

ORIGINAL
ARTICLE

Taxonomic and functional diversity patterns reveal different processes shaping European and Amazonian stream fish assemblages

Kévin Cilleros^{1*}, Luc Allard², Gaël Grenouillet¹ and Sébastien Brosse¹

¹Laboratoire Évolution & Diversité Biologique (EDB UMR5174), Université Paul Sabatier, CNRS, ENFA, 118 route de Narbonne, F-31062 Toulouse Cedex, France, ²Laboratoire Environnement de Petit Saut, HYDRECO, B.P. 823, 97388 Kourou Cedex, French Guiana

ABSTRACT

Aim Differences in dispersal limitation and environmental filtering have been proposed to explain differences in diversity patterns between regions. Incorporating functional traits into studies of assembly rules allows the relative strengths of such processes to be distinguished. We test the predictions that assemblages in a similar environment under strong dispersal limitation should be differentiated taxonomically but not functionally, whereas strong environmental filtering should more differentiate assemblages functionally.

Location French Guiana and France.

Methods We used two datasets on fish assemblage composition: one for French Guiana and one for continental France. We constrained both dataset to have similar geographical extent and similar environment using site location and topographic variables of the French Guiana dataset to select continental France data. We estimated functional diversity using a combination of 15 fish morphological traits. We computed species and functional richness at regional and local scales for both regions. We calculated taxonomic and functional turnover between sites and compared them within and between regions.

Results Taxonomic and functional richness were higher in tropical fish assemblages than in temperate ones both on regional and local scales. Species richness differences between the two regions resulted in very similar functional richness. Temperate assemblages showed a higher functional turnover than tropical assemblages, but a lower taxonomic turnover. We found a stronger turnover in taxonomic diversity than in functional diversity between tropical assemblages, and the opposite pattern between temperate ones.

Main conclusions The higher functional richness in tropical assemblages was mainly caused by an increased number of species compared to temperate assemblages, probably linked with an increase in available niches. Dispersal limitation was the predominant process in structuring Guianese stream fish assemblages causing strong species replacement, whereas French stream fish assemblages were mainly under strong environmental filtering resulting in local adaptations to different environments.

Keywords

assembly rules, community, dispersal limitation, environmental filtering, France, French Guiana, freshwater fish, turnover, α -diversity, β -diversity

*Correspondence: Kévin Cilleros, Laboratoire Évolution & Diversité Biologique (EDB UMR5174), Université Paul Sabatier, CNRS, ENFA, 118 route de Narbonne, F-31062 Toulouse Cedex, France.
E-mail: kevin.cilleros@univ-tlse3.fr

INTRODUCTION

One of the most striking characteristics of tropical regions is their species richness compared to temperate areas. The causes of these differences have been debated for more than

a century, and three nonexclusive groups of hypotheses have been proposed to explain the patterns observed, that is, historical, evolutionary and ecological hypotheses. Historical and evolutionary causes are closely linked and have been handled through a biogeographical context. Ecological

hypotheses refer to mechanisms and factors that promote species presence and coexistence through their ecology, including higher available energy (Wright, 1983), more diverse habitats (Preston, 1962; MacArthur & Wilson, 1967) and/or decreased abiotic harshness in tropical regions (Fischer, 1960).

In addition to the higher local species richness in tropical than in temperate assemblages, a higher turnover in species between localities has also been reported (Soininen *et al.*, 2007). For instance, Kraft *et al.* (2011) reported a global decrease in β -diversity with increasing latitude, and a stronger species turnover occurs in the tropics compared to the temperate areas for both frog and fungus assemblages (Dahl *et al.*, 2009; Bahram *et al.*, 2013). Dispersal limitation and environmental filtering are the two main processes proposed to explain these patterns (Nekola & White, 1999), but their relative roles remain unclear and have been shown to differ between tropical and temperate environments (Kraft *et al.*, 2011; Myers *et al.*, 2013). For instance, Myers *et al.* (2013) reported that tropical tree assemblages are mainly structured by dispersal limitation, whereas temperate assemblages are more influenced by environmental filtering.

Functional diversity approaches have been proposed as a way to disentangle these processes, by examining the correlation between taxonomic and functional facets of diversity (Devictor *et al.*, 2010). Indeed, the assemblages filtered by the environmental characteristics should differ functionally according to the local environmental characteristics, therefore promoting functional turnover between assemblages. In contrast, assemblages dominated by dispersal limitation evolve independently in a homogeneous environment and should therefore differentiate distinct species with similar strategies. Based on this, we predict that (1) if functional turnover and taxonomic turnover cover a similar range, environmental filtering and dispersal limitation have a similar strength (Fig. 1a), (2) if functional turnover is higher than taxonomic

turnover, environmental filtering is stronger than dispersal limitation, and (3) if taxonomic turnover is higher than functional turnover, dispersal limitation is stronger than environmental filtering. Using this theoretical framework, we also predict that if both the taxonomic and the functional turnover in the tropics are higher than in the temperate zones, environmental filtering and dispersal limitation act in the same way in both environments (Fig. 1b). In contrast, if despite an increase in taxonomic turnover between temperate and tropical zones, we show an opposite trend for functional turnover, this would indicate a prominent role of dispersal limitation in tropical assemblages and of environmental filtering in temperate assemblages (Fig. 1c). Such a framework deserves to be built using phylogenetic diversity approaches (Graham & Fine, 2008), but no robust global phylogeny is currently available for South American fishes, especially Guianese ones.

Here, we compared taxonomic and functional diversity of French and Guianese stream fish assemblages. We selected a set of samples having similar topographic characteristics (altitude, stream width) and similar spatial structure (extent and grain size) between the two regions to ensure their comparability (Steinbauer *et al.*, 2012). We first quantified local and regional taxonomic and functional α -diversity in the two regions. Then, we compared the spatial patterns in taxonomic and functional turnover between France and French Guiana, and inferred the processes shaping assemblage structure according to the relationships between taxonomic and functional turnover in temperate and tropical streams.

