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Freshwater fish invasions: A comprehensive review

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Abstract

Freshwater fish have been widely introduced worldwide, and freshwater ecosystems are among the most affected by biological invasions. Consequently, freshwater fish invasions are one of the most documented invasions among animal taxa, with much information available about invasive species, their characteristics, invaded regions, invasion pathways, impacts, and management. While existing reviews address specific aspects of freshwater fish invasions, there is still a gaping lack of comprehensive assessments of freshwater fish invasions that simultaneously address pivotal and connected elements of the invasion process. Here, we provide a holistic review, together with quantitative assessments, divided into four major parts: (1) introduction pathways; (2) characteristics of non-native species and invaded ecosystems to explain successful invasion processes; (3) invasion impacts and their mechanisms; and (4)

management. We highlight data gaps and bias in current databases and point to the basic lack of understanding of several aspects of freshwater fish invasions. Finally, we provide recommendations for future studies.

Keywords: pathways, life history traits, impacts, management, characteristics.

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1. Introduction

The growth of global trade has resulted in the intentional and unintentional displacement of a large number of species around the world beyond their natural geographic ranges (Seebens et al., 2017). From 1800 to 2000, new species introductions increased worldwide, and this trend is expected to continue over the next few decades (Seebens et al., 2017, 2021). These new species introductions can lead to biological invasions, which are a major source of change and decline in global biodiversity (Bellard et al., 2016) as well as economic loss (Haubrock et al., 2021). The invasion process is often divided into five successive stages (Moyle and Light, 1996a; Blackburn et al., 2011): (1) transport of a species beyond its native range through human-mediated pathways, (2) introduction into a new environment, (3) establishment (i.e., population self-reproducing in the wild), (4) spread, and (5) impacts (i.e., when species induce changes in the receiving ecosystem).

Although the history of fish introductions dates back at least to the Zhou Dynasty (1046–256 BCE) in China (Zhao et al., 2015) and the Roman Empire in Europe (1st and 2nd Century CE; Balon, 1995), the introduction rate of fish worldwide has substantially increased since the industrial revolution (18th century). Seebens et al. (2017) reviewed the first records of established non-native freshwater fish species per country, and their data suggest a massive increase in the cumulative number of first records around the mid-20th century and a subsequent stabilization (Fig. S1). Nowadays, freshwater fish species are among the most introduced taxa (Gozlan, 2008) and occur in all biogeographic regions (Leprieur et al., 2008; Fig. 1). At the global scale, 551 non-native freshwater fish species have been recorded as established, with the common carp (*Cyprinus carpio*) being the most widely established species (Fig. 1). If these established fish cause impacts, they are invasive. Invasive freshwater fish have been an important driver of biodiversity changes over the past two centuries (Su et al., 2021). Indeed, a wide range of ecological impacts due to invasive non-native fish have been reported. They

include declines in native fish populations and species extinctions (Aloo et al., 2017), causing profound changes in food webs and even resulting in a global trend toward biotic homogenization (Villeger et al., 2011), not to mention economic and human health impacts (Gozlan, Britton, et al., 2010; Cucherousset and Olden, 2011). Globally, freshwater ecosystems are among the most impacted by biological invasions (Ricciardi and Macisaac, 2010), which is particularly problematic given their importance in terms of ecosystem services (e.g., water supply, food and economic productivity through fisheries and aquaculture; Carpenter et al., 2011).

Fish invasions have been well documented around the world (Rahel, 2000), with several published reviews focusing on notorious invaders such as mosquitofish (*Gambusia spp.*; Pyke, 2008) and Nile perch (*Lates niloticus*; Aloo et al., 2017), on specific regions of ecological or economic importance such as Spain (Elvira and Almodóvar, 2001), Poland (Grabowska et al., 2010), South Africa (Ellender and Weyl, 2014), and the North American Great Lakes (Escobar et al., 2018), on certain stages of the invasion process such as entry routes, impact, and management (Gozlan, Britton, et al., 2010), fisheries and aquaculture pathways (Gozlan, 2017), or ecological impacts (Cucherousset and Olden, 2011). Alongside these species-, region-, or process-focused reviews, several went beyond fish and considered freshwater invasions more broadly (Fuller, 2015; McKnight et al., 2017), thus making it difficult to isolate information that specifically applies to freshwater fish. Consequently, a comprehensive review of introduction pathways, factors influencing invasion success, invasion impacts, and non-native species management is still lacking. Such an integrated overview is necessary in order to understand the role and importance of different introduction pathways, characterize key drivers of invasion success, and summarize the different impact mechanisms and management plans implemented to counter freshwater fish invasions. This will then facilitate integrative analyses that combine the pathways of introductions, life history traits of non-native species, and

characteristics of the receiving ecosystems (Novoa et al., 2020), which in turn are necessary to predict invasions and their impacts and set up effective management actions (IPBES, 2019).

In this review, we focus on fish (i.e., Actinopterygii and Cyclostomata) for which freshwater is the preferred habitat according to FishBase (Froese and Pauly, 2019). Specifically, we assess four aspects of freshwater fish invasions:

1) The pathways by which non-native freshwater fish species are introduced around the world, and their relative importance in terms of the number of non-native fish species established;
2) The characteristics of non-native species and receiving ecosystems, which can affect the success of each stage of the invasion process;
3) The main impacts and impact mechanisms of invasive non-native freshwater fish species, and their relative importance using the Global Invasive Species Database (GISD) (ISSG, 2015);
4) The methodologies and techniques used for management, with special attention paid to recently developed or emerging approaches.

This review provides a state-of-the-art assessment of all key aspects of freshwater fish invasions worldwide, while identifying gaps and limitations in the current literature, which could serve as a roadmap for future studies.

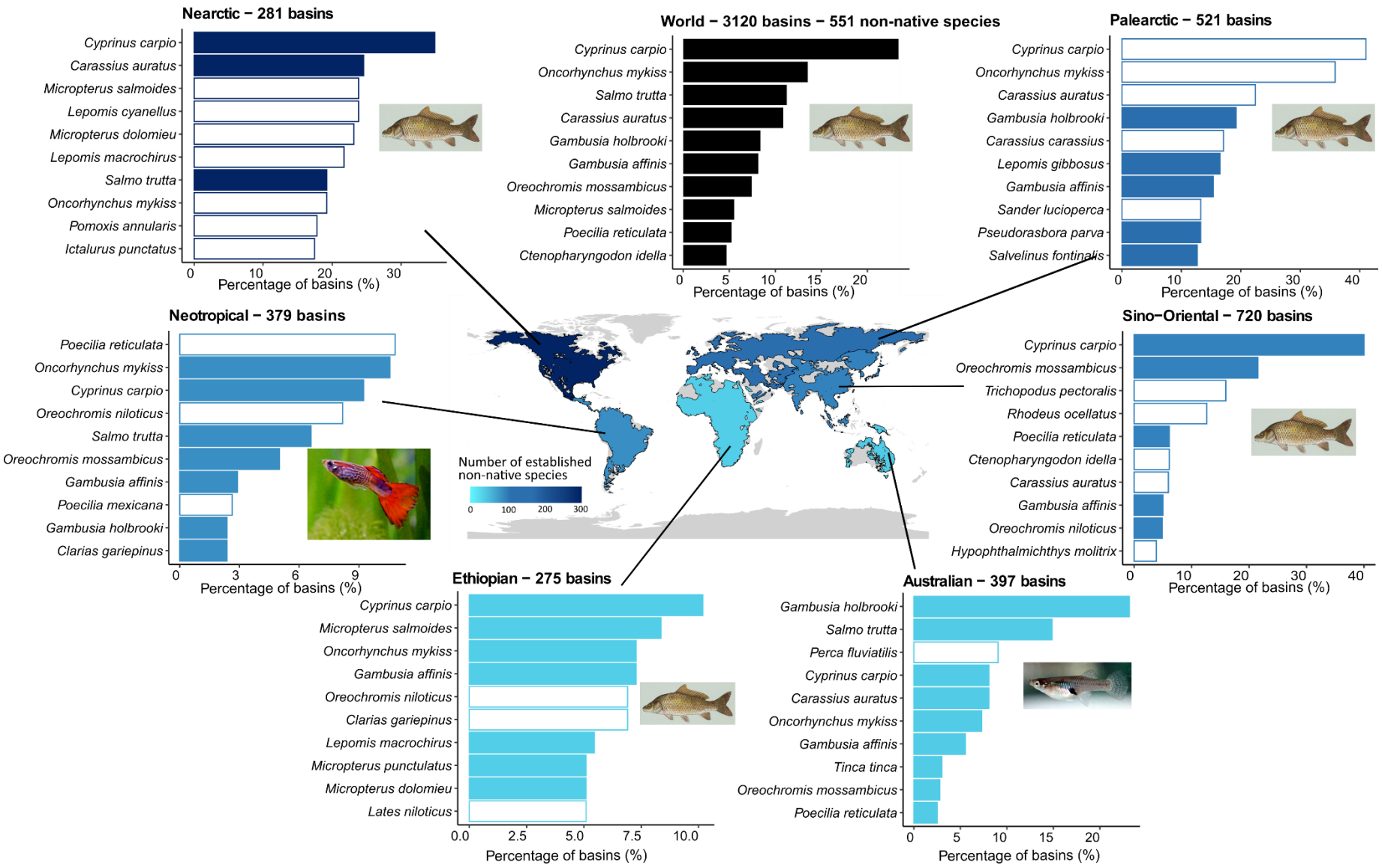

Nearctic – 281 basins
Cyprinus carpio
Carassius auratus
Micropterus salmoides
Lepomis cyanellus
Micropterus dolomieu
Lepomis macrochirus
Salmo trutta
Oncorhynchus mykiss
Pomoxis annularis
Ictalurus punctatus
0 10 20 30
Percentage of basins (%)
World – 3120 basins – 551 non-native species
Cyprinus carpio
Oncorhynchus mykiss
Salmo trutta
Carassius auratus
Gambusia holbrooki
Gambusia affinis
Oreochromis mossambicus
Micropterus salmoides
Poecilia reticulata
Ctenopharyngodon idella
0 5 10 15 20
Percentage of basins (%)
Palearctic – 521 basins
Cyprinus carpio
Oncorhynchus mykiss
Carassius auratus
Gambusia holbrooki
Carassius carassius
Lepomis gibbosus
Gambusia affinis
Sander lucioperca
Pseudorasbora parva
Salvelinus fontinalis
0 10 20 30 40
Percentage of basins (%)
Neotropical – 379 basins
Poecilia reticulata
Oncorhynchus mykiss
Cyprinus carpio
Oreochromis niloticus
Salmo trutta
Oreochromis mossambicus
Gambusia affinis
Poecilia mexicana
Gambusia holbrooki
Clarias gariepinus
0 3 6 9
Percentage of basins (%)
Number of established non-native species
0 100 200 300
Sino–Oriental – 720 basins
Cyprinus carpio
Oreochromis mossambicus
Trichopodus pectoralis
Rhodeus ocellatus
Poecilia reticulata
Ctenopharyngodon idella
Carassius auratus
Gambusia affinis
Oreochromis niloticus
Hypophthalmichthys molitrix
0 10 20 30 40
Percentage of basins (%)
Ethiopian – 275 basins
Cyprinus carpio
Micropterus salmoides
Oncorhynchus mykiss
Gambusia affinis
Oreochromis niloticus
Clarias gariepinus
Lepomis macrochirus
Micropterus punctulatus
Micropterus dolomieu
Lates niloticus
0.0 2.5 5.0 7.5 10.0
Percentage of basins (%)
Australian – 397 basins
Gambusia holbrooki
Salmo trutta
Perca fluviatilis
Cyprinus carpio
Carassius auratus
Oncorhynchus mykiss
Gambusia affinis
Tinca tinca
Oreochromis mossambicus
Poecilia reticulata
0 5 10 15 20
Percentage of basins (%)

Figure 1: Percentage of basins in which non-native freshwater fish species are introduced and established at the bioregional and global (in black) scales. Only the first 10 species with the highest percentage of invaded basins are represented, and we provide a photo of the first one. Open bars indicate translocations. We used data from Tedesco et al. (2017), which were filtered to only take into account species with freshwater recorded as one of their preferred habitats in FishBase (Froese and Pauly, 2019). We used the freshwater fish bioregions of Leroy et al. (2019).

2. Pathways of introduction

The globalization of trade and the value of imported products are known to be linked to the introduction of non-native fish worldwide (Turbelin et al., 2017). Below, we describe the pathways by which non-native freshwater fish species enter receiving environments. Further information and examples on the pathways of introduction are available in Appendix 1.

