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Advancing research on alien species and biological invasions

The economic costs of biological invasions in Central and South America: a first regional assessment

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Abstract

Invasive alien species are responsible for a high economic impact on many sectors worldwide. Nevertheless, there is a scarcity of studies assessing these impacts in Central and South America. Investigating costs of invasions is important to motivate and guide policy responses by increasing stakeholders' awareness and identifying action priorities. Here, we used the InvaCost database to investigate (i) the geographical pattern of biological invasion costs across the region; (ii) the monetary expenditure across taxa and impacted sectors; and (iii) the taxa responsible for more than 50% of the costs (hyper-costly taxa) per impacted sector and type of costs. The total of reliable and observed costs reported for biological invasions in Central and South America was USD 102.5 billion between 1975 and 2020, but about 90% of the total costs were reported for only three countries (Brazil, Argentina and Colombia). Costs per species were associated with geographical regions (i.e., South America, Central America and Islands) and with the area of the countries in km^2. Most of the expenses were associated with damage costs (97.8%), whereas multiple sectors (77.4%), agriculture (15%) and public and social welfare (4.2%) were the most impacted sectors. *Aedes* spp. was the hyper-costly taxon for the terrestrial environment (costs of USD 25 billion) and water hyacinth (*Eichhornia crassipes*) was the hyper-costly taxon for the aquatic environment (USD 179.9 million). Six taxa were classified as hyper-costly for at least one impacted sector and two taxa for at least one type of cost. In conclusion, invasive alien species caused billions of dollars of economic burden in Central and South America, mainly in large countries of South America. Costs caused by invasive alien species were unevenly distributed across countries, impacted sectors, types of costs and taxa (hyper-costly taxa). These results suggest that impacted sectors should drive efforts to manage the species that are draining financial sources.

Abstract in Portuguese

As espécies exóticas invasoras são responsáveis por custos econômicos elevados em diversos setores em todo mundo. No entanto, existe uma falta de estudos que avaliam esses impactos na América Central e do Sul. Investigar os custos com invasões biológicas é importante para estimular e guiar respostas políticas, aumentando a sensibilização de diversos grupos envolvidos e identificando prioridades de ação e gestão. Neste estudo, utilizamos a base de dados do InvaCost para investigar (i) os padrões geográficos dos custos causados por invasões biológicas entre as regiões da América Central e do Sul; (ii) a distribuição dos custos por taxon e setores impactados; e (iii) os taxa responsáveis por mais de 50% dos custos (os taxa hiper-custosos) por setor impactado e tipo de custo. O total de custos observados para a América Central e do Sul e reportados em fontes de elevada confiabilidade foi de 102,5 bilhões de dólares americanos (ou milhares de milhões) entre 1975 e 2020, sendo que cerca de 90% do custo total ocorreu em apenas três países (Brasil, Argentina e Colômbia). Os custos por espécies foram associados com a região geográfica (América do Sul, América Central e ilhas) e com a extensão territorial dos países. A maior parte dos gastos foi associada com danos (97,8%), enquanto setores múltiplos (77,4%), agricultura (15%) e bem-estar público e social (4,2%) foram os setores mais impactados. *Aedes* spp. foi o taxon hiper-custoso no ambiente terrestre (custo de 25 bilhões de dólares americanos) e o aguapé (*Eichhornia crassipes*) foi o taxon hiper-custoso em ambientes aquáticos (179,9 milhões de dólares americanos). Seis taxa foram classificadas como hiper-custosos para pelo menos um setor e dois taxa foram classificados como hiper-custosos para pelo menos um tipo de custo. Em conclusão, espécies exóticas invasoras causam custos econômicos de bilhões de dólares na América Central e do Sul, especialmente nos países mais extensos da América do Sul. Os custos causados pelas espécies exóticas invasoras não foram igualmente distribuídos entre países, setores impactados, tipos de custos e grupos taxonômicos (taxa hiper-custosos). Esses resultados sugerem que os setores impactados devem direcionar esforços para o manejo e prevenção daquelas espécies que são drenos de recursos financeiros.

Abstract in Spanish

Las especies exóticas invasoras son responsables por un alto impacto económico en muchos sectores en todo el mundo. Sin embargo, hay una escasez de estudios que evalúen estos impactos en Centro y Sudamérica. La investigación de los costos de las invasiones es importante para motivar y orientar las respuestas políticas, aumentando la conciencia de las partes interesadas e identificando las prioridades de acción. Aquí, utilizamos la base de datos InvaCost para investigar (i) el patrón geográfico de los costos de invasiones biológicas en la región; (ii) el gasto monetario en cada taxón y sector afectado; y (iii) los taxones responsables de más del 50% de los costos (llamados taxa hiper-costosos) por sector impactado y tipo de costos. El total de costos fiables y observados reportados para las invasiones biológicas en Centro y Sudamérica, fue de 102,5 mil millones de dólares americanos entre 1975 y 2020, pero aproximadamente el 90% de los costos totales se reportaron solo para tres países (Brasil, Argentina y Colombia). Los costos por especie se asociaron con las regiones geográficas (es decir, América del Sur, América Central e islas) y con el área de los países en km^2. La mayoría de los gastos se asociaron con costos de daños (97,8%), siendo los sectores mixtos (p.e. más de un sector involucrado, 77,4%), la agricultura (15%) y el bienestar público y social (4,2%) los sectores más afectados. *Aedes* spp. fue el taxón más costoso para el medio terrestre (con un costo de 25 mil millones de dólares americanos) mientras que el jacinto de agua (*Eichhornia crassipes*) fue el más costoso para el medio acuático (179,9 millones de dólares americanos). Seis taxones fueron clasificados como hiper-costosos para al menos un sector afectado y dos taxones para al menos un tipo de costo. En conclusión, las especies exóticas invasoras causaron miles de millones de dólares de carga económica en Centro y Sudamérica, principalmente en grandes países de Sudamérica. Los costos causados por las especies exóticas invasoras se distribuyeron de manera desigual entre los países, los sectores afectados, los tipos de costos y los taxones (taxones hiper-costosos). Estos resultados sugieren que los sectores afectados deberían impulsar esfuerzos para manejar las especies que están agotando las fuentes financieras.

