

# Economic costs of invasive species in Germany

Phillip J. Haubrock<sup>1,2\*</sup>, Ross N. Cuthbert<sup>3,4\*</sup>, Andrea Sundermann<sup>1,5</sup>,  
Christophe Diagne<sup>6</sup>, Marina Golivets<sup>7</sup>, Franck Courchamp<sup>6</sup>

**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, Zátíší 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](mailto:phillip.haubrock@senckenberg.de))

---

Academic editor: Franz Essl | Received 9 October 2020 | Accepted 7 January 2021 | Published 29 July 2021

---

**Citation:** Haubrock PJ, Cuthbert RN, Sundermann A, Diagne C, Golivets M, Courchamp F (2021) Economic costs of invasive species in Germany. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) The economic costs of biological invasions around the world. NeoBiota 67: 225–246. <https://doi.org/10.3897/neobiota.67.59502>

---

## 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 4<sup>th</sup> 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 4<sup>to</sup> 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 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 invazivní druhy jsou dobře známou a všudypřítomnou hrozbou pro celosvětovou biodiverzitu 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 invazivními druhy v Německu, které je čtvrtou zemí s nejvyšším HDP na světě. Celkově byly ekonomické náklady invazivních 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 invazivní, 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, jež velmi pravděpodobně maskuje existenci podstatně vyšších škod způsobených invazivními druhy v Německu. Jelikož počet invazivních druhů v zemi roste, lze do budoucna očekávat i růst jimi způsobených škod. Je tedy potřeba zlepšit hodnocení a vykazování ekonomických nákladů souvisejících s invazivními 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 (Nehring 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.

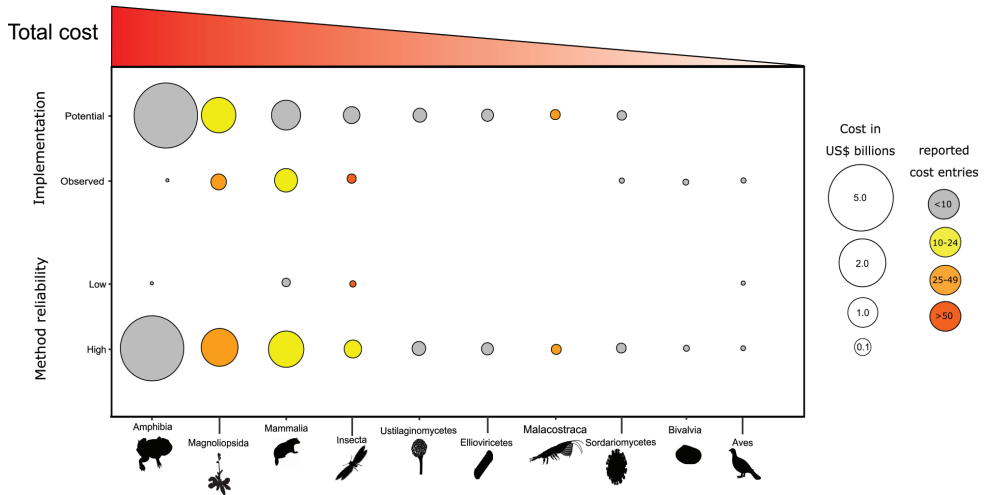
## Temporal dynamics of accumulated costs

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.

