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To cite this article: Andrea Castaño-Sánchez, Laura Valencia, José M. Serrano & Juan A. Delgado (2018) Species introduction and taxonomic homogenization of Spanish freshwater fish fauna in relation to basin size, species richness and dam construction, Journal of Freshwater Ecology, 33:1, 347-360, DOI: [10.1080/02705060.2018.1503101](https://doi.org/10.1080/02705060.2018.1503101)

To link to this article: <https://doi.org/10.1080/02705060.2018.1503101>



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Published online: 13 Nov 2018.



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Species introduction and taxonomic homogenization of Spanish freshwater fish fauna in relation to basin size, species richness and dam construction

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ABSTRACT

The introduction of exotic species is a key global threat to biodiversity. Beyond an increased risk of native species extinction, there exists a loss of biodiversity distinctiveness. Nevertheless, quantitative information on biotic homogenization at the taxonomic level in relation to basin features is rare. We used freshwater fish distribution data in Spain at three different time periods (1952, 1995, and 2007) to assess the species introduction process and the temporal dynamics of taxonomic homogenization among river basins in relation to basin size, native species richness and dam construction variables. The degree of alteration of original faunas by species introduction has increased through time, especially in native richer species, which suggest that the number of non-native and native species covariate with environmental heterogeneity. On the other hand, neither basin size nor habitat modification by dam construction seems to explain the number of introduced species. Our results indicate that the taxonomic homogenization of Spanish fish fauna is a temporally and spatially dynamic process; initial local increases in β -diversity through species introduction could be blurred because of scaling to regional and national levels or by the continuous expansion of a reduced number of exotic species.

ARTICLE HISTORY

Received 18 January 2018
Accepted 17 July 2018

KEYWORDS

Biotic homogenization;
 β -diversity; fish
conservation; multiple-site
similarity index

Introduction

The introduction of non-native species into an ecosystem, have become a widespread problem with important implications for wildlife conservation (Simberloff et al. 2013; Giakoumi et al. 2016). A large number of introduced non-native species in a region increase the likelihood that some of them became an invader. At a global scale, the introduction of species is leading to a loss of biodiversity (α -diversity or species richness) through its contribution to native species extinction (Clavero and García-Berthou 2005;

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Didham et al. 2007; Sax and Gaines 2008), although at a regional scale usually increases biodiversity while at the local scale, both an increase and a decrease in biodiversity are possible (Sax and Gaines 2003). In addition to these changes in species richness, both biotic homogenization and differentiation are possible depending on the interactions between introduced species, native species and the environment (Olden and Poff 2003).

The occurrence of these events may not necessarily be independent since the introduction of non-native species can promote extinctions through predation or competition (Elvira and Almodóvar 2001; Blanchet et al. 2007; Sax and Gaines 2008); or can promote new introductions. For example, the introduction of large-sized predatory game fishes is usually associated with the introduction and translocation of small-sized fish species. These species may be intentionally introduced as forage fish for predatory species or, on the other hand, accidentally introduced when being used as living bait (Elvira and Almodóvar 2001; Ribeiro et al. 2008). In addition, scale relationships are also implicated; taxonomic differentiation prevails at a local scale (Cassey et al. 2007) while homogenization prevails at large scales (Olden and Poff 2004; Clavero and García-Berthou 2006; Baiser et al. 2012), mainly due to the introduction of widespread invaders (Rahel 2000; Vitule et al. 2009; Watanabe 2010; Vitule et al. 2012; Daga et al. 2015; Liu et al. 2017).

Spatial scale is also linked to the perception of the relationship between the invasion process and the original community α -diversity. Communities that are more diverse should have fewer niche opportunities for invaders (Case 1990; Knops et al. 1999; Stachowicz et al. 1999; Levine 2000; Kennedy et al. 2002; Brown and Peet 2003). In large-scale observational studies, positive relationships between native species richness and the number of introduced species have been explained through extrinsic factors; sites with favorable conditions for natives also have favorable conditions for exotics (Levine and D'Antonio 1999; Shea and Chesson 2002; Davies et al. 2005; Fridley et al. 2007).

Nevertheless, introduction of species is not the only driver for changes in species composition within a community. Habitat loss quality has been cited as a main driver of biodiversity loss (Lönnerstedt et al. 2014; Göthe et al. 2015) but it also may favor an increase in the number of introduced species (Didham et al. 2007; Hermoso et al. 2011; Schliserman et al. 2014; Light and Moyle 2015). Therefore, both drivers should be considered simultaneously for a more accurate assessment of changes in α - and β -diversity.

