RESEARCH PAPER

Historical assemblage distinctiveness and the introduction of widespread non-native species explain worldwide changes in freshwater fish taxonomic dissimilarity

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ABSTRACT

Aim Taxonomic dissimilarity between assemblages can result from two processes – the replacement of species (turnover) and differences in richness – but it remains unclear how anthropogenic drivers (introductions and extirpations) affect these processes. Here, we investigate how historical patterns and anthropogenic drivers shape the changes in dissimilarity and its turnover component in freshwater fish assemblages both in historical (i.e. pre-industrial) times and at the present day.

Location World-wide.

Methods We used a global database of fish assemblages in 1054 river basins throughout the world to quantify the change in turnover through its contribution to taxonomic dissimilarity between the two periods. We then used random forests to disentangle the relative roles of historical distinctiveness, species introductions and species extirpations on changes in dissimilarity and on the contribution of its turnover component.

Results The pairs of basins exhibited a decrease in the contribution of turnover to taxonomic dissimilarity of 82% and 61% in homogenized and differentiated pairs, respectively. The historical number of shared species and its change after species introductions and extirpations accounted for more than 60% of the change in dissimilarity and in the turnover contribution in the six biogeographical realms.

Main conclusions The historically high distinctiveness between pairs of basins, due to a low number of shared species, has promoted high levels of taxonomic dissimilarity. The world-wide changes in taxonomic dissimilarity among fish assemblages are to a large extent coupled to a decrease in the contribution of taxonomic turnover to taxonomic dissimilarity. Hence, the dissimilarity between assemblages declines with decreasing species replacement. These changes are mainly explained by introductions of a small set of widespread non-native species, which promote an increase in the number of shared species. Alongside historical distinctiveness, species introduction processes can determine whether assemblages become more homogenized or more differentiated. Our results suggest that taxonomic differentiation can quickly turn to homogenization as the number of species introductions increase.

Keywords
Beta diversity, differentiation, freshwater fish, homogenization, macroecology, partitioning, turnover.

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INTRODUCTION

Human activities and the subsequent environmental disturbances are the major drivers of changes in species composition (Elton, 1958; Vitousek *et al.*, 1997). Anthropogenic pressures such as overexploitation and habitat degradation have undoubtedly contributed to the extirpation of some species from at least part of their native range, and have even driven some endemic species to extinction (Angermeier & Karr, 1994; Pimentel *et al.*, 2000; Scott & Helfman, 2001). Human activities have also led (intentionally or otherwise) to the transportation of species and their establishment in areas where they were not naturally present, bypassing biogeographical barriers (Vitousek *et al.*, 1997; Butchart *et al.*, 2010). The global number of introductions of non-native species has followed the development of intercontinental exchanges for about 150 years, and may therefore increase further through the intensification of global trade (Blanchet *et al.*, 2009).

The addition and removal of species through non-native introductions and native-range extirpations have changed the species composition of local assemblages throughout the world (Rahel, 2007). An intensification of non-native species introductions (e.g. Vander Zanden, 2005) coupled with an accelerated loss of endemic species (Vitousek *et al.*, 1996, 1997) led McKinney & Lockwood (1999) to define the concept of biotic homogenization as the replacement of many endemic species with a few widespread species. This concept then became extended to the changes in dissimilarity between assemblages (i.e. changes in beta diversity due to introductions and extirpations), whether they are due to a decrease in dissimilarity (homogenization) or an increase (differentiation) (Olden & Rooney, 2006).

Changes have been measured for various taxa across the globe and they reveal an overall trend toward biotic homogenization (e.g. Rahel, 2000; Winter *et al.*, 2009; Villéger *et al.*, 2011). Some of these studies nevertheless revealed strong geographical discrepancies in the strength of changes in beta diversity and even, in some cases, in their direction (e.g. Leprieur *et al.*, 2008a; Villéger *et al.*, 2011).

Most previous measurements of changes in beta diversity have used the difference in Jaccard dissimilarity, i.e. the change over time in the percentage of species not shared by a pair of species assemblages (Olden & Rooney, 2006; Villéger & Brosse, 2012). As pointed out by Baselga (2010, 2012) and Carvalho *et al.* (2012), however, beta diversity results from the sum of two independent components: the replacement of species between assemblages (the turnover component) and the difference in richness between assemblages (the nestedness-resultant component).

These decompositions have been used to disentangle the biogeographical processes that drive the patterns of dissimilarity in species composition of different taxa (see Baselga *et al.*, 2011, for amphibians; Leprieur *et al.*, 2011, for freshwater fish; Boieiro *et al.*, 2013, for ground beetles). Their contributions to the change in dissimilarity between historical and current situations have been little studied to date (Baiser *et al.*, 2012), and we believe that their relative importance should shed light on the drivers of changes in dissimilarity (Villéger & Brosse, 2012).

Our aim here was to unravel the contributions of the turnover and nestedness-resultant components to the changes in dissimilarity among freshwater fish assemblages at a global scale. Fish have been intensively exploited and transported through human activities for about two centuries, leading to a decrease in dissimilarity between assemblages across the world (Villéger *et al.*, 2011). This overall homogenization hides more complex patterns, with a third of basin pairs experiencing homogenization, a third exhibiting no changes and a third experiencing differentiation (Villéger *et al.*, 2011). We therefore investigated the determinants of the discrepancies observed in changes in dissimilarity. We first used the decomposition proposed by Baselga (2012) to measure changes in the contribution of turnover to dissimilarity. We then determined the relative contributions of historical species richness, species introductions and species extirpations to the changes in assemblage dissimilarity and turnover.