2.1. Aquaculture

Aquaculture, which primarily refers to the farming of fish and other aquatic species (Kerr et al., 2005), is linked to a substantial share of the establishment events of non-native freshwater fish species worldwide: out of the 1,649 freshwater fish establishment events listed in FishBase *(*Froese and Pauly, 2019*)*, 42% are the result of species introduced through aquaculture (Fig. S2.

Legal aquaculture stocking can cause the introduction of undesirable non-native species due to fish escaping from the aquaculture facilities where they are reared or the accidental release of fish instead of or with others following the misidentification or careless culling of stocks (Mandrak and Cudmore, 2010). The composition of species escaping from aquaculture facilities depends on the species cultivated in the region. For example, in Australia, millions of farmed fish are reported to escape annually (Center of Food Safety 2012), thus resulting in the

introduction of several non-native species such as the shortfin eel (*Anguilla australis*) and Australian bass (*Macquaria novemaculeata*) (Lintermans, 2004).

Aquaculture also involves the trade in live freshwater fish for food, which consists of the import, transfer, distribution, and sale of live freshwater fish for consumption (Kerr et al., 2005). Live fish trade is a significant vector for the transport of non-native fish, but there is no clear evidence of its role in introducing non-native fish, apart from a few anecdotal examples (see Rixon et al., 2005).

The importance of the aquaculture pathway is expected to increase in the future, with the growing development of supplementary hatchery stocking programs worldwide and of non-native fish aquaculture in most tropical developing countries (Britton and Orsi, 2012; Bezerra et al., 2019; Vitule et al., 2019).

2.2. Ornamental trade

Ornamental fish trade is a growing multi-billion dollar industry involving more than 125 countries and 2,500 fish species, with 60% of species being of freshwater origin (Dey, 2016). It is well recognized that ornamental trade is a major pathway for the introduction and establishment of fish (Strecker *et al.*, 2011; Fuller, 2015). According to FishBase data, 17% of establishment events are the result of species introduced through ornamental trade (Fig. S2). Indeed, most ornamental fish sold in pet shops are non-native and can become invasive if released into suitable habitats (Strecker et al., 2011).

The frequency of ornamental species introductions depends on both the frequency of the species in aquarium stores and their popularity, with popular species being discarded more often and in greater numbers (Duggan et al., 2006; Gertzen et al., 2008). Currently, 90% of fish species in the ornamental trade are of tropical origin (Evers et al., 2019) – including the most popular species *Poeciliidae* and tetras (Characiformes; Duggan et al., 2006; Strecker et al., 2011) –,

which makes the establishment and spread of these species unlikely in temperate countries, where most of the ornamental trade has historically taken place (Gozlan et al. 2010). However, major invasion risks exist in tropical countries with significant levels of ornamental trade (e.g., China, Malaysia), as some are trade hubs with the re-exportation of their imports (Dey, 2016).

Introduction threats by ornamental trade are increasing with the recent development of online trade, which has contributed to the transport of over one million fish worldwide in recent years (Olden et al., 2020). Online markets enhance the diversity of traded species and facilitate trade in prohibited species, thus increasing the risk of invasive species introductions.

2.3. Release of bait for angling

Recreational fishing of aquatic animals, most often through angling, involves catching animals that are not a primary source of food and that are not usually sold or traded (Arlinghaus et al., 2012). Anglers frequently use fish as bait, and the majority discard any unused bait (Kilian et al., 2012). Many anglers erroneously believe that releasing bait is beneficial to ecosystems and game fish populations despite the existence of prohibition laws (Kilian *et al.*, 2012; Drake and Mandrak, 2014). Therefore, bait release is an important pathway of introduction into areas where angling is common with high reported rates of establishment (Gascho Landis et al., 2011). According to FishBase, 14% of non-native freshwater fish establishment events worldwide are the result of species introduced through angling and bait release. The causes for this high rate of establishment can be twofold. First, the environmental conditions are usually suitable for released bait due to the physical proximity of the angling and source sites. This is because baiting fish are either caught by anglers or purchased from a local retailer, and then transported to the angling site (Gascho Landis et al., 2011; Drake and Mandrak, 2014). Second, the propagule pressure resulting from this pathway can be significant (e.g., in Maryland, USA, 65% of anglers using fish as bait discarded any unused bait; Kilian et al., 2012). Recreational fishing is currently witnessing an increase in popularity in some regions such as Central Europe

(Lyach and Čech, 2018), Brazil (Freire et al., 2012), and India (Gupta et al., 2015), and other developing countries will likely follow. This increase may lead fishermen to visit a higher number and greater diversity of fishing grounds, thus increasing the likelihood of introducing non-native fish (Lyach and Čech, 2018). Nevertheless, this trend could be reversed by increasing restrictions and controls by fishery guards (Lyach and Čech, 2018).

2.4. Biological control

Non-native fish species have been introduced as biological control agents to control mosquito larvae and pupae, or weeds, among others (Beisel and Lévêque, 2010). However, some non-native species used as biological control agents have become established and invasive, resulting in catastrophic ecological impacts (Copp et al., 2005). According to FishBase, 9% of freshwater fish establishment events are the result of species introduced through biological control (Fig. S2). Typical examples are the mosquitofish species (*Gambusia affinis* and *G. holbrooki*), which were introduced worldwide to control mosquito populations responsible for malaria epidemics (Lintermans, 2004). Biological control has been a major pathway in the past (Beisel and Lévêque, 2010) but is now declining, especially with the increase in regulations preventing such introductions (Pyke, 2008).

2.5. Stocking for fisheries

Fish stocking is the practice of supplying wild stocks with hatchery-reared fish to establish new fisheries, bolster threatened or overfished native populations, or support recreational fisheries. This global management practice has existed for over a century (Gozlan, Britton, et al., 2010; Fuller, 2015). Most stocking occurs with native species, but it can also be used to introduce new species for economically valuable fisheries (Mandrak and Cudmore, 2010; Fuller, 2015; Teletchea, 2019). It is well known that stocking has led to biological invasions worldwide, with disastrous ecological and economic impacts such as invasions caused by the enrichment of wild

fisheries in China (Hulme, 2015) or invasions by Nile perch (*Lates niloticus*) and several species of Nile tilapia in Lake Victoria in Africa (Cucherousset and Olden, 2011) (Appendix 4). According to FishBase, 7% of non-native freshwater fish establishment events are the result of species introduced for fishing (Fig. S2). It is generally difficult to disentangle legal and illegal stocking, so the extent of illegal stocking is unknown. However, several examples suggest that its importance can be high at the local level (e.g., Lintermans, 2004; Kerr et al., 2005; Johnson et al., 2009. For example, a single person introduced 15,000 non-native fish into New Zealand, causing irreversible changes to the country's freshwater ecosystems (Mitchell, 2020). At present, illegal stocking does not have an effective legal framework, although management actions have been proposed to help reduce introductions (Johnson et al., 2009).

2.6. Ballast transport

Since the 1800s, ballast water has been used to increase the stability and maneuverability of ships during voyages. This involves taking on water as the ship leaves port and discharging it in the port of arrival. Although fish represent only a small proportion of the transported organisms (Wonham et al., 2000; Bailey, 2015), it is well established that ballast water is an important pathway for the unintentional introduction of fish. There are potential unconfirmed examples of fish being introduced via ballast water such as the yellow-finned goby (*Acanthogobius flavimanus*) or streaked goby (*Acentrogobius pflaumii*) (Francis et al., 2003; Lintermans, 2004). However, this pathway is less likely to lead to future fish introductions. Indeed, legislation to reduce ballast water introductions, particularly for large ships, has been put in place worldwide, with quotas of viable organisms per cubic meter of ballast water as well as the obligation to conduct oceanic ballast water exchange (Verna and Harris, 2016).

2.7. Interconnected waterways

Human activities can break down natural geographic barriers through the construction of canals or other structures linking two contiguous basins that were originally completely independent (Galil et al., 2007). For example, over the last two centuries, the surface of the catchment areas connected to the Rhine River by inland canals has increased by 21.6 times (Leuven et al., 2009). These connections facilitate freshwater invasions in two ways. First, they allow fish to move between previously inaccessible basins, and second, they allow non-native fish species introduced via another pathway to expand into previously independent river basins. Well-known examples include *Gobiidae*, which can reach new areas through canals connected to the Danube (Rabitsch *et al.*, 2013; Zoric *et al.*, 2014), and several species spreading through the Panama Canal (Smith et al., 2004). In addition to canals, dams can also interconnect waterways, as evidenced by the construction of a hydroelectric dam that allowed 33 fish species to reach the upper part of the Rio Paraná in South America by flooding waterfalls that acted as a natural barrier (Júnior et al., 2009).

Even today, new canal construction projects are underway such as the One Belt One Road (Tsui et al., 2017) and Istanbul Canal (Oxford Analytica, 2017), which may become drivers of future fish introductions and expansions.

2.8. Other reasons

2.8.1. Prayer animal releases

Animal releases as a part of prayer rituals, offerings to gods or as a means of protecting living organisms are practiced in some religions such as Buddhism or Taoism (Everard et al., 2019). Successful introductions of invasive freshwater fish have been attributed to this pathway in China (Everard et al., 2019), Canada (Lintermans, 2004; Beisel and Lévêque, 2010; Liu et al., 2012), and the USA (Fuller, 2015). Overall, this pathway appears to be less notable than the others, and there is no evidence to suggest its increasing trend.

2.8.2. Acclimatization societies

Acclimatization societies aimed not only to establish in colonized countries the species that were familiar and representative of European colonizing countries, but also to promote the spread of non-native species in Europe (Arthington *et al.*, 1997).

These societies have been responsible for the introductions of non-native fish into Australia (Arthington et al., 1997; García-Díaz et al., 2018), Russia, Britain, and Europe (Gherardi *et al.*, 2009). Although this pathway was a major cause of fish introductions before 1970, it is now of minor importance with the global recognition of the negative impacts of non-native species (García-Díaz et al., 2018), leading to laws banning such introductions in several countries (Copp et al., 2005).

2.8.3 Biodiversity conservation

Anecdotally, introductions of non-native freshwater fish can result from translocation programs to prevent species extinctions. This is the case for the huchen (*Hucho hucho*) in Poland (Witkowski *et al.*, 2013) or the Pedder galaxias (*Galaxias pedderensis*) in Tasmania, both of which have been moved outside of their native range to prevent extinction (Chilcott *et al.*, 2013). Nevertheless, future translocations associated with efforts to address climate change could increase the number of species established outside their native range through this pathway (Thomas, 2011).

2.8.4. Unintentional transport via fishing gear or animals

Aquatic animals can be transported from one water body to another on equipment such as boat hulls or fishing gear as well as on animals. The importance of this pathway for fish has only been illustrated anecdotally in the literature. For example, it was shown that nets of eel fishermen in Tasmania (Australia) may be responsible for the movement of redfin perch between adjacent waterbodies (Lintermans, 2004).

3. Factors influencing the invasion success of non-native fish

The invasion success of a non-native species is not only governed by the likelihood of the species being transported and introduced but also by its ability to survive and spread in the new environment. Therefore, the success of the invasion may result from several interacting factors: propagule pressure of non-native species, life history traits, residence time, and characteristics of the receiving ecosystem. In the following sections, we discuss these factors separately, although no single factor is sufficient to explain the invasion success (e.g., Woodford et al., 2013). Further details and examples on these factors are detailed in Appendix 1.

3.1 Propagule pressure

Propagule pressure has two features: propagule size, which is the number of fish individuals arriving during an introduction event, and propagule number, which is the number of introduction events (Simberloff, 2009). Propagule pressure has been shown to significantly increase establishment success, as a larger number of introduced individuals increases the genetic diversity and survival probability of the introduced population (e.g., reduced risk of stochastic extinctions and increased probability of containing individuals with a high dispersal and reproduction capacity) (Woodford *et al.*, 2013). Although a large propagule size facilitates establishment, it is not always necessary. For example, the life history traits of the topmouth gudgeon (*Pseudorasbora parva*) mean that its population can grow rapidly in uncompetitive environments (e.g., fishless environments), thus allowing the species to establish with only a few introduced individuals (Britton and Gozlan, 2013). Indeed, the influence of propagule pressure on invasion success is highly dependent on the life cycle and life history traits of the species in question as well as the suitability of the receiving habitat (Gertzen et al., 2008).

Propagule pressure depends on pathways of introduction and future trends in propagule pressure should follow the expected trends for each pathway.

