Massive economic costs of invasive bivalves in freshwater ecosystems

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Abstract

Many countries lack the economic capacity to effectively manage invasive species. Yet, the direct socioeconomic impact generally much outweighs the expected costs of prevention. A distinct lack of monetary cost quantification associated with key invasive species groups impedes decision-making, and thus resource allocation, by policy makers to address invasions. Here, we synthesize published global economic costs of impacts for one key taxonomic group – freshwater bivalves – whilst explicitly considering the reliability of estimation methodologies, cost types, economic sectors and impacted regions. Although several species from this group are notorious widespread invaders, estimations of their economic costs have remained relatively sparse. Cumulative total global costs of invasive macrofouling bivalves were US$ 63.6 billion (2017 USD) across all regions and socioeconomic sectors between 1980 and 2020. Costs were heavily biased taxonomically and spatially, dominated by two families, Dreissenidae and Cyrenidae (Corbiculidae), and largely constrained to North America. The largest share of reported costs ($ 30.6 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 ($ 30.3 billion) than control or preventative measures ($ 1.7 billion). Moreover, although many impacted socioeconomic sectors lacked specification, the largest shares of costs were incurred through authorities and stakeholders ($ 26.3 billion, e.g. public and private sector interventions) and by public and social welfare ($ 11.6 billion, e.g. via power/drinking water plant and irrigation system damage). Average cost estimates over the entire period amounted to approximately $ 1.6 billion per year, most of which was incurred in North America. We thus present novel cost quantifications that offer a strong economic incentive to invest in preventative management of invasive bivalves in freshwaters. However, these costs are severely underestimated because well-documented economic impacts are lacking for most invaded countries and most invasive bivalve species.

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), including invasive species (Strayer 2010; Poulin et al. 2011). Globally, invasive non-native species are a major driver of erosion of native biodiversity and the disruption of ecosystem functioning (Malcolm and Markham 2000; Stigall 2010; Blackburn et al. 2019). 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 socioeconomic pests (Hassan and 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 better described (e.g. Kumschick et al. 2014; Dick et al. 2017; Crystal-Ornelas et al. 2020). However, whilst categorizations for invader socioeconomic impacts have been designed (Bacher et al. 2017), there remains a paucity of quantified socioeconomic costs incurred by invasions, constraining effective cost/benefit analysis and

rationale for policy makers to invest the sparse available resources toward prevention (but see Lovell et al. 2006; Marbuah et al. 2014). This constraint exists even though preventive measures are generally considered more cost effective than long-term mitigation and control (Keller et al. 2008; Ahmed et al., this issue), and management is less costly than losses from damages (Leung et al. 2002). Pimentel et al. (2000, 2005), and later Kettunen et al. (2009), were among the first to attempt to summarize the costs of invasive species on large scales. Despite methodological shortcomings, these pioneer studies had the benefit of raising awareness of the potentially huge costs associated with non-native species (Hoffmann and Broadhurst 2016). Their shortcomings originate from the problem that some categories of costs are difficult to quantify, especially regarding damages to ecosystem services or other indirect effects (Charles and Dukes 2008) and that they are often not comparable and thus summable. The lack of such synthesis, however, is critical because it can give the false impression that costs for invasive species are lower than empirically observed. In turn, this can result in an under-allocation of economic resources to tackle invasive species. Regional or even global estimations of the cost of invasions rely on the resolution of cost estimation at smaller spatial scales and at various taxonomic levels. In particular, 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 controlling the arrival and spread of such species.

A group of aquatic invasive species that has caused significant ecological and socioeconomic impacts are freshwater bivalves (Sousa et al. 2009; 2014), including, inter alia, several hyper-successful invasive species from the genera *Dreissena*, *Limnoperna*, and *Corbicula* (Boltovskoy et al. 2006; Karatayev et al. 2007; Sousa et al. 2008). These taxa have caused a broad range of impacts (e.g. 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 Karatayev et al. 1997; Boltovskoy et al. 2006; Ward and Ricciardi 2007). As a result, 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 invasions of 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. 2015). On the other hand, invasive freshwater bivalves have, on occasion, been associated with certain perceived beneficial effects for human activities, as with other invaders (Kourantidou et al., *this issue*). For instance, their filtration capacity can substantially increase water clarity (Phelps 1994; Higgins and Vander Zanden 2010; Boltovskoy et al. 2009), 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. 2015).

