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Damage costs from invasive species exceed management expenditure in nations experiencing lower economic activity

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A R T I C L E I N F O

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A B S T R A C T

While data on biological invasions and their economic toll are increasingly available, drivers of susceptibility to damage and cost-effectiveness of management in reducing long-term costs remain poorly understood. We used data describing the damage costs of, and management expenditure on, invasive species among 56 nations between 2000 and 2020 reported in the *InvaCost* database to test the overarching hypothesis that higher-income nations and those with higher trade volume have a higher efficiency to limit the damage incurred by invasive species by spending relatively more on management. We also tested whether nations with (*i*) more corruption have a reduced capacity to manage invasive species, leading to relatively higher damage costs, (*ii*) more educated citizens or greater technological and scientific output allow for improved incentives and ability to manage invasive species, thereby reducing relative damage costs, and (*iii*) economies based on higher primary resource dependencies (e.g., agriculture) are at greater risk of incurring high costs of invasive species, and so all other conditions being equal, have higher relative damage costs compared to management expenditure. By focusing on the ratio between damage costs and management expenditure, we analyse the willingness of countries to invest in management as a function of the extent of the damage suffered. We show that economic activity, measured by

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the volume of trade, is the main determinant of this ratio — the greater the volume, the smaller the ratio. We also found a higher rate of increase in the damage:management ratio as a country's proportion of total land area devoted to agriculture increased, suggesting that a higher economic dependency on agriculture predisposes a country to greater damage costs from invasive species over time. When considering the proportion of total costs identified as damage-related, results indicated that higher government investment in education produced higher proportional damage, and lower corruption and lower trade volume both reduced proportional damage. Our overall results suggest that wealthier nations with high per-capita imports of goods and services are more susceptible to damage, but also have a greater capacity to reduce it, and are therefore less threatened by biological invasions than countries with fewer resources and lower imports.

1. Introduction

There have been considerable recent advances in assessing the costs of invasive species on national economies (Ahmed et al., 2023). Invasive species have been estimated to cost US$423 billion annually at the global scale (Intergovernmental Platform on Biodiversity and Ecosystem Services, 2023), doubling approximately every six years (Diagne et al., 2021; Henry et al., 2023). The rising number of new species introductions as a result of increasing trade of goods and services is partially to blame for the rise in economic impacts over time (Chapman et al., 2017; Hulme, 2009; Perrings et al., 2005; Seebens et al., 2021; Seebens et al., 2017; Turbelin et al., 2022; Westphal et al., 2008), as well as the observed and expected expansion of the ranges of many invasive species — especially invertebrates — from drivers of global change such as climate disruption (Bellard et al., 2013).

Researchers and practitioners recognise that early prevention and control is cost-effective because management becomes increasingly difficult and thus more costly as invasions progress (Ahmed et al., 2022b; Haubrock et al., 2022; Leung et al., 2002). The direct and indirect damage caused by invasive species can take many forms, including reduced agricultural yields (Stenseth et al., 2003), damage to infrastructure (Bradshaw et al., 2016), and health effects (Jones, 2019; Jones and McDermott, 2018), with the total cost of damage exceeding the cost of managing invasive species globally by an order of magnitude (Cuthbert et al., 2022). Early management should therefore reduce relative future damage, although there are likely social and political factors that lead to predictable variation in the extent to which this occurs. Identifying these factors is important to demonstrate support for cost-effective management regimes, whereby proactive or reactive management intervention efficiently reduce damage costs and highlight where improvements can be made. However, there is little information on which countries adopt cost-effective management in terms of magnitude and timing, the political and socio-economic profiles that drive interventions, and the extent to which management efficiently reduces the costs of future damage. In principle, lower-income countries should have fewer financial resources and therefore, less capacity to invest in management, fewer physical capital assets to damage, but also potentially more corruption that weakens their capacity to manage invasive species (Latombe et al., 2023). Conversely, higher-income countries could be more inclined to early management, but can also be expected to have better 'reactive' capacity (Early et al., 2016) to limit relative damage from invasive species (Lira-Noriega and Soberón, 2015; McDermott et al., 2013).

To test these hypotheses, we analysed the ratio between the total recorded cost of damage (D) arising from invasive species and expenditure on their management (M) at a national scale. The larger this ratio (D:M), the higher the relative management expenditure compared to the damage costs incurred in any given country. Examining which main political and socio-economic factors best explain variation in the D:M ratio among countries can therefore indicate the most likely drivers of management intervention. The D:M ratio can decrease by increasing a country capacity to manage invasions (increasing M), or by decreasing its susceptibility to damage (decreasing D). The advantage of analysing the factors explaining variation in the D:M, rather than those determining gross management costs, is to overcome the inevitable positive correlation between national wealth and investments in invasive-species management (Early et al., 2016; Hulme, 2009; Paini et al., 2016). For example, if a high-income nation experiences greater damage costs from invasive species because of the high value of its assets, yet it invests in managing this threat at the same relative proportion of its total wealth as a lower-income nation with less valuable assets, the D:M ratios for the two nations would be the same.

The challenge is to identify and test which socio-economic measures indicate the relative capacity to manage the economic threat of invasive species. We therefore identified the following measures to test components of the main hypothesis. (1) We first predict that higher-income nations — measured as per-capita gross domestic product and importation of goods and services (Hudgins et al., 2023) — have greater capacity to respond to biological invasions (i.e., financial, capital, and human resources available, plus political and cultural (Reo and Ogden, 2018) priorities, to manage invasive species), and so should demonstrate lower D:M compared to lower-income nations. (2) Next, we hypothesise that D:M will be higher for countries with more corruption because they have lower capacity to manage invasive species relative to countries with less corruption. (3) We also predict that countries with more educational attainment and greater technological and scientific output have lower ratios because of factors including greater access to knowledge and tools that enhance management cost-effectiveness, and public acceptance (e.g., Drummond and Fischhoff, 2017) of management measures, among others. From the perspective of susceptibility to the damage caused from invasive species, we also predict that (4) countries more dependent on primary production (e.g., agriculture) for their economic output will be more at risk of incurring damage costs from existing and future biological invasions, and so all other conditions being equal, will have higher D:M.

Because the D:M can also vary given time lags (years; decades) between actions and outcomes (Pendergast et al., 2015; Tobin et al., 2011), we also analysed the determinants of the rate of change of the D:M over time as an indicator of the cost effectiveness of early management. This is because a country with high management expenditure at time t should have reduced damage costs in the future, $t + 1$, and thus a ratio that decreases over time because management expenditure typically reduces alongside lower damage costs. Although in practice the temporal trend in the ratio might reveal other information than the cost effectiveness of early management (for example, costs might lag behind increasing population sizes of established invasive species), we predict that nations with higher capacity should have decreasing rates of D:M over time.