Introduction of non-native species is considered a relevant threat to the conservation of freshwater fish (Clavero and García-Berthou 2005; Light and Marchetti 2007; Darwall et al. 2008; Vitule et al. 2009; Leunda 2010; Hermoso and Clavero 2011; Olden et al. 2018). But it is not the only threat since flow modification, habitat degradation, water pollution and over-exploitation produced by human activities are also included as major threats (Dudgeon et al. 2006). Likely, the most widely distributed anthropogenic alteration of freshwater ecosystems is dam construction, which cause fragmentation within a basin, modify natural flow regimes and disrupt sediment transportation (Osmundson et al. 2002; Leprieur et al. 2008; Renöfält et al. 2010, Liu et al. 2012). In addition, reservoirs themselves have been reported to favor the dispersal and establishment of introduced species (Johnson et al. 2008; Skóra et al. 2015; Liew et al. 2016; Casimiro et al. 2017). And variables related to reservoir morphology such as reservoir capacity have been found to be inversely correlated to biotic integrity (Moyle and Randall 1998). These effects may be grouped under the 'human activity' hypothesis, which predict that human activities promote the establishment of introduced species (Taylor and Irwin 2004).

Nevertheless, there are other two main hypothesis explaining non-native species numbers in a community, both involving the number of native species: the 'biotic resistance' hypothesis that predicts lower number of non-native species in species-rich communities

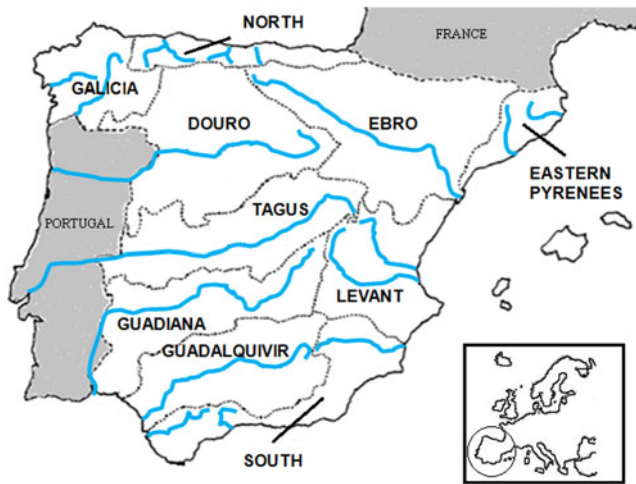


Figure 1. Map showing the Spanish basins from which data on freshwater fish distributions were gathered.

than in species poor communities (Elton 1958); and the ‘biotic acceptance’ hypothesis, that predicts that habitats favoring native species should favor also non-native ones (Fridley et al. 2007). In the current study, we tested these three hypothesis to explain spatial and temporal changes in α - and β -diversity in Spanish freshwater fish communities. To this aim, we used three published data sets (1952, 1995 and 2007) on the presence of stable population of fish species in the 10 main Spanish biogeographical basins. From these data, we established a temporal pattern of fish fauna alteration from the original communities to the current, describing the patterns of homogenization among basins. We used number of reservoirs and total reservoir capacity as proxies for human activity and predict a positive effect on the number of exotic species. We used basin size (as a proxy of habitat heterogeneity) and native fish species richness to test the ‘biotic acceptance’ hypothesis, predicting positive relationships with the number of non-native fish species. Finally, we test the ‘biotic resistance hypothesis’ using also native fish species richness, predicting a negative relationship with the number of non-native fish species. In addition, since the accumulation of changes could mask differences, we also considered temporal variations in α - and β -diversity.

Material and methods

Study area

Continental Spain comprises ten main biogeographical basins covering roughly 5×10^5 km² (Elvira 1995; Figure 1). We obtained data on the presence or absence of the different fish species in each basin and their status as native (N), exotic (non-native) for Spain (E) or translocated (T; native for Spain but non-native for that basin) according to the best available information (Table 1). Only native species with permanent inland populations were used for this study, diadromus species (anadromous, catadromous or amphidromous) were not considered. The presence of non-native species in a basin were considered only when well-established populations were reported. Although four basins are shared with Portugal, all data refer to the Spanish territory, included data on basin area [<http://hispagua.cedex.es/en/instituciones/demarcaciones> (accessed 6/04/2017)].

