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

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40   **Abstract** Mediterranean-climate regions (med-regions) are global hotspots of endemism facing mounting

41   environmental threats associated with human-related activities, including the ecological impacts associated with

42   non-native species introductions. We review freshwater fish introductions across med-regions to evaluate the

43   influences of non-native fishes on the biogeography of taxonomic and functional diversity. Our synthesis

44   revealed that 136 freshwater fish species (26 families, 13 orders) have been introduced into med-regions

45   globally. These introductions, and local extirpations, have increased taxonomic and functional faunal similarity

46   among regions by an average of 7.5% (4.6-11.4%; Jaccard) and 7.2% (1.4-14.0%; Bray-Curtis), respectively.

47   Faunal homogenization was highest in Chile and the western Med Basin, whereas sw Cape and the Aegean Sea

48   drainages showed slight differentiation (decrease in faunal similarity) over time. At present, fish faunas of

49   different med-regions have widespread species in common (e.g. *Gambusia holbrooki, Cyprinus carpio,*

50   *Oncorhynchus mykiss, Carassius auratus,* and *Micropterus salmoides*) which are typically large-bodied, non-

51   migratory, have higher physiological tolerance, and display fast population growth rates. Our findings suggest

52   that intentional and accidental introductions of freshwater fish have dissolved dispersal barriers and significantly

53   changed the present-day biogeography of med-regions across the globe. Conservation challenges in med-regions

54   include understanding the ecosystem consequences of non-native species at macro-ecological scales.

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56   **Keywords** Introduced species · non-native species · conservation biogeography · taxonomic homogenization ·

57   functional homogenization

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Introduction

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62   Mediterranean-climate regions (med-regions) are recognised hotspots of biodiversity and endemism (Cowling et

63   al., 1996). Concurrently, they are among the most densely human-populated regions because of their favourable

64   climates that support valuable agricultural produce (e.g., fruit, winter wheat, and wine). Human enterprise in

65   these regions has resulted in extensive habitat alteration, water pollution, high levels of water extraction and

66   regulation, and the intentional and accidental introduction of many non-native species (Di Castri, 1991). As a

67   result, freshwater ecosystems in med-regions are highly modified and continue to face mounting pressure from

68   growing human populations and water development schemes (Economidis, 1995; Collares-Pereira et al., 2000;

69   Millennium Ecosystem Assessment, 2005; Shumka et al., 2010). Unfortunately, aquatic faunas in these regions

70   are considered to be experiencing among the fastest rates of species imperilment globally (Moyle, 1995).

71   Freshwater ecosystems are particularly affected by non-native species introductions, which produce a

72   range of ecological and economic impacts (Cambray, 2003; Cucherousset & Olden, 2011; García-Berthou &

73   Moyle, 2011). For instance, the zebra mussel *Dreissena polymorpha* and the Asian clam *Corbicula fluminea* act

74   as ecosystem engineers and have caused significant economic impacts in North America and Europe by

75   clogging water intake structures. Crayfishes have been introduced worldwide, such as the red swamp crayfish

76   *Procambarus clarkii* that often reaches high abundance in Mediterranean waters and these introductions have

77   contributed to the decline of native species (e.g., Gherardi & Acquistapace, 2007). Riparian or aquatic plants

78   such as the water hyacinth *Eichhornia crassipes*, Eurasian watermilfoil *Myriophyllum spicatum*, hydrilla

79   *Hydrilla verticillata*, the ferns *Salvinia molesta* and *Azolla filiculoides*, and the giant reed *Arundo donax*, and

80   insects, such as the black locust *Robinia pseudoacacia,* are global invaders that have profound effects on

81   ecosystem structure and functioning (Brunel et al., 2010).

82   Our review focuses on spatial patterns and temporal trends in freshwater fish introductions in med-

83   regions. These regions are hotspots both of endemisms and freshwater fish introductions (Leprieur et al., 2008;

84   Tedesco et al. 2012) and med-region aquatic habitats are severely threatened, in part, because of water scarcity

85   and environmental degradation (Hermoso & Clavero, 2011; Hermoso et al., 2011). Thus, we require a greater

86   understanding of the impacts in these regions to guide management and policy actions. We focus on fish

87   because their native and introduced ranges are well documented across these regions.

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89   **Freshwater fish introductions in mediterranean regions**

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91   Europe's history of non-native fish introductions dates back to the Roman Empire, through the progression of

92   fish culturing in Medieval monasteries and parishes and by the nobility in the Renaissance to the 19th century

93   "Acclimation Societies" that provided incentives for the establishment (acclimation) of non-native plants and

94   animals and the government-sanctioned introductions of the mid-20th century (Copp et al., 2005). At present,

95   numerous non-native fish from a variety of sources have been introduced across Mediterranean Europe for the

96   biological control of aquatic plants and mosquitoes, aquaculture, to compensate for the decline in native fish

97   stocks, and to create new and more diverse recreational fisheries (Cowx, 1997; Hermoso & Clavero, 2011).

98   Although government-sanctioned fish introductions have ceased in many countries, the illegal release of non-

99   native species by anglers and aquarists, including accidental releases from aquaculture facilities, has continued

100   (Elvira & Almodóvar, 2001; Rahel, 2004).

