hard substrates of coral, algal or rocky 'reefs' or occupies an adjacent sand substrate (Floeter *et al.*, 2008). Biogenic reefs, here referred to as coral reefs for simplicity, are those constructed by large, heavily calcified organisms, mainly corals and coralline algae (Wood, 1999).

We categorized species into trophic groups based mainly on Ferreira *et al.* (2004), resulting in seven groups as follows: herbivores, macrocarnivores, mobile invertebrate feeders, omnivores, piscivores, planktivores and sessile invertebrate feeders. The herbivores are those species that feed on macroalgae, seagrass, filamentous algae and associated detritus, i.e. undefined organic material. Piscivores feed primarily on fish. Macrocarnivores eat a variety of large mobile organisms, including crustaceans and fish. The diet of mobile invertebrate feeders consists primarily of small benthic invertebrates (e.g. small crustaceans, molluscs, worms, etc.), while sessile invertebrate feeders consume cnidarians, hydrozoans, bryozoans, ascidians and

sponges. Omnivores eat both animal and plant material in various proportions. Finally, planktivores feed primarily on macro- and microzooplankton.

Reef fish species were also classified into body size categories since this trait is a surrogate for many others (Dumay *et al.*, 2004) and underlies many ecosystems processes (Fisher *et al.*, 2010). We defined four maximum body size categories, based on total length, as follows: small, medium–small, medium and large (< 10, 10–25, 25–50, > 50 cm, respectively; see Halpern & Floeter, 2008 for details).

Data analyses

To understand how historical, biogeographic and environmental factors have shaped the structure of reef fish assemblages across the Atlantic, we focused on taxonomic (family), trophic and body size structures (see our three hypotheses in Fig. 1). We first assessed the distribution of species within families, body size categories and trophic groups for each of the 31 reef fish assemblages. We then performed cluster analyses to classify the 31 locations based on the proportion of fish species within 69 families, four body size categories and seven trophic groups using the Bray–Curtis dissimilarity index and a complete linkage method (Borcard *et al.*, 2008). *P*-values for cluster nodes (AU, approximately unbiased) were calculated using bootstrap resampling (1000 replicates) (Pvclust package in R software) to assess their reliability.

Since the taxonomic structure of assemblages, based on species membership to a given family, may influence the functional structure thanks to phylogenetic trait conservatism (Mouquet *et al.*, 2012), we tested whether closely related fish assemblages, on the basis of their taxonomic structure, were also functionally more similar. To this end, we implemented Mantel tests between pairs of dissimilarity matrices: family versus trophic categories; family versus body size categories; and trophic versus body size categories.

Second, we performed a constrained analysis of principal coordinates (CAP) (Anderson & Willis, 2003) of data on proportions of species to assess the relative influence of environmental and biogeographic factors on the structure of reef fish assemblages, using the Bray–Curtis distance between pairs of locations (Legendre & Legendre, 1998). Assemblage data were previously transformed using the Hellinger distance (Legendre

& Gallagher, 2001). Variations between locations in the observed proportions of species richness within families, trophic groups and body size categories were contrasted with the following explanatory variables: the distance from the biodiversity centre, sea surface temperature (SST), isolation (distance from the mainland in kilometres), coral species richness, coral area (km²) and coastal length (km). The distance from the reef fish biodiversity centre in the Atlantic Ocean, which corresponds to the Caribbean (474 species recorded in Cuba, 22° N 77° W) (Claro & Parenti, 2001; Briggs, 2003; Floeter *et al.*, 2008), was measured in degrees. The average SST for each location was obtained from BIO-oracle (Tyberghein *et al.*, 2012). For each checklist we defined, according to maps and descriptions in the original publications, the area to which the species list pertains, thereby allowing the computation of the coral reef surface and the coastline to which each checklist was referred. Coral reef area derives from the Millennium Coral Reef Mapping Project (UNEP-WCMC, 2012). All this information was converted to a Behrmann equal-area projection before analysis. All data analyses were performed using the software R 2.14.2 (R Core Team, 2012), and packages ‘Vegan’ version 2.0–2 (Oksanen *et al.*, 2011) and ‘Pvclust’ version 1.2-2 (Suzuki, 2011).