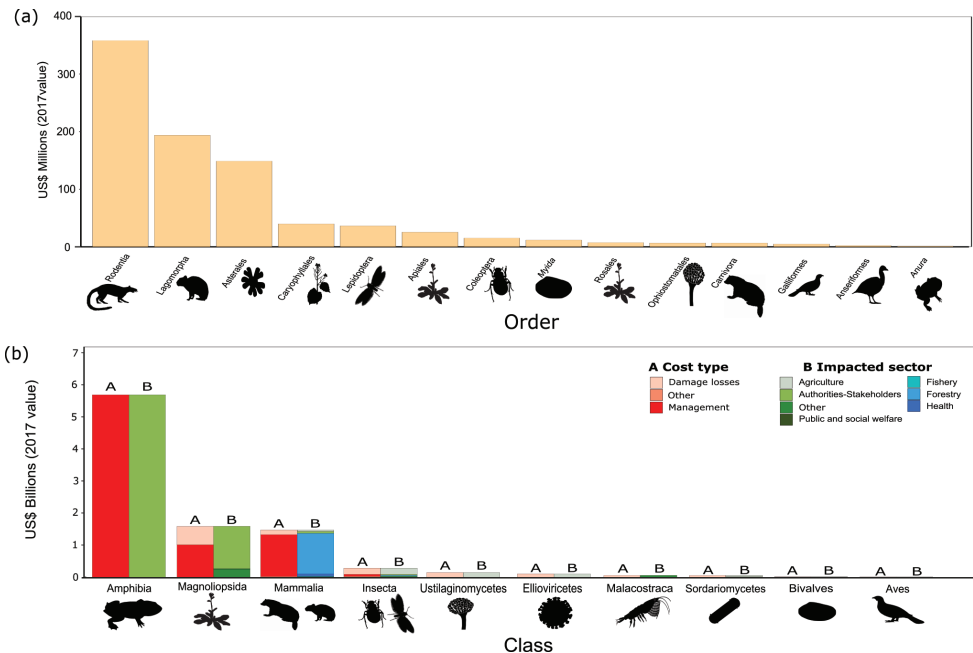
## Results

### 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

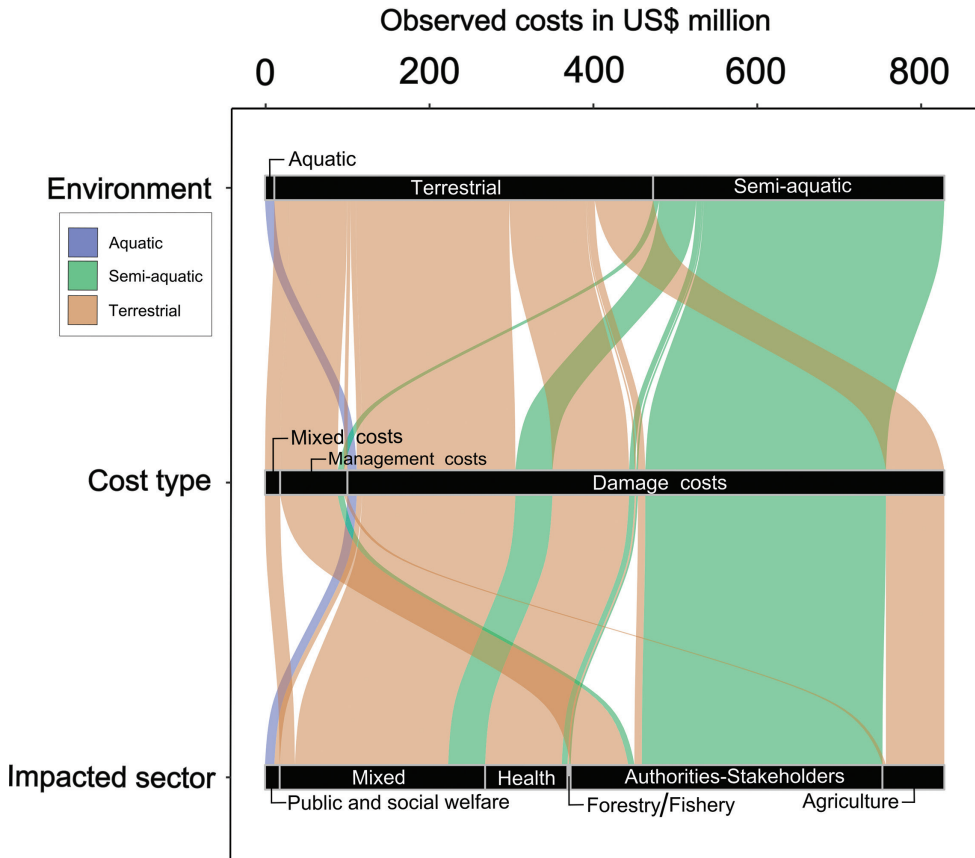


**Figure 1.** Total economic costs of invasions in Germany across taxonomic groups (classes) showing method reliability (high vs. low) and implementation (potential vs. observed costs) in comparison to the overall total cost (indicated by the increasingly red scale). The colour of each balloon corresponds 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.

