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Worldwide freshwater fish homogenization is driven by a few widespread non-native species

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Abstract Introduction of non-native species have changed the composition of freshwater fish assemblages throughout the world and hence the dissimilarity between them, either toward homogenization (i.e. decrease in dissimilarity) or differentiation (i.e. increase in dissimilarity). However, there is still no assessment of individual contributions of non-native species to this overall trend at the global scale. Here, we disentangle individual non-native species effect from the global effect of the whole introduced species pool at the biogeographic realm scale and test which determinant can explain the effect of non-native species on changes in assemblage dissimilarity. Our results show that the contribution of introduced species on changes in dissimilarity is highly variable and all directions of changes are observed through the introduction process, i.e. either toward homogenization, differentiation or no change. Overall, only a few widespread species contribute to the worldwide homogenization pattern, whereas most of introduced species slightly contribute to the global change in dissimilarity. The effect of species on change in dissimilarity was influenced by the introduction pressure but also by whether introduced species were translocated (i.e. introduced to other basins within their biogeographic realm) or exotic (i.e. introduced from other biogeographic realms). Homogenization is strongly determined by the species translocated within a realm and only by few widespread exotic species whereas the majority of exotics contribute to a differentiation effect. Nevertheless, under future intensified human pressure, the exotic species spread across realms is predicted to increase and their differentiation effect might turn towards homogenization, and might trigger the global homogenization trend.

Keywords Freshwater fish · Introduction · Beta-diversity · Translocation · Exotic species

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Introduction

Human activities have strongly altered species composition and richness of the freshwater ecosystems over the world (Vitousek 1997; Butchart et al. 2010; Leprieur et al. 2008a). The increase of global trade and economic activities during the last two centuries have promoted intentional and unintentional dissemination of species throughout the world (Taylor and Irwin 2004; La Sorte and McKinney 2007; Leprieur et al. 2008a). At the end of the twentieth century at least 624 freshwater fish species have been established into areas located outside their natural range (Gozlan et al. 2010), due of trading, aquaculture and game fishing purpose (Rahel 2007). As a consequence, more than half of the river basins in the world currently host at least one non-native fish species (Leprieur et al. 2008a), with consequent changes of large scale faunal dissimilarities among fish species assemblages (Villéger et al. 2011).

Native species extirpations have also modified the species composition of river basins throughout the world (Rahel 2007), but to a lower extent than introductions of non-native species (Olden et al. 2011; Villéger et al. 2011). Indeed, in most regions the number of non-native species introduced exceeds the number of extirpations, which ultimately leads to an increase in local species richness (Sax and Gaines 2003; Cassey and Lockwood 2007; Cadotte et al. 2009).

Besides this change in alpha diversity among river basin assemblages, the addition or deletion of species also alters the compositional dissimilarity between assemblages, i.e. beta-diversity (Olden et al. 2006; Rahel 2007), either inducing a decrease of dissimilarity (i.e. homogenization) or an increase of dissimilarity (i.e. differentiation). Numerous studies on changes in dissimilarity between the river basin assemblages in freshwater fish fauna have reported a global trend toward homogenization (McKinney and Lockwood 1999; Leprieur et al. 2008a; Olden et al. 2008; Villéger et al. 2011), although differentiation has also been reported in a non-negligible number of river basins (Villéger et al. 2011). The direction of change in dissimilarity (i.e. homogenization or differentiation) and its intensity is mainly determined by the historical richness of the assemblages, their historical dissimilarity and the number of the non-native species introduced (Villéger et al. 2011; Toussaint et al. 2014).

In most studies on freshwater fish, all non-native species were pooled to compute the changes in alpha- and/or beta-diversity (Alcaraz et al. 2005; Blanchet et al. 2010; Gozlan et al. 2010; Britton et al. 2011; Clavero 2011). However, at the global scale, the biogeographic regions (also called realms) are characterized by distinct freshwater fish fauna (Lévêque et al. 2008) and the effects of non-native species on change in dissimilarity is likely to be uneven among them within a realm since the most occurring ones may exhibit a higher probability of being transplanted and since their origin may favour their spread (Villéger et al. 2011; Toussaint et al. 2014; Villéger et al. 2015). Indeed, two types of non-native species can be considered based on their realm of origin: (1) 'exotic' species when the species introduced is native from another realm or (2) 'translocated' species when the species is native from the realm. For instance, Leprieur et al. (2008b) showed for European freshwater fish assemblages that translocated species drove assemblages towards homogenization whereas exotic species promoted differentiation.

In the current context of increasing non-native species occurrences, it is urgent to go one step further and we here discriminate the non-native species according to their biogeographic origin, and identify the non-native species that contribute the most to the overall trend toward homogenization of freshwater fish faunas. To this aim, we assessed the role played by each introduced species on change in dissimilarity among fish assemblages. Then, we quantified how their introduction type (i.e. 'exotic' or 'translocated') status and the number of times they were introduced explained the effect of each non-native species on change in dissimilarity in each biogeographic realm.

Methods

Database

We used a global database of 1054 river basins across the world (Brosse et al. 2013) for which the native and non-native status in each basin has been recorded for 9722 freshwater fish species. Therefore, historical (pre-industrial period, before human-mediated species introductions) and current compositions of assemblages (historical composition + non-native species − extirpated

species) are known (Leprieur et al. 2008a; Villéger et al. 2011).

