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Economic costs of biological invasions within North America

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Abstract

Invasive species can have severe impacts on ecosystems, economies, and human health. Though the economic impacts of invasions provide important foundations for management and policy, up-to-date syntheses of these impacts are lacking. To produce the most comprehensive estimate of invasive species costs within North America (including the Greater Antilles) to date, we synthesized economic impact data from the recently published InvaCost database. Here, we report that invasions have cost the North American economy at least US$ 1.26 trillion between 1960 and 2017. Economic costs have climbed over recent decades, averaging US$ 2 billion per year in the early 1960s to over US$ 26 billion per year in the 2010s. Of the countries within North America, the United States (US) had the highest recorded costs, even after controlling for research effort within each country ($5.81 billion per cost source in the US). Of the taxa and habitats that could be classified in our database, invasive vertebrates were associated with the greatest costs, with terrestrial habitats incurring the highest monetary impacts. In particular, invasive species cumulatively (from 1960–2017) cost the agriculture and forestry sectors US$ 527.07 billion and US$ 34.93 billion, respectively. Reporting issues (e.g., data quality or taxonomic granularity) prevented us from synthesizing data from all available studies. Furthermore, very few of the known invasive species in North America had reported economic costs. Therefore, while the costs to the North American economy are massive, our US$ 1.26 trillion estimate is likely very conservative. Accordingly, expanded and more rigorous economic cost reports are necessary to provide more comprehensive invasion impact estimates, and then support data-based management decisions and actions towards species invasions.

Abstract in Spanish

Costos económicos de las invasiones biológicas en Norteamérica. Las especies invasoras pueden tener severos impactos en los ecosistemas, las economías y la salud humana. Aunque los impactos económicos de las invasiones proporcionan bases importantes para la gestión y la política, no existen síntesis actualizadas de estos impactos. Para producir la estimación más completa de los costos de las especies invasoras en Norteamérica (incluidas las Antillas Mayores) hasta la fecha, sintetizamos los datos de impactos económicos de la base de datos InvaCost publicada recientemente. Aquí, reportamos que las invasiones le han costado a la economía de Norteamérica al menos US $1,26 billones entre 1960 y 2017. Los costos económicos han aumentado en las últimas décadas, con un promedio de US $2 mil millones por año a principios de la década de 1960 a más de US $26 mil millones por año en la década de 2010. De los países de Norteamérica, Estados Unidos (EE. UU.) registró los costos más altos, incluso después de controlar el esfuerzo de investigación dentro de cada país (US $5,81 mil millones por fuente de costos en los EE. UU.). De los taxones y hábitats que podrían clasificarse en nuestra base de datos, los vertebrados invasores se asociaron con los mayores costos, y los hábitats terrestres registraron los mayores impactos monetarios. En particular, las especies invasoras de forma acumulada (de 1960 a 2017) le costaron a los sectores agrícola y forestal US $527,07 mil millones y US $34,93 mil millones, respectivamente. Las inconsistencias en los informes (por ejemplo, la calidad de los datos o los detalles en la clasificación taxonómica) nos impidieron sintetizar los datos de todos los estudios disponibles. Además, había informes de costos económicos para muy pocas de las especies invasoras conocidas de Norteamérica. Por consiguiente, si bien los costos para la economía de Norteamérica son enormes, nuestra estimación de US $1,26 billones probablemente es muy conservadora. En consecuencia, se necesitan informes de costos económicos más extensos y rigurosos para proporcionar estimaciones más completas del impacto económico de las invasiones y luego respaldar con los datos las decisiones y acciones de manejo de las invasiones de especies.

Abstract in French

Les espèces exotiques envahissantes ont de fortes répercussions sur les écosystèmes, l'économie et la santé humaine. Bien que les conséquences financières induites par les invasions constituent des données de base importantes pour la définition des politiques publiques et de gestion des invasions biologiques, des synthèses robustes manquent encore à ce jour sur les coûts économiques liés aux invasions. Afin de fournir une estimation la plus complète possible des coûts induits par les espèces exotiques envahissantes en Amérique du Nord (Les Antilles comprises), nous avons compilé les données disponibles au sein de la base de données InvaCost récemment publiée. Ce travail révèle que les invasions ont coûté au moins 1260 milliards de dollars américains entre 1960 et 2017 à l'économie nord-américaine. Les coûts économiques ont été particulièrement accrus au cours des dernières décennies, passant de 2 milliards de dollars par an en moyenne au début des années 1960, à plus de 26 milliards de dollars par an au début des années 2010. Parmi les pays de l'Amérique du Nord, les États-Unis présentent les impacts économiques les plus élevés, même après que ces coûts aient été corrigés par les différences d'efforts de recherche menés par chaque pays (5,81 milliards de dollars par document source de coûts aux États-Unis). Parmi les taxons et les habitats renseignés dans notre base de données, les vertébrés présentent les coûts les plus élevés, et les habitats terrestres sont ceux qui subissent les impacts monétaires les plus importants. Ainsi, les espèces exotiques envahissantes ont, sur la période 1960–2017, coûté 527,07 milliards de dollars de pertes à l'agriculture, et 34,93 milliards de dollars à la foresterie. A noter que la qualité des données sources (par exemple, la fiabilité des estimations de coûts ou encore l'absence de précision sur les taxons spécifiques associés aux coûts) ne nous a pas permis d'utiliser toutes les données disponibles. De surcroît, il existe peu de données de coûts au regard de la diversité des espèces exotiques envahissantes en Amérique du Nord. Par conséquent, même si les coûts pour l'économie nord-américaine sont énormes, notre estimation de 1260 milliards de dollars américains reste probablement très largement sous-estimée. Par conséquent, il est indispensable d'accroître les efforts de recherche sur ces données de coûts afin (*i*) de fournir des estimations plus complètes des impacts économiques des invasions biologiques, et (*ii*) d'appuyer les décisions de gestion fondées sur des données le plus robustes possible.

