Economic costs of invasive rodents worldwide: the tip of the iceberg

Christophe DIAGNE (chrisdiagne89@hotmail.fr)
Universite Paris-Sud https://orcid.org/0000-0002-6406-1270
Liliana Ballesteros-Mejia
Universite Paris-Saclay
Thomas Bodey
University of Aberdeen
Ross Cuthbert
GEOMAR: Helmholtz-Zentrum fur Ozeanforschung Kiel
Jean Fantle-Lepczyk
Auburn University
Elena Angulo
Universite Paris-Saclay
Gauthier Dobigny
Institut de recherche pour le developpement
Franck Courchamp
Centre National de la Recherche Scientifique

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Abstract

Rodents are a notorious group of invaders worldwide. Their invasions have substantially impacted native ecosystems, local infrastructure, and human health and well-being. However, a lack of synthesized estimation of their economic impacts hampers effective management interventions at relevant scales. Here, we used the *InvaCost* database – the most up-to-date and comprehensive synthesis of reported monetary invasion costs – to assess the economic costs of invasive rodents globally. Our conservative analysis showed that reported costs of rodent invasions reached at least US$ 3.28 billion between 1930 and 2018, and were significantly increasing through time. The highest species-specific costs were reported from *Ondatra zibethicus*, *Rattus norvegicus* and *Castor canadensis*, with over 90% of the total costs damage-related, principally impacting agriculture, and predominantly reported in Asia (65%) and Europe (20%). Although minimal compared to damages, the majority of management investments were made on islands, with post-invasion spending always dominant. Importantly, managements expenditures to prevent rodent invasions were entirely absent from mainland areas. However, only approximately one quarter of the 48 known invasive alien rodents had reported costs, highlighting clear taxonomic biases. Obvious cost reporting gaps were also evidenced across different areas, sectors and contexts, suggesting a great underestimation of the costs incurred by invasive rodents globally. Greater and integrative research effort on the direct and indirect costs of rodent invaders – particularly the distinction between native rodent pests and invasive rodents' impacts, or from indirect impacts on human health – would be crucial for bridging these gaps. Ultimately, this would support proactive and sustainable management strategies.

Introduction

Rodents, the most abundant and diversified order of living mammals (~ 40% of mammalian biodiversity; Burgin et al. 2018), are undoubtedly the vertebrate group that has most often accompanied humans throughout their history of global dispersal (e.g. Cucchi et al. 2020). The ever-increasing intensification of human enterprise (e.g. maritime trade, road development) together with habitat modifications (e.g. land-use changes, urbanization) has resulted in a global spread of numerous non-native rodents, with some species continuing to proliferate; Dalecky et al. 2015; Di Febbraro et al. 2019; Hassell et al. 2021). In addition, the ecological flexibility of these rodents has allowed adaptation to heavily human-modified habitats, facilitating both their spread and acclimatization to new areas (Hima et al. 2019; Mazza et al. 2020). Once established, these commensal non-native rodents are usually highly prolific and represent a multisectoral threat to local biodiversity (e.g. (Sainsbury et al. 2020)), public health (Han et al. 2015; Meerburg et al. 2009a), human well-being (Colombe 2019) and socio-economic activities (Murray et al. 2018).

Indeed, invasive rodents have numerous detrimental impacts on invaded ecosystems, resulting from both direct (e.g. competition, predation, destruction through digging and gnawing) and indirect (e.g. transmission of pathogens and parasites, reductions in pollination efficiency and nutrient recycling) mechanisms (e.g. Colombe 2019; Diagne et al. 2016; Russell et al. 2020; Stokes et al. 2009; Wardle et al.

2012). Invasive rodents have been implicated in the decline and extinction of native biota on several islands worldwide, including hundreds of endemic plants (e.g. Shiels et al. 2013), birds (e.g. Jones et al. 2008), reptiles (e.g. Towns et al. 2001), other native rodents (e.g. Sainsbury et al. 2020) and invertebrates (e.g. St Clair 2011). In addition, they are drivers of profound disruption to local ecosystem function and substantial environmental modifications (Fukami et al. 2006). Rodents also spread infectious diseases of major public health importance, as they are reservoirs for at least 60 known zoonotic pathogens (including for instance plague, scrub typhus, leptospirosis and hemorrhagic fevers), which are in turn associated with about 400 million human cases every year (Han et al. 2015; Meerburg et al. 2009a). Particularly damaging are the sudden outbreaks of invasive commensal rodents, in particular mice, which are for example experienced every four years on average in Australia and can result in severe crop losses over thousands of km^2 (Singleton et al. 2005). Through contamination, damage, and consumption of food stocks and crops, rodents increase malnutrition and food security (Colombe 2019), as well as affect economic activities and productivity (e.g. damage to seaport infrastructure; Dossou et al. 2020). Furthermore, rodent infestations are perceived as a hallmark of poverty and unhealthy living conditions (though in reality, rodents damage clothes, blankets and furniture of the wealthiest human populations; Garba et al. 2014). Given the multitude of ways rodents are known to damage economies and environments, it is no surprise that four rodent species (the black rat *Rattus rattus*, the house mouse *Mus musculus*, the grey squirrel *Sciurus carolinensis*, and the coypu/nutria *Myocastor coypus*) are listed as major invasive taxa among the representative list of “100 of the world’s worst invasive alien species” (Lowe et al. 2000; Luque et al. 2014). Indeed, *R. rattus* was found to be the second costliest of the 100 world’s worst invasive alien species based on the available data (Cuthbert et al., submitted in this issue). Had there not been a rule to include only one species per genera, other major invasive *Rattus* species (*R. norvegicus* and *R. exulans*) would have certainly been included as well.

Despite the documented impacts rodents have on environments and economies, management efforts dedicated to mitigate the negative effects of invasive alien rodents remain limited and patchily restricted to post-establishment actions, often in insular areas (i.e. control or eradication campaigns; Duron et al. 2017). Unfortunately, these efforts can be impaired by natural or anthropogenic reinvasions of the targeted rodent species (e.g. Harris et al. 2012). Invasive rodents thus remain a major ecological and societal concern in most parts of the world. As with many invasive species, the discrepancy between the tremendous impacts of rodent invasions and insufficient control efforts is often driven by a lack of clear and applicable information on rodent impacts worldwide (Courchamp et al. 2017). As a result, there is a need for a global and accessible overview of the socioeconomic impacts of invasive rodents to improve public communication on rodent invasion issues, and coordinate transnational efforts of policy makers and local stakeholders (Bacher et al. 2018; Diagne et al. 2020a).

