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Economic costs of invasive non-native species in urban areas: An underexplored financial drain

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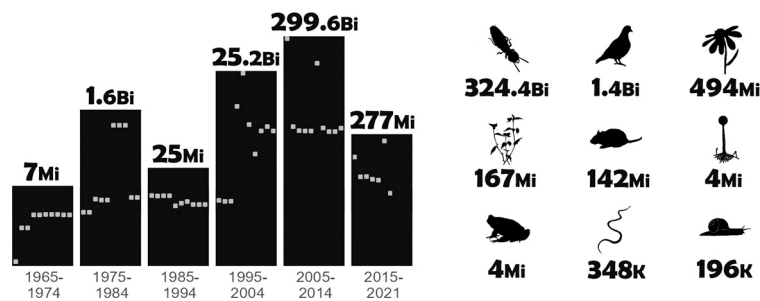
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HIGHLIGHTS

- Biological invasions in urban areas resulted in a total cost of US\$ 326.7 billion.
- Urban costs represent ~15 % of the total costs caused by invasive species.
- Most of these costs were attributed to damage by insects and impacted mostly public and social welfare.
- 73 countries have reports of costly invasive species in urban areas, yet no monetary costs have been reported.
- Taxonomic and geographic gaps can be mitigated with more studies and accurate cost reporting.

GRAPHICAL ABSTRACT

Reported costs of invasive species in urban areas (US\$)



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ABSTRACT

Urbanization is an important driver of global change associated with a set of environmental modifications that affect the introduction and distribution of invasive non-native species (species with populations transported by humans beyond their natural biogeographic range that established and are spreading in their introduced range; hereafter, invasive species). These species are recognized as a cause of large ecological and economic losses. Nevertheless, the economic impacts of these species in urban areas are still poorly understood. Here we present a synthesis of the reported economic costs of invasive species in urban areas using the global *InvaCost* database, and demonstrate that costs are likely underestimated. Sixty-one invasive species have been reported to cause a cumulative cost of US\$ 326.7 billion in urban areas between 1965 and 2021 globally (average annual cost of US\$ 5.7 billion). Class Insecta was responsible for >99 % of reported costs (US\$ 324.4 billion), followed by Aves (US\$ 1.4 billion), and Magnoliopsida (US\$ 494 million). The reported costs were highly uneven with the sum of the five costliest species representing 80 % of reported costs. Most reported costs were a result of damage (77.3 %), principally impacting public and social welfare (77.9 %) and authorities-stakeholders (20.7 %), and were almost entirely in terrestrial environments (99.9 %). We found costs reported for 24 countries. Yet, there are 73 additional countries with no reported costs, but with occurrences of invasive species that have reported costs in other countries. Although covering a relatively small area of the Earth's surface, urban areas represent about 15 % of the total reported costs attributed to invasive species. These results highlight the conservative nature of the estimates and impacts, revealing important biases present in the evaluation and publication of reported data on costs. We emphasize the urgent need for more focused assessments of invasive species' economic impacts in urban areas.

1. Introduction

Urbanization is recognized as one of the predominant drivers of global change, and its ever-increasing intensity contributes to the impacts of climate change and biodiversity collapse (Grimm et al., 2008; Uchida et al., 2020). In 2018, about 55 % of the human population lived in urban areas and it is projected to reach 60 % by 2030 (United Nations, 2018). Urbanization involves substantial alterations in land use and infrastructure development, represented by built areas like streets, houses, parking, squares, and human-made green areas (Grimm et al., 2008; Uchida et al., 2020). Urban areas are also associated with a high frequency of human-caused disturbance, terrestrial, aquatic, and atmospheric pollution, and host a high proportion of hot climatic niches (Grimm et al., 2008; Kowarik, 2011). Environmental change in urban areas, and the high mobility of people and trade flows, facilitate the introduction of non-native species (Bueno et al., 2023; Essl et al., 2020; Heringer et al., 2021b; Kowarik, 2011). Such new introductions have led to profound shifts in species composition, often resulting in a complex interplay between native and non-native species (Borges et al., 2020; Heringer et al., 2021b; Kowarik, 2011). Indeed, urban areas typically foster conditions favorable to the introduction and spread of non-native species and generally act as introduction hubs, from which species subsequently spread (actively or passively) into the surrounding rural and natural environments (Aronson et al., 2016; Kowarik, 2011; McLean

et al., 2017). The species with populations transported beyond their natural biogeographic range that are established and can spread in their introduced range are considered as invasive non-native species or invasive alien species (hereafter, invasive species – Blackburn et al., 2011). This spread is particularly apparent for generalist and opportunistic species that thrive in disturbed environments, with these conditions often favoring the proliferation of invasive species and a homogenization of species composition (McKinney, 2006; Gaertner et al., 2017).

Most taxonomic groups of invasive species are predicted to increase their number globally at least until 2050 (Seebens et al., 2020; Pyšek et al., 2020; IPBES, 2023), with inevitable further increases in their impacts on the environment and human well-being (Pyšek et al., 2020). Invasive species have diverse socio-ecological impacts, such as reducing native species richness, causing native population declines, changing ecosystem functioning, modifying soil properties, damaging infrastructure, and causing or transmitting diseases affecting human health (Vilà et al., 2011; Blackburn et al., 2014; Pyšek et al., 2020; IPBES, 2023). In urbanized areas, the effects of invasive species are an emerging field of research that requires more attention (Francis and Chadwick, 2015; Cadotte et al., 2017). Despite knowledge gaps in this domain, some examples demonstrate the relationship between urbanization and the advent and impacts of invasive species. For example, the Japanese knotweed (*Reynoutria japonica*) promotes changes in soil structure and

reductions in plant richness and cover in urban wastelands (Maurel et al., 2010). Moreover, the magnitude of the impact of invasive mosquitoes, *Aedes aegypti* and *A. albopictus*, on public health (i.e., the transmission of viral diseases such as dengue, yellow fever, chikungunya, and Zika) is closely related to the presence of urbanized areas which provide adequate conditions for proliferation and disease transmission (Li et al., 2014; Kolimenakis et al., 2019). Several non-native plant species occurring in cities produce large quantities of allergenic airborne pollen that represent significant hazards for human health, such as common ragweed (*Ambrosia artemisiifolia*) and groundsel-bush (*Baccharis halimifolia*), and can damage monuments (e.g., *Ailanthus altissima*) (Ham et al., 2013; Nentwig et al., 2017).

A recent initiative found invasive species caused more than US\$ 2.2 trillion in accumulated losses to the world economy, bringing the average incurred cost due to biological invasions to approximately US\$ 37 billion every year for the past six decades (Diagne et al., 2021a; Angulo et al., 2021; for updated values, see Leroy et al., 2022a). In 2019 alone, the annual cost was around US\$ 423 billion globally, according to the last “Thematic Assessment Report on Invasive Alien Species and their Control” of the “Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services” (IPBES, 2023). The majority of this total cost was caused by damage to nature’s contributions to people and good quality of life (IPBES, 2023). There is an increasing number of studies investigating the economic impact of invasive species (Ahmed et al., 2023), but only a few of them examine the economic impacts on particular habitats (i.e., aquatic – accumulated cost of US\$ 345 billion [Cuthbert et al., 2021], islands – accumulated cost of US\$ 36.6 billion [Bodey et al., 2023], and protected areas – accumulated cost of US\$ 22.4 billion [Moodley et al., 2022]). In urban areas, the high density of humans in urban areas increases the likelihood of contact between people and invasive species and may result in greater issues. A good example is a dengue outbreak in Dourados, Brazil, in 2010, which caused economic losses due to hospitalization and treatment, compromising about 2.5 % of the gross domestic product of this middle-sized city (Machado et al., 2014). Although some studies report the costs caused by invasive species in urban areas (e.g., Machado et al., 2014; Wylie and Janssen-May, 2017), a global synthesis is still lacking, yet it would contribute to drawing public and political attention to the topic, as well as functioning as a guide and baseline for future studies. Improving our understanding of the economic impacts of invasive species becomes critical to better describe the array of problems they pose, allowing the improvement of management strategies in urbanized areas (e.g., via better communication with the public and active engagement of stakeholders) and the conservation of urban biodiversity.

Here, we used the *InvaCost* database (Diagne et al., 2020a, 2020b), the first, most comprehensive, and up-to-date global database on the monetary costs of invasive species, to analyze and synthesize the reported economic impacts associated with invasive species in urbanized areas. Specifically, based in the costs reported in the literature available in *InvaCost*, we assessed the (1) total cost of invasive species reported in urbanized areas from 1965 to 2021 and the temporal trend of the costs included; (2) distribution of invasive species reported costs by taxonomic groups, impacted sector, type of cost, and invaded environment; (3) cumulative cost at a national level and the number of invasive species responsible for that in every country; and (4) knowledge gaps triggered by underreporting, particularly for countries lacking references on costs or other documentation. We intend, therefore, to present a global synthesis based on the current literature available and discuss important aspects that must be considered to delimitate future priorities in public policies and scientific studies.

2. Methods

2.1. Data collection and standardization

We retrieved the costs of invasive species from the *InvaCost* database

(version 4.1 – Diagne et al., 2020a, 2020b; Angulo et al., 2021). This database collected cost data from English and other 21 non-English languages using the ISI Web of Science and Google Scholar searches, and by contacting experts and stakeholders to request additional (not publicly available) cost information from official reports. Since its first release in 2020, the *InvaCost* database has been reviewed and updated periodically, including a living figure with a graphical overview of the latest version (Leroy et al., 2022a). The current version of the database used contains 13,553 cost entries related to invasive species and 66 columns with variables that describe in detail each cost entry (such as, reference title, authors, publication year, species, and environment) from 1975 references (Diagne et al., 2020b; Leroy et al., 2022b). Each reference is a unique source of data (e.g., scientific paper, book, or official report) that provides one or more cost entry. One of these descriptors was developed for this study to distinguish the monetary values incurred in urban areas and filter those for further assessment.