Table 1. Spanish freshwater fish species, including their status: native (N), exotic (E) or translocated (T) in the different selected basins in the three studied periods.

	Spain	NO	GA	DO	TA	GN	GL	SO	LE	EB	PY
<i>Lampetra planieri</i> (Bloch 1784)	N	N									
<i>Achondrostoma arcasii</i> (Steindachner 1866)	N		N	N	N	T			N	N	
<i>Achondrostoma salmantium</i> (Doadrio and Elvira 2007)	N			N							
<i>Anaocypris hispanica</i> (Steindachner 1866)	N					N	N				
<i>Barbus haasi</i> (Merterns 1924)	N							N	N	N	
<i>Barbus meridionalis</i> (Risso 1826)	N										N
<i>Gobio lozanoi</i> (Doadrio and Madeira 2004)	N	N	T	N	T	T	T	T	T	N	T
<i>Iberochondrostoma lemmingii</i> (Steindachner 1866)	N				N	N	N				
<i>Iberochondrostoma oretanum</i> (Doadrio and Carmona 2003)	N						N				
<i>Iberocypris alburnoides</i> (Steindachner 1866)	N			N	N	N	N				
<i>Iberocypris palaciosi</i> (Doadrio 1980)	N						N				
<i>Luciobarbus bocagei</i> (Steindachner 1865)	N		N	N	N						
<i>Luciobarbus comiza</i> (Steindachner 1865)	N				N	N					
<i>Luciobarbus graellsii</i> (Steindachner 1866)	N	N							N	N	N
<i>Luciobarbus guiraonis</i> (Steindachner 1866)	N					N			N		
<i>Luciobarbus microcephalus</i> (Almaça 1967)	N					N					
<i>Luciobarbus sclateri</i> (Günther 1868)	N					N	N		N		
<i>Parachondrostoma arrigonis</i> (Steindachner 1866)	N								N		
<i>Parachondrostoma miegii</i> (Steindachner 1866)	N	N			N				N	N	T
<i>Parachondrostoma turiense</i> (Elvira 1987)	N								N		
<i>Phoxinus bigerri</i> (Kottelat 2007)	N		N	T						N	N
<i>Pseudochondrostoma duriense</i> (Coelho 1985)	N	N	N	N							
<i>Pseudochondrostoma polylepis</i> (Steindachner 1865)	N				N			T	T		
<i>Pseudochondrostoma willkommii</i> (Steindachner 1866)	N					N	N	N			
<i>Squalius carolitertii</i> (Doadrio 1987)	N		N	N	N						
<i>Squalius castellanus</i> (Doadrio, Perea y Alonso, 2007)	N				N						
<i>Squalius laietanus</i> (Doadrio, Kottelat y de Sostoa 2007)	N									N	N
<i>Squalius malacitanus</i> (Doadrio and Carmona 2006)	N							N			
<i>Squalius pyrenaicus</i> (Günther 1868)	N				N	N	N	N	N	N	
<i>Squalius valentinus</i> (Doadrio and Carmona 2006)	N								N		
<i>Tinca tinca</i> (L. 1758)	N			N	N	N			N	N	
<i>Cobitis calderoni</i> (Bacescu 1961)	N			N	N					N	
<i>Cobitis paludica</i> (De Buen 1930)	N	T	T	N	N	N	N	N	N	N	
<i>Cobitis vettonica</i> (Doadrio and Perdices 1997)	N				N						
<i>Barbatula quignardi</i> (Bacescu-Mester 1967)	N	N		T						N	
<i>Salmo trutta</i> (L. 1758)	N	N	N	N	N	T	N	N	N	N	N
<i>Aphanius iberus</i> (Valenciennes 1864)	N							N	N	N	N
<i>Aphanius baeticus</i> (Doadrio et al. 2002)	N						N	N			
<i>Valencia hispanica</i> (Valenciennes 1864)	N								N	N	N
<i>Atherina boyeri</i> (Risso 1810)	N						N	N	N	N	N
<i>Gasterosteus gymnurus</i> (Cuvier 1829)	N	N	N						N	N	N
<i>Syngnathus abaster</i> (Risso 1810)	N								N	N	
<i>Cottus hispaniolensis</i> (Bacescu and Bacescu-Mester 1964)	N									N	
<i>Cottus aturi</i> (Freyhof et al. 2005)	N	N									
<i>Salaria fluviatilis</i> (Asso 1801)	N					N		N	N	N	N
<i>Carassius auratus</i> (L. 1758)	E	E	E	E	E	E	E	E	E	E	E
<i>Cyprinus carpio</i> (L. 1758)	E	E	E	E	E	E	E	E	E	E	E
<i>Rutilus rutilus</i> (L. 1758)	E									X	E
<i>Scardinius erythrophthalmus</i> (L. 1758)	E					E				E	E
<i>Ameiurus melas</i> (Rafinesque 1820)	E			X	X	E			E	E	E
<i>Esox lucius</i> (L. 1758)	E	X	E	E	E	E	E	E	E	E	E
<i>Oncorhynchus mykiss</i> (Walbaum 1792)	E	E	E	E	E	E	E	E	E	E	E
<i>Salvelinus fontinalis</i> (Mitchell 1814)	E	E		X	E					E	
<i>Gambusia holbrooki</i> (Agassiz 1859)	E		E	E	E	E	E	E	E	E	E
<i>Lepomis gibbosus</i> (L. 1758)	E			E	E	E	E	E	E	E	E
<i>Silurus glanis</i> (L. 1758)	E									E	
<i>Hucho hucho</i> (L. 1758)	E			E							
<i>Fundulus heteroclitus</i> (L. 1766)	E					X	E	E		E	
<i>Perca fluviatilis</i> (L. 1758)	E				E					E	E
<i>Sander lucioperca</i> (L. 1758)	E			E	E				E	E	X
<i>Micropterus salmoides</i> (Lacépède 1802)	E	E	E	E	E	E	E	E	E	E	E

