LETTER

Non-native species led to marked shifts in functional diversity of the world freshwater fish faunas

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Abstract

Global spread of non-native species profoundly changed the world biodiversity patterns, but how it translates into functional changes remains unanswered at the world scale. We here show that while in two centuries the number of fish species per river increased on average by 15% in 1569 basins worldwide, the diversity of their functional attributes (i.e. functional richness) increased on average by 150%. The inflation of functional richness was paired with changes in the functional structure of assemblages, with shifts of species position toward the border of the functional space of assemblages (i.e. increased functional divergence). Non-native species moreover caused shifts in functional identity toward higher body sized and less elongated species for most of assemblages throughout the world. Although varying between rivers and biogeographic realms, such changes in the different facets of functional diversity might still increase in the future through increasing species invasion and may further modify ecosystem functioning.

Keywords

Biotic exchanges, extinction, functional divergence, functional richness, introduction, macroecology.

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INTRODUCTION

Human activities, by altering and fragmenting habitats, changing climate and overharvesting organisms have pushed hundreds of species to local extinction during the last two centuries (Burkhead 2012; Tedesco *et al.* 2013; Dias *et al.* 2017; IUCN 2018). Meanwhile, human activities have also promoted biotic exchanges between regions, with more than 16 000 successful non-native introductions (animal and vegetal) across the world recorded to date (Seebens *et al.* 2018). These introductions of non-native species have contributed to increase species richness (i.e. taxonomic diversity) in most regions of the world, at least for plants and vertebrates (Sax & Gaines 2003; Leprieur *et al.* 2008).

However, the consequences of the numerous species introductions and extinctions on functional diversity (i.e. diversity of ecological attributes), a key facet of biodiversity (Mouillot *et al.* 2013b), remain only partially documented over large areas (Olden *et al.* 2006, 2008; Blanchet *et al.* 2010; Whittaker *et al.* 2014). Temporal changes in functional diversity result from differences between the functional attributes of native, non-native and extinct species and thus cannot be predicted by measuring the change in species richness alone (Villéger *et al.* 2010; Mouillot *et al.* 2013a). In addition, change in species composition could affect in different ways the complementary facets of functional diversity (Villéger *et al.* 2008, 2011b; Mouillot *et al.* 2013a). For instance, functional richness (FRic), measures the portion of the functional space filled by species from an assemblage and accounts only for the species with the most extreme trait values (Villéger *et al.* 2008), Therefore FRic cannot decrease after introduction of non-native species (and, similarly, extinction cannot increase FRic). However, the magnitude of the change in FRic cannot be predicted only based on the changes in species richness. Thus, if the introduced or extinct species exhibit unique functional attributes, the change in FRic will markedly exceed the change in taxonomic diversity. Contrastingly, if introduced or extinct species are functionally redundant with native species, FRic will show limited change, even if taxonomic diversity varies strongly.

Furthermore, similar change in FRic could hide contrasted changes in complementary facets of functional diversity accounting for position of all species in the functional space, such as functional divergence (i.e. position of species relative to the border of the space filled by an assemblage, FDiv, Villéger *et al.* 2008), and functional identity (average position of species in functional space, FIde). These functional diversity facets could affect differently ecosystem processes (Mouillot *et al.* 2011) and hence their temporal changes should be assessed to disentangle contrasted situations following introduction of non-native species and extinction of native species (Fig. 1). For instance, similar increase in FRic in two species assemblages could be paired with either a decrease in FDiv, if most non-native species have non-extreme traits values (compared to species historically present), or an increase in FDiv if most of the non-native species have extreme traits values (compared to species historically present) (Fig. 1a).

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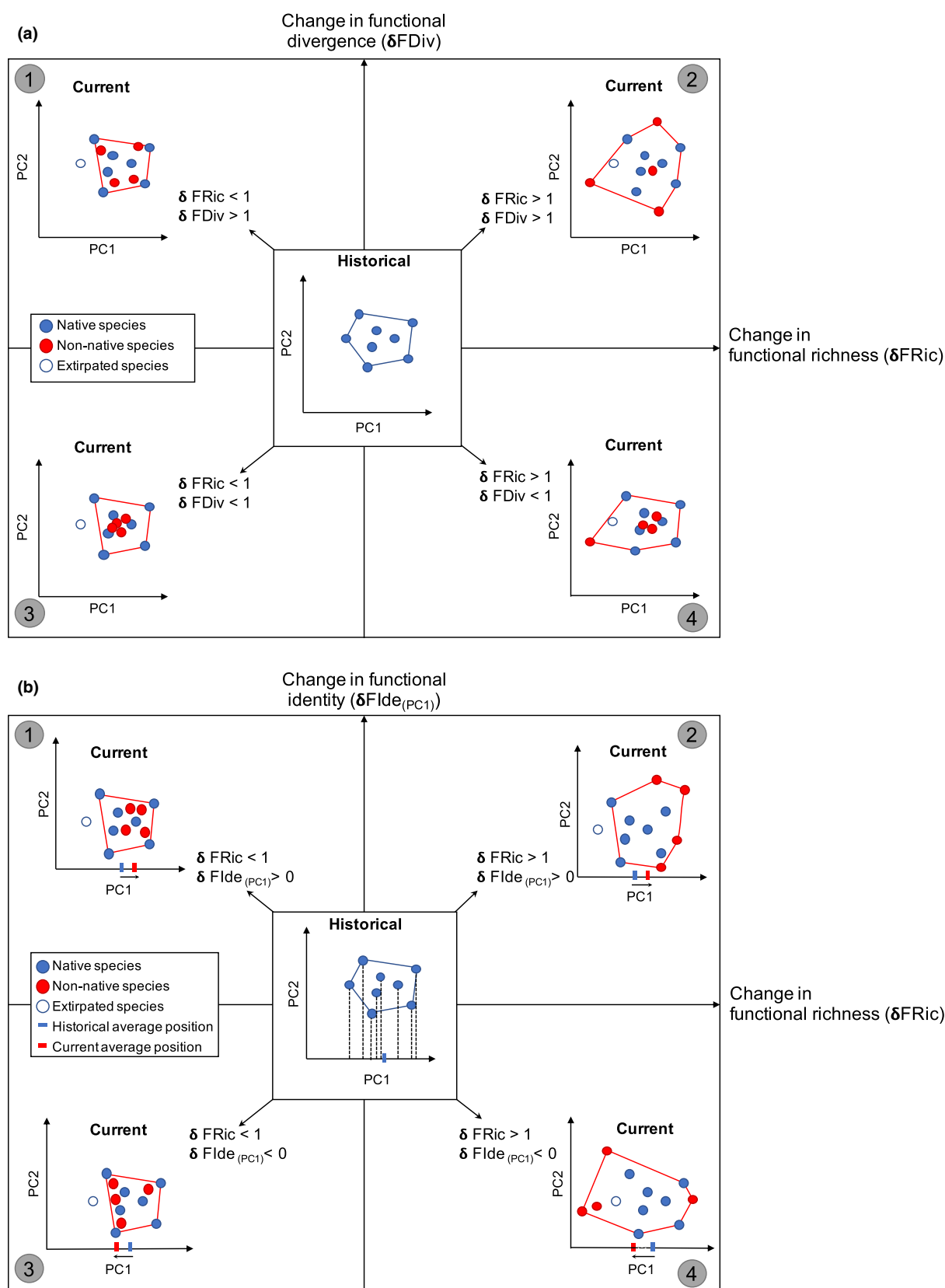
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In addition, increase in FRic can be paired with contrasted shifts in FIde depending on the similarity of functional trait values of introduced and extinct species relative to the native species (Fig. 1b). Therefore, while the change in FRic measures the increase or decrease in the portion of the functional space filled by species, the change in FIde measures the

