



RESEARCH
PAPER

Functional homogenization exceeds taxonomic homogenization among European fish assemblages

Sébastien Villéger^{1*}, Gaël Grenouillet² and Sébastien Brosse²

¹Laboratoire Ecologie des Systèmes Marins Côtiers (UMR5119 ECOSYM), CNRS, IRD, IFREMER, Université Montpellier 2, Place Eugène Bataillon, 34095 Montpellier, France, ²Laboratoire Evolution et Diversité Biologique (UMR5174 EDB), Université Paul Sabatier, CNRS, ENFA, Université Toulouse 3, 31062 Toulouse, France

ABSTRACT

Aim Human activities and the consequent extirpations of native species and introductions of non-native species have been modifying the composition of species assemblages throughout the world. These anthropogenic impacts have modified the richness of assemblages as well as the biological dissimilarity among them. However, while changes in taxonomic dissimilarity (i.e. accounting for species composition) have been assessed intensively during the last decade there are still few assessments of changes in functional dissimilarity (i.e. accounting for the diversity of biological traits). Here, we assess the temporal changes in both taxonomic and functional dissimilarities for freshwater fish assemblages across Europe.

Location Western Palaearctic, 137 river basins.

Methods The Jaccard index was used to quantify the changes in both taxonomic and functional dissimilarity. We then partitioned dissimilarity to extract its turnover component and measured the changes in the contribution of turnover to dissimilarity.

Results Functional homogenization exceeded taxonomic homogenization six-fold. More importantly, we found only a moderate positive correlation between these changes. For instance, 40% of assemblages that experienced taxonomic differentiation were actually functionally homogenized. Taxonomic and functional homogenizations were stronger when the historical level of taxonomic dissimilarity among assemblages was high and when a high number of non-native species were introduced in the assemblages. Moreover, translocated species (i.e. non-native species originating from Europe) played a stronger role than exotic species (i.e. those coming from outside Europe) in this homogenization process, while extirpation did not play a significant role.

Main conclusions Change in taxonomic diversity cannot be used to predict changes in functional diversity. In addition, as functional diversity has been proven to be a better indicator of ecosystem functioning and stability than taxonomic diversity, further studies are required to test the potential effects of functional homogenization at the local scale.

Keywords

Beta-diversity, exotic species, functional diversity, non-native species, taxonomic dissimilarity, translocation.

*Correspondence: Sébastien Villéger, Laboratoire Écologie des Systèmes Marins Côtiers cc93, Université Montpellier 2, Place Eugène Bataillon, 34095 Montpellier, France. E-mail: sebastien.villeger@univ-montp2.fr

INTRODUCTION

The current biodiversity crisis is characterized by an accelerated rate of species extinction due to the increasing anthropogenic impacts on ecosystems, mainly through habitat change,

pollution and exploitation of populations (Cardinale *et al.*, 2012). However, besides the extirpation of some species from their native range, human activities have also been promoting the introduction of species outside their native range (Vander Zanden, 2005; Strayer & Hillebrand, 2012). These extirpation

and introduction processes have acted together to modify the composition and richness of local assemblages, as well as the dissimilarity between them (Olden & Poff, 2004; Villéger & Brosse, 2012). The impacts of species introduction and extirpation on biodiversity have been increasingly studied during the last decade (Olden & Rooney, 2006). For instance, in freshwater ecosystems introductions of non-native fish species have modified the natural patterns of species richness (Leprieur *et al.*, 2008a) and have increased the level of similarity in species composition between faunas (Rahel, 2000; Olden *et al.*, 2008; Villéger *et al.*, 2011a).

This trend towards taxonomic homogenization (i.e. increase in the similarity of species composition among species assemblages over time) has been confirmed for many other taxa across the world (Lockwood *et al.*, 2000; Spear & Chown, 2008; Winter *et al.*, 2009; Olden *et al.*, 2011). In contrast, the impact of introductions and extirpations on the functional facet of biodiversity has seldom been quantified (Baiser & Lockwood, 2011; Luck & Smallbone, 2011; Pool & Olden, 2012; Matsuzaki *et al.*, 2013). Yet there may be no direct relationship between changes in taxonomic and functional dissimilarity among assemblages. For instance, a pair of assemblages that exhibits taxonomic differentiation (i.e. an increase in dissimilarity) can actually be functionally homogenized if the unique non-native species introduced in each assemblage are functionally similar to each other. Within the biotic homogenization framework, the analysis of changes in functional dissimilarity is hence complementary to the assessment of changes in taxonomic dissimilarity. Indeed, functional diversity was recognized as an important dimension of biodiversity in governing ecosystem functioning, and accounting for species functional traits (i.e. biological attributes linked to species niche and role) is necessary to evaluate how change in species composition may affect ecosystem processes (Naeem *et al.*, 2012). By decreasing complementarity among functionally dissimilar communities, functional homogenization is likely to decrease the viability of connected communities facing disturbances (Clavel *et al.*, 2011). Therefore, assessing the level of functional homogenization will permit a better understanding of the potential consequences of biodiversity change on ecosystem functioning than just measuring the level of taxonomic homogenization.

Here, we focused on European freshwater fish assemblages that have experienced frequent introductions of non-native species of species originating from different areas of the globe (Leprieur *et al.*, 2008a,b; Blanchet *et al.*, 2009). We used the frameworks of Baselga (2012) and Villéger *et al.* (2013) to quantify taxonomic and functional dissimilarity between European fish faunas. We assessed the temporal changes in these biodiversity facets following introductions of non-native species and extirpations of native species. We quantified the correlation between the change in functional dissimilarity and the change in taxonomic dissimilarity to test whether the latter could be used as a surrogate of the former. Finally, we disentangled the relative effects of historical dissimilarity and of number of extirpations and introductions on changes in taxonomic and functional dissimilarity.

MATERIAL AND METHODS

Measuring dissimilarity and contribution of turnover

Measuring biological dissimilarity between species assemblages has a long history in ecology since the definition of the concept of beta diversity (Whittaker, 1956). This concept was first proposed to assess differences in species composition, i.e. taxonomic dissimilarity (Koleff *et al.*, 2003), but it has recently been extended to functional (Villéger *et al.*, 2013) and phylogenetic (Leprieur *et al.*, 2012) facets of biodiversity.