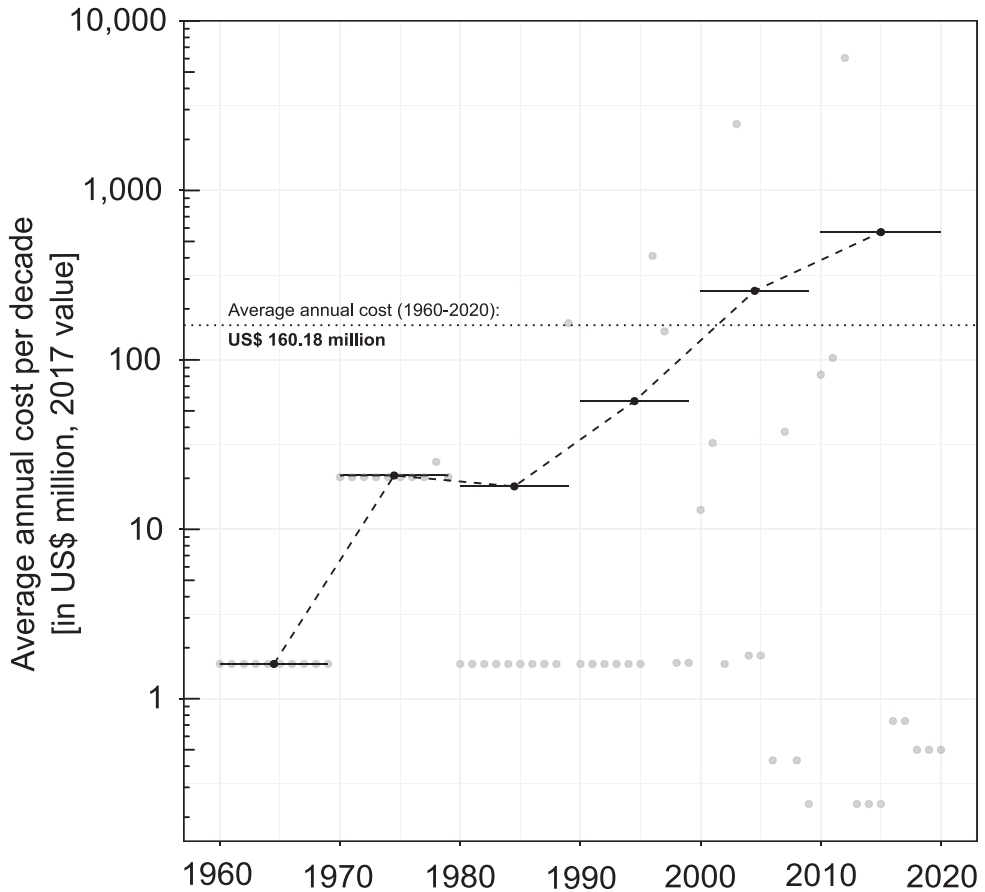




**Figure 3.** Distribution of observed costs across the three descriptors ‘Environment’, ‘Type of cost’ and ‘Impacted sector’, illustrating flows of identified invasion costs in Germany.

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. Health, 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 ob-

served 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.

