Science of the Total Environment 775 (2021) 145238

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Global economic costs of aquatic invasive alien species

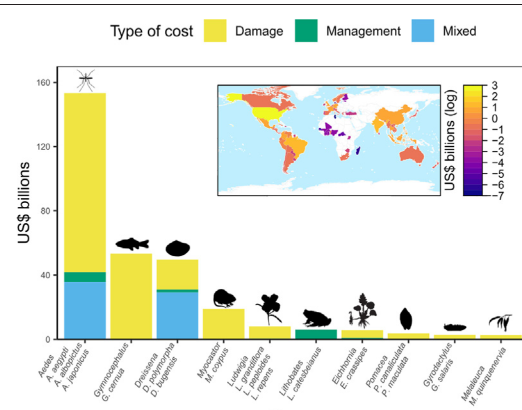
Ross N. Cuthbert [a,b,*], Zarah Pattison [c], Nigel G. Taylor [d], Laura Verbrugge [e,f], Christophe Diagne [g], Danish A. Ahmed [h], Boris Leroy [i], Elena Angulo [g], Elizabeta Briski [a], César Capinha [j], Jane A. Catford [k,l], Tatenda Dalu [m,b], Franz Essl [n], Rodolphe E. Gozlan [o], Phillip J. Haubrock [p,q], Melina Kourantidou [r,s,t], Andrew M. Kramer [u], David Renault [v,w], Ryan J. Wasserman [x,b], Franck Courchamp [g]

[a] GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, 24105 Kiel, Germany
[b] South African Institute for Aquatic Biodiversity, Makhanda 6140, South Africa
[c] Modelling, Evidence and Policy Research Group, School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne NE1 7RU, UK
[d] Tour du Valat, Research Institute for the Conservation of Mediterranean Wetlands, 13200 Arles, France
[e] University of Helsinki, Faculty of Agriculture and Forestry, Department of Forest Sciences, P.O. Box 27, 00014 Helsinki, Finland
[f] Aalto University, Department of Built Environment, Water & Development Research Group, Tietotie 1E, FI-00076 Aalto, Finland
[g] Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405 Orsay, France
[h] Center for Applied Mathematics and Bioinformatics (CAMB), Department of Mathematics and Natural Sciences, Gulf University for Science and Technology, P.O. Box 7207, Hawally 32093, Kuwait
[i] Biologie des Organismes et Ecosystèmes Aquatiques (BOREA), Muséum national d'Histoire naturelle, CNRS, IRD, Sorbonne Université, Université Caen-Normandie, Université des Antilles, 43 rue Cuvier, CP 26, 75005 Paris, France
[j] Centro de Estudos Geográficos, Instituto de Geografia e Ordenamento do Território – IGOT, Universidade de Lisboa, Lisboa, Portugal
[k] Department of Geography, King's College London, Strand WC2B 4BG, UK
[l] School of BioSciences, University of Melbourne, Vic 3010, Australia
[m] School of Biology and Environmental Sciences, University of Mpumalanga, Nelspruit 1200, South Africa
[n] BioInvasions, Global Change, Macroecology-Group, Department of Botany and Biodiversity Research, University Vienna, Rennweg 14, 1030 Vienna, Austria
[o] ISEM UMR226, Université de Montpellier, CNRS, IRD, EPHE, 34090 Montpellier, France
[p] Senckenberg Research Institute and Natural History Museum, Frankfurt, Department of River Ecology and Conservation, Gelnhausen, Germany
[q] 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
[r] Woods Hole Oceanographic Institution, Marine Policy Center, Woods Hole, MA 02543, United States
[s] Institute of Marine Biological Resources and Inland Waters, Hellenic Center for Marine Research, Athens 164 52, Greece
[t] University of Southern Denmark, Department of Sociology, Environmental and Business Economics, Esbjerg 6705, Denmark
[u] Department of Integrative Biology, University of South Florida, Tampa, FL 33620, United States
[v] Univ Rennes, CNRS, ECOBIO [(Ecosystèmes, biodiversité, évolution)], - UMR 6553, F 35000 Rennes, France
[w] Institut Universitaire de France, 1 Rue Descartes, 75231 Paris cedex 05, France
[x] Department of Zoology and Entomology, Rhodes University, Makhanda 6140, South Africa

HIGHLIGHTS

- Aquatic invasions have cost the global economy US$345 billion.
- Most costs are caused by invertebrates, in North America and damages to resources.
- Costs have increased exponentially over time, to at least US$23 billion in 2020.
- Aquatic invasion costs are underrepresented compared to terrestrial invasion costs.
- Taxonomic, geographic and temporal gaps make these costs severely underestimated.

GRAPHICAL ABSTRACT



* Corresponding author at: GEOMAR, Helmholtz-Zentrum für Ozeanforschung Kiel, 24105 Kiel, Germany.
E-mail address: rossnoelcuthbert@gmail.com (R.N. Cuthbert).

https://doi.org/10.1016/j.scitotenv.2021.145238

ARTICLE INFO

Article history:
Received 12 November 2020
Received in revised form 6 January 2021
Accepted 13 January 2021
Available online 20 January 2021

Editor: Damia Barcelo

Keywords:
Brackish
Freshwater
Habitat biases
InvaCost
Marine
Monetary impact

ABSTRACT

Much research effort has been invested in understanding ecological impacts of invasive alien species (IAS) across ecosystems and taxonomic groups, but empirical studies about economic effects lack synthesis. Using a comprehensive global database, we determine patterns and trends in economic costs of aquatic IAS by examining: (*i*) the distribution of these costs across taxa, geographic regions and cost types; (*ii*) the temporal dynamics of global costs; and (*iii*) knowledge gaps, especially compared to terrestrial IAS. Based on the costs recorded from the existing literature, the global cost of aquatic IAS conservatively summed to US$345 billion, with the majority attributed to invertebrates (62%), followed by vertebrates (28%), then plants (6%). The largest costs were reported in North America (48%) and Asia (13%), and were principally a result of resource damages (74%); only 6% of recorded costs were from management. The magnitude and number of reported costs were highest in the United States of America and for semi-aquatic taxa. Many countries and known aquatic alien species had no reported costs, especially in Africa and Asia. Accordingly, a network analysis revealed limited connectivity among countries, indicating disparate cost reporting. Aquatic IAS costs have increased in recent decades by several orders of magnitude, reaching at least US$23 billion in 2020. Costs are likely considerably underrepresented compared to terrestrial IAS; only 5% of reported costs were from aquatic species, despite 26% of known invaders being aquatic. Additionally, only 1% of aquatic invasion costs were from marine species. Costs of aquatic IAS are thus substantial, but likely underreported. Costs have increased over time and are expected to continue rising with future invasions. We urge increased and improved cost reporting by managers, practitioners and researchers to reduce knowledge gaps. Few costs are proactive investments; increased management spending is urgently needed to prevent and limit current and future aquatic IAS damages.

1. Introduction

The impacts of invasive alien species (IAS) on biodiversity (Mollot et al., 2017; Spatz et al., 2017; Shabani et al., 2020), ecosystem services (Vanbergen, 2013; Blackburn et al., 2019) and human wellbeing (Pejchar and Mooney, 2009) are well recognized (Pyšek et al., 2020). Accordingly, there are numerous national and international policies, regulations and mandates in place to prevent new introductions and limit the geographic spread of IAS [e.g. Convention on Biological Diversity (UNEP, 2011); European Union Regulation 1143/2014 on IAS]. However, records of IAS are continuously increasing, owing to factors such as habitat disturbance, climate change, and an increasing diversity, frequency and intensity of anthropogenic vectors associated with globalising trade and transport networks (Capinha et al., 2015; Seebens et al., 2017, 2018; Turbelin et al., 2017; McGeoch and Jetz, 2019). Alien species numbers are burgeoning across geographical regions and habitat types, with the number of established alien species expected to increase by 36% in the next three decades (Seebens et al., 2020).

Aquatic ecosystems can be severely threatened by IAS, which contribute to extinctions of individual species, substantially change the structure of native communities, and alter ecosystem functioning (Vitousek et al., 1997; Ricciardi and MacIsaac, 2011; Jackson et al., 2017). Aquatic ecosystems provide numerous services to people, from food provision to flood protection and recreation; these services can also be critically altered by the presence of IAS (e.g. Katsanevakis et al., 2014). The vulnerability of aquatic ecosystems to invasions is increased by high interconnectedness among habitats, specifically man-made waterways and shipping, as well as other anthropogenic pressures (Strayer and Findlay, 2010; Poulin et al., 2011; Darwall et al., 2018) and climate shifts (Woodward et al., 2010).