MATERIALS AND METHODS

Partitioning changes in taxonomic dissimilarity

We used the Jaccard index (Jaccard, 1901) to calculate taxonomic dissimilarity from presence–absence data (Rahel, 2000; Olden & Rooney, 2006; Villéger & Brosse, 2012). Consider two species assemblages with compositions such that a is the number of species shared by the two assemblages, and b and c are the numbers of species present only in each assemblage with, by convention, $b \geq c$ (Koleff *et al.*, 2003). The Jaccard dissimilarity (β_{diss}) is the proportion of species not shared:

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

Taxonomic dissimilarity results from the sum of two processes, one of which is species turnover (Baselga, 2012). Two distinct frameworks have been proposed to calculate the contribution of turnover to Jaccard dissimilarity – those of Baselga (2012) and of Carvalho *et al.* (2012). In the framework of Carvalho *et al.* (2012), turnover is measured using the β_{-3} index (Williams, 1996), which is not independent of the total species richness in the pair of assemblages (i.e. $a + b + c$). According to the typology of beta diversity measures proposed by Anderson *et al.* (2011), Carvalho's framework allows the measurement of a directional turnover in assemblage structure (e.g. through time or along an environmental gradient). In Baselga's (2012) framework, the turnover component of dissimilarity is measured using an index similar to the β_{sim} index that accounts only for the richness of the poorer assemblage and is thus independent of total species richness in the assemblage pair (see below). Baselga's framework is designed to measure spatial turnover between assemblages, without considering the environmental or distance gradients between them, and thus measures a non-directional variation in assemblage structure (Anderson *et al.*, 2011).

Our aim here was to measure the temporal change in spatial taxonomic dissimilarity for all pairs of assemblages, as well as the temporal change in the contribution of turnover to this spatial dissimilarity. We therefore needed a framework: (1) in which the contribution of turnover to dissimilarity reflects the relative proportion of shared versus unique species in each community (i.e. it must depend on a, b and c), so that a change in any of these components induces a change in the contribution of turnover to dissimilarity; and (2) in which, if no species are shared by the two communities ($a = 0$), dissimilarity is entirely driven by turnover. This second criterion ensures that the contribution of turnover to dissimilarity is not influenced by differences in species richness when no species are shared, and thus that temporal changes in the contribution of turnover to dissimilarity can only occur when dissimilarity remains maximal. Indeed, if two assemblages were historically totally distinct and remain totally distinct in the current situation, the contribution of turnover to this maximal dissimilarity must not change even if different unique non-native species are introduced (or native species extirpated). Baselga's (2012) framework, which meets these two key criteria, was therefore preferred over the framework of Carvalho *et al.* (2012).

In Baselga's (2012) framework, turnover measures species replacement independently of total species richness, $\beta_{turnover} = \dfrac{2 \times c}{a + (2 \times c)}$. It is smallest when the poorer assemblage contains all the species that are present in the richer assemblage ($c = 0$), and largest when the two assemblages have no species in common ($a = 0$). The nestedness-resultant component measures the contribution to dissimilarity that is not due to turnover. It is influenced by the difference in species richness between the two assemblages (Baselga, 2012).

This partitioning allows the relative contribution of species replacement (i.e. taxonomic turnover) to taxonomic dissimilarity (beta diversity) to be assessed and thus allows these two ecologically important concepts to be compared (Koleff *et al.*, 2003; Anderson *et al.*, 2011). We propose a quantification of the relative contribution of taxonomic turnover to taxonomic dissimilarity, hereafter called p_{turn}:

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

The p_{turn} index is defined only when dissimilarity is not null, i.e. when at least one species is not shared by the two assemblages ($c > 0$); This condition is met in most real cases, even at small spatial scales. The value of p_{turn} ranges from 0 to 1: it is minimal when $c = 0$, which means that the two assemblages are nested and thus that turnover is null. In such a situation, dissimilarity is therefore due only to the difference in species richness, regardless of its level. The value of p_{turn} is maximal either when $b = c$, which means that the two assemblages have the same species richness and consequently that turnover equals dissimilarity, or when $a = 0$, which means that the two assemblages exhibit no common species and thus that both dissimilarity and turnover are maximal.

The changes in pairwise taxonomic dissimilarity and the contribution of turnover to taxonomic dissimilarity (hereafter called $\delta\beta_{diss}$ and δp_{turn}, respectively) between historical times (species composition before human influence) and the present day are then:

$$\delta\beta_{diss} = (\beta_{diss})_{current} - (\beta_{diss})_{historical}, \text{ and}$$

$$\delta p_{turn} = \frac{(\beta_{turnover})_{current}}{(\beta_{diss})_{current}} - \frac{(\beta_{turnover})_{historical}}{(\beta_{diss})_{historical}}.$$

If we note e, the change in the number of species shared by the two assemblages ($e \geq -a$), and f and g, the changes in the number of non-shared species in the richer and the poorer assemblages, respectively ($f \geq -b$; $g \geq -c$), then:

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

$$\delta\beta_{turnover} = \frac{2 \times \min(b + f, c + g)}{a + e + 2 \times \min(b + f, c + g)} - \frac{2 \times c}{a + 2 \times c}, \text{ and}$$

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

Both turnover and dissimilarity change range from −1 to +1 (Villéger & Brosse, 2012), as does the change in the contribution of turnover to dissimilarity. These two indices both depend on the historical species richness shared (or not) by the two assemblages (a, b and c) and on the associated changes due to species introductions and extirpations (e, f and g).