## 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 AlienScenario project funded by BiodivERsA and Belmont-Forum Call 2018 on biodiversity scenarios. RC is funded by the Alexander von Humboldt Foundation. MG and CD are funded by the BiodivERsA-Belmont Forum Project “Alien Scenarios” (BMBF/PT DLR 01LC1807C). The authors acknowledge Antonin Kouba for the translation of the abstract to Czech and Elena Angulo for the translation to Spanish. Lastly, the authors would like to acknowledge the meaningful effort from the anonymous reviewers.

## References

- Adelino JRP, Heringer G, Diagne C, Courchamp F, Faria LDB, Zenni RD (2021) The economic costs of biological invasions in Brazil: a first assessment. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The economic costs of biological invasions around the world*. *NeoBiota* 67: 349–374. <https://doi.org/10.3897/neobiota.67.59185>
- AELF (2008) *Die Bekämpfung des Kartoffelkäfers im ökologischen Landbau*. Amt für Ernährung, Landwirtschaft und Forsten Bamberg, L2.8.
- Angulo E, Diagne C, Ballesteros-Mejía L, Akulov EN, Dia CAKM, Adamjy T, Banerjee A-K, Capinha C, Duboscq VG, Dobigny G, Golivets M, Heringer G, Haubrock P, Kirichenko

- N, Kourantidou M, Liu C, Nuñez M, Renault D, Roiz D, Taheri A, Watari Y, Xiong W, Courchamp F (2021a) Non-English languages enrich scientific data: the example of the costs of biological invasions. *Science of the Total Environment* 775: e144441. <https://doi.org/10.1016/j.scitotenv.2020.144441>
- Angulo E, Ballesteros-Mejia L, Novoa A, Duboscq-Carra VG, Diagne C, Courchamp F (2021) Economic costs of invasive alien species in Spain. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The economic costs of biological invasions around the world*. *NeoBiota* 67: 267–297. <https://doi.org/10.3897/neobiota.67.59181>
- Arlinghaus R, Tillner R, Bork M (2015) Explaining participation rates in recreational fishing across industrialised countries. *Fisheries Management and Ecology* 22: 45–55. <https://doi.org/10.1111/fme.12075>
- Arndt E (2009) *Neobiota in Sachsen-Anhalt*. Landesamt für Umweltschutz Sachsen-Anhalt.
- Ballesteros-Mejia L, Angulo E, Diagne C, Courchamp F, Consortia, Invacost (2020) Complementary search database for Invacost. figshare. Dataset. <https://doi.org/10.6084/m9.figshare.12928145.v2>
- Bellard C, Thuiller W, Leroy B, Genovesi P, Bakkenes M, Courchamp F (2013) Will climate change promote future invasions? *Global Change Biology* 19: 3740–3748. <https://doi.org/10.1111/gcb.12344>
- Bernaciak M (2010) Cross-border competition and trade union responses in the enlarged EU: Evidence from the automotive industry in Germany and Poland. *European Journal of Industrial Relations* 16: 119–135. <https://doi.org/10.1177/0959680110364827>
- Blackburn TM, Bellard C, Ricciardi A (2019) Alien versus native species as drivers of recent extinctions. *Frontiers in Ecology and the Environment* 17: 203–207. <https://doi.org/10.1002/fee.2020>
- Borcherding J, Staas S, Krüger S, Ondračková M, Šlapanský L, Jurajda P (2011) Non-native Gobiid species in the lower River Rhine (Germany): recent range extensions and densities. *Journal of Applied Ichthyology* 27: 153–155. <https://doi.org/10.1111/j.1439-0426.2010.01662.x>
- Bradshaw CJA, Hoskins AJ, Haubrock PJ, Cuthbert RN, Diagne C, Leroy B, Andrews L, Page B, Cassey P, Sheppard AW, Courchamp F (2021) Detailed assessment of the reported economic costs of invasive species in Australia. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The economic costs of biological invasions around the world*. *NeoBiota* 67: 511–550. <https://doi.org/10.3897/neobiota.67.58834>
- Cooke SJ, Cowx IG (2006) Contrasting recreational and commercial fishing: searching for common issues to promote unified conservation of fisheries resources and aquatic environments. *Biological Conservation* 128(1): 93–108. <https://doi.org/10.1016/j.biocon.2005.09.019>
- Cooke SJ, Sneddon LU (2007) Animal welfare perspectives on recreational angling. *Applied Animal Behaviour Science* 104: 176–198. <https://doi.org/10.1016/j.applanim.2006.09.002>
- Crystal-Ornelas R, Hudgins EJ, Cuthbert RN, Haubrock PJ, Fantle-Lepczyk J, Angulo E, Kramer AM, Ballesteros-Mejia L, Leroy B, Leung B, López-López E, Diagne C, Courchamp F (2021) Economic costs of biological invasions within North America. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The economic costs of biological invasions around the world*. *NeoBiota* 67: 485–510. <https://doi.org/10.3897/neobiota.67.58038>