Keywords
Alien species, Canada, ecosystem management, Greater Antilles, InvaCost, Mexico, monetary impacts, societal sectors, United States

Introduction

Invasive species can have widespread and severe impacts on ecosystems, human health, and economies (Bradshaw et al. 2016; Iwamura et al. 2020; Pyšek et al. 2020; Diagne et al. 2021a). Ecological impacts from invasions are increasingly well-characterized, including reductions in native species abundances (Bradley et al. 2019), biodiversity (Mollot et al. 2017), fitness (Nunes et al. 2019) and many other detrimental effects on ecosystems (Ehrenfeld 2010). Also, invasions have been shown to severely impact human health (Shepard et al. 2011; Schaffner et al. 2020). In turn, associated economic impacts range from disrupting ecosystem services (Pejchar and Mooney 2010), to decreasing agricultural yields (Oliveira et al. 2001), damaging infrastructure and lowering real estate value and incomes (Sousa et al. 2009; Olden and Tamayo 2014), as well as substantial expenditures from management actions (Hoffmann and Broadhurst 2016). However, while advances have been made in deciphering the extent and intensity of ecological impacts on ecosystems (but see Crystal-Ornelas and Lockwood 2020), economic quantifications of invasive species remain scarce at several scales (Diagne et al. 2020a).

Where economic impacts of biological invasions have been quantified, they have often been limited to particular geographic, taxonomic, socioeconomic or environmental contexts (Pimentel et al. 2000; Aukema et al. 2011; Bradshaw et al. 2016; Hoffmann and Broadhurst 2016; Paini et al. 2016; Cuthbert et al. 2021a). Broadly, systematic reviews in invasion ecology suggest that research efforts are not equal across taxonomic groups and geographic areas (Pyšek et al. 2008; Cameron et al. 2016; Crystal-Ornelas and Lockwood 2020). Furthermore, because specific industries may be impacted more heavily than others by invasive species, we have data that directly link the impact of invasive species to economic losses for individual industries. For example, the tobacco whitefly (*Bemisia tabaci*), which spreads diseases through lettuce crops in Mexico, costs the Mexican economy US$ 20 million annually (Oliveira et al. 2001). Within the US, the annual economic cost to the forestry sector in terms of timber losses due to invasive forest pests is estimated at approximately US$ 150 million. At the same time, local governments and homeowners incur annual losses estimated at US$ 1.7 billion and $830 million due to the impacts wood-boring invasive insects have on healthy community trees (Aukema et al. 2011). Other research suggests that invasive insects could cost North America US$ 27.3 billion per year, with the largest losses incurred by the agricultural sector (Bradshaw et al. 2016).

Cost estimates at national levels are crucial, as they can duly inform policy. However, biological invasions do not respect geopolitical boundaries and intracontinental exchanges of goods and persons are linked to increased invasions (e.g., North American Free Trade Agreement; Barajas et al. 2014). Therefore, without large region-wide estimates of monetary impact across multiple biotic groups, habitat types and societal sectors, policy and management at more local-scales will at best be piecemeal, and at worst may lead to deeper economic impacts (Diagne et al. 2020b; Faulkner et al. 2020). So far, multinational agreements have led to coordinated efforts to reduce invasions in ballast water (Firestone and Corbett 2005) and control sea lamprey populations in the North American Great Lakes (Lodge et al. 2006).

This spatial coordination of management actions is particularly pertinent as the number of invasive species introductions (Aukema et al. 2010) and their ecological impacts are dynamic over time (Gallardo et al. 2016). It follows that their economic impacts may also shift over time. Indeed, because species introductions have increased exponentially over the past 200 years (Seebens et al. 2017), we might expect economic costs of invasions to rise as well. This has been seen in Australia, where an economic impact assessment found that invasive species management cost an average of AU$ 2.31 billion in the early 2000s, with costs then rising to AU$ 3.77 billion per year by 2011 (Hoffmann and Broadhurst 2016). Given the lack of information at the continental scale for North America, it is an open question whether accelerations in introduction and subsequent damage or management are even greater when examined region-wide.

In order to coordinate region-wide policy and management, North America critically needs a comprehensive understanding of cost detection efforts taking place within North American countries. For the US, one country-wide cost detection effort estimated that invasive species cost the US approximately $137 billion per year (Pimentel et al. 2000). However, in the decades since these early quantifications, some of these large-scale efforts have been criticized for the reliability of their extrapolations (e.g., Hoagland and Jin 2006; McDermott et al. 2013; Cuthbert et al. 2020). A robust assessment of economic costs of invasions is necessary to inform policy and management (e.g., by helping to define prioritization of target areas/species and estimate costefficiency of actions), as an inaccurate assessment could lead to an over/underallocation of resources and inefficient management actions. In turn, inadequate contemporary management actions could cause greater invasion costs in future, particularly if pre-invasion management (i.e., biosecurity) fails to prevent new introductions of damaging species (Ricciardi et al. 2020; Ahmed et al. 2021).

Providing continental estimates of economic costs may help spur the development of invasive species guidance that spans large geographic areas (Epanchin-Niell 2017; Aizen et al. 2018). The many disparate ways by which researchers assess invasive species economic impacts (Dana et al. 2014; Jackson 2015) have thus far impeded reliable and robust cost syntheses. The InvaCost database is the most up-to-date repository of invasion costs worldwide (Diagne et al. 2020a). Within InvaCost, detailed cost information is provided alongside each record, including the nature of the cost incurred and the scale at which it was studied.

In this study, we provide an estimate of the total economic cost of invasive species to North America, including to the Greater Antilles (Canada, US, Mexico, Cuba, Jamaica, and Dominican Republic; hereafter, North America). Specifically, we use information from the InvaCost database (Diagne et al. 2020a) to: (i) characterize the invasive taxa, countries (i.e., cost per country and cost per source for that country), habitats and activity sectors bearing the highest economic impacts; (ii) identify the types of costs (damage or management) incurred by the invaders; (iii) describe the temporal dynamics of these monetized impacts within North America; and (iv) identify the major continents and pathways of origin for these species.

Methods

Data collection and filtering

The recently developed InvaCost database (Diagne et al. 2020a) is a publicly available repository that compiles the monetary impacts of invasive species globally. To develop the InvaCost database, Diagne et al. (2020a) conducted standardized literature searches (via Web of Science platform, Google Scholar and Google search engine) and opportunistic targeted searches (i.e., expert consultations by which data gaps were identified). The most up-to-date version of the InvaCost database (InvaCost_3.0, freely accessible at https://doi.org/10.6084/m9.figshare.12668570) was considered in our study. We aggregated this data resource with new costs collected from another study in Mexico (Rico-Sánchez et al. 2021). The resulting initial dataset contained 9,866 cost estimates (standardized to 2017 US$) of invasive species impacts around the world.

