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Edited by

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EDITORIAL

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The economic costs of biological invasions around the world

Rafael Dudeque Zenni[1], Franz Essl[2],
Emili García-Berthou[3], Shana M. McDermott[4]

1 *Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, Universidade Federal de Lavras, Lavras-MG, Brazil* **2** *Bioinvasions. Global Change. Macroecology Group, Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030 Vienna, Austria* **3** *GRECO, Institute of Aquatic Ecology, University of Girona, 17003 Girona, Catalonia, Spain* **4** *Department of Economics, Trinity University, One Trinity Place, San Antonio TX, USA*

Corresponding author: Rafael Dudeque Zenni (rafael.zenni@ufla.br)

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A large and increasing number of ecosystems of the planet are now invaded by alien species, resulting in detrimental impacts on biodiversity, human health, and ecosystem services (IPBES 2019). Many of these impacts can be defined and quantified as economic costs; expenditures to prevent, reduce or mitigate the losses caused by invasive alien species (IAS). Reports on the global economic costs over the last 50 years estimate that IAS are responsible for a minimum of US$1.288 trillion (2017 US dollars) in damages, a number that is steadily rising over time (Diagne et al. 2021a). Understanding and estimating economic damages caused by IAS is particularly important given that new introductions of alien species and impacts are increasing globally with no sign of slowing down (Seebens et al. 2017; Essl et al. 2020). In addition, just as current and future projections of numbers and types of IAS vary across ecosystems (van Kleunen et al. 2015; Essl et al. 2020), impacts and costs of biological invasions differ widely across space and time (Angulo et al. 2021b; Diagne et al. 2021a). Improving economic cost estimates of biological invasions across regions helps scientists, managers, and stakeholders to develop and inform benefit-cost analyses and policies for dealing with invasive alien species. Previous studies have modelled and estimated the economic costs of biological invasions for specific countries (e.g., Pimentel et al. 2005; Hoffmann and Broadhurst 2016) or globally (e.g., Diagne et al. 2021a), but a standardized assessment of costs of biological invasions with detailed information for countries and regions was lacking for most regions of the world. In this special issue on the "The economic costs of biological invasions around the world," 63 authors address this issue by bringing together 19 papers from 13 countries and 6 supra-national regions that report on the economic cost-dimension of biological invasions (Fig. 1, Table 1). Collectively, they provide a global, innovative perspective detailing the economic costs of biological invasions while also providing regional information to help raise public awareness, and support efficient and cost-effective decision-making.

All papers in this special issue are based on the InvaCost database (Diagne et al. 2020). InvaCost is a global database built from a systematic review on reported economic costs of biological invasions in peer-reviewed articles, official reports and gray literature; it considers impacts caused by any alien species that result in economic costs on any human activities (Diagne et al. 2020; Angulo et al. 2021b). With observations obtained from sources across 16 languages, the resulting database is considered the most comprehensive, harmonized and robust global-scale data compilation and description of economic cost estimates associated with alien species reported in the literature (Diagne et al. 2020; Angulo et al. 2021b). Yet, cost accounts of alien species are unavailable or undocumented for many parts of the globe. When costs were available, they were generally concentrated in specific regions and were mainly attributed to agriculture, human health, and terrestrial habitats. Here, we outline some of the key messages from the papers in this special issue and synthesize the main findings.

Despite being widely recognized as a major threat to biodiversity and ecosystem services, reported economic costs of prevention, control, and damage of biological invasions on biodiversity and conservation are surprisingly rare. Perhaps just as perplexing, alien species are rarely identified as a leading threat to global agriculture and human health (but see Nuñez et al. 2020; Eschen et al. 2021; Vilà et al. 2021), but many of the papers in this special issue found some of the largest costs impact these sectors. For instance, agricultural losses and damage were the main component of reported costs for Africa (Diagne et al. 2021b), the Americas (Crystal-Ornelas et al. 2021; Heringer et al. 2021), and Asia (Kirichenko et al. 2021; Liu et al. 2021; Watari et al. 2021). Human health costs were strongly related to mosquitoes of the genus *Aedes* and were a main component of reported costs for Brazil (Adelino et al. 2021), Central America (Heringer et al. 2021) and Singapore (Haubrock et al. 2021b). Conversely, economic costs of preventing or mitigating alien species impacts on biodiversity and ecosystem services were virtually non-existent, with a few exceptions. In Ecuador, most cost reports were from one region only, the Galapagos Islands – a biodiversity hotspot –, aimed at controlling alien species impacting natural habitats (Ballesteros-Mejia et al. 2021). Similarly, Japan intensively invested in alien species management on small islands with high conservation value (Watari et al. 2021).

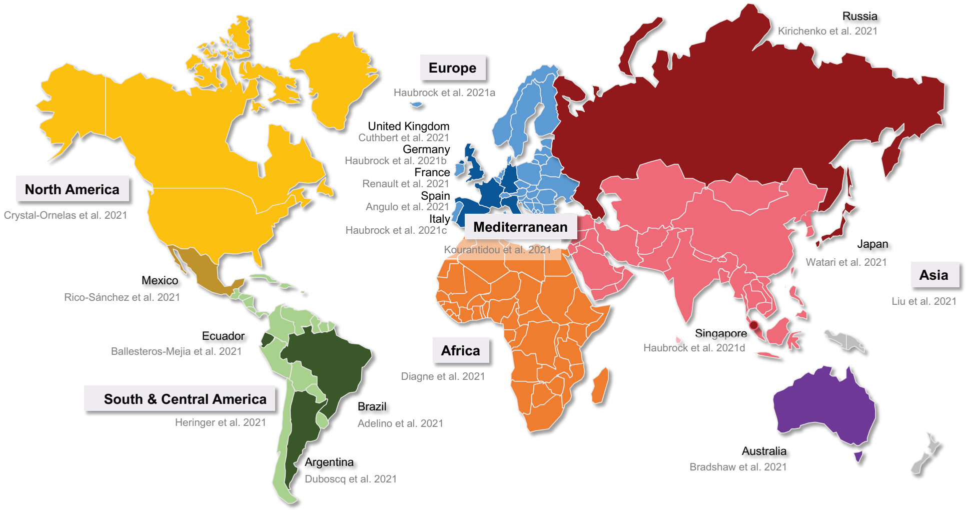

Figure 1. Distribution of studies on economic costs of biological invasions. Lighter tones represent continents and regions covered by the special issue "The Economic Costs of Biological Invasions Around the World." Delineation of countries does not imply data availability for every country depicted in that region or continent. Darker tones represented countries with assessments at national levels. Gray represents regions not included in the special issue.

Table 1. Reported economic cost of invasive alien species for 13 countries and 6 supra-national regions, main type of expenditure reported (realized and expected), ecosystem with most cost reporting, main biological group for which economic cost was reported, number of invasive alien species for which economic cost was found and reference. Expenditure values are not directly comparable as studies have used different analytical approaches. We strongly suggest readers refer to the original papers cited in the table for detailed explanations on data gathering, analytical approach, potential limitations and recommendations.

Region	Expenditure (US$ million)	Main expenditure	Main system	Main group	Number of IAS with cost data	Reference
Africa	**78,900.00**	**Damage**	**Terrestrial**	**Animal**	**62**	**Diagne et al. (2021b)**
Asia	**432,600.00**	**Damage**	**Terrestrial**	**Animal**	**88**	**Liu et al. (2021)**
Japan	728.00	Management	Terrestrial	Animal	54	Watari et al. (2021)
Russia	51,520.00	Damage	Terrestrial	Animal	72	Kirichenko et al. (2021)
Singapore	1,720.00	Damage	Terrestrial	Animal	3	Haubrock et al. (2021b)
Australia	**298,580.00**	**Damage**	**Terrestrial**	**Plants**	**172**	**Bradshaw et al. (2021)**
Central and South America	**146,500.00**	**Damage**	**Terrestrial**	**Animal**	**81**	**Heringer et al. (2021)**
Argentina	6,908	Damage	Terrestrial	Plants	15	Duboscq-Carra et al. (2021)
Brazil	105,530.00	Damage	Terrestrial	Animal	16	Adelino et al. (2021)
Ecuador	626.00	Management	Terrestrial	Animal	37	Ballesteros-Mejia et al. (2021)
Europe	**140,200.00**	**Damage**	**Terrestrial**	**Animal**	**381**	**Haubrock et al. (2021c)**
France	11.535	Damage	Terrestrial	Animal	98	Renault et al. (2021)
Germany	9,800.00	Management	Terrestrial	Animal	28	Haubrock et al. (2021a)
Italy	819.76	Damage	Terrestrial	Animal	15	Haubrock et al. (2021d)
Spain	261.00	Management	Terrestrial	Plants	174	Angulo et al. (2021a)
United Kingdom	17,600.00	Damage	Terrestrial	Animal	42	Cuthbert et al. (2021)
Mediterranean	**27,300.00**	**Damage**	**Terrestrial**	**Animal**	**218**	**Kourantidou et al. (2021)**
North America	**1,260,000.00**	**Damage**	**Terrestrial**	**Animal**	**164**	**Crystal-Ornelas et al. (2021)**
Mexico	5,330.00	Damage	Aquatic	Animal	35	Rico-Sanchez et al. (2021)

We can only speculate why most cost data come from agricultural and health sectors and rarely from the environmental sector. One reason might be that agriculture and human health are more commonly viewed as economic activities, whereas the economic value of biodiversity and ecosystem services preservation is often not recognized (i.e., crops and drugs are economic products, but biodiversity is not). Further, quantifiable economic impacts attributed to biodiversity loss and the environment tend to be indirect, making them more challenging to collect and estimate. Another reason might be that alien species are managed in conservation areas to maximize biodiversity protection, whereas, on farms, they are managed to optimize crop yield and revenue, making it easier to monetize gains and losses in agricultural systems. Overall, many of the papers in this issue encourage people engaged with biodiversity and natural resources management to document and report the costs associated with IAS.

Just like cost data were only available for a select few territories and industries, economic cost estimates were only available for a limited number of alien species (at most, 10% of known IAS in a given region). Europe reported costs for the largest number of species: 381 for the continent (Haubrock et al. 2021c), 174 for Spain (Angulo et al. 2021a), 98 for France (about 10% of known IAS in the region) (Renault et al. 2021), 42 for the United Kingdom (about 8% of known IAS in the region) (Cuthbert et al. 2021), 28 for Germany (Haubrock et al. 2021a), and 15 for Italy (Haubrock et al. 2021d). However, besides Europe, numbers of alien species with cost reports were smaller. For instance, all North America reported costs for 164 species (Crystal-Ornelas et al. 2021), Australia had costs for 172 species (Bradshaw et al. 2021) and South and Central America had costs for 80 species (Heringer et al. 2021). Fungi and microbes were rarely mentioned.

Aside from alien insects, which were frequently reported in the papers of the special issue, data were unavailable for a large number of alien species (Pagad et al. 2018). Thus, it is not possible to compare patterns of costly species across countries and regions. However, Heringer et al. (2021) suggest a promising approach for comparing economic impacts of biological invasions across countries or regions – the concept of hyper-costly species. Comparisons of costs of alien species broken down by control and damage costs, may allow governments, practitioners, and stakeholders to evaluate the pros and cons of different management strategies and actions.

The papers in this special issue also highlight the challenge of comparing economic costs and damages over time. Most of the reported cost estimates are recent, so long-term trends on economic costs of biological invasions are not available in most publications, with the exception of the UK (Cuthbert et al. 2021). It is also important to note that a lag exists between observed and reported impacts, which is why most papers showed a decrease in costs in recent years. For the UK, where long-term trends were examined, authors show that species with longer resident times had higher costs (Cuthbert et al. 2021). Despite reporting mostly recent cost estimates and the observed lag between expenditure and cost reporting, none of the publications in the special issue conclude that economic costs will flatten or decrease in the future. As more alien species become introduced into new regions, and alien species that are already present in a region often spread further, we can only expect that damage and management costs will continue increasing.

Taken together, all publications in this special issue "The Economic Cost of Biological Invasions Around the World" estimate global realized and potential economic impacts of biological invasions around US$2.3 trillion (2017 US dollars) (Table 1, excluding overlapping costs between countries and supra-national regions). However, at the same time, one of the most common themes across all the publications in this special issue is that the true economic costs are underreported, as cost data were unavailable for many groups (e.g., microorganisms), systems (e.g., marine) and regions (e.g., Central America). This special issue highlights the need to publicly document the high economic impact that alien species can have on people's lives, especially since the number of biological invasions is projected to increase (Seebens et al. 2017; Essl et al. 2020). To achieve this, it is imperative that researchers and practitioners collaborate on the assessment and reporting of economic costs of biological invasions. More and better data are needed to evaluate the costs and benefits of IAS management actions, and these costs need improved documentation.

In conclusion, the global map of expenditures with alien species shows that societies have been paying for the post-introduction management of alien species impacts with very little reported investment in prevention of biological invasions. While prevention might not necessarily be cheaper than control and impact mitigation efforts, in many cases it can help diminish the costly environmental, agricultural, and health impacts observed throughout this special issue. As a result, reducing globally the damage costs of biological invasions likely requires spending more money and effort undertaking prevention, early detection, and rapid response. Finding ways to minimize damage is essential because as the articles in this special issue highlight, the economic costs of biological invasions are only likely to increase in the future.

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RESEARCH ARTICLE

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Advancing research on alien species and biological invasions

The economic costs of biological invasions in Africa: a growing but neglected threat?

Christophe Diagne[1*], Anna J. Turbelin[1*], Desika Moodley[2**], Ana Novoa[2**], Boris Leroy[3], Elena Angulo[1], Tasnime Adamjy[4,5], Cheikh A.K.M. Dia[6], Ahmed Taheri[7], Justice Tambo[8], Gauthier Dobigny[4], Franck Courchamp[1]

1 *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405, Orsay, France* **2** *Institute of Botany, Department of Invasion Ecology, Czech Academy of Sciences, 252 43, Průhonice, Czech Republic* **3** *Unité Biologie des Organismes et Ecosystèmes Aquatiques (BOREA, UMR 7208), Muséum national d'Histoire naturelle, Sorbonne Université, Université de Caen Normandie, CNRS, IRD, Université des Antilles, Paris, France* **4** *Institut de Recherche pour le Développement, UMR CBGP (IRD-INRAE-CIRAD-Institut d'Agro), 34988, Montferrier-sur-Lez, France* **5** *Université d'Abomey-Calavi, Ecole Polytechnique d'Abomey-Calavi, Laboratoire de Recherche en Biologie Appliquée, Unité de Recherche sur les Invasions Biologiques, Cotonou, Benin* **6** *Department of Animal Biology, Sciences and Technologies Faculty, Cheikh Anta Diop University, B.P. 5005, Dakar, Senegal* **7** *Département de Biologie, Faculté des Sciences, Université Chouaïb Doukkali, BP 20, El Jadida 24000, Morocco* **8** *CABI, Rue des Grillons 1, 2800, Delémont, Switzerland*

Corresponding authors: Christophe Diagne (christophe.diagne@u-psud.fr); Anna Turbelin (anna.turbelin@u-psud.fr)

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Abstract

Biological invasions can dramatically impact natural ecosystems and human societies. However, although knowledge of the economic impacts of biological invasions provides crucial insights for efficient management and policy, reliable syntheses are still lacking. This is particularly true for low income countries where economic resources are insufficient to control the effects of invasions. In this study, we relied on the recently developed "InvaCost" database – the most comprehensive repository on the monetised impacts of invasive alien species worldwide – to produce the first synthesis of economic costs of biological invasions on the African continent. We found that the reported costs of invasions ranged between US$ 18.2 billion and US$ 78.9 billion between 1970 and 2020. This represents a massive, yet highly underes-

* These authors contributed equally (as lead authors).

** These authors contributed equally (as co-authors).

timated economic burden for African countries. More alarmingly, these costs are exponentially increasing over time, without any signs of abatement in the near future. The reported costs were mostly driven by damage caused by invaders rather than expenses incurred for management. This trend was highly skewed towards a few regions (i.e. Southern and Eastern Africa) and activity sectors (i.e. agriculture) and incurred by a small number of invasive taxa (i.e. mainly three insect pests: *Chilo partellus*, *Tuta absoluta*, *Spodoptera frugiperda*). We also highlight crucial, large gaps in current knowledge on the economic costs of invasions that still need to be bridged with more widespread research effort and management actions across the continent. Finally, our study provides support for developing and implementing preventive measures as well as integrated post-invasion management actions at both national and regional levels. Considering the complex societal and economic realities in African countries, the currently neglected problem of biological invasions should become a priority for sustainable development.

Abstract in Afrikaans

Die ekonomiese koste van uitheemse biologiese indringer spesies in Afrika: ‘n groeiende, maar verwaarloosde bedreiging? Kort titel: Verwaarloosde maar groeiende koste van indringer spesies in Afrika. Uitheemse indringer spesies kan natuurlike ekosisteme en menslike samelewings dramaties beïnvloed. Alhoewel kennis oor die ekonomiese gevolge van indringer spesies belangrike insigte bied vir doeltreffende bestuur en beleid, ontbreek betroubare sintese steeds. Dit geld veral in lande met lae inkomste waar ekonomiese hulpbronne onvoldoende is om die gevolge van indringer spesies te beheer. In hierdie studie het ons vertrou op die onlangs ontwikkelde InvaCost-databasis - die mees omvattende opslagplek vir die monetêre impak van indringer uitheemse spesies wêreldwyd - om die eerste sintese van ekonomiese koste van indringer spesies op die vasteland van Afrika te lewer. Ons het gevind dat die gerapporteerde koste van indringer spesies wissel tussen US $ 18,2 miljard en US $ 78,9 miljard gedurende 1970 tot 2020. Dit verteenwoordig ‘n massiewe, maar tog hoogs onderskatte, ekonomiese las vir Afrikalande. Meer kommerwekkend is dat hierdie koste mettertyd eksponensieel styg, sonder enige tekens van vermindering in die nabye toekoms. Die gerapporteerde koste is meestal weens skade van die indringer spesies eerder as uitgawes wat vir die bestuur daarva aangegaan is. Hierdie neiging was sterk skeefgetrek deur enkele streke (Suider- en Oos-Afrika) en aktiwiteitsektore (veral landbou) en is veroorsaak deur ‘n klein aantal indringer taksa (hoofsaaklik drie insekplae: *Chilo partellus*, *Tuta absoluta*, *Spodoptera frugiperda*). Ons beklemtoon ook belangrike groot leemtes in die huidige kennis oor die ekonomiese koste van indringer spesies wat nog oorbrug moet word met behulp van wyer navorsings en bestuursaksies op die vasteland. Ten slotte bied ons studie ondersteuning vir die ontwikkeling en implementering van voorkomende maatreëls, sowel as geïntegreerde bestuursaksies op beide nasionale en streeksvlak. Met inagneming van die komplekse samelewings- en ekonomiese realiteit in Afrikalande, moet die tans verwaarloosde probleem van indringer spesies ‘n prioriteit word vir volhoubare ontwikkeling.

Abstract in Amharic

የሥነ-ሕይወታዊ ወረራዎች ኢኮኖሚያዊ ወጪዎች - እየጨመረ የመጣ ግን ችላ የተባለ ስጋት?
አጭር ርዕስ፡ ችል የተባለ ግን እየጨመረ የመጣ የሥነ-ሕይወታዊያን ወረራ በአፍሪካ ረቂቅ
ሥነ-ሕይወታዊ ወረራዎች በተፈጥሯዊ ሥነ-ምህዳር እና በሰው ማኅበረሰብ ላይ ከፍተኛ ተጽዕኖ ያሳድራሉ። ሆኖም ምንም እንኳን ስለ ሥነ-ሕይወታዊ ወረራዎች ኢኮኖሚያዊ ተጽዕኖ ያለው እውቀት ቀልጣፋ ቁጥጥርን እና ፖሊሲን በተመለከተ ወሳኝ ግንዛቤዎችን የሚሰጥ ቢሆንም፣ አስተማማኝ ውህደት (ቅንጅት) ግን አሁንም ይጎለዋል። ይህ ሁኔታ በተለይ የሥነ-ሕይወታዊ ወረራዎችን ተፅእኖ ለመቆጣጠር በቂ ኢኮኖሚያዊ ሀብት በሌላቸው አገሮች የሚታይ ሀቅ ነው። በዚህ ጥናት፣ እኛ በቅርቡ ኢንቫኮስት የተባለ የመረጃ ቋት (በዓለም ዙሪያ

በወራሪ የውጭ ዝርያዎች የገንዘብ ተጽዕኖዎች ላይ እጅግ የተሟላ መረጃ ያለው የመረጃ ቋት) ባጠናቀረው መረጃ ላይ ተመርኩዘን የመጀመሪያዉን በአፍሪካ ውስጥ ሥነ-ሕይወታዊ ወረራዎች የሚያደርሱትን ኢኮኖሚያዊ ወጪዎች ማጠናቀር ችለናል። በዚህ መሰረት እ.ኤ.አ. ከ 1970 እስከ 2020 ባሉት ዓመታት የተዘገቡ የሥነ-ሕይወታዊ ወረራዎች ወጪዎች ድምር በ 18.2 ቢሊዮን እና 78.9 ቢሊዮን የአሜሪካ ዶላር መካከል መሆኑን ደርሰንበታል። ይህ አሃዝ በጣም ተቃሎ (ዝቅ ተደርጎ) የተገመተ ወጪ ቢሆንም ለአፍሪካ አገራት እጅግ ከፍተኛ ኢኮኖሚያዊ ሸክምን ይወክላሉ። በጣም በሚያስደነግጥ ሁኔታ እነዚህ ወጪዎች በቅርቡ ምንም የመቀነስ ምልክቶች ሳያሳዩ ከጊዜ ወደ ጊዜ በከፍተኛ ሁኔታ እየጨመሩ ይገኛሉ። ሪፖርት የተደረጉት ወጪዎችም ቢሆኑ በአብዛኛው ወራሪዎቹን ለመቆጣጠር ከሚወጡ ወጪዎች ይልቅ በወራሪዎቹ የሚደርሱ ጉዳቶች ላይ ያተኮሩ ናቸው። ይህም ሂደት ወደ ተወሰኑ የክፍለ አህጉሩ አከባቢዎች (ማለትም ወደ ደቡብ እና ምስራቅ አፍሪካ) እና የስራ ዘርፎች (ማለትም ግብርና) በጣም ያዘነበለ ሆኖ በጥቂት ወራሪ ዝርያዎች (ማለትም በዋናነት በሶስት ተባይ ነፍሳቶት፣ በሳይንስ ስማቸው ቺሎ ፓርቴሉስ፣ ቱታ አብሶሉታ እና ስፖዶፕቴራ ፍሩጂፔርዳ) የደረሰ ጥቃት ላይ ያተኮረ ነው። በተጨማሪም በዚህ ጥናት በአህጉር ደረጃ በተስፋፉ ጥናትና ምርምር ጥረቶች እና መቆጣጠሪያ እርምጃዎች ሊሞሉ የሚገቡ ወሳኝና ትላለቅ የሥነ-ሕይወታዊ ወረራዎች ኢኮኖሚያዊ ወጪዎችን በተመለከተ ያሉ ወቅታዊ የዕውቀት ክፍተቶችን እናሳያለን። በመጨረሻም ጥናታችን የወረራ መከላከያ እርምጃዎችን ለማዘጋጀትና ተግባራዊ ለማድረግ እንዲሁም በብሔራዊም ሆነ ክፍለ-አህጉር ደረጃ የሚተገበሩ የተቀናጁ የድህረ-ወረራ መቆጣጠሪያ እርምጃዎችን ይደግፋል። በአፍሪካ ሀገሮች ውስጥ ያሉትን ውስብስብ ማህበራዊ እና ኢኮኖሚያዊ እውነታዎች ከግምት ውስጥ በማስገባት በአሁኑ ጊዜ ትኩረት ያልተሰጠው የሥነ-ሕይወታዊ ወረራዎች ችግር ለዘላቂ ልማት ጥቅም ቅድሚያ ሊሰጠዉ የሚገባ ጉዳይ ሊሆን ይገባል።

Abstract in Arabic

التكاليف الاقتصادية للغزو البيولوجي في أفريقيا: تهديد متنامٍ، لكن متجاهل؟ يؤثر الغزو البيولوجي بشكل كبير على النظم البيئية الطبيعية، وعلى المجتمعات البشرية. وعلى الرغم من أن المعرفة بالآثار الاقتصادية للغز البيولوجي توفر معلومات بالغة الأهمية من أجل تدبير ناجع وسياسات فعالة، إلا أن التوليفات الموثوقة لا تزال غير متوفرة. وينطبق هذا بشكل خاص على البلدان ذات الدخل المنخفض، حيث الموارد الاقتصادية غير كافية للسيطرة على آثار الغزو. اعتمدنا في هذه الدراسة على قاعدة بيانات InvaCost التي تم تطويرها مؤخرًا - وهي المستودع الأكثر شمولاً للتأثيرات المالية للأنواع الغريبة الغازية في جميع أنحاء العالم – من أجل إنتاج أول توليفة للتكاليف الاقتصادية للغزو البيولوجية في القارة الإفريقية. ولقد تبين أن التكاليف المبلغ عنها للغزو البيولوجي تراوحت بين 18,2 مليار دولار أمريكي و78,9 مليار دولار أمريكي ما بين عامي 1970 و 2020 ، ويمثل هذا عبئا اقتصاديا هائلا على البلدان الإفريقية التي لازالت تقلل من شأنه. كما أن المقلق في الأمر هو أن هذه التكاليف تتزايد بشكل كبير مع مرور الوقت، دون أي علامات على التراجع في المستقبل القريب. وكانت معظم التكاليف المبلغ عنها ناجمة عن الأضرار الناتجة عن الأنواع الغازية بدلاً من المصاريف المتكبدة من أجل التدبير. وتجدر الإشارة إلى أن الاتجاه هم بشدة مناطق قليلة (أي جنوب وشرق أفريقيا) وبعض قطاعات الأنشطة (أي الزراعة) وكبدها عدد قليل من الأصناف الغازية (أي ثلاث آفات حشرية بشكل أساسي: *Chilo partellus* و*Tuta absoluta* و *Spodoptera frugiperda*). كما نسلط الضوء أيضًا في هذه الدراسة على الفجوات الكبيرة والحاسمة في المعرفة الحالية حول التكاليف الاقتصادية للغزو البيولوجي التي لا تزال بحاجة إلى سدها من خلال المزيد من الجهود البحثية الواسعة النطاق والإجراءات الإدارية في جميع أنحاء القارة. وفي الأخير، تقدم دراستنا الدعم لوضع وتنفيذ تدابير وقائية فضلا عن إجراءات إدارية متكاملة بعد الغزو على الصعيدين الوطني والإقليمي.

Abstract in Bamanan Kan

Ɲanamaya finkuraw bɛsekakɛ nɔdyateminɛ taye kungo lahalaw ni sigida lahalaw kan. Alini ayasɔrɔ dɔniya minu bɛ talikɛ ɲanamaya finkuraw cyarili musakakola, ka kunafoni nafamaw jira, ka kɛɲɛ ni maralifɛrɛw ani gilancyoko jonjonw ye, alisa tɔbujɛ. o sɛbɛtyaledo dyamana kono minu ka sɔrɔ ka dɔkɔn, ani u ka nafasɔrɔ finw dɔkɔya kaman, utese ka ɲanamaya finkuraw cyarili kɔlɔsi ani ka dansigi u yɛlɛma cyogola. Nin ɲinini kɔnɔnana anyan sinsin kunafoniwkan min bɔra “InvaCost” la. U ka kunafoniw ye finyé min ni mɔgɔ beseka isinsin akan ɲanamaya finw sɔrɔko kunkan ani finsukuya wɛrɛ min bɛ bɔ dunya fanwɛrɛ fɛ ka dunya minɛ. Kunafoni minu bɛ talikɛ “IvanCost” la u sɛbɛntyala wakati labanw na. Nin bara nunu kɛra sababuye ka dyabi fɔlɔ sinsinlenw sɔrɔ minu bɛ talikɛ ɲanamaya finkuraw musaka kola farafina marabolokan. An ya dyateminɛ ko musaka minuw dantikɛla kakɛɲɛ ni fin nunu yariliye, o ba daminɛ Ameriki wari dolari milyari 18,2 ka ta bila 78,9 ka bɔ san 1970 ka na bila 2020. Nin bɛ musaka cyanma kofɔ, ŋa minuw dyatelentɛ farafina dyamanaw bolo. Dabaliban kowɛrɛ tuguni, nin musakanunuw bɛtaka cyokoyala min ka telin, ka kɛɲɛ ni wagatiye, kasɔrɔ u jigini fɛrɛ foyi yiralentɛ. Musaka minu bɔrama, okun dɛnendo bakurubala minu bɛ talikɛ kɔlɔlɔwla minu bɛ talikɛ fin nunuw cyaribawla katɛmɛ musakako min dyalatikɛlendo labarali kama. Sika kun kɛlendo o famuyali bolonina marayɔrɔ damadɔ fanfɛ minu bɛ farafinakɔnɔ ani cyakɛda bolowla (sɛnɛ bo la) min bara tun geleyalendo fɛnɲanamanw fɛ (inafo finsaba hakɛ: Chilo partellus, Tuta absoluta, Spodoptera frugiperda). An ba yira fana ka fɔ ko dɔnya minunw beye sisan ɲanamaya finw cyarili musaka kowkan, ko belebele be u dyɛ minuw kakan ka dafa ni ɲinininw ani waleya waralenw ye farafina fantyama na. Kuntyɛlila anka ni ɲinini bɛnakɛ dɛmɛ ye fɛrɛkunbɛnanw ani waleya minuw bɛ talikɛ kɔlɔlɔwla minuw dɛn nendo fin nunuw cyarilila ka kɛɲɛ ni marayɔrɔw ye. Ka da farafina jamanaw sigida ni a musakakow gɛlɛyakan, gɛlɛya min bɛyen bi na jatelen tɛ kakɛɲɛ ni ɲanamaya finw cyarili ye, o kan ka kɛ bɛ kunkelena ye, yiriwa badabada kama.

Abstract in French

Les coûts économiques des invasions biologiques en Afrique: une menace croissante mais négligée ? Les invasions biologiques peuvent avoir un impact considérable sur les écosystèmes naturels et les sociétés humaines. Cependant, bien que les connaissances sur les impacts économiques des invasions biologiques fournissent des informations cruciales en termes de gestion, des synthèses récentes et fiables font encore défaut. Cela est particulièrement vrai pour les pays à faible revenu où les ressources économiques sont insuffisantes pour contrôler les effets des invasions. Dans cette étude, nous nous sommes appuyés sur la base de données "InvaCost" développée récemment - le référentiel le plus complet sur les impacts monétaires des espèces exotiques envahissantes dans le monde - pour produire la première synthèse des coûts économiques des invasions biologiques sur le continent africain. Nous avons constaté que les coûts déclarés des invasions varient entre 18,2 milliards de dollars américains (USD) et 78,9 milliards USD entre 1970 et 2020. Cela représente une charge économique énorme, mais encore très sous-estimée, pour les pays africains. Plus alarmant encore, ces coûts augmentent de façon exponentielle au fil du temps, sans aucun signe de réduction pour les années à venir. Les coûts reportés étaient principalement (*i*) dus aux dommages causés par les envahisseurs plutôt qu'aux dépenses engagées pour lutter contre leurs invasions, (*ii*) fortement biaisés vers quelques régions (Afrique australe et orientale) et secteurs d'activité (agriculture) et (*iii*) associés à un nombre restreint de taxons envahissants (essentiellement trois insectes ravageurs: *Chilo partellus*, *Tuta absoluta*, *Spodoptera frugiperda*). Notre étude met également en lumière de cruciales lacunes dans les connaissances actuelles sur les coûts économiques des invasions qui doivent encore être comblées par des efforts de recherche et des actions de gestion plus importants et étendus à travers le continent. Enfin, notre travail souligne la nécessité de l'élaboration et la mise en œuvre de mesures préventives pour empêcher l'introduction des espèces envahissantes, ainsi que l'intégration des actions de gestion aux niveaux national et régional. Compte tenu des réalités sociétales et économiques complexes des pays africains, le problème actuellement négligé des invasions biologiques devrait être une priorité pour le développement durable.

Abstract in Haussa

Ɗaukar nauyin mamayar ƙwayoyin halittu a Afirka : wata barazana mai yaɗuwa amma da aka yi wa kamun sakainar kashi ? Yaɗuwar ƙwayoyin halittu (tsirai ko ƙwari) na iya samun babban tasiri a kan muhalli da al'umomi. Sai dai, ko da yake ilimi da ake da shi a kan tasirin yaɗuwar ƙwayoyin halittun a kan tattalin arziki na bayar da muhimman bayanai don ingantuwar siyasa da gudanarwa, amma amintattun bayanai sun faskara. An fi ganin zahirin hakan musamman a ƙasashe masu raunin tattalin arziki da ba su iya fuskantar lamarin. Cikin wannan binciken, mun yi amfani da rumbun bayanai na InvaCost da aka bunƙasa kwanan nan- kafa mafi cika da inganci a kan tasirin kuɗaɗen da

akan kashe don fuskantar zaukakkin ire-iren ƙwayoyin halittu masu mamaya a faɗin duniya- domin samar da amitattun bayanai a kan kuɗin da ake kashewa ta fuskar mamayar kwayoyin halittu a nahiyar Afirka. Mun gano cewa kuɗaɗen da aka bayyana cewa an kashe da ga shekara ta 1970 sun kai biliyan (miliyar) 18,2 dalar Amerika zuwa biliyan 78,9 a shekara ta 2020.

Wannan wani babban nauyi ne a kan tattalin arzikin ƙasashen Afirka, amma da ba a mizanta da kyau ba. Abu mafi ɗaga hankali kuma shi ne: kashe-kashe kuɗaɗen ƙaruwa yake yau da gobe, ba tare da wata alama ta raguwa ba. Kuɗaɗen da aka bayyana an kashe sun shafi musamman ɓarnar da masu mamayar suka yi, maimakon kashe su ta fuskar gudanar da aiki.

Wannan manufar ta sami komabaya sosai a wasu sassan Afirka (wato sashen kudu na Afirka da gabashin Afirka) da wasu ɓangarorin aiki (wato noma) kuma hakan na da nasaba da wasu ƴan tsirarun irin ƙwayoyin halittu masu mamaya (wato musamman ƙwaro uku maɓarnata albarkatun noma : *Chilo-partellus*, *Tuta absoluta*, *Spodoptera frugiperda*).

Muna kuma jan hankali a kan manyan kura-kurai cikin bayanan da ake da su a halin yanzu da suka shafi ɗaukar nauyin mamayar ƙwayoyin halittu, da ya kamata a magance su ta hanyar ƙoƙarin bincike da faɗaɗa gudanar da ayyuka ko'ina cikin nahiyar.

A ƙarshe, bincikenmu na goyon bayan ɗaukar matakan riga kafi da kuma na gudanar da aiki bayan wanzuwar mamaya a matakin ƙasa da ma na ƙasa da ƙasa. Da la'akari da zahirin yanayin tattalin arziki da rayuwar al'umar ƙasashen Afirka mai sarƙaƙƙiya, ya kamata matsalar mamayar ƙwayoyin halittu da ke gudana a halin yanzu, ta zama a sahun gaba don cimma cigaba mai ɗorewa.

Abstract in Malagasy

Ny totalim-bidy ara-toekarena noho ny fananiham-bohitra biolojika ao Afrika : tsindry tsy mitsaha-mitombo nefa atao tsirambina ? Ny fananiham-bohitra biolojika dia mety hisy fiatraikany lehibe amin'ny tontolo iainana voajanahary sy ny fiarahamonin'ny olombelona. Na dia manome fahalalana betsaka momba ny politika sy ny fitantanana mahomby ny fampahalalana ny voka-dratsy ara-toekarena noho ny fananiham-bohitra biolojika, dia mbola tsy ampy ireo fandravonana azo antoka. Hita taratra izany eo amin'ireo firenena ambany fidiram-bola izay tsy manana ny ampy hifehezana ny vokadratsin'ny fananiham-bohitra. Amin'ity fandinihana ity dia mifototra amin'ny angon-drakitra InvaCost vao novolavolaina tsy ela - ny firaiketana feno kokoa momba ny fiantraika ara-bola ny vokatry ny karazan-javamananaina vahiny mpandrakotra manerantany – mba hamokarana ny fandravonana dingana voalohany ny vidim-piainana noho ny fanafihana biolojika ao amin'ny kaontinanta afrikanina. Tsikaritray fa ny vola lany tamin'ny fananiham-bohitra biologika dia 18,2 miliara $ ka hatramin'ny 78,9 miliara $ teo anelanelan'ny 1970 sy 2020. Fahavoazana lehibe ho an'ny toe-karena izany, nefa dia ambany ny tombatombana ho an'ny firenena afrikanina. Mbola anisan'ny mampatahotra ihany koa ny amin'ireo totalim-bidy ireo izay tsy mitsaha-mitombo hatrany ary tsy misy ny fambara ny amin'ny fihenany. Ny totalim-bidy voalaza dia miompana indrindra amin'ny fahasimbana naterak'ireo mpandrakotra fa tsy ny fandaniana amin'ny fitantanana. Ity fironana voalaza ity dia nitanila tamin'ny faritra vitsivitsy (izany hoe aty amin'ny faritra Afrika atsinanana sy atsimo) sy seha-pikatrohana manokana (izany hoe ny fambolena) ary eo ihany koa ny havitsian'ny karazana mpandrakotra (izany hoe niompana kokoa amin'ireo bibikely mpandrava: *Chilo partellus*, *Tuta absoluta*, *Spodoptera frugiperda*). Tianay ho marihina ihany koa ny tsy fahampiana lehibe eo amin'ny fahalalana momba ny vola lany amin'ny fananiham-bohitra amin'izao fotoana izao izay mbola mila jerena akaiky amin'ny alàlan'ny ezaky ny fikarohana bebe kokoa sy ny hetsika fitantanana manerana ny kaontinanta. Ary farany, ny fandinihanay dia manohana ny famolavolana sy ny fampiharana ny fepetra fisorohana ary koa ny hetsika fitantanana aorian'ny fananiham-bohitra amin'ny sehatra nasionaly sy isam-paritra. Raha ny zava-misy eo amin'ny fahasarotan'ny fiainana ara-piaraha-monina sy ara-toekarena eo amin'ny firenena afrikanina, dia tokony hatao laharam-pahamehana amin'ny fampandrosoana maharitra ny olan'ny fanafihana biolojika amin'izao fotoana izao.

Abstract in Portuguese

Os custos econômicos das invasões biológicas na África: uma crescente, mas negligenciada ameaça? Invasões biológicas podem impactar ambientes naturais e sociedades humanas dramaticamente. No entanto, embora o conhecimento dos impactos econômicos das invasões biológicas forneça uma visão crucial para gestão e políticas eficientes, ainda faltam sínteses confiáveis. Isso é particularmente importante para países com pouca renda, onde recursos econômicos são insuficientes para controlar os efeitos das invasões biológicas. Nesse estudo, nós contamos com o banco de dados recentemente desenvolvido InvaCost – o repositório mais abrangente sobre os impactos financeiros das espécies invasoras em todo o mundo – para produzir a primeira síntese dos custos das invasões biológicas no continente Africano. Nós encontramos que o custo reportado das invasões variou entre 18,2 bilhões de dólares e 78,9 bilhões de dólares, dados de 1970 a 2020. Esse valor representa uma enorme, apesar de subestimada, carga econômica para os países Africanos. Ainda mais alarmante, esses custos crescem exponencialmente com o tempo e sem nenhum sinal de redução no futuro próximo. Os custos reportados foram direcionados principalmente por danos causados pelas espécies invasoras, mais que pelas despesas devido ao manejo. Essa tendência foi altamente enviesada para algumas regiões (tais como, África Austral e Oriental) e setores de atividade (tal como, agricultura), e gerada por um pequeno número de taxa invasores (tais como, três insetos-pragas: *Chilo partellus*, *Tuta absoluta*, *Spodoptera frugiperda*). Nós também destacamos grandes lacunas no atual conhecimento sobre os custos econômicos das invasões biológicas, que ainda precisam ser superados com mais esforços de pesquisa e ações de manejo em todo o continente. Finalmente, nosso estudo fornece suporte para o desenvolvimento e implementação de medidas de prevenção, assim como ações de manejo integrado pós-invasão em escala nacional e regional. Considerando a complexa realidade social e econômica do continente Africano, o problema atualmente negligenciado das invasões biológicas deve se tornar uma prioridade para o desenvolvimento sustentável.

Abstract in Puular

Ko ruudooji mbarakoñ ngarkoñ e Afrik ngardata : bonere mawnde nde reentaaka ? Ruudooji mbarakoñ na mbaawi adude bonere mawnde e kala windere e nguurndam yimbe. Kono, ko gonggo gandal nowoodi faade ko deen bonne ngadorta ko hadatapolitik e jogogal peewngal. Duumdoon tengtikoyleydeele pamdude doole de koomkoomeeji mum en njonaani ngam reentude bonere diin ruudooji. E ndeer nde windere, baariden koy ligeey « InvaCost » tiaraado ko booyaani - liggeey burdo timmu faade e bonere jawdi leyyi niembaadi jaaknudi aduna – ngam yaltinde fibre idiinde holliroore ko diin ruudooji ngadata e leydi Afrik. En njii wonde diin ruudooji edi mbonna hakkunde 18², miliaaruji dolaar e 78,9 dolaar ko fuddori hitande 1970 faade hitannde 2020. Duumko baasal mangal, kono ngal limaaka, e ndeer Afrik. Ko buriko hulbinaade woni bonere ndeni besdo no feewi niande fof, ko adata ustaare yiaaka… Ko adiiko bonere nde no fawondira umiiko e ruudooji he wona e ko wadaako e ngaynaaka.Duumdoon firti no feewi ko e woon nokkuuji e woon ligiyaaji (woni ndemri) tawa adi dum ko seeda e woon ruudoooji : "*Chilo partellus*, *Tuta absoluta*, *Spodoptera frugiperda*". Min kolira kadi waasde gandal nofeewi faade e ko di ruudooji mbonanta e danialmen adanimen fotde tinnaade e witto e neende diawdimen e ndeer Afrik.

Ko watindiiko, jangde men teengtini fotde tinnaade ardinde peeje et bade tiagal ruudooji e ndeer leydimen e ko taariindi ko. Si en ndaari aadaaji men e koomkoom mettudo mbo leydeele afrik, itude tiadeele hande umiidi e ruudooji potden ardinde ngam ndanien ngartam booydam.

Abstract in Spanish

Los costos económicos de las invasiones biológicas en África: ¿una amenaza creciente pero desatendida? Las invasiones biológicas pueden impactar dramáticamente los ecosistemas naturales y las sociedades humanas. Sin embargo, aunque el conocimiento de los impactos económicos de las invasiones biológicas proporciona información crucial para una gestión y política eficientes, todavía faltan síntesis fiables. Esto es particularmente cierto para países de bajos ingresos donde los recursos económicos son insuficientes para controlar los impactos de las invasiones. En este estudio nos basamos en la base de datos

InvaCost, la cual ha sido desarrollada recientemente y constituye el repositorio más completo sobre los impactos económicos de las especies exóticas invasoras a nivel mundial, para producir la primera síntesis de los costos económicos de las invasiones biológicas en el continente Africano. Descubrimos que los costos reportados de las invasiones oscilaron entre US$ 18.2 mil millones y US$ 78.9 mil millones entre 1970 y 2020. Esto representa una carga económica masiva, pero muy subestimada, para los países africanos. Lo que es más alarmante es que estos costos están aumentando exponencialmente con el tiempo, sin mostrar signos de disminución en el futuro cercano. Los costos reportados corresponden principalmente a daños causados por las invasiones, en lugar de a gastos de gestión. Esta tendencia está sesgada hacia unas pocas regiones (África meridional y oriental) y sectores de actividad (agricultura) y resulta de un pequeño número de taxones invasores (principalmente de tres plagas de insectos: *Chilo partellus*, *Tuta absoluta* y *Spodoptera frugiperda*). También destacamos grandes lagunas en el conocimiento actual sobre los costos económicos de las invasiones que deben superarse con esfuerzos de investigación y acciones de gestión más generalizadas en todo el continente. Finalmente, nuestro estudio brinda apoyo para el desarrollo e implementación de medidas preventivas, así como acciones integradas de manejo post-invasión a nivel nacional y regional. Teniendo en cuenta las complejas realidades sociales y económicas de los países africanos, el problema actualmente desatendido de las invasiones biológicas debería convertirse en una prioridad para el desarrollo sostenible.

Abstract in Tamasheq

Alquyuman daɣ awa deqalan emel in almissibaten tin-issudar daɣ Afrik: almissibat tətiiwaḍat mušen war-hin nitawajrah? Almiṣṣibaten tin - issudar adobatnat ad- ilanat takmo maqqorat fil awad eqalan ahinzazaɣ d- timuzdoq n-adinat. Hakid-ijja awendaɣ, kud daɣass imiyiišãn d-musnaten idaqqalnen terk-erché tad-d- tirəwnát almaṣṣibaten ti ikmanen usudar d-ahinzazaɣ, harat wendaɣ kudaɣ amoss ayihakan issalan assoxatnen yi manaɣafan hakid daɣ adabara iwir sarho, hakid ijjawendaɣ wirid inšeš har harwa ayinfan harat.

Harat wendaɣ eqal tidit hulen y-iduwilan wi arkamnén id filas iduwilan windaɣ ibraran hulen daɣ awadeqalan aššujiš in azrəf iškam diš ad- ajjin iniyat yi haratan wi did tiruwnat almaṣṣibaten.

Daɣ taɣare tadaɣ nasihatal fil issalan id išreynen hanaɣid ifalnen awass itawan Inva Cost- ɣas teɣare ten təmoss almintal assoxen daɣ awadeqalan tikmawen meɣ tinfawen in izirfan fil mudaran wi taqalnen almiṣṣibaten daɣ udunia- tə mušɣult ten daɣ kul wir təga ar-yadid tissaɣsil meɣ adid tišinšiš alquyuman daɣ azrəf n almaṣṣibaten ti ikmanen issudar daɣ afriq.

Nijrahin as alquyuman witawassaneen n- almaṣṣibaten ilanant jər 18,2 in milliards USD d- 78,9 milliards USD jər awattay wan 1970 har wan 2020. Awen eqal aẓuk maqqoran daɣ azzruf, hakid-ijjawendaɣ aẓuk wendaɣ atiwalka y i iduwilan win Afriq. Hakid-ijja awendaɣ awa assharahaɣan harwa as alquyuman windaɣ tiwaḍan hak awattay, sas wartila aššamol nas fanzan. Ilquyuman windaɣ attwana ijjan daɣ šaɣšadan ɣas widid orawan almaṣṣibaten issilmadan as waden amašal ayija azrəf daɣ ijjin n-ewatel y almaṣṣibaten waladaɣ ikanan n ayinfan harat. Harat wadaɣ išrayan n iban kanan n išaɣil səmək olaɣan ijja hulen daɣ kalan iyaḍ n afrik (ilmintal ikalan n afrik wi ahanen teje tan agala d- win dinig) d išarajan n təmašɣolen(šund issuduma) hakid ijja awendaɣ marsalan windaɣ erawtanid harat in ilmissibaten in mudaran(imudaran windaɣ amosnen ilmissibaten ijjan daɣ karad šarajan n magadan witajinen šaɣšad : (Chilo partellus, Tuta absoluta, Spodoptera frugiperda). Nissilmad as ilant marsallan ajjotnen daɣ awadeqalan masnat in alquyuman in awaytajašan tabilant tajjat d- ilmissibaten, ɣas anihaja ad- ittiwitir adabara ijjan daɣ umaɣ d- əssimil in təmušɣult tolaɣat təlssat Afrik. Nissilmad ḍarat awen as teɣare tadaɣ tidhal assəmil d- ijji n adabaratan əmosnen ewatel hakidaɣ təmušɣult ibdadnen daɣ ijji n adabara dat assa n- ilmiṣṣibaten daɣ iddiwil hakid daɣ iddiwilan wiyaḍnen. Filas attiwassan attarex d timizdoq n addinant taẓikanẓarat daɣ kalan win afrik, almušaqat ta ti təlat ɣas warhin titawajraj ašilidaɣ təmoss tabilant d- almiṣṣibaten ti ikmanen issudar, tabilant ten-daɣ əntass as anhaja ad taqqal itus ɣəssəmil in effes illan taɣrist.

Abstract in Woloff

Tënk. Ruurum ndundat yi lu aay la ci yàq kéew-kéewaan yu bindare yi ak dundug nit ñi. Ci loolu nag, doonte xam-xam am na ci njeexital i ruurum ndundat ci wàllug koom-koom ba aw yoon tijjiku ngir man a saytu caytu gu am solo ak teg i polotig, waaye jarabu yu doy, yu amul benn laam-laame ; àggaguñu ca ba leegi. Loolu ci réew yu néew doole yi la rawatee nag ndax ñàkk njumtukaay ak alal ju ñu waggaree ruur moomu. Jarabu gii, ñi ngi ko sukkandikoo ci dayu InvaCost bi ñu defar bu yàggul – ndàmb li gën a yomb a nànd ngir xam jeexital i ray-donni doxandéem yi ci àdduna wërngal kapp ci wàllug koppar – ngir jëmmal jarabu gi njëkk ci kembaaru Afrig ñeel li ruurum ndundat di jur ci alal ci koom-koom mi. Gis nanu ne ruur mi, li ko dale 1970 ba 2020, bees ko nattee cig njëg ; toll na ci diggante 18.2 ba 78.9 tamndareet i US$. Alal ju bari jii di naaxsaay, luy nasaxal koomu réewi Afrig yi la. Li ci gën a doy waar, koom mu bari moomu ñuy ñàkk day yokk saa yu ne, te amul luy nuru ab dogal bees jël ngir saafara ko ci ëllag ju jampal. Alal jii ñu fésal nag mooy li ruur mi yàq waaye du lu ñu génne ngir saytug ruur mi. Yàqu-yàquy ruur moomu nag tane na ci yenn tund yi (i.e. Penku ak Bëj-déexu Afrig) ak ci yenn aaneer yi (i.e. mbay mi) boole ci lim bu néew ciy ndundat (taxa) ñoo fay ruur (i.e. ñatti gunóori ruurkat yi gën a ràññiku: *Chilo partellus*, *Tuta absoluta*, *Spodoptera frugiperda*). Gendiku nanu itam lu am solo, fi xam-xamu ruur mi tollandi ak alal ji miy laatul ci koom-koom, soxla na bu baax a baax ñu gën a yaatal góor-góorlu gi ci luññtu yi ak yokk jéego yi ci saytug ruur mi ci kembaar gi. Ngir teeral, sunu jarabu gii jur na cëslaay ngir samp ak fànnoo ay dogal yoo xam ne dinañu sóor nees di saytoo bir yi ginnaaw bu am ruur amee moo xam ci biir réew mi la mbaa ci tundi kembaar gi. Bees bàyyee xel ci ni dundiin wi nosoo ak tolluwaayi koom-koomu réewi Afrig yi, soobantal gii tembe ñu soobantal ruurum ndundat yi lu war a dakk la tey yitte ju jamp ngir ug suqliku gu sont te sax dàkk.

Abstract in isiZulu

Izindleko ezidalwa izimila nezilwanyana zokufika kwizwekazi laseAfrika: Ingozi ekhulayo kodwa enganakiwe. Isihloko esifingqiwe: Izindleko ezikhulayo kodwa ezingakaniwe zemizila nezilwanyana zokufika ezweni-kazi laseAfrika.

Izimila nezilwanyana zokufika zinomthelela omkhulu kwimvelo kanye nenhlalonhle yemiphakathi. Nakuba ukuqondisisa kahle imithelela yezimila nezilwanyana zokufika emnothweni kunikeza imininingwane ebalulekile ikakhulu uma kuzoliwa nokubhebhetheka kwazo kanye nokuhlaziya inqubomgomo yezomthetho, ulwazi olusemqoka noluthembekile lusashoda. Lokhu kuyiqiniso ikakhulukazi emazweni antulayo lapho umnotho ungenele ukuthi kubhekwane nemithelela yezimila nezilwanyana zokufika. Kulolucwaningo, sisebenzise isigcinalwazi iInvaCost esanda kusungulwa- lapho kugcinwe khona ucwaningo olubanzi noluphelele mayelana nemithelela yezimila nezilwanyana zokufika uma kukhulunywa ngomnotho emhlabeni jikelele- lesi sigcina lwazi sizosiza ukudalula izindleko ezivela ngenxa yokubhebhetheka kwezimila nezilwanyana zokufika ezwenikazi lase Afrika. Ngokusebenzisa lesi sigcina lwazi sithole ukuthi izindleko zokumelana nezimila nezilwanyana zokufika zilinganiselwa phakathi kuka $18.2 kuya ku $78.9 wezigidigidi zamadola aseMelika kusekela eminyakeni yo1970 kuya ku2020. Lokhu kutshengisa umthwalo omkhulu, kepha ongazakaze wacwaningwa ngokwanele wezomnotho emazweni ase-Afrika. Okuthusa kakhulu ukuthi lezi zindleko ziyakhula ngokuhamba kwesikhathi kanti futhi azikho izimpawu ezikhomba ukwehla kwazo esikhathini esizayo. Izindleko ezibikiwe zincike kakhulu kumonakalo owenziwa izimila nezilwanyana zokufika kunezindleko zokulwisana nokubhebhetheka kwazo. Lombiko ubususelwe kakhulu ezifundeni ezimbalwa (esizeNingizumu naseMpumalanga yeAfrika) kanye nasemikhakheni embalwa (isb. ezolimo) nakhona kubhekwe izibonelo ezimbalwa (ikakhulukazi izinambuzane ezintathu eziyinkathazo: Chilo partellus, Tuta absoluta, Spodoptera frugiperda). Siphinde siveze ukuntuleka kolwazi olwanele uma kukhulunywa ngezindleko zezomnotho ezidalwa yizo izimila nezilwanyana zokufika, nokusafanele kwenziwe ucwaningo olunzulu ukuze sizoqonda izindlela zokulwisana nokubhebhetheka kwazo ezwenikazi lonke lase Africa. Okokugcina, lolu cwaningo luhlanganiswe ngendlela yokuthi lukwazi ukweseka imizamo yokusungula izindlela ezizokuvimbela ukubhebhetheka kwezimila nezilwanyana zokufika emazingeni amazwe kanye nawezifunda.

Uma kubhekwa inhlalonhle kanye nezomnotho emazweni wonke ase-Afrika, lokhu kuntuleka kolwazi uma kukhulunywa ngezimila zokufika kumele kube yinto ebhekisiswayo ikakhulu uma kukhulunywa ngezentuthuko.

Keywords
Africa, agriculture, biological invasions, damage, economic costs, InvaCost, management

Palabras clave
África, agricultura, invasiones biológicas, daños, costes económicos, InvaCost, gestión

Trefwoorde
Afrika, landbou, indringer spesies, skade, ekonomiese koste, InvaCost, bestuur

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አፍሪካ; ግብርና; ሥነ-ሕይወታዊ ወረራዎች; ጉዳት; ኢኮኖሚያዊ ወጪዎች; ኢንቫኮስት; ቁጥጥር።

Sigiden bakurubaw
Farafina, sɛnɛ, Ɲanamaya finkuraw cyarili, kɔlɔlɔ, musaka, InvaCost, labarali

Mots-clés
Afrique, agriculture, invasions biologiques, pertes et dommages, coûts économiques, InvaCost, gestion

Waat yu am solo yi
Afrig, mbay, ruuri ndundat yi, yàqu-yàyu, njeexital ci koom-koom, InvaCost, saytu gi

Amagama angukhiye
Afrika, ezolimo, izimila nezilwanyana zokufika, umonakalo, izindleko zezomnotho, InvaCost, ukubhekana

Introduction

Biological invasions have become a worldwide problem because of the accelerating rate of globalization, particularly since the end of the 20th century due to increasing modern travel, trade and technology, and these factors are likely to intensify the spread of invasive alien species (IAS) (Seebens 2015; Seebens et al. 2019). Within the context of Africa, the increased threat and spread of IAS will be no exception given the continent's evolving travel and trade (Rouget et al. 2016; Faulkner et al. 2017; Faulkner et al. 2020). Despite the relatively low research effort in invasion biology in most African countries, IAS studied until now across the continent (e.g. 16% of the species currently listed in the Global Invasive Species Database, GISD; www.iucngisd.org/gisd/) represent important drivers of ecological disturbance (e.g. biodiversity loss; Zengeya et al. 2020), social and health issues (e.g. disease transmission and impact on water resources; Wild 2018; Ogden et al. 2019), and economic losses and expenses (e.g. reduction in the yield of agricultural crops; Pratt et al. 2017).

Some of these IAS can become invasive after their intentional introduction by humans. For example, the tree *Prosopis juliflora* was introduced in the Afar region (Ethiopia) for water and soil conservation, shade and wind protection, and as firewood, fencing and building material. *P. juliflora* soon invaded croplands, grasslands, riverbanks and roadsides in the area, reducing native biodiversity, grazing potential and water supply (Shiferaw et al. 2019). Another example is the invasion of the succulent plant *Opuntia stricta* in South Africa, where it was initially introduced as an ornamental plant. *O. stricta* is currently recorded as invasive across most of the country, reducing food production, causing loss of grazing potential, transforming habitats, altering native biodiversity and causing injuries to people due to its spines (Novoa et al. 2016a). The last example is the marbled crayfish, *Procambarus virginalis*, which was first observed in markets in Madagascar around 2005 where it continues to be sold as a valuable food source. *P. virginalis* rapidly became invasive, impacting endemic freshwater biodiversity, rice agriculture and local freshwater fisheries (Andriantsoa et al. 2020). In addition, many IAS can spread across the African continent following their accidental introductions by humans. Some illustrative examples include the fall armyworm, *Spodoptera frugiperda*, a voracious polyphagous pest from tropical and subtropical regions of the Americas which threatens several important crops in Western, Central and Southern Africa (Goergen et al. 2016); the house mouse (*Mus musculus domesticus*), black rat (*Rattus rattus*) and brown rat (*Rattus norvegicus*) that were introduced through seaports and can dramatically decrease the indigenous rodent fauna, increase zoonotic risk and impact food security for human populations (Diagne et al. 2017; Dossou et al. 2020); and the Asian mosquito (*Anopheles stephensi*), which represents a new malaria vector for about 126 million urban dwellers across Africa (Sinka et al. 2020).

These invasions do not show any signs of abatement in the near future (Seebens et al. 2017), and many species that are not yet recorded in Africa are predicted to invade the continent over the coming decades (Faulkner et al. 2020). Consequently, since invasions are a transboundary issue, managing invasions should be prioritized on this continent in a regional manner (Faulkner et al. 2017; Faulkner et al. 2020). However, despite the increasing knowledge of IAS distribution and impacts, biological invasions still remain relatively poorly studied in developing countries (Nghiem et al. 2013), particularly in Africa – with the exception of South Africa (van Wilgen et al. 2020). Yet, this information is crucial for identifying priorities, designing efficient policies and implementing optimal management actions at relevant scales (Latombe et al. 2017; Pagad et al. 2018). As such, understanding the magnitude of impacts of IAS across Africa is a critical step towards efficient mitigation.

Economic aspects are critical in this context, especially regarding the limited economic capacity of most African countries to counteract invasions. Indeed, information on the economic impacts of biological invasions is important at several levels, especially for (*i*) increasing societal awareness on the substantial losses caused by invasions and compelling policymakers to act on the short- and long-terms against the introduction, proliferation and spread of harmful invaders, (*ii*) designing efficient policies and implementing evidence-based decisions through both prioritization of targeted IAS and/or susceptible areas as well as pre-evaluation of measures (e.g. cost-efficiency analyses) and (*iii*) ensuring sustainable management actions according to the economic capacities of countries/regions (Born et al. 2005; Larson et al. 2011; Dana et al. 2013; Caffrey et al. 2014; Diagne et al. 2021). A consistent, broad-scale approach using economic impact data is essential for both research and management purposes (Diagne et al. 2020a). This can contribute to the development of collaborative programs and coordinated responses among countries. However, to the best of our knowledge, the African continent lacks such cost-synthesis. Until now, regional- or continental-scale data relating to the economic impact of invaders in Africa were only available for relatively few species (e.g. *Tuta absoluta*; Rwomushana et al. 2019), sectors (e.g., smallholder livelihoods; Pratt et al. 2017) and regions (South Africa; Wild 2018).

The recent advent of the "InvaCost" database (Diagne et al. 2020b) allowed us to address this limitation by providing the first general overview on the economic costs of biological invasions across the African continent. "InvaCost" is the first comprehensive compilation of the documented economic costs of IAS globally. This freely accessible and updatable catalog contains cost estimates extracted from scientific peer-reviewed articles and grey-literature sources, and covers most taxa, geographical regions and activity sectors worldwide. It thus provides unprecedented opportunities to comprehensively assess and understand the economic impacts of invasions at multiple spatial scales, particularly for Africa where such knowledge is usually poor and highly fragmented (Diagne et al. 2021). Here, we aim to (*i*) provide the first state-of-the-art study on the economic costs of biological invasions in Africa, (*ii*) decipher how these costs are distributed over space, time, taxa, activity sectors and types of costs, and (*iii*) discuss the implications of these costs for invasion research and management in African countries.

Materials and methods

Original data

We relied on cost data recorded in the "InvaCost" database, which is the most up-to-date, comprehensive, and harmonized compilation and description of economic cost estimates associated with biological invasions worldwide (Diagne et al. 2020b). "InvaCost" has been generated following a systematic, standardized methodology to collect information from scientific articles, grey literature, stakeholders and expert elicitation. Each source was checked for relevance and the cost information was collated and standardized to a common and up-to-date currency in the database (i.e. 2017 US dollars). Each cost entry was depicted by a range of descriptive fields pertaining to the original source (e.g. title, authors and publication year of the reporting document), spatial extent (e.g. location and spatial scale), temporal coverage (e.g. time range and period of estimation), estimation methodology (e.g. method reliability and acquisition method) and the nature of cost (e.g. type of cost and impacted sector). All methodological procedures and details for data search (e.g. literature review), collation (e.g. cost standardization), validation (e.g. method repeatability) and improvement (i.e. corrections and inputs) are described elsewhere (Diagne et al. 2020b, 2020c). This updatable and publicly available data resource provides an essential basis for worldwide research and policymaking targeting IAS (Diagne et al. 2020a).

Starting dataset

To get the most complete and up-to-date dataset of the reported economic costs attributable to biological invasions in Africa for the last fifty years (1970–2020), we used the most recent version of the "InvaCost" database (version 3.0; Diagne et al. 2020c). This updated database integrates and refines cost information (9,823 cost entries; 64 descriptive fields) from two other repositories generated in the frame of the broader "InvaCost" initiative (Diagne et al. 2020a), and which include cost data collected from multiple sources and languages throughout the world (Angulo et al. 2021). Using this latest version of "InvaCost" allows us to limit potential gaps in existing literature as well as common language biases due to the exclusive consideration of English in research (Haddaway et al. 2015; Konno et al. 2020; Angulo et al. 2021). Using successive filters in the descriptive fields of the database (i.e. "Geographic region" and "Country" columns), we identified and then extracted all economic costs which were exclusively associated with African countries. Therefore, any cost entry that concerned non-African territories located within African regions (e.g. La Reunion Island) was not considered. We carefully checked the data to correct or remove any potential mistakes or duplicated cost entries. Our final database (hereafter called "starting dataset") consisted of 696 cost entries (Suppl. material 1).

Expanded dataset

We homogenized our "starting dataset" so that each cost entry – realized over a single year, a period of less than a year, or a cost reoccurring over a series of years – corresponds to a single-year estimate, which is repeated over the number of years during which the cost occurred. For this purpose, we used the "expandYearlyCosts" function from the "invacost" package (Leroy et al. 2020) in R version 4.0.2 (R Core Team 2019). This operation allowed us to expand each cost entry over its actual or estimated duration time, which was derived from the difference between the first year ("Probable starting year adjusted" column) and the last year ("Probable ending year adjusted" column) of the recorded cost. Consequently, this process removed any cost entries occurring over an unspecified time period in the database. Nonetheless, this step was necessary to ensure accurate estimations of the cumulative and mean annual costs of invasions over time. The expanded version of our "starting dataset" contained 4,259 cost entries (Suppl. material 1).

Conservative subset

To ensure a realistic and conservative synthesis of cost estimates reported for Africa, we applied two successive filters to this "starting dataset" (Suppl. material 2). The filters used were based on the categories listed for a set of descriptive fields in the "starting dataset" (see Suppl. material 3 for a detailed description of the fields). First, we kept only “observed” costs (rather than “potential” costs, under the "Implementation" column); second, we retained only economic estimates classified as “high” reliability (rather than “low” reliability, under the "Method reliability" column). Subsequently, all cost estimates for the year 2020 were excluded since these estimates were “potential” and/or of “low” reliability. Our final dataset (hereafter referred to as the "conservative subset") contained 2,302 cost entries between 1970 and 2019 (Suppl. material 4).

Categorization of cost data

We categorized the cost data according to different descriptive fields (hereafter called “descriptors”) in our datasets. First, we grouped countries into the five geographical regions defined by the United Nations geoscheme for Africa (available at https://unstats.un.org/): “Western Africa”, “Southern Africa”, “Northern Africa”, “Middle Africa”, and “Eastern Africa” (the latter also includes countries in the Indian Ocean) (Suppl. material 5). Second, we considered information on the typology of the costs ("Type of cost merged" column) that groups each cost estimate under “damage” (i.e. economic losses due to direct and/or indirect impacts of invaders, such as yield losses, damage repair, medical care, infrastructure alteration or income reduction); “management” (i.e. economic resources allocated to actions that aim at avoiding the invasion or dealing with more or less established invaders, such as prevention, control, research, eradication, education or mitigation policies); or “mixed” (i.e. when a single cost simultaneously includes both “damage” and “management” components) category (Suppl. material 6). Third, we determined which sectors were impacted by the reported costs (using information from the "Impacted sector" column); cost estimates that were not allocated exclusively to a single sector were classified under the “mixed” category. Fourth, economically harmful species were classified into different major ‘organism types’ based on information from the "Kingdom", "Phylum", "Class" and "Environment" columns: “Animalia” (i.e. insects, mammals, birds), “Plantae” (i.e. aquatic plants, terrestrial plants, semi-aquatic plants), and “Virus”. For each descriptor, cost estimates that could not be unambiguously and exclusively assigned to one category were labelled as “diverse/unspecified”.

Data analyses

Our purpose was to draw a complete, as well as a robust picture of the cost of biological invasions throughout the African continent. We used the following R packages - ggplot2 (v.3.3.2, Wickham 2011), rnaturalearthdata (v.0.1.0, South 2017) and networkD3 (v.0.4, Allaire et al. 2017) – to generate an array of graphical representations for each descriptor of interest.

First, we used the "starting dataset" to describe the full cost information that was available. To do this, we investigated how individual cost estimates and their source materials (i.e. peer-reviewed articles and grey literature) were distributed over time. We focused on both the number of cost estimates and the total costs accumulated between 1970 and 2020. The latter was obtained by summing all cost estimates provided in the "cost estimate per year 2017 exchange rate" column of the expanded version of the "starting dataset" (Suppl. material 1). We systematically distinguished the proportions of the cost estimates that were of “high” versus “low” reliability, as well as those that were actually realized (i.e. “observed”) or just merely predicted (“potential”).

Second, we used the "conservative subset" to investigate how the cost amounts were distributed across geographic regions, types of costs, impacted sectors and taxonomic groups for the period 1970–2019. Finally, we investigated the trend of costs over time using two strategies.

The first strategy included an estimation of both the cumulative costs incurred between 1970 and 2020 (i.e. the sum of all cost estimates provided in the "cost estimate per year 2017 exchange rate" column of the expanded subset; Suppl. material 4) and the mean cost amount for each decade over the same period (i.e. obtained by dividing the total cost of each decade by ten years).

The second strategy consisted of modelling the long-term trends in economic costs of invasions by fitting models of annual costs as a function of time. Indeed, a reliable estimation of the average annual costs over time should take into account (*i*) the dynamic nature of costs, (*ii*) the time lags between the real occurrence of the costs and their reporting in the literature (called ‘publication delay’ hereafter), (*iii*) the heteroscedastic and temporally auto-correlated nature of cost data, and (*iv*) the effects of potential outliers in the cost estimates. For this purpose, we implemented the "costTrendOverTime" function ("invacost" package; Leroy et al. 2020) on the $\log_{10}$-transformed cost estimates per year, which allowed modelling the trend of costs over time with a range of linear and non-linear modelling techniques while enabling a comparison of the respective outputs of all models generated. As statistical intricacies inherent to econometric data did not allow for a priori identification of the most relevant modelling technique to apply, we relied on ‘ordinary least squares regressions’ (linear, quadratic), ‘robust regressions’ (linear, quadratic - R package "robustbase", Maechler 2020), ‘multiple additive regression splines’ (MARS, R package earth, Milborrow 2017), ‘generalised additive models’ (GAM, R package "mgcv", Wood and Wood 2015) and ‘quantile regressions’ (quantiles 0.1, 0.5, 0.9, R package "quantreg", Koenker 2019). To optimize model performance, all models were calibrated following a robust linear regression using cost data as the response variable and time as a predictor, which allowed to identify obvious outliers in the years of cost occurrence. To account for potential data incompleteness due to the ‘publication delay’, we excluded from model calibration all cost estimates from 2014 onwards because they constituted obvious outliers with a sudden drop of two orders of magnitude. We confirmed these outliers by investigating robust regressions calibrated on all data, which had set the weights of years above 2013 near to zero (Suppl. material 7). Model discussion was based on the assessment of the predictive performance across models (Root-mean-square deviation, RMSE) as well as the goodness-of-fit measure (variance explained). Moreover, combining these diverse modelling procedures offers strong support for the observed temporal trends and provides consistent model outcomes. As this approach is highly data-demanding, we only applied it to the African continent without disentangling types of costs, regions, sectors or taxonomic groups.

Results

Overview of cost data available in the starting dataset

During the 1970–2020 period, economic costs associated with biological invasions in Africa were obtained separately for 33 countries (i.e. 4 from Middle Africa, 3 from Northern Africa, 3 from Southern Africa, 10 from Western Africa, and 13 from Eastern Africa; see Suppl. material 5 for further details). The expanded dataset contained 4,259 cost estimates collected from 103 source documents from both the grey (n = 39) and scientific peer-reviewed (n = 64) documents (Suppl. material 1). Except for sixteen documents that were written in French, all reporting documents used English as the primary language. This shows a clear language bias despite all efforts made for collecting cost information reported in 15 languages in the updated "InvaCost" database (version 3.0; Diagne et al. 2020c). We also showed that since the 1970s, the number of both the cost estimates and source documents steadily increased over the years, along with the total estimated cost amounts (Figure 1). This is despite a slight decline in the number of cost estimates over the last decade, which might be the result of a time lag between the occurrence of the most recent costs and when they were reported in the literature (Figure 1).

About 86% of the cost entries (n = 3,653) collated were only incurred in Southern Africa (Table 1; Figure 2). Far behind, Eastern and Western Africa were the most represented regions, with 287 (7%) and 155 (3%) cost estimates, respectively. These patterns are influenced by a small number of countries with cost entries in each region (Suppl. material 5). Within Southern Africa, South Africa reported the majority of costs (together, the two other countries within this region, Lesotho and Swaziland, were only associated with 33 of the 3,653 cost entries recorded); more than 60% of the costs recorded in Eastern Africa were associated with three of the ten reporting countries (i.e. Kenya, n = 71; Uganda, n = 48; Tanzania, n = 53); and costs recorded in Western Africa mostly concern Benin (n = 78). The other regions harbored fewer than 15 cost entries, with Middle Africa reporting the smallest number of cost data (n = 6). Cost estimates associated simultaneously with two or more countries belonging to (at

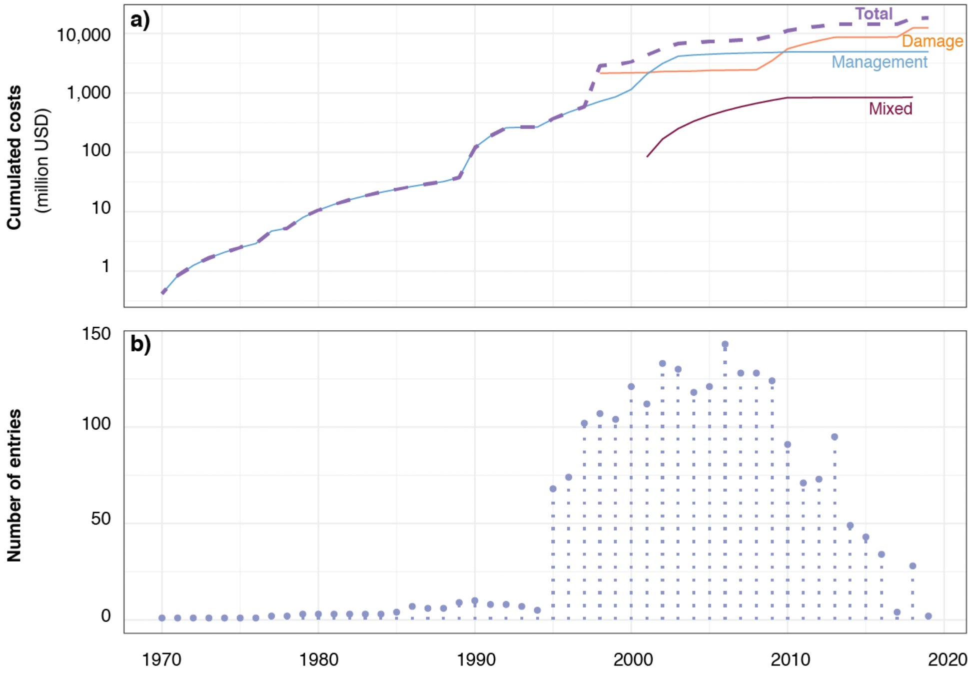

Figure 1. Distribution of cost estimates over time represented by **a** the cumulative cost amounts and **b** the number of cost entries per year between 1970 and 2019. We considered the expanded version of the *starting dataset*. In **a** the dashed line corresponds to the total amounts over the complete period, while the other lines correspond to the amounts of damage losses, management expenditures and mixed costs (i.e. when costs could not be exclusively associated with 'damage' or 'management' type).

least) two distinct regions (i.e. "diverse/unspecified" category) consisted of 146 cost entries (3%) in the "starting dataset".

Except for Southern Africa and "diverse/unspecified" regions, more than two thirds of the recorded cost estimates were considered as having been empirically observed in each region (Figure 2; Suppl. material 8). Conversely for Southern Africa and "diverse/unspecified" regions, respectively about 42% and 66% of the reported data comprised potential costs. Given that Southern Africa is the most represented region in our dataset, this means that a substantial portion of the cost estimates recorded throughout the continent (n = 1,807 out of 4,259) were derived from extrapolation or modelling approaches rather than true observations (Figure 2; Suppl. material 8). Finally, the reported cost data mostly exhibited a high degree of method reliability (Figure 2; Suppl. material 8). Indeed, the proportion of cost entries resulting from highly reliable cost estimations range between 75% (for Northern Africa) and 98% (for Eastern Africa), suggesting that most cost estimates were obtained from relevant estimation methodologies (Figure 2; Suppl. material 8).

Considering all cost entries in our "starting dataset", the accumulated cost of IAS in Africa reached a total of US$ 78.9 billion between 1970 and 2020 (see Table 1 for a detailed cost breakdown by region, taxa, sector, and type of cost).

Table 1. Quantitative summary of the cost data and estimates considered in this study for the African continent and each geographic region. Total cumulative costs (between 1970 and 2020) are provided in 2017-equivalent US$ million using both the *starting dataset* (*'Full' cost*) and *conservative subset* (*'Robust' cost*). Impacted sectors and type of cost are defined in the Suppl. material 3 (fields *Impacted sectors* and *Type of cost merged*). *N* represents the number of cost entries in the datasets (i.e. *starting dataset* and *conservative subset*); in the *Category* column, N corresponds to the number of original and expanded cost entries in the datasets considered – respectively the *starting dataset* and the *conservative subset*.

Descriptive field	Category	Africa		Eastern Africa		Middle Africa		Northern Africa		Southern Africa		Western Africa		Mixed	
		Full' cost (N= 4,259)	*Robust' cost (N= 2,302)*	*Full' cost (N=287)*	*Robust' cost (N=169)*	*Full' cost (N=6)*	*Robust' cost (N=3)*	*Full' cost (N=12)*	*Robust' cost (N=5)*	*Full' cost (N=3,653)*	*Robust' cost (N=1,980)*	*Full' cost (N=155)*	*Robust' cost (N=98)*	*Full' cost (N=146)*	*Robust' cost (N=47)*
Impacted sector	Agriculture	34209,41	8772,82	7189,47	6771,03	267,96	267,96	147,16	0,00	24,00	–	1740,11	1733,83	24840,72	–
	Authorities-Stakeholders	20710,11	4406,07	50,50	28,64	0,10	0,01	593,04	196,53	19028,77	3701,59	460,45	401,74	577,24	77,56
	Environment	17029,18	3277,03	–	–	–	–	–	–	17029,18	3277,03	–	–	–	–
	Fishery	0,36	0,36	–	–	–	–	–	–	–	–	0,36	0,36	–	–
	Forestry	22,29	0,10	–	–	–	–	–	–	0,11	0,10	–	–	22,19	–
	Health	2,20	2,20	2,20	2,20	–	–	–	–	–	–	–	–	–	–
	Mixed	6974,88	1744,35	613,83	10,09	1,80	–	–	–	1149,93	856,69	–	–	5209,33	877,56
	Public and social welfare	0,43	0,14	0,42	0,14	–	–	–	–	–	–	0,00	0,00	–	–
Type of cost	Damage_costs	56739,68	12418,47	7797,90	6773,37	269,76	267,96	147,16	0,00	17245,33	3216,81	2122,70	2116,41	29156,84	43,93
	Management_costs	21280,73	4937,90	45,47	25,68	0,10	0,01	593,04	196,53	19986,66	4618,62	78,23	19,52	577,24	77,56
	Mixed_costs	928,45	846,69	13,05	13,05	–	–	–	–	–	–	–	–	915,40	833,63
Taxon	Animalia	39016,50	7954,63	5666,22	4829,41	269,76	267,96	740,19	196,53	2,56	–	1813,99	1749,55	30523,78	911,19
	Plantae	38093,54	8636,73	435,20	373,05	0,10	0,01	–	–	37227,38	7833,37	386,94	386,38	43,93	43,93
	Viruses	1754,93	1609,57	1754,93	1609,57	–	–	–	–	–	–	–	–	–	–
	Diverse/Unspecified	83,89	2,13	0,07	0,07	–	–	–	–	2,05	2,05	–	–	81,76	–
Total costs for Africa and each region		78948,86	18203,06	7856,42	6812,10	269,86	267,96	740,19	196,53	37231,99	7835,42	2200,92	2135,93	30649,48	955,12

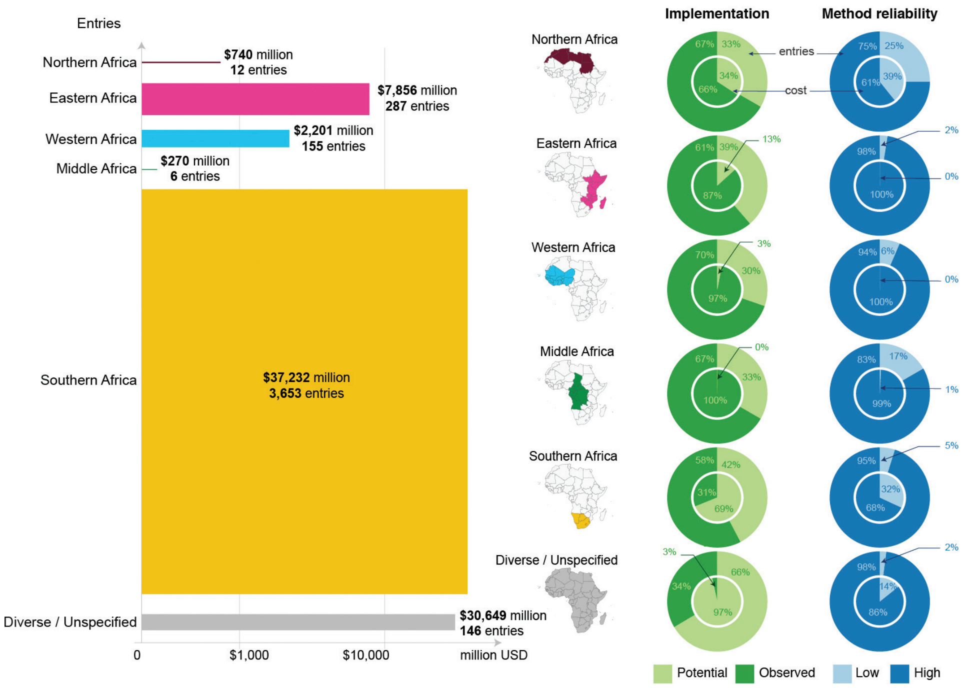

Figure 2. Typology and distribution of costs (number and estimates) recorded in the *starting dataset* according to their reliability ("high" *versus* "low") and their implementation ("potential" *versus* "observed"). We present both cost figures (total cumulative costs in 2017-equivalent US$ million for 1970–2019) and number of expanded cost entries as well as their specific proportion for each official region. *Implementation* states — at the time of the estimation — whether the reported cost was actually "observed" (i.e., cost actually incurred) or "potential" (i.e. not incurred but expected cost). *Method reliability* assesses the methodological approach used for cost estimation as of (*i*) "high" reliability if either provided by officially pre-assessed materials (peer-reviewed articles and official reports) or the estimation method was documented, repeatable and/or traceable if provided by other grey literature, or (*ii*) "low" reliability if not.

Synthesis of the cost estimates from the conservative subset

Biological invasions were estimated to cost a minimum of US$ 18.2 billion in Africa over the period 1970–2019 (Figure 3; Table 1). These conservative costs were not equally distributed across regions, between types of costs, or among sectors and taxa (Table 1).

Geographical regions

Recorded economic costs were spread unevenly across regions, with Southern Africa and Eastern Africa exhibiting the largest estimates (i.e. US$ 7.8 billion and US$ 6.8 billion, respectively). Apart from these two regions, Western Africa was the only region for which total costs exceeded US$ 1 billion (i.e. US$ 2.1 billion). The lowest reported costs included Middle and Northern Africa with US$ 267 million and US$ 196 million, respectively. Again, these cost estimates were mostly driven by a limited number of reporting countries (Suppl. material 5). When considering the reports of Southern Africa, Northern Africa and "diverse/unspecified" regions using the "conservative subset", the total costs were respectively four, twenty-five and thirty times lower compared with those obtained from the "starting dataset". This was mainly due to Southern Africa and 'diverse/unspecified' regions harboring a high proportion of potential costs, and Northern Africa reporting a substantial portion (almost 40%) of low-reliability cost estimates (Figure 2). Conversely, the total costs reported from the other regions decreased by less than 10% following the filtering steps, indicating that most of the costs reported in these areas were actually observed as well as of a high level of reliability.

Type of costs

The majority of cost estimates reported throughout the continent were associated with "damage" costs (US$ 12.4 billion) rather than "management" costs (US$ 4.9 billion) (Table 1). This pattern was consistent across regions and was even exacerbated for Eastern, Central and Western Africa where "damage" costs represented at least 99% of the recorded costs in each region (Figure 3; Suppl. material 5; see Suppl. material 9 for country-specific details). The single exception was Northern Africa for which the economic expenditures were exclusively associated with "management" costs. "Mixed" costs (US$ 846.6 million) were found exclusively and dominantly for "diverse/unspecified" regions, suggesting that costs with low spatial resolution may also have less precise and/or detailed information on the type of costs incurred by invaders.

Impacted sectors

Invasions had the greatest impacts on agriculture with, respectively, about 99% of the costs reported from Eastern and Middle Africa (Figure 3; Table 1). About 80% of the costs reported from Western Africa are also attributable to this economic sector (Figure 3; Table 1). Conversely, economic expenditures by authorities and stakeholders to manage invasions and/or to mitigate their impacts represents almost all costs incurred in Northern Africa and the greater proportion (about one third) of costs reported in Southern Africa (Figure 3; Table 1). Surprisingly, some sectors that we expected to be impacted were under-represented and/or spatially restricted. Indeed, environmental costs were only reported in Southern Africa and represent less than 15% of the total costs for this given region while marginal costs were found for fisheries (US$ 0.36 million from Western Africa), forestry (US$ 0.10 million from Southern Africa), social welfare (US$ 0.14 million from Eastern and Western Africa) and health (US$ 2.19 million from Eastern Africa) (Table 1). Moreover, we found that costs collated from "diverse/unspecified" regions were mostly related to a range of sectors concomitantly, rather than a specific single sector (i.e. about 90% of the total amounts; Figure 3). Overall, these regional patterns were also reflected at the national scale (Suppl. material 9).

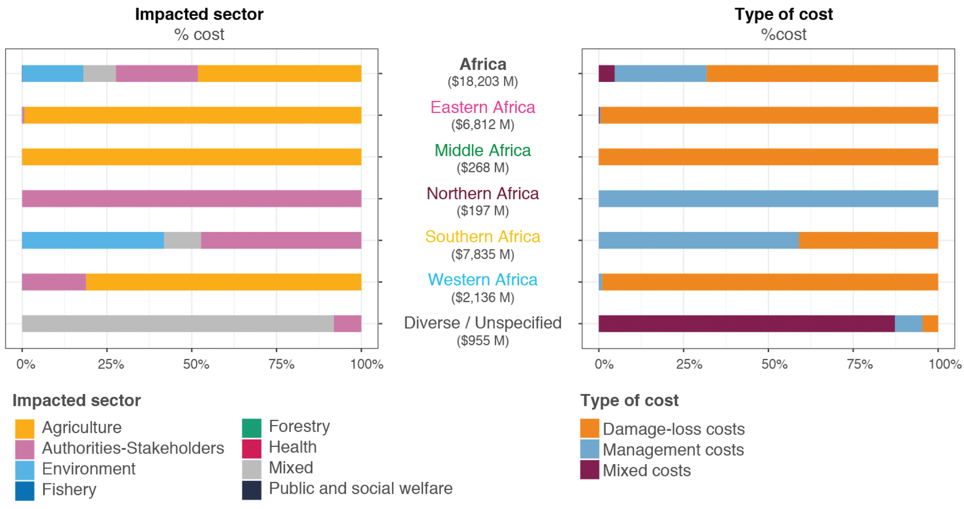

Figure 3. Distribution of reliable observed costs (using the *conservative subset*) following the impacted sectors and type of cost for each geographic region. For both impacted sectors and type of cost, we considered the definition and categories detailed in the Suppl. material 3 (see fields Impacted sectors and Type of cost merged).

Taxonomic groups

Cost estimates were reported for various animals (n = 16 species; US$ 7.9 billion) and plants (n = 45; US$ 8.6 billion), and one virus (US$ 1.6 billion) (Figure 4; Table 1; Suppl. material 10). Most of the recorded economic costs were driven by very few taxa, among which three of the five costliest species included insect pests: the spotted stem borer (*Chilo partellus*; US$ 2.6 billion), the fall armyworm (*Spodoptera frugiperda*; US$ 2,9 billion) and the tomato leafminer (*Tuta absoluta*; US$ 1,15 billion). The two other taxa contributing to the top five costliest species include the virus responsible for maize lethal necrosis (US$ 1.6 billion), attacking agricultural production in Eastern Africa (Pratt et al. 2017), and *Acacia* species (US$ 3.4 billion) which were introduced from Australia in the 19th century and now have strong environmental impacts (e.g. negative impacts on water availability) and management costs in Southern Africa (De Wit et al. 2001).

Temporal dynamics

The costs of biological invasions steadily increased over the period 1970–2019. During this period, invasions cost on average US$ 303 million per year and the mean cost exponentially increased over decades (Figure 5a). The mean cost in the current decade (US$ 919 million) is 310 times higher than those estimated in the 1980s (US$ 2.97 million). All models converged in their results and showed a high goodness-of-fit regarding the cost data (Figure 5b). Indeed, the variance explained by all models exceeds 85% with similar RMSE values; Suppl. material 11). Additionally, all modelling techniques confirmed that costs continuously increased each year since 1970 and there was

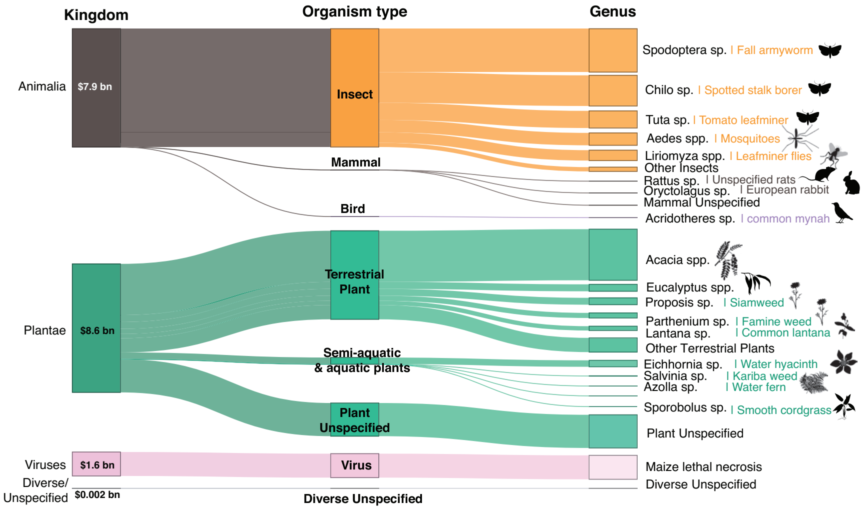

Figure 4. Distribution of the cost amounts (in 2017-equivalent US$ millions) among species recorded in the *conservative subset*. The species are successively grouped into kingdom, organism type and genus. The size of the bars (rectangles) is proportional to the cost value associated with either the kingdom, organism type or genus. For example, we can see that costs associated with the kingdom Animalia are equal to US$11.6 billion. Animalia comprises the organism groups insect, mammal and bird, so the combined height of the rectangles representing costs for insect, mammal and bird is equal to the height of the bar representing the Animalia Kingdom. Insects contribute the most to costs associated with Animalia and amongst insects, the genus Spodoptera sp. is the most costly. Icons are from (http://phylopic.org/).

no sign of abatement of cost amounts in the most recent years. We found an 8-fold increase in the mean cost each decade. Therefore, we estimated that the average annual cost of invasions in 2019 could range between US$ 2.6 billion (predicted by the GAM) and US$ 8.6 billion (predicted by the linear robust regression).

Discussion

Massive economic toll

Our findings undoubtedly illustrate that invasions incur substantial costs to national African economies, most of them being vulnerable and already weak (Lekunze 2020). The reported financial burden accumulated to a conservative total of approximately US$ 18.9 billion (annual average of US$ 303 million) between 1970 and 2019, reaching an estimated annual average of US$ 2.6–8.6 billion in 2019. However, these costs could seem relatively low compared with those from other continents such as North America (Crystal-Ornelas et al., submitted in the current issue), Europe (Haubrock et al., submitted in the current issue) or Asia (Liu et al., submitted in the current issue). On the one hand, this discrepancy likely reflects the strong geographical imbalance in research intensity and financial capacities (Early et al. 2016; Sooryamoorthy 2018)

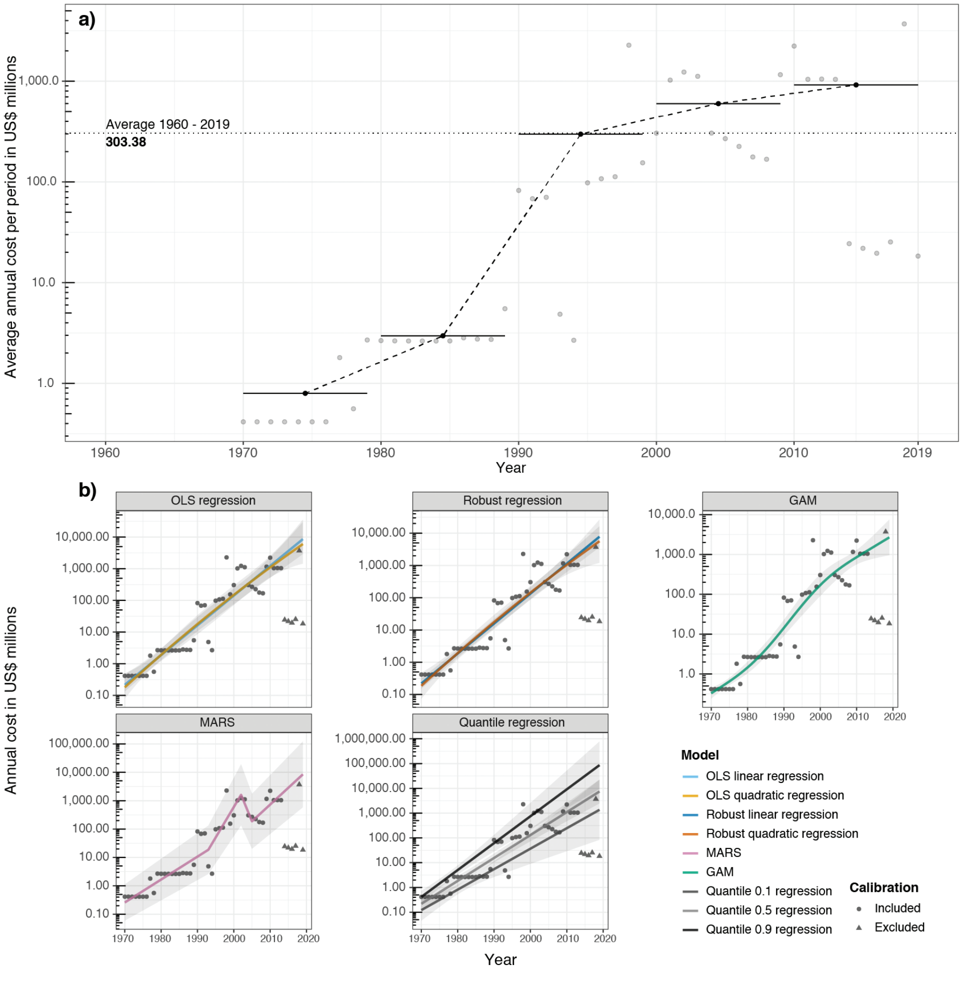

Figure 5. Temporal trends (1970–2019) of costs (in 2017-equivalent US$ millions) **a** considering the actual distribution of the mean amounts provided for each decade in the *conservative subset* and **b** using model predictions (i.e. OLS: ordinary least-squares; GAM: generalized additive model; linear regression, quadratic regression, MARS: multiple adaptive regression splines) and quantile regressions. We considered models calibrated and fitted with at least 75% of cost data completeness from the dataset. We $\log_{10}$-tranformed cost estimates using information from the *cost estimate per year 2017 USD exchange rate* column in the *conservative subset*).

rather than the actual spatial distribution of the costs of invasions. Also, invasion-associated issues may not be perceived as a priority for many African countries where investments in many primary structural needs (e.g. roads, infrastructures, fight against extreme poverty, and building sustainable education and health systems) are still greatly needed (African Development Bank Group 2018; Adamjy et al. 2020). This may logically translate into reduced academic studies and operational programs on biological invasions. Accordingly, IAS were dramatically understudied in Africa compared with other parts of the world (Pysek et al. 2008) – with a notable exception being South Africa (van Wilgen et al. 2020). Moreover, wealthier or developed regions are also those with higher documented invasions and associated impacts (Bellard et al. 2016; Essl et al. 2020). In addition, the significant difference in both values of the money and price levels between areas (e.g. labor costs for similar management actions are likely cheaper in most African countries when compared with those in Europe or North America), might be contributing to increment the observed discrepancy in reported costs between Africa and other regions. Indeed, relevant monetary comparisons at macroeconomic scale require reliance on indicators such as the purchasing power parity (but see Gosh 2018), which reflects the relative purchasing power of different currencies between countries and over time. However, such reliable comparisons are still prevented by very limited information on this indicator for most countries and/or years (Diagne et al. 2020b). We therefore have to also acknowledge that some African countries invest a substantial amount of resources towards the appropriate management of invaders – as evidenced by the increasing successful control of invasive alien plants in several African countries such as South Africa and Namibia (Stafford et al. 2017). The cost estimates presented here are substantial and obviously detrimental for the African continent. An eloquent illustration comes from comparing our estimated costs with the African Union's budget (https://au.int/). In 2019, the expected minimum cost of invasions was more than three times higher than the entire budget available for this continental organization (i.e. US$ 681.5 million in 2019). Therefore, we can safely assume that our conservative estimate of invasion costs largely exceeds the actual funding capacities of the largest regional organizations that support socio-economic development in African countries. Moreover, the highest average value estimated for 2019 (US$ 8.6 billion) is greater than the individual gross domestic products of the seventeen less developed countries across the whole continent.

Increasing costs over time

Worryingly, we found that the economic costs of IAS in Africa are steadily increasing over time without any signs of slowing down, reflecting the continuous increase in the number of IAS worldwide (Seebens et al. 2017). A set of complementary reasons may explain this temporal pattern, and/or why we should not expect any deceleration in invasion costs in the years to come. First, there is a growing awareness of the impacts of invaders as well as a burgeoning interest in reporting their economic impacts along with an associated increase in management actions during recent years (Dana et al. 2013; Simberloff et al. 2013; Diagne et al. 2021). Scrutinizing our dataset reveals that while the first monetized impacts of IAS in Africa dates back to the 1970s, the first document providing IAS costs was published in 1991 (Suppl. material 4). All cost estimates recorded between 1970 and 1985 stemmed from only three sources which reported costs for South Africa and Indian Ocean islands, suggesting that the research interest in other African regions has been growing rapidly over the past few decades. Second, the ongoing globalization and climate change synergistically accelerate the opportunities and rate of species invasions almost everywhere, and Africa should be no exception (Seebens et al. 2015; Faulkner et al. 2020). Third, Africa has been shown to be among the key areas at risk for future invasions by at least 86 of 100 of the world's worst invasive species, with most of these invasions likely to cause severe socio-economic impacts (Faulkner et al. 2020). The role of the socio-economic changes faced by most African areas is undebatable in this particular context. In particular, Africa is currently experiencing a rapid rate of urbanization that is only second to Asia, with an urban population that may at least triple between 2010 and 2050 to reach 1.339 billion people (Matamanda and Nel 2020). Evolutionary socio-ecological features associated with this urbanization process can promote invasion success (Klotz and Kühn 2010; Sinka et al. 2020). For example, the dense and various networks of exchanges of goods and people can create repeated opportunities for the introduction of a wide range of exotic species and a shift towards biotic and abiotic conditions can greatly favor opportunistic, adaptable and prolific species. In that sense, empirical evidence supporting this process was recently provided for different invasive taxa, including rodents in Western African countries (Garba et al. 2014; Hima et al. 2019) and cultivated ornamental plants in South Africa (Potgieter et al. 2020). Unfortunately, these examples constitute only a few among several others which demonstrates the changing context-related spread of harmful invaders throughout the continent (Early et al. 2016). The increasing costs reported here sound alarming, yet there are several reasons which can explain why these costs are likely much higher than we estimated.

Underestimated economic burden

A number of logistical, methodological and cost-intrinsic factors may have prevented the capture of the complete diversity – and thus the full amount – of costs. Costs can remain hidden and/or underestimated due to (*i*) the unclear status of some invasive species (Jarić et al. 2019), (*ii*) inaccessible source materials (e.g. grey literature; Adams et al. 2017), and (*iii*) methodological (e.g. inadequate extrapolations; see Jackson (2015) for a detailed synthesis) as well as ethical issues (e.g. monetary perception of ecosystem services; Meinard et al. 2016) that impair the evaluation process (Bradshaw et al. 2016; Hoffmann and Broadhurst 2016). For instance, costs from well-known economically harmful invaders could have been overlooked simply because they failed to be captured when building the "InvaCost" database (Diagne et al. 2020b, 2021). Moreover, costs are inherently complex and heterogeneous. As a consequence, misconceptions from the lack of reporting consistency in invasion science (Colautti and MacIsaac 2004; Richardson et al. 2020) likely lead to overlooking some cost estimates (Dana et al. 2013). Furthermore, we made highly conservative choices when generating our "conservative subset" in order to ensure reliable cost assessments, which led to consider only 2,302 out of 4,259 cost entries from the "starting dataset" (e.g. for some countries, such as Morocco and Angola, all costs were unreliable or potential, and were therefore discarded following our filtering procedure). More broadly, the skewed cost distribution (see below) revealed taxonomic, sectoral and geographic gaps that may contribute to our underestimations of the actual economic burden of IAS in Africa.

Geographic imbalance in the reported costs

We showed that economic costs are widely but not evenly distributed across regions. Indeed, most cost estimates were associated with a single country (i.e. South Africa), which is internationally recognized as a pioneering and frontline country for research and management in invasion science (van Wilgen et al. 2020). It has been shown that South Africa comprised about two-thirds of the quantified research effort in the field across the African continent (Pysek et al. 2008). A similar unevenness has been found in relation to aquatic invasion costs, where South Africa dominated costs reported on the African continent (Cuthbert et al. 2021). The rich history of species introductions, higher economic capacity (compared with most African countries) and long tradition of large-scale conservation actions in this country may also contribute to this trend (Foxcroft et al. 2020; van Wilgen et al. 2020). Another reason for the higher cost estimates for South Africa comes from the fact that South African studies often rely on extrapolation-based approaches to provide economic estimates of IAS impacts (van Wilgen et al. 2020). Yet, these potential cost data were filtered out of our "conservative subset", explaining why the total cost for Southern Africa significantly decreased after filtering to reach an amount comparable to costs from Eastern Africa (Table 1). The high costs reported for Eastern Africa may be – at least partially – linked to the research activity of the Centre for Agricultural Bioscience International (CABI; www.cabi.org) and work done by the United Nations Environmental Program (UNEP) which have their regional centers located in Nairobi (Kenya).

Moreover, we may expect higher costs for the other regions than those reported here. For instance, Northern Africa has 13 cost entries recorded for only five species, while 157 species are listed in the GISD for this region. Also, Western African countries are historically and contemporarily threatened by a broad variety of biological invaders which is beyond insects and plants that were mostly reported for this region. Indeed, the succession of large international seaports along coastal cities (e.g. Abidjan, Cotonou, Lagos, Dakar) and the parallel development of the extensively urbanizing corridor from Côte d'Ivoire to Nigeria (i.e. the so-called Abidjan-Lagos corridor) may greatly facilitate the introduction of several vertebrate and aquatic invertebrate invaders (Habitat 2014; Bellard et al. 2016; Hima et al. 2019). Consequently, we advocate for increasing research effort towards the economic costs of biological invasions, mainly in the understudied regions where the costs are likely to be much higher than those currently reported.

Biased costs towards agriculture

Across the African continent, most of the reported costs were mainly driven by very few taxa, among which the costliest included three insect pests: the spotted stem borer (*C. partellus*), introduced in Eastern Africa in the 1930s, is suspected to be the most serious pest of maize and sorghum in Eastern and Southern Africa (Yonow et al. 2017); the fall armyworm (*S. frugiperda*) has now been reported in 45 African countries since its first report in Western Africa in late 2016, and is a known voracious consumer of more than 80 crop species of strong nutritional and socio-economic utility (CABI 2020); the tomato leafminer (*T. absoluta*) has now invaded 41 of the 54 African countries since its introduction in Northern Africa in 2007 (Rwomushana et al. 2019). Given the broad distribution (beyond the limited spatial coverage of each of these species in the database) and biological characteristics of these invasive pests, we can safely assume that their economic impacts largely exceed the monetary costs reported here (see Eschen et al. 2021 for a recent extrapolation attempt, using information obtained from the literature and stakeholder consultations). In this study, *T. absoluta* and *S. frugiperda* were still among the five costliest IAS, together with the invasive plants *Eichhornia crassipes*, *Lantana camara* and *Prosopis juliflora*. Typically, the over-representation of agriculture in the reported costs may reflect the direct influence of economic priorities and societal realities in political and research agendas. Indeed, building sustainable agriculture for food security is a priority for most African countries and their economies sometimes strongly rely on food production (Pratt et al. 2017; Wiggins et al. 2010). Given that Africa is highly vulnerable to invasions by exotic pests (Early et al. 2016; Paini et al. 2016), it would seem logical that local authorities invest more on research in the agricultural sector, especially given the very limited economic resources of these countries to fight against invaders (Early et al. 2016; Faulkner et al. 2020).

Focusing solely on major and well documented (and often mediatized) agricultural threats may have an 'umbrella' effect on other less visible but harmful invaders for which the costs may be unsuspected or neglected. Indeed, only a small spectrum of species (about 15%) from those recognized as invading Africa in the GISD were reported here. This strongly corroborates a previous assumption that only a small portion of invaders have been economically analyzed (Aukema et al. 2011). Besides, many of the species recorded in our dataset can have a broader range of economic impacts. An eloquent example of this is provided by rodent species (e.g. *Rattus* spp. and *Mus musculus*) for which only management costs were reported here. Yet, invasive rodents are responsible for significant damage costs to humans (e.g. medical care due to zoonotic infections, losses from consumption of stored food stocks, destruction of infrastructures and electric supply networks) (Drummond 2001; Han et al. 2015), as recently illustrated in different parts of Africa (Leirs et al. 2010; Dossou et al. 2020).

Therefore, it is evident that research intensity is closely connected with societal and economic realities in African countries. Hence, strong collaborations should be established and/or amplified between scientists, authorities, various sectoral stakeholders as well as local communities to understand and deal with the multidimensional issues raised by biological invasions.

Call for integrated and concerted management efforts

Our results clearly highlight that IAS are a significant economic burden in Africa and the costs of these invasions are largely driven by damage induced by invaders. Monetary estimates associated with managing invasions were scarce and the amounts spent were essentially restricted to South Africa and North Africa. This pattern reflects a missed opportunity, since one of the rare examples we have for the entire African continent (i.e. the biological control of the cassava mealybug) suggests a benefit-cost ratio of management of 200 at minimum (Zeddies et al. 2001). If the lower investment in management is real (and not only under-reported), we hypothesize that this lower investment in management could possibly reflect a lack of awareness and/or insufficient capacities and means from national authorities and decision-makers facing invasions. Yet, invaders represent a significant shortfall for low income countries. In addition, this enormous financial toll represents only part of all the impacts incurred from invasions, which are also associated with major ecological and health issues (Kumschick et al. 2014; Ogden et al. 2019). Our findings should therefore be interpreted as an urgent call for considering invasion management as a major piece of sustainable development in these developing countries (Larson et al. 2011; Shackleton et al. 2017), in parallel with many of the Sustainable Development Goals defined by the United Nations and which serve as political, socio-economic and ethical guidelines globally (Sach et al. 2019).

We argue that efficient strategies towards management require cross-disciplinary and cross-sectoral efforts within and between scientists, decision-makers, stakeholders and civil society (Courchamp et al. 2017; Vaz et al. 2017; Richardson et al. 2020). Indeed, if research is necessary to produce knowledge about origin, impacts and spread of invasive species, a supportive political environment is critical to develop and implement long-term policies in Africa (Evans et al. 2018; Adamjy et al. 2020). Moreover, it has been shown that insufficient appreciation of socio-political context, non-existent or perfunctory public and community engagement, as well as unidirectional communications were associated with conflictual invasive species management (Crowley et al. 2017). Since an invasive species can be viewed as detrimental, neutral, or even beneficial in society, people who benefit from IAS may differ from those who suffer the costs (Estévez et al. 2015; Novoa et al. 2016b; Adamjy et al. 2020). As such, applying principles and concepts of sustainability science to invasion research and management should represent a key opportunity within the African context (Gasparatos et al. 2017; Tortell 2020). In addition, scientists and stakeholders need to engage in a joint paradigm for the concerted implementation of context-adapted policies and concerted implementation of management measures at relevant scales (Novoa et al. 2018).

The adoption and implementation of biosecurity measures appear particularly relevant for African countries where economic capacities are often limited. This is particularly true since many invaders introduced from other continents are also spreading within Africa in unpredictable directions (Faulkner et al. 2017; Keller and Kumschick 2017). The ultimate objective should be to act against invaders before they are introduced or become widely established, since controlling widespread invasions is often impossible or may require a high amount of resources. Furthermore, these actions should be applied at regional scales to balance expenditures and improve efficiency of actions (Faulkner et al. 2020). To date, such examples of regional cooperation are still scarce across the continent and the few attempts are restricted to South Africa (e.g. Shackleton et al. 2017). Our findings stress the need for integrating and/or reinforcing the place of biological invasions in the official agendas of African regional organizations.

Conclusion

Our study provides the first comprehensive overview of the reported economic costs of biological invasions in Africa over the last fifty years. We showed that invasions represent a massive, yet highly underestimated economic burden for African countries, and their reported costs are exponentially increasing over time. We also highlighted crucial, large gaps in the current knowledge on invasion costs that still need to be bridged with more active and widespread research and management across the continent. The cost figures presented in this paper should be seen as a snapshot of the cost information currently available in the updatable "InvaCost" database, rather than definitive cost values (and temporal/spatial distribution of costs). We consider this work a sound basis for improving further research on this topic and envision future updates for this first state-of-the-art synthesis of the economic costs of invasions in Africa. Finally, our study provides support for developing and implementing biosecurity measures as well as integrated post-invasion management actions at both national and regional levels. Taking into account the complex societal and economic realities of African countries, the currently neglected problem of invasions should be dealt with using holistic and sustainable approaches. Indeed, beyond their economic impacts, invasions also have substantial impacts on biodiversity, human health and food security. Therefore, we advocate for (*i*) an increase in societal awareness on biological invasions through improved science-society interactions on this topic and (*ii*) the systematic inclusion of invasion costs in the development of regulations and actions targeting invasive species in Africa.

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All data used in this study were made fully accessible as suppl. materials (Suppl. material 1: Suppl. material 4).

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Supplementary material 1

Starting dataset considered in this study

Authors: Christophe Diagne, Anna J. Turbelin, Desika Moodley, Ana Novoa, Boris Leroy, Elena Angulo, Tasnime Adamjy, Cheikh A. K. M. Dia, Ahmed Taheri, Justice Tambo, Gauthier Dobigny, Franck Courchamp

Data type: database

Explanation note: This database results from the combination of data collated in the "InvaCost" database (Diagne et al. 2020b) and two other complementary databases available at https://doi.org/10.6084/m9.figshare.12928145.v1 and https://doi.org/10.6084/m9.figshare.12928136. The first spreadsheet (called "Basic data") contains the complete database focusing on cost data exclusively associated with the African continent. The second spreadsheet (called "Expanded data") contains the expanded version of the complete database.

Link: https://doi.org/10.3897/neobiota.67.59132.suppl1

Supplementary material 2

Data collection and filtering processes

Authors: Christophe Diagne, Anna J. Turbelin, Desika Moodley, Ana Novoa, Boris Leroy, Elena Angulo, Tasnime Adamjy, Cheikh A. K. M. Dia, Ahmed Taheri, Justice Tambo, Gauthier Dobigny, Franck Courchamp

Data type: database

Explanation note: (a) Collection of cost information from the version 3.0 of "InvaCost"; (b) extraction of relevant data using the "Geographic region" and "Country" fields to obtain the "starting dataset"; (c) homogenization of cost entries to cost estimates per year expanded over time and (d) selection of the most "conservative subset" using the "Implementation" and "Reliability" variables.

Link: https://doi.org/10.3897/neobiota.67.59132.suppl2

Supplementary material 3

Summary of the descriptive columns of the database used in this study (from Diagne et al. 2020c)

Authors: Christophe Diagne, Anna J. Turbelin, Desika Moodley, Ana Novoa, Boris Leroy, Elena Angulo, Tasnime Adamjy, Cheikh A. K. M. Dia, Ahmed Taheri, Justice Tambo, Gauthier Dobigny, Franck Courchamp

Data type: database

Explanation note: The different columns (i.e. descriptive variables) are italicized and presented in alphabetical order. The categories used for each descriptive variable are put in bold. All fields actually considered in our study are marked with an asterisk.

Link: https://doi.org/10.3897/neobiota.67.59132.suppl3

Supplementary material 4

Conservative subset obtained following specific filtering steps applied to the starting dataset

Authors: Christophe Diagne, Anna J. Turbelin, Desika Moodley, Ana Novoa, Boris Leroy, Elena Angulo, Tasnime Adamjy, Cheikh A. K. M. Dia, Ahmed Taheri, Justice Tambo, Gauthier Dobigny, Franck Courchamp

Data type: database

Explanation note: This dataset only contains estimates that are considered as actually realized and perceived as of high reliability (based on the type of publication and method of estimation). The first spreadsheet (called "Basic data") contains the complete subset focusing on cost data exclusively associated with the African continent. The second spreadsheet (called "Expanded data") contains the expanded version of the complete subset.

Link: https://doi.org/10.3897/neobiota.67.59132.suppl4

Supplementary material 5

Quantitative summary of the cost data and estimates

Authors: Christophe Diagne, Anna J. Turbelin, Desika Moodley, Ana Novoa, Boris Leroy, Elena Angulo, Tasnime Adamjy, Cheikh A. K. M. Dia, Ahmed Taheri, Justice Tambo, Gauthier Dobigny, Franck Courchamp

Data type: database

Explanation note: Quantitative summary of the cost data and estimates for each African country recorded in the "starting dataset" and the "conservative subset" according to their perceived level of reliability (“high” versus “low”) and implementation (“observed” versus “potential”). We used the expanded version of both datasets to provide the total cumulative costs (between 1970 and 2020) in 2017-equivalent US$ billion. *N* represents the number of cost entries in the datasets. Details about the descriptive fields and their respective categories are provided in the Suppl. material 3.

Link: https://doi.org/10.3897/neobiota.67.59132.suppl5

Supplementary material 6

Categorization of recorded cost data into “damage” costs

Authors: Christophe Diagne, Anna J. Turbelin, Desika Moodley, Ana Novoa, Boris Leroy, Elena Angulo, Tasnime Adamjy, Cheikh A. K. M. Dia, Ahmed Taheri, Justice Tambo, Gauthier Dobigny, Franck Courchamp

Data type: database

Explanation note: Categorization of recorded cost data into “damage”, “management” or “mixed” costs according to criteria considered in Diagne et al. 2020c (see also Suppl. material 3).

Link: https://doi.org/10.3897/neobiota.67.59132.suppl6

Supplementary material 7

Relative weights of predictor categories in the linear robust regression between cost data and time period

Authors: Christophe Diagne, Anna J. Turbelin, Desika Moodley, Ana Novoa, Boris Leroy, Elena Angulo, Tasnime Adamjy, Cheikh A. K. M. Dia, Ahmed Taheri, Justice Tambo, Gauthier Dobigny, Franck Courchamp

Data type: database

Explanation note: 'Cost data' is the response variable: we considered information from the Cost estimate per year USD Exchange rate column in the expanded conservative subset (Suppl. material 4). 'Time period' (in years) is the predictive variable: we considered information from the Impact year column of the expanded subset conservative subset (Suppl. material 4). We identified that the relative weights of all years from 2014 onwards (except 2018) are lower than those from previous years. These years (including 2018) were therefore removed when calibrating the final models investigating the trend of cost over time.

Link: https://doi.org/10.3897/neobiota.67.59132.suppl7

Supplementary material 8

Quantitative summary of the costs reported in each African region

Authors: Christophe Diagne, Anna J. Turbelin, Desika Moodley, Ana Novoa, Boris Leroy, Elena Angulo, Tasnime Adamjy, Cheikh A. K. M. Dia, Ahmed Taheri, Justice Tambo, Gauthier Dobigny, Franck Courchamp

Data type: database

Explanation note: Quantitative summary of the costs reported in each African region following the number of expanded cost entries (*N*), the "method reliability" ("High" or "Low") and the cost "implementation" ("observed" or "potential").

Link: https://doi.org/10.3897/neobiota.67.59132.suppl8

Supplementary material 9

Distribution of the reliable observed costs

Authors: Christophe Diagne, Anna J. Turbelin, Desika Moodley, Ana Novoa, Boris Leroy, Elena Angulo, Tasnime Adamjy, Cheikh A. K. M. Dia, Ahmed Taheri, Justice Tambo, Gauthier Dobigny, Franck Courchamp

Data type: database

Explanation note: Distribution of the reliable observed costs (from the conservative subset) following the impacted sectors and type of cost for each reporting African country. The country names are coloured based on the geographical region they belong to as defined by United Nations geoscheme (available at https://unstats.un.org/): "Western Africa", "Southern Africa", "Northern Africa", "Middle Africa", and "Eastern Africa" (see continental map on the top left corner). For the impacted sectors, we considered the categories proposed by Diagne et al. (2020b) (Suppl. material 3). For the type of cost, we used the information from the type of cost column to classify the cost estimates among "damage" costs (economic losses due to direct and/or indirect impacts of invaders, such as yield loss, health injury, land alteration, infrastructure damage, or income reduction), "management" costs (economic resources allocated to actions to avoid the invasion, or to deal with more or less established invaders such as prevention, control, research, long-term management, eradication) or "mixed" costs (when costs include both damage and management expenditures) (Suppl. material 6).

Link: https://doi.org/10.3897/neobiota.67.59132.suppl9

Supplementary material 10

List of species as well as their cost estimates recorded in our dataset

Authors: Christophe Diagne, Anna J. Turbelin, Desika Moodley, Ana Novoa, Boris Leroy, Elena Angulo, Tasnime Adamjy, Cheikh A. K. M. Dia, Ahmed Taheri, Justice Tambo, Gauthier Dobigny, Franck Courchamp

Data type: database

Explanation note: We provided the total cumulative costs in 2017-equivalent US$ million for 1970-2020 derived from the "starting dataset" (i.e. total cost) and "conservative subset" (i.e. robust cost).

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Supplementary material 11

Summary of the outputs from the different models used for analyzing the temporal trend of invasion costs in Africa between 1970 and 2019

Authors: Christophe Diagne, Anna J. Turbelin, Desika Moodley, Ana Novoa, Boris Leroy, Elena Angulo, Tasnime Adamjy, Cheikh A. K. M. Dia, Ahmed Taheri, Justice Tambo, Gauthier Dobigny, Franck Courchamp

Data type: database

Explanation note: Prediction was based on OLS: ordinary least-squares; GAM: generalized additive model; linear regression, quadratic regression, MARS: multiple adaptive regression splines. We considered models calibrated and fitted with at least 75% of cost data completeness from the dataset. Costs are estimated in 2017-equivalent US$ millions. We $\log_{10}$-tranformed cost estimates (from the 'Cost estimate per year 2017 USD exchange rate' column in the InvaCost database).

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Economic costs of biological invasions in Asia

Chunlong Liu[1,2,3,4], Christophe Diagne[4], Elena Angulo[4], Achyut-Kumar Banerjee[5], Yifeng Chen[6], Ross N. Cuthbert[7], Phillip J. Haubrock[8,9], Natalia Kirichenko[10,11,12], Zarah Pattison[13], Yuya Watari[14], Wen Xiong[15], Franck Courchamp[4]

1 *Institute of Biology, Freie Universität Berlin, Berlin, Germany* **2** *Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany* **3** *Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany* **4** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, Orsay, France* **5** *School of Life Sciences, Sun Yat-sen University, Guangzhou, China* **6** *Laboratory of biological invasion and adaptive evolution, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China* **7** *GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Kiel, Germany* **8** *Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, Gelnhausen, Germany* **9** *University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Vodňany, Czech Republic* **10** *Sukachev Institute of Forest, Siberian Branch of Russian Academy of Sciences, Federal Research Center "Krasnoyarsk Science Center SB RAS", Krasnoyarsk, Russia* **11** *Siberian Federal University, Krasnoyarsk, Russia* **12** *Reshetnev Siberian State University of Science and Technology, Krasnoyarsk, Russia* **13** *School of Natural and Environmental Sciences, Modelling, Evidence and Policy Group, Newcastle University, Newcastle Upon Tyne, UK* **14** *Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba-shi, Ibaraki, Japan* **15** *College of Fisheries, Guangdong Ocean University, Zhanjiang, China*

Corresponding author: Chunlong Liu (liuchunlong113@gmail.com)

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Abstract

Invasive species have caused severe impacts on biodiversity and human society. Although the estimation of environmental impacts caused by invasive species has increased in recent years, economic losses associated with biological invasions are only sporadically estimated in space and time. In this study, we synthesized the losses incurred by invasions in Asia, based on the most comprehensive database of economic costs of invasive species worldwide, including 560 cost records for 88 invasive species in 22 countries. We also assessed the differences in economic costs across taxonomic groups, geographical regions and impacted sectors, and further identified the major gaps of current knowledge in Asia. Reported economic costs of biological invasions were estimated between 1965 and 2017, and reached a total of US$ 432.6 billion (2017 value), with dramatic increases in 2000–2002 and in 2004. The highest costs were recorded for terrestrial ectotherms, for species estimated in South Asia, and for species estimated at the country level, and were related to more than one impacted sector. Two taxonomic groups with the highest reported costs were insects and mammals, and two countries with the highest costs were India and China. Non-English data covered all of 12 taxonomic groups, whereas English data only covered six groups, highlighting the importance of considering data from non-English sources to have a more comprehensive estimation of economic costs associated with biological invasions. However, we found that the estimation of economic costs was lacking for most Asian countries and for more than 96% of introduced species in Asia. Further, the estimation is heavily biased towards insects and mammals and is very limited concerning expenditures on invasion management. To optimize the allocation of limited resources, there is an important need to better and more widely study the economic costs of invasive alien species. In this way, improved cost reporting and more collaborations between scientists and stakeholders are needed across Asia.

Abstract in Chinese

生物入侵在亚洲造成的经济损失. 生物入侵已经造成了严重的生态和经济影响。虽然关于生物入侵生态影响的研究在近年来不断增加，但是生物入侵的经济影响却仅见于零星的研究中。在本研究中，我们整合了当前报道的生物入侵在亚洲造成经济损失的数据，共包含22个国家的88种入侵生物的560条数据。我们进一步分析了经济损失在不同类群、区域以及部门之间的差异，并提出了未来亟待解决的相关问题。在亚洲，生物入侵经济损失的数据报道的时间范围为1965至2017年。经济损失的总量达到了4326亿美元，且在2000 - 2002以及2004年发生了较大幅度的增长。经济损失在陆生变温动物、南亚以及国家尺度上最高，且主要的经济损失与超过一个部门相关。经济损失最高的两个类群为昆虫及哺乳动物、而最高的两个国家为印度和中国。非英语数据涵盖了数据中所有的12个类群，但是英语数据只涵盖了6个类群，这一结果揭示了考虑非英语数据对综合地评估生物入侵经济损失的重要性。然而，我们也发现大多数亚洲国家都缺乏生物入侵造成经济损失的数据，且目前仅有不足4%的外来种有经济损失数据。此外，经济损失的评估显著偏向于昆虫和哺乳动物，严重影响着生物入侵的管理。为了优化生物入侵的管理，需要更加全面且广泛地评估入侵生物所造成的经济损失。这需要亚洲的研究人员和管理人员之间的更加广泛的合作。

Abstract in French

Coûts économiques des invasions biologiques en Asie. Les espèces exotiques envahissantes ont de graves répercussions sur la biodiversité et les sociétés humaines. Bien que l’estimation des impacts environnementaux causés par ces espèces a augmenté ces dernières années, les pertes économiques associées aux invasions biologiques ne sont estimées que sporadiquement dans l’espace et le temps. Dans cette étude, nous présentons la synthèse des pertes économiques associées aux invasions biologiques en Asie, en nous appuyant sur la base de données la plus complète sur les coûts économiques des espèces exotiques envahissantes dans le monde, comprenant 560 rapports de coûts pour 88 espèces exotiques envahissantes dans 22 pays d’Asie. Nous avons également évalué les différences de coûts économiques entre les groupes taxonomiques des espèces exotiques envahissantes, les régions géographiques et les secteurs touchés, et nous avons identifié les principales lacunes des connaissances actuelles en Asie. Les coûts économiques déclarés des invasions biologiques ont été estimés entre 1965 et 2017 et ont atteint un total de 432.6 milliards de dollars (valeur de 2017), avec des augmentations spectaculaires en 2000–2002 et en 2004. Les coûts les plus élevés ont été enregistrés pour les ectothermes terrestres, pour les espèces estimées en Asie du Sud et pour les espèces estimées au niveau des pays, et étaient liés à plus d'un secteur impacté. Les insectes et les mammifères sont les deux groupes taxonomiques dont les coûts déclarés étaient les plus élevés, les deux pays où les coûts étaient les plus élevés étant l'Inde et la Chine. Les données en langue non anglaise couvraient l'ensemble des 12 groupes taxonomiques étudiés, tandis que les données en anglais ne couvraient que six groupes, ce qui souligne l'importance de tenir compte des données provenant de sources non non reportés en anglais pour avoir une estimation plus complète des coûts économiques associés aux invasions biologiques. Cependant, nous avons constaté que l'estimation des coûts économiques est insuffisante pour la plupart des pays asiatiques et pour plus de 96% des espèces introduites en Asie. De plus, elle est fortement biaisée envers les insectes et les mammifères et est très limitée en ce qui concerne les dépenses pour la gestion des invasions. Pour optimiser l'allocation des ressources limitées, il est important d'étudier de façon plus vaste et plus approfondie les coûts économiques des espèces exotiques envahissantes. Également, il faut améliorer la standardisation des études sur les coûts et accroître la collaboration entre les scientifiques et les porteurs d'enjeu en Asie.

Abstract in Japanese

アジアにおける外来種の侵入に伴う経済コスト． 外来種は生物多様性や人間社会に深刻な影響を与えている．近年，侵略的外来種による環境への影響評価は数多くなされてきたが，外来種の侵入に伴う経済的損失の推定は，地理的，時期的に散発的にしか行われてこなかった．本研究では，22カ国，88種の外来種の経済コスト記録560件を含む，世界で最も包括的な外来種の経済コストデータベースをもとに，アジアにおける外来種の侵入による経済コストを集計した．また，分類群，地域，コスト区分間での経済コストの違いを評価し，現時点でのアジアにおける知見の主要なギャップを明らかにした．アジアにおける外来種の侵入の経済コストは，1965年から2017年の期間の推定値が報告されており，計4,326億米ドル（2017年の価値）に達し，特に2000年から2002年と2004年には劇的に増加していた．最も高いコストが記録されたのは，陸生の外温動物，南アジアでコストが生じている種，国家スケールでコストが生じている種であった．これらは2つ以上のコスト区分に関連していた．報告されたコストが最も高かった分類群は昆虫類と哺乳類であった．最も高いコストが推定された国は，インドと中国であった．非英語言語のデータソースから推定されたコストは12の分類群すべてをカバーしていたのに対し，英語のデータソースは6つの分類群しかカバーしていなかったことから，外来種の侵入による経済的コストを網羅的に推定するためには，英語以外の言語の情報を考慮することが重要であることがわかった．しかしながら，経済コストの推定は，アジアのほとんどの国において，またアジアの外来種の96％以上において，不足している状況であることがわかった．さらに，経済コストの報告は昆虫類や哺乳類に大きく偏っており，また，外来種管理のための経済支出についての情報は非常に限られていた．限られた経済的，人的資源の配分を最適化するためには，外来種の侵入に関する経済的コストをより的確に，より広範に調査する必要がある．このように，アジア全域において，経済コストのよりよい報告体制と，科学者とステークホルダーとのより緊密な連携が必要とされている．

Abstract in Russian

Экономические потери от биологических инвазий в Азии. Инвазионные виды оказывают серьезное воздействие на биоразнообразие и человеческое общество. Несмотря на то, что в последние годы воздействие инвазионных организмов на окружающую среду заметно выросло, экономические потери, связанные с биологическими инвазиями, оцениваются все еще редко. Используя количественные данные из наиболее полной мировой базы данных экономических ущербов от инвазионных видов, мы проанализировали сведения об экономических потерях в результате биологических инвазий в Азии: данные насчитывали 560 позиций убытков для 88 инвазионных видов в 22 азиатских странах. Мы также оценили размер экономических потерь в разных таксономических группах инвайдеров, географических регионах и секторах экономики, и кроме того, определили основные пробелы в знаниях о потерях от биологических инвазий в Азии. В 1965–2017 гг. экономические потери от инвайдеров составили около 432.6 млрд долларов США (по курсу валюты на 2017 г.) с резким увеличением убытков в 2000–2002 гг. и в 2004 г. Наиболее высокие траты были связаны с наземными инвазионными холоднокровными организмами как в Южной Азии в целом, так и в ее отдельных странах и отмечались в более чем одном экономическом секторе. Две таксономические группы – насекомые и млекопитающие – обусловили самые высокие экономические потери; наибольший экономический ущерб от них был отмечен в двух странах – Индии и Китае. Данные по экономическим потерям из неанглоязычных (т.е. местных) литературных источников касались всех 12 таксономических групп, тогда как данные из англоязычной литературы по Азии охватывали только шесть групп, что говорит о важности учетов данных из национальных источников для более полной оценки экономических потерь от инвазий. Мы отметили, что оценки экономических потерь от инвазий отсутствуют в большинстве азиатских стран; до сих пор потери не оценивались для 96% видов, интродуцированных в Азию. Имеющиеся данные, преимущественно связанные с инвазиями насекомых и млекопитающих, указывают на низкие расходы на мониторинг чужеродных видов. Существует большая потребность в более тщательных оценках экономических ущербов от инвазий чужеродных видов в разных регионах Азии. Таким образом, статья призывает к улучшению отчетности по экономическим потерям от инвазий и расширению сотрудничества между учеными и заинтересованными сторонами в Азии.

Abstract in Spanish

Los costos económicos de las invasiones biológicas en Asia. Las invasiones biológicas han causado serios impactos en la biodiversidad y en las sociedades humanas. Aunque las estimaciones de los impactos ambientales causados por las especies invasoras han aumentado en los últimos años, las pérdidas económicas asociadas han sido estimadas esporádicamente tanto espacialmente como temporalmente. En este estudio sintetizamos las pérdidas económicas producidas por las invasiones biológicas en Asia, basándonos en la base de datos más exhaustiva sobre los costos económicos de las especies invasoras que existe a nivel mundial, incluyendo 560 entradas de costos para 88 especies invasoras en 22 países. También evaluamos las diferencias en los costos económicos entre grupos taxonómicos, entre regiones geográficas y entre sectores económicos impactados, e identificamos las lagunas del conocimiento actual en Asia. Los costos económicos reportados para las invasiones biológicas fueron estimados entre 1965 y 2017, y alcanzaron un total de 432.6 mil millones de dólares americanos (valor de 2017), incrementando dramáticamente en el período 2000–2002 y en 2004. Los costos más altos fueron reportados para los ectotermos terrestres, para especies reportadas en el sur de Asia, para especies estimadas a nivel de país, y estuvieron relacionados con más de un sector económico. Los mayores costos reportados fueron para los insectos y los mamíferos (en cuanto a grupos taxonómicos), y para India y China (en cuanto a países). Los datos obtenidos a partir de documentos no ingleses cubrieron los 12 grupos taxonómicos reportados, mientras que los documentos en inglés solo cubrieron 6 grupos, poniendo de manifiesto la importancia de considerar los documentos no ingleses para tener una estimación más exhaustiva de los costes económicos asociados a las invasiones biológicas. A pesar de ello, encontramos que hay una falta de estimaciones económicas para la mayoría de los países Asiáticos y para más del 96% de las especies introducidas en Asia. Más aún, las estimaciones reportadas están sesgadas hacia insectos y mamíferos y muy limitadas en cuanto a los gastos en el manejo de las invasiones. Para optimizar el reparto de los recursos limitados que existen, es muy importante estudiar mejor y más ampliamente los costos económicos de las especies invasoras. Por lo tanto, es necesario el aumento de los informes sobre costos y las colaboraciones entre científicos y gestores en Asia.

Keywords

Economic damages, InvaCost, invasive alien species, monetary losses, non-English data, non-native species

Introduction

Biological invasions are one of the most serious threats to biodiversity and human society (Vander Zanden and Olden 2008; Seebens et al. 2018). With increasing anthropogenic activities, thousands of species have been introduced across the globe, causing substantial impacts on ecosystem service and social welfare (Essl et al. 2011; Bradshaw et al. 2016; Hanley and Roberts 2019). To better understand invasion impacts and develop cost-effective management strategies, recent years have seen remarkable increases in the estimation of environmental impacts caused by invasive species (i.e. alien species that have caused impacts on the economy and environment in new ranges) (Lodge et al. 2016; McGeoch et al. 2016). At the global scale, environmental impacts have been estimated for different taxonomic groups, including invasive plants (Vilà et al. 2011), amphibians (Nunes et al. 2019), crayfish (Twardochleb et al. 2013), and marine species (Anton et al. 2019). However, the estimation of their economic impacts lags behind and is still in its infancy (Lodge et al. 2016). Despite the crucial importance for informing invasion management (Aukema et al. 2011; Diagne et al. 2020a), economic impacts of invasive species have only been estimated for certain taxa (e.g. insects; Bradshaw et al. 2016), countries (e.g. China; Xu et al. 2006), regions (e.g. Southeast Asia; Nghiem et al. 2013), or sectors (e.g. agriculture; Paini et al. 2016). Estimating economic impacts is further hampered by the difficulty of compiling a comprehensive list of invasive species (Wilson et al. 2018), and the uncertainty associated with the methods applied for estimation (Bradshaw et al. 2016; Cuthbert et al. 2020). To date, systematic estimation of economic impacts is lacking for most species and regions, limiting our ability to manage biological invasions at a broad scale (Diagne et al. 2020a).

Asia is among the continents suffering most from biological invasions (Pimentel et al. 2001; Ding et al. 2008; Shepard et al. 2013). As the continent with the largest human population and fastest economic growth (International Monetary Fund 2019; https://www.imf.org/), Asia has become a key recipient area for invasive species (Turbelin et al. 2017). Expanding trading activities in Asian countries not only accelerate the introduction of species, but also exacerbate invasion-induced economic impacts

(Nghiem et al. 2013; Seebens et al. 2017). Sardain et al. (2019) reported that China's share of maritime transportations increased from 1.4% in 1990 to 20.1% in 2013, and that Northeast Asia would become the global hotspot of marine invaders in the near future. Paini et al. (2016) predicted that China would suffer the highest economic loss in agriculture from invasive pests worldwide. Many species are also intentionally introduced to increase food production and mitigate environmental impacts (Ding et al. 2008; Wang et al. 2020), or are released for religious purposes (Liu et al. 2012). Asia is the leading continent for aquaculture, with a number of species being introduced for aquaculture practices. But many of them have escaped from facilities and successfully established in the wild (Liu et al. 2017; Ju et al. 2019). In East and Southeast Asia, Buddhist and Taoist practices regularly result in the intentional release of captive alien animals, such as American bullfrogs *Lithobates catesbeianus* and common carp *Cyprinus carpio*, to gain spiritual merit (Liu et al. 2012; Xiong et al. 2015). These species not only cause widespread environmental problems, but also are recognized as a great threat to economic development (Ding et al. 2008; Seebens et al. 2017).

Despite lacking information at the continental scale, economic impacts of invasive species have been estimated in different countries and regions in Asia. In Southeast Asia, Nghiem et al. (2013) reported that the annual economic loss in agriculture, environment and public health accounted for an estimated US$ 33.5 billion. Xu et al. (2006) mentioned that economic loss in China was US$ 14.5 billion in the year 2000, which approximately accounted for 1.36% of China's annual GDP. A more striking case is India, in which invasive weeds were estimated to incur a 30% loss in crop yields, with extrapolated annual economic loss of US$ 91 billion (Pimentel et al. 2001). Economic costs can also be markedly high for individual invasive species. For example, yellow fever mosquito *Aedes aegypti* is reported to cause an annual economic burden of US$ 950 million in 12 countries in Southeast Asia alone, due to its capacity of rapidly transmitting the dengue virus (Shepard et al. 2013). Although these pioneering studies provide useful information, their findings are spatially and temporally sporadic, thus preventing a comprehensive understanding of ongoing economic impacts of invasive species.

Language is another barrier impeding the synthesis of economic impacts across Asian countries. While English dominates current scientific activities (Amano et al. 2016; Tao et al. 2018), it is not the mother tongue in most Asian countries, whereas economic costs of invasions are often reported in grey literature (e.g. government reports and graduate school theses) written in national languages (Hanley and Roberts 2019). Moreover, studies published in non-English languages (e.g. Chinese and Japanese) are substantial (Tao et al. 2018; Konno et al. 2020), suggesting that data of economic impacts from non-English sources might be abundant. In the field of biodiversity conservation, Amano et al. (2016) found that more than one third of scientific studies were published in non-English languages. Language, thus, acts as a hurdle in accessibility and searchability when compiling data of economic impacts in Asia. To account for information gaps of cost estimation due to language barriers, it is, therefore, important to consider studies published in non-English languages.

In this study, we used the most comprehensive database of economic costs of invasive species worldwide (InvaCost; Diagne et al. 2020b) to understand the damages invasive species have caused to the Asian economy. Specifically, we aimed to address three overarching questions: (1) what are the costs and expenditures of invasions in Asia, and how do they change over time; (2) what are the differences in economic costs across taxonomic groups, geographical regions and impacted sectors, and (3) what are the major gaps in current knowledge on invasion costs in Asia across languages, taxonomic groups, geographical regions, and impacted sectors?

Methods

Data compilation

The dataset of economic costs caused by invasive species in Asia was compiled from the original version of the InvaCost database (Diagne et al. 2020b), which was supplemented with data from non-English documents searched in Chinese, Japanese, Russian, and Indian languages (Angulo et al. 2021; data accessible at: https://doi.org/10.6084/m9.figshare.12928136). Economic costs of all records were standardized in US dollar (2017 value). In this study, we selected economic costs solely estimated in Asia, and thus excluded those covering other continent(s). We specifically focused on economic impacts that actually occurred, and excluded costs estimated based on computational modelling and predictions beyond the spatial and/or temporal extents in which species currently exist. To refine recorded information, we carefully checked the data to correct potential mistakes and remove overlaps (i.e. cost records included in another record with larger spatial scale or longer temporal scale) and duplicates (i.e. costs records with the same descriptors were reported by two different sources). Xu et al. (2006) is the only study for which the data are available in both English and Chinese. We only kept the Chinese data which were reported species by species, whereas English data only provided aggregated estimates by ecological groups and impacted sectors. Similarly, a cost for an eradication project of invasive fruit flies was reported in English and Japanese. The latter was kept, as it described the costs with more details (Watari et al. 2021). The final dataset used in this study is provided as a supplementary material (Suppl. material 1: Table S1).

Species were classified into 12 taxa belonging to five ecological groups: aquatic species (crustaceans, fishes, and molluscs), microorganisms (bacteria, fungi, and viruses), plants, terrestrial ectotherms (insects, amphibians and reptiles), and terrestrial endotherms (birds and mammals). In the study, for simplicity, we listed viruses among microorganisms, despite not being cellular. Costs estimated for multiple species belonging to more than one ecological group were labeled as “Unspecified”. Countries were classified into four geographical regions: East Asia, South Asia, Southeast Asia, and Western Asia, following the classification in United Nations Statistics Division (https://unstats.un.org/unsd/methodology/m49/). Our dataset did not include records from Central Asia and North Asia (see Results for more details). Spatial scales of costs were classified into three categories: region-level (i.e. costs estimated across more than one country), country-level, and site-level (i.e. costs estimated within one country subdivision). We further re-assigned costs into seven impacted sectors: agriculture, authorities, environment, fishery, forestry, health, and social welfare (Suppl. material 2: Table S2), and four types of cost: damage, management, knowledge, and damage & management (Suppl. material 3: Table S3). Costs that could not be assigned to one specific sector were labeled as “Multiple”. Cost data were further identified as being of low or high reliability based on the source of the data. Specifically, data were considered of high reliability if they were reported from sources validated by experts, including peer-reviewed articles and official documents; otherwise, data were considered to be of low reliability. InvaCost did not determine data reliability specifically based on the approaches applied to estimate costs, because approaches were quite heterogenous among sources.

Data analyses

The temporal trends of cost estimation were assessed based on the changes in the number of species and cumulated economic costs, for the five ecological groups, for four geographical regions, and for three spatial scales, respectively. Costs labeled with “Unspecified” were excluded from the assessment for ecological groups, and costs covering more than one geographical region were excluded from the assessment for geographical regions.

We then assessed the compositions of species that have been estimated for economic costs in Asia, and the compositions of the total amount of economic costs among different taxonomic groups and countries, respectively. We also assessed the compositions of species that have been introduced in Asia for comparison. Costs estimated for multiple taxa and/or labeled with “Unspecified” were excluded from the assessment for the composition of taxonomic groups. All above analyses were performed using English and non-English data separately to better understand the specific contributions of reporting languages. For 22 countries included in the study (see Results for more details), ten countries only included data of *A. aegypti*. We therefore excluded these countries from the assessment of species composition among countries. To assess the difference in compositions of species already introduced in Asia and species estimated for economic impacts, we collected the data of species that have been introduced in Asia (i.e. introduced species) (see Results for more details) from the Global Alien Species First Records Database (Seebens et al. 2018, accessed in June 2020). To assess the completeness of cost estimation among groups and countries, we calculated the proportion of species being estimated for economic impacts and species being introduced for each of five ecological groups per country. We also assessed the variations in the number of cost records and economic costs among impacted sectors and types of cost. Last, we identified invasive species that were introduced in Asia but were only reported with economic costs in other continents (i.e. outside of Asia) using data from InvaCost database. All analyses were conducted in R software (v 3.5.0.) (R Development Core Team 2018).

Results

Data summary

Our dataset included 560 cost records for 88 invasive species, with the total economic loss reaching US$ 432.6 billion (Table 1). The economic costs captured within this dataset range between 1965 and 2017, with substantially less cost recorded in the 20th century (US$ 64.4 billion) than in the 21th century (US$ 368.2 billion) (Suppl. material 1: Table S1). Instead of increasing steadily over time, the number of species for which costs were estimated showed spikes in 2000 (36 species) and in 2013–2016 (58 species) (Fig. 1a), which were driven by the inclusion of Chinese data (26 species)

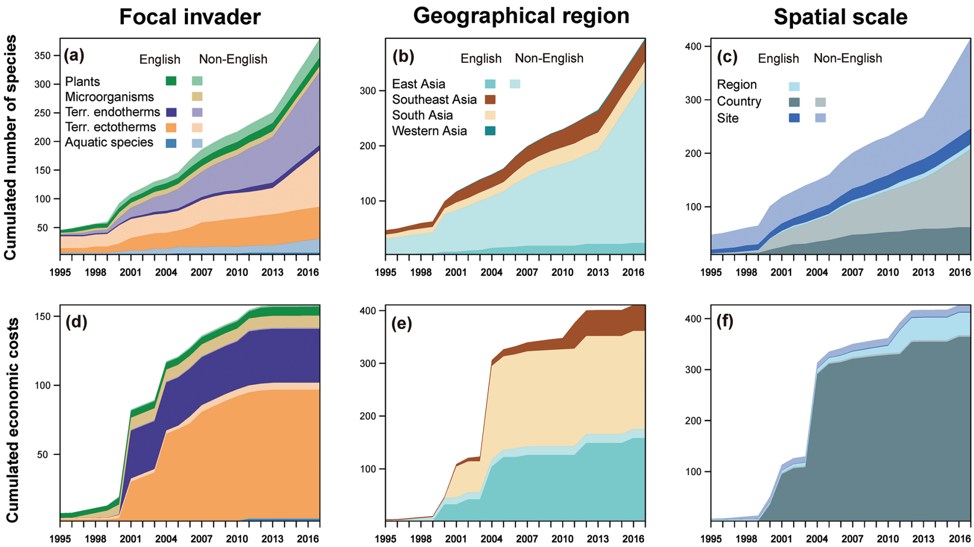

Figure 1. The temporal trends in the cumulated number of species and the amount of economic costs between 1995 and 2017. Focal invaders are classified into: Plants, Microorganisms, Terrestrial endotherms, Terrestrial ectotherms, and Aquatic species. Geographical regions are classified into: East Asia, Southeast Asia, South Asia, and Western Asia. Spatial scales are classified into: Region, Country, and Site. Economic costs are standardized in US billion dollars (2017 value). Note that the contribution of each group at a point in time is represented by the proportionate height width (not the absolute height) of the corresponding color at that particular year. Given some cost data cannot be classified into specific groups of invaders or geographical regions, the number of species and economic costs are different between panels. One species can be estimated in different years and/or different publications. The temporal scale is set since 1995, because economic costs are rarely estimated between 1965 and 1995 (see Results for more details).

Table 1. Data of economic costs of invasive species compiled from English and non-English studies. Economic costs are standardized in US dollar (2017 value).

Language	Temporal range	Number of countries	Number of species	Number of records	Economic costs (US$)
English	1976–2017	22	21	140	415.3 billion
Non-English	1965–2017	2	74	421	17.3 billion

and Japanese data (48 species), respectively (Suppl. material 1: Table S1). Dramatic increases in economic cost occurred in 2000–2002 (US$ 137.4 billion) and in 2004 (US$ 180.3 billion) (Fig. 1d), driven by a few records of high economic cost in China and India, respectively (Suppl. material 1: Table S1). Twenty-two countries reported economic costs; however, nine of these countries only had one record each. Japan had the highest number of records (326); retrieved primarily from non-English studies (99.7%). Among species, economic costs of *A. aegypti* were estimated in the highest number of countries (15), whereas costs of 80 species were only recorded in only one country. Economic costs were markedly different among species: the mosquito *A. aegypti* incurred the highest cost (US$ 44.6 billion) and the whitetop weed *Parthenium hysterophorus* caused the lowest cost (US$ 34.0).

We found marked differences in the number of species and records, and total amount of economic costs between English and non-English data (Table 1). English data covered all of the 22 countries included in the dataset, but the number of species was only 28.4% of the non-English data, which was consisted only of data from China and Japan; all data retrieved in Russian was for the European part of the country and not used here, no data were returned using either of four Indian languages (Hindi, Telugu, Tamil, and Bengali), and other Asiatic languages were not searched. More strikingly, one species (*A. aegypti*) contributed to 47.9% of the English records, and there were only seven species included in both English and non-English data. The costs from non-English data tended to be more numerous and smaller (Table 1). Despite the number of English records being around one third (33.3%) of that of non-English records, the total cost from English references was 24 times higher than that from non-English references. The proportion of records with high reliability was marginally greater for non-English (91.2%) than English data (82.7%), but both were very high. Most of the English records were estimated at country level (65.5%), compared to the majority of records being at site level (56.8%) for non-English data. In addition, we found that 23.8% of species in the English data were among 100 of the world's worst invasive alien species (Global Invasive Species Database; http://www.iucngisd.org/gisd/100_worst.php), and the proportion in non-English data was only 13.5%.

Taxonomic compositions

There are clear differences in the number of species and the total economic costs reported among five ecological groups (Fig. 1a, d). In our dataset, the highest number of species (40.5%) belonged to terrestrial ectotherms, followed by terrestrial endotherms (36.1%), aquatic species (8.2%), plants (6.6%), and microorganisms (2.6%) (Fig. 1a). Surprisingly, only around one third of the total economic costs (US$ 158.2 billion) was attributed to particular species, with most costs (63.4%) being recorded for multiple species (Fig. 1d). Terrestrial ectotherms reportedly caused the highest costs (US$ 98.2 billion), followed by terrestrial endotherms (US$ 39.7 billion); whereas aquatic species caused the lowest costs (US$ 3.6 billion) (Fig. 1d). Economic costs estimated from English data were much higher than records from non-English data for terrestrial ectotherms (18.0 times), terrestrial endotherms (51.8 times), aquatic species (10.6 times), and plants (5.1 times). For marine invaders, our dataset only included two records related to the red tide (i.e. vast concentrations of aquatic single-celled microorganisms, such as protozoans and diatom algae) and one record related to jellyfish invasion.

The completeness of cost estimations was low across countries (Suppl. material 4: Table S4). China was the only country with cost estimation for all of five ecological groups, whereas seven countries only had cost estimation for one group. Microorganisms were the group for which the costs were estimated in most countries (N = 10), whereas the cost of terrestrial endotherms was only estimated in four countries.

The compositions of species introduced in Asia, as well as the invasive alien species for which costs were estimated, and the proportions of economic costs that they have caused were not evenly distributed among taxonomic groups (Fig. 2). For 2,703 species introduced in Asia, plants constituted the group with the highest proportion of introduced species (44%), followed by insects (13.2%), birds (11.5%), and fishes (10.4%) (Fig. 2a). The 88 species estimated for economic costs only accounted for 3.3% of all introduced species.

The two groups having the most species with cost estimates were insects (34.2%) and mammals (29.3%) (Fig. 2b), despite their relatively small contributions to the number of introduced species. The other three groups contributing the most introduced species (plants, birds and fishes) were relatively less estimated in terms of cost. The taxonomic differences in amounts of economic costs were also pronounced (Fig. 2c): insects and mammals caused more than 80% of the total losses (48.9% and 33.2%, respectively), while seven out of 12 taxa contributed to < 1% of the total losses, including amphibians, bacteria, birds, crustaceans, fishes, fungi, and reptiles. We also found that non-English data covered all these 12 taxonomic groups, whereas English data only covered six groups (Fig. 2c). The amount of economic costs showed remarkable variations among species. For example, *Rattus* spp. caused a loss of US$ 34.6 billion in social welfare and *A. aegypti* caused US$ 44.2 billion to the health system. Social welfare and health system were two sectors suffering the greatest economic losses from particular species (US$ 68.3 billion; Fig. 3), which were mainly caused by mammals and insects. Most costs were related to damages caused by invasive species (US$ 91.2 billion), which were reported in East Asia, South Asia and Southeast Asia (Fig. 3).

There were 135 species introduced in Asia for which economic costs were reported in other continents (no reported economic cost in Asia yet) (Suppl. material 5: Table S5). The total amount of their costs outside of Asia reached US$ 126.1 billion. Among seven species with the highest costs, there were six insect species, with the Asian long-horned beetle *Anoplophora glabripennis* (native in China and invasive in Europe, North America and other parts of Asia) causing the highest economic cost (US$ 5.84 billion).

Geographical compositions

The number of species and total economic costs also substantially differed among geographical regions (Fig. 1b, e). Most species were estimated in countries from

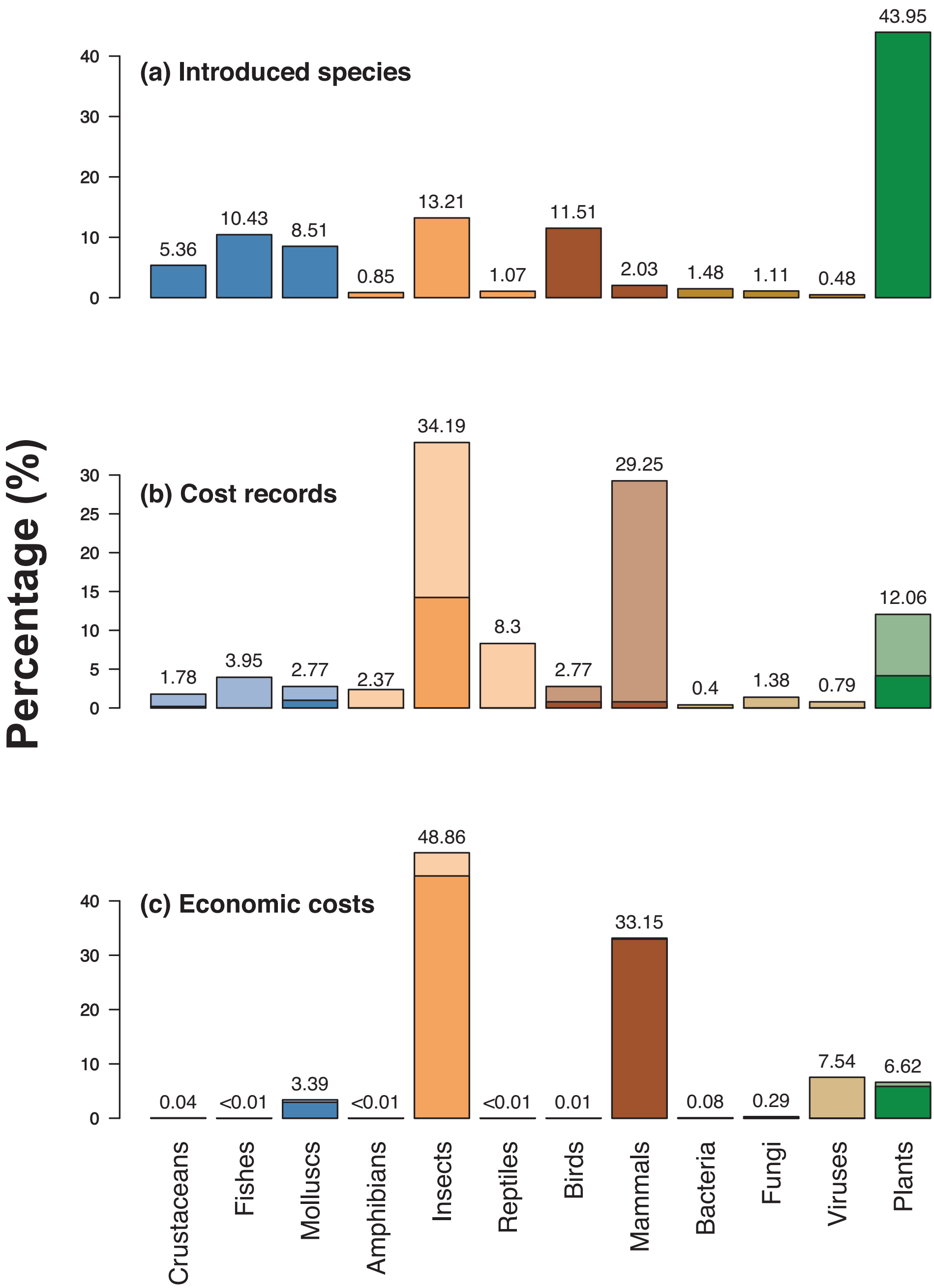

Figure 2. The compositions of (**a**) species introduced in Asia (**b**) species with estimated economic costs, and (**c**) economic costs across 12 taxonomic groups. Data retrieved from English studies are shown in a darker shade and those from non-English studies are in a lighter shade. The percentage of each taxonomic group is shown above the bar. Colors of taxonomic groups correspond to colors of five ecological groups shown in Figure 1. Data of (**a**) are from the Global Alien Species First Records Database, while data of (**b**) and (**c**) from our dataset.