- Cuthbert RN, Bartlett AC, Turbelin AJ, Haubrock PJ, Diagne C, Pattison Z, Courchamp F, Catford JA (2021) Economic costs of biological invasions in the United Kingdom. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) The economic costs of biological invasions around the world. *NeoBiota* 67: 299–328. <https://doi.org/10.3897/neobiota.67.59743>
- Cuthbert RN, Pattison Z, Taylor NG, Verbrugge L, Diagne C, Ahmed DA, Leroy B, Angulo E, Briski E, Capinha C, Catford JA, Dalu T, Essl F, Gozlan RE, Haubrock PJ, Kourantidou M, Kramer AM, Renault D, Wasserman RJ, Courchamp F (2021b) Global economic costs of aquatic invasive alien species. *Science of the Total Environment* 775: e145238. <https://doi.org/10.1016/j.scitotenv.2021.145238>
- De Poorter M, Browne M (2005) The Global Invasive Species Database (GISD) and international information exchange: using global expertise to help in the fight against invasive alien species. *BCPC Symposium Proceedings* 81: 49–54.
- Diagne C, Leroy B, Gozlan R, Vaissière A, Nunninger L, Assailly C, Roiz D, Jourdain F, Jarić I, Courchamp F (2020) InvaCost, a public database of the global economic costs of biological invasions. *Scientific Data* 7: e277. <https://doi.org/10.1038/s41597-020-00586-z>
- Diagne C, Leroy B, Vaissière A-C, Gozlan RE, Roiz D, Jarić I, Salles JM, Bradshaw CJA, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. *Nature* 592: 571–576. <https://doi.org/10.1038/s41586-021-03405-6>
- Didham RK, Tylianakis JM, Hutchison MA, Ewers RM, Gemmill NJ (2005) Are invasive species the drivers of ecological change? *Trends in Ecology Evolution* 20: 470–474. <https://doi.org/10.1016/j.tree.2005.07.006>
- Duboscq-Carra VG, Fernandez RD, Haubrock PJ, Dimarco RD, Angulo E, Ballesteros-Mejia L, Diagne C, Courchamp F, Nuñez MA (2021) Economic impact of invasive alien species in Argentina: a first national synthesis. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) The economic costs of biological invasions around the world. *NeoBiota* 67: 329–348. <https://doi.org/10.3897/neobiota.67.63208>
- Early R, Bradley BA, Dukes JS, Lawler JJ, Olden JD, Blumenthal DM, Sorte CJ (2016) Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications* 7: e12485. <https://doi.org/10.1038/ncomms12485>
- Essl F, Nehring S, Klingenstein F, Milasowszky N, Nowack C, Rabitsch W (2011) Review of risk assessment systems of IAS in Europe and introducing the German–Austrian Black List Information System (GABLIS) *Journal for Nature Conservation* 19: 339–350. <https://doi.org/10.1016/j.jnc.2011.08.005>
- Essl F, Biró K, Brandes D, Broennimann O, Bullock JM, Chapman DS, Karrer G (2015) Biological flora of the British Isles: *Ambrosia artemisiifolia*. *Journal of Ecology* 103: 1069–1098. <https://doi.org/10.1111/1365-2745.12424>
- Gergs R, Rothhaupt KO (2015) Invasive species as driving factors for the structure of benthic communities in Lake Constance, Germany. *Hydrobiologia* 746: 245–254. <https://doi.org/10.1007/s10750-014-1931-4>
- Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? *Trends in Ecology Evolution* 19: 470–474. <https://doi.org/10.1016/j.tree.2004.07.005>
- Hanley N, Roberts M (2019) The economic benefits of invasive species management. *People and Nature* 1(2): 124–137. <https://doi.org/10.1002/pan.3.31>