Taxonomic dissimilarity based on species composition is the percentage of species present only in one assemblage within a pair of assemblages, and it can be measured with the Jaccard index

$$\beta_{\text{diss}} = \frac{b+c}{a+b+c},$$

where a is the number of species shared by the two assemblages and b and c are the number of species unique to each assemblage (Fig. 1a). The index ranges from 0 when the assemblages are identical ($b=c=0$) to 1 when the assemblages have totally distinct species compositions ($a=0$). However, dissimilarity accounts for both the number of unique species and the difference in species richness. For instance, the dissimilarity between two assemblages of similar richness and sharing only few species ($b=c \gg a$) can be close to the dissimilarity between a species-poor assemblage in which composition is a subsample of a species-rich assemblage ($b \gg a > c=0$). To solve this issue, Baselga (2012) proposed an additive partition of taxonomic dissimilarity into a nestedness-resultant component accounting for difference in species richness and a turnover component independent of difference in species richness. This turnover component accounts for the number of species replaced and the species richness in the poorest assemblage:

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

It ranges from 0, when the species present in the poorest assemblage are a subsample of the species present in the richest assemblage ($\min(b, c) = 0$), to 1, when the assemblages share no species ($a = 0$).

As turnover is a component of dissimilarity, we propose to measure its relative contribution to dissimilarity, hereafter denoted p_{turn} (Toussaint *et al.*, 2014):

$$p_{\text{turn}} = \frac{\beta_{\text{turnover}}}{\beta_{\text{diss}}} = \frac{2 \times \min(b, c)}{a + 2 \times \min(b, c)} \times \frac{a+b+c}{b+c}.$$

Measuring the contribution of turnover to dissimilarity is by definition not possible when dissimilarity is null (i.e. when $b=c=0$). However, such a situation of complete similarity in species composition or functional space filling is rare in practice, especially at large spatial scales. The p_{turn} index is minimal and equals 0 when turnover is null ($\min(b, c) = 0$), i.e. when the

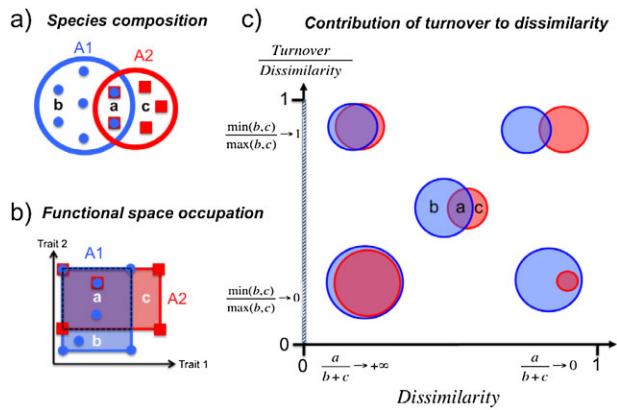


Figure 1 Assessing ecological dissimilarity between a pair of assemblages. (a) Taxonomic dissimilarity is the dissimilarity in species composition between two assemblages (A1 and A2). It can be represented with a Venn diagram where species are symbolized by points (blue dots and red squares for the two assemblages, respectively). The two assemblages share a species and have b and c unique species, respectively. (b) Functional dissimilarity is the dissimilarity in the occupation of the multidimensional functional space defined by functional traits. It can be represented by the overlap between convex hulls shaping assemblages (here coloured rectangles). The intersection between the two hulls is the purple square delimited by the dotted line with an area of a . The portions of the functional space filled only by one assemblage are in red and blue and their area equal b and c , respectively. (c) Taxonomic and functional dissimilarity can be represented using the same quantities (a , b , c), and measured using the Jaccard dissimilarity index: $D = (b + c) / (a + b + c)$. The contribution of turnover (i.e. percentage of replacement given the richness of the poorest assemblage) to dissimilarity can also be measured using a , b and c (see the equation in the text). These two indices allow us to discriminate contrasted situations of proportion of richness shared and difference in richness between assemblages.

diversity of the poorest assemblage is a subset of the diversity present in the richest assemblage. The p_{turn} index is maximal and equals 1 when the two assemblages have the same richness ($b = c > 0$).

This partitioning of taxonomic dissimilarity based on species composition has been recently transferred to functional dissimilarity (Villéger *et al.*, 2013). Indeed, the functional richness of an assemblage can be measured as the volume of the convex hull shaping all the species in a multidimensional functional space (Villéger *et al.*, 2008). The functional dissimilarity between two assemblages can thus be assessed using the percentage of overlap in this functional space (Villéger *et al.*, 2011b). By analogy with the Venn diagram representation for taxonomic dissimilarity, it is hence possible to define the quantity a as the volume of the functional space shared by the two assemblages and b and c as the volume of the functional space they fill independently, respectively (Fig. 1b).

The simultaneous assessment of dissimilarity and contribution of turnover to dissimilarity offers the opportunity to discriminate contrasted ecological situations (Fig. 1c) (Toussaint

et al., 2014). For instance, it allows discrimination of situations where high dissimilarity is driven by a high difference in richness between two nested assemblages (low contribution of turnover) from situations where high dissimilarity is due to a low percentage of biological overlap between assemblages having similar richness (high contribution of turnover).

Assessing changes in taxonomic and functional dissimilarities

The partitioning of taxonomic and functional dissimilarities can be used to describe biogeographic patterns at a given time (Baselga *et al.*, 2012; Villéger *et al.*, 2013). It also allows quantification of temporal changes in the taxonomic and functional facets of biodiversity following changes in species composition. For instance, extirpations of native species and introductions of non-native species modify the species and functional diversity of assemblages but also the proportion of diversity (i.e. number of species or volume of functional space) they share. Let us define e as the change from historical to current period in the diversity shared by two assemblages ($e \geq -a$), and f and g as the changes in the diversity unique to each of the two assemblages ($f \geq -b$ and $g \geq -c$). Change in dissimilarity and change in contribution of turnover to dissimilarity from a historical to a current period (after species introductions and extirpations occurred) can then be written as:

$$\Delta\beta_{\text{diss}} = \frac{b + f + c + g}{a + e + b + f + c + g} - \frac{b + c}{a + b + c}$$

$$\Delta p_{\text{turn}} = \frac{2 \times \min(b + f, c + g)}{a + e + 2 \times \min(b + f, c + g)} \times \frac{a + e + b + f + c + g}{b + f + c + g} - \frac{2 \times \min(b, c)}{a + 2 \times \min(b, c)} \times \frac{a + b + c}{b + c}$$

A decrease in dissimilarity (i.e. an increase in the percentage of species or functional space shared) means that assemblages became homogenized after their composition changed (Fig. 2). On the contrary, an increase in dissimilarity indicates a differentiation (Fig. 2). Interestingly, changes in taxonomic and functional dissimilarities are a priori independent of each other (Fig. 2). For instance, a taxonomic homogenization could induce a functional differentiation if the species added to only one assemblage fill a unique portion of the functional space (Fig. 2). Similarly, a taxonomic differentiation could induce a functional homogenization if the species introduced in only one of the two assemblages fill the same portion of the functional space (Fig. 2).