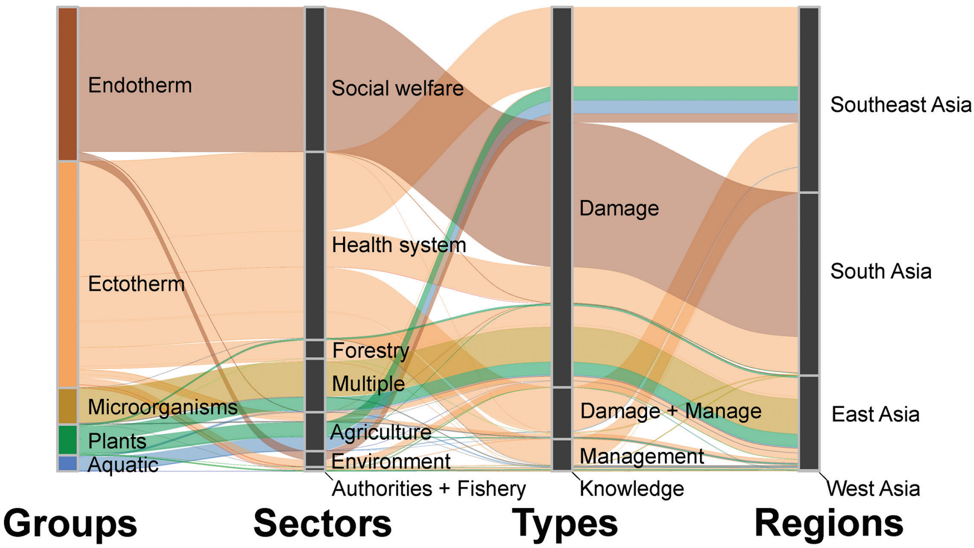

Figure 3. The network showing the composition of economic costs among ecological groups, impacted sectors, types of cost and geographical regions. Only economic costs estimated for particular species were considered, and those estimated for multiple species were excluded. Colors of ecological groups correspond to colors of five ecological groups shown in Figure 1.

East Asia (80.7%), which was mainly driven by species in Chinese and Japanese studies (74.7%) (Fig. 1b). Our dataset did not cover records from Central and North Asia (consisting of the Russian regions eastward of the Ural Mountains): data were unavailable for Central Asia, whereas data for North Asia were combined with those from European Russia and no data were specifically reported for North Asia (Kirichenko et al. 2021). Economic costs were highest in South Asia (US$ 185.8 billion), followed by East Asia (US$ 175.7 billion), with only US$ 0.2 billion in Western Asia (Fig. 1e). Similar patterns were was also found among spatial scales (Fig. 1c, f): economic costs at the site level comprised nearly half of records but only contributed to 3.6% of the total cost, with most of economic costs (86.1%) at the country level (Fig. 1f). Economic costs were nearly all estimated at the country (50.2%) and site (47.6%) levels, with comparatively few (2.2%) at the region level (Fig. 1c).

The variations in introduced species, invasive alien species with estimated costs, and amounts of economic costs were also marked among countries (Fig. 4). Around half (46.9%) of introduced species were recorded in countries from East Asia, with only 7.1% in countries from South Asia. Israel was the country with the highest number of introduced species (596), followed by China (560) and Japan (480) (Fig. 4a). However, records of economic costs were heavily driven by Japan (327) and China (113); all other countries, including Israel, had fewer than 10 records (Fig. 4b). Despite only having eight records, India was the country with the highest

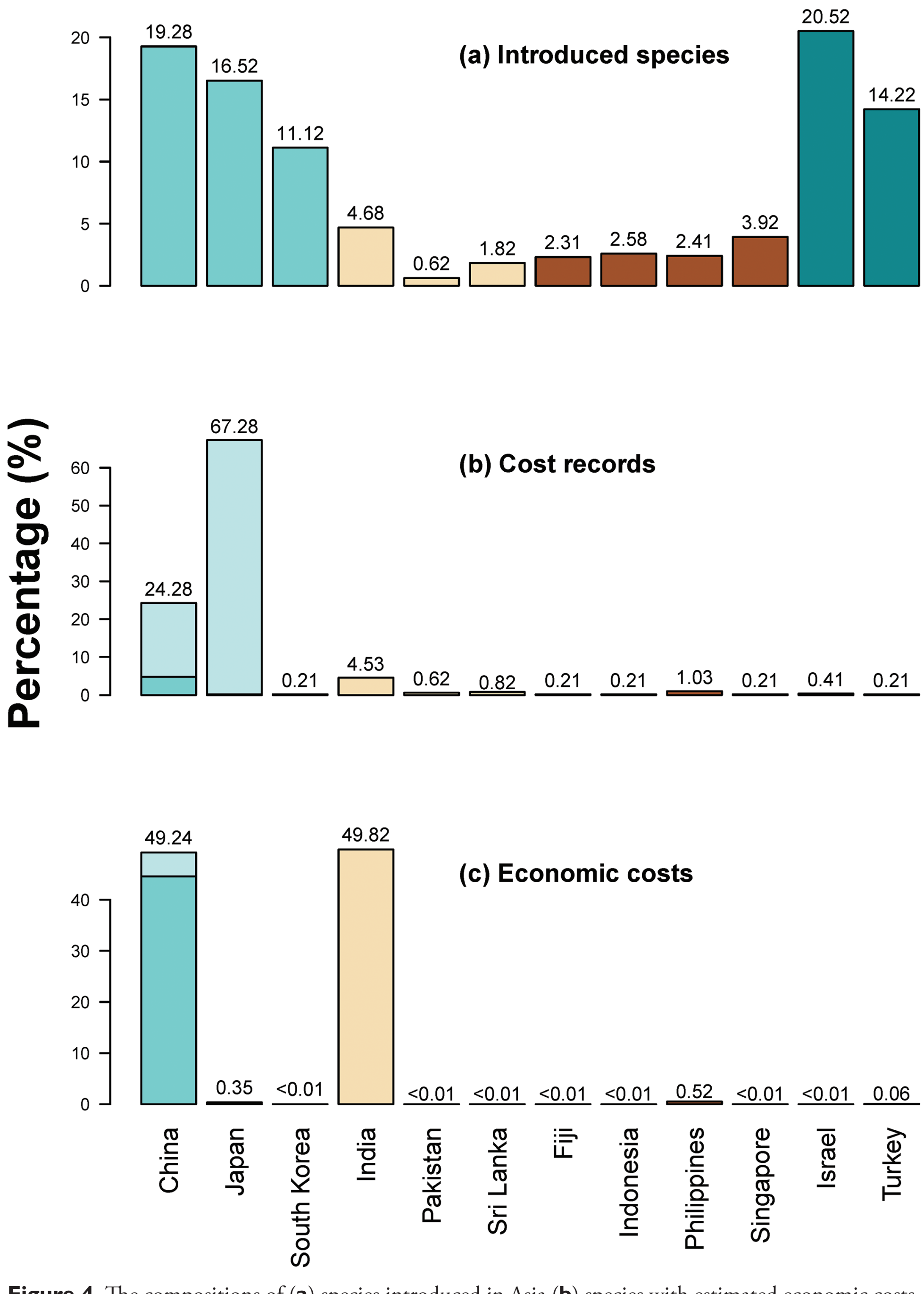

Figure 4. The compositions of (**a**) species introduced in Asia (**b**) species with estimated economic costs, and (**c**) economic costs across 12 countries. Data from English studies are shown in a darker shade and those from non-English studies are in a lighter shade. The percentage of each country is shown above the bar. Colors of countries correspond to colors of four geographical regions shown in Figure 1. Data of (**a**) are from the Global Alien Species First Records Database, while data of (**b**) and (**c**) from our dataset.

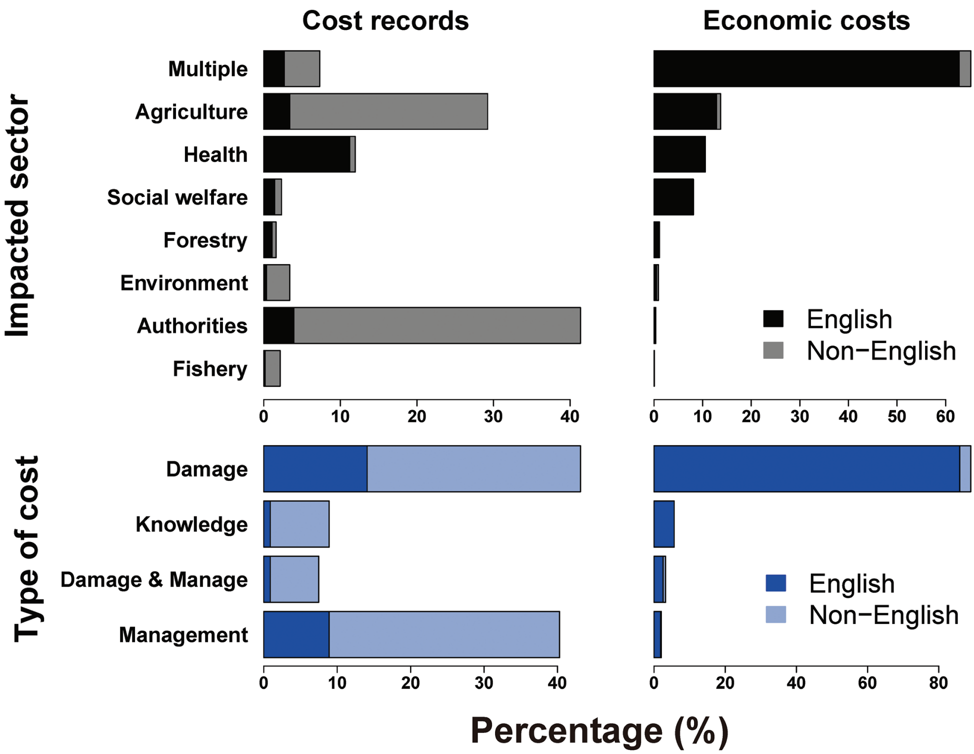

Figure 5. The compositions of records and amounts of economic costs among impacted sectors and types of cost. The categories of impacted sectors and types of costs are ordered according to the amount of economic costs decreasingly. Data from English studies are shown in a darker shade and from non-English studies are in a lighter shade.

economic cost (US$ 176.7 billion). Economic cost was also very high in China (US$ 174.7 billion), whereas all other countries contributed to less than 1% to the total losses (Fig. 4c).

Impacted sectors and types of cost

There were clear differences in the number of records and economic costs among impacted sectors and types of cost (Fig. 5). Economic costs were most frequently estimated for authorities (41.4%) and agriculture (29.2%), but were rarely estimated for social welfare (2.3%), fishery (2.1%), and forestry (1.6%). However, we found that most economic costs (65.2%) were related to more than one sector. Agriculture was the specific sector with the highest economic cost (13.7%), and fishery was the sector with the lowest cost (0.06%). Despite the number of records being similar between types of damage (43.1%) and management (40.3%), economic costs associated with management were much lower than that of damage (2.1% and 89.0%, respectively). Costs associated with knowledge were also quite low (US$ 24.6 billion; 5.7%).

Discussion

Our study synthesized the reported economic impacts of invasive species in Asia and found that the total amount was approximately US$ 432.6 billion, which is much higher than that recorded in South America (US$ 204.0 billion), Oceania (US$ 180.9 billion), Europe (US$ 125.6 billion), and Africa (US$ 18.8 billion) but much lower than that in North America (US$ 6.1 trillion) (Diagne et al. 2020b). Despite this great figure, economic losses are very likely underestimated across Asia. This is because more than 96% of known introduced species have not yet been estimated for costs, corroborating a previous assumption that only a very small proportion of invaders have been economically analyzed so far (Aukema et al. 2011). Although not every introduced species can cause impacts in new ranges, previous studies have found that around 30% of introduced species have been reported with ecological impacts (Measey et al. 2020). As such, we suggest the accumulated economic losses would be inevitably higher if more invaders were estimated, even if their impacts were to be intermediate or even low (Bradshaw et al. 2016; Hanley and Roberts 2019). We also found a clear bias in the number of estimated species and the amount of reported cost across years, suggesting the irregular reporting and improved data accessibility of economic costs of invasive species. For example, the marked increases in the number of estimated species in 2000 and 2013–2016 were driven by the increased data of economic costs reported from Chinese and Japanese references at those times, respectively.

Nevertheless, our study demonstrates the vital importance of considering data from non-English sources in order to have a more completed estimation of economic costs. Non-English data covered all major taxonomic groups of species introduced in Asia and contributed more records than English data, confirming the language barrier in conservation biology (Amano et al. 2016). Despite non-English data contributing more cost records, the total cost of non-English data was much less than that from English data. This finding is probably related to the spatial scale of the English and non-English data. Most of the English records were reported at country level, therefore the cost of English data is inevitably higher than that of non-English data, for which the majority of records were estimated at site level (see Results for more details). Although publishing studies in English has largely facilitated the transfer of scientific knowledge, it remains a big challenge for conservation practitioners and stakeholders for whom English is not the primary language for work and communication (Amano et al. 2016; Nuñez et al. 2019). Most conservation actions at the national level are coordinated in non-English languages in many Asian countries (Nuñez et al. 2019), and the under-representation of national studies might cause biases in scientific information transferred to policy makers and stakeholders in international forums. Despite non-English data being explicitly integrated in the present study, this was insufficiently comprehensive to capture all Asian languages in which invasion costs may be reported. However, India, Russia, China and Japan have been the focus of a more extensive research effort (e.g. local language searches and direct contact with local experts) because: (i) lower income countries often lack resources to conduct national economic analyses (generally in their own language) and (ii) NGOs generally write in English and their reports should therefore have been captured by our search and be included in InvaCost. Consequently, even though our non-English data clearly shows the effect of a lower research effort for many Asian countries, we believe our strategy has allowed us to minimize the number of overlooked records. To tackle language barriers, publishers and/or authors could regularly translate non-English studies to English to maximize the accessibility and effectiveness of these studies (Amano et al. 2016; Tao et al. 2018). It is, thus, essential to initiate the collaborations between English and non-English speakers so that scientists could disseminate information that is not available in English. Moreover, non-English speakers could upload the local data to the global database to facilitate the international collaborations.

The lack of information in most Asian countries suggests a strong geographical bias in the estimation of economic costs. One reason for the biased coverage may be the difference in economic activities among countries, because invasion impacts are assumed to be poorly documented in countries with lower income (Nghiem et al. 2013). However, we argue that it is probably not a key determinant, because our study largely lacks data from South Korea (only one 'Unspecified' record), Saudi Arabia (no record), Turkey (no record), Thailand (only records of *A. aegypti* and *A. albopictus*), and Iran (no record), which are all among the ten countries with the highest GDP in Asia (International Monetary Fund 2019; https://www.imf.org/). Data insufficiency is more marked in Central and North Asia, which covers a large proportion of the territory of Asia and is recognized as a priority area for the management of biological invasions (Turbelin et al. 2017). This geographical bias might be partly diminished after including non-English studies from those countries/regions but would still remain widespread, limiting the capacity to manage invasions at the regional scale (Bellard and Jeschke 2016). In addition, we realize the potential limitation in methods of estimating economic impacts at the country level. For example, despite Pimentel et al. (2001) estimating economic impacts in India with much caution, they still applied a rather simple method which just attributed a fixed proportion (12.6%) of the loss in all crop productions to invasive species. A standardized method is thus urgently needed to unify the estimation of economic impacts across countries (Hanley and Roberts 2019). The development of a more holistic strategy of invasion management also necessitates the close collaboration of countries, because species invasions are not stopped by political boundaries (Bellard and Jeschke 2016; Early et al. 2016).

The estimation of economic costs is heavily biased towards insects and mammals, despite their smaller proportions of introduced species in Asia. It has been well acknowledged that the estimation of invasion impacts mainly focuses on species for which the impacts can be readily quantified (Wilson et al. 2018; Hanley and Roberts 2019). Compared to other taxa, insects and mammals have caused more severe impacts on health systems and social welfare, which can be easily monetized (Bradshaw et al. 2016; Lodge et al. 2016; Hanley and Roberts 2019). The marked taxonomic biases indicate the urgent need of conducting estimation for species from other taxa, especially for taxa currently with limited data. For example, aquatic invasive species (e.g. algae and molluscs) have caused remarkable changes in community structure and ecosystem functioning (Xiong et al. 2015; Anton et al. 2019). Indeed, aquatic species only contributed to 8.5% of cost records and 3.4% of total amount of economic losses in Asia, indicating the considerable knowledge gap concerning both freshwater and marine invaders. A similar trend has been found at the global scale, where aquatic invasions have cost US$ 345 billion in recent decades, but are an order of magnitude lower than terrestrial invasion costs (Cuthbert et al. 2021). One possible reason for this knowledge gap is that current assessment of invasion costs largely ignores the decreased economic value associated with changing biodiversity (e.g. the decrease in the abundance and richness of native species), which is very difficult to estimate (Bradshaw et al. 2016; Lodge et al. 2016). Moreover, invasion costs may be more difficult to observe in submerged environments, or could result from generally fewer assets or research biases compared to terrestrial systems (Cuthbert et al. 2021). Our synthesis does not include any study specifically estimating economic impacts of marine invaders, although countries in Asia produce more than 80% of all marine cultured biomass (The State of World Fisheries and Aquaculture 2020). Moreover, the opening of the Suez Canal sparked the massive invasions of organisms from the Red Sea to the coast of Israel (Galil et al. 2019). Hence, future studies should not only characterize species with high economic impacts, but also assess the relationship between ecological and economic impacts, given the current information of ecological impacts is much more abundant (Jeschke et al. 2014; Lodge et al. 2016; McGeoch et al. 2016).

Compared to the great damages caused by invaders, the expenditures on management contributed to only 2.3% of total economic costs in Asia. Management costs were similarly very low in Central and South America (2.1%, Herigner et al. 2021). In other continents, management expenses were always higher than in Asia, yet consistently much lower than damage and loss costs: Africa (27%, Diagne et al. 2021), Europe (16%, Haubrock et al. 2021), or North America (<20%, Crystal-Ornelas et al. 2021). This suggests the necessity of increasing funding for invasion management in Asia. Although preventing species introduction is the most cost-effective way to manage future invasions (Hulme 2006; Lodge et al. 2016), the majority of Asian countries are still under-equipped to mitigate invasions (Early et al. 2016; Turbelin et al. 2017). The difference in economic costs among impacted sectors echoes the bias among taxonomic groups, with much fewer records being reported for fishery and forestry. Estimating economic impacts is further complicated by the notorious difficulty in some sectors, such as ecosystem-regulating services, for which species impacts depend on recipient contexts and invasion stages (Bradshaw et al. 2016; Lodge et al. 2016; Wilson et al. 2018; Hanley and Roberts 2019). To better inform invasion management, more attention should be paid to estimating sectors currently with limited information.

Invasive species have caused great economic losses in Asia, but we should be aware that reported economic impacts are more related to historical rather than current socioeconomic activities (i.e. invasion debt; Essl et al. 2011): we are now mainly seeing the impacts caused by species that were introduced in the last century, and are yet to endure the impacts of following invasions. In the future, we would expect heightened economic impacts of invasive species in Asia, due to the consequence of considerable increases in trade activities and international travel and tourism (Seebens et al. 2017; Sardain et al. 2019). Rapidly changing climates would further facilitate the expansion of invasive species and exaggerate their impacts (Bellard et al. 2013; Hanley and Roberts 2019; Essl et al. 2020). To optimize the allocation of limited resources, the management of invasions should be prioritized towards species causing higher economic impacts and regions suffering higher losses (Vander Zanden and Olden 2008; McGeoch et al. 2016). We also suggest economic costs should be more comprehensively estimated for species with known environmental impacts, and reported in a centralized and standardized manner to ensure reliable quantifications of impacts at multiple scales. Finally, we call for more collaboration at the national (especially between researchers, stakeholders and decision-makers) and international scales to provide further incentive to estimate economic costs associated with biological invasions in Asia.

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Supplementary material 1

Table S1. The dataset of economic costs caused by invasive species in Asia

Authors: Chunlong Liu, Christophe Diagne, Elena Angulo, Achyut-Kumar Banerjee, Yifeng Chen, Ross N. Cuthbert, Phillip J. Haubrock, Natalia Kirichenko, Zarah Pattison, Yuya Watari, Wen Xiong, Franck Courchamp

Data type: database

Link: https://doi.org/10.3897/neobiota.67.58147.suppl1

Supplementary material 2

Table S2. The classification and description of seven sectors impacted by invasive species

Authors: Chunlong Liu, Christophe Diagne, Elena Angulo, Achyut-Kumar Banerjee, Yifeng Chen, Ross N. Cuthbert, Phillip J. Haubrock, Natalia Kirichenko, Zarah Pattison, Yuya Watari, Wen Xiong, Franck Courchamp

Data type: species data

Link: https://doi.org/10.3897/neobiota.67.58147.suppl2

Supplementary material 3

Table S3. The classification and description of four types of costs caused by invasive species

Authors: Chunlong Liu, Christophe Diagne, Elena Angulo, Achyut-Kumar Banerjee, Yifeng Chen, Ross N. Cuthbert, Phillip J. Haubrock, Natalia Kirichenko, Zarah Pattison, Yuya Watari, Wen Xiong, Franck Courchamp

Data type: species data

Link: https://doi.org/10.3897/neobiota.67.58147.suppl3

Supplementary material 4

Table S4. The completeness of cost estimation for each of five ecological groups per country

Authors: Chunlong Liu, Christophe Diagne, Elena Angulo, Achyut-Kumar Banerjee, Yifeng Chen, Ross N. Cuthbert, Phillip J. Haubrock, Natalia Kirichenko, Zarah Pattison, Yuya Watari, Wen Xiong, Franck Courchamp

Data type: species data

Link: https://doi.org/10.3897/neobiota.67.58147.suppl4

Supplementary material 5

Table S5. Species that have been introduced in Asia and caused economic costs in other continents

Authors: Chunlong Liu, Christophe Diagne, Elena Angulo, Achyut-Kumar Banerjee, Yifeng Chen, Ross N. Cuthbert, Phillip J. Haubrock, Natalia Kirichenko, Zarah Pattison, Yuya Watari, Wen Xiong, Franck Courchamp

Data type: species data

Explanation note: Species are ordered according to the amount of economic cost decreasingly.

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First synthesis of the economic costs of biological invasions in Japan

Yuya Watari[1], Hirotaka Komine[1,2], Elena Angulo[3], Christophe Diagne[3], Liliana Ballesteros-Mejia[3], Franck Courchamp[3]

1 *Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba-shi, Ibaraki 305-8687, Japan* **2** *present adress: Faculty of Agriculture, Yamagata University, 1-23 Wakaba-machi, Tsuruoka, Yamagata, 997-0037 Japan* **3** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405, Orsay, France*

Corresponding author: Yuya Watari (ywatari@affrc.go.jp)

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Abstract
Despite the large body of knowledge recognising the impact of biological invasions on biodiversity, their economic impact has been less evaluated. However, the associated economic costs ought to provide useful information on many different aspects to prevent and manage invasions. Here, we describe the economic costs of biological invasions in Japan using InvaCost, a recently-published global database on monetary costs extracted from English and non-English sources, as well as a complementary search, thereby filling a gap in regional knowledge. We focused on the following four dimensions when analysing the economic costs of biological invasions: damage to biodiversity, damage to human livelihood, management for biodiversity and management for human livelihood. Interestingly, there was no information about biological invasion costs for Japan in English, but the Japanese search and our additional survey provided a total of 630 cost entries, with a total economic cost of 728 million USD (2017 value, equivalent to 62 billion JPY). These entries appeared in 33 documents and corresponded to a total of 54 species. We showed that: 1) damage costs from biological invasions tend not to be assessed as frequently as management costs and are more underestimated; 2) despite the numerous entries, an overwhelmingly limited amount of the management budget was allocated to biodiversity conservation compared to protecting human livelihood; 3) budgets have been intensively invested in invasive species management on small islands, which reflects the vulnerability of small island ecosystems and economies to biological invasions; 4) the recorded costs still seem to be greatly underestimated, mainly due to the lack of recording (and potentially limited access to recorded cost information). These findings are not only specific to Japan, but may also be widely applicable to most other countries. The future recording of economic costs will help to close the gap between actual and recorded costs, leading to more realistic guidelines for tackling biological invasions.

Abstract in Japanese

日本における外来種の侵入が引き起こす経済的コストの初統合. 外来種の侵入が引き起こす生物多様性への影響については，多くの知見がある一方で，その経済的影響はあまり評価されていない．しかし，外来種の侵入が関連する経済的コストを評価することは，侵入の阻止，管理のための様々な側面から役立つ情報を提供してくれるはずである．ここでは，最近公開された英語情報源および英語以外の情報源から抽出した経済コストに関するグローバルなデータベースであるInvaCostを用いて，日本における外来種の侵入の経済的コストを記載するとともに，グローバルデータベースと地域的な知見のギャップを埋めるために，補完的な検索も行った．外来種の侵入の経済的コストを分析する際には，生物多様性への被害，人間の生活への被害，生物多様性のための管理，人間の生活のための管理の4つの次元に注目した．興味深いことに，日本の外来種の侵入のコストに関する情報は英語の情報源には存在しなかったが，日本語検索による情報源と本研究の追加調査により，合計630件のコスト情報件数が得られ，合計で7億2800万米ドル（2017年の価値，620億円相当）の経済コストが計上された．これらのエントリは33のデータソースに記載され，コストが記録された外来種は合計54種であった．本研究では以下のことを示した．1）外来種の侵入による被害コストは管理コストに比べて評価されることが少なく，過小評価される傾向があること，2）外来種管理の予算のうち，生物多様性の保全のための対策は多数の項目があるにもかかわらず，人間生活を守るための予算と比べると額が圧倒的に少ないこと，3）離島の外来種対策に集中的に予算が投入されており，これは離島の生態系や経済が外来種の侵入に脆弱であることを反映していること，4）コストは多くの場合記録されていなかったりアクセスが困難であったりするために，今回計上されたコストは依然として大幅に過小評価されているように思われること．これらの知見は日本だけでなく，他の多くの国にも広く適用可能である．今後，経済的コストを記録することで，実際のコストと計上されるコストのギャップを埋めることができ，外来種の侵入に対応するためのより現実的なガイドラインにつながると考えられる．

Abstract in French

Première synthèse du coût économique des invasions biologiques au Japon. Malgré le vaste cortège de connaissances qui reconnaît l'impact des invasions biologiques sur la biodiversité, leur impact économique a été moins évalué. Pourtant, les coûts économiques associés sont sensés constituer des informations utiles pour bien des aspects de prévention et de gestion des invasions biologiques. Dans cette étude, nous décrivons le coût économique des bioinvasions au Japon en utilisant d'une part InvaCost, une base de données globale récemment publiée sur les coûts monétaires des invasions et extraites à partir de sources rédigées en langues anglaise et non-anglaises, et d'autre part des recherches complémentaires plus spécifiques, comblant ainsi des lacunes de connaissance régionale. Notre analyse des coûts économiques des invasions biologiques est déclinée selon les quatre dimensions suivantes : les dégâts sur la biodiversité, les dégâts sur les moyens humains de subsistance, la gestion de la biodiversité et la gestion des moyens humains de subsistance. De façon intéressante, il n'y a aucune information concernant le coût des invasions biologiques au Japon qui soit disponible en anglais, mais une recherche en Japonais et nos investigations complémentaires ont permis de compiler 630 mentions de coûts, pour un total de 728 millions USD (valeur de 2017, équivalents à 62 milliards yens). Ces mentions ont été identifiées à partir de 33 documents et correspondent à 54 espèces. Nous montrons que: 1) les coûts des dégâts liés aux invasions biologiques ont tendance à ne pas être évalués aussi fréquemment que les coûts liés à leur gestion, et sont davantage sous-estimés ; 2) malgré les nombreuses mentions, le budget alloué à la conservation de la biodiversité est étonnamment faible comparé à celui alloué pour préserver les moyens humains de subsistance ; 3) des budgets ont été massivement investis dans la gestion des espèces envahissantes sur les petites îles, ce qui reflète la vulnérabilité de ces écosystèmes et économies insulaires face aux invasions biologiques ; 4) les coûts mentionnés semblent largement sous-estimés, essentiellement à cause du manque de documentation rapportant ces coûts (et potentiellement d'un accès limité aux informations sur les coûts rapportés). Ces résultats ne sont pas spécifiques au Japon, mais pourraient aussi être largement applicables à la plupart des autres pays. De futurs efforts sur l'estimation et la documentation des coûts économiques permettra de combler l'écart entre les coûts réels et les coûts effectivement enregistrés, ce qui mènera à des recommandations plus réalistes pour lutter contre les invasions biologiques.

Abstract in Spanish

Primera síntesis de los costos económicos de las invasiones biológicas en Japón. A pesar de la gran cantidad de información científica sobre las invasiones biológicas que reconoce los impactos en la biodiversidad, los impactos económicos han sido menos evaluados. Sin embargo, los costos económicos asociados a las invasiones deberían proporcionar información útil en muchos aspectos, para prevenir y gestionar las invasiones. En este trabajo, describimos los costos económicos de las invasiones biológicas en Japón, usando la recientemente publicada base de datos InvaCost, que contiene los costes económicos extraídos a partir de documentos en lengua inglesa y en otras lenguas no inglesas, así como datos obtenidos en una búsqueda complementaria, lo cual ha llenado una laguna del conocimiento regional. Enfocamos el análisis de los costos económicos de las invasiones biológicas en las siguientes cuatro dimensiones: los daños a la biodiversidad, los daños al bienestar humano, la gestión para la biodiversidad y la gestión para el bienestar humano. Es de destacar que no hubo información en inglés para Japón, mientras que nuestra búsqueda adicional resultó en 630 entradas de costos, con un total económico de 728 millones de dólares americanos (valor de 2017, equivalente a 62 mil millones de yenes). Estas entradas de costos procedieron de 33 documentos y correspondieron a un total de 54 especies. Mostramos que: 1) los daños de las invasiones biológicas parecen no haber sido evaluados tan frecuentemente como las estrategias de gestión y por lo tanto parecen más subestimados; 2) a pesar de las numerosas entradas, la cantidad de dinero de gestión asignada a biodiversidad fue abrumadoramente limitada en comparación con la asignada al bienestar humano; 3) el dinero se ha invertido de forma intensiva en el manejo de las especies invasoras en islas pequeñas, lo que refleja la vulnerabilidad de los ecosistemas de las islas pequeñas y sus economías a las invasiones biológicas; 4) los costos reportados parecen estar aún fuertemente subestimados, debido sobre todo a la falta de registros (y por un acceso a la información sobre costos potencialmente limitado). Estos resultados no son específicos de Japón, sino que pueden ser aplicados ampliamente a la mayor parte de los países. Si en el futuro se registran los costes económicos, esto ayudará a cerrar la brecha que existe entre los costes que ocurren y los reportados, lo cual llevará a proponer medidas más realistas para abordar las invasiones biológicas.

Keywords

Actual costs, biodiversity, island, InvaCost, invasive species, Japanese, non-English language, underestimated costs

Introduction

Biological invasions are known to be a leading cause of biodiversity degradation worldwide (Clavero and Garcia-Berthou 2005; Bellard et al. 2016). However, their economic impacts and costs on several sectors, such as the environment, agriculture and fishery, as well as the economic expenses associated with their management, have been less evaluated (Courchamp et al. 2017). The economic evaluation of invasive species may provide useful information at many levels (Dana et al. 2013). For example, it may contribute to raising awareness about the threat posed by invasive species. In addition, prioritising management actions and assessing their cost-effectiveness can help to improve local strategies towards invaders. Up to now, there have been some economic assessments for regions like the United States (Pimentel et al. 2005), Europe (Kettunen et al. 2008) and Southeast Asia (Nghiem et al. 2013). However, regional coverage is lacking and the overview of the economic costs is still unknown (but see Diagne et al. 2020a, 2021; Angulo et al. 2021), indicating the necessity for further research to evaluate the economic costs in many countries and regions. In particular, comprehensive estimates at the national level – the most important unit for designing and implementing management – are in dire need.

Japan has the third largest GDP (International Monetary Fund 2018) in the world, with the fourth largest international trade market (World Trade Statistical Review 2019) and a large pet trade (Auliya et al. 2016; Kitade and Naruse 2020). As a result, Japan is a world centre of both biological invasions and invasion science (Mito and Uesugi 2004; Mizutani and Goka 2010). Although the Global Invasive Species Database (2020) lists 263 invasive species for Japan, the Ecological Society of Japan identified 2,230 species in its list of alien species for the country almost 20 years ago (Ecological Society of Japan 2002). Amongst these species, many invasive species are known to induce severe ecological impacts and agricultural damage. Examples of ecological impacts include predation on endangered species by invasive predators, such as the small Indian mongoose *Urva auropunctata* (Watari et al. 2008), the black rat *Rattus rattus* (Chiba 2010), free-ranging cats *Felis silvestris catus* (Shionosaki et al. 2015; Kobayashi et al. 2019; Maeda et al. 2019; Azumi et al. 2021) and the green anole *Anolis carolinensis* (Abe et al. 2008). Examples of agricultural damage include damage to agricultural products by common raccoons *Procyon lotor* (Suzuki and Ikeda 2019) and alien invasive insects (Kiritani 1998). In addition, the management of invasive alien species is conducted across the country, with several large-scale projects, such as an eradication project on islands (Kiritani 1998; Koyama et al. 2004; Fukasawa et al. 2013a; Watari et al. 2013; Komine et al. 2016; Sato 2019; Yagihashi et al. 2021).

Japan features more than 6,800 islands (Higuchi and Primack 2009) with a wide geographical expanse ranging 3,000 km in both east-west and north-south directions (Fig. 1) and its climate ranges from subarctic to temperate and subtropical (Higuchi and Primack 2009; Japan Meteorological Agency 2016). Therefore, various invasive species in Japan are expected to incur a wide range of costs, although the comprehensive assessment of these economic costs has yet to be conducted. Such an assessment could enable us to estimate the optimal budget size and distribution for targeted management, promote biosecurity policies to prevent future potential costs and assess the cost performance of management strategies. According to the global definition of an island, the entire Japanese territory is an island. However, most Japanese people distinguish between the four largest islands (Honshu, Hokkaido, Kyushu and Shikoku) as the mainland (hereafter, mainland) and the other thousands of smaller islands as islands (hereafter, islands) (Fig. 1). This classification is mainly based on the discontinuous nature of the area (the smallest mainland is Shikoku measuring 18,298 km^2, while the largest island used in this study is Okinawa-jima Island measuring 1,207 km^2) and it features differences in most biogeographical aspects. For example, all four

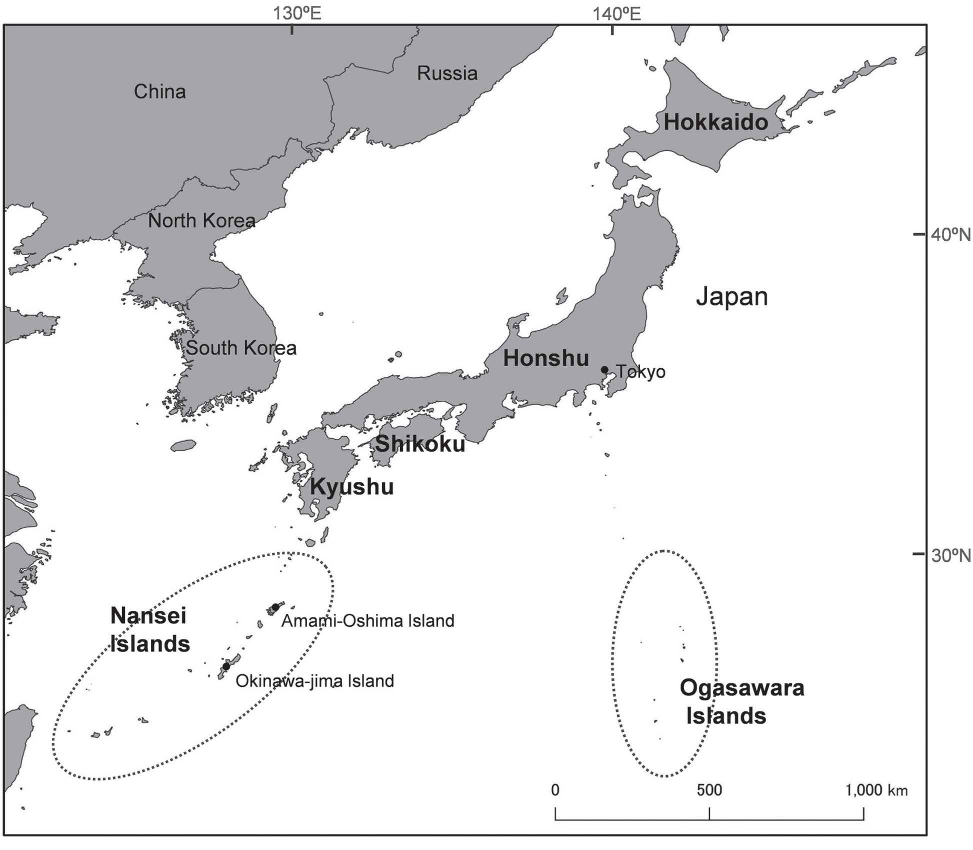

Figure 1. Map of the four main islands (mainland: Hokkaido, Honshu, Shikoku, Kyushu) and Nansei Islands and Ogasawara Islands in Japan.

mainlands have multiple native mammalian carnivore species, whereas they are absent from most islands (Ohdachi et al. 2015), which, instead, have very unique and vulnerable ecosystems, where the impact of invasive species tends to be greater (Courchamp et al. 2003). Across the Japanese territory, high conservation priority has been given to the islands isolated from both the Japanese mainland and the Eurasian continent (Glen and Hoshino 2020), as they harbour many endemic and endangered species and are therefore a major component of biodiversity in Japan. For example, the Ogasawara Islands have been designated as a Natural World Heritage Site (UNESCO World Heritage Centre 2012) and part of the Nansei Islands is a candidate for a Natural World Heritage Site (UNESCO World Heritage Centre 2016). Many of these islands are extremely vulnerable to alien predators, because their native species have evolved in the absence of native predatory mammals. Therefore, assessing the economic costs of biological invasions in these regions can contribute to improving the measures to protect their valuable biodiversity. However, this has not yet been done.

A recently-published database of the economic costs of biological invasions (Angulo et al. 2020, 2021; Diagne et al. 2020b) provides comprehensive information on the economic damage and expenditure associated with invasive species around the world, with an extension that focuses on the entries of economic costs in non-English-speaking countries. Using this database and the results of a complementary search performed for this study, we aimed to describe the outline and details of the recorded economic costs of biological invasions for Japan. In particular, we described the economic costs of invasive species in Japan following two approaches. First, we focused on the difference between the economic damage caused by invasive species and the cost of their management. Invasive species damage represents a substantial economic loss (reactive) that requires scientific knowledge and administrative systems to evaluate the damage, whereas invasive species management is an expense (proactive) that allows us to calculate the cost incurred directly from the management budget. Consequently, the qualities of damage and management as economic costs differ from each other. Second, we differentiate between the targets of each type of damage and management, i.e. between human livelihood (e.g. agricultural productions and human health) and biodiversity. The impact of invasive species on human livelihood is clearly visible and can be easily monetised. Therefore, their management appears to be relatively straightforward to implement (Nuñez and Pauchard 2010; Rose et al. 2018). By contrast, the impacts on biodiversity can have a profound effect on human life in the long term (Rose et al. 2018), but the impacts on human livelihood are indirect, less visible and, hence, difficult to monetise (Courchamp et al. 2017). Therefore, expenses associated with the management of biodiversity conservation probably require increased public awareness of the value of biodiversity and the economic margins involved (Nuñez and Pauchard 2010; Rose et al. 2018). Clarifying the gaps between damage and management costs and between human production and biodiversity will help us to better understand the current situation and challenges in Japan. Ultimately, this would provide us with clues about how to better tackle the problem of invasive species in the future. Based on this framework, we further describe economic costs with a focus on: 1) the differences in taxonomic groups of the reported costs, 2) annual trends in the reported costs and 3) difference in costs between the mainland and islands. Finally, we explore the problems of data accessibility encountered during the compiling of the Japanese entries, consider the possible underestimation of the recorded costs and point out the importance of recording costs in an accessible form.

Methods

Data acquisition and categorisation

To analyse the economic cost of biological invasions in Japan, we used InvaCost (version 3.0, openly available at https://doi.org/10.6084/m9.figshare.12668570), a recently-compiled database which compiles the monetary impacts of invasive species reported in English and non-English documents worldwide (Diagne et al. 2020b; Angulo et al. 2021). InvaCost was developed following a systematic and standardised methodology to collect information from scientific articles, grey literature, stakeholders and expert elicitation. The most up-to-date version (v3.0) of InvaCost contains 9,823 cost entries; each entry refers to a unique cost value with specific descriptors (columns) that describe the spatial and temporal information of the cost, the taxonomy of the species causing the cost, the typology of the cost and the document reporting the cost. A set of columns reports the cost value in both local currencies and in USD, i.e. converted by dividing the cost estimate by the official market exchange rate corresponding to the year of the cost estimation and then to 2017 USD using inflation factors (Diagne et al. 2020b).

Given the importance of the search in Japanese, we summarise here how this search was performed (for more details, see Angulo et al. 2021). First, in the Web of Knowledge, the same search strings were used as in English, i.e. a combination of terms related to the economic costs and invasive species, but setting the Language to Japanese; 64 articles were retrieved but none with costs. Second, we used a similar search string in Google Scholar with Japanese terms: 205 articles were retrieved, including eight with economic costs. Finally, in the Google search engine, the Japanese terms for "budget" AND "exotic organisms" were used, directing the search to the webpage JUDGIT! (JUDGIT! 2019), a volunteer organisation that compiles the budgets of the Japanese government, which provided most of the Japanese-language entries in InvaCost_v3.0. The search of the Japanese entries was conducted for economic costs incurred through 2017.

A total of 329 cost entries was obtained from InvaCost_v3.0. Only one source came from the English database; the remaining 328 entries were Japanese and came from the non-English database (Suppl. material 1: Table S1). However, the English cost entry, based on the description of Armstrong and Ball (2005) citing Kiritani (1998), was excluded from our analyses, because Kiritani (1998) did not present a cost description and, therefore, may be considered misquoted. Moreover, this English entry represented the cost of the eradication project of melon flies *Bactrocera cucurbitae* and oriental flies *Bactrocera dorsalis*, while the Japanese entries (Reference ID: JP_6 in Suppl. material 1: Table S1) described these costs in more detail.

We also conducted additional surveys to avoid the omission of cost data from important invasive alien species in Japan, because the searches conducted in English and non-English emphasised the uniformity of the search methods across countries, which may lead to the omission of locally-important invasive species. Thus, we conducted searches in the JUDGIT! database (JUDGIT! 2019) using the common names (in Japanese) of all species listed in the "100 worst invasive alien species in Japan" (Ecological Society of Japan 2002) as search strings. The JUDGIT! database mostly compiles budgets since 2014 with the exception of a few in 2013. Moreover, JUDGIT! not only extracts each entry, but also shows the budget subjects in which the entries are located, which, in turn, allows us to search for other projects located in each budget subject. Using this function, we also extracted cost entries related to invasive species other than the 100 worst species. Similar to the InvaCost, the search was conducted for economic costs incurred through 2017. The cost entries obtained from this additional search were finally combined with the entries obtained from InvaCost_v3.0 (Suppl. material 1: Table S1).

We re-classified the type of costs associated with the entries by dividing them into two categories: "Damage" and "Management". "Damage" includes the economic loss caused by the invasive alien species and the expenses incurred to repair its impacts, while "Management" includes the expenses associated with managing invasive alien species itself, including prevention, eradication, control, research, buying equipment and environmental education to promote a better understanding of invasive species management. These two categories are then further divided into two categories: "Human" and "Biodiversity", where "Human" refers to the costs directly related to human livelihood-impacted sectors, such as agriculture, fisheries, forestry and human health. "Biodiversity" refers to the costs with respect to natural ecosystems, including the impact of invasive species on native species and ecosystem services (e.g. ecotourism). The classification scheme is shown in Suppl. material 2. Amongst the costs categorised under "Management", it is sometimes difficult to clearly determine whether the purpose of management applies to "Human" or "Biodiversity". For example, the management implemented by the Ministry of Agriculture, Forestry and Fisheries can be clearly categorised as "Human", while the management implemented by the Ministry of the Environment can be categorised as either "Biodiversity" or "Human", because the objectives stated in the law include, not only the conservation of biodiversity, but also the protection of human health. Furthermore, species that can pose a risk to human health also pose a potential and future risk to biodiversity. Therefore, in this study, for species with notable characteristics that may be harmful to human health, such as venomous insects and for which large-scale management is undertaken at the beginning of an invasion, we assumed that the government implemented the management action mainly to prevent risks to human health. In this case, we classified the management costs for such species as Management_Human (e.g. the red imported fire ant *Solenopsis invicta*). Based on these four categories – i.e. damage to biodiversity (Damage_Biodiversity), damage to human livelihood (hereafter, Damage_Human), management for biodiversity (Management_Biodiversity) and management for human livelihood (Management_Human), subsequent analyses were conducted focusing on the number of entries and the amount of economic costs.

Data analyses

We first compared the economic costs reported for each taxonomic group using the Class and species taxonomic classification. Second, to examine the annual change in economic costs, we plotted the costs against the year. Most of the Japanese entries are based on projects conducted by the government, in which the temporal unit of entries is the Fiscal Year (e.g. FY2017 = 2017 April – 2018 March). Here, for the sake of convenience, we treated the fiscal year as the year of the beginning period (FY2017 = 2017). Some of the entries in the database described total costs over multiple years. To determine the annual costs, we used the function "expand-

YearlyCosts" from the invacost package (Leroy et al. 2020). In this case, the total cost was divided by the number of years and converted to a cost per year. Third, to compare the costs between the mainland and islands, we compared between the entries with the ‘Island’ column as “Y”, which corresponded to islands and those with “N”, which corresponded to the mainland and unspecified geographic regions (Suppl. material 1: Table S1). Finally, to compare the number of entries and the amount of economic costs per unit area for the mainland and islands, we calculated the number of entries and economic costs per unit area for the total area of the mainland (361,006 km^2; Honshu, Hokkaido, Kyushu and Shikoku) and the islands (16,968 km^2). However, caution is required, as it is possible that some of the island entries are recorded in the mainland entries due to the limited identification of the location in their information sources.

Results

We obtained a total of 630 cost entries, of which 328 were from the non-English database and 302 from the search performed for this study (there were no recorded costs in English). Based on these entries, invasive species cost a total of 728 million USD (2017 value) to the Japanese economy from 1965 to 2017. These entries came from 33 documents and 16 authors (Suppl. material 1: Table S1). The author with the most entries was JUDGIT!, with 17 data sources (budget subjects of the Japanese government), 499 entries and 86 million USD. Of this information, the budgets of the Ministry of the Environment had the largest number of entries, with 318 entries, followed by 177 entries from the Ministry of Agriculture, Forestry and Fisheries and four entries from the Ministry of Economy, Trade and Industry. In terms of economic costs, the Ministry of Agriculture, Forestry and Fisheries had the largest budget at 48 million USD, followed by the Ministry of the Environment at 37 million USD and the Ministry of Economy, Trade and Industry at 0.7 million USD. The next author with most entries was the Ministry of Agriculture, Forestry and Fisheries with two data sources, which resulted in 93 entries and corresponded to 235 million USD. These were statistics on the economic damage caused by invasive mammals and birds recorded in each area of the country since 1999. The third largest entries were taken from a report from Okinawa Prefecture amounting to 10.55 million USD, which assessed the damage caused by invasive alien species in Okinawa Prefecture; this entry had not been included in the above summary of the Ministry of Agriculture, Forestry and Fisheries. These costs were followed by the report of invasive insect eradications (JP_6 in Suppl. material 1: Table S1) with five entries, with the largest costs being 333 million USD for the eradication project of invasive insects in the Nansei Islands and Ogasawara Islands, which accounted for almost half of Japan’s total costs in our dataset.

The number of entries (Fig. 2a) and the amount of economic costs (Fig. 2b) aggregated for the four categories of Damage_Biodiversity, Damage_Human, Manage-

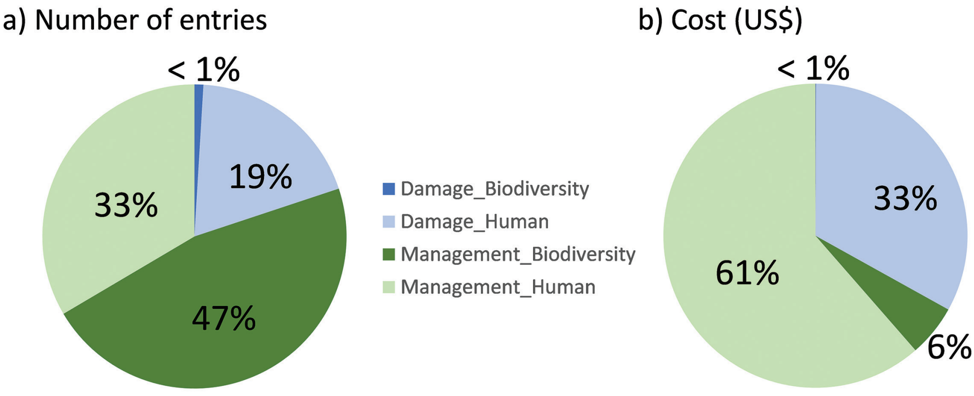

Figure 2. Breakdown of the number of cost entries (**a**) and the amount of costs (US$) (**b**) induced by biological invasions. Damage_Biodiversity and Damage_Human represent damage caused by biological invasions to biodiversity and human livelihood, respectively. Management_Biodiversity and Management_Human represent managements for biodiversity and human livelihood, respectively.

ment_Biodiversity and Management_Human show that the largest number of entries was recorded for Management_Biodiversity, accounting for 47% of the total number of entries. However, these entries only constituted 6% of the total economic costs. By contrast, both Damage_Human and Management_Human had a high proportion of the total economic costs compared to the number of entries. Damage_Biodiversity was < 1% in both cases.

A total of 54 invasive species had reported costs (Fig. 3). As to the number of entries by taxonomic groups (Fig. 3a), mammals had the highest total number of entries (190 entries), followed by nematodes (171 entries) and insects (78 entries). The species with the highest number of entries was the pine wilt nematode *Bursaphelenchus xylophilus* (163 entries), which has caused widespread pine dieback in Japan. The common raccoon and small Indian mongoose both had high Damage_Human and Management_Biodiversity, whereas the Asian black hornet *Vespa velutina* had the second highest number of entries for Management_Human. Other species with more than 15 cost entries were the green anole *Anolis carolinensis*, free-ranging cats, the Argentinean ant *Linepithema humile*, the masked palm civet *Paguma larvata*, the coypu *Myocastor coypus* and the Taiwan squirrel *Callosciurus erythraeus*. Damage_Biodiversity was only recorded in the entries for the green anole, whose costs were associated with a conservation measure targeting the population of endemic insects damaged by the green anole on Ogasawara Islands (Abe et al. 2008).

For the economic cost by taxonomic groups, insects prominently had the largest amount of total costs, followed by mammals and nematodes (Fig. 3b). The costs of the other groups were relatively small. Amongst insects, the economic costs incurred by the melon fly *Bactrocera cucurbitae*, oriental fruit fly *Bactrocera dorsalis* and Sweet potato weevil *Cylas formicarius* were the largest, accounting for Management_Human (Fig. 3a), which corresponded to the eradication project conducted in the Nansei Is-

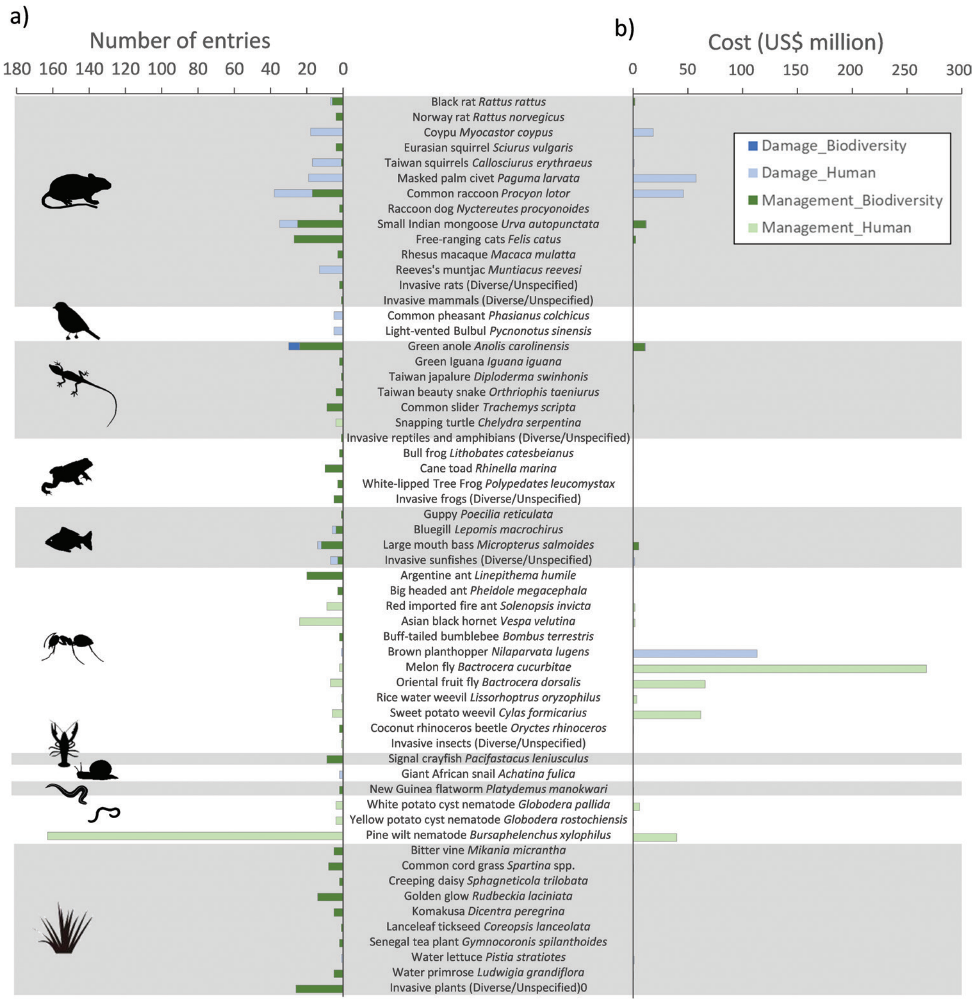

Figure 3. Taxonomic comparison of the number of cost entries (**a**) and the amount of cost (**b**) by species. Damage_Biodiversity and Damage_Human represent damage caused by biological invasions to biodiversity and human livelihood, respectively. Management_Biodiversity and Management_Human represent management for biodiversity and human livelihood, respectively. The square frames grouped, from top to bottom, into invasive mammals, birds, reptiles, amphibians, fishes, insects, crustaceans, gastropods, flatworms, nematodes and plants.

lands and Ogasawara Islands. Another invasive insect associated with large costs was the brown plant-hopper *Nilaparvata lugens*, which related to the emergency nationwide assessment of the economic loss in rice production after the outbreak of this species in 2013 (Ministry of Agriculture, Forestry and Fisheries 2013). By contrast, there was only a small cost associated with the Asian black hornet, even though this species had the largest number of entries. Amongst mammals, the coypu, masked-palm civet and common raccoon had relatively large costs for Damage_Human. The small In-

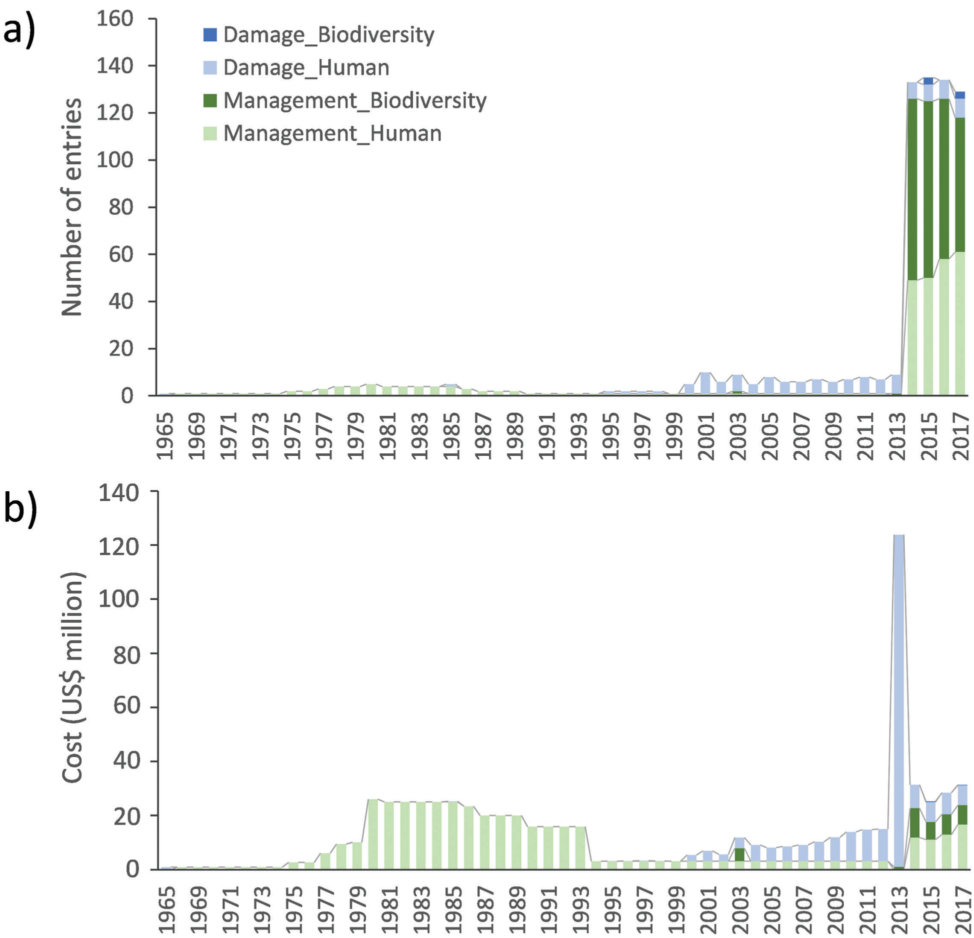

Figure 4. Annual change in the number of cost entries (**a**) and the amount of costs in US$ (**b**). Damage_Biodiversity and Damage_Human represent damage caused by biological invasions to biodiversity and human livelihood, respectively. Management_Biodiversity and Management_Human represent management for biodiversity and human livelihood, respectively.

dian mongoose had the largest costs for Management_Biodiversity, although the values were far smaller than those associated with Damage_Human and Management_Human in other outstanding species. Amongst nematodes, the pine wilt nematode had the largest costs for Management_Human.

Annual changes in the number of expanded entries and the amount of economic costs show that the reported costs began in 1965 (Fig. 4). For the number of entries (Fig. 4a), there is a small peak from the late 1970s to the late 1990s for Management_Human and in the early 2000s for Damage_Human. The largest peak in the number of entries has occurred since 2014, mainly in relation to Management_Biodiversity and Management_Human. By contrast, regarding the annual economic costs (Fig. 4b), the

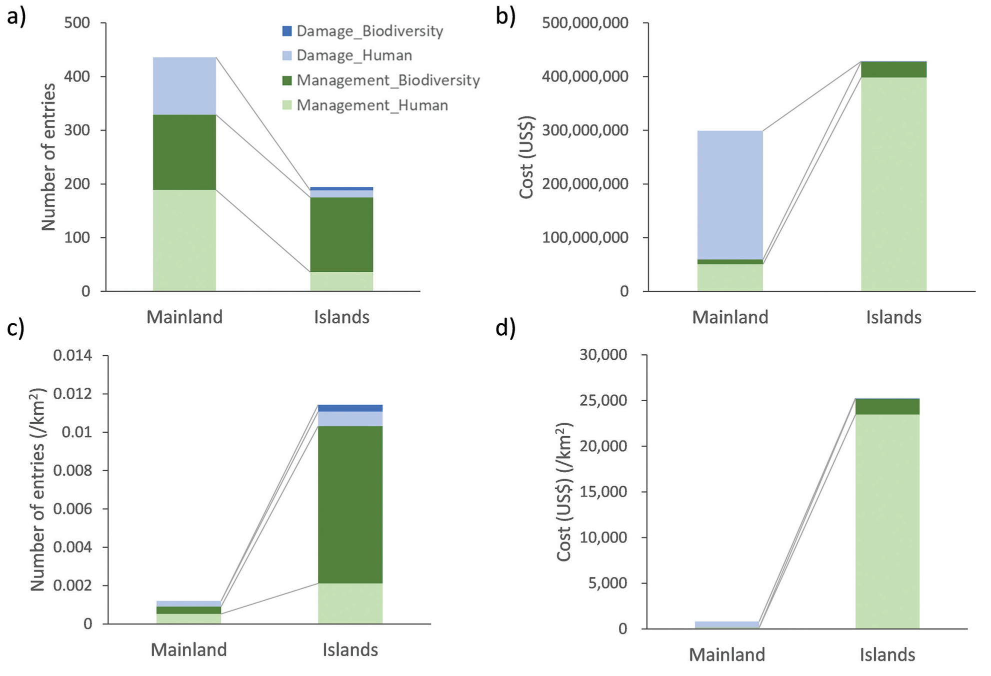

Figure 5. Comparison of (**a**) the mainland and islands for the number of cost entries (**b**) the amount of costs in US$ (**c**) the number of cost entries per unit area and (**d**) the amount of costs per unit area. Damage_Biodiversity and Damage_Human represent damage caused by biological invasions to biodiversity and human livelihood, respectively. Management_Biodiversity and Management_Human represent management for biodiversity and human livelihood, respectively.

highest costs were recorded for Damage_Human in 2013, which corresponded to a nationwide damage assessment of a large outbreak of the brown planthopper. With the exception of this one-off assessment, high cumulative economic costs were recorded for Management_Human from the late 1970s to the early 1990s, mainly in relation to the eradication projects targeting invasive insects on islands. Since 2014, relatively high costs have been recorded by the sum of Damage_Human, Management_Biodiversity and Management_Human.

Comparing of the number of entries between the mainland and islands showed that the mainland had more reported cost entries than the islands in relation to Damage_Human and Management_Human, whereas only the cost entries for Damage_Biodiversity were higher in the islands (Fig. 5a). By contrast, regarding the economic costs, the mainland had a higher cost for Damage_Human, although the islands exceeded the mainland in Management_Biodiversity, Management_Human and total costs (Fig. 5b), despite their smaller total land areas. The number of entries and the amount of economic costs per unit area between the mainland and islands resulted in 9.6 times more entries (Fig. 5c) and 30.5 times more costs (25,285 USD/km^2; Fig. 5d) recorded for the islands.

Discussion

Summary of the major findings

This study is the first attempt to analyse the recorded economic costs of biological invasions in Japan, which only used sources in the Japanese language: 630 cost entries with a total economic cost of 728 million USD (2017 value, equivalent to 62 billion JPY). The following are major findings in this study. First, damage costs caused by biological invasions tend not to be assessed as frequently as management costs and are more underestimated. Second, despite the numerous entries, an overwhelmingly small amount of the management budget was allocated to biodiversity conservation compared to protecting human livelihood. Third, budgets have been intensively invested in invasive species management on islands, which reflects the vulnerability of small island ecosystems and economies to biological invasions. Finally, the recorded costs seemed to be generally greatly underestimated, mainly due to the limited access to cost information.

Costs associated with human livelihoods versus biodiversity

The costs associated with human livelihoods were much higher than those associated with biodiversity. Scrutinising the nature of these costs suggests that Japan is still spending much more money on enduring or repairing damage directly related to human livelihoods rather than focusing on ecosystem conservation. In Japan, the Alien Species Act was enacted in 2005 (Mizutani and Goka 2010) and, since then, a relatively large number of projects for biodiversity conservation have been carried out, as seen in the increased number of cost entries relating to the management of invasive species for biodiversity in recent years. However, the amount of the costs allocated to these management actions for biodiversity is nevertheless very low, resulting in smaller budgets being spread across a large number of projects. This indicates that the priority for biodiversity conservation is still low in the Japanese government as a whole, except for the administrative sectors in charge of environmental conservation (e.g. Ministry of the Environment).

Costs for mainland versus islands

This study revealed that the costs per unit area were disproportionately higher on islands. As some costs incurred on islands may be reported in the costs for the mainland (see Methods), the costs reported on islands are underestimated relative to the mainland costs. To conserve native species on islands, Japan has invested a higher amount of money in managing invasive species, such as the management projects for invasive rats, goats and anole in the Ogasawara Islands (Sato 2019) and the small Indian mongoose on Amami-Oshima Island and Okinawa-jima Island (Watari 2011; Fukasawa et al. 2013b; Watari et al. 2013; Sugimura et al. 2014; Yagihashi et al. 2021), indicating the emphasis placed on the value and vulnerability of island biodiversity. In addition, the amount of costs for human livelihood was far higher than that for biodiversity in islands. This corresponded to the eradication projects targeting agricultural invasive insects, such as melon flies and weevils. As agriculture is a basic industry for most inhabited islands, including the production of sugarcane, sweet potatoes and fruits (e.g. Kagoshima Prefecture 2019), invasive insects could seriously damage the small and fragile economies of islands. The vulnerability of the island ecosystems and economies is thus reflected in the disproportionate cost of invasive species in islands.

Potential gaps between actual costs and available data

In general, the economic costs of biological invasions tend to be underestimated, because some are difficult to assess (e.g. costs incurred for biodiversity), even if they can exert long-term indirect impacts on humans (Nunes and van den Bergh 2001). Given the difficulty of fully filling this gap, the risk of invasive species and the necessity of their management should not only be discussed on the basis of the recorded economic costs. Another reason relates to the availability of data; if they exist, they are often difficult to access. The impacts of invasive species often occur locally and local measures tend to be implemented independently, which could prevent local practitioners and decision-makers from sharing information and technology with other regions (Kueffer et al. 2013), thus making it difficult for the scientific community to access the data. Therefore, economic assessments that only draw on the usual sources of data (i.e. scientific publications) can lead to underestimation and bias.

In this study, the overall management costs were higher than the damage costs in terms of both the number of cost entries and the amount of costs. The major difference between management and damage costs is that the former is an expense for managing biological invasions, which can be assessed by summing up the recorded budgets for human actions, whereas the latter is an economic loss caused by biological invasions, which requires a scientific approach and administrative system in order to be evaluated. For example, while management costs have been reported for many years, damage costs only began to be recorded in around 2000, when the Ministry of Agriculture, Forestry and Fisheries set up the national system to report the economic costs of crop damage by wildlife (Ministry of Agriculture, Forestry and Fisheries 2020). This correlation between recorded economic costs and research efforts implies that many costs actually incurred remain unassessed (Bradshaw et al. 2016; Kourantidou et al. 2021). In addition, it was only recently that damage to biodiversity began to be reported, although the costs recorded as damage to biodiversity in our dataset corresponded to the budget for in situ and ex situ conservation of threatened insects greatly damaged by the green anole (Karube 2019), which did not require additional efforts to evaluate the economic costs of the impact of the invasive species. This suggests that the economic costs of the invasion damage might be greatly underestimated and the degree of underestimation may be more pronounced in the case of damage to the biodiversity. Another indication of this underestimation is that only 54 species were evaluated for the economic costs out of 2,230 known to be present in Japan (Ecological Society of Japan 2002). The real costs, especially in terms of damage, could therefore be much higher. Although it is important to make further efforts to calculate the economic costs, it is still essential to further document the impact of invasive species on ecosystem functions, given the difficulty of adequately assessing the long-term and indirect economic losses caused by biodiversity losses (Nunes and van den Bergh 2001; Jackson 2015).

Insufficient data accessibility can also lead to underestimations. It is, therefore, a major limitation of this first synthesis of the costs of invasive species in Japan. The measures targeting invasive alien species in Japan, which are mainly based on the three laws: "Act on the Prevention of Adverse Ecological Impacts Caused by Designated Invasive Alien Species", "Protection and Control of Wild Birds and Mammals and Hunting Management Law" and "Act on Special Measures for Prevention of Damage Related to Agriculture, Forestry and Fisheries Caused by Wildlife" have been conducted at all levels of government, including the national government, 47 prefectural governments and 1,741 local municipal governments (Okabe et al. 2019). However, the entries in the dataset were biased towards those implemented by the national government, which were accessible on the internet. For example, the relatively large-scale eradication measures such as those implemented against the small Indian mongoose by the Okinawa Prefecture (Watari 2011; Yagihashi et al. 2021) and against Reeves's muntjac (*Muntiacus reevesi*) by Tokyo metropolitan government (Tokyo Metropolitan Government 2016) are not included in the present dataset. In addition, introduced common raccoons and masked palm civets are widespread in Japan (Ohdachi et al. 2015; Suzuki and Ikeda 2019) and many cities, towns and villages capture them to reduce crop damage (Ohdachi et al. 2015), but their economic costs are not included in the entries of the dataset. Moreover, even the national measures, conducted outside of the period and reported on the internet, are not included in the dataset. For example, the mongoose eradication project on Amami-Oshima Island started in 2000 (Watari et al. 2008), but its costs have only been available on the internet since 2014.

Even if the costs are published on the internet, they are not always listed in the dataset. For example, a document in the database summarising the contents of the budget for biological invasion management, based on "Act on the Prevention of Adverse Ecological Impacts Caused by Designated Invasive Alien Species", included a total of 2,512,000,000 JPY (2012–2017), whereas the amount of costs listed in our dataset (Suppl. material 1: Table S1) was 1,615,000,000 JPY (14,766,378 USD in 2017), meaning 38% of the total budget was omitted from the dataset of source documents. This gap is due to the difficulties in identifying the target invasive species from the title of each project listed in the source documents, most of which target multiple invasive species.

To access such data, it is necessary to conduct comprehensive and labour-intensive surveys of paper-based materials, as well as individual interviews with countless local government officials. In order to improve this situation, it is important to establish systems that allow the reporting of invasion costs in a widely-available form, such as a platform for indexing and searching administrative data and an open library to enable not only scientists, but also practitioners and decision-makers to easily access the economic costs.

Importance of including non-English information

Given the current situation where information from non-English sources has been ignored, becoming a barrier to the advancement of ecological scientific knowledge biodiversity conservation (Amano et al. 2016; Nuñez et al. 2019; Konno et al. 2020), using the InvaCost database will help to ensure that information will be shared more equitably, leading to better global and domestic evaluation of economic costs of invasive species.

Japan is one of the countries with a lower proportion of English speakers (Amano and Sutherland 2013) and, hence, information is more prone to be transmitted/published in Japanese, rather than in English (Konno et al. 2020). Indeed, only one entry was found for Japan in the English database (Diagne et al. 2020b). As a result, the English-based scientific community, has significantly overlooked evidence at least in terms of the economic cost evaluation of invasive species from non-English speaking countries. This study is the first attempt to compile and analyse the economic costs from the scattered data written in Japanese, which could be an important part of the global evaluation. It thus provides valuable information for non-Japanese speaking researchers, as well as practitioners and decision-makers. As the use of English information by local practitioners and decision-makers could usually be limited in non-English countries (Amano and Sutherland 2013; Amano et al. 2016; Angulo et al. 2021), we suggest the need for an increase in the collaboration between scientists and practitioners, to facilitate transfer of knowledge about local biological invasions. Here we show that omitting the non-English information would have resulted in an almost non-existent evaluation of economic costs for invasive species in Japan and, therefore, partial and biased, in agreement with previous studies (Konno et al. 2020; Angulo et al. 2021). The knowledge bias caused by neglecting the existing non-English information in the economic cost assessment of biological invasions is about to be significantly reduced with the construction of the non-English database used in this study (Angulo et al. 2021). The fact that the available data sources for this Japanese data synthesis were all from the Japanese literature is a typical example that reflects the biased global trend.

Conclusion

We showed the economic costs of biological invasions in Japan for various taxonomic groups and ecosystems over a period of more than 50 years. These costs mainly focused on humans (as opposed to biodiversity), management (as opposed to damage) and small islands (as opposed to the mainland). This study also showed that the economic costs of biological invasions may be grossly underestimated. Therefore, accepting the amount of economic costs provided here will inevitably lead to an underestimation of the impact of invasive species. To bridge this gap, it is necessary to continue efforts to compile records of economic costs, which will allow us to appropriately balance the impact of invasive species on the one hand and the scale of management measures on the other, hence providing more realistic guidelines for tackling the issue of biological invasions. The findings in this study are not only specific to Japan, but also widely applicable to other countries.

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Supplementary material 1

Table S1. Dataset of the economic costs of biological invasion in Japan

Authors: Yuya Watari, Hirotaka Komine, Elena Angulo, Christophe Diagne, Liliana Ballesteros-Mejia, Franck Courchamp

Data type: database

Explanation note: The dataset of the economic costs of biological invasion in Japan extracted from the InvaCost_v3.0 (openly available at https://doi.org/10.6084/m9.figshare.12668570) and the additional search in this study.

Link: https://doi.org/10.3897/neobiota.67.59186.suppl1

Supplementary material 2

Definition of the categorisation of economic costs

Authors: Yuya Watari, Hirotaka Komine, Elena Angulo, Christophe Diagne, Liliana Ballesteros-Mejia, Franck Courchamp

Data type: adittional data

Explanation note: Damage_Biodiversity and Damage_Human represent damage caused by biological invasions to biodiversity and human livelihood, respectively. Management_Biodiversity and Management_Human represent management for biodiversity and human livelihood, respectively. Categories in each cost entry are shown in Suppl. material 1: Table S1.

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RESEARCH ARTICLE

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Economic costs of biological invasions in terrestrial ecosystems in Russia

Natalia Kirichenko[1,2,3*], Phillip J. Haubrock[4,5*], Ross N. Cuthbert[6,7*], Evgeny Akulov[8], Elena Karimova[9], Yuri Shneyder[9], Chunlong Liu[10,11,12,13], Elena Angulo[13], Christophe Diagne[13], Franck Courchamp[13]

1 *Sukachev Institute of Forest, Siberian Branch of Russian Academy of Sciences, Federal Research Center "Krasnoyarsk Science Center SB RAS", Krasnoyarsk, Russia* **2** *Siberian Federal University, Krasnoyarsk, Russia* **3** *Reshetnev Siberian State University of Science and Technology, Krasnoyarsk, Russia* **4** *Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, Gelnhausen, Germany* **5** *University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Vodňany, Czech Republic* **6** *GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Kiel, Germany* **7** *School of Biological Sciences, Queen's University Belfast, Belfast, Northern Ireland, UK* **8** *All-Russian Plant Quarantine Center, Krasnoyarsk branch, Krasnoyarsk, Russia* **9** *All-Russian Plant Quarantine Center, Bykovo, Ramenskoe, Moscow Oblast, Russia* **10** *Institute of Biology, Freie Universität Berlin, Germany* **11** *Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany* **12** *Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany* **13** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, Orsay, France*

Corresponding author: Natalia Kirichenko (nkirichenko@yahoo.com)

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Abstract

Terrestrial ecosystems, owing to the presence of key socio-economic sectors such as agriculture and forestry, may be particularly economically affected by biological invasions. The present study uses a subset of the recently developed database of global economic costs of biological invasions (InvaCost) to quantify the monetary costs of biological invasions in Russia, the largest country in the world that spans two continents. From 2007 up to 2019, invasions costed the Russian economy at least US$ 51.52 billion (RUB 1.38 trillion, n = 94 cost entries), with the vast majority of these costs based on predictions or extrapolations (US$ 50.86 billion; n = 87) and, therefore, not empirically observed. Most cost entries exhibited

* These authors contributed equally.

low geographic resolution, being split between European and Asian parts of Russia (US$ 44.17 billion; n = 72). Just US$ 7.35 billion (n = 22) was attributed to the European part solely and none to the Asian part. Invasion costs were documented for 72 species and particularly insects (37 species). The empirically-observed costs, summing up to US$ 660 million (n = 7), were reported only for four species: two insects *Agrilus planipennis* Fairmaire and *Cydalima perspectalis* (Walker) and two plants *Ambrosia artemisiifolia* L. and *Heracleum sosnowskyi* Manden. The vast majority of economic costs were related to resource damages and economic losses, with very little reported expenditures on managing invasions in terrestrial ecosystems. In turn, agriculture (US$ 37.42 billion; n = 68) and forestry (US$ 14.0 billion; n = 20) were the most impacted sectors. Overall, we report burgeoning economic costs of invasions in Russia and identify major knowledge gaps, for example, concerning specific habitat types (i.e. aquatic) and management expenditures, as well as for numerous known invasive taxa with no reported economic costs (i.e. vertebrates). Given this massive, largely underestimated economic burden of invasions in Russia, our work is a call for improved reporting of costs nationally and internationally.

Abstract in Russian

Экономические потери от биологических инвазий в наземных экосистемах России. Наземные экосистемы в связи с наличием в них таких ключевых социально-экономических секторов, как сельское и лесное хозяйство, могут испытывать значительные экономические потери в результате биологических инвазий. В работе, основываясь на количественных показателях из недавно разработанной базы данных глобальных экономических потерь от биологических инвазий (InvaCost), проанализированы убытки от биологических инвазий в России – крупной (расположенной на двух континентах) и важной в экономическом плане стране. В 2007–2019 гг. величина ущерба в результате биологических инвазий в стране составила как минимум 51.52 млрд долларов США (1.38 трлн рублей, n = 94 позиции убытков), однако, подавляющее большинство оценок было основано на прогнозах или экстраполяциях (50.86 млрд долларов США; n = 87), требующих верификации. Оценки ущерба демонстрировали низкое географическое разрешение и в основном являлись обобщением прогнозных данных для европейской и азиатской частей страны (44.17 млрд долларов США; n = 72). Исключительно в европейской части России прогнозный экономический ущерб от биологических инвазий составил 7.35 млрд долларов США (n = 22). Экономические убытки в результате инвазий были задокументированы для 72 видов, большинство из которых – насекомые (37 видов). Фактический ущерб в сумме около 660 млн долларов США (n = 7) был связан только с четырьмя видами-инвайдерами: двумя видами насекомых, *Agrilus planipennis* Fairmaire и *Cydalima perspectalis* (Walker), и двумя видами растений, *Ambrosia artemisiifolia* L. и *Heracleum sosnowskyi* Manden. Подавляющее большинство убытков было связано с прямыми потерями при незначительных задокументированных расходах на борьбу с инвайдерами в наземных экосистемах. Сельское хозяйство (прогнозная оценка ущерба: 37.42 млрд долларов США; n = 68) и лесное хозяйство (прогнозная оценка ущерба: 14.0 млрд долларов США; n = 20) являлись наиболее пострадавшими секторами экономики. В целом мы сообщаем о росте экономических потерь, ассоциированных с биологическими инвазиями в России. Мы отмечаем наличие больших пробелов в знаниях об экономических потерях от биологических инвазий в других местообитаниях (в частности, в водных экосистемах), скудность оценок затрат на мониторинг, а также малочисленность или полное отсутствие сведений по экономическим потерям для целого спектра инвазионных видов (для позвоночных организмов). Учитывая крупные и все еще в значительной степени недооцененные экономические убытки, ассоциированные с биологическими инвазиями в России, наша работа призывает к улучшению отчетности по экономическим потерям на национальном и международном уровнях.

Abstract in German

Wirtschaftliche Kosten biologischer Invasionen in terrestrischen Ökosystemen in Russland. Terrestrische Ökosysteme können aufgrund des Vorhandenseins wichtiger sozioökonomischer Sektoren wie Land- und Forstwirtschaft durch biologische Invasionen besonders wirtschaftlich geschädigt werden. Die vorliegende Studie verwendet eine Teilmenge der kürzlich entwickelten Datenbank der globalen wirtschaftlichen Kosten biologischer Invasionen (InvaCost), um die monetären Kosten biologischer Invasionen in Russland, einer Wirtschafts die sich über zwei Kontinente erstreckt, zu quantifizieren. Von 2007 bis 2019 haben Invasionen die russische Wirtschaft mindestens 51.52 Milliarden US-Dollar gekostet (1.38 Billionen Rubel, n = 94 Kosten-Einträge), wobei die überwiegende Mehrheit dieser Kosten auf Vorhersagen oder Hochrechnungen basiert (50.86 Milliarden US-Dollar; n = 87) und daher nicht empirisch beobachtet wurden. Die meisten Kosten wiesen eine geringe geografische Auflösung auf und wurden zwischen europäischen und asiatischen Teilen Russlands aufgeteilt (44.17 Mrd. USD; n = 72). Nur 7.35 Milliarden US-Dollar (n = 22) wurden ausschließlich dem europäischen Teil und keiner dem asiatischen Teil zugerechnet. Die Kosten biologischer Invasionen wurden für 72 Arten und insbesondere für Insekten (37 Arten) dokumentiert. Die empirisch beobachteten Kosten, die sich auf 660 Mio. USD (n = 7) summierten, wurden nur für vier Arten angegeben: zwei Insekten *Agrilus planipennis* Fairmaire und *Cydalima Perspectalis* (Walker) sowie zwei Pflanzen *Ambrosia artemisiifolia* L. und *Heracleum sosnowskyi* Manden. Die überwiegende Mehrheit der wirtschaftlichen Kosten stand im Zusammenhang mit Schäden an Ressourcen und wirtschaftlichen Verlusten, wobei nur sehr geringe Ausgaben für die Bewältigung von Invasionen in terrestrische Ökosysteme gemeldet wurden. Die Landwirtschaft (37.42 Mrd. USD; n = 68) und die Forstwirtschaft (14.0 Mrd. USD; n = 20) waren wiederum die am stärksten betroffenen Sektoren. Insgesamt berichten wir über aufkeimende wirtschaftliche Kosten von Invasionen in Russland und identifizieren große Wissenslücken, beispielsweise in Bezug auf bestimmte Lebensraumtypen (d. H. Wasser) und Verwaltungsausgaben sowie für zahlreiche bekannte invasive Taxa ohne gemeldete wirtschaftliche Kosten (d. H. Wirbeltiere). Angesichts dieser massiven, weitgehend unterschätzten wirtschaftlichen Belastung durch Invasionen in Russland ist unsere Arbeit ein Aufruf zur verbesserten Berichterstattung über die Kosten im In- und Ausland.

Abstract in French

Coûts économiques des invasions biologiques dans les écosystèmes terrestres en Russie. Les écosystèmes terrestres peuvent être particulièrement endommagés économiquement par les invasions biologiques, notamment de part la présence de secteurs socio-économiques clés tels que l'agriculture et la foresterie. Cette étude utilise un sous-ensemble de la base de données récemment développée sur les coûts économiques mondiaux des invasions biologiques (InvaCost) pour quantifier les coûts monétaires des invasions biologiques en Russie, un pays à économie majeure qui s'étend sur deux continents. De 2007 à 2019, les invasions ont coûté à l'économie russe au moins 51.52 milliards USD (1.38 billion RUB, n = 94 entrées de coûts), la grande majorité de ces coûts étant basée sur des prévisions ou des extrapolations (50.86 milliards USD; n = 87) et, par conséquent, non observée empiriquement. La plupart des entrées de coût présentaient une faible résolution géographique, étant réparties entre les parties européennes et asiatiques de la Russie (44.17 milliards USD; n = 72). Seuls 7.35 milliards USD (n = 22) ont été attribués à la partie européenne uniquement et aucun à la partie asiatique. Les coûts d'invasion ont été documentés pour 72 espèces et en particulier les insectes (37 espèces). Les coûts observés empiriquement, totalisant 660 millions USD (n = 7), n'ont été rapportés que pour quatre espèces: deux insectes *Agrilus planipennis Fairmaire* et *Cydalima perspectalis* (Walker) et deux plantes *Ambrosia artemisiifolia L.* et *Heracleum sosnowskyi Manden*. La grande majorité des coûts économiques étaient liés aux dommages aux ressources et aux pertes économiques, avec très peu de dépenses déclarées pour la gestion des invasions dans les écosystèmes terrestres. L'agriculture (37.42 milliards USD; n = 68) et la foresterie (14.0 milliards USD; n = 20) ont été les secteurs les plus touchés. Dans l'ensemble, nous rapportons les coûts économiques croissants des invasions en Russie et identifions les principales lacunes dans les connaissances, par exemple, concernant des types d'habitats spécifiques (c.-à-d. Aquatiques) et des dépenses de gestion, ainsi que pour de nombreux taxons invasifs connus sans coûts économiques déclarés (c.-à-d. les vertébrés). Compte tenu de ce poids économique massif et largement sous-estimé des invasions en Russie, notre travail est un appel à une meilleure communication des coûts aux niveaux national et international.

Abstract in Spanish

Los costos económicos de las invasiones biológicas en los ecosistemas terrestres de Russia. Los ecosistemas terrestres, debido a la presencia de sectores socio-económicos clave, como la agricultura o la silvicultura, pueden verse particularmente dañados por las invasiones biológicas a nivel económico. Este estudio utiliza la base de datos InvaCost, desarrollada recientemente para cuantificar los costes monetarios de las invasiones biológicas a nivel global, extrayendo el subconjunto de datos correspondiente a Rusia, un país con una economía importante que se extiende por dos continentes. Desde 2007 hasta 2019, las invasiones han costado a la economía Rusa al menos 51.52 mil millones de dólares americanos (RUB 1.38 billones, n = 94 entradas de costos); la mayoría de los costos estuvieron basados en predicciones o extrapolaciones (50.86 mil millones de dólares; n = 87) y por lo tanto no fueron empíricamente observados. La mayoría de las entradas de costos tuvieron una baja resolución geográfica, ocupando ambos continentes, Europa y Asia (44.17 mil millones de dólares; n = 72). Sólamente 7.35 mil millones de dólares (n = 22) fueron asignados a la parte Europea, pero ninguno fue atribuido únicamente a la parte Rusa. Los costos de las invasiones fueron documentados para 72 especies y particularmente para insectos (37 especies). Los costos empíricamente observados alcanzaron los 660 millones de dólares (n = 7), y fueron reportados para tan sólo 4 especies: dos insectos, *Agrilus planipennis* Fairmaire y *Cydalima perspectalis* (Walker), y dos plantas, *Ambrosia artemisiifolia* L. y *Heracleum sosnowskyi* Manden. La mayoría de los costos económicos estuvieron en relación con daños y pérdidas económicas, mientras que se reportaron mucho menos los gastos para manejar las invasiones en los ecosistemas terrestres. Por su parte, la agricultura (37.42 mil millones de dólares; n = 68) y la silvicultura (14.0 mil millones de dólares; n = 20) fueron los sectores económicos más impactados. En general, mostramos los crecientes costos económicos de las invasiones en Rusia e identificamos las principales lagunas del conocimiento, por ejemplo, en relación con los gastos de manejo, o con hábitat específicos (como el medio acuático), así como con numerosos taxones reconocidos como invasores pero sin datos económicos (como los vertebrados). Dada esta carga económica masiva de las invasiones en Rusia, en gran parte subestimada, nuestro trabajo hace un llamamiento para mejorar el reporte de los costos económicos tanto a nivel nacional como internacional.

Keywords

Direct and indirect losses, insects, InvaCost, invasive species, pathogens, Russian Federation, weeds

Introduction

Biological invasions are recognised as a global threat to biodiversity, ecosystem functioning and economic development worldwide (Elliott 2003; Kovac et al. 2010; Bradshaw et al. 2016; Seebens et al. 2018). Globalisation and ongoing environmental changes (i.e. climate change and habitat alteration) have accelerated the introduction of invasive species at an unparalleled rate, leading to the circumvention of historic biogeographical barriers by many species (Maslyakov and Izhevskii 2011; Seebens et al. 2017).

Terrestrial ecosystems are known to experience severe impacts from invasive species (Stephens et al. 2019). Terrestrial invaders can disrupt the structuring and functioning of ecosystems (Holmes et al. 2009; Roques 2010; Aukema et al. 2011; David et al. 2017; Eyre et al. 2017; Kirichenko et al. 2019). Phytophagous insects and phytopathogens are amongst the most diverse and notorious invaders, causing noteworthy damage to their host plants (up to their extirpation from large areas), leading to crop harm and further irreparable economical losses (Lockwood et al. 2013; Paini et al. 2016; Musolin et al. 2018). Whilst invasions can cause significant changes in ecosystems that, in turn, lead to massive economic losses (Pimentel 2005; Aukema et al. 2011; Lockwood et al. 2013; Diagne et al. 2021), the severity of these economic impacts remains unquantified at many geographic scales where policy decisions are made.

Russia, transcontinentally located in Eastern Europe and Northern Asia, is the largest country in the world. It covers a territory of more than 17 million km^2, i.e. about 1/8 of the Earth's land surface (Borodko 2020). The country is globally known as a major exporter of natural resources, increasing connectivity to various nations and geographical regions (Bradshaw and Connolly 2016). It possesses the largest natural forests in the world, predominated by coniferous species (boreal forest, or taiga) (FAO 2012). Furthermore, Russia has a well-developed agricultural sector, which significantly contributes to the world's crop production (Liefert and Liefert 2020). By nominal gross domestic product, Russia has the 11th largest economy in the world and the 6th largest by purchasing power parity (World Bank 2020). Both these market values are known to be associated with invasion risk (Haubrock et al. 2021c; Kourantidou et al. 2021). Indeed, these extensive commerce and goods exchanges within and outside of the country have facilitated the introduction of invasive species, especially pests of plants, phytopathogens and weeds (Maslyakov and Izhevsky 2011; Izhevsky 2013; Ebel et al. 2016; Orlova-Bienkowskaja 2016; Karpun 2019).

Russian national literature provides extensive ecological data on the threats posed by invasive organisms to terrestrial ecosystems, in particular to forestry and agriculture. Dgebuadze et al. (2018) overviewed the biology, distribution and ecological impacts of the top 100 invasive species in Russia, i.e. the most ecologically impactful, amongst which 60% (mainly plants and insects) are affecting agriculture, forestry and urbanised ecosystems. Vinogradova et al. (2009) and Ebel et al. (2016) compiled the Black Books of invasive flora by gathering together data on diversity, primary and secondary ranges and ecological hazards of invasive plants aggressively spreading in European and Asian Russia. Kuznetsov (2005) provided the list of invasive insects and discussed their impact on the terrestrial ecosystems of easternmost Russia. More recently, Orlova-Bienkowskaja (2016) analysed the threat of invasive beetles to agriculture and forestry in European Russia, whilst Karpun (2019) focused on invasive insects causing damage to the subtropical area of the country. Baranchikov et al. (2008) and Orlova-Bienkowskaja (2014) studied the threat posed by the invasive emerald ash borer *Agrilus planipennis* (Coleoptera: Buprestidae) to ash species (*Fraxinus* spp.) in European Russia, whereas Baranchikov et al. (2011), Kerchev and Krivets (2012) and Debkov et al. (2019) estimated the ecological impact of the far eastern four-eyed fir bark beetle

Polygraphus proximus Blandford that invaded Siberia. Within the group of phytophagous insects solely, around 200 invasive species are presently known in Russia, largely in its European part (Maslyakov and Izhevsky 2011). Amongst them, a number of notorious insect pests attacking woody and herbaceous plants in forests and orchards, as well as different crops in agricultural fields have been documented in the country in the last few decades (Maslyakov and Izhevsky 2011). Despite diverse ecological studies on invasive organisms in Russia, there are few published data on economic costs associated with invasions of arthropods, phytopathogens and weeds, even on species being of economic significance in the country.

In this regard, the present paper is the first attempt to gather together data on economic losses due to biological invasions to estimate the overall costs of invasive species in terrestrial ecosystems in Russia. Specifically, it aims to define the distribution of those costs amongst taxa and economic sectors, as well as temporal trends in their development. Using data retrieved from federal sources, mainly from official pest risk assessment reports and publicly available research papers, as compiled in the InvaCost database (Diagne et al. 2020b), we synthesised the current data on actual and potential costs of invasive organisms that have recorded monetary impacts on terrestrial ecosystems in Russia. Given the increasing number of invasions documented in the country (Maslyakov and Izhevsky 2011; Orlova-Bienkowskaja 2016; Karpun 2019), we suspect an increase in overall costs associated with actual and potential invaders and, in particular, arthropods, phytopathogens and plants in terrestrial ecosystems over time, given they have been most intensively studied. We also expect a remarkable economic loss primarily due to resource damage from invasive arthropods, in particular insects, given that those invasion cases have been recorded widely in the country, both in its European and Asian parts (Maslyakov and Izhevsky 2011; Orlova-Bienkowskaja 2016; Karpun 2019), and that the group is known to be costly globally (Bradshaw et al. 2016). Moreover, we examined the compositions of costs in terms of reliability of monetary sources and whether they are based on extrapolations or empirical observations.

Methods

Data collection, filtering and standardisation

To describe the costs of biological invasions in Russia, we used cost data collected in the InvaCost database v.1.0 (2,419 entries; Diagne et al. 2020b; data link: https://doi.org/10.6084/m9.figshare.11627406). This database was complemented following two specific ways: by adding cost data collected globally from non-English documents (5,212 entries; Angulo et al. 2021b; https://doi.org/10.6084/m9.figshare.12928136) and by including costs from complementary database (ca. 2,300 entries; https://doi.org/10.6084/m9.figshare.12928145). An updated version of each of these databases is now incorporated within the core InvaCost Database (https://doi.org/10.6084/m9.figshare.12668570). The majority of recorded cost data of invasive species (i.e. cost entries, indicated as “n” in the paper) in Russia were obtained from pest risk analysis reports of the All-Russian Plant Quarantine Center (VNIIKR, Bykovo, Moscow Oblast). These data cover both categories of actual and potential invaders (often having quarantine status in the country) that have a threat to plants, especially in forestry and/or agriculture. According to the legislation of the Russian Federation in plant quarantine, the quarantine organism/agent is a species that is so far absent but has a risk of introduction, or a species that already invaded but still has a limited distribution in the territory of the country and that may significantly impact plants, resulting in economic losses (On Plant Quarantine 2014). Cost entries provided in national currency were converted to US$, based on the 2017 value (Diagne et al. 2020b). Altogether, we extracted all costs (accounting for 94 entries) related to Russia for the purpose of our analyses by filtering the “Country” column to include “Russia”. The extracted dataset is provided in Suppl. material 1: Fig. S1.

Cost analyses

The analysis of costs from the InvaCost database was performed using the invacost R package v0.2-4 (Leroy et al. 2020) in R v4.0.2 (R Core Team 2019). Using the filtered data, the total invasion costs were examined according to different descriptive columns of the database (see Diagne et al. 2020b for further details):

1. Method reliability: illustrating the perceived reliability of cost estimates, based on the type of publication and method of estimation;
2. Implementation: referring to whether the cost estimate was actually realised (observed) or whether it was expected (potential);
3. Taxonomic grouping: the kingdom, class, order and species from which the cost emanated. Here, we refer to the organisms from the kingdoms: Animalia, Plantae, Fungi, and Bacteria. Nomenclature of viruses is independent of other biological nomenclature (ICTV Code 2020), with nine kingdoms defined (Virus Taxonomy 2020). For simplicity, we do not list virus kingdoms in the study but rather operate the general term “viruses”.

In Animalia, as an exception, besides costs of actual and potential invaders, our study also analysed impacts of six native longhorn beetles: *Monochamus galloprovincialis*, *M. impluviatus*, *M. nitens*, *M. saltuarius*, *M. sutor*, and *M. urussovi* (Coleoptera: Cerambycidae). Distributed in some parts of Russia, they are subjected to national quarantine control because they are considered vectors of a potentially-invasive pine wood nematode, *Bursaphelenchus xylophilus* (Steiner et Buhrer) Nickle (Aphelenchida: Parasitaphelenchidae). To avoid counting native species, these beetles, represented in InvaCost database by 14 entries (cost IDs: NE4445–NE4456, NE4474 and NE4475; Suppl. material 1: Fig. S1), were excluded from the analysis and their potential economic losses were summarised and attributed to the pine wood nematode, the species that was counted in the analysis of taxonomic groups. That is because control actions for the species aim to manage the vectoring of pine wood nematode, rather than control the native species per se. On the contrary, the cost of the North American *Monochamus scutellatus* (Say) (cost ID NE4434 in Suppl. material 1: Fig. S1) was not attributed to the nematode. This non-native species may directly affect wood by boring holes and it also has a potential to distribute the nematode (Akbulut and Stamps 2020). As such, *M. scutellatus* is itself considered as being potentially invasive to Russia and was counted in the study accordingly.

4. Type of cost: grouping of categories of cost types into: (1) "Damage-Loss" referring to damages or losses incurred by invasion (i.e. costs for damage repair, resource losses, medical care), (2) "Management" comprising control-related expenditure (i.e. monitoring, prevention, eradication) and (3) "General" including mixed damage-loss and control costs (cases where reported costs were not clearly distinguished);
5. Impacted sector: the activity, societal or market sector that was impacted by the invasive species (Suppl. material 1: Fig. S1).

We also analysed the dynamics of cost reporting for the period from 2007 to 2019, given this is the range of years from which invasion costs were available for Russia in serveyed sources. We estimated the absolute and average annual costs of invaders reported in this period in Russia and the number of cost entries represented in the InvaCost database and quantified the temporal trends in accumulations of these indicators. The data entries were assigned to the year mentioned in the original source (if a single year was mentioned), to the most recent year (if a period of years was mentioned) or to the year of publication (if the year was not assigned to the cost).

In addition, we ranked all species involved in the study according to their costs (descending ranking) to show the distribution of costs across taxa. We also classified species by their quarantine status in Russia (i.e. whether they are assigned to quarantine or non-quarantine species in the country) and estimated their costs according to these groups and the taxonomic kingdom. Information on the quarantine status of species was found in legislation documents (On approval 2014, 2019). Data on quarantine status of species is given in Suppl. material 2: Tables S1.

Results

Economic costs in European and Asian Russia

The 94 invasion cost entries for Russia totalled at US$ 51.52 billion between 2007 and 2019, which was equivalent to around RUB 1.38 trillion (Suppl. material 1: Fig. S1). From these, all recorded entries were of high reliability, based on pest risk analyses and approved estimation methods (Suppl. material 1: Fig. S1). However, just 1.3% of the total costs were empirically observed (US$ 660 million; n = 7), whereas the remaining potential costs were largely based on extrapolations (US$ 50.86 billion; n = 87). Whilst

Russia spans substantial parts of continental Europe and Asia, the majority of costs were associated with both macro-regions (US$ 44.17 billion; n = 72), while US$ 7.35 billion (n = 22) was associated solely with the European part. No costs were attributed to the Asian part exclusively.

Taxonomic grouping

Overall, the 94 cost entries analysed in the study corresponded to 77 species. We reclassified the costs of six native longhorn beetle species of the genus *Monochamus*, attributing them instead to the potentially-invasive pine wood nematode. These insect species (and their 14 entries) were not counted in taxonomic grouping analysis, but instead a single entry for the pine wood nematode was taken into account. Thus, the resultant overall invasive species number, included into the analysis, was 72 (represented by 81 entries). Amongst them, insects were the leading group (37 species, 51%), followed by plants (9 species, 13%), fungi and viruses (8 species, 11% each) and bacteria (7 species, 10%) (Fig. 1). Nematodes and mites were represented by 2 (3%) and 1 (1%) species each (Fig. 1). Across insects, beetles (Coleoptera) and moths (Lepidoptera) were the most represented groups (23 species overall, i.e. 32% of all species in the study).

Quarantine vs. non-quarantine species

Amongst the 72 analysed species, 61 species (84.7%) have a quarantine status in Russia (i.e. are predicted to invade to the country from abroad, already have a limited present extent in Russia or serve vectors of potentially-invasive species). The majority of those species (i.e. 33 species) are from Animalia, followed by the representatives from Plantae and viruses (eight species each), Bacteria and Fungi (six species each). The remaining 11 species have no quarantine status in Russia, with seven species from Animalia, two species from Fungi and one species each from Bacteria and Plantae. The data on the quarantine status of the species in Russia, species origin and cost of their invasions are given in Suppl. material 2: Table S1.

Overall, species with a quarantine status accounted for US$ 50.64 billion (98.3% of all economic losses) (Table 1). Amongst organisms with quarantine status, there were in total 18 species, i.e. 16 species that already invaded Russia from abroad (they accounted for US$ 8.41 billion, i.e. 16.3%) and two national invaders that moved to the western part of the country from the eastern part (the emerald ash borer *A. planipennis* and the San Jose scale *Quadraspidiotus perniciosus* Comstock). The latter two species accounted for US$ 1.12 billion (2.2%). The potential losses from other species that are predicted to invade Russia and, thus, subjected to quarantine control there (43 species in the analysed dataset), accounted for US$ 41.11 billion (Suppl. material 2: Table S1), i.e. about four times greater than the cost of 18 quarantine invasive species. Amongst quarantine species, the potentially invasive pine wood nematode was the most costly organism, at US$ 13.93 billion (i.e. 27.5% of economic losses across quarantine organisms in Russia).

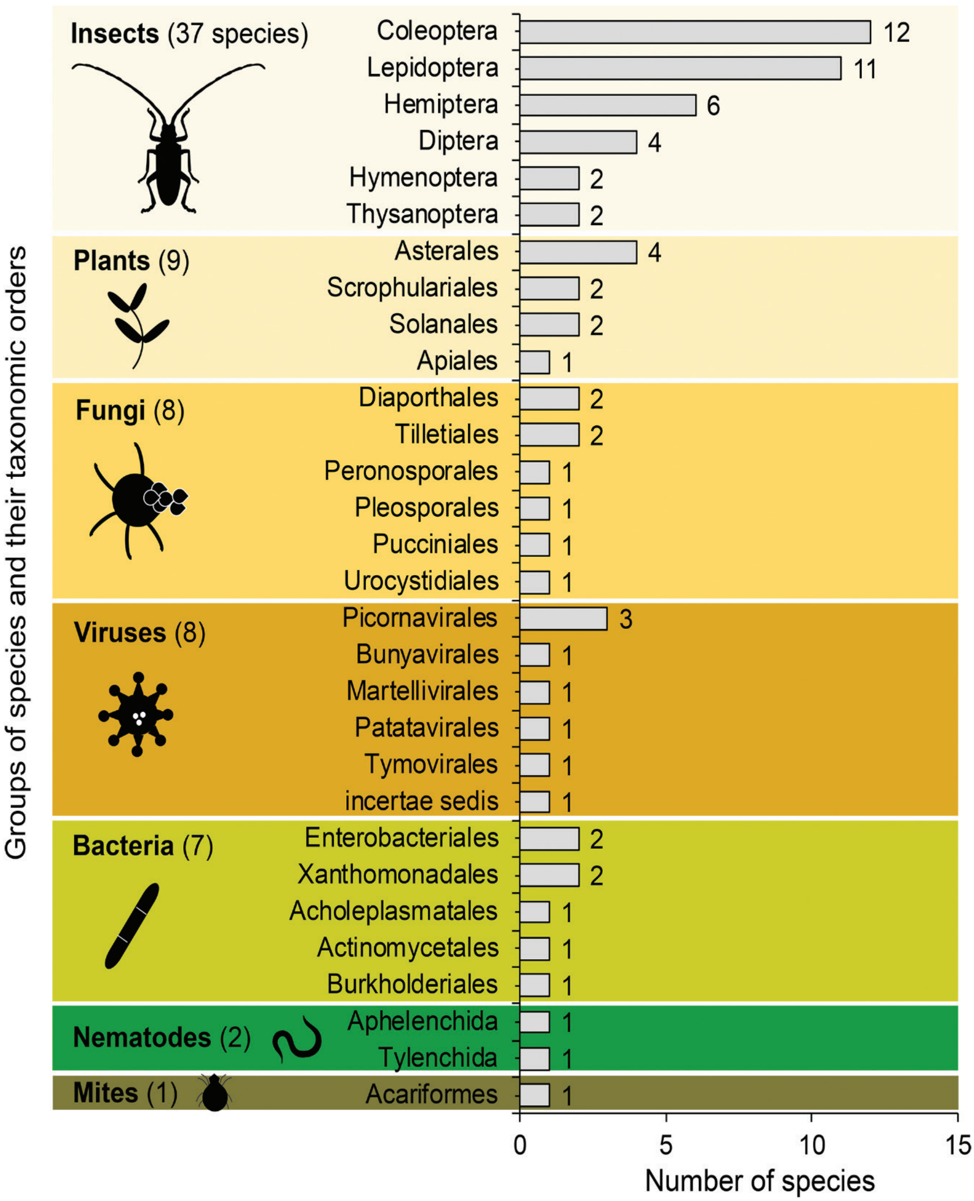

Figure 1. Number of species with estimated economic costs across respective taxonomic groups in Russia.

Non-quarantine species accounted for just US$ 0.88 billion (1.7% of all economic losses), that is around 58 times less than the cost of quarantine species. Amongst them, there are two insects, namely, *Cydalima perspectalis* and the lime leaf-miner *Phyllonorycter issikii* (Kumata) (Lepidoptera: Gracillariidae), the plant *H. sosnowskyi* and the fungal pathogen *Diaporthe helianthi* Munt.-Cvet. et al. (Diaporthales: Diaporthaceae), with those economic losses comprising US$ 0.60 billion (Suppl.

Table 1. Economic costs of quarantine and non-quarantine species in Russia*.

Species category	Number of species	Cost, US$ billion	Proportion in total cost, %
Quarantine species			
Invaded Russia from abroad	16	8.41	16.3
National invaders	2	1.12	2.2
Predicted to invade Russia	43	41.11	79.81
Non-quarantine species			
Invaded Russia	4	0.60	1.2
Predicted to invade Russia	7	0.28	0.5
Overall for quarantine species	**61**	**50.64**	**98.3**
Overall for non-quarantine species	**11**	**0.88**	**1.7**
TOTAL		**51.52**	**100**

*Data by species is provided in Suppl. material 2: Table S1.

material 2: Table S1). The remaining US$ 0.28 billion is due to seven potentially-invasive organisms (four insects, one mite, one bacterium, one fungal pathogen) (Suppl. material 2: Table S1).

Costs per taxonomic group

Overall, costs associated with invasive species from the Animalia kingdom dominated (US$ 31.48 billion; n = 46 entries), followed by Plantae (US$ 11.28 billion; n = 12), Fungi (US$ 4.46 billion; n = 8), viruses (US$ 2.94 billion; n = 8) and, lastly, Bacteria (US$ 1.36 billion; n = 7) (Fig. 2).

Amongst animals, the costs of invasions by insects represented the largest part (US$ 16.44 billion, n = 43). The proportion of other animals made US$ 15.01 billion for nematodes (n = 2) and US$ 0.02 billion for mites (n = 1). The total cost for the nematodes comprised that of the potentially-invasive pine wood nematode *B. xylophilus* (US$ 13.93 billion) and the Columbia root-knot nematode *Meloidogyne chitwoodi* Golden, O'Bannon, Santo & Finley, the agricultural crop pest (US$ 1.08 billion).

Amongst the costliest top-3 species, there were two representatives of Animalia (one nematode and one insect) and one representative of Plantae (herb). Of them, the most costly species was the potentially-invasive pine wood nematode *B. xylophilus* (Suppl. material 2: Table S1). The other two invasive species were the 28-spotted potato ladybird *Henosepilachna vigintioctopunctata* Fabricius (Coleoptera: Coccinellidae) and black-jack *Bidens pilosa* L. (Asterales: Asteraceae), with the potential damage from each estimated at around US$ 4.31 and 4.07 billion, respectively (Suppl. material 2: Table S1). Altogether, the contribution of these top-3 species to the economic losses of the country accounted for US$ 22.32 billion, i.e. 43% of costs of all species covered by the study. The species with the lowest reported cost was the potentially-invasive North American longhorn beetle, *Monochamus scutellatus*, accounting for US$ 0.015 million (Suppl. material 2: Table S1).

The distribution of costs across species was skewed, with just a few species causing high economic impacts (> US$ 1 billion) and most with a substantially lower economic impact (Fig. 3). Indeed, few individual species, i.e. 15 out of 72 (20.8%), exhibited

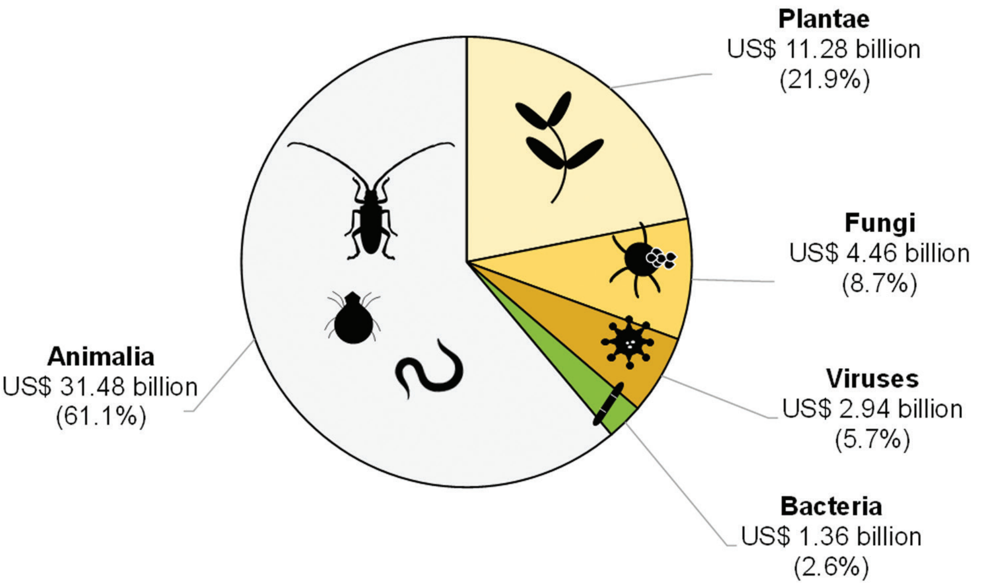

Figure 2. Distribution of economic costs across different taxonomic kingdoms in Russia, in US$ billion. For viruses, the kingdoms are not indicated and, thus, all species are treated under the general term "viruses".

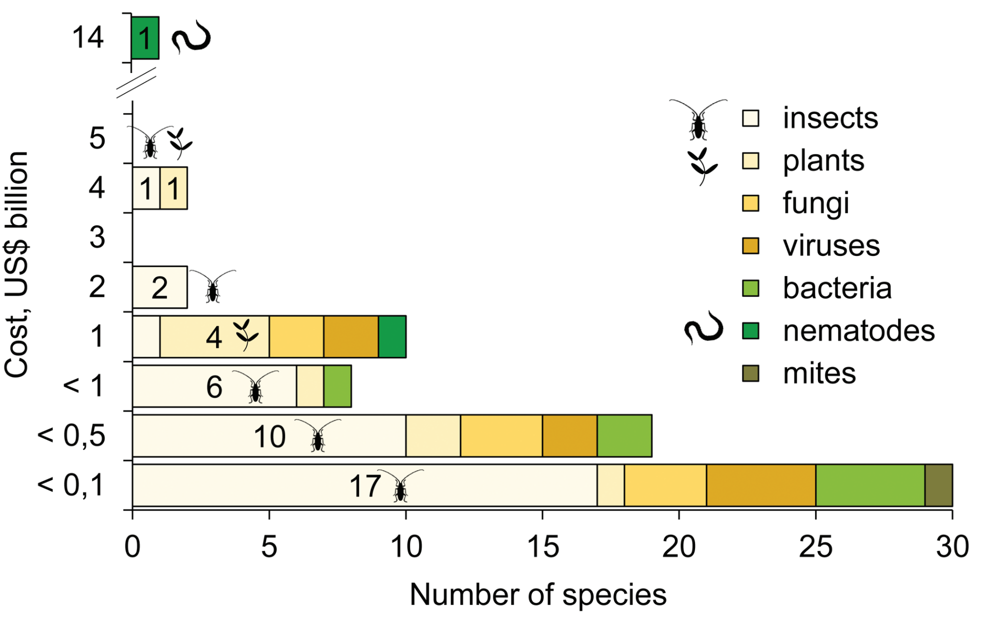

Figure 3. The ranked economic costs in different taxonomic groups of invasive species in Russia. The group with the highest number of species is indicated within each cost category (additionally marked by the respective organism pictogram).

costs greater than US$ 1 billion (Fig. 3). Conversely, twice as many species, i.e. 30 out of 72 (41.6%; amongst which, 17 species are insects), led each to an economic loss of at least a magnitude lower (Fig. 3).

Table 2. Actual losses (observed costs) in different sectors due to invasions of insect pests and weeds in Russia.

Impacted sector	Kingdom	Order	Species	Cost, US$ million
Agriculture	Plantae	Asterales	*Ambrosia artemisiifolia*	307.9
Forestry	Animalia	Coleoptera	*Agrilus planipennis*	258.9
Health	Plantae	Asterales	*A. artemisiifolia*	90.6
Public and social welfare	Animalia	Lepidoptera	*Cydalima perspectalis*	1.1
Environment	Animalia	Lepidoptera	*C. perspectalis*	0.9
Authorities-Stakeholders	Plantae	Apiales	*Heracleum sosnowskyi*	0.6
TOTAL				**660.0**

While several species contributed to the list of costly invasive species with extrapolated economic losses, only four species (two insects and two plants) remained when focusing on only observed costs (Table 2; Fig. 4). Amongst them, there were two weeds: common ragweed *A. artemisiifolia* (Asterales: Asteraceae) and Sosnowsky's hogweed *H. sosnowskyi* (Apiales: Apiaceae), those actual economic losses altogether reached around US$ 400 million in the years 2011 and 2015. The other two species were phytophagous insect pests, the emerald ash borer *A. planipennis* and the box-tree moth *C. perspectalis*, those observed costs amounting to around US$ 260 million during the period of 2011–2016 (Table 2).

Impacted sectors

The majority (97%) of the total inferred costs of US$ 51.52 billion were categorised as damage-losses in the terrestrial environment. Impacted sectors were diverse, with agriculture being the most heavily impacted sector (US$ 37.42 billion; n = 68 entries), followed by forestry (US$ 14.0 billion; n = 20). Costs inferred to health (US$ 91.92 million; n = 2), public and social welfare (US$ 1.1 million; n = 1), the environment (US$ 944.3 thousand; n = 1), authorities and stakeholders (US$ 706.7 thousand; n = 2) were of a lower magnitude (Fig. 5). The contribution of different invasive species classed to the above-mentioned sectors can be found in Suppl. material 1: Fig. S1.

Overall, 46% of all losses in agriculture (US$ 17.22 billion) were caused by Animalia, followed by Plantae (30%, US$ 11.19 billion); the contribution of phytopathogens accounted overall for 24% (US$ 8.76 billion). In total cost analysis, forestry was solely impacted by Animalia (in particular by insects and nematodes). Other sectors (health, public and social welfare, authorities and stakeholders) were affected by Plantae (herbaceous weeds), overall accounting for US$ 92.99 million, whereas the environment sector had losses due to insects solely (US$ 944.3 thousand).

Similar to the total costs, the observed costs were the highest in the agricultural sector (US$ 307.9 million; n = 1), followed closely by those in forestry (US$ 258.9 million; n = 1), health (US$ 90.6 million; n = 2), public and social welfare (US$ 1.1 million; n = 1), the environment (US$ 0.9 million; n = 1), the authorities and stakeholder sectors (US$ 0.6 million; n = 1) (full data are given in Suppl. material 1: Fig. S1). The observed costs were driven entirely by insect and plant species (Table 2).

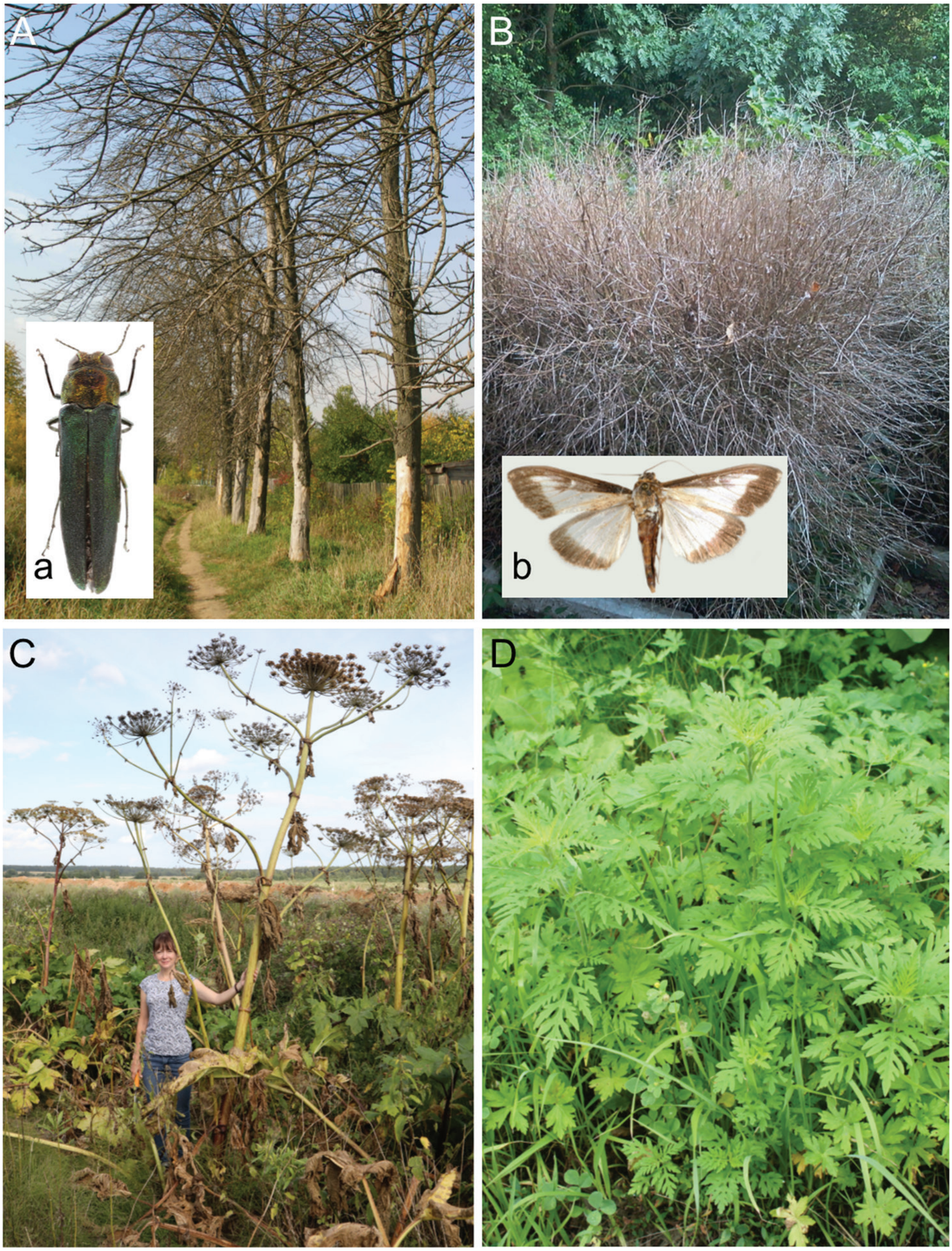

Figure 4. Four notorious invasive species with observed costs in Russia **A** the emerald ash borer *Agrilus planipennis* and associated dead trees of *Fraxinus pennsylvanica* **B** the box-tree moth *Cydalima perspectalis* and associated dead bushes of *Buxus sempervirens* **C** Sosnowsky's hogweed *Heracleum sosnowskyi* invading an agricultural field **D** common ragweed *Ambrosia artemisiifolia* in the forest canopy. **A–C** Moscow Oblast (**B** an experimental trial) **D** Primorsky Krai. Photos taken by **A, B** V. Ponomarev **C** V. Kulakov (the photo is published with the permission from the photographed person) **D** N. Kirichenko **a, b** D. Kasatkin.

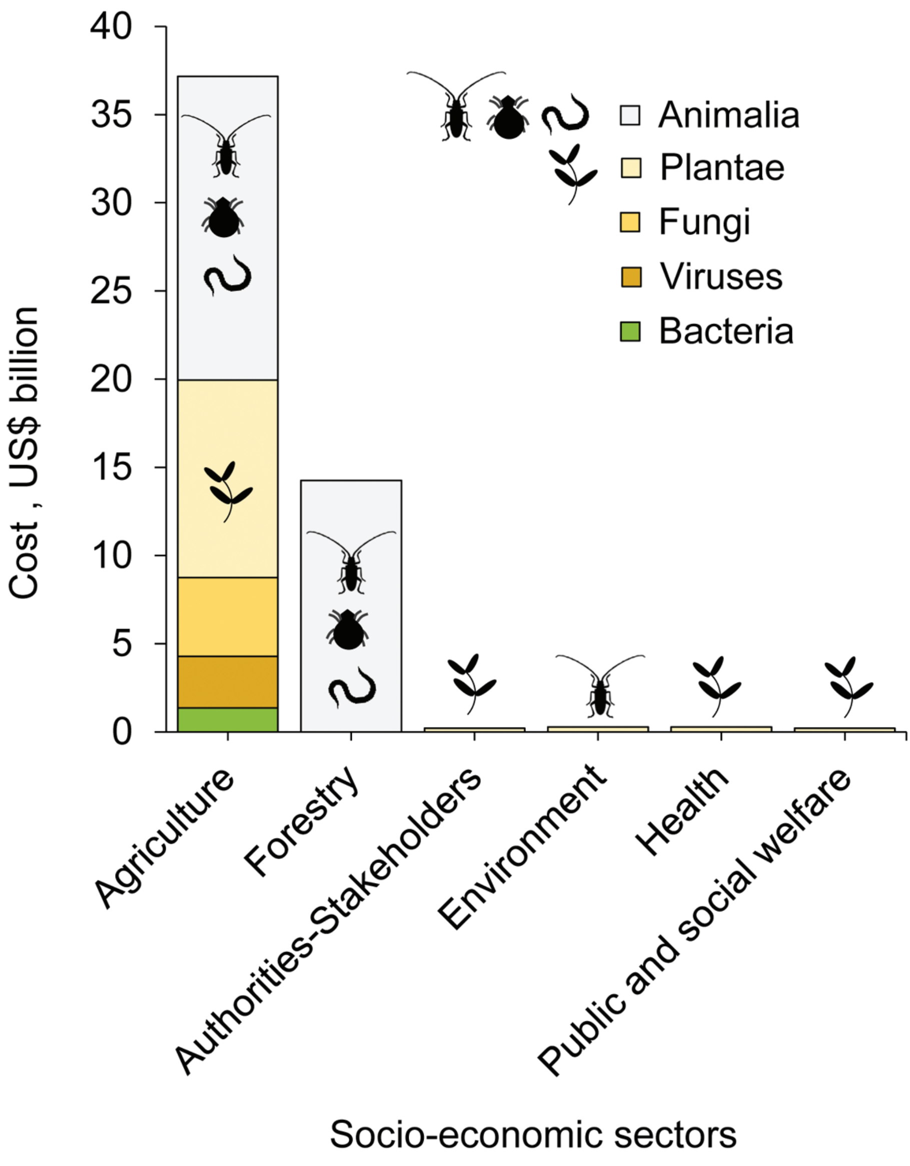

Figure 5. Total economic costs related to socio-economic sectors in Russia according to taxonomic kingdoms. The dominant groups of organisms in different socio-economic sectors are additionally marked by the respective organism pictogram.

Cost dynamics

Reported invasion costs averaged US$ 3.96 ± 3.03 billion per year (2007–2019) when considering all costs (Fig. 6A) and US$ 110.2 million per year (2011–2016) when considering only observed costs (not shown). The reported costs (analysed in absolute

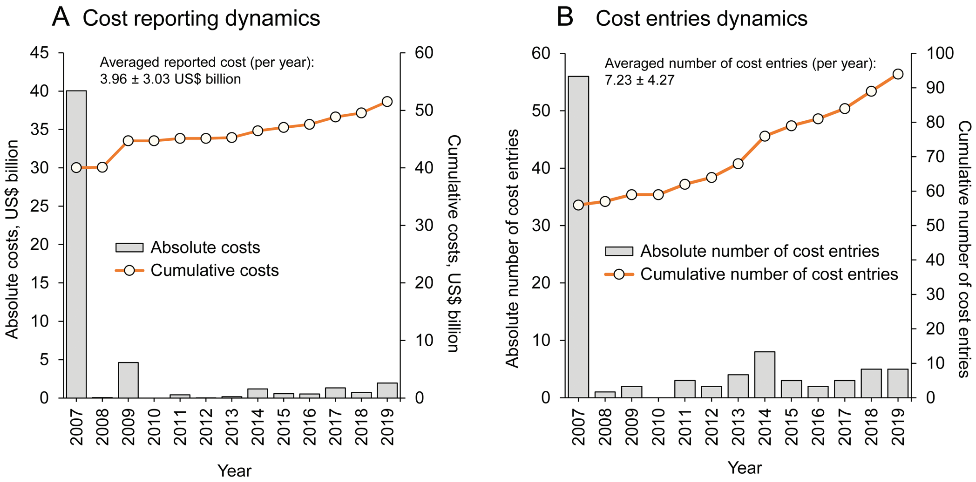

Figure 6. Temporal trends in the cost reporting (**A**) and in the number of cost entries (**B**) in Russia in 2007–2019. In both cases, the cumulative trends are additionally computed.

values) displayed a pronounced peak in 2007 (US$ 40.04 billion), followed by fluctuation from US$ 0.05 billion to US$ 1.96 billion in the period 2008–2019 (Fig. 6A). Fluctuations in dynamics were also observed when considering the total number of cost entries, with a pronounced peak in 2007 (56 entries), followed by a decrease and unstable dynamics in the following years (i.e. from 0 to 8 entries per year) (Fig. 6B). As such, it was reflecting the transition in the methodology used for assessing invasion costs in Russia after 2007, but also potentially indicating a time lag in cost reporting in the following years (see Discussion). The cumulative curves showed just a slight increase in both cases (Fig. 6A and B). No particular trend was defined when analysing the observed costs (not shown).

Discussion

Our study summarised, for the first time, the recorded economic costs of invasive species in Russia from 2007 to 2019 and showed that they amounted to a total of US$ 51.52 billion. In particular, it analysed actual and potential economic losses associated with 72 species of insects, mites, nematodes, phytopathogens and weeds, of which the majority (i.e. 85%) has a quarantine status in Russia, i.e. is subjected to federal phytosanitary control (Suppl. material 2: Tables S1). For those species, monetary data were available in pest risk assessment reports and scarce national publications, accessible online.

Despite being based on a representative number of cost entries for different taxa, it should be understood that our results do not reflect the total monetary losses associated with terrestrial invasions in Russia for the studied period, 2007–2019. In general in Russia, there are very few studies estimating resource damage and losses associated with invasive and quarantine organisms in monetary terms (Magomedov et al. 2013; Gninenko et al. 2016; Dalke et al. 2018). Further, there are hardly any publicly-available data on costs attributed to management expenditure, despite the potential cost-effectiveness of early preventative measures for invasions compared to longer term approaches (Leung et al. 2002; Ahmed et al. 2021). For those reasons, the estimates presented in this study can be considered as being very conservative.

The structure of economic costs reported here largely reflects taxonomic interests of the All-Russian Plant Quarantine Center related to the range of species posing phytosanitary risks, given that those data served as a main source for the present analysis. Thus, our study largely focuses on species (invertebrates, phytopahogens and plants) affecting the key socio-economic sectors of agriculture and forestry, but is lacking analyses of other terrestrial organisms (such as vertebrates). Those economic losses have been seldom reported in national literature (Fokin and Airapetyants 2004), despite known ecological impacts, in particular caused by mammals (Bobrov et al. 2008; Khlyap et al. 2008). Moreover, our study did not include aquatic invasive species in Russia, simply because hardly any data on economic losses associated with those organisms are available in Russian literature (Dgebuadze et al. 2018). Despite all these limitations, our study still shows that expenditures associated with terrestrial invaders and their monetary impacts to different sectors are very important in Russia and suggests they also might be important where data are missing.

Surprisingly, our analysis of recorded costs did not show a clear increase in overall costs associated with invasive species over time. This is despite a pronounced increase in global invasion rates worldwide across taxonomic groups (Seebens et al. 2017), with invasions projected to increase markedly in the coming decades (Seebens et al. 2020), as well as increasing invasion costs at the global scale (Diagne et al. 2021; Cuthbert et al. 2021b). The main explanation is that the monetary estimates have been published not in all pest risk analysis reports for organisms subjected to such analysis in Russia. Overall, in the country pest risk analysis is based on an integrative approach to define phytosanitary risks of invasive species by computing an integral index (Orlinski 2006). This index takes into account expert opinions regarding the probability of different risks (including economic) associated with invasive species and is expressed in quantitative units (Analysis of Phytosanitary Risk 2018). This, therefore, can bias our results temporally, as for the latest years we failed to extract monetary data for a number of species from pest risk analysis reports. Further, in 2008–2019, we observed significant fluctuations of costs reporting, i.e. the increase in 2009 followed by the decrease in 2010 and subsequent unstable dynamics in the following years, that overall, may indicate a time lag in cost reporting in the country.

Thus, whilst biological invasions have been a major element of global change for many recent decades (Seebens et al. 2017; Elton 2020), costs are available in Russia for only around the last two decades (Magomedov et al. 2013), further narrowing the temporal scale of our study. In turn, the lack of reported observed costs in Russia may further negate comprehensive appraisals of temporal trends in economic costs, whereas the extrapolated costs, which dominated, may potentially be more sporadic over time. In contrast to other countries within the database which are predominantly English-speaking (e.g. Bradshaw et al. 2021; Cuthbert et al. 2021a; Crystal-Ornelas et al. 2021), cost entries for the Russian economy mainly originated from non-English sources rather than from English scientific publications (Diagne et al. 2020b). This further indicates the value in considering non-English materials to improve the comprehensiveness of literature syntheses (Angulo et al. 2021b).

In accordance with our expectation, economic losses in Russia were primarily driven by invasive arthropods, in particular insects. We showed that records for insects accounted for US$ 16.44 billion, i.e. 32% of total economic losses associated with invasive species involved in the study. Indeed, it was the most diverse group of invasive species with reported costs in our study and this group is regularly documented as invasive in Russia (Maslyakov and Izhevsky 2011). This group is ecologically very plastic, having great potential to invade new regions and adapt to ongoing global changes (Garnas et al. 2016; Deutsch et al. 2018; Lehmann et al. 2020). At the world scale, insects have been identified as causing a considerable risk to agricultural and forestry practices, whereby major forest and agricultural producers and developing countries may be most severely damaged in future (Paini et al. 2016; Liu et al. 2021). In turn, global estimates of the costs of invasive insects have been determined at least US$ 76.9 billion (embracing associated goods, service and health costs), yet have been likely significantly underestimated, given the knowledge gaps at many national scales (Bradshaw et al. 2016; Diagne et al. 2021). Overall, in agricultural ecosystems of Russia, the range of harmful species having economic impacts is more diverse than the ones causing costs in forestry. Insects may lead to significant monetary losses in agriculture, accounting for around 46% of all recorded losses associated with invaders in this sector in Russia. The other half of recorded losses has occurred due to weeds and crop pathogens (fungi, bacteria and viruses).

As we showed, economic losses associated with biological invasions in forestry are also significant but still lower than in agriculture. Russia is a forested country and thus the problems emerging in the forest sector due to invasions of pestiferous organisms are of a special concern. In our study, as an exception, we analysed economic losses associated with six native-to-Russia longhorn beetles: *Monochamus galloprovincialis*, *M. impluviatus*, *M. nitens*, *M. saltuarius*, *M. sutor* and *M. urussovi* that can potentially serve as vectors of the pine wood nematode. The invasion of *Bursaphelenchus xylophilus* to Russia is considered as highly likely due to favourable climatic conditions and vast distribution of the native vectors here (Kulinich et al. 2017). It may lead to US$ 13.93 billion in annual losses (as estimated for the year 2007 in the study, see Suppl. material 1: Fig. S1 and Suppl. material 2: Table S1), which is the highest cost for terrestrial ecosystems in Russia. The pine wood nematode is known as a notorious pest causing pronounced economic losses also in some European and Asian countries (Haubrock et al. 2021c; Watari et al. 2021). In Spain, the related species of the pine wood nematode, *Bursaphelenchus mucronatus* Mamiya et Enda, has been predicted to cause loss in the forestry stock of around US$ 28 billion (estimated over a period of 22 years, i.e. about

US$ 1.27 billion per year), which is the highest economic cost associated with the invasive organisms in the country (Angulo et al. 2021a).

Despite our study having analysed a wide range of different species, the observed invasion costs were recorded only for four species: two insects (the emerald ash borer and box tree moth) and two weeds (common ragweed and Sosnowsky's hogweed). These notorious species have attracted significant attention in Russia, given their pronounced impacts on forestry (via invasive insects), agriculture and human health (via invasive weeds) (Dgebuadze et al. 2018). The cascading problems associated with their invasions in the country have resulted in a number of publications on their ecological impacts (Baranchikov et al. 2008; Reznik 2009; Orlova-Bienkowskaja 2014, 2016; Karpun 2019), including a few studies presenting data on observed economic losses due to these species, i.e. direct and indirect loss (environment) and those linked to health issues (Magomedov et al. 2013; Gninenko et al. 2016; Dalke et al. 2018). Meanwhile, a number of other invasive species, having known ecological and economic impacts in agriculture and forestry, lack cost assessments in Russia, for example, the insects: the Grape phylloxera *Daktulosphaira vitifoliae* (Fitch) (= *Viteus vitifoliae*), the silverleaf whitefly *Bemisia tabaci* (Gennadius), the western flower thrips *Frankliniella occidentalis* Pergande, the oriental fruit moth *Grapholita molesta* (Busck), the brown marmorated stink bug *Halyomorpha halys* (Stål), the potato tuber moth *Phthorimaea operculella* (Zeller), the tomato leaf-miner *Tuta absoluta* (Meyrick), *Polygraphus proximus* Blandford and harmful invasive species from other taxonomic kingdoms (National Report 2020).

Overall, the 'true' economic impact of biological invasions in Russia remains unidentified. Given that around 1,000 alien invasive species have been documented in Russia across different habitat types (Petrosyan et al. 2020), the number of species that cause economic losses, as well as over which geographic and monetary scales and in which economic sectors, remains unknown. It is, however, certain that the number of invasive species records and associated economic costs analysed in our study are much lower than aggregate economic losses which Russia faces due to biological invasions, as in the case of other countries (e.g. Haubrock et al. 2021a, b; Rico-Sánchez et al. 2021).

Conclusions

The present study provides the most comprehensive quantification of economic costs associated with invasive species in terrestrial ecosystems, in particular in forestry and agriculture, in Russia. Reported economic costs have reached US$ 51.52 billion in total for the studied period 2007–2019. In turn, we identified a number of gaps and biases in cost estimation which could provide information for future compilations of invasion costs within Russia. Firstly, a minority of costs reported in Russia from invasions have been empirically observed, with the vast majority being based on extrapolations from smaller scales. Moreover, costs were not geographically resolute, with the majority of expenditures split between European and Asian parts of Russia, impeding local-scale appraisals of costs and thus fine-scale decision-making. Secondly, terrestrial biota drove the entirety of reported costs in Russia, with no impacts reported from invasive aquatic or semi-aquatic biota, despite the massive extent of coastal and freshwater systems nationally and burgeoning global costs from aquatic invaders (Cuthbert et al. 2021b). We note, however, that this study focused on terrestrial ecosystems, because we did not intensively seek to obtain aquatic invasion costs for Russia from sources outside of published literature. Reported costs were also dominated by resource damage and losses to agricultural and forestry sectors, with very little in terms of management. This is concerning, as a lack of early-stage intervention measures could drive much greater invasion costs in future (Leung et al. 2002; Ahmed et al. 2021). Thirdly, less than 10% of recorded non-native species in Russia have recorded costs and entire taxonomic groups, such as vertebrates, are currently lacking cost estimation. Overall, we thus encourage to improve cost estimation resolution across environmental, spatial, temporal and taxonomic scales, including appraisals for costs of management interventions, not only for terrestrial invaders (including vertebrates), but also for organisms invading aquatic ecosystems in Russia. In that context, InvaCost offers an opportunity to standardise and centralise invasion cost reporting for the Russian economy and elsewhere, in a publicly available and comprehensive manner (Diagne et al. 2020a).

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Supplementary material 1

Figure S1. The distribution of economic costs across different species in Russia, in US$ billions

Authors: Natalia Kirichenko, Phillip J. Haubrock, Ross N. Cuthbert, Evgeny Akulov, Elena Karimova, Yuri Shneyder, Chunlong Liu, Elena Angulo, Christophe Diagne, Franck Courchamp

Data type: Figure

Explanation note: Cost data for particular species. A – beginning half of the graph; B – the end half. Abbreviations (see axis OX): **Henosepilachna vigintioctomaculata*, ***Stenocarpella maydis/S. macrospora*; ****Pantoea stewartii* subsp. *stewartii*; *****Xanthomonas oryzae* pv. *oryzae*; ******Clavibacter michiganensis* subsp. *sepedonicum*; APL tymovirus – Andean potato latent tymovirus; APM comovirus – Andean potato mottle comovirus; PRM nepovirus – Peach rosette mosaic nepovirus.

Link: https://doi.org/10.3897/neobiota.67.58529.suppl1

Supplementary material 2

Table S1. Dataset on economic losses associated with biological invasions in terrestrial ecosystems in Russia

Authors: Natalia Kirichenko, Phillip J. Haubrock, Ross N. Cuthbert, Evgeny Akulov, Elena Karimova, Yuri Shneyder, Chunlong Liu, Elena Angulo, Christophe Diagne, Franck Courchamp

Data type: Table (xslx. file)

Explanation note: Data on economic costs associated with bioinvasions in Russia. Based on InvaCost databases: Diagne et al. (2020a), Angulo et al. (2021b).

Link: https://doi.org/10.3897/neobiota.67.58529.suppl2

Supplementary material 3

Table S2. The region of origin and the quarantine status of the species in Russia involved in the study

Authors: Natalia Kirichenko, Phillip J. Haubrock, Ross N. Cuthbert, Evgeny Akulov, Elena Karimova, Yuri Shneyder, Chunlong Liu, Elena Angulo, Christophe Diagne, Franck Courchamp

Data type: Table (xslx. file)

Explanation note: Native ranges of the studied species and their quarantine status in Russia.

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RESEARCH ARTICLE

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Biological invasions in Singapore and Southeast Asia: data gaps fail to mask potentially massive economic costs

Phillip J. Haubrock[1,2*], Ross N. Cuthbert[3,4*], Darren C.J. Yeo[5,6], Achyut Kumar Banerjee[7], Chunlong Liu[8,9,10,11], Christophe Diagne[11], Franck Courchamp[11]

1 *Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, 63571 Gelnhausen, Germany* **2** *University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Zátiší 728/II, 389 25, Vodňany, Czech Republic* **3** *GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, 24105, Kiel, Germany* **4** *School of Biological Sciences, Queen's University Belfast, 19 Chlorine Gardens, Belfast, BT9 5DL, Northern Ireland, UK* **5** *Department of Biological Sciences, National University of Singapore, 16 Science Drive 4, Singapore 117558, Republic of Singapore* **6** *Lee Kong Chian Natural History Museum, National University of Singapore, 2 Conservatory Drive, Singapore 117377, Republic of Singapore* **7** *School of Life Sciences, Sun Yat-sen University, 510275, Guangzhou, China* **8** *Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany* **9** *Institute of Biology, Freie Universität Berlin, Germany* **10** *Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany* **11** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405, Orsay, France*

Corresponding authors: Phillip J. Haubrock (phillip.haubrock@senckenberg.de); Darren C.J. Yeo (darrenyeo@nus.edu.sg)

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Abstract

The impacts of invasive alien species are well-known and are categorised as a leading contributor to biodiversity loss globally. However, relatively little is known about the monetary costs incurred from invasions on national economies, hampering management responses. In this study, we used published data to describe the economic cost of invasions in Southeast Asia, with a focus on Singapore – a biodiversity-rich, tropical island city state with small size, high human density and high trade volume, three factors likely to increase invasions. In this country, as well as in others in Southeast Asia, cost data were scarce,

* These two authors contributed equally

with recorded costs available for only a small fraction of the species known to be invasive. Yet, the overall available economic costs to Singapore were estimated to be ~ US$ 1.72 billion in total since 1975 (after accounting for inflation), which is approximately one tenth of the total cost recorded in all of Southeast Asia (US$ 16.9 billion). These costs, in Singapore and Southeast Asia, were mostly linked to insects in the family Culicidae (principally *Aedes* spp.) and associated with damage, resource loss, healthcare and control-related spending. Projections for 11 additional species known to be invasive in Singapore, but with recorded costs only from abroad, amounted to an additional US$ 893.13 million, showing the potential huge gap between recorded and actual costs (cost records remain missing for over 90% of invasive species). No costs within the database for Singapore – or for other Southeast Asian countries – were exclusively associated with proactive management, highlighting that a shortage of reporting on the costs of invasions is mirrored by a lack of investment in management. Moreover, invasion cost entries in Singapore were under-reported relative to import levels, but total costs exceeded expectations, based on land area and population size, and to a greater extent than in other Southeast Asian countries. Therefore, the evaluation and reporting of economic costs of invasions need to be improved in this region to provide efficient data-based support for mitigation and management of their impacts.

Abstract (Chinese)

外来物种入侵新加坡和东南亚：数据缺乏不能掩盖潜在巨大的经济损失 众所周知，外来物种入侵的影响是导致全球生物多样性降低的一个重要因素。然而，对于外来物种入侵造成国家经济损失知之甚少，从而阻碍了有效的管理响应。在这项研究中，我们使用已发表的数据揭示外来物种入侵东南亚造成的经济损失，重点关注新加坡：一个生物多样性丰富的热带岛屿城市国家，面积小、人口密度高、进出口贸易量大，这三个因素可能会增加入侵。新加坡和东南亚的其他国家一样缺乏外来物种入侵造成经济损失的数据，只有一小部分已知的入侵物种造成经济损失的记录。然而，自1975年以来，外来物种入侵在新加坡造成经济损失估计约为17.2亿美元（考虑到通货膨胀），约占整个东南亚经济损失（169亿美元）的十分之一。外来物种入侵在新加坡和东南亚的造成的经济损失主要与蚊科（Culicidae）昆虫（主要是伊蚊）有关，与其造成的直接伤害、资源损失、医疗保障和防治的开支有关。根据在其他国家造成损失的经验，估算另外11种在新加坡入侵物种造成了8.9313亿美元的经济损失，这一结果表明记录和实际损失之间的巨大差距（超过90%的入侵物种的缺乏造成经济损失的记录）。在新加坡或其他东南亚国家的数据库中，没有外来入侵物种造成经济损失的记录，因此缺乏前瞻性的管理措施。这突出表明，对于入侵物种造成经济损失报告的短缺与相关管理投资的缺乏是一致的。此外，相对于进口水平，新加坡的入侵物种造成的经济损失是被低估的，根据土地面积和人口规模，总的经济损失超过了预期，远远高于其他东南亚国家。因此，在这个地区需要加强对入侵物种造成经济损失的评估和报告，从而为减轻和管理其影响提供有效的数据支持。

Abstract (Malay)

Penaklukan spesis di Singapura dan Asia Tenggara: jurang data gagal untuk menutup kos ekonomi yang berpotensi besar). Kesan buruk spesies asing invasif diketahui ramai dan dikategorikan sebagai penyumbang utama kehilangan biodiversiti di peringkat global. Walau bagaimanapun, tindak balas pengurusan terhalang kerana kekurangan maklumat tentang penilaian kewangan yang timbul daripada penaklukan spesis asing invasif terhadap ekonomi negara. Dalam kajian ini, kami menggunakan data yang telah diterbitkan untuk menggambarkan kos ekonomi penaklukan spesis di Asia Tenggara, dengan fokus pada Singapura – sebuah negara pulau tropika yang kaya dengan biodiversiti, mempunyai saiz kecil, kepadatan manusia yang tinggi dan jumlah perdagangan yang tinggi, tiga faktor yang berkemungkinan meningkatkan penaklukan spesis. Di negara ini, dan juga di negara-negara lain di Asia Tenggara, data kos masih kekurangan, dengan kos yang sedia ada cuma untuk sebilangan kecil spesies yang diketahui invasif. Namun, keseluruhan kos ekonomi yang tersedia untuk Singapura dianggarkan ~ US$ 1.72 bilion secara keseluruhan sejak tahun 1975 (setelah memperhitungkan inflasi), yang merupakan kira-kira sepersepuluh daripada jumlah kos yang dilaporkan di seluruh Asia Tenggara (US$ 16.9 bilion). Kos ini, di Singapura dan Asia Tenggara, kebanyakannya berkaitan dengan serangga dalam keluarga Culicidae (terutamanya, *Aedes* spp.) dan berkaitan dengan kerosakan, kehilangan sumber daya, penjagaan kesihatan dan perbelanjaan yang berkaitan dengan kawalan. Jangkaan untuk 11 spesies tambahan yang diketahui invasif di Singapura, tetapi hanya dengan menggunakan kos yang dilaporkan dari luar negara, berjumlah US$ 893.13 juta tambahan, menunjukkan potensi adanya jurang besar antara kos yang direkodkan dan yang sebenar (laporan kos masih tiada untuk lebih daripada 90% invasif spesies). Kos dalam pangkalan data untuk Singapura – atau untuk negara-negara Asia Tenggara lain – tidak dikaitkan secara eksklusif dengan pengurusan proaktif. Ini menunjukkan bahawa kekurangan laporan tentang kos penaklukan spesis dicerminkan oleh kekurang pelaburan untuk pengurusan. Lebih-lebih lagi, kemasukan kos penaklukan spesis di Singapura kurang dilaporkan berkaitan dengan tahap import, tetapi jumlah kos melebihi jangkaan, berdasarkan keluasan tanah dan saiz penduduk, dan di tahap yang lebih tinggi daripada negara-negara Asia Tenggara yang lain. Oleh itu, penilaian dan pelaporan kos ekonomi penaklukan spesis perlu ditingkatkan di rantau ini untuk memberikan sokongan berasaskan data yang efisien untuk mengurangkan dan menguruskan kesan buruk akibat spesis asing invasif.

Abstract (French)

Invasions biologiques à Singapour et en Asie du Sud-Est: les lacunes dans les données ne masquent pas des coûts économiques potentiellement énormes. Les impacts des espèces exotiques envahissantes (EEE) sont bien connus et sont classés comme l’un des principaux contributeurs à la perte de biodiversité à l’échelle mondiale. Cependant, on en sait relativement peu sur les coûts monétaires induits par les invasions sur les économies nationales, qui entravent les décisions de gestion. Dans cette étude, nous avons utilisé des données publiées pour décrire le coût économique des invasions en Asie du Sud-Est, en mettant l’accent sur Singapour - une ville-état insulaire tropicale riche en biodiversité de petite taille, avec une densité humaine et un volume commercial élevés; trois facteurs susceptibles d’augmenter les invasions. Dans ce pays, ainsi que dans d’autres en Asie du Sud-Est, les données sur les coûts étaient rares, les coûts enregistrés n’étant disponibles que pour une petite fraction des espèces réputées envahissantes. Pourtant, les coûts économiques globaux disponibles pour Singapour ont été estimés à au moins ~ 1,72 milliard de dollars américains, soit environ un dixième du coût total enregistré dans toute l’Asie du Sud-Est (16,9 milliards de dollars américains). Ces coûts, à Singapour et en Asie du Sud-Est, étaient principalement liés aux insectes de la famille des Culicidae (principalement Aedes spp.) et associés aux dommages, à la perte de ressources, aux soins de santé et aux dépenses liées au contrôle. Les projections pour 11 espèces supplémentaires connues pour être envahissantes à Singapour, mais avec des coûts enregistrés uniquement en provenance de l’étranger, se sont élevées à 893,13 millions USD supplémentaires, montrant l’énorme écart potentiel entre les coûts enregistrés et réels (les enregistrements de coûts restent manquants pour plus de 90% des espèces envahissantes). Aucun coût dans la base de données pour Singapour - ou pour d’autres pays d’Asie du Sud-Est - n’était exclusivement associé à une gestion proactive, ce qui souligne qu’un manque de rapports sur les coûts des invasions se traduit par un manque d’investissement dans la gestion. De plus, les entrées de coûts d’invasion à Singapour ont été sous-déclarées par rapport aux niveaux d’importation, mais les coûts totaux ont dépassé les attentes fondées sur la superficie des terres et la taille de la population, et dans une plus grande mesure que dans d’autres pays d’Asie du Sud-Est. Par conséquent, l’évaluation et la communication des coûts économiques des invasions doivent être améliorées dans cette région pour fournir un soutien efficace basé sur des données pour l’atténuation et la gestion de leurs impacts.

Abstract (Spanish)

Invasiones biológicas en Singapur y el sudeste asiático: la falta de datos no logra enmascarar costos económicos potencialmente masivos. Los impactos de las especies invasoras son bien conocidos y se caracterizan por ser uno de los principales contribuyentes para la pérdida de la biodiversidad a nivel global. No obstante, se conoce relativamente poco sobre el impacto monetario que las invasiones provocan en las economías de las naciones, lo cual obstaculiza las respuestas de manejo. En el presente estudio, se emplearon datos publicados para describir los costes económicos de las especies invasoras en el sudeste asiático, con un enfoque en Singapur –una pequeña ciudad isleña tropical con alta riqueza biológica, alta densidad poblacional y un alto volumen del mercado; tres factores que se asocian con el incremento de invasiones biológicas–. En este país, como en otros del sudeste de Asia, los datos sobre los costes son escasos, donde los registros de costes disponibles representaron solo una fracción de las especies que se conocen como invasoras. No obstante, los datos sobre los costes económicos disponibles en general se estimaron al menos en ~ US $1.72 mil millones en Singapur, lo cual corresponde aproximadamente a una onceava parte de los costes reportados en todo el sudeste de Asia (US $16.9 mil millones). Los costes identificados en Singapur y el sudeste asiático se asociaron principalmente con insectos de la familia Culicidae (principalmente *Aedes* spp.) y se asociaron con gastos por daños, pérdida de recursos, cuidado de la salud, y aquellos relacionados con el control. Las proyecciones para las 11 especies adicionales que se sabe que son invasoras en Singapur, pero con registros superficiales en sus costes, alcanzaron un total de US $893.13 millones, mostrando un gran vacío potencial entre la información registrada y los costes actuales (los registros mantienen una ausencia sobre los costes del 90% de las especies invasoras). Ningún coste en la base de datos de Singapur –o para otro país sudasiático– se asoció exclusivamente con manejo proactivo, destacando que la escasez de información sobre los costes de las invasiones se refleja en la falta de inversión en el manejo. Además, las entradas de los costes de invasoras se mostraron inferiores a los niveles de importación en Singapur, pero los costes totales superaron las expectativas basadas en la extensión del área y el tamaño de la población, y en mayor medida que en otros países del sudeste de Asia. Por lo tanto, es necesario mejorar la evaluación y la presentación de informes sobre los costes económicos de las invasiones en esta región a fin de proporcionar un apoyo eficaz basado en datos para la mitigación y el manejo de sus impactos.

Keywords

Ecosystem services, imports, InvaCost, monetary impact, tropics, socioeconomic sectors

Introduction

Biological invasions cause significant ecological impacts around the world, posing profound impediments to conservation efforts and potentially driving marked socioeconomic costs (Hulme et al. 2009; Early et al. 2016; Seebens et al. 2017). Invasive species are amongst the main drivers of biodiversity loss worldwide (Malcolm and Markham 2000; Stigall 2010; Bellard et al. 2016; Haubrock et al. 2021). In a socioeconomic context, invasions can directly affect human health, damage goods and services, compromise public and social welfare and impact agriculture (Bradshaw et al. 2016; Paini et al. 2016; Jones 2017; Shackleton et al. 2019). Yet, disproportionately few economic resources are allocated to remediate the large-scale consequences of such invasions in different parts of the world (Hulme et al. 2009; Scaler, 2010; Early et al. 2016). One of the reasons underlying this discrepancy is undoubtedly related to the limited knowledge and societal awareness of their actual impacts (Courchamp et al. 2017).

Whilst the ecological impacts of invasive species are well-described (see, for example, Gurevitch and Padilla 2004; Didham et al. 2005; Cuthbert et al. 2019a, 2020; Mofu et al. 2019), relatively few studies have synthesised monetary aspects associated with biological invasions (but see Pimentel et al. 2005 for the USA; Kettunen et al. 2009 for Europe; Oreska and Aldridge 2011 for the UK; Gren et al. 2009 for Sweden; Hoffmann and Broadhurst 2016 for Australia; Xu et al. 2006 for China). Yet, highlighting the economic costs of invasions can actually represent a key awareness-building tool for both the general public and authorities, as well as an efficient way for motivating policies, guiding decision-making and prioritising management actions towards invasive species (Dana et al. 2014; McConnachie et al. 2016; Hiatt et al. 2019; Diagne et al. 2020a). Such economic costs might relate to a large variety of impacts, through damage directly or indirectly driven by invaders (e.g. Shwiff et al. 2010), to different types of expenditure dedicated to preventing, controlling or eradicating invasions (e.g. Hoffmann and Broadhurst 2016). Nonetheless, the scarcely reported economic costs are spatially, temporally and taxonomically fragmented (Diagne et al. 2020a), leading to a lack of a holistic understanding of the monetary aspects of invasions. This represents a major challenge for decision-making as invasions represent an ever-increasing trans-boundary socio-ecological challenge (Lovell et al. 2006; Marbuah et al. 2014; Diagne et al. 2020a). Particularly, while regional estimates have highlighted the diversity of costs (e.g. Pimentel et al. 2000, 2005; Kettunen et al. 2009; Nghiem et al. 2013), limited spatial resolution has resulted in piecemeal financial commitments to tackle the growing economic problem of invasions at relevant scales. More detailed and comparable information on specific costs is urgently needed at the government-level, where budgets are established and managed.

As an international travel and trade hub with numerous introduction pathways, Singapore is a country facing high risk of biological invasions (Yeo and Chia 2010; Seebens et al. 2013; Wong 2018) and may thus be a particularly useful example for such nationally-scaled cost estimation. Thus, Singapore is outstanding amongst other Southeast Asian countries due to its very dynamic economic connectivity, despite a relatively small surface area. Singapore is a highly urbanised and densely populated, but biodiverse, tropical island city state, centrally located within Southeast Asia (Tan et al. 2010; Ng et al. 2011; World Bank 2019). The few publications reporting costs of invasive species in Singapore have suggested they might be important (Nghiem et al. 2013), yet costs have lacked synthesis. At least 142 non-native animal species have been reported in Singapore (Yeo and Chia 2010), including species listed on several 'worst invasive alien species' lists (e.g. IUCN).

Recently, the available literature on economic costs of invasive species globally was compiled in the InvaCost database (Diagne et al. 2020b) with the aim of generating the means to fill knowledge gaps on invasion costs worldwide. Using data available from this database, we synthesised and described the available information on economic costs of invasions in Southeast Asia, focusing on Singapore in particular.

