Freshwater Fish Invasions: A Comprehensive Review

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Abstract

Freshwater fish have been widely introduced worldwide, and freshwater ecosystems are among those 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: (*a*) introduction pathways, (*b*) characteristics of nonnative species and invaded ecosystems that explain successful invasion processes, (*c*) invasion impacts and their mechanisms, and (*d*) management. We highlight data gaps and biases in the current databases and highlight a basic lack of understanding of several aspects of freshwater fish invasions. In addition, we provide recommendations for future studies.

1. INTRODUCTION

The growth of global trade has resulted in the intentional and unintentional displacement of many species 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 a major source of economic loss (Haubrock et al. 2022). The invasion process is often divided into five successive stages (Moyle & Light 1996a, Blackburn et al. 2011): (*a*) transport of a species beyond its native range through human-mediated pathways, (*b*) introduction into a new environment, (*c*) establishment (i.e., generation of a self-reproducing population), (*d*) spread, and (*e*) impacts (i.e., changes induced by the invasive species in the receiving ecosystem).

Although the history of fish transportation dates back to at least the Zhou Dynasty (1046–256 BCE) in China (Zhao et al. 2015) and the Roman Empire in Europe (first and second century CE) (Balon 1995), the rate of global transportation and introduction of fish has substantially increased since the industrial revolution (eighteenth century). Seebens et al. (2017) reviewed the first records of established nonnative freshwater fish species per country, and this data suggest a massive increase in the cumulative number of first records during the mid-twentieth century followed by a short period with fewer additions (**Supplemental Figure 1**). Nowadays, freshwater fish species are among the most introduced taxa (Gozlan 2008), and they occur in all biogeographic regions (Leprieur et al. 2008) (**Figure 1**). At the global scale, 551 nonnative freshwater fish species have been recorded as established, with the common carp (*Cyprinus carpio*) being the most widely established species (**Figure 1**). Once established, nonnative fish can proliferate, spread, and cause ecological and/or socioeconomic impacts, in which case we define them as invasive following (Lewis et al. 2016). Note that the definition of invasiveness can vary in the literature, depending on whether or not the impact is included (Pyšek & Richardson 2010, Blackburn et al. 2011), be it ecological or socioeconomic. 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 nonnative fish have been reported, including declines in native fish populations and species extinctions (Aloo et al. 2017), which cause profound changes in food webs and even an overall trend toward biotic homogenization (Villéger et al. 2011). Freshwater fish invasions also result in economic and human health impacts (Gozlan et al. 2010b, Cucherousset & Olden 2011, Haubrock et al. 2022). Globally, freshwater ecosystems are among the most affected by biological invasions (Ricciardi & 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 reviews focusing on notorious invaders such as mosquitofish (*Gambusia* spp.) (Pyke 2008) and Nile perch (*Lates niloticus*) (Aloo et al. 2017) or on specific regions of ecological or economic importance such as Spain (Elvira & Almodóvar 2001), Poland (Grabowska et al. 2010), South Africa (Ellender & Weyl 2014), and the North American Great Lakes (Escobar et al. 2018). Other reviews focus on certain stages of the invasion process such as entry routes, impact, and management (Gozlan et al.

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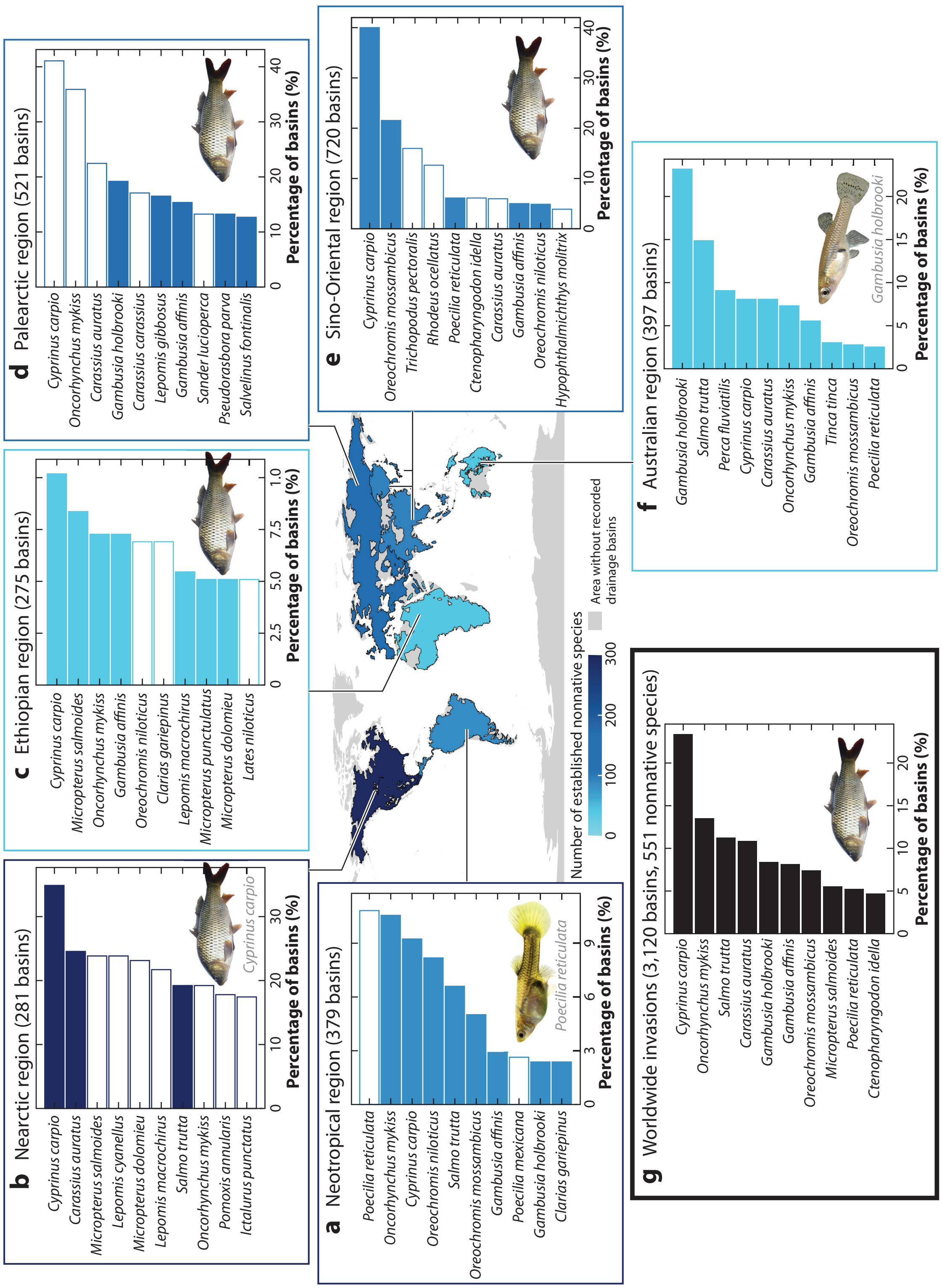


