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Introduction pathways of economically costly invasive alien species

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Abstract Introduction pathways play a pivotal role in the success of Invasive Alien Species (IAS)—the subset of alien species that have a negative environmental and/or socio-economic impact. Pathways refer to the fundamental processes that leads to the introduction of a species from one geographical location to another—marking the beginning of all alien species invasions. Increased knowledge of pathways is essential to help reduce the number of introductions and impacts of IAS and ultimately improve their management. Here we use the *InvaCost* database, a comprehensive repository on the global monetary impacts of IAS, combined with pathway data classified using the Convention on Biological Diversity (CBD) hierarchical classification and compiled from CABI Invasive Species Compendium, the Global Invasive Species Database (GISD) and the published literature to address five key points. Data were available for 478 individual IAS. For these, we found that both the total and annual average cost per species introduced through the 'Stowaway'

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(US$144.9bn; US$89.4m) and 'Contaminant' pathways (US$99.3bn; US$158.0m) were higher than species introduced primarily through the 'Escape' (US$87.4bn; US$25.4m) and 'Release' pathways (US$64.2bn; US$16.4m). Second, the recorded costs (both total and average) of species introduced unintentionally was higher than that from species introduced intentionally. Third, insects and mammals, respectively, accounted for the greatest proportion of the total cost of species introduced unintentionally and intentionally respectively, at least of the available records; 'Stowaway' had the highest recorded costs in Asia, Central America, North America and Diverse/Unspecified regions. Fourthly, the total cost of a species in a given location is not related to the year of first record of introduction, but time gaps might blur the true pattern. Finally, the total and average cost of IAS were not related to their number of introduction pathways. Although our findings are directly limited by the available data, they provide important material which can contribute to pathway priority measures, notably by complementing studies on pathways associated with ecologically harmful IAS. They also highlight the crucial need to fill the remaining data gaps—something that will be critical in prioritising limited management budgets to combat the current acceleration of species invasions.

Introduction

All alien species invasions begin with the intentional or accidental transportation of individuals or propagules by humans outside of their historical biogeographic boundaries (Blackburn et al. 2011; Lehan et al. 2013; Essl et al. 2015). Introduction pathways (henceforth 'pathways') refer to the fundamental processes that leads to the introduction of a species from

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one geographical location to another (Richardson et al. 2011). Consequently, pathways play a pivotal role in the success of Invasive Alien Species (IAS)—the subset of alien species that have a negative environmental and/or socio-economic impact—as they influence the number, frequency and geographic range of propagules dispersed (Pyšek et al. 2020; Gippet and Bertelsmeier, 2021). Increased knowledge of pathways is crucial to help reduce the movement and impacts of IAS (Leung et al. 2002; Essl et al. 2015) and ultimately improve their management (Simberloff and Rejmanek 2011; Novoa et al. 2020). In recent years, research and policy have focused on identifying and classifying pathways and prioritising which pathways to manage in order to prevent biological invasions. This was illustrated by the Strategic Plan for Biodiversity 2011–2020 (Target 9; Convention on Biological Diversity 2014; https://www.cbd.int/sp/targets/rationale/target-9/) in which parties aspired that *'by 2020, invasive alien species and pathways are identified and prioritized'*.

Many pathways have already been identified through assessments at regional levels and across ecosystems. These assessments help advance our understanding of IAS flows and support the development of policy tools (Hulme et al. 2008; Essl et al. 2015; Katsanevakis et al. 2013; Pyšek et al. 2011; Nunes et al. 2015; García-Berthou et al. 2005; Pergl et al. 2017). Global databases of IAS such as the IUCN's Global Invasive Species Database (GISD, www.iucngisd.org) and the CABI Invasive Species Compendium (CABI ISC, www.cabi.org/isc) list between 34 and 80 different pathways through which alien species can be introduced to new locations. Examples of pathways include horticulture (e.g. purple loosestrife, *Lythrum salicaria*; Maki and Galatowitsch 2004), agriculture (e.g. sisal hemp, *Agave sisalana;* Ortega et al. 2019), pet trade (e.g. Burmese python, *Python bivittatus*; Wilson et al. 2011) and biofouling (e.g. zebra mussel, *Dreissena polymorpha*; Carlton 2008). Such lists are neither exhaustive nor static; as societies evolve and economic activities continue to grow, and so more pathways are expected to emerge. To facilitate comparative studies on pathways, Hulme et al. (2008) proposed a pathway classification, which was further developed and subsequently adopted by the Convention on Biological Diversity (CBD, 2014). The CBD's hierarchical framework encompasses three levels; the first level is three broad mechanisms through which

species may arrive to a new location: movement of commodities, arrival of a transport vector, and/or natural spread from a neighbouring region. These three mechanisms then encompass six primary pathways (Hulme et al. 2008): 'Release' (intentional introduction as a commodity for release), 'Escape' (intentional introduction as a commodity but unintentional escape; includes the release of alien organisms from captivity), 'Contaminant' (unintentional introduction with a specific commodity), 'Stowaway' (unintentional introduction attached to or within a transport vector), 'Corridor' (unintentional introduction via human infrastructures linking previously unconnected regions), and 'Unaided' movement (unintentional introduction through natural dispersal of alien species across political borders). These six pathways are further divided into 44 subcategories, covering pathways applicable to alien species from a wide range of taxonomic groups and environments (Pergl et al. 2020) (Fig. 1).

Prioritizing the management of high-risk pathways is necessary to achieve cost-effective management of IAS, essentially by preventing additional introductions of species that have already been introduced as well as new harmful alien species (McGeoch et al. 2016). IAS can generate substantial costs in terms of damage to ecosystems, impacts on human well-being and expenditures on management (Diagne et al. 2021a). At the same time, there is evidence that investing in the prevention of IAS introduction (proactive management) is less costly—and likely more efficient—compared to allocating resources and funds to reactive management once they establish and become invasive (Leung et al. 2002; Ahmed et al., this Special Issue).

Pathways can be prioritized using (i) the number of IAS introduced per pathway and/or (ii) an assessment of the observed or potential impact caused by species introduced through different pathways (Essl et al. 2015; McGeoch et al. 2016). Studies investigating the number of species per pathway have found that, where pathway information had been deduced, movement of commodities was associated with the most documented introductions. Indeed, 'Escape' is identified as the most prevalent pathway for IAS (Faulkner et al. 2016; McGrannachan, et al. 2020), predominantly through horticulture trade (Turbelin et al. 2017) and the most important for plants and vertebrates (Saul et al. 2017). It is worth noting

that pathway information is still lacking for a number of IAS, particularly plant and invertebrate taxa (Faulkner et al. 2016). Other studies showed that invaders associated with a high number of pathways are more likely to have an ecological impact in newly invaded sites (Pergl et al. 2017; Saul et al. 2017). Particularly for plants, both the number and types of pathways may influence invasion success and the likelihood of impact (Pysek et al. 2011; Pergl et al. 2017). Plants introduced through 'Release', 'Corridor' and 'Unaided' pathways are more likely to have an ecological impact than when introduced as 'Contaminants' (Pergl et al. 2017). Plants introduced through these pathways are also more likely to successfully establish and be accepted in society when grown as animal food or for environmental uses (van Kleunen et al. 2020). Similarly, certain pathways may favor successful invaders, e.g. pet trade particularly favors invasive species (Gippet and Bertelsmeier, 2021).

Whilst a number of publications have examined the links between ecological impacts and pathways of IAS (e.g. Pergl et al. 2017; Saul et al. 2017), there are currently no studies assessing relationships between pathways and economic impacts of IAS. Although economic impact may overlook aspects of ecological impacts, it is a very useful metric of the impact of IAS, as it can be quantitative, and if costs are standardized, they can be compiled across regions or taxa and compared between pathways. A better understanding of the economic costs of invasions is also a key way to raise global awareness about IAS, optimise transboundary legislation and help the prioritisation of management actions (Diagne et al. 2020a).