2. Data and methods

2.1. Standardising and comparing costs

Using the *InvaCost* database (Diagne et al., 2020b) available from the `invacost` package (Leroy et al., 2020) in R (R Core Team, 2023), we compiled all derived annual costs (in 2017 US$; column 'Cost_estimate_per_year_2017_USD_exchange_rate') by country from 2000 to 2020 (observed, highly reliable costs only, meaning that these costs were realised or empirically incurred within the invaded habitat and that they originate from peer-reviewed articles and official reports, or grey material but with documented, repeatable and traceable methods). We chose this period as a trade-off between maximising the number of years and cost data available for the highest number of countries to include in our sample. To make costs comparable, we applied the *expandYearlyCosts* function in the `invacost` package using the fields 'Probable_starting_year_adjusted' and 'Probable_ending_year_adjusted' to expand costs through their probable duration (Leroy et al., 2022) (therefore, we retained costs from before 2000 expanded into that year, but removed expanded costs prior to 2000).

To account for different sampling rates among countries and time periods (we excluded countries without recorded damage cost or management expenditure data), we divided the 20-year period into 3-year intervals, and then resampled (with replacement) each interval based on the maximum number of cost estimates within the expanded database for any 3-year interval for that country between 2000 and 2020. Resampling was necessary to standardise the number of cost and expenditure estimates available across countries. We then took the median (± 95% confidence limits) annual values per category (damage costs or management expenditure based on the column 'Type_of_cost_merged') per interval and calculated the ratio of the two quantities (i.e., D:M). From these intervals, we calculated a bootstrapped (10,000 samples) median ratio based on all data for each country over the entire 20-year interval. We also calculated the proportion of the total reported costs identified as 'damage' as a separate response variable.

2.2. Temporal trends in relative damage costs and management expenditure

We first describe seven plausible scenarios of temporal change in D:M (Fig. 1a,b). Under the assumption of increasing management expenditure over time, D:M declines at an increasing rate from a situation of weakly increasing damage costs (Scenario 1) to rapidly declining damage costs (Scenario 4; Fig. 1a). When assuming constant management expenditure over time (Fig. 1b), D:M shifts from an increase over time when damage costs are increasing slowly (Scenario 5), to a rapidly decreasing trend when damage costs decrease rapidly (Scenario 7). As such, the mean rate of change of D:M, calculated as the median instantaneous exponential rate of change (*r*) over all 3-year intervals per country:

$$r_t = log_e\frac{(\mathrm{D:M})_{t+1}}{(\mathrm{D:M})_t}$$

where $t =$ any 3-year interval, becomes increasingly negative assuming an increasing management expenditure, or from positive to increasingly negative assuming constant management expenditure (Fig. 1c). We do not consider the rare cases where management expenditure decreases over time, considering the prevalent lack of cost-effectiveness in present day-management given the general trend in reactive rather than proactive management and spending (Epanchin-Niell and Hastings, 2010; Lodge et al., 2006; Simberloff et al., 2013).

Different nations will likely have different starting points along the D:M trajectory for the interval of interest due to their unique invasion histories, so differences in D:M itself among nations might not

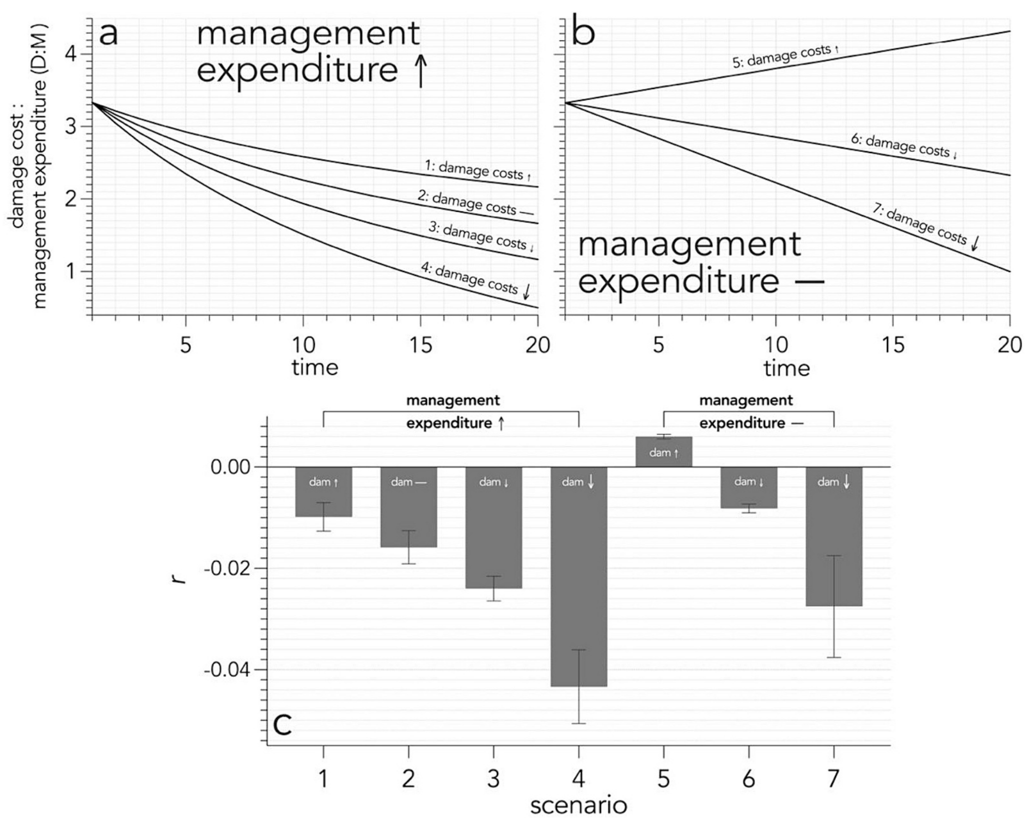

Fig. 1. Relative scenario schematic for hypothesis testing. (a) Assuming management expenditure is increasing over time, the damage cost:management expenditure ratio (D:M) declines slowly when damage costs increase slowly (Scenario 1), with increasingly rapid declines in D:M as damage costs either remain constant (—; Scenario 2), decrease slowly (Scenario 3), or decrease rapidly (Scenario 4). In all four scenarios, management expenditure is cost-effective for reducing relative damage costs, but at increasing rates. (b) Assuming management expenditure remains constant over time, D:M increases when damage costs increase slowly over time (Scenario 5), or D:M decreases slowly when damage costs decline slowly (Scenario 6), or rapidly when damage costs decrease rapidly (Scenario 7). Only in the latter scenarios (6, 7) is management cost-effective for reducing relative damage costs. (c) The mean rate of change ($r_t = \log_e([\mathrm{D:M}]_{t+1}$ / $[\mathrm{D:M}]_t)$) of D:M declines monotonically from Scenarios 1–4 (management expenditure increasing), and from Scenarios 5–7 (management expenditure constant).

necessarily reveal the whole picture of inter-country differences in the capacity to manage invasions. However, the rate of change in D:M should control for the potential differences where any given nation begins its D:M trajectory. We also considered an additional response — the proportion of total costs arising from damage — to test our hypotheses, with the proviso that proportional data often compromise linear models because of inflation of variance at the extremes (near 0 or 1).