The decomposition of dissimilarity according to Baselga's framework meets two important conditions required for assessing temporal change in taxonomic dissimilarity in pairs of assemblages and change in contribution of turnover to this spatial dissimilarity (Toussaint *et al.*, 2014): (1) the change in contribution of turnover to dissimilarity reflects the change in the proportion of shared versus unique richness, i.e. it accounts for the six variables a , b , c , e , f , g ; (2) if the two assemblages were

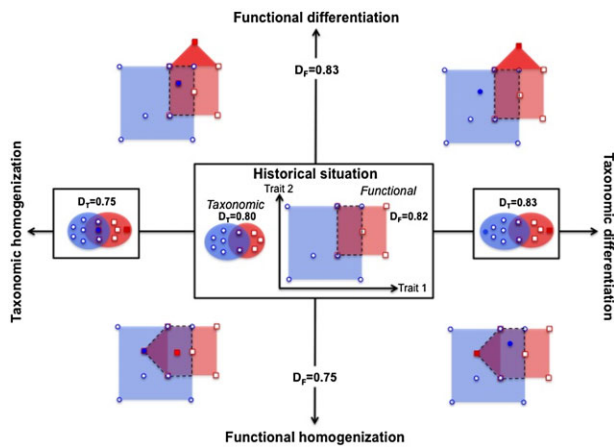


Figure 2 Illustration of the independence of temporal changes in taxonomic and functional dissimilarity in a pair of species assemblages. The two species assemblages are represented in red and blue with species being symbolized by squares and circles, respectively. Taxonomic dissimilarity is illustrated by the overlap of ellipses following the classical Venn diagram representation. Functional dissimilarity is illustrated as the intersection of the convex hulls shaping species assemblages in a multidimensional functional space. Here, for graphical convenience, there are only two functional axes and convex hulls are thus polygons. The functional space shared by the two assemblages is delimited by a dashed line. A hypothetical historical situation is shown in the central box of the figure. The two assemblages shared only two species while they have five and three unique species, respectively. Similarly, the two assemblages shared only a small part of the functional space. Taxonomic and functional dissimilarity (D_T and D_F) are thus historically high (≥ 0.80). An example of taxonomic homogenization is shown on the left part of the figure, it results from the introduction of one non-native species in the poorest assemblage and one non-native species in the two assemblages. An example of taxonomic differentiation resulting from the introduction of two non-native species (colour-filled symbols), one in the richest assemblage and one in the poorest assemblage, is shown on the right part of the figure. For each of these two situations, examples of functional differentiation and functional homogenization are provided at the top and bottom of the figure, respectively. The values of change in functional dissimilarity are the same for the taxonomic differentiation and taxonomic homogenization examples, to illustrate the a priori independence of changes in taxonomic and functional dissimilarity.

historically totally distinct ($a = 0$), dissimilarity was entirely driven by turnover, as all the diversity present in the poorest assemblage was also present in the richest one (Koleff *et al.*, 2003). This property ensures that temporal changes in contribution of turnover to dissimilarity cannot occur when dissimilarity is maximal in both historical and current periods.

Datasets and statistical analyses

Fish occurrences in 137 river basins of western Europe were extracted from a world-wide database on freshwater fish faunas that compiles the available literature (including scientific

reports, books, online data and grey literature) on species lists at the river-basin scale. Details on the database and references used per river basin are available in Brosse *et al.* (2013) and on the Biofresh data platform (<http://www.freshwaterbiodiversity.eu/>). The western European river basins cover most of the terrestrial area from the Iberian Peninsula to north-western Russia and from Norway to Greece (see Fig. S1 in Supporting Information). This area was selected as it benefits from extensive knowledge on the species composition of most river basins, as well as on species introductions or extirpations in each basin (see, e.g., Kottelat & Freyhof, 2007, for a synthesis). However, it remains possible that a few human-mediated translocations between adjacent basins have been considered as native occurrences or that rare species have been considered as extinct. Such potential bias is probably limited given that western Europe remains, with North America, one of the most intensively studied area of the world. Indeed, European data on fish occurrences, as well as introduction and extirpation events, are continuously updated in international collaborative platforms such as Fishbase (<http://www.fishbase.org>) and Biofresh. Those platforms were used to check and complement information in our database on species introductions and extirpations. Our database hence accounts for the status of each species (native, native extirpated and non-native) in each river basin and thus allows us to infer historical and current species composition (Brosse *et al.*, 2013). Non-native species only refers to established species, and two different kinds of non-native fishes have been considered: translocated species that are native in western European basins and exotic species that originate from elsewhere in the world (Leprieur *et al.*, 2008b; Brosse *et al.*, 2013). Historical composition refers to the period before human activities affected fish faunas. Industrialization and associated exchanges of goods are responsible for most human-mediated fish introductions and extirpations (Leprieur *et al.*, 2008a), and according to Ricciardi (2007) we considered the pre-industrial period (before the 18th century) as a reference for historical composition. Historical composition hence includes native species currently present and native species that are documented in the scientific literature (see Brosse *et al.*, 2013, for a list of references) to have been extirpated (mostly during the 20th century). Current composition refers to the end of the 20th century, i.e. accounting for non-native species occurrences and for extirpation of some native species (Olden & Rooney, 2006; Villéger *et al.*, 2011a).

The functional strategy of the 286 species present in the 137 assemblages studied was described using six functional traits commonly used in studies on fish functional diversity to describe two facets of fish ecology: food acquisition and locomotion (Olden *et al.*, 2006; Buisson *et al.*, 2013; Villéger *et al.*, 2013). Two traits were measured as continuous variables: body length and body shape ratio (total length/maximal body depth). Three traits, diet, rheophily and vertical position in the water column, were coded as ordered traits (with five, three and three modalities respectively), and prey vertical position was coded using two categories (Table S1). Categorical traits and common adult body length were taken from Fishbase (Froese & Pauly, 2013) and Kottelat & Freyhof (2007). Morphological traits were

estimated from pictures of adult individuals from these two references. 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 principal coordinates analysis (PCoA) was carried out on this functional distance matrix (Villéger *et al.*, 2008). The indices of functional dissimilarity and turnover were computed in the functional space made by the first three principal axes of the PCoA, following a trade-off between information quality and computation time (Villéger *et al.*, 2011b, 2013). Indeed, the three-dimensional functional space provided an accurate representation of the functional dissimilarity between species (Mantel's test between Gower's distance on traits values and Euclidean distance in the three-dimensional functional space: $r = 0.936$, $P < 0.001$).

