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Analysis

Unevenly distributed biological invasion costs among origin and recipient regions

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Abstract

Globalization challenges sustainability by intensifying the ecological and economic impacts of biological invasions. These impacts may be unevenly distributed worldwide, with costs disproportionately incurred by a few regions. We identify economic cost distributions of invasions among origin and recipient countries and continents and determine socio-economic and biodiversity-related predictors of cost dynamics. Using data filtered from the *InvaCost* database, which inevitably includes geographic biases in cost reporting, we found that recorded costly invasive alien species have originated from almost all regions, most frequently causing impacts to Europe. In terms of cost magnitude, reported monetary costs predominantly resulted from species with origins in Asia impacting North America. High reported cost linkages (flows) between species' native countries and their invaded countries were related to proxies of shared environments and shared trade history. This pattern can be partly attributed to the legacy of colonial expansion and trade patterns. The characterization of 'sender' and 'receiver' regions of invasive alien species and their associated cost can contribute to more sustainable economies and societies, while protecting biodiversity by informing biosecurity planning and the prioritization of control efforts across invasion routes.

Anthropogenic global changes challenge the conservation and sustainability of natural and economic systems [1]. Trends such as human population growth, intensifying international trade and travel, and growth of material transport networks may accelerate ecological, social, and economic impacts of environmentally destructive practices [2,3]. Consequently, future economic growth could be offset by a growing monetary burden attributable to global change [4,5]. However, these impacts may be unevenly distributed around the globe [6,7,8]. A potential decoupling between countries where costs originate and are incurred could hamper opportunities for sustainable development, particularly if developing economies are the most impacted [6].

Invasive alien species (IAS) — defined in a management context as species introduced outside their native range as a result of anthropogenic activity, and which have harmful effects — are among the main threats to biodiversity, biogeographic relationships and ecosystem functioning worldwide [3,9]. In addition to ecological impacts, the economic impacts of IAS and their related capacity to undermine human and social wellbeing are burgeoning [5,9]. IAS weaken progress towards many of the United Nations Sustainable Development Goals [10]. With rapidly growing invasion rates worldwide [8], the magnitude of these impacts is expected to increase further in the future [11]. While not all impacts can be easily monetized [12], prominent ones include costs to human healthcare systems, production enterprises (agriculture, fisheries, aquaculture, forestry), tourism and real estate, human-made infrastructures, and ecosystem services [9,13,14].

Recent syntheses of invasion costs have shown that reported costs of IAS vary hugely across geographic regions [5] (e.g., three orders of magnitude among European countries [15]). Regional variability in incurred costs is likely attributable, among other reasons, to the extent of connectivity to the rest of the world through trade and transport networks [2,16] differences in introduction pathways [17,18], the scale and type of economic activity [13], and any ecosystem resistance to invasions conferred by local biodiversity [19]. Additionally, factors such as research effort contribute to regional variability in *reported* costs [11], whilst publication language influences their inclusion in syntheses [20].

In our increasingly globalized world, sustainable development depends on understanding the interactions between geographically disparate human-natural systems [21]. In the context of biological invasions, this means understanding the flows of IAS and their effects among regions. However, research has tended to focus on IAS flows without extending their examination to resulting impacts [22,23]. There has been no research thus far that identifies sender and recipient regions, nor the structure and determinants of flows amongst them in the context of impacts caused by IAS. We focus on monetary impacts and define 'sender' regions as those from which IAS originate, and 'recipient' regions as those invaded and where costs occur. Note that sender regions are not necessarily responsible for the subsequent invasion and its impacts; rather, they are simply part of the native range of these IAS. For simplicity, we describe the costs associated with the movement of IAS from a particular origin to a recipient region as 'flows' (while we acknowledge that it is the IAS that flow), to emphasise the inherent linkage of species movement to cost dynamics.

An understanding of how impacts of globalization, and specifically costs of invasions, are distributed across space and time could contribute to sustainability in multiple ways. For example, it could identify regions that disproportionately suffer costs from invasions due to the uneven impact of trade activities with distant nations. Similarly, it can identify inequalities — such as continents, countries or other regions that are net receivers of IAS and their costs, or with low research capacity relative to the invasion pressure they face — that should be addressed to meet the Sustainable Development Goals (for instance Goal 10 [24]). It could also highlight opportunities for prioritized biosecurity actions, such as risk screenings for imported goods or early-warning surveillance systems for potentially costly IAS from specific origins. Identification of socio-economic and environmental predictors of invasion costs could also help to inform proactive management [25].

The *InvaCost* database (Supplementary Note 1) documents globally reported monetary costs of IAS. Notwithstanding known regional biases in the reporting of costs, it allows comparisons of standardized costs at taxonomic [11], sectoral [15], regional [15], and global levels [5]. To investigate the spatial distribution of senders and receivers of sustainability challenges triggered by invasions, we quantify the monetary burden within and flowing between sender and recipient regions (continents or countries). Specifically, we examine: (*i*) whether some continents or countries send or receive a disproportionate amount of economically costly IAS, and costs associated with those IAS; and (*ii*) whether socio-economic and environmental variables predict cost flows between country pairs.

