BIODIVERSITY RESEARCH

Null model of biotic homogenization: a test with the European freshwater fish fauna

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ABSTRACT

In recent years, there has been growing concern about how species invasions and extinctions could change the distinctiveness of formerly disparate fauna and flora, a process called biotic homogenization. In the present study, a null model of biotic of homogenization was developed and applied to the European freshwater fish fauna. We found that non-native fish species led to the greatest homogenization in south-western Europe and greatest differentiation in north-eastern Europe. Comparing these observed patterns to those expected by our null model empirically demonstrated that biotic homogenization is a non-random ecological pattern, providing evidence for previous assumptions. The place of origin of non-native species was also considered by distinguishing between exotic (originating from outside Europe) and translocated species (originating from within Europe). We showed that exotic and translocated species generated distinct geographical patterns of biotic homogenization across Europe because of their contrasting effects on the changes in community similarity among river basins. Translocated species promoted homogenization among basins, whereas exotic species tended to decrease their compositional similarity. Quantifying the individual effect of exotic and translocated species is therefore an absolute prerequisite to accurately assess the spatial dynamics of biotic homogenization.

Keywords

biotic homogenization, exotic species, freshwater fish, null model, translocated species.

INTRODUCTION

The introduction of non-native species and the extinction of native species have together caused loss of taxonomic regional distinctiveness among formerly disparate faunas and floras (reviewed by Olden & Rooney, 2006). This decrease in beta-diversity, also called biotic homogenization (BH) by McKinney & Lockwood (1999), is expected to have important evolutionary and ecological consequences (Olden *et al.*, 2004). BH is now an important research agenda for ecologists as it represents a process including both species invasions and extirpations, two key components of the modern biodiversity crisis (Olden, 2006).

Three distinct forms of BH (genetic, taxonomic and functional) were defined by Olden *et al.* (2004). Among them, taxonomic homogenization (TH) has been empirically studied for various taxonomic groups (reviewed by Olden, 2006), and has been explicitly formalized by Olden & Poff (2003, 2004) into a mechanistic model incorporating scenarios of invasion and extinction. These scenarios show how species invasions and/or extinctions can lead to TH (i.e. increase in community similarity) or to taxonomic differentiation (i.e. decrease in community similarity). Although TH patterns have been commonly related to environmental and human factors in homogenization studies (e.g. Marchetti *et al.*, 2001; Rooney *et al.*, 2004; Olden *et al.*, 2006), few have tested whether TH is geographically structured (Smith, 2006). In addition, none of these studies addressed whether the place of origin of non-native species influenced TH patterns. Recently, McKinney (2005) found that translocated species (i.e. species introduced within their native biogeographical zone in localities where they did not historically occur) have a greater homogenization effect than exotic species (i.e. species originating from another biogeographical area). However, tests of this assumption are scarce (La Sorte & McKinney, 2005), and to our knowledge the joint and individual effects of translocated and exotic species on TH have never been compared.

In this context, this study aims (i) to identify the relative roles of exotic and translocated species in driving TH patterns and (ii) to test whether these patterns are geographically structured. We explored fish homogenization and differentiation in the 25 major European river basins as extended information is available on native and non-native fish species in these basins. Moreover, almost all homogenization studies have been conducted in North

America, and homogenization processes need evidence from other continents to allow general validation. To quantify TH, we applied the quantitative framework of Olden & Poff (2003, 2004) and among the 14 scenarios proposed by these authors, we tested those without extinction events. Indeed, these scenarios correspond to the European situation as no basin-scale extinctions among non-migratory freshwater fish were reported in large European river basins (e.g. Keith & Allardi, 2001; Clavero & García-Berthou, 2006).

Previous studies exploring BH assumed that non-native species were not randomly distributed across localities as species introductions are primarily related to human purposes (Blackburn & Duncan, 2001; Jeschke & Strayer, 2006). This led to the assumption that BH is a non-random ecological pattern (e.g. Duncan & Lockwood, 2001; Olden *et al.*, 2004). However, these studies did not compare observed patterns to those expected under a null hypothesis. Then, the quantification of TH is commonly based on similarity indices, such as the Jaccard index (Olden & Rooney, 2006), that are notoriously difficult to interpret without knowing their expected values under null hypotheses of random distribution of species among localities (Henderson & Heron, 1977; Connor & Simberloff, 1978; Raup & Crick, 1979). Last, the change in community similarity among pairwise localities is negatively related to the initial similarity (Olden & Poff, 2004), preventing direct comparison between pairwise values. In this context, we generated random assemblages of non-native species using Monte Carlo simulations to compare observed TH patterns with regard to null models. These models are widely used to test specific hypotheses about patterns in nature by creating artificial data sets that could be expected if a given null hypothesis is true (e.g. Gotelli, 2000). Compared to other modelling approaches, a null model deliberately excludes the mechanism on interest being tested. In this study, we expect that if TH is generated by a non-random distribution of non-native species, observed TH patterns should differ from those expected by chance alone. Particularly, if the slope of the relationship between the change in community similarity and the initial similarity among basins is lower than predicted by the null model, this would imply that basins that are initially similar in their species composition are more likely than expected by chance to be invaded by the same species.