2.3. Hypothesis-testing framework

Given the small sample size of countries with cost and national-scale socio-economic data available in *InvaCost*, we split our hypothesis framework into three phases from which we selected the most supported correlates and then combined these into a final analysis phase.

Phase 1: This phase analyses whether a country's economic activities, health capacity index, and corruption affect management performance. We first predict that D:M would decline as per-capita wealth (gross domestic product), per-capita imports of goods and services, and global health security (ability to deal with infectious disease outbreaks)

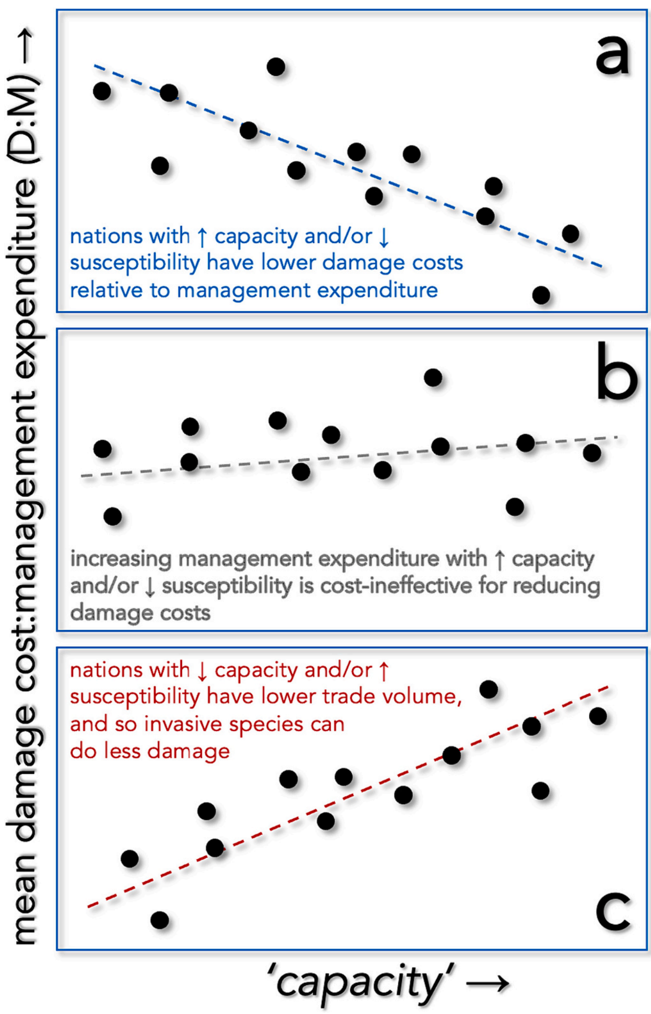

Fig. 2. Schematic for hypothesis testing. With the mean ratio of damage cost: management expenditure (D:M) per country, (a) the first hypothesis is that nations with higher 'capacity' to manage invasions and/or lower susceptibility to invasions have lower damage costs relative to management expenditure (black dots represent individual countries). In contrast, (b) higher capacity and/or lower susceptibility is cost-ineffective at reducing D:M. The third contrasting hypothesis in (c) predicts that nations with the lowest 'capacity' and/or highest susceptibility have fewer resources to be damaged, so D:M would in fact increase with capacity.

increases, and that D:M would increase as its corruption declines (Fig. 2a). Or, one can hypothesise that increasing management expenditure is cost-ineffective for reducing D:M (Fig. 2b), or even that countries with less capacity to manage invasive species have lower gross domestic product and so invasive species do less relative damage (Fig. 2c). For each country, we took the median r for the available time series (i.e., countries with declining D:M over time have lower r compared to countries with stable or increasing D:M over time).

We obtained the relevant data to test these hypotheses from the following sources: World Bank (data.worldbank.org) — per-capita gross domestic product (GDP) and per-capita imports of goods and services (mean of last five years); Global Health Security Index (ghsindex.org); Transparency International (transparency.org) — 2021 corruption perception index. We also considered another metric of trade (container port traffic), but there were too few data to provide reliable sample sizes.

Phase 2: This phase encompasses a country's *reliance on and engagement in primary production*. We predict that countries with a higher reliance on primary production (agriculture, fisheries, and forestry) have a higher D:M (primarily due to a higher proportion of costs arising from damages by invasive species) than those with a more diverse economic portfolio incorporating secondary and tertiary sectors. In essence, this represents a country's susceptibility to incur direct economic losses from biological invasions. We included two different metrics of primary production from the following sources: Food and Agriculture Organization of the United Nations (fao.org/faostat) — value-added net output of the agriculture, fishing, and forestry (primary production) sectors (% GDP); and World Bank (data.worldbank.org) — proportion of total land area devoted to agriculture.

Phase 3: This phase includes metrics of a country's *educational and research capability*. We predict that countries with greater investment in education and a higher research output would have lower D:M driven primarily from a concomitant higher investment in the management of invasive species (higher proportion of management costs) than countries with lower research investment. We acquired data describing these components from the following sources: World Bank (data.worldbank.org) — government expenditure on total education (% of gross domestic product) and per-capita number of scientific and technical journal articles produced. We also considered including the number of researchers and research and development expenditure per country, but there were too many missing data to provide reliable sample sizes.

2.4. Multiple imputation

We then applied multiple imputation by chained equations using the `mice` library (van Buuren and Groothuis-Oudshoorn, 2011) in R (R Core Team, 2023) to impute any missing values in the predictor variables to maintain the highest-possible sample size for subsequent analysis. Multiple imputation using this method is robust for up to 75% missing values (Takahashi, 2017), and provides stronger inferences than ignoring missing data (Nakagawa and Freckleton, 2008). Assuming values were missing at random, we employed predictive means matching in the mice function with 500 maximum iterations to impute the missing data. There were 56 countries with cost data from *InvaCost* to derive the response variables. For the hypothesised explanatory variables, we applied multiple imputation to avoid having to delete records with missing data — total percent missing values were: 40.9% (value-added primary production); 34.8% (corruption perception index); 29.3% (global health security index); 15.2% (imports of goods and services); 14.1% (government expenditure on education); 11.6% (per-capita scientific and technical journal articles); 6.9% (% agricultural land); and 5.4% (per-capita gross domestic product). We then transformed and scaled each component variable as follows: $\log_{10}$ of the scaled (not centred) (*i*) D:M, (*ii*) per-capita gross domestic product, (*iii*) per-capita imports of goods and services, and (*iv*) per capita production of scientific and technical journal articles; scaled (not centred) logit of the proportions for (*i*) damage costs, (*ii*) agricultural land, (*iii*) value-added primary production, and (*iv*) government expenditure on education; and scaled (not centred) (*i*) corruption perception index and (*ii*) global health security index.

