The ecological dimension of global trade: origin and recipient regions of biological invasion costs

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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. Here, we identify how invasion economic costs are distributed among origin and recipient regions at country and continent levels, and determine socio-economic and biodiversity-related predictors of invasion cost dynamics. Flows of invasive alien species causing costs originated from several regions, most frequently flowing to Europe, whereas monetary costs predominantly flowed from Asia to North America. High cost flows between countries were related to various environmental and socio-economic factors, such as shared biomes, high GDP and a common language. This characterization of 'sender' and 'receiver' regions of invasive alien species and their associated cost can inform biosecurity planning and the prioritization of control efforts across invasion routes, to achieve more sustainable economies and societies, while protecting biodiversity.

introduction

Ongoing anthropogenic global changes challenge the conservation and sustainability of natural and economic systems worldwide [1]. Trends such as human population growth, intensifying 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 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]. They undermine progress towards many of the United Nations Sustainable Development Goals [10]. With rapidly growing invasion rates worldwide [8, 1], 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, national 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 *recorded* costs [11], whilst publication language influences their inclusion in syntheses [20].

In our increasingly globalized world, sustainable development depends on understanding telecouplings: 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 between regions. However, research has tended to

focus on IAS flows without extending their examination to resulting impacts [22,23]. In particular, there has been no research thus far that identifies the composition and determinants of sender and recipient regions, and the flows amongst them, in the context of costs caused by IAS. We 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 to blame for the subsequent invasion and its impacts [24]; rather, they are simply part of the native range of these IAS.

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 or their costs — that should be addressed to meet the Sustainable Development Goals (for instance Goal 10 [25]). 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 [26].

The InvaCost database (Supplementary Note 1) documents economic costs of IAS reported globally. It allows for standardizing and comparing costs at taxonomic [11], sectoral [15], regional [27], 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 costs were unevenly distributed across continents (Figures 1). 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 (see Methods). The Northern continents also sent 82% and received 95% of the total invasion cost in our dataset ($467 billion from 459 IAS; all costs reported herein are in 2017 United States of America [USA] dollars). Our database did not contain any costs attributable to single species in Antarctica.

Asia sent the largest share of IAS (29%), followed by North America (25%), Europe (13%), South America (13%), Africa (13%) and Oceania (7%). Europe had the greatest share of IAS received (40%). Oceania ranked second in the number of IAS received (20%), followed by North America (17%), while 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 (Figure 1). 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 2). There were particularly large flows from Asia and North America to Europe.

Not all IAS bear the same economic cost. Compared to the pattern in the flow of IAS, the pattern of costs was more unevenly distributed among continents (Figure 1). Seventy percent of 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 costs. Most costs were received in North America (82% of received costs, predominantly from Asia; Figure 2), followed by Asia (10%). The remaining continents each received 3% of total costs or less. Accordingly, most continents were net senders of costs (Figure 1): 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, costs flowed between all pairs of continents, except from Oceania to Asia (Figure 2).

While we do not focus on temporal trends, we note that across continents, costs and species sent and received tended to increase over time (Supplementary Note 2; Supplementary Figures 1,2).

Country-level patterns

The country sending the most costs was China ($279 billion; Figure 3a), substantially exceeding other sender countries, and the country receiving the most costs was the USA ($339 billion; Figure 3b). Several countries appeared as both top receivers and senders (China, Canada, Colombia, USA, Australia, Russia). The costliest pairwise flow of IAS was from China to the USA, amounting to $275 billion, or 98.6% of the total cost from China to other countries, largely due to the invasion of the Formosan termite *Coptetermes formosanus* (Figure 3c). Six of the top ten pairwise relationships included the USA at the receiving end. South Africa was a top receiver of costs from Australia, while Canada was a top receiver from China, and China was a top receiver from Brazil and Colombia. Additional analyses including species without country-level origin information substantially changed the top ten receiver countries, resulting in several more entries from Asia (Supplementary Figure 4).

Of the 223 countries in our dataset, only 17 were net receivers (that is, costs incurred from IAS in these countries were greater than 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, costs of IAS native to these countries were greater than costs incurred from IAS in these countries); 143 of these sent costs without receiving any, 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

The country-level cost flow model indicated significant positive effects for the number of IAS, total cost sent by each country, recipient country area, presence of a shared biome across the two countries, presence of a common language, and gross domestic product (GDP) of the two countries (Figure 4, Supplementary Table 3). This model fits significant negative effects for the existence of a present-day free trade agreement between countries, the presence of a shared border between the countries, the distance between countries, the number of cost references included in InvaCost for the origin country, population size of the receiving country, and historical (1990s) trade volumes. In other words, countries *receiving* the highest costs had a larger area, higher GDP and smaller human populations. Countries responsible for *sending* large costs had a higher GDP, a smaller number of references in InvaCost, and tended to send a higher total cost across all their country partners. Cost flows between country pairs tended to be higher when they shared biomes or common languages or were

geographically close, but lower when they had a free trade agreement, shared a common border or had a trading history in the 1990s.

