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## **Deliverable D5.D: Report on the position of exotic species in the context of estuaries, rivers and lakes multi-stressors and regarding ecosystem services**

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## Non-technical summary

Non-native species, i.e. species occurring outside of their native range, have been recognised as a major threat for ecosystem functioning. Indeed, the number of non-native species introduced at all continents to support human activities or needs has increased during the last decades and several non-native species are now spread worldwide, e.g. mosquitofish species or salmonids. Aquatic ecosystems are particularly sensitive to these introductions. Numerous evidences were provided concerning their impact on native biota, at different levels of organisation (genetic, individual, population, community and ecosystem). Invasion biology is a complex discipline as the success of establishment of non-native species in new locations is driven by numerous factors that depend on the local context. Local environmental conditions, species tolerance, native biota and life history traits were hypothesised as key factors controlling the invasion success of an introduced species.

The main objective of this study was to assess the impacts of non-native species on fish assemblages all along the freshwater-marine continuum at large scale in Europe. We thus considered lakes, rivers and estuaries of France, Spain and Portugal. The status of each species was defined at the national level (native, translocated or exotic) and served to assess the relative abundance of non-native species in fish assemblages. In order to understand the ability of non-native species to colonise new areas, we compared their characteristics to those of the native species through two components of functional diversity: specificity and originality.

Results showed that estuaries were very different from lakes and rivers, with less non-native species. All were freshwater species with low occurrence and low abundances (*Lepomis gibbosus*, *Ameiurus melas*, *Sander lucioperca*, *Silurus glanis*, *Carassius carassius*, *Cyprinus carpio*). In contrast, in lakes and rivers, non-native fish species occurred in about 25% of fish assemblages, although with heterogeneous distributions across systems. Lakes were approximately four times more affected by the occurrences of non-native species than rivers. In France, Portugal and Spain, almost 1/3 of the regional species pools were composed of non-native fish species, with the pikeperch (*Sander lucioperca*), the pumpkinseed (*Lepomis gibbosus*), the largemouth bass (*Micropterus salmoides*) and the European catfish (*Silurus glanis*) being the most common non-native species encountered. With the exception of some particular locations, when non-native species were present, they only accounted for a small proportion of local fish abundances (on average 16.78% of catches). We also observed that the non-native species pool was overall more functionally original and specialized than the native species pool. This pattern suggests that non-native fish species exhibit functional traits that tend to differ from those of native species, which is consistent with previous observations. Moreover, this highlights the role played by non-native species in the functional richness of some assemblages, especially on the Iberian Peninsula, where local species and functional richness were generally low.

A majority of non-native fish species investigated is known to be of interest, either for commercial or recreational fishing and, consequently, they have a high economic value. This

observation is especially true on the Iberian Peninsula, where approximately half of the fished species represent non-native species. However, some of these non-native species with fishing interest are also known to deteriorate water quality, i.e. to increase nutrients and thus contributing to eutrophication of reservoirs. The management of non-native species (removal, control, etc.) should be integrated within an ecosystem service assessment framework, to weight the cost/benefits of given actions.

## Introduction

The increasing concern about biodiversity conservation in face of a generalization of anthropogenic activities and their impacts gave rise to a huge literature focusing on the risk associated to introduced and invasive species in new environments (Lodge 1993). Indeed, it was claimed that introductions of non-native species may impair composition and structure of the communities, modify the whole ecosystem functioning and lead to an homogenization of communities (Vitousek 1990, Williamson 1996, Olden and Poff 2004, Villéger et al. 2014, Villéger et al. 2015).

From an evolutionary point of view, the geomorphological structure of freshwater ecosystems has been viewed as isolated biogeographic islands (Hugueny 1989), as natural barriers (ocean and land) limit connections between watersheds, with the exception for species tolerant to brackish waters (e.g. long distance migratory fish). These barriers to migration could have been overcome in some rare situations such as ice melting at the end of the last-glacial maximum (Hewitt 2000). The spread of non-native species after their introduction could potentially be limited in aquatic systems, as these natural barriers would prevent fish migration between basins. In spite of this limitation, non-native fish species are also now found in a large number of waterbodies (Welcomme 1988, Cowx 1998, Irz et al. 2004). It has been hypothesized that both artificial connections (i.e. channels) between waterbodies (Rahel 2007, Leuven et al. 2009) and fish stocking play a major role of in the spread of non-native fish into new habitats (Goudswaard et al. 2008, Gozlan et al. 2010b). Fish introduction could be accidental, when undesirable individuals are introduced with another native fish itself introduced to support natural population. It could also be intentional, as non-native fish are stocked to enhance recreational or professional fishing activities (Welcomme et al. 1983, Welcomme 1988, Holčík 1991, Cowx 1994, Crivelli 1995, Cowx 1998).

Even if most introduced species do not succeed in settling (Williamson and Fitter 1996, Marchetti et al. 2004, Ribeiro et al. 2008), several non-native species are now irreversibly established (Manchester and Bullock 2000) and attempts to remove them are most often unfruitful or highly expensive (Gozlan et al. 2010b). As non-native species have been introduced worldwide since decades (Roule 1938, Pyke 2005, Lecomte et al. 2013), numerous consequences of their introductions were reported. The most famous introduction of fish species and its deleterious consequences is probably the Nile perch in Lake Victoria, which led to the extinction of several hundreds of haplochromine species (Goudswaard et al. 2008). In their review, Cucherousset and Olden (2011) detailed the potential effects of fish introduction on various levels of organization, from genetic diversity to ecosystem functioning. Very often the contributions, role and impacts of non-native species on assemblages are studied at a small spatial extent. Moreover, even if lakes (natural and artificial), rivers and estuaries are connected and participate to a freshwater-marine continuum, these water categories and their biocenoses are generally studied separately, independently of their links.

Trying to explain why some species could successfully invade locations outside of their native range (Marchetti et al. 2004, Olden et al. 2006, García-Berthou 2007, Ribeiro et al. 2008) is also of major importance to estimate their potential of invasion (Copp et al. 2009). Several studies aimed to identify the key attributes of species to overcome the different phases of species introduction. Very often, these studies focused on life history traits (demographic traits), such as fecundity (clutch size), longevity and investment in parental care to progeny. The Winemiller and Rose model (1992) resumes these three main strategies (Olden et al. 2006, Logez et al. 2016a). Functional traits (Lavorel and Garnier 2002) are defined as species attributes that are directly or indirectly linked to ecosystem functioning. They could also be of major importance to explain species success of introduction (Marchetti et al. 2004), as several ecological theories suggest that only species with an adapted suite of traits could maintain and develop themselves in given environmental conditions (Tonn et al. 1990, Keddy 1992, Poff 1997).

Therefore, do those successful non-native species exhibit similar suite of traits than native species? Or on contrary, can they display different combinations of traits that could explain their implantation, by reducing their functional overlap with native-species or to exploit other resources (*sensu* niche definition)?

Functional originality and specificity are two components of functional diversity (Mouillot et al. 2013) that enable assessing the functional similarity among species, by comparing the position of species functional niches relative to others (Buisson et al. 2013). At the assemblage level, niche overlap between native and non-native species could be studied through Functional Richness (FRic) (Mason et al. 2005). FRic measures the amount of functional space occupied by a species in a given assemblage (Villéger et al. 2008). Therefore, if a non-native species has functional attributes different from native species occurring at same locations, their presence will increase FRic. Similarly, if non-native species are removed from the communities, the FRic values will decrease. On the contrary, if non-native species have relatively similar attributes to native species, then FRic would not be affected by their removal.

Finally, considering in particular the relationship between biodiversity and ecosystem functions (Connolly et al. 2013, Abson et al. 2014, Bennett et al. 2015), we can hypothesize about possible impacts of fish introductions on ecosystem services. These aspects are seldom documented in the literature and when they are, conclusions are not necessary convergent. First, biodiversity can be intrinsically considered to support wellbeing, due to its impacts on ecosystem functioning. Nevertheless when species are introduced, their impacts are often reported via modification of trophic status and on the taxonomic diversity of the manipulated taxon, without consideration of the whole diversity as well as the impacted ecosystem functions. Concerning fisheries, both positive and negative effects of introductions are reported (Cowx 1998). A limited/null impact of introduced species on the communities was reported for French lowland lakes; conversely, fish stocking seems at the origin of most of the

established Salmonid populations of the altitudinal lakes supporting recreational activities (Argillier et al. 2002).

The first objective of this study was to assess the relative contribution of non-native species (either translocated or exotic) to the fish assemblages along the freshwater-marine continuum (lakes, rivers and estuaries) at a large scale: Portugal, Spain and France. The second aim of this study was to get a better understanding of the mechanisms that are linked to the introduction success of fish species, by comparing the functional attributes of native and non-natives species. We thus used Functional Originality (FOri) and Functional Specificity (FSpe) as metrics to compare species to an average functional species or to their closest neighbour. Then, we studied the relative influence of non-native species on the functional diversity of local fish assemblages and ecosystem services, by taking into account the fishing interest of these species.

## Methods

### Available data

We used various sources of data collected within monitoring programs related to the EU Water Framework Directive (WFD; 2000/60/EC) to obtain estimates of fish abundance in estuaries, lakes, and rivers distributed in France, Spain and Portugal. The WFD requirements ensure the availability of relatively homogeneous fish datasets for each aquatic system in terms of standardization of sampling efforts and fishing techniques (Birk et al. 2012, Pérez-Domínguez et al. 2012).

For estuarine systems, fish abundances were estimated on the basis of trawl surveys conducted between 2005 and 2013. Briefly, the protocol consists of performing several hauls distributed across the whole salinity gradient by using a beam trawl (from 1.5 to 3 m large, 8-20 mm mesh size). Trawling was performed against the current during 5 to 20 min, at a speed ranging from 1 to 3.5 knots. The number of hauls (from 5 to 71 hauls per estuary) was defined according to the system size to ensure the sampling representativeness. Abundances of all taxa were expressed in density by dividing the number of individuals by the sampled surface (number of individuals per 1000 m<sup>2</sup>).

For lakes, fish data were obtained in application of the Norden gillnet standardised protocol (C.E.N., 2005). Benthic multi-mesh gillnets (12 different panels with mesh sizes ranging between 5 mm and 55 mm, following a geometric series) and pelagic gillnets (11 different panels with mesh sizes ranging between 6.25 mm and 55 mm) were set in different depth strata during the summer period. The sampling effort (gillnet-nights) depended on lake depth and area. Nets were set before dusk and lifted after dawn in order to cover the activity peaks of all the fish species. Lakes in this dataset are either natural or artificial (reservoirs).

For rivers, fish data were extracted from an extensive database (EFI+Consortium, 2007) containing fish surveys conducted by several academic institutions and environmental agencies across Europe. Sites were sampled by electrofishing (wading) during low flow periods using European standards (C.E.N., 2003). To minimise the risk of false absences, only sites where sampled areas were greater than 100 m<sup>2</sup> with more than 50 individuals caught were included. Abundances were expressed in number of individuals per m<sup>2</sup>.

The fish assemblages were determined in terms of species occurrence and abundance by gathering the available samples of each system.

## Sites description

The global data set was composed of 1 118 sites from 38 estuaries, 317 lakes and 763 river reaches sampled between 2000 and 2015. The distribution of sites was highly contrasted among countries and water categories (Table 1). Rivers and lakes (especially in France) were the most abundant water categories in the dataset, while estuaries represented a small amount of sites, especially in the Iberian Peninsula. The sampling sites of the rivers category were more abundant but their locations were more geographically limited, not evenly covering national territories (Figure 1). For Spain, data are mainly distributed along the Atlantic coast; for Portugal they are concentrated on the North and some French large watersheds such as the Loire River basin were not represented.

Table 1. Number of sampling sites per country and water category.

Water category	Country			Total
	<i>France</i>	<i>Portugal</i>	<i>Spain</i>	
Estuaries	27	9	2	38
Lakes	245	18	54	317
Rivers	375	174	214	763

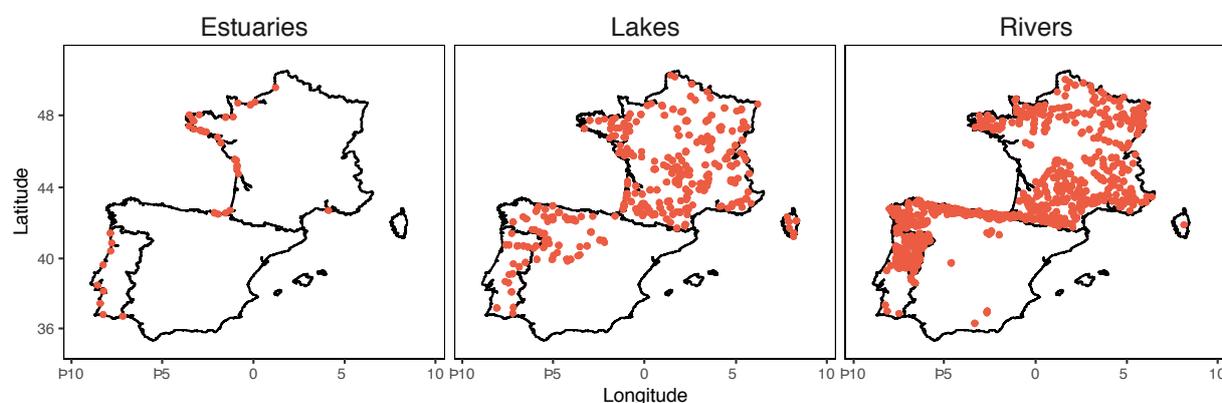


Figure 1. Site locations in estuaries, lakes and rivers.

## Fish species status

At each site, individuals were identified at the species level and their scientific names were assigned in accordance with the current classification proposed on Fishbase (Froese and Pauly, 2016). The status of the species (origin and fishing interest, see below) was defined at the national level. It was not possible to gather this information at lower spatial scales (e.g. the basin level).

The origin of species was based on the available literature (Kottelat and Freyhof 2007, IUCN France 2010, Keith et al. 2011, Froese and Pauly 2016). Following Trochine et al. (in prep), a species was considered:

- Native (N) only when present in the country before year 1500,
- Translocated (T) when introduced in the country and known as native in another European country,
- Exotic (E) when non-native in entire Europe.

The fishing interest of each species ('Yes' or 'No') was defined based on expert judgment and on Maire et al. (2013) for fish species occurring in France. A species was classified as of fishing interest if this species was known to be of interest either for commercial or recreational fishing. Some species occurring both in estuarine and freshwater ecosystems exhibited different fishing interests depending on the systems. For this reason, we decided to separate analyses between estuarine and freshwater ecosystems. See supplementary materials (Table S1, Table S2) for the origin and the fishing interest of the species.

## Fish functional traits

Following the work of Teichert et al. (2016), we used five common traits to describe the functional attributes of fish (Pont et al. 2006, Eros et al. 2009, Guillemot et al. 2011, Buisson et al. 2013, Mouillot et al. 2014, Pool et al. 2014): fish size, vertical position, spawning substratum, reproductive guild, and trophic group (Table 2). These traits were chosen to reflect different ecological functions of species in ecosystems according to Teichert et al. (2016). Beside fish size which is a continuous number, the remaining traits are of categorical nature and only one trait category was assigned to each species. Trait assignment was either based in expert judgment (EFI+Consortium 2007, Caussé et al. 2011) or derived from Fishbase (Froese and Pauly, 2016). Only fish attributes at the adult stage were considered.

Table 2. Fish traits classification and description.