101   Strong commonalities in human land use and invasion histories are evident across med-regions of the

102   world. Non-native species of California were predominantly introduced for recreational angling, commercial

103   fisheries, and forage/bait fish, or intentionally through the ornamental fish trade (Moyle, 1976). Populations of

104   native fish have continued to decline as a result of a suite of threats (Moyle et al., 2011), with some salmonid

105   species now approaching extinction (Katz et al., 2012). In Chile, the creation of recreational fisheries was the

106   primary reason for fish introductions prior to the 1980s (Basulto, 2003), whereas government-sponsored

107   aquaculture has been the major driving force for fish introductions in recent decades (Iriarte et al., 2005;

108   Arismendi et al., 2009). Chile is currently one of the world's largest producers of cultured salmonids,

109   accounting for more than 73% of Chile's aquaculture production (Buschmann et al., 2009). Introduced

110   salmonids dominate the total fish abundance and biomass in streams and lakes (Soto et al., 2006; Arismendi et

111   al., 2009). For example, in southern Chile native fish are absent from 40% of the streams in which salmonids are

112   now present (Soto et al., 2006). The rapid colonisation of South American streams by escapees from salmonid

113   culture facilities has raised concerns regarding the impact of these escapees on the native fish assemblages (Soto

114   et al., 2001; Arismendi et al., 2009; Garcia de Leaniz et al., 2010).

115   In south-western Australia (sw Australia) and the south-western Cape of South Africa (sw Cape), initial

116   introductions involved ornamental fish and food fish for sailors, followed by salmonids for recreational angling,

117   and biological control agents for mosquitoes (de Moor & Bruton, 1988; Morgan et al., 2004; Marr et al., 2012).

118   The illegal release of angling, ornamental, and mosquito control species continues in both regions (Morgan et

119   al., 2004; Impson, 2007). Recent estimates suggest that more than 90% of the river habitat in the sw Cape of

120   Africa is currently invaded by non-native fishes (Marr et al., 2012). As in other med-regions, the rivers in sw

121   Australia and the sw Cape are subject to high levels of water abstraction, habitat degradation, eutrophication,

122   salinization, fragmentation, and pollution (Morgan et al., 2003; Impson, 2007).

123   Despite some benefits (contribution to fishery production, recreational fishery, aquaculture development,

124   mosquito control, and reduction of heavy algal blooms), fish introductions have been associated with significant

125   negative ecological and socio-economic impacts. The ecological impacts are manifested at: genetic (gene

126   transcription, hybridisation); individual (behaviour, morphology, vital rates); population (transmission of

127   parasites/diseases, demographic effects, distributional effects); community (species extirpations, compositional

128   changes, alterations in food webs); and ecosystem (biochemical cycles, energy fluxes between ecosystems,

129   ecological engineering) levels (Cucherousset & Olden, 2011). Phylogenetic history and human affiliation have

130   been identified as predictors favouring species of freshwater fish selected for introduction in med-regions

131   (Alcaraz et al., 2005; Marr et al., 2010). Certain fish families are represented by disproportionally higher

132   numbers of non-native species because of strong human biases towards introducing species, such as game fish,

133   forage fish, and bio-control agents for aquatic weeds or mosquitoes (Clavero & García-Berthou, 2006; García-

134   Berthou, 2007; Marr et al., 2010). The introduction of freshwater fishes has reduced the characteristic endemism

135   of freshwater fish assemblages in med-regions regions (Marr et al., 2010) and the risk of further introductions

136   remains extremely high because of increasing interest in angling, low public awareness about the impacts of

137   non-native fish, and poor mechanisms to enforce bans on non-native fish introductions (Zenetos et al., 2009;

138   Gozlan et al., 2010).

139   By dissolving physical barriers to movement and connecting formerly isolated regions, human-mediated

140   species introductions have dramatically reshuffled the present-day biogeography of freshwater fishes (Leprieur

141   et al., 2008). A growing pattern is emerging where the range expansion of ubiquitous non-native species and the

142   loss of endemic forms tend to be driving the homogenization of the species pools of fish faunas (i.e., decreasing

143   beta-diversity) over time (Olden, 2006). Species introductions have caused shifts in fish community

144   composition, including regional-scale biotic homogenization. It has been emphasised that the importance of

145   identifying and understanding present-day patterns of biotic homogenization with the intention of establishing

146   conservation goals aimed at reducing potential future ecological impacts (Olden, 2006). Although a number of

147   biotic homogenization studies of freshwater fish assemblages have been completed, the majority have focused

148   on taxonomic homogenization in temperate latitudes of the Northern Hemisphere. In contrast, comparative

149   studies between different regions or over multiple scales are lacking (Olden et al., 2010; 2011), but see Velliger

150   et al. (2011), Hermoso et al. (2012) and Vitule et al. (2012). A comparison of introductions across climatically

151   similar regions promotes an understanding of invasion processes by isolating large-scale drivers other than

152   regional climate (Pauchard et al., 2004), and focuses on the role of human activities (Jiménez et al., 2008) and

153   the characteristics of the invading species (Moyle & Marchetti, 2006). Comparative studies may also provide

154   valuable information for the conservation of native species and the management of non-native species by

155   establishing priority lists of potentially harmful species, evaluating the risk of homogenization of the invaded

156   communities, developing guidelines for sustainable ecosystem management, and targeting dispersal pathways

157   for the management of non-native species (Pauchard et al., 2004).

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159   **Analysis of freshwater fish introductions**

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161   Freshwater fish are among the most widely introduced vertebrate groups and will continue to be introduced even

162   though their detrimental impacts have been well-documented (Lintermans, 2004; Cucherousset & Olden, 2011).