Abstract in French

Les espèces exotiques envahissantes sont responsables d'un impact économique important pour de nombreux secteurs dans le monde. Néanmoins, les études évaluant ces impacts sont rares en Amérique centrale et en Amérique du Sud. Il est important d'enquêter sur les coûts des invasions biologiques pour motiver et orienter les réponses politiques en sensibilisant davantage les parties prenantes et en identifiant les priorités d'action spécifiques à chaque contexte. Ici, nous avons utilisé la base de données InvaCost pour étudier (i) la structure géographique des coûts des invasions biologiques dans la région; (ii) les dépenses monétaires à travers les taxons impliqués et les secteurs touchés; et (iii) les taxons responsables de plus de la moitié des coûts enregistrés (taxons 'hyper-coûteux') par secteur impacté et type de coûts. Le total des coûts observés et associés à des données fiables était de 102,5 milliards de dollars américains (USD) en Amérique centrale et en Amérique du Sud entre 1975 et 2020; cependant, environ 90% de ce coût total sont associés à seulement trois pays (Brésil, Argentine et Colombie). La distribution des coûts par espèce était étroitement liée aux régions géographiques (Amérique du Sud, Amérique centrale et les îles) et à la superficie des pays. La plupart des dépenses étaient associées aux coûts de dommages (97,8%), tandis que les secteurs multiples (77,4%), l'agriculture (15%) et le bien-être public et social (4,2%) étaient les secteurs les plus touchés. Les moustiques du genre *Aedes* représente le taxon hyper-coûteux principal pour l'environnement terrestre (25 milliards USD) et la jacinthe d'eau (*Eichhornia crassipes*) était le taxon hyper-coûteux pour l'environnement aquatique (179,9 millions USD). En outre, six taxons ont été classés comme hyper-coûteux pour au moins un secteur touché et deux taxons pour au moins un type de coût. En conclusion, les espèces exotiques envahissantes ont causé un fardeau économique à hauteur de plusieurs milliards de dollars en Amérique centrale et du Sud, principalement dans les grands pays d'Amérique du Sud. Les coûts engendrés par les espèces exotiques envahissantes étaient inégalement répartis entre les pays, les secteurs touchés, les types de coûts et les taxons (taxons hyper-coûteux). Ces résultats soulignent fortement l'urgence des efforts de gestion pour limiter les impacts des invasions biologiques sur les secteurs touchés.

Keywords

Biological invasions, Central America, economic costs, economic impact, hyper-costly species, InvaCost, South America

Introduction

Invasive alien species are responsible for promoting changes in biological diversity, ecosystem functioning (e.g., Bellard et al. 2016a; Heringer et al. 2019), ecosystem services (Walsh et al. 2016; Castro-Díez et al. 2019) and for causing and transmitting diseases (e.g., Alfaro-Murillo et al. 2016; Ogden et al. 2019). As a result of the actions needed to hinder and mitigate environmental impacts, as well as direct impacts on economic sectors, several studies have reported high economic costs of invasive alien species (e.g., Martelli et al. 2015; Hoffmann and Broadhurst 2016; Diagne et al. 2021a). Recently, the global reported costs of invasive species were estimated at more than USD 1.288 trillion (Diagne et al. 2021a) with the addition of UDS 214 billion when considering non-English references (Angulo et al. 2021). Twenty years ago, Pimentel and colleagues estimated that the economic cost associated with invasive alien species was around USD 300 billion per year in the United States, United Kingdom, Australia, South Africa, India, and Brazil and about USD 42.6 billion per year in Brazil alone, the only Central or South American country evaluated (Pimentel et al. 2001). Martelli et al. (2015) estimated the cost of dengue fever, a disease transmitted by invasive alien mosquitos of the genus *Aedes*, to be about USD 468 million for the Brazilian health sector in 2013 alone. Understanding the nature, typology and magnitude of these costs at a regional scale is essential for developing efficient management planning, for prioritising actions towards species and countries and for assisting decision-making (Born et al. 2005; Dana et al. 2013; Jackson 2015; Diagne et al. 2020a).

Invasive alien species impact economic sectors differently because the characteristics of invasive alien species vary widely. For example, invasive alien insects cause direct economic losses to the agriculture and forestry sectors by damaging crops and tree plantations, and on human health by acting as vectors of diseases (e.g., Oliveira et al. 2013; Martelli et al. 2015; Bradshaw et al. 2016). Freshwater molluscs, such as golden mussel (*Limnoperna fortunei*), are a major concern to the hydropower sector in southern South America. This species can inlay firmly in different submerged surfaces, such as pipelines and block them resulting in water flow reduction and, thus, electricity production, also increasing the operating costs due to stops for maintenance and the actions to control the infestation (Faria et al. 2006; Campos et al. 2014). Hence, the comprehension of the economic impact caused by each invasive species can contribute towards increases in social and political awareness (Simberloff et al. 2013) and assist decision-making by allowing cost-related analyses adequate for each sector specifically.

It is known that there is a lack of articles written in English and published in indexed journals about some regions highly impacted by invasive alien species (Bellard and Jeschke 2015). Developing countries, located in the Global South and Central Asia, are under-represented because of low funding for ecological research, a low proportion of scientific researchers and also because of overlooking of non-English knowledge sources by researchers (Nuñez et al. 2019; Angulo et al. 2021). Thus, despite the damage caused by many invasive alien species in Central and South America, there is a gap in the studies addressing the combined economic impact of biological invasions outside North America and Europe (Bradshaw 2016). The lack of information associated with a potential increase of invasive alien species in countries such as Argentina, Brazil, Chile, and Peru (Seebens et al. 2015; but see Zenni 2015), shows the need to investigate the economic impact of invasive alien species in the region. Further, there is a lack of information on the identity and characteristics of the species causing greater losses in the region, hindering decision-making and control policies to reduce their impact and economic burden. Knowing which invasive alien species are responsible for disproportionate economic impacts can provide a way to evaluate economic impacts and to increase the focus of control in species that are causing the largest monetary losses. Here, we define these taxa responsible for more than 50% of the economic impact as hyper-costly taxa. The concept was adapted from ter Steege et al. (2013) that showed that 1.4% of the species in the Amazon represents more than 50% of the abundance in the region. This approach is particularly interesting in our context because a few species commonly drive the economic costs (e.g., Pimentel et al. 2000, 2005; Oliveira et al. 2013; Bradshaw et al. 2016), whereas most species cause lower economic impact proportionally. Thus, the hyper-costly approach allows us to know the taxa that are shaping the economic costs, as well as to drive conservation efforts against invasive alien species in a more effective way (i.e., focused on the few taxa that are draining financial sources). In addition, this approach can be easily applied and replicable to different ecosystems, scales and sectors.

Recognising the invasive alien species responsible for most of the economic impact can be relevant for priority-setting, as well as for understanding the efficiency and gaps in the management actions in Central and South America (Courchamp et al. 2017). Thus, the aims of this study were to gather and summarise the reported costs generated by invasive alien species in Central and South America and to identify the hyper-costly invasive alien species in the region (those responsible for more than 50% of the costs). Specifically, we aimed at investigating (i) the geographical pattern of cost with invasive alien species across Central and South America; (ii) the monetary expenditure across species and impacted sectors; and (iii) the hyper-costly taxa per impacted sector and type of costs.

Methods

Study area

For this study, we investigated the cost of invasive alien species in the Southern America continent, here defined according to the Taxonomic Database Working Group – TDWG (tdwg.org/). This area encompasses Central America, corresponding to the continental region and Caribbean Islands and South America (Fig. 1). Continental Central America extends from Guatemala to Panama, the Caribbean Islands from the Bahamas to Trinidad and Tobago and South America from Colombia to Chile.