We specifically investigated (a) how recorded costs and species are characterised across Southeast Asian countries and (b) Singapore as a more detailed example or case study to describe recorded costs impacting its economy, according to (*i*) taxa, (*ii*) cost types and (*iii*) activity sectors. We also deciphered whether the level of reliability of estimates may impact the financial burden of invaders. Furthermore, we extrapolated additional costs for invaders reported in Singapore, but with unknown costs there. Finally, we correlated invasion costs with importation levels, surface area and population size amongst countries to assess the specificities of Southeast Asian countries. We hypothesised that the costs of invasive species in Singapore are underestimated and yet substantial, as are probably those of other Southeast Asian countries.

Methods

Data acquisition

Information on the economic cost of invasions in all the Southeast Asian countries (Brunei, Cambodia, East Timor, Indonesia, Laos, Malaysia, Myanmar, Philippine, Singapore, Thailand and Vietnam) was extracted from the InvaCost database (Diagne et al. 2020b; Angulo et al. 2021) concerning the global costs of invasive species, based on published literature, enabling comprehensive quantification of costs associated with invasive species at various spatio-temporal scales. The latest version of the database, as well as a summary of the whole procedure used to build and update it, can be directly accessed at https://doi.org/10.6084/m9.figshare.12668570. Briefly, the data in InvaCost were collected following (*i*) a series of literature searches using the Web of Science platform (https://webofknowledge.com/), Google Scholar database (https://scholar.google.com/) and the Google search engine (https://www.google.com/) and (*ii*) targeted searches through contacting experts and stakeholders to request potentially unpublished and/or publicly unavailable documents containing cost information. All the retrieved costs were standardised in an up-to-date currency (2017 USD), while also taking into account an inflation factor (Diagne et al. 2020b). We performed descriptive analyses of a subset of this database, by filtering data ('Official_country' column) to exclusively ascertain invasion costs in each country.

Cost calculation and description

We considered the total costs of invasions by amalgamating the recorded raw costs (column 'Cost_estimate_per_year_2017_USD_exchange_rate') per year from our subset. Due to the variability of temporal scales of cost estimates in InvaCost, we annualised the data, based on the difference between the "Probable_starting_year_adjusted" and "Probable_starting_year_adjusted" columns using the "summarizeCosts" function of the 'invacost' package (v.0.3-4) in R (v.4.0.2) (Leroy et al. 2020). Each expanded entry thus corresponded to a single year for which costs were available following this expansion process (i.e. costs spanning multiple years were divided amongst those same years). The resulting costs attributed to recorded species were examined according to different descriptive fields of the database (an updated description of these descriptive fields is openly available at https://doi.org/10.6084/m9.figshare.12668570):

i. Method_reliability: illustrating the perceived reliability of cost estimates, based on the type of publication and method of estimation. Estimates in peer-reviewed publications or official reports or with documented, repeatable and/or traceable methods were designated as "High reliability"; all other estimates were designated as "Low reliability" (Diagne et al. 2020b);

ii. Implementation: referring to whether the cost estimate was actually realised in the invaded habitat ("Observed") or whether it was only predicted to occur ("Potential");

iii. Type_of_cost_merged: grouping of costs according to the categories: (a) "Damage-Loss" referring to damages or losses incurred by invasion (e.g. costs for damage repair, resource losses, medical care), (b) "Management" comprising control-related expenditure (for example monitoring, prevention, management, eradication) and money spent on education and maintenance costs, (c) "Diverse/Unspecified" including mixed damage-loss and management costs (cases where reported costs were not clearly distinguished amongst cost types);

iv. Impacted_sector: the activity, societal or market sector that was impacted by the cost (Suppl. material 2); note that individual cost entries not allocated to a single sector were classified under "Mixed" in the "Impacted_sector" column. A detailed summary of all descriptors can be found in Suppl. material 1 (see also Diagne et al. 2020b) and the final dataset in Suppl. material 2.

Temporal dynamics and cost extrapolations

To investigate the temporal dynamics of invasion costs, we used the "summarizeCosts" function implemented in the R package 'invacost' (Leroy et al. 2020). With this method, we calculated the observed cumulative and average annual costs covering the period for which costs were recorded, displaying the changes in invasion costs over time.

As cost information for invasive alien species in Singapore, which we used as an example, was limited (three species; see Results for more details), we also extrapolated potential costs for a few additional known invasive species present in Singapore, but which had recorded costs outside Singapore. For this, we used the most recent comprehensive list of alien animal species in Singapore (n = 142; Yeo and Chia 2010). With this information, we first estimated the mean annual cost of the species listed in Yeo and Chia (2010) outside Singapore (at the "country" scale) that was available in InvaCost, assuming the InvaCost database contained recorded cost information for Singapore over the same period (1975–2015). We then applied a correction factor that considers the cost difference between the average costs of all invasive alien species in Singapore and the average costs of all invasive alien species outside Singapore (excluding extreme values, i.e. the upper and lower 12.5% when implementing the correction factor to cost data). The corrected mean cost of each of these species was then summed to obtain an additional cost of biological invasions not directly available from records in Singapore.

Southeast Asia and national comparisons

Given Singapore is an economic centre, we compared the available cost information of Singapore – in terms of cost entries and number of recorded species (Liu et al. 2021) – to other available information on invasive alien species costs in Southeast Asian countries recorded in InvaCost (via the aforementioned data processing methods). Furthermore, we compared invasion cost entries with other countries worldwide using a linear regression, based on import value (collected from the International Trade Centre (https://www.trademap.org/tradestat/Country_SelProduct_TS.aspx) to (i) see how the lack of available data can affect the estimated economic costs and (ii) examine the relationship between trade volume and economic activities with the cost recording of invasive species. We focused on the 50 countries ranking highest in import value, but with recorded data in InvaCost. Further, we collected the data of species that have been introduced in all countries in Southeast Asia (see Results for more details) from the Global Alien Species First Records Database (Seebens et al. 2018; accessed in June 2020).

Finally, we examined the relationships between invasion costs (observed and high reliability costs only) and (i) land area and (ii) human population size using linear regressions (log-transformed) and examined how Singapore compared to other countries globally and in Southeast Asia particularly. Land area and population size per country were obtained using 2020 data from worldometer (https://www.worldometers.info/world-population/population-by-country/).

Results

Costs across taxa, types and sectors in Singapore

Cost data originated from seven records from six different published sources (n = 34 expanded entries). The recorded costs were found to have occurred after 1975 and amounted to US$ 1.720 billion in total (Figure 1).

At the taxonomic level, cost estimates were available for species from two families, Culicidae (n = 6 estimates) and Corvidae (n = 1). Within Culicidae, *Aedes* spp. drove all of the recorded costs, with four records attributed to *A. aegypti* alone and two as a combination of *A. aegypti* and *A. albopictus*. Although *A. albopictus* is native to Singapore, it was not possible to separate joint cost estimates, which accounted for < 0.05% of total Culicidae costs. For Corvidae, the single cost estimate was associated with *Corvus splendens*.

The overall estimated cost was mainly caused by *Aedes* spp. with a total of US$ 1.72 billion split between damage-losses (US$ 1.14 billion) and management costs (US$ 578.01 million). For *C. splendens*, the single cost estimate reached US$ 765.24

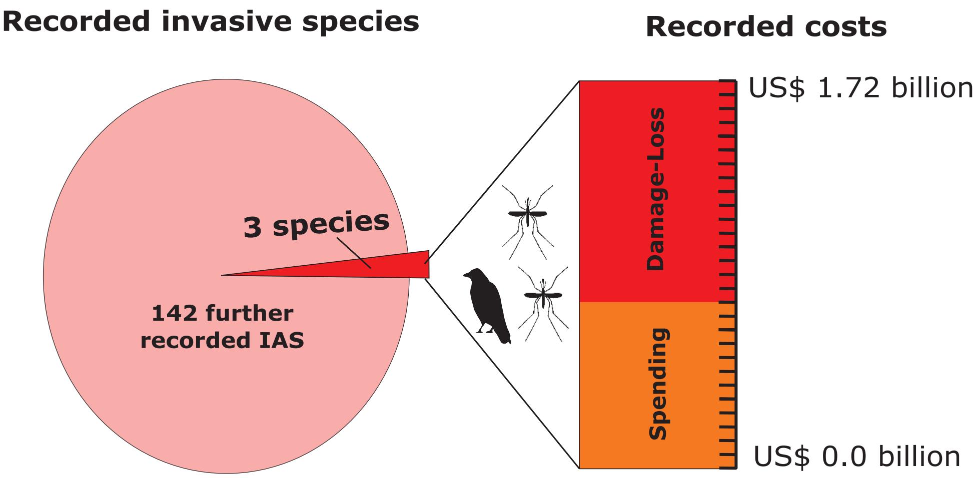

Figure 1. Relative proportions of known alien species present and recorded costs in Singapore as of 2010 (Yeo and Chia 2010), alongside type categorisations for reported costs.

thousand and concerned costs attributed to control-related management efforts (Figure 2a). With respect to the impacted sector, all *Aedes* spp. costs were associated with a combination of impacts on authorities-stakeholders, health and public and social welfare. The single recorded costs for *C. splendens* impacted authorities-stakeholders (Figure 2b). The reported economic costs were associated with terrestrial systems alone and, thus, no costs were documented in aquatic invasions.

From a methodological point of view, all reported costs were classified as "Observed", i.e. considered as actually occurring and not based on predictions or extrapolations from outside the invaded area. Every documented *Aedes* spp. cost was obtained from accessible peer-reviewed literature and thus deemed "High reliability". Conversely, the single cost estimate of *C. splendens* was deemed to be of "Low reliability" (Figure 2c). Accordingly, more than 99.9% of costs were deemed "High reliability".

Temporal cost accumulations, extrapolations and correlations in Singapore

Costs for invasive species were recorded between 1975 and 2014. These costs tended to increase over time, both in terms of reported costs (1975–1994: n = 2; 1995–2014: n = 32), but also average annual costs (1975–1994: US$ 1.66 million per year; 1995–2014: US$ 80.24 million per year), with an annual average cost total of US$ 41.91 million across the entire period (Suppl. material 3).

Comparing the costs of recorded species in Singapore with their average annual costs per country outside of Singapore, after excluding extreme values (removing 25% extreme values, i.e. the top and bottom 12.5%), costs and expenditure in Singapore were around three times lower than those in the rest of the world. From the 142 species recorded in Yeo and Chia (2010), only an additional 11 were recorded in the InvaCost database (Suppl. material 4). Applying the average annual monetary cost discrepancy

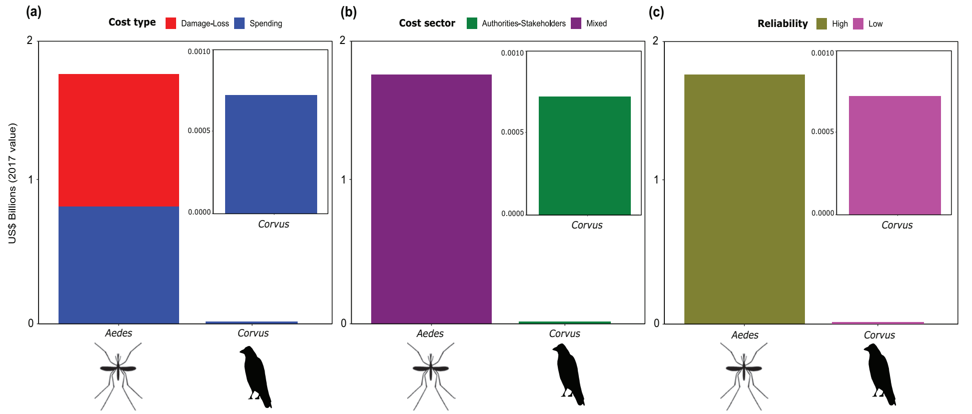

Figure 2. Total costs generated by the two genera of invasive species in Singapore with available cost estimates considering **a** cost type **b** impacted sector and **c** reliability of cost estimations.

Table 1. Comparison of recorded invasive alien species and their costs amongst countries in Southeast Asia. Proportions of species with reported costs, relative to numbers of known reported alien species originating from the Global Alien Species First Records Database (Seebens et al. 2018; accessed in June 2020), are also displayed.

Southeast Asian country	Recorded species	Database entries	Total cost in US$ billion (2017 value)	Species reported	Proportion of recorded established alien species
Brunei	1 (*Aedes aegypti*)	1	0.007	-	-
Cambodia	1 (*Aedes aegypti*)	7	0.208	10	10%
East Timor	1 (*Aedes aegypti*)	1	0.004		
Indonesia	2 (*Aedes aegypti*; *Rattus* sp.)	5	3.406	75	2.7%
Laos	1 (*Aedes aegypti*)	1	0.054	10	10%
Malaysia	4 (*Aedes aegypti*; *Aedes albopictus, Mus musculus, Rattus norvegicus*)	10	2.673	36	5.6%
Myanmar	3 (*Aedes aegypti, Mus musculus, Rattus norvegicus*)	3	0.152	15	6.7%
Philippines	3 (*Aedes aegypti*; *Pomacea canaliculata*; *Sternochetus frigidus*)	10	3.169	70	4.3%
Singapore	3 (*Aedes aegypti*; *Aedes albopictus*; *Corvus splendens*)	7	1.718	142	2.6%
Thailand	4 (*Aedes aegypti*; *Aedes albopictus, Mus musculus, Rattus norvegicus*)	13	5.176	45	4.4%
Vietnam	1 (*Aedes aegypti*)	6	0.327	20	5%

as a correcting factor to the average annual costs of the 11 invasive species, using the InvaCost data from outside Singapore, resulted in an additional projected annual average cost of US$ 22.33 million per year and a total of US$ 893.13 million additional costs considering the period 1975–2015.

Southeast Asia and national comparisons

The monetary impact of invasions recorded in Southeast Asia totalled US$ 16.89 billion between 1960 and 2020. Amongst these, Singapore ranked fifth relative to other countries in terms of reported costs, with two recorded invasive alien species and seven recorded cost entries in InvaCost. Notably, Brunei had the lowest number of recorded

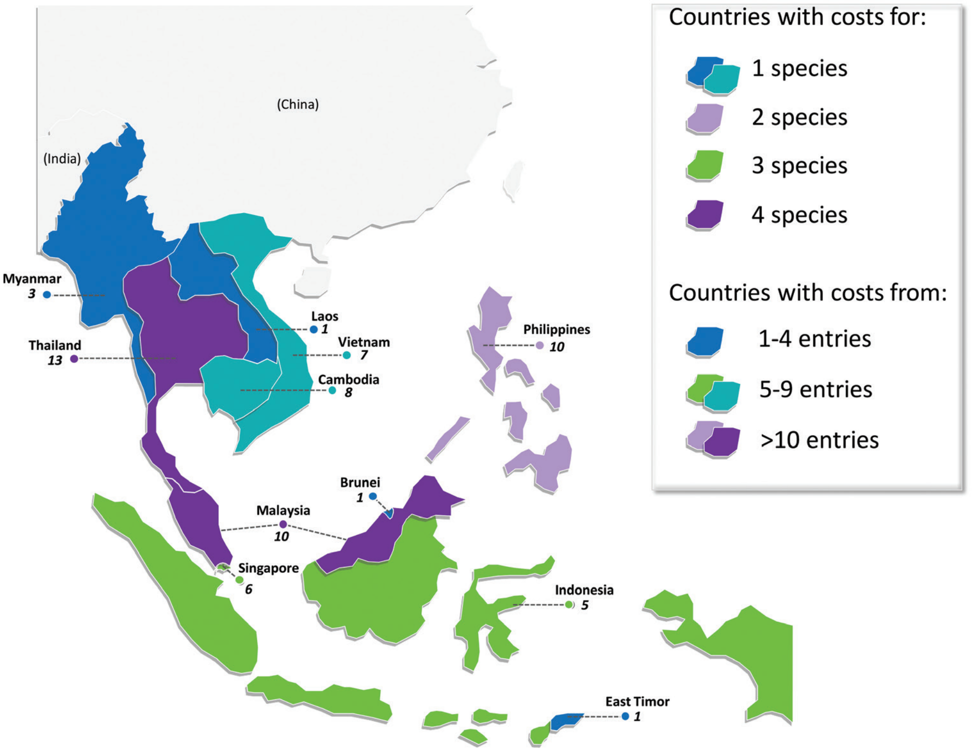

Figure 3. Recorded costs and species for Southeast Asian countries.

entries (1), species (1) and costs (US$ 6.7 million), while Thailand had the highest costs (US$ 5.2 billion) and most recorded entries (13) according to InvaCost (Table 1), suggesting considerable spatial heterogeneity in the region (Figure 3). In countries where lists of known invasive alien species were available (Liu et al. 2021), all had reported costs for 10% or less of known invasive alien species, with Singapore having the lowest proportion of aliens with costs (< 3%).

We further identified a significant correlation between trade volume and the number of recorded entries in InvaCost (Suppl. material 5). When the number of records from Singapore is related to the volume of trade imports (Figure 4), which has been shown to be strongly related to cost entries (Haubrock et al. 2021b; Kourantidou et al. 2021), the relationship highlights a number of entries 40 times lower than expected. The under-reporting of cost entries in Singapore was considerably more apparent than other high-ranking Southeast Asian countries (i.e. amongst top 50 globally in terms of imports), with Thailand, Vietnam, Malaysia and Indonesia also having fewer records than expected based on imports, but the Philippines having more cost records than expected (Figure 4).

Considering all countries, invasion costs related significantly positively to both land area and population size (Supplement 5). When compared to other countries with costs, Singapore displayed considerably greater costs relative to those variables, even relative to other Southeast Asian nations which mostly clustered together (Figures

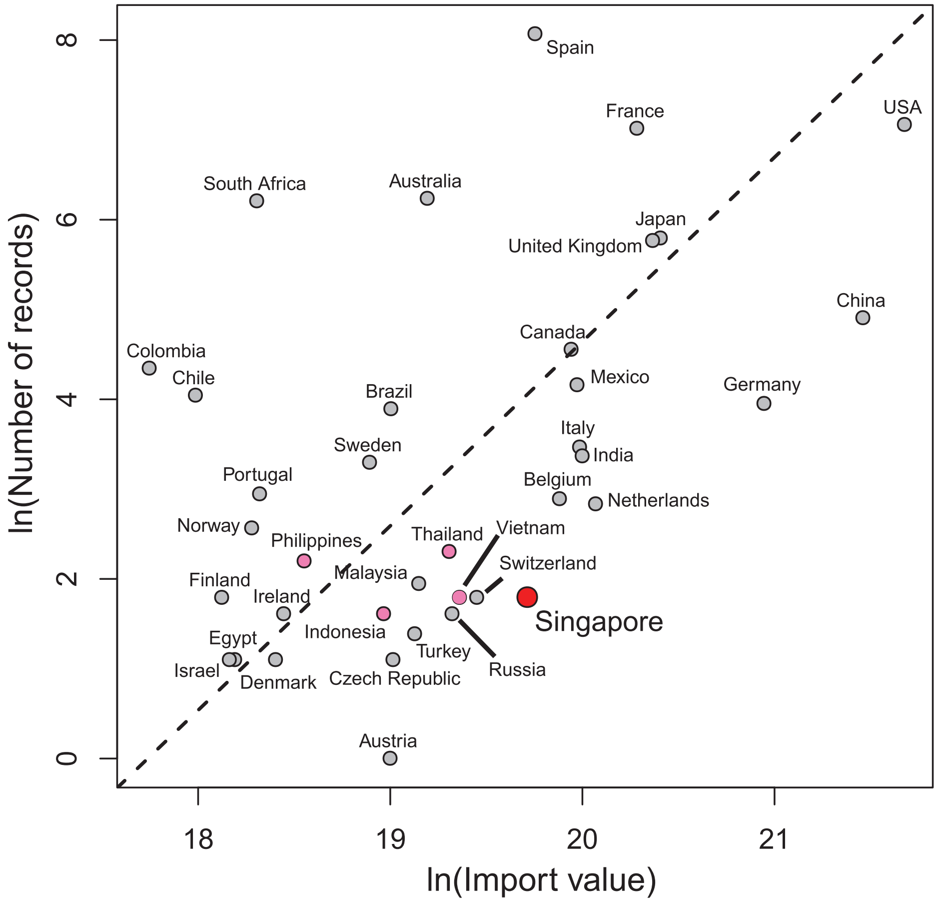

Figure 4. Relationship between the import value and the number of records in InvaCost, focusing on the 50 countries ranking highest in both GDP and import values, but with recorded data in InvaCost. Note that all variables are displayed on a ln-scale. Singapore shows a large deficit of records related to expectations from its import value.

5a, b). Indonesia, Myanmar and Vietnam (and Laos in the case of surface area) had lower invasion costs than expected, based on surface area and human population.

Discussion

The recorded invasion costs in Singapore over the past 40 years have reached US$ 1.72 billion in total which represents about ⅚ of the Ministry of the Environment and Water Resources (S$ 2.83 billion; US$ 2.12 billion), ⅔ of the Ministry of Trade and Industry (S$ 3.68 billion; US$ 2.76 billion) or more than ⅓ of the Ministry of National Developments (S$ 4.8 billion; US$ 3.67 billion) annual budgets in 2017 (https://www.singaporebudget.gov.sg). Despite these costs being high, our study shows that the available entries in the da-

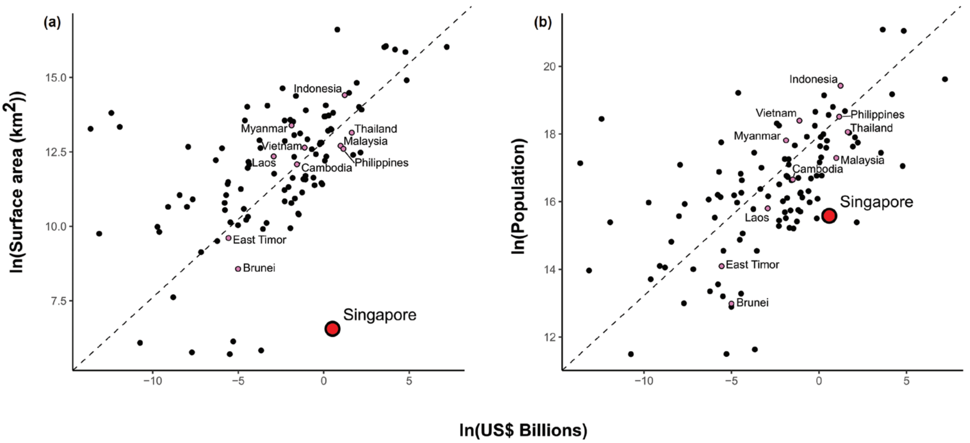

Figure 5. Relationships between invasion costs and **a** land area and **b** human population of countries. Note that variables are presented on a ln-scale. Each node represents an individual country with costs in InvaCost, while Singapore is highlighted.

tabase were highly fragmentary, with the majority of documented alien animal species in Singapore being absent from the cost estimation (Yeo and Chia 2010). This further puts into perspective overall costs that are already surprisingly high for such a small area, especially when actual costs are expected to be more numerous and thus overall higher than the few recorded costs. Indeed, we show not only that Singapore has few cost entries, but also that it has about 40 times fewer than expected from its trade volume. Contrastingly, comparisons, based on costs relative to land area and human population size, evidenced considerably higher costs in Singapore *pro rata*, based on those variables, with costs comparable to countries approximately 600-times larger and 10-times more populous. These trends were even more marked when compared to relationships amongst other Southeast Asian countries, which were more in line with the global cost pattern.

The very few recorded costs were linked principally to the human health sector and mainly driven by mosquitoes, with large incurred costs listed for healthcare and their control. This is mostly related to costs arising from limiting the risk of infectious human diseases, such as Zika, dengue or chikungunya, which are caused by pathogens, vectored principally by *A. aegypti* and *A. albopictus*, as well as losses through direct healthcare costs (Beltrame et al. 2007; Zammarchi et al. 2015). Indeed, mosquitoes are considered as a severe problem in Singapore, underlined by the considerable costs on control and the medical field (Carrasco et al. 2011). These total costs relating to human health in Singapore are significant, considering previous estimation of annual costs on human health and environment in the entirety of Southeast Asia (US$ 1.85 billion; US$ 1.4–2.5 billion per year) estimated by Nghiem et al. (2013). Moreover, our extrapolations for species known to be present in Singapore, but with no reported costs there, indicated further economic impacts summing to US$ 893.13 million over 1975–2014. Although this figure has to be taken with caution, it underlines the magnitude of potentially occurring costs which are not accounted for in published literature. These numbers are still likely underestimated (Diagne et al. 2021), given that these additional costs stem from just 11 of the 142 known animal invaders in Singapore that were available in InvaCost, with plant species missing entirely. Indeed, information on plant invasions in Singapore and, particularly, with regard to their monetary impacts, are scarce (Meyer 2000), with Yeo and Chia (2010) listing only relatively few invasive examples, such as the water hyacinth *Eichhornia crassipes*, which entered Singapore's waterways and proliferated to a damaging extent. As such, most invaders lack cost information at the Singapore scale, yet also internationally. Nevertheless, this lack of information, although striking, is neither surprising nor different from what is found in similar studies elsewhere. First, we showed that this is a general pattern in the region, with Singapore amongst the countries with most cost entries in Southeast Asia. Second, national or regional studies on the economic costs of biological invasions outside this region also consistently reported only between 2% and 10% of invasive alien species having recorded costs, for example, Argentina (Duboscq-Carra et al. 20201), Asia (Liu et al. 2021), Australia (Bradshaw et al. 2021), France (Renault et al. 2021), Germany (Haubrock et al. 2021c), Mexico (Rico-Sánchez et al. 2021) and United Kingdom (Cuthbert et al. 2021a).

In the context of Southeast Asia, this national bias is even more pronounced; amidst differences in economic activities amongst countries (note that Singapore has the highest GDP per capita in Southeast Asia), the lack of cost information for invasive alien species more broadly across Southeast Asian countries is striking. Singapore had the lowest proportion of known invasive alien species with reported costs, while all Southeast Asian countries had costs for 10% or below in terms of listed invasive alien species. This is also noteworthy in an all-Asia context (Liu et al. 2021), as shown by a lack of cost information in, for example, South Korea (only one 'Unspecified' record), Saudi Arabia (no records), Turkey (no records), Thailand (only records considering *A. aegypti* and *A. albopictus*) and Iran (no records), which are all amongst the 10 countries with the highest GDP in Asia (International Monetary Fund 2019; https://www.imf.org/). This suggests that lower economic wealth is likely not to be a determinant of how biological invasions – and their monetary costs – are documented (Nghiem et al. 2013).

Regarding the overall cost estimation, it is possible to overestimate costs if one assumes that the costs repeatedly occurring over time are repeated for a longer duration than it actually occurs (if total duration is not reported). To stay conservative, we assigned a single duration year for cost entries for which such information was missing and the cost was potentially ongoing. Furthermore, it is possible that the annual monetary burden increased over the years due to frequent descriptions of new invaders. In addition, the spatial scale for estimating costs in InvaCost reflect 'site' and/or 'country' level estimates, meaning that the national burden could be higher as some 'regional' costs may not have specified specific countries. Additionally, we show that the relatively large number of alien species present in Singapore (see Yeo and Chia 2010) potentially contributes further costs exceeding those that were recorded in InvaCost. However, one should consider that a) Yeo and Chia (2010) presented detailed information only for animals, excluding plants and microbes in this assessment; and b) the difficulties in quantifying certain types of economic impact – especially concerning ecosystem services and the many forms of damage that occur indirectly (Spangenberg and Settele 2010). For all these reasons, it could be assumed that the presented costs may represent potentially a massive underestimation of the real economic costs of biological invasions in Singapore and Southeast Asia.

Our work also reveals a considerable taxonomic bias in the reported economic impacts of the 142 reported alien animal species in Singapore. The weighting of costs towards taxa in the database does not reflect the 'true' taxonomic composition of alien species in Singapore. Freshwater fishes and reptiles together make up the majority of alien species in this country (61%) (Yeo and Chia 2010), but no cost data were found for any of these taxa here. Yet, Yeo and Chia (2010) present anecdotal information that several non-native plant species (e.g. the South American water hyacinth, *Eichhornia crassipes*) are likely to have necessitated regular management at various scales, sometimes at considerable (yet unquantified) financial cost. This information, however, mostly relied on Wee and Corlett (1986), who, although most likely being outdated, listed 34 potentially invasive plant species present in Singapore. Nevertheless, these two accounts together are only about one quarter of the 648 species listed by GRIIS (Kwek et al. 2020), underlining the gap of cost reporting for invasive species in Singapore.

Whilst we cannot exclude that some existing cost data may have not been captured by the InvaCost database, this taxonomic discrepancy should be discussed. Singapore has a history of freshwater species introductions (Yeo and Chia 2010; Ng et al. 2010; Liew et al. 2012; Ng and Yeo 2012; Kwik et al. 2013; Ng et al. 2015, 2016a, b). Accidental releases/escapes aside, key drivers of intentional releases can often be cultural (e.g. for aesthetic, recreational or religious reasons; Yeo and Chia 2010). Usually, impacts on aquatic habitats or native communities are less obviously perceived by the public and authorities or are perceived as beneficial for local municipalities (Selge et al. 2011; Kilian et al. 2012). This could partially explain the overall bias towards costs on terrestrial habitats and the lack of information regarding aquatic habitats (Cuthbert et al. 2021b). Yet, as Singapore and many other countries of Southeast Asia are (or include) islands and, in many cases, have extensive and economically-important inland water systems, it is striking that no cost exists here for aquatic invasions. Furthermore, birds are known to be commonly released for religious purposes (Su et al. 2016); however the present study contained costs for just one species, indicating additional knowledge gaps.

Given that management and control costs usually outweigh the costs of prevention and surveillance (Leung et al. 2002), the presence of various introduction pathways in Singapore (Yeo and Chia 2010; Jaafar et al. 2012) raises the concern about how economic costs are related to pathways (Liu et al. 2019). Indeed, this should be evaluated for framing management policies by relevant stakeholders, because currently, Singapore does not have specific management plans in place that address threats from major invasive alien species, but has implemented various surveillance/monitoring programmes (National Parks Board Singapore 2015).

Despite most of the economic costs in Singapore being related to the control of invasive species and the costs of healthcare, it can be assumed that other damage or losses have not yet been estimated. For example, similarly data-poor studies found major costs for agriculture in Argentina or the UK (Duboscq-Carra et al. 2021; Cuthbert et al. 2021a) or forestry in Sweden (Haubrock et al. 2021b). In each case, it seemed clear that these trends were driven by few records, suggesting that a richer cost record might, in each case, reveal costs for other activity sectors, substantially raising the overall estimates. In Southeast Asia, biological invasions could exert a very significant toll on major economic sectors, such as forestry in Indonesia, agriculture in Vietnam, fisheries in the Philippines or tourism in Thailand. In the case of many invasive species, only with more costs being described can we get a better understanding of the cost distribution for each descriptor. Furthermore, without information on the financial pressures that invasive species apply to an economy, efforts to tackle these, whether through prevention, surveillance or applied control and monitoring efforts, might fail at an underestimated monetary value due to inadequate investments. Given the likely underestimated costs identified for biodiversity-rich Southeast Asian countries and illustrated with Singapore, alongside their rapidly growing population densities, trade volumes and GDP, the need for effective invasive species management and cost reporting is paramount.

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Supplementary material 1

Description of the procedure used for collecting and describing cost data in the InvaCost database (adapted from Diagne et al. 2020)

Authors: Phillip J. Haubrock, Ross N. Cuthbert, Darren CJ Yeo, Achyut Kumar Banerjee, Chunlong Liu, Christophe Diagne, Franck Courchamp

Data type: database description

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Supplementary material 2

Database subset

Authors: Phillip J. Haubrock, Ross N. Cuthbert, Darren CJ Yeo, Achyut Kumar Banerjee, Chunlong Liu, Christophe Diagne, Franck Courchamp

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Supplementary material 3

Annual average costs of biological invasions in Singapore. Note the y-axis is on a $\log_{10}$ scale

Authors: Phillip J. Haubrock, Ross N. Cuthbert, Darren CJ Yeo, Achyut Kumar Banerjee, Chunlong Liu, Christophe Diagne, Franck Courchamp

Data type: database

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Supplementary material 4

Extrapolated annual average costs for those invasive species known to be in Singapore with recorded costs in InvaCost

Authors: Phillip J. Haubrock, Ross N. Cuthbert, Darren CJ Yeo, Achyut Kumar Banerjee, Chunlong Liu, Christophe Diagne, Franck Courchamp

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Supplementary material 5

Relationships between trade value and recorded cost entries per country in InvaCost, as well as land area and human population with total cost

Authors: Phillip J. Haubrock, Ross N. Cuthbert, Darren CJ Yeo, Achyut Kumar Banerjee, Chunlong Liu, Christophe Diagne, Franck Courchamp

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RESEARCH ARTICLE

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Economic costs of invasive alien species across Europe

Phillip J. Haubrock[1,2*], Anna J. Turbelin[3*], Ross N. Cuthbert[4,5*], Ana Novoa[6*], Nigel G. Taylor[7*], Elena Angulo[3], Liliana Ballesteros-Mejia[3], Thomas W. Bodey[8,9], César Capinha[10], Christophe Diagne[3], Franz Essl[11], Marina Golivets[12], Natalia Kirichenko[13,14], Melina Kourantidou[15,16], Boris Leroy[17], David Renault[18,19], Laura Verbrugge[20,21], Franck Courchamp[3,*]

1 *Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, 63571 Gelnhausen, Germany* **2** *University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Zátiší 728/II, 389 25, Vodňany, Czech Republic* **3** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405, Orsay, France* **4** *Queen's University Belfast, School of Biological Sciences, 19 Chlorine Gardens, Belfast, BT9 5DL, Northern Ireland, UK* **5** *GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, 24105, Kiel, Germany* **6** *Czech Academy of Sciences, Institute of Botany, Department of Invasion Ecology, CZ-25243, Průhonice, Czech Republic* **7** *Tour du Valat, Research Institute for the Conservation of Mediterranean Wetlands, 13200, Arles, France* **8** *University of Aberdeen, King's College, School of Biological Sciences, Aberdeen, AB24 3FX, UK* **9** *University of Exeter, Penryn, Environment & Sustainability Institute, Cornwall, TR10 9FE, UK* **10** *Universidade de Lisboa, Centre for Geographical Studies, Institute of Geography and Spatial Planning, Edifício IGOT, Rua Branca Edmée Marques, 1600-276, Lisbon, Portugal* **11** *University Vienna, Department for Botany and Biodiversity Research, BioInvasions, Global Change, Macroecology-Group, Rennweg 14, 1030, Vienna, Austria* **12** *Helmholtz-Centre for Environmental Research – UFZ, Department of Community Ecology, 06120, Halle (Saale), Germany* **13** *Sukachev Institute of Forest Siberian Branch of Russian Academy of Sciences, Federal Research Center «Krasnoyarsk Science Center SB RAS», Krasnoyarsk, 660036, Russia* **14** *Siberian Federal University, Krasnoyarsk, 660041, Russia* **15** *Woods Hole Oceanographic Institution, Marine Policy Center, Woods Hole, MA 02543, United States* **16** *University of Southern Denmark, Department of Sociology, Environmental and Business Economics, Esbjerg, 6700, Denmark* **17** *Unité Biologie des Organismes et Ecosystèmes Aquatiques (BOREA UMR 7208), Muséum National d'Histoire Naturelle, Sorbonne Universités, Université de Caen Normandie, Université des Antilles, CNRS, IRD, Paris, France* **18** *University of Rennes 1, UMR CNRS 6553, EcoBio, Rennes, France* **19** *Institut Universitaire de France, 1 rue Descartes, Paris, France* **20** *Aalto University, Water & Development Research Group, Espoo, Finland* **21** *University of Helsinki, Faculty of Agriculture and Forestry, Department of Forest Sciences, P.O. Box 27, 00014, Helsinki, Finland*

Corresponding authors: Phillip J. Haubrock (Phillip.Haubrock@Senckenberg.de); Franck Courchamp (Franck.Courchamp@u-psud.fr)

* These authors contributed equally.

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Abstract

Biological invasions continue to threaten the stability of ecosystems and societies that are dependent on their services. Whilst the ecological impacts of invasive alien species (IAS) have been widely reported in recent decades, there remains a paucity of information concerning their economic impacts. Europe has strong trade and transport links with the rest of the world, facilitating hundreds of IAS incursions, and largely centralised decision-making frameworks. The present study is the first comprehensive and detailed effort that quantifies the costs of IAS collectively across European countries and examines temporal trends in these data. In addition, the distributions of costs across countries, socioeconomic sectors and taxonomic groups are examined, as are socio-economic correlates of management and damage costs. Total costs of IAS in Europe summed to US$140.20 billion (or €116.61 billion) between 1960 and 2020, with the majority (60%) being damage-related and impacting multiple sectors. Costs were also geographically widespread but dominated by impacts in large western and central European countries, i.e. the UK, Spain, France, and Germany. Human population size, land area, GDP, and tourism were significant predictors of invasion costs, with management costs additionally predicted by numbers of introduced species, research effort and trade. Temporally, invasion costs have increased exponentially through time, with up to US$23.58 billion (€19.64 billion) in 2013, and US$139.56 billion (€116.24 billion) in impacts extrapolated in 2020. Importantly, although these costs are substantial, there remain knowledge gaps on several geographic and taxonomic scales, indicating that these costs are severely underestimated. We, thus, urge increased and improved cost reporting for economic impacts of IAS and coordinated international action to prevent further spread and mitigate impacts of IAS populations.

Abstract in Czech

Ekonomické náklady na invazní nepůvodní druhy v celé Evropě. Biologické invaze nadále ohrožují stabilitu ekosystémů i naší společnosti, která je na těchto ekosystémech závislá. Zatímco ekologické dopady nepůvodních invazních druhů byly v posledních desetiletích podrobně studovány, existuje jen mámo informací o ekonomických dopadech těchto invazí. Evropa má silné obchodní a dopravní vazby se zbytkem světa i značně decentralizované řízení, což usnadňuje stovkám nepůvodních druhů jejich invazní vpád. Tato studie je prvním komplexním a podrobným příspěvkem, který kvantifikuje ekonomické náklady spojené s invazními druhy, jež se vyskytují v evropských zemí, a to včetně jejich časového vývoje. Dále bylo zkoumáno rozdělení nákladů mezi zeměmi, socioekonomickými odvětvími, taxonomickými skupinami a typy nákladů. Celkové náklady invazních druhů v Evropě dosáhly v letech 1960 až 2020 výše 140,20 miliardy americké dolary (116.6 miliardy eur), přičemž většina (60%) byla spojena s přímými škodami a měla dopad na více odvětví. Tyto náklady byly plošné, ale dominovaly dopady ve velkých západoevropských a středoevropských zemích, jako je Velká Británie, Španělsko, Francie a Německo. Velikost lidské populace, rozloha státu, výše hrubého domácího produktu a úroveň cestovního ruchu byly významnými prediktory nákladů způsobených invazními druhy, přičemž náklady na jejich management byly dány počtem těchto druhů, výzkumným úsilím na ně vynaloženým a úrovní rozvoje obchodu. Časově nákladovost invazních druhů rostla z 23,58 miliardy americké dolary (19.6 miliardy eur) v roce 2013 na odhadovaných 139,56 miliardy americké dolary (116.2 miliardy eur) v roce 2020. Ačkoliv jsou tyto náklady značné, existují stále významné mezery v našich znalostech o jejich úrovni v řadě evropských regionů, stejně jako pro početné taxonomické skupiny invazních druhů. Zde prezentovaná výše škod je tak stále významnou měrou podhodnocena. Vyzýváme tedy ke zvýšenému a lepšímu vykazování ekonomických nákladů způsobených invazními druhy a koordinovaným mezinárodní aktivitám, jež mají za cíl omezovat šíření a dopady těchto druhů.

Abstract in French

Coûts économiques des espèces exotiques envahissantes en Europe. Les invasions biologiques continuent de menacer la stabilité des écosystèmes et des sociétés qui dépendent de leurs services. Alors que les impacts écologiques des espèces exotiques envahissantes (EEE) ont été largement signalés au cours des dernières décennies, il reste peu d'informations concernant les impacts économiques des EEE. L'Europe a de solides liens commerciaux et de transport avec le reste du monde, facilitant des centaines d'incursions d'EEE et des cadres décisionnels largement centralisés. Cette étude est le premier effort complet et détaillé qui quantifie les coûts des EEE collectivement dans les pays européens et examine les tendances temporelles de ces données. En outre, la répartition des coûts entre les pays, les secteurs socio-économiques et les groupes taxonomiques est examinée, de même que les corrélats socio-économiques des coûts de gestion et des dommages. Le coût total des EEE en Europe s'est élevé à 140,20 milliards de dollars américains (ou 116,61 milliards d'euros) entre 1960 et 2020, la majorité (60%) étant liée aux dommages et ayant un impact sur plusieurs secteurs. Les coûts étaient également géographiquement répandus, mais dominés par les impacts dans les grands pays d'Europe occidentale et centrale, à savoir le Royaume-Uni, l'Espagne, la France et l'Allemagne. La taille de la population humaine, la superficie terrestre, le PIB et le tourisme étaient des prédicteurs importants des coûts d'invasion, les coûts de gestion étant en outre prédits par le nombre d'espèces introduites, l'effort de recherche et le commerce. Temporairement, les coûts d'invasion ont augmenté de façon exponentielle au fil du temps, atteignant jusqu'à 23,58 milliards de dollars (19,64 milliards d'euros) en 2013 et 139,56 milliards de dollars (116,24 milliards d'euros) d'impacts extrapolés en 2020. Il est important de noter qu'il subsiste des lacunes dans les connaissances à plusieurs échelles géographiques et taxonomiques bien que ces coûts soient substantiels, ce qui indique que ces coûts sont fortement sous-estimés. Nous suggérons donc une augmentation et une amélioration des rapports sur les coûts des impacts économiques des EEE et une action internationale coordonnée pour prévenir la propagation et atténuer les impacts des populations d'EEE.

Abstract in Russian

Экономические издержки инвазивных чужеродных видов в Европе. Биологические инвазии продолжают угрожать стабильности экосистем и зависящих от экосистемных услуг обществ. Несмотря на активное документирование экологических воздействий инвазионных чужеродных видов (invasive alien species, IAS) в последние десятилетия, данные об экономических потерях, ассоциированных с инвазиями, все еще малочисленны. Европа имеет прочные торговые и транспортные связи с остальным миром, которые могут способствовать инвазиям сотен чужеродных видов, и характеризуется выраженной централизованностью структур, отвечающих за принятие управленческих решений. Данная работа является первым подробным комплексным исследованием, позволившим оценить выраженный в денежном эквиваленте ущерб от инвазий чужеродных видов в европейских странах, и проанализировать временные тренды экономических потерь. Нами также изучалось распределение убытков по странам, социально-экономическим секторам и таксономическим группам, а кроме того, оценивались социально-экономические корреляты затрат на мониторинг и контроль инвазий. В Европе в 1960–2020 гг. общие затраты, ассоциированные с инвазионными чужеродными видами, составили 140.20 млрд долларов США (или 116.61 млрд евро), и большая часть (60%) затрат была связана с убытками в разных экономических секторах. Сведения по экономическим потерям получены из многих регионов Европы, но их преобладающий объем поступает из крупных стран Западной и Центральной Европы, в частности, Великобритании, Испании, Франции и Германии. Численность населения, площадь суши, размер валового внутреннего продукта (ВВП) и туризм являются важными предикторами экономических потерь, включая затраты на контроль инвайдеров, спрогнозированные на основе числа интродуцированных видов, исследовательских усилий и торговой активности. В Европе ущерб от инвазий показывает экспоненциальный рост: от 23.58 млрд долларов США (1964 млрд евро) в 2013 г. до 139.56 млрд долларов США (116.24 млрд евро) по прогнозным оценкам в 2020 г. Важно отметить, что эти затраты хотя и являются значительными, все еще сохраняются пробелы в знаниях об экономических потерях по отдельным таксонам инвайдеров и отдельным европейским странам, что указывает на недооценку тотального ущерба от инвазий в Европе. Таким образом, мы призываем к улучшению отчетности по экономическим последствиям инвазий чужеродных видов и к координированным международным действиям по предотвращению дальнейшего распространения видов-инвайдеров и смягчению их воздействия.

Abstract in Spanish

Costos económicos de las especies exóticas invasoras en Europa. Las invasiones biológicas continúan amenazando la estabilidad de los ecosistemas y de las sociedades que dependen de sus servicios. Si bien en las últimas décadas los impactos ecológicos de las especies exóticas invasoras (EEI) han sido ampliamente registrados, sigue habiendo escasez de información sobre sus impactos económicos. Europa tiene fuertes vínculos comerciales y de transporte con el resto del mundo, lo que facilita la introducción de cientos de EEI y la existencia de marcos de toma de decisiones en gran parte centralizados. Este estudio representa el primer esfuerzo completo y detallado de cuantificar los costos económicos de las EEI en los países europeos y examina las tendencias temporales en estos datos. Además, analiza las distribuciones de costos entre países, sectores socioeconómicos y grupos taxonómicos, así como las correlaciones socioeconómicas de los costos de gestión y daños de las EEI. Los costos totales de las EEI en Europa ascendieron a 140.20 mil millones de dólares (o 116.61 mil millones de euros) entre 1960 y 2020, y la mayoría (60%) están relacionados con daños y afectan a múltiples sectores. Los costos están geográficamente extendidos pero dominados por los daños de las EEI en los grandes países de Europa occidental y central, es decir, Reino Unido, España, Francia y Alemania. La población humana, la superficie terrestre, el PIB y el turismo fueron predictores importantes de los costos relacionados con los daños de las EEI, mientras que para los costos de gestión, el número de especies introducidas, el esfuerzo de investigación y el comercio fueron los predictores más importantes. Temporalmente, los costos de invasión han aumentado exponencialmente a lo largo del tiempo, con hasta 23.58 mil millones de dólares (19.64 mil millones de euros) en 2013 y 139.56 mil millones de dólares (116.24 mil millones de euros) en impactos extrapolados en 2020. Sigue habiendo lagunas de conocimiento en varias escalas geográficas y taxonómicas, lo que indica que estos costos están muy subestimados. Por lo tanto, instamos a que se incrementen y mejoren los informes de costos de los impactos económicos de las EEI y a la acción internacional coordinada para evitar una mayor propagación de EEI y mitigar sus impactos.

Abstract in Greek

Οικονομικό κόστος επεμβατικών ξένων ειδών σε ολόκληρη την Ευρώπη. Οι βιολογικές εισβολές εξακολουθούν να απειλούν την σταθερότητα των οικοσυστημάτων και των κοινωνιών που εξαρτώνται από τις υπηρεσίες τους. Ενώ οι οικολογικές επιπτώσεις των εισβολικών ειδών έχουν καταγραφεί ευρέως τις τελευταίες δεκαετίες, εξακολουθεί να υπάρχει μια έλλειψη πληροφορίας για τις οικονομικές επιπτώσεις των ειδών αυτών. Η Ευρώπη συνδέεται στενά με τον υπόλοιπο κόσμο μέσω του δικτύου εμπορίου και μεταφοράς, επιτρέποντας έτσι εκατοντάδες περιστατικά βιολογικών εισβολών και σε μεγάλο βαθμό κεντροποιημένα συστήματα λήψης αποφάσεων. Η παρούσα εργασία είναι η πρώτη ολοκληρωμένη και λεπτομερής προσπάθεια που ποσοτικοποιεί τα κόστη των εισβολικών ειδών συνολικά για τις Ευρωπαϊκές χώρες και εξετάζει τις τάσεις των δεδομένων αυτών στην πορεία του χρόνου. Επιπρόσθετα, αναλύεται η κατανομή του κόστους σε χώρες, τομείς της οικονομίας και της κοινωνίας, καθώς και ταξινομικές ομάδες, όπως επίσης αναλύονται και κοινωνικό-οικονομικές συσχετίσεις του κόστους από βλάβες και διαχείριση. Τα συνολικά κόστη των εισβολικών ειδών στην Ευρώπη εκτιμήθηκαν σε US 140.20 δις (ή € 116.61 δις) για το διάστημα 1960 – 2020, με την πλειονότητα αυτών (60%) να αποδίδονται σε βλάβες και να επηρεάζουν πολλαπλούς τομείς. Επίσης η γεωγραφική κατανομή του κόστους ήταν ευρεία, ωστόσο κυριάρχησαν οι επιπτώσεις σε μεγάλες χώρες της κεντρικής και δυτικής Ευρώπης, π.χ. Ηνωμένο Βασίλειο, Ισπανία, Γαλλία και Γερμανία. Το μέγεθος του πληθυσμού, η έκταση, το ΑΕΠ και ο τουρισμός βρέθηκαν να είναι σημαντικοί παράμετροι που εξηγούν τα κόστη των εισβολικών ειδών, με τον αριθμό των εισαχθέντων ειδών, την ερευνητική προσπάθεια και το εμπόριο να εξηγούν επιπρόσθετα τα κόστη διαχείρισης. Τα κόστη των εισβολικών ειδών έδειξαν να αυξάνονται εκθετικά στη διάρκεια του χρόνου, με κόστη που φτάνουν τα US$ 23.58 δις (€ 19.64 δις) το 2013 και US$ 139.56 δις (€ 116.24 δις) σε επιπτώσεις τα κόστη των οποίων προεκτάθηκαν ως το 2020. Είναι σημαντικό το ότι παρόλο που τα κόστη αυτά είναι υψηλά, εξακολουθούν να υπάρχουν κενά γνώσης σε διάφορες γεωγραφικές και ταξινομικές κλίμακες, υποδεικνύοντας ότι τα κόστη έχουν υποεκτιμηθεί σε μεγάλο βαθμό. Έτσι προτρέπουμε αύξηση και βελτίωση στην καταγραφή των οικονομικών επιπτώσεων και συντονισμένη δράση σε διεθνές επίπεδο για την αποφυγή επιπλέον επέκτασης και για την μείωση των επιπτώσεων των εισβολικών πληθυσμών.

Abstract in Italian

Costi economici delle specie esotiche invasive in tutta Europa. Le invasioni biologiche continuano a minacciare la stabilità degli ecosistemi e delle società dipendenti dai loro servizi. Mentre gli impatti ecologici delle specie aliene invasive (SAI) sono stati largamente riportati negli ultimi decenni, rimane una scarsità di informazioni riguardo agli impatti economici delle SAI. L'Europa ha forti rapporti di commercio e trasporto col resto del mondo, favorendo centinaia di incursioni di SAI. Questo studio è il primo sforzo comprensivo e dettagliato a quantificare collettivamente i costi delle SAI nei Paesi europei e ad esaminare le tendenze temporali di questi dati. Inoltre, sono esaminate le distribuzioni dei costi tra Paesi, settori socioeconomici e gruppi tassonomici, così come i correlati socioeconomici dei costi della gestione e dei danni. I costi totali delle SAI in Europa tra il 1960 e il 2020 ammontano a 140.20 miliardi di $ americani (116.61 miliardi di €), la maggior parte dei quali (60%) sono legati ai danni e colpiscono più settori. I costi sono anche geograficamente diffusi, ma dominati dagli impatti nei grandi Paesi dell'Europa occidentale e centrale, ovvero Regno Unito, Spagna, Francia e Germania. La dimensione della popolazione umana, l'estensione dell'area, PIL e il turismo sono predittori significativi dei costi delle invasioni, con i costi gestionali predetti anche dal numero di specie introdotte, gli sforzi di ricerca e il commercio. Nel tempo, i costi delle invasioni sono aumentati esponenzialmente, con un picco estrapolato di impatti di 23.58 miliardi di $ americani (19.64 miliardi di €) nel 2013 e di 139.56 miliardi di $ americani (116.24 miliardi di €) nel 2020. Importantemente, sebbene questi costi siano notevoli, rimangono ancora delle lacune nella conoscenza di alcune scale geografiche e tassonomiche, il che indica che questi costi sono considerevolmente sottostimati. Pertanto, abbiamo bisogno di una maggiore e migliore rendicontazione dei costi per gli impatti economici delle SAI e di un'azione internazionale coordinata per prevenire ulteriori diffusioni e mitigare gli impatti delle SAI.

Abstract in German

Wirtschaftliche Kosten invasiver gebietsfremder Arten in ganz Europa. Biologische Invasionen bedrohen die Stabilität von Ökosystemen und Gesellschaften, die von ihren Dienstleistungen abhängig sind. Während über die ökologischen Auswirkungen invasiver gebietsfremder Arten in den letzten Jahrzehnten ausführlich berichtet wurde, fehlen Informationen über die wirtschaftlichen Auswirkungen. Europa verfügt über starke Handels- und Verkehrsverbindungen mit dem Rest der Welt, wodurch die Etablierung hunderter von nichtheimischen Arten erleichtert wird. Die vorliegende Studie ist die erste umfassende und detaillierte Studie, die die Kosten von gebietsfremden Arten in allen europäischen Ländern gemeinsam quantifiziert und zeitliche Trends untersucht. Darüber hinaus werden die Kostenverteilung auf Länder, sozioökonomische Sektoren und taxonomische Gruppen sowie sozioökonomische Korrelationen von Management- und Schadenskosten untersucht. Die Gesamtkosten der IAS in Europa beliefen sich zwischen 1960 und 2020 auf 140.20

Mrd. USD (oder 116.61 Mrd. EUR), wobei die Mehrheit (60%) schadensbedingt war und mehrere Sektoren betraf. Die Kosten waren auch geografisch weit verbreitet, wurden jedoch von Auswirkungen in großen westeuropäischen und mitteleuropäischen Ländern dominiert, d.h. in Großbritannien, Spanien, Frankreich und Deutschland. Die Bevölkerungszahl, die Landfläche, das BIP und der Tourismus waren wichtige Indikatoren für die Kosten biologischer Invasionen, wobei die Verwaltungskosten zusätzlich durch die Anzahl der eingeführten Arten, den Forschungsaufwand und den Handel prognostiziert wurden. Zeitlich gesehen sind diese Kosten im Laufe der Zeit, mit bis zu 23.58 Mrd. USD (19.64 Mrd. EUR) im Jahr 2013 und 139.56 Mrd. USD (116.24 Mrd. EUR) im Jahr 2020, exponentiell angestiegen. Obwohl die Kosten erheblich sind, verbleiben wichtige geografische und taxonomische Wissenslücken, wodurch diese Kosten stark unterschätzt werden. Wir fordern daher eine verstärkte und verbesserte Kosten-Berichterstattung für die wirtschaftlichen Auswirkungen gebietsfremder Arten in Europa sowie koordinierte internationale Maßnahmen, um eine weitere Verbreitung zu verhindern und dessen Auswirkungen zu mildern.

Abstract in Irish

Costais eacnamaíocha speiceas coimhthíoch ionrach ar fud na hEorpa. Tá ionraí bitheolaíochta go fóill ina mbagairt ar chobhsaíocht éiceachóras agus sochaithe atá ag brath ar a gcuid seirbhísí. Cé gur tuairiscíodh tionchair éiceolaíochta speicis choimhthíocha ionracha (SCI) go forleathan le blianta beaga anuas, tá ganntanas eolais ann go fóill maidir leis na tionchair gheilleagracha a bhaineann le SCI. Tá caidreamh láidir trádála agus iompair ag an Eoraip leis an chuid eile den domhan, rud a éascaíonn na céadta ionradh SCI, agus creata cinnteoireachta aici atá láraithe den chuid is mó. Is é an staidéar seo an chéad iarracht chuimsitheach, mhionsonraithe a mheasann ar bhonn cainníochtúil comhchostais SCI ar fud thíortha na hEorpa trí chéile agus a scrúdaíonn treochtaí ama sna sonraí seo. Lena chois sin, scrúdaítear ann dáileadh costas ó thír go tír, ó earnáil shocheacnamaíoch go chéile, agus ó ghrúpa tacsanomaíoch go chéile, mar aon le comhghaolaigh shocheacnamaíocha costais bhainistithe agus damáiste. SA$140.20 billiún (nó €116.61 billiún) na costais a bhí ar SCI san iomlán san Eoraip idir 1960 agus 2020, agus bhí baint ag a bhformhór (60%) le damáiste agus tionchar acu sin ar earnálacha iomadúla. Bhí costais leitheadach chomh maith, ó thaobh na tíreolaíochta de, ach is i dtíortha móra in iarthar agus i lár na hEorpa, i. an Ríocht Aontaithe, an Spáinn, an Fhrainc, agus an Ghearmáin, a bhí na tionchair ba shuntasaí. Ba réamhaithriseoirí tábhachtacha ar chostais ionraidh iad líon na ndaoine, limistéar talún, OTI, agus an turasóireacht, agus ba iad líon na speiceas a tugadh isteach, dua taighde, agus trádáil ba bhonn le costais bhainistithe a thuar chomh maith leis sin. Ó thaobh ama de, tá costais ionraidh i ndiaidh méadú as cuimse trí na blianta agus eachtarshuíodh suas le SA$23.58 billiún (€19.64 billiún) in 2013 agus suas le SA$139.56 billiún (€116.24 billiún) in 2020 de bharr tionchar. Is tábhachtach a aithint, cé go bhfuil na costais seo suntasach, go bhfuil bearnaí eolais ann go fóill ar roinnt scálaí tíreolaíocha agus tacsanomaíocha, rud a thaispeánann gur gannmheasadh na costais seo go mór. Molaimid, dá réir sin, méadú agus feabhsú ar thuairisciú costas maidir le tionchair gheilleagracha SCI agus gníomh Idirnáisiúnta comheagraithe chun nach leathfaidh líon SCI a thuilleadh agus chun a dtionchair a mhaolú.

Abstract in Croatian

Ekonomski troškovi invazivnih stranih vrsta širom Europe. Biološke invazije nastavljaju prijetiti stabilnosti ekosustava i društvima koja ovise o njihovim uslugama. Iako su posljednjim desetljećima ekološki utjecaji invazivnih stranih vrsta široko izvještavani, i dalje nema dovoljno podataka o ekonomskim utjecajima invazivnih stranih vrsta. Europa ima snažne trgovinske i prometne veze s ostatkom svijeta, olakšavajući stotine upada invazivnih stranih vrsta, i uglavnom centralizirane okvire za donošenje odluka. Ova studija je prvi sveobuhvatan i detaljan napor koji kvantificira troškove invazivnih stranih vrsta kolektivno diljem europskih zemalja i ispituje privremene trendove u tim podacima. Uz to se ispituje raspodjela troškova po zemljama, socioekonomskim sektorima i taksonomskim skupinama, kao i socioekonomske korelacije troškova upravljanja i štete. Ukupni troškovi ivnazivnih stranih vrsta u Europi iznosili su 140.20 milijardi američkih dolara (ili 116.61 milijardi eura) između 1960. i 2020. godine, pri čemu je većina (60%) povezana sa štetom i utječe na više sektora. Troškovi su također bili zemljopisno rašireni, ali su dominirali utjecaji u velikim zemljama zapadne i srednje Europe, tj. Velikoj Britaniji, Španjolskoj, Francuskoj i Njemačkoj. Veličina ljudske populacije, površina zemljišta, BDP i turizam bili su značajni prognozeri troškova invazije, a troškovi upravljanja dodatno su predviđeni brojem unesenih vrsta, istraživačkim naporima i trgovinom. Troškovi invazije su se s vremenom eksponencijalno povećali na 23.58 milijardi američkih dolara (19.64 milijardi eura) do 2013. godine i na 139..56 milijardi američkih dolara (116.24 milijardi eura) za utjecaje koji su ekstrapolirani u 2020 godini. Iako su ti troškovi znatni važno je naglasiti da i dalje postoje praznine u znanju na nekoliko zemljopisnih i taksonomskih razmjera, što ukazuje da su ti troškovi ozbiljno podcijenjeni. Stoga zahtijevamo povećano i poboljšano izvještavanje o troškovima za ekonomske utjecaje invazivnih stranih vrsta i koordiniranu međunarodnu akciju kako bi se spriječilo daljnje širenje i ublažili utjecaji populacija invazivnih stranih vrsta.

Abstract in Arabic

التكاليف الاقتصادية للأنواع الغريبة الغازية في أوروبا. من المعلوم أن أوروبا، بالإضافة إلى مسألة تمركز القرار الاقتصادي، تتمتع بروابط تجارية مهمة وحركة نقل واسعة النطاق مع بقية العالم، الأمر الذي يسهل معه دخول العديد من "الأنواع الغريبة". وبالرغم من الجهود المهمة المبذولة، في العقود الأخيرة، في مجال "الاستعلام" وتوفير إمكانات "الإبلاغ" عن التأثيرات البيئية "للأنواع الغريبة الغازية"، إلا أنه يسجل ندرة بخصوص المعلومات المتعلقة بالتأثير على المجال الاقتصادي؛ وهو ما جعل الخبراء في هذا المجال يرفعون شعار "الغزو البيولوجي يُهدد استقرار النظم البيئية والمجتمعات التي تعتمد على خدماتها".

الدراسة التي بين أيدينا، تعتبر، اليوم، الأولى من نوعها من حيث الجهد الجماعي والتفصيل الدقيق فيما يخص تكاليف "الأنواع الغريبة الغازية" في البلدان الأوروبية، وتدرس الاتجاهات الزمنية الممكنة في البيانات المحصل عليها. وتنطلق الدراسة من تحليل توزيع التكاليف عبر البلدان والقطاعات الاجتماعية والاقتصادية والمجموعات التصنيفية، وكذلك تكلفة الأضرار المرتبطة بتدبير الروابط الاجتماعية-الاقتصادية.

وحسب هذه الدراسة، بلغ إجمالي تكاليف "الأنواع الغريبة الغازية" في أوروبا 140.20 مليار دولار أمريكي (أو 116.61 مليار يورو) بين عامي 1960 و2020 وغالبيتها (60٪) مرتبطة بالأضرار، كما تؤثر هذه الأنواع على قطاعات متعددة. ويسجل بهذا الخصوص، أن التكاليف ظهرت منتشرة جغرافياً في كل أوروبا مع هيمنة التأثيرات في دول أوروبا الوسطى والغربية، مثل المملكة المتحدة وإسبانيا وفرنسا وألمانيا. كما شكل عدد السكان، ومساحة البلد، والناتج المحلي الإجمالي والسياحة المؤشرات الأساسية لتحديد تكاليف الغزو البيولوجي، مع تكاليف التدبير الإضافية المتوقعة من خلال عدد الأنواع التي تم إدخالها وجهود البحث والتجارة.

زمنيا، إذن، زادت تكاليف "الغزو البيولوجي" بشكل كبير لتصل إلى 23.58 مليار دولار أمريكي (19.64 مليار يورو) في عام 2013، و139.56 مليار دولار أمريكي (116.24 مليار يورو) في التأثيرات التي تم استقراءها في سنة 2020. والأهم من ذلك، هو أنه على الرغم من أن هذه التكاليف كبيرة، فإنه لا تزال هناك فجوات معرفية على عدة نطاقات جغرافية وتصنيفية، مما يشير إلى أن هذه التكاليف تم التقليل من شأنها بشدة.

وعطفا على ما سبق، فإننا نحث، كتوصية، العمل على زيادة وتحسين تقارير التكلفة للتأثيرات الاقتصادية "للأنواع الغازات الغريبة" والعمل الدولي المنظم من أجل منع المزيد من الانتشار والتخفيف من آثار مجموعات الأنواع الغريبة الغازية.

Keywords

Bodiversity, European Union, InvaCost, monetary impacts, non-native biota, socio-economic correlates, socioeconomic sectors

Introduction

Despite an increasing number of indicators and alarming reports on the rapid decline of biodiversity globally (Díaz et al. 2020; Haubrock et al. 2021b), efforts to halt biodiversity losses have remained insufficient (Hulme 2009; Scalera 2010; Rayment et al. 2018). Notwithstanding the multiple signals of the rapid decline of natural capital worldwide, global economic resources allocated to prevent and mitigate such losses have not proven adequate to meet conservation management goals, or have been designated inefficiently (Murdoch et al. 2007; Underwood et al. 2008; Stokstad 2010; McCarthy et al. 2012; Waldron et al. 2013, 2017). In a highly connected world, with escalating trade and demand for resources, the number of invasive alien species (IAS) is rapidly increasing (Seebens et al. 2017). In fact, biological invasions are one of the most eminent global threats to biodiversity, ecosystem services and livelihoods (Bellard et al. 2016; Pysek et al. 2020). Whilst much effort has been directed to improve understanding of the ecological impacts of IAS, knowledge about their economic impacts is limited to a few species, habitats, and/or regions, and often only to direct costs that are straightforward to properly quantify or estimate (Kettunen et al. 2009; Bradshaw et al. 2016).

As a historic epicenter of migration, tourism and trade, Europe represents a hub for alien species introductions (Turbelin et al. 2017). Although several studies have attempted to assess the environmental and socio-economic impacts of IAS in Europe (Weber and Gut 2004; Vilà et al. 2009, 2010; Keller et al. 2011), only a few have quantified them in monetary terms (Gren et al. 2009; Kettunen et al. 2009). Pimentel et al. (2000, 2005) and Kettunen et al. (2009) were among the first to attempt to summarize the economic impact of IAS on a continental scale, raising awareness of the actual and potential costs associated with IAS (Hensley 2012). However, due to limited availability of published data at the time, they had to rely heavily on personal communications and technical reports. Kettunen et al. (2009) reported total annual costs of IAS of ~€12 billion across Europe, although given the scarcity of data available at this time, sources and methods used were generally scant (Bradshaw et al. 2016; Diagne et al. 2020a, 2020b). Other publications have attempted to collectively assess the costs of IAS (Hoffmann and Broadhurst 2016), for different organism types (Lovell et al. 2006; Van der Veer and Nentwig 2015; Bradshaw et al. 2016; Barbet-Massin et al. 2020; Cuthbert et al. 2021b), and for different countries (e.g. Great Britain: Williams et al. 2010). Scalera (2010), for example, reviewed EU-funded projects on IAS and reported an investment of more than €132 million between 1992 and 2006. Substantial variation in estimations of management and damage costs of IAS and the methodologies used, due to many sources being somewhat scattered and providing only anecdotal information at local, regional and national scales, have limited the estimation of IAS costs so far (e.g. Britton et al. 2010; Oreska and Aldridge 2011). Importantly, in several cases, data reporting the costs of IAS are often found in the grey literature (IUCN 2018), not easily accessible, sometimes not publicly available and not written in English (Angulo et al. 2021b).

This lack of reliable, readily-available data on IAS costs remains a critical knowledge gap in assessing the diversity of impacts associated with biological invasions. Its absence can give the false impression that this information is limited, as costs may be rarely reported in a systematic manner. In addition, the lack of reliable and comprehensive quantification of IAS costs leads to an absence of an economic rationale serving as a solid basis for decision-making by policy makers and other stakeholders. A robust and transparent assessment of costs of IAS at the scale of continents, European states, or trading blocs is currently lacking. While cost estimates are useful at a national scale, their calculation at broader scales may be even more crucial. For example, within both the European Union (EU) and European Economic Area (EEA), where trade agreements encourage the free movement of goods and potentially facilitate the spread of IAS, information on the economic impact of each species could demonstrate the requirements for a greater or lower emphasis on continent-wide biosecurity and control measures. Such an evidence base would also indicate the extent to which different countries are investing into relevant actions, and where funds or political pressure may be targeted to enhance the economic security of both nations and wider trading blocs.

In this context, the InvaCost initiative (Diagne et al. 2020a, 2020b) tackles this lack of collated data, presenting a comprehensive and urgently-needed database that can be used to thoroughly investigate the costs of IAS at a range of scales, from subnational to continental. Here, we use the InvaCost database to (i) describe Europe-wide impacts of IAS among countries, cost types and economic sectors, (ii) investigate the causes for differences in these costs among European countries, and (iii) examine the temporal trends in costs of IAS in recent decades.

Methods

Data compilation and extraction

IAS in InvaCost represent those which have established and spread in novel ranges and have reported socioeconomic impacts (i.e. monetary costs). To estimate the cost of biological invasions on the European economy, we used the InvaCost database (InvaCost v.1.0; Diagne et al. 2020a and subsequent additions, see below). The InvaCost v.1.0 database comprises 2,419 entries of reported economic costs of IAS retrieved from published peer-reviewed and grey literature (as of December 2017). Data in InvaCost v.1.0 were retrieved from publications in English identified in the Web of Science platform (https://webofknowledge.com/), Google Scholar (https://scholar.google.com/), Google (https://www.google.com/), and through direct contacts with regional experts. InvaCost is a living database for which correction of potential errors and addition of new cost entries are further expected (Diagne et al. 2020a). The InvaCost v.1.0 database has been extended recently with 5,212 data entries from non-English sources (Angulo et al. 2020). This dataset was derived from a search in fifteen languages, including languages relevant for Europe: French, Spanish, Portuguese, German, Greek, Dutch, Ukrainian, and Russian (as of May 2020). The cost search protocol was similar to the original InvaCost protocol (Diagne et al. 2020a); however, the majority of these entries resulted from targeted searches, i.e. via searching web pages and directly contacting IAS experts and stakeholders to request for potentially unpublished/publicly unavailable documents containing cost information. We further added supplementary cost data from new references containing cost information, obtained through the same search protocol as used for InvaCost v.1.0 (2,374 entries; Ballesteros-Mejia et al. 2020). Individual cost records were standardized to a common currency: 2017 US$ (see Diagne et al. 2020a for detailed information on conversion; exchange rate for 2017: US$1 = €0.8852; World Bank 2020).

Data processing

First, we cleaned the raw data in the InvaCost database. We removed obvious duplicate or overlapping costs, identified through chains of citations or identical cost details. Where necessary, we split aggregated costs (e.g. if the InvaCost database contained a single cost for Europe but the original source contained costs for each individual country). The period of estimation across reported costs varied considerably, spanning periods of several months to several years. For the purpose of the analysis, and in order to obtain comparable IAS costs, we considered all costs for a period of less than a year as annual costs, and re-calculated costs covering several years on an annual basis. This was performed using the "expandYearlyCosts" function of the 'invacost' package version 0.3–4 (Leroy et al. 2020) in R version 4.0.2 (R Core Team 2020). We thus estimated average annual costs represented in the InvaCost database. Deriving the total cumulative cost of invasions over time requires consideration of the probable duration time of each cost occurrence. The duration consisted of the number of years between the probable starting ("Probable_starting_year") and ending ("Probable_ending_year") years of the costs reported by each publication included in the InvaCost database (Diagne et al. 2020a). When information was missing for the starting year, we conservatively considered the publication year of the original reference. For the ending year of costs, however, information was missing only for costs likely to be repeated over years (i.e. "potentially ongoing", contrary to "one-time" costs occurring only once along a specific period). Therefore, we considered that these costs might still occur until 2020: the last year from which publications were included in InvaCost and in the non-English dataset. Subsequently, to obtain a comparable total cumulative cost for each estimate over each defined invasion period, we multiplied each annual estimate by the respective duration (in years). All analyses were performed for the period from 1960 to 2020, as monetary exchange rates could not be obtained from official institutions (e.g. World Bank) prior to 1960. The overall number of cost entries before expansion was 4867 and 7461 after expansion, whereby "expansion" refers to the process of annualising cost data of different durations using the aforementioned "expandYearlyCosts" function.

Economic cost descriptors

To examine the costs of IAS incurred within Europe, we filtered the full dataset based on the geographic region "Europe". We provide our final dataset used as a supplement (Suppl. material 1). Naturally, these analyses include species which are native in some European countries, but invasive in others (e.g. European rabbit), but invasion costs are only documented in novel ranges. Costs that were incurred from multiple or unspecified taxa were included in analyses but categorised as "Diverse/Unspecified". The resulting invasion cost totals were examined according to different descriptive fields of the most up-to-date database available when writing this manuscript:

i. Official_country: describing the national origin of the listed cost for European countries only. For technical reasons, Kosovo and Serbia were considered as one country, while Turkey was excluded entirely as costs were not clearly attributable to Europe. For transcontinental Russia, we considered and presented only the European part for the total cost, while not considering it for further analyses which were based on fully European countries. As such, Turkey and Russia were excluded from detailed analyses to avoid ambiguities given their transcontinental nature, whereby there was a lack of European-scale indicators that would permit comparison with other European states. Moreover, the underlying spatial resolution of data often precluded determination of European and Asian contributions as costs were presented at national, not regional, scales. Overseas territories (e.g. French Guiana, Reunion, Pitcairn and the Canary Islands) were also excluded;

ii. Method_reliability: illustrating the perceived reliability of cost estimates based on the type of publication and method of estimation. Estimates in peer-reviewed publications or official reports, or with documented, repeatable and/or traceable methods were designated as "High" reliability (hereafter, "reliable"); all other estimates were designated as "Low" reliability (Diagne et al. 2020a);

iii. Implementation: referring to whether the cost estimate was actually realised in the invaded habitat ("Observed") or whether it was expected ("Potential");

iv. Type_of_cost_merged: grouping of costs according to the categories: (a) "Damage-Loss" referring to damages or losses incurred by invasion (e.g. costs for damage repair, resource losses, medical care), (b) "Management" comprising control-related expenditure (for example monitoring, prevention, management, eradication, research, communication) and money spent on education and maintenance costs, (c) "Diverse/Unspecified" including mixed damage-loss and management costs (cases where reported costs were not clearly distinguished among cost types);

v. Impacted_sector: the activity, societal or market sector that was impacted by the cost (Suppl. material 2); note that individual cost entries not allocated to a single sector were classified under "Mixed" in the "Impacted_sector" column.

Economic cost correlations

We first explored whether the two main types of costs, "Management" and "Damage-Loss", can be explained by country-specific factors. To do so, we calculated the cumulative reliable observed costs for 1960–2020 of each type of cost at the country level and selected a range of socio-economic variables that we hypothesize could be linked to biological invasions (Suppl. material 3). Then, we calculated Spearman rank correlations (r_s) between the country-level expenditures and damage costs and the selected socio-economic variables using the R package 'ggpubr' (Kassambara 2017). Further, we also explored correlations between country-level expenditures and damage costs.

Spatial and taxonomic connectivity of costs

To examine the spatial and taxonomic connectivity of invasion costs in Europe, we constructed a bipartite network composed of two types of nodes: (1) countries and (2) taxonomic groupings (excluding studies reporting costs on diverse taxonomic groups). For taxonomic groupings, we also captured habitat types of each taxon (e.g. "terrestrial arthropod" instead of "arthropod"). When an IAS group economically impacted a given country, a link was drawn between the associated nodes with a weight proportional to the economic impact. As such, the size of the nodes, and thickness of the links, correspond to the magnitude of cumulative economic costs incurred for the 1960–2020 period. To investigate spatial and taxonomic patterns of costs in Europe, we applied the Map Equation community-detection algorithm (version 0.19.12, www.mapequation.org; Rosvall and Bergstrom 2008). This approach groups nodes into clusters with high intragroup connectivity, enabling clusters of similar costs to be established (i.e. countries sharing costs from the same invasive taxa) (Leroy et al. 2019). Network analyses were performed with the 'biogeonetworks' R package version 0.1.2 (Leroy 2020), and the network was represented with Gephi 0.9.2 using the ForceAtlas2 algorithm (Bastian et al. 2009).

Temporal dynamics of accumulated costs

For the temporal estimation of the average annual costs, we used the 'invacost' package in R (Leroy et al. 2020). This package allows modelling the trend of costs over time with an array of linear and non-linear model types and enables a summary and comparison of their respective outputs. Given the evidence that numbers of IAS show no sign of saturation (Seebens et al. 2017), we expected their associated costs to be stable or increasing. In addition, we can expect a time lag between the occurrence of costs, their publication, and their reporting in InvaCost (Leroy et al. 2020). Therefore, as per Seebens et al. (2017), we excluded recent years from model calibration. The last eight years appear to have less than 75% completeness within the global InvaCost database (Leroy et al. 2020); therefore, we chose to exclude them from model calibration (i.e. years post-2013).

A range of modelling techniques were then applied to model the temporal dynamics of reported costs ("modelCosts" function): ordinary least squares regressions (linear, quadratic), robust regressions (linear, quadratic – R package 'robustbase'; Maechler et al. 2020), multivariate additive regression splines (MARS – R package 'earth'; Milborrow et al. 2018), generalised additive models (GAM – R package 'mgcv'; Wood et al. 2016) and quantile regressions (quantiles 0.1, 0.5, 0.9 – R package 'quantreg'; Koenker 2020). These approaches enabled quantification of average annual costs, measurements of variation in cost estimates over time and assessment of predictive performance across models (based on RMSE). Model selection was also performed on the basis of techniques that are relatively robust to issues of heteroskedasticity, outliers and temporal autocorrelation that are common in econometric data (Leroy et al. 2020). Moreover, the diverse modelling approach enabled potential generalities in trends to be determined, such as whether all models were consistent in projecting cost increases through time.

As a separate analysis, we further used the aforementioned combination of approaches to examine temporal trends in economic costs, based on the GDP-qualified economic costs of the European countries from the year the cost occurred (i.e., costs divided by GDP per year), elucidating whether invasion costs are still increasing relative to economic growth. For this, we utilized robust regressions modelling as implemented in the 'invacost' package, since those are based on iteratively reweighted least squares, which makes them less sensitive to outliers compared to ordinary least square regressions (Yohai 1987; Koller and Stahel 2011).

Results

Composition and scale of economic costs

Overall, economic losses associated with biological invasions were obtained for 39 European countries (including the European part of Russia). Costs of biological invasions in Europe between 1960 and 2020 accumulated to a reported total of US$140.20 billion (or €116.61 billion). The vast majority of the reported costs exhibited a high degree of reliability (US$113.16 billion; n = 7034; 80.71%). Slightly more than half of cost estimates (US$77.66 billion; n = 6489; 55.4%) were derived from actual observations, while the rest (US$62.54 billion; n = 972; 44.6%) were potential costs that were not empirically observed (Figure 1). Economic costs were spread unevenly across countries (Figure 1): the United Kingdom (UK) (US$17.60 billion, n = 709), Spain (US$16.19 billion, n = 4162), France (US$11.41 billion, n = 1268), Germany (US$9.76 billion, n = 193), European Russia (US$8.48 billion; n = 29), Portugal (US$7.89 billion, n = 60), and the Netherlands (US$3.44 billion; n = 161) reported the largest invasion costs (Figure 1). Considering only reliable observed costs (US$50.97 billion; n = 6153), the UK again reported the highest total (US$6.89 billion; n = 538), and was followed by European Russia (US$1.82 billion; n = 10), Ukraine (US$1.51 billion; n = 96), and Romania (US$1.61 billion; n = 3). Reliable observed costs reported for other countries were less than US$1 billion per country.

The majority of total reported economic costs were related to damage and loss (total costs: US$84.18 billion; 60%; reliable observed costs: US$21.52 billion; 42%) (Figure 2a). Management costs (e.g. for prevention, control, education) totalled to US$28.17 billion (20%) considering all costs, and US$2.76 billion (5%) when considering only reliable observed costs. The remaining costs were classified under the category "Mixed" (i.e. combining both damage-loss and management; total costs: US$27.85 billion; 20%; reliable observed costs: US$26.69 billion; 52%). The proportion of damage-loss and management costs differed substantially across European countries (Figure 3). The distribution of reliable, observed cost types also varied by impacted sectors (Figure 2b). Damage-loss costs constituted the majority of costs for agriculture (94%), forestry (91%), fisheries (83%), environment (67%), health (>99%), and public and social welfare (92%), whilst management costs represented the majority of costs incurred by authorities and stakeholders (81%) (Figure 2b).

From impacted sectors, agriculture was the most impacted by biological invasions (US$36.00 billion, 26%), followed by forestry (US$25.08 billion, 18%), authorities and stakeholders (US$21.44 billion, 15%), public and social welfare (US$9.12 billion, 7%), health (US$5.97 billion; 4%), environment (US$938.74 million; <1%), and fisheries (US$495.5 million; <1%) considering total costs. Considering only reliable, observed costs (Figure 2c), agriculture remained the most impacted sector (US$11.96 billion; 23%), followed by authorities and stakeholders (US$2.17 billion; 4%) and the health sector (US$1.54 billion; 3%). With US$34.81 billion (68%), costs attributed to multiple sectors contributed the largest share. Invasion costs to all other sectors were less than US$1 billion per sector. The relative proportion of impacted sectors was not uniformly distributed across European states (Figure 3).

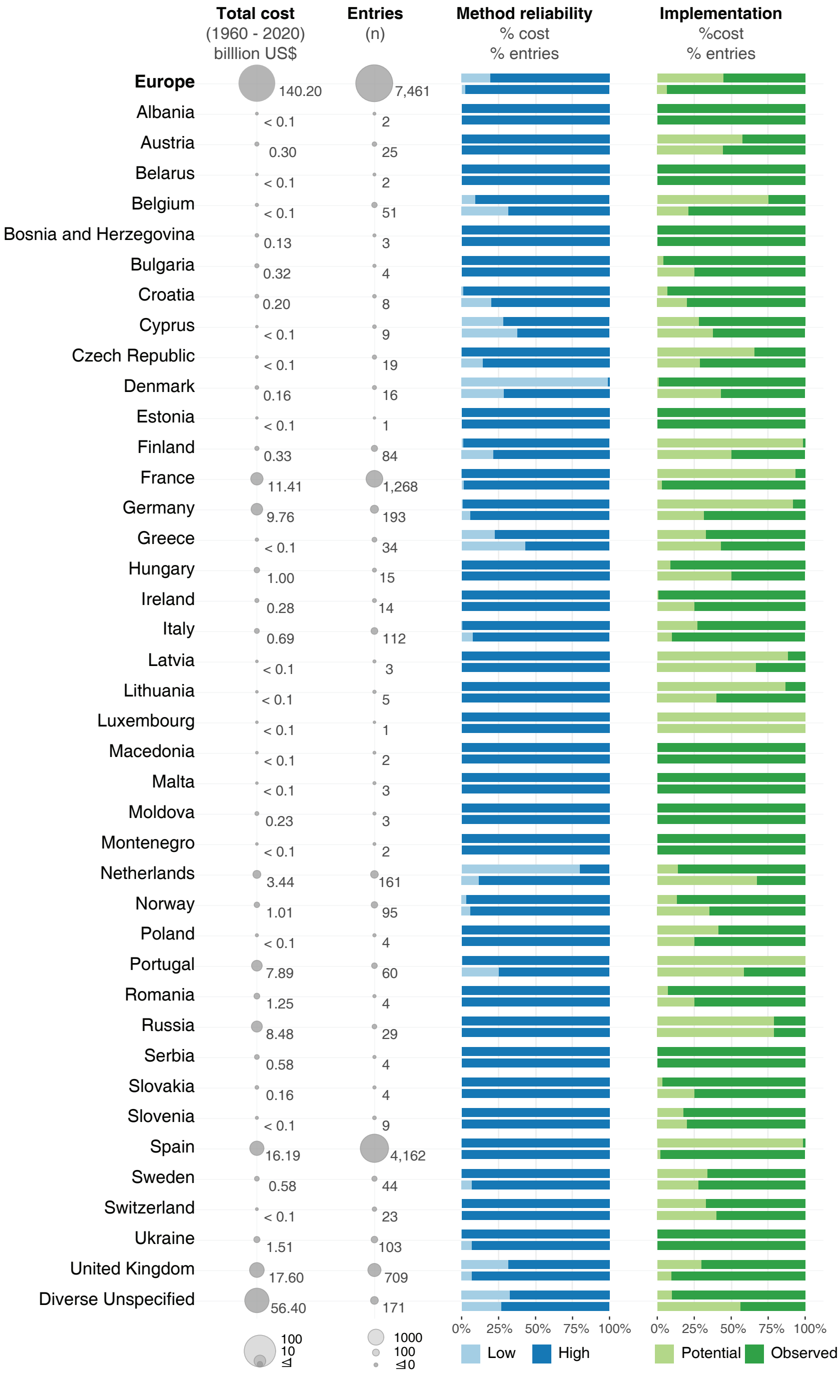

Figure 1. Nature of reported costs (monetary totals and numbers of database entries) for IAS across European countries according to percentages considering method reliability (high vs. low) and implementation type (potential vs. observed). Highly reliable figures are from peer-reviewed, official and/or reproducible sources; observed costs have been empirically realised (i.e. excluding expected cost estimations).

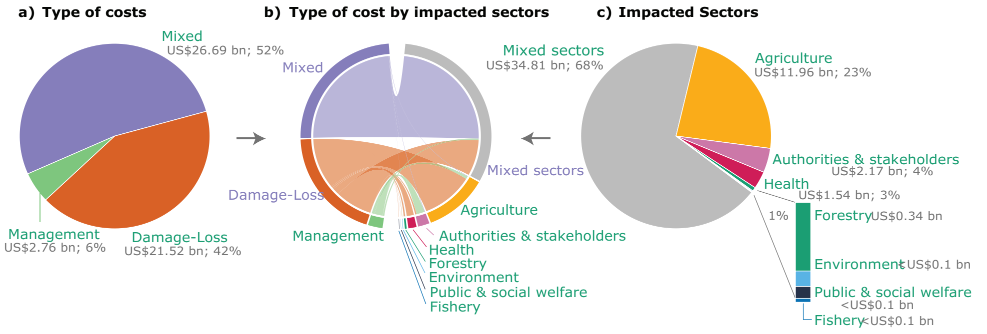

Figure 2. Distribution of IAS costs in Europe by **a** type of cost **b** cost type (left half) and impacted sector (right half) and **c** impacted sector. Panel **b** highlights linkages between cost types and impacted sectors, for example 5% (US$2.76/50.97 billion) of total costs were attributed to management, and 64% (US$1.76/2.76 billion) of these costs were incurred in the Authorities and Stakeholders sector, representing 81% (US$1.76/2.17 billion) of costs incurred by the Authorities and Stakeholders sector. Only reliable observed costs are considered (i.e. excluding irreproducible cost estimations and expected costs).

A list of the costliest invasive alien species in Europe can be found in Table 1. Considering all costs, five invertebrates, three vertebrates, and two plants were present in the top 10. When considering only reliable observed costs, three invertebrates, four vertebrates, two plants and one fungi genera were included in the top 10. *Rattus* species had the highest reliable observed costs (4th highest when considering all costs) (reliable: US$6.60 billion; all: US$6.67 billion) spanning across 2 countries. Hereafter, all analyses are performed with Russia omitted.

Economic cost correlations

Figure 4 highlights the geographical variations in the total cost of invasions throughout Europe, without and with standardization by GDP. There is a positive relationship between the total cost of invasions and country GDP, i.e. countries with a higher GDP tend to have higher reported observed costs (Figure 4c). High costs of invasion compared to GDP were observed in eastern European countries such as Ukraine, Serbia, Romania, Moldova and Hungary, suggesting that this trend may also change when more studies are undertaken or translated (Suppl. material 4).

We found significant positive correlations between damage-loss and management costs with the following socio-economic variables of the considered countries: human population size, land area, GDP, international tourism as expenditures and as number of arrivals. We also found significant positive correlations between management costs and the number of introduced alien species, research effort as the number of papers on the topic of biological invasions and expenditure in R&D, number of researchers, and imports of goods and services, with other tested socio-economic variables showing no significant correlations (Table 2). Moreover, the EU country-specific expenditure in IAS management and in damages-losses induced by IAS were not significantly correlated ($r_s = 0.10$, $p = 0.560$).

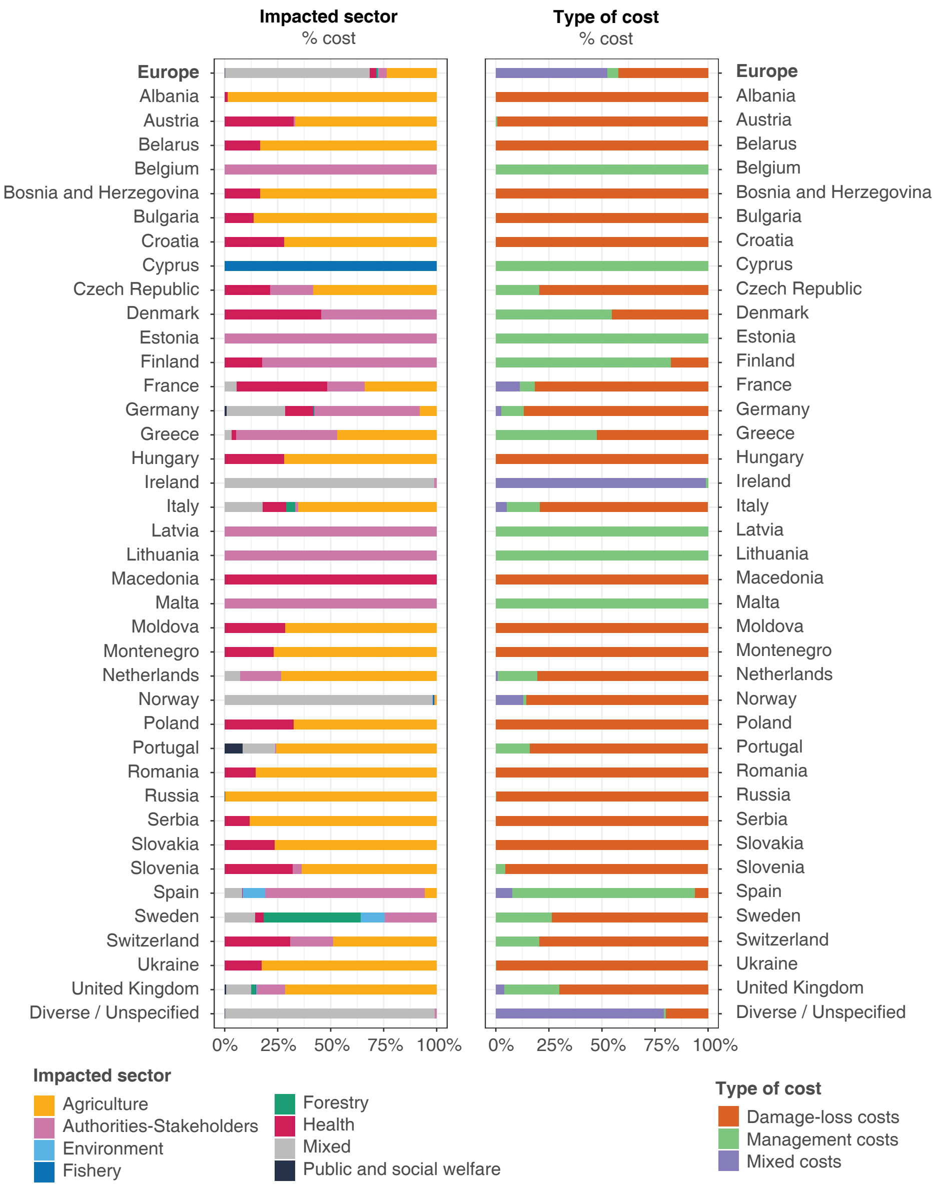

Figure 3. Percentage contributions of different impacted sectors and cost types according to country. Only reliable observed costs are considered (i.e. excluding irreproducible cost estimates and expected costs).

Spatial and taxonomic connectivity of costs

Eight distinct clusters of nodes were found to be strongly interconnected across taxa and countries (Figure 5). These clusters comprised assemblages of typically one or two countries, alongside one or more groups of organisms. The UK was primarily

Table 1. Top 10 cost-contributing genera considering (**a**) total and (**b**) reliable observed costs (i.e. excluding irreproducible cost estimations and expected costs), illustrating species taxonomy, total costs and numbers of database entries. Numbers of impacted countries per genus are also shown. Note that costs and entries are pooled across the entire genus (i.e. for all species), with constituent species listed therein.

(a) Total costs							
Rank	**Common name**	**Kingdom**	**Phylum**	**Species**	**Total cost (US$ billion, 2017 value)**	**Data entries**	**Number of impacted countries**
1	Nematode	Animalia	Nematoda	*Bursaphelenchus mucronatus*	23.38	178	7
2	Ragweed	Plantae	Tracheophyta	*Ambrosia artemisiifolia* *Ambrosia polystachya*	11.61	368	29
3	Water-primrose	Plantae	Tracheophyta	*Ludwigia grandiflora* *Ludwigia peploides* *Ludwigia repens*	8.01	262	5
4	Rat	Animalia	Chordata	*Rattus norvegicus* *Rattus rattus*	6.67	45	4
5	American bullfrog	Animalia	Chordata	*Lithobates catesbeianus*	6.04	38	6
6	European rabbit	Animalia	Chordata	*Oryctolagus cuniculus*	4.32	57	3
7	Salmon fluke	Animalia	Platyhelminthes	*Gyrodactylus salaris*	2.85	69	2
8	Termite	Animalia	Arthropoda	*Cryptotermes brevis*	2.81	4	1
9	Cucumber beetle	Animalia	Arthropoda	*Diabrotica undecimpunctata* *Diabrotica virgifera*	2.68	59	20
10	Asian longhorn beetle	Animalia	Arthropoda	*Anoplophora chinensis* *Anoplophora glabripennis*	1.91	35	6
(b) Reliable observed costs							
Rank	**Common name**	**Kingdom**	**Phylum**	**Species**	**Total cost (US$ billion, 2017 value)**	**Data entries**	**Number of impacted countries**
1	Rat	Animalia	Chordata	*Rattus norvegicus*	6.60	41	2
2	Ragweed	Plantae	Tracheophyta	*Ambrosia artemisiifolia* *Ambrosia polystachya*	6.57	269	29
3	European rabbit	Animalia	Chordata	*Oryctolagus cuniculus*	2.31	23	2
4	Emerald ash borer	Animalia	Arthropoda	*Agrilus planipennis* *Rattus rattus*	1.81	7	1
5	Salmon fluke	Animalia	Platyhelminthes	*Gyrodactylus salaris*	0.75	32	1
6	Japanese knotweed	Plantae	Tracheophyta	*Reynoutria japonica*	0.54	91	2
7	Common pigeon	Animalia	Chordata	*Columba livia*	0.37	1	1
8	Muskrat	Animalia	Chordata	*Ondatra zibethicus*	0.35	10	3
9	Dutch elm disease	Fungi		*Ophiostoma ulmi*	0.18	5	2
10	Biting midge	Animalia	Arthropoda	*Culicoides imicola*	0.16	1	1

highly impacted by terrestrial mammals, birds, forbs and aquatic organisms; the Netherlands and Finland by terrestrial arthropods; Norway by aquatic microorganisms; Germany and Estonia by semi-aquatic mammals; Sweden by microorganisms, molluscs and aquatic arthropods/plants; Spain by a diverse array of groups, excepting taxa such as macroalgae and nematodes; and Belgium by semi-aquatic amphibians and terrestrial plants. In turn, the main impacts in France, Italy, as well as in multiple eastern European countries, were caused by terrestrial forbs which turned out to be the costliest group in Europe. Nevertheless, the substantial array of inter-cluster links suggested that European states were each impacted by a diverse array of invasive alien taxa (Figure 5).

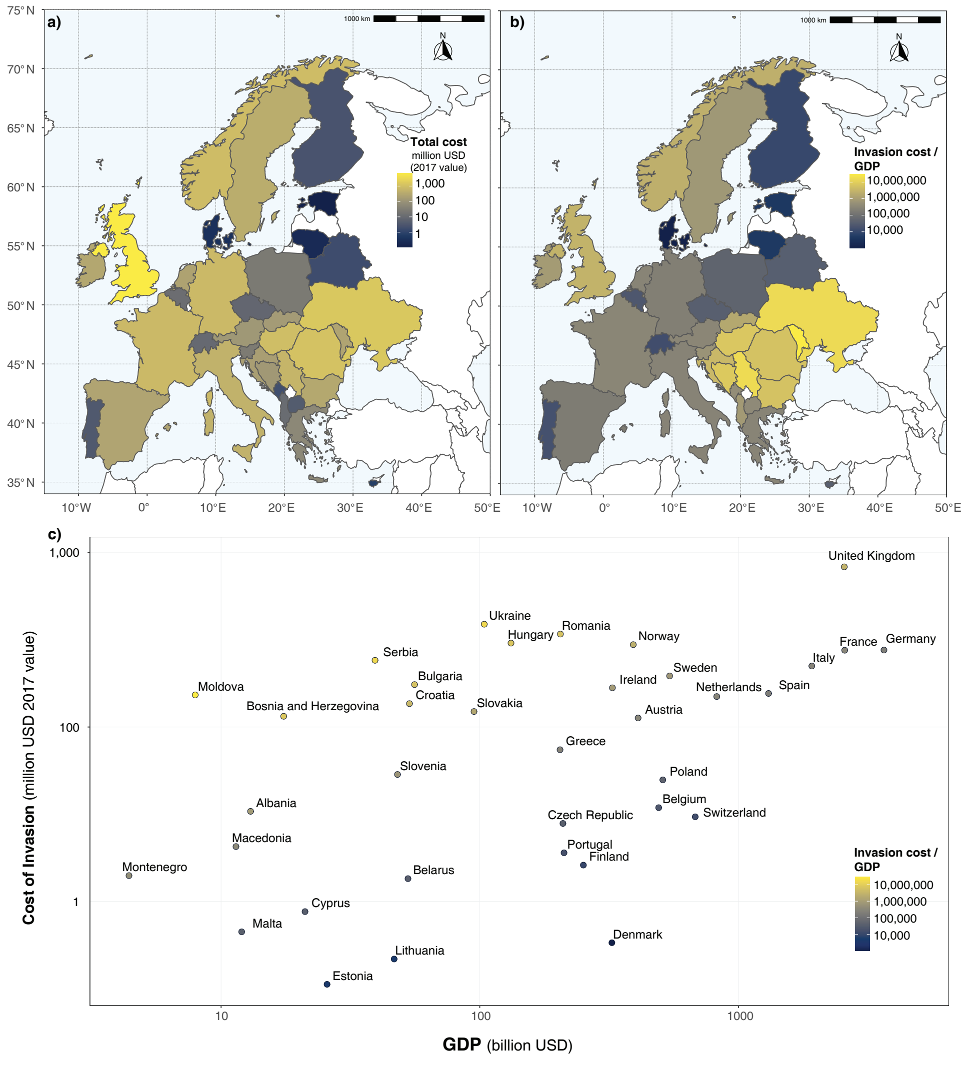

Figure 4. Maps showing for each European country where data were available: **a** total reliable observed costs of IAS for the period 1960–2020 in million US$ (i.e. excluding irreproducible cost estimations and expected costs) **b** total reliable observed costs of IAS standardised by GDP (US$), and **c** scatter plot of total cost of IAS against GDP. Data are from **a–c** InvaCost (Ballesteros-Mejia et al. 2020; Diagne et al. 2020a; Angulo et al. 2021b) **b, c** World Bank (2020). Countries in white located in Europe did not have reported costs in the InvaCost database, or in the case of Russia and Turkey were excluded from this analysis due to their transcontinental nature.

Temporal cost cumulations

Across Europe, biological invasions on average cost 2017 US$2.3 billion (2017 €1.91 billion) annually over the period 1960–2020. While the average annual cost

Table 2. Relationships of cost of IAS in European countries with country-specific factors. Two types of costs are included: cost of "Damage-Loss" and cost of "Management". Country-specific factors are presented in Suppl. material 3. Statistics shown are Spearman correlation coefficients (*p*-values associated). Bold numbers indicate significance at the 0.05 level.

Factor	Damage-Loss		Management	
	r_s	*p*	r_s	*p*
Human population size	**0.45**	**0.004**	**0.50**	**0.001**
Area	**0.55**	**<0.001**	**0.43**	**0.006**
GDP	**0.33**	**0.041**	**0.73**	**<0.001**
Number of introduced species	0.14	0.420	**0.50**	**0.002**
Number of invasive alien species	0.03	0.850	0.10	0.550
Research effort in invasion biology as number of papers on that topic	0.22	0.190	**0.58**	**<0.001**
Research effort as expenditure in R&D in % of GDP	0.02	0.920	**0.64**	**<0.001**
Research effort as expenditure in R&D	0.29	0.086	**0.75**	**<0.001**
Number of researchers	0.23	0.180	**0.65**	**<0.001**
International tourism as expenditures	**0.33**	**0.042**	**0.75**	**<0.001**
International tourism as number of arrivals	**0.34**	**0.038**	**0.55**	**<0.001**
Imports of goods and services	0.26	0.110	**0.70**	**<0.001**

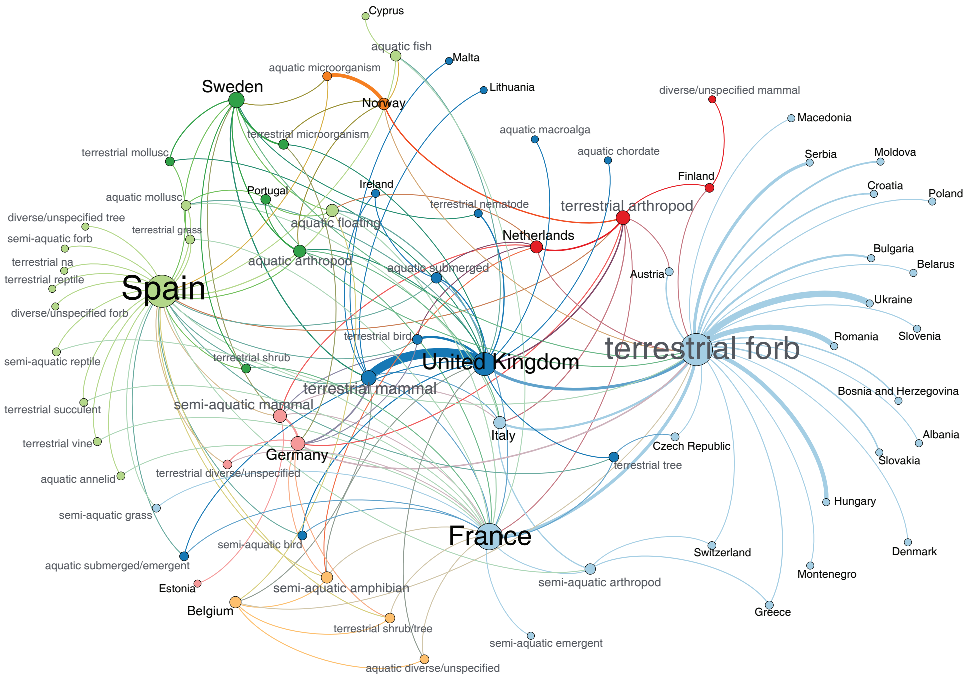

Figure 5. European network of IAS costs. This bipartite network is composed of both species and country nodes. Links indicate the cumulative costs of species in European countries over 1960–2020. The larger the link, the higher the cost. Likewise, node size is proportional to the total cumulative cost. For species nodes, node size represents the total cost they had over all countries. For country nodes, the node size represents the total cost of all species in that country. Note that studies reporting costs on 'diverse' groups of organisms rather than specific species were excluded from this network.

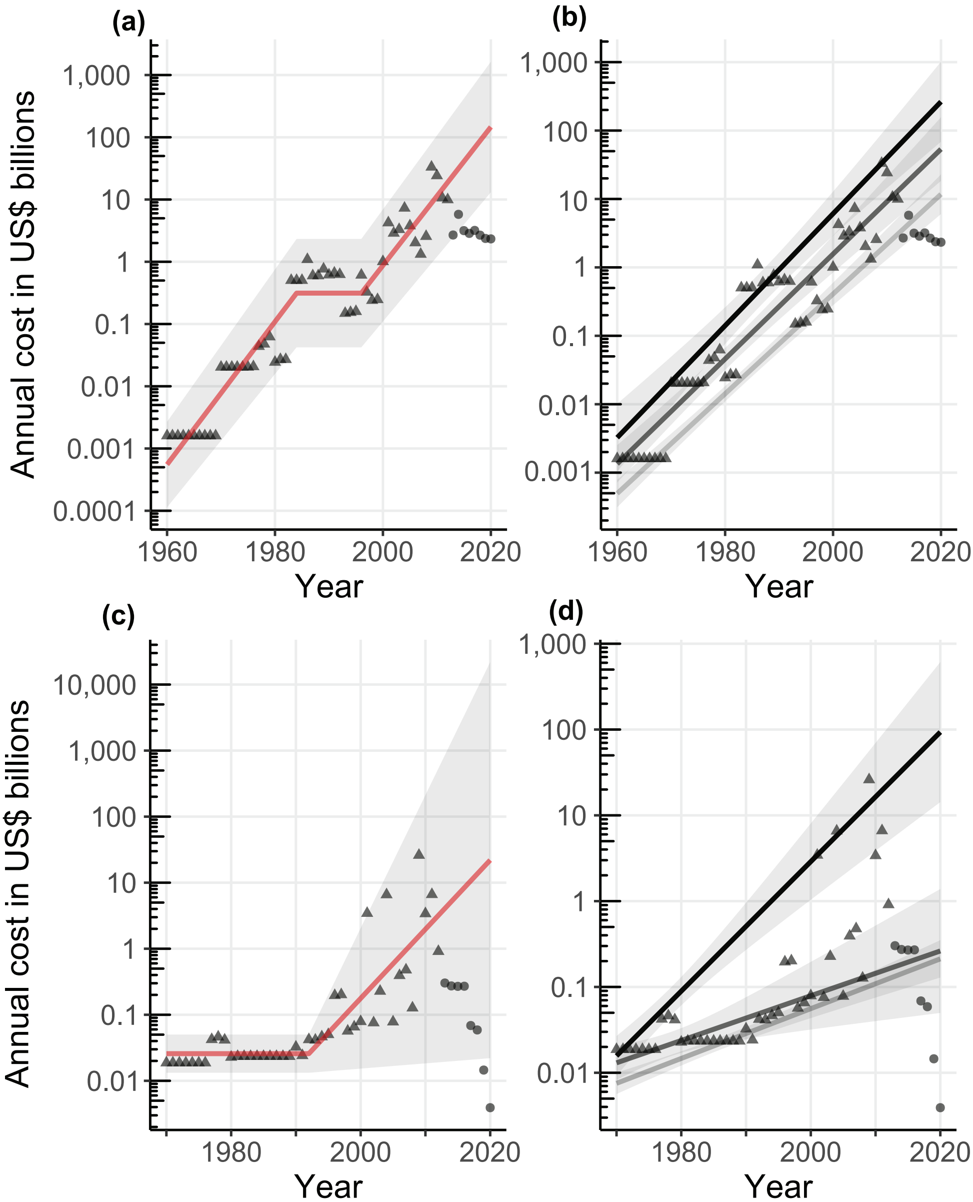

Figure 6. Temporal trend of total annual invasion costs recorded in Europe according to multivariate adaptive regression splines (MARS) (**a** red) and quantile regressions; from bottom to top: 0.1: light grey, 0.5: grey, 0.9: dark grey (**b**) between 1960 and 2020, as well as reliable observed costs, MARS (**c** red) and quantile regressions; from bottom to top: 0.1: light grey, 0.5: grey, 0.9: dark grey (**d**) between 1970 and 2020. Error bands on MARS represent prediction intervals (i.e. the interval of cost that any individual year can have). Error bands on quantile regressions represent 95% confidence intervals. Yearly data are triangles (until 2013) and circles (after); only the former are used in the models.

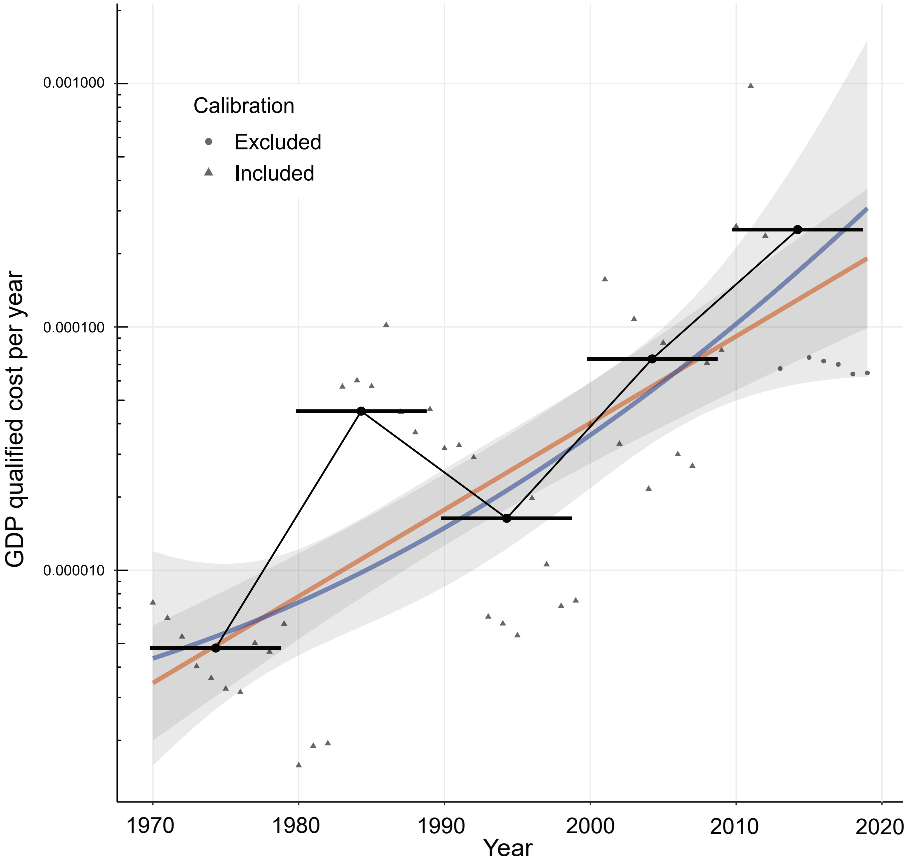

Figure 7. Temporal trend of costs considering the GDP-standardized average decadal costs (black bars) and total annual GDP-standardized invasion costs (triangles until 2013, circles after) recorded in Europe (on a log scale). Robust regression analysis between 1970 (the first year of documented reliable observed costs) and 2019 (last year with available GDP data) is overlaid, showing linear regression in orange and quadratic regression in blue. Error bands on robust regressions represent 95% confidence intervals. Model coefficients are presented in Suppl. material 7.

between 1960–1969 was below US$0.16 billion, it increased to an average annual cost of US$6.35 billion per year in 2010–2020. Considering only reliable, observed costs, the first database entry occurred a decade later than when considering all costs, totalling at an average annual cost of US$963.9 million per year (€802.9 million annually). Reliable costs between 1970–1979 averaged US$26.1 million per year, increasing to US$3.75 billion per year in 2000–2010 before dropping to US$944.3 million in 2010–2020, likely due to lags between costs and their reporting.

However, averaging across such long time periods may not clearly demonstrate temporal trends. As such, the best fitting models of temporal cost trends (MARS and quadratic OLS, see Suppl. materials 5, 6) both predict a steep linear increase on a log-scale in IAS driven costs to Europe over the 1960–2013 period (Figure 6). Considering all costs, the best model (MARS: predicted 2013 costs of US$23.58 billion / €19.64 billion; OLS: 0.1st quantile: US$3.62 billion; 0.5th quantile: US$15.57 billion; 0.9th quantile: US$59.02 billion) indicated a 12.6 to 14.1-fold increase every ten years of costs incurred from IAS (Figure 6a, b), while considering only reliable costs (MARS: predicted 2013 costs US$4.07 billion / €3.39 billion; OLS: (0.1st quantile: US$133.18 million; 0.5th quantile: US$172.52 million; 0.9th quantile: US$27.68 billion) suggested a 10.7-fold increase every ten years of reliable observed costs inferred from IAS (Figure 6c, d). If these trends were to continue over the most recent years for which data is incomplete, then extrapolations in 2020 based on MARS models would yield US$139.56 billion / €116.24 for all costs and US$21.98 billion / €18.31 billion for reliable observed costs only.

Considering GDP-qualified economic costs, monetary impacts continued to significantly increase in recent decades (model coefficients shown in Suppl. material 7), irrespective of concurrent economic growth in Europe (Figure 7). Accordingly, the proportional share of GDP devoted to invasion costs has been increasing through time, with invasion costs rising at a greater rate than the rate of economic growth, as evidenced by the steep increase in recent years.

Discussion

The total cumulative cost of IAS in Europe between 1960 and 2020 was estimated at US$140.20 billion. We identified an exponential increase in the costs of IAS over the studied time period, with costs increasing at least ten-fold every decade. Invasion costs reached US$24 billion in 2013 alone (the last year with 'complete' data), and our model extrapolated 2020 costs of up to US$140 billion. While the reported annual cost of IAS in Europe represented < 0.01% of the European Union (EU) GDP (2017 US$15.3 trillion), it was considerably larger than the annual GDP of national economies such as Malta – in recent years (US$12.8 billion).

While this total may overestimate some individual costs (e.g. in those cases where reported timelines of expenditure for a specific project were unclear in the literature), it remains a highly conservative value given the many challenges attached to assigning costs to IAS impacts. For the purposes of this analysis, we have considered reported costs and expenditure. However, we note that costs of IAS are generally not restricted to directly quantifiable damages or expenditure on management, but also include various indirect costs that are not always easily quantifiable, and therefore not as commonly reported in the literature. For example, many IAS have substantial impacts on human health, native species or ecosystem services that indirectly harm ecosystems and undermine human wellbeing, yet these costs are not easy to capture or quantify (Medlock et al. 2012; Hamaoui-Laguel et al. 2015; Ogden et al. 2019). A striking illustration has been published by Walsh et al. (2016) who reported a significant decrease in the biomass of the grazer *Daphnia pulicaria* in lakes invaded by the spiny water flea *Bythotrephes longimanus*, in turn causing a substantial decrease in water quality by affecting its clarity and total phosphorus content. Other examples include biting nuisances by invasive mosquito species (e.g. *Aedes albopictus*) or invasive ant species (e.g. *Solenopsis invicta*) which can negate recreational activities (e.g. Angulo et al. 2021c); and adverse impacts by invasive tree-boring insects (e.g. *Agrilus planipennis*) on trees that could be costly for the respective economy, although these costs are seldom quantified. Indirect costs are often overlooked or at best underestimated, resulting in minimal investments for alleviation (Rogers et al. 2017; Linders et al. 2019). Although our cost estimations cover 410 species (340 species when considering only reliable observed costs), there remain over ~4,000 IAS in Europe without reported costs (Pagad et al. 2018), indicating that our estimates are highly conservative. Moreover, often costs such as salaries of invasion researchers or managers are not published or accounted for.

Marked differences in cost reporting and totals were found among European countries, with impacts to the UK, Spanish, French, Russian and German economies being most pervasive considering all costs (see Cuthbert et al. 2021a; Angulo et al. 2021a; Renault et al. 2021; Kirichenko et al. 2021; and Haubrock et al. 2021a, respectively). The highest observed costs were found in the UK (Cuthbert et al. 2021a), a country with a long colonial history highly reliant on trade (Clark et al. 2014) and previously identified as a "receiver and donor" country (e.g. for aquatic invasions see García-Berthou et al. 2005). Similar to the UK, the rest of the aforementioned countries with the highest total costs have large economies and most of them were colonial powers, all factors that putatively contribute to high levels of invasions and impacts (Hulme 2009; Hulme et al. 2009). However, the west-European dominance in IAS costs may also be explained by the limited reporting of costs for Eastern European, and potentially also some Nordic, countries. Additionally, the limited reporting of the invasion costs may partly be attributed to the gap of the InvaCost database in sources/documents in languages other than English. The non-English data were collected for only a subset of European languages (Angulo et al. 2021b), leaving aside several languages from Eastern and Northern Europe (e.g. Romanian, Hungarian, Serbian, Polish, and Nordic languages – Finnish, Swedish, Danish etc.). For Eastern European countries, e.g. those of the former communist bloc, one reason for their low reported costs may be that up until 1990, there was little documentation of monetary impacts or, if there was, this information was not made publicly available. Further, differences in societal norms, awareness or regulations may contribute to the lower reported costs for Eastern European countries. However, we note that, considering highly reliable observed costs only, Eastern Russia, Ukraine and Romania exhibited relatively high costs. Regardless of the drivers of this limited reporting, it is a concern, considering that coordinated responses and cooperation are key to efficiently managing invasions and mitigating their impacts (Kark et al. 2015; Latombe et al. 2017; Ogden et al. 2019).

Cultural differences among countries, regional perceptions and national priorities may also influence the level and way of reporting, for example through perceived country-specific sectors of economic importance e.g. forestry and agriculture. In some countries, alien taxa such as trees have been perceived to provide cultural heritage services, particularly in areas with lower levels of development and life satisfaction (Vaz et al. 2018), which might influence cost reporting. Our results also reflect the difficulties of identifying how different sectors may have been impacted – a substantial share of reported costs (29%; US$41.17 billion) were not attributed to a single affected sector. Another important driver of differences in reporting across European countries may lie in differences in perceptions of the severity of IAS impacts. For example, a European-wide survey on attitudes towards biodiversity indicated substantial differences between citizens of different countries in their perceptions towards newly introduced plants and animals. Residents of Spain, Portugal and Slovenia were most likely to view them as a great threat to biodiversity, while those from Finland, the Netherlands and Eastern European countries were less likely to be concerned about the threats of introduced species (European Commission 2013, 2015). For Eastern European countries, initiatives during the Soviet Union times to increase production (i.e. in agriculture, fisheries etc.) and support regional employment may have contributed to the view that new species introductions hold large positive economic potential, which later on may have shaped public views and research agendas towards favoring and/or accepting these species (Kourantidou and Kaiser 2019). Furthermore, in European aquatic systems, alien taxa were reportedly introduced to improve yields from fish farming historically, and particularly in human-altered waterbodies (Arbačiauskas et al. 2010). Although the reasons for the differences in perception of IAS as a threat are not well understood, with perception and values attributed to biodiversity being complex but consistent among social categories, gender and age (Atlan and van Tilbeurgh 2019), higher levels of awareness of their harmful impacts can help support more management actions, research investments and increased efforts to document and report costs. However, these also depend on public support, and this may also vary across specific actions or environments (e.g. Perry and Perry 2008; Crowley et al. 2017). Ultimately, the differences in perceptions of IAS among European states could be a major driver in unevenness of cost reporting among nations, as well as through differences in national-scale policy frameworks. A lack of reporting from many states likely renders our totals as underestimates, but the extent of this underestimation probably differs among countries.

Despite this variability in reported economic costs among European countries (in France, for example, <1% of total reported costs were associated with management as compared with 86% in Germany or 92% in the Netherlands; see e.g. Renault et al. 2021; Haubrock et al. 2021a), the majority of costs (US$84.18 billion; 60%) comprised expenditure on damages and losses, while control-related expenditure represented only 20% of all costs (US$28.17 billion). This dominance of damage costs over management investments is paralleled in other regions, such as Asia (Liu et al. 2021), Africa (Diagne et al. 2021b), North America (Crystal-Ornelas et al. 2021), Central/South America (Heringer et al. 2021), and Australia (Bradshaw et al. 2021); but some individual countries appear to have more management costs (Angulo et al. 2021a for Spain; Ballesteros-Mejia et al. 2021 for Ecuador; Watari et al. 2021 for Japan). Similar to Kourantidou et al. (2021), a number of socio-economic factors significantly correlated with both the reported damages and management costs of IAS, namely: human population size, land area, GDP, and international tourism of the studied countries. These predictors help explain some of the discrepancies in shares of IAS management and damages cost across European countries. First, in countries with higher population, larger land areas, and more international tourism, new species are more likely to be introduced, propagate and invade, while higher human population may also result in increased awareness of specific damage types, e.g. to infrastructure (Mooney and Cleland 2001; Hulme et al. 2009; Hall 2015). This might lead to an increased willingness to pay for managing them. On the other hand, higher GDP might lead to higher resources (e.g. funding and capacity) available to understand and manage IAS. Indeed, the strong relationship found between research effort and numbers of researchers and management cost magnitudes exemplifies this point: greater research investments align with higher reporting of management costs. Our results also indicate that increasing imports of goods and services are associated with greater management spending. It may be assumed that money spent on IAS management would be at least a partial reflection of the total damages incurred. However, there was no significant relationship between reported damage-loss and management costs (Table 2). If management expenditure is largely independent of the number of IAS present and their negative economic impacts, this may reflect a fixed budgetary availability (i.e. the funding available for IAS management is independent of the number of IAS and their impacts in the country). Moreover, the overall three-fold difference in damage-related compared to management costs (eight-fold for observed reliable costs) is alarming, particularly given that preventative measures for invasions (which are classified under management in this study) are shown to be effective at reducing costs than longer-term interventions (Leung et al. 2002; Ahmed et al. 2021), and that countries with a higher proportion of money spent on biosecurity experience generally lower damage costs (Jay et al. 2003; Kritikos et al. 2005).

The InvaCost data also indicate more than a 10-fold increase every ten years in costs associated with IAS since 1960. This finding is likely a result of several trends: foremost the increasing number of IAS in Europe (Seebens et al. 2017), global cost trends (Diagne et al. 2021a; Cuthbert et al. 2021c) and the increasing number of publications within the field of invasion science (Richardson and Pyšek 2008). This is followed by the increase in the GDP of most European countries; and the increasing awareness and number of legislative instruments (at national and EU levels) adopted to tackle IAS (Garcıa de Lomas and Vilà 2015; Turbelin et al. 2017, but see Coughlan et al. 2020). These factors likely contribute to a growth in reported costs and also to an increase in budgets over time. With several thousand alien species established in Europe (Dawson et al. 2017) and legislation in place to tackle IAS throughout the continent, it is somewhat surprising that management and mixed costs (which comprise some management component) represent a small proportion of the total. However, this disconnect between resources made available to mitigate invasion impacts and the large number of IAS worldwide is not a trend unique to Europe (Andreu et al. 2009). Management of IAS can be compromised by a range of factors including insufficient knowledge of species origin and biology, lack of appropriate management strategies, societal ignorance, and lack of resources (Sharp et al. 2011; Courchamp et al. 2017; Kirichenko et al. 2019). Financing provided for biomonitoring and/or eradication plans is frequently of insufficient length, compromising outcomes while simultaneously increasing both management and damage costs (Sutcliffe et al. 2018;

Pergl et al. 2019). Further, the insufficient cooperation among and within countries, for example in implementing risk assessments and management planning for IAS, can result in ineffective management strategies (Sharp et al. 2011; Keller et al. 2011). Even if such planning deficiencies are specifically considered, as in the framework proposed by the Convention on Biological Diversity (CBD 2020), the feasibility of management actions remains impaired by the paucity of resources (Heink et al. 2018).

Conclusion

The cost estimations presented in this publication synthesize the state of knowledge on economic costs associated with IAS at the European level. Such cost information on biological invasions at regional scales is especially important for planning coordinated responses, cooperative action but also for interaction at multiple levels among European countries within the EU or EEA and with non-European countries through e.g. trade agreements. Further, we identified significantly higher costs in recent years than previous estimates of ~€12 billion (Kettunen et al. 2009), despite the identified knowledge gaps for various IAS. This becomes particularly important in light of the effects of past agreements such as the freedoms guaranteed by Article 21 of the Treaty on the Functioning of the EU, with the freedom of movement being linked to the enhanced displacement of various species within Europe (de Sadeleer 2014). From a management co-operation standpoint, whether within the EU or between trading partners within Europe, the economic burden imposed by IAS becomes particularly relevant, given that increasing costs burden certain countries disproportionately, likely putting monetary strain on economically weaker countries. A comprehensive appraisal of costs would ultimately contribute to well-targeted investments into conservation measures on an EU and continental scale.

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Supplementary material 1

Dataset used as basis for the analysis

Authors: Phillip J. Haubrock, Anna J. Turbelin, Ross N. Cuthbert, Ana Novoa, Nigel G. Taylor, Elena Angulo, Liliana Ballesteros-Mejia, Thomas W. Bodey, César Capinha, Christophe Diagne, Franz Essl, Marina Golivets, Natalia Kirichenko, Melina Kourantidou, Boris Leroy, David Renault, Laura Verbrugge, Franck Courchamp

Data type: Dataset/Excel-sheet

Link: https://doi.org/10.3897/neobiota.67.58196.suppl1

Supplementary material 2

Description of the impacted sector categories considered in analyses of European invasion costs

Authors: Phillip J. Haubrock, Anna J. Turbelin, Ross N. Cuthbert, Ana Novoa, Nigel G. Taylor, Elena Angulo, Liliana Ballesteros-Mejia, Thomas W. Bodey, César Capinha, Christophe Diagne, Franz Essl, Marina Golivets, Natalia Kirichenko, Melina Kourantidou, Boris Leroy, David Renault, Laura Verbrugge, Franck Courchamp

Data type: Description/Word-file

Link: https://doi.org/10.3897/neobiota.67.58196.suppl2

Supplementary material 3

Descriptions of socio-economic explanatory variables considered at the country level as potential correlates of invasion costs

Authors: Phillip J. Haubrock, Anna J. Turbelin, Ross N. Cuthbert, Ana Novoa, Nigel G. Taylor, Elena Angulo, Liliana Ballesteros-Mejia, Thomas W. Bodey, César Capinha, Christophe Diagne, Franz Essl, Marina Golivets, Natalia Kirichenko, Melina Kourantidou, Boris Leroy, David Renault, Laura Verbrugge, Franck Courchamp

Data type: Description/Word-file

Explanation note: Descriptions of socio-economic explanatory variables considered at the country level as potential correlates of invasion costs. Factor names are presented alongside their units, description, source and associated hypotheses.

Link: https://doi.org/10.3897/neobiota.67.58196.suppl3

Supplementary material 4

Map of Europe showing (a) the number of alien species, (b) the number of researchers at a scale of thousands, (c) total cost of invasion normalised by the number of alien species and (d) total cost of invasions normalised by the number of researchers by country

Authors: Phillip J. Haubrock, Anna J. Turbelin, Ross N. Cuthbert, Ana Novoa, Nigel G. Taylor, Elena Angulo, Liliana Ballesteros-Mejia, Thomas W. Bodey, César Capinha, Christophe Diagne, Franz Essl, Marina Golivets, Natalia Kirichenko, Melina Kourantidou, Boris Leroy, David Renault, Laura Verbrugge, Franck Courchamp

Data type: Figure/Word-file

Explanation note: Map of Europe showing (**a**) the number of alien species, (**b**) the number of researchers at a scale of thousands, (**c**) total cost of invasion normalised by the number of alien species and (**d**) total cost of invasions normalised by the number of researchers by country. Data from (**a**) GRIIS (2020), (**b**) UNESCO statistics (2020), **c**) Angulo et al., (2020), Diagne et al. (2021) and GRIIS (2020) and d) Diagne et al. (2020) and UNESCO statistics (2020).

Link: https://doi.org/10.3897/neobiota.67.58196.suppl4

Supplementary material 5

Temporal trends in invasion costs considering all and reliable observed data (i.e. excluding irreproducible cost estimates and expected costs), calculated until 2013

Authors: Phillip J. Haubrock, Anna J. Turbelin, Ross N. Cuthbert, Ana Novoa, Nigel G. Taylor, Elena Angulo, Liliana Ballesteros-Mejia, Thomas W. Bodey, César Capinha, Christophe Diagne, Franz Essl, Marina Golivets, Natalia Kirichenko, Melina Kourantidou, Boris Leroy, David Renault, Laura Verbrugge, Franck Courchamp

Data type: Figure/Word-file

Explanation note: Temporal trends in invasion costs considering all and reliable observed data (i.e. excluding irreproducible cost estimates and expected costs), calculated until 2013. Fitted models are: ordinary least squares regression (OLS; linear and quadratic), robust regression (linear and quadratic), generalised additive (GAM), multiple additive regression splines (MARS) and quantile-quantile regression (0.1, 0.5 and 0.9). Points represent annual invasion costs totals, whilst grey areas represent 95% confidence intervals (prediction intervals in case of MARS); they are represented by circles until 2013 and triangles after.

Link: https://doi.org/10.3897/neobiota.67.58196.suppl5

Supplementary material 6

Root-mean-square errors (RMSE) corresponding to models of temporal trends in invasion costs

Authors: Phillip J. Haubrock, Anna J. Turbelin, Ross N. Cuthbert, Ana Novoa, Nigel G. Taylor, Elena Angulo, Liliana Ballesteros-Mejia, Thomas W. Bodey, César Capinha, Christophe Diagne, Franz Essl, Marina Golivets, Natalia Kirichenko, Melina Kourantidou, Boris Leroy, David Renault, Laura Verbrugge, Franck Courchamp

Data type: Table/Word-file

Explanation note: Root-mean-square errors (RMSE) corresponding to models of temporal trends in invasion costs (ordinary least squares regression: OLS; robust regression: RR; multiple additive regression splines (MARS); generalised additive model: GAM; quantile: QT) and considering all data (a) and reliable observed data (b) (i.e. excluding irreproducible cost estimates and expected cots). Calibrated data applies adjustments to account for time lags in recent years, in contrast to the unadjusted raw data (i.e. all data).

Link: https://doi.org/10.3897/neobiota.67.58196.suppl6

Supplementary material 7

Coefficients from linear robust regression model considering temporal trends in invasion costs, qualified per annual GDP among European countries

Authors: Phillip J. Haubrock, Anna J. Turbelin, Ross N. Cuthbert, Ana Novoa, Nigel G. Taylor, Elena Angulo, Liliana Ballesteros-Mejia, Thomas W. Bodey, César Capinha, Christophe Diagne, Franz Essl, Marina Golivets, Natalia Kirichenko, Melina Kourantidou, Boris Leroy, David Renault, Laura Verbrugge, Franck Courchamp

Data type: Table/Word-file

Explanation note: Coefficients from linear robust regression model considering temporal trends in invasion costs, qualified per annual GDP among European countries.

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RESEARCH ARTICLE

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Advancing research on alien species and biological invasions

Biological invasions in France: Alarming costs and even more alarming knowledge gaps

David Renault[1,2], Eléna Manfrini[3], Boris Leroy[4], Christophe Diagne[3], Liliana Ballesteros-Mejia[3], Elena Angulo[3], Franck Courchamp[3]

1 *University of Rennes, CNRS, ECOBIO [(Ecosystèmes, biodiversité, évolution)] – UMR 6553, Rennes, France* **2** *Institut Universitaire de France, 1 Rue Descartes, Paris, France* **3** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, Orsay, France* **4** *Unité Biologie des Organismes et Ecosystèmes Aquatiques (BOREA UMR 7208), Muséum National d'Histoire Naturelle, Sorbonne Universités, Université de Caen Normandie, Université des Antilles, CNRS, IRD, Paris, France*

Corresponding author: David Renault (david.renault@univ-rennes1.fr)

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Abstract

The ever-increasing number of introduced species profoundly threatens global biodiversity. While the ecological and evolutionary consequences of invasive alien species are receiving increasing attention, their economic impacts have largely remained understudied, especially in France. Here, we aimed at providing a general overview of the monetary losses (damages caused by) and expenditures (management of) associated with invasive alien species in France. This country has a long history of alien species presence, partly due to its long-standing global trade activities, highly developed tourism, and presence of overseas territories in different regions of the globe, resulting in a conservative minimum of 2,750 introduced and invasive alien species. By synthesizing for the first time the monetary losses and expenditures incurred by invasive alien species in Metropolitan France and French overseas territories, we obtained 1,583 cost records for 98 invasive alien species. We found that they caused a conservative total amount ranging between US$ 1,280 million and 11,535 million in costs over the period 1993–2018. We extrapolated costs for species invading France, for which costs were reported in other countries but not in France, which yielded an additional cost ranging from US$ 151 to 3,030 millions. Damage costs were nearly eight times higher than management expenditure. Insects, and in particular the Asian tiger mosquito *Aedes albopictus* and the yellow fever mosquito *Ae. aegypti*, totalled very high economic costs, followed by non-graminoid terrestrial flowering and aquatic plants (*Ambrosia artemisiifolia*, *Ludwigia* sp. and *Lagarosiphon major*).

Over 90% of alien species currently recorded in France had no costs reported in the literature, resulting in high biases in taxonomic, regional and activity sector coverages. To conclude, we report alarming costs and even more alarming knowledge gaps. Our results should raise awareness of the importance of biosecurity and biosurveillance in France, and beyond, as well as the crucial need for better reporting and documentation of cost data.

Abstract in Chinese

法国的生物入侵：造成令人震惊的经济损失和更令人震惊的知识差距

David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

快速增加的外来物种已经对全球生物多样性造成了严重威胁。虽然对于外来入侵物种的生态和进化影响受到关注持续增加，但对于外来物种经济影响却很少研究关注，特别是在法国。本项研究评估了法国外来入侵物种造成的直接经济损失和相关管理控制的经济花费。由于长期积极参与全球贸易活动、高度发达的旅游业以及在全球不同地区拥有多个海外领地，所以法国有着悠久的外来物种的引入历史，保守估计至少有2750种外来物种被引入了法国。本研究首次整理法国大都市和法国海外领地的外来入侵物种造成直接经济损失和相关管理支出的资料，我们查询到有关98种外来入侵物种1583条造成经济损失的相关研究。保守估算法国的外来物种在1993–2018年期间造成115.35亿美元的经济损失。对于那些已经入侵到法国但尚未有经济损失数据报道的物种，我们根据它们在其他国家已造成的经济损失估算它们造成的额外经济损失为1.51 至 30.3亿美元。在法国外来入侵物种造成的直接经济损害大约是对外来入侵物种管理控制费用的8倍。在所有外来入侵物种类群中，昆虫造成的非常高的经济损失，尤其是白纹伊蚊（*Aedes albopictus*）和埃及伊蚊（*A. aegypti*）。其次是非禾本科的陆生花卉和水生植物，如豚草（*Ambrosia artemisiifolia*）、蓼科植物（*Ludwigia* spp）和软骨草（*Lagarosiphon major*)。目前超过90%的法国外来入侵物种缺乏研究其造成的经济损失，由于外来入侵物种分类类群，分布地区和使用部门不同，所以对其造成经济损失的研究存在很大的不均衡性。因此，我们这项研究报告外来入侵物种在法国造成巨大的经济损失，并存在更加巨大的知识差距。我们研究结果表明应提高对法国及其海外领地生物安全和生物监测重要性，急需更好的研究报告和记录外来入侵物种造成经济损失。

Abstract in French

Invasions biologiques en France : des coûts alarmants et des lacunes de connaissances encore plus alarmantes

David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

La croissance ininterrompue de transport et d'introduction d'espèces menace dangereusement la biodiversité mondiale. Bien que les conséquences éco-évolutives liées à la présence d'espèces exotiques envahissantes fassent l'objet d'un nombre d'études de plus en plus conséquent, les impacts économiques générés par les invasions biologiques restent insuffisamment étudiés, notamment en France. Dans cette étude, nous présentons une vue générale des pertes monétaires (dommages, dégâts) et des dépenses (gestion) induites par les espèces exotiques envahissantes en France. Ce pays dispose d'une longue histoire de présence d'espèces exotiques en raison d'importantes activités de commerce international de longue date, d'un tourisme fortement développé, et de nombreux territoires d'outre-mer dans différentes régions du monde; ceci contribue à expliquer l'estimation conservatrice de la présence de 2750 espèces exotiques (introduites ou envahissantes) en France. En synthétisant pour la première fois les pertes monétaires et les dépenses induites par la présence des espèces exotiques envahissantes en France métropolitaine et dans ses territoires d'outre-mer, nous avons pu identifier 1583 données de coûts concernant 98 espèces exotiques envahissantes. Nous avons estimé que les espèces exotiques envahissantes ont généré un montant conservateur de 1280 à 11535 millions $US sur la période 1993–2018. Nous avons extrapolé les coûts pour les espèces envahissant la France, pour lesquelles des données de coûts existent dans le monde mais pas en France, ce qui a abouti à un coût additionnel compris entre 151 et 3 030 millions $US. Les coûts des dégâts étaient 8 fois plus élevés que les coûts liés aux dépenses de gestion. Les insectes, en particulier le moustique tigre, *Aedes albopictus*, et le moustique de la fièvre jaune, *Ae. Aegypti*, génèrent les coûts économiques les plus importants, suivis par les plantes à fleurs terrestres et les plantes aquatiques (*Ambrosia artemisiifolia*, *Ludwigia* sp. et *Lagarosiphon major*). Plus de 90% des espèces exotiques actuellement enregistrées en France ne font l'objet d'aucune mention de coût dans la littérature, ce qui traduit un fort biais taxonomique, et un fort biais de couvertures régionale et sectorielle des impacts de ces espèces. En conclusion, notre étude pointe des coûts alarmants et des lacunes de connaissances entre plus grandes au regard des impacts financiers liés aux espèces exotiques envahissantes. Nos résultats doivent alerter sur l'importance de la biosécurité et de la biosurveillance en France et, au-delà, sur le besoin crucial d'une meilleure documentation et d'une meilleure compilation des données de coût.

Abstract in Spanish

Invasiones biológicas en Francia: Alarmantes costos y lagunas de conocimiento aún más alarmantes.
David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp
El número cada vez mayor de especies introducidas amenaza profundamente la biodiversidad mundial. Si bien las consecuencias ecológicas y evolutivas de las especies exóticas invasoras (EEI) están recibiendo cada vez más atención, sus impactos económicos han permanecido poco estudiados, especialmente en Francia. Nuestro objetivo en este artículo, fue proporcionar una descripción general de las pérdidas monetarias (daños causados por) y los gastos (gestión de) asociados con las especies exóticas invasoras en Francia. Este país tiene una larga historia de presencia de especies exóticas, debido a su tradición de actividades comerciales en todo el mundo, su turismo altamente desarrollado y presencia de territorios de ultramar en diferentes regiones del mundo, lo que nos lleva a tener un mínimo conservador de 2.750 especies exóticas introducidas e invasoras.

Esta primera síntesis de las pérdidas monetarias y los gastos incurridos por las EEI en la Francia metropolitana y sus territorios de ultramar, arrojó un total de 1.583 registros de costos para 98 especies exóticas invasoras. También descubrimos que durante el período de 1993 a 2018, las EEI causaron un monto total conservador de entre US $ 1.280 millones y 11.535 millones en costos. Extrapolamos los costos de las especies que invaden Francia, cuyos costos se reportaron en otros países pero no en Francia, lo que generó un costo adicional que oscila entre los 151 y los 3.030 millones de dólares. Los costos de daños fueron alrededor de 8 veces más altos que los gastos de gestión. Los insectos, y en particular el mosquito tigre asiático *Aedes albopictus* y el mosquito de la fiebre amarilla *Ae. aegypti*, sumaron costos económicos muy altos, seguidos de plantas acuáticas y de flores terrestres no gramíneas (p. ej. *Ambrosia artemisiifolia*, *Ludwigia* sp. y *Lagarosiphon major*). Más del 90% de las especies exóticas registradas actualmente en Francia no tienen costos reportados en la literatura, lo que resulta en un alto sesgo en cuanto a la cobertura taxonómica, regional y en sectores socioeconómicos. En conclusión, reportamos costos alarmantes y lagunas de conocimiento aún más alarmantes. Nuestros resultados deberían crear conciencia sobre la importancia de la bioseguridad y el biocontrol en Francia y más allá, así como sobre la necesidad crucial de mejorar la calidad de la información y la documentación de los datos de costos sobre especies invasoras.

Abstract in Russian

Биологические инвазии во Франции: тревожные убытки и еще более тревожные пробелы в знаниях
David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp
Постоянный рост числа интродуцированных видов серьезно угрожает глобальному биоразнообразию. Хотя экологическим и эволюционным последствиям инвазий чужеродных

видов уделяется огромное внимание, экономические потери от их деятельности в значительной степени остаются недостаточно изученными, особенно во Франции. Мы представляем обзор экономических потерь (в результате причиненных повреждений) и расходов на контроль инвазионных чужеродных видов во Франции. Эта страна имеет долгую историю присутствия на ее территории чужеродных видов, отчасти из-за давней глобальной торговой деятельности, высокоразвитого туризма и наличия заморских французских территорий в разных регионах земного шара. Сегодня во Франции насчитывается 2750 интродуцированных и инвазионных чужеродных видов. Мы впервые обобщили данные по экономическим потерям в результате инвазий чужеродных видов во Франции и на ее заморских территориях, проанализировав 1583 позиции убытков в результате инвазий 98 чужеродного вида. В 1993–2018 гг. эти виды причинили ущерб на общую сумму 11,535 млн долларов США. Мы экстраполировали затраты на виды, вторгшиеся во Францию (расходы по которым были известны по другим странам, но не для Франции), что увеличило денежные потери в диапазоне от 151 до 3030 миллионов долларов США. Экономические потери в результате причиненных повреждений (прямые убытки) были в 8 раз выше, чем затраты на контроль инвайдеров. Насекомые, в частности, азиатский тигровый комар *Aedes albopictus* и желтолихорадочный комар *Aedes aegypti,* являлись причиной самых высоких экономических потерь; за ними следовали травянистые (кроме злаков, бобовых и осоковых) и водные растения (*Ambrosia artemisiifolia*, *Ludwigia* sp. и *Lagarosiphon major*). Для более чем 90 % зарегистрированных во Франции чужеродных видов в литературе отсутствуют сведения об экономических потерях, что не может не сказываться на точности оценок экономических ущербов при анализе таксономических групп, регионов и секторов экономики. Таким образом, мы сообщаем о тревожных убытках и еще более тревожных пробелах в знаниях. Наши результаты должны повысить осведомленность о важности биологической безопасности и надзора за инвайдерами во Франции и за ее пределами, а также о необходимости улучшения отчетности и документирования экономических потерь.

Abstract in Arabic

ملخص

الغزو البيولوجي في فرنسا: تكاليف مقلقة وفجوات معرفية مفزعة.

يشكل النمو المستمر في النقل وإدخال الأنواع تهديدًا خطيرًا للتنوع البيولوجي العالمي. وعلى الرغم من أن نتائج التطور الإيكولوجي لوجود "الأنواع الغازية" هي موضوع عدد متزايد من الدراسات، فإن الآثار الاقتصادية الناجمة عن الغزو البيولوجي لا تزال غير مدروسة بما فيه الكفاية، لا سيما في فرنسا. نقدم في هذه الدراسة لمحة عامة عن التكلفة المالية للأضرار والخسائر ونفقات التسيير التي تسببها الأنواع الغازية في فرنسا. لهذه الدولة تاريخ طويل فيما يخص تواجد الأنواع "الدخيلة" بسبب الأنشطة التجارية الدولية المهمة والطويلة الأمد، والسياحة المتطورة وامتدادها في العديد من الأقاليم "ما وراء البحار" المتواجدة في مناطق مختلفة من العالم؛ يساعد كل هذا في تفسير "التقديرات المتحفظة" لوجود ٢٧٥٠ نوعًا غازيًا في فرنسا. من خلال تجميعنا لأول مرة لمختلف الخسائر المالية والنفقات الناتجة عن وجود الأنواع الغازية في فرنسا وأقاليمها "ما وراء البحار"، استطعنا تحديد ١٥٨٣ بيان تكلفة يتعلق بـ ٩٨ صنفا مختلفا. ولقد قدرنا التكلفة الإجمالية للأنواع الغازية في ١١٥٣٥ مليون دولار أمريكي خلال الفترة ١٩٩٣-٢٠١٨. ومن خلال استقرائنا لتكاليف الأنواع التي تغزو فرنسا، والتي توجد بيانات عنها في العالم ولكن ليس في فرنسا، فإن هناك تكلفة إضافية تتراوح بين ١٥١ و٣٠٣٠ مليون دولار أمريكي. إضافة إلى ذلك، فإن التكاليف الناتجة عن الأضرار كانت أعلى ٨ مرات من تكاليف مصاريف التسيير. وقد جاءت الحشرات، وخاصة بعوضة النمر وبعوضة الحمى الصفراء في الرتبة الأولى من حيث التكلفة الاقتصادية، تليها النباتات الزهرية الأرضية والنباتات المائية. وكان من اللافت أن أكثر من ٩٠٪ من الأنواع الدخيلة المسجلة حاليًا في فرنسا لم تتم الإشارة إلى تكلفتها الاقتصادية في المراجع المعتمدة، مما يعكس وجود تحيز قوي لا من الناحية التصنيفية ولا من ناحية التغطية الإقليمية والقطاعية لتأثيرات هذه الأنواع. في الختام، نبلغ في هذه الدراسة عن تكاليف مقلقة وفجوات معرفية مهولة فيما يهم الاثار المالية المرتبطة بالأنواع الغازية. كما نأمل أن تزيد هذه النتائج في نسبة الوعي بأهمية الأمن البيولوجي والرصد البيولوجي في فرنسا وخارجها، وتساهم في تحسين عملية توثيق وتجميع مختلف بيانات التكاليف.

Keywords

damage costs, economic threat, exotic, InvaCost, invasive alien species, management costs, non-indigenous, non-native

Introduction

Biological invasions, alongside climate change, pollution, habitats destruction and overexploitation, are direct drivers of change and loss in biodiversity (Bellard et al. 2012; Elbakidze et al. 2018; Hughes et al. 2020; Liu et al. 2020; Verma et al. 2020). With the continuous escalation in the number of transported species (Seebens et al. 2017), the threat to biodiversity incurred by invasive alien species, i.e. those populations introduced by humans and expanding in regions outside their past or current distribution areas, has become particularly concerning. Worse, recent predictions suggest that increasing shipping traffic may further enhance invasion phenomena, much more than climate change alone; for instance, models estimate a 3- to 20-fold increase of the marine invasion risks on the globe towards the 2050 horizon (Sardain et al. 2020). The resulting biogeographic changes in biodiversity distribution have several far-reaching ecological and evolutionary consequences (Alp et al. 2016; Carbonell et al. 2017; Colautti et al. 2017). In particular, the impacts of invasive alien species on biodiversity may profoundly alter the functioning of communities and ecosystems (Braun et al. 2019; Papier et al. 2019), in turn altering the delivery of ecosystem services (Castro-Diez et al. 2016), biodiversity and human health (Elbakidze et al. 2018; Shackleton et al. 2019; Kumar Rai and Singh 2020; Pyšek et al. 2020). When expanding their range, several invasive alien species can also act as ecosystem engineers, gradually transforming invaded communities and existing ecological structures (Guy-Haim et al. 2017; Lebouvier et al. 2020).

The accumulating evidence of the environmental impacts generated by biological invasions worldwide has considerably increased the attention of researchers towards invasive alien species over the years. In particular, databases documenting invasive alien species distributions are flourishing (e.g., Seebens et al. 2020; CABI; Global Register of Introduced and Invasive Species (GRIIS); The Invasive Species Specialist Group), in addition to investigations assessing existing vectors/pathways (Hulme 2009; Saul et al. 2017; Turbelin et al. 2017; Mohanty and Measey 2019) and the future distribution of invasive species (e.g., Bellard et al. 2013; Bertelsmeier et al. 2015; Fournier et al. 2019; Bazzichetto et al. 2020; Louppe et al. 2020). Continuous research effort improves our comprehension of the large array of effects incurred by invasive alien species, and contributes to identifying those species having the greatest impacts on ecosystems, habitats or biodiversity. These investigations subsequently allow for the establishment of action prioritisations for the management of invasive alien species. Yet, and surprisingly, while our understanding of the effects of biological invasions on biodiversity and the environment is growing (Simberloff et al. 2013; Castro-Diez et al. 2016; Braun et al. 2019; Verma et al. 2020), their impacts on economic activities, and the overall costs they are generating, have in parallel remained understudied (IUCN 2018). Information on the socio-economic impacts of invasive species is essential to identify effective management approaches and optimise transboundary legislation (Dana et al. 2013; Caffrey et al. 2014; Chaffin et al. 2016; Diagne et al. 2020a). Filling this gap in the invasion literature could also be beneficial to attract the attention of the non-academic actors (stakeholders, industry, and the general public), as recommended in the assessments of the Intergovernmental Platform for Biodiversity & Ecosystem Services (IPBES, Elbakidze et al. 2018). Since the first estimations of economic costs of invasive alien species at large spatial scales by Pimentel et al. (2005), other studies have attempted to increase this knowledge (e.g., Scalera et al. 2010; Paini et al. 2017). However, available data remain scattered, and approaches remain methodologically questionable (Cuthbert et al. 2020).

To date, previous studies have suggested very high economic costs, i.e. damage and losses (e.g., damage repair, medical care, value of crop losses) incurred by an invasion, or means dedicated to understand or predict (research), prevent (education, biosecurity), early detect (monitoring, surveillance) and/or manage (control, eradication) invasive alien species. For instance, the global cost averages at about US$ 76 billion per year globally for invasive insects (Bradshaw et al. 2016). In Europe, economic costs caused by invasive alien species were extrapolated at about 2017 US$ 14 billion per year (Kettunen et al. 2009). In aquatic ecosystems, cumulated costs had reached at least US$ 23 billion in the year 2020 (Cuthbert et al. 2021). Yet, detailed and thorough assessments of such costs at the national level are still lacking for most countries, while the country scale is often the first level of action regarding the management of biological invasions. In particular, France is highly impacted by the presence of invasive alien species, with a long history of global trade and tourism that has greatly favoured the introduction of non-native species. Currently, a conservative minimum of 2,750 introduced and invasive alien species with accepted names (as recorded on September 24th, 2020 in GRIIS; Pagad et al. 2018; Thevenot et al. 2020) have been recorded from metropolitan France. This large list of non-native records likely results from several concomitant factors. First, the central geographic position of France is unique, comparatively with the other countries of the European Union: France has frontiers with five other countries, coastlines on three different seas or oceans, and overseas territories distributed all over the world. This situation enhances the possibility for substantial national and transnational traffic from regions and countries hosting different native species. Second, France has the 7th highest gross domestic product worldwide (The World Bank, https://www.worldbank.org/), is the 7th largest importer of goods (World Trade Organization, https://www.wto.org/), is ranked 10th for transportation of persons and even ranked 1st in 2018 in terms of international tourist arrival (World Tourism Organization, UNWTO, https://www.unwto.org/). France welcomes over 80 million tourists annually (more than its own population) from all continents. Both trade of goods and transportation of people are known to increase biological invasions and their costs (Hulme 2009; Gippet et al. 2019; Essl et al. 2020; Haubrock et al. 2021a). Third, as is the case in general in Europe, the legislation concerning biological invasions in France is inadequate to slow down the flux of introductions of species (Caffrey et al. 2014). For example, there is no restriction of living species transportations from/to the many overseas territories.

In this context, a general overview of the monetary losses and expenditures associated with invasive species is urgently needed for France. This national cost assessment would be particularly important to fully capture the complex and diverse nature of costs incurred by biological invaders. To that aim, we synthesised for the first time the economic costs of invasive alien species in France (Metropolitan France and French overseas) over a large time range. Then, we calculated the total economic costs caused by invasive alien species in France, and, using annualised cost values, examined how these costs have evolved over time. To obtain a comprehensive insight on the nature of the monetary impacts, we then examined the repartition of costs among different economic sectors and across French regions. Finally, we identified the distribution of economic costs across taxonomic groups of invasive alien species, and established a list of the costliest invasive alien species in France.

Material and methods

Data collection, compilation and filtering

To estimate the costs of biological invasions in France, we benefited from the InvaCost initiative (Diagne et al. 2020a, b) that compiles the most comprehensive and up-to-date information on the economic costs of invasive alien species worldwide. Data collection was mainly based on systematic literature searches, complemented by both opportunistic and targeted data collection through contacting experts and stakeholders. One of these searches targeted cost data in non-English languages, such as French (Angulo et al. 2021a), and is detailed below. All cost information retrieved were assembled in a common database structured following the descriptive columns of the InvaCost database (see 'Descriptors' file available at https://doi.org/10.6084/m9.figshare.12668570 for a complete description of the descriptive fields considered). Thus, each cost entry refers to a unique cost value with specific descriptors (columns) about the document reporting the cost, the spatial and temporal information of the cost, the taxonomy of the species causing the cost and the typology of the cost (see Suppl. material 1 for details on the descriptors used in this manuscript). As cost entries were obtained from different years and currencies, all costs were standardised to a unique and common currency, i.e. 2017 equivalent US dollars (US$) using official market exchange rates and taking into account the inflation since the year of cost estimation (see Diagne et al. 2020b for complete details about formulas and calculations associated with the cost standardisation, as well as Diagne et al. 2020a for a detailed description of the different steps of the construction of the InvaCost database). The latest version of this updatable database (9,823 cost entries), along with all related details and associated information, is fully accessible and openly available online (version 3.0; https://doi.org/10.6084/m9.figshare.12668570).

The InvaCost version 3.0 incorporates the cost data we collected when specifically searching for costs of invasive alien species in France. Indeed, we performed a double-stage strategy for collating more cost information for our study. First, monetized impacts of invasions were collected by screening the available literature containing invasion costs in the research engines Web of science and Google scholar. The topic search was restricted to the literature published in either English or French, with no timespan restriction. Second, we gathered additional – often unpublished – cost estimates from active communication efforts with conservation managers and practitioners to collect information that we may have missed with more traditional searches. Specifically, we (*i*) directly contacted the French coordinator of IUCN (International Union for Conservation of Nature), the French Invasive Alien Species Resource Center ("*Centre des Ressources Espèces Exotiques Envahissantes*"), the National Botanical Conservatory ("*Conservatoire Botanique National"*), the Conservatories of Natural Spaces ("*Conservatoires d'Espaces Naturels"*) and their federation; and (*ii*) circulated a request among managers from French reserves and protected territories in order to collate specific cost data from these areas.

For the analyses, we filtered the InvaCost version 3.0 by the "Official country" descriptor to get the entries corresponding to France (Suppl. material 1). We carefully checked the data, identifying potential mistakes or double counting. Finally, we refined the data by excluding all cost entries deemed as less reliable from the database (i.e. assigned 'low' in the "Method reliability" column; Suppl. material 1), as well as those cost entries with partial temporal information. We restricted the temporal interval to the end of 2018, as it was the last year for which we had economic costs. After these filtering steps, our final dataset for France contained 1,118 entries for the 1993–2018 time period.

Total and annualised economic costs

Cost information could be reported for a single year in some documents, while it was occurring over several successive years in other studies. Therefore, we expanded the assembled French dataset to standardise all cost entries to yearly estimates using the *expandYearlyCosts* function of the *invacost* R package (Leroy et al. 2020). This function uses the original information about the time range, i.e. columns reporting the probable starting and ending years of each cost entry included in the database, to derive annual costs. This resulted in a total number of 1,583 annualised cost entries. We thus estimated both total and average annual costs by, respectively, totalling the annual costs of a given period of time (i.e. total costs), and then divided them by the number of years of this period of time (i.e. annual costs). We calculated the temporal trends of the invasion costs in France by using the function *summarizeCosts* in the Invacost package version 1.0 (Leroy et al. 2020) in R version 4.0.2 (R Core Team 2020), which allowed the calculation of mean annual cost between 1993 and 2018, providing averages in 4-year periods throughout the study period.