2.5. Models to test hypotheses

Using the imputed and transformed dataset, we first built a set of general linear mixed-effects models with different combinations of the best-supported predictor variables from each of the three phases because we suspected potential non-independence among the country values (i.e., similarity among countries within a region). We used the lme4 package (Bates et al., 2013) in R (R Core Team, 2023), coding a random effect according to continental region — North America & Caribbean (n = 6 countries); South America (n = 8); Africa (n = 9); Europe and Middle East (n = 18); Asia & Oceania (n = 15) — to account partially for spatial non-independence (no further subdivision of the random effect is possible given inadequate replicates [countries] to do so). We determined both the evidence for a non-random effect of the variables on D:M, as well as the goodness of fit (percent deviance explained per model). We ranked all models according to Akaike's information criterion corrected for small samples (AIC_c), which not only identifies relative model probabilities, it also explicitly reduces the impact of potential collinearity among variables by downweighting models containing highly correlated predictors (Burnham and Anderson, 2002; Burnham and Anderson, 2004). Nonetheless, we also tested for collinearity among variables using the *check_collinearity* function in the performance library (Lüdecke et al., 2021) in R (R Core Team, 2023).

We also built boosted-regression trees (Elith et al., 2008) with the imputed dataset using the `gbm` library (Greenwell et al., 2022) in R (R Core Team, 2023) to account for potential nonlinearity in the relationships between the response (D:M, proportion of total costs arising from damage, or the D:M rate of change r) and the phase-specific indicators. Machine-learning methods such as boosted regression trees are also generally insensitive to collinearity among predictor variables (Breiman, 2001; Cutler et al., 2007; Dormann et al., 2013; Elith et al., 2008). All boosted regressions had a bag fraction = 0.75 and a tree complexity = 2, but depending on response and analysis phase in question, the learning rate varied between 10^{-7} and 10^{-4}, and the tolerance varied between 10^{-6} and 10^{-4} (see R code at doi: 10.5281/zenodo.10801170 and https://zenodo.org/doi/10.5281/zenodo.10801170 for test-specific values). The general linear mixed-effects models developed in the previous section potentially miss sub-regional spatial non-independence, so to account for a deeper level of potential non-independence, and to quantify uncertainty in the relationships between the responses and each explanatory variable, we resampled countries from the dataset with replacement 1000 times. We then passed each resampled dataset to the boosted regression tree algorithm and then calculated the 2.5th and 97.5th percentiles for the respective distribution for each predicted ratio as the uncertainty bounds. We applied kappa (κ) limitation to the resampled selections to limit the influence of outliers (Bradshaw and Brook, 2016), where we retained only the resampled mean ranks within $\kappa\sigma$ of the overall average mean ($\kappa = 2$). We then recalculated the average and standard deviation of the mean rank, with the process repeated five times.

Finally, we applied general least-squares models that are designed explicitly to account for spatial autocorrelation among spatial units (countries, in this case) to the final model set using the *gls* function in the `nlme` library (Pinheiro et al., 2019) in R (R Core Team, 2023). For each country, we coded the centroid coordinates (in latitude/longitude) using the `rworldmap` (South, 2011) and `rgeos` (Bivand and Rundel, 2021) libraries in R (R Core Team, 2023), and determined which within-group spatial correlation structure was the top-ranked for the saturated model; we therefore ran the models in the final phase as per the general linear mixed-effects models. We ranked the ensuing models according to $wAIC_c$, and calculated relative goodness-of-fit using three different pseudo-R^2 metrics: McFadden, Cox and Snell, and Craig and Uhler (Bradshaw et al., 2019) using the *nagelkerke* function in the library `rcompanion` (Mangiafico, 2020) in R (R Core Team, 2023). We ran all code on the Flinders University High-Performance Computing facility *DeepThought* (Flinders University, 2023), and the R code and data to reproduce the analysis are available at doi: 10.5281/zenodo.10801170 https://zenodo.org/doi/10.5281/zenodo.10801170.

3. Results

The expanded database included 22,433 entries, of which 5208 related to damage costs (sum = US\$1.578 trillion) and 16,638 to management expenditure (US\$147.545 billion); 587 were 'mixed'). Damage costs were predominately (90.5%) due to loss of capital and repair of damaged goods (\$US142.463 trillion), and management expenditure was predominately (73.4%) intervention/control (US\$108.245 billion).

There were 56 countries with sufficient *InvaCost* data to calculate the bootstrapped median D:M (Fig. 3). In general, there was evidence for a power-law relationship between mean annual damage costs and mean annual management expenditure among countries (Fig. 4). However, the region-specific slopes and intercepts of this relationship varied markedly (Fig. 4), justifying the inclusion of region as a random effect in the general linear mixed-effects models.

We initially anticipated that we would need to control for the number of invasive species per country to compare costs among countries, but we found no relationship between either damage costs or management expenditure and the number of reported genera (Fig. S1; see also Discussion). For the correlates we considered, the median

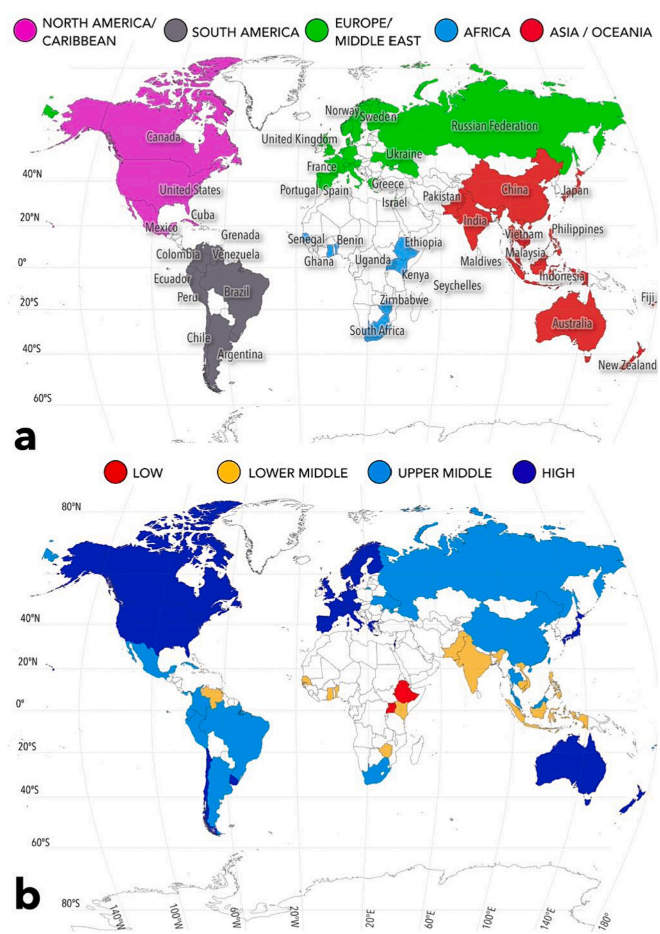

Fig. 3. Map showing distribution of countries included in our analyses, (a) their regional classification for the general linear mixed-effects models, and (b) their 2021–2022 income category according to the World Bank (data.worldbank.org).