Data collection

We collected cost data for invasive alien species from a publicly available repository that compiles the economic impacts of invasive species worldwide, the InvaCost database (originally 2,419 entries; Diagne et al. 2020b). The original dataset was complemented by incorporating data collected from non-English references (5,212 entries; Angulo et al. 2020) and by adding supplementary cost data from new references containing cost information (2,374 entries; Ballesteros-Mejia et al. 2020). These

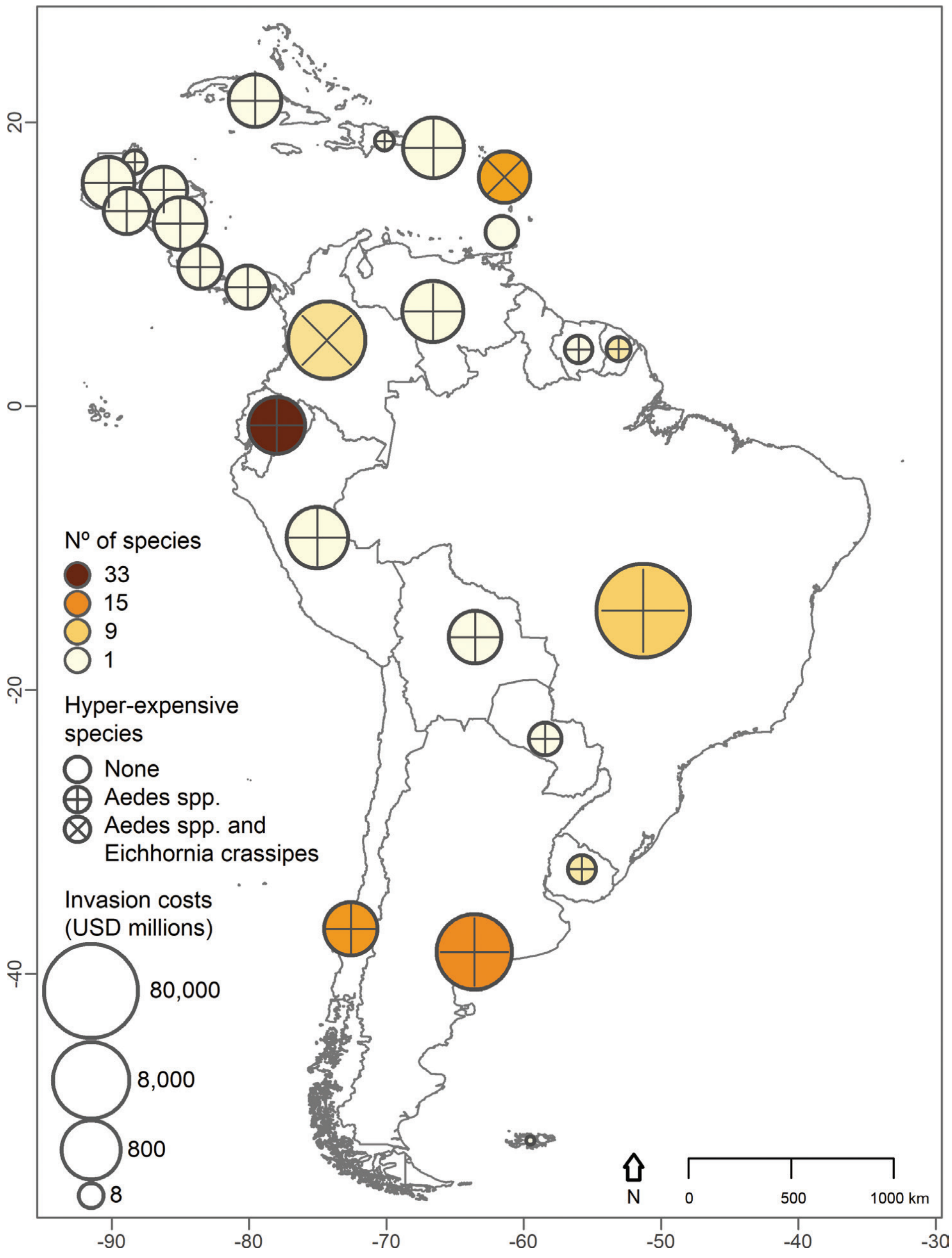

Figure 1. Map of Central and South America showing the number of invasive alien species registered in the InvaCost database (colour of circles), countries where costs with the hyper-costly taxa *Aedes* spp. and *Eichhornia crassipes* were related (crosses in the circles), and costs per country (size of the circles). Aedes spp. represents *Aedes aegypti* and *Aedes albopictus*.

data resources were reviewed and merged into a single database, which is the current and most up-to-date version of InvaCost (version 3.0; accessible at https://doi.org/10.6084/m9.figshare.12668570.v3). The data were filtered to contain only the countries of interest (see below). Cost entries with low reliability or reporting only potential costs (as classified by Diagne et al. 2020b) were also removed to allow for a standardised multi-country comparison. In short, low reliability identify grey source documents that used an estimation methodology based on no traceable or relevant references, ambiguous underlying assumptions or irreproducible calculations (see Diagne et al. 2020b). Next, we used the "expandYearlyCosts" function of the "invacost" R package v. 0.1-3 (Leroy et al. 2020) to expand the 442 cost entries to 960 cost entries in total, so that each cost entry corresponds to a single-year cost estimate (see Leroy et al. 2020 for a detailed explanation). In the InvaCost database, references reporting costs for a multi-year period can be inserted in one row and need to be expanded as previously explained to allow the assessment of the cumulative and mean yearly costs (Leroy et al. 2020). In addition, to facilitate the interpretation of the results, we made two changes in the original data. First, the entries of the economic cost associated with more than two taxa (multiple taxa) were reclassified as the name of the genus or as "Diverse/Unspecified" when species belong to different genera. Second, to understand how the economic costs were caused and associate it with the stage of invasion, we reclassified the original data from the "Type_of_cost" column. The "Type_of_cost" column describes the reason for the economic cost associated with an invasive species, such as control or prevention (Diagne et al. 2020b). Thus, costs arising from initiatives aiming to avoid the transportation or the introduction of the species were classified into "prevention cost" (e.g. early detection); cost occurring after species introduction aiming to hamper establishment or spreading were classified into "management cost" (e.g. control, eradication and management); and costs related to the impact of invasive species were classified as "damage cost" (e.g. damage-repair and medical care) (Suppl. material 1: Table S1). For studies that reported more than one of these new classes, we used the term "mixed cost." Similarly, the references that reported more than one impacted sector are assigned as "mixed" and, here, we used the term "multiple sectors" ("Impacted_sector_2" column, Suppl. material 1: Table S1).

The resulting subset of data corresponding to Central and South America have 960 cost entries, 97 references, 81 taxa and covered 26 countries in the region (see details below and in Suppl. material 1: Table S2). It is important to note that the United Kingdom and France are listed amongst the countries owing to their overseas territories. In South America, there are the Falklands/Malvinas, which are part of the United Kingdom and French Guiana as part of France and, amongst the Caribbean Islands, there are Guadalupe, Martinique and Saint-Martin also as part of France. In the subset used here, there are no data for Guyana in South America and the Bahamas, Barbados, Dominica, Haiti, Jamaica, Saint Kitts and Nevis, Saint Lucia, Saint Vincent and the Grenadines and Trinidad and Tobago in the Caribbean Region. The dataset used for this study is provided as Suppl. material 1: Table S2.

