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Economic costs of invasive bivalves in freshwater ecosystems

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Abstract

Aim: To assess spatio-temporal and taxonomic patterns of available information on the costs of invasive freshwater bivalves, as well as to identify knowledge gaps.

Location: Global.

Time period: 1980–2020.

Taxon studied: Bivalvia.

Methods: We synthesize published global economic costs of impacts from freshwater bivalves using the InvaCost database and associated R package, explicitly considering the reliability of estimation methodologies, cost types, economic sectors and impacted regions.

Results: Cumulative total global costs of invasive macrofouling bivalves were \$ 63.7 billion (2017 US\$) across all regions and socio-economic sectors between 1980 and 2020. Costs were heavily biased taxonomically and spatially, dominated by two families, Dreissenidae and Cyrenidae (Corbiculidae), and largely reported in North America. The greatest share of reported costs (\$ 31.5 billion) did not make the distinction between damage and management. However, of those that did, damages and resource losses were one order of magnitude higher (\$ 30.5 billion) than control or preventative measures (\$ 1.7 billion). Moreover, although many impacted socio-economic sectors lacked specification, the largest shares of costs were incurred by authorities and stakeholders (\$ 27.7 billion, e.g., public and private sector interventions) and through impacts on public and social welfare (\$ 10.1 billion, e.g., via power/drinking water plant and irrigation system damage) in North America. Average cost estimates over the entire period amounted to approximately \$ 1.6 billion per year, most of which was incurred in North America.

Main conclusions: Our results highlight the burgeoning economic threat caused by invasive freshwater bivalves, offering a strong economic incentive to invest in preventative management such as biosecurity and rapid response eradications. Even if the damages and resource losses are severely understated because economic impacts are lacking for most invaded countries and invasive bivalve species, these impacts are substantial and likely growing.

Phillip J. Haubrock and Ross N. Cuthbert contributed equally to this work.

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KEYWORDS

Cyrenidae, Dreissenidae, InvaCost, macrofouling, mussel, non-native, socio-economic impact

1 | INTRODUCTION

Freshwater ecosystems have been identified as among the most threatened worldwide, owing to their sensitivity to the effects of climate change (Woodward et al., 2010) and a range of other anthropogenic pressures (Darwell et al., 2018; Haubrock et al., 2021), including invasive species (Poulin et al., 2011; Strayer, 2010). Globally, invasive non-native species are a major driver of erosion of native biodiversity and the disruption of ecosystem functioning (Blackburn et al., 2019; Malcolm & Markham, 2000; Stigall, 2010). Furthermore, they are a burgeoning economic stressor on virtually all resource sectors—especially those associated with inland waters, where they are several times more likely than natives to become socio-economic pests (Hassan & Ricciardi, 2014). Indeed, invasion rates worldwide have been steadily increasing with no sign of saturation (Seebens et al., 2017), owing to increasing globalization, intensification of global transport networks and accessibility of new non-native source pools (Seebens et al., 2018). At present, most countries have limited capacity to manage invasions (Early et al., 2016) and are increasingly forced to make decisions regarding investment in biosecurity versus other societal needs.

In recent years, the ecological impacts of invasive species on recipient ecosystems have been quantified (e.g., Crystal-Ornelas et al., 2021; Dick et al., 2017; Kumschick et al., 2015). However, while categorizations for invader socio-economic impacts have been designed (Bacher et al., 2017), there remains a paucity of quantified socio-economic costs for key taxonomic groups, hampering effective cost-benefit analysis and rationale for policymakers to invest the sparse available resources towards prevention and control (but see Cuthbert, Pattison, et al., 2021; Diagne et al., 2021, for analyses at the global scale across taxa). This constraint to invest still exists even though it has been shown that preventive measures are generally considered more cost-effective than long-term damages and control (Ahmed et al., 2021; Keller et al., 2008), with pre-invasion management remaining underfunded (Leung et al., 2002). Indeed, proactive preventative measures have the potential to yield trillion-dollar savings over just a few decades compared with delayed management actions (Cuthbert et al., 2022). Accordingly, as invasions are increasing globally (Seebens et al., 2017; 2021), it is important to document the economic costs of taxonomic groups known to include damaging invasive species, as it could help to inform decision-making at the national level and thus provide appropriate economic incentives for proactively managing the arrival and spread of such species.

A group of aquatic invasive species that has caused significant ecological and socio-economic impacts are freshwater bivalves (Cuthbert et al., 2021; Sousa et al., 2009, 2014), including, inter alia, several hyper-successful invasive species from the genera *Dreissena*, *Limnoperna* and *Corbicula* (Bódis et al., 2014; Boltovskoy et al., 2006;

Karatayev et al., 2007; Sousa et al., 2008). These taxa have caused a broad range of impacts, such as macrofouling, habitat modification, restructuring communities and food webs, nutrient mineralization, contaminant transfer, alteration of oxygen availability and sedimentation rates, and promotion of excessive macrophyte and algal growth (see reviews by Boltovskoy et al., 2006; Karatayev et al., 2007; Ward & Ricciardi, 2007). Recognized as ecosystem engineers, invasive bivalves have a particularly marked effect on suspended particle concentrations and water clarity by filter feeding, as well as sediment bioturbation and the provisioning of shells, which alter habitat (Sousa et al., 2014). In turn, they affect various sectors of society (e.g., infrastructure, municipal and industrial water supply systems, and fisheries; Hoyle et al., 1999; Minchin et al., 2002; Waterfield, 2009). Arguably, the enormous costs associated with invasive bivalves such as the Asian clam *Corbicula fluminea* and the zebra mussel *Dreissena polymorpha* have done more to raise public awareness of aquatic invasions than their respective ecological impacts, although the economic and ecological impacts are often linked (e.g., Kao et al., 2016). On the contrary, invasive freshwater bivalves have, on occasion, been associated with certain perceived beneficial effects for human activities, as with other invaders (Kourantidou et al., 2022). For instance, their filtration capacity can substantially increase water clarity (Boltovskoy et al., 2009; Higgins & Vander Zanden, 2010; Phelps, 1994), which may benefit certain recreational activities (e.g., scuba diving and angling), while at the same time causing food web disruptions that harm fisheries (Kao et al., 2016).