Trait	Category	Description
Maximum size (mm)	-	Maximum reported size of the species in the literature.
Vertical position	Benthic (BENT)	Fish prefer to live near the bottom from where they obtain food. They usually do not go to the surface for feeding purposes.
	Water column (WC)	Species that live and feed in the water column. They usually do not go to the bottom to search for food.
Trophic guild	Detritivorous (DETR)	Adult diet consists of high proportion of detritus, the digestive tract is unspecialized.
	Herbivorous (HERB)	Adult diet consists of more than 75% plant material.
	Invertivorous (INV)	Adult diet consists of more than 75% invertebrates.
	Omnivorous (OMNI)	Adult consists of more than 25% plant material and more than 25% animal material.
	Parasitic (PARA)	Fish that exhibit a parasitic feeding mode.
	Piscivorous (PISC)	Adult diet consists of more than 75% of other fish.
	Planctivorous (PLAN)	Adult diet consists of more than 75% zooplankton and/or phytoplankton.
Reproductive guild	Bearer	Fish bears the eggs (internal or external).
	Guarder	Fish guards the eggs after spawning.
	Nonguarder	Fish leaves the eggs after spawning.
Spawning substratum	Ariadnophilic (ARIAD)	Specialized nest building fish that may exhibit some form of parental care.
	Lithophilic (LITH)	Fish spawn exclusively on gravel, rocks, stones, rubbles or pebbles. Hatchlings are photophobic.
	Ostracophilic (OSTR)	Spawning takes place in shells of bivalve mollusks.
	Pelagophilic (PELA)	Fish spawn into the pelagic zone.
	Phytolithophilic (PHLI)	Fish deposit eggs in clear water habitats on submerged plants or on other submerged items. Larvae are photophobic.
	Phytophilic (PHYT)	Fish deposit eggs in clear water habitats on submerged plants.
	Polyphilic (POLY)	Non-specialized spawners.
	Psamnophilic (PSAM)	Fish spawn on roots or grass above sandy bottom or on the sand itself.
	Speleophilic (SPEL)	Fish spawn in interstitial spaces, crevices or caves.
	Viviparous (VIVI)	Live bearers or internal brooder fish.

## Functional diversity

To assess the impact of non-native species on the functional diversity of fish assemblages, we used a multivariate functional space (Mouillot et al. 2013). First, we computed the functional dissimilarity between each pair of species using the Gower distance (Gower 1971). This distance was used as it handles both continuous and categorical variables (traits) and because of its efficiency to reflect dissimilarities based on functional traits (Podani and Schmera

2006). The functional space was defined as the first three axes of a Principal Coordinate Analysis (PCoA) on the matrix of Gower distances.

To assess if functional attributes of non-native species could explain their success outside of their native distribution area, we computed for each species their functional specificity (FSpe; Mouillot et al. 2013) and originality (FOri; Buisson et al. 2013). For a given species, FSpe is defined as the Euclidean distance between its location on the functional space and the barycentre of all species locations ('average species'). A high value of FSpe suggests that this species is more specialized as it has a suite of traits highly different from most of the other species. FOri is defined as the Euclidean distance to the closest neighbour species in the functional space. If a species has a value of 0 for FOri, it indicates that a second species has exactly the same suite of traits. Therefore, a species with a high FSpe could simultaneously show a low FOri in case it is included in a group of two or more species that share similar traits but that markedly differs from the main cloud of species in the multivariate space. On the other hand, a species could have a high value of FOri because of a unique suite of traits but a low value of FSpe, if this species is close to the 'average species', whereas all the others are far from the barycentre. These two indexes were standardized by their respective maximum values.

Functional richness (FRic) was used as a measure of functional diversity of fish assemblages (Villéger et al. 2008). FRic measures the amount of space occupied by species along functional axes. In a multivariate functional space, FRic is the convex hull volumes computed from species locations. If species composing a given assemblages are functionally close to each other, they will occupy a restraint volume of the functional space and thus the FRic value will be low. To estimate the relative importance of non-native species in a fish assemblage, we computed the deviation between FRic based on all species and FRic based only on native species.

## Results

### Regional species pool

#### *Species distribution*

A total of 188 fish species have been identified among the different habitats and countries, but 39 species were only recorded once. Estuaries were the most speciose water category (Figure 2) with 126 species observed, followed by rivers (78) and lakes (61). The species pool in estuaries was mainly composed of species only present in this system (99), while among freshwater systems, almost all species observed in lakes were also observed in rivers (Figure 2). Five species were specific or only recorded in lakes: *Coregonus lavaretus*, *Leuciscus burdigalensis*, *Salvelinus namaycush*, *S. umbla* and *Scardinius hesperidicus*. These species were collected in a small number of lakes (from 1 to 9, mean value 3.6). Only species

belonging to *Salvelinus* genus were highly abundant in some lakes (up to 50 % of the catches). Then, twenty two species were only observed in rivers and several of these species were endemic (mainly of the Iberian Peninsula), such as *Iberochondrostoma almakai*, *I. lemmingii* and *Zingel asper*, or only observed in one country (e.g. *Gambusia holbrooki*). Finally, 17 species were present in the three water categories (Figure 2), comprising mainly freshwater species (see Table S3 for the species list). With the exception of European eel (*Anguilla anguilla*), and in a less extent the white bream (*Blicca bjoerkna*), these 17 species were only recorded in three estuaries and represented less than 5 % of the catches (0.1 % on average).

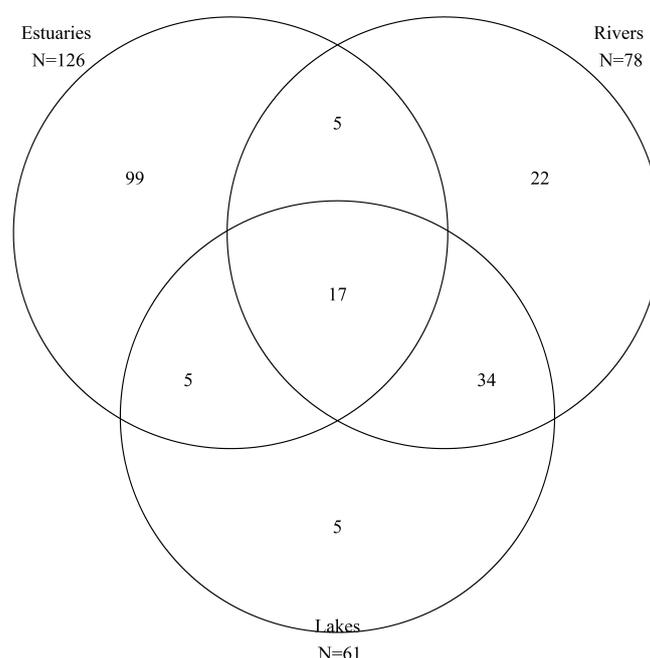


Figure 2. Venn diagram representing the number of species in estuaries, lakes and rivers. Circle overlaps represent the number of species that are shared between the different systems.

As for site distribution, we observed consistent differences between countries. In French sites (all water categories confounded), 146 species were sampled. In comparison, the Iberian Peninsula displayed depauperate fish fauna with 88 species sampled in Portugal and 33 in Spain. In each country, species richness was highly variable between the three water categories (



Table 3).

Table 3. Number of species recorded per country and water category.

System	Country			All
	France	Portugal	Spain	
Estuaries	107	59	3	126
Lakes	49	17	18	61
Rivers	51	29	25	78

### *Alpha diversity*

The specific richness of fish communities was highly dependent on both the water category and the country, but also highly variable within water category and countries. The highest local species richness (39 species) was observed for French estuaries, whereas the lowest species richness (only one species) was observed for some rivers and lakes of the three countries. Within water categories, French sites were on average always more speciose than Iberian sites. The lowest alpha diversities were observed for the two Spanish estuaries (Table 4).

Table 4. Average local species richness observed per water category and country (min – max).

Water category	Country		
	France	Portugal	Spain
Estuaries	22.1 (11 - 39)	15.1 (4 - 26)	1.5 (1 - 2)
Lakes	9.2 (1 - 15)	4.2 (1 - 6)	3.4 (1 - 8)
Rivers	7.8 (1 - 20)	4.0 (1 - 8)	2.9 (1 - 9)

In addition, local species richness was much more diverse for France than for the Iberian Peninsula. For lakes and rivers, more than half of the French sites showed an alpha diversity exceeding the maximum diversity observed for the two other countries (Figure 3). Nevertheless, the number of sites available per country was highly unbalanced.

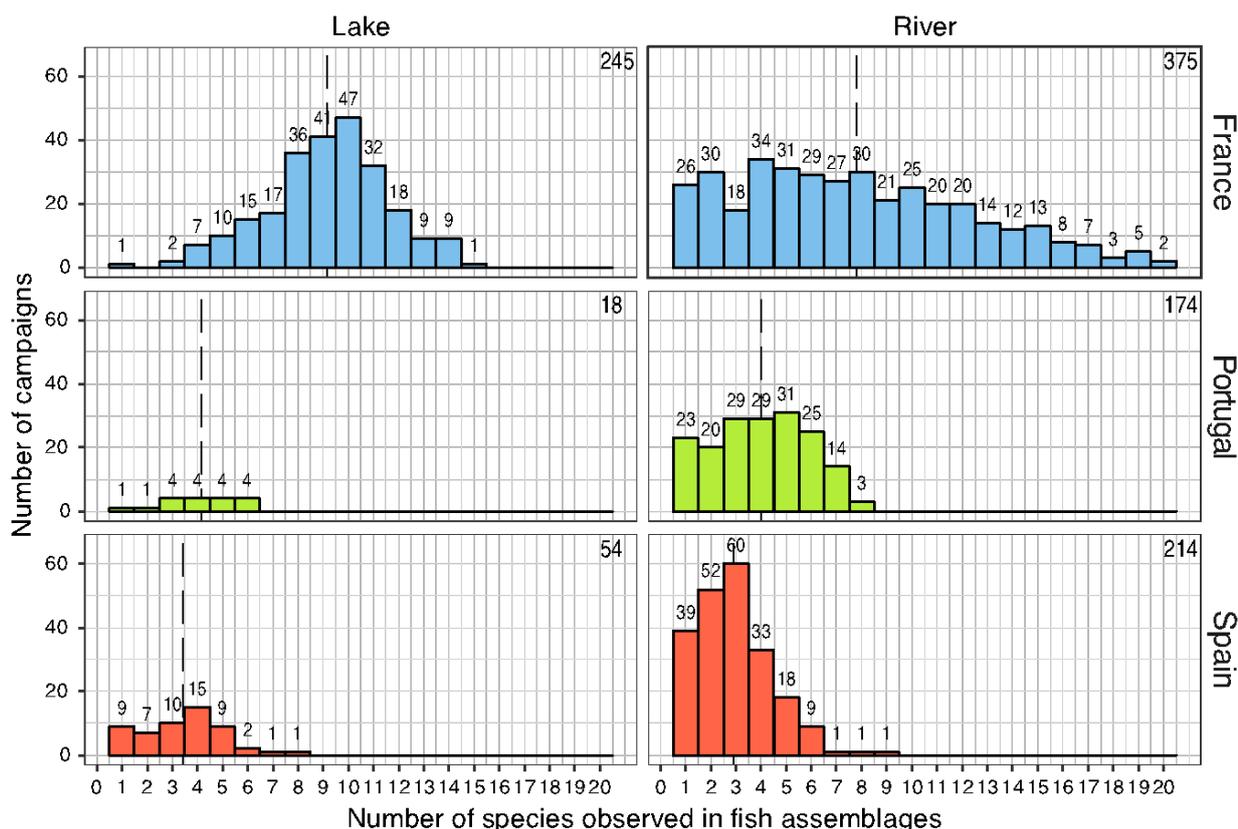


Figure 3. Local species richness observed in freshwater systems. In each panel, horizontal dashed line corresponds to the mean richness value and top right number is the total number of sites sampled in the corresponding system and country.

### Distribution of native, translocated and exotic species

As species inhabiting transitional and freshwater systems were relatively different (see above), in this analyse, estuaries were distinguished from lakes and rivers. Non-native species (both translocated and exotic species) were almost absent of estuaries (Table 5). In the most speciose system, French estuaries, only five non-native species composed the species pool: *Ameiurus melas*, *Carassius carassius*, *C. gibelio*, *Leuciscus idus* and *Sander lucioperca*. None of these species occurred in more than three estuaries and they represented less than 3 per thousand of the individuals sampled in each system.

Table 5. Origin of species observed in estuaries.

Origin	Country		
	France	Portugal	Spain
Native	102	58	3
Translocated	4	-	-
Exotic	1	1	-

Non-native species were clearly more important in lakes and rivers, with 12 exotic and 12 translocated species recorded. The proportion of non-native and translocated species in the

national species pool was comparable in France, Spain and Portugal and represented up to 30% of the national species pools (Table 6). Ten exotic species and 8 translocated species were observed in rivers and lakes compared to 1 and 4 respectively for French estuaries. Analogous situation was true for Iberian species pools.

Table 6. Species status in freshwater species pools.

Origin	Country			
	France	Portugal	Spain	All
Native	42 (75%)	24 (71%)	22 (73%)	68 (74%)
Translocated	8 (13%)	4 (12%)	4 (13%)	12 (13%)
Exotic	10 (17%)	6 (18%)	4 (13%)	12 (13%)

Among the 12 exotic species found in our dataset, 8 originated from North America (*Ameiurus melas*, *Gambusia affinis*, *G. holbrooki*, *Lepomis gibbosus*, *Micropterus salmoides*, *Oncorhynchus mykiss*, *Salvelinus fontinalis*, *S. namaycush*), 1 from South America (*Australoheros facetus*) and three from Asia (*Carassius auratus*, *Hypophthalmichthys molitrix*, *Pseudorasbora parva*). Goldfish, pumpkinseed and largemouth bass were the only three exotic species occurring in the three countries. On contrary, mosquitofish, silver carp, *Pseudorasbora parva*, brook trout and lake trout were observed only in France; chameleon cyclid and Eastern mosquitofish only in Portugal and no specific exotic species were observed only in the Spanish dataset.

Similarly to exotic species, most of the translocated species only occurred in France: *Carassius carassius*, *C. gibelio*, *Leuciscus aspius*, *L. idus*, *Pachychilon pictum*, *Scardinius hesperidicus* and *Silurus glanis*. *Gobio lozanoi* was the only translocated species specific of Portugal while *Gobio gobio* was specific of Spain. Two species were considered as translocated in the Iberian Peninsula: *Alburnus alburnus* and *Esox Lucius*, but native of France (Table 7). Pike-perch (*Sander lucioperca*) was the unique translocated species common to the three countries.

Table 7. Species with changing status in freshwater species pools.

Species	Status		
	France	Portugal	Spain
<i>Alburnus alburnus</i>	Native	Translocated	Translocated
<i>Esox lucius</i>	Native	Translocated	Translocated
<i>Gobio gobio</i>	Native	-	Translocated
<i>Gobio lozanoi</i>	-	Translocated	Native

The number of non-native species observed within each sample site varied greatly, depending both on water category and country. On overall, the alpha diversity of non-native species was higher in lakes (1.71 species) than in rivers (0.31 species). This pattern was constant among

countries even if Spanish lakes had fewer non-native species in their communities (0.76 species) than the two other countries (1.93 and 1.72 respectively for French and Portuguese lakes; Figure 4).