Despite the notoriety of invasive freshwater bivalves in invasion science, information on economic costs for invasive bivalves in freshwater ecosystems is often scanty or anecdotal, which challenges efforts to prioritize management action. To broadly address this pervasive lack of information and provide a basis for quantifications of costs associated with most 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, etc.) 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, anticipating unevenness in cost reporting towards a few regions and a few highly conspicuous invasive species. Moreover, we investigate how these costs are structured, and identify knowledge gaps in cost estimations for key invasive freshwater bivalves.

Methods

Original data

To estimate the cost of bivalve invasions of fresh waters on the global economy, we considered cost data from version 3 of the InvaCost database (full database and descriptive files are available at https://doi.org/10.6084/m9.figshare.12668570). This database (9,823 entries; Diagne et al. 2020; Angulo et al. 2021) compiles entries that extensively describe documented costs globally, enabling large-scale cost synthesis associated with invasive species in different spatial and temporal frames. We note that this database only reports monetary values for invasion costs, without considering monetised benefits of invasive species quantitatively. Therefore, the analyses which follow reflect that scope and only consider costs. Grey and published references were retrieved from standardised searches in online repositories (ISI Web of Science, Google Scholar and Google search engine) and opportunistic collection based on targeted searches. Full information on the search terms (see Supplementary material 1) 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; Supplementary Material 2). From this full database, 231 cost data entries were identified as exclusively belonging to the Bivalvia class using the 'Class' column filter and 226 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).

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 (4th step in Figure 1). This was done by 'expanding' the database via the *expandYearlyCosts* function of the 'invacost' R package (Leroy et al. 2020) – 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 US$ 10,000 would become ten entries at US$ 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. (2020). 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 468 expanded database entries (Figure 1). The dataset was then reduced to 443 entries by removing entries before 1980 to ensure comparability of currency translations ("recent" in Figure 1) and is provided in Supplementary Material 3.

Finally, the invasion costs were specifically estimated by summing all entries according to different descriptive columns of the database (see Supplementary Material 2):

(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. 2020b). We acknowledge that this approach, which categorises costs as *High* reliability based on their presence in peer-reviewed 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 realised 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 (for example monitoring, prevention, management, eradication) and money spent on education, research and maintenance costs, (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) Impacted_sector (i.e. the activity, societal or market sector where the cost occurred; see Supplement 4). Individual cost entries not allocated to a single sector were modified to "Other".

Temporal dynamics of costs

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

Results

Economic costs among taxonomic groups

The InvaCost database contained information on five families of bivalves: Cyrenidae, Dreissenidae, Mytilidae, and Unionidae (Figure 1). The collective costs of the 443 expanded entries in the InvaCost database for freshwater bivalves amounted to $ 63.6 billion covering the impacted years 1980–2020. At the family-level, 366 cost entries were attributable to Dreissenidae ($ 51.2 billion), 28 to Cyrenidae (formerly Corbiculidae; $ 12.4 billion), 43 to Mytilidae ($ 11.8 million), and 2 to Unionidae ($ 16.4 thousand). Four cost entries were inferred by both Dreissenidae and Cyrenidae simultaneously ($ 9.3 thousand).

Within Dreissenidae, 368 cost entries were linked to the zebra mussel *D. polymorpha* ($ 19.4 billion; n = 255) and quagga mussel *D. bugensis* ($ 4.6 million; n = 2), either singularly or in congeneric combination ($ 31.8 billion; n = 108). Forty-three cost entries were found for the golden mussel *Limnoperna fortunei* ($ 1.2 million), two for the Chinese pond mussel *Sinanodonta woodiana* ($ 1.6 thousand) and only one for the false mussel (*Mytilopsis trautwineana* $ 68.3 thousand). Further, 4 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).

Economic costs among method reliability and implementation types

Although constituting the majority of cost entries (n = 328), highly reliable cost estimates comprised only 10 % of the documented total ($ 6.2 billion), with the remaining costs not originating from accessible peer-reviewed or official sources. *Observed* costs accounted for 77 % from freshwater bivalves, 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, as well as 99% of Cyrenidae costs were observed.

