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Main Manuscript

Biological invasions as burdens to primary economic sectors.

Keywords: *InvaCost*; non-native species; monetary impact; agriculture; forestry; fisheries

Abstract:

Many human-introduced alien species economically impact industries worldwide. Management prioritization and coordination efforts towards biological invasions are hampered by a lack of comprehensive quantification of costs to key economic sectors. Here, we quantify and estimate global invasion costs to seven major sectors and unravel the introduction pathways of species causing these costs — focusing mainly on primary economic sectors: agriculture, fishery and forestry. From 1970 to 2020, costs reported in the InvaCost database as pertaining to *Agriculture, Fisheries*, and *Forestry* totaled $509 bn, $1.3 bn, and $134 bn, respectively (in 2017 United States dollars). Pathways of costly species were diverse, arising predominantly from cultural and agricultural activities, through unintentional contaminants with trade, and often impacted different sectors than those for which species were initially introduced. Costs to *Agriculture* were pervasive and greatest in at least 37% (n = 46/123) of the countries assessed, with the United States accumulating the greatest costs for primary sectors ($365 bn), followed by China ($101 bn), and Australia ($36 bn). We further identified 19 countries highly economically reliant on *Agriculture*, *Fisheries*, and *Forestry* that are experiencing massive economic impacts from biological invasions, especially in the Global South. Based on an extrapolation to fill cost data gaps, we estimated total global costs ranging from at least $517–1,400 bn for *Agriculture*, $5.7–6.5 bn for *Fisheries*, and $142–768 bn for *Forestry*, evidencing substantial underreporting in the *Forestry* sector in particular. Burgeoning global invasion costs challenge sustainable development and highlight the need for improved management action to reduce future impacts on industry.

Significance

With rapidly rising biological invasion rates, efficient management is critical for economic and environmental impact mitigation. Specifically, improved quantification of the economic cost of biological invasions to the world's primary economic sectors could help policymakers prioritize actions to limit ongoing and future impacts. We show that since 1970, over $600 bn in impacts has been incurred across *Agriculture*, *Fisheries* and *Forestry*, with the largest share reported in *Agriculture*. We further identify 19 countries, which rely heavily on primary sectors, facing comparatively high impacts from invasions, requiring urgent action. However, gaps in cost reporting across invasive taxa and countries suggest that these impacts are grossly underestimated. Proactive prioritization by policymakers is needed to mitigate future impacts to primary sectors.

1. Introduction

Invasive alien species (hereafter, invasive species) can cause substantial health[1], ecological[2] and economic impacts[3]. For example, maize crop damage caused by the fall armyworm (*Spodoptera frugiperda*) in 12 African countries was estimated to reach up to $6.1 bn (United States dollars), with yield losses forecasted between 8.3 and 20.6 million tonnes per annum[4]. By virtue of being introduced by humans, alien species invasions are closely interconnected with the globalization of human activities, trade and transport. Alien plant species, for example, are commonly introduced for and used in agriculture and pasture production[5] and alien fish are introduced for the fishery industry[6]. Economic sectors related to primary production — such as agriculture, fishery and forestry — can, however, be caught in a causal nexus between economic growth, which promotes species introductions into new areas, and uncontrolled spread of invasive species, which in turn can adversely impact economic productivity[7-11]. Indeed, even species introduced for economic benefits in one sector may incur large economic costs for that and other economic sectors — as seen, for example, in aquaculture and fisheries, where the Nile tilapia and perch can both increase and decrease economic returns[12,13].

A global overview of the economic costs of biological invasions to major industries such as agriculture, forestry and fisheries is still lacking, although such information would facilitate more efficient management of invasive species[14]. So far, efforts to assess the economic costs of invasions to economic sectors have tended to focus on a specific sector[7,15], and often on a single invasive species or taxon impacting the targeted sector[4,16,17]. When multiple sectors have been considered, they have been geographically limited[18], or only reported in relative terms[3,19], reducing their value in directing management actions.

A consistent, broad-scale approach using economic impact data can *(i)* motivate policymakers and civil society to take proactive management action, *(ii)* contribute to the development of collaborative programs and coordinated responses at the international level, and *(iii)* enable evidence-based and cost-effective policies through the prioritization of management actions and pre-evaluation of their outcomes[20-23]. Further, such results will aid in sector-specific pathway-level biosecurity policy, which has been identified as a future priority for effective invasive species management[11,24]. To achieve these outcomes, it is imperative to understand the pathways through which impactful biological invasions are incurred, while identifying country-level trends at the scale under which most management decisions are made. Country-level analyses are additionally critical owing to differential reliance on activity sectors, whereby the most reliant countries as a share of GDP could be at the highest risk when faced with impactful invasions. Previous studies have identified pathways of costly biological invasions[11] and that country-level management actions are predominantly reactive[23], but assessments in relation to specific activity sectors across countries have not been considered. Moreover, filling the pervasive knowledge gaps for invasive species with known impacts but unknown costs is paramount given widespread underestimation of impacts, considering that only 2% of biological invasions have a reported cost so far (Cuthbert et al., 2024).

As such, here we aimed to *(i)* investigate the costs of invasive species to the seven sectors listed in InvaCost — the most comprehensive global repository of reported invasive species costs[14] — *Agriculture*, *Authorities-Stakeholders, Environment, Fisheries*, *Forestry, Health, Public and Social Welfare*, and more specifically the costs of invasive species to the three main primary sectors (*Agriculture*, *Fisheries* and *Forestry*[25]); *(ii)* identify introduction pathways of invasive species responsible for observed economics losses to *Agriculture*, *Fisheries* and *Forestry*; *(iii)* evaluate economic losses of countries in the context of economic reliance on *Agriculture*, *Fisheries* and *Forestry*; and *(iv)* estimate unrecorded costs of known invasive species impacting primary sectors, based on extrapolations of impacts from invasive species known to cause harm to activity sectors but which are not yet captured in InvaCost.