Discussion

Invasive alien species causing costs have originated from, and invaded all, inhabited continents globally. 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. Cost sender-recipient dynamics are dominated by one main sender continent (Asia, in particular China) and one main receiver continent (North America, in particular the USA). Previous studies identified both growing rates of biological invasions [11] and associated economic impacts in these regions [27] and globally [5], but did not consider differences in sender and recipient dynamics tied to costly IAS [22]. Only 17 individual countries were net receivers of costs, with the USA dominant amongst these. It is notable that Asia sends a relatively large economic cost (5–70 times that of other continents) for the number of IAS it sends (only 1–4 times the other continents). Similarly, North America receives a far greater 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, research effort and publication language. Given our modelling focus on individual cost flows rather than patterns of net costs, we can only speculate on these results.

Trade and economic impact dynamics

While our cost data come from recent decades (1960–2020), invasion dynamics can exhibit considerable lag times — often spanning many decades [28] — 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 from the 1990s. However, many of the largest 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 [29]. For the USA, costs received from China and India were pervasive, perhaps reflecting import dominance from these rapidly developing economies over recent decades [30], and/or due to flows of immigration for intentionally introduced invaders [31]. The presence of five common biomes likely underpins the cost flows from Australia to South Africa, however we also found strong historical trade links across these two countries (2.7 million kg/yr of imports 1995–1999 to Australia, ranking 3rd in South Africa's imports). Similar trade linkages exist from emerging South American countries, such as Brazil, to China (332 million kg/yr 2015–2019, ranking 2nd for Chinese imports, Supplementary Table 3). Given the fitted negative impact of historical trade volumes on cost flows, it is possible that other modelled predictors account for trading relationships, such as GDP and distance, while historical trade may be acting as a proxy for wealth (discussed below in relation to free trade agreements).

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 [2]. These shifts could result in regions transitioning from net senders to receivers of costs, as increased production leads to stronger export and ultimately to higher GDP, and greater GDP is in turn associated with cost incurrence (as found in this, and previous, studies [11]). Particularly, planned transport networks (such as China's Belt and Road Initiative; [32]; Arctic shipping routes; [33]) will make new species source pools available biogeographically to these and other

regions that could increase future invasion costs. Nevertheless, it is possible that such dismal future trends could be offset by the development of better proactive, prevention measures [34,35,36].

An additional consideration is that within these uneven dynamics, the stakeholders or countries which record the greatest IAS economic impacts may be separate from the parties which gain the most from trading arrangements. Indeed, even below our scale of analysis, while impacts can be incurred by many (for example, tax-paying citizens bearing management costs or a higher price of damaged agricultural goods), benefits are more likely to be accrued by few (for example, individual companies or stakeholders who benefit from the importation). This phenomenon of inequities in sender and receiver regions of sustainability challenges is common across contemporary environmental problems, including inequities in the production of greenhouse gases and impacts of related climate change [6-7].

Socio-economic and biological predictors of cost flows

Our cost flow model results have clear implications for biodiversity conservation and policy. 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 prioritization of measures to limit propagule flow among regions of the greatest environmental similarity. In contrast, we found that cost flows were lower between countries that shared borders, which could dampen the likelihood of ecological novelty owing to shared native ranges. Impactful invasions could be more likely to emanate from non-adjacent biogeographic regions, where communities lack shared eco-evolutionary history, up to a limit where environmental dissimilarity is too high [37], as captured in the negative distance term in our model. While it has been demonstrated at the level of IAS establishment [19], we did not find support for biotic resistance at the level of IAS economic costs, since species richness was not a significant predictor in our model. Somewhat surprisingly, costs from biological invasions largely flowed within northern continents, whereas highly biodiverse areas — mostly in the southern continents — have been posited to be key donor regions for damaging IAS [but see 38]. This suggests that ecological factors that mediate invasion success and impact could be superseded by human activities, such as those proxied by historical trade intensity.

