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Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages

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ABSTRACT

Aim One of the main gaps in the assessment of biodiversity is the lack of a unified framework for measuring its taxonomic and functional facets and for unveiling the underlying patterns.

Location Europe, 25 large river basins.

Methods Here, we develop a decomposition of functional β-diversity, i.e. the dissimilarity in functional composition between communities, into a functional turnover and a functional nestedness-resultant component.

Results We found that functional β-diversity was lower than taxonomic β-diversity. This difference was driven by a lower functional turnover compared with taxonomic turnover while the nestedness-resultant component was similar for taxonomic and functional β-diversity.

Main conclusions Fish faunas with different species tend to share the same functional attributes. The framework presented in this paper will help to analyse biogeographical patterns as well as to measure the impact of human activities on the functional facets of biodiversity.

Keywords
Beta-diversity, convex hull volume, Europe, freshwater fish, functional diversity, functional richness, functional traits, overlap.

INTRODUCTION

One of the key issues in ecology is the measurement of biodiversity, to understand its determinants and prioritize its conservation (Purvis & Hector, 2000; McKnight *et al*., 2007; Devictor *et al*., 2010; Leprieur *et al*., 2011). Biodiversity is a multifaceted concept which goes further than simply the number of species present in a given place, i.e. taxonomic α-diversity. Indeed, beyond local diversity (α), β-diversity, defined as the variation in species composition, is another key feature which has been considered for a long time in ecological studies (Whittaker, 1960; Koleff *et al*., 2003; Anderson *et al*., 2011).

The simplest meaning of taxonomic β-diversity, and one of the most frequently used, is the percentage of dissimilarity in species composition between two communities (Koleff *et al*., 2003). Recently, a series of papers brought key conceptual advances for the disentanglement of the patterns underlying pairwise dissimilarity in species composition (Baselga, 2010, 2012; Carvalho *et al*., 2012). Taxonomic β-diversity can indeed be decomposed into taxonomic turnover (i.e. species replacement between communities) and nestedness-resultant components (i.e. those that reflect the difference in the number of species among communities). For instance, a high level of β-diversity can characterize two contrasting situations. It can result from a low proportion of shared species between two communities with a similar number of species, leading to a high contribution of the turnover component and a low value for the nestedness-resultant component. In contrast, it can also result from a species richness difference between two communities, when the poorer is a subset of the richer, leading to a low value for turnover but a high value for the nestedness-resultant component.

Both α- and β-diversity approaches have frequently been conducted on the taxonomic facet of biodiversity. It is, however,

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widely acknowledged that taxonomy is not sufficient to understand the structure of species assemblages (Villéger *et al.*, 2008; Swenson *et al.*, 2012) and their effects on ecosystem functioning (Díaz *et al.*, 2007; Lavorel *et al.*, 2011; Mouillot *et al.*, 2011) without considering the functional facet of biodiversity (i.e. the diversity of biological strategies, McGill *et al.*, 2006). Towards this objective, many indices of functional diversity have been proposed over the last decade (Petchey & Gaston, 2006; Mouchet *et al.*, 2010), including indices to assess the level of functional dissimilarity among communities (Anderson *et al.*, 2006; Ricotta & Burrascano, 2008; de Bello *et al.*, 2010; Swenson *et al.*, 2011; Villéger *et al.*, 2011a). Indeed, functional β-diversity is a key facet of biodiversity as it helps disentangle community assembly processes across environmental gradients or spatial scales (Pavoine & Bonsall, 2011; Stegen & Hurlbert, 2011; Swenson, 2011; Swenson *et al.*, 2011; Münkemüller *et al.*, 2012). For instance, two communities with few species in common (high taxonomic β-diversity) would show a low functional β-diversity if their respective species are functionally similar.

Nevertheless, comparing only taxonomic and functional β-diversity does not unveil the underlying patterns, i.e. replacement of species (or functional strategies) and difference in species (or functional) richness. Indeed, as for taxonomic β-diversity, a high level of functional β-diversity can actually result from a high level of functional turnover (i.e. the communities host different functional strategies) or a low level of functional turnover (i.e. one community hosts a small subset of the diversified functional strategies present in the other one). Analysing taxonomic and functional β-diversity and their respective components offers a unique opportunity to test the ecological processes structuring communities. For instance, for two communities having similar species richness but only a few species in common (i.e. high taxonomic β-diversity due to a high taxonomic turnover), a high functional β-diversity can have multiple meanings (Fig. 1). In one way, it can be driven by a high functional turnover if unique species from each community are functionally very different, indicating niche differentiation between communities. But in another way a high functional β-diversity can also result from a low functional turnover, if the species hosted by one community represent only a small subset of the functional strategies present in the other community, indicating different niche filtering intensity between communities. On the contrary, low functional β-diversity is expected if the species present in the two communities, although different, have the same functional strategies (i.e. functional convergence).

Currently available functional β-diversity indices use several approaches, such as a dissimilarity index based on trait composition (Anderson *et al.*, 2006; Stegen & Hurlbert, 2011; Swenson *et al.*, 2011), overlap of communities in a multidimensional functional space (Villéger *et al.*, 2011a) or an entropy-derived index including pairwise functional distances between species as well as their abundances (Ricotta & Szeidl, 2009). Nevertheless, decomposition of functional β-diversity into its turnover and nestedness-resultant components is still lacking, although it would be a keystone towards a unified framework allowing comparison of taxonomic and functional β-diversity patterns and hence testing of ecological processes.