In recent years there have been significant advances across habitat types in understanding ecological impacts of IAS (Kumschick et al., 2015; Dick et al., 2017; but see Crystal-Ornelas and Lockwood, 2020) and the drivers of invasion success (Cuthbert et al., 2019, 2020; Fournier et al., 2019; van Kleunen et al., 2020), as well as methodological advances in assessing the economic dimensions of IAS and their management (Lovell et al., 2006; Hanley and Roberts, 2019). However, studies of economic aspects of IAS have been limited to certain taxonomic groups (Bradshaw et al., 2016), communities, or regions (Pimentel et al., 2000; 2005; Kettunen et al., 2009; Cuthbert et al., 2021; Haubrock et al., 2021). In particular, costs of aquatic IAS are generally less well understood than costs of terrestrial IAS, despite some estimates indicating high costs (Lovell et al., 2006; Aldridge and Oreska, 2011). Comprehensive and systematically-assembled data on the costs of aquatic IAS would greatly help planning and prioritisation for their management, in the context of limited resources (McGeoch et al., 2015). Such data would also provide a useful resource for communications with policymakers and the general public: impacts expressed in economic terms are more tangible and comprehensible than complex ecological impacts (Diagne et al., 2020a).

This paper is the first systematic effort to describe global patterns and trends in reported costs of aquatic IAS. Our analysis, based on the recently developed InvaCost database (Diagne et al., 2020b), allows us to synthesise standardised costs, identify knowledge gaps and provide recommendations for management and further research. We describe the global monetary costs associated with aquatic IAS based on taxonomic, geographic and temporal descriptors, as well as between fully aquatic and semi-aquatic taxa. In doing so, we examine (*i*) how costs are structured by implementation method (i.e. observed vs. potential/expected), (*ii*) reliabilities of cost estimates and (*iii*) their typology, i.e., whether costs result from damages and losses or management expenditure. Further, we model the yearly and cumulative dynamics of costs and investigate whether they are likely to saturate in the near future. Finally, we assess potential biases between aquatic and terrestrial cost reporting. These biases are then used to identify gaps in management spending between habitats.

2. Materials and methods

2.1. Original data

For the purpose of quantifying global costs of aquatic IAS, we used the most comprehensive and up-to-date dataset of costs caused by alien species globally, assembled by the InvaCost project (Diagne et al., 2020a, 2020b). At time of writing, this includes 9823 entries in various languages from systematic and opportunistic literature searches (Diagne et al., 2020b; Angulo et al., 2021; full database version 3 at https://doi.org/10.6084/m9.figshare.12668570). This database captures any reported economic costs associated with IAS in their novel range, including those for species that have already become invasive (e.g. management, damages and losses) and species that may become invasive in the future (e.g. prevention and rapid eradication).

The InvaCost version 3 database contains a column ("Environment_IAS") which classifies species as either aquatic (species with a close association with aquatic systems at any life stage, including for reproduction, development and/or foraging; $n = 2317$ cost entries after our below corrections) or terrestrial ($n = 6433$ cost entries after our below corrections), independently of where costs occurred. For some analyses, we split out costs for semi-aquatic species: the subset of aquatic species with a looser association with aquatic systems (see Supplementary Material 1). Remaining entries, linked to species from diverse habitats (i.e. a mixture of aquatic and terrestrial) or unspecified habitats, were excluded from analyses. We also carefully screened the published database, removing clear duplicates and correcting clear mistakes. All modifications made in our dataset were sent to updates@invacost.fr as recommended by the database managers.

Briefly, costs in InvaCost are standardised against a single currency for comparability (2017 US$); costs in the database may be 'expanded' so that entries can be considered on an annual basis. That means that costs spanning multiple years (e.g. $10 million between 2001 and 2010) are divided according to their duration (e.g. $1 million for each year between 2001 and 2010); we considered this expanded database version in all analyses (Supplementary Materials 1; $n = 5682$ aquatic entries). Expansion was done using the *expandYearlyCosts* function of the 'invacost' R package (R Core Team, 2020; Leroy et al., 2020). The final, unexpanded dataset used in our analyses is provided as Supplementary Material 2. We note that 1 billion $= 1 \times 10^9$.

2.2. Cost descriptors

To obtain a general overview of the costs associated with IAS, we first illustrated them across a number of key database descriptors (see Supplementary Material 1 and https://doi.org/10.6084/m9.figshare.12668570 for complete details). These included (1) broad taxonomic grouping of species presenting costs (invertebrates, vertebrates, plants, other), (2) perceived reliability of each cost entry ("High" vs. "Low"), (3) cost implementation type ("Observed" vs. "Potential"), (4) geographic region in which the cost occurred (within continent- and country- scales) and (5) cost type ("Damage" vs. "Management"). We summed the expanded entries (see above) to quantify cost totals among these descriptors.

2.3. Spatial and taxonomic connectivity

We investigated spatial and taxonomic patterns in costs of aquatic IAS with a network analysis (see Supplementary Material 1). Here, we created a bipartite network composed of two types of nodes: countries and IAS. When a species had a reported economic impact in a country, a link was drawn between the two nodes. The weight of the link was equal to the cumulative cost, since 1960. We defined the size of nodes on the network as proportional to their total costs with a log spline, such that country or species nodes with higher costs are easier to distinguish from those with lower economic impacts.

2.4. Prediction of annual costs for aquatic IAS

To examine the most appropriate temporal relationship for the accumulation of costs over time, we used the *modelCosts* function of the 'invacost' package (Leroy et al., 2020). We fitted multiple models to the data and identified the best model(s) by quantitative and qualitative criteria (see Supplementary Material 1). As we were dealing with econometric data, we selected models that were robust to issues of heteroskedasticity, temporal autocorrelation and outliers. We examined the long-term trend of annual costs worldwide between 1960 and 2020, i.e., we predicted costs as a function of years. First, owing to time lags in cost reporting, we corrected the data by removing the most recent, thus incomplete years; not making this correction would result in an inherent underestimation of costs (Supplementary Material 1). Second, we employed and compared a range of statistical techniques on the resulting data: ordinary least squares regression (linear and quadratic), robust regression (linear and quadratic), multivariate adaptive regression splines, generalised additive models (GAMs) and quantile regression [0.1 (lower boundary of cost), 0.5 (median cost value), 0.9 (upper boundary of cost)].

2.5. Trend in cumulated costs for aquatic IAS

In addition to modelling annual costs, we mathematically described temporal changes in cumulated costs of aquatic IAS. We chose to rely on a variation of the functional form proposed by Yokomizo et al. (2009) for density-impact curves, where we considered the cumulative cost C in terms of population density u. By assuming logistic growth in the population, C can then be expressed as a function of time and therefore serves as a model for the cumulative temporal cost of impacts (Supplementary Material 1). We used a non-linear regression curve-fitting tool to estimate the best fit parameters, such as cost saturation $C_{\max}$, carrying capacity K and intrinsic growth rate α. We quantified the fit by computing the squared correlation coefficient (r^2) and root mean square error (RMSE).

2.6. Reporting of invasion costs from aquatic IAS compared to terrestrial IAS

We obtained known numbers of established alien species ($n = 13{,}867$) in aquatic and terrestrial habitats globally, using databases such as the inventory of IAS in Europe (DAISIE; see Supplementary Material 1 for full list of sources). Categorising entries originating from either aquatic or terrestrial species, we then counted for the two habitats in InvaCost: the numbers of species having costs (excluding unspecific entries), the number of documents reporting these costs, total costs, and costs only reporting management actions (not reporting damage). Then, we compared these numbers to the proportions of known established IAS between habitats. Finally, we predicted the expected costs of management actions for aquatic IAS, under the hypothesis of an unbiased expenditure between aquatic and terrestrial habitats (based on the known proportion of global aliens that are aquatic).

3. Results

3.1. Global costs and taxonomic groupings

Global costs of aquatic IAS summed to US$345 billion, based on 5682 records from the expanded InvaCost database. These were all published since 1971. Semi-aquatic species cost US$185 billion ($n = 2971$ records) and fully aquatic species US$149 billion ($n = 2518$ records), with diverse costs (that spanned semi-aquatic and fully aquatic species) comprising the remaining US$11 billion ($n = 193$ records). Only 1% of the cost was from fully marine species (US$3.6 billion; $n = 234$ records).

Costs were unevenly distributed across taxonomic groups, with the majority (62%, US$214 billion) attributed to invertebrates, 28% (US$97 billion) to vertebrates and 6% (US$20 billion) to plants. All other taxonomic groups accounted collectively for 4% (US$14 billion) of the total costs (Fig. 1). Highly reliable (i.e. peer-reviewed or traceable) sources contributed 79% (US$274 billion) of the documented total costs of aquatic IAS (Fig. 1a). The majority of the total costs for animals (invertebrates: 76%; vertebrates: 88%) and plants (65%) were based on highly reliable sources.

Most (65%, US$224 billion) of the costs were derived from empirical observations, rather than predictions (Fig. 1b). The majority of costs for aquatic invertebrates were derived from empirical observations (92%). However, just 17% of the costs for aquatic vertebrates and 42% of plant costs, were based on empirical observations.