RESULTS

The relationships between locations based on the proportions of species within the 69 families reveal the influence of species geographic distributions: the eastern and western Atlantic are separated and, in the western portion, the Caribbean and the Brazilian coast with its oceanic islands form two distinct branches, the north-western and south-western Atlantic, respectively (Fig. 3). The only exception to that global pattern is the Brazilian oceanic island of St Paul’s Rocks, which is grouped with the islands of St Helena and Ascension. The proportions of the 10 most species-rich families differ greatly between assemblages: Serranidae, Labrisomidae and Gobiidae species dominate in Caribbean assemblages, while the Carangidae family has the highest proportion of species in St Paul’s Rocks, St Helena and Ascension. In the eastern Atlantic, the proportions of Bleniidae, Sparidae and Scorpaenidae species are higher when compared with those of the western Atlantic (Fig. 3, see histograms).

Figure 3 Cluster analyses (Bray–Curtis; complete linkage) summarize the relationship among Atlantic reef fish assemblages based on (from left to right) the taxonomic, body size and trophic group structure (bottom). Histograms represent the proportion of species in: (1) the 10 most species-rich Atlantic reef fish families; (2) the four maximum body-size categories and (3) the seven diet categories. Values at cluster nodes correspond to approximately unbiased (AU) *P*-values (%) supported by bootstrap (1000 replicates). For the sake of simplicity, histograms grouped locations within cluster nodes exhibiting AU values > 70. Elements coloured in red refer to locations of biogenic reefs. Symbols indicate regions within the Atlantic Province (*sensu* Floeter *et al.*, 2008). Families: SERR, Serranidae; GOBI, Gobiidae; LABS, Labrisomidae; LABR, Labridae; CARA, Carangidae; CHAE, Chaenopsidae; SYNG, Syngnathidae; SCOR, Scorpaenidae; SPAR, Sparidae; BLEN, Bleniidae. Trophic groups: MINV, mobile invertebrate feeders; PLANK, planktivores; MCAR, macrocarnivores; HERB, herbivores; PISC, piscivores; OMNI, omnivores; SINV, sessile invertebrate feeders. Body size categories: SMALL, small; MSMALL, medium–small; MED, medium; LARG, large (< 10, 10–25, 25–50, > 50 cm, respectively).

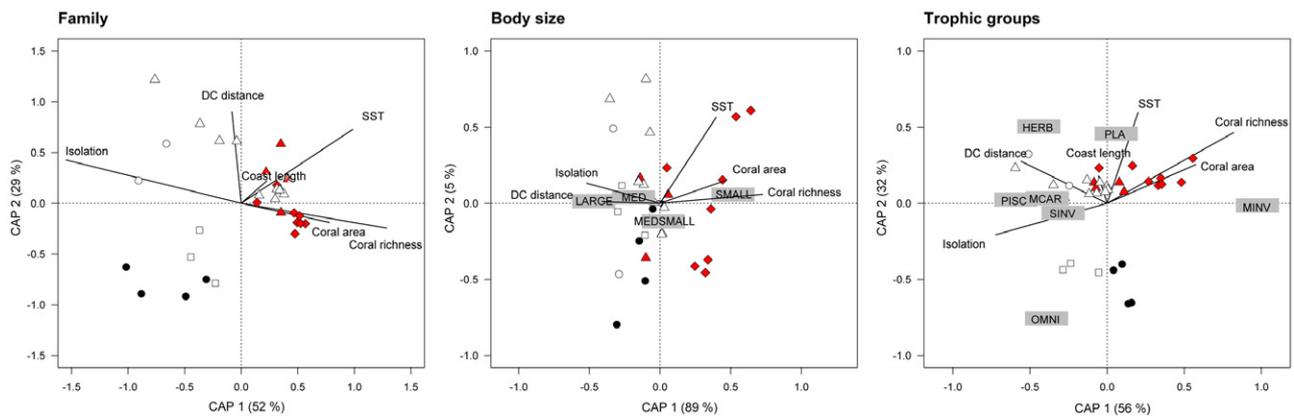


Figure 4 Biplots of constrained analyses of principal coordinates (CAP) explaining the proportions of species within (a) families, (b) body size categories and (c) trophic groups in 31 Atlantic reef fish assemblages as a function of biogeographic and environmental factors. Symbols indicate regions within the Atlantic Province (*sensu* Floeter *et al.*, 2008): \blacklozenge , north-western Atlantic; \blacktriangle , south-western Atlantic; \circ , Ascension and St Helena; \bullet , north-eastern Atlantic; \square , tropical eastern Atlantic. Red symbols represent locations of biogenic reefs. DC distance, distance from the diversity centre; SST, sea surface temperature. Abbreviations for body size and trophic groups are the same as those in the caption to Fig. 3.