Despite the notoriety of invasive freshwater bivalves in invasion science, information on their economic costs has not been synthesized. To broadly address this pervasive lack of information and provide a basis for quantifications of costs associated with invasive species worldwide, the InvaCost database has recently been developed (Diagne et al., 2020). This database contains extensive information on the costs (e.g., cost types, impacted sectors, regional attributes, cost estimation reliability) associated with ~500 invasive species. In the present study, we use a subset of the database to describe global costs associated with invasive freshwater bivalves and how they are structured, anticipating unevenness in cost reporting towards a few regions and a few highly conspicuous invasive species.

2 | METHODS

2.1 | Original data

To estimate the cost of bivalve invasions of freshwaters on the global economy, we considered data from the latest version of the InvaCost database at the time of writing this manuscript (version 4.0; full database and descriptive files are available at <https://doi.org/10.6084/>

m9.figshare.12668570). We note that although some IAS can provide both benefits and costs to economies (Kouranditou et al., 2022), InvaCost does not quantify benefits provided by IAS and potential beneficial effects are thus outside the scope of this study. This database (13,123 entries; Diagne et al., 2020; Angulo et al., 2021) compiles entries that extensively describe documented costs globally, enabling large-scale cost syntheses associated with invasive species in different spatial and temporal frames. Grey and published references were retrieved from standardized searches in online repositories (Web of Science, Google Scholar and Google search engine) and opportunistic collection based on targeted searches. Full information on the search terms (see Appendix S1) is provided in Diagne et al. (2020) and Angulo et al. (2021). Gathered references were thoroughly examined to assess relevance and then scrutinized for collating cost estimates associated with invasive species. Every cost entry was recorded, depicted by 64 parameters, and finally converted to a common and up-to-date currency (US dollars (US\$) 2017; see Diagne et al., 2020, for detailed information; Appendix S2). From this full database, 241 cost data entries were identified as exclusively belonging to the Bivalvia class using the “Class” column filter and 233 cost data entries belonging to bivalves which impact freshwaters (see Figure 1). We therefore excluded fully marine species, but focused on various taxa such as *D. polymorpha* and *Mytilopsis* spp. that occur in both brackish and freshwater ecosystems (e.g., Leppäkoski et al., 2002).

2.2 | Estimating the total costs

Deriving the total cumulative cost of invasions over time requires consideration of the probable duration time of each cost

occurrence. This duration consisted of the number of years between those mentioned in the “Probable_starting_year_adjusted” and the “Probable_ending_year_adjusted” columns. When information was missing for the “Probable_starting_year_adjusted” column, we conservatively considered the publication year of the original reference. For the “Probable_ending_year_adjusted” column, information was missing only for *potentially ongoing* costs (“Occurrence” column), which are costs likely to be repeated over years (contrary to *one-time* costs occurring only once along a precise period). We used this temporal information to annualize the invasion cost entries (3rd step in Figure 1). This was done by “expanding” the database via the *expandYearlyCosts* function of the “invacost” R package (Leroy et al., 2021)—a process that causes each entry in the database to correspond to a single year, thereby increasing the number of entries beyond that of the original data. For example, an initial single cost between 2000 and 2009 that totalled at \$ 10,000 would become ten entries at \$ 1,000 each after the expansion. All analyses were performed using this version of the database. A full explanation of this and other functions used is available in Leroy et al. (2021). For one cost entry, the probable ending year was presumably after 2020. Hence, all resulting cost estimates projected beyond 2020 were not taken into account. Similarly, costs were not available before 1980. This resulted in a subset of 461 expanded database entries (Figure 1). The dataset was then reduced to 461 entries by removing entries before 1980 to ensure comparability of currency translations (“recent” in Figure 1) and is provided in Appendix S3.

Finally, the invasion costs were specifically estimated by summing all entries according to different descriptive columns of the database (see Appendix S2):