Simultaneously assessing changes in taxonomic dissimilarity and the relative contribution of turnover can help to disentangle the interlaced consequences of species introductions and extirpations (Fig. 1):
• Homogenization (i.e. decrease in β_{diss}) coupled with a decreased contribution of turnover reveals an increase in the proportion of shared species and no decrease in the richness difference between assemblages, corresponding to an increase of the contribution of the nestedness-resultant component, as defined by Baselga (2012). This could result, for instance, from the introduction of the same species into both assemblages (Fig. 1, bottom left).
• Homogenization coupled with an increased contribution of turnover reveals an increase in the proportion of shared species and a decrease in the richness difference between assemblages. This can occur when the number of species introduced into the two assemblages exceeds the number of species introduced only in the poorer assemblage, while extirpation may occur in the richer assemblage (Fig. 1, top left).
• Differentiation (i.e. increase in β_{diss}) coupled with an increased contribution of turnover reveals a decrease in the proportion of shared species and a decrease in the richness difference between assemblages. This can occur when the poorer assemblage receives non-native species, while the richer assemblage loses some of its non-shared species (Fig. 1, top right).
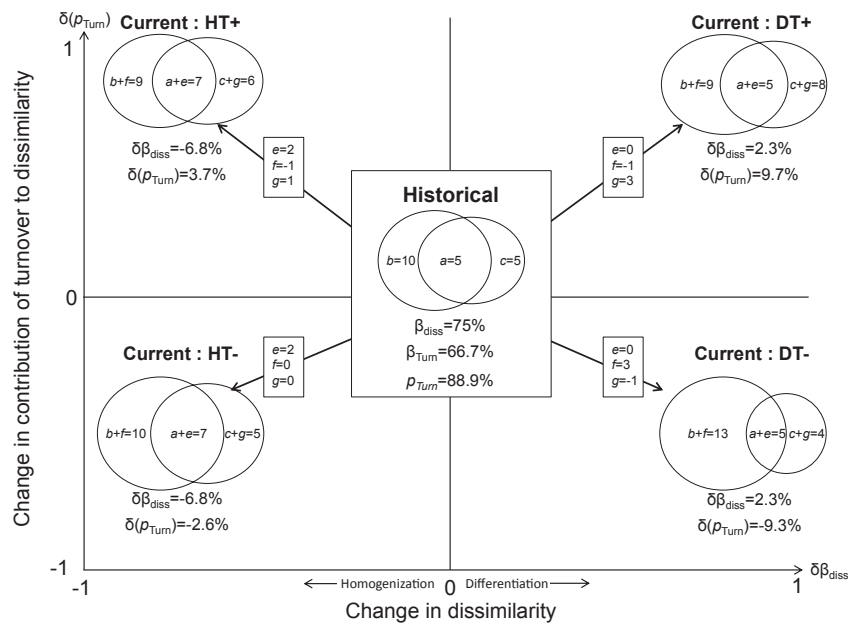
Figure 1 Change in taxonomic dissimilarity ($\delta\beta_{diss}$) versus change in contribution of taxonomic turnover to taxonomic dissimilarity (δp_{turn}) between historical and current situations for global freshwater fish assemblages. Taxonomic dissimilarity between two assemblages is represented using the classical Venn diagram representation, where ovals represent species assemblages, their size being scaled to their respective number of species and the size of their intersection symbolizing the number of species shared by the two assemblages. A hypothetical historical situation is illustrated in the centre of Fig. 1; a is the number of species that were historically shared, and b and c are the numbers of species historically present only in each of the two assemblages. Four contrasting current situations corresponding to different levels of introduction and extirpation in the two assemblages considered are provided in the four corners; e is the change in the number of species shared; f and g are the changes in the number of species present only in the richer and poorer assemblages, respectively. The resulting homogenization (H) or differentiation (D) as well as the increase or decrease of contribution of turnover (T+ and T−) are indicated for each current situation. Nil values (0, 0 coordinates) account for no change in taxonomic dissimilarity between the historical and the current situation.

• Differentiation coupled with a decreased contribution of turnover reveals a decrease in the proportion of shared species and no decrease in the richness difference between assemblages. This could be the case when the richer assemblage receives non-native species and the poorer one loses some of its non-shared species (Fig. 1, bottom right).

Identifying the determinants of change in dissimilarity

We used a database of 9722 fish species occurring in 1054 river basins, covering more than 80% of the earth's continental surface (Brosse *et al.*, 2013). Native and non-native status was recorded for each species occurrence. Both historical composition (before human intervention, i.e. before the industrial period) and current assemblages (historical composition + non-natives − extirpated) are therefore available (Leprieur *et al.*, 2008a; Villéger *et al.*, 2011). We computed the change in taxonomic dissimilarity and the change in the relative contribution of turnover to dissimilarity from the historical to the current situation for all pairs of basins in each of the six biogeographical realms: Afrotropical, Australian (including Oceania), Nearctic, Neotropical, Oriental and Palaearctic.

To investigate the determinants of changes in dissimilarity and contribution of turnover, we split the pairs of assemblages into five groups according to the sign of the change. HT+ and HT− refer to the basin pairs exhibiting a pattern of homogenization associated with a decrease (HT−) or increase (HT+) in the contribution of turnover. NC refers to basins that experienced no change in taxonomic dissimilarity over time. DT+ and DT− refer to the basin pairs experiencing differentiation and a decrease (DT−) or increase (DT+) in the contribution of turnover.

