Functional richness and turnover patterns reveal assembly rules structuring marine fish communities on the continental shelf of French Guiana

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ABSTRACT: The presence and coexistence of species in a community depend on their abilities to survive and to maintain their fitness in a given environment. Determining how assembly processes structure communities across scales, also called 'assembly rules,' is still a subject of debate. These mechanisms are related to biotic and abiotic factors. At local scales, they are represented by 2 main assumptions: the limiting similarity hypothesis (interspecific competition) and the niche or environmental filtering hypothesis. At regional scales, dispersal limitation and environmental filtering are assumed to be the 2 main processes explaining the community assembly patterns. We tested these hypotheses using the trait-based approach and functional relationships between species in fish communities from the continental shelf of French Guiana. This study was based on 2 scientific surveys conducted in November 2016 and 2017 at 33 stations by bottom trawling. At the local scale, i.e. a single haul, co-existing species tended to be more functionally closely related than what would be expected randomly, indicating a dominant influence of environmental filters over interspecific competition. These observations revealed assemblages composed of species showing similar ecological functions and, thus, high functional redundancies. At the regional scale, i.e. the study area, comparisons between pairs of stations showed that species replacements (taxonomic turnover) between local assemblages corresponded to random variations while functional profile replacements (functional turnover) tended to be higher than random expectations. Results suggest that abiotic characteristics of habitats have a stronger effect on fish community assembly at local and regional scales than biotic interactions.

KEY WORDS: Community assembly · Environmental filtering · Tropical fish · Functional diversity · Traits · α-diversity · β-diversity · French Guiana

1. INTRODUCTION

Understanding the distribution and the composition of biodiversity in ecosystems is a great challenge in community ecology (Sutherland et al. 2013). One of the most fundamental issues is to explain how biological communities are assembled and what controls biodiversity patterns across scales (Mouillot et al. 2013c). Changes in species distribution are still a crucial question in biological community studies. Knowing what controls biodiversity patterns and how local assemblages are structured from species' regional pools remains an outstanding issue that has generated more than a century of debates among ecologists (Clements 1916, Gleason 1926, Macarthur & Levins 1967, Pacala & Tilman 1994, Hubbell 2001, Lortie et al. 2004, Cadotte & Tucker 2017). These debates have led to the establishment of 2 main eco-

logical theories: the spatial-based neutral theory and the niche-based deterministic process theory. The former considers that demographic stochasticity and migration processes are the major processes structuring observed biodiversity patterns (Hubbell 2001), whereas the latter assumes that biotic and abiotic parameters play key roles in generating differences and controlling intra- and interspecific interaction strengths, and hence, act as assembly rules that govern species assemblages (Macarthur & Levins 1967, Diamond 1975). From a neutral theory perspective, the coexistence of species is possible assuming a constant species flow into the community, whereas a niche-based theory would assume that it is controlled by the strength of species' niche overlap. Both processes can co-occur in a system at different scales in various ways as extremities of a continuum and have been widely used to explain community assembly patterns (Whittaker et al. 2001, Gravel et al. 2006). The relative importance of each hypothesis in controlling community dynamics in a system remains complex to test, and as we lack information on species dispersal capabilities, we will focus more on niche processes in our study.

The most striking and well-established biodiversity pattern is probably the latitudinal gradient observed at the global scale that describes the decrease in α- and β-diversity with increasing latitude from the equator to the poles (Rohde 1992, Willig et al. 2003, Kraft et al. 2011). However, at finer scales, these processes are more complex to describe. At the local scale, the presence of species in an ecosystem depends on their capacities to survive and, thus, to maintain their fitness in their own ecological niche (Drake 1990). Species' co-existence in a given environment could be regulated by both abiotic filters and biotic interactions acting simultaneously (Mouillot et al. 2007). On the one hand, abiotic control, also known as the 'niche or environmental filtering' hypothesis, acts as a sieve on the presence of certain combinations of functional traits and allows only a certain spectrum of species to survive. This hypothesis assumes that co-existing species are likely to share most similar ecological and functional characteristics, as they respond to the same environmental filters (Keddy 1992, Violle et al. 2007). Thus, in the case of a dominant abiotic control, the functional diversity will be relatively low and assemblages will be composed of functionally closely related species, thereby increasing functional redundancy, i.e. the number of different species that exhibit similar ecological functions (Walker 1992, Guillemot et al. 2011). On the other hand, biotic control, also called the 'lim-

iting similarity' hypothesis, considers that interspecific competition prevents the co-existence of species with similar ecological niches (Macarthur & Levins 1967). As competition is greater between species sharing many ecological and functional characteristics, a dominant biotic control will result in a community with the most dissimilar and complementary species and will be functionally diverse (Mouillot et al. 2007). Therefore, the stronger the competition between species, the higher is the functional diversity and the co-existence of complementary species. Inversely, the stronger the environmental filtering, the lower is the functional diversity and the higher is the co-existence of functionally redundant species. At the regional scale, environmental filtering and dispersal limitation are assumed to be the 2 dominant processes explaining community assembly patterns (Nekola & White 1999, Kraft et al. 2011, Myers et al. 2013). By using the theoretical framework proposed by Cilleros et al. 2016), the relative influences of these structuring processes can be described by the study of β-diversity patterns and more precisely by the correlation between taxonomic and functional turnovers between pairs of species assemblages.

