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Abstract

Invasive alien fishes have caused pernicious ecological impacts on aquatic ecosystems. However, there has not been a global appraisal of associated economic impacts. Here, we compiled reported economic impacts of invasive alien fishes using the most comprehensive global database of invasion costs (InvaCost). We analyze how fish invasion costs are distributed geographically and temporally, as well as which socioeconomic sectors are most impacted. Fish invasions have caused the economic loss of at least US$32.8 billion globally (2017 value), from only 26 reported species (of 128 known invasive alien fish species). North America had the highest costs (> 99%), followed by Europe and Asia, with no costs reported in Africa, Oceania nor South America. Very few costs from invasive fish in the marine realm were reported (0.1%). Most costs are related to resource damages and losses (97%), with relatively little spent on management; mainly impacting the fisheries sector (93%). However, when only considering empirically observed costs (without predictions), most costs were incurred by authorities and stakeholders through management, indicating that damage costs from invasive fishes are often extrapolated and/or difficult to quantify. Fish invasion costs increase markedly over time, from US$0.57 billion/year in the 1980s to US$1 billion/year in the 2000s. Fish invasions have been relatively well studied; however, economic costs have been lower than expected based on overall numbers of alien species. Accordingly, although costs are increasing, improved reporting is required to better understand how fish invasion costs are distributed across time, space and economic sectors.

Introduction

Around the globe, numbers of alien invasive fish incursions are growing (Avlijaš et al., 2018; Cucherousset & Olden, 2011). Concomitantly, fish invaders are increasingly recognized as a direct driver of aquatic biodiversity declines (e.g. topmouth gudgeon *Pseudorasbora parva*, European catfish *Silurus glanis* and Sea lamprey *Petromyzon marinus*; Schuldt & Goold, 1980; Ercan et al., 2019; Vejřík et al., 2017; Ruiz-Navarro et al., 2020). In line with increasing numbers of fish invasions, most associated invasion drivers are on the rise (Copp et al., 2010; Turbelin et al., 2017; Zieritz et al., 2017).

In particular, increasing anthropogenic activities, especially in emerging market economies, are expected to facilitate new introductions of alien fish species and the following invasions through pathways such as tourism, trade (e.g. aquaculture and aquarium trade) and infrastructure development (e.g. waterways/channel construction; Hulme, 2015). Some of the key introduction pathways resulting in invasions are intentional, such as aquaculture, recreational or commercial fisheries, the ornamental fish trade, or religious releases. Others are unintentional, for example, through ballast water (e.g. Pratt et al., 1992), canals (e.g. Mills et al., 1993) and through environmental changes (e.g. climate, pollution, land use) that lead to increased susceptibility to invasions (e.g. Britton et al., 2010a).

Ecological impacts of alien invasive fishes include the displacement and extinction of native species (Mills et al., 2004; Haubrock et al., 2018), modification of trophic interactions (Martin et al., 2010; Haubrock et al., 2019) and disruption of ecosystem functioning (Capps & Flecker, 2013). Fish invaders can also transmit novel pathogens (Gozlan et al., 2005; Waicheim et al., 2014; Ercan et al., 2019; Boonthai et al., 2017) as well as cause genetic pollution via the hybridization with native species (Oliveira et al. 2006, Gunnell et al. 2007). Introductions of alien fish species into previously fishless insular systems can additionally exacerbate impacts due to resident species naiveté (Knapp et al., 2001, Lecomte et al., 2013; Cuthbert et al., 2018).

Nevertheless, despite evidence for increasing numbers of fish invasions globally and their increasing ecological impacts (Leprieur et al., 2008; Seebens et al., 2020), their economic impacts remain poorly understood, largely due to data scarcity. This scarcity in cost data has spurred debate among scientists regarding estimates of invasion costs (Cuthbert et al., 2020), which have often been over-reliant on extrapolations and presented untraceable sources. In a fisheries context, that could involve estimating costs from local scales to entire fisheries. This knowledge gap in costs, in turn, impedes decision-making and largely limits the ability of policy makers and stakeholders to design successful and cost-effective management strategies (Britton et al., 2010b; Hyytiäinen et al., 2013). In those cases where invasive fish populations may hold a positive value, understanding trade-offs and designing socially optimal management is also impeded by the lack of cost data. Examples of these positive values include invasive fishes with commercial value (Gollasch & Leppäkoski, 1999), aesthetic and/or cultural values associated to recreational uses (Downing et al., 2013, Schlaepfer et al., 2011, Katsanevakis et al., 2014, Gozlan 2015, 2016), or other perceived ecosystem benefits (Pejchar & Mooney, 2009).

To address this pervasive knowledge gap and provide a baseline for cost quantifications, we characterise, for the first time, the current status of knowledge on global costs of alien invasive fishes using the InvaCost database (Diagne et al., 2020). This database contains detailed information on reported costs (e.g. cost types, impacted sectors, regional attributes, reliability of cost estimations, etc.) over the past 60 years, associated with ~ 800 invasive species from all ecosystem types globally. In the present study, we use a subset of this database to which we add complementary cost information from other sources. Our aims were to describe the global costs associated with alien invasive fish species, explore the structure of these costs, and to identify potential knowledge gaps and biases in the estimation of past and current economic impacts.

Methods

Cost data sourcing and filtering

To estimate the cost of alien fish invasions reported globally, we considered cost data from the InvaCost database (Diagne et al., 2020). This database compiles 2,419 cost entries in a sufficiently detailed manner for large-scale syntheses of costs associated with invasive species at different spatial and temporal scales. We complemented the data of the InvaCost database in two ways. First, we added cost data collected from a number of additional sources in 15 non-English languages (5,212 cost entries; Angulo et al. in prep., https://doi.org/10.6084/m9.figshare.12928136). We further supplemented the original InvaCost database with new references (ca. 2,314 cost entries: https://doi.org/10.6084/m9.figshare.12928145.v1). Following the InvaCost protocol (Diagne et al., 2020), data were retrieved using a series of search strings entered into the ISI 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 relevant references with costs of invasions. These new references were thoroughly assessed to identify relevance and extract cost information. Ultimately, all costs were converted to 2017 US$ values (see Diagne et al. 2020 for detailed information). The enhanced database used for this analysis includes information on monetary costs across taxonomic, regional and sectoral descriptors, and allows the distinction between *observed* (i.e. costs of a realized impact) and *potential* costs (i.e. costs of a predicted/expected impact), as well as the reliability of methodologies used for cost estimates (*high* or *low* reliability).

