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The magnitude, diversity, and distribution of the economic costs of invasive terrestrial invertebrates worldwide

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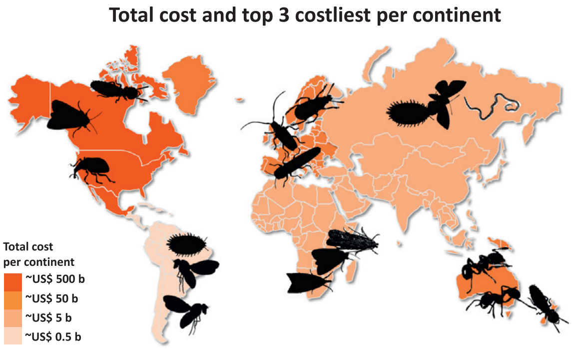
HIGHLIGHTS

- Invasive terrestrial invertebrates cost the global economy US$ 712.44 billion up to 2020.
- These costs are rising and were mostly due to invasive insects (88%).
- The highest costs were reported from North America (73% of the global costs).
- These costs mainly resulted from direct resource damages and losses (75%).
- Knowledge gaps imply that these costs are severely underestimated.

GRAPHICAL ABSTRACT



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ABSTRACT

Invasive alien species (IAS) are a major driver of global biodiversity loss, hampering conservation efforts and disrupting ecosystem functions and services. While accumulating evidence documented ecological impacts of IAS across major geographic regions, habitat types and taxonomic groups, appraisals for economic costs remained relatively sparse. This has hindered effective cost-benefit analyses that inform expenditure on management interventions to prevent, control, and eradicate IAS. Terrestrial invertebrates are a particularly pervasive and damaging group of invaders, with many species compromising primary economic sectors such as forestry, agriculture and health. The present study provides synthesised quantifications of economic costs caused by invasive terrestrial invertebrates on the global scale and across a range of descriptors, using the InvaCost database. Invasive terrestrial invertebrates cost the global economy US$ 712.44 billion over the investigated period (up to 2020), considering only high-reliability source reports. Overall, costs were not equally distributed geographically, with North America (73%) reporting the greatest costs, with far lower costs reported in Europe (7%), Oceania (6%), Africa (5%), Asia (3%), and South America (<

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1%). These costs were mostly due to invasive insects (88%) and mostly resulted from direct resource damages and losses (75%), particularly in agriculture and forestry; relatively little (8%) was invested in management. A minority of monetary costs was directly observed (17%). Economic costs displayed an increasing trend with time, with an average annual cost of US$ 11.40 billion since 1960, but as much as US$ 165.01 billion in 2020, but reporting lags reduced costs in recent years. The massive global economic costs of invasive terrestrial invertebrates require urgent consideration and investment by policymakers and managers, in order to prevent and remediate the economic and ecological impacts of these and other IAS groups.

1. Introduction

Invasive alien species (IAS) have massive adverse effects on biodiversity, ecosystem structure and function (Blackburn et al., 2019). These impacts can result in cascading effects on ecosystem services (Pejchar and Mooney, 2009) as well as human welfare through, for example, the vectoring of pathogens and parasites which cause diseases (Hulme, 2014; Medlock et al., 2015) or health issues from reactions to stings or bites (e.g., Vinson, 1997). By spreading and developing in a large variety of natural and anthropogenic habitats, IAS are also burgeoning stressors in several economic sectors (Diagne et al., 2021). Yet, despite increasing awareness of the burden generated by IAS, and legislation aimed at limiting their threats to biodiversity and ecosystem functioning, our capacity to contain invasions has often remained weak (Early et al., 2016). While IAS monitoring and management efforts have progressively increased over the past years in protected areas (but see Liu et al., 2020; Rico-Sánchez et al., 2020), resource allocations for biosecurity and post-invasion management are generally made ad hoc in many areas (Liebhold and Kean, 2019). The paucity, or even absence for certain IAS, of quantified socioeconomic costs incurred by invasions (see Lodge et al., 2016 and references therein) likely contributes to explaining these reduced investment incentives. Accordingly, awareness about the economic costs of IAS is increasingly recognised as critical to strengthen the rationale for policymaking and for better-informed decisions (Leung et al., 2002; Caffrey et al., 2014; Hoffmann and Broadhurst, 2016; Diagne et al., 2020; Ahmed et al., 2022).

Pimentel et al. (2000, 2005), and later Kettunen et al. (2009), pioneered large-scale (i.e., regional or national) summations of costs, in monetary terms, of IAS. These studies had the benefit of pointing out the huge costs associated with IAS, which until then had lacked synthesis. However, the acknowledged difficulties in monetizing some types of costs, in particular those not directly linked to primary economic activities, such as alterations of ecosystem services, and to standardise very different costs, resulted in important shortcomings in the presented figures (see for example, Hoagland and Jin, 2006; Hoffmann and Broadhurst, 2016). The accounting of all types of impacts is critical for capturing the full dimension of invasion costs, which in turn should inform evidence-based decision-making. Underestimated figures can, for example, mislead decision-makers into a lower allocation of resources than what is actually needed, or vice-versa (Lovell et al., 2006; Marbuah et al., 2014), and thus cause an inefficient prioritisation of management efforts. Such quantifications should pay particular attention to taxonomic groups known to cause disproportionate economic impact and losses, such as insects (e.g., Bradshaw et al., 2016; Paini et al., 2016). This knowledge would facilitate monetary comparisons of cost types between resource damages and invasion management.

Terrestrial invertebrates include several IAS that have been described as species producing major alteration of ecosystem structure and functioning (Holway et al., 2002; Bertelsmeier et al., 2015; Wong et al., 2020), thereby causing a diversity of economic impacts. For example, termites that compromise infrastructure (Buczkowski and Bertelsmeier, 2017), or insect disease vectors causing rising medical (Renault et al., 2021) and veterinary costs (Narladkar, 2018). It is probable that this economic burden has risen steadily along with the significant increase in the establishment of alien terrestrial invertebrate species reported in the literature over the past decades (Roques et al., 2009; Roques, 2010; Seebens et al., 2017). Several invasive invertebrates, in particular insects, also greatly affect biodiversity, with critical consequences for native species (Lebouvier et al., 2020; Liu et al., 2020). Predicted future range shifts that accompany globalisation and climate change will likely add to these effects (Bebber et al., 2013; Bellard et al., 2013; Bertelsmeier et al., 2015). Despite these critical ecological impacts, there remains a significant lack of information on economic costs caused by invasive terrestrial invertebrates other than a preliminary estimation of US$70 billion per year for insects in goods and services damages globally (Bradshaw et al., 2016). Some well-known examples of damaging invasive invertebrate groups other than insects include terrestrial gastropods (Cowie et al., 2008), earthworms (Hendrix, 2006) or flatworms (Sugiura, 2010). Nevertheless, the overall economic costs of these reported taxa, and that of invasive terrestrial invertebrates in general, is still lacking.