In this paper, we investigate pathways of economically-harmful IAS using the most up-to-date compilation of monetary cost information on IAS—the *InvaCost* database (Diagne et al. 2020b) and pathway data classified using the CBD hierarchical classification (CBD, 2014; Hulme et al. 2008) and compiled from CABI ISC, the GISD and the published literature. Specifically, we address the following questions: (*i*) Have some introduction pathways facilitated the introduction of more economically costly species than others? (*ii*) Are there differences in costs between species introduced intentionally and unintentionally? (*iii*) How are costs taxonomically and spatially distributed across introduction pathways? (iv) Is there a relationship between the cost of species and the year of first record of introduction? and (*v*) Is there a
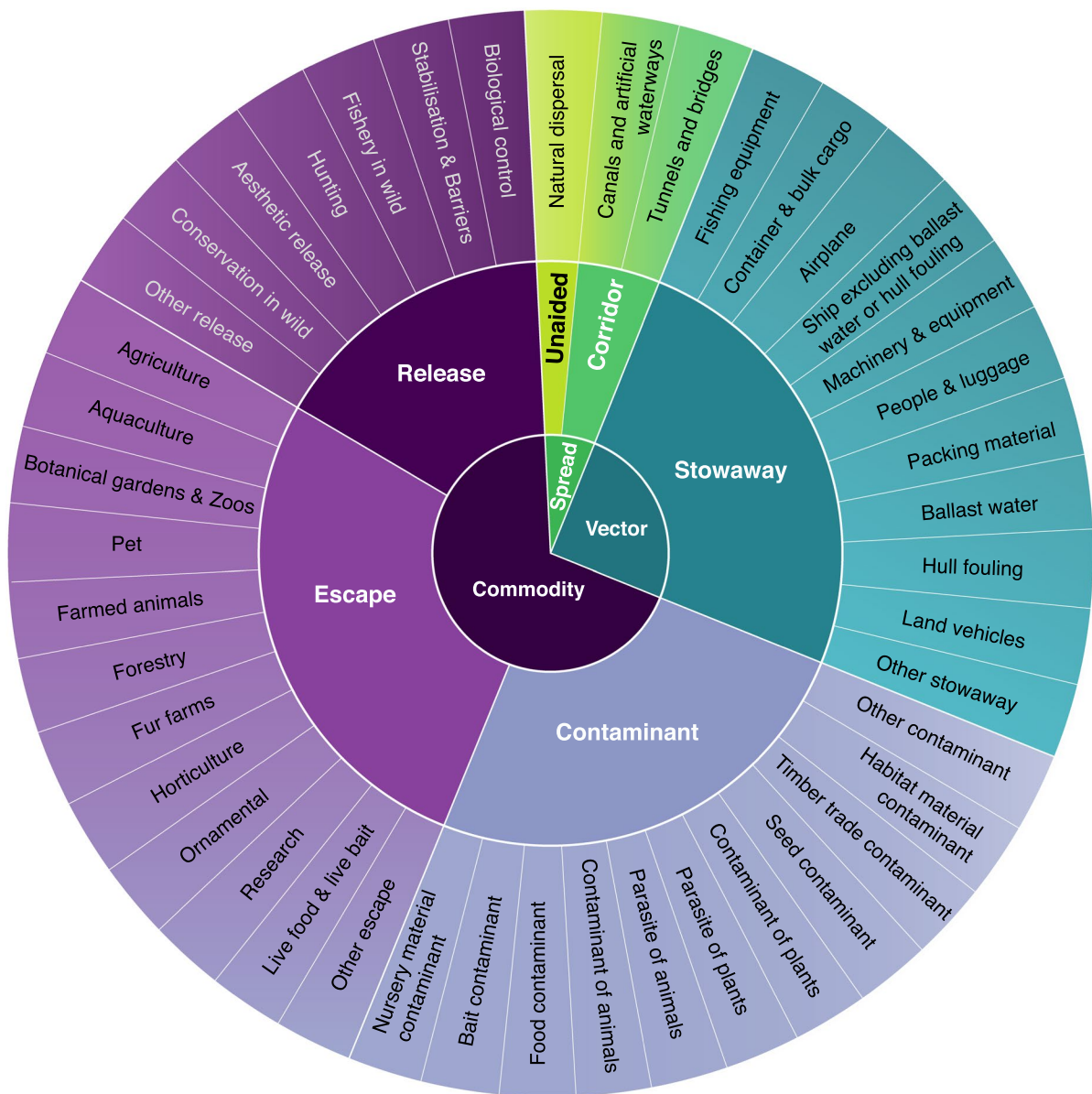
Fig. 1 Convention on Biological Diversity (CBD) pathway classification. This framework uses a hierarchical approach in which alien species may arrive in a new location through three broad mechanisms (i.e. movement of a commodity, arrival of a transport vector, or spread from a neighbouring region), 6 main pathways (i.e. release, escape, contaminant, stowaway, corridor, and unaided) and 44 pathway subcategories (e.g. ornamental, aquaculture, seed contaminant, etc.). Changes adopted from suggestions by Harrower et al. (2018) include the addition of 'Other contaminant' and the removal of 'Release in nature for use'. Figure adapted from Harrower et al. (2018). 'Intentional' pathways include 'Release' and 'Escape' and 'Unintentional' pathways include 'Contaminant', 'Stowaway', 'Corridor' and 'Unaided'

relationship between the number of possible introduction pathways of IAS and their costs?

Methods

Cost data collection and filtering

To assess the economic impact of IAS over the last 50 years (1970–2020), we relied on cost data recorded in the latest version of *InvaCost* (version 4.0, openly available at https://doi.org/10.6084/m9.figshare.12668570.v4), which is the most complete and up-to-date global dataset of the reported economic costs attributable to biological invasions (Diagne et al. 2020b). *InvaCost* has been built by a combination of both systematic literature searches (e.g., specific search strings used in Web of Science and Google Scholar) and direct solicitations (e.g., stakeholders, scientific experts) in more than 10 languages, to gather any cost information available in written documents. After ensuring the relevance of each document, cost information was collated, standardised to a common and up-to-date currency in the database (i.e. 2017 US dollars), and finally classified into categories using a range of descriptive fields (complete description and details on these descriptive fields are available at https://doi.org/10.6084/m9.figshare.12668570)(See Table 1 for a description of the fields used in this study). This updatable and publicly available resource contains 13,123 cost entries (as of June 2021), therefore providing an essential basis for worldwide research and policymaking targeting IAS (Diagne et al. 2020a; 2020b). The 'living' nature of the dataset allows for the taxonomic and geographic gaps in cost information to be addressed over time, and then keeps all users and stakeholders informed on cost dynamics and distribution (Diagne et al. 2021a).

We used successive filters from the *InvaCost* database to identify relevant cost entries for our analysis and obtain a conservative and realistic estimate of costs. First, we extracted costs empirically "observed" in the invaded environment and left out all "potential" costs (not yet actually realised but rather expected and/or predicted over time within or beyond their actual distribution area). Second, we then retained costs classified as "high" reliability—therefore discarding "low" reliability costs—thereby keeping only cost estimates either provided by officially pre-assessed documents (peer-reviewed articles

Table 1 Definition of fields from the InvaCost Database. Source: https://doi.org/10.6084/m9.figshare.12668570