Results

Continent-level patterns

Numbers of IAS sent and their reported costs were unevenly distributed across continents (Figure 1). Note that the same was true for reporting effort, and that our results should be interpreted with this in mind (Figure 1a). Together, the Northern continents (Europe, Asia and North America) both sent (67%) and received (66%) the majority of IAS. "IAS" here, and throughout the results, refers only to non-domesticated species, with costs in the *InvaCost* database, and for which we could identify ≥1 native continent or country (Figure 2, see Methods). The Northern continents also sent 82% and received 95% of the total reported invasion cost in our dataset ($467 billion from 459 IAS; all costs reported herein are in 2017 United States of America [USA] dollars). Our dataset did not contain any costs attributable to single species in Antarctica.

Asia sent the largest share of IAS (29%), followed by North America, Europe, South America, Africa, and Oceania (Figure 1b). Europe had the greatest share of IAS received (40%), followed by Oceania and North America. Other continents received under 10% of IAS. Asia sent three times more IAS than it received, while Africa, North America and South America were also net IAS senders. Both Europe and Oceania were net receivers of approximately three times more IAS than they sent. All continents received flows of IAS from all other continents, except for Asia, which did not receive IAS from Oceania (Figure 3a). There were particularly large flows from Asia and North America to Europe.

Compared to the pattern in the flow of IAS, the pattern of reported costs was more unevenly distributed among continents (Figure 1). Seventy percent of reported costs were sent by (that is, due to species native to) Asia and 13% by Africa, with the remaining continents each sending below 10% of total reported costs. Most reported costs were received in North America (82% of received costs, predominantly from Asia; Figure 2b, Extended Data Fig. 1), followed by Asia. The remaining continents each received 3% of reported total costs or less. Accordingly, most continents were net senders of costs (Figure 1c): Africa and Asia sent over seven times more costs than they received, while Europe and South America were also net cost senders, by about two-fold. Conversely, North America received 18 times more costs than it sent, and Oceania was also a net receiver by two-fold. As for species, reported costs flowed between all pairs of continents, except from Oceania to Asia (Figure 3b).

These regional patterns were similar when accounting for research effort (number of publications in our dataset) as a simple proxy for capacity to report IAS costs, although South America became a net receiver (Figure 1d). Furthermore, these patterns are relatively insensitive to additional data, as substantial increases in research effort would be required to override these results (446–1,446% to override the top sender and 729–5,267% to override the top receiver, Supplementary Table 1). While we do not focus on temporal trends, we note that across continents, species and reported costs (both raw and per publication) sent and received tended to increase over time (Supplementary Note 2; Extended Data Figures 2–4). Reported cost flows among continents according to cost types and activity sectors are shown in Supplementary Tables 2–3.

Country-level patterns

The country sending the most reported costs was China ($279 billion, $1.6 billion per publication reporting costs due to Chinese-native species; Figure 4a, Extended Data Fig. 5a), substantially exceeding other sender countries. The country receiving the most reported costs was the USA ($339 billion, $2.8 billion per publication reporting costs incurred in the USA; Figure 4b, Extended Data Fig. 5b), although second to Colombia when considering reported cost per publication ($3.3 billion). Several countries appeared as both top senders and receivers (China, Canada, Colombia, USA, Australia, Russia; Canada and USA only when considering reported cost per publication).

The strongest pairwise flow of reported IAS costs was from China to the USA, amounting to $275 billion, or 99% of the total reported cost from China to other countries (Figure 4c, Extended Data Fig. 5c). Six of the top 10 pairwise relationships included the USA at the receiving end (seven when corrected by research effort). South Africa was a top receiver of costs from Australia (for raw reported costs only), while Canada was a top receiver from China, and China was a top receiver from Brazil and Colombia (for both raw reported costs and cost per publication). The top 10 was very similar when considering cost flows per publication (Extended Data Fig. 5). Additional analyses including species without country-level origin information changed the top 10 receiver countries, resulting in several more entries from Asia (Supplementary Figure 1).

Of the 223 countries in our dataset, only 17 were net receivers (that is, reported costs incurred from IAS in these countries were greater than reported costs of IAS native to these countries). The largest net receivers were the USA ($335 billion), Canada ($10 billion), and the Philippines ($2 billion). There was at least one net receiver country on every inhabited continent. The other 206 countries were net senders (that is, reported costs of IAS native to these countries were greater than reported costs incurred from IAS in these countries); 143 of these sent costs without reporting any costs received whilst 63 both sent and received costs. The largest net senders were China ($274 billion), India ($23 billion) and Mexico ($4 billion).