Economic costs among geographic regions and cost types

Approximately 99% of the total costs were incurred in North America (Figure 2a). For Dreissenidae, the single *M. trautwineana* cost was incurred in South America ($ 0.007 billion), 69 specific *D. polymorpha* cost entries were incurred in North America ($ 18.2 billion), 13 in Europe and North America combined ($ 1.10 billion), and 173 in Europe ($ 0.06 billion). No invasive bivalve costs were reported for Africa, Asia or Oceania. All costs of the family Mytilidae (*L. fortunei*; *n* = 31; $ 0.012 billion) were incurred in South America, while the two entries of Unionidae (*S. woodiana*, $ 0.002 million) originated from Europe.

With respect to cost types, 48% of bivalve-related costs were categorised as due to damages or resource losses ($ 30.3 billion), with relatively little (3%; $ 1.7 billion) spent on control singularly (Figure 3b). The largest share of costs (50%; $ 31.6 billion) was, however, categorized as general (mixed) as they contained elements relating to several types and were thus not specific. For Cyrenidae, the majority of costs were due to damages, whereas the remainder were associated with mixed control and damages exclusively.

Economic costs across North American sectors

In North America specifically, where the vast majority of bivalve costs were reported, 39% ($ 24.2 billion; n = 51) of bivalve costs was incurred by undefined or unspecified socioeconomic sectors (Figure 4), whilst 19% ($ 11.6 billion; n = 25) impacted public and social welfare directly (e.g. via power/drinking water plant and irrigation system damage), only being surpassed by 41% of costs ($ 26.3 billion; n = 93) attributed to authorities and stakeholders (e.g. public and private sector interventions; see Diagne et al. 2020 for full definition of each category). Of the remaining sector types, 'Environment' was listed with $ 369.6 million, followed by 'Fisheries' with $ 7.4 million. At the species-level, *C. fluminea* had lower specific costs to the public and social welfare sector than *D. polymorpha* ($ 2.2 vs. 9.0 billion).

Economic cost accumulations through time

Cost accumulations 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 $ 63.6 billion, with an average annual cost over the entire period of $ 1.6 billion. Whilst 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 gap in cost reporting.

Discussion

The present study demonstrates massive economic costs associated with invasive freshwater bivalves, estimated at a total of $ 63.6 billion USD over the period 1980-2020. The resulting average annual cost of $ 1.6 billion is lower than the previous annual cost estimation ($ 2 billion USD) 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. Within the InvaCost database, Dreissenidae constituted the majority of data sources and costs, while fewer cost entries referred to Cyrenidae and none for other families, excepting minor additions from the Mytilidae and Unionidae. Within these families, *D. polymorpha*, *D. bugensis*, and *C. fluminea* were implicated in the vast majority of economic damage, 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 southeast Asia and South America (e.g. Sousa et al. 2014; Boltovskoy and Correa 2015). 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).

On a taxonomic level, some key species of freshwater bivalves with well-known invasion histories (e.g. the golden mussel *L. fortunei,* the dark false mussel *Mytilopsis leucophaeta,* 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 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, and corrosion of surfaces that result in system shutdowns, chemical/mechanical treatment, and equipment replacement (Magara et al. 2001; Montalto and De Drago 2003; Rajagopal et al. 2003; Boltovskoy et al. 2015), 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 USD. 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 USD per year in lost power generation (reviewed by Boltovskoy et al. 2015).

Moreover, the geographic bias 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. While North America is unique in its cultural history, leading to a substantially higher study effort, it is also possible that actually exerted impacts of invasive bivalves are unevenly distributed owing to differences in economic activity. Further, it may be possible that early estimates for invasion costs in the USA led to greater reporting efforts for invasion economic effects in the last two decades (Pimentel et al. 2000). Indeed, the zebra mussel invaded most of the waterways in central and western Europe well before the mid-20th century (Dediu, 1980). We speculate that this produced a baseline bias in which subsequent costs were not viewed as novel and thus, were not reported – in contrast with 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). However, this trend was already highlighted more broadly in invasion science (Early et al. 2016). In turn, less than 1 % of the globally reported costs of invasive bivalves were estimated from within Europe or South America; but an absence of evidence is not evidence of absence.

Our analyses indicated that studies reporting invasive freshwater bivalve costs have remained at a similar magnitude in recent decades. Whilst 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 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 on-going 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 (Wakida-Kusunoki et al. 2015; Enders et al. 2019) and / or (ii) the very conservative

nature of our approach. An outstanding example of the latter 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 USD 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 USA and other regions many decades before (Crespo et al., 2015). Further, these costs only pertain to power plants in the US, 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 emphasised, therefore, that we consider the presented costs to be highly conservative overall, particularly given the prominent cost reporting gaps, both taxonomically and spatially.