163   We conducted a global assessment of freshwater fish introductions across med-regions to compare the

164   taxonomic and functional dimensions of biotic homogenization resulting from the introduction of non-native

165   species and the extirpation of native species. We compiled data on freshwater bony fish (Osteichthyes) in med-

166   regions, excluding marine species that only occasionally enter freshwaters. We examined the northern

167   Mediterranean Sea Basin (Med Basin) and four additional med-regions: California, central Chile, sw Australia,

168   and the sw Cape of South Africa (Table 1). The Med Basin includes data from Portugal, Spain, France, Italy,

169   Slovenia, Bosnia-Herzegovina, Montenegro, Croatia, Macedonia (Former Yugoslav Republic of Macedonia),

170   Serbia, Albania, Greece, Bulgaria, and Turkey. Catchments from the southern and eastern Med Basin countries

171   were not considered due to the paucity of reliable data available for these countries. A catchment-level database

172   for freshwater fish presence-absence records was compiled from available literature (see Table S1 Supplemental

173   Material for a list of sources) for 374 catchments within these regions: the Iberian Peninsula (35), France (20),

174   Italy (36), the eastern Adriatic Coast (17), Greece (90), Turkey (40), California (32), Chile (13), sw Australia

175   (33), and the sw Cape (48). For each catchment, we recorded the number of historical native (including

176   extirpations), extirpated native, and non-native fishes. Non-native species were defined as species that did not

177   historically occur in the area, but have subsequently established self-sustaining populations as a result of human

178   activities and included translocations (i.e., species native to the region but not a particular catchment). The

179   "historical" species assemblage for each region was reconstructed from the literature, whereas the "present"

180   species assemblage was based on the most recent available data, taking into account recorded introductions and

181   extirpations. For some analyses, the catchment-level data were aggregated to regional level using the

182   biogeographic regions delineated by Abell et al. (2008).

183   A total of 136 species of fishes from 26 families in 13 orders have been recorded as introduced and

184   established into the med-regions included in this study (Table 1). The Med Basin has received 88 species from

185   21 families and 10 orders while other med-regions received 68 species from 19 families in 10 orders. Some

186   regions such as California or the Italian Peninsula currently have more species of introduced than of native

187   origin. The most widely introduced fish are global invaders such as the eastern mosquitofish *Gambusia*

188   *holbrooki*, common carp *Cyprinus carpio*, rainbow trout *Oncorhynchus mykiss,* goldfish *Carassius auratus,* and

189   similar species generally from European or North American origin and introduced for sport fisheries or

190   aquaculture (Table 2). Species translocation within regions has been more frequent in California (12 species)

191   and the Cantabric coast-Languedoc region (10) but not recorded in numerous regions (Aegean Sea, Western,

192   Southern, and Central Anatolia, Chile, and sw Australia drainages). Ten regions recorded regional extirpations

193   (Table 1), particularly Central Anatolia (8 species) followed by California, Cantabric coast-Languedoc, and

194   Southern Iberia (3 spp. each). California, Central Anatolia, and the South-eastern Adriatic Coast are the only

195   regions with known global extirpations: *Gila crassicauda* and *Pogonichthys ciscoides* in California; *Alburnus*

196   *akili* and *Pseudophoxinus handlirschi* in Central Anatolia; and *Chondrostoma scodrense* in the Southern

197   Adriatic Coast.

198   The introduction of non-native fishes has resulted in the loss of faunal uniqueness of these regions while

199   increasing the total number of fish species (see also Leprieur et al., 2008; Marr et al., 2010). The highest number

200   of introduced species is found for California, followed by Peninsular Italy, the Gulf of Venice Drainages, and

201   the Dalmatian Coast. The high number of non-native fishes found in Italy can be explained by the higher lack of

202   control on freshwater fish introductions there (Copp et al., 2005; García-Berthou et al., 2005). Further, our

203   results confirm that California is an invasion hotspot (e.g., freshwater fishes, Leprieur et al., 2008; plants,

204   Jiménez et al., 2008).

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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 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 and they 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 overrepresented 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

237   their low economic value as recreational and aquaculture human purposes. Overall, our results provide evidence

238   that taxonomic preference and human association are important factors predicting successful freshwater fish

239   introductions (see also Alcarazet al., 2005, Blanchet et al., 2010).

240   The regional level analysis reveals that each region received species from a unique set of geographical

241   origins. The diversity of geographical origins poses a challenge to conservation authorities to identify potential

242   source regions of species that would successfully become established. A similar result was obtained for plants in

243   central Chile and California (Jiménez et al., 2008). The diversity of origins highlights the importance of studies

244   aimed at identifying characteristics of species that have successfully established self-sustaining populations in

245   other regions.

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247   **Patterns of taxonomic homogenization**

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249   The analysis of taxonomic homogenization provides an indication of whether species assemblages in the

250   respective med-regions are becoming more, or less, similar in taxonomic composition over time. Taxonomic

251   homogenization of the freshwater fish faunas of the med-regions was calculated using presence absence data at

252   both regional- and catchment-level; see Supplemental Material for detailed methods. Jaccard's index of

253   similarity was selected for the taxonomic data because it is the most commonly used index in taxonomic

254   homogenization studies (Olden & Rooney, 2006); but Baiser et al. (2012) has discussed other appropriate

255   indices for this type of analysis.