We also found lower cost flows, all else being equal, into countries with larger human populations. We note that this does not necessarily discount low *per capita* costs in less populated 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) in our model, whose export-driven trade patterns may limit the costs received.

Our controls for biases yielded unexpected results. Contrary to expectations, we found a negative effect of research effort on cost flows from origin countries, possibly due to a relationship between research effort and increased understanding of mitigation tactics, as well as interest and financial/resource capacity to manage those invasions. Alternatively, it could reflect a shift in wealthier countries away from research funding to commerce.

Country-level GDP and recipient country surface area were significant positive terms in our model, suggesting countries with higher economic output are more likely to send and receive costs, and that larger countries receive

and report larger costs [15]. The greatest sources of costs sent tended to be wealthier countries (based on total GDP), implying that these countries could have the greatest capacity to reduce impacts if they were to take on more proactive approaches to invasion prevention in their exports. Further, this positive GDP effect could be an artefact based on better origin range data availability within wealthier countries. Given the inherent bias embedded in the reported costs from poorer countries, where infrastructure damage, management costs and salaries are valued lower, these costs are likely still underestimated. Overall, these results support the primary role of socio-economic factors as determinants of invasion costs [28].

One might have expected free trade to increase IAS flows between countries, but we found the opposite result: free trade agreements were associated with lower IAS costs. Free trade agreements could be markers of greater surveillance and oversight capacity, as well as greater international cooperation to mitigate invasion impacts. This could ultimately reduce the number of unintentional invasions, leading to lower costs [18]. Alternatively, since biosecurity policies only became commonplace in recent decades, this finding could reflect the fact that wealthier countries have both more free trade agreements and greater invasion management capacity, with our data largely concentrated in recent decades and subject to time lags. Regions sharing trade agreements may have also had more historical invasions whose costs were incurred prior to 1960. Finally, we found more intense flows between countries that shared a language, which may reflect greater access to IAS reporting between countries, and therefore to subsequent cost detection, but may also be a marker for human movements, such as tourism and 19th or 20th Century trade, that have transported invasive propagules. 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. Firstly, InvaCost is entirely dependent upon recorded 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 (for example, Formosan termite, yellow fever mosquito, *Aedes aegypti* and boll weevil, *Anthonomus grandis*) likely to disproportionately influence global trends, while indicating massive data gaps for other known damaging IAS [39]. Secondly, publication biases may influence cost flows, where regions with greater reporting effort in common languages (English) such as North America are better represented. 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]. 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. 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]. 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 'stepping stone' regions that had been already invaded [23,40]. This phenomenon challenges the precise attribution of economic cost sources, with invasions potentially caused by trade patterns spatio-temporally independent of the initial origin region. Finally, we are subject to the limitations and gaps of the various sources of species origin information we used for this analysis. We provide more detail on these factors in Supplementary Note 3. 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. 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 to focus biosecurity efforts and associated investments. Identification of major donor regions for costs allows prioritisation of species sources in early warning systems to prevent future impacts, which complements pathway determination for informing management [18]. Our link between shared borders, socio-economic variables and IAS cost flows suggests that decreased reliance on distant resources in favour of developing local resources could decrease flows of costly IAS. Our results suggest that increased biosecurity efforts for trade linking Asia and North America and for trade linking several regions to Europe are priorities to limit known economic impacts. IAS economic cost considerations could become an additional factor to include in designing international trade treaties. 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, 41]). 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 [41]. 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, 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 [42]. 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 ten entries following expansion, each amounting to $500 per year. Accounting for these dimensions of costs also allowed for assessments of the dynamics of cost occurrence over time [42]. 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. 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, human pathogens) from the data, as these taxa are equivocally identified as non-native, 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) because of the higher likelihood of double-counting with costs at larger geographic scales, and because 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 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.

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; [39]) as well as synonyms in the Integrated Taxonomic Information System (ITIS) database via the *taxize* R package [43]. 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 "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 [44]. We used present day political border definitions for each country as defined by ISO3C codes in the *countrycode* package [45].

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 transcontinental 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 3 for details of species impacted). In these two cases, we classified recipient regions based on human population, because of the role of humans in transporting IAS [46] 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 sources 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 4. 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 [47]. 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 5).