To address our aims, we first used the 'invacost' R package[26], which allows complete processing and investigation of the InvaCost database, to decipher the distribution and dynamics of recorded costs over a number of parameters (e.g., time, space, taxa and sectors). Second, we examined the pathways of entry and establishment resulting in the greatest impacts to each sector based on Turbelin et al. (2022). Third, we examined whether particular countries incurred a high burden of economic impact relative to the value of their primary sectors, by visualizing each country's economic impact as a function of the amount of their GDP contributed from these industries. Finally, we extrapolated unrecorded costs of all invasive species for these primary sectors with a more comprehensive list of potential invasive species threats that are directly linked to the harvest of biological resources. To create a more complete list of the total set of identified invasive species impacting *Agriculture, Fisheries* and *Forestry,* we used an independent pest database to extrapolate the potential cost of the entire set of invasive species known to impact a particular sector, both reported in InvaCost and unreported. Together, these approaches allowed us to examine the observed costs of biological invasions to primary sectors, unravel their introduction pathways, fill knowledge gaps and extrapolate risks among countries.

2. Materials and Methods

2.1. Data preparation

2.1.1. Global costs to sectors

Cost data were extracted from the InvaCost Database[14] using the R *invacost* package version 1.1–4 (R Core Team 2020) [26,39]. We extracted entries for all species that were reported at the country level within any country from 1970-2020 inclusive. We conservatively excluded low-reliability estimates (those from gray material sources lacking documented, repeatable or traceable methods) and potential costs (those not incurred but rather expected and/or predicted over time within or beyond the species' actual distribution area), as defined within the InvaCost database[14]. We extracted the years over which impacts were reported within each InvaCost entry ("Impact_year" column of the database extracted with the *invacost* R package). All cost information was transformed to an annual cost in 2017 USD based on reported exchange rates and the implicit price deflator for GDP[14]. Reported costs were separated by the economic sectors ('Impacted Sector' within InvaCost) (see **Table 1** for sector descriptions), and were reported as 'Mixed/Unspecified' when they were either attributed to more than one sector or could not be assigned confidently to a single sector. All reported costs designated within InvaCost as either "damage-loss cost", "management cost", or "mixed cost" were summed across species and countries within a given year to obtain a cumulative global cost over time. Any cost that was reported at a geographic scale above the country level was removed, as well as any cost reported in terms of per unit area (due to difficulties in understanding the realized area over which the cost was incurred). Broad taxonomic groups used to classify data are available in **Dataset S1**. The R-script used to prepare the data is available in **SI R-script S1.**

Table 1. Description of sectors as provided in InvaCost (version 4.1) Descriptors

Sector impacted by biological invasion as per InvaCost	**Sector description (from InvaCost)**
Agriculture	Considered at its broadest sense, food and other useful products produced by human activities through using natural and/plant resources from their ecosystems such as crop growing, livestock breeding, beekeeping, land management
Authorities-Stakeholders	Governmental services and/or official organisations such as conservation agencies, forest services, associations, that allocate efforts for the management *sensu lato* of biological invasions (e.g. control programs, eradication campaigns, research funding)
Environment	Impacts on natural resources, ecological processes and/or ecosystem services that have been valued by authors such as disruption of native habitats or degradation of local habitats
Fishery	Fish-based activities and services such as fishing and aquaculture
Forestry	Forest-based activities and services such as timber production/industries and private forests

Health	Every item directly or indirectly related to the sanitary state of people such as vector control, medical care and other derived damage on human productivity and well-being
Public and social welfare	Activities, goods or services contributing — directly or indirectly — to the human well-being and safety in our societies, including local infrastructures such as electric system, quality of life (e.g. income, recreational activities), personal goods (e.g. private properties, lands), public services (e.g. transports, water regulation), and market activities (e.g. tourism, trade)
Mixed / Unspecified	Either impacts multiple sectors and costs cannot be distinguished or if no information is given in the source

2.1.2. Pathways of introduction

We acquired pathway information for individual species listed in InvaCost (i.e., where the cost was attributed to a single species as opposed to multi-species or genus-level) from Turbelin et al. [11]. Existing pathway data were based on InvaCost version 4.0, so we completed pathway information for 48 additional species with highly reliable observed costs listed in version 4.1 following the methods described in [11]. Pathway information for the species was mainly gathered from CABI ISC (www.cabi.org/isc/), the GISD (http://www.iucngisd.org/gisd), and other sources when information was not available in the aforementioned databases (e.g., targeted searches of the published literature; national checklists). Pathway descriptions were recorded and matched to both the CABI ISC pathway description and the pathway mechanisms, categories, and subcategories of the CBD scheme using the published guidelines for the scheme[40]. For the purpose of our study, we further classified pathways of introduction to identify species introduced for 'Agriculture', 'Forestry', 'Fisheries' and 'Culture' (where the latter relates to aesthetic and sociocultural purposes). We used 'Contaminant' to refer to indirect introductions from the movement of commodities relating to 'Agriculture', 'Forestry' and 'Fisheries' (See **Table S4**). All other pathways were listed in the category 'Other', which includes most stowaways. These are available in **Table S5**. As species can have multiple pathways, we reduced the number of pathways attributed to a species introduced for 'Agriculture', 'Forestry', 'Fisheries', 'Culture' and 'Other' by only including pathways that were classified as direct (pathway is related directly to the species being introduced) and primary (clearly recognised as one of the most important pathways in the source document); see[11]. To avoid duplication of species in the 'Other' and 'Contaminant' categories, we removed species from the 'Other' category if they were also a 'Contaminant' of 'Agriculture', 'Forestry' or 'Fisheries'.