256   The average historical taxonomic similarity among native freshwater fish faunas of the northern Med

257   Basin, calculated as the average of the pair-wise similarity, was 8.6%, whereas that for the other med-regions

258   was 0.1% (California 0%; Chile 0.2%; sw Australia 0.2%; and sw Cape 0%). Our results show strong evidence

259   of on-going taxonomic homogenization in the fish faunas of the med-regions (~ 7.5% when considering all the

260   studied regions: northern Med 7.8%; California 5.5%; Chile 7.7%; sw Australia 6.5%; and sw Cape 5.3%). The

261   level of taxonomic homogenization differs among regions (from 4.6 to 10.4%, Table 1) and appears to be

262   independent of the number of species historically native to the area. Taxonomic homogenization was highest in

263   Med Basin regions west of the Adriatic Sea (Cantabric Coast > Vardar > Thrace > Gulf of Venice; Table 1).

264   Multivariate ordination analysis (N-MDS) on Jaccard's similarity index among regions supports a strong overall

265   tendency toward increasing similarity of fish fauna over time (Fig. 1a). Although present-day faunal

266 assemblages remain more similar to their historical assemblages than to those of any other regions, regions have

267 become considerably more similar in present times (PERMANOVA, $P < 0.05$).

268   The catchment-level analysis shows taxonomic homogenization in all regions, with the exception of the

269 sw Cape and the Aegean Sea drainages, which shows differentiation in more than 50% of their catchments (Fig.

270 2). Homogenization is highest in Chile and the western Med Basin. The overall change in regional multivariate

271 dispersion of catchments (i.e., variability in species composition) between the historical and present-day

272 assemblages is significant (PERMDISP, $P < 0.05$), but mainly as a result of changes for Western Iberia,

273 California, Chile and the sw Cape. The overall change in the position of the regional centroids between the

274 historical and present-day catchments is significant for all regions (PERMANOVA, $P < 0.05$) with the

275 exception of the Med Basin east of the Ionian Sea.

276   This high level of taxonomic homogenization found at across med-regions can be explained by the

277 widespread introduction of a common set of non-native fishes (e.g., *G. holbrooki*, *C. carpio*, *O. mykiss*, *C.*

278 *auratus*, *Micropterus salmoides*, *Lepomis gibbosus*, *Carassius gibelio*, *Salmo trutta*, *Lepomis macrochirus*,

279 *Gambusia affinis*, *Pseudorasbora parva,* and *Oreochromis mossambicus*). For instance, our results show that 10

280 species were introduced into five or more regions and that the above 12 species were introduced into more than

281 10% of the studied catchments.

282   Our results contrast with those found by Villéger et al. (2011), who showed that the current level of

283 taxonomic homogenization for freshwater fishes was rather low (0.5%), hence concluding that the

284 "Homogocene era" is not yet the case for the freshwater fish fauna at the worldwide scale. However, Villéger et

285 al. (2011) studied taxonomic homogenization across different climatic regions by quantifying the changes in

286 similarity caused by non-native fishes introductions between tropical and temperate catchments. We indeed

287 expect that catchments from different climatic regions are more likely to be colonised by different non-native

288 species as result of environmental filtering (e.g., Lapointe & Light, 2012), hence explaining the low level of

289 taxonomic homogenization found by Villéger et al. (2011). Previous large-scale analyses of multiple climate

290 regions support this perspective (Olden et al., 2008; Baiser et al., 2012). Overall, we concur with Pauchard et al.

291 (2004) that analysing global-scale patterns of biotic homogenization across climatically similar regions allows a

292 better understanding of biotic homogenization processes by isolating large-scale factors other than regional

293 climate, e.g. by focusing on the role of human use of non-native species and the characteristics of the recipient

294 pool of native species.

295

Patterns of functional homogenization

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298 Most biotic homogenization studies focus on changes in the taxonomic composition of faunas and floras (see

299 Olden et al., 2010), whereas changes in functional trait composition have received considerably less attention

300 (but see Pool & Olden, 2012). Yet, the functional component of biodiversity has been shown to explain

301 ecosystem functioning better than classical taxonomic measures of diversity (see Hooper et al., 2005). We

302 calculated functional homogenization of the freshwater fish faunas of the med-regions using presence-absence

303 data (at regional- and catchment-levels) and functional trait data compiled from FishBase (Froese & Pauly,

304 2010) (see Supplemental Material for detailed methods). The Bray-Curtis similarity coefficient was used to

305 evaluate the functional homogenization between the regions/catchments.

306 The average historical functional similarity among native freshwater fish faunas of the northern Med

307 Basin was 71.8%, whereas that for the other med-regions was 61.7% (California 72.1%; Chile 66.6%; sw

308 Australia 68.2%; and sw Cape 68.2%). The functional composition of regional fish assemblages in med-regions

309 has also changed over recent time (PERMANOVA, $P < 0.005$); mean compositional similarity has increased

310 between 1.2 and 14.0% (mean 6.8%: northern Med 6.7%; California 2.6%; Chile 9.7%; sw Australia 9.7%; and

311 sw Cape 7.7%, Table 2). Functional homogenization is highest in Peninsular Italy (14.0%) and Central Anatolia

312 (13.7%) and lowest in the Aegean drainages (1.2%) and California (2.6%) (Table 1). The N-MDS analysis

313 shows a strong overall tendency toward more functionally similar fish faunas (Fig. 1b). Six functional traits

314 contributed to more than 60% of the increase in similarity of the faunal assemblages, each increasing in

315 frequency by more than 5% between the historical and present-day assemblages. Current assemblages have

316 more species with the following functional traits: being non-migratory, with a population doubling time between

317 1.4-4.4 years, invertivores, exhibiting no parental care, having moderate levels of tolerance, and with large body

318 sizes (ranges of 40-160 cm) (Fig. 3).