The 10 aquatic genera with the highest documented costs accounted for US$304 billion (88%) of total costs (Fig. 2). These taxa included four invertebrates, three vertebrates and three plants. Mosquitoes belonging

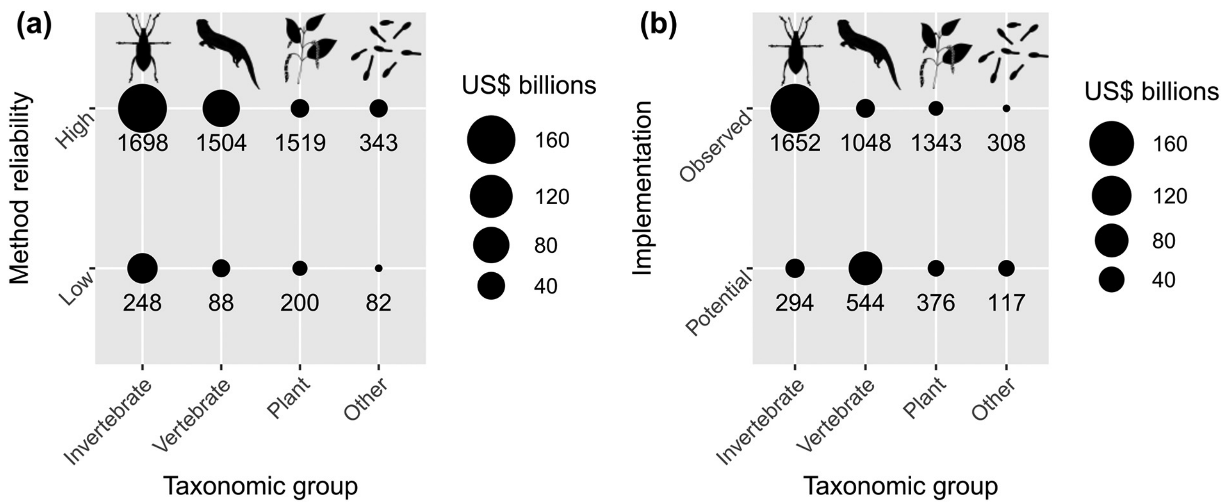


Fig. 1. Balloon plots illustrating global monetary costs of aquatic invasive alien species across major taxonomic groupings, with respect to (a) method reliability and (b) implementation type. Figures below each balloon correspond to the numbers of entries from the expanded database.

to three species of the *Aedes* genus caused 50% (US$153 billion) of the total top 10 cost. These were followed by ruffes *Gymnocephalus cernua* (18%, US$53 billion), mussels *Dreissena* spp. (two species, 16%, US$50 billion), coypus *Myocastor coypus* (6%, US$19 billion) and primroses *Ludwigia* spp. (three species, 3%, US$8 billion). Contributions from the remaining genera were relatively small. For all genera, excepting *Lithobates*, damages outweighed reported management spending (Fig. 2).

3.2. Geographic regions

Reported economic costs of aquatic IAS were unevenly distributed across geographic regions (Fig. 3). North America, owing to costs primarily from the United States of America (USA), reported the highest costs (48%, US$166 billion), followed by costs that were not attributed to specific regions (26%, US$91 billion) and costs from Asia (13%, US $45 billion). The costs in Europe and South America accounted collectively for 12% (US$41 billion) of total reported costs, whilst Africa, Oceania-Pacific Islands and the Antarctic-Subantarctic, combined accounted for 0.6% (US$2.1 billion) (Fig. 3). Regarding cost types, 74% (US$256 billion) of global costs were driven by damages, whereas only 6% (US$21 billion) consisted of management-related expenditure (Fig. 3b). Mixed spending (i.e. combined records of damage and management-related spending) comprised 20% of global costs (US$68 billion). Further information on taxonomic and cost typology breakdowns per region is provided in Supplementary Material 1.

At the country level, the USA had the highest recorded cost for aquatic IAS, followed by Brazil, India and France (Fig. 4a); other

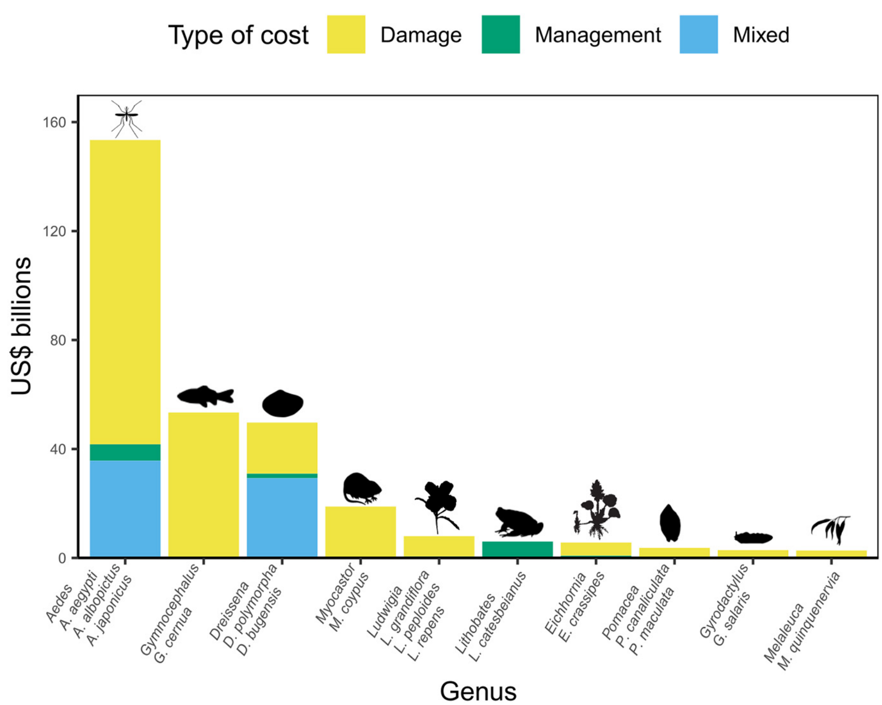


Fig. 2. Total monetary costs of the top 10 costly aquatic invasive alien genera, alongside species-specific information of underlying data pertaining to each genus. Unspecified species within each genus were also included. Fills illustrate cost type contributions per genus. Note that "Management" corresponds to expenditure related to activities such as prevention, control, eradication and research, whilst "Mixed" is a mixture of cost types.

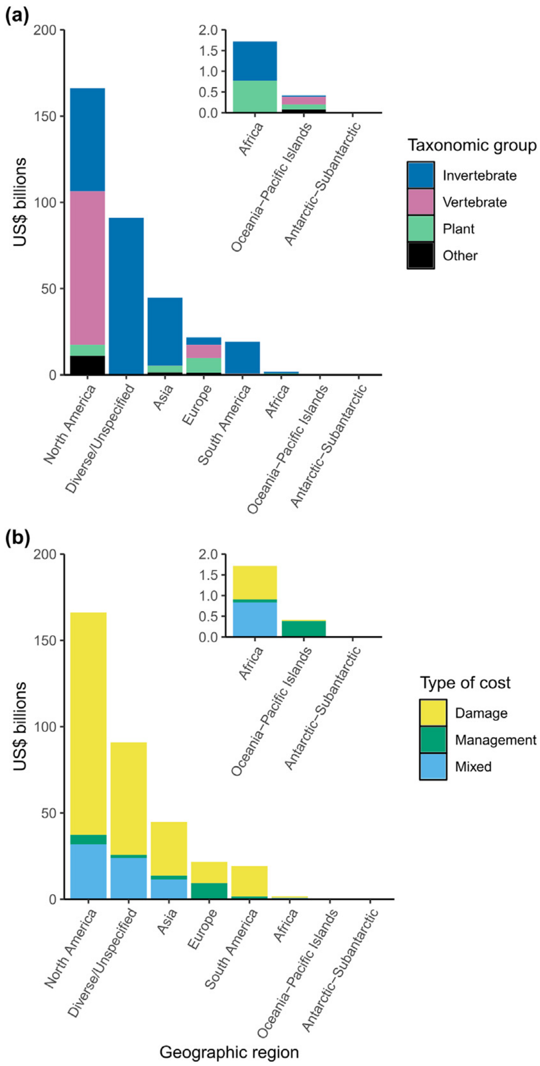


Fig. 3. Total aquatic invasion costs across geographic regions with respect to (a) taxonomic groupings and (b) cost types. Note in (b), that "Management" corresponds to expenditure related to activities such as prevention, control, eradication and research, whilst "Mixed" is a mixture of cost types.

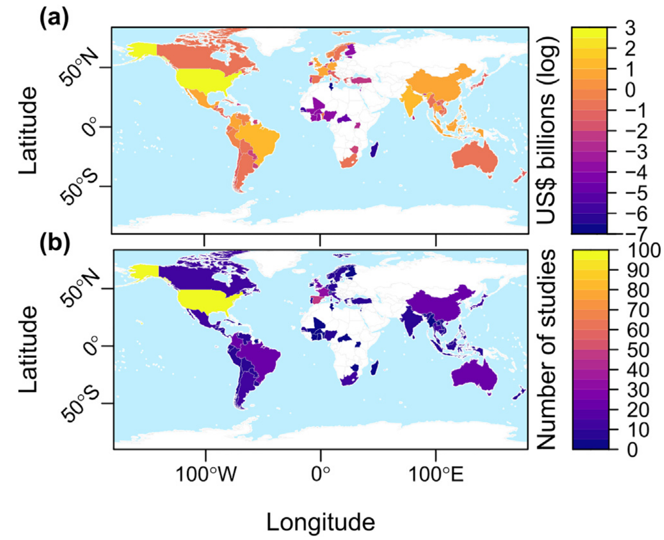


Fig. 4. Maps illustrating global distribution of (a) total economic costs and (b) number of studies (i.e. unique documents) for aquatic invasive alien species. Costs unattributable to individual countries were excluded (US$110 billion, out of a total US$345 billion; n = 37 study per country data points, out of a total 526). Costs with a known location in the territorial waters of each country are also included in the displayed data. Total costs are presented on a $\log_{10}$ scale.

countries were relatively similar in costs. The USA also had the largest number of studies. Other countries that reported costs generally had similar numbers of studies, with numbers from, for example, Spain, Brazil and Australia relatively high (Fig. 4b). We found no reported costs for aquatic IAS from the majority of African and Asian countries.