For this classification into costs incurred in urban vs. non-urban spaces, all references in the *InvaCost* database were reviewed, and costs incurred strictly in urban areas or specific to urban habitats were classified as “urban”. This included sites characterized by high population density, provision of essential services (e.g., electricity and water supply), a high proportion of built area, or human-made sites with infrastructure highly associated with cities, such as airports and harbors. Therefore, while assessing the references, we observed the terms clearly related to urban areas, such as cities, metropolises, towns, or human settlements, as well as the context of the study. It is important to highlight that urban areas are complex and encompass a heterogeneous set of ecosystems, and different authors or regions may apply concepts slightly differently. Those studies reporting costs associated with non-urban areas or where urban and non-urban areas could not be clearly differentiated were classified as “other” (such as costs reported collectively for a whole country). In many studies, the costs were not explicitly associated with habitat (urban/rural areas, forest, agricultural lands, etc.) but rather mentioned the economic impacts incurred at local/regional/national scales. For studies that computed costs incurred in urban vs. non-urban areas but were not reported separately in *InvaCost* database, we used the term “both”.

We therefore constrained the database to costs incurred in urban areas, cost entries classified as “highly reliable”, and classified as “observed” costs in the *InvaCost* (Fig. 1). Records are classified as “highly reliable” when they come from peer-reviewed sources, official reports, or grey material but with documented, repeatable, and traceable methods. In turn, “observed” costs did not include potential anticipated costs but only those realized or empirically incurred. For comparability purposes, we maintained the costs converted to 2017 US\$ used in *InvaCost* and reported the total cost considering “observed” and “potential” as some studies using *InvaCost* consider both. The dataset following the aforementioned filtering steps can be found in Supplementary material 1 (Table S1). For more details on the *InvaCost* database, see Diagne et al. (2020a, 2020b). In one case, where we had costs on several species without the species-wise cost breakdown, we reclassified that entry as “Diverse/Unspecified” (the species were *Clidemia hirta*, *Limnocharis flava*, *Mikania micrantha*, *Miconia calvescens*, *Miconia nervosa*, and *Miconia racemosa*). Moreover, we combined *Aedes aegypti* and *A. albopictus* as *Aedes* spp., since both species have similar behavior and impact, and the two are not always specified when costs are reported.

Before analysis, we expanded this dataset using the “expandYearlyCosts” function of the “invaCost” R package (Leroy et al., 2022b). This function is based on the difference between the “Probable_starting_year_adjusted” and “Probable_ending_year_adjusted” columns for each cost entry. It transforms the compacted structure of *InvaCost* database to an expanded form where each row represents a unique entry with costs per year, species/taxa, and reference (for details see Leroy et al., 2022b). After expanding our dataset, we obtained a total of 819 annualized cost entries for the period of 1965–2021, i.e., 57

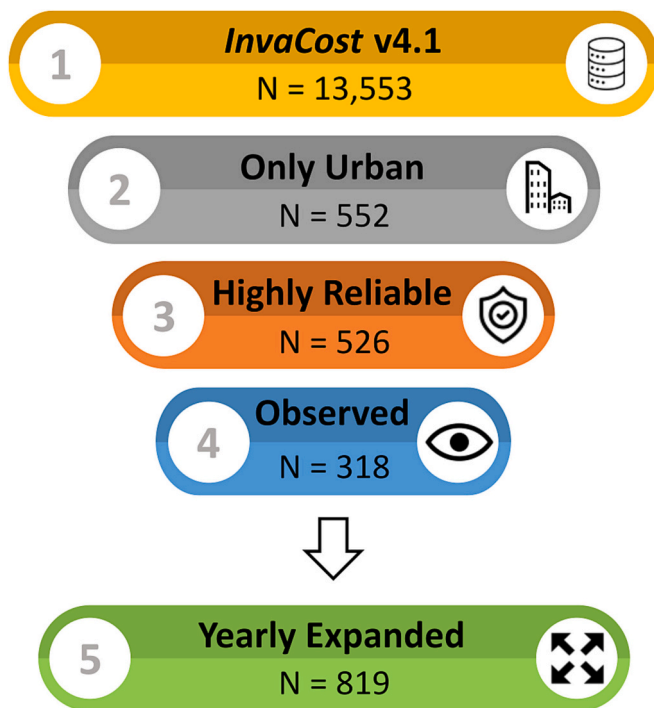


Fig. 1. Flowchart detailing the stepwise data filtering process to reach the final database used in this study, along with the number of entries at each step.

years. With this database, we estimated the total economic cost of invasive species reported in urban areas for this period.

2.2. Cost analyses

We described the distribution of invasive species costs incurred in urban areas over time (aim 1). To meet the second aim, we assessed the patterns of cost by taxonomic group (column “Species” and column “Class”), impacted sector (i.e., agriculture, authorities-stakeholders, forestry, health, multiple, and public and social welfare; column “Impacted_sector”), type of cost (i.e., damage, management, or mixed cost; column “Type_of_cost_merged”), and living environment of the invasive species (i.e., terrestrial, aquatic, or aquatic/terrestrial; column “Environment_IAS”) (Supplementary material 1, Table S1). Here, impacted sector describes the economic or societal activity related to the cost reported. For instance, expenses from governmental or official organizations focused on the management of invasive species, such as control programs or research funding, were assigned as “authorities-stakeholders” (for details see Diagne et al., 2020b). Damage costs corresponded to monetary losses, such as infrastructure losses, monetized health issues, and reductions in ecosystem productivity. Management-related costs included mitigation costs/expenditure, such as prevention, control, eradication, and research of invasive species. Finally, mixed costs are costs that do not explicitly mention if costs result from either of the two previous categories.

2.3. Cost per country and knowledge gaps

To meet the third aim, we calculated the cumulative cost incurred in urban areas per country (dependent variable) and the number of invasive species that cause costs reported in urban areas per country (independent variable). We used, therefore, a linear model to test whether cost incurred in urban areas is affected by the number of costly invasive species (i.e., those that caused costs in urban areas). Both variables were log₁₀ transformed and the assumptions of normality and linearity of residuals were assessed visually by the residual-diagnostic plot, whereas

homoscedasticity was assessed using Breusch-Pagan test ($BP = 0.91$, $df = 1$, $p = 0.34$). We also tested the existence of spatial autocorrelation using Mantel correlogram and Principal Coordinates of Neighbour Matrices – PCNM (Borcard et al., 2011). In short, the PCNM method consists of computing a PCoA using a truncated distance matrix. The output PCNM eigenvectors are orthogonal spatial variables that represent the structure of the data from broad to finer scales (from first to last axes) (Borcard et al., 2011). We then tested the 14 PCNM eigenvectors as independent variables in a global linear model against economic cost and applied a backward selection using the “drop1” function to remove non-significant variables with smaller F-value progressively (package “stats”; R Core Team, 2023). In both cases, we did not find a significant effect of space on economic cost caused by invasive species incurred in urban areas.

We could not run a similar test at the urban area scale due to the lack of variability in the available data (95 % of urban areas presented only one invasive species, with the other 5 % having two). However, we assume that many, if not most, actions related to research and management of invasive species are planned at the country level, and analyses at country levels are still necessary to guide them.

Finally, we investigated the countries with potential costs in urban areas currently neglected in the literature (fourth aim). For this, (i) we searched for occurrences of the species that caused economic costs in urban areas in the Global Biodiversity Information Facility platform (GBIF.org, 2023). (ii) We filtered the data to remove records without geographical coordinates, geographical uncertainty >1000 m, and geospatial issues that could affect the quality of the records (e.g., coordinates exactly equal 0 longitude and 0 latitude or mismatch between country and coordinates). (iii) We applied a data cleaning process to improve the quality of the data by removing records with spatial or temporal inconsistencies using functions from the “CoordinateCleaner” package (Zizka et al., 2019). To ensure occurrences in medium and small capitals would not be removed entirely, we set up a buffer size of 1000 in the “cc_cap” function. (iv) Finally, we selected only the occurrences inside urban areas, using the “cc_urb” function to flag the records into urban areas in the “CoordinateCleaner” package. This produced the occurrences of invasive species that caused costs incurred in urban areas beyond locations reported in the *InvaCost* database. To ensure we dealt only with the occurrences where these species are non-native, we cross-checked data with the Global Register of Introduced and Invasive Species (GRIIS – Pagad et al., 2018). We then plotted the occurrence of invasive species in urban areas on a map to highlight the countries with potential missing costs. All analyses were done in R environment (version 4.3.1 – R Core Team, 2023).

3. Results

The total reported cost of invasive species in urban areas was US\$ 326.7 billion, with an average annual cost of US\$ 5.7 billion from 1965 to 2021 (a total of 819 entries after expanding the data) (Fig. 2A). We observed a clear trend of increasing costs over time, with the peak of costs being reached in the decade between 2005 and 2014. Sixty-one invasive species caused these costs, in 24 countries across all continents except Antarctica. Although this paper focusses on assessing the “observed” economic impact of invasive species, it is worth mentioning that if we consider both “observed” and “potential” (i.e., with temporal or spatial extrapolation) then the total cost reaches US\$ 507.4 billion (average annual cost of US\$ 8.9 billion).

