

A global assessment of freshwater fish introductions in mediterranean-climate regions

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Abstract Mediterranean-climate regions (med-regions) are global hotspots of endemism facing mounting environmental threats associated with human-related activities, including the ecological impacts associated with non-native species introductions. We review freshwater fish introductions across med-regions to evaluate the influences of non-native fishes on the biogeography of taxonomic and functional diversity. Our synthesis revealed that 136 freshwater fish species (26 families, 13 orders) have

been introduced into med-regions globally. These introductions, and local extirpations, have increased taxonomic and functional faunal similarity among regions by an average of 7.5% (4.6–11.4%; Jaccard) and 7.2% (1.4–14.0%; Bray–Curtis), respectively. Faunal homogenisation was highest in Chile and the western Med Basin, whereas sw Cape and the Aegean Sea drainages showed slight differentiation (decrease in faunal similarity) over time. At present, fish faunas of different med-regions have widespread species in common (e.g. *Gambusia holbrooki*, *Cyprinus carpio*, *Oncorhynchus mykiss*, *Carassius auratus*, and *Micropopterus salmoides*) which are typically large-bodied, non-migratory, have higher physiological tolerance, and display fast population growth rates. Our findings suggest that intentional and accidental introductions of

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freshwater fish have dissolved dispersal barriers and significantly changed the present-day biogeography of med-regions across the globe. Conservation challenges in med-regions include understanding the ecosystem consequences of non-native species introductions at macro-ecological scales.

Keywords Introduced species · Non-native species · Conservation biogeography · Taxonomic homogenisation · Functional homogenisation

Introduction

Mediterranean-climate regions (med-regions) are recognised hotspots of biodiversity and endemism (Cowling et al., 1996). Concurrently, they are among the most densely human-populated regions because of their favourable climates that support valuable agricultural produce (e.g. fruit, winter wheat, and wine). Human enterprise in these regions has resulted in extensive habitat alteration, water pollution, high levels of water extraction and regulation, and the intentional and accidental introduction of many non-native species (Di Castri, 1991). As a result, freshwater ecosystems in med-regions are highly modified and continue to face mounting pressure from growing human populations and water development schemes (Economidis, 1995; Collares-Pereira et al., 2000; Millennium Ecosystem Assessment, 2005; Shumka et al., 2010). Unfortunately, aquatic faunas in these regions are considered to be experiencing among the fastest rates of species imperilment globally (Moyle, 1995).

Freshwater ecosystems are particularly affected by non-native species introductions, which produce a range of ecological and economic impacts (Cambray, 2003; Cucherousset & Olden, 2011; García-Berthou &

Moyle, 2011). For instance, the zebra mussel *Dreissena polymorpha* and the Asian clam *Corbicula fluminea* act as ecosystem engineers and have caused significant economic impacts in North America and Europe by clogging water intake structures. Crayfishes, such as the red swamp crayfish *Procambarus clarkii*, have been introduced worldwide, often reaching high abundance in Mediterranean waters, and have contributed to the decline of native species (e.g. Gherardi & Acquistapace, 2007). Riparian or aquatic plants such as the water hyacinth *Eichhornia crassipes*, Eurasian watermilfoil *Myriophyllum spicatum*, hydrilla *Hydrilla verticillata*, the ferns *Salvinia molesta* and *Azolla filiculoides*, and the giant reed *Arundo donax*, and insects, such as the black locust *Robinia pseudoacacia*, are global invaders that have profound effects on ecosystem structure and functioning (Brunel et al., 2010).

Our review focuses on spatial patterns and temporal trends in freshwater fish introductions in med-regions. These regions are hotspots both of endemisms and freshwater fish introductions (Leprieur et al., 2008; Tedesco et al., 2012) and med-region aquatic habitats are severely threatened, in part, because of water scarcity and environmental degradation (Hermoso & Clavero, 2011; Hermoso et al., 2011). Thus, we require a greater understanding of the impacts in these regions to guide management and policy actions. We focus on fish because their native and introduced ranges are well documented across these regions.

Freshwater fish introductions in mediterranean regions

Europe's history of non-native fish introductions dates back to the Roman Empire, through the progression of fish culturing in Medieval monasteries and parishes and by the nobility in the Renaissance to the 19th century "Acclimation Societies" that provided incentives for the establishment (acclimation) of non-native plants and animals and the government-sanctioned introductions of the mid-20th century (Copp et al., 2005). At present, numerous non-native fish from a variety of sources have been introduced across Mediterranean Europe for the biological control of aquatic plants and mosquitoes, aquaculture, to compensate for the decline in native fish stocks, and to create new and more diverse recreational fisheries (Cowx, 1997;

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Hermoso & Clavero, 2011). Although government-sanctioned fish introductions have ceased in many countries, the illegal release of non-native species by anglers and aquarists, including accidental releases from aquaculture facilities, has continued (Elvira & Almodóvar, 2001; Rahel, 2004).