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 numbers of species with costs, 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. For example, if a species was native to three countries and was reported to cause impacts to two countries in all of 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 in a cost entry, 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 causing the impact 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 [48]. 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' BACI database [49] for the years 1995–1999 inclusive and 2015–2019 inclusive, selecting the HS92 designation of harmonized import and export records (see Supplementary Table 2 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 [48]), 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 [50]. As a proxy for environmental matching, we identified countries that shared at least one terrestrial biome using data from [51] and 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) from the World Bank using the *wbstats* R package, and the distance between countries variable from the Centre for Prospective Studies and International Information (CEPII) database (calculated between two most populous cities), which has been previously employed to model invasional flows [2]. From this same paper, we also extracted information on common language (spoken by at least 9% of the population in each country), shared geographical borders, the existence of a free trade agreement between countries, and a shared colonial history (CEPII GeoDist and Gravity Databases). Missing predictor variable values were filled in with either the closest decade of available data (372 missing sender country+decade pairs for GDP, one missing sender

country+decade pair for population), or the mean value of the predictor across data points where no information was unavailable (96 interpolated countries for sender species richness, 42 interpolated countries for recipient species richness, 131 missing country pairs for distance, and one missing sender country for GDP [Democratic People's Republic of Korea]). No pair of predictor variables was highly correlated (all $r < 0.80$), and thus all predictors were retained in the models.

Statistical modelling

We built predictive models of the cost flow between each country pair for all complete (non-zero) flows recorded in InvaCost (Fig. 5). To do this, we first summed our cost data within each decade and within each origin-recipient country combination, employing the *countrycode* R package [45] 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 [52], 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 with costs' 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; [52]), where 'worst case' concurvity values of >0.8 were taken to indicate model overfitting.

Declarations

Data availability

The InvaCost database version 4.1 is available in the form of a publicly available repository doi:10.6084/m9.figshare.12668570.

Code availability

All code and derived data are available at github.com/emmajhudgins/Givers_Takers, and will be archived in Zenodo with a DOI upon acceptance.

Author Contribution 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

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Competing interests

The authors declare no competing interests.