3.2 Life history traits

Each stage of the invasion process is influenced by life history traits, although the relative importance of specific traits varies between stages of invasion (Kolar and Lodge, 2002). Indeed, the traits associated with the transport and introduction stages are highly diverse and depend on whether or not the introduction was intentional. Intentionally introduced species have human-selected traits. For example, species intentionally introduced for stocking are often large fish, which are preferred by anglers and consumers (Fuller, 2015; Su et al., 2020). By contrast, the morphological and ecological traits of unintentionally introduced species are filtered out depending on the nature of the pathway. Species transported and introduced by ballast water are generally small with pre-adapted traits that allow them to survive in ballast water such as a specialized lateral line for hunting in the dark (e.g., *Gobiidae* ;Wonham et al., 2000; Fuller, 2015). Other examples can be found in Appendix 2 (see also García-Berthou, 2007).

Traits associated with successfully established species appear to be less diverse than those of transported or introduced species due to the environmental filtering effect (Su et al., 2020). Existing evidence suggests that established species have a generalist diet, broad environmental tolerance, and high plasticity, which allows them to adapt to a wide range of environmental conditions (Kolar and Lodge, 2002; Tonella *et al.*, 2018). This is the case with the invasive topmouth gudgeon found in 32 countries, characterized by high phenotypic plasticity in its growth and reproductive traits (Gozlan et al., 2010a). However, specialist species may occasionally become established due to their ability to exploit specific resources, which are not limited in the environment (e.g., detritivores (Moyle and Light, 1996a; Tonella et al., 2018). In addition to these general patterns, there is an interaction between the traits of the established species and the environmental conditions of the receiving ecosystem. In highly variable environments, successfully established species have high fecundity, early maturity, rapid growth, and small adult size, all of which tend to increase the likelihood of successful invasions

in contrast to stable environments (Moyle and Marchetti, 2006). For example, invasive species of the Iberian Peninsula colonized different types of streams according to seasonal flow patterns: small species with high offspring numbers preferentially colonized streams with high seasonality, while large fish with a slower life rates invaded streams with regular flows (Vila-Gispert et al., 2005).

Traits associated with the spread and impact of non-native species have rarely been studied, except in predictive and profiling studies, which means that assumptions about the underlying mechanisms tend to be speculative (Kolar and Lodge, 2002; Marchetti, Light, et al., 2004; Marchetti, Moyle, et al., 2004; Moyle and Marchetti, 2006; Ribeiro et al., 2008). In general, the successful spread and impact seems to depend on broad physiological tolerance and being native to a nearby region, which highlights the importance of pre-adaptation to invaded ecosystems. However, there is a lack of consistency between studies in terms of impact measures, so the relationship between traits and impacts remains unresolved for freshwater fish (Howeth et al., 2016). Some studies have predicted that small species produce greater impacts than large ones (e.g., Marchetti, Moyle, et al., 2004), although existing evidence suggests that large fish can cause catastrophic ecological impacts as in the case of the Nile perch (Aloo et al., 2017) (Appendix 4) or largemouth bass *Micropterus salmoides* (Gratwicke and Marshall, 2001). The correlative nature of the existing studies means that understanding the underlying mechanisms is speculative or limited. For example, species with small eggs are correlated with high impacts, but this correlation is poorly understood (Kolar and Lodge, 2002; Snyder et al., 2014).

3.3 Residence time

The residence time of non-native species, or the time since the first recorded introduction, plays an important role during the spread and impact stages (Wilson *et al.*, 2007). Residence time has been shown to be linked to the spread of non-native species via colonization success

(Buckwalter et al., 2020) and size of the introduced range (Rabitsch *et al.*, 2013). Species impacts may evolve over time and can sometimes increase even without new introductions (Rabitsch et al., 2013), as illustrated by the Nile perch, the impacts of which increased significantly 20 years after its first introduction (Taabu-Munyaho *et al.*, 2016; Appendix 4). The mechanisms by which residence time may affect establishment, spread, and impacts can be associated with various hypotheses from invasion science, including adaptation, evolution of increased competitive capacity, defense displacement, windows of opportunity, and biotic acceptance (Jeschke et al., 2018).

3.4. Inherent characteristics of invaded ecosystems

3.4.1 Niche similarity

Apart from propagule pressure, life history traits, and residence time, the characteristics of the receiving environment are also very important in explaining invasion success. Thus, the ecological and geographic proximity between the donor and recipient ecosystems plays a role in the establishment of non-native species, with these two components often being linked (Nekola and White, 1999). Species originating from a nearby region are most likely to encounter the same climatic and physiological conditions in the receiving environment and thus be pre-adapted there (Moyle and Light, 1996b; Moyle and Marchetti, 2006). Most introduced species are introduced into the same biogeographic region as their native region, and therefore they experience similar climatic conditions in their native and introduced regions (Blanchet et al., 2009; Boris Leroy, unpublished data). For example, fish that are intentionally introduced for economic or recreational reasons tend to be released in places where they are expected to do well (Ruesink, 2005). Nevertheless, some species can become invasive in climatically different regions due to their high plasticity and adaptability (e.g., the topmouth gudgeon, goldfish, or mosquitofish; Fletcher et al., 2016).

3.4.2 Anthropization and perturbations

Abrupt environmental changes are also known to facilitate biological invasions (Zhang et al., 2006). When disturbances are too rapid, native species cannot cope, leading to their lower abundance, extinctions, and unoccupied niches left free for non-native species (Havel *et al.*, 2005; Clavero *et al.*, 2013). Therefore, aquatic ecosystems, which are heavily or frequently disturbed by humans, seem to be highly susceptible to invasions. For example, dam density and reservoir area, which are related to the alteration, destruction, or fragmentation of freshwater habitats as well as to hydrological changes (Leprieur et al., 2008; Clavero et al., 2013), are positively associated with the number of non-native aquatic species (Marchetti, Light, et al., 2004; Clavero et al., 2013; Su et al., 2021). Artificially created habitats such as water impoundments may also facilitate invasions, because they are more accessible to humans than natural lakes, and also because they reduce the average distance between invaded and non-invaded areas, thus increasing the likelihood that natural lakes will in turn be invaded (Johnson et al., 2008). Water consumption for energy production or irrigation also generates water-level fluctuations and temperature changes that profoundly alter aquatic habitats and exclude some native species, which are often replaced by more tolerant non-native species (Hudon, 1997).

At a larger scale, climate change may also influence freshwater fish invasions by creating new niches for non-native species, causing temperate zones to match the climatic requirements of tropical or subtropical species, as is the case for tropical snakeheads (Channidae) in the USA (Herborg et al., 2007). In addition, climate change may also affect other aspects of freshwater invasions, ranging from pathways (e.g., emergence of a new optimal area for aquaculture) to their impacts (e.g., shifts in competitive dominance; Rahel and Olden, 2008).

3.4.3 Native community diversity

Species diversity in recipient communities also plays an important role in invasion success, via three main mechanisms detailed below: biotic resistance, enemy release, and invasion meltdown hypotheses. Other hypotheses have also been proposed to explain the effects of native community diversity on invasion processes such as biotic indirect effects, novel associations, and missed mutualisms (Jeschke et al., 2018; Enders et al., 2020). However, these hypotheses are not well described or explored in the literature on freshwater fish.

3.4.3.1 Biotic resistance

The biotic resistance hypothesis suggests that richer communities are characterized by stronger competition and fewer unoccupied niches than poorer communities, which reduces their susceptibility to invasion (Havel *et al.*, 2015). Conversely, fish communities with a low level of functional redundancy would be more vulnerable to disturbance (Gozlan, Britton, et al., 2010; Pelletier et al., 2020). However, the biotic resistance hypothesis for freshwater fish is not yet validated. Of the nine studies examining this issue for freshwater fish between 2001 and 2015, four supported the biotic resistance hypothesis, four questioned it, and one neither supported nor rejected it (Jeschke et al., 2018). We speculate that these divergent observations may be explained by the scale of the studies: those supporting the hypothesis were conducted at local or regional scales (Habit et al., 2012), while those not supporting it were at larger scales where the species-area relationship may have stronger effects (Fitzgerald et al., 2016).

3.4.3.2 Enemy release

The enemy release hypothesis states that an introduced species often experiences a reduction in parasites, predators, or pathogens in its new ecosystem compared to its native range (Torchin *et al.*, 2003). Of the twelve studies examining the enemy release hypothesis for freshwater fish between 2008 and 2016, seven supported the hypothesis, one questioned it, and four neither supported nor rejected it (Jeschke et al. 2018). Nevertheless, only parasitism was studied. Indeed, native parasites may have difficulties adapting to new hosts, and introduced fish tend

to be parasitized by fewer individuals than native fish, especially because of the low probability of invasive species introducing their parasites (Torchin et al., 2003; Roche et al., 2010). Moreover, even when introduced fish do not avoid parasites, they can be free of their negative effects, as shown by Lacerda et al. (2013). Overall, it is recognized that the enemy release hypothesis is an important factor explaining the success of invasions, although the amount of published evidence remains incomplete for fish (Roche et al., 2010; Jeschke et al. 2018).

3.4.3.3 Invasional meltdown

While the presence of some established non-native species can negatively affect or prevent new invasions, others may directly or indirectly increase the chances of success of new invasive species in a process known as invasional meltdown (Simberloff, 2006). Of the twenty-three studies investigating invasional meltdown for freshwater fish between 2008 and 2016, nine supported the hypothesis, twelve questioned it, and two neither supported nor rejected it (Jeschke et al. 2018). For example, in the North American Great Lakes, the invasive sea lamprey (*Petromyzon marinus*) has caused the collapse of trout, the dominant piscivore, thus indirectly allowing the invasion of two planktivores, alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) (Mooney, 2005).

4. Impacts

Invasive freshwater fish are directly responsible for ecological impacts in natural ecosystems as well as economic damage to fisheries, aquaculture, and human infrastructure and health (Haubrock *et al.*, 2022). Although the ecological and socioeconomic impacts have very different effects, they share common mechanisms (Levine et al., 2003). In this section, we will first explore the main mechanisms responsible for the impacts of invasive freshwater fish, and then discuss the associated ecological and socioeconomic impacts (Table S1, Appendix 3).

4.1. Mechanisms

Several mechanisms are described in the GISD, each related to how invasive freshwater fish species interact with native and other invasive species (i.e., competition, predation, disease and parasite transmission, and hybridization) as well as with the native habitat (i.e., burrowing and browsing) (ISSG, 2015). The main mechanisms involve interactions with native species (96% of 198 described cases), followed by interactions with the native habitat (3% of cases described; Fig. 2A).

4.1.1. Competition

Competition is the main mechanism described in both the GISD database (53% of cases; Fig. 2A) and the literature on ecological impacts. Indeed, field data and experiments have repeatedly shown that the trophic niches of invasive and native fish species overlap (Schleuter, 2007; Sampson et al., 2009; Minder et al., 2020). In addition, invasive fish also compete with organisms found outside their freshwater habitats, such as riparian spiders and birds (Epanchin et al., 2010; Jackson et al., 2016).

Invasive fish have been shown to outcompete native fish, which may be facilitated by specific traits such as aggressive behavior or increased foraging abilities, particularly in degraded ecosystems (Bergstrom and Mensinger, 2009; Abrahams et al., 2017). Overall, the indirect and cascading effects of competition from invasive fish on ecosystems have been suggested in a limited number of studies (Eby et al., 2006) but remain anecdotal at this time.

4.1.2. Predation

Predation is the second most frequently described mechanism for the ecological and socioeconomic impacts of invasive freshwater fish (30% of cases described) (Fig. 2A). Many examples illustrate the strong influence of predation such as the case of peacock bass introduced in Lake Gatun (Panama) suggesting that invasive predatory fish can have irreversible consequences on the composition and functional diversity of native ecosystems (Sharpe et al., 2017).

4.1.3. Hybridization

Hybridization involves the crossing of individuals of two genetically distinct populations (Harrison and Larson, 2014) (8% of cases described; Fig. 2A). Hybridization between closely related invasive and native fish species is common due to their external mode of fertilization (Olden et al., 2004; Ludwig et al., 2009; Blackwell et al., 2020). For example, in the UK, about 40% of the British population of crucian carp (*Carassius carassius*) contains hybrids with goldfish (Hänfling et al., 2005). Hybridization between native and invasive fish is likely to increase in the coming years due to shifts in species distributions as a result of climate change (Muhlfeld et al., 2017) and the increased transportation and introductions of fish for aquaculture and fisheries. Stocking non-native populations that are genetically distant from locally adapted native populations of the same species can also cause inbreeding or outbreeding depression and impact the fitness of individuals (Ludwig, 2006; Ludwig et al., 2009).