Strong commonalities in human land use and invasion histories are evident across med-regions of the world. Non-native species of California were predominantly introduced for recreational angling, commercial fisheries, and forage/bait fish, or intentionally through the ornamental fish trade (Moyle, 1976). Populations of native fish have continued to decline as a result of a suite of threats (Moyle et al., 2011), with some salmonid species now approaching extinction (Katz et al., 2012). In Chile, the creation of recreational fisheries was the primary reason for fish introductions prior to the 1980s (Basulto, 2003), whereas government-sponsored aquaculture has been the major driving force for fish introductions in recent decades (Iriarte et al., 2005; Arismendi et al., 2009). Chile is currently one of the world's largest producers of cultured salmonids, accounting for more than 73% of Chile's aquaculture production (Buschmann et al., 2009). Introduced salmonids dominate the total fish abundance and biomass in streams and lakes (Soto et al., 2006; Arismendi et al., 2009). For example, in southern Chile native fish are absent from 40% of the streams in which salmonids are now present (Soto et al., 2006). The rapid colonisation of South American streams by escapees from salmonid culture facilities has raised concerns regarding the impact of these escapees on the native fish assemblages (Soto et al., 2001; Arismendi et al., 2009; Garcia de Leaniz et al., 2010).

In south-western Australia (sw Australia) and the south-western Cape of South Africa (sw Cape), initial introductions involved ornamental fish and food fish for sailors, followed by salmonids for recreational angling, and biological control agents for mosquitoes (de Moor & Bruton, 1988; Morgan et al., 2004; Marr et al., 2012). The illegal release of angling, ornamental, and mosquito control species continues in both regions (Morgan et al., 2004; Impson, 2007). Recent estimates suggest that more than 90% of the river habitat in the sw Cape is currently invaded by non-native fishes (Marr et al., 2012). As in other med-regions, the rivers in sw Australia and the sw Cape are subject to high levels of water abstraction, habitat

degradation, eutrophication, salinisation, fragmentation, and pollution (Morgan et al., 2003; Impson, 2007).

Despite some benefits (contribution to fishery production, recreational fishery, aquaculture development, mosquito control, and reduction of heavy algal blooms), fish introductions have been associated with significant negative ecological and socio-economic impacts. The ecological impacts are manifested at: genetic (gene transcription, hybridisation); individual (behaviour, morphology, vital rates); population (transmission of parasites/diseases, demographic effects, distributional effects); community (species extirpations, compositional changes, alterations in food webs); and ecosystem (biochemical cycles, energy fluxes between ecosystems, ecological engineering) levels (Cucherousset & Olden, 2011). Phylogenetic history and human affiliation have been identified as predictors favouring species of freshwater fish selected for introduction in med-regions (Alcaraz et al., 2005; Marr et al., 2010). Certain fish families are represented by disproportionately higher numbers of non-native species because of strong human biases towards introducing species, such as game fish, forage fish, and bio-control agents for aquatic weeds or mosquitoes (Clavero & García-Berthou, 2006; García-Berthou, 2007; Marr et al., 2010). The introduction of freshwater fishes has reduced the characteristic endemism of freshwater fish assemblages in med-regions (Marr et al., 2010) and the risk of further introductions remains extremely high because of increasing interest in angling, low public awareness about the impacts of non-native fish, and poor mechanisms to enforce bans on non-native fish introductions (Zenetos et al., 2009; Gozlan et al., 2010).

By dissolving physical barriers to movement and connecting formerly isolated regions, human-mediated species introductions have dramatically reshuffled the present-day biogeography of freshwater fishes (Leprieur et al., 2008). A growing pattern is emerging where the range expansion of ubiquitous non-native species and the loss of endemic forms tend to be driving the homogenisation of the species pools of fish faunas (i.e. decreasing beta-diversity) over time (Olden, 2006). Species introductions have caused shifts in fish community composition, including regional-scale biotic homogenisation. It has been emphasised that the importance of identifying and

understanding present-day patterns of biotic homogenisation with the intention of establishing conservation goals aimed at reducing potential future ecological impacts (Olden, 2006). Although a number of biotic homogenisation studies of freshwater fish assemblages have been completed, the majority have focused on taxonomic homogenisation in temperate latitudes of the Northern Hemisphere. In contrast, comparative studies between different regions or over multiple scales are lacking (Olden et al., 2010, 2011), but see Villéger et al. (2011), Hermoso et al. (2012), and Vitule et al. (2012). A comparison of introductions across climatically similar regions promotes an understanding of invasion processes by isolating large-scale drivers other than regional climate (Pauchard et al., 2004), and focuses on the role of human activities (Jiménez et al., 2008) and the characteristics of the invading species (Moyle & Marchetti, 2006). Comparative studies may also provide valuable information for the conservation of native species and the management of non-native species by establishing priority lists of potentially harmful species, evaluating the risk of homogenisation of the invaded communities, developing guidelines for sustainable ecosystem management, and targeting dispersal pathways for the management of non-native species (Pauchard et al., 2004).

