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Increased geographical distribution and richness of non-native freshwater fish species in Argentina: evidence from a literature review

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Abstract The present study is a full review of the non-native freshwater fish species introduced into Argentina and their relationship to the main environmental features and introduction vectors of each freshwater ecoregion. The total number of non-native freshwater fish species was compiled through a literature survey; information on spatial–temporal patterns of species records and invasion vectors was retrieved for all ten freshwater ecoregions of Argentina. Our survey revealed that 18–22 non-native fish species had been recorded up to 1999, and a total of 40 introduced fish species, of which 18 are invasive and five potentially invasive, had been registered in seven Argentinean ecoregions as of May 2020. According to georeferenced records, the rainbow trout *Oncorhynchus mykiss* and common carp *Cyprinus carpio* were the non-native fish species with the greatest number of records and largest invaded areas, probably due to their species-specific ecological traits. Invasive fish species differed clearly between the Patagonia, Lower Paraná, and Lower Uruguay ecoregions, probably because of a combination of the environmental

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conditions, structure of native assemblages, and invasion pathways in each ecoregion. Except for the recognized impact of non-native salmonids, the adverse effects of introduced fish species have been little studied, indicating the need for further research to clarify the role of ecological shifts triggered by the introduction and establishment of non-native fish species in Argentina. In contrast to the high diversity of aquatic species and freshwater environments, the spread and impact of invasive fish species in Argentina is little known, particularly compared with other South American countries.

Keywords Ecoregions · Invasive species · Spatial–temporal distributions · Species introduction · Non-native fish species

Introduction

Globalization has led to a progressive increase in species movement, reaching unprecedented levels in the last century (Bezerra et al. 2019; Vitule et al. 2019). As a result, non-native species have expanded their ranges at great speed (Seebens et al. 2017) and become established all over the world (Pyšek et al. 2020). Although invasion processes are not yet fully understood, it is clear that introduced species represent one of the main drivers of global biodiversity loss (Moyle and Light 1996; Gu et al. 2019). In this sense, current national and international biosecurity measures have been ineffective in regulating the transportation of non-native species and preventing their accidental and intentional release (Perrings et al. 2005).

Invasion processes are complex, depending on the characteristics of the non-native species (invasiveness component) and the intrinsic characteristics of the environment invaded (invasibility component). When both components are positively correlated the chance of a non-native species becoming established rises considerably, increasing the risk of its spread throughout the introduced region and its becoming invasive (Colautti et al. 2006).

Although freshwater systems harbour disproportionally high levels of biodiversity, they are the most threatened ecosystems on Earth (Saunders et al. 2002; Dudgeon et al. 2006; Abell et al. 2008; Gatti 2016; Vitule et al. 2017). These systems suffer from a wide range and magnitude of human impacts (e.g., surface and groundwater use, industrial and domestic pollution, dam construction and operation, Dudgeon et al. 2006; Gatti 2016) that increase their susceptibility to biological invasions (Gallardo et al. 2016) and facilitate the spread of non-native species (Rosenzweig 2001; Vitule et al. 2012; Doherty et al. 2016). Apart from intentional introductions, human activities often surpass biogeographical barriers by creating artificial connections between previously separated catchments, or removing barriers such as waterfalls (Moyle and Light 1996; Vitule et al. 2012; Daga et al. 2016). They also increase ecosystem invasibility through habitat modification, as in the case of dams (Vitule et al. 2012), through changes in the submerged structures of navigable rivers, as noted in European rivers (Uehlinger et al. 2009), or the construction of fish passages (Pelicice and Agostinho 2008; Kerr et al. 2021).

Despite the significant ecological damage non-native fishes cause in freshwater environments in comparison with other introduced species (Simberloff and Rejmánek 2010), they continue to be introduced worldwide (Ribeiro et al. 2017). Invasive fishes have led to severe economic (loss of ecosystem services) and ecological (native community reshaping, changes in natural habitat conditions, biotic homogenization) impacts, which are well-documented (e.g., Rahel 2002; Espínola et al. 2010; Cucherousset and Olden 2011; Santos et al. 2019; Vidal et al. 2020).

Therefore, updated knowledge of non-native species distributions on broad spatial scales are crucial for understanding of the invasion process and prevention or mitigation of the impact caused by new introductions.

Argentina (total area 2,780,400 km^2) is the eighth largest country in the world and the second largest country in South America, encompassing broad latitudinal and altitudinal ranges and ten biogeographical ecoregions. These freshwater ecoregions contain a wide variety of lentic and lotic environments with high levels of aquatic biodiversity, especially fishes (570 species) (López et al. 2008; Mirande and Koerber 2020). Linking the varying levels of environmental heterogeneity to patterns of species diversity and distribution (Abell et al. 2008) enables the identification of evolutionary ecological processes and patterns on an ecoregional scale (Baselga et al. 2012), and the testing of hypotheses regarding mechanisms that generate and maintain aquatic ecosystem biodiversity (Legendre and De Cáceres, 2013). The ecoregional approach also enables the development of biodiversity management and conservation policies at varying geographic levels (Groves et al. 2002). Therefore, applying the approach of freshwater ecoregions may give a more comprehensive perspective of the processes that have facilitated the introduction and eventual establishment of non-native species in the water bodies of Argentina.

The introduction of non-native fish species in this country dates back to the beginning of the twentieth century (Baigún and Quirós, 1985). Ringuelet et al. (1967) documented seven non-native fish species, but this total rose to the 13 invasive fish species registered by Baigún and Quirós (1985), who carried out the first exhaustive review of the presence of non-native species throughout Argentina. Subsequent inventories and compilations have detected an increase to 18 non-native fish species (e.g., Liotta 2005; Mirande and Koerber 2015; Koerber et al. 2019), but none of these studies attempted to explain the factors that shaped the distribution of these invaders (Mirande and Koerber 2020). Most studies in Argentina have focused mainly on salmonids (e.g., Vigliano and Alonso 2007; Pascual et al. 2002; 2007; Aigo et al. 2008) and common carp (Maiztegui et al. 2016; 2019). Besides these, except for Baigún and Quiros (1985) and Vigliano and Darrigran (2002), there has been no in-depth attempt to track the distribution of all non-native fish species currently found in Argentina.

The purpose of this study is to update knowledge on the number of non-native freshwater fish species introduced and established in Argentina. Based on scientific literature and validated technical reports on these species, we describe the trend of recorded species over a period of more than 100 years (1908–2020). In contrast to previous studies that tended to list non-native fishes or target certain species (e.g., salmonids and common carp), our study tracks the temporal evolution of all publications on non-native fish species up to the present. We also provide the distribution patterns and main introduction vectors of invasive fish species throughout the Argentine ecoregions.

Materials and methods

The large-scale classification approach of freshwater ecoregions of the world (FEOW; Abell et al. 2008) was used to identify Argentine ecoregions and their characteristics.

A search for information on non-native species was conducted in peer-reviewed articles up to May 2020, using the Scopus (https://www.scopus.com) and Google Scholar database (https://scholar.google.com.ar) search platforms. The combined keywords (English and Spanish) used for searches were the following: 'fish' OR 'ichthyofauna' OR 'introduction' OR 'alien' OR 'non-native' OR 'invasive' OR 'exotic' OR 'introduced' AND 'Argentina' OR 'Patagonia' OR 'Cuyo' OR 'Buenos Aires' OR 'Northwest Argentina' OR 'Littoral Argentina' OR 'Central Argentina', and the time span covered was from 1908 to May 31, 2020. Using both search platforms we carried out a survey of all available publications addressing the topic of "non-native fish species in freshwater environments in Argentina". In addition, newspaper articles, government reports and provincial legislation were reviewed and evaluated. Using the results from searches in both English and Spanish, the following information was retrieved for each non-native species: date of publication, source, type of publication, and geographic location. Two other specific lists (Liotta 2005; Mirande and Koerber 2020) available for native and non-native freshwater fishes in Argentina were also examined to extract the same information as retrieved from electronic surveys.