(Caption appears on following page)

Figure 1 (*Figure appears on preceding page*)

Percentage of basins in which introduced nonnative freshwater fish species have established at the bioregional (*blue gradient*) and global (*black*) scales. Only the ten species with the highest percentage of invaded basins are represented for each bioregion; the most common species for each bioregion is illustrated. Solid bars indicate introductions of species not native to the biogeographical region, whereas open bars indicate introductions of species within their native biogeographical region (i.e., a species can be native to part of a region but introduced elsewhere in that region). We used data from Tedesco et al. (2017), which were filtered to include only species for which freshwater is recorded as one of their habitats in FishBase (Froese & Pauly 2022). We used the freshwater fish biogeographical regions defined by Leroy et al. (2019). Photo in panels *a–e* reproduced from BlueBreezeWiki/Wikimedia (**https://upload.wikimedia.org/wikipedia/commons/5/5f/190729_Guppy_01.jpg**) (CC-BY SA 3.0). Photo in panel *b* reproduced from George Chernilevsky/Wikimedia (**https://upload.wikimedia.org/wikipedia/commons/3/3b/Cyprinus_carpio_2008_G1_%28cropped%29.jpg**) (CC-BY SA 3.0). Photo in panel *f* reproduced from MarshBunny/Wikimedia (**https://upload.wikimedia.org/wikipedia/commons/d/d3/EasternMosquitoFishJG_Female.jpg**) (CC-BY SA 4.0).

2010b); fisheries and aquaculture pathways (Gozlan 2017); or ecological impacts (Cucherousset & Olden 2011). Alongside these species-, region-, or process-focused reviews, several studies went beyond fish and considered freshwater invasions more broadly (Fuller 2015, McKnight et al. 2017), which makes it difficult to isolate information that specifically pertains to freshwater fish. Consequently, a comprehensive review of introduction pathways and the factors influencing invasion success, impacts, and management is still lacking. Such an integrated overview is necessary to understand the role and importance of different introduction pathways, to characterize the key drivers of invasion success, and to summarize the different impact mechanisms and management plans implemented to counter freshwater fish invasions. This overview facilitates integrative analyses, combining the pathways of introduction, the life history traits of nonnative species, and the characteristics of the receiving ecosystems (Novoa et al. 2020), which allows us to better predict invasions and their impacts and to set up effective management actions (Elbakidze et al. 2018).

In this review, we focus on fish (i.e., Actinopterygii and Cyclostomata) that have freshwater listed as one of their habitats in FishBase (Froese & Pauly 2022). Fish living only in brackish water and/or saltwater were not considered (e.g., *Sparus aurata*). Specifically, we assess four aspects of freshwater fish invasions:

1. The pathways by which nonnative freshwater fish species are introduced around the world and their relative importance in terms of the number of established nonnative fish species
2. The characteristics of nonnative species and receiving ecosystems, which can affect the success of each stage of the invasion process
3. The main impacts and the impact mechanisms of invasive nonnative freshwater fish species and their relative importance according to the Global Invasive Species Database (GISD) (ISSG 2015)
4. The methods 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 the key aspects of freshwater fish invasions worldwide, while identifying gaps and limitations in the current literature, and can serve as a roadmap for future studies.

2. PATHWAYS OF INTRODUCTION

The globalization of trade and the value of imported products are known to be linked to the introduction of nonnative fish worldwide (Turbelin et al. 2017). In this section, we describe the pathways by which nonnative freshwater fish species enter receiving environments. Further information and examples of introduction pathways are available in **Supplemental Appendix 1**.

2.1. Aquaculture

Aquaculture, which primarily refers to the farming of fish and other aquatic species (Kerr et al. 2005), contributes to a substantial share of establishment events for nonnative freshwater fish species worldwide: Out of the 1,649 freshwater fish establishment events listed in FishBase (Froese & Pauly 2022), 42% are the result of species introduced through aquaculture (**Supplemental Figure 2**).

Legal aquaculture stocking can introduce undesirable nonnative species due to fish escaping from the aquaculture facilities where they are reared. They may also be accidentally released instead of or along with the intended fish, following the misidentification or careless culling of stocks (Mandrak & Cudmore 2010). The composition of species escaping from aquaculture facilities depends on the species cultivated in the region (Center of Food Safety 2012). For example, in Australia, fish escaping from aquaculture facilities resulted in the introduction of several nonnative species such as the shortfin eel (*Anguilla australis*) and Australian bass (*Macquaria novemaculeata*) (Lintermans 2004).

Aquaculture also involves the trade in live freshwater fish, which consists of their import, transfer, and distribution (Kerr et al. 2005). The live fish trade is a significant vector for the transportation of nonnative fish, but there is no clear evidence of its role in introducing nonnative 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 predicted growth in supplementary hatchery stocking programs worldwide and in nonnative fish aquaculture in most tropical developing countries (Britton & Orsi 2012, Bezerra et al. 2019, Vitule et al. 2019).

2.2. Ornamental Trade

The ornamental fish trade is a growing, multi-billion dollar industry involving more than 125 countries and 2,500 fish species, with 60% of these species being of freshwater origin (Dey 2016). It is well recognized that the ornamental fish 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 the ornamental trade (**Supplemental Figure 2**). Indeed, most ornamental fish sold in pet shops are nonnative and can become invasive if released into suitable habitats (Strecker et al. 2011).

The frequency of ornamental species introductions depends on their popularity, with popular species being discarded more frequently 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). The tropical origin of ornamental fish species makes their establishment and spread unlikely in temperate countries, where most ornamental trade has historically taken place (Gozlan et al. 2010b). However, there are major invasion risks in tropical countries with significant levels of ornamental trade (e.g., China, Malaysia), as some are trade hubs where the reexportation of their imports occurs (Dey 2016). Climate change may also create new invasion opportunities for tropical species in temperate areas in the near future (e.g., Herborg et al. 2007).