METHODS

Data sources

Freshwater fish occurrences were compiled from published data on the major European river basins. We selected the 25 basins (Fig. 1a) for which sufficient information on the fish fauna is available at the basin scale (see Appendix S1 in Supplementary Material for a full list of references). This avoided potential bias in our analysis due to incomplete surveys of both native and non-native fish species. For each basin, we distinguished three categories of species: natives, exotics (i.e. species originating from outside Europe) and translocated (i.e. species native to Europe introduced into drainages where they did not historically

occur). We considered as non-native a species with self-reproducing populations or populations artificially maintained by regular and long-term restocking. Only strictly freshwater fish were considered because (i) migratory and brackish species would introduce potential bias in the analysis as we considered each basin as a biogeographical island, and (ii) information availability on the distribution of migratory and brackish species is much more limited than for resident species.

Quantifying homogenization/differentiation

For each pair of basins ($n = 300$), we calculated the Jaccard similarity index corresponding to two time situations, i.e. initial ($J_{initial}$) and final (J_{final}) situations. This similarity index is commonly applied in homogenization studies dealing with presence/absence matrices (Olden & Rooney, 2006). The initial situation only included native species that represented the historical pool of species (Olden & Rooney, 2006). On the contrary, the final situation included native species plus non-native species (i.e. the contemporary species pool). TH was quantified from differences in Jaccard index (expressed as percentage) for each pair of basins between the final and initial situations (i.e. the change in similarity among pairwise basins: Pairwise ΔCS; Rahel 2000; Olden & Poff, 2003). Positive values of Pairwise ΔCS indicate a TH among pairwise basins, whereas negative values indicate a taxonomic differentiation among pairwise basins.

We explored TH patterns using different metrics and quantitative representations. First, we investigated the relationship between Pairwise ΔCS and the initial similarity among basins (i.e. initial situation, $J_{initial}$). As geographical distance and species similarity are generally inversely related at large spatial scales (Nekola & White, 1999), we also considered $J_{initial}$ as a surrogate of geographical distance among basins (e.g. Reyjol *et al.*, 2006). The relationship between Pairwise ΔCS and $J_{initial}$ permitted us to relate observed patterns to the prediction of the two invasion-only scenarios of Olden & Poff (2003, 2004): (scenario I1) the same species invade driving TH; (scenario I2) different species invade driving taxonomic differentiation. Second, to understand how each basin changed relative to all others in Europe, we computed the average of Pairwise ΔCS between each basin and the 24 other basins (i.e. Basin ΔCS or rate of homogenization/differentiation per basin). We then mapped the Basin ΔCS to explore geographical patterns of TH across Europe and applied a Mantel's test to assess whether the Basin ΔCS was geographically structured (i.e. to determine if the basins that are close together had more similar rates of homogenization/differentiation than distant ones). The Mantel's test consists of testing the correlation between two distance matrices using a randomization procedure (10,000 permutations; see Legendre & Legendre, 1998). We used the Euclidean distance to compute the matrices of (i) geographical distance (based on mean latitude and longitude of each basin) and (ii) Basin ΔCS distance (based on the rates homogenization/differentiation per basin). Last, we quantified the continental level of homogenization or differentiation in Europe by averaging the 300 Pairwise ΔCS (Continental ΔCS).
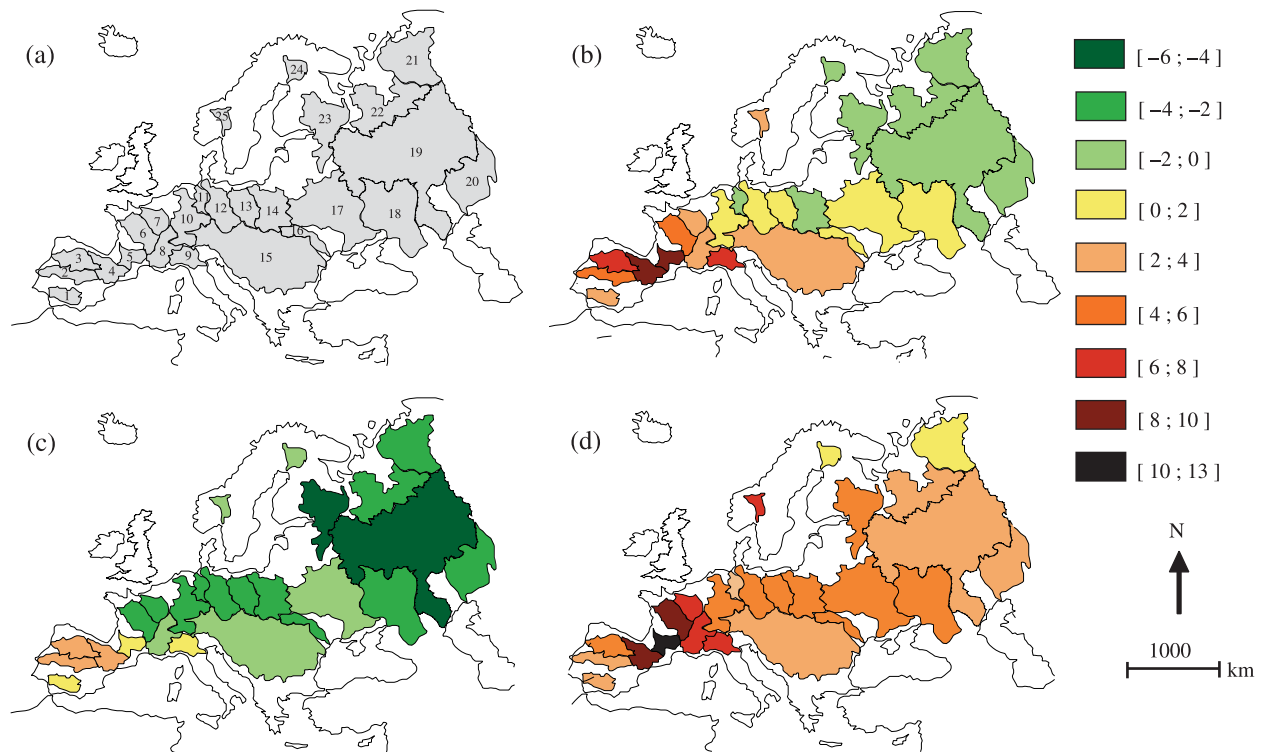
Figure 1 Geographical distribution of the rates of homogenization/differentiation per basin (Basin ΔCS;%). (a) Map of the 25 major European river basins (1: Guadalquivir; 2: Tagus; 3: Douro; 4: Ebro; 5: Garonne; 6: Loire; 7: Seine; 8: Rhône; 9: Pô; 10: Rhine; 11: Weser; 12: Elbe; 13: Oder; 14: Wisla; 15: Danube; 16: Dniestr; 17: Dniepr; 18: Don; 19: Volga; 20: Ural; 21: Petchora; 22: Dniva; 23: Neva; 24: Kemijoki; 25: Glomma). (b) Basin ΔCS (%) based on non-native species (both exotic and translocated species). (c) Basin ΔCS (%) based on exotic species alone. (d) Basin ΔCS (%) based on translocated species alone. The graduation of green indicates a taxonomic differentiation and the graduation of red indicates a taxonomic homogenization. See Methods for more details.

