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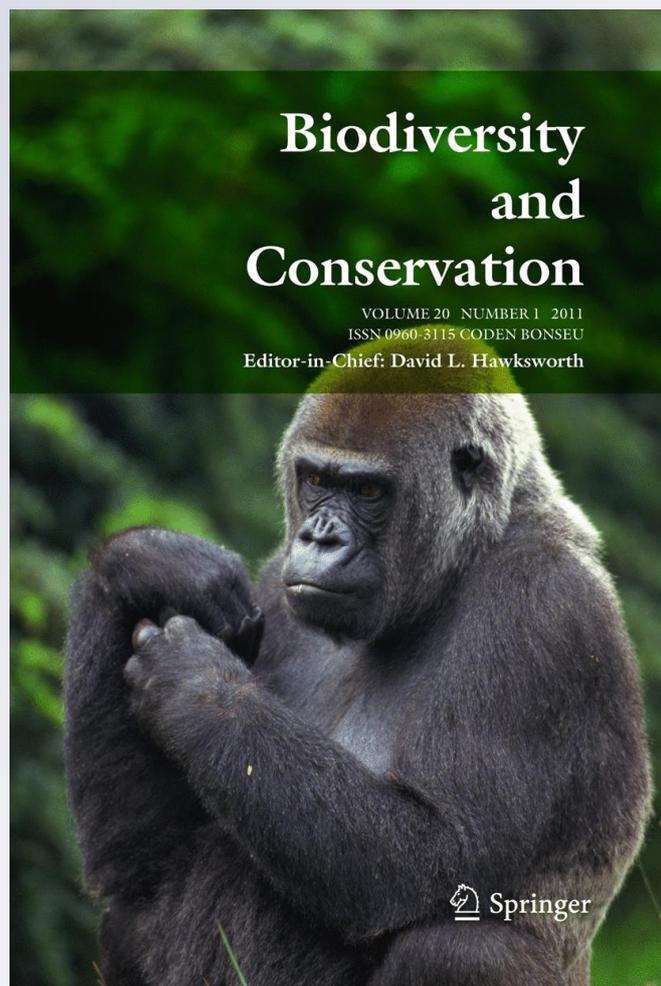
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Reservoirs promote the taxonomic homogenization of fish communities within river basins

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Abstract Most studies analyzing patterns in biotic homogenization of fish communities have used large-scale approaches, while the community-level effects of species introductions and local extinctions within river basins have been sparsely analyzed. In this article, we examine patterns in freshwater fish α- and β-diversity in relation to the presence of reservoirs in a Mediterranean river (Guadiana river; Iberian Peninsula). We used fish samples from 182 river localities and 59 reservoir ones to address two main questions: (i) do reservoirs favor the establishment of invasive fish species?; and (ii) do reservoirs bear taxonomically homogenized fish communities? Although total species richness was not different between rivers and reservoirs, the latter had more invasive species and less native ones. Fish species found in reservoirs tended to be larger ones, but invasive species of any size showed higher preferences for reservoirs. Native species that were rare or absent in reservoirs were those that showed higher sensitivity to invasive species in rivers. Reservoir fish communities were taxonomically homogenized in relation to river ones, both when considering all fish species and using only natives or only invasive ones. Our results suggest that invasive species occupying reservoirs constitute an ecological filter excluding most native species from such systems. Invasive species in the study area are often widely introduced elsewhere, while native species found in reservoirs are congeneric and ecologically similar to those found in other Iberian studies. Thus, we conclude that reservoirs

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promote taxonomic homogenization at multiple spatial scales, while could also be promoting the functional homogenization of Iberian fish communities.

Keywords Biotic homogenization · β-diversity · Freshwater fish · Fish conservation · Mediterranean rivers · Invasive species · Regulated rivers

Introduction

Changes in the composition of communities, including species extirpations and introductions, are ubiquitous consequences of human's activities. The combined effects of extinctions and invasions (with the latter often exacerbating the former) have given rise to important shifts in the distribution of biologic diversity, which are often dependent on the scale of observation. While at the global scale there is a rapid loss of biodiversity driven by species extinctions, at the regional scales species introductions often cause increases in species richness (Sax and Gaines 2003). At the local scale, both reduced and increased numbers of species can result after extinctions and introductions. These patterns in the variations of α-diversity (i.e., species richness) were the main focus of studies dealing with invasions and extinctions until the seminal paper of McKinney and Lockwood (1999) revealed that these processes could be also reducing the biologic distinctiveness of communities (i.e., β-diversity). This loss of biologic uniqueness, caused by the non-random identity of species involved in invasion and extinction events, was termed biotic homogenization. While invaders are usually widely distributed species, which are repeatedly introduced in many areas, declining native species tend to be range-restricted ones. Biotic homogenization was later put in a bigger picture, and defined as an ecological process by which biotas lose biologic distinctiveness at any level of organization, whether genetic, taxonomic, or functional (Olden and Rooney 2006).

The taxonomic component of the homogenization process, or taxonomic homogenization, has been more extensively studied than its functional and genetic aspects (Olden and Rooney 2006). Rahel (2000) showed that freshwater fish faunas in continental USA had lost taxonomic distinctiveness mainly due to the introduction of widespread invasive species. Subsequently, increases in taxonomic similarities have been reported in a variety of organisms and regions, including plants (McKinney 2004), birds (Lockwood 2006), and ungulates (Spear and Chown 2008). However, the increase in taxonomic similarity is only one of the possible outcomes of the combination of extinctions and introductions, with taxonomic differentiation (i.e., a decrease in similarity) being the other side of the coin (Olden and Poff 2003). Differentiation among two areas may happen when one of them receives non-native species that are absent in the other, and/or when one area loses species that were initially shared by both. As the changes in α-diversity, those of β-diversity are also dependent on the scale of observation, whether spatial or temporal (Olden and Poff 2004; Clavero and García-Berthou 2006). While at larger scales there is usually a clear trend toward taxonomic homogenization, trends toward taxonomic differentiation are often recorded at the local scale (e.g., Marchetti et al. 2001; Cassey et al. 2007).