Here, we use the recently developed InvaCost database (Diagne et al., 2020) to provide a global-scale assessment of the reported economic costs of invasive terrestrial invertebrates. Recent works using the InvaCost database have highlighted economic impacts at regional and country scales (e.g., Haubrock et al., 2021a; Heringer et al., 2021; Kourantidou et al., 2021; Liu et al., 2021; Bang et al., 2022) as well as for specific taxonomic groups (e.g., Angulo et al., 2021b; Haubrock et al., 2022; Kouba et al., 2022). Yet, the effects of many widespread invasive taxa remain unquantified at the global scale using these novel, comprehensive data. This is the case for invasive terrestrial invertebrates, for which the types of costs caused, economic sectors affected, and the geographical patterns and temporal trends of these costs remain largely unassessed. To address this important knowledge gap, we analysed the InvaCost database to examine how the monetary costs of invasive terrestrial invertebrates are distributed across taxonomic groups, geographic regions, cost types, and socioeconomic sectors. Moreover, we modelled the global temporal trends in these reported economic costs over recent decades. Given uneven cost distributions at the global scale (Diagne et al., 2021), we predicted that invasion costs of invasive terrestrial invertebrates will be high and burgeoning, but dominated by a small number of well-studied taxonomic groups that impact anthropocentric socioeconomic sectors in a few geographic regions.

2. Methods

2.1. Data extraction

To estimate the economic costs of terrestrial invertebrate invasions, we considered data from the InvaCost database (InvaCost v.4.1; Diagne et al., 2020; Angulo et al., 2021a; doi:https://doi.org/10.6084/m9.figshare.12668570). This database was developed to provide standardised quantification of the costs caused by IAS worldwide, including extensive information about the nature of these costs. Grey and published references in different languages were retrieved from standardised searches in online repositories (Web of Science, Google Scholar and Google search engine), an opportunistic collection based on targeted searches, and contacting experts and stakeholders to request documents or files containing cost information. Every cost entry was recorded with more than 60 parameters (**Table A.1**, Tab_1 “Descriptors”), and converted to a common currency (US dollars (US$) 2017; see Diagne et al., 2020 for detailed information).

The extraction and analysis of cost data from the InvaCost database were performed using the “invacost” package v0.3–4 (Leroy et al., 2021) in R v4.1.1 (R Core Team, 2021). To specifically examine terrestrial invertebrates, a two-step filtering process was performed. First, we selected the ‘Terrestrial’ category (**Table A.1**, Tab_2 “Data4.1” column V “Environment_IAS” of the database), and second, we kept only ‘Arthropoda’, ‘Mollusca’, ‘Platyhelminthes’ and ‘Nematoda’ phyla (**Table A.1**, Tab_2 “Data4.1”, column “Phylum”). In doing so, we excluded any terrestrial species which have an aquatic life-history stage (for instance, mosquitoes which are categorised as ‘Semi-aquatic’), or those that are associated with water for foraging and/or reproduction. These costs are presented elsewhere (Cuthbert et al., 2021a). Assuming that the database contains errors, a screening of data relevant to this study was performed at different levels in order to minimise them: first, we searched for exact duplicates and removed bias; second, we checked for spatial, temporal or other overlaps in costs entries, and when a case was detected, we retained for the analysis the cost for the longest period and/or the largest area, while prioritising species-, country- or yearly-specific costs over lump-sum costs. While duplicates no longer appear in the dataset or in InvaCost v4.1, decisions on whether to include overlapping costs in the analyses are available in the **Table A.1** (Tab_2_“Data4.1”). Even if some errors could still remain, the analysis was aimed to present orders of magnitude rather than exact estimation of the cost associated with invasions by terrestrial invertebrates.

Whenever a cost was reported for a combination of more than one category in the column “Geographic region” or taxonomy below “Phylum”, data were changed to ‘Diverse/Unspecified’. Collated data comprised a total of 1965 entries (**Table A.1**, Tab_3 “DatasetTerrestrialInvertebrates”).

Because the temporal extent of these reported costs varied considerably across records (i.e., within-years, yearly, and among years), we used the *expandYearlyCosts* function of the “invacost” R package to obtain comparable annual costs for all cost estimates (Leroy et al., 2021). In brief, this function provides yearly cost estimates for all entries, based on the time range represented in the original cost data (Diagne et al., 2020; doi:https://doi.org/10.6084/m9.figshare.12668570, and **Table A.1**, Tab_1 “Descriptors”). We based this on the difference between the starting (**Table A.1**, Tab_3 “DatasetTerrestrialInvertebrates”, column “Probable starting year adjusted”) and ending (**Table A.1**, Tab_3 “DatasetTerrestrialInvertebrates”, column “Probable ending year adjusted”) years of the reported costs. For example, a cost of $100,000 spanning 10 years would be expanded to $10,000 per year. When no period of impact was specified in one or more columns, one single year was considered (even though the cost might have been repeated over many years, even up to the present time). This resulted in 7177 expanded entries (i.e., per year) from the initial 1965 entries. These expanded data were further filtered by (i) removing costs with an “Impact year” after 2020; (ii) and omitting costs that were not converted to 2017 US$. This resulted in a final, expanded dataset for analysis with 5906 entries (Fig. 1).

2.2. Cost description

The invasion costs totals were examined according to different descriptors of the costs available in the database (**Table A.1**, Tab_1 “Descriptors”). First, we focused on taxonomic grouping (“Class” and “Species”) and geographic region (“Geographic region”) where the cost occurred, the type of cost, and the economic sector impacted. For the type of cost, we used two columns: (i) the “Type of cost merged” column that categorised the cost into “Damage” referring to damages or losses incurred by invasion (i.e., costs for damage repair, resource losses, medical care), “Management” comprising control-related expenditure (i.e., monitoring, prevention, control, eradication), and “Mixed” including mixed damage and management costs (cases where reported costs were not clearly distinguished); every cost for which the exact nature of the cost was not clearly defined was assigned to “Unspecified”; (ii) the “Management type” column, which differentiates between pre- and post-invasion management expenditures, and actions including research or funding for IAS, or mixed actions. For the economic sector that was impacted by the cost (activity, societal or market sector), we used the column “Impacted sector” (**Table A.1**, Tab_4 “ImpactedSector”); individual cost entries that were unspecified or not allocated to a single sector were re-assigned to a new category called “Mixed”. The column “Implementation” was used to distinguish whether the cost estimate was actually realised (“Observed”) or whether it was expected (“Potential”).