For each non-native species, we determined its realm of origin, i.e. the realm where the species was historically present. We studied changes in taxonomic dissimilarity among fish assemblages in the six biogeographic realms: Afrotropical, Australian (including Oceania), Nearctic, Neotropical, Oriental, and Palearctic (Lévêque et al. 2008). In addition, each occurrence of a non-native species was classified as 'translocated' if the species was historically present in another river basin from the same realm, or as 'exotic', if the species did not historically occur in the realm.

Measuring change in taxonomic dissimilarity

For each pair of river basins belonging to the same realm, we computed dissimilarity using the Jaccard dissimilarity index (Jaccard 1901) as follow:

$$\beta_{Jaccard} = \frac{\text{Number of unshared species}}{\text{Total number of species}} = \frac{b + c}{a + b + c}$$

with b and c the number of species present only in each river basin assemblages and a the number of species shared by the two assemblages (Villéger and Brosse 2012).

These measures were assessed for historical and current periods to compute a change in taxonomic dissimilarity from historical to current period. A negative change in taxonomic dissimilarity reveals that the species assemblages of a pair of river basins become more similar from historical to current period. This change is called homogenization. On the contrary, the differentiation refers to basin pairs that become more dissimilar with time. For each realm we then computed the mean change in dissimilarity among all pairs of basins. These analyses were performed using the *betapart* package (Baselga and Orme 2012).

Assessing the effect of each non-native species

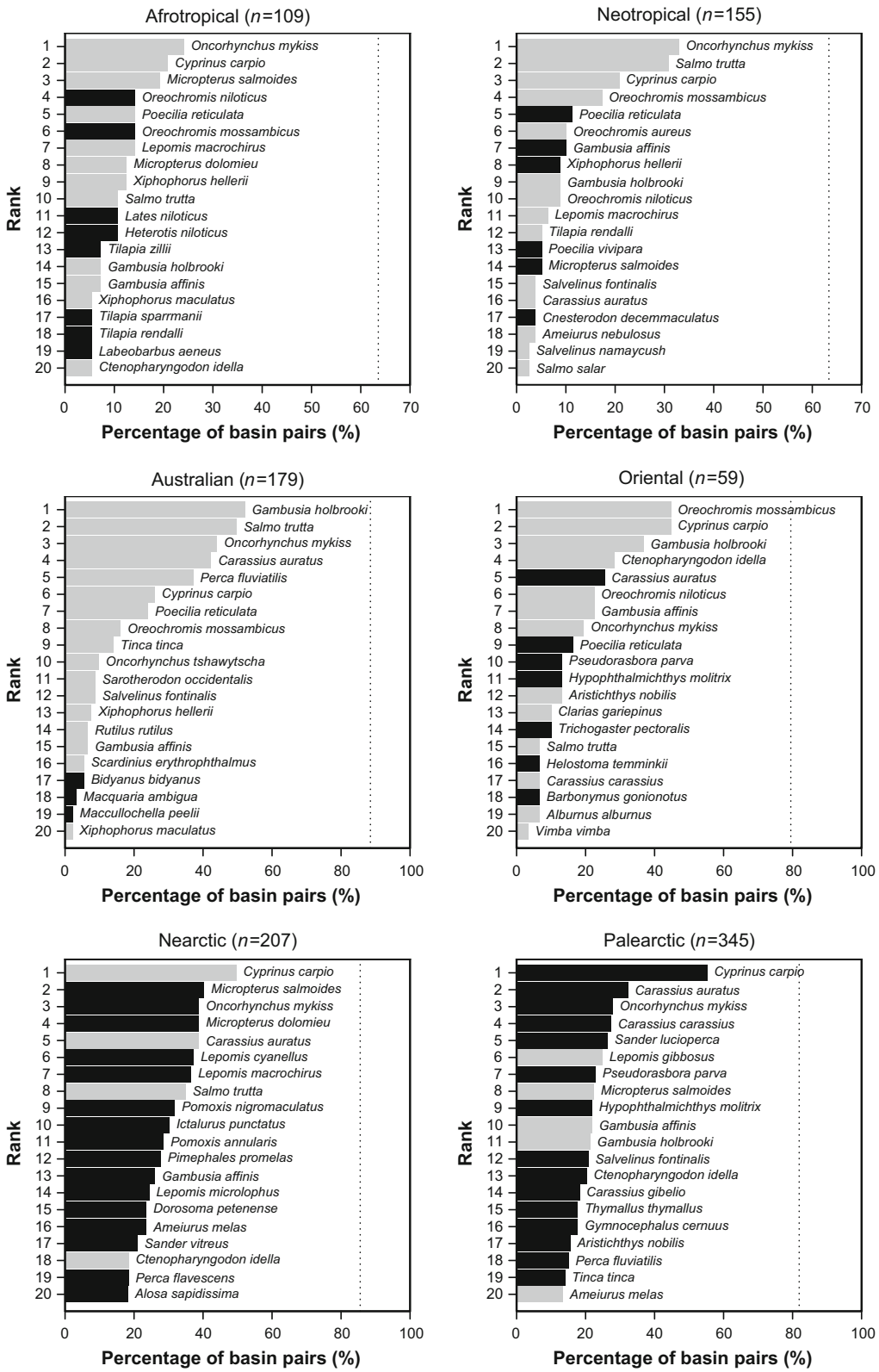
We assessed the effect of each non-native species on taxonomic dissimilarity independently of other species introductions; this was done for each pair of river basins as the change in Jaccard's dissimilarity between the historical situation and a hypothetical current situation where only the occurrences of the focal non-native species were kept (i.e. introductions of other non-native species and extirpations were ignored). Then, we computed the average change in dissimilarity among all river basin pairs in a realm to produce an indicator translating the independent effect of each non-native species in a realm. The sign of the effect gives the direction of the change due to the introduction of each non-native species. A positive effect indicates that the non-native species drives the overall change in dissimilarity toward differentiation whereas a negative value indicates that the non-native species drives the overall change in dissimilarity toward homogenization.