Functional diversity has already been used to reveal assembly processes structuring fish communities at local scales (Mouillot et al. 2007) and at regional scales (Mouillot et al. 2007, Pecuchet et al. 2016, Cilleros et al. 2016) but never at both scales in the same study. Functional diversity represents the range of species' ecological strategies (Violle et al. 2007) and, thus, the niche availability in habitats (Mouillot et al. 2013a). Here we used a trait-based approach which provides information regarding ecological processes inferred from any measurable morphological, physiological and phenological trait that affects individual performance, e.g. growth, reproduction and survival (Violle et al. 2007, Mouchet et al. 2010). Fish functional traits have already revealed ecological mechanisms underlying community structure with the use of null models (Mason et al. 2007, 2008). Currently, functional diversity is probably the best means with which to understand biological community structure and functioning.

The present work aims to describe the relative influences of the main processes structuring tropical fish communities from the French Guiana shelf at both local and regional scales to better understand their community structure. The continental shelf of French Guiana has undergone important variations in its habitats and exploitation over the last 3 decades. The shrimp fishery began to decrease in the mid-1980s, while the mean sea surface temperature

of its coastal waters has increased by more than 1°C since 1990 (V. Vallée et al. unpubl.) Hence, the need to better understand its fish community structure in a changing environment is pressing. To this aim, the relationship between functional and taxonomic diversity combined with null models was employed. Null models were used to generate random associations from observed communities in order to highlight assembly rules. The identification and understanding of these ecological community assembly processes is a crucial key to understand ecosystem functioning. These processes are often not considered in fisheries models despite their potential impacts on altering fish stock dynamics, abundance and composition, as well as their importance in the regulation of fish populations. Tropical marine communities will probably be the most severely affected by biodiversity losses in the next decades due to potential local extinction of less thermally resilient species following climate change leading to poleward migrations of tropical species (Worm et al. 2006, Cheung et al. 2009). Our study can provide community- and population-level information on ecological processes that may be useful to understanding how anthropogenic-linked changes can affect fish stocks for future management of such high biodiversity systems. Hence, a better understanding of tropical fish community assembly and functioning is essential for future sustainable management of such threatened ecosystems. The challenge is to provide useful information to mitigate ecosystem and economic losses from exploitations and future climate changes in French Guiana and in fragile tropical regions.

2. MATERIALS AND METHODS

2.1. Study area

The study area was the inner continental shelf of French Guiana (4.5°–6.5° N, 51.5°–54° W; Fig. 1). In this area, the equatorial climate is strongly influenced by seasonal variations due to the Inter-Tropical Convergence Zone, which brings heavy rainfalls and defines the regional climate of the Amazonian region (Hu et al. 2004). The rainy season occurs from January to June, while the dry season lasts from July to December (Amatali 1993). Coastal marine ecosystems from the north of Brazil to Venezuela are highly influenced by the turbid freshwater discharge from the Amazon River, which is flushed out into the ocean and transported from east to west by the North Brazilian Current and its extension, the Guiana Current (Cadée 1975, Smith & Demaster 1996).

2.2. Sampling protocol and data set

The present work was based on fish data compiled from 2 scientific trawl surveys conducted at 33 stations along the coast of French Guiana in November 2016 and 2017 (Fig. 1). Teleosts and Chondrichthyes were collected (hereafter simply 'fish'). Stations were distributed by a stratified random sampling protocol between 15 and 60 m depth from the Brazilian border in the east to the Surinamese border in the west. This sampling plan covered a surface of approximately 25 000 km^2. For each station, fish communities were sampled using a bottom shrimp trawl (horizontal mouth opening: 6.7 m; vertical mouth opening: 1.5 m; cod end mesh size: 45 mm), towed for 30 min westward at a constant speed of 2.5 knots. When possible, all individual fish collected were identified to the species level.

The entire data set, including rare and pelagic fish species, was considered in the following statistical analyses. Rare species are often excluded from analyses as they could lead to misinterpretations due to their low abundances. However, studies have shown that they represent highly distinct combinations of
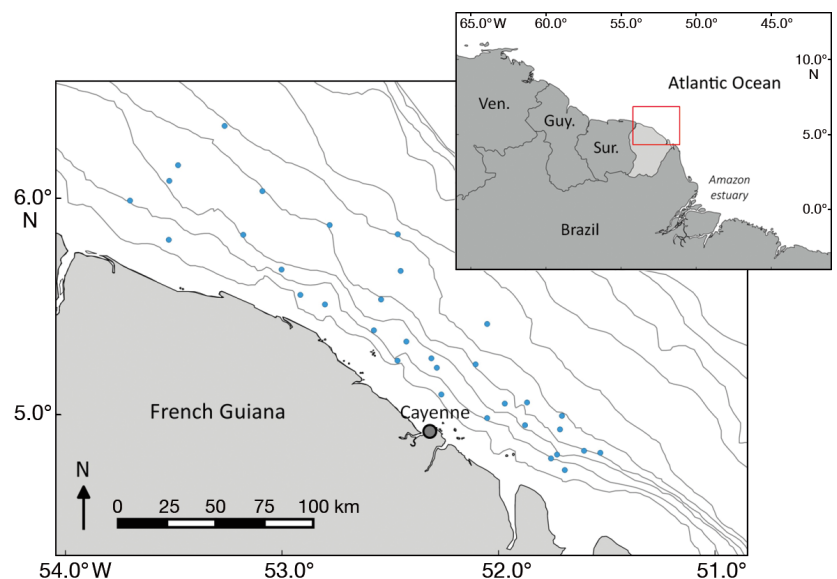