Description of impacted sectors and costliest species

To describe the patterns of invasive alien species costs in France, and their impacts on different sectors, we used different descriptors of the cost entries. First, we focused on the type of costs (column "Type of cost merged") which categorises the cost reported as: 'Damage' referring to damages or losses incurred by the invasion (e.g., costs for damage repair, resource losses, medical care), or 'Management' comprising expenditure such as control, monitoring, prevention, or eradication of invasive alien species. For the analyses pertaining to these cost categories, we classified as 'mixed' the cases where the specific nature of the reported costs was unclear, i.e. when it was not possible to separately attribute monetary values to either damages or management of invasive alien species. Second, we explored socio-economic sectors (column "Impacted sector"), which were classified into seven major categories reflecting the main activity, societal or market sectors impacted by costs (see Suppl. material 2 for a full description of the impacted sectors that are considered in the InvaCost database).

For the distribution of costs among taxa, we used the taxonomic information as reported in the InvaCost database. However, to understand how the different socio-economic sectors were impacted by invasive alien species, we also applied taxonomic groupings in combination with environment of the invasive species causing the cost (e.g., "terrestrial mammal", "aquatic arthropod", "semi-aquatic bird"). The list of environment-taxonomic groupings is available in Suppl. material 3.

To provide an InvaCost-based list of the costliest invasive species currently documented in France (i.e. those that had economic impacts exceeding US$ 1 million in the period 1993–2018), the "Species" column was reclassified (i) to merge costs assigned to multiple species within the category diverse/unspecified, and (ii) to aggregate by genus all species with cost estimates provided at both the species and the genus level (i.e., *Impatiens glandulifera* and *Impatiens* spp.; *Ludwigia grandiflora*, *L. peploides*, *Ludwigia* spp., and *Ludwigia* sp., *Rattus norvegicus*, *Rattus* sp. and *Rattus* spp.; and *Reynoutria japonica* and *Reynoutria* sp.). Then, the geographic origin of the costliest invaders was collected from the Global Invasive Species Database (GISD 2020) and from the GRIIS (Pagad et al. 2018). Data were filtered and only 'observed' (incurred) costs were used for all these analyses; 'potential' (expected) costs (column "Implementation", Suppl. material 1) were thus excluded.

Regional mapping of economic costs

To present a regional mapping of economic costs incurred by invasive alien species in metropolitan France and French overseas territories, data were filtered per region (column "Location", Suppl. material 1), and only observed costs were selected (column "Implementation", Suppl. material 1). The cost entries corresponding to multiple regions or with unspecified invasive alien species were removed from this analysis. Then, for each French region and French overseas, we mapped the total costs and the associated number of invasive alien species causing these costs.

Estimation of the cost of invasive alien species with no recorded cost in France

We also provide a coarse approximation of the potential costs of invasive alien species known to occur in France, but without cost data for France in InvaCost version 3.0, with a two-step extrapolation procedure based on available data. First, to identify the species reported from France that have no cost data, we collected (i) 2,750 introduced and invasive species with accepted scientific names from the GRIIS (Suppl. material 4, which also presents the distribution of species per taxonomic groups; Pagad et al. 2018;

Thevenot et al. 2020), (ii) 254 invasive alien species listed in GISD, and (iii) 630 alien taxa documented from French overseas territories (Soubeyran et al. 2015), of which some are also non-native in metropolitan France. We merged this information, and after having removed duplicated species and subspecies, we obtained a total of 2,621 introduced and invasive species occurring in France. From this list, we identified the species for which we had economic costs in InvaCost version 3.0: 67 species with both observed and potential costs, and 63 species with only observed costs. We used these species with economic cost data for both France and the world, to establish a linear regression model of the cost in France as a function of cost worldwide (all costs were log-10 transformed). Finally, we used this relationship to provide a coarse extrapolation of costs to the species known to occur in France, with cost data worldwide in Invacost 3.0, but for which we had no cost information in France.

Data analysis

All analyses were conducted in R 4.0.2 (R Development Core Team 2020). We used the invacost R package (Leroy et al. 2020) for all cost estimations (see above).

Results

Cost data collected

In a first step, the InvaCost database reported initially only 28 cost entries from 16 English-written articles. Then, our complementary search made using French as a language (Angulo et al. 2020) in the Web of Science and Google Scholar returned 26 papers mentioning economic costs caused by invasive alien species in France. Yet, only four articles, representing 14 cost entries, reported monetary cost values. In a third step, our efforts to personally contact experts allowed us to collect a high quantity of new cost information (1,106 cost entries from 39 documents written in French as of September 1st, 2020). In total, we obtained 1,583 annualised cost estimates, corresponding to 98 invasive alien species.

Overall costs and temporal trend

Invasive alien species incurred a total amount of US$ 11,535 million in France over the period 1993–2018, with an average of US$ 444 million annually (Figure 1A). The highest costs were documented in the time range 2009–2012 (ca. US$ 4,172 million, corresponding to US$ 1,043 million annually). A large part of the reported costs of invasive alien species for France were not empirically observed, i.e. they were obtained from extrapolations of the potential cost should these invasive alien species further invade favourable habitats/regions. Hence, the costs actually observed amounted up to US$ 1,280 million for the 1993–2018 time period (average annual: US$ 49.2 million) (Figure 1A).

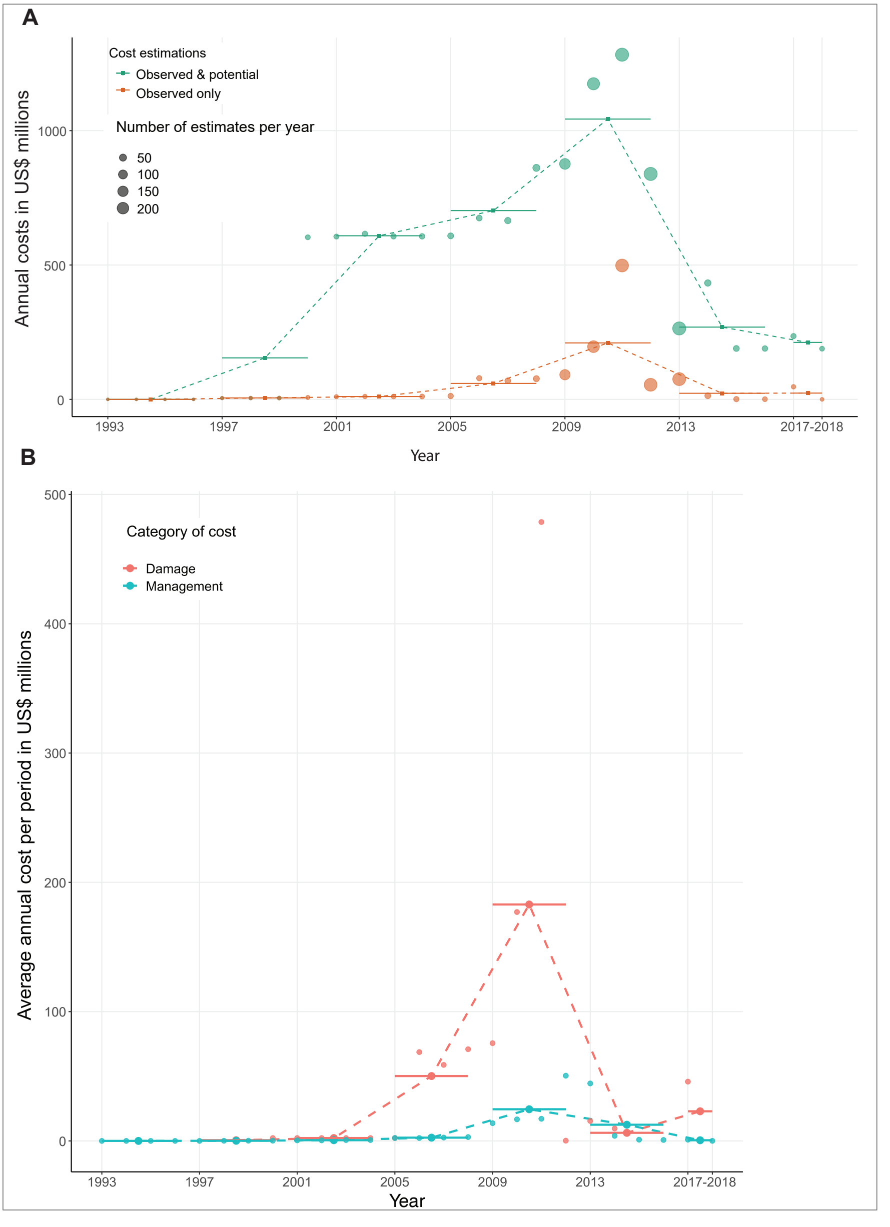

Figure 1. Presentation of the costs incurred by invasive alien species in France over the period 1993–2018 **A** total cost values (in 2017 US$) per year of invasive alien species in metropolitan France and French overseas territories. The reported amounts are calculated from observed costs (orange), or from both observed (i.e. incurred) and potential (i.e. predicted to occur) costs (green). Each point represents the cumulative cost for a given year; the size of each point is proportional to the number of estimates for that year. Average annual costs for 4-year periods are represented by squares and horizontal solid lines; dashed lines connect the average annual costs across these 4-year periods **B** temporal changes in observed costs (2017 value) for 'Damage-Loss' (simplified as Damage in the figure legend) vs. 'Management' (control, monitoring, prevention, management, and eradication of alien invasive species) costs.

The number of cost entries per year was also the highest in this period (2009–2012), ranging from 168 to 283 entries per year. There were only 13 costs reported before 2000, and these documents only reported low cost values. The temporal trend in costs suggested that costs continuously increased from 1993 to 2012, and decreased afterwards. This decrease after 2012 is, however, concomitant with the decrease in the number of reported cost estimates and indicative of a time lag in cost reporting (see Suppl. material 5).

Nature of the costs and impacted sectors

As most of the costs started to be reported from the early 2000s in France, the paucity of information makes it impossible to obtain a comprehensive picture of how damage and management costs impacted the different sectors over time. Before 2000, it can only be mentioned that costs corresponded to damage and loss only, without any management expenditure. From 2000 to 2018, observed damage costs were almost always higher than observed management costs. For the most complete time period (2009–2012), observed damage costs were in general characterised by amounts 7–8 times higher than those observed costs documented for management, totalling to US$ 732million for 'Damage-Loss' costs vs. US$ 98 million for 'Management' costs (Figure 1B).

Four activity sectors were mainly impacted by invasive alien species in France over the time range (1993–2018) from which cost information was obtained: Health (US$ 324 million; cumulative cost), Agriculture (US$ 258 million) and Authorities and Stakeholders (US$ 230 million) (Figure 2, Suppl. material 6). A fourth, mixed category (i.e., several sectors impacted together) was higher than the three above specific activity sectors (US$ 425 million). We also found that each sector category could be affected by different groups of invaders (Figure 2). Semi-aquatic arthropods often had large impacts on a combination of sectors, as suggested by their large impact on the "Mixed" category (Figure 2). Costs to Agriculture and Health sectors were mostly caused by terrestrial forbs, whereas Authorities and Stakeholders were impacted by a diversity of invaders.

Regional mapping of economic costs

The reported economic costs and the number of associated species greatly varied among the different French regions, both metropolitan and overseas (Figure 3). Over the period 1993–2018, the regions with the lowest numbers of species and cumulative cost (< 10 species and < US$5 million) were the northernmost regions (Grand Est, Ile de France, Hauts de France and Normandie). Auvergne-Rhône-Alpes and La Réunion were the regions with the highest cumulative costs (US$238 million and US$137 million, respectively) and had the highest number of invasive species with costs. Provence Alpes Côte d'Azur, Bretagne, Pays de la Loire, Nouvelle Aquitaine and New Caledonia had more than 15 invasive species with costs, and a cumulative cost ranging from US$5 to US$100 million. For each region, the listing of the genus / species for which we had cost information is available in Suppl. material 7.

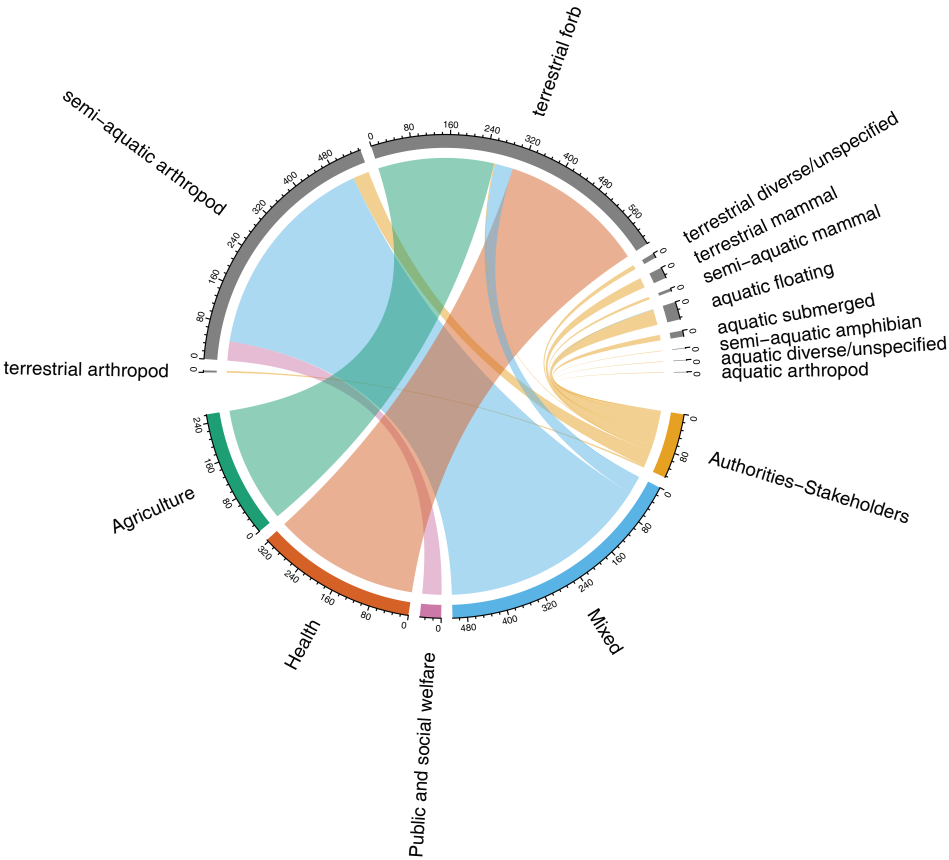

Figure 2. Cumulative costs (in 2017 US$ million) incurred to each sector per major group of invaders in France in the period 1993–2018. The "Mixed" sector indicates that two or more sectors were economically impacted by invasive alien species. Note that diverse/unspecified groups of invaders were excluded, as well as groups of invaders whose cumulative impact was less than US$ 1 million over the duration of the period (1993–2018).

Taxonomic group distribution and costliest species

The analysis of economic costs across taxonomic groups revealed that invasive alien plants and invertebrates accounted for most of the reported costs in France (Figure 4, Suppl. material 6). For plants, the great majority of the costs was attributed to the Magnoliopsida class, totalling US$ 8,421 million in terms of potential costs, and US$ 664 million for observed costs (Figure 4A, B); it included the 18 following plant taxa: *Acacia mangium*, *Acer negundo*, *Ambrosia artemisiifolia*, *A. polystachya*, *Baccharis halimifolia*, *Crassula helmsii*, *Elaeagnus angustifolia*, *Flemingia strobilifera*, *Ludwigia* spp., *Miconia calvescens*, *Myriophyllum aquaticum*, *Opuntia rosea*, *Prunus serotina*, *Reynoutria* spp., *Robinia pseudoacacia*, *Rhododendron ponticum*, *Rubus alceifolius* and

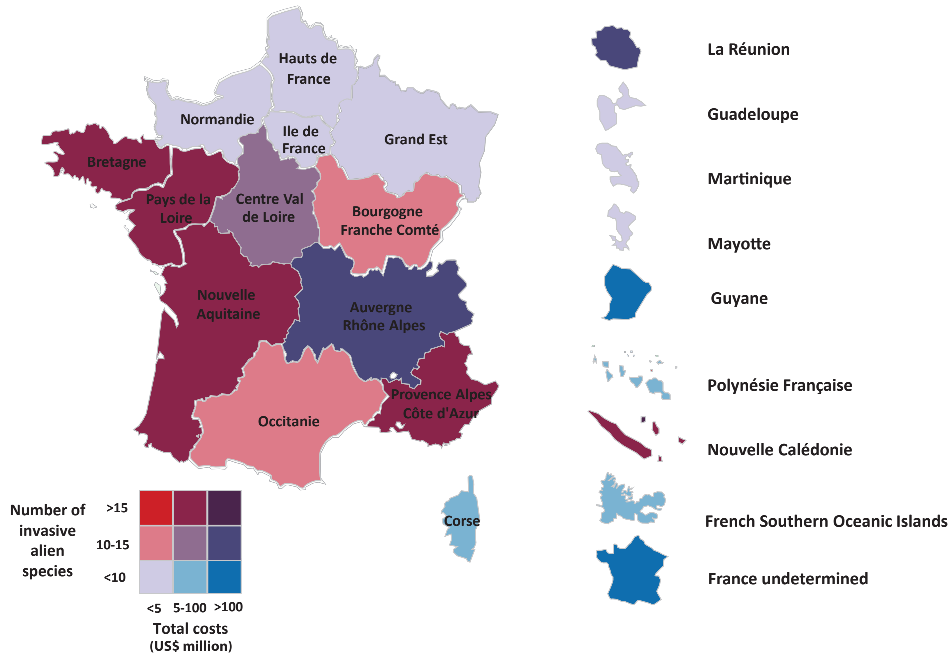

Figure 3. Gradient map of the cumulated numbers of invasive alien species and of total economic costs (US$ million) recorded from each region of metropolitan France (and French overseas territories on the right) over the period 1993–2018. When the impacted region of the cost was not specified, it was mapped as 'France undetermined'.

Table 1. Listing of the costliest invasive alien species in France (> 1 million in observed cumulated costs).

Species/Genus	Common name	Sum of cost US$2017	Geographic Origin
Ambrosia artemisiifolia	Common ragweed	551 261 394	North America
Aedes aegypti	Yellow fever mosquito	333 089 505	Africa
Aedes albopictus	Asian tiger mosquito	128 523 816	Asia
Ambrosia polystachya	Cuman ragweed	70 588 450	South America
Ludwigia spp.	Water primrose	35 226 942	America
Rusa timorensis	Javan rusa	8 300 398	Asia
Rattus spp.	Rats	2 811 942	Asia
Vespa velutina	Yellow legged-hornet	2 588 307	Asia
Reynoutria spp.	Knotweed	2 090 356	Asia
Lagarosiphon major	African elodea	1 605 914	Africa
Lithobates catesbeianus	American bullfrog	1 594 127	North America
Procambarus clarkii	Red swamp crayfish	1 394 047	North America
Felis catus	Feral cat	1 258 480	Africa
Baccharis halimifolia	Eastern baccharis	1 104 942	North America

Saururus cernuus. For invertebrates, most of the cost entries were attributed to insects, totalling US$ 890 million for potential and observed costs, and US$ 466 million for observed costs (Figure 4A, B); these costs were incurred from the nine following insect species: *Aedes aegypti*, *Ae. albopictus*, *Anoplolepis gracilipes*, *Anoplophora glabripennis,*

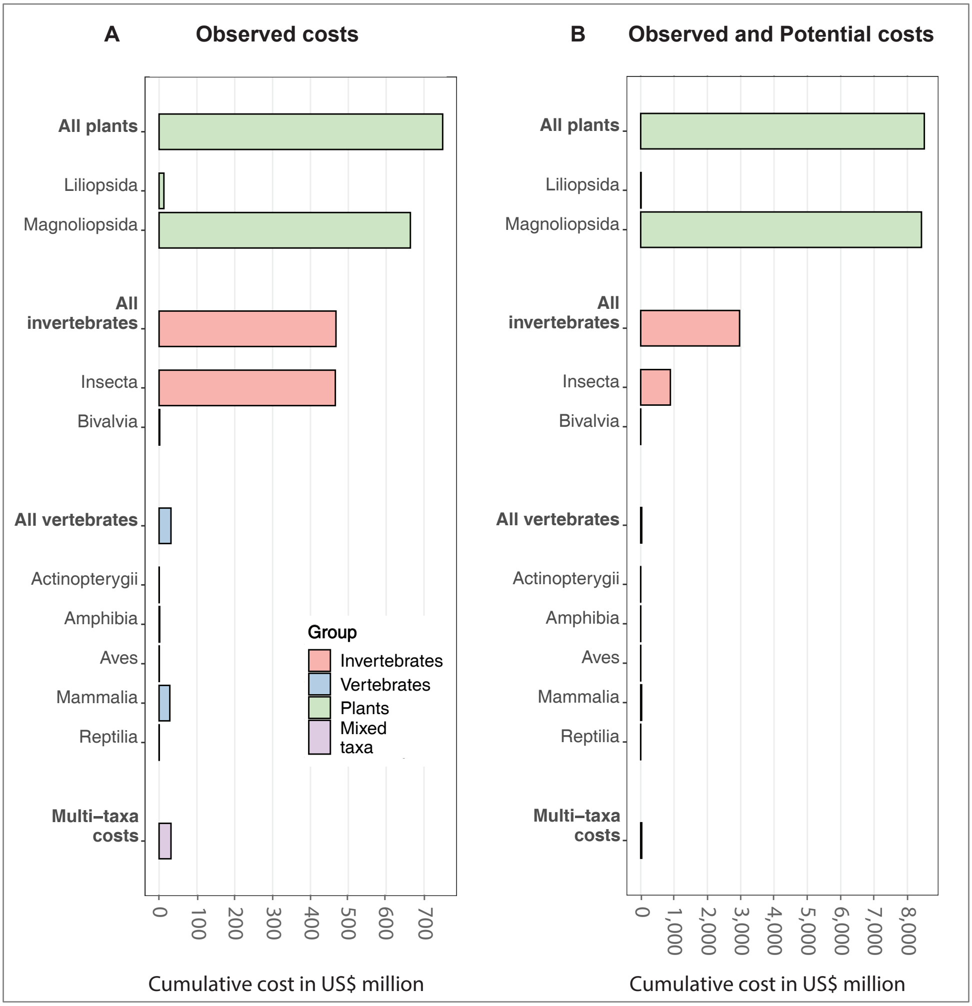

Figure 4. Cumulative costs (in 2017 US$) by taxonomic groups of invasive alien species in France over the time range 1993–2018 for **A** observed cost amounts and **B** both observed and potential costs. The "Multi-taxa costs" group refers to entries that presented costs without separating the different taxa.

Apis mellifera, *Brontispa longissima*, *Bactrocera tryoni*, *Vespa velutina* and *Wasmannia auropunctata*. Little cost information was found for vertebrates in metropolitan France and French overseas territories.

The costliest invasive alien species in France are presented in Table 1. They include four invertebrates (*Ae. aegypti*, *Ae. albopictus*, *V. velutina*, *Procambarus clarkii*), four vertebrates (*Felis catus*, *Lithobates catesbeianus*, *Rattus* spp., *Rusa timorensis,*) and six plants (*A. artemisiifolia*, *A. polystachya*, *Baccharis halimifolia*, *Lagarosiphon major*, *Ludwigia* spp., *Reynoutria* spp.); these species originate from all continents except Europe and Oceania (Figure 5).

Figure 5. Representation of the geographic origin of the costliest invasive alien species in France over the period 1993–2018 (all those >1 million in cumulated cost). Some of the costliest invaders have multiple continental origins. The coloured bar on the right part of the figure shows the number of species for each continental area (North and South Americas, Arctic, Africa, Europe, Asia, Oceania). See Table 1 for the names of the costliest invasive taxa in metropolitan France and French overseas.

Estimation of the potential costs for species which cost information is missing in France

We found that costs in France represent a small proportion of worldwide species costs, weakly increasing with the global cost value (observed and potential costs:

$$cost_{France} = 0.172 \times cost_{(Global–France)} + 3.500;$$

observed costs only:

$$cost_{France} = 0.163 \times cost_{(Global–France)} + 3.462).$$

We used these relationships to make a first extrapolation of the costs of species known to occur in France, with cost data available worldwide, but no recorded costs in France, which resulted in an estimation of an additional US$ 3,030 million for both observed and potential costs, and US$ 151 millions when only considering observed costs.

Discussion

Based on 1,583 records for 98 invasive alien species, we found that biological invasions incurred a total cost ranging between US$ 1,280 (only observed, incurred costs considered) and 11,535 (observed and potential costs) million in France over the period 1993–2018. These values are likely underestimated since we considered only highly reliable costs and cost data were missing for the vast majority (97.6%) of invasive species in France. If we add to these numbers our coarse extrapolations of missing cost data, the total cost would range between US$ 1,431 million (only observed costs) and 14,565 million (observed and potential costs). However, even these rough extrapolations still do not account for over 90% of the species invading France, for which there is no cost information whatsoever. The highest recorded costs correspond to the period 2009–2012, and overall most were damage and loss costs, with relatively few costs corresponding to management expenditures. Many regions had very little information on economic costs of biological invasions, whether in metropolitan France or in French overseas territories. The fractionary nature of the existing data pointed to aquatic insects (mosquitoes, in particular *Aedes* sp.) and terrestrial forbs (non-graminoid herbaceous flowering plants, in particular *Ambrosia* sp.) as belonging to the costliest invasive alien species in France, both severely impacting the human health sector. Yet, many more species had high costs in different sectors.

The economic costs incurred by invasive alien species in France greatly increased in the period 2009–2012. We suggest that the increasing consideration of biological invasions in France and elsewhere in the past years (decades), and the improved awareness of invasive species and biodiversity, may have contributed to explaining this pattern. In particular, the 'Delivering alien invasive species in Europe' initiative over the period 2002–2006 (DAISIE 2009), the development of GRIIS by the Species Survival Commission of the International Union for Conservation of Nature in 2006, the Aichi Biodiversity Target 9 for the period 2011–2020 (https://www.cbd.int/sp/targets/rationale/target-9/), and the European report published by Kettunen et al. (2009) may have significantly contributed to raising awareness of the ecological and economic burdens caused by invasive alien species. The emergence of these influential initiatives may have subsequently motivated the community to collect and publish information on invasive alien species costs. The decrease of recorded costs after 2012 is at least in part due to the time lag between occurrence of a cost, its record and its publication.

A large majority of the economic costs caused by invasive alien species in France are related to damages and losses. Regarding damages and losses, infrastructures and recreational activities were frequently reported as some of the sectors impacted by invasive alien species. As already reported in other countries, biological invasions can greatly interfere with recreational activities in France (Legrand 2002), especially in water bodies where, for instance, fishing or canoeing are practised; yet, these costs were not reported from several French regions where they are most probably occurring. Agriculture and Health were by far the most impacted sectors in France, followed by Authorities-Stakeholders (surveillance, prevention, control, and education), within which management costs were most often associated and of high reliability (Sarat et al. 2015a, Sarat et al. 2015b; Sarat et al. 2019). Agricultural, industrial or recreational losses, seem less straightforward to accurately estimate, most probably because of their intertwined relationships with several other confounding factors, but also because the invasive status species is not always specified in these sources (e.g. for "pests"), and may thus have been missed by our searches. For example, the lack of cost data of invasive insects on the agricultural sector is surprising given their known costs worldwide

(Bradshaw et al. 2016), and suggests a gap or bias in the reporting of their economic impacts in France. Recent research on invasive ants corroborates this hypothesis, suggesting a total cost over US$ 45 million for France (Angulo et al. 2021b).

In this study, non-graminoid terrestrial flowering and aquatic plants totalled the highest economic costs followed by invertebrates, and more particularly insects. Five plants totalling a large proportion of the costs: *Ambrosia* spp., *Ludwigia* spp., *B. halimifolia*, *Reynoutria* spp., and *L. major*. Ambrosia and Ludwigia were also among the most costliest species in Europe (Haubrock et al. 2021a). Pollens produced by the different *Ambrosia* species, and more particularly by *A. artemisiifolia*, cause allergies to humans (Chen et al. 2018). In France, populations from the Auvergne-Rhône-Alpes region are particularly threatened by the pollens produced by *Ambrosia* spp., and pollen sensitivity of the inhabitants is increasing (from 5% in 1980 to about 13% in 2014; ORS Rhône-Alpes 2017). In Europe, the estimated health costs from treating pollen allergies have reached US$ 8.3 billion annually (Schaffner et al. 2020). As predictive studies suggest that the numbers of inhabitants sensitive to *A. artemisiifolia* pollens should be at least doubled in France by 2041–2060 (Lake et al. 2017), it is likely that medical care costs will significantly rise in this country if mitigation measures aimed at limiting the proliferation of *A. artemisiifolia* are not further increased.

The curly waterweed *L. major* was introduced for aquariophilie and was first observed outdoors in France after the Second World War. By quickly forming very dense beds in ponds and lakes, this submergent plant has strong ecological (extirpation of native hydrophytes, accelerated sedimentation, enhanced transparency of the water), recreational (boating activities, fishing) and industrial (hydroelectric plants) impacts. As part of the invasive alien species list of EU concern (Roy et al. 2014), preventive measures are established to avoid new introductions of *L. major* in the EU, including France, and management plans are implemented for preventing its proliferation. Consistently, our study revealed that in many instances, available costs were related to harvesting of *L. major*, be it mechanised or manual, to labour costs, and to the cost of storage and destruction of this plant, which has 495 occurrences in France (over 3,102 occurrences worldwide; GRIIS, Pagad et al. 2018). Because manual or mechanical harvesting can cause propagation of invasive macrophytes, increased investment in biosecurity is warranted to prevent secondary spread (e.g. Crane et al. 2019). A similar observation can be raised for *Ludwigia* spp., also listed as an invasive alien species of EU concern due to its high ecological and socio-economic impacts (Thouvenot et al. 2013). In our study, all of the costs of *Ludwigia* spp., but one, were related to Authorities-Stakeholders, with more than 90% of the costs being associated with the management of this species.

Following plants, invertebrates (and in particular Insects) constitute the second costliest invasive alien taxonomic group in France. Among them, members of the Culicidae family, including the Asian tiger mosquito *A. albopictus* and the yellow fever mosquito *A. aegypti*, represent growing threats to human populations, due to being harmful mosquitoes swarming in both urban and peri-urban landscapes (Darriet 2014). Females of *A. albopictus* play a significant role in the transmission of many pathogens, and this results in a strong threat to the public health system (Schaffner et al. 2013). Vega-Rua et al. (2013) showed that this species was particularly efficient in transmitting chikungunya and dengue in the southeast of France, and can also harbour and transmit yellow fever virus (Amraoui et al. 2016). The *Aedes* genus has also been shown to cause the greatest costs of all aquatic and semi-aquatic taxa (Cuthbert et al. 2021). In this study, we found that monitoring, surveillance prevention, research and control costs reached ca. US$ 62 million in France over the period 2009–2013 for *A. albopictus*, and US$ 48 million for *A. aegypti* in the same time range. Wittmann and Flores-Ferrer (2015) previously reported that 55% of the costs related to invasive alien species in France in 2013 were related solely to *A. albopictus*, with the number of cost data growing over the period they studied (76 cost entries in 2009 for *A. albopictus*, 81 in 2010, 101 in 2011, 144 in 2012, and 133 in 2013). Yet, the direct medical costs resulting from the expanding populations of vector mosquitoes remain poorly documented. High costs for Aedes species were expected in the French territories located in the Americas (French Guiana, Martinique and Guadeloupe), as these species were also the costliest species in the Central and South America region and in specific countries therein such as Ecuador or Argentina (Ballesteros-Mejia et al. 2021; Duboscq-Carra et al. 2021; Heringer et al. 2021). For these French territories in the Americas, Uhart et al. (2016) documented 4,574 hospitalisations of approximately 4.3 days each for patients affected by dengue, with a mean cost per stay of US$ 2,849. These monetary values are, however, region-dependent, and thus cannot be used for obtaining accurate estimates of the economic impacts of the species in other regions. As an illustration, the direct medical cost per person (hospitalisation, diagnosis, specialised services, drug usage and medical supplies) from dengue fever was about US$ 48.10 per dengue episode in Vietnam (Vo et al. 2017), US$ 307 in Central America and Mexico, and US$ 3,154 in North America (Shepard et al. 2011). Also, we highlight that many costs incurred by invasive alien vectors have not been recorded or monetised (for instance, lost income of hospitalised patients). Finally, as global warming is rapidly boosting the fecundity, development, survival rate and the frequency of blood meals of hematophagous insects, and hence the intensity with which they transmit pathogens (Ryan et al. 2019; Iwamura et al. 2020), the geographic expansion of vector-borne disease insects in France should be considered urgently. In Corsica for instance, there remains a major reintroduction risk of *Plasmodium falciparum* with the presence of populations of *Anopheles labranchiae* on the island (this species is native to northern Africa and vector of the most serious form of malaria, Toty et al. 2010). Given this background, and despite the continuous expansion of *Aedes* sp. in France and Europe, and the massive medical costs they cause, it is surprising that these insects have remained absent from the European list of invasive alien species of concern to the EU (Roy et al. 2014; Consolidated version of the Union list 2019: https://ec.europa.eu/environment/nature/invasivealien/list/index_en.htm).

In the context of global warming, another alien insect species could further expand its range in France, and could potentially have huge monetary impacts: the pinewood nematode *Bursaphelenchus xylophilus*. As several entries corresponded to potential costs for this species in InvaCost, and because we worked with entries of high reliability only, relatively low costs are reported from the pinewood nematode in France in our work. Meanwhile, Soliman et al. (2012) suggested that the species could be distributed in the southern part of France, as well as in Bourgogne, Poitou-Charentes, Aquitaine, Midi-Pyrénées, Limousin, Rhône-Alpes, Provence-Alpes Côte d'Azur and Auvergne, with potential huge direct impacts varying from US$ 18 to 102 per km² of infested pinewood, depending on the considered region. Globally, these authors projected US$ 14.08 billion in damage costs of pinewood nematode *B. xylophilus* in forests in Spain, France and Italy, should the species not be contained. These were not considered in our national estimate, but constituted 99% of the costs in Spain if potential costs were included (Angulo et al. 2021c); a similar amount of annual losses was estimated in Russia (Kirichenko et al. 2021)

The Asian hornet, accidentally introduced in southwestern France in 2004, is the second costliest insect genus (after *Aedes* sp.) in France. This species has colonised urban, agricultural and forest areas, and continues its expansion throughout Europe (Monceau et al. 2014). The Asian hornet has severe impacts on beekeeping and pollination services provided by domestic bees on which it predates (Rome et al. 2011). A study dedicated to the monetary cost of the control of *V. velutina* suggested a US$ 26 million cost for the destruction of nests in France from 2006 to 2015, and mentioned that this cost could increase by US$ 13.4 million per year due to the expansion of the species (Barbet-Massin et al. 2020). Yet, this study had no data to report on the probable high costs to beekeepers or to decreased pollination due to the hornet's predation on wild and domestic pollinators. Given that the apiculture revenue was € 135 million in France (corresponding to 2017 US$ 152.5 million) (Barbet-Massin et al. 2020) and the yearly pollination services to agriculture were estimated at € 2 billion in France (2017 US$ 2.26 billion) (Gallai et al. 2009), the actual economic impact of the Asian hornet is probably massive. The high costs found for France are very similar to the costs found in Spain for the same species (US$ 5.33 billion; Angulo et al. 2021c).

Overall, our study revealed very high economic costs of biological invasions, and yet, they remain very conservative, for several reasons. First, we remained conservative here and used only highly reliable cost entries. Second, many existing costs are simply unknown, or unreported, because the scientific literature reporting the economic consequences of biological invasions is still in its infancy in France, as evidenced by the 3% of currently introduced or invasive species having cost entries in InvaCost in France (Diagne et al. 2020b, Angulo et al. 2020). Out of the 2,621 invasive species in total, the remaining 97% of species likely represent a very high additional cost, as shown by the high extrapolations derived for invasive alien species invading France but with known costs only outside France. During our literature search, we also observed that a large number of studies (22 out of 26) stated that invasive alien species have monetary impacts in France, without supplying cost information or referring to published material reporting these costs. Third, monetising the costs remains a difficult task, and we found that pricing the effects of invasive alien species was often achieved by different ways (e.g., costs based from direct observations, estimations, models, extrapolations,...) (Diagne et al. 2020a; Angulo et al. 2021a), with all of these procedures being challenging to synthesise. Fourth, access is probably one of the major hurdles, as cost information exists in relatively large amounts of (a) unpublished and not publicly available documents, (b) documents not published in English, and (c) documents aggregated by non-academic entities. In France, it is especially difficult to obtain cost values because of the large diversity of entities running investigations on alien species and the diversity of protection designations for terrestrial and aquatic areas (Guignier and Prieur 2010).

As reported elsewhere (e.g., IUCN 2018), direct contacts with academic and non-academic actors had here too proven the most efficient means of retrieving cost information, and partially resolved the issue of the paucity of publicly available cost information. By using phone calls, e-mailing, and by circulating questionnaires, we have been able to collect the majority of cost information (1,106 cost entries collected from 39 documents, as compared with 26 cost entries with the classical InvaCost Database search), revealing that even if cost data were poorly documented in France and overseas territories, those data do exist as grey literature. High percentages of non-English costs were also reported in other countries, such as in Spain or Japan (98%, Angulo et al. 2021c; and 100%, Watari et al. 2021, respectively), and this percentage was lower but also important in countries such as Germany or Ecuador (69%, Haubrock et al. 2021b; 52%, Ballesteros-Mejias et al. 2021) or in general in the Central and South America continent and in Asia (Heringer et al. 2021; Liu et al. 2021). In line with the recent suggestion from Blackburn et al. (2020), this observation proves that academics must continue their engagements towards a more collaborative science for improving the sharing of knowledge and having adequate communication of invasion science findings to the public (Mattingly et al. 2020), and ultimately an ability to better tackle the issues caused by invasive alien species.

The paucity of literature reporting the monetary impacts of invasive alien species in France is problematic, as it results in decision-makers failing to be convinced at local and national levels of the need to make investments towards improving our understanding of ecological and economic impacts linked with invasion. The absence of more quantitative studies on costs is startling, as many introduced populations present very serious risks to public health in France, including the allergenic common ragweed and the irritant giant hogweed (*Heracleum mantegazzianum*), both of which mobilize significant economic resources for their control (Sarat et al. 2015a, b) and for medical care (Schaffner et al. 2020). Some years ago, the overview published by Mazza et al. (2014) summarised the different threats posed by invasive alien species to human health, reemphasising the crucial need for stringent policies to reduce invasion-driven health effects. Our study points out the crucial need for considering invasive alien species costs more generally, i.e. not only the species having health impacts or being listed as invasive alien species of union concern, to reveal and address the significant burden invasive alien species have on the economy in France and beyond.

Conclusion

Our knowledge of the ecological effects of invasive alien species is progressing constantly (Laverty et al. 2017; Cuthbert et al. 2019), and results in frequent warning of the deleterious effects they cause on biodiversity and human societies (e.g., Simberloff et al. 2013; Pyšek et al. 2020). Climate change is additionally enhancing the geographic expansion of aliens (Bellard et al. 2013; March-Salas and Pertierra 2020), in turn increasing their role as drivers of biodiversity decline (Butchart et al. 2010; McGeoch et al. 2010; Lebouvier et al. 2020). The increased scientific awareness and communication of the negative effects of alien species on biodiversity and ecosystem services have fostered their consideration by a wide array of actors, and a complete and robust assessment of economic costs was hitherto missing. In this study, we provided the first synthesis on the economic costs incurred from invasive alien species to the French economy. We report alarming costs and even more alarming knowledge gaps. The growing number of invasive alien species in France, while budgets dedicated to their management remain very low, has pushed managers to optimize the use of limited funds. By collecting information on the costs incurred by invasive alien species, we hope to raise awareness on the need to monitor and prevent new invasions, but also to supply managers with additional information to better prioritise the species already invasive in France. The costs that we are reporting provide evidence of the significant damages invasive alien species can cause to economies, in addition to their threats to biodiversity. At present, a national coordination compiling the effects of all known invasive alien species in monetary terms is missing. This aspect should be urgently solved, as it would greatly enhance communications towards decision-makers and the public, facilitating our ability to raise awareness of the importance of biosecurity and biosurveillance in France and overseas. The InvaCost initiative partially addresses this need, and offers a platform for standardised cost reporting by environmental managers.

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Supplementary material 1

Datasets of the economic costs of invasive alien species in France and descriptive variables (from Diagne et al. 2020b)

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: Description of the structure of the database

Explanation note: Spreadsheet 'DB-Descriptor': summary of the content of the descriptive columns of the database used in this study (from Diagne et al. 2020b). The different columns (i.e. descriptive variables) are presented by alphabetical order and between inverted commas (‘’); note that the ‘Taxonomy’ information groups several columns. The categories used for each descriptive variable are italicized. Spreadsheet 'RawData': Raw data for France from InvaCost v3.0. Spreadsheet 'DB_Expanded_High': expanded data filtered with only high reliable cost entries. Spreadsheet 'DB_Expanded_High_Observed': expanded data filtered with only high reliable and observed costs.

Link: https://doi.org/10.3897/neobiota.67.59134.suppl1

Supplementary material 2

Description of the different sectors of the InvaCost database

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: Description of the structure of the database

Link: https://doi.org/10.3897/neobiota.67.59134.suppl2

Supplementary material 3

Listing of the environment-taxonomic groupings

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: Description of the structure of the database

Link: https://doi.org/10.3897/neobiota.67.59134.suppl3

Supplementary material 4

Listing of the 2750 introduced or invasive alien species with accepted names in France

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: listing of Invasive Alien Species

Explanation note: Data were extracted from the Global Register of Introduced and Invasive Species database.

Link: https://doi.org/10.3897/neobiota.67.59134.suppl4

Supplementary material 5

Number of cost estimates per year for France

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: cost data

Explanation note: The dashed line illustrates the sudden decrease in the number of cost estimates after 2013.

Link: https://doi.org/10.3897/neobiota.67.59134.suppl5

Supplementary material 6

Categorical representation of the cumulated costs caused by invasive alien species in metropolitan France and French overseas over the period 1993–2018

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: distribution of costs incurred by Invasive Alien Species

Explanation note: Categorical representation of the cumulated costs caused by invasive alien species in metropolitan France and French overseas over the period 1993–2018 per (a) activity sectors, (b) cost types, and (c) taxonomic groups. Pie charts show the cost contribution of alien invasive species to the different categories; inner circle shows information based on all costs (i.e. observed and potential costs), whereas the outer circle restricts the information to the costliest invaders ((i.e. observed costs > 1 US$ million) from France (*Aedes* sp., *Ambrosia* sp., *Lagorasiphon* sp., *Lithobates catesbeianus*, *Ludwigia* sp., *Procambarus clarkii*, *Rattus* sp., *Reynoutria* sp., Rusa timorensis russa, *Vespa velutina*, *Felis catus*, *Baccharis halimifolia*).

Link: https://doi.org/10.3897/neobiota.67.59134.suppl6

Supplementary material 7

For each French region, listing of the taxa for which we had cost information in the InvaCost database over the time range 1993–2018

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: occurences

Link: https://doi.org/10.3897/neobiota.67.59134.suppl7

Supplementary material 8

List of the 68 invasive alien species in metropolitan France for which no economic cost was documented in our database

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: Listing of Invasive Alien Species

Explanation note: The potential costs incurred by these 68 invasive alien species in France were estimated from cost data obtained from other countries (see Material and methods).

Link: https://doi.org/10.3897/neobiota.67.59134.suppl8

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RESEARCH ARTICLE

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Economic costs of invasive species in Germany

Phillip J. Haubrock[1,2*], Ross N. Cuthbert[3,4*], Andrea Sundermann[1,5], Christophe Diagne[6], Marina Golivets[7], Franck Courchamp[6]

1 *Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, 63571 Gelnhausen, Germany* **2** *University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Zátiší 728/II, 389 25, Vodňany, Czech Republic* **3** *GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, 24105, Kiel, Germany* **4** *School of Biological Sciences, Queen's University Belfast, 19 Chlorine Gardens, Belfast, BT9 5DL, Northern Ireland, UK* **5** *Goethe University Frankfurt am Main, Faculty of Biology, Department Aquatic Ecotoxicology, Max-von-Laue-Str. 13, 60438, Frankfurt am Main, Germany* **6** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405, Orsay, France* **7** *Department of Community Ecology, Helmholtz-Centre for Environmental Research – UFZ, Theodor-Lieser-Str. 4, 06120, Halle (Saale), Germany*

Corresponding author: Phillip J. Haubrock (phillip.haubrock@senckenberg.de)

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Abstract
Invasive alien species are a well-known and pervasive threat to global biodiversity and human well-being. Despite substantial impacts of invasive alien species, quantitative syntheses of monetary costs incurred from invasions in national economies are often missing. As a consequence, adequate resource allocation for management responses to invasions has been inhibited, because cost-benefit analysis of management actions cannot be derived. To determine the economic cost of invasions in Germany, a Central European country with the 4th largest GDP in the world, we analysed published data collected from the first global assessment of economic costs of invasive alien species. Overall, economic costs were estimated at US$ 9.8 billion between 1960 and 2020, including US$ 8.9 billion in potential costs. The potential costs were mostly linked to extrapolated costs of the American bullfrog *Lithobates catesbeianus*, the black cherry *Prunus serotina* and two mammals: the muskrat *Ondatra zibethicus* and the American mink *Neovison vison*. Observed costs were driven by a broad range of taxa and mostly associated with control-related spending and resource damages or losses. We identified a considerable increase in costs relative to previous estimates and through time. Importantly, of the 2,249 alien and 181 invasive species reported in Germany, only 28

* These authors contributed equally.

species had recorded economic costs. Therefore, total quantifications of invasive species costs here should be seen as very conservative. Our findings highlight a distinct lack of information in the openly-accessible literature and governmental sources on invasion costs at the national level, masking the highly-probable existence of much greater costs of invasions in Germany. In addition, given that invasion rates are increasing, economic costs are expected to further increase. The evaluation and reporting of economic costs need to be improved in order to deliver a basis for effective mitigation and management of invasions on national and international economies.

Abstract in German

Wirtschaftliche Kosten invasiver Arten in Deutschland. Invasive gebietsfremde Arten sind eine bekannte und weit verbreitete Bedrohung für die globale Artenvielfalt und das Wohlergehen des Menschen. Trotz erheblicher Auswirkungen invasiver gebietsfremder Arten fehlen häufig quantitative Synthesen der finanziellen Kosten, die durch Invasionen entstehen. Infolgedessen wurde eine angemessene Ressourcenzuweisung für Managementreaktionen auf Invasionen verhindert, da keine Kosten-Nutzen-Analyse von Managementmaßnahmen abgeleitet werden kann. Um die wirtschaftlichen Kosten von Invasionen in Deutschland, einem mitteleuropäischen Land mit dem viertgrößten BIP der Welt, zu ermitteln, haben wir veröffentlichte Daten analysiert, die aus der ersten globalen Bewertung der wirtschaftlichen Kosten invasiver gebietsfremder Arten stammen. Insgesamt wurden die wirtschaftlichen Kosten zwischen 1960 und 2020 auf 9.8 Milliarden US-Dollar geschätzt, einschließlich potenzieller Kosten in Höhe von 8.9 Milliarden US-Dollar. Die potenziellen Kosten waren hauptsächlich auf die extrapolierten Kosten des amerikanischen Ochsenfrosches *Lithobates catesbeianus*, der Tollkirsche *Prunus serotina* und zweier Säugetiere zurückzuführen: des Bisamratten *Ondatra zibethicus* und des amerikanischen Nerz *Neovison vison*. Die beobachteten Kosten wurden von einer breiten Palette von Taxa getrieben und waren hauptsächlich mit kontrollbezogenen Ausgaben und Ressourcenschäden oder -verlusten verbunden. Wir haben einen erheblichen Anstieg der Kosten im Vergleich zu früheren Schätzungen und im Laufe der Zeit festgestellt. Wichtig ist, dass von den in Deutschland gemeldeten 2.249 gebietsfremden und 181 invasiven Arten nur 28 Arten wirtschaftliche Kosten verzeichneten. Daher sollte die Gesamtquantifizierung der Kosten invasiver Arten hier als sehr konservativ angesehen werden. Unsere Ergebnisse zeigen einen deutlichen Mangel an Informationen in der öffentlich zugänglichen Literatur und in staatlichen Quellen zu Invasionskosten auf nationaler Ebene, was die höchstwahrscheinliche Existenz viel höherer Invasionskosten in Deutschland maskiert. Angesichts der steigenden Invasionsraten werden die wirtschaftlichen Kosten voraussichtlich weiter steigen. Die Bewertung und Berichterstattung der wirtschaftlichen Kosten muss verbessert werden, um eine Grundlage für eine wirksame Eindämmung und Bewältigung der Invasionen in die nationale und internationale Wirtschaft zu schaffen.

Abstract in Spanish

Costos económicos de las especies invasoras en Alemania. Las especies invasoras representan una conocida amenaza en general para la biodiversidad del planeta y el bienestar humano. A menudo se omite la cuantificación de los costes económicos que provocan las especies invasoras, a pesar de los impactos sustanciales que ellas provocan. En consecuencia, el reparto de los recursos para el manejo de las respuestas es inadecuado ante las invasiones, por lo tanto no es posible obtener un análisis de los costos y beneficios de las acciones de manejo. Para determinar los costos económicos de las invasiones en Alemania, un país Centroeuropeo con el 4to producto interno bruto más grande del planeta, se analizaron datos publicados en la primera evaluación global de los costes económicos de especies invasoras. En general se estimaron costes económicos de US $9.8 mil millones entre los años 1960 y 2020, incluyendo US $8.9 mil millones en costos potenciales. Los costos potenciales se asociaron con los costes extrapolados de la rana toro americana *Lithobates catesbeianus*, el cerezo negro *Prunus serotina* y dos mamíferos: la rata almizclera

Ondatra zibethicus y el visón americano *Neovison vison.* Los costes observados se condujeron entre una amplia variedad de taxa de los cuales la mayoría se asociaron con gastos relacionados con el control de las especies y daños a los recursos o pérdidas relacionadas con invasiones. Se identificó un incremento considerable de los costes relacionados con estimaciones previas y a través del tiempo. De manera importante, de las 2,249 especies exóticas y 181 especies invasoras, solo se han reportado costes de 28 especies invasoras en Alemania. Por lo tanto, el total de los costes cuantificados de las especies invasoras que se presentan aquí deben de mostrarse como muy moderados. Se destaca una ausencia de información entre la literatura de acceso libre y las fuentes gubernamentales sobre los costes de las invasiones s a nivel nacional, enmascarando así la alta probabilidad de que existan mayores costes por invasiones en Alemania. Adicionalmente, dado que la tasa de invasión se encuentra en incremento, se espera que los costes económicos sufran un incremento. Se requiere mejorar la evaluación y el reporte de los costes económicos para sentar un adecuado precedente para la mitigación y manejo efectivo de las invasiones en la economía nacional e internacional.

Abstract in Czech

Ekonomické náklady na invazivní druhy v Německu. Nepůvodní invazní druhy jsou dobře známou a všudypřítomnou hrozbou pro celosvětovou biodiversitu i blahobyt člověka. Navzdory podstatným dopadům biologických invazí však často postrádáme přehled o jejich nákladovosti pro národní ekonomiky. V důsledku toho byla omezena i adekvátní alokace zdrojů pro management biologických invazí, jelikož nebylo možné vypracovat analýzu nákladů a přínosů takových akcí. Cílem této studie bylo pomocí speciálně vytvořené databáze zhodnotit náklady způsobené invazními druhy v Německu, které je čtvrtou zemí s nejvyšším HDP na světě. Celkově byly ekonomické náklady invazních druhů mezi lety 1960 a 2020 odhadnuty na 9.8 miliardy amerických dolarů. Jednalo se především o potenciální odhadnuté náklady způsobené severoamerickým skokanem volským *Lithobates catesbeianus*, střemchou pozdní *Prunus serotina* a dvěma savci – ondatrou pižmovou *Ondatra zibethicus* a norkem americký *Neovison vison*. Pozorované náklady byla způsobené různými skupinami organismů a většinou byly spojeny s kontrolou jejich šíření a jimi způsobenými škodami. V průběhu času bylo oproti dřívějším odhadům zaznamenáno značné zvýšení těchto ekonomických škod. V Německu žije 2249 nepůvodních organismů, z nichž je 181 považováno za invazní, avšak pouze u 28 existují ekonomicky vyčíslené škody. Reálná výše těchto škod je tedy očekávatelně podstatně vyšší. Tato zjištění poukazují na značný nedostatek takových údajů v dosažitelných informačních zdrojích, jenž velmi pravděpodobně maskuje existenci podstatně vyšších škod způsobených invazními druhy v Německu. Jelikož počet invazních druhů v zemi roste, lze do budoucna očekávat i růst jimi způsobených škod. Je tedy potřeba zlepšit hodnocení a vykazování ekonomických nákladů souvisejících s invazními druhy, aby bylo možné vytvořit podmínky pro jejich eliminaci a management na národní i mezinárodní úrovni.

Abstract in French

Coûts économiques des espèces envahissantes en Allemagne. Les espèces exotiques envahissantes sont une menace bien connue et omniprésente pour la biodiversité mondiale et le bien-être humain. Malgré les connaissances sur les impacts substantiels de ces espèces, les synthèses quantitatives des coûts monétaires induits par les invasions sur les économies nationales font souvent défaut. De fait, le rapport coûts-avantages des mesures de gestion des invasions biologiques est souvent difficile à obtenir. Cela a nécessairement des conséquences négatives sur l’allocation adéquate de ressources dédiées à ces mesures et actions destinées à prévenir ou contrôler les espèces exotiques envahissantes. Pour déterminer le coût économique des invasions en Allemagne (pays européen avec le quatrième PIB le plus important au monde), nous avons analysé les données publiées collectées à partir de la première compilation mondiale des coûts économiques des espèces exotiques envahissantes. Dans l'ensemble, les coûts économiques ont été estimés à 9,8 milliards de dollars entre 1960 et 2020, dont 8,9 milliards de dollars de coûts potentiels.

Les coûts potentiels étaient principalement liés aux coûts extrapolés du ouaouaron d'Amérique *Lithobates catesbeianus*, du cerisier noir *Prunus serotina* et de deux mammifères: le rat musqué *Ondatra zibethicus* et le vison d'Amérique *Neovison vison*. Les coûts observés étaient attribuables à un large éventail de taxons et principalement associés aux dépenses liées au contrôle et aux dommages ou pertes affectant les ressources humaines. Nous avons identifié une augmentation considérable des coûts au cours du temps, avec des coûts supérieurs aux estimations réalisées précédemment. Il est important de noter que sur les 2249 espèces exotiques et 181 espèces envahissantes signalées en Allemagne, seules 28 espèces ont des coûts économiques reportés dans la base de données considérée. Par conséquent, les coûts quantifiés ici doivent être interprétés avec prudence. Nos résultats mettent donc en évidence un manque flagrant d'informations dans la littérature librement accessible et les sources gouvernementales sur les coûts des invasions au niveau national, masquant l'existence hautement probable de coûts beaucoup plus élevés en Allemagne. De plus, il ne fait aucun doute que l'augmentation toujours croissante des phénomènes d'invasion biologique sera liée à l'augmentation concomitante des coûts économiques associés. L'évaluation et la communication des coûts économiques doivent nécessairement être améliorées pour contribuer à l'établissement et l'implémentation de mesures de gestion efficaces des invasions aux échelles nationale et internationale.

Keywords
Alien species, biodiversity, ecosystem management, InvaCost, monetary impacts, resource losses, socio-economic sectors

Introduction

Invasive alien species (hereafter, invasive species) have been linked to manifold ecological and socioeconomic impacts (Malcolm and Markham 2000; Stigall 2010; Diagne et al. 2020) and substantially contribute to the decline in global biodiversity (Blackburn et al. 2019), threatening economic enterprises (Paini et al. 2016). However, few economic resources are allocated to tackle biodiversity declines and invasions, despite the range of ecosystem services inherently linked to species diversity that are at risk (Hulme et al. 2009; Scalera 2010; Early et al. 2016; Vanbergen et al. 2018). In particular, despite the well-described impacts of invasive species on recipient ecosystems and communities (Gurevitch and Padilla 2004; Didham et al. 2005), relatively few studies have synthesised monetary aspects associated with the management of – and damages from – invasive species. Moreover, the reported costs from invasive species are often disparate and lack standardisation in monetary terms across spatial and temporal scales. They are also subject to spatial, taxonomic and temporal biases. This prevents obtaining broader estimations of costs, the understanding of their key drivers and the development of management actions (Lovell et al. 2006; Marbuah et al. 2014). The first comprehensive estimations of invasive species costs were made by Pimentel (2000, 2005) for North America and by Kettunen et al. (2009) for Europe, successfully raising awareness of burgeoning invasion costs at regional scales. However, in both cases, cost estimations omitted cost appraisals for smaller decision-making units, such as those at the level of specific states. Consequently, limited quantification and low spatial resolution of invasion economic costs have undermined financial efforts to tackle the growing economic and ecological problems of invasive species at the regional or country-level. As management budgets are often established at the governance level, quantifying and characterising the cost of invasions at the national level is crucial (Hanley and Roberts 2019).

International trade has been shown to be linked to both high numbers of invasive species and high associated costs (Haubrock et al. 2021). Germany, due to its central location, has intense trade with other European states (Bernaciak 2010), yet management practices to reduce alien species introductions via trade and other pathways are lacking (Nehrung and Klingenstein 2008; Hussner et al. 2010). Beyond the EU list of Invasive Alien Species of Union Concern (Regulation (EU) 1143/2014), specific lists of potentially dangerous or permitted species exist ("German Blacklist"; Essl et al. 2011). However, no comprehensive list of invasive species present in Germany is maintained by the government and management actions aimed at tackling invasions remain scarce and inconsistent. The number of potentially-invasive species introduced through trade is not negligible in Germany. In particular, the pet trade has been linked to multiple invasive alien species introductions at the national level (Hussner et al. 2010; Lipták and Vitázková 2015). Despite the presence of many invasive species in Germany, no thorough cost estimations for these species are available. Indeed, governmental reports on the costs of invasive species mostly refer to pioneering, but now outdated international publications (e.g. Pimentel et al. 2005; Kettunen et al. 2009) or Reinhardt et al. (2003), which presented national cost quantifications predominantly based on anecdotal information. As a result, almost two decades later, substantial economic losses can be expected due to the intensified use of fisheries, agriculture and forestry.

Using the literature-based data on the economic costs of invasive species compiled in the InvaCost database (Diagne et al. 2020), we synthesise and describe the costs of invasions for the German economy. Our study is more comprehensive in presenting economic costs inferred from invasions than previous assessments at the national level (see, for example, Reinhardt et al. 2003). Indeed, data included in this database are more rigorous and complete, with rich ancillary information allowing a more detailed examination of the origin of costs and methodologies used in primary studies. Moreover, the database compiled cost information using a standardised and annualised currency, enhancing comparisons among data sources within and beyond the country. Focusing on the period of 1960–2020 in Germany, we asked: (*i*) what is the economic cost of biological invasions in that country; (*ii*) which taxonomic groups cause the highest economic costs, which economic sectors are most impacted and how amounts are distributed between damage and management costs; (*iii*) what proportion of costs are from highly reliable sources (i.e. peer-reviewed or official) and have been empirically observed rather than predicted/extrapolated (see Methods); and (*iv*) how economic costs have evolved over time? We anticipate that large proportions of identified costs are attributed to currently applied management practices and that costs have steadily increased over recent decades, but differ amongst taxa and sectors. We expect invasive taxa that affect agricultural enterprises to be most costly overall, given the economic threat that has already been identified to that sector from invasions globally (Paini et al. 2016). In turn, we expect to identify potential knowledge gaps and biases in costs reporting on different scales.

Methods

Data collection

To determine the cost of invasions on the German economy, we used data from the InvaCost database (2,419 entries; Diagne et al. 2020) on the published economic costs of biological invasions globally, enabling comprehensive quantification of costs associated with invasive species at various spatio-temporal scales. The data in InvaCost were collected following a series of literature searches using the Web of Science platform (https://webofknowledge.com/), Google Scholar database (https://scholar.google.com/), the Google search engine (https://www.google.com/) and all of the retrieved costs were converted to a common, up-to-date currency (2017 USD; World Bank 2019; Suppl. material 1). The InvaCost database has been recently complemented with data from non-English literature (5,212 entries; Angulo et al. 2021a) and additional data from English sources (ca. 2,300 entries; Ballesteros-Mejia et al. 2020). Potential duplicates were also carefully checked and removed from the database. The resulting complete InvaCost database (version 3.0) is available and detailed elsewhere (https://figshare.com/s/c88d2e0dbe7b3e8a4edc). Following our data processing (see below), we extracted 71 entries for Germany for the purpose of our analyses (Suppl. material 2).

The estimated period for reported costs varied considerably, spanning periods of several months to several years. For the purpose of the analysis and in order to obtain comparable invasion costs, we considered all costs for a period of less than a year as annual costs and re-calculated costs covering several years on an annual basis. That is, costs spanning several years were divided equally amongst those years, so as to not inflate costs artificially. Equally, costs covering a time period of under one year were not increased in value to span that entire year, to remain conservative. This was performed using the "expandYearlyCosts" function of the ‘invacost’ package version 0.3-4 (Leroy et al. 2020) in R version 4.0.2 (R Core Team 2020). In using this function, we estimated average annual costs represented in the InvaCost database. Deriving the total cumulative cost of invasions over time requires consideration of the probable duration time of each cost occurrence. The duration consisted of the number of years between the probable starting and ending years of the costs reported by each publication included in the InvaCost database. When information was missing for the starting year, we conservatively considered the publication year of the original reference. For the ending year of costs, however, information was missing only for costs likely to recur over years (i.e. "potentially ongoing", contrary to "one-time" costs occurring only once within a specific period). Therefore, we assumed that these costs occurred every year. Subsequently, to obtain a comparable total cumulative cost for each estimate over each defined invasion period, we multiplied each estimate by the respective duration (in years). All analyses were performed for the period from 1960 to 2020, as monetary exchange rates could not be obtained from official institutions (e.g. World Bank) prior to 1960. The resulting costs were therefore annualised, allowing comparability on a temporal basis.

Economic cost descriptors

The invasion costs in Germany were estimated by summing all annualised estimates according to the five descriptors, i.e. by quantifying aggregate cost totals amongst the categories within each descriptor:

1. Method reliability: based on whether the assessed material was peer-reviewed or an official document ("high" reliability) or from an inaccessible source or a document that followed irreproducible methods ("low" reliability) (see Suppl. material 1). We acknowledge that this binary classification inherently does not capture the full range of reliabilities of sources, but provided an objective basis to categorise costs;
2. Implementation form: referring to whether the cost estimate was actually realised in the invaded habitat (i.e. "observed") or extrapolated (i.e. "potential"), see Suppl. material 1;
3. Species environment: "aquatic", "semi-aquatic", "terrestrial" or "diverse/unspecified" (i.e. where multiple species across several environments were present in a single entry or were unspecified);
4. Type of cost: (a) "damage", referring to damage or losses incurred by invasion, (b) "management", comprising control-related (i.e. monitoring, prevention, management, eradication) expenditure and (c) "other" costs, including research and administrative costs;
5. Impacted sector (i.e. the activity, societal or market sector where the cost occurred; see Suppl. material 2). Individual cost entries not allocated to a single sector were modified to "other" in the “Impacted sector” column, see Suppl. material 2 and Suppl. material 3.

Temporal dynamics of accumulated costs

To analyse the economic costs of invasive species over time, we used the "summarizeCosts" function in the R package ‘invacost’ (Leroy et al. 2020). With this function, we calculated the average annual costs between 1960–2020 at 10-year intervals, as well as over the entire period. We note that this function is based on raw trends and thus does not account for the effects of time lags in recent years between cost incurrence and publication.

Results

Economic cost descriptors

Based on the 71 entries found for invasive species in Germany, the InvaCost database contained 194 annualised cost estimates distributed across twenty taxonomic orders and twenty-eight species, amounting to a total of US$ 9.77 billion or € 8.14 billion (2017 value). Of all the reported costs, 36.60% of the entries (n = 71) and 91.50% of the total cost (US$ 8.94 billion) were potential (Fig. 1). These were mostly driven

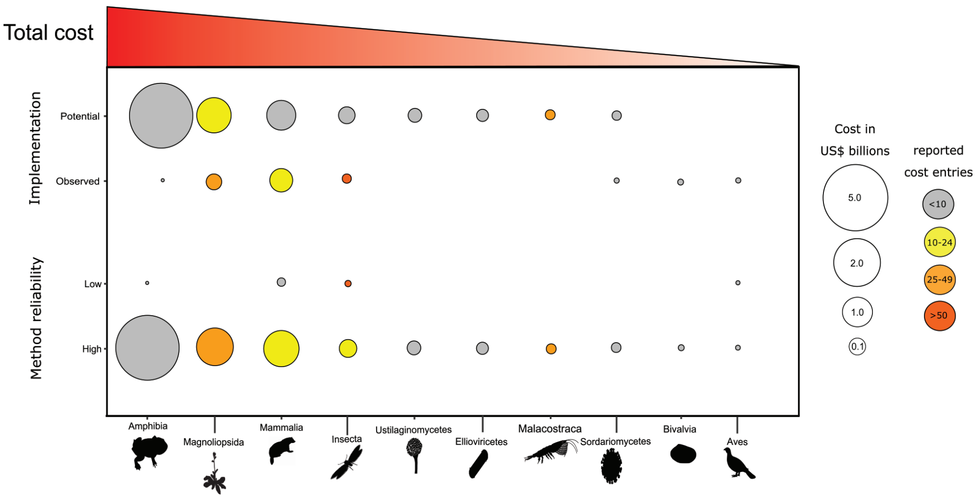

Figure 1. Total economic costs of invasions in Germany across taxonomic groups (classes) showing method reliability (high vs. low) and implementation (potential vs. observed costs) in comparison to the overall total cost (indicated by the increasingly red scale). The colour of each balloon corresponds to the group sample size, based on annualised cost numbers (n = 194) and the size of the balloons to the respective cost (in US$ billions). We note that these sizes are not constrained to the four categories shown on the legend (i.e. they scale continuously).

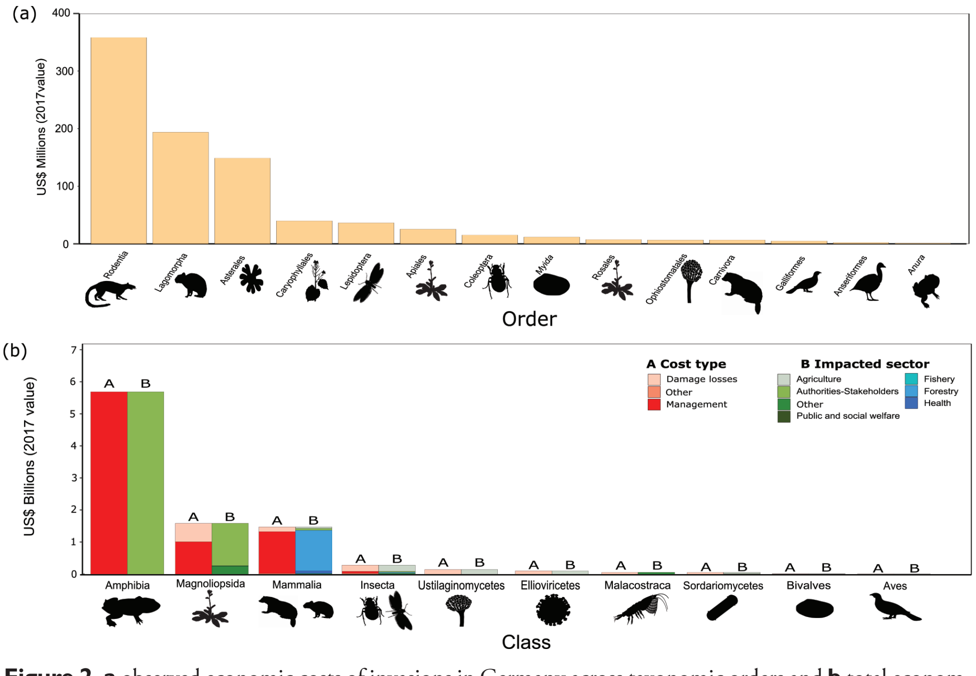

Figure 2. a observed economic costs of invasions in Germany across taxonomic orders and **b** total economic costs of invasions in Germany across taxonomic classes considering all cost types and impacted sectors.

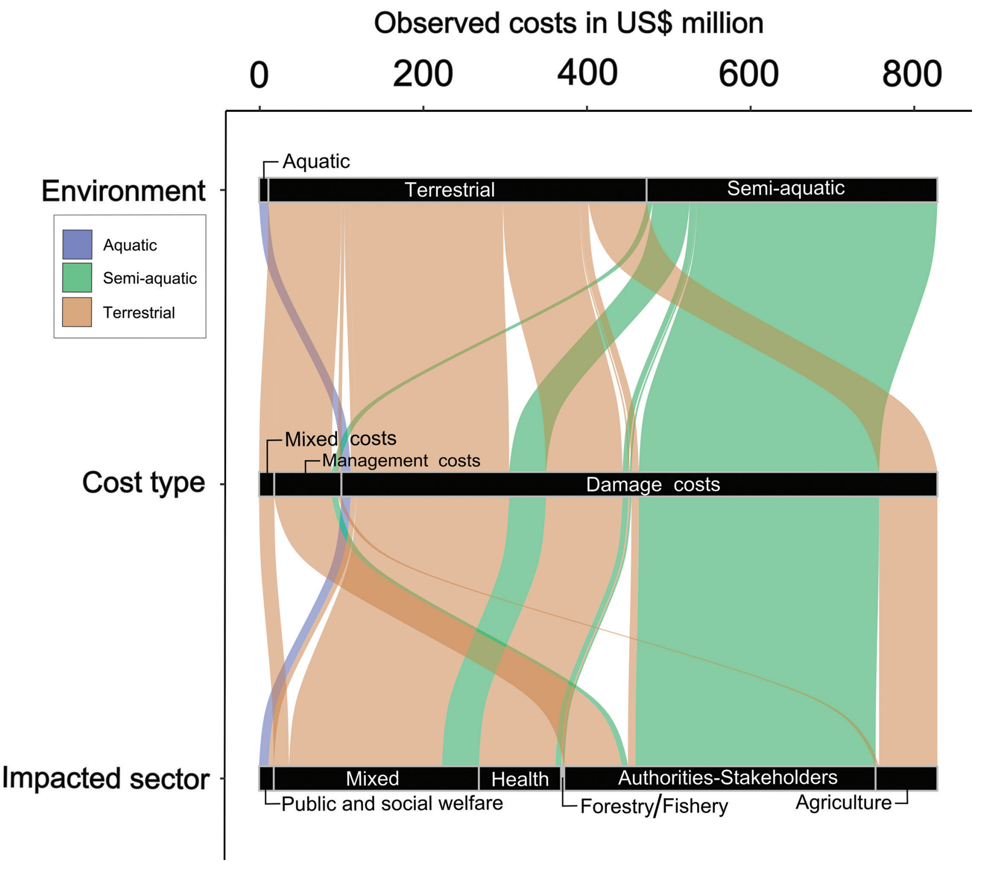

Figure 3. Distribution of observed costs across the three descriptors 'Environment', 'Type of cost' and 'Impacted sector', illustrating flows of identified invasion costs in Germany.

by extrapolations considering Amphibia (*Lithobates catesbeianus*; US$ 6.04 billion; n = 1), Magnoliopsida (mostly constituted by *Prunus serotina*; US$ 1.32 billion; n = 2), Mammalia (multiple species; US$ 0.93 billion; n = 4) and Insecta (multiple species; US$ 0.25 billion; n = 5). The majority of the costs were deemed to be highly reliable (Fig. 1) and the only cost estimates of low reliability were for the families Anatidae (waterfowls), Ranidae (true frogs), Cricetidae (rodents) and Chrysomelidae (leaf-beetles).

Observed costs (i.e. excluding extrapolations) across Germany amounted to US$ 829.11 million. These costs were unequally distributed amongst kingdoms (Animalia: US$ 608.64 million; Plantae: US$ 213.95 million; Fungi: US$ 6.52 million). The order Rodentia (represented by *Ondatra zibethicus*) was the costliest reported (US$ 345.80 million), followed by Lagomorpha (US$ 187.10 million) and Asterales (US$ 143.8 million). All other taxonomic orders (i.e. Anseriformes, Anura, Apiales, Caryophyllales, Carnivora, Coleoptera, Galliformes, Lepidoptera, Myida, Ophiostomatales and Rosales) each contributed costs up to US$ 100 million (Fig. 2a). Observed costs differed

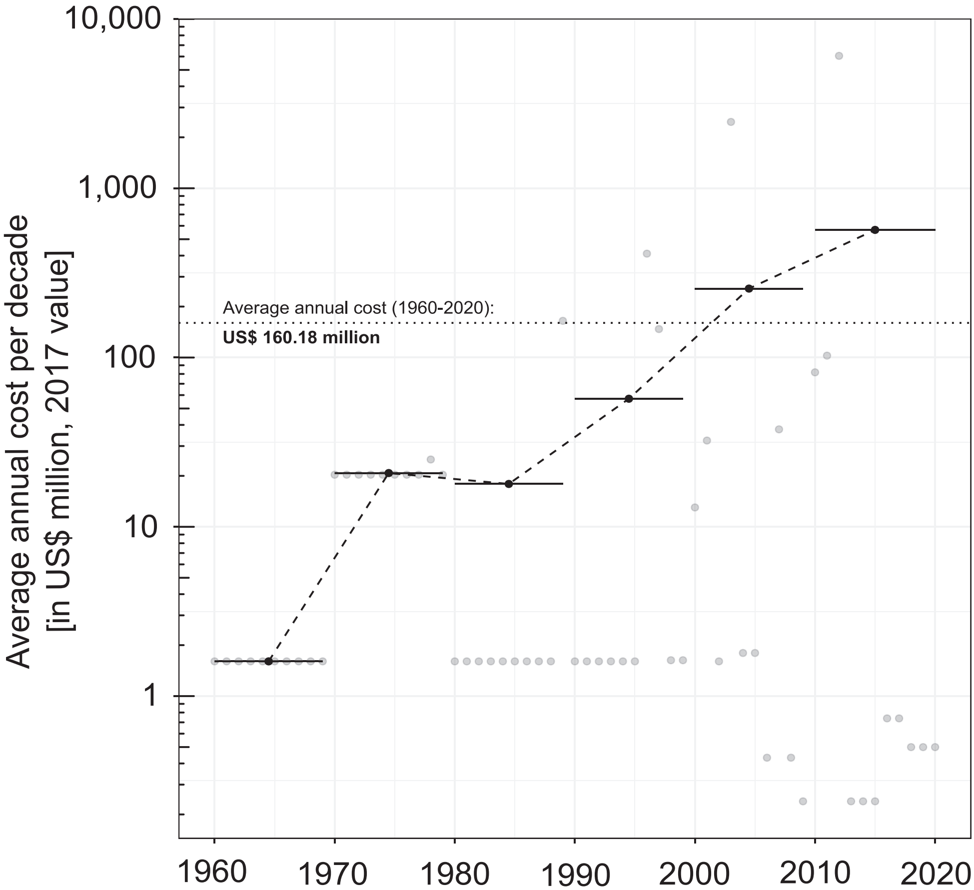

Figure 4. Average decadal costs of invasive species in Germany between 1960 and 2020. Black points represent decadal means and adjacent lines highlight the specific period, whilst grey points represent annual totals from which the decadal means were calculated. Note that the costs trends are not cumulative, with average costs determined for each individual decade. Note the log-transformed *y*-axis scale.

amongst environments, with costs in terrestrial systems (US$ 462.3 million) outweighing those in semi-aquatic (US$ 355.4 million) and aquatic systems (US$ 11.4 million).

The majority of economic costs (86.28%; US$ 8.43 billion) arose from management-related expenditure, followed by damage (13.30%; US$ 1.30 billion) and other costs (< 1%; US$ 47.7 million; Fig. 2b). When considering only observed costs, damage-loss (87.86%; US$ 728.46 million) outweighed expenditure on management (9.9%; US$ 82.13 million).

With respect to the impacted sector, 75.33% of all costs (US$ 7.36 billion) were attributed to authorities and stakeholders, 13.92% (US$ 1.36 billion) to forestry and 5.95% (US$ 581.65 million) to agriculture. Heath, public and social welfare and fishery sectors each bore less than US$ 200 million of costs (Fig. 2b). Other sectors (i.e. unspecified or mixed) contributed 3.50% (US$ 342.71 million). Considering only observed costs, authorities and stakeholders again comprised the largest share (45.90%; US$ 380.55 million), followed by other sectors (30.24%; US$ 250.75 million), health (12.12%; US$ 100.45 million), agriculture (9.14%; US$ 75.75 million), public and social welfare (2.16%; US$ 17.92 million), fishery (< 1%; US$2.08 million) and forestry (< 1%; US$ 1.80 million) sectors.

Considering observed costs, across reported sectors and cost types, impacts within terrestrial environments were dominant, followed by semi-aquatic and with relatively few contributions from aquatic environments overall in terms of invasion costs. Costs from management actions were mostly inferred through the terrestrial environment, while monetary damages from the semi-aquatic and aquatic environments predominantly related to damage (Fig. 3). In turn, authorities-stakeholders incurred most costs related to semi-aquatic species, public and social welfare was impacted predominantly by aquatic species and health, agriculture and other sectors affected by terrestrial species.

Temporal dynamics of accumulated costs

The cost of invasions increased by two orders of magnitude between 1960 and 2020, with an annual average cost estimated at US$ 160.18 million across the entire period (Fig. 4). Considering only observed costs, an annual average cost was estimated at a total of US$ 13.59 million across the entire period. Whilst the effects of time lags were not incorporated into the analysis, decadal cost estimates have continued to increase markedly into the current decade.

Discussion

Economic costs of invasive species in Germany can be considered as massive, despite the disproportional contribution of potential, extrapolated costs (US$ 8.9 billion) compared to observed costs (US$ 829.1 million). However, literature on German national costs was overall scarce, which points to the lack of coordinated effort at the national level to collect these data. For instance, Reinhardt et al. (2003) listed various alien invasive species and their potential costs in Germany, while lacking precise information on the origin of estimates and combining the beneficial and negative aspects of invasive species in monetary terms. The search of literature in German revealed only a few additional publications, but these contributed data on taxonomic groups that were absent in the English sources. However, publications in German mostly referred to the costs reported by Reinhardt et al. (2003), while adding only a few additional cost estimations (see, for instance, Pehl et al. 2003; AELF 2008; Arndt 2009). In contrast, similar studies for economically-comparable countries yielded many more (unexpanded) cost records. For example, InvaCost data for Spain (2384 entries, Angulo et al. 2021b), France (595 entries, Renault et al. 2021) and the UK (353 entries, Cuthbert et al. 2021a) highlight the data deficiency in Germany (71 entries).

Several supranational lists of potentially invasive species exist for Germany; specifically, the Global Invasive Species Database (GISD; De Poorter and Browne 2005) currently lists 181 invasive species in Germany and the Global Register of Introduced and Invasive Species (GRIIS; Pagad et al. 2018) lists 2,249 introduced and invasive species, of which 48 are known to have negative impacts. These numbers contrast markedly with the 28 species in our dataset, which highlights a considerable mismatch between species present and studies or management efforts reporting economic costs. For example, non-native fish species listed in the German Blacklist (Essl et al. 2011) were missing entirely, indicating a profound lack of cost information. Alien fish species, in particular, are known to be very costly in other regions, such as North America (Haubrock et al. 2021b). Other regional studies of the InvaCost database have similarly found that the number of species with recorded costs represent a very small percentage of known alien species. For example, costs evaluations were missing for over 90% of alien species in the UK (Cuthbert et al. 2021a), 97% of alien species in France (Renault et al. 2021) and 96% of all alien species both in Asia (Liu et al. 2021) and in Argentina (Duboscq-Carra et al. 2021). There are an estimated 2700 exotic plant species established in Australia, but recorded costs for only about 1% of these plant species (Bradshaw et al. 2021). In contrast, the research effort in other regions seems much higher: costs were present for about 50% of all invasive species in North America (Crystal-Ornelas et al. 2021), indicating these knowledge gaps are not ubiquitously low. Nevertheless, we acknowledge that not all invasive alien species will be associated with economic costs, with some having relatively-benign impacts or being characterised by indirect effects that are difficult to monetise or even associated with economic benefits mixed with impacts (Vimercati et al. 2020; Haubrock et al. 2021c).

Invasion costs have also recently been synthesised at the European scale (Haubrock et al. 2021a), amounting to US$ 140 billion and allowing Germany to be formally compared with other European countries in terms of monetary impacts. Amongst those countries, Germany was ranked fourth in terms of invasion costs, despite having the greatest GDP and total wealth across Europe. Indeed, that same study found invasion costs incurring in Germany to be low relative to GDP, whereas countries, such as those in the UK, Ukraine, Serbia and Moldova, exhibited invasion costs of a much greater magnitude as a proportion of their GDP. Across Europe, invasion costs in terms of both management and damage have been found to relate significantly positively with parameters such as human population size, geographic area and tourism (Haubrock et al. 2021a). As such, given Germany has the largest population size in Europe (excluding transcontinental countries), allocates approximately 3% of GDP to research and development and has the greatest amount of goods and services imports, invasion costs appear to be under-represented nationally. Improved cost reporting infrastructures are therefore urgently required in Germany, particularly given that biological invasions are predicted to increase in coming decades across all habitat types and geographic regions (Bellard et al. 2013; Seebens et al. 2020).

Future costs reporting should additionally focus on quantifying empirically observed costs rather than relying on predictions, as the vast majority of costs in the present study were potential. Considering the observed costs only, plants and rodents dominated, trailed by a diverse group of invertebrates, amphibians and other taxa. In contrast, the major contributors of potential costs were single studies reporting costs that could arise following the potential spread of species like the American bullfrog (*L. catesbeianus*), an aquatic invader suspected to cause substantial ecological damage (European Environment Agency 2012) or of the tomato spotted wilt virus, a known agricultural pest present in Germany (Kehlenbeck 1996) or following the necessary forest actions to prune the black cherry (*P. serotina*; Reinhardt et al. 2003). Although it is not surprising that an agricultural disease contributed such high costs, the dominance of just one study exemplifies a lack of cost reporting, as (a) three other recorded fungi (*Tilletia indica*, *Ophiostoma ulmi* and *Ceratocystis fimbriata* pv. *platani*) are known to have affected the forestry and agricultural sectors and (b) no further study investigated their respective economic impacts in the following ~25 years. By comparison, similar national studies found a high predominance of agricultural costs in Argentina (Duboscq-Carra et al. 2021), Brazil (Adelino et al. 2021), the UK (Cuthbert et al. 2021a), Australia (Bradshaw et al. 2021) and the USA (Crystal-Ornelas et al. 2021), showing that the low costs recorded for Germany might be due to further data deficiency.

Another interesting example of data deficiency is *Ambrosia artemisiifolia* (common ragweed), an allergenic plant known for its impact on human health (Essl et al. 2015), whose monetary impact on the EU was recently extrapolated at EUR€ 7.4 billion annually (Schaffner et al. 2020). The InvaCost database lists four “observed” cost entries totalling EUR€ 117.14 million for *A. artemisiifolia* in Germany for the period until 2020. The cost estimated in Schaffner et al. (2020) underlines how conservative the cost estimates here likely are (see also Diagne et al. 2021) – indirectly showing that the actual cost of invasions in Germany could be one or two orders of magnitude higher. In addition, fisheries were only impacted slightly according to the data at hand, although this sector is known to suffer high costs elsewhere (such as Mexico, Rico-Sánchez et al. 2021). Economic activities in aquatic systems, such as angling and recreational activities (Cooke and Cowx 2006), have been long associated with aquatic alien species introductions in Germany. This utilisation, however, contributes major economic gains that should be considered in parallel with economic costs (Steffens and Winkel 2002; Cooke and Sneddon 2007). As such, communities and the hydro-morphology of aquatic ecosystems have long been transformed as a result of anthropogenic activities (Vörösmarty et al. 2004; Arlinghaus et al. 2015), while at the same time being managed by fishing associations. An obvious lack of economic impact estimation, positive or negative, of invasions into inland fisheries in Germany may thus result from a lack of governmental regulation or public and scientific perception.

Similarly, non-native molluscs lack cost information, even though they are known to have caused significant damage to the German economy (Martens et al. 2007; Schöll et al. 2012). Nevertheless, costs of invasive dreissenid bivalves, as often reported from other countries (Vegega and Manissero 1996; Venkatesan and Murphy 2008), have not been reported in Germany. A lack of costs for aquatic species in Germany aligns with trends on the global scale, where very few known alien species have reported economic impacts (Cuthbert et al. 2021b). More broadly, whilst certain invasive species might be associated with concomitant economic benefits to certain sectors, the lack of synthesis of invasion benefits remains a knowledge gap that precludes formal comparison with costs. However, we suspect that any benefits would be magnitudes lower than reported costs.

The observed data limitations are not restricted only to aquatic species. Another currently infamous example that is gaining increasing attention is the introduced insect *Ctenolepisma longicaudata* (long-tailed silverfish), which is causing substantial economic and cultural losses of museum material (Thomsen et al. 2019). Other examples of invasive species causing consistent damages in Germany are rodents, such as the racoon *Procyon lotor*, which are, however, not recorded in InvaCost. That is because there were no reported impacts in monetary terms captured following our search strategy for this species. Furthermore, health costs have yet to be captured for north-spreading pathogen vectors, such as ticks or mosquitoes (Hartelt et al. 2008; Werner et al. 2012; Walther et al. 2017). For example, in France, the health sector is associated with the highest costs (Renault et al. 2021), mostly because of insect vectors and allergenic plants, although these appear under-represented in our study. As a result, the actual, unreported or unevaluated economic costs of invasive species in Germany can likely be evaluated as magnitudes higher than reported here.

Furthermore, it must be realised that such an obvious lack of cost quantifications on a national scale can impede decision-making by policy-makers and stakeholders, owing to a distinct absence of an economic rationale for prioritising actions. The investment in prevention and control can lower the impacts and thus costs of invasive species. Whilst management costs were substantial in Germany considering all data, when considering only empirically-observed costs, damage far exceeded management spending. Moreover, it must be assumed that, without adequate future investments into control and prevention (i.e. cost category "Management"), damage-related costs will likely increase further. Given the blatant lack of information for various known invasive species in Germany, it can be assumed that no governmental body is responsible for actively accounting for invasive species costs and, apart from Reinhardt et al. (2003), little to no scientific effort has been given to this issue on a national level. Moreover, the lack of available cost estimates, despite the recurring problems with invasive species (Gergs and Rothhaupt 2015), confirms the finding that invasive species have not yet been realised as a potential danger for native biodiversity, the German economy and health (Jarić et al. 2020). Reinhardt et al. (2003) highlighted the available information on invasive species costs and extrapolated mean costs of non-native species in Germany on various sectors to be approximately EU€ 150 million every year, including health, forestry, agriculture and waterways. This compares well with the annual average estimated in this study, despite presented costs by Reinhardt et al. (2003) dating back two decades and not extrapolating any costs. However, as costs are lacking for various species and especially affected sectors, the current empirical costs might be at least two orders of magnitudes higher.

Conclusions

The high economic costs of biological invasions in Germany presented in this study could provide information for decision-making at the national level, thus providing economic incentives for mitigating the arrival and spread of alien species. These costs underline the need for invasive screenings and impact assessments, as costs of pre-invasion biosecurity protocols are, on average, at least one magnitude lower than costs of active management (Leung et al. 2002). Knowledge gaps are also apparent given the low numbers of species with cost estimates in InvaCost, compared to known numbers of invaders in Germany. Considering this, costs presented here should be taken into account for prospective prevention and surveillance efforts. Furthermore, our study demonstrates the need for national and regional authorities to produce more structured reporting of costs in order to refine these estimates further (Diagne et al. 2020). Future projections have also indicated an urgently-needed increase in national budgets to tackle the threat of alien species (Silva et al. 2014; OECD 2019). Across Europe, better-coordinated international actions and policy changes are required to mitigate economic costs of invasive species.

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Supplementary material 1

Description of the procedure used for collecting and describing cost data in the InvaCost database (adapted from Diagne et al. 2020)

Authors: Phillip J. Haubrock, Ross N. Cuthbert, Andrea Sundermann, Christophe Diagne, Marina Golivets, Franck Courchamp

Data type: procedure

Explanation note: This file contains detailed information the collation and processing of the data contained within the InvaCost database.

Link: https://doi.org/10.3897/neobiota.67.59502.suppl1

Supplementary material 2

Database subset used for this manuscript

Authors: Phillip J. Haubrock, Ross N. Cuthbert, Andrea Sundermann, Christophe Diagne, Marina Golivets, Franck Courchamp

Data type: table

Explanation note: This file contains the subset underlying the results presented in this manuscript after applying the described filtering criteria.

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Supplementary material 3

Description of the sectors considered in the InvaCost database

Authors: Phillip J. Haubrock, Ross N. Cuthbert, Andrea Sundermann, Christophe Diagne, Marina Golivets, Franck Courchamp

Data type: table

Explanation note: This table contains the information on impacted sector reclassification as practiced for this manuscript.

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The recorded economic costs of alien invasive species in Italy

Phillip J. Haubrock[1,2*], Ross N. Cuthbert[3,4*], Elena Tricarico[5], Christophe Diagne[6], Franck Courchamp[6], Rodolphe E. Gozlan[7,8]

1 *Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, 63571 Gelnhausen, Germany* **2** *University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Zátiší 728/II, 389 25 Vodňany, Czech Republic* **3** *GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, 24105 Kiel, Germany* **4** *School of Biological Sciences, Queen's University Belfast, 19 Chlorine Gardens, Belfast, BT9 5DL, Northern Ireland, UK* **5** *University of Florence, Department of Biology, Via Madonna del Piano 6, 50019 Sesto Fiorentino (FI), Italy* **6** *School of Natural and Environmental Sciences, Newcastle University, NE1 7RU, UK* **7** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405, Orsay, France* **8** *ISEM, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France*

Corresponding authors: Phillip J. Haubrock (phillip.haubrock@senckenberg.de); Elena Tricarico (elena.tricarico@unifi.it)

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Abstract

Whilst the ecological impacts of invasion by alien species have been well documented, little is known of the economic costs incurred. The impacts of invasive alien species on the economy can be wide-ranging, from management costs, to loss of crops, to infrastructure damage. However, details on these cost estimates are still lacking, particularly at national and regional scales. In this study, we use data from the first global assessment of economic costs of invasive alien species (InvaCost), where published economic cost data were systematically gathered from scientific and grey literature. We aimed to describe the economic cost of invasions in Italy, one of the most invaded countries in Europe, with an estimate of more than 3,000 alien species. The overall economic cost of invasions to Italy between 1990 and 2020 was estimated at US$ 819.76 million (EUR€ 704.78 million). This cost was highest within terrestrial habitats, with considerably fewer costs being exclusively associated with aquatic habitats and management methods, highlighting a bias within current literature. There was also a clear indication of informational gaps, with only

* Contributed equally as the first authors.

15 recorded species with costs. Further, we observed a tendency towards particular taxonomic groups, with insect species accounting for the majority of cost estimates in Italy. Globally, invasion rates are not slowing down and the associated economic impact is thus expected to increase. Therefore, the evaluation and reporting of economic costs need to be improved across taxa, in order to mitigate and efficiently manage the impact of invasions on economies.

Abstract in Italian

I costi economici riportati per le specie aliene invasive in Italia. Sono ancora poco noti i costi economici causati dalle invasioni biologiche, mentre gli impatti ecologici sono stati ben documentati. Gli impatti delle specie aliene invasive sull'economia possono essere vari: si va dai costi di gestione, alla perdita dei raccolti e ai danni alle infrastrutture. Tuttavia, non ci sono ancora dettagli su questi costi stimati, in particolare a livello nazionale e regionale. In questo studio, vengono utilizzati i dati della prima valutazione globale sui costi economici delle specie aliene invasive (InvaCost), dove i dati pubblicati sui costi economici sono stati raccolti dalla letteratura scientifica e grigia. L'obiettivo è stato descrivere i costi economici delle invasioni biologiche in Italia, uno dei paesi più invasi in Europa con oltre 3000 specie aliene stimate. Nel complesso, il costo economico stimato delle invasioni in Italia tra il 1990 e il 2020 si aggira sugli 819.76 milioni US$ (che corrispondono a 704.78 milioni di euro). Il costo maggiore è stato rilevato per gli habitat terrestri, mentre molto pochi sono stati i costi trovati associati strettamente agli habitat acquatici e alla gestione, sottolineando una disparità nella letteratura odierna. Si è evidenziato anche una mancanza di informazioni, con costi riportati solo per 15 specie. Inoltre, è stata osservata una preponderanza di dati per alcuni gruppi tassonomici: gli insetti sono responsabili della maggior parte dei costi stimati in Italia. A livello globale, i tassi di invasione non stanno rallentando e ci si aspetta, quindi, che gli impatti economici associati crescano. Di conseguenza, è necessario migliorare la valutazione e riportare i costi economici tra i vari taxa per mitigare e gestire in maniera efficace gli impatti delle invasioni sulle attività economiche.

Abstract in Deutsch

Die erfassten wirtschaftlichen Kosten gebietsfremder invasiver Arten in Italien. Während die ökologischen Auswirkungen der Invasion gebietsfremder Arten gut dokumentiert sind, ist wenig über die wirtschaftlichen Kosten bekannt. Die Auswirkungen invasiver gebietsfremder Arten auf die Wirtschaft können weitreichend sein, von Verwaltungskosten über Ernteverluste bis hin zu Infrastrukturschäden. Einzelinformationen zu diesen Kostenschätzungen fehlen jedoch noch, insbesondere auf nationaler und regionaler Ebene. In dieser Studie verwenden wir Daten aus der ersten globalen Datenbank der wirtschaftlichen Kosten invasiver gebietsfremder Arten (InvaCost), bei der veröffentlichte wirtschaftliche Kostendaten systematisch aus wissenschaftlicher und grauer Literatur gesammelt wurden. Wir wollten die wirtschaftlichen Kosten von Invasionen in Italien, einem der am stärksten von biologischen Invasionen beeinflussten Länder Europas (geschätzt mehr als 3.000 gebietsfremden Arten) beschreiben. Die gesamtwirtschaftlichen Kosten von Invasionen in Italien zwischen 1990 und 2020 wurden auf 819,76 Mio. USD (704,78 Mio. EUR) geschätzt. Diese Kosten waren in terrestrischen Lebensräumen am höchsten, wobei erheblich weniger Kosten ausschließlich mit aquatischen Lebensräumen und Bewirtschaftungsmethoden verbunden waren, was auf eine Verzerrung in der aktuellen Literatur hinweist. Es gab auch deutliche Hinweise auf Informationslücken, da Kosten nur für 15 Arten registriert waren. Darüber hinaus beobachteten wir eine Tendenz zu bestimmten taxonomischen Gruppen, wobei Insektenarten den größten Teil der Kostenschätzungen in Italien ausmachen. Die Raten biologischer Invasionen verlangsamen sich weltweit nicht und die damit verbundenen wirtschaftlichen Auswirkungen werden voraussichtlich zunehmen. Daher muss die Bewertung und Berichterstattung der wirtschaftlichen Kosten in allen Taxa verbessert werden, um die Auswirkungen von Invasionen auf die Volkswirtschaften abzuschwächen und effizient zu steuern.

Abstract in Spanish

Los costos económicos registrados de las especies exóticas invasoras en Italia. Poco se conoce sobre los costes económicos que provocan las especies invasoras, mientras que los impactos ecológicos se caracterizan por estar bien documentados. Los impactos económicos que provocan las especies invasoras pueden provenir de una amplia gama, desde costes de manejo, pérdidas en cultivos, hasta daños a la infraestructura. Sin embargo, los detalles sobre los costes aún se desconocen, particularmente a una escala regional y nacional. En el presente estudio, se emplearon datos de la primera evaluación global de los costes económicos de las especies invasoras (InvaCost), donde se publicaron datos económicos colectados sistemáticamente de literatura científica y literatura gris. El objetivo del presente estudio es describir los costes económicos de las especies invasoras en Italia, uno de los países con la mayor presencia de invasiones en Europa, con un estimado de más de 3,000 especies exóticas presentes. Los costes económicos generales se estimaron en US $817.76 millones (EUR€ 704.78 millones) entre 1990 y 2020 en Italia. Los costes se observaron mayores entre los hábitats terrestres y los métodos de manejo, destacando una desviación entre los datos presentados en la literatura actual. Se observó también una clara evidencia de vacíos de información, donde solo 15 especies se reportaron en los costes. Adicionalmente, se observó una tendencia hacia algunos grupos taxonómicos en particular, en donde las especies de insectos presentaron la mayoría de los datos para estimar los costes de sus invasiones en Italia. Mundialmente, las tasas de invasión no están disminuyendo, por lo que se espera que los impactos económicos se eleven. Asimismo, la evaluación y reporte de los costes económicos requieren de mejores estimaciones entre los taxa, para una mitigación y manejo eficiente del impacto sobre la economía de las especies invasoras.

Keywords

biodiversity, ecosystem services, Europe, InvaCost, resource damages, socioeconomic indicators

Introduction

Despite an increasing number of indicators, targets and alarming reports on the rapid decline of biodiversity worldwide, limited economic resources have been allocated to tackle the ongoing erosion of biodiversity (Gren et al. 2009; Hulme et al. 2009; Scalera 2010). Amongst the key drivers of biodiversity decline are the ecological impacts of invasive alien species (IAS) on native species and ecosystems (Malcolm and Markham 2000; Stigall 2010), with the spread of alien species showing no sign of abatement (Seebens et al. 2017). Alien species have been shown to be major drivers of extinction globally across multiple taxonomic groups and geographic regions, being the second most common threat associated with extinct species since AD 1500 (Bellard et al. 2016).

The ecological impacts of biological invasions have been well-described and reported in abundance in scientific literature (see Gurevich and Padilla 2004; Didham et al. 2005; Dick et al. 2017; Haubrock et al. 2021a). For example, plant invasions have been shown to have significant impacts at the species, community and ecosystem level, reducing the diversity and abundance of native assemblages (Vilà et al. 2011). In turn, impacts from groups, such as mammalian predators, have been shown to be particularly marked on native birds, mammals and reptiles, especially on islands (Doherty et al. 2016). However, relatively-few studies have synthesised impacts in monetary terms

(Bradshaw et al. 2016; Diagne et al. 2020a, b), limiting economic quantifications of invasion costs. Indeed, reported economic costs of IAS are fragmented across habitats (e.g. terrestrial, aquatic), specific management actions (e.g. control, eradication) or activity sectors (e.g. agriculture, fisheries; Lovell et al. 2006; Marbuah et al. 2014). Accordingly, there is a distinct lack of comprehensive quantification regarding economic costs of invasive species across multiple systems and geographic regions. Characterising the cost of invasions at the national level, the main governance level at which budgets are established, is essential to provide basic economic elements necessary for states to implement internationally-binding regulations on biodiversity and to promote management actions towards IAS.

Despite some acknowledged methodological flaws (Holmes et al. 2009; Perrings 2011; Cuthbert et al. 2020), Pimentel's studies (Pimentel et al. 2000, 2005) have effectively raised awareness on the grossly underestimated costs associated with alien species introductions (Hensley 2012; Bradshaw et al. 2016). In these works, most of the costs related to invasive species were analysed for the United States. Therefore, invasion costs incurred in Europe have been understudied, despite Europe being a historic centre of globalisation (Reba et al. 2016), and, by virtue, a hub for alien species introductions. Nonetheless, Kettunen et al. (2009) estimated a total cost of approximately 12 billion Euro (€) per year across Europe (Haubrock et al. 2021b). However, many of these cost estimations are untraceable (and thus potentially unreliable) and information at national scales has remained anecdotal at best. Such national-scale information is essential, as it is at this level that budgeting and decision-making are often made.

One particular example is Italy, which has been considered as one of the financial and cultural centres for the development of Europe (James and O'Rourke 2011), with a history of many alien species introductions (Occhipinti-Ambrogi 2002; Nunes et al. 2014, 2015; Tricarico et al. 2018). In total, the Global Register of Introduced and Invasive Species (GRIIS, Pagad et al. 2018; National Database on Alien Species, ISPRA) lists in excess of 3,000 known alien species in Italy, at present, with 15% of those species considered invasive. These have occurred through various pathways, such as agriculture, angling or horticulture, to name only a few. As such, Italy is today referred to as a hotspot and gateway for several groups of invasive species (Occhipinti-Ambrogi 2002; Occhipinti-Ambrogi et al. 2011; Castaldelli et al. 2013; Nunes et al. 2014, 2015). In particular, aquatic ecosystems in Italy have been burdened with well-intentioned introduction efforts in support of recreational angling (Occhipinti-Ambrogi 2002; Gherardi et al. 2008; Gravili et al. 2010). This has led to the establishment of more than 150 freshwater aquatic species (at least 64 invertebrates and 48 vertebrates), reported in 2008 to contribute at least 2% of the inland-water fauna (Gherardi et al. 2008; Tricarico E. pers. comm.). In addition, approximately 165 alien marine species have been recorded along the 7,000 km long coastline, aided by increased, human-mediated habitat connectivity (Occhipinti-Ambrogi et al. 2010). In terrestrial ecosystems, at least 923 insect species taxa have been introduced (Inghilesi et al. 2013).

Despite these burgeoning numbers of high-impact invasions in Italy, cost data on the Italian economy are still scarce. The lack of cost quantifications impedes decision-making by policy-makers and stakeholders, owing to a distinct absence of an economic rationale for environmental priority actions. We hypothesise that these costs are substantial, although a considerable difference in costs amongst ecosystem types can be expected. Based on data from current literature, we synthesised and described, for the first time, the costs of invasions on the Italian economy. More particularly, we first aimed at depicting how these costs are distributed according to the a) invasive species or broader taxonomic groups (i.e. classes or orders), b) socioeconomic sectors, c) geographic regions and d) cost types, whilst examining the effects of habitat type within each of these descriptors. Second, we determined how the overall costs have changed since cost reporting began and whether these costs of invasions are depicting a particular trend over time.

Methods

To investigate the invasion costs on the Italian economy, we used cost data collected in the InvaCost database (2,419 entries; Diagne et al. 2020a, b) concerning the global costs of invasive species, based on published literature, enabling comprehensive quantification of costs associated with invasive species at various spatial and temporal scales. This updatable database was constructed, based on both published and grey literature and enables the most comprehensive cost quantifications associated with invasive species. All the methodological procedures, from literature searches to data collation, have been detailed elsewhere (Diagne et al. 2020b; Angulo et al. 2021a). All cost entries were standardised to a common and up-to-date currency (US dollars (US$) 2017). We complemented the data following two specific ways: on one hand, we have added cost data collected from non-English documents, including Italian (5,212 entries; Angulo et al. 2021a. https://doi.org/10.6084/m9.figshare.12928136). Further, we added supplementary cost data from new references containing cost information (ca. 2,300 entries; https://doi.org/10.6084/m9.figshare.12928145.v1).

The period of estimation across reported costs varied considerably, spanning periods of several months to several years. For the purpose of the analysis and to derive the total cumulative cost of invasions over time, we considered the duration time (i.e. number of years) over which each cost occurred. For this purpose, we defined the duration of each cost entry. We based this on the difference between the starting ("Probable starting year low margin" column) and ending ("Probable ending year low margin" column) years of the reported costs. When no period of impact was specified in one and/or the other column(s), we counted only a single year unless the authors were certain that the costs had been repeated up to a certain year. The obtained figures corresponded to the total cumulative cost along a defined period for each entry.

From the full database, we identified cost entries related to the Italian economy by filtering data using the 'Official country' column. In addition to the already available information present in the database, we added six further cost records, summarised in the work of one of the authors (Tricarico et al. 2018) and sent them to invacost@updates.fr to be integrated into the InvaCost database. The final dataset can be found in Suppl. material 1. Finally, the invasion costs were specifically estimated from all entries according to method reliability, i.e. indicating the reliability of cost estimates, based on the type of publication and method of estimation. Estimates in peer-reviewed publications or official reports or with documented, repeatable and/or traceable methods were designated as *High* reliability; all other estimates were designated as *Low* reliability (Diagne et al. 2020b); the taxonomic group ('Class', 'Order' and 'Species' columns); activity sector (the activity, societal or market sector that was impacted by the cost; 'Impacted sector' column, see Suppl. material 2); invaded habitat ('Environment' column); and lastly the cost type ('Type of cost' column) by grouping costs according to the categories: (a) *Damage* referring to damages or losses incurred from invasion (e.g. costs for damage repair, resource losses, medical care), (b) *Management* comprising control-related expenditure (e.g. monitoring, prevention, management, eradication) and money spent on education, research and maintenance costs, (c) *Mixed* including mixed damage and management costs (cases where reported costs were not clearly distinguished amongst cost types). In addition, for the purpose of investigating the costs in different habitats, we defined costs on wetlands and riparian zones generated by organisms that have an association with both terrestrial and aquatic environments, as *Semi-aquatic*. For costs that were estimated at a spatial scale below the *Country* level within Italy, we considered them in a finer-scale *Regional* analysis, using the 'Spatial scale' and 'Details' columns.

We estimated global average annual costs of invasive species in Italy represented in the InvaCost database by quantifying the temporal trends in cost accumulations. We performed these estimates for the period from 1990 to 2020. To investigate invasion costs in Italy over time and, hence, to identify whether costs are saturating over time or continuously increasing, we used the *summarizeCosts* function of the 'invacost' R package (Leroy et al. 2021). We thus determined decadal average costs since 1990, as well as the cumulative and average annual cost of that entire time period. Overall, this approach allowed for trends in raw data cost to be examined over time, corresponding to the impacted year when the cost was incurred.

Results

There were 50 economic cost entries (40 of which from the original InvaCost database) associated with Italy. After expansion, the collective 207 expanded database entries totalled US$ 819.76 million between 1990 and 2020 (US$ 26.44 million per year). From these, 76% of costs were actually realised (i.e. assigned to *Observed* category in the 'Implementation' column) and 97% of the total costs were considered as of *High* reliability ('Method reliability' column) and, thus, derived from peer-reviewed or traceable sources.

Economic costs by taxonomic group

A high proportion of the filtered database entries concerned invasive mammal species (number of expanded database entries n = 88; US$ 149.81 million, Table 1). Invasive

Table 1. List of invasive alien species entries with reported costs in Italy, alongside associated taxonomic groupings. Data sourced from the InvaCost database.

Class	Order	Family	Genus	Species	Database entries	Cost in US$ million
Insecta	Diptera	Culicidae	*Aedes*	*albopictus*	21	95.95
		Lauxaniidae	*Drosophila*	*suzukii*	7	20.27
	Hemiptera	Pentatomidae	*Halyomorpha*	*halys*	1	3.40
	Coleoptera	Cerambycidae	*Anoplophora*	*chinensis*	23	8.99
		Curculionidae	*Rhynchophorus*	*ferrugineus*	4	6.70
		Chrysomelidae	*Diabrotica*	*virgifera*	1	138.12
Plantae	Asterales	Asteraceae	*Ambrosia*	*artemisiifolia*	5	344.80
Mammalia	Artiodactyla	Cervidae	*Dama*	*dama*	6	0.38
	Rodentia	Muridae	*Rattus*	*rattus*	1	2.34
		Sciuridae	*Sciurus*	*carolinensis*	1	0.02
		Myocastoridae	*Myocastor*	*coypus*	80	147.07
Secernentea		Aphelenchidae	*Bursaphelenchus*	*mucronatus*	13	26.91
Bivalvia	Myida	Dreissenidae	*Dreissena*	*polymorpha*	11	0.37
Malacostraca	Amphipoda	Gammaridae	*Dikerogammarus*	*villosus*	6	0.18
	Decapoda	Diverse	Diverse	Diverse	27	24.27

insects represented the second most reported class (n = 57; US$ 273.42 million), followed by invasive Malacostraca (n = 33; US$ 24.45 million). In turn, invasive plants (n = 5) and invasive nematodes (n = 13) had a combined overall cost of US$ 371.72 million. Looking at specific orders, invasive Asterales contributed, with US$ 344.80 million, the most to the cost burden, followed by invasive Coleoptera (US$ 153.81 million), Rodentia (US$ 149.43 million) and Diptera (US$ 116.22 million). Taken together, all other orders accounted for less than US$ 100.00 million (Table 1; Fig. 1).

Economic costs by invaded habitat, sector and type

Economic costs of invasions differed by invaded habitat type. Costs associated with impacts in terrestrial habitats summed to US$ 647.88 million (n = 83), inferred to 12 taxa. From these, US$ 480.51 million (n = 68) was classified as observed. Cost estimates associated with aquatic-only environments accumulated to just US$ 24.82 million (n = 44), inferred only to *Dikerogammarus villosus* (US$ 178.83 thousand; n = 6), *Dreissena polymorpha* (US$ 368.38 thousand; n = 11) and further unspecified freshwater crayfish (US$ 24.27 million; n = 27). Semi-aquatic habitats (mostly linked to the semi-aquatic coypu *Myocastor coypus*; Guichón et al. 2003) totalled US$ 147.07 million (n = 80).

The overall cost distribution across taxa, sectors and types is shown in Fig. 2. Overall, agriculture (US$ 476.27 million; n = 53) and authorities-stakeholders (US$ 65.37 million; n = 69) were the primarily impacted sectors, followed by costs associated with the health sector (US$ 54.32 million; n = 3), forestry (US$ 33.61 million; n = 17) and, lastly, public and social welfare (US$ 14.97 million; n = 12) and the environment (US$ 13.72 million; n = 6). Mixed sectors (i.e. costs that were not specifically assigned to one sector) contributed an additional US$ 161.61 million (n = 47). The costs of invasive species in terrestrial habitats were predominantly associated with agriculture (US$ 453.79 million; n = 21), mixed sectors (US$ 84.89 million; n = 11 entries),

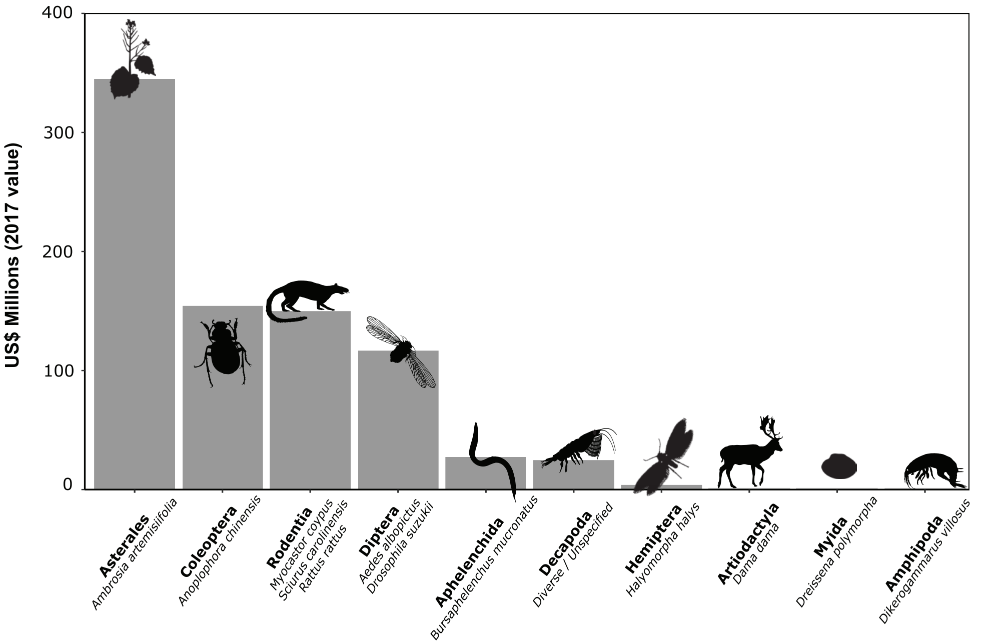

Figure 1. Total costs generated by invasive alien species in Italy between 1990 and 2020 (in US$ millions). Bold names on the x-axis represent orders, while indicating species belonging to that class, as recorded in InvaCost.

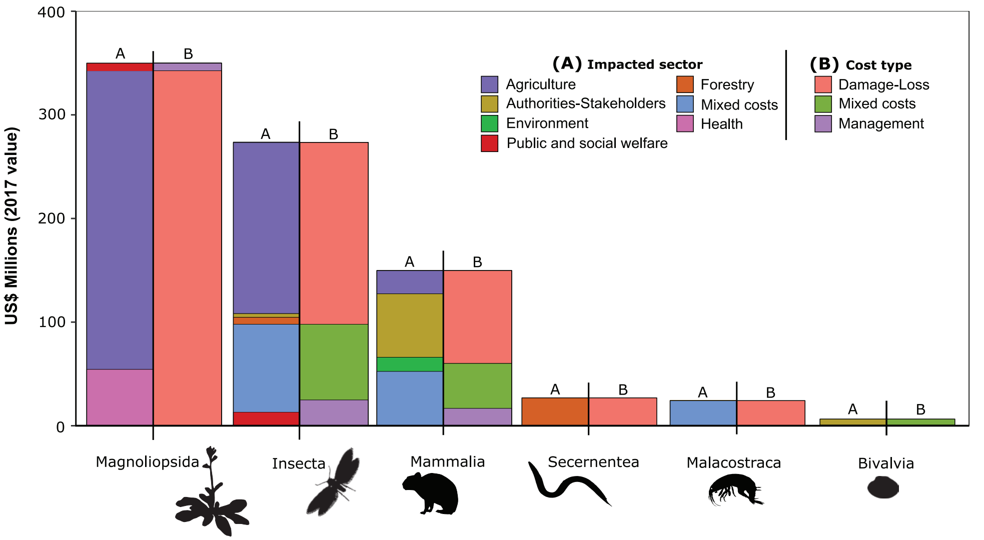

Figure 2. Total invasion costs estimates (in US$ millions) in Italy between 1990 and 2020 according to cost types and impacted sectors according to the species classes.

health costs (US$ 54.32 million; n = 3), forestry (US$ 33.61 million; n = 17), authorities-stakeholders (i.e. all management policies, US$ 6.31 million; n = 19 entries) and public and social welfare (US$ 14.97 million; n = 12). Aquatic costs were only

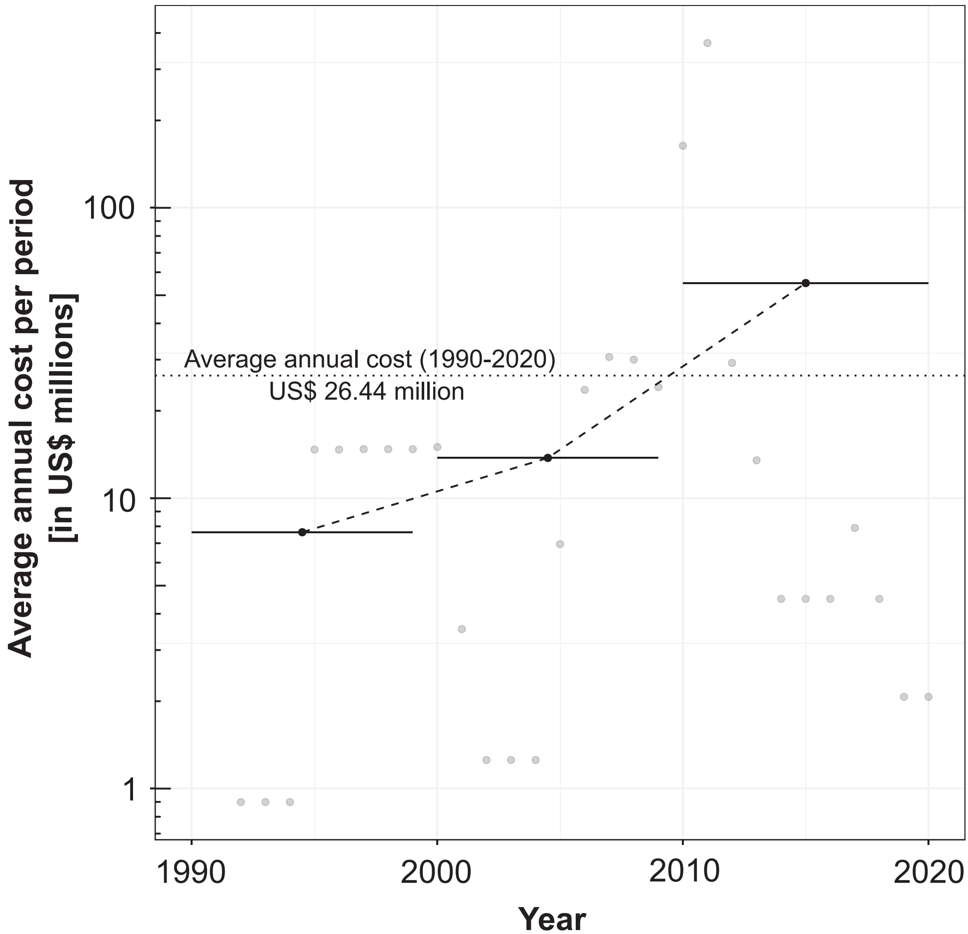

Figure 3. Average costs between 1990 and 2020 of invasive species in Italy. Bars represent decadal means and grey points indicate annual cost totals, whilst the dotted line illustrates the mean cost over the entire period. Note that the *y*-axis is on a log scale.

related to mixed sectors (US$ 24.27 million; n = 27) or to authorities and stakeholders (US$ 547.21 thousand; n = 17) and were mostly incurred by decapods (> 99%) and marginally by amphipods (< 1%). Semi-aquatic costs were mostly incurred by authorities-stakeholders (US$ 58.51 million; n = 33), followed by mixed sectors (US$ 52.36 million; n = 9), agriculture (US$ 22.48 million; n = 32) and costs inferred to the environment (US$ 13.72 million; n = 6; Fig. 3). The Insecta class drove primarily costs to agricultural (US$ 165.59 million) and mixed sectors (US$ 84.89 million), while Magnoliopsida drove costs associated with agriculture mostly (US$ 288.20 million). The single Secernentea reported cost impacted forestry (US$ 26.91 million).

Damage and losses dominated by far (US$ 659.07 million; n = 110), followed by management costs (US$ 116.91 million; n = 68). Mixed type costs contributed a further US$ 43.78 million (n = 29). The division of cost types within terrestrial habitats was as follows: US$ 544.94 million for resource damages and losses (n = 25 entries), US$ 75.85 million for control interventions (n = 30 entries), and US$ 27.09 million for mixed costs (n = 28) (Fig. 2). Costs associated with aquatic environments were mostly inferred from damage-losses (US$ 24.25 million, n = 33), with low management costs (US$ 368.38 thousand; n = 11). Similarly, cost types in semi-aquatic habitats comprised resource damage and losses (US$ 89.68 million; n = 52 entries), control interventions (US$ 40.69 million; n = 27 entries) and mixed costs (US$ 16.69 million; n = 1 entry).

Economic costs by geographical region

For several publications within the database, specific information about the region where the cost actually occurred was provided. This indicated a difference in economic cost data between the north and the south of Italy. Regional information was present only for northern/central regions, which included Emilia-Romagna (US$ 99.05 million; n = 27), Latium (US$ 24.27 million; n = 27), Trentino (US$ 20.27 million; n = 7), Lombardia (US$ 10.45 million; n = 14), Piedmont (US$ 762.63 thousand; n = 15), Tuscany (US$ 547.21 thousand; n = 17), and Umbria (US$ 22.33 thousand; n = 1). From southern regions, only Sicily had reported costs (US$ 6.70 million; n = 4). Accordingly, there was a distinct lack of cost estimation concerning States in southern Italy. The other entries were given either at national level (US$84.83 million; n = 40) or from unspecified locations (US$572.85 million; n = 55).

Temporal accumulation of costs

The recorded average annual cost between 1990 and 2020 amounted to an average US$ 26.44 million, with an exponential increase in decadal means over time (Fig. 3; note the y-axis is $\log_{10}$-transformed). In the most recent years, recorded costs of invasions in Italy have surpassed US$ 50 million per year.

Discussion

The overall cost of invasive species in Italy has been estimated at US$ 819.76 million (€ 704.78 million) between 1990 and 2020. This can be seen as a conservative total cost (Diagne et al. 2021) and is most likely an underestimate of the actual costs, especially as costs have been occurring for several decades prior to the first Italian record and because very few known invasive taxa have reported costs. Indeed, many species or invasions have not been studied for their economic impact and many of those that have been studied are not publicly available (e.g. governmental reports, grey literature) and costs present therein were thus not recorded in the InvaCost database. Furthermore, it should be noted that some types of costs are simply difficult to quantify, especially regarding ecosystem services or damages and losses (Spangenberg and Settele 2010). The lack of such data is critical because it can give the false impression that costs due to invasive species are lower than they actually are. Consequently, due to a lack of synthesis of cost information from multiple sources, as well as disparate reporting amongst invasive taxa and invaded regions, decision-makers may not have the necessary information to evaluate the costs and benefits of invasive species management actions. As a result, this limits rationale to invest in preventative or control measures to reduce or manage invasions. However, while we acknowledge that the InvaCost database does not capture all available costs through the systematic searches employed, our data indicate that the economic costs of invasions and studies are growing exponentially over time and are unlikely to saturate soon.

Taxonomic, habitat and regional biases across current literature are prevalent, resulting in only a subset of invasions being evaluated. For example, to our knowledge, costs associated with phytosanitary inspections are not available. Moreover, several aquatic invasive species which are known to damage Italian freshwater ecosystems (e.g. freshwater crayfish) were only anecdotally recorded in the database without identifiable species, given a distinct lack of cost estimation. Additionally, impacts associated with invasive crayfish species, such as levee damaging burrowing behaviour (Haubrock et al. 2019), habitat engineering (Barbaresi et al. 2004), in addition to direct impact on native biodiversity (Gherardi and Acquistapace 2007), were not present in the InvaCost database. This may be due to the cultural and financial benefits of introductions outweighing potential economic cost or the nature of ecological impact, leading to non-value costs, which are inherently harder to estimate (e.g. native community changes, ecosystems changes) and, therefore, not reported.

Despite the number of invasive species in Italy exceeding 3000 (Gherardi et al. 2008; Pagad et al. 2018; National Database on Alien Species, ISPRA), the recorded costs of invasive species in Italy concerned only very few species. For example, fish were totally missing, despite known invasions and costs. In addition, reported costs in Italy were lower than in many other EU countries (Haubrock et al. 2021b). Indeed, national-scale costs were an order of magnitude higher in the UK (Cuthbert et al. 2021a), Germany (Haubrock et al. 2021c), France (Renault et al. 2021) and Spain (Angulo et al. 2021b). This could reflect the insufficient investment by the Italian public services into the surveillance and management of these species (i.e. via control, monitoring) relative to the direct impact cost on health and crops (i.e. health care, damage cost), as well as non-market values linked to biodiversity, ecosystem services, well-being or cultural benefits (Plieninger et al. 2013). Our results also show that the highest incurred costs are linked to the control of insects. It does not mean that invasive alien insects are more frequent in Italy, but only that these are seen by public authorities as a priority to limit the damage to agriculture and forestry and the risk of emerging vector- borne human diseases, such as yellow fever, Zika, dengue or chikungunya, which are pathogens vectored principally by *Aedes aegypti* and *Ae. albopictus* (Beltrame et al. 2007; Zammarchi et al. 2015). Damage-losses through mammals (i.e. rodents) played only a subordinate role compared to insects. This could be due to several factors, such as lack of dedicated funds and coordinated and continuous control plans, public perception against the control of mammals (especially for squirrels and even for coypu) and problems with legislation (i.e. before EU Regulation 1143/2014, the change of juridical status of the coypu caused a decrease in control actions). Yet, amidst the noted lack of reported costs for insects and mammals, these taxonomic groups may present the complete records amongst all recorded groups.

Nevertheless, the lack of information on invasion-related costs could be due to the search terms used to identify economic cost literature when building InvaCost or to the lack of specific data available. For instance, a search in Italian, using a different search string including species names that are known to cause damage in Italy, yielded two additional cost estimations (as included in our data analysis). This highlights the existence, but restricted availability of important information, as (1) in the Region of Latium, central Italy, economic impacts of alien crayfish species were estimated between €140,000 and 1.17 million per year, including damage to angling, aquaculture and agriculture (Gherardi et al. 2014); (2) in the Region of Piedmont, damage in rice fields due to burrowing activities of *Procambarus clarkii* led to a decrease of 6% in the annual rice production, while in 'Consorzio di Bonifica dell'Emilia Centrale' €1000 per m^2 was necessary to rebuild levees damaged by its burrowing activity (Gherardi et al. 2014). Similarly, damage caused to agriculture by coypu was estimated at around €1 million, while damage and restoration of levees incurred costs of nearly €11 million (Panzacchi et al. 2007).

Regionally, economic costs of invasive alien species were reportedly higher in the north of Italy (North: US$ 155.37 million; South: US$ 6.70 million). Regions in northern Italy are commonly associated with higher population densities and human activities (Gherardi et al. 2008). Northern Italy also belongs to a different climatic zone (Grapow and Blasi 1998; Celesti-Grapow et al. 2010). It is, however, difficult to be confident that these observed regional cost differences reflect true differences in governance or monetised impacts, rather than a discrepancy in reporting costs between northern and southern regions. That is due to the fact that reporting of costs can be described as limited, considering that only 15 invasive species had recorded costs. Further, a considerable share of the total costs (~ 80%) was not clearly distinguishable for any region, with this low resolution negating a more comprehensive regional analysis. However, extensive/intensive agriculture (CREA 2017) and drainage basins (Gherardi et al. 2008) are concentrated in the north, potentially explaining part of the bias in reported economic costs that were available in InvaCost. As a result, the described lack of aquatic costs entries in the north is a cause for concern, as the numbers of invasive species and affected freshwater ecosystems are relatively high in the north of Italy, indicating a severe neglect of invasive aquatic species costs for Italy overall. The overall bias towards costs on terrestrial habitats and the scarcity of information regarding aquatic habitats could be explained by the nature of the damaged economic sectors with terrestrial ecosystems being more commonly perceived, leading to more public awareness amongst populations. This trend also reflects that on the global scale, whereby aquatic species invasion costs have been underreported compared to terrestrial taxa, relative to known numbers of alien species between those habitat types (Cuthbert et al. 2021b). Additionally, Italy has a long history of active species introduction into freshwater ecosystems. Amongst species like the red swamp crayfish *P. clarkii* (Gherardi and Acquistapace 2007) or the pond slider *Trachemys scripta* (Ficetola and Scali 2010), a very well-known example is the black bullhead *Ameiurus melas*, which first appeared in 1904 (Tortonese 1970) and has now spread throughout Italy, reaching high densities in, for example, the River Tiber and the Corbara Reservoir (Pedicillo et al. 2008). The key drivers for these introductions have often been cultural, because the introduction of alien freshwater species is often perceived as favourable and beneficial for local municipalities (Selge et al. 2011; Kilian et al. 2012), as it increases the attraction of fisheries, for example, for recreational angling. Therefore, in future studies, it would be important to address the costs of invasions for the economy, whilst considering potential values, particularly in terms of angling.

In addition, we identified an exponential increase in costs through time since 1990, with annual average cost exceeding US$ 50 million in recent years. Given that the US$ 819.76 million total is attributed to only 15 out of the more than 3,000 known alien species in Italy (Pagad et al. 2018; National Database on Alien Species, ISPRA) and probably far from exhaustively for these 15 species (see above), it can be easily appreciated how significantly underestimated this overall cost is, regardless of how they are representative of these few species. For instance, only one database entry referred to the grey squirrel (*Sciurus carolinensis*), which has been studied and managed thoroughly in Italy (Genovesi and Bertolino 2001; Martinoli et al. 2010) and no entries regarded the well-investigated costs from the impacts of invasive crayfish were found (Gherardi et al. 2014). Further, the costs of management activities in Italy spent solely on IAS within the Union Concern list of EU Regulation 1143/2014, between 2016 and 2018 (in total 48 listed species for this period, 31 of which are present in Italy and 20 that were managed between 2016 and 2018), were estimated at EU€1.85 million (~ US$2.17 million) for those two years (Alonzi et al. 2020). Annually, this figure suggests that the monetary investments into management efforts were between 24-times (considering the entire period) and 46-times (considering only the two recent years) lower than the total costs inferred by IAS at the national level. However, it should be noted that (i) today, 42 of the now 66 IAS listed are present in Italy and, (ii) this cost does not consider the allocated funds for IAS at regional levels. As a result, the actual, unreported or unevaluated economic costs of all IAS in Italy must be staggering.

In conclusion, the presented economic costs of biological invasions in Italy will contribute to informed decision-making at the national level and, thus, providing economic incentives for mitigating the arrival, spread and damage of invasive species. The relatively-high costs reported for Italy, despite the low number of entries in the database contrasting with the high number of invasive species, underlines the need for prevention and surveillance programmes, as costs spent on these are generally considered several magnitudes lower than active management (Leung et al. 2002). Our study highlights the need for national and regional authorities to produce more structured reporting of costs in order to refine these figures further (Diagne et al. 2020b, 2021). However, future perspectives indicate an urgently-needed increase in national budgets to tackle the threat of alien species (Silva et al. 2014; OECD 2019). Further studies are also required to examine costs attributed to invasive species in other EU countries, as these may facilitate better-coordinated international actions and drive policy change to mitigate economic costs of invasive species. Nevertheless, we highlighted the increase in annual costs for Italy: the numbers of invasions will increase over time (Seebens et al. 2017) and, thus, it is most likely that reported costs will continue to rapidly increase during the coming decades.

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Supplementary material 1

Data used for the estimation of invasive species costs in Italy

Authors: Phillip J. Haubrock, Ross N. Cuthbert, Elena Tricarico, Christophe Diagne, Franck Courchamp, Rodolphe E. Gozlan

Data type: cost data

Explanation note: This table contains collected information for invasive species recorded in Italy as listed in the InvaCost database.

Link: https://doi.org/10.3897/neobiota.67.57747.suppl1

Supplementary material 2

Description of the Impacted Sector categories

Authors: Christophe Diagne, Franck Courchamp

Data type: classification

Explanation note: This table contains the information on impacted sector reclassification as practiced for this manuscript.

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Supplementary material 3

Number of recorded studies over the cumulative estimates

Authors: Phillip J. Haubrock, Ross N. Cuthbert

Data type: figure, trend

Explanation note: Estimation of the relationship between recorded studies and cumulative estimates from the Italian InvaCost datasubset.

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Economic costs of invasive alien species in Spain

Elena Angulo[1], Liliana Ballesteros-Mejia[1], Ana Novoa[2],
Virginia G. Duboscq-Carra[3], Christophe Diagne[1], Franck Courchamp[1]

1 *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405, Orsay, France* **2** *Department of Invasion Ecology, Institute of Botany, Czech Academy of Sciences, CZ-252 43 Průhonice, Czech Republic* **3** *Grupo de Ecología de Invasiones, INIBIOMA, CONICET, Universidad Nacional del Comahue, Quintral 1250, San Carlos de Bariloche, CP 8400, Argentina*

Corresponding author: Elena Angulo (elenaanguloaguado@gmail.com)

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Abstract

Economic assessments for invasive alien species (IAS) are an urgent requirement for informed decision-making, coordinating and motivating the allocation of economic and human resources for the management of IAS. We searched for economic costs of IAS occurring in Spain, by using the InvaCost database and requesting data to regional governments and national authorities, which resulted in over 3,000 cost entries. Considering only robust data (i.e. excluding extrapolated, potential (not-incurred or expected) and low reliability costs), economic costs in Spain were estimated at US$ 261 million (€ 232 million) from 1997 to 2022. There was an increase from US$ 4 million per year before 2000 to US$ 15 million per year in the last years (from € 4 to 13 million). Robust data showed that most reported costs of IAS in Spain (> 90%) corresponded to management costs, while damage costs were only found for 2 out of the 174 species with reported costs. Economic costs relied mostly on regional and inter-regional administrations that spent 66% of costs in post-invasion management actions, contrary to all international guidelines, which recommend investing more in prevention. Regional administrations unequally reported costs. Moreover, 36% of the invasive species, reported to incur management costs, were not included in national or European regulations (i.e. Black Lists), suggesting the need to review these policies; besides, neighbouring regions seem to manage different groups of species. We suggest the need of a national lead agency to effectively coordinate actions, facilitate communication and collaboration amongst regional governments, national agencies and neighbouring countries. This will motivate the continuity of long-lasting management actions and the increase in efforts to report IAS costs by regional and inter-regional managers which will adequately provide information for future budgets gaining management effectiveness.

Abstract in Spanish

Costos económicos de las especies exóticas invasoras en España. Las evaluaciones de los costos de las especies exóticas invasoras (EEI) son un requisito urgente para informar en la toma de decisiones, coordinar y motivar la asignación de recursos económicos y humanos para la gestión de las EEI. En este estudio, buscamos información sobre los costos económicos de las EEI en España, usando la base de datos InvaCost, y solicitando datos a las administraciones regionales y nacionales, lo que resultó en más de 3000 entradas de costos. Considerando solamente los costos robustos (es decir, excluyendo los costos extrapolados, potenciales (no observados o esperados) o de baja fiabilidad), los costos económicos de EEI en España fueron estimados en 261 millones de dólares americanos (US$, 232 millones de €) entre 1997 y 2022. Observamos un incremento desde 4 millones de US$ por año antes del año 2000 hasta 15 millones de US$ por año en los últimos años (de 4 a 13 millones de €). Los datos robustos indicaron que la mayoría de los costos reportados en España (>90%) correspondieron a costos de gestión, mientras que los daños económicos sólo fueron observados para 2 de las 174 especies con costos reportados. Los costos económicos correspondieron principalmente a las administraciones regionales o inter-regionales que gastaron 66% de los costos en acciones de manejo después de la invasión, al contrario de lo recomendado en las guías internacionales, que es invertir más en prevención. Las administraciones regionales reportaron de manera desigual los costos. En este sentido, el 36% de las especies invasoras reportadas con costos de gestión no estaban incluidas en las leyes nacionales o Europeas (listas negras), lo que sugiere la necesidad de revisar esas leyes; además, las regiones vecinas parecen gestionar diferentes grupos de especies. Sugerimos la necesidad de una agencia que coordine las acciones de manera efectiva a nivel nacional, y facilite la comunicación y la colaboración entre gobiernos regionales, agencias nacionales y países vecinos. Esto motivará la continuidad de las acciones de gestión a largo plazo, que proveerán de información adecuada a los futuros presupuestos, ganando en efectividad en la gestión.

Abstract in French

Coûts économiques des espèces exotiques envahissantes en Espagne. Les évaluations économiques des espèces exotiques envahissantes (EEE) sont une nécessité urgente pour motiver et orienter les actions des autorités et décideurs en matière de gestion des EEE. Nous avons recherché les coûts économiques des EEE en Espagne via (i) la base de données InvaCost et (ii) des sollicitations adressées aux gouvernements régionaux et autorités nationales. Ce travail a abouti à l'obtention de plus de 3000 données individuelles de coûts. Si l'on ne tient compte que des données considérées comme les plus robustes (c'est-à-dire lorsqu'on exclut les coûts extrapolés, potentiels (i.e. prédits ou non-observés) et/ou peu fiables d'un point de vue méthodologique), les coûts économiques en Espagne ont été estimés à 261 millions de dollars américain (232 millions d'euros) entre 1997 et 2022. Il y a eu une augmentation annuelle de 4 millions de dollars avant 2000, puis de 15 millions de dollars par an ces dernières années. Ces données robustes ont montré que la plupart des coûts déclarés des EEE en Espagne (> 90%) correspondaient aux coûts de gestion, tandis que les coûts des dommages n'ont été constatés que pour 2 des 174 espèces dont les coûts étaient reportés. Nous avons montré que les coûts économiques reposaient principalement sur les administrations régionales et interrégionales; celles-ci ont consacré 66% des coûts enregistrés aux actions de gestion post-invasion, contrairement aux directives internationales qui recommandent d'investir davantage dans la prévention. Les administrations régionales ont déclaré les coûts de manière inégale. De plus, 36% des espèces envahissantes, déclarées comme entraînant des coûts de gestion, n'étaient pas incluses dans les réglementations nationales ou européennes (c'est-à-dire les listes noires). Ceci suggère la nécessité de revoir ces politiques; en outre, les régions voisines semblent gérer différents groupes d'espèces. Nous suggérons la nécessité d'une agence nationale 'chef de file' pour coordonner efficacement les actions, faciliter la communication et la collaboration entre les gouvernements régionaux, les agences nationales et les pays voisins. Cela motivera la continuité des actions de gestion à long terme et l'intensification des efforts pour rendre compte des coûts des EEE par les gestionnaires régionaux et interrégionaux. Tout ceci permettra de fournir des informations adéquates pour les budgets futurs, avec un bénéfice certain pour l'efficacité des mesures de gestion.

Abstract in Italian

Costi economici delle specie aliene invasive in Spagna. Le valutazioni economiche delle specie aliene invasive (SAI) sono un requisito urgente per processi decisionali informati, e per coordinare e motivare l'allocazione di risorse economiche e umane per la gestione delle SAI. Usando la banca dati InvaCost e richiedendo i dati ai governi regionali e alle autorità nazionali, abbiamo cercato i costi economici delle SAI presenti in Spagna, ottenendo come risultato 3000 voci di costi. Considerando solo i dati robusti (i.e. escludendo i costi estrapolati, potenziali (non sostenuti od attesi) e con bassa attendibilità), i costi economici in Spagna dal 1997 al 2022 stati stimati a 261 milioni di $ americani (232 milioni di €). C'è stato un aumento da 4 milioni di $ americani all'anno prima del 2000 a 15 milioni di $ americani all'anno negli ultimi anni (da 4 a 13 milioni di €). I dati robusti hanno mostrato che la maggior parte (> 90%) dei costi riportati per le SAI in Spagna corrispondeva a costi di gestione, mentre i costi riferiti ai danni sono stati trovati solo per 2 delle 174 specie con costi riportati. I costi economici si basano soprattutto sulle amministrazioni regionali e interregionali, che hanno speso il 66% dei costi in azioni di gestione post invasione, contrariamente a tutte le linee guida internazionali, che raccomandano di investire di più nella prevenzione. Le amministrazioni regionali hanno riportato i costi in modo diseguale. Inoltre, il 36% delle specie invasive per cui sono riportati costi di gestione non era incluso nei regolamenti nazionali o europei (i.e. Liste Nere), il che suggerisce il bisogno di rivedere queste politiche; inoltre, regioni limitrofe sembrano gestire gruppi diversi di specie. Suggeriamo la necessità di un'agenzia principale nazionale per coordinare efficacemente le azioni, facilitare la comunicazione e la collaborazione tra i governi regionali, le agenzie nazionali e i Paesi vicini. Questo motiverà la continuità di azioni di gestione a lungo termine e l'aumento degli sforzi per riportare i costi delle SAI da parte dei gestori regionali e interregionali, che forniranno informazioni adeguatamente per far sì che i futuri bilanci acquisiscano efficacia gestionale.

Abstract in Portuguese

Custos econômicos das espécies invasoras na Espanha. Avaliações econômicas para espécies exóticas invasoras (EEI) são uma necessidade urgente para informar, coordenar e motivar tomadores de decisão na alocação de recursos econômicos e humanos para a gestão das EEI. Nós buscamos por custos econômicos de EEI na Espanha utilizando o banco de dados InvaCost e solicitamos dados para governos regionais e autoridades nacionais, o que resultou em mais de 3.000 registros de entrada. Considerando apenas dados robustos (ou seja, excluindo custos extrapolados, potenciais (não observados ou esperados) e custos de baixa confiabilidade), os custos econômicos na Espanha foram estimados em 261 milhões de dólares (232 milhões de euros) de 1997 até 2022. Houve um aumento de 4 milhões de dólares por ano, antes do ano 2000, para 15 milhões anuais nos anos mais recentes (de 4 para 13 milhões de euros). Com base nos dados robustos, os custos com manejo foram os mais reportados na Espanha (> 90%), enquanto custos com danos foram encontrados apenas para 2 das 171 espécies com custos reportados. Os custos econômicos dependem principalmente de administrações regionais e inter-regionais que gastaram 66% do recurso com ações de manejo pós-invasão, ao contrário de todas as diretrizes internacionais que recomendam investir mais em prevenção. Administrações regionais reportaram os custos de forma desigual. Além disso, 36% das espécies invasoras, que foram responsáveis por custos com manejo, não foram incluídas em regulamentações nacionais ou europeias (tal como, listas de espécies indesejadas), sugerindo a necessidade de revisão dessas políticas. Ainda, regiões vizinhas parecem gerir diferentes grupos de espécies. Nós sugerimos a necessidade de uma agência nacional central para coordenar ações de forma efetiva, facilitar a comunicação e a colaboração entre os governos regionais, agências nacionais e países vizinhos. Isso irá motivar a continuidade de ações de gestão a longo prazo e o aumento dos esforços para reportar custos com EEI por gestores regionais e inter-regionais, que fornecerão informações adequadas para orçamentos futuros ganhando eficácia na gestão.

Abstract in Arabic

التكاليف الاقتصادية للأنواع الغريبة الغازية في إسبانيا. تعتبر التقييمات الاقتصادية للأنواع الغريبة الغازية حاجة ملحة لتحفيز وتوجيه إجراءات السلطات وصناع القرار في إدارة وتسيير الأنواع الغريبة الغازية. لقد بحثنا، من خلال الدراسة التي بين أيدينا، في التكاليف الاقتصادية للأنواع الغريبة الغازية في إسبانيا، وذلك باستثمار المعلومات المتاحة في قاعدة بيانات أنفاكوست وبتوجيه طلبات إلى الحكومات الإقليمية والسلطات الوطنية الإسبانية. وقد نتج عن هذا العمل الحصول على أكثر من 3000 بيانات تكلفة فردية مختلفة للأنواع الغازية. وإذا ما اعتبرنا فقط البيانات الأقوى (أي عند استبعاد التكاليف المستقرأة (أي المتوقعة أو غير الملاحظة) و/أو غير الموثوق بها من وجهة نظر منهجية)، فقد بلغت التكاليف الاقتصادية في إسبانيا نحو 261 مليون دولار أمريكي (232 مليون يورو) بين عامي 1997 و2022. وكانت هناك زيادة سنوية قدرها 4 ملايين دولار قبل عام 2000، ثم 15 مليون دولار سنويًا في السنوات الأخيرة. وقد أظهرت هذه البيانات القوية أن معظم التكاليف المبلغ عنها للأنواع الغريبة الغازية في إسبانيا (أكثر من 90%) ترتبط بتكاليف التسيير، في حين تم العثور على تكاليف الضرر لنوعين فقط من أصل 175 نوعا تم تحديد تكلفتها. كما أظهرت هذه الدراسة أن التكاليف الاقتصادية تقع بشكل رئيسي على عاتق الإدارات الإقليمية وبين-الإقليمية. هذا وقد خصصت هذه الأخيرة 66% من التكاليف المسجلة لإجراءات التسيير ما بعد الغزو البيولوجي، خلافًا للتوجيهات الدولية التي توصي بزيادة الاستثمار في مجالات الوقاية القبلية. كما أبلغت هذه الإدارات الإقليمية عن التكاليف بشكل متفاوت. وبالإضافة إلى ذلك، فإن 36% من الأنواع الغازية، التي أبلغ عن أنها تسبب في تكاليف التسيير، لم تكن مدرجة في التشريعات الوطنية أو الأوروبية (أي القوائم السوداء). وهذا يشير إلى الحاجة الماسة إلى مراجعة هذه السياسات؛ وعلاوة على ذلك، يبدو أن المناطق المجاورة تدير مجموعات مختلفة من الأنواع. وعطفا على ما سبق، فإننا نحث، كتوصية، على خلق وكالة وطنية رائدة لتنسيق الإجراءات بشكل فعال وتسهيل الاتصال والتعاون بين الحكومات الإقليمية والوكالات الوطنية والبلدان المجاورة. وسيحفز ذلك، لا محالة، على استمرارية إجراءات الإدارة على المدى الطويل وتكثيف الجهود لتحديد دقيق لتكاليف الأنواع الغريبة الغازية من قبل المسيرين الإقليميين وبين-الإقاليميين

Abstract in Galician

Custos económicos das especies exóticas invasoras en España. As avaliacións económicas para especies exóticas invasoras (EEI) son un requisito urxente para a toma de decisións informadas e a coordinación e motivación da asignación de recursos económicos e humanos para a súa xestión. Neste estudo buscamos información dos custos económicos das EEI en España mediante a utilización da base de datos InvaCost e solicitude de datos aos gobernos rexionais e autoridades nacionais, o que deu lugar a máis de 3.000 entradas de custos. Considerando só datos sólidos (é dicir, excluíndo os custos extrapolables, potenciais (non ocasionados ou esperados) e de baixa fiabilidade), os custos económicos en España estimáronse en US$ 261 millóns (232 millóns de euros) entre 1997 e 2022. Houbo un aumento de US$ 4 millóns ao ano antes do 2000 a US$ 15 millóns ao ano nos últimos anos (de 4 a 13 millóns de euros). Os datos sólidos mostraron que a maioría dos custos reportados das EEI en España (> 90%) corresponden a custos de xestión, mentres que os custos dos danos só se atoparon en 2 das 174 especies con custos notificados. Os custos económicos dependen principalmente das administracións rexionais e interrexionais que gastaron o 66% dos custos en accións de xestión posterior á invasión, en contra de todas as directrices internacionais, que recomendan investir máis en prevención. As administracións rexionais informaron desigualmente dos custos. Ademais, o 36% das especies invasoras con custos de xestión reportados, non foron incluídas na normativa nacional ou europea (é dicir, as listas negras), o que suxire a necesidade de revisar estas políticas; ademais, as rexións veciñas parecen xestionar diferentes grupos de especies. Suxerimos a necesidade dunha axencia líder nacional para coordinar de xeito eficaz as accións de xestión, e facilitar a comunicación e a colaboración entre gobernos rexionais, axencias nacionais e países veciños. Isto motivará a continuidade das accións de xestión de longa duración e o aumento dos esforzos para reportar os custos das EEI por parte dos xestores rexionais e interrexionais, o cal proporcionará información para os futuros orzamentos que mellorarán a eficacia da xestión de EEI.

Abstract in Catalan

Custos Costos econòmics de les espècies exòtiques invasores a Espanya. L'avaluació econòmica del impacte d'espècies exòtiques invasores (EEI) és un requisit urgent per a la presa de decisions informades, promovent i coordinant l'assignació de recursos humans i econòmics per a una gestió adequada de les EEI. Hem cercat informació sobre els costos econòmics de les EEI a Espanya, mitjançant la base de dades InvaCost i consultes als governs regionals i les autoritats nacionals, amb un resultat de més de

3.000 entrades sobre costos. Tenint en compte només dades sòlides (és a dir, excloent els costos extrapolats, potencials (no incorreguts o esperats) i costos de baixa fiabilitat), els costos econòmics a Espanya es van estimar en 261 milions de dòlars (US$, 232 milions d'euros) des del 1997 fins al 2022. Hi va haver un augment de 4 milions de dòlars per any abans del 2000 a 15 milions de dòlars en als darrers anys (de 4 a 13 milions d'euros). Les dades sòlides van mostrar que la majoria dels costos reportats de les EEI a Espanya (> 90%) corresponien als costos de gestió, mentre que els costos de danys només es van trobar en 2 de les 174 espècies amb els costos reportats. Els costos econòmics es basaven principalment en administracions regionals i interregionals que gastaven el 66% dels recursos en accions de gestió postinvasió, contràriament a totes les directrius internacionals, que recomanen invertir més en prevenció. Les administracions regionals van informar desigualment de costos. D'altra banda, el 36% de les espècies invasores, que suposaven un cost de gestió, no estaven incloses en les regulacions nacionals o europees (és a dir, les llistes negres), cosa que suggereix la necessitat de revisar aquestes polítiques; a més, les regions veïnes semblen gestionar diferents grups d'espècies. Suggerim la necessitat d'una agència líder nacional per coordinar eficaçment les accions, facilitar la comunicació i la col·laboració entre governs regionals, agències nacionals i països veïns. Això motivarà la continuïtat de les accions de gestió de llarga durada i una millora de la informació sobre els costos derivats de les EEI per part dels gestors regionals i interregionals, proporcionant la informació adequada per tal de maximitzar una eficaç gestió en futurs pressupostos.

Abstract in Basque

Espezie exotiko inbaditzaileen kostu ekonomikoak Espainian. Espezie exotiko inbaditzaileen (EEI) kudeaketarako kostuen ebaluazioa ezinbestekoa da, bai erabakiak hartzeko, informazioa emateko zein baliabide ekonomikoen eta giza baliabideen esleipena koordinatu eta motibatzeko. Ikerketa honetarako Espainiako EEIen kostu ekonomikoei buruzko informazioa bilatu genuen. Horretarako InvaCost datubasea erabiliz gain, eskualdeko eta nazioko administrazioei datuak eskatu genizkien. Guztira, bilaketak 3.000 kostu-sarrera baino gehiago ekarri zituen. Kostu sendoak bakarrik kontuan hartuta (hau da, espero ziren kostuak, aurreikusiak edo potentzialak alde batera utzita), 1997 eta 2022 bitartean Espainian EEIren kostu ekonomikoak 261 milioi dolar (232 milioi €) izan zirela kalkulatu zen. 2000. urtea baino lehen urteko kostua 4 milioi US$-koa bazen, azken urteetan 15 milioira igo da (hau da, 4 milioi eurotik 13 milioi eurora). Datu sendoen arabera, Espainian jakinarazitako kostu gehienak (>90%) kudeaketakostuei zegozkien. Kalte ekonomikoak, berriz, 174 espezieetatik 2rekin bakarrik erlazionatu ziren. Kostu ekonomikoak eskualdeko edo eskualde arteko administrazioenak izan ziren batez ere. Nazioarteko gidetan gomendatzen den moduan prebentzioan gehiago inbertitu beharrean, kostuen %66 inbasioaren ondorengo erabilera-ekintzetan gastatu zuten. Eskualdeetako administrazioek ez zituzten kostuak modu berean aurkeztu. Kudeaketarako kostuak ezarritako espezie inbaditzaileen artean, %36a ez zen lege nazionaletan edo Europako legeetan agertzen (zerrenda beltzak). Gertaera honek, legeak berrikusteko beharra adierazten du. Horrez gain, aldameneko eskualdeek espezie-talde desberdinak kudeatzen dituztela dirudi. Hori dela eta, estatu mailan ekintzak eraginkortasunez koordinatuko dituen agentzia baten beharra iradokitzen dugu. Agentziak gainera eskualdeetako gobernuen, agentzia nazionalen eta auzoko herrialdeen arteko komunikazioa eta lankidetza erraztu beharko luke. Kudeaketa eraginkorragoa izan dadin, agentziaren sorrerak epe luzeko kudeaketa-ekintzak aurrera jarraituko dutela eta etorkizuneko aurrekontuei buruzko informazio egokia emango dela ziurtatuko luke.

Keywords

Iberian Peninsula, InvaCost, management costs, monetary impacts, non-native species, prevention costs, socioecology, stakeholders

Introduction

Invasive alien species (IAS) can cause significant negative environmental and socioeconomic impacts (Blackburn et al. 2019). These include loss of biodiversity (Simberloff et al. 2013; Bellard et al. 2016), changes to ecosystem functioning (Ehrenfeld 2011), impacts on human health and well-being (Jeschke et al. 2014) and large economic losses. Knowledge about the economic impact of IAS is, however, generally limited geographically, taxonomically or to some socioeconomic sectors. In the 2000s, Pimentel et al. (2005) provided the first estimations of the economic costs of IAS at large spatial scales. Since then, other studies have attempted to collect further data on these costs, such as in Europe (Kettunen et al. 2009), in invasion research and management (Scalera 2010) or for specific taxonomic groups (e.g. insects, Bradshaw et al. 2016). However, available data are scarce, scattered and not easily accessible and extrapolation-based approaches underlying most of these estimates are methodologically questionable (Cuthbert et al. 2020). These fragmented data and methodological flaws are reflected by critical knowledge gaps on the economic costs of IAS for most taxa, countries and regions of the world (Aukema et al. 2011). Such economic assessments are, therefore, an urgent requirement for informed decision-making by policy-makers and other stakeholders, for coordinating and motivating the allocation of economic and human resources for the management of IAS and for raising public awareness (Hulme 2006; Andreu et al. 2009; Diagne et al. 2020a, 2021a).

Europe represents a hub for alien species introductions (Turbelin et al. 2017), of which several thousands are already established (Dawson et al. 2017), inducing substantial economic impacts to the continent (Haubrock et al. 2021a). As a consequence, there is an increasing awareness to tackle IAS throughout the continent (García-de-Lomas and Vilà 2015; Turbelin et al. 2017). With an area of 505,992 km^2, Spain is one of the largest countries in Europe, presenting a considerable geographical, topographical, climatic, geological and species diversity. It also has a large diversity of IAS: the Spanish Government estimates that up to 190 alien species have already established invasive populations in the country (Spanish Catalogue of Invasive Alien Species, Royal Decree 630/2013). Spain has adopted legislation aiming at tackling biological invasions for the last 25 years. However, although the introduction of IAS was already considered as a criminal offence since 1995 (through an Organic Law, 10/1995) and the Spanish Strategy for the Conservation and Sustainable Use of Biodiversity (following the Convention of the Biological Diversity's recommendations to protect biodiversity from IAS) was developed in 1998, it was not until 2007 when policies for preventing and managing IAS were strengthened. The Law of Natural and Biodiversity Heritage (Law 42/2007) includes not only the need for prevention (through the Spanish Catalogue of Invasive Alien Species, Royal Decree 630/2013), but also the creation of strategic management plans for those IAS that threaten native species, natural habitats, agronomy and economic resources associated with environmental resources. The responsibility for implementing the Law falls into the "competent authorities", which are mainly the regional governments (i.e. the autonomous communities) and the national authorities (e.g. national authorities managing borders, continental waters or national parks that spatially correspond to more than one region).

Andreu et al. (2009) showed that environmental managers from regional authorities in Spain were generally aware of the risks posed by biological invasions. However, they claimed that there were limited economic funds to manage invasive alien species, and a lack of coordination amongst different regional and national administrations, scientific research on the performance of different strategies to manage invasive alien species and knowledge on the economic costs of IAS in the country (Andreu et al. 2009). The latter is known to be essential to help regional and national authorities to set up efficient budgets for IAS management. In this context, the InvaCost database (Diagne et al. 2020b), the most up-to-date repository of invasion costs worldwide, provides an excellent opportunity to tackle the current lack of data on the economic costs of IAS in Spain. Here, we extracted the data available in the InvaCost database regarding the economic costs of IAS in Spain. We expanded these data by requesting further information directly from Spanish regional and national environmental managers. Our aims were to (i) describe the distribution of reported economic costs of IAS across regions, environments, taxonomic groups, cost types and economic sectors; (ii) identify those IAS causing the highest costs; and (iii) examine the temporal trends of the economic costs reported over the last decades.