- Hartelt K, Pluta S, Oehme R, Kimmig P (2008) Spread of ticks and tick-borne diseases in Germany due to global warming. *Parasitology Research* 103: 109–116. <https://doi.org/10.1007/s00436-008-1059-4>
- Haubrock PJ, Turbelin AJ, Cuthbert RN, Novoa A, Taylor NG, Angulo E, Ballesteros-Mejia L, Bodey TW, Capinha C, Diagne C, Essl F, Golivets M, Kirichenko N, Kourantidou M, Leroy B, Renault D, Verbrugge L, Courchamp F (2020) Economic costs of invasive alien species across Europe In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The economic costs of biological invasions around the world*. *NeoBiota* 67: 153–190. <https://doi.org/10.3897/neobiota.67.58196>
- Haubrock PJ, Bernery C, Cuthbert RN, Liu C, Kourantidou M, Leroy B, Turbelin AJ, Kramer AM, Verbrugge L, Diagne C, Courchamp F, Gozlan RE (2021b) What is the recorded economic cost of alien invasive fishes worldwide?. <https://doi.org/10.21203/rs.3.rs-381243/v1>
- Haubrock PJ, Pilotto F, Innocenti G, Cianfanelli S, Haase P (2021c) Two centuries for an almost complete community turnover from native to non-native species in a riverine ecosystem. *Global Change Biology* 27(3): 606–623. <https://doi.org/10.1111/gcb.15442>
- Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18. <https://doi.org/10.1111/j.1365-2664.2008.01600.x>
- Hussner A, van de Weyer K, Gross EM, Hilt S (2010) Comments on increasing number and abundance of non-indigenous aquatic macrophyte species in Germany. *Weed Research* 50: 519–526. <https://doi.org/10.1111/j.1365-3180.2010.00812.x>
- Jarić I, Bellard C, Courchamp F, Kalinkat G, Meinard Y, Roberts DL, Correia RA (2020) Societal attention toward extinction threats: a comparison between climate change and biological invasions. *Scientific Reports* 10: 1–9. <https://doi.org/10.1038/s41598-020-67931-5>
- Kehlenbeck H (1998) Kosten und Nutzen der Auswirkungen von EG-Binnenmarktregelungen zur Pflanzengesundheit. Teil 2: Nutzen der Pflanzenbeschau und Zusammenfassende Wertung. *Nachrichtenblatt des Deutschen Pflanzenschutzdienstes* 50: 217–224.
- Kettunen M, Genovesi P, Gollasch S, Pagad S, Starfinger U, ten Brink P, Shine C (2009) Technical support to EU strategy on invasive alien species (IAS) Institute for European Environmental Policy (IEEP), Brussels, 124 pp.
- Kochalski S, Riepe C, Fujitani M, Aas Ø, Arlinghaus R (2019) Public perception of river fish biodiversity in four European countries. *Conservation Biology* 33: 164–175. <https://doi.org/10.1111/cobi.13180>
- Leroy B, Kramer AM, 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>
- Lipták B, Vitázková B (2015) Beautiful, but also potentially invasive. *Ekológia (Bratislava)* 34: 155–162. <https://doi.org/10.1515/eko-2015-0016>
- Liu C, Diagne C, Angulo E, Banerjee A-K, Chen Y, Cuthbert RN, Haubrock PJ, Kirichenko N, Pattison Z, Watari Y, Xiong W, Courchamp F (2021) Economic costs of biological invasions in Asia. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The eco-*