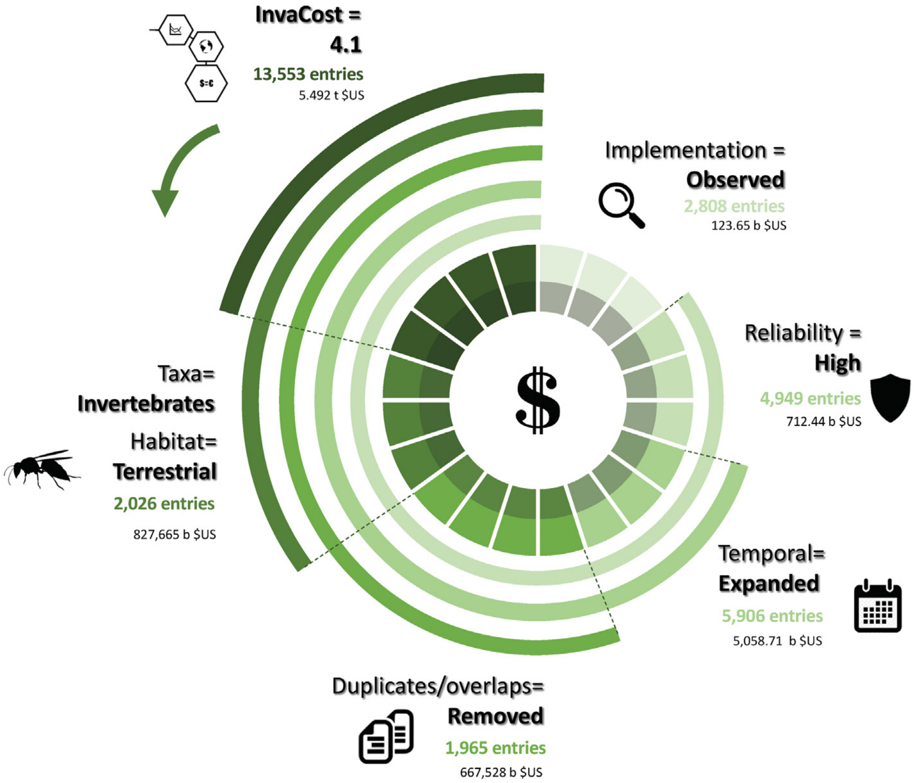

Fig. 1. Successive filters applied to the InvaCost dataset, with the resulting number of entries and total cost at each step. Counterclockwise, the following filters have been applied: invertebrates living in terrestrial habitats, then removal of potential duplicates and overlaps, then temporal expansion, then only highly reliable data, and finally only observed data. This last filter provides a subset of 2808 entries totalling $US 123.65 billion.

2.3. Temporal trends

We estimated global average annual costs of terrestrial invertebrate invaders represented in the InvaCost database by quantifying the temporal trends in cost accumulation. These estimates were performed for the period 1960–2020. We accounted for the effects of time lags between the occurrence of the costs and their reporting in analysed documents through the examination of the "Impact year" column relative to the "Publication year" within the terrestrial invertebrate subset of the expanded database **(Table A.1**, Tab_3 "DatasetTerrestrialInvertebrates"). Examination of quantiles from this relationship indicated that years following 2011 were incomplete (<75% cost completeness), and we thus excluded those years from temporal analyses. Then, a range of modelling techniques was applied to examine the temporal dynamics of reported costs (*modelCosts* function in "invacost" R package, Leroy et al., 2021), including regression (linear and quadratic terms), multivariate adaptive regression splines (MARS), generalised additive models (GAM), and quantile regression (quantiles 0.1, 0.5, 0.9). This range of modelling approaches was selected to account for issues related to econometric data, such as heteroscedasticity and presence of outliers, allowing for selection among several linear and non-linear candidate models. We used the root mean square error (RMSE) to examine and compare model fits.

3. Results

3.1. Geographic and taxonomic distribution of costs

Total cost incurred by terrestrial invertebrate invasions amounted to US$ 5058.71 billion ($n = 5906$) up to the year 2020. Highly reliable costs constituted about 14% of the total costs (US$ 712.44 billion; $n = 4949$ expanded entries) **(**Fig. 1**)**. From these, about one-sixth of the highly reliable costs (17.4%; US$ 123.65 billion; $n = 2808$ expanded entries) were empirically observed, with the remainder predicted using costs from a small area extrapolated to a broader scale, or expected from extending an existing impact over time (potential costs).

The vast majority of total invasion costs was caused by Insecta (Fig. 2), while other taxonomic classes were lower by at least one order of magnitude. Most costs associated with Insecta were empirically observed, but relatively large shares of the total costs were from poorly reliable sources (Fig. 2). Variable cost distributions between implementation forms and reliability classifications were exhibited for other taxonomic classes, which contributed little to the overall cost (Fig. 2).

Overall, the highly reliable compiled data covered 206 species from 80 families (**Table A.1,** Tab_5 "SummaryCostPerSpecies"). Only highly reliable data were used for subsequent analyses, providing a conservative but reliable cost estimation. Again, when considering highly reliable costs alone, the majority of costs within the expanded database was caused by the Insecta (Phylum: Arthropoda; $n = 4203$; US$ 625.66 billion). These were followed by costs for Secernentea (Phylum: Nematoda; $n = 614$; US$ 46.59 billion) and Arachnida (Phylum: Arthropoda; $n = 46$; US$ 4.01 billion). Costs caused by Gastropoda (Phylum: Mollusca; n = 42; US$ 0.17 billion), and Collembola (Phylum: Arthropoda; $n = 7$; US$ 0.03 billion) were much lower. Costs attributed to multiple taxonomic groupings ("Diverse/Unspecified"; $n = 37$) amounted to US$ 35.98 billion.