2.1.2. External impact data

While many economic sectors are reported within InvaCost, we focused our extrapolation on three major primary economic sectors (resource-based sectors) that have a well defined list of invasive species known to be impactful: *Agriculture*, *Fisheries*, and *Forestry*. Other sectors contain a more diverse set of actors (e.g., *Authorities-Stakeholders*, *Public and Social Welfare*) and are less easily linked to impacts listed by databases such as CABI's Invasive Species Compendium (ISC) (https://www.cabi.org/ISC).

We assigned each InvaCost species a dominant associated economic sector by matching InvaCost records to species listed in the CABI Invasive species compendium[41] that reported negative impacts to a given sector (see **SI Methods**).

2.1.3. Completeness of costs

We considered any species listed in CABI ISC with impacts to a sector that was not listed in InvaCost to be missing as a cost estimate to that sector. We conservatively extrapolated missing costs only to new, entirely missing species, and did not attempt to fill in the remainder of species' known invaded ranges with costs for the set of InvaCost species. This is an important area for future work, since these costs could be extremely large for regions with lower reporting ability and/or discoverability (e.g., African and Asian languages remain heavily underrepresented in InvaCost 4.1[27]).

2.2. Economic losses of countries and economic reliance

We examined the burden of the economic impact from biological invasions to the three main primary sectors, as defined by the French National Institute for Statistics and Economic Studies[25], relative to the value added from their primary sectors, by visualizing: each country's average annual recorded cost of invasive species (1970-2020) (USD 2017) *(i)* compared to the *Agriculture*, *Fisheries* and *Forestry* average annual value added for the same period, and *(ii)* as a percentage of *Agriculture*, *Fisheries* and *Forestry* annual average value added compared to the annual average *Agriculture*, *Fisheries* and *Forestry* value added as a percentage of GDP for that country. Both datasets used as a proxy for each country's economic reliance on *Agriculture*, *Fisheries* and *Forestry* were obtained from the World Bank national accounts data (https://data.worldbank.org/) on the 1st of June, 2022. See **SI Methods** for more information.

2.3. Cost extrapolation

We identified species missing from the InvaCost database by matching InvaCost records to species listed in the CABI ISC that reported negative impacts to a given sector. In the attribute-based scenario, we built a boosted regression tree model for observed costs, and used this model to predict the missing species. In the distributional scenario, we used a Bayesian approach[16,42] to fit the probability distribution of all costs across missing and reported species (**SI Methods**), employing Bayesian model averaging across four potential curve families. We integrated the area under the resulting cost curve to obtain an estimate of the global cost across all missing species to the sector of interest. Across both scenarios, we calculated extrapolated costs by adding reported costs to these estimated missing costs for each sector. See **SI Methods** for more information.

3. Results

3.1. Observed economic losses

We focused on a portion of the InvaCost database that contains only *Observed* costs, i.e., those cost estimates that were actually realized due to an invasive species within the invaded region (**Fig. 1**). The costs estimated here ranged from $1 bn for *Fishery* (including aquaculture) to $509 bn for *Agriculture* between 1970 and 2020. Over $732 bn in losses from biological invasions were attributed to mixed or unspecified sectors. Of these, ~53% were a combination of an impact on *Agriculture* and one or more other sectors — the highest type of mixed-sector costs (inset in **Fig. 1a**).