Methods

Data collection

We extracted data on the costs of IAS from the most updated version of the InvaCost database: InvaCost_v.3.0 (9,823 entries, Diagne et al. 2020b, https://doi.org/10.6084/m9.figshare.12668570) (Fig. 1a). This database consists of cost data extracted from documents obtained through standardised literature searches (i.e. using SI Web of Science platform, Google Scholar and the Google search engine) and opportunistic targeted searches (i.e. expert consultations for which data gaps were identified). One of these targeted searches addressed cost data in non-English languages (Angulo et al. 2020, https://doi.org/10.6084/m9.figshare.12928136). Cost values (including Spanish) recorded in InvaCost_v.3.0 were converted from local currencies to US$ by dividing the cost estimate by the official market exchange rate corresponding to the year of the cost estimation and then to 2017 US$ using inflation factors (Diagne et al. 2020b). From InvaCost_v.3.0, we extracted specific relevant data, resulting in a total of 3,260 entries of economic costs of IAS in Spain (Suppl. material 1; Fig. 1b).

Due to the importance of the non-English targeted search for the Spanish dataset (i.e. only 49 of the 3,260 entries in our dataset were extracted from documents written in English – 20 vs. 61 documents), we expand here the methods used by Angulo et al. (2021) to collect cost data in non-English languages. Spain is administratively divided into 17 autonomous regions (herein "regions"). Each of these regions manages IAS independently. We explored the web pages of regional government offices in charge of managing invasive species in each region and, when available, emailed environmental managers or sent administrative forms requesting economic data on the costs of IAS.

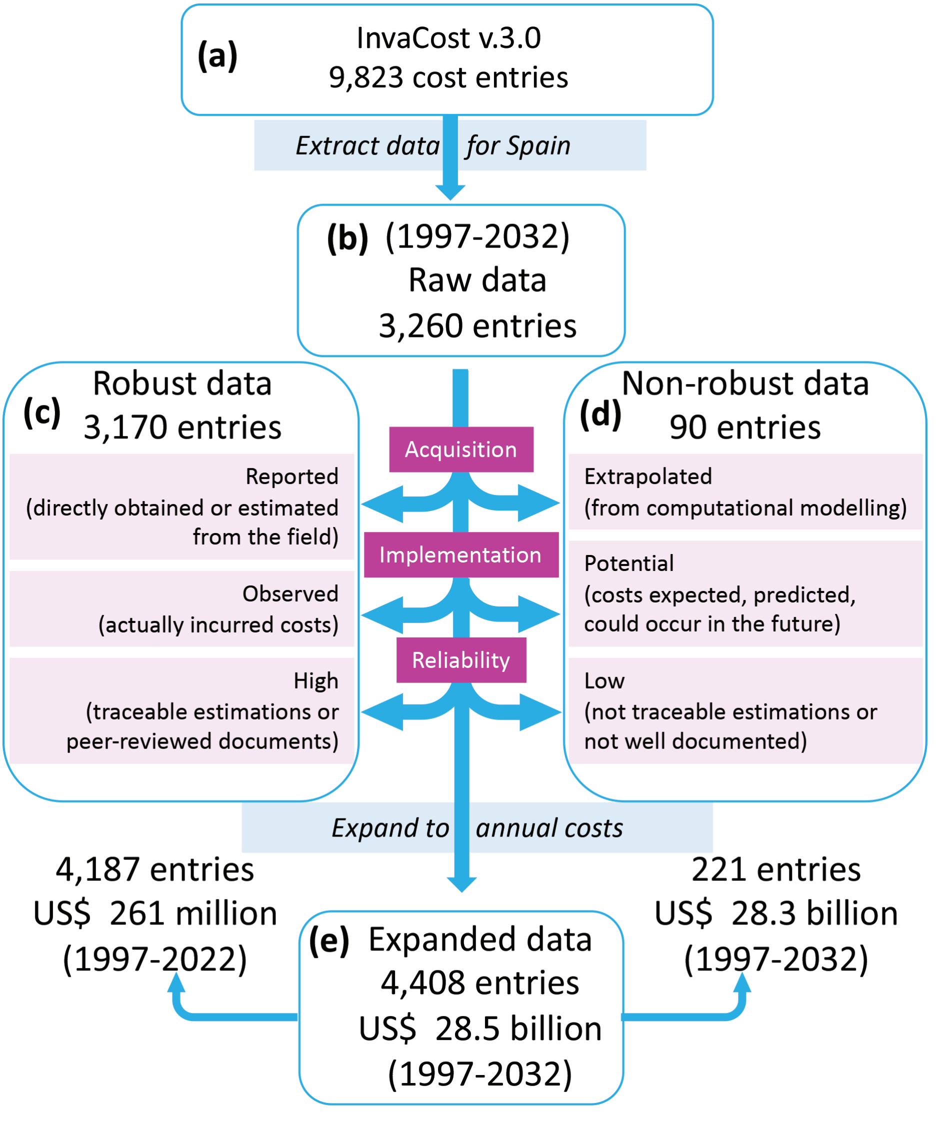

Figure 1. Data collection and filtering processes (**a**) data sources (**b**) raw data (timeframe and number of entries) obtained after extracting the data for Spain; raw data were segregated in two groups (**c**) robust data and (**d**) non-robust data using three variables, acquisition, implementation and reliability (**e**) expanded data to obtain comparable yearly costs.

Moreover, Spanish continental waters are managed in coordination with the Ministry for the Ecologic Transition and Demographic Challenge, through independent river basin authorities (hydrographic confederations). Therefore, we searched for available information in their web pages and contacted those river basin authorities from whom we could obtain the contact details of their environmental managers (i.e. Guadiana, Tajo, Segura, Basque Country, Cantábrico). In the region of Valencia, costs were reported as working days and we transformed them into economic costs by multiplying the reported number of working days by € 128 (i.e. cost per day, Vicente del Toro, Biodiversity Service, Generalitat Valenciana, pers. comm.). We obtained data for Spain up to December 2020, with costs being reported in Spanish and in two co-official languages: Catalan and Galician (Suppl. material 1: Tab InvaCost_3.0_Spain, column "language").

Data structure

Cost data extracted for Spain (herein raw data, Fig. 1b, Suppl. material 1: Tab InfoVariables) were described with a set of variables pertaining to: (i) information on the document reporting the cost, (ii) spatial information (e.g. location, spatial scale, environment – aquatic or terrestrial – and whether the location corresponds to a protected area or to an island), (iii) taxonomy of the invasive species incurring the cost, (iv) temporal information, (v) typology of costs reported (e.g. management actions or economic damages, impacted sector) and (vi) a set of variables reporting the raw cost estimates, currency used and the converted US$ values.

With respect to the type of cost, we first used the column "type_of_cost_merged" which included three categories: "damage" costs: economic losses due to direct and/or indirect impacts of invaders, such as yield loss, health injury, land alteration, infrastructure damage or income reduction; "management" costs: economic resources allocated to prevention, control, research, long-term management, or eradication; "mixed" costs: when costs include both damage and management expenditure. We also used the column "management_type" to divide further management costs in the following categories: "pre-invasion management": monetary investments for preventing successful invasions in an area (including quarantine or border inspection, risk analyses, biosecurity management, etc.); "post-invasion management": money spent for managing IAS in invaded areas (including control, eradication, containment); "knowledge/funding": money allocated to all actions and operations that could be of interest at all steps of management at pre- and post-invasion stages (including administration, communication, education, research etc.); "unspecified" for costs without detailed types; and a "mixed" category was assigned when costs included at least two of the above categories.

Categories for the economic sector included: "agriculture": considered at its broadest sense, such as crop growing, livestock breeding, beekeeping, land management; "authorities-stakeholders": governmental services and/or official organisations – such as conservation agencies and forest services – that allocate efforts for the management of biological invasions (e.g. control programmes, eradication campaigns, research funding); "environment": impacts on natural resources, ecological processes and/or ecosystem services; "forestry": forest-based activities and services, such as timber production/industries and private forests; "health": for every item directly or indirectly related to human health, such as control of disease vectors (e.g. mosquitoes transmitting pathogens to humans) or medical care and damage to work productivity due to impacts on health; "public and social welfare": activities, goods or services contributing to human well-being and safety in our societies, including local infrastructure, such as the electricity system, quality of life (e.g. income, recreational activities), personal goods (e.g. private properties, lands), public services (e.g. transport, water regulation) and market activities (e.g. tourism, trade).

Data processing

Three variables about the typology of the costs are important for the further selection of the data we used (Diagne et al. 2020b): (i) the acquisition method for the cost value ("reported" if the cost data were directly obtained or derived using inference methods from field-based information or "extrapolated" if the cost data were obtained using computational modelling), (ii) the implementation of the cost ("observed" if the cost was actually incurred or "potential" if the cost is predicted to occur over time) and (iii) the reliability of the cost value reported ("high" or "low", based on whether the approach used for cost estimation in the document was reported and traceable). We filtered our dataset to differentiate the most robust data, i.e. directly reported, observed and highly reliable costs (corresponding to 3,170 raw entries, Fig. 1c). Indeed, we considered as non-robust data 90 cost entries that were extrapolated, not yet actually incurred and/or of low reliability (Fig. 1d).

We considered the full dataset (raw data, 3,260 entries, Fig. 1b) to explore general differences in the number of cost entries for Spain amongst descriptors. The number of entries is a good indicator of how detailed reported costs are (e.g. costs obtained from a single report for one region covering all invasive species, invaded locations, years and types of management can be assumed to be less detailed than costs obtained from several reports, each of them covering different invasive species and their management). Moreover, since the period of estimation across reported costs varied from months to years, we homogenised the cost values for the full dataset (including both robust and non-robust data) as follows: we recalculated costs covering several years on an annual basis and repeated these annual values over the duration time (in number of years) of each cost occurrence. For example, a cost reporting US$ 500 occurring in the period 1996–2000 was transformed into five identical costs of US$ 100 for each of those years. Costs occurring in less than one year were assumed as having occurred during a single complete year in order to avoid overestimation. Hence, we obtained comparable annual costs for all cost entries. This was performed using the "expandYearlyCosts" function of the 'invacost' package version 0.3-4 (Leroy et al. 2020 in R version 3.6.3 (R Core Team 2020). The expanded full dataset resulted in 4,408 entries (Fig. 1e) from which 4,187 cost entries correspond to robust data and 221 to non-robust data. All the analyses presented in the main text were carried out with the robust data. Results including the non-robust data are briefly presented in the first sentences of the results and shown in Figure 1 and in Suppl. material 2: Fig. S1.

Data analysis

We first described the number of entries and the economic costs for each of the 17 autonomous regions and mapped the information across the country using the package "ggplot" in R version 4.0.2 (R Core Team 2020). We also described the costs across specific descriptors: main taxonomic groups, main environments in which the costs occurred, economic sectors impacted by the cost, the spatial scale at which the costs occurred and whether or not the costs occurred in protected areas.

We calculated the temporal trends of IAS economic impacts in Spain by using the function summarizeCosts of the "invacost package" version 0.3-4 (Leroy et al. 2020) in R version 3.6.3 (R Core Team 2020). This function allowed us to calculate average annual costs between 1997 and 2019, providing averages in 4-year periods throughout the study period using the extended entries calculated by the "expandYearlyCosts" function described above.

Finally, we identified the costliest IAS in Spain and assessed whether the species causing economic costs in Spain are those recorded as invasive in the country or included in European or national regulations. We collected information on the identity of those alien species (i) recorded as invasive in Spain (sensu the Global Invasive Species Database; http://www.issg.org/database); (ii) included in the Spanish Catalogue of Invasive Alien Species (Royal Decree 630/2013), (iii) included in the List of Invasive Species of Union Concern (EU, No 1143/2014 of the European Parliament); and (iv) proposed as potential candidates to be included in the List of Invasive Species of Union Concern (Carboneras et al. 2018). Besides European and National regulations, some Spanish regions also present regional invasive alien species regulations. For example, in the region of Aragon, it is not allowed to introduce, catch, keep, transport or sell any freshwater alien crayfish species (Decreto 127/2006 of the Aragon Government). However, most regions rely exclusively on national and European regulations and have no specific lists of invasive alien species (with the exception of Valencia; Decreto 14/2013 of the Consell). Therefore, we only considered national and European regulations in our analysis.

Results

Costs of invasive species in Spain amounted to US$ 28.52 billion (€ 25.38 billion, using the 0.89 conversion factor for 2017) from 1997 to 2032 (Fig. 1e). However, although only 90 out of 3,260 raw entries were extrapolated, potential and/or unreliable costs, these constituted 99.08% of the economic costs in our dataset (Fig. 1e). Most of these high costs were driven by one single entry: a cost derived from an extrapolation of the potential loss of forestry stock caused by *Bursaphelenchus mucronatus*, the pine wood nematode, over a period of 22 years (2008–2030, Suppl. material 2: Fig. S1). Without considering non-robust data, the reported, observed and reliable costs for invasive species in Spain constituted US$ 261.28 million (€ 232.54 million). These costs occurred from 1997 to 2020, except for two raw entries that went over this year: one corresponding to a LIFE+ project ranging from 2019 to 2022 aimed at controlling *Lampropeltis californiae* in the Canary Islands and the second corresponding to an annual management programme for invasive plants in Sierra Espuña Regional Park (Murcia) that included part of the year 2021. Thus, both reported budgets are considered already delivered costs.

Only using the robust dataset, we showed that the highest amount of costs was reported for plants (66%; especially from the orders Myrtales and Commelinales), followed by arthropods (12%; mainly insects) and mollusca (11%; mostly bivalves) (Fig. 2a–e). Most costs corresponded to IAS from terrestrial environments (53%), while

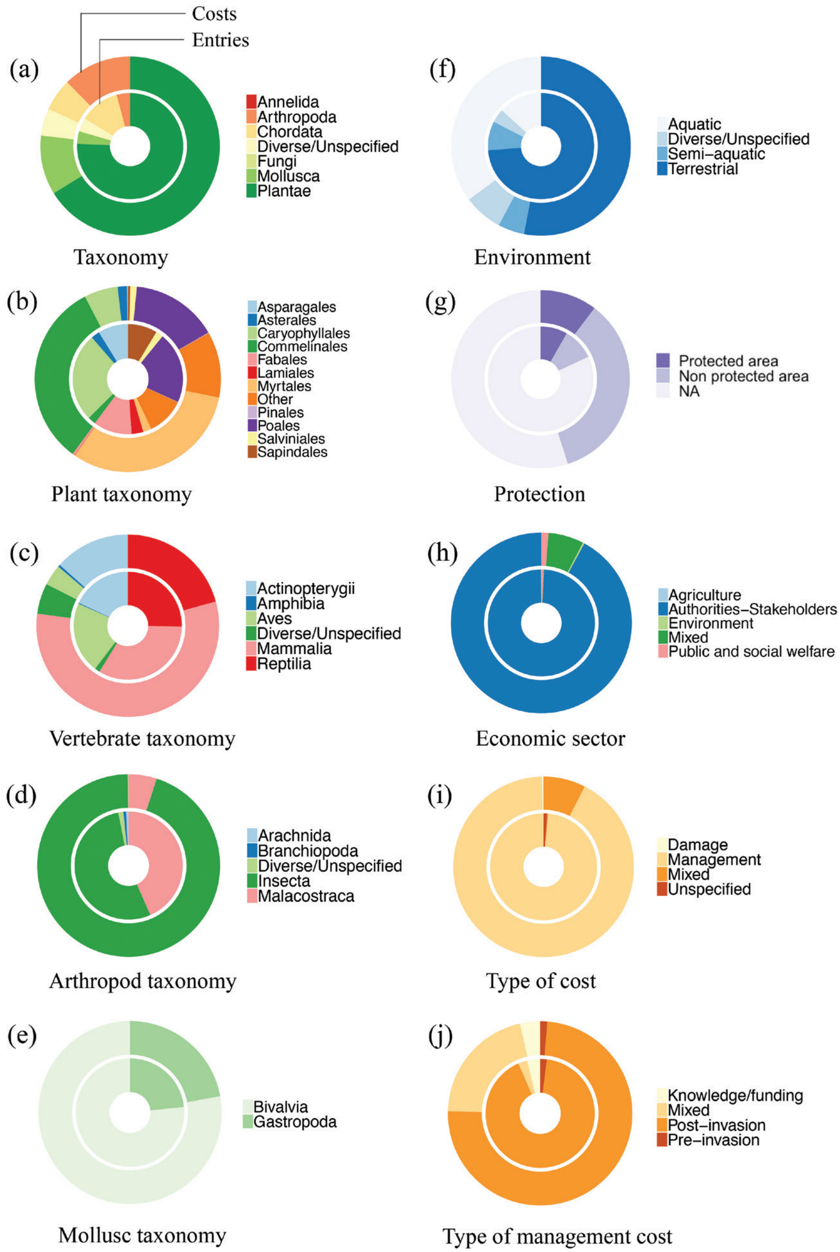

Figure 2. Total economic costs (outer circles) and number of entries (inner circles) for invasive species in Spain for each cost descriptor (**a**) taxonomy in general (**b**) plant taxonomy (**c**) vertebrate taxonomy (**d**) arthropod taxonomy (**e**) mollusc taxonomy (**f**) environment (**g**) protection (**h**) economic sector (**i**) type of cost and (**j**) type of management cost. See methods for description of categories.

aquatic and semi-aquatic environments contributed with 35% and 5% of the costs, respectively; the number of entries was much higher for terrestrial environments (Fig. 2f). Only 10% of the total costs were reported to occur specifically in protected areas

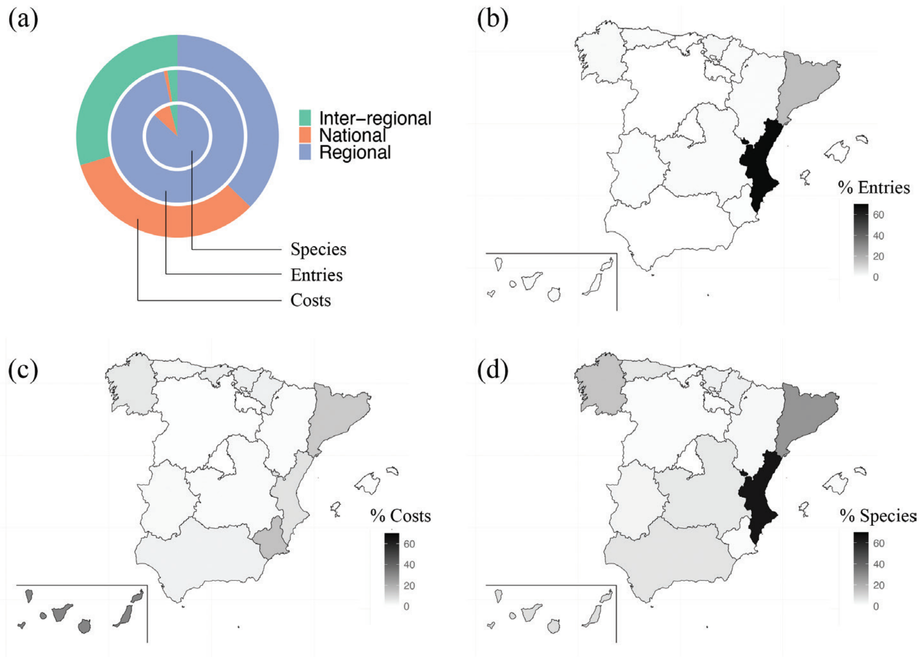

Figure 3. Distribution of the observed economic costs of biological invasions in Spain across the autonomous regions (**a**) relative importance of country, inter-regional and regional levels in costs and number of species with costs (**b**) proportion of entries (**c**) total economic costs (US$ million), and (**d**) number of species with costs. All values correspond to the robust data (reported, incurred and reliable costs); values in (**b**) and (**d**) correspond to the raw data and (**c**) to the expanded data.

(Fig. 2g). The most impacted sector was authorities and stakeholders (92%, Fig. 2h); i.e. governmental services and/or official organisations (e.g. conservation departments) that allocate efforts to the management of IAS (e.g. prevention, eradication campaigns, control or monitoring programmes, research funding). The forestry and health economic sectors had only one (for *B. mucronatus*) and two (for *Ambrosia artemisiifolia*) entries, respectively. These entries consisted of extrapolated amounts and, therefore, were not considered as robust data. Costs impacting agriculture came from both scientific papers (three entries that consisted of extrapolated costs and, thus, not included in the robust data) and information obtained directly from managers (four entries for *Pomacea* spp.). Less than 1% of the costs corresponded to economic damage while 92% corresponded to management costs (Fig. 2i). Taking into account only management costs, most costs reporting management actions consisted in post-invasion management (74%), while relatively low costs were spent for knowledge/funding (3%, including education, communication etc.) and pre-invasion management actions (1%, Fig. 2j).

Although a high number of entries corresponded to information obtained directly from the regional autonomous communities, economic costs were divided almost equally at the country (33%), inter-regional (30%, such as river basins situated across regions) and regional levels (37%, Fig. 3a). Within the autonomous regions, there were differences in the amount of costs and number of entries amongst them (Fig. 3b, c).

Both variables showed different patterns; for example, Valencia reported a high number of detailed entries (i.e. including information on time, location, type of management etc.), while their costs were not as high as those reported by other regions, such as Murcia and Canary Islands. In other cases, for example, Catalonia, a high number of entries corresponded to a high amount of costs. Valencia had the highest number of entries, expanding from 2009 to 2019, followed by Catalonia, from 2014 to 2018 (Fig. 3b). Canary Islands constituted the region with the highest reported costs, followed by Murcia, Catalonia, Valencia and Galicia (Fig. 3c). The rest of the regions accounted for less than US$ 5 million. Castilla y León and La Rioja showed the lowest costs (i.e. lower than US$ 1 million). With respect to the number of IAS managed by region, these largely differed amongst regions, ranging from 1 to 111 IAS (Fig. 3d). Mean number of IAS reported to incur costs amongst regions (16.5) was intermediate between the ones managed at the country level (18) and the ones managed at the inter-regional level (8).

The average annual costs of biological invasions in Spain, taking into account only the robust data, was US$ 10.85 million (€ 9.66 million) over a time period from 1997 to 2020 (Fig. 4). Most of the robust data were reported between 2017 and 2020. Annual costs increased from US$ 4.22 million per year (€ 376 million) before 2000 to US$ 14.60 million per year (€ 12.99 million) in the last four years (Fig. 4). Using the robust dataset, trends of costs in Spain showed an initial increase during the first decade of cost reporting (1997–2007) and seemed to stabilise afterwards (Fig. 4). The apparent decrease in reported costs between 2013 and 2016 is most likely an artefact arising from a lack of cost estimates, given the multi-year delay between occurrence and reporting in literature.

Robust data show that economic damage in Spain was only observed for two species (*Dreissena polymorpha* and *Procambarus clarkii*), while the rest of the costs corresponded to managing IAS (Fig. 5a). Of the 174 IAS incurring management costs in Spain (robust data), 63 (36%) were not recorded as invasive for the country (GISD; http://www.issg.org/database) nor included in the current European or national regulations or proposed to be assessed to potentially include them in European regulations (Fig. 5a, Suppl. material 3). The management costs corresponding to these 63 invasive species (US$ 48.24 million, € 42.93 million) were recorded in the regions of Asturias (1 species), Balearic Islands (1), Canary Islands (4), Cantabria (1), Castilla La Mancha (1), Catalonia (4), Galicia (4), Navarra (2) and Valencia (46). Most of the costs invested in managing IAS that are not included in national or European regulations corresponded to terrestrial and aquatic plants (Fig. 5b, Suppl. material 3).

The 10 IAS presenting the highest economic costs (considering only robust management costs) include five terrestrial plants, one aquatic plant, two terrestrial animals and two aquatic animals (Table 1). Of these, seven species are included in the national regulations (*Arundo donax*, *Carpobrotus* sp., *Cenchrus setaceus*, *Cylindropuntia rosea*, *Eichhornia crassipes*, *Rhynchophorus ferrugineus* and *Vespa velutina*) and four in the European regulations of IAS (*E. crassipes*, *C. setaceus*, *C. rosea* and *V. velutina*). Regarding the number of cost entries of IAS in Spain, 50% of the entries corresponded to 15

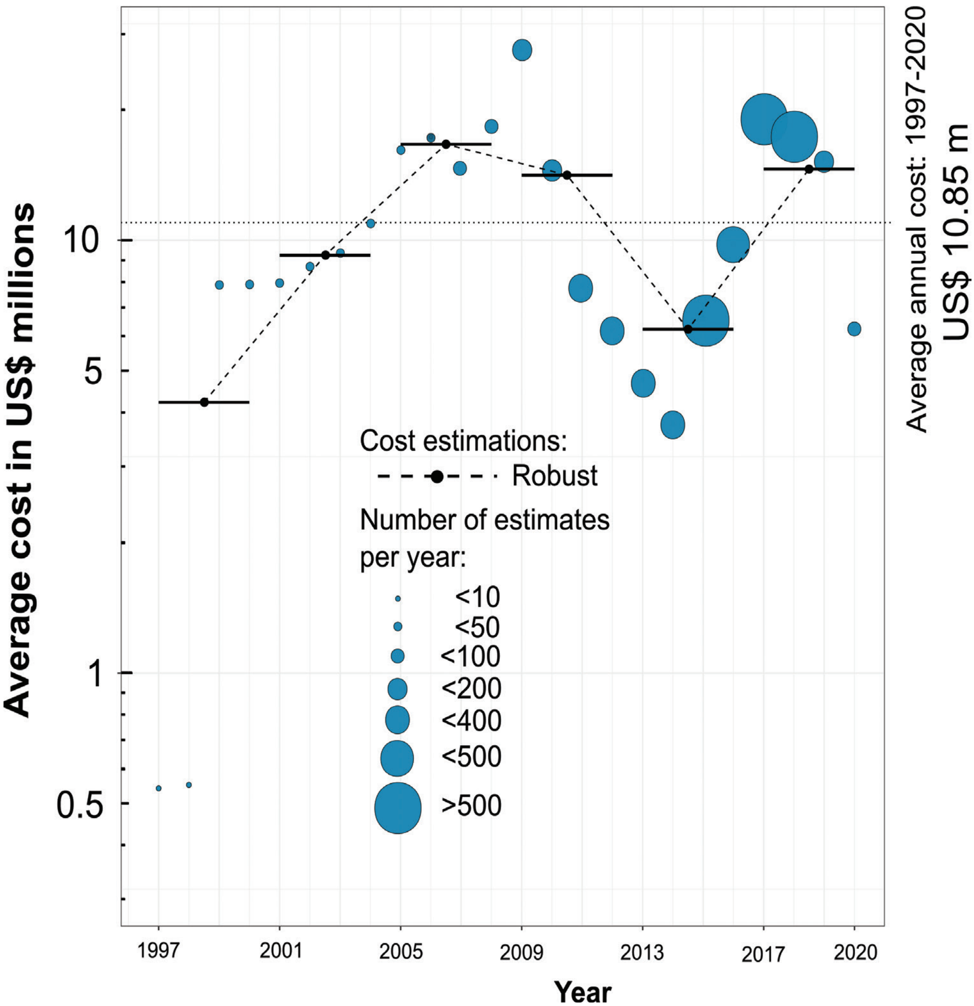

Figure 4. Temporal trends of the economic costs (US$, log) of invasive alien species in Spain using the robust data (reported, incurred and reliable costs). Each blue circle represents the cumulative cost for a given year, whereas its size is proportional to the number of estimates for that particular year. Average annual costs are calculated in 4-year periods and are represented by black dots and horizontal solid lines. Dashed lines connect the average annual costs for these 4-year periods.

species, all registering more than 50 cost entries each (Suppl. material 4: Fig. S2). The species with the highest number of entries was *Cylindropuntia pallida*, with a total of 203 records that represent 6.40% of the data, extracted from a total of six documents from Valencia. The 15 species with the highest number of cost entries did not vary when considering only management costs, while the 15 species with the highest economic costs slightly differed due to the damage reported for *D. polymorpha* (Suppl. material 4).

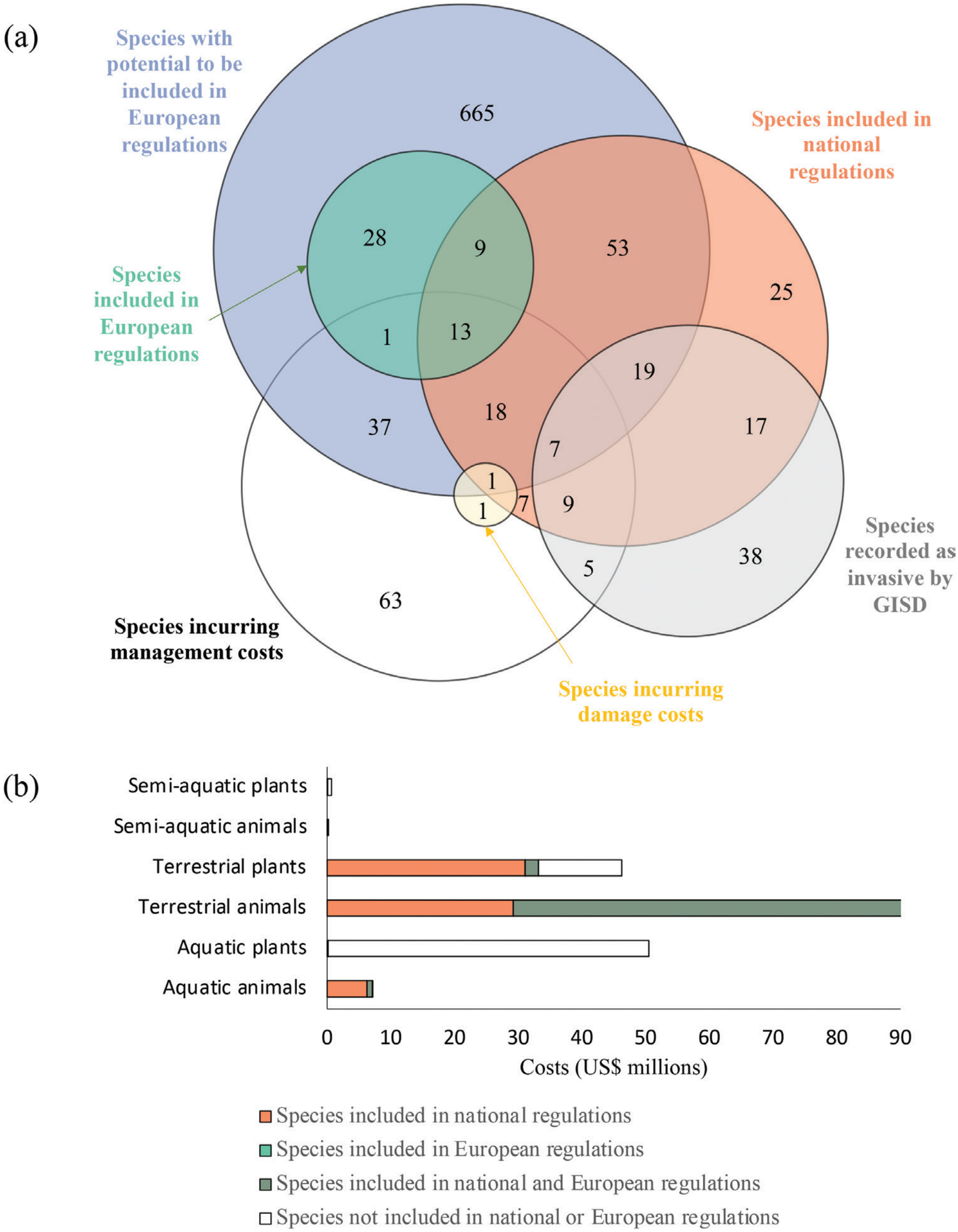

Figure 5. Invasive species with cost data in Spain with respect to national and international regulations (**a**) Venn Diagram illustrating the number of invasive species incurring management costs in Spain that are not recorded as invasive in the country (GISD; Pagad et al. 2018), listed in European or national regulations or proposed as potential candidates to be included in European regulations. Numbers indicate the number of invasive species (**b**) costs (in US$ millions) incurred by taxonomy and environment of those IAS incurring management costs in Spain, that are included in national regulations, in European regulations or in neither one.

Table 1. Lists of the ten costliest species in Spain considering only robust management costs. Costs are in US$ million; "Environ" corresponds to the environment where the cost occurred, "Taxon" refers to the taxonomic group of the species; "Regulation" indicates whether the species is listed in national (SP) and/or European (EU) regulations.

Species	Costs	Environ	Taxon	Regulation
Eichhornia crassipes	55.63	Aquatic	Plant	SP & EU
Eucalyptus sp.	50.25	Terrestrial	Plant	–
Rhynchophorus ferrugineus	24.12	Terrestrial	Animal	SP
Arundo donax	13.98	Terrestrial	Plant	SP
Cenchrus setaceus	10.13	Terrestrial	Plant	SP & EU
Neovison vison	7.91	Aquatic	Animal	–
*Pomacea maculata**	6.20	Aquatic	Animal	–
Vespa velutina	5.33	Terrestrial	Animal	SP & EU
Carpobrotus sp.	4.92	Terrestrial	Plant	SP
Cylindropuntia rosea	2.92	Terrestrial	Plant	SP & EU

* The taxonomy of *P. maculata* is not clear; however, it was reported with this name in the InvaCost database.

Discussion

General costs of IAS in Spain

We analysed economic costs of IAS occurring in Spain and explored more than 3,000 entries, using the InvaCost database and additional sources. Invasive species cost Spain at least US$ 261.28 million between 1997 and 2019. Contrary to what Haubrock et al. (2021a) found at the European continent scale, our estimations of expenditure were mostly incurred by governmental organisations (including regional administrations and river basin authorities) in managing IAS (92% of all costs). Damage costs were only found for two species (i.e. *D. polymorpha* and *Procambarus clarkii*). Since a large number of invasive species are known to cause high environmental and socioeconomic impacts in Spain (Andreu et al. 2009), these results highlight the need for future investments in research efforts to understand and quantify the economic damage of biological invasions in the country. Such knowledge on the economic damages of IAS in Spain could help increasing societal awareness, prioritising the management of IAS and motivating further investments in IAS management actions.

Compared with other countries of the Mediterranean basin, Spain has been reported as the fifth most impacted country regarding observed costs associated with IAS (Kourantidou et al. 2021), after France (US$781 billion, n = 1,036 cost entries), Italy (US$503 million, n = 94), Libya (US$340 million, n = 4) and Turkey (US$326 million, n = 11). From a continental perspective, Haubrock et al. (2021a) ranked Spain at a similar place than The Netherlands and Ireland, both countries being much smaller than Spain.

As for other countries and regions, our results show that not accounting for sources of information besides those written in English would have led to a significant knowledge gap and bias for this first assessment of global costs of invasive species in Spain (Angulo et al. 2021). The majority of costs and entries in our dataset came from non-English sources, mainly consisting of unpublished documents in Spanish, which resulted in a high percentage of cost entries reported in Spanish (98%), consistent with findings in some other European countries that reported costs in their native language (e.g. 97% for France, Renault et al. 2021; 69% for Germany, Haubrock et al. 2021b). For instance, in Central and South America over 40% of cost estimates came from Spanish and Portuguese sources (Heringer et al. 2021); and in Ecuador 51.8% of the costs were reported in Spanish (Ballesteros-Mejia et al. 2021). An extreme situation is observed in Japan, where all recorded costs were in Japanese (Watari et al. 2021), although this was a common trend in Asia (reviewed in Liu et al. 2021).

Management costs focused in aquatic and terrestrial environments, but mostly targeting invasive plants. The costliest invasive species in Spain was the aquatic plant *E. crassipes* (commonly known as water hyacinth), which was first recorded in the Guadiana River in 2004 and by 2005 it was already covering 75 km of the river surface. A large research effort has been invested in understanding the management options available to control this invasive plant. For example, in 2008, a workshop, arranged by European organisations, was attended by international experts, aiming to share experiences in the management of *E. crassipes* (e.g. the successes or failures resulting from applying different management actions) to facilitate the design of management actions in the Guadiana River (http://archives.eppo.int/meeTingS/2008_conferences/eic-chornia_workshop.htm). However, its management is still a challenge for the area (Téllez et al. 2008; Kriticos and Brunel 2016). This species, together with *D. polymorpha* or *Neovison vison*, which are amongst the ten costliest species in Spain, are also amongst the invasive aquatic species causing the most widespread economic impacts (Cuthbert et al. 2021a). *E. crassipes* also seems to be one of the costliest species in several African countries, in Asia and in North American countries, such as Mexico (Diagne et al. 2021b; Liu et al. 2021; Rico-Sánchez 2021); while *D. polymorpha* seems to be very costly in the USA and *N. vison* in other European countries such as Germany (Crystal-Ornelas et al. 2021; Haubrock et al. 2021b). Being in the list of the 100 of the worst invasive species, *D. polymorpha* was also ranked as the 8th costliest species of that list (Cuthbert et al. 2021b).

Regional management and the need for effective national coordination of actions

Regional administrations unequally reported costs, with regions, such as Catalonia or Valencia, reporting detailed annual economic costs from the last decade and others reporting relatively low amounts of costs. Many of the regions reporting high numbers of entries and large amounts of costs present high levels of development, trading and tourism activities, which are normally associated with biological invasions (Pyšek et al. 2010; Haubrock et al. 2021a). However, regional administrations reporting low numbers of entries and low costs are also largely invaded by IAS (e.g. Dana et al. 2009) and, therefore, might need further investments in reporting and managing IAS in the future.

The use of lists including IAS with known invasive potential is a widely used regulation tool at international and national levels (García-de-Lomas and Vila 2015). Most Spanish regions relied on the national catalogue of IAS rather than establishing their own regional listing (except, for example, Valencia). Based on the national list, managers can prioritise either IAS already present and expanded in their regions or the ones identified as potentially harmful in the future, in order to prevent their entrance. However, our results show that economic costs for pre-invasion management actions related to biosecurity issues, such as early detection, early warning, risk assessment or prioritisation analyses, constituted less than 1% of all costs; while most economic costs (74%) were spent in post-invasion management actions, such as monitoring, control or eradication. Although the importance of prevention rather than post-invasion management to efficiently manage IAS is known (Leung et al. 2012; Wilson et al. 2016), there could be an under-estimation of the costs of pre-invasion management actions in the data analysed for Spain. In many cases, managers communicating costs recognised that some prevention actions, such as risk analyses or monitoring for early detection, were not included in the reported costs, as no additional funding was required to implement such actions (e.g. managers use already existing resources, their time, computers or cars), while eradication or control campaigns need extra work (i.e. worker teams, machinery etc.).

A large number of the managed invasive species (63 IAS, 36% of all managed species) were not listed as invasive in Spain (sensu the GISD database; http://www.issg.org/database), included in European regulations or proposed to be assessed to potentially include them in European regulations. This suggests that Spanish environmental managers do not prioritise the management of invasive species according to current regulations or tools, such as the Global Invasive Species Database, or published expert assessments. The rationale for prioritising the management of IAS in the country, therefore, remains unknown. One possible explanation is that some managers are following the common approach of developing and implementing management actions for groups of species with similar management requirements, instead of doing this separately for individual species (van Wilgen et al. 2011). For example, in 2019, the Global Cactus Working Group (GCWG) identified a set of invasive and potentially-invasive cacti and key actions that can be taken to manage them worldwide (Novoa et al. 2019). In our dataset, six of the cactus species identified as invasive by the GCWG have reported management costs. However, only two of these are included in national regulations. Additionally, our data showed that, in aquatic environments, control of known invasive species, such as invasive turtles, fishes or crayfishes, lead to capture of other non-native species as a by-catch, such as other turtles of different genera (e.g. *Graptemys*, *Mauremys* or *Pelodiscus*), fishes (e.g. *Carassius auratus*) or crayfishes (e.g. *Callinectes sapidus*), not included in national regulations. Managing species that are not included in national lists is not uncommon; for example, Elvira and Almodóvar (2019) showed that only 2 out of 11 fish species introduced in Spain since 2000 are included in the national catalogue. Even if it is laudable and even encouraging that most managers are proactive and in advance of regulations, we suggest that the national catalogue should be revised to account for all species that are or should be managed.

A substantial amount of research has been recently focused on developing strategies to prioritise the management of IAS, including optimisation frameworks and decision processes (e.g. McGeoch et al. 2016; Curtois et al. 2018; Novoa et al. 2018), all in collaboration with different stakeholder groups (Novoa et al. 2020). Our results suggest that future efforts should focus on stakeholder engagement in Spain, in order to develop transparent and evidence-based management decisions. Moreover, inter-regional management costs, such as those incurred in river basins, were equal to the sum of the costs of all regions together. Such inter-regional management actions are generally more effective than single regional ones, since managing different species pools in neighbouring regions can hinder the effectiveness of the actions at larger geographic scales (Faulkner et al. 2020). Therefore, species prioritisation should ideally be done in collaboration with neighbouring regions in order to achieve effective management results (Sutcliffe et al. 2017).

Our results suggest that there is a need for a country-level organism responsible for the management of IAS that can effectively coordinate joint management strategies, facilitate communication and collaboration between regional governments, national and inter-regional agencies (such as river basin authorities), neighbouring countries and other stakeholders (Caffrey et al. 2014; Piria et al. 2017). This will motivate the continuity of long-lasting management actions and reporting of the costs of IAS that will adequately provide information for future budgets increasing management effectiveness (Pergl et al. 2020). The non-native species secretariat in the UK (http://www.nonnativespecies.org/) is a good reference for this, while a starting point in clarifying competencies across different administrations is suggested.

The good and the bad: high costs in aquatic environments and low costs in protected areas

Although terrestrial environments had more and higher reported costs than other environments(US$ 138.6 million), invasions were also relatively costly in aquatic (US$ 91.9 million) and semi-aquatic environments (US$ 12.4 million). There are generally few reports on the global economic impacts of invasive species in aquatic ecosystems (Lovell et al. 2006). However, compared with the whole InvaCost database (Diagne et al. 2020b), our estimates for these ecosystems are exceptionally high (but see the case of Mexico, Rico-Sánchez et al. 2021). A global assessment of all data included in InvaCost reported that the monetary costs of aquatic invasive species only constituted 5% of the total reported costs. This percentage increased to only 9% when considering management costs only (Cuthbert et al. 2021a). In contrast, we show that, in Spain, 35% of the funds allocated to the management of invasive species were spent in aquatic environments (plus 5% in semi-aquatic environments). Interestingly, some of the management costs reported by the river basin authorities along the Iberian Peninsula river basins were really high, such those reported in the Guadiana River related to the control of the water hyacinth (*E. crassipes*) since 2005 or that from the Ebro Basin related to the control of the Zebra mussel (*D. polymorpha*) in the 2000s (Table 1).

Protected areas in the Iberian Peninsula are known to be effective as natural biodiversity refugia (Araújo, Lobo and Moreno 2007; Gaston et al. 2008). In some Spanish regions, such as Andalusia, protected areas represent 30.5% of the total surface, which was reported as more than twice the European average (13.7%, Angulo et al. 2016). However, our results show that only 10.3% of the economic costs of IAS in the country (8.2% of cost entries) incurred specifically in protected areas in Spain. These low numbers suggest a lower reporting of costs or a lower investment in managing IAS in protected areas than in non-protected land, which is worrisome given the high ecological impacts of IAS in protected areas in the country. For example, Gallardo et al. (2017) showed that 38% of marine and 24% of inland protected areas in Europe were already affected by at least one of the 86 most threatening invasive species in Europe. Moreover, Capdevilla-Argüelles and Gallardo (2019) ranked a set of top-invaders by their menace to the Spanish national parks and some of those that constituted the highest menace, are amongst the ones we reported here with the highest costs, such as *E. crassipes*, *Cenchrus setaceus*, *N. vison*, *V. velutina* or *Cortaderia selloana*. Furthermore, Moodley et al. (2021) classified *Baccharis halimifolia* and *V. velutina* among the costliest species in European protected areas, while *N. vison* was among the costliest in semi-aquatic environments within protected areas (*B. halimifolia* was ranked 11th in Spain when looking only at management costs). However, it could be that our data are conservative regarding the real costs incurred in protected areas. For example, Saavedra and Medina (2020) showed that an eradication programme implemented in La Palma Island, Spain, prevented the expansion of the ring-necked parakeet (*Psittacula krameri*) into La Palma Island Biosphere. These costs were, however, recorded at the island level, not only in the protected lands.

Limitations of the study

Our study shows high economic costs of IAS in Spain, despite our conservative selection of data. Mainly, four potential sources of costs in Spain remained unexplored. On the one hand, while most protected areas are managed by the regional authorities, national parks, the most important figure of conservation for protected areas in Spain, are managed by a national authority, the Autonomous Organism of National Parks (OAPN). Although we also contacted environmental managers from the OAPN, they could not provide us with data on the economic costs of IAS, since this was not readily available. The main reason for this was that their management is shared by a number of private enterprises (mainly from the TRAGSA group) that work for the administration in broad public services, not only in the management of invasive species (Pep Amegual, Chief of Research Office in the OAPN, pers. comm.). Therefore, future engagement with these enterprises is needed to include these data in further analysis.

On the other hand, many research projects in Spain, commonly founded by national or international agencies, study biological invasions, despite few entries reporting research costs (n = 166). Scalera (2010) reported an increasing number of EU funded projects focusing on IAS from 1992 to 2006, with a budget for this period exceeding € 132 million; Spain, together with Italy and France, hosted 52% of these projects. Although we approached European Programmes' Advisors from the Spanish National Research Council (CSIC) and searched the web of the Ministry for Education and Professional Career, the information on these costs was difficult to obtain. We only consider costs of a few European projects that took place in Spain, for which cost information was available on the web or was reported by targeted researchers (i.e. Invasep, Ripisilva, Lampropeltis, ConHabit, Margal Ulla, La Rioja Life, Estuarios del Pais Vasco). New ways to obtain this information are needed in order to include such economic costs in future assessments.

Third, even if costs for invasive aquatic species were well reported in our database, costs for marine species were not reported in Spain; a possible explanation is that we did not specifically target national administrations with governance in marine species. However, this is a common problem for the global InvaCost project, since only 2% of all global aquatic invasion costs were related to marine-tolerant invasive species (Cuthbert et al. 2021a).

Finally, border controls, phytosanitary measures against invasive pests or private efforts to control invaders, have not been searched specifically. Border control measures exist in Spain. For example, in the Canary Islands, there are strict border controls, but control of invasive species is difficult to quantify separately from other border activities. Some private efforts have been recorded, such as those targeting the eradication of the first outbreak of the invasive termite *Reticulitermes flavipes* in Tenerife Island between 2010 and 2015 (Hernández-Teixidor et al. 2019) or the management of *D. polymorpha* in the Ebro Basin, which costs € 615,000/year to energy companies and € 321,450 in 2009 to the private companies using its water (Durán et al. 2012). However, we argue for a better reporting of these private costs. In relation to damage caused by invaders, it is likely that our targeted research did not succeed in obtaining such information from the public administrations that could hold such data. For example, our database does not include data on damage caused to agriculture or forestry by invasive pest species, such as apple snails or bark beetles (Golzanadera et al. 2012; Joshi and Parera 2017) or damage caused by disease vectors, such as health-associated costs by invasive *Aedes* sp. mosquitoes (Collantes et al. 2015). However, it could also depend on how local funds are distributed, prioritising management actions rather than damage evaluation, which would require additional resources and scientific skills.

Conclusion

This study is the first one attempting to economically evaluate the impact of IAS in Spain. We collected cost data mainly from the literature, regional governments and river basin authorities. Beside certain extrapolated costs on the economic impacts of IAS in the forestry sector, most of the reported costs consisted of funding used for managing established IAS (such as control or monitoring costs). Despite invasive species posing high environmental and economic impacts in Spain (Andreu et al. 2009), most of the collected costs corresponded to management actions, while damage costs were only found for two species. These results suggest the need for further investment in understanding the damage costs of IAS in the country and reporting them. Taxonomically, Spanish environmental managers expended more funds in managing invasive plants than animals and substantial efforts were directed to manage IAS in aquatic environments. From a geographic perspective, a country-level organism responsible for the management of IAS could promote long-lasting research-based management strategies and reporting of costs that expand political borders amongst regions and efficiently coordinate actions amongst all the implicated actors.

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Supplementary material 1

Dataset of the economic costs of invasive alien species in Spain and descriptive variables

Authors: Elena Angulo, Liliana Ballesteros-Mejia, Ana Novoa, Virginia G. Duboscq-Carra, Christophe Diagne, Franck Courchamp

Data type: excel file

Explanation note: Spreadsheets: "InvaCost_3.0_Spain" contains the 3,260 raw entries; "InfoVariables" contains information on each variable and their categories; "Corrections": report of corrections made with respect to the original source (Invacost_3.0).

Link: https://doi.org/10.3897/neobiota.67.59181.suppl1

Supplementary material 2

Figure S1

Authors: Elena Angulo, Liliana Ballesteros-Mejia, Ana Novoa, Virginia G. Duboscq-Carra, Christophe Diagne, Franck Courchamp

Data type: pdf file

Explanation note: (a) Descriptors of the economic costs of invasive alien species in Spain using the non-robust data (extrapolated cost, not occurring and/or unreliable costs) and (b) temporal trends of these economic costs (US$). In (b), each blue circle represents the cumulative cost for a given year, whereas its size is proportional to the number of estimates for that particular year. Average annual costs are calculated in 4-year periods and are represented by black points and horizontal solid lines. Dashed lines connect the average annual costs for these 4-year periods. Non-robust data started with low values in the 2000s increasing highly (mainly due to the predicted costs for the pine wood nematode) for the period between 2008 and 2030. See sample size in Fig. 1.

Link: https://doi.org/10.3897/neobiota.67.59181.suppl2

Supplementary material 3

Lists of species used in Figure 5

Authors: Elena Angulo, Liliana Ballesteros-Mejia, Ana Novoa, Virginia G. Duboscq-Carra, Christophe Diagne, Franck Courchamp

Data type: excel file

Explanation note: Spreadsheets: "Management and damage" contains species recorded as invasive in the country (GISD; Pagad et al. 2018); species in national regulations, European regulations or proposed as potential candidates to be included in European regulations (Carboneras et al. 2018); species having management costs and damage costs in InvaCost. "Management" contains only managed species with their presence in the lists reported in the previous spreadsheet and information about their environment and taxonomy (Env/Phyl), as well as their costs in US$. "Management_non_listed" contains the species not listed in any of the previous lists and the regions where each one has been reported as having management costs. Codes 1-0 mean presence or absence in the list, respectively.

Link: https://doi.org/10.3897/neobiota.67.59181.suppl3

Supplementary material 4

Figure S2

Authors: Elena Angulo, Liliana Ballesteros-Mejia, Ana Novoa, Virginia G. Duboscq-Carra, Christophe Diagne, Franck Courchamp

Data type: PDF file

Explanation note: Lists of the costliest species in Spain considering all the cost types or only management costs and separating robust and non-robust data. (A) Economic costs (US$ million) and (B) number of entries. Colours in the tenth costliest invasive species using the robust data facilitate comparison of species amongst different lists.

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RESEARCH ARTICLE

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Economic costs of biological invasions in the United Kingdom

Ross N. Cuthbert[1,2], Angela C. Bartlett[3], Anna J. Turbelin[4], Phillip J. Haubrock[5,6], Christophe Diagne[4], Zarah Pattison[7], Franck Courchamp[4], Jane A. Catford[3,8]

1 *GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Kiel, Germany* **2** *School of Biological Sciences, Queen's University Belfast, Belfast, UK* **3** *Department of Geography, King's College London, London, UK* **4** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, Orsay, France* **5** *Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, Gelnhausen, Germany* **6** *Faculty of Fisheries and Protection of Waters, South Bohemian Research Centre of Aquaculture and Biodiversity of Hydrocenoses, University of South Bohemia, Vodňany, Czech Republic* **7** *School of Natural and Environmental Sciences; Modelling, Evidence and Policy Group, Newcastle University, Newcastle Upon Tyne, UK* **8** *School of BioSciences, University of Melbourne, Melbourne, Australia*

Corresponding author: Ross N. Cuthbert (rossnoelcuthbert@gmail.com)

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Abstract

Although the high costs of invasion are frequently cited and are a key motivation for environmental management and policy, synthesised data on invasion costs are scarce. Here, we quantify and examine the monetary costs of biological invasions in the United Kingdom (UK) using a global synthesis of reported invasion costs. Invasive alien species have cost the UK economy between US$6.9 billion and $17.6 billion (£5.4 – £13.7 billion) in reported losses and expenses since 1976. Most costs were reported for the entire UK or Great Britain (97%); country-scale cost reporting for the UK's four constituent countries was scarce. Reports of animal invasions were the costliest ($4.7 billion), then plant ($1.3 billion) and fungal ($206.7 million) invasions. Reported damage costs (i.e. excluding management costs) were higher in terrestrial ($4.8 billion) than aquatic or semi-aquatic environments ($29.8 million), and primarily impacted agriculture ($4.2 billion). Invaders with earlier introduction years accrued significantly higher total invasion costs. Invasion costs have been increasing rapidly since 1976, and have cost the UK economy $157.1 million (£122.1 million) per annum, on average. Published information on specific economic costs included only 42 of 520 invaders reported in the UK and was generally available only for the most intensively studied taxa, with just four species contributing 90% of species-specific costs. Given that many of the invasive species lacking cost data are actively managed and have well-recognised impacts, this suggests that cost information is incomplete and that totals presented here are vast underestimates owing to knowledge gaps. Financial expenditure on managing invasions is a fraction (37%) of the costs incurred through damage from invaders; greater investments in UK invasive species research and management are, therefore, urgently required.

Abstract in Welsh

Er bod costau uchel rhywogaethau ymledol yn cael eu nodi'n aml fel rhesymeg allweddol ar gyfer gweithredu polisïau a rheolaeth amgylcheddol, mae data syntheseiddiedig ar gostau ymlediad yn brin. Yma, rydym yn meintioli ac yn archwilio costau ariannol ymlediadau biolegol yn y Deyrnas Unedig (DU) gan ddefnyddio synthesis byd-eang o gostau ymlediadau cyhoeddedig. Mae rhywogaethau ymledol estron wedi costio rhwng UD$ 6.9 biliwn a $17.6 biliwn (£5.4 – £13.7 biliwn) i economi'r DU mewn colledion a threuliau ag adroddwyd ers 1976. Adroddwyd y mwyafrif o gostau ar gyfer y DU neu Brydain Fawr yn ei chyfanrwydd (97%) ac felly roedd adroddiadau costau i'r gwledydd unigol yn brin. Adroddiadau ar ymlediad anifeiliaid oedd yr ymlediadau mwyaf costus ($4.7 biliwn), yna planhigion ($1.3 biliwn), yna ffwng ($206.7 miliwn). Roedd costau difrod yr adroddwyd arnynt (h.y. heb gynnwys costau rheoli) yn uwch mewn amgylcheddau daearol ($4.8 biliwn) nag amgylcheddau dyfrol neu led-ddyfrol ($29.8 miliwn), gan effeithio'n bennaf ar amaethyddiaeth ($4.2 biliwn). Roedd ymledwyr â gyflwynwyd yn gynharach wedi cronni cyfanswm costau ymlediadau roedd yn uwch o lawer 'na rhai a gyflwynwyd yn fwy diweddar. Mae costau ymlediadau wedi bod yn cynyddu'n gyflym ers 1976, gan gostio ar gyfartaledd $157.1 miliwn (£122.1 miliwn) y flwyddyn i economi'r DU. Dim ond ar gyfer 42 o'r 520 o rywogaethau ymledol a gyhoeddwyd costau economaidd penodol yn y DU, a hynny gan amlaf ar gyfer y tacsa a astudiwyd yn fwyaf dwys yn unig, gyda pedair rhywogaeth yn gyfrifol am 90% o'r costau penodol. O ystyried bod llawer o rywogaethau ymledol sydd heb ddata costau yn cael eu rheoli'n weithredol, awgrymir fod gwybodaeth am gostau yn anghyflawn a bod y cyfansymiau a gyflwynir yma ond yn amcangyfrif isel oblegid diffyg gwybodaeth. Mae gwariant ariannol ar reoli ymlediadau yn cynrychioli ffracsiwn (37%) o'r costau a achosir trwy ddifrod gan ymledwyr; felly mae angen buddsoddiadau ychwanegol ar reoli rhywogaethau ymledol y DU ar frys.

Abstract in Irish

D'ainneoin gur minic a luaitear na costais arda a bhaineann le hionradh agus gur cúis an-tábhachtach iad le bainistiú agus polasaí comhshaoil, is annamh a fhaightear sonraí sintéisithe faoi chostais ionraidh. Sa pháipéar seo, measaimid ar bhonn cainníochtúil agus scrúdaímid costais airgeadaíochta ionraí bitheolaíochta sa Ríocht Aontaithe (RA) agus leas á bhaint againn as sintéis dhomhanda ar chostais ionraidh a thuairiscítear. Tá geilleagar na RA thíos idir SA$6.9 billiún agus $17.6 billiún (£5.4 – £13.7 billiún) le speicis choimhthíocha ionracha ó bhí 1976 ann maidir le caillteanais agus costais a tuairiscíodh. Is i gcás na RA nó i gcás na Breataine Móire a tuairiscíodh formhór na gcostas agus, mar sin de, is annamh a tuairiscíodh costais ar scála tíre. Ba iad tuairiscí ar ionraí ainmhithe ba mhó a raibh costais ag baint leo ($4.7 billiún), ansin ionraí plandaí ($1.3 billiún) agus ionraí fungasacha ($206.7 milliún). B'airde na costais damáiste a tuairiscíodh (.i. gan costais bhainistithe san áireamh) i dtimpeallachtaí talún ($4.8 billiún), agus tionchar acu seo, go príomha, ar an talmhaíocht ($4.2 billiún), ná i dtimpeallachtaí uisceacha nó leathuisceacha ($29.8 milliún). B'airde i bhfad na costais ionraidh a d'fhabhraigh ionróirí a tugadh isteach ar bhonn níos óige. Tá méadú tapa ag teacht ar chostais ionraidh ó bhí 1976 ann, agus $157.1 milliún (£122.1 milliún) de chostas ar gheilleagar na RA in aghaidh na bliana, ar an mheán mar gheall orthu. Níor chuimsigh eolas a foilsíodh faoi chostais gheilleagracha shonracha ach 42 de chuid na 520 ionróir a tuairiscíodh sa RA agus ní raibh sé ar fáil, go ginearálta, ach i gcás na dtacsón is mó a ndearnadh mionstaidéar orthu, agus gan ach ceithre speiceas bainteach le 90% de na costais sainspeicis. Nuair a chuirtear san áireamh go mbainistítear go gníomhach mórán de na speicis ionracha a bhfuil sonraí costas ina leith ar iarraidh agus go bhfuil tionchair an-aitheanta ag baint leo, tugann sé seo le fios go bhfuil an t-eolas a bhaineann le costais neamhiomlán agus gur meastacháin faoina luach ollmhóra iad, de bharr bearnaí eolais, na hiomláin a chuirtear i láthair anseo. Is cuid bheag (37%) de na costais a thabhaítear de bharr damáiste a dhéanann ionróirí is ea caiteachas airgeadais ar bhainistiú ionraí; tá géarghá, dá réir sin, le hinfheistíochtaí níos mó i mbainistiú speicis ionracha na RA.

Abstract in French

Bien que les coûts élevés des invasions biologiques soient fréquemment évoqués et qu'ils constituent une motivation clé pour les politiques et la gestion environnementale, les données synthétiques sur ces coûts sont rares. Dans cette étude, nous quantifions et examinons le coût monétaire des invasions biologiques au Royaume-Uni (UK) à l'aide d'une synthèse globale des coûts effectivement reportés. Selon les informations disponibles sur les pertes et les dépenses depuis 1976, les espèces exotiques envahissantes ont coûté à l'économie de l'UK entre 6,9 et 17,6 milliards USD (entre 5,4 et 13,7 milliards £). La plupart des coûts proviennent de l'ensemble de la Grande Bretagne (97%) et, ainsi, les données à l'échelle de chaque pays sont rares. Les invasions animales sont les plus coûteuses (4,7 milliards USD), puis viennent les invasions végétales (1,3 milliard USD) et fongiques (206,7 millions USD). Les coûts des dégâts (i.e. en excluant les coûts de gestion) sont plus élevés dans les environnements terrestres (4,8 milliards USD) que dans les milieux aquatiques ou semi-aquatiques (29,8 millions USD), et concernent majoritairement l'agriculture (4,2 milliards USD). Les organismes envahissants avec des années d'introduction plus précoces sont ceux qui sont associés aux coûts les plus élevés. Le coût des invasions ont augmenté rapidement depuis 1976, avec un coût annuel moyen à l'économie anglaise de 157,1 millions USD (122,1 millions £). Les informations publiées sur des coûts espèce-spécifiques concernent seulement 42 des 520 organismes envahissants connus au Royaume-Uni, et sont généralement disponibles seulement pour les taxons les plus étudiés, avec seulement quatre espèces qui contribuent pour 90% des coûts espèces-spécifiques documentés. Compte tenu du nombre important d'espèces exotiques pour lesquelles il n'existe aucune donnée mais qui sont pourtant activement gérées pour leurs impacts parfaitement reconnus, cela suggère que les informations sur le coût des invasions biologiques sont incomplètes et que les totaux présentés ici sont largement sous-estimés à cause des lacunes de connaissance. Les dépenses liées à la gestion des invasions ne représentent qu'une fraction (37%) des coûts provoqués par les dégâts des espèces exotiques envahissantes. Des investissements plus importants en matière de gestion des espèces envahissantes en UK sont donc nécessaires et urgents pour limiter au maximum les impacts de ces invasions biologiques.

Abstract in Spanish

Aunque los altos costos de las invasiones se mencionan con frecuencia y son una motivación clave para la gestión y las políticas ambientales, aún las síntesis de datos de los costos de las invasiones son escasas. Aquí, cuantificamos y examinamos los costos monetarios de las invasiones biológicas en el Reino Unido (UK) utilizando una síntesis global de los costos reportados sobre invasiones biológicas. Las especies exóticas invasoras le han costado a la economía del Reino Unido entre US$6,9 mil millones y US$17,6 mil millones (£ 5.4 – £ 13.7 mil millones) en pérdidas y gastos reportados desde 1976. La mayoría de los costos se reportaron a la escala del Reino Unido o Gran Bretaña (97%) y, por lo tanto, la representación de informes de costos a escala individual de cada país dentro del Reino Unido fue escasa. Los informes de invasiones de animales fueron los más costosos ($4,7 mil millones), seguidos por las invasiones de plantas ($1,3 mil millones) y de hongos ($206,7 millones). Los costos de daños reportados (es decir, excluyendo los costos de gestión) fueron más altos en ambientes terrestres ($4.8 mil millones) que en ambientes acuáticos o semiacuáticos ($29.8 millones), afectando principalmente a la agricultura ($4.2 mil millones). Los invasores con introducciones más antiguas acumularon costos totales de invasión significativamente más altos.

Los costos de invasión han aumentado rápidamente desde 1976, lo que le ha costado a la economía del Reino Unido unos $157,1 millones (£122,1 millones) por año, en promedio. La información publicada sobre costos económicos específicos incluyó sólo 42 de las 520 invasores reportados en el Reino Unido y generalmente estaba disponible solo para los taxones más estudiados, con solo cuatro especies contribuyendo con el 90% de los costos específicos de cada especie. Dado que muchas de las especies invasoras que carecen de datos de costos se gestionan activamente y tienen impactos bien conocidos, esto sugiere que la información de costos es incompleta y que los totales presentados aquí son subestimaciones enormes debido a lagunas de conocimiento. El gasto financiero en el manejo de invasiones es una fracción (37%) de los costos incurridos por los daños causados por los invasores; por lo tanto, se requieren con urgencia mayores inversiones en la gestión de especies invasoras del Reino Unido.

Abstract in German

Obwohl die hohen Kosten biologischer Invasionen häufig aufgezeigt werden und eine wichtige Motivation für das Umweltmanagement und die Umweltpolitik darstellen, sind synthetisierte Daten rar. Hier quantifizieren und untersuchen wir die monetären Kosten biologischer Invasionen im Vereinigten Königreich anhand einer globalen Synthese der gemeldeten Invasionskosten. Invasive gebietsfremde Arten haben die britische Wirtschaft seit 1976 zwischen 6,9 und 17,6 Milliarden US-Dollar (5,4 bis 13,7 Milliarden Pfund) an gemeldeten Verlusten und Ausgaben gekostet. Die meisten Kosten wurden für das Vereinigte Königreich oder Großbritannien (97%) und damit für das gesamte Land gemeldet. Berichte über invasive Tiere waren die teuersten (4,7 Mrd. USD), gefolgt von Pflanzen (1,3 Mrd. USD) und Pilzen (206,7 Mio. USD). Die gemeldeten Schäden (d.h. ohne Verwaltungskosten) waren in terrestrischen Habitaten (4,8 Mrd. USD) höher als in aquatischen oder semi-aquatischen (29,8 Mio. USD) und wirkten sich hauptsächlich auf die Landwirtschaft aus (4,2 Mrd. USD). Invasoren mit früheren Einführungsjahren verursachten signifikant höhere Gesamtinvasionskosten. Die Invasionskosten sind seit 1976 rapide gestiegen und kosten die britische Wirtschaft durchschnittlich 157,1 Mio. USD (122,1 Mio. GBP) pro Jahr. Zu den veröffentlichten Informationen zu spezifischen wirtschaftlichen Kosten gehörten nur 42 von 520 im Vereinigten Königreich gemeldeten Invasoren, die im Allgemeinen nur für die am intensivsten untersuchten Taxa verfügbar waren, wobei nur vier Arten 90% der art-spezifischen Kosten beisteuern. Angesichts der Tatsache, dass viele der invasiven Arten, denen Kostendaten fehlen, aktiv verwaltet werden und allgemein anerkannte Auswirkungen haben, deutet dies darauf hin, dass die Kosteninformationen unvollständig sind und dass die hier dargestellten Summen aufgrund von Wissenslücken stark unterschätzt werden. Die finanziellen Ausgaben für das Management von Invasionen machen einen Bruchteil (37%) der Kosten aus, die durch Schäden durch Eindringlinge entstehen. Daher sind dringend größere Investitionen in das Management invasiver Arten im Vereinigten Königreich erforderlich.

Keywords

England, InvaCost, invasive alien species, non-native species, Northern Ireland, published monetary impacts, Scotland, socioeconomic sector, Wales

Introduction

Biological invasions can cause far-reaching ecological, environmental, social and economic impacts in invaded ranges (Simberloff et al. 2013; Linders et al. 2019; Pyšek et al. 2020; Diagne et al. 2021). In the last two decades, there has been an increasing number of studies examining the ecological impacts of invasive alien species (hereon, invasive species) (Crystal-Ornelas and Lockwood 2020). However, notwithstanding a few national-scale studies (e.g. Pimentel et al. 2000, 2005; Williams et al. 2010; Hoffman and Broadhurst 2016), the socioeconomic implications have generally lacked synthesis until recently (Bacher et al. 2018; Shackelton et al. 2019; Diagne et al. 2020a; Cuthbert et al. 2021a; Diagne et al. 2021). A lack of cost-reporting reduces monetary incentives for policy-makers to implement management measures aimed at preventing the introduction, spread and impacts of invasions (Diagne et al. 2020b). That is despite management, especially when applied at an early invasion stage (Leung et al. 2002; Ahmed et al. 2021), being highly cost-effective in reducing longer-term management expenditure or damage to resources (Aukema et al. 2011; Paini et al. 2016).

Until recently, large-scale studies into the economic costs of invasive species have been limited to major geographic entities, such as the United States (Pimentel et al. 2000, 2005), Europe (Kettunen et al. 2009) and Australia (Hoffman and Broadhurst 2016). Importantly, these studies have raised societal and policy-maker awareness of the massive economic costs of biological invasions, yet many nations lack assessment. In 2020, the United Kingdom (UK) was the 5th largest economy in the world (World Economic Outlook Database 2020) and has experienced high levels of invasion success (Roy et al. 2014a; van Kleunen et al. 2015), with economic factors, such as GDP, known to influence invasion rates (Lin et al. 2011) and invader economic costs (Haubrock et al. 2021a; Kourantidou et al. 2021).

Despite invasive species being increasingly recognised as a concern for the UK government (EAC 2019), in-depth and up-to-date cost reporting of invasions to the UK economy is lacking. Early estimates of the total cost of invasive species to the UK economy have, however, been made (e.g. White and Harris 2002; Williamson 2002), albeit with a focus on relatively few, well-known taxa. In 2010, invasion costs were estimated at around £1.7 billion per year in England, Scotland and Wales (Williams et al. 2010). In Northern Ireland, invasion costs have been estimated at £46.5 million per year (Kelly et al. 2013). Williams et al. (2010) found that rabbits, Japanese knotweed and wild oats were the costliest invasive species in the UK and agriculture was the most impacted sector, especially in England. Other UK studies have focused on specific environments and cost types. For freshwater invasions in Great Britain, costs of controlling invasive species have been projected at £43.5 million per year in the case of management being undertaken at all invaded locations (Oreska and Aldridge 2011). That pioneering study also highlighted aquatic macrophytes and zebra mussels as two particularly expensive species for management. These same species groups have since been targeted in biosecurity campaigns such as Check, Clean, Dry in the UK (Anderson et al. 2015). However, whilst having raised important awareness, often such studies are outdated, based on extrapolations and have a limited focus on one specific cost type and there thus remains a lack of wide-scale cost estimation for impacts that are empirically observed. There is also no basis to test the notion that observed management investments are less costly than resource damages and losses from invasions in a standardised way, despite Williams et al. (2010) identifying that prevention is cheaper than longer term control in the UK.

Overall, the economic costs of invasions for the UK lack a finer-scale, up-to-date synthesis across multiple environmental, social and temporal contexts, with different types of costs compiled in a comparable way. There have been few appraisals of the biases and knowledge gaps in cost reporting amongst invasive species, despite the presence of 'flagship' invaders in the UK that receive high attention from scientists and media outlets (Roy et al. 2014b). As such, whether costs correlate with the degree of scientific interest towards a given taxon lacks examination. More broadly, invasion science has been shown to be taxonomically biased and only a minority of invasive species are studied in detail (Jarić et al. 2020). This unevenness leads to knowledge gaps in the costs of invasions, which can make management, prioritisation and policy creation difficult. Robust analyses of economic costs are urgently required to enable cost-benefit analyses and efficient allocations of limited economic resources.

The need to comprehensively understand costs of invasive species on the UK economy is particularly crucial given their escalating numbers (Manchester and Bullock 2000; Roy et al. 2014b; Seebens et al. 2017, 2021). The Great Britain Non-Native Species Secretariat estimates that approximately ten new alien species have become established in the UK each year since 1950 and, on average, two of these have become invasive since 2000 (EAC 2019). As the rate of invasion across the UK increases over time, so too are the expected costs associated with these invasions (Diagne et al. 2020a). However, how economic costs relate to the length of time an alien species has been established remains unclear; species that invaded earlier might accrue greater costs or, on the contrary, these costs might diminish as species become naturalised. This needs to be assessed and temporal dynamics in total costs need to be characterised. Likewise, whether certain pathways of introduction are associated with higher costs than others at different times require consideration.

To address these knowledge gaps, we use UK-specific data from 1976 to 2020 in the InvaCost database (Diagne et al. 2020a), a global compilation of the available literature on the economic costs of invasive species. This database compiles detailed cost information suitable for large-scale syntheses of costs associated with invasive species at different spatial, taxonomic and temporal scales. Specifically, we ask:

Question 1: What is the reported economic cost of invasive species in the UK and how is it distributed amongst taxonomic groups, habitat types and socioeconomic sectors? Given its economic importance, we expect costs to be higher from species impacting agriculturally-intensive terrestrial environments.

Question 2: Are studies and recorded costs shared equally amongst all invasive species? We expect that most costs are caused by relatively few species and that these species are particularly well-known and studied, reflecting a positive feedback between documented costs and study effort.

Question 3: How do costs of invasions vary over time and are species with early introductions costlier than more recent invaders considering their introduction pathways? We expect that costs per species will increase with residence time, given a longer time period over which to accrue costs and that common introduction pathways will be dominant (e.g. ornamental; van Kleunen et al. 2020).

Overall, answering these questions allows us to synthesise cost information across numerous ecological and socioeconomic contexts in the UK, helping to make informed current and future management strategies. Further, they will help in pointing out potential biases in available invasion-related cost data and guide further research avenues in this topic.

Methods

Data collection and filtering

To estimate the cost of invasive species on the UK economy, we used UK-relevant cost data from the latest available version of the InvaCost database (version 3.0; Diagne et al. 2020a; https://doi.org/10.6084/m9.figshare.12668570) up to the year 2020. We note that InvaCost is a 'living' database that is subject to further additions and improvements. Following the InvaCost protocol (Diagne et al 2020a), all references were retrieved using standardised searches within selected repositories [Web of Science (https://webofknowledge.com/); Google Scholar (https://scholar.google.com/); Google search engine, (https://www.google.com/)] and targeted collection through gathering opportunistic literature and contacting experts and stakeholders. Collected materials were thoroughly assessed to identify relevance and extract cost information. Specifically, titles, keywords, abstracts and full texts were checked hierarchically to ensure that (1) they were in English, as per the language competencies of the review team, (2) they contained at least one cost estimate and (3) each cost estimate was attributed exclusively to invasive species (see Diagne et al. 2020a for full details). InvaCost only includes invasive species for which there are documented economic impacts and our cost analysis reflects that scope. The database effectively defines invasive species as human-introduced alien species that cause some economic cost. Duplicates that reported the same or overlapping costs were also removed from the data. We note that, for the most part, InvaCost includes species that are currently invasive in the UK. However, in some cases, costs pertaining to past successful eradications are included, such as for coypu *Myocastor coypus*. Costs from the Channel Islands, British Overseas Territories and the Isle of Man were excluded to tighten the biogeographical focus. All costs were converted to a common, up-to-date currency (2017 US$); we also provided certain cost estimates in 2017 GBP [1 USD = 0.777 GBP (World Bank 2017 exchange range)].

Data processing

The period of estimation across reported costs varied considerably, spanning periods of several months to several years. In order to obtain comparable costs, we considered all costs for a period of less than a year as annual costs and re-calculated costs covering several years on an annual basis (i.e. costs accumulated over multiple years were divided amongst those years, giving annual cost estimates). Therefore, costs that spanned multiple years were divided equally amongst those years (e.g. a cost totalling $10,000 over ten years would equal $1,000 per year). If there was no evidence for a cost occurring in more than one year (i.e. *One-time* cost), we conservatively counted it for one year only and likewise for costs that were *Potentially-ongoing* (Occurrence column in InvaCost). In cases where the timespan for the costs was not described in the data publication, we used publication year as a surrogate for starting year and – if the cost was *Potentially-ongoing* – publication year as a surrogate for ending year.

The conversion of all costs into an annual basis resulted in a total of 709 expanded entries (Suppl. material 1; 353 initial entries). This was accomplished using the *expandYearlyCosts* function of the 'invacost' package version 0.3–4 (Leroy et al. 2020) in R version 4.0.2 (R Core Team 2020); this function considers both the probable starting and ending years of each cost entry in the InvaCost database to annualise costs (see Suppl. material 2; https://doi.org/10.6084/m9.figshare.12668570). The first cost entry in our dataset was recorded in 1976, so all analyses were performed for the period 1976 to 2019, because that was the last year with robust reported costs. Costs in InvaCost are reported at different spatial scales (Spatial scale column), from site-specific to regional and national estimates. We carefully considered this information and checked for potential duplications in costs within or amongst scales, with costs estimated at all spatial scales (i.e. unit, site or country) included in the analyses.

Question 1: Invasion costs distributions through space and sectors

We categorised the invasion costs using seven criteria. The first two criteria were used to filter and subset the costs and the other five were used in analysis. See Suppl. material 2 for further information on the considered categories.

(i) Method reliability (*High* or *Low*): Cost estimates, extracted from peer-reviewed publications or official reports or with documented, repeatable and/or traceable methods, were considered to have *High* reliability; all other estimates were designated as *Low* reliability (Diagne et al. 2020a);

(ii) Implementation (*Observed* or *Potential*): Cost estimates that occurred in the invaded habitat were designated *Observed* and those or that were extrapolated or predicted to occur were deemed *Potential*.

We calculated full costs, which include potential and low reliability estimates, but excluded these more speculative estimates when examining the data in detail (as well as for the following subsections). The more detailed, conservative analysis, therefore, considered only the following descriptors:

(iii) Country (*England*, *Scotland*, *Wales*, *Northern Ireland*). Where costs were attributed to a particular country, we presented costs to that country; other costs were recorded as spanning multiple countries, i.e. *Great Britain* (i.e. excluding Northern Ireland) or the *UK* (i.e. including Northern Ireland);

(iv) Environment of the invasive species (*Terrestrial*, *Aquatic*, *Semi-aquatic* or *Diverse/Unspecified*): the habitat from which the species causing the cost originated. Here, we considered that *Semi-aquatic* corresponds to species that are closely associated with water for development, reproduction and/or foraging (e.g. *M. coypus* is a semi-aquatic rodent);

(v) Type of cost: (a) *Damage* referring to damages or losses incurred by invasion (e.g. costs for damage repair, resource losses, medical care), (b) *Management* comprising control-related expenditure (e.g. monitoring, prevention, management, eradication) and money spent on education, research and maintenance costs, (c) *Mixed* including mixed damage and management costs (cases where reported costs were not clearly distinguished amongst cost types);

(vi) Impacted sector: the activity, societal or market sector that was impacted by the cost (*Agriculture*, *Authorities-Stakeholders*, *Environment*, *Fishery*, *Forestry*, *Public and social welfare*); individual cost entries not allocated to a single sector were classified as *Mixed*;

(vii) Kingdom: the taxonomic kingdom of the species associated with each cost entry. Where this information was missing, taxa were deemed to be *Diverse/Unspecified*. Viruses were included as a general 'kingdom', but only counted if they were vectored by an invasive species in the UK subset (e.g. squirrelpox virus vectored by the grey squirrel *Sciurus carolinensis*).

Question 2: Taxonomic biases in invasion costs

To identify the proportions of invasive species in the UK for which cost data are available, the list of individual species in InvaCost was compared with comprehensive lists of invasive species in the UK. Lists of known invasive species were extracted and compiled for the UK from the following databases: (1) InvaCost version 3.0; (2) the Global Invasive Species Database (GISD); (3) the sTwist database; and (4) the Great Britain Non-native Species Information Portal (GB-NNSIP) (Table 1). Only species listed within the UK were extracted from each database, with listed species checked to confirm their alien status and refined accordingly. We classify all of these species as "invasive", but note that the definitions of invasiveness differ slightly amongst these datasets (Table 1). We used the GBIF.org Backbone Taxonomy to standardise species names.

Rank-abundance analyses were used to determine the unevenness of species' costs according to cost types (management and damage), environments (aquatic, semi-aquatic and terrestrial) and kingdoms (plants and animals).

A keyword search on the Web of Science over the period 1960 to 2020 was used to quantify research effort (i.e. publication numbers) towards individual species listed as invasive in the UK (Table 1). Global and UK-only searches were conducted to determine research effort, as indicated by numbers of publications. The Global search string used species' scientific names only; the UK-only search string combined the scientific name of the species with "UK" OR "United Kingdom" OR "Great Britain" OR "England" OR "Scotland" OR "Wales" OR "Northern Ireland". For example, the search string used to retrieve the number of studies for *Oryctolagus cuniculus* was: TS=("Oryctolagus cuniculus") AND TS=("UK" OR "United Kingdom" OR "Great Britain" OR "England" OR "Scotland" OR "Wales" OR "Northern Ireland"), where TS is the "Topic". The results and specific search terms are provided in Suppl. material 3.

We used a Kruskal-Wallis test to compare research efforts for invasive species that were present vs. absent from InvaCost. This tested the null hypothesis that research effort was equal across species with and without published impact costs. We also used

Table 1. Initial numbers of known invasive species extracted from the InvaCost, GISD, sTwist and GB-NNSIP databases for the UK. Definitions of invasiveness are provided in relation to each database, along with underlying sources of data extracted.

Database	Species (*n*)	Invasive definition	Data source
InvaCost	42	Invasive alien species with reported economic impacts.	Version 3.0, Diagne et al. (2020a; https://doi.org/10.6084/m9.figshare.12668570).
GISD	216	Alien species with known negative impacts on biodiversity in the region where they are invasive.	GISD (www.iucngisd.org/gisd).
sTwist	321	A taxon whose introduction and/or spread threatens biological diversity (Convention on Biological Diversity).	Version 1.2.3, https://doi.org/10.5281/zenodo.3763222. Underlying data sources: Caphina et al. (2017); GAVIA (Dyer et al. 2017); Global Alien First Records Database (Seebens et al. 2017); GloNAF (van Kleunen et al. 2015); GRIIS (available via: GBIF.org).
GB-NNSIP	282	An introduced taxon designated as having a negative ecological or human impact.	Roy et al. (2014b).

linear regression to test the relationship between species' total economic costs and their research effort, on a $\log_{10}$ scale to normalise residuals and homogenise variances. Here, a significant positive relationship would indicate that greater invasion costs are reported for invasive species with larger numbers of studies.

Question 3: Temporal dynamics of invasion costs

The cost over time of all UK invasive species was calculated via the *summarizeCosts* function of the 'invacost' R package (Leroy et al. 2020). This function illustrates the dynamics of costs over time, projecting the mean cost per decade, as well as the mean cost over the entire reported period (i.e. from 1976 to 2019; the last year with robust, reported costs).

Using first record information from the sTwist database, we used linear regression to examine the relationship between the length of time a species has been reported as invasive in the UK and its total invasion cost. First record information was available for 35 species reported in InvaCost (of the 42 species with individual cost entries). Both time since introduction and total economic costs were modelled on a $\log_{10}$ scale to normalise residuals and homogenise variances. We thus tested whether species with an earlier year of introduction accrued greater impacts than species that were introduced more recently. For each species and year of introduction, we also examined introduction pathway information (Suppl. material 4), as reported in the DAISIE database (Roy et al. 2020). This database is an inventory of invasive species in Europe, in the form of a checklist; we used UK-specific data only.

Results

Question 1: Invasion costs distributions through space and sectors

Biological invasions cost the UK economy an amount estimated from \$6.9 billion to \$17.6 billion (£5.4 billion – £13.7 billion) between 1976 and 2019. The lower, more conservative cost estimate excludes *Potential* costs ($5.2 billion; £4.0 billion; 103 entries) and *Low* reliability costs ($5.5 billion; £4.3 billion; 101 entries). We use the more conservative estimates for all further analyses below (538 entries).

Of the total for the whole of the UK, $4.3 billion (£3.3 billion) was attributed to the UK and $2.4 (£1.9 billion) billion to Great Britain. Much lower cost totals were recorded per country, with $81.5 million (£63.3 million) to Northern Ireland, $76.2 million (£59.2 million) to England, $34.9 million (£27.1 million) to Scotland and $2.4 million (£1.9 million) to Wales. Therefore, the vast majority of invasion costs were reported at larger spatial scales.

Where costs were assigned to specific taxa, the majority were attributed to animals ($4.7 billion, 267 entries; including $2.4 billion to mammals and $1.5 billion to insects), followed by plants ($1.3 billion, 99 entries) and then fungi ($206.7 million, 2 entries). Invasive chromists (16 entries) and viruses (10 entries) cost $771,575 and $775,451, respectively. However, a large sum of invasion costs in the UK was either not taxonomically defined or spanned multiple kingdoms (i.e. *Diverse/Unspecified*; $781.6 million, 144 entries).

Terrestrial habitats were most impacted overall ($6.4 billion, 245 entries) and had the highest number of cost entries. Impacts to aquatic ($258.5 million, 116 entries) and semi-aquatic habitats ($51.7 million, 86 entries) were, respectively, one and two orders of magnitude lower (Fig. 1), despite high numbers of cost entries. A relatively small portion of total economic costs was reported from entries that affected multiple or unspecified environment types ($172.0 million, 91 entries) (Fig. 1).

The costliest impacts of invasions in the UK were incurred by the agricultural sector ($4.9 billion, 32 entries), followed by authorities and stakeholders (i.e. governmental services and/or official organisations, $955.9 million, 436 entries), mixed sectors ($824.6 million, 41 entries), as well as forestry ($144.2 million, 11 entries). Public and social welfare ($37.8 million, 10 entries), fisheries ($11.0 million, 5 entries) and the environment ($7.8 million, 3 entries) were reportedly impacted to a much lesser degree. Agricultural, mixed and forestry impacts were typically incurred through direct damage or losses to resources, whilst impacts to authorities and stakeholders were mostly related to management expenditure. Across these sectors and cost types, terrestrial environments were dominant, with relatively few contributions from aquatic and semi-aquatic environments overall in terms of invasion costs. In contrast to terrestrial environments, where costs were mostly damage-related, aquatic and semi-aquatic costs were more likely to be from management actions (Fig. 1).

Question 2: Taxonomic biases in invasion costs

Overall, cost data in the UK were reported for 42 invasive species in InvaCost (with individual cost entries; n = 56 including species within 'mixed' entries). However, there were 520 unique invasive species in the UK reported in InvaCost, sTwist, GISD or GB-NNSIP, thus meaning that approximately 8% of known invasive species in the UK have documented economic costs (Fig. 2a). Invasive species with reported cost data

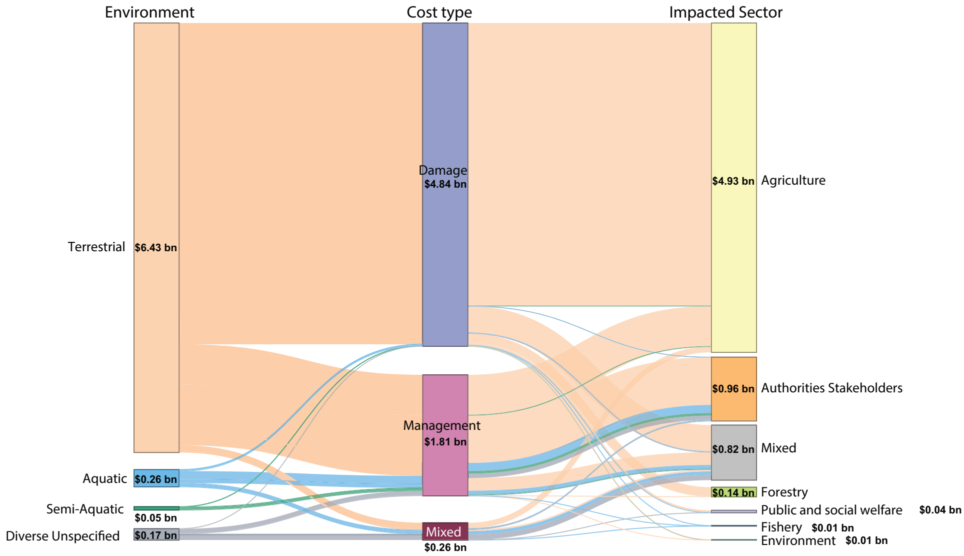

Figure 1. Alluvial plot illustrating flows of identified invasion cost types in the UK amongst environments and socioeconomic sectors. Abbreviations: bn is billion (2017 US$).

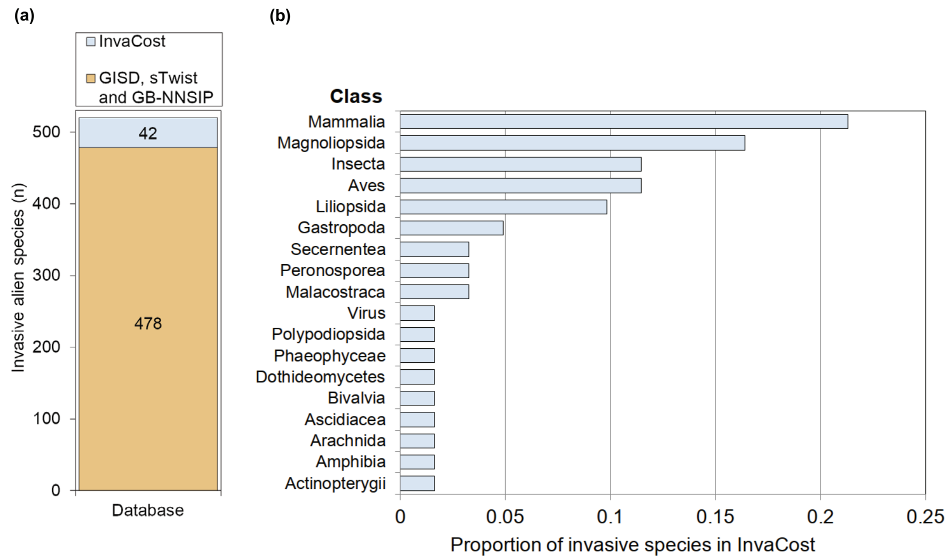

Figure 2. Barplots showing **a** total numbers of all known invasive species in the UK (i.e. species within GISD, sTwist and GB-NNSIP) and UK invasive species in InvaCost; and **b** proportions of UK invasive species in InvaCost across classes.

mainly belonged to the Mammalia (21%), Magnoliopsida (16%), Insecta (11%) and Aves (11%) classes (Fig. 2b).

Cost contributions were highly uneven across species overall (Fig. 3). Considering total costs, the European rabbit *O. cuniculus* contributed 62%, followed by Japanese

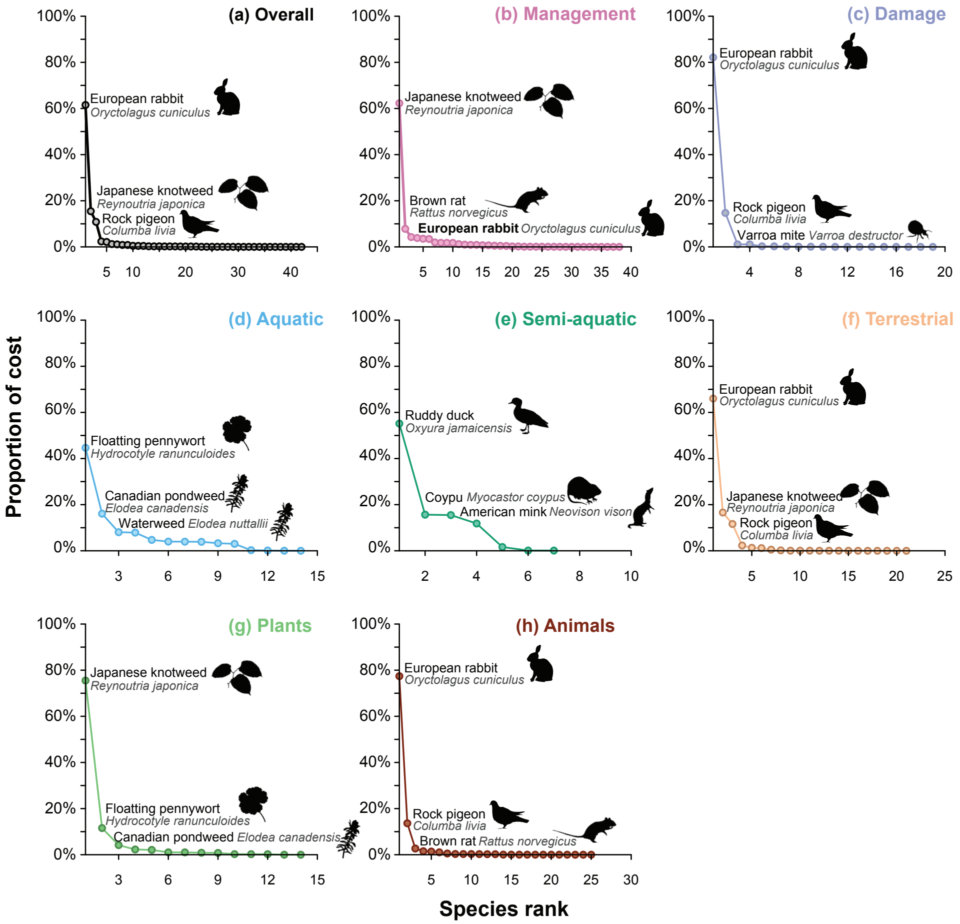

Figure 3. Whittaker plots illustrating ranked proportional cost contributions across species for **a** overall **b** management **c** damage **d** aquatic **e** semi-aquatic **f** terrestrial **g** plant and **h** animal cost categories. The top three highest-contributing species are labelled on each subplot, for example, the European rabbit ranks as the costliest species **a** overall, for **c** damage costs and amongst the terrestrial organisms (**f**) and animal kingdom (**h**), representing 62%, 82%, 66% and 77% of costs in the respective categories. Note the differences in *x*-axes scaling.

knotweed (*Reynoutria japonica*) and the rock pigeon (*Columba livia*). Japanese knotweed dominated management costs (62%), followed by the brown rat (*R. norvegicus*) and European rabbit. Damage costs were again dominated by the European rabbit (82%), followed by the rock pigeon, with Varroa mite (*Varroa destructor*) third.

Aquatic environments were mostly impacted by floating pennywort (*Hydrocotyle ranunculoides*) (45%) and Canadian pondweed (*Elodea canadensis*) (16%), thereafter waterweed (*Elodea nuttallii*). Semi-aquatic taxa costs were mostly driven by the ruddy duck (*Oxyura jamaicensis*) (55%), coypu (*Myocastor coypus*) and American mink (*Neovison vison*). Costs in terrestrial environments were driven predominantly by the European rabbit (66%), Japanese knotweed and rock pigeon. Overall, the majority of spe-

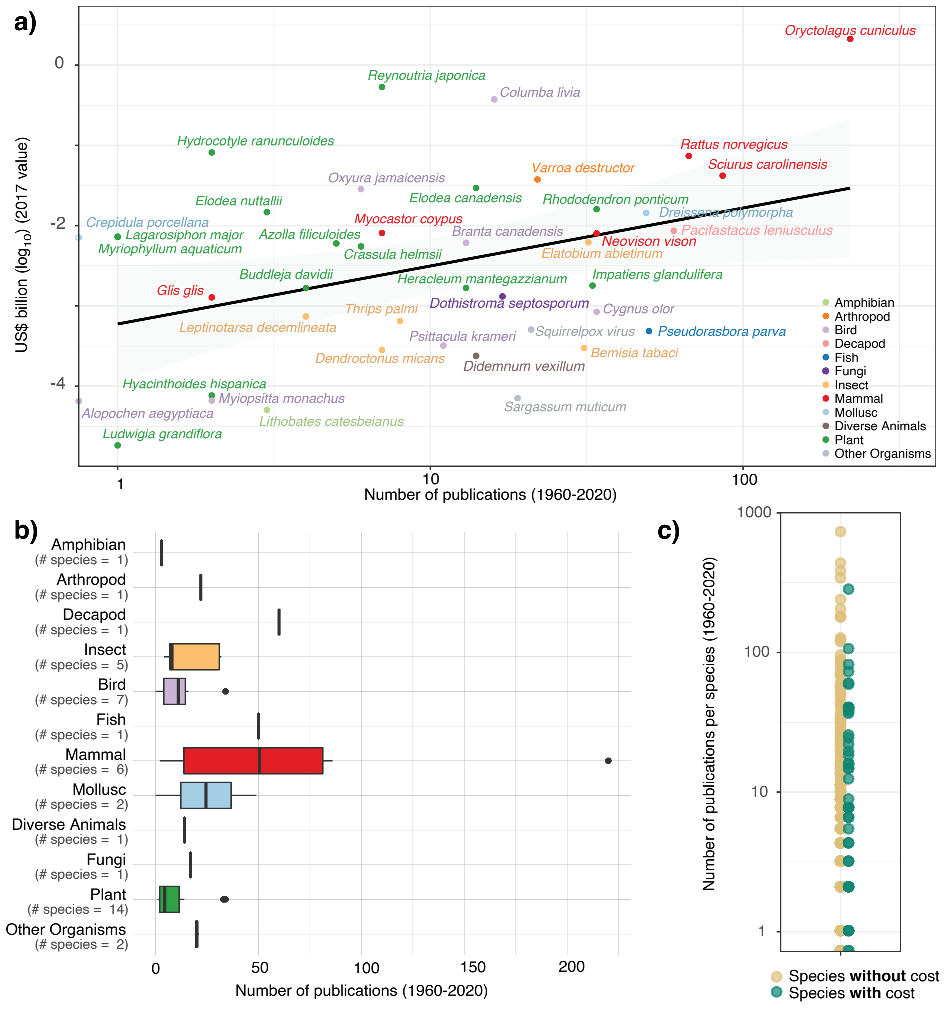

Figure 4. Per-species invasion costs and study efforts showing **a** the number of publications available in Web of Science for the period 1960–2020 for each species with InvaCost records against the total cost for each species in billion US$ (2017 value; log_{10} scale; shaded area is 95% confidence interval) **b** the distribution of the number of publications available in Web of Science for the period 1960–2020 for each species with invasion costs by organism group ("# species" refers to numbers of species in InvaCost within that group) and **c** distribution of publication numbers of invasive species with and without costs.

cies with monetary costs (83%) each contributed less than 1% of the respective total cost (Fig. 3). Costs of the European rabbit were incurred predominantly by agricultural impacts (93%); Japanese knotweed through impacts to authorities and stakeholders (97%); and rock pigeon towards mixed sectors (100%).

Invasive species with economic costs were associated with significantly more publications than UK invasive species without costs ($\chi^2 = 32.79$, df = 1, $p < 0.001$; Suppl. material 5: Fig. S1; Fig. 4). Of those invasive species present in InvaCost, total per-

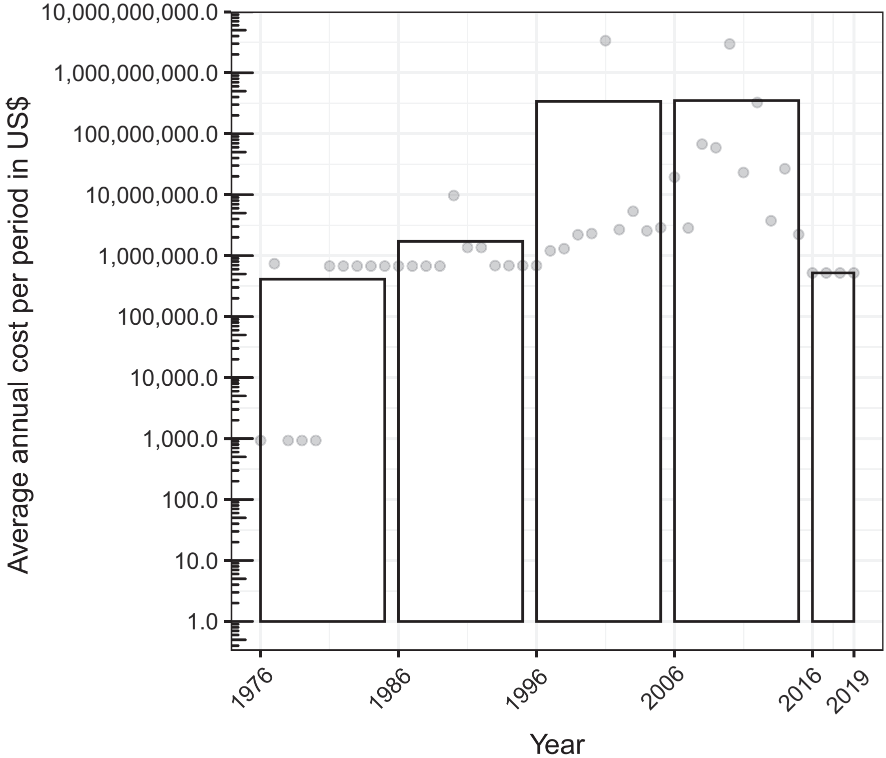

Figure 5. Annual average costs of biological invasions in the United Kingdom, considering decadal means (except 2016 to 2019: four years mean). Grey points indicate annual total costs. Note the *y*-axis is on a $\log_{10}$ scale.

species costs were positively related to numbers of studies per species ($t = 3.32$, $p < 0.01$; Fig. 4a). Plants, birds, mammals and insects had the highest numbers of species with costs (Fig. 4b), whilst many other taxa comprised just one species. Plants had relatively few publications per species, yet many invasive plants exhibited high costs relative to their study effort (e.g. floating pennywort, *H. ranunculoides*; Japanese knotweed, *R. japonica*). For birds, the rock pigeon (*C. livia*) and ruddy duck (*O. jamaicensis*) had the highest costs relative to publications. Mammals were generally the focus of the most published studies, with taxa such as the coypu (*M. coypus*) and European rabbit (*O. cuniculus*) having especially high costs relative to their study intensity (Fig. 4).

Question 3: Temporal dynamics of invasion costs

In examining the raw cost trends over time, between 1976 and 2019, the accumulated costs of \$6.9 billion (\$157.1 million per year; £5.4 billion and £122.1 million, respectively) increased steadily until 2005, being between \$411,987 (1976–1985) and \$1.7 million (1986–1995) per year until 1995. Costs then grew rapidly to between \$338.7 million and \$350.0 million per year after 1995 (Fig. 5). Cost reporting reduced in

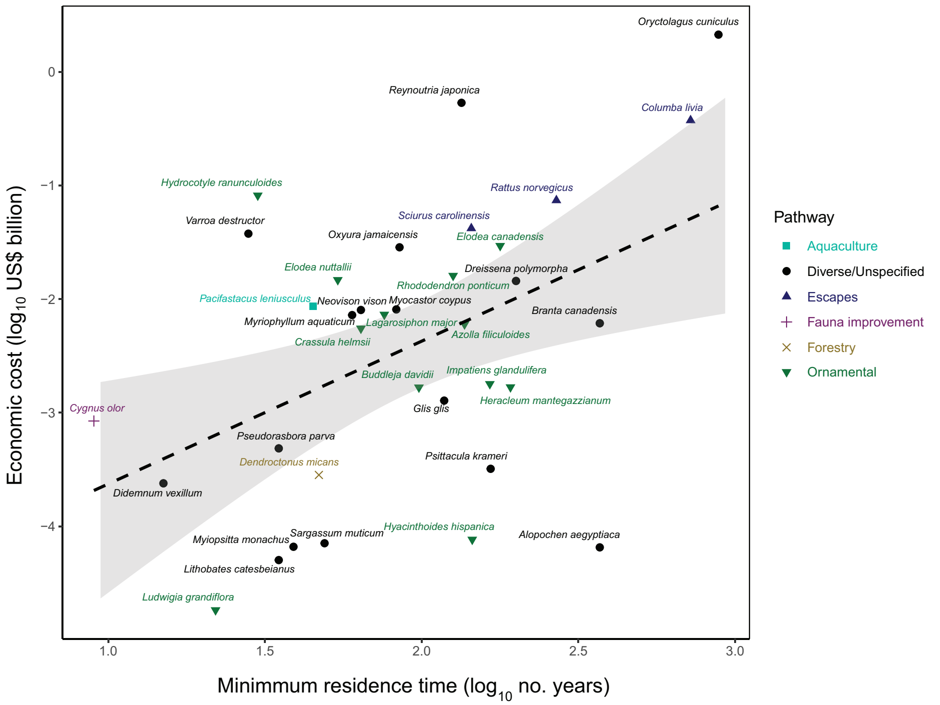

Figure 6. Invasion costs (US$ billions) as a function of number of years since introduction for UK invasive species. Note that both the *x*- and *y*-axes are on a log_{10} scale. The dashed line represents a linear regression model fit and the shaded area the 95% confidence interval. Pathways of introduction per species are indicated by different fill shapes and colours.

recent years, causing lower average costs in the last four years, likely due to time lags in cost reporting.

Of the 35 UK invasive species present in InvaCost with first record information, there was high variation in species' costs ($18,300 to $2.12 billion) and minimum residence times (9 to 885 years; time since first record of introduction; Fig. 6). Nonetheless, species that have been present in the UK for longer tended to have significantly higher invasion costs (t = 2.93, p < 0.01). There were several anomalies, however, to this trend, with species, such as the floating pennywort (*H. ranunculoides*), Varroa mite (*Varroa destructor*) and European rabbit (*O. cuniculus*), displaying disproportionately high impacts relative to their minimum residence time. Conversely, species, such as the Egyptian goose (*Alopochen aegyptiaca*), Spanish bluebell (*Hyacinthoides hispanica*) and edible dormouse (*Glis glis*), had relatively low economic effects, despite their early record of introduction (Fig. 6).

Of the five specified pathways of UK invasive species introductions, species introduced via the ornamental pathway were most common (12 species), followed by escapes (3 species); almost half of species were introduced via multiple (diverse) or unspecified pathways (17 species). In turn, diverse and unspecified pathways contributed the greatest costs ($2.8 billion), followed by escapes ($0.49 billion) and ornamental species ($0.17 billion). There was, however, generally no trend between pathway prevalence and minimum residence time for the assessed UK invasive species (Fig. 6).

Discussion

Biological invasions have cost the UK economy at least $6.9 billion (£5.4 billion) since 1976 and possibly at least $17.6 billion (£13.7 billion) if we include low reliability and potential costs (Diagne et al. 2020a). Costs have been rising rapidly over time and species with longer residence times have accrued higher invasion costs. However, there were no cost estimates for 90% of invasive species recorded so far in the UK. Of the costs reported for individual species, 90% were caused by approximately 10% of all invasive species in the UK with costs. Although the more costly species are also the most studied, the lack of any cost data for the majority of invasive species suggests that knowledge gaps are pervasive and that total costs of invasive species in the UK are underestimated. If cost reporting was complete for all invasive taxa, activity sectors, geographic regions and through time, UK invasion costs would likely be far greater than those reported here. Our totals also exclude invasion costs based on extrapolations or predictions ($5.2 billion), which calls for further research effort to decipher economic costs empirically. Impacts to certain activity sectors, such as fisheries and the environment, require urgent quantification, given the available means of quantifying economic impacts from environmental degradation and losses of ecosystem services from invasions (Hanley and Roberts 2019).

Question 1: Invasion costs distributions through space and sectors

Invasion costs were mostly reported at UK or Great Britain scales and, thus, further cost reporting is required at country-level scales or lower within the UK to improve and pinpoint management actions. Most costs stemmed from direct damage rather than management spending and principally impacted the agriculture sector. This dominance of damage-related costs over management aligns with trends in other geographic regions worldwide (Crystal-Ornelas et al. 2021; Haubrock et al. 2021a; Heringer et al. 2021; Liu et al. 2021). Invasion impacts in the UK were largely driven by animals, which were both the most studied and costliest taxa. Terrestrial invasion costs were most frequently documented and accounted for 93% of reported impacts overall. Contrastingly, there were comparatively few studies documenting economic impacts of aquatic and semi-aquatic invasions, despite the presence of multiple aquatic invaders that are recognised as a high management priority in the UK (e.g. Oreska and Aldridge 2011; Booy et al. 2020) and high global aquatic invasion costs (Cuthbert et al. 2021a). This trend might also reflect broader research biases within ecology towards terrestrial over aquatic environments (Menge et al. 2009; Cuthbert et al. 2021a) or perhaps reflect that aquatic invasion costs are more difficult to be observed empirically and thus likely to be predicted (and therefore excluded from our data subset).

Reported management costs were substantially lower than reported damage costs. Management costs were primarily incurred by authorities and stakeholders that are responsible for ecosystem management practices in the UK, rather than through primary sectors (e.g. agriculture and forestry). Aquatic and semi-aquatic invaders were more likely to incur management costs than direct damage, but the converse was true for terrestrial species. A study by Oreska and Aldridge (2011) found that aquatic invaders cost Great Britain £26.5–£43.5 million per year; like our study, most costs were attributed to macrophytes and bivalves. This suggests that observed management cost totals for aquatic systems ($258.5 million since 1976; £200.9 million) in our study may be underestimated. Nonetheless, aquatic invasion costs were found to be at least one order of magnitude lower than terrestrial impacts overall. A similar finding has been made at the global scale, where aquatic invasion costs have been found to have reached over $20 billion in the year 2020 alone, but remain an order of magnitude lower than terrestrial invasion costs in total (Cuthbert et al. 2021a). A lack of observed aquatic invasion costs in the UK may stem from a paucity in damage reporting from aquatic taxa or suggest that aquatic invasion costs are more likely to be predicted or extrapolated, given the difficulty in monitoring submerged environments. Awareness campaigns such as Check, Clean, Dry have spearheaded aquatic biosecurity in the UK, with recent methods developed to improve invader decontaminations (Anderson et al. 2015; Bradbeer et al. 2020). Recent criticisms have, however, been raised surrounding the efficacy of existing biosecurity protocols to prevent aquatic invasions and invasive species secondary spread across Europe (Coughlan et al. 2020).

More effective and coordinated management strategies are required to help limit future invasion costs in the UK, particularly in the terrestrial realm where damages are most burgeoning. Such management strategies should consider the range of pathways through which costly invaders have established (Robertson et al. 2020), as well as scientific evidence which indicates the most damaging species. Proactive management strategies, such as biosecurity, can prove disproportionately more cost-effective than longer-term, reactive interventions at more advanced invasion stages (Leung et al. 2002; Williams et al. 2010; Ahmed et al. 2021). Moreover, nations that fail to develop sufficient management strategies, at any invasion stage, could incur greater resource damages and losses as a result of biological invasions, such as through impacts to agriculture, forestry and human health sectors (Aukema et al. 2011; Paini et al. 2016).

Similar to prior estimates of UK invasion costs (Williams et al. 2010), we found the agricultural sector to be the most impacted overall and with cost types dominated by damages and losses, principally by animals. More broadly, this trend is congruent with a growing threat to agricultural enterprises worldwide by invasive species, threatening food production (Paini et al. 2016). Economic impacts were accordingly dominated by taxa affecting agriculturally-intensive terrestrial environments (e.g. European rabbit, brown rat, Varroa mite), where damage can be more readily perceived than in submerged realms. These results also corroborate Williams et al. (2010), where economic impacts from rabbits were dominant in the UK. Indeed, most studies on UK invasive species have focused on invasive mammals, despite alien plants constituting the highest number of alien species established by far (Roy et al. 2014b). Other studies have highlighted the extent of knowledge gaps (in terms of understudied taxonomic groups, regions and habitat types), indicating that previous invasion cost quantifications could be gross underestimates at the global scale (Bradshaw et al. 2016; Diagne et al. 2020a; Diagne et al. 2021).

Question 2: Taxonomic biases in invasion costs

Across all habitat types and taxonomic groups, where reported, invasion costs in the UK were always dominated by very few species. Similar trends have been found in other countries, with costs dominated by few species in, for example, Italy (Haubrock et al. 2021b), Singapore (Haubock et al. 2021c), Brazil (Adelino et al. 2021) and Argentina (Duboscq-Carra et al. 2021), as well as on the global scale (Cuthbert et al. 2021b). Strikingly, 90% of costs were attributable to just four individual species in the UK. Disproportionately high costs were associated with European rabbit, Japanese knotweed, rock pigeon and floating pennywort, corroborating other UK estimates (Williams et al. 2010). These species were particularly costly compared to their research effort. The disproportionate cost data, which represent 8% of the total invasive species pool in the UK, are somewhat indicative of the Tens Rule.

The Tens Rule hypothesizes that, where 10% of introduced species invade, 10% of those species naturalise and 10% of those become invasive (Williamson 1996). Whilst our results suggest that this hypothesis might be extended to the economic cost incurred by invasive species, absence of information does not indicate absence of impact. Accordingly, this fraction may reflect study effort rather than distribution of economic impacts. Indeed, studies have found much greater invasion success rates than predicted by the Tens Rule, with a success rate of 50% at each invasion stage shown for vertebrates (Jeschke and Strayer 2005). Moreover, the Tens Rule has been stated to be more of an indicator of lack of understanding, than the actual ratio of species that precipitate impacts (Jarić and Cvijanović 2012).

We also note that, because species present as part of 'mixed' cost entries were excluded from species-specific analyses here, numbers of invaders with costs would be higher with their inclusion (totalling 56 species with these 'grouped' costs). Nevertheless, the biases in cost reporting evidenced here were due to sustained focus on a few species, notwithstanding the substantial number of invasive species that are absent from InvaCost. In particular, mammals represented the class with the greatest proportion of reported invasive species with costs, despite not being the most diverse group of invaders in the UK (Roy et al. 2014b).

Cost reporting is lacking for many less notorious invasive species, evidenced by the relationship between those species with reported costs also having a greater number of studies. In the UK, some of the most notorious invaders that feature in targeted management campaigns do not have accessible cost data. The killer shrimp

(*Dikerogammarus villosus*) and quagga mussel (*Dreissena bugensis*) have no reported costs in the UK in InvaCost, despite being amongst 'keystone' invasive species targeted through management campaigns, such as Check, Clean, Dry (Anderson et al. 2015), launched by the UK Government's Department of Environment, Food and Rural Affairs in 2010. Another example is the topmouth gudgeon *Pseudorasbora parva*, which was introduced into the UK in 1985; a species which has been managed to curtail disease risk at high cost (Gozlan et al. 2010; Britton et al. 2011). Similarly, there were no reported costs for the Asian hornet (*Vespa velutina*) (Keeling et al. 2017; Barbet-Massin et al. 2020) nor the ash dieback fungus (*Hymenoscyphus fraxineus*) (Broome et al. 2018), despite their impact and concurrent management responses. The 2019 Environmental Audit Committee recognised a lack of consolidated information across UK organisations for these and other invasive species. This can lead to lost opportunities in managing new invasions in the UK, such as the delayed response in tackling the arrival of oak processionary moth (*Thaumetopoea processionea*) in 2006 (EAC 2019). This now established invasive species is a serious concern for forestry and public health and its unpredictable outbreaks make it difficult and costly to manage (Godefroid et al. 2020).

Overall, relative to three of the most robust databases of invasive species in the UK and beyond (sTwist, GISD and GB-NNSIP), numbers of species represented in InvaCost comprised less than one tenth and the few which are present reflect a bias towards intensively studied invasive species. These numbers also exclude species that are not yet reported as being alien in the UK or those that are introduced or naturalised and not invasive; the mismatch between numbers of invaders present and numbers economically appraised is therefore likely to be vast.

Question 3: Temporal dynamics of invasion costs

Over half of invaders with individual costs and first records have only been present in the UK for under 100 years. Despite marked species-specific variabilities, our results show that taxa present for longer (i.e. > 100 years) generally have more potential to accrue invasion costs, further highlighting that early-stage management measures are likely to be most cost-effective (Leung et al. 2002, Robertson et al. 2020; Ahmed et al. 2021). In that vein, early-stage prevention has been shown to be hugely more efficient than post-invasion management strategies in the UK (Williams et al. 2010). Furthermore, invasion costs across the UK are increasing rapidly through time, by at least three orders of magnitude since 1976.

Although our overall average annual cost estimate for the whole of the UK since 1976 ($157.1 million; £122.1 million) and, even in the most recent years, is considerably lower than previous estimates (GB: £1.7 billion; Williams et al. 2010), this is likely because prior works did not account for temporal dynamics. We also included only the most robust subset of estimates characterised by being of high method reliability and being empirically observed, i.e. not extrapolations or predictions. In contrast to those previous studies, our cost acquisition methods were centralised and standardised across a comprehensive suite of predictors (Diagne et al. 2020a), improving their comparability.

Given alien species incursions are expected to increase by 36% globally in the next three decades (Seebens et al. 2021) and costs are rising worldwide (Diagne et al. 2021; Cuthbert et al. 2021a), we expect UK costs to increase by further orders of magnitudes in coming years, with factors, such as climate change, as well as trade and transport intensifications, driving invasion rates (Bellard et al. 2013; Seebens et al. 2018; Hulme 2021).

Costs have been rising over time and species with longer residence times had higher costs. Even without further invasions, this means that costs in future will continue to accumulate (signalling an invasion economic impact debt; Essl et al. 2011). Whilst several pathways were identified in the present study, many species were from multiple or unspecified pathways. Nonetheless, the ornamental trade was especially pervasive considering numbers of introductions of costly invasive plants (van Kleunen et al. 2020). This trade activity is known to be increasing over time, with the UK market based on more than 73,000 plant species and varieties (Perrings et al. 2005). In contrast, most animal invasions were through diverse or unspecified pathways or via escapes from captivity (e.g. via pet trade). Horizon scanning has additionally identified a range of high risk invaders that are likely to arrive in the coming years, with 93 identified as constituting at least a medium risk of arriving, establishing and threatening ecosystems (Roy et al. 2014a). We, therefore, expect costs to increase markedly also because many new invaders will arrive in the UK. Indeed, recent UK invaders have shown an ability to rapidly establish and spread and cause impact, such as ash dieback fungus (Broome et al. 2018); with ash accounting for ~ 34 million m^3 of the timber volume in UK woodlands, the potential impacts could be massive (Broome et al. 2014). Further, the Asian hornet, which was first known to have arrived in 2016, has been the subject of rapid response control measures in the UK and has the potential to spread rapidly in mainland areas, threatening economically-important pollinators, such as bees (Keeling et al. 2017; Barbet-Massin et al. 2020).

Conclusion

Despite long-standing knowledge of ecological impacts of invasive species in the UK (Manchester and Bullock 2000), economic costs of invasions have been quantified for less than 10% of the UK's invasive species (42/520 species). If we were to consider species not yet reported as alien in the UK or those that have been introduced, but not yet invasive (Seebens et al. 2017), the proportion of alien species for which we have cost data becomes even smaller. For taxa with reported costs, cost contributions were highly unequally distributed, with infamous and well-studied invaders dominating costs. We acknowledge that not all invaders will cause discernible economic impacts. However, given the striking absence of cost data for species that are known to yield high economic costs (e.g. killer shrimp, Asian hornet, quagga mussel, ash dieback fungus), the general absence of cost data for the great majority of invasive species in the UK seems to point to a lack of data rather than a lack of costs. As such, it is likely that the reported costs, presented in this study, vastly underestimate the true cost of invasions in the UK. Accordingly, we urge greater cost reporting for all known invasive species in the UK and at sufficient resolution to provide information for efficient management practices at local and regional scales. This would enable greater awareness of the costs of UK invasions, supporting and motivating greater investment in management, as well as policy aimed at reducing the economic burden of damage and losses caused by current and future invasive species.

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Supplementary material 1

Subset of InvaCost database used for analyses of UK invasion costs. Note that cost data are not annualised.

Authors: Ross N. Cuthbert, Angela C. Bartlett, Anna J. Turbelin, Phillip J. Haubrock, Christophe Diagne, Zarah Pattison, Franck Courchamp, Jane A. Catford

Data type: database

Link: https://doi.org/10.3897/neobiota.67.59743.suppl1

Supplementary material 2

Summary of the content of the descriptive columns of the database used in this study (adapted from Diagne et al. 2020a)

Authors: Ross N. Cuthbert, Angela C. Bartlett, Anna J. Turbelin, Phillip J. Haubrock, Christophe Diagne, Zarah Pattison, Franck Courchamp, Jane A. Catford

Data type: explanation

Link: https://doi.org/10.3897/neobiota.67.59743.suppl2

Supplementary material 3

Web of Science search terms for UK invasive species publication numbers, alongside resulting study numbers

Authors: Ross N. Cuthbert, Angela C. Bartlett, Anna J. Turbelin, Phillip J. Haubrock, Christophe Diagne, Zarah Pattison, Franck Courchamp, Jane A. Catford

Data type: database

Link: https://doi.org/10.3897/neobiota.67.59743.suppl3

Supplementary material 4

Total costs of species with individual cost entries, alongside first record years and introduction pathways

Authors: Ross N. Cuthbert, Angela C. Bartlett, Anna J. Turbelin, Phillip J. Haubrock, Christophe Diagne, Zarah Pattison, Franck Courchamp, Jane A. Catford

Data type: database

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Supplementary material 5

Figure S1

Authors: Ross N. Cuthbert, Angela C. Bartlett, Anna J. Turbelin, Phillip J. Haubrock, Christophe Diagne, Zarah Pattison, Franck Courchamp, Jane A. Catford

Data type: figure

Explanation note: Boxplots of the number of publications recorded in Web of Science for species listed as invasive in the United Kingdom (UK) in the Global Invasive Species Database (GISD), sTwist database and Great Britain Non-native Species Information Portal (GB-NNSIP), but with no specific cost records in InvaCost (beige) and for invasive species with cost records in the UK in InvaCost (green).

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RESEARCH ARTICLE

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Economic impact of invasive alien species in Argentina: a first national synthesis

Virginia G. Duboscq-Carra[1*], Romina D. Fernandez[2*], Phillip J. Haubrock[3,4], Romina D. Dimarco[5], Elena Angulo[6], Liliana Ballesteros-Mejia[6], Christophe Diagne[6], Franck Courchamp[6], Martin A. Nuñez[1,7]

1 *Grupo de Ecología de Invasiones, INIBIOMA, CONICET, Universidad Nacional del Comahue, Quintral 1250, San Carlos de Bariloche, CP 8400, Argentina* **2** *Instituto de Ecología Regional, Universidad Nacional de Tucumán-CONICET. CC 34, 4107, Yerba Buena, Tucumán, Argentina* **3** *Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, Gelnhausen, Germany* **4** *University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Zátiší 728/II, 389 25, Vodňany, Czech Republic* **5** *Grupo de Ecología de Poblaciones de Insectos, IFAB (INTA-CONICET), Modesta Victoria 4450, San Carlos de Bariloche, CP 8400, Argentina* **6** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405, Orsay, France* **7** *Department of Biology and Biochemistry, University of Houston, Houston, Texas, 77204, USA*

Corresponding author: Romina D. Fernandez (romi.d.fernandez@gmail.com)

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Abstract

Invasive alien species (IAS) affect natural ecosystems and services fundamental to human well-being, human health and economies. However, the economic costs associated with IAS have been less studied than other impacts. This information can be particularly important for developing countries such as Argentina, where monetary resources for invasion management are scarce and economic costs are more impactful. The present study provides the first analysis of the economic cost of IAS in Argentina at the national level, using the InvaCost database (expanded with new data sources in Spanish), the first global compilation of the reported economic costs of invasions. We analyzed the temporal development of invasions costs, distinguishing costs according to the method reliability (i.e. reproducibility of the estimation methodology) and describing the economic costs of invasions by invaded environment, cost type, activity sector affected and taxonomic group of IAS. The total economic cost of IAS in Argentina between 1995 and 2019 was estimated at US$ 6,908 mil-

* These authors contributed equally to this work.

lion. All costs were incurred and 93% were highly reliable. The recorded costs were mainly related to terrestrial environments and the agricultural sector, with lack of costs in other sectors, making it difficult to discuss the actual distribution of invasion costs in Argentina. Nevertheless, the reported costs of IAS in this country are very high and yet likely much underestimated due to important data gaps and biases in the literature. Considering that Argentina has an underdeveloped economy, costs associated with biological invasions should be taken into consideration for preventing invasions, and to achieve a more effective use of available resources.

Abstract in Spanish

Impacto económico de las especies exóticas invasoras en Argentina: primera síntesis nacional. Las especies exóticas invasoras (EEI) afectan a la naturaleza y a servicios ecosistémicos fundamentales para el bienestar humano, la salud humana y las economías. Sin embargo, los costos económicos asociados a las EEI han sido menos estudiados en comparación con otros impactos. Esta información puede ser particularmente importante para países en vías de desarrollo como Argentina, donde los recursos económicos para el manejo de invasiones biológicas son escasos y los costos económicos son más impactantes. El presente estudio proporciona el primer análisis de los costos económicos de las EEI en Argentina a nivel nacional, utilizando la base de datos InvaCost (ampliada con nuevas fuentes de datos en español), la primera compilación global de los costos económicos registrados de las EEI. Analizamos el desarrollo temporal de los costos de las invasiones, distinguiendo los costos según la confiabilidad del método (es decir, reproducibilidad de la metodología de estimación) y describiendo los costos económicos de las invasiones por ambiente invadido, tipo de costo, sectores de actividad impactados y grupo taxonómico de las EEI. El costo económico total de las EEI en Argentina entre 1995 y 2019 se estimó en US$ 6,9 mil millones. Todos los costos económicos de las EEI fueron observados y el 93% fue altamente confiable. Los costos de las EEI se registraron principalmente en ambientes terrestres y en el sector agrícola, con pocos costos registrados en otros sectores, lo que dificulta discutir la distribución real de los costos de las invasiones en Argentina. No obstante, los costos económicos registrados de las EEI en este país son muy altos y probablemente estén muy subestimados debido a importantes lagunas de datos y sesgos en la literatura. Dado que Argentina tiene una economía en vías de desarrollo, los costos asociados a las invasiones biológicas deben considerarse para prevenir las invasiones y lograr un uso más efectivo de los recursos disponibles.

Abstract in Portuguese

Impacto econômico das espécies exóticas invasoras na Argentina: uma primeira síntese nacional. Espécies exóticas invasoras (EEI) afetam ecossistemas naturais e serviços ecossistêmicos fundamentais para o bem-estar humano, saúde humana e economia. No entanto, os custos econômicos associados com EEI é menos estudado que os outros impactos. Essa informação pode ser particularmente importante para países em desenvolvimento como Argentina, onde recursos financeiros para o manejo de invasões biológicas é escasso e os custos econômicos são mais impactantes. O presente estudo fornece a primeira análise dos custos econômicos de EEI na Argentina em nível nacional, utilizando a base de dados InvaCost (ampliada com novas fontes de dados em espanhol), o primeiro compilado global dos custos econômicos reportados de EEI. Nós analisamos a evolução temporal dos custos de invasãoes biológicas, diferenciamos os custos de acordo com a confiabilidade do método (isto é, facilidade de reprodução do método de estimativa) e descrevemos os custos econômicos das invasãoes biológicas pelo ambiente invadido, tipo de custo, setor de atividade afetado e grupo taxonômico de EEI. O custo total das EEI na Argentina entre 1995 e 2019 foi estimado em 6,908 milhões de dólares. Todo os custos foram observados e 93% deles são altamente confiáveis. Os custos reportados foram principalmente relacionados ao ambiente terrestre e ao setor de agricultura, com ausência de custos para outros setores, dificultando a discussão sobre a real distribuição de custos das EEI na Argentina. Ainda assim, os custos das EEI reportados no país são muito altos e, provavelmente, muito subestimados devido à falta de dados e viés na literatura. Considerando que a Argentina é uma economia em desenvolvimento, os custos associados com invasões biológicas devem ser levados em consideração para prevenir invasões e atingir um uso mais eficiente dos recursos disponíveis.

Abstract in French

Impact économique des espèces exotiques envahissantes en Argentine: première synthèse nationale. Les espèces exotiques envahissantes (EEE) affectent les écosystèmes naturels et les services écosystémiques essentiels au bien-être humain, à la santé humaine et aux économies. Cependant, les coûts économiques associés aux EEE ont été moins étudiés que les autres impacts. Cette information peut pourtant être particulièrement importante pour les pays en développement comme l'Argentine, où les ressources économiques pour la gestion des invasions sont rares et les coûts plus importants. Cette étude fournit la première analyse du coût économique des EEE en Argentine au niveau national, en utilisant la base de données InvaCost (étendue à d'autres sources de données), la première compilation mondiale des coûts économiques des invasions. Nous avons analysé l'évolution temporelle des coûts des invasions, distingué les coûts selon la forme d'implémentation (c.-à-d. observée empiriquement ou prévue) et décrit les coûts économiques des invasions selon l'environnement envahi, le type de coût, le secteur d'activité affecté et le groupe taxonomique des EEE. Le coût économique total des EEE en Argentine entre 1995 et 2019 a été estimé à 6,908 milliards de dollars américains. Tous les coûts ont été observés et 93% étaient hautement fiables. Les coûts enregistrés étaient principalement liés aux environnements terrestres et au secteur agricole, les autres coûts manquant de données, ce qui rend difficile la discussion de la répartition réelle des coûts d'invasion en Argentine. Néanmoins, les coûts déclarés des EEE dans ce pays sont très élevés, et probablement sous-estimés en raison d'importants lacunes et biais dans la littérature existante. Étant donné que l'Argentine a une économie sous-développée, les coûts associés aux invasions biologiques devraient être pris en considération pour prévenir les invasions et parvenir à une utilisation plus efficace des ressources disponibles.

Keywords

Damage costs, developing country, economic threat, InvaCost, management costs, non-native species

Introduction

Scientific literature provides robust and abundant evidence of negative impacts of invasive alien species (IAS) (e.g., Vilà et al. 2010, 2011; Pyšek et al. 2012; Castro-Díez et al. 2019). Notably, IAS threaten native biodiversity worldwide (Vilà et al. 2011; Pyšek et al. 2012; IPBES 2019) and burden human health, the production of food and other important goods, as well as ecosystem services that are fundamental for human well-being (Vilà et al. 2011; Simberloff et al. 2013; Shackleton et al. 2019). All these impacts on nature, health and production can also have important economic consequences. Although the problem of IAS is as much an economic as an ecological problem (Cuthbert et al. 2020), the economic costs associated with invasions have been relatively less studied (Pimentel et al. 2005; Bradshaw et al. 2016; Early et al. 2016; Cuthbert et al. 2020). For example, results of a meta-analysis on management of IAS showed that very few studies quantitatively evaluated the economic costs of invasive species control (Kettenring and Adams 2011). In addition, control costs were estimated in studies carried out at rather small spatial scales and over a considerably short period of time (Kettenring and Adams 2011), although quantifying damages and control costs at national levels is key to prioritizing management actions for IAS.

Research on IAS mostly focuses on developed countries (Pyšek et al. 2008), and this holds also for monetary impacts of invasions (Kettenring and Adams 2011). The scarce information on the monetary impact of IAS is especially true for areas where such information is desperately needed, as being unaware of these costs can limit the ability to timely respond (Leung et al. 2002). Research in developing countries is more focused on addressing basic aspects of invasions such as the distribution and ecology of IAS (Pauchard et al. 2011; Schwindt and Bortolus 2017). However, there is a great interest in the scientific community in addressing the issue of invasion costs in these areas (Pauchard et al. 2011; Schwindt and Bortolus 2017). Increasing such knowledge is important as prioritization and management of IAS in developing and developed countries may differ (Nuñez and Pauchard 2010). In this regard, developing countries such as Argentina present a flowering scientific community working on different socio-ecological aspects of biological invasions, which is reflected in the increasing number of publications in this field (e.g., Schwindt and Bortolus 2017; Kay et al. 2018; Nuñez and Paritsis 2018; Urcelay et al. 2019; Ballari et al. 2020; Fernandez et al. 2020; Huertas Herrera et al. 2020). In addition, in the last six years IAS became a priority of the Argentina government through a national strategy that aims to study, control and eradicate invasive species and to improve institutional capacities to manage biological invasions (MAyDS and FAO 2019). As an integral part of this strategy, the Argentine government seeks to promote the generation of public policies to minimize the impact of biological invasions on the national economy. For example, based on this strategy, the Argentine government approved risk analysis systems for the introduction of plants, fish and terrestrial vertebrates which are functioning and they elaborated an official list of IAS and, potentially, IAS in the country. However, to date, there is no public, open-access database that would facilitate collection and access to information on economic costs incurred by all IAS that could guide policy-makers. Moreover, very few studies report how much is actually spent on research or management of IAS (Fernandez et al. 2020, but see Zilio 2019). Consequently, there is a lack of consistent and complete information on the economic cost of biological invasions in Argentina.

Recently, the InvaCost database has been created to gather all the published data on the economic costs of invasive species (Diagne et al. 2020a, b). In the present study, we used this database to provide the first country-level synthesis of the economic cost of IAS in Argentina. More specifically, we analyzed how the reported costs of IAS evolved over time, distinguished costs according to the method reliability (i.e. reproducibility of the estimation methodology) and described their distribution by invaded environment, cost type, impacted sector and taxonomic group of IAS.

Methods

We retrieved economic costs data of IAS exclusively associated with Argentina that were collected in the frame of the InvaCost project (Diagne et al. 2020a), as of September 2020. Most of the original Invacost data was collected using traditional search engines, such as Web of Science and Google Scholar (Diagne et al. 2020b). However, these search engines provided extremely little information on the search topic for Argentina (only five references). To complete the dataset, we have added cost data collected from non-English sources (11 references), relying on both identical search strategies in existing repositories and more targeted collection through contacting experts and stakeholders (Angulo et al. 2021a). All cost entries were standardized to a common and up-to-date currency (US dollars exchange rate in 2017). Data were carefully checked to identify potential errors; all modifications to the original data were sent to updates@invacost.fr for further correction and consideration in the subsequent updated version(s) of the global database (latest version openly available at https://doi.org/10.6084/m9.figshare.12668570). Further details about the InvaCost database used here are provided by Diagne et al. (2020b).

From these 16 references (5 in English and 11 in Spanish), a total of 54 cost entries were selected for Argentina (Suppl. material 1). This dataset was expanded using the 'expandYearlyCosts' function of the R package "Invacost" (Leroy et al. 2020) considering the time period of each estimated cost entry using the database information (columns probable starting year adjusted and probable ending year adjusted, Suppl. material 1). Subsequently, this function multiplied the duration time (in years) by the cost per year to obtain the total cumulative cost along the defined period. When information was missing, we conservatively decided to consider the same year for both the starting and ending year if the cost was expected to occur over a single year, or used the publication year as a basis for calculating the duration if information was missing from both years. The reported annualized cost entries after costs were expanded totaled 68.

To investigate the temporal dynamics of the economic costs caused in Argentina by the IAS reported in the 68 annualized cost entries, we used the 'summarizeCosts' function implemented in the R package "invacost" (Leroy et al. 2020). With this method, we calculated the observed cumulative and average annual costs between 1995 and 2019, considering 5-year intervals for the mean costs. We also distinguished costs according to the implementation form and method reliability. The implementation form refers to whether the cost estimate was actually realized or incurred in the invaded habitat ("Observed") or whether it was a predicted or expected cost to be spent ("Potential"), (column implementation, Suppl. material 1). Method reliability refers to the perceived reliability of cost estimates based on the type of publication and method of estimation; "Low" vs. "High". Peer-reviewed or other official documents from the grey literature in which the original sources, assumptions and methods to estimate the cost were accessible and fully described were classified as "High" (column reliability, Suppl. material 1).

Finally, we described the distribution of costs by:

- **Invaded environment:** Aquatic, terrestrial, or semi-aquatic habitats (i.e. cost of IAS that spent part of their life in water) (column Environment, Suppl. material 1).
- **Cost type:** (a) "Damage-Loss", referring to damages or losses incurred by IAS, (b) "Management", comprising control-related expenditures (i.e., research, monitoring, prevention, management, eradication), and (c) "Mixed" costs, including undifferentiated damage and management costs (column Type_2 that we added based on information provided in the 'Type_of_cost' column, Suppl. material 1).

- **Impacted sector:** The activity, societal or market sector that was impacted by the cost of IAS (column "impacted_sector_2", Suppl. material 1). The sectors included were agriculture, authorities-stakeholders (briefly, institutions that manage IAS), environment (briefly, economic quantifications of impacts in ecosystem services, natural resources), fishery, forestry, health and public and social welfare (for the complete description of these categories see Suppl. material 2).
- **Taxonomic group of IAS** (columns "Class", "Order", "Family", "Genus" and "Species", Suppl. material 1).

Results

The total economic cost of invasive species reported in Argentina was estimated at US$ 6,908 million (AR$ 590,300 million, calculated considering the value of the dollar in 2017) over the entire period between 1995 and 2019, and the annual average was US$ 276 million (Fig. 1). The majority of the cost information (95%) was concentrated in the 2015–2019 period, concomitant with the majority of invasion cost records being published in 2016 (28 annualized cost entries out of 68). All costs were observed and 93% were highly reliable (i.e., costs were collected from peer-reviewed articles and official documents).

Economic costs by invaded environment

Economic costs of biological invasions differed according to the environment. Most of the costs associated with IAS were registered in the terrestrial environment (n = 52) with a total cost of US$ 6,816 million, while those associated with aquatic environments were much lower, amounting to US$ 87.91 million (n = 15). Only one record was found in a semi-aquatic environment, amounting to US$ 3.76 million (Fig. 2a).

Economic costs by cost type

The vast majority of the costs of IAS (98.9%) were related to damage-loss (US$ 6,835 million), while management costs represented 1.03% of the total (US$ 71.19 million). Costs belonging concomitantly to damage and management cost (Mixed costs; 0.03%) accumulated to US$ 1.69 million (Fig. 2a).

Economic costs by impacted sector

In general, the costs of invasive species were predominantly associated with agriculture (US$ 4,307 million). These costs were related with control or eradication actions or damages to crops of seven species; *Ceratitis capitata* (Mediterranean fruit fly), *Anthonomus grandis* (cotton boll weevil), *Anastrepha fraterculus* (fruit fly), *Cydia pomonella* (codling moth), *Castor canadensis* (beaver), *Sturnus vulgaris* (common starling) and

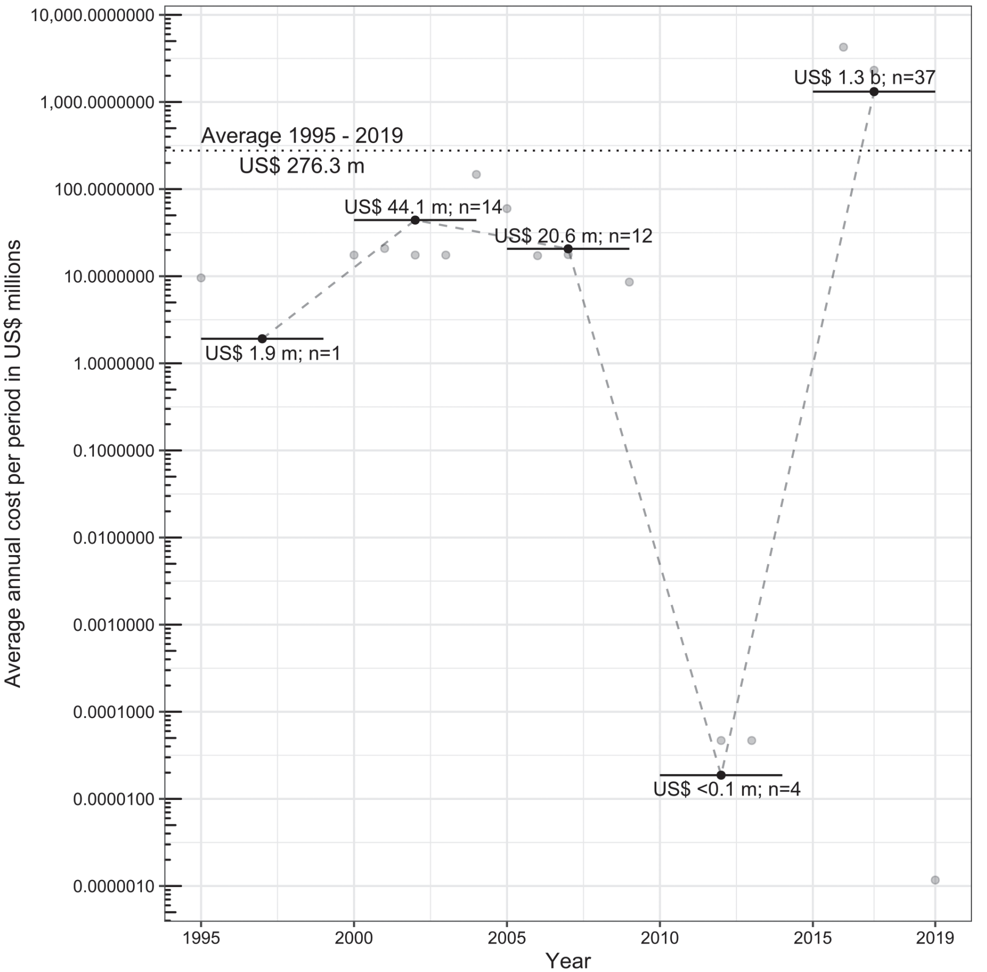

Figure 1. Cumulative economic costs of IAS in Argentina over time. Costs expanded between 1995 and 2019. Points are total annual costs for every year (i.e., all individual costs for a specific year are summed). Lines represent the average annual cost for 5 year intervals and the "n" in each line indicates the number of records in each period.

Tamarix sp. (saltcedar). The second most impacted sector was authorities-stakeholders (i.e., IAS management agencies/institutions, US$ 2,333 million). These costs impacting the authorities-stakeholders sector were associated with control, eradication, research, communication or damages caused by the species *C. capitata*, *Undaria pinnatifida* (Asian kelp), *Limnoperna fortunei* (golden mussels), *Ligustrum lucidum* (glossy privet), *C. canadensis* and *Sus scrofa* (wild boar). Particularly, the health costs were driven by the Insecta class (associated with medical care, direct medical costs, research, damage loss and control costs to *Aedes* mosquitoes transmitting dengue), fishery costs were driven by the algae *U. pinnatifida* and the public and social welfare costs were driven by *Tamarix* sp. (Fig. 2b).

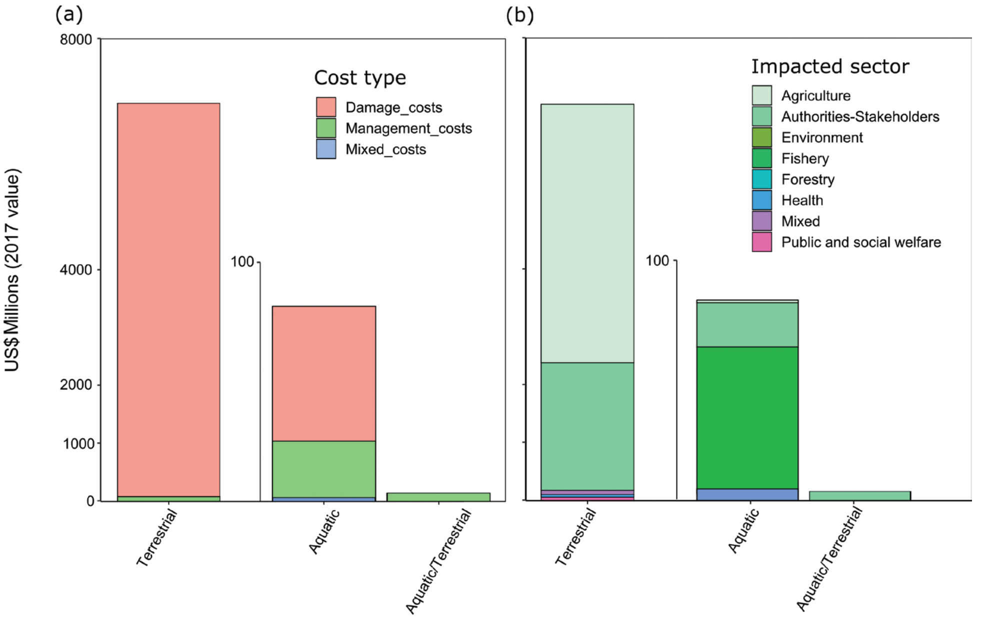

Figure 2. Economic cost of IAS in Argentina in each type of environment by **a** cost type and **b** impacted sectors.

Table 1. List of invasive species with reported economic costs for Argentina. Data sourced from the InvaCost database (Diagne et al. 2020b).

Class	Order	Family	Genus	Species	Cost $US	Database entries
Aves	Passeriformes	Sturnidae	Sturnus	Vulgaris	134,008,341.80	1
Bivalvia	Mytilida	Mytilidae	Limnoperna	fortunei	2,032,315	3
Insecta	Coleoptera	Curculionidae	Anthonomus	grandis	3,324,066.02	2
	Diptera	Culicidae	Aedes	aegypti	24,124,104.73	12
	Diptera	Culicidae	Aedes	aegypti/albopictus	155,807,802.40	10
	Diptera	Tephritidae	Anastrepha	fraterculus	38,242,382.17	2
	Diptera	Tephritidae	Ceratitis	capitata	129,773,008.00	2
	Hymenoptera	Siricidae	Sirex	noctilio	1,657,922.89	6
	Lepidoptera	Tortricidae	Cydia	pomonella	217,644.84	2
Magnoliopsida	Caryophyllales	Tamaricaceae	Tamarix	NA	4,035,079,013	6
	Lamiales	Oleaceae	Ligustrum	lucidum	94.74	6
Mammalia	Artiodactyla	Suidae	Sus	scrofa	2,293,673,994	5
	Rodentia	Castoridae	Castor	Canadensis	66,556,973	9
Phaeophyceae	Laminariales	Alariaceae	Undaria	pinnatifida	168,490	2
Pinopsida	Pinales	Pinaceae	Pinus	halepensis	78.15	1

Economic costs by taxonomic group of IAS

The majority of the 68 cost entries belonged to the Insecta class (n = 36), mainly of *Aedes Aegypti*. The second class with the highest number of cost entries was Mammalia (n = 14) represented by beavers and wild boars, and the third class was Magnoliopsida (n = 9) with the species glossy privet and saltcedar (Table 1). However, the Magnoliopsida class (“flowering plants”) produced most of the costs, with US$ 4,035 million concentrated mainly in saltcedar; second were Mammalia with US$ 2,360 million (Table 1; Fig. 3).

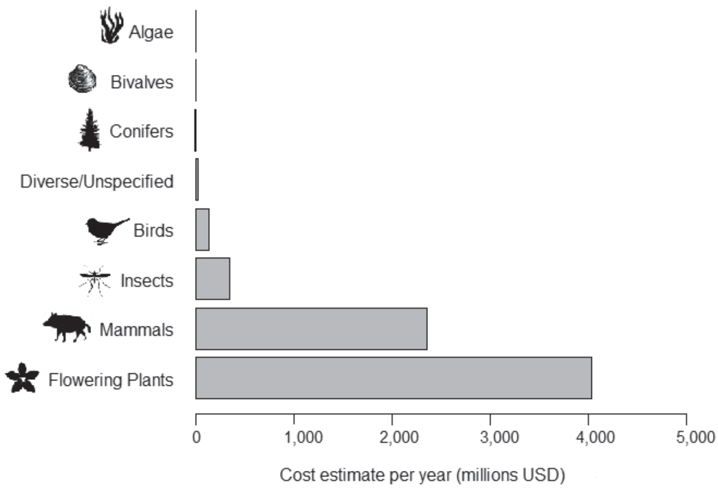

Figure 3. Economic costs of IAS in Argentina by taxonomic groups (Class).

Discussion

Our results show that the reported cost of IAS in Argentina accumulated to a total of US$ 6,908 million (AR$ 590,300 million) between 1995 and 2019. Despite the extensive search and the millions in costs observed, we consider that this value can be seen as highly conservative because the costs reported here were produced by just 15 species, which represent only 2% of the IAS registered for Argentina. Indeed, according to the National Invasive Exotic Species Information System, Argentina registers 654 IAS and 319 evidenced negative ecological impacts according to the global database of introduced and invasive alien species (Zalba et al. 2020). Although very problematic, this is not specific to Argentina, and similar knowledge gaps have been highlighted elsewhere, for example in economic assessments in Germany (Haubrock et al. 2021), France (Renault et al. 2021), United-Kingdom, (Cuthbert et al. 2021a), Asia (Liu et al. 2021) or Australia (Bradshaw et al. 2021). Furthermore, there are only very few entries in the database on economic costs for several sectors (e.g. forestry, fishery and health) of major importance in Argentina, which could still account for very large sums. For example, in the health sector, there are 12 entries about the high costs associated with direct medical costs, research, damage loss and control costs of invasive mosquitoes vectoring diseases like dengue, Zika and chikungunya fever, and all but one come from observed costs of only one year, 2016 (FAO FMAM Estrategia Nacional sobre Especies Invasoras; Ministerio de Medio Ambiente y Desarrollo Sostenible 2017). However, it is important to note that several dengue prevention and control actions were performed in Argentina, which implies high management expenditures, but these are not usually published (Vezzani and Carbajo 2008). Unsurprisingly, there is no record on monetized impacts of IAS on biodiversity and some ecosystem services (e.g. cultural services) because these are generally difficult to quantify (Vilà et al. 2010; Cerda et al. 2017; Diagne et al. 2020b). Yet, some countries invest more in biodiversity conservation and therefore have a higher percentage of management investment of

IAS, showing it is not a fate (e.g. Ecuador, Ballesteros-Mejia et al. 2021; Spain, Angulo et al. 2021b; Japan, Watari et al. 2021). More generally, the cost amounts shown here represent only a small part of the actual economic burden of IAS, as they are only based on the few documented costs that were collated in the InvaCost resource.

There is considerable variability in these reported economic costs of IAS in Argentina throughout the period analyzed, which is strongly linked with the publication effort. Most of the total costs are concentrated in the last 5 years of the period analyzed, because 50% of the studies on IAS costs are concentrated in that time. There is limited information about economic costs of IAS in Argentina and we noted that part of this may be related to the accessibility of information. Web search engines such as Web of Science, for example, that have been very useful in countries like the United Kingdom, proved to have really limited efficiency here, with less than 4% of the references analyzed coming from this tool. We believe that there may be technical reports on the impacts of invasive species in the agriculture, fishery, forestry and health sectors, but they are not available to the scientific community, and therefore not attainable through traditional search methods. As a result, some cost information could be missing in the InvaCost database despite having used a wide range of search terms in Spanish and English languages. This situation highlights clear gaps in the available data. In comparison, other Latin American countries like Brazil, Ecuador (mostly from Galapagos Islands), and Mexico, have respectively, two, six, and four times more entries than Argentina (174 entries in expanded database, Adelino et al. 2021; 464 entries in expanded database, Ballesteros-Mejia et al. 2021; 251 entries in expanded database, Rico-Sánchez et al. 2021). From there, scientists need to improve interactions with some official organisms to communicate the importance of increasing accessibility to this information. Given the standardization of the InvaCost database used, it would be interesting to have this type of analysis carried out in Argentina, Brazil, Ecuador and Mexico also applied to other Latin American countries.

In 2016, the year with the highest estimated costs, the total annual cost was US$ 4,260 million, which corresponds to 0.76% of the Argentina's Gross Domestic Product (GDP) of US$ 557,500 million in the same year, and is comparable to the health budget for the entire country of US$ 4,560 million for 2016 (Senado y Cámara de Diputados de la Nación Argentina 2016). This indicates that despite the limited information of the economic impact of IAS in Argentina, the costs are still high. In line with this idea, it is possible that other countries reported higher costs than in Argentina such as Brazil (US$ 105.53 billion, Adelino et al. 2021) and Mexico (US$ 10.77 billion, Rico-Sánchez et al. 2021) mainly because they have better data records (as mentioned above) and not because the IAS generated higher economic problems than in Argentina. Based on our conservative estimation and the clear missing data, the real cost of IAS in Argentina likely represents a significant problem for the developing economy of the country.

Our results also showed that there are important data biases. Indeed, the entire pattern of the costs reported was driven by one environment type (terrestrial), one sector (agriculture) and a single taxon (*Tamarix* sp.) of invasive species in Argentina. These costs based on data records to date do not represent the overwhelming majority of the real costs due to the prevalence of habitat, sector and taxonomic biases. Consequently, it is difficult to discuss the distribution patterns of invasion costs in this country. In fact, most of the cost records (76%) come from the terrestrial environment. This trend has been also observed in general for the InvaCost database, for which only 5% of reported costs were from aquatic species (Cuthbert et al. 2021b). This is not surprising given that, in general, invasion studies predominate in the terrestrial environment (e.g. Puth and Post 2005; Dana et al. 2014). Part of this disparity in invasion studies in aquatic and terrestrial environments may be related to a bias in social perception. In aquatic environments, IAS are perceived mostly by scientists who work in aquatic ecosystems or by fewer people who perform water-based recreational activities compared to activities in terrestrial environments (Eiswerth et al. 2011). There are several gaps in aquatic invasion research (Schwindt and Bortolus 2017) including economic impacts (Cuthbert et al. 2021b), which can be high considering that some invasive species can negatively affect numerous sectors. An important example of IAS in aquatic environments in Argentina is the mammalian *C. canadensis* (beavers). This species is an ecosystem engineer that produced large and dramatic ecological and economic impacts by invading forests, grasslands and peatlands in southern Argentina (Anderson et al. 2009; Zilio 2019). According to our records, the beavers' invasions affected forestry, agriculture, and environment sectors with an estimated cost of US$ 66.56 million (Table 1). Given the magnitude of its impacts both in aquatic and terrestrial ecosystems, it is likely that the real damage and management costs of this species are higher than those reported in this study. Another example of IAS in this environment with substantial impacts is the bivalve golden mussels. All costs of golden mussels accounted for US$ 0.007 billion and were registered in South America entirely (Haubrock et al. in prep). We know that in Argentina this species negatively affected several sectors that use water (e.g. nuclear and thermal power plants, food plants, commercial and tourist boats) (Boltovskoy et al. 2006), but these damage costs have not been estimated yet. The costs inferred to freshwater bivalves can be considerably higher. This is, for instance, indicated by the costs of another freshwater invasive macrofouling bivalve, *Dreissena polymorpha* (zebra mussel), in North America alone, totaling at US$ 24.8 billion (Haubrock et al., in prep).

We found an overwhelming predominance of reported costs related to damage or loss rather than to management of IAS. High damage-loss cost of invasions could be related to the incipient, and much needed, investment in prevention and control of IAS in Argentina. It is important to mention that the non-implementation of invasive species management and control strategies could increase the negative impact for both the national and private economies. Additionally, few control studies carried out in Argentina reported the costs of the different treatments evaluated, although these costs can easily be quantified since they are observable. Indeed, they are fundamental to evaluate the costs-benefits of applied management. This problem is not exclusive to Argentina, because in general studies on control of IAS do not report the costs associated with management actions of these species (Kettenring and Adams 2011; Dana et al. 2014). However, our results show a growing interest from the scientific community in considering this aspect of invasions, since the highest number of entries of invasions costs in Argentina were reported in the last 5 years.

Invasive species represent a threat to global agriculture, in particular for the economy of developing countries (Paini et al. 2016). Agriculture is an important economic sector for Argentina. This country is the second largest agricultural and food exporter in Latin America (US$ 35 billion in 2017; Food and Agriculture Organization of the UN, 2019) and it was the sector that registered the highest costs associated with invasions (more than 62%), even without including the costs of several exotic pests and weeds such as *Cirsium vulgare* (spear thistle), *Carduus acanthoides* (welted thistle) and *Vespula germanica* (German wasp) that also affect agriculture (Ziller et al. 2005; Masciocchi and Corley 2013; Renzi and Cantamutto 2013) but for which there is no economic cost evaluation associated. The invasive species also generated high costs on the authorities-stakeholders' sector (33% of the total), which includes all management policies of biological invasions, and the costs associated with research and management of IAS in protected areas. Given that invasive species represent a growing problem in protected areas in Argentina (e.g. Merino et al. 2009; Ballari et al. 2015) it is not surprising that the costs are high. Moreover, some sectors that may be much impacted by IAS in Argentina might be understudied there, and present an artificially low cost. For example, there was only one cost in Argentina for fisheries, and yet the costs for this activity sector could be very high; it was the most impacted sector in Mexico (US$ 5.96 billion, Rico-Sánchez et al. 2021).