Indices of taxonomic and functional dissimilarity and contribution of turnover to dissimilarity between each pair of fish assemblages were computed for historical and current species composition. Temporal changes from the historical to the current period were computed for these four indices (a positive value indicates an increase in dissimilarity or in contribution of turnover from the historical to the current period). Correlations between changes in taxonomic dissimilarity and changes in functional dissimilarity were tested using Mantel's permutation test.

To disentangle the drivers of changes in taxonomic dissimilarity we used multiple regression on distance matrices (MRM; Lichstein, 2007) with historical taxonomic dissimilarity, total number of native species extirpations, total number of exotic species introductions and total number of translocations in each pair of assemblages as explanatory matrices. *P*-values for MRM models were obtained by comparing each observed regression coefficient with a distribution of 10,000 permuted values. The same analysis was conducted to analyse changes in functional dissimilarity.

We tested the sensitivity of change in functional dissimilarity to the set of functional traits used to describe species. We built six functional traits matrices by removing one of the six functional traits from the initial dataset. We then ran all the analyses (i.e. computing functional distances between species, building a three-dimensional functional space and computing changes in functional dissimilarity) on these six functional datasets.

Statistical analyses were carried out using R (R Core Team, 2013), including the libraries *betapart* for computing dissimilarity indices (Baselga & Orme, 2012; Baselga *et al.*, 2013) and *ecodist* for MRM analyses (Goslee & Urban, 2007).

RESULTS

The 137 European river basins considered in this study host 244 native fish species. Among these native species 23 were extirpated from at least one basin where they historically occurred and 84 were translocated to at least one basin where they historically did not occur. A total of 42 exotic species have been imported and subsequently established in the studied region. The number of native species extirpated from a basin was only weakly correlated with the total number of non-native species introduced ($r = 0.175$, $P = 0.041$). The species richness per river basin increased on average by 30% from the historical to the current period (from 24.0 ± 15.3 to 31.4 ± 19.7).

Historical patterns of taxonomic and functional dissimilarities

Historical taxonomic dissimilarity among European fish assemblages (i.e. before human activities contributed to the extirpation of some native species and the introduction of non-native species) was high with a mean value of 0.74 (SD ± 0.19 ; Table 1). Contribution of turnover to the taxonomic dissimilarity was also high (0.74 ± 0.26). In contrast, historical functional dissimilarity was lower (0.44 ± 0.26), as was contribution of turnover to dissimilarity (0.32 ± 0.32 , Table 1). Difference in richness between assemblages was on average higher for species richness than for functional richness (minimum/maximum ratio of 0.56 and 0.64, respectively, Table 1).

Temporal changes in taxonomic and functional dissimilarities

Overall, fish assemblages in western Europe showed a weak trend towards taxonomic homogenization from the historical to the current period (mean change of -0.01 ± 0.15 ; Table 1). However, this low average value hid a great variability, with only 47% of assemblage pairs showing homogenization while 53.1%

		Taxonomic	Functional
Dissimilarity	Historical	0.74 ± 0.19 (0.27;0.97)	0.44 ± 0.26 (0.06;0.93)
	Current	0.73 ± 0.18 (0.31;0.96)	0.38 ± 0.26 (0.05;0.87)
	Change	-0.01 ± 0.07 (-0.18;0.14)	-0.06 ± 0.14 (-0.46;0.09)
Contribution of turnover to dissimilarity	Historical	0.74 ± 0.26 (0;1)	0.32 ± 0.32 (0;0.97)
	Current	0.72 ± 0.26 (0;1)	0.30 ± 0.31 (0;0.97)
	Change	-0.02 ± 0.14 (-0.32;0.26)	-0.02 ± 0.24 (-0.60;0.52)
Richness ratio	Historical	0.56 ± 0.24 (0.15;1.00)	0.64 ± 0.26 (0.12;0.99)
	Current	0.55 ± 0.24 (0.14;0.97)	0.68 ± 0.26 (0.17;0.99)
	Change	-0.01 ± 0.15 (-0.30;0.32)	0.05 ± 0.16 (-0.20;0.49)

Table 1 Summary of taxonomic and functional dissimilarities and contribution of turnover to dissimilarity, for historical and current periods. Temporal change corresponds to the current value minus the historical one. Richness ratios (minimum richness/maximum richness for each pair of assemblages) are also indicated. Values are mean \pm standard deviation with confidence interval at 95% in parentheses.

showed no change or differentiation (Table 2, Fig. 3a). Contribution of turnover to taxonomic dissimilarity also showed a slight decrease (-0.02 ± 0.14 ; Table 1).

Change in functional dissimilarity was on average higher than change in taxonomic dissimilarity (-0.06 ± 0.14 ; Table 1). Cases of functional homogenization (i.e. assemblages that became functionally more similar) were more frequent than cases of functional differentiation (62.3 vs. 37.7%; Table 2, Fig. 3b). Contribution of turnover to functional dissimilarity decreased in the same proportion as for taxonomic dissimilarity (-0.02 ± 0.24 ; Table 1). However, there was strong variability of this index among assemblage pairs (Table 2, Fig. 3b). Among the 37.7% of pairs that showed functional differentiation, 27.3% also showed a decrease in the contribution of turnover while only 10.3% showed an increase. Among the 62.3% of functional homogenization cases, change in contribution of turnover was more balanced with 29.3% of assemblage pairs showing an increase in the contribution of turnover and 33% showing a decrease. The ratio of species richness between the poorest and the richest assemblage in each pair decreased slightly (-0.01 ± 0.15 ; Table 1). In contrast, the ratio of functional richness increased on average by 0.05 ± 0.16 (Table 1).

Change in dissimilarity and change in contribution of turnover to dissimilarity were weakly correlated for both taxonomic and functional facets (Fig. 3a,b). Changes in taxonomic and functional dissimilarity were positively correlated (Spearman's correlation coefficient $\rho = 0.630$; Mantel test $P < 0.001$; Fig. 3c). Changes in the contribution of turnover to taxonomic and functional dissimilarity were also positively correlated ($\rho = 0.284$; $P < 0.001$; Fig. 3d).

Changes in functional dissimilarity were robust to the trait sensitivity analysis (Fig. S2). These results demonstrate that the observed trend towards functional homogenization was not driven by a single trait but actually reflected an overall trend towards more similar combinations of traits among assemblages.