To prevent contradiction or confusion in relation to the terminology commonly employed for introduced organisms, the terms used in this manuscript are as follows: *native species* was assigned to species occurring in a region as a product of natural processes of dispersal (IUCN 2014; Convention on Biological Diversity 2014), whereas *non-native species* refers to those transported outside their natural range by humans (whether intentionally or accidentally), even within the same country (Guo and Ricklefs 2010). However, only species introduced by humans and natural causes from other countries were considered here (i.e. species translocations between ecoregions within Argentina were not evaluated); *non-established* were considered non-native species found or reported in nature (lotic-lentic ecosystems) but not known to maintain self-reproductive populations; *established* were species known to have reproducing, self-sustainable populations (Williamson and Fitter 1996b); and *invasive* were considered established species capable of spreading (Colautti and MacIsaac 2004). This terminology was applied because these terms have an ecological rather than an anthropocentric connotation, thus avoiding the use of confounding terms such as exotic, alien, invasive, and naturalized species (Espínola and Ferreira 2007).

The bibliographic information was used to compile a full list of non-native fish species recorded in Argentina, and one of the four invasion statuses was assigned to each non-native fish species, according to the following criteria: (1) *risk of being introduced* (RBI) was assigned to species that were recorded or detected within Argentinean territory but had no official records of introduction into natural or seminatural systems (e.g. species registered on websites for the aquarium trade or used as biological models in research centres); (2) *introduced* (INT) was ascribed to non-native fish species with official or validated stocking records in natural or seminatural systems but never reported after their release into the wild; (3) *invasive* (INV) was assigned to non-indigenous fish species repeatedly reported through experimental, artisanal or sport/recreational fisheries, and which were also found breeding or their larvae or juveniles inhabiting natural or semi-natural systems; and (4) *potentially invasive* (PI) was ascribed to species reported only very occasionally as a product of stocking or fish farm escapes, even from sectors of the basins in neighbouring countries, but without evidence that they can establish self-sustainable populations. This means that the number of invasive species given here could be regarded as relatively conservative (see Williamson and Fitter, 1996a), but could increase rapidly if further findings are published. We also disregarded cases of translocation, i.e., species that were moved between ecoregions within the same country (Copp et al. 2005).

Data analysis

Based on information collected from FishBase (Froese, and Pauly 2017) about non-native fish species, we determined the natural range, invaded ecoregions and ecological characteristics of these species. In addition, through the bibliography we identified the possible introduction vectors of these species, and determined the total number of publications referring to invasive and potentially invasive fish species in freshwater environments in Argentina. A map with georeferenced records of invasive and potentially invasive species by freshwater ecoregion (FEOW) was generated using QGIS (QGIS Development Team 2019). Based on the publications reviewed, the full study period (1908–2020) was divided into three time periods: 1908–1958 (the early studies on non-native fish species carried out in the worldwide before publication of the pivotal book of Charles Elton in 1958 (See Richardson and Pyšek (2008); 1959–1999 (the intermediate stage of studies on non-native fish species, which coincided with enforcement of the first national law aiming to control non-native species introductions, Law N°10,081, 1983); and 2000–2019 (the stage of contemporary studies on non-native fish species in Argentina, which coincided with the period of increased international awareness of the risk of introduced species and the definition of worldwide policy against new introductions).

Results

Non-native fish species introduced into Argentina

A total of 109 peer-reviewed publications, four government reports**,** and eight journalistic articles that met the selection criteria were used; they showed that a total of 40 non-native fish species belonging to seven orders and 11 families had been recorded in Argentina (Table 1).

The first publication on non-native fish species in Argentina, considering the two databases analysed, was published in 1908 (See Tulian, 1908). Two other articles (reviews of the introduced salmonids) were published in 1936 (Marini, 1936) and 1940 (Thompson, 1940), and two others in 1944 (Bruno Videla, 1944) and 1945 (Mac-Donagh, 1945), showing that until 1958 the total number of publications addressing non-native fish species was very low. Despite the study of Baigún and Quiros (1985), who suggested that the period 1904–1930 corresponded to the fundamental introductions of non-native species, the total number of publications addressing non-native fish species remained low up to the middle of the twentieth century and even up

Table 1 First published record, classification, introduction vector, native range and invades ecoregions

Family	Species	First record published in	RBI	INT	INV	PI	Introduction vector	Native range	Invaded ecoregions
Acipenseriformes									
Acipenseridae									
	Acipenser baerii Brandt, 1869	Azpelicueta and Almirón (1999)				X	Aquaculture	ASI	LPA, LUR, MCS
	Acipenser gueldenstaedtii Brandt and Ratzeburg, 1833	Demonte et al. (2017)				X	Aquaculture	ASI, EUR	LPA, MCS
	Huso huso (Linnaeus, 1758)	MAGyP (2012)		X			Aquaculture	ASI, EUR	MCS
Beloniformes									
Adrianichthyidae	*Oryzias latipes** (Temminick and Schlegel, 1846)	Website sales	X				Experimental model	ASI	
Cypriniformes									
Cyprinidae	*Carassius auratus* (Linnaeus, 1758)	Pozzi (1945)			X		Aquarium trade	ASI	CDE, LPA
	Ctenopharyngodon idella (Valenciennes, 1866)	Arámburu (1971)			X		Aquaculture / Biological Control	ASI	BDR, CDE, LPA, MCS
	Cyprinus carpio Linnaeus, 1758	Mac Donagh (1945)			X		Aquaculture/ Sportfishing	ASI, EUR	BDR, CDE, LPA, MCS, CHA, IGU, LUR, PAT
	*Danio rerio** (Hammilton, 1822)	website sales	X				Experimental model/ Aquarium trade	ASI	
	Hypophthalmichthys molitrix (Valenciennes, 1844)	García Romero et al. (1998)			X		Aquaculture /Biological Control /Sportfishing	ASI	CHA, LPA
	Hypophthalmichthys nobilis (Richardson, 1845)	Vigliano and Darrigran (2002)			X		Aquaculture	ASI	LPA
Cyprinodontiformes									
Poeciliidae	*Gambusia affinis* (Baird and Girard, 1853)	Pozzi (1945)			X		Biological Control	NAM	CDE, LPA, MCS
	Gambusia holbrooki Girard, 1859	Cabrera et al. (2017)			X		Biological Control	NAM	CDE, LPA, MCS
	Poecilia reticulata Peters, 1859	Rosso et al. (2017)			X		Biological Control/Aquarium trade	CAM, SAM	CHA
	*Xiphophorus maculatus** (Günther, 1866)	MAGyP (2014a, b)	X				Aquarium trade	CAM, NAM	MCS
Centrarchiformes									
Centrarchidae	*Micropterus salmoides* (Lacepède, 1802)	Baigún and Quirós (1985)		X			Aquaculture/ Sportfishing	NAM	BDR

Table 1 (continued)

Family	Species	First record published in	RBI	INT	INV	PI	Introduction vector	Native range	Invaded ecoregions
Cichliformes									
Cichlidae	*Cichla kelberi** Kullander and Ferreira, 2006	MAyDS (2016)	?				Aquarium trade	SAM	
	*Cichla piquiti** Kullander and-Ferreira, 2006	website sales	?				Aquarium trade	SAM	
	Coptodon rendalli (Boulenger, 1987)	López et al. (2003)				X	Aquaculture/Biological Control	AFR	LPA, IGU
	Geophagus brasiliensis (Quoy and Gaimard, 1824)	Ringuelet et al. (1967)			X		Aquarium trade	SAM	LPA, IGU
	Geophagus sveni Lucinda, Lucena and Assis, 2010	Benitez et al. (2018)				X	Aquarium trade	SAM	LPA
	Oreochromis niloticus (Linnaeus, 1758)	MAGyP (2012)			X		Aquaculture	AFR	LPA, BDR, IGU
	*Rocío octofasciata** (Regan, 1903)	MAGyP (2014b)	X				Aquarium trade	CAM, NAM	MCS
Perciformes									
Moronidae	*Morone saxatilis* (Walbaum, 1792)	Vigliano and Darrigran (2002)		X			Aquaculture/ Sportfishing	NAM	LPA
Sciaenidae	*Plagioscion squamosissimus* (Heckel, 1840)	Bó et al. (2002)			X		Aquaculture	SAM	LPA