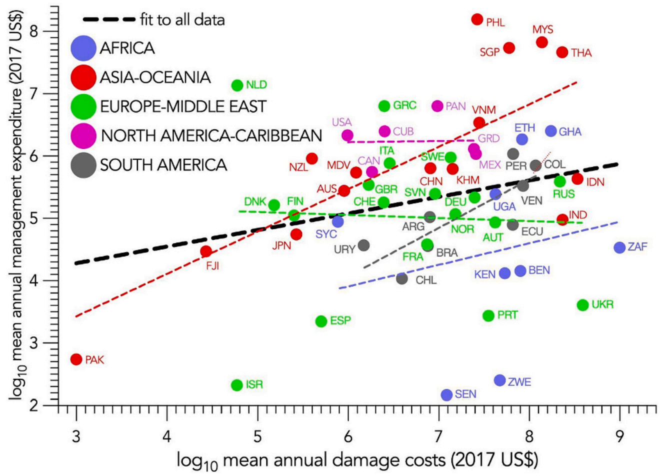

Fig. 4. Power-law relationship between resampled mean annual management expenditure and damage costs from invasive species across 56 countries. There is a weak, non-random linear increase in the $\log_{10}$ of damage cost as $\log_{10}$ management expenditure rises (information-theoretic evidence ratio for the entire dataset $>5.12 \times 10^{28}$; $R^2 = 0.04$). Also shown are the power-law lines of best fit for the entire dataset (black, dashed) and for each region separately (dashed). Also see Fig. 3 for a map of sampled countries.

ISO3 country codes: **ARG** = Argentina; **AUS** = Australia; **AUT** = Austria; **BEN** = Benin; **BRA** = Brazil; **CAN** = Canada; **CHE** = Switzerland; **CHL** = Chile; **CHN** = China; **COL** = Columbia; **CUB** = Cuba; **DEU** = Germany; **DNK** = Denmark; **ECU** = Ecuador; **ESP** = Spain; **ETH** = Ethiopia; **FIN** = Finland; **FJI** = Fiji; **FRA** = France; **GBR** = United Kingdom; **GHA** = Ghana; **GRC** = Greece; **GRD** = Grenada; **IDN** = Indonesia; **IND** = India; **ISR** = Israel; **ITA** = Italy; **JPN** = Japan; **KEN** = Kenya; **KHM** = Cambodia; **MDV** = Maldives; **MEX** = Mexico; **MYS** = Malaysia; **NLD** = Netherlands; **NOR** = Norway; **NZL** = New Zealand; **PAK** = Pakistan; **PAN** = Panama; **PER** = Peru; **PHL** = Philippines; **PRT** = Portugal; **RUS** = Russia; **SEN** = Senegal; **SGP** = Singapore; **SVN** = Slovenia; **SWE** = Sweden; **SYC** = Seychelles; **THA** = Thailand; **UGA** = Uganda; **UKR** = Ukraine; **URY** = Uruguay; **USA** = United States; **VEN** = Venezuela; **VNM** = Vietnam; **ZAF** = South Africa; **ZWE** = Zimbabwe.

absolute Kendall's τ across all correlate combinations was = 0.41, and the maximum absolute τ was = 0.79 (Fig. S2; Table S1). Per-capita gross domestic product and imports of goods and services had the highest positive correlation (0.79; Table S1).

3.1. Damage cost:management expenditure ratio (D:M)

a. Phase 1: economics/health security/corruption — Per-capita gross domestic product was collinear and correlated positively with per-capita imports of goods and services (Appendices 1 and 2), so we removed the former from all subsequent analyses. The general linear mixed-effects models demonstrated support for per-capita imports of goods and services, and the corruption perception index, but weak to no support for the global health security index in explaining variation in D:M among countries (Table S2). The boosted regression tree for Phase 1 also supported the inclusion of per-capita imports of goods and services and much weaker support for the corruption perception index, with a final coefficient of variation = 29.4 ± 16.9% for 37,500 trees (Fig. S3).

b. Phase 2: Reliance and engagement in primary production — According to the general linear mixed-effects models, neither value-added %GDP from primary production (agriculture, fisheries, and forestry) nor the proportion of terrestrial land area devoted to agriculture explained much variation in D:M (marginal $R^2 = 4.6$–5.3%; Table S3). The boosted regression tree for Phase 2 supported the inclusion of value-added % GDP from primary production (agriculture, fisheries, and forestry), but little support for the proportion of terrestrial land area devoted to agriculture, with a final coefficient of variation = 6.9 ± 22.8% for 5700 trees (Fig. S4).

c. Phase 3: Educational and research capability — There was little support from the general linear mixed-effects models to include per-capita production of scientific and technical journal articles (marginal $R^2 = 4.4\%$) or government investment in education in the combined-phase analysis (marginal $R^2 = 0.6\%$; Table S4). While the boosted regression tree for Phase 3 suggested approximately equal contribution of per-capita production of scientific and technical journal articles and government investment in education to variation in D:M, there was more support for the former. The final coefficient of variation = 40.8 ± 12.9% for 48,600 trees (Fig. S5).

d. Combined phases — We therefore retained the following four variables for the combined-phase analysis: (*i*) per-capita imports of goods and services, (*ii*) corruption perception index, (*iii*) value-added % GDP from primary production (agriculture, fisheries, and forestry), and (*iv*) per-capita production of scientific and technical journal articles. According to the general linear mixed-effects models, the economic indicator per-capita imports of goods and services) had the highest individual contribution (R_m = 22%) to explaining the variance in D:M among countries (Table 1), supporting the hypothesis that increasing economic activity reduces the D:M. All other variables provided low explanatory power in comparison (R_m = 4.5%–9.6%; Table 1), and none added much additional explanation when combined with imports of goods and services (Table 1).

The resampled-dataset boosted regression tree analyses for the combined phases had a final coefficient of variation = 51.5–80.8%, and also showed that per-capita imports of goods and services explained the most variation in the D:M ratio among countries (Fig. 5). Here, greater imports led to reduced damage costs relative to management expenditure (Fig. 5b).

While the corruption index (CPI) had some support in the boosted regression trees in terms of relative influence (Fig. 5c), it had a complex, non-monotonic relationship to D:M (Fig. 5c), which only partially supports our hypothesis that increasing corruption led to a higher D:M. The influences of value-added primary production (VAPP) and science/technology journal articles (STJA) on variation in D:M were weak (Fig. 5d,e).