In this context, using monetary costs to represent quantitative impacts is a relevant strategy for raising societal and authority awareness, helping to set actions and priorities in management programmes, and assessing cost-effectiveness of relevant responses (Diagne et al. 2020a; Gruber et al. 2021). Understanding costs is particularly relevant for invasive rodents, which are responsible for substantial economic losses throughout the world each year (Diagne et al. 2021). Annual production losses attributed to rodents have been assessed at US $1.9 billion in Asia (Nghiem et al. 2013), US$ 45 million in the United Republic of Tanzania (Leirs 2003), US$ 19 billion in the United States of America (Pimentel et al. 2005), and US$ 60 million in Australia (Brown & Singleton 2000). However, we lack an essential, global overview of these economic costs, which is necessary for both research needs (e.g. identifying gaps and priorities) and management strategies (e.g. providing a basis for coordinating regional biosecurity measures) (Diagne et al. 2020a; Early et al. 2016).

Here, we provide the first global synthesis of the reported economic costs of invasive alien rodents. For this purpose, we relied on the recently developed *InvaCost* database, which is the most up-to-date and comprehensive living database of the economic costs of invasive alien species reported worldwide (Diagne et al. 2020b). Specifically, our goal was to describe and model the cost of invasive rodents to human society over time, and summarize how costs are distributed across rodent taxa, geographic space, socio-economic sectors and types of costs. From this, we identify research needs for consistent identification and use of costs across disparate sectors as well as crucial societal interactions in the perspective of an efficient management of invasive alien rodent impacts.

Materials And Methods

Data collection and processing

We considered the most recent version of the *InvaCost* database (version 3.0, available at https://doi.org/10.6084/m9.figshare.12668570). This database includes 9,823 cost entries collated from scientific and grey materials in multiple languages (Angulo et al. 2021; Diagne et al. 2020b). Each cost entry recorded is standardized to 2017 US dollars and categorized by a range of 64 descriptive fields (Online Resource 1, Tab Descriptors). We selected cost entries identified as *Rodentia* in the 'Order' column of the database (Fig. 1). We carefully checked the data for any duplicates or mistakes, and all modifications made were sent to updates@invacost.fr as recommended by the database managers. The resulting dataset (n = 349 cost entries) is provided as the *suitable subset* in the Online Resource 1 (Tab. Original subset). This suitable subset was homogenized so that all cost entries were considered on an annual basis, meaning that costs spanning multiple years were divided according to their duration (e.g. $20 million between 1991 and 2000 becomes $2 million annually across those years). Annual costs were calculated through a subset 'expansion' process using the *expandYearlyCosts* function of the 'invacost' R package (Leroy et al. 2020; R Core Team 2019). The duration time of each cost occurrence was calculated as the number of years between the recorded cost entry's starting ('Probable starting year adjusted' column) and ending ('Probable ending year adjusted' column) years. Any cost entries without available information in one or both columns were conservatively removed from this expansion process, and thus our analyses. The resulting subset (n = 718 cost entries) is provided as the *expanded subset* in the Online Resource 1 (Tab. Expanded subset). In addition, we applied two successive filters to this expanded subset to obtain a *conservative subset* (Fig. 1): first, we kept only *observed* costs (rather than *potential* costs, under the 'Implementation' column ; thereby removing, for example, all predicted costs);

second, we retained only *high*-reliability costs (rather than *low*-reliability costs, under the 'Method reliability' column; thereby removing, for examples, all costs without sourced information) – see Online Resource 2 for distribution of cost data within both descriptive fields. Our conservative subset contained 426 annualized cost entries between 1930 and 2018 (Fig. 1, Online Resource 1, Tab. Conservative subset). From there, total costs were obtained by summing all annualized cost entries ('Cost_estimate_per_year_2017_USD_exchange_rate' column) from this conservative subset.

Temporal dynamics of costs

We examined how costs developed over time (since 1980) using the *modelCosts* function to fit multiple models to the conservative subset. Such modelling of the trend of costs over time allows for a more reliable estimation of the dynamics of total annual costs by taking into account the time lags between the real occurrence of the costs and their reporting in the literature, as well as the heteroscedastic and temporally auto-correlated nature of cost data (Leroy et al. 2020). We therefore removed post-2013 years from this analysis, due to time lags in cost reporting. We subsequently employed a range of modelling techniques on the conservative subset data: ordinary least squares regression (linear and quadratic), robust regression (linear and quadratic), multivariate adaptive regression splines (MARS), generalised additive models (GAMs) and quantile regression [0.1 (lower boundary of cost), 0.5 (median cost value), 0.9 (upper boundary of cost)]. Model evaluation was based on the assessment of their predictive performance (via root-mean-square deviation, RMSE) and the level of variance explained. Although predictions will inherently vary among models, combining these diverse modelling procedures offers strong support for the resulting temporal trends if most or all of them provide consistent outcomes.

Taxonomic bias

To identify the proportion of invasive rodent species for which cost data is available, we compared the individual rodent species reported in the original subset with comprehensive lists of invasive rodents recorded worldwide, following an approach similar to Cuthbert et al. (2021). Lists of known invasive rodents were extracted and compiled from the Global Invasive Species Database (GISD; http://www.iucngisd.org/gisd/) and the sTwist database (version 1.2; Seebens et al. 2020b). We filtered these databases to select only species belonging to the order *Rodentia* and used the GBIF.org Backbone Taxonomy to standardize species names and removed any duplicated species. Then, for the latter first records (sTwist) database, we selected only taxa that were known to be presently established. We classified all such species as invasive, but note that the definitions of invasiveness may differ slightly between these datasets (Cuthbert et al. in press). Within each taxonomic family, we thus obtained the proportion of invasive rodent species with costs recorded in *InvaCost*.

Cost distribution

We subsequently investigated how economic costs of invasive rodents were distributed across key database descriptors using the conservative subset (see Online Resource 1, Tab Descriptors for details on all descriptors and categories). We included the *(i)* 'Species' (undetermined species were aggregated by genus, where possible), *(ii)* 'Geographic region' and 'Official country' where the cost occurred, *(iii)* 'Type of cost' (*Damage* [economic losses due to direct and indirect impacts of rodents] *vs*. *Management* [monetary investments to prevent and/or mitigate impacts, further separated according to type of actions undertaken: *pre-invasion management*, *post-invasion management* and *research/funding*]) and *(iv)* 'Impacted sector' *(Agriculture, Authorities-Stakeholders, Environment, Fishery, Forestry, Public and social welfare).* We also included an additional comparison *(v)* insular habitat status ('Island' = *yes* or *no*). For each descriptor, we grouped under *mixed* all cost entries that were not unambiguously assigned with one of the above-mentioned specific categories.