3.1. Economic costs by taxonomic group

Class Insecta was responsible for the largest percentage of the total cost (US\$ 324.4 billion [99.3 %]) and represented the majority of the expanded cost entries ($n = 616$ out of 819 total expanded entries) (Fig. 2B; Supplementary material 1, Table S2). Class Aves carried the second-highest costs (US\$ 1.4 billion [0.4 %]; $n = 11$) followed by

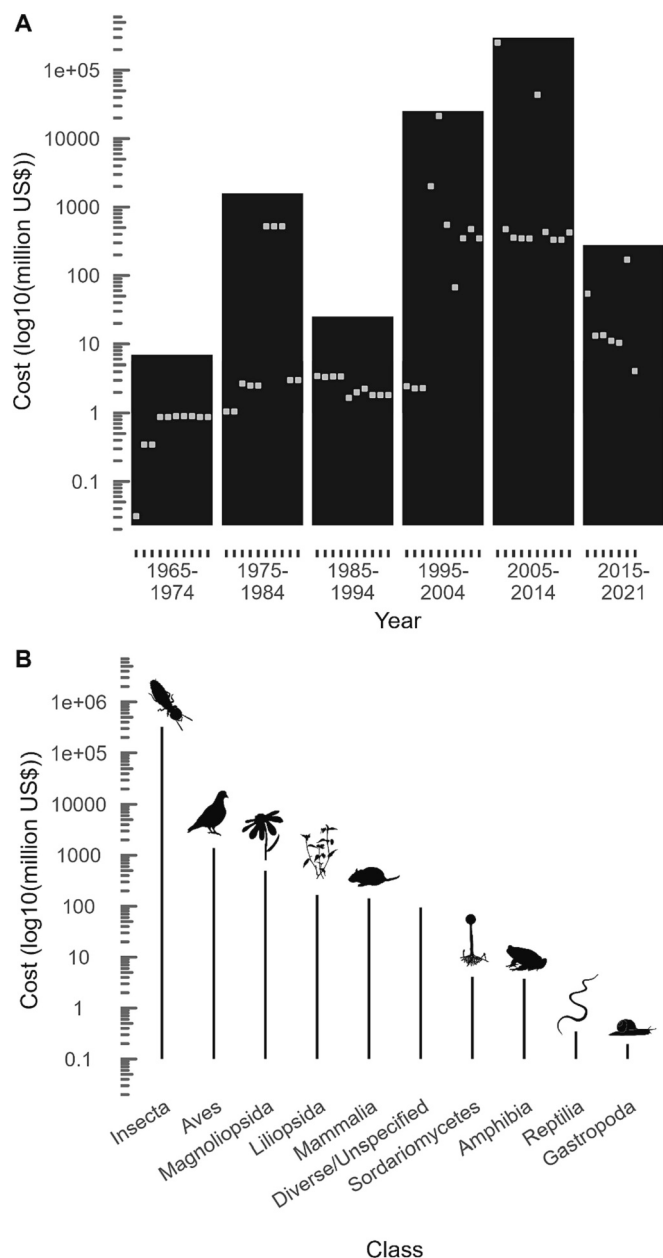


Fig. 2. Reported monetary costs for invasive non-native species in urban areas. Costs per year and decade (A). Reported monetary costs per class (B). In both cases, note the logarithmic y-axis scale. In A, squares show the sum of costs per year and bars show the sum of costs per decade. Silhouettes were obtained with the “rphylopic” package (Gearty and Jones, 2023).

Magnoliopsida (US\$ 494 million [0.15 %]; $n = 90$), Liliopsida (US\$ 167 million [0.05 %]; $n = 14$), and Mammalia (US\$ 142 million [0.04 %]; $n = 21$) (Fig. 2B).

The five costliest species, according to reported costs in the database, were the Formosan subterranean termite (*Coptotermes formosanus*, US\$ 252.1 billion [77.2 %], $n = 42$), the emerald ash borer (*Agrilus planipennis* US\$ 3.7 billion [1.1 %], $n = 13$), the red fire ant (*Solenopsis invicta* US\$ 1.6 billion [0.49 %], $n = 77$), the Mediterranean fruit fly (*Ceratitis capitata* US\$ 1.6 billion [0.48 %], $n = 3$), and the feral pigeon (*Columba livia* US\$ 1.4 billion [0.42 %], $n = 1$) (Fig. 3; Table 1; Supplementary material 1, Table S3). The sum of costs assigned to these five species accounted for 80 % of the total costs incurred in urban areas (Table 1; Supplementary material 1, Table S3). Despite representing only 0.7 % of the total sum, the actual cost values for these other species are still

massive (US\$ 2.1 billion, $n = 637$).

Costs caused by animals mainly impacted the public and social welfare sector, followed by the authorities-stakeholders sector (Fig. 3). The Formosan subterranean termite was responsible for >77 % of the costs caused by animals and affected exclusively public and social welfare due to damage and management (Fig. 2A; Supplementary material 1, Table S4 and S8). Invasive non-native plants, which presented lower recorded total cost than animals, affected mostly the health, authorities-stakeholders, and agriculture sectors (Fig. 3). The two invasive non-native plants with highest reported costs caused 95 % of the total costs recorded for invasive plants; common ragweed (*Ambrosia artemisiifolia*) affecting the health sector due to damage losses, and halfa grass (*Sporobolus cynosuroides*) affecting the authorities-stakeholders sector due to management costs (Fig. 2B; Supplementary material 1, Table S5 and S9). *Ophiostoma ulmi*, the causal agent of the Dutch elm disease, was the only fungal species and impacted mainly the public and social welfare sector because of damage costs (Fig. 3C; Supplementary material 1, Table S6 and S10).

3.2. Economic costs by impacted sector and type of cost

The costs caused by invasive species were predominantly associated with public and social welfare (US\$ 254.3 billion; $n = 89$), authorities-stakeholders (US\$ 67.7 billion, $n = 631$), and multiple sectors (US\$ 4 billion; $n = 64$) (Fig. 4; Supplementary material 1, Table S12). All other sectors incurred relatively lower impacts, ranging from US\$ 13.8 million in the health sector to US\$ 550.9 million in the forestry sector. The costs reported in public and social welfare were mostly related to damage, whereas management and mixed were the costs more related to authorities-stakeholders (Fig. 4A; Supplementary material 1, Table S15).

Far more of the costs of invasive species in urban areas were related to damage (US\$ 252.4 billion; $n = 89$), followed by mixed (US\$ 66.1 billion; $n = 26$) and management (US\$ 8.2 billion; $n = 703$) (Fig. 4; Supplementary material 1, Table S13). Costs related to damage were incurred mainly in public and social welfare and health sectors, whereas costs related to management were reported mostly in multiple sectors, authorities-stakeholders, and public and social welfare sectors (Fig. 4A; Supplementary material 1, Table S15). The mixed type of cost impacted mainly the authorities-stakeholders sectors (Fig. 4A; Supplementary material 1, Table S15).

3.3. Economic costs by urban-invaded environments

Most of the costs associated with invasive species in urban areas were reported to terrestrial environments, totaling US\$ 326.6 billion ($n = 750$), while those associated with aquatic and aquatic/terrestrial environments were much lower, amounting to US\$ 44.4 million ($n = 53$) and US\$ 14 million ($n = 15$), respectively (Fig. 3D; Supplementary material 1, Table S14). Costs caused by aquatic taxa were associated with the authorities-stakeholders sector due to management and damage (costs of US\$ 35.8 million and 1.7 million, respectively) and public and social welfare (US\$ 6.9 million).

The taxa responsible for the costs reported in terrestrial environments correspond to the costliest taxa listed in Table 1. The reported costs in aquatic environments were caused by two invasive non-native plants, the spiked milfoil (*Myriophyllum spicatum*) and the water hyacinth (*Pontederia crassipes*, formerly known as *Eichhornia crassipes*) (Supplementary material 1, Table S3), as well as taxa classified as Diverse/Unspecified (US\$ 28.9 million). The costs in aquatic/terrestrial environments were caused by taxa classified as Diverse/Unspecified (US\$ 13.6 million) and the American bullfrog (*Lithobates catesbeianus*) whose adult life is associated with both environments (Supplementary material 1, Table S3).

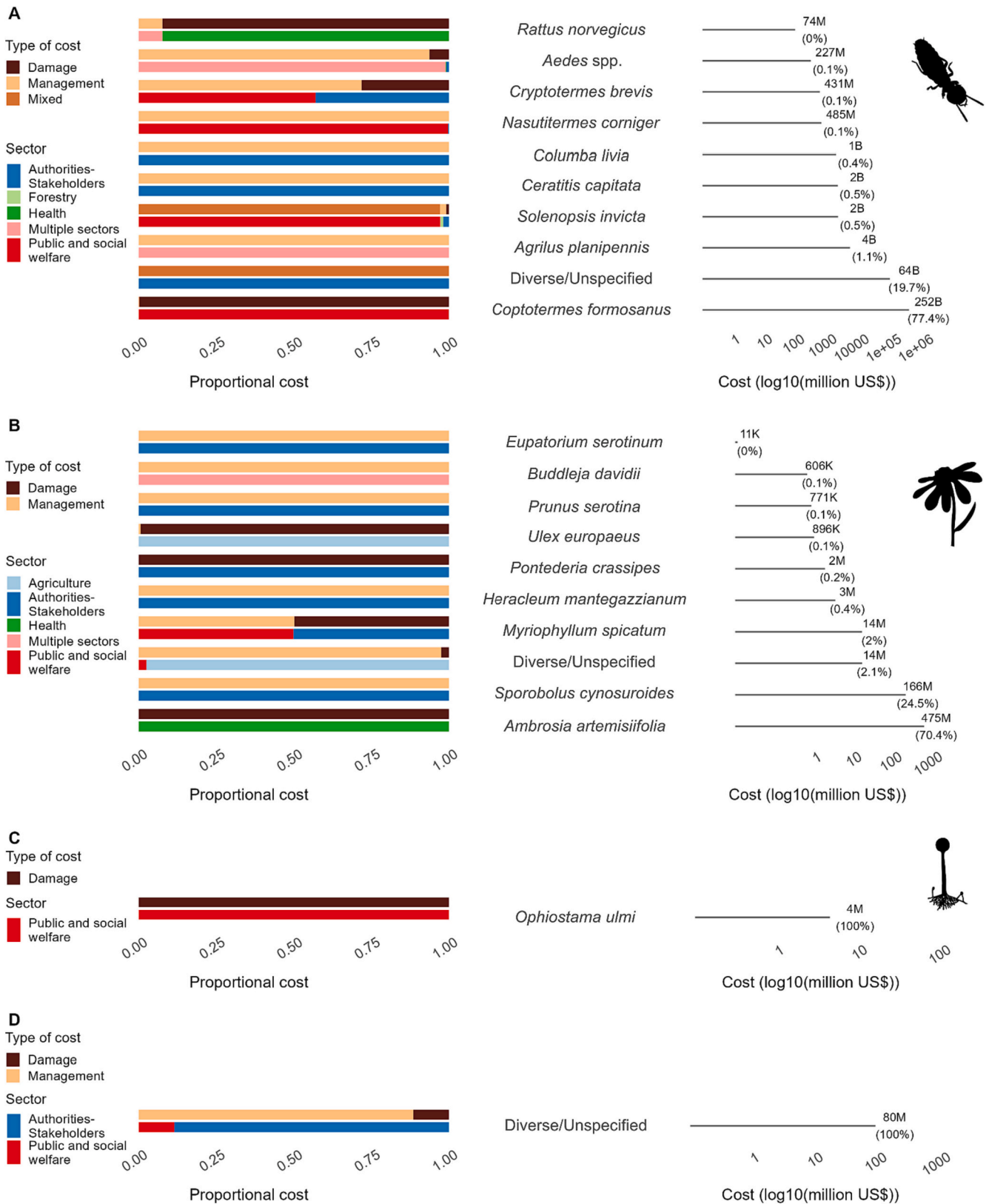


Fig. 3. Economic costs observed incurred in urban areas per species per kingdom (top-10 costliest taxa are shown). Animalia (A); Plantae (B); Fungi (C); Diverse/Unspecified (D). Bars on the left side show the proportion of economic costs per type of cost (top) and impacted sector (bottom), whereas bars on the right side show the economic costs where K = thousand, M = million, and B = billion. Silhouettes were obtained with the “rphylopic” package (Gearty and Jones, 2023).