The relative importance of the historical situation (i.e. the number of species shared or not by the pair of assemblages) and of introduction and extirpation processes (i.e. respective changes in the number of non-shared or shared species) in discriminating these five types of change was determined using a random forest modelling method (Breiman, 2001). The random forest algorithm has been widely used in ecology to carry out multivariate analyses without making assumptions about the input variables. The importance of each predictor was measured using the Gini index (Strobl *et al.*, 2007). Analyses were carried out using the randomForest package (Liaw & Wiener, 2002) in R (R Development Core Team, 2011); following the recommendations of Breiman (2001), 500 trees were generated to obtain a reliable estimation of the contribution of each predictor.

	Basins	*a*	*b*	*c*	*e*	*f*	*g*
Afrotropical	109	0 [0; 135]	61 [0; 793]	8 [0; 396]	0 [0; 8]	1 [−26; 12]	1 [−27; 12]
Australian	179	0 [0; 37]	16 [0; 69]	7 [0; 47]	0 [−1; 10]	2 [−5; 13]	1 [−6; 13]
Nearctic	207	1 [0; 139]	36 [0; 243]	7 [0; 106]	0 [−5; 49]	3 [−25; 60]	0 [−13; 51]
Neotropical	155	0 [0; 610]	34 [0; 1798]	9 [0; 564]	0 [−1; 9]	0 [−5; 17]	2 [−4; 17]
Oriental	59	0 [0; 247]	50 [2; 691]	10 [0; 260]	0 [−6; 14]	2 [−12; 31]	0 [−10; 11]
Palaearctic	345	1 [0; 76]	23 [0; 340]	6 [0; 91]	0 [−3; 26]	3 [−16; 33]	0 [−8; 33]

Table 1 Median and range (in square brackets) of the historical number of fish species shared (*a*), or not (*b* and *c*) between pairs of assemblages in six biogeographical realms, and their respective changes (*e*, *f* and *g*) after species introductions and extirpations. See text and Figure 1 caption for the detailed meanings of parameters *a* to *g*.

The predictors exhibiting a relative contribution greater than 10% (as measured by the Gini index) were used to construct a synthetic decision tree to illustrate how these variables discriminate the five types of change. We then calculated the frequency of each of the five groups of combinations of change in dissimilarity and change in contribution of turnover in each leaf of this synthetic tree.

RESULTS

Historical taxonomic dissimilarity and taxonomic turnover among assemblages

For freshwater fish, historical dissimilarities were characterized by a large proportion of non-shared species (*b* and *c*), which represent on average more than 95% of the total species richness in assemblage pairs (Table 1). The number of species in common (*a*) was very low; with a median value of 1 in the Palaearctic and Nearctic realms and a median value of 0 in the other four realms. The number of species present only in the richer assemblage of the pair (*b*) was on average 9.9 times higher than the number of species present only in the poorer assemblage (*c*) (Table 1).

Of the 116,124 pairs of assemblages in the six realms, 2% (2741 pairs) were nested (*c* = 0; *b* > 0) and only 106 pairs (0.1%) were identical (*b* = *c* = 0). As a consequence, the average values of the Jaccard dissimilarity index for the historical time-point were higher than 90% in the six realms (see Appendix S1 in Supporting Information). These assemblage dissimilarities were mainly due to the turnover component, which accounted for more than 90% of the overall dissimilarity (Appendix S1).

Changes in taxonomic dissimilarity and contribution of turnover

Around half of the basin pairs (49.8%) experienced a change in dissimilarity as well as a change in the contribution of turnover to dissimilarity. For each of the six realms, we found a significant positive correlation between dissimilarity and turnover changes (Spearman's rank correlation coefficient ranged from 0.138 to 0.472; $P < 0.001$; Fig. 2). Because these values were rather low, however, all types of change combining dissimilarity and turnover occurred (Fig. 2).

Among the homogenized basin pairs, 82% underwent a decrease in turnover contribution (Fig. 2). For this subset of pairs, significant positive correlations were found between dissimilarity and changes in the turnover contribution in each biogeographical realm (Table 2). Similarly, 61% of the basin pairs that showed differentiation over time exhibited a decrease in the turnover contribution, as well as a negative correlation between change in taxonomic dissimilarity and the change in the turnover contribution (Table 2).

Influence of historical situation, introductions and extirpations

The random forest analyses provided a relevant discrimination of the determinants of change in dissimilarity, with a small proportion of wrong classifications (< 3%; Fig. 3). The ranking of the determinants of change was similar among the six realms. Three main variables discriminated the five types of change. The number of historically shared species (*a*) and the associated change in the number of shared species following species introductions and/or extirpations (*e*) provided the greatest contribution to the classification tree (Gini index > 25% for each variable in each realm; Fig. 3). In contrast, the number of historically non-shared species (*b* and *c*) only weakly discriminated the five types of change (Gini index < 10% in all six realms). The change in the number of species present only at the poorer site (*g*) represented the third most important variable, with a Gini index ranging from 10% to 20% (Fig. 3).