Freshwater environments are among the most intensively threatened by human activities, having at the same time important proportions of range-restricted imperilled organisms and large numbers of invasive species (e.g., Darwall et al. 2008). Among human-related alterations of freshwater environments, dam construction is one of the most widely distributed across the globe, causing alterations of the natural flow regimes, fragmentation of fluvial networks, and large-scale disruption of sediment transport (Poff et al. 1997; Nilsson et al.

2005). Poff et al. (2007) showed that dams drive the homogenization of flow regimes of river systems with originally distinct hydrologic cycles. Furthermore, reservoirs have been shown to favor the establishment of invasive species and facilitate their spread through natural habitats (Johnson et al. 2008). Moyle and Mount (2007) suggested that all these environmental alterations would tend to homogenize both reservoir and riverine biologic communities, although these issues have been sparsely quantified (Marchetti et al. 2001).

Freshwater fish has been the most widely used biologic group in the analyses of taxonomic homogenization patterns. Studies in faunal similarities among drainages or regions have been performed in the USA in different occasions and at different spatial scales (see Olden and Poff 2004), and in Canada (Taylor 2004), Europe (Clavero and García-Berthou 2006; Leprieur et al. 2008) or Australia (Olden et al. 2008). Most of these studies used large geographical scales, and focused on basins or political entities for faunal similarity comparisons. The patterns of taxonomic homogenization among fish assemblages within river basins have received much less attention (but see Gido et al. 2009), even though basins are the main meaningful biogeographical units for freshwater communities. An increase of faunal similarity among basins, as those previously reported, means that basins are loosing their biologic distinctiveness, while the homogenization of communities within basins would imply a loss of ecological complexity, which is a fundamental component of biodiversity (Lambdon et al. 2008).

In this study, we examine the spatial and temporal patterns of taxonomic homogenization of fish communities in relation to the presence of reservoirs within a Mediterranean river basin in the Iberian Peninsula. To this aim, we used a data set of 241 sampling sites, 59 located in reservoirs and 182 in rivers and streams. First, we analyze α-diversity patterns, to compare patterns in species richness (whether total or that of native and invasive species) between reservoirs and running waters. We also analyze the preferences of fish species (both native and invasive) for river and reservoir environments. Then, we calculated pair-wise similarities among river communities and among reservoir ones, and compared values from both situations. The specific hypotheses to be tested were (1) reservoirs favor the establishment of invasive fish species; and (2) reservoirs have taxonomically homogenized fish communities in relation to those of running waters.

Materials and methods

Study area

The Guadiana river basin occupies ca. 67,500 km^2 in southern Iberian Peninsula, with a main axis some 800 km long that flows through Spain and Portugal (Fig. 1). The whole basin has a Mediterranean climate, with hot and dry summers and a concentration of precipitations in autumn and spring. Average annual precipitation across the basin is around 450 mm. About half of the basin is devoted to agriculture and over 30% to intensive agricultural uses (Urrea and Sabater 2009). This has generated a strong water demand that has resulted in an important alteration of flow regimes, due both to water abstraction in wells (either legal or illegal) and to the construction of dams. The basin is highly regulated by 88 large reservoirs (>1 hm^3) and hundreds of smaller ones, aggregating to a total storage capacity of over 11,000 hm^3.

The native fish fauna in the Guadiana stands out as one of the richest in a Mediterranean context (Smith and Darwall 2006). From a pool of 16 native species (this number may vary as a function of the estuarine-diadromous species considered) 11 are primary freshwater
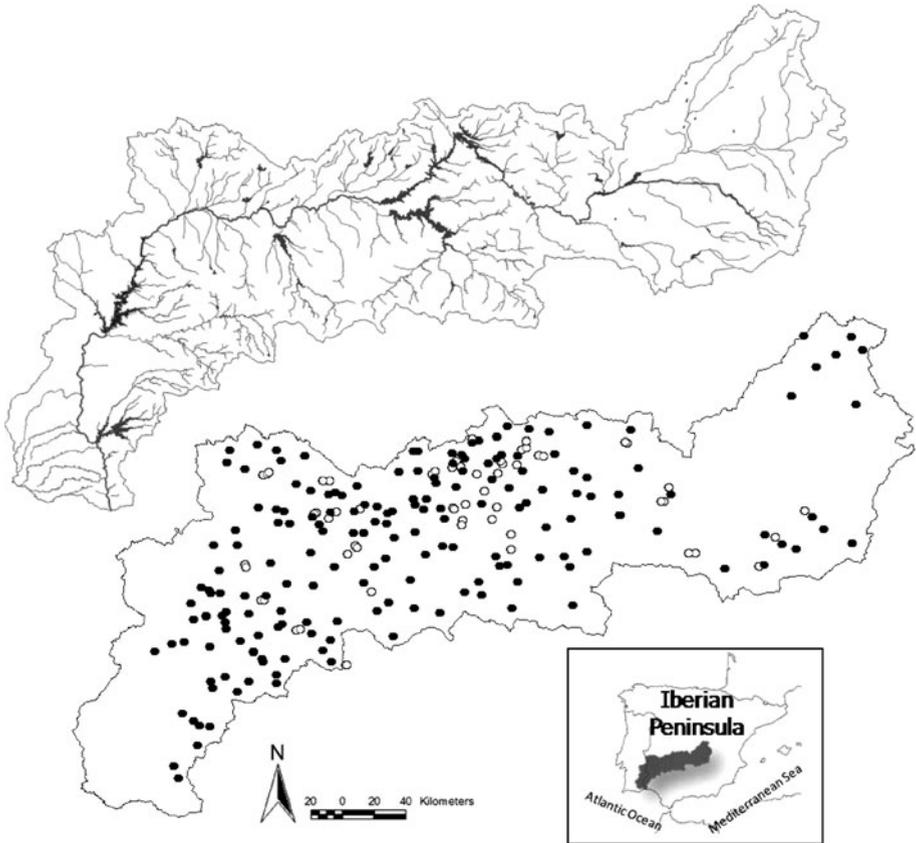
Fig. 1 Maps of the Guadiana basin showing: (i) its main water courses and the location of reservoirs (*upper map*); and (ii) the location of surveyed localities (*lower map*). *Filled circles* denote river localities and *empty circles* denote reservoir ones