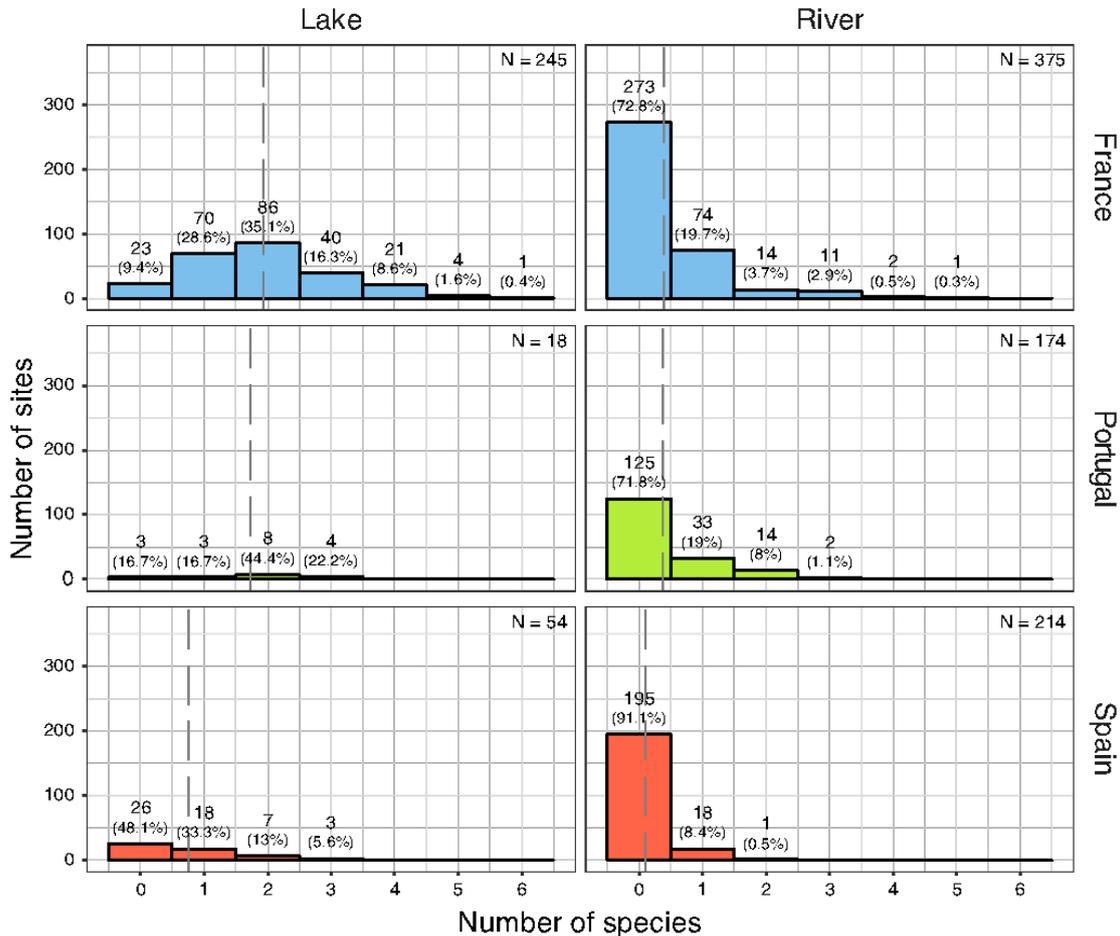


Figure 4. Number of non-native species in fish assemblages.

Accordingly with previous observed patterns, the triangular plots (Figure 5) revealed that the relative abundance of native, translocated and exotic species varied among water categories and countries. With rare exceptions, in France and Spain, riverine assemblages were dominated by native species. When non-native species were abundant in French and Spanish rivers, it was mainly due to exotic species (dots located along the N-E axis, Figure 5). Communities of Portuguese rivers were more contrasted. Either exotic or translocated species could dominate assemblages (dots along the T-N axis, Figure 5).

Regarding Portuguese fish communities in lakes, conversely to the observations on rivers, native species were generally dominant. In Spain, lake communities could be dominated either by native or exotic species, or by translocated species. Both species categories could dominate French lakes. We did not observe assemblages dominated conjointly by exotic and translocated species (no dots observed along the T-E axes, Figure 5) but some assemblages were almost uniquely composed of exotic species (dots relatively close to the lowest right side

of the triangular graphs, Figure 5). Some French lake assemblages exhibited mixed assemblages melting individuals from the three origins, native, translocated and exotic.

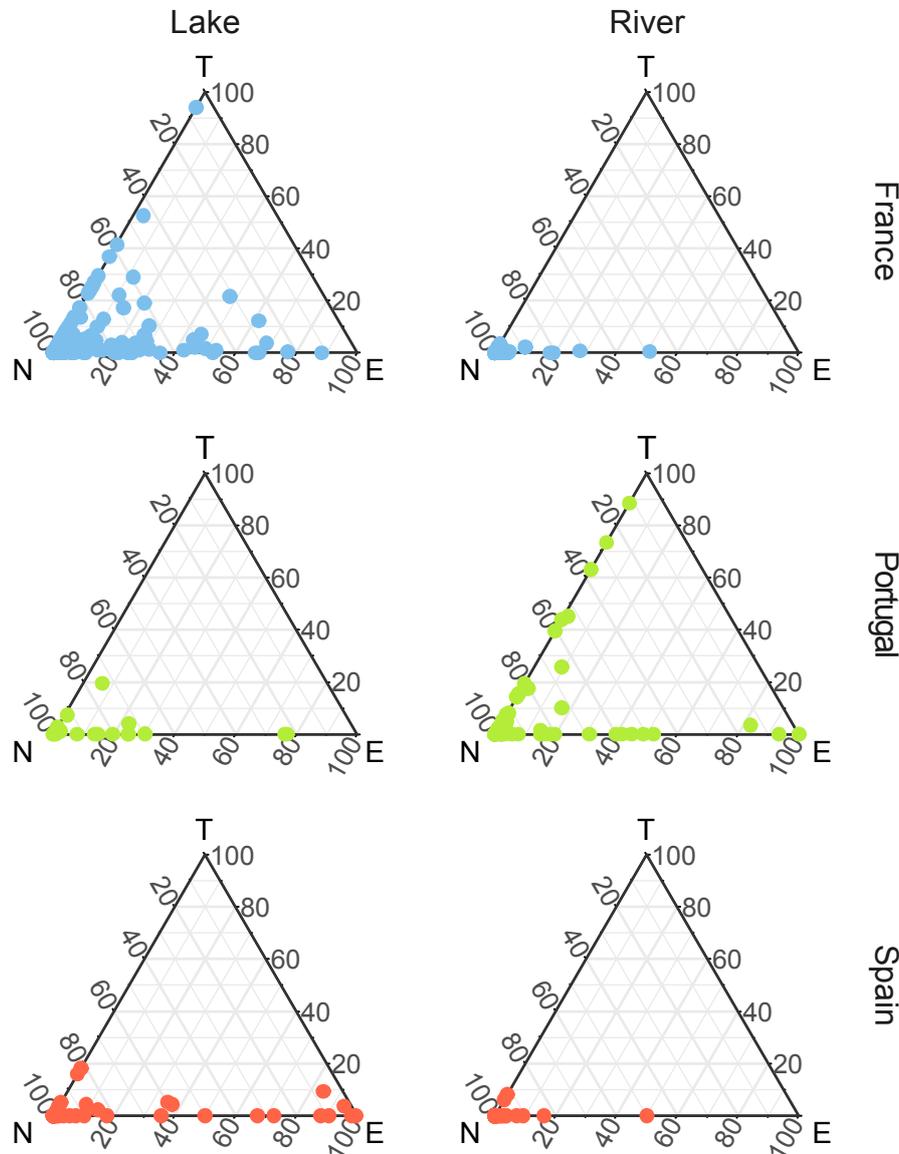


Figure 5. Relative abundance of native (N), translocated (T) and exotic species (E) in freshwater fish assemblages. Assemblages composed of native and exotic species only will be located along the N-E axis, communities composed of native and translocated species only will be located along the N-T axis and assemblages only composed of non-native species will be located along the E-T axis.

Non-native species occurring in the three countries and within each water category type were relatively different (Figure 6). Pike-perch was the most widespread non-native species (translocated) among French lakes, occurring in more than 75% of the sites. While this species was also observed in Iberian lakes, its occurrence rate did not exceed 25% for Portugal and 6% for Spanish lakes. Pumpkinseed and largemouth bass (exotic species) were also observed in the three countries, but were much more common in Portuguese lakes, sampled in more than half of these systems. Pumpkinseed was also an important species in French and Spanish lacustrine assemblages, occurring in a quarter of the lakes. The

largemouth bass was not observed in the Spanish subset. *Silurus glanis* was only observed in France. The occurrences of non-native species in rivers were by far lower than in lakes. The only noticeable species were Pumpkinseed and *Gobio lozanoi* (for Portugal only). Mosquitofishes were almost never present in our dataset.

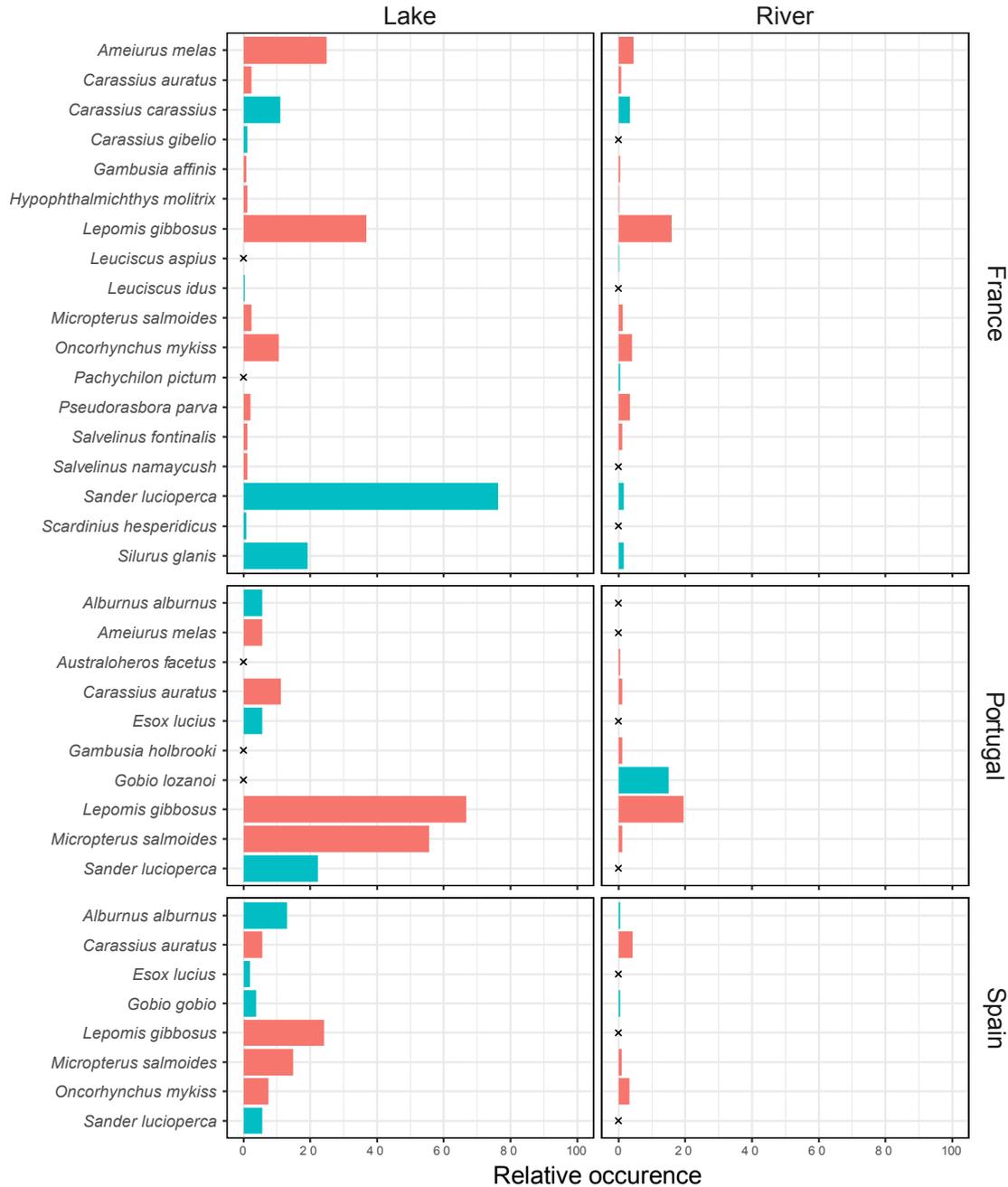


Figure 6. Relative occurrence of non-native species among countries and water categories (translocated in blue-green and exotic in red).

The relative abundance of non-native species gave a complete different insight about the role played by these species in fish assemblages as revealed by the boxplots (Figure 7). Overall, their relative abundances in fish assemblages were relatively limited, while some of these species were widespread (see above). This was all the most visible for pike-perch that did not

exceed 10% of the total number of individuals in 75% of the French lakes, where it was sampled. Nonetheless, in some lakes this species could have been highly abundant (grey dots corresponding to outliers on the boxplot).

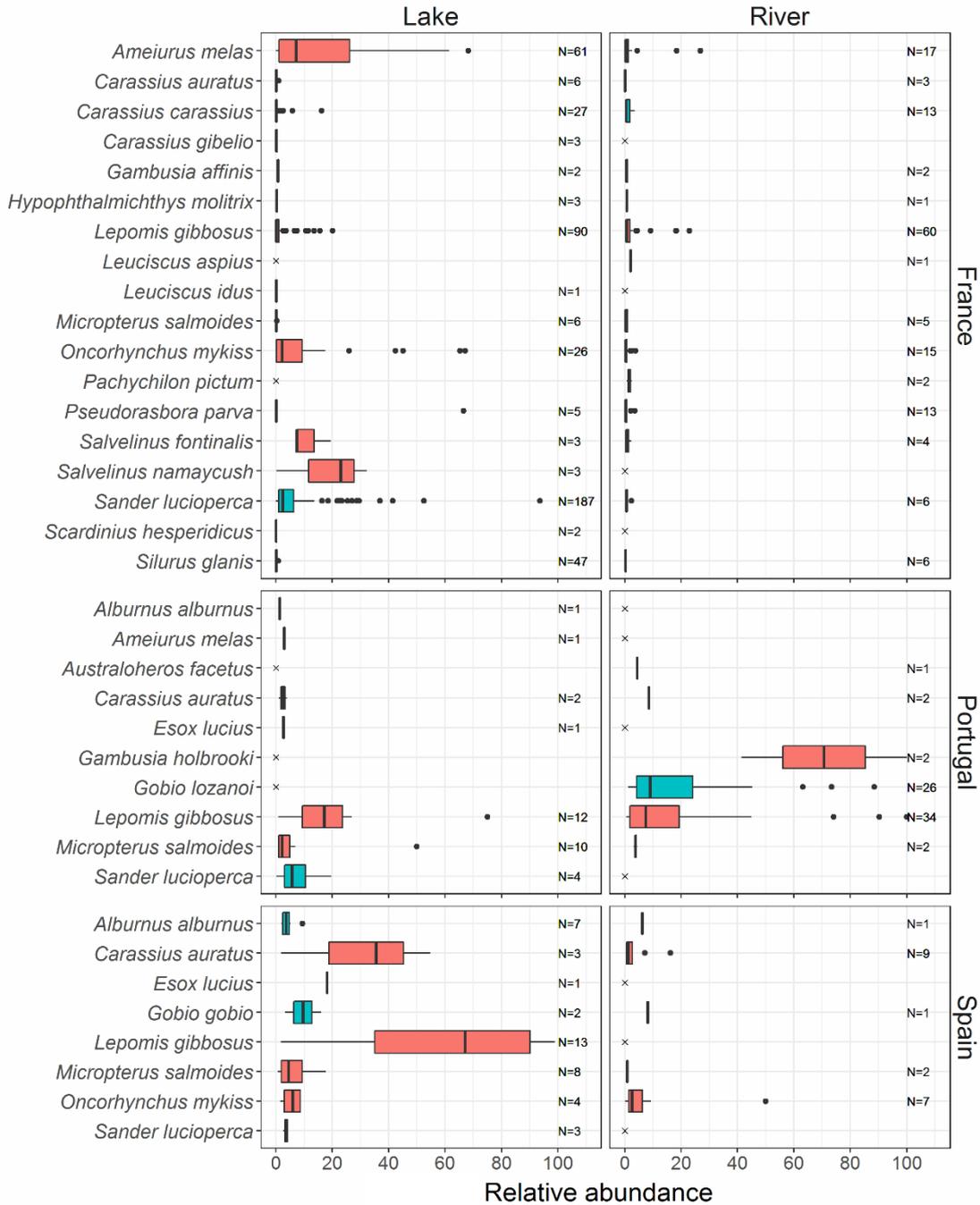


Figure 7. Boxplot of the relative abundance of non-native species among countries and water categories considering only samples where species were recorded (otherwise the box of species with low prevalence would have been concentrated around 0; translocated species are filled in blue-green and exotic in red).