Analysis

To describe the costs of invasive alien species over the years, we calculated the average annual cost caused by invasive alien species between 1975 and 2020, considering intervals of 5 years, using the "summarizeCosts" function in "invacost" R package (Leroy et al. 2020). To investigate the geographical pattern of costs amongst the countries, we ran two non-metric multidimensional scaling (NMDS) analyses, using the "metaMDS" function, from the "vegan" package (Oksanen et al. 2019). NMDS is an ordination method to represent a distance matrix in a predetermined number of axes (Borcard et al. 2011). Thus, first, to represent the countries according to the differences in presence and absence of invasive alien species presented in the database, we ran the analysis using a Jaccard distance matrix. Second, to represent the countries according to the differences in the economic costs per species, we based our analysis in a Bray-Curtis distance matrix. Thus, in the first case, the countries were represented in a two-dimensional graph according to the differences amongst species composition, whereas in the second case, the ordination was based on the differences amongst the cost promoted per species. To avoid noise during the ordination, we removed the species with single cost records from these analyses (e.g., Neves et al. 2015; Rezende et al. 2018). Both ordinations were then used to test their correlation with five descriptive variables per country: the number of cost entries in the expanded subset used here, the central latitude and area of each country provided by Google Earth (earth.google.com), gross domestic product per capita from World Bank (GDP per capita; data.worldbank.org) and the region in which each country occurs. The categorical variable region has three levels: Central America, South America and Islands (Caribbean Islands and Falklands/Malvinas Islands). These analyses consist of fitting vectors or factors, usually environmental variables, in an ordination and the significance between ordination and descriptive variables are tested by permutations using the "envfit" function, in the "vegan" package v. 2.5-6 (Oksanen et al. 2019). All analyses in this study were conducted in the R environment (R Core Team 2020).

Results

The total reported cost of biological invasions in Central and South America between 1975 and 2020 was USD 102.5 billion (USD 146.5 billion, when including the data with low reliability or potential costs). On average, reported costs were USD 2.2 billion per year, but the costs were unevenly distributed amongst the countries. Brazil had a total reported cost of USD 76.8 billion with an annual average of USD 1.7 billion, whereas Colombia had a total reported cost of USD 8.8 billion, with an annual average of USD 0.19 billion and Argentina had USD 6.9 billion reported, with an annual average of USD 0.15 billion. These three countries had the greatest expenditure and together were responsible for more than 90% of the total costs reported for the region (Fig. 1; Table 1; Suppl. material 2). More than 40% of the expanded cost entries came from documents in non-English languages (mostly Spanish (34.2%), followed by French (4.0%) and Portuguese (2.2%); Suppl. material 1: Table S3). These data constituted 10.7% of the amount of costs reported. We found a clear increase in annual expenses after 1995, when more than 99% of the total costs in the region were reported (Fig. 2).

Table 1. Reported economic costs of biological invasions between 1975 and 2020 in the countries of Central, South America and the Caribbean Islands (USD million). The Table is ordered from the country with highest cost to lowest cumulated cost.

Country	Geographic region	Cumulated cost	Average annual cost
Brazil	South America	76,784.76	1669.23
Colombia	South America	8,821.61	191.77
Argentina	South America	6,902.13	150.05
Diverse/Unspecified	Central America	2,948.15	64.09
Peru	South America	1,131.73	24.60
Venezuela	South America	1,033.56	22.47
Puerto Rico (USA)	Central America (Islands)	1,011.57	21.99
Diverse/Unspecified	Central America/South America	852.91	18.54
Ecuador	South America	604.87	13.15
Bolivia	South America	349.14	7.59
Nicaragua	Central America	343.00	7.46
Cuba	Central America (Islands)	342.04	7.44
Guatemala	Central America	307.51	6.69
Guadeloupe, Martinique, Saint-Martin (France)	Central America (Islands)	288.44	6.27
Honduras	Central America	161.39	3.51
Chile	South America	156.26	3.40
El Salvador	Central America	142.71	3.10
Costa Rica	Central America	101.62	2.21
Panama	Central America	100.46	2.18
Diverse/Unspecified	South America	37.15	0.81
Grenada	Central America (Islands)	25.68	0.56
French Guiana (France)	South America	24.67	0.54
Paraguay	South America	23.46	0.51
Uruguay	South America	12.76	0.28
Suriname	South America	11.70	0.25
Belize	Central America	6.66	0.14
Dominican Republic	Central America (Islands)	3.05	0.07
Antigua	Central America (Islands)	0.02	0.0005
Falklands/Malvinas (UK)	South America (Islands)	0.01	0.0002

The lower amounts between 2017 and 2020 was likely caused by the lag between expenses and their reporting (Fig. 2; for details about the lag, see Leroy et al. 2020).

Most of the economic costs of invasive alien species were related to damage costs (97.8% of the total cost), whereas a small proportion was generated by management costs (2.1%), mixed costs (0.1%) and prevention costs (0.009%). Most of the costs were associated with mixed sectors (77.4%), agriculture (15%), public and social welfare (4.2%) and authorities and stakeholders (2.6%). In the InvaCost database, the authorities and stakeholders sector correspond to "governmental services and/or official organizations that allocate efforts for the management *sensu lato* of biological invasion" Diagne et al. (2020b). Damage costs were the predominant type of cost for all sectors, except for the health sector where management was the largest type of cost (Fig. 3). Except for authorities and stakeholders, none of the impacted sectors reported spent money on prevention.

Based on the NMDS ordination (Table 2), species occurrences and costs per species amongst countries were spatially structured across the three regions (Central America, South America and Islands; Fig. 1; Suppl. material 3: Fig. S1). The three regions presented different species assemblages ($R^2 = 0.28$, $p = 0.008$), which means that

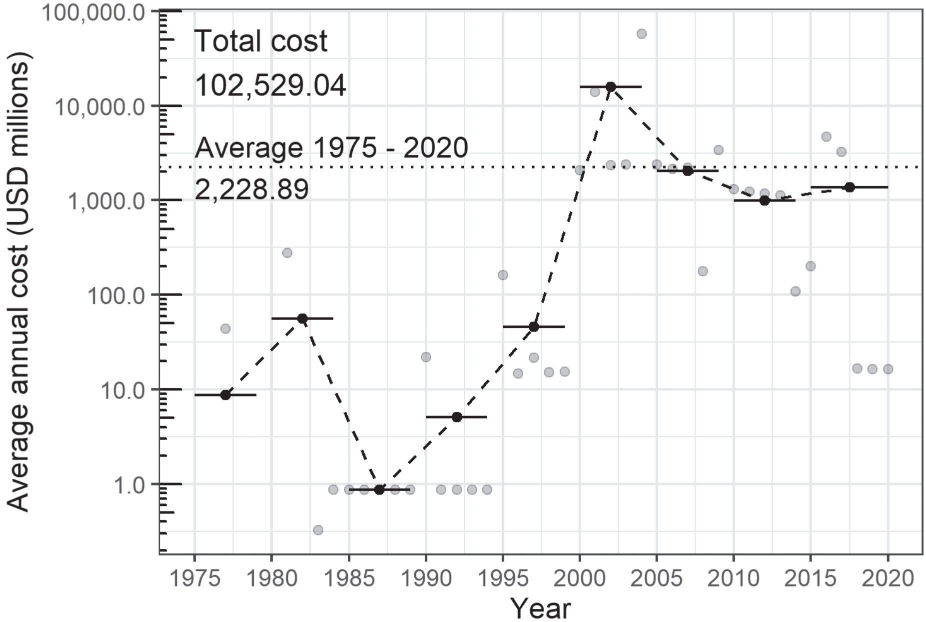

Figure 2. Annual costs of biological invasions observed over time in Central and South America. Grey dots represent the annual costs, horizontal lines and black dots represent the average annual cost per 5 years and the dashed horizontal line represents the general average between 1975 and 2020.