We filtered the complete database to focus on the economic impacts of invasive species within North America that occurred between 1960 and 2017. This resulted in a full dataset of a total of 1,727 cost entries (hereafter, "full dataset"; See Suppl. material 1: full_dataset). We provide a visual depiction of our data cleaning and filtering processing using a Preferred Reporting Items for Systematic Reviews and Meta-

Analyses (PRISMA) diagram (Moher et al. 2009; Fig. 1). As a first step, we considered the full dataset to provide an estimate closer to the upper bound of costs recorded in the database for this region without any filtering of the database. Then, we performed two filtering steps to obtain the most robust subset for our North American analyses (hereafter "robust dataset"; See Suppl. material 1: robust_dataset). First, we subset the data to retain only "observed" costs (actually incurred) rather than a combination of "observed" and "potential" costs (costs expected, predicted over time or potentially occurring in the future). By constraining our analyses to focus on only observed costs, we synthesized data on directly measured economic impacts. Second, we retained only economic impacts classified as "highly reliable" (Diagne et al. 2020a), meaning that the economic impacts were either published in peer-reviewed journals, official reports or if found in grey literature, the costs reported had justified and replicable methods. These filtering steps removed the small number of entries in our database on invasive species in Jamaica. Using this robust subset of the full dataset for North America, we examined the economic impact of invasive species in North America across a range of descriptors: taxonomic grouping, habitat affected, impacted sector, cost type, and time (See Suppl. material 1: field_description for description of fields in database). We describe these analyses below.

Quantifying economic impacts by descriptors

Cost entries in the InvaCost database occur over different timescales. Accordingly, entries within the database were expanded to obtain annualized estimates using the *expandYearlyCosts* function of the *invacost* R package (Leroy et al. 2020 *v*1.0, R Core Team 2020 *v*4.0.2). This function provides annualized cost estimates for all entries, based upon the adjusted probable starting and ending years provided in the InvaCost Database (Diagne et al. 2020a).

In order to determine which taxonomic groups had the highest economic impacts within North America, we organized all invasive species in the database into four phylum-level groups (invertebrates, vertebrates, plants, or other) based on the phyla recorded in the InvaCost database. We note that for vertebrates, we grouped all chordates, but highlight that not all chordates are vertebrates. The "other" grouping captured unspecified or mixed phyla entries as well as groups with very few cost estimates (viruses, bacteria, fungi, and algae). Mixed entries correspond to those with impacts attributed to multiple invasive species in a single cost entry, where it is not possible to split apart each of their impacts. Unspecified entries have no specific invasive species attributed to an individual cost.

To characterize the economic impact in different countries within North America, we standardized the total costs incurred by each country within North America by the number of cost sources (the "Reference_title" field) captured in InvaCost. We controlled for the number of cost sources published from research in each country so that we could make fairer comparisons between countries-had we not taken this step of controlling for a proxy of research effort, costs would have inevitably risen with a greater number of

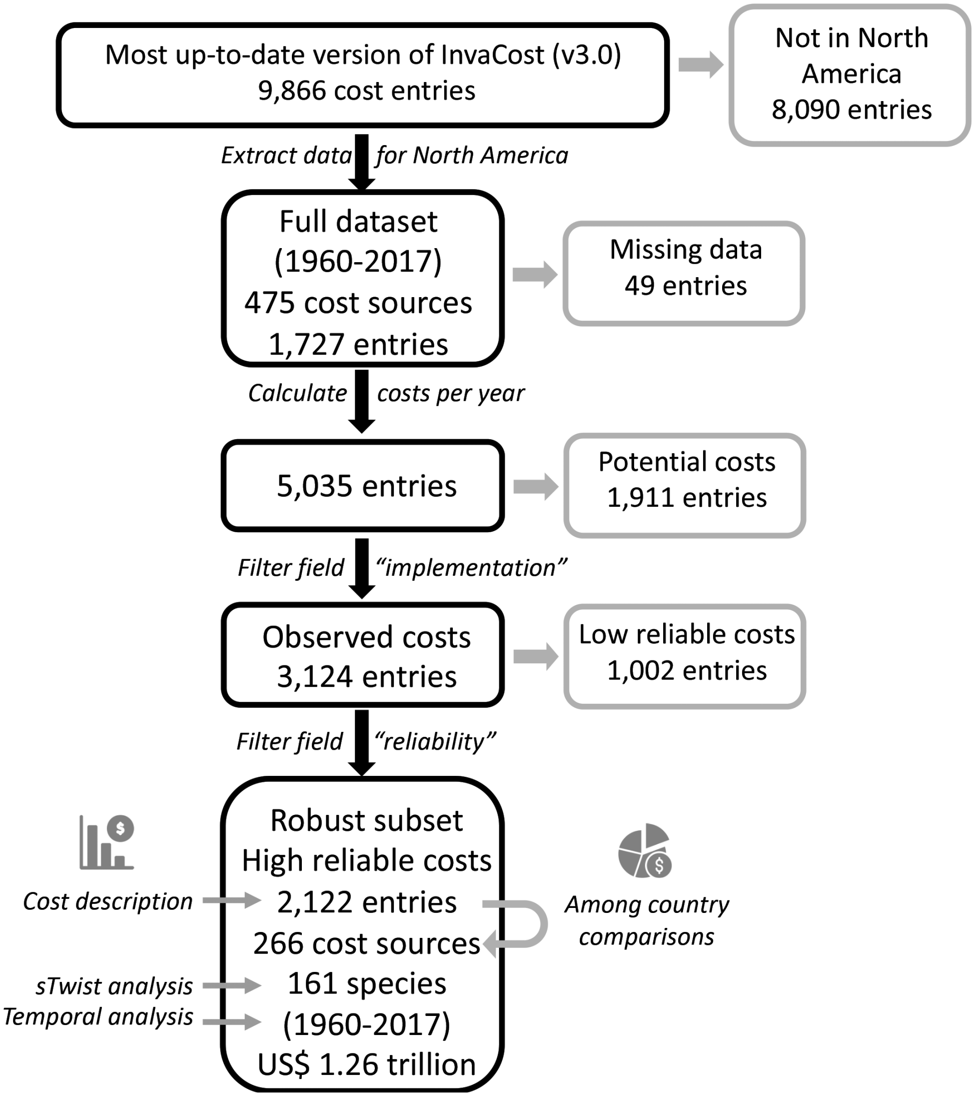

Figure 1. PRISMA flowchart (Moher et al. 2009) to depict our process for identifying the subset of economic data we used in this manuscript. Black boxes indicate the number of entries retained at every screening step. Gray boxes indicate the number of entries removed at every screening step. We began with 9,866 cost entries that include data from InvaCost 3.0 as well as recently collected data from invasion costs in Mexico (Rico-Sánchez et al. 2021) Ultimately, we retained 2,122 expanded entries that occurred within North America, and were classified as being reliable and directly observed.

sources. Thus, we present an average economic cost of invasive species impacts for each country controlling for the proxy of research effort, as well as the raw cost totals.