In turn, Eastern mosquitofish was highly abundant in the two Portuguese river reaches where it occurred. A similar pattern was observed for pumpkinseed and goldfish in Spanish lakes. Pumpkinseed was also abundant in rivers independently of the country, while *Gobio lozanoi*

was abundant in Portuguese rivers. Generally the abundance of non-native species in rivers remained low.

## Functional attributes of fish species

In this section, we only considered freshwater systems as no non-native estuarine species were recorded (only few non-native freshwater species were observed, see above).

The functional space, defined by the three first axes of the PCoA, was representative of the functional similarity between species measured with Gowers' distances on functional traits (Mantel test ;  $r = 0.817$ ;  $p < 0.001$ ). The first PCoA axis was strongly correlated with the position of species in the water column, opposing benthic species to species preferring the water column (Figure 8). The second axis opposed omnivorous species to lithophilic invertivorous species, while the third axis was mainly correlated with parental cares (guarders, non-guarders species) and maximum size (right panel of Figure 8).

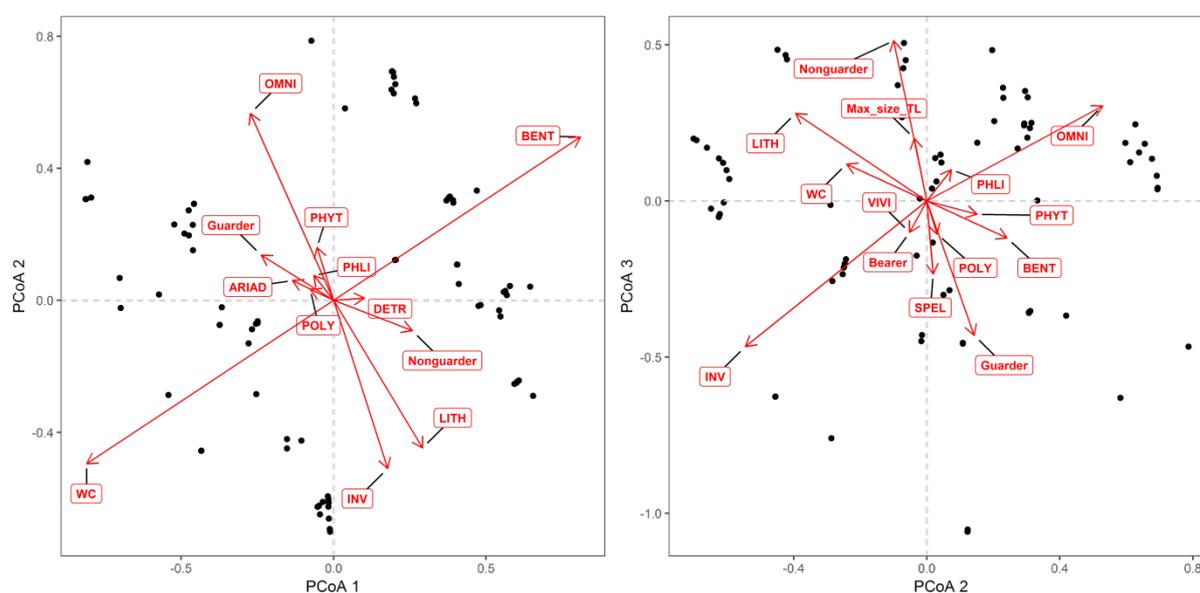


Figure 8. Traits distribution inside the functional space (axes 1 and 2 of the PCoA on the left panel and axes 2 and 3 on the right panel). Each point represents a species. Only the significant correlations ( $p < 0.05$ ) between the fish functional traits and the PCoA axes are represented (red arrows). The intensity of the correlation is proportional to arrow lengths.

This 3D functional space was used to assess species functional specificities (FSpe), i.e. the distance of a given species to the “average species” (Figure 9), and species functional originalities (FOri), i.e. the distance of a given species to its closest neighbour (Figure 10).

Twelve out of the eighteen most functionally specific species (with the highest FSpe values) were non-native species and predominantly exotic species: *Lepomis gibbosus*, *Australoheros facetus*, *Ameiurus melas*, *Gambusia affinis*, *Gambusia holbrooki*, *Silurus glanis*, *Micropterus salmoides*, *Sander lucioperca*, *Carassius carassius*, *Carassius auratus*, *Carassius gibelio* and *Salvelinus namaycush* (red dots on Figure 9).

This pattern was less pronounced when looking at the functional originality of species (FOri; Figure 10). Among these 12 species, only five were also among the most original species: *S.*

*glanis*, *A. melas*, *L. gibbosus*, *S.lucioperca* and *M. salmoides*. At the same time, two other non-native species (*Pseudorasbora parva* and *Leuciscus idus*) showed high F<sub>ori</sub> values but low F<sub>Spe</sub> values.

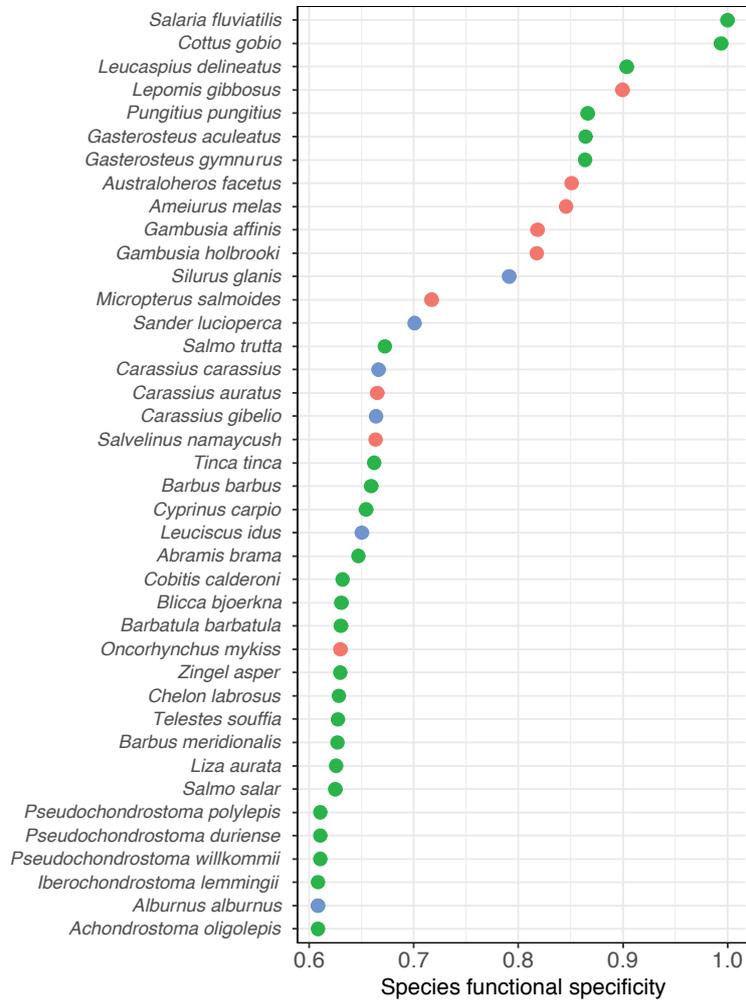


Figure 9. Functional specificity of fish species. Only the 40 species with the highest index values were represented. Green dots correspond to native species, blue dots to translocated species and red dots to exotic species.

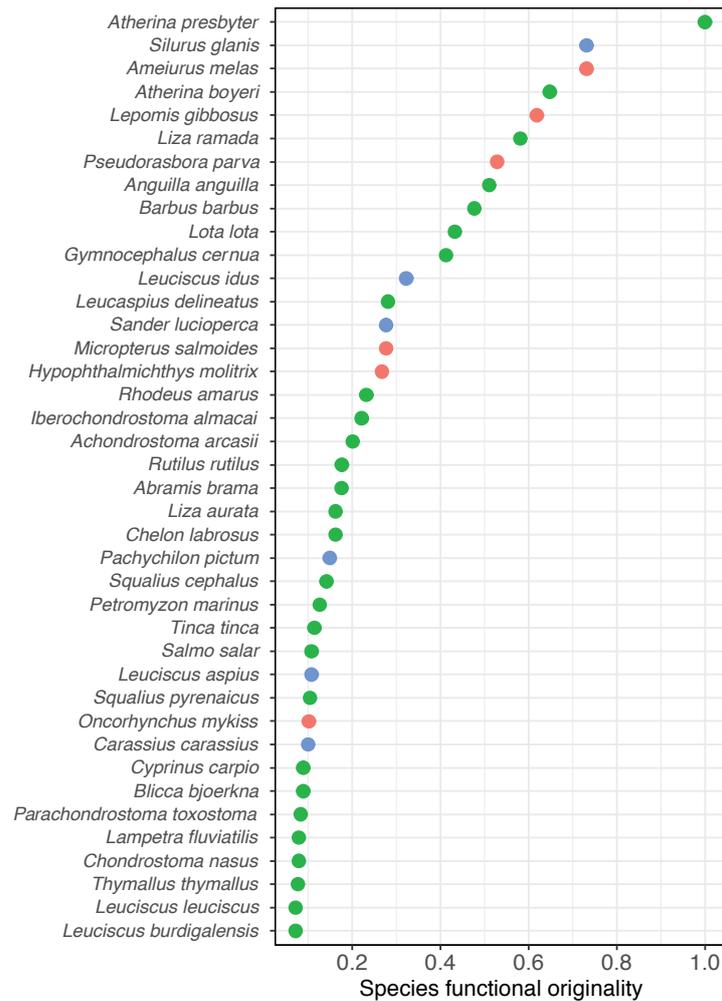


Figure 10. Functional originality of fish species. Only the 40 species with the highest index values were represented. Green dots correspond to native species, blue dots to translocated species and red dots to exotic species.

Non-native species pools were overall more functionally specialized than native species pools, even if some differences were only slight. Patterns were more marked for originality, especially in Iberian species pools. Indeed, native species pools of Portuguese freshwaters and Spanish lakes were soundly less original than non-native species pools (Figure 11). Spanish rivers displayed antagonist patterns for originality, with the native species pools being more original than the non-native species pools.

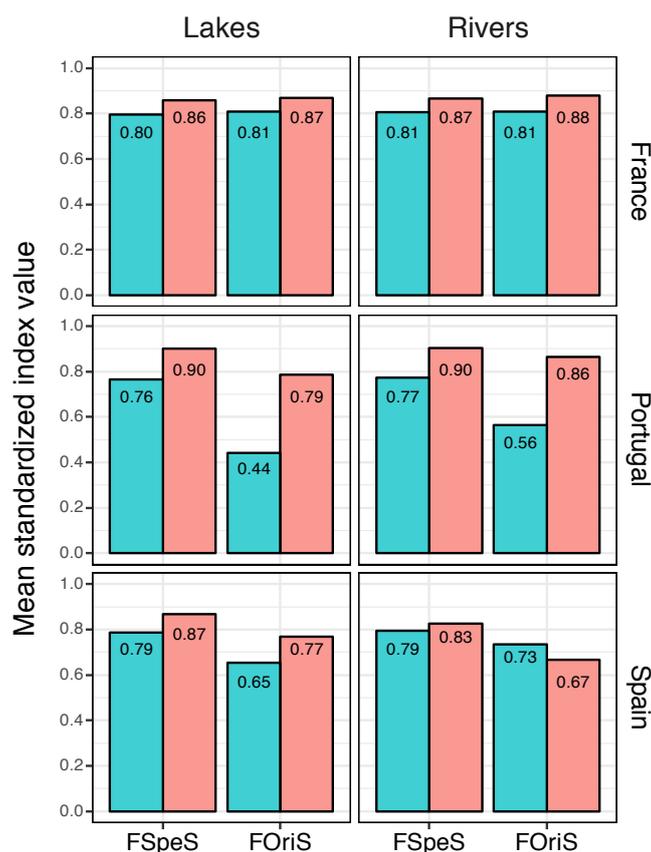


Figure 11. Average functional specificity (FSpeS) and originality (FOriS) of native (blue-green) and non-native (red) species among species pools.

The role played by non-native species on the functional richness (FRic) of fish assemblages was assessed only on lakes and rivers assemblages composed by at least 4 native species (N = 711 sites). Setting this limit was due to the method used to compute FRic (to compute complex hull volume the number of points, species, must exceed the number of axes).

When non-native species were present in fish assemblages, their relative importance on FRic varied considerably among countries and within water categories (Figure 12). In French lakes and rivers and in Portuguese rivers, they support one quarter of the functional richness, while they accounted for more than half of FRic in Spanish rivers and lakes. The number of Portuguese lakes with more than 4 native species is low, thus preventing any interpretation.

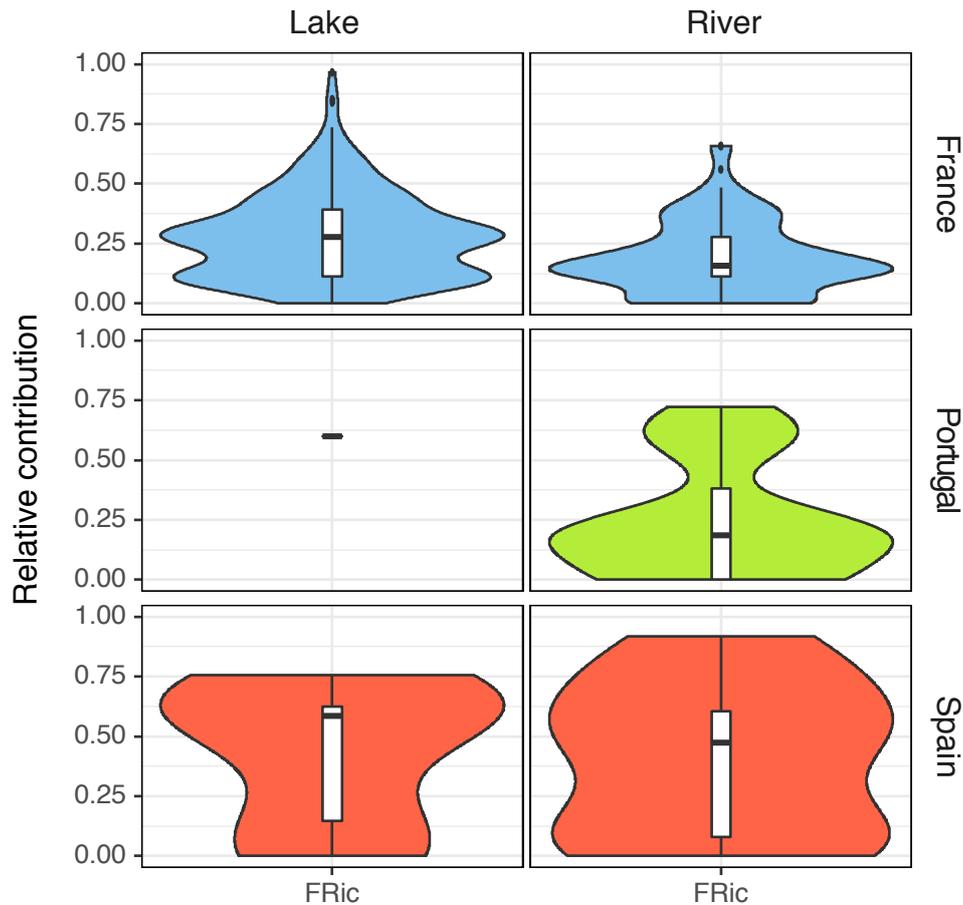


Figure 12. Proportion of the functional richness supported by non-native species in fish assemblages (polygons are estimations of the densities of the FRic values, ‘violin’ plots).