The random forest analysis identified the variables *a*, *e* and *g* as the most important for sequentially discriminating the five types of change in taxonomic dissimilarity (Fig. 4). The number of species shared historically (*a*) and the change in shared species following the introduction of non-native species and species extirpation (*e*) discriminated assemblage pairs exhibiting no change (NC) from homogenized pairs (HT−, HT+). In the cases of homogenization, the contribution of turnover decreased in 97% of the pairs when *e* > 0. Additionally, for *a* > 0, the change in the number of species present only in the poorer assemblage (*g*) discriminated two groups among differentiated pairs: for *e* = 0 and *g* > 0 (non-shared species introduction), 87.5% of pairs differentiated and showed an increase in the contribution of turnover, whereas for *e* = 0 and *g* ≤ 0 (non-shared species extirpation), differentiation was accompanied by a decrease in the contribution of turnover. Similar decision trees were built for each biogeographical realm, and provided similar results (see Appendix S2).
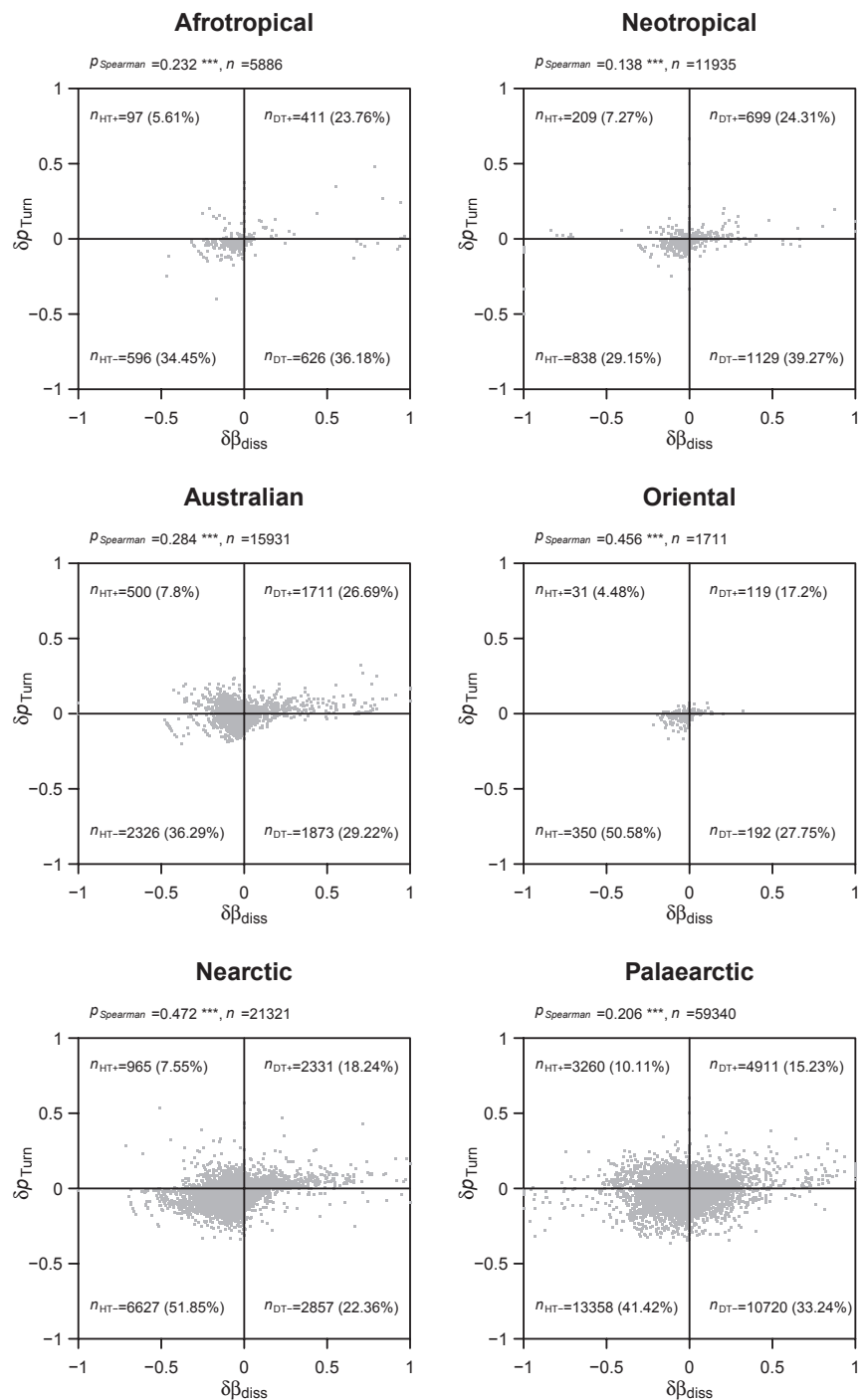
Figure 2 Relationship between change in taxonomic dissimilarity ($\delta\beta_{diss}$) and change in contribution of taxonomic turnover to taxonomic dissimilarity (δp_{turn}) for freshwater fish assemblages in six biogeographical realms. Number of basin pairs (n), Spearman's correlation coefficient, and associated Mantel test are provided for each realms (***$P < 0.001$). For each panel, the number of basin pairs in each of the four non-null combinations of direction of change is indicated, and the percentage of each of the four combinations is given in parentheses.

DISCUSSION

Studying patterns of beta diversity is fundamental for understanding the ecological processes that shape differences in species assemblages, and for assessing the impact of human activities on biodiversity (Olden & Rooney, 2006; Devictor *et al.*, 2010; Leprieur *et al.*, 2011). Human-mediated species introductions and extirpations are known to affect freshwater fish faunas and push them towards global homogenization (Rahel, 2000; Olden *et al.*, 2008; Leprieur *et al.*, 2008a; Villéger *et al.*, 2011).

