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2 Introduction pathways of economically costly invasive alien 3 species

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9 **Abstract** Introduction pathways play a pivotal role
10 in the success of Invasive Alien Species (IAS)—the
11 subset of alien species that have a negative environ-
12 mental and/or socio-economic impact. Pathways
13 refer to the fundamental processes that lead to the

introduction of a species from one geographical loca- 14
tion to another—marking the beginning of all alien 15
species invasions. Increased knowledge of pathways 16
is essential to help reduce the number of introduc- 17
tions and impacts of IAS and ultimately improve 18
their management. Here we use the *InvaCost* data- 19
base, a comprehensive repository on the global 20
monetary impacts of IAS, combined with pathway 21

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A2 contains supplementary material available at [https://doi.](https://doi.org/10.1007/s10530-022-02796-5)
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22 data classified using the Convention on Biological
 23 Diversity (CBD) hierarchical classification and com-
 24 piled from CABI Invasive Species Compendium, the
 25 Global Invasive Species Database (GISD) and the
 26 published literature to address five key points. Data
 27 was available for 478 individual IAS. For these, we
 28 found that both the total and annual average cost
 29 per species introduced through the ‘Stowaway’
 30 (US\$144.9bn; US\$89.4 m) and ‘Contaminant’ path-
 31 ways (US\$99.3bn; US\$158.0 m) were higher than that
 32 for species introduced primarily through the ‘Escape’
 33 (US\$87.4bn; US\$25.4 m) and ‘Release’ pathways
 34 (US\$64.2bn; US\$16.4 m). Second, the recorded costs
 35 (both total and average) of species introduced unin-
 36 tentionally was higher than that of species introduced
 37 intentionally. Third, insects and mammals, respec-
 38 tively, accounted for the greatest proportion of the
 39 total cost of species introduced unintentionally and
 40 intentionally respectively, at least of the available
 41 records; ‘Stowaway’ had the highest recorded costs in
 42 Asia, Central America, North America and Diverse/
 43 Unspecified regions. Fourthly, the total cost of a spe-
 44 cies in a given location is not related to the year of
 45 first record of introduction, but time gaps might blur
 46 the true pattern. Finally, the total and average cost of
 47 IAS were not related to their number of introduction
 48 pathways. Although our findings are directly limited
 49 by the available data, they provide important mate-
 50 rial which can contribute to pathway priority meas-
 51 ures notably by complementing studies on pathways
 52 associated with ecologically harmful IAS. They also
 53 highlight the crucial need to fill the remaining data
 54 gaps—something that will be critical in prioritising
 55 limited management budgets to combat the current
 56 acceleration of species invasions.

57 **Keywords** Introduction pathways · *InvaCost* ·
 58 Invasive alien species · Monetary impact · Exotic
 59 mammals · Non-native insects · Management · Policy

60 Introduction

61 All alien species invasions begin with the intentional
 62 or accidental transportation of individuals or prop-
 63 agules by humans outside of their historical biogeog-
 64 raphic boundaries (Blackburn et al. 2011; Lehan
 65 et al. 2013; Essl et al. 2015). Introduction pathways
 66 (henceforth ‘pathways’) refer to the fundamental

67 processes that lead to the introduction of a species
 68 from one geographical location to another (Rich-
 69 ardson et al. 2011). Consequently, pathways play a
 70 pivotal role in the success of Invasive Alien Species
 71 (IAS)—the subset of alien species that have a nega-
 72 tive environmental and/or socio-economic impact—
 73 as they influence the number, frequency and geo-
 74 graphic range of propagules dispersed (Pyšek et al.
 75 2020; Gippet and Bertelsmeier, 2021). Increased
 76 knowledge of pathways is crucial to help reduce the
 77 movement and impacts of IAS (Leung et al. 2002;
 78 Essl et al. 2015) and ultimately improve their man-
 79 agement (Simberloff and Rejmanek 2011; Novoa
 80 et al. 2020). In recent years, research and policy have
 81 focused on identifying and classifying pathways and
 82 prioritising which pathways to manage in order to
 83 prevent biological invasions. This was illustrated by
 84 the Strategic Plan for Biodiversity 2011–2020 (Target
 85 9; Convention on Biological Diversity 2014; [https://
 86 www.cbd.int/sp/targets/rationale/target-9/](https://www.cbd.int/sp/targets/rationale/target-9/)) in which
 87 parties aspired that ‘by 2020, invasive alien species
 88 and pathways are identified and prioritized’.

89 Many pathways have already been identified
 90 through assessments at regional levels and across eco-
 91 systems. These assessments help advance our under-
 92 standing of IAS flows and support the development
 93 of policy tools (Hulme et al. 2008; Essl et al. 2015;
 94 Katsanevakis et al. 2013; Pyšek et al. 2011; Nuñez
 95 et al. 2015; García-Berthou et al. 2005; Pergl et al.
 96 2017). Global databases of IAS such as the IUCN’s
 97 Global Invasive Species Database (GISD, [www.iucng
 98 isd.org](http://www.iucngis.org)) and the CABI Invasive Species Compendium
 99 (CABI ISC, www.cabi.org/isc) list between 34 and 80
 100 different pathways through which alien species can be
 101 introduced to new locations. Examples of pathways
 102 include horticulture (e.g. purple loosestrife, *Lythrum
 103 salicaria*; Maki and Galatowitsch 2004), agriculture
 104 (e.g. sisal hemp, *Agave sisalana*; Ortega et al. 2019),
 105 pet trade (e.g. Burmese python, *Python bivittatus*;
 106 Wilson et al. 2011) and biofouling (e.g. zebra mus-
 107 sel, *Dreissena polymorpha*; Carlton 2008). Such lists
 108 are neither exhaustive nor static; as societies evolve
 109 and economic activities continue to grow, and so
 110 more pathways are expected to emerge. To facilitate
 111 comparative studies on pathways, Hulme et al. (2008)
 112 proposed a pathway classification, which was further
 113 developed and subsequently adopted by the Conven-
 114 tion on Biological Diversity (CBD, 2014). The CBD’s
 115 hierarchical framework encompasses three levels; the

116 first level is three broad mechanisms through which
 117 species may arrive to a new location: movement of
 118 commodities, arrival of a transport vector, and/or nat-
 119 ural spread from a neighbouring region. These three
 120 mechanisms then encompass six primary pathways
 121 (Hulme et al. 2008): ‘Release’ (intentional introduc-
 122 tion as a commodity for release), ‘Escape’ (inten-
 123 tional introduction as a commodity but unintentional
 124 escape; includes the release of alien organisms from
 125 captivity), ‘Contaminant’ (unintentional introduction
 126 with a specific commodity), ‘Stowaway’ (uninten-
 127 tional introduction attached to or within a transport
 128 vector), ‘Corridor’ (unintentional introduction via
 129 human infrastructures linking previously unconnected
 130 regions), and ‘Unaided’ movement (unintentional
 131 introduction through natural dispersal of alien species
 132 across political borders). These six pathways are fur-
 133 ther divided into 44 subcategories, covering pathways
 134 applicable to alien species from a wide range of taxo-
 135 nomic groups and environments (Pergl et al. 2020)
 136 (Fig. 1).

