Knowledge gaps in economic costs of invasive alien fish worldwide

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Running head: Costs of fish invasions

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Highlights:

- Invasive alien fish species have cost at least $37.08 billion globally since 1960s
- Annual costs increased from < $0.01 million in the 1960s to $1 billion since 2000
- Reported costs are unevenly distributed, with a bias towards North America
- Impacts are less reported than other taxa based on research effort
- Gaps in available data indicate underestimation and a need to improve cost reporting

Abstract

Invasive alien fishes have had pernicious ecological and economic impacts on both aquatic ecosystems and human societies. However, a comprehensive and collective assessment of their monetary costs is still lacking. We reviewed reported data on the economic impacts of invasive alien fishes using InvaCost, the most comprehensive global database of invasion costs, and analysed how total (i.e. observed and potential/predicted) and observed (i.e. empirically incurred) costs of fish invasions are distributed geographically and temporally and assessed which socioeconomic sectors are most affected. Fish invasions have potentially caused the economic loss of at least US$37.08 billion globally, from just 27 reported species. North America reported the highest costs (>85% of the total economic loss), followed by Europe, Oceania and Asia, with no costs yet reported from Africa or South America. Only 6.6% of the total reported costs were from invasive alien marine fish. Costs that were observed amounted to US$2.28 billion (6.1% of total costs), indicating that costs of damages caused by invasive alien fishes are often extrapolated and/or difficult to quantify. Most of the observed costs were related to damage and resource losses (89%). Observed costs mainly affected public and social welfare (63%), with the remainder borne by fisheries, authorities and stakeholders through management actions, environmental, and mixed sectors. Total costs have increased significantly over time, from <US$0.01 million/year in the 1960s to over US$1 billion/year in the 2000s, and observed costs have followed a similar trajectory. Despite the growing body of work on fish invasions, information on costs has been much less than expected, given the overall number of invasive alien fish species documented and the high costs of the few cases reported. Both invasions and their economic costs are increasing, exacerbating the need for improved cost reporting across socioeconomic sectors and geographic regions, for more effective management.

Keywords: biodiversity conservation; fisheries; InvaCost; marine and freshwater; non-native species; socio-economic damages

Introduction

Invasive alien fish introductions are increasing in number globally (Leprieur et al., 2008; Avlijaš et al., 2018). In turn, the drivers of these invasions are also rising (Turbelin et al., 2017; Zieritz et al., 2017), with the potential to intensify future impacts. In particular, the increase in anthropogenic activities, especially in emerging market economies, is expected to facilitate new introductions of invasive alien fish species and subsequent invasions through pathways such as tourism, trade (e.g. aquaculture and aquarium trade) and infrastructure development (e.g. waterways/channel construction) (Hulme, 2015; Haubrock et al., 2021a).

Ecological impacts of invasive alien fishes (Cucherousset & Olden, 2011) include the displacement and extinction of native species (Mills et al., 2004; Haubrock et al., 2018), alteration of trophic interactions (Martin et al., 2010; Cuthbert et al., 2018; Haubrock et al., 2019), and disruption of ecosystem functioning (Capps & Flecker, 2013). Invasive alien fish can also transmit new pathogens (Gozlan et al., 2005; Waicheim et al., 2014; Boonthai et al., 2017; Ercan et al., 2019) and threaten native species' genetic diversity through hybridization (Oliveira et al., 2006; Gunnell et al., 2007). However, despite evidence for increasing numbers of fish invasions worldwide and their growing ecological impacts (Leprieur et al., 2008; Seebens et al., 2020; Raick et al., 2020), their economic impacts remain poorly understood, largely due to a lack of data for numerous sectors and difficulties in monetizing ecological impacts. This paucity of cost data has led to debate among scientists about previous estimates of invasion costs (Cuthbert et al., 2020), which have often relied on over-extrapolation and presented untraceable sources. In the context of fisheries, this could involve projecting costs from local scales to entire fisheries.

This lack of knowledge of costs of invasive alien fish, in turn, hampers decision-making and severely limits the ability of policymakers to design cost-effective management strategies (Britton et al., 2010; Hyytiäinen et al., 2013). In cases where invasive alien fish populations may have a positive value, understanding the trade-offs and designing socially optimal management are also hampered by the lack of cost data. Examples of such positive values include invasive alien fishes with commercial benefits (Gollasch & Leppäkoski, 1999), aesthetic and/or cultural values associated with recreational uses (Downing et al., 2013, Schlaepfer et al., 2011, Katsanevakis et al., 2014, Gozlan 2015, 2016), or other perceived ecosystem benefits (Gozlan, 2008; Pejchar & Mooney, 2009; Britton & Orsi, 2012).

Despite the potential benefits of some taxa, recent works have highlighted the increasing negative economic impacts of invasive alien species globally (Bradshaw et al., 2016), with economic costs of invasions exceeding US$1.2 trillion in recent decades across all habitat types (Diagne et al., 2021). In a first global synthesis of the cost of aquatic invasive alien species, impacts have reached $345 billion worldwide, which is likely an underestimate given that impacts of aquatic invasions are generally under-represented compared to terrestrial taxa. That is because their costs are lower than expected based on numbers of alien species between those habitats (Cuthbert et al., 2021). Further, Cuthbert et al. (2021) found that the ruffe *Gymnocephalus cernua* was the second most costly invasive aquatic taxon in the world, considering total costs which include predictions and extrapolationsIn addition, significant gaps in reporting on the costs of aquatic invasions were found in Asia and Africa, with many countries reporting no invasion costs, despite the presence of known harmful invasive alien species (Cuthbert et al., 2021). While the increasing economic impacts of aquatic invasions are alarming, there remain knowledge gaps at more granular scales regarding the specific nature of impacts of key taxonomic groups, such as fish, which must be filled to fully understand biases and inform taxon-specific management (Haubrock et al., 2021b; Cuthbert et al., 2021; Kouba et al., 2021).

Following recent advances addressing costs of invasive alien species at different regional scales (Bradshaw et al., 2021; Crystal-Ornelas et al., 2021; Haubrock et al., 2021c; Kourantidou et al., 2021; Liu et al., 2021) and across taxonomic groups (Cuthbert et al., 2021), we aim to better understand costs of fish invasions. To provide a necessary baseline for the economic impact of this taxon, we have therefore characterised, for the first time, the current status of knowledge on the global costs of invasive alien fishes using the InvaCost database (Diagne et al., 2020a). This database contains detailed information on reported costs (e.g. types of costs, sectors affected, regional attributes, reliability of cost estimates, etc.) over the last 60 years, associated with ~ 1000 invasive alien species from all ecosystem types worldwide (i.e. impacts occurring outside their native range). Invasive alien species included in the InvaCost database are thus those that spread outside of their geographic range of origin (Blackburn et al., 2011) and have a negative economic impact that was quantified in monetary terms. Our aims were to describe the reported global costs associated with invasive alien fish species, to explore the structure of these costs, and to identify gaps and potential biases in the estimation of past and current economic impacts.