Here, we fill this gap by proposing a decomposition of functional β-diversity allowing the quantification of the contribution of functional turnover and functional nestedness-resultant components, and their comparison with taxonomic β-diversity. We then applied this framework to European freshwater fish faunas to compare taxonomic and functional β-diversity and their respective turnover and nestedness-resultant components. Finally, we tested whether functional richness and functional β-diversity were significantly different from null-expectation given the observed patterns of taxonomic richness and β-diversity.

MATERIAL AND METHODS

Partitioning taxonomic β-diversity into turnover and nestedness-resultant components

Dissimilarity in species composition between a pair of communities (C1 and C2) is classically illustrated using a Venn diagram (Fig. 1a) where each community is represented by a two-dimensional object with an area proportional to its species richness (Koleff *et al.*, 2003; Villéger & Brosse, 2012). The number of species shared (a) is symbolized by the area at the intersection between the two objects. The total number of species is symbolized by the union of the two objects and equals $a + b + c$, with b and c being respectively the number of species present only in the first and second community (Fig. 1a). Species richness (hereafter denoted S) in the two communities is thus $S(\mathrm{C1}) = a + b$ and $S(\mathrm{C2}) = a + c$.

This representation led to one of the multiple meanings of taxonomic β-diversity (Anderson *et al.*, 2011; Baselga, 2012), i.e. the percentage of dissimilarity in species composition between two communities: taxonomic β-diversity = (number of species not shared)/(total number of species). This pairwise taxonomic β-diversity is measured using Jaccard's dissimilarity index (Anderson *et al.*, 2011; Baselga, 2012; Carvalho *et al.*, 2012):

$$\text{taxonomic }\beta\text{-diversity} = \frac{b+c}{a+b+c} = \frac{S(C1)+S(C2)-2\times S(C1\cap C2)}{S(C1)+S(C2)-S(C1\cap C2)} \tag{1}$$

Taxonomic β-diversity equals zero when the two communities host the same species ($b = c = 0$) and equals one when the two communities share no species ($a = 0$). However, it can be noticed that taxonomic β-diversity could be close to its maximal value even if the two communities share some species ($a > 0$), provided that one community has a much larger number of species than the other ($a + \min(b,c) << \max(b,c)$). Thus, taxonomic β-diversity is not only determined by species turnover among communities but also by difference in species richness (Baselga, 2010, 2012). Therefore, Baselga (2012) suggested that taxonomic β-diversity is the sum of a turnover component (i.e. species replacement in the two communities)