Results

Global cost and temporal dynamics

Based on costs reported in our conservative data subset, we found that invasive alien rodents have already cost the global economy at least US$ 3.28 billion between 1930 and 2018 (Online Resource 2). A less conservative approach would have produced a figure of around US$ 35.53 billion worldwide (Fig. 1). Models considering the temporal dynamics of costs were generally convergent in showing an increase in invasion costs over time (Fig. 2), confirming the raw temporal trends directly based on the cost estimates (Online Resource 3). All models displayed a relatively similar goodness of fit (RMSE 0.75–0.77), with costs in the year 2020 projected between US$ 511 million (linear ordinary least squares regression) and US$ 10 billion (quadratic robust regression) (Online Resource 2). Quantiles were increasingly divergent through time, indicating greater amplitudes between lower and upper cost quantiles in recent years. This global cost was unevenly distributed across taxonomic groups, geographic areas, types of costs and societal sectors (see below). Note that all costs provided here are summarized in the Online Resource 4.

Taxonomic cost distribution and bias

Invasion costs were reported for 12 individual rodent species in our conservative subset, while there are 48 invasive alien rodents recorded worldwide (i.e. across InvaCost, sTwist, GISD; Fig. 3). Two further species recorded in the original InvaCost database were not included in our conservative subset (Fig. 1; Fig. 3). Specifically, costs for *Hystrix brachyura* and *Sciurus niger*, either reported (for *H. brachyura* in the UK) or expected (for *S. niger* should it arrive in the Netherlands), were respectively deemed as *low*-reliability or *potential* estimates. The most underrepresented rodent families in our subset include Sciuridae (13 species without costs out of 17), Muridae (9 species out of 13) and Cricetidae (5 species out of 6). Additionally, the families Cavidae, Dasyproctidae and Heteromyidae did not have any reported costs (Fig. 3).

Costs were skewed towards the muskrat *Ondatra zibethicus* (US$ 378.1 million; n = 18 annualized cost entries), undefined rats *Rattus* spp., (US$ 329.3 million; n = 82), the brown rat *R. norvegicus* (US$ 145.8 million; n = 29) and the North American beaver *Castor canadensis* (US$ 103.9 million; n = 15). These four taxa constituted about a third of the total costs reported. All remaining species-specific costs totaled less than US$ 100 million, but *mixed costs* (diverse or nonspecific taxa) collectively amounted to US$ 2.17 billion. Despite being the species with the higher number of annualized entries (n = 110) in our conservative subset, costs from the coypu *M. coypus* totaled only US$ 70 million.

Cost distribution across types, space and sectors

Most costs were due to resource damages or losses (91%; US$ 2.99 billion, n = 134). Management actions (or mixed damage-management) comprised the remainder, though they had a higher number of annualized entries (n = 269 for management actions, 21 for mixed damage-management). In turn, management spending was dominated by post-invasion management (US$ 260 million, n = 196), which was over 170-times greater than pre-invasion management (Fig. 4a). While the aforementioned costliest species remain overall the same regardless of cost type, their relative ranking changes when considering damage versus management. Regarding damage costs, *O. zibethicus* (US$ 328.6 million; n = 8) was the costliest species, followed by *R. norvegicus* (US$ 68.5 million; n = 2) and *C. canadensis* (US$ 65.4 million; n = 9). The only specific species with more than 10 damage cost entries were *M. coypus* (n = 69) and *Callosciurus erythraeus* (n = 32), which totaled, respectively, US$ 64.3 million and US$ 1.98 million. Conversely, management costs were mostly associated with *R. norvegicus* (US$ 68.6 million; n = 26), and then *O. zibethicus* (US$ 49.5 million; n = 10) and *C. canadensis* (US$ 38.5 million; n = 6). While being the species complex incurring the highest damage costs (US$ 304.2 million; n = 4), undefined *Rattus* spp. represented the fourth taxon for which money was spent for management actions (US$ 24.9 million; n = 75).

Regionally, most costs were incurred in Asia (65%; US$ 2.16 billion, n = 87), followed by Europe (20%; US$ 659.3 million, n = 206) and North America (9 %; US$ 297.9 million, n = 21), with remaining regions contributing around US$ 100 million or less each. Most species recorded impacts in only a few geographic regions (Fig. 4b). In particular, the costliest species *O. zibethicus* only incurred costs in Europe. Where defined, mainland areas incurred higher rodent invasion costs than islands overall (US$ 457.3 million, n = 199 vs. US$ 314.2 million, n = 179) (Fig. 5). Rodent damage represented most costs (88%) on mainland areas, but only a third of the total costs reported in islands. Conversely, management spending was considerably greater on islands (US$ 192.7 million, n = 157) compared to mainland areas (US$ 54.5 million, n = 89). While post-invasion actions dominated management spending overall, pre-invasion management actions were only reported for islands (Fig. 5).

Regarding impacted sectors, most costs were incurred by the Agricultural sector (66%; US$ 2.16 billion; n = 102) with two-thirds of this cost recorded in Asia, followed by expenditures by Authorities and stakeholders (22%; US$ 741.4 million; n = 288), of which slightly more than half occurred in Europe. Almost all (~ 95%) of the agricultural costs were attributed to diverse or unspecified taxa, while for the costliest species, *O. zibethicus*, 46% of the costs were borne by Authorities and stakeholders. All other specified sectors represented less than US$ 10 million and ten annualized entries.

Discussion

Tremendous, increasing and uneven economic costs

Rodent invaders have conservatively cost the global economy at least US$ 3.28 billion between 1930 and 2018. Inclusion of all costs through less conservative data filtering leads to a global amount more than ten times higher (US$ 35.53 billion; Fig. 1). Whatever the actual cost figure, these costs are undeniably increasing. All models of temporal cost dynamics converged to depict an exponential increase over time in invasive rodent costs (Fig. 2). Although projections were variable due to underlying model characteristics, annual costs of rodent invasions were predicted to reach as much as US$ 10 billion in 2020. This figure is striking, and to provide perspective, is higher than the European Union's negotiated budget for addressing the COVID-19 crisis (US$ 7.3 billion, consilium.europa.eu) during the same year. The fact that these annual costs show no sign of slowing reflects the ongoing increase in rates of biological invasions globally (Seebens et al. 2020; Seebens et al. 2017). Although increasing reporting of costs cannot be clearly disentangled from empirically rising cost figures, the ongoing intensification of global trade, transport networks and human-induced habitat modification continues to provide new opportunities for further rodent invasions, and their associated costs worldwide (Hassell et al. 2021; Seebens et al. 2020).