Methods

Cost data sourcing and filtering

To estimate the cost of fish invasions reported globally, we considered cost data from the latest version of the InvaCost database (version 4.0, https://doi.org/10.6084/m9.figshare.12668570; released in June 2021). This version of the database compiles 13,123 cost entries reported from both English and non-English sources in a sufficiently detailed manner to allow a large-scale synthesis of the costs associated with invasive alien species at different spatial, taxonomic and temporal scales (Diagne et al., 2020a; Angulo et al., 2021). These cost data were primarily retrieved using a series of search strings entered into the Web of Science platform (https://webofknowledge.com/), Google

Scholar database (https://scholar.google.com/) and the Google search engine (https://www.google.com/) to identify and collate relevant references on invasion costs. Local stakeholders and experts on invasions were also contacted as part of the search process. All references were thoroughly evaluated to identify their relevance and to extract information on costs. In the invasive alien species literature, there is a wide variety of costing practices which have an associated risk of misunderstandings and causing discrepancies among reported costs (Diagne et al., 2021). These may include, for example, differences in discounting across studies or in cost estimation methodologies. Despite the obvious challenges of standardizing heterogeneous costs, InvaCost is the most comprehensive database on the economic costs of IAS that has largely succeeded in resolving the problems associated with standardisation over time and across countries where they have been reported (Diagne et al., 2020b). In addition, this database is public and regularly updated with either corrections if mistakes are detected and/or new data as they become available. With regard to monetary units, all costs published in the literature and included in the database were converted to 2017 US$ values (see Diagne et al., 2020a and Supplementary Material 1 for detailed information). The database used for this analysis includes information on monetary costs across taxonomic, regional and sectoral descriptors, and allows for a distinction between *observed* (i.e. costs of a realized impact) and *potential* costs (i.e. costs of a predicted/expected impact over time within or beyond the actual distribution area of the IAS). It also allows for a classification based on the reliability of the source and the methodologies used for the cost estimates (*high* or *low* reliability, with *high* implying that the source is from pre-assessed material such as peer-reviewed articles and official reports or from grey material but with documented, repeatable and traceable methods, and with *low* referring to all other estimates).

We filtered the InvaCost database to retain costs related to fishes belonging to the classes Cephalaspidomorphi and Actinopterygii; these were the only fish taxa in the database with reported costs, but also included an entry listed as “Osteichthyes” (see Pimentel et al., 2000).

Because the available information did not allow us to distinguish this entry among ray-finned fish (Actinopterygii) and lobe-finned fish (Sarcopterygii), it was kept as a "diverse" entry. In total, we identified 177 entries, from which 7 were excluded as no starting and / or ending year for the listed costs could be identified. After expansion, these entries resulted in 384 annualized cost entries (see expansion process below). Cost entries that were not attributable to single species, sectors or cost types within these classes were classified as "Diverse/Unspecified". All analyses were conducted for the period between 1960 to 2020, as (i) monetary exchange rates prior to 1960 were not available, and (ii) 2020 was the last year for which cost data were available in the database. The final dataset used for the analysis is provided in Supplementary Material 2.

Global cost descriptions

In order to describe the costs of invasive alien fish over time, we used the *expandYearlyCosts* function of the 'invacost' package (v0.3-4; Leroy et al., 2020) in R version 4.0.2 (R Core Team, 2020). This function facilitates consideration of the temporal dimensions of the data, with the estimated costs per year being expanded over time according to the length of time over which they occurred or were expected to have occurred (i.e. the length of time between the *Probable_starting_year_adjusted* and *Probable_ending_year_adjusted* columns). In order to obtain a comparable cumulative total cost for each estimate over the period during which costs were incurred for each invasion, we multiplied each annual estimate by the respective duration (in years). The analyses were therefore conducted on the basis of these 'expanded' entries to reflect the likely duration of the costs as reported in each study analysed. This means that costs covering several years (e.g. US$10 million between 2001 and 2010) are divided according to their duration (i.e. US$1 million for each year between 2001 and 2010). Finally, the cumulative costs of the invasion were estimated based on their classification in the following cost descriptors (i.e. columns) included in the database (Supplementary Material 1):

(i) Method_reliability: indicating the perceived reliability of cost estimates based on the publication type and estimation method. Costs are considered to be of *low* reliability in those cases where they were derived from grey literature and/or are lacking documented, repeatable or traceable methods. On the contrary, costs are considered of *high* reliability if they come from peer-reviewed articles, official documents, or grey literature but with a fully documented, repeatable and traceable method (Diagne et al., 2020a). While we acknowledge that this binary classification does not capture the widely varying methodologies of underlying studies, it provides a practical, reproducible and objective means of cost assessment and filtering;

(ii) Implementation: whether the cost estimate was actually incurred in the invaded area (*observed*; e.g. a cost directly incurred from investment in managing an invasive alien fish population, or an invasion-driven decline in a native fishery that resulted in a realised loss of income) or whether it was extrapolated or predicted over time within or beyond the actual distribution area of the IAS (*potential*), and thus not empirically incurred (Diagne et al., 2020a; see Supplementary Material 1). We emphasize that costs were compiled in InvaCost based on the information in each cost document (i.e. we did not extrapolate or predict cost estimates independently here, and simply compiled reported costs). For example, *potential* costs may include estimated reductions in fisheries income because of an invasion (Scheibel et al., 2016), known local costs that are extrapolated to a larger system than the one they occur in (Oreska and Aldridge, 2011), and costs extrapolated over several years based on estimates from a shorter period (Leigh, 1998).

(iii) Geographic_region: description of the continental geographic location of the cost;

(iv) Type_of_cost_merged: grouping of costs into categories: (i) "*Damage*" referring to damages or loss incurred by the invasion (i.e. costs of repairing damage, losses of

resources, medical care), (ii) "*Management*" including expenditure related to control (i.e. surveillance, prevention, management, eradication), (iii) and "*Mixed*" including mixed cost of damage and control (cases where the reported costs were not clearly distinguishable);

(v) Impacted_sector: the activity, societal or market sector that was affected by the cost. Seven sectors are described in the database: *agriculture*, *authorities-stakeholders* (official structures allocating efforts to manage biological invasions), *environment*, *fishery*, *forestry*, *health*, and *public and social welfare* (Diagne et al., 2020a; see Supplementary Material 1).