Determinants of changes in taxonomic and functional dissimilarities

Change in taxonomic dissimilarity could be significantly predicted from historical period and introduction and extirpation pressures (MRM, $R^2 = 0.248$, $P < 0.001$; Fig. 4). The historical level of taxonomic dissimilarity had a significant negative effect, i.e. pairs of assemblages with a high historical dissimilarity tended to be the more homogenized (Fig. 4). The total number of native species extirpations from the pair of assemblages did not have a significant contribution. The total number of introductions of non-native species coming from Europe (i.e. translocated species) in a pair of assemblages had a significant negative effect on change in taxonomic dissimilarity, i.e. pairs that received more translocated species tended to be more homogenized. In contrast, the total number of exotic species (i.e. coming from other continents) introduced had a positive, although weak, effect on change in taxonomic dissimilarity, i.e. pairs that received more exotic species tended to be more

Table 2 Summary of frequency and intensity of changes in taxonomic dissimilarity, functional dissimilarity and contribution of functional turnover to functional dissimilarity. Percentages of taxonomic and functional differentiation include assemblage pairs that show no change. Values in parentheses are mean \pm standard deviation of change in functional dissimilarity.

	Functional homogenization		Functional differentiation		Total taxonomic change	
	Total	Increase in contribution of turnover	Decrease in contribution of turnover	Increase in contribution of turnover	Decrease in contribution of turnover	Total
Taxonomic homogenization	41.5% (-0.15 ± 0.16)	23.6% (-0.16 ± 0.15)	17.9% (-0.13 ± 0.16)	5.4% (0.03 ± 0.04)	4.2% (0.04 ± 0.04)	46.9% (-0.13 ± 0.16)
Taxonomic differentiation	20.8% (-0.06 ± 0.08)	9.4% (-0.07 ± 0.08)	11.4% (-0.06 ± 0.07)	32.3% (0.03 ± 0.04)	23.1% (0.03 ± 0.05)	53.1% (-0.01 ± 0.07)
Total functional change	62.3% (-0.12 ± 0.14)			37.7% (0.03 ± 0.04)		

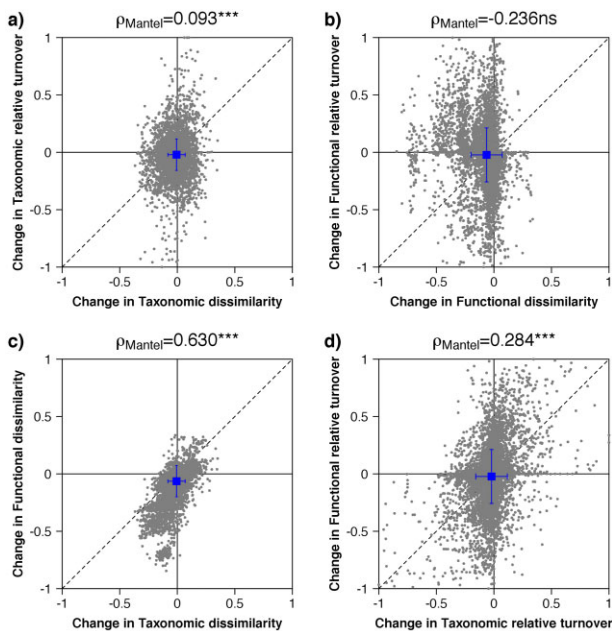


Figure 3 Changes in taxonomic and functional dissimilarity versus changes in contribution of turnover to dissimilarity. Spearman's correlation coefficient and associated Mantel permutation test are provided at the top of each panel. The mean value (and associated standard deviation) among pairs of fish faunas (grey points) is shown by the dark square.

differentiated. Changes in functional dissimilarity were influenced by the same factors but the effects of historical dissimilarity and the total number of translocations were stronger (MRM, $R^2 = 0.318$, $P < 0.001$; Fig. 4).

DISCUSSION

The biogeography of the European freshwater fish fauna is marked by the legacy of the last glaciation and the subsequent recolonization from the Ponto-Caspian and Mediterranean refuges (Griffiths, 2006; Reyjol *et al.*, 2007). For instance, native species richness across Europe shows a positive longitudinal gradient from east to west in addition to a positive latitudinal gradient from south to north (Reyjol *et al.*, 2007). Because of these historical and ecological contingencies there was a high historical level of taxonomic dissimilarity between fish assemblages, especially across physical barriers such as the Alps and the Pyrenean mountains (Leprieur *et al.*, 2011). Furthermore, the high level of taxonomic dissimilarity observed among the 137 river basins was mainly due to species replacement, as the contribution of turnover to taxonomic dissimilarity was also high (Fig. 3). However, despite this high level of taxonomic dissimilarity, functional dissimilarity remained moderate with a low contribution of turnover to dissimilarity (i.e. most of the functional dissimilarity was due to difference in functional richness). These results confirm the patterns found for 25 large European drainage basins (Villéger *et al.*, 2013), i.e. lower functional dissimilarity than taxonomic dissimilarity and lower

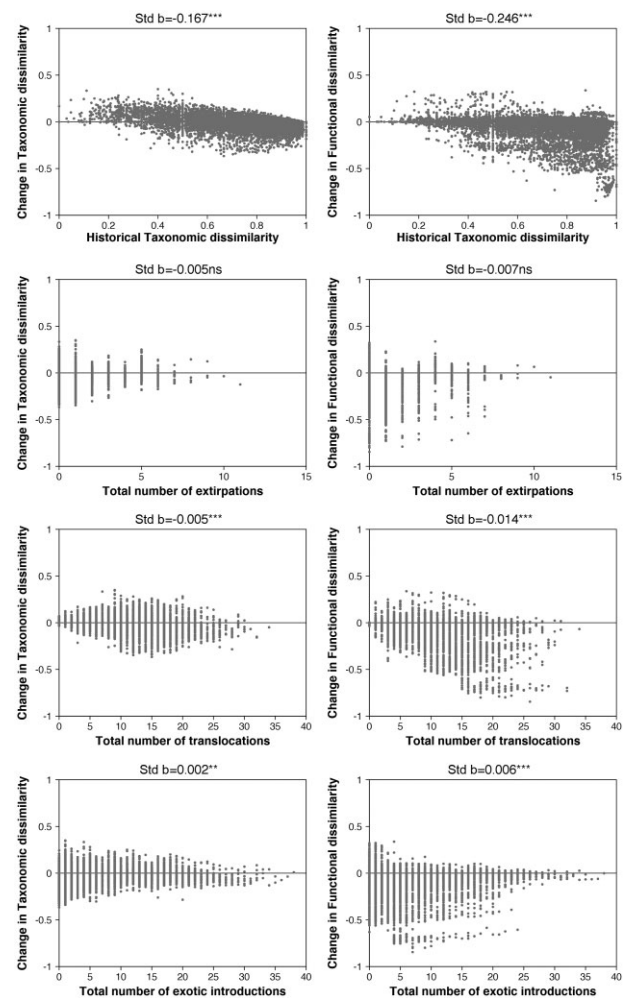


Figure 4 Effect of historical dissimilarity and extirpation/introduction pressures on changes in taxonomic and functional dissimilarities. Standard partial regression coefficient (Std b) and associated P-value from multiple regression on distance matrices are given for each variable (** $P < 0.001$, ** $P < 0.01$, ns not significant).

contribution of turnover to functional dissimilarity than to taxonomic dissimilarity. Thus, even if European freshwater fish assemblages contain distinct species (and different numbers of species) they share the same core combinations of trait values.