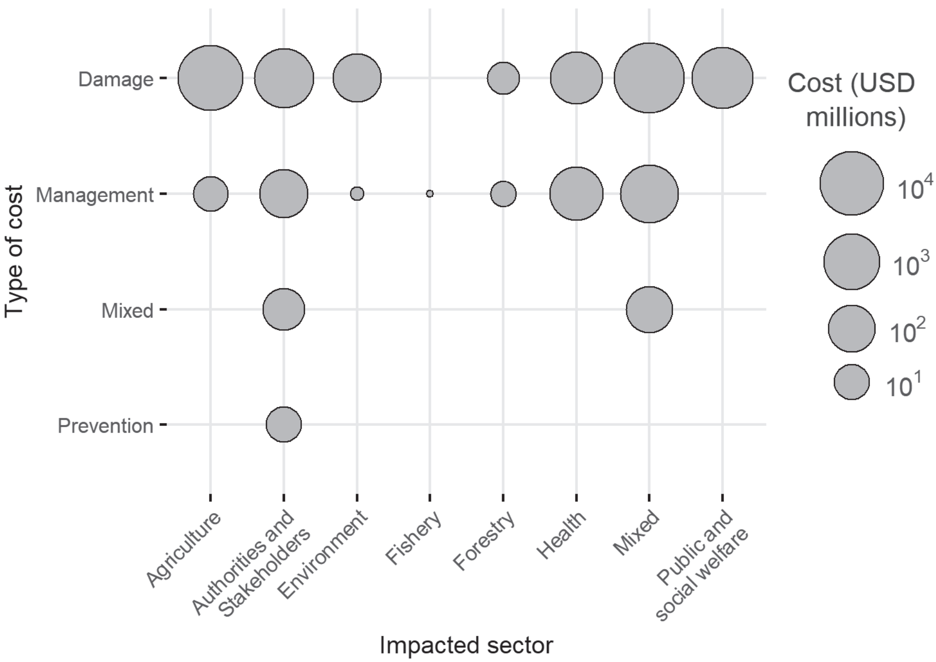

Figure 3. Cost of biological invasions shared amongst impacted sectors and type of costs in Central and South America.

Table 2. Model fitting of geographical and socioeconomic variables in the ordinations, based on occurrence of alien species and costs per alien species in Central and South America. Number of permutations = 10000.

	NMDS1	NMDS2	R^2	*p*
Occurrence of invasive alien species per country (Jaccard distance)				
Entries	-0.304	0.953	0.206	0.1311
Lat	0.587	-0.810	0.407	0.0052**
GDP per capita	-0.959	-0.284	0.269	0.0375*
Area	-0.322	0.947	0.187	0.1421
Region			0.283	0.0084**
Costs per invasive alien species per country (Bray-Curtis distance)				
Entries	0.402	0.916	0.188	0.1324
Lat	0.675	-0.738	0.015	0.8618
GDP per capita	-0.993	0.118	0.103	0.2822
Area	0.148	0.989	0.408	0.0194*
Region			0.198	0.0364*

each region had costs reported for a different set of invasive species (Suppl. material 3: Fig. S1A); and also showed different patterns of cost per species ($R^2 = 0.19$, $p = 0.036$), which means that reported costs for invasive species were different amongst regions (Suppl. material 3: Fig. S1B). In addition, ordination based on alien invasive species occurrences, was correlated with latitude ($R^2 = 0.41$, $p = 0.005$) and GDP per capita ($R^2 = 0.27$, $p = 0.037$), whereas the ordination, based on the costs per species, showed a correlation with area of the country ($R^2 = 0.41$, $p = 0.019$).

Costs reported for multiple taxa were responsible for more than 53.9% of the accumulated expenses and represented more than USD 55 billion of the total cost. Although we could not highlight any hyper-costly taxon in general (Fig. 4A; Suppl. material 1: Table S4), *Aedes* spp. was the unique hyper-costly taxon in the terrestrial environment, whereas water hyacinth (*Eichhornia crassipes*) was the unique hyper-costly taxon in the aquatic environment (Fig. 4B, C). In addition, aquatic species had lower reported economic impact than terrestrial species (USD 274 million vs. USD 47 billion, respectively; Fig. 4B).

Several taxa were classified as hyper-costly for specific impacted sectors (Fig. 5A; Suppl. material 3: Figs S2, S3). The feral pig (*Sus scrofa*) was the hyper-costly taxon for both the "authorities and stakeholders" and the environmental sectors, whereas the American beaver (*Castor canadensis*) was the hyper-costly taxon for the environmental and forestry sectors. The salt cedars (*Tamarix* spp.) and woodwasp (*Sirex noctilio*) were the hyper-costly taxa for the public and social welfare sector and the forestry sector, respectively. Two sectors were reportedly impacted only by one taxon; *Aedes* spp. was the only taxon with a reported economic impact on the health sector (USD 783 million) and the Japanese kelp (*Undaria pinnatifida*) was the only taxon with reported cost on the fishery sector (USD 4.5 thousand; Fig. 5A). Considering the type of costs, *Aedes* spp. was the hyper-costly taxon for management and mixed costs, whereas patas monkey and Rhesus macaque (*Erythrocebus patas* and *Macaca mulatta*) were listed as hyper-costly taxa for the costs related to prevention (Fig. 5B).