Field	Definition
Method reliability (Method_reliability column)	Assessment of the methodological approach used for cost estimation as of (i) high reliability if either provided by officially pre-assessed materials (peer-reviewed articles and official reports) or the estimation method was documented, repeatable and/or traceable if provided by other grey literature, or (ii) low reliability if not
Implementation (Implementation *column*)	This states — at the time of the estimation — whether the reported cost was actually observed (i.e., cost actually incurred) or potential (i.e., not incurred but expected cost)
Cost type (Type_of_cost_merged column)	Categories of the Type of cost column reassigned into **damage** (economic losses due to direct and/or indirect impacts of invaders, such as yield loss, health injury, land alteration, infrastructure damage, or income reduction), **management** (monetary resources allocated to mitigate the spread or impacts of invaders, such as prevention, control, research, long-term management, eradication) or **mixed** (when costs included both 'damage' and 'management' components); every cost for which the exact nature of cost was not clearly defined was assigned to **unspecified**
Management type (*Management_type* column)	**Pre-invasion management** (monetary investments for preventing successful invasions in an area—including quarantine or border inspection, risk analyses, biosecurity management, etc.), **post-invasion management** (money spent for managing invasions in invaded areas—including control, eradication, containment), **knowledge/funding** (money allocated to all actions and operations that could be of interest at all steps of management at pre- and post-invasion stages—including administration, communication, education, research, etc.), or **mixed** was assigned when costs include at least (and without possibility to disentangle the specific proportion of) two of the previous categories; every cost for which the exact nature of cost was not clearly defined was assigned to **unspecified**. Every entry that has partly or fully associated with damage costs was assigned to **NA**
Geographic Region (*Geographic_region* column)	Geographical region(s) where the cost occurred (**Africa, Antarctic-Subantarctic, Asia, Central America, Europe, North America, Oceania, Pacific islands, South America**) In this analysis Oceania and Pacific islands are classified as one category: "Oceania / Pacific islands". Diverse/Unspecified is assigned when costs are incurred over multiple regions or the geographic location was not specified

and official reports) or associated with an estimation methodology that was deemed reproducible when building the database (Diagne et al. 2020b). Lastly, we focused on cost estimates exclusively attributed to individual species, therefore multi-species costs or genus-level costs were removed (e.g. when the value in the *Species* field included "sp." or "spp." or was simultaneously associated with several species without any possibility to disentangle specific contribution of each taxon to the overall cost). Following these filtering steps, our dataset (hereafter called *filtered_subset*) contained 7,175 entries (Supplementary Material 1). Finally, we extracted the list of individual species with recorded costs. After checking for discrepancies in species names (i.e., where entries for the same species have different scientific names, we opted for the internationally preferred scientific name as described in CABI), the number of individual species with cost records amounted to 606.

Collection and compilation of pathway information

Pathways were categorised using Harrower et al. (2018), a guidance document for interpreting the Convention on Biological Diversity (CBD, 2014) pathway classification framework (Fig. 1). This pathway classification system has limitations, especially regarding uncertainty linked to subcategories (Faulkner et al. 2016, 2020; Pergl et al. 2020), however McGrannachan et al. (2021) suggested that it is a reliable framework for reporting on IAS pathways at a global level. Pathway mechanisms and categories are defined, and subcategories are listed in Supplementary Material 2. We compiled pathway data for each of the 606 species with reported economic costs in our *filtered_subset* (Supplementary Material 3, which contains all columns hereafter mentioned) mainly using information from CABI ISC (www.cabi.org/isc/) and the GISD (http://www.iucngisd.org/gisd), resulting in a total of 478 species with information on their specific pathways. When the pathway information needed was not available in one of these repositories, we opportunistically extended our searches to other databases on biological invasions (e.g. the Galapagos Species Checklist), and performed targeted searches in the published literature. Pathway descriptions provided in databases or

publications were recorded, along with the source of the data (CABI ISC, GISD, etc.), in our pathways dataset. These descriptions do not always match the CBD pathway sub-categories. Each pathway description was initially matched to the CABI ISC pathway description and then classified into the mechanisms, categories, and subcategories of the CBD scheme using the published guidelines for the scheme (i.e. Harrower et al. 2018). Pathways were further classified into pathway types with 'Intentional' pathways including 'Release' and 'Escape' and 'Unintentional' pathways including 'Contaminant', 'Stowaway', 'Corridor' and 'Unaided'.

As stated by Harrower et al. (2018; p.88): "*Moreover, the pathway category assigned to a species is typically the pathway(s) that relates directly to the species being introduced. However, the introduction of a species may also be indirectly dependent on another pathway, particularly when the species is contaminant of another species or product. Although these dependent pathways are not directly related to the species they play a part in understanding the process of introduction and are, therefore, important for decision-making and particularly in relation to prevention through management of pathways. As these dependent pathways are important they should be recorded, but as they are not directly related to the species it is important they are not confused with the pathway information that directly relates to the species.*" As such, to highlight pathway dependency, we classified pathways as 'Direct' or 'Indirect' to indicate whether the pathway was related directly to the species being introduced (*Direct*) or when the pathway was related to a species or product that the species being introduced is dependent upon (*Indirect*) (*Direct_or_Indirect* column).

Finally, as IAS can have multiple pathways, we determined the most important pathways for each species and classified each pathway as 'primary' or 'secondary' (*Primary_or_Secondary* column) based on the above-mentioned source information. A pathway was categorised as 'primary' when it was clearly recognised as one of the most important in the source document, i.e. likely leading to successful long-distance introductions as a result of increased propagule pressure (number, frequency and range of propagules) or by facilitating escape. Conversely, a pathway was categorised as 'secondary' when it was less likely to lead to the successful establishment of a

species, generally due to either low propagule pressure (i.e. low number of introduction events, low number of individuals per introduction event) or due to it mainly promoting short distance/local dispersal of the species. We classified pathways as 'secondary' only when the information provided in databases or publications enabled us to identify primary pathways. Otherwise, pathways were classified as primary. It was thus possible for a species to have more than one primary pathway. See Supplementary Material 4 for an example of how species pathways were classified as 'direct' or 'indirect' and 'primary' or 'secondary'.

There is a level of inherent uncertainty associated with the compilation of data collated in large-scale databases. We minimized the level of uncertainty associated with pathway-related data input in two ways depending on the source of uncertainty. First, data collation and the merging of different data sources may be a source of potential confusion and errors. Therefore, we checked for and then systematically corrected obvious mistakes in pathway assignment resulting from the merging of datasets using our expert judgement. For example, if the pathway recorded in the database of an invertebrate was 'Forestry' but this was a known contaminant, then the new pathway description would be 'Contaminant of plants'. Second, given that uncertainty may also arise from the varying quality of the source attributing a pathway to a particular species, we assessed pathways based on (i) information from the peer-reviewed literature—providing evidence of transport of a species from one region to another, (ii) indirect evidence of pathway use reported in grey literature (e.g. individuals found near botanic gardens), and (iii) assumptions/deductions made from similar species' introduction pathways (Harrower et al. 2018).

Data processing

We used the *expandYearlyCosts*() function from the 'invacost' package version 0.3–4 (Leroy et al. 2020) in R version 4.0.3 (R Core Team 2020) to ensure that each cost entry—which could correspond to either a single or a multi-year estimate—was consistently recorded on an annual basis for the amount of years that the cost was incurred. The expanded version of our *filtered_subset* contained 21,250 cost entries (hereafter called *expanded_subset*). Finally, we used the R package dplyr (version 1.0.2.)(Wickham et al.

2020) to merge the *expanded_subset* with the pathways dataset (Supplementary Material 3) and generate our *final dataset,* available in Supplementary Material 5. Our *final dataset* contained 77,826 entries covering over 108 countries.

We organised this *final dataset* for further analyses (see below). First, IAS were classified into 13 broad "organism types" based on information from the *Kingdom*, *Phylum*, and *Class* columns: amphibian, arthropods, bird, decapod, fish, fungi, insect, mammal, mollusc, plant, reptile, animalia diverse and other organisms. "Animalia diverse" include invertebrate species from the *Kingdom* Animalia that are not listed in the above animal categories, namely species of the phylum Nematoda, Cnidaria, Platyhelminthes and class Ascidiacea. The category "other organisms" is made up of all organisms not included in the aforementioned categories (e.g. species with *Kingdom* column entries Bacteria, Virus, Chromista). Second, we included information from the *Type_of_cost_merged* column (Table 1) in our *final dataset*, which classifies the cost estimates as "damage" (i.e. economic losses due to direct and/or indirect impacts of invaders, such as yield losses, damage repair, etc.), "management" (i.e. economic resources allocated to actions related to the prevention, management and control of alien species) or "mixed" (i.e. when costs incorporate both 'damage' and 'management' elements) costs.