Predictors of cost flows

A wide range of environmental and socio-economic variables were predictive of the value of cost flows between sender and receiver countries with differing effect sizes. Significant positive predictors of pairwise cost flows were: total reported cost sent (by sender country), latitude (of receiver country), country area (sender and receiver), and distance between countries, number of species involved, shared biome, common language, and shared colonial history. Significant negative predictors of pairwise cost flows were: research effort (in sender country), human population and road density (in receiver country), primary industry values added (in sender and receiver), and pairwise trade volume and presence of a free trade agreement (Figure 5). These effects were largely similar when accounting for research effort as cost per publication, and testing sensitivity to increased non-USA data and weighting of cost flows across multi-country origin regions (Supplementary Figures 3-6).

Discussion

Invasive alien species causing economic costs have originated from, and invaded all, inhabited continents globally. This worldwide problem challenges sustainable development and requires urgent international cooperation for effective mitigation. While known regional research biases underlie cost flows, particularly large numbers of IAS with reported costs have been sent from (that is, are native to) Asia and North America, and received in Europe and Oceania. Sender-recipient dynamics for reported costs have been dominated by Asia as the main sender and North America as the main receiver. Only 17 countries were net receivers of reported costs, with the USA dominant amongst these. It is notable that Asia sends a relatively large reported economic cost (5–70 times that of other continents) relative to the number of IAS it sends (only 1–4 times the other continents). Similarly, North America receives a far greater reported cost (8–54 times that of other continents) than would be expected given the number of IAS it receives (2–6 times the other continents). These patterns likely reflect a complex, interacting mixture of influences such as trade volume and direction, the identity of species sent and received, and publication language.

Trade and economic impact dynamics

While our cost data are recent (1960–2020), invasion dynamics can exhibit considerable lag times — often spanning many decades [26] — and so current sender-recipient dynamics likely reflect historical patterns of trade and colonialism [16]. Contrary to our expectations, cost flows were significantly negatively influenced by trade volumes in the 1990s and 2010a. However, many of the largest reported cost flows are between major contemporary trading partners. For instance, Asia’s share of global exports rose from 15% in the 1970s to 36% in 2010 [27]. For the USA, costs received from China and India were pervasive, perhaps reflecting import dominance from these rapidly developing economies over recent decades, driven by the USA’s consumption-based economy [28], flows of immigration for intentionally introduced invasive species [29], and/or regional cost reporting biases owing to underlying differences in research capacities among countries. Indeed, countries such as the

USA were both high net importers and received high costs, whereas China bore much lower reported invasion costs relative to trade (Extended Data Fig.6, Supplementary Note 3).

Cost flows displayed similarities and differences to global alien species flows. Invasion cost flows corroborate dominant plant movements from Asia and Europe to North America, for example [16]. Similarly, flows of alien reptiles have largely been from Asia and Africa to the Americas, but flows of alien amphibians have largely been between the Americas and within [30]. Alien aquatic macroinvertebrates in North America often originate from the Ponto-Caspian region in eastern Europe/western Asia [31]. As with alien species flows, bridgehead effects might distort direct economic impact flows between origin and recipient regions [23]. At the country level, our cost flows corroborate previous research highlighting the USA as the largest recipient of IAS, and China and India as the largest senders globally [32].

While previous studies have examined spread and establishment dynamics of IAS [2], they have fallen short at predicting impacts or in considering sender-recipient dynamics of these impacts. An increase in invasion rates and socio-economic impacts is expected to accompany future economic growth [2,15]. For example, Northeast Asia’s GDP is expected to increase 21-fold by 2050 [2]. These shifts could result in regions transitioning from net senders to receivers of costs, if they become more import-dominant. It is also probable that future changes in country-level research capacities to document biological invasion costs will influence the recorded dynamics of their senders and receivers.

Socio-economic and biological predictors of cost flows

Our cost flow results have clear implications for biodiversity conservation and policy. Previous studies have shown that invasion dynamics are shaped by importation volume and species richness [33], as well as national wealth and human population density [34], suggesting that unsustainable wealth generation and human population growth has contributed substantially to biological invasion rates. However, no previous studies have examined pairwise flows in the context of invasion impacts, despite the fact that IAS impacts are independent of invasion success [35].

We found greater cost flows between country pairs that share at least one biome, indicating that invasion impacts are greater at lower environmental distances. This finding supports the prioritisation of measures to limit propagule flow among regions of the greatest environmental similarity. In contrast, we found that cost flows were larger between physically distant countries, perhaps because physical distance increases the likelihood of ecological novelty and invasion impact. While demonstrated at the level of IAS establishment [19,33], we did not find support for biotic resistance influencing reported IAS economic costs, since species richness in the recipient country was not significant. Environmental drivers of IAS impacts may therefore be superseded by socio-economic factors.

We found lower pairwise cost flows into countries with larger human populations. We note that this does not necessarily discount high total costs in these areas, as in [33], if supplied by a greater number of sender countries. Although what may be driving this population trend remains unclear, it is possible that these countries may have more capacity to respond proactively to invasion risks, and/or may represent larger urban areas where both native biodiversity and heavily invasion-impacted industries, such as forestry and agriculture, are less prominent. Alternatively, it could reflect the influence of substantial human populations in emerging economies (such as India, Brazil, and China), whose export-driven trade patterns or lesser research capacities may limit the costs received and reported.