MATERIALS AND METHODS

Fish data

Analyses were based on complete fish inventories in small streams in both French Guiana and continental France. In

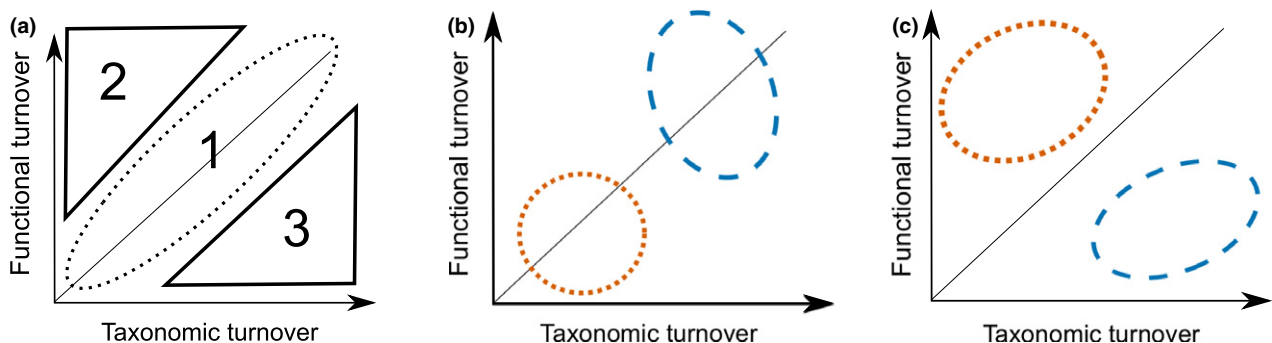


Figure 1 Theoretical framework (a) and expectations (b, c) about the relative strength of environmental filtering and dispersal limitation based on the relationship between taxonomic and functional turnover. (a) Assemblages with similar taxonomic and functional turnover (area 1) are structured with similar strengths of environmental filtering and dispersal limitation. Outside this area, pairs of assemblages with higher functional turnover are structured by different environmental filters and promote species with different ecological strategies (area 2), whereas pairs with higher taxonomic turnover are dominated by dispersal limitation, with distinct species sharing similar strategies (area 3). We hence expect that a higher functional turnover in tropical assemblages (blue dashed line) than in temperate ones (orange dotted line) will reveal that both processes act in the same way in the two regions (b). In contrast, a higher functional turnover in temperate assemblages will reveal that the relative strength of dispersal limitation and environmental filtering differs between the two regions (c).

both cases, fish abundances were converted into species occurrences to avoid potential bias due to differences in sampling techniques and potential differences in sampling efficiency between sites and between climate zones (Oberdorff *et al.*, 2001; Macnaughton *et al.*, 2015). Species lists obtained at the same location from 2008 to 2013 were merged to get the most complete image of fish assemblages. The Guianese database contained the occurrence of freshwater fish species in 84 stream reaches dispersed throughout French Guiana (Fig. 2a). The fish surveys that were used to build this database were conducted under several different research projects (CNRS-Nouragues, PAG-DEAL-HYDRECO project, CEBA-DIADEMA project). The sampling protocol was standardized for all sites (Allard *et al.*, 2016). At each site, a river section located upstream of a confluence was isolated using two fine mesh (4 mm) stop nets. Fish were collected after releasing a small quantity of rotenone a few metres upstream from the first net. At the end of each sampling session we searched for fishes lying on the bottom or hidden in the leaves and debris. In almost all sites, cryptic fish were collected, including highly cryptic silurids such as *Farlowella* or *Harttiella*, bottom-dwelling fishes such as *Ituglanis* or *Loricaria*, and litter bank fishes such as small killifishes (see Appendix S1 in Supporting Information for lists of species). Gymnotids,

although known as resistant to rotenone, were also captured in almost all the sites. For continental France, we used a database compiled by the French National Agency for Water and Aquatic Environments (Onema). Extensive surveys were conducted on stream sections with a standardized two-pass removal electrofishing protocol [see Poulet *et al.* (2011)].

All the fish captures were in accordance with French laws and guidelines concerning live animals, and all the experiments were approved by the Direction of Environment of the French ministry of Environment (DEAL), the French Guiana National Park (Parc Amazonien de Guyane), and the Onema.

Site selection

These two databases were built in order to characterize local fish assemblages in the two regions. French and Guianese sampling sites were thus selected to balance environmental, spatial and topographic discrepancies between the two regions that can bias comparisons between distant areas. Among the French sites, we selected those having the same physical characteristics (slope, altitude and distance from the source) and sampled during the same time period (2008–2013) as Guianese sites. All sites were upstream sites located between 0.5 and 16 km from the source. They belonged to