Fig. 1. Study area off the coast of French Guiana, showing the location of the 33 sampling stations (isobaths are represented every 10 m). Ven.: Venezuela, Guy.: Guyana, Sur.: Suriname

traits regarding the total species pool (Diaz et al. 2007), and therefore, they occupy specific niches and perform unique ecological roles important in ecosystem functioning (Mouillot et al. 2013a, Leitão et al. 2016). Excluding such important species may thus affect our understanding of community functioning (Solan et al. 2004). It is therefore important to retain these species, in order to properly describe processes ruling community assembly (Mouillot et al. 2013a). In this study, rare species represented 12% of the total species pool in 2016 and 14% in 2017. In other studies using bottom trawling, pelagic species were removed from analyses considering that their catchability and, consequently, their abundances might be underrepresented due to the sampling method (Pecuchet et al. 2016). Nevertheless, we decided to keep the pelagic species in our analyses for several reasons. Firstly, despite being underestimated due to the sampling method, in the present study only presence/absence data of species were used in order to describe structuring processes. Secondly, pelagic species could be excluded from analyses because they belong to the pelagic zone and are thought to have few interactions with the demersal and benthic zones. However, the height of the water column was relatively low in the study area (60 m depth maximum) compared to other studies which excluded pelagic species (up to several hundred meters) (Pecuchet et al. 2016). Almost all pelagic species identified in our database have an ecological relationship with the benthic zone. For instance, 15 of the 17 pelagic species (typical pelagic species such as carangids, scombrids or clupeids) are omnivorous and feed on pelagic prey but also on shrimps and benthic invertebrates (Table S1 in the Supplement at www.int-res.com/articles/suppl/m630p183_supp.pdf). Therefore, even if pelagic species have relatively few interactions with benthic and demersal compartments, they probably play a role in the structure of assemblages as they interact with them.

2.3. Functional characterization

Fish functional diversity was characterized by using 16 traits, i.e. 2 ecological and 14 morphological traits, grouped into 3 ecological functional categories: food acquisition, locomotion and habitat use. Ecological traits were based on their trophic and habitat affinities. We considered 4 'trophic group' categories (planktivorous, benthic invertivorous, piscivorous and omnivorous) and 3 'habitat use' categories (benthic, demersal and pelagic) (Table S1).

Morphological traits are unitless ratios (Table S2) computed from 14 measures taken from the lateral view of digital pictures of individual fish (Fig. S1) using IMAGEJ© software (https://imagej.nih.gov/ij/) as proposed by (Villéger et al. 2010). Among the 14 morphological traits, the maximum fish size was described using the log-transformed maximum standard length obtained from FishBase (Froese & Pauly 2018). Measures for the rarest species that were sampled only once were characterized from 1 picture while species that occurred 2 times were characterized from 2 pictures, etc. For more abundant species that were sampled frequently, measures were taken from 10 pictures of similar fish species with heterogeneous sizes. For each species, mean trait values were computed from individual measures assuming that intraspecific variations were lower than interspecific variations (Dumay et al. 2004). For each trait, mean species ratios were standardized so that the mean was 0 and standard deviation was 1 to give the same weight to each morphological trait. The functional distance matrix was computed using Gower's distance (Gower 1971), as recommended by Pavoine et al. (2009), which allows different types of traits (i.e. traits coded as continuous, ordinal and categorical) to be mixed while giving them equal weight (Buisson et al. 2013). A principal coordinate analysis (PCoA) was then performed on the functional distance matrix to obtain coordinates of the species in a multidimensional space (Villéger et al. 2008, Laliberté & Legendre 2010). We used the method of Maire et al. (2015) to assess the best compromise to represent the functional information while keeping the number of dimensions as low as possible. Following this procedure, we kept the species coordinates on the first 4 axes to describe the functional space representing 81.28% (33.53, 21.55, 14.51 and 11.69% for the first 4 principal components) and 83.76% of the inertia (34.13, 24.10, 14.92 and 10.61% for the first 4 principal components) for the 2016 and 2017 surveys, respectively. The mean square deviation was lower than 0.01 for both surveys.

2.4. Taxonomic and functional diversity indices

At the local scale, which is defined here as a single haul, α-diversity was defined by the species richness (SR) and the functional richness (FR) computed per station. SR is the number of species and FR represents the percentage (from 0 to 1) of the convex hull volume occupied by the local species assemblage given that the total FR from the species' regional pool

is equal to 1 (Villéger et al. 2008). FR was computed with the 'qual_funct_space' and 'multidimFD' updated functions provided at http://villeger.sebastien.free.fr/.