Null model of homogenization/differentiation

Monte Carlo simulations were developed to generate 10,000 matrices of Pairwise ΔCS expected by chance alone (i.e. Pairwise ΔCS generated by a random distribution of non-native species). We first tested whether the observed values of Basin ΔCS and Continental ΔCS were generated by a non-random distribution of non-native species. Observed values of Basin ΔCS and Continental ΔCS were compared to their null distributions that derived from the simulated Pairwise ΔCS (two-tailed test, α = 5%). Then, we determined whether the relationship observed between Pairwise ΔCS and $J_{initial}$ differed from those expected by chance alone by calculating the regression parameters (i.e. slope and intercept) from the 10,000 simulations and comparing the observed values to their null distributions (two-tailed test, α = 5%).

Our Monte Carlo simulations consisted in randomly assigning each non-native fish species into the 25 basins (translocated species were randomly assigned only in basins where they do not naturally occur). We applied a fixed-equiprobable algorithm (Gotelli, 2000) to generate the random matrices of non-native species occurrences. This algorithm implied that occurrences of non-native species were conserved as in the original matrix (i.e. the number of basins in which each non-native species occurs is fixed), whereas the total number of non-native species per basin was allowed to vary randomly (i.e. columns equiprobable).

Non-native species occurrences were maintained constant during simulations to account for interspecific differences in colonization ability and/or human induced propagule pressure. An equiprobable total of columns means that (i) all the basins are equiprobably sustainable for all the non-native species, and (ii) the non-native species are distributed randomly among the basins as all of them can colonize all the basins. According to Gotelli (2000), the fixed-equiprobable algorithm is efficient to avoid type I and II errors concerning statistically significant patterns for a random matrix. When selecting a null model, every feature of the randomized data would be preserved as in the observed data, except the feature that the study aims to test (Tokeshi, 1986). This ensures that the model does not become biologically too unrealistic. In our null model, we did not maintain the number of non-native species per basin constant as in the original matrix because it is well accepted that most communities in nature are not saturated (e.g. Hugueny & Paugy, 1995; Smith & Shurin, 2006). This means that all communities may be susceptible to invasion by non-native species regardless of native species richness (e.g. Moyle & Light, 1996; Gido & Brown, 1999; Smith & Shurin, 2006). Then, Olden & Rooney (2006) argued that BH should not be systematically confused with patterns of species invasions (i.e. number of invaders) as is commonly done in the literature. Therefore, allowing the number of non-native species to vary in each basin permitted

Table 1 Number of native, exotic and translocated freshwater fish in the 25 major European river basins. The basin numbers (Code) are those used in Fig. 1a.