- conomic costs of biological invasions around the world. *NeoBiota* 67: 53–78. <https://doi.org/10.3897/neobiota.67.58147>
- Lovell SJ, Stone SF, Fernandez L (2006) The economic impacts of aquatic invasive species: a review of the literature. *Agricultural and Resource Economics Review* 35: 195–208. <https://doi.org/10.1017/S1068280500010157>
- Malcolm JR, Markham A (2000) Global warming and terrestrial biodiversity decline. WWF, Washington.
- Marbuah G, Gren IM, McKie B (2014) Economics of harmful invasive species: a review. *Diversity* 6: 500–523. <https://doi.org/10.3390/d6030500>
- Martens A, Grabow K, Schoolmann G (2007) Die Quagga-Muschel *Dreissena rostriformis bugensis* (Andrusov, 1897) am Oberrhein (Bivalvia: Dreissenidae). *Lauterbornia* 61: 145–152.
- Nehring S, Klingenstein F (2008) Aquatic alien species in Germany – listing system and options for action. *Neobiota* 7: 19–33.
- Pagad S, Genovesi P, Carnevali L, Schigel D, McGeoch MA (2018) Introducing the global register of introduced and invasive species. *Scientific data* 5: 1–12. <https://doi.org/10.1038/sdata.2017.202>
- Paini DR, Sheppard AW, Cook DC, De Barro PJ, Worner SP, Thomas MB (2016) Global threat to agriculture from invasive species. *Proceedings of the National Academy of Sciences* 113(27): 7575–7579. <https://doi.org/10.1073/pnas.1602205113>
- Pehl L, Kehr R, Wulf A (2003) Rosskastanienminiermotte, *Cameraria ohridella* Deschka Dimic. Für die Praxis: Krankheiten und Schädlinge an Gehölzen. Biologische Bundesanstalt für Land- und Forstwirtschaft(BBA): 1–6.
- Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs of non-indigenous species in the United States. *BioScience* 50: 53–66. [https://doi.org/10.1641/0006-3568\(2000\)050\[0053:EAECON\]2.3.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0053:EAECON]2.3.CO;2)
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273–288. <https://doi.org/10.1016/j.ecolecon.2004.10.002>
- Reinhardt F, Herle M, Bastiansen F, Streit B (2003) Ökonomische Folgen der Ausbreitung von Neobiota. *Forschungsbericht* 201, 248 pp.
- Renault D, Manfrini E, Leroy B, Diagne C, Ballesteros-Mejia L, Angulo E, Courchamp F (2021) Biological invasions in France: Alarming costs and even more alarming knowledge gaps. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The economic costs of biological invasions around the world*. *NeoBiota* 67: 191–224. <https://doi.org/10.3897/neobiota.67.59134>
- Rico-Sánchez AE, Haubrock PJ, Cuthbert RN, Angulo E, Ballesteros-Mejia L, López-López E, Duboscq-Carra VG, Nuñez MA, Diagne C, Courchamp F (2021) Economic costs of invasive alien species in Mexico. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The economic costs of biological invasions around the world*. *NeoBiota* 67: 459–483. <https://doi.org/10.3897/neobiota.67.63846>
- Scalera R (2010) How much is Europe spending on invasive alien species? *Biological Invasions* 12: 173–177. <https://doi.org/10.1007/s10530-009-9440-5>