Beyond this overall decrease in taxonomic dissimilarity, both homogenization and differentiation have occurred among fish assemblages in North America (Rahel, 2000) and Europe (Clavero & García-Berthou, 2006; Leprieur *et al.*, 2008b), and on a global scale (Villéger *et al.*, 2011).

Here, we highlight the complexity of dissimilarity changes when adding or removing species. Such heterogeneous situations arise from the complex nature of assemblage dissimilarity, which combines two independent components, namely the turnover component (i.e. species replacement from one assem-

Table 2 Spearman's correlation coefficient and associated Mantel's test between the change in taxonomic dissimilarity of freshwater fish assemblages in six biogeographical realms and the change in the contribution of turnover to taxonomic dissimilarity for the basin pairs experiencing taxonomic homogenization or differentiation. (***$P < 0.001$).

Realm	Homogenization			Differentiation		
	ρ	P	n	ρ	P	n
Afrotropical	0.423	***	697	−0.312	***	1048
Australian	0.209	***	2910	−0.176	***	3775
Nearctic	0.230	***	7746	−0.077	***	5418
Neotropical	0.290	***	1097	−0.089	***	1871
Oriental	0.227	***	385	−0.194	***	315
Palaearctic	0.085	***	16,779	−0.243	***	16,185

blage to another, independent of species richness) and the nestedness-resultant component (Baselga, 2012; Qian & Ricklefs, 2012). Exploring changes in the contribution of turnover to taxonomic dissimilarity gives us an opportunity to provide mechanistic explanations for the changes that follow anthropogenic disturbance (Koleff *et al.*, 2003; Villéger & Brosse, 2012). More precisely, we have shown here how assessing both dissimilarity and turnover changes can shed light on the relative effects of historical contingency, species extirpations and introduction pressure on an important facet of biodiversity.

For freshwater fish faunas, every combination of change in taxonomic dissimilarity and in the contribution of turnover occurred within each biogeographical realm. Although significant, the strength of the correlation between change in taxonomic dissimilarity and change in the contribution of turnover remains low, confirming that these two indices provide complementary information on changes in beta diversity among assemblages. Homogenization associated with a decrease in the turnover contribution was the most frequent combination of change in dissimilarity and contribution of turnover in all realms. Such a situation represents, for example, more than 87% of cases of homogenization in the Nearctic realm. In contrast, for pairs experiencing differentiation, the proportions of increased and decreased contributions of turnover were much more balanced in all realms (around 40% and 60%, respectively).

These contrasting situations are not only explained by species introductions and/or extirpations, but also by the historical composition of assemblages, supporting previous studies (Rahel, 2000; Villéger *et al.*, 2011). Indeed, the historical situation plays a major role, with the number of historically shared species (a) being the factor best explaining changes in species dissimilarity. The importance of the historical situation is due to the high turnover between freshwater fish faunas, which results from the inability of freshwater fish to cross dry land or salt water (Hugueny, 1989). Fish assemblages from each river basin are therefore isolated from their neighbours, creating an insular aquatic system that is prone to independent evolution (Rosenzweig, 1995, 2001; Burridge *et al.*, 2008). The isolation of

assemblages may be triggered by extinction events such as glaciations, to which riverine freshwater fish are especially sensitive, rendering recolonization after glacial periods a long and stochastic process (Leprieur *et al.*, 2011; Oberdorff *et al.*, 2011). These processes explain why historical situations are characterized by the rarity of shared species among basins, as underlined by the relatively high proportion (almost 50%) of basin pairs without any species in common (historical dissimilarity and historical turnover are therefore maximal in these pairs; Baselga, 2012). The introduction of the same species in the two assemblages thus leads to a decrease both in taxonomic dissimilarity and in the turnover contribution. To illustrate this, 41% of the basin pairs that showed this trend (HT−; Fig. 4) were historically entirely dissimilar. For basin pairs which shared at least one species historically, the number of shared species remains lower than the number of unshared species (Table 1), and even in this case the introduction of at least one species in common will have more impact on the change in dissimilarity than the introduction of different species in the two assemblages.

The world's freshwater fish faunas are currently undergoing changes in taxonomic dissimilarity across all biogeographical realms, leading to homogenization for most basin pairs that experience species introductions (Villéger *et al.*, 2011). Introductions of the same species in numerous basins are the main cause of worldwide homogenization. As underlined by Gozlan *et al.* (2010), a few species, such as the rainbow trout (*Oncorhynchus mykiss*), the Mozambique tilapia (*Oreochromis mossambicus*) and the common carp (*Cyprinus carpio*), have been widely introduced across the world, mainly for commercial and recreational purposes. The dominance of cases of homogenization, coupled with the decrease in the contribution of turnover found in this study (Fig. 2, bottom left), highlights the impact of the intentional introduction of a few species over large areas.

As well as the predominant homogenization trend, cases of differentiation have also been reported at both global (Villéger *et al.*, 2011) and regional scales (Leprieur *et al.*, 2008b). Such situations result from introductions and/or extirpations that only occur in one of the two assemblages without affecting the number of shared species ($a > 0$ and $e = 0$). This leads to a slight increase in dissimilarity (differentiation) that can be associated with either an increase or a decrease of the turnover contribution (Fig. 4). Indeed, turnover variation is controlled by the proportion of non-shared species in the poorer assemblage (g). Hence, species introduction ($g > 0$) tends to increase the turnover contribution by reducing the difference in richness between assemblages. In contrast, when the richer assemblages receives non-native species without introduction into the poorer assemblage ($g = 0$) or with species extirpation there ($g < 0$), the contribution of turnover decreases.

