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Geographic and taxonomic trends of rising biological invasion costs

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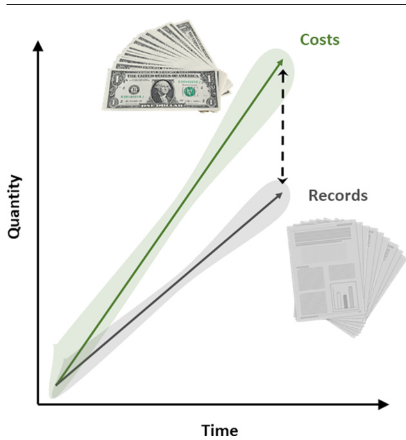
HIGHLIGHTS

- Research interest and economic impacts of biological invasions are globally increasing.
- Invasive alien species costs grew faster than reports of costs.
- Invasive alien species cost trends differ across geographic regions.
- Different taxonomic groups drive global and regional trends differently.

GRAPHICAL ABSTRACT



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ABSTRACT

Invasive alien species (IAS) are a growing global ecological problem. Reports on the socio-economic impacts of biological invasions are accumulating, but our understanding of temporal trends across regions and taxa remains scarce. Accordingly, we investigated temporal trends in the economic cost of IAS and cost-reporting literature using the InvaCost database and meta-regression modelling approaches. Overall, we found that both the cost reporting literature and monetary costs increased significantly over time at the global scale, but costs increased faster than reports. Differences in global trends suggest that cost literature has accumulated most rapidly in North America and Oceania, while

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monetary costs have exhibited the steepest increase in Oceania, followed by Europe, Africa and North America. Moreover, the costs for certain taxonomic groups were more prominent than others and the distribution also differed spatially, reflecting a potential lack of generality in cost-causing taxa and disparate patterns of cost reporting. With regard to global trends within the Animalia and Plantae kingdoms, costs for flatworms, mammals, flowering and vascular plants significantly increased. Our results highlight significantly increasing research interest and monetary impacts of biological invasions globally, but uncover key regional differences driven by variability in reporting of costs across countries and taxa. Our findings also suggest that regions which previously had lower research effort (e.g., Africa) exhibit rapidly increasing costs, comparable to regions historically at the forefront of invasion research. While these increases may be driven by specific countries within regions, we illustrate that even after accounting for research effort (cost reporting), costs of biological invasions are rising.

1. Introduction

The ecological, social, and economic effects triggered by global environmental changes are growing (Pyšek et al., 2020; Diagne et al., 2021a, 2021b). Accordingly, there is an urgent need to analyse biological trends over large spatial scales (e.g., patterns and potential discrepancies across local and global contexts) and across multiple taxonomic groups. This includes trends in biodiversity (Dornelas et al., 2014; Pilotto et al., 2020), and particularly cumulative effects incurred from global and regional changes (Diagne et al., 2021a; Haubrock et al., 2021a, 2021b). Despite the growing availability and resolution of large-scale data from long-term observations and research projects, such syntheses remain rare. One particularly profound aspect of global change is the growing rate of biological invasions over time, largely due to ongoing globalisation of transportation and trade networks (Seebens et al., 2017). Indeed, as globalisation intensifies, introduction pathways and trade patterns expand and erode natural barriers to the massive global pool of potential invasive alien species (IAS), leading to an increase in invasion rates (Seebens et al., 2018; Gippet and Bertelsmeier, 2021; Kaiser and Kourantidou, 2021).

The annual rate of first records of established alien species worldwide has been increasing over the last two centuries, with more than a third (37%) reported after 1970 (Seebens et al., 2017). Further, the acceleration in trade during the twentieth century along with the diaspora of European settlers in the nineteenth century likely caused considerable spatial variation in invasion rates across species and taxonomic groups (Cuthbert et al., 2022). More recent estimates predict that established alien species will increase by 36% from 2005 to 2050 (Seebens et al., 2021a, 2021b). This rapid global increase will likely vary across taxa, space, and time, and depend on introduction rates, pathways, and patterns across these dimensions. These trends are further complicated by the presence of time lags across many invasion stages and levels of human intervention at different stages, including establishment, spread, species detection, and economic impact identification, meaning that contemporary invasion and impact dynamics often reflect historical contexts (Crooks, 2005; Essl et al., 2011; Coutts et al., 2018). In turn, growing invasion rates and shifting dynamics could accelerate and intensify both ecological and economic impacts over time.