At the regional scale, which is defined here as the study area, pairwise taxonomic β-diversity (βTj) and pairwise functional β-diversity (βFj) were calculated between each pair of local assemblages (Cilleros et al. 2016). Taxonomic β-diversity was computed using Jaccard's dissimilarity index (Koleff et al. 2003). This measure is the percentage of unshared species between 2 stations, and it represents the sum of species replacements (turnover) and the difference in species richness between them (nestedness). The taxonomic turnover (Baselga 2012) equals 0 when 1 assemblage contains all species from the other and equals 1 when 2 assemblages have no species in common. In the same way as with taxonomic β-diversity, functional β-diversity was computed using convex hull volumes of assemblages instead of SR (Villéger et al. 2011). Functional turnover and nestedness were also expressed and calculated (Villéger et al. 2013). Here, functional turnover represents the overlap within convex hull volumes between 2 local assemblages and is a value equal to 0 when 2 functional spaces are identical (perfect overlap) and equals 1 when volumes do not overlap at all (without intersection).

2.5. Theoretical frameworks and statistical analyses

First, at the local scale, defined as a single haul, we compared the observed relationship between SR and FR to simulated values obtained from a random distribution using a null model (Mouillot et al. 2007, Pecuchet et al. 2016). The null model generates simulated values by randomization from the total species pool in order to build random communities. Since FR is calculated with presence/absence data, the randomization process was realized by holding constant both row sums (i.e. the occurrence number of species) and column sums (i.e. the species richness by station) using the 'permatswap()' function in the 'vegan' package (Oksanen 2018). We repeated this operation 999 times. Following the method of Pecuchet et al. (2016), observed FR values were compared to the null model and its 50 and 95% distribution. These comparisons allowed us to describe how stations are influenced by environmental filtering and competitive exclusion. To this aim, we considered that observed values within the interquartile range (25–75%) of the null model distribution corre-

spond to communities where neither the niche filtering nor the limiting similarity process dominates. This observation indicates random assembly which occurs when communities are influenced by both processes acting at similar strengths. Observed values below the 25% quartile zone indicate communities which are more structured by niche filtering and strictly shaped by this process for values below the 2.5% quartile zone. A similar assumption is made for values above the 75 and 97.5% quartile zones structured by a dominant and a strict influence of interspecific competition, respectively (Pecuchet et al. 2016).

At the regional scale, defined here as the entire study area, environmental filtering and dispersal limitation are the 2 major processes proposed to describe observed biodiversity patterns (Nekola & White 1999). However, their relative roles are difficult to disentangle and could vary as a response to climate and environment changes (Kraft et al. 2011, Myers et al. 2013). For this purpose, Cilleros et al. (2016) proposed a theoretical framework based on the correlation between taxonomic and functional turnovers between pairs of local assemblages. If functional and taxonomic turnovers cover a similar range, both processes have a similar strength. As proposed by Cilleros et al. (2016), if pairs of assemblages have a higher functional turnover, they are structured by different environmental filters promoting species with different ecological strategies. In contrast, pairs of assemblages with higher taxonomic turnover are dominated by dispersal limitation, with distinct species sharing most similar ecological strategies. However, this is a theoretical framework where the 1:1 linear relationship between both turnovers implies that each species plays a unique functional role, whereas we assume that functional redundancies exist in ecosystems (Micheli & Halpern 2005, Guillemot et al. 2011). Indeed, one species could support several functions and several species could hold the same functions (Bond & Chase 2002, Mouillot et al. 2014). For instance, for the same number of species, functionally redundant or complementary communities will not have the same relationship between taxonomic and functional components (Micheli & Halpern 2005). Therefore, regional processes cannot be revealed only by the observed relationship of both turnovers. Thus, we tested whether observed taxonomic and functional turnovers differed from randomly simulated communities using 2 null models to disentangle the relative roles of processes shaping community assembly. The first model tested if the observed taxonomic turn-

over differed from random expectations from the total pool of species, in order to assess the relative strength of both dispersal limitation and environmental filtering compared to stochasticity. To achieve this, random assemblages were generated by maintaining the observed SR per sampling station and the species occurrence in each survey using a trial swap algorithm (Miklós & Podani 2004). The second null model then tested if the observed functional turnover differed from random expectations in which species traits were randomly distributed among fish communities. Using the same method as Cilleros et al. (2016), species identity was permuted in the species–trait matrix while keeping the site–species matrix and, thus, the local SR and taxonomic turnover using 'functional.betapart.core()' and 'functional.beta.pair()' functions in the 'betapart' package (Baselga et al. 2018). For both null models, a standardized effect size (SES) was calculated, representing the difference between observed values and the mean of 999 simulated values, divided by the standard deviation of the simulated values. Pairs of assemblages with an SES value between −1.96 and 1.96 did not differ significantly from random expectations. Medians of SES values were tested for departure from 0 to determine if environmental filtering or dispersal limitation shapes community assembly (Stegen et al. 2012). No departure from 0 means that stochastic processes rule community assembly (Cilleros et al. 2016). All statistical analyses were performed using the R software (R Core Team 2013).

3. RESULTS

In 2016, 96 taxa and 24 814 individuals were collected and identified for a total weight of 3.36 t. In 2017, 103 taxa and 13 349 individuals were collected and identified for a total weight of 2.60 t. Combining these 2 surveys, a total of 115 different taxa were collected, identified and considered in our analyses, while 534 pictures of individuals were used in order to characterize morphological traits of these taxa. In 2016, SR and FR values obtained ranged from 10 to 36 species and from 0.03 to 0.5, respectively. In 2017, SR ranged from 11 to 39 species and FR from 0.03 to 0.27. Mean estimated β-diversity was 0.75 in 2016 and 0.81 in 2017.