Table 1 (continued)

Family	Species	First record published in	RBI	INT	INV	PI	Introduction vector	Native range	Invaded ecoregions
Salmoniformes									
Salmonidae	*Coregonus clupeaformis* (Mitchill, 1818)	Baigún and Quiróz (1985)		X			Aquaculture/ Sportfishing	NAM	PAT
	Oncorhynchus gorbuscha (Walbaum, 1792)	Crawford and Muir (2008)		X			Aquaculture/ Sportfishing	ASI, NAM	PAT
	Oncorhynchus kisutch (Walbaum, 1792)	Marini (1936)			X		Aquaculture/ Sportfishing	ASI, NAM	PAT
	Oncorhynchus masou (Brevoort, 1856)	Ortubay et al. (1991)		X			Aquaculture/ Sportfishing	ASI	PAT
	Oncorhynchus mykiss (Walbaum, 1792)	Tulian (1908)			X		Aquaculture/ Sportfishing	NAM	CDE, MCS, PAT
	Oncorhynchus nerka (Walbaum, 1792)	Tulian (1908)		X			Aquaculture/ Sportfishing	ASI, NAM	PAT
	Oncorhynchus tshawytscha (Walbaum, 1792)	Tulian (1908)			X		Aquaculture/ Sportfishing	ASI, NAM	PAT
	Salmo salar Linnaeus, 1758	Tulian (1908)			X		Aquaculture/ Sportfishing	EUR, NAM	PAT
	Salmo trutta Linnaeus, 1758	Tulian (1908)			X		Aquaculture/ Sportfishing	ASI, EUR	PAT
	Salvelinus alpinus (Linnaeus, 1758)	Buria and Ortubey (2016)		X			Sportfishing	EUR, NAM	PAT
	Salvelinus fontinalis (Mitchell, 1814)	Tulian (1908)			X		Aquaculture/ Sportfishing	NAM	CDE, MCS, PAT
	Salvelinus namaycush (Walbaum, 1792)	Tulian (1908)			X		Aquaculture/ Sportfishing	NAM	PAT
Siluriformes									
Clariidae	*Clarias angolensis* Steindachner, 1866	Chebez et al. (2008)		X			Aquaculture	AFR	
	Clarias gariepinus (Burchell, 1822)	Vigliano and Darrigran (2002)				X	Aquaculture	AFR, ASI	IGU, LPA
Ictaluridae	*Ameriurus nebulosus* (Lasueur, 1819)	Gómez (2015)		X			Aquaculture	NAM	IGU
	Ictalurus punctatus (Rafinesque, 1818)	Gómez (2015)		X			Aquaculture	NAM	IGU

Order, family, and species name of the non-native fishes recorded in Argentina and discriminated by, risk of being introduced (RBI), introduced (INT), invasive (INV) and potentially invasive (PI)

Native range: (South American: SAM; North American: NAM; Central American: CAM; Europe: EUR; Africa: AFR; Asia: ASI)

Ecoregions (Bonaerensean-Drainages: BDR; Chaco: CHA; Cuyan-Desaguadero: CDE; Iguassu: IGU; Mar Chiquita-Salinas Grandes: MCS; Lower Parana: LPA; Lower Uruguay: LUR; Patagonia: PAT

[*] Only registered on websites for the aquarium market and as biological models (produced and used in research centers)

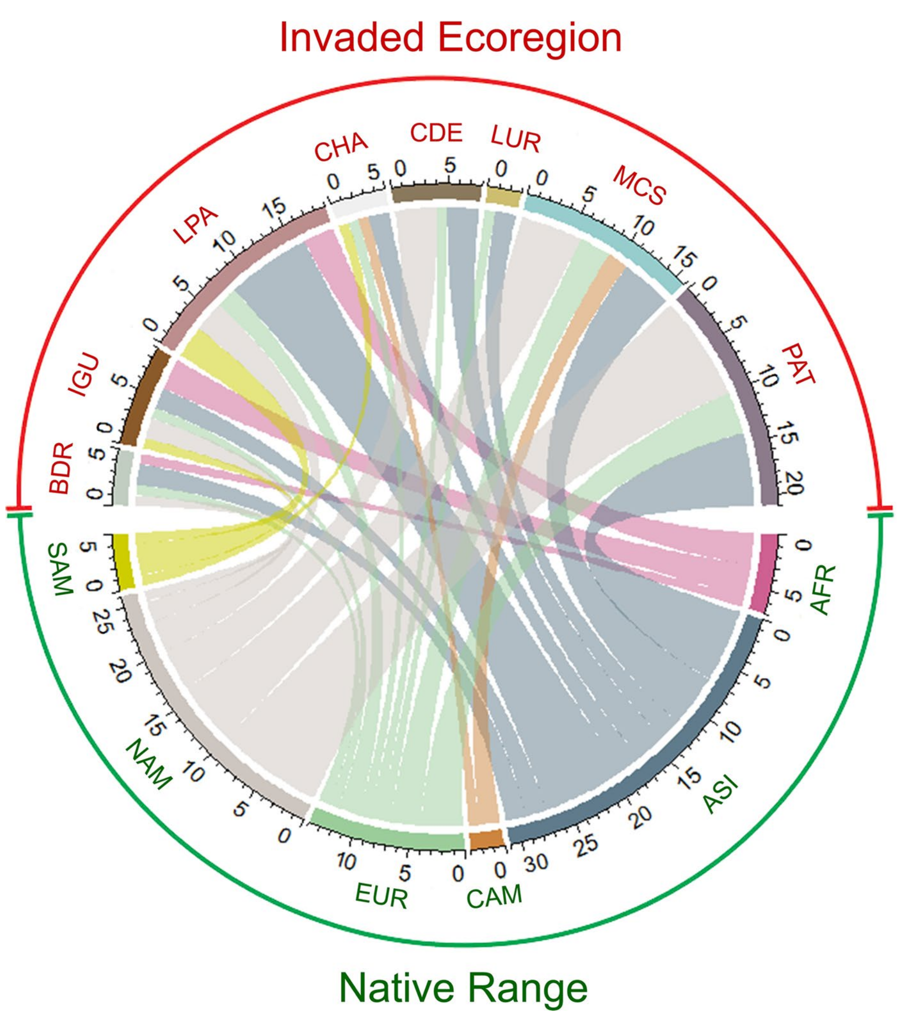
(?) Questionable publication

to the year 2000. After that the number of publications began to increase, slowly at first, but escalating rapidly after the first peak in publications in 2008. The maximum number of publications was recorded in 2015, including a total of 16 studies that targeted the genera *Oncorhynchus*, *Salvelinus* and *Salmo* (Fig. 1).

The invasive species with the highest number of publications ($N=64$) was the rainbow trout *Oncorhynchus mykiss*, one of the first species introduced into Argentina at the beginning of the nineteenth century (Tulian 1908; Baigún and Quiros 1985), followed by the brown trout *Salmo trutta* ($N=37$), the brook trout *Salvelinus fontinalis* ($N=30$), the common carp *Cyprinus carpio* ($N=19$), and the Atlantic salmon *Salmo salar* ($N=18$) (Fig. 2). Salmonids comprised almost 62% of the records in the publications studied.