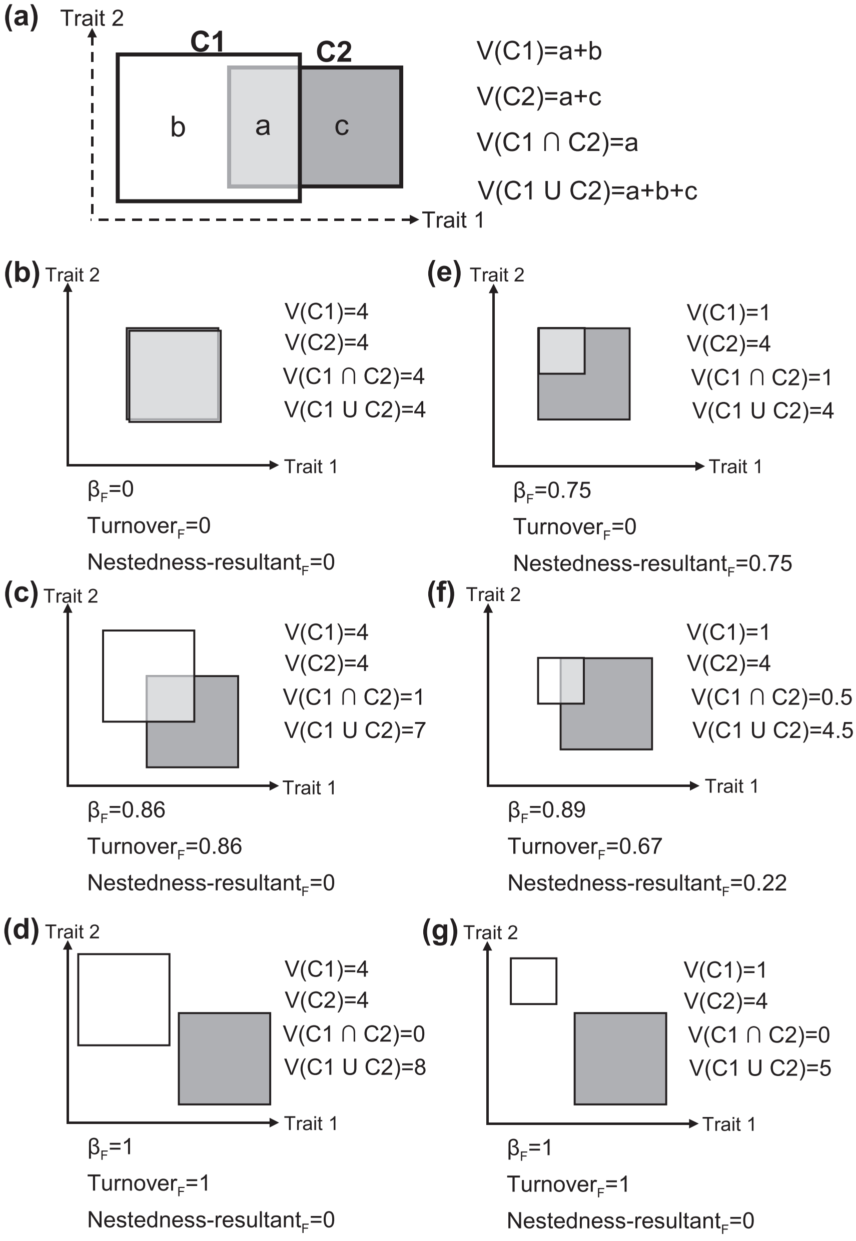

Figure 1 Conceptual framework for the decomposition of functional β-diversity. (a) Classical representation of taxonomic β-diversity for a pair of two communities (C1 and C2) using a Venn diagram (for graphical simplicity, polygons instead of ellipses are used). *a* is the number of species shared by the two communities and *b* and *c* are the number of species present only in C1 and C2, respectively. This representation can be directly transposed to functional β-diversity by considering the convex hull shaping the two communities in a functional space defined by functional axes (dashed arrows, only two for graphical convenience). Correspondences between *a*, *b*, *c* and the volumes of convex hulls, their intersection and union are given on the right. (b)–(g) Six hypothetical case studies. For each panel the convex hull of two communities (C1 in white, C2 in grey) are plotted in a hypothetical functional space. The number of species is not represented as it could be equal or differ between the two communities. For graphical simplicity the convex hulls are squares and their respective volumes are provided on the right as well as the volume of their intersection. Functional β-diversity (β_F) and its two components, functional turnover and functional nestedness-resultant components, are provided under each panel (see text for formulae).

and a nestedness-resultant component (i.e. influenced by the difference in number of species between the two communities). This can be written as

$$\frac{b+c}{a+b+c}=\frac{2\times\min(b,c)}{a+2\times\min(b,c)}+\frac{|b-c|}{a+b+c}\times\frac{a}{a+2\times\min(b,c)} \qquad (2)$$

Like taxonomic β-diversity, turnover and nestedness-resultant components vary between 0 and 1 (Baselga, 2012). Taxonomic turnover equals zero when one community hosts a subset of species present in the other one ($b = 0$ or $c = 0$). It equals one when no species are shared by the two communities ($a = 0$). The nestedness-resultant component of taxonomic β-diversity equals zero when the two communities have the same number of species ($b = c$) or have a unique composition ($a = 0$). It tends to one when one community hosts a small subset of the species present in the other community ($\max(b,c) >> a > \min(b,c) = 0$).

Partitioning functional β-diversity into functional turnover and functional richness difference

Measuring functional diversity based on community composition and species functional traits could be achieved using a multidimensional functional space (Villéger *et al.*, 2008), where axes are functional traits or synthetic components summarizing functional traits [e.g. from principal coordinates analysis (PCoA); Villéger *et al.*, 2008]. Species are plotted in this multidimensional functional space according to their respective functional trait values. The functional richness of a community thus corresponds to the proportion of functional space it fills

(Villéger *et al.*, 2008; Mouchet *et al.*, 2010). The functional richness of a community is measured using the volume inside the convex hull (i.e. the minimum convex polytope) that contains all of its species (Cornwell *et al.*, 2006).

Then, according to Villéger *et al.* (2011a), by analogy with taxonomic β-diversity, the functional β-diversity between two communities (*C1* and *C2*) is: functional β-diversity = (functional space not shared)/(total functional spce filled) (Fig. 1a).

Given the volume of the convex hulls of each of the two communities (V(C1) and V(C2)) and of their intersection V(C1∩C2), we thus have:

$$\text{functional }\beta\text{-diversity} = \frac{V(C1)+V(C2)-2\times V(C1\cap C2)}{V(C1)+V(C2)-V(C1\cap C2)}. \quad (3)$$

It appears that equations (1) and (3) are equivalent, i.e. the functional β-diversity of Villéger *et al.* (2011a) based on convex hull volume is equivalent to Jaccard's dissimilarity index based on the number of species. Therefore, functional β-diversity can be decomposed into functional turnover and functional nestedness-resultant components following the framework of Baselga (2012). According to equation (2) and the following equivalences: $a = V(\mathrm{C1}\cap\mathrm{C2})$, $b = V(\mathrm{C1}) - V(\mathrm{C1}\cap\mathrm{C2})$ and $c = V(\mathrm{C2}) - V(\mathrm{C1}\cap\mathrm{C2})$ (Fig. 1a):

$$\text{functional }\beta\text{-diversity} = \text{functional turnover} + \text{functional nestedness-resultant}$$

with

$$\text{functional turnover} = \frac{2\times \min(V(C1),V(C2)) - 2\times V(C1\cap C2)}{2\times \min(V(C1),V(C2)) - V(C1\cap C2)} \quad (4)$$

and

$$\text{functional nestedness-resultant} = \frac{|V(C1)-V(C2)|}{V(C1)+V(C2)-V(C1\cap C2)} \times \frac{V(C1\cap C2)}{2\times \min(V(C1),V(C2)) - V(C1\cap C2)}. \quad (5)$$