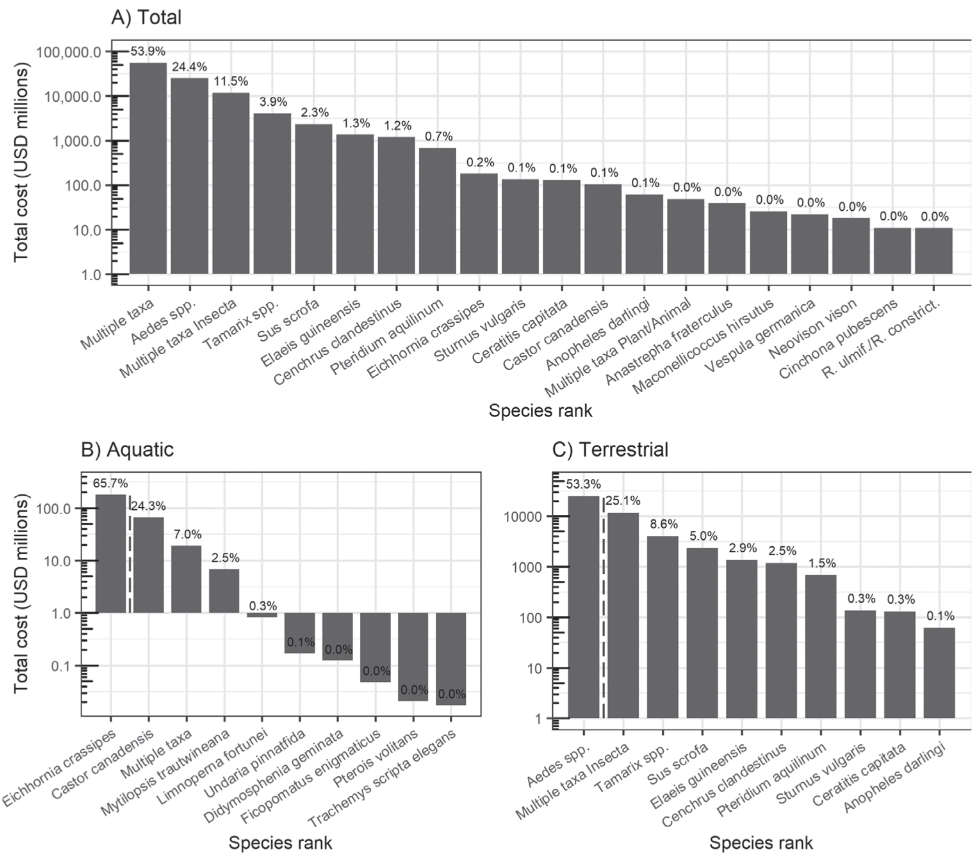

Figure 4. Costs of biological invasions per taxa in Central and South America **A** twenty costliest taxa **B** the ten costliest taxa on aquatic environments, and **C** the ten costliest taxa on the terrestrial environments. The hyper-costly taxa appear on the left side of the dashed line. Aedes spp. represents *Aedes aegypti* and *Aedes albopictus*; R. ulmif./R. constrict. represents *Rubus ulmifolius* and *Rubus constrictus*.

Discussion

General patterns

We found a significant economic impact of invasive alien species in Central and South America (USD 102.5 billion, with an annual average of USD 2.2 billion) caused mainly in the terrestrial environment and by insects. Invasive alien species have already caused high economic impacts in the region and are affecting important economic sectors and social well-being. Some high economic costs reported included more than one impacted sector (USD 79 billion). These were probably caused by the high number of costs classified as multiple taxa, but also by the fact that some species are indeed affecting more than one sector (e.g., *Aedes* spp., *Anopheles darlingi* and *Ulex europaeus*). In addition, there were high economic costs of invasive alien species reported for the agriculture and public and social welfare. This fact is not surprising

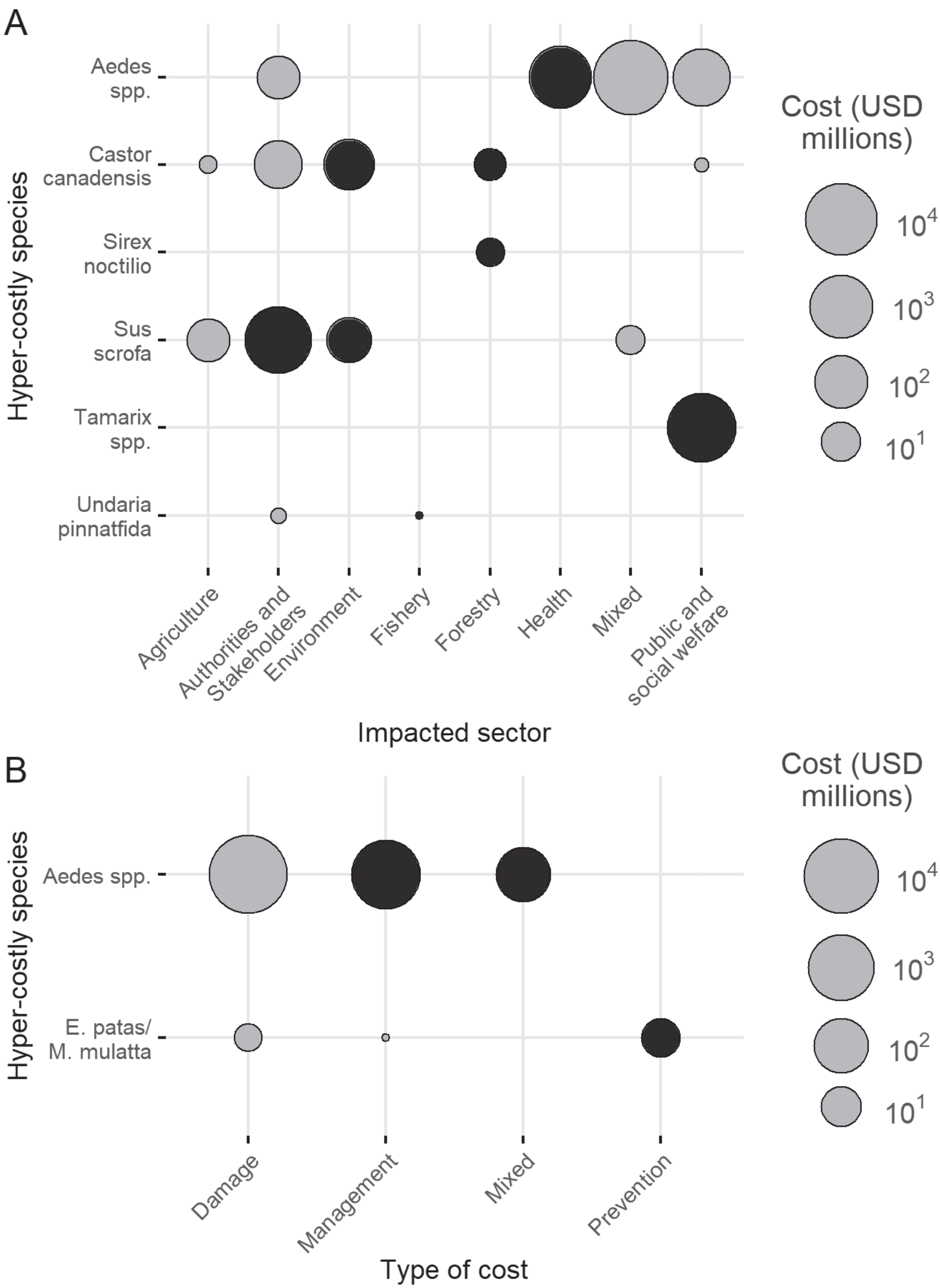

Figure 5. Costs of invasions by hyper-costly taxa **A** impacted sector and **B** type of cost. Black circles represent the hyper-costly taxa per impacted sector or type of cost and the grey circles represent the costs of each taxa in the impacted sector or type of costs where the taxa are not hyper-costly. Aedes spp. represents *Aedes aegypti* and *Aedes albopictus*; *E. patas*/*M. mulatta* represents *Erythrocebus patas* and *Macaca mulatta*.

considering that agriculture is one of the most prominent economic activities in most of the countries in South America, and the high impact caused by *Aedes* spp. and *Tamarix* spp. on public and social welfare.