### Distribution of species with fishing interest

In accordance with the number of species observed in the species pools, estuaries exhibited the highest number of species with fishing interest, except in Spain (Table 8). Concerning freshwater water types, the greatest number of species with fishing interest was found in France. In Spanish and Portuguese species pools, the same number of species with fishing interest was observed.

Table 8. Number of species with fishing interest per water category.

Water category	Country			All
	France	Portugal	Spain	
Estuaries	59	40	2	71
Freshwater	34	15	14	44

### Estuaries

All species with fishing interest were native species. This is not surprising because of the very low contribution of non-native species to estuarine species pools.

Overall, no differences were found between France and Portugal when looking at the occurrences of species with fishing interest in estuaries (Figure 13). Indeed, *Anguilla anguilla*, *Dicentrarchus labrax*, *Platichthys flesus* and *Solea solea* had the highest occurrence rates. Some species were more or less specific of each country, for instance *Diplodus vulgaris* (Portugal), and *Trisopterus luscus* (France). Due to the low number of sites available, it was not possible to discuss the patterns observed for Spanish estuaries consistently.

The relative abundances of these species were generally low, suggesting a wide diversity of species with fishing interest available for anglers (Figure 14). This pattern was highly marked for France and Portugal, even if in this latest country some species stood out from the remaining, such as *Atherina presbyter*, *Diplodus bellottii* and *Solea solea*.

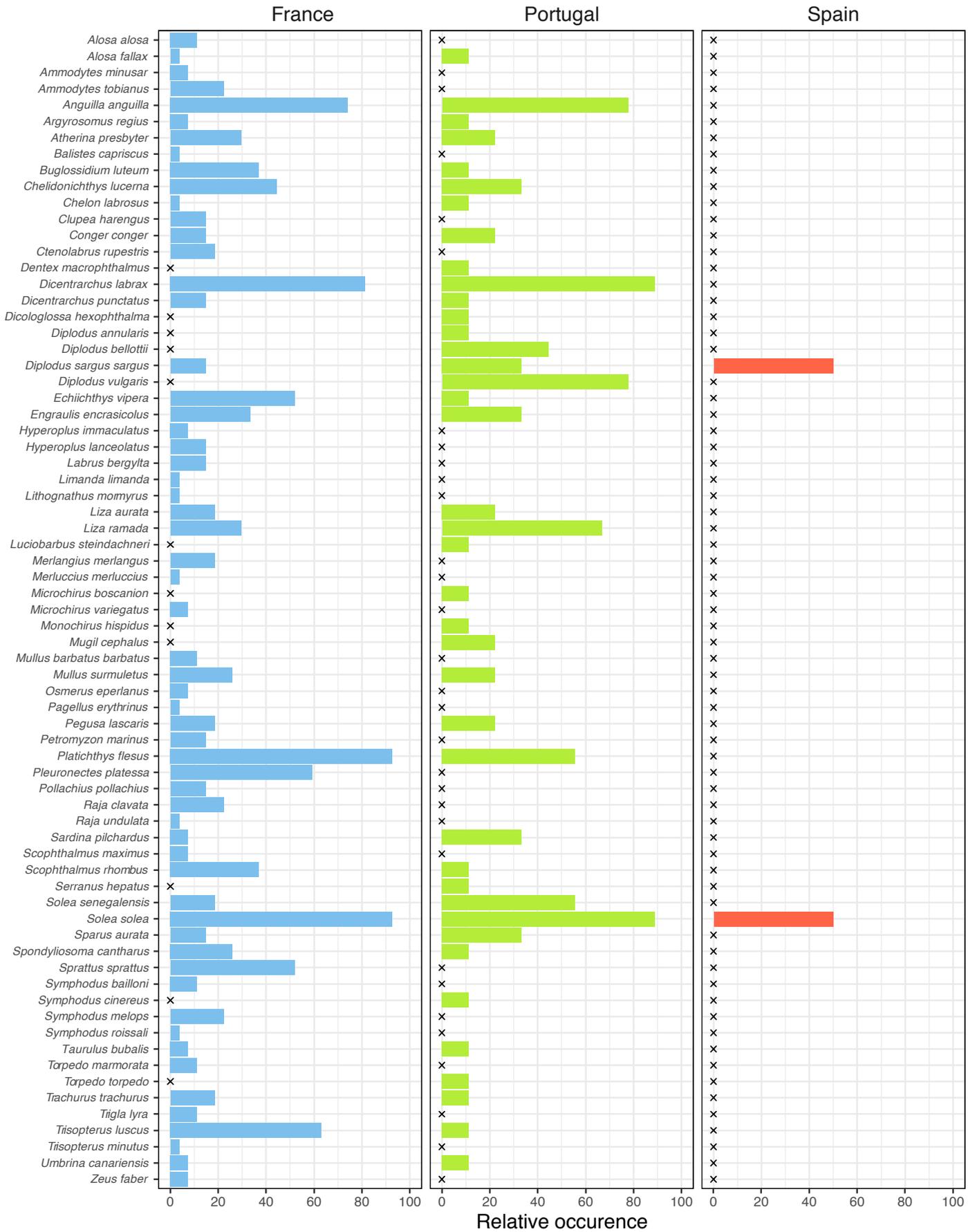


Figure 13. Relative occurrence of species with fishing interest among estuaries.

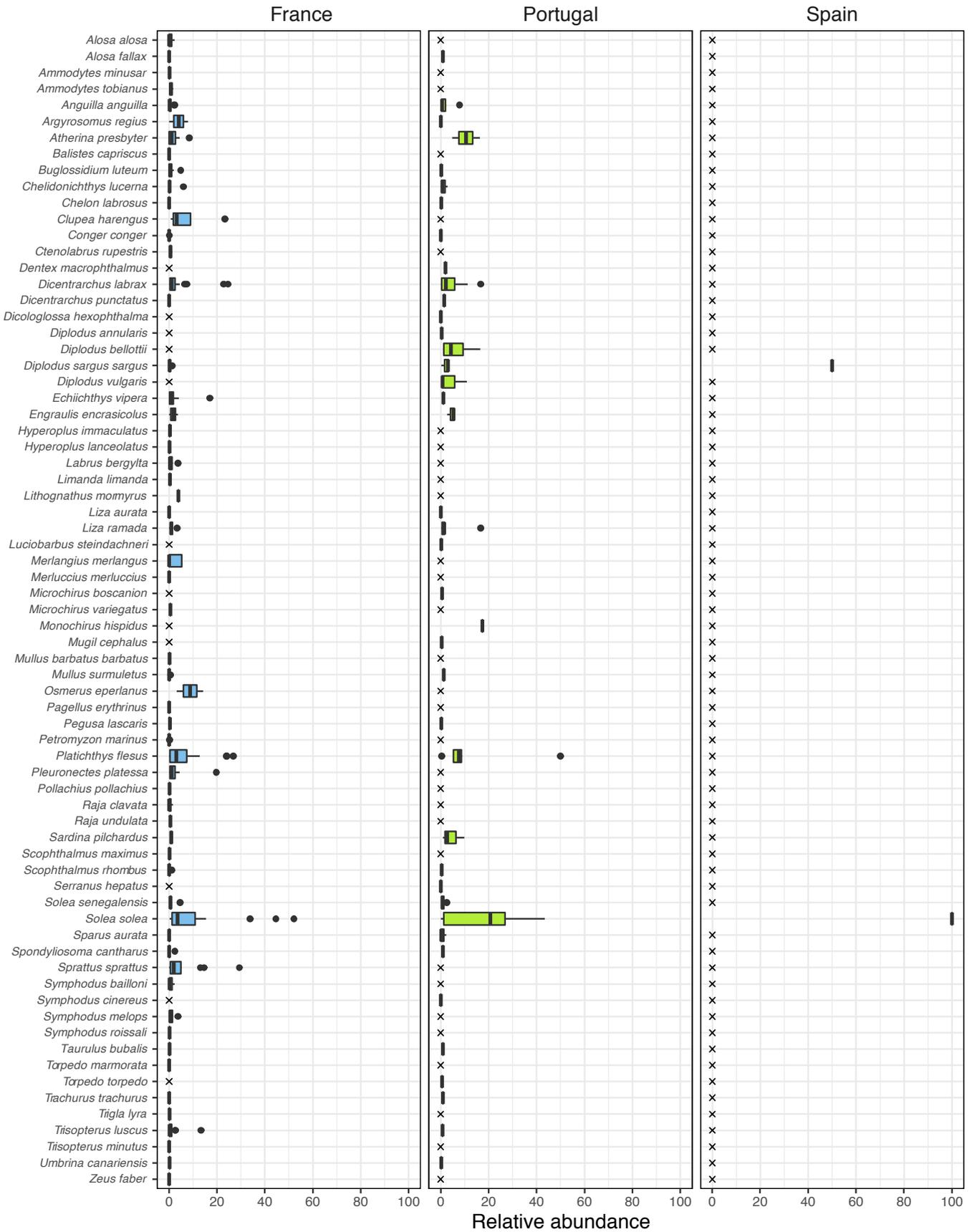


Figure 14: Relative abundance of species with fishing interest among estuaries.

### Lakes and rivers

For lakes and rivers, the situation was more contrasted. A large number of species with fishing interest were non-native (Table 9).

Table 9. Number of species with fishing interest per country and origin.

Origin	Country		
	France	Portugal	Spain
Native	23	7	7
Translocated	5	3	3
Exotic	6	5	4

Indeed, even if in freshwater fish assemblages species with fishing interest were mainly native species (Figure 15), non-native species accounted for about half of the species with fishing interest in the Iberian Peninsula and for 32% of the species in France. Except in some French lakes, translocated species were not attractive for anglers at local scale. On the other hand, exotic species with fishing interest were more abundant, especially in Spanish lakes (several dots very close from ‘E’ in Figure 16).

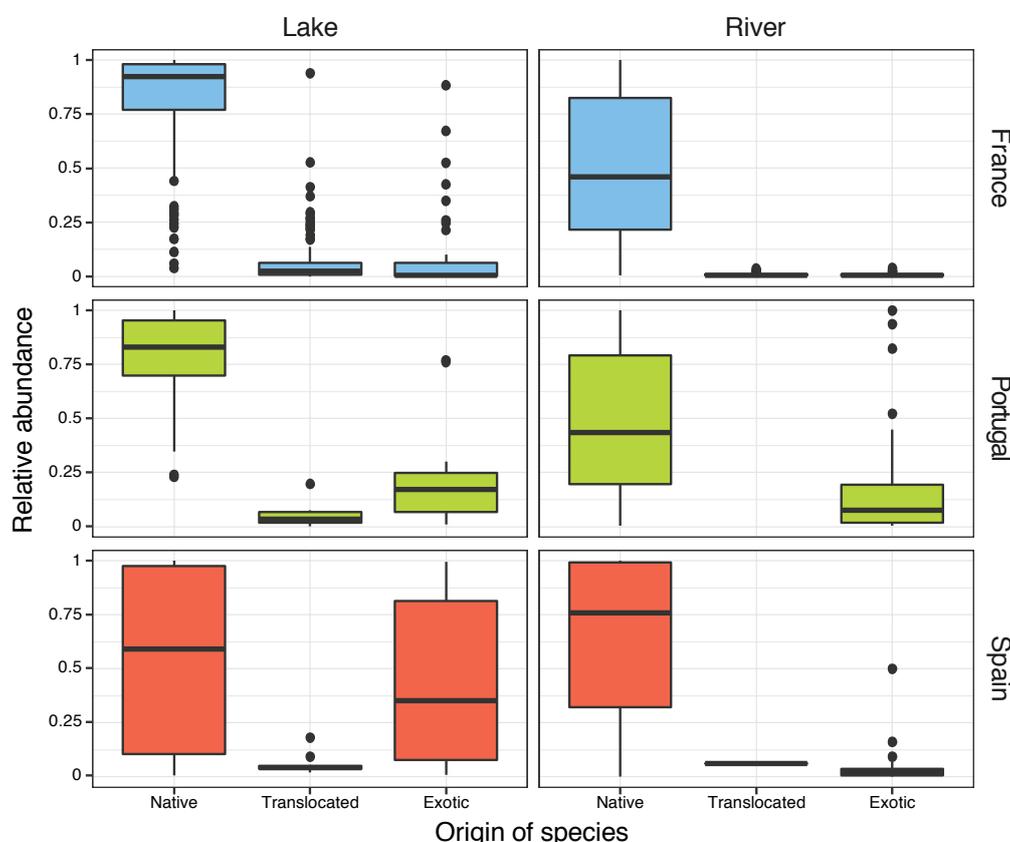


Figure 15. Relative abundance of species with fishing interest per origin of species, country and water category.

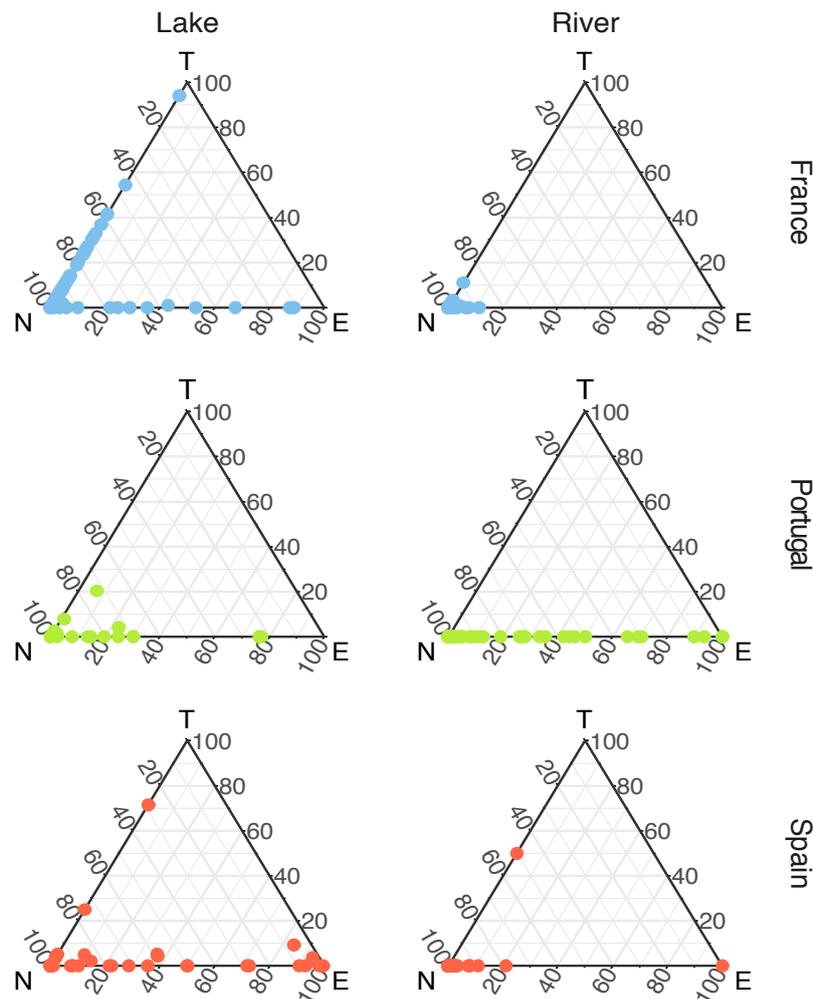


Figure 16. Relative contribution to individuals of fishing interest in assemblage of native (N), translocated (T) and exotic (E) species.

At the species level, interests for angling/fishing were highly contrasted, both in terms of occurrence and abundance (Figure 17 and Figure 18). Regarding native species with fishing interest, we observed a clear distinction between rivers and lakes and between water bodies of the same category. The native species with the highest prevalence rates in rivers was the brown trout (*Salmo trutta*), sometimes associated with cyprinid species such as *Luciobarbus bocagei* in Portugal. Not surprisingly, French rivers were the most speciose, as they exhibit the widest diversity of species of fishing interest (Figure 17).