The most-supported spatial autocorrelation structure in the general least-squares models was spheroid, with the country centroids explaining 21–23% of the variation in the D:M. After accounting for spatial relationships, there was support for all variables considered, although per-capita imports of goods and services had the highest relative explanatory power among the single-parameter models for variation in D:M among countries (Appendix 2, Table S5).

3.2. Proportion of total costs from damage

Changing the response to the proportion of total costs arising from damage (damage cost ÷ [damage cost + management expenditure]), per-capita gross domestic product was also identified as collinear with this response (as for when D:M was the response; Section 3.1), so we removed it from subsequent analyses. In Phase 1 we again found most support for the import of goods and services (Appendix 4, Table S6; Fig. S7). After completing each phase analysis (Appendix 4), we retained per-capita imports of goods and services, corruption perception index, proportion of terrestrial land area devoted to agriculture, government investment in education, and per-capita production of scientific and technical journal articles in the final phase (Table S9, Fig. S9). Overall, the general linear mixed-effects models revealed lower explanatory power (~ half) for the response of proportional damage (R_m = 10.5–13.8% for the highest-ranked models; Table S9) compared to when the response was D:M (R_m = 19.2–23.4% for the highest-ranked models; Table 1), consistent with our expectation that proportions can often be problematic for linear models. The resampled boosted regression trees in the final phase showed the strongest influence of government investment in education (more investment = higher proportional damage), followed by the corruption perception index (lower corruption = lower

Table 1
General linear mixed-effects models of the relationship between the ratio of damage cost to management expenditure (D:M) among countries and four predictor variables for the combined-phase analysis (only models where $\Sigma w\mathrm{AIC}_c > 0.8$ shown): IGS = per-capita imports of goods and services; CPI = corruption perception index; VAPP = value-added %GDP from primary production (agriculture, fisheries, and forestry), and STJA = per-capita production of science/technology journal articles. k = number of model parameters; ℓ = log-likelihood; AIC_c = Akaike's information criterion corrected for small samples; $\Delta\mathrm{AIC}_c$ = difference in AIC_c between model and top-ranked model; $w\mathrm{AIC}_c$ = AIC_c weight (≈ model probability); R_m = marginal R^2; R_c = conditional R^2 (%).

model	k	ℓ	AIC_c	$\Delta\mathrm{AIC}_c$	$w\mathrm{AIC}_c$	R_m	R_c
~IGS + VAPP	5	−91.711	193.961	0	0.311	23.4	42.5
~IGS	4	−94.187	195.533	1.571	0.142	22.0	41.6
~IGS + CPI + VAPP	6	−91.122	195.690	1.728	0.131	22.9	43.1
~IGS + VAPP+STJA	6	−91.585	195.844	1.882	0.121	22.6	42.0
~IGS + STJA	5	−93.606	196.278	2.316	0.098	20.6	40.7
~IGS + CPI + VAPP+STJA	7	−90.542	197.082	3.120	0.065	21.1	43.6
~IGS + CPI + STJA	6	−92.434	197.268	3.306	0.060	19.2	42.4
~IGS + CPI	5	−93.726	197.505	3.544	0.053	21.6	41.4
~CPI	4	−96.537	201.314	7.353	0.008	9.6	36.8
~CPI + STJA	5	−95.911	202.620	8.658	0.004	8.4	41.0
~CPI + VAPP	5	−95.915	203.314	9.352	0.003	9.4	37.1
~CPI + VAPP+STJA	6	−95.098	204.430	10.468	0.002	8.7	40.3
~VAPP	4	−98.190	205.057	11.095	0.001	5.3	31.2
~STJA	4	−99.054	205.568	11.606	0.001	4.5	30.1
intercept-only	3	−99.754	205.657	11.695	0.001	0.0	32.2
~VAPP+STJA	5	−97.966	206.876	12.915	0.000	6.0	31.0