The relationships among locations based on the proportions of species within body size categories reveal a different pattern from that found for the taxonomic composition (Fig. 3) with a weaker influence of biogeography, since locations that belong to different biogeographic regions can be in the same clusters, e.g. the Canaries (north-eastern Atlantic) along with São Paulo and Bahia (south-western Atlantic); Bermuda (north-western Atlantic) grouped with Espírito Santo (south-western Atlantic); and the Azores (north-eastern Atlantic) with St Helena (Mid-Atlantic Ridge). Overall there is discrimination between most of the Caribbean locations at the top of the cluster, forming one group, and a second group that includes the remaining 24 locations. Histograms (Fig. 3; body size categories) show that in Caribbean assemblages there is a large proportion of small-bodied species, the opposite pattern to that exhibited at Cape Verde, São Tomé and St Paul's Rocks.

For trophic categories, the cluster analysis reveals that most locations of biogenic reef formation, including Arolhos reefs and the Hump of Brazil, are grouped in the south-western Atlantic (Fig. 3). In those assemblages, there is a large proportion of mobile invertebrate feeder species compared with other trophic categories (see histograms in Fig. 3). The islands of Ascension and St Paul's Rocks form a clearly separated group, possibly an outcome of the equitable distribution of species within trophic categories and the increased proportion of macrocarnivorous species, compared with other assemblages. Tropical eastern Atlantic and north-eastern Atlantic locations form one separate group, where the proportion of omnivorous species is greater than in other locations. Bermuda, a site of coral reef formation, is grouped with sites of the Brazilian coast (south-western Atlantic).

The taxonomic dissimilarity between pairs of reef fish assemblages was positively correlated with both the trophic dissimilarity (Mantel test $r=0.73$; $P<0.001$) and the body size dissimilarity (Mantel test $r=0.58$; $P<0.001$), indicating a

strong influence of phylogeny on these ecological traits. Moreover, trophic and body size dissimilarities between reef fish assemblages are also positively correlated (Mantel test $r=0.61$; $P<0.001$).

Among the examined variables that may explain the patterns of dissimilarity among reef fish assemblages, SST and coral species richness play an important role, be it on taxonomic, trophic or body size structure (Fig. 4). Since coral richness and coral reef area were positively correlated (Appendix S1 in Supporting Information), relationships between these variables and the structure of reef fish assemblages can be an outcome of any of these variables, or a combination thereof. Coral richness was negatively correlated with the distance from the biodiversity centre; thus these variables have antagonistic effects on the structure of certain components of reef fish assemblages. The distance from the biodiversity centre and isolation are also significant terms in the CAP analysis, explaining variation of trophic and taxonomic structure among fish assemblages. Isolation influences the taxonomic structure of fish assemblages with high proportions of Muraenidae and Carangidae species in the oceanic islands of St Helena and Ascension in the Mid-Atlantic Ridge; whereas coral species richness was related to higher proportions of Chaenopsidae and Labrisomidae as in north-western Atlantic locations (Fig. 4).

For trophic groups and body size categories, results are very consistent with the taxonomic analysis. In all cases, the first coordinate discriminates the antagonistic effects of SST, coral reef area and richness on the one hand, and isolation and distance from the biodiversity centre on the other. This coordinate alone explains more than 50% of the variation in all analyses, and accounts for 89% of all the variation in body size structure observed across assemblages (Fig. 4). Consequently, for body size these antagonistic effects can be embedded into a single dimension that clearly discriminates rocky from biogenic reefs (Figs. 3 & 4). For trophic categories the pattern is qualitatively

similar, but in this case the variation across assemblages could not be embedded into a single dimension as with body size (Fig. 4). Nonetheless, the first coordinate, explaining 56% of the total variation, discriminates those assemblages in which mobile invertebrate feeders prevail and those in which the contribution of piscivores, herbivores or omnivores is proportionally higher. The second coordinate, accounting for 32% of the variation in trophic structure unravels the overall contribution of herbivores to assemblages (Fig. 4).