137 Prioritizing the management of high-risk pathways
 138 is necessary to achieve cost-effective management of
 139 IAS, essentially by preventing additional introduc-
 140 tions of species that have already been introduced as
 141 well as new harmful alien species (McGeoch et al.
 142 2016). IAS can generate substantial costs in terms
 143 of damage to ecosystems, impacts on human well-
 144 being and expenditures on management (Diagne
 145 et al. 2021a). At the same time, there is evidence
 146 that investing in the prevention of IAS introduction
 147 (proactive management) is less costly—and likely
 148 more efficient—compared to allocating resources and
 149 funds to reactive management once they establish and
 150 become invasive (Leung et al. 2002; Ahmed et al.,
 151 this Special Issue).

152 Pathways can be prioritized using (i) the number of
 153 IAS introduced per pathway and/or (ii) an assessment
 154 of the observed or potential impact caused by spe-
 155 cies introduced through different pathways (Essl et al.
 156 2015; McGeoch et al. 2016). Studies investigating the
 157 number of species per pathway have found that, where
 158 pathway information had been deduced, movement
 159 of commodities was associated with the most docu-
 160 mented introductions. Indeed, ‘Escape’ is identified
 161 as the most prevalent pathway for IAS (Faulkner et al.
 162 2016; McGrannachan, et al. 2020), predominantly
 163 through horticulture trade (Turbelin et al. 2017) and
 164 the most important for plants and vertebrates (Saul

165 et al. 2017). It is worth noting that pathway informa-
 166 tion is still lacking for a number of IAS, particularly
 167 plant and invertebrate taxa (Faulkner et al. 2016).
 168 Other studies showed that invaders associated with
 169 a high number of pathways are more likely to have
 170 an ecological impact in newly invaded sites (Pergl
 171 et al. 2017; Saul et al. 2017). Particularly for plants,
 172 both the number and types of pathways may influ-
 173 ence invasion success and the likelihood of impact
 174 (Pysek et al. 2011; Pergl et al. 2017). Plants intro-
 175 duced through ‘Release’, ‘Corridor’ and ‘Unaided’
 176 pathways are more likely to have an ecological impact
 177 than when introduced as ‘Contaminants’ (Pergl et al.
 178 2017). Plants introduced through these pathways
 179 are also more likely to successfully establish and be
 180 accepted in society when grown as animal food or for
 181 environmental uses (van Kleunen et al. 2020). Simi-
 182 larly, certain pathways may favor successful invad-
 183 ers, e.g. pet trade particularly favors invasive species
 184 (Gippet and Bertelsmeier, 2021).

185 Whilst a number of publications have examined
 186 the links between ecological impacts and pathways of
 187 IAS (e.g. Pergl et al. 2017; Saul et al. 2017), there are
 188 currently no studies assessing relationships between
 189 pathways and economic impacts of IAS. Although
 190 economic impact may overlook aspects of ecologi-
 191 cal impacts, it is a very useful metric of the impact of
 192 IAS, as it can be quantitative, and if costs are stand-
 193 ardized, they can be compiled across regions or taxa
 194 and compared between pathways. A better under-
 195 standing of the economic costs of invasions is also
 196 a key way to raise global awareness about IAS, opti-
 197 mize transboundary legislation and help the priori-
 198 tisation of management actions (Diagne et al. 2020a).

199 In this paper, we investigate pathways of economi-
 200 cally-harmful IAS using the most up-to-date com-
 201 pilation of monetary cost information on IAS—the
 202 *InvaCost* database (Diagne et al. 2020b) and pathway
 203 data classified using the CBD hierarchical classifica-
 204 tion (CBD, 2014; Hulme et al. 2008) and compiled
 205 from CABI ISC, the GISD and the published litera-
 206 ture. Specifically, we address the following questions:
 207 (i) Have some introduction pathways facilitated the
 208 introduction of more economically costly species than
 209 others? (ii) Are there differences in costs between
 210 species introduced intentionally and unintentionally?
 211 (iii) How are costs taxonomically and spatially dis-
 212 tributed across introduction pathways? (iv) Is there a
 213 relationship between the cost of species and the year