(continued)

Table 1. Continued.

	Spain	NO	GA	DO	TA	GN	GL	SO	LE	EB	PY
<i>Cichlasoma facetum</i> (Jenyns 1842)	E					E					
<i>Alburnus alburnus</i> (L. 1758)	E			E	E	E	E	E	E	E	E
<i>Oncorhynchus kisutch</i> (Walbaum 1792)	E			E							
<i>Misgurnus anguillicaudatus</i> (Cantor 1842)	E									E	E
<i>Abramis bjoerkna</i> (Linnaeus 1758)	E								E		
<i>Ictalurus punctatus</i> (Rafinesque 1818)	E									E	
<i>Aphanius fasciatus</i> (Nardo 1827)	E									E	
<i>Poecilia reticulata</i> (Peters 1859)	E								E		
<i>Cobitis bilineata</i> (Canestrini 1865)	E										E
<i>Pseudorasbora parva</i> (Temminck and Schlegels 1846)	E									E	
<i>Acipenser baeri</i> (Brandt 1869)	E						E				

Regular font for the status in 1952 (IFIE 1952; García-Berthou and Moreno-Amich 2000), bold for the status in 1995 (Elvira 1995; Doadrio and Aldeguer 2007), and grey for the status in 2007 (Doadrio and Aldeguer 2007). Only species with permanent inland populations were considered. Changes in scientific names and taxonomic status were corrected for all datasets following Doadrio and Aldeguer (2007).

Basin codes: DO, Douro; TA, Tagus; GN, Guadiana; GU, Guadalquivir; EB, Ebro; NO, North; GA, Galicia; SO, South, LE, Levant; PY, Eastern Pyrenees.

X: Exotic species extirpated in 1995 but present in 1952.

X: Exotic species extirpated in 2007 but present in 1995.