We filtered the InvaCost database in order to only keep costs related to fishes belonging to the classes *Cephalaspidomorphi* and *Actinopterygii*. Database entries not attributable to unique species, sectors, or cost types within those classes were categorized as "Diverse/Unspecified". All analyses were performed for the period between 1960 to 2020, given that (a) monetary exchange rates prior to 1960 were unavailable, and (b) 2020 was the last year for which cost data were considered in the database. The final dataset used for the analysis is provided in Supplementary Material 1.

Global cost descriptions

For the purposes of describing costs of invasive fish through time, we used the *expandYearlyCosts* function of the 'invacost' package (v0.3-4; Leroy et al., in prep) in R version 4.0.2 (R Core Team, 2020). This function facilitates consideration of temporal data dimensions, whereby the estimated costs per year are expanded over time according to the duration of time over which they occured or were expected to have occurred (i.e. duration time between *Probable_starting_year_low_margin* and *Probable_ending_year_low_margin* columns). The analyses were therefore conducted based on these 'expanded' entries to account for the probable duration of the costs as they were reported in each analysed study. For the purposes of obtaining a comparable total cumulative cost for each estimate over the period that costs incurred for each invasion, we multiplied each annual estimate by the respective duration (in years). Finally, the cumulative invasion costs were estimated based on their classification under the following cost descriptors (i.e., columns) included in the database (Supplementary Material 2):

(i) Method_reliability: illustrating the perceived reliability of cost estimates based on the type of publication and method of estimation. Costs are considered as of *low* reliability when materials cannot be assessed for full-text investigation or if costs come from grey literature with no fully described method. On the contrary, costs are considered as of *high* reliability they come from peer-reviewed articles, official documents, or grey literature with fully described method (Diagne *et al.*, 2020);

(ii)Implementation: referring to whether the cost estimate was actually realised in the invaded habitat (*observed*) or whether it was extrapolated (*potential*). For example, potential costs can include estimated reductions in fishery income (Scheibel et al., 2016), known local costs that are extrapolated to a larger system in which they occur (Oreska and Aldridge, 2011), and costs extrapolated over multiple years based on estimates from a shorter period (Leigh, 1998);

(iii) Geographic_region: describing the continental geographic origin of the listed cost;

(iv) Type_2: grouping of costs according to the categories: (i) "*Damage costs*" referring to damages or losses incurred by invasion (i.e., costs for damage repair, resource losses, medical care), (ii) "*Management costs*" comprising control-related expenditure (i.e., monitoring, prevention, management, eradication), (iii) and "*General costs*" including mixed damage-loss and control costs (cases where reported costs were not clearly distinguishable);

(v) Impacted_sector_2: the activity, societal or market sector that was impacted by the cost. Seven sectors are described in the database : *agriculture*, *authorities-stakeholders* (official structures allocating efforts for the management of biological invasions), *environment*, *fishery*, *forestry*, *health* and *public and social welfare* (Diagne *et al.* 2020).

Temporal cost accumulations

To assess temporal trends of invasive fish species, we considered 10-year means since 1980, because cost data concerning fish invasions were reported solely after the 1980s. We examined costs as a function of the *year of impact*, which reflects the time at which the invasion cost likely occurred and expanding it over years during which the costs was realised (using the *probable_starting_year* and *probable_ending_year* columns; see Leroy et al., in prep.). This allowed for an estimation of annual average costs over the entire reported period, as well as over decadal increments.

Comparison with other taxonomic groups

In order to put costs of alien invasive fish species in a wider taxonomic perspective, we compared the economic costs of fishes with those of invasive birds and mammals. The comparison was based on the total cost and the number of cost entries in the InvaCost database, coupled with the number of invasive species per taxon, as well as the numbers of scientific publications in invasion science. First, total monetary costs and database entry numbers for birds and mammals were calculated following the methods detailed above. Second, we estimated the available literature for each group using the same search protocol as the one used for the InvaCost database (see Diagne et al. 2020), excluding words that refer to costs and adding the biotic group name (i.e 'fish", "mammal", or "bird"), in order to get a comparative proxy of research effort in invasion biology for these three taxa. Exact search strings used can be found in Supplementary Material 3. The information considered in this comparison was gathered using the Web of Science. Third, the numbers of alien species for each of the three aforementioned taxonomic groups were estimated using the IUCN Red List database (https://www.iucnredlist.org/). We categorized alien species according to their IUCN status, either "Extant and Introduced", "Possibly extinct and Introduced", "Presence Uncertain and Introduced" or "Possibly extant and Introduced". Last, we used Pearson's Chi-squared test to assess whether the data of three taxonomic groups had the same distribution of variable values (number of alien species, number of cost entries, number of studies reporting invasion costs and total costs).

Results

A total of 228 cost entries for 26 alien invasive species from 17 fish families were identified in the database, summing up to US$32.80 billion. The majority of costs, however, was deemed as potential (US$31.27 billion; n = 164, hereafter the number of cost entries), while observed costs summed up to just US$1.53

billion (n = 64). In turn, the majority of costs (US$20.29 billion; n = 182) were deemed as highly reliable, with US$12.51 billion (n = 46) evaluated as of low reliability (Supplementary Material 4).

Costs across regions and taxa

According to our recorded costs, North America was found to be the region reported with the highest number of economic costs (US$32.78 billion; n = 78), followed by Europe (US$9.75 million; n = 101) and Asia (US$8.37 million; n = 43) (Figure 1). Costs inferred from Central America and polar regions (e.g. French Southern and Antarctic Lands) were both below US$ 1 million each. When considering observed costs alone, invasive fish costs in North America were estimated at US$1.51 billion (n = 25), which was again more than 10 times higher compared to observed costs recorded in Europe (US$7.67 million; n = 101) and Asia (US$8.37 million; n = 43). Notably, there were no economic costs reported from Africa, Oceania and South America. Reported costs were attributed to multiple species in North America (n = 8) and Europe (n = 15), but were less diverse in Asia (n = 2) and Central America (n = 1) (Figure 2) (note that these do not include taxa at coarser groupings than species level).