The number of IAS with costs sent and country surface areas were significant positive terms in our model, suggesting that future rises in invasion rates will drive higher costs and larger countries receive and send greater costs [15] — despite country area previously demonstrating no clear influence on the degree of invasion in recipient countries [33].

We found that wealth (proxied by gross capital formation) had a non-significant relationship with cost flows, while the values added by primary industries in sender and recipient countries were negative predictors. The negative relationship between value added and cost flow in both directions suggests that primary resource-producing countries are relatively less involved in IAS cost flows in general. Previous studies have found that GDP does not necessarily determine the degree of invasion at the national scale [33].

One might have expected recipient country road density and free trade to increase cost flows between countries, but we found the opposite result: high road densities and free trade agreements were associated with lower reported pairwise flows of IAS costs. This does not preclude there being higher total cost to these countries if they receive more pairwise flows. Alternatively, countries with lower road densities could incur greater cost flows if these represent more isolated, pristine regions that are vulnerable to IAS. Free trade agreements could be markers of greater surveillance and oversight capacity, which could reflect greater international cooperation to mitigate invasion impacts. This could ultimately reduce the number of unintentional invasions, and/or invasions by species known to have high economic impacts and therefore placed on blacklists or watch lists, leading to lower cost flows [18]. Alternatively, this finding could reflect the fact that wealthier countries have both higher numbers of free-trade agreements and greater invasion management capacity. Regions sharing trade agreements may have also had more historical invasions whose costs were incurred prior to 1960. The negative effect of 20th and 21st Century trade on cost flows additionally differs from the positive effect of historical trade on invasion success previously reported [26], although our earliest trade period (1995-1999) is relatively late in this century. Finally, we found more intense flows between countries that shared a language and colonial history. These may be a marker for human movements, such as colonialism and 19th or 20th Century trade, that have transported invasive propagules [36]. A more granular analysis of the role of such factors is an important area of future research.

Data gaps and caveats

It is important to highlight and caveat factors that may have strongly influenced the trends exhibited in the present study. We provide more detail on the following factors in Supplementary Note 4.

Firstly, *InvaCost* is dependent upon costs reported in original studies, and such reporting of economic costs of biological invasions is distributed highly unevenly geographically and taxonomically [5], and frequently lacks specificity. Indeed, costs in *InvaCost* are known to be skewed towards just a few well-studied taxa in certain places [5], with several hyper-costly species likely to disproportionately influence global trends and massive data gaps for other known damaging IAS [37]. Publication biases undoubtedly influence cost flows, whereby particularly high levels of reporting of impacts in North America could have emanated from relatively early efforts to report invasion costs in the USA, which prompted further research into the effects on the economy in the last two decades [38]. We aimed to address this descriptively and statistically by including research effort and number of IAS as individual terms across countries and regions. Hence, all environmental and socio-economic effects can be considered in the context of research effort and invasion rates, and are thereby over and above the strength of these terms. We also present reported costs corrected for research effort in our dataset. However, we caution that our proxies probably do not capture all aspects of regional capacities to report IAS and their impacts, and therefore our results are likely still influenced by differences in reporting capacity.

Secondly, publication language may influence perceived cost flows, where regions with greater reporting effort in common languages (English), such as North America, are better represented in our dataset. Although updates to *InvaCost* now include data in 21 non-English languages, regions such as Asia and Africa remain heavily underrepresented, with numerous countries having no costs in *InvaCost* [20]. Whilst our analyses accounting for research effort would have controlled for some of these biases, they could not account for entirely missing data.

Thirdly, purchasing power affects the cost of damage and management incurred by a region; all else being equal, regions with higher purchasing power (such as Asia, Europe, and North America) would inherently incur higher costs. Given this inherent bias and the probable link between lower economic output and research capacity, invasion costs from lower-income countries are likely particularly underestimated. Therefore, research investments in low-to-middle income nations should be promoted to bridge these gaps and support biosecurity.

Fourth, socio-cultural factors will also change the likelihood of invasion management in ways we cannot capture in this analysis. For instance, impacts on ecosystems and health are difficult to monetize, but are also a key motivator for management action [9]. Considering differences in research effort, it is likely that capacities to report costs from ecosystem-based impacts are particularly limited in countries with lower research capacities.

Fifth, we do not account for the many IAS of unknown origin, or for the precise invasion trajectory taken by each one. It is possible that IAS with costs in a receiver region did not originate directly from the species' native region, but rather from 'steppingstone' regions that had been already invaded [23,39]. This phenomenon challenges the precise attribution of economic cost sources, with invasions potentially caused by trade patterns that are spatially and temporally independent of the initial origin region and of direct trade between senders and receivers. It was impossible to account for this phenomenon in our analyses given the absence of information on invasion trajectories for most species.

Our results call for more systematic data reporting and collation — in particular, on species' native ranges, initial source populations of invasive propagules, invasion trajectories, invasion pathways, and invasion costs. Future extrapolation efforts could also help to resolve unreported costs. We highlight specific areas for focused research (for example, pathways and vectors involved in cost flows from China to the USA) to provide a basis for future predictions of how negative economic impacts from burgeoning biological invasions will unfold.