We made a complete data set of native and exotic fish species present in each basin at three different temporal points (1952, 1995 and 2007) using data provided in published taxonomic list for all Spanish territory. Only these temporal points were used because there exist reliable published datasets about the distribution of the whole Spanish fish fauna, including native and exotic species. The 2007 dataset was gathered from a report on the status of Spanish fish fauna (Doadrio and Aldeguer 2007). The 1995 dataset was obtained from a study on the zoological integrity of the main Spanish biogeographical basins (Elvira 1995); the 1952 dataset were composed from data collected from a list of species from many different sample points around Spanish geography (IFIE 1952) and a paper reviewing several historical introductions of exotic fishes in the Eastern Pyrenees basin (García-Berthou and Moreno-Amich 2000). Divergencies among lists were solved considering the most recent data source. We considered changes in scientific nomenclature and taxonomic status that have taken place during this long period following Doadrio and Aldeguer (2007). These changes include the modification of the taxonomic affiliation of many native Cyprinidae species passing from 20 native species cited in Elvira (1995) to 30 native species cited in Doadrio and Aldeguer (2007). Within these changes it must be stressed the taxonomic status of *Gobio lozanoi*, that was formerly considered as *Gobio gobio* L. a species exotic for Spain but based on genetic studies has recently been considered as a new native species for Spain (Doadrio and Madeira 2004). More native species were also included along the studied period belonging to different families. *Cobitis vettonica* in the Cobitidae family (Doadrio and Perdices 1997); *Aphanius baeticus* in the Cyprinodontidae family (Doadrio et al. 2002) and *Cottus aturi* (Freyhof et al. 2005) in the Cottidae family. All these new accepted native species were included in all the datasets.

The list of historical fish fauna in Spain was elaborated considering only native species, since there has been not reported extinction of native species with permanent inland populations in the main biogeographical basins considered in this study (Elvira 1995, Doadrio and Aldeguer 2007).

Data on number of dams constructed and reservoir capacity were obtained consulting two online databases [<http://www.embalses.net/> and <http://www.seprem.es/presases.php>

(accessed 6/04/2017)]. We calculated total number of dams and total reservoir capacity per each basin at each studied temporal point (1952, 1995 and 2007).

Statistical analysis

We assessed changes in the number of exotic species through stepwise regression analysis, with basin size, number of native species, number of reservoirs and total reservoir capacity as independent variables. All variables were log-transformed to achieve normality and homoscedasticity assumptions. Because of low sample size (only ten biogeographical basins in Spain), we considered as significant models with $p < .1$ in order to decrease Type II error due to low statistical power (Zar 1996).

To assess variations in β -diversity, we analyzed the taxonomic similarities of communities at the community composition level (i.e. using presence-absence data) in two ways: (1) considering only native species; and (2) using all species on the three different dates. Data from the first analysis allow the assessment of the degree of differentiation of original communities. This information combined with that from the second analysis allows the assessment of the variation in taxonomic homogenization patterns over time.

Therefore, we measured the taxonomic similarity of fish communities for the historical composition (only native species), and for the 1952, 1995 years 2007 datasets. First of all, we make comparisons among pairs of basins using the Jaccard's similarity index, which provides the proportion of shared species between two basins in relation to the total number of species present in those basins. This index varies from 0 (no shared species) to 1 (identical species composition). Nevertheless, since pairwise dissimilarities do not account for patterns of co-occurrence among more than two sites, we also calculate both: (1) the Whittaker's beta, $\beta_w = S_T / \bar{S}_{\text{within}}$, where S_T is total number of species and \bar{S}_{within} is the average species richness for the A_1 to A_T sites; and 2) a Sørensen based multiple-site similarity index proposed by Diserud and Ødegaard (2007).

$$C_S^T = \frac{T}{T-1} \left(1 - \frac{S_T}{\sum_i a_i} \right)$$

where S_T is the total number of species and a_i is the number of species in site A_i , $i = 1, \dots, T$. Greater values of this index indicate that there are few species differences between sites, and then, lower β -diversity values.

Results

α -Diversity analyses

Our study showed 45 native species from 11 different taxonomic families (Table 1) with most species (66.7%) belonging to the Cyprinid family. There was a weak positive correlation between area and the number of native species (log transformed values; $r = 0.59$, $p = .07$).

The number of exotic species increased over time (Table 1). The taxonomic origin of the 27 exotic species was diverse (12 families) and again the Cyprinid family was the most highly represented (25.9%).

Regressions results showed that the number of exotic species was not related to any independent variables considered using data from 1952. Nevertheless, the analyses of the

Table 2. Results of multiple regression analysis to explain the number of exotic species in Spanish river basins for the 1995 and 2007 datasets; analysis on 1952 dataset resulted in no significant model.

Dataset	Model	R^2	F	B (standardized)	t	p value
1995	Native	0.371	4.722	0.609	2.173	.062
2007	Native	0.462	6.878	0.680	2.623	.031

other data sets showed that the number of native species was the only variable explaining the number of exotic species (Table 2).