Similarly to taxonomic β-diversity and its components, functional β-diversity and its turnover and nestedness-resultant components vary between zero and one depending on the respective functional richness of the two communities and their overlap in the functional space. Functional β-diversity is minimal when the two communities overlap totally (i.e. $V(\mathrm{C1}) = V(\mathrm{C2}) = V(\mathrm{C1}\cap\mathrm{C2})$), which implies that both functional turnover and functional nestedness-resultant components also equal zero (Fig. 1b).

As for taxonomic β-diversity, a high level of functional β-diversity can result from a high functional turnover due to low overlap in the functional space between two communities (i.e. $V(\mathrm{C1}\cap\mathrm{C2}) = 0$, Fig. 1d, g). A high functional β-diversity could also result from a low level of functional turnover but a high functional nestedness-resultant dissimilarity (Fig. 1e), when one community fills only a small portion of the functional space filled by the other (i.e. $\min(V(\mathrm{C1}), V(\mathrm{C2})) = V(\mathrm{C1}\cap\mathrm{C2}) << \max(V(\mathrm{C1}),V(\mathrm{C2}))$). More generally, similar levels of functional β-diversity could result from contrasting levels of turnover and nestedness-resultant components (Fig. 1c, f).

Measuring taxonomic and functional β-diversity in European fish faunas

We measured the taxonomic and functional β-diversity and their respective turnover and nestedness-resultant components among 25 European fish faunas. The fish faunas correspond to native species lists reported in the literature for 25 large European drainage basins (Leprieur *et al.*, 2008). These basins cover most of western Europe from the south-west of the Iberian Peninsula to the north-west of Russia (Fig. 2).

Fish functional niche was characterized for its two main facets, food acquisition and locomotion, using seven functional traits commonly included in studies on fish functional diversity (e.g. Lamouroux *et al.*, 2002; Olden *et al.*, 2006). Three traits were continuous: body length, body shape ratio (total length/maximal body depth) and swimming factor (minimum caudal peduncle depth/maximal caudal fin depth), and four traits were coded as ordered categorical variables: diet, feeding position, rheophily and position in the water column (see Table S1 in Supporting Information). These seven functional traits were assessed for all the fish present in this database based on pictures and information available in FishBase (Froese & Pauly, 2011) and Kottelat & Freyhof (2007).

Functional distances between each pair of species were computed using Gower's distance which allows different types of variables to be mixed while giving them equal weights (Gower, 1971). Then, a PCoA was carried out on this functional distance matrix (Villéger *et al.*, 2008; Laliberté & Legendre, 2010). Following a trade-off between information quality and computation time, we finally kept the species coordinates on the first three axes as the values of three synthetic functional traits describing fish functional strategies (Villéger *et al.*, 2011a).

For each of the 300 pairs of fish faunas, taxonomic β-diversity and its turnover and nestedness-resultant components were computed following equation 2. For each of these pairs, functional β-diversity and its turnover and nestedness-resultant components were computed following the subsequent equations 3–5. An R function for computing taxonomic and functional β-diversity and their respective turnover and nestedness-resultant components is provided in Appendix S1.

The correlations between taxonomic and functional β-diversity as well as between their respective components were tested using Mantel permutational tests. Partial Mantel tests were also carried out to account for geographical distance between basins, difference in species richness and the combination of these two variables. These analyses aimed to disentangle the correlation between taxonomic and functional β-diversity and their components from potential biogeographical effects.