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

2.3. Release of Bait for Angling

Recreational fishing, 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 live 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 prohibitory laws (Kilian et al. 2012, Drake & 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 nonnative freshwater fish establishment events worldwide are the result of species introduced through angling and bait release (**Supplemental Figure 2**). The causes of this high rate of establishment are twofold. First, environmental conditions are usually suitable for the released bait due to the physical proximity of the angling and source sites. Indeed, baiting fish are either caught by anglers themselves or purchased from local retailers and then transported to a nearby angling site (Gascho Landis et al. 2011, Drake & Mandrak 2014). Second, the propagule pressure resulting from this pathway can be significant [e.g., in Maryland, USA, 65% of anglers using live fish as bait discarded any unused bait (Kilian et al. 2012)]. Recreational fishing is currently growing in popularity in some regions such as Central Europe (Lyach & Čech 2018), Brazil (Freire et al. 2012), and India (Gupta et al. 2015), and other developing countries will likely follow. This increase may lead anglers to visit a higher number and greater diversity of fishing grounds, thereby increasing the likelihood of introducing nonnative fish (Lyach & Čech 2018). Nevertheless, this trend could be reversed by increasing awareness through the introduction of more appropriate restrictions and controls by fishery guards (Lyach & Čech 2018).

2.4. Biological control

Nonnative fish species have been introduced as biological control agents to control weeds or mosquitoes, among other pests (Beisel & Lévêque 2010). However, some nonnative species used as biological control agents have become established and invasive, leading to 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 (**Supplemental Figure 2**). Typical examples are the mosquitofish species (*Gambusia affinis* and *Gambusia holbrooki*), which were introduced worldwide to control the mosquito populations responsible for malaria epidemics (Lintermans 2004). Biological control has been a major pathway for invasion in the past (Beisel & Lévêque 2010). Regulations preventing such introductions have increased in the last few years, although there is a lack of evidence regarding their effectiveness. In the near future, climate change is likely to favor the emergence of mosquito-borne pathogens in new locations, leading to the possible introduction of nonnative fish to control mosquitoes (Azevedo-Santos et al. 2017). For these two reasons, biological control is likely to remain an important introduction pathway in the future (Pyke 2008, Azevedo-Santos et al. 2017).

2.5. Stocking for Fisheries

Fish stocking is the practice of supplementing 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 et al. 2010b, Fuller 2015). Most stocking occurs with native species, but it can also be used to introduce new species for economically valuable fisheries (Mandrak & Cudmore 2010, Fuller 2015, Teletchea 2019). Stocking has led to biological invasions worldwide, with disastrous ecological and economic impacts, such as the invasions caused by the enrichment of wild fisheries in China (Hulme 2015) or invasions by Nile perch (*Lates niloticus*) and Nile tilapia (*Oreochromis niloticus*) in Lake Victoria in Africa (Cucherousset & Olden 2011) (**Supplemental Appendix 2**). According to FishBase, 7% of nonnative freshwater fish establishment events result from species introduced for fishing (**Supplemental Figure 2**). As it is generally difficult to disentangle legal and illegal stocking, the extent of illegal stocking is unknown. However, several examples suggest that it can be substantial at a local level (e.g., Lintermans 2004, Kerr et al. 2005, Johnson et al. 2009). For example, a single person introduced 15,000 nonnative fish into New Zealand and irreversibly changed the country's freshwater ecosystems (Mitchell 2020). Legal frameworks to regulate illegal stocking are increasingly being adopted, although they have been widely criticized for their ineffectiveness (Johnson et al. 2009), which is still demonstrated by recent examples (Fernández et al. 2019).

2.6. Ballast Transport

Since the 1800s, ballast water has been used to increase the stability and maneuverability of ships during voyages. This procedure involves taking on very large volumes of water as a ship leaves port and discharging them in the port of arrival. Although fish constitute only a small proportion of the transported organisms (Wonham et al. 2000, Bailey 2015), it is well established that ballast water is a nonnegligible pathway for the unintentional introduction of fish, even if it is less significant for freshwater than for marine fish (Wonham et al. 2000, Fuller 2015). So far, there are unconfirmed examples, such as the yellow-finned goby (*Acanthogobius flavimanus*) and the streaked goby (*Acentrogobius pflaumii*) (Francis et al. 2003, Lintermans 2004). However, this pathway is less likely to lead to future fish introductions. Legislation to reduce ballast water introductions, particularly for large ships, has been implemented worldwide, with the inclusion of quotas of viable organisms per cubic meter of ballast water and the obligation to conduct mid-oceanic ballast water exchange (Verna & Harris 2016) to kill any freshwater organisms in the ballast water.

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 21.6-fold (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 nonnative fish species introduced via another pathway to expand into previously independent river basins. Well-known examples include *Gobiidae*, which can now reach new areas through canals connected to the Danube (Rabitsch et al. 2013, Zoric et al. 2014), and several species from the Panama canal region. Indeed, construction of the Panama canal allowed the connection of the Rio Chagres and the Rio Grande drainage basins, leading to species exchanges between them (Smith et al. 2004). In addition to canals, dams can also connect 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 after 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 project (Wong et al. 2017). One Belt One Road is a major construction strategy 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, canals, and dams. These new structures are expected to become a driver of future freshwater fish introductions and expansions.

2.8. Other Pathways of Introduction

2.8.1. Prayer animal releases. Animal releases, as a part of prayer rituals and offerings 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 & Lévêque 2010, Liu et al. 2012), and the United States (Fuller 2015). Overall, this pathway appears to be less notable than the other pathways, and there is no evidence to suggest it is increasing.

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 nonnative species throughout Europe (Arthington & McKenzie 1997). These societies have been responsible for introducing nonnative fish into Australia (Arthington & McKenzie 1997, García-Díaz et al. 2018), Russia, Britain, Europe (Gherardi et al. 2009), and New Zealand (McDowall 1994). Although this pathway was a major cause of fish introductions before 1970, it is now of minor importance due to global recognition of the negative impacts of nonnative 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 nonnative 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) and the Pedder galaxias (*Galaxias pedderensis*) in Australia, both of which have been moved outside of their native range to prevent extinction (Chilcott et al. 2013). Nevertheless, future translocations associated with climate change initiatives 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 been illustrated only anecdotally in the literature. For example, it was shown that the nets of eel fishermen in Tasmania, Australia, may be responsible for moving redfin perch between adjacent water bodies (Lintermans 2004).