European rivers constitute a hot-spot of non-native species introductions (Clavero & García-Berthou, 2006; Leprieur *et al.*, 2008a; Marr *et al.*, 2010), due to the high demand for recreational fishing and aquaculture activities and to the high commercial activity within Europe and between Europe and other continents (Blanchet *et al.*, 2009; Clavero, 2011). Meanwhile, anthropogenic pressure on freshwater ecosystems, through pollution, habitat modification (e.g. dams) and exploitation of fish populations, have led some fish species towards local extirpation (Kottelat & Freyhof, 2007; Freyhof & Brooks, 2011). However, the number of native species extirpated remains low at the river-basin scale compared with the number of introduced species (Leprieur *et al.*, 2008a; Villéger *et al.*, 2011a). The direction and

intensity of change in taxonomic dissimilarity among pairs of fish assemblages was variable, but on average we found a weak trend towards taxonomic homogenization (Tables 1 & 2, Fig. 3), which is consistent with previous studies on freshwater fish faunas in Europe (Clavero & García-Berthou, 2006; Leprieur *et al.*, 2008b; Villéger *et al.*, 2011a; Hermoso *et al.*, 2012). We also found that the contribution of turnover to dissimilarity tended to decrease, but this change was marked by a high variability among pairs of assemblages, a pattern also found at the global scale (Toussaint *et al.*, 2014). Furthermore, the change in taxonomic dissimilarity was independent of the change in the contribution of turnover (Fig. 3). This independence could be explained by the lack of a clear trend in the ratio of richness difference among assemblages. Indeed, the ratio between species richness of assemblage pairs decreased slightly from the historical to the current period but this average value hid a high variability (Table 1). Indeed, as human activities are the main determinant of non-native fish richness (i.e. there is no strong biotic resistance or biotic acceptance; Blanchet *et al.*, 2009), the number of species introductions and extirpations is independent of native species richness, and thus these two processes did not affect the difference in species richness between assemblages.

The change in functional dissimilarity was higher than taxonomic change, with a global trend towards functional homogenization of 0.05; more than 10% of pairs experienced a functional homogenization greater than 0.20. However, functional differentiation remained frequent (38% of assemblage pairs) but of lower magnitude than homogenization. More importantly, even if there was a significant positive correlation between changes in taxonomic and functional dissimilarities (Fig. 3), in more than a quarter of assemblage pairs the changes were in the opposite direction (Table 2). For instance, 39% of the assemblage pairs that showed taxonomic differentiation were actually functionally homogenized and more than 10% of the assemblage pairs taxonomically homogenized were functionally differentiated (Table 2). For the remaining cases where taxonomic and functional dissimilarities changed in the same direction, the change in functional dissimilarity was most often of higher magnitude than the change in taxonomic dissimilarity, despite a high variability in the magnitude of this difference (Fig. 3). This discrepancy highlights the need to consider explicitly the functional facet of biodiversity, as changes in functional dissimilarity cannot be predicted by the change in taxonomic dissimilarity. Indeed, other than the number of non-native species added in a pair, the functional identity of the non-native species introduced is a determining factor of functional homogenization (Fig. 2).

Change in the contribution of turnover to dissimilarity was of the same magnitude for both taxonomic and functional dissimilarities (Table 1), with an average decrease of 0.02. However, the changes in the contribution of turnover to taxonomic and functional dissimilarities were weakly correlated (Fig. 3). More precisely, the decrease in the percentage of functional space filled by two assemblages was mainly due to an increase in the functional richness of the richest assemblage. However, when the percentage of functional space filled by the two assemblages increased,

it could be coupled to either an increase or a decrease in the functional richness of the richest assemblage.

Changes in taxonomic and functional dissimilarity were significantly related to the historical level of taxonomic dissimilarity. This historical contingency is intuitive for extreme levels of taxonomic dissimilarity; for instance a pair of assemblages that historically had few species in common cannot experience a high taxonomic differentiation. The number of species extirpated did not play a significant role in explaining the change in dissimilarity (Fig. 4), confirming previous studies (Villéger *et al.*, 2011a). This weak effect could be explained by the large spatial grain of our analyses (i.e. river basins) at which species extirpations are still scarce. In contrast, the number of non-native species introductions had a significant effect on both taxonomic and functional dissimilarity. However, the number of species widely translocated within Europe had a negative effect whereas the number of species introduced from other regions had a positive, although weak, effect on both taxonomic and functional dissimilarity (Fig. 4). This result parallels the conclusions of Leprieur *et al.* (2008b) on only taxonomic dissimilarity for 25 large European basins, and extends them to a much more complete set of European river basins (137 basins were considered in this study; Fig. S1) encompassing a wider range of basin sizes. Such a taxonomic pattern results from the large native range of the species that have been translocated (e.g. top predators such as the zander, *Sander lucioperca*) that by definition lead to homogenization between the assemblages that contain this species either as native or as introduced. On the contrary, exotic species have generally been introduced (and established) in few river basins (e.g. the mosquitofish, *Gambusia affinis*, only established in south-western Europe or the brook trout, *Salvelinus fontinalis*, only established in cold-water ecosystems) and thus they tend to differentiate the composition of assemblages.

More importantly, translocated and exotic species also have different effects on functional dissimilarity (Fig. 4). Indeed, increasing the number of translocated species increased the magnitude of functional homogenization, while increasing the number of exotic species tended to reduce functional homogenization. This discrepancy could be explained by the high functional richness and the low functional dissimilarity among European freshwater fish assemblages (Schleuter *et al.*, 2012; Villéger *et al.*, 2013) and by the low functional dissimilarity between native and translocated species that have evolved in basins with similar ecological conditions. On the contrary, several exotic species from North America that have been introduced in European basins have a particular morphology (e.g. *Gambusia affinis* or the black bullhead, *Ameiurus melas*) (Clavero & García-Berthou, 2006; Leprieur *et al.*, 2008b). These functionally original species thus tend to increase both the functional richness of their recipient assemblage and the functional dissimilarity from other assemblages. Given the high number of species considered here, we only consider a small set of traits describing the main facets of fish functional niche (food acquisition and locomotion ability). To go further than our large-scale measure of functional dissimilarity it would be necessary to assess change in functional dissimilarity at the local scale,

which would require accounting for species relative biomass and more directly including functional traits linked to the effects of fish on ecosystem processes such as detailed fish diet, behaviour and nutrient excretion (Boulêtreau *et al.*, 2011; Cucherousset & Olden, 2011; Capps & Flecker, 2013).