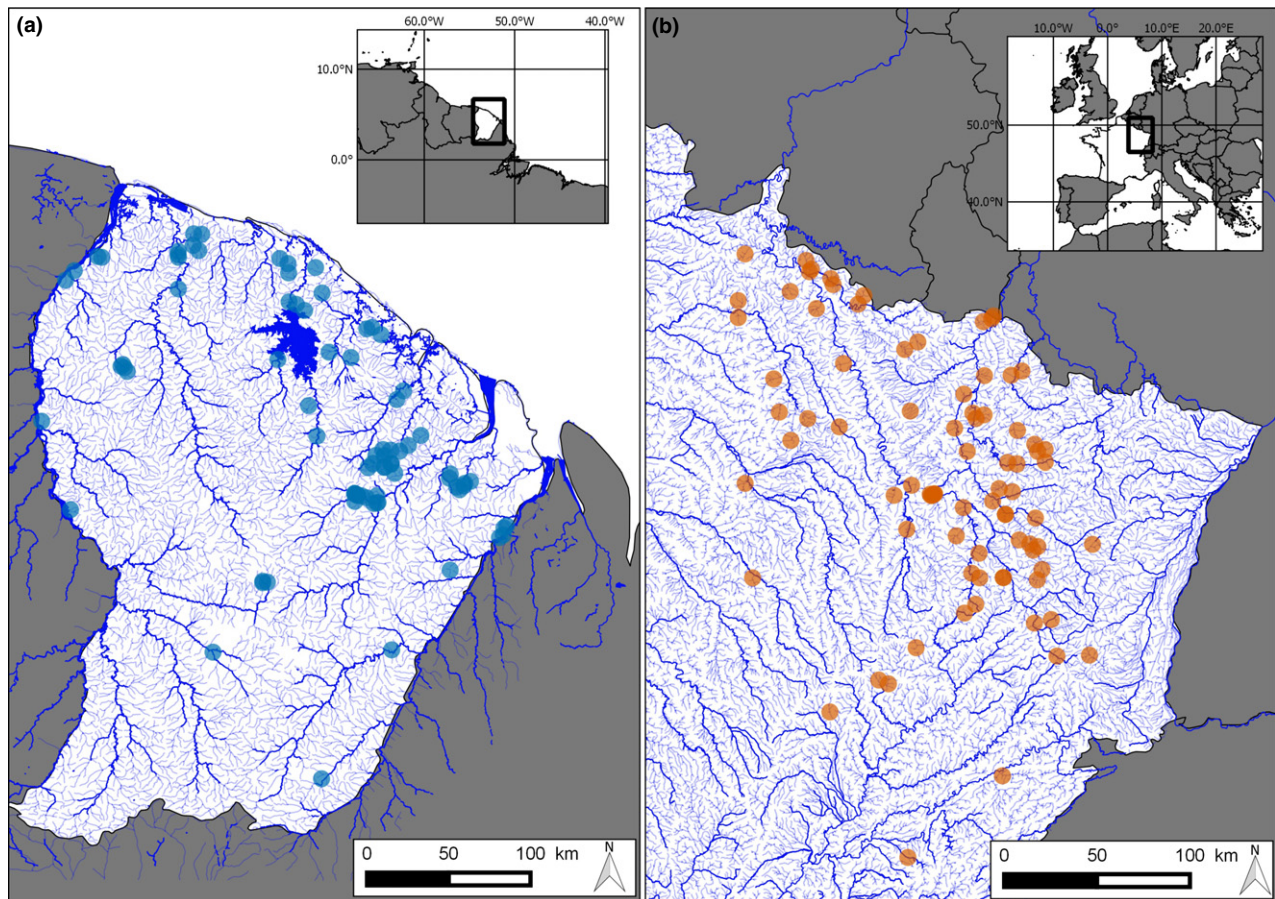


Figure 2 The location of the 84 studied fish assemblages within French Guiana (a) and continental France (b).

lowland and piedmont rivers and were located from 27 to 633 m above sea level, with a slope between 0.57‰ and 18.77‰. Then, to ensure a similar spatial structure between Guianese and French sites, we translated Guianese site coordinates to the part of mainland France where the spatial congruence was the best, corresponding here to the north-east of the country. We then selected French sites with more than four species (because the functional space was calculated in four dimensions, see below) that best matched Guianese site location (Fig. 2b). The resulting selection of 84 French sites showed similar spatial structure to the Guianese sites (see Appendix S2). This selection procedure provided two comparable databases of freshwater fish species occurrence in 84 assemblages for each region.

Functional data

We characterized fish for two main functions, locomotion and food acquisition, combining 14 morpho-anatomic measures taken on a picture (lateral view) of one adult individual per species using IMAGEJ software (<http://imagej.nih.gov/ij/>) and fish size was described using the log-transformed maximum body length (values taken from Fishbase (Froese & Pauly, 2015); see Appendix S3a and Toussaint *et al.* (2016) for details). Juveniles were not considered as morphological changes can occur during ontogeny. The effect of intraspecific variability on our results was assessed with all the species with several individuals measured (i.e. all French species and 17 Guianese species). Intraspecific variation in each trait was lower than interspecific variation for all the species, with interspecific variability accounting for $75.10 \pm 18.83\%$ (mean \pm SD) of the total variability. Moreover, a simulation analysis randomly selecting individuals within species (999 replicates) showed that the French functional richness reported here was never underestimated, and overestimated in 30% of the local sites. The Guianese fish functional richness never differed. This means that intraspecific variability did not affect our conclusions, however, in 30% of the sites it did accentuate the magnitude of the difference between French and Guianese functional richness.

Morpho-anatomic measures were combined as 14 unitless ratios (see Appendix S3b). Their use has first been recommended by Webb (1984) and Winemiller (1991), and these unitless ratios still remain the most commonly used to describe fish locomotion and nutrition (e.g. Bellwood *et al.*, 2014; Brandl *et al.*, 2015; Leitão *et al.*, 2016; Toussaint *et al.*, 2016). We then computed functional distance matrix between species with Gower's distance based on the morphological ratios and the fish size to consider missing data. We used a principal coordinate analysis (PCoA) on the functional distance matrix encompassing 192 species (155 species from French Guiana and 37 species from continental France) to obtain coordinates of the species in a multidimensional space (Villéger *et al.*, 2008; Leitão *et al.*, 2016). The method of Maire *et al.* (2015) was used to evaluate the

best compromise to represent the functional information and keep the number of dimensions as low as possible (and hence keep considering assemblages with a few species). It revealed that a 4-D approach was the most appropriate. We, therefore, kept the first four principal components to describe the functional space, representing 80.45% of the inertia (32.18%, 22.51%, 16.19% and 9.58% for the first four axes of the PCoA respectively). Allometric or isometric relationships existing between morpho-anatomic measures can bias species ordination in a multivariate space toward a first component representing a size effect rather than a shape or functional difference between species (Winemiller, 1991; Baur & Leuenberger, 2011). We thus checked that species ordination was not driven by a few variables having a preponderant effect by inspecting correlations between functional traits and the four PCoA components (see Appendix S4). For instance, fish body length has been considered as an integrative functional variable (Winemiller & Rose, 1992), but here its effect did not blur the effect of the others variables.