Temporal cost accumulations

To assess temporal trends of invasive alien fish species, we considered 10-year averages since 1960. We examined the costs in terms of the *year of impact*, which reflects the time at which the invasion cost likely occurred and extended it over years in which the costs were realised using the *summarizeCost*s function of the 'invacost' R package (using the *Probable_starting_year_adjusted* and *Probable_ending_year_adjusted* columns; see Leroy et al., 2020). This allowed the estimation of average annual costs over the whole period considered, as well as over decadal increments, for both *observed* and *potential* costs.

Comparison with other taxonomic groups

In order to put the costs of invasive alien fish species in a broader taxonomic perspective, we compared the economic costs of invasive alien fish with other invasive vertebrates: birds and mammals. The comparison was based on the total cost and the number of documents reporting costs in the InvaCost database, coupled with the number of invasive alien species per taxon, and the numbers of scientific publications in the field of invasion science. First, total monetary costs and number of entries for birds and mammals were calculated following the same methods and database version as for fishes (as detailed above). Secondly, we estimated the number of publications available for each group using the same search protocol as for the InvaCost database (see Diagne et al., 2020a), excluding words referring to costs and adding the name of the biotic group (i.e. "fish", "mammal", or "bird"), in order to obtain a comparative approximation of the research effort in invasion ecology for these three taxa. The exact search strings used can be found in Supplementary Material 3. The information considered in this comparison was collected using the Web of Science Core collection. Thirdly, the numbers of alien species for each of the three taxonomic groups mentioned above was estimated using the IUCN Red List database (https://www.iucnredlist.org/). We classified a species as alien according to the IUCN legends of the countries where they occur. If a species is considered as introduced in at least one country, then we consider this species as alien. Finally, we used Pearson's Chi-squared test of independence to assess whether the data for the three taxonomic groups had the same distribution of values (number of alien species, number of cost entries, number of studies reporting invasion costs, and total costs).

Results

A total of 384 annualized cost entries for 27 invasive alien species belonging to 18 fish families were available in the database, totalling US$37.08 billion. The majority of costs was deemed as potential (US$34.79 billion; n = 88, hereafter the number of cost entries), while observed costs amounted to only US$2.28 billion ($n$ = 296). Furthermore, the majority of costs (US$25.31 billion; n = 295) were considered of high reliability, while US$11.77 billion ($n$ = 89) were considered of low reliability (Supplementary Material 4).

Costs across regions and taxa

North America was the region with the highest reported economic costs of invasive alien fish species, followed by Europe, Oceania , Asia and Central America (Figure 1). Costs inferred from polar regions (e.g. French Southern and Antarctic Lands) were below US$ 1 million (no costs for invasive alien fish were reported for Arctic regions).

When considering only observed costs, the costs of invasive alien fish in North America (*n* = 46), were again about 10 times higher than observed costs recorded in Oceania (*n* = 12), and over 60 times higher than costs in Asia (*n* = 59; Figure 2). Reported observed costs were attributed to several species in North America, Europe and Asia, but were least diverse in Central America, Oceania and polar regions (Figure 2) (note that these do not include taxa at coarser groupings than species level).

The Actinopterygii class included 26 invasive alien fish species with reported costs (US$34.26 billion). The class Cephalasdomorphi, on the other hand, included only one species, the sea lamprey *P. marinus* (US$1.39 billion in North America) (Table 1). Observed costs listed for the class Osteichthyes (i.e. bony fish; US$1.42 billion) were deemed diverse, as this cost entry could not be assigned to a lower taxonomic level (see Pimentel et al., 2000 for details). Globally, the ruffe *G. cernua* was the costliest species, followed by the topmouth gudgeon *Pseudorasbora parva*, the sea lamprey *P. marinus*, the common carp *Cyprinus carpio*, the red lionfish *Pterois volitans*, unspecific species belonging to *Tilapia* sp., the silver-cheeked toadfish *Lagocephalus sceleratu*s, the black bass *Micropterus salmoides*, white bass *Morone chrysops* , the brown trout *Salmo trutta*, and common minnow *Phoxinus phoxinus* (Table 1). All other species contributed less than US$ 1 million (Table 1).

Considering total costs (*potential* and *observed*) inferred in North America, the ruffe *G. cernua* was the costliest species (US$28.93 billion), followed by *P. marinus* (US$1.39 billion), white bass *M. chrysops* (US$3.39 million) and brown trout *S. trutta* (US$1.78 million). All other species, such as the northern pike *Esox lucius* and the northern snakehead *Channa argus*, contributed less than US$1 million.

Considering only observed costs globally, *P. marinus* was the costliest species, followed *by C. carpio*, *P. volitans*, *Tilapia* sp., *L. sceleratus*, *M. salmoides*, *M. chrysops*, *S.*

trutta, and *P. phoxinus* (Table 1). All other species contributed up to US$1 million (Table 1; Figure 2). Observed costs of *P. marinu*s, *S. trutta* and *M. chrysops* were only reported in North America.

Cost types and impacted sectors

Costs related to damages and resource losses represented approximately 89% of the observed cost (*n* = 96; Figure 3). Costs associated with management (i.e. control, detection and eradication costs) were an order of magnitude lower, despite having more entries (*n* = 196), while mixed costs amounted to less than US$1 million (*n* = 4) (Figure 3). In North America, most of the observed cost (US$1.77 billion) was attributed to damages and losses, with the remaining US$231.16 million (11.5%) classified as management costs.

Considering observed costs, public and social welfare was the most affected sector , followed by costs to fisheries, authorities and stakeholders, the environment and mixed sectors (Figure 3). Inferring only observed costs to impacted sectors in North America, the distribution of costs across sectors was similar, with public and social welfare (US$1.44 billion) predominantly impacted, followed by fisheries (US$349.81 million), authorities and stakeholders (US$208.70 million), and mixed sectors (US$3.27 million).

Temporal cost accumulations

In total, costs averaged to US$607.78 million per year between 1960 and 2020 (Figure 4), with a strong increase from < US$0.01 million per year in the 1960s to US$603.08 million per year in the 1980s, before surpassing US$1 billion by the 2010s. Observed costs averaged to US$37.43 million per year between 1960 and 2020. Annual observed costs first increased from < US$0.01 million in the 1960s to US$159.96 million per year in the 2000s, then decreased after 2010 to US$7.27 million per year. It should be noted, however, that time lags (i.e. between the occurrence of costs and official reporting) were not accounted for in the last decade (2010 – 2020), and thus cost estimates are therefore likely to be more underestimated in recent years.