Most of the total costs registered were produced by *Tamarix* sp., which has several negative ecological impacts and important social and economic impacts because it consumes large amounts of water and invades productive lands and subsistence agriculture areas (Natale et al. 2008; Natale et al. 2012; Zilio 2019). However, it is important to mention that the costs of this species registered in the invaCost database were estimated extrapolating the current areas invaded and the known cost for irrigation due to consumption of water in areas destined for agriculture on the large arid areas where it invades. Although *Tamarix* sp. was the species with the highest recorded economic costs in Argentina in our database, it is not certain if this is the one with the actual higher costs. This could be due to the lack of detailed studies on the economic cost of other important invasive species with very high impacts and with a larger number of reports such as *A. aegypti*, *S. scrofa* and *C. canadensis*. In Argentina, there are other invasive species such as *Pinus* spp, *L. lucidum*, *Bombus terrestris*, *Achatina fulica*, *Didymosphenia geminata*, *Neovison vison* and *Callosciurus erythraeus* whose negative ecological impacts are well known (e.g. Benitez et al. 2013; Valenzuela et al. 2013; Nuñez et al. 2017; Aizen et al. 2019; Fernandez et al. 2020), but lack economic impact assessments (or with a few, clearly underestimated costs). For example, the invasion of *B. terrestris* has caused a decrease in the populations of native bees and severe impacts on the natural and agricultural ecosystems of southern Argentina, but we lack information on the economic cost of these impacts (Aizen et al. 2019). Another problem is that several articles on the economic impacts of weeds do not differentiate whether the weeds are native species or not, which makes it difficult to estimate the impact of the latter. Having a biased sample of costs from a literature review is not something unexpected on an understudied topic, and we hope that our report will help reduce these biases. Additionally, studies are required to examine the costs caused by IAS for which there are no estimated costs in order to obtain a comprehensive database of the real economic costs of invasions at the national level. In this sense, future studies should evaluate the potential economic costs of IAS with the most negative impact in different sectors of the country considering the spatial scale of their distribution and the vulnerability of the invaded habitat.

One aspect that has been understudied is the positive economic benefits of invasions. We recognize that some IAS can be seen ambivalently, causing as they do both economic costs and benefits. For example, sport fisheries in Patagonia – based on nonnative salmonids – is a multimillion-dollar business that brings tourists from all over the world (Vigliano et al 2007). However, these reported economic benefits are in order of magnitude of millions of dollars rather than billions as we obtained here for economic costs of IAS. This suggests that the costs of IAS are notably higher than the benefits, but a case-by-case analysis is necessary for a deeper understanding of the impact of IAS on the local economies. Finally, considering the perceptions that different stakeholders have about IAS and their economic costs or benefits can contribute to estimating the cost-benefit ratio of IAS in the country.

Conclusions

The results of this study highlight the high economic burden of IAS for Argentina, which may be even more important given that the amounts presented are based only on the little documented cost information reported in the data resource considered here. They also underline a significant need to develop more research on the economic impacts of IAS as well as to improve the accessibility of that information in Argentina. The cost of IAS reported here is very high considering the low representation of taxa with cost estimates relative to the number of invasive taxa registered in Argentina, and the few data recorded of the taxa with cost information. Considering that Argentina has an underdeveloped economy, costs associated with biological invasions should be taken into consideration for prevention efforts of invasions and to achieve a more effective use of resources. The information about costs of IAS that we reported in the present study, could contribute to the objectives of the Argentine government which seeks to promote the development and implementation of public policies that minimize the impact of biological invasions on the economy (MAyDS and FAO 2019). Significantly, management (i.e., proactive costs) represented a very small fraction of the recorded costs, the rest being damages and losses (i.e., reactive costs). There is a need to improve the interaction with both market sectors and the government in order to develop an open access database on the economic costs associated with biological invasions (e.g. fumigation costs for prevention, and hospitalization cost related to *Aedes* mosquitoes). The development of collaboratively applied projects between decision makers and scientists could contribute to this objective. Further, we encourage researchers to report the quantity of public resources committed to evaluate the impacts of invasive species, and to report the economic costs of managing invasive species in the country in a thorough and standardized way (Diagne et al. 2020a). All this information could help to have a better picture of the real economic costs of IAS in Argentina and also may be useful to alert the public and policy-makers about the magnitude of the economic problem of biological invasions in this country.

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Supplementary material 1

Dataset of economic costs of IAS for Argentina, extracted from InvaCost Database

Authors: Virginia G. Duboscq-Carra, Romina D. Fernandez, Phillip J. Haubrock, Romina D. Dimarco, Elena Angulo, Liliana Ballesteros-Mejia, Christophe Diagne, Franck Courchamp, Martin A. Nuñez

Data type: table

Link: https://doi.org/10.3897/neobiota.67.63208.suppl1

Supplementary material 2

Description of the sectors considered in the InvaCost database

Authors: Virginia G. Duboscq-Carra, Romina D. Fernandez, Phillip J. Haubrock, Romina D. Dimarco, Elena Angulo, Liliana Ballesteros-Mejia, Christophe Diagne, Franck Courchamp, Martin A. Nuñez

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RESEARCH ARTICLE

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The economic costs of biological invasions in Brazil: a first assessment

José Ricardo Pires Adelino[1], Gustavo Heringer[2], Christophe Diagne[3], Franck Courchamp[3], Lucas Del Bianco Faria[2], Rafael Dudeque Zenni[2]

1 *Programa de Pós-Graduação em Ciências Biológicas, Centro de Ciências Biológicas, Departamento de Biologia Animal e Vegetal, Universidade Estadual de Londrina, CP 6001, 86051-970, Londrina, Brazil* **2** *Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, Universidade Federal de Lavras, CEP 37200-900, Lavras-MG, Brazil* **3** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405, Orsay, France*

Corresponding author: Rafael Dudeque Zenni (rafael.zenni@ufla.br)

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Abstract

Biological invasions are one of the leading causes of global environmental change and their impacts can affect biodiversity, ecosystem services, human health and the economy. Yet, the understanding on the impacts of invasive alien species is still limited and mostly related to alien species outbreaks and losses in agricultural yield, followed by the understanding of the ecological impacts on natural systems. Notably, the economic impacts of biological invasions have rarely been quantified. Brazil has at least 1214 known alien species from which 460 are recognized as invasive alien species. Still, there are no comprehensive estimates of the cost of their impact and management. Here, we aimed at filling this gap by providing a comprehensive estimate of the economic cost of biological invasions in Brazil. In order to quantify these costs for species, ecosystems and human well-being we used the InvaCost database which is the first global compilation of the economic costs of biological invasions. We found that Brazil reportedly spent a minimum of USD 105.53 billions over 35 years (1984–2019), with an average spent of USD 3.02 (± 9.8) billions per year. Furthermore, USD 104.33 billion were due to damages and losses caused by invaders, whereas only USD 1.19 billion were invested in their management (prevention, control or eradication). We also found that recorded costs were unevenly distributed across ecosystems, and socio-economic sectors, and were rarely evaluated and published. We found that the economic costs with losses and damages were substantially greater than those used for prevention, control or eradication of IAS. Since our data show costs reported in Brazil for only 16 invasive alien species, our estimates are likely a conservative minimum of the actual economic costs of biological invasions in Brazil. Taken together, they indicate that invasive alien species are an important cause of economic losses and that Brazil has mostly opted for paying for the damage incurred by biological invasions rather than investing in preventing them from happening.

Abstract in Portuguese

Os impactos resultantes da introdução de espécies exóticas e invasoras (t.c.p. invasão biológica) é um dos principais fatores associados as mudanças ambientais em escala global, cujos impactos afetam direta e indiretamente a biodiversidade, os serviços ecossistêmicos, o bem estar e a saúde humana, e a economia. Contudo, muito do conhecimento sobre os impactos das espécies exóticas e invasoras ainda é limitado aos prejuízos observados em áreas de cultivo e plantações, negligenciando o impacto de surtos de espécies exóticas em sistemas ecológicos e naturais. Somado a isso, é notável o desconhecimento dos impactos econômicos da invasão biológica que são raramente quantificados e reportados. No Brasil estima-se a ocorrência de ao menos 1214 espécies exóticas estabelecidas das quais 460 são reconhecidas como espécies invasoras. Ainda assim, as estimativas dos custos relacionados aos respectivos impactos por prejuízos e por manejo de espécies exóticas e invasoras são desconhecidos. Neste estudo, pretendemos contribuir para preencher esta lacuna sumarizando os custos econômicos da invasão biológica para o Brasil. Para quantificar os custos econômicos da invasão biológica usamos informações em nível de espécie, ecossistemas, bem estar e saúde humana, e setores socio-econômicos disponíveis no primeiro levantamento de dados global para custos econômicos da invasão biológica, InvaCost. Encontramos que os custos reportados para o Brasil apresentam valor mínimo de USD 105,3 bilhões ao longo dos últimos 35 anos (1984–2019), com custo médio de USD 3,02 (± 9,8) bilhões ao ano. Detectamos que USD 104,33 bilhões estão relacionados a prejuízos (danos e perdas) causados por espécies invasoras, enquanto USD 1,9 bilhões foram investidos em ações preventivas como o de manejo, controle ou erradicação de espécies. Além disso, nossos resultados apontam para uma significativa disparidade dos custos econômicos entre os diferentes setores analisados (ecológicos, sociais e econômicos) reforçando a escassez de dados econômicos reportados e ou disponíveis para análise. Com os dados disponiveis observamos que os custos econômicos dos prejuízos (perdas e danos) foram mais representativos do que os custos de prevenção, controle e erradicação de espécies exóticas e invasoras. Uma vez que nossos dados de custo disponíveis para o Brasil estão associados apenas à presença de 16 espécies invasoras, certamente nossos resultados representam uma estimativa conservadora que reflete o valor mínimo esperado para os custos atuais dos impactos econômicos referente a presença de espécies exótico invasoras para o Brasil. Em conjunto, providenciamos a primeira análise de custos econômicos baseado em evidências que indicam que o custo com espécies exótico invasoras no país está associado à reversão dos prejuízos acometidos pela invasão biológica ao invés do incentivo em investimento para a prevenção de danos. Portanto, concluímos que espécies exótico invasoras são uma importante fonte do prejuízo econômico ao país.

Keywords

Biological invasions, economic cost, economic damage, Invasive species impact, InvaCost database, invasive alien species, Invasion management

Introduction

The pervasive impacts of invasive alien species (IAS hereafter) are complex and multifaceted, since IAS are responsible for substantial damages in social, ecological, and human health worldwide (Strayer 2012; Jones 2017; Bradley et al. 2019; Crystal-Ornelas and Lockwood 2020a). Among the wide range of impacts imposed by IAS are changes in native species composition (Vilà et al. 2011; but see Crystal-Ornellas and Lockwood 2020b), the decline in biodiversity (Bellard et al. 2016; Doherty et al. 2016), disturbance in ecosystem services and environmental functioning (Ricciardi et al. 2013), spreading diseases that affect human well-being (Shepard et al. 2011; Shackleton et al. 2019; Nuñez et al. 2020) and destruction of croplands (Paini et al. 2016). However, public awareness of the impacts associated with IAS seems to be insufficient to support effective management efforts in prevention, control, and eradication. Thus, mitigation of biological invasions remains a challenge. For instance, although the ecological impacts of IAS have been more thoroughly scrutinized (Blackburn et al. 2014; Gallardo et al. 2016; Crystal-Ornelas and Lockwood 2020b), there is a scarcity of information on economic costs imposed by IAS. Because economic costs are distributed over the market and non-market sectors (Bradshaw et al. 2016), understanding the type and the magnitude of economic costs associated with IAS are key for environmental management and for raising public awareness. Therefore, knowing IAS impacts becomes more relevant in the current context where many more species are expected to be introduced and become invasive worldwide (Seebens et al. 2017; Seebens et al. 2020).

Despite the growing knowledge in IAS distribution patterns and drivers (e.g., Dawson et al. 2017), estimating the impact of IAS remains a challenge owing to the temporal and spatial scales in which they occur, and the potential myriad of indirect effects that some IAS can have on ecological and human systems (Shackleton et al. 2019). With the recent development of standardized ecological (Blackburn et al. 2014, IUCN 2020) and socio-economic assessments (Bacher et al. 2018) of IAS impacts, it is increasingly clear that high-quality and comprehensive information is still lacking for most taxa, systems and regions. Yet, these data are necessary for researchers, managers and policy makers to develop and implement effective management programs towards IAS.

The economic cost of biological invasions tends to incur even when the ecological or human health impacts decrease. Indeed, managing invasions to reduce their ecological impact also produces an economic impact by consuming monetary and human resources. However, different sectors of activity differ in their required costs for managing IAS. In Brazil, IAS can rapidly damage crops fields and directly impact a wide range of commodities imposing billions of Reais (R$) in cost distributed over damage repair, species invasion mitigation, and prevention strategies (Oliveira et al. 2013; Oliveira et al. 2014; Pozebon et al. 2020). Furthermore, in tropical regions, IAS impact can be more severe and threat human well-being substantially by spreading multiple zoonotic diseases (i.e., dengue, chikungunya, and zika virus spread by species of the genus *Aedes*), consequently causing severe economic impact associated with human care (Teichi et al. 2017). Finally, IAS spread diseases into Forestry plantations (Schnell e Schühli et al. 2016) and imposes severe costs with IAS management and eradication in conservation areas (Guimarães et al. 2017). Therefore, partitioning of the economic impact of IAS over multiple activity sectors is central for understanding and planning effective impact reduction.

Despite the comprehensive impacts generated by IAS, the economic costs of biological invasions are rarely assessed (Diagne et al. 2020; Heringer et al. 2021 for the costs in Latin America) and effective management and policy decisions for the best possible resource allocation remains doubtful in most cases. Knowledge of the economic effects of IAS in a region can help inform management and policy decisions as well as raise public awareness regarding the implications of biological invasions on people's lives. Globally, the economic impact of biological invasions was estimated to reach at least USD 1.288 trillion between 1970 and 2017 (Diagne et al. 2021) owing to impacts associated with biodiversity loss, spread and cause of human diseases, damage to goods and infrastructure, and increased costs of travel and international trade. For Central and South Americas, when applying the same criteria used here, the known economic impact of invasive alien species has recently been estimated at USD 146.5 billion (see Heringer et al. 2021). In South America, Brazil is one of the world's rising economies (Shukla et al. 2018) that hosts two global biodiversity hotspots covering 17.25% of the hotspots surface area worldwide (Myers et al. 2000; Mittermeier et al. 2011). However, its biodiversity, ecological structure and ecosystem services (Pauchard et al. 2018) have been severely impacted by the damage imposed by human activities (Soares-Filho et al. 2014; Venter et al. 2016) which in turn raise opportunities for new IAS impacts. For Brazil, even though studies have shown the widespread presence and negative impacts of many invasive alien species (e.g., Zenni and Ziller 2011; Fontoura et al. 2013; da Rosa et al. 2017), the only general estimation for the economic impact of invasive alien species for the country was made 20 years ago based solely on the estimated impacts of rats and human diseases (Pimentel et al. 2001). Therefore, there is a knowledge gap regarding the costs with IAS in Brazil.

Here, we investigated the economic costs associated with the presence of IAS in Brazil. For the purpose of this study, invasive alien species are any non-native species that generate economic impact on ecological, societal or environmental sectors of activity. Using studies that report the economic impact of alien species we evaluated the reported expenses based on IAS identities, intervention classes and costs in environmental and societal sectors. Furthermore, by using InvaCost, a global dataset of the economic costs of invasive species (Diagne et al. 2020), we estimated the total cost of biological invasions in Brazil, as well as the distribution of these costs over the different economic sectors and type of costs. Finally, we tested whether the economic costs associated with the presence of IAS reflect preventive actions for managing or enduring damages and losses caused by IAS.

Method

The species list used in this study was obtained from the InvaCost database (Diagne et al. 2020). InvaCost is a global database (N = 9,823 entries) constructed from a systematic review in peer-reviewed articles, official reports and grey material that considers as IAS any non-native species that results in economic impact on the ecological, societal or environmental sector of activity (for details see Diagne et. al 2020 and Angulo et al. 2021). The resulting database is the most comprehensive, harmonized and robust global-scale data compilation and description of economic cost estimates associated with IAS reported in the existing literature (Diagne et al. 2020; https://doi.org/10.6084/m9.figshare.12668570). To compile these data, the Web of Science, Google Scholar, and Google search engines were used with standardized search strings (for details see Diagne et al. 2020). Additionally, institutions, researchers and managers were contacted in order to find all possible references. For Brazil, both English and Portuguese literature were used (Angulo et al. 2021).

From the InvaCost database, we selected all entries referring to Brazil (N = 54) by using the 'Official country' column of the dataset and used the 'expandYearlyCosts' function of the R package invacost (Leroy et al. 2020) to expand the dataset. This function expands the annual cost to the period of time higher than one year. Thus, each estimate cost corresponds to an annual cost, which was repeated as many times as the number of years over which the cost occurred. Then, the total reported cost entries after data 'expansion' (N = 173) was used in further analysis. However, owing to the small number of resulting cost information (N= 173 for 16 species), we did not remove the data classified as having low reliability (N = 55) and as potential implementation (N = 11), contrary to other studies using the InvaCost database which did not include these data (e.g., Heringer et al. 2021). The variable reliability refers to the accessibility of cost based on the availability of the information (i.e., low for not fully accessible information) and implementation indicates if the costs were incurred (i.e., observed) or expected, for example through modelling or extrapolation (i.e., potential). Therefore, these metrics represent the confidence attributed to the observed costs (Suppl. material 1: Table S1). Importantly, all cost data were converted to 2017 US Dollars (USD).

To estimate the total economic cost of IAS, we summed up all annual costs considering the ecological and societal sectors of activity for which information was available (i.e., without considering management or damage repair as distinct classes). The former is represented by the costs directly linked with species information on terrestrial, aquatic or both terrestrial and aquatic ecosystems (i.e., there is no marine species in the Brazil dataset). For the societal costs we used the market sector and the type of cost classes of reported economic costs. The market sector is a categorical variable that links the economic costs in the following six business classes: agriculture, stakeholders or decision makers, environment, forestry, health, and public and social welfare (for definition of each market sector see Table 1). Similarly, the type of cost classes directly links the economic costs with the following seven categories: control, damage repair, damage loss, eradication, medical care, prevention and research (for definition of each type of cost see Table 2).

In order to evaluate if the economic costs differed between costs used to repairing damage from costs used to IAS management, we used the impact year and the costs associated to create a new variable derived from the type of costs, here named of intervention group ("Type_2" in InvaCost database). The latter is a categorical variable where the seven types of cost classes explained above were reorganized into the

Table 1. Description of market sectors impacted by IAS in Brazil. Descriptions follow the classification used in the InvaCost database (Diagne et al. 2020).

Market sector	Description
Agriculture	Food and other useful products produced by human activities (i.e., plant resources, crop growing, livestock breeding, land management).
Stakeholders or decision makers	Governmental services or official organizations that allocate efforts and resources for the management, control, and eradication of IAS.
Environment	Impacts impose by IAS on natural resources, ecological processes or ecosystem services.
Forestry	Impacts impose by IAS on forest-based activities and services (i.e., timber production, industries).
Health	Directly or indirectly impact imposed by IAS that negatively affect human well-being or and the sanitary state of people (i.e., vector control, medical care and other derived damage on human productivity).
Public and social welfare	Directly or indirectly impact imposed by IAS on activities, goods or services that contribute to the human well-being and safety in our societies, including local infrastructures (e.g. electric system), quality of life (e.g. income, recreational activities), personal goods (e.g. private properties, lands), public services (e.g. transports, water regulation), and market activities (e.g. tourism, trade).

Table 2. Description of Type of Cost imposed by IAS in Brazil.

Type of cost	Description
Control	Costs used to control IAS population.
Damage repair	Costs used to repair the damages associated with IAS on local infrastructures or other human activity that affect the quality of life, personal goods, public services and market activities.
Damage loss	Costs used to repair the losses associated with IAS on food and other useful products produced by human activities.
Eradication	Costs used on activities that act on IAS mitigation aimed towards complete removal of IAS (e.g., authorized hunting).
Medical care	Costs used to medical care and other human well-being treatment (e.g., treatment of vector borne diseases).
Prevention	Costs used in surveillance, monitoring and other activities that help to prevents the trade, transport and/or introduction of alien species.
Research	Costs on theoretical (e.g., academic research on IAS), applied (e.g., evidence-based decisions plans) and technological (e.g., technological tools) knowledge that support strategies to reduce, control or mitigate the impacts imposed by IAS.

following group of intervention: damage, management, and mixed (Suppl. material 2: Table S2). This predictor indicates the type of intervention that caused the following expending: 1) damage – for costs related to the losses and repairs of damages associated with invasive species; 2) management – for costs related to the management of invasive alien species and other costs not included in damage repair; and 3) mixed – for costs related to the expenses reported without differentiation between damage and management. Then, using the intervention group variable, we fit an ANOVA comparing the three groups of costs with post-hoc Tukey contrast by least-squares means from *emmeans* package and tested the residual normality by Shapiro-Wilk.

Results

We found reports of economic costs for 16 IAS (Table 3). Together, the reported costs accumulate to USD 105.53 billion, or ca. R$ 349.3 billion, representing an average annual cost of USD 3.02 (± 9.8) billion (Fig. 1). From the total, USD 28.3 billion were based on cost entries with low reliability or expected costs and USD 76.8 billion

Table 3. Profile table of invasive alien species. Species: indicates species name. Impact descriptor: A brief overview of the available information of the impacts imposed by each of 16 invasive alien species.

Species	Impact descriptor
Aedes spp.	Is the vector of the most important mosquito-borne disease that impacts human health in the world (Gould et al. 2017). In Brazil, it is responsible for the spread of at least three different arboviruses (i.e., Dengue, Zika and Chikungunha) that threaten human well-being (Marcondes et al. 2016) costing millions of reais with insecticides, larvicides and medical care (Teich et al. 2017).
Artocarpus heterophyllus	Is associated with the Brazilian Atlantic forest (i.e., the most fragmented biomes of the country, see Ribeiro et al. 2009). In Brazil, *A. heterophyllus* occurs closer to human settlements as a fruit tree and ornamental species (Zenni and Ziller 2011) where it usually dominates species biomass and reduce small mammal composition (Boni et al. 2009; Abreu and Rodrigues 2010; Fabricante et al. 2012; Mello et al. 2015).
Bemisia tabaci	Is one of the most economically detrimental invasive alien species that damage a wide variety of horticultural, ornamental, and field crops worldwide (De Barro et al. 2011). In Brazil, its occurrence is associated with ornamental plants (de Moraes et al. 2017), and its economic costs with insecticides production, biological control plans, and virus diseases in field crops (Navas-Castillo et al. 2011; Gilbertson et al. 2015; Cavalcante et al. 2015; Inoue-Nagata et al. 2016).
Brachiaria eminii	Is one of the ecologically impactful invasive alien species that belongs to the group of invasive grasses (Zenni and Ziller 2011). Its costs are associated with fire disturbance (Ribeiro et al. 2000; Gorgone-Barbosa et al. 2016), cattle poisoning (Riet-Correa et al. 2011), competitive exclusion by allelopathic compounds (Barbosa et al. 2008; Damasceno et al. 2018) and reduction of floristic and native species diversity (Durigan et al. 2007; Almeida-Neto et al. 2010).
Cinara spp.	Initially recorded in Brazil in 1996, the species specifically affect the pine plantations productivity which are composed by *Pinus taeda* and *Pinus elliottii* species (Penteado et al. 2000). The economic costs are associated with the Forestry sectors that manage biological control programs and technology development (Schnell e Schühli et al. 2016).
Cydia pomonella	Is one of the most economically detrimental apple pests in the world (Beers et al. 2009; Jiang et al. 2018), and its damage can cause complete crop losses. In Brazil, its economic costs are associated with the development of species eradication planning (PNEPC) that costs US$ 398,000 annually (Kovaleski and Mumford 2007; Kovaleski et al. 2015). Since 2014 the species is considered eradicated (Kovaleski et al. 2015).
Drosophila suzukii	Reported by the first time in 2013 in Brazil's southern provinces (Deprá et al. 2014), its impact is poorly known. However, because of the several economic impacts on fruits growers in North America (Goodhue et al. 2011; Walsh et al. 2011), predictive models indicate wide economic impact in the Brazil's Southern region suggesting fig and pear crops as the main impacted host species (Benito et al. 2016).
Eragrostis plana	The species impacts more than one million hectares in Brazil's southern grasslands (Medeiros and Focht 2007). Its spread imposes impact by outcompeting with native species (Ferreira et al. 2008). Its costs are associated with the development of new technologies in order to mitigate and prevent species spreading as well as the low yield in feeding animals (Zenni and Ziller 2011; Baggio et al. 2018).
Helicoverpa armigera/*Tuta absoluta*	Are economically impactful invasive alien species that damage a wide variety of field crops worldwide including tomatoes. In Brazil, its economic impact is associated with crop damages (Czepak et al. 2013) and the development of advanced genetic modification technologies in order to improve the crop resistance to its respective pest (Thomazoni et al. 2013; Silva et al. 2016).
Limnoperna fortunei	Is one of the economically impactful invasive alien species that damage ecological, economical and human wellbeing worldwide (Boltovskoy 2015). Is responsible for impact the hydropower generation (Darrigran et al. 2007), water quality (Darrigran and Damborenea 2011), structure and function of the ecosystem (Boltovskoy and Correa 2015) and damage man-made structures (Boltovskoy 2015). In Brazil, its economic costs are distributed over multiple ecological and social activities sectors.
Panicum maximum	This is an invasive alien species that belongs to the group of invasive grasses. Its ecological impact is associated with the overconsumption of soil nitrogen (Leite et al. 2019) and slowing ecological succession (Montoani and Torezan 2016). Its economic costs are associated with herbicide and fertilization chemical production.
Pinus spp.	The species are one of the most common alien species used in forest plantations and management. In Brazil, its ecological and economic impacts are associated with negative effects in the native community (Brewer et al. 2018), water consumption and quality (Mello et al. 2018), citizen engagements in order to design effective species management (Dechoum et al. 2019), impacts on phytosanitary diseases (Schnell e Schühli et al. 2016), and changes in ecosystem services, functions, soil composition and nutrient cycling (Valduga et al. 2016).
Rhinella marina	Impacts and costs with this species are associated with biodiversity damage and eradication control. However, information of its impact in Brazil seems to be scarce (Forti et al. 2017).
Salvator merianae	Invasive in the Fernando de Noronha archipelago the species is considered a threat to the native community species by hosting, transporting, and spreading parasites to new regions (Ramalho et al. 2009). Further, effective management of the species is a challenge which incurs in economic costs associated with conservation plans design and in its absence the species can harm the livelihood of the local population by spreading zoonotic diseases (Abrahão 2019).

Table 3. Continued.

Species	Impact descriptor
Sirex noctilio	Is one of the most relevant threats to plantation forestry in South America and its impact is mainly associated with disease outbreaks in both natural and planted forests resulting in high levels of tree mortality (Corley et al. 2019). In Brazil, its presence is associated with *Pinus* spp. plantations which is composed by *Pinus taeda* and *Pinus elliotti* species (Iede et al. 2016) which the economic cost of species is estimated in USD 9 million annually over 4 hundred thousands of tree hectare (Schnell e Schühli et al. 2016).
Sus scrofa	Is one of the largest and most widespread invasive alien species in Brazil and it is responsible for several damages in vegetation surface, herbivory, rooting, soil overturning and crop fields damage (Hegel and Marini 2013; Pedrosa et al. 2015). Its economic costs are associated with species eradication control programs and crops damage.

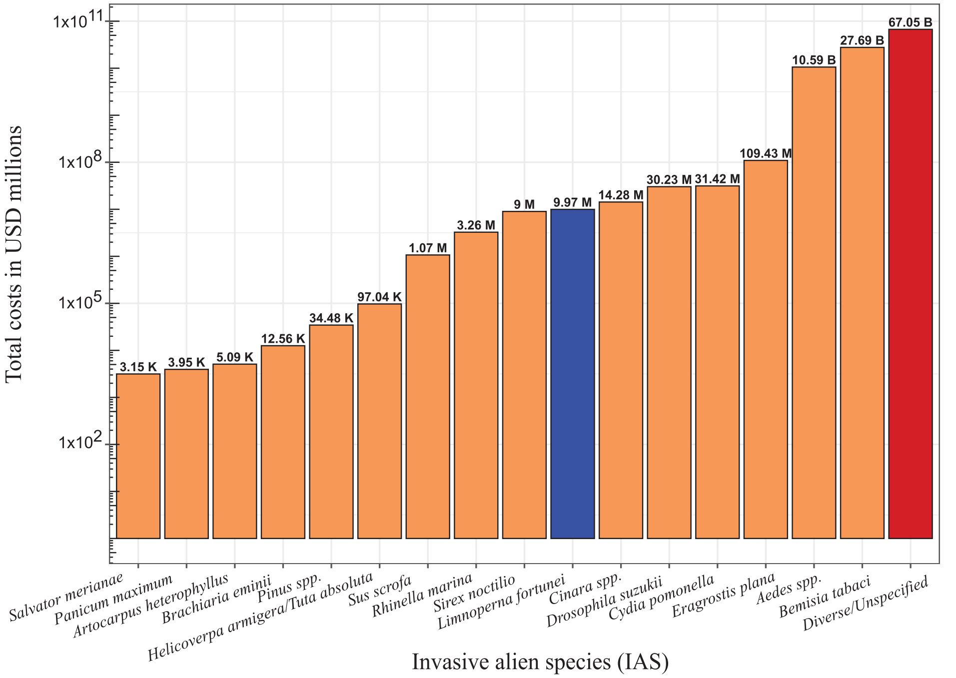

Figure 1. Economic costs incurred by the 16 invasive alien species in Brazil. Numbers above the bars indicate the abbreviated cost in thousand (K), millions (M) and Billions (B) of US dollars. Orange indicates costs assigned to the terrestrial ecosystem. Blue (i.e., *Limnoperna fortunei*) indicates costs assigned to the aquatic ecosystem. Red (in Diverse/unspecified) indicates costs assigned to both terrestrial and aquatic ecosystems.

were based on high-reliability and incurred costs. The reported economic costs among species ranged from USD 3.15 thousand (*S. merianae,* Fig. 1) to USD 27.68 billion (*B. tabaci,* Fig. 1). The five costliest invasive alien species together had a cumulated reported cost of USD 38.44 billion and were distributed within the damage intervention group (Fig. 2, ANOVA; F = 7.123; p = 0.046). Two of the top five costliest species occurred within the management intervention group. None of the top five species occurred within the mixed intervention group (Fig. 2).

In respect to ecosystem type, 52.4% of the costs (USD 55.28 billion) were distributed across both aquatic and terrestrial ecosystems. The costs reported exclusively for terrestrial ecosystems totaled USD 50.24 billion and had *Aedes* spp. as the costliest

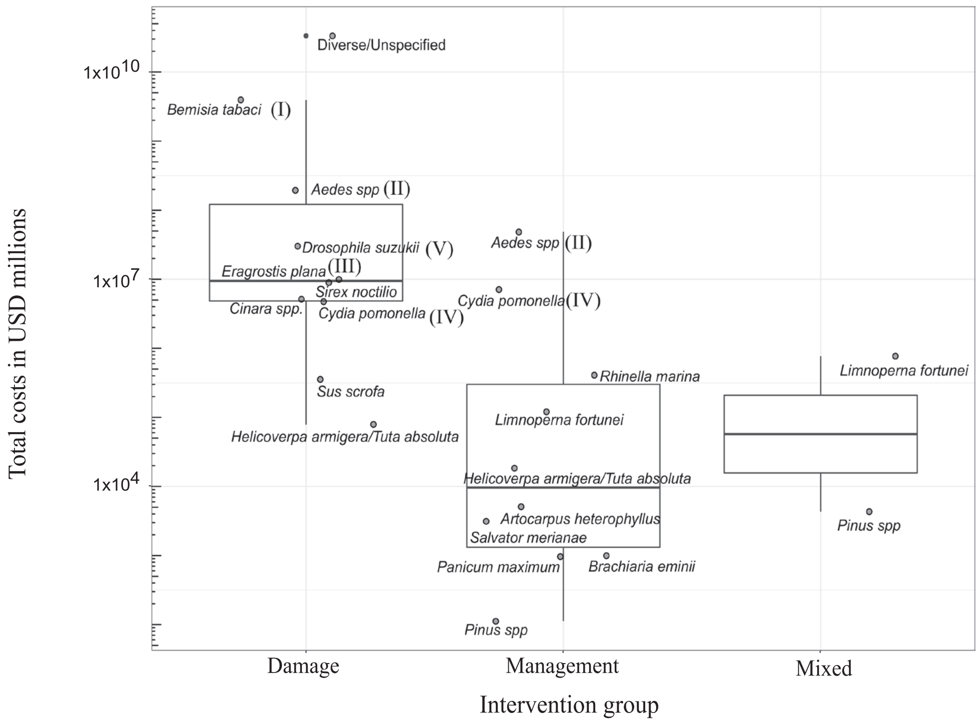

Figure 2. Invasive alien species economic impact associated with type of cost. The post hoc Tukey test for the differences shown statistically significance between damage and management type of cost (Estimate = 2.895 ± 0.78, t value = 3.692, p-value = 0.003). The differences between Damage to Mixed (Estimate = 2.608 ± 1.35, t value = 1.921, p-value = 0.102) and Management to Mixed (Estimate = -0.2864 ± 1.35, t value = -0.211, p-value = 0.835) were not statistically significant. Filled circles indicate species within each type of cost group. The costliest species are pointed out by roman numbers according to the top five costly species rank.

species. The costs reported exclusively for aquatic ecosystems totaled USD 9.97 million and were only due to expenses caused by *L. fortunei*. Considering both terrestrial and aquatic ecosystems, the class Insecta was over-represented, followed by Bivalvia and Liliopsida. The species *Aedes* spp., *L. fortunei, B. eminii* and *E. plana* were the costliest species in Brazil (Figure 3). Surprisingly, there were no costs reported for marine ecosystems.

The economic costs reported as damage contributed with 98.9% of the available cost information and was estimated at USD 104.33 billion, whereas management contributed with 1.13% of the total, reportedly costing USD 1.19 billion. Mixed costs represented less than 1%, at USD 7.7 million (see Suppl. material 3: Table S3). When partitioning the economic costs into classes of market sectors we observed that mixed sectors contributed 61.8% of the total cost, corresponding to USD 65.2 billion. Apart from mixed sectors, agriculture was the most impacted sector with an economic cost estimated at USD 39.61 billion, followed by health with USD 665.85 million and authorities-stakeholders with USD 24.37 million. The remaining impacted sectors

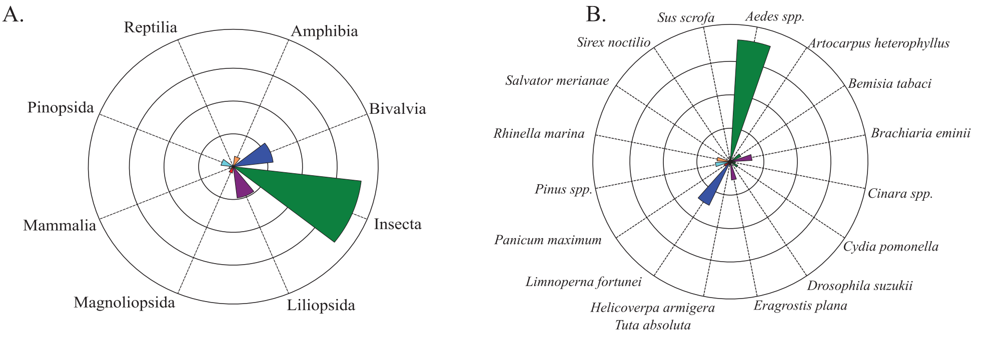

Figure 3. Radar plot showing the frequency of invasive taxonomic classes **(A)** and invasive alien species **(B)** distributed across different ecosystem types. Overrepresented species were: *Aedes* spp. (N = 73), *Limnoperna fortunei* (N = 29), *Brachiaria eminii* (N = 13) and *Eragrostis plana* (N = 11). Species with intermediate representativeness were *Pinus* spp. (N = 9), *Rhinella marina* (N = 8), *Bemisia tabaci* (N=7) and *Cydia pomonella* (N=5). The remaining species were underrepresented (N < 5). The overrepresented taxonomic classes were Insecta (N =93), Bivalvia (N=29) and Liliopsida (N=24), whereas the remaining ones were underrepresented (N <10).

were forestry with a cost of USD 14.28 million, public and social welfare with USD 9.97 million and environment with USD 59.24 thousand (Figure 4). The reported cost of each species by sector varies from USD 96.65 thousands for *B. eminii* in the environment sector to USD 3.96 billion incurred by *B. tabaci* in the agriculture sector (Suppl. material 4: Table S4). Representativeness of species on economic impact over the market sectors indicates that agriculture and environment were impacted by more species than the remaining market sectors, six species each one (see Fig. 6A). Agriculture suffered the highest economic impact caused by *B. tabaci, C. pomonela, E. plana* and *D. suzukii,* followed by the forestry sector, which was impacted by *Cinara* spp. and *S. noctilio,* and the health sector which was impacted by *Aedes* spp.

Regarding the type of intervention, damage losses contributed 89.9% of the available cost estimation at USD 94.91 billion, followed by medical care with USD 9.29 billion and species control with USD 1.19 billion (Fig. 5, see Suppl. material 3: Table S3). The remaining types of costs were indirect costs (USD 126.16 million reported), damage repair (USD 7.67 million), research (USD 3.91 million), prevention (USD 864.24 thousand) and eradication (USD 411.61 thousand) (Figure 5). The cost of each species by activity sectors varied from USD 96.65 thousand by *B. eminii* in the control to USD 3.96 billion incurred by *B. tabaci* in the damage-loss (Suppl. material 5: Table S5). Representativeness of species on economic impact over the type of costs indicated that control had nine species associated with economic impact. The highest impact was caused by *Aedes* spp. and *C. pomonella*. Similarly, damage-loss was reported for eight species, of which two species (*S. scrofa* and *H. armigera*) had the lowest cost reported (see Fig. 6B). Conversely, six species had considerably high impact in the damage-loss, with *B. tabaci* as costliest species. Finally, costs associated with medical care were reported exclusively for *Aedes* spp. (Fig. 6B).

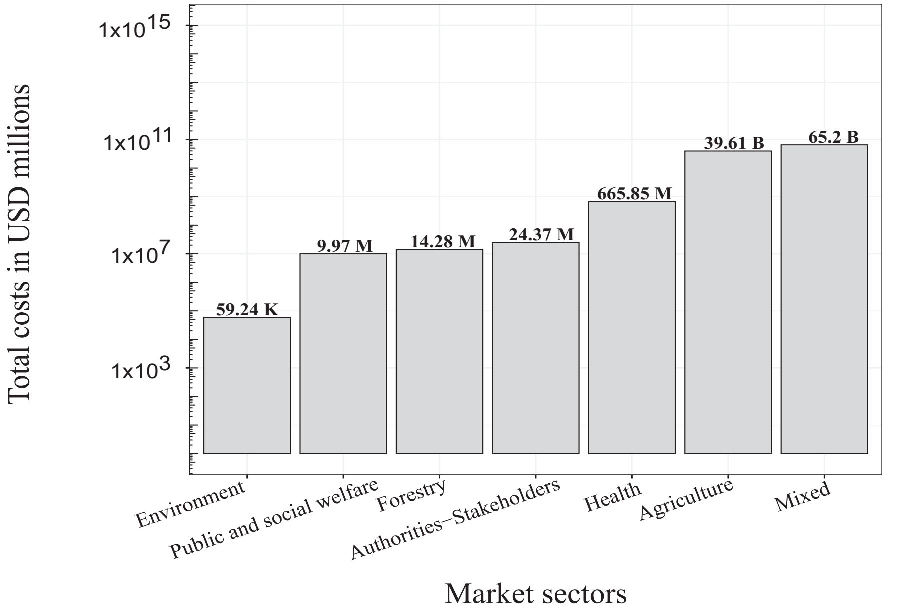

Figure 4. Economical costs with invasive alien species partitioned over seven market sectors. Numbers above the bars indicate the abbreviated cost in thousand (K), millions (M) and Billions (B) in 2017 US dollars over a time span of 35 years.

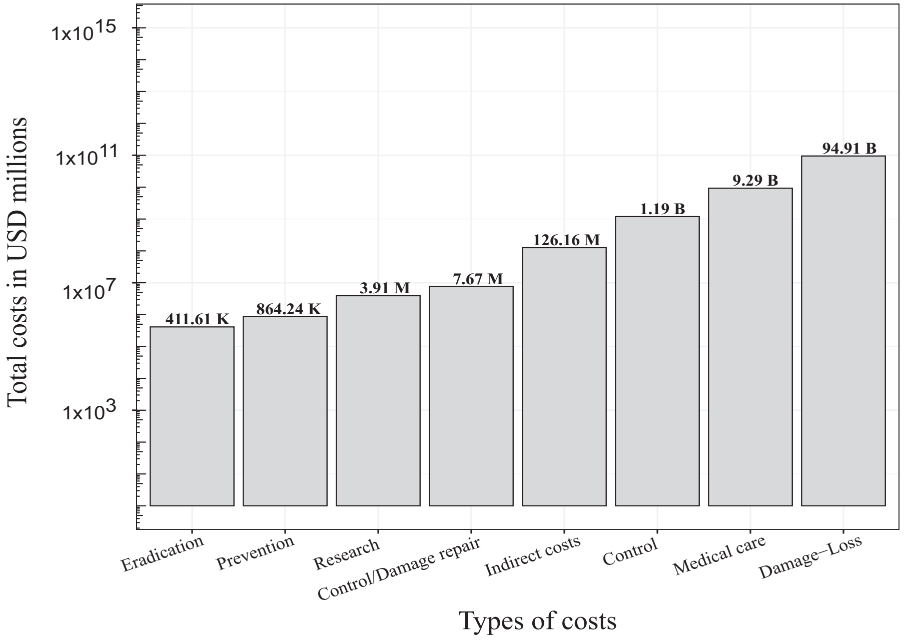

Figure 5. Economical costs with invasive alien species partitioned over eight types of costs. Numbers above the bars indicate the abbreviated cost in thousand (K), millions (M) and Billions (B) in 2017 US dollars over a time span of 35 years.

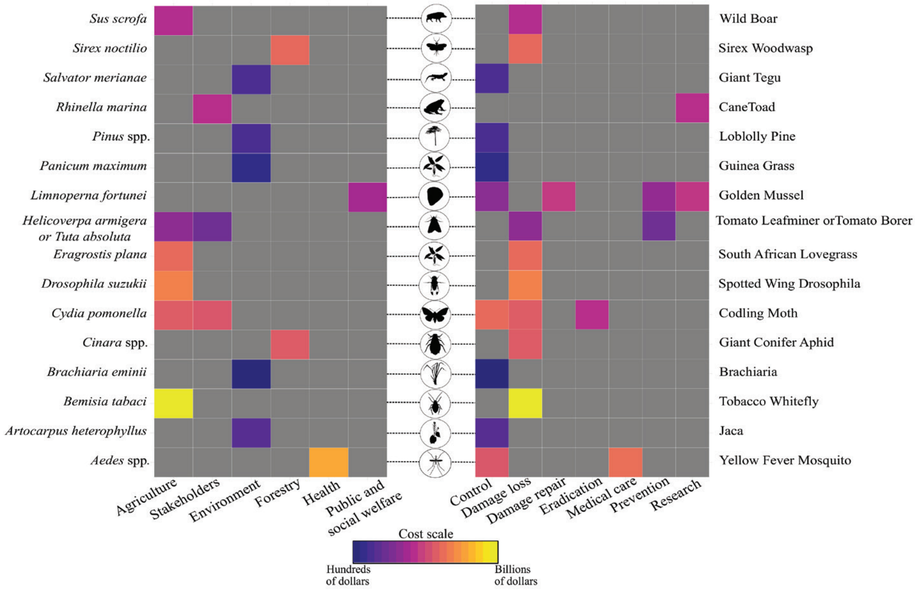

Figure 6. Heat map depicting the economic costs associated with species, market sectors and cost type. Each block indicates the cost incurred by each species over a specific market sector (in left) and cost type (in right). Gray blocks are associations with no available cost information and colorful blocks indicate the intensity of the economic cost incurred by each species. Low cost intensity (i.e. hundreds and thousands of dollars) are represented by blue to purple color transitions and high cost intensity (i.e. billions of dollars) are represented by orange to yellow color transitions. The remaining colors represent intermediate cost intensity (i.e., millions of dollars). Each row of the heatmap corresponds to one species and the species name and its vernacular name are depicted in the left and right margins of the heatmap respectively. Each column of the heat map corresponds to an impacted market sector and the type of cost required to overcome invasive species impact. The circles in the middle depicts a visual representation of invasive organisms. All silhouettes were freely obtained from www.phylopic.org.

Discussion

Here, we have provided the first detailed assessment of the economic costs of biological invasions in Brazil since the study of Pimentel et al. (2001). The relevance of the information provided here lies in incorporating detailed information of the estimated economic impact of invasive alien species, their impact on natural ecosystems, and multiple relevant economic sectors in Brazil. The present study represents a substantial improvement in the knowledge of IAS impacts, environmental and social perception and differ from previous studies that provide economic costs with no indication of the invasive status of the species (Oliveira et al. 2013; Oliveira et al 2014; Teich et al. 2017). Considering that we found economic costs for only 16 species from at least 460 known alien species classified as invasive in Brazil (Ziller et al. 2020), we caution that the USD 105.53 billion figure is a conservative minimum estimate of the actual economic impact. Still, the estimated costs with invasive alien species corresponded to 0.26% of the sum of Brazil's Gross Domestic Product from 1984 to 2019.

The quantification and reporting of economic costs of biological invasions were not a common practice in Brazil. Also, part of the available reports lack in accuracy, as there were 55 entries (*ca*. 31%) classified as low reliability. For instance, despite the high relevance of freshwater ecosystems in Brazil and the harmful effects of invasive alien species in aquatic environments (Pelicice et al. 2013), there were economic costs estimated for only one aquatic invasive alien species – the Golden mussel (*L. fortunei*) which impacts hydropower plant systems (de Campos et al. 2014). In addition, there were no costs associated with invasive alien species in marine ecosystems despite the fact that prevention, surveillance, and eradication of invasive species in marine ecosystems are officially one of the 10 goals established by the ministry of the environment as a strategy to conserve and mitigate the negative effects of invasive species in marine ecosystems. For example, the invasive lionfish *Pterois volitans* and orange cup coral *Tubastraea coccinea* are considered in Brazil's biodiversity plan for protecting coral reefs environments (PAN/Corais). Lionfish is an aggressive predatory IAS that impacts ecosystem functioning and threatens human well-being with human poisoning (Carlos-Júnior et al. 2015; Haddad Jr et al. 2015; Bumbeer et al. 2018). Orange cup corals (a species of sun coral) impact ecosystem dynamics and structure of native reef communities (Miranda et al. 2018; Silva et al. 2019). However, despite the intense efforts to understand the impacts of these invasive alien species, information on economic costs has not been formally gathered or published. In fact, the tendency of skewed evidence on environmental and conservation practices towards terrestrial ecosystems have previously been reported (Overbeck et al. 2015; Azevedo-Santos et al. 2019), including in the context of invasion costs (Cuthbert et al. 2021). Therefore, the actual costs of biological invasions in Brazil are probably much greater than the reported costs presented in this study.

Considering terrestrial ecosystems, we observed high costs by invasive insects (Fig. 3). Invasive alien insects are globally recognized as the main cause of agriculture (Bradshaw et al. 2016; Paini et al. 2016) and forestry damages (Aukema et al. 2011). Similarly, in Brazil insects (i.e., native and alien) are the main source of costs incurred in crop fields (Oliveira et al. 2013; Oliveira et al. 2014) and forestry plantations (Schnell e Schühli et al. 2016). Further, it is known that at least 24 insect species, four of which are present in this study, constitute the most important crop pests in Brazil since 1900, costing billions of dollars for the economy (Oliveira et al. 2013). The prevalence of invasive insects in the reported economic costs reflects the relevance of the agriculture and forestry sectors in the economic expenses associated with invasive species. Also, invasive alien insects (e.g., *Aedes* spp.) also affect public health by spreading vector-borne human diseases, increasing the economic impact perception (Taichi et al. 2017). Furthermore, and although it is well-known that mammals have high environmental impacts in Brazil (da Rosa et al. 2017), little is known about economic costs of invasive alien mammals.

The association between the agriculture sector and economic costs incurred by invasive alien species is not surprising (Oliveira et al. 2013; Oliveira et al. 2014). Indeed, agriculture represents one of the greatest portions of the Brazilian economy and has been responsible for 24.31% (± 4.06) of the country's Gross Domestic Product over the last 23 years on average (CEPEA). However, effective strategies to mitigate the impact of invasive alien species likely occur with the engagement of the private sectors' interests that support technological progress. For example, Kovaleski et al (2015) highlight that the eradication of the Codling moth only occurred due to the combined activity among multiple Brazilian apple private sector institutions. However, planning effective design seemed to be more feasible for species that impose a direct impact like invasive crop pests. For species with indirect impacts on the economy, such as environmental impacts, new challenges are imposed for planning effective design that require the engagement of multiple sectors.

Clear information on prevention strategies for invasive alien species and costs were missing and indicate the necessity for a country-level integrated database of invasive alien species, management programs and research, such as indicated in the Brazil's National Strategy for Invasive Alien Species – CONABIO Resolution 05/2019 – and its implementation plan (SBio/MMA Ordinance 3/2018; Resolution 05/2019). Indeed, 10 entries (USD 824.64 thousand) reported prevention as a type of cost in Brazil. Prevention strategies for IAS exist in Brazil but are currently limited and lack operational coordination (but see Brazil's National Strategy for Invasive Alien Species – CONABIO Resolution 05/2019). This supports the notion that in Brazil, as well as in Central and South America in general (Heringer et al. 2021), resource allocation for biological invasions focus on IAS with large observed impacts at later stages of invasion (i.e., *Aedes* spp. and *L. fortunei*). This represents a reactive approach that tends to be more expensive and less effective than preventing the alien species invasion and impacts (Wittenberg and Cock 2001; Leung et al. 2002).

In summary, here we have provided a first national estimate of the total economic cost of biological invasions in Brazil. The reported USD 105.53 billion of expenses in 35 years for 16 species is a conservative estimate of the total cost of biological invasions, as it only included direct and publicly available costs, which remain strikingly few. In addition to the clear biases in taxonomic groups, regions and activity sectors, some costs dissolved in broader actions, such as sanitary border control, ecosystem restoration efforts and environmental research were not estimated (Brancalion 2019). Costs of losses owing to biological invasions, such as ecosystem services degradation and yield reductions were also lacking from the literature. Brazil has at least 460 invasive alien species (Ziller et al. 2020) and hundreds more of naturalized species with invasive potential (Zenni 2015; da Rosa et al. 2017; Forti et al. 2017; Ziller et al. 2020; Bueno et al. 2021) and costs were reported for only 16 of them. Yet, Brazil is the country with the highest reported cost with invasive alien species in Latin America (Heringer et al. 2021; Rico-Sánchez et al. 2021; Crystal-Ornelas et al. 2021), and still the cost is unknown for most IAS. There is an urgent need for better reporting of both economic losses and costs imposed by IAS, as well as effective policy and management actions to reduce these costs.

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Supplementary material 1

Table S1. Observed costs for Brazil from the invacost database including the confidence attributed to the observed costs

Authors: José Ricardo Pires Adelino, Gustavo Heringer, Christophe Diagne, Franck Courchamp, Lucas Del Bianco Faria, Rafael Dudeque Zenni

Data type: cost

Explanation note: https://doi.org/10.6084/m9.figshare.12668570

Link: https://doi.org/10.3897/neobiota.67.59185.suppl1

Supplementary material 2

Table S2. Observed costs for Brazil from the invacost database organized into the following group of intervention: damage, management, and mixed

Authors: José Ricardo Pires Adelino, Gustavo Heringer, Christophe Diagne, Franck Courchamp, Lucas Del Bianco Faria, Rafael Dudeque Zenni

Data type: cost

Explanation note: https://doi.org/10.6084/m9.figshare.12668570

Link: https://doi.org/10.3897/neobiota.67.59185.suppl2

Supplementary material 3

Table S3. Observed mixed costs for Brazil from the invacost database

Authors: José Ricardo Pires Adelino, Gustavo Heringer, Christophe Diagne, Franck Courchamp, Lucas Del Bianco Faria, Rafael Dudeque Zenni

Data type: cost

Explanation note: https://doi.org/10.6084/m9.figshare.12668570

Link: https://doi.org/10.3897/neobiota.67.59185.suppl3

Supplementary material 4

Table S4

Authors: José Ricardo Pires Adelino, Gustavo Heringer, Christophe Diagne, Franck Courchamp, Lucas Del Bianco Faria, Rafael Dudeque Zenni

Data type: cost

Explanation note: All costs for Brazil present in the invacost database at the time of the analysis: https://doi.org/10.6084/m9.figshare.12668570

Link: https://doi.org/10.3897/neobiota.67.59185.suppl4

Supplementary material 5

Table S5

Authors: José Ricardo Pires Adelino, Gustavo Heringer, Christophe Diagne, Franck Courchamp, Lucas Del Bianco Faria, Rafael Dudeque Zenni

Data type: cost

Explanation note: Cost of species by activity sectors

Link: https://doi.org/10.3897/neobiota.67.59185.suppl5

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RESEARCH ARTICLE

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Economic costs of biological invasions in Ecuador: the importance of the Galapagos Islands

Liliana Ballesteros-Mejia[1], Elena Angulo[1], Christophe Diagne[1], Brian Cooke[2], Martin A. Nuñez[3,4], Franck Courchamp[1]

1 *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405, Orsay, France* **2** *Institute for Applied Ecology, University of Canberra, Bruce 2617, ACT, Australia* **3** *Grupo de Ecología de Invasiones, INIBIOMA, CONICET, Universidad Nacional del Comahue, Quintral 1250, San Carlos de Bariloche, CP 8400, Argentina* **4** *Department of Biology and Biochemistry, University of Houston, Houston, Texas, 77204, USA*

Corresponding author: Liliana Ballesteros-Mejia (ballesteros.liliana@gmail.com)

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Abstract

Biological invasions, as a result of human intervention through trade and mobility, are the second biggest cause of biodiversity loss. The impacts of invasive alien species (IAS) on the environment are well known, however, economic impacts are poorly estimated, especially in mega-diverse countries where both economic and ecological consequences of these effects can be catastrophic. Ecuador, one of the smallest mega-diverse countries, lacks a comprehensive description of the economic costs of IAS within its territory. Here, using "InvaCost", a public database that compiles all recorded monetary costs associated with IAS from English and Non-English sources, we investigated the economic costs of biological invasions. We found that between 1983 and 2017, the reported costs associated with biological invasions ranged between US$86.17 million (when considering only the most robust data) and US$626 million (when including all cost data) belonging to 37 species and 27 genera. Furthermore, 99% of the recorded cost entries were from the Galapagos Islands. From only robust data, the costliest identified taxonomic group was feral goats (*Capra hircus*; US$20 million), followed by *Aedes* mosquitoes (US$2.14 million) while organisms like plant species from the genus *Rubus*, a parasitic fly (*Philornis downsi*), black rats (*Rattus rattus*) and terrestrial gastropods (*Achatina fulica*) represented less than US$2 million each. Costs of "mixed-taxa" (i.e. plants and animals) represented the highest (61% of total robust costs; US$52.44 million). The most impacted activity sector was the national park authorities, which spent about US$84 million. Results from robust data also revealed that management expenditures were the major type of costs recorded in the Galapagos Islands; however, costs reported for medical losses related to *Aedes* mosquitoes causing dengue fever in mainland Ecuador would have ranked first if more detailed information had allowed us to categorize them as robust data. Over 70% of the IAS reported for Ecuador did not have reported costs. These results suggest that costs reported here are a massive underestimate of the actual economic toll of invasions in the country.

Abstract in Spanish

Costos económicos de las invasiones biológicas en Ecuador: La importancia de las islas Galápagos. Las invasiones biológicas, al ser resultado de la intervención humana a través del comercio y la movilidad, son la segunda causa más importante de pérdida de biodiversidad. Los impactos de las especies exóticas invasoras (EEI) en el medio ambiente son bien conocidos, sin embargo, los impactos económicos aún son poco estimados, especialmente en países megadiversos donde las consecuencias económicas y ecológicas de estos efectos pueden ser catastróficas. Ecuador, uno de los países megadiversos más pequeños, carece de una descripción completa de los costos económicos de las EEI dentro de su territorio. En este estudio, investigamos los costos de las investigaciones biológicas, utilizando "InvaCost", una base de datos pública que compila todos los costos monetarios registrados asociados con las EEI de fuentes tanto en inglés como en español. Encontramos que entre 1983 y 2017, los costos reportados asociados con las invasiones biológicas oscilaron entre US$86,17 millones (considerando sólo los datos más robustos) y US$626 millones (incluyendo todos los datos de costos) pertenecientes a 37 especies y 27 géneros. Además, el 99% de los costos registrados fueron en las Islas Galápagos. Al utilizar sólo datos robustos, el grupo taxonómico identificado más costoso fueron las cabras salvajes (*Capra hircus*; US$20 millones), seguido de los mosquitos *Aedes* (US$2,14 millones), mientras que organismos como especies de plantas del género *Rubus*, la mosca parásita (*Philornis downsi*), las ratas negras (*Rattus rattus*) y los gasterópodos terrestres (*Achatina fulica*) representaron menos de 2 millones de dólares cada uno. Los costos de los taxones mixtos (es decir, plantas y animales) representaron los más altos (61% de los costos robustos totales; US$52,44 millones). El sector de actividad más afectado fue el de las autoridades del parque nacional, que gastó alrededor de 84 millones de dólares. Los resultados de datos robustos también revelaron que los gastos de gestión fueron el principal tipo de costos registrados en las Islas Galápagos; sin embargo, los costos reportados por pérdidas médicas relacionadas con los mosquitos *Aedes* que causan la fiebre del dengue en el Ecuador se habrían clasificado en primer lugar, si la existencia de información más detallada nos hubiera permitido clasificarlos como datos robustos. Más del 70% de las EEI conocidas para Ecuador no tuvieron costos reportados. Estos resultados sugieren que los costos aquí discutidos son una subestimación masiva del costo económico real de las invasiones en el país.

Abstract in Portuguese

Custos econômicos das invasões biológicas no Equador: importância das Ilhas Galápagos. As invasões biológicas, como resultado da intervenção humana por meio do comércio e da mobilidade, são a segunda maior causa da perda de biodiversidade. Os impactos das espécies exóticas invasoras (EEI) no meio ambiente são bem conhecidos. No entanto, os impactos econômicos ainda nem tanto, especialmente em países megadiversos onde as consequências econômicas e ecológicas desses efeitos podem ser catastróficas. O Equador, um dos menores países megadiversos, carece de uma descrição abrangente dos custos econômicos das EEI em seu território. Neste estudo, usando o "InvaCost", um banco de dados público que compila todos os custos monetários associados às EEI de fontes em inglês e espanhol, investigamos os custos econômicos das invasões biológicas. Descobrimos que, entre 1983 e 2017, os custos relatados associados às invasões biológicas variaram entre US$86,17 milhões (considerando apenas os dados mais robustos) e US$626 milhões (incluindo todos os dados) pertencentes a 37 espécies e 27 gêneros. Além disso, 99% das entradas de custos registradas eram das Ilhas Galápagos. Apenas com dados robustos, o grupo taxonômico mais custoso identificado foi de cabras selvagens (*Capra hircus*; US$20 milhões), seguido por mosquitos Aedes (US$2,14 milhões). Por outro lado, organismos como espécies de plantas do gênero Rubus, uma mosca parasita (Philornis downsi), o rato-preto (Rattus rattus) e os gastrópodes terrestres (Achatina fulica) representaram menos de US$ 2 milhões cada. Os custos dos táxons mistos (ou seja, plantas e animais) representaram os mais altos (61% dos custos robustos totais; US$52,44 milhões). O setor de atividade mais impactado por esses custos foram as autoridades do parque nacional, que gastaram cerca de US$84 milhões. Os resultados de dados robustos também revelaram que as despesas de gerenciamento foram o principal tipo de custo registrado nas Ilhas Galápagos. No entanto, os custos registrados de perdas médicas relacionadas aos mosquitos Aedes, que causam a dengue no Equador, teriam ficado em primeiro lugar, se tivéssemos informações mais detalhadas que nos permitiram classificá-los como dados robustos. Mais de 70% das espécies invasoras não apresentam custos para o Equador. Esses resultados sugerem que os custos relatados, neste trabalho, estão subestimados quanto ao custo real das invasões no país.

Abstract in French

Coûts économiques des invasions biologiques en Équateur : l'importance des îles Galapagos. Les invasions biologiques, résultant de l'intervention humaine par le commerce et la mobilité internationaux, sont la deuxième cause de perte de biodiversité. Les impacts des espèces exotiques envahissantes (EEE) sur l'environnement sont bien connus, mais les impacts économiques sont mal estimés, en particulier dans les pays à biodiversité méga-diverse où les conséquences économiques et écologiques de ces effets peuvent être catastrophiques. L'Équateur, l'un des plus petits pays méga-divers, ne bénéficie toujours pas de description complète des coûts économiques des espèces exotiques envahissantes pour son territoire. Ici, nous avons étudié les coûts économiques des invasions biologiques en utilisant "InvaCost", une base de données publique qui compile tous les coûts monétaires associés a ces invasions, provenant de sources en langues anglaise et non-anglaise. Nous avons constaté qu'entre 1983 et 2017, les coûts déclarés associés aux invasions biologiques variaient entre 86,17 millions de dollars américains (si l'on considère uniquement les données les plus robustes) et 626 millions de dollars américains (si l'on inclut toutes les données disponibles), appartenant à 37 espèces et 27 genres. De plus, 99 % des entrées de coûts enregistrées pour l'Équateur provenaient des îles Galápagos. D'après les données les plus robustes, le groupe taxonomique le plus coûteux est celui des chèvres sauvages (*Capra hircus*; 20 millions de dollars), suivi des moustiques du genre *Aedes* (2,14 millions de dollars), tandis que des organismes comme des espèces végétales du genre *Rubus*, des mouches parasites (*Philornis downsi*), les rats noirs (*Rattus rattus*). et des gastéropodes terrestres (*Achatina fulica*) représentaient moins de 2 millions de dollars US chacun. Les coûts des taxons mixtes (c.-à-d. plantes et animaux indifférenciés) sont les plus élevés (61 % des coûts robustes totaux, soit 52,44 millions de dollars américains). Le secteur d'activité le plus impacté est représenté par les autorités des parcs nationaux, qui ont dépensé environ 84 millions de dollars. Les données les plus robustes ont également révélé que les dépenses de gestion constituaient le principal type de coûts enregistrés dans les îles Galápagos; toutefois, les coûts déclarés pour les pertes médicales liées aux moustiques *Aedes* causant la dengue en Équateur continental auraient été classés au premier rang si des informations plus détaillées nous avaient permis de les catégoriser comme des données robustes. Plus de 70 % des EEE recencées en Équateur n'ont pas de coûts déclarés. Ces résultats suggèrent que les coûts rapportés ici sont une sous-estimation massive du fardeau économique réel des invasions biologiques dans le pays.

Abstract in German

Wirtschaftliche Kosten biologischer Invasionen in Ecuador: die Bedeutung der Galapagos-Inseln. Biologische Invasionen infolge menschlicher Eingriffe durch Handel und Mobilität sind die zweitgrößte Ursache für den Verlust der biologischen Vielfalt. Die Auswirkungen invasiver gebietsfremder Arten

(IAS) auf die Umwelt sind allgemein bekannt. Die wirtschaftlichen Auswirkungen werden jedoch nur unzureichend geschätzt, insbesondere in Ländern mit großer Vielfalt, in denen die wirtschaftlichen und ökologischen Folgen dieser Auswirkungen katastrophal sein können. In Ecuador, einem der kleinsten Länder mit großer Vielfalt, fehlt eine umfassende Beschreibung der wirtschaftlichen Kosten von IAS in seinem Hoheitsgebiet. Hier haben wir mithilfe von "InvaCost", einer öffentlichen Datenbank, die alle mit IAS verbundenen monetären Kosten aus englischen und nicht englischen Quellen zusammenstellt, die wirtschaftlichen Kosten biologischer Invasionen untersucht. Wir haben festgestellt, dass zwischen 1983 und 2017 die mit biologischen Invasionen verbundenen Kosten zwischen 86,17 Mio. USD (unter Berücksichtigung nur der robustesten Daten) und 626 Mio. USD (unter Einbeziehung aller Kostendaten) zu 37 Arten und 27 Gattungen lagen. Darüber hinaus stammten 99% der erfassten Kosteneinträge von den Galapagos-Inseln. Aus nur belastbaren Daten ging hervor, dass Wildziegen (*Capra hircus*; 20 Mio. USD) die teuerste taxonomische Gruppe waren, gefolgt von *Aedes*-Mücken (2,14 Mio. USD). Jedoch, Organismen wie Pflanzenarten der Gattung Rubus, einer parasitären Fliege (*Philornis downsi*), schwarze Ratten (*Rattus rattus*) und terrestrische Gastropoden (*Achatina fulica*) machten jeweils weniger als 2 Millionen US-Dollar aus. Die Kosten für gemischte Taxa (d. H. Pflanzen und Tiere) waren am höchsten (61% der gesamten robusten Kosten; 52,44 Mio. USD). Der am stärksten betroffene Aktivitätssektor waren die Nationalparkbehörden, die rund 84 Millionen US-Dollar ausgaben. Die Ergebnisse robuster Daten zeigten auch, dass die Verwaltungsausgaben die Hauptkosten auf den Galapagos-Inseln waren. Die Kosten für medizinische Verluste im Zusammenhang mit *Aedes*-Mücken, die auf dem ecuadorianischen Festland Dengue-Fieber verursachen, wären jedoch an erster Stelle gestanden, wenn wir durch detailliertere Informationen als robuste Daten eingestuft werden könnten. Über 70% der für Ecuador gemeldeten IAS hatten keine Kosten gemeldet. Diese Ergebnisse deuten darauf hin, dass die hier gemeldeten Kosten die tatsächliche wirtschaftliche Belastung durch Invasionen im Land massiv unterschätzen.

Keywords
Damages, economic costs, InvaCost, invasive alien species, mainland Ecuador, management

Introduction

Invasive alien species (IAS) are defined as non-native species that, as a result of human transportation or trade, establish in a new ecosystem where they may cause environmental impact, economic harm or affect human health (Convention on Biological Diversity 2009). Most worrisome is that the number of invasive species and invasion events – as well as their associated deleterious impacts in invaded areas – shows no sign of abatement in the near future (Seebens et al. 2017, 2018). Whether their introduction has been intentional or accidental (McNeely 2001), IAS pose serious threats to biodiversity, ecosystem stability (Vilà et al. 2010), health (Shepard et al. 2011; Schaffner et al. 2020), human livelihood and well-being (Pejchar and Mooney 2009; Simberloff et al. 2013), and the economy (e.g., Pratt et al. 2017; Diagne et al. 2021a; Cuthbert et al. 2021). Some examples of their numerous ecological impacts include the transformation of landscapes by removing trees (e.g. the beaver *Castor canadensis* in Chile and Argentina; Papier et al. 2019), decline or elimination of native species through competition or predation (e.g. by the ant *Solenopsis geminata* in the Galapagos Islands; Herrera and Causton 2008), ecosystem and restructuration and function modification (e.g. by invasive aquatic bivalves *Dreissenia* spp.; Karatayev et al. 2014), and decreasing biodiversity in protected areas and islands (Bellard et al. 2017; Holmes et al. 2019).

Invasive alien species are also responsible for a variety of substantial losses across many socio-economic sectors (Bacher et al. 2018). As an illustration, it has been shown that a reduction of 10–16% of yield crops globally was associated with invasive insects (Bebber et al. 2013), but invasive species can also cause losses of human-made goods and services (Binimelis et al. 2007), destruction of infrastructure over sectors like forestry (Scheibel et al. 2016), fisheries (Rosaen et al. 2012), and agriculture (Paini et al. 2016), among others. Such sectors often drive the economy of a country, and the effects of biological invasions can hinder its sustainable economic growth, especially in developing countries (Early et al. 2016). Yet, only a few studies have reported monetary estimates of the costs of biological invasions. The existing assessments report losses worth billions yearly; for instance, previous studies estimated costs of around US$120 billion in the USA (Pimentel et al. 2005), US$14.45 billion in China (Xu et al. 2006), EUR 12 billion in Europe (Kettunen et al. 2008) and US$70 billion globally for invasive insects alone (Bradshaw et al. 2016). Moreover, across most activity sectors, the economic costs of biological invasions can be divided into two categories: "Damage", referring to the direct and indirect economic losses caused by invasive species, and "Management" referring to the expenditures on actions dedicated to controlling or eliminating invasive species (Bradshaw et al. 2016; Diagne et al. 2020a). However, these economic assessments come from less diverse regions of the world, highlighting the lack of such evaluations for mega-diverse countries (i.e. hotspots for biodiversity), where biological invasions might pose bigger ecological threats and where these studies can provide guidance for better redirection of resources (i.e. monitoring, management and mitigation) to counter IAS impacts.

Ecuador, one of the smallest of the world's 17 mega-diverse countries, harbors unique ecosystems as well as an extraordinary number of endemic species (Mittermeier et al. 1998; Myers et al. 2000). It is divided into three continental regions (i.e. Amazon, mountains, coast) plus the Galapagos Islands. Ecuador is among the five richest places in the world for birds, reptiles and amphibians (Bass et al. 2010). Approximately 20% of its national territory – distributed across 50 protected areas- is under the maximum category of protection, according to the national environmental legislation and the National System of Protected Areas (SNAP, Ministerio de Ambiente de Ecuador 2014). The most famous of these protected areas are the Galapagos Islands, declared a UNESCO World Heritage Natural Site in 1978. They are regarded as a "living museum and showcase of evolution" due to their peculiar fauna and flora (UNESCO, 2020). They attract interest not only from tourism (more than 271,238 visitors in 2019; Dirección del Parque Nacional Galápagos 2019), but also from international funding to invest in their protection and conservation, for example, a major contribution from the UNESCO-World Heritage over US$2.19 million for the "Galapagos Invasive Species" account (UNESCO 2008).

The Galapagos Islands have been invaded by many species from a variety of taxa representing an exceptional threat to this vulnerable insular ecosystem. Up to 2017, the number of alien terrestrial and marine species recorded in the islands was 1,522

(Shackleton et al. 2020, appendix 2). Among these, 810 were plant species, 63 pathogens, 50 marine invertebrates and 3 marine plants (Shackleton et al. 2020, appendix 2). Of the introduced plant species, at least 32 were considered invasive (Atkinson et al. 2012). Many plant species, out of control today, were introduced with ornamental and/or agricultural purposes in the four inhabited islands of the archipelago (i.e. Floreana, Isabela, San Cristobal and Santa Cruz). Among the worst plants regarding their impacts on biodiversity and ecosystems services are *Cedrela odorata* (Spanish cedar), *Cestrum auriculatum* (orange cestrum), *Cinchona pubescens* (quinine tree), *Lantana camara* (multicoloured lantana), *Psidium guajava* (guava), *Rubus niveus* (blackberry) and *Tradescantia fluminensis* (small-leaf spiderwort) (Gardener et al. 2013), which outcompete Galapagos endemic and native flora (Guézou et al. 2010).

In addition, there are 545 species of introduced insects and 77 other terrestrial invertebrates (Toral-Granda et al. 2017) from which at least six species are considered invasive (Atkinson et al. 2012). Two species of ants, *Wasmannia auropunctata* (little fire ant) and *S. geminata* (tropical fire ant), are considered the most serious threats to the hatchlings of endemic birds and reptiles in the Galapagos Islands. Particularly, *S. geminata* is regarded as an environmental and economic pest, being documented on 20 islands and islets and having major impacts on around 25 endemic or threatened taxa including land tortoises, iguanas and many seabirds (Wauters et al. 2014). But undoubtedly, vertebrates have the most devastating impacts on the biodiversity on the islands. These invasions originated from the introduction of pigs, goats, cattle, cats, dogs and birds in the early 19th century. Since then, 27 vertebrate species have been reported to live on the islands from which 20 have established feral populations (Phillips et al. 2012a). Introductions of vertebrates have driven some local extinction; for example, the land iguana (*Conolophus subcristatus*) on Santiago Island (Phillips et al. 2005; Cayot 2008). Feral goats threaten 55–60% of the endemic plant species (Atkinson et al. 2012). Over the course of 50 years, invasive alien species in the Galapagos Islands have therefore been the focus of numerous management projects, which in total have been costly, yet not systematically compiled. Identifying these costs would help to inform and prioritize optimal management planning.

Invasive species also have impacts on mainland Ecuador. For example, in the public health system, *Aedes* mosquitoes are a medically important vector of arboviral diseases, such as dengue fever and chikungunya in the whole country and throughout Latin America. Control of the *Aedes* species remains the principal means of preventing and managing outbreaks but it requires considerable investment of time and resources. People living on the urban periphery are particularly vulnerable and are in need of public health management strategies that integrate local, policy-relevant research that guides the design, implementation and evaluation of dengue management (Stewart Ibarra et al. 2014). Invasive species also greatly impact the agriculture sector. Fruit exportation depends on the appropriate control of fruit flies from the family *Tephritidae* and their presence has triggered monitoring and eradication campaigns in areas of papaya, melon and mango cultivation in the Santa Elena and Los Ríos regions in Ecuador (Cañadas et al. 2014). Invasive potato tube moths (PTM, Lepidoptera: Gelechiidae), in their larval stage, feed on potato, a major staple crop in highland Ecuador (i.e. Andean region), representing serious agricultural problems in the poorest regions of Central Ecuador where monitoring programs are most needed (Dangles et al. 2010). Yet, these costs are generally unknown, very case-specific and/or difficult to contextualize.

So far, there has been no national assessment of all the economic costs incurred by IAS in Ecuador, although such cost assessments are of strong interest for both research and management purposes (Dana et al. 2013; Diagne et al. 2020a). Using the "InvaCost" database, we addressed this knowledge gap. Our aims were to (*i*) quantify all the reported economic costs of IAS in Ecuador, (*ii*) evaluate the distribution of such costs across space, taxonomic groups, impacted sectors and over time, and (*iii*) assess the highest types of costs incurred, whether damage costs or management expenditures.

Methods

Data compilation, structure, and extraction

We extracted costs data associated with IAS from the "InvaCost" database (Invacost 3.0; Diagne et al. 2020b). "InvaCost" is a comprehensive and harmonized compilation and description of monetary costs associated with biological invasions (9,823 entries, full data and details in https://doi.org/10.6084/m9.figshare.12668570). This database results from a systematic literature search made in three bibliographic repositories (i.e. Web of Science, Google Scholar and Google search engine), as well as specific searches directed towards pre-defined sources, experts and stakeholders (i.e. "Targeted Collection" through e.g. webpages of official organizations and institutions, national biodiversity managers, conservation practitioners, researchers specialized in biological invasions). As a result, "InvaCost" also includes data published in languages other than English (Angulo et al. 2021a). All sources were screened for relevant cost information and collated to a standardized currency, i.e. 2017 equivalent US Dollars (US$), based on exchange rates provided by the World Bank (see Diagne et al. 2020b for details). Each entry collated in "InvaCost" contains a cost estimate depicted by a unique combination of cost descriptors (currently >60 columns in the database) including: (i) the bibliographic information of the documents reporting the costs; (ii) the information on the impacted area (e.g. location, spatial scale, environment – aquatic or terrestrial, and whether the location corresponded to a protected area and/or an island); (iii) the taxonomy of the IAS causing the cost, (iv) the temporal extent over which the cost occurred, or was predicted to occur; and (v) the typology of each reported cost (e.g. type of cost – management actions or economic damages; impacted sector – activity, market or societal sector related to the cost; and the reliability of the cost value). Finally, a set of variables reported the raw and standardized cost values (see below), as well as the original currencies.

From this data assembly we selected cost entries specific to the country of Ecuador (column “Official_country”), resulting in 153 entries (herein, "raw data"; Data are provided in the Suppl. material 1: S1a). Data for Ecuador comes from 19 references collected in the Web of Science (two references corresponding to six entries), Google Scholar (two references corresponding to 19 entries) and Google (two references corresponding to eleven entries). The remaining 14 references (117 "raw data" entries) were collected by the "Targeted Collection" specifically focused on Ecuador. Together, these data provided information about 27 Genera and 37 invasive species. All cost data were carefully revised and checked to identify potential duplicates and errors, and all modifications to the original data were sent to the dedicated email address (updates@invacost.fr) for consideration and correction in a future update of "InvaCost".

Data processing

We annualized all "raw data" entries (except six entries due to lack of precise information about the duration of the costs) to consider the temporal frame in which they occurred. This was necessary because the duration of reported costs is very heterogeneous, varying from few months to several years. To estimate annual costs of invasions, our cost entries were expanded along the number of years during which each cost occurred. For this purpose, we used the "expandedYearlyCosts" function of the "invacost" R package (Leroy et al. 2020; R version 3.6.2, R Core Team 2020) to derive each cost entry of the raw robust data to annual estimates for each year of cost occurrence. This function considers information provided on both the starting and ending years ("probable starting year adjusted" and "probable ending year adjusted" columns; Suppl. material 1: S1a) of each cost occurrence. When information was not available on the actual years of the cost, we used the publication year of the original reference as a basis for estimating the duration (Diagne et al. 2020b). This way, we obtained a total of 464 annualized costs entries (Suppl. material 1: Table S1b).

Temporal description of the costs

From the resulting expanded database and the year in which the costs occurred, we calculated the cumulative and average costs of invasive species in Ecuador for the period 1983 to 2017, using the function "summarizeCosts" from the same "invacost" R package. We analyzed and provided average costs in five-year intervals over the above-targeted period.

Data filtering

Once all the data were annualized, we filtered the data using two important descriptors of the costs: the reliability of the cost estimate and the implementation of the cost (columns “Method_Reliability”, and “Implementation” respectively of the database, Suppl. material 1: Table S1b). The reliability of the cost entries was categorized as ‘High’ if the approach used for cost estimation in the original source was reported, reproducible and traceable, and ‘Low’ if otherwise. The implementation of the cost entries was categorized as ‘Observed’ if the cost was actually incurred in the focal area, and ‘Potential’ if the cost was not empirically observed but only predicted to occur (see

Diagne et al. 2020b for details on criteria used). Costs that were both observed and of highly reliable were considered “robust”. Thus, we obtained a first dataset that we called herein "robust data" containing 317 entries representing data for 26 genera and 36 species (Suppl. material 2: Table S2). Excluded entries are classified as "non-robust" (147 entries, i.e. ‘Low’ reliability and/or ‘Potential’ implementation), this group of entries reports costs for one additional genus and species that is thus not included in the "robust data" (Suppl. material 2: Table S3).

Analyses of the robust data using cost descriptors

Invasion costs estimates were analyzed based on three descriptors:

i. Taxonomy of the invasive species causing the cost at the Genus level of (“Genus” column in the database; Suppl. material 1: Table S1). However, when multiple species were associated with the same costs, those entries were reclassified as "Mixed-taxa".

ii. Socio-economic sectors impacted by the invasive species cost (“Impacted_sector” column in the database; Suppl. material 1: Table S1) as the following: "Agriculture", "Authorities-stakeholders", "Forestry", "Health", "Environment" and "Mixed". The "Mixed" category was assigned when reported costs affected two or more economic sectors and it was not possible to assign individual values.

iii. Type of cost reported (“Type of cost_merged” column in the database; Suppl. material 1: S1) as (a) "Management" costs, i.e. expenditures associated with impeding the spread of the invasive species (i.e. management, control, eradication, monitoring), (b) "Damage" costs, monetary losses either direct (e.g. yield reduction, degradation of infrastructures) or indirect (e.g. repairing the impact of the invasive species, medical care of ill patients), (c) "Unspecified"costs, referring to other costs that could not be unambiguously associated to exclusively one of two previous categories (i.e. indirect costs).

Results

Overall description of costs over time

Taking into account only the "robust data" (i.e. "observed" and "highly reliable" cost data), the total economic costs of biological invasions in Ecuador amounted to US$86.17 million from 1983 to 2017 (n = 317, Fig. 1). On average, expenditure on invasive species was US$3.75 million per year (Fig. 2). Annual costs increased from ca. US$0.35 million per year in the second half of the 1990s, to ca. US$6.37 million per year during the 2000s but decreased to ca. US$2.5 million per year during the last decade (probably in part due to the time lag to report costs). Most of these costs were documented between 2007 and 2009 (Fig. 2), when international projects for eradication of invasive species, mostly in the Galapagos Islands, were put into place (Carrión

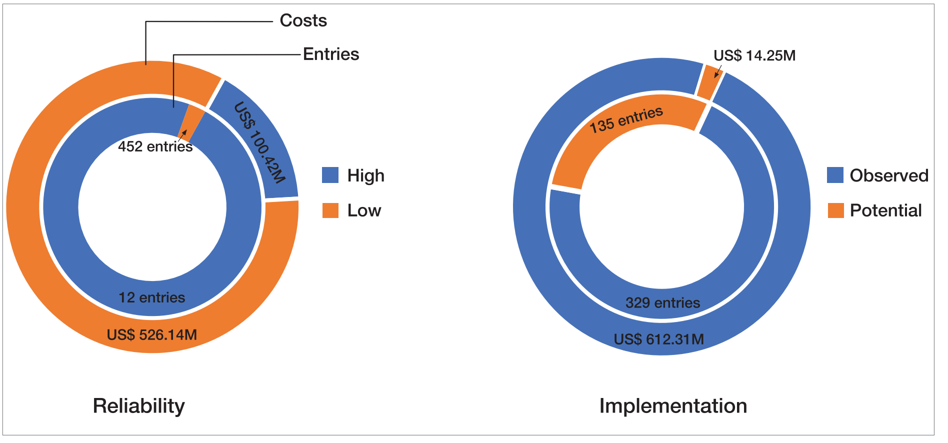

Figure 1. Distribution of economic costs (outer circles US$ million) and number of entries (inner circles) of invasive species in Ecuador according to: (**a**) level of reliability of the cost entries (High and Low); (**b**) implementation of the cost reported (Observed and Potential). "Robust data" is the combination of highly reliable entries and observed implementation, whereas "Non-robust" data is otherwise.

et al. 2011). Accounting for all cost entries (i.e. including both "low reliability" and "potential" costs), the total economic cost was US$626.56 million ($n$ = 464 annualized costs). From this amount, the 85.72% were driven by costs deemed either as potentially occurring (i.e. predicted; US$14.25 million) and/or marked as low reliability (US$526.14 million; Fig. 1). Specifically, the low reliability data correspond mostly to data on *Aedes* mosquitoes dengue fever cases (Suppl. material 1: Table S1). From here on, all results are based on "robust data" unless stated otherwise.

The costs entries of Ecuador came almost exclusively from the Galapagos Islands (99%, corresponding to US$86.17 million, n = 315 entries, Fig. 3), whereas the remaining 1% were reported for either the entire country and/or for mainland Ecuador (US$1.67 million, n = 2 entries, Fig. 3). Including "non-robust data" only increased the percentage of cost entries reported for mainland to 5%. Costs from islands were reported for either the entire archipelago or for independent islands (Fig. 3). The island with most costs was Isabela Island (US$13.91 million, n = 38 entries), followed by Santiago Island (US$8.97 million, n = 38 entries). The islands of Pinzón and Santa Cruz each reported costs of ca. US$1 million (n = 3 and n = 155 entries, respectively), whereas San Cristobal, Marchena and Pinta islands reported costs less than US$1 million (n = 9, and two n = 5 entries, respectively). Costs at the scale of the entire archipelago amounted to US$48.45 million (n = 38 entries).

Cost descriptors

Expenditures on "Management" constituted the large majority of the type of economic costs reported for Ecuador, with US$86.06 million (99.8%; n = 314 entries) involving control, eradication, monitoring and administrative management actions. The remaining 0.2% of the costs are divided between economic costs due to "Damage"

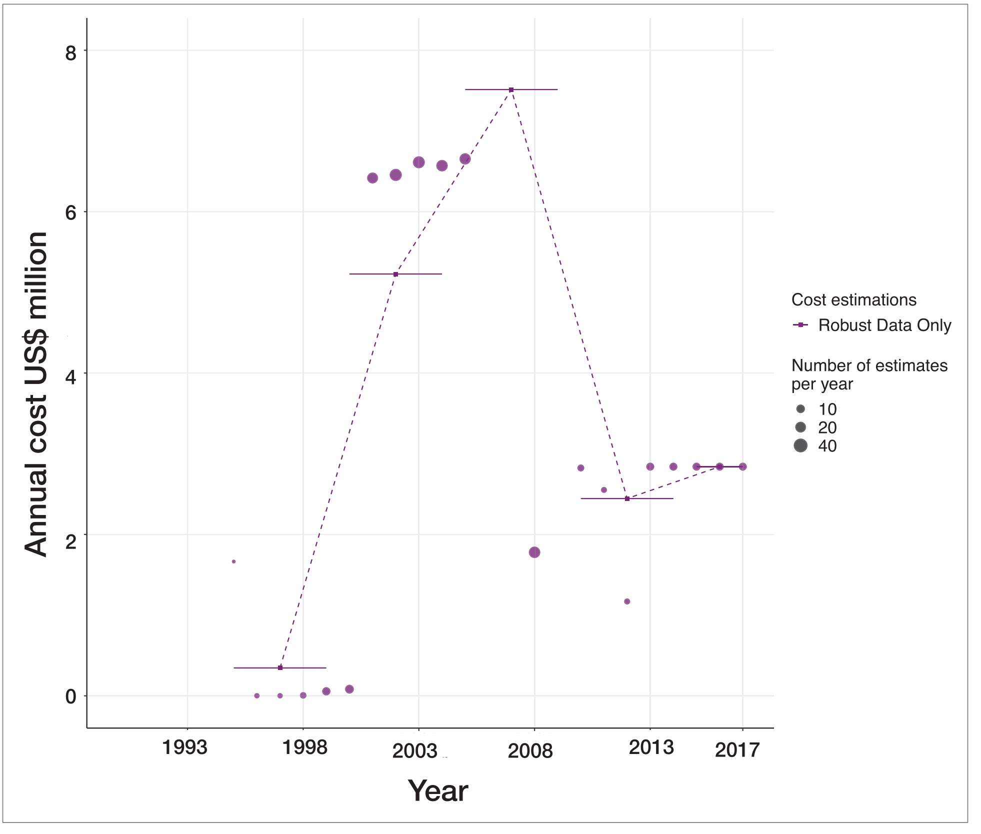

Figure 2. Temporal trend of the total costs in 2017-equivalent US dollars incurred by invasive species in Ecuador over time. Only *robust data* is represented (i.e. both observed and highly reliable). Each point represents the cumulative cost for a given year whereas its size is proportional to the number of estimates for that particular year. Average annual costs are calculated in 5-year periods and are represented by dots and horizontal solid lines. Dashed lines connect the average annual costs for these 5-year periods.

of US$0.01 million (n = 1 entry) and "unspecified" costs amounting to US$0.107 million (referring to indirect costs; n = 2 entries). When including "non-robust data", damage losses, are all associated with medical care (US$525.9 million; eight entries, Suppl. material 2: Table S3) due to dengue cases, which is about five times higher than the reported expenditures on management of the *Aedes* mosquitoes (US$2.14 million, "robust data", n = 6 entries, Suppl. material 2: Table S4).

The most impacted activity sector was "Authorities-stakeholders" (i.e. those governmental services or organizations allocating efforts and resources for managing invasive species, Diagne et al. 2020b) with US$84.03 million; N = 309 entries (Table 1). Costs impacting "Mixed" sectors amounted to US$2.14 million (particularly mixed costs affecting both "Authorities-stakeholders" and "Health" US$2.14 million n = 6 entries, Table 1). "Agriculture" reported costs for US$0.001 million (n = 1 entry). With the inclusion of "non-robust data", the "Mixed" sector (mixing "Authorities-stakeholders" and "Health") would have been ranked in first place due to US$525.9

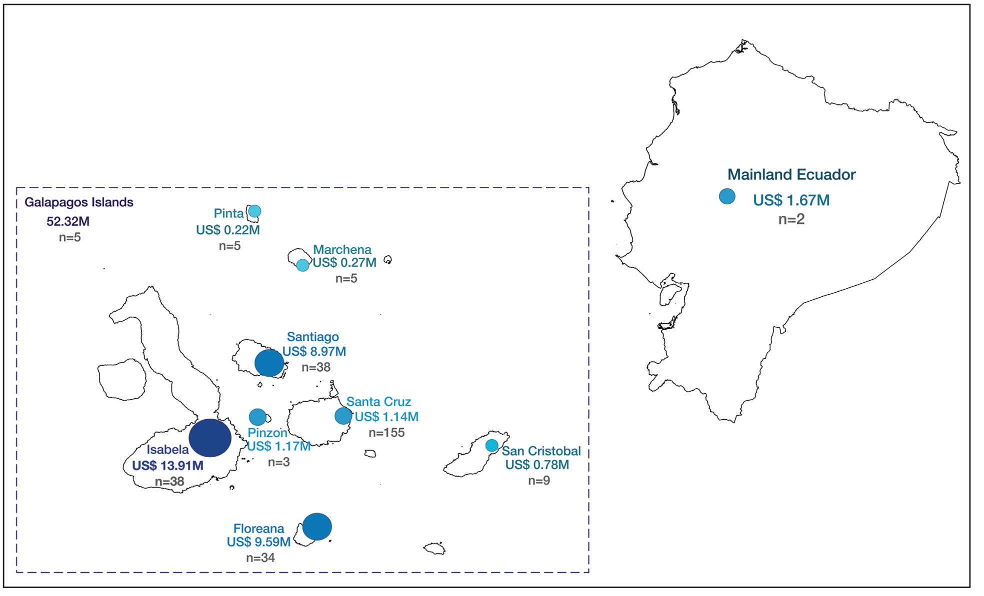

Figure 3. Maps of the economic costs of invasive species in Ecuador: Only *robust data* is represented (i.e. observed and highly reliable). Values are reported for islands and mainland Ecuador. Bubble size represents the amount of costs in US$ millions grouped by similar colors. Dashed lines denote the costs reported for the entire archipelago.

Table 1. Total economic management costs per impacted activity sector taking into account only *robust data* (i.e. observed and highly reliable).

Impacted sector	Total cost US$ million	Number entries
Authorities-Stakeholders	84.03	309
Mixed	2.14	7
Agriculture	0.001	1

million on damage costs (eight entries, Suppl. material 2: Table S3) caused by *Aedes* mosquitoes dengue fever cases.

Regarding taxonomy, the highest economic costs were reported for "mixed-taxa" (61.4%; US$52.44 million, n = 12 entries, Fig. 4). Animal species were responsible for 35% of the total economic costs (US$30.64 million n = 73 entries) and plant species for 3.6% (US$3.09 million, n = 232). The costliest invasive organisms that we could assign costs to were feral goats with US$23.75 million (n = 38 entries, Fig. 4), followed by *Aedes* mosquitoes with US$2.14 (n = 6 entries). The third most costly organisms were plants belonging to the genus *Rubus* (*R. niveus*, *R. adenotrichos*, *R. glaucus*, *R. ulmifolius* and *R. megalococcus*), whose management caused high costs to "Authorities-stakeholders" (US$2.07 million, n = 118 entries; Fig. 4; Suppl. material 2: Table S4). The parasitic fly (*Philornis downsi*) that affects the survivorship of several species of birds in the Galapagos Islands, has incurred control costs of US$1.60 million (n = 5 entries). In ninth place as the costliest invasive genus in Galapagos was the timber tree

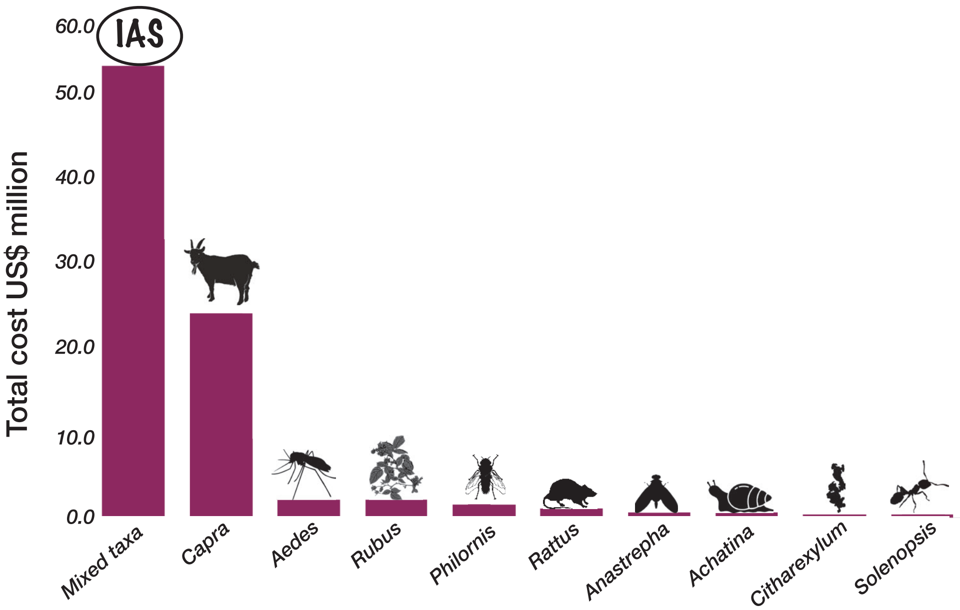

Figure 4. The ten costliest genus in Ecuador. IAS represents costs for multiple species. Costs are reported in million US dollars.

(*Citharexylum gentryi*), a native tree from lowland coastal and Amazonian Ecuador and considered highly invasive in the Galapagos Islands and which incurred costs of US$0.47 million (n = 25 entries). Information for all the 27 genera causing costs in Ecuador is given in Suppl. material 2: Tables S3, S5. The entire costs reported in the database came from organisms in terrestrial environments. Here, we considered the *Aedes* mosquitoes terrestrial, since all the incurred costs are related to their adult life stage (i.e. control – for health and resources spent by health authorities due to dengue fever).

Management actions on "mixed-taxa" of invasive species have fallen most heavily upon governmental organisms such as the Galapagos National Park Directorate and/or other institutions such as the Charles Darwin Foundation, incurring expenditures of US$52.44 million (n = 12 entries; Suppl. material 2: Tables S2, S4).

Discussion

Central role of the Galapagos Islands in invasion costs reported for Ecuador

Our findings showed that biological invasions cost the Ecuadorian economy at least US$86.17 million between 1983 and 2017, and that most of these expenses were reported between 2007–2009 (Fig. 2). The highest recorded costs were associated with a combination of two or more plant/animal species, but the costliest identified taxonomic group was the goat, followed by the *Aedes* mosquito. We also found that the economic sector "Authorities-stakeholders" sustained the largest economic costs, mostly through management actions in the Galapagos Islands. Our conservative approach of only retaining "robust" data (i.e. both observed and highly reliable) excluded another US$526.14 million that were classified as potential and/or unreliable costs (i.e. "non-robust data"). The high predominance of management expenditures in the Galapagos Islands might be explained by two reasons that we explore below: the emblematic history of this unique archipelago that helps secure funding to control and/or eradicate invasive species more than in mainland Ecuador, and island isolation, coupled with increasing tourism, as a reason to invest in management actions to protect these ecosystems from the damage caused by invasive species.

The World Heritage status and the history of Charles Darwin formulating his theory of evolution after visiting Galapagos, promoted the Galapagos Islands to a flagship conservation area that helps attract major resources for both research and conservation. It has led to the establishment of institutions like the Charles Darwin Foundation and its Research Station that attracts researchers from all around the world and in turn has promoted the transfer of ideas and expertise (in both directions, local and international institutions and individuals). This has also enabled the securing of substantial amounts of funding for conservation. For example, the funding of a multi-partner 6-year program (US$43 million) for managing invasive species (Gardener et al. 2009), from which a US$6.1 million program was established to eliminate feral goats from Santiago Island (Cruz et al. 2009) as part of the Project Isabela (~10.5 million US$) – the world's largest restoration effort – for the elimination of invasive mammals at the archipelago level (Carrión et al. 2011). Twenty-one plant eradication programs began in 1996, but only four were successful, eradicating *Rubus adenotrichos*, *R. megalococcus*, *Pueraria phaseoloides* and *Cenchrus pilosus* from Santa Cruz Island (Atkinson et al. 2012). It seems that plant species are much more difficult to eradicate than other groups of organisms (Gardener et al. 2009). Several eradication programs for invasive ants have been conducted across the archipelago, achieving local removal from Santa Fe and Isabela islands for the tropical fire ant (Wauters et al. 2014), and from Santa Fe and Marchena for the little fire ant (Causton et al. 2005). The joint efforts between researchers and local authorities have also helped to put in place legislation and oversee the proper implementation of programs to control invasive pests such as feral pigeons and limit the spread of dengue-carrying mosquitoes (Phillips et al. 2012b; Toral-Granda et al. 2017).

At the same time, the status as a protected area and a World Heritage site makes the Galapagos Islands an important hub for ecotourism that now underpins the national economy. Tourism has grown from 1,000 tourists per year in 1960 up to >270,000 tourists in 2019 (Dirección del Parque Nacional Galápagos 2019). The continuous pressure posed by tourism, population growth and the increasing trade between mainland and the archipelago resulted in the official establishment of biosecurity protocols in 1999. They started in 2000 with the release of a list of permitted, restricted and prohibited products and goods from the Quarantine Inspection System of Galapagos (SICGAL), and inspection of goods from cargos and luggage from new arrivals to stop potential harmful organisms from becoming established (Zapata 2007; Cruz Martínez et al. 2007). Then, in 2007, the invasive alien species management plan (Plan de Control Total de Especies Introducidas) was developed (Toral-Granda et al. 2017). Finally, in 2012, a dedicated agency of biosecurity (ABG; Agencia de Regulación y Control de la Bioseguridad y Cuarentena para Galápagos) was established with its mission to control, regulate and reduce the risk of introduction and spreading of exotic species that endanger the biodiversity of the islands, the local economy and human well-being (Toral-Granda et al. 2017; https://www.gob.ec/abg). Moreover, getting a comprehensive legal and administrative framework to address already established invasive populations (i.e. control and eradication programs, quarantine actions, and legislation) was crucial for the Galapagos Islands and in turn for Ecuador's economic interests because of the high value of tourism; an industry whose net benefits were extrapolated to be around US$392 million in 2016 (Schep et al. 2014). The investment of US$86 million over the last three decades protecting both the Galapagos unique biodiversity and dependent tourism revenues is a good choice for conservation but at the same time a very cost-effective economic strategy. The Galapagos Islands' main source of revenue is their endemic species (i.e. tourism, conservation) which leads to a differential managing strategy in comparison to mainland Ecuador where introduced species can be the major source of revenue such as crops (e.g. bananas and coffee) and other introduced species that are not invasive. Therefore, the perception and pressure for management can be very different (Nuñez et al. 2018).

Limitations and ways forward

Quality control in databases is crucial for ensuring accurate assessments and conclusions, particularly in invasion science, where results are used to inform conservation managers, practitioners and environmental policy makers. We chose to use a highly conservative and robust dataset to draw our conclusions, and then delineated the pitfalls in our interpretation of the cost distribution. We are aware that our decisions to include or exclude some data might have consequences on our quantitative conclusions. For example, *Aedes* mosquitoes occupied third place in our list of the costliest species in Ecuador because we excluded its data from the most robust dataset; yet this species complex ranks much higher in economic costs assessments for other South American countries (such as Argentina, Duboscq-Carra et al. 2021) or even the whole continent (Central and South America, ranked 2nd -US$12.9 million; Heringer et al. 2021). Sheppard et al. (2011) provides a detailed account of the high costs of *Aedes* mosquitoes across the Americas between 2000 and 2007 (Reference ID 73; Suppl. material 1: Table S1a). Yet, we can only speculate about the real economic burden that this species generated in Ecuador due to dengue fever, as national details were not provided in that case. Dengue cases are considered under-reported in Latin America in general (Hotez et al. 2008) despite estimated losses being in the same order of magnitude as other neglected diseases such as tuberculosis, leishmaniasis or intestinal helminths (Torres and Castro 2007). Furthermore, this finding emphasizes that managers and researchers, whenever possible, should provide finer-scale and more complete information, when providing economic cost data for invasive species impacts; e.g. at least the main descriptors, such as spatial and temporal scale of the cost, the taxa involved, the type of costs and the economic sector impacted (Diagne et al. 2020a, b). In fact, due to the lack of precise information about the duration of the costs, six entries ("raw entries", Suppl. material 1: Table S1a: L149–153) had to be excluded from the entire analysis. One of the excluded entries belonged to *Culex* mosquitoes reported for mainland Ecuador (i.e. an area with not many records), and was the only cost entry we have for the species (Suppl. material 1: Table S1a).

The leading type of costs reported across the assembled dataset was expenditure in management. This is in contrast to results from the analysis of "InvaCost" data in other regions, where damage costs far outweighed management investments, for example, in Asia (Liu et al. 2021), Africa (Diagne et al. 2021b), Central and South America (Heringer et al. 2021), Europe (Haubrock et al. 2021a) or North America (Crystal-Ornelas et al. 2021). Ecuador, particularly the Galapagos National Park, significantly invests in management actions such as prevention (e.g. with the establishment of ABG), monitoring, control or eradication since most invasions controlled, both in the past and currently, are in a late stage of invasions generating high management costs. Yet, it is surprising that Ecuador reports almost no data for damage and loss, although a similar situation occurred in Spain where > 90% of the robust data corresponded to management costs of IAS, while damage costs were only found for 2 out of the 174 species with reported costs (Angulo et al. 2021b). It is, for example, also striking that no damage costs have been recorded for agriculture, forestry or fisheries activities in Ecuador. Agriculture, for instance, is an important sector that makes up 33.9% of the employment in rural areas of Ecuador (which is higher than the 24% reported in other Andean countries of the region (Martínez Valle 2017). It was also the most impacted activity sector by invasive alien species in Brazil (Adelino et al. 2021) and Argentina (Duboscq-Carra et al. 2021), while fisheries was ranked first for Mexico (Rico-Sánchez et al. 2021). In fact, the scarcity of scientific reports on the economic impacts of invasive species from mainland Ecuador makes it difficult to assess the real cost on most activity sectors. Low funding for ecological research in comparison to other disciplines might be one of the causes for the lack of records (Nuñez et al. 2019; Nuñez and Pauchard 2010). Economic evaluation studies are often limited by available data (Gren et al. 2009), that is biased taxonomically and/or geographically (Pyšek et al. 2008) but also on differential funding allocation (Baker 2017). In addition, the complexity of evaluating some types of impacts (e.g. value of extinct or living species, ecosystem services, non-market items) is also probably part of the reason for the undervaluation of damage and losses (Kallis et al. 2013; Meinard et al. 2016; Diagne et al. 2020a).

We found robust costs for only 36 invasive species, whereas the Global Invasive species database reports 125 species known to be invasive in Ecuador (GISD, Pagad et al. 2018). Therefore, more than 70% of the species reported as invasive in Ecuador do not have reported economic costs that are easily accessible. Even higher gaps between the number of species to be known as invasive and the number of species from which costs are reported, have been found in other countries in Central and South America, for example in Argentina and Mexico, where they report costs for only 10% of the known invasive species (Duboscq-Carra et al. 2021; Rico-Sánchez et al. 2021) and other parts of the world, such as Germany (Haubrook et al. 2021b) or France (Renault et al. 2021). In this study, we further noticed the bias on publication language. Half of the cost entries (51%, 78 out of 153 raw entries) were derived from the search in

Spanish. Not only were there fewer publications about economic costs for Ecuador when compiling data with the most common search engines, but a large portion of the publications were obtained from directly contacting conservationists and managers ("Targeted Collection", Suppl. material 1: Table S1a). This strong bias was also found in other countries, such as Russia, (Kirichenko et al. 2021), Japan (Watari et al. 2021), France (Renault et al. 2021) or Spain (Angulo et al. 2021b). For all these reasons, despite our dedicated efforts for assembling the most complete database (Angulo et al. 2021a; Diagne et al. 2020a, 2020b), our cost estimations probably remain much underestimated. All the foregoing emphasizes the complexity of estimating costs accurately and completely, and stresses the need for most reliable cost assessments in the future – particularly for those countries (such as Ecuador) that have limited capacities to act against invasive species (Early et al. 2016; Rouget et al. 2016; Faulkner et al. 2020).

Conclusions

This study is the first attempt to construct an economic assessment of biological invasions of Ecuador, by standardizing and compiling available information from both English and Spanish sources. Our results show a disproportionate lack of investment in mainland Ecuador compared to the Galapagos Islands. However, the lack of accessible published data limits our effective assessment of the economic costs of biological invasion in the whole territory. Despite our efforts to find more information, there is still a need to investigate other sources of information (e.g. internal reports, theses, conference proceedings and the grey literature in general) to gain a more comprehensive overview. In turn, assessments of economic impacts of invasive species might benefit from having reports and projects published more accessible to the public.

Contrary to other countries in the region – whether mega-diverse or not (Heringer et al. 2021; Adelino et al. 2021; Duboscq-Carra et al. 2021), Ecuadorian institutional authorities, at least in the Galapagos Islands, have invested actively in invasive species management actions. One of the reasons is the body of research about the massive impact that invasive species have on the Galapagos resident biota (Jäger et al. 2009; Jäger et al. 2013; Rivas-Torres and Rivas 2018; Cooke et al. 2020), triggering investment to control or eradicate these species. However, ecological damage is more difficult to monetize and consequently, fewer costs are reported. Despite the massive economic costs reported here, and the important knowledge gaps we identified for these costs, we stress that economic costs are but one aspect of the impact of biological invasions, and that the biodiversity impacted by this threat is infinitely invaluable, in Ecuador and beyond.

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Supplementary material 1

Database of Economic costs of biological invasions in Ecuador

Authors: Liliana Ballesteros-Mejia, Elena Angulo, Christophe Diagne, Brian Cooke, Martin A. Nuñez, Franck Courchamp

Data type: database

Explanation note: Dataset on costs of invasive species in Ecuador extracted from InvaCost database (Diagne et al 2020) and descriptions of the column names.

Link: https://doi.org/10.3897/neobiota.67.59116.suppl1

Supplementary material 2

Tables S2–S5

Authors: Liliana Ballesteros-Mejia, Elena Angulo, Christophe Diagne, Brian Cooke, Martin A. Nuñez, Franck Courchamp

Data type: tables

Explanation note: **Table S2.** Economic costs (only robust data; US$ million) discriminated per genus, impacted sector and type of cost in Ecuador. Impacted sectors are: Authorities-stakeholders (Auth-stak), Mixed (combination of two or more) and Agriculture. Costs are sorted in decreasing order per sector. **Table S3.** Economic costs (only non-robust data; US$ million) discriminated per genus, impacted sector and type of cost in Ecuador. Impacted sectors are: Authorities-stakeholders, Mixed (combination of two or more sectors). Costs are sorted by alphabetic order of the genus. **Table S4.** Economic costs (only robust data; US$ million) and number of cost entries of all the invasive species reported for Ecuador grouped by genus and ordered decreasingly from the costliest to the less costly. **Table S5.** Economic costs (only non-robust data; US$ million) and number of cost entries of all the invasive species reported for Ecuador grouped by genus and ordered decreasingly from the costliest to the less costly. Note that genus *Felis* is the only genus that does not report entries considered robust data.

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RESEARCH ARTICLE

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

Gustavo Heringer[1], Elena Angulo[2], Liliana Ballesteros-Mejia[2], César Capinha[3], Franck Courchamp[2], Christophe Diagne[2], Virginia Gisela Duboscq-Carra[4], Martín Andrés Nuñez[4,5], Rafael Dudeque Zenni[1]

1 *Programa de Pós-Graduação em Ecologia Aplicada, Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, Universidade Federal de Lavras – UFLA, 37200-900, Lavras, Minas Gerais, Brazil* **2** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, Orsay, France* **3** *Centro de Estudos Geográficos, Instituto de Geografia e Ordenamento do Território – IGOT, Universidade de Lisboa, Lisboa, Portugal* **4** *Grupo de Ecología de Invasiones, INIBIOMA, CONICET/ Universidad Nacional del Comahue, Av. de los Pioneros 2350, Bariloche 8400, Argentina* **5** *Department of Biology and Biochemistry, University of Houston, Houston, Texas, 77204, USA*

Corresponding author: Gustavo Heringer (gustavoheringer@hotmail.com)

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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

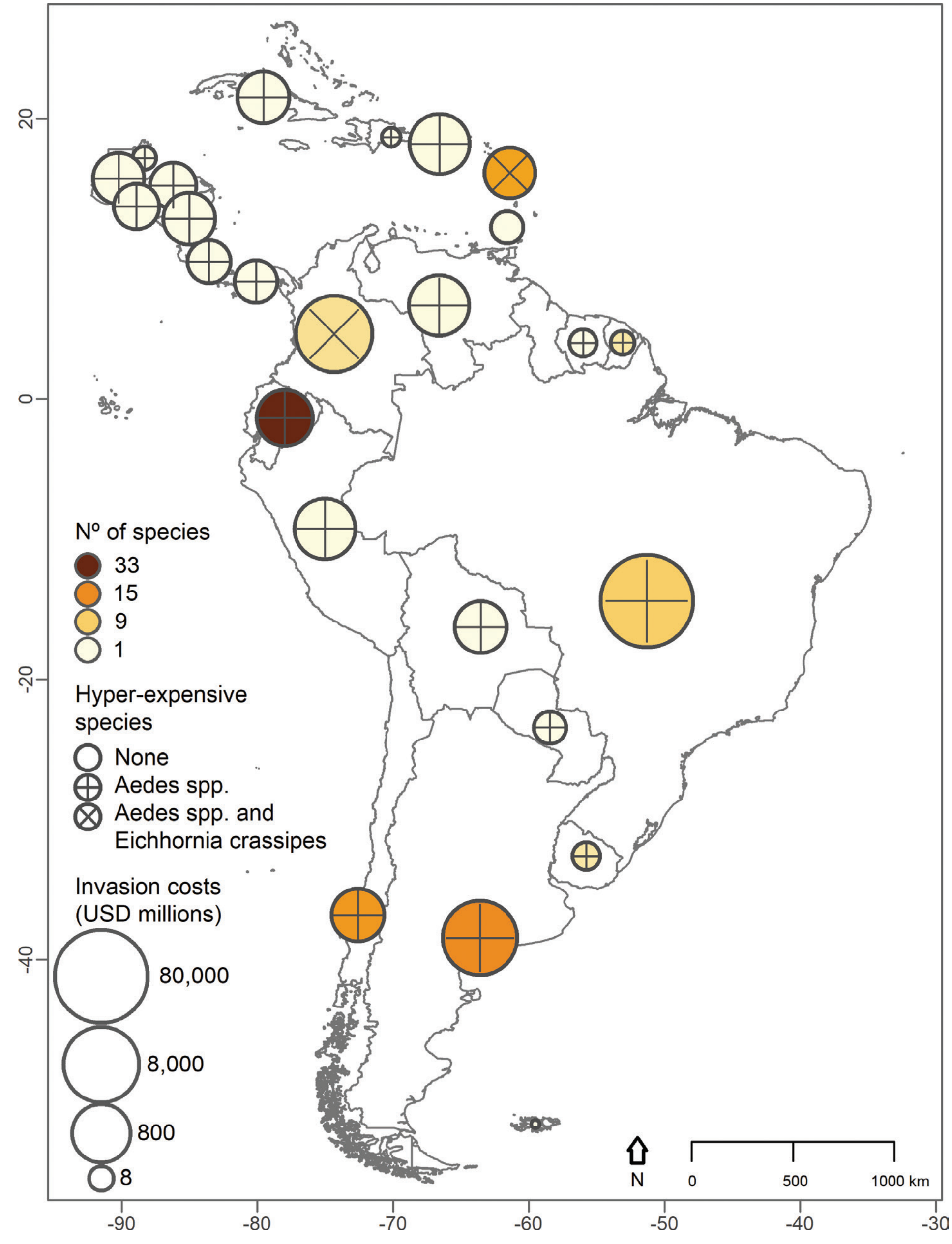

Figure 1. Map of Central and South America showing the number of invasive alien species registered in the InvaCost database (colour of circles), countries where costs with the hyper-costly taxa *Aedes* spp. and *Eichhornia crassipes* were related (crosses in the circles), and costs per country (size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

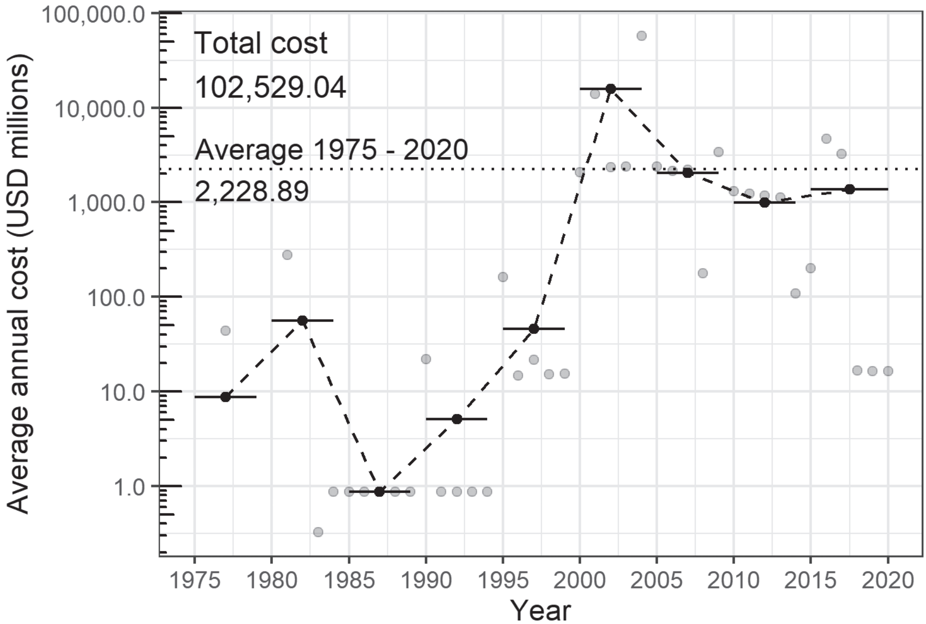

Figure 2. Annual costs of biological invasions observed over time in Central and South America. Grey dots represent the annual costs, horizontal lines and black dots represent the average annual cost per 5 years and the dashed horizontal line represents the general average between 1975 and 2020.

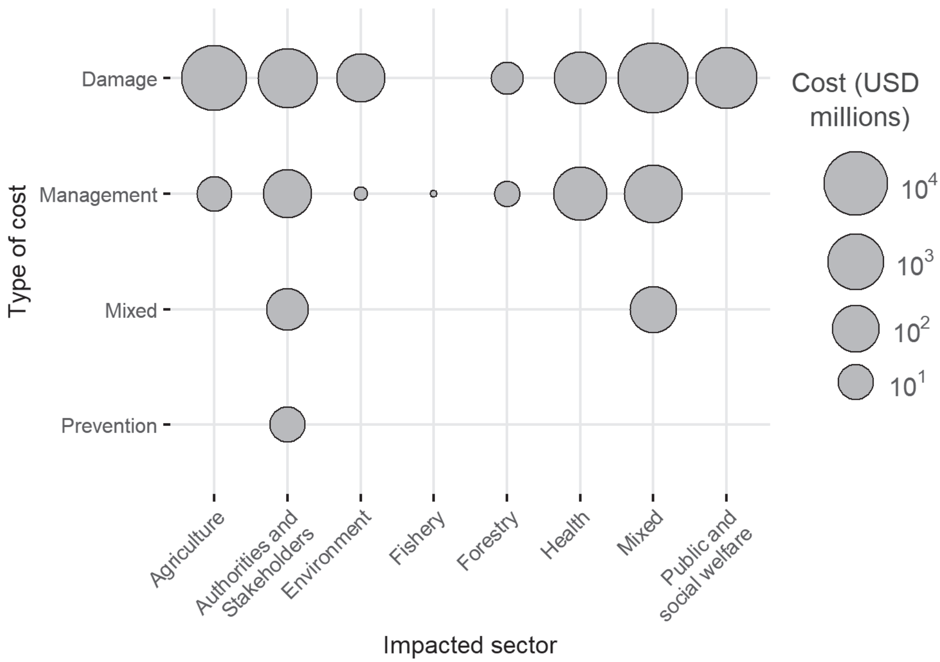

Figure 3. Cost of biological invasions shared amongst impacted sectors and type of costs in Central and South America.

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).

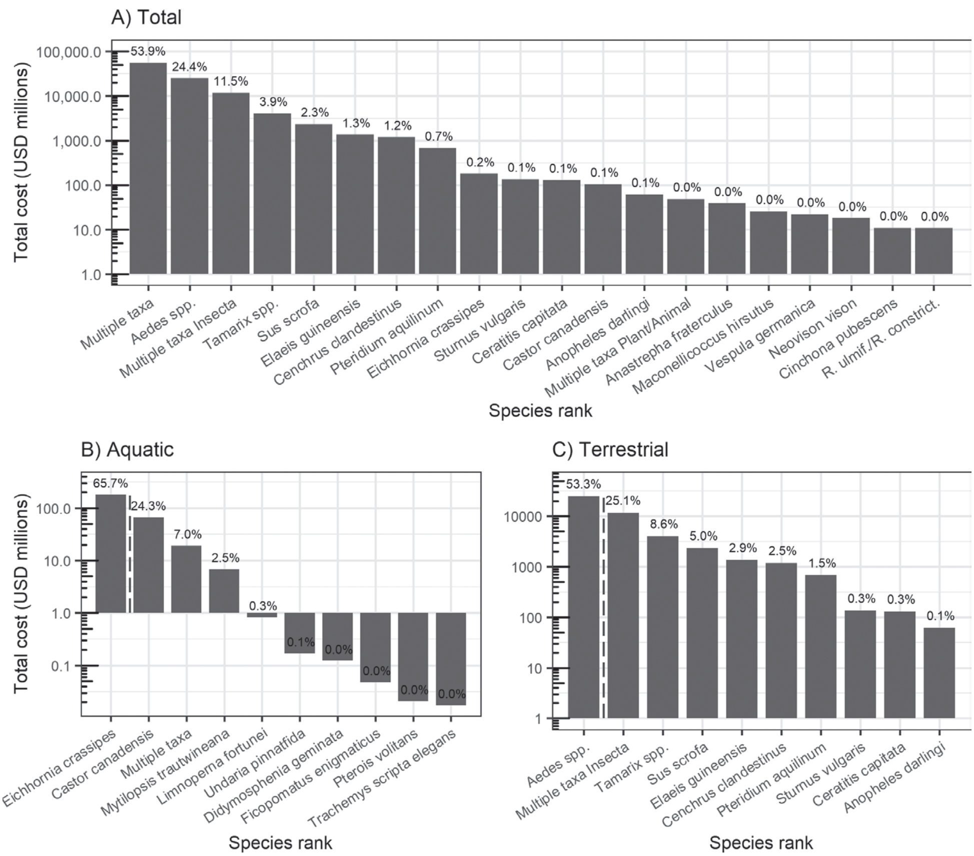

Figure 4. Costs of biological invasions per taxa in Central and South America **A** twenty costliest taxa **B** the ten costliest taxa on aquatic environments, and **C** the ten costliest taxa on the terrestrial environments. The hyper-costly taxa appear on the left side of the dashed line. Aedes spp. 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

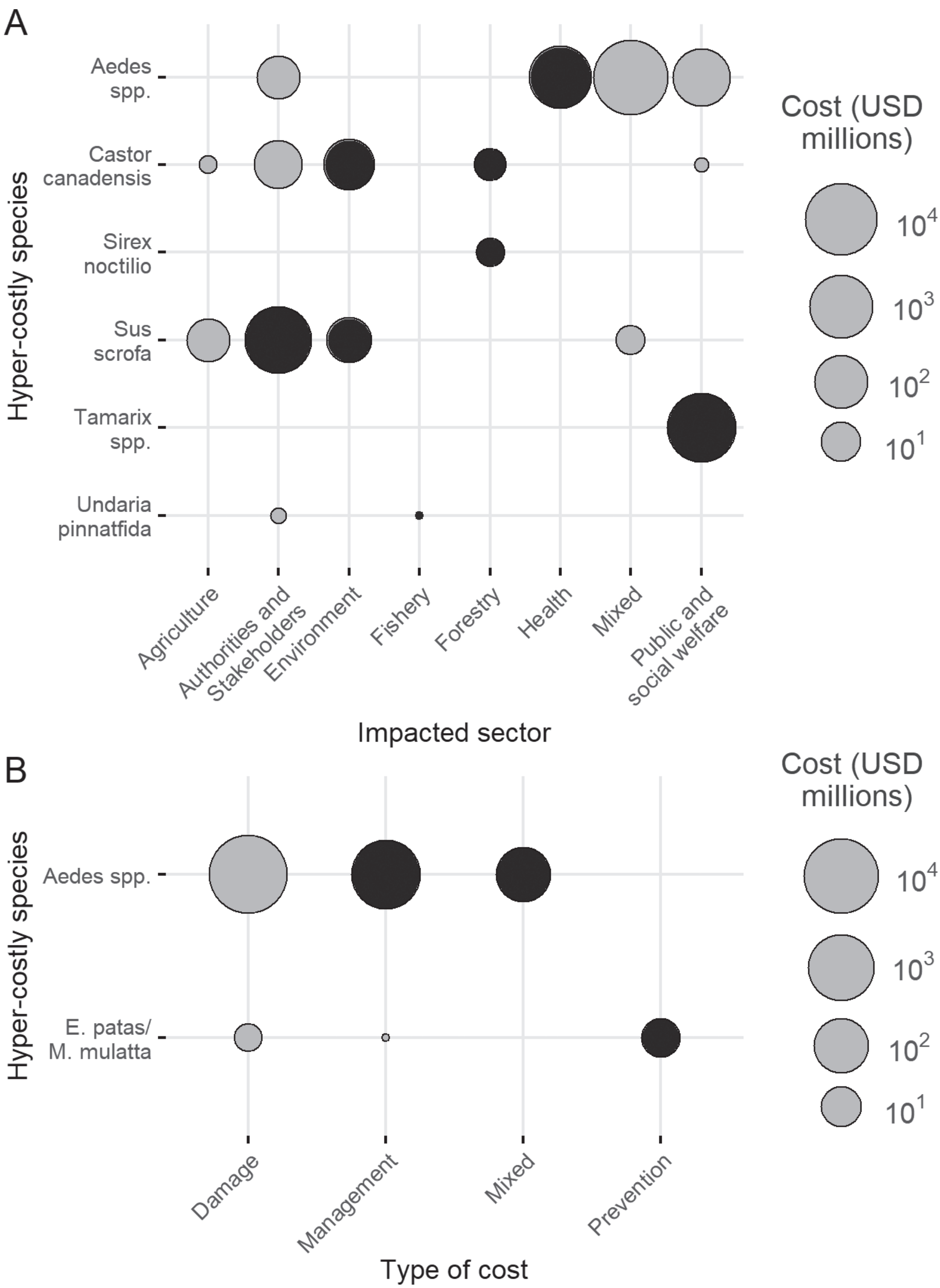

Figure 5. Costs of invasions by hyper-costly taxa **A** impacted sector and **B** type of cost. Black circles represent the hyper-costly taxa per impacted sector or type of cost and the grey circles represent the costs of each taxa in the impacted sector or type of costs where the taxa are not hyper-costly. 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

Authors: Gustavo Heringer, Elena Angulo, Liliana Ballesteros-Mejia, César Capinha, Franck Courchamp, Christophe Diagne, Virginia Gisela Duboscq-Carra, Martín Andrés Nuñez, Rafael Dudeque Zenni

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

Authors: Gustavo Heringer, Elena Angulo, Liliana Ballesteros-Mejia, César Capinha, Franck Courchamp, Christophe Diagne, Virginia Gisela Duboscq-Carra, Martín Andrés Nuñez, Rafael Dudeque Zenni

Data type: measurement

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

Supplementary material 3

Figures S1–S3

Authors: Gustavo Heringer, Elena Angulo, Liliana Ballesteros-Mejia, César Capinha, Franck Courchamp, Christophe Diagne, Virginia Gisela Duboscq-Carra, Martín Andrés Nuñez, Rafael Dudeque Zenni

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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RESEARCH ARTICLE

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Economic costs of invasive alien species in the Mediterranean basin

Melina Kourantidou[1,2*], Ross N. Cuthbert[3,4*], Phillip J. Haubrock[5,6*], Ana Novoa[7*], Nigel G. Taylor[8*], Boris Leroy[9], César Capinha[10], David Renault[11,12], Elena Angulo[13], Christophe Diagne[13], Franck Courchamp[13]

1 *Woods Hole Oceanographic Institution, Marine Policy Center, Woods Hole, MA 02543, USA* **2** *Institute of Marine Biological Resources and Inland Waters, Hellenic Center for Marine Research, Athens 164 52, Greece* **3** *GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, 24105, Kiel, Germany* **4** *School of Biological Sciences, Queen's University Belfast, Belfast BT9 5DL, Northern Ireland, UK* **5** *Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, Gelnhausen 63571, Germany* **6** *University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Zátiší 728/II, 389 25, Vodňany, Czech Republic* **7** *Department of Invasion Ecology, Institute of Botany, Czech Academy of Sciences, CZ-252 43, Průhonice, Czech Republic* **8** *Tour du Valat, Research Institute for the Conservation of Mediterranean Wetlands, 13200, Arles, France* **9** *Unité Biologie des Organismes et Ecosystèmes Aquatiques (BOREA UMR 7208), Muséum National d'Histoire Naturelle, Sorbonne Universités, Université de Caen Normandie, Université des Antilles, CNRS, IRD, Paris, France* **10** *Centro de Estudos Geográficos, Instituto de Geografia e Ordenamento do Território – 26 IGOT, Universidade de Lisboa, Lisboa, Portugal* **11** *University of Rennes, CNRS, ECOBIO [(Ecosystèmes, biodiversité, évolution)] – UMR 6553, F 35000, Rennes, France* **12** *Institut Universitaire de France, 1 Rue Descartes, 75231 Paris cedex 05, France* **13** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405, Orsay, France*

Corresponding author: Melina Kourantidou (mkour@dal.ca)

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Abstract

Invasive alien species (IAS) negatively impact the environment and undermine human well-being, often resulting in considerable economic costs. The Mediterranean basin is a culturally, socially and economically diverse region, harbouring many IAS that threaten economic and societal integrity in multiple ways. This paper is the first attempt to collectively quantify the reported economic costs of IAS in the Medi-

* Contributed equally as the first suthors.

terranean basin, across a range of taxonomic, temporal and spatial descriptors. We identify correlates of costs from invasion damages and management expenditures among key socioeconomic variables, and determine network structures that link countries and invasive taxonomic groups. The total reported invasion costs in the Mediterranean basin amounted to $27.3 billion, or $3.6 billion when only realised costs were considered, and were found to have occurred over the last three decades. Our understanding of costs of invasions in the Mediterranean was largely limited to a few, primarily western European countries and to terrestrial ecosystems, despite the known presence of numerous high-impact aquatic invasive taxa. The vast majority of costs were attributed to damages or losses from invasions ($25.2 billion) and were mostly driven by France, Spain and to a lesser extent Italy and Libya, with significantly fewer costs attributed to management expenditure ($1.7 billion). Overall, invasion costs increased through time, with average annual costs between 1990 and 2017 estimated at $975.5 million. The lack of information from a large proportion of Mediterranean countries, reflected in the spatial and taxonomic connectivity analysis and the relationship of costs with socioeconomic variables, highlights the limits of the available data and the research effort needed to improve a collective understanding of the different facets of the costs of biological invasions. Our analysis of the reported costs associated with invasions in the Mediterranean sheds light on key knowledge gaps and provides a baseline for a Mediterranean-centric approach towards building policies and designing coordinated responses. In turn, these could help reach socially desirable outcomes and efficient use of resources invested in invasive species research and management.

Abstract in French

Coûts économiques des espèces exotiques envahissantes dans le bassin méditerrannéen. Les espèces exotiques envahissantes (EEE) impactent négativement l'environnement et le bien-être humain, et résultent souvent en des coûts économiques considérables. Le bassin méditerranéen est une région culturellement, socialement et économiquement variée; elle abrite de nombreuses EEE qui menacent son intégrité économique et sociétale de multiples façons. Cet article constitue la première tentative de quantification collective des coûts économiques associés aux EEE dans le bassin méditerranéen au travers de divers descripteurs taxonomiques, temporels et spatiaux. Nous identifions les corrélations des coûts dûs aux dégâts des EEE et aux dépenses induites par leur gestion avec des variables socio-économiques clés, et nous déterminons les structures des réseaux qui lient les pays et les différents groupes taxonomiques envahissants. Le montant total du coût des invasions dans le bassin méditerranéen s'élève à $27,3 milliards, et $3,6 milliards si seuls les coûts réalisés sont pris en compte au cours des trois dernières décennies. Notre compréhension du coût des invasions biologiques en Méditerranée est largement réduite aux données concernant quelques pays, essentiellement d'Europe de l'Ouest, et aux écosystèmes terrestres, malgré la présence avérée de nombreux organismes aquatiques envahissants à fort impact. La grande majorité des coûts reportés correspondent à des dégâts ou des pertes ($25,2 milliards) et concerne essentiellement la France, l'Espagne et, dans une moindre mesure, l'Italie et la Libye, avec significativement moins de coûts correspondant à des dépenses de gestion ($1,7 milliard). De façon générale, les coûts liés aux invasions augmentent avec le temps, avec un coût annuel moyen entre 1990 et 2017 estimé à $975,5 millions. Le manque d'information pour une grande part des pays méditerranéen, qui se reflète dans l'analyse de connectivité spatiale et taxonomique et les relations entre les coûts et les variables socio-économiques, met en évidence les limites des données disponibles, ainsi que l'effort de recherche qui est nécessaire pour une compréhension plus globale des différentes facettes des coûts des invasions biologiques. Notre analyse des coûts reportés pour la région méditerranéenne met en lumière les principales lacunes de connaissance et pose les bases d'une approche Méditerranée-centrée visant la mise en place de politiques et le design de réponses coordonnées. En retour, celles-ci pourront aider à atteindre une utilisation efficace et socialement acceptable des ressources investies dans la recherche sur les espèces envahissantes et dans leur gestion.

Abstract in Spanish

Costos económicos de las especies exóticas invasoras en la cuenca mediterránea. Las especies exóticas invasoras (EEI) tienen un impacto negativo en el medio ambiente y perjudican el bienestar humano, lo que a menudo genera costos económicos considerables. La cuenca del Mediterráneo es una región cultural, social y económicamente diversa, que alberga un gran número de especies exóticas invasoras que amenazan la integridad económica y social de múltiples maneras. Este artículo es el primer intento de cuantificar colectivamente los costos económicos reportados de las EEI en la cuenca del Mediterráneo, a través de una variedad de descriptores taxonómicos, temporales y espaciales. Identificamos las correlaciones de los costos causados por los daños de las EEI y los gastos relacionados con su gestión con una serie de variables socioeconómicas clave y determinamos las estructuras de red que vinculan a los países de la cuenca Mediterránea y los grupos taxonómicos invasores. Los costos totales de invasión reportados en la cuenca del Mediterráneo ascendieron a $27.3 mil millones, o $3.6 mil millones cuando solamente se consideraron los costos realizados, los cuales ocurrieron durante las últimas tres décadas. Nuestro conocimiento de los costos de las invasiones en el Mediterráneo se limitó en gran medida a unos pocos países, principalmente de Europa occidental, y a ecosistemas terrestres, a pesar de la presencia conocida de numerosos taxones invasores acuáticos de alto impacto. La gran mayoría de los costos se atribuyeron a daños o pérdidas por invasiones ($25.2 mil millones) y fueron impulsados principalmente por Francia, España y, en menor medida, Italia y Libia, con costos significativamente menores atribuidos a los gastos de gestión ($1.7 mil millones). En general, los costos aumentaron con el tiempo, con costos anuales promedio entre 1990 y 2017 estimados en $975.5 millones. La falta de información de costos en una gran proporción de países mediterráneos, reflejada en el análisis de conectividad espacial y taxonómica y la relación de los costes con las variables socioeconómicas, pone de manifiesto los límites de los datos disponibles y el esfuerzo investigador necesario para mejorar la comprensión colectiva de las diferentes facetas de los costos de las invasiones biológicas. Nuestro análisis de los costes reportados asociados con las invasiones en el Mediterráneo pone de relieve las actuales lagunas de conocimiento y proporciona una línea de base para un enfoque centrado en el Mediterráneo hacia la creación de políticas y el diseño de respuestas coordinadas. A su vez, este estudio podría ayudar a alcanzar resultados socialmente deseables y un uso eficiente de los recursos invertidos en la investigación y el manejo de EEI en la cuenca del Mediterráneo.

Abstract in Italian

Costi economici delle specie aliene invasive nel bacino del Mediterraneo. Le specie aliene invasive (SAI) impattano negativamente l'ambiente e minacciano il benessere umano, spesso con conseguenti costi economici. Il bacino Mediterraneo è una regione culturalmente, socialmente ed economicamente diversa, ospitando molte SAI che minacciano l'integrità economica e sociale in molti modi. Questo articolo è il primo tentativo di quantificare collettivamente i costi economici riportati per le SAI nel bacino Mediterraneo, con un uno spettro di descrittori tassonomici, temporali e spaziali. Identifichiamo i correlati dei costi dai danni delle invasioni e le spese di gestione tra le variabili socioeconomiche chiave, e determiniamo strutture a rete che collegano Paesi e gruppi tassonomici invasivi. I costi totali delle invasioni riportati nel bacino Mediterraneo ammontano a $27,3 miliardi, o $3,6 miliardi se si considerano solo i costi realizzati, e si sono verificati nel corso degli ultimi tre decenni. La nostra comprensione dei costi delle invasioni nel Mediterraneo era ampiamente limitata a pochi Paesi Europei, soprattutto quelli occidentali, e agli ecosistemi terrestri, nonostante la nota presenza di numerosi taxa acquatici invasivi di alto impatto. La grande maggioranza dei costi delle invasioni sono stati attribuiti a danni o perdite ($25,2 miliardi) e sono stati principalmente determinati dalla Francia, dalla Spagna e, in misura minore, dall'Italia e dalla Libia, con costi significativamente minori attribuiti alle spese di gestione ($1,7 miliardi). In generale, i costi delle invasioni sono aumentati nel tempo, con un costo annuale medio tra il 1990 e il 2017 stimato a $975,5 miliardi. La mancanza di informazioni da una larga proporzione di Paesi del Mediterraneo, riflessa nell'analisi di connettività spaziale e tassonomica e nella relazione tra i costi e le variabili socioeconomiche, sottolinea i limiti dei dati disponibili e delle ricerche necessarie per migliorare la conoscenza collettiva dei diversi aspetti dei costi delle invasioni biologiche. La nostra analisi dei costi riportati associate alle invasioni nel Mediterraneo fa luce sulle lacune chiave nella conoscenza e fornisce una base per un approccio Mediterraneo-centrico verso la formulazione di politiche e di risposte coordinate. A sua volta, queste potrebbero aiutare a raggiungere risultati socialmente desiderabili e un uso efficiente delle risorse investite nella ricerca e nella gestione delle specie invasive.

Abstract in Greek

Οικονομικά κόστη εισβολικών ειδών στην λεκάνη της Μεσογείου. Τα εισβολικά είδη επηρεάζουν αρνητικά το περιβάλλον και υποβαθμίζουν την ανθρώπινη ευημερία, κάτι που συχνά καταλήγει σε σημαντικά οικονομικά κόστη. Η λεκάνη της Μεσογείου είναι μια πολιτιστικά, κοινωνικά και οικονομικά ποικιλόμορφη περιοχή που φιλοξενεί πολλά εισβολικά είδη τα οποία απειλούν την οικονομική και κοινωνική συνοχή με διάφορους τρόπους. Η εργασία αυτή είναι μια πρώτη προσπάθεια να ποσοτικοποιήσει συνολικά τα οικονομικά κόστη εισβολικών ειδών που έχουν αναφερθεί για την λεκάνη της Μεσογείου με τη χρήση ενός εύρους ταξινομικών, χρονικών και χωρικών περιγραφέων. Προσδιορίζουμε συσχετίσεις του κόστους από τις ζημιές και διαχείριση των εισβολικών ειδών με βασικές κοινωνικό-οικονομικές μεταβλητές, καθώς επίσης και τις δομές του δικτύου που συνδέουν τις χώρες με τις εισβολικές ταξινομικές ομάδες. Το συνολικά κόστη από εισβολές στην λεκάνη της Μεσογείου εκτιμήθηκαν σε $27,3 δις, ή $3,6 δις λαμβάνοντας υπόψη μόνο τα πραγματικά/υλοποιηθέντα κόστη, και έλαβαν χώρα στη διάρκεια των τριών τελευταίων δεκαετιών. Η γνώση μας για τα κόστη των εισβολικών ειδών στην Μεσόγειο περιορίστηκε σε μεγάλο βαθμό σε λίγες, κυρίως δυτικό-Ευρωπαϊκές χώρες και σε χερσαία οικοσυστήματα, παρά το ότι γνωρίζουμε για την παρουσία πολλών εισβολικών ειδών σε υδάτινα οικοσυστήματα με σημαντικές επιπτώσεις. Η συντριπτική πλειοψηφία του κόστους αποδόθηκε σε ζημιές ή απώλειες από εισβολές ($25,2 δις) και κυρίως από την Γαλλία, Ισπανία και σε μικρότερο βαθμό από την Ιταλία και την Λιβύη, ενώ σημαντικά λιγότερα κόστη αποδόθηκαν στη διαχείριση ($1,7 δις). Συνολικά, τα κόστη των εισβολικών ειδών αυξήθηκαν στην διάρκεια του χρόνου με το μέσο ετήσιο κόστος μεταξύ του 1990 και 2017 να εκτιμάται στα $975,5 εκατομμύρια. Η έλλειψη πληροφορίας από μεγάλη μερίδα Μεσογειακών χωρών, που αντικατοπτρίζεται στην χωρική και ταξινομική ανάλυση συσχέτισης και στην σχέση μεταξύ του κόστους και κοινωνικό-οικονομικών μεταβλητών, αναδεικνύει τους περιορισμούς που θέτουν τα διαθέσιμα δεδομένα και την ανάγκη για έρευνα, για μια καλύτερη συλλογική κατανόηση των διαφορετικών πτυχών του κόστους των βιολογικών εισβολών. Η ανάλυσή μας για τα καταγεγραμμένα κόστη εισβολικών ειδών στη Μεσόγειο φέρνει στο φως σημαντικά κενά γνώσης και προσφέρει την βάση για μια προσέγγιση με επίκεντρο την Μεσόγειο, για τον σχεδιασμό συντονισμένων δράσεων και την δημιουργία πολιτικών. Με τη σειρά τους αυτές μπορούν να βοηθήσουν στην επίτευξη επιθυμητών αποτελεσμάτων και αποδοτικής χρήσης των πόρων που επενδύονται στην έρευνα και διαχείριση εισβολικών ειδών.

Abstract in German

Kosten invasive Arten Kosten invasiver gebietsfremder Arten im Mittelmeerraum. Invasive gebietsfremde Arten wirken sich negativ auf die Umwelt aus und beeinträchtigen das Wohlbefinden des Menschen, was häufig zu erheblichen wirtschaftlichen Kosten führt. Das Mittelmeerbecken ist eine kulturell, sozial und wirtschaftlich vielfältige Region mit vielen gebietsfremden Arten, die die wirtschaftliche und gesellschaftliche Integrität auf vielfältige Weise gefährden. Dieses Arbeit ist der erste Versuch, die gemeldeten wirtschaftlichen Kosten dieser Arten im Mittelmeerraum über eine Reihe taxonomischer, zeitlicher und räumlicher Deskriptoren hinweg kollektiv zu quantifizieren. Wir identifizieren Korrelationen von Kosten biologischer Invasionen und Verwaltungsausgaben unter den wichtigsten sozioökonomischen Variablen und bestimmen Netzwerkstrukturen, die Länder und invasive taxonomische Gruppen verbinden. Die gesamten gemeldeten Kosten im Mittelmeerraum beliefen sich auf $27,3 Mrd. oder $3,6 Mrd., wenn nur realisierte Kosten berücksichtigt wurden, und wurden in den letzten drei Jahrzehnten festgestellt. Unser Verständnis der Kosten biologischer Invasionen im Mittelmeerraum war trotz des bekannten Vorhandenseins zahlreicher hoch-invasiver aquatischer invasiver Taxa weitgehend auf einige wenige, hauptsächlich westeuropäische Länder und terrestrische Ökosysteme beschränkt. Die überwiegende Mehrheit der Kosten entfiel auf Schäden oder Verluste an Ressourcen durch Invasionen ($25,2 Mrd.) und wurde hauptsächlich von Frankreich, Spanien und in geringerem Maße von Italien und Libyen getragen, wobei die Verwaltungsausgaben ($1,7 Mrd.) erheblich geringer waren. Insgesamt stiegen diese Kosten im Laufe der Zeit, wobei die durchschnittlichen jährlichen Kosten zwischen 1990 und 2017 auf $975,5 Mio. geschätzt wurden. Der Mangel an Informationen aus einem großen Teil der Mittelmeerländer, der sich in der räumlichen und taxonomischen Konnektivitätsanalyse und dem Verhältnis der Kosten zu sozioökonomischen Variablen widerspiegelt, zeigt die Grenzen der verfügbaren Daten und den Forschungsaufwand auf, der erforderlich ist, um ein kollektives Verständnis der verschiedenen Facetten der Kosten für biologische Invasionen zu verbessern. Unsere Analyse der gemeldeten Kosten im Zusammenhang mit Invasionen im Mittelmeerraum beleuchtet wichtige Wissenslücken und bietet eine Grundlage für einen auf den Mittelmeerraum ausgerichteten Ansatz zur Erstellung von Strategien und zur Gestaltung koordinierter Reaktionen. Dies könnte wiederum dazu beitragen, sozial wünschenswerte Ergebnisse zu erzielen und die Ressourcen die in die Forschung an invasiven Arten und deren Bewirtschaftung investiert werden, effizient zu nutzen.

Abstract in Croatian

Ekonomski troškovi invazivnih stranih vrsta u mediteranskom bazenu. Invazivne strane vrste negativno utječu na okoliš i sabotiraju dobrobit ljudi, što često rezultira značajnim ekonomskim troškovima. Mediteranski bazen je kulturno, socijalno i ekonomski raznolika regija u kojoj se nalaze mnoge invazivne strane vrste koje na više načina ugrožavaju njezin ekonomski i društveni integritet. Ovaj rad je prvi pokušaj kolektivnog kvantificiranja prijavljenih ekonomskih troškova invazivnih stranih vrsta u mediteranskom bazenu, kroz niz taksonomskih, vremenskih i prostornih deskriptori. Utvrdili smo korelati troškova od štete prouzorčene invazivnim stranim vrstama i izdataka za upravljanje među ključnih socioekonomskih varijabli, i utvrdili mrežne strukture koje povezuju države i invazivne taksonomske skupine. Ukupni prijavljeni troškovi invazije u mediteranskom bazenu iznosili su 27,3 milijarde dolara, odnosno 3,6 milijardi dolara kada su se uzimali u obzir samo ostvareni troškovi, a koji su zabilježeni u posljednja tri desetljeća. Naše razumijevanje troškova invazije na Sredozemlju uglavnom je bilo ograničeno na nekoliko, prvenstveno zapadnoeuropskih zemalja i kopnene ekosustave, unatoč poznatoj prisutnosti brojnih vodenih invazivnih svojti s prepoznatim velikim utjecajem. Velika većina troškova pripisana je šteti ili gubicima od strane invazija (25,2 milijarde dolara), uglavnom predvođenim od strane Francuske i Španjolske te u manjoj mjeri Italije i Libije, uz znatno manje troškova pripisanih izdacima za upravljanje (1,7 milijardi dolara). Sveukupni troškovi invazije s vremenom su se povećavali, a prosječni godišnji troškovi između 1990. i 2017. procjenjuju se na 975,5 milijuna dolara. Nedostatak informacija iz velikog dijela mediteranskih zemalja, koji se ogleda u analizi prostorne i taksonomske povezanosti te odnosu troškova sa socioekonomskim varijablama, ukazuje na ograničenost dostupnih podataka i istraživačkog napora potrebnim za poboljšanje kolektivnog razumijevanja različitih aspekata troškova bioloških invazija. Naša analiza prijavljenih troškova povezanih s invazijama na Mediteranu ukazuje na ključne nedostatke u znanju i daje osnovu za mediteranski usmjeren pristup izgradnji politika i osmišljavanju koordiniranih odgovora. Takav pristup bi zauzvrat mogao pomoći u postizanju društveno poželjnih rezultata i učinkovitom korištenju resursa uloženih u istraživanje i upravljanje invazivnim stranim vrstama.

Abstract in Arabic

التكاليف الاقتصادية للأنواع الغريبة الغازية في حوض البحر الأبيض المتوسط.

تؤثر "الأنواع الغريبة الغازية" سلبًا على البيئة ورفاهية الإنسان، وغالبًا ما تؤدي إلى تكاليف اقتصادية مهمة. من جهتها، تعتبر منطقة حوض البحر الأبيض المتوسط مجالا متنوعا ثقافياً واجتماعياً واقتصادياً،

مما جعل منها موطنا للعديد من "الأنواع الغريبة الغازية" التي تهدد سلامتها الاقتصادية والاجتماعية بطرق شتى. تشكل الدراسة التي بين أيدينا محاولة أولية لتقدير جماعي للتكاليف الاقتصادية المرتبطة بـ "الأنواع الغريبة الغازية" في حوض البحر الأبيض المتوسط، وذلك من خلال واصفات تصنيفية وزمنية ومكانية مختلفة. كما نحدد ارتباطات التكاليف الاقتصادية التي سببها أضرار "الأنواع الغريبة الغازية" وتكاليف تسييرها مع المتغيرات الاجتماعية والاقتصادية الرئيسية، ونحدد كذلك بينة الشبكات التي تربط البلدان والمجموعات التصنيفية الغازية المختلفة. وحسب هذه الدراسة، بلغ إجمالي تكاليف "الأنواع الغريبة الغازية" في حوض البحر الأبيض المتوسط 27.3 مليار دولار، و3.6 مليار دولار إذا تم أخذ التكاليف المحققة فقط بعين الاعتبار على مدى العقود الثلاثة الماضية.

إن فهمنا لتكلفة الغزو البيولوجي في حوض البحر الأبيض المتوسط اقتصر إلى حد كبير على البيانات المتعلقة بعدد قليل من البلدان، خاصة من أوروبا الغربية، وبعض النظم الإيكولوجية القارية، على الرغم من الوجود المؤكد للعديد من الكائنات المائية الغازية ذات التأثير الكبير. إن الغالبية العظمى من التكاليف المبلغ عنها تتعلق بالأضرار أو الخسائر (25.2 مليار دولار) وتهم بشكل رئيسي فرنسا وإسبانيا وبدرجة أقل إيطاليا وليبيا، مع تكاليف أقل بكثير تخص نفقات التسيير الاداري (1.7 مليار دولار). بشكل عام، تزداد التكاليف المرتبطة بالغزو البيولوجي بمرور الوقت وذلك بمتوسط تكلفة سنوية تقدر بـ 975.5 مليون دولار بين عامي 1990 و2017. إن نقص المعلومات في جزء كبير من دول البحر الأبيض المتوسط، الشيء الذي ينعكس من خلال تحليل الربط المكاني والتصنيفي والعلاقات بين التكاليف والمتغيرات الاجتماعية والاقتصادية، يسلط الضوء على حدود البيانات المتاحة، وكذلك جهود البحث الضرورية من أجل فهم أكثر شمولاً للجوانب المختلفة لتكاليف الغزو البيولوجي.

لقد سلط تحليلنا للتكاليف المرتبطة بمنطقة البحر الأبيض المتوسط الضوء على الفجوات المعرفية الرئيسية ووضع الأسس لمقاربة "متوسطية" تهدف إلى وضع سياسات ملائمة وتصاميم تدخلات متناسقة، مما يمكن أن يؤمن استخدام فعال ومقبول اجتماعيًا للموارد المستثمرة في الأبحاث حول الأنواع الغازية وكيفية إدارتها.

Keywords

geographic connectivity, InvaCost, monetary impacts, non-indigenous species, resource losses, socioeconomic dimensions

Introduction

The ongoing spread of invasive alien species (IAS) is a key driver of biodiversity and ecosystem degradation that continues to adversely affect human and social well-being at local, national and global scales (Pyšek et al. 2020; Secretariat of the Convention on Biological Diversity 2020). With increasingly globalised trade and transport networks, there is no sign of abatement in invasion rates worldwide (Seebens et al. 2017), owing to high propagule and colonisation pressures sustained from increasingly interconnected biogeographic regions (Seebens et al. 2018). Despite the relatively well-characterised ecological impacts of several IAS among ecosystem types and geographic regions (Dick et al. 2017; Crystal-Ornelas and Lockwood 2020), a paucity in estimation of economic costs, along with a poor understanding of socioeconomic impacts, limits monetary investments in management (Courchamp et al. 2017). In turn, this also hampers rationale for timely management of IAS at national or regional scales. That is despite the well-known and accepted fact that investments in prevention are far more economically efficient than longer-term control protocols (Leung et al. 2002).

Large-scale efforts to quantify invasion costs have primarily focused on a single country (e.g. the U.S.; Pimentel et al. 2000, 2005 or Australia; Hoffmann and Broadhurst 2016), taxonomic group (e.g., insects; Bradshaw et al. 2016) or economic sector (e.g., agriculture; Paini et al. 2016). Whilst these studies have promoted attention towards burgeoning economic costs of invasions, a lack of understanding of these costs at smaller spatial scales, across countries, species or sectors, presently impairs regional-scale interventions, and particularly for regions that are interconnected biogeographically. Moreover, extrapolations in previous estimations of IAS costs have prompted debate on their relevance and reliability (Cuthbert et al. 2020). For interconnected countries with borders lacking natural or anthropogenic barriers for species' movement, a unified approach to IAS management may be most efficient: investments from one country could offset future costs in another, given the ease at which invaders can spread. However, the factors driving invasion success are also often highly context-dependent, and can vary depending on many parameters, such as taxa, introduction pathways, spread mechanisms, characteristics and vulnerability of recipient ecosystems (Novoa et al. 2020). Factors that mediate the economic impacts of IAS have yet to be considered in monetary quantifications to better inform decision-making and management.

The Mediterranean basin is a major biogeographic unit, whether defined by its shared climate or marine resources, its distinct biome (Dinerstein et al. 2017), or as one of the world's most diverse biodiversity hotspots (CEPF 2020). Spanning three continents, countries within the Mediterranean basin are highly connected through terrestrial and aquatic routes and often share similar pathways and ecosystem characteristics (e.g. Katsanevakis et al. 2013). This interconnectedness calls for coordinated responses and management actions (Traveset et al. 2008; Tempesti et al. 2020). For example, in the Mediterranean Sea, the opening of the Suez Canal in 1869 facilitated the widespread introduction of numerous alien marine taxa. The speed of invasion and range of Lessepsian IAS have been increasing ever since, owing to a number of factors such as currents, climate change, removal of high and low-salinity barriers, overexploitation of native fish, etc (Lasram et al. 2008, 2010; Raitsos et al. 2010; Edelist et al. 2011, 2013; Vergés et al. 2014). Indeed, for marine taxa, recorded species introductions into the Mediterranean Sea significantly exceed the numbers of species introductions in other European seas, with the eastern Mediterranean possibly the most heavily impacted (Edelist et al. 2013; Galil et al. 2014).

Aside from the marine realm, terrestrial and freshwater ecosystems also share similar invasion patterns across countries of the Mediterranean basin, such as similar species traits of successful invaders or habitat vulnerability (e.g., Arianoutsou et al. 2013), and deserve attention given the diversity and impacts of invasions there (Clavero et al. 2010).

The millenary history of trade and travel, and multiple other anthropogenic disturbances in the region, has led to a biogeographically diverse set of invaders (Arianoutsou et al. 2013). These IAS have strong socioeconomic and geographical imprints which are particularly high in both the mainland and islands of the basin (Groves and di Castri 1991; Vilà and Pujadas 2001; Pyšek and Richardson 2010). Notably, the Mediterranean-type climate imposes stringent regulatory effects over the invasion potential of many species, hindering the establishment of species requiring colder or wetter conditions, and leading to the development of circum-Mediterranean or quasi-circum-Mediterranean ranges for well-adapted ones. Among the latter are many highly damaging species, such as the Asian tiger mosquito (*Aedes albopictus*) (Gasperi et al. 2012), the red swamp crayfish (*Procambarus clarkii*) (Gherardi and Acquistapace 2007), or the palm moth (*Paysandisia archon*) (Muñoz-Adalia and Colinas 2020). Despite efforts to understand economic dimensions for some of the most prominent IAS in this region along with their impact on human well-being, integrated analyses encompassing impacts and costs at the scale of the Mediterranean basin are still largely missing.

Recognising this gap and the often-expected connectivity of invasions across ecosystems in the region, a useful approach for prioritising the allocation of resources aimed at IAS management is to identify which species pose the greatest economic risks and build collaborative strategies for their management. Additionally, lessons gained from the successes and failures of managing a species in one country can guide managers in others. Indeed, regional approaches are recognised to be essential in sustainable and efficient prevention against IAS (Faulkner et al. 2020). Identifying in which habitat types costs are reported, which socioeconomic sectors are affected, and how costs accrue over time further informs targeted management interventions. However, at present, economic impacts attributable to IAS are not centrally examined, categorised or systematically reported within the Mediterranean basin, impeding effective ecosystem management responses, and reducing efficiencies of investments. The Mediterranean region is also a cradle of civilisations that encompasses a wide range of environmental, socioeconomic and cultural elements. Well-being, social and economic development are highly dependent on natural resources and a vulnerable environment that, similar to the rest of the world, is at risk from biological invasions.

The present study thus builds on the InvaCost initiative (Diagne et al. 2020a, c) to present the first large scale analysis of invasion costs in the Mediterranean basin. We examine how costs in this region are distributed over time and across countries, habitat types, taxonomic groups and economic sectors. We also estimate the influence of socioeconomic drivers (e.g., trade, tourism, research) on the reporting of IAS costs. Moreover, countries with the highest economic costs are identified, as well as similarities and differences in their cost characteristics and network structures that indicate countries impacted by similar taxa.