DISCUSSION

Our results indicate that the taxonomic structure of Atlantic reef fish assemblages varies among locations, reflecting both historic and biogeographic influences (Floeter *et al.*, 2008). This heterogeneous pattern is not concordant with the scenario based on assembly rules identified for reef fish families in the Indo-Pacific (Bellwood & Hughes, 2001) (Fig. 1b). In fish assemblages of the Indo-Pacific, Bellwood & Hughes (2001) identified a relatively constant taxonomic membership and highly correlated family species richness (mean of $r = 0.83$). In the Atlantic, similar analysis revealed considerably lower correlation values between family richness across assemblages ($r = 0.43 \pm 0.3$), which means that the patterns of taxonomic composition are not homogeneous (Appendix S2). The absence of generality in this pattern between oceans may be explained by: (1) the independent evolutionary history of the Atlantic compared with the Indo-Pacific (Floeter *et al.*, 2008; Renema *et al.*, 2008; Cowman & Bellwood, 2013), (2) different habitat availability through time (Bellwood & Wainwright, 2002; Cowman & Bellwood, 2013), (3) the differences between coral and rocky reefs, and (4) the influence of strong biogeographic barriers in the Atlantic (Floeter *et al.*, 2008; Luiz *et al.*, 2012). The Indo-Pacific is characterized by an extensive shallow-water geological complexity (Bellwood & Wainwright, 2002) that promoted species survival, origination and range extension, enhancing diversification (Cowman & Bellwood, 2013). Moreover, this diversity has remained connected over time due to the availability of increased shallow-water areas and the existence of fewer barriers in the Indo-Pacific than in the Atlantic Ocean (Floeter *et al.*, 2008; Bellwood *et al.*, 2012; Mora *et al.*, 2012).

By contrast, a number of historical events have deeply influenced the Atlantic reef fish fauna in the last 50 million years (Eocene) (Budd, 2000; Floeter *et al.*, 2008), including extinctions, the closure of the Isthmus of Panama (Bermingham *et al.*, 1997; Floeter *et al.*, 2008) and Pleistocene glaciations; the latter caused severe reductions in the shallow-water habitat available for the reef biota (Bellwood & Wainwright, 2002). The greater availability of shallow-water habitat in the Caribbean compared with other areas in the Atlantic made this region the centre of fish and coral biodiversity in the Atlantic Ocean (Briggs, 2003; Floeter *et al.*, 2008). The shared history of the coral and fish faunas might explain the role of reef isolation and coral species richness as filters to fish richness for some families of Atlantic reef fishes. The families Gobiidae, Labrisomidae and Chaenopsidae, having small cryptobenthic fish, have far more species in

the Caribbean region than elsewhere in the Atlantic (Floeter *et al.*, 2008). This may be attributed to limited dispersal abilities, leading to high rates of diversification within those families (Munday & Jones, 1998). Isolation, on the other hand, might have favoured higher proportions of Carangidae and Muraenidae species in Mid-Atlantic Ridge assemblages (Ascension and St Helena). Muraenidae species are pelagic spawners with long pelagic larval durations (Victor, 1991), while Carangidae species are rafters – they raft with floating debris in the open sea (Luiz *et al.*, 2012). These traits improve species dispersal potential across long distances (Thiel & Gutow, 2005; Luiz *et al.*, 2012). Although the Caribbean is the region of the Atlantic Ocean that most resembles the Indo-Pacific with respect to shallow biogenic habitats and connectivity, evolutionary history and diversity patterns are different between these regions, explaining the differences in the proportions of various families.