Comparisons across biotic groups

Records for alien fishes from the IUCN Red List database (n = 147, hereafter the number of species) were 30% fewer than recorded alien birds (n = 210) and 39% more than recorded alien mammals (n = 106). Conversely, fishes were the taxonomic group with the highest number of scientific publications on alien species (17,864 papers), about twice the number of publications on birds (8,759) and four times the number on mammals (4,880) (Figure 5). Nevertheless, invasive alien fish species had the lowest number of unique references reporting costs in the InvaCost database (55) compared to mammals (378) and birds (64). In turn, the total cost of invasive alien fish species (US$37.08 billion) was much lower than that of mammals (US$ 424.56 billion), but higher than that of birds (US$7.52 billion). The distribution of values for each biotic group thus differed significantly (fish *vs.* birds: $\chi 2$ = 2738, df = 3, $p < 0.001$; fish *vs.* mammals: $\chi 2$ = 100,000, df = 3, p < 0.001; Figure 5), with costs and inputs for fish disproportionately lower than expected based on the number of studies and alien species.

Discussion

The total economic cost of invasive alien fishes was US$37.08 billion globally, from just 27 species with reported cost data. These costs are the result of reported/published estimates only which, because of the lack of reported costs in several regions (i.e. Africa and South America) and for several species, suggest that the overall cost estimate is significantly underestimated compared to the actual costs.

The reported observed costs are, in fact, very few and are mainly based on damages and resource losses to fisheries, as well as on the costs of large-scale management interventions. For example, the cost of the Eurasian ruffe invasion *(G. cernua),* which accounts for a significant portion of the total cost of invasive alien fish in North America, was extrapolated from population density estimates in Lake Superior to the types of impacts it could have if it were to spread more widely in the Great Lakes basin, resulting in economic costs (potentially reaching US$500 million by 2050) by impacting recreational fisheries and causing a decline in yellow perch (*Perca flavescens*) populations. This resulted in an estimate of US$13.6 million for a two-year control program and US$119 million to US$1.05 billion in benefits from control programmes for recreational and commercial fisheries over a 50-year time period (Lovell et al., 2006). However, because these estimated economic costs have not yet been confirmed, the limited information available on the socio-economic impacts of *G. cernua* in the Great Lakes precludes an adequate assessment of economic cost. Nevertheless, it is possible that these potential costs were not overestimated, but rather that the expected impact was mitigated by management, suggesting that the extrapolation may have been robust (and useful) at the time it was made. Other harmful invasive alien fish, such as Asian carp species in the Mississippi River basin, have no current cost estimates, despite the expectation of potential future economic and ecological costs large enough to require the expenditure of US$831 million to try to prevent spread in the Great Lakes (USACE, 2018).

We also showed that the costs of invasive alien fish were significantly lower compared to birds and mammals and the research effort devoted to them. This could be due to a perception bias where damage to habitats or aquatic communities goes unnoticed by the public and authorities because of the difficulties in timely detecting fish invasions compared to other taxa. At the same time, the introduction of aquatic species has often been seen as beneficial to some local communities, especially those engaged in harvesting, processing or recreational tourism (Selge et al., 2011), which leads to a risk of ignoring the negative impacts of the invasion. Invasive alien fish have diverse impacts on ecosystems and understanding their indirect effects will benefit from advances in non-market valuation methods to infer the full range of their impacts (e.g. decline of native species, displacement, extinctions, disease, etc.) (Hanley and Roberts, 2019). Compared to mammals and birds, fish invasions and their vectors of introduction are well studied, with a high number of publications in the natural sciences and reports on the number of invasive alien species (Semmens et al., 2004; Castellanos-Galindo et al., 2020). The low number of reported costs for fish invasions, despite this wealth of literature documenting their presence, likely reflects the difficulties in quantifying their costs and possibly in some cases the fact that certain fish have a long history of intentional introductions (Gozlan, 2008).

Taxonomic, regional and environmental biases

In total, economic costs were available for only 27 out of the more than 147 invasive alien fish species worldwide (IUCN, 204 according to FishBase (Froese and Pauly, 2019), with some highly invasive and impactful fish species being completely absent. For example, observed costs have not been reported for the Chinese or Amur sleeper (*P. glenii)* in Europe, although it is a known vector of parasites (Reshetnikov & Sokolov, 2011; Kvach et al., 2013) which may have an important impact on the aquaculture sector (Ondračková et al., 2012).

Documented costs of invasive alien fish species also show marked regional disparities, with the majority of reported costs attributed to North America and significantly lower costs reported elsewhere. These regional disparities are not only reflected in the massive differences in costs, but also in the spatial scale of their reporting; a higher proportion of costs in North America were reported at the national level (89 %) compared to costs at the regional (1 %) or local level (10%). These large-scale estimates likely increase the magnitude of reported costs and underscore the need for large-scale estimates outside North America. Despite the fact that a number of fish species have been intentionally introduced to meet the rapidly increasing demand for farmed fish (Lin et al., 2015; Xiong et al., 2015; Grosholz et al., 2015; Zhao et al., 2015; Gozlan 2016), costs of only five invasive alien fish species have been reported in Asia. This is amidst evidence that multiple introduced fish species escape from aquaculture facilities or are released into the wild (Marchetti et al., 2004; Saba et al., 2021). Similarly, the total lack of reporting on the costs of fish invasions in South America and Africa is surprising given the multiple high-profile examples of fish invasions on these continents. For example, in parts of South America (e.g. northern Bolivia), the introduction of *Arapaima gigas* has had serious environmental impacts and is aggressively replacing commercially valuable native fisheries (although *A. gigas* is also fished commercially) (Miranda-Chumacero et al., 2012; Liu et al., 2017; Ju et al., 2019). In East Africa, although the introduction of Nile perch has increased commercial fishing yields, stimulated fish processing and generated income from recreational tourism, it has also had negative effects on local communities by displacing small-scale fishermen and increasing food insecurity and health problems around Lake Victoria (Abila, 2000; Yongo et al., 2005; Aloo et al., 2017). The invasion has also altered the ecological community composition and food web of the lake (Witte et al., 2013), reducing water quality and causing the extinction of around 200 native species (many of them endemic), resulting in one of the largest anthropogenic ecosystem changes ever recorded (Ligtvoet et al., 1991; Kaufman, 1992; Mugidde et al., 2005).