Non-native species with fishing interest were most widespread in lakes and differed between countries. In France it was roach, perch and bream; in Portugal *L. bocagei* and carp, and in Spain brown trout associated and *L. bocagei*. It is noticeable that the occurrence rates of native species in Portuguese lakes were lower than those of non-native (mainly exotic) species.

The most widespread non-native species of interest was pike-perch (translocated species) in French lakes, and pumpkinseed and large mouth bass (two exotic species) in Portuguese lakes and to a lesser extent in Spanish lakes. This does not mean that pumpkinseed was not abundant in French lakes; it just revealed that this species did not have the same fishing interest between France and Iberian Peninsula.

Species of fishing interest differed between countries due to different anglers' preferences (as for pumpkinseed) and national species pools. Indeed, species belonging to the genera *Luciobarbus* and *Pseudochondrostoma* are endemic of the Iberian Peninsula, while species belonging to the genera *Coregonus* or *Salvelinus* were only observed in the French dataset.

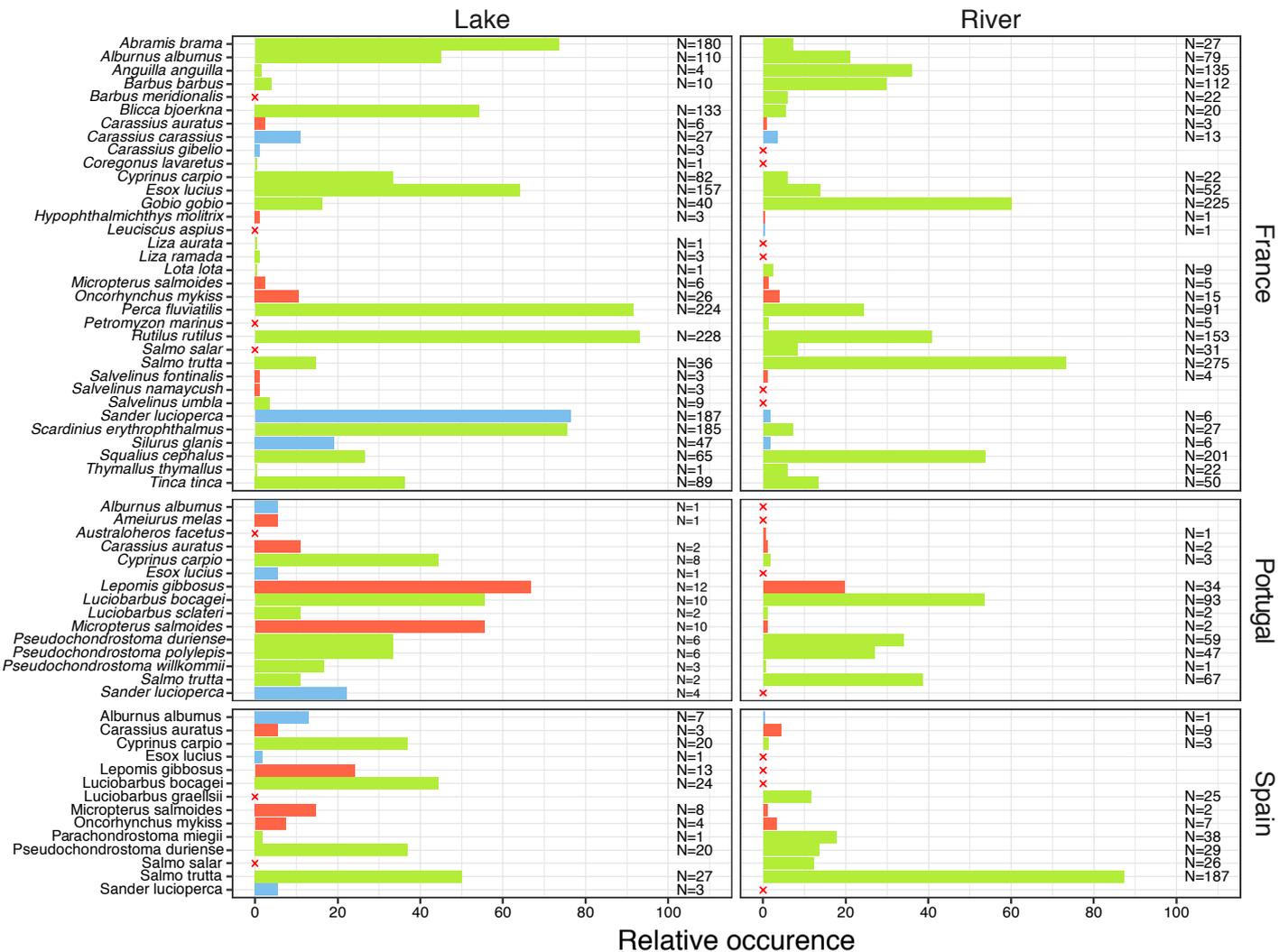


Figure 17. Relative occurrence of species with fishing interest per origin of species (native in green, translocated in blue and exotic in red) per country and water category.

As already observed before, occurrences and abundances could provide two contrasted points of view on fish assemblages. For France, the most widespread native species with fishing interest were also the most abundant ones when they occurred (Figure 18). The most widespread translocated species, pike-perch, showed relatively low abundances but the exotic *Salvelinus namaycush*, which only occurred in three lakes could be relatively abundant.

For Portuguese systems, the most abundant species targeted by anglers were the native species. The pumpkinseed relative abundances were generally low (or lower than those of native species).

For Spain, the situation was completely different. Even if pumpkinseed was not often observed in lakes, when it occurred it could be the most abundant species. In rivers, brown trout was the most widespread and abundant species.

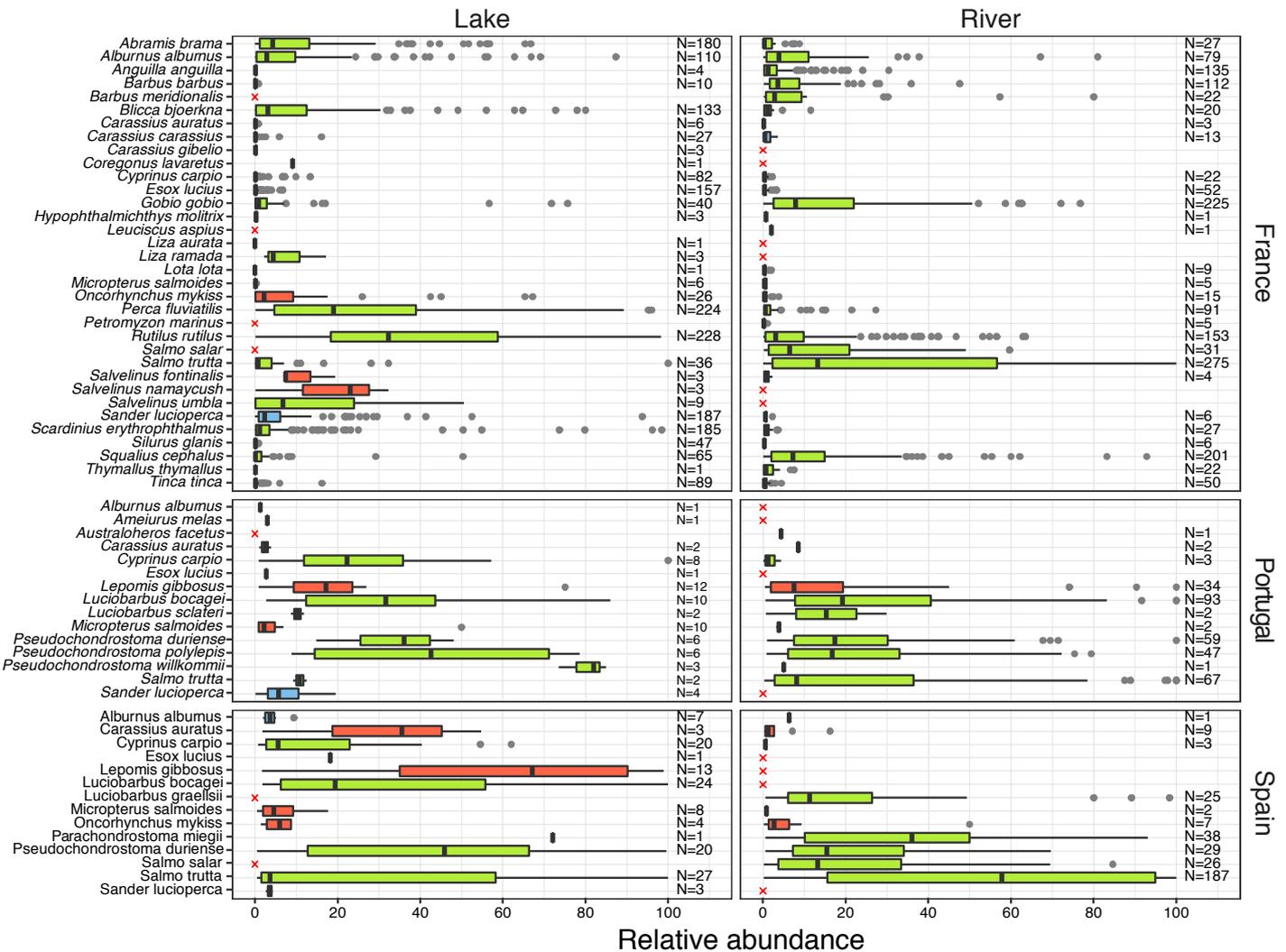


Figure 18. Relative abundance of species with fishing interest per origin of species (native in green, translocated in blue and exotic in red), country and water category.

### Impact of non-native species on species of fishing interest

Figure 19 shows the relationship between proportion of native species with fishing interest and proportion of non-native species among assemblages. These two proportions could theoretically vary between 0 and 1, but they are not independent, as their sum could not exceed 1 (symbolised by the dashed lines on the six panels). The impact of non-native fish species on native species with fishing interest seemed more intense for lakes than for rivers,

especially in France. Indeed numerous assemblages (represented by dots) were very close to the dashed-lines or located on it. This revealed that removing non-native species from these assemblages would be beneficial to native species with fishing interests only (especially for assemblages of the right side of the *x*-axis). This pattern was less evident for rivers. For the same proportion of non-native species (e.g. between 0 to 10%), a large range of proportion of native species with fishing interest could have been observed (e.g. between 30 to 80%).

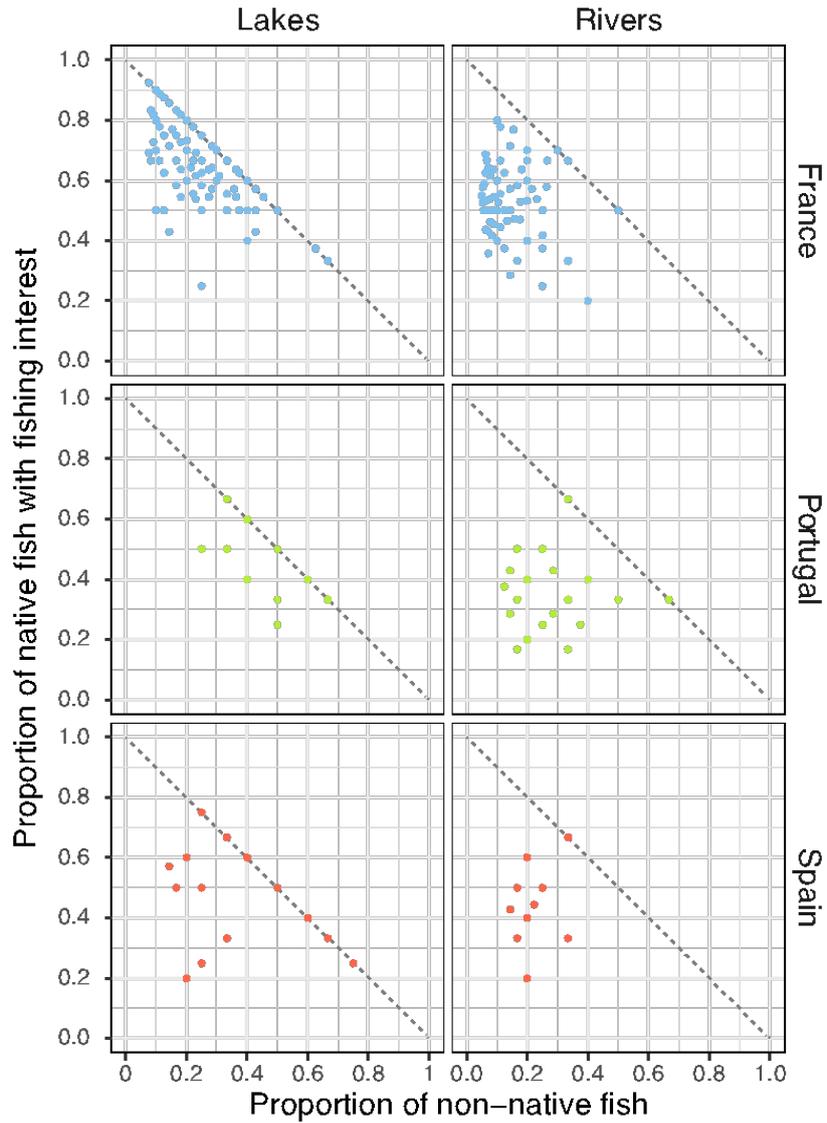


Figure 19. Relationships between the proportion of non-native fish (*x*-axis) and the proportion of native fish with fishing interest. As these two proportions could be completely linked to each other (their sum could not exceed 1), no dots could be observed above the dashed line.

## Discussion

This study compares fish assemblages of three water realms, i.e. estuaries, rivers and lakes, by exploring the role played by non-native species (translocated or exotic) on these assemblages at a large spatial scale. As expected, fish assemblages in estuaries differed in their response from those of freshwater systems. Indeed, for the same geographical area, in estuaries (except the small Spanish estuaries), the species pool and the local species richness were higher and markedly distinct from those of lakes and rivers. Among these speciose assemblages, the only non-native species, recorded in low occurrences and low abundances, were freshwater species. Finally, species with fishing interest were very diverse in estuarine sites. All these reasons contribute to the uniqueness of estuaries compared to freshwater ecosystems, together with the heterogeneous and naturally disturbed habitat conditions prevalent in estuaries.

Considering the two investigated freshwater categories and countries altogether, non-native species represented 26% of the species pool, with an equal number of translocated and exotic species (mainly originating from America). Their relative occurrences and abundances were on average low in rivers when compared to lakes. Non-native species were functionally distinct from native faunas as revealed by high values of FSpe and FOri. Their impact on the community functional structure seemed maximal in Iberian systems, with important deviation of FSpe, FOri and FRic. In the peninsular regions of southern Europe, the rarity of natural lakes where fish species could speciate in lacustrine conditions, and the massive water storage in reservoirs, resulted in habitats that are not easy to colonize for native species. In this region, the native populations present relatively few functional types and top predatory niches remain largely unoccupied. These niches have been occupied by exotic species, therefore profoundly influencing the functional structure of assemblages.

The relationship between non-native species and native species with fishing interest was contrasted. Lakes, especially those located in France, seemed to be the most ‘sensitive system’. Indeed for several French lakes, the proportions of native species with fishing interest and the proportion of non-native species were perfectly negatively correlated (their sums were equal to one). Fishing pressure or stockings are important in many waterbodies, but not equally, and detailed data on these activities are missing. Nonetheless, France is likely to have the more important angling pressure, as in Iberia, inland angling is a modest leisure activity.