Analysis of freshwater fish introductions

Freshwater fish are among the most widely introduced vertebrate groups and will continue to be introduced even though their detrimental impacts have been well-documented (Lintermans, 2004; Cucherousset & Olden, 2011). We conducted a global assessment of freshwater fish introductions across med-regions to compare the taxonomic and functional dimensions of biotic homogenisation resulting from the introduction of non-native species and the extirpation of native species. We compiled data on freshwater bony fish (Osteichthyes) in med-regions, excluding marine species that only occasionally enter freshwaters. We examined the northern Mediterranean Sea Basin (Med Basin) and four additional med-regions: California, central Chile, sw Australia, and the sw Cape of South Africa (Table 1). The Med Basin includes data from Portugal, Spain, France, Italy, Slovenia, Bosnia-Herzegovina, Montenegro, Croatia, Macedonia (Former

Yugoslav Republic of Macedonia), Serbia, Albania, Greece, Bulgaria, and Turkey. Catchments from the southern and eastern Med Basin countries were not considered due to the paucity of reliable data available for these countries. A catchment-level database for freshwater fish presence–absence records was compiled from available literature (see Table S1 Supplemental Material for a list of sources) for 374 catchments within these regions: the Iberian Peninsula (35), France (20), Italy (36), the eastern Adriatic Coast (17), Greece (90), Turkey (40), California (32), Chile (13), sw Australia (33), and the sw Cape (48). For each catchment, we recorded the number of historical native (including extirpations), extirpated native, and non-native fishes. Non-native species were defined as species that did not historically occur in the area, but have subsequently established self-sustaining populations as a result of human activities and included translocations (i.e. species native to the region but not a particular catchment). The “historical” species assemblage for each region was reconstructed from the literature, whereas the “present” species assemblage was based on the most recent available data, taking into account recorded introductions and extirpations. For some analyses, the catchment-level data were aggregated to regional level using the biogeographic regions delineated by Abell et al. (2008).

A total of 136 species of fishes from 26 families in 13 orders have been recorded as introduced and established into the med-regions included in this study (Table 1). The Med Basin has received 88 species from 21 families and 10 orders while other med-regions received 68 species from 19 families in 10 orders. Some regions such as California or the Italian Peninsula currently have more species of introduced than of native origin. The most widely introduced fish are global invaders such as the eastern mosquitofish *Gambusia holbrooki*, common carp *Cyprinus carpio*, rainbow trout *Oncorhynchus mykiss*, goldfish *Carassius auratus*, and similar species generally from European or North American origin and introduced for sport fisheries or aquaculture (Table 2). Species translocation within regions has been more frequent in California (12 species) and the Cantabric coast-Languedoc region (10) but not recorded in numerous regions (Aegean Sea, Western, Southern, and Central Anatolia, Chile, and sw Australia drainages). Ten regions recorded regional extirpations (Table 1), particularly Central Anatolia (8 species) followed by California, Cantabric coast-Languedoc,