Outlook

This work can help promote international cooperation to mitigate economically damaging IAS. Our results should be considered in the context of uneven regional research efforts to report the impacts of IAS and should not be used to support unnecessary economic barriers among countries (such as from the Global South). Identification of major donor regions for costs nevertheless allows prioritisation of species sources in early warning systems to prevent future impacts, which complements pathway determination for informing management [18]. Our links among physical distance, socio-economic variables and IAS cost flows suggest that decreased reliance on distant resources in favour of developing local resources could decrease flows of costly IAS. Our results suggest that biosecurity efforts should be prioritized for trade between Asia and North America, and for trade linking several regions to Europe, but that research capacities should be improved to globally report invasion costs and inform on their impact dynamics. IAS economic cost considerations could become an additional factor to include in designing international trade treaties as well as legal frameworks and policy targets for biodiversity protections. Due to the cost and missed economic opportunities associated with decreasing exports, which may dissuade any individual nation from increasing their export-level restrictions, an international governing body for biosecurity may be better positioned to assess risks associated with global trade to decrease biological invasions.

Methods

Cost data and processing

We extracted cost data from the latest version of the *InvaCost* database (version 4.1, publicly available at 10.6084/m9.figshare.12668570 [20, 40]). *InvaCost* has been generated following a systematic, standardized methodology to collate invasion costs from peer-reviewed scientific articles, official reports, grey literature, and stakeholder and expert elicitation. Following a thorough and hierarchical screening of each source document for relevance, costs were extracted, standardized to a common currency (2017 USA dollars/US$), and adjusted for inflation through the Consumer Price Index (https://data.worldbank.org/indicator/FP.CPI.TOTL?end=2017&start=1960) to be comparable across space and over time [40]. Costs were categorized under a range of descriptive fields pertaining to the original source (such as title, authors, and publication year), spatial and temporal coverage (such as period of estimation and study area), cost estimation methodology (such as method reliability and acquisition method) and the cost estimates *per se* (such as nature and typology of cost relating to damage and/or management costs). Detailed information on all descriptive variables can be found in an online repository of the *InvaCost* database (https://doi.org/10.6084/m9.figshare.12668570, “Descriptors4.1.xlsx”).

Costs can occur over varying periods; for example, a one-off cost associated with a one-time eradication effort versus a multi-year cost associated with recurrent, annually estimated damages to crop production. To homogenize the temporal occurrence of these cost entries in the database, they were all converted to annual costs using the *expandYearlyCosts* function of the *invacost* R package [41]. This function provides annualized cost estimates for all entries, based upon the probable starting and ending years of the cost occurrence provided in the database ('Probable_starting_year_adjusted' and 'Probable_ending_year_adjusted' columns). For example, a single cost entry of $5,000 that occurred between 2000 and 2009 would be transformed to 10 entries following expansion, each amounting to $500 per year. Thereby, if costs are reported over a multiannual period, the total cost over that given period is divided by the number of years, resulting in an equal annual cost per year that does not inflate the overall cost. Accounting for these dimensions of costs also allowed for assessments of the dynamics of cost occurrence over time [41]. Furthermore, for this analysis, we considered costs with impact years between 1960 and 2020, given limited *InvaCost* data before 1960, and constraints on the availability of relevant socio-economic variables beyond this period (see *Predictor variables*).

We further considered species-specific cost entries only, thus excluding those for diverse (where costs were reported collectively for multiple taxa) or unspecific (where species-level information was missing) taxa, where 1,557 or 11.6% of entries were excluded (Supplementary Figure 1). Likewise, we removed costs reported in unspecified geographic regions (those that could not be attributed to any continents or countries) and blank cost entries. We additionally removed cost entries for disease agents (viruses, bacteria, and human pathogens) from the data, as these taxa are equivocally identified as alien, and we are typically more interested in the movement of their vector species. For example, invasive alien mosquitoes (*Aedes* spp.) would be included, while the viral diseases they vector (yellow fever, Zika, chikungunya, etc.) would be excluded. We also opted to use the most robust subset of these resulting data, by considering only costs that were of high method reliability (from peer-reviewed literature or other sources with documented, reproducible, and traceable methods) and empirically observed (costs actually incurred, rather than expected or predicted). Further, we removed cost entries at the ‘unit’ spatial scale (belonging to various minor scales below the site level, for example, per m^2). This scale has a higher likelihood of being duplicated with costs at larger geographic scales through nesting (for example, unit-level costs might be captured already in an overlapping site-level cost). Further, the total area over which these costs were incurred was variable and often unreported (for example, costs reported per m^2 without indicating the total size of the area impacted). These filters thus allowed us to consider costs (*i*) from individual IAS in defined recipient continents or nations, and for which regional origins could, in theory, be determined, *(ii*) that were actually incurred, reported, and estimated through “highly reliable” methods, and (*iii*) at appropriate, distinct spatial scales. The aforementioned filters, however, also mean our reported costs are underestimated and uneven due to reporting differences regionally. Unless specified differently, all results are provided for the filtered dataset, which represents 30.3% of all *InvaCost* records for continent-level analyses, and 27.2% of all records for country-level analysis (see *Species origins* and Figure 2 for more details).