319 All studied regions showed catchment-level functional homogenization in more than 50% of their

320 catchments with the exception of Central Anatolia and the Aegean Sea drainages, which show differentiation

321 (Fig. 2). Functional homogenization is highest in Chile, followed by Western Iberia and the Adriatic Sea

322 drainages. The change between the historical and present-day assemblages is significant for all regions

323 (PERMANOVA, $P < 0.05$) with the exception of the Med Basin east of the southern Adriatic drainages. The

324 changes in functional similarity are the result of the introduction of species with the traits highlighted in the

325 regional-level analysis. Our catchment-scale analysis reveals changes in functional composition of fish

326 assemblages for all regions as a result of non-native fish introductions and native species extirpations (circa 7%

327 when considering all the studied regions). We also found that catchments exhibiting taxonomic homogenization

328 are also homogenized in terms of their trait composition, a pattern also highlighted by Pool & Olden (2012) in a

329 finer spatial scale study.

330   Overall, our results are concordant with one of the general predictions of biotic homogenization: specialist

331 species with limited ranges are being replaced by widespread generalist species (McKinney & Lockwood, 1999;

332 Clavel et al., 2010). Present-day assemblages across regions have more large-bodied species, display non-

333 migratory behaviour, exhibit faster population doubling times, and are characterized as invertivores, with no

334 parental care (and presumable higher fecundity), and moderate levels of physiological tolerance. These shifts in

335 the functional composition may have many subtle impacts on the recipient systems. For instance, the increase in

336 large bodied and long lived species may result in the increased hold-up of nutrients in the freshwater system,

337 which reduces transport of freshwater-derived nutrients to estuaries and inshore marine systems. With regards to

338 body size, our results have important implications because there is increasing empirical evidence that changing

339 the body size structure of assemblages affects ecosystem functioning (Long & Morin, 2005; Woodward et al.,

340 2005).

341

342 **Concluding remarks**

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344 Overall, this study emphasizes that the introduction of non-native fish species has resulted in the loss of

345 uniqueness of med-regions while increasing the total number of fish species. Specifically, our results suggest

346 that the introduction of non-native fish species and the loss of native fish species affected the functional

347 composition of freshwater fish assemblages, which may have important consequences for the functioning of

348 freshwater ecosystems in such regions.

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

350 native fish introductions and habitat alteration. In many of the med-regions, the remaining native populations are

351 restricted to ever decreasing river fragments that have not been invaded by non-native species or altered by

352 unsustainable water consumption. We predict that the patterns of biotic homogenization seen in freshwater

353 ecosystems of med-regions will intensify in the future unless these regions are recognised as highly valuable

354 ecosystems for conservation and long-term sustainable management.

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Fig. 1 Non-metric multidimensional scaling summarising a) taxonomic and b) functional changes in fish composition between the historical (▲) and present-day (Δ) assemblages in Mediterranean-climate regions. Convergence of region position in multivariate space provides evidence for taxonomic homogenization over time. See Table 1 for region codes.

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.