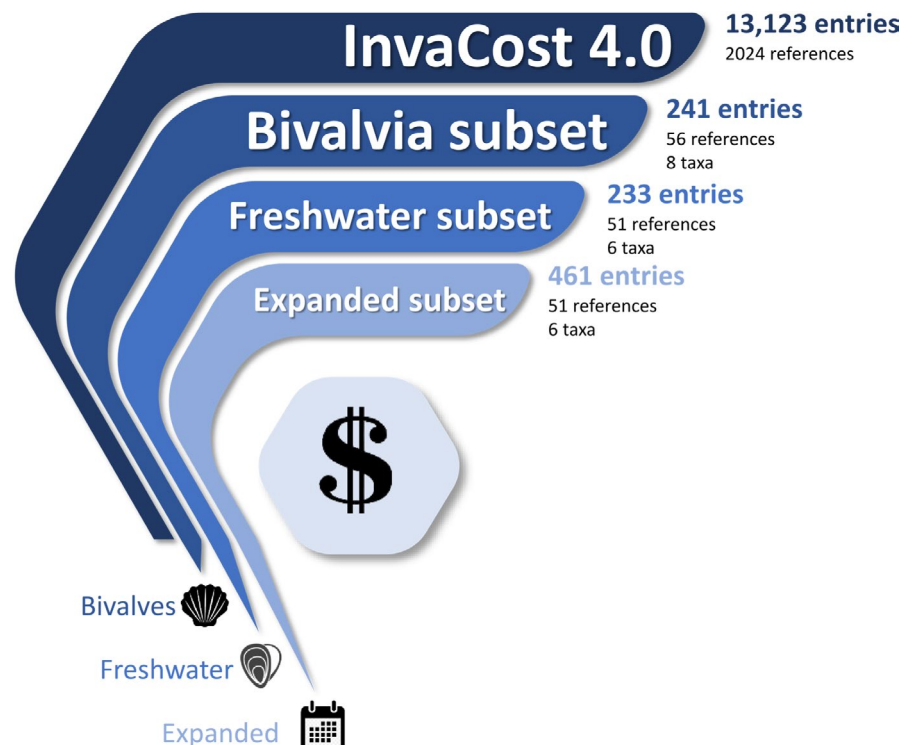


FIGURE 1 Successive steps of filtering from the entire InvaCost database to the subset analysed for annualized costs of freshwater bivalves between 1980 and 2020. Each step is detailed in the text

- (i) Method reliability: illustrating the perceived reliability of cost estimates based on the type of publication and method of estimation. Estimates in peer-reviewed publications or official reports, or with documented, repeatable and/or traceable methods were designated as *high* reliability; all other estimates were designated as *low* reliability (Diagne et al., 2020). We acknowledge that this approach, which categorizes costs as *high* reliability based on their presence in peer-reviewed or official material, may not be fully representative of the diverse forms of method reliability of cost estimates. Nevertheless, these criteria provided clear, objective and reproducible means of assessing material, as it was not feasible to assess method reliability on a broader categorical scale;
- (ii) Implementation: referring to whether the cost estimate was actually realized in the invaded habitat (observed) or whether it was extrapolated (potential), based on the methods reported in the underlying study (i.e. we did not perform extrapolations ourselves);
- (iii) Geographic region: describing the geographic origin of the listed cost;
- (iv) Type of cost merged: grouping of costs according to the categories: (a) *damage* costs referring to damages or losses incurred from invasion (e.g., costs for damage repair, resource losses, medical care), (b) *management* costs comprising control-related expenditure (e.g., monitoring, prevention, management, eradication) and money spent on education, research and maintenance costs, and (c) *mixed* costs including mixed damage and management costs (cases where reported costs were not clearly distinguished among cost types). We note that *management* costs include also research spending, irrespective of the findings, because this work often aims to better understand the ecology of invaders and their impacts, in turn informing management options;
- (v) Management type: breaking down if management costs were incurred by pre-invasion management (i.e. costs inferred from, e.g., early detection, biosecurity and/or monitoring efforts) and post-invasion management (i.e. costs inferred from control and/or eradication efforts), or rather originated from research-related efforts (knowledge funding); and
- (vi) Impacted sector (i.e. the activity, societal or market sector where the cost occurred; see Appendix S4). Individual cost entries not allocated to a single sector were modified to “mixed or unspecified”.

2.3 | Temporal dynamics of costs

We analysed the economic costs of invasive macrofouling bivalves over time. For this, we used the `summarizeCosts`-function implemented in the R package “`invacost`” (Leroy et al., 2021). With this method, we calculated the observed cumulative and average annual costs between 1980 and 2020 considering 10-year intervals.

3 | RESULTS

3.1 | Economic costs among bivalve families

The InvaCost database contained information on four out of five families of bivalves: Cyrenidae, Dreissenidae, Mytilidae and Unionidae, but not Sphaeriidae (Figure 2; Appendix 3). The collective costs of the 461 expanded entries in the InvaCost database for freshwater bivalves amounted to \$ 63.7 billion covering the impacted years 1980–2020. At the family level, 381 cost entries were attributable to Dreissenidae (\$ 51.1 billion), 28 to Cyrenidae (formerly Corbiculidae; \$ 12.4 billion), 46 to Mytilidae (\$ 140.5 million) and two to Unionidae (\$ 16.4 thousand). Four cost entries were inferred by diverse families of bivalves (\$ 9.3 thousand).

Within Dreissenidae, 380 cost entries were linked to the zebra mussel *D. polymorpha* (\$ 19.3 billion; $n = 271$) and quagga mussel *D. bugensis* (\$ 46.4 million; $n = 2$), either singularly or in congeneric combination (\$ 31.7 billion; $n = 107$), as well as one entry for the false mussel (*Mytilopsis trautwineana* \$ 68.3 thousand). Forty-six cost entries were found for the golden mussel *Limnoperna fortunei* (*Mytilidae*) (\$ 140.5 million) and two for the Chinese pond mussel *Sinanodonta woodiana* (*Unionidae*) (\$ 1.6 thousand). Further, four undefined species cost entries were derived, accounting for <1% of the documented total costs (\$ 9.3 thousand). All Cyrenidae entries ($n = 28$) were attributable to the Asian clam *C. fluminea* singularly (\$ 12.4 billion).

3.2 | Economic costs among method reliability and implementation types

Although constituting the majority of cost entries ($n = 346$), highly reliable cost estimates comprised only 10% of the documented total cost (\$ 6.2 billion), with the remaining costs not originating from accessible peer-reviewed or official sources. *Observed* costs accounted for 77% of costs from freshwater bivalves (\$ 49.0/63.7 billion; $n = 340/461$), whereas other *potential* costs were derived in the absence of the invader in the study area based on observed costs in other regions (i.e. in the case the species were to be introduced) or based on extrapolated predictions of an existing impact over time (see Diagne et al., 2020, for details). In particular, 72% of documented Dreissenidae costs (\$ 36.6/51.1 billion; $n = 262/381$), as well as 99% (\$ 12.43/12.44 billion; $n = 27/28$) of Cyrenidae costs, were observed.