With respect to the large difference in costs between North America and Europe, one possible contributing factor worth considering is that the fauna of the Western Palearctic is depleted due to glaciations (Oberdorff et al., 1997). While Nearctic fish faunas were less impacted by glaciations and remained relatively diverse, most fish species in European rivers were intentionally introduced or colonized as a result of anthropogenic activities e.g., the Danube (Levêque et al., 2007). Therefore, invasions in Europe might have an impact, at best, on a limited number of freshwater fishes (or might even have been economically beneficial historically), whereas invasions in North America would necessarily have an impact on a larger number of native species (Levêque et al., 2007). Therefore, compared to other regions, higher costs may also result from the economic importance of the respective freshwater fisheries, which are much more developed in North America than in Europe (e.g. especially for recreational activities such as angling and boating; Franklin, 1998; Mordue 2009). Another potential bias may exist with respect to the regional variation in the number of researchers and institutions studying the impacts of invasive alien fish. That is, that a disproportionately large number of North American researchers may be studying invasive alien fish. This may explain the relatively large investment in management efforts in North America (e.g. for sea lampreys; Stewart et al., 2003; Twohey et al., 2003). Nevertheless, the discrepancies in invasive alien fish costs between North America and Europe cannot be fully explained by differences in economic activity or severity of impacts triggered by invasions. It is also often unclear whether management of invasive populations is driven by ecological or economic rationale between these regions or elsewhere, and InvaCost does not record this information.

In contrast to freshwater fish invasions, very few costs are associated with invasive alien marine fish species (Anton et al., 2019, 2020). This is notable given their well-known impacts on marine ecosystems (i.e. on habitat or other native species via competition for food) and on spatially-overlapping commercial fisheries for native species (i.e. costs incurred by bycatch, gear damage, injury, increased fuel consumption to reach invasive-free areas, etc.). Key examples include the angelfish *Pomacanthus* sp. (Semmens et al., 2004), the round herring *Etrumeus golanii* (Galil et al., 2019), the rabbitfish *Siganus rivulatus* and *S. luridus*, the pufferfish *L. sceleratus* in the Mediterranean (Kalogirou et al., 2013; Giakoumi, 2014) and the lionfish *P. miles* (Moonsammy et al., 2011). We think that the low number of entries in the database for marine fish, and for fishes in general, reflect limited knowledge of the costs being incurred, rather than their absence.

Conservative nature of reported costs

Considering the biases described above, the cost estimates presented here are likely to be very conservative, as cost data are scarce for most invasive alien fish species and for most regions of the world (see also Diagne et al., 2021 for an overview of the reasons for cost underestimation). A limited understanding of the costs of invasive alien fish is likely to hamper effective communication, investments in detection, control, prevention and management, and relegate them to the bottom of the priority list of policy makers and/or resource managers facing budgetary constraints. This is despite the fact that much of the funding used to manage invasive alien fish in North America comes directly from angling licence sales and taxes on fishing gear and boat fuel, and was therefore not reported or tracked in InvaCost. For example, in 2011, anglers in freshwater ecosystems in the US generated more than US$40 billion in retail sales, with an estimated total economic impact of US$115 billion and more than 800,000 jobs (Hughes, 2015). Although not reflected in our results for the costs of invasive marine fish, the expenditure of marine anglers is also substantial ($31 billion in 2012), as is the economic impact (US$82 billion and 500,000 jobs in 2012) (Hughes, 2015). Of course, most of these species are not invasive, but since some of them are, it contributes to the difficulty of comparing costs and benefits of invasive alien fishes.

In addition, many of the costs associated with research activities seeking to advance knowledge of invasive alien fish, controlling their populations and mitigating their impacts are generally unreported or inaccessible in the public domain, resulting in an underestimation of investment in relevant research. This is an important driver of limitations inherent in the InvaCost database. Firstly, the monetary costs recorded in InvaCost were largely based on a systematic use of research terms (Diagne et al., 2020a), however, different studies and parties use different terminology to describe invasive alien species. As a result, costs may have been missed in these searches given the pervasive differences in keywords across cost reporting documents. Another similar reason is the fact that some source documents may use the vernacular names that were not considered in the search strings. Additionally, despite the effort to include literature in multiple languages (15 additional non-English languages in InvaCost searches, see Angulo et al., 2021), it has not been possible to cover all languages that may be reporting costs for invasive alien fish globally. This may have exacerbated perceived knowledge gaps in Asia and Africa in particular for which the linguistic coverage was limited. InvaCost is further limited in that only impacts that can be readily monetised are included, resulting in the omission of potential impacts assessed via other measures and metrics, or that are non-market in nature. Furthermore, the methods used to quantify these impacts differ considerably among studies — and although InvaCost uses an objective binary classification for reliability and implementation of the method as a standardised repository for reported costs — it has not been possible to fully account for the variable methodological nature of the underlying studies. The costs in InvaCost therefore directly reflect those reported in the underlying studies, and are subject to their respective potential criticisms. It is important to stress that many of these aforementioned limitations likely make our results substantial underestimates. Considering that InvaCost is a living database meant to be updated on an ongoing basis by authors and future users (Diagne et al., 2020a), we expect that these limitations can be alleviated in the future, yielding improved and more realistic estimates of costs for invasive alien fish and other species.

Finally, we note that invasive alien fish species are also known to have economic benefits (especially when they have commercial value) as well as aesthetic and spiritual values (Gozlan, 2010), which requires a better understanding of the trade-offs and incentives to introduce new species and/or maintain a long-term sustainable stock of their invasive population. Considering the benefits of invasive alien fish and understanding these trade-offs was beyond the scope of both the InvaCost database and this paper. However it is an important dimension of managing these species for the greater public good, and one that deserves further exploration in future research. Nevertheless, a comprehensive understanding of the costs and benefits of invasive alien fish is difficult because fish often disperse freely across international borders in seas and rivers, and trade pathways differ greatly between neighbouring countries, while neither costs nor benefits are equally shared.

Conclusion

Our work highlights the known and unknown economic costs of invasive alien fish species on a global as well as regional scale. A better understanding of the costs of invasive alien fish species should contribute, for example, to more responsible aquaculture practices, increased awareness of the risk of recreational introductions, and more effective regulatory instruments to prevent accidental species introductions. While it is difficult to predict how the cost of invasive alien fish will evolve worldwide, it is certain that the numbers of introductions of invasive alien species will continue to increase over time (Seebens et al., 2017, 2020). There is accordingly an urgent need to develop more effective and proactive management strategies to prevent fish invasions and promote mitigation of their impacts.

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Table 1. Cost-contributing invasive fish species for total and observed costs, illustrating species, total costs and numbers of database entries; F = Freshwater, M = Marine, B=Brackish (according to the environment classification of Froese and Pauly, 2019).