The *Actinopterygii* class included 25 invasive fish species with costs (US$30.38 billion), as opposed to the Cephalasdomorphi class, which was represented by just one species, the sea lamprey *P. marinus* (US$2.41 billion in North America) (Table 1; Figure 2). Considering all costs in North America, the Ruffe *Gymnocephalus cernua* was the costliest species (US$28.93 billion), followed by the sea lamprey *P. marinus* (US$2.41 billion), the white bass *Morone chrysops* (US$3.39 million) and brown trout *Salmo 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, *P. marinus* was, with US$61.35 million, the costliest species, followed by *Micropterus salmoides* (US$5.29 million), *Lagocephalus sceleratus* (US$3.87 million), *Cyprinus carpio* (US$1.85 million), and *Phoxinus phoxinus* (US$1.21 million). All other species contributed up to US$1 million (Table 1).

Impacted sectors and cost types

Most costs were linked to the damages and losses of resources (n = 48; US$31.82 billion), which represented approximately 97% of the total reported costs. Costs associated with management (i.e. costs of control, detection and eradication) were therefore two orders of magnitude lower (US$975.43 million), while general costs (costs either unspecified or classified under multiple cost types) summed to just US$953.73 thousand. In North America, US$31.82 billion was attributed to damages and losses, with the remaining US$963.04 million classified as management costs.

On a worldwide scale, the fisheries is the sector most impacted (US$30.40 billion), followed by costs to public and social welfare (US$1.42 billion) and lastly costs to authorities and stakeholders (US$971.96 million). Inferring only costs to impacted sectors in North America, the distribution of costs across sectors was similar, with fisheries (US$30.39 billion) predominantly impacted, followed by public and social welfare (US$1.42 billion) and authorities and stakeholders (US$959.49 million) (Supplementary Material 5).

As for the subset of species with observed costs, the majority were conversely incurred through management expenditures, with comparatively little via direct damages. In turn, management expenditures were predominantly incurred by authorities-stakeholders, whilst damages were incurred by fisheries (Figure 3). Accordingly, the majority of fishery impacts in terms of damages and losses were extrapolative, whilst empirically incurred costs were mostly management-orientated. Yet, many of these extrapolations were deemed to be of high reliability and thus could be methodologically robust.

Temporal cost accumulations

In total, these costs averaged to US$0.80 billion per year between 1980 and 2020 (Figure 4). Average costs generally increased over the years, from US$0.57 billion per year in the 1980s to US$ 1 billion in the 2000s and eventually dropped to US$0.79 billion in the 2010s. Note, however, that time lags (i.e. between cost incurrence and formal reporting) were not accounted for in the last decade, and thus cost estimates are likely more underestimated in recent years.

Comparisons across biotic groups

Records for alien fishes from the IUCN Red List database (n = 128), were approximately half the number of recorded alien birds (n = 207), but were very close to the number of recorded alien mammals (n = 108). Conversely, fishes comprised the taxonomic group with the largest number of scientific publications on alien species (15,969 papers), which was approximately double the number of publications for birds (7,900) and four times more than mammals (4,334) (Figure 5). Invasive fish species, however, had the lowest number of entries before expansion over time (33) compared to mammals (292) and birds (43). In turn, the total cost of invasive fish species (US$32.80 billion) was found to be much lower than mammals (US$261.24 billion), but greater than birds (US$6.55 billion). The distribution of values for each biotic group therefore differed significantly (fish vs birds: $\chi 2 = 1606.3$, $p < 0.001$; fish vs mammals: $\chi 2 = 145.2$, $p < 0.001$; Figure 5), with fish costs and entries disproportionately lower than expected based on numbers of studies and alien species.

Discussion

Invasive fishes have caused economic costs of at least US$32.80 billion from just 26 recognised invaders with reported monetary impacts globally. These costs largely resulted from potential estimations and were mostly incurred through damages rather than management spending. However, when considering empirically observed costs only, most of them were due to management actions, with damages reportedly being a minority. For instance, a large portion of invasive fish species costs were based solely on extrapolations. For the Eurasian ruffe *(G. cernua),* which accounted for a substantial share of total costs from invasive fish in North America, their reported observed costs are very few and were mostly based on potential annual losses to fisheries should invasions not be controlled, as well as potential costs of large-scale management interventions. Similarly, the Chinese or Amur sleeper (*P. glenii)* in Europe had no reported observed costs, although being a known vector for e.g., parasites (Reshetnikov & Sokolov, 2011; Kvach et al., 2013) which can impact especially aquaculture (Ondračková et al., 2012). Other damaging invasive fish, such as species of Asian carp in the Mississippi River basin, lack current cost estimates, despite expectation of potential future economic and ecological costs large enough to require spending US$831 million to attempt to prevent spread into the Great Lakes (USACE, 2018). This tendency towards extrapolated or potential costs may arise because of (i) the inconspicuousness of damages to socioeconomic sectors such as fisheries in submerged environments, (ii) because markets such as fisheries may fail to report such damage costs in publications despite their proven existence, and (iii) because management actions are more easily reported, as they are often based on planned budgets published in official documents (compared to damage-costs that need to be estimated from sometimes not monetizable foundations). Nevertheless, over recent decades, fish invasions have become more costly, increasing by an order of magnitude in total. However, despite invasive fishes being diverse and relatively well studied, significantly disproportionately fewer costs are reported for this group compared to other taxa, with cost totals reaching a considerably lower magnitude than, for example, non-native invasive mammals. Accordingly, further cost reporting is urged to address these gaps and refine the spatial resolution and coverage of cost information on the global scale.