Figure 1 A multifaceted approach of functional diversity to assess the effects of introductions of non-native species and extinction of native species. Contrasted changes in functional richness and changes in functional divergence (a) or changes in functional identity (b) are illustrated for an hypothetical historical situation (centre) and 4 current situations (corners) after the same changes in taxonomic diversity (4 introductions and 1 extinction). Functional richness (FRic) is measured as the volume of the minimum convex hull (illustrated by the blue or red polygons) that includes all the species in the multidimensional functional space built based on trait values among all species present in the study case (here only 2 axes from a Principal Component analysis for graphical convenience). Functional divergence (FDiv) is measured as the relative position of species from the gravity centre of the species present in an assemblage. Functional identity (FIde) is computed for each functional axis (here PC1) as the average of species position along this axis (illustrated by dashed lines and colored dash on axis). Change in FRic and change in FDiv were calculated as the ratio between current (i.e. after introduction and/or extinction) and historical values, and they thus range from 0 (extreme decrease) to infinity (extreme increase). Change in FIde was calculated as the difference between current (i.e. after introduction and/or extinction) and historical average position of species on the axis (here PC1), divided by the range filled by the species in the historical situation. Change in FIde thus ranges from -1 to $+1$.

direction on each dimension of the functional space. An increase in FIde on one functional axis (e.g. PC1, on Fig. 1b) indicates that the assemblage received non-natives species with higher values of the traits contributing to this axis compared to species historically present (e.g. cases 1 and 2, Fig. 1b), whereas a decrease indicates the opposite situation (e.g. cases 3 and 4, Fig. 1b). Therefore, a same increase in FRic can be paired with contrasted changes in FIde.

Here, we analysed for the first time the change in functional diversity of freshwater fish assemblages at the world scale. Freshwater ecosystems host more than 13 000 fish species (i.e., 25% of all vertebrate species (Nelson *et al.* 2016), and are among the most imperilled faunas worldwide (Vörösmarty *et al.* 2000). Meanwhile, human activities have also promoted biotic exchange between rivers, with more than 3500 successful non-native fish introductions across the world rivers recorded to date (Villéger *et al.* 2011a). These introductions of non-native species have contributed to increase fish species richness (i.e. taxonomic diversity) in over half of the world river basins (Leprieur *et al.* 2008), and changes in functional diversity have been reported in several regions (Matsuzaki *et al.* 2013; Villéger *et al.* 2014; Kuczynski *et al.* 2018). Using a database of functional traits, related to food acquisition and locomotion for more than 9500 freshwater fish species, we assessed the effect of non-native species introductions and native species extinctions on complementary facets of functional diversity in 1569 river basins throughout the world. We first quantified the changes in FRic experienced by those 1569 fish assemblages across the 6 biogeographic realms. We then tested the relative role of invasions and extinctions on those changes. We here hypothesise that the contribution of non-native species to those changes is not only explained by the number of species introduced but also by the biogeographic origin of those species and the functional traits of the native fauna. Indeed, since fish faunas are distinct between realms (Lévêque *et al.* 2008) and show distinct morphologies (Toussaint *et al.* 2016b), non-native species might drive functional change in different directions between realms, causing idiosyncratic FIde shifts. We also hypothesise that exotic species introduced from another realm might cause a stronger change in functional diversity than the species introduced from other rivers of the considered realm (i.e. translocated species). We therefore investigated how those taxonomic changes translate into FRic and whether most or a few of the introduced or extinct species support those changes by examining changes in FDiv and FIde.