Using one frequently studied ecological impact indicator (i.e., species richness), a recent meta-analysis suggested that the published evidence has stabilized around an average 21% decrease in richness in invaded ecosystems (Crystal-Ornelas and Lockwood, 2020a). In contrast, economic impacts from invasions have increased in severity by several orders of magnitude on the global scale in the last decades (Diagne et al., 2021a). As invasion science is a growing field (e.g., based on numbers of publications; Richardson and Pyšek, 2008), a similar increasing pattern in the economic cost of IAS can also be found across regional and local scales, taxa and environments (e.g., Cuthbert et al., 2021, 2022; Haubrock et al., 2021a), with both increasing numbers of studies and costs documented over time. Whereas these works have repeatedly shown invasion costs to be increasing over time (e.g., see also Diagne et al., 2021a, 2021b) and indicated a positive correlation between monetary costs and publications (e.g., Haubrock et al., 2021a), there is an urgent need to investigate whether the cost increase is solely due to increased research effort (i.e., whether costs are increasing at a greater rate than reporting effort).

Evidence for these patterns can be identified using the InvaCost database, the largest and most comprehensive global compilation of published costs incurred due to IAS, which offers a sound basis for the synthesis and comparison of monetary costs at several scales (Diagne et al., 2020). Using currency as a common global metric, InvaCost provides evidence for much-needed investments to curtail future biological invasions and their impacts (Ahmed et al., 2021), albeit falling short at capturing non-market impacts as they are seldom reported in monetary terms (Hanley and Roberts, 2019). The InvaCost database includes both damage and management costs, incurred by both primary sectors (e.g., agriculture, forestry, fisheries) and wider society (e.g., health, public and social welfare) at a variety of spatial and temporal scales, per the reporting by underlying studies compiled (full list of descriptor variables at doi:https://doi.org/10.6084/m9.figshare.12668570). Within this database, standardisation protocols have enabled the assessment of temporal dynamics in invasion costs across a range of cost descriptors (e.g., from spatial and taxonomic to sectors of the economy affected). Harnessing these data permits the comparative analysis of temporal trends in invasion costs at global and more granular scales, to identify the countries associated with increasing economic costs from invasions and the taxa driving them. However, large discrepancies can exist between trends at global and local scales, with global patterns potentially masking smaller-scale dynamics. Accordingly, advancing the understanding of costs at sufficient spatial and taxonomic resolution is key to IAS policy and governance at levels where policy decisions are made, and management is designed.

Space for time substitutions (Haubrock et al., 2020), autoregressive mixed effects model approaches (Van Klink et al., 2020), and monotonic trend-based meta-analysis (Pilotto et al., 2020) have been shown to be useful tools in describing past trends in biodiversity changes. These, and other studies (e.g., Dornelas et al., 2014), have suggested declines in terrestrial, but increases in aquatic biodiversity and species abundances, highlighting the need for multi-location, high-resolution time-series for the identification of larger (temporal and spatial) patterns. Yet, trends in the monetary burden posed by IAS and the underlying research effort have not been investigated or linked formally using a comprehensive global dataset. With an increased understanding of the monetary burden posed by IAS, the present study aims to analyse the temporal trends in cost reporting and monetary costs of IAS at continental (regional) and national scales over time. Specifically, we ask: (1) Are costs increasing beyond what we expect due to increasing research effort? (2) Are long-term trends in IAS costs different across geographic regions? (3) If so, to what extent are such trends driven by different taxonomic groups? As a result of ongoing globalisation and the predicted increase in biological invasions (Seebens et al., 2021a, 2021b), as well as advances in invasion science, we expect to observe: (i) greater increases in the trajectory of monetary costs than that of cost reporting documents across all geographic regions, but (ii) differing taxon contributions to the potential variability of cost increases across regional trajectories. Given the difference in reported economic costs among continents and countries, these questions are answered at both global and continental scales, with countries in Europe included specifically as an additional case study owing to relatively high cost reporting levels.