Simultaneously assessing changes in taxonomic and functional dissimilarities as well as the changes in their turnover components allowed us to understand the consequences of non-native species introductions and native species extirpations on the biodiversity of assemblages.

Here, for European freshwater fish faunas, we demonstrate that there is an overall trend towards functional homogenization that exceeds the magnitude of the trend to taxonomic homogenization. Indeed most of the non-native introductions were actually species translocations within Europe, which promoted a higher level of taxonomic and functional similarity between faunas. As translocated species are functionally similar to native species, they contributed to an increase in the functional richness of fish assemblages as well as to a decrease in the functional dissimilarity among them.

More importantly, there is no direct relation between change in taxonomic dissimilarity and change in functional dissimilarity, and thus the former cannot be used as a proxy for the latter. Hence, the direction and intensity of change in functional dissimilarity depend on several interacting factors such as historical dissimilarity and number and identity of the non-native species. The changes in functional dissimilarity reported in this study call for further assessment of functional homogenization of other taxa for which change in taxonomic dissimilarity has already been demonstrated, e.g. plants (Winter *et al.*, 2009), birds (Lockwood *et al.*, 2000) and ungulates (Spear & Chown, 2008). Furthermore, studying the local consequences of functional homogenization on the functioning and stability of ecosystems is of the utmost importance for understanding, predicting and mitigating the effects of global change on aquatic ecosystems.

ACKNOWLEDGEMENTS

We thank three anonymous referees and the editors for their constructive comments that helped us to improve this article. This work was supported by the EU BIOFRESH project (7th Framework European Program, contract N°226874). EDB is part of the 'Laboratoire d'Excellence' (LABEX) entitled TULIP (ANR -10-LABX-41).

REFERENCES

- Baiser, B. & Lockwood, J.L. (2011) The relationship between functional and taxonomic homogenization. *Global Ecology and Biogeography*, **20**, 134–144.
- Baselga, A. (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, **21**, 1223–1232.
- Baselga, A. & Orme, C.D.L. (2012) Betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, **3**, 808–812.
- Baselga, A., Gómez-Rodríguez, C. & Lobo, J.M. (2012) Historical legacies in world amphibian diversity revealed by the turnover and nestedness components of beta diversity. *PLoS ONE*, **7**, e32341.
- Baselga, A., Orme, C.D.L. & Villéger, S. (2013) Betapart: partitioning beta diversity into turnover and nestedness components.
- Blanchet, S., Leprieur, F., Beauchard, O., Staes, J., Oberdorff, T. & Brosse, S. (2009) Broad-scale determinants of non-native fish species richness are context-dependent. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 2385–2394.
- Boulêtreau, S., Cucherousset, J., Villéger, S., Masson, R. & Santoul, F. (2011) Colossal aggregations of giant alien freshwater fish as a potential biogeochemical hotspot. *PLoS ONE*, **6**, e25732.
- Brosse, S., Beauchard, O., Blanchet, S., Dürr, H.H., Grenouillet, G., Hugueny, B., Lauzeral, C., Leprieur, F., Tedesco, P.A., Villéger, S. & Oberdorff, T. (2013) Fish-SPRICH: a database of freshwater fish species richness throughout the world. *Hydrobiologia*, **700**, 343–349.
- Buisson, L., Grenouillet, G., Villéger, S., Canal, J. & Laffaille, P. (2013) Toward a loss of functional diversity in stream fish assemblages under climate change. *Global Change Biology*, **19**, 387–400.
- Capps, K.A. & Flecker, A.S. (2013) Invasive fishes generate biogeochemical hotspots in a nutrient-limited system. *PLoS ONE*, **8**, e54093.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.
- Clavel, J., Julliard, R. & Devictor, V. (2011) Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment*, **9**, 222–228.
- Clavero, M. (2011) Assessing the risk of freshwater fish introductions into the Iberian Peninsula. *Freshwater Biology*, **56**, 2145–2155.
- Clavero, M. & García-Berthou, E. (2006) Homogenization dynamics and introduction routes of invasive freshwater fish in the Iberian Peninsula. *Ecological Applications*, **16**, 2313–2324.
- Cucherousset, J. & Olden, J.D. (2011) Ecological impacts of non-native freshwater fishes. *Fisheries*, **36**, 215–230.
- Freyhof, J. & Brooks, E. (2011) *European Red List of freshwater fishes*. Publications Office of the European Union, Luxembourg.
- Froese, R. & Pauly, D. (2013) FishBase. Available at: <http://www.fishbase.org>.
- Goslee, S.C. & Urban, D.L. (2007) The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, **22**, 1–19.
- Griffiths, D. (2006) Pattern and process in the ecological biogeography of European freshwater fish. *Journal of Animal Ecology*, **75**, 734–751.