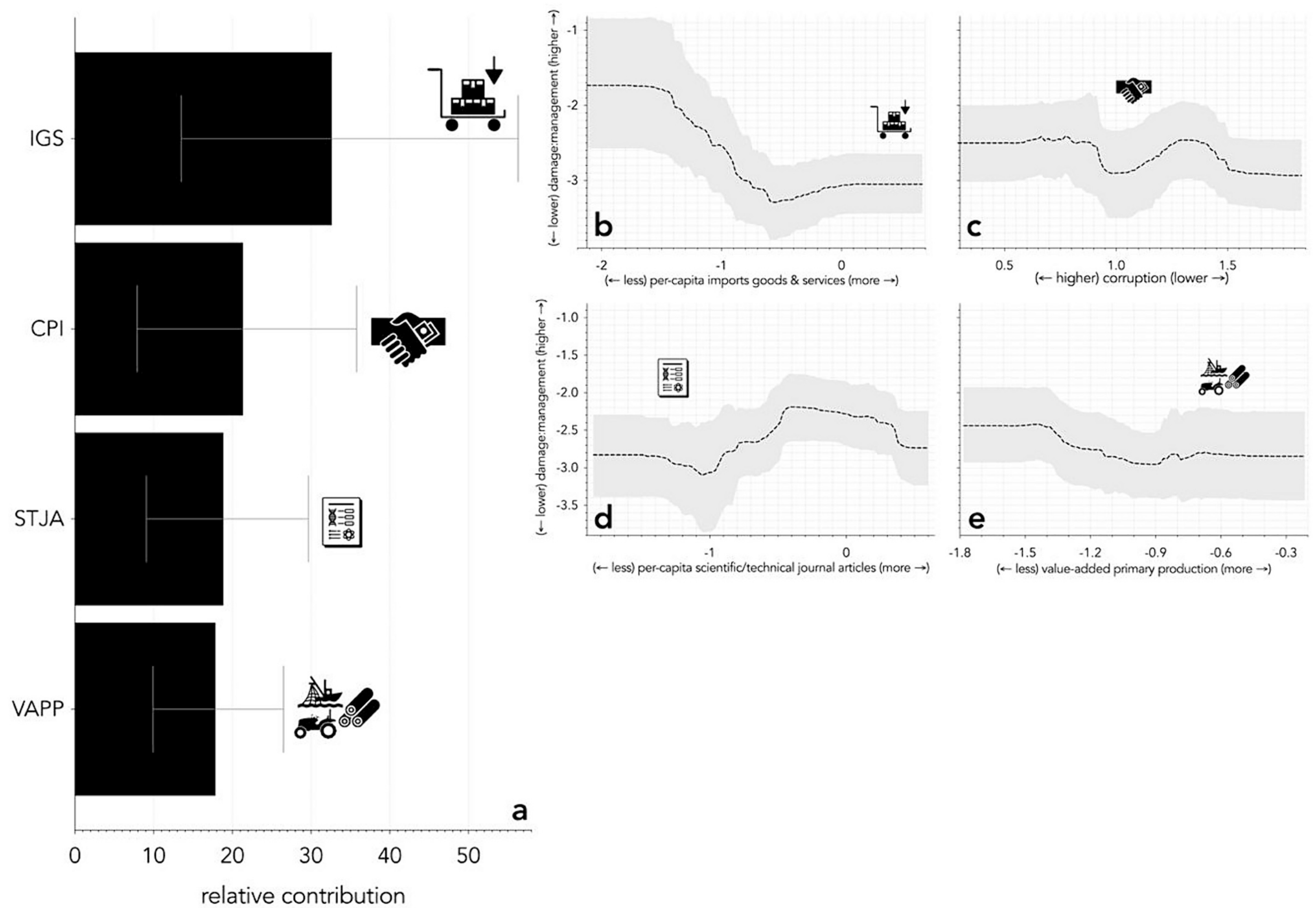

Fig. 5. Final-phase boosted regression trees (Phase 1–3 results shown in Supplementary Information, Appendix 3, Fig. S4–S6, Tables S2–S4) for the D:M ratio after removing per-capita gross domestic product (GDP) because of high collinearity (Appendix 2). (**a**) Relative contribution and relationships in predictor variables (**b**–**e**) to variation in the ratio of damage cost:management expenditure (D:M) derived from boosted regression trees, explaining 48.2–80.3% of the deviance. (**a**) Bars represent the relative influence of the resampled-dataset boosted regression trees (± 95% confidence bounds) for the variables described below. Predicted D:M expressed as a function of variation in (**b**) per-capita imports of goods and services, (**c**) corruption perception index (higher values = lower corruption), (**d**) per-capita scientific/technological journal articles, and (**e**) value-added primary production. In panels **b**–**e**, centred and scaled covariate values are displayed along the x axis.

proportional damage), and per-capita imports of goods and services (higher imports = lower proportional damage) (Fig. S9). The coefficient of variation for the final-phase boosted regression trees was slightly higher for the D:M responses (51.5–80.8%) compared to the proportion damage response (44.4–78.4%).

3.3. Median instantaneous exponential rate of change in D:M (r)

The phase-specific tests (Appendix 5; Tables S10–S12) revealed support only for the inclusion of proportion of land area devoted to agriculture (Table S11, Fig. S10) to explain variation in *r*. According to the general linear mixed-effects model, the proportion of land area devoted to agriculture alone explained 13.1% of the variation in *r* among countries (Table 2).

The resampled-dataset boosted regression tree analyses had a coefficient of variation = 9.4–56.1%, and revealed that as the proportion of agricultural land increased, the rate of temporal change (*r*) in D:M also increased (Fig. 6). There is therefore support for the hypothesis that an increasing dependence on agriculture results in an increasing *r*.

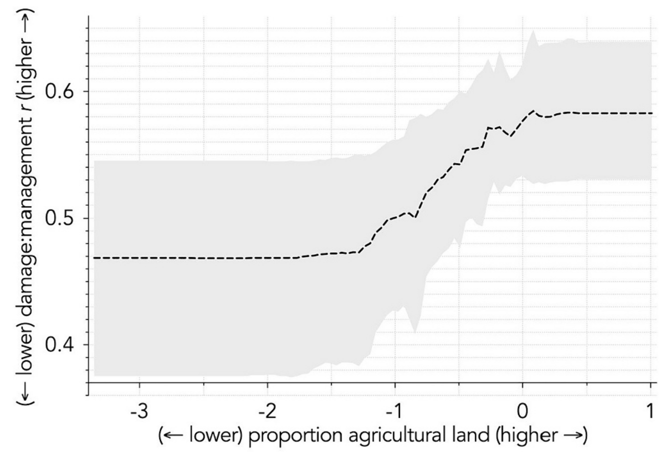

Fig. 6. Predicted median *r* of D:M expressed as a function of variation in proportion of total land area devoted to agriculture from the boosted regression tree analysis.

4. Discussion

Our study highlights that countries with lower per-capita imports of goods and services as an indicator of economic activity generally have a lower capacity to control and prevent potential damages caused by invasive species. Using the ratio of reported damage costs to reported management expenditure, we found that nations with greater trade volume tend to have lower damage cost:management expenditure ratios (Fig. 5). Our results thus suggest that even if the risks of biological invasions are higher as trade increases (Hulme, 2021), more economically active nations appear to be able to prevent at least some invasions and/or limit the damage of those invasive species that do establish.

Importantly, our results appear to support the notion that management expenditure reduces overall damage costs, because those nations investing more in management have lower relative damage costs. Although less likely, a high ratio might also indicate a laissez-faire attitude towards the invasion process, and potentially a lack of capacity to manage the threats cost-effectively. This suggests an implicit (conscious or unconscious) acceptance of accumulating damage caused by biological invasions because it is either too costly to manage the invasion relative to the damage it causes, or the perceived magnitude of the damage is not high enough to justify intervention. In addition, the D:M could potentially remain high when damage costs of biological invasions are not ultimately borne by those paying for their management — for example, retail customers paying higher produce prices following reductions in crop yield due to damage by invasive species, but the industry itself avoids the additional costs from neglecting to invest in cost-effective biosecurity measures.

Changing the response variable to proportion of the total costs identified as damage provided lower explanatory power, possibly because proportions are constrained between 0 and 1, but revealed again the importance of trade volume as a predictor of changing proportions among nations. However, using this response also identified the counter-intuitive outcome that greater educational investment led to higher proportional damage, a result we cannot easily explain. Perhaps another cultural or economic component we could not measure here might be responsible (e.g., more informed people might in fact challenge management intervention), warranting further investigation. Additionally, we found some evidence for corruption increasing proportional damage, probably because it prevents the implementation of cost-effective management. Finally, that higher proportions of land devoted to agriculture were correlated with higher rates of increase in the D:M suggest that all other conditions being equal, a greater economic reliance on agriculture might predispose nations to a greater potential for damage from invasive species. This could arise because agricultural activity generally occurs over spatial scales much broader than individual ownership (e.g., many independent actors), so efficiently managing established invasive species in the agriculture sector would require exceptional jurisdictional coordination and landowner cooperation.