Regional biases

Global documented costs of alien invasive fish species exhibited marked regional disparities, with the majority of reported costs attributed to North America and significantly fewer costs reported from other geographic regions. These regional disparities are not only reflected by massive differences in costs, but also in their spatial scale of reporting; a much higher proportion of costs in North America were reported at country or regional scales (39 %) compared to other areas (10 %). These large-scale appraisals in turn likely increase the magnitude of reported costs and highlights a need for larger-scale estimates outside of North America (e.g., in Europe). Furthermore, this difference in magnitude of costs between invasive fish species in North America and other continents is noteworthy given North America accounted for only 27.1 % of all cost entries for invasive fishes (78 out of 228) and 39.1% of entries of solely observed costs (25 out of 64 entries). Low economic costs based on few entries were associated with alien fish invasions in Asia. This is despite a number of fish species having been intentionally introduced to meet the rapid increase in demand for farmed fish (Lin et al. 2015; Xiong et al. 2015), and aquaculture enterprises in Asia producing 80 % of all marine cultured biomass (The State of World Fisheries and Aquaculture 2020) despite being a known vector for aquatic invasions (Grosholz et al., 2015). In fact, costs for only two invasive fish species have been reported in Asia, regardless of evidence of multiple introduced fish species escaping from aquaculture facilities or being released in the wild (Marchetti et al., 2004). Similarly, the absence of reported costs from fish invasions in South America, Africa and Oceania is surprising given multiple notorious examples of fish invasions in these continents. For example, in certain regions in South America (e.g., North Bolivia), the introduction of *Arapaima gigas* has had severe environmental impacts and is aggressively displacing native commercially valuable fisheries (although *A.gigas* is fished commercially as well) (Miranda-Chumacero et al. 2012; Liu et al., 2017; Ju et al., 2019). In East Africa, although the the introduction of Nile perch resulted in an increase in commercial fishery yields, boosted fish processing, and provided revenues from recreational tourism, it also adversely affected local communities by edging-out of local small-scale fishers and increasing in both insecurity and health issues around Lake Victoria (Aloo et al., 2017; Yongo et al., 2005; Abila, 2000). That invasion also altered the lake's community composition and trophic network (Witte et al., 2013), reducing water quality, and causing the extinction of around 200 native species (including many endemic), altogether causing one of the largest anthropogenic-driven ecosystems shifts on record (Ligtvoet et al., 1991; Kaufman, 1992; Mugidde et al., 2005). Australia also has a history of fish invasions, which have affected freshwaters systems and triggered high-risk management strategies, such as carp management through the introduction of viruses (Marshall et al., 2018). One further noteworthy example in this regard is New Zealand, which had no reported cost entries in InvaCost for invasive fish species, despite having been impacted by their deliberate releases, the well-known importance of IAS, and the dedicated management efforts (Collier & Grainger, 2015). The lack of reported costs from fish invasions in these regions and the discrepancy in costs reported between North America and elsewhere points both a likely much greater actual cost than currently recorded, and an urgent need to better quantify monetary impacts of invasive fishes. A possible contributing factor that deserves consideration is that the fauna of the western Palearctic is depauperate 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). Indeed, historical and cultural drivers are dominant, especially in southern Europe, where countries have a long history of species intentional introductions (Occhipinti-Ambrogi et al., 2011; Castaldelli et al., 2013; Nunes et al., 2014). Therefore, invasions in Europe could impact, at best, a limited number of freshwater fishes (or may even have been economically beneficial historically), whereas invasions in North America would necessarily impact a greater number of native species (Levêque et al., 2007). Hence, compared to other regions, higher costs may also arise from the economic importance of the respective freshwater fisheries, which is far more developed in North America compared to Europe (e.g. especially for recreational activities such as angling and boating; Franklin, 1998; Mordue 2009). This may explain the relatively large investment in management efforts, i.e., observed costs, in North America compared to other regions, which had the largest share of observed costs globally (e.g., for sea lampreys; Stewart et al., 2003; Twohey et al., 2003). Nevertheless, the regional discrepancies in invasive fish costs between North America and Europe cannot be fully explained by the difference in economic activity or the severity of monetary impacts due to invasions, nor can they explain the low costs and lack of data in other regions.

Cultural biases

In Europe, the topmouth gudgeon (*P. parva*) was identified as the costliest fish invasion based on solely six studies reporting reliable and observed costs, and despite the availability of further cost information which have not been incorporated into the InvaCost database. That is, its introduction in UK waters in 1985, has led to the largest and costliest eradication programme ever taken on for a fish species (Britton et al., 2010). With an average annual cost of about £190 thousand (~ US$244 thousand) over a three-year period, about thirty populations distributed across England and Wales have now been eradicated (Britton et al., 2011). Another economic impact assessment that considered potential future distributions for *P. parva* indicated potential resource damages and losses totalling between £2.9 and £3.1 billion (Defra 2005), and an annual total of US$39.6 million in damages and losses (Britton et al., 2010b). However, it was the emerging infectious disease risk associated with the presence of *P. parva* (Gozlan et al., 2005), which has fuelled this unique management action. Today, it is still the only global example of a national eradication program taken on by an environmental agency (Britton et al., 2010b).

Moreover, cultural differences in attitudes and/or awareness towards invasive aquatic species in North America could have further led to a greater willingness for expenditure to combat freshwater fish invasions. Most of the costs of invasive fish species in North America impacted the fisheries sector (93%), while in Asia costs for fisheries were not reported. However, these costs were largely potential damages and losses and therefore may not have yet been incurred or realised, or full damage extents could have been extrapolated from smaller scales as they are difficult to quantify in submerged environments. Furthermore, the difference in costs between North America (particularly the US) and other regions globally can be explained by the fact that the value of fisheries in the US is significantly higher compared to other places, resulting in more pressure to manage invasive fish and therefore higher budgets allocated for this purpose as well as damages and losses. Indeed, much of this funding derives directly from licence sales and taxes on fishing gear and boat fuels. Indicatively, 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 costs of marine invasive fish, the expenditure of marine anglers is also substantial ($31 billion in 2012) and so is the economic impact (US$82 billion and 500,000 jobs in 2012) (Hughes, 2015). The expenditure, economic impact and jobs supported through recreational fishing has been much smaller in Europe (e.g., see for example Hyder et al., 2017; European Parliament, 2017) and the same applies to participation rates in recreational fisheries (Steffen and Winkel, 2003; Arlinghaus et al., 2015).

Environmental and taxonomic biases

In contrast to these manifold freshwater fish invasions, very few costs are associated with invasive fish species from the marine realm. This is especially noteworthy given their well-known impacts to marine ecosystems (with impacts to e.g., habitat or other native species via competition for food) and to spatially overlapping commercial fisheries for native species (with costs incurring from bycatch, damage to gear, injuries, increased fuel consumption to reach invasive-free areas etc). Prominent examples include for instance the angelfish *Pomacanthus* sp. (Semmens et al., 2004), lionfish, *P. miles* (Moonsammy et al., 2011), the round herring *Etrumeus golanii* (Galil et al., 2019), the rabbitfishes *Siganus rivulatus and S. luridus*, and the pufferfish *L. sceleratus* in the Mediterrenean (Kalogirou et al., 2013; Giakoumi, 2014).