- Schaffner U, Steinbach S, Sun Y, Skjøth CA, de Weger LA, Lommen ST, Thibaudon M (2020) Biological weed control to relieve millions from Ambrosia allergies in Europe. *Nature Communications* 11(1): 1–7. <https://doi.org/10.1038/s41467-020-15586-1>
- Schöll F, Eggers TO, Haybach A, Gorka M, Klima M, König B (2012) Verbreitung von *Dreissena rostriformis bugensis* (Andrusov, 1897) in Deutschland (Mollusca: Bivalvia). *Lauterbornia* 74: 111–115.
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Bacher S (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications* 8: e14435. <https://doi.org/10.1038/ncomms14435>
- Seebens H, Bacher S, Blackburn T M, Capinha C, Dawson W, Dullinger S, Jeschke JM (2020) Projecting the continental accumulation of alien species through to 2050. *Global Change Biology* 27(5): 970–982. <https://doi.org/10.1111/gcb.15333>
- Steffens W, Winkel M (2002) Evaluating recreational fishing in Germany. *Recreational fisheries: ecological, economic, and social evaluation*. Blackwell Scientific Publications, Oxford, 130–136. <https://doi.org/10.1002/9780470995402.ch10>
- Stigall AL (2010) Invasive species and biodiversity crises: testing the link in the Late Devonian. *PLoS ONE* 5: e15584. <https://doi.org/10.1371/journal.pone.0015584>
- Thomsen E, Dahl HA, Mikalsen SO (2019) *Ctenolepisma longicaudata* (Escherich, 1905): a common, but previously unregistered, species of silverfish in the Faroe Islands. *BioInvasions Record* 8(3): 540–550. <https://doi.org/10.3391/bir.2019.8.3.09>
- Vanbergen AJ, Espíndola A, Aizen MA (2018) Risks to pollinators and pollination from invasive alien species. *Nature Ecology and Evolution* 2(1): 16–25. <https://doi.org/10.1038/s41559-017-0412-3>
- Vegea AM, Manissero CE (1996) U.S. Patent No. 5,550,157. U.S. Patent and Trademark Office, Washington.
- Venkatesan R, Murthy PS (2008) Macrofouling control in power plants. In: Flemming H-C, Murthy S, Venkatesan R, Cooksey KE (Eds) *Marine and Industrial Biofouling*. Springer Series on Biofilms (Vol. 4). Springer, Berlin, Heidelberg, 265–291. [https://doi.org/10.1007/978-3-540-69796-1\\_14](https://doi.org/10.1007/978-3-540-69796-1_14)
- Vimercati G, Kumschick S, Probert AF, Volery L, Bacher S (2020) The importance of assessing positive and beneficial impacts of alien species. *NeoBiota* 62: 525–545. <https://doi.org/10.3897/neobiota.62.52793>
- Vörösmarty C, Lettenmaier D, Leveque C, Meybeck M, Pahl-Wostl C, Alcamo J, Lansigan F (2004) Humans transforming the global water system. *Eos, Transactions American Geophysical Union* 85: 509–514. <https://doi.org/10.1029/2004EO480001>
- Walther D, Scheuch DE, Kampen H (2017) The invasive Asian tiger mosquito *Aedes albopictus* (Diptera: Culicidae) in Germany: Local reproduction and overwintering. *Acta Tropica* 166: 186–192. <https://doi.org/10.1016/j.actatropica.2016.11.024>
- Werner D, Kronefeld M, Schaffner F, Kampen H (2012) Two invasive mosquito species, *Aedes albopictus* and *Aedes japonicus japonicus*, trapped in south-west Germany, July to August 2011. *Eurosurveillance* 17(4): e20067. [4 pp.] <https://doi.org/10.2807/ese.17.04.20067-en>

Wolter C, Röhr F (2010) Distribution history of non-native freshwater fish species in Germany: how invasive are they? *Journal of Applied Ichthyology* 26: 19–27. <https://doi.org/10.1111/j.1439-0426.2010.01505.x>

World Bank World Development Indicators (2019) Population density (people per sq. km of land area). <https://data.worldbank.org/indicator/EN.POP.DNST> [Retrieved on 10 Dec 2019]

## 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.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

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.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neobiota.67.59502.suppl2>

### **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.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neobiota.67.59502.suppl3>