4.1.4. Disease and parasite transmission

Invasive fish can carry diseases and parasites from their native ranges, which are then transported and introduced along with their host into the new territory (Kuchta *et al.*, 2018; Spikmans *et al.*, 2020). Co-introduced parasites become invasive if they spread into native host populations in the new area (Lymbery et al., 2014). These co-invasive parasites are generally simple life-cycle parasites with no need for intermediate hosts (Sheath *et al.*, 2015). Co-invasive parasites of freshwater fish are the fourth most described mechanism in the GISD database (5% of cases described; Fig. 2A). Co-invasive parasites can be spread by multiple invaders such as the Asian fish tapeworm (*Schyzocotyle acheilognathi*) co-introduced around the world with carps, guppies, and mosquitofish (Kuchta et al., 2018). Intriguingly, co-invasive parasites are considered disproportionately important for freshwater fish: studies on host fish accounted for more than 50% of the studies on co-introductions (Lymbery et al., 2014). Existing evidence suggests that co-invasive parasites tend to have more detrimental effects on native fish

populations than on their vectors due to the lack of resistance in native hosts (Kirk, 2003; Lymbery et al., 2014). For example, the nematode *Anguillicola crassus*, introduced into Europe with Japanese eels, has had a greater impact on native eels than on Japanese eels (Kirk, 2003). However, the true impact of co-invasive parasites may be underestimated, as many parasites tend to go unnoticed, or their non-native origin is often unresolved, while their consequences on native fish populations are difficult to demonstrate (Jarić *et al.*, 2019).

We can also note here the mechanism of direct parasitism, which involves the parasitism of the native species directly by the invasive fish. However, direct parasitism is a rare mechanism for freshwater fish (*sensu lato*), as it has only been demonstrated, to our knowledge, for sea lampreys, which have invaded the North American Great Lakes (Cucherousset and Olden, 2011; Siefkes, 2017).

4.1.5. Interaction with native habitat: Digging and grazing/browsing

A more anecdotal, though probably overlooked, mechanism that can have a direct impact on habitats is the foraging and reproductive behavior of invasive engineer fish species (Fig. 2A). For example, some invasive carp as well as the invasive pumpkinseed (*Lepomis gibbosus*) are responsible for suspending sediments due to their burrowing feeding habits or nest construction, respectively, leading to an increase in turbidity and erosion (Matsuzaki et al., 2009; Emery-Butcher et al., 2020) and to the release of pollutants trapped in the soil (Matsuzaki et al., 2009; Emery-Butcher et al., 2020).

4.2. Ecological and socioeconomic impacts

Ecological impacts are the most described impact category for non-native freshwater fish (89%; Fig. 2B). These impacts were mainly documented at the ecosystem level (76% of 303 cases; Fig. 2B) but can occur at all biological levels (genetic, individual, population, ecosystem, and biogeographic levels; Fig. 2B; Table S1: Appendix 3). For example, in Columbia, rainbow trout

is known to hybridize with the native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), thus reducing its fitness through lower reproductive success and altering genetic resources (Muhlfeld *et al.*, 2009). At the ecosystem level, invasive fish can be responsible of the modification of nutrient fluxes At biogeographic levels, introductions have caused an overall increase in fish species richness throughout basins worldwide, exceeding extinction rates (Villeger et al. 2011). This increase in richness has been associated with an increase in the functional diversity of assemblages (Toussaint et al., 2018). However, these changes in biodiversity were mainly caused by the introduction of a limited number of widespread species (Toussaint et al., 2016), leading to an increase in both taxonomic and functional similarity between aquatic systems and regions (Villeger et al. 2011; Su et al. 2021). This process, known as biotic homogenization, has been intensively studied in recent years (Rahel, 2000; Villeger et al., 2011; Pool and Olden, 2012; Villéger et al., 2014; Vargas et al., 2015; Campbell and Mandrak, 2020) (Table S1).

The socioeconomic impacts of non-native fish are less studied and represent only a minor part (13%) of the 303 cases described in the GISD database (Fig. 2B). Non-native fish can damage aquaculture, fisheries, and infrastructures (GISD), thus adding to the costs of management plans implemented to prevent ecological impacts and economic damage; for example, the sea lamprey eradication plan in the North American Great Lakes in 2001 cost US$13.5 million (Smith and Swink, 2003). A recent study showed that only 27 invasive fish species have estimated damage costs but with a cumulative cost of about US$37 billion between 1960 and 2020 (Haubrock et al., 2022). Most costs were related to North America as well as to damage and resource loss (e.g., impacts on native fish stocks through predation). However, most of these costs were based on extrapolations, while the observed costs were “only” US$2.28 billion. The discrepancy between cost estimates and reporting reflects the critical underreporting of the economic costs for freshwater fish and the difficulty of estimating the loss of ecosystems services (Gozlan,

Britton, et al., 2010; Haubrock et al., 2022). The substantial underestimation of non-native fish costs may partly be related to the economic benefits associated with non-native fish species (e.g., farmed fish, sport fishing; Gozlan, 2008). In this uncertain context, Leprieur et al. (2009) and Vitule et al. (2009) have called for a precautionary principle against the introduction of non-native freshwater fish.

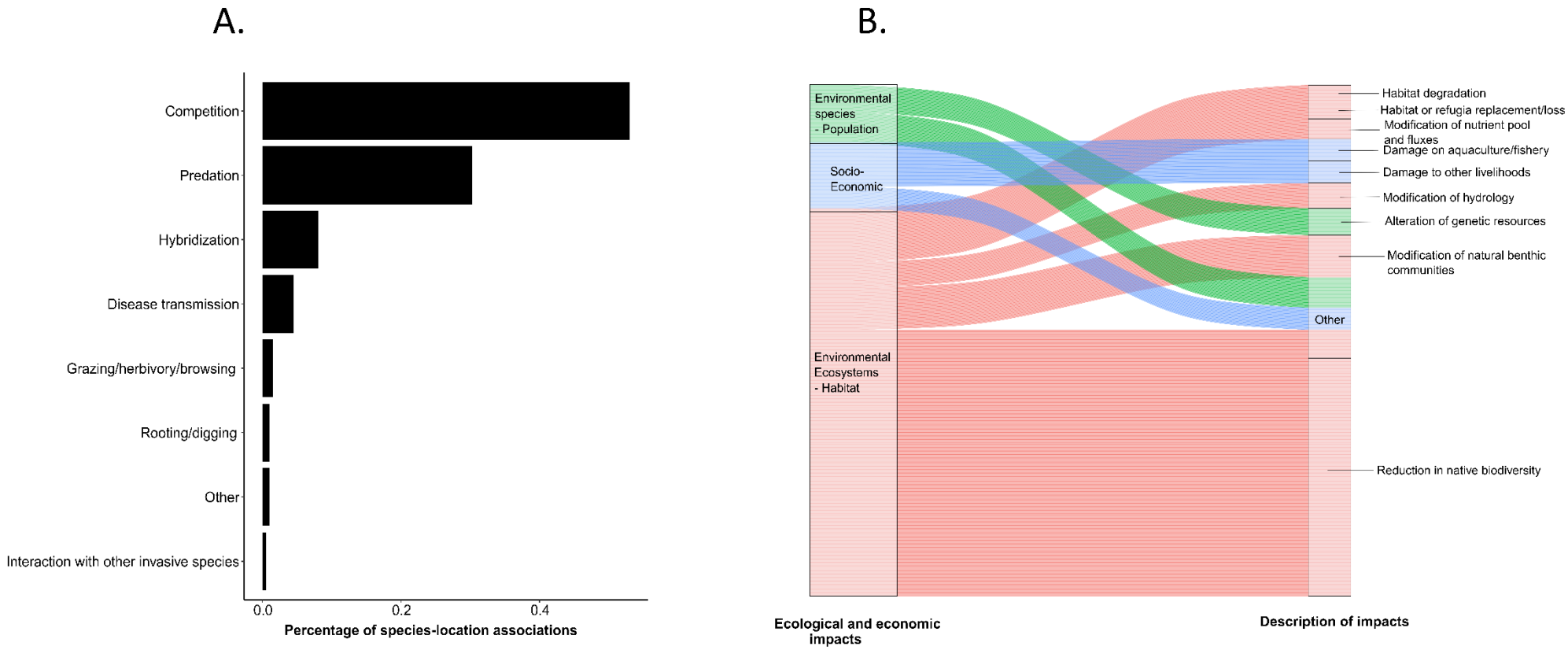


Figure 2: Percentage of species-location associations per mechanism (A: 198 species-location associations) and impact (B: 303 species-location associations) of non-native freshwater fish species. Data are taken from the GISD dataset (ISSG, 2015).

5. Management

Management techniques for dealing with freshwater fish invasions are numerous and depend on the stage of invasion. While prevention and early detection can prevent the introduction and establishment of invasive non-native fish species, control and eradication techniques are required when the invasion is at a more advanced stage (Robertson et al., 2020).

5.1. Prevention, early detection, and monitoring

Prevention is used to act before introduction by avoiding the transport of fish species or their introduction into the wild (Robertson et al., 2020). For freshwater fish, legal frameworks have been put in place to mandate the treatment of ballast waters and thereby reduce the transport of species through this pathway (Werschkun et al., 2014; Robertson et al., 2020). In addition, laws have been passed to prohibit the illegal stocking of fish (Johnson et al., 2009), and barriers can also be set up to avoid the introduction of fish species after the construction of a canal (Noatch and Suski, 2012). According to the GISD database containing information about the management approach used for 40 species-country associations (i.e., 27 non-native freshwater fish species and 14 countries), prevention is the second most common management strategy, with 15 of the 40 species-location associations linked to management actions.

Once a non-native species is introduced, it is important to detect it as early as possible. In addition to traditional techniques (e.g., netting, trapping, and electrofishing), which have a limited effectiveness when the target species is represented by only a few individuals, several monitoring techniques can detect and track trends in non-native species. For example, bio-acoustic sensors are a non-invasive method that has been used to detect non-native fish species (e.g., spotted Tilapia (*Tilapia mariae*) in Australia (Kottege et al., 2012, 2015). Another non-invasive technique is the use of environmental DNA (eDNA), which involves analyzing DNA from an environmental sample to detect species (Rees et al., 2014). The eDNA technique is

more sensitive in detecting rare introduced fish species than traditional detection methods (Jerde et al., 2011) but do not always provide the accurate location of target species in fast-flowing environments (Pont et al., 2018).

Detection techniques can also be used to study the invasion history of species and identify the pathway of introduction. For example, Reshetnikov et al. (2011, 2017) used parasitological analysis to detect and study the introduction pathways of the invasive Amur sleeper (*Perccottus glenii*). Indeed, the detection of the specific parasite *Nippotaenia mogurndae* led to the detection of an invasive population of Amur sleeper and supported the hypothesis of an out-of-aquarium introduction, as this parasite cannot survive with prolonged aquarium maintenance.

Finally, citizen science and internet data are also promising monitoring tools for early detection and rapid response. For example, mobile phone applications such as “Find a Pest” or “Invasive Alien Species Europe” are general monitoring and information tools for the general public with tracking and identification tools (Pawson et al., 2020). Similarly, posts and conversations on social media can also be useful sources of information, as they may contain photos, species names, and/or be geo-referenced (Daume and Galaz, 2016). For example, the introduction of the non-native buffalo fish (*Ictiobus cyprinellus* and *I. niger*) into Czech rivers was detected from anglers’ posts on online forums and websites (Kalous et al., 2018). Prevention and early response are recognized as the most effective (and cheapest) ways to manage invasive non-native species (Leung *et al.*, 2002). However, these measures obviously require the public’s prior awareness of biological invasions. Monitoring tools used for early detection can also be useful for monitoring the abundance of the non-native population after eradication. Unfortunately, monitoring is the least documented management strategy for freshwater fish according to the GISD database, as it was used for only 2 out of 40 species-location associations.

5.2. Eradication, containment, and suppression

As long as the area of invasion is very limited, and the non-native population is small, eradication is logistically and financially feasible using several possible methods. Chemical treatments such as the use of rotenone have been used for years to rapidly eradicate species but are also toxic to non-target species (Knapp and Matthews, 1998; Britton et al., 2011). Nevertheless, some chemical methods known for their selectivity and effectiveness are still used such as lampricides to control sea lampreys (Siefkes, 2017). However, chemical control is generally not well accepted by the public (Bremner and Park, 2007). Electrofishing and gill netting can be effective eradication methods, although they are far more expensive and time-consuming than chemical treatments (Knapp and Matthews, 1998; Bosch et al., 2019). More recently, genetic biocontrol methods aimed at reducing the ratio of females to males within a population have been developed, but are still rarely used (Teem and Gutierrez, 2014). Biological eradication techniques using specific viruses to control populations have also been considered for freshwater fish (e.g., common carp in Australia using the host-specific CyHV-3 virus) (McColl et al., 2014). This method requires a thorough knowledge of the targeted species as well as the epidemiology, virulence, and transmissibility of the virus, but it is also necessary to manage the evolution of its host resistance (McColl et al., 2014, 2016) and the potential spillover of the virus to other species.