METHODS

Functional traits

We used the most comprehensive functional database existing to date to describe freshwater fish morphology (Toussaint *et al.* 2016b). This database encompasses 9534 freshwater fish species out of the *ca.* 13 000 described strictly freshwater fish species (Nelson *et al.* 2016), and hence covers 73% of the documented world freshwater fish fauna. Each species is described with ten functional traits (see Fig. S1 for details), among which body size is a key trait related to all functions driven by metabolism (Blanchet *et al.* 2010) and was estimated as the maximum body length registered on Fishbase (www.fishbase.org, Froese & Pauly 2012). The remaining nine traits describe the shape and position of the external anatomical characteristics of fishes (i.e. head, eyes, mouth, pectoral and caudal fins, see details in Fig. S1) that affect their feeding and locomotion. These traits were computed as unit-less ratios between morphological measures on side view picture, using one specimen by species as in Villéger *et al.* (2010) and Toussaint *et al.* (2016b). Although these ten morphological traits cannot account for all the actual roles played by fish in ecosystems (e.g. nutrient recycling or trophic control of other taxa), they remain informative to describe at least two key functions performed by fish, i.e. food acquisition and locomotion (Winemiller 1991; Villéger *et al.* 2010, 2017). Complementary functional traits (e.g. gut length, oral gape area and shape, fecundity) were not included because they are currently unavailable for most species (i.e. more than 70% of the > 9000 species considered).

Fish occurrence databases

Historical and current occurrences of freshwater fish species in more than 3000 river basins across the globe were obtained by combining two spatial databases (Brosse *et al.* 2013; Tedesco *et al.* 2017). Each river basin was assigned to one of the six biogeographic realms (i.e. Afrotropical, Australian (including Oceania), Nearctic, Neotropical, Oriental and Palearctic) defined for freshwater fish (Brosse *et al.* 2013; Tedesco *et al.* 2017). Historical composition of the river basins refers to the past fauna with only native species, and thus roughly corresponds to the preindustrial period (i.e., before the 18th century), because industrialisation and associated goods exchanges are recognised as the main driver of the introduction of fish (as well as of other animals) mainly for aquaculture, fishing, and ornamental purposes (Leprieur *et al.* 2008;

Seebens *et al.* 2017). Current composition refers to present fauna with the non-native species and without the extinct native ones. Extinct species refers to extinctions within each river basin and were extracted from Brosse *et al.* (2013) and Dias *et al.* (2017) and updated using IUCN Red lists (IUCN 2018). Non-native species occurrences were separated into 'exotic' for species introduced in a realm where they were not present as native, and 'translocated' for species introduced in a river basin belonging to a realm where they were present as native (Blanchet *et al.* 2009). Combining the functional and occurrence databases permitted to describe the temporal changes in functional diversity of 1569 freshwater fish assemblages across the world, for which more than 80% of the species were functionally described.

Functional space

The ten functional traits were standardised so that the mean of each trait was 0 and its standard deviation was 1 in order to give the same weight to each trait. Then, they were ordered in a multidimensional functional space using a Principal Components Analysis. Because of the quality of the pictures did not allow the measurement of all morphological traits in all species (i.e. 18% of the morphological measurements were not obtained, see details in Toussaint *et al.* 2016b), we used a regularised algorithm designed for ordination analysis to handle the missing values (Josse & Husson 2012). The first five axes, accounting for 80.5% of the total variance and having eigenvalues > 1 (Table S1), were kept to build a five-dimensional functional space that faithfully represented the trait-based functional distance between species (Maire *et al.* 2015). Mean squared deviation between initial distance between species (i.e. computed according to their scaled trait values) and final distance (i.e. Euclidean distance in the 5D space) is of 0.11 which is 0.67% of maximum initial distance testifying for the high quality of 5D space. We measured the distance between each species and its closest neighbour in order to look for potential hole within the functional space. We found that the maximal distance between 2 neighbour species corresponds to 11% of the two most distant species in the functional space. On average distance between two neighbour species was of 0.002% (± 0.001) testifying that species are continuously distributed in the functional space.

We then tested the sensitivity of distance between species in the functional space to the set of functional traits considered. We computed the functional distance between species for all combinations of nine functional traits out of ten. The distance between species in these 9-dimensional functional spaces were congruent with distance in the 10-dimensional space (Mantel tests $r > 0.900$, $P < 0.001$, see details in Toussaint *et al.* 2016b) demonstrating that relative position of species in the functional space was not driven by a single trait.

We also tested the potential effect of intra-specific traits variability on functional diversity indices (i.e. FRic and FSpe, see below for details). As intra-specific variation is unknown for most of the species, we used a subset of 60 species (including non-native species) occurring in 36 European assemblages for which between 3 and 6 adult individuals per species were morphologically described. Intra-specific trait variability hardly affect patterns of functional diversity measured at the river basin scale (Fig. S2).

Assessing fish biodiversity

For each assemblage, we calculated taxonomic richness (TRic) as the number of species in each river basin. Functional structure of fish assemblages in each river basin was assessed using three complementary functional diversity indices: functional richness (FRic), functional divergence (FDiv) and functional identity (FIde).

Functional richness (FRic, Villéger *et al.* 2008), measures the volume of the minimum convex hull that includes all the species in the five-dimensional functional space. The higher the FRic, the higher the range of functional trait values in the species assemblage considered. Thus, FRic accounts only for the species with the most extreme trait values (Villéger *et al.* 2008).

Functional divergence (FDiv) measures how species are distributed within the volume filled by the assemblage (Mouillot *et al.* 2013a). FDiv measures the relative position of species from the gravity centre of the most extreme species (i.e. those at the edge of the convex hull). FDiv is close to 1 if most species are close to the border of the convex hull and is close to 0 if most species are close to the gravity centre of the volume filled by the assemblage.

Functional identity (FIde) measures how the species distribute in the functional space and is calculated as the average position of the species from an assemblage on each axis of the functional space.

Measuring changes in biodiversity

For each river basin, the consequences of species introductions and extinctions on TRic were assessed as the relative changes from the historical to the current period.

$$\delta TRic = \frac{TRic_{Current}}{TRic_{Historic}}$$

$TRic_{Historic}$ represented the number of species historically occurring in each river basin and the $TRic_{Current}$ represented the number of species currently present, namely after introductions and extinctions. As for TRic, the changes in FRic ($\delta FRic$) and FDiv ($\delta FDiv$) were calculated as the ratio between the current and the historic situation. A change lower than 1 means that diversity facet has decreased between the two periods, whereas a change > 1 means that assemblage richness has increased.