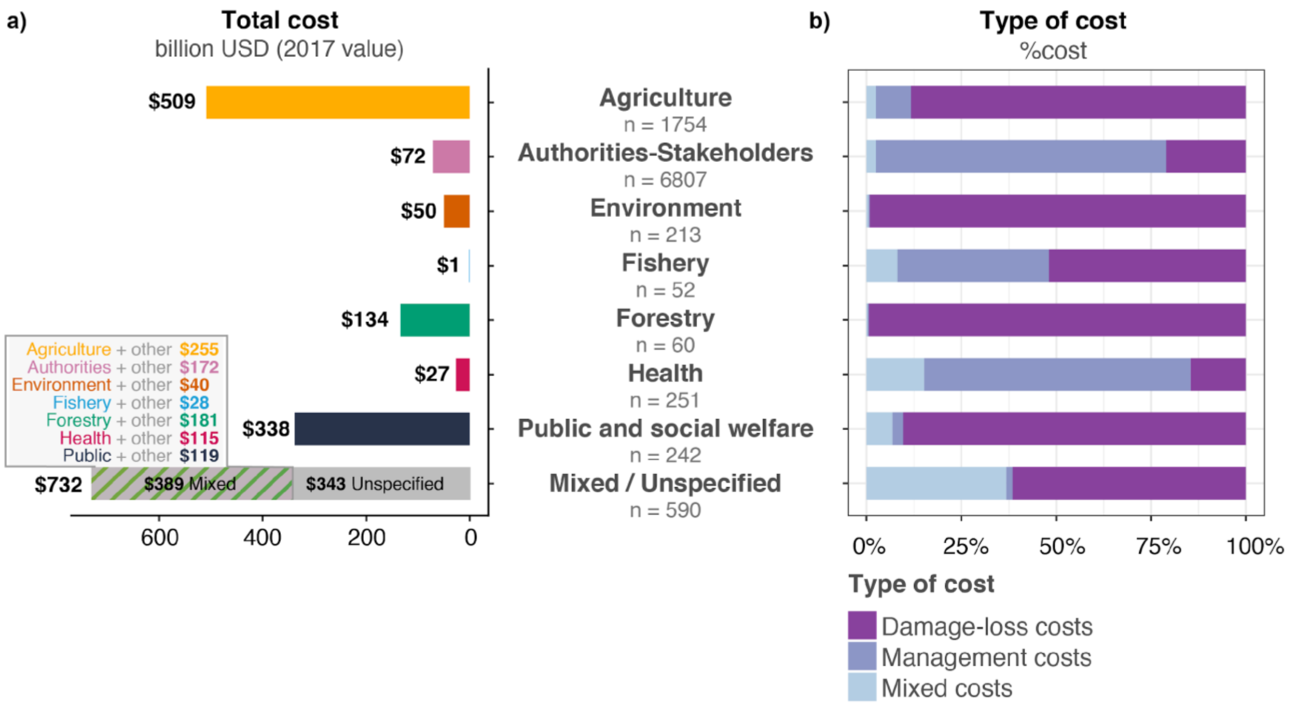

Figure 1. Total cost of invasive alien species by sector (1970–2020) and breakdown by type of cost. Mixed/Unspecified costs amount to $732bn, 47% of which are unspecified and 53% are associated with multiple sectors. For example, $255bn is attributed to *Agriculture* and one or more other sectors. Values attributed to sectors within the '+ other' categories in the left panel do not add up to the $389bn, as costs can be part of multiple categories in this list. For example, the $176bn attributed to *Agriculture* and *Forestry* combined are included in both the $255bn attributed to *Agriculture* (+ other) and the $181bn attributed to *Forestry* (+ other). In Fig. 1a. Authorities refers to *Authorities-Stakeholders* and Public refers to *Public and social welfare*.

When considering the type of cost incurred, *Damage-loss* costs accounted for over 50% of economic losses to all resource-based economic sectors (*Agriculture*, *Fishery* & *Forestry*), as well as to *Environment*, *Public and social welfare* and *Mixed / Unspecified* (**Fig. 1b**). *Management* costs represented more than 50% of recorded economic losses to *Authorities-Stakeholders* and *Health* sectors. The preponderance of management costs to *Authorities-Stakeholders* was expected, as this category mostly incorporates governmental services or official organizations responsible for the management of biological invasions[3] (**Table 1**).

From a geographic standpoint, biological invasions have predominantly impacted the *Agriculture* sector, where 46 out of 123 countries had the highest costs to agriculture across sectors, including the United States, Russia, 19 European countries and 19 African countries (**Fig. 2**). *Mixed / Unspecified* sectors were the most impacted sector category in 39 countries (e.g., Brazil, Australia, Mexico, India), with *Agriculture* being the most commonly reported component in Brazil and Australia. *Forestry* was the most impacted sector in Canada ($14.8bn), China ($97.9bn) and Sweden ($0.18bn). *Fishery* was the most impacted sector in Côte d'Ivoire ($0.36 million) and the second most impacted sector in Mexico after *Mixed / Unspecified*. There were no reported economic impacts in 72 countries worldwide.