3. FACTORS INFLUENCING THE INVASION SUCCESS OF NONNATIVE FISH

The invasion success of a nonnative species is governed not only 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 one of several interacting factors: the propagule pressure of the nonnative species, life history traits, residence time, and characteristics of the receiving ecosystem. In the following sections, we discuss these factors separately, although invasion success may be driven by multiple factors simultaneously (e.g., Woodford et al. 2013). Further details and examples of these factors are described in **Supplemental 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 the larger number of introduced individuals increases both the genetic diversity and the survival probability of the introduced population (e.g., due to reduced risk of stochastic extinctions and increased probability of having 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 & Gozlan 2013). Indeed, the influence of propagule pressure on invasion success is highly dependent on the life cycle and life history traits of the introduced species, as well as on the suitability of the receiving habitat (Gertzen et al. 2008). Propagule pressure also depends on the 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 (Kolar & 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 can be expected to have traits selected in relation to their utility to humans. 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 depend on the nature of the pathway. Species that are transported and introduced by ballast water are generally small, with preadapted 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 **Supplemental Appendix 3** (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 tend to have a generalist diet, broad environmental tolerance, and high plasticity (i.e., traits that allow them to adapt to a wide range of environmental conditions) (Kolar & Lodge 2002, Tonella et al. 2018). This is the case with the invasive topmouth gudgeon, which is found in 32 countries and 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 that are not limited in the environment [e.g., detritivores (Moyle & 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. Species established in highly variable environments tend to have higher fecundity, earlier maturity, faster growth, and smaller adult size compared to those established in stable environments (Moyle & Marchetti 2006). For example, invasive species in the Iberian Peninsula colonized different types of streams depending on the seasonal flow patterns: Small species with high offspring numbers preferentially colonized streams with high seasonality, while large fish with delayed maturity and a lower spawning rate invaded streams with regular flows (Vila-Gispert et al. 2005).

Traits associated with the spread and impact of nonnative species have rarely been studied, except in predictive and profiling studies, which means that assumptions about the underlying mechanisms remain unresolved and speculative (Kolar & Lodge 2002; Marchetti et al. 2004a, 2004b; Moyle & Marchetti 2006; Ribeiro et al. 2008). In general, the successful spread and impact of species seem to depend on their broad physiological tolerance and origin from a nearby region; this highlights the importance of preadaptation to invaded ecosystems. However, studies are inconsistent regarding the impact measures; hence, the relationship between traits and impacts remains unresolved for freshwater fish (Howeth et al. 2016). Some studies predict that small species produce greater impacts than large ones (e.g., Marchetti et al. 2004b), although existing evidence suggests that large fish can cause catastrophic ecological impacts, as in the cases of the Nile perch (Aloo et al. 2017) (**Supplemental Appendix 2**) and largemouth bass (*Micropterus salmoides*) (Gratwicke & Marshall 2001). The correlative nature of the existing studies means that our understanding of the underlying mechanisms is speculative or limited. For example, species with small eggs are correlated with high impacts, although this correlation is poorly understood (Kolar & Lodge 2002, Snyder et al. 2014).

3.3. Residence Time

The residence time of nonnative species, or the time since the first recorded introduction, plays an important role in the spread and impact stages (Wilson et al. 2007). Residence time has been shown to be linked to the spread of nonnative species via colonization success (Buckwalter et al. 2020) and the 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); for example, the impacts of the Nile perch increased significantly 20 years after its first introduction (Taabu-Munyaho et al. 2016) (**Supplemental Appendix 2**). The mechanisms by which residence time may affect establishment, spread, and impacts can be linked to 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. Proximity between donor and receiving environments. Apart from propagule pressure, life history traits, and residence time, the characteristics of the receiving environment are also very important in explaining invasion success. Therefore, the ecological and geographic proximity between the donor and recipient ecosystems is likely to contribute to the establishment of nonnative species, with these two components often being linked (Nekola & White 1999). Species originating from a nearby region are most likely to encounter the same abiotic conditions (e.g., temperature) in the receiving environment and therefore be preadapted there (Moyle & Light 1996b, Moyle & Marchetti 2006). Most introduced species are introduced into the same biogeographic region as their native region, where they experience similar climatic conditions (Blanchet et al. 2009; B. 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 thrive (Ruesink 2005). Nevertheless, some species can become invasive in climatically different regions due to their high plasticity and adaptability [e.g., topmouth gudgeon, goldfish, and 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 occur too rapidly, many native species cannot cope, leading to their lower abundance, local extinction and the creation of unoccupied niches left free for nonnative species (Havel et al. 2005, Clavero et al. 2013). Aquatic ecosystems that are heavily or frequently disturbed by humans therefore seem to be highly susceptible to invasions. For example, dam density and reservoir area, which are related to the alteration, destruction, and 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 nonnative aquatic species (Marchetti et al. 2004a, 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 distance between invaded and noninvaded 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 nonnative species (Hudon 1997).

At a larger scale, climate change may also influence freshwater fish invasions by causing temperate zones to match the climatic requirements of tropical or subtropical species, thus creating new niches for nonnative 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 & 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 in the following sections: biotic resistance, enemy release, and invasion meltdown. Other mechanisms have also been hypothesized to explain the effects of native community diversity on invasion processes such as indirect biotic 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 higher functional redundancy, stronger competition, and fewer unoccupied niches than poorer communities, which reduce their susceptibility to invasion (Gozlan et al. 2010b, Havel et al. 2015, Pelletier et al. 2020). However, the biotic resistance hypothesis for freshwater fish has not yet been 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 conducted at larger scales at which the species–area relationship may have had 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 predators, parasites, 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). However, only parasitism was studied. Native parasites may have difficulties adapting to new hosts, and introduced fish tend to be parasitized by fewer individuals than native fish, in part 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 infection with parasites, they can avoid their negative effects, as shown by Lacerda et al. (2013). Overall, the enemy release hypothesis has been recognized as an important factor for explaining the success of invasions, although the amount of published evidence regarding fish remains incomplete (Roche et al. 2010, Jeschke et al. 2018).

3.4.3.3. Invasional meltdown. Although the presence of some established nonnative species can negatively affect or prevent new invasions, others may directly or indirectly increase the chances of success for new invasive species, through 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, the invasive topmouth gudgeon carries the rosette agent parasite *Sphaerothecum destruens* without being affected by it. This intracellular parasite can, however, cause massive declines in native fish populations, which in turn allows the topmouth gudgeon to overcome native competition, establish, and invade environments (Ercan et al. 2015).

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 first explore the main mechanisms responsible for the impacts of invasive freshwater fish and then discuss the associated ecological and socioeconomic impacts (**Supplemental Appendix 4**).

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 (e.g., competition, predation, disease and parasite transmission, and hybridization), as well as with the native habitat (e.g., 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) (**Figure 2*a***).

4.1.1. Competition. Competition is the main mechanism described in both the GISD (53% of cases) (**Figure 2*a***) 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). Specific traits of some invasive fish such as aggressive behavior or increased foraging abilities help invasive species to outcompete native species for food, particularly in degraded ecosystems (Bergstrom & 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) (**Figure 2*a***). Many examples illustrate the strong influence of predation such as the case of peacock bass (*Cichla monoculus*) introduced in Lake Gatun, Panama. This example suggests that invasive predatory fish can have irreversible consequences on the composition and functional diversity of native ecosystems (Sharpe et al. 2017). Another famous example is the predation by the invasive Nile perch in the Lake Victoria, which led to "the first mass extinction of vertebrates that scientists have ever had the opportunity to observe" (Kaufman 1992, p. 846) (**Supplemental Appendix 2**).