We also tested whether the changes in FRic (i.e. filling of functional space) were paired with a shift in functional identity ($\delta FIde$). We computed the relative change in functional identity along each of the five-functional axes for each assemblage as the difference in average position on each axis between species present in the current situation (i.e. after introduction and/or extinction) and species present in the historical situation, divided by the range of each axis filled by the species present in the historical situation.

Disentangling drivers of changes in FRic and FDiv

Functional richness is expected to increase with increasing taxonomic richness but the strength and slope of this relationship could vary across situations because of species trait values. We first tested the explanatory power of δTRic on δFRic in the six biogeographic realms independently, using linear regressions on $\log_2$-transformed values of δTRic and δFRic.

We then tested the contribution of four variables that could explain δFRic and δFDiv: historical FRic on δFRic or historical FDiv on δFDiv, the number of non-native species introduced, the proportion of exotic species among the non-native species introduced in the river basin (i.e. non-native species introduced in a realm where they were not historically present) and the number of extinct species. All predictors were log-transformed and scaled. We used linear mixed models including simple effects and pairwise interactions between these four variables. In addition, we considered the biogeographic realm as a random factor in order to test for potential variation between them. The model was built using 'lme' function (nlme package) available in R and simplified using a stepwise selection procedure based on Akaike Information Criterion (AIC) using the 'stepAIC' function (MASS package) available in R.

Finally, we tested the deviation between observed change in FRic and expectation given the number of introduced and/or extinct species and given trait values of native, non-native and threatened species from each realm. More precisely, for each river basin the identity of translocated and exotic non-native species were sorted randomly within the pool of non-native species occurring in the biogeographic realm and identity of extinct species within the pool the IUCN-Threatened species (IUCN 2018) occurring in the biogeographic realm. The threatened species were defined as the species listed as Critically Endangered (CR), Endangered (EN), Vulnerable (VU) or Near Threatened (NT) in the most recent IUCN Red List assessment (IUCN 2018). Randomisations were repeated 999 times. The significance of the difference from null expectations (p) was tested using a two-tailed test ($\alpha < 0.05$).

Comparing functional specialisation of native, non-native and extinct species

For each biogeographic realm, we tested whether non-native and extinct species have more extreme traits values than native species. We first computed the centroid of all the native species historically occurring in the realm (including extinct species). Then we computed for each species occurring in the realm (native and non-native) its functional specialisation (FSpe) as the Euclidean distance to this centroid (Villéger et al. 2010). We finally tested for differences in FSpe between all native species and (i) extinct native species, (ii) all non-native species, (iii) translocated species (non-native species introduced in river basins belonging to a realm where they were already present) and (iv) exotic non-native species, using non-parametric Wilcoxon tests.

All statistical analyses were performed with R software version 3.0 (R Core Team 2017).

RESULTS

The changes in species composition in the river basins across the world have led to a global increase in both taxonomic and functional richness. Indeed, river basins experienced a 1.15-fold increase in TRic (i.e. species richness increased by 15% on average) that turned into a 2.50-fold increase in FRic (i.e. functional richness increased by 150% on average). Among the 1569 rivers considered, current FRic values range from 0.12-fold to 441-fold of historical FRic while current TRic ranges from 0.60-fold to 5.00-fold of historical TRic (Table 1, Fig. S3). The higher increase in FRic compared to the increase in TRic was significant in all the 6 biogeographic realms (Paired t-test: $t = 4.08$, d.f. = 1568, $P < 0.001$, Table 1). Fish FRic has increased more than twice in 14% of the river basins across the world (i.e. magnitude of change in FRic between historical and current situations exceeded 2). In contrast, TRic has more than doubled in < 2% of the world river basins (Fig. S4).

Although δFRic was expected to correlate positively with δTRic, the increase in FRic of freshwater fish assemblages was steeper than increase in TRic and even followed a power-like function (Fig. 2). Indeed, in the six biogeographic realms, the slope of the relationship between $\log_2$-δTRic and $\log_2$-δFRic was higher than 2 (from 2.83 in Palearctic to 3.82 in Oriental, Fig. 2). For most of the river basins, the observed change in fish FRic did not differ from the change expected

Table 1 Changes in taxonomic and functional richness of freshwater fish assemblages following native species extinctions and non-native species introductions

Biogeographic realm	Change in functional richness (δFRic)	Change in taxonomic richness (δTRic)	Ratio δFRic/δTRic
Afrotropical (n = 148)	1.50 ± 1.90 [1.00−7.24]	1.06 ± 0.17 [1.00−1.63]	1.28 ± 1.09 [0.95−4.66]
Australian (n = 217)	1.87 ± 2.86 [1.00−6.45]	1.13 ± 0.19 [1.00−1.71]	1.51 ± 1.72 [0.95−4.44]
Nearctic (n = 204)	6.18 ± 34.17 [0.81−34.57]	1.27 ± 0.58 [0.96−3.08]	2.47 ± 8.81 [0.86−13.33]
Neotropical (n = 287)	1.34 ± 1.66 [1.00−3.46]	1.05 ± 0.12 [1.00−1.43]	1.22 ± 1.20 [0.99−2.51]
Oriental (n = 169)	1.35 ± 1.56 [1.00−4.53]	1.05 ± 0.12 [1.00−1.37]	1.23 ± 1.04 [0.95−2.92]
Palearctic (n = 544)	2.62 ± 8.05 [1.00−19.48]	1.20 ± 0.35 [1.00−1.93]	1.75 ± 3.18 [0.87−9.14]
World (n = 1569)	2.50 ± 13.35 [1.00−11.99]	1.15 ± 0.3 [1.00−1.88]	1.61 ± 3.82 [0.90−6.55]