3.1. Assembly rules at the local scale

Since adding new species to an assemblage can only increase the functional diversity or its redundancy (Guillemot et al. 2011), the relationship between SR and FR is necessarily positive (Fig. 2). However, most stations showed relatively low FR values, causing a gentle slope in the relationship between SR and FR, which indicates high redundancies in existing functions within assemblages. For instance, 39 species were collected at a station in 2017 (Fig. 2b). Estimated FR for this local assemblage was 0.15, which means that it represents only 15% of the total FR from the species' regional pool even though this is
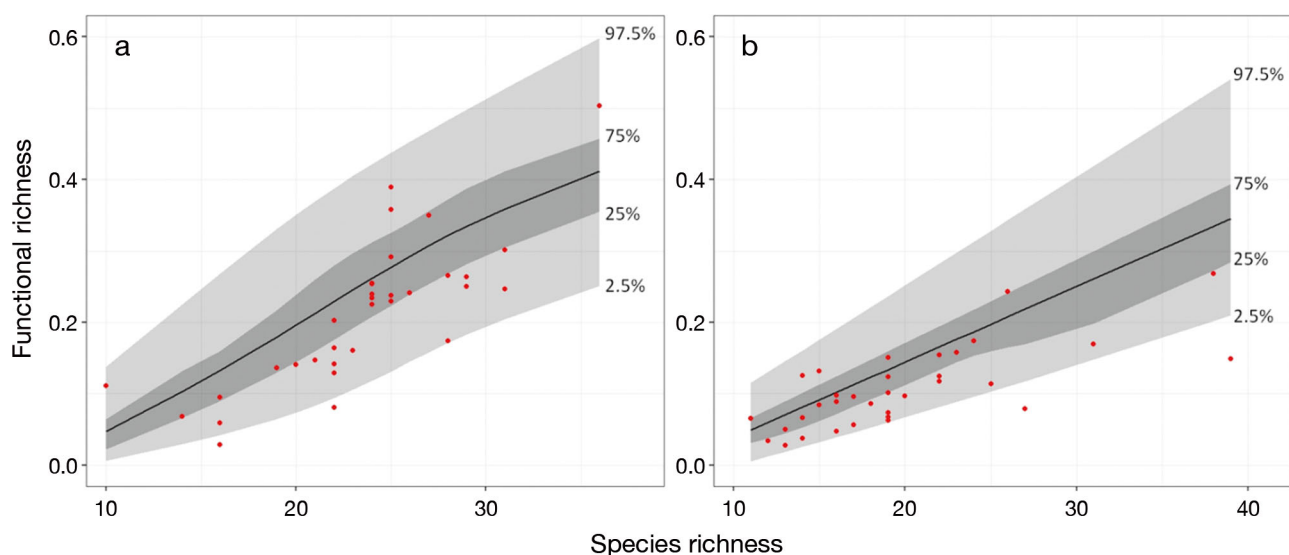

Fig. 2. Observed (dots) and simulated functional richness values based on a null model (grey zones) in (a) 2016 and (b) 2017. The black line is the mean of 999 random permutations. Areas in dark and light grey are respectively the 50th and the 95th percentiles, smoothed using a generalized additive model function

the highest SR value recorded for both surveys. Mean FR per station was 0.21 in 2016 and 0.11 in 2017.

In 2016, 4 observed values were above the 75th percentile, 14 were within the interquartile range, and 15 were below the 25th percentile of the null distribution (Fig. 2a). In 2017, 3 observed values were above the 75th percentile, 12 were within the interquartile range, and 18 were below the 25th percentile of the null distribution (Fig. 2b). According to our assumptions, these results indicate that interspecific competition is more influential for only 12 and 9% of fish assemblages in 2016 and 2017, respectively, whereas environmental filtering is the dominant structuring process for 45 and 54% of fish assemblages in 2016 and 2017, respectively. Moreover, for both surveys, 2 observed values were below the 2.5% quartile zone (Fig. 2), indicating assemblages strictly shaped by environmental filtering. The remaining observed values were distributed within the interquartile range (dark grey zone), indicating communities where neither process dominated.

3.2. Assembly rules at the regional scale

For both surveys, taxonomic β-diversity and functional β-diversity were significantly correlated (2016:

Table 1. Parameters of standardized effect size (SES) values for taxonomic and functional turnovers. 'Median' is the median of all SES values computed. The z-statistic represents the z distribution. If z is less than −1.96 or greater than 1.96, the null hypothesis (random distribution following the null model) is rejected. Pc represents pairwise comparisons between assemblages which are different from random expectations over the 528 comparisons possible

	SES of taxonomic turnovers				SES of functional turnovers			
	Median	z	p	Pc	Median	z	p	Pc
2016	−0.0905	−1.5965	0.1104	251	0.93	9.3854	<0.001	220
2017	0.245	−1.5092	0.1312	266	0.9956	13.3	<0.001	194

r = 0.75, p < 0.001; 2017: r = 0.84, p < 0.001), as were taxonomic and functional turnovers (2016: r = 0.60, p < 0.01; 2017: r = 0.85, p < 0.001). In 2016 and 2017, taxonomic β-diversity and turnover were higher than functional β-diversity and turnover (in 2016: βTj-βFj: Wilcoxon signed-rank test: z = 8.67, p < 0.001; turnover: Fig. 3a; z = 17.08, p < 0.001 and in 2017: βTj-βFj: Wilcoxon signed-rank test: z = 6.92, p < 0.001; turnover: Fig. 3b; z = 15.89, p < 0.001).