Considering global patterns of homogenization and differentiation from a dynamic point of view opens new considerations about the outcome of 'single' introductions (i.e. species introduced in only one assemblage of a pair). Single introductions can be considered as isolated species that are under an initial invasion stage and that, if established, might undertake the next
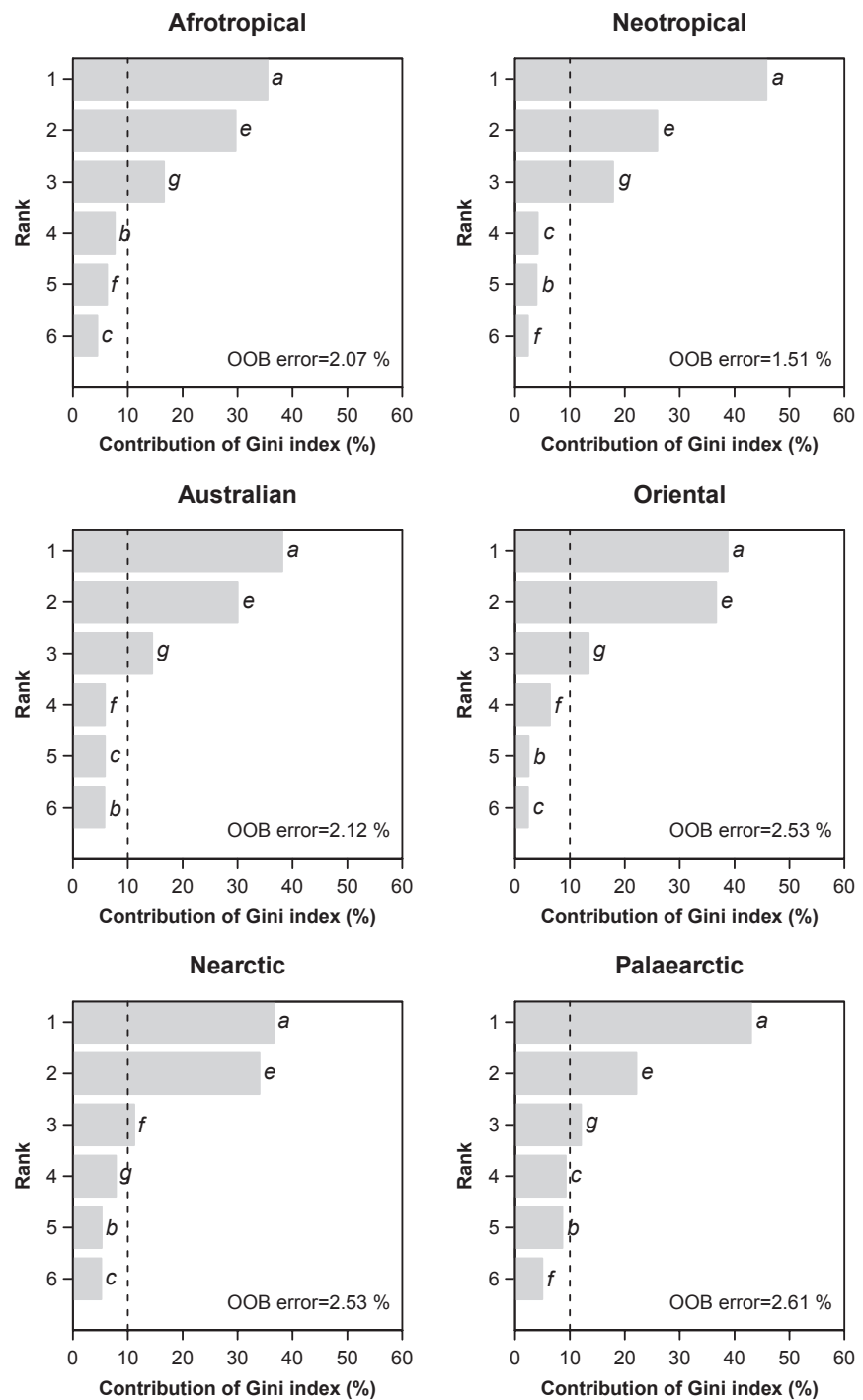
Figure 3 Relative contribution of historical situation, and introduction and extirpation processes, to the change in taxonomic dissimilarity and the change in the contribution of taxonomic turnover to dissimilarity in freshwater fish assemblages in six biogeographical realms. Values are percentage contribution to the Gini index given by the random forest model for each realm; *a* is the number of species shared historically and *b*, *c* are the number of historically unique species in the richer and the poorer assemblages, respectively; *e* is the change in the number of shared species through introduction and extirpations; *f* and *g* are the changes through introduction and extirpations in the number of species unique to *b* and *c*, respectively. The dashed line indicates the 10% contribution threshold. The percentage of error of the model (or percentage of incorrect classification) is given by the out-of-bag (OOB) error.