- Gower, J.C. (1971) General coefficient of similarity and some of its properties. *Biometrics*, **27**, 857–871.
- Hermoso, V., Clavero, M. & Kennard, M.J. (2012) Determinants of fine-scale homogenization and differentiation of native freshwater fish faunas in a Mediterranean Basin: implications for conservation. *Diversity and Distributions*, **18**, 236–247.
- Koleff, P., Gaston, K.J. & Lennon, J.J. (2003) Measuring beta diversity for presence–absence data. *Journal of Animal Ecology*, **72**, 367–382.
- Kottelat, M. & Freyhof, J. (2007) *Handbook of European freshwater fishes*. Kottelat & Freyhof, Cornol, Switzerland.
- Leprieur, F., Beauchard, O., Blanchet, S., Oberdorff, T. & Brosse, S. (2008a) Fish invasions in the world's river systems: when natural processes are blurred by human activities. *PLoS Biology*, **6**, e28.
- Leprieur, F., Beauchard, O., Hugueny, B., Grenouillet, G. & Brosse, S. (2008b) Null model of biotic homogenization: a test with the European freshwater fish fauna. *Diversity and Distributions*, **14**, 291–300.
- Leprieur, F., Tedesco, P.A., Hugueny, B., Beauchard, O., Dürr, H.H., Brosse, S. & Oberdorff, T. (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters*, **14**, 325–334.
- Leprieur, F., Albouy, C., De Bortoli, J., Cowman, P.F., Bellwood, D.R. & Mouillot, D. (2012) Quantifying phylogenetic beta diversity: distinguishing between 'true' turnover of lineages and phylogenetic diversity gradients. *PLoS ONE*, **7**, e42760.
- Lichstein, J. (2007) Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecology*, **188**, 117–131.
- Lockwood, J.L., Brooks, T.M. & McKinney, M.L. (2000) Taxonomic homogenization of the global avifauna. *Animal Conservation*, **3**, 27–35.
- Luck, G.W. & Smallbone, L.T. (2011) The impact of urbanization on taxonomic and functional similarity among bird communities. *Journal of Biogeography*, **38**, 894–906.
- Marr, S.M., Marchetti, M.P., Olden, J.D., García-Berthou, E., Morgan, D.L., Arismendi, I., Day, J.A., Griffiths, C.L. & Skelton, P.H. (2010) Freshwater fish introductions in mediterranean-climate regions: are there commonalities in the conservation problem? *Diversity and Distributions*, **16**, 606–619.
- Matsuzaki, S.S., Sasaki, T. & Akasaka, M. (2013) Consequences of the introduction of exotic and translocated species and future extirpations on the functional diversity of freshwater fish assemblages. *Global Ecology and Biogeography*, **22**, 1071–1082.
- Naem, S., Duffy, J.E. & Zavaleta, E. (2012) The functions of biological diversity in an age of extinction. *Science*, **336**, 1401–1406.
- Olden, J.D. & Poff, N.L. (2004) Ecological processes driving biotic homogenization: testing a mechanistic model using fish faunas. *Ecology*, **85**, 1867–1875.
- Olden, J.D. & Rooney, T.P. (2006) On defining and quantifying biotic homogenization. *Global Ecology and Biogeography*, **15**, 113–120.
- Olden, J.D., Poff, N.L. & Bestgen, K.R. (2006) Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecological Monographs*, **76**, 25–40.
- Olden, J.D., Kennard, M.J. & Pusey, B.J. (2008) Species invasions and the changing biogeography of Australian freshwater fishes. *Global Ecology and Biogeography*, **17**, 25–37.
- Olden, J.D., Lockwood, J.L. & Parr, C.L. (2011) Biological invasions and the homogenization of faunas and floras. *Conservation biogeography* (ed. by R.J. Ladle and R.J. Whittaker), pp. 224–243. Wiley-Blackwell, Chichester.
- Pool, T.K. & Olden, J.D. (2012) Taxonomic and functional homogenization of an endemic desert fish fauna. *Diversity and Distributions*, **18**, 366–376.
- R Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rahel, F.J. (2000) Homogenization of fish faunas across the United States. *Science*, **288**, 854–856.
- Reyjol, Y., Hugueny, B., Pont, D., Bianco, P.G., Beier, U., Caiola, N., Casals, F., Cowx, I., Ferreira, T., Haidvogel, G. & Noble, R. (2007) Patterns in species richness and endemism of European freshwater fish. *Global Ecology and Biogeography*, **16**, 65–75.
- Ricciardi, A. (2007) Are modern biological invasions an unprecedented form of global change? *Conservation Biology*, **21**, 329–336.
- Schleuter, D., Daufresne, M., Veslot, J., Mason, N.W.H., Lanoiselée, C., Brosse, S., Beauchard, O. & Argillier, C. (2012) Geographic isolation and climate govern the functional diversity of native fish communities in European drainage basins. *Global Ecology and Biogeography*, **21**, 1083–1095.
- Spear, D. & Chown, S.L. (2008) Taxonomic homogenization in ungulates: patterns and mechanisms at local and global scales. *Journal of Biogeography*, **35**, 1962–1975.
- Strayer, D.L. & Hillebrand, H. (2012) Eight questions about invasions and ecosystem functioning. *Ecology Letters*, **15**, 1199–1210.
- Toussaint, A., Beauchard, O., Oberdorff, T., Brosse, S. & Villéger, S. (2014) Historical assemblage distinctiveness and the introduction of widespread non-native species explain worldwide change in freshwater fish taxonomic dissimilarity. *Global Ecology and Biogeography*, **23**, 574–584.
- Vander Zanden, M.J. (2005) The success of animal invaders. *Proceedings of the National Academy of Sciences USA*, **102**, 7055–7056.
- Villéger, S. & Brosse, S. (2012) Measuring changes in taxonomic dissimilarity following species introductions and extirpations. *Ecological Indicators*, **18**, 552–558.
- Villéger, S., Mason, N.W.H. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**, 2290–2301.

- Villéger, S., Blanchet, S., Beauchard, O., Oberdorff, T. & Brosse, S. (2011a) Homogenization patterns of the world's freshwater fish faunas. *Proceedings of the National Academy of Sciences USA*, **108**, 18003–18008.
- Villéger, S., Novack-Gottshall, P.M. & Mouillot, D. (2011b) The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecology Letters*, **14**, 561–568.
- Villéger, S., Grenouillet, G. & Brosse, S. (2013) Decomposing functional β -diversity reveals that low functional β -diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography*, **22**, 671–681.
- Whittaker, R.H. (1956) Vegetation of the great smoky mountains. *Ecological Monographs*, **26**, 1–80.
- Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Arianoutsou, M., Basnou, C., Delipetrou, P., Didziulis, V., Hejda, M., Hulme, P.E., Lambdon, P.W., Pergl, J., Pysek, P., Roy, D.B. & Kühn, I. (2009) Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proceedings of the National Academy of Sciences USA*, **106**, 21721–21725.

SUPPORTING INFORMATION

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

Figure S1 Map of the 137 river basins.

Figure S2 Results of the traits sensitivity analysis.

Table S1 Functional traits used to describe fish functional strategy.

BIOSKETCHES

Sébastien Villéger is a CNRS researcher in the laboratory 'Ecologie des Systèmes Marins Côtiers' (University of Montpellier, France). He uses taxonomic and functional approaches to understand the determinants of fish diversity and to assess their impacts on ecosystem functioning.

Gaël Grenouillet is an associate professor in the laboratory 'Evolution et Diversité Biologique' (University of Toulouse, France). He has experience in species distribution modelling and stream ecology. He is working on the impact of climate change on fish assemblages, currently with emphasis on the influence of species traits on the sensitivity of species.

Sébastien Brosse is a professor in the laboratory 'Evolution et Diversité Biologique' (University of Toulouse, France). He has experience in fish ecology at both local and macroecological scales and has a particular interest in human impacts on freshwater ecosystems.

Editor: Janne Soininen