In 2016, null models showed that 251 out of 528 (47.5%) pairwise comparisons of taxonomic turnover were significantly different from random expectations, while the median of distribution did not differ significantly from 0 (Table 1). Fewer pairs of communities were different from random expectations for the functional turnover while conserving the observed taxonomic turnover (220 out of 528, i.e. 41.7%). The median of its simulated distribution was significantly
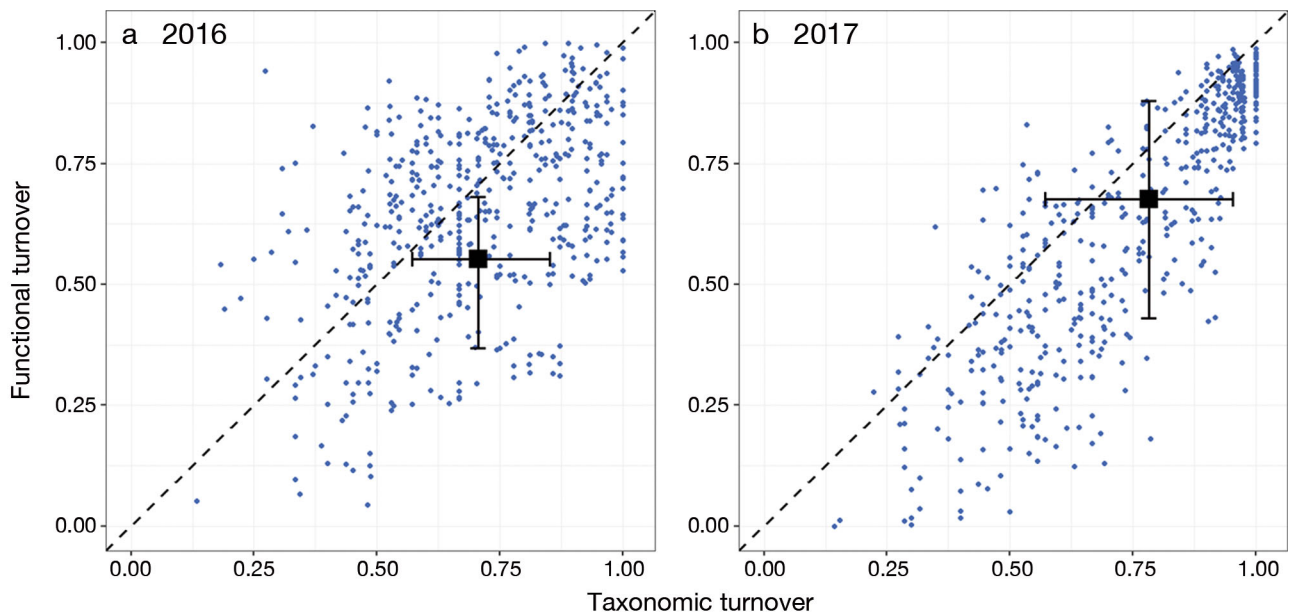

Fig. 3. Relationships between pairwise taxonomic and functional observed turnovers among the 33 assemblages in (a) 2016 and (b) 2017. Black squares and bars represent medians and 25th/75th percentiles, respectively. The theoretical line 1:1 is represented by the dashed line

different from 0 (Table 1). In 2017, null models showed that 50.4% of comparisons of the taxonomic turnover were significantly different from random expectations while the median of distribution did not differ significantly from 0 (Table 1). 36.7% of pairs were different from random expectations for the functional turnover. The median of its simulated distribution was significantly different from 0. Observed taxonomic turnovers in 2016 and 2017 did not differ significantly from random expectations. However, functional turnovers differed significantly from random expectations, with positive medians for both surveys indicating higher functional turnovers than expected by chance following the null model.

4. DISCUSSION

This work demonstrated that environmental filtering was the most influential process shaping local fish species assemblages in French Guiana. Results underlined the dominance of niche filtering over the limiting similarity hypothesis for both surveys. Only 4 (12%) and 3 (9%) of the 33 local fish assemblages showed a higher influence of interspecific competition in 2016 and 2017, respectively (Fig. 2). Approximately half of the stations (45 and 54% in 2016 and 2017, respectively) were dominated by environmental filtering, while the remaining stations (43 and 37% in 2016 and 2017, respectively) distributed in the neutral zone were structured by both processes acting simultaneously with more equal strength, where neither niche filtering nor limiting similarity processes dominated. Moreover, 2 assemblages for each survey were below the 2.5% quartile zone, indicating fish assemblages purely structured through abiotic filters (Fig. 2).