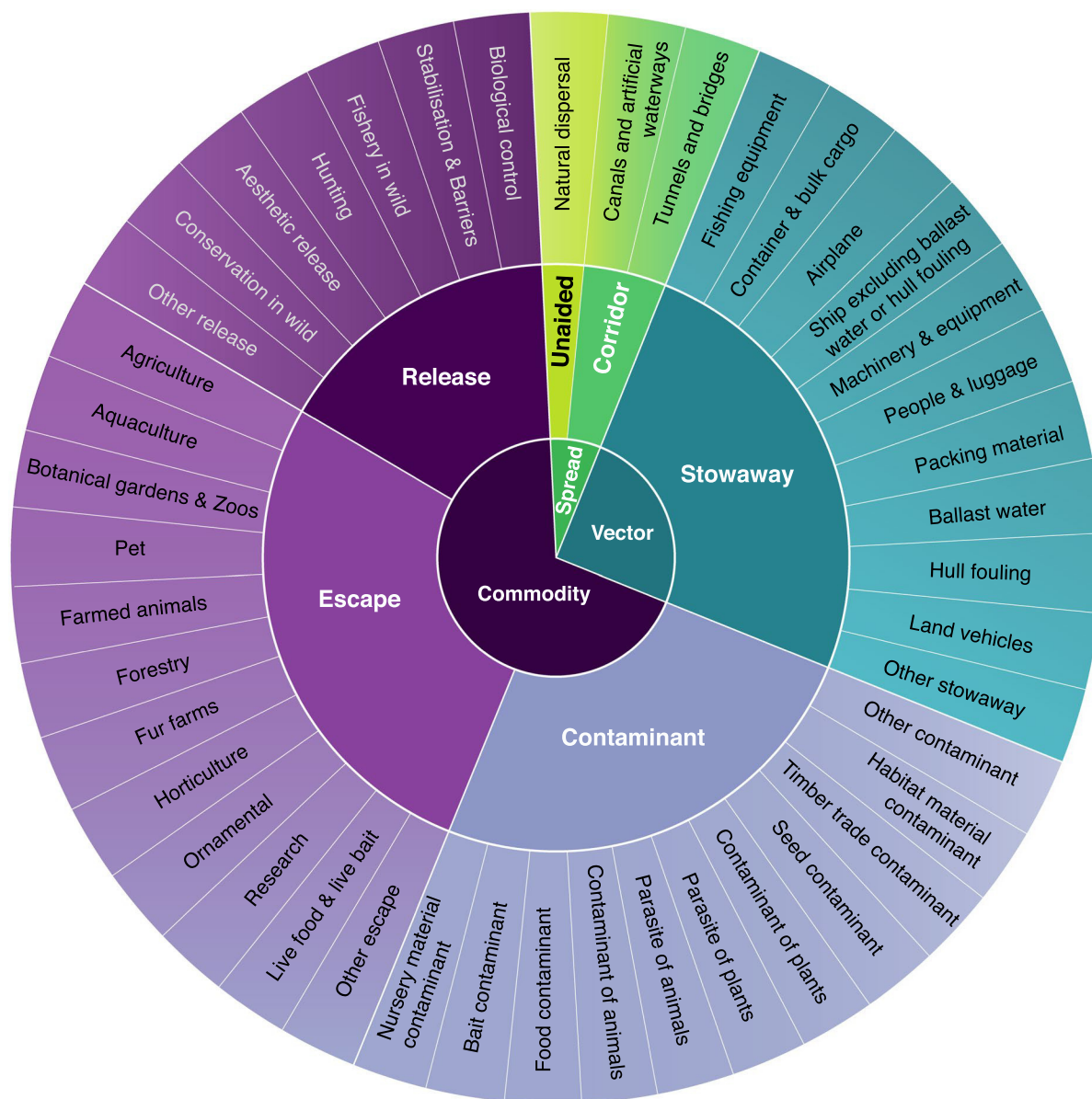


Fig. 1 Convention on Biological Diversity (CBD) pathway classification. This framework uses a hierarchical approach in which alien species may arrive in a new location through three broad mechanisms (i.e. movement of a commodity, arrival of a transport vector, or spread from a neighbouring region), 6 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'

214 of first record of introduction? and (v) Is there a rela-
215 tionship between the number of possible introduction
216 pathways of IAS and their costs?

Methods

Cost data collection and filtering

217

218

219 To assess the economic impact of IAS over the
 220 last 50 years (1970–2020), we relied on cost data
 221 recorded in the latest version of *InvaCost* (version
 222 4.0, openly available at [https://doi.org/10.6084/](https://doi.org/10.6084/m9.figshare.12668570.v4)
 223 [m9.figshare.12668570.v4](https://doi.org/10.6084/m9.figshare.12668570.v4)), which is the most com-
 224 plete and up-to-date global dataset of the reported
 225 economic costs attributable to biological invasions
 226 (Diagne et al. 2020b). *InvaCost* has been built by a
 227 combination of both systematic literature searches
 228 (e.g., specific search strings used in Web of Science
 229 and Google Scholar) and direct solicitations (e.g.,
 230 stakeholders, scientific experts) in more than 10 lan-
 231 guages, to gather any cost information available in
 232 written documents. After ensuring the relevance of
 233 each document, cost information was collated, stand-
 234 ardised to a common and up-to-date currency in the
 235 database (i.e. 2017 US dollars), and finally classi-
 236 fied into categories using a range of descriptive fields
 237 (complete description and details on these descriptive
 238 fields are available at [https://doi.org/10.6084/m9.figsh](https://doi.org/10.6084/m9.figshare.12668570)
 239 [are.12668570](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 240
 available resource contains 13,123 cost entries (as of 241
 June 2021), therefore providing an essential basis for 242
 worldwide research and policymaking targeting IAS 243
 (Diagne et al. 2020a; 2020b). The 'living' nature of 244
 the dataset allows for the taxonomic and geographic 245
 gaps in cost information to be addressed over time, 246
 and then keep informed all users and stakeholders on 247
 cost dynamics and distribution (Diagne et al. 2021a). 248

We used successive filters from the *InvaCost* 249
 database to identify relevant cost entries for our 250
 analysis and obtain a conservative and realistic esti- 251
 mate of costs. First, we extracted costs empirically 252
 "observed" in the invaded environment and left out 253
 all "potential" costs (not yet actually realised but 254
 rather expected and/or predicted over time within or 255
 beyond their actual distribution area). Second, we 256
 then retained costs classified as "high" reliability— 257
 therefore discarding "low" reliability costs—thereby 258
 keeping only cost estimates either provided by offi- 259
 cially pre-assessed documents (peer-reviewed articles 260

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 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

261 and official reports) or associated with an estimation
 262 methodology that was deemed reproducible when
 263 building the database (Diagne et al. 2020b). Lastly,
 264 we focused on cost estimates exclusively attributed
 265 to individual species, therefore multi-species costs
 266 or genus-level costs were removed (e.g. when the
 267 value in the *Species* field included “sp.” or “spp.” or
 268 was simultaneously associated with several species
 269 without any possibility to disentangle specific contri-
 270 bution of each taxon to the overall cost). Following
 271 these filtering steps, our dataset (hereafter called *fil-*
 272 *tered_subset*) contained 7,175 entries (Supplementary
 273 Material 1). Finally, we extracted the list of individual
 274 species with recorded costs. After checking for dis-
 275 crepancies in species names (i.e., where entries for
 276 the same species have different scientific names, we
 277 opted for the internationally preferred scientific name
 278 as described in CABI), the number of individual spe-
 279 cies with cost records amounted to 606.

280 Collection and compilation of pathway 281 information

282 Pathways were categorised using Harrower et al.
 283 (2018), a guidance document for interpreting the
 284 Convention on Biological Diversity (CBD, 2014)
 285 pathway classification framework (Fig. 1). This
 286 pathway classification system has limitations, espe-
 287 cially regarding uncertainty linked to subcategories
 288 (Faulkner et al. 2016, 2020; Pergl et al., 2020), how-
 289 ever McGrannachan et al. (2021) suggested that it is
 290 a reliable framework for reporting on IAS pathways
 291 at a global level. Pathway mechanisms and catego-
 292 ries are defined, and subcategories are listed in Sup-
 293plementary Material 2. We compiled pathway data
 294 for each of the 606 species with reported economic
 295 costs in our *filtered_subset* (Supplementary Material
 296 3, which contains all columns hereafter mentioned)
 297 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 infor-
 300 mation on their specific pathways. When the path-
 301 way information needed was not available in one of
 302 these repositories, we opportunistically extended
 303 our searches to other databases on biological inva-
 304 sions (e.g. the Galapagos Species Checklist), and
 305 performed targeted searches in the published litera-
 306 ture. 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 descrip-
 tion 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 classi-
 fied into pathway types with ‘Intentional’ pathways
 including ‘Release’ and ‘Escape’ and ‘Unintentional’
 pathways including ‘Contaminant’, ‘Stowaway’, ‘Cor-
 ridor’ and ‘Unaided’.