To investigate which variables might experience differing levels of impact, we summarized cost totals by habitat ("Environment"), economic sector ("Impacted_sector"), and type of cost ("Type_of_cost_merged"). For a full explanation of variables and the levels of classification within those variables, see Suppl. material 1: "field_description". Here, we highlight some of the classification levels for the variables in our analysis. For the "Environment" variable, we grouped economic impacts into high-level habitat categories of either aquatic, semi-aquatic, terrestrial, or unspecified as provided by the InvaCost database. The "Impacted_sector" field of the InvaCost database allows users to view the costs of invasive species within any of the 9 major sectors of economic activity captured in the database, such as agriculture, forestry, health and fisheries. The InvaCost database separates economic costs based on the type of cost incurred in the recipient location (the "Type_of_cost_merged" field): damage, management, or mixed. We characterized the magnitude of economic impacts within North America for each of these types of costs. For a more detailed classification of cost types, see Suppl. material 2: Table S1.

We analyzed temporal trends of invasive species' economic impacts within North America by using the *summarizeCosts* function in the *invacost* R package. This function used yearly costs calculated by the *expandYearlyCosts* function described above to calculate average annual costs as well as decadal averages over the 1960–2017 study period.

Linkage with CABI and sTwist

We linked each InvaCost entry with a species' geographic region(s) of origin based on "Native" region entries within their "Distribution table" where provided by CABI's Invasive Species Compendium (ISC, CABI 2020). We used the *rvest* package (Wickham 2016) to obtain the content of each CABI ISC webpage within the set of species with "Full" coverage as defined by CABI ISC (i.e., those with fully-referenced, peer-reviewed entries, 2,620 species globally). From the resulting files, we extracted the "Distribution table" element of each species' webpage and took note of all countries it contained. We also linked each species to any dominant pathways of introduction provided within CABI's "Species Transported by Cause" listing for five major groupings of pathways: pet trade (includes ornamental plants), forestry, agriculture (includes livestock), fisheries, and health (defined in Suppl. material 2: Table S2). We set the pathway cause for a species to "Other" if it could not be assigned to any of these dominant pathways. When a species reported multiple pathways, we divided its weight (or total cost) equally across all reported pathways, thereby assuming equal contribution of all pathways.

In order to determine the set of species known to have invaded North America, as well as their known invaded ranges, we relied on a recent publication that provides the most up-to-date distributional information for all known invasive alien species globally (sTwist, Seebens et al. 2020). This database also synthesized first record information where available for each species at the country level. We considered only records of successful establishment within the set of countries in the robust dataset (n = 439), rather than all known sTwist records of introduction for this set of countries (n = 19,159). We used the *countrycode* R package to assign country names within sTwist and InvaCost records to ISO3C country codes (Arel-Bundock et al. 2018), and the *gbif_parse* function within the *taxize* library to resolve species names based on GBIF taxonomy (Chamberlain et al. 2020 v0.9.98). We then merged entries based on matching country codes and species names. We considered a cost missing if InvaCost did not report a cost for any country listed as part of the invader's range within the sTwist database (Seebens et al. 2020). This approach assumed that all known invasive species produce some nonzero economic impact. However, we acknowledge that there may be a small number of invasive species that produce no measurable economic impacts in any of the dimensions covered by the InvaCost database. A more holistic valuation of the myriad impacts of invasive species remains an important long-term objective (Pejchar and Mooney 2009). For incomplete entries that had at least one cost recorded in InvaCost, we extrapolated potential total cost by dividing the total cost recorded for each species across all North American countries by the proportion of the known invaded range area over which costs were reported. For example, if a species were established in the USA, Mexico and Canada, but costs were only reported for the USA, we would divide the total USA cost by the USA's proportional contribution to the total area occupied by the USA, Canada and Mexico (i.e., area of USA/area of USA+Canada+Mexico). This extrapolation assumes that species have the same average economic impact in countries where costs have not been reported, which provides a reasonable upper bound, but may overestimate costs due to a likely correlation between the magnitude of economic impact and the likelihood of its detection. We combined all species within the *Aedes* genus for this portion of the analysis, as they were not always identified to species level, though costs predominantly related to *A. aegypti* and *A. albopictus*.

Results

From 1960 to 2017, our robust dataset suggests that invasive species cost the North American economy at least US$ 1.26 trillion (n = 2,122 expanded database entries). We emphasize that this is likely a highly conservative cost estimate because we constrained our analysis to only recorded economic data, classified as both directly observed and highly reliable. When we relax these constraints and include recorded costs of low reliability (US$ 1.02 trillion) and/or that are potential (US$ 902.19 billion), our full dataset suggests costs may be US$ 3.18 trillion. As outlined in the methods section, hereafter all results that we discuss are based on the filtered set of highly robust data.

Database descriptors

Taxonomically, the highest economic costs to North America were reported for species that could not be resolved to the species level or complexes of more than one species (US$ 845.21 billion, n = 343). The second highest costs were from the vertebrate group (US$ 252.97 billion, *n* = 365). Third highest were invertebrates with costs of US$ 140.80 billion (*n* = 795).

At the country level, our results showed that from 1960–2017, the US incurred US$ 1.21 trillion in costs. When we scaled this estimate by the number of references describing costs in the US (*n* = 209) each source found an average cost of US$ 5.81 billion from invasions. Invasive species cost the Canadian economy a total of US$ 34.49 billion (*n* = 22), with an average economic impact per source of US$ 1.57 billion. Total costs incurred in Mexico from invasions were US$ 3.75 billion (*n* = 28) and the average cost of impacts found per source was US$ 133.81 million. The total cost to the Cuban economy was US$ 342.04 million (*n* = 6), averaging US$ 57.01 million per source. Our robust database had a single entry from the Dominican Republic, and the cost to this country was US$ 3.05 million. Note that the cost per source metric was used only to account for the relationship between recorded costs and research effort, and is not used hereafter.

The most impacted habitat within North America was terrestrial (US$ 675.39 billion), and we note that this was also the most frequently studied system in our subset of the InvaCost database, with 1,509 expanded entries (Fig. 2). Invasive species categorized as impacting semi-aquatic habitats were the second most damaging (US$ 292.85 billion, *n* = 178). Habitats that contained entries of unknown or mixed systems ("diverse/unspecified") were the third most costly (US$ 272.35 billion, *n* = 85). While invasive species impacting aquatic habitats had the second highest number of entries in our robust database (*n* = 350), they had the lowest costs (US$ 14.69 billion).