Materials and methods

Data collection and extraction

For the purposes of quantifying the costs associated with IAS in the Mediterranean basin, we combined information from databases linked to the InvaCost project, the first global effort to systematically compile and synthesise the monetary costs of invasive species (Diagne et al. 2020a) (Fig. 1).

InvaCost is a living database, meant to be updated on an ongoing basis by authors and future users (Diagne et al. 2020a). We used the cost entries available at

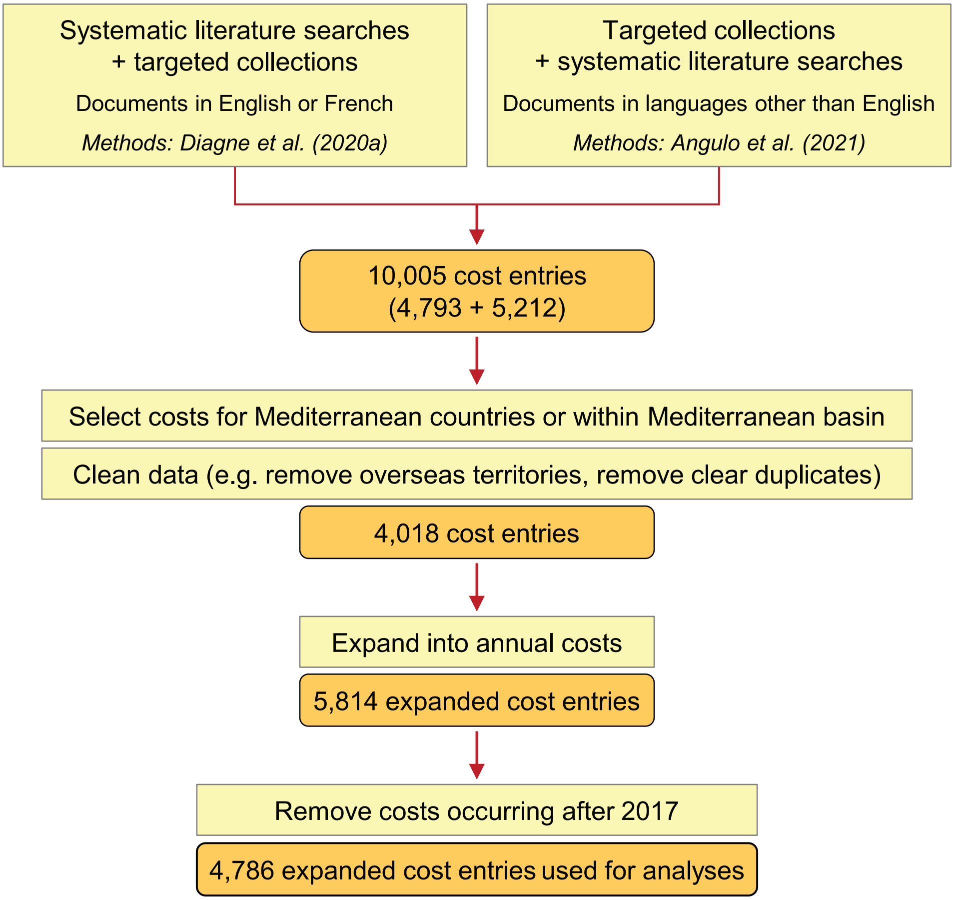

Figure 1. Process of compiling data sources for a database of invasion costs for the Mediterranean.

the time of writing (November, 2020; 4,793 entries, Ballesteros-Mejia et al. 2020; Diagne et al. 2020b), which were the result of both systematic and targeted searches, conducted through standardised English-language search strings in Web of Science, Google Scholar and Google. Targeted searches allowed opportunistic addition of supplementary cost entries, in both English and French. These searches were conducted in a number of different ways which span from examining the content of relevant web pages to contacting national and international experts for obtaining published or unpublished documents. Further methodological details regarding the search strategies, search terms used, material included, the screening process and the inclusion criteria, can be found in Diagne et al. (2020a).

These data were further complemented with 5,212 cost entries extracted from literature in 15 languages other than English (Angulo et al. 2020, 2021). These cost estimates were collated through a) a standardised literature search that used the InvaCost protocol described in Diagne et al. (2020a) and b) a more targeted opportunistic search through national databases, web pages of national institutions, NGOs and other organisations, as well as through contacts with regional national experts (Angulo et al. 2021).

We filtered the cost entries compiled (n = 10,005) to select only costs of IAS in the 26 countries having a coastline on the Mediterranean Sea (or countries within these countries, i.e. Andorra, San Marino, Vatican City), or costs in the Mediterranean Sea. Costs of IAS explicitly occurring in overseas territories of these countries (e.g. French Guiana) were excluded from our analyses.

Prior to analyses, all cost entries in our database were expanded so that each entry was annualised (i.e. corresponding to a single year), given that original cost estimates may have corresponded to either a cost realised over a single year, a period of less than a year, or a cost reoccurring over a series of years. For the purpose of expanding these original cost entries, we used the *expandYearlyCosts* function of the 'invacost' R package (Leroy et al. 2020), based on the difference between the probable starting and ending years of each cost entry presented in the database. Note that this process removed any cost entries (including one for Israel, Morocco and Tunisia) that occurred over an unspecified time period following the procedure described in Diagne et al. (2020a). Our analysis is therefore based on the 4,786 "expanded" cost entries resulting from this process and occurring up until 2017 (the last complete year included in all systematic searches). These mostly originated from the following 15 Mediterranean countries: Albania, Bosnia and Herzegovina, Croatia, Cyprus, Egypt, France, Greece, Israel, Italy, Libya, Malta, Montenegro, Slovenia, Spain and Turkey.

All cost estimates were standardised to 2017 equivalent US dollars (US$) using the market exchange rate (World Bank), and accounting for inflation (Consumer Price Index of the year the cost was estimated for in each study) (Diagne et al. 2020a, b). The dataset used for the analysis is provided as a Suppl. material (Suppl. material 1: Mediterranean database).

Cost descriptors, temporal cost dynamics and correlation with socioeconomic variables

The extracted cost data were classified according to temporal, spatial, and taxonomic descriptors (see Diagne et al. 2020a for more details): (*i*) Publication year: referring to the year in which the study and/or costs were published; (*ii*) Method reliability: illustrating the perceived reliability of the type of publication and methodological approach used for cost estimation; estimates obtained from officially pre-assessed materials (peer-reviewed articles and official reports), or from grey material but with documented, repeatable and traceable methods, were designated as "High" reliability. All other estimates were designated as having a "Low" reliability; (*iii*) Implementation: referring to whether the cost estimate was actually realised or empirically incurred due to an invasive species within the invaded habitat ("Observed"), or whether it was not incurred but rather expected and/or predicted over time within or beyond its actual distribution area ("Potential"); (*iv*) Country: describing the origin country of the listed cost; (*v*) Taxonomy, referring to the taxonomic grouping of the cost; (*vi*) Habitat of species: corresponding to where the species occurs (i.e. "Aquatic", "Semi-aquatic", "Terrestrial" or "Diverse/Unspecified") (Suppl. material 2: Table S1a); (*vii*) Type of cost: grouping of costs according to the categories: (a) "Damage" referring to damages or losses incurred due to the invasion (i.e., costs for damage repair, resource losses, medical care), (b) "Management" comprising expenditure such as control, monitoring, prevention, eradication, (c) "Mixed" including a mix of categories (a) and (b) (cases where reported costs were undistinguishable damage and management costs); (*viii*) Impacted sector: the activity, societal or market sector that was impacted by the cost (Suppl. material 2: Table S1b); note that individual cost entries not allocated to a single sector were classified as "Mixed" in the "Impacted sector" column. Costs that were incurred from multiple or unspecified taxa, or countries, were categorised as "Diverse/Unspecified".

To assess temporal trends of invasion costs in the Mediterranean over time, we considered 5-year means since 1990 (the first year with invasion costs in our database). We examined costs as a function of the "Impact year", which reflects the time at which the invasion cost likely occurred based on probable starting and ending years (Leroy et al. 2020). This allowed for an estimation of annual average costs over the entire reported period.

In addition to the data included in our cost database, we collected complementary elements from the Centre for Agriculture and Bioscience International (CABI 2020) to obtain information on the geographic origin of each invasive species causing observed damage costs in the studied area, including their presence in each country, pathways of introduction, impacts and uses (if any). To improve our analysis and interpretation of invasion costs, we also extracted information on several country indicators from the World Bank (2020) (Suppl. material 2: Table S2) to further assess whether costs in each country could be correlated to key socioeconomic variables. To that aim, the ggcorr function of the 'GGally' package in R 4.0.0 was used. We found significant correlations between some of these indicators (Suppl. material 2: Fig. S1). However, since we aimed to study the relation of each indicator with the observed costs independently, we estimated Spearman rank correlations between each extracted indicator and country-level expenditures and damage costs using the 'ggpubr' package in R 4.0.0.

Network analysis of costs

Spatial and taxonomic aspects of Mediterranean invasion costs were concurrently examined using a bipartite network of two types of nodes: (1) countries and (2) taxonomic groups (excluding studies reporting costs on diverse taxonomic groups, or in other words costs for species belonging to different taxonomic groups that were reported together). For taxa, broad groupings were created from combinations of habitat and animal taxonomic group (e.g. "terrestrial mammal", "aquatic arthropod") or plant guild e.g. ("terrestrial forb" or "aquatic floating") to facilitate broad-scale taxonomic linking among countries. The taxonomic groupings used can be found in Suppl. material 1: Mediterranean database. In brief, links were produced among nodes where a group had a cost in a given country, and the link thicknesses and node sizes were attributed to respective cost totals. As such, the size of the nodes, and thickness of the links, correspond to the magnitude of cumulative economic costs incurred for the 1990–2017 period. The network was illustrated in Gephi 0.9.2 using the ForceaAtlas2 algorithm (Bastian et al. 2009). We applied the Map Equation community-detection algorithm (version 0.19.12, www.mapequation.org; Rosvall and Bergstrom 2008, Rosvall et al. 2009) to examine clusters of countries which exhibited similar combinations of invasion costs. Clusters within this network reflect groups of nodes sharing costs (e.g., an invasive group that impacted multiple countries, or multiple groups that impacted altogether one to several countries). The network analysis was performed using the 'biogeonetworks' R package (Leroy et al. 2019; Leroy 2020), and based on the Map Equation algorithm optimised for a two-level partition of the network with 1,000 trials.

Results

Overview of invasion costs

Between 1990 and 2017, the total cost of IAS in the Mediterranean basin was estimated at \$27.31 billion (in 2017 US\$ values). The majority of the costs for the Mediterranean in our database were published after the mid-2000s (orange line, Fig. 2). The number of costs occurring per year exhibited a general increase over time, especially after 2006 (red line, Fig. 2)

The vast majority (87%) of total costs for the region were derived from expectations or predictions (Potential, \$23.73 billion), rather than empirical observations (Observed, \$3.59 billion). However, these potential costs correspond to a relatively small number of database entries (n = 279) with the majority of entries corresponding to empirical observations (n = 4,507, Fig. 3). Additionally, close to 98% of the cost entries for the Mediterranean basin (n = 4,672), corresponding to \$25.89 billion, were deemed highly reliable based on the method of estimation (see also Suppl. material 2: Fig. S2, for method reliability in observed costs). Most of the costs (69%, \$18.81 billion) originated from English-language references.

Spatial distribution of costs

Between 1990 and 2017, the majority of Mediterranean invasion costs were recorded in the western part of Europe: Spain (\$12.47 billion, n = 3,367), France (\$10.85 billion, n = 1,237) and Italy (\$680.76 million, n = 107). Costs were also high in Libya (\$593.04 billion; n = 8). The sum of costs in the remaining 11 countries for which data were available (i.e. Albania, Bosnia and Herzegovina, Croatia, Cyprus, Egypt, Greece, Israel, Malta, Montenegro, Slovenia and Turkey) were found to be relatively low, corroborating low numbers of cost entries (Fig. 4).

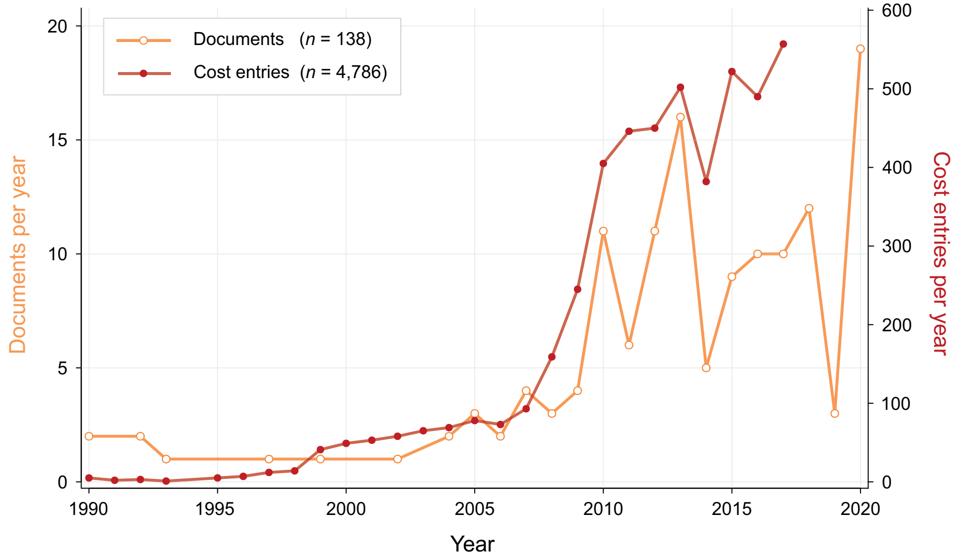

Figure 2. Temporal trends in numbers of documents reporting costs (left y-axis) and cost entries (right y-axis) concerning invasive alien species within the Mediterranean basin published during 1990–2020. Note the different scales for the two vertical axes. All data shown here reflect costs occurring in 2017 or earlier, as used in our analysis (note that some of these costs were published after 2017).

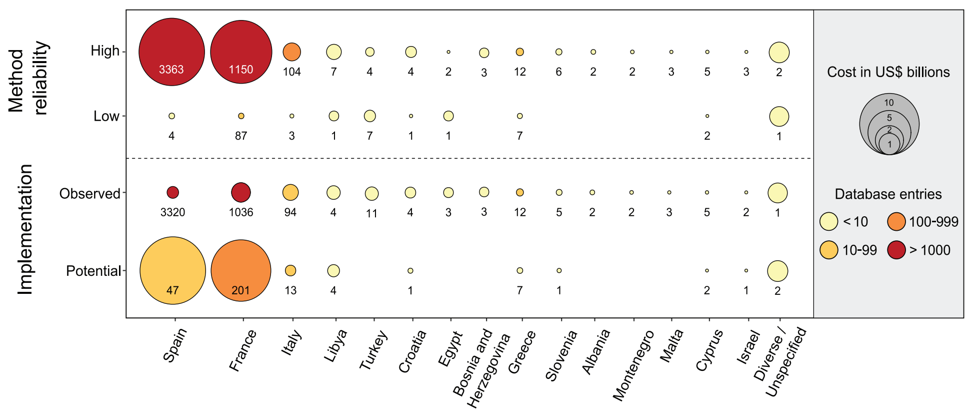

Figure 3. Balloon plot indicating invasion costs (total) and cost entry numbers for Mediterranean countries available, according to implementation type (Observed/Potential) and method reliability (High/Low). The numbers inside or adjacent to each balloon correspond to the sample size (also indicated by shading).

When "Observed" costs were considered, France ($780.71 billion, *n* = 1,036), Italy ($502.9 million, *n* = 94), and Libya ($339.77 million, *n* = 4) were the top three countries, with Turkey ($325.84 million, *n* = 11) ranking fourth and Spain ($234.48 million, *n* = 3,320) fifth. Our dataset contained no costs for the following 11 countries: Algeria, Andorra, Gibraltar, Lebanon, Monaco, Morocco, Palestine, San Marino, Syria, Tunisia and Vatican City.

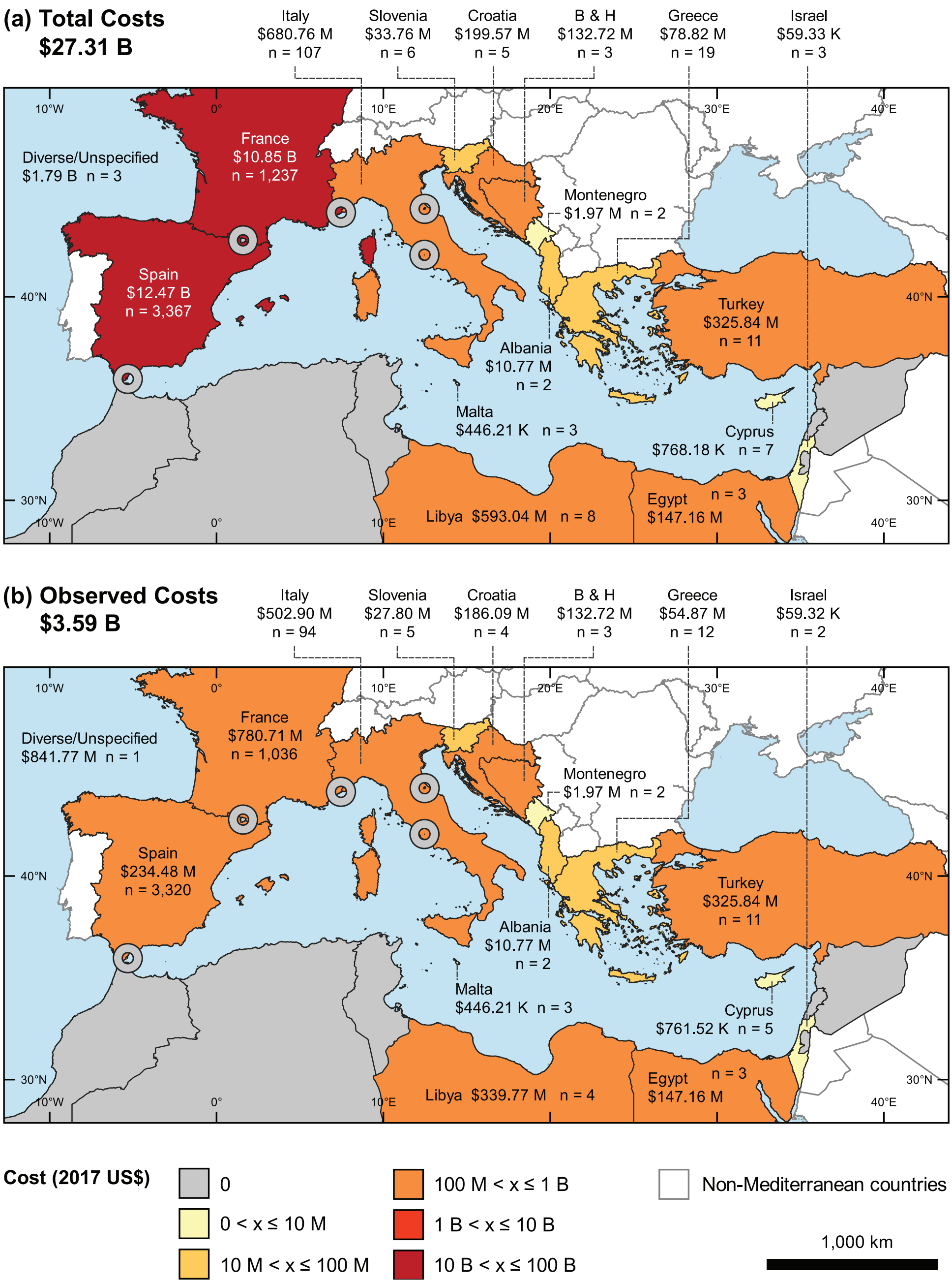

Figure 4. Reported costs of IAS in countries of the Mediterranean basin over the period 1990–2017. Subplots display (**a**) total costs (observed and potential costs), and (**b**) observed costs only. *n* = number of cost entries in expanded InvaCost database, B: Billions, M: Millions, K: Thousands. Circles highlight small-sized countries (Andorra, Gibraltar, Monaco, San Marino, Vatican City, all with no recorded cost). National borders are based on data from https://gadm.org/data.html and are for illustration purposes only. Cyprus is represented as a single geographical unit; all costs were from the Greek part. Map Projection: World Mercator.

Distribution of costs across taxonomic groups

Overall, close to two thirds of the costs ($17.76 billion) were attributed to animals, and one third ($9.54 billion) to plants, although the number of entries was much smaller for animals (n = 1,140 entries) than for plants (n = 3,516 entries). When considering "Observed" costs only, invasions from animals ($1.81 billion, n = 998 entries) were found to be slightly more costly than those from plants ($1.76 billion, n = 3,399 entries).

The vast majority of costs were caused by invertebrates, driven predominantly by the secernentean nematodes ($14.08 billion, 52% of total costs, n = 110 entries) and insects ($3.55 billion, 13% of total costs, n = 143 entries). Vertebrates accounted for <1% of total costs ($74.01 million, n = 563 entries), with mammals accounting for 88% of vertebrate costs ($65.07 million, n = 272 entries). Plant costs were driven primarily by the flowering plants Magnoliopsida ($9.35 billion, 34% of total costs). When observed costs were considered solely, Magnoliopsida was the costliest class of species, with total reported costs of $1.59 billion ($n$ = 2,049 entries), followed by insects, with $1.74 billion ($n$ = 128 entries) (see also Suppl. material 2: Table S3).

The database for the Mediterranean contains costs for 218 species and 187 genera (considering only costs attributable to individual species or genera). The pine wood nematode *Bursaphelenchus xylophilus*, the only species within the class of Secernentea, was by far the costliest invasive species across the Mediterranean basin, with total costs peaking at $14.08 billion (Suppl. material 2: Table S3). The New World screwworm *Cochliomyia hominivorax* and the common ragweed *Ambrosia artemisiifolia* followed in the list of the top three most costly species, with total costs of $1.54 and $1.39 billion, respectively (Suppl. material 2: Table S4).

When accounting for "Observed" costs only, the common ragweed *Ambrosia artemisiifolia* was the costliest IAS ($1.39 billion), followed by the olive fruit fly *Bactrocera oleae* with $0.84 billion, the New World screwworm *Cochliomyia hominivorax* with close to $0.34 billion and the tomato leafminer *Tuta absoluta* with $0.22 billion.

Spatial and taxonomic connectivity of costs

In examining spatial and taxonomic group connectivity across the Mediterranean basin, six clusters identified marked patterns of invasion costs (Fig. 5).

Two major clusters emerged in the Mediterranean basin. First, France, Italy, Greece, as well as Turkey and several Balkan countries constituted the largest cluster. All countries in this cluster were affected by terrestrial forbs; this cluster was also characterized by multiple groups of invaders affecting one to a few countries (notably, semi-aquatic arthropods). The second major cluster was composed of Spain and the highly diverse array of invasive groups impacting this country. The remaining clusters were composed of one to two countries economically impacted by a specific group of organisms: Libya and Egypt by terrestrial arthropods, Malta by terrestrial mammals, Cyprus by fishes and Israel by cnidarians. Nonetheless, despite these marked areas of interrelatedness, there were many inter-cluster linkages which indicate that most clusters are impacted

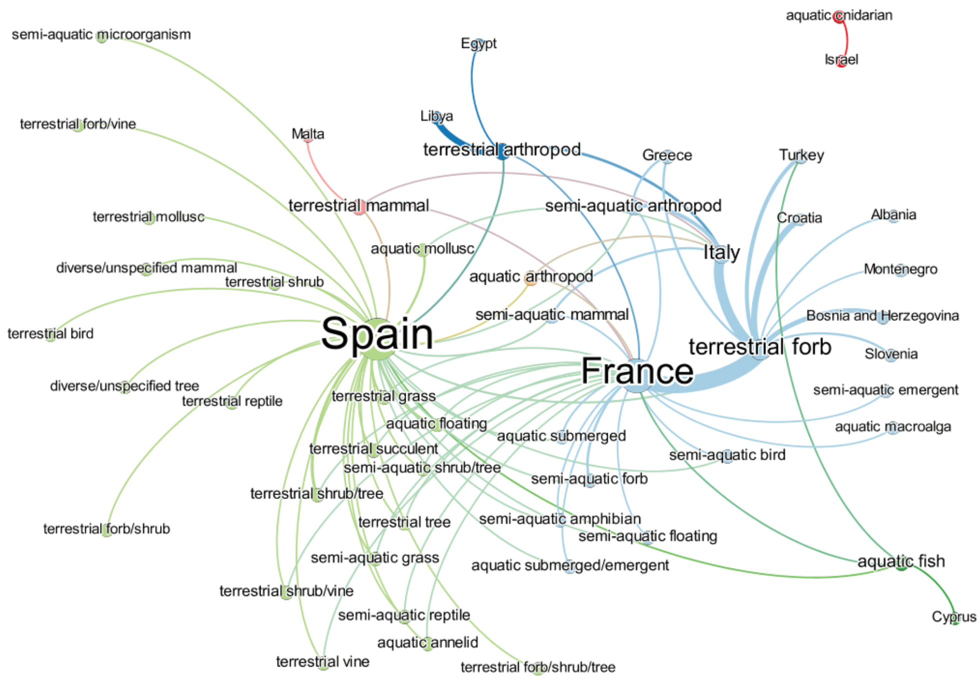

Figure 5. Network of observed invasive alien species costs per country in the Mediterranean. This bipartite network is composed of both species groups and country nodes. Links indicate the cumulative costs of species in countries over 1990–2017. Node size and link thickness corresponds to the cumulative costs. For species nodes, node size represents the total cost they had over all countries. For country nodes, the node size represents the total cost of all species in that country, so large country nodes imply that those countries had large invasion costs.

economically by several taxonomic groups. Note, for example, the numerous groups reported to impact both France and Spain. Overall, a relative lack of reported invasion costs for other Mediterranean countries negated their prominence in the network, indicating a disparity in cost reporting in the region.

Distribution of costs across habitats, cost types and sectors impacted

Considering both "Total" and "Observed" costs, terrestrial species accounted for the vast majority of both total ($19.09 billion, 70%) and observed costs ($3.2 billion, 89%) (Fig. 6a, b). Costs characterised as purely "Aquatic" were estimated at $7.9 billion (29% of all costs) and considering only observed costs at $0.12 billion (3.2% of all costs) (Fig. 6a, b). In both cases, "Semi-aquatic" species contributions were relatively minor (Total costs: $0.24 billion; Observed costs: $0.20 billion). "Diverse/unspecified" costs were $80.92 million and $75.79 million, respectively. Costs from marine taxa comprised only a minor part ($4.24 million, n = 18) of the total aquatic cost ($7.9 billion).

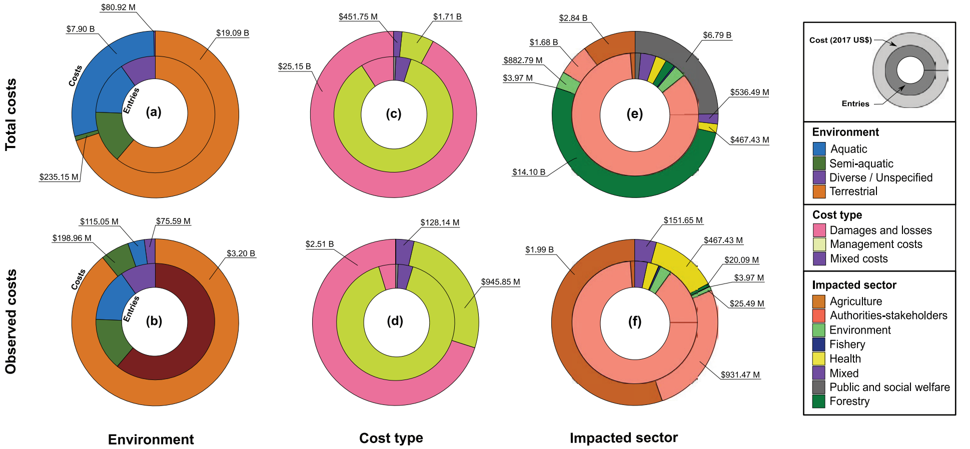

Figure 6. Invasion costs (outer circle) and cost entries (inner circle) in the Mediterranean basin by Environment (left), Type of cost (middle) and Impacted sector (right), considering all costs (upper) and observed costs alone (bottom).

The vast majority of costs associated with biological invasions in the Mediterranean basin were due to damages or losses (92.1% of total costs, $25.15 billion), followed by much lower management costs (6.3% of total costs, $1.71 billion) (Fig. 6c). The majority of damage costs were reported in Spain and France, and were largely due to the pine wood nematode invasion. When only observed costs were considered, damage costs again dominated (60% of observed costs, $2.51 billion), but to a lesser extent compared to total costs (Fig. 6d). France incurred the highest damage costs ($621.18 million observed) and Italy the second highest ($400.26 million observed). Notably, more than half of the observed damage costs were attributed to the common ragweed (55%, $1.39 billion).

The forestry industry was the most severely affected overall, with approximately $14.1 billion ($n$ = 114 entries) in total costs (Fig. 6c). The high costs attributed to forestry in the Mediterranean basin are primarily due to the pine wood nematode invasion in Spain and France, and the predictions described earlier. Costs to "Public and social welfare" ($6.79 billion, n = 68 entries) followed by "Agriculture" ($2.84 billion, n = 60 entries) and "Authorities-Stakeholders" ($1.68 billion, n = 4,059 entries) were found to be the next highest among all other sectors. Costs that could not be assigned to a single sector (i.e., "Mixed") were lower than costs incurred under the category "Environment" ($536.49 million, n = 186 and $882.79 million, n = 145 entries for "Mixed" and "Environment" respectively). The least impacted sectors according to data records were "Health" ($467.43 million, n = 134 entries) and "Fishery" ($3.97 million, n = 20) owing to the very low number of cost entries (20 in total) (Fig. 6e).

When "Observed" costs only were considered, "Agriculture" ($1.99 billion, n = 51 entries) came out as the most impacted sector, followed by "Authorities-Stakeholders" ($931.47 million, n = 4,018 entries), "Health" costs ($467.43 million, n = 134 entries), and costs to “Mixed” sectors ($151.65 million, n = 148 entries) then “Environment” ($25.49 million, n = 132 entries) and “Forestry” ($20.09 million, n = 4) (Fig. 6c). Costs to the “Fishery” sector were found, again, to have the lowest cost value ($3.97 million, n = 20 entries), while there were no observed costs for “Public and social welfare”, despite high total costs for that sector. This is because all relevant costs were estimates based on models and/or theoretical assumptions such as for example scenarios under which the IAS under consideration were to spread beyond their current range.

A more detailed breakdown of costs per sector in each country is available in Suppl. material 2: Fig. S3.

Correlations between costs and key socioeconomic variables

For observed cost entries, significant positive correlations were identified between both damages and management costs and research effort (reflected through expenditure in R&D). There were also positive strong correlations between a) observed damage-loss costs and the size of forest areas, GDP, international trade (reflected through container port traffic), and research effort (reflected also through number of journal publications, beyond just expenditure in R&D) and b) observed management costs and international trade (reflected through imports of goods and services) (Table 1).

Temporal trends of costs

The average annual cost throughout the entire period of 1990–2017 was estimated at $975.5 million, exhibiting an initial decrease throughout the 1990s, followed by a sharp increase in the early 2000s, and a further substantial increase afterwards (Fig. 7). Damages and losses comprised most of the average annual costs throughout this period, with management costs comprising less than 6% of all the costs. The average

Table 1. Relationships of observed “Damage” and “Management” costs of IAS in Mediterranean countries with country-specific indicators derived from the World Bank (2020). Details on these country-specific indicators are presented in Suppl. material 2: Table S2. Statistics shown are Spearman correlation coefficients and associated p-values (in brackets). Cells in bold indicate significance at the 0.05 level.

	Damage costs	Management costs
Total area (km^2)	0.10 (0.670)	0.08 (0.740)
Agricultural area (km^2)	0.11 (0.650)	0.03 (0.900)
Forest area (km^2)	**0.63 (0.003)**	0.24 (0.310)
Urban area (km^2)	0.34 (0.160)	0.31 (0.200)
Human population (thousands of people)	0.22 (0.360)	0.04 (0.880)
GDP (US$)	**0.46 (0.039)**	0.39 (0.086)
Container port traffic (TEU: 20-foot equivalent units)	**0.47 (0.050)**	0.33 (0.180)
Research and development expenditure (US$)	**0.49 (0.041)**	**0.61 (0.007)**
Scientific and technical journal articles	**0.47 (0.035)**	0.28 (0.230)
Number of researchers	0.41 (0.088)	0.45 (0.060)
Imports of goods and services (US$)	0.44 (0.054)	**0.49 (0.027)**

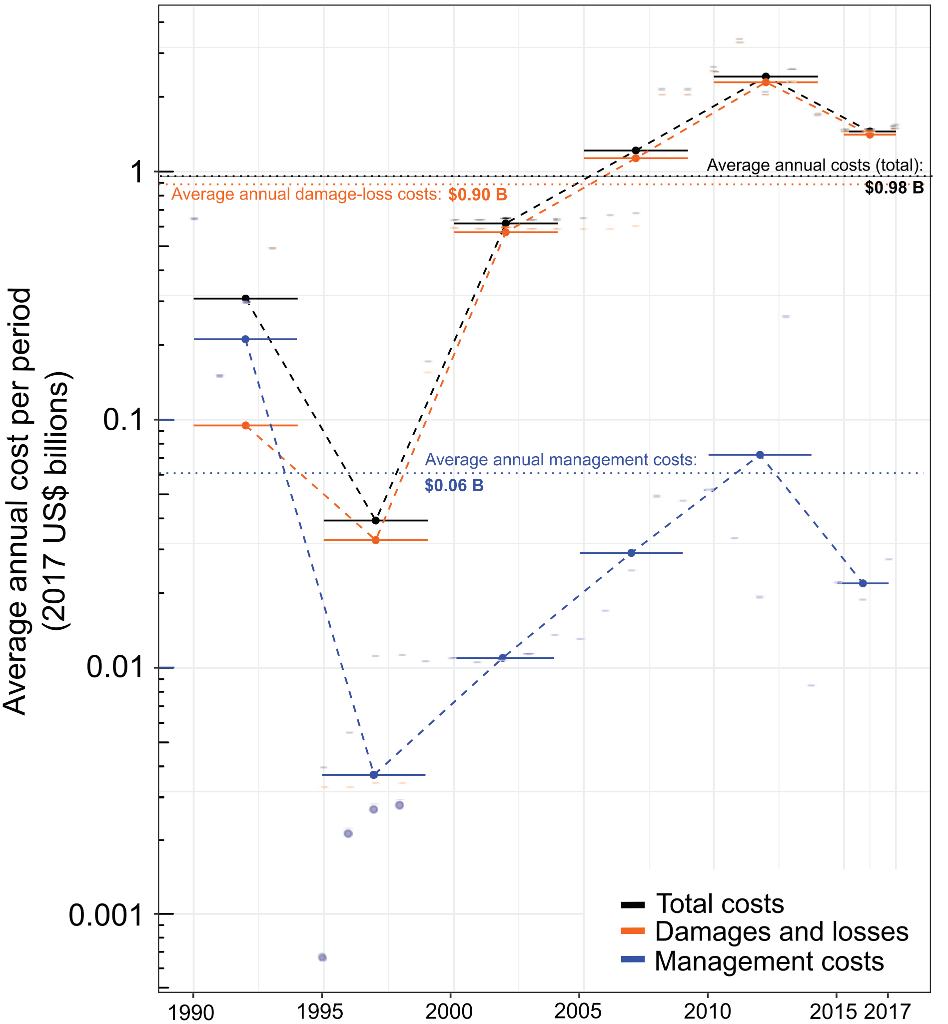

Figure 7. Total (observed and potential) annual costs resulting from invasions in the Mediterranean region from 1990–2017 at five-year increments (except for the last three years of the dataset which cover the period 2015–2017). Data are presented for all costs combined, plus "Damage" and "Management" costs separately. Solid points and horizontal lines represent annual means over their respective 5-year intervals. Note that the y-axis is shown on a $\log_{10}$ scale. The slight decrease observed for the last three years is likely indicative of the incomplete sampling of cost for these last years, because of the delay between cost occurrence and reporting/publication.

annual costs of damages and losses, estimated at $898.3 million, have been steadily increasing through time, reaching their peak between 2010 and 2015 and declining over the last three years. Average annual management costs were estimated at $61 million and had their peak in the early 1990s, reaching a low in the late 1990s and generally did not exhibit a consistent pattern through time. Reductions in costs in recent years likely emanate from time lags (i.e. between timing of cost incurrence and publication) and thus reflect incompleteness, as there is no evidence that biological invasions are slowing down (Seebens et al. 2017).

Discussion

Between 1990 and 2017, the total recorded economic costs of biological invasions in Mediterranean countries amounted to \$27.31 billion. However, most costs are the result of predictions or expectations (87% of total costs, \$23.73 billion) rather than realised costs, meaning that costs were projected in time and/or space by the original authors, so these costs have not necessarily been borne in practice. It is important to acknowledge this as a limitation in our understanding of actual economic impacts of invasions in the region. Observed costs of biological invasions were still substantial, at \$3.59 billion over the same time period. Note again though that our database includes reported costs only, implying that costs are likely a substantial underestimate. Additionally, and as suggested by our results, costs may reflect reporting effort as much as real costs. Biases and gaps in our database likely reflect an absence of published material or a failure of the InvaCost literature searches to find this or unpublished material, rather than a genuine absence of costs. Nevertheless, our analysis of temporal trends identified marked increases in invasion costs over time (during the last three decades), particularly for resource damages, in line with evidence of increasing rates of invasion worldwide (Seebens et al. 2017) and increasing publication rates.

Our understanding of the economic impacts of biological invasions in the Mediterranean basin is largely limited to studies from a subset of countries: cost data were found for only 15 out of 26 countries, with the Western European countries (France, Spain and Italy) dominating reported costs. While most of the invasive species causing the highest monetary losses in the Mediterranean are present in many countries, their observed costs are only reported by a few. For example, our database only contains observed costs for cnidarians in Israel, despite the presence of a number of invasive species of jellyfish all over the Mediterranean (Brotz and Pauly 2012). Furthermore, previous findings (Capinha et al. 2014; Essl et al. 2015; Schertler et al. 2020; Zhang et al. 2020) have shown that large areas of the Mediterranean basin are predicted to be currently climatically suitable for some of the IAS presenting observed damage costs in other regions. Assuming the presence of suitable dispersal vectors, costs are likely already occurring in these regions (but have not been reported or captured in our database) or likely to occur in additional countries as IAS distributions expand.

Not surprisingly and in line with earlier literature establishing correlations between economic development and invasions (Nuñez and Pauchard 2010), we identified research effort (reflected through expenditure in R&D) to be positively and significantly correlated with both damage and management costs of IAS. This significant correlation indicates that greater research investments enhance capacities to report economic impacts, and may also bolster incentives for management actions. As expected, with greater economic activity in a country (e.g. higher GDP, greater value of imports etc), there is a larger scope for a) economic losses, which manifest especially through directly quantifiable damages to human infrastructure, health or different sectors of the economy, and b) increased expenditure on management driven by increased awareness of ecological damages and sufficient resources to invest in alleviating them (Dickie et al. 2014). However, there may also be reporting biases at play here, whereby more developed countries with more resources and higher expenditure on research (World Bank 2020) document invasion costs more thoroughly. Accordingly, France, Spain and Italy, the three countries found to dominate total reported costs in our data, are the highest-scoring Mediterranean countries in several of these indicators (World Bank 2020). Interestingly, we found no significant correlation between the observed costs and agricultural area, despite the fact that the sector bears a large proportion (55%) of the observed costs. However, these results should be carefully interpreted, given the aforementioned correlations between costs and research effort.

Impacts generally spanned various sectors affecting a diverse set of stakeholders; however, the vast majority of reported costs were attributed to damages or losses (92.1% of total costs, $25.15 billion), possibly indicating relatively limited investments in management or, at best, limited reporting of management expenditure. Our results also provide evidence for strong taxonomic gaps and biases, with most costs derived from few invasive species or taxonomic groups. The top 10 costliest species (Suppl. material 2: Table S4) account for 70% of total costs and 91% of observed costs. A key cluster of reported costs was identified for terrestrial forbs in Western Europe and the Balkans. Costs from two publications and three species dominate the database, driving patterns in total costs. First, Issanchou (2012) estimated, by extrapolation, the economic losses to tourism and recreation caused by floating primrose willow *Ludwigia peploides* and water primrose *Ludwigia grandiflora*. Although this study focuses on a single French marsh, the annual cost is substantial and is described as extending over 13 years, resulting in a large total cost ($7.74 billion), that comprises a large part of costs to “Public and social welfare” and contributes to the high ranking of France in the list of countries most affected by IAS. Second, Soliman et al. (2012) projected $14.08 billion in damage costs of pine wood nematode *Bursaphelenchus xylophilus* in forests in Spain, France and Italy. Note that this is an approximate estimate given that our analysis of costs spans until 2017 (whereas the original paper projects costs to 2030) and assumes a linear accumulation of costs over time. This single reference greatly contributes to the dominance of: a) costs in terrestrial over other ecosystems, b) damages over other types of expenditure (e.g. management), c) effects on the forestry sector over other sectors/groups bearing costs, and d) Spain and France over all other countries. However, in reality, pine wood nematode has not spread extensively in the Mediterranean beyond Portugal, where it was introduced in 1999 (de la Fuente et al. 2018), implying that widespread damage has not yet occurred and therefore these damage costs have not yet been realised. This emphasises the importance of distinguishing between observed costs and total costs (which includes potential or expected costs; see Results subsection “Overview of invasion costs”). At the same time, however, investments in understanding potential costs, along with efforts for control, early detection and rapid response measures for this species may reduce the likelihood of spread and therefore the likelihood of costs being realised (see for example 2012/535/EU in EU (2012)). The high reported costs for a single species may also highlight the role of research agendas along with researchers’ and research funders’ incentives, in determining those IAS of utmost importance and driving research investments in understanding their costs. These agendas and incentives, which differ across countries depending on e.g. national priorities on certain sectors of the economy, largely shape our understanding of costs at a regional scale, likely creating bias over ecosystems, sectors and countries affected (Kourantidou and Kaiser 2019).

Our database contains no information on the economic cost of several IAS known to have large costs in invaded habitats elsewhere in the world, or at the global scale. Such species present as aliens in the Mediterranean, include for example the diamondback moth *Plutella xylostella*, the carpet sea squirt *Didemnum vexillum* and kikuyu grass *Cenchrus clandestinus* or *Pennisetum clandestinum* (Musil et al. 2005; Mendieta and Cardenas 2010; Ordóñez et al. 2015; Bradshaw et al. 2016). Similarly, the database is missing information on costs of several IAS or alien species known or expected to have large social and/or ecological impacts in the Mediterranean – which may be linked to high economic costs – such as the common myna *Acridotheres tristis*, the seaweed *Codium parvulum* and the Pacific oyster *Crassostrea gigas* (Katsanevakis et al. 2016; Peyton et al. 2019). An absence of such species from our database should not necessarily be interpreted as an absence of realised economic costs. In addition, several highly costly species in some countries are also invasive in others, but with no recorded costs. As an example, a study of the costs of invasions in France calculated the potential costs of all IAS known to be present but with no cost record, from the cost records in other countries (Renault et al. 2021). This estimation increased the economic costs of IAS in France by $968 million over the period 1993–2018 (i.e. more than 8%). These examples highlight the need to expand research efforts quantifying the economic impacts of existing, ongoing and expected invasions.

These gaps in species reported are also reflected in the ecological literature for the region that describes the presence of many IAS (Zenetos et al. 2005; Di Castri et al. 2012; ISSG 2015), as well as in national and European legislation and regulatory instruments such as the EU (2014) Regulation 1143/2014. These knowledge gaps, which may also come along with a paucity of quantitative information on ecological impacts of invasions on goods and services, limit our ability to assess with accuracy the true costs of invasive species in the region and indicate that costs presented here are substantial underestimates.

Reported costs of aquatic species ($7.9 billion, only $0.12 billion of which were observed) were less than half of the reported costs for terrestrial species. These covered only 37 aquatic and 28 semi-aquatic species with species-specific costs. This is despite many reports of high-impact and newer high-risk invasions in Mediterranean aquatic environments, especially the Mediterranean Sea which is among the world’s most invaded (Zenetos et al. 2005; Edelist et al. 2013; Kalogirou 2013; Giakoumi 2014; Katsanevakis et al. 2014; Clavero et al. 2015; Kletou et al. 2016; Zenetos and Galanidi 2020). Limited capacity for reporting costs of aquatic invasions may be related to the difficulty of understanding their social and economic dimensions, which may in turn lead to limited investments in research and management in these ecosystems. This becomes particularly important given that by the time aquatic invasions are observed and attract researchers' and/or resource managers' attention, they are typically at a quite advanced stage of the invasion (Beric and MacIsaac 2015), which increases the likelihood of more pronounced impacts. The absence of such reported expenditure in the Mediterranean is likely a combination of limited management at an early stage of the introduction and a lack of knowledge, strategies and/or frameworks for these types of investments. Despite the economic importance of coastal tourism and the socioeconomic value of fisheries in the Mediterranean, we do not exclude the possibility that economic impacts of IAS may be genuinely lower in aquatic than terrestrial systems, given that most human activities and infrastructure that could be affected by invasions are on dry land (e.g. 64% of costs in the U.S. linked to arable and livestock farming; Pimentel et al. 2005).

Notably, the costs from invasions identified in marine ecosystems (less than 0.01% of aquatic species costs) and were limited to a three species only, when there are multiple well-known invasive fish, marine mollusks and invertebrates, crustaceans, foraminifera, polychaetes and algae in the Mediterranean Sea (Rilov and Galil 2009; Edelist et al. 2013). Considering invasive fish, the Mediterranean has the most invasions worldwide, with at least 84 known Indo–Pacific fish that have invaded the eastern part since the opening of the Suez Canal, close to two thirds of which have established permanent populations in the Mediterranean (Edelist et al. 2013). Costs for marine invasions are generally underrepresented at a global scale, with about 2% of all aquatic invasion costs globally attributed to marine species (Angulo et al. 2020; Ballesteros-Mejia et al. 2020; Diagne et al. 2020b).

Costs to the fishery sector were only \$3.97 million (all observed), originating from two species: the tube worm *Ficopomatus enigmaticus*, and the red swamp crayfish *Procambarus clarkii.* Costs to the sector of several well-known marine invaders that have been affecting fishers directly (e.g. through damages to gear, injuries, bycatch costs etc) and/or indirectly (e.g. through ecosystem degradation, competition for food etc), such as the pufferfish *Lagocephalus sceleratus*, the round herring *Etrumeus golanii*, the lionfish *Pterois miles* or the rabbitfishes *Siganus rivulatus* and *S. luridus* have not yet been quantified (e.g. see Kalogirou 2013; Giakoumi 2014).

Efforts to understand the spatial and taxonomic connectivity additionally highlighted the limits of the available data and the research effort conducted in the region to understand the different facets of invasion costs in the Mediterranean basin. Few broad taxonomic groups, such as terrestrial forbs and arthropods, as well as fish, had relatively far-reaching invasion costs, evidenced by network clustering. Conversely, other taxa were structurally disparate in the network, being linked to just single, or few, countries (e.g., cnidarians in Israel; aquatic plants in France and Spain), despite the wider known extent and damages of such taxa across the Mediterranean region (e.g., Brundu 2015). Our network analysis revealed that the taxonomic composition of costs differed across countries, indicating that the reported assemblages of IAS impacts that drive economic impacts are strongly dictated by low publication effort (with the knowledge gaps and biases it entails), or that invaders have truly unique compositions with unevenly distributed impacts across nations.

Conclusions

Having shed light on many of the limitations of the current understanding of economic impacts from invasions in the Mediterranean, we suggest that these shortcomings should be addressed in future research and also considered in resource managers' and policy makers' agendas. However, we also caution that management decisions should not be based on reported monetary costs alone, as difficult-to-quantify ecological invasion ramifications should also warrant interventions. As opposed to what one may have expected for an interconnected region such as the Mediterranean basin, no clear pattern can be identified regarding the origin of the invasive species causing costs in the area (Suppl. material 2: Table S5). This may be attributed to limited reporting of costs from several countries. Most of the terrestrial species occupy disturbed areas, cultivated lands or forests. No clear pattern has been identified for aquatic invasions which may reflect, among other factors, underreporting of invasions in aquatic systems. With 42% of countries in the Mediterranean basin completely absent from our database, very few recorded costs from the vast majority of the rest and collective action on combating invasions largely missing in the Mediterranean basin, it becomes clear that there is an urgent need for comprehensive, resolute and standardised reporting of how invasions impact human and social wellbeing and economies. This is especially the case in aquatic environments and the Mediterranean Sea in particular, which is known to be among the world's most invaded.

Such efforts will allow for specifying high-risk and/or high-impact invasive taxa and identifying with more accuracy the spatial and temporal scale of realized and expected impacts. Investments in standardising both costs of damages and management (Iacona et al. 2018; Diagne et al. 2021) can be of great value for an improved collective understanding of invasion impacts regionally as well as for designing cross-border collaborative policies that can help mitigate impacts in the Mediterranean, one of the world's richest biodiversity hotspots.

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Supplementary material 1

Mediterranean database

Authors: Melina Kourantidou, Ross N. Cuthbert, Phillip J. Haubrock, Ana Novoa, Nigel G. Taylor, Boris Leroy, César Capinha, David Renault, Elena Angulo, Christophe Diagne, Franck Courchamp

Data type: xlsx file database with cost entries for the Mediterranean basin

Explanation note: The dataset used for the analysis of costs of invasive species for the Mediterranean basin.

Link: https://doi.org/10.3897/neobiota.67.58926.suppl1

Supplementary material 2

Appendix

Authors: Melina Kourantidou, Ross N. Cuthbert, Phillip J. Haubrock, Ana Novoa, Nigel G. Taylor, Boris Leroy, César Capinha, David Renault, Elena Angulo, Christophe Diagne, Franck Courchamp

Data type: tables and figures

Explanation note: The Appendix contains additional tables and figures referred to in the text in the form of Fig. S4; Figs S1, S2; Table S2; Appendix, as required by the journal.

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Economic costs of invasive alien species in Mexico

Axel Eduardo Rico-Sánchez[1*], Phillip J. Haubrock[2,3*], Ross N. Cuthbert[4,5*], Elena Angulo[6*], Liliana Ballesteros-Mejia[6], Eugenia López-López[1], Virginia G. Duboscq-Carra[7], Martin A. Nuñez[7,8], Christophe Diagne[6], Franck Courchamp[6]

1 *Laboratorio de Evaluación de la Salud de los Ecosistemas Acuáticos, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Prolongación de Carpio y Plan de Ayala s/n, Col. Santo Tomás, C.P. 11340, Miguel Hidalgo, Ciudad de México, México* **2** *Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, 63571 Gelnhausen, Germany* **3** *University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Zátiší 728/II, 389 25, Vodňany, Czech Republic* **4** *GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, 24105, Kiel, Germany* **5** *School of Biological Sciences, Queen's University Belfast, 19 Chlorine Gardens, Belfast, BT9 5DL, Northern Ireland, UK* **6** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405, Orsay, France* **7** *Grupo de Ecología de Invasiones, INIBIOMA, CONICET, Universidad Nacional del Comahue, Quintral 1250, San Carlos de Bariloche, CP 8400, Argentina* **8** *Department of Biology and Biochemistry, University of Houston, Houston, Texas, 77204, USA*

Corresponding author: Axel Eduardo Rico-Sánchez (axelskx@gmail.com)

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Abstract

Invasive alien species (IAS) are a leading driver of biodiversity loss worldwide, and have negative impacts on human societies. In most countries, available data on monetary costs of IAS are scarce, while being crucial for developing efficient management. In this study, we use available data collected from the first global assessment of economic costs of IAS (InvaCost) to quantify and describe the economic cost of invasions in Mexico. This description was made across a range of taxonomic, sectoral and temporal variables, and allowed us to identify knowledge gaps within these areas. Overall, costs of invasions in Mexico were estimated at US\$ 5.33 billion (i.e., 10^9) (\$MXN 100.84 billion) during the period from 1992 to 2019.

* These authors contributed equally to this work.

Biological invasion costs were split relatively evenly between aquatic (US$ 1.16 billion; $MXN 21.95 billion) and terrestrial (US$ 1.17 billion; $MXN 22.14 billion) invaders, but semi-aquatic taxa dominated (US$ 2.99 billion; $MXN 56.57 billion), with costs from damages to resources four times higher than those from management of IAS (US$ 4.29 billion vs. US$ 1.04 billion; $MXN 81.17 billion vs $MXN 19.68 billion). The agriculture sector incurred the highest costs (US$ 1.01 billion; $MXN 19.1 billion), followed by fisheries (US$ 517.24 million; $MXN 9.79 billion), whilst most other costs simultaneously impacted mixed or unspecified sectors. When defined, costs to Mexican natural protected areas were mostly associated with management actions in terrestrial environments, and were incurred through official authorities via monitoring, control or eradication. On natural protected islands, mainly mammals were managed (i.e. rodents, cats and goats), to a total of US$ 3.99 million, while feral cows, fishes and plants were mostly managed in protected mainland areas, amounting to US$ 1.11 million in total. *Pterygoplichthys* sp. and *Eichhornia crassipes* caused the greatest reported costs in unprotected aquatic ecosystems in Mexico, and *Bemisia tabaci* to terrestrial systems. Although reported damages from invasions appeared to be fluctuating through time in Mexico, management spending has been increasing. These estimates, albeit conservative, underline the monetary pressure that invasions put on the Mexican economy, calling for urgent actions alongside comprehensive cost reporting in national states such as Mexico.

Abstract in Spanish

Costos económicos de las especies invasoras en México. Las especies invasoras implican una pérdida de biodiversidad a nivel mundial, y presentan impactos negativos en la sociedad humana. En la mayoría de los países, es escasa la información disponible sobre los costes monetarios de las especies invasoras, la cual es información crucial para el desarrollo de un manejo eficiente. En el presente estudio, se empleó información disponible recolectada de la primera evaluación global de los costes económicos de las especies invasoras (InvaCost), para cuantificar y describir los costes económicos de las invasiones en México. Se elaboró la descripción a través de diferentes categorías taxonómicas, descriptores sectoriales y temporales, lo que permitió identificar los vacíos de información en esas áreas. Los costes por invasiones en México en general, se estimaron en US$ 5.33 mil millones (i.e., 10^9) ($MXN 100.84 mil millones) durante el periodo de 1992 a 2019. Los costes de las invasiones biológicas se separaron en forma relativamente equitativa entre los invasores acuáticos (US$ 1.16 mil millones; $MXN 21.95 mil millones) y los invasores terrestres (US$ 1.17 mil millones; $MXN 22.14 mil millones), pero los taxa semiacuáticos dominaron (US$ 2.99 mil millones; $MXN 56.57 mil millones), con costes donde el daño a recursos fue cuatro veces más elevado que aquellos por el manejo de especies invasoras (US$ 4.29 mil millones vs US$ 1.04 mil millones; $MXN 81.17 mil millones vs $MXN 19.68 mil millones). El sector de la agricultura obtuvo los mayores costes (US$ 1.01 mil millones; $MXN 19.1 mil millones), seguido por la pesquería (US$ 517.24 millones; $MXN 9.79 mil millones), mientras que la mayoría de otros costes impactan simultáneamente en sectores mezclados o inespecíficos. Cuando se definieron, los costes en las áreas naturales protegidas mexicanas se relacionaron en mayor medida con acciones de manejo en ambientes terrestres y se llevaron a cabo por autoridades gubernamentales vía monitoreo, control o erradicación. En islas naturales protegidas principalmente se manejaron mamíferos (i.e. roedores, gatos y cabras), para un total de US$ 3.99 millones, mientras que las vacas ferales, peces y plantas se manejaron predominantemente en áreas continentales protegidas, alcanzando un total de US$ 1.11 millones. Se reportó que el pez diablo (*Pterygoplichthys* sp.) y el lirio acuático (*Eichhornia crassipes*) causaron los costes más elevados en ambientes acuáticos no protegidos en México, y la mosca blanca (aleuródidos) en sistemas terrestres. A pesar de que los daños reportados por invasiones aparentemente parecen fluctuar a través del tiempo en México, la inversión en manejo ha ido en incremento. Estas estimaciones, aunque conservadoras, señalan la presión monetaria que las invasiones ejercen sobre la economía mexicana, haciendo un llamado a las acciones urgentes en conjunto con informes integrales de los costes en estados nacionales como México.

Abstract in Fench

Coûts économiques des espèces exotiques envahissantes au Mexique. Les espèces invasives constituent l'un des principaux facteurs de perte de biodiversité dans le monde, et ont de nombreuses répercussions négatives sur les activités humaines. Dans la plupart des pays, les données relatives aux coûts monétaires induits par la présence d'espèces invasives sont rares, bien que ces informations soient cruciales dans l'optique du déploiement d'actions de gestion efficaces. Dans cette étude, nous avons analysé les données issues de la première base de données mondiale centralisant les coûts économiques générés par les espèces invasives (InvaCost) pour quantifier et décrire le coût monétaire de la présence de ces espèces au Mexique. Cette description s'appuie sur un éventail de descripteurs, incluant différents taxons, et secteurs d'activités sur une large période. Cette étude nous a également permis d'identifier les manques de connaissances des impacts économiques générés par les espèces invasives. En cumulé, le coût des invasions biologiques au Mexique s'élève à 5,33 milliards de dollars américains (100,84 milliards de dollars MXN) au cours de la période 1992–2019. Le coût des invasions biologiques se répartit de façon égale entre les espèces invasives aquatiques (1,16 milliard de dollars US; 21,95 milliards de dollars MXN) et terrestres (1,17 milliard de dollars US; 22,14 milliards de dollars MXN). Néanmoins, les taxons semi-aquatiques excèdent largement ces valeurs (2,99 milliards de dollars US; 56,57 milliards de dollars MXN). Les coûts résultant des dommages sont quant à eux quatre fois supérieurs à ceux liés à la gestion des espèces invasives (4,29 milliards de dollars américains contre 1,04 milliard de dollars américains; 81,17 milliards de dollars MXN contre 19,68 milliards de dollars MXN). Le secteur agricole a subi les coûts les plus élevés (1,01 milliard de dollars US; 19,1 milliards de MXN), suivi de la pêche (517,24 millions de dollars US; 9,79 milliards de MXN), tandis que la plupart des autres coûts ont eu des répercussions sur différents secteurs, et sur des secteurs non renseignés dans les données sources. Lorsqu'ils ont été définis, les coûts pour les aires naturelles protégées du Mexique étaient principalement associés aux mesures de gestion des milieux terrestres, et ont été engagés par les autorités par des actions de surveillance, de contrôle ou d'éradication des espèces invasives. Sur les îles bénéficiant d'un statut de protection, la gestion des mammifères envahissants (c.-à-d. rongeurs, chats et chèvres) a induit un coût total de 3,99 millions de dollars ; les vaches sauvages, les poissons et les plantes ont été principalement gérés dans des zones continentales protégées, et ont conduit à une dépense totale de 1,11 million de dollars. Le pléco (poisson, *Pterygoplichthys* sp.) et la jacinthe d'eau (plante, *Eichhornia crassipes*) ont entraîné les coûts les plus élevés dans les écosystèmes aquatiques non protégés au Mexique, et les aleurodes dans les systèmes terrestres. Bien que les dommages signalés à la suite d'invasions semblent fluctuer au fil du temps au Mexique, les dépenses liées à la gestion des espèces invasives ont quant à elles augmenté. Ces estimations, bien que prudentes, soulignent l'impact financier important que les invasions exercent sur l'économie mexicaine, appelant à des mesures urgentes de gestion parallèlement à la publication de rapports détaillant les coûts induits par les espèces invasives.

Keywords

Damages, InvaCost, islands, management, monetary impact, non-native species, North America, protected areas

Introduction

Biological invasions have become a major international concern and pervasive driver of global change, causing ecological, social and economic issues in impacted countries (Hulme et al. 2009; Early et al. 2016; Seebens et al. 2017, 2020). Invasive alien species (IAS), translocated through human-mediated vectors, have been identified as one main driver of global biodiversity loss (Malcolm and Markham 2000; Stigall 2010; Bellard et al. 2016). The magnitude of ecological impacts driven by IAS has received increasing attention across taxonomic groups and habitat types (e.g., Didham et al. 2005; Courchamp et al. 2017; Cuthbert et al. 2019; Haubrock et al. 2019; Mofu et al. 2019). However, relatively few studies have synthesised monetary impacts of biological invasions at national scales (Pimentel et al. 2000, 2005; Hoffmann and Broadhurst 2016). As a result, investments in safeguarding ecosystems from IAS have remained lackluster, given that knowledge of their economic costs at national levels is essential. Indeed, this is the main scale at which legislation is implemented and management responses are funded (Eiswerth and Johnson 2002).

Economic costs from IAS can arise through a large variety of impacts, including damages directly or indirectly caused by invaders on environments, resources or infrastructures (e.g. Shwiff et al. 2010), to different types of expenditures dedicated to preventing, controlling or eradicating invasions (e.g. Hoffmann and Broadhurst 2016). Invasive alien species can also negatively affect opportunities for income generation by compromising the supply of natural resources for e.g. aquaculture and agriculture, and can lead to severe health issues by vectoring pathogens (Shackleton et al. 2007; Medlock et al. 2012; Selck et al. 2014). Quantifications of economic costs associated with IAS have been limited to a few taxa globally (insects: Bradshaw et al. 2016), or certain geographic areas (USA: Pimentel et al. 2000, 2005; Europe: Kettunen et al. 2009; Australia: Hoffmann and Broadhurst 2016). However, some previous large-scale studies concerning biological invasion costs have been criticised for an overreliance on the upscaling of small-scale estimates, with limited method reproducibility that, in turn, detracts from monetary estimate reliability (Hoffmann and Broadhurst 2016; Cuthbert et al. 2020). As such, more resolute, comprehensive and harmonised cost reporting is crucial for enabling efficient decision-making at governmental levels for invasions (Dana et al. 2014; McConnachie et al. 2016; Hiatt et al. 2019; Diagne et al. 2020a).

Mexico is a major national economy within Latin America; with a surface area of 1,947,156 km^2 and being located in a transition zone between the Nearctic and Neotropic, it features a mostly arid and tropical climate, and has one of the most diverse biotas among temperate zones (Mastretta-Yanes et al. 2015). Due to geological and climatic changes during the Pliocene-Pleistocene and Neogene, respectively, it is one of the most biodiverse ecoregions (Salzmann et al. 2011). Mexico has undertaken substantial environmental actions in terms of, for example, protected area designations (2% increase; update on global statistics from Protected Planet Report 2016). Consequently, 182 natural protected areas have been designated to date (Armendáriz-Villegas et al. 2015), and 12 protected areas belong to islands in Mexico, such as the National Parks of Archipiélago Espíritu Santo, Archipiélago de Revillagigedo Biosphere Reserve, and Isla Guadalupe Biosphere Reserve (CONABIO 2020). The protected areas possess great biological diversity and a high degree of endemism, and islands in particular harbour a high diversity of birds, mammals and reptiles (Aguirre-Muñoz et al. 2011). Hence, the Mexican flora and fauna contribute a considerable degree to global biodiversity, making conservation efforts and impacts of IAS particularly important (Rico-

Sánchez et al. 2020). Protected areas have been identified as cornerstones of biodiversity conservation and are essential for maintaining ecosystem function, yet are increasingly at risk from biological invasions (Liu et al. 2020). However, appraisals of how invasion costs are structured in protected areas are lacking in Mexico, despite approximately 800 non-native species having been reported (350 of which are invasive) (Mifsut and Jiménez 2007). Prominent invasive species in Mexico include, among many others, several species classified among the IUCN list of "100 of the world's worst invasive alien species", such as the feral cat (*Felis catus*), the American bullfrog (*Lithobates catesbeianus*), the water hyacinth (*Eichhornia crassipes*), the red imported fire ant (*Solenopsis invicta*), the red-eared turtle (*Trachemys scripta*) and the black bass *Micropterus salmoides*. The listed "100 of the world's worst" IAS have been found to be more economically impactful than unlisted IAS on average (Cuthbert et al. 2021a). On Mexican islands, 20% of endemic mammals and 12% of endemic birds are now extinct because of introduced species (Aguirre-Muñoz et al. 2009). Marine and freshwater ecosystems are also much affected by IAS such as fish, lampreys, aquatic plants or snails.

For example, two lionfish species, *Pterois miles* and *P. volitans* are predators of fish and invertebrates in mangrove swamps and in reefs of the Gulf of Mexico, affecting some species of great economic importance (Mendoza and Koleff 2014). The introduction of bumblebees, such as *Bombus impatiens* from the USA or *B. terrestris* from Europe, North Africa, and Asia as pollinators of commercial crops has significantly affected native pollinators and plants (CANsEI 2010). As in several other countries, large-scale plantations of Eucalyptus (*Eucalyptus globulus*) were actively promoted in Mexico until this century, both to alter ecosystems and thereby reduce incidences of malaria and to boost the paper industry (Hinke 2000). It has since become one of the seven most damaging invasive plants in Mexico, the six others being *Ricinus communis*, *Pennisetum clandestinum*, *Eragrostis lehmanniana*, *Cenchrus ciliaris*, *Rhynchelytrum repens* and *Tamarix ramosissima* (Mifsut and Jiménez 2007). Notorious invasive birds in Mexico include the house sparrow *Passer domesticus*, the Monk Parakeet *Myiopsitta monachus* and the rock dove *Columba livia*, affecting native bird species, damaging buildings and reducing crop yields (Pineda-López et al. 2013).

In recent years, Mexico has also undertaken actions derived from a national strategy on IAS presented in the Global Environment Facility ("GEF invaders") (De Alba et al. 2017), which have highlighted the economic impact of invasions on agriculture, forestry and wildlife. Previous studies (Ramírez-Albores et al. 2019) compiled pioneering information about references on biological invasions in Mexico. The "GEF invaders" strategy has contributed to increasing the knowledge of economic costs over the period of 2014 to 2018 via a project managed by the National Commission for the Knowledge and Use of Biodiversity (CONABIO). Despite all these efforts, information regarding costs of IAS in Mexico has not yet been synthesised in a standardised manner, hampering management actions and appraisals of the costs and benefits of interventions (Aguirre Muñoz et al. 2009). In consequence, data on IAS costs in Mexico are unavailable for stakeholders or authorities to make relevant decisions; recent records or estimates of costs are missing entirely.

The InvaCost database (Diagne et al. 2020b) has recently been developed in a global effort to quantify known economic costs of biological invasions. InvaCost is an accessible, broad inventory of economic costs based on a large pool of both scientific and grey literature, as well as unpublished data gathered from international experts and local stakeholders. Monetary estimations of damages and expenditures associated with IAS are considered. The structure of this database enables detailed quantification of invasion costs across different taxonomic, spatial, temporal and environmental scales. Moreover, economic costs of IAS are linked to a set of descriptors indicating which activity, societal or market sectors were related to each cost estimate (socioeconomic sectors); or which type of costs was reported, ranging from the economic damages and losses incurred by the invasion (e.g., value of crop losses, damage repair) to different management actions against the invaders (e.g., prevention, control, eradication). Using data available from this database, we analysed the economic costs of invasions currently available in Mexico. For this purpose, we describe costs among taxa, environments, cost types, and socioeconomic sectors. We also explored reported costs from protected areas, both from mainland and island areas, owing to their contribution to the biodiversity of Mexico. To understand the full dimensions of invasion costs, we distinguished cost estimates on the basis of their implementation (i.e. predicted or empirically observed) and method reliability (i.e. reproducibility of the estimation methodology). Furthermore, we describe the trend in reported costs to infer their development over time, as well as future trajectories.

Methods

Data compilation and extraction

To estimate the cost of biological invasions to the Mexican economy, we used the most up-to-date version of the InvaCost database (InvaCost_3.0; Diagne et al. 2020b). This database comprises 9,823 cost entries compiled from three data resources (full details and data openly available at https://doi.org/10.6084/m9.figshare.12668570), including costs from non-English sources (Angulo et al. 2021a). In order to gather additional cost data from Mexico, we contacted several specialists from national authorities; among them the secretary of environment (Secretaría de Medio Ambiente y Recursos Naturales), GBIF representatives of the Latin-American node, and authorities from the project "GEF – invaders" carried out by the National Commission for the Knowledge and Use of Biodiversity web page (https://biodiversidad.gob.mx/especies/Invasoras/informacion-proyecto) (CONABIO 2020). These additional data were included in addition to the InvaCost v3.0 data aforementioned (see Suppl. material 1). Individual cost records from 35 individual species were standardized to a common currency: 2017 US$ (see Diagne et al. 2020b for detailed information on conversion). Using the "Official_country" column, we filtered entries for Mexico (n = 107) and consequently costs were presented as MXN$ (exchange rate for 2017: US$ 1 = MXN$

18.92; World Bank 2020). As we filtered costs at this country-scale, we thus omitted larger-scale regional or continental costs that might have included Mexico and inflated our costs. Thus to our knowledge, InvaCost is the most comprehensive repository of the costs that have been reported for IAS in Mexico, following a systematic and standardised methodology to collect any related information (Diagne et al. 2020b). We provide our final dataset in Suppl. material 1.

Estimating total costs across descriptors

Deriving the total cumulative cost of invasions over time requires consideration of the duration of each cost occurrence. We thus estimated the duration of a cost as the number of years between the probable starting and ending years (i.e., the reported duration over which the cost was incurred) considering information provided in the "probable starting year adjusted" and "probable ending year adjusted" columns (Suppl. material 1). For example, a cost of US$ 10,000 between 1991 and 2000 would be expanded to become US$ 1,000 per year, with this latter cost estimate representing a single entry associated to the same source reference in the expanded database. When the exact starting and/or ending year were unknown, the year of publication of the primary data source was conservatively considered as the starting or ending year, and then the other information was derived (starting or ending year) based on the duration of costs, if explicitly provided in the source. To estimate the total cumulative cost, we thus expressed all the costs on an annual basis for the defined periods of their occurrence using the function "expandedYearlyCosts" from the invacost R package (Leroy et al. 2020; R version 3.6.2, R Core Team 2020) and then summed them. As such, the initial 107 entries (Suppl. material 1) became 251 entries when cost data were provided on an annual basis (and two missing cost figures removed that could not be annualised), with each expanded entry thus corresponding to a single year. We used the expanded database for the following analyses because it was necessary for cost comparability, and it further allowed us to decode temporal cost dynamics in a relevant way. Further information on this process is provided in Leroy et al. (2020).

The invasion costs were specifically described by summing all entries according to five descriptive columns of the most up-to-date version of the database (specific details on each descriptive field of the database are available at doi.org/10.6084/m9.figshare.12668570):

(i) Method reliability: illustrating the perceived reliability of cost estimates based on the type of publication and method of estimation ("high" or "low"). We acknowledge that the nature of reported costs differed markedly among sources; we classified entries as highly reliable when they originated from peer-reviewed material or official reports, as well as grey literature with reproducible methods. On the other hand, low reliability entries did not fulfil these criteria;

(ii) Implementation: referring to whether the cost estimate was actually realised in the invaded habitat ("observed") or whether it was expected ("potential");

*(iii)*Environment (column: Environment_IAS): corresponding to whether the cost was incurred from biota that are either “aquatic”, “terrestrial”, or “semi-aquatic” (species that spend part of their life cycle in water or are associated with it for foraging/reproduction);

(iv) Type of cost (column: Type_of_cost_merged): grouping of costs according to the categories: “damage”, referring to damages or losses incurred by invasion (i.e., costs for damage repair, resource losses), and “management”, comprising control-related expenditure (i.e., monitoring, prevention, management, eradication).

(v) Impacted sector: the activity (agriculture, environment, forestry, authorities-stakeholders, public and social welfare, fishery or health) that was impacted by the cost. Individual cost entries not allocated to a single sector were modified to “mixed”.

We used variables (*i*) and (*ii*) to separate the robust cost estimates from the non-robust (Suppl. material 1: Tab “InfoVariables”). Robust estimates comprised those cost entries that were at the same time observed and reliable. Non-robust cost estimates comprised those cost entries reporting potential costs and/or unreliable costs.

We also analysed whether the reported costs pertained to protected areas by distinguishing protected island and protected mainland areas from unprotected ones. We excluded entries for this analysis which spanned both protected and unprotected areas, or which were unspecific. Finally, to analyse the economic costs of IAS over time, we used the "summarizeCosts" function in the R package “invacost” (Leroy et al. 2020). With this function, we estimated the cumulative and average annual costs between 1990–2019 at 5-year intervals. Although costs started in 1992, we opted to project trends from 1990 to capture means from the last two decades completely. This analysis was performed separately according to cost type (damage vs. management), for both robust and total costs.

Results

The total reported cost of IAS to the Mexican economy was US$ 5.33 billion ($MXN 100.84 billion; i.e., 10^9 here and throughout). This monetary cost was estimated on the basis of 251 annualized costs (n = 107 original entries) from 1992 to 2019. From the overall costs, US$ 5.03 billion (n = 238) was empirically observed, whereas only US$ 295.96 million (n = 13) was deemed as potentially occurring (i.e., predicted). The majority of the economic costs was of high reliability compared to low reliability (US$ 4.71 billion, n = 245, vs. US$ 620.99 million, n = 6) (Fig. 1).

Costs across environments, taxa and sectors

Within Mexico, costs inferred from aquatic or semi-aquatic taxa were the greatest (US$ 4.14 billion, n = 75), followed by terrestrial ones (US$ 1.17 billion; n = 131). In the aquatic realm (US$ 1.16 billion), costs were contributed by eight species with individual cost records, including the water hyacinth (*Eichhornia crassipes*) that cost US$ 633.58 million, but also a diverse group of fishes that cost US$ 492.88 million (Suppl. material 3).

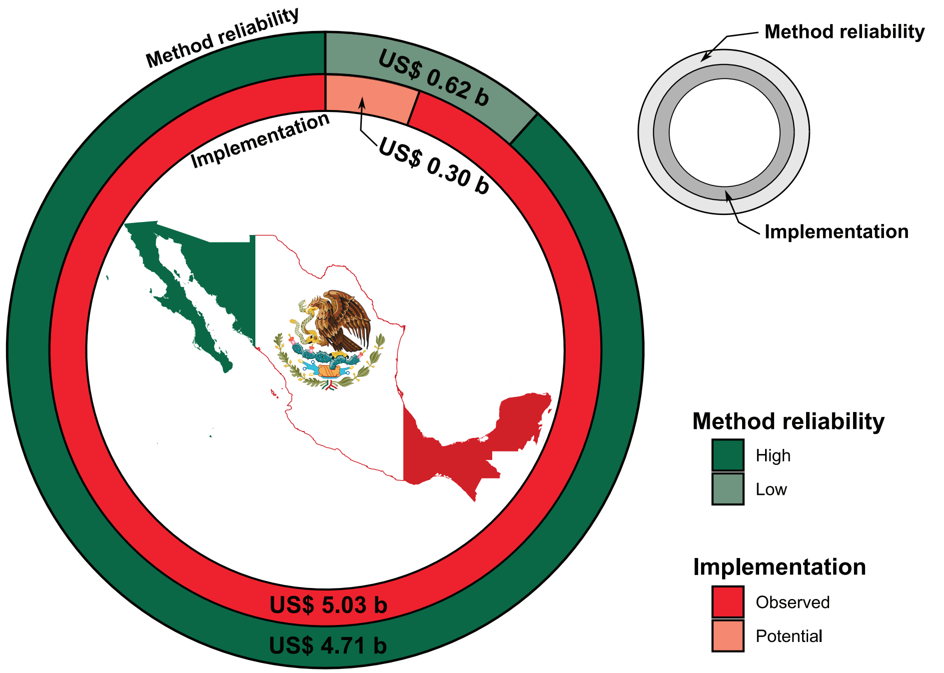

Figure 1. Total economic cost for invasive species in Mexico according to the level of reliability of the cost estimates and whether the costs were empirically observed or not (implementation). Costs are reported in US $, billion (i.e., 10^9).

In the terrestrial realm, the class Insecta dominated (US$ 1.07 billion; n = 56), followed by six further classes, each contributing cost below US$ 25 million. Costs inferred from semi-aquatic taxa (US$ 2.99 billion; n = 17) were mostly caused by mosquitoes of the *Aedes* genus (US$ 2.99 billion; n = 14), with further minor contributions from the American bullfrog *L. catesbeianus* (US$ 9.71 thousand; n = 3). Costs with unspecified or mixed habitat designations (US$ 17.51 million; n = 45) contributed the remainder (Fig. 2).

The majority of reported economic costs were due to resource damages and losses (US$ 4.29 billion; 81%, n = 57). Management costs (e.g. for prevention, control and eradication) totalled substantially less at US$ 1.04 billion (19%, n = 194; Fig. 2). From impacted sectors, the highest costs were incurred by the agriculture activity sector (US$ 1.01 billion; n = 43), followed by costs characterized as impacting fisheries (US$ 517.24 million; n = 39). Costs impacting mixed sectors comprised the largest share (US$ 3.76 billion; n = 33; Fig. 2). All other sectors incurred less than US$ 100 million (Suppl. material 2).

Overall, 12 recorded classes, and 35 species (including viruses taxa), were associated with economic costs. Insecta was the most diverse (n = 9 species), followed by Mammalia (n = 7), Liliopsida (n = 4), Actinopterygii (n = 3), and Magnoliopsida (n = 3). Similarly, insects were the costliest (US$ 4.05 billion), followed by the class Liliopsida, containing *E. crassipes* totalling at US$ 633.63 million. All other specific classes, including mammals which contributed only US$ 14.31 million despite their diversity, caused less than US$ 100 million in costs (Suppl. material 3).

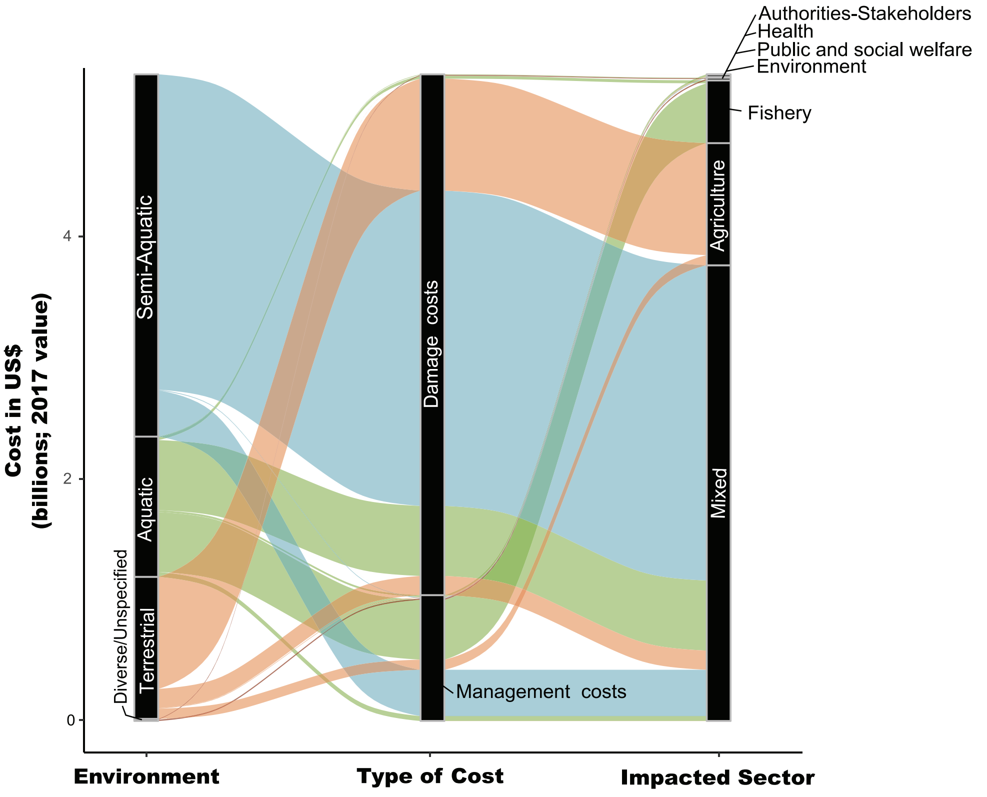

Figure 2. Alluvial plot illustrating flows of invasion costs from different environments to socioeconomic sectors according to types of costs associated with invasive species in Mexico. Costs are reported in US$, billion (i.e., 10^9).

Protected area impacts

When considering only the data that had explicit information for protected areas, we observed higher costs in unprotected lands than in protected areas in Mexico. Interestingly, costs on protected islands were all robust and most of the cost in protected mainlands was not (Fig. 3a). Invaders in unprotected areas (n = 20 entries), such as silverleaf whitefly *Bemisia tabaci*, showed the highest costs through agricultural impacts (Fig. 3b). Janitor fish (*Pterygoplichthys* sp.) and *E. crassipes* caused the greatest impacts in unprotected aquatic ecosystems in Mexico. The costs in unprotected terrestrial areas were focused on IAS of agricultural importance, relating exclusively to damages in that sector. Otherwise, in protected areas the highest costs were assigned to be incurred by authorities and stakeholders and were not species-specific (Fig. 3c, d). Without considering these costs for unspecified species, invasive mammals presented the greatest shares of economic impacts in protected areas on islands (Fig. 3c), with most economic impacts by rodents (mainly rats), cats and goats, and through management interventions from official authorities. In mainland protected areas, most species-specific economic costs

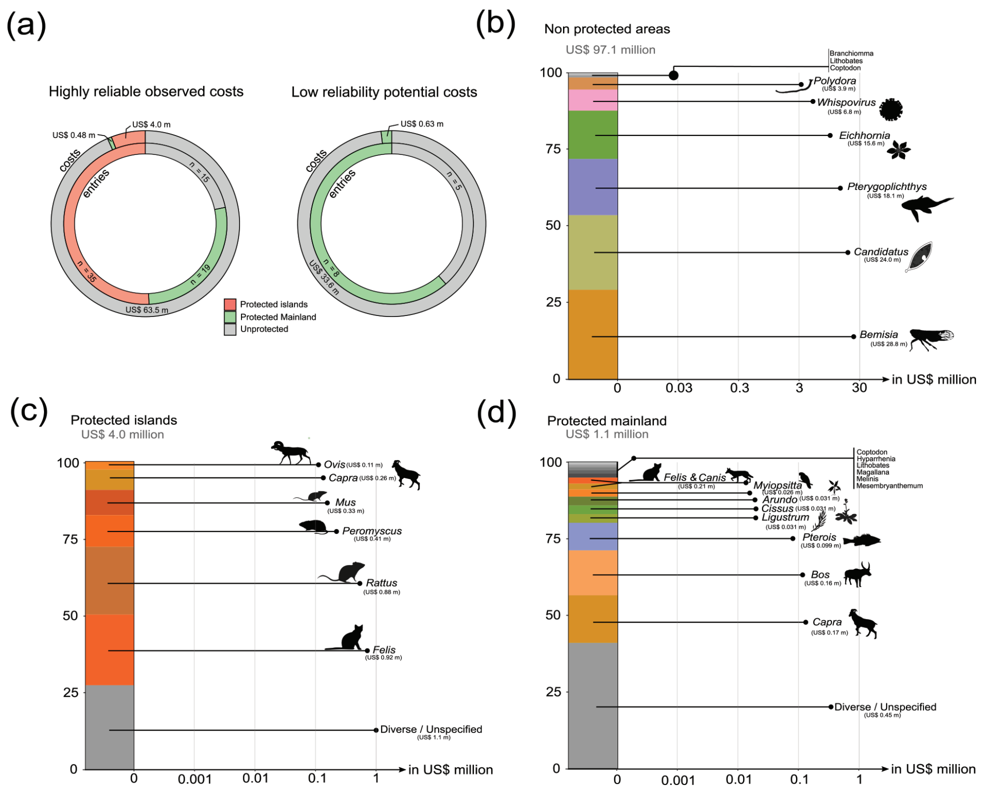

Figure 3. Invasion costs of invasive alien species with regards to the protection status of lands **a** relative number of entries and invasion costs in unprotected lands, protected islands and protected mainland for robust cost estimates (reliable and observed costs), and for non-robust cost estimates (unreliable and/or potential costs). Invasion costs in **b** unprotected lands **c** protected islands and **d** protected mainlands, considering percentage cost contributions in Mexico across taxa. For (**b, c** and **d**) costs include reliable and unreliable as well as observed and potential.

were caused by invasive goats and cows, as well as jointly between palm weevils and mites (Fig. 3d), mainly through monitoring, control, or mitigation also performed by official authorities. Plants showed minor economic impacts versus animals in mainland protected areas (US$ 0.12 million, Fig. 3d), and protected islands (US$ 0.03 million).

Temporal cost development

Between 1992 and 2019 the available cost estimates reached a total of US$ 5.33 billion, which led to an average annual cost of US$ 177.64 million overall. Disentangling costs by their level of robustness indicated opposing trends between robust costs estimates (Fig. 4a) and total cost estimates (Fig. 4b). Focusing on the highly reliable and observed costs, we in turn found different temporal patterns between damage and management costs. Recorded damages and losses (average annual cost of US$ 114.39

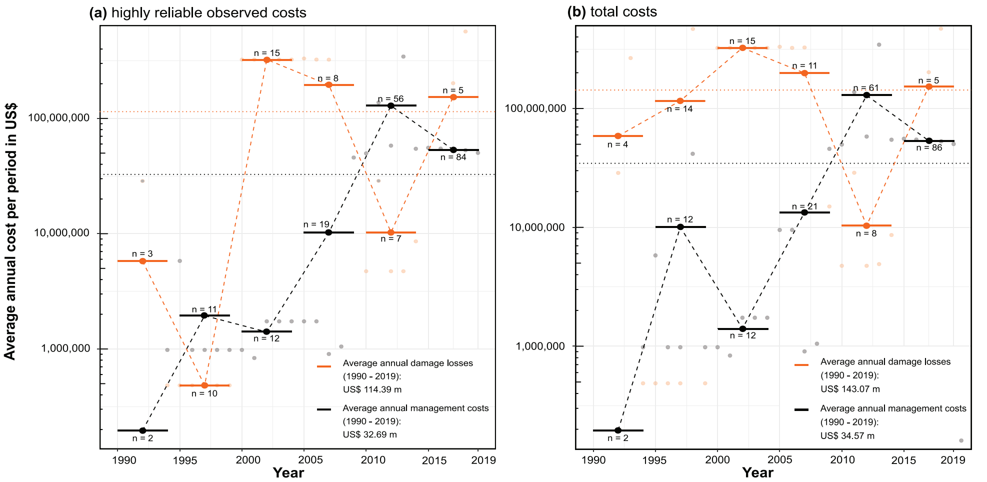

Figure 4. Temporal trends using **a** robust cost estimates (reliable and observed costs) and **b** total cost estimates, in management costs (black) and damage costs (brown) from 1990 to 2019. Periodic averages are presented on a $\log_{10}$ scale. Points represent annual totals. Numbers indicate annualized cost entries per 5-year intervals.

million per year) showed fluctuating dynamics over time, but a general upwards trend marked by a significant increase between the mid-1990s and 2005. In contrast, management costs (average annual costs of US$ 32.69 million per year) showed an apparent increase over time, even though the mean annual cost tended to decrease for the most recent years (Fig. 4a). For total costs (Fig. 4b), damage costs similarly fluctuated at a relatively stable magnitude, with an average of US$ 143.07 million per year, whereas management increased and averaged at US$ 34.57 million per year.

Discussion

In the present study, we report the first synthesis of monetary costs from IAS in Mexico. The total cost of over US$ 5 billion was determined using reported costs of IAS from 1992 to 2019 in the country. Most of the available costs were empirically observed and highly reliable, incurred in aquatic or semi-aquatic environments, and impacted primarily agriculture and fisheries, where specified. Moreover, the present study identifies key structural differences in invasion costs between protected and unprotected areas, with protected areas incurring far lower invasion costs, and those that occurred being primarily driven by management actions from authorities – in contrast to unprotected sites that mostly reported damages. However, many costs in protected islands and mainland areas were not unambiguously associated with the species that were managed.

Recently, IAS in Mexico have been most notably investigated by the project "GEF invaders" (De Alba et al. 2017). This project, managed by the National Commission of the Knowledge and Use of Biodiversity (CONABIO), invested more than US$ 30 million on IAS costs between 2014 and 2018. Furthermore, another office in Mexico which contribute to the study of IAS, i.e. the National Commission of Natural Protected Areas (CONANP) belonging to the Ministry of Environmental and Natural Resources (SEMARNAT), has a budget of US$ 224 million per year (SEMARNAT 2021). Even if all was counted as targeting IAS, these expenditures would overall still remain lower than 5% of the total cost of invasions in Mexico, highlighting a need for much higher investment if this country is to lighten the burden that biological invasions have on its economy. By comparison, the US$ 5.33 billion of total costs of invasions represents no less than a fifth of the amounts Mexican migrants working abroad sent home in 2017: the single largest foreign source of income for Mexico and an amount higher than any other sector (including the oil industry) (BBVA-CONAPO 2017).

There are nearly 350 recognised IAS reported in Mexico (CONABIO 2020). However, InvaCost only reported cost data for 35 species, suggesting a huge underestimation of invasion costs in Mexico – since costs are available for only 10% of known IAS. This proportion is similar to that reported in other studies, which have found that less than 10% of invaders have reported costs: Germany (Haubrock et al. 2021a), France (Renault et al. 2021), the United Kingdom, (Cuthbert et al. 2021b), Asia (Liu et al. 2021), Argentina (Duboscq-Carra et al. 2021) or Australia (Bradshaw et al. 2021). Even if one cannot conclude that actual costs should be ten times higher, the very high overall economic costs we found for only 10% of IAS in Mexico hints at a real, total cost that is staggering. These unreported costs included species that are widely established in Mexico, such as fishes of the *Tilapia* genus, which were introduced to increase food supply and are now considered to be competitively displacing and driving extinction of native species (Fitzsimmons 2000), or recently recorded invaders such as the redclaw crayfish *Cherax quadricarinatus* (Haubrock et al. 2021b). Other examples include the freshwater snail *Tarebia granifera*, that causes severe damages on rice cultures, displacing native species (Contreras-Arquieta and Contreras-Balderas 2000), as well as the tree *Eucalyptus globulus*, that has degraded habitat quality and altered the availability of vulnerable water resources (Morton 1980; Becerra et al. 2018). Nevertheless, our results underline the costs of some known most harmful species which occur in the country, the costliest being mosquitoes which drive marked impacts through the vectoring of pathogens and parasites that cause disease (Medlock et al. 2012), impacting the health system economically. According to Contreras-Balderas and Gutiérrez (2009), at least 36 of the IUCN 100 of the world's worst IAS (van der Weijden et al. 2007) are established in Mexico, and many of them were included in the present study, such as *Eichhornia crassipes*, *Arundo donax*, *L. catesbeianus*, *Felis catus*, *Capra hircus*, *Mus musculus*, *Rattus rattus*, among others, and are particularly economically costly (Cuthbert et al. 2021a). *E. crassipes* and *A. donax* were also among the costliest species in Spain (Angulo et al. 2021b), while mammals appear to be also very costly in other countries such as France (*Rattus* and *Felis*, (Renault et al. 2021)), Japan (*Rattus*, (Watari et al. 2021)) or Ecuador (*Capra* and *Rattus*, (Ballesteros-Mejia et al. 2021)), mainly due to the management of these species in islands (e.g. invasive rodents, (Diagne et al.

2021a)). Nevertheless, increased efforts to determine the economic impact from other species (as we mentioned above) with currently no recorded costs in InvaCost are urgently needed to fill this knowledge gap.

Major investments have only been applied to manage IAS in Mexico over recent years. In 2007, the Mexican government – through the established CONABIO – called upon academic and government institutions as well as representatives of organized civil society to assemble the National Advisory Committee on IAS that developed the National Strategy on Invasive Species in Mexico (NSISM). The NSISM acted as a guiding document to strategically and coordinately face the challenges posed by biological invasions and their costs, allowing compliance with the commitments acquired by Mexico as part of the Convention on Biological Diversity. There have been several policies in response to the need to control IAS in protected areas of the world according to Aichi Biodiversity Targets, i.e. Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization to the Convention on Biological Diversity (IPBES 2019). Therefore, these increasing national developments by the NSISM may explain the rapid growth in management costs for IAS in Mexico in the early 2000s, as well as cost reporting. Contrastingly, fluctuations in damage costs might reflect inconsistencies in cost reporting over time, rather than an actual, empirical reduction in that type of economic impact. No costs were reported in Mexico before 1992, which is relatively late compared to other countries (Haubrock et al. 2021a).

In addition, CONABIO has worked together with the National Commission of Protected Natural Areas (CONANP), which has undertaken actions to manage IAS within protected areas. This has led to the recovery of key ecosystems, both on the mainland and on Mexican islands. Islands and protected areas are highlighted in Mexico due to their biological diversity and high grade of recognized endemism (Donlan et al. 2000). However, the great diversity in protected areas in Mexico is threatened by IAS (Rico-Sánchez et al. 2020). Islands are especially important due to their high diversity of birds and reptiles (Latofski-Robles et al. 2015), generating an attractive target to invest economic resources to potential conservation strategies. The present study thus provides new knowledge on the costs of IAS management in protected areas, and particularly in protected islands.

Overall, costs in protected areas have been shown here to be much lower than costs in unprotected lands, showing also that protected islands, protected mainland or unprotected lands seemed to be threatened by a different suite of species. Disparity in costs among protected and unprotected areas might reflect a lesser extent of human activity in protected areas, in turn resulting in fewer damage costs, but a higher proportion of management costs. Invasive mammals were shown to be particularly costly in protected areas, especially in protected islands, through management by authorities and stakeholders. Indeed, this invasive group has been historically recognized as the principal conservation issue in islands. Rodents, cats and goats appeared the costliest species in Mexican protected islands, as has been found in other countries, such as goats in Galapagos Islands (Ballesteros-Mejia et al. 2021). Strategies for controlling invasive mammals in Mexico, and in particular in islands, have been mostly successful (Aguirre-

Muñoz et al. 2011; Robertson et al. 2017; Samaniego-Herrera et al. 2018), while associated cost information has remained scarce. However, in marine habitats (highly related to the fisheries activity sector where we show costs to the Mexican economy reaching US$ 517 million), eradication represents a greater challenge. For example, we observed control costs or damage to fisheries, such as those for oysters and polychaetes, of more than US$ 3 million. The high connectivity of marine environments through pathways such as shipping favours the dispersal of IAS, making it challenging to regulate invasive marine species arrivals (Giakoumi et al. 2019). Indeed, even new treatments for ballast water can be ineffective towards certain taxonomic groups (Lin et al. 2020).

Nonetheless, the most impactful species in Mexico were from aquatic or semi-aquatic habitats, similar to Spain (Angulo et al. 2021b) but in contrast to other countries such as Germany (e.g. Haubrock et al. 2021a). Although cost differences between these two habitats were small, there is a great difference with regards to the number of entries (n = 75 aquatic/semi-aquatic vs. n = 131 terrestrial), suggesting that the aquatic environment could contribute an additional major cost if data availability increases. This disparity also highlights potential biases in research attention between terrestrial and aquatic environments (Menge et al. 2009), with aquatic invasion costs generally underepresented compared to terrestrial with respect to numbers of alien species (Cuthbert et al. 2021a). Frequently, impacts of IAS are imparted through the vectoring of pathogens in aquaculture, impacting several species cultured for food, which creates lost incomes. Bondad-Reantaso et al. (2005) have summarized impacts of infectious diseases, such as losses in production, income, employment, market interactions, investment, and consumer confidence. In the present study, we excluded certain documented impacts on the aquaculture of shrimps (Lightner 1999), because costs were presented at a continental scale beyond only Mexico; this would further contribute substantially to the aquatic costs reported here. Indeed, diseases in shrimp culture due to pathogenic IAS have been recognized as among the costliest in the world. A study from Israngkura et al. (2002) recognized loss incomes up to US$ 3 billion in 11 countries (including Mexico) in the period of 1987 to 1994. Nonetheless, aquatic invasions have been found to comprise just 5% of costs at the global scale, and are thus under-represented more generally (Cuthbert et al. 2021a, b).

In addition, aquatic costs may be driven by the high economic costs associated with the fishery sector in Mexico, while there were higher costs in the agriculture sector, despite both sectors having similar database entries (n = 39 and n = 43, respectively). These results may also be related to the fact that the terrestrial environment has been the focus of programs aimed at eradicating IAS, as well as strict dispersion controls to avoid invasions, principally by arthropods in Mexico (De Alba et al. 2017). Consequently, there are national programs that address the main IAS for agriculture (i.e., as the most famous and successful efforts to eradicate *Cactoblastis cactorum*) and forestry (i.e., to control *Eucalyptus* disease by the jumping plant lice *Glycaspis brimblecombei*), which have successfully diminished their impacts and consequently monetary damages (De Alba et al. 2017). However, in the aquatic environment, greater efforts to control IAS are required, as species such as shrimps, one of the main fishery products (20% of the production) (INEGI 2010), have been strongly affected by IAS, provoking serious losses to this sector. Moreover, increased investment should be aimed at controlling vector mosquitoes which substantially damage the health sector through human diseases (Medlock et al. 2012); joint costs between *Aedes aegypti* and *Aedes albopictus* caused the greatest economic impacts in Mexico. These species caused high costs also in other American countries such as Ecuador (Ballesteros-Mejia et al. 2021), Argentina (Duboscq-Carra et al. 2021) or even in Central and South America (Heringer et al. 2021) and in the French territories located in the Americas (Renault et al. 2021).

Our results additionally showed that resource damages and losses were higher (US$ 4.29 billion) than management costs (US$ 1.04 billion). These results emphasize that although there are a larger number of entries on management costs, their costs are generally much lower than those of damages and losses to resources. Overall, damage costs are difficult to determine due to often indirect impacts, but further documentation might support the relevance of increasing management efforts, if the actions undertaken are sufficient to mitigate the impacts of IAS. Nevertheless, IAS costs were higher than other natural disasters in Mexico, such as flooding (US$ 1.79 billion) (Haer et al. 2017), droughts (US$ 1.2 billion) (Neri and Magaña 2016), or fires (US$ 8 million) (CONAFOR 2019). Therefore, increased focus is needed in Mexican policies in order to recognize critical impacts that contribute to costs of IAS in the country. In consideration, preventative measures can be highly cost-effective compared to longer-term impacts (Leung et al. 2002), and should be applied at early invasion stages (Ahmed et al. 2021). Accordingly, we suggest further management interventions to be made, particularly at the pre-invasion stage via biosecurity management actions (only 19 out of 107 raw entries reported specifically early detection or prevention measures against IAS in Mexico), to help to reduce longer-term control costs as well as potential damages. Alternatively, that trend could simply reflect a lack of willingness to invest. However, damage and management costs exhibited different trajectories in trends over time, with damages tending to fluctuate overall, and management increase. There may be several reasons for this disparity, including (1) the potential offsetting of damages by higher management investment and (2) cost reporting reflecting research priorities, which may have shifted towards management actions in recent years. However, we stress that damage costs are unlikely to be decreasing empirically, given increasing rates of biological invasion (Seebens et al. 2017), the lack of reported costs for many taxa, and the fact that many impacts from IAS are not monetised (Diagne et al. 2021b).

Conclusion

Invasive alien species have been shown in the present study to have massive impacts on the Mexican economy. However, more information is needed about the specific cost of invasions, with the results presented here likely massively underestimated. Indeed, our data set comprises only 35 of the ~350 IAS (10%) recorded in Mexico (CONABIO 2020). Despite this small percentage of species compiled in this study, it presents the first approximation of IAS costs for Mexico, indicating the magnitude of the impacts that might be realised if a greater number of invasive taxa from the Mexican territory was assessed. Overall, decision making needs to account for the cost of IAS to develop appropriate policy and management responses.

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Supplementary material 1

Database of the economic costs of biological invasions in Mexico

Authors: Axel Eduardo Rico-Sánchez, Phillip J. Haubrock, Ross N. Cuthbert,Elena Angulo, Liliana Ballesteros-Mejia, Eugenia López-López, Virginia G. Duboscq-Carra, Martin A. Nuñez, Christophe Diagne, Franck Courchamp

Data type: Dataset

Explanation note: Dataset on costs of invasive species in Mexico extracted from InvaCost v3.0 and descriptions of the column names.

Link: https://doi.org/10.3897/neobiota.67.63846.suppl1

Supplementary material 2

Economic sectors impacted by IAS in Mexico

Authors: Axel Eduardo Rico-Sánchez, Phillip J. Haubrock, Ross N. Cuthbert,Elena Angulo, Liliana Ballesteros-Mejia, Eugenia López-López, Virginia G. Duboscq-Carra, Martin A. Nuñez, Christophe Diagne, Franck Courchamp

Data type: Number of entries per sector

Explanation note: Economic sectors impacted by IAS in Mexico. Total economic costs in US$ and the number of cost entries are shown. (bil: 10^9).

Link: https://doi.org/10.3897/neobiota.67.63846.suppl2

Supplementary material 3

Economic costs of invasive alien species in Mexico

Authors: Axel Eduardo Rico-Sánchez, Phillip J. Haubrock, Ross N. Cuthbert,Elena Angulo, Liliana Ballesteros-Mejia, Eugenia López-López, Virginia G. Duboscq-Carra, Martin A. Nuñez, Christophe Diagne, Franck Courchamp

Data type: Costs and robustness of invasive alien species in Mexico

Explanation note: Economic costs of IAS in Mexico. Species are sorted by their costs (US$ million); taxonomic class (Class) and environment of each IAS (Environment_IAS) are described; the percentage of robust costs is indicated (Robust) as well as the number of entries for each species. * Class for WSSV (white stain syndrome Baculovirus) is incertae sedis so Family has been added instead.

Link: https://doi.org/10.3897/neobiota.67.63846.suppl3

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RESEARCH ARTICLE

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Economic costs of biological invasions within North America

Robert Crystal-Ornelas[1], Emma J. Hudgins[2], Ross N. Cuthbert[3], Phillip J. Haubrock[4,5], Jean Fantle-Lepczyk[6], Elena Angulo[7], Andrew M. Kramer[8], Liliana Ballesteros-Mejia[7], Boris Leroy[9], Brian Leung[2], Eugenia López-López[10], Christophe Diagne[7], Franck Courchamp[7]

1 *Ecology, Evolution, and Natural Resources, Rutgers University, 14 College Farm Road, New Brunswick, NJ 08901, USA* **2** *Department of Biology, McGill University, Montreal, H3A 1B1, Québec, Canada* **3** *GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, 24105 Kiel, Germany* **4** *Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, 63571, Gelnhausen, Germany* **5** *University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Zátiší 728/II, 389 25, Vodňany, Czech Republic* **6** *Auburn University, School of Forestry & Wildlife Sciences, Auburn, AL, 36849, USA* **7** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405, Orsay, France* **8** *University of South Florida, Department of Integrative Biology, Tampa, FL, 33610, USA* **9** *Unité Biologie des Organismes et Ecosystèmes Aquatiques (BOREA UMR 7208), Muséum National d'Histoire Naturelle, Sorbonne Universités, Université de Caen Normandie, Université des Antilles, CNRS, IRD, Paris, France* **10** *Instituto Politécnico Nacional. Escuela Nacional de Ciencias Biológicas. Carpio y Plan de Ayala, Col. Sto. Tomás 11340, CDMX, México*

Corresponding author: Robert Crystal-Ornelas (rob.crystal.ornelas@rutgers.edu)

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Abstract

Invasive species can have severe impacts on ecosystems, economies, and human health. Though the economic impacts of invasions provide important foundations for management and policy, up-to-date syntheses of these impacts are lacking. To produce the most comprehensive estimate of invasive species costs within North America (including the Greater Antilles) to date, we synthesized economic impact data from the recently published InvaCost database. Here, we report that invasions have cost the North American economy at least US$ 1.26 trillion between 1960 and 2017. Economic costs have climbed over recent decades, averaging US$ 2 billion per year in the early 1960s to over US$ 26 billion per year in the 2010s. Of the countries within North America, the United States (US) had the highest recorded costs, even after controlling for research effort within each country ($5.81 billion per cost source in the US). Of the taxa and habitats that could be classified in our database, invasive vertebrates were associated with the greatest costs, with terrestrial habitats incurring the highest monetary impacts. In particular, invasive species cumulatively (from 1960–2017) cost the agriculture and forestry sectors US$ 527.07 billion and US$ 34.93 billion, respectively. Reporting issues (e.g., data quality or taxonomic granularity) prevented us from synthesizing data from all available studies. Furthermore, very few of the known invasive species in North America had reported economic costs. Therefore, while the costs to the North American economy are massive, our US$ 1.26 trillion estimate is likely very conservative. Accordingly, expanded and more rigorous economic cost reports are necessary to provide more comprehensive invasion impact estimates, and then support data-based management decisions and actions towards species invasions.

Abstract in Spanish

Costos económicos de las invasiones biológicas en Norteamérica. Las especies invasoras pueden tener severos impactos en los ecosistemas, las economías y la salud humana. Aunque los impactos económicos de las invasiones proporcionan bases importantes para la gestión y la política, no existen síntesis actualizadas de estos impactos. Para producir la estimación más completa de los costos de las especies invasoras en Norteamérica (incluidas las Antillas Mayores) hasta la fecha, sintetizamos los datos de impactos económicos de la base de datos InvaCost publicada recientemente. Aquí, reportamos que las invasiones le han costado a la economía de Norteamérica al menos US $1,26 billones entre 1960 y 2017. Los costos económicos han aumentado en las últimas décadas, con un promedio de US $2 mil millones por año a principios de la década de 1960 a más de US $26 mil millones por año en la década de 2010. De los países de Norteamérica, Estados Unidos (EE. UU.) registró los costos más altos, incluso después de controlar el esfuerzo de investigación dentro de cada país (US $5,81 mil millones por fuente de costos en los EE. UU.). De los taxones y hábitats que podrían clasificarse en nuestra base de datos, los vertebrados invasores se asociaron con los mayores costos, y los hábitats terrestres registraron los mayores impactos monetarios. En particular, las especies invasoras de forma acumulada (de 1960 a 2017) le costaron a los sectores agrícola y forestal US $527,07 mil millones y US $34,93 mil millones, respectivamente. Las inconsistencias en los informes (por ejemplo, la calidad de los datos o los detalles en la clasificación taxonómica) nos impidieron sintetizar los datos de todos los estudios disponibles. Además, había informes de costos económicos para muy pocas de las especies invasoras conocidas de Norteamérica. Por consiguiente, si bien los costos para la economía de Norteamérica son enormes, nuestra estimación de US $1,26 billones probablemente es muy conservadora. En consecuencia, se necesitan informes de costos económicos más extensos y rigurosos para proporcionar estimaciones más completas del impacto económico de las invasiones y luego respaldar con los datos las decisiones y acciones de manejo de las invasiones de especies.

Abstract in French

Les espèces exotiques envahissantes ont de fortes répercussions sur les écosystèmes, l'économie et la santé humaine. Bien que les conséquences financières induites par les invasions constituent des données de base importantes pour la définition des politiques publiques et de gestion des invasions biologiques, des synthèses robustes manquent encore à ce jour sur les coûts économiques liés aux invasions. Afin de fournir une estimation la plus complète possible des coûts induits par les espèces exotiques envahissantes en Amérique du Nord (Les Antilles comprises), nous avons compilé les données disponibles au sein de la base de données InvaCost récemment publiée. Ce travail révèle que les invasions ont coûté au moins 1260 milliards de dollars américains entre 1960 et 2017 à l'économie nord-américaine. Les coûts économiques ont été particulièrement accrus au cours des dernières décennies, passant de 2 milliards de dollars par an en moyenne au début des années 1960, à plus de 26 milliards de dollars par an au début des années 2010. Parmi les pays de l'Amérique du Nord, les États-Unis présentent les impacts économiques les plus élevés, même après que ces coûts aient été corrigés par les différences d'efforts de recherche menés par chaque pays (5,81 milliards de dollars par document source de coûts aux États-Unis). Parmi les taxons et les habitats renseignés dans notre base de données, les vertébrés présentent les coûts les plus élevés, et les habitats terrestres sont ceux qui subissent les impacts monétaires les plus importants. Ainsi, les espèces exotiques envahissantes ont, sur la période 1960–2017, coûté 527,07 milliards de dollars de pertes à l'agriculture, et 34,93 milliards de dollars à la foresterie. A noter que la qualité des données sources (par exemple, la fiabilité des estimations de coûts ou encore l'absence de précision sur les taxons spécifiques associés aux coûts) ne nous a pas permis d'utiliser toutes les données disponibles. De surcroît, il existe peu de données de coûts au regard de la diversité des espèces exotiques envahissantes en Amérique du Nord. Par conséquent, même si les coûts pour l'économie nord-américaine sont énormes, notre estimation de 1260 milliards de dollars américains reste probablement très largement sous-estimée. Par conséquent, il est indispensable d'accroître les efforts de recherche sur ces données de coûts afin (*i*) de fournir des estimations plus complètes des impacts économiques des invasions biologiques, et (*ii*) d'appuyer les décisions de gestion fondées sur des données le plus robustes possible.

Keywords

Alien species, Canada, ecosystem management, Greater Antilles, InvaCost, Mexico, monetary impacts, societal sectors, United States

Introduction

Invasive species can have widespread and severe impacts on ecosystems, human health, and economies (Bradshaw et al. 2016; Iwamura et al. 2020; Pyšek et al. 2020; Diagne et al. 2021a). Ecological impacts from invasions are increasingly well-characterized, including reductions in native species abundances (Bradley et al. 2019), biodiversity (Mollot et al. 2017), fitness (Nunes et al. 2019) and many other detrimental effects on ecosystems (Ehrenfeld 2010). Also, invasions have been shown to severely impact human health (Shepard et al. 2011; Schaffner et al. 2020). In turn, associated economic impacts range from disrupting ecosystem services (Pejchar and Mooney 2010), to decreasing agricultural yields (Oliveira et al. 2001), damaging infrastructure and lowering real estate value and incomes (Sousa et al. 2009; Olden and Tamayo 2014), as well as substantial expenditures from management actions (Hoffmann and Broadhurst 2016). However, while advances have been made in deciphering the extent and intensity of ecological impacts on ecosystems (but see Crystal-Ornelas and Lockwood 2020), economic quantifications of invasive species remain scarce at several scales (Diagne et al. 2020a).

Where economic impacts of biological invasions have been quantified, they have often been limited to particular geographic, taxonomic, socioeconomic or environmental contexts (Pimentel et al. 2000; Aukema et al. 2011; Bradshaw et al. 2016; Hoffmann and Broadhurst 2016; Paini et al. 2016; Cuthbert et al. 2021a). Broadly, systematic reviews in invasion ecology suggest that research efforts are not equal across taxonomic groups and geographic areas (Pyšek et al. 2008; Cameron et al. 2016; Crystal-Ornelas and Lockwood 2020). Furthermore, because specific industries may be impacted more heavily than others by invasive species, we have data that directly link the impact of invasive species to economic losses for individual industries. For example, the tobacco whitefly (*Bemisia tabaci*), which spreads diseases through lettuce crops in Mexico, costs the Mexican economy US$ 20 million annually (Oliveira et al. 2001). Within the US, the annual economic cost to the forestry sector in terms of timber losses due to invasive forest pests is estimated at approximately US$ 150 million. At the same time, local governments and homeowners incur annual losses estimated at US$ 1.7 billion and $830 million due to the impacts wood-boring invasive insects have on healthy community trees (Aukema et al. 2011). Other research suggests that invasive insects could cost North America US$ 27.3 billion per year, with the largest losses incurred by the agricultural sector (Bradshaw et al. 2016).

Cost estimates at national levels are crucial, as they can duly inform policy. However, biological invasions do not respect geopolitical boundaries and intracontinental exchanges of goods and persons are linked to increased invasions (e.g., North American Free Trade Agreement; Barajas et al. 2014). Therefore, without large region-wide estimates of monetary impact across multiple biotic groups, habitat types and societal sectors, policy and management at more local-scales will at best be piecemeal, and at worst may lead to deeper economic impacts (Diagne et al. 2020b; Faulkner et al. 2020). So far, multinational agreements have led to coordinated efforts to reduce invasions in ballast water (Firestone and Corbett 2005) and control sea lamprey populations in the North American Great Lakes (Lodge et al. 2006).

This spatial coordination of management actions is particularly pertinent as the number of invasive species introductions (Aukema et al. 2010) and their ecological impacts are dynamic over time (Gallardo et al. 2016). It follows that their economic impacts may also shift over time. Indeed, because species introductions have increased exponentially over the past 200 years (Seebens et al. 2017), we might expect economic costs of invasions to rise as well. This has been seen in Australia, where an economic impact assessment found that invasive species management cost an average of AU$ 2.31 billion in the early 2000s, with costs then rising to AU$ 3.77 billion per year by 2011 (Hoffmann and Broadhurst 2016). Given the lack of information at the continental scale for North America, it is an open question whether accelerations in introduction and subsequent damage or management are even greater when examined region-wide.

In order to coordinate region-wide policy and management, North America critically needs a comprehensive understanding of cost detection efforts taking place within North American countries. For the US, one country-wide cost detection effort estimated that invasive species cost the US approximately $137 billion per year (Pimentel et al. 2000). However, in the decades since these early quantifications, some of these large-scale efforts have been criticized for the reliability of their extrapolations (e.g., Hoagland and Jin 2006; McDermott et al. 2013; Cuthbert et al. 2020). A robust assessment of economic costs of invasions is necessary to inform policy and management (e.g., by helping to define prioritization of target areas/species and estimate cost-efficiency of actions), as an inaccurate assessment could lead to an over/underallocation of resources and inefficient management actions. In turn, inadequate contemporary management actions could cause greater invasion costs in future, particularly if pre-invasion management (i.e., biosecurity) fails to prevent new introductions of damaging species (Ricciardi et al. 2020; Ahmed et al. 2021).

Providing continental estimates of economic costs may help spur the development of invasive species guidance that spans large geographic areas (Epanchin-Niell 2017; Aizen et al. 2018). The many disparate ways by which researchers assess invasive species economic impacts (Dana et al. 2014; Jackson 2015) have thus far impeded reliable and robust cost syntheses. The InvaCost database is the most up-to-date repository of invasion costs worldwide (Diagne et al. 2020a). Within InvaCost, detailed cost information is provided alongside each record, including the nature of the cost incurred and the scale at which it was studied.

In this study, we provide an estimate of the total economic cost of invasive species to North America, including to the Greater Antilles (Canada, US, Mexico, Cuba, Jamaica, and Dominican Republic; hereafter, North America). Specifically, we use information from the InvaCost database (Diagne et al. 2020a) to: (i) characterize the invasive taxa, countries (i.e., cost per country and cost per source for that country), habitats and activity sectors bearing the highest economic impacts; (ii) identify the types of costs (damage or management) incurred by the invaders; (iii) describe the temporal dynamics of these monetized impacts within North America; and (iv) identify the major continents and pathways of origin for these species.

Methods

Data collection and filtering

The recently developed InvaCost database (Diagne et al. 2020a) is a publicly available repository that compiles the monetary impacts of invasive species globally. To develop the InvaCost database, Diagne et al. (2020a) conducted standardized literature searches (via Web of Science platform, Google Scholar and Google search engine) and opportunistic targeted searches (i.e., expert consultations by which data gaps were identified). The most up-to-date version of the InvaCost database (InvaCost_3.0, freely accessible at https://doi.org/10.6084/m9.figshare.12668570) was considered in our study. We aggregated this data resource with new costs collected from another study in Mexico (Rico-Sánchez et al. 2021). The resulting initial dataset contained 9,866 cost estimates (standardized to 2017 US$) of invasive species impacts around the world.

We filtered the complete database to focus on the economic impacts of invasive species within North America that occurred between 1960 and 2017. This resulted in a full dataset of a total of 1,727 cost entries (hereafter, "full dataset"; See Suppl. material 1: full_dataset). We provide a visual depiction of our data cleaning and filtering processing using a Preferred Reporting Items for Systematic Reviews and Meta-

Analyses (PRISMA) diagram (Moher et al. 2009; Fig. 1). As a first step, we considered the full dataset to provide an estimate closer to the upper bound of costs recorded in the database for this region without any filtering of the database. Then, we performed two filtering steps to obtain the most robust subset for our North American analyses (hereafter “robust dataset”; See Suppl. material 1: robust_dataset). First, we subset the data to retain only “observed” costs (actually incurred) rather than a combination of “observed” and “potential” costs (costs expected, predicted over time or potentially occurring in the future). By constraining our analyses to focus on only observed costs, we synthesized data on directly measured economic impacts. Second, we retained only economic impacts classified as “highly reliable” (Diagne et al. 2020a), meaning that the economic impacts were either published in peer-reviewed journals, official reports or if found in grey literature, the costs reported had justified and replicable methods. These filtering steps removed the small number of entries in our database on invasive species in Jamaica. Using this robust subset of the full dataset for North America, we examined the economic impact of invasive species in North America across a range of descriptors: taxonomic grouping, habitat affected, impacted sector, cost type, and time (See Suppl. material 1: field_description for description of fields in database). We describe these analyses below.

Quantifying economic impacts by descriptors

Cost entries in the InvaCost database occur over different timescales. Accordingly, entries within the database were expanded to obtain annualized estimates using the *expandYearlyCosts* function of the *invacost* R package (Leroy et al. 2020 *v*1.0, R Core Team 2020 *v*4.0.2). This function provides annualized cost estimates for all entries, based upon the adjusted probable starting and ending years provided in the InvaCost Database (Diagne et al. 2020a).

In order to determine which taxonomic groups had the highest economic impacts within North America, we organized all invasive species in the database into four phylum-level groups (invertebrates, vertebrates, plants, or other) based on the phyla recorded in the InvaCost database. We note that for vertebrates, we grouped all chordates, but highlight that not all chordates are vertebrates. The “other” grouping captured unspecified or mixed phyla entries as well as groups with very few cost estimates (viruses, bacteria, fungi, and algae). Mixed entries correspond to those with impacts attributed to multiple invasive species in a single cost entry, where it is not possible to split apart each of their impacts. Unspecified entries have no specific invasive species attributed to an individual cost.

To characterize the economic impact in different countries within North America, we standardized the total costs incurred by each country within North America by the number of cost sources (the “Reference_title” field) captured in InvaCost. We controlled for the number of cost sources published from research in each country so that we could make fairer comparisons between countries-had we not taken this step of controlling for a proxy of research effort, costs would have inevitably risen with a greater number of

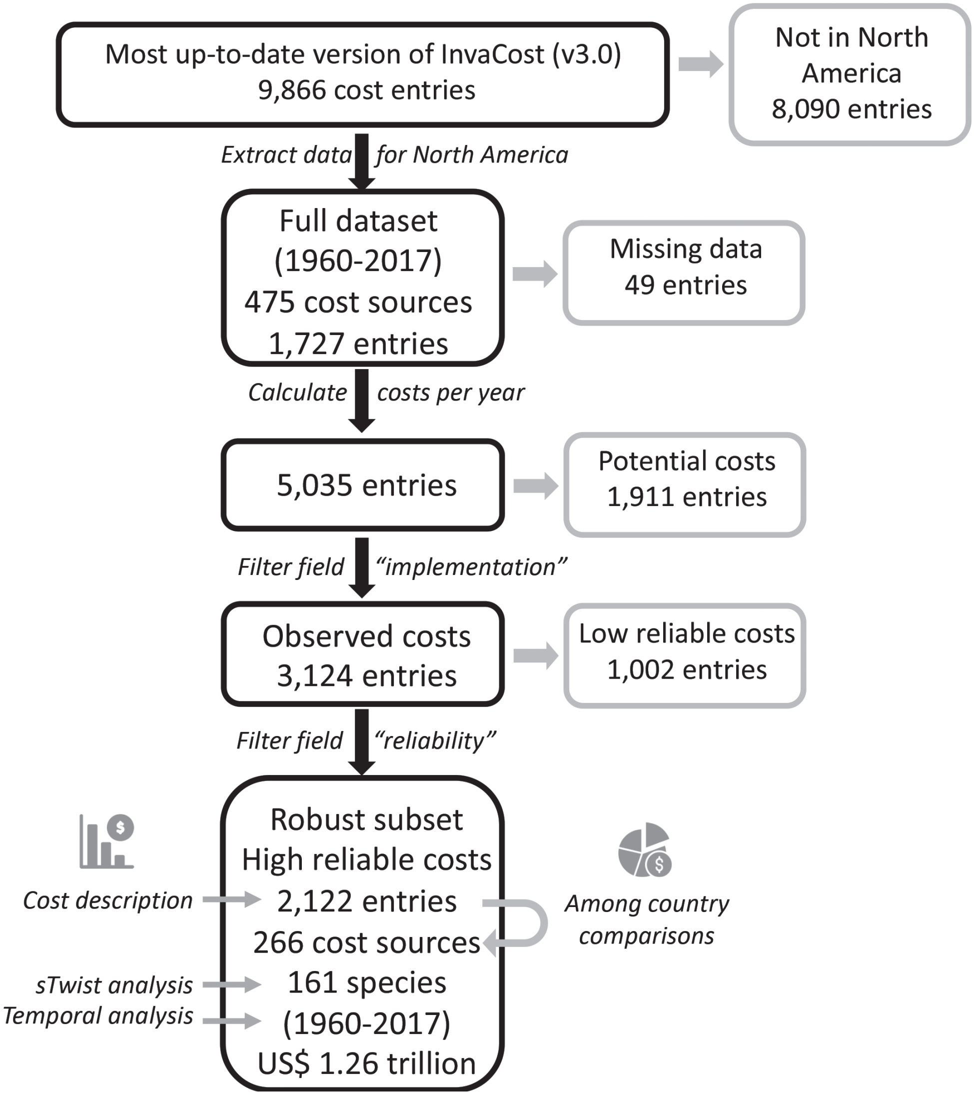

Figure 1. PRISMA flowchart (Moher et al. 2009) to depict our process for identifying the subset of economic data we used in this manuscript. Black boxes indicate the number of entries retained at every screening step. Gray boxes indicate the number of entries removed at every screening step. We began with 9,866 cost entries that include data from InvaCost 3.0 as well as recently collected data from invasion costs in Mexico (Rico-Sánchez et al. 2021) Ultimately, we retained 2,122 expanded entries that occurred within North America, and were classified as being reliable and directly observed.

sources. Thus, we present an average economic cost of invasive species impacts for each country controlling for the proxy of research effort, as well as the raw cost totals.

To investigate which variables might experience differing levels of impact, we summarized cost totals by habitat ("Environment"), economic sector ("Impacted_sector"), and type of cost ("Type_of_cost_merged"). For a full explanation of variables and the levels of classification within those variables, see Suppl. material 1: "field_description". Here, we highlight some of the classification levels for the variables in our analysis. For the "Environment" variable, we grouped economic impacts into high-level habitat categories of either aquatic, semi-aquatic, terrestrial, or unspecified as provided by the InvaCost database. The "Impacted_sector" field of the InvaCost database allows users to view the costs of invasive species within any of the 9 major sectors of economic activity captured in the database, such as agriculture, forestry, health and fisheries. The InvaCost database separates economic costs based on the type of cost incurred in the recipient location (the "Type_of_cost_merged" field): damage, management, or mixed. We characterized the magnitude of economic impacts within North America for each of these types of costs. For a more detailed classification of cost types, see Suppl. material 2: Table S1.

We analyzed temporal trends of invasive species' economic impacts within North America by using the *summarizeCosts* function in the *invacost* R package. This function used yearly costs calculated by the *expandYearlyCosts* function described above to calculate average annual costs as well as decadal averages over the 1960–2017 study period.

Linkage with CABI and sTwist

We linked each InvaCost entry with a species' geographic region(s) of origin based on "Native" region entries within their "Distribution table" where provided by CABI's Invasive Species Compendium (ISC, CABI 2020). We used the *rvest* package (Wickham 2016) to obtain the content of each CABI ISC webpage within the set of species with "Full" coverage as defined by CABI ISC (i.e., those with fully-referenced, peer-reviewed entries, 2,620 species globally). From the resulting files, we extracted the "Distribution table" element of each species' webpage and took note of all countries it contained. We also linked each species to any dominant pathways of introduction provided within CABI's "Species Transported by Cause" listing for five major groupings of pathways: pet trade (includes ornamental plants), forestry, agriculture (includes livestock), fisheries, and health (defined in Suppl. material 2: Table S2). We set the pathway cause for a species to "Other" if it could not be assigned to any of these dominant pathways. When a species reported multiple pathways, we divided its weight (or total cost) equally across all reported pathways, thereby assuming equal contribution of all pathways.

In order to determine the set of species known to have invaded North America, as well as their known invaded ranges, we relied on a recent publication that provides the most up-to-date distributional information for all known invasive alien species globally (sTwist, Seebens et al. 2020). This database also synthesized first record information where available for each species at the country level. We considered only records of successful establishment within the set of countries in the robust dataset (n = 439), rather than all known sTwist records of introduction for this set of countries (n = 19,159). We used the *countrycode* R package to assign country names within sTwist and InvaCost records to ISO3C country codes (Arel-Bundock et al. 2018), and the *gbif_parse* function within the *taxize* library to resolve species names based on GBIF taxonomy (Chamberlain et al. 2020 v0.9.98). We then merged entries based on matching country codes and species names. We considered a cost missing if InvaCost did not report a cost for any country listed as part of the invader's range within the sTwist database (Seebens et al. 2020). This approach assumed that all known invasive species produce some nonzero economic impact. However, we acknowledge that there may be a small number of invasive species that produce no measurable economic impacts in any of the dimensions covered by the InvaCost database. A more holistic valuation of the myriad impacts of invasive species remains an important long-term objective (Pejchar and Mooney 2009). For incomplete entries that had at least one cost recorded in InvaCost, we extrapolated potential total cost by dividing the total cost recorded for each species across all North American countries by the proportion of the known invaded range area over which costs were reported. For example, if a species were established in the USA, Mexico and Canada, but costs were only reported for the USA, we would divide the total USA cost by the USA's proportional contribution to the total area occupied by the USA, Canada and Mexico (i.e., area of USA/area of USA+Canada+Mexico). This extrapolation assumes that species have the same average economic impact in countries where costs have not been reported, which provides a reasonable upper bound, but may overestimate costs due to a likely correlation between the magnitude of economic impact and the likelihood of its detection. We combined all species within the *Aedes* genus for this portion of the analysis, as they were not always identified to species level, though costs predominantly related to *A. aegypti* and *A. albopictus*.

Results

From 1960 to 2017, our robust dataset suggests that invasive species cost the North American economy at least US$ 1.26 trillion (n = 2,122 expanded database entries). We emphasize that this is likely a highly conservative cost estimate because we constrained our analysis to only recorded economic data, classified as both directly observed and highly reliable. When we relax these constraints and include recorded costs of low reliability (US$ 1.02 trillion) and/or that are potential (US$ 902.19 billion), our full dataset suggests costs may be US$ 3.18 trillion. As outlined in the methods section, hereafter all results that we discuss are based on the filtered set of highly robust data.

Database descriptors

Taxonomically, the highest economic costs to North America were reported for species that could not be resolved to the species level or complexes of more than one species (US$ 845.21 billion, n = 343). The second highest costs were from the vertebrate group (US$ 252.97 billion, n = 365). Third highest were invertebrates with costs of US$ 140.80 billion (n = 795).

At the country level, our results showed that from 1960–2017, the US incurred US$ 1.21 trillion in costs. When we scaled this estimate by the number of references describing costs in the US (n = 209) each source found an average cost of US$ 5.81 billion from invasions. Invasive species cost the Canadian economy a total of US$ 34.49 billion (n = 22), with an average economic impact per source of US$ 1.57 billion. Total costs incurred in Mexico from invasions were US$ 3.75 billion (n = 28) and the average cost of impacts found per source was US$ 133.81 million. The total cost to the Cuban economy was US$ 342.04 million (n = 6), averaging US$ 57.01 million per source. Our robust database had a single entry from the Dominican Republic, and the cost to this country was US$ 3.05 million. Note that the cost per source metric was used only to account for the relationship between recorded costs and research effort, and is not used hereafter.

The most impacted habitat within North America was terrestrial (US$ 675.39 billion), and we note that this was also the most frequently studied system in our subset of the InvaCost database, with 1,509 expanded entries (Fig. 2). Invasive species categorized as impacting semi-aquatic habitats were the second most damaging (US$ 292.85 billion, n = 178). Habitats that contained entries of unknown or mixed systems ("diverse/unspecified") were the third most costly (US$ 272.35 billion, n = 85). While invasive species impacting aquatic habitats had the second highest number of entries in our robust database (n = 350), they had the lowest costs (US$ 14.69 billion).

Within North America, the agricultural activity sector was the most impacted group, incurring US$ 527.07 billion in costs (n = 309; Table 1). The second highest costs were recorded in the authorities-stakeholders sector (US$ 45.01 billion, n = 979). Next was the environmental sector with US$ 41.93 billion in costs with 114 entries in our database. The forestry sector incurred US$ 34.93 billion in costs (n = 18). Costs associated with public and social welfare sectors were US$ 41.07 billion (n = 158), and health costs were US$ 19.49 billion (n = 78). Fisheries had the lowest economic costs in our database (US$ 924 million, n = 45). Costs related to sectors that were classified as either "mixed" or "unspecified" also had large economic costs (US$ 94.99 billion, n = 326; US$ 449.86 billion, n = 95, respectively).

Damage costs far outweighed either management costs or mixed costs within North America. We estimated that the North American region-wide cost for direct damage by invasive species is approximately US$ 837.09 billion (n = 690). Our database recorded almost twice as many management costs within North America (n = 1,273) compared to direct damage, yet the measured costs of management were approximately 11% that of direct damage costs (US$ 99.52 billion).

On average, from 1960 to 2017 invasive species cost the North American economy US$ 21.64 billion per year. Annual costs increased from approximately US$ 2.13 billion per year in the 1960s to at least US$ 26.26 billion per year in the 2010s (Fig. 3). However, our estimates in the decade that spans 2010–2017 are likely extremely conservative for two reasons. First, the number of robust data entries from the current

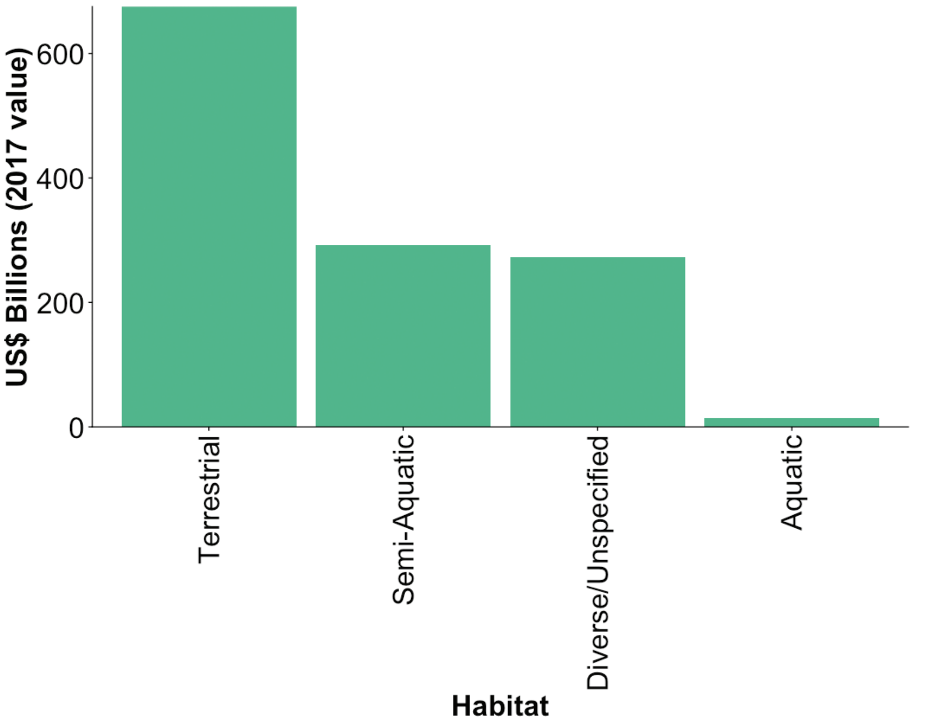

Figure 2. Cost estimates for impacts of invasive species within North America across impacted environments.

Table 1. Reported cost impacts to activity sectors of the North American economy. Numbers of entries are shown in parentheses.

Sector	Cost (in US$ billions)
Agriculture (*n* = 309)	527.07
Unspecified (*n* = 95)	449.86
Mixed (*n* = 326)	94.99
Authorities-stakeholders (*n* = 979)	45.01
Environment (*n* = 114)	41.93
Public and social welfare (*n* = 158)	41.07
Forestry (*n* = 18)	34.93
Health (*n* = 78)	19.49
Fisheries (*n* = 45)	0.92

decade should grow before this decade's end. Second, time lags between occurrence of costs and when the costs are reported may lead to underestimates of economic burdens by invasions for more recent years.

Linkage with CABI and sTwist

There were a large number of species known to be established within North America from the sTwist database that were not present within our robust dataset (161 species

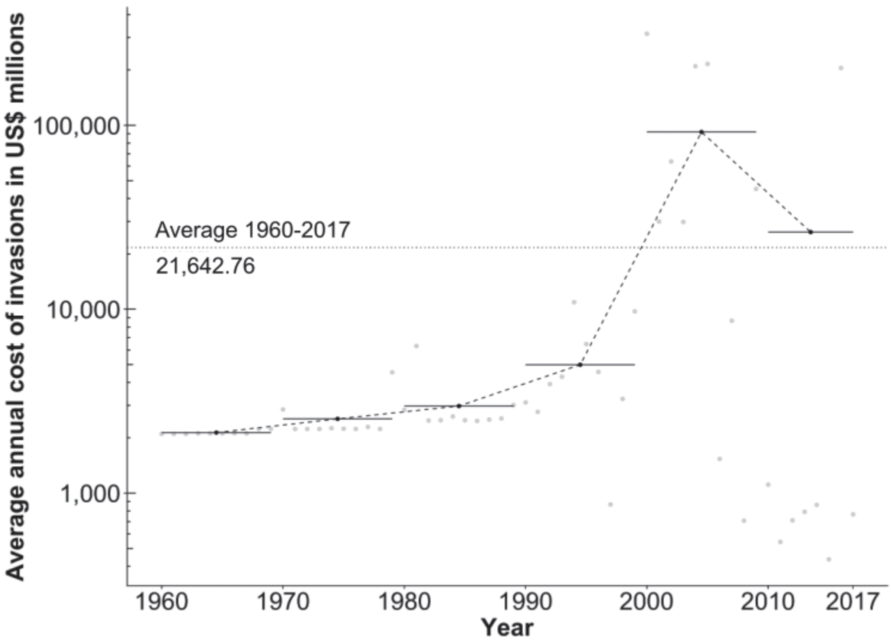

Figure 3. Annual robust costs of invasive species to the North American economy from 1960–2017. Each gray dot represents total annual costs and horizontal lines are decadal averages of economic costs. The dotted line represents the average over the entire period.

or species complexes vs. 305 species reported within sTwist). Establishment dates were unknown in at least one country within the robust dataset (final box in Fig. 1) for 27 of these known established species. Approximately one quarter of establishments were known to have taken place after 1970 (*n* = 113 species-country combinations). The largest discrepancies between sTwist and InvaCost appear to exist for Cuba (Suppl. material 2: Fig. S1, InvaCost 5% complete) and the Dominican Republic (3% complete), while the lowest appears to be for Mexico (75% complete). Canada and the US have an intermediate level of completeness (both 45% complete). When a species was listed in both databases, the total area of the countries over which it was recorded within InvaCost was 96% of the total area of the known set of established countries within sTwist. Of the species within our robust subset that had at least one known date of establishment listed within sTwist (*n* = 12), they averaged 2.7 independent establishments within North America (i.e., not due to secondary spread). There were 145 species within our robust subset where no information on establishment means was present. If we assume that the 161 identified species or species complexes (i.e., not "diverse/unspecified") within our robust subset have caused similar average damages throughout their invaded ranges as defined by sTwist, the total damages incurred within the region due to these species jumps from US$ 353 to 396 billion.

North American InvaCost species have known native ranges spanning all continents outside of Oceania and Antarctica (Fig. 4; S2, *n* = 86). Many species have unknown regions of origin (red flows in Suppl. material 2: Fig. S2a), while many

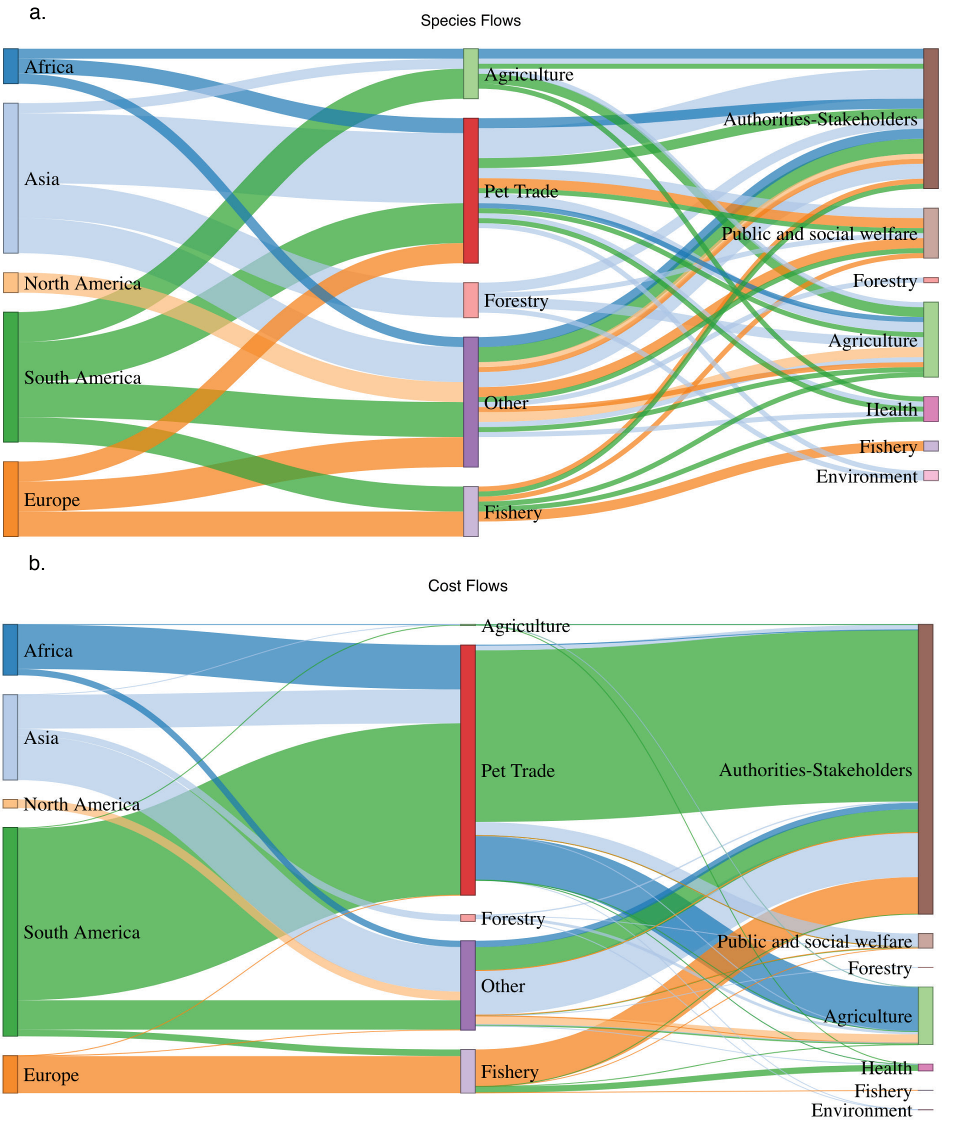

Figure 4. Flows from pathways of entry to impacted sectors proportional to **a** the number of species originating from each continent, and **b** the costs incurred estimated from our robust dataset (2017 US$). Originating nodes and colored flows in this diagram correspond to the continent of origin of each species when available from CABI. The center node labels correspond to dominant entry pathways characterized by CABI (n = 86 species with pathway information), while the destination node labels correspond to impacted sectors within the robust dataset. See Suppl. material 2: Fig. S2 for a more complete examination of flows, including diverse and unknown continents of origin, and impacts to multiple or unspecified sectors.

others possess native ranges spanning multiple continents (dark orange flows in Suppl. material 2: Fig. S2a). Asian, South American and European species have been reported more frequently than North American and African species. The majority of all species have entered via pathways beyond those in Suppl. material 2: Table S2 (mostly via unknown pathways, $n = 73$; but also pathways such as hitchhiking, $n = 15$; and escape from gardens or confinement, $n = 22$). Within the focal pathways we examined, the pet trade was the largest contributor of invaders ($n = 66$, Fig. 4a), followed by agriculture ($n = 24$) and fisheries ($n = 20$). Forestry was the source of a smaller share of invaders, and only one of the invaders was introduced for health purposes. The spread of regions of origin was quite mixed within all pathways. North American species (light orange flows) have been spread primarily via diverse pathways, while Asian species (light blue flows) have been frequently introduced via the pet trade pathway, and have mostly impacted the authorities-stakeholders sector.

When we analyzed invasional flows in terms of costs rather than numbers of species (Fig. 4b; Suppl. material 2: Fig. S2b), the dominant flows were far less complex. The largest costs were due to species with an unknown native range (Suppl. material 2: Fig. S2b), and pet trade and fisheries pathways were the main pathways of introduction that led to costs (Fig. 4b, Suppl. material 2: Fig. S2b). Of species with a known native range, South American species (dark green flows) have dominated the influx of costs from the pet trade pathway (Fig. 4b), and European species (dark orange flows) have done the same for the fisheries pathway, Asian natives have primarily entered via pet trade and diverse pathways (Fig. 4b). Where sectors could be disentangled, South American species (dark green flows) make up a substantial portion of the costs to the authorities-stakeholders sector (Fig. 4b). Asian and European natives also impact this sector to a lesser degree. The small number of African invaders have mostly impacted the agriculture sector after entry via the pet trade pathway. While the small share of North American invaders mentioned previously have produced small costs, they make up a notable share of the costs to the agriculture sector.

Discussion

We show that invasive species cost the North American economy at least US$ 1.26 trillion from 1960–2017. The highest costs from specified taxonomic groups were associated with invasive vertebrates, costs were greatest in the US even when scaled by the number of cost sources, and costs impacting the terrestrial ecosystem were higher than those impacting other habitats. We also found that the agricultural sector bore the largest economic costs across North America, and that yearly costs have been increasing from approximately US$ 2 billion per year in the 1960s to over US$ 26 billion per year in the 2010s. Our robust dataset excluded US$ 1.92 trillion in costs that were classified as having low reliability or predicted costs; when we relax the constraints of our robust dataset, our full dataset suggests costs exceed US$ 3 trillion.

Our analysis of economic impacts of different taxonomic groups suggests that the largest economic impacts come from entries in our database that assigned costs to multiple invasive species (“diverse” entries; US$ 845.21 billion). This finding emphasizes that researchers, when providing economic cost data for invasive species impacts, should provide finer-scale information about their study system (e.g., taxa, impacted sector, years, and habitat) so that further data integration is possible (Diagne et al. 2020b). Besides this rather broad taxonomic category, we showed vertebrates had the highest reported economic impact, in contrast to other reviews that focused on the ecological impacts of invasive species, which indicate that plants are the most studied taxonomic group (Pyšek et al. 2008; Crystal-Ornelas and Lockwood 2020). The discrepancy between our findings for economic impacts and that of ecological-impact syntheses may be due to a lack of taxonomic granularity we mentioned above, or could be due to discrepancies between the species that are studied for their ecological impacts and those that are studied for their economic impacts (Jeschke et al. 2014).

Even when controlling for the number of cost sources produced by each country in our database, invasion costs in the US far outweighed other countries within North America (US$ 5.81 billion in costs per source in the US). However, costs in other countries, scaled by the number of cost sources were still large (e.g., US$ 57.01 million per cost source in Cuba), despite a low sample size (n = 6, including non-English cost sources). Furthermore, costs in North America as a whole were substantially higher than other geographic regions, including Africa (Diagne et al. 2021b), Asia (Liu et al. 2021), Europe (Haubrock et al. 2021) and South America (Heringer et al. 2021). National-scale differences within North America indicate that the low magnitude of reported costs for some countries are either a result of the entrenched geographical biases in invasion ecology (Pyšek et al. 2008; Bellard and Jeschke 2016; Crystal-Ornelas and Lockwood 2020; Angulo et al. 2021a) and more broadly in ecology (Nuñez and Pauchard 2010; Martin et al. 2012; Nuñez et al. 2019), or that they reflect actual differences in invasion histories and international trade that promote opportunities for introduction and potential economic impacts. Cuba and the Dominican Republic have similar numbers of records in sTwist compared to Mexico, but Mexico has many more records within our robust (both observed and highly reliable) dataset (Rico-Sánchez et al. 2021), suggesting that our cost underestimation is greater in Cuba and the Dominican Republic. Further, while the US has roughly twice as many InvaCost records compared to Canada, it has more than four times the number of sTwist records. This suggests the 30-fold difference in economic impact between the US and Canada derived from InvaCost could be a substantial underestimate of the difference in total cost to each nation (i.e., an even more important underestimation of costs in Canada). Last, despite the presence of known damaging invaders, our robust subset of InvaCost included no reports of economic costs in Jamaica.

Only one species (of 161) within the robust dataset is known to be established in all 5 countries (*Columba livia*), and none have cost records in each country. However, three other species are predicted to have region-wide distributions in the more complete sTwist database (*Cyprinus carpio*, *Passer domesticus*, *Phasianus colchicus*). If we assume that *C. livia* has the same average costs across the entire North American region, its total estimated costs jump from US$ 2.95 billion to US$ 6.7 billion.

The most economically impacted habitat within North America was the terrestrial system, and this may be driven by the high economic costs associated with agriculture and forestry sectors within North America. This concurs with other predictions that the US would experience massive agricultural, and therefore terrestrial, costs from invasive species (Paini et al. 2016). We note that a substantial amount of impact (US$ 272.35 billion) was attributed to habitats that could not be classified into a single category ("diverse/unspecified" in our database), suggesting that a non-negligible portion of reported costs was not clearly associated with specific information for this descriptor. Fisheries showed the lowest amount of economic impact (US$ 924 million), although this sector was important in individual countries such as Mexico (Rico-Sánchez et al. 2021). This was likely due to the relatively low number of expanded entries (*n* = 45), since studies across the continent suggest invasions can have negative impacts on fisheries (Walsh et al. 2016), even if some studies do not directly quantify the economic costs (Dunlop et al. 2019). Furthermore, many impacts to fisheries are extrapolated due to the difficulties in quantifying damages in submerged habitats, and thus were excluded largely from our analyses. More broadly within InvaCost, impacts from aquatic invaders have been found to be several times lower than from terrestrial taxa, and disproportionately low relative to known numbers of alien taxa between those habitats worldwide (Cuthbert et al. 2021a). Such a low degree of cost reporting in aquatic realms may reflect a lack of human assets in those systems, or reflect a wider bias in ecology towards terrestrial ecosystems (Menge et al. 2009).

We found that direct damage costs were much higher than management costs (US$ 837.09 billion and US$ 99.52 billion, respectively). This pattern is consistent with global findings (Diagne et al. 2020b, 2021a), although some individual countries presented the opposite pattern (e.g. Spain, Ecuador or Japan; Angulo et al. 2021b; Ballesteros-Mejia et al. 2021; Watari et al. 2021). Previous research suggests rapid intervention (Leung et al. 2005; Simberloff et al. 2013; Ahmed et al. 2021) can potentially offset greater direct damage costs in the future, and we may be seeing patterns of this trade-off where locations incurring higher damage costs spend less on management. Moreover, management costs are relatively easier to track and reliably quantify, so this may be why our database contains nearly twice as many entries for management as it does for damages.

Given that invasion rates have increased over the past 200 years (Seebens et al. 2017), we predicted that the economic costs of invasions would follow the same trend from 1960–2017. Whilst this expectation held true, we highlight that the dip in economic costs from 2010–2017 compared to the previous decade is likely due to a lag between when costs are incurred and when the costs are reported, such that the most recent years in the database (2010–2017) have fewer entries (*n* = 224 [28/year]) than the previous decade (2000–2009, *n* = 401 [40/year]). We also suggest that invasion debt is an important concept for tracking economic costs of invasions over time. Research on invasion debt suggests that some of the most ecologically impactful species in the early 2000s had arrived in the early 1900s (Essl et al. 2011). It follows, then, that the species having the most severe economic impacts to North American sectors and habitats at the present time may be more reflective of socioeconomic conditions decades ago, and that the present socioeconomic conditions may result in a new suite of species having different economic impacts. Indeed, invasion costs have been found to be significantly positively related to the length of time an alien species has been present (Cuthbert et al. 2021b). This particular analysis should be updated when additional reliable cost estimates from 2010–2019 are available.

Most North American invasive species have not been assessed for economic impacts, and often, invasive species cause impacts that are non-market in nature (Hanley and Roberts 2019; Diagne et al. 2020a). We accept that not all invasive species will have a measurable economic impact, with many affecting non-market sectors that are difficult to monetize. Nonetheless, the considerable difference between sTwist and the species recorded for North America in our dataset is surely yet another indication that the overall cost estimated here is a huge underestimation of the real cost, as we suspect that many of the species causing non-market impacts could be missed by both our dataset and sTwist. The set of species recorded within sTwist alone remains quite data poor, as establishment dates are unknown in at least one country within the North American invaded range for the majority of these species, indicating that they are poorly studied. The remaining discrepancy does not appear to be due to a large number of pre-colonial invaders within sTwist (which are not considered invasive by InvaCost), as only 21 records are from before 1800. Instead, the difference may be due to lags between initial detection and economic impact (Coutts et al. 2018). Roughly one quarter of the sTwist establishment records correspond to establishments after 1970, placing them well within previously identified lag periods (Essl et al. 2011). While some of these more contemporary invaders may already be causing substantial ecological and/or economic impacts, the worst costs may only be incurred in the next 50 years or more, and/or they may have yet to have their impacts measured by researchers. Canada appears to have benefitted from more consistent effort in detecting invasive species over time, potentially leading to better detection of subsequent damages, while the other countries have seen an increase in detection in more recent years, potentially indicating a greater likelihood of lags in damage detection.

Economically-damaging invaders to North America come from all over the world and have been introduced due to a variety of pathways. As expected, the pet trade, agriculture, and fisheries pathways have led to the invasion of many species (Aizen et al. 2018; Stringham and Lockwood 2018), but less well-examined pathways have also led to substantial costs. Invasive North American natives have produced detectable, but nevertheless small, costs within the region. In contrast, several species are reported to have invaded North America repeatedly. This suggests that countries within the region are at risk to the same suites of species, and may benefit from increasing information sharing on potential threat species (e.g., through initiatives such as the proposed North America Multilateral Invasive Species Project Inventory). To date, the greatest threats are from species native to South America and Asia, particularly those entering via the pet trade and diverse pathways, as they are the source of a disproportionate amount of the costs incurred.

Syntheses like ours are limited in scope by the available knowledge base from which we constructed our database. Other factors related to climate change or the importance of global trade routes make it difficult to predict the sectors and habitats that will bear costs in the future (Bradshaw et al. 2016). Moreover, economic impacts for most invasive species are still yet to be quantified, and a 2010 review suggested that economic impacts were recorded for only 13% of the known invasive species in Europe (Vilà et al. 2010). This is an underestimate compared to our analysis of completeness relative to sTwist (~50% complete), but we note that species may be missing from both databases. We also stress that while the costs for Canada, Mexico, and Cuba were substantial, the number of entries in our database were small compared to those of the US, without any a priori reason to believe they reflect fewer actual costs. In summary, we present the first estimate of how much invasive species cost the North American economy, and our estimate of over US$ 1 trillion is likely very conservative. Building more robust economic assessments of invasion impacts in these countries will make for even more accurate, and likely higher, cost estimates for North America.

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Supplementary material 1

Supplementary file. Dataset of the costs of biological invasions in North America.

Authors: Robert Crystal-Ornelas, Emma J. Hudgins, Ross N. Cuthbert, Phillip J. Haubrock, Jean Fantle-Lepczyk, Elena Angulo, Andrew M. Kramer, Liliana Ballesteros-Mejia, Boris Leroy, Brian Leung, Eugenia López-López, Christophe Diagne, Franck Courchamp

Data type: table

Explanation note: This supplementary file contains the cost estimates from the InvaCost database that were used to estimate invasion costs in North America. The spreadsheet 'full_dataset' shows cost information for invasions across all of North America. The 'robust_dataset' spreadsheet shows the filtered dataset used for the analyses in our manuscript. The 'field_description' spreadsheet provides definitions for each column name in the InvaCost database. The spreadsheet 'field_classifications' shows the different categories available for each field in the InvaCost database.

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Supplementary material 2

Tables S1, S2 and Figures S1, S2

Authors: Robert Crystal-Ornelas, Emma J. Hudgins, Ross N. Cuthbert, Phillip J.Haubrock, Jean Fantle-Lepczyk, Elena Angulo, Andrew M. Kramer, Liliana Ballesteros-Mejia, Boris Leroy, Brian Leung, Eugenia López-López, Christophe Diagne, Franck Courchamp

Data type: table and figures

Explanation note: **Table S1.** Classification of the types of costs ("Type of cost" column in the InvaCost database) into "damage" (economic losses due to direct and/or indirect impacts of invaders), "management" (monetary resources allocated to mitigate the spread and/or impacts of invaders), or "mixed" (when costs correspond both previous categories simultaneously). We assigned unspecified when the nature of cost was not defined. **Table S2.** Search terms used to match invasive species that have economic impacts in North America to pathways of introduction from CABI. **Figure S1.** Comparison of the timeline of establishment records of invasive species within the sTwist database (upper violin plots, black species counts) and records of species economic costs within our robust subset of InvaCost (lower violin plots, grey species counts) over time. **Figure S2.** Flows from pathways of entry to impacted sectors proportional to a) the number of species originating from each continent (including unknown and diverse origins), and b) to the costs incurred estimated from our robust dataset (2017 US$).