These species came from different parts of the world, some originating from two or more continents, like *Salmo trutta*, which is native to Europe and Asia. It was found that 45% of the non-native fish species were native to North America (United States, Canada or Mexico), 42.55% came from Asia and 15% from Europe. Only 15% of the non-native species were introduced from South American countries (Brazil and Uruguay). A smaller percentage came from Africa (10%) and Central America (7.5%). Thus, the main donor continents for introduced non-native fish species were North America and Asia; fish from these continents were recorded in six and eight Argentine ecoregions, respectively. Non-native fishes were also introduced from Europe into eight ecoregions; however, the flow of introductions was lower (Fig. 3). The main vectors of non-native fish

Fig. 1 Total number of scientific publications recorded per year referring to non-native fish species in Argentina



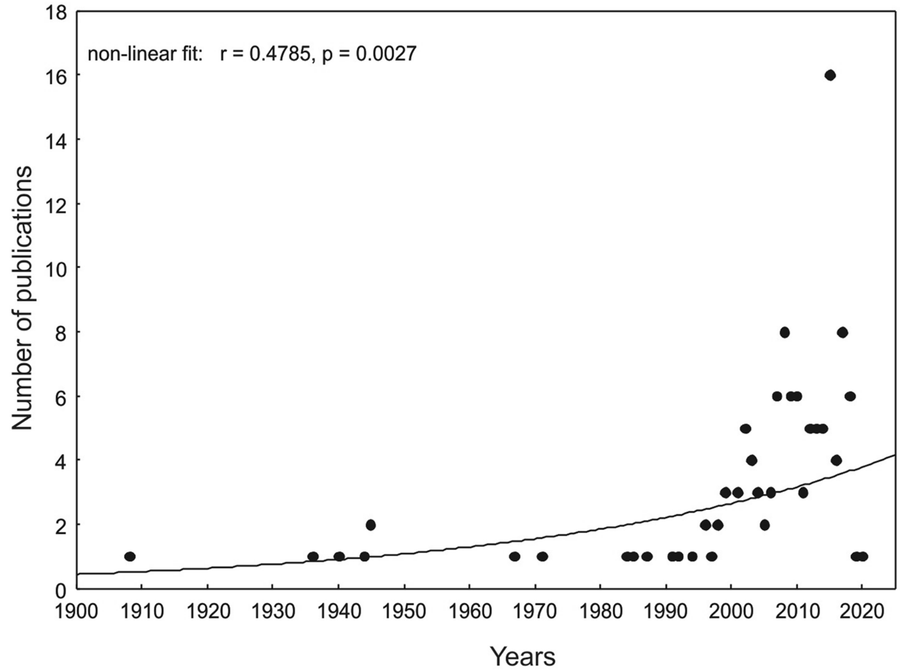


Fig. 2 Total number of scientific publications per invasive and potentially invasive (*) fish species recorded in Argentina

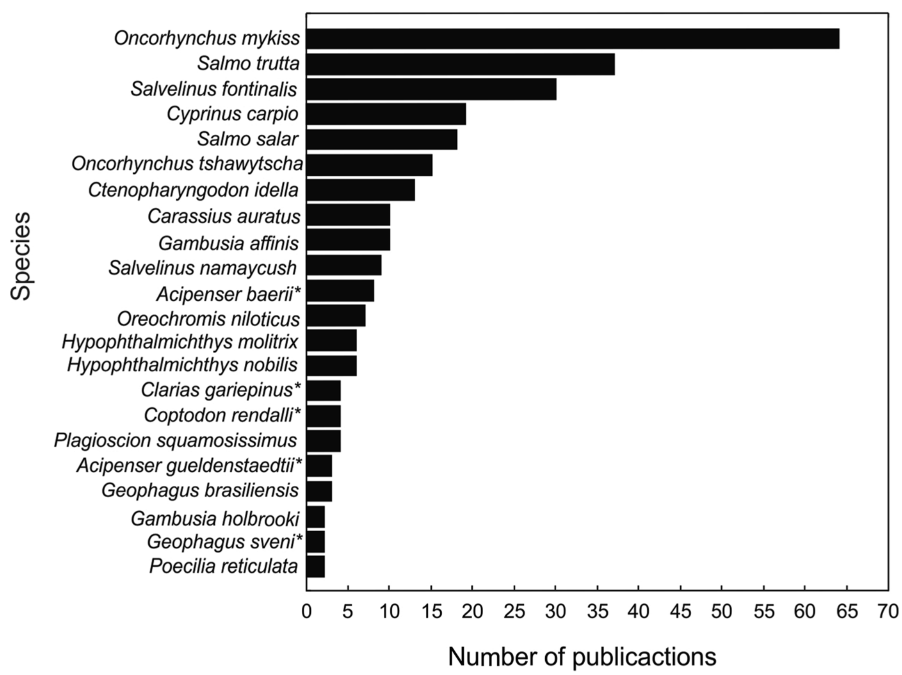


Fig. 3 Number of non-native species that invaded ecoregions of Argentina (red) from their native range (green). Ecoregions (Bonaerensean Drainages: BDR; Chaco: CHA; Cuyan-Desaguadero: CDE; Iguassu: IGU; Mar Chiquita-Salinas Grandes: MCS; Lower Parana: LPA; Lower Uruguay: LUR; Patagonia: PAT. Native range: (South American: SAM; North American: NAM; Central American: CAM; Europe: EUR; Africa: AFR; Asia: ASI)

introductions identified were aquaculture (67.5%; 27 species), sportfishing (40%; 16 species), aquarium trade (22.5%; 9 species), biological control (15%; 6 species) and use as biological models in experiments (5%; 2 species).

Regarding non-native species classification, seventeen non-established (6 RBI; 11 INT), 18 invasive, and 5 potentially invasive fish species were classified according to our categories (Table 1). The most recently recorded species that met the criteria to be considered invasive included *Gambusia holbrooki,* and *Poecilia reticulata* (2017), and potentially invasive species included the Danube sturgeon *Acipenser gueldenstaedtii* (2017) and eartheater *Geophagus sveni* (2018). The RBI species (the peacock basses *Cichla kelberi* and *C. piquiti,* the swordfish *Xiphophorus maculatus*, the Jack Dempsey *Rocio octofasciata*, the zebrafish *Danio rerio* and the Japanese rice fish *Oryzias latipes*) were recorded as introduced but not registered in the wild. Both *C. kelberi* and *C. piquiti* were found on a website for ornamental aquarium sales. However, in a report that summarized the presence of non-native fish in Argentina, SAyDS (2017) identified *C. kelberi* as present in natural ecosystems. Species imported for the aquarium trade, aquaculture, sport fishing and experimental modelling also represent potential invaders, but are not generally considered.

Spatial–temporal distribution of invasive and potentially invasive fish species

The occurrence of non-native fish species in Argentinean ecoregions differed between the three time periods (1908–1958, 1959–2000, and 2001–2019), (Table 2). The 11 fish species recorded for 1908–1958 occurred in the Cuyan-Desaguadero, Lower Paraná, Mar Chiquita-Salinas Grandes and Patagonia ecoregions. It should be noted that most of the non-native species recorded during this period were temperate species such as salmonids (Table 2).

During the 1959–2000 period, five new invasive and two potentially invasive species were recorded, while most invasive species recorded in the previous period, such as the goldfish *Carassius auratus* in the Lower Paraná, and the *Cyprinus carpio* in the Lower Uruguay and Mar Chiquita-Salinas Grandes ecoregions, spread to other ones. During this period the first records of tropical species such as cichlids were published.

Finally, between 2001 and 2019 four invasive species and three new potentially invasive species were recorded for the Lower Uruguay (one) and Lower Paraná (four) ecoregions. Four and five non-native species were also first recorded for Chaco and Cuyan-Desaguadero ecoregions, respectively, contrasting with previous periods presenting no records. On the other hand, no new non-native species was detected in the Patagonia ecoregion.