species, out of which 10 species are Iberian endemics. There is even a monospecific genus endemic to the basin (*Anaecypris*) (Kottelat and Freyhof 2007). This important biodiversity hotspot is presently highly imperilled, and 80% of the Iberian endemic fish fauna in the basin is considered threatened after IUCN criteria (Smith and Darwall 2006). Invasive species are one of the main threats to freshwater fish both throughout the Mediterranean basin and in the particular case of the Guadiana river. Presently there are over 15 non-native fish species cited in the Guadiana, out of which at least 12 are definitely established and, in most cases, expanding their ranges (Hermoso et al. 2008).

Fish sampling

During the years 2005 and 2006, we carried out extensive fish surveys in the Guadiana basin in which 241 localities were sampled, 182 in rivers and 59 in reservoirs (Fig. 1). We sampled rivers stretches in spring (April–June) through single-pass electrofishing without blocking along a minimum 100 m, as thoughtfully described in Hermoso et al. (2009, in press). Reservoir localities were sampled in summer, using a constant unit of effort consisting in a combination of passive capture techniques that were set overnight, with an aim

to capture the widest possible range of fish species and sizes and to cover as much as possible of the microhabitats found in reservoirs. Passive gears used at each locality included two trammel nets, which were 10 m long and had two different inner panel mesh sizes (25 and 50 mm), three large-meshed fyke nets (7-mm mesh), three small-meshed fyke nets (3.5 mm mesh), 15 metal minnow traps (6-mm mesh), and 10 pairs (surface and bottom) of plastic minnow traps made with soda bottles (see Clavero et al. 2006 for further details on traps and fyke nets). All devices were set near reservoir shores (up to 25–30 m), and so we did not sample pure open water habitats.

Data analyses

For the most common species, we calculated an index to estimate species' preference for rivers or reservoirs, after the formula:

$$\text{Habitat preference} = \frac{\text{PRO}_{\text{river}} - \text{PRO}_{\text{reservoir}}}{\text{PRO}_{\text{river}} + \text{PRO}_{\text{reservoir}}}$$

where $\text{PRO}_{\text{river}}$ and $\text{PRO}_{\text{reservoirs}}$ are, respectively, the proportions of river and reservoirs sites in which the species had been detected (see Table 1). The values of the index vary between -1 (absolute preference for reservoirs) and $+1$ (absolute preference for rivers) with values near zero denoting no clear preferences. In an attempt to identify biologic characteristics related to the preference of a given species for river or reservoir habitats, we recorded the maximum size of each species from the Portuguese Freshwater Fishbase (Ribeiro et al. 2007). We studied the influence of species' size (covariate) and status (factor with two levels, native/invasive) on habitat preference through an analysis of covariance (ANCOVA). If the interaction term (factor × covariate) was non-significant ($P < 0.1$), then it was deleted from the ANCOVA design. For common native species, we further calculated an index of sensitivity to invasive species using exclusively data from river locations. This index was based in the richness of invasive species in localities where a certain species was present or absent, using the following formula:

$$\text{Sensitivity to invasive spp}_i = \frac{\text{SI}_{i\text{abs}} - \text{SI}_{i\text{pre}}}{\text{SI}_{\text{average}}}$$

where $\text{SI}_{i\text{abs}}$ is the average richness of invasive species in localities where species i was absent, $\text{SI}_{i\text{pre}}$ is the same value for localities where species i was present and $\text{SI}_{\text{average}}$ is the average number of invasive species among all surveyed river localities. We analyzed the influence of the sensitivity to invasive species on habitat preference through a simple linear regression analysis.

To identify the possible role played by reservoirs in the process of taxonomic homogenization of fish communities, we analyzed the similarities of communities at two levels: (i) community composition (i.e., using only the presence–absence data); and (ii) community structure (i.e., using the percentage of individuals belonging to each species detected). Previous studies have shown that taxonomic homogenization patterns may differ when using the presence/absence or abundance data, the former often underestimating the level of homogenization (La Sorte and McKinney 2007). Both for community composition and structure, we analyzed similarities in three ways: (i) considering all species; (ii) using only native species; and (iii) using only invasive species. In all cases, for similarity analyses, we only used those localities in which at least two fish species from the considered pool (all species, natives, or invasives) had been recorded.

Table 1 List of the fish species identified during the field survey in the Guadiana basin