Determinants of the effect of each non-native species

We performed linear models to measure the contribution of the following drivers to the effect of each non-native species on change in dissimilarity in each biogeographic realm. The drivers we considered were (1) the number of river basins of the realm in which the non-native species was historically present (i.e. the occurrence as native, which is positive for a translocated species and nil for an exotic species), (2) the introduction type (i.e. translocated or exotic), and (3) the number of river basins in which the non-native species was introduced (i.e. the occurrence of introduction). This analysis was run independently for each biogeographic realm, and both simple effects and pairwise interaction between drivers were considered. For each biogeographic realm, influential outliers, defined according to the Cook's distance cut-off (Cook 1977) defined as $D = 4/(n - k - 1)$, where n is the number of observations and k is the number of variables in the model, were removed prior analysis to prevent from biased model outputs (Hair et al. 2009). All analyses were carried out using R, v. 3.0.2 (R Core Team 2014).

Results

The 20 most frequently introduced species in each realm represented only a small fraction of the introduced species in the Nearctic and Palearctic realms (8.9 and 11.8 %, respectively), but account for more than half of the introduction events. Indeed, those 20 species account for 52 and 60 % of the total number of


Afrotropical (n=109)
1 Oncorhynchus mykiss
2 Cyprinus carpio
3 Micropterus salmoides
4 Oreochromis niloticus
5 Poecilia reticulata
6 Oreochromis mossambicus
7 Lepomis macrochirus
8 Micropterus dolomieu
9 Xiphophorus hellerii
10 Salmo trutta
11 Lates niloticus
12 Heterotis niloticus
13 Tilapia zillii
14 Gambusia holbrooki
15 Gambusia affinis
16 Xiphophorus maculatus
17 Tilapia sparrmanii
18 Tilapia rendalli
19 Labeobarbus aeneus
20 Ctenopharyngodon idella
Rank
0 10 20 30 40 50 60 70
Percentage of basin pairs (%)
Neotropical (n=155)
1 Oncorhynchus mykiss
2 Salmo trutta
3 Cyprinus carpio
4 Oreochromis mossambicus
5 Poecilia reticulata
6 Oreochromis aureus
7 Gambusia affinis
8 Xiphophorus hellerii
9 Gambusia holbrooki
10 Oreochromis niloticus
11 Lepomis macrochirus
12 Tilapia rendalli
13 Poecilia vivipara
14 Micropterus salmoides
15 Salvelinus fontinalis
16 Carassius auratus
17 Cnesterodon decemmaculatus
18 Ameiurus nebulosus
19 Salvelinus namaycush
20 Salmo salar
Rank
0 10 20 30 40 50 60 70
Percentage of basin pairs (%)
Australian (n=179)
1 Gambusia holbrooki
2 Salmo trutta
3 Oncorhynchus mykiss
4 Carassius auratus
5 Perca fluviatilis
6 Cyprinus carpio
7 Poecilia reticulata
8 Oreochromis mossambicus
9 Tinca tinca
10 Oncorhynchus tshawytscha
11 Sarotherodon occidentalis
12 Salvelinus fontinalis
13 Xiphophorus hellerii
14 Rutilus rutilus
15 Gambusia affinis
16 Scardinius erythrophthalmus
17 Bidyanus bidyanus
18 Macquaria ambigua
19 Maccullochella peelii
20 Xiphophorus maculatus
Rank
0 20 40 60 80 100
Percentage of basin pairs (%)
Oriental (n=59)
1 Oreochromis mossambicus
2 Cyprinus carpio
3 Gambusia holbrooki
4 Ctenopharyngodon idella
5 Carassius auratus
6 Oreochromis niloticus
7 Gambusia affinis
8 Oncorhynchus mykiss
9 Poecilia reticulata
10 Pseudorasbora parva
11 Hypophthalmichthys molitrix
12 Aristichthys nobilis
13 Clarias gariepinus
14 Trichogaster pectoralis
15 Salmo trutta
16 Helostoma temminkii
17 Carassius carassius
18 Barbonymus gonionotus
19 Alburnus alburnus
20 Vimba vimba
Rank
0 20 40 60 80 100
Percentage of basin pairs (%)
Nearctic (n=207)
1 Cyprinus carpio
2 Micropterus salmoides
3 Oncorhynchus mykiss
4 Micropterus dolomieu
5 Carassius auratus
6 Lepomis cyanellus
7 Lepomis macrochirus
8 Salmo trutta
9 Pomoxis nigromaculatus
10 Ictalurus punctatus
11 Pomoxis annularis
12 Pimephales promelas
13 Gambusia affinis
14 Lepomis microlophus
15 Dorosoma petenense
16 Ameiurus melas
17 Sander vitreus
18 Ctenopharyngodon idella
19 Perca flavescens
20 Alosa sapidissima
Rank
0 20 40 60 80 100
Percentage of basin pairs (%)
Palearctic (n=345)
1 Cyprinus carpio
2 Carassius auratus
3 Oncorhynchus mykiss
4 Carassius carassius
5 Sander lucioperca
6 Lepomis gibbosus
7 Pseudorasbora parva
8 Micropterus salmoides
9 Hypophthalmichthys molitrix
10 Gambusia affinis
11 Gambusia holbrooki
12 Salvelinus fontinalis
13 Ctenopharyngodon idella
14 Carassius gibelio
15 Thymallus thymallus
16 Gymnocephalus cernuus
17 Aristichthys nobilis
18 Perca fluviatilis
19 Tinca tinca
20 Ameiurus melas
Rank
0 20 40 60 80 100
Percentage of basin pairs (%)