Species origins

As a first step in determining species’ countries of origin, we employed a web scraping script to gather data from the *Centre for Agriculture and Bioscience International (CABI) Invasive Species Compendium* (ISC, www.cabi.org/isc), the *International Union for Conservation of Nature (IUCN) Global Invasive Species Database* (GISD, http://www.iucngisd.org/gisd/) and the *Global Biodiversity Information Facility* (GBIF, www.gbif.org) (see www.github.com/emmajhudgins/Givers_Takers for more information). CABI’s ISC contains a variety of information on IAS around the world, including their current distribution and countries of origin [18]. Our script searched using the species names as entered within *InvaCost* (harmonized using the GBIF.org Backbone Taxonomy; [40]) as well as synonyms in the *Integrated Taxonomic Information System* (ITIS) database via the `taxize` R package [42]. If a species match was found within the CABI ISC, we searched for a "Distribution Table" portion of the species entry. If found, we extracted country or region (within country) names tagged as "Native" within this table. GISD contains geographical information for many IAS and was used as an alternative to CABI where distributional data were missing. Our script searched for GISD distributional data points tagged as "Native" and compiled them at the country level. Finally, we checked for matching entries in GBIF — a global database of all types of species distribution — tagged as "Native" at the country level within the *occ_search* function of the `rgbif` package version 3.6.0 [43]. We used present day political border definitions for each country as defined by ISO3C codes in the `countrycode` package [44].

Next, where possible, we used country-scale origins to infer continental regions. Countries designated in *InvaCost* to be part of Central America were assigned to North America (and we refer to them henceforth as North America). Following *InvaCost* protocols, overseas territories were linked with the continent that matched their geographic, rather than political, designation. As exceptions, Turkey and Russia were identified as multi-continent sender and recipient countries. Origin continents within Turkey and Russia were selected on a case-by-case basis for each species, considering published data on the finer-scale distribution of each species within these countries as well as the continental designation of other countries listed (for example, if all other origin countries listed were European, we considered the native range to be European; see Supplementary Table 5 for details of species impacted). In these two country cases, we classified recipient regions based on human population, because of the role of humans in transporting IAS [45] and incurring economic impacts [15]. Since most of Turkey's population is in Asia and the majority of Russia's population is in Europe, we assigned them accordingly to these continents. As a third exception, China's Special Autonomous Regions (Hong Kong and Macau) and Taiwan were merged with mainland China due to them representing a much smaller landmass, as well as being strongly linked to China politically, economically, and geographically.

All origin assignments were checked manually by co-authors (where we ensured that there existed ≥ 1 reliable source[s] that agreed on the origin continent at least) or were entered for the first time when information was unavailable from GISD and CABI, using available literature and databases. Literature was identified through *ad hoc*, informal searches, so it is possible that some known native countries were missed. However, this is likely to be a small issue compared to the number of native countries that have never been identified in the literature. A list of literature sources used to check the species' origins is provided in Supplementary Note 5. Some species were allocated only to a continent of origin, due to the absence of country-level data (see later).

Origin information was identified for 467 unique species with cost records that met our aforementioned filters (high reliability, observed records within defined continents, cost incurred 1960–2020, non-pathogens). Of these, eight were removed due to a domesticated status (cat, *Felis catus*; dog/wolf, *Canis lupus*; sheep, *Ovis aries*; dromedary camel, *Camelus dromedarius*; pig, *Sus scrofa*; horse, *Equus caballus*; donkey, *Equus asinus*; and goat, *Capra hircus*; and with cow, *Bos taurus*; and ferret, *Mustela furo* having been removed by previous filters). This set of species does not have clear native ranges due to their long domestication and/or hybridization history. In contrast, we opted to retain species such as the European rabbit (*Oryctolagus cuniculus*) with a well-defined native range [46]. The remaining 459 unique species were recorded in six origin and recipient continents, amounting to 4,107 cost entries reported across 539 independent publications (expanded to 8,060 total entries; Figure 2).

When subset to entries with a country-level resolution, our dataset was further restricted to 412 unique species in 223 origin and 80 recipient countries, corresponding to 3,685 raw cost entries, 436 unique publications, and 7,112 expanded entries. Overseas territories were removed from this portion of the analysis because they lacked trade volume, GDP, and/or population data, which were implemented in models (see *Predictor variables*).