Within North America, the agricultural activity sector was the most impacted group, incurring US$ 527.07 billion in costs (*n* = 309; Table 1). The second highest costs were recorded in the authorities-stakeholders sector (US$ 45.01 billion, *n* = 979). Next was the environmental sector with US$ 41.93 billion in costs with 114 entries in our database. The forestry sector incurred US$ 34.93 billion in costs (*n* = 18). Costs associated with public and social welfare sectors were US$ 41.07 billion (*n* = 158), and health costs were US$ 19.49 billion (*n* = 78). Fisheries had the lowest economic costs in our database (US$ 924 million, *n* = 45). Costs related to sectors that were classified as either "mixed" or "unspecified" also had large economic costs (US$ 94.99 billion, *n* = 326; US$ 449.86 billion, *n* = 95, respectively).

Damage costs far outweighed either management costs or mixed costs within North America. We estimated that the North American region-wide cost for direct damage by invasive species is approximately US$ 837.09 billion (*n* = 690). Our database recorded almost twice as many management costs within North America (*n* = 1,273) compared to direct damage, yet the measured costs of management were approximately 11% that of direct damage costs (US$ 99.52 billion).

On average, from 1960 to 2017 invasive species cost the North American economy US$ 21.64 billion per year. Annual costs increased from approximately US$ 2.13 billion per year in the 1960s to at least US$ 26.26 billion per year in the 2010s (Fig. 3). However, our estimates in the decade that spans 2010–2017 are likely extremely conservative for two reasons. First, the number of robust data entries from the current

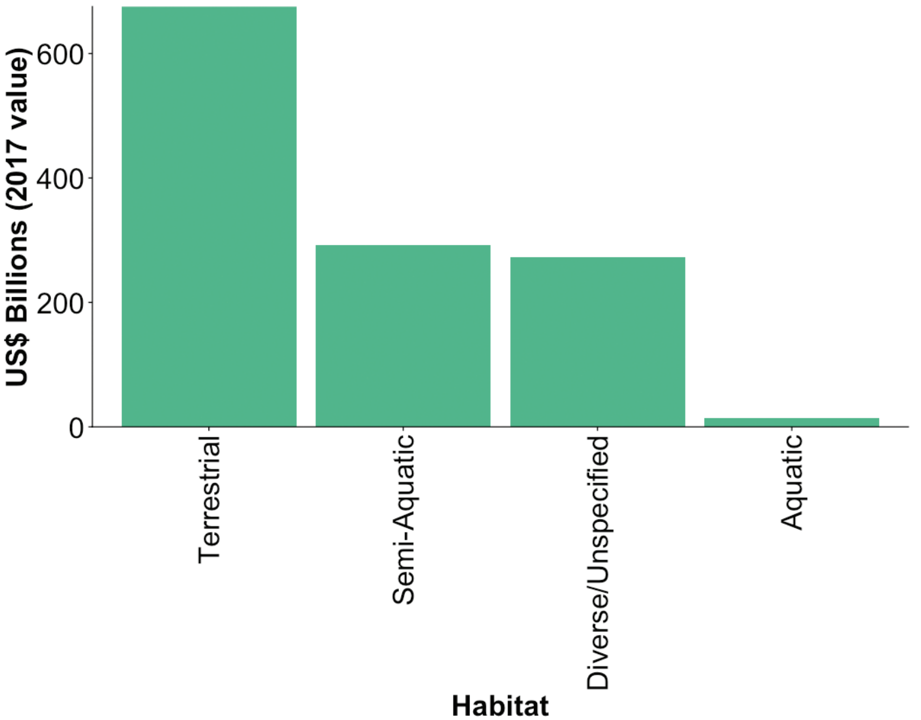

Figure 2. Cost estimates for impacts of invasive species within North America across impacted environments.

Table 1. Reported cost impacts to activity sectors of the North American economy. Numbers of entries are shown in parentheses.

Sector	Cost (in US$ billions)
Agriculture (n = 309)	527.07
Unspecified (n = 95)	449.86
Mixed (n = 326)	94.99
Authorities-stakeholders (n = 979)	45.01
Environment (n = 114)	41.93
Public and social welfare (n = 158)	41.07
Forestry (n = 18)	34.93
Health (n = 78)	19.49
Fisheries (n = 45)	0.92

decade should grow before this decade's end. Second, time lags between occurrence of costs and when the costs are reported may lead to underestimates of economic burdens by invasions for more recent years.

Linkage with CABI and sTwist

There were a large number of species known to be established within North America from the sTwist database that were not present within our robust dataset (161 species

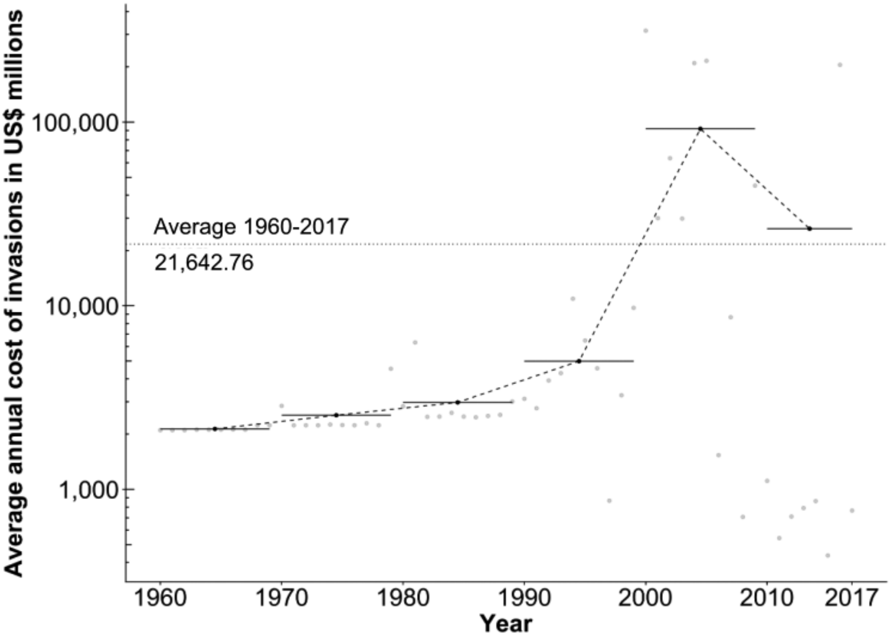

Figure 3. Annual robust costs of invasive species to the North American economy from 1960–2017. Each gray dot represents total annual costs and horizontal lines are decadal averages of economic costs. The dotted line represents the average over the entire period.