Table 1

Total costs and percentage share of the top 20 invasive non-native species with the highest reported costs for urban areas (complete list of species' costs available in Supplementary material 1, Table S3).

Taxa (mostly species)	English common name of the species/genera	Cost incurred in urban areas (US\$ million)	Percentage
<i>Coptotermes formosanus</i>	Formosan subterranean termite	252,127.36	77.18
Diverse/Unspecified	n/a	64,157.03	19.64
<i>Agrilus planipennis</i>	Emerald ash borer	3717.54	1.14
<i>Solenopsis invicta</i>	Red fire ant	1586.94	0.49
<i>Ceratitis capitata</i>	Mediterranean fruit fly	1562.76	0.48
<i>Columba livia</i>	Feral pigeon	1380.66	0.42
<i>Nasutitermes corniger</i>	Termite	485.44	0.15
<i>Ambrosia artemisiifolia</i>	Ragweed	475.10	0.15
<i>Cryptotermes brevis</i>	Powderpost termite	431.35	0.13
<i>Aedes</i> spp.	Mosquitoes	227.03	0.07
<i>Sporobolus cynosuroides</i>	Halfa grass	165.51	0.05
<i>Rattus norvegicus</i>	Brown rat	74.08	0.02
<i>Blatta orientalis/Blatella germanica</i>	Oriental cockroach/ German cockroach	59.72	0.02
<i>Wasmannia auropunctata</i>	Little fire ant	30.20	0.01
<i>Cameraria ohridella</i>	Horse-chestnut leaf miner	28.87	0.01
<i>Canis familiaris dingo/Vulpes vulpes</i>	Dingo/Red fox	28.26	0.01
<i>Sciurus aureogaster</i>	Mexican grey squirrel	19.77	0.01
<i>Linepithema humile</i>	Argentine ant	16.96	0.01
<i>Myriophyllum spicatum</i>	Spike watermilfoil	13.81	<0.01
<i>Ondatra zibethicus</i>	Muskrat	12.78	<0.01

3.4. Economic cost by country

The costs caused, at country level, by invasive species in urban areas ranged from US\$ 17 to US\$ 261.5 billion (median: US\$ 10.9 billion). Australia, China, and the USA presented the highest expenses caused by invasive species in urban areas (US\$ 169 million, 518 million, and 261.5 billion, respectively) (Fig. 5A; Supplementary material 1, Table S16). The number of invasive species that cause costs in urban areas ranged between one and 18 (median: 3.4; Fig. 5B; Supplementary material 1, Table S17), with Germany, Australia, and the USA showing the highest number of these species (9, 14, and 18, respectively). The observed number of costly invasive species in urban areas was positively related to the costs incurred in urban areas per country ($F_{1, 22} = 16.5, p < 0.001, r_{adj}^2 = 0.40$; Supplementary material 2, Fig. S1). Importantly, there are 73 additional countries with no reported costs in the *InvaCost* database, but with occurrences of invasive species that have reported costs in other countries (Fig. 5C; Supplementary material 1, Table S17). In other words, in these countries, invasive species are likely to have costs that were not documented or reported in available sources.

4. Discussion

We found that just 61 invasive species caused a reported cost of US\$ 326.7 billion between 1965 and 2021 in urban areas worldwide. These massive monetary losses represent about 15 % of the total costs reported for invasive species (about US\$ 2.2 trillion – Diagne et al., 2021a; Angulo et al., 2021; for the latest values, see Leroy et al., 2022a), yet urban areas cover only between 0.6 and 3 % of the Earth's surface (Liu et al., 2014; Zhao et al., 2022). Such costs can be attributed to the success of invasive species in urban environments – where they can achieve higher abundance and diversity (Cadotte et al., 2017) alongside

a high concentration of human population, economic, research and management activities and assets. Despite these figures, a large number of countries without any reported costs caused by invasive species in urban areas (as documented in *InvaCost*) have occurrence records of known impactful species in urban locations. This gap strongly implies that the already massive costs associated with urban invasions reported in this study remain significantly underestimated, and more primary and systematic assessments are needed, particularly for data poor regions.

4.1. Economic costs by taxonomic group

Invasive non-native insects are frequently reported as the costliest taxonomic group (e.g., Adelino et al., 2021; Bradshaw et al., 2016; Diagne et al., 2021a; Heringer et al., 2021a; Renault et al., 2022). Additionally, a study at the continental scale found that non-native insects and plants invade mostly human-made (e.g., urban and cultivated) habitats (Pyšek et al., 2010) which partially aligns with our results, where several insects are among the costliest invasive species reported in urban areas. For instance, the Formosan subterranean termite, red fire ant, and *Aedes* mosquitoes. The Formosan subterranean termite is a widely distributed species that threatens buildings and other wooden structures and materials and damages living trees (Evans et al., 2019; Rust and Su, 2012). These impacts result in high economic costs incurred by the public and welfare and authorities-stakeholders sectors due to damage and management costs. Red fire ants represent a severe problem for human health, recreation, tourism, and farming as the species has a painful sting and aggressive behavior, while also severely impacting native biodiversity (Kenis et al., 2009; Angulo et al., 2022). *Aedes* spp. cause more than US\$ 87 billion of costs worldwide (Roiz et al., 2023), but we found that a relatively small fraction of this reportedly incurred in urban areas. This is surprising as *Aedes* spp. mosquitoes are strongly associated with urban areas, where higher human densities favor disease transmission. This can be caused by the fact that many relevant studies reported costs at broader regional or continental scales, so the proportion occurring in urban areas was not explicit (e.g., Kolimenakis et al., 2019). Our conservative approach of only assigning costs to urban areas when explicitly stated in the original reference meant that the number and impacts of species, including *Aedes* spp., remain vastly underestimated in urban areas.

The high cost reported in urban areas due to damages caused by brown rats (*Rattus norvegicus*) and management actions associated with feral pigeons seems to be widely underestimated, as only three studies limited to China, UK, and the USA report these economic impacts. Nevertheless, most residents of large cities worldwide invest in mitigating the impact caused by those species, such as the use of traps for rats or the use of nets and skewers to avoid feral pigeons on buildings and monuments. The lack of published studies reporting costs caused by invasive species in urban areas, the difficulty of accessing and evaluating the reliability of grey literature, and the misattribution of costs to “pests” without mentioning their ecological status as invasive species, are potential reasons to explain the underestimation of costs of rodents (Diagne et al., 2023), and are potentially relevant to most urban species.

We found that the costs recorded for invasive non-native plants in urban areas were lower than the costs associated with the invasion of non-native animals. Possibly, this result is strongly related to a data deficiency related to plants in the *InvaCost* database (Novoa et al., 2021). Nevertheless, the ratio between costs caused by the invasion of non-native plants and the total costs is much smaller in urban areas than when considering the overall cost (see Leroy et al., 2022a). For instance, of the 72 invasive non-native trees reported in the literature causing costs (Fernandez et al., 2023), only black cherry (*Prunus serotina*) appears as a costly species in urban areas. Thus, we can expect that other factors are also influencing the low reported costs caused by plants in urban areas. For example, invasive plants in urban areas can also promote ecosystem services (Potgieter et al., 2017), and this can influence the public perception of such species. An additional consideration is that