Globally, the majority of the reported highly reliable cost was from North America ($n = 1975$; US$ 521.57 billion), followed by Europe ($n = 657$; US$ 50.45 billion), Oceania ($n = 1048$; US$ 43.46 billion), Africa ($n = 332$; US$ 32.83 billion), Asia ($n = 826$; US$ 24.05 billion), and South America ($n = 56$; US$ 0.24 billion) **(**Fig. 3**)**. Regionally diverse or unspecified costs accumulated to a total of US$ 39.82 billion ($n = 59$). Across all regions except South America, potential costs were dominant. The top three costliest species per region were always insects, except the nematode *Bursaphelenchus mucronatus* in Asia, but differed entirely in species-level composition among regions (Fig. 3),

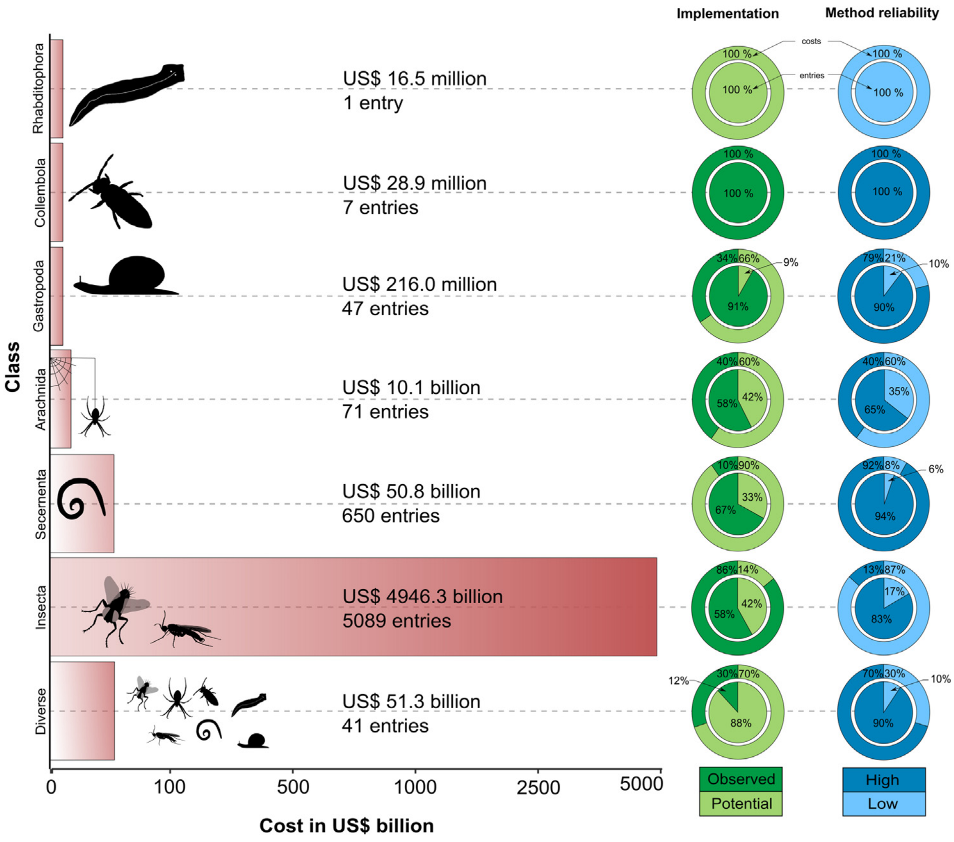

Fig. 2. Costs incurred from invasive terrestrial invertebrates worldwide over the period 1869–2020, according to cost implementation nature (potential versus observed) and method reliability (lower versus higher) among taxonomic classes. Percent values are rounded to the nearest whole number.

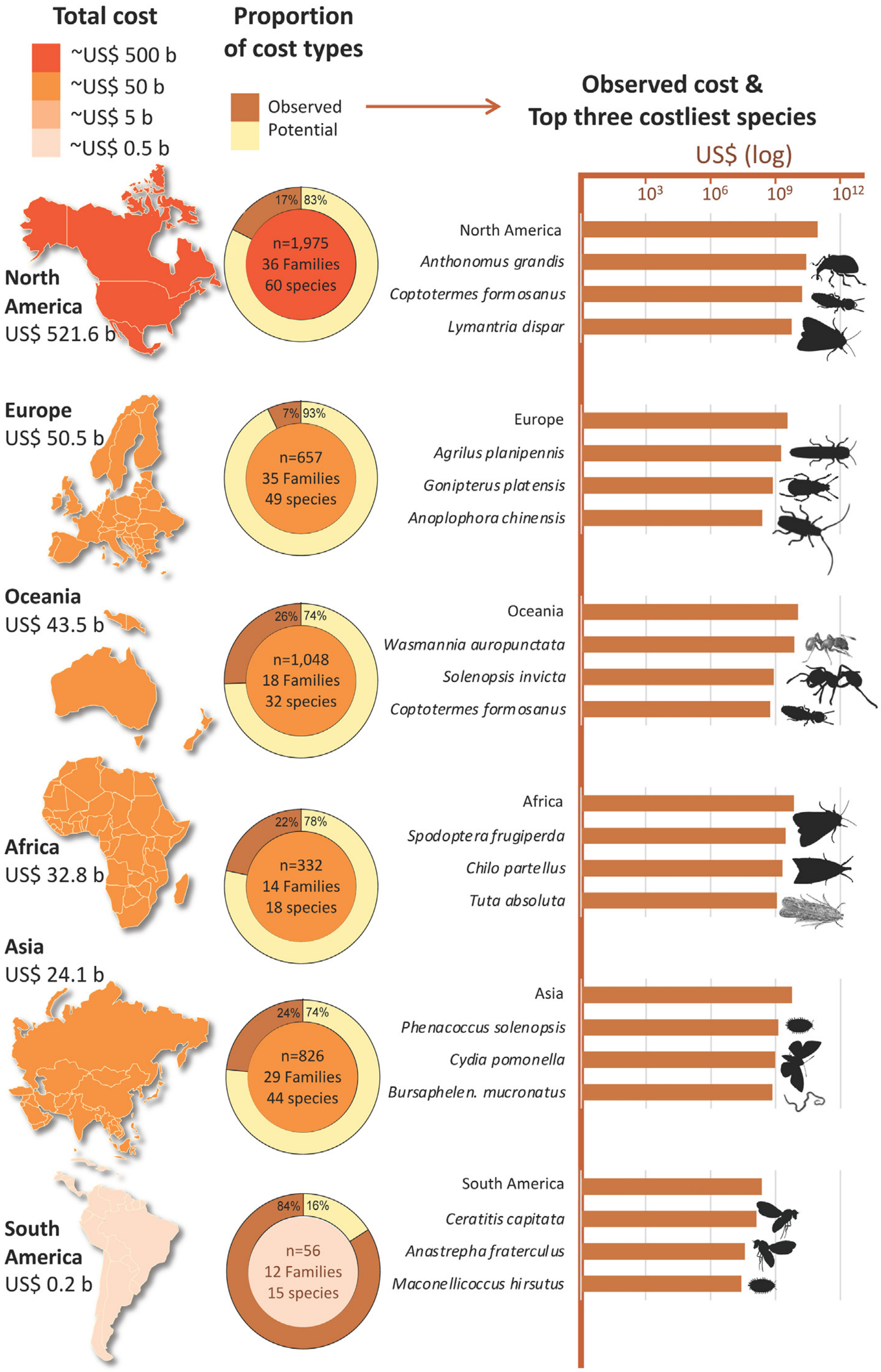

Fig. 3. Total costs of recorded terrestrial invertebrates according to affected geographic regions (US$). For each continent, costs are split according to cost implementation nature (potential versus observed, %) and number of entries and the number of families and species (inside the circles) are shown. For observed costs, the total and the three costliest species for each continent (bars) are shown.