Finally, when non-native fish reproduce and spread over larger areas, eradication ceases to be possible (Ali Ahmed et al., 2021). In this case, management responses involve mitigating the invasive species or its impacts. Indeed, the control of freshwater fish is currently the main management measure that has been used for 23 of the 40 species-location associations listed in the GISD database. Thus, containment measures can be implemented to limit the spread of invasive species. Species can be contained using physical barriers (e.g., common carp in New Zealand; Tempero et al., 2019) or non-physical barriers, which alter the behavior of invasive

species, such as electrical barriers, pheromones, altered flow regimes, magnetic fields, or carbon dioxide and oxygen to create low oxygen zones (Noatch and Suski, 2012). Suppression actions (i.e., reducing the distribution or abundance of the non-native population in an area) can also be implemented to reduce the distribution and abundance of the non-native population (Robertson et al., 2020), as well as selective capture, which can be promoted through public awareness and incentives.

Freshwater fish invasions remain difficult to control, although new management techniques are increasingly becoming available for their control and eradication. Nevertheless, the prevention of invasions remains the most effective solution. Consequently, legal frameworks are required most urgently at a global scale.

6. Shortfalls, gaps, and bias in knowledge and data

More than 60 years after Elton's seminal work on invasions (Elton, 1958), much has been learned about invasion records and spatial patterns. Since then, a large amount of theoretical knowledge has been developed on invasion processes and mechanisms for freshwater fish. In short, non-native freshwater fish are introduced through several pathways, two of which stand out, namely aquaculture and ornamental trade. These two trade sectors are likely to grow further in the future and may involve even more species if no regulation is put in place (Fig. 3). The main parameters associated with successful invasions are propagule pressure, life history traits of introduced species (e.g., a broad physiological tolerance facilitates the establishment, spread, and impact stages), and characteristics of the receiving environment (e.g., strong anthropogenic disturbances facilitate invasions). We highlighted that the success of an invasion is most often explained by a combination of parameters such as high propagule pressure combined with niche similarity. Invasive freshwater fish impact native ecosystems through multiple mechanisms, especially competition and predation. These mechanisms are mainly related to ecological

impacts, although their economic impacts are still greatly underestimated. Finally, to address freshwater fish invasions, the most widely used method is population control, even though prevention is the most efficient means. New management techniques are constantly being developed, thus allowing eradications that were previously impossible. Despite the abundance of studies on freshwater fish invasions, there is still a clear lack of understanding about certain aspects of freshwater fish invasions. This poor understanding stems from the inadequate exploration of certain key hypotheses as well as the lack of available data along with geographic and temporal biases.

6.1. Lack of key hypotheses

Our review highlighted that although some aspects of freshwater fish invasions are well known (e.g., pathway of introduction), several important aspects and hypotheses have been insufficiently explored in the literature (Fig. 3), notably with regard to the ecological hypotheses proposed to explain invasion success (Jeschke et al., 2018). In this respect, we still struggle to link mechanisms to observations. For example, we are unable to fully profile invaders while taking into account all the characteristics that influence invasion success (i.e., species traits, environment, and socioeconomic characteristics), and thus predict the outcome when a new non-native species is established in the receiving ecosystem (Marchetti, Moyle, et al., 2004; Pyšek et al., 2020). This hinders the development of effective actions to prevent and manage biological invasions.

6.2. Lack of data

In addition, there is a severe lack of data on several aspects of freshwater fish invasions. For example, there is a lack of data on the propagule pressure of freshwater fish species (García-Berthou, 2007). Only minimal figures on fish production and commerce are given by the FAO (FAO, 2011), while the figures for ornamental fish releases are restricted to North America and

based on predictive models (Strecker et al., 2011). There is also a lack of data regarding the economic impacts of freshwater fish invasions despite the potential high cost associated with them (Haubrock et al., 2022). The same applies to their ecological impacts. While the ecological impact classification of invasive species exists for several taxa through the Environmental Impact Classification for Alien Taxa (EICAT) database (Hawkins et al., 2015), this classification is not available for freshwater fish species. Likewise, the only database listing management plans implemented for invasive freshwater fish species by country is the GISD database. However, this database is incomplete, as it only contains management information for 27 non-native freshwater fish species in 14 countries, even though at least 551 non-native freshwater fish are established worldwide (Fig. 1). For example, some iconic invasive species with known management plans are not included in the database (e.g., sea lamprey).

However, several other databases reporting information on freshwater fish invasions do exist (e.g., economic impacts, Diagne et al. (2020); exotic species per basin, and Tedesco et al. (2017)). Nevertheless, these databases do not cover all the aforementioned data gaps. They are also affected by unquantified incompleteness biases, which necessarily impact the predictions and conclusions relating to freshwater fish invasion patterns.

6.3. Geographic and temporal bias

Our knowledge of the success of biological invasions of freshwater fish is heavily biased toward a few well-studied regions. In this review, we highlighted that the understanding of freshwater fish invasions is heavily biased toward developed countries, with a large concentration of studies conducted in North America. For example, studies on the traits and characteristics influencing invasion success mainly focus on the invasive freshwater fish of North America, while only a few studies explore other locations such as Iberian rivers (Ribeiro et al., 2008), Mediterranean streams (Vila-Gispert et al., 2005), and South America (Tonella et al., 2018) (see Appendix 2). The same bias was demonstrated for the economic impacts of freshwater fish

species in Haubrock et al. (2022). Nevertheless, it is important to observe that this trend is not specific to freshwater fish, as it has already been demonstrated for other taxa in the context of biological invasions (Bellard and Jeschke, 2016). As the characteristics of recipient ecosystems (e.g., climatic conditions) are an important factor influencing invasions, the accumulated knowledge on North American species is not representative of invasive species in other regions of the world. In particular, we know that the African region is heavily exposed to invasive freshwater fish, although studies are still severely lacking in this region (Pyšek et al., 2020; Haubrock et al., 2022).

Furthermore, the available databases on invasions are not updated within a sufficient timeframe to allow for the real-time monitoring of invasions. For example, Tedesco et al. (2017) only list a few introductions in the Amazon drainage, even though recent reports show an increase in invasions (Vitule et al., 2019; Magalhães et al., 2020). Similarly, Guianese rivers have long been considered among the most pristine, but recent reports point to introductions of several non-native fish species that must be considered as an early sign of potential invasions (Brosse et al., 2021). This problem can even be quantified in the database of Seebens et al. (2017) on first records of established species. Indeed, the first record rate of non-native established fish species declined after 2000, partly due to the detection delay (Seebens et al., 2017). Comprehensive and up-to-date databases are therefore essential for building reliable invasion models, especially as ecosystems and the global economy are likely to face major changes in the coming years.

6.4. Future trends

The maintenance or development of human activities in the coming years will certainly lead to changes in future patterns of freshwater fish invasions. While the majority of introduction pathways are expected to decline, some are predicted to retain the same importance such as the prayer animal release pathway, while others will increase as in the case of pathways related to

biodiversity conservation, aquaculture, and ornamental trade (Fig. 3). The latter two are documented as the two main pathways of introduction of non-native species, and they will certainly become increasingly important thanks to the growth in online trade and their development in developing countries (e.g., increase in the aquarium trade in South America; Magalhaes and Jacobi, 2013; Magalhães et al., 2020). For example, a major construction strategy known as the "One Belt One Road" was adopted in 2013 by the Chinese government to develop roads across Asia, reaching as far as Africa and Southern Europe, with planned infrastructure including ports and dams (Tsui et al., 2017). These constructions are a major potential pathway for further introductions of invasive species from East Asia to the West.

Climate change will also be a driver of change in the coming years. However, the literature on the influence of climate change on future invasions of freshwater fish species remains scarce. Nonetheless, we can expect that climate change will affect introduction pathways. The optimal temperatures for the aquaculture of some fish are expected to shift upward, which could lead to changes regarding the regions in which species are reared, thus bringing about new species introductions (Rahel and Olden, 2008). Climate change will also continue to open new niches for invasive species and may even create new opportunities of establishment in temperate countries for species currently unable to establish (Vilizzi et al., 2021). With the known ecological and socioeconomic impacts, these niche shifts could also create new possibilities for hybridization (Muhlfeld et al., 2017).

To avoid these potential impacts of new invasions, management plans need to be strengthened. In view of the current trends toward the development of laws and citizen sciences, we can expect that the prevention and early detection methods will evolve and be increasingly used (Fig. 3).

6.5. Recommendations

In this review, we provided an overview of the different aspects of freshwater fish invasions, from pathways of introduction to management techniques. We have also highlighted several research gaps that need to be filled. Accordingly, we provide a few recommendations on the main issues that should be addressed in future studies.

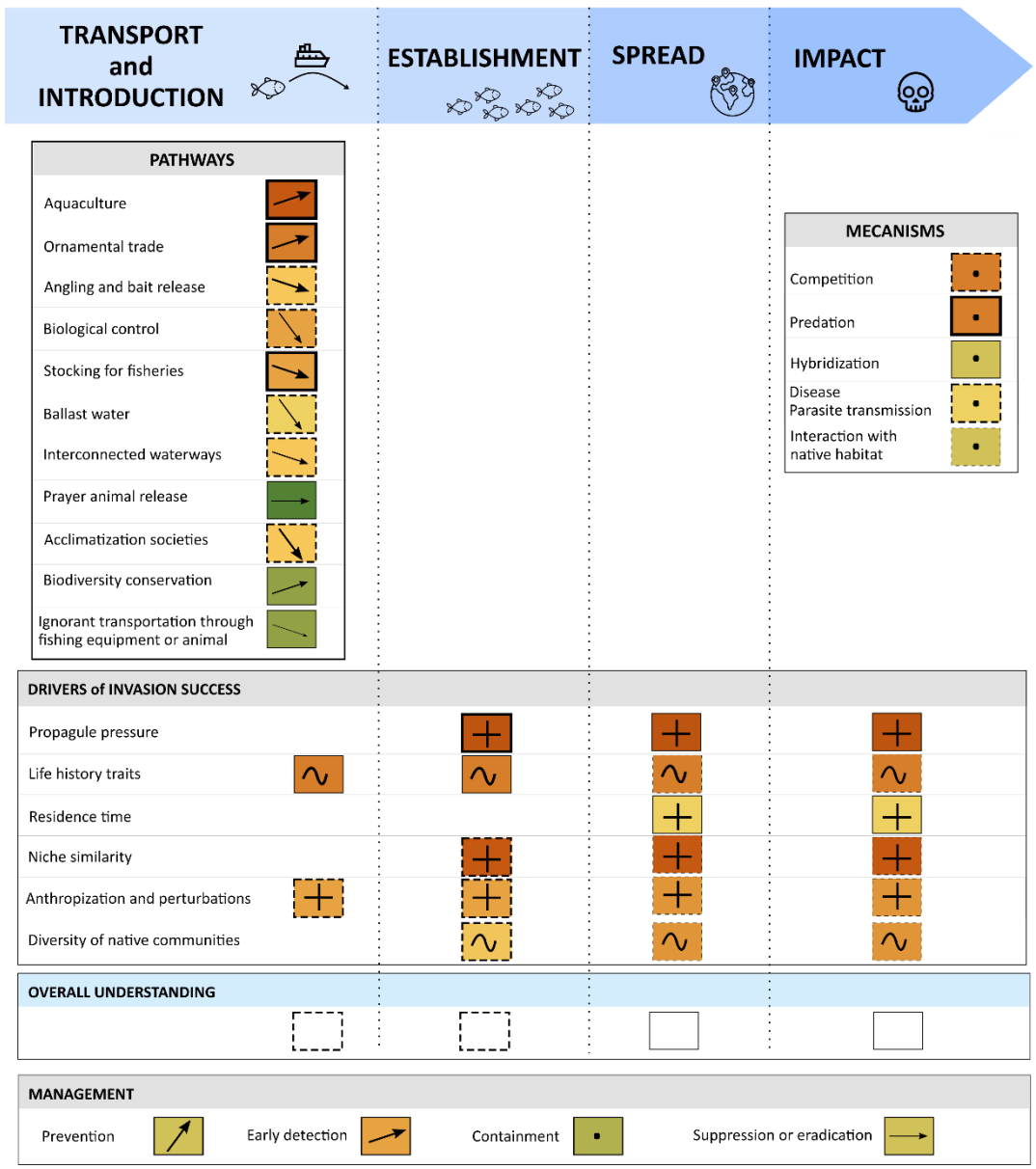
First, data collection efforts should focus on specific areas (e.g., Africa, South America) and aspects of fish invasions where data are poor or non-existent. Comprehensive data on the propagule pressure of introduced fish would greatly benefit from being collected and gathered in a single comprehensive database. We are aware that gathering this information is difficult, but the collection of proxies for propagule pressure such as import data or ballast water volume could also be a potential solution to fill this gap (Drake *et al.*, 2015). Regarding impacts, tremendous progress in research could be achieved by classifying the ecological impacts using the EICAT classification and completing the data on economic impacts with a focus on less studied species and regions like Africa. In addition, it is well known that some invasive freshwater fish species can simultaneously bring benefits to the economy (Gozlan, 2008), so the extent to which the positive economic aspects outweigh the negative ones should be addressed. The development of a comprehensive database on the positive and negative economic and ecological impacts of freshwater fish invasions could help clarify the question about the benefits of certain species and consequently inform management decisions (Vimercati et al., 2020). Finally, regarding the lack of management data, the large number of articles on the management of freshwater fish species could help with the development of a database based on the literature, which could be the first step toward creating a comprehensive database.