This global cost figure is unevenly distributed across taxa, space, sectors and types of costs. From a taxonomic perspective, most costs were attributed to species belonging to the genus *Rattus*, with a cumulative cost of around US$ 480 million. Whether due to their actual impacts (e.g. role as disease reservoir; Morand et al. 2015); alteration of socio-economic activities, Murray et al. 2018; impacts on biodiversity and ecosystems; Doherty et al. 2016)) or intensive research effort (this is probably the most documented rodent genus worldwide: e.g. invasion history and introduction pathways; Zeng et al. 2018), *Rattus* spp. are recognized among the worst invaders worldwide (Lowe et al. 2000; Luque et al. 2014). *Ondatra zibethicus*, the individual species with the highest reported costs but exclusively in Europe) causes huge impacts through its burrowing ability (which can severely damage local habitats, roads and hydraulic systems) and its capacity to transmit zoonotic diseases (Nentwig et al. 2018).

From a geographic perspective, Asia (US$ 2.16 billion) comprises the highest proportion of the total cost, mainly due to a single estimate associated with agricultural losses from *Mus* and *Rattus* species in Malaysia, Myanmar and Thailand (Nghiem et al. 2013). Interestingly, despite having the third highest number of cost entries (n = 48), Oceania ranked 5th regarding total costs, likely because this region is mainly associated with management costs rather than more costly damages. The higher reporting rate (number of entries) of cost estimates observed in Europe, North America and Oceania could also reflect biases in research efforts and/or economic capacities rather than an accurate spatial distribution of costs, as shown for invasion science in general (Pysek et al. 2008). In turn, scarce cost reporting in low income regions likely reflects low priority given to IAS research and/or limited capabilities to act against invasions (Early et al. 2016). Indeed, costs of invasive rodents in Africa represented less than 1% of the total cost estimates among continents. Yet, globally common invasive rodents (*R. rattus, R. norvegicus* and *M. musculus*) are known to have the same described detrimental impacts there (Dossou et al. 2020; van Wilgen et al. 2020).

From a sectoral perspective, our results highlight that most costs from invasive rodents are simultaneously associated with several societal and activity sectors, illustrating the intrinsic multi-sectoral nature of rodent impacts (Colombe 2019). For example, a single invasive rodent – the Eastern grey squirrel *S. carolinensis* – may simultaneously impact local biodiversity, affect people's possessions, consume ornamental plants and bark stripping activity (Broughton 2020). Considering individual sectors, agricultural losses unsurprisingly comprised the greatest proportion. Globally, rodents are among humans' most important competitors for food resources, particularly through the damage they cause to growing crops and stored products (Belmain et al. 2015). Relative to agriculture, other sectors have reported more marginal rodent impacts, but this should clearly be viewed in light of the difficulties present in monetizing substantial ecological and health impacts (Diagne et al. 2021).

An undervalued economic burden

However high these costs may be, there is no doubt that they are a massive underestimation of the total costs incurred by invasive alien rodents globally. As for all invasive alien species (IAS) costs, there are a number of logistical, methodological and cost-intrinsic factors that fail to encompass the full diversity, and thus total cost of invasive rodents (Diagne et al. 2021). Although our synthesis is based on the most complete and up-to-date compilation of reported IAS costs worldwide, it is not exhaustively comprehensive. For example, the accessibility of grey literature materials varies (Angulo et al. 2021; Diagne et al. 2020a), monetary valuation of non-market ecosystem services is not straightforward (Kallis et al. 2013; Spangenberg and Settele 2010), and there is active ethical debate surrounding the principles of monetary valuation processes (Meinard et al. 2016). In addition, our choice to only examine the most robust subset (Fig. 1), and thus exclude any unsubstantiated costs (e.g. those relying on unsourced hypothetical calculations) also contributed to reduce the total cost over 1930–2018, which also contribute to explain the striking discrepancy between the resulting global annual cost (US$ 7.71 million) and some local estimates previously provided elsewhere (e.g. US$ 19 billion per year in the United States; Pimentel et al. 2005).

Further evidence of underestimation is seen in the number of invasive rodents for which no invasion costs have been reported so far (Fig. 3). In fact, reported costs were only available for one-quarter of known invaders, though it is unlikely the other species have no significant economic impacts. Another challenge to estimating costs from rodent IAS is the lack of systematic distinction between invasive and native rodent species when assessing economic losses and expenditure. This may be because of difficulty in attributing costs between often morphologically similar species. Moreover, particularly for invasive mice and rats, their commensal habits and long-standing invasion history may mean that most of the time they are classified as generic pests rather than specifically as invasive species (Stenseth et al. 2003), and so are treated differently within the literature, especially outside ecology (e.g. agriculture and health). In this instance, the search terms used within *InvaCost* may be not optimally designed for capturing such costs. Additionally, rodents (including most invasive ones) are also major reservoirs of pathogenic agents responsible for both zoonotic and veterinary diseases (Colombe 2019; Han et al. 2015; Meerburg et al. 2009a). These diseases are associate with substantial costs from both direct (e.g.

disease control; medical care) and indirect impacts (e.g. disabilities resulting in decreased productivity and loss of income; disturbed tourism). However, such costs can again be difficult to monetize (Diagne et al. 2021), or they may be attributed to the pathogens or arthropod vectors rather than explicitly to invasive rodents. In the same vein, economic losses or expenditures associated with (invasive) rodents are often provided in terms of incurred damage rather than in specific monetary terms. For example, rats were estimated to consume food crops that could feed 200 million people in Asia for an entire year (Singleton 2003), and it was estimated that 280 million cases of undernourishment could be avoided worldwide through proactive rodent control (Meerburg et al. 2009b). Similarly, rodent-borne zoonoses are responsible for over 400 million human illness cases each year, leading thus to a cascade of socio-economic consequences (Meerburg et al. 2009a); as an illustration, the invasive *R. norvegicus* plays a pivotal role in the epidemiological cycle of leptospirosis in many urban settings, which is associated with a global loss of 2.9 million Disability Adjusted Life Years (DALY) annually (Torgerson et al. 2015). Such gaps and underestimates of costs identified by our synthesis highlight the need for improved explicit monetary valuation of the economic impacts of invasive alien rodents to better disseminate the cost-benefit tradeoffs of addressing this global problem.