Homogenization of fish faunas

The distribution of changes in similarity in relation to original fish faunas is being displaced to positive values from the 1952 to the 2007 dataset (Figure 2). Positive increments over 20% are absent in the 1952 dataset but are progressively larger from the 1995 to the 2007 datasets. Furthermore, negative values showing decreases in similarity among basins is only relevant in 1952, when species introduction decreases similarity in 17 comparisons from 45. Nevertheless, negative values almost disappear in the rest of the years with only 3 and 1 negative values for the 1995 and 2007 data sets, respectively. In addition, the averaged values of Jaccard index of the 45 pairwise combinations of the 10 Spanish biogeographical basins are increasing with time (Table 3). All these results suggest that similarity in fish fauna composition among basins is increasing from historical times to nowadays. The same idea could be derived from the assessment of the variation with time of the averaged values of the Jaccard index comparisons, the multiple-site similarity index, and the values of Whittaker's β -diversity (Table 3). None of these parameters detected an increase in β -diversity from historical conditions (only native species) to 1952, derived from decreases in similarity among basins detected in that period.

Discussion

Results show that the number of exotic species is increasing with time and that basins with higher native species richness presented also higher number of exotic species. This result gives support to the 'biotic acceptance' hypothesis and suggesting the rejection of the 'biotic resistance' hypothesis. This last hypothesis predicts a negative relationship between native species richness and the number of exotic species, especially when basin size is controlled, since there should be fewer niche opportunities for invaders (Elton 1958). Or, alternatively, because the extinction of native species through predation by or competition with exotic species (Yonekura et al. 2004). Nevertheless, there have been no native species extinction at the main basin scale in our study. In this introduction-only scenario, 'biotic acceptance' hypothesis is more likely to be supported (Fridley et al. 2007). In addition, at large spatial scales, both, native and non-native species richness, should be positively correlated with habitat heterogeneity (Davies et al. 2005). Nevertheless, we have not found a positive relationship between basin area and non-native species richness, which suggest that more reliable indicators of habitat heterogeneity and energy availability other than basin size should be included in the analysis. The use of geographical, climatic, and hydrological variables such as altitudinal range and dendritic configuration could be useful to further test the 'biotic acceptance' hypothesis.