◀**Fig. 1** Freshwater fish species introduced in the six biogeographic realms. Species are ranked according to their decreasing frequency of occurrence as non-native in the realm. The *bars* represent the percentage of river basin pairs where the considered species is introduced. Only the twenty most frequently introduced species in each realm are represented for clarity. 'Exotic' species (i.e. native from another realm) are in *grey*, and 'translocated' species (i.e. native from the same realm) are in *black* (e.g. carp, *Cyprinus carpio*, occurs as translocated species in 55 % of the Palearctic river basin pairs). The *dotted line* represents the percentage of basin pairs which have received at least one non-native species in each realm. The number of river basins considered in each realm is indicated under *brackets*

non-native introductions within the Nearctic (691/1330 introduction events) and Palearctic (851/1407) realms, respectively. In the four remaining realms, the 20 most frequently introduced species account for 28.6 (in the Neotropics) to 45.5 % (in the Afrotropics) of the number of species introduced in each realm. As for northern realms, the 20 species account for more than half of the introduction events. This proportion reached 74 % (691/1222) of the introduction events in the Neotropics, 76 % (113/149) in Oriental, 82 % (128/156) in Afrotropical and 91 % (369/406) in Australian realms. These introductions of non-native species have impacted the dissimilarity of more than 60 % of river basin pairs in Afrotropical (64 %) and Neotropical (62 %) realms, and more than 80 % of basin pairs in Australian (90 %), Nearctic (83 %), Oriental (80 %) and Palearctic (81 %) realms (Fig. 1).

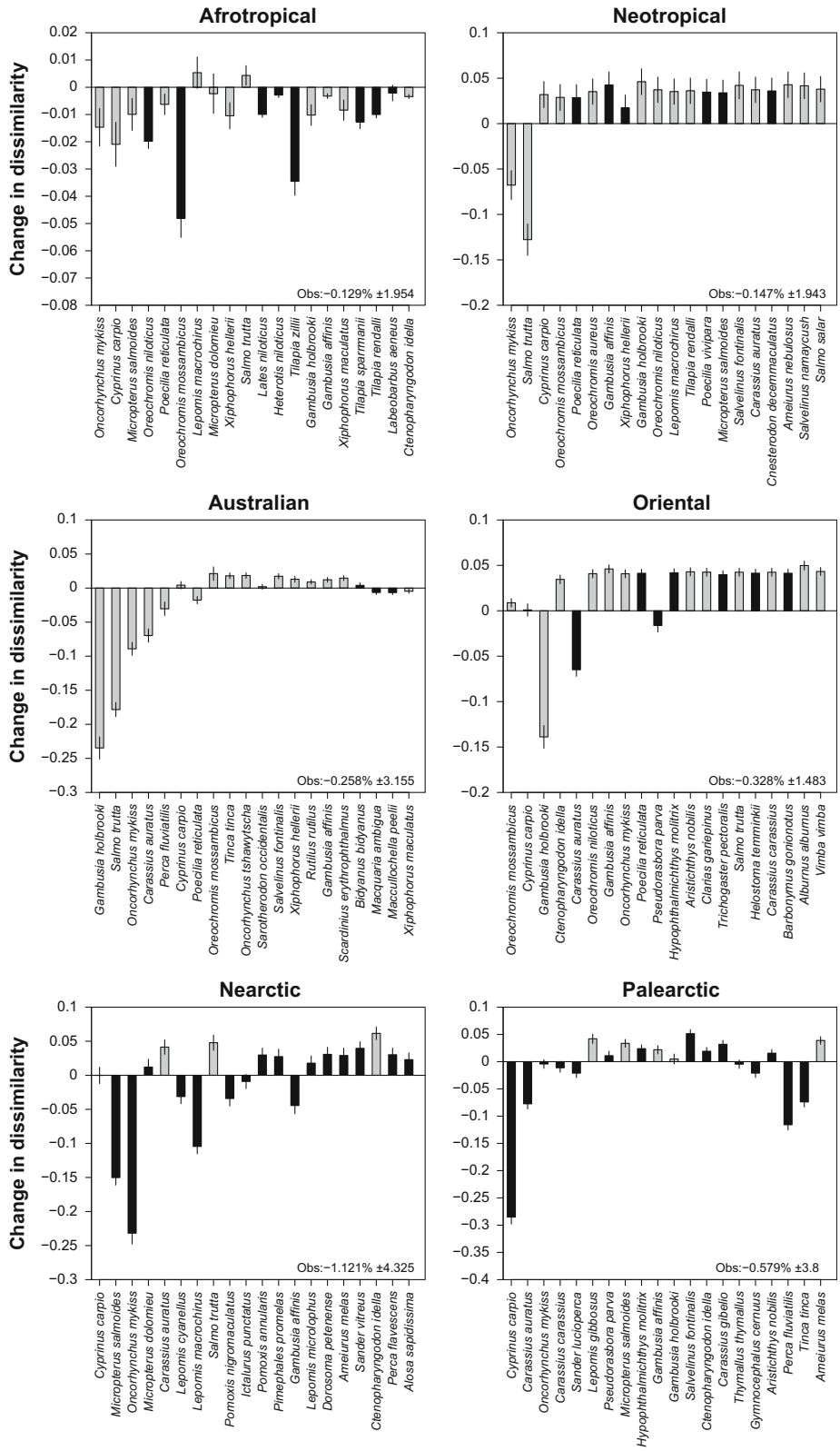
The effect of each of the twenty most frequently introduced non-native species on changes in dissimilarity was highly variable between species and realms both in terms of direction of change and intensity (Fig. 2). A non-native species introduced in different realms can have opposite effects, either towards homogenization or differentiation (Fig. 2). For instance, the brown trout (*Salmo trutta*) drove Australian and Neotropical realms toward homogenization whereas it was responsible from differentiation in the Oriental and Nearctic realms (Fig. 2).