3.3. Spatial and taxonomic connectivity

We found eight clusters of IAS costs that were composed of at least five nodes (coloured clusters in Fig. 5), and eleven minor clusters that were composed of only two nodes (grey nodes in Fig. 5). We found two types of clusters. First, most clusters were composed of one or a few countries and a unique combination of IAS. This was the case, for example, for countries with the highest costs (mainly European and North American countries), which often had clusters of their own. Among these unique country clusters, the USA example was pervasive, with highest reported costs for *Dreissena* spp., *G. cernua* and *Melaleuca quinquenervia*, alongside many other IAS that were unique to that country. Second, there was one cluster that was driven by one genus, *Aedes*, which had pantropical economic impacts as well as impacts in temperate countries. For most of the Southern Hemisphere countries, *Aedes* was the only genus for which costs were reported. Despite these specific clusters of costly IAS per country, several IAS taxa had widespread economic impacts on multiple countries, such as *Lithobates catesbeianus*, *M. coypus*, *Neovison vison*, *Dreissena* spp., *Hydrocotyle ranunculoides* and *Eichhornia crassipes*. Interestingly, we found no strong biogeographical structure in the network. Australia, for example, shared costly IAS with geographically disparate regions such as European countries, South Africa, Argentina and Chile.

3.4. Prediction of annual costs for aquatic IAS

The linear models projected the highest costs of aquatic IAS in the year 2020 (since 1960; data from years 2013 to 2020 were removed owing to <75% completeness), however they had a relatively poor fit, with high RMSE (Fig. 6; Supplementary Material 1). The quadratic robust regression was removed owing to cost reductions in recent years, but it also had the highest RMSE (0.63). The GAM approach thus provided the best fit to the data (ΔRMSE ≥0.08; Fig. 6). This model indicated a rapid increase in costs by three orders of magnitude between 1970 and 2000, followed by a relatively gradual increase within a further magnitude since 2000 (Fig. 6c). Overall, the best-fitting GAM predicted a cost of aquatic IAS of US$23 billion globally in the year 2020.

3.5. Trend in cumulated costs for aquatic IAS

We found that the linear curve and high threshold curve models performed well, with the former providing a slightly better fit (Table S1; Supplementary Material 1). In the long term, the cumulative cost saturates to a fixed value C_{max} (i.e. maximum cumulative cost of impact), where the invasion is completely controlled and no further impact costs are incurred (Fig. 7). A clear saturation in costs (i.e. carrying capacity) was not reached for either the full or adjusted dataset (with outliers removed), indicating that costs will continue to increase in the near future. The reduction in rate of cost increases over recent years was likely an artefact of time lags in cost reporting versus occurrence.

3.6. Reporting of invasion costs of aquatic IAS compared to terrestrial IAS

Of 13,867 known established alien species worldwide (see Supplementary Material 1), 26% are associated with aquatic habitats, compared

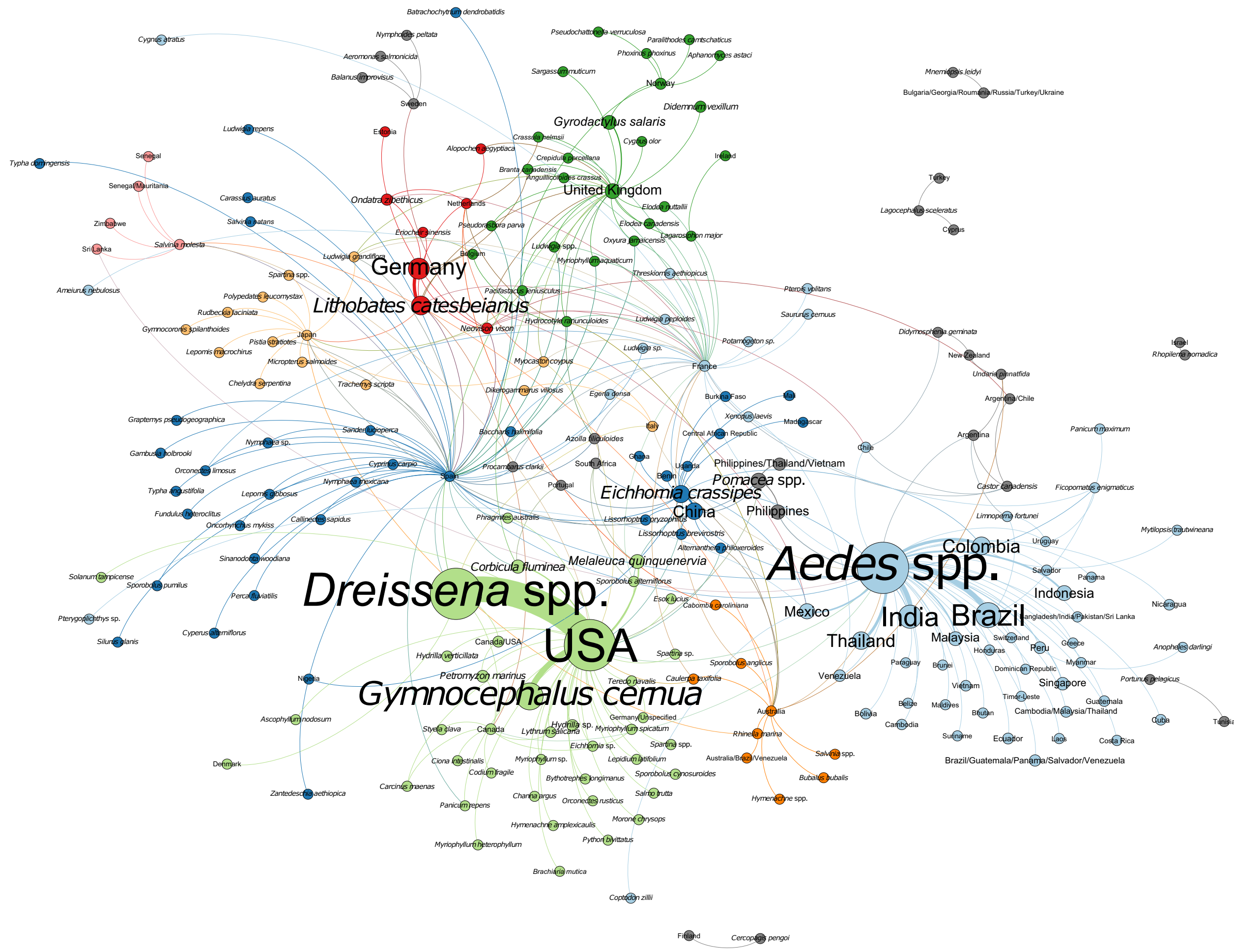


Fig. 5. Global network of aquatic invasive alien species costs per country. This bipartite network is composed of both species and country nodes. Links indicate the cumulative costs of species in countries. The thicker the link, the higher the cost. Likewise, node size is proportional to the total cumulative cost, with a log spline. 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.

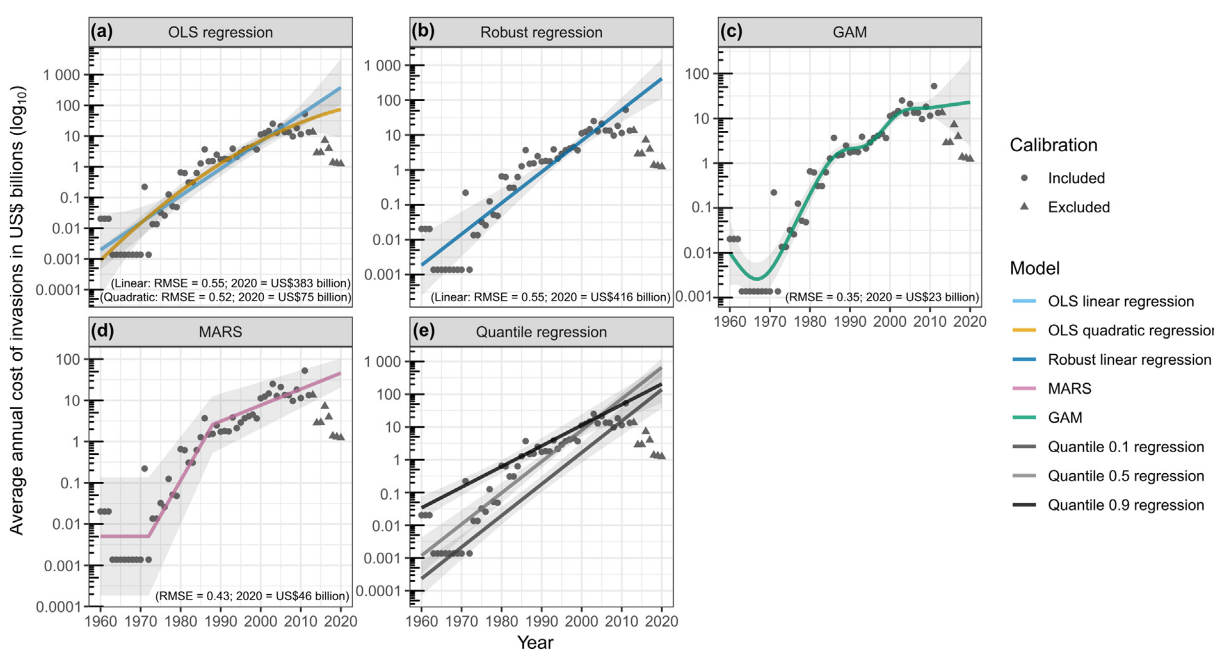


Fig. 6. Five modelling techniques considering global aquatic invasion costs over time [ordinary least squares (OLS) regressions (a), robust regression (b), generalised additive model (GAM) (c), multivariate adaptive regression splines (MARS) (d) and quantile regressions (e)]. Points are annual total costs. Note the scales differ among subplots. Shaded areas are 95% confidence intervals, and prediction intervals in the case of MARS. Root mean square error (RMSE) is shown for all appropriate models as well as 2020 cost predictions.