As stated by Harrower et al. (2018; p.88): “*More-*
over, the pathway category assigned to a species is
typically the pathway(s) that relates directly to the
species being introduced. However, the introduc-
tion 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 pro-
cess of introduction and are, therefore, important for
decision-making and particularly in relation to pre-
vention 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 spe-
cies.” As such, to highlight pathway dependency, we
 classified pathways as ‘Direct’ or ‘Indirect’ to indi-
 cate whether the pathway was related directly to the
 species being introduced (*Direct*) or when the path-
 way was related to a species or product that the spe-
 cies 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).

392 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

450 probability of a species being assigned a pathway was
 451 dependent on the organism group of that species as
 452 it was weighted by the proportion of species in each
 453 pathway for a given organism group. We repeated that
 454 process 200 times and recorded the average, mini-
 455 mum and maximum of the total cost per pathway and
 456 the average annual average cost per species for each
 457 pathway.

458 To compare the total and annual average cost per
 459 species across pathway categories and subcatego-
 460 ries and for “types of cost” (Table 1), we used the
 461 Kruskal–Wallis rank sum test. Multiple comparisons
 462 were further carried out with pairwise Wilcoxon rank
 463 sum tests (95% family-wise confidence level). All
 464 these analyses were conducted for ‘direct primary’
 465 pathways only.

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

471 To determine if the number of pathways influenced
 472 the cost of a species, the number of pathways per spe-
 473 cies was calculated for both pathway categories and
 474 subcategories by (i) summing the number of direct
 475 pathways (*CBD_pathway* column) and (ii) summing
 476 the number of direct pathways subcategory (*CBD_*
 477 *subcategory* column) for each species. We used
 478 Spearman’s rank correlation to assess the correlation
 479 between the total and annual average cost per species
 480 and the number of pathways subcategories.

481 For all analyses we use ‘direct primary’ pathways
 482 to minimise the duplication of cost across pathways,
 483 except when (i) investigating the relationship between
 484 the number of pathways and cost of species where
 485 both primary and secondary pathways are considered
 486 and (ii) identifying indirect pathways subcategories
 487 of species introduced unintentionally where we use
 488 ‘indirect’ pathways.

489 We used ggplot2 (v.3.3.2, Wickham 2011) R pack-
 490 age and Adobe illustrator to generate and format all
 491 figures.

492 Results

493 Our final dataset contained cost data for 606 indi-
 494 vidual species. Pathway information was available

for 478 species (79%), whilst 128 species (21%) cur- 495
 496 rently have unknown pathways.

497 Have some pathways facilitated the introduction 498 of more economically costly species than others?

499 As shown in Fig. 2, when considering direct primary 500
 501 pathways only, we found that ‘Stowaways’ and ‘Con- 502
 503 taminants’ were globally associated with the highest 504
 505 monetary losses and expenditures. This pattern was 506
 507 consistent when considering both the (i) total cost 508
 509 per species over the last 50 years (1970–2020)(KW 510
 511 test=56.666; $p < 0.001$; Supplementary Material 7) 512
 513 as well as (ii) the annual average cost per species per 514
 515 pathway (KW test=84.438; $p < 0.001$; Fig. 2b). See 516
 517 Supplementary Material 6 for the annual average 518
 519 cost and total cost per species per pathway and Sup- 520
 521 plementary Material 7 for details on Kruskal–Wal- 522
 523 lis rank sum test and Wilcoxon pairwise compari- 524
 525 sons. Contrastingly the greatest number of species 526
 527 was found to be introduced through ‘Escape’ (243) 528
 529 followed by ‘Contaminant’ (159), ‘Release’ (121) 530
 531 and ‘Stowaway’ (113) pathways (see Supplemen- 532
 533 tary Material 8). Equally when randomly assigning a 534
 535 pathway to the 128 species with unknown pathways 536
 537 ‘Stowaways’ and ‘Contaminants’ were still associated 538
 539 with the highest monetary losses and expenditures 540
 541 with a maximum total cost of \$159.5bn and \$126.7bn 542
 543 respectively. Whilst ‘Escape’ and ‘Release’ had a 544
 545 maximum total cost of \$56.7bn and \$26.8bn respec- 546
 547 tively (Supplementary Material 8). 548

549 ‘Corridor’ and ‘Unaided’, were generally classi- 550
 551 fied as secondary pathways and thus their contribu- 552
 553 tion to economic costs in this study was minimal 554
 555 (Fig. 2a); nevertheless for a relatively small amount 556
 557 of species ($n=18$) (e.g. *Salvinia molesta*, *Gymno-* 558
 559 *cephalus cernuus*) these were also classified as the 560
 561 primary means of dispersal. The total costs incurred 562
 563 as a result of species introduced through ‘Corridors’ 564
 565 and ‘Unaided’ pathways over the last 50 years were 566
 567 the lowest, costing \$0.04bn and \$2.2bn, respec- 568
 569 tively. However, the average annual average cost per 569
 570 species spread through ‘Corridor’ was \$0.5 m and 571
 572 ‘Unaided’ \$25.0 m and the median species costs were 573
 574 comparable to the other pathways (\$0.5 and \$7.5 m 575
 576 respectively). 577