except for the Formosan termite *Coptotermes formosanus* between Oceania and North America.

3.2. Type of economic costs and activity sectors affected

The majority of reported costs resulted from direct damages or resource losses (n = 1780; US$ 532.66 billion) (Fig. 4). Strikingly, only US$ 54.01 billion (n = 2350) was directly spent on management interventions. Mixed costs contributed US$ 116.43 billion (n = 670). Within the reported management interventions, US$ 49.29 billion (n = 1814) was spent on post-invasion management (e.g., control, eradication), but only US$ 0.18 (n = 105) billion on pre-invasion management (e.g., biosecurity, surveillance). The remaining management spending was mixed in type or related to knowledge and funding. About 90% of the total damage costs were incurred in only two sectors, viz. forestry (n = 606; US$ 255.93 billion) and agriculture (n = 810; US$ 221.65 billion). Contrastingly, 87% of total management costs was incurred by a single sector, viz. authorities and stakeholders (n = 2063; US$ 47.04 billion). Mixed costs, comprising damage and management costs, were incurred in agriculture (n = 142; US$ 28.55 billion), forestry (n = 305; US$ 32.34 billion), authorities and

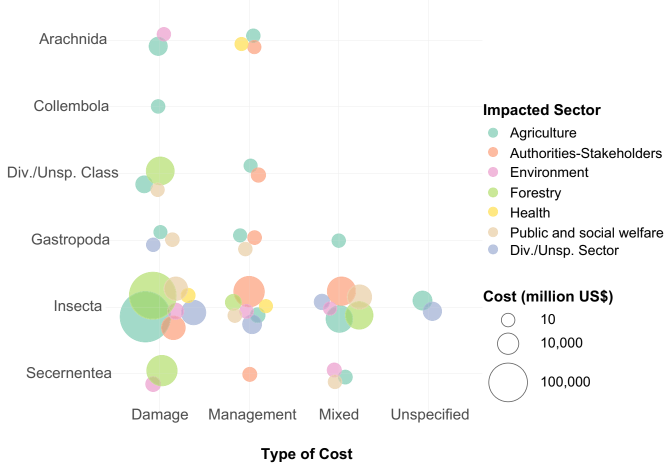

Fig. 4. Highly reliable cost contributions among different cost types and taxonomic groups, with fills corresponding to impacted sectors. Node sizes are scaled based on the magnitude of incurred costs across these three variables.

stakeholders (n = 150; US$ 35.64 billion), and public and social welfare (n = 27; US$ 18.97 billion). These four sectors together contributed to more than 99% of mixed costs.

According to reported data, the largest shares of terrestrial invertebrate costs affected the forestry (n = 938; US$ 289.45 billion) and agriculture (n = 1239; US$ 255.98 billion) sectors; mostly driven by insects (Fig. 4). Insects also affected other sectors (e.g., authorities-stakeholders, public and social welfare, and mixed categories), while Secernentea impacted forestry primarily, and other taxa mostly affected agriculture. Other sectors considerably impacted by the costs of invasive terrestrial invertebrates were authorities-stakeholders (n = 2290; US$ 99.85 billion), and public and social welfare (n = 231; US$ 35.30 billion). Comparably lower reported costs were inferred to the environment (n = 65; US$ 2.09 billion) and health sectors (n = 51; US$ 0.22 billion). Mixed costs, i.e., costs not impacting specific sectors and/or impacted multiple sectors, contributed the remainder.

3.3. Annual cost accumulation

The estimated US$ 695.49 billion over the period of 1960 to 2020 resulted in an average of US$ 11.40 billion per year over the entire period. In this period, both potential (US$ 588.37 billion) and observed (US$ 107.11 billion) highly reliable costs increased, with average annual costs totalling at US$ 9.65 billion per year for potential costs, and US$ 1.72 billion per year for observed costs, respectively (Fig. 5a).

At the beginning of the investigated period (1960–2020), highly reliable observed management costs (1960–1969: US$ 0.25 billion in total) were higher than those inferred by damages (1960–1969: US$ 0.01 billion in total) (Fig. 5b). Then, damage costs substantially outweighed management spending after a turning point in the decade 1990–1999, resulting in an average annual management cost of US$ 0.33 billion and US$ 20.10 billion in total, compared to US$ 0.91 billion per year and US$ 55.69 billion in total in damages.

The predicted trend of cost accumulations from 1960 to 2020 differed among regression models (Fig. 6). Ordinary least squares (OLS), robust and quantile regressions, GAM and the MARS revealed that economic costs incurred by invasive terrestrial invertebrates continuously increased over the period 1960–2020. The OLS regression estimated the costs of these IAS in 2020 at between US$ 131.83 and 165.01 billion (Fig. 6a), while it was estimated at between US$ 113.68 and 130.37 billion by the robust regression (Fig. 6b). The generalised additive model, with the second lowest RMSE, also predicted a rapid increase in costs of invasive terrestrial invertebrates over the 1960–2000 period and an annual cost of US$ 120.35 billion in 2020 (Fig. 6c). Multivariate adaptive regression splines, which showed the best fit as revealed by the RMSE of the calibrated models (Table A.2), suggested costs peaking at US$ 34.51 billion in 2020 (Fig. 6d). Quantile regression revealed relatively similar cost amplitudes over time (Fig. 6e).

3.4. Synthesis of the monetary costs incurred

A general overview of the economic costs caused by invasive terrestrial invertebrates among taxa, implementations, geographic regions, impacted sectors, and cost types, is presented in Fig. 7. A significant part of the highly reliable costs is attributed to economic losses in North American countries (US$ 521.57 billion, corresponding to 73% of total reported costs). Agriculture and forestry were the main impacted sectors (US$ 255.98 billion and US$ 289.45 billion, respectively), and impacts were mostly damage-related and potential in type. Taxonomic unevenness was also evident, with insects being responsible for 88% of the total costs (US$ 625.66 billion).