The number of river basins (n) considered for each realm is indicated in brackets. Change in taxonomic richness (δTRic) and change in functional richness (δFRic) were calculated as the ratio between their current and historical values (i.e. values higher than 1 indicate an increase from historical to current situation). A value higher than 1 for the ratio δFRic/δTRic indicates that change in functional richness (δFRic) was greater than the change in taxonomic richness (δTRic). For each biogeographic realm and the world, the mean and standard deviation for each biodiversity metric are given with corresponding confidence interval at 95% in square brackets.
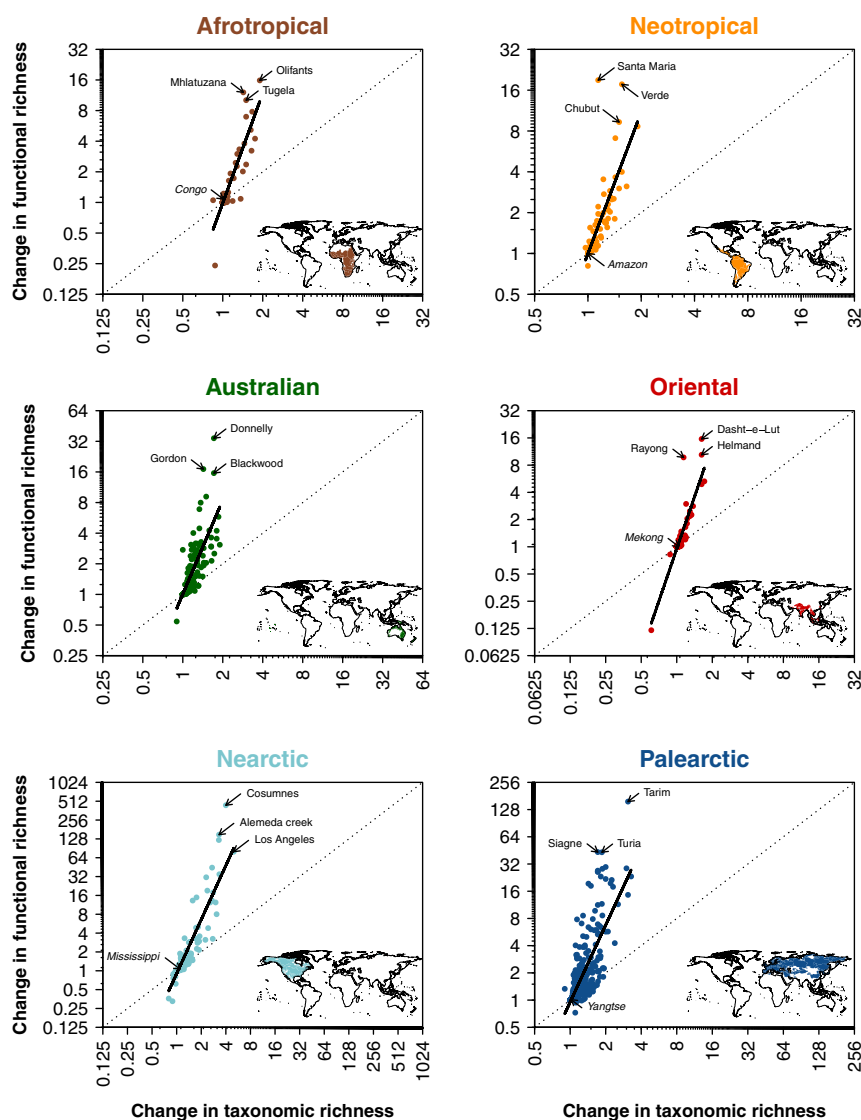
Figure 2 Relation between change in taxonomic richness and change in functional richness of freshwater fish assemblages following native species extinctions and non-native species introductions. Changes in taxonomic richness (δTRic) and functional richness (δFRic) were calculated as the relative change between current and historical values of indices (NB: scales of axes are $\log_2$-scales and differ between panels). The dotted line represents the identity line (δFRic = δTRic). For each biogeographic realm, the relationship between δTRic and δFRic was tested using linear regression. The black lines represent the linear regression line between $\log_2$-transformed δTRic and $\log_2$-transformed δFRic. For each biogeographic realm, the names of the three river basins experiencing the greater increase in functional richness are given. Some large rivers are also indicated in italic on the figure. The inset maps show the river basins considered in each realm.

given the number of species introduced and/or extinct and the trait values of non-native species already established in the biogeographic realm (Table S2).

The global increase in FRic was associated with a change in the functional structure of fish assemblage. More than 60% of the fish assemblages that experienced an increase in FRic also experienced an increase in FDiv (Fig. 3). In addition, the increase in FRic was not coupled to a change in a single functional trait but rather paired with shifts in the average position (FIde) along the five axes of the functional space that differ in terms of both direction and intensity among river basins and realms (Table S5 and Fig. 4). Only the functional axis PC4, related to body elongation (Table S1), was

congruent for the six biogeographic realms and significantly positively correlated to the changes in FRic (Spearman's rank correlation tests: Rho ranges from 0.444 in Afrotropical to 0.664 in Australian, Table S5).