We showed that costs from invasive fish are underrepresented compared to other taxonomic groups and relative to the research effort devoted to them. This could arise from a perception bias where damages to aquatic habitats or communities go unnoticed by the public and authorities owing to the difficulties in detecting fish invasions compared to other taxa. At the same time, the introduction of aquatic species has often been considered as beneficial for some local communities, especially those engaged in harvesting, processing, or recreational tourism (Selge et al., 2011), which results in a risk of ignoring negative impacts from the invasion. Invasive fish have diverse impacts on ecosystems and understanding their indirect effects will benefit from advancing non-market valuation methods to deduce the full range of their impact (including e.g. native species decline, displacement, extirpations, diseases etc) (Hanley and Roberts, 2019). Compared to mammals and birds, fish invasions and their introduction vectors are well studied, with high numbers of publications and reported numbers of alien species (Semmens et al., 2004; Castellanos-Galindo et al., 2020). The low number of reported costs for fish invasions inferred from this large body of research likely reflects the fact that some fishes, unlike most birds or mammals, are purposefully introduced (Gozlan, 2008).

Conservative nature of reported costs

The cost estimates presented here are therefore likely very conservative, as cost data are deficient for most invasive fish species and parts of the world. Average cost estimates for invasive fish species have generally increased through time, despite some levelling off in recent years, which likely reflects time lags in cost reporting following their occurrence. The limited understanding of costs of invasive fish likely hinders investments in detection, control, prevention and management and lowers them in the priority list of decision-makers and/or resource managers who face budgetary constraints. Invasive fish species are also known for their economic benefits (especially when they hold a commercial value) as well as aesthetic and spiritual values (Gozlan 2010), which calls for a better understanding of trade-offs and incentives to introduce new species and/or maintain a sustainable, long-term stock of their invasive population. Considering the benefits of invasive fish and understanding such trade-offs was beyond the scope of this paper, but it is an important dimension to managing these species for the greater public good, that is worth pursuing in future research. Nevertheless, a global understanding of the costs and benefits of alien fish is challenging because fish often freely across international borders in seas and rivers, and trade vectors and pathways differ greatly between neighbouring countries, while neither costs nor benefits are equally shared. In addition, the complexity of estimating the cost of non-market impacts (e.g., ecosystem impacts) represents an immense challenge that may limit policy makers from taking action. However, efforts have been made in recent years to develop user friendly risk assessment tools (see e.g., Copp et al., 2005, 2009) that could be used by environmental agencies around the world to evaluate risks associated with invasive fish species and thus prioritize relevant management actions. In the light of the potential high cost of invasive fish species, particularly if these continue to fail attracting resource managers' attention as indicated by the low management costs in our study, the natural, social and economic disruptions can be expected to exacerbate. Liability issues with respect to fish invasions may be worth being brought forward to the policy arena in ways that would allow for control and/or other management costs to be borne by industries with a key role in new species introductions (e.g., aquaculture, fisheries, aquarium trade).

Conclusion

Our work sheds light on the known and likely increasing costs of alien invasive fish species globally and brings to the surface regional gaps as well as biases in the reporting of costs relative to invasions within other taxa. An improved understanding of their costs is expected to contribute to more responsible aquaculture practices, increased awareness on the risk of species introductions for recreational purposes and more effective regulatory instruments to prevent accidental species introductions (e.g., via ballast water). While it is difficult to predict how global invasive fish costs will evolve throughout time, it is certain that the numbers of alien introductions and hence, invaded areas will keep increasing over time (Seebens et al., 2017, 2020). There is thus an urgent need to develop more effective and proactive management strategies to prevent alien fish invasions and their impacts.

Declarations

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Data availability statement

All the data used in this study was made available as supplementary material.

Conflicts of interest/Competing interests

No conflict of interest has to be declared.

Availability of data and material

The underlying data was provided as supplementary material.

Code availability

The R code required for the analyses has been referenced in the related sections within the methods.

Authors' contributions

PJH, CB and RNC led the writing and analysis. CL, MK, BL, AJT, AMK, LV provided valuable insights and contributed to the writing and presentation. CD, REG and FC provided the database and contributed to all aspects of the manuscript production.

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Table

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).

			Total costs		Observed costs	
Common name	Species	Environment	Costs (US$2017 in millions)	Database entries	Costs (US$2017 in millions)	Database entries
Ruffe	*Gymnocephalus cernua*	F,B	28,933.600	48	0.383	1
Sea lamprey	*Petromyzon marinus*	M, F , B	2,413.636	12	61.359	4
Black bass	*Micropterus salmoides*	F	5.293	34	5.293	34
Silver-cheeked toadfish	*Lagocephalus sceleratus*	M	4.186	14	3.873	6
White bass	*Morone chrysops*	F	3.394	1		
Topmouth gudgeon	*Pseudorasbora parva*	F,B	2.193	11	0.575	6
Common carp	*Cyprinus carpio*	F,B	1.859	16	1.859	16
Brown trout	*Salmo trutta*	M,F,B	1.782	10		
Common minnow	*Phoxinus phoxinus*	F,B	1.21	3	1.210	3
Chinese sleeper	*Perccottus glenii*	F,B	0.173	4		
Northern snakehead	*Channa argus*	F	0.138	1	0.138	1
Bluegill	*Lepomis macrochirus*	F	0.073	10	0.073	10
Pumpkinseed	*Lepomis gibbosus*	F,B	0.03	13	0.03	13
Zander	*Sander lucioperca*	F,B	0.022	4	0.022	4
Red lionfish	*Pterois volitans*	M	0.021	2	0.021	2
Northern pike	*Esox lucius*	F,B	0.021	1		
Mummichog	*Fundulus heteroclitus*	M,F,B	0.017	5	0.017	5
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
Eastern mosquitofish	*Gambusia holbrooki*	F,B	0.009	10	0.009	10
Redbelly tilapia	*Coptodon zillii*	F,B	0.006	2	0.006	2
Janitor fish	*Pterygoplichthys sp.*	F	0.002	1	0.002	1
European catfish	*Silurus glanis*	F,B	0.002	1	0.002	1
Brown bullhead	*Ameiurus nebulosus*		0.001	3	0.001	3