In the Australian, Neotropical and Palearctic realms, the two most introduced species contributed strongly to homogenization (Fig. 2). On the contrary, in the other three realms, the non-native species having the strongest effect on change in dissimilarity were not the one with the highest number of introductions. For instance, in the Oriental realm, the eastern mosquitofish (*Gambusia holbrooki*) had the strongest homogenization effect (−0.14 %, Fig. 2), while being less frequently introduced than the common carp (*Cyprinus carpio*) or the Mozambique tilapias (*Oreochromis mossambicus*) that accounted for only 0.001 and 0.01 % of change in dissimilarity (Fig. 2). A similar trend was found in the Nearctic realm where the rainbow trout (*Oncorhynchus mykiss*) has a strong homogenization effect (−0.23 %) although being less frequently introduced than the common carp that hardly affected changes in dissimilarity (−0.0001 %, Fig. 2). This was confirmed by Table 1 which shows that the occurrence of introduction was not the only driver explaining the homogenization effect of each non-native species. Indeed, in all the biogeographic realms except the Australian, the introduction type (i.e. translocated or exotic) and/or the native occurrence of the species significantly affected (directly or interacting with the occurrence of introduction) the homogenization effect of each non-native species. Moreover, the native occurrences of the species in the realm has a significant effect, or interact with the occurrence of introduction, in all those 5 realms (Table 1), testifying for the strong homogenization effect of translocated species (Fig. 2).

Discussion

Among the 624 freshwater fish species introduced over the world (Rahel 2007; Gozlan et al. 2010; Lauzeral et al. 2011), fourteen have been introduced into at least one river basin in the six realms, and 90 non-native species have been introduced in realms other than their native one (Rahel 2007; Villéger et al. 2015). Leprieur et al. (2008a) emphasized the role of human activities, which promoted the introduction of species of economic interest, leading to the introduction of a few species over large areas. Those widespread processes have received attention in previous local studies on homogenization patterns reporting the important role of a small pool of species of interest as part of human activities (Rahel 2000; Clavero and García-Berthou 2006; Rahel 2007). Although a few non-native species can synergistically contributed to the global trends of freshwater fish homogenization, we showed here that the overall pattern could hide contrasted species individual contributions.

Indeed, analysing species individual effects enabled to highlight strong discrepancies among species and


Afrotropical
Change in dissimilarity
Obs:−0.129% ±1.954
Oncorhynchus mykiss
Cyprinus carpio
Micropterus salmoides
Oreochromis niloticus
Poecilia reticulata
Oreochromis mossambicus
Lepomis macrochirus
Micropterus dolomieu
Xiphophorus helleri
Salmo trutta
Lates niloticus
Heterotis niloticus
Tilapia zillii
Gambusia holbrooki
Gambusia affinis
Xiphophorus maculatus
Tilapia sparrmanii
Tilapia rendalli
Labeobarbus aeneus
Ctenopharyngodon idella
Neotropical
Obs:−0.147% ±1.943
Oncorhynchus mykiss
Salmo trutta
Cyprinus carpio
Oreochromis mossambicus
Poecilia reticulata
Oreochromis aureus
Gambusia affinis
Xiphophorus helleri
Gambusia holbrooki
Oreochromis niloticus
Lepomis macrochirus
Tilapia rendalli
Poecilia vivipara
Micropterus salmoides
Salvelinus fontinalis
Carassius auratus
Cnesterodon decemmaculatus
Ameiurus nebulosus
Salvelinus namaycush
Salmo salar
Australian
Change in dissimilarity
Obs:−0.258% ±3.155
Gambusia holbrooki
Salmo trutta
Oncorhynchus mykiss
Carassius auratus
Perca fluviatilis
Cyprinus carpio
Poecilia reticulata
Oreochromis mossambicus
Tinca tinca
Oncorhynchus tshawytscha
Sarotherodon occidentalis
Salvelinus fontinalis
Xiphophorus hellerii
Rutilus rutilus
Gambusia affinis
Scardinius erythrophthalmus
Bidyanus bidyanus
Macquaria ambigua
Maccullochella peelii
Xiphophorus maculatus
Oriental
Obs:−0.328% ±1.483
Oreochromis mossambicus
Cyprinus carpio
Gambusia holbrooki
Ctenopharyngodon idella
Carassius auratus
Oreochromis niloticus
Gambusia affinis
Oncorhynchus mykiss
Poecilia reticulata
Pseudorasbora parva
Hypophthalmichthys molitrix
Aristichthys nobilis
Clarias gariepinus
Trichogaster pectoralis
Salmo trutta
Helostoma temminkii
Carassius carassius
Barbonymus gonionotus
Alburnus alburnus
Vimba vimba
Nearctic
Change in dissimilarity
Obs:−1.121% ±4.325
Cyprinus carpio
Micropterus salmoides
Oncorhynchus mykiss
Micropterus dolomieu
Carassius auratus
Lepomis cyanellus
Lepomis macrochirus
Salmo trutta
Pomoxis nigromaculatus
Ictalurus punctatus
Pomoxis annularis
Pimephales promelas
Gambusia affinis
Lepomis microlophus
Dorosoma petenense
Ameiurus melas
Sander vitreus
Ctenopharyngodon idella
Perca flavescens
Alosa sapidissima
Palearctic
Obs:−0.579% ±3.8
Cyprinus carpio
Carassius auratus
Oncorhynchus mykiss
Carassius carassius
Sander lucioperca
Lepomis gibbosus
Pseudorasbora parva
Micropterus salmoides
Hypophthalmichthys molitrix
Gambusia affinis
Gambusia holbrooki
Salvelinus fontinalis
Ctenopharyngodon idella
Carassius gibelio
Thymallus thymallus
Gymnocephalus cernuus
Aristichthys nobilis
Perca fluviatilis
Tinca tinca
Ameiurus melas