Common name	**Genus**	**Species**	**Environment**	**Total costs**		**Observed costs**	
				Cost (US$ 2017 value) in million	**database entries**	**Cost (US$ 2017 value) in million**	**database entries**
Brown bullhead	*Ameiurus*	*nebulosus*	F	0.001	3	0.001	3
Goldfish	*Carassius*	*auratus*	F,B	0.001	3	0.0010	3
Northern snakehead	*Channa*	*argus*	F	0.138	1	0.138	1
Redbelly tilapia	*Coptodon*	*zillii*	F,B	0.011	3	0.011	3
Common carp	*Cyprinus*	*carpio*	F,B	216.978	48	216.773	28
Northern pike	*Esox*	*lucius*	F,B	0.021	1	-	-
Mummichog	*Fundulus*	*heteroclitus*	M,F,B	0.017	5	0.017	5
Eastern mosquitofish	*Gambusia*	*holbrooki*	F,B	0.009	10	0.009	10
Ruffe	*Gymnocephalus*	*cernua*	F,B	28,933.217	47	-	-
Silver-cheeked toadfish	*Lagocephalus*	*sceleratus*	M	6.540	15	6.247	13
Pumpkinseed	*Lepomis*	*gibbosus*	F,B	0.030	13	0.030	13
Bluegill	*Lepomis*	*macrochirus*	F	0.073	10	0.073	10
Black bass	*Micropterus*	*salmoides*	F	5.293	34	5.293	34
White bass	*Morone*	*chrysops*	F	3.394	1	3.394	1
Rainbow trout	*Oncorhynchus*	*mykiss*	M,F,B	0.016	2	0.016	2
European perch	*Perca*	*fluviatilis*	F,B	0.014	3	0.014	3

Chinese sleeper	*Perccottus*	*glenii*	F,B	0.173	4	-	-
Sea lamprey	*Petromyzon*	*marinus*	M, F , B	1,389.395	15	534.887	12
Common minnow	*Phoxinus*	*phoxinus*	F,B	1.210	3	1.210	3
Guppy	*Poecilia*	*reticulata*	F	0.017	2	0.017	2
Topmouth gudgeon	*Pseudorasbora*	*parva*	F,B	5,004.319	22	0.818	11
Red lionfish	*Pterois*	*volitans*	M	24.528	85	24.528	85
Janitor fish	*Pterygoplichthys*	sp.	F	0.002	1	0.002	1
Brown trout	*Salmo*	*trutta*	M,F,B	1.782	10	1.782	10
Zander	*Sander*	*lucioperca*	F,B	0.022	4	0.022	4
European catfish	*Silurus*	*glanis*	F,B	0.002	1	0.002	1
Tilapia	*Tilapia*	sp.	F	20.039	1	20.039	1
	Diverse/unspecified			1,467.556	31	1,467. 556	31

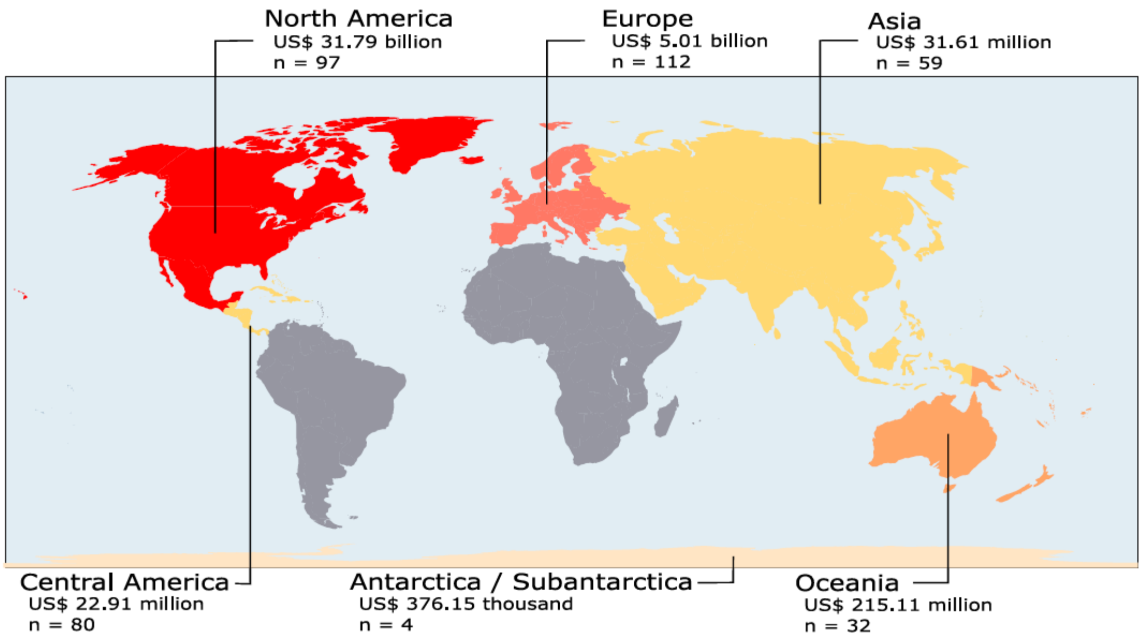


Figure 1. Total costs (observed and potential) of invasive fishes by geographical region. Grey indicates no cost information being available for that region, yellow to red indicates the magnitude of the reported costs.