		F				
Goldfish	*Carassius auratus*	F,B	0.001	3	0.001	3

Figures

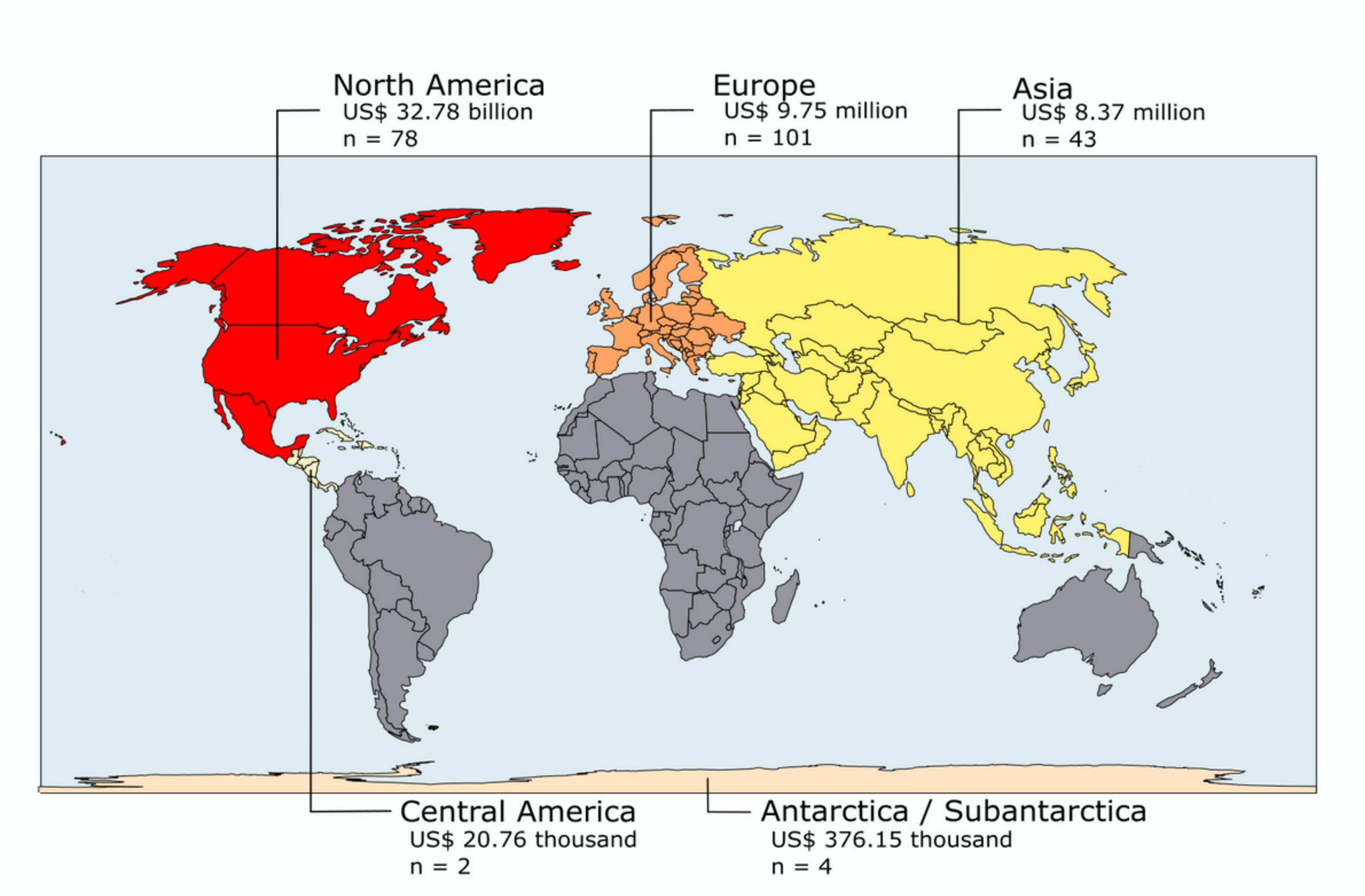

Figure 1

Total (observed and potential) costs from invasive fishes per geographical region. Grey indicates no cost information being available for that region, yellow to red indicated the magnitude of reported costs. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

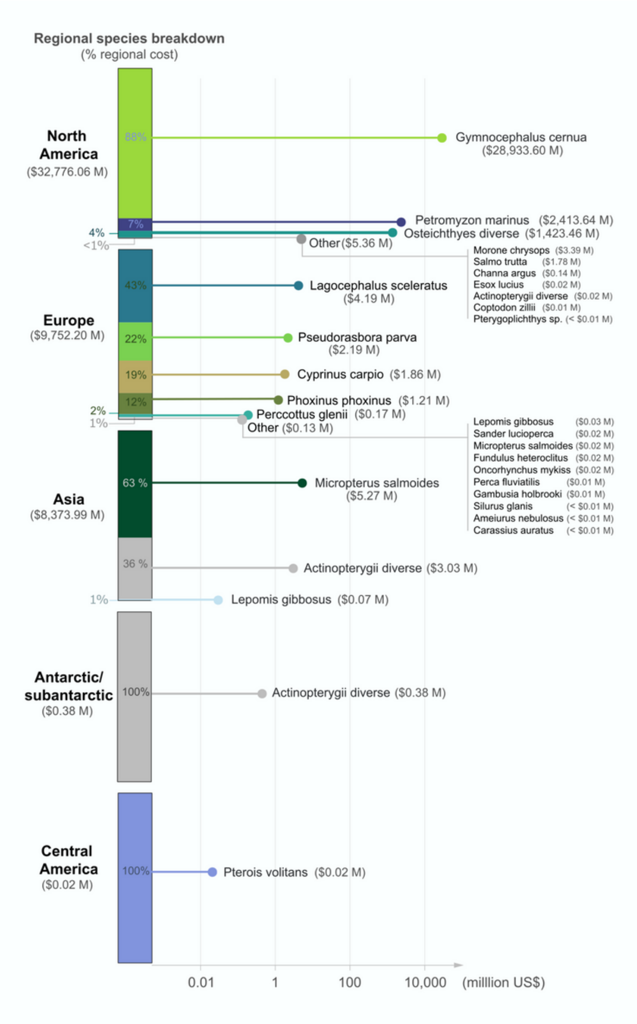

Figure 2

Total costs of invasive fish species across regions (North America, Europe, Asia, Antarctic/subantarctic and Central America) indicating the contribution of species to the respective total. For example, Pterois volitans represents 100% of invasive fish costs in Central America and contributes $0.02 million to the total cost of invasive species. Note that the x-axis is on a log10 scale.