Another factor contributing to uncertainty surrounding our estimate is the difficulty in quantifying types of economic damage associated with ecosystem services (Spangenberg and Settele 2010). Invasive freshwater bivalves can be ecosystem engineers and keystone species where they have disproportionate effects on ecosystem structure and function– and thus, the various services they provide to humans (e.g. aquaculture). For instance, dreissenid mussels indirectly stimulate benthic algal growth (Boegman et al. 2008), invasive aquatic weed proliferation (Zhu et al. 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; Hogan et al. 2007; Carrasco et al. 2008). These effects likely result in substantial indirect socioeconomic impacts that are difficult, if not impossible, to evaluate in terms of monetary losses. 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 USA 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 inhibits recognition of any potential benefits these species provide to humans, and thus impedes comprehensive cost-benefit analyses which could further inform and direct management actions among different economic sectors or regions. For example, filtration activities of dense populations of *Dreissena* spp. and *C. fluminea* have been shown to substantially increase water clarity (Phelps, 1994; Higgins and Vander Zanden 2010; Boltovskoy et al. 2009), which (while causing myriad ecological disruptions and harm 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, which in turn 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.

Whilst 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 $ 63.6 billion USD.

In conclusion, our study highlights very fragmented data that calls 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., 2013) 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 billion US$ per year) and should provide added incentive to manage invasive bivalves in freshwater systems. When specific cost types were known, damages and resource losses were an order of magnitude higher than control or management costs, suggesting that more management is needed to prevent the spread and establishment. Given that invasion rates are expected to keep increasing over time (Seebens et al. 2017, 2020), we predict that the costs of invasive macrofouling freshwater bivalves will increase substantially in the future.

Declarations

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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 code required has been referenced in the related sections within the methods.

Authors' contributions

PJH and RNC led the writing and analysis. AR provided valuable insights and contributed to the writing. CD and FC provided the database and contributed to all aspects of the manuscript production.