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Figures

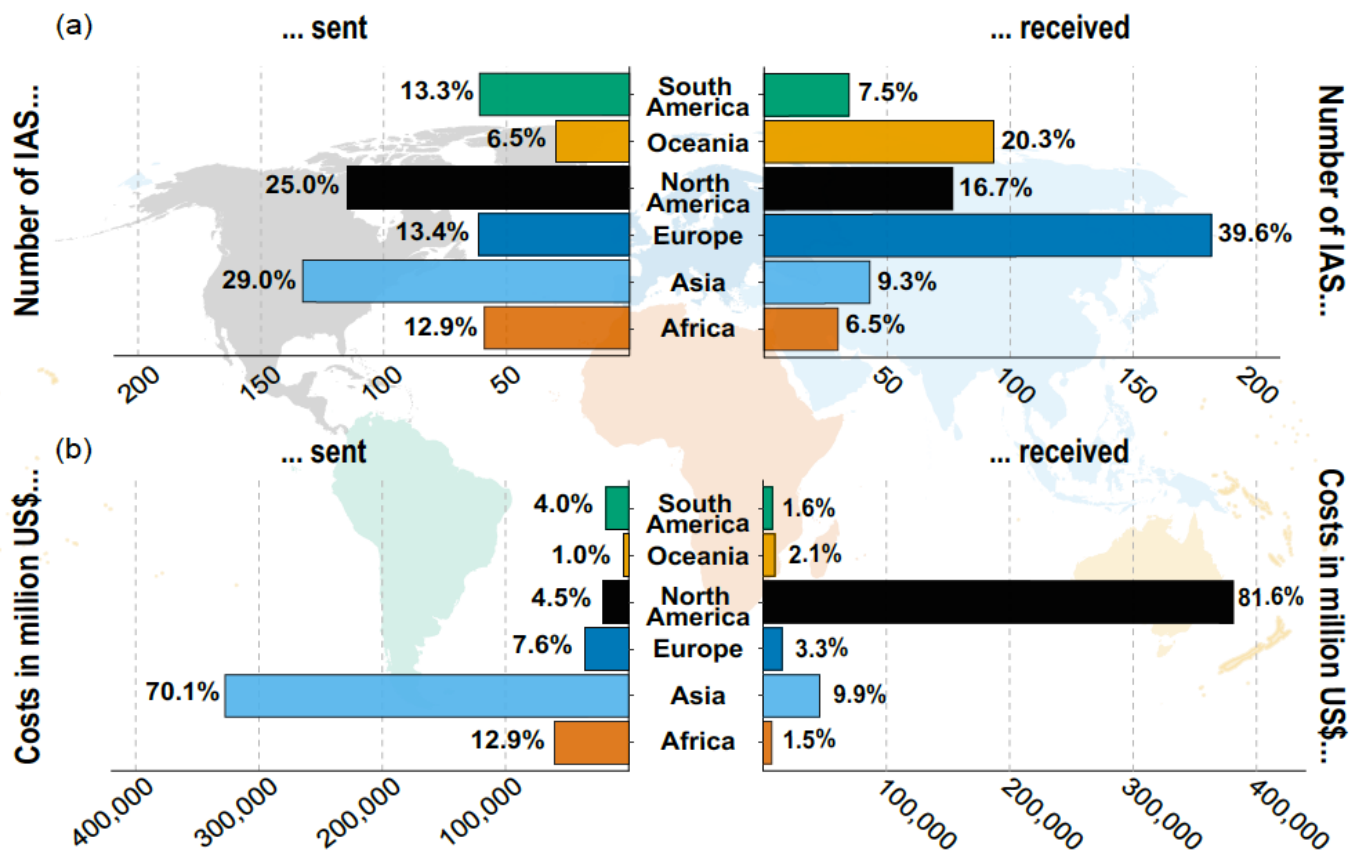

Figure 1

(a) Number of IAS associated with costs, and (b) monetary cost in 2017 US$ millions, sent and received by each continent. Percentages in each panel correspond to the share of the total per region.