The temporal pattern found for the accumulated number of invasive and potentially invasive fish species retrieved from publication records agreed overall with the accumulated number of publication records (Fig. 4). Until 1958, the non-native invasive fishes in Argentina were mostly salmonids (four species), followed by cyprinids and cyprinodontids (two species each), and a single cichlid species. Few other fish species (e.g., a single centrarchid species, a single sturgeon species, and two other cyprinid species) were recorded until 1999, indicating a long period of stagnation in the number of studies on non-native fish species. Since the year 2000, both the records and numbers of non-native fish species have increased, reaching nine new established fish species and more than 800 new records. Considering the time span of each period, the rate of species establishment was 1 fish species per 4.33 years for the early period (1908–1958), decreasing to 1 fish species per 10.25 years for the intermediate period (1959–1999), and sharply increasing to 1 fish species per 2.22 years for the contemporary period (2000–2019).

According to the records obtained from the scientific literature, *Cyprinus carpio* can be considered invasive in seven of the 10 ecoregions of Argentina. The grass carp, *Ctenopharyngodon idella*, and the two-mosquito fish species (*Gambusia spp*) are found in four ecoregions, whereas the brook trout *Salvelinus fontinalis*, and *Oncorhynchus mykiss* are invasive in four and three ecoregions, respectively. *C. carpio* can be considered the non-native species with the most extensive distribution in Argentina (Table 3); however, *O. mykiss* was recorded in three ecoregions and had the highest number of records ($N=222$). Moreover, although no scientific literature has validated the presence of this species in the northern portion of Argentina, the occurrence of *O. mykiss* has often been reported by the regulatory technical reports of the provinces of Salta, Tucuman, and Jujuy, which belongs to the Mar Chiquita-Salinas Grandes ecoregion. In turn, *C. carpio,* the species with the second highest number of georeferenced records ($N=181$), spread least in the Cuyan-Desaguadero and Patagonia ecoregions, but dominated the Bonaerensean Drainage. *Salvelinus fontinalis* is another invasive fish species that spread widely (~100 georeferenced records), being present in the same ecoregions as *O. mykiss* (Cuyan-Desaguadero, Mar Chiquita-Salinas Grandes, and Patagonia). Other invasive species, such

Table 2 Temporal and spatial evolution of invasive and potentially invasive (**) fish species by Argentinean ecoregion. Species names typed in bold indicate their establishment within each period

Species	Ecoregions							
	Bonaerensean-Drainages	Chaco	Cuyan-Desaguadero	Iguassu	Lower Parana	Lower Uruguay	Mar Chiquita—Salinas Grandes	Patagonia
					1908–1958			
Carassius auratus			1					
Cyprinus carpio					1			
Gambusia affinis			1		1		1	
Gambusia holbrooki					1			
Oncorhynchus kisutch								1
Oncorhynchus nerka*								1
Oncorhynchus tschawytscha								1
Oncorhynchus mykiss								1
Salmo salar								1
Salmo trutta								1
Salvelinus fontinalis			1					1
					1959–2000			
Acipenser baerii**					1			
Carassius auratus					1		1	
Coptodon rendalli				1				
Ctenopharyngodon idella	1							
Cyprinus carpio							1	
Gambusia affinis					1		1	
Gambusia holbrooki					1			
Geophagus brasiliensis				1				
Hypophthalmichthys molitrix					1			
Micropterus salmoides*	1				1			
Oreochormis niloticus				1				
Oncorhynchus mykiss								1
Oncorhynchus tschawytscha								1
Salmo salar								1
Salmo trutta								1
Salvelinus fontinalis								1
					2000–2020			
*Acipenser baerii***					1	1		
Acipenser gueldenstaedtii**					1			
Carassius auratus			1					
Clarias gariepinus**				1	1			
Coptodon rendalli**					1			
Ctenopharyngodon idella			1		1		1	
Cyprinus carpio	1	1	1		1	1	1	1

Table 2 (continued)

Species	Ecoregions							
	Bonaerensean-Drainages	Chaco	Cuyan-Desaguadero	Iguassu	Lower Parana	Lower Uruguay	Mar Chiquita—Salinas Grandes	Patagonia
Gambusia affinis			1				1	
Gambusia holbrooki			1		1		1	
Geophagus brasiliensis					1			
Geophagus sveni**					1			
Hypophthalmichthys molitrix					1			
Hypophthalmichthys nobilis		1			1			
Oreochromis niloticus	1							
Plagioscion squamosissimus		1			1			
Poecilia reticulata		1						
Oncorhynchus mykiss			1				1	1
Oncorhynchus tshawytscha								1
Salmo salar								1
Salmo trutta								1
Salvelinus fontinalis							1	1
Salvelinus namaycush								1

(*)Species that have not been recorded since introduction

(**) Species potentially invasive

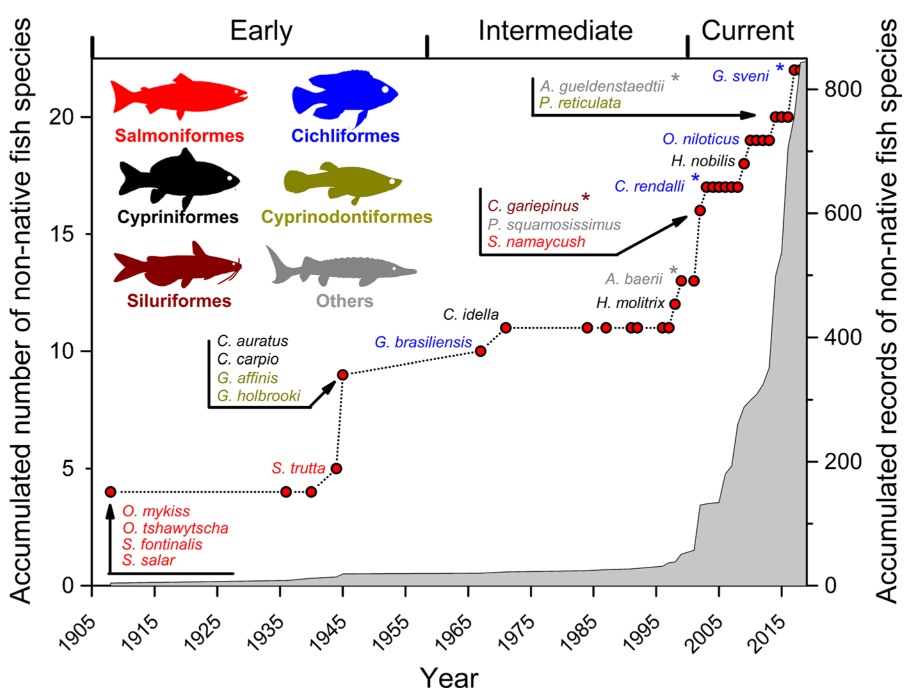


Fig. 4 Accumulated number (left axis) and number of records (right axis) of non-native fish species established in Argentina from 1908 to 2019. The first record of each established fish species is shown near the year of its first appearance and according to the colour of its taxonomic group. Red = Salmoniformes; blue = Cichliformes; black = Cypriniformes; brown = Cyprinodontiformes; dark red = Siluriformes; grey = others (Acipenseriformes, Perciformes, and Centrarchiformes)

Table 3 Total number of records of invasive and potentially invasive species (*) by Argentinean ecoregion

Order/species	Ecoregions							
	Bonaerensean-Drainages	Chaco	Cuyan-Desaguadero	Iguassu	Lower Parana	Lower Uruguay	Mar Chiquita-Salinas Grandes	Patagonia
Cichliformes								
*Coptodon rendalli**				2	1			
Geophagus brasiliensis				2	1			
*Geophagus sveni**					1			
Oreochromis niloticus	1			1	1			
Cypriniformes								
Carassius auratus			3		1		3	
Ctenopharyngodon idella	1		2		3		2	
Cyprinus carpio	56	1	15		43	5	39	22
Hypophthalmichthys molitrix					1			
Hypophthalmichthys nobilis					1			
Cyprinodontiformes								
Gambusia affinis			4		1		14	
Gambusia holbrooki			1		4		9	
Poecilia reticulata		13						
Salmoniformes								
Oncorhynchus mykiss			1				3	218
Oncorhynchus tshawytscha								38
Salmo salar								42
Salmo trutta								143
Salvelinus fontinalis			3				2	112
Salvelinus namaycush								10
Siluriformes								
*Clarias gariepinus**				1	1			
Others								
Acipenseriformes								
*Acipenser baerii**					10	2		
*Acipenser gueldenstaedtii**					7			
Perciformes								
Plagioscion squamosissimus		1			2			
Total ecoregions records	58	15	29	8	79	7	72	587

as the two bighead carps (*Hypophthalmichthys molitrix and H. nobilis*), and potentially invasive species such as *Acipenser gueldenstaedtii,* the African catfish *Clarias gariepinus* and the redbreast tilapia *Coptodon rendalli,* were recorded only in the Lower Paraná ecoregion and in low numbers. The silver croaker *Plagioscion squamosissimus* was also recorded few times, and only in the Chaco and Lower Parana ecoregions (Table 3).