Table 1 Fish richness and biotic homogenisation in med-regions

	Region codes	No. species				Taxonomic similarity (%)			Functional similarity (%)		
		<i>N</i>	<i>X</i>	<i>T</i>	<i>I</i>	TS	TS _H	ΔTS	FS	FS _H	ΔFS
All regions		482	11	46	136		6.83	7.47		68.69	6.80
Northern Mediterranean		374	8	33	88		8.63	7.80		71.83	6.65
California, Chile, sw Aus, sw Cape		108	3	14	68		0.08	6.24		61.68	7.39
Western Iberia	W Ib	31	1	2	15	65.22	7.91	8.24	80.70	73.96	3.96
Southern Iberia	S Ib	28	2	2	17	57.78	9.46	7.09	77.00	71.71	5.14
Eastern Iberia	E Ib	27	1	5	24	50.98	9.84	10.35	69.26	71.01	9.25
Cantabric Coast-Languedoc	Cant	48	2	10	22	65.71	11.44	9.27	82.47	73.57	7.07
Italian Peninsula	It P	23	1	^a	45	32.35	10.47	9.47	51.11	67.45	14.03
Gulf of Venice (Po drainages)	Po	39	2	^a	34	50.68	10.70	10.21	70.91	76.55	3.15
Dalmatian coast	Dal	58	2	1	27	65.88	6.71	10.39	81.32	70.02	6.76
South East Adriatic	Adr	50	3	6	28	60.26	5.84	8.60	80.00	74.43	5.45
Ionian drainages	Ion	39	1	9	26	58.46	7.28	8.90	75.73	76.35	5.36
Aegean drainages	Aeg	29	0	0	10	74.36	7.18	4.62	85.29	71.48	1.20
Vardar	Var	38	0	4	12	76.00	11.03	6.48	86.36	76.44	3.72
Thrace	Thr	66	0	7	17	79.52	10.83	6.65	88.59	68.04	9.02
Western Anatolia	W An	53	0	0	9	85.48	8.10	5.96	92.17	73.78	7.47
Southern Anatolia	S An	45	0	0	7	86.54	6.53	5.34	92.78	74.05	4.48
Central Anatolia	C An	81	3	0	8	86.52	6.16	5.45	97.36	58.18	13.66
California	Cal	38	3	12	44	42.68	0.00	5.53	64.96	72.12	2.56
Chile	Chl	28	0	0	23	54.90	0.15	7.65	70.89	66.55	9.65
SW Australia	SW Aus	10	0	0	10	50.00	0.15	6.53	66.67	39.89	9.68
SW Cape	SW Cape	33	0	2	16	67.35	0.00	5.25	80.49	68.16	7.66

Reported statistics include the number of freshwater fish species that are native (*N*), extirpated (*X*), translocated within the region (*T*), and introduced or exotic (excluding translocated) to the region (*I*); the pairwise taxonomic similarity between historical and present-day communities (*TS*), the average historical pairwise taxonomic similarity (*TS_H*), the average change in pairwise taxonomic similarity (*ΔTS*); the pairwise functional similarity between historical and present-day communities (*FS*), the average historical pairwise functional similarity (*FS_H*), and the average change in pairwise functional similarity (*ΔFS*) between the historical and present-day fish faunas

^a Levels of translocation in the Italian regions could not be calculated from the available data

and Southern Iberia (3 spp. each). California, Central Anatolia, and the South-eastern Adriatic Coast are the only regions with known global extirpations: *Gila crassicauda* and *Pogonichthys ciscooides* in California; *Alburnus akili* and *Pseudophoxinus handlirschi* in Central Anatolia; and *Chondrostoma scodrense* in the Southern Adriatic Coast.

The introduction of non-native fishes has resulted in the loss of faunal uniqueness of these regions while increasing the total number of fish species (see also Leprieur et al., 2008; Marr et al., 2010). The highest number of introduced species is found for California, followed by Peninsular Italy, the Gulf of Venice Drainages, and the Dalmatian Coast. The high number

of non-native fishes found in Italy can be explained by the higher lack of control on freshwater fish introductions there (Copp et al., 2005; García-Berthou et al., 2005). Further, our results confirm that California is an invasion hotspot (e.g. freshwater fishes, Leprieur et al., 2008; plants, Jiménez et al., 2008).

Taxonomic and geographical patterns

The analysis of taxonomic and geographical patterns of freshwater fish introductions highlights the role of human mediation in the selection of the species introduced into med-regions. Our analyses reveal that

Table 2 Summary of the 20 freshwater fishes most widely introduced in the 19 med-regions studied