or species complexes vs. 305 species reported within sTwist). Establishment dates were unknown in at least one country within the robust dataset (final box in Fig. 1) for 27 of these known established species. Approximately one quarter of establishments were known to have taken place after 1970 (*n* = 113 species-country combinations). The largest discrepancies between sTwist and InvaCost appear to exist for Cuba (Suppl. material 2: Fig. S1, InvaCost 5% complete) and the Dominican Republic (3% complete), while the lowest appears to be for Mexico (75% complete). Canada and the US have an intermediate level of completeness (both 45% complete). When a species was listed in both databases, the total area of the countries over which it was recorded within InvaCost was 96% of the total area of the known set of established countries within sTwist. Of the species within our robust subset that had at least one known date of establishment listed within sTwist (*n* = 12), they averaged 2.7 independent establishments within North America (i.e., not due to secondary spread). There were 145 species within our robust subset where no information on establishment means was present. If we assume that the 161 identified species or species complexes (i.e., not "diverse/unspecified") within our robust subset have caused similar average damages throughout their invaded ranges as defined by sTwist, the total damages incurred within the region due to these species jumps from US$ 353 to 396 billion.

North American InvaCost species have known native ranges spanning all continents outside of Oceania and Antarctica (Fig. 4; S2, *n* = 86). Many species have unknown regions of origin (red flows in Suppl. material 2: Fig. S2a), while many

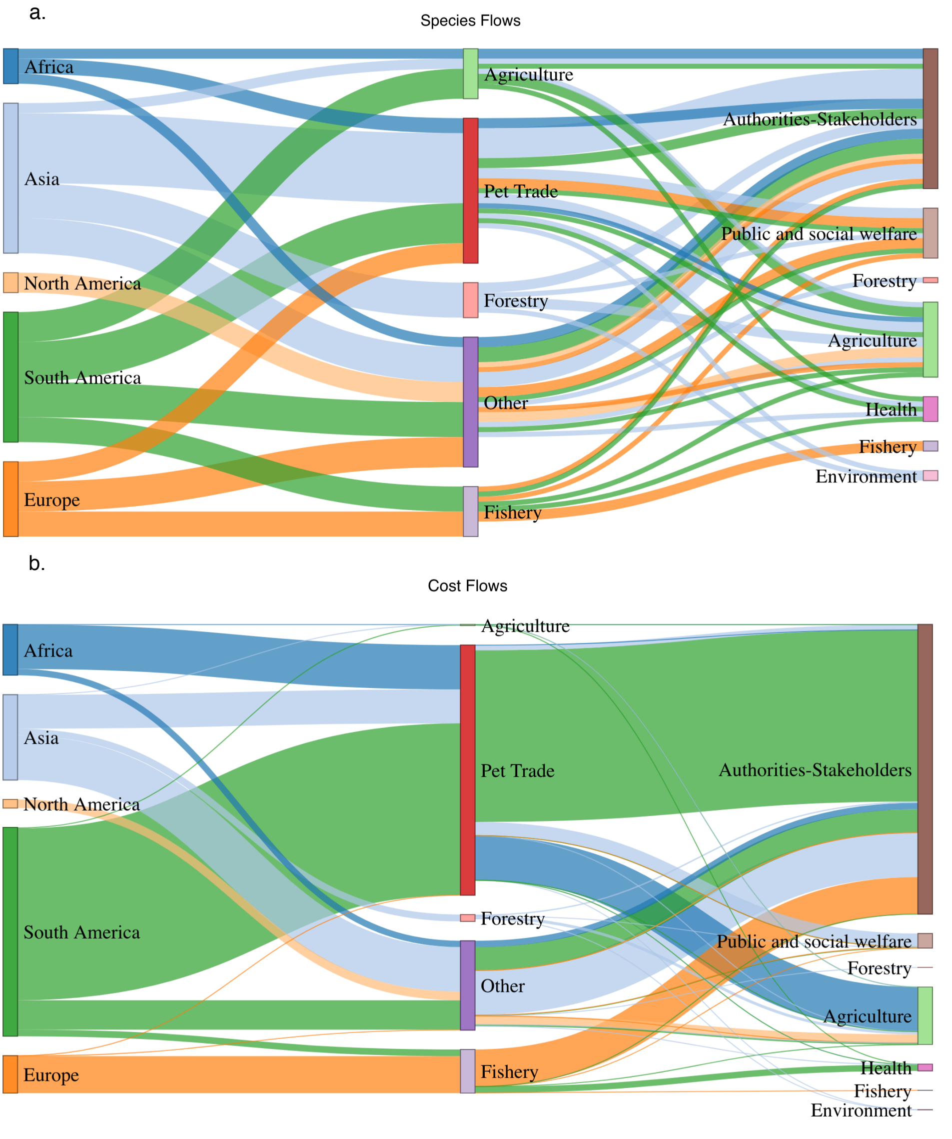

Figure 4. Flows from pathways of entry to impacted sectors proportional to **a** the number of species originating from each continent, and **b** the costs incurred estimated from our robust dataset (2017 US$). Originating nodes and colored flows in this diagram correspond to the continent of origin of each species when available from CABI. The center node labels correspond to dominant entry pathways characterized by CABI (n = 86 species with pathway information), while the destination node labels correspond to impacted sectors within the robust dataset. See Suppl. material 2: Fig. S2 for a more complete examination of flows, including diverse and unknown continents of origin, and impacts to multiple or unspecified sectors.

others possess native ranges spanning multiple continents (dark orange flows in Suppl. material 2: Fig. S2a). Asian, South American and European species have been reported more frequently than North American and African species. The majority of all species have entered via pathways beyond those in Suppl. material 2: Table S2 (mostly via unknown pathways, n = 73; but also pathways such as hitchhiking, n = 15; and escape from gardens or confinement, n = 22). Within the focal pathways we examined, the pet trade was the largest contributor of invaders (n = 66, Fig. 4a), followed by agriculture (n = 24) and fisheries (n = 20). Forestry was the source of a smaller share of invaders, and only one of the invaders was introduced for health purposes. The spread of regions of origin was quite mixed within all pathways. North American species (light orange flows) have been spread primarily via diverse pathways, while Asian species (light blue flows) have been frequently introduced via the pet trade pathway, and have mostly impacted the authorities-stakeholders sector.