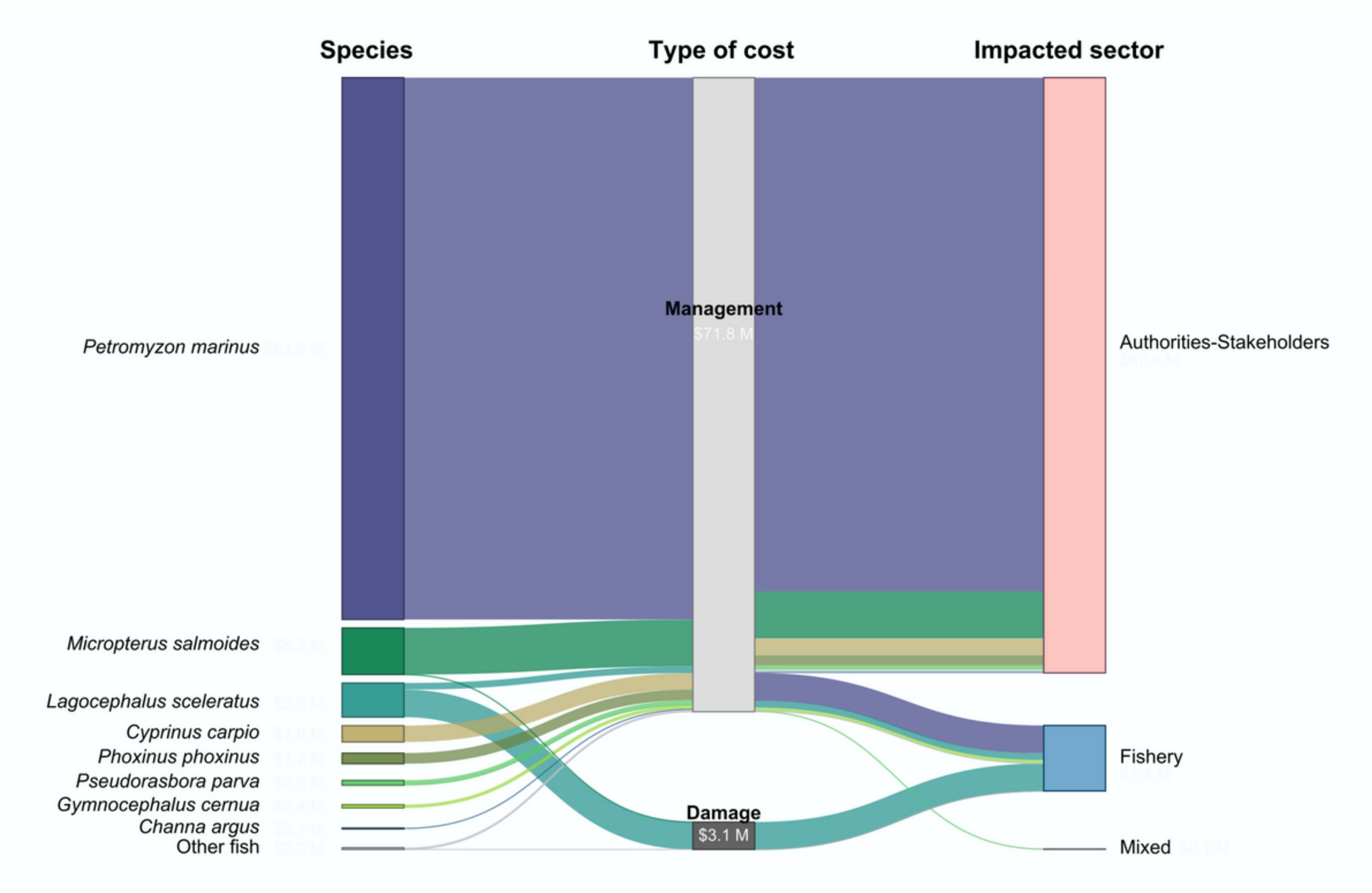

Figure 3

Distribution of highly reliable observed fish invasion costs across species, types of costs and impacted sectors. Costs are shown in US$ 2017 million.