Species	W Ib	S Ib	E Ib	Cant	It P	Po	Dal	Adr	Ion	Aeg
<i>Gambusia holbrooki</i>	0.90	1.00	0.71	0.50	0.39	0.42	1.00	1.00	0.58	0.32
<i>Cyprinus carpio</i>	1.00	0.88	1.00	0.85	0.87	0.75	0.88	0.89	0.42	0.12
<i>Oncorhynchus mykiss</i>	0.45	0.38	0.71	0.85	0.39	0.58	0.75	0.67	0.29	0.12
<i>Carassius auratus</i>	1.00	0.75	1.00	0.35	0.87	0.83	0.25	0.33	0.05	
<i>Lepomis gibbosus</i>	0.75	0.75	0.43	0.65	0.65	0.50	1.00	0.22	0.05	
<i>Salmo trutta</i>	0.35	0.13	0.29	0.25	1.00	1.00	0.50		0.03	
<i>Carassius gibelio</i>				0.40			0.88	0.44	0.18	0.08
<i>Micropterus salmoides</i>	0.75	0.88	0.43	0.10	0.35	0.33	0.13		0.03	
<i>Pseudorasbora parva</i>			0.29	0.30	0.43	0.75	0.38	0.78	0.05	
<i>Esox lucius</i>	0.15	1.00	0.71	0.15	0.04		0.50	0.11		
<i>Sander lucioperca</i>	0.10	0.13	0.43	0.45	0.13	0.33	0.25	0.11		
<i>Gobio lozanoi</i>	1.00	0.75	0.71							
<i>Tinca tinca</i>		0.13					0.88	0.22	0.16	
<i>Ameiurus melas</i>	0.50	0.25	0.14	0.25	0.26	0.50	0.13	0.11		
<i>Ctenopharyngodon idella</i>					0.09	0.08	0.25	0.33	0.16	0.08
<i>Silurus glanis</i>	0.50		0.29	0.35	0.13	0.42	0.25	0.11	0.08	
<i>Gambusia affinis</i>										
<i>Salvelinus fontinalis</i>	0.50		0.29		0.04	0.08	0.13	0.11	0.03	
<i>Perca fluviatilis</i>			0.29	0.40	0.09		0.25	0.11	0.05	
<i>Carassius carassius</i>				0.60	0.13	0.08	0.25			

Species	Var	Thr	W An	S An	C An	Cal	Chl	SW Aus	SW Cape
<i>Gambusia holbrooki</i>	0.71	0.61	0.75	1.00	0.50		0.92	0.76	
<i>Cyprinus carpio</i>	0.14					0.47	1.00	0.09	0.35
<i>Oncorhynchus mykiss</i>	0.57	0.22	0.25	0.67	0.56		1.00	0.30	0.33
<i>Carassius auratus</i>		0.09	0.08		0.11	0.38	0.77	0.30	0.15
<i>Lepomis gibbosus</i>	0.57	0.22	0.25	0.17		0.09			
<i>Salmo trutta</i>	0.14					0.31	1.00	0.06	0.17
<i>Carassius gibelio</i>	0.86	0.57	0.50	0.50	0.33				
<i>Micropterus salmoides</i>						0.59			0.54
<i>Pseudorasbora parva</i>	0.43	0.22	0.17	0.17	0.11				
<i>Esox lucius</i>	0.14	0.04							
<i>Sander lucioperca</i>		0.04	0.33		0.28				
<i>Gobio lozanoi</i>									
<i>Tinca tinca</i>	0.14						0.69		0.02
<i>Ameiurus melas</i>						0.31	0.15		
<i>Ctenopharyngodon idella</i>	0.29	0.04					0.38		
<i>Silurus glanis</i>									
<i>Gambusia affinis</i>						0.50	0.92		0.23
<i>Salvelinus fontinalis</i>	0.14	0.04				0.16	0.54		
<i>Perca fluviatilis</i>	0.14							0.27	
<i>Carassius carassius</i>		0.09			0.11				

The proportion of catchments by region occupied by the species is given (blank entries = species has not been introduced) ordered by level of introduction. See Table 1 for region codes

the majority of non-native fish species (121 out of 136) introduced in these regions belong to five taxonomic orders (Cypriniformes, Cyprinodontiformes, Perciformes, Salmoniformes, and Siluriformes), as noted in previous regional-scale studies in California (Moyle & Marchetti, 2006), the Iberian Peninsula (Alcaraz et al., 2005), sw Australia (Morgan et al., 2004), and five med-regions (Marr et al., 2010). In this review, nine families of freshwater fish have been found to be non-randomly introduced (i.e. Cyprinidae, Salmonidae, Centrarchidae, Cichlidae, Gobiidae, Acipenseridae, Ictaluridae, Poeciliidae, and Percidae) accounting for 81% of the species established. Similarly, Kark & Sol (2004) found that only six bird families represent more than 78% of introductions into the Med Basin that were also non-randomly introduced. In addition, all the med-regions we examined currently contain orders or families not historically present. This is particularly noticeable in the Southern Hemisphere. Historically, Salmoniformes and Cyprinodontiformes were not present in any of the Southern Hemisphere's med-regions, while Cypriniformes were absent from sw Australia and Chile. Moreover, the families Centrarchidae and Cichlidae were never present in any of the med-regions of the Southern Hemisphere.

All nine families of freshwater fish have been introduced in med-regions because they are of interest to humans (see also Alcaraz et al., 2005). Salmoniformes of the family Salmonidae are important recreational angling and aquaculture species and they are significantly over-represented in most regions, with the exception of Anatolia, where non-native salmonids appear to be unable to establish self-sustaining populations (Çelikkale, 2002). Perciformes contain important recreational angling (e.g. Centrarchidae) and aquaculture (e.g. Cichlidae) species and were over-represented only in California and the sw Cape. The family Centrarchidae were over-represented in the Med Basin west of the Aegean Sea, California, and the sw Cape, highlighting the importance of recreational fisheries in these regions.