578 Supplementary Material 9 shows that over the last 579
 580 50 years, species introduced unintentionally through 581

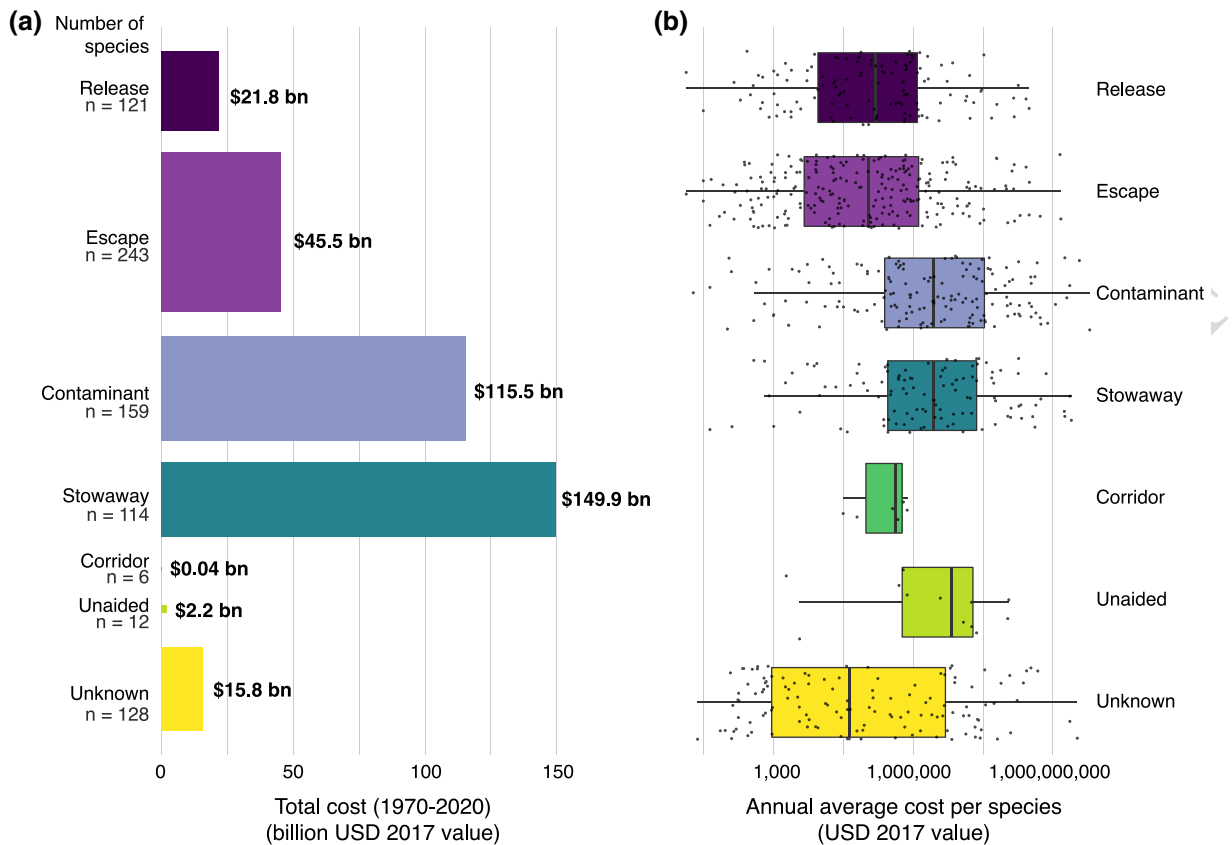


Fig. 2 Cost of species by introduction pathways. (a) Total cost of invasive alien species by pathway for the period (1970–2020) and (b) annual average cost per invasive alien species per pathway. The solid line in (b) shows the median, the lower and upper hinges of the box correspond to the 25th and 75th percentiles. The upper [lower] whisker extend to the largest [smallest] value no further than $1.5 \times$ the 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’

541 ‘Packing material’ and ‘Contaminant of plants’
 542 accounted for the highest total costs (\$83bn and
 543 \$73bn, respectively). For intentional pathways, spe-
 544 cies introduced through ‘Pet trade’, ‘Other release’
 545 and ‘Live food & live bait’ amassed the highest total
 546 cost of \$14bn, \$11bn and \$10bn. In Fig. 3 we see that
 547 the three direct, primary pathway subcategories with
 548 the highest median annual average cost per species
 549 were ‘Timber trade contaminant’, ‘Food contaminant’
 550 and ‘Parasites on animals’ whilst the three pathway
 551 subcategories with the lowest median annual average
 552 cost per species were ‘Fishery in the wild’, ‘Agricul-
 553 ture’, and ‘Ornamental’. Species sample size becomes
 554 more varied across pathway sub-categories and may

generate higher uncertainty in the results. It is impor- 555
 tant to take this into consideration when interpreting 556
 pathway subcategories results as these are likely to 557
 change with time. As shown in Supplementary Mate- 558
 rial 10, we found that the ‘indirect’ pathways uninten- 559
 tional introductions of species were most frequently 560
 associated with were: ‘Agriculture’, ‘Horticulture’ 561
 and ‘Ornamental trade’. 562

Are there differences in costs between species 563
 introduced intentionally and unintentionally? 564

Figure 4 shows the total and average cost per species 565
 of intentional and unintentional introductions 566

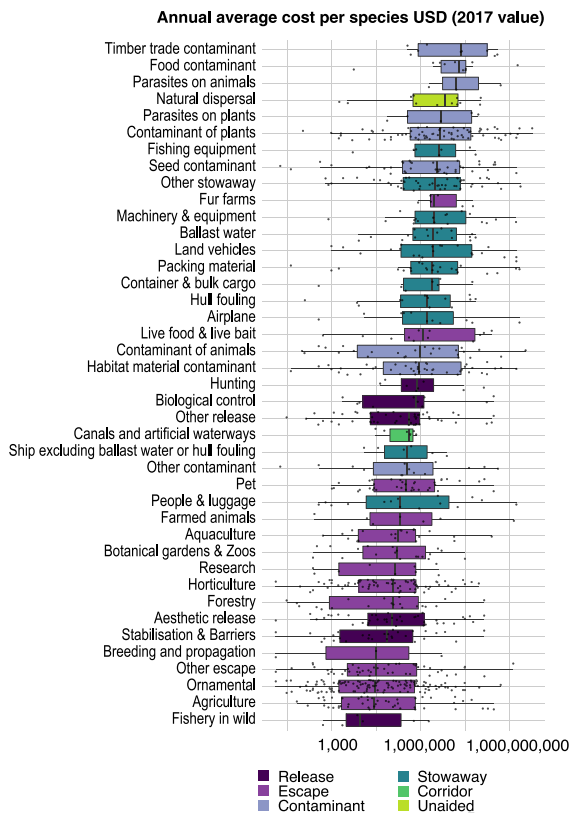


Fig. 3 Annual average cost per invasive alien species by introduction pathway sub-category (1970–2020) (USD 2017 value). Species can have multiple pathways. Only direct ‘primary’ pathways are included in this figure. Boxes are coloured based on the main CBD pathway classification and ranked according 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’

by cost type. The total cost of species introduced 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