English name	Latin name	Code	Status	N	% rivers	% reservoirs
Calandino	*Iberocypris alburnoides*	IAL	N	110	57.1	10.2
Southern Iberian spined-loach	*Cobitis paludica*	CPA	N	107	56.6	6.8
Iberian long-snout barbel	*Luciobarbus comizo*	LCO	N	61	20.3	40.7
Iberian small-head barbel	*Luciobarbus microcephalus*	LMI	N	58	26.9	15.3
Southern Iberian chub	*Squalius pyrenaicus*	SPY	N	49	26.4	1.7
Southern straight-mouth nase	*Pseudochondrostoma willkommii*	PWI	N	47	14.8	33.9
Iberian arched-mouth nase	*Iberochondrostoma lemmingii*	ILE	N	43	23.6	0
Freshwater blenny	*Salaria fluviatilis*	SFL	N	29	11.5	10.2
Southern Iberian barbel	*Luciobarbus sclateri*	LSC	N	25	9.3	13.6
Jarabugo	*Anaecypris hispanica*	AHI	N	9	4.9	0
Eastern Iberian barbel	*Luciobarbus guiraonis*	–	N	3	1.6	0
Eel	*Anguilla anguilla*	–	N	2	1.1	0
Big-scale sand smelt	*Atherina boyeri*	–	N	1	0.5	0
Allis shad	*Alosa alosa*	–	N	1	0.5	0
Pumpkinseed	*Lepomis gibbosus*	LGI	I	135	46.2	86.4
Eastern mosquitofish	*Gambusia holbrooki*	GHO	I	78	34.6	25.4
Largemouth bass	*Microperus salmoides*	MSA	I	67	16.5	62.7
Common carp	*Cyprinus carpio*	CCA	I	37	6.0	44.1
Northern pike	*Esox lucius*	ELU	I	18	5.5.	13.6
Bleak	*Alburnus alburnus*	AAL	I	15	2.7	16.9
Goldfish	*Carassius auratus*	CAU	I	15	2.2	18.6
Black bullhead	*Ameiurus melas*	AME	I	10	4.4	3.4
Pyrenean gudgeon	*Gobio lozanoi*	–	I[a]	5	2.7	0
Channel catfish	*Ictalurus punctatus*	–	I	4	0	6.8
Roach	*Rutilus rutilus*	–	I	4	0.5	5.1
Tench	*Tinca tinca*	–	I	4	0	6.8
Chameleon cichlid	*Australoheros facetus*	–	I	1	0.5	0
Brown trout	*Salmo trutta*	–	I[a]	1	0.5	0

The total number of presences (*N*), and the percentage of river and reservoir localities in which each species was detected is also given. Status codes are *N* for native species and *I* for invasive species

[a] Species that are native to the Iberian Peninsula, but not to the Guadiana basin

For the presence/absence data, the similarity of fish communities among pairs of localities was measured using the Jaccard's similarity index. This index gives the proportion of species shared between two sites in relation to the total number of species present in the same sites. The similarity in community structure was assessed through multivariate statistics. The same process was followed for the total, native and invasive species data sets. We submitted the matrix of species × localities to a principal components analysis (PCA) to extract the main gradients of variation in community structure. We only included in the PCA those fish species occurring in at least 5% of the localities. We retained the scores of localities along the first four principal components (PCs) extracted by the PCA and calculated the Euclidean squared distance between all possible pairs of

localities for each PC. The distance for any pair of localities was then calculated as the average of their distances along the four PCs weighed through their *eigenvalues*, following the formula:

$$\text{Distance} = \frac{\sum_{i=1}^{i=4} e_i \times (a_i - b_i)^2}{4}$$

where e_i is the *eigenvalue* of PC_i, and a_i and b_i are the scores of locality A and locality B along PC_i. We transformed distances into community structure similarities by subtracting distance to 1 (i.e., the similarity of two localities occupying the same point in the multidimensional space defined by PC 1–4 would be 1). In order to facilitate comparisons with Jaccard's similarities, community structure similarity values were transformed to range from 0 to 1, by subtracting the minimum and dividing by the total range (i.e., maximum − minimum).

The main question addressed in this study is whether reservoirs drive taxonomic homogenization of fish communities. We analyze this by comparing the similarities of communities (both for composition and structure) among rivers and among reservoir localities, using the whole community or concentrating in native or invasive species. Homogenization process is therefore described here as a spatial increase in the similarity of freshwater fish communities in relation to the presence of dams.

Results

The field study resulted in the detection of 28 fish species, half of which are native to the Guadiana basin (Table 1). The total number of fish species was not statistically different between river and reservoir localities, but differences were clear when analyzing separately native and invasive species (Fig. 2). Reservoirs had impoverished native fish communities in comparison with rivers, and we did not detect any native species in almost 40% of reservoir localities. In contrast, reservoirs tended to have more invasive species than rivers. There was not a single reservoir locality in which invasive fish were not detected, while in over 85% of the cases we found two or more invasive species. Notwithstanding the presence of invasives in river localities was also very high, since up to 70% of them had at least one invasive species (Fig. 2) and up to 40% of river localities had as many invasive species as native ones.

The ANCOVA relating maximum size and status of species with their habitat preference explained 71% of variation in the latter variable and showed that smaller species tend to prefer rivers ($P = 0.002$) and that invasive species, whatever its size, had a higher preference for reservoirs than native ones ($P = 0.003$) (Fig. 3). The relationships between size and habitat preference were not statistically different between native and invasive species, as shown by the non-significant effect of the factor × covariate interaction ($P = 0.20$), which was consequently deleted from the ANCOVA. Native fish species that occurred in localities with few invasive species in rivers were also those that tended to be absent from reservoirs (simple regression analysis; $n = 10$; $P = 0.001$) (Fig. 3). The sensitivity to invasive species was also negatively correlated with fish size (Pearson's $r = -0.69$; $n = 10$; $P = 0.026$), i.e., smaller species tended to occur in river localities with few or no invasive species.

The four first principal components (PC) of the PCA explained 58, 74, and 75% of the original variance for the total, native and invasive species data sets, respectively (Fig. 4).