4. Discussion

Global economic costs documented for invasive terrestrial invertebrates were found to sum to US$ 712.44 billion in the present study (highly reliable costs only), with an average reported cost of US$ 11.40 billion per year since 1960, showing a rapid increase since 1960 over several orders of magnitude. These costs show that invasive terrestrial invertebrates have placed tremendous pressure on the global economy across a range of sectors and cost categories in recent decades. We identified clear geographic biases towards North America regarding the costs incurred by terrestrial invertebrates, and taxonomic biases, particularly towards invasive insects in North America (Fig. 7). These findings mean that the reported figures are likely underestimations of already conservative costs in other regions, missing many terrestrial invertebrate invasions where costs are unreported. These gaps are further compounded with insufficient research on IAS impacts at numerous biological and environmental scales (Crystal-Ornelas and Lockwood, 2020), and research gaps due to the omission of non-English information (Angulo et al., 2021a). Costs were driven primarily by resource damages or losses, and were unevenly distributed across the full range of economic sectors, with agriculture and forestry sectors disproportionately reporting the highest costs, but also with many other costs inferred for diverse or unspecified sectors (Fig. 7).

Moreover, our examination of cost accumulations through time showed a general pattern of increase temporally. Indeed, as the rate of terrestrial invertebrate invasions continues to increase (Seebens et al., 2017, 2020), it is probable that there will be further concurrent increases in economic costs. In a regional context, most costs were located in North America, potentially indicating a higher awareness and compliance in reporting IAS associated costs in that region. Alternatively, higher resource damages and losses in North America may be due to more assets likely to be damaged. Indeed, specific species like the gypsy moth *Lymantria dispar* and the emerald ash borer *Agrilus planipennis* are well known for their costly impacts in North America (Régnière et al., 2008; Herms and McCullough, 2014). A striking example of a data gap is the absence of the lesser mealworm *Alphitobius diaperinus* from our database, despite the massive efforts deployed worldwide for combating the pullulations of this poultry house pest (Wolf et al., 2015). Nevertheless, non-English searches (15 languages) and specific targeting of grey literature sources have helped to fill these geographic knowledge gaps in the database — particularly considering African, Asian and South American countries. In addition, cost research needs to be conducted in future to bolster accessibility of costs. Specific cost searches have still to be conducted in numerous African and Asian languages, further rendering the results of the present study as conservative.

Our average annual estimate since 1960 (US$ 11.40 billion) is about 4-times higher than the average annual United Nations budget in the last decade (US$ 2.76 billion). Moreover, our peak annual cost in 2020 (US$ 165.01 billion) is even higher, relative to the entire gross domestic product (GDP) of rich countries such as Luxembourg (US$ 64.02 billion in 2017), or

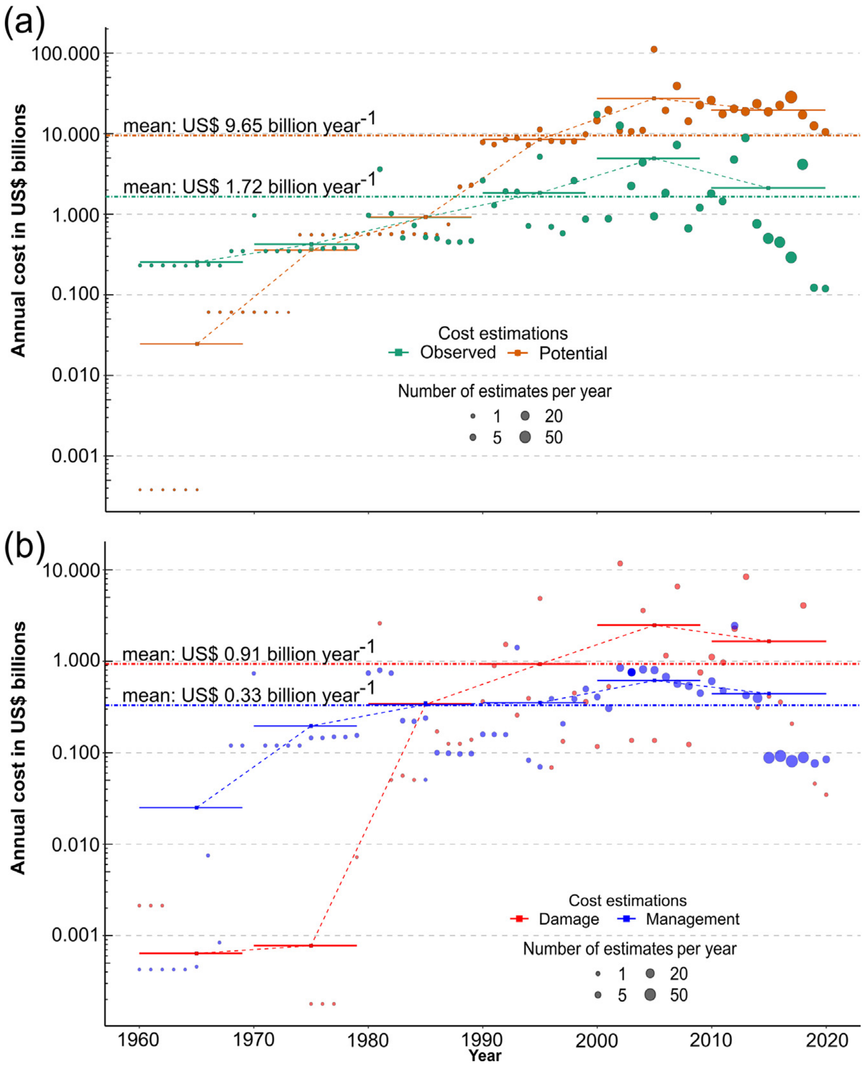

Fig. 5. Temporal distribution of highly reliable annual costs according to (a) cost implementation nature (potential versus observed) and (b) cost type (management vs damage). Decadal and overall means are represented by the solid and dashed lines, respectively.