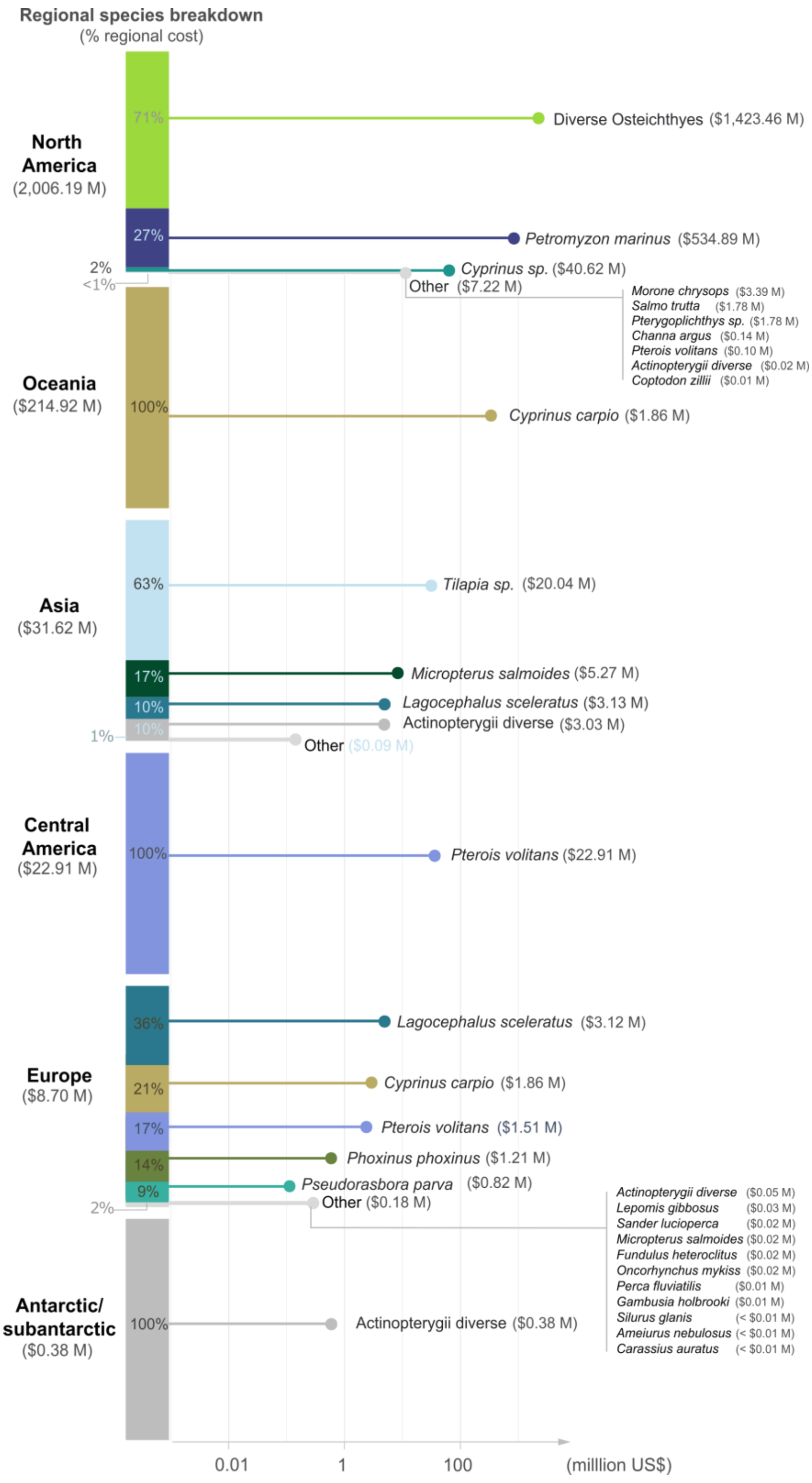


Figure 2. Observed costs of invasive fish species across regions (North America, Europe, Asia, Antarctic/Sub-Antarctic and Central America) indicating the contribution of the species to the respective total. For example, *Pterois volitans* accounts for 100% of the costs of invasive fish in Central America and contributes US$0.02 million to the total cost of invasive species. Note that the *x*-axis is on a $\log_{10}$ scale.

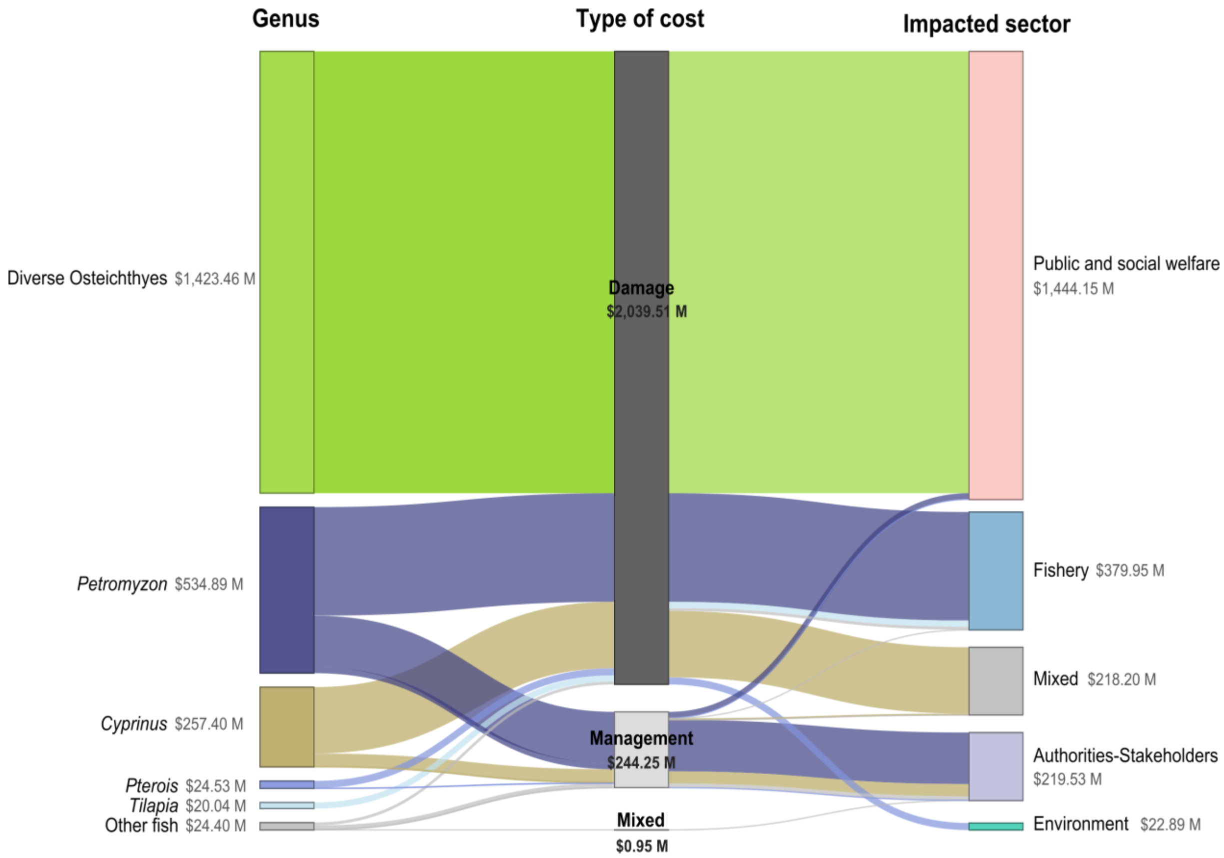


Figure 3. Sankey diagram showing the distribution of observed costs of alien fish invasions across genera, types of costs and sectors affected. Costs are shown in millions of US 2017 dollars.