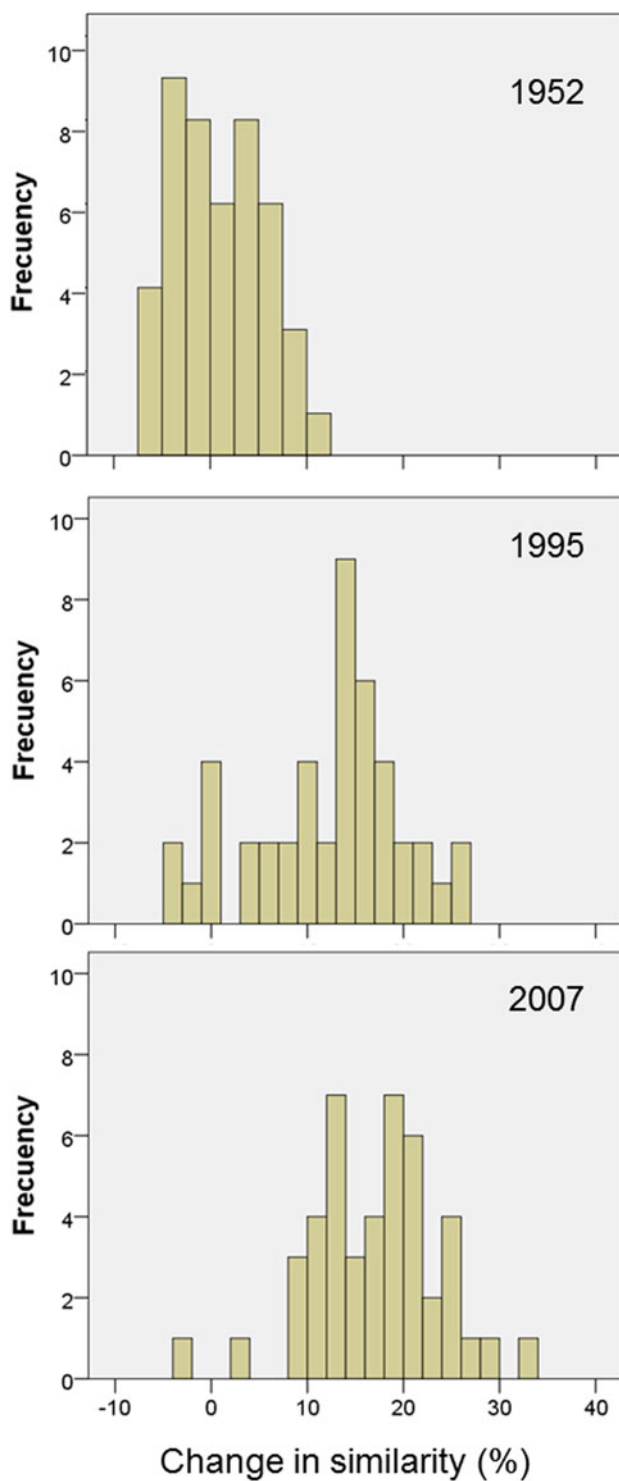


Figure 2. Changes in similarity of fish faunas among 45 pairwise combinations of the 10 Spanish biogeographical basins. Data show differences in the Jaccard index values when comparing historical communities to those obtained with databases from different years.

Table 3. Variation of taxonomic similarity and β -diversity in Spanish basins through time.

Date	Averaged Jaccard index	Multiple similarity index	Whittaker's β diversity
Historical	0.204 \pm 0.128	0.714	3.462
1952	0.212 \pm 0.121	0.717	3.438
1997	0.323 \pm 0.130	0.786	2.864
2007	0.370 \pm 0.095	0.790	2.880

Our results do not support the 'human activity' hypothesis, since the presence and size of reservoirs did not correlate with the number of exotic species. This effect was expected since dam construction introduced a permanent lentic freshwater habitat absent in most Spanish fluvial systems (Berga-Casafont 2003), opening new niche opportunities for species. The construction of dams in Spain until 1955 was mainly for water supply or irrigation. After 1955, the rapid construction of dams for hydroelectrical power doubled the number of dams and increased their total capacity by sixfold (Berga-Casafont 2003). Dam construction modifies disturbance regimes and is one of the main causes of habitat degradation, dampening the temporal and spatial variability characteristic of Mediterranean fluvial systems (Gasith and Resh 1999; Magalhães et al. 2002; Poff et al. 2007). Although this kind of habitat degradation has been shown to play a role in freshwater diversity loss, this may be an indirect effect through the facilitation of the establishment of exotic species (Corbacho and Sánchez 2001; Johnson et al. 2008; Hermoso et al. 2011).

Reservoirs could favor the presence of several lymnophilic exotic species as, *Carassius auratus*, *Cyprinus carpio*, *Esox lucius*, *Micropterus salmoides*, *Lepomis gibbosus* and *Alburnus alburnus* (Elvira 1995). The first fish introductions in Spain (s. XVII) were *C. carpio* and *C. auratus*, linked to their use in ornamental pools (Elvira and Almodóvar 2001; Doadrio et al. 2011). Both species are well adapted to lentic habitats and are introduced to reservoirs by sport fishing because of the large size of the former and the use as bait of the latter. And, although a second wave of introductions were performed by environmental authorities to promote sport fishing activities, many other species have been introduced or translocated illegally (García-Berthou et al. 2005; Doadrio et al. 2011). In fact, dam construction has been reported to be correlated to the introduction of exotic species (Johnson et al. 2008). In addition, fish communities in reservoirs are more affected by species introduction than are those from fluvial ecosystems (Clavero and Hermoso 2011) or natural lakes (Johnson et al. 2008). This fact has been explained by an increase in propagule pressure due mainly to illegal introductions related to recreation activities (Elvira and Almodóvar 2001; Johnson et al. 2008; Ribeiro et al. 2008; Vitule et al. 2014).

Nevertheless, there was several extinctions of exotic species in basins where they were introduced, *Ameiurus melas* became extinct in two basins and *Rutilus rutilus*, *Salvelinus fontinalis*, *Fundulus heteroclitus* and *Sander lucioperca* in one basin). The analysis of the causes of the success and the fail of this introductions in the different basins could be useful to assess the vulnerability of basins to introduction and to evaluate the invasive risk of species. This analysis could be performed in the context of the phylogenetic relationships among exotic and native species within each basin attending to increased competition between relatives, 'Darwins' naturalization hypothesis', or shared adaptative traits, 'adaptation hypothesis' (Skóra et al. 2015). This analysis will be also valuable because will include the study of functional homogenization that has been studied less more than taxonomic homogenization (Olden et al. 2018).