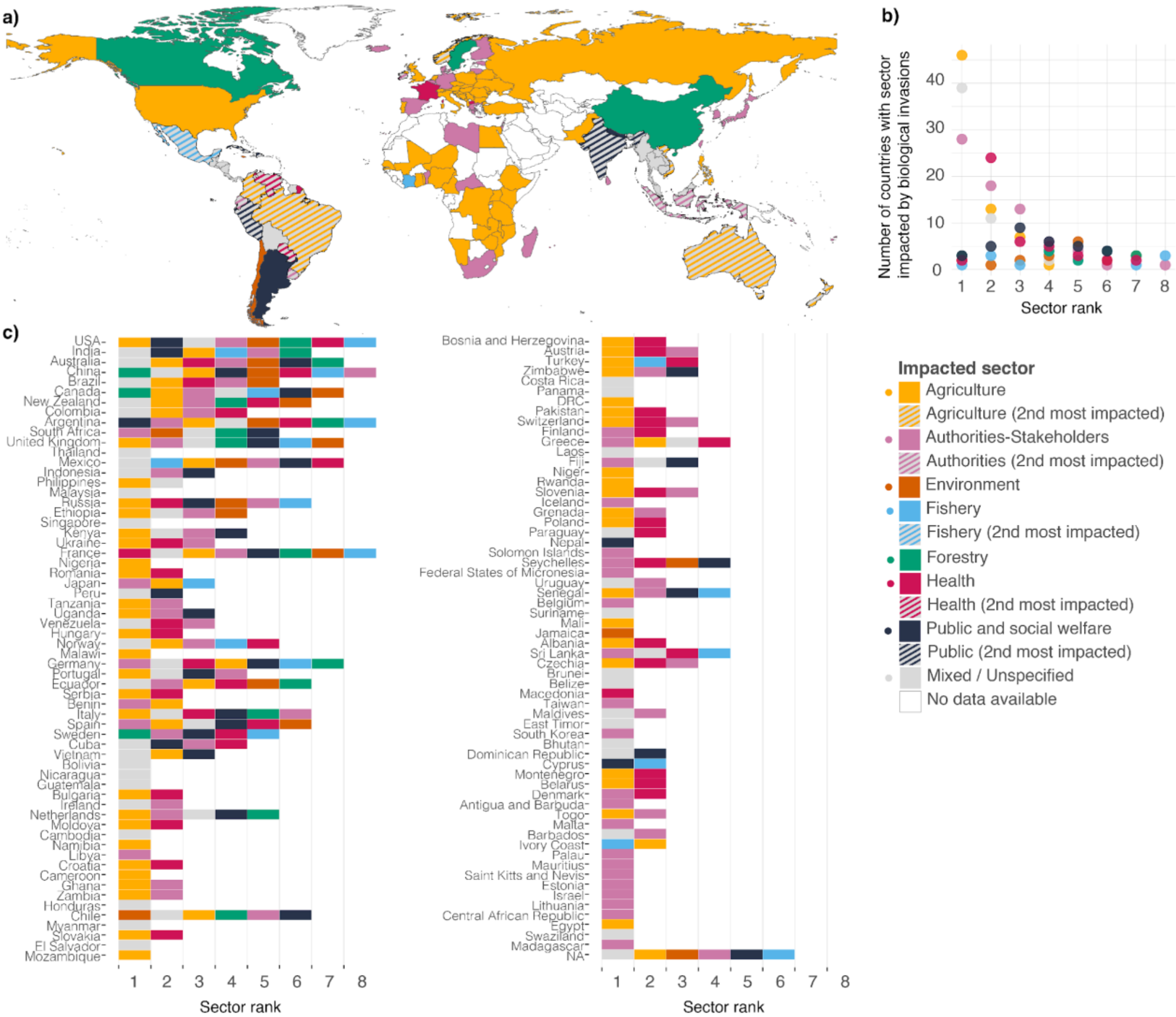

Figure 2. Monetarily impacted sectors by country showing (a) the most impacted sector for each country (solid colours) and second most impacted sector for each country (stripes) when the most impacted is *Mixed / Unspecified*, (b) number of countries where a given sector ranks in a position from 1 to 8, where 1 is the most impacted sector in a country (e.g,. 46 countries report *Agriculture* as the most impacted sector and 24 countries report *Health* as the second most impacted sector) and (c) sectors ranked from most impacted to least impacted (1:8). Countries in (c) are ordered by total cost for the period (1970-2020) — cost data are available in Supporting Dataset S2.

From a taxonomic standpoint, the proportion of cost incurred by different sectors and the number of impacted sectors varied across taxonomic groups (**SI Figure S1**). Mammals and insects caused the most damage to *Agriculture*, whilst insects and other uncategorized animals generated the most costs to *Forestry*, and fish and plants to *Fisheries* (**SI Table S1**).

3.2. Introduction pathways

We gathered pathway data for 180 individual species with costs recorded in InvaCost that impact the *Agriculture*, *Forestry* and *Fisheries* sectors. These represent 31% of costs incurred by the three sectors and 53% of cost entries. The remaining costs to these sectors (69%; $446bn) were attributed to *Diverse/Unspecified* species (including costs assessed at genus or kingdom level) ($436bn) or species with unknown pathways ($10bn). The proportion of costs from *Diverse/Unspecified* species was particularly significant for the *Agriculture* sector, which represented 83% of costs incurred by that sector ($86bn), and less so for *Forestry*, where 84% of costs were attributed to individual, identified species.

The greatest number of individual species with economic costs impacting the three primary sectors (i.e., collectively *Agriculture*, *Forestry* and *Fisheries*) was introduced through the 'Other' pathway (n=103), costing $48 bn (**Fig. 3)**. Species introduced through the 'Other' pathway, also accounted for the greatest number of species impacting *Agriculture* and *Fisheries* (n=89 and n=10; respectively). The 46 species unintentionally introduced as a by-product of agriculture, forestry and fishing practices — often as contaminants of plants, animals, seeds or habitat material — represented 68% of costs incurred by the three sectors ($135bn/$198bn). Four of the species unintentionally introduced through the movement of commodities went on to cause the majority of costs to the *Forestry* sector ($100bn). Species introduced for economic benefits in one sector may go on to cause large economic costs on another sector. We found that species intentionally introduced for 'Culture' (n=56), 'Agriculture' (n=31), 'Fishery' (n=7) and 'Forestry' (n=4) generated costs to the three primary sectors of $10bn, $23bn, $3bn and $0.04bn, respectively.

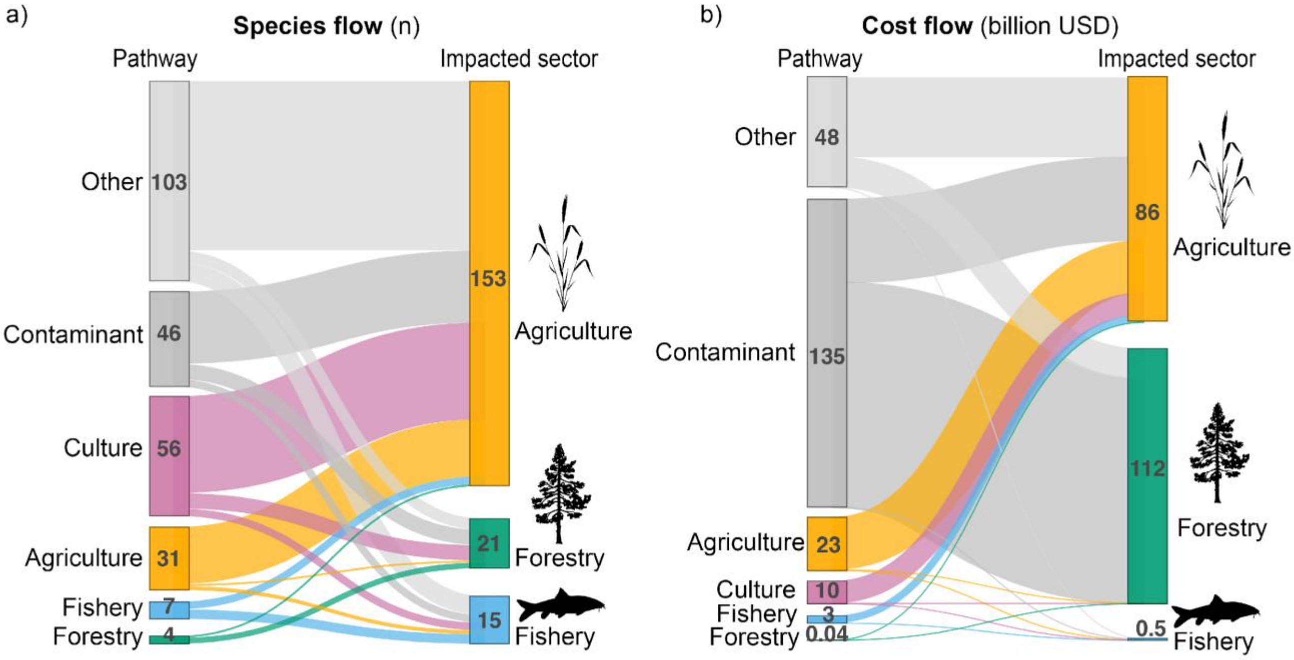

Figure 3. Network diagram showing the flow of a) number of invasive alien species and b) cost from invasive alien species from the driving pathway of introduction to the impacted primary sector. *For example, 31 species with costs in InvaCost have been introduced for agricultural purposes, 24 of which have generated costs to the* Agriculture *Sector. Species introduced for cultural purposes have generated $10bn in costs, over $9bn of which were incurred by the* Agriculture *sector. Species may be introduced via multiple pathways and impact multiple sectors. Pathways were grouped into six broad categories: 'Agriculture' (species introduced as a result of agricultural practices), 'Fishery' (species introduced as a result of fishing and aquaculture practices), 'Forestry' (species introduced as a result of forestry practices; e.g. timber production), 'Culture' (species introduced for aesthetic and sociocultural reasons), 'Other' (species introduced through other pathways such as stowaways) and 'Contaminant' (species unintentionally introduced through the movement of commodities relating to 'Agriculture', 'Forestry' and 'Fishery').*