Fig. 2 Fish species richness frequency histograms showed separately for river ($N = 182$) and reservoir ($N = 59$) locations, and for total, native and invasive species. *P* values are those resulting from one-way ANOVAs, while the *squares* show the direction of the observed differences
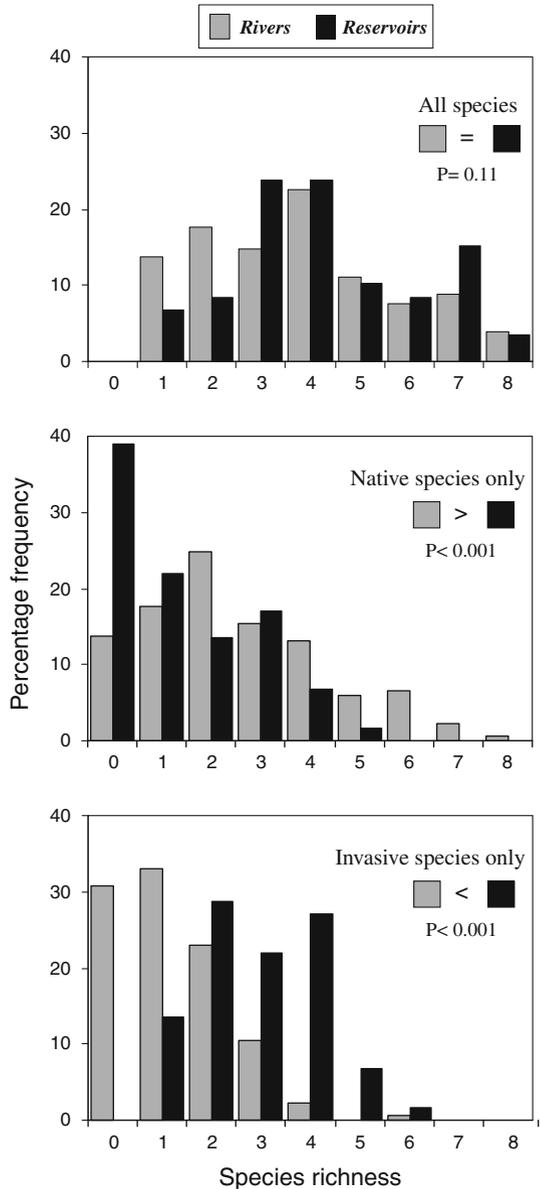
In the PCA applied to the total dataset reservoir localities tended to be associated with the dominance of invasive species [especially pumpkinseed (*Lepomis gibbosus*), largemouth bass (*Micropterus salmoides*) and common carp (*Cyprinus carpio*)] and with the presence of large native cyprinids [mainly Iberian long snout-barbel (*Luciobarbus comizo*) and southern straight-mouth nase (*Pseudochondrostoma willkommii*)]. While reservoirs localities scored toward the negative end of the first PC of this PCA all species with positive scores were native. Similar species associations with reservoir localities were obtained when analyzing the native and the invasive data sets.
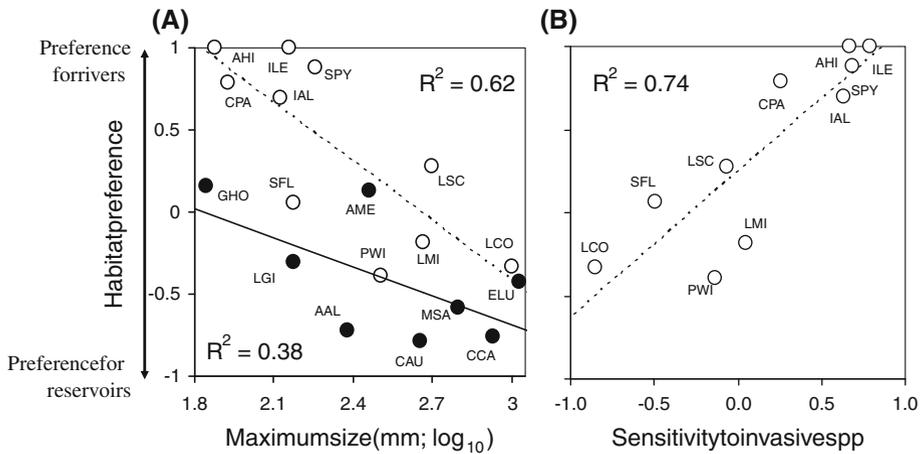
Fig. 3 Linear relationships between preferences for river or reservoir environments of the most common species in the Guadiana river basin and: **a** the maximum body size, represented separately for native (*empty circles*, *dotted line*) and non native (*filled circles*, *solid line*) species; and **b** the sensitivity of native species to invasive species, calculated using only river localities (see "Materials and methods" section). Coefficients of determination (R^2) for each regression line are also given. Species acronyms as in Table 1

Reservoir localities tended to have more similar fish communities than rivers, a pattern that was relatively constant for the total, native and invasive data sets (Fig. 5). It can be thus stated that reservoirs favor the homogenization of fish communities. In terms of species composition both communities and the native component of communities were clearly homogenized in reservoirs in relation to rivers, while there was a slight taxonomic differentiation in reservoirs when considering only invasive species. When analyzing community structure all three data sets showed a clear homogenizing effect of reservoirs, which was maximal for the total dataset.

Discussion

We have shown that reservoirs promote a shift from native-dominated fish communities to invasive-dominated ones, that only a subset of native species, mainly large-sized ones, are commonly found in reservoirs and that reservoir communities have lost β-diversity in relation to river ones. Thus, changes in fish communities following dam construction are associated to a loss of distinctiveness among local assemblages.