Code	Basin	Native	Exotic	Translocated
1	Guadalquivir	12	5	5
2	Tagus	18	6	7
3	Douro	13	8	7
4	Ebro	19	8	11
5	Garonne	18	11	13
6	Loire	21	9	11
7	Seine	22	8	10
8	Rhône	31	11	9
9	Pô	28	11	10
10	Rhine	31	16	11
11	Weser	29	7	7
12	Elbe	34	8	4
13	Oder	39	12	5
14	Wisla	31	11	3
15	Danube	67	18	2
16	Dniestr	48	12	0
17	Dniepr	49	10	0
18	Don	45	13	1
19	Volga	51	16	2
20	Ural	35	4	0
21	Petchora	20	0	0
22	Dvina	25	1	0
23	Neva	35	0	1
24	Kemijoki	17	2	0
25	Glomma	17	2	1

[Correction added after online publication 28 August 2007: values of Native, Exotic and Translocated freshwater fish are corrected as above].

us to test the null hypothesis that the rates of homogenization/ differentiation per basin (Basin ΔCS) were dependent of the number of non-natives in each basin. We quantified TH and applied our null model by first considering overall non-native species (exotic and translocated species were pooled) and then by distinguishing between exotic and translocated species. The null model program was computed by the authors with the open source R software (Ihaka & Gentleman, 1996).

RESULTS

General trends in native and non-native species richness

The native non-migratory freshwater fish fauna of the 25 major European river basins was composed of 136 species. We identified 38 exotic species and 40 translocated species with a large variation in species richness between basins (Table 1). Native species richness was independent of the number of non-native species (Pearson's correlation: $r = 0.151$, $P = 0.236$). However, when distinguishing between exotic and translocated species, native and exotic species richness was positively correlated (Pearson's correlation: $r = 0.575$, $P = 0.001$), whereas native

and translocated species richness was negatively correlated (Pearson's correlation: $r = -0.449$, $P = 0.012$). This relationship was strongly influenced by the basin area, as when controlling for this variable with partial regressions, these correlations became marginal (partial Pearson's correlation: $r = 0.406$, $P = 0.049$) or non-significant (partial Pearson's correlation: $r = -0.321$, $P = 0.126$) for exotic and translocated species, respectively.

Pairwise change in community similarity (Pairwise ΔCS)

Pairwise ΔCS and the initial similarity among basins displayed a negative linear relationship as predicted by the invasion-only scenarios of Olden & Poff (2004) (Fig. 2). When first analysing the joint effect of exotic and translocated species, both homogenization (i.e. 60% of Pairwise ΔCS > 0%) and differentiation (i.e. 40% of Pairwise ΔCS < 0%) among basins were observed (Fig. 2a). Then, when analysing the effect of exotic and translocated species separately, we noticed (i) a general trend of differentiation among basins for exotic species (i.e. 75% of Pairwise ΔCS < 0%), except for basins sharing few native species (i.e. low $J_{initial}$) that became more similar (Fig. 2b), and (ii) a general trend of homogenization among basins (i.e. 93% of Pairwise ΔCS > 0%) within the entire range of $J_{initial}$ for translocated species (Fig. 2c). The slopes of these relationships were less steep than those expected by the null model (two-tailed test, $P = 0.000$, Fig. 2). The intercepts were significantly lower than those expected by the null model (two-tailed test, $P = 0.000$).

Fish homogenization/differentiation in Europe (Continental ΔCS, Basin ΔCS)

A continental level of homogenization was observed when analysing the joint effect of exotic and translocated species (Continental ΔCS = 2.2%, $n = 300$), which was greater than expected by the null model (two-tailed test, $P < 0.0001$). A general trend of homogenization was also observed at the basin scale (i.e. 17 basins out of 25; Fig. 1b). The Basin ΔCS were spatially autocorrelated (Mantel test, $r = 0.357$, $P = 0.006$) and differed from those expected by the null model in nine basins (Table 2).

Then, analysing exotic species alone revealed a continental level of differentiation (Continental ΔCS = –1.6%, $n = 300$), which was lower than expected by the null model (two-tailed test, $P = 0.0003$). A general trend of differentiation was also observed at the basin scale (i.e. 19 out of 25 basins, Fig. 1c). The Basin ΔCS were spatially autocorrelated (Mantel test, $r = 0.3218$, $P < 0.001$) and differed from those expected by the null model in most basins (i.e. 20 out of 25, Table 2). No significant linear relationship was established between the observed Basin ΔCS and the number of exotic species per basin ($R^2 = 0.015$, $P = 0.565$).