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 - potamadromous, Mig2 - diadromous, Mig3 – amphidromous).
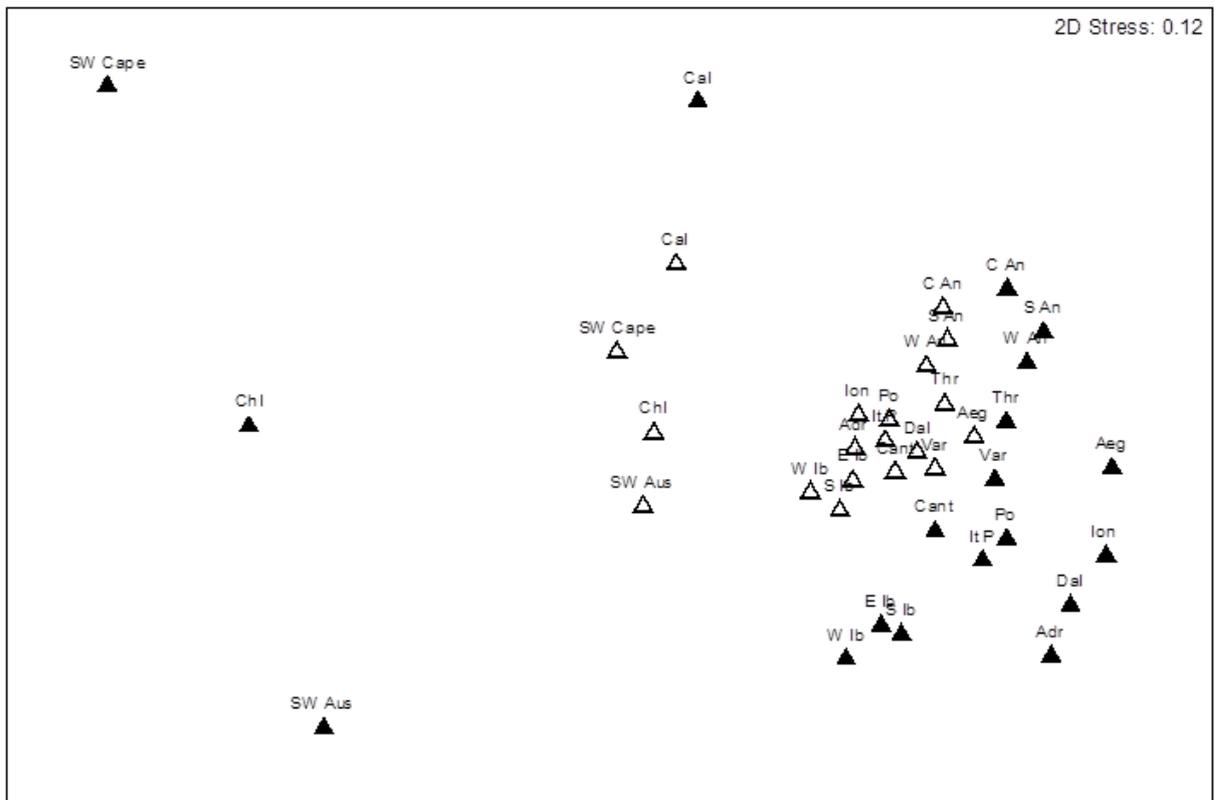
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Fig. 1a Taxonomic homogenization
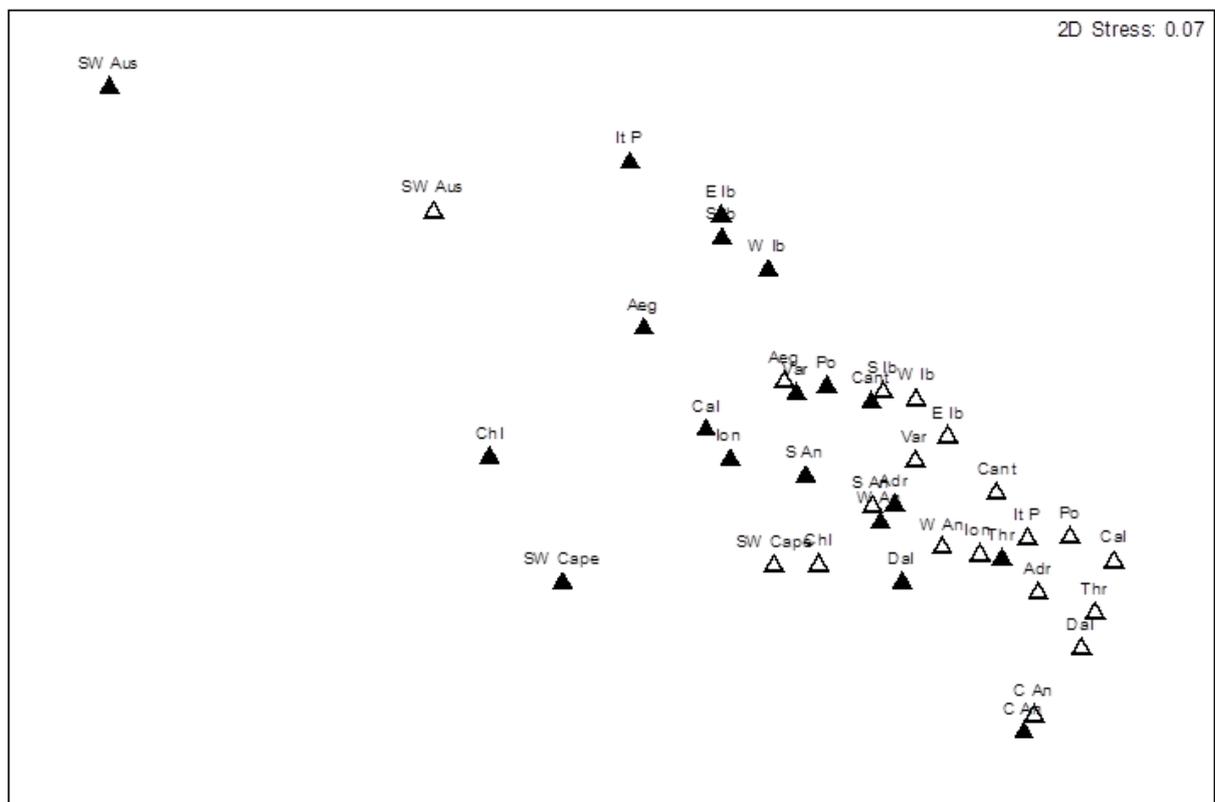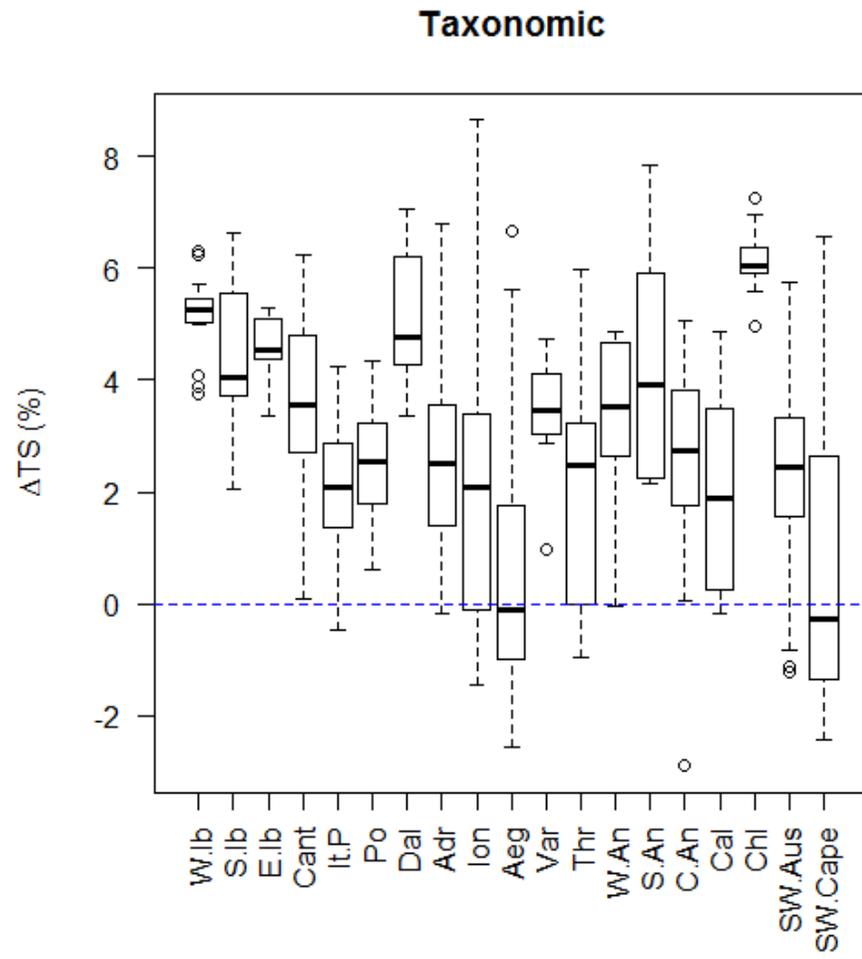