Impact distributions

Our analyses illustrate the distributions of both *(i)* numbers of IAS with costs and *(ii)* monetary costs, each among sender and recipient regions. Therefore, our analysis of IAS flows considers only those with reported costs in *InvaCost*. For *(ii)*, we further qualified the costs per region by dividing the total costs by the numbers of publications reporting them, as one way to account for research effort, in a separate analysis. For *(i)*, each species' contribution was divided by the number of origin regions known for the species and/or destination regions recorded in *InvaCost*. This ensured that each species' contribution summed to '1' in the total number of species sent or received [32]. For example, if a species was native to three countries and was reported to cause impacts to two countries in *InvaCost*, it would contribute a value of 0.33 species sent from each country and 0.5 species received to each country. We acknowledge that this may not be an accurate representation of the weight of particular origins of the invasion, but this information was unavailable given the complexity and changeability of pathways and vectors. For costs, when a single cost entry was reported in two or more geographic regions or countries, the cost was split equally among those recipient regions or countries. Similarly, if an IAS originated from two or more origin regions or countries, the aggregate cost from that IAS was split equally among those origin regions or countries.

Predictor variables

We separated our analysis by decade. Then, from *InvaCost* version 4.1, we generated a variety of predictor variables that we hypothesized would influence the magnitude of cost flow to and from different locations (where the cost flow from Region A to B refers to the costs of IAS in Region B that are due to native species from Region A). Firstly, we extracted the number of unique cost references associated with each receiving country in each decade, as a proxy for research effort (“Reference_ID” field in the *InvaCost* database). Secondly, we summed the total number of species involved in the cost flows between countries for each decade. Thirdly, we summed the total cost, incurred between 1960 and 2020, of IAS originating from each country.

Beyond these *InvaCost*-specific predictors, we employed several external variables hypothesized to influence the magnitude of cost flows due to biological invasions [47]. We extracted the total volume of imported goods (in metric tonnes) for each country pair from the *Centre d'Études Prospectives et d'Informations Internationales'* (CEPII) *Base pour l'Analyse du Commerce International* (BACI) database [48] for the years 1995–1999 inclusive and 2015–2019 inclusive, selecting the HS92 designation of harmonized import and export records (see Supplementary Table 6 example data from 10 pairs). We calculated the mean annual flow of goods between each country pair for the 1995–1999 period and dubbed this ‘historical trade’. Historical trade can be more predictive of present-day invasion risk due to invasion lags (see [47]), but we note that consistent import data are not available for the entire period of our cost data. The mean annual flows for 2015–2019 reflect recent trade (prior to the COVID-19 pandemic). To assess the role of origin and recipient biodiversity in dictating the flow of invasion impacts, we downloaded species richness data for each country from Mongabay, which tallies species richness for amphibian, bird, fish, mammal, reptile, and vascular plant species [49]. As a proxy for environmental matching, we identified countries that shared at least one terrestrial biome [50] and using data from *Global Administrative Areas* v3.6. We assume that country pairs sharing terrestrial biome(s) also share some freshwater and marine environments with similar conditions. Note that we also tested the effect of a shared climate zone variable, but the biome model had greater deviance explained. We also used the mean annual GDP and human population of each decade, and surface land area (reported in 2018, and measured in square km, including inland waters, but excluding marine Exclusive Economic Zones), tourism expenses (in 2022 US$), tourism receipts (in 2022 US$), agriculture, fisheries and forestry value added (in 2022 US$), gross capital formation (in 2022 US$), road density (km per 100 hectares), and percent of imports relating to food (as a percentage of all imports) from the World Bank using the `wbstats` R package [51], the latitude of each country from the `rworldmaps` R package [r52], and the distance between countries variable from the CEPII *GeoDist* database (calculated between two most populous cities), which has been previously employed to model invasional flows [2]. Based on [2], we also extracted information on common language (spoken by at least 9% of the population in each country), the existence of a free trade agreement between countries, and a shared colonial history (CEPII *Gravity* Database), and shared geographical borders (reported in [2]). To test whether cost flows could be predicted from the number of total IAS (with and without costs) that occur in a recipient region, we obtained data on IAS load per country from [32].

Missing predictor variable values were filled in with either the closest decade of available data or the mean of non-missing values when entirely missing (Supplementary Note 6). High levels of multicollinearity among variables led to the removal of GDP and tourism variables (collinear with gross capital formation and research effort) as well as gross capital formation in the receiving country (collinear with research effort), and the total IAS load per country (collinear with tourism, research effort, and recipient country area) from our model (all r>0.70) [53]. We considered human population and economic output instead of human population density and output *per capita*, because the qualifying variables (surface land area for human population and human population for output) were already included in the model. Moreover, ratio variables are well-known to cause spurious effects if there is a correlation between the denominator of the ratio and the response variable [54]. Our approach therefore allows for greater non-linearity and flexibility in considering these independent variables and their partial effects.