Contrary to exotic species, translocated species have led to a continental level of homogenization (Continental ΔCS = 5% in average, $n = 300$), which was greater than expected by the null model (two-tailed test, $P < 0.0001$). Fish homogenization was also recorded at the basin scale (Fig. 1d). The Basin ΔCS were not
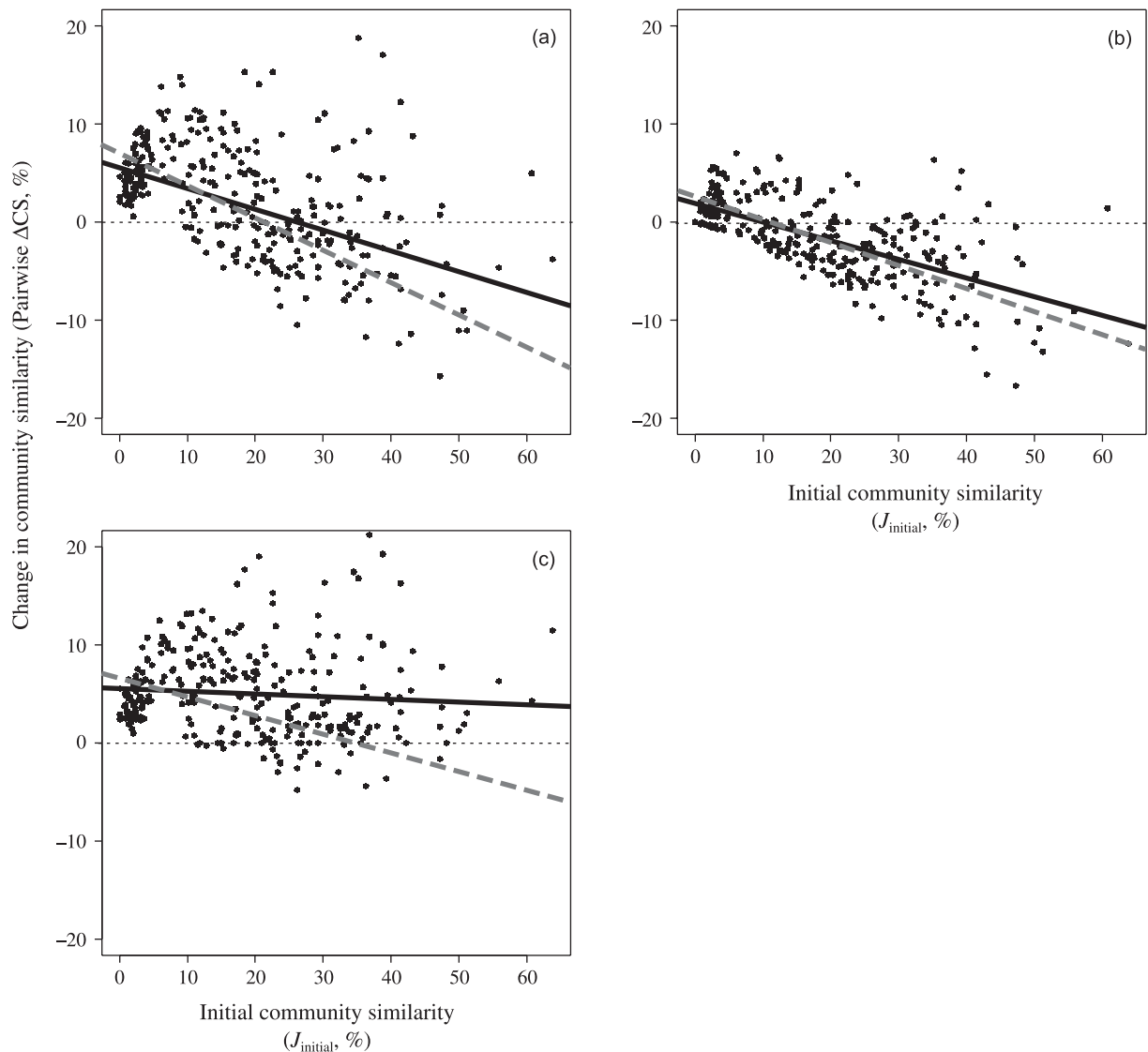
Figure 2 Change in community similarity (Pairwise ΔCS,%) of the freshwater fish fauna among 300 pairwise comparisons of the 25 major European river basins in relation with their initial similarity ($J_{initial}$,%). Solid black lines represent observed relationships and dashed grey lines represent the average simulated relationship ($n = 10,000$). (a) Non-native species (both exotic and translocated species), observed relationship: Pairwise ΔCS = $-0.21 J_{initial} + 0.06$, average simulated relationship: Pairwise ΔCS = $-0.37 J_{initial} + 0.08$. (b) Exotic species alone, observed relationship Pairwise: ΔCS = -0.19; $J_{initial} + 0.023$; average simulated relationship: Pairwise ΔCS = $-0.26 J_{initial} + 0.03$. (c) Translocated species alone, observed relationship: Pairwise ΔCS = $-0.04 \ J_{initial} + 0.055$; average simulated relationship: Pairwise ΔCS = $-0.18 J_{initial} + 0.08$.

spatially autocorrelated (Mantel test, $r = 0.107$, $P = 0.15$) and differed from those expected by the null model in only four basins (Table 2). A significant linear relationship was established between the observed Basin ΔCS and the number of translocated species per basin ($R^2 = 0.6441$, $P < 0.0001$).

DISCUSSION

As mentioned by Schoener (1987), although an ecological pattern might be statistically significant, its features may not differ significantly from the output of a null model. To our knowledge, this is the first study that aimed to test whether the observed TH patterns differed from those expected by a null

model. To generate null assemblages of non-native species, we did not maintain constant the number of non-native species as in the original matrix. We considered that each basin was equivalent in its susceptibility to invasion independently of the number of native species present. As expected, we did not observe a strong relationship between the number of native species and the number of exotic and translocated species, respectively, when controlling for the basin area. This confirms that the positive correlation between the number of native and non-native species that is commonly observed on large spatial scales, may be related to covarying factors (e.g. Davies *et al.*, 2005).