Research and management implications

In light of the evident knowledge gaps currently impairing our quantitative understanding of the economic costs of invasive rodents, we suggest efforts need to be targeted at multiple scales towards currently under-reported regions, taxa and sectors. In addition to multiscale studies, we stress the need for more accurate and standardized economic estimations in order to improve cost reporting following recommendations from Diagne et al. (2021). A key insight from these is to provide cost estimates at the finest taxonomic resolution possible. In this study, 66% of the total estimated costs were associated with *mixed* rodent species. This means that there is no possibility to disentangle species-specific contributions to this total cost, thereby limiting opportunities to set priorities and evaluate cost-effectiveness of management actions at the species level (Gruber et al. 2021). For instance, currently underestimated health costs are expected to dramatically increase as ongoing trends in land-use change and urbanization lead to amplification of the role of (invasive) rodents as important zoonotic reservoirs in many locations (Gibb et al. 2020; Hassell et al. 2021; Mendoza et al. 2020). Obtaining accurate estimates of the true magnitude of these health costs will be imperative for incentivizing control efforts targeting multiple invasive rodent hosts. Along with increased reporting of species-specific costs, we strongly encourage separation of invasive *versus* native status in rodent impact assessments, rather than considering both species as pests *versus* non-pests. Producing this greater granularity across scales will enhance our understanding of the rodent impacts, but will also help to improve the effectiveness of rodent management actions (Diagne et al. 2021; Gruber et al. 2021). As a support, we showed that management costs predominated on islands generally, with damage costs more common in mainland areas. Islands supported disproportionately high levels of native species endemism and extinction risk, often partly as a result of invasive rodents (Bellard et al. 2017). The higher prevalence of management spending on islands may thus represent expenditures for local conservation purposes - particularly the costs invested in pre-invasion prevention and detection methods (Bodey et al, submitted in this issue).

While it is possible that the relative lack of management expenditure in mainland areas might indicate cost-efficient actions at local scales, the evident ongoing temporal increase in damage costs over time suggests this is unlikely. Notably, our results highlight the apparent complete lack of pre-invasion surveillance costs in these mainland areas.

Consistent and accurate accounting of the economic costs of rodents is therefore integral to coordinated, efficient and sustainable management of rodent invasions and their impacts. Furthermore, comprehensive estimates of the true costs of invasive rodents is essential to raising awareness (of both authorities and citizens) of rodents' impact, and obtaining community buy-in to control and prevention actions. Given the crucial importance of invasive rodent management as a priority for national governments, communicating the magnitude of these impacts is critical to creating a supportive legislative, political and societal environment which will implement long-term policies on rodent invasions (Novoa et al. 2017; Adamjy et al., 2020). Ultimately, this would help to design locally adapted - and thus sustainable - management strategies that account for the economic and societal realities (e.g. implementation of ecologically-based rodent management (EBRM) approaches with local communities; (Constant et al. 2020). This is particularly critical in low- and middle-income countries where economic resources are scarce, and societal concerns are dominated by food and health security (Crowley et al. 2017; Evans et al. 2018). Given the societal difficulties and costs involved in minimizing the impacts of established invasive rodents, our results demonstrate the urgent, global need for increased policy development and effective measures to prevent further rodent invasions worldwide. Therefore, we encourage efforts to improve the efficiency of management actions through closer science-society interactions (Novoa et al. 2018), which should ultimately involve sustainable partnerships and interactions within/between local actors (biodiversity managers, funders and directly-impacted people, political leaders, socio-economic stakeholders) and scientists from different fields (e.g. economists, sociologists, biomedical and data scientists). Whether they are long term commensals of humans (rats, mice), invaders of specific habitats (beavers, muskrats, coypus) or newly invasive from exotic pets (squirrels, dormice), invasive rodents remain relatively inconspicuous. Yet, they are particularly widespread and ubiquitous. We showed here that the small fraction of their impact that has been monetized is sufficient to warrant much more focus on this invasive group.

Table 1

Estimates (2017 US$) and root mean square errors (RMSE) for ordinary least squares (OLS), robust regression (RR), multivariate adaptive regression splines (MARS) and generalised additive model (GAM), as well as quantile regressions. Models considered annual total invasion costs as a function of time, between 1980 and 2012.

Model	2020 cost (US$ million)	RMSE
OLS (linear)	511.27	0.76
OLS (quadratic)	1,610.80	0.76
RR (linear)	520.67	0.76
RR (quadratic)	10,187.70	0.77
MARS	1,496.42	0.75
GAM	1,651.28	0.76
Quantile 0.1	9.92	1.13
Quantile 0.5	420.33	0.76
Quantile 0.9	16,787.75	1.32

Online Resources

Online Resource 1 Data considered in this study on the economic costs of invasive alien rodents. The spreadsheets are the following: 'Descriptors' provides full definition and details about the descriptive columns used in InvaCost as well as those added for the purposes of our analyses; 'Suitable subset' contains the raw cost entries pertaining to the order *Rodentia* in the original InvaCost database (version 3.0; complete database available at); 'Expanded subset' contains the annualized cost entries following data expansion through the *invacost* package (Leroy et al. 2020); 'Conservative subset' is the most robust subset of the 'Expanded subset' obtained after keeping only the *observed* ("Implementation" column) and *high* ("Method reliability" column) cost entries.

Online Resource 2 Distribution of cost entries and estimates recorded in our original subset according to their reliability (high **versus** low**) and their implementation (**potential **versus** observed**).** All details on the descriptive fields considered are provided in the Online Resource 1.

Online Resource 3 Temporal trends of the cost estimates of invasive alien rodents from our study. We considered (a) the original subset, (b) the conservative subset and (c) the non-conservative subset (see Fig. 1 and Online Resource 1 for further details on the subset and filtering steps). In (a), trend is described separately for *potential* and *observed* cost entries (see "Implementation" column; Online Resource 1). In (b) and (c), trends are described separately for *damage*, *management* and *mixed* costs (see "Type of cost merged" column; Online Resource 1). Costs are provided in 2017 US$ dollars. The horizontal dotted lines represent annual averages over the entire time period, solid bars represent 10-year means and filled circles represent annual costs scaled by size to match the number of entries.

Online Resource 4 Summary of the cost distribution per invasive alien rodent taxon, impacted sector, geographic region and type of costs from the conservative subset used in our analyses. Costs are provided in 2017-equivalent US$ million. The number of annualized cost entries is provided in parenthesis. All details on the descriptive fields considered are provided in the Online Resource 1.

Declarations

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Availability of data and material. The data considered in this study provided as an Electronic Supplementary Material (Online Resource 1.

Author's contribution. CD and FC led the project. CD conceived the study with inputs from all co-authors. CD, LBM, TB, JFL and EA managed the data collection, processing and/or filtering. CD, LBM and RC carried out the analyses. LBM, RC, EA and FC generated the graphical items. CD took the lead in writing the paper with inputs from all co-authors.

Code availability. Not applicable here.

Compliance with ethical standards. Disclosure of potential conflicts of interest.

Conflict of interest. The authors declare that they have no conflict of interest.

Consent for publication. All authors have read and approved the submitted version of the manuscript.