Taxonomic and functional diversity measures

We defined regional richness as the total richness found in each of the two regions considered, with the number of species found in all the French and Guianese sites, respectively, being the regional taxonomic richness and the percentage of convex hull volume occupied by all the species from one region being the functional richness (Cornwell *et al.*, 2006; Villéger *et al.*, 2008). Local richness (α -diversity) was defined as the taxonomic richness (the number of species) and functional richness (the volume occupied in the functional space by the species present in one local assemblage) in one stream reach assemblage.

Pairwise taxonomic β -diversity (hereafter β_{Tj}) between two assemblages was computed using Jaccard's dissimilarity index. This index is widely used in ecology (Koleff *et al.*, 2003; Myers *et al.*, 2013) and its meaning is easily understandable (the percentage of unshared species between two assemblages). It is based on a 'broad-sense' measure of dissimilarity (Koleff *et al.*, 2003), representing the sum of the species replacement between two assemblages (hereafter called turnover) and the difference in species richness between them (nestedness). The turnover was calculated according to Baselga (2012):

$$\text{taxonomic turnover} = \frac{2 \times \min(b, c)}{a + 2 \times \min(b, c)}.$$

Taxonomic turnover is null when one assemblage contains all the species from the other and equals 1 (i.e. β_{Tj}) when assemblages have no species in common.

We then calculated the relative contribution of the turnover component to overall dissimilarity (p_{turn}) to get an easily interpretable measure of the importance of species turnover on β -diversity (Toussaint *et al.*, 2014), with:

$$p_{\text{turn}} = \frac{\text{taxonomic turnover}}{\beta T_j}.$$

The p_{turn} metric is defined only if dissimilarity is not null, meaning that a pair of assemblages differs by at least one species. It is null when assemblages are nested and it equals 1 when assemblages have the same species richness (taxonomic nestedness component is null) or when they have no species in common.

We computed pairwise functional β -diversity (βF_j) within the same framework as for taxonomy, but using convex hull volumes of assemblage instead of species richness (Villéger *et al.*, 2011). So βF_j can be computed with the a , b and c quantities with a being the intersection of volumes of two assemblages, and b and c the volumes unique to each assemblage. Functional dissimilarity will be equal to 1 when volumes do not overlap and 0 when volumes are identical. The same decomposition in turnover and nestedness of functional dissimilarity were also computed as for taxonomy (Villéger *et al.*, 2013). Functional turnover here represents the overlap within functional spaces between assemblages. The relative contribution of the functional turnover component is computed in the same way as its taxonomic counterpart.

Statistical analysis

We compared functional richness at the regional scale while accounting for differences in species richness. We randomly selected as many Guianese species as French species and then calculated the functional richness that they represented. We repeated this 9999 times and compared the regional functional richness of continental France to this distribution. For the local functional richness, we used the same approach by replacing the French species by the selected Guianese species, thus conserving the occurrence matrix. We then calculated local functional richness for each site and compared, for each site, the French local functional richness to the simulated values for the corresponding sites.

To check for the potential effect of the difference in the number of drainage basins between the two regions on taxonomic and functional diversity measures, taxonomic pairwise comparisons were classified in either intra- or inter-basin comparison. We tested whether intra-basin and inter-basin comparisons significantly differed for each region with a permutation procedure as implemented in 'diffmean' function in R package 'simba' (Jurasinski & Retzer, 2012) with 9999 permutations.

We tested the difference in βT_j , βF_j and their turnover component between continental France and French Guiana using analysis of homogeneity of multivariate dispersion based on distance-to-centroids (Anderson *et al.*, 2011). In this context, β -diversity was defined as the average distance of sites from the centroid formed by all the sites of a group. Distance-to-centroid and average dissimilarity were highly correlated (Pearson's correlation > 0.92, $P < 0.001$ for each

metric). We thus used Jaccard's framework to represent graphically β -diversity.

Taxonomic and functional dissimilarity and turnover were regressed against the logarithm of the pairwise geodesic distance between sites to test the difference in spatial pattern between continental France and French Guiana. We used the Mantel test with 9999 permutations and the Spearman correlation coefficient to test the significance of the relationship between dissimilarity and distance. Intercept and slope were estimated with a 95% confidence interval by bootstrap with 9999 replicates (Davidar *et al.*, 2007). Differences in slope and intercept between continental France and French Guiana were tested using 9999 permutations, following Nekola & White (1999) with 'diffslope' and 'diffic' functions. For each run, couples of value dissimilarity/turnover – distance were randomly attributed to one of the two regions and the difference in slope or intercept was calculated. The differences calculated were used as a null distribution to compare with observed difference.

We tested whether observed turnover differed from random expectations using two null models to disentangle which processes had a predominant influence on community assembly between environmental filtering, dispersal limitation and stochastic processes. The first model tested if the observed taxonomic turnover differed from random sampling of species from the regional pool and evaluated the strength of both dispersal limitation and environmental filtering compared to stochasticity. For this, we constructed random assemblages by maintaining the species richness observed in the sites and the species occurrence in the database using a trial swap algorithm (Miklós & Podani, 2004). The second model tested if observed functional turnover differed from expectation where species traits are randomly distributed among assemblages and thus discriminate environmental filtering from stochastic processes. We permuted species identity in the species-trait matrix while maintaining the sites-species matrix and thus the local species richness and taxonomic turnover. For each null model, we calculated a standardized effect size (SES) as the difference between observed values and the mean of 999 simulated values, divided by the standard deviation of the simulated values. Pairs with an SES value between -1.96 and 1.96 did not differ significantly from random expectations. The medians of SES values were tested for departure from zero to assess if environmental filtering or dispersal limitation govern community assembly (Stegen *et al.*, 2012). In contrast, no departure from zero would indicate that stochastic processes govern community assembly.