Since the earliest recorded cost in 1977, there has been an enormous increase in reported costs, from an average cost of USD 8.7 million in the first five years since 1977 to USD 1.3 billion in the last five years. The remarkable rise observed here was probably the result of a combination of factors. Firstly, the potential increase of invasive alien species in the region (Seebens et al. 2015, 2017, 2020). Secondly, the growth of Invasion Science in the region (Frehse et al. 2016; Zenni et al. 2016) and the number of published cost estimations in both the scientific and grey literature. Lastly, we suggest the increases in the number of reported economic costs of invasions are a consequence of the increasing reactive response of affected sectors to biological invasions in Central and South America generated by damage losses (e.g., damage repair and medical care) and management actions (e.g., control and eradication). These reactive responses are expected to generate higher costs than preventative actions (Simberloff et al. 2013; Bradshaw et al. 2016). Furthermore, preventative actions have advantages as they also hamper the invasive alien species introduction and, consequently, reduce other impacts promoted by invasive species (e.g., native species replacement and changes in ecosystem functions and services). Thus, even in cases where preventative actions are more expensive, they must be considered by decision-makers and practitioners in order to prevent the impact of invasive alien species as a whole, as well as future costs due to reactive actions.

Compared to other regions, Central and South America have higher accumulated costs than Africa (USD 18.2 billion; Diagne et al. 2021b) and a similar cost to that found in Europe when we used the same inclusion criteria, considering low reliability or potential costs (USD 140.2 billion; Haubrock et al. 2021). However, Central and South America have lower costs than North America and Asia (USD 1.26 trillion and USD 432.6 billion, respectively; Crystal-Ornelas et al. 2021; Liu et al. 2021). These differences were not entirely surprising considering the lower number of invasive alien species in Central and South America compared with North America (van Kleunen et al. 2015; Pyšek et al. 2019), as well as the research deficit in invasion biology in Central and South America (Bellard and Jeschke 2015), which can negatively affect the number of reported costs to the continents. In addition, although our study is the first regional assessment in Central and South America and was based on the most up-to-date database, we highlight that the costs reported here are a conservative baseline. We did not include cost entries classified as low reliability or reporting expected-only costs in the analysis and there were no published costs for some relevant invasive alien species in the region (e.g., *Pterois volitans* and *Tubastraea coccinea*; Adelino et al. 2021); furthermore, it is difficult to disentangle costs associated with multiple practices (e.g., restoration; Brancalion et al. 2019). Hence, the economic cost of biological invasions in the region is higher and must be evaluated continuously.

The differences amongst the costs found here and other country-level assessments in the region are due to different methodological choices. Adelino et al. (2021) found a higher accumulated cost than us for Brazil because they did not remove entries from the original InvaCost dataset (USD 105.5 billion vs. USD 76.8 billion). For the same reason, Duboscq-Carra et al. (2021) found an accumulated cost USD 5.5 million higher than us for Argentina (USD 6,907.6 million vs. USD 6,902.1 million). Conversely, Ballesteros-Mejia et al. (2021) found smaller costs for Ecuador because one of the entries with high economic impact was classified in their study as low reliability and therefore removed from the main analyses (USD 86.2 million vs. USD 604.9 million; see details at Ballesteros-Mejia et al. 2021). In country-level assessments with limited data availability, it is essential to use all available data for the most comprehensive assessment possible. However, multi-country assessments need higher standardisation of data reporting across countries in order to decrease uncertainty in the analyses. Hence, all results reported are conservative estimates of the cost of biological invasions for multi-country comparisons.

Geographic pattern

We found that the distribution of recorded costs of invasive alien species were spatially structured amongst the three regions (Central America, South America and Islands), as they have different species assemblages and costs per species (Table 2; Suppl. material 3: Fig. S1). However, it is important to note that latitude was correlated only with the occurrence of invasive alien species. We hypothesised that countries with higher GDP per capita and more intense trading would share higher numbers of alien species, as observed in previous studies (Seebens et al. 2015; Bellard et al. 2016b; Dawson et al. 2017), eventually increasing their economic burden. Nevertheless, we only found a correlation between GDP per capita and the ordination based on alien species occurrence. This may indicate that better socioeconomic conditions did not reflect higher investments in preventing and controlling invasive alien species in the region, possibly owing to the deficit of knowledge about them, even in the countries with higher GDP per capita. The pattern observed here, of larger countries having higher costs with invasive alien species, was a consequence of the area impacted by the invasive alien species and the costs to manage or repair. *Aedes* spp. and *S. scrofa*, for instance, are widely distributed throughout tropical America and can generate economic impacts proportional to their large area of occurrence (Barrios-Garcia and Ballari 2012; Martelli et al. 2015; Alfaro-Murillo 2016, see discussion below). Although the expenses with invasive alien species were probably limited by socioeconomic conditions of the country, we observed that geographical variables, such as country area and region, are relevant and must be considered in further investigations.

Hyper-costly taxa

The distribution of recorded costs amongst species was highly uneven and, in a few cases, the multiple taxa category presented the highest costs (see Fig. 1A; Suppl. material 3: Figs S2A, E, S3A). However, in most rankings, few taxa were responsible for a greater portion of the economic costs for most sectors and types of costs in Central and South America. The economic impact was directly related to the damage caused by some species in essential sectors, such as agriculture and public and social welfare (Fig. 3). The hyper-costly taxon in the terrestrial environment, *Aedes* spp., are distributed across all tropical regions of the globe and transmit the viruses that cause chikungunya, dengue, yellow fever and Zika (WHO 2009; Bhatt et al. 2013). In the Central and South America region, these mosquitoes affect mainly human health and have been reported in the InvaCost database since 1977, causing expenses due to damage, management and mixed. The reactive actions (i.e., damage repair and management) and long-term economic costs associated with the high costs of public health programmes can explain the high economic impact associated with *Aedes* spp. in Central and South America. We did not find any cost exclusively related to the prevention of *Aedes* spp. However, in regions with widely-established *Aedes* spp., the integrated *Aedes* management includes a set of surveillance actions that could be considered as prevention, for example, seasonal dynamics and hot-spots mapping and monitoring trends (Roiz et al. 2018). This reinforces our interpretation that the investments for dealing with invasive alien species tend to be reactive in Central and South America (e.g., eradication, control and damage repair), leading to higher economic expenses due to later actions (Simberloff et al. 2013).