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Figures

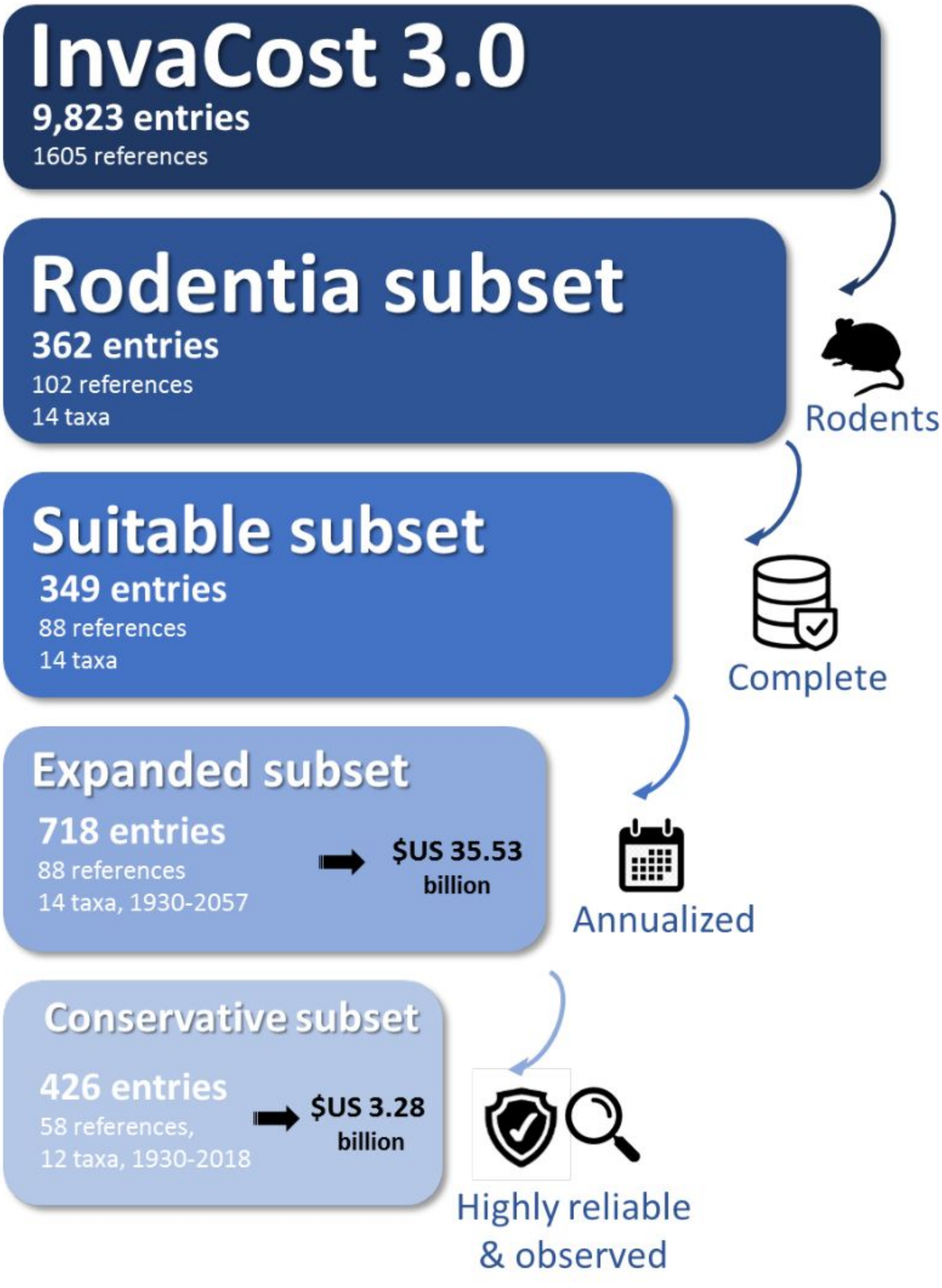

Figure 1

Workflow depicting the data collection and filtering process. Thirteen cost entries were excluded to limit dubious data (9 cost entries) and potential spatial overlaps (3 cost entries provided at the continental scale and 1 cost entry provided at the global scale) when generating the suitable subset. The expanded subset was obtained through the 'expansion' of the suitable subset using the 'invacost' R package (Leroy et al. 2020). The criteria used for generating the conservative subset were based on the descriptive fields of the InvaCost database (Online Resource 1, Tab Descriptors), i.e. the ‘Implementation’ (observed versus potential costs) and ‘Method_reliability’ (high versus low-reliability costs). The number of taxa includes both individual species and undefined species aggregated at the genus level.