The successive introductions of non-native fish species (i.e. the joint effect of exotic and translocated species) increased on

Table 2 Observed rates of homogenization/differentiation per basin (Basin ΔCS percentage) compared to those expected by the null model (two-tailed test). The results are indicated for non-native species (i.e. exotic and translocated species were pooled) and for exotic and translocated species alone, respectively. The alphabetical codes in parentheses correspond to the conclusion of a two-tailed test: (HS) observed rates of homogenization are significantly smaller than expected by the null model; (HG) observed rates of homogenization are significantly greater than expected by the null model; (DS) observed rates of differentiation are significantly smaller than expected by the null model; (DG) observed rates of differentiation are significantly greater than expected by the null model. No indications in parentheses mean that observed rates of homogenization/differentiation did not differ from those expected by the null model. $*P < 0.001$ (Bonferroni correction), ns = non-significant. The basin numbers (Code) are those used in Fig. 1a.

| Code | Basin | Basin ΔCS (%) | | | | | |
		Non-native species		Exotic species		Translocated species	
1	Guadalquivir	3.55	ns	1.52 (HG)	*	2.77	ns
2	Tagus	4.95	ns	2.24 (HG)	*	3.68	ns
3	Douro	6.19	ns	2.44 (HG)	*	5.14	ns
4	Ebro	8.98	ns	2.27 (HG)	*	8.66	ns
5	Garonne	9.08 (HG)	*	0.34 (HG)	*	12.28 (HG)	*
6	Loire	4.64 (HG)	*	−2.10 (DS)	*	9.08 (HG)	*
7	Seine	3.53 (HG)	*	−2.43 (DS)	*	7.76	ns
8	Rhône	3.56 (HG)	*	−1.23 (DS)	*	6.26	ns
9	Pô	6.61 (HG)	*	1.69 (HG)	*	6.4	ns
10	Rhine	0.21	ns	−3.80 (DS)	*	5.24	ns
11	Weser	−0.91	ns	−3.19	ns	2.59	ns
12	Elbe	1.09 (HG)	*	−3.04 (DS)	*	5.42	ns
13	Oder	1.91 (HG)	*	−2.19 (DS)	*	5.35 (HG)	*
14	Wistula	−0.84	ns	−4.51	ns	4.36	ns
15	Danube	2.07 (HG)	*	−0.62 (DS)	*	3.41 (HG)	*
16	Dnestr	1.02	ns	−2.09	ns	4.14	ns
17	Dnepr	1.62	ns	−1.61 (DS)	*	4.09	ns
18	Don	0.37	ns	−2.97	ns	4.62	ns
19	Volga	−1.80 (DG)	*	−4.41 (DG)	*	3.7	ns
20	Ural	−0.01	ns	−3.21 (DG)	*	3.84	ns
21	Petchora	−0.49	ns	−2.28 (DG)	*	1.91	ns
22	Dvina	−1.23	ns	−3.66 (DG)	*	2.88	ns
23	Neva	−0.73	ns	−4.51 (DG)	*	4.57	ns
24	Kemijoki	−1.20	ns	−2.00	ns	0.68	ns
25	Glomma	3.77	ns	−1.84 (DG)	*	6.47	ns

average the taxonomic similarity among the 25 major European basins (Continental ΔCS = 2.2%), which is consistent with other empirical case studies analysing TH at the regional and continental scales as reviewed by Olden (2006). This continental level of homogenization was significantly greater than those expected under the null hypothesis, indicating that random assemblages of non-native species have a higher differentiation effect than actually observed. This was predictable as our null model allowed all non-native species to colonize all the basins. Overall, these results indicate that fish homogenization in Europe was not random in regards to the geographical distribution of both exotic and translocated species. This finding is supported by previous studies suggesting that the geographical distribution of non-native species was not random due to (i) differences or similarities in human-selected species and propagule pressure (e.g. Blackburn & Duncan, 2001); (ii) dispersal abilities and environmental tolerances of the introduced species (e.g. Kennard *et al.*, 2005); and (iii) the environmental and biological attributes of the recipient region (i.e. climate, human-modified habitats and

biotic resistance, e.g. Moyle & Marchetti, 2006). Several studies clearly point out intentional human activities (e.g. angling, aquaculture, biological control) as being the main determinants of fish introductions in European states (e.g. Vooren, 1972; Holcík, 1991). For example, *Gambusia affinis* Baird & Girard and *Gambusia holbrooki* Girard were mainly introduced in southern Europe for mosquito control (Keith & Allardi, 2001; Doadrio, 2002). Similarly, exotic fish assemblages were spatially structured along a latitudinal gradient in the Iberian Peninsula, with species related to sport fishing being characteristic of northern basins (Clavero & García-Berthou, 2006).