4.1.3. Hybridization. Hybridization involves the mating of individuals from two genetically distinct populations (Harrison & Larson 2014) (8% of cases described) (**Figure 2*a***). 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

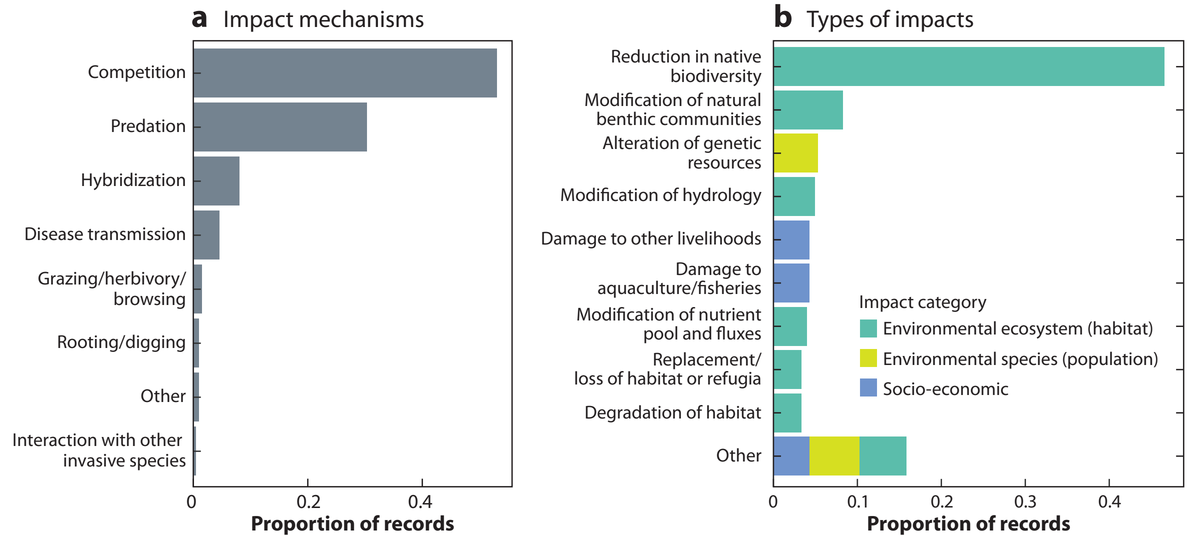


Figure 2

Bar charts illustrating the relative proportion of records of (*a*) impact mechanisms (198 records) and (*b*) types of impacts (303 records) for nonnative freshwater fish. Data are taken from the Global Invasive Species Database (GISD) (ISSG 2015). The GISD compiles impacts and mechanisms of invasive species worldwide with geographic and temporal details. Each record is defined here as the documented observation of (*a*) a mechanism or (*b*) an impact of one species in one location. The spatial resolution of records is variable; some records were recorded at the country level, whereas others were recorded at the scale of a drainage basin. Note that a species can have multiple records in each panel, either in the same category or in different categories.

United Kingdom, approximately 40% of the British population of crucian carp (*Carassius carassius*) consists of hybrids with goldfish (Hänfling et al. 2005). In the Pecos River in Texas, the nonnative sheepshead pupfish (*Cyprinodon variegatus*) has hybridized with the native Pecos pupfish (*Cyprinodon pecosensis*). Hybrids were shown to replace Pecos pupfish populations, due to better swimming endurance and rapid growth rate (Rosenfield et al. 2004). In some cases, low rates of introgression can also have important impacts on the population. For example, hybrids between bull trout (*Salvelinus confluentus*) and brook trout (*Salvelinus fontinalis*) are often sterile, involving only a little introgression risk, as their genes are not passed to the next generation. However, this hybridization led to local declines of the bull trout, due to their loss of reproductive potential (Kanda et al. 2002) (**Supplemental Appendix 4**). 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 to the increased transportation and introduction of fish from aquaculture and fisheries. Stocking nonnative populations that are genetically distant from locally adapted native populations of the same species can also cause inbreeding or outbreeding depression, and as a result, 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 that are transported and introduced along with their host into the new territory (Kuchta et al. 2018, Spikmans et al. 2020). Cointroduced 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 requirement for intermediate hosts (Sheath et al. 2015). Coinvasive parasites of freshwater fish are the fourth most common impact mechanism described in the GISD (5% of cases described) (**Figure 2*a***). Coinvasive parasites can be spread by multiple invaders such as the Asian fish tapeworm (*Schyzocotyle acheilognathi*), which has been co-introduced around the world with carps, guppies, and mosquitofish (Kuchta et al. 2018). Coinvasive parasites are considered to be disproportionately important for freshwater fish: Studies on host fish accounted for more than 50% of all studies on co-introductions (Lymbery et al. 2014). Evidence suggests that co-invasive parasites tend to have more detrimental effects in native fish populations than in their introduced 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 it had on Japanese eels (Kirk 2003). However, the true impact of co-invasive parasites may be underestimated, because many parasites tend to go unnoticed and because their nonnative origin is often unresolved. Furthermore, their effects on native fish populations are difficult to demonstrate (Jarić et al. 2019).

We also note the mechanism of direct parasitism, which involves the parasitism of a native species directly by an invasive fish. However, direct parasitism is a rare mechanism for freshwater fish, as it has been demonstrated, to our knowledge, only for sea lampreys, a major invader in the North American Great Lakes (Cucherousset & Olden 2011, Siefkes 2017).

4.1.5. Interaction with native habitats: Digging and grazing or browsing. Ecosystem engineers are species that modify the resources and abiotic conditions of habitats, which, in turn, influence community composition (Emery-Butcher et al. 2020). Some invasive fish are known to be ecosystem engineers and to impact habitats through their foraging and reproductive behavior (**Figure 2*a***). For example, some invasive carp are responsible for suspending sediments due to their burrowing feeding habits, thereby increasing turbidity and erosion and releasing pollutants trapped in the soil (Matsuzaki et al. 2009, Emery-Butcher et al. 2020). The same behavior has been described for the invasive pumpkinseed (*Lepomis gibbosus*) during their nest construction (Beisel & Lévêque 2010).