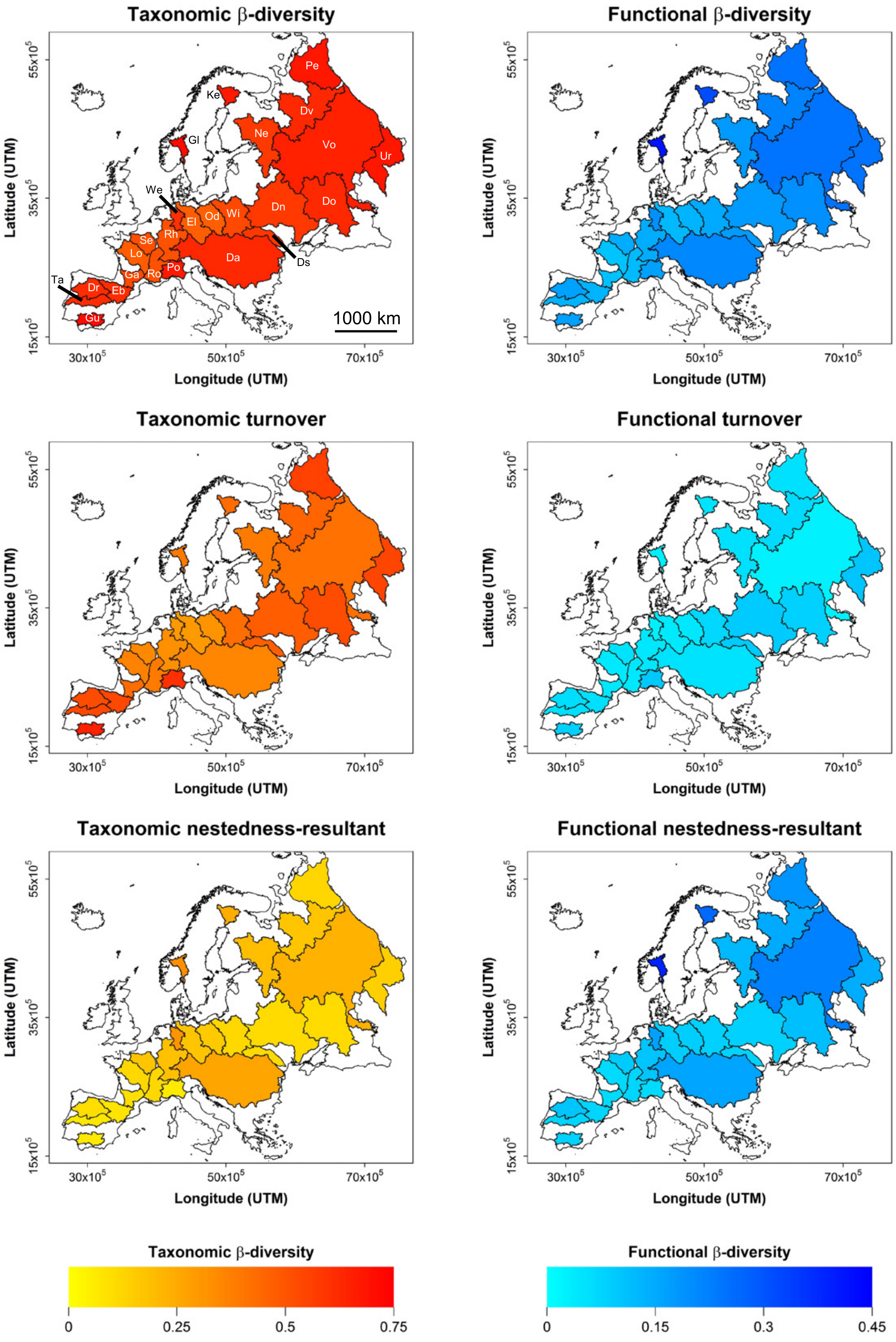

Figure 2 Spatial patterns of taxonomic and functional β-diversity and their respective turnover and nestedness-resultant components for the 25 European fish faunas. Index values for each fauna correspond to the average of the pairwise comparisons between that fauna and the 24 others weighted by the inverse of their geographical distances. River basin names are shown in top left panel: Da, Danube; Dn, Dnieper; Ds, Dniester; Dv, Dniva; Do, Don; Dr, Douros; Eb, Ebro; El, Elbe; Ga, Garonne; Gl, Glomma; Gu, Guadalquivir; Ke, Kemijoki; Lo, Loire; Ne, Neva; Od, Oder; Pe, Petchora; Rh, Rhine; Ro, Rhone; Se, Seine; Ta, Tagus; Ur, Ural; Vo, Volga; We, Weser; Wi, Wisla. UTM, Universal Transverse Mercator.

For each river basin, we considered average values of taxonomic and functional β-diversity by computing the weighted mean of the pairwise comparisons between each focal basin and the 24 remaining basins using the inverse of geographical distance between basins as weights. This weighting strengthened the importance of the changes occurring between focal and adjacent basins compared with distant ones (Leprieur *et al.*, 2011).

Testing functional β-diversity in European fish faunas

Comparing the observed patterns of taxonomic and functional diversity is of interest but to go further a key question is to test whether the observed functional diversity values result from non-random assembly processes.

As a first step we tested whether the functional richness of each basin differs from a random expectation given its taxonomic richness. We thus designed a null-model in which the observed number of species in each basin was kept constant, but species identity was randomly chosen among the global pool of species (i.e. present in the 25 basins). For each basin, 999 communities were generated and simulated values of functional richness were computed accordingly. Then we compared the distribution of simulated values to the observed one using a two-tailed test. If fewer than 2.5% of the simulated values were lower than the observed one, we concluded that the species present in the basin were significantly clustered in the functional space. In contrast, if more than 2.5% of the simulated values were higher than the observed one, we concluded that the species present in the basin were significantly overdispersed in the functional space.

Then we tested the null hypothesis that the observed values of functional β-diversity (and its two components) are not significantly different from a random expectation given the observed values of taxonomic β-diversity (and its two components) and the pool of species present in the two assemblages. To this end we designed a null-model for each pair of fish assemblages which randomly permuted, separately, the identity of the species unique to each assemblage and those of the species shared by the two assemblages. Therefore, this permutation process kept constant (1) the species richness of each river basin, (2) taxonomic β-diversity and its turnover and nestedness-resultant components of each river basin pair, and (3) the pool of functional strategies present in each pair of basins. The permutations were repeated 999 times for each pair of assemblages and the simulated values of functional β-diversity (and of its two components) were compared with the corresponding observed values to compute a *P*-value (bilateral test with a confidence level of 5%).