Distinguishing between exotic and translocated species revealed that translocated species generated a higher continental level of homogenization (Continental ΔCS = 5%) than overall non-native species. Indeed, exotic species decreased, on average, the taxonomic similarity among basins (Continental ΔCS = −1.6%), counteracting therefore the homogenization effect of translocated species. These opposite effects of exotic and translocated species on TH were clearly distinguished when

plotting the pairwise change in community similarity against the initial similarity among basins (Fig. 2). Translocated species produced homogenization among both neighbouring basins (high $J_{initial}$) and distant ones (low $J_{initial}$), whereas exotic species had an overall differentiation effect (i.e. decreased the compositional similarity among basins with an initial similarity ranging from 0.1 to 0.6). These results support the predictions of the two invasion-only scenarios of Olden & Poff (2004). Then, they are consistent with recent works of La Sorte & McKinney (2005), suggesting that differences in homogenization effect between exotic and translocated species may be related to their differences in geographical distribution patterns. Indeed, different sets of exotic species were introduced in different sets of neighbouring basins, i.e. 4.8 basins per species on average (e.g. *Lepomis gibbosus* Linnaeus, *Ameirus melas* Rafinesque in western Europe and *Perccottus glenii* Dybowski, *Mylopharyngodon piceus* Richardson in eastern Europe), which led to an overall decrease in species similarity among basins (scenario I2, Olden & Poff, 2004). In contrast, most translocated fish species in Europe are native to eastern basins (e.g. *Sander lucioperca* Linnaeus, *Silurus glanis* Linnaeus) and were widely introduced in less speciose drainages of western and southern Europe (Keith & Allardi, 2001; Doadrio, 2002). This led to an increase in the size of their geographical ranges (i.e. from an average historical range of 8.3 basins per species to a current range of 12.3) and hence in species similarity among basins (scenario I1, Olden & Poff, 2004). Such a pattern of homogenization has also been reported in the USA, where increased similarity among states is partly due to the expansion of cosmopolitan US fish from eastern to western basins (Fuller *et al.*, 1999; Rahel, 2000).

The fact that the observed slope of the relationship between Pairwise ΔCS and $J_{initial}$ was lower than predicted by the null model means that basins that are initially similar in their species composition are more likely than expected by chance to be invaded by the same species. Many factors may lead to this pattern but two are probably important: (i) environmental filters (e.g. Mediterranean basins are likely to be naturally inhabited and invaded by drought resistant species) and (ii) geographical structure in introduction pathways (i.e. neighbouring basins having high initial faunal similarity are likely to receive similar non-native species, see Clavero & García-Berthou, 2006). While in both cases (translocated and exotics), the observed slope was significantly lower than those expected under the null model, the deviation from the null expectation was much more pronounced for translocated species. Indeed, contrary to exotic species, the observed distribution of translocated species is mainly asymmetric (i.e. introduction pathway from eastern to western Europe). In contrast, our simulations generated symmetrical distribution patterns by allowing all the translocated species to colonize all the basins where they did not naturally occur (i.e. in both western and eastern Europe). This produced therefore different 'null subsets' of translocated species across Europe and hence an overall decrease in community similarity among initially similar basins (see Rahel, 2002; Olden & Poff, 2004).

Although TH is commonly presented as the average change in community similarity among regions of a given biogeographical area (e.g. Rahel, 2000; Taylor, 2004; Olden, 2006), complementary information can be obtained by quantifying TH at the regional scale (as expressed by Basin ΔCS). Indeed, when considering both exotic and translocated species, our spatial autocorrelation analysis revealed that neighbouring basins tend to display more similar rates of homogenization/differentiation than distant basins. This results in greatest rates of homogenization for south-western basins and greatest rates of differentiation for north-eastern basins (see Fig. 1b). Such a latitudinal pattern of TH is consistent with the introduction pathways of fish species in Europe, recently analysed by García-Berthou *et al.* (2005). These authors reported a higher ratio of received to given introductions in southern countries and a lower one in northern countries. Particularly, numerous non-European and European fish species were introduced from France to the Iberian Peninsula (García-Berthou *et al.*, 2005; Clavero & García-Berthou, 2006), which differs from the rest of Europe by its low number of native species and high level of fish endemism (Doadrio, 2002). This explains why French and Iberian basins experienced similar changes in their species composition (i.e. homogenization, see Fig. 1b). Similarly, a significant latitudinal gradient of TH was observed when analysing the individual effect of exotic species (see Fig. 1c), except that fish fauna homogenization occurred only in southern Europe (i.e. the Garonne and Pô river basins and the basins of the Iberian Peninsula). Overall, the European river basins were homogenized or differentiated independently of the number of exotic species as almost all of the observed rates of homogenization/differentiation per basin differed from those expected by the null model. This was confirmed by the lack of a significant linear relationship between the observed rates of homogenization/differentiation per basin and the number of exotic species. In contrast, our spatial autocorrelation analysis revealed that the homogenization pattern resulting from translocated species did not match a latitudinal gradient as it did for exotics (Fig. 1d). However, we noticed that the nearby Ebro, Pô, and French river basins displayed the highest rates of homogenization. These basins are also characterized by numerous translocated species (9.8 species on average, $n = 6$) compared to other basins (2.4 species on average, $n = 19$). This suggests that the number of translocated species strongly influenced the rate of homogenization in each basin. Indeed, we found that (i) almost none of the rates of homogenization per basin differed from those expected by the null model and (ii) the rate of homogenization per basin was significantly related to the number of translocated species. Although we showed that the rate of homogenization in a given basin could be accurately predicted by the number of translocated species, we do not encourage future studies to explore geographical patterns of TH only on the basis of the number of invaders. Indeed, we clearly demonstrated that for exotics, this conclusion was not accurate. This implies that tracing the identity of species (and not the number of species) is a fundamental prerequisite for quantifying the changes in community similarity among localities (e.g. Olden & Rooney, 2006; Qian & Ricklefs, 2006; Smart *et al.*, 2006).