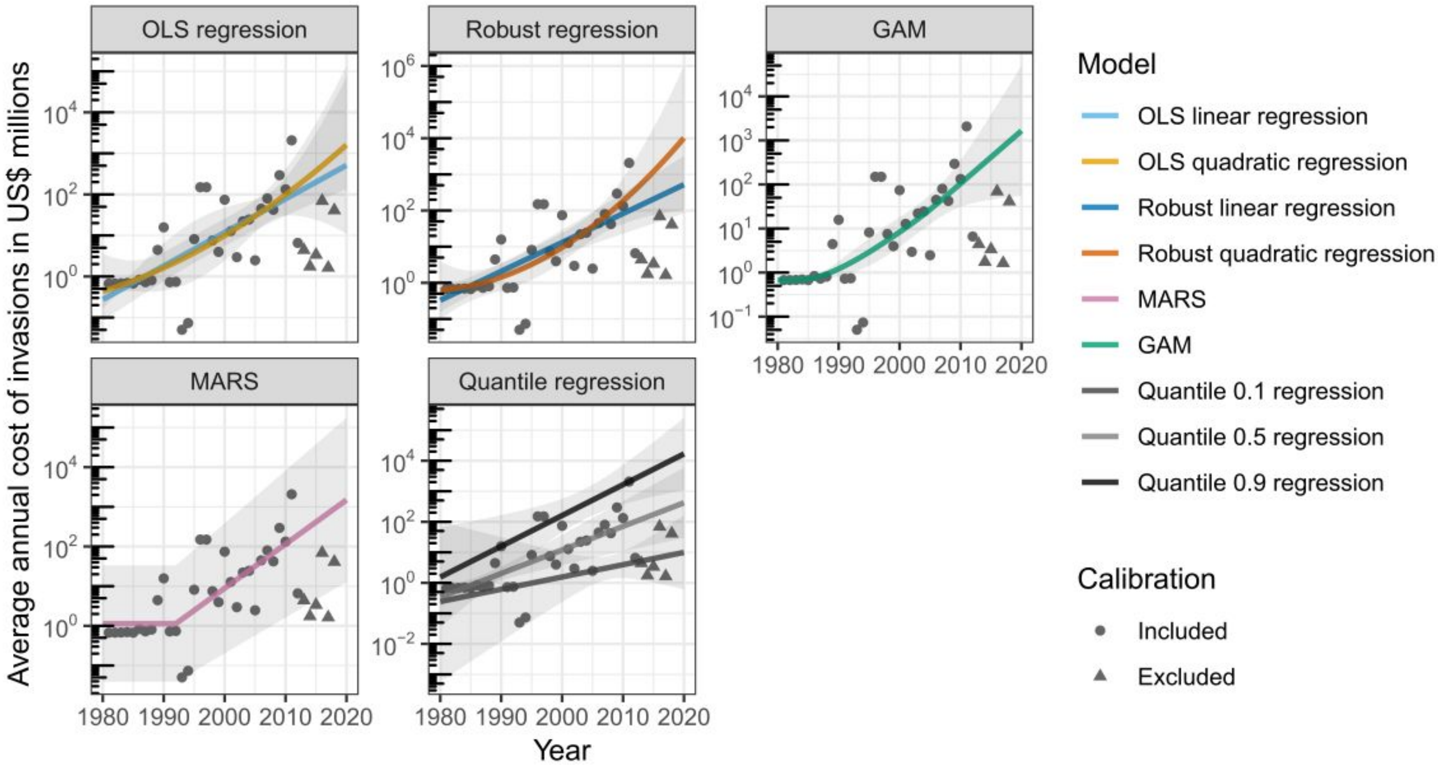

Figure 2

Temporal trends in rodent invasion costs considering a range of statistical models. Ordinary least squares (OLS), robust regression, generalised additive model (GAM), multivariate adaptive regression splines (MARS) and quantile regressions. Shaded areas are 95 % confidence intervals; points represent annual totals. The y axes are on a log10 scale, and are scaled separately among subplots.

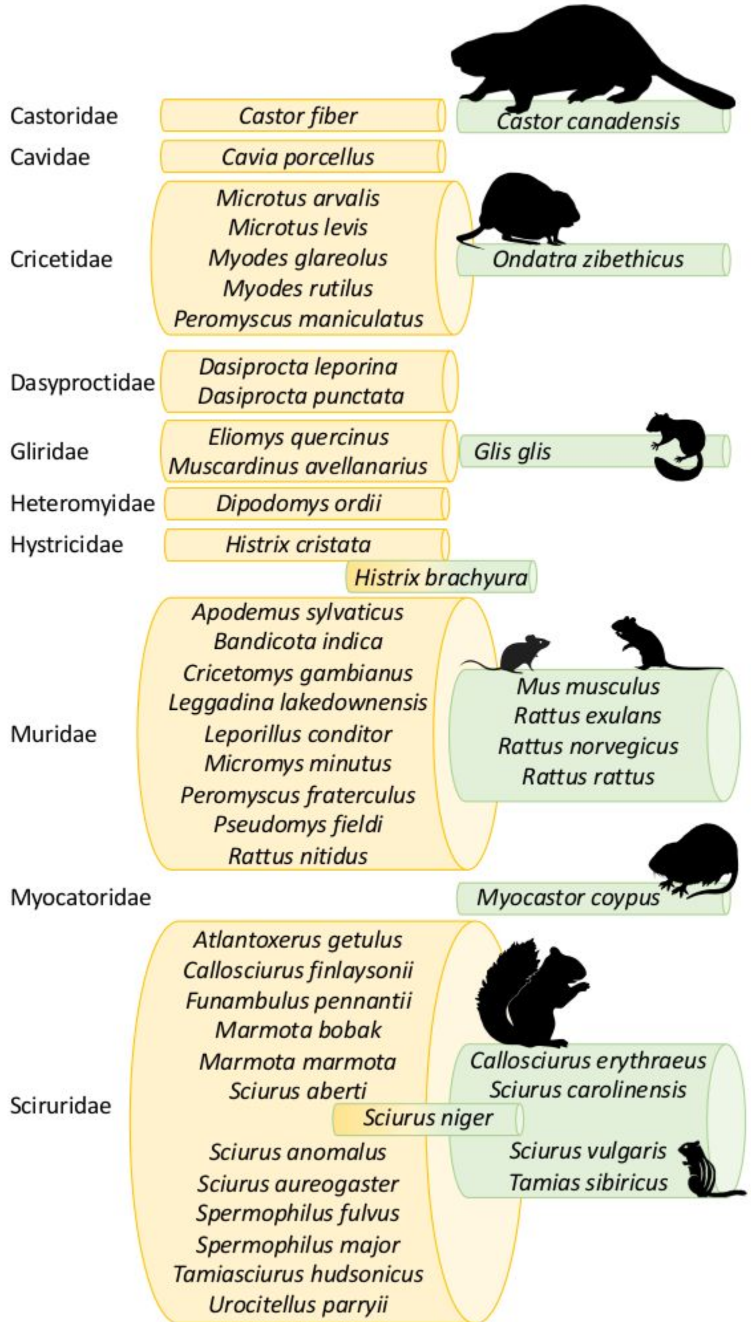

Figure 3

Taxonomic bias in rodent invasion costs. Invasive rodent species are those recorded in the InvaCost database, the Global Invasive Species Database (GISD; http://www.iucngisd.org/gisd/) and the sTwist database (version 1.2; Seebens et al., 2018). Species with dichromatic rolls (H. brachyura, S. niger) are in the original subset, but were not considered in our conservative subset. All listed species are grouped by family. Species with blended colors are not considered in the conservative subset used for our analysis.

Roll height is scaled to the number of species within each group and species silhouettes are sized to scale