3.3. Economic reliance on primary economic sectors

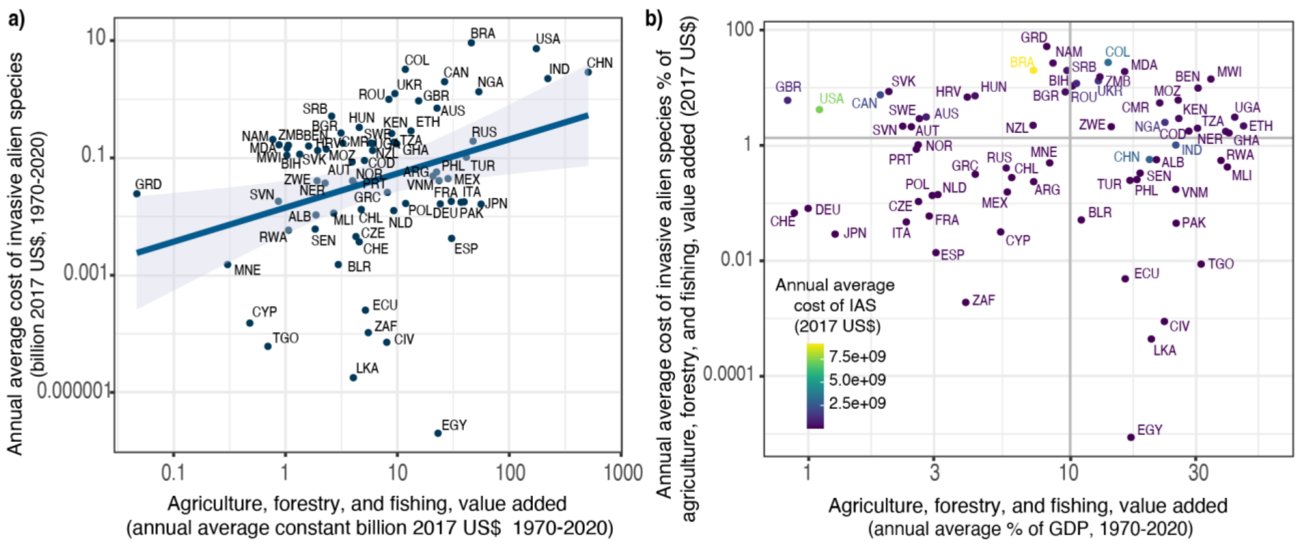

Figure 4. Burden of invasive alien species to primary sectors showing a) the annual average cost of invasive alien species (1970-2020) compared to the agriculture, forestry and fishing annual average value

added (2017 USD) for each country with costs recorded in InvaCost, b) the annual average cost of invasive alien species as a percentage of agriculture, forestry and fishing annual average value added. The dark gray lines in b) represent the 50th percentile of the observed values of the axis across all countries.

Comparing the average annual value added from primary sectors to national economies (1970-2020) to the average annual cost of invasive species to the sectors of these countries (**Fig. 4a.**), shows that countries with higher GDP proportions owing to these sectors also tend to bear higher costs from biological invasions.

The economic burden on individual countries from invasive species also differed considerably according to the value added from *Agriculture*, *Fisheries* and *Forestry* and GDP (**Fig. 4b.; Table 2**). Countries above the 50th percentile of both the percentage of invasive species cost to *Agriculture*, *Fisheries* and *Forestry* value added and value added to GDP (top right area on the plot) included Ethiopia, Uganda, Malawi and Benin. These countries' economies are more likely to suffer from the economic impact of biological invasions than countries with relatively high costs from invasive species but which are less reliant on *Agriculture*, *Fisheries* and *Forestry* (as a proportion of GDP) (e.g. the USA, Canada). See **SI text** for a further description of the results.

Table 2. Countries more likely to suffer from the economic impacts of biological invasions. List of 19 countries that are highly reliant on agriculture, forestry and fishing — with annual average added value as % of GDP higher than the 50th percentile — and for which the proportion of costs from invasive alien species to the *Agriculture*, *Forestry* and *Fishery* to the value added by the three sectors within the country are higher than the 50th percentile.

Country	ISO3	Annual average cost of invasive alien species (million 2017 US$, 1970-2020)	Agriculture, forestry, and fishing, value added (annual average million 2017 US$ 1970-2020)	Annual average cost of invasive alien species % of agriculture, forestry, and fishing, value added (2017 US$)	Agriculture, forestry, and fishing, value added (annual average % of GDP, 1970-2020)
Benin	BEN	$159.11	$1,612.38	9.87	30.60
Bosnia and Herzegovina	BIH	$110.73	$1,029.18	10.76	10.16
Cameroon	CMR	$177.86	$3,256.90	5.46	21.85
Colombia	COL	$3,232.29	$11,779.91	27.44	13.89
Democratic Republic of the Congo	COD	$90.10	$5,083.28	1.77	28.22
Ethiopia	ETH	$288.22	$13,235.02	2.18	45.66
Ghana	GHA	$173.07	$9,875.03	1.75	39.02
Kenya	KEN	$260.85	$8,897.33	2.93	25.84
Malawi	MWI	$146.07	$1,033.63	14.13	34.25