3.3 | Economic costs among geographic regions and cost types

Approximately 98% of the total costs were incurred in North America (Figure 3a). For Dreissenidae, the single *M. trautwineana* cost was incurred in South America (\$ 0.007 billion), and 79 specific *D. polymorpha* cost entries were incurred in North America (\$ 18.2

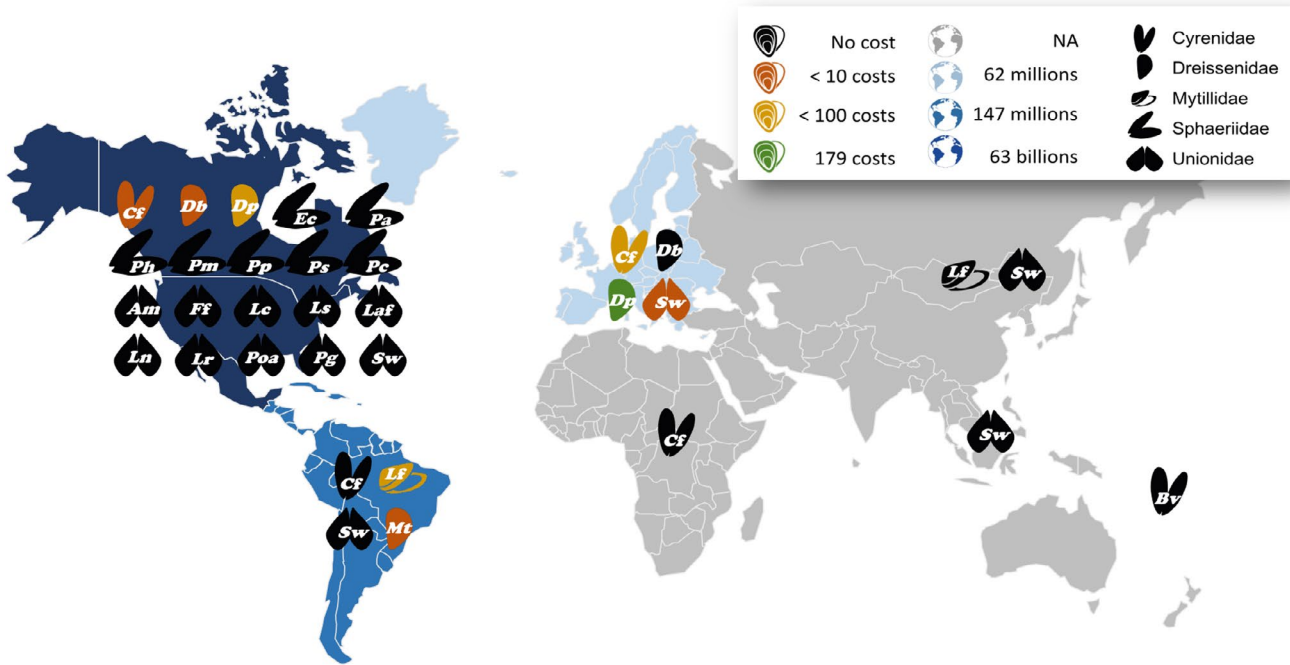


FIGURE 2 Distribution of known invasive bivalves according to Sousa et al. (2014), Lopes-Lima et al. (2020) and species listed in InvaCost. Costs are classified according to magnitude across geographic regions and number of cost entries (in InvaCost) per species. Entries inferred to unspecified regions or by unspecific taxa are not displayed. Species are as follows: *Corbicula fluminea* (Cf); *Batissa violacea* (Bv); *Dreissena bugensis* (Db); *Dreissena polymorpha* (Dp); *Limnoperna fortunei* (Lf); *Eupera cubensis* (Ec); *Pisidium amnicum* (Pa); *Pisidium henslowanum* (Ph); *Pisidium moitessierianum* (Pm); *Pisidium punctiferum* (Pp); *Pisidium supinum* (Ps); *Sphaerium corneum* (Sc); *Alasmidonta marginata* (Am); *Fusconaia flava* (Ff); *Lampsilis cardium* (Lc); *Lasmigona subviridis* (Ls); *Leptodea fragilis* (Laf); *Ligumia nasuta* (Ln); *Ligumia recta* (Lr); *Mytilopsis trautwineana* (Mt); *Potamilus alatus* (Poa); *Pyganodon grandis* (Pg); and *Sinanodonta woodiana* (Sw)