### *Non-native species*

The list of translocated or exotic species observed in our study is in accordance with the 20<sup>th</sup> most frequently introduced species in Palearctic realm (Toussaint et al. 2016): *Carassius auratus*, *Oncorhynchus mykiss*, *Carassius carassius*, *Sander lucioperca*, *Lepomis gibbosus*,

*Pseudorasbora parva*, *Micropterus salmoides*, *Hypophthalmichthys molitrix*, *Gambusia affinis*, *G. holbrooki*, *Salvelinus fontinalis*, etc. Most of these species were also successfully introduced elsewhere in the world (Toussaint et al. 2016). All these species introductions lead to worldwide homogenization of the fish faunas (Villéger et al. 2015, Toussaint et al. 2016). Moreover, the potential invasiveness of these species was important as demonstrated by their very high values of FISK (Fish Invasiveness Score Kit; Copp et al. 2009).

These introductions served various objectives or had various reasons. The mosquitofish species, *G. affinis* and *G. holbrooki*, are two small species that were introduced for the biological control of mosquito populations (Pyke 2005). The main objective was to limit disease spread such as malaria. These species are still largely introduced, while its efficiency to feed on mosquito larvae is still questionable, although their negative effects on aquatic biota are more and more reported (Pyke 2008). For instance, Caiola and De Sostoa (2005) reported the decline of two native species of toothcarp (*Aphanius iberus* and *Valencia hispanica*) through feeding competition with mosquitofish.

Pumpkinseed (*Lepomis gibbosus*) is a small exotic species that was introduced as a potential sport fish, as a garden pond fish (Copp et al. 2004) or to improve wild stocks (Elvira and Almodóvar 2001). It was introduced since the 19<sup>th</sup> century (Vivier 1951, Cucherousset et al. 2009) and it is now spread all over Europe (Copp et al. 2004). Its relatively high prevalence rate was thus not so surprising.

Top predators, European catfish, pikeperch, pike and largemouth bass were introduced in France, Spain and Portugal for recreational purposes (Elvira and Almodóvar 2001), with distinct impacts among regions. For example, the native fish from Iberian region are likely more affected by these introductions. Iberian fish had a long evolution period, as this region was not affected by the last glacial maximum (it served as a glacial refuge, Hewitt 1999, 2000, 2004) leading to a high endemism rate (Marr et al. 2010, Marr et al. 2013). Because this evolution was performed in the absence of top predators, the more recent introductions of top predators, mainly from France, may represent a serious threat to native populations (Clavero and Garcia-Berthou 2006).

#### *Suitable conditions for non-native species dispersal and establishment*

Reservoirs were thought to play a major role in the spreading of non-native fish species. These systems were built to store water to meet the growing human needs, i.e. drinking water, irrigation, electricity and recreation. All Iberian lakes from our dataset and more than two-thirds of the French lakes considered in this study were reservoirs. These artificial systems, by disturbing the natural environmental conditions (Stanford and Ward 2001), were thought to facilitate spreading of non-native species and to promote the decline of native species (Salette Daga et al. 2016). In some of these reservoirs, the proportion of non-native species was high in accordance with previous observations (Godinho et al. 1998, Clavero et al. 2013). These proportions could have been even more important if *C. carpio* were considered as non-native

in Spain and Portugal, depending on the date of introduction considered (García-Berthou 2007).

Damming the former river course led to new environmental conditions (Garcia de Jalon et al. 1992), much closer to lentic environments. New habitats were created and very often non-native species were promoted in these systems because of their stronger capacity to use these new vacant niches than former native river species. This is the case of numerous non-native species observed here, as they can develop and maintain themselves in reservoirs and are more able to cope with water level fluctuations than native species (Logez et al. 2016b). In addition to the creation of new niches, reservoirs could also serve as starting spreading points or stepping-stones for non-native dispersion. For example, riverine populations of largemouth bass were observed downstream from the reservoir Encinarejo (southern Spain), where these populations were not able to reproduce. Conversely, this species was able to accomplish its entire biological cycle in the reservoir (Almeida and Grossman 2014). Therefore, reservoirs could serve as source for river populations, as some small individuals were able to get through the turbines. Almeida and Grossman (2014) hypothesized that even if largemouth bass was not able to reproduce immediately downstream the dam, it would be able to complete its life cycle further downstream. This source-sink mechanism ensures the spreading of a species in a catchment.

These non-native species that benefit from artificial new habitats or human alterations (Alcaraz et al. 2005) exhibit suite of traits (syndrome or strategy depending of the authors) that are more suitable than native species traits (Olden et al. 2006, García-Berthou 2007). Previous studies intended to find key traits that could explain the success of species invasion along the different phases of the process (García-Berthou 2007, Gozlan et al. 2010b), i.e. release, establishment, dispersal and integration. The main objective of this study was to compare the functional singularity of non-natives species already established in their new environment with those of native species. This was done through functional specificity and originality, two aspects of the functional diversity (Buisson et al. 2013, Mouillot et al. 2013). We highlighted that the most widespread non-native species were among the species with the highest functional specificity and/or the highest functional originality. Therefore, non-native species presented very distinct suite of traits, either extreme (specificity) or non-observed in other species (originality). This is in accordance with Olden et al. (2006), who found that introduced species had much more extreme strategies than native species, which get extinct due to long term alterations of natural environmental conditions. It is noticeable that even though these authors used different type of traits than those we used, conclusions are relatively similar. Olden et al. based their analyses on life history traits (mainly demographic), whereas we used the triangular model of Winemiller and Rose (1992) that classifies species along three main strategies (axes) based on their life history traits (Logez et al. 2016a).

The differences of the species' location in the functional space between native and non-native species reveal a relatively low niche overlap that could explain the introduction success of non-native species. Occupying different niches could give a competitive advantage over non-

native species, especially in altered systems (Olden et al. 2006). These differences between functional characteristics of native and non-native species were deeply marked at the species pool levels, especially in the site-poor fish fauna of the Iberian Peninsula (though regional richness is very high). Various mechanisms were responsible for this pattern. The low richness of the Iberian species pools increases the probability that an introduced species has different functional attributes (i.e. no native top-predators in Spain and Portugal), whereas in species-rich faunas this probability decreases. Phylogeny is probably an important factor too. Indeed, numerous native fish species of Spain and Portugal belong to the same lineage and had similar traits (e.g. the various species of barbel and straight-mouth nase), which could lead to low functional originality (Alcaraz et al. 2005). In addition, most introduced species belong to lineage originated from other regions of the world (Alcaraz et al. 2005). Finally, alteration of natural systems must have been an important issue, as altered environmental conditions are known to promote non-native species with different traits (Olden et al. 2006).

Other traits or different aspects of species introduction not considered here could have been important factors to the spread of non-native species (Cucherousset et al. 2009, Grabowska and Przybylski 2014). Probably one of the most important traits is the ability of these species to adapt their traits to novel environmental conditions. For instance, pumpkinseed exhibited different life history traits between its original area, North America, and European systems (Copp et al. 2004, Fox and Copp 2014), including the ones studied here (Bhagat et al. 2011). This phenotypic plasticity was also observed among different areas where this species has been introduced (Cucherousset et al. 2009). A similar pattern of adaptation is observed with another widespread species, the topmouth gudgeon *Pseudorasbora parva*, also very plastic in fitness related traits (Gozlan et al. 2010a).

#### *Non-native species and ecosystem services*

In addition to their impact on native faunas (Cucherousset and Olden 2011, Schlaepfer et al. 2011), the introduction and the success of non-native species in the European hydrographical network lead to the question of their impact on ecosystem services (Pejchar and Mooney 2009). Indeed, non-native species being introduced for very diverse reasons (Gozlan et al. 2010b) may contribute to sustain several ecosystem services (Schlaepfer et al. 2011).

Many species introduced for recreational purposes, i.e. species with sport fishing interest, contribute to ‘cultural’ services (angling corresponding to service class: ‘Physical and experiential interactions with biota’ *sensu* CICES v4.3). In some locations, we observed fish assemblages almost composed of non-native species with sport fishing interest, and high socio-economic implications and spinoffs (fishing gear, fishing licence, angling vacation, etc.) (Amaral et al. 2015). Indeed, in Iberian Peninsula anglers declared to have preferences in catching large predator non-native species (Banha et al. 2016) and thousands of anglers are participating to angling competitions (Amaral et al. 2015). In these circumstances, where only non-native species are currently occurring and are beneficial to local populations, protection

of these species can be questioned with regard to conflicting “environmental objectives” advocating pristine or low disturbance conditions.

Conflicts between services could also arise due to direct and indirect negative effects of non-native species (it could also be true for native species) on water quality and potable water (provisioning service, ‘Nutrition – Potable water’, CICES v4.3), especially by enhancing eutrophication (Angeler et al. 2002, Starling et al. 2002, Amaral et al. 2015). Allochthonous nutrients are sometimes introduced into the systems through groundbait released by anglers to improve fish catchability. The additional stock of nutrient inputs (Arlinghaus 2005) depends not only on the amount but also on the types of groundbait used (Amaral et al. 2015). A direct effect on water-quality was observed, when non-native species are feeding on zooplankton (e.g. mosquitofish and pumpkinseed) or on sediment (e.g. benthivorous carp). As a result, phytoplankton assemblages and productivity are modified by a cascade effect, conducting to an increase in nutrient concentration and eutrophication (Bernes et al. 2015). Similar patterns were observed in systems hosting carps but for different reasons (natural enrichment due to this species and bioturbation).

In this study, it was not really possible to analyse the impact of the introduction of non-native species on biodiversity. Indeed, historical information on species introductions is not easily accessible. Only a few and short time series on species abundance were available and were not analysed, and data on biomasses were lacking.

### *Management of non-native species*

Without considering the fact that removing non-native species in a water body is technically very difficult and expensive (Gozlan et al. 2010b), eradication of non-native species can be discussed considering the goods and services previously mentioned.

In case of non-native species targeted by fishing, their impact on the ecosystem functioning is often poorly assessed. A removal of such non-native species could appear unjustified and not cost effective considering economical activities linked to fishing. In that condition, reconciling environmental and cultural objectives can be conflicting. Only if non-native species are at the origin of water quality degradation, it might be easier to solve such conflicts, as eradication of non-native species then could satisfy different services. The utility to remove a non-native species could also be debated when this species is part of ‘pest and disease control’ and therefore benefitting human health. This is the case of the two mosquito fish species. For these reasons, such species could be seen as highly important by providing services for human well-being. Nonetheless, the efficiency of mosquito fish into biological control is still debated and contested more than one century after its worldwide spreading (Pyke 2005, 2008). On the other hand, the negative effects of mosquito fish species are more and more reported in the literature, which questions the benefits of their introduction for human well-being (Pyke 2008).

We believe that the debate concerning the importance of non-native species and their implications in ecosystem services is far from being closed. As discussed by Gozlan et al. (2010b), the socio-economic issue related to the introduction of non-native species and ecosystem services must be addressed. The existence of impacts of non-native species should also be considered regarding to the context of environmental conditions, native biotas (absence of native species in newly created reservoirs) and former system functioning. Therefore, we advocate that realistic projections of the system functioning and ecosystems services derived are taken into account in related future decision-making processes.

### *Limits of the study*

Assessing the consequences and the effects of non-native species presence on native assemblages and/or on hydrosystem functioning constitute an issue that should be supported by long-term monitoring programs (Gozlan et al. 2010b). In this study, for each site, only the latest sampling date was considered. One year of data is obviously not sufficient to consistently estimate the effects of non-native species on native fauna. For instance, in a stream reach of the southeastern Iberian Peninsula, Ruiz-Navarro et al. (2013) showed that five years of monitoring were required to demonstrate the recovery of native fish densities after a control of *G. affinis*. In addition, long-term data on the Rhone River showed a fast increase in the density of *P. parva* in a couple of years after 1989 (its first record in the system). Then the densities stabilised and seemed to vary accordingly with hydrological events (Carrel, *pers. comm.*), justifying the need for long term monitoring programs.

The time period covered by the datasets was a second limit to our work. Data for rivers were provided by the EFI+ Consortium (2007). These data were very useful to understand patterns shaping fish assemblages (Logez et al. 2013) and to evaluate anthropogenic pressures at large scale (Schinegger et al. 2012). Nonetheless, none of the river data was collected after 2006. For the non-native species issue this could constitute a limit. In the Iberian Peninsula, several non-native species were introduced recently (García-Berthou 2007, Ribeiro et al. 2009, Leunda 2010) and are still spreading in the hydrographical networks (Aparicio et al. 2012, Gago et al. 2016). Thus we are probably underestimating the occurrence of non-native species at present.

Two other factors could lead to an underestimation of non-native species occurrences or abundances: spatial location of sites and sampling efficiency. Even if a large number of sampling sites for rivers was available, our dataset in Spain was limited to the Atlantic coast and in Portugal to the central and northern regions. It probably means that we had a limited overview of Mediterranean rivers from a climatic point of view. The great majority of rivers were sampled by wading and thus had limited depth, suggesting a bias toward small and medium-size rivers. Large rivers were almost absent, while they offer habitat conditions not observed in smallest rivers such as lentic habitat and/or warmer conditions that could be suitable for pumpkinseed, bleak, European catfish, mosquito fish (Pyke 2008) and several

other non-native species. Conversely, most of the study lakes were large lakes, where the standardised sampling strategy does not allow catching all fish species present. Small littoral species for example are very likely underrepresented/absent in the samples. The several aforementioned reasons might explain the low number of non-native species recorded in our study when compared to the numbers reported in the literature. For example, 20-30 non-native species were introduced in the Iberian Peninsula (Elvira and Almodóvar 2001, Sabater et al. 2009, Leunda 2010, Marr et al. 2010), and many are under-represented in the data set.

### *Concluding remarks*

By integrating all water categories along the freshwater-marine continuum, our study enables a broad overview contributing with new insights concerning the effects of non-native species on European fish assemblages. The presence of non-native fish species appeared very distinct among waterbodies and countries. These results highlighted that management of non-native species should be the prime concern in lakes and Iberian hydrosystems. Their presence in these systems is already common and may lead to irreversible ecological impacts. On the contrary, non-native species appeared relatively scarce in estuaries, calling for prevention and vigilance in these systems. Non-native fish species generally appeared to be functionally apart from native species and we hypothesized that these differences may explain their introduction success in European freshwaters. Our results also support the need for national monitoring programs, as the occurrences, the abundances and the identity of non-native species come along with a strong geographic pattern. Finally, the management of non-native species (removal, control, etc.) should be integrated within an ecosystem service assessment framework, to weight the cost/benefits of given actions.

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## Supporting Materials

Table S1. Status of the 88 fish present in lakes and rivers.