By contrast, we found that Characiformes and Siluriformes were under-represented when all regions were considered together, but not for any specific region. Indeed, Siluriformes and Characiformes have large numbers of tropical species that may not be able to readily establish in med-regions, where environmental conditions may extend beyond their physiological tolerances (Marr et al., 2010). Cypriniformes is

a large order which has not been introduced to the same extent as smaller families, such as Salmonidae, probably because of their low economic value as recreational and aquaculture species. Overall, our results provide evidence that taxonomic preference and human association are important factors predicting successful freshwater fish introductions (see also Alcaraz et al., 2005; Blanchet et al., 2010).

The regional-level analysis reveals that each region received species from a unique set of geographical origins. The diversity of geographical origins poses a challenge to conservation authorities to identify potential source regions of species that would successfully become established. A similar result was obtained for plants in central Chile and California (Jiménez et al., 2008). The diversity of origins highlights the importance of studies aimed at identifying characteristics of species that have successfully established self-sustaining populations in other regions.

Patterns of taxonomic homogenisation

The analysis of taxonomic homogenisation provides an indication of whether the taxonomic composition of species assemblages in the respective med-regions are becoming more, or less, similar over time. Taxonomic homogenisation of the freshwater fish faunas of the med-regions was calculated using presence–absence data at both regional- and catchment-level; see Supplemental Material for detailed methods. Jaccard's index of similarity was selected for the taxonomic data because it is the most commonly used index in taxonomic homogenisation studies (Olden & Rooney, 2006); but Baiser et al. (2012) has discussed other appropriate indices for this type of analysis.

The average historical taxonomic similarity among native freshwater fish faunas of the northern Med Basin, calculated as the average of the pairwise similarity, was 8.6%, whereas that for the other med-regions was 0.1% (California 0%; Chile 0.2%; sw Australia 0.2%; and sw Cape 0%). Our results show strong evidence of on-going taxonomic homogenisation in the fish faunas of the med-regions (~7.5% when considering all the studied regions: northern Med 7.8%; California 5.5%; Chile 7.7%; sw Australia 6.5%; and sw Cape 5.3%). The level of taxonomic homogenisation differs among regions (from 4.6 to 10.4%, Table 1) and appears to be independent of the

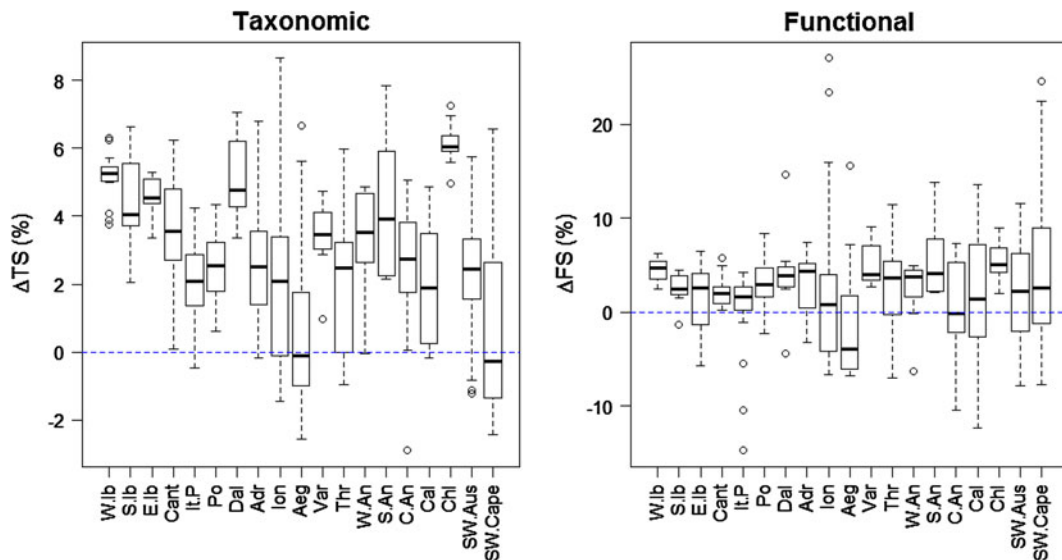


Fig. 2 Box and whisker plots summarising the catchment-level changes in taxonomic (ΔTS) and functional (ΔFS) compositional similarity between the present-day and historical freshwater fish assemblages in the northern Mediterranean Basin, California, Chile, south-western Australia, and the south-

western Cape. Each box corresponds to 25th and 75th percentiles; the dark line inside each box represents the median; error bars show the minima and maxima except for outliers (*open circles*, corresponding to values >1.5 box heights from the box). See Table 1 for region codes

historical and present-day assemblages is significant (PERMDISP, $P < 0.05$), but mainly as a result of changes for Western Iberia, California, Chile, and the sw Cape. The overall change in the position of the regional centroids between the historical and present-day catchments is significant for all regions (PERMANOVA, $P < 0.05$) with the exception of the Med Basin east of the Ionian Sea.