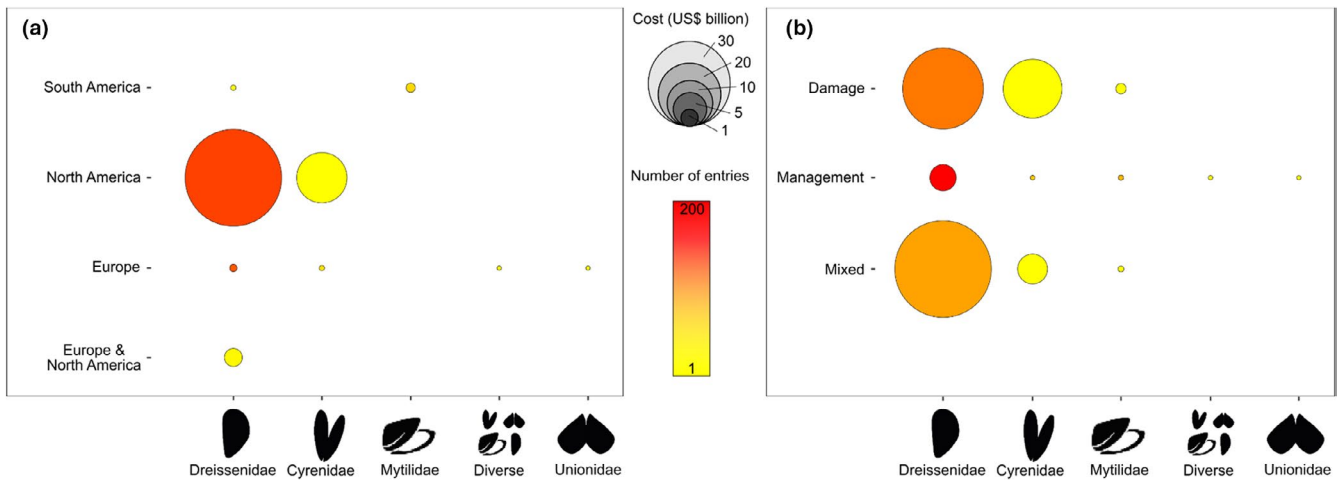


FIGURE 3 Global costs of recorded invasive freshwater bivalve taxa according to the affected continent (a) and cost type (b). The colour ramp corresponds to cost entries

billion), 13 in Europe and North America combined (\$ 1.10 billion) and 179 in Europe (\$ 0.06 billion). Mixed *D. polymorpha* and *D. bugensis* entries cost North America a further \$ 31.7 billion ($n = 107$). Cyrenidae costs were also mostly in North America (\$ 12.4 billion; $n = 9$), with some coverage in Europe (\$ 6.2 million; $n = 19$). No invasive bivalve costs were reported for Africa, Asia or Oceania. All costs of the family Mytilidae (*L. fortunei*; $n = 46$; \$ 0.14 billion) were

incurred in South America, while the two cost entries of Unionidae (*S. woodiana*, \$ 0.02 million) were incurred in Europe.

With respect to cost types, 48% of the total bivalve-related cost was categorized as due to damages or resource losses (\$ 30.5 billion; $n = 98$), with relatively little (3%; \$ 1.7 billion; $n = 293$) spent on management singularly (Figure 3b). The largest share of the total cost (49%; \$ 31.5 billion; $n = 70$) was, however, categorized as general (mixed) as

they contained elements relating to several cost types and were thus not specific. Dreissenidae costs were largely mixed in type, followed by exclusive damages, then management. For Cyrenidae, the majority of costs was due to damages, whereas most of the remainder was associated with mixed management and damages. Mytilidae costs were distributed relatively minorly across all cost types, whereas Unionidae was solely management-related. For the \$ 1.7 billion in total management costs, \$ 1.6 billion was invested reactively post-invasion, whereas only \$ 0.002 billion was invested proactively pre-invasion, and with just \$ 0.04 billion spent on knowledge funding.

3.4 | Economic costs across North American sectors

In North America specifically, where the vast majority of bivalve costs were reported, 10% (\$ 6.2 of 62.4 billion) of the total bivalve cost was incurred by mixed or unspecified socio-economic sectors (Figure 4). Then, 16.2% (\$ 10.1 billion) impacted public and social welfare directly (e.g., via power/drinking water plant and irrigation system damage), only being surpassed by 44.4% of costs (\$ 27.7 billion; $n = 94$) attributed to authorities and stakeholders (e.g. public and private sector interventions; see Appendix 4 and Diagne et al., 2020, for full definition of each category). Of the remaining sector types, “Environment” was reportedly impacted to the sum of \$ 369.6 million ($n = 16$), followed by “Fisheries” with \$ 4.2 million ($n = 2$). At the species level, *C. fluminea* had lower costs to the public and social welfare sector than *D. polymorpha* (\$ 2.2 vs. 7.6 billion).

3.5 | Economic cost accumulations through time

Average costs between 1980 and 2020 are presented in Figure 5. In total, these costs remained at a consistent magnitude over the past decade and amounted to \$ 63.7 billion, with an average annual cost

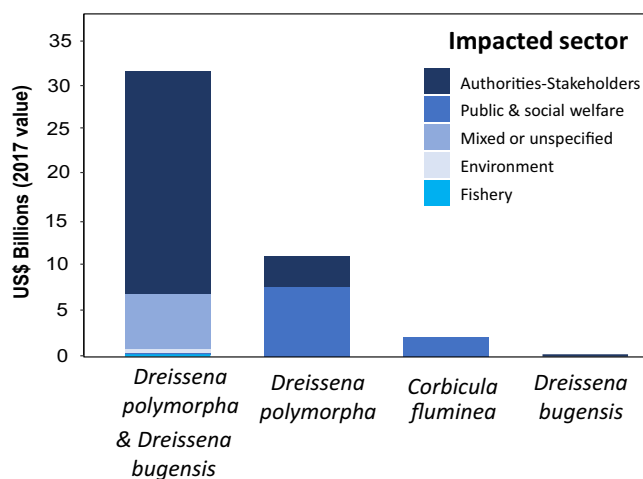


FIGURE 4 Total cost estimates for the major contributing invasive freshwater bivalve species according to the impacted sectors in North America

over the entire period of \$ 1.55 billion. Whereas the effects of time-lags in cost reporting were not incorporated into analyses, average cost estimates became reduced slightly towards the end of the last decade, indicating a temporal gap in cost reporting.