Table 2
General linear mixed-effects models of the relationship between the median instantaneous exponential rate of temporal change (*r*) in the ratio of damage cost:management expenditure (D:M) among countries and one predictor variables for the combined-phase analysis: AGRL = proportion of total land area devoted to agriculture. k = number of model parameters; ℓ = log-likelihood; AIC_c = Akaike's information criterion corrected for small samples; ΔAIC_c = difference in AIC_c between model and top-ranked model; $wAIC_c$ = AIC_c weight (≈ model probability); R_m = marginal R^2; R_c = conditional R^2 (%).

model	k	ℓ	AIC_c	ΔAIC_c	$wAIC_c$	R_m	R_c
~AGRL	4	10.220	−22.901	–	0.945	13.1	17.1
intercept-only	3	9.064	−17.207	5.695	0.055	–	4.5

We found no relationship between the number of invasive genera reported in the database and the total costs, either expressed as damage costs or management expenditure (Fig. S1). This result is counter-intuitive given suggestions that future increases in invasions will likely precipitate higher costs (Hudgins et al., 2023). However, there are many non-exclusive explanations for this inconsistency, including high variance in damage costs and/or reporting rates among countries, the disproportionate focus on reporting the damage from the worst invaders (and managing their damage), conflation of damage caused by native or invasive 'pests' (Diagne et al., 2023), and perhaps the notion that the most affected countries might not always have the capacity or will to manage all their invasive species, but only a (perceived-to-be-tractable or costliest in terms of damage) subset. Indeed, only about 3% of invasive species have associated cost data (Henry et al., 2023; Intergovernmental Platform on Biodiversity and Ecosystem Services, 2023).

The emergence of statistically supported relationships despite the high uncertainty and irregular sampling effort among nations is an important outcome, but there are still several caveats regarding the general interpretation. We were unable to distinguish ratios between damage cost and pre- (preventative; proactive) versus post- (reactive) invasion management expenditure, even though there are different relationships with damage costs between these two categories. For example, there is evidence that pre-invasion management is more cost-effective in limiting future damage costs compared to post-invasion investment (Cuthbert et al., 2022; Leung et al., 2002). While proactive management expenditure is approximately one order of magnitude lower than reactive management (Cuthbert et al., 2022), higher proactive spending would likely reduce the D:M further. In addition, the types of management expenditure likely vary in response to the particular groups of species any one nation intends to manage, meaning that monetary damages might not capture all of the negative aspects of the invasions (i.e., intangible impacts, non-use values, intrinsic values, etc.). Another issue is that, while the damage costs:management expenditure ratio controls for some of the impact of reporting bias when it is consistent across these two cost dimensions, values might be reported differently by different actors driven by different reporting capacities. For instance, management expenditure records might be more often provided in more obscure government reports and grey literature, whereas many damage costs might be more likely in the form of readily available academic articles. The quality and availability of record-keeping can also introduce bias, especially in cases where data from low-income regions are under-represented. This limitation is particularly pertinent for regions like sub-Saharan Africa where record-keeping practices might not be as comprehensive or consistent as in higher-income regions. This phenomenon could potentially inflate the D:M, especially in nations where expenditure records are difficult to procure. For example, different socio-political drivers could also alter patterns in the relative reporting bias of these cost types across countries, with some species not deemed to warrant concern in some regions, whereas they can be considered harmful and worthy of reporting in others (Carneiro et al., 2024). Future research will benefit from enhanced sensitivity analyses to understand the impact of missing data or incorporate additional data sources/proxies that fill the gaps in regions with sparse record-keeping.

The scenarios in Fig. 1 consider D:M ratios when gross damage costs either increase or decrease at different rates, or remain constant, in combination with either increasing or stagnant management expenditure. Although informative, we concede that this might present a simplistic overview, because temporal cost dynamics within countries can be more complex. For example, they can exhibit fundamental differences in the duration of the invasion, the ecology of the species involved, the dominant pathways of spread (Hudgins et al., 2023), or the impacted economic sectors (Cuthbert et al., 2021; Diagne et al., 2021; Henry et al., 2023). This is supported by empirical cost data for many taxonomic groups (Diagne et al., 2020a), where reported costs can be smaller by several orders of magnitude than the maximum values, indicating a tendency towards diminishing costs over time. Moreover, this has been substantiated by analysing damage costs for several genera (Ahmed et al., 2022a), and at the global scale when pooling all invasive species (Cuthbert et al., 2022). Although untested, it is plausible to assume that the same trends apply at the national scale, at least for some of the nations we considered. Ahmed et al. (2022b) formulated such logistic-type cost functions to quantify the cost of inaction — the additional expenditure due to delayed management. These cost functions can be parametrised using national damage cost and management expenditure data to construct a more dynamic D:M ratio, while still allowing for variable delays and efficiencies in management. We therefore require additional analyses to contrast nations with varying socio-economic capacities based on a D:M that accounts for time lags between management actions and outcomes, as well as cost effectiveness.

5. Conclusions

The ability to reveal the potential drivers of variation in the economic implications of invasive species across countries without explicit information on marginal costs and benefits maximises the utility of analysing data in global cost databases such as *InvaCost*. Improvements to the database could include, at least for well-studied systems or species, additional information on the methods underlying cost estimation (Ahmed et al., 2023; Hulme et al., 2024), as well as estimates of marginal costs that take management efficiency into account. Our analyses were able to control for the uneven sampling and potential reporting biases in these costs among countries, and demonstrate that nations with lower trade volume have a clear disadvantage in tackling the massive economic losses incurred from invasive species (Diagne et al., 2021). The implications are profound for countries with a relatively low capacity to address such losses, suggesting that because more economically active nations are susceptible to additional invasions originating from their potentially less management-capable neighbours, they would be wise to invest in the management of invasive species abroad. Such a form of international aid is self-serving, but could ultimately reduce the impact of invasive species across entire regions of the globe (Henry et al., 2023; Hulme, 2021).

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CRediT authorship contribution statement

Corey J.A. Bradshaw: Writing – review & editing, Writing – original draft, Visualization, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Philip E. Hulme:** Writing – review & editing, Writing – original draft, Methodology. **Emma J. Hudgins:** Writing – review & editing, Writing – original draft, Methodology. **Brian Leung:** Writing – review & editing, Writing – original draft, Conceptualization. **Melina Kourantidou:** Writing – review & editing, Writing – original draft. **Pierre Courtois:** Writing – review & editing, Writing – original draft, Conceptualization. **Anna J. Turbelin:** Writing – review & editing, Writing – original draft, Data curation. **Shana M. McDermott:** Writing – review & editing, Writing – original draft, Conceptualization. **Katherine Lee:** Writing – review & editing, Writing – original draft, Conceptualization. **Danish A. Ahmed:** Writing – review & editing, Writing – original draft. **Guillaume Latombe:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Alok Bang:** Writing – review & editing, Writing – original draft. **Thomas W. Bodey:** Writing – review & editing, Writing – original draft. **Phillip J. Haubrock:** Writing – review & editing, Writing – original draft. **Frédérik Saltré:** Writing – review & editing, Writing – original draft. **Franck Courchamp:** Writing – review & editing, Writing – original draft, Validation, Supervision, Funding acquisition, Data curation, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author did not use any AI or AI-assisted technologies in the writing process.

Declaration of competing interest

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Data availability

All data presented are available via the invacost R package. Related code and data available at https://zenodo.org/doi/10.5281/zenodo.10801170.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolecon.2024.108166.

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