This high level of taxonomic homogenisation found at across med-regions can be explained by the widespread introduction of a common set of non-native fishes (e.g. *G. holbrooki*, *C. carpio*, *O. mykiss*, *C. auratus*, *Micropterus salmoides*, *Lepomis gibbosus*, *Carassius gibelio*, *Salmo trutta*, *Lepomis macrochirus*, *Gambusia affinis*, *Pseudorasbora parva*, and *Oreochromis mossambicus*). For instance, our results show that 10 species were introduced into five or more regions and that the above 12 species were introduced into more than 10% of the studied catchments.

Our results contrast with those found by Villéger et al. (2011), who showed that the current level of taxonomic homogenisation for freshwater fishes was rather low (0.5%), hence concluding that the “Homogocene era” is not yet the case for the freshwater fish fauna at the worldwide scale. However, Villéger et al. (2011) studied taxonomic homogenisation across

different climatic regions by quantifying the changes in similarity caused by non-native fishes introductions between tropical and temperate catchments. We indeed expect that catchments from different climatic regions are more likely to be colonised by different non-native species as result of environmental filtering (e.g. Lapointe & Light, 2012), hence explaining the low level of taxonomic homogenisation found by Villéger et al. (2011). Previous large-scale analyses of multiple climate regions support this perspective (Olden et al., 2008; Baiser et al., 2012). Overall, we concur with Pauchard et al. (2004) that analysing global-scale patterns of biotic homogenisation across climatically similar regions allows a better understanding of biotic homogenisation processes by isolating large-scale factors other than regional climate, e.g. by focusing on the role of human use of non-native species and the characteristics of the recipient pool of native species.

Patterns of functional homogenisation

Most biotic homogenisation studies focus on changes in the taxonomic composition of faunas and floras (see Olden et al., 2010), whereas changes in functional trait

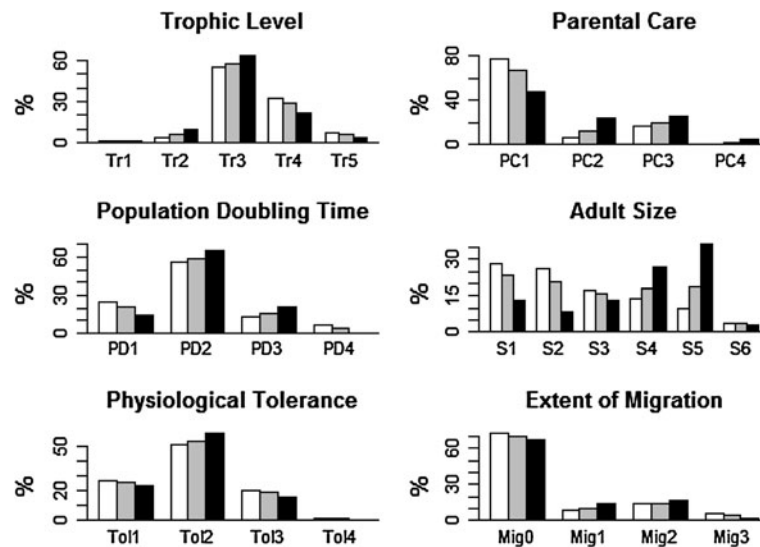


Fig. 3 Bar plots summarising the changes in functional trait composition of the freshwater fish assemblages over all med-regions (%) included in this study. The *white bars* represent the historical fish assemblage, the *grey bars* the present day fish assemblages, and the *black bars* represent the introduced fish assemblage. The trait codes are adult trophic status (*Tr1* planktivore; *Tr2* herbivore and detritivore; *Tr3* invertivore; *Tr4* omnivore; *Tr5* piscivore); degree of parental care (*PC1* no parental care; *PC2* brood hiders; *PC3* guarders; *PC4* bearers);