Our results suggest that local environment tends to shape fish assemblages by favoring co-existing species with functional traits more similar than expected randomly under the null model. The dominance of environmental filters was revealed by low FR values observed for many assemblages in comparison with the null model (Fig. 2). At the local scale, despite high SR values (from 10 to 39 species), estimated FR values remained relatively low (from 0.03 to 0.5; the second highest value is 0.39) compared to the regional FR (1.0). We cannot properly compare our results to the work of Pecuchet et al. (2016) conducted on fish communities in the Baltic Sea, as we did not use exactly the same functional traits, and the 2 ecosystems are very different. However, local FR values can reach 0.75 in the Baltic Sea. Taking this into account,

with a mean local FR of 0.21 in 2016 and 0.11 in 2017, the fish communities on the continental shelf of French Guiana can be considered to be highly functionally redundant. Functional redundancy decreases with the increase in functional traits, since 2 different species rarely share all considered functions (Gamfeldt et al. 2008). However, even though we considered 16 functional traits (which is relatively high) in the present study, functional redundancy remains well pronounced. The dominant effect of abiotic filters against interspecific competition enhances the co-existence of functionally closely related species. French Guiana's coastal waters are considered highly productive ecosystems (>300 g C m^{-2} yr^{-1}), which certainly weakens competition for food acquisition (Vieira & Castello 1997). Furthermore, the abundance of omnivorous species may also limit competition for specific trophic resources. Based on available trophic behavior information, the majority (68%) of fish species collected was omnivorous (Table S1), feeding on several different resources. Another possible mechanism, not investigated in this study, is the limitation of biotic interactions by a complementary use of trophic resources. Species can avoid partial or complete resource overlaps and thus competition by restraining their spatial realized (Eltonian) niche or by temporally segregating their food acquisition during the night and/or the day (Devictor et al. 2010, Mouchet et al. 2013). Our results are in accordance with previous studies on fish communities which revealed functionally redundant assemblages more structured by environmental filtering than by biotic interactions at local scales (Oberdorff et al. 1998, Hoeinghaus et al. 2007, Mouillot et al. 2007, Mouchet et al. 2013).

Assembly rules may vary along environmental gradients in space and/or time (Mason et al. 2007, Pecuchet et al. 2016). Changes in the relative influence of processes shaping fish communities have been observed in environments presenting very different seasonal conditions and involving changes in the species composition (Córdova-Tapia et al. 2018). In French Guiana, rainy season conditions could induce migrations of coastal species depending on their salinity tolerances due to the increasing freshwater outflow from rivers during this period (Guéguen 2000, Vendeville & Baudrier 2006, Willems et al. 2015). Therefore, we can ask whether the relative influence of shaping processes could vary between both seasons. In order to evaluate a potential seasonal effect on assembly rules, we performed the same analyses realized in the present study on a dataset for which fishes were sampled during the dry and rainy seasons in 2007. Environmental filtering

remains the most influential shaping process throughout the year, with similar conclusion between both seasons (Fig. S2). In the Guianese region, offshore waters are subject to seasonal variations (Ffield 2007) but less than estuaries where very strong variations were reported (Rousseau et al. 2018). In the Amazonian estuary, the salinity concentration is probably the most important variable conditioning taxonomic and functional diversity. In future research, it would be interesting to investigate how species composition and assembly rules vary along a salinity gradient from coastal marine waters to freshwaters in French Guiana.

Results of studies on the relationship between regional and local diversity suggested that local richness is mostly determined by regional richness (Cornell & Lawton 1992, Oberdorff et al. 1998, Bellwood & Hughes 2001, Bond & Chase 2002, Hillebrand & Blenckner 2002). However, understanding how communities are structured in a large area such as the continental shelf of French Guiana requires the determination of both local and regional assembly rules. The transition from α- to β-diversity patterns allowed us to describe assembly processes that structure local and regional assemblages. Observed medians of taxonomic turnovers were higher than observed medians of functional turnovers for both surveys, indicating that species replacements were higher than functional profile replacements between sites. Therefore, no conclusion on the relative influence of structuring mechanisms can be drawn considering only these results. By using null models, for both surveys, simulated medians of taxonomic turnover distribution did not differ significantly from random expectations. Those results are in contradiction with our hypothesis, since a non-random and higher taxonomic turnover was expected due to the spatial shift pattern from coastal to offshore fish assemblages in French Guiana and Suriname (Guéguen 2000, Vendeville & Baudrier 2006, Willems et al. 2015). However, species replacements between sites correspond to random variations and cannot be assigned to a specific process. Simulated medians of functional turnovers differed significantly from random expectations for both surveys. This means that functional profile replacements between sites were higher than expected by chance, indicating that fish assemblages were distributed in habitats with different abiotic characteristics requiring different functional adaptations. Since FR increases with the SR (Guillemot et al. 2011), we assume that the FR measured in French Guiana is relatively high due to the high regional SR and to the wide variety of shapes of

collected fishes. Therefore, regional results are congruent with those observed at the local scale. Indeed, functional turnovers must be high between pairs of functionally redundant assemblages in such a highly biodiverse fish community (Guillemot et al. 2011). At the regional scale as well, our results suggest a dominant influence of environmental filters.

Overall at the regional scale, species replacements correspond to random variations due to the joint effects of dispersal limitation and environmental filtering acting with more or less equal strength. However, functional turnover revealed a stronger influence of environmental filtering. Local habitats in the study area are generally homogeneous, but regional environments seem sufficiently heterogeneous to provoke a higher change in fish functional profiles than what could be expected randomly. Several reasons could explain the dominance of environmental filters and a weaker influence of dispersal limitation. Firstly, we can expect a high dispersal in marine fish species, as most of them are characterized by high dispersal abilities and a greater prevalence of planktonic larval stages due to the buoyancy of seawater (Cornell & Harrison 2013, Srivastava & Kratina 2013). Moreover, these movements are also enhanced by the North Brazilian and Guiana Currents (Smith & Demaster 1996). Furthermore, as mentioned above, previous studies in the Guianese region showed a spatial shift pattern from coastal to offshore fish communities corresponding to 2 different habitats, separated around the 30 m isobath (Vendeville & Baudrier 2006, Willems et al. 2015). This species distribution is mainly influenced by sediment characteristics (Willems et al. 2015). Species living in the coastal zone are more adapted to mudflats with a very fine grain size and are subjected to important freshwater outflow from the Amazon and other local rivers such as the Oyapock and Approuague.