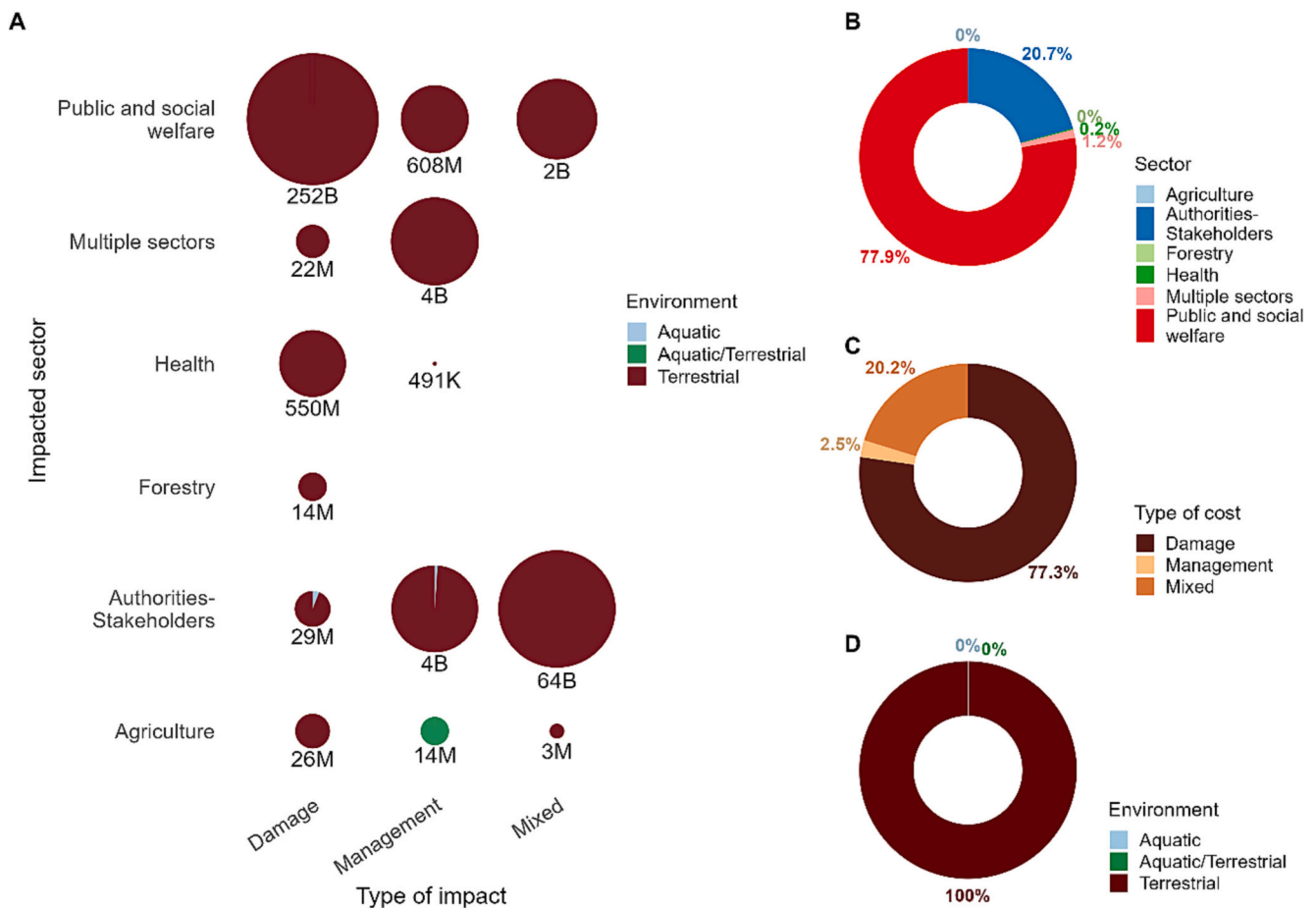


Fig. 4. Economic costs observed incurred in urban areas per Impacted sector, Type of costs, and Environment. Association between economic costs and Impacted sector, Type of costs, and Environment (A); Economic costs per Impacted sector (B); Economic costs per Type of costs (C); Economic costs per Environment (D). In A, the values of costs observed are presented below the circles where K = thousand, M = million, and B = billion.

generalized control of ‘weeds’ in urban areas (e.g., road edges or parks) may not differentiate between invasive and native species, making costs both difficult to find in the literature and to attribute to their invasive status. Although we lack evidence on why reported costs of invasive non-native plants in urban areas are lower compared to other habitats, studies designed to investigate this question can elucidate whether this result is biased.

4.2. Economic costs by type of cost and impacted sector

The management of invasive species in urban areas can be complex because of the numerous actors involved that may have different perceptions and stakes in the invasive species (Gaertner et al., 2017; Potgieter et al., 2019; Potgieter et al., 2021). In addition, management in urban areas can be at times controversial (Kourantidou et al., 2022); the greatest conflict may occur with those charismatic non-native species, which were intentionally introduced into urban areas as pets or to provide some ecosystem service (Dickie et al., 2014; Jarić et al., 2020). This can explain why most of the costs were triggered by damage losses rather than management, and affected the public and social welfare sector. Although the disproportionately high costs of the Formosan subterranean termite are likely the driver of this imbalance, it is plausible that reactive conservation actions against invasive species, which is a general pattern observed (e.g., Adelino et al., 2021; Cuthbert et al., 2022; Heringer et al., 2021a), will result in more extensive economic impacts. Our results corroborate the need to invest in proactive actions which, in general, are less costly and can prevent future impacts associated with biological invasions (Cuthbert et al., 2022; Heringer et al.,

2021a).

4.3. Economic costs by invaded urban environments

In general, more studies have been conducted on the impacts of invasive species in terrestrial than in aquatic environments (Cuthbert et al., 2021; Heringer et al., 2021a), and our results confirm this trend, with a very small proportion of the economic impacts occurring in aquatic ecosystems of urban areas. The absence of reported costs caused by fish in urban areas caught our attention. Although the high degree of modification of aquatic environments in urban areas may be a barrier even for invasive fish, we believe the lack of studies is a more parsimonious reason. Most of the costs reported in aquatic environments were caused by the invasive plants spiked milfoil and water hyacinth. These species can become dominant and promote a set of ecosystem changes in the waterbody (e.g., light availability and water chemical composition), affecting native species, hindering navigation and impacting upon recreational activities (e.g., Smith and Barko, 1990; Olden and Tamayo, 2014; Kriticos and Brunel, 2016).

4.4. Economic cost by country

The reported costs associated with the invasion of non-native species in urban areas were especially high in the USA, which could be expected as the USA is the country with the highest reported costs imposed by invasive species in the world (Crystal-Ornelas et al., 2021), and the highest proportion of studies of managing invasive species in urban areas (Potgieter et al., 2021). In addition, as an English-speaking country

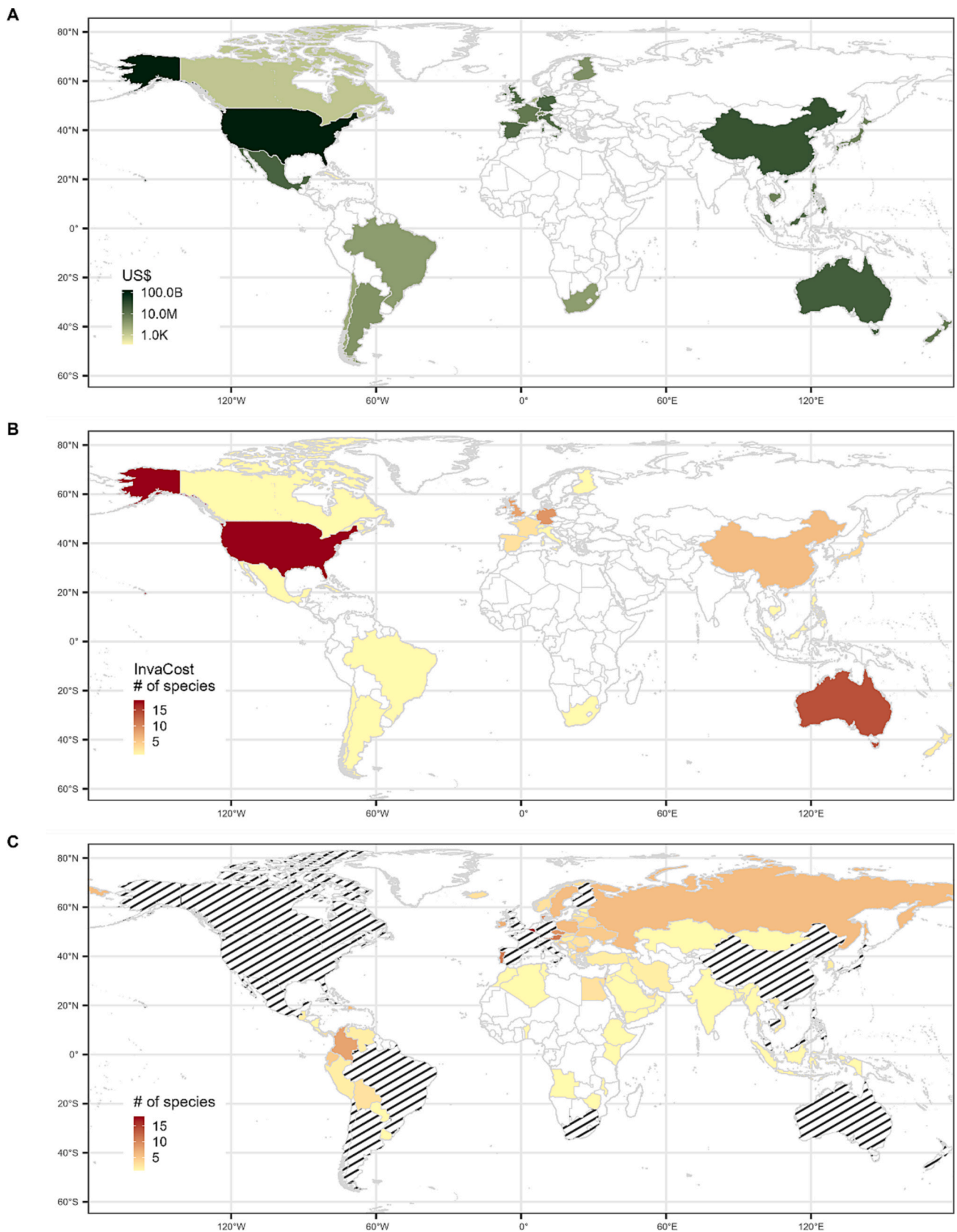


Fig. 5. Global distribution of reported costs and number of invasive non-native species in urban areas per country. Costs reported in urban areas per country (A); the number of invasive non-native species with recorded economic costs in urban areas included in the *InvaCost* database per country (B); the number of invasive non-native species with recorded economic costs in urban areas based in GBIF records that overlap with urban areas (C). In A, the values of costs observed are presented below the circles where K = thousand, M = million, and B = billion. In C, only invasive non-native species that already have costs incurred in urban areas were considered and countries with costs incurred in urban areas reported are represented with transversal stripes.

with relatively abundant resources for research, researchers may face lower barriers to publishing their studies in scientific journals, and papers are accessed more frequently (Angulo et al., 2021; Amano et al., 2021). Although there were monetary costs of invasive species reported in urban areas from all continents (except for Antarctica), these were restricted to 24 countries. Except for North America and Western Europe, there is a large proportion of all continents where countries have no reported data. The costs caused by invasive species are poorly reported in many countries and regions (e.g., Adelino et al., 2021; Diagne et al., 2021b; Duboscq-Carra et al., 2021; Heringer et al., 2021a; Liu et al., 2021). According to our findings, even where they are known to occur, studies focusing on urban areas are notably missing. The lack of costs generated by invasive species in the literature is a challenge that must be addressed through stronger engagement with stakeholders and research investments (Ahmed et al., 2023). In our case, for instance, several studies investigated the economic impact incurred in urban areas, but then combined these with costs incurred in non-urban areas, so reporting only total values (e.g., Kolimenakis et al., 2019; Vyn, 2019).

Because of their similar physical environment, urban areas induce a strong biological homogenization: the same species adapted to urban habitats tend to be widespread in cities across the planet (McKinney, 2006). Successful invaders are typically ecological generalists with wide distributional ranges, which are common in their native range (Pyšek et al., 2009) and are often introduced in urban areas (Aronson et al., 2016). As a result, invasive species that cause economic impacts in one urban area have the potential to cause an economic impact in any urban area across the world. However, it is clear from our analyses (Fig. 5) that these issues are likely not recognized or fully reported, resulting in a large underestimation in the costs caused by invasive species in urban areas. This is compounded by studies that combine costs from urban areas with non-urban areas, making it impossible to attribute the scale of impact of a species in either. More effective actions to assess and explicitly report the costs related to the invasion of non-native species in urban areas, combined with more applied research on the effectiveness of control actions, might pave the way to the implementation of cost-effective proactive management strategies reducing and preventing impacts in urban areas.