Invasive fish, native fish, and reservoirs

The relationships between reservoirs and the introduction and establishment of invasive fish species have been previously noted by several authors, both in the Iberian Peninsula (e.g., Elvira et al. 1998; Clavero et al. 2004) and elsewhere (e.g., Moyle and Light 1996; Kolar and Lodge 2000). These studies mainly refer to the differences between reservoirs and running water systems. However, Johnson et al. (2008) analyzed over 1,000 water bodies in the Great Lakes Region (USA) and found that reservoirs were also more likely to be invaded and to host multiple invaders than neighboring natural lakes. The main
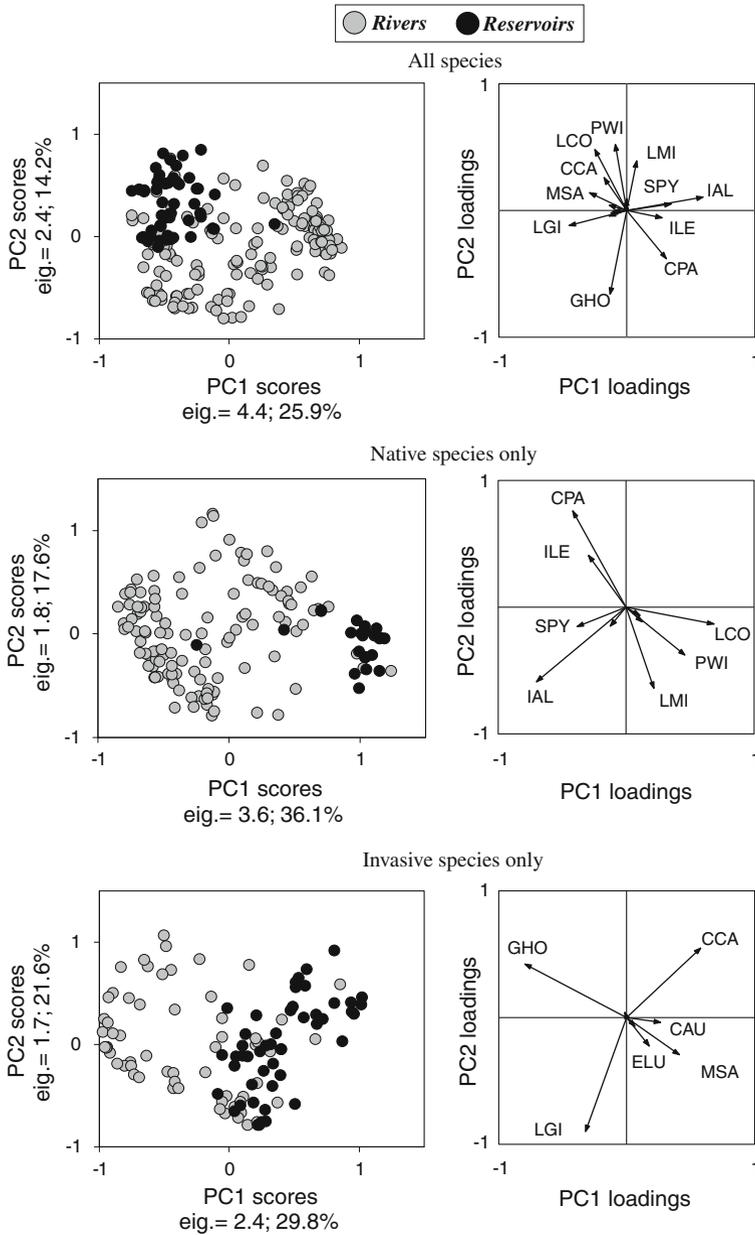
Fig. 4 Results of three complementary principal components analyses (PCAs) applied the % composition of fish communities [log$_{10}$ $(X + 1)$ transformed values]. *Graphics* show sampling localities' scores (separately for rivers and reservoirs) and species' loadings along the first two principal components. Community structure similarity values (see Fig. 4) were calculated from the pair-wise distances between sampling locations in the 4-dimension multivariate spaces defined by these PCAs. Species acronyms are the same as those in Table 1
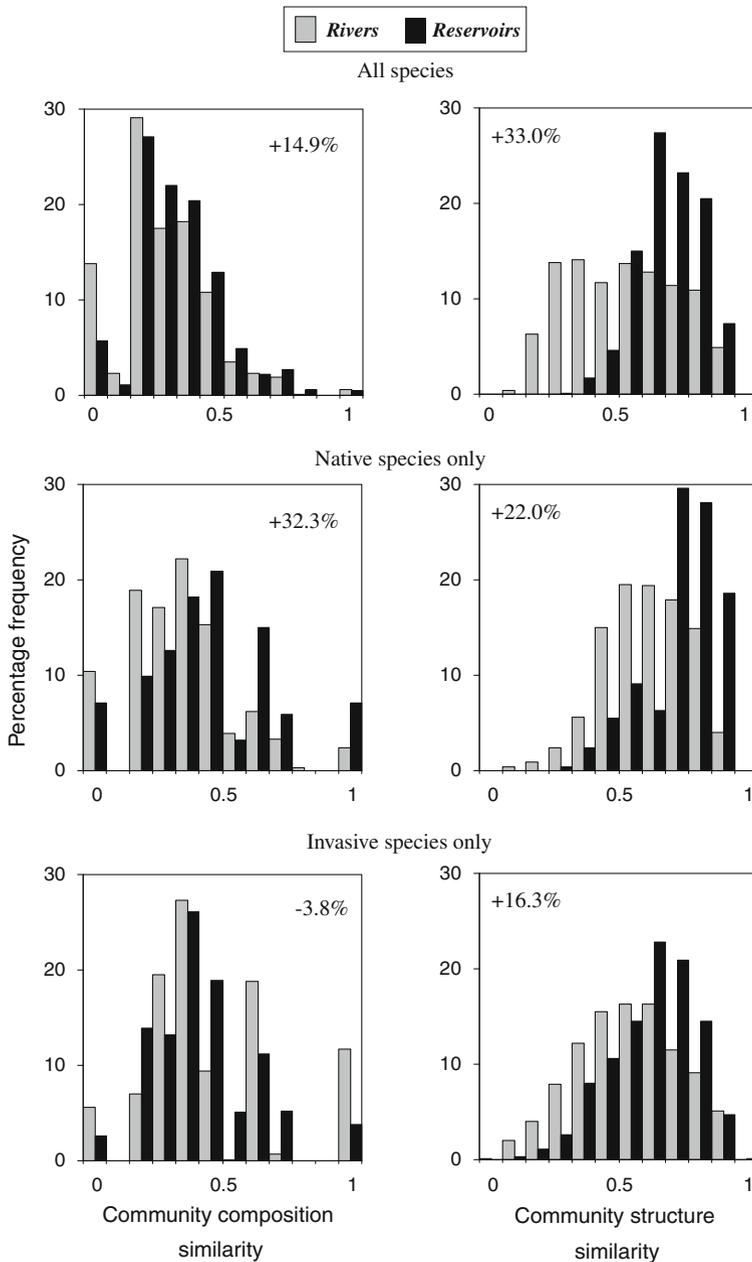
Fig. 5 Frequency histograms of similarities among river locations and reservoir ones presented separately for all fish species and native only and invasive only species pools. Community composition similarities are Jaccard's coefficient of similarity values, while those of community structure similarity were derived from the principal component analyses presented in Fig. 4. Shown percentages are the mean increases in similarity from river to reservoir values (i.e., mean reservoir similarity − mean river similarity)

mechanisms proposed to explain the link between reservoirs and invasive species have been the increased propagule pressure (i.e., invasive species tend to be introduced into reservoirs), the low biotic resistance of the newly formed communities following the construction of dams and alterations of disturbance regimes.