Country	ISO3	Annual average cost of invasive alien species (million 2017 US$, 1970-2020)	Agriculture, forestry, and fishing, value added (annual average million 2017 US$ 1970-2020)	Annual average cost of invasive alien species % of agriculture, forestry, and fishing, value added (2017 US$)	Agriculture, forestry, and fishing, value added (annual average % of GDP, 1970-2020)
Moldova	MDA	$166.85	$875.97	19.05	16.06
Mozambique	MOZ	$141.25	$2,314.08	6.10	25.71
Niger	NER	$37.09	$2,260.77	1.64	40.17
Nigeria	NGA	$1,340.56	$53,500.49	2.51	22.87
Romania	ROU	$996.56	$8,393.70	11.87	10.51
Uganda	UGA	$178.43	$5,777.74	3.09	42.25
Ukraine	UKR	$1,248.35	$9,502.55	13.14	12.75
United Republic of Tanzania	TZA	$184.72	$9,296.31	1.99	30.46
Zambia	ZMB	$163.99	$1,062.23	15.44	12.92
Zimbabwe	ZWE	$40.51	$1,918.40	2.11	14.27

3.4. Estimating unrecorded economic losses

To create a more complete list of the total set of identified invasive species impacting *Agriculture, Fisheries* and *Forestry*, independently of those for which economic costs are recorded, we compiled species records from the CABI Invasive Species Compendium (www.cabi.org/isc), and used the difference as a set of 'missing' cost records. We extrapolated these missing costs to obtain the potential cost of the entire set of invasive species known to impact a particular sector. Given the propensity to report data on particularly costly species, we used two contrasting scenarios of missing data. One scenario (attributed-based) (ABSc) assumed that missing species had predictable relationships with cost based on their attributes and invasion history. The other scenario (distributional) (DSc) assumed that missing data followed a similar frequency distribution to the reported cost data, where the majority of species were more likely to have medium to low costs and a few rare species caused very high economic impacts[16]. In the attribute-based scenario, missing costs were modeled using boosted regression trees fit to the attributes in **Table S2**. In the distributional scenario, reported economic costs were fit to probability distributions via Bayesian methods and missing species were assumed to follow the same distribution. We found that extrapolated costs were proximal to reported costs in *Agriculture* and *Forestry* in the attribute-based scenario, but were much higher in the distributional scenario (2.7 times and 5.7 times, respectively) (**SI Figure S2, Table S3**). Extrapolated costs were much higher than observed costs for *Fisheries* across both scenarios (attributed-based scenario = 5.0 times, distributional scenario = 4.4 times).

After extrapolation, *Agriculture* still had by far the greatest cost. The large increase in the estimate for the distributional scenario relative to the attribute-based scenario indicates that species missing from InvaCost have attributes more similar to lower-cost species within InvaCost.

4. Discussion

Biological invasions have cost economies hundreds of billions of dollars between 1970 and 2020. Despite these widespread impacts of biological invasions across sectors, our extrapolations indicate that costs could be several times higher than currently reported. Further, our extrapolations should be considered conservative in that they assume all sectoral and geographic impacts of species present in InvaCost are fully reported, when inclusion in this database is subject to well-described underreporting[3,27].

Costs were borne unevenly among sectors, ranging from $1 bn for *Fishery* to $509 bn for *Agriculture*. Except for *Authorities-Stakeholders* and *Health*, the majority of reported costs to other sectors were related to resource damage and losses. Of the seven sectors we assessed, current data show that *Agriculture* incurs the highest costs from biological invasions, both globally and in at least 46/123 of assessed countries (including the USA, Russia, Nigeria). The high observed economic impact from biological invasions to *Agriculture* compared to other sectors is unsurprising, considering that the number of cost records (n = 1754) is 3–30 times higher than that of other sectors, except *Authorities-Stakeholders* (n = 6807). Both the high number of cost records for *Agriculture* and associated high observed losses can be explained by a combination of factors[28], including (i) costs being easily monetised, (ii) impacts being monitored consistently and (iii) the size of the sector — agriculture represents 4% of global GDP[29] (see **SI Discussion**). Pathways for costly invasive species were diverse, with impacts frequently incurred by sectors disconnected to the initial introduction pathway (e.g., cultural introductions damaging agriculture).

Species introduced unintentionally (e.g., contaminants of plants or animals) or for reasons other than agriculture, forestry, fishing or cultural purposes (e.g., biological control, research) accounted for the highest number of species impacting primary sectors and the highest costs. This is consistent with a study on introduction pathways of costly invasive species, which found that species introduced as stowaways or contaminants had accumulated the greatest costs over the last 50 years[11]. Importantly, over 30 of these species were unintentionally introduced through the movement of commodities, including those destined for *Agriculture*, *Forestry* or *Fishery*, paradoxically generating costs of $127bn in those same sectors. Four species were particularly damaging to the *Forestry* sector, costing nearly $100bn in management and damage losses, including the emerald ash borer (*Agrilus planipennis*), Asian long-horned beetle (*Anoplophora glabripennis*), pine wilt nematode (*Bursaphelenchus mucronatus*) and white pine blister rust (*Cronartium ribicola*). This overwhelming contribution of contamination from various sectors should serve as a warning to growing industries, to ensure they are not harming their long-term sustainability by failing to implement biosecurity (e.g., ISPM10[30]).