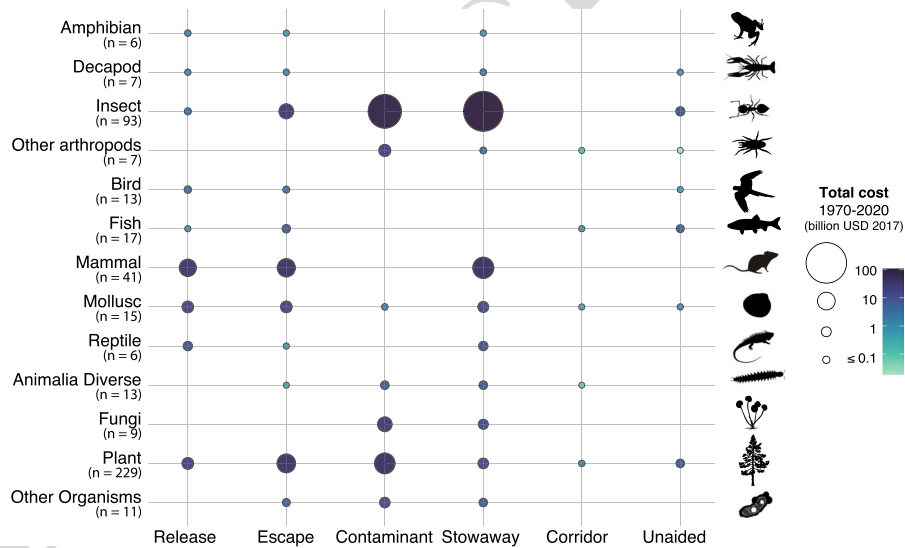
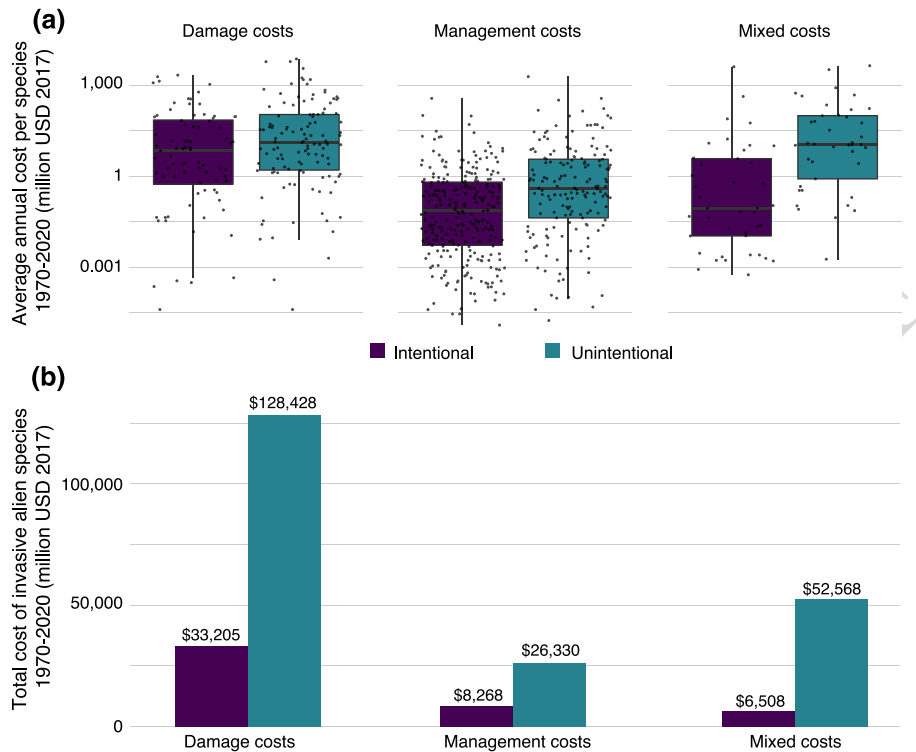


Fig. 5 Total cost of invasive alien species by introduction pathway and organism group (1970–2020) (USD 2017 value). Only direct ‘primary’ pathways are included in this figure. The colour and the size of the bubble represents the total cost of invasive alien species by broad organism group and pathway.

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’

Author Proof

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

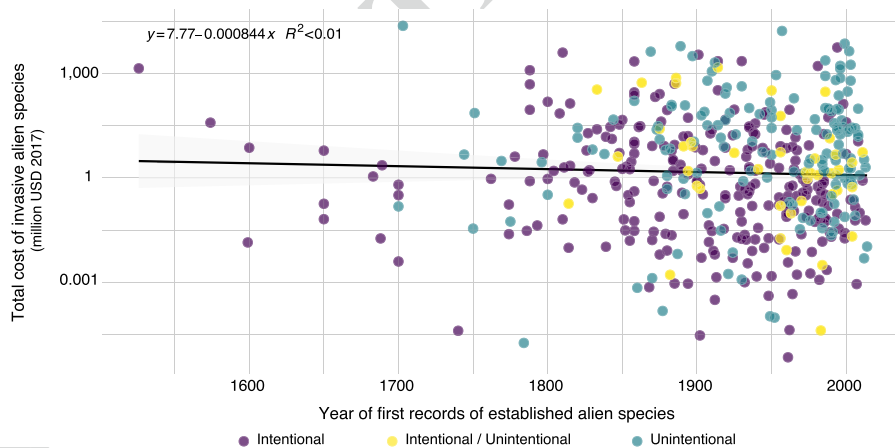
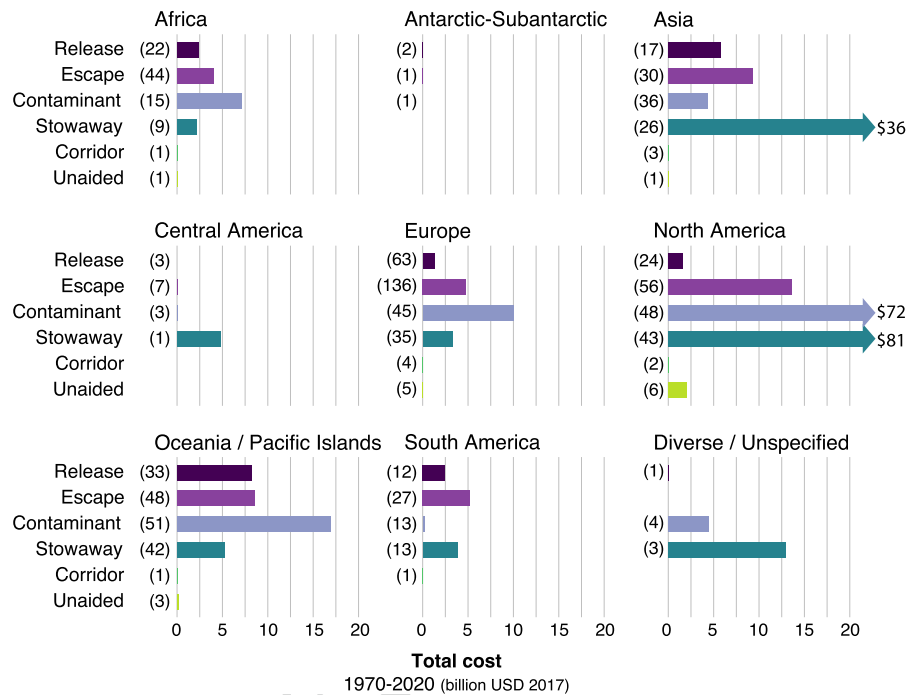


Fig. 7 Invasive alien species cost (1970–2020)(million USD 2017) against the year of the first record of the species in a given location. Only ‘primary’ and ‘direct’ pathways are included in this figure. The colours represent whether the pri-

mary 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

623 Is there a relationship between the cost of species and
624 the year of first record of introduction?

625 Figure 7 plots the total cost of a species over the
626 period 1970–2020 in a given location against the
627 year of first record of introduction of the species in

628 that location. We found no significant relationship
629 between the total cost of a species and the year of
630 first record of introduction (Spearman’s rho = -0.056;
631 $p = 0.202$). So, although there was a slight decreasing
632 trend between the cost of IAS and the year of
633 first record of introduction, the observed total cost

634 of recent introductions is not significantly lower than
635 the observed total cost of species introduced in earlier
636 years.