RESULTS

Regional species richness was higher in French Guiana than in continental France, with 155 and 37 species respectively (Fig. 3a). Regional functional richness showed a similar pattern. Guianese species occupied 87.29% of the total functional volume, whereas French species accounted for 14.77%

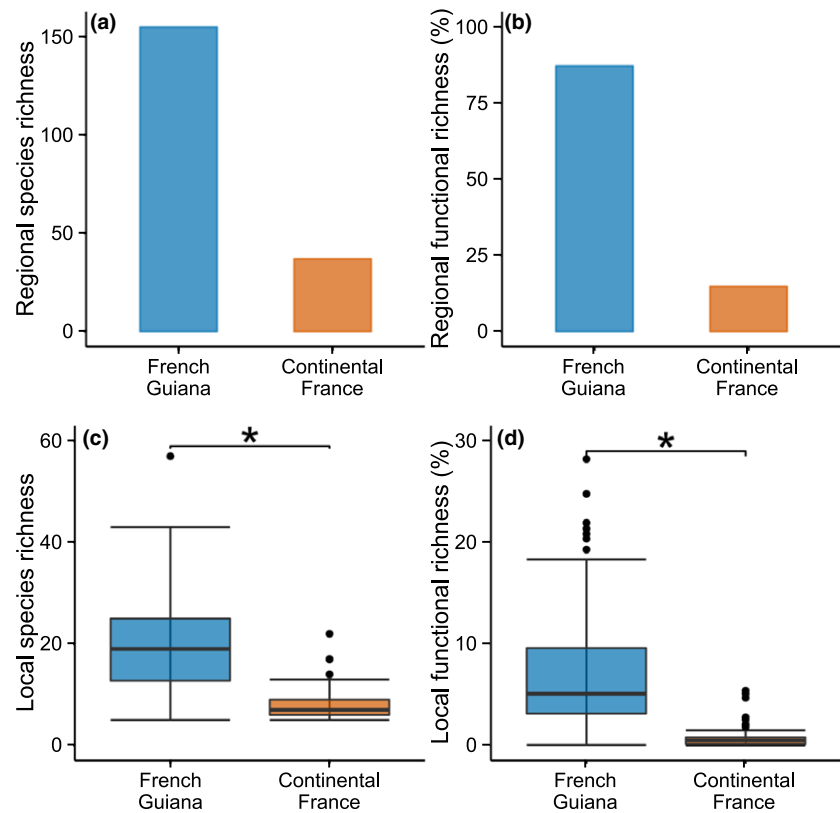


Figure 3 Taxonomic and functional α -diversity of fish at regional scale (a, b) and at local scale (c, d). The functional richness represents the percentage of the convex hull volume occupied by all the species of one region (b) or of one site (d) out of the total convex hull volume of all the species. Significant differences between the two regions are indicated above the boxes (*).

of this volume (Fig. 3b). It should be noted that the ratio between Guianese and French diversity increased when turning from taxonomic to functional diversity (4.19 vs. 5.91). Moreover, the functional space occupied by French species was largely included in the functional space of Guianese species. Indeed, only 4.88% of the French functional space was not shared with Guianese functional space (Fig. 4, see Appendix S5). However, controlling for species richness differences between the two regions revealed that the regional functional richness of French Guiana was not different from the functional richness of continental France ($P = 0.21$), and hence the functional differences observed between the two regions were due to a species richness effect.

At the local scale, French assemblages contained fewer species (7.88 ± 3.05) than Guianese assemblages (19.92 ± 9.32) (Fig. 3c; Wilcoxon rank-sum test: $z = 9.46$, $P < 0.001$) which were less functionally diverse ($0.74 \pm 1.02\%$ vs. $7.26 \pm 6.28\%$) (Fig. 3d; Wilcoxon rank-sum test: $z = 9.64$, $P < 0.001$). Again, the distinction between Guianese and French streams was more marked from a functional than from a taxonomic point of view. Accounting for species richness differences by randomly replacing French species by Guianese species showed that only four French sites had a lower local functional diversity ($P < 0.05$). The functional diversity of the 80 remaining French sites did not significantly differ from a random replacement of French species by Guianese species. Hence, the functional differences reported between Guianese and French sites were mainly due to a species richness effect.

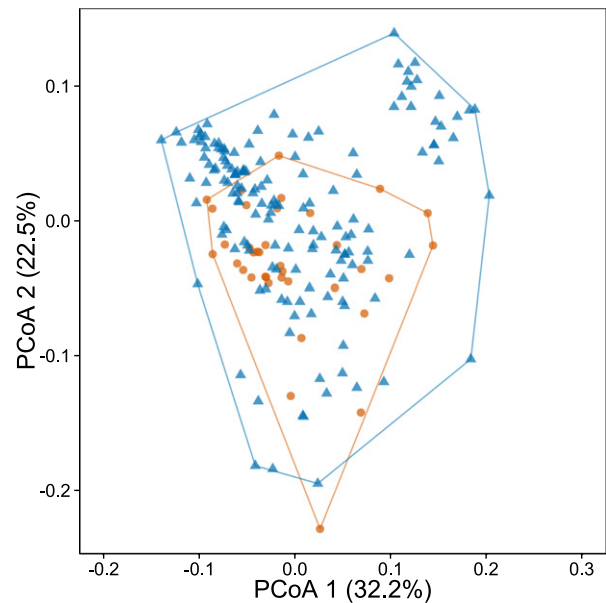


Figure 4 Ordination of fish species along the axes of the first two principal components (representing 54.7% of the total inertia) based on the functional distance matrix computed with Gower's distance on the 15 morpho-anatomic measures. Convex hulls for continental France (●) and French Guiana (▲) are represented.