◀**Fig. 2** Effect of the introduced species on change in dissimilarity in each realm. Species are ranked according to their decreasing frequency of occurrence as non-native in the realm. *Vertical bars* represent the change in dissimilarity caused by each non-native species (i.e. if it has been the only non-native species introduced, see "Methods" section for details). The observed value of the percentage of change in dissimilarity while considering all the non-native species (*obs*) is given for each biogeographic realm (mean ± standard deviation). Note that the *obs* value can be lower than the individual species effect sum. *Positive values* indicate an increase of dissimilarity (differentiation), whereas *negative values* indicate a decrease (homogenization). *Bars* for translocated and exotic species are filled in *black* and *grey*, respectively

among realms, suggesting that non-native species contributed differently to the homogenization process. Among the 61 most frequently introduced species in the world (i.e. the global pool made by the 20 most frequently introduced species in each of the six realms, that account for 69 % of the global number of introductions, Fig. 1), only 10 non-native species (*Carassius auratus, Cyprinus carpio, Gambusia holbrooki, Micropterus salmoides, Oncorhynchus mykiss, Oreochromis mossambicus, Oreochromis niloticus, Perca fluviatilis, Salmo trutta, Tilapia zillii*) had an effect toward homogenization higher than 10 % of the realm homogenization level. Those species are all known to be highly invasive, often reaching high abundances (Gherardi and Acquistapace 2007; Rahel 2007; Lauzeral et al. 2011), but we nevertheless found a low correlation between the number of introductions and the effect of each of these species on change in dissimilarity (Table 1). This suggested that the number of introduction was not the only determinant of the potential effect on change in dissimilarity. This was particularly striking for common carp (*Cyprinus carpio*), which although being the most frequently introduced species in Oriental, Nearctic and Palearctic realms, had only a weak impact on change in dissimilarity in Nearctic and Oriental realms. On the contrary, this species had a strong effect toward homogenization in the Palearctic realm. A similar pattern was observed for several species (e.g. *Oreochromis mossambicus* or *Tilapia* sp.), suggesting that the identity or the occurrence of the species itself did not explain its role in the change in dissimilarity.

Indeed, the type of introduction (i.e. translocated vs. exotic) was a significant predictor of the changes in dissimilarity in five out the six biogeographic realms. The translocated species had a strong effect on homogenization patterns because they were historically already present as native species. Hence, their introduction in more basins of the realm could only lead to homogenization for all the basin pairs where the species was historically present. Such a situation is one of the major drivers of homogenization worldwide (Olden and Poff 2004; Toussaint et al. 2014).

In contrast, exotic species were often introduced in a few basins and some of them then spread in nearby basins (Arthington 1991; Lintermans 2004). Exotic species hence tend to favour differentiation at the early stages of invasion, as shown by Leprieur et al. (2008b) for Western Europe. Nevertheless, when those species expand over their invasion area, the number of river basin pairs where they occur increases and can contribute to homogenization (Toussaint et al. 2014). This reversal effect was observed, for instance, for eastern mosquitofish (*Gambusia holbrooki*) that quickly invaded large areas in Australian and Oriental realms since its initial introduction in the early twentieth century (Welcomme 1988; Milner and Petts 1994; Pyke 2008; Ayres and Clunie 2010), and hence currently has a strong homogenization effect in those realms (Fig. 2).

Focusing conservation efforts in controlling a few species that have a prominent effect on the global homogenization process (e.g. *Carassius auratus, Cyprinus carpio, Gambusia holbrooki, Micropterus salmoides, Oncorhynchus mykiss, Oreochromis mossambicus, Oreochromis niloticus, Perca fluviatilis, Salmo trutta, Tilapia zillii*) may be more relevant to counteract the current homogenization trend and its local detrimental effects on species community integrity. We should nevertheless be aware that the homogenization rate of an area results from complex combinations of individual species homogenization and differentiation effects. Therefore, the homogenization strength measured here at the species individual level did not represent the complete species effect when considering other non-native species introductions. Nevertheless, our approach and results provide interesting perspectives to optimize management and conservation efforts by focusing on a limited number of species influencing global homogenization patterns.