Data analyses

To estimate the economic cost of invasive species for the period 1970–2020, we calculated the total cost per pathway observed over this period, by summing all cost estimates provided in the *Cost_estimate_per_ year_2017_USD_exchange_rate* column of our *final dataset*. We also calculated (i) the annual average cost per species, by averaging the total cost per year calculated for every species and (ii) the average annual average cost per species per pathway by averaging the annual average cost per species for each pathway.

To assess the potential effects of unknown pathways on the cost distribution shown, we randomly assigned one of the 6 main pathways ('Release', 'Escape', 'Contaminant', 'Stowaway', 'Corridor', 'Unaided') to each species from the InvaCost database which lacked pathway information. We then calculated the total cost per pathway and the average annual average cost per species for each pathway. The

probability of a species being assigned a pathway was dependent on the organism group of that species as it was weighted by the proportion of species in each pathway for a given organism group. We repeated that process 200 times and recorded the average, minimum and maximum of the total cost per pathway and the average annual average cost per species for each pathway.

To compare the total and annual average cost per species across pathway categories and subcategories and for "types of cost" (Table 1), we used the Kruskal–Wallis rank sum test. Multiple comparisons were further carried out with pairwise Wilcoxon rank sum tests (95% family-wise confidence level). All these analyses were conducted for 'direct primary' pathways only.

We used a linear regression and Spearman's rank correlation to assess the correlation between the cost of species and the year of first record of introduction. First records data are from the Global Alien Species First Record Database (Seebens et al. 2017).

To determine if the number of pathways influenced the cost of a species, the number of pathways per species was calculated for both pathway categories and subcategories by (i) summing the number of direct pathways (*CBD_pathway* column) and (ii) summing the number of direct pathways subcategory (*CBD_subcategory* column) for each species. We used Spearman's rank correlation to assess the correlation between the total and annual average cost per species and the number of pathways subcategories.

For all analyses we use 'direct primary' pathways to minimise the duplication of cost across pathways, except when (i) investigating the relationship between the number of pathways and cost of species where both primary and secondary pathways are considered and (ii) identifying indirect pathways subcategories of species introduced unintentionally where we use 'indirect' pathways.

We used ggplot2 (v.3.3.2, Wickham 2011) R package and Adobe illustrator to generate and format all figures.

Results

Our final dataset contained cost data for 606 individual species. Pathway information was available for 478 species (79%), whilst 128 species (21%) currently have unknown pathways.

Have some pathways facilitated the introduction of more economically costly species than others?

As shown in Fig. 2, when considering direct primary pathways only, we found that 'Stowaways' and 'Contaminants' were globally associated with the highest monetary losses and expenditures. This pattern was consistent when considering both the *(i)* total cost per species over the last 50 years (1970–2020) (KW test = 56.666; *p < 0.001;* Supplementary Material 7) as well as *(ii)* the annual average cost per species per pathway (KW test = 84.438; *p < 0.001*; Fig. 2b). See Supplementary Material 6 for the annual average cost and total cost per species per pathway and Supplementary Material 7 for details on Kruskal–Wallis rank sum test and Wilcoxon pairwise comparisons. Contrastingly the greatest number of species was found to be introduced through 'Escape' (243) followed by 'Contaminant' (159), 'Release' (121) and 'Stowaway' (113) pathways (see Supplementary Material 8). Equally when randomly assigning a pathway to the 128 species with unknown pathways 'Stowaways' and 'Contaminants' were still associated with the highest monetary losses and expenditures with a maximum total cost of $159.5bn and $126.7bn respectively. Whilst 'Escape' and 'Release' had a maximum total cost of $56.7bn and $26.8bn respectively (Supplementary Material 8).

'Corridor' and 'Unaided', were generally classified as secondary pathways and thus their contribution to economic costs in this study was minimal (Fig. 2a); nevertheless for a relatively small amount of species (n = 18) (e.g. *Salvinia molesta, Gymnocephalus cernuus*) these were also classified as the primary means of dispersal. The total costs incurred as a result of species introduced through 'Corridors' and 'Unaided' pathways over the last 50 years were the lowest, costing $0.04bn and $2.2bn, respectively. However, the average annual cost per species spread through 'Corridor' was $0.5m and 'Unaided' $25.0m and the median species costs were comparable to the other pathways ($0.5 and $7.5m respectively).

Supplementary Material 9 shows that over the last 50 years, species introduced unintentionally through 'Packing material' and 'Contaminant of plants'
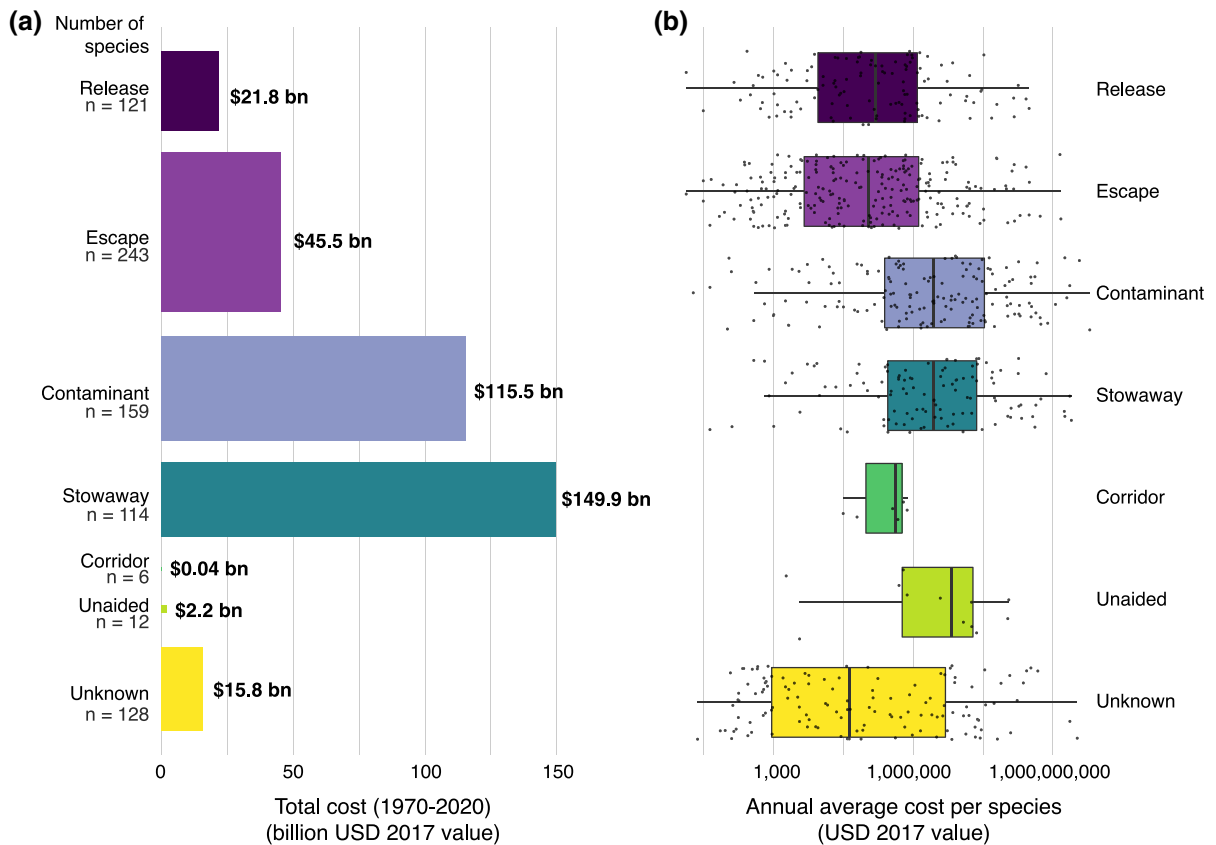
Fig. 2 Cost of species by introduction pathways. (a) Total cost of invasive alien species by pathway for the period (1970–2020) and (b) annual average cost per invasive alien species per pathway. The solid line in (b) shows the median, the lower and upper hinges of the box correspond to the 25th and 75th percentiles. The upper [lower] whisker extend to the largest [smallest] value no further than 1.5 * t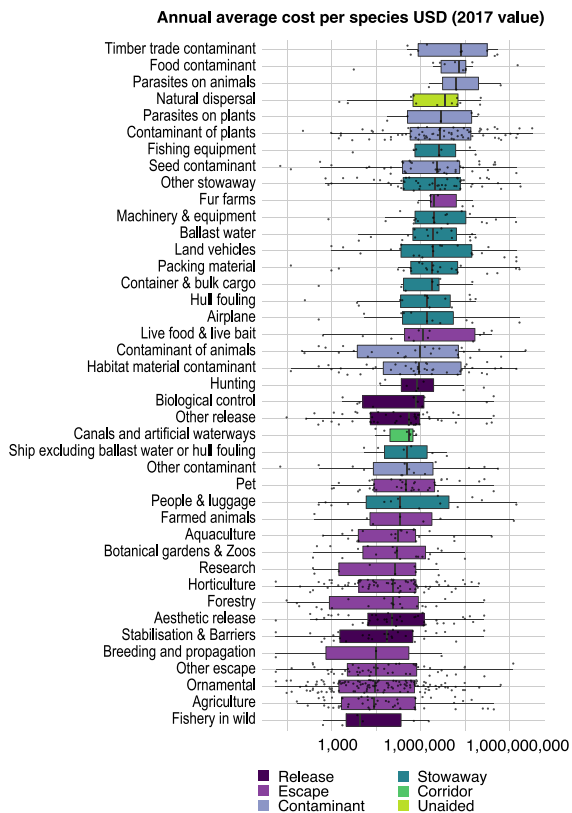he distance between the first and third quartiles from the hinge. Species can have multiple pathways although in this figure we only present direct 'primary' pathways that are likely to lead to successful long-distance introductions (see methods), which reduces the number of pathways per species. The width of the bars in (a) is equivalent to the number of species. 'Intentional' pathways include 'Release' and 'Escape' and 'Unintentional' pathways include 'Contaminant', 'Stowaway', 'Corridor' and 'Unaided'