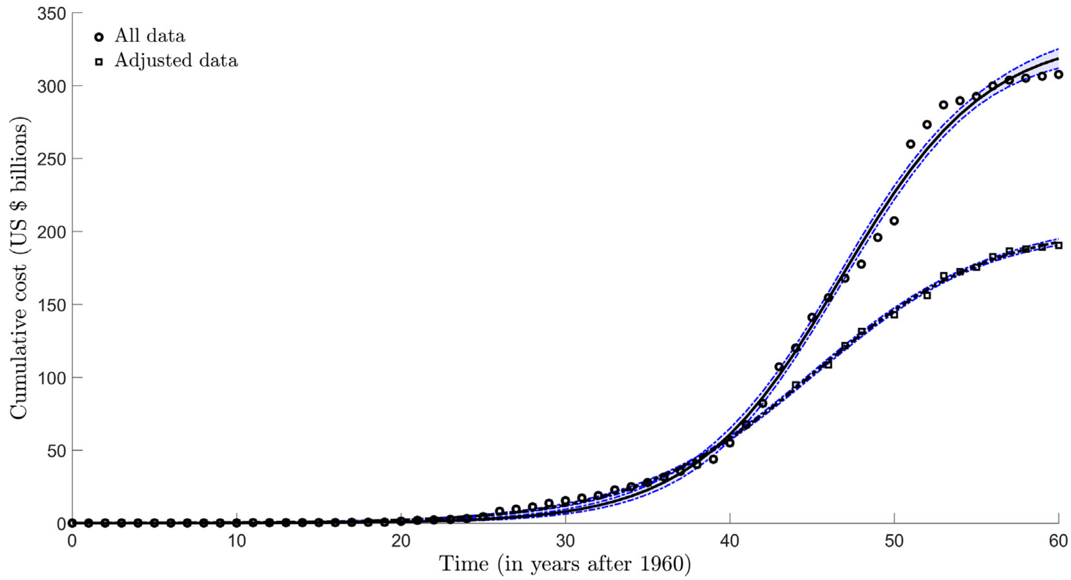


Fig. 7. Plot of the linear curve model given by Eq. (3) (Supplementary Material 1) against the cumulative cost data. Circular markers represent all the data. We computed best fit parameter values $C_{max} = 335.1$, $K = 26274$, $\alpha = 0.22$ and metric values $r^2 = 0.996$, RMSE $= 6.73$. Square markers represent the adjusted data set, which excludes four upper end extreme values (any cost value greater than $Q_3 + 1.5 \times \text{IQR} =$ US\$14.66 billion, where Q_3 is the upper quartile and the IQR is the interquartile range of the dataset), i.e. (2003, US\$25.06 billion), (2005, US\$21.07 billion), (2009, US\$18.34 billion) and (2011, US\$52.61 billion), corresponding to times $t = 43, 45, 49$ and 51, respectively. We found that $C_{max} = 205.6$, $K = 2882$, $\alpha = 0.18$, $r^2 = 0.999$ and RMSE $= 2.26$. The shaded areas represent 95% confidence regions indicating the range of predicted cumulative costs.

to 74% associated with terrestrial habitats (Fig. 8). Although in InvaCost the number of aquatic species and the number of documents reporting their costs constituted relatively similar percentages (20% and 28%, respectively), the value of their reported cost comprised just 5% of the global total. This increased to just 9% when considering only costs reported from management strategies. If management expenditure was unbiased between habitat types according to numbers of known established aliens, we estimated that a further US$39 billion should have been spent on aquatic species to date.

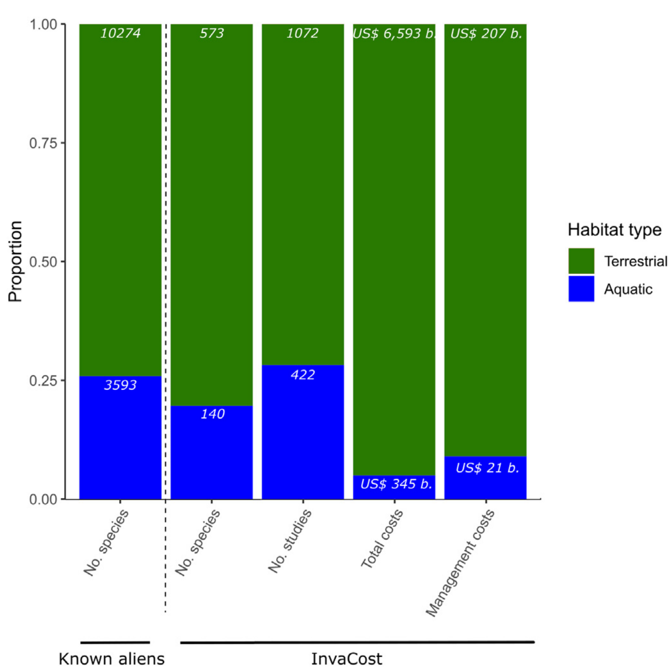


Fig. 8. Proportions of known established alien species, and with respect to InvaCost estimates: numbers of species, documents, total costs and management costs between terrestrial and aquatic habitats. Raw values are presented per habitat type; abbreviations: *b.* = billion.

4. Discussion

Our study reveals that aquatic IAS have likely cost the global economy at least US$345 billion. This estimate is probably highly conservative as it only includes costs that have been documented and captured in the InvaCost database. Moreover, the taxonomic, geographic, temporal and habitat trends among these costs suggest that cost reporting is very uneven, with many IAS and countries entirely lacking reported costs. Most costs were attributed to aquatic invertebrates (US$214 billion), with lower costs for vertebrates (US$97 billion) and plants (US$20 billion). Our estimate of the costs of aquatic IAS globally in the year 2020 – US $23 billion, much higher in magnitude than the cost, for example, of managing global marine protected areas (US$5–19 billion; Balmford et al., 2004) – calls for increased investments in management of IAS.

4.1. Cost distributions across taxa

Globally, mosquitoes are major contributors to the burden of diseases, with vector-borne pathogens and parasites causing over one billion infections and one million deaths annually (Kilpatrick and Randolph, 2012; Campbell-Lendrum et al., 2015). The massive costs attributed to vector-borne diseases from invasive mosquitoes are thus not surprising, given the costs to healthcare systems worldwide. In Brazil, for example, the government invested approximately US$48 million per year from 2015 to 2017 for limiting population outbreaks of *A. aegypti* (Bueno et al., 2017). In Columbia, total medical costs for the treatment of dengue-infected patients reached US$3 billion between 2010 and 2012 (Rodríguez et al., 2015), and the recent chikungunya outbreak cost about US$76 million to the healthcare system (Cardano et al., 2015). Mosquitoes can also lead to economic losses associated with recreation and tourism, as they discourage people from carrying out certain activities or visiting certain sites (Claeys-Mekdade and Morales, 2002). In the present study, damages to sectors such as health comprised 73% of mosquito costs, with just 4% spent on management. Future range expansions of invasive mosquitoes are expected to increase their economic impact (Iwamura et al., 2020). Although mosquitoes vector diseases in their terrestrial-based adult life stage, where most costs are incurred, larval and pupal life stages are invariably spent in water where management is often targeted, with the characteristics and distribution of aquatic habitat patches determining mosquito distributions at various scales via key trait- and density-mediated processes (Pintar et al., 2018; Cuthbert et al., 2019).

The Eurasian ruffe (*G. cernua*) was second most costly and has caused declines of native fish by predation and competition, with considerable economic impacts through reductions in commercially- and recreationally-valuable fish species (Leigh, 1998). In turn, the zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*) are hyper-successful macrofouling freshwater bivalves, which are highly costly to infrastructure through impeding navigation structures, obstruction of water flow in pipes and occlusion of water filters (Sousa et al., 2014). The coypu (*M. coypus*) has caused substantial economic losses through agricultural impacts, as well as infrastructural damage (Panzacchi et al., 2007). The primroses (*Ludwigia* spp.) are known to reduce water quality that can affect economically important taxa such as fish, and can be extremely costly to control (Williams et al., 2010).