Species	Origin			Fishing Interest		
	France	Portugal	Spain	France	Portugal	Spain
<i>Abramis brama</i>	N	-	-	Yes	-	-
<i>Achondrostoma arcasii</i>	-	N	N	-	No	No
<i>Achondrostoma oligolepis</i>	-	N	-	-	No	-
<i>Alburnoides bipunctatus</i>	N	-	-	No	-	-
<i>Alburnus alburnus</i>	N	T	T	Yes	Yes	Yes
<i>Ameiurus melas</i>	E	E	-	No	Yes	-
<i>Anguilla anguilla</i>	N	N	N	Yes	No	No
<i>Atherina boyeri</i>	-	N	-	-	No	-
<i>Atherina presbyter</i>	-	-	N	-	-	No
<i>Australoheros facetus</i>	-	E	-	-	Yes	-
<i>Barbatula barbatula</i>	N	-	N	No	-	No
<i>Barbus barbus</i>	N	-	-	Yes	-	-
<i>Barbus meridionalis</i>	N	-	-	Yes	-	-
<i>Blicca bjoerkna</i>	N	-	-	Yes	-	-
<i>Carassius auratus</i>	E	E	E	Yes	Yes	Yes
<i>Carassius carassius</i>	T	-	-	Yes	-	-
<i>Carassius gibelio</i>	T	-	-	Yes	-	-
<i>Chelon labrosus</i>	-	-	N	-	-	No
<i>Chondrostoma nasus</i>	N	-	-	No	-	-
<i>Cobitis calderoni</i>	-	N	N	-	No	No
<i>Cobitis paludica</i>	-	N	N	-	No	No
<i>Cobitis taenia</i>	N	-	-	No	-	-
<i>Coregonus lavaretus</i>	N	-	-	Yes	-	-
<i>Cottus gobio</i>	N	-	-	No	-	-
<i>Cyprinus carpio</i>	N	N	N	Yes	Yes	Yes
<i>Esox lucius</i>	N	T	T	Yes	Yes	Yes
<i>Gambusia affinis</i>	E	-	-	No	-	-
<i>Gambusia holbrooki</i>	-	E	-	-	No	-
<i>Gasterosteus aculeatus</i>	N	-	-	No	-	-
<i>Gasterosteus gymnurus</i>	-	N	N	-	No	No
<i>Gobio gobio</i>	N	-	T	Yes	-	No
<i>Gobio lozanoi</i>	-	T	N	-	No	No
<i>Gymnocephalus cernua</i>	N	-	-	No	-	-
<i>Hypophthalmichthys molitrix</i>	E	-	-	Yes	-	-
<i>Iberochondrostoma almakai</i>	-	N	-	-	No	-
<i>Iberochondrostoma lemmingii</i>	-	N	-	-	No	-
<i>Lampetra fluviatilis</i>	N	-	-	No	-	-
<i>Lampetra planeri</i>	N	N	N	No	No	No
<i>Lepomis gibbosus</i>	E	E	E	No	Yes	Yes
<i>Leucaspis delineatus</i>	N	-	-	No	-	-
<i>Leuciscus aspius</i>	T	-	-	Yes	-	-
<i>Leuciscus burdigalensis</i>	N	-	-	No	-	-

<i>Leuciscus idus</i>	T	-	-	No	-	-
<i>Leuciscus leuciscus</i>	N	-	-	No	-	-
<i>Liza aurata</i>	N	-	-	Yes	-	-
<i>Liza ramada</i>	N	-	-	Yes	-	-
<i>Lota lota</i>	N	-	-	Yes	-	-
<i>Luciobarbus bocagei</i>	-	N	N	-	Yes	Yes
<i>Luciobarbus graellsii</i>	-	-	N	-	-	Yes
<i>Luciobarbus microcephalus</i>	-	N	-	-	No	-
<i>Luciobarbus sclateri</i>	-	N	-	-	Yes	-
<i>Micropterus salmoides</i>	E	E	E	Yes	Yes	Yes
<i>Mugil cephalus</i>	-	N	-	-	No	-
<i>Oncorhynchus mykiss</i>	E	-	E	Yes	-	Yes
<i>Pachychilon pictum</i>	T	-	-	No	-	-
<i>Parachondrostoma miegii</i>	-	-	N	-	-	Yes
<i>Parachondrostoma toxostoma</i>	N	-	-	No	-	-
<i>Perca fluviatilis</i>	N	-	-	Yes	-	-
<i>Petromyzon marinus</i>	N	-	N	Yes	-	No
<i>Phoxinus phoxinus</i>	N	-	N	No	-	No
<i>Platichthys flesus</i>	-	-	N	-	-	No
<i>Pseudochondrostoma duriense</i>	-	N	N	-	Yes	Yes
<i>Pseudochondrostoma polylepis</i>	-	N	-	-	Yes	-
<i>Pseudochondrostoma willkommii</i>	-	N	-	-	Yes	-
<i>Pseudorasbora parva</i>	E	-	-	No	-	-
<i>Pungitius pungitius</i>	N	-	-	No	-	-
<i>Rhodeus amarus</i>	N	-	-	No	-	-
<i>Rutilus rutilus</i>	N	-	-	Yes	-	-
<i>Salaria fluviatilis</i>	N	-	-	No	-	-
<i>Salmo salar</i>	N	-	N	Yes	-	Yes
<i>Salmo trutta</i>	N	N	N	Yes	Yes	Yes
<i>Salvelinus fontinalis</i>	E	-	-	Yes	-	-
<i>Salvelinus namaycush</i>	E	-	-	Yes	-	-
<i>Salvelinus umbla</i>	N	-	-	Yes	-	-
<i>Sander lucioperca</i>	T	T	T	Yes	Yes	Yes
<i>Scardinius erythrophthalmus</i>	N	-	-	Yes	-	-
<i>Scardinius hesperidicus</i>	T	-	-	No	-	-
<i>Silurus glanis</i>	T	-	-	Yes	-	-
<i>Squalius alburnoides</i>	-	N	-	-	No	-
<i>Squalius aradensis</i>	-	N	-	-	No	-
<i>Squalius carolitertii</i>	-	N	N	-	No	No
<i>Squalius cephalus</i>	N	-	-	Yes	-	-
<i>Squalius pyrenaicus</i>	-	N	N	-	No	No
<i>Squalius torgalensis</i>	-	N	-	-	No	-
<i>Telestes souffia</i>	N	-	-	No	-	-
<i>Thymallus thymallus</i>	N	-	-	Yes	-	-
<i>Tinca tinca</i>	N	-	-	Yes	-	-
<i>Zingel asper</i>	N	-	-	No	-	-

E=Exotic, N=Native, T=Translocated; - codes for the absence of the species in the dataset.

Table S2. Status of the 126 fish present in estuaries.

Species	Presence			Origin			Fishing Interest		
	France	Portugal	Spain	France	Portugal	Spain	France	Portugal	Spain
<i>Abramis brama</i>	1	0	0	N	-	-	No	-	-
<i>Agonus cataphractus</i>	1	0	0	N	-	-	No	-	-
<i>Alburnus alburnus</i>	1	0	0	N	-	-	No	-	-
<i>Alosa alosa</i>	1	0	0	N	-	-	Yes	-	-
<i>Alosa fallax</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Ameiurus melas</i>	1	1	0	E	E	-	No	No	-
<i>Ammodytes marinus</i>	1	0	0	N	-	-	Yes	-	-
<i>Ammodytes tobianus</i>	1	0	0	N	-	-	Yes	-	-
<i>Anguilla anguilla</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Aphia minuta</i>	1	1	0	N	N	-	No	No	-
<i>Argyrosomus regius</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Arnoglossus imperialis</i>	1	0	0	N	-	-	No	-	-
<i>Arnoglossus laterna</i>	1	1	0	N	N	-	No	No	-
<i>Arnoglossus thori</i>	1	0	0	N	-	-	No	-	-
<i>Atherina presbyter</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Balistes capriscus</i>	1	0	0	N	-	-	Yes	-	-
<i>Barbus barbus</i>	1	0	0	N	-	-	No	-	-
<i>Blicca bjoerkna</i>	1	0	0	N	-	-	No	-	-
<i>Bothus podas</i>	0	1	0	-	N	-	-	No	-
<i>Buglossidium luteum</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Callionymus lyra</i>	1	1	0	N	N	-	No	No	-
<i>Callionymus maculatus</i>	0	1	0	-	N	-	-	No	-
<i>Callionymus risso</i>	1	1	0	N	N	-	No	No	-
<i>Carassius carassius</i>	1	0	0	T	-	-	No	-	-
<i>Carassius gibelio</i>	1	0	0	T	-	-	No	-	-
<i>Chelidonichthys lucerna</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Chelon labrosus</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Ciliata mustela</i>	1	0	0	N	-	-	No	-	-
<i>Clupea harengus</i>	1	0	0	N	-	-	Yes	-	-
<i>Conger conger</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Ctenolabrus rupestris</i>	1	0	0	N	-	-	Yes	-	-
<i>Cyprinus carpio</i>	1	1	0	N	N	-	No	No	-
<i>Dentex macrophthalmus</i>	0	1	0	-	N	-	-	Yes	-
<i>Dicentrarchus labrax</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Dicentrarchus punctatus</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Dicologlossa hexophthalma</i>	0	1	0	-	N	-	-	Yes	-
<i>Diplecogaster bimaculata</i>	1	0	0	N	-	-	No	-	-
<i>Diplodus annularis</i>	0	1	0	-	N	-	-	Yes	-
<i>Diplodus bellottii</i>	0	1	0	-	N	-	-	Yes	-
<i>Diplodus sargus sargus</i>	1	1	1	N	N	N	Yes	Yes	Yes
<i>Diplodus vulgaris</i>	0	1	0	-	N	-	-	Yes	-
<i>Echiichthys vipera</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Engraulis encrasicolus</i>	1	1	0	N	N	-	Yes	Yes	-

<i>Entelurus aequoreus</i>	1	0	0	N	-	-	No	-	-
<i>Gasterosteus aculeatus</i>	1	0	0	N	-	-	No	-	-
<i>Gobius niger</i>	1	1	0	N	N	-	No	No	-
<i>Gobius paganellus</i>	1	1	0	N	N	-	No	No	-
<i>Gobiusculus flavescens</i>	1	0	0	N	-	-	No	-	-
<i>Gymnocephalus cernua</i>	1	0	0	N	-	-	No	-	-
<i>Halobatrachus didactylus</i>	0	1	0	-	N	-	-	No	-
<i>Hippocampus guttulatus</i>	1	0	0	N	-	-	No	-	-
<i>Hippocampus hippocampus</i>	1	1	0	N	N	-	No	No	-
<i>Hyperoplus immaculatus</i>	1	0	0	N	-	-	Yes	-	-
<i>Hyperoplus lanceolatus</i>	1	0	0	N	-	-	Yes	-	-
<i>Labrus bergylta</i>	1	0	0	N	-	-	Yes	-	-
<i>Lepadogaster candolii</i>	1	0	0	N	-	-	No	-	-
<i>Lesueurigobius friesii</i>	0	0	1	-	-	N	-	-	No
<i>Leuciscus idus</i>	1	0	0	T	-	-	No	-	-
<i>Limanda limanda</i>	1	0	0	N	-	-	Yes	-	-
<i>Lithognathus mormyrus</i>	1	0	0	N	-	-	Yes	-	-
<i>Liza aurata</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Liza ramada</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Luciobarbus bocagei</i>	0	1	0	-	N	-	-	No	-
<i>Luciobarbus comizo</i>	0	1	0	-	N	-	-	No	-
<i>Luciobarbus steindachneri</i>	0	1	0	-	N	-	-	Yes	-
<i>Merlangius merlangus</i>	1	0	0	N	-	-	Yes	-	-
<i>Merluccius merluccius</i>	1	0	0	N	-	-	Yes	-	-
<i>Microchirus boscanion</i>	0	1	0	-	N	-	-	Yes	-
<i>Microchirus variegatus</i>	1	0	0	N	-	-	Yes	-	-
<i>Monochirus hispidus</i>	0	1	0	-	N	-	-	Yes	-
<i>Mugil cephalus</i>	0	1	0	-	N	-	-	Yes	-
<i>Mullus barbatus barbatus</i>	1	0	0	N	-	-	Yes	-	-
<i>Mullus surmuletus</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Nerophis lumbriciformis</i>	1	0	0	N	-	-	No	-	-
<i>Nerophis maculatus</i>	1	0	0	N	-	-	No	-	-
<i>Nerophis ophidion</i>	1	0	0	N	-	-	No	-	-
<i>Osmerus eperlanus</i>	1	0	0	N	-	-	Yes	-	-
<i>Pagellus erythrinus</i>	1	0	0	N	-	-	Yes	-	-
<i>Parablennius gattorugine</i>	1	0	0	N	-	-	No	-	-
<i>Pegusa lascaris</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Perca fluviatilis</i>	1	0	0	N	-	-	No	-	-
<i>Petromyzon marinus</i>	1	0	0	N	-	-	Yes	-	-
<i>Pholis gunnellus</i>	1	0	0	N	-	-	No	-	-
<i>Platichthys flesus</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Pleuronectes platessa</i>	1	0	0	N	-	-	Yes	-	-
<i>Pollachius pollachius</i>	1	0	0	N	-	-	Yes	-	-
<i>Pomatoschistus lozanoi</i>	1	0	0	N	-	-	No	-	-
<i>Pomatoschistus marmoratus</i>	1	0	0	N	-	-	No	-	-
<i>Pomatoschistus microps</i>	1	1	0	N	N	-	No	No	-
<i>Pomatoschistus minutus</i>	1	1	0	N	N	-	No	No	-

<i>Pomatoschistus pictus</i>	1	1	0	N	N	-	No	No	-
<i>Raja clavata</i>	1	0	0	N	-	-	Yes	-	-
<i>Raja undulata</i>	1	0	0	N	-	-	Yes	-	-
<i>Rutilus rutilus</i>	1	0	0	N	-	-	No	-	-
<i>Sander lucioperca</i>	1	0	0	T	-	-	No	-	-
<i>Sardina pilchardus</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Scardinius erythrophthalmus</i>	1	0	0	N	-	-	No	-	-
<i>Scophthalmus maximus</i>	1	0	0	N	-	-	Yes	-	-
<i>Scophthalmus rhombus</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Serranus hepatus</i>	0	1	0	-	N	-	-	Yes	-
<i>Solea senegalensis</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Solea solea</i>	1	1	1	N	N	N	Yes	Yes	Yes
<i>Sparus aurata</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Spinachia spinachia</i>	1	0	0	N	-	-	No	-	-
<i>Spondyliosoma cantharus</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Sprattus sprattus</i>	1	0	0	N	-	-	Yes	-	-
<i>Squalius cephalus</i>	1	0	0	N	-	-	No	-	-
<i>Symphodus bailloni</i>	1	0	0	N	-	-	Yes	-	-
<i>Symphodus cinereus</i>	0	1	0	-	N	-	-	Yes	-
<i>Symphodus melops</i>	1	0	0	N	-	-	Yes	-	-
<i>Symphodus roissali</i>	1	0	0	N	-	-	Yes	-	-
<i>Syngnathus abaster</i>	0	1	0	-	N	-	-	No	-
<i>Syngnathus acus</i>	1	1	0	N	N	-	No	No	-
<i>Syngnathus rostellatus</i>	1	0	0	N	-	-	No	-	-
<i>Syngnathus typhle</i>	1	0	0	N	-	-	No	-	-
<i>Taurulus bubalis</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Thorogobius ephippiatus</i>	1	0	0	N	-	-	No	-	-
<i>Tinca tinca</i>	1	0	0	N	-	-	No	-	-
<i>Torpedo marmorata</i>	1	0	0	N	-	-	Yes	-	-
<i>Torpedo torpedo</i>	0	1	0	-	N	-	-	Yes	-
<i>Trachurus trachurus</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Trigla lyra</i>	1	0	0	N	-	-	Yes	-	-
<i>Trisopterus luscus</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Trisopterus minutus</i>	1	0	0	N	-	-	Yes	-	-
<i>Umbrina canariensis</i>	1	1	0	N	N	-	Yes	Yes	-
<i>Zeus faber</i>	1	0	0	N	-	-	Yes	-	-

Table S3. Occurrence of the 17 fish present in the three water categories.

Species	Water categories		
	Estuaries	Lakes	Rivers
<i>Abramis brama</i>	3	180	27
<i>Alburnus alburnus</i>	3	118	80
<i>Ameiurus melas</i>	3	62	17
<i>Anguilla anguilla</i>	27	5	265
<i>Barbus barbus</i>	2	10	112
<i>Blicca bjoerkna</i>	6	133	20
<i>Carassius carassius</i>	2	27	13
<i>Cyprinus carpio</i>	4	110	28
<i>Gasterosteus aculeatus</i>	5	1	35
<i>Gymnocephalus cernua</i>	1	137	23
<i>Luciobarbus bocagei</i>	1	34	93
<i>Perca fluviatilis</i>	2	224	91
<i>Rutilus rutilus</i>	3	228	153
<i>Sander lucioperca</i>	2	194	6
<i>Scardinius erythrophthalmus</i>	2	185	27
<i>Squalius cephalus</i>	1	65	201
<i>Tinca tinca</i>	1	89	50