637 In Supplementary Material 14, we individually
638 plotted the total cost of species introduced intention-
639 ally, both intentionally and unintentionally and unin-
640 tentionally against the year of first record of species.
641 Again, there was no significant relationship between
642 the total cost of a species over the period 1970–2020
643 against the year of the first record of introduction of
644 the species. There was a slight decreasing trend for
645 species introduced intentionally and both intention-
646 ally and unintentionally whilst for species introduced
647 unintentionally we found a slight increasing trend.

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

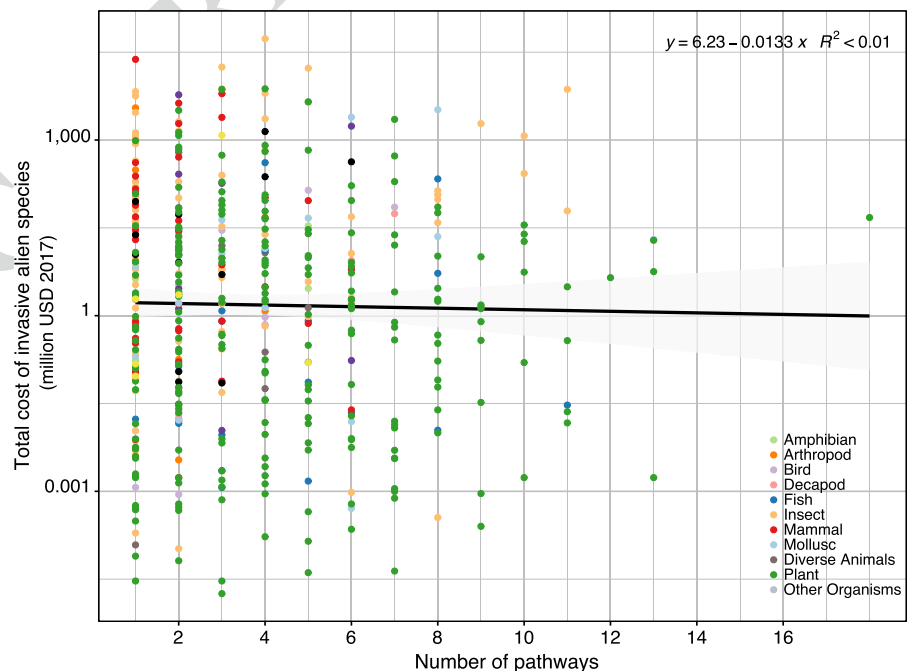
650 Figure 8 depicts the total cost of a species for the
651 period 1970–2020 against the number of pathways
652 attributed to that species. There was a slight decreas-
653 ing trend between costs of IAS and the number of
654 pathways through which they are transported. How-
655 ever, we found no significant relationship between the
656 total cost and the number of pathways (Spearman's
657 $\rho = -0.025$; $p = 0.521$) or pathway sub-categories
658 (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 introduc-
tions, 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 aver-
age cost per species introduced through ‘Contami-
nants’ 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 spe-
cies tends to be much higher for species introduced
unintentionally than species introduced intention-
ally. 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 considera-
tion when formulating policies (Fig. 5 and 6). Fourth,

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



683 the observed total cost of recent introductions is not
684 significantly lower than the observed total cost of
685 species introduced in earlier years (Fig. 7). Finally,
686 unlike ecological impacts—where multiple pathways
687 increase the likelihood of species’ having an impact
688 (Pergl et al. 2017)—we found no relationship between
689 the total and annual average cost per species and the
690 number of pathways through which it is transported
691 (Fig. 8).

692 More than 40% of species with cost records had
693 ‘Escape’ as a primary pathway of introduction mak-
694 ing it the most common IAS pathway, followed by
695 ‘Contaminants’ (26%), ‘Release’ (20%) and ‘Stowa-
696 ways’ (19%) (Supplementary Material 8). Although
697 species introduced through ‘Escape’ and ‘Release’
698 are more numerous than species introduced as ‘Con-
699 taminants’ or ‘Stowaways’, their annual average and
700 overall costs are significantly lower (see Fig. 1).
701 While the patterns and trends depicted here are based
702 on only a subset of known IAS—i.e. those recorded
703 in the *InvaCost* database vs. 3352 species in GRIIS
704 considered to have evidence of impacts (Chamberlain
705 and Bartomeus, 2021), our results are aligned with
706 previous findings in terms of proportion of IAS by
707 pathways (Saul et al. 2017) and proportion of intro-
708 duction events by pathways (McGrannachan et al.
709 2021). Hence, our study provides a sound basis for
710 further improved pathway-based cost assessments for
711 many more IAS.

712 Observed patterns can be attributed to sev-
713 eral factors including lack of records, possibly
714 in turn affected by species’ charisma, perceived
715 utility, and ease of management. IAS charisma—
716 “characteristics that affect people’s perceptions,
717 attitudes, and behaviors toward them”—can influ-
718 ence public support or contribute to social conflicts
719 thereby affecting perceptions of costs and manage-
720 ment actions (Jarić et al. 2020, p. 346; Kouranti-
721 dou et al. 2021). As such, charismatic species are
722 not only more likely to be introduced intentionally
723 through, for example, the ornamental trade (van
724 Kleunen et al. 2018) but are also more likely to
725 receive social acceptance in the receiving region
726 and generate public opposition to control measures
727 (Jarić et al. 2020). This could lead to low reports of
728 damage costs and paltry investment in management
729 actions. For example, proposed controlled measures
730 of the grey squirrel (*Sciurus carolinensis*) in the
731 UK and Italy generated strong backlash from the

public despite its known impact on native red squir- 732
rel (*Sciurus vulgaris*) populations and potentially 733
high economic damage cost (Bertolino and Geno- 734
vesi 2003; Gurnell et al. 2004; Mayle and Broome 735
2013). Moreover, intentional releases and escapes 736
should in theory be more straightforward to moni- 737
tor and control (Hulme et al. 2008) and therefore 738
less costly. Although further evidence is needed to 739
support this hypothesis, Pluess et al. (2012) suggest 740
that eradication campaigns were more likely to suc- 741
ceed for plants introduced for cultivation and subse- 742
quently escaped, than for plants introduced through 743
unintentional pathways in semi-natural environ- 744
ments. Another theory that would require further 745
research is that species introduced unintentionally 746
may be able to spread undetected for longer, lead- 747
ing to greater economic costs compared to species 748
introduced intentionally, for which one expects that 749
better measures are already in place to prevent and 750
control invasions. 751