Costs attributed to invasive aquatic invertebrates such as the zebra and quagga mussels were deemed highly reliable and mostly based on empirical observations rather than extrapolations. In contrast, a large share of vertebrate costs was potential costs, as in the case of the three most costly vertebrate taxa, Eurasian ruffe *G. cernua*, coypu *M. coypus* and American bullfrog *L. catesbeianus*. Therefore, realised vertebrate costs require improved validation and reporting to the extent possible from their actual invaded habitat. Similarly, reported costs of plants, including the highly damaging *Ludwigia* species and broad-leaved paper bark *M. quinquenervia*, were primarily potential costs, not incurred at the time of estimation. Although ecological impacts of aquatic plants have been well-studied by invasion scientists (Pyšek et al., 2008; Gallardo et al., 2016), there is scope for more thorough recording of realised economic impacts.

4.2. Cost distributions across geographic regions and types

The costs of aquatic IAS were also unevenly distributed across geographic regions, with particularly high reported costs in North America (US$166 billion) and Asia (US$45 billion). In turn, a substantial proportion (26%) of the costs were unattributed to specific geographic regions. Moreover, most costs were driven by damages (74%), whilst management (principally control-related) costs were just 6%. It may be expected that management costs are lower than damage or loss costs: if the inverse were true, management would not be economically justifiable. However, the InvaCost search strategy may have exacerbated this difference. Reports of management costs may have been disproportionately missed by the systematic literature searches because management studies often do not mention costs, economics or other InvaCost search terms (Diagne et al., 2020b) in their title, abstract or keywords (e.g. Sandodden and Johnsen, 2010).

At the country scale, the USA exhibited both the highest magnitude of costs and the greatest number of studies compared to all other countries. The high degree of cost reporting in the USA is unsurprising given that early estimates of costs focused on this country (Pimentel et al., 2000, Pimentel et al., 2005), which sparked research efforts to better understand costs and provide a more refined spatial and temporal description for those costs. The USA also scores highly on several socio-economic variables that have been found to correlate positively with reported costs of IAS (Haubrock et al., 2021; Kourantidou et al., 2021), such as GDP (1st in world), human population (3rd), international tourism arrivals (3rd) and research expenditure (9th).

In contrast, the InvaCost database contains no aquatic IAS costs at all for many countries, particularly in Asia and Africa. However, even in countries such as South Africa, where research on biological invasion is leading (van Wilgen et al., 2020), large gaps in our knowledge of economic costs are evident. For example, South Africa is a global invasion hotspot for freshwater fish and has been invaded by numerous invertebrate taxa in freshwater, estuarine and marine environments, with well-known impacts on human wellbeing (Appleton et al., 2009; Ellender and Weyl, 2014; Weyl et al., 2020; Robinson et al., 2020). However, we captured no monetary costs for such taxa. Similarly, in other African countries, IAS without formally documented or quantified costs are known to affect human societies via impacts to biological communities, local fisheries and water storage infrastructures (e.g. Nile perch in East Africa; Harris et al., 1995; Kwena et al., 2012; Aloo et al., 2017, and crayfish in Lake Naivasha, Kenya; Kafue River, Zambia; Madzivanzira et al., 2020). Limited cost reporting in Africa and Asia is likely reflective of a low priority given to IAS research, or capabilities (Pyšek et al., 2008), despite high levels of introduction via, for example, aquaculture (Lin et al., 2015). However, there may have been some bias introduced by the original InvaCost search string, as no currencies from these continents were explicitly included as search terms (even if searches were performed in 15 non-English languages, Angulo et al., 2021).

Nonetheless, limited cost reporting in Africa and Asia is alarming given that invasions in these countries may disproportionately impact livelihoods, given high levels of poverty, limited resources for research and management, and an overall limited preparedness to meet challenges brought by IAS (Early et al., 2016). Limited cost reporting also hinders management actions, as the extent of IAS cost is not fully realised by managers.

Network analyses additionally revealed a distinct lack of global structuring of costs, whereby clustering appeared disparate across taxa and countries, insinuating a largely random distribution of costs and vast gaps in cost reporting of well-known aquatic IAS. That is, for many countries, there was generally only one cluster, indicating unique combinations of economic impacts associated with particular species, despite some of these species being highly widespread. One example of an exception to this is *Aedes* spp., which had a consistent and pantropical impact, resulting in a distinct cost cluster. Nonetheless, other context-dependencies, such as differences in climate and pathways, likely also influence IAS compositions.

4.3. Temporal trends in costs

The majority of fitted models indicated exponentially increasing annual costs of aquatic IAS since 1960 over several magnitudes, to a best-fit extrapolated annual global cost of US$23 billion in 2020. Model differences in recent years likely reflect differential sensitivities to time lags in cost reporting. Model predictions of cost increases over time align with increasing rates of biological invasions worldwide (Seebens et al., 2017), as globalisation and intensification of trade and transport networks result in high propagule and colonisation pressures from novel source pools (Seebens et al., 2018). Given that invasion rates will increase further in future (Seebens et al., 2020), we can expect further increases in economic costs – although investments in management, especially prevention and rapid eradication, could limit realised costs (Leung et al., 2002). Moreover, these results align with the findings of Bradshaw et al. (2016) who have suggested, specifically for invasive insects such as mosquitoes, that costs are generally largely underestimated and are expected to increase through time. Our mathematically-modelled density-impact curves also suggest that costs of IAS to the global economy will continue to increase, as they were far from an asymptotic plateau, even where extreme values were removed and time lags not incorporated. Moreover, this population-level approach does not account for unreported costs or those arising from future IAS spread, and this likely results in further underestimation.

4.4. Reporting of invasion costs of aquatic IAS compared to terrestrial IAS

Despite over one quarter of known alien species using aquatic environments, only 5% of the total cost in the InvaCost database was attributed to aquatic species. Further, the majority (54%) of these costs were from semi-aquatic rather than fully aquatic species. On one hand, this finding potentially reflects a bias in cost reporting towards terrestrial systems, in line with ecological research in general (Menge et al., 2009; Richardson and Poloczanska, 2008). With respect to management costs of IAS, if investments of equivalent magnitude to terrestrial were made for aquatic systems, one would anticipate a further US $39 billion to have been spent to date. Note that this extrapolation does not consider potentially lower costs in aquatic ecosystems (i.e. less infrastructure to damage) or differences in management efficiencies between terrestrial and aquatic environments. On the other hand, the disparity between aquatic and terrestrial costs may thus reflect genuinely lower costs of aquatic – particularly marine – IAS relative to terrestrial IAS. There are limited human assets and infrastructures in aquatic systems, limiting the scope for easily-quantifiable damages and resulting in minimal investments in prevention and management. For example, terrestrial agricultural practices are heavily impacted by crop pests (Paini et al., 2016; Ahmed and Petrovskii, 2019), whereas agricultural activities in aquatic systems (e.g. rice fields) are relatively scarce. However, aquatic systems do offer highly valuable ecosystem services that could be affected by IAS, such as aquaculture, and often through cascading effects that are difficult to predict (Walsh et al., 2016). Thus, we encourage investment in management of IAS in aquatic systems to limit future costs that stem from damage and loss (Leung et al., 2002).

5. Conclusions

Urgent and coordinated management actions are required globally to reduce economic and ecological impacts from aquatic IAS. Whilst costs of aquatic IAS are escalating, knowledge of impacts across major taxonomic groupings, geographic regions and habitat types remains diffuse. These knowledge gaps suggest costs of aquatic IAS are underestimated, particularly relative to their ecological impacts and to the more intensively-studied terrestrial species. Equally, geographical biases in reported costs highlight the need for increased and improved cost reporting, given that allocation of finite resources to manage IAS is underpinned by adequate understandings of costs. We urge our results to be applied as an incentive for managers, stakeholders and scientists to increase and improve cost reporting and invest in a more adequate protection of aquatic ecosystems.

CRediT authorship contribution statement

Ross N. Cuthbert: Conceptualization, Data curation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Zarah Pattison:** Conceptualization, Data curation, Writing - review & editing. **Nigel G. Taylor:** Conceptualization, Data curation, Writing - review & editing. **Laura Verbrugge:** Conceptualization, Data curation, Writing - review & editing. **Christophe Diagne:** Conceptualization, Data curation, Writing - review & editing. **Danish A. Ahmed:** Conceptualization, Formal analysis, Visualization, Writing - review & editing. **Boris Leroy:** Conceptualization, Data curation, Formal analysis, Visualization, Writing - review & editing. **Elena Angulo:** Conceptualization, Data curation, Writing – review & editing. **Elizabeta Briski:** Conceptualization, Writing - review & editing. **César Capinha:** Conceptualization, Writing - review & editing. **Jane A. Catford:** Conceptualization, Writing - review & editing. **Tatenda Dalu:** Conceptualization, Writing - review & editing. **Franz Essl:** Conceptualization, Writing - review & editing. **Rodolphe E. Gozlan:** Conceptualization, Writing - review & editing. **Phillip J. Haubrock:** Conceptualization, Writing - review & editing. **Melina Kourantidou:** Conceptualization, Writing - review & editing. **Andrew M. Kramer:** Conceptualization, Formal analysis, Visualization, Writing - review & editing. **David Renault:** Conceptualization, Data curation, Writing - review & editing. **Ryan J. Wasserman:** Conceptualization, Writing - review & editing. **Franck Courchamp:** Conceptualization, Data curation, Writing - review & editing.