4.2. Ecological and Socioeconomic Impacts

Ecological impacts are the most frequently described impact category for nonnative freshwater fish (87%) (**Figure 2*b***). These impacts have mainly been documented at the ecosystem level (76% of 303 cases) (**Figure 2*b***), although they can occur at all biological levels (genetic, individual, population, ecosystem, and biogeographic) (**Figure 2*b*, Supplemental Appendix 4**). For example, in Montana, USA, rainbow trout are known to hybridize with the native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), thus reducing the fitness of the latter species by lowering reproductive success and altering genetic resources (Muhlfeld et al. 2009). At the ecosystem level, invasive fish can be responsible for modifying nutrient fluxes (Matsuzaki et al. 2009). At biogeographic levels, introductions have caused an overall increase in fish species richness throughout basins worldwide by exceeding extinction rates (Villéger 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 among aquatic systems and regions (Villéger et al. 2011, Su et al. 2021). This process, known as biotic homogenization, has been intensively studied in recent years (Rahel 2000, Villéger et al. 2011, Pool & Olden 2012, Villéger et al. 2014, Vargas et al. 2015, Campbell & Mandrak 2020) (**Supplemental Appendix 4**).

The socioeconomic impacts of nonnative fish are less studied and constitute only a minor part (13%) of the 303 cases described in the GISD (**Figure 2*b***). Nonnative fish can damage aquaculture, fisheries, and infrastructure, 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 & Swink 2003). A recent study showed that impact costs have been estimated for only 27 invasive fish species, but these totaled approximately US$37 billion between 1960 and 2020 (Haubrock et al. 2022). As most species lack cost studies, these records are not only severely underestimated but also geographically and taxonomically biased. Most costs were recorded in North America; in addition, the majority of costs pertained to damage and resource loss (e.g., impacts on native fish stocks through predation), with very few management-related costs. 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 economic costs for freshwater fish and the difficulty of estimating the cost of lost ecosystem services (Gozlan et al. 2010b, Haubrock et al. 2022). The substantial underestimation of nonnative fish costs may partly be related to the economic benefits associated with nonnative fish species [e.g., farmed fish, sport fishing (Gozlan 2008)]. In this uncertain context, Leprieur et al. (2009) and Vitule et al. (2009) have argued for a precautionary principle against introducing nonnative freshwater fish.

5. MANAGEMENT

Management techniques for dealing with freshwater fish invasions are numerous and depend on the stage of the invasion process. While prevention and early detection plus a rapid response can limit the introduction and establishment of invasive nonnative fish species, respectively, 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 entails acting before introduction takes place by avoiding the transport of fish species or their introduction into the wild (Robertson et al. 2020). For freshwater fish, legal frameworks have been implemented 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). Risk assessment tools, such as the fish invasiveness scoring kit are also used by policymakers to distinguish between potentially invasive and noninvasive species of nonnative fish and provide an aid for developing legislation (Copp et al. 2008). Barriers can also be set up to avoid the introduction of fish species after the construction of a canal (Noatch & Suski 2012). The GISD contains information about the management approach used for 27 species through 40 records. A record is defined here as a management plan implemented for one species in one location. Based on these 40 records, prevention is the second most common management strategy, with 15 records linked to such management actions.

Once a nonnative 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 limited effectiveness when the target species is represented by only a few individuals, several monitoring techniques can detect and track trends in nonnative species. For example, bioacoustic sensors are a noninvasive method that has been used to detect nonnative fish species [e.g., spotted Tilapia (*Tilapia mariae*) in Australia (Kottege et al. 2012, 2015)]. Another noninvasive 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 at detecting rare introduced fish species than traditional detection methods (Jerde et al. 2011) but cannot 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 introduction pathway. 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 that it came from a nonaquarium introduction, as this parasite cannot survive with prolonged aquarium maintenance.

Additionally, 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 monitoring, tracking, identification, and information tools for the general public (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 geo-references (Daume & Galaz 2016). For example, the introductions of nonnative buffalo fish (*Ictiobus cyprinellus* and *Ictiobus niger*) into Czech rivers were 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 nonnative 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 nonnative population after an eradication effort. Unfortunately, monitoring is the least documented management strategy for freshwater fish according to the GISD, as it was used for only 2 out of 40 records.

5.2. Eradication, Containment, and Suppression

As long as the area of invasion is very limited, and the nonnative population is small, eradication using several possible methods may be logistically and financially feasible. Chemical treatments such as rotenone have been widely used for years to eradicate species rapidly and efficiently, but they are also toxic to nontarget species (Knapp & Matthews 1998, Britton et al. 2011, Rytwinski et al. 2019) and not well accepted by the public (Bremner & Park 2007). Nevertheless, some chemical methods known for their selectivity and effectiveness are still used, such as lampricides to control sea lampreys (Siefkes 2017). Electrofishing and gill netting can be effective eradication methods, although they are far more expensive and time consuming than chemical treatments (Knapp & Matthews 1998, Bosch et al. 2019). More recently, new management techniques have been explored, such as genetic biocontrol methods to alter the sex ratio within a population, but they are still under development (Teem & Gutierrez 2014). In North America, a Trojan Y chromosome strategy is used to produce YY males of the invasive brook trout (Schill et al. 2016). Field evaluations of the efficiency of stocking YY male brook trout are ongoing in North American lakes and streams with encouraging results (Roth et al. 2020). 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 remains risky due to the potential spillover of the virus to other species and requires a thorough knowledge of the targeted species as well as the epidemiology, virulence, and transmissibility of the virus (McColl et al. 2014, 2016).

In addition, when nonnative fish reproduce, spread over larger areas, and establish large populations, eradication ceases to be possible (Ahmed et al. 2022). 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 records listed in the GISD. For instance, 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 nonphysical barriers that alter the behavior of invasive species, e.g., electrical barriers, altered flow regimes, magnetic fields, or the addition of carbon dioxide and oxygen to create low oxygen zones (Noatch & Suski 2012). Suppression actions (i.e., reducing the distribution or abundance of the nonnative population in an area) can also be implemented (Robertson et al. 2020), as can selective capture, which can be promoted through public awareness and incentives. In addition the exploitation of invasive freshwater fish as a food source can be an effective suppression technique (Seaman et al. 2022). For example, in Lake Victoria, fishing of Nile Perch has led to a decline in these fish (Yongo et al. 2018). More recently, Bouska et al. (2020) showed that, with sufficient market demand, harvest could be an effective way to control the invasive bighead carp (*Hypophthalmichthys nobilis*) in the Mississippi River basin. In addition, management techniques formerly used for terrestrial invasions are beginning to be applied to freshwater fish (Simberloff 2021). This is the case with the sterile male technique (Bravener & Twohey 2016, Simberloff 2021), which has been recently applied to sea lampreys in the Great Lakes (Bravener & Twohey 2016) and with pheromones, which have great potential, as fish use pheromones to communicate. The pheromone technique has been tested for sea lampreys and common carp in order to reduce mating and reproductive success, redirect migratory invasive fish, or mass trap fish, with some encouraging results (Sorensen & Johnson 2016).