When we analyzed invasional flows in terms of costs rather than numbers of species (Fig. 4b; Suppl. material 2: Fig. S2b), the dominant flows were far less complex. The largest costs were due to species with an unknown native range (Suppl. material 2: Fig. S2b), and pet trade and fisheries pathways were the main pathways of introduction that led to costs (Fig. 4b, Suppl. material 2: Fig. S2b). Of species with a known native range, South American species (dark green flows) have dominated the influx of costs from the pet trade pathway (Fig. 4b), and European species (dark orange flows) have done the same for the fisheries pathway, Asian natives have primarily entered via pet trade and diverse pathways (Fig. 4b). Where sectors could be disentangled, South American species (dark green flows) make up a substantial portion of the costs to the authorities-stakeholders sector (Fig. 4b). Asian and European natives also impact this sector to a lesser degree. The small number of African invaders have mostly impacted the agriculture sector after entry via the pet trade pathway. While the small share of North American invaders mentioned previously have produced small costs, they make up a notable share of the costs to the agriculture sector.

Discussion

We show that invasive species cost the North American economy at least US$ 1.26 trillion from 1960–2017. The highest costs from specified taxonomic groups were associated with invasive vertebrates, costs were greatest in the US even when scaled by the number of cost sources, and costs impacting the terrestrial ecosystem were higher than those impacting other habitats. We also found that the agricultural sector bore the largest economic costs across North America, and that yearly costs have been increasing from approximately US$ 2 billion per year in the 1960s to over US$ 26 billion per year in the 2010s. Our robust dataset excluded US$ 1.92 trillion in costs that were classified as having low reliability or predicted costs; when we relax the constraints of our robust dataset, our full dataset suggests costs exceed US$ 3 trillion.

Our analysis of economic impacts of different taxonomic groups suggests that the largest economic impacts come from entries in our database that assigned costs to multiple invasive species (“diverse” entries; US$ 845.21 billion). This finding emphasizes that researchers, when providing economic cost data for invasive species impacts, should provide finer-scale information about their study system (e.g., taxa, impacted sector, years, and habitat) so that further data integration is possible (Diagne et al. 2020b). Besides this rather broad taxonomic category, we showed vertebrates had the highest reported economic impact, in contrast to other reviews that focused on the ecological impacts of invasive species, which indicate that plants are the most studied taxonomic group (Pyšek et al. 2008; Crystal-Ornelas and Lockwood 2020). The discrepancy between our findings for economic impacts and that of ecological-impact syntheses may be due to a lack of taxonomic granularity we mentioned above, or could be due to discrepancies between the species that are studied for their ecological impacts and those that are studied for their economic impacts (Jeschke et al. 2014).

Even when controlling for the number of cost sources produced by each country in our database, invasion costs in the US far outweighed other countries within North America (US$ 5.81 billion in costs per source in the US). However, costs in other countries, scaled by the number of cost sources were still large (e.g., US$ 57.01 million per cost source in Cuba), despite a low sample size (n = 6, including non-English cost sources). Furthermore, costs in North America as a whole were substantially higher than other geographic regions, including Africa (Diagne et al. 2021b), Asia (Liu et al. 2021), Europe (Haubrock et al. 2021) and South America (Heringer et al. 2021). National-scale differences within North America indicate that the low magnitude of reported costs for some countries are either a result of the entrenched geographical biases in invasion ecology (Pyšek et al. 2008; Bellard and Jeschke 2016; Crystal-Ornelas and Lockwood 2020; Angulo et al. 2021a) and more broadly in ecology (Nuñez and Pauchard 2010; Martin et al. 2012; Nuñez et al. 2019), or that they reflect actual differences in invasion histories and international trade that promote opportunities for introduction and potential economic impacts. Cuba and the Dominican Republic have similar numbers of records in sTwist compared to Mexico, but Mexico has many more records within our robust (both observed and highly reliable) dataset (Rico-Sánchez et al. 2021), suggesting that our cost underestimation is greater in Cuba and the Dominican Republic. Further, while the US has roughly twice as many InvaCost records compared to Canada, it has more than four times the number of sTwist records. This suggests the 30-fold difference in economic impact between the US and Canada derived from InvaCost could be a substantial underestimate of the difference in total cost to each nation (i.e., an even more important underestimation of costs in Canada). Last, despite the presence of known damaging invaders, our robust subset of InvaCost included no reports of economic costs in Jamaica.

Only one species (of 161) within the robust dataset is known to be established in all 5 countries (*Columba livia*), and none have cost records in each country. However, three other species are predicted to have region-wide distributions in the more complete sTwist database (*Cyprinus carpio*, *Passer domesticus*, *Phasianus colchicus*). If we assume that *C. livia* has the same average costs across the entire North American region, its total estimated costs jump from US$ 2.95 billion to US$ 6.7 billion.

The most economically impacted habitat within North America was the terrestrial system, and this may be driven by the high economic costs associated with agriculture and forestry sectors within North America. This concurs with other predictions that the US would experience massive agricultural, and therefore terrestrial, costs from invasive species (Paini et al. 2016). We note that a substantial amount of impact (US$ 272.35 billion) was attributed to habitats that could not be classified into a single category ("diverse/unspecified" in our database), suggesting that a non-negligible portion of reported costs was not clearly associated with specific information for this descriptor. Fisheries showed the lowest amount of economic impact (US$ 924 million), although this sector was important in individual countries such as Mexico (Rico-Sánchez et al. 2021). This was likely due to the relatively low number of expanded entries (*n* = 45), since studies across the continent suggest invasions can have negative impacts on fisheries (Walsh et al. 2016), even if some studies do not directly quantify the economic costs (Dunlop et al. 2019). Furthermore, many impacts to fisheries are extrapolated due to the difficulties in quantifying damages in submerged habitats, and thus were excluded largely from our analyses. More broadly within InvaCost, impacts from aquatic invaders have been found to be several times lower than from terrestrial taxa, and disproportionately low relative to known numbers of alien taxa between those habitats worldwide (Cuthbert et al. 2021a). Such a low degree of cost reporting in aquatic realms may reflect a lack of human assets in those systems, or reflect a wider bias in ecology towards terrestrial ecosystems (Menge et al. 2009).