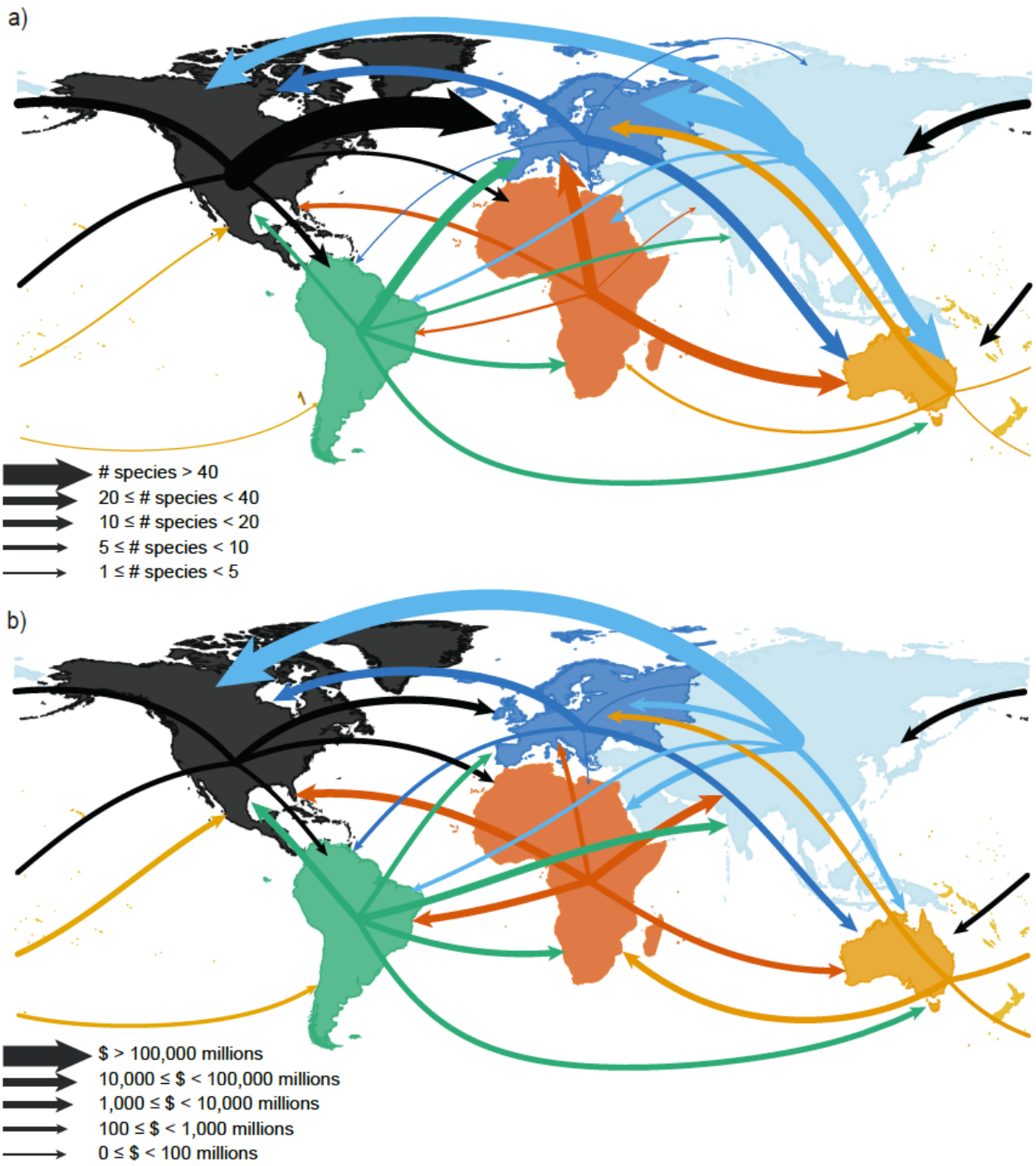

Figure 2

The (a) number of species associated with intercontinental cost flows and (b) cost of these species flows in 2017 US$ millions. Arrow thickness indicates the number of species in (a) and the magnitude of costs in (b). Arrows indicate species' known native ranges and final recipient regions of costs, and therefore do not necessarily indicate direct flows between continents.

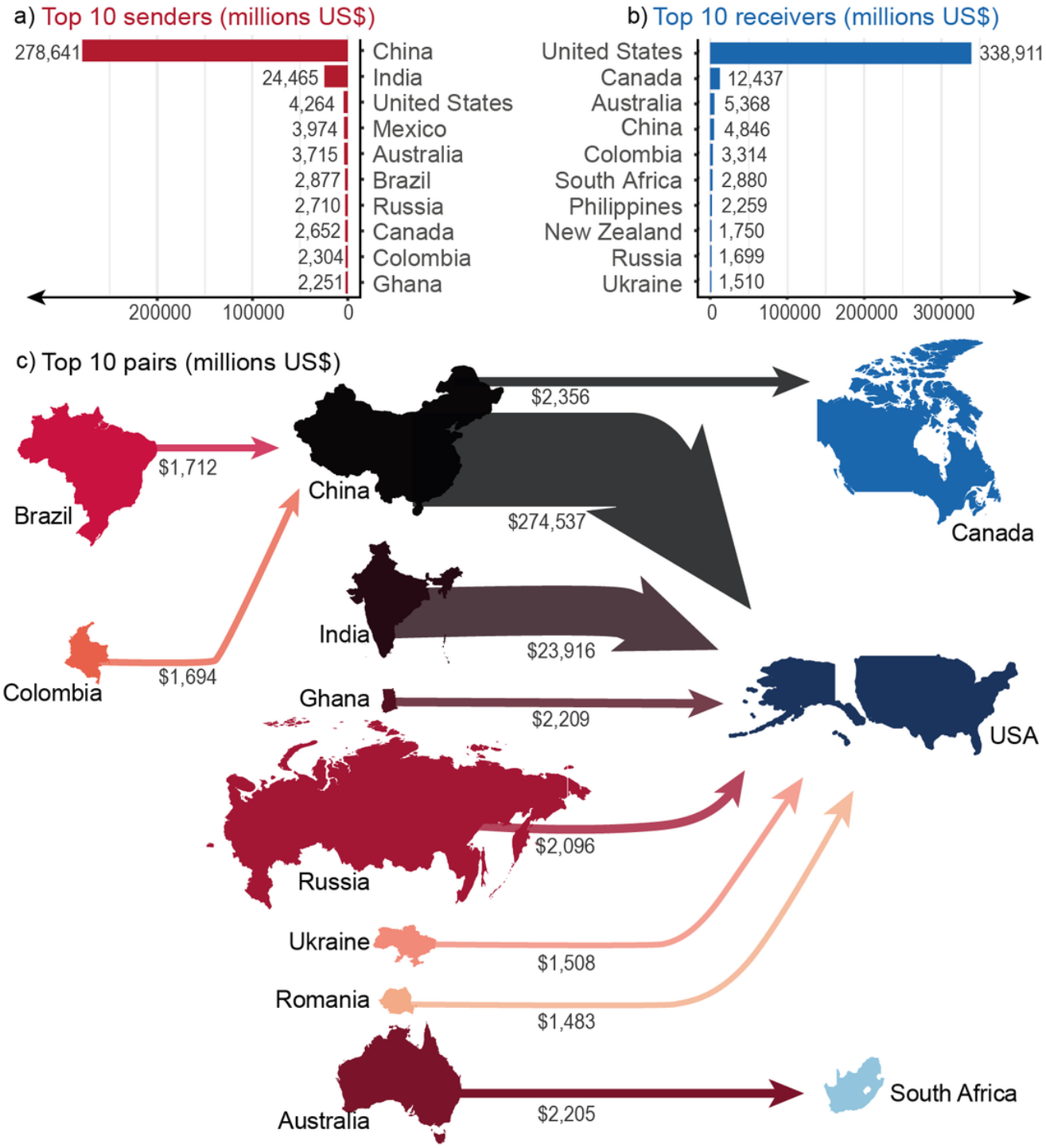

Figure 3

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 invasion impacts in 2017 US$ values of species native to a country across all receiving countries (a), total invasion costs per country attributable to individual species native to any other country (b), and 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.