In the particular case of the Iberian Peninsula, which is extremely poor in natural lakes, over 1,200 large reservoirs [storage capacity > 1 hm^3 (Berga-Casafont 2003)] have created a huge amount of new lentic freshwater habitat. The environmental characteristics of reservoirs clearly contrast with those of surrounding natural freshwater systems. Most Iberian running water ecosystems are under Mediterranean climatic conditions, having a summer dry period during which surface flow is low or inexistent and unpredictable floods occurring between autumn and spring. The intensity of droughts and floods is higher in low- and medium-order water courses. This temporal and spatial variability in environmental conditions is the main force structuring Mediterranean freshwater communities (Gasith and Resh 1999; Magalhães et al. 2002). Dams soften, eliminate or even reverse the natural variability of freshwater systems, both in the reservoir itself and in downstream water courses, through the contention of floods and the artificial maintenance of water flows in summer months (Poff et al. 2007).

We have shown that invasive species richness is higher in reservoirs than in rivers. While in river localities invasive species comprised on average 33% of the total species richness, in reservoirs this value was 71%. This latter figure is almost equal to that reported by Carol et al. (2006) for 14 reservoirs in Catalonia (north-eastern Iberian Peninsula), in which, on average, 72% of species were invasive. Most invasive fish species are unable to thrive in Mediterranean water courses with natural flow regimes (e.g., Marchetti and Moyle 2001), but their establishment is facilitated in the lentic habitats created by reservoirs (Clavero et al. 2004) as well as in rivers with attenuated variability in flow regimes. For example, using also data from river localities in the Guadiana basin, Hermoso et al. (in press) showed that invasive species tended to be more abundant near reservoirs. On the other hand, a large proportion of fish introductions recorded in the Iberian Peninsula are related to sport fishing, implying both species of fishing interest and bait fish (Elvira and Almodóvar 2001; Ribeiro et al. 2008), and sport fishing activities in the Iberian Peninsula tend to be concentrated in reservoirs (Marta et al. 2001). While it is known that government-promoted introductions in the second half of the twentieth century were made mainly in reservoirs (both in Spain and Portugal), it can also be assumed that present-day illegal introductions are being performed into reservoirs. Thus, the proliferation of invasive species in Iberian reservoirs, and elsewhere in Mediterranean areas, is probably owed to a combination of altered environmental conditions (mainly the elimination of natural instability) and an increased propagule pressure (e.g., Marchetti et al. 2004).

However, why do reservoir localities host less native species than river ones? The most probable explanations to this pattern are (i) that native species are not able to occupy reservoirs due to habitat modifications and alterations; (ii) that invasive species that are established and thriving in reservoirs exclude native species; or (iii) the one based on a combined or synergistic effect of these two mechanisms. The discussion on the role of habitat alterations and invasive species in biodiversity loss has gained importance in the last decade (e.g., Didham et al. 2005). The issue is often difficult to address due to the frequent spatial and temporal coincidence of the dominance of invasive species and habitat degradation. This is the case of our reservoir data, since we did not find a single reservoir locality without invasive species, and also the general situation in Iberian reservoirs (Godinho et al. 1998; Carol et al. 2006). In fact, invasive species such as common carp and

largemouth bass appear in reservoirs soon after dam construction, due to illegal intro-
ductions arguably performed by particulars (e.g., Ruiz 1998).

However, there are some reasons that point toward a major role of invasive species in
the low occupancy of reservoirs by native fish. First, Mediterranean freshwater fish species
have evolved in highly instable environments and their ecological specialization, espe-
cially in relation to habitat characteristics, is generally low. For example, since flows are
scarce or inexistent during summers, there are few strictly rheophilic fish species, which
would be the most negatively affected by dam construction. We believe that there are no
clear arguments to support that most native Mediterranean freshwater fish would not be
able to occupy reservoirs. On the other hand, native species that are absent or scarce in
reservoirs strongly tend to be those that in rivers are most sensitive to the presence of
invasive species. The strong bias toward large-sized species among native fish occupying
reservoirs also suggests that the filter limiting native species richness in such systems is
related to processes predominantly affecting small species. Predation by invasive species
seems the most likely mechanisms to explain the lack of small native fish in reservoirs
(e.g., Gido et al. 2009). Previous studies had already related the lack of small native species
in Iberian reservoirs to the presence of large invasive predators, especially largemouth bass
(Godinho et al. 1998). Iberian fish have evolved in an almost complete absence of
piscivorous fish [with the exception of the eel (*Anguilla anguilla*)] and seem to be espe-
cially sensitive to introduced fish predators (Rincón et al. 1990; Godinho et al. 1998). Apart
from the large species, the exception to this pattern is the small-bodied freshwater blenny
(*Salaria fluviatilis*), which was found in reservoirs almost as often as in rivers. In fact, the
ability of freshwater blenny to coexist with invasive species have been previously
described both in lotic (e.g., Blanco-Garrido et al. 2009) and lotic environments (e.g.,
García-Berthou and Moreno-Amich 2000). This coexistence has been related to the cryptic
coloration and benthic habits of the species that would allow a lower predation pressure
than that suffered by cyprinids (García-Berthou and Moreno-Amich 2000).