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RESEARCH ARTICLE

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Advancing research on alien species and biological invasions

Detailed assessment of the reported economic costs of invasive species in Australia

Corey J.A. Bradshaw[1,2], Andrew J. Hoskins[3], Phillip J. Haubrock[4,5], Ross N. Cuthbert[6,7], Christophe Diagne[8], Boris Leroy[9], Lindell Andrews[10], Brad Page[10], Phillip Cassey[11], Andy W. Sheppard[12], Franck Courchamp[8]

1 *Global Ecology Partuyarta Ngadluku Wardli Kuu, College of Science and Engineering, Flinders University, GPO Box 2100, Tarndanya (Adelaide), South Australia 5001, Australia* **2** *ARC Centre of Excellence for Australian Biodiversity and Heritage. EpicAustralia.org.au, Australia* **3** *Commonwealth Scientific and Industrial Research Organisation, Health and Biosecurity, James Cook Drive, Townsville, Queensland 4811, Australia* **4** *Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, Gelnhausen, Germany* **5** *University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Centre of Aquaculture and Biodiversity of Hydrocenoses, Zátiší 728/II, 389 25, Vodňany, Czech Republic* **6** *GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Düsternbrooker Weg 20, Kiel, Germany* **7** *School of Biological Sciences, Queen's University Belfast, 19 Chlorine Gardens, Belfast, BT9 5DL, Northern Ireland, UK* **8** *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405, Orsay, France* **9** *Unité Biologie des Organismes et Ecosystèmes Aquatiques (BOREA, UMR 7208), Muséum national d'Histoire naturelle, Sorbonne Université, Université de Caen Normandie, CNRS, IRD, Université des Antilles, Paris, France* **10** *Department of Primary Industries and Regions South Australia, Government of South Australia, CSIRO Building 1, Entry 4, Waite Road Urrbrae, Adelaide, South Australia 5001, Australia* **11** *School of Biological Sciences, University of Adelaide, Adelaide, South Australia 5005, Australia* **12** *Commonwealth Scientific and Industrial Research Organisation, Health and Biosecurity, GPO BOX 1700, Canberra, Australian Capital Territory 2601, Australia*

Corresponding author: Corey J.A. Bradshaw (corey.bradshaw@flinders.edu.au)

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Abstract

The legacy of deliberate and accidental introductions of invasive alien species to Australia has had a hefty economic toll, yet quantifying the magnitude of the costs associated with direct loss and damage, as well as for management interventions, remains elusive. This is because the reliability of cost estimates and under-sampling have not been determined. We provide the first detailed analysis of the reported costs associated with invasive species to the Australian economy since the 1960s, based on the recently published InvaCost database and supplementary information, for a total of 2078 unique cost entries. Since the 1960s, Australia has spent or incurred losses totalling at least US$298.58 billion (2017 value) or AU$389.59 billion (2017 average exchange rate) from invasive species. However, this is an underestimate given that costs rise as the number of estimates increases following a power law. There was an average 1.8–6.3-fold increase in the total costs per decade since the 1970s to the present, producing estimated costs of US$6.09–57.91 billion year^{-1} (all costs combined) or US$225.31 million–6.84 billion year^{-1} (observed, highly reliable costs only). Costs arising from plant species were the highest among kingdoms (US$151.68 billion), although most of the costs were not attributable to single species. Of the identified weedy species, the costliest were annual ryegrass (*Lolium rigidum*), parthenium (*Parthenium hysterophorus*) and ragwort (*Senecio jacobaea*). The four costliest classes were mammals (US$48.63 billion), insects (US$11.95 billion), eudicots (US$4.10 billion) and monocots (US$1.92 billion). The three costliest species were all animals – cats (*Felis catus*), rabbits (*Oryctolagus cuniculus*) and red imported fire ants (*Solenopsis invicta*). Each State/Territory had a different suite of major costs by species, but with most (3–62%) costs derived from one to three species per political unit. Most (61%) of the reported costs applied to multiple environments and 73% of the total pertained to direct damage or loss compared to management costs only, with both of these findings reflecting the availability of data. Rising incursions of invasive species will continue to have substantial costs for the Australian economy, but with better investment, standardised assessments and reporting and coordinated interventions (including eradications), some of these costs could be substantially reduced.

Abstract in Pitjantjatjara

Kuka munu ukiri kutjupa tjutangku manta nganampa kurantja alatjitu. Kuli kutjupa kuli kutjupa anangu kutjupa tjutangku kuka kutjupa kutjupa tjuta munu punu kutjupa kutjupa tjuta ngura kutjupa pararinguru ngalya-katipai Australiala-kutu. Ka kuka munu punu nyanga malikitja tjutangku ngura nganampa kuralpai alatjitu, kala palulanguru nganana mani pulkangka payamilalpai ngura wirura kanyintjikitjangku, mani nampa nyangangka 6,000,000,000 dollars, mani pulka mulata. Palu nganana mani pulka mulata manti payamilalpai mani panya palula munkara alatjitu, panya nganana tjukutjukuku kutju ninti kukaku munu punuku paluru tjana panya manta nyanga kurannyangka. Panya kuka munu punu tjutangku manti ngura nyanga palunya pulkara kurani, kala tjukutjukuku kutju nintiringu. Ka kutjupa tjutangku ngura kutjupanguru uninypa kura ngalya-katira manta nyanga palula para-wanira wanannyangka ukiri kura mulapa pakara pulkaringkupai munu lipiringkupai manta winkingka uninypa panya palulanguru, munu manta kuralpai alatjitu. Ka pala palu purunytju kuka kutjupa tjutangku pulkara kuralpai manta nyanga nganampa, kuka nyangantu: ngaya, putji, rapita munu minga kura, minga panya mututa, pikati pulka. Kuka nyanga paluru tjana manta kuralpai alatjitu ukiringka munkara alatjitu. Tjinguru anangu tjutangku titutjarangku kutjupa kutjupa tjuta ngura kutjupa-nguru ngalya-katinyangkampa ka paluru tjana pulkara kuralku manta nyanga palunya. Palu nganana uti manta panya wirura kanyinma, kutjupa tjutangku kurantjaku-tawara. Munu palulanguru nganana mani pulkangka payamilantja wiya ngura nyangatja palya ngaranyangka.

Abstract in Chinese

对澳大利亚已报道的入侵物种造成经济损失的详细评估

无意和有意引入的外来入侵物种已经给澳大利亚的经济造成了巨大损失。然而，对生物入侵造成的经济损失和相应的管理投入进行定量仍较困难，因为我们当前缺乏可靠且全面的生物入侵造成经济损失的数据。为填补这一空缺，我们利用最近发表的InvaCost数据库及其相应的补充信息，根据自20世纪60年代以来报道的2078条数据，首次分析了生物入侵对澳大利亚经济造成的损失。自20世纪60年代以来，生物入侵已经澳大利亚造成了至少2985.8亿美元（2017年的价值）或3895.9亿澳元的经济损失（2017年的平均汇率)。然而，这一数字仍被

低估，因为经济损失会随着数据数量的增加而呈幂律上升。20世纪70年代至今，经济损失平均每十年便会增加1.8–6.3倍，其对应的增长速度为60.9–57.1亿美元/年（所有损失的数据)，或2.2531亿-68.4亿美 元/年（仅考虑实测到的且可靠较高的数据)。外来植物入侵产生的损失为各生物界中最高的(1516.8亿美元)，尽管大部分的损失不是由单一物种造成。在已确定的入侵杂草中，造成经济损失最高的物种是硬直黑麦草 (*Lolium rigidum*)、银胶菊 (*Parthenium hysterophorus*) 和新疆千里光 (*Senecio jacobaea*)。造成经济损失最高的四个类群分别是哺乳动物 (486.3亿美元)、昆虫 (119.5亿美元)、真双子叶植物 (41.0亿美元)和单子叶植物 (19.2亿美元)。造成经济损失最高的 三个物种都是动物，分别为家猫 (*Felis catus*)、家兔 (*Oryctolagus cuniculus*) 和入侵红火蚁 (*Solenopsis invicta*)。每个州/领地的主要经济损失由不同 物种造成，但是各行政单元的大多数 (3–62%) 损失可归于一至三个物种。大多数 (61%) 经济损失是由入侵物种在多个环境中造成 的，且73%的总损失与直接的经济损失相关，而非与管理投入相关。这两个结果反映了数据的可用性。日益增多的入侵物种将持续对澳大利亚的经济造成巨大损失。但是，如果有更合理的经费投入、标准化的评估和报告、以及协调的干预措施 (包括根除)，生物入侵造成的经济损失 可被极大地降低。

Abstract in Bahasa Indonesia

Kajian lengkap mengenai kerugian ekonomi yang diakibatkan oleh spesies invasif di Australia. Dampak dari masuknya spesies invasif, baik secara sengaja maupun tidak, ke dalam Australia telah mengakibatkan kerugian perekonomian yang besar, namun mengukur besarnya kerugian yang terkait biaya dan kerusakan secara langsung, juga terkait pengeluaran untuk manajemen intervensi, masih sulit untuk dilakukan. Hal ini karena tingkat keandalan dari estimasi kerugian dan pengambilan sampel belum diketahui. Di sini kami memaparkan analisis mendetil untuk pertama kalinya mengenai kerugian yang terkait dengan keberadaan spesies invasif terhadap perekonomian Australia sejak tahun 1960an, berdasarkan *database* InvaCost yang baru-baru ini dipublikasikan dan informasi tambahan lainnya, dengan total 2078 buah entri unik terkait biaya kerugian. Sejak tahun 1960an, Australia telah mengeluarkan atau mengalami kerugian yang mencapai setidaknya US$295.58 milyar (nilai tahun 2017) atau AU$389.59 milyar (nilai tukar 2017) akibat keberadaan spesies invasif. Namun, nilai ini masih merupakan estimasi yang lebih rendah dari yang sesungguhnya dikarenakan oleh peningkatan kerugian secara eksponensial seiring bertambahnya data. Secara rata-rata terdapat peningkatan secara 1.8–6.3 kali dari biaya kerugian total untuk setiap dekade sejak 1970an hingga sekarang, menghasilkan estimasi kerugian sebesar US$6.09–57.91 milyar per tahun (seluruh biaya disatukan) atau US$225.31 juta–6.84 milyar per tahun (teramati, hanya nilai kerugian yang dapat diandalkan). Kerugian yang dihasilkan dari spesies tumbuhan paling tinggi diantara kingdom yang lain (US$151.68 milyar), namun sebagian besar dari kerugian ini tidak diakibatkan oleh spesies tunggal. Dari tanaman rumput liar yang teridentifikasi, yang paling besar mengakibatkan kerugian adalah rumput *Lolium rigidum*, rumput *Parthenium hysterophorus*, dan rumput *Senecio jacobaea*. Untuk tingkatan kelas, yang mengakibatkan kerugian paling besar adalah mamalia (US$48.63 milyar), serangga (US$11.95 milyar), tanaman dikotil sejati/eudikot (US$4.10 milyar) dan monokotil (US$1.92 milyar). Untuk tingkatan spesies, tiga spesies yang paling mengakibatkan kerugian adalah spesies hewan, yaitu kucing (*Felis catus*), kelinci (*Oryctolagus cuniculus*) dan semut api (*Solenopsis invicta*). Setiap negara bagian memiliki pola kerugian terbesar yang berbeda berdasarkan jenis spesies, namun kerugian terbesar (3–62%) datang dari satu hingga tiga spesies per unit politik. Sebagian besar (61%) dari kerugian yang terlaporkan terjadi pada berberapa jenis lingkungan dan 73% dari keseluruhan termasuk ke dalam kerusakan atau kerugian secara langsung dibandingkan dengan biaya manajemen saja, dengan catatan bahwa kedua penemuan ini mencerminkan ketersediaan data. Peningkatan masuknya spesies invasif akan terus menghasilkan kerugian yang nyata untuk perekonomian Australia, namun dengan investasi yang lebih baik, penyeragaman dari pengukuran dan pelaporan dan juga pengkoordinasian intervensi (termasuk pembasmian), beberapa kerugian ini dapat dikurangi secara substansial.

Abstract in Tok Pisin

Stadi lon painim aut kostim lon ol nogut binatang na diwai kam insait lon Austrelia. Taim ol nogut binatang na diwai bilong longwe ples kamap lo Austrelia, ol bagarapim kantri stret. Tasol em hatwok yet lon lukim hamas stret moni dispela bagarap em givim lo kantri. Dispela em bikos nogat gutpela stadi lo kostim em kamap yet. Tasol nau, dispela em nambawan stadi em lukluk lon hamas stret moni Austrelia usim lon lukautim na managim dispela wari (lon ol nogut binatang na diwai kam insait lo kantri), lon 1960s kam inap nau; ol wokman lo stadi lukluk lon kainkain save lon mekim dispela kostim. Bifo lon 1960s kam inap nau, Austrelia givim moni mak olsem US$298.58 billion (lon 2017) or AU$389.59 billion (lon 2017 namel namba) lo lukautim ol yet lon binatang nogut. Tasol dispela moni mak em ino stret tumas bilong wanem ol namba save senis olgeta taim. Na tu, lon 1970s kam, ibin gat 1.8–6.3% moa kostim olgeta tenpela yia kam inap tede, moni mak olsem US$6.09–57.91 billion yia-1 (olgeta kostim wantaim) or US$225.31 million–6.84 billion. Ol kostim bilong olgeta nogut diwai wantaim em bikpela olgeta (US$151.68 billion). Lo sait blo gras nogut, sampela olsem *ryegrass* (*Lolium rigidum*), *parthenium* (*Parthenium hysterophorus*) na *ragwort* (*Senecio jacobaea*) em planti moni stret. Na tu, lon sait lon banisim ol abus, ol *mammal* (US$48.63 billion), binatang (US$11.95 billion), *eudicots* (US$4.10 billion) na *monocot* (US$1.92 billion) usim planti moni tu. Lon sait lon banisim olgeta abus wantaim, ol pusi (*Felis catus*), *rabbit* (*Oryctolagus cuniculus*) na retpela paia anis (*Solenopsis invicta*) usim bikpela moni stret. Olgeta provins lo Austrelia givim planti moni lo lukautim ol yet lon ol nogut binatang na diwai, tasol dispela moni ol givim (3–62%) save go lon wanpla or tripela binatang/diwai nogut tasol. Planti lon dispela moni (61%) em ol provins givim lon lukautim planti kainkain bus/bikbus insait lo graun blo ol, na 73% lo dispela olgeta moni em ol usim lon lukautim bus/bikbus we binatang bagarapim pinis; ol no usim moni lo sait lo lukautim bifo bus/bikbus bagarup. Tede, ol nogut binatang na diwai kam insait lo Austrelia na wok lon bagarapim kantri yet, tasol sapos igat moa moni, and tu ol ripot na wok bung wantaim kamap, sampela dispela ol kostim bai go daun.

Abstract in French

Estimation de l'ensemble des coûts économiques des espèces exotiques envahissantes en Australie. L'histoire des introductions intentionnelles et accidentelles des espèces exotiques envahissantes en Australie a un coût économique élevé. La quantification de l'ampleur de ce coût associé aux pertes directes ainsi qu'aux dommages demeure pourtant inconnue. La difficulté d'arriver à une estimation robuste du montant total est exacerbée par un échantillonnage insuffisant et un manque de protocoles pour déterminer la robustesse des estimations de coûts individuels. Nous fournissons le premier bilan des coûts associés aux espèces envahissantes à l'économie australienne depuis les années 1960, à partir de la base de données InvaCost récemment publiée, enrichie d'estimations supplémentaires. À partir de 2078 estimations uniques de coûts, nous estimons que l'Australie a subi un coût total de US$298,58 milliards (valeur 2017, soit AU$389,59 milliards). Ce total doit cependant être une sous-estimation parce que les coûts augmentent exponentiellement avec le nombre d'estimations. Le taux d'augmentation des coûts par décennie était de 1,8 à 6,3 fois depuis les années 1970 jusqu'au présent, ce qui indique un montant annuel de US$6,09–57,91 milliards (tous les coûts compris), soit US$2,25 millions à 6,84 milliards par an (coûts observés et robustes uniquement). Les coûts associés aux espèces végétales (US$151,68 milliards) étaient les plus élevés parmi les règnes que nous avons considérés, même si la plupart de ce montant était associée aux groupements d'espèces et non aux espèces individuelles. Parmi les plantes, les coûts les plus élevés sont venus de l'ivraie raide (*Lolium rigidum*), l'absinthe marron (*Parthenium hysterophorus*) et le séneçon jacobé (*Senecio jacobaea*). Les classes les plus coûteuses étaient respectivement les mammifères (US$48,63 milliards), les insectes (US$11,95 milliards), les Eudicotylédones (US$4,10 milliards) et les Monocotylédones (US$1,92 milliards). Les espèces individuelles les plus coûteuses étaient tous les animaux : le chat haret (*Felis catus*), le lapin européen (*Oryctolagus cuniculus*) et la fourmi de feu (*Solenopsis invicta*). Le bilan de coûts dominants différait selon l'unité politique (états et territoires), mais la plupart (entre 3 et 62% selon l'unité politique) provenait d'une à trois espèces. La majorité (61%) des coûts se rapportait aux plusieurs environnements et 73% du montant total était associés aux dommages ou aux pertes directes (ex, coûts de gestion), qui reflètent la disponibilité des données. L'augmentation des espèces exotiques envahissantes va occasionner des coûts considérables à l'économie australienne dans les années à venir. De meilleurs investissements, des évaluations standardisées, et des interventions bien organisées pourraient cependant contribuer à une réduction considérable des coûts venant des espèces exotiques envahissantes dans le pays.

Abstract in Spanish

Evaluación detallada de los costos económicos registrados de las especies invasoras en Australia. El legado de introducciones deliberadas y accidentales de especies exóticas invasoras en Australia ha tenido un costo económico considerable, sin embargo la cuantificación de la magnitud de los costos asociados con las pérdidas y daños directos, así como de las intervenciones de manejo, sigue siendo difícil de realizar. Esto se debe a que no se ha determinado la confiabilidad de las estimaciones de costos y el submuestreo. En este trabajo, proporcionamos el primer análisis detallado de los costos reportados asociados a especies invasoras para la economía australiana desde la década de 1960, basado en la base de datos InvaCost recientemente publicada e información complementaria para un total de 2078 registros únicos de costos. Desde la década de 1960, Australia ha gastado o incurrido en pérdidas un total de al menos US $298,58 mil millones (valor de 2017) o AU $389,59 mil millones (tipo de cambio promedio de 2017) debido a especies invasoras. Sin embargo, esto es una subestimación dado que los costos aumentan a medida que aumenta el número de estimaciones siguiendo una ley de potencia. Hubo un aumento promedio de 1.8 a 6.3 veces en los costos totales por década desde la década de 1970 hasta el presente, produciendo costos estimados de US $6,09 a 57,91 mil millones año^{-1} (todos los costos combinados) o US $225,31 millones a US $6,84 mil millones año^{-1} (solo costos observados, altamente confiables). Los costos derivados de especies de plantas fueron los más altos entre todos los reinos (US $151,68 mil millones), aunque la mayoría de los costos no se atribuyeron a una sola especie. De las especies de malezas identificadas, las más costosas fueron el raigrás anual (*Lolium rigidum*), la falsa altamisa (*Parthenium hysterophorus*) y la hierba cana (*Senecio jacobaea*). Las cuatro clases más costosas fueron mamíferos (US $48,63 mil millones), insectos (US $11,95 mil millones), eudicotiledoneas (US $4,10 mil millones) y monocotiledóneas (US $1,92 mil millones). Las tres especies que produjeron los mayores costos fueron animales: gatos (*Felis catus*), conejos (*Oryctolagus cuniculus*) y hormigas rojas importadas (*Solenopsis invicta*). Cada estado / territorio tuvo un conjunto diferente de costos principales por especie, pero la mayoría de los costos (3–62%) derivaron de una a tres especies por unidad política. La mayoría (61%) de los costos reportados aplicaron a múltiples hábitats y el 73% del total de costos correspondió a daños o pérdidas directas en comparación con los costos de manejo únicamente, ambos hallazgos reflejan la disponibilidad de datos. El aumento de las incursiones de especies invasoras seguirá teniendo costos sustanciales para la economía australiana, pero con una mejor inversión, estandarización de evaluaciones y de informes e intervenciones coordinadas (incluidas las erradicaciones), algunos de estos costos podrían reducirse considerablemente.

Abstract in Portuguese

Avaliacão detalhada dos registos de custos económicos associados a espécies invasoras na Austrália. O legado de introduções deliberadas e acidentais de espécies exóticas invasoras na Austrália tem resultado em custos económicos consideráveis. Contudo, calcular a magnitude dos custos associados a perdas diretas e danos, bem como dos custos associados com intervenções de gestão, não é imediato. Este desfazamento está relacionado com o nível indeterminado de confiança nas estimativas de custo e com a sub-amostragem. Nós providenciamos a primeira análise detalhada dos registos australianos de custos associados a espécies invasoras desde os anos 60, com base na publicação recente da database InvaCost e respectiva informação complementar, para o total de 2078 registos únicos de custo. Desde a década de 1960, a Austrália incorreu um gasto total de, no mínimo, US$298.58 mil milhões (valor de 2017) ou AU$389.59 mil milhões (ao câmbio medio de 2017) devido a espécies invasoras. Este valor está contudo subestimado, uma vez que o custo aumenta com o aumento de estimativas de custo de acordo com o modelo da lei de potência. Houve, em média, um aumento de 1.8 a 6.3 vezes no custo total por década desde os anos 70 até ao presente, levando a uma estimativa de custo de US$6.09 a 57.91 mil milhões ano^{-1} (para todos os custos combinados) ou US$225.31 milhões a 6.84 mil milhões ano^{-1} (só para custos observados, de elevada confiança). Os custos derivados de espécies de plantas foram os mais altos de entre todos os reinos taxonómicos (US$151.68 mil milhões), embora a maioria dos custos não possam ser atribuídos a uma única espécie. Das espécies de ervas daninhas identificadas, as que resultaram em custos mais elevados foram o azevém anual (*Lolium rigidum*), a artemísia falsa (*Parthenium hysterophorus*) e a tasninha (*Senecio jacobaea*). As quatro classes taxonómicas mais caras foram: mamíferos (US$48.63 mil milhões), insectos (US$11.95 mil milhões), eudicotiledóneas (US$4.10 mil milhões) e monocotiledóneas (US$1.92 mil milhões). As três espécies mais caras corresponderam aos seguintes animais – gatos (*Felis catus*), coelhos (*Oryctolagus cuniculus*) e formigas de fogo (*Solenopsis invicta*). Cada Estado ou Território australiano teve um conjunto diferente de custos principais por espécie, mas a maioria (3–62%) dos custos foram associados com uma, ou até três, espécies por unidade política. A maioria (61%) dos custos registados foram aplicados a múltiplos ambientes e 73% do total de custos correspondeu a danos ou perdas diretas em comparação com apenas os custos de gestão; ambos os resultados refletindo a disponibilidade de dados. O aumento de espécies invasoras vai continuar a ter um custo substancial na economia Australiana, mas com um melhor plano de investimento, com padrões iguais para avaliações e registos e com intervenções coordenadas (incluindo extermínio), alguns destes custos podem ser substancialmente reduzidos.

Abstract in Italian

Stima dei costi economici riportati delle specie esotiche invasive in Australia. Il lascito delle introduzioni intenzionali o accidentali di specie aliene invasive in Australia ha avuto un pesante conto, ciononostante, la quantificazione della magnitudine dei costi associati alla perdita diretta e ai danni, così come agli interventi di gestione, rimane elusiva. Questo perché l'attendibilità delle stime dei costi e i sottocampionamenti non sono stati determinati. Noi forniamo la prima analisi dettagliata dei costi riportati per l'economia australiana associati alle specie invasive dagli anni '60, basati sulla banca dati recentemente pubblicata InvaCost e informazioni supplementari, per un totale di 2078 voci di costo univoche. Dagli anni '60, l'Australia ha speso o ha subito perdite per un totale di almeno 298,58 miliardi di $ americani (valore del 2017) o 389,59 miliardi di $ australiani (tasso medio di conversione del 2017) per le specie invasive. Comunque, questa è una sottostima, dato che i costi aumentano all'aumentare del numero di stime, seguendo una legge di potenza. C'è un aumento medio nei costi totali di 1,8–6,3 volte per decennio dagli anni '70 ad oggi, producendo costi stimati a 6,09–57,91 miliardi di $ americani all'anno (tutti i costi combinati) o 225,31 milioni-6,84 miliardi di $ americani all'anno (solo costi osservati e con alta attendibilità). I costi derivanti dalle specie vegetali sono quelli più alti tra i regni (151,68 miliardi di $ americani), sebbene la maggior parte dei costi non sia attribuibile a singole specie. Tra le specie infestanti identificate, le più costose sono il loglio rigido (*Lolium rigidum*), il partenio (*Parthenium hysterophorus*) e il senecione di S. Giacomo (*Senecio jacobaea*). Le quattro classi più costose sono: mammiferi (48,63 miliardi di $ americani), insetti (11,95 miliardi di $ americani), eudicotiledoni (4,10 miliardi di $ americani) e monocotiledoni (1,92 miliardi di $ americani). Le tre specie più costose sono animali: il gatto domestico (*Felis catus*), il coniglio selvatico europeo (*Oryctolagus cuniculus*) e la formica fuoco (*Solenopsis invicta*). Ogni Stato/territorio ha una diversa serie di costi principali per specie, ma la maggior parte dei costi (3–62%) deriva da una a tre specie per unità politica. La maggior parte dei costi riportati (61%) si applica a più ambienti e il 73% del totale riguarda il danno diretto o la perdita, piuttosto che i costi di sola gestione, con entrambi questi risultati che riflettono la disponibilità di dati. Le crescenti incursioni delle specie invasive continueranno ad avere costi notevoli per l'economia australiana, ma con un migliore investimento, monitoraggi e rendicontazioni standardizzati e interventi coordinati (comprese le eradicazioni), alcuni di questi costi potrebbero essere sostanzialmente ridotti.

Abstract in German

Detaillierte Bewertung der gemeldeten wirtschaftlichen Kosten invasiver Arten in Australien. Die absichtlichen und versehentlichen Einschleppungen invasiver gebietsfremder Arten in Australien haben einen hohen wirtschaftlichen Tribut gefordert, doch die Quantifizierung der Höhe der Kosten, die mit direkten Verlusten und Schäden sowie für Management-Interventionen verbunden sind, ist nach wie vor schwer fassbar. Dies liegt daran, dass die Zuverlässigkeit von Kostenschätzungen nicht ermittelt wurde. Diese erste detaillierte Analyse der gemeldeten Kosten für invasive Arten für die australische Wirtschaft basiert auf der Grundlage der kürzlich veröffentlichten InvaCost-Datenbank und zusätzlich bezogener Informationen und somit insgesamt 2078 eindeutigen Kosten-Einträgen. Seit den 1960er Jahren hat Australien Verluste in Höhe von mindestens 298,58 Mrd. USD (Wert 2017) oder 389,59 Mrd. AU $ (durchschnittlicher Wechselkurs 2017) für invasive Arten verzeichnet. Dies ist jedoch eine Unterschätzung, da die Kosten steigen, wenn die Anzahl der Schätzungen nach dem Potenzgesetz zunimmt. Seit den 1970er Jahren haben sich die Gesamtkosten pro Jahrzehnt um das 1,8- bis 6,3-fache erhöht, was geschätzte Kosten von 6,09 bis 57,91 Milliarden US-Dollar (alle Kosten) oder 225,31 Millionen US-Dollar bis 6,84 Milliarden US-Dollar (empirisch beobachtete, zuverlässige Kosten) pro Jahr zur Folge hatte. Die Kosten für Pflanzenarten waren am höchsten (151,68 Mrd. USD), obwohl die meisten Kosten nicht auf einzelne Arten entfielen. Von den identifizierten Unkraut-Artigen Pflanzen waren die teuersten das einjährige Weidelgras (*Lolium Rigidum*), Parthenium (*Parthenium hysterophorus*) und das Kreuzkraut *(Senecio jacobaea*). Die vier teuersten Klassen waren Säugetiere (48,63 Milliarden US-Dollar), Insekten (11,95 Milliarden US-Dollar), Eudicots (4,10 Milliarden US-Dollar) und Monocots (1,92 Milliarden US-Dollar). Die drei teuersten Arten waren alle Tiere – Katzen (*Felis catus*), Kaninchen (*Oryctolagus cuniculus*) und die rote Feuerameise (*Solenopsis invicta*). Jeder Staat bzw. jedes Territorium hatte eine andere Reihe von Hauptkosten nach Arten, wobei die meisten (3–62%) Kosten von je ein bis drei Arten stammen. Die meisten (61%) der gemeldeten Kosten entfielen auf mehrere Umgebungen und 73% der Gesamtkosten betrafen direkte Schäden oder Verluste im Vergleich zu nur den Verwaltungskosten, wobei beide Ergebnisse die Verfügbarkeit von Daten widerspiegeln. Ansteigende Raten biologischer Invasionen werden weiterhin erhebliche Kosten für die australische Wirtschaft verursachen, aber durch bessere Investitionen, standardisierte Bewertungen und Berichterstattung sowie koordinierte Interventionen (einschließlich Ausrottungen) könnten einige dieser Kosten erheblich gesenkt werden.

Abstract in Swedish

Detaljerad bedömning av de rapporterade ekonomiska kostnaderna för invasiva arter i Australien. Arvet efter avsiktlig och oavsiktlig introduktion av invasiva främmande arter till Australien har medfört en kraftig ekonomisk skada, men att kvantifiera storleken på kostnaderna förknippade med direkt förlust och skada, liksom för ledningsinsatser, är fortfarande svårgripbart. Detta beror på att tillförlitligheten hos kostnadsberäkningar och underprovtagning inte har fastställts. Vi tillhandahåller den första detaljerade analysen av de rapporterade kostnaderna för invasiva arter till den australiensiska ekonomin sedan 1960-talet, baserat på den nyligen publicerade InvaCost-databasen och kompletterande information, för totalt 2078 unika kostnadsuppgifter. Sedan 1960-talet har Australien spenderat eller drabbats av förluster på minst 298,58 miljarder USD (2017 års värde) eller 389,59 miljarder AUD (genomsnittlig växelkurs 2017) från invasiva arter. Detta är dock en underskattning med tanke på att kostnaderna stiger när antalet uppskattningar ökar enligt en potenslag. De totala kostnaderna per årtionde sedan 1970-talet fram till idag ökade i genomsnitt 1,8–6,3 gånger vilket gav uppskattade kostnader på 6,09–57,91 miljarder USD/år (alla kostnader sammanlagt) eller 225,31 miljoner – 6,84 miljarder USD/år (observerade, endast mycket tillförlitliga kostnader). Kostnaderna för växtarter var de högsta bland rikena (151,68 miljarder USD), även om de flesta kostnaderna inte kan hänföras till enskilda arter. Av de identifierade ogräsarterna var de dyraste årlig Styvrepe (*Lolium rigidum*), Flikpartenium (*Parthenium hysterophorus*) och Stånds (*Senecio jacobaea*). De fyra dyraste klasserna var däggdjur (48,63 miljarder USD), insekter (11,95 miljarder USD), eudicots (4,10 miljarder USD) och monocots (1,92 miljarder USD). De tre dyraste arterna var alla djur – katter (*Felis catus*), kaniner (*Oryctolagus cuniculus*) och röda importerade eldmyror (*Solenopsis invicta*). Varje stat/territorium hade en skild uppsättning av kostnader per art, men de flesta (3–62%) av kostnaderna härrör från en till tre arter per politisk enhet. De flesta (61%) av de rapporterade kostnaderna tillämpades på flera miljöer och 73% av totalen avsåg direkt skada eller förlust jämfört med endast förvaltningskostnader, varvid båda dessa resultat återspeglar tillgängligheten av data. Stigande invasioner av invasiva arter kommer att fortsätta medföra betydande kostnader för den australiensiska ekonomin men med bättre investeringar, standardiserade bedömningar och rapportering och samordnade insatser (inklusive utrotningar) kan en del av dessa kostnader minskas avsevärt.

Abstract in Greek

Λεπτομερής εκτίμηση του καταγεγραμμένου οικονομικού κόστους των χωροκατακτητικών ειδών στην Αυστραλία. Οι συνέπειες των τυχαίων και μη εισαγωγών χωροκατακτητικών ειδών στην Αυστραλία έχουν βαρύ οικονομικό τίμημα, αν και η ποσοτικοποίηση του κόστους, το οποίο σχετίζεται με την άμεση εξαφάνιση ή βλάβη, όπως και με τις διαχειριστικές παρεμβάσεις, παραμένει ελλιπής. Αυτό συμβαίνει διότι η αξιοπιστία των εκτιμήσεων κόστους και η μη-αντιπροσωπευτική δειγματοληψία δεν έχουν διερευνηθεί. Εδώ παρέχουμε την πρώτη λεπτομερή ανάλυση του αναφερθέντος οικονομικού αντίκτυπου που είχαν τα χωροκατακτητικά είδη στην οικονομία της Αυστραλίας από τη δεκαετία του 1960, βασιζόμενοι στην βάση δεδομένων InvaCost, η οποία δημοσιεύθηκε πρόσφατα, και άλλες συμπληρωματικές πληροφορίες, για ένα σύνολο 2078 μοναδικών καταχωρίσεων κόστους. Από τη δεκαετία του 1960, η Αυστραλία έχει δαπανήσει ή υπόκειται σε απώλειες συνολικού ύψους τουλάχιστον 298,58 δις δολαρίων (σε αξία 2017) ή 389,59 δις δολαρίων Αυστραλίας (μέσος δείκτης συναλλαγματικής ισοτιμίας του 2017) εξαιτίας των χωροκατακτητικών ειδών. Ωστόσο, πρόκειται σαφώς για υποτίμηση, δεδομένου ότι το κόστος αυξάνεται όσο αυξάνεται ο αριθμός των εκτιμήσεων ακολουθώντας κατανομή νόμου δύναμης. Από τη δεκαετία του 1970 μέχρι σήμερα, το συνολικό κόστος αυξήθηκε κατά μέσο όρο 1,8–6,3 φορές ανά δεκαετία, δημιουργώντας εκτιμώμενο οικονομικό αντίκτυπο της τάξης των 6,09–57,91 δις δολαρίων το χρόνο (για όλα τα κόστη) ή 225,31 εκατομμυρίων-6,84 δις δολαρίων το χρόνο (συνυπολογίζονται μόνο στοιχεία κόστους υψηλής αξιοπιστίας που υλοποιήθηκαν). Το οικονομικό αντίκτυπο που προκύπτει από είδη φυτών ήταν το υψηλότερο συγκριτικά με τα υπόλοιπα βασίλεια (151,68 δις δολάρια), παρόλο που τα περισσότερα κόστη δεν μπορούν να αποδοθούν σε ένα μόνο είδος. Από τα αναγνωρισμένα αγρωστώδη, αυτά με το υψηλότερο οικονομικό αντίκτυπο ήταν η Ήρα (*Lolium rigidum*), το Παρθένιο (*Parthenium hysterophorus*) και το Ιακώβαιο (*Senecio jacobaea*). Οι τέσσερις τάξεις με το υψηλότερο κόστος ήταν τα Θηλαστικά (48,63 δις δολάρια), τα Έντομα (11,95 δις δολάρια), τα Ευδικοτυλήδονα φυτά (4,10 δις δολάρια) και τα Μονοκοτυλήδονα φυτά (1,92 δις δολάρια). Τα τρία είδη με το μεγαλύτερο οικονομικό αντίκτυπο ήταν όλα ζώα — γάτες (*Felis catus*), κουνέλια (*Oryctolagus cuniculus*) και Αμερικάνικα κόκκινα μυρμήγκια (*Solenopsis invicta*). Η σύνθεση των κύριων στοιχείων κόστους ανά είδος ήταν διαφορετική για κάθε πολιτεία/επικράτεια, με τα περισσότερα κόστη (3–62%) ωστόσο να προέρχονται από ένα έως τρία είδη ανά διοικητική μονάδα. Η πλειονότητα (61%) των καταγεγραμμένων στοιχείων κόστους αφορούσε σε πολλαπλά περιβάλλοντα και 73% του συνόλου αυτών αφορούσε σε άμεση βλάβη ή εξαφάνιση, σε σύγκριση με το κόστος διαχείρισης αποκλειστικά, με τα δύο αυτά αποτελέσματα να αντανακλούν την διαθεσιμότητα των δεδομένων. Η αύξηση στην εισαγωγή χωροκατακτητικών ειδών θα συνεχίσει να έχει σημαντικό οικονομικό αντίκτυπο για την Αυστραλιανή οικονομία, αλλά με καλύτερες επενδύσεις, τυποποιημένες αξιολογήσεις και αναφορές, καθώς και με συντονισμένες παρεμβάσεις (συμπεριλαμβανομένης της εξολόθρευσης), μέρος του κόστους μπορεί να μειωθεί σημαντικά.

Abstract in Japanese

オーストラリアにおける侵入種の経済的影響の包括的な評価

オーストラリアへの侵略的外来種の故意かつ偶発的な導入の余波は多大な経済的犠牲をもたらしたが、直接的な損失と被害、および管理介入に関連する経済的影響（コスト）の大きさを定量化することは、とらえどころのないままである。これは、推定値とアンダーサンプリングの信頼性が決定されていないためである。最近公開されたInvaCostデータベースと補足情報に基づいて、1960年代以降、オーストラリア経済への侵入種に関連して報告されたコストの詳細な分析をはじめて提供し、合計2078の固有のコストエントリを提供することができた。1960年代以降、オーストラリアは、侵入種から少なくとも合計2985.8億米ドル（2017年の価値）あるいは3895.9億豪ドル（2017年の平均為替レート）の損失を費やした。ただし、べき法則に従って見積もりの数が増えるとコストが上がることを考えると、これは過小評価である。1970年代から現在までの10年間の総コストは平均1.8～6.3倍に増加し、推定コストは1年目で60億9千万～57.9億ドル（合計）、1年目で2億2,531万～68.4億ドルになった（観察された、信頼性の高いコストのみ）。植物種から生じる費用は、植物界と動物界の間で最も高かった（1516.8億米ドル）が、費用のほとんどは単一種に起因するものではなかった。同定された雑草種の中で、最も高価なのは、毎年恒例のライグラス（*Lolium_rigidum*）、パルテニウム（*Parthenium_hysterophorus*）、およびラグワート（*Senecio_jacobaea*）だった。最も費用のかかる4つのクラスは、哺乳類（486.3億米ドル）、昆虫（119.5億米ドル）、真正双子類（41.0億米ドル）、単子葉植物（19億2000万米ドル）だった。最も高価な3種は、猫（*Felis_catus*）、ウサギ（*Oryctolagus_cuniculus*）、ヒアリ（*Solenopsis_invicta*）のすべての動物でした。各州/準州には、種ごとに異なる一連の主要なコストがあったが、ほとんど（3～62%）のコストは、政治単位ごとに1～3種に由来していた。報告されたコストのほとんど（61%）は複数の環境に適用され、全体の73%は管理コストのみと比較して直接的な損傷または損失に関連しており、これらの調査結果は両方ともデータの可用性を反映している。侵入種の侵入の増加は、オーストラリア経済にとって引き続きかなりのコストがかかるが、より良い投資、標準化された評価と報告、および調整された介入（根絶を含む）により、これらのコストの一部は大幅に削減される可能性がある。

Abstract in Korean

오스트레일리아의 외래침입종의 경제적 비용에 대한 상세 평가

의도적이거나 우연히 호주로 유입된 외래 침입종은 막대한 경제적 손실을 발생시켰지만, 외래종의 유입으로 인한 직접적인 손실 및 피해와 관련된 직접적인 비용뿐만 아니라 관리 비용 등의 규모는 여전히 수치화되지 못하고 있다. 이는 비용 추정치 및 과소 표집의 신뢰성이 부족하기 때문이다. 우리는 총 2078개의 고유 비용 항목에 대해 최근 발표된 InvaCost 데이터베이스를 기반으로 1960년대 이후 오스트레일리아로 유입된 외래 침입종의 경제 비용에 대한 상세 분석을 진행하였다. 1960년대 이후 오스트레일리아는 외래 침입종으로 인하여 최소 2985억 8천만 달러 (2017년 미화 가치 기준) 또는 3895억 9천만 달러 (2017년 평균 환율 적용한 오스트레일리아화 기준)의 경제적 손실을 보았다. 그러나 추정치의 수가 증가함에 따라 비용이 증가한다는 멱 법칙을 고려하였을 때 이는 과소평가되었다고 볼 수 있다. 1970년대 이후 현재까지 매 10년간 총비용은 1.8 ~ 6.3배 증가하였으며, 추정비용은 연간 미화 609 ~ 579억 (모든 비용을 포함하였을 경우) 혹은 미화 2억 253만 1천 ~ 68억 4천만 (신뢰성이 높은 알려진 비용만 포함한 경우) 달러 수준이다. 연구에 포함된 계 중 식물 종에서 발생한 비용이 가장 높았으나 (미화 1516억 8천만 달러) 단일종 큰 집중적으로 비용을 발생시키지는 않았다. 확인된 잡초종

중에서 가장 큰 비용을 발생시킨 종은 호밀 (*Lolium rigidum*), 파르테늄 (*Parthenium hysterophorus*) and 래그워트 (*Senecio jacobaea*) 등이었다. 강 분류 별로 포유류 (미화 486억 3000만 달러), 곤충 (119억 5천만 달러), 진정쌍떡잎식물 (미화 41억 1천만 달러), 외떡잎식물 (미화 19억 2천만 달러) 등이 가장 큰 비용을 발생시켰다. 종 분류 별로 가장 큰 비용을 발생시킨 종은 고양이 (*Felis catus*), 토끼 (*Oryctolagus cuniculus*), 붉은 불개미 (*Solenopsis invicta*) 등의 동물들이었다. 각각의 주 별로 비용을 발생시킨 주요 종이 다르지만, 대부분 (3 ~ 62%)의 비용은 주별로 1 ~ 3개의 종에 의해서 발생하였다. 보고된 비용의 대부분 (61%) 은 다양한 환경에 적용되었고, 전체 비용의 73%는 관리 비용보다는 직접적인 손실에 관련되어 있으며, 두 결과 모두 데이터의 가용성을 반영한다. 외래 침입종의 유입 증가는 오스트레일리아 경제에 상당한 비용을 부담시킬 것이다. 그러나 적절한 투자와, 표준화된 평가 및 보고 방법, 조직적인 개입 (퇴치 포함)은 이러한 비용을 상당히 감수할 수 있을 것이다.

Abstract in Russian

Подробная оценка фактических экономических потерь от инвазионных видов в Австралии. Наследие осознанной и случайной интродукции инвазионных чужеродных видов в Австралии привело к огромным экономическим потерям, однако же количественные оценки величин экономических потерь, связанных с прямым ущербом, а также с расходами на контроль инвайдеров все еще единичны. Это имеет отношение в том числе и к проблеме надежности оценок и их недостаточности. Мы предоставляем первый подробный анализ фактических экономических потерь от инвазионных видов для австралийской экономики начиная с 1960-х гг., проведенный на основе данных из недавно опубликованной базы данных InvaCost и дополнительной информации; всего было проанализировано 2078 позиций убытков. С 1960-х гг. фактические и прогнозные убытки от инвазионных видов в Австралии в совокупности составили около 298,58 млрд долларов США (по курсу валюты на 2017 г.), или 389,59 млрд австралийских долларов (по среднему обменному курсу на 2017 г.). Однако это заниженная оценка, учитывая тот факт, что величина потерь растет с увеличением числа оценок согласно степенному закону. С 1970-х гг. по настоящее время общие потери увеличивались в среднем в 1,8–6,3 раза за десятилетие, в результате чего предполагаемые потери составили 6,09–57,91 млрд долларов США в год$^{-1}$ (все потери вместе взятые) или от 225,31 млн до 6,84 млрд долларов США в год$^{-1}$ (только фактические высоконадежные оценки). Потери, связанные с чужеродными растениями, были самыми высокими в сравнении с таковыми в разных таксономических царствах (151,68 млрд долларов США), вместе с тем значительная часть экономических потерь не относилась к одному конкретному биологическому виду. Среди сорных растений наибольшие убытки были связаны с райграсом однолетним (*Lolium rigidum*), партенией (*Parthenium hysterophorus*) и крестовником луговым (*Senecio jacobaea*). Значительные потери были вызваны инвазиями представителей четырех таксономических классов: млекопитающих (48,63 млрд долларов США), насекомых (11,95 млрд долларов США), эвдикотов (4,10 млрд долларов США) и однодольных растений (1,92 млрд долларов США). Среди животных наибольший ущерб был отмечен от кошек (*Felis catus*), кроликов (*Oryctolagus cuniculus*) и красных огненных муравьев (*Solenopsis invicta*). Каждый штат или территория характеризовался разными типами потерь от видов-инвайдеров, но большинство потерь (3–62%) приходилось на 1–3 вида-инвайдера на административно-территориальную единицу. Большая часть (61%) экономических потерь была задокументирована для нескольких сред обитания, а 73% от общей суммы убытков относились к прямым потерям или тратам на контроль, что обусловлено наличием таких оценок. Рост инвазий будет продолжать приносить существенные расходы экономике Австралии, но при более эффективных инвестициях, стандартизированных оценках и отчетности, а также скоординированных действиях (включая искоренение видов-инвайдеров) некоторые из этих затрат могут быть существенно сокращены.

Abstract in Arabic

ايلارتسأ يف ةيزاغلا عاونألل اهنع نلعملا ةيداصتقالا فيلاكتلل يليصفت مييقت
ىلإ ىدأ ايلارتسأ ىلإ يضرعلا وأ دّمعتملا ًءاوس ةبيرغلا ةيزاغلا عاونألا لاخدإ ىدأ :صلختسملا
رارضألاو رئاسخلاب ةطبترملا فيلاكتلا مجح ديدحت لازي الف كلذ عمو ،ةظهاب ةيداصتقا فيلاكت
تاريدقت ةقد ديدحت مدع ىلإ كلذ يف ببسلا دوعيو .قيقحتلا ةديعب ةيرادإلا تالخدتلاو ةرشابملا
ليلحت لوأ مييقتلا اذه يف مدقنو .عاونألا هذه نم تانيعلا ذخأ يف صقنلا كلذكو ةيداصتقالا ةفلكتلا
ةيداليملا تانيتسلا ذنم يلارتسألا داصتقالل ةيزاغلا عاونألاب ةطبترملاو اهنع نلعملا فيلاكتلل
2078 يلامجإب اهيف ةيليمكتلا تامولعملاو ًارخؤم ةروشنملا InvaCost تانايب ةدعاق ىلع ًءانب كلذو
ةيزاغلا عاونألا هذه نم ةيداليملا تانيتسلا ذنم ايلارتسأ رئاسخ عومجم تغلب ثيح .درفتم لخدم
389.59 لداعي ام وه و 2017 ماع تانايب ىلع ًءانب لقألا ىلع يكيرمأ رالود رايلم 298.58 برقاي ام
نأل ًارظن عقاولا نم لقأ مقرلا اذه دعي كلذ عمو .ماعلا سفنل فرصلا رعس بسح كلذو يلارتسأ رالود
طسوتم ناك ثيح .ةيمسرلا نيناوقلل اقبط تاريدقتلا ددع ةدايز عم عفترت ةيداصتقالا فيلاكتلا
ىتحو ةيداليملا تاينيعبسلا ذنم دقع لكل فيلاكتلا يلامجإ يف 6.3 ىلإ 1.8 نيب ام حوارتي ةدايزلا
رالود رايلم 57.91 ىلإ 6.09 نيب ام حوارتت ةيريدقت فيلاكت ديدحت ىلإ ىدأ امم ،رضاحلا تقولا
ًايونس يكيرمأ رالود رايلم 6.84 – يكيرمأ رالود نويلم 225.31 وأ (فيلاكتلا ةلمج)ًايونس يكيرمأ
نم ىلعألا يه ةيزاغلا ةيتابنلا عاونألا نع ةئشانلا فيلاكتلا تناك .(ةيزاغلل ةقوثوم فيلاكت ،ةظوحلم)
مظعم نأ نم مغرلاب يكيرمأ رالود رايلم 151.68 نم برقاي ام ةفلكتلا تغلب ثيح ىرخألا عاونألا نيب
تاتابن اهديدحت مت يتلا باشعألا عاونأ نيب نم ةفلكت ىلعألا تناكو .ددحم عون ىلإ زعُت مل فيلاكتلا
ناوزلا نشخلا يونسلا (*Lolium rigidum*) موينيثرابلاو (*Parthenium hysterophorus*) خيشلا ةرهزو (*Sene-*
(يكيرمأ رالود رايلم 48.63) تاييدثلا لمشت ًةفلكت رثكألا عبرألا تائفلا تناك امك .(*cio jacobaea*
(يكيرمأ رالود رايلم 4.10) ةيقيقحلا ةقلفلا تايئانثو (يكيرمأ رالود رايلم 11.95) تارشحلاو
عيمج لمشت ةفلكت رثكألا ةثالثلا عاونألا تناكو .(يكيرمأ رالود رايلم 1.92) ةقلفلا تايداحأو
دروتسملا يرانلا رمحألا لمنلاو (*Oryctolagus cuniculus*) بنارألاو (*Felis catus*) ًالثم طقلاك تاناويحلا
عاونألا بسح ةريبكلا فيلاكتلا نم ةفلتخم ةعومجم ميلقإ وأ ةيالو لكل ناك امك .(*Solenopsis invicta*)
لكل عاونأ ةثالث ىلإ عون نم تقتشا (3 -26%) فيلاكتلا مظعم نكلو ميلقإلا وأ ةيالولا هذه يف ةدوجوملا
قلعتي امنيب ةددعتم تائيب ىلع اهقيبطت مت (61%) اهنع غلُب يتلا فيلاكتلا مظعم .ةيسايس ةدحو
.طقف ةيرادإلا فيلاكتلاب ًةنراقم ةرشابملا رئاسخلا وأ ررضلاب تاغالبلا يلامجإ نم 73% برقاي ام
ديازتم لكشب ةيزاغلا عاونألا ةدايز رمتستسو .تانايبلا رفاوت ناسكعت نيتجيتنلا نيتاه الكو
هذه ضعب ضيفخت نكمي نكلو .ةريبك فيلاكت يلارتسألا داصتقالا لّمحيس امم لبقتسملا يف
ةفاضإلاب فيلاكتلاو راثآلل مييقتلا ديحوتو رامثتسالا نيسحت لالخ نم ريبكٍ لكشب فيلاكتلا
.رمألا مزل نأ لاصئتسالا كلذ يف امب تالخدتلا قيسنت ىلإ

Abstract in Farsi

ایلارتسا رد یموب ریغ یاههنوگ یداصتقا نایز شرازگ یبایزرا
هتشاد رب رد یداصتقا نیگنس یاهدمایپ ایلارتسا هب یموب ریغ یاه هنوگ یفداصت و یدمع دورو
رد ام .تسا راوشد نآ)لرتنک(نارحب تیریدم نیچمه و نایز و ررض هنیزه دروآرب ،دوجو نیا اب تسا
۱۹۶۰ لاس زا یموب ریغ یاههنوگ دورو زا هدش شرازگ یداصتقا یاههنیزه راب نیلوا یارب هلاقم نیا
یسررب)دشابیم هعلاطم ۲۰۷۸ دادعت لماش هک(تسکونیا یتاعالطا عبنم ساسا رب ار ایلارتسا هب
۲۹۸.۵۸ لقادح لداعم یلام ررض لمحتم یموب ریغ یاههنوگ لیلد هب روشک نیا ،۱۹۶۰ لاس زا .میدرک
.تسا هدش)۲۰۱۷ لاس رد رالد خرن باستحا هب(ایلارتسا رالد نویلیب ۳۸۹.۵۹ ای اکیرمآ رالد نویلیب
نیرتالاب .تسا هدش ربارب ۶.۳ ات ۱.۸ طسوتم روط هب اههنیزه نازیم ههد ره رد ،نونک ات ۱۹۷۰ لاس زا
صتخم هچ رگا ،)اکیرمآ رالد نویلیب ۱۵۱.۶۸(تسا یهایگ یاههنوگ هب طوبرم اههلسلس نایم رد هنیزه
،سرگ یار لماش اههنیرت هنیزه رپ ،هدش ییاسانش یفلع یاههنوگ نایم زا .دشاب یمن یصاخ هنوگ هب
،)اکیرمآ رالد نویلیب ۴۸.۶۳(نرادناتسپ لماش هنیزه رپ ُهدر راهچ .دنا هدوب ترووگار و مویننتراپ
۱.۹۲(اه یاهپلک و)اکیرمآ رالد نویلیب ۴.۱۰(اهیا هپل ود ،)اکیرمآ رالد نویلیب ۱۱.۹۵(تارشح
اهشوگرخ ،اههبرگ ـدنا هدوب تاناویح زا یگمه هنیزه رپ ُهنوگ هس .تسا هدوب)اکیرمآ رالد نویلیب
۷۳ و هاگتسیز دنچ هب طوبرم اههنیزه لک دصرد ۶۱ هک تسا هداد ناشن دهاوش .یموب ریغ زمرق یاههچروم

درصد هزینهها مربوط به ضرر و زیان میباشد (این آمار شامل هزینه مدیریت بحران نمی باشد) و تاکید میکنیم که این ارقام بر اساس اسناد ثبت شده بوده و امکان تغییر آن بر اساس اسناد ثبت نشده وجود دارد. تحمیل ضرر و زیان اقتصادی به کشور استرالیا به خاطر ورود عمدی و تصادفی گونه های غیر بومی ادامه خواهد داشت، ولی با سرمایهگذاری بهتر میتوان برخی از هزینهها را کاهش داد

Abstract in Czech

Podrobné zhodnocení vykázaných ekonomických nákladů způsobených invazivními druhy v Austrálii. Úmyslné i náhodné zavlečení nepůvodních invazních druhů do Austrálie si vyžádalo značné ekonomické náklady. Výše těchto nákladů ve vztahu ke způsobeným škodám a managementu těchto druhů je však do značné míry neznámá. Hlavním důvodem je nedostatečná dostupnost a spolehlivost takovýchto odhadů. Tato studie představuje první podrobnou analýzu vykázaných nákladů způsobených invazními druhy australskému hospodářství od 60. let minulého století. Studie vychází z nedávno zveřejněné databáze InvaCost a doplňujících zdrojů, jenž celkem podchycují 2078 jedinečných záznamů takovýchto nákladů. Od šedesátých let minulého století již vynaložila Austrálie za dopady invazních druhů nejméně 298,6 miliardy amerických dolarů (hodnota pro rok 2017). Tyto náklady jsou však podhodnoceny, jelikož jejich úroveň roste s počtem dostupných odhadů. Od 70. let do současnosti došlo v průměru k 1,8–6,3násobnému nárůstu celkových nákladů za desetiletí, což vedlo k odhadovaným nákladům 6,09–57,91 miliardy amerických dolarů ročně (souhrn všech nákladů) nebo 225,3 milionu až 6,84 miliard amerických dolarů ročně za pozorované, vysoce spolehlivě prokázané náklady. Nejvyšší náklady byly na invazní rostliny (151,7 miliard amerických dolarů), ačkoli jejich většinu nelze přičíst jednomu druhu. Nejvýznamnějšími byli jílek tuhý (*Lolium rigidum*), sambaba obecná (*Parthenium hysterophorus*) a starček přímětník (*Senecio jacobaea*). Čtyřmi nejnákladnějšími třídami byli savci (48,63 miliard amerických dolarů), hmyz (11,95 miliard amerických dolarů), dvouděložné (4,10 miliard amerických dolarů) a jednoděložné rostliny (1,92 miliard amerických dolarů). Třemi nejnákladnější živočichy byla kočka domácí (*Felis catus*), králík divoký (*Oryctolagus cuniculus*) a mravenec (*Solenopsis invicta*). Každý stát/teritorium měl jinou skupinu nejnákladnějších druhů, ale většina (3–62%) nákladů vždy pocházela od jednoho až tří druhů. Většina (61%) vykázaných nákladů se vztahovala k více typům prostředí a 73% z této částky se týkalo přímých škod, na rozdíl od nákladů na management těchto druhů, jak ukazují dostupná data. Počet invazních druhů se bude zvyšovat, což bude mít za následek rostoucí náklady pro australské hospodářství, avšak lepšími investicemi, standardizovaným hodnocením i vykazováním a koordinovanými zásahy (včetně eradikací) lze některé z těchto nákladů podstatně snížit.

Abstract in Polish

Kompleksowa ocena kosztów ekonomicznych gatunków inwazyjnych w Australii. Dziedzictwo celowego i przypadkowego wprowadzenia inwazyjnych gatunków obcych do Australii miało ogromny wpływ na gospodarkę, jakkolwiek wycena wielkości kosztów związanych z bezpośrednimi stratami i szkodami oraz interwencją w zakresie zarządzania, pozostaje nieuchwytna. Wynika to z tego, że nie określono wiarygodności szacunków kosztów i niedostatecznego pobierania próbek. Dostarczamy pierwszej szczegółowej analizy kosztów poniesionych przez australijską gospodarkę, związanych z gatunkami inwazyjnymi, zgłoszonych od 1960 roku. Analiza ta została oparta o niedawno opublikowaną bazę danych InvaCost oraz informacje uzupełniające, w sumie 2078 indywidualnych wpisów kosztów. Od 1960 roku Australia poniosła koszty i straty z powodu gatunków inwazyjnych w łącznej wysokości co najmniej 298,58 mld USD (wartość z 2017 r.), co stanowi rownowartość 389,59 mld AUD (średni kurs wymiany z 2017 r.). Jest to jednak niedoszacowanie, biorąc pod uwagę, że koszty się potęgują wraz ze wzrostem liczby szacunków. Od lat 1970-tych do chwili obecnej nastąpił średnio 1,8–6,3-krotny wzrost całkowitych kosztów na dekadę, co oznacza wzrost szacowanych kosztów w wysokości 6,09–57,91 mld USD rocznie (wszystkie koszty łącznie) lub 225,31 mln–6,84 mld USD rocznie (dotyczące tylko bardzo wiarygodnych kosztów). Koszty związane z gatunkami roślinnymi były najwyższe wśród królestw (151,68 mld USD), chociaż większość kosztów nie była przypisywana pojedynczym gatunkom. Ze zidentyfikowanych gatunków chwastów najwyższych kosztów przysporzyły życica sztywna (*Lolium rigidum*), partenium ambrozjowate (*Parthenium histerophorus*) i starzec jakubek (*Senecio jacobaea*). Czterema klasami powodującymi najwyższe koszty były ssaki (48,63 mld USD), owady (11,95 mld USD), rośliny dwuliścienne (4,10 mld USD) i jednoliścienne (1,92 mld USD). Trzema gatunkami powodującymi najwyższe koszty były zwierzęta – koty (*Felis catus*), króliki (*Oryctolagus cuniculus*) i mrówki ogniste (*Solenopsis invicta*). Każdy stan/terytorium miał inny zestaw głównych kosztów według gatunków, ale większość tych kosztów (3–62%) pochodziła z jednego do trzech gatunków na jednostkę polityczną. Najwięcej (61%) zgłoszonych kosztów odnosiło się do wielu środowisk, a 73% całkowitej kwoty dotyczyło bezpośrednich szkód lub strat w porównaniu tylko z kosztami zarządzania, przy czym oba te ustalenia odzwierciedlają dostępność danych. Wzrost ilości gatunków inwazyjnych nadal będzie się wiązał ze znacznymi kosztami dla australijskiej gospodarki, ale dzięki zastosowaniu lepszych inwestycji, znormalizowanych ocen i sprawozdawczości oraz skoordynowaniu interwencji (w tym likwidacji), niektóre z tych kosztów mogłyby zostać znacznie zmniejszone.

Abstract in Bosnian/Croatian

Detaljna procjena prijavljenih ekonomskih troškova invazivnih zivotinjski i biljni vrsta u Australiji. Nasljeđe namjernog i slučajnog unošenja invazivnih stranih zivotinjski i biljni vrsta u Australiju imalo je pozamašan ekonomski utjecaj, ali kvantificirajući veličinu troškova povezanih sa izravnim gubicima i štetom, kao troskove za upravljanje intervencije i dalje je nedostižno. Razlog ovoga he zato sto pouzdanost procjena troškova i nedovoljno uzorkovanje nisu utvrđene i standarizovane. Ovdje dajemo prvu detaljnu analizu prijavljenih troškova povezanih s invazivnim zivotinjskim i biljnim vrstama za Australsko gospodarstvo od 1960-ih, na temelju nedavno objavljene baze podataka InvaCost i dodatnih podataka, za ukupno 2078 jedinstvenih unosa troškova. Od šezdesetih godina Australija je od invazivnih zivotinjskin i biljni vrsta potrošila ili pretrpjela gubitke u ukupnom iznosu od najmanje 298,58 milijardi američkih dolara (vrijednost 2017.) ili 389,59 milijardi američkih dolara (prosječni tečaj 2017.). Međutim, ovo je znacajno podcijenjeno s obzirom na to da troškovi rastu kako se broj procjena povećava slijedeći zakonske promjene. Ukupni troškovi po desetljeću od 1970-ih do danas u prosjeku su porasli za 1,8–6,3 puta, što je prouzrokovalo procijenjene troškove od 6,09–57,91 milijardi USD[1] (svi troškovi zajedno) ili 225,31 milijuna– 6,84 milijarde USD[1] (uočeno, samo vrlo pouzdani troškovi). Troškovi biljnih vrsta bili su najveći među kraljevstvima (151,68 milijardi USD), iako se većina troškova nije pripisala jednoj vrsti biljki. Od identificiranih korovitih vrsta biljki najskuplji su bili jednogodišnji ljulj (*Lolium rigidum*), partenij (*Parthenium hysterophorus*) i krpa (*Senecio jacobaea*). Četiri najskuplje klase bili su sisavci (48,63 milijarde USD), insekti (11,95 milijardi USD), eudikoti (4,10 milijardi USD) i monokoti (1,92 milijarde USD). Tri najskuplje vrste bile su sve životinje – mačke (*Felis catus*), zečevi (*Oryctolagus cuniculus*) i crveni uvezeni vatreni mravi (*Solenopsis invicta*). Svaka država / teritorij imala je različit skup glavnih troškova po vrstama, ali s većinom (3–62%) troškova koji proizlaze iz jedne do tri vrste po političkoj jedinici. Većina (61%) prijavljenih troškova odnosila se na više okruženja, a 73% ukupnih troškova odnosilo se na izravnu štetu ili gubitak u usporedbi samo s troškovima upravljanja, s tim da oba ova otkrića directno ovise o dostupnost podataka. Rastući napadi invazivnih zivotinjski i biljni vrsta i dalje će imati značajne troškove za Australsko gospodarstvo, ali boljim ulaganjem, standardiziranim procjenama i izvješćivanjem te koordiniranim intervencijama (uključujući iskorjenjivanje), neki od tih troškova mogli bi se znatno smanjiti u buducnosti.

Abstract in Punjabi

ਆਸਟਰੇਲੀਆ ਵਿਚ ਧਾੜਵੀ ਪ੍ਰਜਾਤੀਆਂ ਦੀਆਂ ਰਿਪੋਰਟ ਕੀਤੀਆਂ ਆਰਥਕਿ ਕੀਮਤਾਂ ਦਾ ਵਸਿਤਰਤਿ ਮੁਲਾਂਕਣ
ਆਸਟਰੇਲੀਆ ਵਿਚ ਗੈਰ-ਮੂਲ ਪਰਦੇਸੀ ਜਾਤੀਆਂ ਦੀ ਜਾਣੇ-ਅਣਜਾਣੇ ਵਿਚ ਕੀਤੀ ਗਈ ਅਸ੍ਥਾਪ੍ਨਾ ਨਾਲ ਭਾਰੀ ਆਰਥਕਿ ਘਾਟਾ ਪਿਆ ਹੈ, ਫਰਿ ਵੀ ਸੱਿਧੇ ਘਾਟੇ ਅਤੇ ਨੁਕਸਾਨ ਦੇ ਨਾਲ-ਨਾਲ ਪ੍ਰਬੰਧਨ ਦੇ ਦਖਲਅੰਦਾਜ਼ੀ ਨਾਲ ਜੁੜੇ ਖਰਚਿਆਂ ਦੀ ਵਆਿਖਆਿ ਮੁਸ਼ਕਲ ਹੈ| ਅਜੇਹਾ ਇਸ ਲਈ ਹੈ ਕਉਿਂਕ ਲਾਗਤ ਦੇ ਅਨੁਮਾਨਾਂ ਅਤੇ ਘੱਟ ਨਮੂਨੇ ਲੈਣ ਦੀ ਭਰੋਸੇਯੋਗਤਾ ਨਰਿਧਾਰਤ ਨਹੀ ਕੀਤੀ ਗਈ ਹੈ| ਅਸੀ ਹਾਲ ਹੀ ਵੱਿਚ ਪ੍ਰਕਾਸ਼ਤ ਇਨਵਾਕੋਸਟ ਡੇਟਾਬੇਸ (InvaCost database) ਅਤੇ

ਪੂਰਕ ਜਾਣਕਾਰੀ ਦੇ ਅਧਾਰ ਤੇ, ਕੁੱਲ 2078 ਵਿਲੱਖਣ ਲਾਗਤ ਐਂਟਰੀਆਂ ਲਈ, 1960 ਤੋਂ ਆਸਟਰੇਲੀਆਈ ਆਰਥਿਕਤਾ ਉੱਤੇ ਧਾੜਵੀ ਪ੍ਰਜਾਤੀਆਂ ਨਾਲ ਜੁੜੀਆਂ ਖਬਰਾਂ ਦਾ ਪਹਿਲਾ ਵਿਸਥਾਰਤ ਵਿਸ਼ਲੇਸ਼ਣ ਪ੍ਰਦਾਨ ਕਰਦੇ ਹਾਂ| 1960ਵਿਆਂ ਤੋਂ ਲੈਕੇ, ਆਸਟਰੇਲੀਆ ਨੇ ਧਾੜਵੀ ਪ੍ਰਜਾਤੀਆਂ ਤੇ ਘੱਟੋ ਘੱਟ 298.58 US ਬਿਲੀਅਨ ਡਾਲਰ (2017 ਮੁੱਲ) ਜਾਂ 389.59 AU ਬਿਲੀਅਨ ਡਾਲਰ (2017 ਔਸਤ ਐਕਸਚੇਂਜ ਰੇਟ) ਦਾ ਖਰਚ ਕੀਤਾ ਹੈ ਜਾਂ ਨੁਕਸਾਨ ਪਾਇਆ ਹੈ| ਹਾਲਾਂਕਿ, ਇਹ ਇੱਕ ਘੱਟ ਅੰਦਾਜ਼ਾ ਹੈ ਕਿ ਜਿਵੇਂ ਜਿਵੇਂ ਸ਼ਕਤੀ ਕਾਨੂੰਨ ਦੇ ਬਾਅਦ ਅਨੁਮਾਨਾਂ ਦੀ ਗਿਣਤੀ ਵਧਦੀ ਹੈ, ਲਾਗਤਾਂ ਵਿੱਚ ਵਾਧਾ ਹੁੰਦਾ ਹੈ| 1970 ਵਿਆਂ ਤੋਂ ਲੈ ਕੇ ਹੁਣ ਤੱਕ, ਹਰ ਦਹਾਕੇ ਵਿੱਚ ਕੁਲ ਖਰਚਿਆਂ ਵਿੱਚ ਔਸਤ 1.8–6.3 ਗੁਣਾ ਵਾਧਾ ਹੋਇਆ ਹੈ, ਜੋ ਕਿ 6.09–57.91US ਬਿਲੀਅਨ ਡਾਲਰ ਪ੍ਰਤਿ ਸਾਲ (ਸਾਰੇ ਖਰਚੇ ਜੋੜ ਕੇ) ਜਾਂ 225.31 ਮਿਲੀਅਨ – 6.84 US ਬਿਲੀਅਨ ਡਾਲਰ ਪ੍ਰਤਿ ਸਾਲ (ਨਿਰੀਖਅਤ, ਸਿਰਫ ਬਹੁਤ ਭਰੋਸੇਮੰਦ ਖਰਚੇ)ਦਾ ਅਨੁਮਾਨਤ ਖਰਚਾ ਸੀ। ਪੌਦਿਆਂ ਦੀਆਂ ਪ੍ਰਜਾਤੀਆਂ ਤੋਂ ਪੈਦਾ ਹੋਣ ਵਾਲੀਆਂ ਲਾਗਤਾਂ ਰਾਜ ਵਿਚ ਸਭ ਤੋਂ ਵੱਧ ਸਨ (151.68 ਬਿਲੀਅਨ ਡਾਲਰ), ਹਾਲਾਂਕਿ ਜ਼ਿਆਦਾਤਰ ਲਾਗਤਾਂ ਇਕ ਪ੍ਰਜਾਤੀ ਕਰਕੇ ਨਹੀਂ ਸਨ| ਨਦੀਨਾਂ ਦੀ ਪਛਾਣ ਕੀਤੀ ਪ੍ਰਜਾਤੀਆਂ ਵਿਚੋਂ, ਸਭ ਤੋਂ ਮਹਿੰਗੀਆਂ ਸਨ ਸਾਲਾਨਾ ਰਾਈਗ੍ਰਾਸ (ਲੋਲੀਅਮ ਰਿਜੀਡਮ), ਪਾਰਥੀਨੀਅਮ (ਪਾਰਥੀਨੀਅਮ ਹਿਸਟੇਰੋਫੋਰਸ) ਅਤੇ ਰੈਗਵੌਰਟ (ਸੇਨੇਸੀਓ ਜਾਕੋਬੀਆ)| ਚਾਰ ਸਭ ਤੋਂ ਮਹਿੰਗੀਆਂ ਸ਼੍ਰੇਣੀਆਂ ਥਣਧਾਰੀਆਂ (48.63 ਬਿਲੀਅਨ ਡਾਲਰ), ਕੀੜੇ (11.95 ਬਿਲੀਅਨ ਡਾਲਰ), ਯੂਡਿਕੌਟਸ (4.10 ਬਿਲੀਅਨ ਡਾਲਰ) ਅਤੇ ਮੋਨੋਕੋਟਸ (1.92 ਬਿਲੀਅਨ ਡਾਲਰ) ਸਨ। ਤਿੰਨ ਮਹਿੰਗੀਆਂ ਪ੍ਰਜਾਤੀਆਂ ਸਨ – ਬਿੱਲੀਆਂ (ਫੇਲਿਸ ਕੈਟਸ), ਖਰਗੋਸ਼ (ਓਰੀਕਟੋਲਾਗਸ ਕਨਿਕੂਲਸ) ਅਤੇ ਲਾਲ ਆਯਾਤ ਕੀਤੀ ਅੱਗ ਕੀੜੀਆਂ (ਸੋਲੇਨੋਪਸਿਸ ਇਨਵਿਕਟਾ)| ਹਰੇਕ ਰਾਜ / ਖਿੱਤੇ ਵਿੱਚ ਪ੍ਰਜਾਤੀਆਂ ਦੁਆਰਾ ਵੱਡੇ ਖਰਚਿਆਂ ਦਾ ਵੱਖਰਾ ਸਮੂਹ ਸੀ, ਪਰ ਪ੍ਰਤੀ ਰਾਜਨੀਤਿਕ ਇਕਾਈ ਵਿਚ ਜ਼ਿਆਦਾਤਰ (3–62%), ਇਕ ਤੋਂ ਤਿੰਨ ਪ੍ਰਜਾਤੀਆਂ ਲਈ ਖਰਚਾ ਕੀਤਾ ਜਾਂਦਾ ਸੀ| ਰਿਪੋਰਟ ਕੀਤੇ ਖਰਚਿਆਂ ਵਿਚੋਂ ਜ਼ਿਆਦਾਤਰ (61%) ਬਹੁਤੇ ਵਾਤਾਵਰਣ ਤੇ ਲਾਗੂ ਹੁੰਦੇ ਹਨ ਅਤੇ ਕੁੱਲ ਦਾ 73% ਕੇਵਲ ਪ੍ਰਬੰਧਨ ਖਰਚਿਆਂ ਦੇ ਮੁਕਾਬਲੇ ਸਿੱਧੇ ਨੁਕਸਾਨ ਜਾਂ ਘਾਟੇ ਨਾਲ ਸਬੰਧਤ ਹੈ, ਜਦਕਿ ਇਹ ਦੋਵੇਂ ਖੋਜਾਂ ਅੰਕੜਿਆਂ ਦੀ ਉਪਲਬਧਤਾ ਨੂੰ ਦਰਸ਼ਾਉਂਦੀਆਂ ਹਨ| ਧਾੜਵੀ ਪ੍ਰਜਾਤੀਆਂ ਦੇ ਵੱਧ ਰਹੇ ਹਮਲਿਆਂ ਦੇ ਖਰਚਿਆਂ ਦਾ ਭਾਰ ਆਸਟਰੇਲੀਆਈ ਆਰਥਿਕਤਾ ਤੇ ਜਾਰੀ ਰਹੇਗਾ, ਪਰ ਬਿਹਤਰ ਨਿਵੇਸ਼, ਮਿਆਰੀਕਰਨ ਕੀਤੇ ਮੁਲਾਂਕਣਾਂ ਅਤੇ ਰਿਪੋਰਟ ਕਰਨ ਅਤੇ ਤਾਲਮੇਲ ਵਾਲੀਆਂ ਦਖਲਅੰਦਾਜ਼ੀਆਂ (ਖਾਤਮੇ ਸਮੇਤ) ਨਾਲ, ਇਹਨਾਂ ਵਿੱਚੋਂ ਕੁਝ ਖਰਚਿਆਂ ਨੂੰ ਕਾਫ਼ੀ ਹੱਦ ਤੱਕ ਘਟਾਇਆ ਜਾ ਸਕਦਾ ਹੈ|

Abstract in Gujarati

ઓસ્ટ્રેલિયામાં નોંધાયેલ આક્રમક પ્રજાતિઓના આર્થિક ખર્ચનું વિગતવાર મૂલ્યાંકન

ઓસ્ટ્રેલિયાને આક્રમક પરપ્રાંતીય પ્રજાતિઓના ઇરાદાપૂર્વક અને આકસ્મિક પ્રવેશના લીધે ભારે આર્થિક નુકસાન થયું છે. તેમ છતાંય સીધા નુકસાન અને નુકસાન સાથે સંકળાયેલા ખર્ચની મર્યાદા તેમજ વ્યવસ્થાપન દરમિયાનગીરીઓનો અંદાજ લગાવવો હંમેશા મુશ્કેલ રહ્યો છે. જેનું મુખ્ય કારણ વિશ્વસનીય ખર્ચ અંદાજ અને નમૂનાઓની સાપેક્ષતા છે. અમે આ સાથે ઇનવાકોસ્ટ ડાટાબેઝ અને પૂરક માહિતીમાંથી કુલ ૨૦૭૮ નોંધણીઓના આધારે ૧૯૬૦ના દાયકાથી ઓસ્ટ્રેલિયાના આક્રમક પ્રજાતિઓ સાથે સંકળાયેલા ખર્ચની ઓસ્ટ્રલિયાના અર્થતંત્ર પરની અસરનું પ્રથમ વિગતવાર વિશ્લેષણ પ્રસ્તુત કરીએ છીએ. ઓસ્ટ્રેલિયાને ૧૯૬૦ના દાયકાથી આક્રમક પ્રજાતિઓ પાછળ ઓછામાં ઓછું ૨૯૮.૫૮ અબજ અમેરીકન ડોલર (વર્ષ ૨૦૧૭ની કિંમત પ્રમાણે) અથવા ૩૮૯.૫૮ (વર્ષ ૨૦૧૭નો સરેરાશ વિનિમયદર પ્રમાણે) અબજ ઓસ્ટ્રેલિયન ડોલરનો કુલ ખર્ચ અથવા નુકસાન થયુ છે. જોકે, આ એક નીચો અંદાજ છે કારણકે ઘાતાંકના નિયમ પ્રમાણે વધતા ખર્ચના લીધે અંદાજમાં વધારો થાય છે. વર્ષ ૧૯૭૦થી અત્યાર સુધી પ્રત્યેક દાયકા દીઠ કુલ સરેરાશ ખર્ચમાં ૧.૮ થી ૬.૩ ગણા વધારાના લીધે વાર્ષિક અંદાજિત ખર્ચની મર્યાદા ૬૦.૯ થી ૫૭.૯૧ અબજ અમેરીકન ડોલર પ્રતિ વર્ષ (તમામ ખર્ચ સંયુક્ત) અથવા ૨૨.૫૩૧ કરોડ થી ૬.૮૪ અબજ અમેરીકન ડોલર પ્રતિ વર્ષ (અવલોકન, માત્ર ખુબ જ વિશ્વસનીય ખર્ચ) અંકાઈ છે. વનસ્પતિ પ્રજાતિઓથી થયેલ ખર્ચ સૌથી વધુ હતો (૧૫૧.૬૮ અબજ અમેરીકન ડોલર), જો કે મોટાભાગના ખર્ચ કોઈ એક પ્રજાતિને આભારી ન હતા. જાણીતી નીંદણ પ્રજાતિઓ પૈકી સૌથી ખર્ચાળ રાયગ્રાસ (લોલીયમ રિગિડમ), પાર્થેનિયમ (પાર્થેનિય હિસ્ટરોફોરસ) અને રાગવોર્ટ (સેનેસિઓ જેકોબીયા) હતા. ચાર સૌથી ખર્ચાળ વર્ગોમાં, સસ્તન પ્રાણીઓ (૪૮.૬૩ અબજ અમેરીકન ડોલર), જંતુઓ/કિટકો (૧૧.૯૫ અબજ અમેરીકન ડોલર), યુડિકોટ્સ (૪.૧૦ અબજ અમેરીકન ડોલર) અને એકદળીય વનસ્પતિ (૧.૯૨ અબજ અમેરીકન ડોલર) હતા. ત્રણ સૌથી ખર્ચાળ પ્રજાતિઓમાં બધા જ પ્રાણીઓ હતા – બિલાડીઓ (ફેલિસ કેટસ), સસલા (ઓરીકટોલાગસ ક્યુનીક્યુલસ) અને લાલ આયાતી ફાયર કીડીઓ (સોલેનોપસીસ ઈનવિકટા) હતા. દરેક રાજ્ય/પ્રદેશોમાં પ્રજાતિદીઠ ખર્ચ અલગ અલગ હતા. પરંતુ રાજકીય એકમ દીઠ મોટા ભાગનો (૩–૬૨%) ના ખર્ચ એકથી ત્રણ પ્રજાતિઓમાંથી તારવેલ હતો. મોટાભાગના નોંધાયેલ ખર્ચ (૬૧%) વિવિધ પર્યાવરણ અને કુલ ખર્ચના ૭૩%, સીધા નુકશાન અને વ્યવસ્થાપન દરમિયાનગીરીઓનો હતો. આ બંને તારણો માહિતીની ઉપલબ્ધતા દર્શાવે છે. આક્રમક પ્રજાતિઓના વધતા જતા આક્રમણથી ઓસ્ટ્રેલિયન

અર્થતંત્રના ખર્ચમાં નોંધપાત્ર વધારો થતો રહેશે. પરંતુ વધુ સારૂં રોકાણ, પ્રમાણિત આકારણી અને અહેવાલ તથા સંકલિત હસ્તક્ષેપ (નાબૂદી સહિત) ની સહાયથી આ ખર્ચમાં નોંધપાત્ર ઘટાડો થઈ શકે છે.

Abstract in Telugu

ఆస్ట్రేలియాలో ఆక్రమణ మొక్కలు మరియు జంతు జాతుల నివేదించబడిన ఆర్థిక ఖర్చుల వివరణాత్మక పరిశీలన

ఆస్ట్రేలియాకు ఉద్దేశపూర్వకంగా మరియు అనుకోకుండా ఆక్రమణ మొక్కలు మరియు జంతు జాతులను తీసుకొనిరావడంతో ఆస్ట్రేలియాకు భారీ ఆర్థిక నష్టాన్ని కలిగిస్తున్నాయి, ఇంకా ప్రత్యక్ష నష్టం మరియు నష్టంతో సంబంధం ఉన్న ఖర్చుల పరిమాణాన్ని లెక్కించడం, అలాగే నిర్వహణ జోక్యాల ఖర్చు కూడా అస్పష్టంగానే ఉంది. ఎందుకంటే ఖర్చు అంచనాల విశ్వసనీయత మరియు అండర్-శాంప్లింగ్ ఇంకా నిర్ణయించబడలేదు. 1960 ల నుండి ఆస్ట్రేలియన్ ఆర్థిక వ్యవస్థకు ఆక్రమణ మొక్కలు మరియు జంతు జాతులతో సంబంధం ఉన్న నివేదించబడిన ఖర్చుల యొక్క మొదటి వివరణాత్మక విశ్లేషణను మేము అందిస్తున్నాము, ఇది మొత్తం 2078 ప్రత్యేక ఖర్చుల ఎంట్రీల కోసం ఇటీవల ప్రచురించిన ఇన్వాకోస్ట్ డేటాబేస్ (InvaCost Database) మరియు అనుబంధ సమాచారం ఆధారంగా రూపొందించబడింది. 1960 ల నుండి, ఆస్ట్రేలియా ఆక్రమణ మొక్కలు మరియు జంతు జాతుల నుండి కనీసం US $ 298.58 బిలియన్ (2017 విలువ) లేదా AU $ 389.59 బిలియన్ (2017 సగటు మార్పిడి రేటు) మొత్తం నష్టపరిచింది. ఏది ఏమైనా, ఇది తక్కువ అంచనా, గణాంక శక్తి చట్టాన్ని (*a statistical power law*) అనుసరించి అంచనాల సంఖ్య పెరిగేకొద్దీ ఖర్చులు పెరుగుతాయి, 1970 నుండి ఇప్పటి వరకు ప్రతి దశాబ్దానికి మొత్తం ఖర్చులు సగటున 1.8–6.3 రెట్లు పెరిగాయి, అంచనా ఖర్చులు US $ 6.09–57.91 బిలియన్ ఒక సంవత్సరం కి (అన్ని ఖర్చులు కలిపి) లేదా US $ 225.31 మిలియన్ – 6.84 బిలియన్ ఒక సంవత్సరం కి (గమనించబడింది, అత్యంత నమ్మదగిన ఖర్చులు మాత్రమే). మొక్కల జాతుల నుండి ఉత్పన్నమయ్యే ఖర్చులు అత్యధికంగా ఉన్నాయి (US $ 151.68 బిలియన్), అయినప్పటికీ చాలా ఖర్చులు ఒకే మొక్కజాతికి ఆపాదించబడమ. గుర్తించిన కలుపు జాతులలో, ఖరీదైనవి వార్షిక రైగ్రాస్ (*Lolium rigidum*), పార్థేనియం (*Parthenium hysterophorus*) మరియు రాగ్వోర్ట్ (*Senecio jacobaea*). నాలుగు ఖరీదైన తరగతులు క్షీరదాలు (పాలిచ్చు జంతుమలు) (US $ 48.63 బిలియన్), కీటకాలు (US $ 11.95 బిలియన్), డైకాట్స్ (US $ 4.10 బిలియన్) మరియు మోనోకట్స్ (US $ 1.92 బిలియన్). మూడు ఖరీదైన జంతుమల జాతులు – పిల్లులు (*Felis catus*), కుందేళ్ళు (*Oryctolagus cuniculus*) మరియు దిగుమతి చేసుకున్న ఎరుపు అగ్ని చీమలు (*Solenopsis invicta*). ప్రతి రాష్ట్రం (లేదా భూభాగం) జాతుల వారీగా వేర్వేరు ఖర్చులు అంచనాలను వేశారు, అయితే చాలా (3–62%) ఖర్చులు ప్రతి రాష్ట్రం (లేదా భూభాగం) ఒకటి నుండి మూడు జాతుల వరకు తీసుకోబడ్డాయి. నివేదించబడిన ఖర్చులలో ఎక్కువ (61%) బహుళ వాతావరణాలకు వర్తింపజేయబడ్డాయి మరియు మొత్తం 73% నిర్వహణ ఖర్చులతో పోలిస్తే ప్రత్యక్ష నష్టం లేదా నష్టానికి సంబంధించినవి, ఈ రెండు ఫలితాలు డేటా లభ్యతను ప్రతిబింబిస్తాయి. ఆక్రమణ జాతుల పెరుగుతున్న ప్రవేశం ఆస్ట్రేలియన్ ఆర్థిక వ్యవస్థకు చాలా ఖర్చులను కలిగిస్తాయి, అయితే మంచి పెట్టుబడి, ప్రామాణిక అంచనాలు మరియు రిపోర్టింగ్ మరియు సమన్వయ జోక్యాలతో (నిర్మూలనతో సహా), కొన్ని ఈ ఖర్చులు గణనీయంగా తగ్గించబడతాయి.

Abstract in Sinhala

ඕස්ට්‍රේලියාවේ පැතිරී තිබෙන ආක්‍රමණශීලී ශාක හේතුවෙන් සිදුව ඇති ආර්ථික හානිය පිළිබඳ විස්තරාත්මක ඇගයීමක්

සිතාමතා සහ අත්වැරදීම් තුලින් ඕස්ට්‍රේලියාවට හඳුන්වා දී ඇති පිටස්තර ශාක සහ සත්ව විශේෂ හේතුවෙන් සිදුව ඇති අති විශාල ආර්ථික හානිය විවිධාකාර වේ. ඍජු සහ වක්‍රව සිදුව ඇති හානි, එනිසා සිදුවන පාලන කටයුතු වෙනුවෙන් යන වියදම සහ එතුලින් මතුව ඇති ප්‍රශ්ණ විසඳීම සඳහා මැදිහත් වීමට සිදුවීම වෙනුවෙන් වන

වැය මේ දක්වා නිවැරදිව සහ ප්‍රමාණාත්මකව ගණනය කිරීමක් සිදු නොවීම හේතුවෙන් ඒ පිළිබඳව පැහැදිලි අවබෝධයක් නොමැත. එයට ප්‍රධානතම හේතු වශයෙන් දැක්විය හැක්කේ විශ්වාසදායී ඇගයීම් සහ නියැදි එකතු කිරීමේ ක්‍රමයක් තවම තීරණය කර නොතිබීමයි. මෙහි අපි විස්තරාත්මක ඇගයීමක් සමග ආක්‍රමණික ශාක සහ සත්ව විශේෂ වලින් ඕස්ට්‍රේලියානු ආර්ථිකයට 1960 දශකයේ සිට මේ දක්වා වී ඇති හානිය වාර්තා කරමු. මේ සඳහා Invacost දත්ත සහ සහායක තොරතුරු භාවිත කර ඇත. 1960 දශකයේ සිට ඇමරිකානු ඩොලර් බිලියන 389.59 (2017) පමණ ආර්ථික හානියක් ආක්‍රමණික ශාක සහ සත්ව විශේෂ වලින් සිදුව ඇත.මයෙද අවතක්සේරුවකි. හානිය 1.8 – සිට 6.3 ගුනයකින් වැඩිවීමක් දශකයකට වී ඇති බව 1970 සිට මේ දක්වා දක්නට ඇති අතර ඇස්තමේන්තු අගය වසරකට ඇමරිකානු ඩොලර් බිලියන 6.09–57.91 (සියලු වියදම්) හෝ ඇමරිකානු ඩොලර් මිලියන 225.31–6.84 බිලියන (නිරීක්ෂණය වී ඇති විශ්වාසදායී) වී ඇත. ශාක වලින් සිදුවූ හානිය ඉහලම අගයක් වන අතර (ඇමරිකානු ඩොලර් බිලියන 151.68) එක් විශේෂයකට පමනක් මයෙ සීමාවී නැත. හඳුනාගත් වල් පැළ අතර වැඩිම වියදම වාර්ෂික රයිග්‍රාස් (*Lolium rigidum*), *parthenium* (*Parthenium hysterophorus*) සහ රැග්වෝට් (*Senecio jacobaea*). සතුන් අතරින් වැඩිම ආර්ථික අලාභය වී ඇත්තේ ක්ෂීරපායීන් ගනේ වන අතර (ඇමරිකු ඩොලර් බිලියන 48.63) , කෘමීන් (බිලියන 11.95) ද්විබීජ පත්‍ර (බිලියන 4.10) සහ ඒකබීජ පත්‍ර (බිලියන 1.92) වැඩිම වියදමක් දැරූ විශේෂ තුන වනුයේ පුසන් (*Felis catus*) හාවන් (*Oryctolagus cuniculus*) සහ රතු කුහුඹුවන් (*Solenopsis invicta*) ගනේ. එක් එක් පළාත් වලට අනුව මයෙ වනෙස් විය හැකි වුවද 3% – 6%ක් පමණ වියදම වී ඇත්තේ විශේෂ 1–3 එක් ප්‍රදේශයකට ලසෙයි.61% පමණ වාර්තා වී ඇති හානිය විවිධ පරිසර වලට වන අතර සහ 73% වී ඇත්තේය සෘජු හානිය හෝ ඒවා පාලනය කිරීම සඳහා වූ වියදමයි. වැඩිවන ආක්‍රමණික විශේෂ ඕස්ට්‍රේලියානු ආර්ථිකයට බරපතල හානියක් කරයි.නමුත් ප්‍රමිතිගත ඇගයීම්, වාර්තා කිරීම් සහ සංවිධානාත්මක මැදිහත්වීම් තුලින් මේ ආර්ථික හානිය සැලකිය යුතු ලසෙ පියවා ගත හැක.

Abstract in Hindi

ऑस्ट्रेलयिा में आक्रामक प्रजातयिों की प्रकाशति आर्थकि लागत का वसि्तृत मूल्यांकन

तेज़ीसे फैलने वाली वदिशी प्रजातयिों का आकस्मकि और असावधानी से कयि गये आयात के फलस्वरूप आस्ट्रेलयिा को भारी आर्थकि नुकसान उठाना पड़ा है। फलिहाल प्रत्यक्ष नुकसान, क्षतिएवं प्रबंधन-उपायों का हानिनर्िधारण कठनि है। लागत अनुमानों और नमूने लेने कीप्रक्रयिा की वशि्वसनीयता का उचति आंकलन न कयिा कयिा जाना इसका मुख्य कारण है। हम हाल ही में प्रकाशति हुए इनोवाकोस्ट आंकड़ासंचय (डेटाबेस) और पूरक जानकारी से प्राप्त कुल २०७८ अद्वतीय लागत प्रवष्टियिों के आधार पर ऑस्ट्रेलयिाई अर्थव्यवस्था के लिए १९६० के बाद से आक्रामक प्रजातयिों के साथ जुड़े आख्या की लागत का पहला वसि्तृत वशि्लेषण प्रदान करते हैं। १९६० के दशक के बाद से, ऑस्ट्रेलयिा ने आक्रामक प्रजातयिों के कारण कम से कम कुल यू.एस. डॉलर २९८.५८ बलियिन (२०१७ मूल्य) या ऑस्ट्रेलयिाई डॉलर ३८९.५९ बलियिन (२०१७ औसत वनिमिय दर) नुकसान या खर्च कयिा है। हालाँकि, यह एक कम अंदाजा है क्योंकी घात के नयिाम अनुसार बढ़ते खर्च से अनुमान की सखंया में बढ़ोतरी होती है। १९७० से वर्तमान तक की कुल लागतों में प्रतिदशक कुल औसतन १.८–६.३ गुना वृद्धिके कारण अनुमानति लागत की सीमाएं परसिर यू.एस. डॉलर ६.०९–५७.९१ बलियिन प्रतवि़र्ष (सभी संयुक्त लागत) या यू.एस. डॉलर २२५.31 मलियिन – ६.८४ बलियिन प्रतवि़र्ष हुई (अवलोकति, केवल अत्यधकि वशि्वसनीय लागत)। पौधों की प्रजातयिों से उत्पन्न होने वाली लागत जातयिों में सबसे अधकि थी (यू.एस. डॉलर १५१.६८ बलियिन), हालांकिएकल प्रजातिअधकिांश लागत के लिए जम्मिेदार नहीं थीं। पहचान की गई खरपतवार प्रजातयिों में से, सबसे महंगा वार्षकि राईग्रास (लोलयिम रगिडिम), पार्थेनयिम (पार्थेनयिम हसि्टेरोफोरस) और रैगवॉर्ट (सेनेसओि जेकोबयिा) थे। चार महंगे वर्ग स्तनधारी (यू.एस. डॉलर ४८.६३ बलियिन), कीड़े (यू.एस. डॉलर ११.९५ बलियिन), यूडकिोट्स (यू.एस. डॉलर ४.१० बलियिन) और एकबीजपत्री (यू.एस. डॉलर १.९२ बलियिन) थे। तीन महंगी प्रजातयिों में सभी जानवर थे – बलि्लयिां (फेलसि कैटस), खरगोश (ओरीक्टोलैगस क्यूनकिुलस) और लाल आयातति आग चींटी (सोलेनोप्ससि इनवक्टिा)। प्रत्येक राज्य / क्षेत्र में प्रजातयिों द्वारा प्रमुख लागतों का एक अलग समूह था, लेकनि प्रतिराजनीतकि इकाई में अधकिांश (३–६२%) लागत एक से तीन प्रजातयिों से प्राप्त हुई थी। प्रकाशति की गई अधकिांश लागतों (६१%) ववििधि परसि्तिथियिों को लागु पडते है और कुल लागत का ७३%, प्रबंधन दरमयिानगरियिो की तुलना में, प्रत्यक्ष क्षतिया हानिसे संबंधति था, यह दो तारणो माहतिी की उपलब्धता भी दर्शाते है। आक्रामक प्रजातयिों की बढ़ती घटनाओं से ऑस्ट्रेलयिाई अर्थव्यवस्था पर भारी लागत जारी रहेगी, लेकनि बेहतर नवशि, मानकीकृत आकलन और प्रतविदन और समन्वति दखल (उन्मूलन सहति) के सहाय से इनमें से कुछ लागतों को काफी हद तक कम कयिा जा सकता है।

Keywords
Ecosystem management expenditure, InvaCost, monetary impacts, non-native species, Oceania, socioeconomic damage

Introduction

Biological invasions continue to erode economies, ecosystems and societies worldwide, with no sign of abatement (Simberloff et al. 2013; Bradshaw et al. 2016; Pyšek et al. 2020). As the rate of introductions of invasive alien species accelerates given an increasingly connected world (Seebens et al. 2017), the extent and magnitude of these impacts will *ipso facto* also increase. While in recent decades, much research has examined the ecological effects of invasive species across habitat types, geographic regions and taxonomic groups (Crystal-Ornelas and Lockwood 2020, and references therein), quantification of the economic impacts has remained diffuse. In particular, a lack of resolute, comprehensive and synthesised economic cost estimates precludes adequate comparisons and compilation at, for example, the national level. Such information can help to assist in setting priorities by policy-makers and organisations for managing invasive species in some of the most impacted countries.

Recently, the InvaCost database was developed to provide the most comprehensive and standardised compilation of invasion costs globally (Diagne et al. 2020b). This advance now addresses the aforementioned limitations by presenting economic costs at a global scale, yet with sufficient resolution to enable assessment in more granular national, taxonomic and socioeconomic contexts. Further, InvaCost allows for assessment of the reliability of cost estimates, as well as for whether costs are predicted to occur or have been empirically observed. While broad-scale perspectives of the economic costs of invasive species are needed because of the transboundary nature of invasions, national or regional assessments are still required in much greater detail (Diagne et al. 2020a).

Australia – the sixth largest country (7,688,287 km^2) and thirteenth largest economy (2017 gross domestic product = US$1.23 trillion; worldbank.org) in the world, as well as the only true 'island' continent apart from Antarctica – has a long history of deliberate and accidental introductions of invasive species (Hoffmann and Broadhurst 2016). Introductions by humans go back as far as 5,000–10,000 years with the deliberate introduction of the dingo (*Canis dingo*) (Smith et al. 2019) and, today, many different alien species occupy almost every terrestrial, freshwater and marine habitat in the country. Indeed, some of the most infamous international examples of deleterious invasive species are Australian – cane toads (*Rhinella marina*) (Lever 2001), prickly pear cactus (*Opuntia* spp.) (Freeman 1992), swamp buffalo (*Bubalus bubalis*) (Ridpath and Waithman 1988), foxes (*Vulpes vulpes*) (Saunders et al. 2010) and European rabbits (*Oryctolagus cuniculus*) – to name a few. While there have been some successes in suppressing various alien species using biological control and corresponding savings in averted damage, such as the prickly pear cactus (Raghu and Walton 2007) and European rabbits (Cooke et al. 2013), most invasive species represent major ongoing ecological, agricultural and economic problems for the country.

While there have been previous attempts to evaluate the costs of invasive species to the Australian economy, these have either focussed on one or only a few taxa, or have been restricted to particular regions. Only the impacts of invasive plants have been the subject of analyses at the kingdom level (e.g., Sinden et al. 2004). Moreover, most assessments have been reliant on flawed assumptions (Sagoff 2008; Holmes et al. 2009) and extrapolations (Pimentel et al. 2001) or have applied more top-down approaches to estimate costs by sector, rather than to divide the estimates among species, regions, sectors or decades (McLeod 2004; Sinden et al. 2004; Gong et al. 2009; Hoffmann and Broadhurst 2016; Llewellyn et al. 2016).

Here we focus on Australia and its territories to provide the first detailed assessment of the reported economic costs of invasive species since the 1960s, based on records extracted from the recently published InvaCost database (Diagne et al. 2020b), combined with both an independent database of costs restricted to invasive herbivore species (previously unpublished) and recent data describing the costs of invasive plants and other disease-causing agents. Our aims are to (*i*) assess the reliability (values based on actual measures as opposed to non-sourced estimates) of the Australian cost estimates, as has been done previously for invasive insects (Bradshaw et al. 2016) and invasive species globally (Diagne et al. 2021), (*ii*) provide a State/Territory summary of those costs, (*iii*) identify the costliest species nationally and by State/Territory, (*iv*) investigate the most impacted environments and sectors and (*v*) estimate robust temporal trends in the economic costs of invasive species over the last five decades.

Methods

Data collection

To determine the cost of invasive species to the Australian economy, we used cost data collected in the InvaCost database (Diagne et al. 2020a, b) (n = 2,419 entries) concerning the global costs of invasive species, based on published literature, enabling comprehensive quantification of costs associated with invasive species at various spatio-temporal scales. Of these, 877 (36%) entries pertained to Australia. The data in InvaCost were collected following a series of literature searches using the Web of Science platform (webofknowledge.com), Google Scholar (scholar.google.com) and the Google search engine (google.com) and all the retrieved costs were converted to a common, up-to-date currency (2017 US$; data.worldbank.org).

We complemented the InvaCost data in three ways. We first added supplementary cost data from new references containing cost information (~ 2300 entries; https://doi.org/10.6084/m9.figshare.12928145). Next, we added data from the "Costs of Invasive Herbivores in Australia" database compiled by Biosecurity South Australia in 2018. The latter is an unpublished database compiled by L.A. to collate peer-reviewed and government documents reporting estimated costs specifically for 'invasive' herbivores [this can include native species, which compete with human interests in some cases – for example, kangaroos (various species, notably *Osphranter* and *Macropus* spp.)]. That database also includes pigs (*Sus scrofa*) and birds, even though these species are not all strictly herbivores. Based on the top five commodities in each of the categories of livestock, crops and horticulture as a starting point, the impacts from pest animals on those commodities were compiled for each. Estimates were identified using Google Scholar and Google search engine for peer-reviewed papers, conference papers, surveys and reports (e.g. Australian Bureau of Agricultural and Resource Economics, Invasive Animals Cooperative Research Centre, government and industry reports).

As a last step, we augmented the database with additional, missing cost estimates identified during the review process, as well as additional searching. We included all new costs following the structure, decision points and rules of the original InvaCost data (Diagne et al. 2020b). Many of the additional costs were derived from a single, large report on weeds of cropping systems by Llewellyn et al. (2016). The reporting units used in that report were the Grain Research and Development Corporation agroecological zones and some of these zones crossed state-government boundaries. To assign costs to the State level where an agroecological zone crossed State boundaries, we assumed that costs were evenly distributed across each zone and divided the reported costs proportionally into their respective States. Furthermore, Llewellyn et al. (2016) reported the annual ongoing costs of weed management and these costs were updated by McLeod (2018) for the year 2018 and onwards. To avoid double counting these costs, we extended the Llewellyn et al. (2016) costs up to 2017 and used McLeod (2018) from 2018 onwards. These added costs included new estimates that included the present year (2020). At the time of writing, there were no exchange rates or consumer price index data available from the chosen InvaCost sources. As such, we used an 11-month average (Jan–Nov 2020) exchange rate taken from rba.gov.au/statistics/historical-data.html. We calculated the relevant consumer price index by taking the 12-month average change to November 2020 reported at bls.gov and applied it to the 2019 consumer price index reported by the chosen InvaCost data source (data.worldbank.org).

We reviewed all sources, as well as the references they cited, to identify additional sources. Each entry recorded: (*i*) species identity ('general' if unspecified); (*ii*) reported cost (including range if available; no hypothetical costs included); (*iii*) jurisdiction (including area of coverage if provided); (*iv*) applicable year(s) (set to year of publication if not provided); (*v*) implementation (observed or extrapolated); (*vi*) method (field, desktop, both); (*vii*) verification (whether approach could be identified/repeated); and (*viii*) type (control, loss, research, damage, mixed).

After combining the separate databases and standardising/aligning columns, we removed obvious duplicate cost estimates (i.e. same cost figures from (non-)identical sources) following previous protocols (Bradshaw et al. 2016; Diagne et al. 2020b). Following our data processing (see below), we finished with a total of n = 2257 unique entries pertaining to Australia for analysis (database available for download at https://doi.org/10.5281/zenodo.4455979).

Estimating total costs

Deriving the total cumulative costs of the impacts and management of invasive species over time requires considering the temporal period to which a particular cost estimate applies. We calculated the duration of a cost as the number of years between the probable start and end years provided in the full database. When the exact start year was unknown, we conservatively considered the year of publication of a primary data source as either the start year or the end year, to which the duration (if mentioned) in number of years was considered (by adding or subtracting the number of years) to derive either, respectively, the end or the start year (Diagne et al. 2020b). We did not use data describing costs prior to 1960 to avoid inconsistencies in currency conversion. We also removed all costs identified as 'avoided' because of a given intervention (i.e. unrealised costs).

To calculate the total cumulative cost, we first recalculated all the annual costs for the defined periods of their occurrence using the `invacost` package in R via the *expandYearlyCosts* function (Leroy et al. 2020) and then summed them to obtain total costs. We also estimated the invasion costs for a series of sub-categories by summing all entries according to six descriptive columns in the database: (1) **method reliability** – the perceived reliability of cost estimates, based on the type of publication and method of estimation (*low* or *high*); following Diagne et al. (2020b), 'high reliability' is accorded if either provided by pre-assessed materials (e.g. peer review, official reports) or using a documented, repeatable and/or traceable method when provided in other grey literature; (2) **region** – here, we split costs by major political unit in Australia (States and Territories), as well as costs not associated with any particular unit (i.e. national-scale or multiple states/not stated); (3) **implementation form** – this refers to whether the cost estimate was actually realised in the invaded habitat or merely predicted (*observed* or *potential*); (4) **type of environment**: *aquatic*, *terrestrial* or *mixed* habitats (species that spend part of their life cycle in water); (5) **type of cost** – (*i*) *damage/loss* (damage or losses incurred by invasion), (*ii*) *expenditure* (control-related expenditure, such as monitoring, prevention, management or eradication), (*iii*) *general* costs, including research and administrative costs and (*iv*) *mixed* types; and (6) **impacted sector** – the activity, societal or market sector that was affected by the cost – these were *agriculture*, *authorities-stakeholders*, *energy*, *environment*, *forestry*, *health*, *public and social welfare*, *protected areas* and *trade*. We modified individual cost entries not allocated to a single sector to *mixed* in the **impacted sector** column. We also provide several taxonomic summaries of the costs to provide the reader with a full appreciation of the relative scale of costs among different contributors. These include by taxonomic Kingdom and taxonomic Class.

Temporal development of costs

For the temporal estimation of the average annual costs, we used the custom `invacost` package in R (Leroy et al. 2020). This package provides functions for modelling the temporal trend of costs using a selection of both linear and non-linear models to provide a summary and comparison of their respective outputs. Given the evidence that numbers of invasive species show no sign of saturation (Seebens et al. 2017), we expected their associated costs to be stable or increase. We accounted for the effects of time lags between the occurrence of the costs and their reporting by examining ‘impact year’ relative to ‘publication year’. This is because there were often several years between the occurrence of costs and the time when they were reported in the literature (Diagne et al. 2021). Here, we determined from both the highly reliable, observed costs and all costs combined that the lag quantiles were: 25% = 0 year; 50% = 1 year and 75% = 3 years. We therefore estimated the ‘final’ costs for the year 2017 (i.e. three years prior to 2020) in the trend analysis described below – this ensures that we include only the most complete years in the trend analysis (i.e. years expected to have > 75% of cost data).

We applied five different models to quantify the temporal dynamics of reported $\log_{10}$ costs (*costTrendOverTime* function in the `invacost` package; now *modelCosts* in the latest version of R) because we had no *a priori* reason to assume that the trends were monotonic (linear or otherwise). The simplest approach is an ordinary least-squares regression (two variants: linear and quadratic to test for monotonic trends or non-linear behaviour, respectively). Additionally, we applied two variants of a robust regression (linear, quadratic – R package `robustbase`) (Maechler et al. 2020) because the cost data are heteroscedastic (unequal variances) and temporally autocorrelated. We therefore estimated the covariance matrix with heteroscedasticity and autocorrelation-consistent estimators (Andrews 1991) to derive 95% confidence intervals for our models. Robust (MM-type) regression (Yohai et al. 1991; Koller and Stahel 2011) applies iteratively reweighted least-squares to reduce the influence of outliers on parameters estimates. Finally, we applied a generalised additive model (GAM – R package `mgcv`) (Wood et al. 2016). Generalised additive models use smoothing functions to account for heteroscedasticity, based on a Gaussian location-scale model family. A more detailed description of the methods we applied is provided in Diagne et al. (2021).

We applied these five different models to both the entire cost dataset for Australia, as well as the highly reliable, observed costs only, to predict model-averaged ‘final’ (for 2017) (Diagne et al. 2021) estimated costs, based on the temporal trends of the full and subset data. This incorporates both parameter uncertainty estimated in individual models, as well as model uncertainty regarding the true underlying fit. We did this in two ways: (1) we first calculated Akaike’s information criterion weights (Burnham and Anderson 2002) for the three likelihood-based models (ordinary least-squares regressions and generalised additive model) and (2) using the root mean-squared errors as weights to calculate a weighted-mean cost in 2017 (all five models). In addition to the `invacost` package, all R code and the Australia-specific dataset needed to reproduce the analyses can be accessed on Github via https://doi.org/10.5281/zenodo.4455979.

Results

Total cost

Since 1960, the total estimated cost of invasive species to Australia was US$298.58 billion (2017 value), based on 2078 unique entries (after removing 179 records pertain-

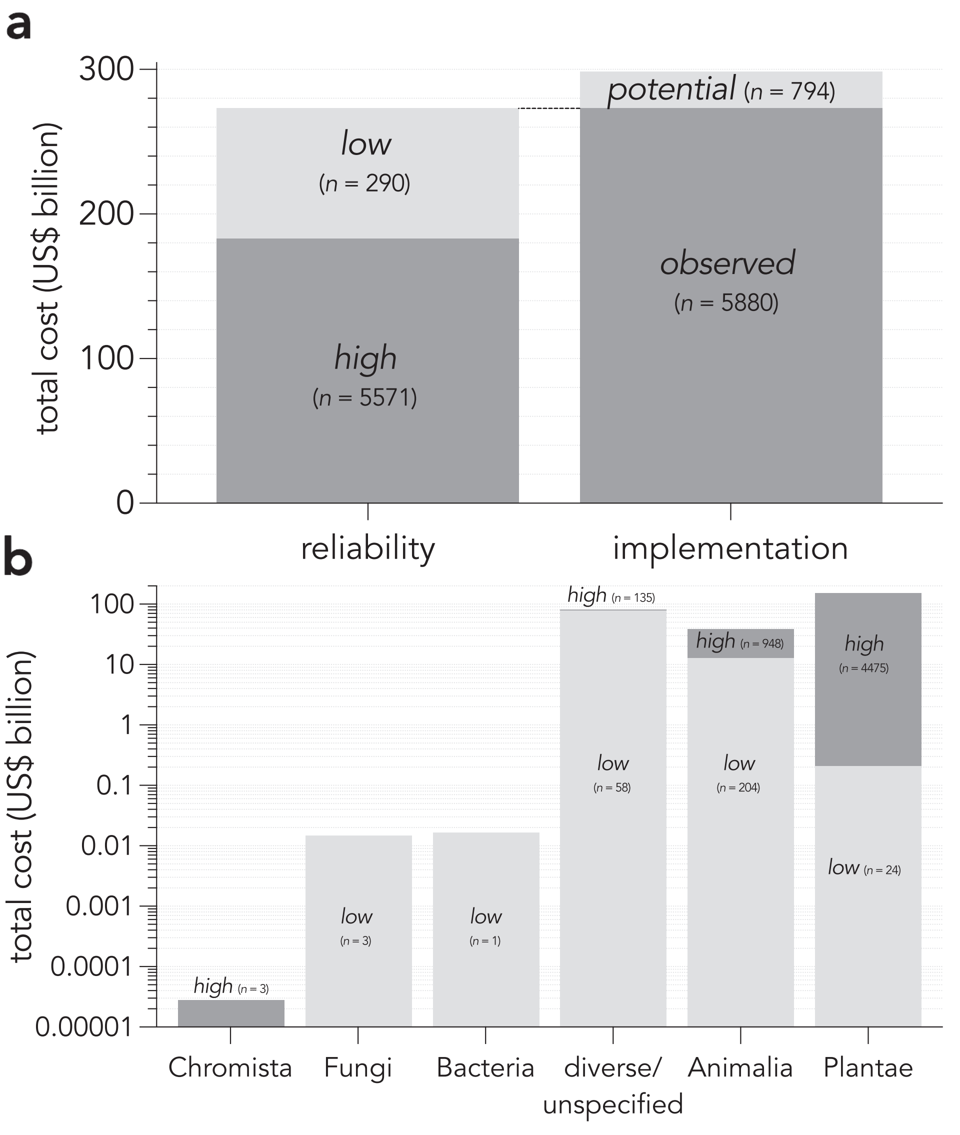

Figure 1. Division of total costs of invasive species in Australia relative to **a** reliability (*high*: dark grey or *low*: light grey) and the form of implementation (i.e. whether the cost estimate was realised [*observed*] or predicted [*potential*]) **b** costs according to major kingdoms. The number of unique database entries (*n*) in each category is indicated in brackets.

ing to avoided costs) in the combined database (6674 expanded yearly values), which is approximately equivalent to AU$389.59 billion (2017 average exchange rate). Of the total costs, the majority (91.6%) were observed (US$273.37 billion) rather than predicted or extrapolated ('potential'; US$25.21 billion) (Fig. 1a). Of the observed costs, most (61.3%) were considered highly reliable (US$183.04 billion).

Considering all costs regardless of reliability and implementation type, 27.6% of the total (US$82.29 billion) was not attributable to a single kingdom or was unspecified (Fig. 1b). This arises mainly from a multi-species assessment of costs of invasive species across all of Australia (Hoffmann and Broadhurst 2016). However, when considering only observed, highly reliable estimates, the costliest kingdom of invasive species was plants (US$151.68 billion), followed by animals (US$26.43 billion), with 'diverse/unspecified' making up only 2.7% of these (135 estimates amounting to US$4.93 billion) (Fig. 1b). There were few entries for Kingdoms Chromista (n = 3; US$27,970), Fungi ($n$ = 3; US$14.69 million; all low reliability; many of the fungal plant pathogens were not specified to Kingdom in the source data and so were designated 'diverse/unspecified') and Bacteria (n = 1; US$16.49 million; low reliability) (Fig. 1b).

There was a large disparity in the proportional attribution of costs by major political unit (States and Territories) whether estimating all costs or focussing on the highly reliable, observed costs only. Aside from the costs not clearly associated with a particular State or Territory (i.e. nation-wide or not specified), Western Australia had the highest total costs (52.7%) when considering all costs (US$17.88 billion) (Fig. 2a) – 69.3% of this value is attributed to rats *Rattus rattus* (US$12.39 billion), but > 99% of this estimate is considered to be of low reliability. When considering only the highly reliable, observed costs, New South Wales had the highest costs (US$5.25 billion), followed by Western Australia (US$4.58 billion) and Victoria (US$3.09 billion) (Fig. 2b).

There was an approximate power-law relationship between the number of unique database entries and the total costs per political unit for both all costs combined (Fig. 2c) or highly reliable, observed costs only (Fig. 2d). These relationships indicate that, with an increase of one order of magnitude in the number of estimates, the estimated costs increase on average by 2.0 (all costs) or 1.9 (highly reliable, observed costs) orders of magnitude. These power-law relationships were also evident for the cumulative data over time (Suppl. material 1: Fig. S1). The magnitude-order increase in costs with the number of database entries appears to be driven mainly by the variation in land surface area among political units (Suppl. material 1: Fig. S2); however, there is no relationship between costs and the number of database entries per unit area (Suppl. material 1: Fig. S2e, f), suggesting that the intensity of assessment of costs among political units is not systematically different. The Australia-wide or unspecified (to State/Territory) values probably represent some inevitable overlap with the cumulative estimates from the different regions; however, it is impossible to discern to what extent given unspecified attribution in many national-scale analyses (e.g., Hoffmann and Broadhurst 2016).

The costliest kingdom (plants) grouped most (96.5%) of its costs into the 'diverse/unspecified' category (Fig. 3b). Of the remaining highly reliable, observed costs identified to species, six species accounted for most (61%) of the remaining costs: annual ryegrass (*Lolium rigidum*), parthenium (*Parthenium hysterophorus*), ragwort (*Senecio jacobaea*), cucumis melons (*Cucumis* spp.), common heliotrope (*Heliotropium europaeum*) and wild radish (*Raphanus raphanistrum*) (Fig. 3b). Other invasive plants have

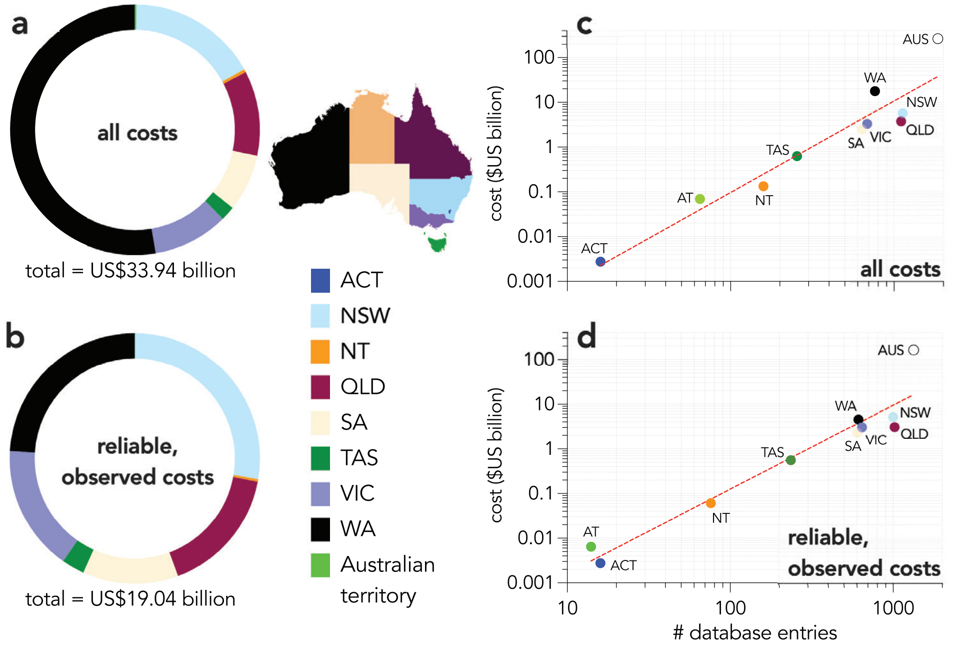

Figure 2. a sum of all costs according to attributable major political unit (States and Territories) **b** sum of highly reliable costs only by political unit **c** relationship between the number of database entries and all cost estimates by political unit – this also includes the estimate for 'Australia' ('AUS'; not directly attributable to a single State or Territory). The power-law relationship is also shown (evidence ratio = 18013, R^2 = 0.90) **d** relationship between number of database entries for highly reliable costs estimates by political unit (evidence ratio = 38550, R^2 = 0.91). Abbreviations: ACT = Australian Capital Territory; NSW = New South Wales; NT = Northern Territory; QLD = Queensland; SA = South Australia; TAS = Tasmania; VIC = Victoria; WA = Western Australia; AUS = nation-wide or not specified to which political unit the estimate belongs. 'Australian territory' refers to regions outside State/Territory jurisdication (e.g. Christmas Island, Lord Howe Island).

historically had enormous negative impacts on Australian agriculture, but successful biological control programmes have largely eliminated these costs (e.g. prickly pear cactus and Paterson's curse *Echium plantagineum*) (Cullen et al. 2012). Some high-cost invasive grasses, such as gamba grass (*Andropogon gayanus*) (Northern Territory Government 2008), were invariably grouped within this 'diverse/unspecified' category and so species-specific cost estimates were not available. In Australia, exotic grasses have major environmental (e.g. gamba and buffel *Cenchrus ciliaris* grasses) and agricultural impacts (e.g. *Nassella* tussocks).

The costliest taxonomic classes of invasive species across all of Australia are mammals, insects and eudicots (respectively), although most estimates cannot be attributed to a single class (Fig. 3a). Among the mammals, cats, rodents (mice *Mus musculus* and rats *Rattus* spp.), pigs, rabbits and foxes had the highest costs, accounting for 95% of the total highly reliable, observed costs in this class (US$20.19 billion; Fig. 3c).

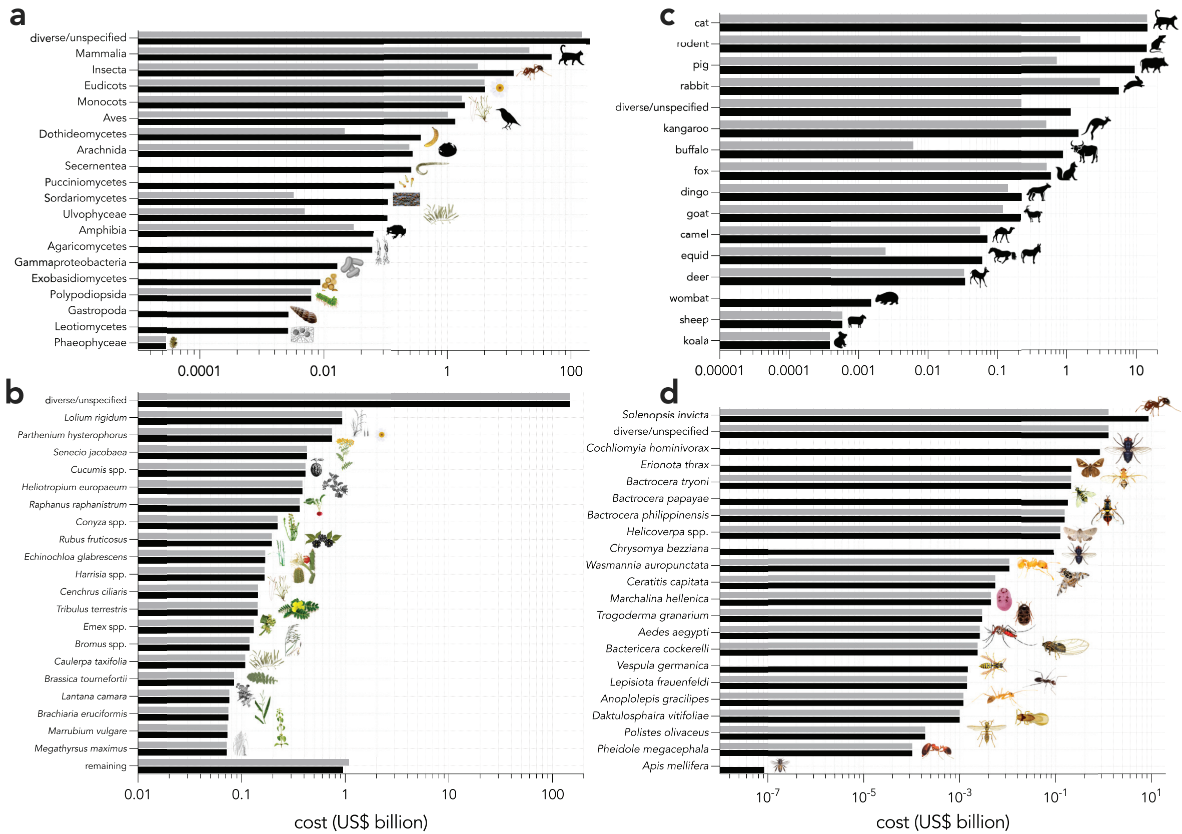

Figure 3. Sum of all (black) and highly reliable-only (grey) costs according to **a** taxonomic class **b** by plant species **c** by mammal species and **d** by insect species. We generally ordered these by the highly reliable costs, but, in some cases where there were no highly reliable costs for a particular category, we placed the category in the order suggested by total costs.

In fact, the category of 'diverse/unspecified' included these five taxa in many multi-species assessments; so, the costs attributed to these are actually higher. Including low-reliability costs would suggest that rodents – namely, house mice and rats *Rattus* spp. – were the second-costliest mammals, but most (89%) of this total was attributed to the low-reliability category. We also reported cost estimates for five native species groups, including various kangaroo species, koalas (*Phascolarctos cinereus*), common wombats (*Vombatus ursinus*), dingoes (*Canis dingo*) and Queensland fruit flies (*Bactrocera tryoni*) given that they are often considered 'overabundant' native 'pest' species because they compete for grazing resources (kangaroos), consume trees in *Eucalyptus* spp. plantations (koalas), burrow in paddocks (wombats), kill livestock (dingoes) or damage crops outside their native region (Queensland fruit fly). Kangaroos, koalas and wombats together account for only 3.1% of the total including all costs and 2.4% of the total highly reliable, observed costs (99.9% of which is attributed to kangaroos alone). Dingoes are native to Australia (Smith et al. 2019), but here we included all accounts of 'wild dogs', 'dogs' and 'dingoes' as dingoes – adding dingoes to the native-species groups increases the percentage represented to 3.5% (all) and 3.1% (highly reliable) (although this percentage is slightly higher in reality because dingo-related costs are sometimes combined with other species). Of course, many other native species cause extensive damage to the agricultural industry, such as birds and many insect species, but reliable estimates of the costs associated with most of these species have not been made for Australia.

Within the second-costliest class (insects), most (41.5%) of the highly reliable, observed total is within the 'diverse/unspecified' category (Fig. 3d). Of the highly reliable, observed cost estimates attributed to single species, 70.7% of the total is from the red imported fire ant *Solenopsis invicta* (US$1.29 billion), 11.8% from the (native to tropical Australia, but considered invasive elsewhere) Queensland fruit fly *Bactrocera tryoni* (US$215.45 million), 8.7% from the Pacific fruit fly *Bactrocera philippinensis* (US$158.91 million) and 7.1% from the bollworm *Helicovera* spp. (US$129.2 million) (Fig. 3d).

For the third-costliest class, based on all costs combined (Eudicots), five species account for most (56.7%) of all costs attributed to this class: parthenium (18.1%; US$740.66 million), ragwort (10.4%; US$425.37 million), cucumis melons (10.1%; US$412.12 million), common heliotrope (9.4%; US$384.25 million) and wild radish (8.8%; US$361.42 million) (Fig. 3b). Many of the other classes are dominated by one or a few species (Suppl. material 1: Table S1); for example, bird costs are either unspecified or from a single species: the common starling (*Sturnus vulgaris*); the Arachnids include only two mites: the red-legged earth mite *Halotydeus destructor* and varroa mite *Varroa destructor*; the Ulvophytes are represented solely by *Caulerpa taxifolia*; the Secernentids include only two nematode species (*Heterodera avenae* and *Pratylenchus* spp.); the Amphibia include only the cane toad *Rhinella marina*; the Polypodiopsids are represented only by *Salvinia molesta*; and the Phaeophyceae (brown algae) include only one species, wakame *Undaria pinnatifida* (see full species list in Suppl. material 1: Table S1).

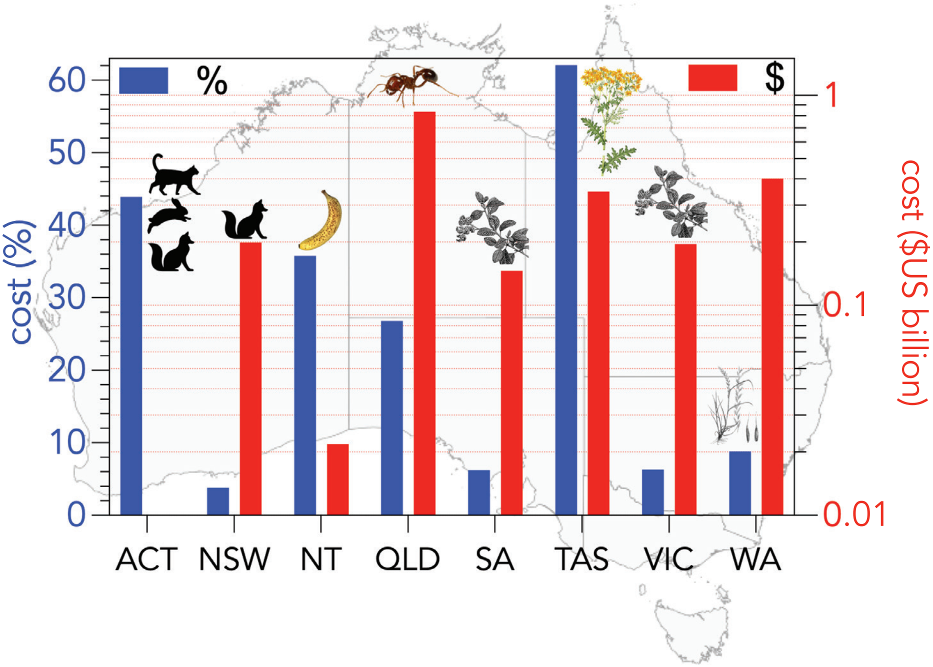

Figure 4. The costliest species (or group of species) per State/Territory. The left axis shows the percentage of the State's/Territory's total highly reliable, observed costs attributable to the species indicated and the right axis shows the value of these species in $US billion (2017 value). For all States/Territories, except Australian Capital Territory (ACT), Northern Territory (NT) and Tasmania, the costliest category is in fact diverse/unspecified. State/Territory abbreviations and species icons refer to: ACT = Australian Capital Territory (cats, foxes, rabbits); NSW = New South Wales (foxes); NT = Northern Territory (banana freckle disease *Phyllosticta cavendishii*), QLD = Queensland (red imported fire ants); SA = South Australia (common heliotrope *Heliotropium europaeum*); TAS = Tasmania (ragwort *Senecio jacobaea*); VIC = Victoria (common heliotrope); WA = Western Australia (annual ryegrass *Lolium rigidum*).

Various fungal rusts, smuts, rots, mildews and other plant pathogens were also featured in the database, accounting for > $697 million of the total reported costs (but only $25.1 million of the highly reliable, observed costs) (Fig. 3a). These included the Dothideomycetes (e.g. banana freckle disease *Phyllosticta cavendishii*), Sordariomycetes (e.g. wheat crown rot *Fusarium pseudograminearum*), Pucciniomycetes (e.g. wheat stripe rust *Puccinia striiformis*), Agaricomycetes (e.g. rhizoctonia disease *Rhizoctonia* spp.), Exobasidiomycetes (e.g. grass smut *Tilletia* spp.) and Leotiomycetes (powdery mildew *Blumeria graminis*).

The costliest species also vary among States/Territories (Fig. 4; also see Fig. 5). Mammals (cats *Felis catus*, red foxes, rabbits) are the costliest species only for Australian Capital Territory and New South Wales (Fig. 4). The Northern Territory's costliest species (36% of its costs) is the fungus *Phyllosticta cavendishii* that causes banana freckle disease. Queensland's costliest species is the red imported fire ant, representing 27% of the total

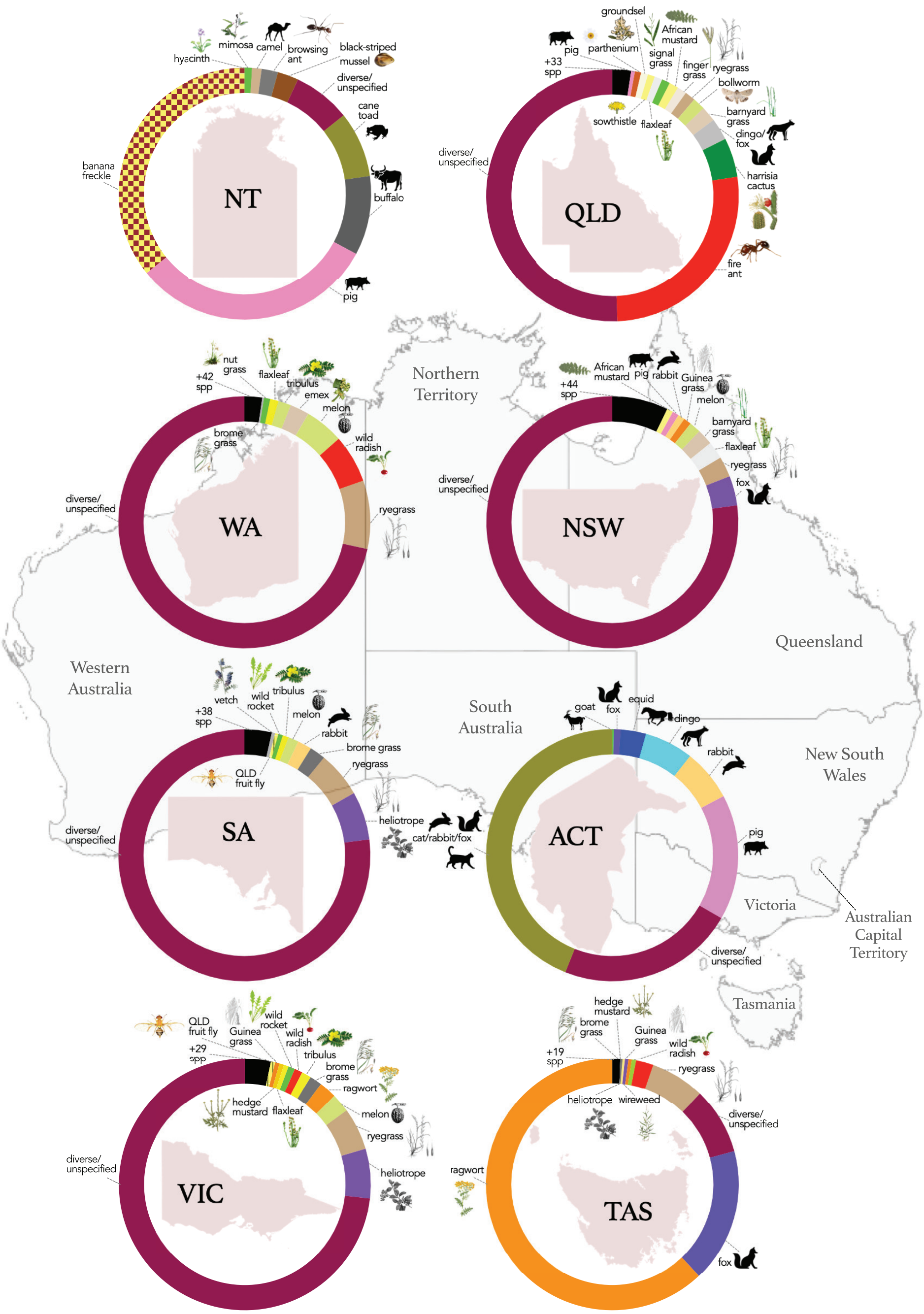

Figure 5. Proportional attribution of costs by species per State and Territory (highly reliable, observed costs only; refer also to Fig. 4). State/Territory abbreviations: ACT = Australian Capital Territory; NSW = New South Wales; NT = Northern Territory, QLD = Queensland; SA = South Australia; TAS = Tasmania; VIC = Victoria; WA = Western Australia. The full list of species (common and scientific names) is provided in Suppl. material 1: Table S1.

highly reliable, observed cost for that State (Fig. 4), whereas the common heliotrope is the costliest species for both South Australia and Victoria (6% of the total highly reliable, observed costs for those States). Tasmania's costliest species (62% of all costs) is the ragwort and Western Australia's is annual ryegrass (9% of total costs) (Fig. 4).

The proportional attribution of the highly reliable, observed costs by species per State/Territory is presented in Fig. 5.

The most impacted habitat is the terrestrial environment (39%), although most (60%) of the total highly reliable, observed costs could not be attributed to a single habitat type (Fig. 6a). Damage by or loss of economic opportunity (cf. management) from invasive species has the highest value (US$133.35 billion) among cost types (Fig. 6b), representing 72.9% of the total highly reliable, observed costs. The most-affected sectors are the agriculture (24.1%; US$44.03 billion), health (4.6%; US$8.37 billion) and environment (4.1%; US$7.58 billion) sectors, although most (65.8% of the total highly reliable, observed costs) affected multiple sectors (*mixed*; Fig. 6c).

Tracking temporal trends (Diagne et al. 2021), the costs attributed to invasive species in Australia increased from the 1970s to the present. Using all costs irrespective of reliability, the average annual cost increased from US$57.65 million in the 1970s to $20.19 billion during the last decade (Fig. 7a). Although highly variable from decade to decade, this equates to an average decadal increase of ~ 6.3-fold (or 3.2-fold, based on the slope coefficient for the linear robust regression only to compare directly to the 3-fold increase estimated from the global dataset) (Diagne et al. 2021). Taking only the reliable, observed costs, the average annual cost increased from over US$52.35 million in the 1970s to US$15.12 billion during the last decade (Fig. 7a) or an average 6.0-fold increase per decade (or 1.8-fold, based on the slope coefficient for the linear robust regression). This translates into a mean annual cost of US$5.85 billion (all costs) or US$3.58 billion (reliable, observed only) over the study interval (Fig. 7a). Examining the temporal trends in the observed, reliable costs only for three of the main taxonomic groups (plants, mammals, insects) shows the general increasing trend, although the most recent decade's increase is driven primarily by costs attributed to plants (Suppl. material 1: Fig. S3).

For both all-costs and observed, reliable datasets, the general additive model had the best fit assessed using the highest Akaike's information criterion weights (*w*AIC). However, the quadratic ordinary least-squares model had the best fit for the highly reliable, observed costs, based on the lowest root mean-squared error (RMSE; Table 1).

Using these weights to predict the annual costs in 2017 for both datasets, those based on *w*AIC are dominated by the GAM prediction, whereas those based on RMSE weights accord relatively more importance to the quadratic models (Fig. 7b, c).

For the all-costs dataset, the estimated annual costs in 2017 are US$18.77 billion (US$6.09 billion–US$57.91 billion) according to *w*AIC or US$17.88 billion (US$7.56 billion–US$45.44 billion) according to RMSE (Fig. 7b). For the highly reliable, observed data only, the predictions for 2017 are US$731.48 million (US$225.31 million–US$2.38 billion) according to *w*AIC or US$1.85 billion (US$484.85 million–US$6.84 billion) according to RMSE (Fig. 7c).

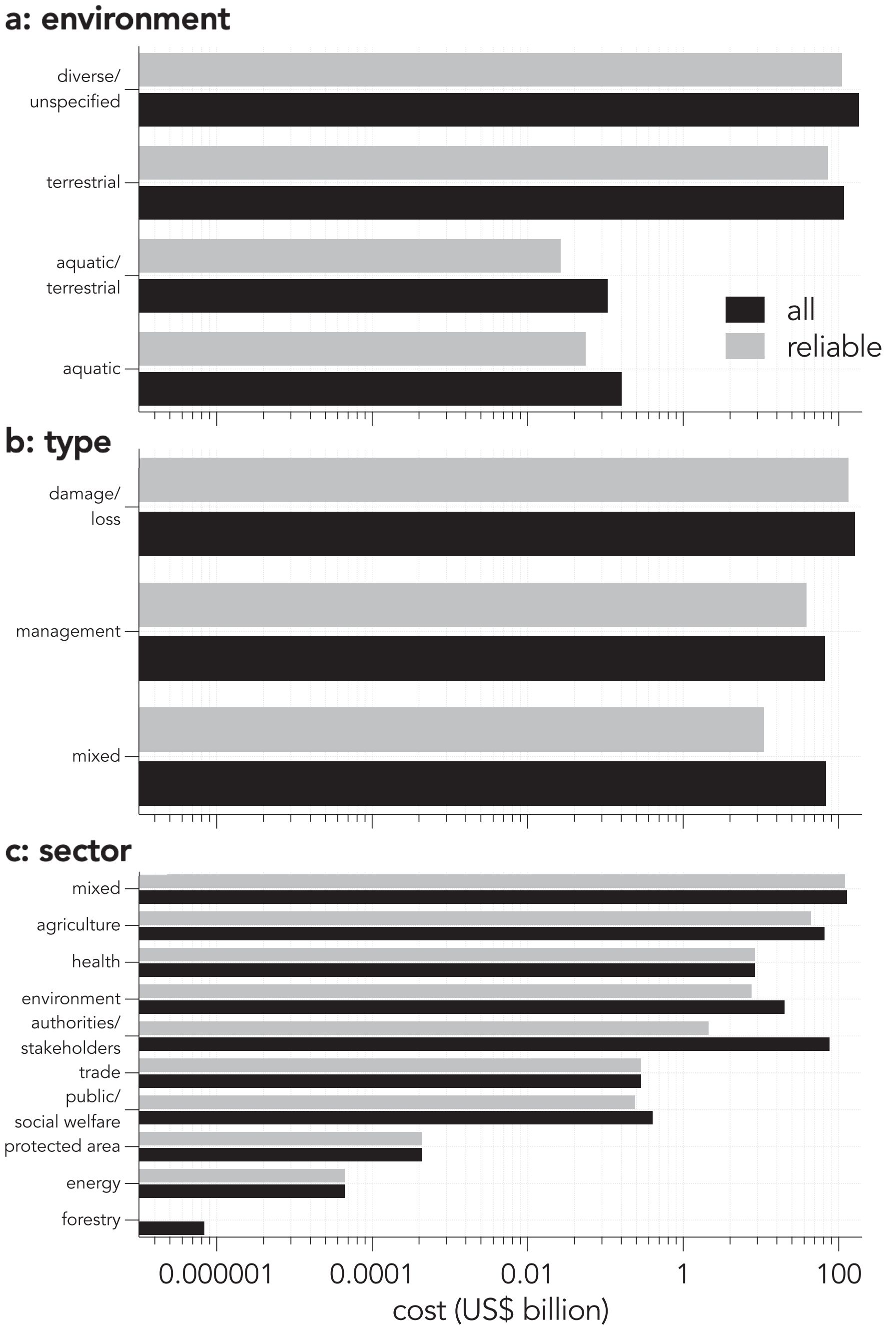

Figure 6. a sum of all (black) and reliable-only (grey) costs ($\log_{10}$ scale) according the impacted environment **b** cost type and (c) the major impacted sector.

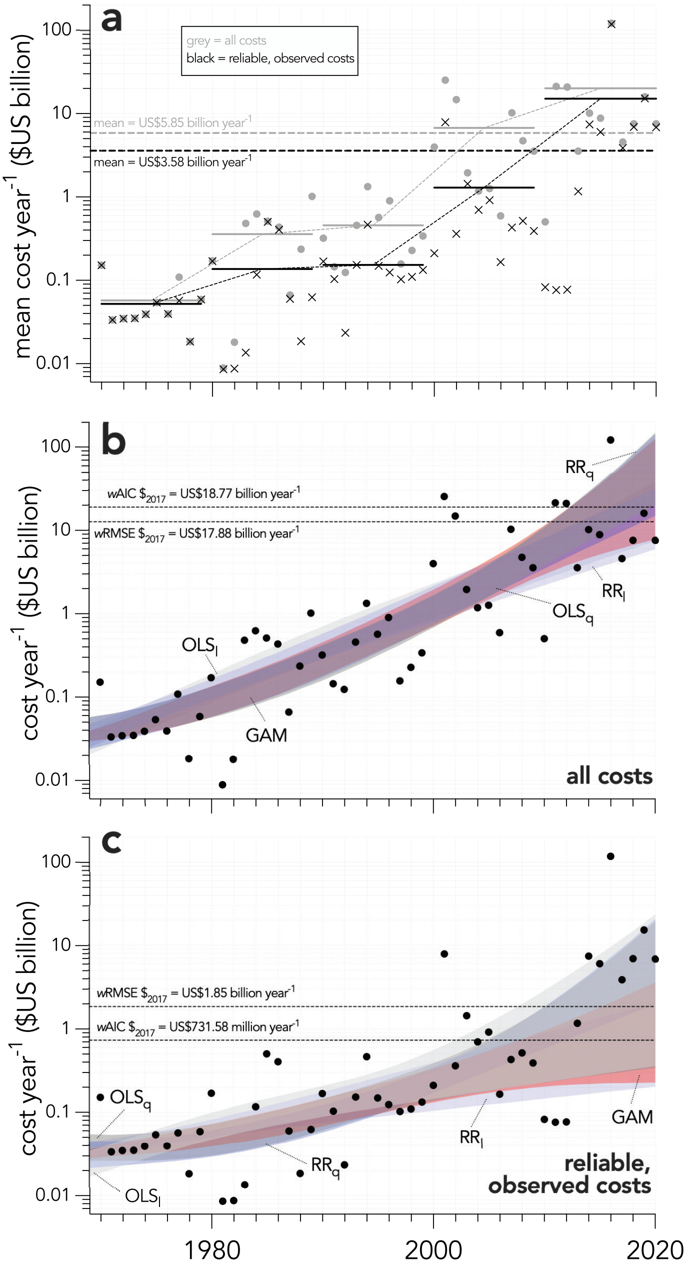

Figure 7. a raw annual costs for all costs (black) and reliable, observed costs (grey). Also shown are the decadal and overall means **b** predicted annual costs across Australia from 1970 to 2020 for all costs and **c** reliable, observed costs only. Fitted models include OLS_l = linear ordinary least-squares, OLS_q = quadratic ordinary least-squares, RR_l = linear robust regression, RR_q = quadratic robust regression, GAM = general additive model. Also shown in each panel are *w*AIC $\$_{2017}$ = Akaike's information criterion-weighted (*w*AIC)-average of the predicted annual cost in 2017 (all costs; OLS_l, OLS_q, GAM only), *w*RMSE $\$_{2017}$ = root mean-squared error-weighted average of the predicted annual cost in 2017 (all costs; all models), *w*AIC $\$_{2017}$, and *w*RMSE $\$_{2017}$ (reliable, observed costs only).

Table 1. Model fits to the temporal trend of annual costs from 1970 to 2020 for all data combined and for reliable, observed data only. Fitted models include OLS_l = linear ordinary least-squares, OLS_q = quadratic ordinary least-squares, RR_l = linear robust regression, RR_q = quadratic robust regression, GAM = general additive model. Also shown are Akaike's information criterion weights (*w*AIC) for the three likelihood-based models (OLS_l, OLS_q, GAM), the root mean-squared error (RMSE) for all models, the R^2 for each model (% deviance explained in the case of GAM) and the estimates of the relevant model coefficients (β_{year} and β_{year}^2) and their standard errors (± SE). See also Fig. 7.

model	*w*AIC	RMSE	R^2	β_{year} ± SE	β_{year}^2 ± SE
all data					
OLS_l	< 0.0001	0.4791	0.76	0.0528 ± 0.0041	–
OLS_q	< 0.0001	0.4798	0.78	-2.5449 ± 0.8721	0.0007 ± 0.0002
RR_l	–	0.4786	0.76	0.0509 ± 0.0041	–
RR_q	–	0.4779	0.79	-2.5807 ± 1.0377	0.0007 ± 0.0003
GAM	> 0.9999	0.4676	0.99	–	–
reliable, observed					
OLS_l	< 0.0001	0.5585	0.50	0.0337 ± 0.0074	–
OLS_q	< 0.0001	0.5271	0.55	-2.9986 ± 1.7180	0.0008 ± 0.0004
RR_l	–	0.5816	0.51	0.0251 ± 0.0055	–
RR_q	–	0.5277	0.71	-3.2653 ± 0.9690	0.0008 ± 0.0002
GAM	> 0.9999	0.5622	0.99	–	–

Discussion

Aggregated economic costs of the impacts and management of invasive species in Australia have amounted to at least US$298.58 billion (~ AU$389.59 billion) since the 1960s and US$183.04 billion (~ AU$238.83 billion) when conservatively considering highly reliable, observed costs only. Sampling biases notwithstanding (see below), the greatest economic burden to Australia imposed by invasive species originates from weedy plants, although most of these costs are shared across a wide range of species. This arises because of the 'top-down' approaches employed by others previously to estimate costs associated with losses and control specific to particular industries, rather than individual species (e.g., McLeod 2004; Sinden et al. 2004; Gong et al. 2009; Llewellyn et al. 2016). In many circumstances, this approach is more tractable and efficient for estimating total costs to particular sectors.

There are an estimated 2700 exotic plant species established in Australia, of which > 400 are declared weedy or noxious (Hoffmann and Broadhurst 2016). Our database contained highly reliable cost estimates for only ~ 100 species of declared weeds and many weeds did not have species-specific costs as described above. The cost of controlling and the damage done by weeds to the Australian agriculture sector alone are estimated at ~ AU$4 billion year^{-1} (Sinden et al. 2004; Hoffmann and Broadhurst 2016). However, from the perspective of single species, exotic mammals dominate the costs, with cats and rabbits, in particular, showing some of the highest estimates across the entire sample across Australia. For rabbits, it has been estimated that, without the highly successful biological control programme started in the 1950s, the impacts of rabbits in Australia would have been at least US$53.5 billion (~ AU$70 billion) higher over the last 50 years (Cooke et al. 2013). However, the impacts of invasive mammals vary markedly by region, with the tropical regions suffering more from invasive fungi (i.e. banana freckle disease in the Northern Territory) and insects (i.e. red imported fire ant in Queensland) instead.

Hoffmann and Broadhurst (2016) estimated annual costs of invasive species in Australia (loss and management) in 2001–2002 at AU$12.9 billion and in 2011–2012 at AU$13.6 billion (2012 values), equivalent to approximately US$14.26 billion and US$15.03 billion (2017 value) for direct comparison to our estimates. The estimates of Hoffmann and Broadhurst (2016) hail from five different sources (Canyon et al. 2002; McLeod 2004; Sinden et al. 2004; Gong et al. 2009; de Hayr 2013) of unknown reliability and/or derived from stakeholder surveys. The management ('national') expenditure component of these were AU$3.0 billion and AU$3.8 billion for 2001–2002 and 2011–2012, respectively (or US$3.93 billion and US$4.20 billion, respectively; 2017 value). In contrast, our study incorporated appraisals of method reliability and implementation type when considering economic costs, presenting both 'total' and more conservative figures. Considering only those more conservative numbers, we found that damage and resource losses attributable to invasive species outweigh (73% of that total) management expenditure, but to a greater extent than indicated in those previous studies. This likely mirrors the relatively small investment of government funding for the management of most invasive species (Hoffmann and Broadhurst 2016) compared to the actual economic damages they incur. However, we acknowledge that our broad categorisations of cost type and implementation likely obscure subtleties associated with production losses, control costs and environmental impacts on a case-by-case basis. Reporting cost categories at finer resolution would likely invoke unacceptable subjectivity in reporting given the diversity of species, approaches, sectors, cost types, analyses and assumptions made in individual reports. We acknowledge, however, that the environmental and social costs recorded in InvaCost should be considered with some caution regarding their interpretation, because they are not strictly similar to market costs recorded in economic sectors (Diagne et al. 2020b). Further, cost categorisations for particular species likely shift in terms of emphasis during the course of invasions, meaning that management investment for many species begins with eradication costs and ultimately changes to suppression via control management as the species becomes established. Indeed, government investments typically target new incursions first, meaning that many of these are unlikely to be captured in the relevant literature.

As most cost estimates are damage arising from invasive plants (weeds), it is understandable why management-related costs represent such a small proportion of the total. However, one invasive mammal species is problematic in this regard – cats. According to the definition of 'reliable' provided for the overall InvaCost database – "Peer-reviewed articles and official documents (e.g. institutional or governmental reports) are likely validated by experts before publication. We assumed, therefore, that all cost estimates collected from these materials may likely be of high reliability" (Diagne et al. 2020b) – we were objectively obliged to include the damage estimate of US$5.95 billion for this species from Pimentel et al. (2001). However, that particular estimate was based on an unverified national population of 18 million feral cats and a subjective value of a bird eaten of US$30 (amount to US$540 million year^{-1}) (Gregory et al. 2014). The subjective extrapolation of the costs of cats was also noted for the USA (Fantle-Lepczyk et al. 2021).

Compared to the global estimates (Diagne et al. 2021), the relatively well-sampled region of Oceania represents ~ 8% (range: 3–22%) of the total average annual costs globally in 2017 according to our database. Further, we found that Australia's rate of cost increase was up to ~ 2 times the rate of cost increase estimated from the global dataset (Diagne et al. 2021), although this observation might be explained in part by a lack of data in other regions compared to relatively well-studied Australia. However, Australia is still likely to be recording only a portion of the total costs of invasive species in the region. Although InvaCost, in general, as well as our enhanced sample from Australia more specifically, represent the most comprehensive and resolute assessments of the costs of invasive species yet available, there are several lines of evidence to suggest that the totals we report here still represent a vast underestimate of the real costs.

The first line of evidence is that the estimated total costs increased by approximately two orders of magnitude with every order-of-magnitude increase in the number of entries. This accords well with other assessments revealing that, as the number of estimates increases, so too do the total costs (Bradshaw et al. 2016; Cuthbert et al. 2021a; Diagne et al. 2021) – in other words, the more economic assessments are done, the more costs are discovered. While this could arise in part from the increasing rate of scientific and related publishing over the last 50 years (Richardson and Pyšek 2008), under-sampled or under-assessed species and regions will necessarily underestimate total costs. This particularly holds true to aquatic and semi-aquatic alien taxa in Australia, with the majority (99.9%) of costs attributed to a particular habitat (i.e. excluding mixed-habitat costs) being terrestrial (observed, highly reliable costs) and terrestrial taxa dominating in most regions. On the global scale, this aligns with the under-representation of aquatic invaders relative to terrestrial ones (Cuthbert et al. 2021b).

The second line of evidence is that many well-known invasive species established in Australia have no associated cost estimates in the database. For example, there was not a single estimate from the Reptilia in the database, yet species like red-eared sliders (*Trachemys scripta elegans*) and corn snakes (*Pantherophis guttatus*) are potentially costly species in some States of Australia (García-Díaz et al. 2017; Toomes et al. 2020). Neither were pet trade-sourced bird species like rose-ringed parakeets (*Psittacula krameri*) (Vall-llosera et al. 2017; Toomes et al. 2020) or fish pests, such as European carp (*Cyprinus carpio*) (Koehn 2004), identified in our cost database. Neither have native birds (Bomford and Sinclair 2002) or insects (Gu et al. 2007) that can heavily damage various crops been adequately assessed for costs (apart from the Queensland fruit fly). Indeed, Gong et al. (2009) reported that birds were the costliest vertebrate group to Australian agriculture. Despite reporting the costs for several fungal plant pathogens, there were notable absences; for example, we could not identify any reasonable costs estimates for *Phytophthora cinnamomi*, despite its being a major cause of crop losses and damage to biodiversity in Australia (Cahill et al. 2008; Hee et al. 2013).

The third line of evidence is that the InvaCost approach mandates avoiding the extrapolation of on-going costs beyond the time period specified by a particular source (Diagne et al. 2020b). We therefore included costs without a specified time window as single-year costs, meaning that the resultant annualised costs represent a lower boundary of the true costs. While this avoids propagating positive errors through time, it downwardly biases the true mean costs. The fourth line of evidence is that the number of invasions in Australia has been increasing linearly for some time (CSIRO 2020), which is a notable improvement from the current exponential trend seen globally (Seebens et al. 2017); this accords well with our temporal analysis indicating an ongoing increase in recorded costs over last few decades (Fig. 7b, c). More broadly, lags in invader impacts considering their year of introduction (Rouget et al. 2016) could mean that it takes decades for economic costs to be realised and reported, just as it takes decades of introductions to become invasions (Essl et al. 2011). Accordingly, future economic impacts will likely result from a different suite of invasive species for which the effects have not yet been fully realised.

Conclusions

While the major costs of loss and damage arising from invasive species, where tangible, are probably captured reasonably well by our database (the under-sampling bias notwithstanding), management-expenditure estimates are perhaps less reliable. The component of the total costs of invasive species attributed to management expenditure is particularly problematic for several reasons. Indeed, there is no standard procedure for reporting expenditure or costs at any level of government or for private organisations, nor is there a national database of expenditure available (Hoffmann and Broadhurst 2016). A similar argument could also be mounted for damage and loss assessments regarding a lack of a standardised reporting protocol.

As our assessment highlights, the large and growing costs of invasive species to the Australian economy are substantial, but under-estimated because of insufficient coverage and a lack of standardised reporting by management authorities and other agencies. As invasive species continue to increase their ranges and associated impacts across the planet (Bellard et al. 2013, 2016; Seebens et al. 2017; Seebens et al. 2021), we can reasonably surmise that Australia will also suffer many additional, negative economic repercussions from invasive species over the coming decades. Developing better methods of estimating environmental impacts of invasive alien species will also contribute to this. We recognise that such types of economically intangible costs arising from invasive species (Bradshaw et al. 2016) are not captured by the database – for example, ecological damage, erosion of ecosystem services and loss of cultural values are inherently challenging to measure in this regard.

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Supplementary material 1

Figures S1–S3 and Table S1

Authors: Corey J.A. Bradshaw, Andrew J. Hoskins, Phillip J. Haubrock, Ross N. Cuthbert, Christophe Diagne, Boris Leroy, Lindell Andrews, Brad Page, Phillip Cassey, Andy W. Sheppard, Franck Courchamp

Data type: Additional data and analyses

Explanation note: **Figure S1.** Cumulative costs across Australia expressed relative to the cumulative number of estimates, with an approximate power-law model fit to (a) all costs and (b) highly reliable, observed costs only (also see Fig. 2). **Figure S2.** Power-law relationships between (a, b) total costs and land-surface area of different States/Territories, (c, d) database entries and total land-surface area and (e, f) total costs and database entries per unit area for all costs (top row) and highly reliable, observed costs only (bottom row). **Figure S3.** (a) Raw annual (observed, highly reliable) costs for plants, mammals and insects. Also shown are the overall annual means for each taxonomic group. **Table S1.** List of common and scientific names of species to which costs have been attributed in the Australian database.

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