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Figures

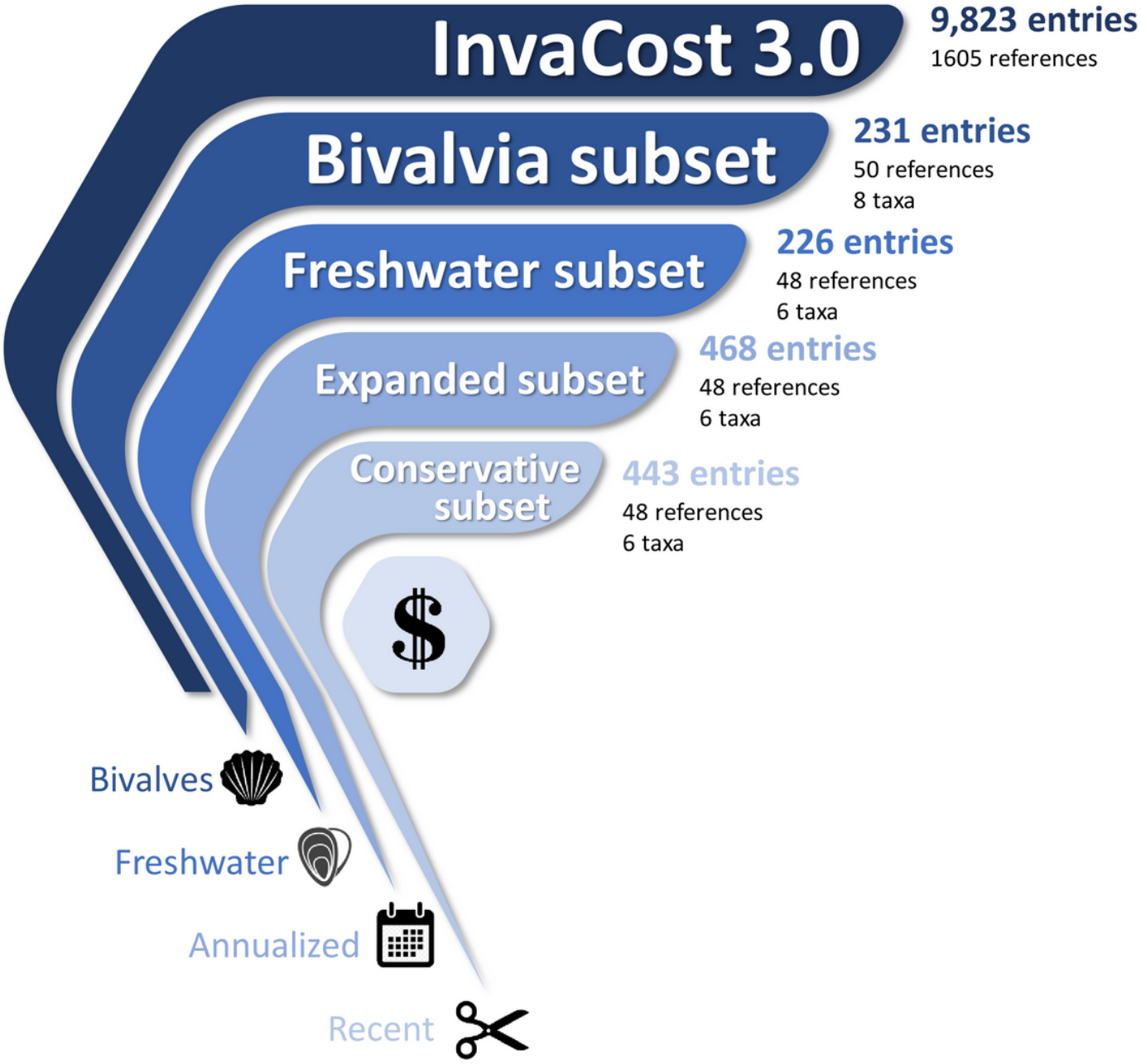

Figure 1

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

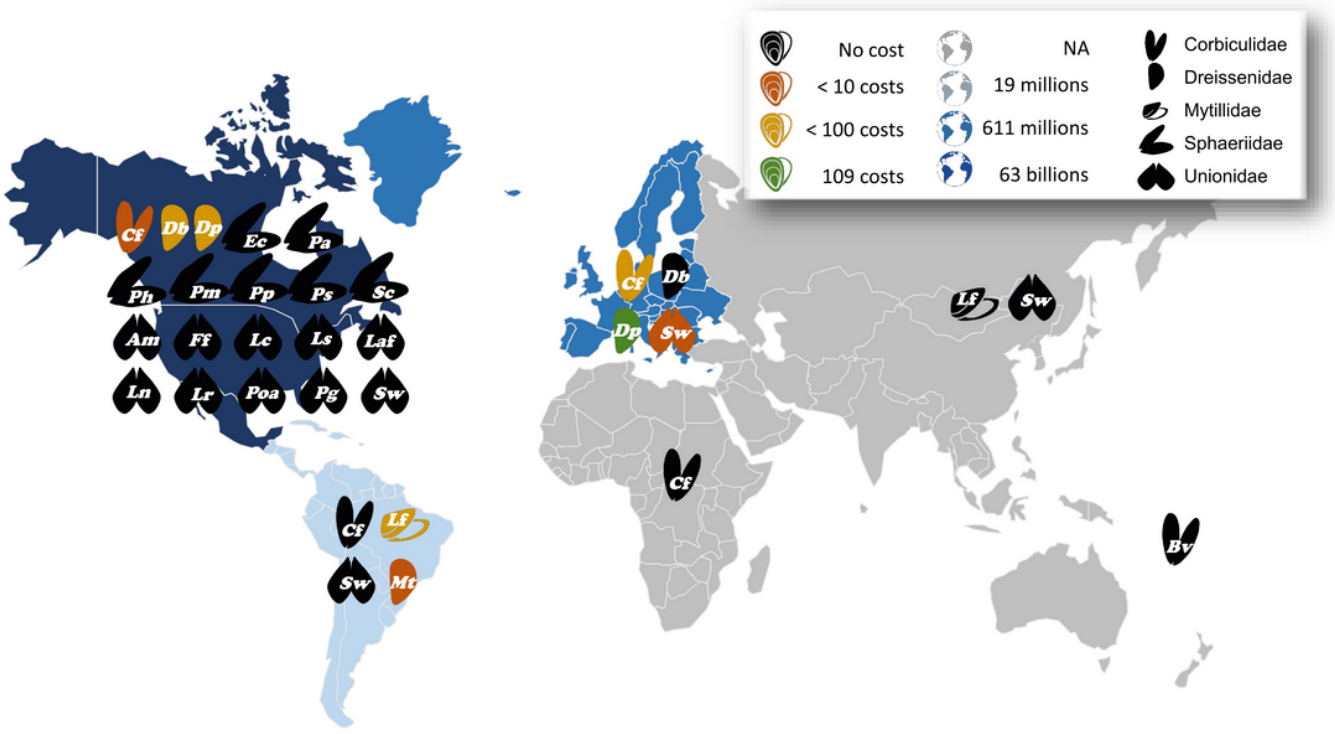

Figure 2

Distribution of known invasive bivalves according to Sousa et al. (2014) and species listed in InvaCost. Costs are classified according to magnitude across geographic regions and number of cost entries (in InvaCost) per species. Species are: Corbicula fluminea (Cf); Batissa violacea (Bv); Dreissena bugensis (Db); Dreissena polymorpha (Dp); Limnoperla fortunei (Lf); Eupera cubensis (Ec); Pisidium amnicum (Pa); Pisidium henslowanum (Ph); Pisidium moitesserianum (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); Potamilus alatus (Poa); Pyganodon grandis (Pg); Sinanodonta woodiana (Sw). 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.

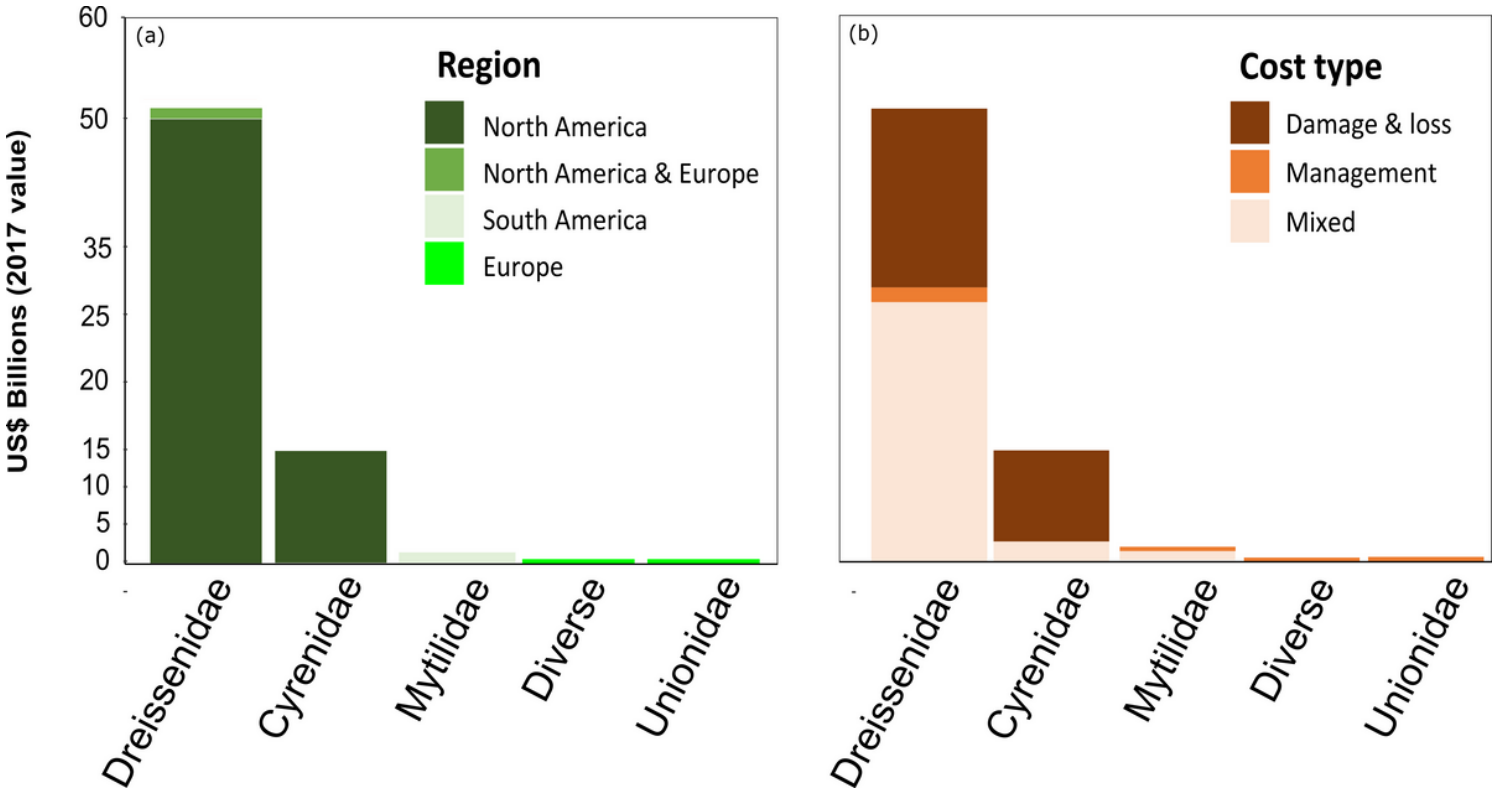

Figure 3

Global costs of recorded bivalve taxa according to affected continent (a) and cost type (b).