Environmental filtering is the dominant process shaping communities in several environments from terrestrial to aquatic ecosystems (Diaz et al. 1998, Mouillot et al. 2007, Lebrija-Trejos et al. 2010). In many cases, studies on fish communities revealed functionally redundant assemblages not limited by interspecific competition and dominated by niche filtering (Mouillot et al. 2007, Mouchet et al. 2013). Nevertheless, most of these studies concerned fish assemblages in closed or spatially limited habitats such as lakes (Mason et al. 2007, 2008), lagoons (Mouillot et al. 2007, Mouillot 2007, Mouchet et al. 2013) or rivers (Hoeinghaus et al. 2007, Cilleros et al. 2016). Investigations on assembly rules governing marine fish communities are scarce (Pecuchet et al.

2016), especially in tropical ecosystems (Guillemot et al. 2011). Several studies suggested that environmental filters become more dominant in harsher abiotic conditions (Villanueva 2015, Pecuchet et al. 2016). In the present study, stations dominated by the niche filtering or limiting similarity hypothesis were randomly distributed with no particular spatial pattern. The salinity gradient in the study area is probably not strong enough to observe a spatial pattern regarding the relative influence of structuring processes. That is why it would be interesting to pursue these analyses along a wider salinity gradient from freshwaters to marine waters in French Guiana. We have analyzed some environmental data collected during the different surveys mentioned above to identify the significant factors structuring the fish community at our study site. Preliminary results obtained show that sea surface temperature seems to be the most significant factor structuring the fish assemblage at our study site (V. Vallee et al. unpubl.).

The definition of the scale is always an important point in ecological studies. The 'local scale' in the present study was defined as 1 haul, which represents approximately $12\,500$ m^2. This area could be considered very large for a local scale relative to other studies in which local scale was defined as 1 m^2 (Fukami et al. 2005, Götzenberger et al. 2012) or a few dozen square meters (Mason et al. 2008, Mouchet et al. 2013). Interspecific competition is dominant at the local scale, whereas environmental filtering is dominant at the larger scale for biological communities for which the local scale could be relatively fine (from 1 to several dozen square meters), such as plant or insect communities (Stubbs & Wilson 2004, Slingsby & Verboom 2006). However, it does not make sense to ask whether interspecific competition would be more important at a fine scale of about few dozen square meters in the present study, since fishes are generally mobile animals. Moreover, very few fish species examined in our study are sedentary and thus restricted to small areas as mentioned above. Nevertheless, it would be interesting to apply the method used here at finer scales than in the present study, on fish assemblages from heterogeneous ecosystems such as reef fish communities. In coral reef ecosystems, taxonomic and functional diversity are high as a result of the complex 3-dimensional habitat structure allowing communities to be functionally diverse and complementary. Moreover, coral reef species tend to be more territorial than in the present study and, thus, restricted to areas around a few hundred or thousand square meters (Guillemot et al. 2011). Hence, we can ask whether interspecific competition would be stronger than environmental filtering in coral reef fish communities considering a local scale defined by transects about 50 m long, for instance (Guillemot et al. 2011). Several studies on biogeography have shown that the distance from biodiversity centers dominates community structure in coral reef fish communities, particularly around the Coral Triangle in the Indo-Pacific region (Bellwood et al. 2005, Mouillot et al. 2013b). These biogeographical scale patterns have been well identified and studied, but processes structuring fish assemblages at finer scales remain incomplete in these ecosystems (Drew & Amatangelo 2017). Finally, the primary productivity of such ecosystems is often low, providing the conditions for the emergence of competition for trophic resources. Biodiversity in tropical reef ecosystems is assumed to be the most diverse in the world (Mouillot et al. 2013b, Drew & Amatangelo 2017) and is likely to be impacted by higher rates of local extinction due to climate change (Worm et al. 2006). Therefore, a better understanding of their functioning at several geographic scales will be very useful in order to conserve such important ecosystems in the face of future climatic changes.

The present study provides more information concerning assembly rules on tropical fish communities in large marine ecosystems. To our knowledge, this study is the first to provide the assessment of assembly rules on fish communities, at both local and regional scales. This work is also the first to characterize the functional diversity of marine fish communities in the Guianese region (Mouillot et al. 2014). It would be interesting to continue this work on a long-term basis to better understand how assembly processes respond to climate change. Environmental changes are occurring fast (Hoegh-Guldberg et al. 2018), and tropical communities are expected to be especially impacted by those changes with high rates of biodiversity losses (Worm et al. 2006, Cheung et al. 2009). Our study has demonstrated that the structure of fish communities in French Guiana is particularly sensitive to environmental parameters. We therefore assume that it would be easily affected by future changes in climatic conditions. The study of communities' functional diversity will allow us to point out major mechanisms in the ecosystem structure and functioning to mitigate biodiversity and economic losses in these fragile regions.

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