This study highlights the invasion-related vulnerabilities to global livelihoods through an estimation of the impact invasions have had to *Agriculture*, *Fisheries* and *Forestry*. The global cost from biological invasions to the three primary economic sectors for the last 50 years amounted to over $644bn, which is 0.5% of the value of agricultural production over the same period ($122,000bn; https://www.fao.org/faostat). Costs are unevenly distributed across countries, with the United States accumulating the highest costs ($365bn), followed by China ($101bn), Australia ($36bn), Canada ($30bn) and India ($25bn); and Egypt, South Africa, Côte d'Ivoire, Togo, and Sri Lanka recording the lowest costs (all under $500,000). While these latter countries incur the lowest impacts, countries bearing the lowest costs are not necessarily the least impacted by invasions in terms of *Agriculture, Fisheries* and *Forestry*. Economies highly reliant on *Agriculture*, *Fisheries* and *Forestry* (as a proportion of GDP) are more likely to suffer from the economic impact of biological invasions. In comparing the cost from biological invasions to the value added by the primary sectors to GDP, we showed that a number of countries in Africa (e.g., Ethiopia, Uganda, Malawi, Benin) are disproportionately affected. As a consequence, these vulnerabilities impede realization of Sustainable Development Goals pertaining to food security, health, economic growth and ecosystem integrity (e.g., SDG 2, 3, 8, 12).

While we identify a suite of high-risk countries based on both relatively high invasive species costs and high reliance on primary sectors, other countries might also suffer as a result of invasive species. Indeed, current data gaps and analysis limitations (see **SI text**) preclude a full assessment of the true economic burden. Especially for countries that are highly reliant on primary sectors (i.e., in the right half of Fig. 4b.), a single invasive species can have devastating impacts. Given the long-tailed nature of the distribution of invasive species impacts we fit, a small subset of invaders are subject to far greater costs than the average invasive species (see also[31]). Beyond the country where the initial impacts are recorded, there can also be important knock-on effects on agricultural and even industrial collapse in any one country, as impacts reverberate across supply chains in our globalized economy. One pertinent example of this is the impact on global production systems stemming from the ongoing (at time of writing) war in Ukraine[32]. Moreover, biological invasions are predicted to increase[9,33], while climate changes and other anthropogenic stresses are predicted to compromise primary sector yields[34-36]. As such, impacts of invasions on *Agriculture*, *Fisheries* and *Forestry* are likely to be exacerbated in the near future without improved management interventions.

When extrapolating missing costs from species listed as invasive species impacting *Agriculture*, *Fisheries* and *Forestry* in CABI, we found that reported costs to the *Fishery* sector were substantially underestimated relative to our predictions across both scenarios, indicating less cost information for this sector in InvaCost, consistent with known aquatic-terrestrial research unevenness[13,37]. In particular, marine biological invasions have been severely underrepresented even among aquatic data entries in InvaCost, which could reflect reduced research efforts, unrefined biogeographies, or a lack of human assets in offshore systems[37]. It is therefore likely that a substantial share of missing Fishery costs arose from marine bioinvasions. Species missing from *Fishery* had attributes associated with species of higher economic impact than average contained within the database, compared to species missing from the other two sectors. This is evidenced by the increase in the extrapolated cost in the attribute-based model relative to the Bayesian model (which does not take species attributes into account). When not considering species traits, species missing from *Agriculture* and *Forestry* were expected to increase extrapolated costs. Since this was only the case for one scenario, this result is less robust. Nevertheless, impacts to both sectors may be much higher than reported, which can have important implications due to their increasing role in global food security[38]. As expected, across all sectors, a large fraction of invasive species had not been assessed and reported in InvaCost, where *Agriculture* was 24% complete, *Fishery* was 34% complete, and *Forestry* was 25% complete.

In providing the first detailed analyses of biological invasion costs among activity sectors alongside estimates of missing costs worldwide, we can make clear recommendations to decision making for policy. First, agriculture bore the highest invasion cost while also having among the smallest management shares relative to resource damages and losses. As impacts to agriculture were the most prevalent among countries, there is a need to implement more stringent and proactive management strategies for this sector to reduce costs by mitigating invasion impacts, such as prevention, monitoring and rapid eradication. Second, we explicitly highlight pathways which are linked to high costs to all major activity sectors. High risk sources of costly invaders to agriculture, forestry and fishery sectors include contaminant and cultural pathways, alongside species introduced to benefit those three sectors directly. Pinpointing these specific sources helps to improve and target biosecurity strategies towards pervasive threats to each sector; this is particularly important for countries with a high and increasing reliance on these sectors relative to GDP, which often include lower income nations. Thirdly, large shares of biological invasion costs to primary sectors have gone unrecorded and therefore lack integration into global syntheses. There is a need for national economies to develop structured approaches to cost reporting, using frameworks such as InvaCost, such that data gaps can be resolved with greater certainty and in sufficient detail. Our estimates of unrecorded costs constitute a conservative step towards this goal.

We have uncovered that the last 50 years have resulted in hundreds of billions of dollars in reported costs to *Agriculture*, *Fisheries*, and *Forestry*, in large part due to contaminants of these same three sectors. The prevalence of contaminant-related costs increases the risk of failure of our attainment of the Sustainable Development Goals regarding sustainable production due to ignorance of biosecurity risks. Across extrapolation scenarios, we show that these costs may in fact be in the trillions to *Agriculture*. While these total, global costs are remarkable, we expect the greatest risks from invasive species are to countries that do not necessarily record the greatest costs, but that bear costs that are large compared to the size of their economy and their reliance on these primary sectors. We caution countries presently reliant on or working to expand their primary sectors to do so in combination with biosecurity policies to ensure long-term sustainability of these sectors.

5. Data and materials availability:

Cost data on biological invasions are from the InvaCost database version 4.1 — the most up-to-date, comprehensive, standardized and robust data compilation and description of economic cost estimates associated with invasive species worldwide — available from www.invacost.fr. Diagne, C. Leroy, B., Gozlan, R., Vaissière, A.C., Assailly, C. Nuninger, L.; et al. (2020): InvaCost: Economic cost estimates associated with biological invasions worldwide. figshare. Dataset. https://doi.org/10.6084/m9.figshare.12668570.v5

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