Overall, our results confirm and generalize to a global scale the previous local or regional studies on the consequences of fish introductions on changes in dissimilarity (Rahel 2000, 2007; Clavero and García-Berthou 2006; Leprieur et al. 2008b). We also pointed

Table 1 Analysis of variance testing the influence of the occurrence of the species as native, as introduced and of the type of introduction (translocated vs. exotic) on the change in dissimilarity due to each non-native species in the six biogeographic realms

Biogeographic realm	Variables	*df*	Sum of squares	*F*	*P*
Afrotropical					
	Native occur.	1	2111.94	50.89	<0.001***
	Intro. occur.	1	37.51	0.90	0.347*ns*
	Intro. type	1	1927.74	46.45	<0.001***
	Native occur. X Intro. occur.	1	200.59	4.83	0.034*
	Intro. type X Intro. occur.	1	110.14	2.65	0.111*ns*
	Residuals	41	41.50		
Australian					
	Native occur.	1	21.97	0.85	0.363*ns*
	Intro. occur.	1	1186.97	45.76	<0.001***
	Intro. type	1	49.32	1.90	0.175*ns*
	Native occur. X Intro. occur.	1	25.75	0.99	0.325*ns*
	Intro. type X Intro. occur.	1	7.02	0.27	0.606*ns*
	Residuals	43	25.94		
Nearctic					
	Native occur.	1	382.71	15.50	<0.001***
	Intro. occur.	1	803.48	32.53	<0.001***
	Intro. type	1	314.79	12.75	<0.001***
	Native occur. X Intro. occur.	1	253.97	10.28	0.002**
	Intro. type X Intro. occur.	1	134.04	5.43	0.021*
	Residuals	211	24.70		
Neotropical					
	Native occur.	1	1097.16	93.91	<0.001***
	Intro. occur.	1	461.79	39.53	<0.001***
	Intro. type	1	4425.14	378.78	<0.001***
	Native occur. X Intro. occur.	1	0.56	0.05	0.827*ns*
	Intro. type X Intro. occur.	1	147.70	12.64	0.001***
	Residuals	70	11.68		
Oriental					
	Native occur.	1	205.78	170.96	<0.001***
	Intro. occur.	1	504.07	418.77	<0.001***
	Intro. type	1	319.95	265.81	<0.001***
	Native occur. X Intro. occur.	1	444.24	369.06	<0.001***
	Intro. type X Intro. occur.	1	0.13	0.11	0.744*ns*
	Residuals	26	1.20		
Palearctic					
	Native occur.	1	1652.22	69.82	<0.001***
	Intro. occur.	1	1602.82	67.73	<0.001***
	Intro. type	1	1501.86	63.46	<0.001***
	Native occur. X Intro. occur.	1	1096.24	46.32	<0.001***
	Intro. type X Intro. occur.	1	264.84	11.19	0.001***
	Residuals	174	23.67		

The contribution of the native occurrences (Native occur.), the occurrence of the species as non-native (Intro. occur.) and the introduction type (Intro. type) on change in dissimilarity was tested using linear model. Analyses were run independently for each biogeographic realm, and both simple effects and pairwise interactions between drivers were considered

ns non-significant ($P > 0.05$); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

out that a few freshwater fish species widely introduced across the world have largely contributed to the observed changes. Those species are characterized by their large distribution over considered areas, and are hence either the species introduced for a long time, such as common carp in the Palearctic (Welcomme 1988; Balon 2004), or brown trout in the Nearctic (Crawford and Muir 2008), or recent introductions of fast spreading species, such as *Gambusia* spp. in Australia (Welcomme 1988; Milner and Petts 1994; Pyke 2008; Ayres and Clunie 2010).

Intercontinental fish exchanges should decrease owing to the development of national and international laws regulating the transport and introduction of exotic species (Costello et al. 2005; Hulme et al. 2009). But under the current accelerated rates of non-native species spread within realms (Britton and Gozlan 2013), exotic species are expected to establish over larger areas in the near future, and then turn their differentiation effect toward homogenization. Thus, this would favour a global homogenization, as forecasted by Villéger et al. (2015) using mathematical simulations. From a conservation point of view, the origin, as well as the occurrence of the non-native species should be considered to better control the forthcoming changes in taxonomic dissimilarity across realms. Controlling the spread of a few species might significantly reduce the global homogenization trend. Such actions are nevertheless pending for a better assessment of the ecological consequences of homogenization, that to date, remain largely unknown (France and Duffy 2006; Olden 2006).

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References

Alcaraz C, Vila-Gispert A, García-Berthou E (2005) Profiling invasive fish species: the importance of phylogeny and human use. Divers Distrib 11:289–298

Arthington AH (1991) Ecological and genetic impacts of introduced and translocated freshwater fishes in Australia. Can J Fish Aquat Sci 48:33–43

Ayres R, Clunie P (2010) Toward a national emergency response system for freshwater fish incursion. Canberra, Australia

Balon EK (2004) About the oldest domesticates among fishes. J Fish Biol 65:1–27

Baselga A, Orme CDL (2012) betapart: an R package for the study of beta diversity. Methods Ecol Evol 3:808–812

Blanchet S, Grenouillet G, Beauchard O et al (2010) Non-native species disrupt the worldwide patterns of freshwater fish body size: implications for Bergmann's rule. Ecol Lett 13:421–431

Britton JR, Gozlan RE (2013) Geo-politics and freshwater fish introductions: how the Cold War shaped Europe's fish allodiversity. Glob Environ Change 23:1566–1574

Britton JR, Gozlan RE, Copp GH (2011) Managing non-native fish in the environment. Fish Fish 12:256–274

Brosse S, Beauchard O, Blanchet S et al (2013) Fish-SPRICH: a database of freshwater fish species richness throughout the World. Hydrobiologia 700:343–349

Butchart SHM, Walpole M, Collen B et al (2010) Global biodiversity: indicators of recent declines. Science 328:1164–1168

Cadotte MW, Hamilton MA, Murray BR (2009) Phylogenetic relatedness and plant invader success across two spatial scales. Divers Distrib 15:481–488