Overall, our results are consistent with previous studies exploring patterns of BH over large spatial scales (i.e. region,

continent), especially for plants (e.g. Rejmánek, 2000; Schwartz *et al.*, 2006). Indeed, we showed that non-native fish species produced differentiation among neighbouring basins (i.e. with high initial similarity) and homogenization among distant ones (i.e. with low initial similarity). According to Marchetti *et al.* (2001), these opposite patterns (homogenization vs. differentiation) can be also explained by the spatial scale of the study. Here we highlight that when considering a single spatial scale, distinguishing between exotic and translocated species produced opposite patterns whatever the distance is between basins. When discussing BH, the place of origin of non-native species constitutes therefore a crucial consideration, together with distance between sites and spatial scale.

The overall differentiation effect of exotic freshwater fish in Europe contrasts with that recently reported on plants by Qian & Ricklefs (2006). Indeed, exotic plant species (i.e. originating from outside North America) introduced in North American provinces had an overall homogenization effect, due to a lower spatial turnover rate than the natives. Such a difference between our results and those of Qian & Ricklefs (2006) can be related to intrinsic differences between fish and plants. Indeed, freshwater fish can hardly disperse from one basin to another without human transports as river basins are separated by barriers insurmountable for fish. In contrast, plants can naturally disperse after introduction due to well-known passive dispersal mechanisms (e.g. winds, animals). The role of dispersion should therefore be considered in future homogenization studies by conducting cross-taxonomic comparisons within and between regions.

Recently, Rooney *et al.* (2007) addressed whether measures of BH were relevant to conservation efforts. They highlighted that conservation significance of BH depends on the scale of the study. The introduction of non-native fish species in European basins promoted the greatest homogenization of species composition in south-western Europe. This should be interpreted with caution as it can result from two distinct scenarios: (i) invasion of non-native species and extinction of native species leading to a biotic impoverishment or (ii) invasion without extinction of native species (see Olden & Poff, 2003, 2004). The current situation in the major European river basins follows the second scenario as no basin-scale extinctions were recorded. However, in southern Europe, several studies reported declines and extirpations of native and endemic fish species at local scales (i.e. in localities within a river basin) due to the spread of non-native species (Bianco, 1995; Elvira & Almodóvar, 2001). Moreover, the process of extinction itself may occur on a much longer timescale than invasions, which would make the perceived impact of invasions dependent on the timescale of observation (Sax *et al.*, 2002). Although our basin scale approach does not permit to quantify the risks of biotic impoverishment, it indicates that southern European basins are the most prone to homogenization. Indeed, ongoing fish invasions (Clavero & García-Berthou, 2006), combined with the spread of the highly seasonal Mediterranean climate in southern Europe, may increase the risk of extinction for endemic fish that are already threatened (Reynolds *et al.*, 2005; Griffiths, 2006). A particular attention should therefore be given to the outcome of fish invasions in southern European basins that are recognized as hotspots of fish diversity in Europe (Reyjol *et al.*, 2006).

CONCLUSION

In this study, we clearly showed that exotic and translocated fish species generated distinct geographical patterns of BH across Europe because of their contrasting effects on the changes in community similarity among river basins. Therefore, pooling translocated and exotic species as is commonly done in homogenization studies (e.g. Marchetti *et al.*, 2001; Rooney *et al.*, 2004; Castro *et al.*, 2006; Smith, 2006) can introduce a major drawback in the quantification of the geographical pattern of TH. We therefore recommend that future efforts in homogenization studies focus on making a clear distinction between exotic and translocated species to accurately assess the spatial dynamics of BH.

Comparing the observed TH patterns to those expected by a null model empirically demonstrated that BH is a non-random ecological pattern, therefore providing evidences in favour of previous assumptions (McKinney & Lockwood, 1999; Duncan & Lockwood, 2001; Olden *et al.*, 2004). Because species invasions and extinctions are likely to continue increasing over time with increasing human activities (Sala *et al.*, 2000), we expect that homogenization of the world biota will also continue to intensify. We feel that the null model approach presented here has useful implications in the field of conservation biology and biogeography. Indeed, null models were lacking in the exploration of BH, whereas these models have long been applied to testing large-scale ecological patterns (e.g. Connor & Simberloff, 1978). We invite biogeographers and ecologists to extend our null model approach to other empirical data involving both species invasions and extinctions. This will enable a relationship to be established between each scenario of the mechanistic model of Olden & Poff (2003) and a rigorous null model. We also encourage future researches to apply other algorithms generating null distributions of non-native and extinct species such as those with fixed rows and columns sums that account for both interspecies differences and environmental variability among localities (i.e. the swap algorithm, Gotelli, 2000). However, such an algorithm cannot be easily achieved as it requires reshuffling translocated species only in the localities where they did not naturally occur. Specific algorithms should be developed in this aim.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Bibliographic sources used to set up the freshwater fish database of the 25 major European river basins.

This material is available as part of the online article from http://www.blackwell-synergy.com/doi/abs/10.1111/j.1472-4642.2007.00409.x
(This link will take you to the article abstract).

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