752 In line with vertebrates being often character- 753
ized as deliberate ‘Releases’, plants as ‘Escapes’ and 754
invertebrates as ‘Contaminants’ (Hulme et al. 2008), 755
in our dataset mammals drive the total cost of inten- 756
tional ‘Release’ (61%), plants account for the great- 757
est proportion of ‘Escape’ costs (37%), whilst insects 758
drive the total costs of unintentional introductions 759
(68%) (Supplementary Material 9). Indeed, domesti- 760
cated cats (*Felis catus*), wild boars (*Sus scrofa*) and 761
rabbits (*Oryctolagus cuniculus*) represent 57% of 762
intentional ‘Release’ costs (Supplementary Material 763
6). Their close proximity and value to humans either 764
as game animals or as pets is a likely cause for their 765
uncontrolled range and population expansion, con- 766
sequently leading to extensive damage costs. On the 767
other hand, insects are inconspicuous, so their sheer 768
numbers and predominant impacts on sectors such 769
as agriculture, health and forestry probably contrib- 770
ute to their high costs. The high reported costs of 771
insects are the opposite of what we would expect if 772
detection bias drove our results. Contrastively the low 773
costs attributed to fungi and other microorganisms 774
is likely due to detection bias. When looking at the 775
annual average cost per species, fungi and mammals, 776
notably rats, stand out as the most costly ‘Stowaway’ 777
species, and fungi and arthropods (other than insects) 778
have the highest annual average species cost for ‘Con- 779
taminants’ (Supplementary Material 12). Indeed, rats 780
are amongst the most impactful IAS with both global

781 and multi-sectoral economic impacts, pertaining to
782 disease transmission, damage to infrastructures and
783 social disruption among others (WHO 2019; Diagne
784 et al., 2021b).

785 Pergl et al. (2017) found that plants introduced
786 through ‘Release’, ‘Corridor’ and ‘Unaided’ are
787 more likely to have ecological impacts than those
788 introduced as ‘Contaminants’. We found that the
789 annual average cost per plant introduced as ‘Con-
790 taminants’ and the total cost of plants introduced as
791 ‘Stowaways’ were higher compared to other path-
792 ways, despite more plant species being introduced
793 intentionally. Moreover, Pyšek et al. (2011) note that
794 plants introduced deliberately have a higher estab-
795 lishment success rate than plants introduced unin-
796 tentionally, although ‘Contaminants’ were as widely
797 distributed as intentionally introduced species, and
798 invaded a wider range of semi-natural habitats. This
799 could explain the higher costs caused by ‘Contami-
800 nants’, despite the high number of ‘Escape’ plant spe-
801 cies as one may expect a high number of low impact
802 ‘Escape’.

803 Some plants with the greatest associated costs
804 were originally released through the aquarium trade
805 or for aquatic horticulture (e.g. *Eichhornia crassipes*,
806 *Hydrilla verticillata*, *Hydrocotyle ranunculoides*,
807 *Lagarosiphon major*) (Brundu et al. 2013; Brunel
808 2009; Madeira et al. 2007). Aquatic ecosystems are
809 susceptible to invasions due to the discrete nature of
810 their coevolved communities (i.e. individual lakes)
811 combined with the accelerating levels of human trans-
812 port among them that may spread plant propagules
813 (Francis et al. 2019). Increased awareness of biosecu-
814 rity issues around the trade in aquatic plants is needed
815 to help counter the future emergence of costly inva-
816 sions (Champion et al. 2010), just as there has been
817 increased recognition of the risks of fish introductions
818 through this mechanism (Gertzen et al. 2008; Nunes
819 et al. 2015; Lockwood et al. 2019).

820 Costs incurred as a result of unintentional introduc-
821 tions are the greatest globally and for most regions,
822 except for Antarctic-Subantarctic, where costs from
823 ‘Release’ species have accrued the most over the last
824 50 years, mostly in the earlier years. With low levels
825 of human activity in the Antarctic region, it is not sur-
826 prising that cost records mainly relate to management
827 measures of intentionally introduced mammals, even
828 though both deliberate and accidental introductions
829 have been reported (Frenot et al. 2005). Monetary

830 quantification of damage from invasions may be more
831 difficult when the impact is primarily environmental;
832 especially since humans are perhaps more inclined to
833 spend money to mitigate impacts that cause economic
834 losses. It is worth noting that all costs in our dataset
835 were standardised based on the classical exchange
836 rates, meaning that the purchasing power of different
837 currencies was not equalised between countries. We
838 did not consider costs standardised based on the Pur-
839 chase Power Parity (PPP) in *InvaCost* (Diagne et al.
840 2020b) because (i) this information is still missing
841 for a number of countries and years from the official
842 sources (i.e. World Bank website; see Diagne et al.
843 2020b for details) and (ii) of limitations of PPP as an
844 adequate conversion factor (Avalos and Alley, 2014).
845 Thus we should be cautious about the geographic pat-
846 terns shown here.

847 Our results should not be taken as leads to recom-
848 mendation of lower investment in the management
849 of pathways where the recorded costs were shown
850 to be lower, at least for two main reasons. **First**, the
851 trends and patterns drawn here only reflect a snapshot
852 of a portion of the cost data available in the *InvaCost*
853 database at the time of writing (i.e. only observed
854 highly reliable costs). Our work should therefore be
855 seen as the first state-of-the-art on the topic, given
856 both qualitative and quantitative findings will be
857 refined as knowledge on pathways and costs of IAS
858 will continue to increase in the future. Precise knowl-
859 edge on pathways is still lacking for a number of
860 IAS—as illustrated by the costs associated with the
861 category ‘unknown’ pathway (Fig. 2). Nonetheless,
862 we can assume that our findings are not only driven
863 or blurred by data availability. Indeed, if the magni-
864 tude of cost information available across pathways
865 was likely to have directly driven the cost distribution
866 evidenced here, one could expect that the higher the
867 number of species or cost data recorded for a particu-
868 lar pathway, the higher the estimated costs. However,
869 we found that ‘stowaway’—the pathway associated
870 with the costliest estimates—is among the pathways
871 with the lowest number of cost information cur-
872 rently recorded in the database. **Second**, although our
873 results currently highlight ‘contaminant’ and ‘stowa-
874 way’ as the costliest pathways, we must keep in mind
875 that the impacts of IAS are far beyond their estimated
876 economic burden and affect health and biodiversity
877 in ways that are often hard to quantify in monetary
878 terms (Charles and Dukes, 2008; Hanley and Roberts, 2004)

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 (Goldsmid 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.

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990 **Author contributions** AJT, CD and FC managed the pro-
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 992 EJH, CB, PJH, MK, REG and AN compiled the pathway data-
 993 set. AJT, CD, DM and REG checked the pathway dataset. AJT
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 996 in writing the first draft of the paper with inputs from CD fol-
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999 **Data availability** All data used in this study were made fully
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1002 Declarations

1003 **Conflict of interest** The authors have declared that no com-
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