step of the invasion process (Lockwood *et al*., 2007). Hence, the differentiating role of early invaders will become a homogenization trend when the species disperses (either naturally or with human assistance) to other nearby basins. Differentiation is traditionally considered the opposite of homogenization (Olden & Poff, 2004; Leprieur *et al*., 2008b; Villéger *et al*., 2011), but it could quickly turn into homogenization under higher propagule pressure or invasion progress. In this context, differentiation could be considered as an indicator metric of homogenization risk, and it might therefore be used to focus management actions on vulnerable areas in order to prevent future homogenization. In the modern world, where increasing global trade will promote the introduction of non-native species in relatively unaffected areas such as the Neotropical and Afrotropical realms (Leprieur *et al*., 2008a), particular attention should be given to increases of dissimilarity as they can rapidly change toward a homogenization situation. Moreover, many assemblages of other taxa (e.g. plants, birds) are also experiencing the introduction of non-native species and the extirpation of native species, but the intensity and nature (e.g. deliberate versus
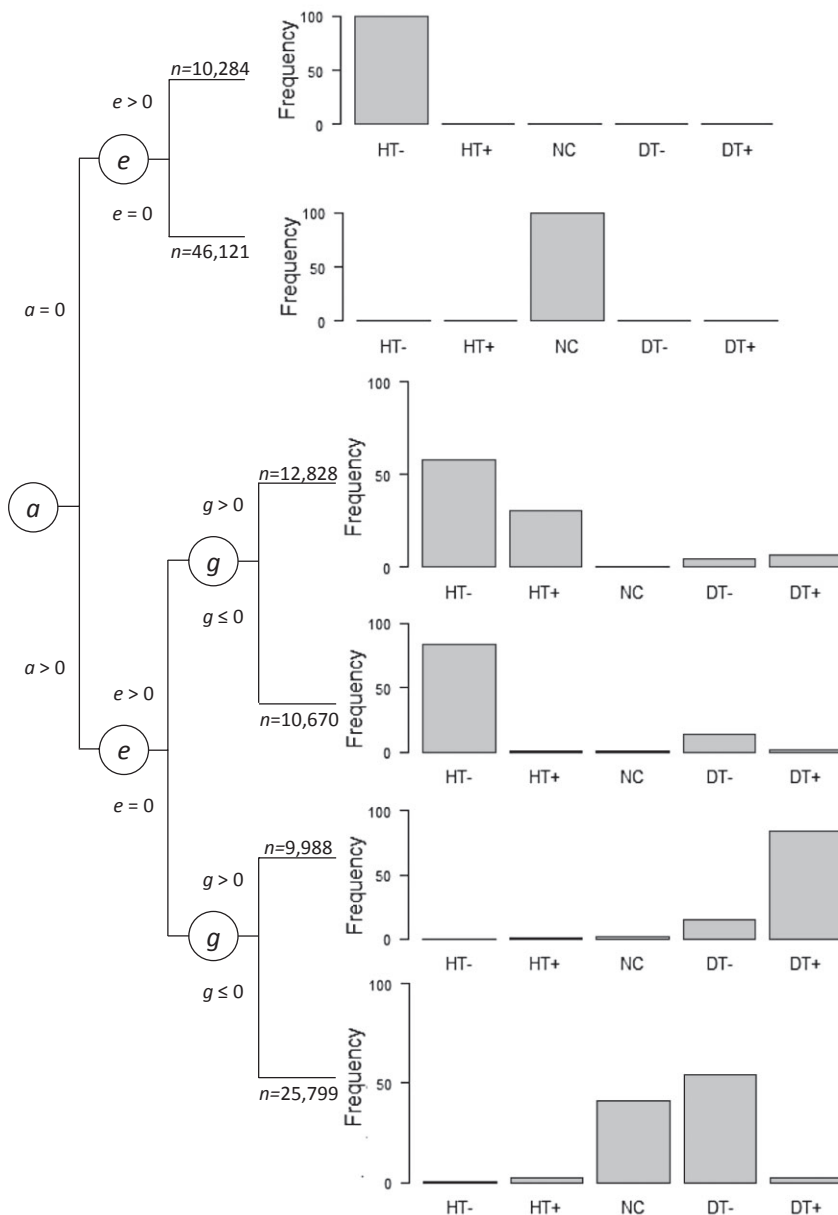
Figure 4 Decision tree illustrating how the three most important variables obtained with the random forest analysis discriminate the different groups of change in dissimilarity and contribution of turnover, for global freshwater fish assemblages. NC means no change in dissimilarity; DT− and DT+ are cases of taxonomic differentiation (i.e. increase in dissimilarity) coupled to decrease and increase in the contribution of turnover to dissimilarity, respectively; HT− and HT+ are cases of taxonomic homogenization coupled to decrease and increase in the contribution of turnover to dissimilarity, respectively; a is the number of species shared historically and e and g are changes in the number of shared species, and the number of species unique to the poorer assemblage. Panels at the end of each branch show the proportion of basin pairs in each combination of change in dissimilarity and contribution of turnover among all the pairs from the six biogeographical realms combined ($n = 116,124$ pairs). The n value associated with each branch is the number of pairs of assemblages. The case $a > 0$ and $e < 0$ is not represented because of its scarcity ($< 0.01\%$) in the six realms.

accidental introduction) of these two processes differ between taxa and between spatial scales. The historical patterns of dissimilarity and the turnover contribution are also likely to vary between studies. The framework presented here could therefore help to better assess the effects of global changes on the beta component of biodiversity.

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SUPPORTING INFORMATION

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

Appendix S1 Mean historical and current taxonomic dissimilarity and turnover between basin pairs in each realm.
Appendix S2 Decision tree illustrating how the three most important variables obtained with the random forest analysis discriminate the different groups of change in dissimilarity and contribution of turnover in the six realms.

BIOSKETCH

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