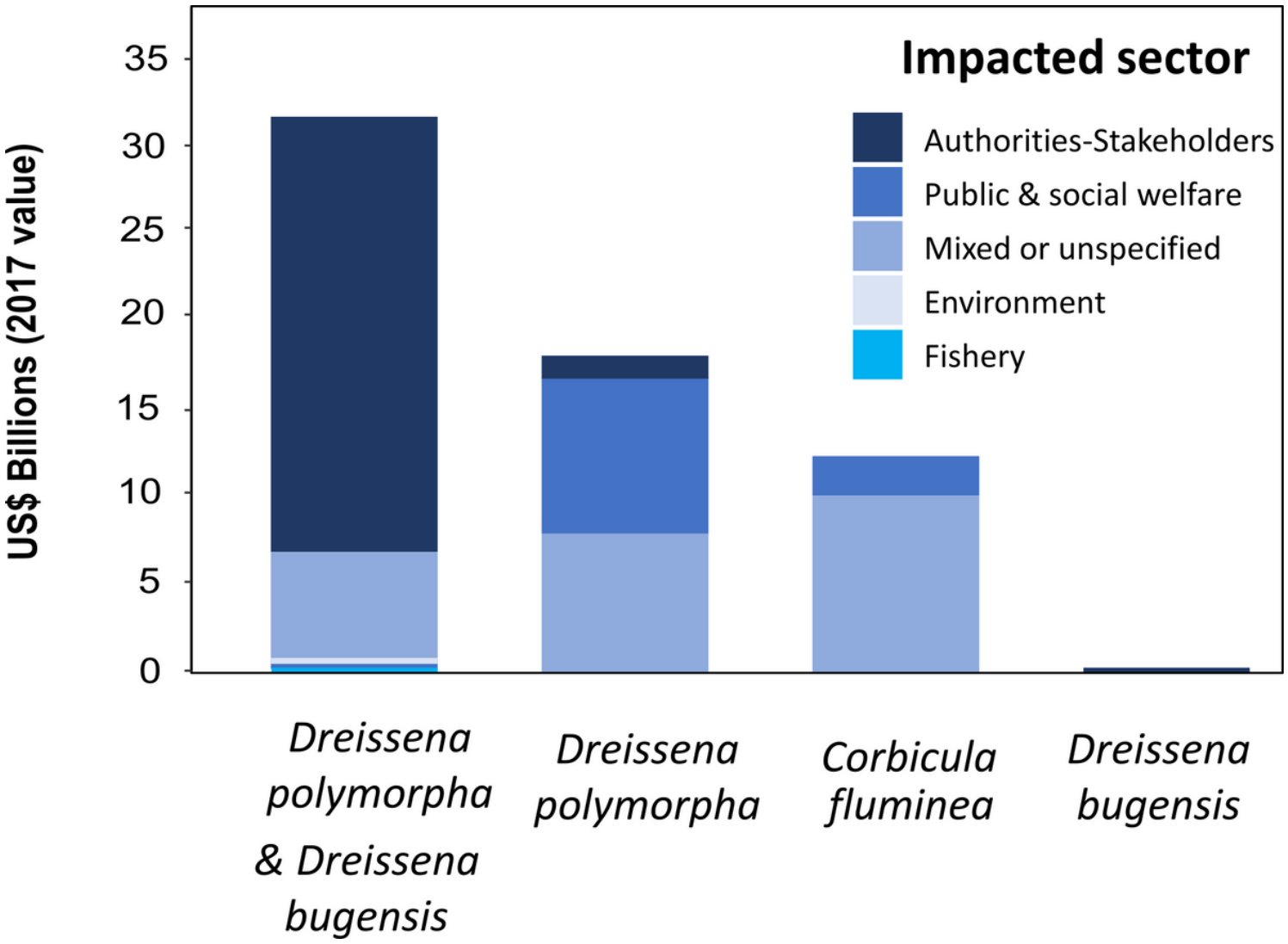

Figure 4

Total cost estimates for the major contributing species according to the impacted sectors in North America.