5. Conclusion

In this study, we provided the first global estimation of the economic impact of biological invasions in urban areas, where 15 % of global costs were attributable to these anthropogenic habitats that cover <3 % of the total global terrestrial area. Importantly, we identified many countries where known invasive species with reported costs in urban areas elsewhere were present but lacked documented monetary costs. We recognize the biases in reported costs of these species, that were strongly unevenly distributed across taxonomic groups, regions, sectors, and cost types, and call for broader scientific community involvement to help refine the database and improve the accuracy of future analyses with support from governments and citizens. Thus, our results highlight the conservative nature of the reported invasive species' economic impacts in urban areas available to date and emphasize the need for continued contributions to this database. Nevertheless, recognizing that invasive species are already a financial drain in urban areas can enhance public and political awareness, and social and policy-related engagement on their management. Amidst the mounting pressures on urban environments, it is crucial to recognize the significance of awareness and policy for invasions, particularly in light of the ongoing expansion of human populations in urban areas and their pivotal role as a driver for biological invasions.

CRedit authorship contribution statement

Gustavo Heringer: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing –

review & editing. **Romina D. Fernandez:** Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Alok Bang:** Investigation, Methodology, Writing – review & editing. **Marion Cordonnier:** Conceptualization, Investigation, Writing – review & editing. **Ana Novoa:** Investigation, Writing – review & editing. **Bernd Lenzer:** Investigation, Writing – review & editing. **César Capinha:** Investigation, Writing – review & editing. **David Renault:** Investigation, Writing – review & editing. **David Roiz:** Investigation, Writing – review & editing. **Desika Moodley:** Investigation, Writing – review & editing. **Elena Tricarico:** Investigation, Writing – review & editing. **Kathrin Holenstein:** Investigation, Writing – review & editing. **Melina Kourantidou:** Investigation, Writing – review & editing. **Natalia I. Kirichenko:** Investigation, Writing – review & editing. **José Ricardo Pires Adelino:** Investigation, Writing – review & editing. **Romina D. Dimarco:** Investigation, Writing – review & editing. **Thomas W. Bodey:** Investigation, Writing – review & editing. **Yuya Watari:** Investigation, Writing – review & editing. **Franck Courchamp:** Funding acquisition, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are available as supplementary material

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.170336>.