accounted for the highest total costs ($83bn and $73bn, respectively). For intentional pathways, species introduced through 'Pet trade', 'Other release' and 'Live food & live bait' amassed the highest total cost of $14bn, $11bn and $10bn. In Fig. 3 we see that the three direct, primary pathway subcategories with the highest median annual average cost per species were 'Timber trade contaminant, 'Food contaminant' and 'Parasites on animals' whilst the three pathway subcategories with the lowest median annual average cost per species were 'Fishery in the wild', 'Agriculture', and 'Ornamental'. Species sample size becomes more varied across pathway sub-categories and may generate higher uncertainty in the results.

It is important to take this into consideration when interpreting pathway subcategories results as these are likely to change with time. As shown in Supplementary Material 10, we found that the 'indirect' pathways unintentional introductions of species were most frequently associated with were: 'Agriculture', 'Horticulture' and 'Ornamental trade'.

Are there differences in costs between species introduced intentionally and unintentionally?

Figure 4 shows the total and average cost per species of intentional and unintentional introductions by cost type. The total cost of species introduced

Annual average cost per species USD (2017 value)

Fig. 3 Annual average cost per invasive alien species by introduction pathway sub-category (1970–2020) (USD 2017 value). Species can have multiple pathways. Only direct 'primary' pathways are included in this figure. Boxes are coloured based on the main CBD pathway classification and ranked according to the median cost of species in each pathway sub-category. The solid line shows the median, the lower and upper hinges of the box correspond to the 25th and 75th percentiles. The upper [lower] whisker extend to the largest [smallest] value no further than 1.5 * the distance between the first and third quartiles from the hinge. 'Intentional' pathways include 'Release' and 'Escape' and 'Unintentional' pathways include 'Contaminant', 'Stowaway', 'Corridor' and 'Unaided'

unintentionally is more than four times the cost of species introduced intentionally ($207bn vs. $48bn respectively). The annual average cost per species tended to be higher for species introduced unintentionally in terms of damage (KW test = 3.381; $p = 0.066$), management (KW test = 27.994; $p < 0.001$) and mixed costs (KW test = 20.191; $p < 0.001$) than species introduced intentionally (Fig. 4a). Similar to this trend, over the period 1970–2020, total costs due to species introduced unintentionally were found to be more in terms of

damage, management and mixed costs than species introduced intentionally (Fig. 4b). When considering the different types of management costs (e.g. pre-invasion, post-invasion), unintentional introductions still generated more costs than intentional introductions (see Supplementary Material 11).

How are costs taxonomically and spatially distributed across pathways?

Figure 5 shows the total cost and number of IAS by pathway and organism group (See Supplementary Material 12 for all values). The cost of species introduced as 'Contaminants' and 'Stowaways' were the highest for insects, with a total cost of $78bn and $116bn, respectively, followed by plants ($$22bn) for 'Contaminants' and mammals ($24bn) for 'Stowaways'. The cost of species introduced intentionally and released into nature ('Release') was the highest for mammals ($13bn), followed by plants ($3.5bn). Whilst the cost of species introduced intentionally and subsequently escaped ('Escape') is highest for plants ($17bn), followed by mammals ($16bn). Plants accounted for the highest number of species introduced intentionally (n = 68 for 'Release' and n = 174 for 'Escape') and insects had the highest number of species introduced as 'Contaminants' (n = 74) and 'Stowaways' (n = 43).

Figure 6 shows the total cost of IAS by pathway and geographical region. The total cost associated with each IAS pathway varied across regions. 'Stowaways' had the highest costs in Asia, Central America, North America and Diverse/Unspecified regions, whilst Antarctic-Subantarctic incurred the greatest costs from species intentionally released into nature ('Release'). In Africa, Europe and Oceania/Pacific Islands, 'Contaminants' generated the highest costs, followed by 'Escape' species.

As shown in Supplementary Material 13, when considering the average yearly cost per species for each pathway, 'Escape' species were the costliest in South America, 'Contaminants' were the most costly in Africa and Oceania/Pacific Islands region and 'Stowaways' cost the most in Antarctic-Subantarctic, Asia, Europe, Central and North America and Diverse/Unspecified.