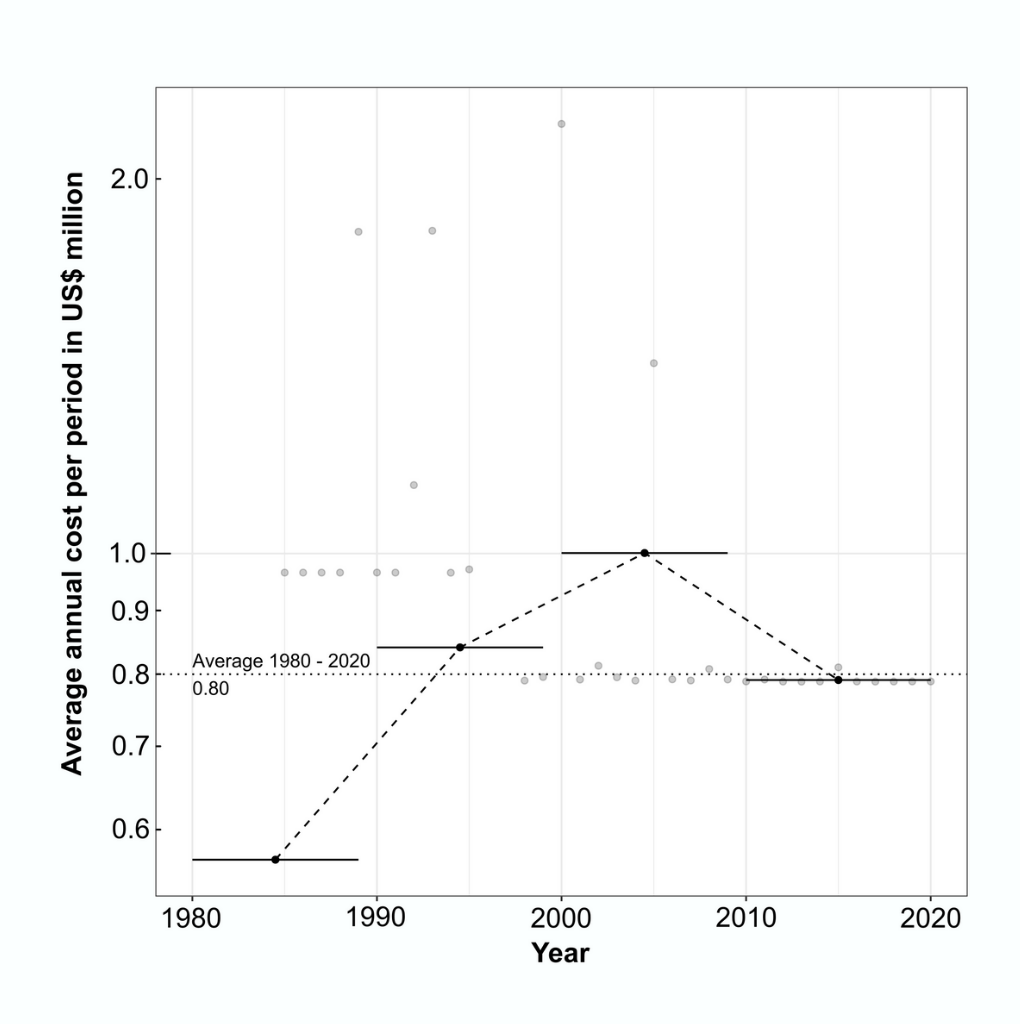

Figure 4

Average annual costs (in 2017 US$ billion) resulting from global invasive fish invasions. Points are annual totals. Note that the y-axis is shown on a log10 scale.

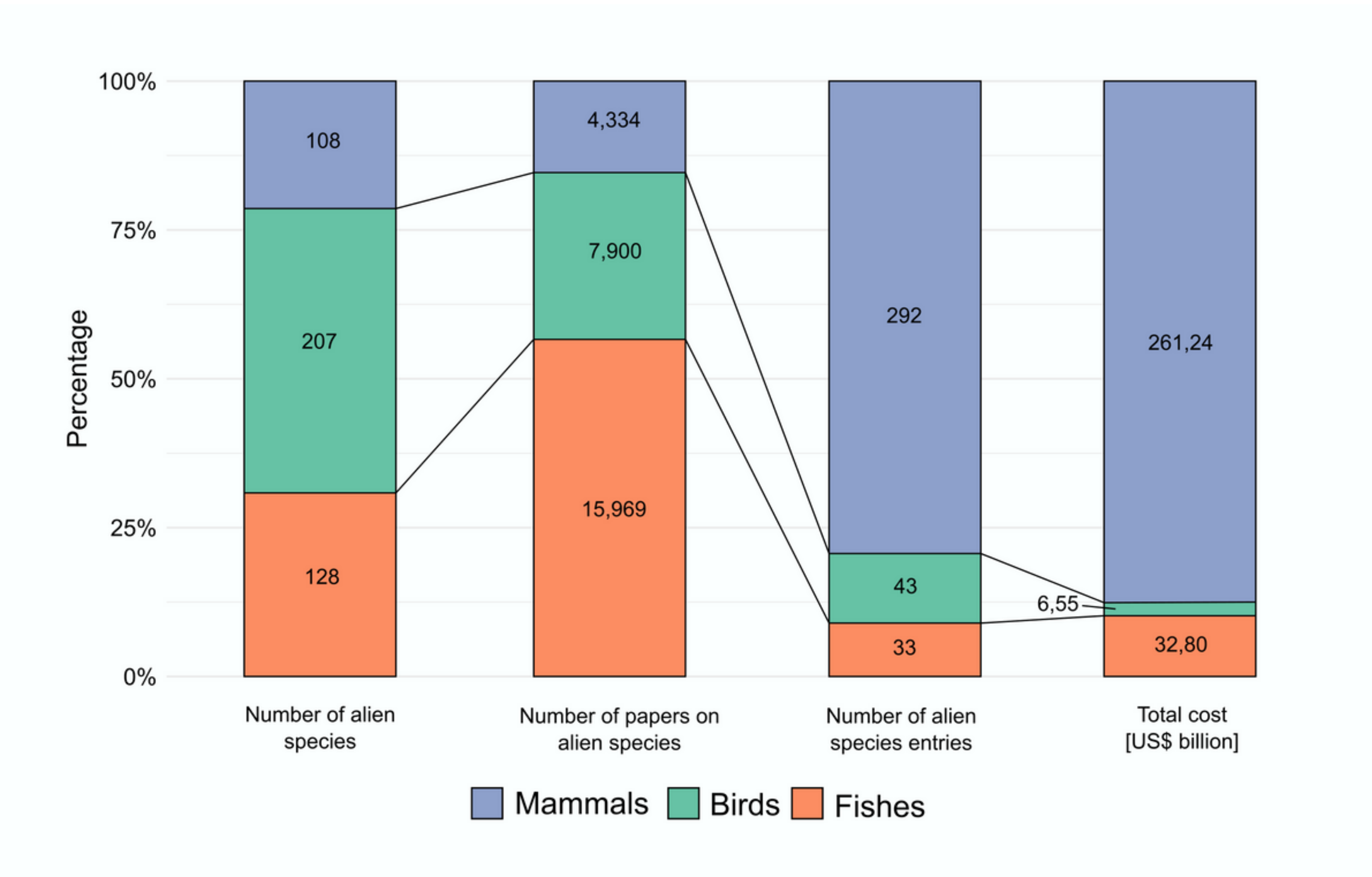

Figure 5

Comparison across fishes, birds and mammals based on the numbers of alien species, numbers of papers on alien species, entries and costs in the InvaCost database.

Supplementary Files

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- Supplement3.docx
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