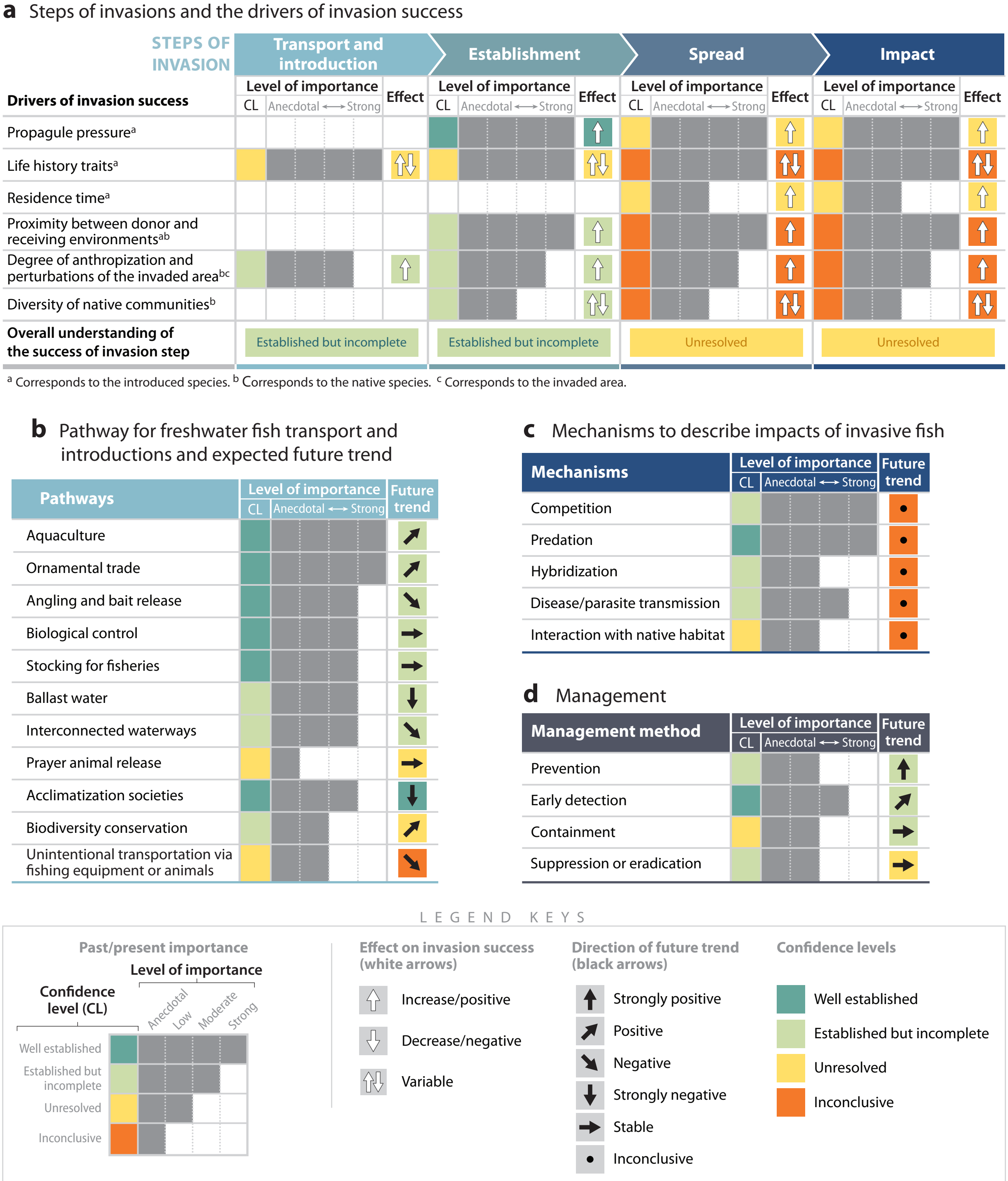
Overall, it remains very challenging to control freshwater fish invasions despite new management options (e.g., genetic biocontrol methods). Consequently, legal frameworks are urgently required at a global scale, since prevention is by far the most effective and least costly management approach.

6. SHORTFALLS, GAPS, AND BIASES IN KNOWLEDGE AND DATA

More than 60 years after Elton's seminal work on invasions [Elton 2020 (1958)], much has been learned about invasion records and spatial patterns. Since then, a large amount of theoretical knowledge has been amassed regarding invasion processes and mechanisms for freshwater fish. In short, nonnative freshwater fish are introduced through several pathways, two of which stand out, namely aquaculture and the ornamental trade. These two trade sectors are likely to grow further in the future and may involve even more species if no regulation is implemented (**Figure 3**). The main factors associated with successful invasions are propagule pressure, the life history traits of introduced species (e.g., a broad physiological tolerance facilitates the establishment, spread, and impact of the invasion), and the characteristics of the receiving environment (e.g., strong anthropogenic disturbances facilitate invasions). We demonstrate that the success of an invasion is most often explained by a combination of factors such as high propagule pressure combined with proximity between donor and receiving environments. Invasive freshwater fish affect 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. The most widely used method to address freshwater fish invasions is population control, even though prevention would be the most effective to implement. New management techniques are constantly being developed, thus allowing for efficient and targeted eradications that were previously impossible without impacting the entire ecosystem. Despite the abundance of studies on freshwater fish invasions, there is still a clear lack of understanding of certain aspects that stems from inadequate exploration of certain key hypotheses, a lack of available data, and geographic and temporal biases.