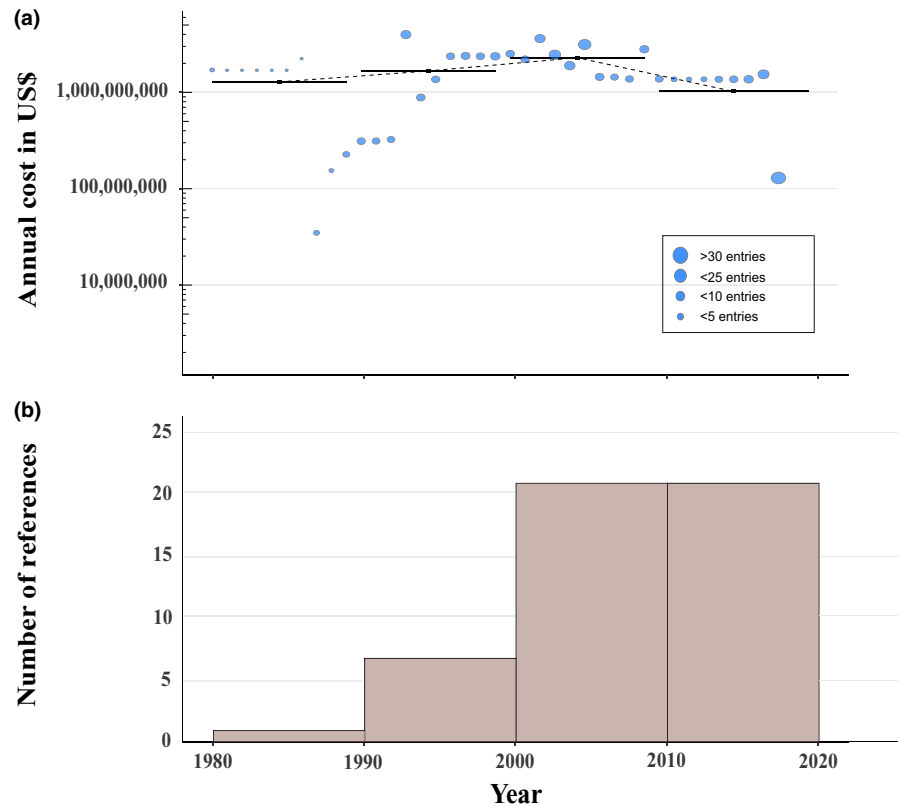
4 | DISCUSSION

The present study demonstrates massive economic costs associated with invasive freshwater bivalves, estimated at a total of \$ 63.7 billion over the period 1980–2020. The resulting average annual cost of \$ 1.55 billion is approximately half the 2020 United Nations budget (<https://news.un.org/en/story/2019/12/1054431>).

Invasive freshwater bivalves can transform entire ecosystems, thereby affecting fisheries and other resources of economic importance (Hansen et al., 2020; Kao et al., 2018; Strayer et al., 1999). However, the implications of these ecosystem engineering effects on economies had not yet been synthesized at the global scale. Within the InvaCost database, Dreissenidae constituted the majority of data sources and costs, while fewer cost entries referred to Cyrenidae and none to other families, excepting minor additions from Mytilidae and Unionidae. Within these families, *D. polymorpha*, *D. bugensis* and *C. fluminea* were implicated in the vast majority of economic damages, particularly in North America where they are widespread and locally abundant. Nonetheless, species such as *C. fluminea* are global invaders (Sousa et al., 2008), and thus, a lack of cost estimation for such taxa on a wide scale is surprising and indicates a profound lack of reporting. Furthermore, few documented costs were reported for the golden mussel *L. fortunei*, which is invasive in South-East Asia and South America (e.g., Boltovskoy & Correa, 2015; Sousa et al., 2014). Accordingly, the current availability of costs identified is inherently species-specific, and thus, costs likely represent a gross underestimation of the full scale of economic impacts across taxonomic groups, given the range of impact types associated with many macrofouling freshwater species and entirely unreported groups (Sousa et al., 2009, 2014). This is further evidenced by our results, in that just six known freshwater invasive bivalves had reported costs—which are themselves likely underestimated numbers.

On a taxonomic level, the present study found that some key species of freshwater bivalves with well-known invasion histories (e.g., the golden mussel *L. fortunei*, the false mussel *Mytilopsis trautwineana*, the Chinese pond mussel *Sinanodonta woodiana*) account for only a few entries in the InvaCost database, owing to a lack of published or traceable cost data. Macrofouling induced by *L. fortunei* and *M. leucophaeta* (a predominantly brackish-water species that was not represented in InvaCost), in particular, has been recognized as an economic problem for South America and Europe, respectively, where they foul municipal and industrial water supply systems (Verween et al., 2010). Yet, their invaded regions contributed very little or none of the total documented costs of freshwater invasive bivalves. Both *L. fortunei* and *M. leucophaeta* generate dense colonies causing obstructed water flow in pipes, occlusion of water filters,