References

- Adelino, J.R.P., Heringer, G., Diagne, C., Courchamp, F., Faria, L.D.B., Zenni, R.D., 2021. The economic costs of biological invasions in Brazil: a first assessment. *Neobiota* 67, 349–374. <https://doi.org/10.3897/neobiota.67.59185>.
- Ahmed, D.A., Haubrock, P.J., Cuthbert, R.N., Bang, A., Soto, I., Balzani, P., Tarkan, A.S., Macêdo, R.L., Carneiro, L., Bodey, T.W., Oficialdegui, F.J., Courtois, P., Kourantidou, M., Angulo, E., Heringer, G., Renault, D., Turbelin, A.J., Hudgins, E.J., Liu, C., Gojery, S.A., Arbiou, U., Diagne, C., Leroy, B., Briski, E., Bradshaw, C.J.A., Courchamp, F., 2023. Recent advances in availability and synthesis of the economic costs of biological invasions. *Bioscience* 73 (8), 550–574. <https://doi.org/10.1093/biosci/biad060>.
- Amano, T., Berdejo-Espinola, V., Christie, A.P., Willott, K., Akasaka, M., Baldi, A., Berthinussen, A., Bertolino, S., Bladon, A.J., Chen, M., Choi, C.Y., Kharrat, M.B.D., De Oliveira, L.G., Farhat, P., Golivets, M., Aranzamendi, N.H., Jantke, K., Kajzer-Bonk, J., Cisel Kemahli Aytekin, M., Khorozyan, I., Kito, K., Konno, K., Lin, D.L., Littlewood, N., Liu, Yang, Liu, Yifan, Loretto, M.C., Marconi, V., Martin, P.A., Morgan, W.H., Narvaez-Gomez, J.P., Negret, P.J., Nourani, E., Ochoa Quintero, J.M., Ockendon, N., Oh, R.R.Y., Petrovan, S.O., Piovezan-Borges, A.C., Pollet, I.L., Ramos, D.L., Reboredo Segovia, A.L., Nayelli Rivera-Villanueva, A., Rocha, R., Rouyer, M.M., Sainsbury, K.A., Schuster, R., Schwab, D., Sekercioglu, C.H., Seo, H.M., Shackelford, G., Shinoda, Y., Smith, R.K., Tao, S.D., Tsai, M.S., Tyler, E.H.M., Vajna, F., Valdebenito, J.O., Vozykova, S., Waryszak, P., Zamora-Gutierrez, V., Zenni, R.D., Zhou, W., Sutherland, W.J., 2021. Tapping into non-English-language science for the conservation of global biodiversity. *PLoS Biol.* 19, 1–29. <https://doi.org/10.1371/journal.pbio.3001296>.
- Angulo, E., Diagne, C., Ballesteros-Mejia, L., Adamjy, T., Ahmed, D.A., Akulov, E., Banerjee, A.K., Capinha, C., Dia, C.A.K.M., Dobigny, G., Duboscq-Carra, V.G., Golivets, M., Haubrock, P.J., Heringer, G., Kirichenko, N., Kourantidou, M., Liu, C., Nuñez, M.A., Renault, D., Roiz, D., Taheri, A., Verbrugge, L.N.H., Watari, Y., Xiong, W., Courchamp, F., 2021. Non-English languages enrich scientific knowledge: the example of economic costs of biological invasions. *Sci. Total Environ.* 775, 144441 <https://doi.org/10.1016/j.scitotenv.2020.144441>.
- Angulo, E., Hoffmann, B.D., Ballesteros-Mejia, L., Taheri, A., Balzani, P., Bang, A., Renault, D., Cordonnier, M., Bellard, C., Diagne, C., Ahmed, D.A., Watari, Y., Courchamp, F., 2022. Economic costs of invasive alien ants worldwide. *Biol. Invasions* 24, 2041–2060. <https://doi.org/10.1007/s10530-022-02791-w>.
- Aronson, M.F.J., Nilon, C.H., Lepczyk, C.A., Parker, T.S., Warren, P.S., Gilliers, S.S., Goddard, M.A., Hahs, A.K., Herzog, C., Katti, M., La Sorte, F.A., Williams, N.S.G., Zipperer, W., 2016. Hierarchical filters determine community assembly of urban species pools. *Ecology* 97, 2952–2963. <https://doi.org/10.1002/ecy.1535>.
- Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarosík, V., Wilson, J.R.U., Richardson, D.M., 2011. A proposed unified framework for biological invasions. *Trends Ecol. Evol.* 26, 333–339. <https://doi.org/10.1016/j.tree.2011.03.023>.
- Blackburn, T.M., Essl, F., Evans, T., Hulme, P.E., Jeschke, J.M., Kühn, I., Kumschick, S., Marková, Z., Mrugała, A., Nentwig, W., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D.M., Sendek, A., Vilà, M., Wilson, J.R.U., Winter, M., Genovesi, P., Bacher, S., 2014. A unified classification of alien species based on the magnitude of their environmental impacts. *PLoS Biol.* 12, e1001850 <https://doi.org/10.1371/journal.pbio.1001850>.
- Bodey, T., Angulo, E., Bang, A., Bellard, C., Fantle-Lepczyk, J., Lenzer, B., Turbelin, A., Watari, Y., Courchamp, F., 2023. Economic costs of protecting islands from invasive alien species. *Conserv. Biol.* 37, e14034 <https://doi.org/10.1111/cobi.14034>.
- Borcard, D., Gillet, F., Legendre, P., 2011. *Numerical Ecology* with R. Springer, New York. <https://doi.org/10.1007/978-0-387-78171-6>.
- Borges, E.R., Dexter, K.G., Bueno, M.L., Pontara, V., Carvalho, F.A., 2020. The evolutionary diversity of urban forests depends on their land-use history. *Urban Ecosyst.* 23, 631–643. <https://doi.org/10.1007/s11252-020-00938-y>.
- Bradshaw, C.J.A., Leroy, B., Bellard, C., Roiz, D., Albert, C., Fournier, A., Barbet-Massin, M., Salles, J.M., Simard, F., Courchamp, F., 2016. Massive yet grossly underestimated global costs of invasive insects. *Nat. Commun.* 7 <https://doi.org/10.1038/ncomms12986>.
- Bueno, M.L., Heringer, G., Carvalho, D.R. de, Robinson, T.B., Pompeu, P.S., Zenni, R.D., 2023. Ecosystem variables importance in the presence and abundance of a globally invasive fish. *Sci. Total Environ.* 876, 162795 <https://doi.org/10.1016/j.scitotenv.2023.162795>.
- Cadotte, M.W., Yasui, S.L.E., Livingstone, S., MacIvor, J.S., 2017. Are urban systems beneficial, detrimental, or indifferent for biological invasion? *Biol. Invasions* 19 (12), 3489–3503.
- Crystal-Ornelas, R., Hudgins, E.J., Cuthbert, R.N., Haubrock, P.J., Fantle-Lepczyk, J., Angulo, E., Kramer, A.M., Ballesteros-Mejia, L., Leroy, B., Leung, B., López-López, E., Diagne, C., Courchamp, F., 2021. Economic costs of biological invasions within North America. *Neobiota* 67, 485–510. <https://doi.org/10.3897/neobiota.67.58038>.
- Cuthbert, R.N., Pattison, Z., Taylor, N.G., Verbrugge, L., Diagne, C., Ahmed, D.A., Leroy, B., Angulo, E., Briski, E., Capinha, C., Catford, J.A., Dalu, T., Essl, F., Gozlan, R.E., Haubrock, P.J., Kourantidou, M., Kramer, A.M., Renault, D., Wasserman, R.J., Courchamp, F., 2021. Global economic costs of aquatic invasive alien species. *Sci. Total Environ.* 775 <https://doi.org/10.1016/j.scitotenv.2021.145238>.
- Cuthbert, R.N., Diagne, C., Hudgins, E.J., Turbelin, A., Ahmed, D.A., Albert, C., Bodey, T.W., Briski, E., Essl, F., Haubrock, P.J., Gozlan, R.E., Kirichenko, N., Kourantidou, M., Kramer, A.M., Courchamp, F., 2022. Biological invasion costs reveal insufficient proactive management worldwide. *Sci. Total Environ.* 819 <https://doi.org/10.1016/j.scitotenv.2022.153404>.
- Diagne, C., Catford, J.A., Essl, F., Nuñez, M.A., Courchamp, F., 2020a. What are the economic costs of biological invasions? A complex topic requiring international and interdisciplinary expertise. *Neobiota* 63, 25–37. <https://doi.org/10.3897/neobiota.63.55260>.
- Diagne, C., Leroy, B., Gozlan, R.E., Vaissiere, A.C., Assailly, C., Nuninger, L., Roiz, D., Jourdain, F., Jarić, I., Courchamp, F., 2020b. InvaCost, a public database of the economic costs of biological invasions worldwide. *Sci. Data* 7, 1–12. <https://doi.org/10.1038/s41597-020-00586-z>.
- Diagne, C., Leroy, B., Vaissiere, A.-C., Gozlan, R.E., Roiz, D., Jarić, I., Salles, J.M., Bradshaw, C.J.A., Courchamp, F., 2021a. High and rising economic costs of biological invasions worldwide. *Nature* 592, 571–576. <https://doi.org/10.1038/s41586-021-03405-6>.
- Diagne, C., Turbelin, A.J., Moodley, D., Novoa, A., Leroy, B., Angulo, E., Adamjy, T., Dia, C.A.K.M., Taheri, A., Tambo, J., Dobigny, G., Courchamp, F., 2021b. The economic costs of biological invasions in Africa: a growing but neglected threat? *Neobiota* 67, 11–51. <https://doi.org/10.3897/neobiota.67.59132>.
- Diagne, C., Ballesteros-Mejia, L., Cuthbert, R.N., Bodey, T.W., Fantle-Lepczyk, J., Angulo, E., Bang, A., Dobigny, G., Courchamp, F., 2023. Economic costs of invasive rodents worldwide: the tip of the iceberg. *PeerJ* 11, e14935. <https://doi.org/10.7717/peerj.14935>.
- Dickie, I.A., Bennett, B.M., Burrows, L.E., Nuñez, M.A., Peltzer, D.A., Porté, A., Richardson, D.M., Rejmánek, M., Rundel, P.W., van Wilgen, B.W., 2014. Conflicting values: ecosystem services and invasive tree management. *Biol. Invasions* 16, 705–719. <https://doi.org/10.1007/s10530-013-0609-6>.
- Duboscq-Carra, V.G., Fernandez, R.D., Haubrock, P.J., Dimarco, R.D., Angulo, E., Ballesteros-Mejia, L., Diagne, C., Courchamp, F., Nuñez, M.A., 2021. Economic impact of invasive alien species in Argentina: a first national synthesis. *Neobiota* 67, 329–348. <https://doi.org/10.3897/neobiota.67.63208>.
- Essl, F., Lenzer, B., Bacher, S., Bailey, S., Capinha, C., Daehler, C., Dullinger, S., Genovesi, P., Hui, C., Hulme, P.E., Jeschke, J.M., Katsanevakis, S., Kühn, I., Leung, B., Liebhold, A., Liu, C., MacIsaac, H.J., Meyerson, L.A., Nuñez, M.A., Pauchard, A., Pyšek, P., Rabitsch, W., Richardson, D.M., Roy, H.E., Ruiz, G.M., Russell, J.C., Sanders, N.J., Sax, D.F., Scalera, R., Seebens, H., Springborn, M., Turbelin, A., van Kleunen, M., von Holle, B., Winter, M., Zenni, R.D., Mattsson, B.J., Roura-Pascual, N., 2020. Drivers of future alien species impacts: an expert-based assessment. *Glob. Chang. Biol.* 26, 4880–4893. <https://doi.org/10.1111/gcb.15199>.
- Evans, T.A., Forschler, B.T., Trettin, C.C., 2019. Not just urban: the Formosan subterranean termite, *Coptotermes formosanus*, is invading forests in the Southeastern USA. *Biol. Invasions* 21, 1283–1294. <https://doi.org/10.1007/s10530-018-1899-5>.
- Fernandez, R.D., Haubrock, P.J., Cuthbert, R.N., Heringer, G., Kourantidou, M., Hudgins, E.J., Angulo, E., Diagne, C.A., Courchamp, F., Nuñez, M.A., 2023. Underexplored and growing economic costs of invasive alien trees. *Sci. Rep.* 13, 8945. <https://doi.org/10.1038/s41598-023-35802-4>.
- Francis, R.A., Chadwick, M.A., 2015. Urban invasions: non-native and invasive species in cities. *Geography* 100, 144–151.
- Gaertner, M., Novoa, A., Fried, J., Richardson, D.M., 2017. Managing invasive species in cities: a decision support framework applied to Cape Town. *Biol. Invasions* 19 (12), 3707–3723.
- GBIF.org, 2023. GBIF Occurrence Download. <https://doi.org/10.15468/dl.bkt7x5>. Accessed on 19 June 2023.
- Gearty, W., Jones, L.A., 2023. rphylopic: An R Package for Fetching, Transforming, and Visualising PhyloPic silhouettes. *bioRxiv*. <https://doi.org/10.1101/2023.06.22.546191>.
- Grimm, N.B., Foster, D., Groffman, P., Grove, J.M., Hopkinson, C.S., Nadelhoffer, K.J., Pataki, D.E., Peters, D.P.C., 2008. The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. *Front. Ecol. Environ.* 6, 264–272. <https://doi.org/10.1890/070147>.
- Ham, C., van, Genovesi, P., Scalera, R., 2013. *Invasive Alien Species: The Urban Dimension - Case Studies on Strengthening Local Action in Europe*. Brussels.
- Heringer, G., Angulo, E., Ballesteros-Mejia, L., Capinha, C., Courchamp, F., Diagne, C., Duboscq-Carra, V.G., Nuñez, M.A., Zenni, R.D., 2021a. The economic costs of biological invasions in Central and South America: a first regional assessment. *Neobiota* 67, 401–426. <https://doi.org/10.3897/neobiota.67.59193>.
- Heringer, G., Faria, L.D.B., Villa, P.M., Araújo, A.U., Botan, A.L.M., Zenni, R.D., 2021b. Urbanization affects the richness of invasive alien trees but has limited influence on species composition. *Urban Ecosyst.* 25, 753–763. <https://doi.org/10.1007/s11252-021-01189-1>.
- IPBES-Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, 2023. In: Roy, H.E., Pauchard, A., Stoett, P., Renard Truong, T., Bacher, S., Galil, B.S., Hulme, P.E., Ikeda, T., Sankaran, K.V., McGeoch, M.A., Meyerson, L.A., Nuñez, M.A., Ordóñez, A., Rahlao, S.J., Schwindt, E., Seebens, H., Sheppard, A.W., Vandvik, V. (Eds.), Summary for Policymakers of the Thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-policy Platform on Biodiversity and Ecosystem Services. IPBES secretariat, Bonn, Germany. <https://doi.org/10.5281/zenodo.7430692>.
- Jarić, I., Courchamp, F., Correia, R.A., Crowley, S.L., Essl, F., Fischer, A., González-Moreno, P., Kalinkat, G., Lambin, X., Lenzer, B., Meinard, Y., Mill, A., Musseau, C., Novoa, A., Pergl, J., Pyšek, P., Pyšková, K., Robertson, P., von Schmalensee, M., Shackleton, R.T., Stefansson, R.A., Stajerová, K., Veríssimo, D., Jeschke, J.M., 2020.