Declaration of competing interest

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

Acknowledgements

The authors acknowledge the French National Research Agency (ANR-14-CE02-0021) and the BNP-Paribas Foundation Climate Initiative for funding the InvaCost project that allowed the construction of the InvaCost database. The present work was conducted following a workshop funded by the AXA Research Fund Chair of Invasion Biology and is part of the AlienScenarios project funded by BiodivERsA and Belmont-Forum call 2018 on biodiversity scenarios. RNC is funded through a Humboldt Research Fellowship from the Alexander von Humboldt Foundation. DAA is funded by the Kuwait Foundation for the Advancement of Sciences (KFAS) (PR1914SM-01) and the Gulf University for Science and Technology (GUST) internal seed fund (187092). CD was funded by the BiodivERsA-Belmont Forum Project AlienScenarios (BMBF/PT DLR 01LC1807C). EA was funded by the AXA Research Fund Chair of Invasion Biology of University Paris Saclay. CC was supported by Portuguese National Funds through Fundação para a Ciência e a Tecnologia (CEECIND/02037/2017; UIDB/00295/2020 and UIDP/00295/2020). TD acknowledges funding from National Research Foundation (NRF_ZA) (Grant Number: 117700). FE appreciates funding by the Austrian Science Foundation (FWF project no I 4011-B32). AMK was supported by the NSF Macrosystems Biology program under grant 1834548. DR thanks InEE-CNRS who supports the French national network Biological Invasions (Groupement de Recherche InvaBio, 2014–2022).

Appendix A. Supplementary material

Underlying data are publicly available in an online repository (https://doi.org/10.6084/m9.figshare.12668570). The dataset used for analysis is provided in the Supplementary Material. Supplementary data to this article can be found online at doi:https://doi.org/10.1016/j.scitotenv.2021.145238.

References

Ahmed, D.A., Petrovskii, S.V., 2019. Analysing the impact of trap shape and movement behaviour of ground-dwelling arthropods on trap efficiency. Methods Ecol. Evol. 10, 1246–1264.

Aldridge, D.C., Oreska, M.P.J., 2011. Estimating the financial costs of freshwater invasive species in Great Britain: a standardized approach to invasive species costing. Biol. Invasions 13, 305–319.

Aloo, P.A., Njiru, J., Balirwa, J.S., Nyamweya, C.S., 2017. Impacts of Nile perch, *Lates niloticus*, introduction on the ecology, economy and conservation of Lake Victoria, East Africa. Lakes Reserv. Res. Manag. 22, 320–333.

Angulo, E., Diagne, C., Ballesteros-Mejia, L., Akulov, E.N., Dia, C.A.K.M., Adamjy, T., et al., 2021. Non-English languages enrich scientific data: the example of the costs of biological invasions. Sci. Total Environ. (in press).

Appleton, C.C., Forbes, A.T., Demetriades, N.T., 2009. The occurrence, bionomics and potential impacts of the invasive freshwater snail *Tarebia granifera* (Lamarck, 1822) in South Africa. Zoölogische Medelingen 83, 525–536.

Balmford, A., Gravestock, P., Hockley, N., McClean, C.J., Roberts, C.M., 2004. The worldwide costs of marine protected areas. Proc. Natl. Acad. Sci. 101, 9694–9697.

Blackburn, T.M., Bellard, C., Ricciardi, A., 2019. Alien versus native species as drivers of recent extinctions. Front. Ecol. Environ. 17, 203–207.

Bradshaw, C.J., Leroy, B., Bellard, C., Roiz, D., Albert, C., et al., 2016. Massive yet grossly underestimated global costs of invasive insects. Nat. Commun. 7, 12986.

Bueno, C.C., Almeida, P.R., Retamero, A., Clark, L.G., 2017. *Aedes aegypti*: economic impact of prevention versus palliation of diseases caused by the mosquito. Value Health 20, A929.

Campbell-Lendrum, D., Manga, L., Bagayoko, M., Sommerfeld, J., 2015. Climate change and vector-borne diseases: what are the implications for public health research and policy? Philos. Trans. R. Soc. B 370, 20130552.

Capinha, C., Essl, F., Seebens, H., Moser, D., Pereira, H.M., 2015. The dispersal of alien species redefines biogeography in the Anthropocene. Science 348, 1248–1251.

Cardano, J.A., Villamil-Gómez, W.E., Jimenez-Canizales, C.E., Castañeda-Hernández, D.M., Rodríguez-Morales, A.J., 2015. Estimating the burden of disease and the economic