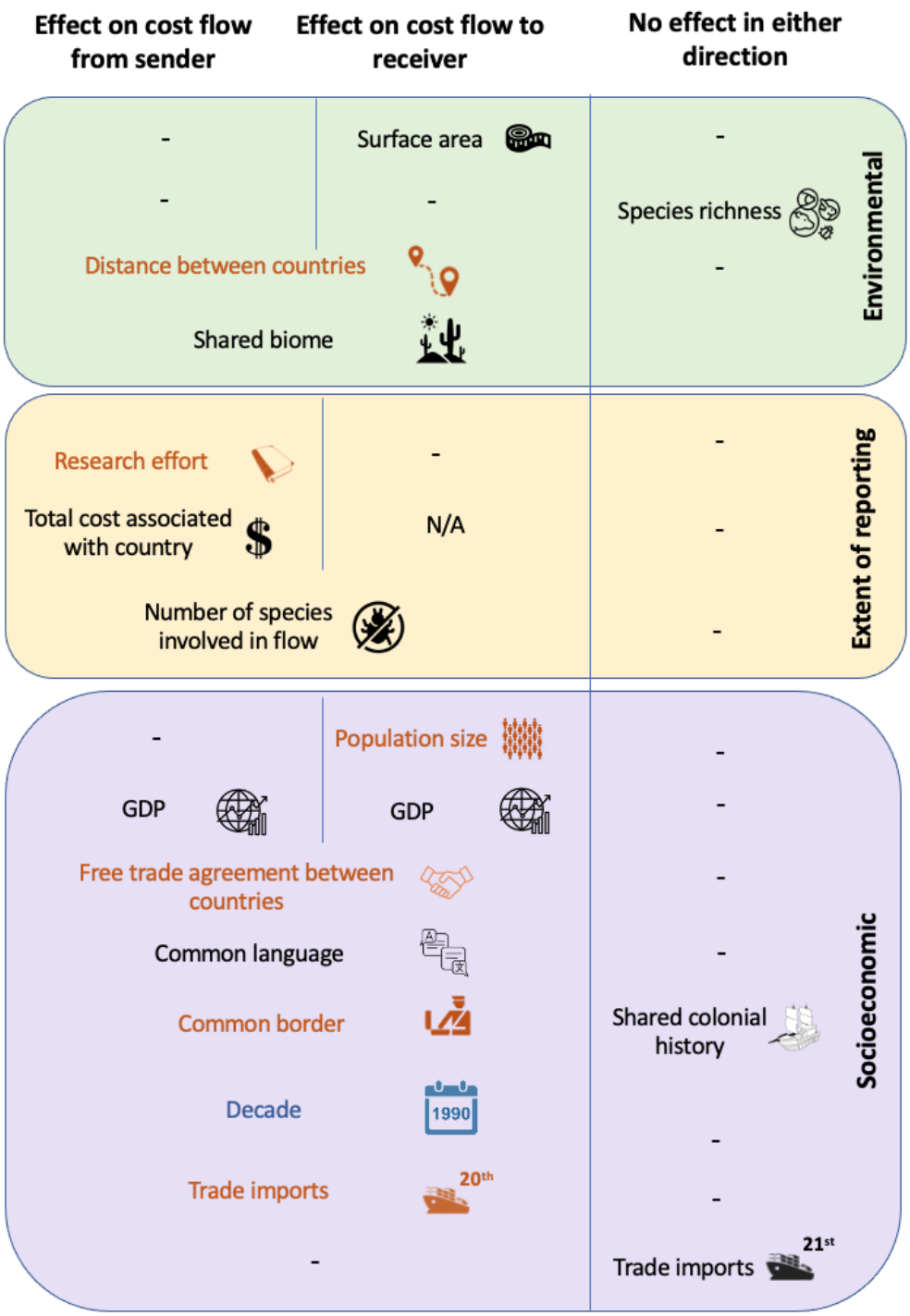

Figure 4

Results of GAM for log-scaled country-level cost flows with log-scaled predictors. The smoother for Decade had empirical degrees of freedom of 3.36, and a p-value of <0.0001 (Supplementary Figure 3). The overall model had 25.6% deviance explained (n = 5362). Black terms indicate significant positive effects, orange terms indicate significant negative effects, and blue terms indicate nonlinear effects. See Supplementary Table 3 for the complete list of estimates and associated p-values. All models displayed a 'worst-case' concurvity value below 0.8, indicating they were not overfit.