- The role of species charisma in biological invasions. *Front. Ecol. Environ.* 18, 345–353. <https://doi.org/10.1002/fee.2195>.
- Kenis, M., Auger-Rozenberg, M.-A., Roques, A., Timms, L., Péré, C., Cock, M.J.W., Settele, J., Augustin, S., Lopez-Vaamonde, C., 2009. Ecological effects of invasive alien insects. *Biol. Invasions* 11, 21–45. <https://doi.org/10.1007/s10530-008-9318-y>.
- Kolimarakis, A., Bithas, K., Latinopoulos, D., Richardson, C., 2019. On lifestyle trends, health and mosquitoes: formulating welfare levels for control of the Asian tiger mosquito in Greece. *PLoS Negl. Trop. Dis.* 13, e0007467 <https://doi.org/10.1371/journal.pntd.0007467>.
- Kourantidou, M., Haubrock, P.J., Cuthbert, R.N., Bodey, T.W., Lenzner, B., Gozlan, R.E., Nuñez, M.A., Salles, J.-M., Diagne, C., Courchamp, F., 2022. Invasive alien species as simultaneous benefits and burdens: trends, stakeholder perceptions and management. *Biol. Invasions* 24, 1905–1926. <https://doi.org/10.1007/s10530-021-02727-w>.
- Kowarik, I., 2011. Novel urban ecosystems, biodiversity, and conservation. *Environ. Pollut.* 159 (8–9), 1974–1983.
- Kriticos, D.J., Brunel, S., 2016. Assessing and managing the current and future pest risk from water hyacinth, (*Eichhornia crassipes*), an invasive aquatic plant threatening the environment and water security. *PLoS One* 11, e0120054. <https://doi.org/10.1371/journal.pone.0120054>.
- Leroy, B., Kramer, A.M., Vaissière, A.C., Kourantidou, M., Courchamp, F., Diagne, C., 2022. Analysing economic costs of invasive alien species with the *invacost* R package. *Methods Ecol. Evol.* 13, 1930–1937. <https://doi.org/10.1111/2041-210X.13929>.
- Leroy, B., Diagne, C., Angulo, E., Ballesteros-Mejia, L., Adamjy, T., Assailly, C., Albert, C., Andrews, L., Balzani, P., Banerjee, A., Bang, A., Bartlett, A., Bernery, C., Bodey, T., Bradshaw, C., Bufford, J., Capinha, C., Catford, J., Cuthbert, R., Mbacké Dia, C., Dimarco, R., Dobigny, G., Duboscq, V., Essl, F., Fantle-Lepczyk, J., Golivets, M., Gozlan, R., Haubrock, P., Heringer, G., Hoskins, A., Hudgins, E., Jarić, I., Jourdain, F., Kirichenko, N., Kourantidou, M., Kramer, A., Leung, B., Liu, C., Lopez, E., Manfrini, E., Moodley, D., Novoa, A., Nuñez, A., Nuninger, L., Pattison, Z., Renault, D., Rico-Sanchez, A., Robuchon, M., Roiz, D., Salles, J., Taheri, A., Tambo, J., Taylor, N., Tricarico, E., Turbelin, A., Vaissière, A., Verbrugge, L., Watari, Y., Welsh, M., Xiong, W., Courchamp, F., 2022a. Global costs of biological invasions: living figure. https://borisleroy.com/invacost/invacost_livingfigure.html. (Accessed 25 June 2023).
- Li, Y., Kamara, F., Zhou, G., Puthiyakunnon, S., Li, C., Liu, Y., Zhou, Y., Yao, L., Yan, G., Chen, X.G., 2014. Urbanization increases *Aedes albopictus* larval habitats and accelerates mosquito development and survivorship. *PLoS Negl. Trop. Dis.* 8 <https://doi.org/10.1371/journal.pntd.0003301>.
- Liu, Z., He, C., Zhou, Y., Wu, J., 2014. How much of the world's land has been urbanized, really? A hierarchical framework for avoiding confusion. *Landsc. Ecol.* 29, 763–771. <https://doi.org/10.1007/s10980-014-0034-y>.
- Liu, C., Diagne, C., Angulo, E., Banerjee, A.-K., Chen, Y., Cuthbert, R.N., Haubrock, P.J., Kirichenko, N., Pattison, Z., Watari, Y., Xiong, W., Courchamp, F., 2021. Economic costs of biological invasions in Asia. *Neobiota* 67, 53–78. <https://doi.org/10.3897/neobiota.67.58147>.
- Machado, A.A.V., Estevan, A.O., Sales, A., Brabes, K.C. da S., Croda, J., Negrão, F.J., 2014. Direct costs of dengue hospitalization in Brazil: public and private health care systems and use of WHO guidelines. *PLoS Negl. Trop. Dis.* 8 <https://doi.org/10.1371/journal.pntd.0003104>.
- Maurel, N., Salmon, S., Ponge, J.F., Machon, N., Moret, J., Muratet, A., 2010. Does the invasive species *Reynoutria japonica* have an impact on soil and flora in urban wastelands? *Biol. Invasions* 12, 1709–1719. <https://doi.org/10.1007/s10530-009-9583-4>.
- McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* 127, 247–260. <https://doi.org/10.1016/j.biocon.2005.09.005>.
- McLean, P., Gallien, L., Wilson, J.R.U., Gaertner, M., Richardson, D.M., 2017. Small urban centres as launching sites for plant invasions in natural areas: insights from South Africa. *Biol. Invasions* 19, 3541–3555. <https://doi.org/10.1007/s10530-017-1600-4>.
- Moodley, D., Angulo, E., Cuthbert, R.N., Leung, B., Turbelin, A., Novoa, A., Kourantidou, M., Heringer, G., Haubrock, P.J., Renault, D., Robuchon, M., Fantle-Lepczyk, J., Courchamp, F., Diagne, C., 2022. Surprisingly high economic costs of biological invasions in protected areas. *Biol. Invasions* 24, 1995–2016. <https://doi.org/10.1007/s10530-022-02732-7>.
- Nentwig, W., Mebs, D., Vilà, M., 2017. Impact of non-native animals and plants on human health. In: Vilà, M., Hulme, P. (Eds.), *Impact of Biological Invasions on Ecosystem Services*. Invading Nature-Springer Series in Invasion Ecology, vol. 12. Springer, Cham. https://doi.org/10.1007/978-3-319-45121-3_18.
- Novoa, A., Moodley, D., Catford, J.A., Golivets, M., Bufford, J., Essl, F., Lenzner, B., Pattison, Z., Pyšek, P., 2021. Global costs of plant invasions must not be underestimated. *Neobiota* 69, 75–78. <https://doi.org/10.3897/neobiota.69.74121>.
- Olden, J.D., Tamayo, M., 2014. Incentivizing the public to support invasive species management: Eurasian milfoil reduces lakefront property values. *PLoS One* 9 (10), e110458.
- Pagad, S., Genovesi, P., Carnevali, L., Schigel, D., McGeoch, M.A., 2018. Introducing the global register of introduced and invasive species. *Sci. Data* 5, 170202.
- Potgieter, L.J., Gaertner, M., Kueffer, C., Larson, B.M.H., Livingstone, S.W., O'Farrell, P. J., Richardson, D.M., 2017. Alien plants as mediators of ecosystem services and disservices in urban systems: a global review. *Biol. Invasions* 19, 3571–3588. <https://doi.org/10.1007/s10530-017-1589-8>.
- Potgieter, L.J., Gaertner, M., O'Farrell, P.J., Richardson, D.M., 2019. Perceptions of impact: invasive alien plants in the urban environment. *J. Environ. Manage.* 229, 76–87. <https://doi.org/10.1016/j.jenvman.2018.05.080>.
- Potgieter, L.J., Aronson, M.F.J., Brandt, A.J., Cook, C.N., Gaertner, M., Mandrak, N.E., Richardson, D.M., Cadotte, M.W., 2021. Prioritization and thresholds for managing biological invasions in urban ecosystems. *Urban Ecosyst.* 1–19.
- Pyšek, P., Jarošík, V., Pergl, J., Randall, R., Chytrý, M., Kühn, I., Tichý, L., Danihelka, J., Chrtěk Jun, J., Sádlo, J., 2009. The global invasion success of central European plants is related to distribution characteristics in their native range and species traits. *Divers. Distrib.* 15, 891–903. <https://doi.org/10.1111/j.1472-4642.2009.00602.x>.
- Pyšek, P., Bacher, S., Chytrý, M., Jarošík, V., Wild, J., Celesti-Grappo, L., Gassó, N., Kenis, M., Lambdon, P.W., Nentwig, W., Pergl, J., Roques, A., Sádlo, J., Solarz, W., Vilà, M., Hulme, P.E., 2010. Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. *Glob. Ecol. Biogeogr.* 19, 317–331. <https://doi.org/10.1111/j.1466-8238.2009.00514.x>.
- Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., Dawson, W., Essl, F., Foxcroft, L.C., Genovesi, P., Jeschke, J.M., Kühn, I., Liebhold, A.M., Mandrak, N.E., Meyerson, L.A., Pauchard, A., Pergl, J., Roy, H.E., Seebens, H., van Kleunen, M., Vilà, M., Wingfield, M.J., Richardson, D.M., 2020. Scientists' warning on invasive alien species. *Biol. Rev.* 95, 1511–1534. <https://doi.org/10.1111/brv.12627>.
- R Core Team, 2023. R: A Language and Environment for Statistical Computing R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Renault, D., Angulo, E., Cuthbert, R.N., Haubrock, P.J., Capinha, C., Bang, A., Kramer, A. M., Courchamp, F., 2022. The magnitude, diversity, and distribution of the economic costs of invasive terrestrial invertebrates worldwide. *Sci. Total Environ.* 835, 155391 <https://doi.org/10.1016/j.scitotenv.2022.155391>.
- Roiz, D., Pontifes, P., Jourdain, F., Diagne, C., Leroy, B., Vaissière, A.-C., Tolsá, M.J., Salles, J.-M., Simard, F., Courchamp, F., 2023. The rising global economic costs of *Aedes* and *Aedes*-borne diseases. *Res. Sq. Prepr.* <https://doi.org/10.21203/rs.3.rs-2679030/v1>.
- Rust, M.K., Su, N.Y., 2012. Managing social insects of urban importance. *Annu. Rev. Entomol.* 57, 355–375. <https://doi.org/10.1146/annurev-ento-120710-100634>.
- Seebens, H., Bacher, S., Blackburn, T.M., Capinha, C., Dawson, W., Dullinger, S., Genovesi, P., Hulme, P.E., van Kleunen, M., Kühn, I., Jeschke, J.M., Lenzner, B., Liebhold, A.M., Pattison, Z., Pergl, J., Pyšek, P., Winter, M., Essl, F., 2020. Projecting the continental accumulation of alien species through to 2050. *Glob. Chang. Biol.* 1–13 <https://doi.org/10.1111/gcb.15333>.
- Smith, C., Barko, J., 1990. Ecology of Eurasian watermilfoil. *J. Aquat. Plant Manag.* 28, 55–64.
- Uchida, K., Blakey, R.V., Burger, J.R., Cooper, D.S., Niesner, C.A., Blumstein, D.T., 2020. Urban biodiversity and the importance of scale. *Trends Ecol. Evol.* 36, 123–131. <https://doi.org/10.1016/j.tree.2020.10.011>.
- United Nations—Department of Economic and Social Affairs, Population Division, 2018. The world's cities in 2018 – Data Booklet (ST/ESA/SER.A/417). Available at <http://population.un.org/wup/publications/>. (Accessed 19 May 2023).
- Vilá, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., Pyšek, P., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* 14, 702–708. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>.
- Vyn, R.J., 2019. Estimated expenditures on invasive species in Ontario: 2019 survey results. Sault Ste. Marie Available at invasivespeciescentre.ca/wp-content/uploads/2020/02/Final-Report-2019-Survey-Results-No-Appendix-A.pdf. (Accessed 19 May 2023).
- Wylie, F.R., Janssen-May, S., 2017. Red imported fire ant in Australia: what if we lose the war? *Ecol. Manag. Restor.* 18, 32–44. <https://doi.org/10.1111/emr.12238>.
- Zhao, M., Cheng, C., Zhou, Y., Li, X., Shen, S., Song, C., 2022. A global dataset of annual urban extents (1992–2020) from harmonized nighttime lights. *Earth Syst. Sci. Data* 14, 517–534. <https://doi.org/10.5194/essd-14-517-2022>.
- Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., Svantesson, S., Wengström, N., Zizka, V., Antonelli, A., 2019. CoordinateCleaner: standardized cleaning of occurrence records from biological collection databases. *Methods Ecol. Evol.* 10, 744–751. <https://doi.org/10.1111/2041-210X.13152>.