FIGURE 5 Annual costs between 1980 and 2020 for invasive macrofouling freshwater bivalves (a) and total number of cost reporting references (i.e. number of studies) per decade (b). On (a), black squares and adjacent bars represent decadal means; blue circles represent annual total costs and are scaled according to the number of database entries (i.e. number of costs within studies). Note the broken y-axis on a \log_{10} scale in (a)



and corrosion of surfaces that result in system shutdowns, chemical/mechanical treatment and equipment replacement (Boltovskoy et al., 2015; Magara et al., 2001; Montalto & De Drago, 2003; Rajagopal et al., 2003), virtually identical to the biofouling impacts associated with *Dreissena* and *Corbicula*. In a review of the economic impacts of *L. fortunei* on man-made structures, Boltovskoy et al. (2015) noted that “objective estimates of the economic losses are extremely rare”, but nevertheless, economic impacts are probably quite substantial. The authors mentioned that the annual costs of maintenance and cleaning tasks owing to *Limnoperna* biofouling in one pipeline project in China, for example, have been anecdotally reported at over \$ 1 million. However, this cost was not included in the analysis as no citable reference could be located. In Brazil, over 30 hydroelectric power plants along the Paraná River and its tributaries have been colonized by *L. fortunei*; a shutdown of a single 40 MW turbine for servicing as a result of biofouling could cost \$ 6.2 million per year in lost power generation (reviewed by Boltovskoy et al., 2015). Concomitantly, the lack of costs of clogging due to *Dreissena* sp. invasions in, for example, Europe is an obvious lack of reported cost data (Adams, 2010). Indeed, the zebra mussel invaded most of the waterways in central and western Europe well before the mid-20th century (Dediú, 1980; Padilla, 1997).

Moreover, the geographic unevenness of cost estimations towards North America and the complete lack of documented cost estimation within Asia, Africa and Oceania reflect major knowledge gaps in the economic costs of invasive bivalves spatially. In the case of North America, it may be possible that early estimates for invasion costs in the United States led to greater

reporting efforts for invasion economic effects in the last two decades (Pimentel et al., 2000). Furthermore, there is a characteristic discrepancy in the importance, valuation and the spatial size of lakes in North America (i.e. the Laurentian Great Lakes) and riverine ecosystems in Europe, which has likely led to an imbalance in the research effort and impacted sectors. Accordingly, we speculate that this produced a baseline bias leading to unevenly reported costs in Europe—in contrast to the sudden incursion and recognition of massive costs following the more recent invasion of North America. Moreover, zebra mussel densities in the Great Lakes reached peaks that were 1 – 2 orders of magnitude larger than what is typically reported in Europe, probably because as invasions progress, mussel densities tend to level off at a lower equilibrium density (Burlakova et al., 2006; Jernelöv, 2017). Less than 1% of the globally reported costs of invasive bivalves was estimated from solely within Europe or South America, but an absence of evidence is not evidence of absence, suggesting that the real costs may be several magnitudes higher. In line with this argumentation, it is likely that regional biases are—at least in part—explainable by language barriers, and thus, relevant costs have not yet been identified in some regions (Angulo et al., 2021). Indeed, whereas InvaCost includes cost data searched for in over 15 non-English languages (Angulo et al., 2021), several languages have not yet been included in searches, particularly across Asia and Africa. A further barrier to the collation of invasion costs is their lack of publication, where costs may have been incurred but are not yet publicly accessible or require targeted contacting of relevant parties. Similarly, reported costs may not be detailed enough to

be informative, for example, by not distinguishing particular taxa causing the costs, or sectors in which they are incurred.

The annual average cost of \$ 1.5 billion is lower than the previous annual cost estimation (\$ 2 billion) for the zebra mussel and Asian clam in the United States (Pimentel et al., 2005). However, here we explicitly account for temporal dynamics in costs over a longer period, using a more conservative methodology and more robust data than the heavily criticized approach presented by Pimentel et al. (Hoffmann & Broadhurst, 2016). Our analyses indicated that studies reporting invasive freshwater bivalve costs have remained at a similar magnitude in recent decades. While average decadal cost estimates tended to decline slightly in recent years, this is likely to be an artefact of time-lags in cost estimation, rather than an empirical reduction in economic impact. The relative stability in cost increases for freshwater bivalves might also relate, in some cases, to improved management efficiencies—in spite of increases in both invasive species numbers (Seebens et al., 2017) and global invasion costs (Diagne et al., 2021, see also Cuthbert, Pattison, et al., 2021, for aquatic IAS) through time. For example, once being initially impacted by pipe-clogging and having to shut down for cleaning, industries will typically bleed chlorine in their water intakes to eliminate further fouling, thus reducing ongoing costs. On the contrary, it is also entirely possible that the annual monetary burden actually increased between years owing to new invasions, interventions or damages, leading to a gross underestimation of costs, owing to (i) insufficient reporting (Enders et al., 2019; Wakida-Kusunoki et al., 2015) and / or (ii) the very conservative nature of our approach. It should be recognized that given increasing invasion rates, it is likely that costs are rising, but true economic effects over time are masked by cost reporting artefacts (e.g., a lag time of several years between establishment and reported costs in a new region; Haubrock et al., 2022).

An outstanding example of our conservative approach to estimation is the impact of biofouling by the Asian clam *Corbicula fluminea* on the operation of power plants in the United States over several decades, compromising fail-safe operations and causing emergency shutdowns of nuclear facilities. The control and mitigation costs, as well as costs related to reduced plant operating efficiencies, were estimated by Isom (1986) to exceed \$ 1 billion per year, based on various anecdotal costs recorded primarily before 1980. Our approach led us to ignore all costs prior to 1980, despite *C. fluminea* having invaded the United States and other regions many decades before (Crespo et al., 2015). Further, these costs only pertain to power plants in the United States, whereas *C. fluminea* is globally invasive and has fouled water supply systems in other countries. In addition to impacts on technological systems, *C. fluminea* is known to negatively impact native bivalve abundance and diversity (Sousa et al., 2008), and to alter physical habitat structure including water quality, sediment composition and submerged vegetation (Phelps, 1994), thus producing ecosystem impacts that can be difficult to quantify in monetary terms (Darrigan, 2002). It should be emphasized therefore that we consider the presented costs to be highly conservative overall, particularly given the prominent cost reporting gaps, both

taxonomically and spatially. Inclusion of less reliable material, such as that with unclear temporal duration, could cause costs to be substantially higher than documented here.