The orders of the invasive species are also unevenly represented in the different ecoregions. The Salmoniformes are mostly restricted to the

Patagonian ecoregion, contrasting with the Cypriniformes and Cyprinodontiformes which are distributed mainly within the ecoregions of Cuyan-Desaguadero, Bonaerensean Drainages, and Mar Chiquita-Salinas Grandes. Other less represented orders, such as the Siluriformes, Cichliformes, Acipenseriformes and Perciformes are found in the Lower Paraná, Lower Uruguay, Iguassu, and Chaco ecoregions (Fig. 5).

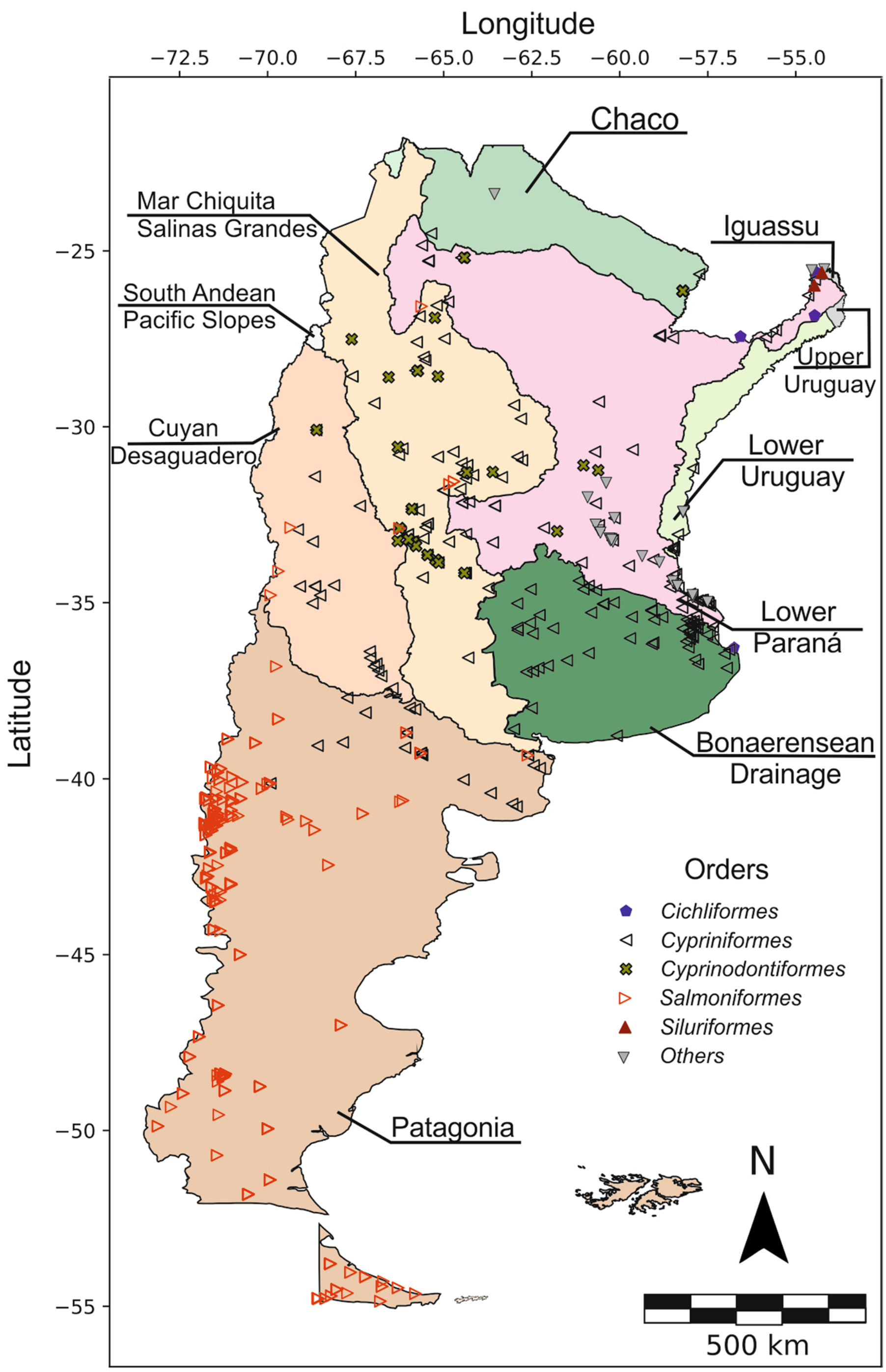


Fig. 5 Spatial distribution of the orders of invasive and potentially invasive fish species by Argentinean ecoregion, based on georeferenced records

Discussion

Our literature review of non-native fishes in Argentina retrieved 65 more peer-reviewed papers than those retrieved (44) by the most recent literature review (Gubiani et al. 2018). (i.e., up to 2017 by Gubiani et al. (2018) vs. May 2020 in our study) (Fig. 1). However, despite the national programme for protection of native biodiversity and control of invasive species, the number of publications on non-native introduced fish in Argentina is still lower than that of other South American countries. Gubiani et al. (2018) found that most studies (56%, N = 164 articles) on the occurrence of non-native freshwater fish species in the Neotropical region were conducted in Brazil, whereas Argentina was ranked only fourth (~40 articles). The use of only one search platform in this study could explain the low number of publications on non-native freshwater fish in Argentina, and the fact that the search was not very country specific. Moreover, the small number of publications found indicate that there are at least 40 introduced non-native fish species recorded in our current dataset. However, it is expected that the actual number is much higher, considering that our list was retrieved from publications available in the literature, and new introductions are likely to be ongoing.

Despite salmonid introductions at the beginning of the twentieth century, the first record of non-native fish species in Argentina provided by SCOPUS database corresponded to Bruno Videla (1944). Depending on the platforms used, the pioneer studies of Tulian (1908), Marini (1936) and Thompson (1940) were also reported, which all referred to salmonid introductions in Argentina. These divergences suggest that the scientific literature has not been accurate enough to adequately reflect the process of introduction of non-native fish species in Argentina during the first half of the twentieth century. In addition, the lack of internet and specific databases may also have contributed to precluding records of non-native species during the early period of studies (i.e., before 1959). Since the 1960s and particularly after the year 2000, the increase in numbers of specialized journals on biological invasions and new zoogeographic records may have contributed to the increased reports of the presence of non-native fish species in Argentina.

Although the first massive introductions of non-native species occurred at the beginning of the twentieth century, few reports document this activity, and those which do correspond to non-scientific literature.