Fig. 1b Functional homogenization

Fig. 2

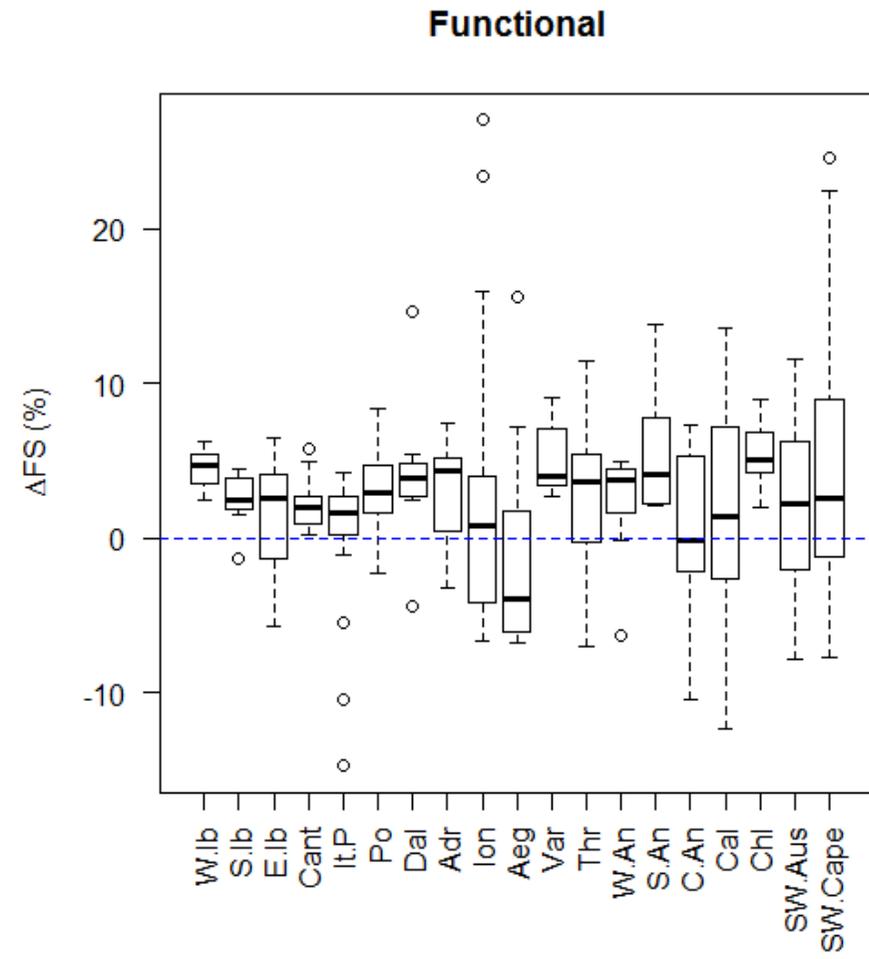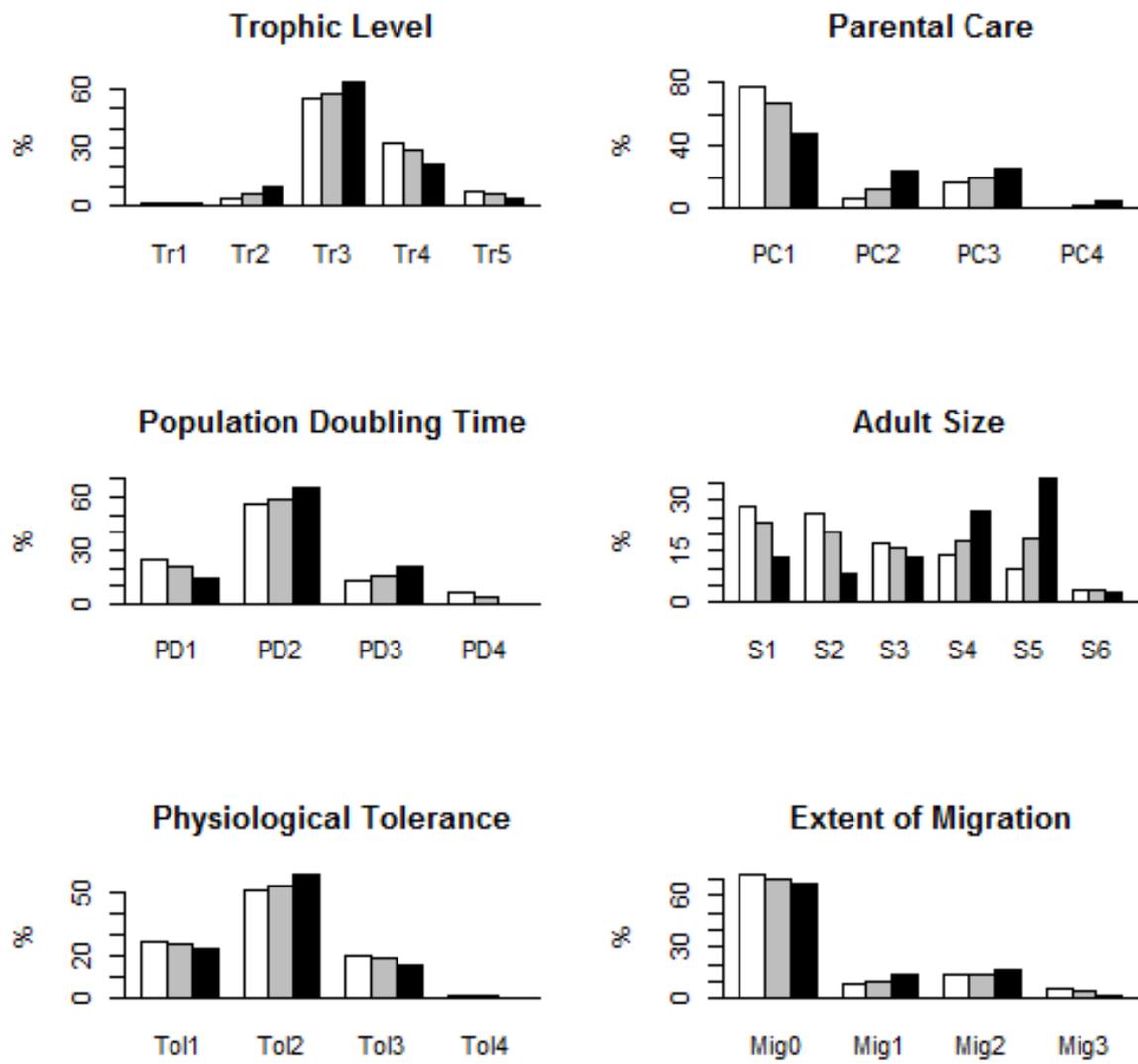**Taxonomic**