RESULTS

Taxonomic and functional richness

The 25 basins hosted a total of 230 fish species with a mean taxonomic richness of 57 species per basin (± SD 22, range 23–112).

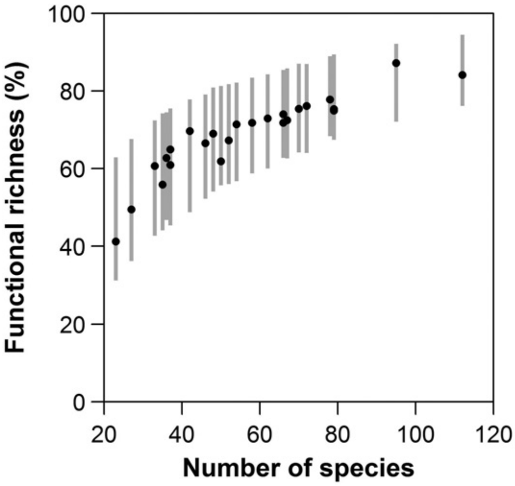

Figure 3 Taxonomic and functional richness. Black points show observed values of number of species and percentage of the available functional space filled by each of the 25 fish assemblages. Grey bars show the 95% confidence-intervals obtained from the null model testing the expected functional richness given the taxonomic richness and the global pool of species.

The Euclidean distances between species in the three-dimensional functional space obtained using PCoA were strongly correlated with the functional distances computed on species traits using Gower's metric (Mantel test, $r = 0.887$, $P < 0.001$). The largest interval between two neighbouring species was only 7% of the axis range (on PC1), and overall, for most species the closest neighbour was very close (median = 0.17%, third quartile = 0.41%). There were therefore no large gaps in our functional space.

Functional richness per basin ranged from 41 to 87% of the total functional space filled by the 230 species of the regional pool, with a mean of 68.7 ± 10.1%. Functional richness increased with species richness (Spearman's correlation of 0.96, $P < 0.001$; Fig. 3). However, in all the basins, the observed functional richness was not significantly different from the null expectation postulating a random species pool given the species richness (Fig. 3).

Taxonomic and functional β-diversity

The number of species shared by fish assemblages was on average half the total number of unique species (Table 1). Taxonomic β-diversity ranged from 0.22 to 0.95 with a mean value of 0.67 (± 0.16) (Table 1, Figs 4 & S1). On average, the turnover (0.53 ± 0.21) was higher by 0.39 than the nestedness-resultant component (0.14 ± 0.13, Table 1) and contributed to 77% (± 21%) of taxonomic β-diversity (Fig. 4d).

The overlap between fish assemblages in the functional space was almost four times higher than the functional space occupied by only one assemblage (Table 1). Functional β-diversity was significantly correlated with taxonomic β-diversity (Mantel test, $r = 0.599$, $P < 0.001$; Fig. 4a) but was on average lower with a

Table 1 Taxonomic and functional β-diversity.

	Taxonomic	Functional
β-diversity	0.67 ± 0.16 (0.22–0.95)	0.21 ± 0.10 (0.01–0.53)
Turnover	0.53 ± 0.21 (0.04–0.94)	0.07 ± 0.05 (0.00–0.25)
Nestedness-resultant	0.14 ± 0.13 (0.00–0.62)	0.14 ± 0.11 (0.00–0.53)
a	0.12 ± 0.06 (0.01–0.30)	0.61 ± 0.09 (0.37–0.78)
b + *c*	0.25 ± 0.09 (0.06–0.53)	0.16 ± 0.08 (0.00–0.46)

The three first rows summarize β-diversity and its two components; mean ± standard deviation and range (in parentheses).

The last two rows present a summary of taxonomic and functional richness shared (*a*) or unique (*b* + *c*) among the 300 pairs of fish communities studied. Values are expressed relative to the total richness present in the regional pool of species.