Non-native species classification in Argentinean ecoregions

In the present study 23 non-native species (18 INV and 5 PI), were recorded, updating the last revision by Mirande and Koeber (2020), who reported 22 species but used a different classification criterion. The other 17 introduced species found in our study were not considered established in the wild. In addition, six of these 17 species were introduced for the aquarium trade, fish farms, or as part of experimental models, but have never been recorded in natural environments. Gubiani et al. (2018) reported only 11 introduced fish species in Argentina, nine of which were considered invasive in our study. Unlike this author we do not consider the Creole perch *Percichthys trucha* and the Argentinean silverside *Odontesthes bonariensis* invasive, despite both species having been widely translocated to some Argentinean ecoregions (Liotta 2005; Lopéz et al. 2008; Mirande and Koerber 2015). Specifically, *O. bonariensis* has been introduced into other Argentinean regions for aquaculture and recreational fisheries (López et al. 2008) and may become invasive in these regions, as documented for other non-native populations of these species in Brazil (see Pelicice and Agostinho 2008; Vitule et al. 2019).

Of the non-native fish species recorded in our study, 12 were salmonids that have been introduced since the beginning of the twentieth century with varying degrees of success (Baigún and Quirós 1985; Pascual et al. 2002; Menni 2004). From a total of ten species stocked between 1904 and 1930, however, only *Onchorrynchus mykiss*, *Salvelinus fontinalis*, *Salmo trutta*, *Salmo salar*, and *Salvelinus namaycush* were able to establish self-sustainable populations and spread, whereas the pink salmon *Oncorhynchus gorbuscha*, sockeye salmon *Oncorhynchus nerka*), lake whitefish *Coregonus clupeaformis,* and Arctic char *Salvelinus alpinus* failed to develop self-sustainable populations. All the established salmonids in Patagonia display resident life histories except the chinook salmon *Oncorhynchus tschawystcha*, the anadromous ecotypes of *O. mykiss,* the sea-run brown trout *S. trutta* and *Oncorhynchus kisutch* (Ciancio et al. 2015; Chalde et al. 2019).

More than a century after its first introduction, *O. mykiss* can be considered the most successful and widely distributed salmonid (Pascual et al. 2002) and, together with *S. trutta,* is widespread throughout the entire Patagonian ecoregion. Macchi and Vigliano (2014) mentioned that these species occurred in 85% and 97% of the basins where they were stocked, respectively, whereas *S. fontinalis* was found in only 42%. The great expansion of this species can be accounted for by sport fishing demands (Macchi 2004). A highly negative example of the pressure to introduce salmonids without understanding their potential impact is found in Valcheta basin, which is inhabited by the naked characin *Gymnocharacinus bergi*, a species categorized as endangered due to its extreme endemism (Cussac et al. 2016, 2020).

On the other hand, it is interesting to note that over recent decades *O. tshawytscha* has colonized several Patagonian basins after escaping from Chilean fish farms and net pens (Ciancio et al. 2005, 2015; Di Prinzio and Pascual 2008; Riva Rossi et al. 2012). Stray *Oncorhynchus kisutch* individuals have been reported in south Patagonia (Chalde and Llompart 2021). Salmonids have also been introduced outside the Patagonian region, but almost all records were related to *O. mykiss*. Regarded as the most successful invasive salmonid in Argentina, *O. mykiss* is also considered one of the most damaging non-native fish species for Argentinean aquatic ecosystems (Quiroga et al. 2017) and one of the most frequently recorded non-native fish species in Neotropical rivers (Gubiani et al. 2018). Trophic interference is probably the most significant mechanism triggered by invasive salmonids that negatively affects the native fish species (García de Leaniz et al. 2010).

Invasiveness and invasibility characteristics

Species invasiveness and ecosystem invasibility are important factors in determining invasion success (Davis 2005; Colautti et al. 2006). High biodiversity and competitive species traits in native fauna may hamper non-native species establishment (Shea and Chesson 2002; Moyle and Ellsworth 2004; Maiztegui et al. 2016). Even if environmental conditions are not suitable, propagule pressure may occasionally compensate and enable the establishment of non-native species. The ecological characteristics of Argentine ecoregions also define differences in fish assemblages and food web structures, thus accounting for potential differences in their invasiveness and invasion characteristics (Romanuk et al. 2009; Rooney and McCann 2012). The invasive success of non-native species in Argentina can be related to very different factors, similar to those of their native environment (Relva 2014): their evolutionary history, environmental tolerance throughout their life history (Fausch 2008), and ability to cope with biotic interactions (Korsu et al. 2007).

Despite high transboundary hydrological connectivity, the Lower Paraná and Lower Uruguay ecoregions present a low number of non-native species (N = 14 and 11, respectively) with respect to native species (N = 310 and 309, respectively). This could be due to the complex spatio-temporal variability of the environments of these ecoregions. In contrast, in Patagonia the low richness of native fishes (N = 15) (Baigún and Ferriz 2003), environmental stability of most aquatic environments, high propagule pressure due to recurrent stocking to satisfy angler demands, and connectivity between water bodies (Macchi and Vigliano 2014) have probably favoured the successful invasion of salmonid populations in the Patagonian basins. The successful introduction of salmonids in the Patagonia ecoregion illustrates the case of novel predators that impacted on native species due to direct predation (e.g., Macchi et al. 1999; Milano et al. 2002, 2006; Macchi et al. 2008; Vigliano et al. 2009), and trophic interference (García de Leaniz et al. 2010; Elgueta et al. 2013).

On the other hand, Baigún and Quirós (1985) proposed that species-specific thermal tolerance is the critical ecological factor determining the establishment of non-native salmonids, which explains why these species have successfully colonized some mountain sites located in warm temperate areas of Argentina. Furthermore, their success is also related to their feeding plasticity and evolutionary history, as well as the development of intensive fish farming policies on a regional scale (Mac-Donagh 1945, 1950; Baigún and Quirós 1985; Macchi and Vigliano 2014). *Cyprinus carpio* can be ranked as the species with the second broadest spatial distribution, encompassing warm temperate lotic and lentic shallow lakes and reservoirs of central Argentina (Maiztegui et al. 2016). This species was first introduced in the mid-nineteenth century for ornamental and aquaculture purposes (Baigún and Quirós, 1985), but in the early and middle twentieth century it was also stocked in several reservoirs of central and northern Argentina for commercial harvesting and recreational fishing (Baigún and Quirós, 1985). Over the last three decades its remarkable expansion seems to be associated not only with its natural dispersal capability (Stuart and Jones, 2006), but also with the construction of impoundments, channels and direct stocking (Maiztegui et al. 2016). The physiological plasticity of this cyprinid to environmental disturbance enables it to survive in a wide range of abiotic conditions (e.g., with variations in temperature, dissolved oxygen, pH, and turbidity) (Crivelli 1981, 1983; Panek 1987; Koehn 2004; Zambrano et al. 2006). It is also an omnivorous benthic consumer that can feed on a wide range of prey species, from benthic invertebrates to seeds of aquatic plants (Colautti 1997; Koehn 2004), and can inhabit either environment despite the wide range of temperatures implied (Panek 1987; Koehn 2004). Its main survival restriction is related to reproduction, as its optimum temperature for spawning is between 19 and 23 °C; reproduction does not take place at temperatures below 14 °C or above 28 °C (Swee and McCrimmon 1966; Horvath 1985; Maiztegui et al. 2016).

The Bonaerensean Drainages ecoregion offers, in turn, great hydrological variability (Serra 1994) that affects the ecological dynamics of the shallow lakes, in which at least 30 native fish species have been recorded (Colautti et al. 2015). In addition, a complex network of channels and levees developed for water regulation have promoted severe hydrological modifications, thus creating favourable conditions for carp and other generalist species (Maiztegui et al. 2016). Habitat alterations generated by the building of structures for water management have also been identified as facilitators of *C. carpio* recruitment in other countries (Bice and Zampatti, 2011) and have probably facilitated its rapid spread in several ecoregions of Argentina, including the north of Patagonia (Alvear et al. 2007; Maiztegui et al. 2016) (Table 3).