Functional

Fig. 3.

Table 1 Fish richness and biotic homogenization in med-regions. 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.

	Region codes	No. species				Taxonomic similarity (%)			Functional similarity (%)		
		N	X	T	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	*	45	32.35	10.47	9.47	51.11	67.45	14.03
Gulf of Venice (Po drainages)	Po	39	2	*	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

Note

* levels of translocation in the Italian regions could not be calculated from the available data.

1

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

Species	W Ib	S Ib	E Ib	Cant	It P	Po	Dal	Adr	Ion	Aeg	Var	Thr	W An	S An	C An	Cal	Chl	SW Aus	SW Cape
Gambusia holbrooki	0.90	1.00	0.71	0.50	0.39	0.42	1.00	1.00	0.58	0.32	0.71	0.61	0.75	1.00	0.50		0.92	0.76	
Cyprinus carpio	1.00	0.88	1.00	0.85	0.87	0.75	0.88	0.89	0.42	0.12	0.14					0.47	1.00	0.09	0.35
Oncorhynchus mykiss	0.45	0.38	0.71	0.85	0.39	0.58	0.75	0.67	0.29	0.12	0.57	0.22	0.25	0.67	0.56		1.00	0.30	0.33
Carassius auratus	1.00	0.75	1.00	0.35	0.87	0.83	0.25	0.33	0.05			0.09	0.08		0.11	0.38	0.77	0.30	0.15
Lepomis gibbosus	0.75	0.75	0.43	0.65	0.65	0.50	1.00	0.22	0.05		0.57	0.22	0.25	0.17		0.09			
Salmo trutta	0.35	0.13	0.29	0.25	1.00	1.00	0.50		0.03		0.14					0.31	1.00	0.06	0.17
Carassius gibelio				0.40			0.88	0.44	0.18	0.08	0.86	0.57	0.50	0.50	0.33				
Micropterus salmoides	0.75	0.88	0.43	0.10	0.35	0.33	0.13		0.03							0.59			0.54
Pseudorasbora parva			0.29	0.30	0.43	0.75	0.38	0.78	0.05		0.43	0.22	0.17	0.17	0.11				
Esox lucius	0.15	1.00	0.71	0.15	0.04		0.50	0.11			0.14	0.04							
Sander lucioperca	0.10	0.13	0.43	0.45	0.13	0.33	0.25	0.11				0.04	0.33		0.28				
Gobio lozanoi	1.00	0.75	0.71																
Tinca tinca		0.13					0.88	0.22	0.16		0.14						0.69		0.02
Ameiurus melas	0.50	0.25	0.14	0.25	0.26	0.50	0.13	0.11								0.31	0.15		
Ctenopharyngodon idella					0.09	0.08	0.25	0.33	0.16	0.08	0.29	0.04					0.38		
Silurus glanis	0.50		0.29	0.35	0.13	0.42	0.25	0.11	0.08										
Gambusia affinis																0.50	0.92		0.23
Salvelinus fontinalis	0.50		0.29		0.04	0.08	0.13	0.11	0.03		0.14	0.04				0.16	0.54		
Perca fluviatilis			0.29	0.40	0.09		0.25	0.11	0.05		0.14							0.27	
Carassius carassius				0.60	0.13	0.08	0.25					0.09			0.11				

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