the combined GDPs of 59 nation-states with the smallest economies (US$ 161.36 billion in 2020, World Bank). The previously reported economic costs of invasive insects alone amounted to a minimum of US$ 70 billion per year (Bradshaw et al., 2016). Importantly, in contrast to that study, we did not include insects with an aquatic life stage or associated with water for reproduction or foraging. As semi-aquatic invertebrates such as mosquitoes drive huge impacts, exceeding US$ 100 billion since 1960 (Cuthbert et al., 2021a), our costs would have been much higher with their inclusion, and would have likely matched or exceeded those formerly reported in Bradshaw et al. (2016). Indeed, our average annual costs of wholly terrestrial insects alone were estimated to be higher than US$ 110 billion in 2020. Finally, some invasive insects have expanded rapidly in recent years, as is the case, for example, the spotted-wing Drosophila *Drosophila suzukii*, devastating cherries, plums and grapes in several European countries (Nikolouli et al., 2018). The rapidly growing outbreaks of this pest are associated with additional production costs and lower revenues for the producers (Knapp et al., 2020). While potentially highly significant, we only have 30 expanded cost entries collected from 13 distinct references for this insect pest. Similarly, the fall armyworm *Spodoptera frugiperda*, which is heavily impacting agriculture in Africa and Asia (Naganna et al., 2020; Tambo et al., 2020), has only 36 expanded cost entries, again exemplifying the gap in between the observation of pullulations and pest damages and the publication of the associated economic losses.

There were clear differences among taxonomic groups causing costs, with insects dominating, while other groups contributing relatively little to the total cost (**Fig. 7**). Insect impacts on agriculture and human health are well-known (Akiner et al., 2016; Sileshi et al., 2019), but this result does not mean that costs attributed to other taxonomic groups are unimportant, but rather that their impacts are less clearly assessed, making them more difficult to quantify. Groups seemingly less costly are probably less studied overall (e.g., invasive micro-invertebrates). For instance, relatively few costs were reported for invasive spiders. This is also the case for invasive snails and slugs and for invasive earthworms, all of which are particularly impactful species, with relatively few or no costs reported in InvaCost. For example, there are at least 175 species of terrestrial gastropods established outside of their native ranges (Capinha et al., 2015). Many of these are very damaging land snails, among which are the two infamous carnivorous snails, the rosy wolfsnail (*Euglandina rosea*) and the giant African snail (*Achatina fulica*), which caused the extinction of many endemic snails on the islands of Hawaii, Tahiti, Moorea, and other Pacific islands (e.g., Davis-Berg, 2012). The giant African snail is one of the largest land snails globally, reaching up to 19 cm in length, a ferocious predator and a vector of at least two human diseases (Meyer et al., 2008). Given the substantial damage that these gastropod species cause (Kozłowski, 2012; Martín et al., 2019), and the existence of management programs developed to control them (Le Gall and Tooker, 2017; Barua et al., 2021; Schurkman and Dillman, 2021), it is surprising that relatively few costs are recorded

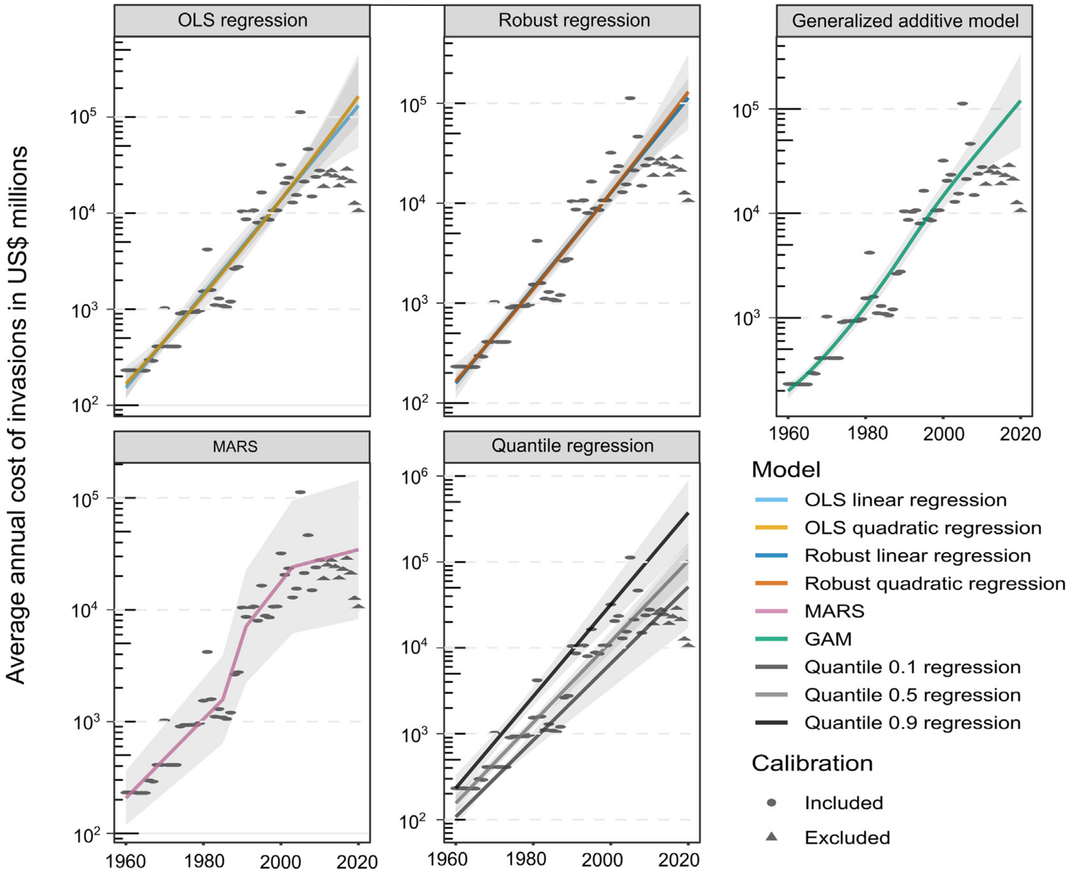

Fig. 6. Modelled temporal trends in highly reliable economic costs of invasive terrestrial invertebrates according to (a) ordinary least squares (OLS) regressions, (b) robust regressions, (c) generalised additive model (GAM), (d) multiple adaptive regression splines (MARS) and (e) quantile regressions. Shaded areas are 95% confidence intervals, and prediction intervals for MARS.

for gastropods. Similarly, over 100 alien species of earthworms have been documented globally (Hendrix, 2006), and they have now spread into habitats such as in North America (McCay and Scull, 2019), the Taiga region in Russia, and the coniferous forests of Scandinavia (Hendrix, 2006), where these species were absent since the last glacial age. As they thrive underground, invasive earthworms have been mostly neglected until very recently, despite the fact that they are ecosystem engineers, and their impacts are believed to be large (Migge-Kleia et al., 2006). Yet, economic costs are absent from recorded invasions for this group. Other groups of invasive terrestrial invertebrates are likewise entirely or largely lacking.