The effects of biogeography are also reflected in the body size structure of fish assemblages, with cluster analyses and CAP discriminating the Caribbean from any other location (Fig. 3). This pattern is mainly due to the large proportions of small-bodied species in the Caribbean, which reaches up to 42% in the Bahamas and 45% in Belize. The structural complexity and niche availability of coral reef habitats combined with the short life cycles of small-bodied fish species have facilitated the diversification of Gobiidae, Labrisomidae and Chaenopsidae in the Caribbean (Munday & Jones, 1998; Floeter *et al.*, 2008). On the other hand, large-bodied species not only have greater potential to colonize new habitats, but also to expand their ranges across dispersal barriers (Luiz *et al.*, 2012). This seems a plausible explanation for the high proportions of large-bodied species (> 50 cm) – reaching up to 40% – in isolated locations such as St Paul's Rocks, São Tomé and Cape Verde. It is also possible that small migrants which eventually reach these locations cannot sustain viable populations in such poor environments and environmental filtering is taking place, as suggested by the patterns found for trophic groups.

Reef type has a large influence on the trophic structure of Atlantic reef fish assemblages, as demonstrated by the close relationship between locations of biogenic reef formation and non-biogenic ones (see Fig. 3). This assembly pattern is in accordance with the habitat affinity scenario (Fig. 1c). The distinction of locations characterized by biogenic reefs is partly driven by the high proportion of mobile invertebrate feeders, encapsulated in the first coordinate of the CAP analysis (Fig. 4). The diversity and abundance of mobile invertebrates in reef ecosystems is favoured by the complexity and productivity of coral reefs, which sustain a high diversity of fish feeding on such prey, as in the Indo-Pacific (Bellwood *et al.*, 2006). This richness of mobile invertebrate feeders is logically related to the high proportion of small-bodied species, and the richness of Gobiidae and Chaenopsidae families in the Caribbean (Floeter *et al.*, 2008).

The second CAP coordinate discriminates trophic groups across the eastern and western Atlantic (Fig. 4), with omnivores prevailing in the former while herbivores and planktivores dominate in the latter. CAP analyses suggest that differences in SST might partly explain this pattern, which is supported by

previous evidence (Floeter *et al.*, 2004, 2005) and illustrates why the latitudinal and thermal range of the Atlantic makes this biogeographic province truly unique as a system for studying the impact of environmental conditions on the functional structure of marine communities. The adaptation of herbivores to the use of relatively low-energy food resources (e.g. algae, detritus, coral) combined with the high availability of such resources in the tropics (lower latitudes and warm waters) has boosted speciation rates in this trophic group (Harmelin-Vivien, 2002). By contrast, in colder peripheral locations, most fish need to exploit higher-energy resources associated with animal protein; in order to fulfil the metabolic needs associated with inhabiting these environments (Floeter *et al.*, 2004). This metabolic constraint associated with historical environmental disturbances of these locations may have favoured the diversification of omnivores (Ferreira *et al.*, 2004). Omnivores in the eastern Atlantic belong mainly to the Sparidae and Blenniidae families, which are particularly diverse in that region (Floeter *et al.*, 2008).

We find that, overall, biogeographic and environmental variables exert combined high influences on the taxonomic and functional structure components of Atlantic reef fish assemblages. Small invertebrate feeders prevail in the warm waters of the Caribbean, whereas larger species consuming other trophic items dominate elsewhere. This footprint of biogeography in the structure of assemblages has also been shown through the importance of large-scale processes on boreal lake fish assemblages (Van Zyll de Jong *et al.*, 2004), the geographic patterns of habitat use in emydid turtle communities (Stephens & Wiens, 2009) and the phylogenetic structure of palm species assemblages (Kissling *et al.*, 2012). The identification of different levels of influence in those components enables a better understanding of the forces determining assemblage structures and how they may vary along richness gradients. This is especially important given the rapid changes that marine ecosystems are experiencing, such as erosion of biodiversity (Jackson *et al.*, 2001; Bellwood *et al.*, 2004; Worm *et al.*, 2006). The subsequent loss of key functional groups of reef fishes and trait diversity in assemblages might seriously compromise the functioning of reef ecosystems and the provision of services.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Pair-wise correlation values between environmental variables considered in our constrained analyses of principal coordinates.

Appendix S2 Pair-wise correlation coefficients between family richness across reef fish assemblages of the Atlantic Ocean.

BIOSKETCH

Mariana Bender is interested in macroecology, biogeography, community assembly rules and the conservation of reef fishes.

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