population doubling time (*PD1* <15 months; *PD2* 1.4–4.4 years; *PD3* 4.4–14 years; *PD4* >14 years); maximum adult size (*S1* <10 cm; *S2* 11–20 cm; *S3* 21–40 cm; *S4* 41–80 cm; *S5* 81–160 cm; *S6* >160 cm standard length); physiological tolerance (*Tol1* intolerant fishes; *Tol2* moderately tolerant fishes; *Tol3* tolerant fishes; *Tol4* extremely tolerant fishes); and extent of migration (*Mig0* non-migratory, *Mig1* potamodromous, *Mig2* diadromous, *Mig3* amphidromous)

composition have received considerably less attention (but see Pool & Olden, 2012). Yet, the functional component of biodiversity has been shown to explain ecosystem functioning better than classical taxonomic measures of diversity (see Hooper et al., 2005). We calculated functional homogenisation of the freshwater fish faunas of the med-regions using presence–absence data (at regional- and catchment-levels) and functional trait data compiled from FishBase (Froese & Pauly, 2010) (see Supplemental Material for detailed methods). The Bray–Curtis similarity coefficient was used to evaluate the functional homogenisation between the regions/catchments.

The average historical functional similarity among native freshwater fish faunas of the northern Med Basin was 71.8%, whereas that for the other med-regions was 61.7% (California 72.1%; Chile 66.6%; sw Australia 68.2%; and sw Cape 68.2%). The functional composition of regional fish assemblages in med-regions has also changed over recent time (PERMANOVA, $P < 0.005$); mean compositional similarity has increased between 1.2 and 14.0% (mean 6.8%: northern Med 6.7%; California 2.6%; Chile 9.7%; sw Australia 9.7%; and sw Cape 7.7%,

Table 2). Functional homogenisation is highest in Peninsular Italy (14.0%) and Central Anatolia (13.7%) and lowest in the Aegean drainages (1.2%) and California (2.6%) (Table 1). The N-MDS analysis shows a strong overall tendency toward more functionally similar fish faunas (Fig. 1b). Six functional traits contributed to more than 60% of the increase in similarity of the faunal assemblages, each increasing in frequency by more than 5% between the historical and present-day assemblages. Current assemblages have more species with the following functional traits: being non-migratory, with a population doubling time between 1.4–4.4 years, invertivores, exhibiting no parental care, having moderate levels of tolerance, and with large body sizes (ranges of 40–160 cm) (Fig. 3).

All studied regions showed catchment-level functional homogenisation in more than 50% of their catchments with the exception of Central Anatolia and the Aegean Sea drainages, which show differentiation (Fig. 2). Functional homogenisation is highest in Chile, followed by Western Iberia and the Adriatic Sea drainages. The change between the historical and present-day assemblages is significant for all regions (PERMANOVA, $P < 0.05$) with the exception of the

Med Basin east of the southern Adriatic drainages. The changes in functional similarity are the result of the introduction of species with the traits highlighted in the regional-level analysis. Our catchment-scale analysis reveals changes in functional composition of fish assemblages for all regions as a result of non-native fish introductions and native species extirpations (circa 7% when considering all the studied regions). We also found that catchments exhibiting taxonomic homogenisation are also homogenised in terms of their functional trait composition, a pattern also highlighted by Pool & Olden, (2012) in a finer spatial scale study.

Overall, our results are concordant with one of the general predictions of biotic homogenisation: specialist species with limited ranges are being replaced by widespread generalist species (McKinney & Lockwood, 1999; Clavel et al., 2010). Present-day assemblages across regions have more large-bodied species, display non-migratory behaviour, exhibit faster population doubling times, and are characterised as invertivores, with no parental care (and presumable higher fecundity), and moderate levels of physiological tolerance. These shifts in the functional composition may have many subtle impacts on the recipient systems. For instance, the increase in large-bodied and long-lived species may result in the increased hold-up of nutrients in the freshwater system, which reduces transport of freshwater-derived nutrients to estuaries and inshore marine systems. With regards to body size, our results have important implications because there is increasing empirical evidence that changing the body size structure of assemblages affects ecosystem functioning (Long & Morin, 2005; Woodward et al., 2005).

Concluding remarks

Overall, this study emphasises that the introduction of non-native fish species has resulted in the loss of uniqueness of med-regions while increasing the total number of fish species. Specifically, our results suggest that the introduction of non-native fish species and the loss of native fish species affected the functional composition of freshwater fish assemblages, which may have important consequences for the functioning of freshwater ecosystems in med-regions.

The extent of these alterations requires further attention by focusing on the interactive effects of non-

native fish introductions and habitat alteration. In many of the med-regions, the remaining native populations are restricted to ever decreasing river fragments that have not been invaded by non-native species or altered by unsustainable water consumption. We predict that the patterns of biotic homogenisation seen in freshwater ecosystems of med-regions will intensify in the future unless these regions are recognised as highly valuable ecosystems for conservation and long-term sustainable management.

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