Fig. 4 Cost of intentional and unintentional introductions by cost type (1970–2020) (USD 2017 value). Figure showing **a** a boxplot of the average cost of species introduced intentionally and unintentionally by cost type and **b** bar plot of the total cost of species introduced intentionally and unintentionally by cost type. The solid line in (**a**) shows the median, the lower and upper hinges of the box correspond to the 25th and 75th percentiles. The upper [lower] whisker extend to the largest [smallest] value no further than 1.5 * the distance between the first and third quartiles from the hinge. Only 'primary' and 'direct' pathways of introduction are included in this figure
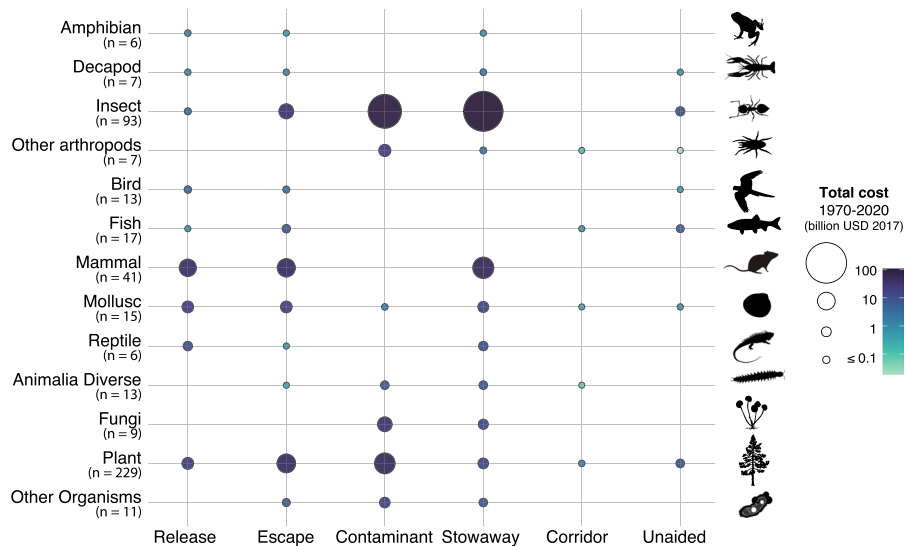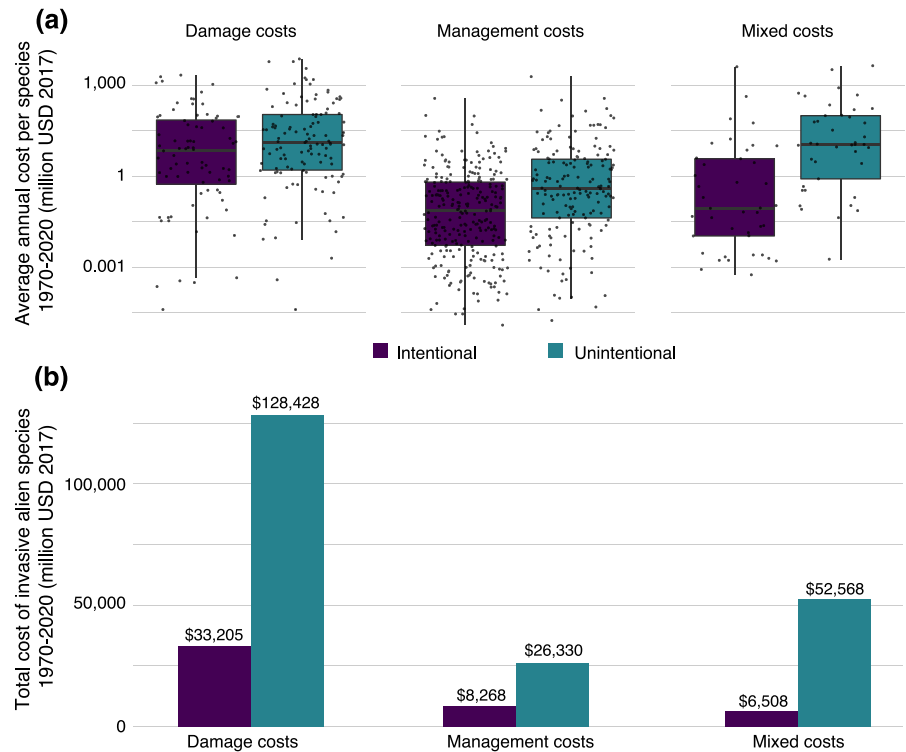
Fig. 5 Total cost of invasive alien species by introduction pathway and organism group (1970–2020) (USD 2017 value). Only direct 'primary' pathways are included in this figure. The colour and the size of the bubble represents the total cost of invasive alien species by broad organism group and pathway.

For example, the total cost incurred for plants introduced through 'escape' for the period 1970–2020 is $ 16.9 billion. 'Intentional' pathways include 'Release' and 'Escape' and 'Unintentional' pathways include 'Contaminant', 'Stowaway', 'Corridor' and 'Unaided'

Fig. 6 Total cost of invasive alien species by introduction pathway and geographical region (1970–2020) (USD 2017 value). Only direct 'primary' pathways of introduction are included in this figure. 'Intentional' pathways include 'Release' and 'Escape' and 'Unintentional' pathways include 'Contaminant', 'Stowaway', 'Corridor' and 'Unaided'. Values in brackets represent the number of species with reported costs introduced in each pathway/region
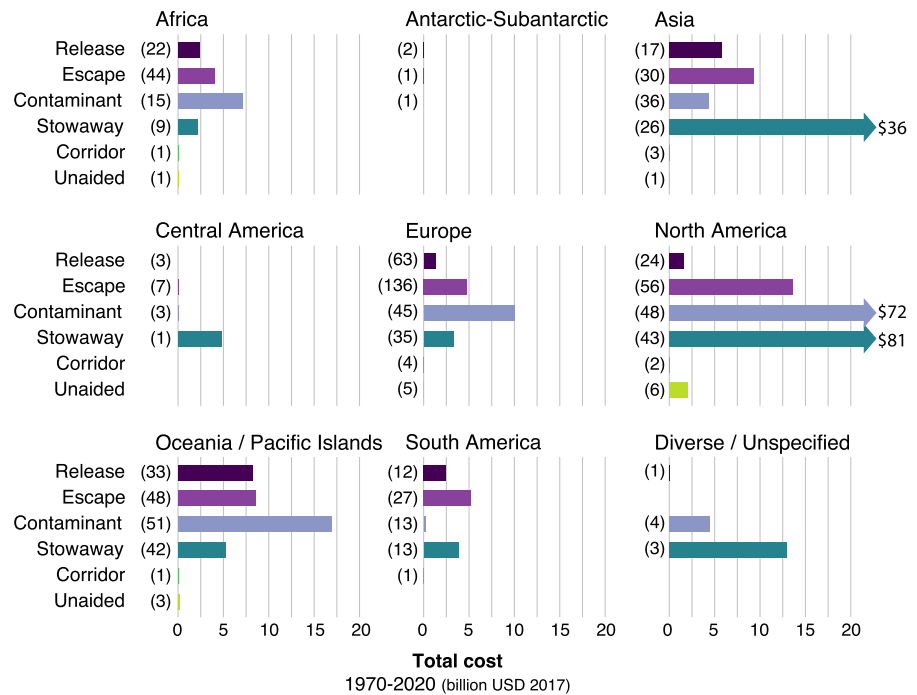
Is there a relationship between the cost of species and the year of first record of introduction?

Figure 7 plots the total cost of a species over the period 1970–2020 in a given location against the year of first record of introduction of the species in that location. We found no significant relationship between the total cost of a species and the year of first record of introduction (Spearman's rho = -0.056; $p = 0.202$). So, although there was a slight decreasing trend between the cost of IAS and the year of first record of introduction, the observed total cost of recent introductions is not significantly lower than the observed total cost of species introduced in earlier years.

In Supplementary Material 14, we individually plotted the total cost of species introduced intentionally, both intentionally and unintentionally and unintentionally against the year of first record of species. Again, there was no significant relationship between the total cost of a species over the period 1970–2020 against the year of the first record of introduction of the species. There was a slight decreasing trend for species introduced intentionally and both intentionally and unintentionally whilst for species introduced unintentionally we found a slight increasing trend.

Is there a relationship between the number of pathways and species cost?

Figure 8 depicts the total cost of a species for the period 1970–2020 against the number of pathways attributed to that species. There was a slight decreasing trend between costs of IAS and the number of pathways through which they are transported. However, we found no significant relationship between the total cost and the number of pathways (Spearman's rho = -0.025; $p = 0.521$) or pathway sub-categories (Spearman's rho = -0.025; $p = 0.594$). Although we note that perhaps it has not been long enough since the first introduction date for many of the species transported via multiple pathways to have accrued additional impacts due to these sources of introductions, we see no reason why these time lags would be absent for species transported via a single pathway.