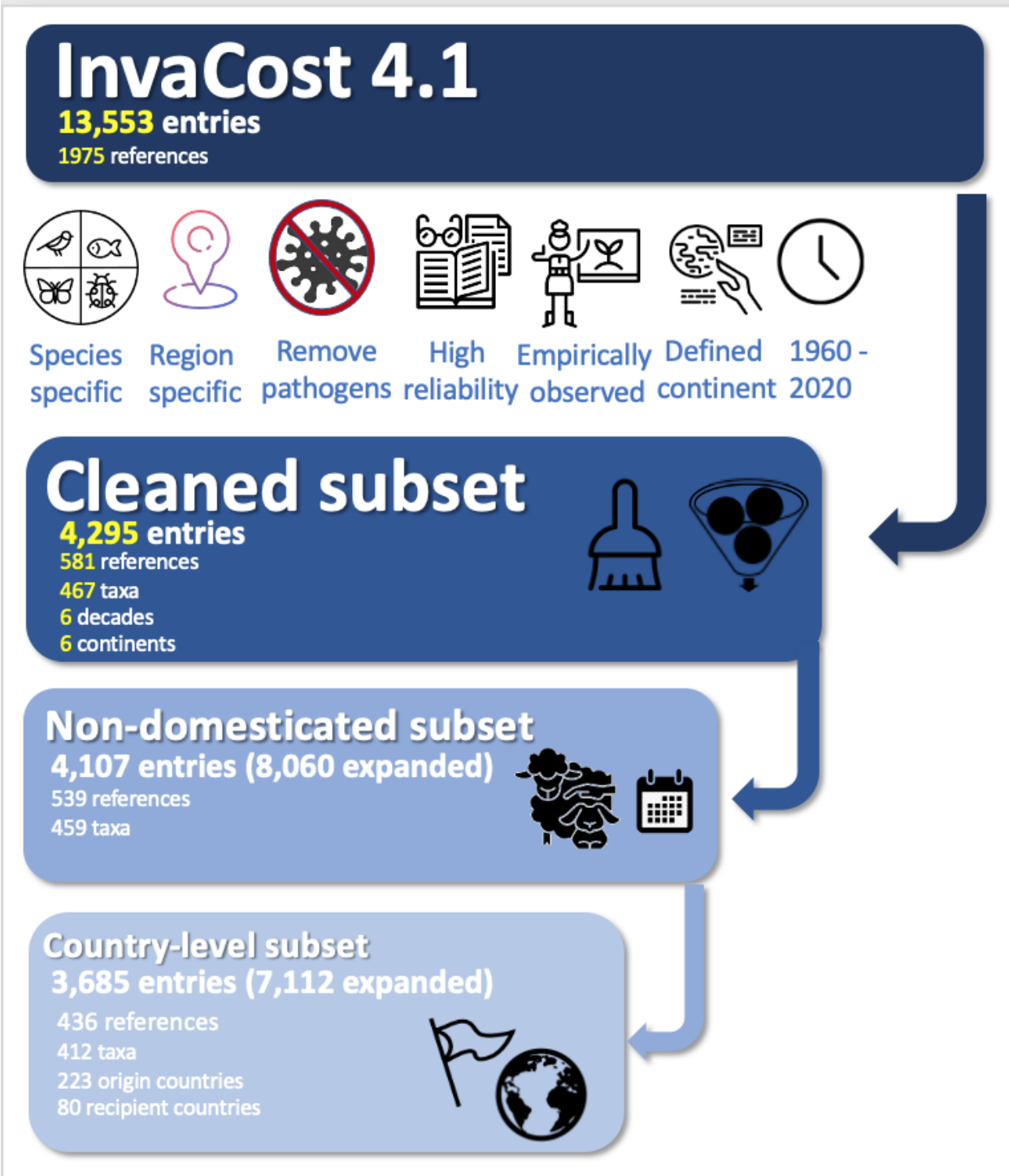

Figure 5

Workflow illustrating the cost filtering process from the InvaCost database to permit analyses.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryData.docx