Species introduction and homogenization dynamics

The freshwater fish fauna of Spain has been subjected to a taxonomic homogenization process due mainly to the widespread introduction of exotic species, but also to translocation of species (native for Spain) among basins. The homogeneity of species as measured by the Jaccard's similarity index increased 16.6% from historical conditions to those of 2007. These values are like those obtained by Marchetti et al. (2001) for California zoogeographic provinces (20.3%) and higher than those reported for the continental United States (7.2%; Rahel 2000); 13 Canadian provinces and territories (1.2%; Taylor 2004); 27 regions in Japan (9%; Watanabe 2010); major drainages in Australia (3%; Olden et al. 2008) and the Parana river (a total of 10.5%, 6–7.5% only considering a dam construction; Vitule et al. 2012). Average values for all basins were nearly identical to those obtained by Clavero and García-Berthou (2006) in the Iberian Peninsula (Spain and Portugal) in 2001. The inclusion of data from Portugal was expected to have no influence on the results because no additional basins were included and almost all species are shared with Spain.

The observed pattern of biotic homogenization agrees with predictions of a scenario without native extirpations and the spread of non-native species in different regions (Olden and Poff 2003). Although the introduction of species led to an increase in the taxonomic homogeneity, this variation was not homogeneous over time but rather seemed to accelerate. We detected relevant biotic differentiation in Spanish fish fauna in the 1952 dataset. Most of this variation was due to species introductions performed between 1910 and 1913 by environmental authorities to improve the economic value of natural fish populations (García-Berthou and Moreno-Amich 2000; Doadrio 2002). In 1995 and 2007 datasets, only a few basin pair comparisons were negative, in other words, only in few cases, species introductions produced faunas more different at that time than historically were. These results agree with those reported for California (Marchetti et al. 2001), Canada (Taylor 2010), Australia, river basins of north-eastern Australia (Olden et al. 2008) and the Iberian Peninsula (Clavero and García-Berthou 2006). It was suggested that the similar patterns of biotic homogenization in California and the Iberian Peninsula is due not only to the shared abiotic (Mediterranean climate) and biotic features (biogeographical isolation, high endemism), but also to the link between dam construction and fish introductions (Clavero and García-Berthou 2006). Nevertheless, no relationship between homogenization and dam construction seems to be revealed by our data.

It must be stressed that the observed changes in the effects of species introduction over the changes in taxonomic similarity, with biotic differentiation first and biotic homogenization later, could be detected only because of the use of a temporal approach. The loss of the particularities in homogenization processes produced by initial species introductions were lost quickly, likely due to the transfer of the same exotic species to other basins. Furthermore, these effects of similarity decrease in some basin comparisons were not relevant for β -diversity values, since their integration at larger spatial scales were compensated by similarity increases in other pairwise comparisons.

Therefore, the results of this study suggest that homogenization is a temporally and spatially dynamic process. The temporal resolution (i.e. both total period covered by data and the length of the intervals) could affect the perception of the homogenization process as previously suggested by other authors (Radomski and Goeman 1995; Olden and Poff 2003; Rooney et al. 2004; Clavero and García-Berthou 2006). The spatial scale could blur the effects of species introduction at local scales and, therefore, it should be considered when comparing results from different studies. In addition, the assessment of pairwise comparisons as a complementary tool of multiple similarity and β -diversity indexes should be useful.

The taxonomic homogenization process due to species introduction is expected to continue in Spanish river basins, since several species typical of reservoirs are not in all basins. In addition, the ability of a basin to incorporate more exotic species could depend mainly on habitat heterogeneity. Including spatial heterogeneity in our analytical approaches could reveal straighter forward relationships with the number of exotic species. Finally, we stress the need of performing studies on finest temporal scales, since in our study we only have reliable list for three periods. The inclusion of more, shorter time periods and larger total temporal extent, will increase statistical power. These studies would confirm whether basins with different characteristics follow different temporal homogenization trajectories, assessing its utility in predicting the temporal dimension of basin vulnerability.

Acknowledgements

We would like to thank to F. Morcillo and F. Aranda for helping us to find relevant information on dam construction. We also thank an anonymous referee for their constructive comments that help to improve an early version of this manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Community of Madrid [REMEDINAL3-CM (S2013/MAE-2719)].

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