Discussion

Using data from the global database of reported monetary costs of IAS—*InvaCost*—we set out to address five principal questions. First, we found that the total cost of species, as well as the annual average cost

$y = 7.77 - 0.000844x \quad R^2 < 0.01$
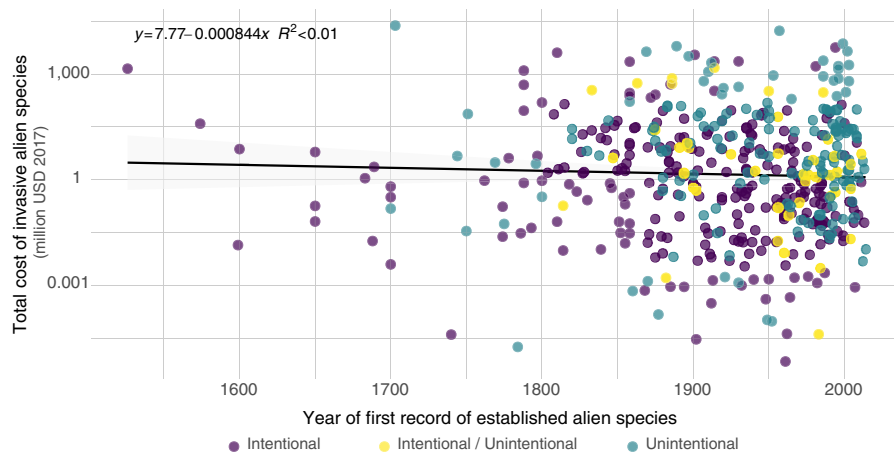
Fig. 7 Invasive alien species cost (1970–2020) (million USD 2017) against the year of the first record of the species in a given location. Only 'primary' and 'direct' pathways are included in this figure. The colours represent whether the primary pathway for a species in a given location is intentional (purple), unintentional (teal) or both intentional and unintentional (yellow). Species were assigned both categories when it was not possible to identify a primary pathway

per species introduced through 'Contaminants' and 'Stowaways' were more costly than species introduced primarily through 'Escape' and 'Release', with 'Unaided' and 'Corridor' being the least costly (Fig. 2; Supplementary Material 6). Second, the total cost of species and the average annual cost per species tends to be much higher for species introduced

unintentionally than species introduced intentionally. This pattern is the same across different types of costs (i.e. damage, management and mixed costs) (Fig. 4). Third, patterns vary spatially and across taxonomic groups, which is an important consideration when formulating policies (Fig. 5 and 6). Fourth, the observed total cost of recent introductions is not

Fig. 8 Total cost per invasive alien species (1970–2020) (million USD 2017) against the number of introduction pathways. Both primary and secondary pathways are considered; however only direct pathway subcategories are included in this figure. The colours represent the broad organism group each species belongs to

$y = 6.23 - 0.0133x \quad R^2 < 0.01$
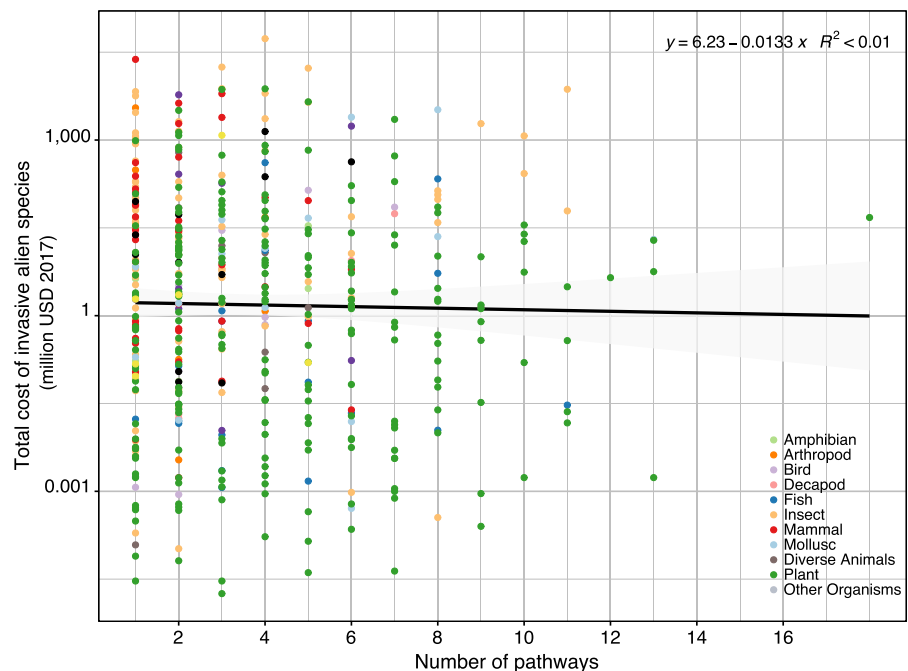
significantly lower than the observed total cost of species introduced in earlier years (Fig. 7). Finally, unlike ecological impacts—where multiple pathways increase the likelihood of species' having an impact (Pergl et al. 2017)—we found no relationship between the total and annual average cost per species and the number of pathways through which it is transported (Fig. 8).

More than 40% of species with cost records had 'Escape' as a primary pathway of introduction making it the most common IAS pathway, followed by 'Contaminants' (26%), 'Release' (20%) and 'Stowaways' (19%) (Supplementary Material 8). Although species introduced through 'Escape' and 'Release' are more numerous than species introduced as 'Contaminants' or 'Stowaways', their annual average and overall costs are significantly lower (see Fig. 1). While the patterns and trends depicted here are based on only a subset of known IAS—i.e. those recorded in the *InvaCost* database vs. 3352 species in GRIIS considered to have evidence of impacts (Chamberlain and Bartomeus, 2021), our results are aligned with previous findings in terms of proportion of IAS by pathways (Saul et al. 2017) and proportion of introduction events by pathways (McGrannachan et al. 2021). Hence, our study provides a sound basis for further improved pathway-based cost assessments for many more IAS.

Observed patterns can be attributed to several factors including lack of records, possibly in turn affected by species' charisma, perceived utility, and ease of management. IAS charisma— "characteristics that affect people's perceptions, attitudes, and behaviors toward them"—can influence public support or contribute to social conflicts thereby affecting perceptions of costs and management actions (Jarić et al. 2020, p. 346; Kourantidou et al. 2021). As such, charismatic species are not only more likely to be introduced intentionally through, for example, the ornamental trade (van Kleunen et al. 2018) but are also more likely to receive social acceptance in the receiving region and generate public opposition to control measures (Jarić et al. 2020). This could lead to low reports of damage costs and paltry investment in management actions. For example, proposed controlled measures of the grey squirrel (*Sciurus carolinensis*) in the UK and Italy generated strong backlash from the public despite its known impact on native red squirrel

(*Sciurus vulgaris*) populations and potentially high economic damage cost (Bertolino and Genovesi 2003; Gurnell et al. 2004; Mayle and Broome 2013). Moreover, intentional releases and escapes should in theory be more straightforward to monitor and control (Hulme et al. 2008) and therefore less costly. Although further evidence is needed to support this hypothesis, Pluess et al. (2012) suggest that eradication campaigns were more likely to succeed for plants introduced for cultivation and subsequently escaped, than for plants introduced through unintentional pathways in semi-natural environments. Another theory that would require further research is that species introduced unintentionally may be able to spread undetected for longer, leading to greater economic costs compared to species introduced intentionally, for which one expects that better measures are already in place to prevent and control invasions.

In line with vertebrates being often characterized as deliberate 'Releases', plants as 'Escapes' and invertebrates as 'Contaminants' (Hulme et al. 2008), in our dataset mammals drive the total cost of intentional 'Release' (61%), plants account for the greatest proportion of 'Escape' costs (37%), whilst insects drive the total costs of unintentional introductions (68%) (Supplementary Material 9). Indeed, domesticated cats (*Felis catus*), wild boars (*Sus scrofa*) and rabbits (*Oryctolagus cuniculus*) represent 57% of intentional 'Release' costs (Supplementary Material 6). Their close proximity and value to humans either as game animals or as pets is a likely cause for their uncontrolled range and population expansion, consequently leading to extensive damage costs. On the other hand, insects are inconspicuous, so their sheer numbers and predominant impacts on sectors such as agriculture, health and forestry probably contribute to their high costs. The high reported costs of insects are the opposite of what we would expect if detection bias drove our results. Contrastively the low costs attributed to fungi and other microorganisms is likely due to detection bias. When looking at the annual average cost per species, fungi and mammals, notably rats, stand out as the most costly 'Stowaway' species, and fungi and arthropods (other than insects) have the highest annual average species cost for 'Contaminants' (Supplementary Material 12). Indeed, rats are amongst the most impactful IAS with both global and multi-sectoral economic impacts, pertaining to

disease transmission, damage to infrastructures and social disruption among others (WHO 2019; Diagne et al., 2021b).