We then suggest that the reduction in the number of native fish species in reservoirs in
relation to rivers is mainly driven by the proliferation of invasive species in the former. In
fact, Hermoso et al. (in press) reported that in river within the Guadiana basin invasive fish
species were the main factor promoting biodiversity loss among native fish communities.
However, it is also plausible that habitat characteristics found in reservoirs could increase
the vulnerability of native species to invasive ones. For example, the simplification of
structural complexity in reservoirs if compared with rivers leads to an increased predation
pressure (e.g., Santos et al. 2008). This could represent an example of a synergistic
interaction between the effects of species invasions and habitat degradation (see Didham
et al. 2007), since simplified reservoir environments would be modifying predator–prey
interactions through an increase of prey vulnerability.

Reservoirs and taxonomic homogenization within basins

Fish community changes that follow the establishment of reservoirs have led to their
generalized homogenization in relation to rivers within the Guadiana basin. Reservoirs
localities were more similar than river ones both in terms of community composition and in
terms of the relative abundance of fish species. Gido et al. (2009) found similar results
when analyzing littoral fish communities in river and reservoirs from three basins in central
USA. This study reported a higher similarity of reservoir communities in comparison to
river ones, both within and among basins. There is, however, a fundamental difference
between our data and those presented by Gido et al. (2009). While in central USA the

proportion of species that had been introduced to each basin was lower than 10% in reservoirs (8 out of 82 species), in the Guadiana basin this figure rose up to 59% (11 out of 19). Carol et al. (2006) had previously reported the same numbers from Catalan reservoirs (8 native and 11 invasive species), while Godinho et al. (1998) found 14 native and 10 exotic species in Portuguese reservoirs. Then, while Gido et al. (2009) propose that the increased similarity of reservoirs community is mainly due to the effects of ecological filters favoring certain traits (e.g., planktivory or preference for large rivers), our results suggest a homogenization process driven by the combined effects of local extinctions of native species and species introductions, with the latter enhancing the former. This scenario is similar to that described by Marchetti et al. (2001) for reservoirs in California, a region that shares many features with the Iberian Peninsula, such as similar climate regime, a widespread regulation of freshwater resources, a high endemicity of the fish fauna (implying high β-diversity values) and a high proportion of invasive species within river basins (e.g., Moyle 2002).

Both our results and others previously reported by other authors indicate that reservoirs would promote the taxonomic homogenization of fish communities at different spatial scales. Our results show that the disappearance of certain native species (especially small-bodied ones that are sensitive to invasive species) from reservoirs and the introduction of invasive ones has led to a reduction in the β-diversity in reservoirs within the Guadiana basin. However, the effects of reservoirs on fish communities can be also promoting a larger-scale process of taxonomic homogenization, such as that described in Clavero and García-Berthou (2006) for the main Iberian river basins. In the Iberian Peninsula the homogenization of fish faunas has taken place under an invasion-only scenario, since up to present there have been no extinctions of native species from whole basins. Clavero and García-Berthou (2006) showed that the continuous introductions of new species and the generalized spread (including many inter-basin movements) of established invasive species was producing a clear reduction in the taxonomic distinctiveness of Iberian basins, both within the Iberian Peninsula and in relation to neighboring European basins. The role of reservoirs as introduction sites, facilitators of the establishment of invasive species and stepping-stones to colonize new habitats (Johnson et al. 2008) would thus be critical to promote and accelerate the ongoing process of taxonomic homogenization of the Iberian fish fauna. Moreover, altered flow regimes in river systems due to reservoir management (Poff et al. 2007) enhance fish invasions in Mediterranean water courses (Marchetti and Moyle 2001). Then, reservoirs would be implied in the homogenization process at multiple levels, both by boring a homogenized fish fauna and through their effect on running water systems.

The same invasive fish species [the few 'winners' after McKinney and Lockwood (1999)] are repeatedly introduced and become established within the Guadiana basin, in the Iberian Peninsula and in many areas of the world. For example, most of the invasive species listed in Table 1 are frequently found in homogenized rivers in Italy (Lorenzoni et al. 2006) or North America (Moyle and Mount 2007). On the other, only a small fraction of the native species pool present in rivers is able to occupy reservoirs, and they tend to be large-bodied ones and those that cope well with the presence of invasive species. In the Guadiana basin these species are mainly barbels (genus *Luciobarbus*) and southern straight-mouth nase. Although belonging to different species as a function of the hydrologic basin, other studies in Iberian reservoirs repeatedly identify *Luciobarbus* species and large nases as the most common native species in reservoirs (Godinho et al. 1998; Encina et al. 2004; Carol et al. 2006; Sales-Luís et al. 2007). The proliferation of invasive species within reservoirs may then drive not only the within-basin increase in the taxonomic

similarity of native communities, but also a decrease of the functional diversity among different basins, since native species found in reservoirs tend to be those with an equivalent functional role (Olden and Rooney 2006).

Final remarks

Our results give support to the idea launched by Moyle and Mount (2007), suggesting that homogenized rivers due to damming and flow management would support homogenized faunas. Reservoirs bore highly invaded fish communities that show little spatial variability in relation to that recorded in rivers. A few native species are the only ones repeatedly found in reservoirs, where fish communities are numerically dominated by a group of invasive species that are widespread distributed across the Guadiana basin, the Iberian Peninsula and often worldwide. The homogenizing effect of reservoirs, and especially their influence on river systems, could be softened by the implementation of environmental flows that mimic as much as possible natural flow regimes. However, a great amount of work is needed to reduce the number of illegal introduction events that allow both intra- and inter-basin spread of invasive species and that are mainly localized in reservoirs. Measures to control those particular initiatives should include regulatory issues (e.g., restricting sport fishing of certain species) as well as environmental education aspects, mainly implying the fishing collective.

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