The hyper-costly aquatic species, water hyacinth (*E. crassipes*), cost about USD 179.9 million in total to the authorities and stakeholder sector. This species is listed amongst the 100 worst invasive alien species in the world (GISD 2020) and is distributed in the tropical and subtropical regions of the world (Kriticos and Brunel 2016). *Eichhornia crassipes* can grow fast in lentic environments and form large mats in the water body, hindering navigation and water supply (Kriticos and Brunel 2016). The species competes with other plants, decreases the light and oxygen availability for the submerged community and tends to negatively affect phytoplankton density (Villamagna and Murphy 2010; Kriticos and Brunel 2016). Despite its impact on the aquatic environment, agriculture and water supply and human activities, only two entries reported costs of *E. crassipes* invasions. This suggests that actions against this species in the region have been poorly reported or the costs were not included in the database because the species is native to a large portion of South America and, therefore, was not captured by the set of terms used in the search engine (see Diagne et al. 2020b). The lack of publications could also explain part of the large difference between the costs caused by invasive alien species on aquatic and terrestrial environments (about 170 times smaller on aquatic environments). Furthermore, although our study reveals a conspicuous difference between the economic costs in both terrestrial and aquatic environments, we cannot determine whether such differences resulted from the fact that aquatic species cause less impact or are neglected in terms of the economic cost they cause. Indeed, aquatic invasion costs have been reported less than expected based on numbers of alien species between habitat types (Cuthbert et al. 2021).

As a general rule, all taxa classified as hyper-costly here are well reported in literature as causing massive environmental impact and with wide distributions in the invaded ranges (e.g., Barrios-Garcia and Ballari 2012; Natale et al. 2008; Kriticos and Brunel 2016; GISD 2020). The feral pig (*S. scrofa*), for instance, can be found on all continents, except Antarctica and it is considered one of the 100 worst invasive species in the world because of the range of impacts the species causes (Barrios-Garcia and Ballari 2012; GISD 2020). This species feeds the below-ground organisms, promoting changes in the soil properties and plant cover and diversity, they harm native animals' populations by predation, cause damage in croplands and many other impacts (Barrios-Garcia and Ballari 2012; Pedrosa et al. 2015). In addition, the salt cedars (*Tamarix* spp.), the costliest taxon for the public and social welfare sector, causes a negative impact on the uses of residential, industrial and agricultural water specifically. *Tamarix* spp. invasions are associated with the impoverishment of forage, a decrease in irrigation water, an increase in soil salinity and the frequency of fires (Natale et al. 2008). Of note, some potential hyper-costly taxa could have been missed here due to the inherent limitations of the database, such as the lack of precise information, the terms applied for literature searching and the availability of researchers that contributed with information (see discussion in Diagne et al. 2020b; Angulo et al. 2021).

It is important to note that many references reported the costs for multiple invasive alien species jointly (assigned as "Diverse/Unspecified" by Diagne et al. 2020b) and, therefore, gathered the economic impact of distinct sets of taxa. These reports prevented us from more precisely assessing the hyper-costly species in general, as well as for agriculture and mixed impacted sectors and for damage type of cost (Figs 4A, 5A, B). Thus, considering the importance of identifying priorities and that invasive alien species can present synergistic impacts (Simberloff 2006; Ricciardi et al. 2011; Zenni et al. 2020), we recommend that future studies on the cost of biological invasions report costs in a more standardised way (Diagne et al. 2021b) and, in particular, by species separately. Such detailed input information will allow researchers to improve the quality and accuracy of the InvaCost database and, consequently, favour the application of the hyper-costly taxa concept in distinct situations with even more effective practical results. For instance, the woodwasp (*S. noctilio*) was the 29th taxon in the ranking of cost per taxon, but it was the second hyper-costly taxa in the forestry sector. This species is widespread in Argentina, Brazil, Chile and Uruguay and causes loss of productivity due to the damage to the timber production (Corley et al. 2019). Therefore, successful actions to prevent or control this species can lead to considerable financial savings for the forestry sector, as the species generated more than USD 1.7 million in management costs. The hyper-costly taxa approach is a useful way to highlight the species that are draining financial sources and evaluate the strategies used to more efficiently avoid or mitigate their impact, as well as to increase social and political awareness. The advance in knowledge of economic costs has been shown as a necessary tool to deal with invasive species (Courchamp et al. 2017).

Although the hyper-costly concept is helpful to establish priorities and can be easily applied at different scales, we emphasise that it must be considered with caution. Some species that were not classified as hyper-costly are responsible for a large economic impact and could be a target of additional conservation efforts (e.g., *Pteridium aquilinum* that caused cumulative costs of around USD 680 million, see Suppl. material 1: Table S4). We also emphasise the fact that our study only accessed reported costs and, therefore, depended on previous studies, with potential data gaps for other very costly species. Thus, the increase of scientific publications or reports by managers addressing the economic impact of invasive alien species with clear distinctions amongst the taxa, impacted sectors and type of costs will favour a better understanding and further studies in order to investigate the association amongst economic impact and diversity loss, environmental change, ecosystem services and management actions. In addition, dealing with invasive alien species is not a simple task and involves a network of disciplines to assess their impact and management strategies (Roiz et al. 2018; Nuñez et al. 2020).

Conclusion

Invasive alien species have caused tens of billions of dollars in economic burden to Central and South America. The high expenses were mainly reported in larger countries in South America and were significantly uneven across countries, impacted sectors, type of costs and taxa. We claim for more and better reporting of the costs of invasive species (e.g., detailed costs by species and impacted sector) as it will allow a more insightful analysis of the costs in the region and favour the overall understanding of the economic impact of invasive species. Despite this caveat, we showed that most reported costs were associated with agriculture, one of the largest economic sectors in the region and generated mainly by reactive actions, whereas preventative actions were much less reported. A few invasive taxa were responsible for the highest costs reported; hence, effective actions to reduce the impact from these few invasive species would likely considerably reduce the cost of biological invasions in the region. Prioritising these invasive species as targets for management and incorporating preventative actions together with reactive actions should lead to higher efficiency in the management of invasive species in this region and reach more effective results.

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Supplementary material 1

Tables S1–S4

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Data type: Supplementary tables

Explanation note: **Table S1.** Type of cost reclasified to prevention, management, and damage. **Table S2.** Expanded database used in this study. **Table S3.** Economic costs of biological invasion (USD million) and number of entries per language of the source of data. **Table S4.** Economic costs of biological invasion (USD million) and countries with costs reported per species.

Link: https://doi.org/10.3897/neobiota.67.59193.suppl1

Supplementary material 2

Cumulative Costs (USD) of Invasive Alien Species in Central and South America per Year: 1977–2020

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Data type: measurement

Link: https://doi.org/10.3897/neobiota.67.59193.suppl2

Supplementary material 3

Figures S1–S3

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Data type: statistical data

Explanation note: **Figure S1.** Non-metric multidimensional scaling with the vectors representing the correlation among ordinations and descriptive variables resulting from "envifit" function, in "vegan" package. **Figure S2.** Costs of biological invasion per impacted sector and taxa. Taxa on the left side of the dashed red line are considered hyper-costly (cause more than 50% of the total costs). **Figure S3.** Costs of biological invasion per type of cost and taxa. Taxa on the left side of the dashed red line are considered hyper-costly (cause more than 50% of the total costs)

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