Second, some aspects of freshwater fish invasions should be further studied in priority. For example, several hypotheses regarding freshwater fish invasions are yet to be explored (see Jeschke et al., 2018) or fully understood (e.g., enemy release, biological resistance hypotheses). More generally, the spread and impact stages of the invasion process are less investigated than

the other stages, and they could benefit from a better understanding if reliable data were collected (Fig. 3).

Third, the prediction of future trends in invasions using predictive models and scenarios must consider all the drivers of invasion success. Indeed, a comprehensive framework with a combination of socioeconomic characteristics, ecological characteristics, and life history traits of species while including global drivers of changes (e.g., climate change), would allow us to better predict future trends in freshwater fish invasions (Novoa et al., 2020). Reliable predictions are essential for global conservation reports such as the Global Assessment Report on Biodiversity and Ecosystem Service (IPBES) to advise managers and decision-makers at the international level and guide international and national public policies about freshwater fish invasions.

In conclusion, many aspects about the biological invasions of freshwater fish are addressed in the literature, ranging from the pathways of introduction of non-native freshwater fish species to their impacts and management methods. Nonetheless, data gaps and biases still remain, and unresolved aspects of freshwater fish invasion should be addressed in future studies to effectively manage these invasions at the international scale.


TRANSPORT and INTRODUCTION
ESTABLISHMENT
SPREAD
IMPACT
PATHWAYS
Aquaculture
Ornamental trade
Angling and bait release
Biological control
Stocking for fisheries
Ballast water
Interconnected waterways
Prayer animal release
Acclimatization societies
Biodiversity conservation
Ignorant transportation through fishing equipment or animal
MECANISMS
Competition
Predation
Hybridization
Disease Parasite transmission
Interaction with native habitat
DRIVERS of INVASION SUCCESS
Propagule pressure
Life history traits
Residence time
Niche similarity
Anthropization and perturbations
Diversity of native communities
OVERALL UNDERSTANDING
MANAGEMENT
Prevention
Early detection
Containment
Suppression or eradication

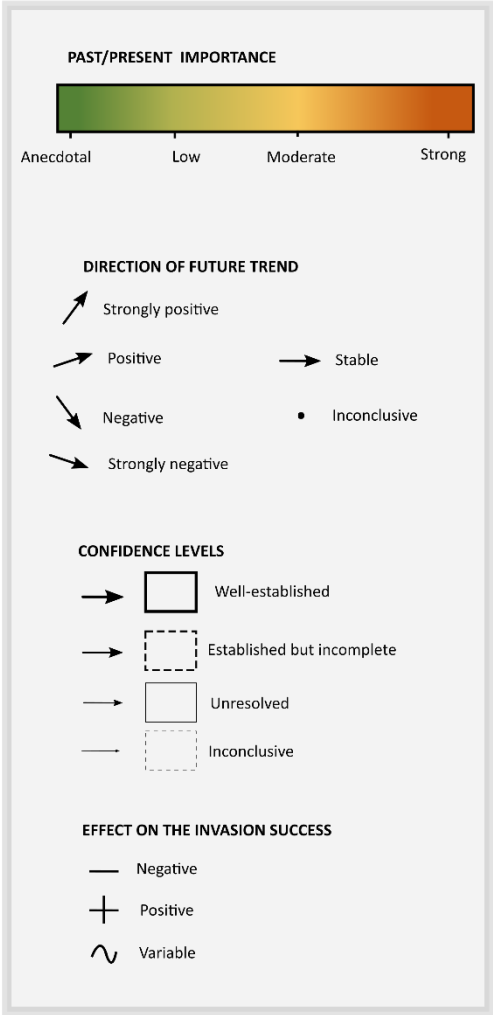

PAST/PRESENT IMPORTANCE
Anecdotal
Low
Moderate
Strong
DIRECTION OF FUTURE TREND
Strongly positive
Positive
Stable
Negative
Inconclusive
Strongly negative
CONFIDENCE LEVELS
Well-established
Established but incomplete
Unresolved
Inconclusive
EFFECT ON THE INVASION SUCCESS
Negative
Positive
Variable

Figure 3: Importance and future trends of introduction pathways, impact mechanisms, drivers of invasion success, and management of invasive freshwater fish species. Concerning the drivers of invasion success, life history traits have a variable effect depending on the trait under consideration, the receiving environment, and the introduction pathway.

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SUPPLEMENTARY MATERIAL :

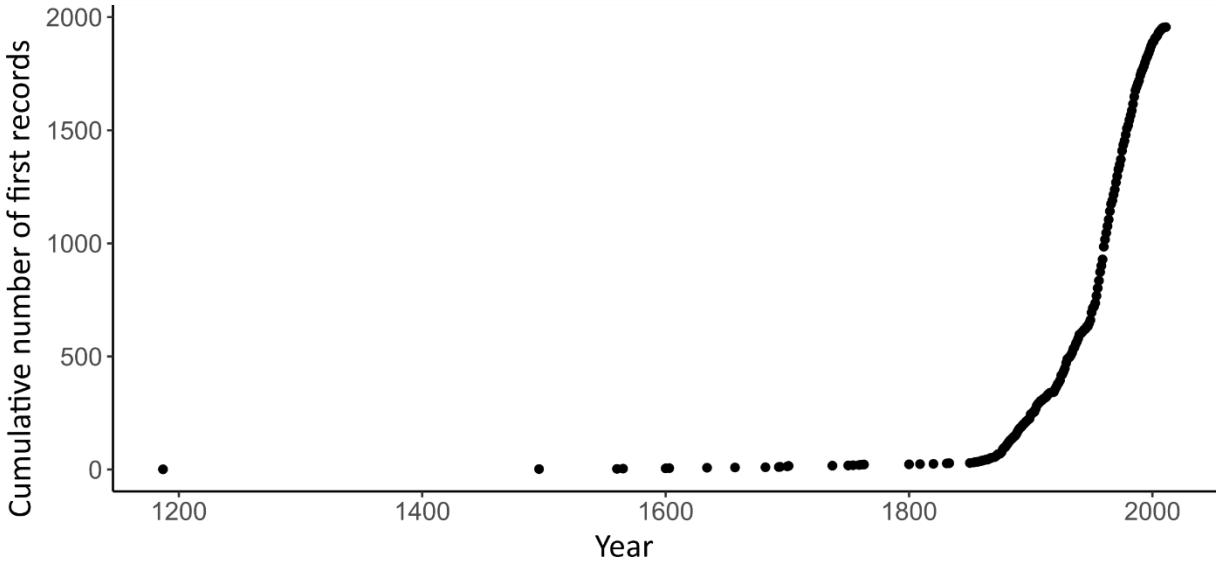

Figure S1: Cumulative number of first records for freshwater fish species (342 species considered). As first records are reported at the country scale, species may be included multiple times in the figure. Data are taken from Seebens et al. (2017)

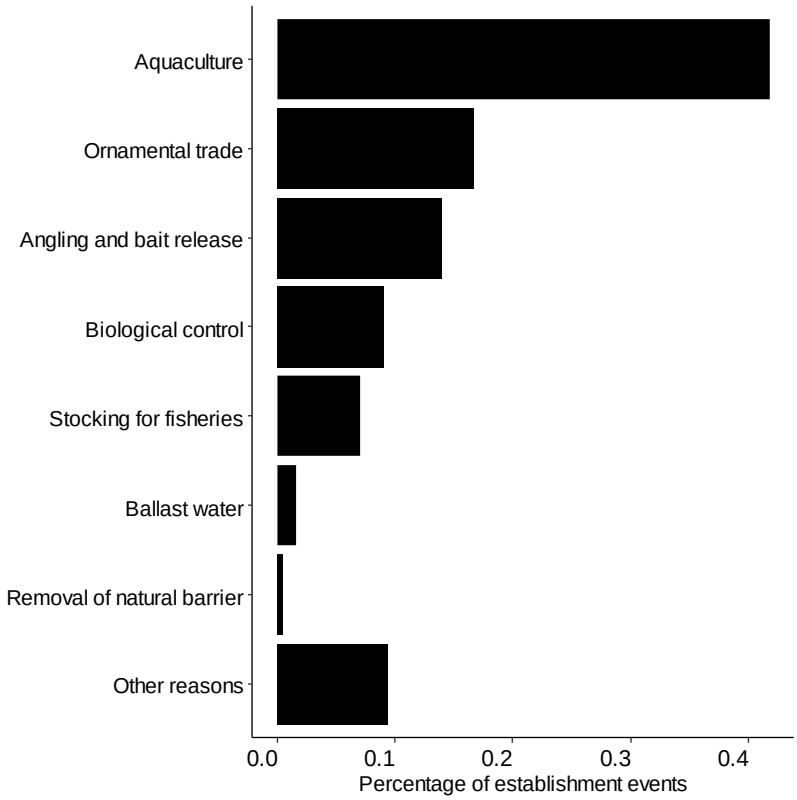

Figure S2: Percentage of establishment events of non-native freshwater fish species per introduction pathway. Note that some species may be introduced by multiple pathways, and a species can be counted multiple times for the same pathway if it becomes established at different locations along the same pathway. We used data from FishBase (Froese and Pauly, 2019) sorted to consider only freshwater fish species (i.e., species with freshwater recorded as one of their preferred habitats). We grouped several categories together (see Appendix 5) and considered 292 species and 1,649 establishment events.

Appendix 1: Additional information

Bait release in recreational fishing

In Maryland (US), 43% of anglers used fishes as bait and the majority of them release their unused bait (Kilian *et al.*, 2012). Various species of small bodied fish can be used as bait, such as those belonging to the Cyprinidae – e.g., the goldfish (*Carassius auratus*) and the fathead minnow (*Pimephales promelas*), Percidae – e.g., redfin perch (*Perca fluviatilis*) and pygmy perch (*Nannoperca sp.*), Cichlidae – e.g., *Tilapia sp.*, Gymnotidae, and Gasterosteidae (Lintermans, 2004; Kilian *et al.*, 2012; Drake and Mandrak, 2014). Fishes are among the top selling bait types, but fish baits are also captured in the wild and then released in another waterbody (Litvak and Mandrak, 1993; Mandrak and Cudmore, 2010; Drake and Mandrak, 2014). Harvest of live bait in the wild raises also the problem of bycatches because identification of species is challenging, especially for juveniles, and they can be consequently unknowingly introduced in new waterbodies (Drake and Mandrak, 2014).

Biological control

The mosquitofish (*Gambusia affinis* and *Gambusia holbrooki*), native to North America, are a classic example of biocontrol. These two closely related species have been widely introduced in many countries of southern Europe, Asia and also in Australia in the early 1920s in order to control mosquito populations responsible for malaria epidemics (Lintermans, 2004; Copp *et al.*, 2005; Beisel and Lévêque, 2010). Mosquitofishes are now distributed on multiple continents and have been included in the list of 100 of the world's worst invasive species because of their impacts (Lowe *et al.*, 2000). Other species of Poeciliidae, such as the guppy (*Poecilia reticulata*), have also been released for mosquitoes control, but not as widely as the mosquitoe fish (Lintermans, 2004). The black carp (*Mylopharyngodon piceus*) has been introduced in North America in order to control snails, which are intermediate hosts of the yellow grub (*Clinostomum margaritum)* that parasitizes cultivated fishes (Haag, 2008)(Nico and Neilson,

2020). Other Chinese carp species such as the silver carp (*Hypophthalmichthys molitrix*) and the grass carp (*Ctenopharyngodon idella)* have been introduced in many countries to counter the proliferation of aquatic plants (Beisel and Lévêque, 2010).

Biodiversity conservation

In the early 1950s, the degradation of the native ecosystems of the huchen (*Hucho hucho*) in Poland caused its decline, and led to translocation initiatives to save the species by moving individuals out of their natural range (Nowak *et al.*, 2008; Witkowski *et al.*, 2013).