6.1. Lack of Exploration of Key Hypotheses

Our review highlights the fact that although some aspects of freshwater fish invasions are well known (e.g., pathways of introduction), several important aspects and hypotheses have not been sufficiently explored (**Figure 3**), notably with regard to the ecological hypotheses proposed to



(*Caption appears on following page*)

Figure 3 (*Figure appears on preceding page*)

Summary of the state of knowledge regarding freshwater fish invasions. The content of this summary figure was derived from an expert-based assessment from all coauthors based on the reviewed literature. We evaluated the level of confidence in our assessments on the basis of both the amount of scientific evidence and the degree of convergence in evidence among studies. (*a*) Our assessment of the past and present importance of each driver for the success of invasion (indicated by the length of the *gray bars*), shown for each step of the invasion process (*top row*), as well as the perceived effect of the driver on invasion success (positive, negative or variable; indicated by the direction of the *white arrows*). The last row of panel *a* indicates the level of overall understanding of each step of the invasion; the transport and introduction and establishment steps are relatively well documented in the literature, whereas the spread and impact steps are still insufficiently documented in the literature. (*b*) The past and present importance of each pathway (*gray bars*) for freshwater fish transport and introductions, with an assessment of the expected future trend (*black arrows*) for each pathway. (*c*) The past and present importance of the known and documented mechanisms by which invasive fish impact native ecosystems (*gray bars*), with an assessment of the expected future trend (*black arrows*). Note that the future trend for all mechanisms was deemed inconclusive because of the lack of literature addressing this aspect. (*d*) The past and present importance of management methods (*gray bars*), with an assessment of the expected future trend (*black arrows*) for each method.

explain invasion success (Jeschke et al. 2018). For example, among the 39 hypotheses about invasion success and impacts proposed by Enders et al. (2020), only a few have been investigated with regard to freshwater fish invasions (biotic resistance, invasional meltdown, and enemy release). Another example is the effect of life history traits on the spread and impacts of invasive fish, which remains unresolved because it has been explored only in a limited number of modeling studies. Because of these unresolved hypotheses, we still struggle to link mechanisms to observations. We are also 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 to predict the outcome when a new nonnative species is established in a receiving ecosystem (Marchetti et al. 2004b, Pyšek et al. 2020). This inability hinders the development of effective actions to manage biological invasions.

6.2. Gaps in Data Coverage

There is a severe lack of data on several aspects of freshwater fish invasions, including essential aspects such as the number of invasion occurrences, particularly in specific regions that are poorly documented. For example, there are limited data on the propagule pressure of freshwater fish species (García-Berthou 2007). Only minimal figures on fish production and commerce are given by the Food and Agriculture Organization of the United Nations (Food Agric. Org. UN 2016), while statistics on 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 costs associated with them (Haubrock et al. 2022). Likewise, invasive freshwater fish have not been classified in the SocioEconomic Impact Classification of Alien Taxa (Bacher et al. 2018). The same paucity 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 that lists management plans implemented for invasive freshwater fish species by country is the GISD. However, this database is incomplete, as it contains management information for only 27 nonnative freshwater fish species in 14 countries, even though at least 551 nonnative freshwater fish are established worldwide (**Figure 1**). For example, some iconic invasive species with known management plans are not included in the database (e.g., sea lamprey). Previous studies such as that by Rytwinski et al. (2019) have already raised the issue of poorly documented evaluations of eradication methods.

However, several other databases reporting information on freshwater fish invasions do exist [e.g., economic impacts (Diagne et al. 2020), occurrence in drainage basins (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 affect predictions and conclusions relating to freshwater fish invasion patterns.

6.3. Geographic and Temporal Biases

Our knowledge of the success of biological invasions of freshwater fish 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 invasive freshwater fish in 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 **Supplemental Appendix 3**). The same bias was demonstrated for the economic impacts of freshwater fish species by 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 & 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, but 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 real-time monitoring of invasions. For example, Tedesco et al. (2017) list only a few introductions in the Amazon drainage basin, 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 nonnative fish species that must be considered an early sign of potential invasions (Brosse et al. 2021). These examples are not documented in the Tedesco et al. (2017) database, thereby preventing users from obtaining up-to-date and accurate information on invasions. This problem can even be quantified in the database of first records of established species created by Seebens et al. (2017). Indeed, the first-record rate of nonnative 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. One solution might be the development of long-term projects with sufficient funding to ensure the regular updating of such important databases.

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 is the case for pathways related to biodiversity conservation, aquaculture, and the ornamental trade (**Figure 3**). The latter two are documented as the two main pathways of introduction of nonnative species, and they will certainly become increasingly important due to the growth in online trade and their development in developing countries [e.g., the increase in the aquarium trade in South America (Magalhães & Jacobi 2013, Magalhães et al. 2020)]. For example, as described in Section 2.7, the One Belt One Road project includes plans to build ports, canals, and dams across Asia and into Africa and Southern Europe (Wong et al. 2017). This construction project is a major potential pathway for further introductions of invasive species from East Asia to the West.

Climate change will also drive changes in the near future. 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. Areas with optimal temperatures for the aquaculture of some fish are expected to shift, possibly leading to changes in the regions in which species are reared, thus bringing about new species introductions (Rahel & Olden 2008). Climate change will also continue to open new niches for invasive species and may even create new opportunities for the establishment of species currently unable to establish in temperate countries (Vilizzi et al. 2021). These niche shifts could also create new possibilities for hybridization (Muhlfeld et al. 2017).

To avoid the potential impacts of new invasions, management plans need to be strengthened. In view of current trends toward the development of laws and expansion of citizen science, we expect that prevention and early detection methods will evolve and be increasingly useful (**Figure 3**).

6.5. Recommendations

In this review, we provide an overview of different aspects of freshwater fish invasions, from pathways of introduction to management techniques. We also highlight several research gaps that need to be filled. Here, 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 nonexistent. Comprehensive data on the propagule pressure of introduced fish could be 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 specific focus on less-studied species and regions [e.g., the Nile perch is known to impact local communities of fishermen in East Africa, but its costs are not recorded (Haubrock et al. 2022)] (**Supplemental Appendix 2**). In addition, it is well known that some invasive freshwater fish species can simultaneously bring benefits to the economy (Gozlan 2008), but the balance between impacts and benefits is still unresolved. The development of a comprehensive database of the positive and negative economic and ecological impacts of freshwater fish invasions could help clarify the benefits of certain species and consequently inform management decisions (Vimercati et al. 2020). Regarding the lack of management data, the large number of articles on the management of freshwater fish species could provide the basis for a comprehensive database.

Second, the further study of some aspects of freshwater fish invasions should be a priority. For example, several hypotheses regarding freshwater fish invasions are yet to be explored (see Jeschke et al. 2018) or fully understood (e.g., the enemy release and biological resistance hypotheses). More generally, the spread and impact stages of the invasion process are less well studied than the other stages, and they could benefit from a better understanding if reliable data were collected (**Figure 3**).

Third, the prediction of future invasion trends 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, along with global drivers of change (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 (Brondizio et al. 2019) to advise managers and decision makers at the international level and to guide international and national public policies concerning freshwater fish invasions.

In conclusion, biological invasions of freshwater fish are among the most important invasions worldwide, and many aspects have already been addressed in the literature, ranging from the introduction pathways of nonnative freshwater fish species to their impacts and management methods. Nonetheless, data gaps and biases remain, and unresolved aspects of freshwater fish invasion should be addressed in future studies to better understand and manage them more effectively.

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