The Amazonian *Cichla kelberi* is one non-native fish species of great concern. It was recorded as introduced but not established in the wild, and is apparently available for aquariums through online sales. Neme (2017), however, mentioned *C. kelberi* as an introduced species (present in nature) in Argentina, and Casciotta et al. (2016), reported this species in the Iguassu river, but only within Brazilian territory and not yet in the Argentinean sector. Resende et al. (2008) reported that following the establishment in 2004 of *Cichla piquiti* (another Amazonian peacock bass species reported in our study as introduced but not yet established) on the left riverbank of the Paraguay river, in the Pantanal, the next year a few specimens were detected on the right riverbank. These species also exhibit high invasive potential due to their reproductive strategy (e.g., laying more than one group of eggs in a reproductive period, parental care of the eggs and young), becoming dominant in the environments where they become established (Espínola et al. 2010; Santos et al. 2016). Both cichlid species are very aggressive piscivores, and if established in rivers in the northwest of the territory, they could cause a mayor reduction in species diversity due to the high degree of native endemism in these rivers (Espínola et al. 2010). In ecosystems where these species were introduced, they have caused serious ecological damage (Resende et al. 2008; Pelicice and Agostinho 2009; Franco et al. 2021). In particular, the Iguassu river basin has been exposed to recurring invasions of non-native species due to multiple and non-mutually exclusive pathways, such as fish farm escapes, intentional species transference between different basins for sport fishing purposes, crossbreeding between related species, and their use as live bait for fishing (Baumgartner et al. 2012). Other introduced species of the Cichlid family, such as the redbreast tilapia *Coptodon rendalli,* the eartheaters *Geophagus brasiliensis* and *Geophagus sveni*, and *Oreochromis niloticus* (See Fig. 3) deserve attention because of their high risk of becoming invasive across several ecoregions of Argentina, due to biological characteristics also shared by *C. kelberi* and *C. piquiti.*

Some considerations regarding fish invasion in Argentina

In the context of climate change (Li et al. 2016) and due to its large north–south latitudinal range, Argentina is potentially vulnerable to the invasion of species from different climates, as demonstrated by the differences between the northern and southern sets of invaders. Policies for preserving native fauna must consider this a 'double' risk. In the colder southern portions of Argentina, increasing water temperatures due to climate change could further intensify the risk of invasion by thermophilic species, as recently suggested for invasive invertebrates (Hesselschwerdt and Wantzen 2018) and fishes of Amazonian origin (Lopes et al. 2017). The temperature increase predicted for Patagonia would reduce the natural distribution of salmonids, particularly in North Patagonia (Cussac et al. 2009; Becker et al. 2018), affect their recreational fisheries (Winfield et al. 2016), and promote the extinction of populations inhabiting other ecoregions with water temperatures close to their upper tolerance limit. On the other hand, the increase in temperature predicted for the La Plata Basin (Barros et al. 2005) would cause a shift in thermal barriers towards the south of the basin, creating favourable conditions for the establishment of more non-native Neotropical species (Lopes et al. 2017).

Geographical connectivity may also play a critical role in increasing the dispersal risk of species introduced for sport and recreational fishing purposes. In the warmer northern portions of Argentina, for instance, the free-flowing (i.e., undammed) Paraguay-Parana corridor still exhibits natural connectivity (Baigún and Minotti 2021) that could facilitate the dispersion of stocked species. Considering the increase in the number of farms of non-native species in neighbouring countries and the growing pressure of sport fishing, the number of non-native fishes in Argentina is probably higher and their distribution wider than currently known. Escapes from netted tanks placed in Brazilian reservoirs could thus cause significant ecological damage to the native aquatic biodiversity of neighbouring countries, such as Argentina, Paraguay, and Uruguay. Fish species escaping from farms or being released for sport fishing purposes in reservoirs of the upper Paraná and Iguassu river basins (both in Brazil) should be considered prime candidates for further introduction and/or invasions in Argentina (Espínola et al. 2010, 2016). A real case study of these predictions is the reported captures in April 2007 and February 2021 of the cachama *Colossoma macropomum* from the Argentinian stretch of the Paraná River. This species has been introduced for fish farming into most of the Brazilian basins (Barçante and Sousa 2015). It was first recorded in Argentina in the vicinity of the Yacyreta dam in 2007 (Aquahoy 2007) and the second report was in the city of Esquina, Corrientes province, located downstream of the Paraná-Paraguay confluence and 574 km downstream of Yacyreta (Espínola comm. per.). It is expected that this situation will be repeated, or even increase, because the Brazilian government has withdrawn or eased most of the environmental regulatory norms that applied to fish farms with non-native fish species (Thomaz et al. 2020). The current policy facilitates new introductions of non-native fish into Brazilian dams for novel aquaculture projects (Dias et al. 2021). The invasion of fish species through escapes from neighbouring countries may also have a permanent critical impact on the native fish fauna of the Argentinean reaches of the Iguassu River, due to the high level of endemism in this region (Espínola et al. 2010). These impacts include biotic homogenization (Rahel 2002; Vitule et al. 2012), native community restructuring, species extirpation and extinction (Zaret and Pine 1973; David et al. 2017), and disease and parasite propagation (Reading et al. 2011; Lymbery et al. 2014). Management plans are thus necessary for early detection of non-native species in transboundary basins, in order to reduce the potential establishment and spread of these invaders throughout Argentinean water bodies.

In addition, it is critical that the Argentine Ministry of Environment and Sustainable Development (MAyDS) begin to consider the presence of non-native fish species as a relevant issue, to ensure the protection of native biodiversity. Current regulations at provincial and national levels are apparently insufficient to control species introduction, which may be fostered by provincial policies that have the authority to manage their own natural resources, often in questionable ways. As a consequence, policies may differ within river basins and among provincial management agencies.

Our extensive literature review, based on both scientific and technical information, revealed that the introduction of non-native fish species into Argentina has increased over recent decades, currently totalling 18 invasive and 5 potentially invasive species. Furthermore, the most common invasive fish species, such as the salmonids, have expanded their geographical range. This is due to an aggressive stocking initiative in the ecoregions outside Patagonia, fostered by angler organizations and fisheries development programmes that were, surprisingly, never evaluated. Other successful species such as carps have been favoured by an increase in water use (water extraction, livestock, and agriculture) and infrastructure development. However, the total number of non-native species in Argentina appears low compared with other South American countries. This may be due to several non-mutually exclusive factors, such as the low number of publications dealing with biological invasions in the country, the high level of environmental diversity in Argentina, the complexity of the Argentine hydrographic network, and the high native species richness in some ecoregions that prevents non-native species from becoming established and spreading.

Our review of the historical success and failure of introduced fish species in Argentina suggests that aquaculture, recreational fishing, biological control, and to a lesser extent, the aquarium trade and use of species as biological models were the main vectors of introduction of non-native freshwater fishes. Even though the ecological damage that can be caused by the introduction of freshwater fishes is widely known, the evaluation and control of species introductions in Argentina are still inadequate. Most scientific information has been gathered from salmonid introduction into Patagonia, but little is known about other ecoregions, and particularly about new species entering through the La Plata basin. In-depth information on non-native fish species distribution should be complemented by information from specific fishing websites and fisheries magazines. This type of source is currently underused and underestimated, but for certain regions of the country probably represents the best source of information available for the detection of new introductions in progress. There is a need to foster studies and promote innovative research projects oriented toward tracking the effects of non-native fish introduction and establishment, in order to improve our knowledge of the risks and impact on native biodiversity. This kind of information may be crucial to prevent further introductions into the last remaining pristine, as yet uninvaded, environments of Argentina, and to aid the recovery of native populations. Even if the cost is high, programmes of non-native species extirpation or control should be applied in highly valuable aquatic ecosystems where native species are at risk of extinction.

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Authors' contribution LAE, APR, CB and LNS conceptualized and led this study; LAE, NC and EMCF carried out the bibliographic research and wrote the first version of this manuscript; EA, FY, MCMB and KM provided useful insight into the structuring of the manuscript. All authors contributed and approved the final version of this letter.

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Declarations

Conflict of interest The authors declare no competing interests. I declare that all co-authors are aware and agree with the submission.

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