Another example is the Pedder galaxias (*Galaxias pedderensis*) species. The flooding of the Pedder lake of Tasmania in 1972 increased the abundance of predators in the small native range of the species. The Pedder galaxias was consequently translocated out of its native range and the species is now extinct from its natural range, but persists with two translocated populations at Strathgordon Dam and Lake Oberon in Tasmania (Chilcott *et al.*, 2013) (TSSC, 2016).

Ballast transport

About 3,500 million tons of ballast water are transferred annually around the world with their associated biota, via trans-oceanic shipping and shipping within inland waters (Endresen *et al.*, 2004; Mandrak and Cudmore, 2010; Bailey, 2015). Although ballast water is often cited as a medium for fish introductions, fishes represent a small part of the transported organisms, most of them being invertebrates (Wonham *et al.*, 2000; Bailey, 2015).

There are several famous examples of fishes introduced by ballast water. Gobies such as the yellowfin goby (*Acanthogobius flavimanus*) or the streaked goby (*Acentrogobius pflaumii*), native to Asia, were introduced in Australia and New Zealand via contaminated ballast water (Francis *et al.*, 2003; Lintermans, 2004). This pathway may also be responsible for six fish species introductions into the Great Lakes (Mandrak and Cudmore, 2010). Nonetheless, this

pathway is less likely to drive future fish introductions, as legislations on ballast water of large ships have been put in place at a global scale (Verna and Harris, 2016).

Concerning prevention of ballast transport introductions, several management measures are implemented. For example, the International Maritime Organization (IMO) established quotas of viable organisms per cubic meter in ballast waters (Verna and Harris, 2016). IMO also imposed mid-ocean ballast water exchanges in order to release species taken in the coastal or inland waters in open ocean, where they are not supposed to survive, and replace them with saltwater species that cannot survive in inland or coastal waters (Ricciardi, 2006; Verna and Harris, 2016).

Aquaculture

Non-native fishes represent 17% of the global aquaculture production (Fuller, 2015; Ju *et al.*, 2020). China currently dominates the world in this field, accounting for 60% of the worldwide finfish inland production (i.e, 26 million tons) in 2014 (Gozlan, 2008; FAO, 2016; Ju *et al.*, 2020). In China, 91 freshwater fish species have been introduced for aquaculture, mostly from Asia, North America and Europe, and tilapia, catfish, eel and pirapatinga are the 4 most dominant fish groups cultured (Xiong *et al.*, 2015). At a worldwide scale, in 2009, 106 freshwater fish species and 24 diadromous fish species were farmed worldwide (Fuller, 2015; Gozlan, 2017; Ju *et al.*, 2020). Thus, the greater the aquaculture production, the more non-native fish species are likely to be introduced. As a results, billions of farmed fishes are intentionally or unintentionally released in nature, following the strong development of aquaculture and supplementary hatchery stocking programs (Britton and Gozlan, 2013)(Britton and Gozlan, 2013; Teletchea, 2019) and fishes non-native to their culture site contribute with 17% of the global aquaculture production.

Larger-scale introductions from aquaculture often occur through accidents and natural disasters, such as floods. In China, the destruction of aquaculture facilities by typhoons and floods in 2005 has enabled the escape of many non-native fishes (Ju *et al.*, 2020).

Between 1996 and 2012, the Center of Food Safety (2012) reported about 26 million escaped fishes from fish farms., the main species concerned being salmons and trouts.

Aquaculture is greatly influenced by the socio-economic and political situation. For instance, wars can have an impact on the species farmed, limiting the introduction of certain species and the trade between countries (Britton and Gozlan, 2013).

Interconnected waterways

Interconnected waterways were one of the earliest and most important pathways of fish introductions in the past (Mandrak and Cudmore, 2010), especially for species from the same biogeographic region (Ellender and Weyl, 2014; Nunes *et al.*, 2015). For example, the majority of species introduced in Europe through inland canals are species native to another part of Europe (Nunes *et al.*, 2015).

Factors impacting non-native fish invasion success:

Propagule pressure

It has been suggested that propagule pressure may also play a role in impacts via an additional dimension which is the colonization pressure. The colonization pressure assumes that the number of non-native taxa introduced in the new environment will affect the likelihood of introducing high-impact fishes (Richardson, 2011; MacIsaac and Johansson, 2017).

Inherent characteristics of the invaded ecosystems

Niche similarity

In California, 25% of the extant native species are invasive in other watersheds of the region: this is considered to be linked with the climatic and physiological similarities in adjacent watersheds (Moyle, 2002; Marchetti *et al.*, 2004). Conversely, aquarium fishes coming from tropical regions cannot establish easily in the cold waters of the St. Lawrence seaway in North America (Gertzen *et al.*, 2008).

Anthropization and perturbation

Another set of heavily disturbed ecosystems are estuarine ecosystems, which are subject to intensive use and alteration by humans, which has been linked to the long-term success of invasive species (Moyle and Light, 1996b).

Enemy release

In the Great Lakes, the invasive round goby (*Apollonia melanostoma*) is parasitized by only 22 species, compared to 72 in its native region (Kvach and Stepien, 2008). Moreover, Sheath *et al.* (2015) demonstrated that non-native species in England and Wales have less than 9% of the parasites species they have in their native ranges, and that parasites which survived were above all parasites with no intermediate hosts.

Invasion meltdown

It is noteworthy that already established species can facilitate the invasion of other species. For instance, the bullfrog invasion in the United States has been indirectly facilitated by the non-native sunfish: the sunfish reduced the dragonfly density, whose nymphs feed on bullfrog tadpoles (Adams *et al.*, 2003).

Furthermore, the invasive topmouth gudgeon is the healthy carrier of the rosette agent parasite *Sphaerothecum destruens*, thus leading to its invasion. This intracellular parasite then causes massive declines in native fish populations, allowing the topmouth gudgeon to overcome native competition and establish and colonize environments (Ercan *et al.*, 2015).

Impacts and mechanisms :

Homogenization and differentiation processes

The impacts of introductions and extinctions of fishes on the similarity of fish assemblages and the functions they support is a process called biotic homogenization when similarity increases, or biotic differentiation when similarity decreases. These processes have been intensively studied over the recent years (Rahel, 2000; Villeger *et al.*, 2011; Pool and Olden, 2012; Villéger *et al.*, 2014; Vargas *et al.*, 2015; Campbell and Mandrak, 2020). Species introductions appear to be the main driver of change in taxonomic and functional homogenization at regional or river basin scales (Rahel, 2000; Villeger *et al.*, 2011; Villéger *et al.*, 2014). However, not all introductions have similar impacts: translocated species (i.e. non-native species originated from the same region) may have a stronger role in taxonomic and functional homogenization upon the considered region than true non-native species (i.e. species originating from a distinct region) (Villéger *et al.*, 2014). In addition, wide-range species play a preponderant role in the taxonomic homogenization (Vargas *et al.*, 2015; Toussaint *et al.*, 2016).

The habitat alteration is also positively correlated with homogenization (Rahel, 2000; Pool and Olden, 2012). Indeed, habitat alteration increases the non-native species richness which, in turn, facilitates homogenization (Rahel, 2000; Pool and Olden, 2012).

Non-native species generally drive biotic homogenization from regional to global scales (Villéger et al. 2011, Toussaint et al. 2014, Vargas et al. 2015), with some areas homogenizing

faster (e.g., Nearctic and Palearctic realms) than the others. Some areas can display taxonomic differentiation (Villeger *et al.*, 2011; Vargas *et al.*, 2015). However, this differentiation may be due to the establishment of distinct non-native species among river basins of the same region, which has been deemed to be an early signal of future homogenization, because as the number of species introductions increase, differentiation quickly turns into homogenization (Toussaint et al. 2014, Villeger et al. 2015). Functional homogenization, i.e. the increase in functional similarity of biotas through the establishment of species with already represented traits and the disappearance of species with unique traits (Olden *et al.*, 2004), has also been documented for freshwater fishes (Villéger *et al.*, 2014; Campbell and Mandrak, 2020).

The global trend of increasing biotic homogenization is expected to continue in the future because of the trends in pathways of species introductions. However, it is difficult to predict how the regionally heterogeneous trends in homogenization will evolve, because homogenization patterns are not linear and depend on the species and assemblages involved (Olden and Rooney, 2006; Pool and Olden, 2012; Villéger *et al.*, 2014; Campbell and Mandrak, 2020).

Appendix 2: Examples of trait associated with each invasion step. It is important to note that the traits filled are not exhaustive and reflect tendencies and examples of traits that are found in literature and which are known to increase the chance of success at each step. The influence of traits on the invasion steps success depends on many factors such as the physical conditions in the invaded region, and exceptions exist.

Invasion step	Specificities at each step	Example of traits associated with invasion steps success	Scale / Region	Method	References
INTRODUCTION	**Ballast water**	Small size Extensive lateral line system	World	Literature review	Wonham et al., 2000
	Aquaculture (intentional introductions)	Large size Laterally compressed	World	Observation	Su *et al.*, 2020
	Aquarium releases	Relatively large size (compared to other aquarium fishes) High popularity (high frequency in aquarium stores)	Canada and United States	Observation	Duggan *et al.*, 2006
		Aggressiveness	St. Lawrence Seaway (Canada)	Observation / Modelling	Gertzen *et al.*, 2008

ESTABLISHMENT	**Environments with highly variable conditions**	Small size Short lifespan Many spawning occasions per year Relatively low fecundity	Mediterranean streams	Observation / Literature review	Vila-Gispert *et al.*, 2005
	Environments with stable conditions	Large size Long lifespan Late maturity Few spawning occasions per year High fecundity	Mediterranean streams	Observation / Literature review	Vila-Gispert *et al.*, 2005
		Piscivorous	World	Literature review	Moyle and Light, 1996a
	All environments	Strong parental care Wide physiological tolerance	California	Observation	Marchetti, Moyle, *et al.*, 2004b
		Small body size Broad food spectrum	World	Observation	Ruesink, 2005
		Piscivorous Omnivorous Specialist feeder if their food items are highly available in the invaded ecosystem (i.e. detrivorous)	Parana river	Observation	Tonella *et al.*, 2018

	Pre-adaptation (low environmental distance)			
	Pre-adaptation (low environmental distance)	World	Literature review	Moyle and Light, 1996a
	Small size Regional origin (low geographical distance)	Iberian watershed	Observation	Ribeiro *et al.*, 2008
	Laterally compressed	World	Observation	Su et al., 2020
	Relatively fast growth Wide tolerance to temperature and salinity	Great Lakes, North America	Observation	Kolar and Lodge, 2002
	Wide salinity and temperature tolerance Higher growth rate	Great Lakes, North America	Literature review	Snyder *et al.*, 2014
SPREAD	Large size Small native range Low parental care (i.e, no parental care at all or brood hiders with no additional care) Detritivorous	Iberian watershed	Observation	Ribeiro *et al.*, 2008
	Long lifespan Not a herbivore Regional origin (low geographical distance)	California	Observation	Marchetti, Moyle, *et al.*, 2004b
	Slow relative growth rate Low tolerance to high temperatures Wide temperature tolerance	Great Lakes, North America	Observation	Kolar and Lodge, 2002 (for quickly spreading fishes compared to slowly spreading fishes)

	Slow relative growth rate Wide salinity and temperature tolerance Low tolerance to high temperatures	Great Lakes, North America	Review of articles	Snyder *et al.*, 2014
IMPACT	Small eggs Wide salinity tolerance High tolerance to low temperatures	Great Lakes, North America	Observation	Kolar and Lodge, 2002
	Small size Regional origin Not an invertivore	California	Observation	Marchetti, Moyle, et al., 2004
	Piscivorous	World	Review of articles	Moyle and Light, 1996a
	Wide physiological tolerance Small native range	Iberian watershed	Observation	Ribeiro *et al.*, 2008 *(integration)*
	Low tolerance to low temperatures Small eggs	Great Lakes, North America	Review of articles	Snyder *et al.*, 2014
	Regional origin (low geographical distance)	California	Observation	Marchetti, Moyle, *et al.*, 2004b)
	Top trophic levels (piscivorous) High fecundity (more than one million eggs per spawning season)	Great Lakes, North America	Observation	Howeth *et al.*, 2016 *(comparaison between low-impact and high-impact invaders)*

Table S1: Examples of the ecological impacts of non-native freshwater fish at each scale. The description of the impact corresponds to illustrations in Figure 2.