Statistical modelling

We built predictive models of the cost flow between each country pair for all complete (non-zero) flows recorded in *InvaCost* (Figure 2). To do this, we first summed our cost data within each decade and within each sender-recipient country combination, employing the `countrycode` R package [44] to ensure consistent country naming by converting all *InvaCost* country records to ISO3C codes. All models were fit as generalized additive models (GAMs) using the `mgcv` package [55], where all quantitative predictors and the cost flows (in millions of $) were logarithmically scaled. Decade was included as a thin-plate smoother term with five knots (a maximum of four inflection points in its functional form) to de-trend the cost flows for consistent variability in time. This variability could be due, for instance, to periods of global economic growth and decline. The 'numbers of species involved' predictor per cost flow controlled for the expected increase in IAS impacts due to a simple increase in IAS sent or received. Within each GAM, we employed the *select* method to avoid the overparameterization of our smoother terms. This method uses a cross-validation approach to penalize overfitted smoother terms (using the *GCV.Cp* method). All non-smoothed variables were $\log_e$-transformed prior to analysis to meet model assumptions, as determined by GAM model-checking results. Models were checked for high concurvity using the `mcgv` function *concurvity* (the GAM equivalent of multicollinearity; [55]), where 'worst case' concurvity values of >0.8 were taken to indicate model overfitting. Model residual and quantile-quantile plots were produced to check log-log model goodness-of-fit relative to an untransformed model (Supplementary Figures 7-8). Sensitivity to research effort was further tested by reanalyzing the model in terms of cost per publication associated with each pairwise country flow. Sensitivity of parameter relationships to high amounts of data from the USA was tested by adding 10%, 50%, and 100% more bootstrapped data rows from non-USA countries. Sensitivity to the assumption that sender costs were spread evenly across native range countries was tested by reweighting costs for species with multi-country native ranges by each native range country's wealth (acknowledging that this is not necessarily any more reflective of true sender dynamics than an equal split).

Data availability

The *InvaCost* database version 4.1 is available in the form of a publicly available repository at https://doi.org/10.6084/m9.figshare.12668570. All derived data have been archived on Zenodo https://doi.org/10.5281/zenodo.7778972.

Code availability

All code used for data analysis and producing figures has been archived on Zenodo https://doi.org/10.5281/zenodo.7778972

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Author Contributions Statement

Conceptualization: EJH; RNC; PJH; FC
Data screening: EJH; RNC; PJH; NGT; MK; DN; AB; AJT; DM; EB; SGK
Analysis: EJH; RNC; DN
Writing: EJH; RNC; PJH; FC; NGT; MK; AB
Editing: All authors
Figure creation: EJH; PJH; AJT; FC

Competing Interests Statement

The authors declare no competing interests.

Figure Legends

Figure 1. (a) Number of studies from each recipient continent published in *InvaCost* and retained in our filtered dataset, (b) number of IAS associated with reported costs, (c) reported monetary cost, and (d) average reported cost per publication associated with continent pairs, sent and received by each continent. Costs are in 2017 US$ millions. Percentages in panels (b–c) correspond to the share of the total per region. Base map is public domain, courtesy of Wikimedia Commons.

Figure 2. Workflow illustrating the cost filtering process from the *InvaCost* database to permit analyses. All icons are public domain, courtesy of Microsoft PowerPoint.

Figure 3. The (a) number of species associated with intercontinental reported cost flows and (b) reported cost of these species flows in 2017 US$ millions. Arrow thickness indicates the number of species in (a) and the magnitude of reported costs in (b). Arrows indicate species' known native ranges and final recipient regions of reported costs, and therefore do not necessarily indicate direct flows between continents. Base map is the intellectual property of Esri and its licensors and is used under license. Copyright © 2013 Esri and its licensors. All rights reserved.

Figure 4. Top 10 IAS cost sender countries (a), top 10 IAS cost receiver countries (b), and top 10 sender-receiver country pairs (c) in the *InvaCost* database. Costs correspond to total reported invasion impacts in 2017 US$ values of species native to a country across all receiving countries (a); total reported invasion costs per country attributable to individual species native to any other country (b); and reported invasion costs incurred per receiver country attributable to species native to the corresponding sender country (c). In (c), darker red hues indicate greater senders of costs, darker blue hues indicate greater receivers of costs, and blacker hues represent countries that both receive and send high costs. Countries are not to scale. Arrows indicate species' known native ranges and final recipient regions of costs and therefore do not

necessarily indicate direct flows between countries. Base map is the intellectual property of Esri and its licensors and is used under license. Copyright © 2013 Esri and its licensors. All rights reserved.

Figure 5. Variable importance in the GAM pairwise cost flow model for log-scaled country-level cost flows with log-scaled predictors, as measured by each parametric term's t-statistic (Supplementary Table 4). The smoother for Decade had empirical degrees of freedom of 3.40, and a p-value of <0.0001 (Supplementary Figure 6). The overall model had 26.2% deviance explained (n = 5362). The red line represents an effect of 0, and more significant positive effects are shown to the right of the plot while more significant negative effects are shown to the left of the plot, where log-log slope terms are shown in text on each bar. Log-log slopes are to be interpreted as the exponent of a power-law relationship, and therefore a doubled value of the associated predictor would result in 2^b times the cost flow, where b is the associated parameter estimate. Insignificant terms are shown in darker blue. All models displayed a 'worst-case' concurvity value below 0.8, indicating they were not overfit.

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