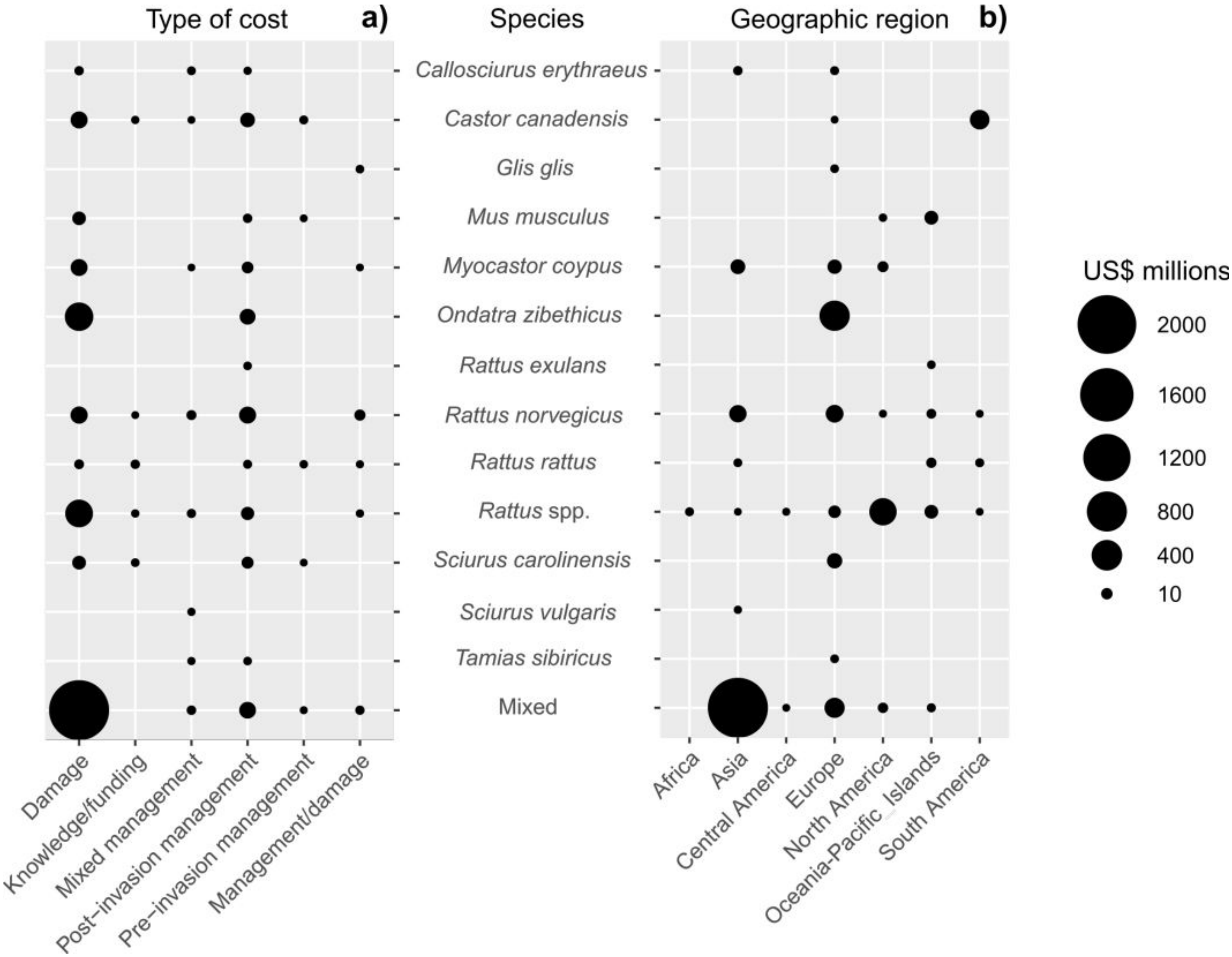

Figure 4

Cost distributions across species according to a) cost type and b) geographic region. The size of each node corresponds to the cost total. Costs are expressed in 2017 US$ millions

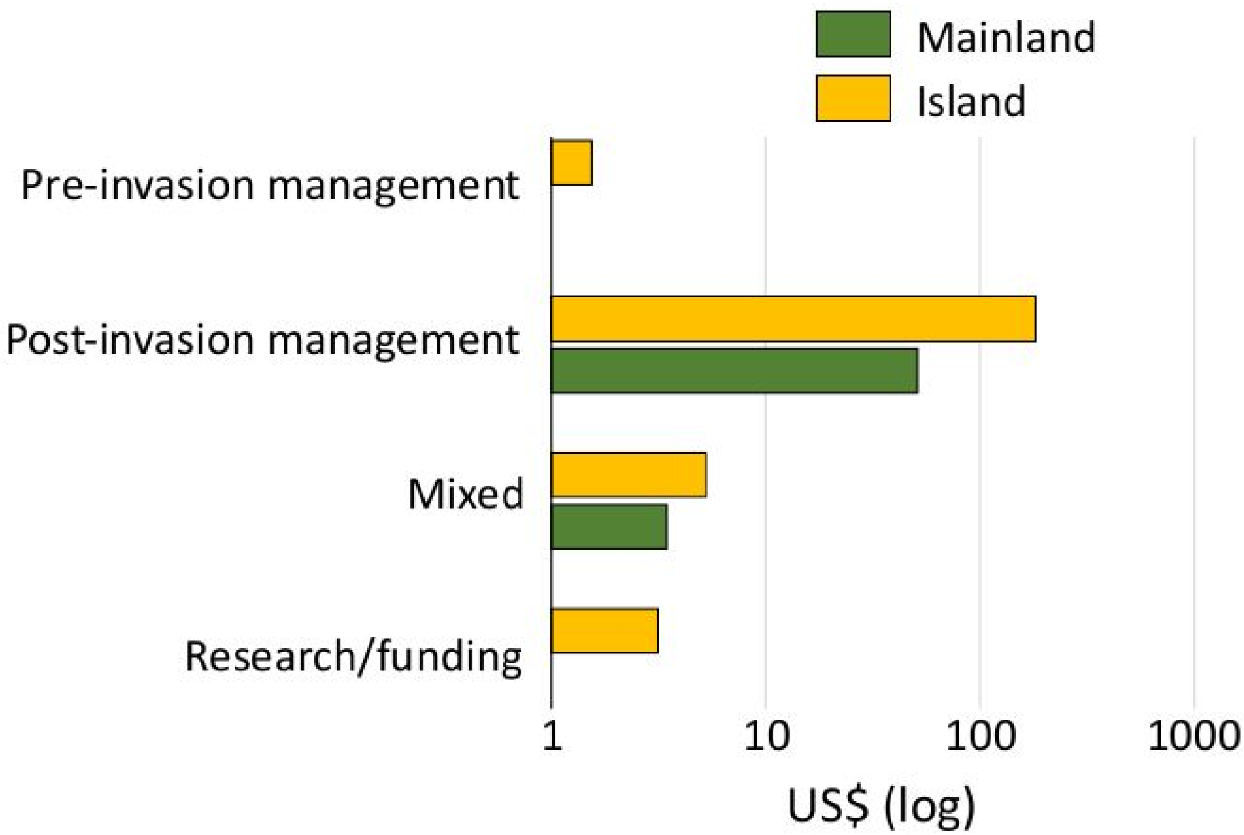

Figure 5

Cost estimates (using log10 distribution) according to the type of management expenditures between mainland (in green) and island (in orange) areas. Pre-invasion management: monetary investments for preventing successful invasions in an area (including quarantine or border inspection, risk analyses, biosecurity management, etc.); post-invasion management: money spent for managing invasions in invaded areas (including control, eradication, containment); research/funding: money allocated to all actions and operations that could be of interest at all steps of management at pre- and post-invasion stages (including administration, communication, education, research), or mixed was assigned when costs include at least (and without possibility to disentangle the specific proportion of) two of the previous categories. Costs are expressed in 2017 US$ millions

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- DiagneetalOnlineresource2.pdf
- DiagneetalOnlineresource3.pdf
- DiagneetalOnlineresource1.xlsx
- DiagneetalOnlineresource4.xlsx