The most significant predictors of change in FRic and FDiv were the historical functional richness and the number of introduced species, whereas the number of extinctions hardly affected the change in FRic and FDiv (Table 2). Rivers with a low historical TRic were more sensitive to the introduction of non-native species as demonstrated by the ten most impacted river basins worldwide (i.e. δFRic > 30) which hosted < 15 species historically (Fig. 2). In contrast, the most species-rich river basins had δFRic similar to those observed
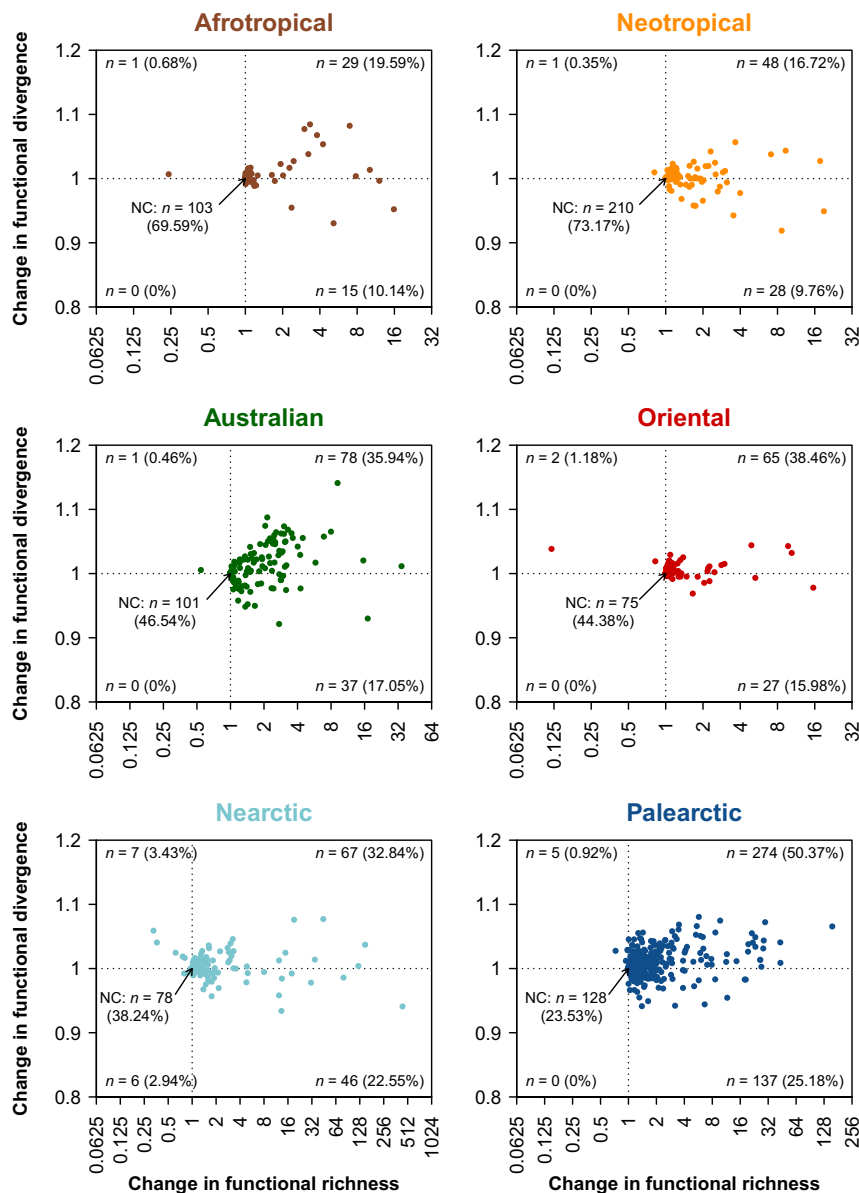
Figure 3 Relationship between change in functional richness and change in functional divergence of freshwater fish assemblages following native species extinctions and non-native species introductions for the six biogeographic realms. Change for each index is calculated as the ratio between current and historical values of indices (NB: scale of x-axis is $\log_2$-scaled and differ between panels). The number of basins (n) and associated relative percentage among all river basins of the biogeographic realm of the 5 combinations of change in functional richness (δFRic) and functional divergence (δFDiv) are indicated in the 4 corners and near the centre of each plot (NC means 'No Change' in functional richness and in functional divergence, i.e. δFRic=δFDiv=1).

for δTRic: both δFRic and δTRic ranged between 1.00 and 1.07 for the Amazon, Congo, Mekong, and Yangtze (Fig. 2).

The higher the proportion of introduced species that were exotic (i.e. non-native species introduced in a realm where they were previously absent), the greater the increase in FDiv (Table 2). Indeed, for five biogeographic realms, the non-native species have significantly more extreme trait values than those of the native freshwater fish fauna (Table S3). These differences in functional specialisation were mainly due to the exotic species that have significantly more extreme trait value than native species in four biogeographic realms but Australian and Palearctic. Contrastingly, translocated species

were functionally similar compared to extant native in all realms but Palearctic (Table S3).