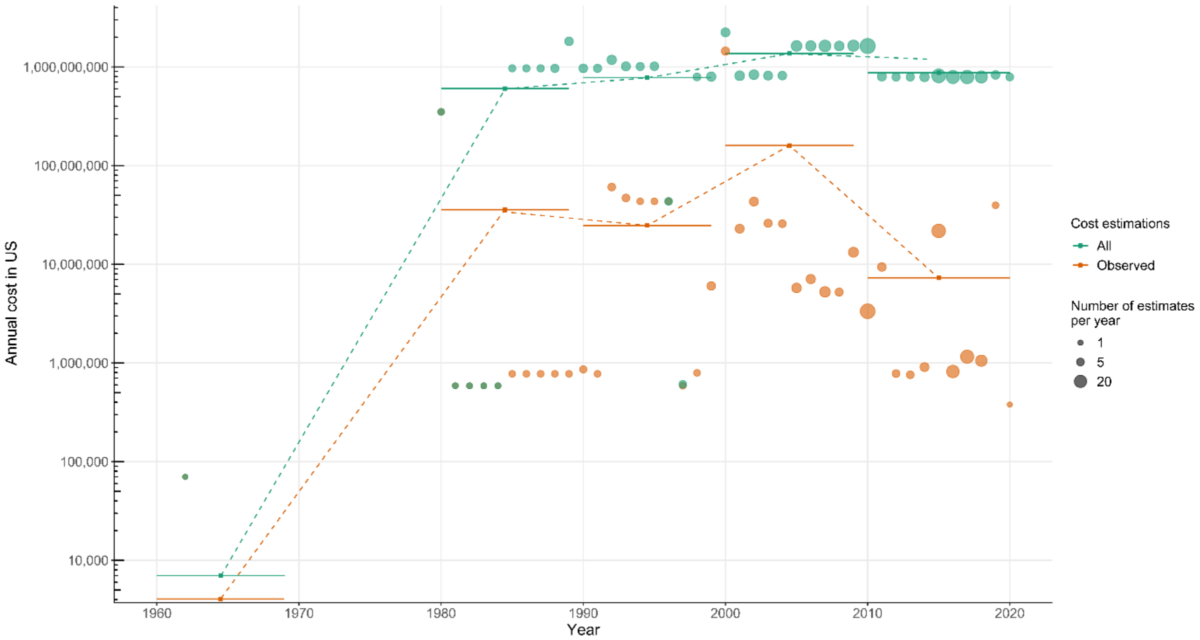
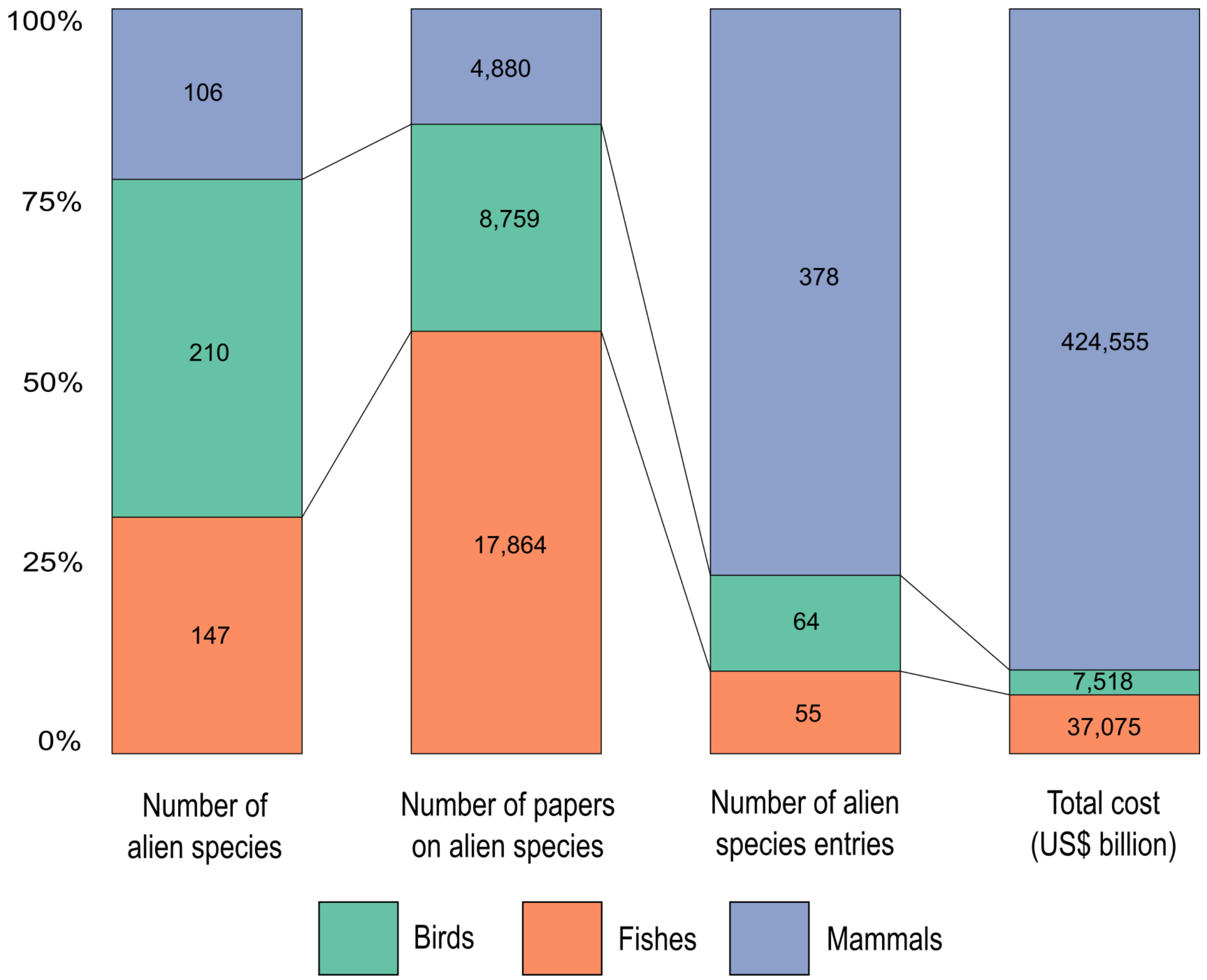


Figure 4. Total (green) and observed (orange) average annual costs in billions of 2017 US$ resulting from global invasions by fish. Points are annual values scaled by the number of annual estimates. Note that the *y*-axis is represented on a $\log_{10}$ scale.



780
781 **Figure 5.** Comparison among fishes, birds and mammals based on the numbers of alien species,
782 numbers of articles on alien species, entries and costs in the InvaCost database.