Cassey P, Lockwood J (2007) The varying role of population abundance in structuring indices of biotic homogenization. J Biogeogr 35:884–892

Clavero M (2011) Assessing the risk of freshwater fish introductions into the Iberian Peninsula. Freshw Biol 56:2145–2155

Clavero M, García-Berthou E (2006) Homogenization dynamics and introduction routes of invasive freshwater fish in the Iberian Peninsula. Ecol Appl 16:2313–2324

Cook RD (1977) Detection of influential observation in linear regression. Technometrics 19:15–18

Costello C, McAusland C, Solow A, Springborn M (2005) International trade and the risk of biological invasions. Santa Barbara, California

Crawford SS, Muir AM (2008) Global introductions of salmon and trout in the genus Oncorhynchus: 1870–2007. Rev Fish Biol Fish 18:313–344

France KE, Duffy JE (2006) Diversity and dispersal interactively affect predictability of ecosystem function. Nature 441:1139–1143

Gherardi F, Acquistapace P (2007) Invasive crayfish in Europe: the impact of *Procambarus clarkii* on the littoral community of a Mediterranean lake. Freshw Biol 52:1249–1259

Gozlan RE, Britton JR, Cowx I, Copp GH (2010) Current knowledge on non-native freshwater fish introductions. J Fish Biol 76:751–786

Hair JF, Black WC, Babin BJ et al (2009) Multivariate data analysis, 7th edn. Upper Saddle River, New Jersey, Prentice-Hall

Hulme P, Roy D, Cunha T, Larsson T (2009) A pan-European inventory of alien species: rationale, implementation and implications for managing biological invasions. In: Handbook of alien species in Europe. Springer, pp 1–14

Jaccard P (1901) Étude comparative de la distribution florale dans une portion des Alpes et du Jura. Bull la Société Vaudoise des Sci Nat 37:547–579

La Sorte FA, McKinney ML (2007) Compositional changes over space and time along an occurrence–abundance continuum: anthropogenic homogenization of the North American avifauna. J Biogeogr 34:2159–2167

Lauzeral C, Leprieur F, Beauchard O et al (2011) Identifying climatic niche shifts using coarse-grained occurrence data: a test with non-native freshwater fish. Glob Ecol Biogeogr 20:407–414

Leprieur F, Beauchard O, Blanchet S et al (2008a) Fish invasions in the world's river systems: when natural processes are blurred by human activities. PLoS Biol 6:e28

Leprieur F, Beauchard O, Hugueny B et al (2008b) Null model of biotic homogenization: a test with the European freshwater fish fauna. Divers Distrib 14:291–300

Lévêque C, Oberdorff T, Paugy D, Stiassny MLJ, Tedesco PA (2008) Global diversity of fish (Pisces) in freshwater. Hydrobiologia 595:545–567

Lintermans M (2004) Human-assisted dispersal of alien freshwater fish in Australia. N Z J Mar Freshw Res 38:481–501

McKinney M, Lockwood J (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453

Milner AM, Petts GE (1994) Glacial rivers: physical habitat and ecology. Freshw Biol 32:295–307

Olden J (2006) Biotic homogenization: a new research agenda for conservation biogeography. J Biogeogr 33:2027–2039

Olden J, Poff N (2004) Ecological processes driving biotic homogenization: testing a mechanistic model using fish faunas. Ecology 85:1867–1875

Olden JD, Poff NL, McKinney ML (2006) Forecasting faunal and floral homogenization associated with human population geography in North America. Biol Conserv 127:261–271

Olden JD, Kennard M, Pusey B (2008) Species invasions and the changing biogeography of Australian freshwater fishes. Glob Ecol Biogeogr 17:25–37

Olden JD, Lockwood J, Parr C (2011) Biological invasions and the homogenization of faunas and floras. In: Conservation biogeography. Wiley, pp 224–243

Pyke GH (2008) Plague minnow or mosquito fish? A review of the biology and impacts of introduced Gambusia species. Annu Rev Ecol Evol Syst 39:171–191

R Development Core Team (2014) R: a language and environment for statistical computing. Austria, Vienna

Rahel F (2000) Homogenization of fish faunas across the United States. Science 288:854–856

Rahel F (2007) Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. Freshw Biol 52:696–710

Sax DF, Gaines SD (2003) Species diversity: from global decreases to local increases. Trends Ecol Evol 18:561–566

Taylor BW, Irwin RE (2004) Linking economic activities to the distribution of exotic plants. Proc Natl Acad Sci USA 101:17725–17730

Toussaint A, Beauchard O, Oberdorff T et al (2014) Historical assemblage distinctiveness and the introduction of widespread non-native species explain worldwide changes in freshwater fish taxonomic dissimilarity. Glob Ecol Biogeogr 23:574–584

Villéger S, Brosse S (2012) Measuring changes in taxonomic dissimilarity following species introductions and extirpations. Ecol Indic 18:552–558

Villéger S, Blanchet S, Beauchard O et al (2011) Homogenization patterns of the world's freshwater fish faunas. Proc Natl Acad Sci USA 108:18003–18008

Villéger S, Blanchet S, Beauchard O et al (2015) From current distinctiveness to future homogenization of the world's freshwater fish faunas. Divers Distrib 21:223–235

Vitousek PM (1997) Human domination of Earth's ecosystems. Science 277:494–499

Welcomme RL (1988) International introductions of inland aquatic species. Food and Agriculture Organization of the United Nations, Fisheries Technical Paper 294. Rome, Italy, pp 1–318