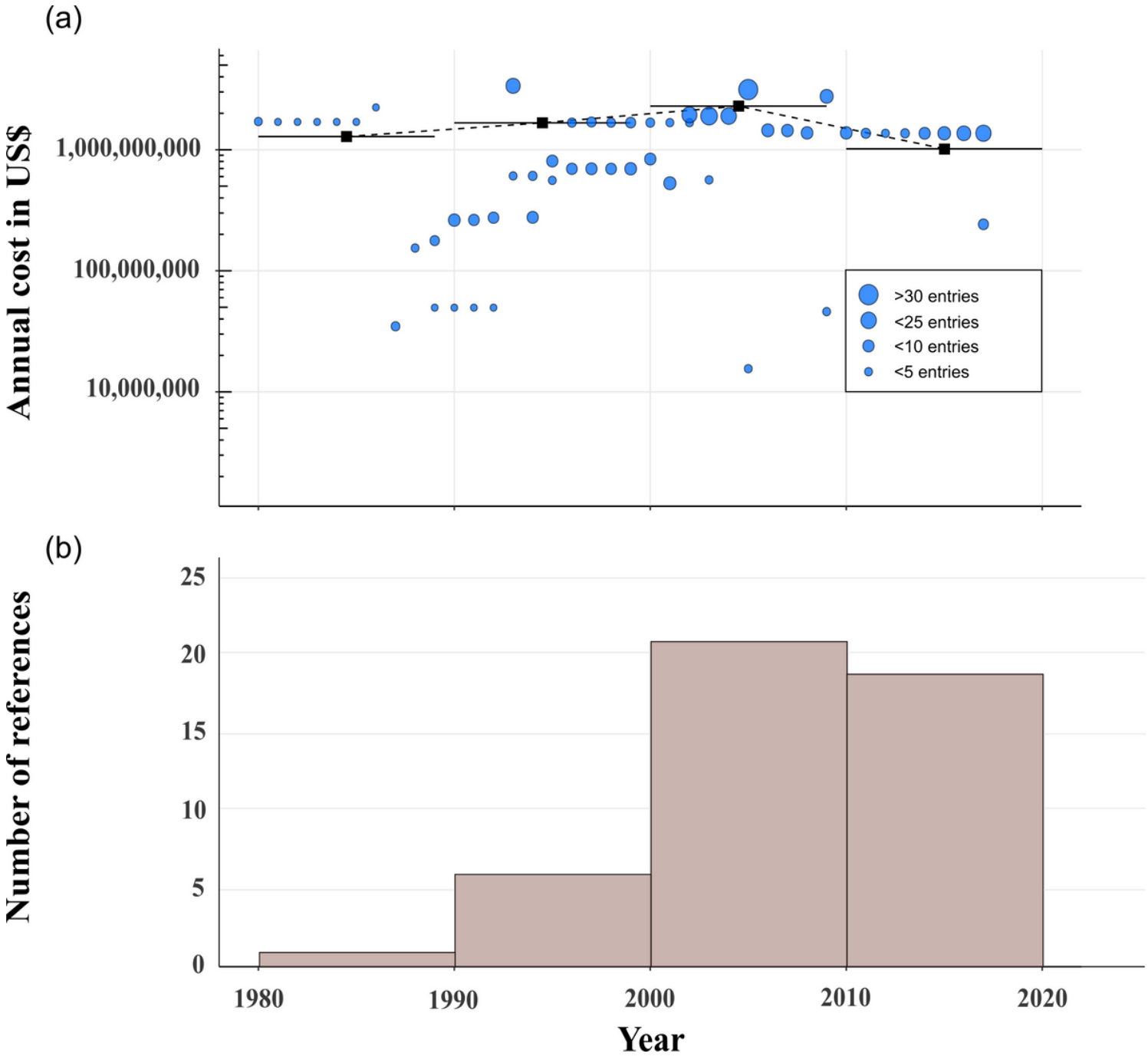

Figure 5

Annual total and observed costs between 1980 – 2020 of invasive macrofouling freshwater bivalves and the number of published cost entries between the same period. Points with bars represent decadal means. Note the broken y-axis scale.

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