cost attributable to chikungunya, Colombia, 2014. Tropical Medicine and Hygiene 109, 793–802.
Claeys-Mekdade, C., Morales, A., 2002. Moustiques et démoustication: une enquête sociologique auprès des Arlésiens et des Camarguais. Rapport final de l'Etude d'impact d'un éventuel traitement au B.t.i. sur le territoire du Parc naturel régional de Camargue. DESMID-IMEP.
Crystal-Ornelas, R., Lockwood, J.L., 2020. The 'known unknowns' of invasive species impact measurement. Biol. Invasions 22, 1513–1525.
Cuthbert, R.N., Callaghan, A., Dick, J.T.A., 2019. A novel metric reveals biotic resistance potential and informs predictions of invasion success. Sci. Rep. 9, 15314.
Cuthbert, R.N., Kotronaki, S.G., Dick, J.T.A., Briski, E., 2020. Salinity tolerance and geographic origin predict global alien amphipod invasions. Biol. Lett. 16, 20200354.
Cuthbert, R.N., Bartlett, A.C., Turbelin, A., Haubrock, P.J., Diagne, C., et al., 2021. Economic costs of biological invasions in the United Kingdom. NeoBiota (in press).
Darwall, W., Bremerich, V., De Wever, A., Dell, A.I., Freyhof, J., et al., 2018. The *Alliance for Freshwater Life*: a global call to unite efforts for freshwater biodiversity science and conservation. Aquat. Conserv. Mar. Freshwat. Ecosyst. 28, 1015–1022.
Diagne, C., Catford, J.A., Essl, F., Nuñez, M.A., Courchamp, F., 2020a. What are the economic costs of biological invasions? A complex topic requiring international and interdisciplinary expertise. NeoBiota 63, 25–37.
Diagne, C., Leroy, B., Gozlan, R.E., Vaissiere, A.C., Assailly, C., et al., 2020b. InvaCost: a public database of the economic costs of biological invasions worldwide. Scientific Data 7, 277.
Dick, J.T.A., Laverty, C., Lennon, J.J., Barrios-O'Neill, D., Mensink, P.J., et al., 2017. Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. J. Appl. Ecol. 54, 1259–1267.
Early, R., Bradley, B., Dukes, J., Lawler, J.J., Olden, J.D., et al., 2016. Global threats from invasive alien species in the twenty-first century and national response capacities. Nat. Commun. 7, 12485.
Ellender, B.R., Weyl, O.L.F., 2014. A review of current knowledge, risk and ecological impacts associated with non-native freshwater fish introductions in South Africa. Aquat. Invasions 9, 117–132.
Fournier, A., Penone, C., Pennino, M.G., Courchamp, F., 2019. Predicting future invaders and future invasions. Proc. Natl. Acad. Sci. 116, 7905–7910.
Gallardo, B., Clavero, M., Sánchez, M.I., Vilà, M., 2016. Global ecological impacts of invasive species in aquatic ecosystems. Glob. Chang. Biol. 22, 151–163.
Hanley, N., Roberts, M., 2019. The economic benefits of invasive species management. People and Nature 1, 124–137.
Harris, C.K., Wiley, D.S., Wilson, D.C., 1995. Socioeconomic impacts of introduced species in Lake Victoria fisheries. In: Pitcher, T.J., Hart, P.J.B. (Eds.), Impact of Species Changes in African Lakes. Chapman and Hall, London.
Haubrock, P.J., Turbelin, A.J., Cuthbert, R.N., Novoa, A., Angulo, E., et al., 2021. Economic costs of invasive alien species across Europe. NeoBiota (in press).
Iwamura, T., Guzman-Holst, A., Murray, K.A., 2020. Accelerating invasion potential of disease vector *Aedes aegypti* under climate change. Nat. Commun. 11, 2130.
Jackson, M.C., Wasserman, R.J., Grey, J., Ricciardi, A., Dick, J.T.A., et al., 2017. Novel and disrupted trophic links following invasion in freshwater ecosystems. Adv. Ecol. Res. 57, 55–97.
Katsanevakis, S., Wallentinus, I., Zenetos, A., Leppäkoski, E., Çinar, M.E., et al., 2014. Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. Aquat. Invasions 9, 391–423.
Kettunen, M., Genovesi, P., Gollasch, S., Pagad, S., Starfinger, U., et al., 2009. Technical Support to EU Strategy on Invasive Alien Species (IAS). Institute for European Environmental Policy (IEEP), Brussels, p. 44.
Kilpatrick, A.M., Randolph, S.E., 2012. Drivers, dynamics, and control of emerging vector-borne zoonotic diseases. Lancet 380, 1946–1955.
van Kleunen, M., Xu, X., Yang, Q., Maurel, N., Zhang, Z., et al., 2020. Economic use of plants is key to their naturalization success. Nat. Commun. 11, 3201.
Kourantidou, M., Cuthbert, R.N., Haubrock, P.J., Novoa, A., Taylor, N.G., et al., 2021. Economic costs of invasive alien species in the Mediterranean basin. NeoBiota (in press).
Kumschick, S., Gaertner, M., Vilà, M., Essl, F., Jeschke, J.M., et al., 2015. Ecological impacts of alien species: quantification, scope, caveats, and recommendations. BioScience 65, 55–63.
Kwena, Z.A., Bukusi, E., Omondi, E., Ng'ayo, M., Holmes, K.K., 2012. Transactional sex in the fishing communities along Lake Victoria, Kenya: a catalyst for the spread of HIV. Afr. J. AIDS Res. 11, 9–15.
Leigh, P., 1998. Benefits and costs of the ruffe control program for the Great Lakes fishery. J. Great Lakes Res. 24, 351–360.
Leroy, B., Kramer, A., Vaissière, A.-C., Courchamp, F., Diagne, C., 2020. Analysing global economic costs of invasive alien species with the invacost R package. biorXiv https://doi.org/10.1101/2020.12.10.419432.
Leung, B., Lodge, D.M., Finnoff, D., Shogren, J.F., Lewis, M.A., et al., 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proc. R. Soc. B Biol. Sci. 269, 2407–2413.
Lin, Y.P., Gao, Z.X., Zhan, A.B., 2015. Introduction and use of nonnative species for aquaculture in China: status, risks and management solutions. Rev. Aquac. 7, 28–58.
Lovell, S.J., Stone, S.F., Fernandez, L., 2006. The economic impacts of aquatic invasive species: a review of the literature. Agricultural and Resource Economics Review 35, 195–208.
Madzivanzira, T.C., South, J., Wood, L.E., Nunes, A.L., Weyl, O.L.F., 2020. A review of freshwater crayfish introductions in Africa. Reviews in Fisheries Science and Aquaculture. (in press).
McGeoch, M.A., Jetz, W., 2019. Measure and reduce the harm caused by biological invasions. One Earth 1, 171–174.
McGeoch, M.A., Genovesi, P., Bellingham, P.J., Costello, M.J., McGrannachan, C., et al., 2015. Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion. Biol. Invasions 18, 299–314.
Menge, B.A., Chan, F., Dudas, S., Eerkes-Medrano, D., Grorud-Colvert, K., et al., 2009. Terrestrial ecologists ignore aquatic literature: asymmetry in citation breadth in ecological publications and implications for generality and progress in ecology. J. Exp. Mar. Biol. Ecol. 377, 93–100.
Mollot, G., Pantel, J.H., Romanuk, T.N., 2017. Chapter two - the effects of invasive species on the decline in species richness: a global meta-analysis. Adv. Ecol. Res. 56, 61–83.
Paini, D.R., Sheppard, A.W., Cook, D.C., De Barro, P.J., Worner, S.P., et al., 2016. Global threat to agriculture from invasive species. Proc. Natl. Acad. Sci. 113, 7575–7579.
Panzacchi, M., Cocchi, R., Genovesi, P., Bertolini, S., 2007. Population control of coypu *Myocastor coypus* in Italy compared to eradication in UK: a cost-benefit analysis. Wildl. Biol. 13, 159–171.
Pejchar, L., Mooney, H.A., 2009. Invasive species, ecosystem services and human well-being. Trends Ecol. Evol. 24, 497–504.
Pimentel, D., Lach, L., Zuniga, R., Morrison, D., 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50, 53–66.
Pimentel, D., Zuniga, R., Morrison, D., 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol. Econ. 52, 273–288.
Pintar, M.R., Bohenek, J.R., Eveland, L.L., Restarits Jr., W.J., 2018. Colonization across gradients of risk and reward: nutrients and predators generate species-specific responses among aquatic insects. Funct. Ecol. 32, 1589–1598.
Poulin, M., Natacha, F., Line, R., 2011. Restoration of pool margin communities in cutover peatlands. Aquat. Bot. 94, 107–111.
Pyšek, P., Richardson, D.M., Pergl, J., Jarošík, V., Weber, E., 2008. Geographical and taxonomic biases in invasion ecology. Trends Ecol. Evol. 23, 237–244.
Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., et al., 2020. Scientists' warning on invasive alien species. Biol. Rev. 95, 1511–1534.
R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
Ricciardi, A., MacIsaac, H.J., 2011. Impacts of biological invasions on freshwater ecosystems. In: Richardson, D.M. (Ed.), Fifty Years of Invasion Ecology: The Legacy of Charles Elton, 1st Wiley-Blackwell, Chichester.
Richardson, A.J., Poloczanska, E.S., 2008. Under-resourced, under threat. Science 320, 1294–1295.
Robinson, T.B., Peters, K., Brooker, B., 2020. Coastal invasions: The South African context. In: van Wilgen, B.W., Measey, J., Richardson, D.M., Wilson, J.R., Zengeya, T.A. (Eds.), Biological Invasions in South Africa. Springer, Berlin.
Rodríguez, P.C., Galera-Galvez, K., Yescas, J.G.L., Rueda-Gallardo, J.A., 2015. Costs of dengue to the health system and individuals in Colombia from 2010 to 2012. Am. J. Trop. Med. Hyg. 9, 709–714.
Sandodden, R., Johnsen, S.I., 2010. Eradication of introduced signal crayfish *Pasifastacus leniusculus* using the pharmaceutical BETAMAX VET.®. Aquat. Invasions 5, 75–81.
Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., et al., 2017. No saturation in the accumulation of alien species worldwide. Nat. Commun. 8, 14435.
Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., et al., 2018. Global rise in emerging alien species results from increased accessibility of new source pools. Proc. Natl. Acad. Sci. 115, E2264–E2273.
Seebens, H., Bacher, S., Blackburn, T.M., Capinha, C., Dawson, W., et al., 2020. Projecting the continental accumulation of alien species through to 2050. Glob. Chang. Biol. (in press).
Shabani, F., Ahmadi, M., Kumar, L., Sohljouy-fard, S., Tehrany, M.S., et al., 2020. Invasive weed species' threats to global biodiversity: future scenarios of changes in the number of invasive species in a changing climate. Ecol. Indic. 116, 106436.
Sousa, R., Novais, A., Costa, R., Strayer, D.L., 2014. Invasive bivalves in fresh waters: impacts from individuals to ecosystems and possible control strategies. Hydrobiologia 735, 233–251.
Spatz, D.R., Zilliacus, K.M., Holmes, N.D., Butchart, S.H.M., Genovesi, P., et al., 2017. Globally threatened vertebrates on islands with invasive species. Sci. Adv. 3, e1603080.
Strayer, D.L., Findlay, S.E., 2010. Ecology of freshwater shore zones. Aquat. Sci. 72, 127–163.
Turbelin, A.J., Malamud, B.D., Francis, R.A., 2017. Mapping the global state of invasive alien species: patterns of invasion and policy responses. Glob. Ecol. Biogeogr. 26, 78–92.
UNEP, 2011. The Strategic Plan for Biodiversity 2011–2020 and the Aichi Biodiversity Targets. COP CBD Tenth Meeting UNEP/CBD/COP/DEC/X/2. Nagoya.
Vanbergen, A.J., the Insect Pollinators Initiative, 2013. Threats to an ecosystem service: pressures on pollinators. Front. Ecol. Environ. 11, 251–259.
Vitousek, P.M., D'antonio, C.M., Loope, L.L., Rejmanek, M., Westbrooks, R., 1997. Introduced species: a significant component of human-caused global change. N. Z. J. Ecol. 21, 1–16.
Walsh, J.R., Carpenter, S.R., Zanden, M.J.V., 2016. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. Proc. Natl. Acad. Sci. 113, 4081–4085.
Weyl, O.L.F., Ellender, B.R., Wasserman, R.J., Truter, M., Dalu, T., et al., 2020. Alien Freshwater Fauna in South Africa. In: van Wilgen, B.W., Measey, J., Richardson, D.M., Wilson, J.R., Zengeya, T.A. (Eds.), Biological Invasions in South Africa. Springer, Berlin.
van Wilgen, B., Measey, J., Richardon, D.M., Wilson, J.R., Zengeya, T.A., 2020. Biological Invasions in South Africa. Springer, Berlin.
Williams, F., Eschen, R., Harris, A., Djeddour, D., Pratt, C., et al., 2010. The Economic Cost of Invasive Non-native Species to Great Britain. CABI, Egham, Egham.
Woodward, G., Perkins, D.M., Brown, L.E., 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. Philosophical Transactions of the Royal Society B: Biological Sciences 365, 2093–2106.
Yokomizo, H., Possingham, H., Thomas, M., Buckley, Y., 2009. Managing the impact of invasive species: the value of knowing the density-impact curve. Ecol. Appl. 19, 376–386.