Testing the effect of the difference in the number of drainage basins revealed that both βT_j and taxonomic turnover showed higher mean inter-basin dissimilarity values than

intra-basin values for continental France (permutation tests: βT_j , $F = 52.4$, $P < 0.001$; taxonomic turnover, $F = 43.6$, $P < 0.001$) and French Guiana (βT_j , $F = 14.2$, $P < 0.001$; taxonomic turnover, $F = 44.6$, $P < 0.001$).

βT_j and taxonomic turnover were higher for Guianese assemblages ($\beta T_j = 0.84 \pm 0.096$; taxonomic turnover = 0.76 ± 0.14) than for French assemblages ($\beta T_j = 0.65 \pm 0.16$; taxonomic turnover = 0.52 ± 0.23) (Fig. 5a; homogeneity of multivariate dispersion test on average distance-to-centroids: $F = 117.17$, $P < 0.001$ for βT_j and $F = 86.77$, $P < 0.001$ for taxonomic turnover). Contribution of turnover to taxonomic dissimilarity was high for both regions, but its contribution was higher for French Guiana (0.91 ± 0.11) than for continental France (0.77 ± 0.26) (Fig. 5b; permutation test: $F = 738$, $P < 0.001$). In contrast, βF_j and functional turnover were greater for French assemblages ($\beta F_j = 0.88 \pm 0.14$; functional turnover = 0.63 ± 0.33) than for Guianese assemblages ($\beta F_j = 0.79 \pm 0.14$; functional turnover = 0.49 ± 0.25) (Fig. 5c; homogeneity of multivariate dispersion test on average distance-to-centroids: $F = 77.99$, $P < 0.001$ for βF_j and $F = 47.42$, $P < 0.001$ for functional turnover). Contribution of turnover to functional dissimilarity was lower for French Guiana (0.62 ± 0.29) than for continental France (0.70 ± 0.33) (Fig. 5d; permutation test: $F = 114$, $P < 0.001$).

For both French Guiana and continental France, βF_j and βT_j were significantly correlated (French Guiana: $r = 0.60$, $P < 0.001$; continental France: $r = 0.56$, $P < 0.001$) as well as taxonomic and functional turnover components (French

Guiana: $r = 0.49$, $P < 0.001$; continental France: $r = 0.72$, $P < 0.001$). However, the magnitude of the taxonomic and of the functional β -diversity and turnover differed between the two regions. For French Guiana, taxonomic β -diversity and turnover were higher than functional β -diversity and turnover ($\beta F_j - \beta T_j$: Wilcoxon signed-rank test: $z = -21.62$, $P < 0.001$; turnover: Fig. 6a; $z = 48.05$, $P < 0.001$). In contrast, in continental France, functional β -diversity and turnover were higher than taxonomic β -diversity and turnover ($\beta F_j - \beta T_j$: $z = 48.05$, $P < 0.001$; turnover: Fig. 6b; $z = -0.52$, $P < 0.001$).

We found significant distance decay relationships for the Guianese βT_j and taxonomic turnover for both regions (Table 1). Slopes of the regressions of βT_j and taxonomic turnover did not differ between continental France and French Guiana (βT_j : $P = 0.074$; taxonomic turnover: $P = 0.12$), but the intercept differed (βT_j : $P < 0.001$; taxonomic turnover: $P < 0.001$), being higher for French Guiana. Both slopes and intercepts differed for βF_j (slope: $P = 0.0033$; intercept: $P = 0.023$), with higher intercept and a more pronounced distance decay for French assemblages. The slope for functional turnover in French assemblages was higher than the slope for French Guiana ($P < 0.001$), but the intercept did not differ between the two regions ($P = 0.13$).

For French Guiana, null models showed that 23 comparisons of 3486 for taxonomic turnover were significantly different from random expectations. The median of distribution differed significantly from zero (median = 0.10, $z = 5.99$, $P < 0.001$). A greater number of pairs of communities were

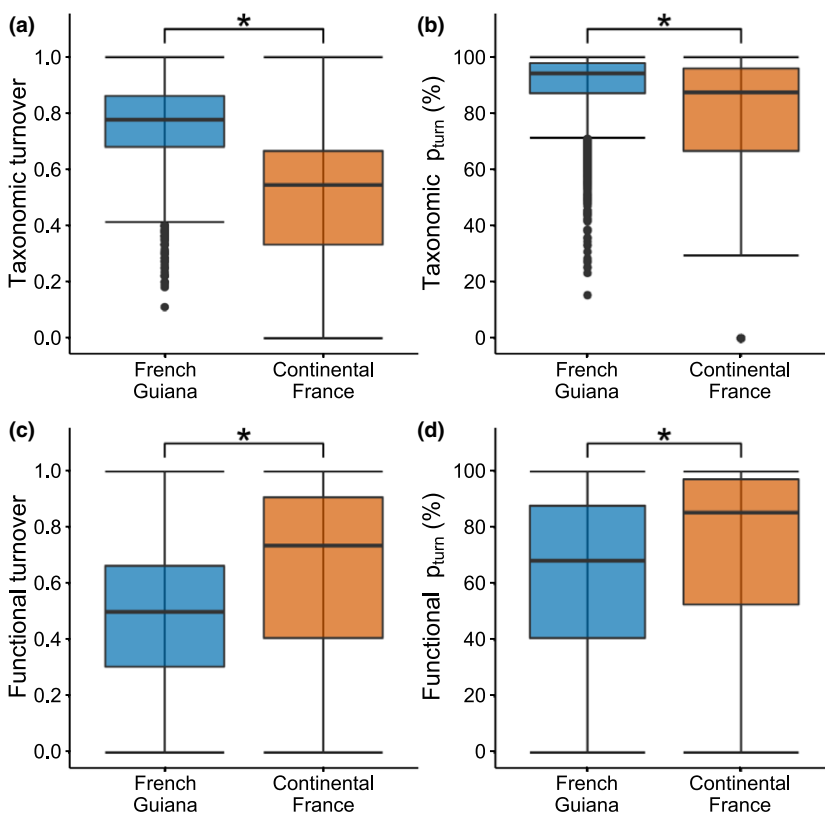


Figure 5 Pairwise taxonomic and functional β -diversity among the 84 fish assemblages (a, c) and the relative contribution of the turnover component to overall dissimilarity (p_{turn}) (b, d) for continental France and French Guiana. Significant differences between the two regions are indicated above the boxes (*), and based on the homogeneity of multivariate dispersion test on average distance-to-centroids and permutation procedure.