Another factor contributing to uncertainty surrounding our estimate is the difficulty in quantifying types of economic damage associated with ecosystem services (Spangenberg & Settele, 2010). Invasive freshwater bivalves can be ecosystem engineers where they have substantial effects on ecosystem structure and function—and thus the various services they can provide to humans (e.g., aquaculture, water purification, sourcing of raw materials). For instance, dreissenid mussels indirectly stimulate benthic algal growth (Boegman et al., 2008), invasive aquatic weed proliferation (Crane et al., 2020; Zhu et al., 2006, 2007) and harmful algal *Microcystis* blooms (Vanderploeg et al., 2001). Furthermore, dreissenid species have been shown to create new pathways for the transfer of contaminants (e.g., Hg, Cd, PCBs, botulism toxin; Carrasco et al., 2008; Hogan et al., 2007). These effects likely result in substantial indirect socio-economic impacts that are difficult, if not impossible, to evaluate in terms of monetary losses. Contrastingly, dreissenid mussels have reportedly led to reduced cyanobacteria and diatom abundances in invaded reservoirs (Reynolds & Aldridge, 2021). More directly, costs of invasive macrofouling bivalves incurred for technological systems other than power plants (municipal and industrial water supply systems in general; fouling of lock-and-dam structures and aquaculture equipment) are virtually undocumented for most regions of the world other than the United States and Canada. Research effort into freshwater bivalves is concentrated in North America and Europe (Lopes-Lima et al., 2014), with a consequent lack of detailed reporting of basic aspects of invasions in other regions (Lopes-Lima et al., 2018), where invasive freshwater bivalves have been reported only relatively recently (e.g., Africa; Clavero et al., 2012). In these cases, published documentation of ongoing costs is urged to fully account for monetary aspects of invasion within emerging economies.

The sparse economic data for invasive freshwater bivalves also inhibit recognition of any potential benefits these species provide to humans, and thus impede comprehensive cost-benefit analyses, which could further inform and direct management actions among different economic sectors or regions (Kouranditou et al., 2022). For example, filtration activities of dense populations of *Dreissena* spp. and *C. fluminea* have been shown to substantially increase water clarity (Boltovskoy et al., 2009; Higgins & Vander Zanden, 2010; Phelps, 1994). These, while causing myriad ecological disruptions and harming fisheries whose focal species depend on prey that are competing with mussels for resources (Kao et al., 2018), could benefit certain recreational activities such as scuba diving. Concomitantly, this could conceivably drive tourist revenue and increase the property value of neighbouring real estate. Conversely, accumulations of sharp shells on beach sands are a hazard to the feet of swimmers (Ilarri et al., 2011; Ilarri & Sousa, 2012). While many beneficial effects are difficult to quantify in monetary terms, or are yet to be shown, it is unlikely that they will outweigh the presently documented (and underestimated) costs of \$ 63.7 billion.

Overall, our study highlights very fragmented data that call for national and regional authorities to produce more and better structured reporting of invasion costs. Given that many known invasive freshwater bivalve species (such as *Batissa violacea*, *Sphaerium corneum* and *Pisidium* spp.; see Sousa et al., 2014) and invaded regions completely lacked reported economic costs, our figures are likely gross underestimations. Nonetheless, the monetary costs reported in this study are still very high (e.g., over \$ 1.5 billion per year) and should provide added incentive to manage invasive bivalves in freshwater systems. In this regard, Ahmed et al. (2022) demonstrated how timely investments into early management of invasive species rapidly reduce long-term economic impacts, whereas delayed investments—especially in pre-invasion management—increase the costs ultimately incurred via post-invasion management and damage (Cuthbert et al., 2022). Therefore, the fact that management spending is a fraction of damages incurred suggests that not enough is being invested, and particularly in proactive biosecurity measures pre-invasion to prevent secondary spread, as well as in the few measures to rapidly eradicate populations at early invasion stages (e.g., Coughlan, Cunningham, et al., 2020; Tang & Aldridge, 2019). Pre-invasion biosecurity measures such as ballast-water management-treatment (Bailey, 2015; Ricciardi & MacIsaac, 2022), the cleaning of boats and fishing equipment between waters (Coughlan, Bradbeer, et al., 2020), and the establishment of rapid response teams (Caffrey et al., 2018) could be effective yet less cost-intensive means to prevent further spread and new arrivals.

Indeed, when specific cost types were known for invasive freshwater bivalves, damages and resource losses were an order of magnitude higher than control or management costs. Given that invasion rates are expected to keep increasing over time (Seebens et al., 2017; 2021), we suppose that the costs of invasive macrofouling freshwater bivalves will increase substantially in future, leading to staggering costs for stakeholders and governments (Scalera, 2010). This calls for an increase in efforts to quantify costs of invasive freshwater bivalves to fill knowledge gaps and to improve the ability to prioritize targeted management interventions. These knowledge gaps could be partly resolved by improving the reporting of cost information in a publicly available form, such that data can be readily captured and included in InvaCost via systematic literature searches. Further research efforts are also required to quantify costs for understudied taxa and parts of the world with lower research capacity, where ecological but not economic impacts are known. Nevertheless, the already substantial costs warrant greater management efforts immediately to curtail the further arrival and spread of existing and emerging macrofouling freshwater bivalves, by providing rationale to invest for stakeholders and decision-makers.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data used in this work are available as supporting information.

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BIOSKETCH

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Author contributions: FC and AR conceived the idea; CD and FC created the database; PJH and RNC analysed the data; and all authors contributed critically to drafts and gave final approval for publication.

SUPPORTING INFORMATION

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