DISCUSSION

Over the last two centuries, human-driven alterations of riverine fish assemblages (i.e. species introductions and extinctions) have led to a global increase in both taxonomic and functional richness (Fig. 2) and the increase in functional richness was 10-times higher, on average, than the increase in taxonomic richness (150% for FRic vs. 15% for TRic). These marked rises in functional richness demonstrate the profound
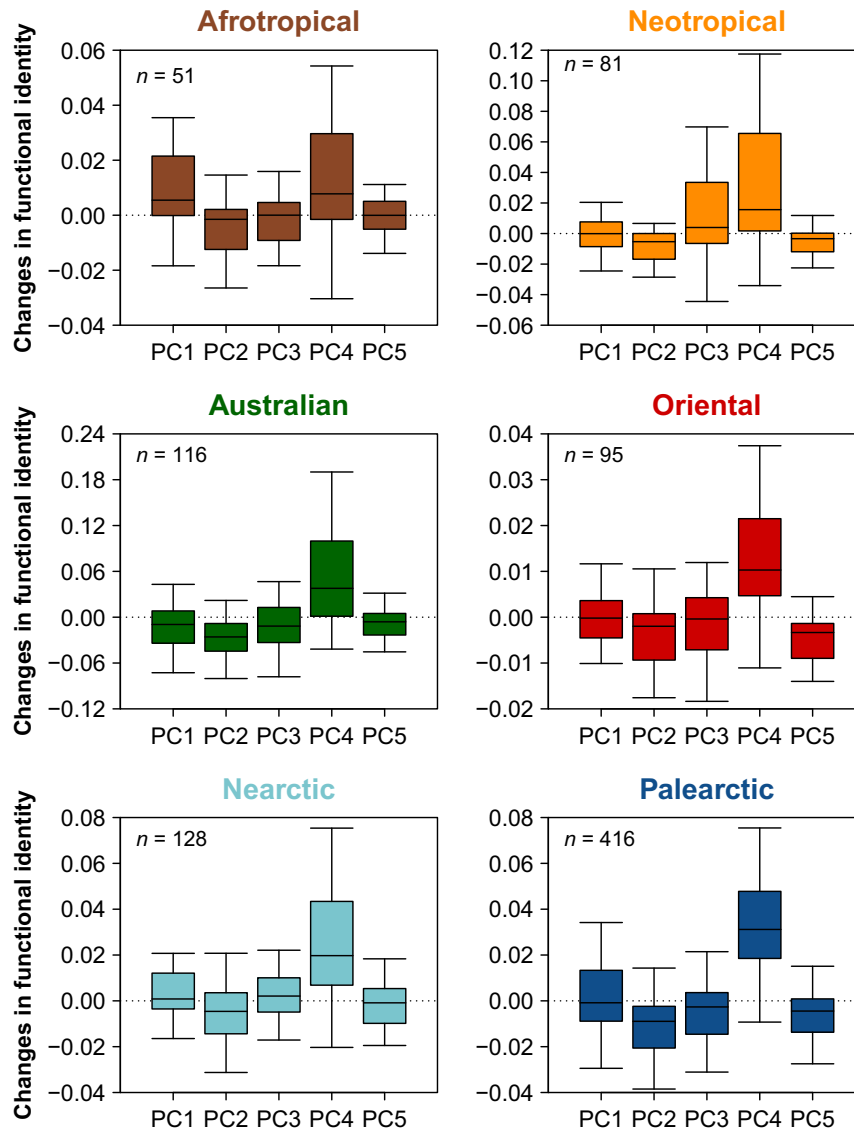
Figure 4 Change in functional identity of freshwater fish assemblages due to non-native species introductions and native species extinctions. For each assemblage, relative change in functional identity was computed for each of the 5 functional space axes (PCk with k from 1 to 5, see Fig. S5) as the difference between current (i.e. after introduction and/or extinction) and historical average position of species on the axis divided by the range filled by the species in the historical situation. Only the assemblages experiencing a change in species composition (i.e. introduction and/or extinction) were considered (number of basins considered for each realm is indicated on each panel, n). The boxes represent the 1st and 3rd quartile, the whiskers represent the confidence interval at 95% and horizontal line represents the median of the distribution for each functional space axis.

biodiversity change experienced by the world riverine ecosystems (Fig. 2). Our global scale results, although based on morphological traits that deserve to be completed, nevertheless call for caution when using only taxonomic diversity as an essential biodiversity variable (Pereira *et al.* 2013) for measuring consequences of human activities on biodiversity, and highlight the need to also consider complementary functional diversity indices to get a comprehensive image of change in biodiversity following alterations of species assemblages.

Marked alterations in FRic occurred even when only a few non-native species have been introduced. For instance, the introduction of 5–6 non-native species in the Turia river (Spain) and in the Siagne river (France), led to 1.85- and

1.71-fold increases in TRic, coupled to 43.19- and 43.37-fold increases in FRic. On another side, the Los Angeles river (CA, USA), for example, experienced the introduction of 32 non-native species, resulting in a 80-fold increase in FRic but only a five-fold increase in TRic (Fig. S3). Such extreme changes occurred mainly in arid and Mediterranean regions (Fig. 2) that are among the most imperilled ecosystems on earth (Vörösmarty *et al.* 2000; Tedesco *et al.* 2013).

Change in FRic was mostly explained by historical FRic and number of non-native species (Table 2). Particularly, the large river basins that historically gathered a rich fauna with diverse functional attributes (Table S5) are less likely to gain new functional attributes through introduction of non-native species, independently of the number of species introduced

Table 2 Determinants of changes in functional richness and functional divergence of freshwater fish assemblages following native species extinctions and non-native species introductions

Index	Variables	Coefficients (±SE)	df	*F* value	*P* value
Functional richness (FRic)					
	FRic Historical (log)	−0.138 ± 0.002	1;1554	1695.52	< 0.001***
	Nb. Non-native species (log+1)	0.207 ± 0.004	1;1554	4530.74	< 0.001***
	Prop. Exotic species	0.021 ± 0.005	1;1554	0.52	0.468[ns]
	Nb. Ext. species (log+1)	−0.046 ± 0.004	1;1554	192.93	< 0.001***
	FRic Historical (log) × Nb. Non-native species (log+1)	−0.140 ± 0.004	1;1554	3612.26	< 0.001***
	FRic Historical (log) × Prop. Exotic species	0.027 ± 0.004	1;1554	51.31	< 0.001***
	FRic Historical (log) × Nb. Ext. species (log+1)	0.019 ± 0.003	1;1554	78.68	< 0.001***
	Nb. Non-native species (log+1) × Prop. Exotic species	−0.024 ± 0.003	1;1554	90.98	< 0.001***
	AIC			−1591.08	
	Pseudo *R*-squared			0.82	< 0.001***
Functional divergence (FDiv)					
	FDiv Historical (log)	−0.0024 ± 0.0002	1;1557	203.75	< 0.001***
	Nb. Non-native species (log+1)	0.0024 ± 0.0003	1;1557	121.82	< 0.001***
	Prop. Exotic species	0.0011 ± 0.0003	1;1557	13.20	< 0.001***
	Nb. Ext. species (log+1)	0.0009 ± 0.0002	1;1557	6.61	< 0.05**
	FDiv Historical (log) × Nb. Non-native species (log+1)	−0.0027 ± 0.0002	1;1557	227.94	< 0.001***
	Nb. Non-native species (log+1) × Prop. Exotic species	−0.0005 ± 0.0001	1;1557	13.89	< 0.001***
	AIC			−11462.93	
	Pseudo *R*-squared			0.29	< 0.001***