We found that direct damage costs were much higher than management costs (US$ 837.09 billion and US$ 99.52 billion, respectively). This pattern is consistent with global findings (Diagne et al. 2020b, 2021a), although some individual countries presented the opposite pattern (e.g. Spain, Ecuador or Japan; Angulo et al. 2021b; Ballesteros-Mejia et al. 2021; Watari et al. 2021). Previous research suggests rapid intervention (Leung et al. 2005; Simberloff et al. 2013; Ahmed et al. 2021) can potentially offset greater direct damage costs in the future, and we may be seeing patterns of this trade-off where locations incurring higher damage costs spend less on management. Moreover, management costs are relatively easier to track and reliably quantify, so this may be why our database contains nearly twice as many entries for management as it does for damages.

Given that invasion rates have increased over the past 200 years (Seebens et al. 2017), we predicted that the economic costs of invasions would follow the same trend from 1960–2017. Whilst this expectation held true, we highlight that the dip in economic costs from 2010–2017 compared to the previous decade is likely due to a lag between when costs are incurred and when the costs are reported, such that the most recent years in the database (2010–2017) have fewer entries (*n* = 224 [28/year]) than the previous decade (2000–2009, *n* = 401 [40/year]). We also suggest that invasion debt is an important concept for tracking economic costs of invasions over time. Research on invasion debt suggests that some of the most ecologically impactful species in the early 2000s had arrived in the early 1900s (Essl et al. 2011). It follows, then, that the species having the most severe economic impacts to North American sectors and habitats at the present time may be more reflective of socioeconomic conditions decades ago, and that the present socioeconomic conditions may result in a new suite of species having different economic impacts. Indeed, invasion costs have been found to be significantly positively related to the length of time an alien species has been present (Cuthbert et al. 2021b). This particular analysis should be updated when additional reliable cost estimates from 2010–2019 are available.

Most North American invasive species have not been assessed for economic impacts, and often, invasive species cause impacts that are non-market in nature (Hanley and Roberts 2019; Diagne et al. 2020a). We accept that not all invasive species will have a measurable economic impact, with many affecting non-market sectors that are difficult to monetize. Nonetheless, the considerable difference between sTwist and the species recorded for North America in our dataset is surely yet another indication that the overall cost estimated here is a huge underestimation of the real cost, as we suspect that many of the species causing non-market impacts could be missed by both our dataset and sTwist. The set of species recorded within sTwist alone remains quite data poor, as establishment dates are unknown in at least one country within the North American invaded range for the majority of these species, indicating that they are poorly studied. The remaining discrepancy does not appear to be due to a large number of pre-colonial invaders within sTwist (which are not considered invasive by InvaCost), as only 21 records are from before 1800. Instead, the difference may be due to lags between initial detection and economic impact (Coutts et al. 2018). Roughly one quarter of the sTwist establishment records correspond to establishments after 1970, placing them well within previously identified lag periods (Essl et al. 2011). While some of these more contemporary invaders may already be causing substantial ecological and/or economic impacts, the worst costs may only be incurred in the next 50 years or more, and/or they may have yet to have their impacts measured by researchers. Canada appears to have benefitted from more consistent effort in detecting invasive species over time, potentially leading to better detection of subsequent damages, while the other countries have seen an increase in detection in more recent years, potentially indicating a greater likelihood of lags in damage detection.

Economically-damaging invaders to North America come from all over the world and have been introduced due to a variety of pathways. As expected, the pet trade, agriculture, and fisheries pathways have led to the invasion of many species (Aizen et al. 2018; Stringham and Lockwood 2018), but less well-examined pathways have also led to substantial costs. Invasive North American natives have produced detectable, but nevertheless small, costs within the region. In contrast, several species are reported to have invaded North America repeatedly. This suggests that countries within the region are at risk to the same suites of species, and may benefit from increasing information sharing on potential threat species (e.g., through initiatives such as the proposed North America Multilateral Invasive Species Project Inventory). To date, the greatest threats are from species native to South America and Asia, particularly those entering via the pet trade and diverse pathways, as they are the source of a disproportionate amount of the costs incurred.

Syntheses like ours are limited in scope by the available knowledge base from which we constructed our database. Other factors related to climate change or the importance of global trade routes make it difficult to predict the sectors and habitats that will bear costs in the future (Bradshaw et al. 2016). Moreover, economic impacts for most invasive species are still yet to be quantified, and a 2010 review suggested that economic impacts were recorded for only 13% of the known invasive species in Europe (Vilà et al. 2010). This is an underestimate compared to our analysis of completeness relative to sTwist (~50% complete), but we note that species may be missing from both databases. We also stress that while the costs for Canada, Mexico, and Cuba were substantial, the number of entries in our database were small compared to those of the US, without any a priori reason to believe they reflect fewer actual costs. In summary, we present the first estimate of how much invasive species cost the North American economy, and our estimate of over US$ 1 trillion is likely very conservative. Building more robust economic assessments of invasion impacts in these countries will make for even more accurate, and likely higher, cost estimates for North America.

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Supplementary material 1

Supplementary file. Dataset of the costs of biological invasions in North America.

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Data type: table

Explanation note: This supplementary file contains the cost estimates from the InvaCost database that were used to estimate invasion costs in North America. The spreadsheet 'full_dataset' shows cost information for invasions across all of North America. The 'robust_dataset' spreadsheet shows the filtered dataset used for the analyses in our manuscript. The 'field_description' spreadsheet provides definitions for each column name in the InvaCost database. The spreadsheet 'field_classifications' shows the different categories available for each field in the InvaCost database.

Link: https://doi.org/10.3897/neobiota.67.58038.suppl1

Supplementary material 2

Tables S1, S2 and Figures S1, S2

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Data type: table and figures

Explanation note: **Table S1.** Classification of the types of costs ("Type of cost" column in the InvaCost database) into "damage" (economic losses due to direct and/or indirect impacts of invaders), "management" (monetary resources allocated to mitigate the spread and/or impacts of invaders), or "mixed" (when costs correspond both previous categories simultaneously). We assigned unspecified when the nature of cost was not defined. **Table S2.** Search terms used to match invasive species that have economic impacts in North America to pathways of introduction from CABI. **Figure S1.** Comparison of the timeline of establishment records of invasive species within the sTwist database (upper violin plots, black species counts) and records of species economic costs within our robust subset of InvaCost (lower violin plots, grey species counts) over time. **Figure S2.** Flows from pathways of entry to impacted sectors proportional to a) the number of species originating from each continent (including unknown and diverse origins), and b) to the costs incurred estimated from our robust dataset (2017 US$).

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