Conversely, the high relative contribution of invasive insect costs may reflect their high diversity, both in terms of overall biodiversity and IAS richness (Finlay et al., 2006; Roques et al., 2009), in addition to being the most studied taxa. Economic costs, particularly non-market costs of environmental degradation, are also more challenging to quantify with certainty (Epanchin-Niell, 2017). Likewise, certain direct monetary losses attributed to IAS are more difficult to ascertain, as evidenced for non-native earthworms invading forests (Addison, 2009). This difficulty results from the multiple dimensions of the effects caused by IAS, and the valuation of ecological consequences in monetary units, which often remains difficult. Limited research effort has also been pointed out, but some studies that reported economic costs usually concern less than 1–10% of IAS (e.g., Bradshaw et al., 2021; Cuthbert et al., 2021b; Haubrock et al., 2021b; Liu et al., 2021; Renault et al., 2021; Bang et al., 2022) and this

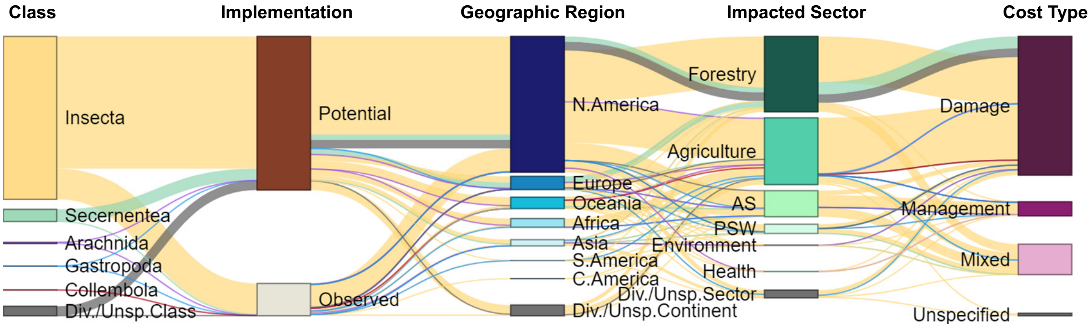

Fig. 7. Figure summarising the distribution of highly reliable costs of invasive terrestrial invertebrates globally. Cost flows originate from different taxonomic groups, before being partitioned sequentially according to their implementation form, geographic region, impacted sector and cost type. Div./Unsp Class refers to costs concerning diverse/unspecified taxonomic classes, regions and impacted sectors. AS: Authorities-Stakeholders; PSW: Public and Social Welfare.

likely applies to insects too. Future studies should address this knowledge gap using a range of improved assessment measures and taxa (Hanley and Roberts, 2019).

Within insects, three groups dominated the costs: Curculionidae (true weevils; US$ 106.04 billion; especially European spruce bark beetle *Ips typographus*), Noctuidae (owlet moths; US$ 105.68 billion; especially cotton bollworm *Helicoverpa armigera*), and Buprestidae (jewel beetles; US$ 64.69 billion; especially emerald ash borer *Agrilus planipennis*). As voracious defoliators, moth caterpillars and beetles are major pests in forests (Liu et al., 2003; Haynes et al., 2014), and alongside weevils, threaten also the production of cotton (Rajendran et al., 2018) and food (Vreysen et al., 2007, 2016). The majority of costs in the present study were attributed to direct resource damages or losses, which primarily emanate from agricultural and forestry enterprises. In contrast, spending from health sector-related damages and losses was relatively minor. This is surprising, as ticks and dust mites are well-known vectors of arthropod-borne diseases and can also cause allergies (Marcondes and Dantas-Torres, 2017). The minimal level of control-related expenditure reported is additionally concerning (but see the costs of the red imported fire ant *Solenopsis invicta* in Oceania, Angulo et al., 2021b) given that preventative measures (i.e., biosecurity actions) can prove to be far more economical than ongoing control measures (Ahmed et al., 2022; Cuthbert et al., 2022). That is because it is comparatively challenging to eradicate or manage invaders following establishment (Leung et al., 2002).

We identified a general increase in average annual reported costs since 1960, reflecting the increase in terrestrial invertebrate introductions described by Roques et al. (2009) and Seebens et al. (2017). In turn, this highlights the urgent need to improve current management and control, but also prevention efforts and cost reporting. Indeed, as globalisation and interconnection facilitate introductions from novel non-native source pools, the numbers and costs of invasive terrestrial invertebrates are expected to increase owing to trade pathways (Seebens et al., 2018). Furthermore, range expansion of invertebrate invaders can be expected to occur with climate change. Bellard et al. (2013) projected an average net increase in the range expansion of 100 worst non-native terrestrial invertebrates of 18% by 2050, with likely increasing costs.

In sum, our findings raise questions about the lack of cost estimations for IAS and highlight taxonomic and geographic knowledge gaps. The economic costs of invasive terrestrial invertebrates presented here should be an incentive for decision-makers to invest in preventing the arrival and spread of such species. Our study highlights the need for national and regional authorities to provide structured reporting of costs to improve the accuracy of cost estimates, with more substantial efforts being required for underrepresented regions and taxonomic groups. In addition, the discrepancy between the relatively small amounts spent on control and prevention strategies directly, compared to costs of damage incurred from well-established invader populations, justifies greater investment in preventative biosecurity protocols (Cuthbert et al., 2022). Given current and future invasion rates (Seebens et al., 2017, 2020), and the likelihood that documented costs are broadly underestimated and poorly monetised, we expect further examination to reveal that the actual costs of invasive terrestrial invertebrates are substantially higher than what we have presented here.

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Availability of data and material

Underlying data are publicly available in an online repository (doi: https://doi.org/10.6084/m9.figshare.12668570) and in the Appendix 1.

Code availability

Not applicable.

CRediT authorship contribution statement

Conceptualization: all co-authors; Project administration: FC; Funding acquisition: AMK, CC, DR, FC, RNC; Production of the underlying database: EA, FC; Visualization: AB, EA, PJH, RNC; Data analysis: AMK, EA, PJH, RNC; Writing: DR, EA, RNC and PJH wrote the original draft, which was reviewed and edited by all co-authors.

Ethics approval

Not applicable.

Consent to participate

Not applicable.

Consent for publication

All authors have seen and approved the manuscript and have consented for publication.

Declaration of competing interest

The authors declare that there are no conflicting or competing interests.

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