Pergl et al. (2017) found that plants introduced through 'Release', 'Corridor' and 'Unaided' are more likely to have ecological impacts than those introduced as 'Contaminants'. We found that the annual average cost per plant introduced as 'Contaminants' and the total cost of plants introduced as 'Stowaways' were higher compared to other pathways, despite more plant species being introduced intentionally. Moreover, Pyšek et al. (2011) note that plants introduced deliberately have a higher establishment success rate than plants introduced unintentionally, although 'Contaminants' were as widely distributed as intentionally introduced species, and invaded a wider range of semi-natural habitats. This could explain the higher costs caused by 'Contaminants', despite the high number of 'Escape' plant species as one may expect a high number of low impact 'Escape'.

Some plants with the greatest associated costs were originally released through the aquarium trade or for aquatic horticulture (e.g. *Eichhornia crassipes, Hydrilla verticillata, Hydrocotyle ranunculoides, Lagarosiphon major*) (Brundu et al. 2013; Brunel 2009; Madeira et al. 2007). Aquatic ecosystems are susceptible to invasions due to the discrete nature of their coevolved communities (i.e. individual lakes) combined with the accelerating levels of human transport among them that may spread plant propagules (Francis et al. 2019). Increased awareness of biosecurity issues around the trade in aquatic plants is needed to help counter the future emergence of costly invasions (Champion et al. 2010), just as there has been increased recognition of the risks of fish introductions through this mechanism (Gertzen et al. 2008; Nunes et al. 2015; Lockwood et al. 2019).

Costs incurred as a result of unintentional introductions are the greatest globally and for most regions, except for Antarctic-Subantarctic, where costs from 'Release' species have accrued the most over the last 50 years, mostly in the earlier years. With low levels of human activity in the Antarctic region, it is not surprising that cost records mainly relate to management measures of intentionally introduced mammals, even though both deliberate and accidental introductions have been reported (Frenot et al. 2005). Monetary quantification of damage from invasions may be more difficult when the impact is primarily environmental; especially since humans are perhaps more inclined to spend money to mitigate impacts that cause economic losses. It is worth noting that all costs in our dataset were standardised based on the classical exchange rates, meaning that the purchasing power of different currencies was not equalised between countries. We did not consider costs standardised based on the Purchase Power Parity (PPP) in *InvaCost* (Diagne et al. 2020b) because (i) this information is still missing for a number of countries and years from the official sources (i.e. World Bank website; see Diagne et al. 2020b for details) and (ii) of limitations of PPP as an adequate conversion factor (Avalos and Alley, 2014). Thus we should be cautious about the geographic patterns shown here.

Our results should not be taken as leads to recommendation of lower investment in the management of pathways where the recorded costs were shown to be lower, at least for two main reasons. ***First***, the trends and patterns drawn here only reflect a snapshot of a portion of the cost data available in the InvaCost database at the time of writing (i.e. only observed highly reliable costs). Our work should therefore be seen as the first state-of-the-art on the topic, given both qualitative and quantitative findings will be refined as knowledge on pathways and costs of IAS will continue to increase in the future. Precise knowledge on pathways is still lacking for a number of IAS—as illustrated by the costs associated with the category 'unknown' pathway (Fig. 2). Nonetheless, we can assume that our findings are not only driven or blurred by data availability. Indeed, if the magnitude of cost information available across pathways was likely to have directly driven the cost distribution evidenced here, one could expect that the higher the number of species or cost data recorded for a particular pathway, the higher the estimated costs. However, we found that 'stowaway'—the pathway associated with the costliest estimates—is among the pathways with the lowest number of cost information currently recorded in the database. ***Second***, although our results currently highlight 'contaminant' and 'stowaway' as the costliest pathways, we must keep in mind that the impacts of IAS are far beyond their estimated economic burden and affect health and biodiversity in ways that are often hard to quantify in monetary terms (Charles and Dukes 2008; Hanley and Roberts 2019). As such, considering all dimensions of IAS

impacts (ecological, economic and sanitary) is key when prioritising pathways in terms of management actions.

Therefore, our results should, rather, be viewed as (i) a sound basis providing avenues for future improvement on this research topic, (ii) complementary knowledge to existing studies on IAS impacts and pathways to improve prioritization and (iii) a call to further invest in the management of all pathways given their massive—and likely much underestimated—costs to our society. Moving from our empirical results to actual management recommendations requires, for instance, (i) deciphering how pathways—and associated number/identity of introduced species—vary across space and time, (ii) identifying how local contexts influence the introduction opportunities from specific pathways (e.g. implementation of regulations), and (iii) bridging current gaps (e.g. CBD pathway classification scheme is heavily biased towards Europe; Faulkner et al. 2020) in research on pathways. This objective is beyond the scope of our manuscript which rather aims at using evidence from the relationship between pathways and costs to highlight the need for transdisciplinary approaches in invasion science, at the interface between science and society (Vaz et al. 2017; Novoa et al. 2018; Diagne et al 2020a, b, 2021a). Accordingly, given the high economic impacts depicted here, managing unintentional pathways (i.e. 'Stowaway' and 'Contaminants') should be a key item for future biosecurity efforts, which must adapt to growing trends in global shipping (Sardain et al. 2019), and increased survivability of stowaways due to climate change (Pyke et al. 2008; Della Venezia et al. 2018; Kourantidou et al. 2015; Kaiser and Kourantidou 2021). Embracing emerging technologies for safer shipping such as eDNA detection techniques, recyclable plastic pallets (i.e. IKEA's OptiLedge), and the application of fouling-resistant paints to ship hulls will help meet these challenges (Callow and Callow 2011; Guan et al. 2019). At the level of international policy, agreements such as the Ballast Water Management (BWM) which finally entered into force in 2017 (close to 27 years after its initial design and 13 years after its adoption) (IMO 2020) and the creation of global biofouling policy are instrumental to establishing a worldwide standard to mitigate stowaways on ship hulls (Davidson et al. 2016; Ojaveer et al. 2018; Galil et al. 2019). The upholding of existing international ballast water

regulations, as well as improved ballast water management in Arctic regions, will be key in the face of warming arctic waters (Goldsmit et al. 2019; Kourantidou et al. 2015; Kaiser and Kourantidou 2021). Stricter enforcement of wood packing material protocols such as ISPM15 can help limit the transport of wood boring insects in wood pallets (Leung et al. 2014). Similarly, adopting a 'pest free status' (ISPM10) prior to the export of goods—especially through 'Agriculture', 'Horticulture', and 'Ornamental trade'—may help reduce costs associated with 'Contaminants' and 'Stowaways'. Interception of IAS by trained staff at ports of entries (airports, seaports) could also be a very efficient measure. More broadly, we advocate for the implementation of measures and actions ever-increasingly proposed in the recent scientific literature to improve at-border systems. These aimed at controlling both intentional and unintentional introduction events through, for instance, (i) appropriate sampling strategies, (ii) suitable inspection methods, (iii) continuous, transnational recording of organisms detected, and (iv) risk assessment and education (Essl et al. 2015; Saccaggi et al. 2016 and references therein; Carpio et al. 2020).

To conclude, using the most up-to-date compilation of monetary cost information on IAS we show that 'Stowaway' and 'Contaminant' pathways (particularly 'Timber trade' and 'Food' contaminants) have a particularly high economic impact globally. In line with existing research, our work supports the need to prevent and control unintentional species introductions in order to reduce the overall economic burden of IAS. We also stress the importance of conducting risk assessments before introducing species into new environments and raising public awareness of the potential impacts of non-native species, especially those introduced through the pet and aquarium trade. Moreover, we expect that our findings can stimulate the need for more and better cost assessments and their association with IAS pathways and impacts, in line with existing evidence that targeted management implemented to prevent IAS introduction is the most efficient way to limit further impacts to our ecosystems and our economies.

Declarations

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