Figure 6 Relationships between pairwise taxonomic and functional turnover among the 84 fish assemblages for French Guiana (a) and continental France (b). Squares and bars represent medians and 25th/75th percentiles respectively. The line 1:1 is represented.

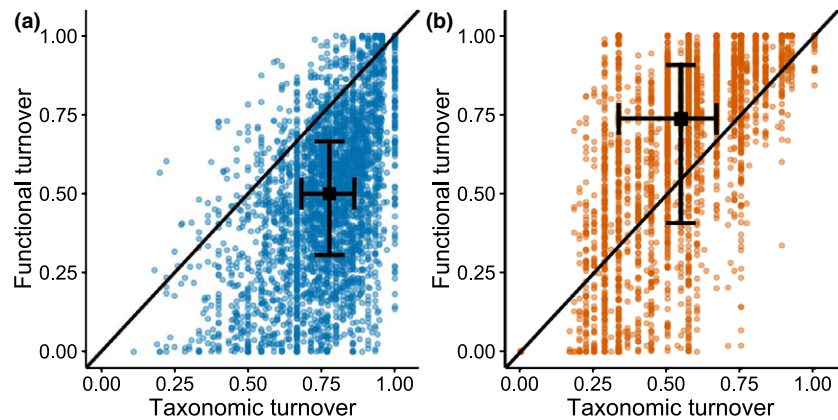


Table 1 Regression parameters of the relationship between diversity metrics (βT_j , βF_j and turnover) of the fish faunas and the pairwise geodesic distance (logged value) between sites for continental France and French Guiana estimated by bootstrap based on 9999 permutations. Spearman correlation coefficient r and P were obtained from Mantel tests with 9999 permutations.

Metric	Region	Intercept (95% CI)	Slope (95% CI)	r	P
βT_j	Continental France	0.54 (0.51–0.57)	0.026 (0.019–0.032)	0.069	0.069
	French Guiana	0.75 (0.73–0.76)	0.021 (0.017–0.024)	0.13	0.0043
Taxonomic turnover	Continental France	0.37 (0.33–0.41)	0.034 (0.025–0.043)	0.087	0.034
	French Guiana	0.64 (0.61–0.66)	0.029 (0.024–0.034)	0.14	0.001
βF_j	Continental France	0.80 (0.77–0.84)	0.018 (0.010–0.026)	0.015	0.39
	French Guiana	0.76 (0.74–0.79)	0.0064 (0.0016–0.011)	0.026	0.31
Functional turnover	Continental France	0.48 (0.42–0.54)	0.034 (0.021–0.049)	0.034	0.23
	French Guiana	0.44 (0.41–0.48)	0.010 (0.0024–0.018)	0.040	0.20

different from random expectation when looking at functional diversity turnover while conserving the observed taxonomic turnover (131 out of 3486). The median of simulated functional turnover distribution was significantly different from zero (median = 0.19, $z = 7.79$, $P < 0.001$). In continental France, 197 taxonomic turnover measures were not consistent with random assembly. Taxonomic turnover distribution showed a median of 0.052 that did not differ from zero ($z = 0.47$, $P = 0.64$). A lower number of pairs of communities were different from random expectation when looking at the functional diversity facet while conserving the observed taxonomic β -diversity (113 pairs). However, the median of the simulated distribution was significantly different from zero (functional turnover: median = 0.50, $z = 17.88$, $P < 0.001$).

DISCUSSION

A major limitation in studies comparing biodiversity patterns from distant areas is the availability of databases collected at similar grain and extents. The total species pool and the distance between samples are affected by the geographical extent of the studies (Steinbauer *et al.*, 2012), and grain size affects α -diversity through a species–area effect, with an increase in habitat heterogeneity (Devictor *et al.*, 2010). β -diversity is also sensitive to grain size as smaller grains are less species-rich than larger ones and thus more likely to

share fewer species between each other than larger grains (Garzon-Lopez *et al.*, 2014). In addition, to compare community assembly processes across regions, data should also encompass similar environmental or topographic gradients between regions (e.g. altitude range or stream order), as these gradients have a profound effect on assemblages structure (Melo *et al.*, 2009; Jaramillo-Villa *et al.*, 2010). Here, these potential biases were controlled by collecting European and South American data at the same grain size and by constraining European data to fit the spatial extent and the topographic gradient encompassed by South American sites, therefore allowing us to explore differences between temperate and tropical faunas independently of scale and environmental gradient effects.

The higher taxonomic diversity we report in Guiana compared to France at both regional and local grains is known for most taxa (Ricklefs & O'Rourke, 1975; Novotny *et al.*, 2006). A similar trend is also forecast for functional richness, which may be positively related to the number of species (Safi *et al.*, 2011; Lamanna *et al.*, 2014). The differences we report between temperate and tropical environments increased when turning from taxonomic to functional diversity, at both regional and local scales. However, when controlling for the number of species, the Guianese fish fauna is not more functionally diverse than the French fauna. This was also the case at the local scale and suggests that the higher functional diversity in Guiana mainly results from an

addition of functional attributes across the region. The greater functional richness found in the tropical region was hence not driven by a triggered functional diversity of the tropical species, but more probably by a higher diversity of habitats which allows a greater diversity of ecological niches and thus a greater number of species (Koeck *et al.*, 2014).