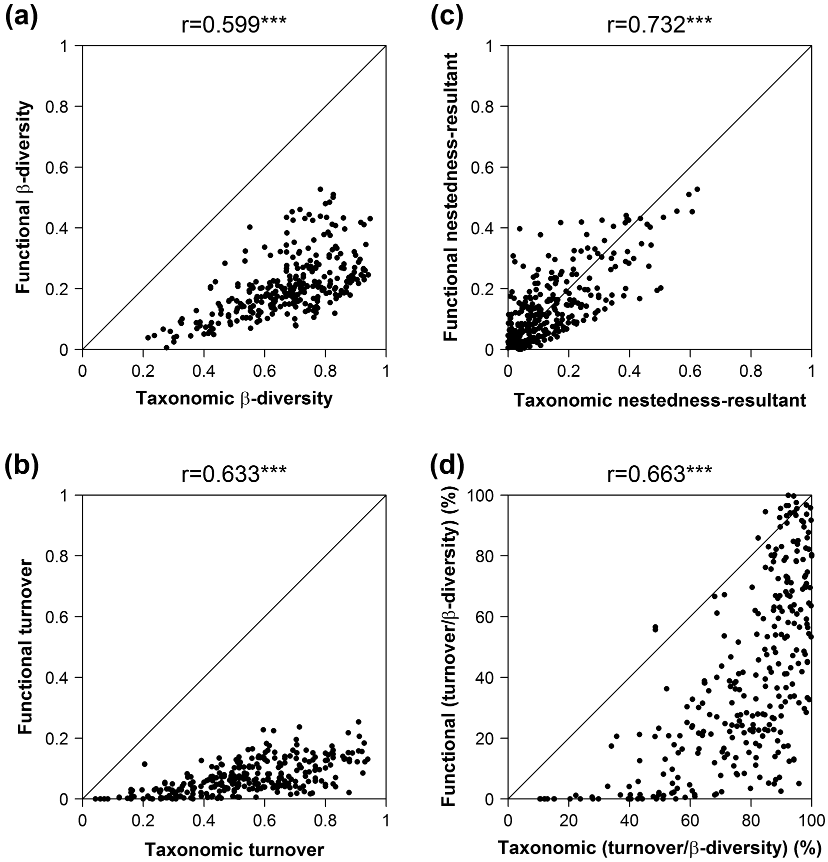

Figure 4 Correlations between taxonomic and functional β-diversity for the 300 pairs of European freshwater fish faunas (a) and their respective turnover (b) and nestedness-resultant (c) components. (d) Relative contribution of turnover to β-diversity for taxonomic and functional β-diversity. Values above each panel are Pearson's correlation coefficients and associated Mantel test *P*-value (***$P < 0.001$).

mean of 0.21 (± 0.10) (Table 1, Fig. S1). Nestedness-resultant components of taxonomic and functional β-diversity were strongly correlated ($r = 0.732$, $P < 0.001$; Fig. 4c) with a similar average value of 0.14 (± 0.11). In contrast, functional turnover was almost four times lower than taxonomic turnover with a mean of only 0.07 (± 0.06), even if the two metrics were also strongly correlated ($r = 0.633$, $P < 0.001$; Fig. 4b). Functional turnover contributed on average to only 40% (± 20%) of functional β-diversity (Fig. 4d).

When accounting for geographical distance between river basins and difference in number of fish species, correlation between taxonomic β-diversity and functional β-diversity was lower but remained significant (Table S2). Similar patterns were observed for turnover and nestedness-resultant components of both taxonomic and functional β-diversity even though the decrease of correlation strength when accounting for geography and species richness was of lower magnitude (Table S2).

Significance of observed functional β-diversity

Observed values of functional β-diversity were not significantly different from the null expectation of random species assemblages in all but seven pairs of fish assemblages (which showed significantly lower values). Similarly, values of turnover and nestedness-resultant components of functional β-diversity were not significantly different from the null expectation in 295 and 298 out of the 300 pairs of fish assemblages, respectively.

DISCUSSION

The original decomposition of functional β-diversity presented above allows the quantification of the respective contributions of functional turnover (i.e. functional space not shared by communities) and functional nestedness-resultant component (i.e. influenced by the difference in the functional space filled by communities) to the functional dissimilarity between communities. This framework is based on a particular view of functional β-diversity, i.e. the percentage overlap between two communities in a multidimensional functional space (Villéger *et al.*, 2011a). Therefore, the metrics depend on the functional richness of the communities and as such are influenced by the range of functional traits present (Cornwell *et al.*, 2006; Villéger *et al.*, 2008; Mouchet *et al.*, 2010). As a result, species with the most extreme trait combinations play a key role by shaping the portion of the functional space filled by communities but species with intermediate trait values affect the level of overlap by shaping the intersection between convex hulls.

This framework for measuring functional β-diversity is complementary to the distance-based methods which consider pairwise distances between species either directly (Ricotta & Szeidl, 2009; de Bello *et al.*, 2010), in a functional space after PCoA (Anderson *et al.*, 2006) or on a functional dendrogram (Mouchet & Mouillot, 2011; Swenson *et al.*, 2011). In particular, some of these metrics (Ricotta & Szeidl, 2009; Mouchet & Mouillot, 2011) allow species abundances to be considered, which is of interest when assessing functional β-diversity at the community level (de Bello *et al.*, 2010). However, to date, the convex hull method is the only one which allows functional β-diversity and its turnover and nestedness-resultant components to be measured in a way similar to those proposed for taxonomic β-diversity by Baselga (2012). Thus comparison of taxonomic and functional β-diversity and their respective components can easily be done. The framework is well suited to large-scale biogeographical studies where the data are often restricted to assemblage species composition and the number of species is often high, which allows the computation of convex hulls in multidimensional spaces.

For European fish faunas, it appears that the lower functional β-diversity compared with taxonomic β-diversity was mainly due to a lower functional turnover, while nestedness-resultant components of taxonomic and functional β-diversity were similarly low (Figs 3, 4 & S1). However, null-models revealed that this low level of functional β-diversity is consistent with the observed patterns of taxonomic β-diversity given the regional pool of species.

To understand this finding, it has to be noticed first that fish species richness in river basins was on average relatively low compared with the global pool of species (basin richness was on average 57 species, i.e. 25% of the 230 species considered). In contrast, fish functional richness in the river basins was globally high (the average functional richness per basin accounting for 70% of the total functional richness; Fig. 3) which indicates that fish species present in each river basin tend to fill most of the functional space available. The null model revealed that in all the basins, the functional richness was not significantly different from a random expectation given the regional pool of species and the species richness. Therefore, there is no evidence of niche filtering in the fish assemblages studied, at least given the set of traits considered. This pattern could result from the large biogeographical scale considered, that does not allow the detection of potential environmental constraints or competition effects that could nevertheless be locally strong. Yet this pattern is consistent with a previous study showing that niche filtering has a low effect, compared with historical events, on the spatial turnover of freshwater fish assemblages over Europe (Leprieur *et al.*, 2009). This contrasts with other regions and organisms for which environmental filtering has a substantial effect (e.g. Mandrak (1995) for North American freshwater fish or Baselga, (2008) for European longhorn beetles).