The contributions of four variables and their pairwise interactions to the change in functional richness and functional divergence were assessed using a mixed model where the biogeographic realm was considered as a random factor. Predictor variables were log-transformed historical functional richness (FRic Historical (log)) for FRic, historical functional divergence (FDiv Historical (log)) for FDiv, log-transformed number of non-native species (Nb. Non-natives species (log+1)), proportion of exotic species (i.e. native from another realm, Prop. Exotic species) and log-transformed number of extinct species (Nb. Ext. species (log+1)). All predictor variables were scaled. For each index independently, a complete model was built and simplified using an AIC-step-wise procedure. Only the best model for each index (i.e. with the lowest AIC) is shown.

(Fig. S3). In contrast the rivers with a low historical TRic experienced drastic functional changes due to the introduction of species with functional characteristics historically absent from those ecosystems. Such a trend, well documented for island fauna (Walsh *et al.* 2012; Dyer *et al.* 2017) and isolated lakes (Dyer *et al.* 2017), probably explains why those isolated environments with limited historical functional richness are subjected to strong functional changes through invasions, causing, at least in some cases, important changes on ecosystem structure and function (Kumschick *et al.* 2015).

The increase in FRic was coupled with an increase in FDiv for most of the river basins throughout the world (Fig. 3), because most non-native species have more extreme traits values than native species (Table S3). Therefore, FRic and FDiv together contribute to the functional change. Moreover, the proportion of exotic species is higher among the river basins that experienced an increase in both FRic and FDiv (Table S6). For instance, in the Nearctic realm, exotic species such as sailfin catfish (*Pterygoplichthys multiradiatus*) and Chinese carp (*Ctenopharyngodon idella*) have extreme functional attributes compared to the native fauna (Table S3) while the more numerous translocated species are more functionally redundant with some native species (e.g. case 4, Fig. 1a). In contrast, the increasing pattern of FRic and FDiv (Fig. 3) in the Palearctic was mostly explained by a few translocated species (e.g. Blanchet *et al.* 2009), which have also extreme characteristics compared to some riverine native fauna (Table S3), such as common carp (*Cyprinus carpio*) and European catfish (*Silurus glanis*).

Such distinct morphological characteristics of the non-native species compared to the native fauna caused shifts in FIde (Fig. 4). Non-native species introduction tends to increase average fish body size (Blanchet *et al.* 2010) and reduce body elongation in all realms (see PC4 on Figs 4 and S5 and Tables S1 and S4). Those large and deep bodied species are favoured in slow flowing habitats, and therefore benefit from the current global rise of dams construction throughout the world (Zarfl *et al.* 2015; Winemiller *et al.* 2016). Moreover, the success of large-bodied species can be related to their higher dispersal ability compared to smaller species (Blanchet *et al.* 2010), making them better at colonising new habitats and thus expanding their ranges. However, large deep bodied fish show distinct traits related to feeding habits between realms (e.g. PC1 on Figs 4 and S5 and Tables S1 and S4). For instance, Palearctic and Australian realms received mostly large detritivorous fishes with basal mouth like carps, whereas Afrotropical and Nearctic realms mostly received predators with terminal mouth like basses (*Micropterus salmoides* and *M. dolomieu*) (Rahel 2007; Toussaint *et al.* 2016a). However, beyond these overall trends, shifts in FIde varied between fish assemblages within each biogeographic realm (Fig. 4) testifying that the change in FIde is highly dependent of the functional characteristics of both native and introduced species of each assemblage. It therefore appears that the consistent changes in fish functional richness throughout the world are mainly due to a preeminent effect of a few non-native extreme species displaying extreme functional attributes and this whatever their exotic or translocated status. The most successful

non-native species are often favoured by aquaculture, ornamental trade and angling (Padilla & Williams 2004) and are selected based on their original morphological characteristics (e.g. size, morphology based aesthetic display) (Marchetti et al. 2004) which ultimately maximise their effect on the functional diversity of recipient river. Such trend towards introduction of particular morphologies might modify ecosystem functioning through change in trophic networks (Cucherousset et al. 2012) or contribute to a faster cycling of organic matter by detritivorous species (Taylor 2006). Testing this hypothesis will require measuring more traits related to the role of fishes in ecosystem functions, as well as information about species abundances and intraspecific variation (including evolutionary consequences of invasions for both native and non-native species; Phillips & Shine 2004; Phillips et al. 2006). Determining the causes of introductions (intentional or not), their age and frequency (date of first introduction, number of introductions of each species in each site) as well as the distance from the native range of each exotic species, might also contribute to refine our results. Nevertheless, such data are currently available only at local scales and for a limited set of species (but see Sagouis et al. 2015; Seebens et al. 2018). Expanding functional and abundance data over more ecosystems is then a key agenda for future large scale studies on the effect of non-native species invasion.

In addition, the inflation of the fish functional diversity we report might in the near future interfere with the predicted increase in extinction rates (Tedesco et al. 2013) and eventually lead to a loss of functional diversity, since the most vulnerable species usually support unique functional attributes (Mouillot et al. 2013a; Leitão et al. 2016). Forecasting whether non-native species will compensate for future loss in functional diversity through extinction still remains a key question to determine potential shifts in ecosystem functioning.

AUTHORSHIP

A.T., S.B and S.V. designed the study. A.T., N.C., S.B and S.V. built the fish functional database, O.B., S.B., P.T. and T.O. built the fish occurrence databases, and A.T. and G.G. performed the analyses. A.T., S.B and S.V. discussed the results and led the writing of the manuscript that involved all authors.

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