Turning from α - to β -diversity patterns sheds light on the assembly processes that structure the fish faunas. Species replacement between sites (turnover) was higher in Guianese assemblages, which are thus composed of a higher number of species whose identity differed in a large part between sites. In contrast, functional turnover was higher in French assemblages than in Guianese ones. According to our predictions, Guianese fish assemblages result from a prominent effect of dispersal limitation that promotes a stronger taxonomic turnover than functional turnover (Swenson *et al.*, 2012b; Myers *et al.*, 2013). However, French assemblages appear more strongly influenced by environmental filtering that promotes lower taxonomic turnover than functional turnover (Swenson *et al.*, 2012a; Myers *et al.*, 2013). Null models confirmed this with species more aggregated within assemblages than expected in French Guiana and a greater functional dissimilarity than expected between assemblages in continental France.

The differences in diversity patterns and processes governing assemblage structure between the two regions might root in their biogeographical history and evolutionary causes. First, tropical climates have been hypothesized to have been more stable than temperate climates and thus led a longer time for species diversification than temperate regions (Gaston & Blackburn, 1996). Moreover, faster diversification in tropical regions has been found in equal time periods, linked with less drastic extinction events during Quaternary climatic fluctuations (Rolland *et al.*, 2014). Secondly, the Guianese ichthyofauna results from the ancient complex biogeographical history of the Neotropical region, involving events of marine incursions, uplift of the Andes and the raising of palaeoarches that modified South America's hydrological network (Lujan & Armbruster, 2011), and from more recent dispersal events via coastal routes from the Amazon in the south and from the Orinoco in the Northwest that occurred during the Miocene (Hubert & Renno, 2006; Cardoso & Montoya-Burgos, 2009). The current fauna thus presents different species pools that contribute to the high regional taxonomic α - and β -diversity in French Guiana. The studied French fauna on the other hand results mainly from a more recent recolonization of Western Europe by a single Danubian species pool after the Last Glacial Maximum (26,500–19,000 years ago) (Taberlet *et al.*, 1998; Kotlík & Berrebi, 2001). The recolonization from a single pool of species hence reduced both the richness in species and the taxonomic turnover across Western Europe.

Although differences in biogeographical history explain taxonomic patterns, they do not provide information on assembly rule processes. Here, we show that in Guianese streams, despite the density of the river network that could

favour faunistic exchanges between basins, the local fish assemblages were effected of by both inter- and intra-basin dispersal limitation. Despite this high turnover in species composition, we report a moderate functional turnover in Guianese streams. Functional diversity represents the range of ecological strategies of the species (Violle *et al.*, 2007; Cadotte *et al.*, 2011; Mouillot *et al.*, 2011) and thus niche availability in local habitats. The high local species richness in Guianese streams hence testifies for a high local diversity of niches, but the same niches are probably shared by most sites explaining therefore the low functional β -diversity (Weinstein *et al.*, 2014). The limited effect of environmental filtering may be due to the relative homogeneity in available habitats between sites. Guianese fish fauna, even historically resulting from different biogeographical origins, is thus composed of species that converged in the use of similar niches, and the co-occurrence of those species being allowed by the high complexity in local habitats.

In the French fish assemblages, functional turnover was higher than taxonomic turnover meaning that the fauna exhibited local adaptations to different environments. Such environmental filtering might be due to the low similarity of available niches between sites (Weinstein *et al.*, 2014). Indeed, under temperate climates, the thermal regime of streams can be markedly different between lowland and piedmont areas, therefore constituting a strong environmental filter for the fauna. Cool-water (lowland) and cold-water (piedmont and mountain) streams are indeed inhabited by phylogenetically and functionally distinct fish faunas (Blanchet *et al.*, 2014). Moreover, the reduced strength of dispersal limitation in France also has historical roots, as the French fauna results from a recent post-glacial recolonization by high-dispersal species (Griffiths, 2006; Hof *et al.*, 2008), that are hence likely to cross longer distances than Guianese stream fishes.

The use of phylogenetic diversity in combination with taxonomic and functional diversity may allow a more complete view of community assembly rules to be assessed (Weinstein *et al.*, 2014). An assumption behind this framework is that closely related species tend to have similar functional traits and ecological niches (Webb, 2000). If true, then environmental filtering should result in communities with more closely related species than randomly assembled communities. Conversely, communities with more distant-related species than random communities should be driven by competitive interactions. So, developing and using a robust phylogeny of freshwater fish present in both regions (or for all fish species) will be a major future step in comparative analyses of assembly processes.

Beyond their conceptual interest, understanding the processes affecting species assembly are also informative in a biodiversity conservation context (Mouillot, 2007; Rossetto *et al.*, 2008). Indeed, faunas assembled through dispersal limitation, such as Guianese stream fishes, are sensitive to local extinctions, because the recolonization of disturbed sites from distant assemblages is almost impossible. Therefore, the

restoration of sites after human disturbance might not result in the re-establishment of the initial fauna. This might explain why local studies report limited post-disturbance recolonization, even after a complete recovery of the stream physical and chemical characteristics (Brosse *et al.*, 2011; Allard *et al.*, 2016). Particular attention should therefore be devoted to the conservation of pristine sites to avoid local species extirpations. In contrast, in Europe, restoring and managing habitat diversity may be a priority, as assemblages being less constrained by dispersal limitations could have more chance to recolonize restored streams.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of fish species.

Appendix S2 Physical characteristics and pairwise distances among the selected French Guiana and continental sites.

Appendix S3 Morphological measurements and functional traits measured.

Appendix S4 Correlations between functional traits and PCoA components.

Appendix S5 Ordination of species along 1st, 3rd and 4th PCoA components.

BIOSKETCH

Kévin Cilleros is a PhD student in the laboratory 'Evolution et Diversité Biologique' (University of Toulouse, France). He is interested in diversity patterns and assembly rules of fish assemblages in French Guiana and how to use different aspects of diversity to unravel these processes.

Author contributions: K.C., G.G. and S.B. conceived the ideas; L.A., G.G. and S.B. collected the data for French Guiana; K.C. analysed the data; and K.C. led the writing, with contributions of L.A., G.G. and S.B.

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