In addition to the low fish species richness within each river basin, the proportion of species shared by assemblages is also low. Therefore, the high level of taxonomic β-diversity (0.67) is mainly due to a high level of taxonomic turnover (0.53). This high taxonomic turnover could be explained by historical contingency since the last glaciation period. Indeed, the current distribution of freshwater fish in Europe follows a decreasing gradient from the Ponto-Caspian region that was the main refuge during the Last Glacial Maximum (Pleistocene, 24,000 to 18,000 years ago; Reyjol *et al.*, 2007). As freshwater fish cannot cross marine or terrestrial barriers (e.g. mountains), inter-basin recolonization is a rare and slow process that occurs only as an exceptional event (e.g. river capture, exceptional floods; Hugueny, 1989), post glacial fish recolonization is therefore still at work in Europe. At the same time, there was a diversification during the recolonization process, especially at the margins of Europe (e.g. the Mediterranean regions). For instance, fish faunas from the Iberian Peninsula (Figs 2 & S1) have the highest values of taxonomic turnover (and hence β-diversity) as they host endemic species (that differentiated in this isolated glacial refuge) and only a low proportion of the common species of western Europe that still have not (re)colonized the peninsula (Reyjol *et al.*, 2007). In contrast, the river basins close to the Danube Basin (e.g. Oder, Weser, Elbe) have the lowest values of taxonomic β-diversity (Figs 2 & S1).

Despite the high taxonomic β-diversity, the large overlap between fish assemblages in the functional space explains the low level of functional turnover (0.07) and hence of functional β-diversity (0.21). Therefore, the frequent species replacements occurring between fish faunas are mostly between species that are functionally redundant, including species with the most extreme trait combinations. For instance, while the fish faunas from Guadalquivir and Elbe have a taxonomic turnover of 0.82, their functional turnover is of only 0.15 (Fig. S1). Consequently, the low level of functional turnover and hence of functional β-diversity might result from either functional convergence among fish assemblages (Logez *et al.*, 2010) or allopatric speciation derived from dispersal limitation (Svenning *et al.*, 2011;

Baselga *et al.*, 2012). The only exceptions to this general pattern are the few high-latitude basins (e.g. Glomma, Kemijoki) which host low species richness and thus lower functional richness. Therefore, these basins tend to present a large difference in functional richness compared with the other basins and hence a high functional β-diversity due to greater values for the nestedness-resultant component (Figs 2 & S1).

Investigations on functional β-diversity are scarce compared with taxonomic β-diversity studies, although the two facets of biodiversity are complementary ecological indicators as illustrated by our study case on European fish faunas. Assessments of taxonomic β-diversity and functional β-diversity for other ecosystems and taxa as well as their respective turnover and nestedness-resultant components could help to prioritize conservation efforts (McKnight *et al.*, 2007; Devictor *et al.*, 2010). Besides describing the spatial patterns of taxonomic and functional β-diversity and analysing their biogeographical determinants, it is also urgent to assess their temporal trends in the current context of global change. Indeed, the changes in local biodiversity due to human activities are also affecting the biotic dissimilarity between communities (Lockwood & McKinney, 2001; Olden, 2006; Olden & Rooney, 2006). For more than a decade, studies on various ecosystems and taxa revealed a global trend towards taxonomic homogenization (i.e. a decrease of β-diversity) following species introductions and/or extirpations (e.g. Qian & Ricklefs, 2006; Spear & Chown, 2008; Villéger *et al.*, 2011b). In contrast, very few studies have examined the other facets of biotic homogenization by assessing functional or phylogenetic β-diversity (but see Winter *et al.*, 2009; Luck & Smallbone, 2011; Pool & Olden, 2012). Future investigations will thus aim to test whether the changes in taxonomic β-diversity patterns are paired with changes in functional β-diversity and to assess how the two components of functional β-diversity respond to abiotic and biotic changes. It is indeed crucial to determine whether the observed species replacement and corresponding changes in taxonomic richness induce functional turnover (i.e. whether 'loser' and 'winner' species are functionally different) and/or change in functional richness. The general framework presented above is thus of particular interest as it allows the assessment of both taxonomic and functional β-diversity and hence the comparison of their patterns and changes for any taxon whether on a local or global scale.

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SUPPORTING INFORMATION

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Figure S1 Taxonomic and functional β-diversity and their respective turnover and nestedness-resultant components for the 300 pairs of European fish faunas.

Table S1 Functional traits used for functional characterization of the fish faunas.

Table S2 Mantel tests of correlations between taxonomic and functional β-diversity components.

Appendix S1 R function for computing taxonomic and functional β-diversity and their respective turnover and nestedness-resultant components for a pair of communities.

BIOSKETCHES

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