Scale	Impacts	Mechanism	Examples	Description of the impact	Reference
Genetic	Altering genetic resources	Hybridization	Rainbow trout (*Oncorhynchus mykiss*)	In Columbia, rainbow trout is known to hybridize with the native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), thus reducing its fitness through lower reproductive success.	Muhlfeld et al., 2009
Individual	Other – Plant/animal health	Disease – parasite transmission	Japanese eel (*Anguilla japonica*)	Japanese eel indirectly causes infections in populations of native European eel (*Anguilla anguilla*) via the nematode *Anguillicola crassus.*	Kirk, 2003
Population	Population size decline – Species range contraction	Parasitism	Sea lamprey (*Petromyzon marinus*)	Immature sea lampreys contribute to the decline of several native large predatory fish species in the American Great Lakes.	Cucherousset and Olden, 2011
Ecosystem	Reduction in native biodiversity	Predation	Nile perch (*Lates niloticus*)	The invasive Nile perch is responsible for the decline and disappearance of hundreds of endemic cichlid species in Lake Victoria.	Witte et al., 1992; Appendix 4
	Modification of nutrient pools and fluxes	Competition	Trout (e.g., brown trout *Salmo trutta*)	Invasive trout prevent the emergence of insects, which are food resources for riparian birds and spiders.	Epanchin et al., 2010
	Habitat or refuge loss / replacement	Predation	Nile tilapia (*Oreochromis niloticus*)	Laboratory experiments showed that the presence of the invasive Nile tilapia in the Gulf of Mexico estuaries resulted in the displacement of the native redspotted sunfish (*Lepomis miniatus*) from their preferred habitats.	Martin et al., 2010
	Other – Soil or sediment modification	Digging and grazing/browsing	Carp (e.g., *Cyprinus carpio*)	Common carp is responsible for increasing turbidity via sediment resuspension.	Emery-Butcher et al., 2020
Biogeographic	Biotic homogenizatio			In the USA, states have on average 15.4 more species in common now than before	Rahel, 2000

	n		European settlement (7.2% more similar).	
			In the Lower Colorado basin, fish fauna is increasingly homogenized, both taxonomically and functionally	Pool and Olden, 2012

Appendix 3: Additional examples of ecological impacts of non-native freshwater fishes at each scale.

Scale	Impacts categories	Examples of non-native species	Description of the impact	References
Genetic	Alteration of genetic ressources	Rainbow trout (*Oncorhynchus mykiss*)	In Columbia, the rainbow trout is known to hybridize and to alter the genome of the native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), which results in a reduction of its fitness through a decrease of the reproductive success.	(Muhlfeld *et al.*, 2009)
		Pecos pupfish (*Cyprinodon pecosensis*)	In the Pecos River in Texas, the native Pecos pupfish (*Cyprinodon pecosensis*) hybridized with the non-native sheepshead pupfish (*C. variegatus*). Hybrids were shown to have better swimming endurance and to grow more rapidly than the purebred *C. pecosensis*. This led to the replacement of *C. pecosensis* population by hybrids.	(Echelle and Connor, 1989; Olden *et al.*, 2004; Rosenfield *et al.*, 2004)
Individual	Reduce/inhibits the growth of other species	Common carp (*Cyprinus carpio*), grass carp (*Ctenopharyngodon idella*), guppies, mosquito fishes (*Gambusia sp.*)	Common carps, grass carps, guppies and mosquito fishes are indirectly linked with developmental problems of several fish species worldwide (e.g. cyprinids).	(Kuchta *et al.*, 2018)
	Plant/animal health	Japaneese eel (*Anguilla japonica*)	Japaneese eels are indirectly causing infections in farmed and wild population of the native European eel (*Anguilla anguilla*) through the nematode *Anguillicola crassus*	(Kirk, 2003)

Population	Population size decline – Species range contraction	Brook trout (*Salvelinus fontinalis*)	The brook trout introductions result in the displacement and decline of many native trout species and of many endangered amphibian species, such as the marbled newt (*Triturus marmoratus*) and the Pacific tree frog (*Pseudacris regilla*)	GISD, 2015
		Peacock bass (*Cichla monoculus*)	In Lake Gatun in Panama, the peacock bass led to a decline of several native species. This decline has been sustained even 45 years after the peackock bass introduction, leading some species to be locally extirpated.	(Sharpe *et al.*, 2017)
		Sea lamprey (*Petromyzon marinus*)	Immature sea lampreys contribute to the decline of several native large predatory fish species in the Great Lakes.	(Cucherous set and Olden, 2011)
Ecosystem	Reduction in native biodiversity	Nile perch (*Lates niloticus*)	The invasive Nile perch is responsible for the decline and disappearance of hundreds of endemic cichlid species in Lake Victoria.	(Witte *et al.*, 1992)
		Largemouth bass (*Micropterus salmoides*), yellow-belly bream (*Serranochromis robustus*)	In Zimbabwe, the largemouth bass and the yellow-belly bream dramatically decrease abundances of native fishes, especially *Barbus* species whose abundance collapsed by 99% in some cases and became functionally extinct.	(Gratwicke and Marshall, 2001)
		Brown trout (*Salmo trutta*)	In New Zealand streams, trouts are responsible for the disappearance of native galaxiids, a family containing mainly threatened species, in almost all the sites where the trout has been introduced.	(Townsend and Simon, 2006; McIntosh *et al.*, 2010)
	Modification of food webs / Modification of nutrient pool and fluxes / Primary production alteration	Trouts - e.g. rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*)	Introduced trouts prevent the emergence of insects, which are food resources for rosy-finch birds and riparian spiders. This can lead to cascading effects in the terrestrial food webs.	(Baxter *et al.*, 2004; Epanchin *et al.*, 2010)
		Peacock bass (*Cichla monoculus*)	The decline of several native species of the Lake Gatun in Panama resulted in changes in the trophic structure of the Lake, which is now dominated by large-bodied non-native omnivores and piscivores, while small native insectivores are becoming scarcer.	(Sharpe *et al.*, 2017)

	Catfishes (*Pterygoplichtys sp.)*	Excretions and egestions of non-native catfishes are known to redistribute nutrients as they graze and excrete in different areas, and to produce biochemical hotspots.	(Capps and Flecker, 2013; Rubio *et al.*, 2016)
	Common carp (*Cyprinus carpio*)	Common carps are known to affect nutrient cycling, to impact the phytoplankton biomass and composition and to decrease the macrophyte biomass.	(Matsuzaki *et al.*, 2007)
Habitat or refugia loss / replacement	Nile tilapia (*Oreochromis niloticus*)	Laboratory experiments showed that the presence of the introduced Nile tilapia in the Gulf of Mexico estuaries resulted in the displacement of the native redspotted sunfish from their preferred habitats.	(Martin *et al.*, 2010)
Soil or sediment modification: modification of structure	Carps - e.g., goldfish (*Carassius auratus*) and common carp (*Cyprinus carpio*)	Goldfish and common carp are responsible for the increase of turbidity through the resuspension of sediments and excretion.	(Richardson *et al.*, 1995; Matsuzaki *et al.*, 2009; Emery-Butcher *et al.*, 2020)
	Catfishes (*Pterygoplichthys* sp.)	Catfishes are known to be responsible for bank erosion.	(Nico *et al.*, 2009); GISD, 2015
	Pumpkinseed sunfish (*Lepomis gibbosus*)	Invasive pumpkinseed sunfish (*Lepomis gibbosus*) increase the turbidity during their nest construction.	(Beisel and Lévêque, 2010)
Biotic homogenization		Rahel (2000) have shown that fish faunas between states have become more similar than before European settlement, pairs of States gaining on average 15 more species in common and fish faunas became 7.2% more similar.	(Rahel, 2000)
		In the Laurentian Great Lakes, fish communities have functionally differentiated among all lakes considered, but have been taxonomically homogenized since 1870.	(Campbell and Mandrak, 2020)
		In the Lower Colorado basin, fish fauna became increasingly homogenized, both taxonomically and functionally	(Pool and Olden, 2012)

Appendix 4: The Nile perch invasion, a relevant example of invasive fish impacts

The Nile perch (*Lates niloticus*) is a good example of the extent and the diversity of impacts that can be produced by an invasive freshwater species. The Nile perch was introduced in 1963 in Victoria Lake, an African lake characterized by its hundreds of endemic species, with a majority of endemic haplochromines species (Taabu-Munyaho *et al.*, 2016). The Nile perch introduction aimed to increase the economic value of fisheries from Victoria Lake, as Nile perch feeds on small-size haplochromines of low economic value (Cucherousset and Olden, 2011; Taabu-Munyaho *et al.*, 2016). Twenty years later, the Nile perch population in the Lake exploded, Nile perch catches rising from 5000t in 1980 to 315,000t in 1989 (Taabu-Munyaho *et al.*, 2016). Many consequences followed the Nile perch invasion.

Negative interactions

As the diet of the Nile perch consists mainly of haplochromines (Aloo *et al.*, 2017), its invasion resulted in a collapse of their populations, in addition to tilapiine species: according to Witte *et al.* (1992), about 200 endemic cichlid species were pushed to extinction, especially algae-feeding haplochromines. Moreover, haplochromines with overlapping habitats with the Nile perch are likely to experience population crash more rapidly than those with no overlap (such as species living in the littoral areas or on rocky shores), which in some cases were not even affected (Witte *et al.*, 1992). Nile perch invasion led to "the first mass extinction of vertebrates that scientists have ever had the opportunity to observe" (Kaufman, 1992) and had repercussions on the trophic network of the lake (Witte *et al.*, 2013).

However, the Nile perch's predation was so strong that it was partly responsible for its own decline, due to the exhaustion of its prey. The decline led to a reappearance of a few native species feared extinct, but at least 200 endemic native species are definitely extinct (Matsuishi *et al.*, 2006).

- **Socio-economic consequences:**

The presence of the Nile perch has radically changed local fisheries of the Victoria Lake. It replaced previously fished native species, multiplying the annual harvest by a factor of four in less than ten years (Witte *et al.*, 1992). Such increase in harvesting was followed by the development of local processing industries, the creation of new jobs, the increase of fishing effort and the huge increase of the population around the lake (Shoko *et al.*, 2005; Matsuishi *et al.*, 2006). More than 1.2 million people and the regional development of riparian countries of the Victoria Lake highly depend on fisheries through the foreign exchanges (Matsuishi *et al.*, 2006).

Nevertheless, it seems that the Nile perch fishing is unsustainable as the Nile perch population is in decline, partly due to the intense fishing pressure (Matsuishi *et al.*, 2006).

The Nile perch also has negative impacts on the local communities, deteriorating their living conditions. Local fishers have to invest into new fishing equipment to efficiently fish Nile perch, but they cannot invest enough to ameliorate their living conditions (Onyango and Jentoft, 2010). Moreover, in about 40 years, the number of fishermen have doubled, intensifying the competition and the conflicts among fishermen and leading to the appearance of foreign leading groups controlling the equipment used and the prices paid, forcing local fishers to be price takers (Onyango and Jentoft, 2010). The disappearance of local fish species due to the Nile perch predation also raises the prices of the remaining fish species, endangering the food security of 30 million riparian people of the Victoria Lake. (Shoko *et al.*, 2005). Morever, the decreasing catches indirectly contributed to increasing prevalence of HIV/AIDS among the fisher communities, as women fishmongers have to secure the fish caught by fishermen in return of sexual relationships (Aloo *et al.*, 2017).

- **Habitat alteration**

Nile perch's impacts on habitat are mostly indirect, driven by its exploitation by humans. Rapid growth of the human population around the Victoria Lake resulted in an increase in human activities (e.g. use of fertilizers, farming), and consequently in the elevated nutrient input to the lake and its eutrophication (Shoko *et al.*, 2005). Moreover, it was also triggered by the Nile perch processing industry which is different from the one used for native fish. The Nile perch needs to be smoked, which requires firewood, leading to an aggravation of the deforestation around the lake, and in turn contributing to the increase of soil erosion, siltation and eutrophication (Aloo et al., 2017). The marked eutrophication experienced by the lake since the late 90ties decreased the water transparency and water oxygen content, worsening the loss of cichlids species diversity by reducing species home range and mating efficiency (Balirwa *et al.*, 2003).

Appendix 5: Gathering pathways together

New categories	Fishbase categories
Biological control	"mosquito control", "other pest control", "snail control", "weed control" , "phyto-zooplankton control"
Aquaculture	"aquaculture", "Aquaculture"
"Unknown"	"no data", "unknown", "unknown", "forage", "research"
Stocking for fisheries	fisheries
Accidental release	"accidental"
Ballast water	"accidental with ships"
Other reason	"off-site preservation", "fill ecological niche", "other reasons", "diffused from other countries"
Angling and bait release	"angling/sport", "bait"
Removal of natural barrier	"removal of natural barrier", "Lessepsian migration"
Ornamental trade	"ornamental"

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