2. Methods

2.1. Data processing

As a basis for the analysis, we used the latest available version of the InvaCost database (Diagne et al., 2020; Angulo et al., 2021; version 4, https://doi.org/10.6084/m9.figshare.12668570). This database version contains 13,123 cost entries described in a sufficiently detailed manner for large-scale syntheses of costs associated with IAS at different spatial, taxonomic and temporal scales. Following the InvaCost protocol (Diagne et al., 2020), data were mostly retrieved using a series of search strings entered into the Web of Science platform (https://webofknowledge.com/), Google Scholar database (https://scholar.google.com/) and the Google search engine (https://www.google.com/) to identify relevant references with monetary costs of invasions. Full details of the descriptor variables used to compile costs in the database are provided on an open access repository (https://doi.org/10.6084/m9.figshare.12668570), but these reflect the scale and context of the underlying reporting literature. In addition to systematic literature searches, opportunistic target searches (e.g., enquiries to regional experts for unpublished relevant material) were also performed. The references compiled were thoroughly assessed to assure relevance and extract cost information along with descriptors. However, note that within the IAS literature there is a great variety of costing practises which may lead to misunderstandings and discrepancies across reported costs. This may include, for example, differences in discounting across studies or other differences in methods to derive costs. While there are inherent difficulties in standardising costs because of such discrepancies, InvaCost generally accounts for a series of factors to ensure that cost records can be suitable for synthesis and analysis of trends. For example, it classifies costs with regard to their reliability with respect to source (classified as 'high' or 'low' depending on the type of publication and methodological approach used for cost estimation) and implementation (classified as 'potential' or 'observed', depending on whether the cost was extrapolated and/or predicted over time within or beyond its actual distribution area, or whether it was actually realised or empirically incurred, respectively). While in some cases potential costs may not have been necessarily currently realised (though older published potential costs may have since become realised, De Groote et al., 2020) or even expected to be realised, we decided to maintain the 'observed' vs. 'potential' costs classification as a distinct characteristic of the nature of costs reported in each reference. Despite the challenges in standardising costs and the presence of limitations, InvaCost is the most comprehensive database of reported economic costs of IAS to date that has largely succeeded in addressing issues related to standardisation across time and countries where costs were reported. In addition, this database is public and regularly updated with new cost data as they become known. All costs registered in the database were converted to US$ 2017 values (see Diagne et al., 2020 and Supplement 1 for detailed information). An inflation factor was used in the database through division of the Consumer Price Index (https://data.worldbank.org/indicator/FP.CPI.TOTL?end=2017&start=1960) of 2017 by that of the year of cost estimation. We note that InvaCost also converts costs using purchasing power parity (Diagne et al., 2020; https://doi.org/10.6084/m9.figshare.12668570), accounting for differences in price level and purchasing power across countries. However, this conversion could not be made for all cost entries, therefore potentially hampering our analysis. Additionally, using purchasing power parity would reduce comparability with other cost papers from InvaCost, which tend to use 2017 US$ based on classical exchange rates (Cuthbert et al., 2021, 2022; Haubrock et al., 2021a, 2021b; Diagne et al., 2021b; Fantle-Lepczyk et al., 2022), and results here would be qualitatively the same.

Deriving the cumulative cost of invasions over time requires consideration of the duration of each cost occurrence. Entries in the InvaCost database include the adjusted "probable starting" and "probable ending" years, referring to the year range in which the cost was known or assumed to occur, based on details described in the references. In those cases where information on the "probable starting" year was absent, we conservatively considered the year of publication of the primary data source as a benchmark, and derived the required information based on other temporal details provided in the source, if available. Using this information, we calculated the duration of each cost as the number of years between the probable starting and ending years. In doing so, some cost estimates with unspecified durations were either deemed to occur over a single year only, if they were provided on an annual basis, or not annualised if they have occurred over (unknown) longer periods. We acknowledge that this may cause some bias in temporal trends towards certain years, however, it does not inflate costs overall, but rather likely underestimates them. To ensure comparability of costs, we first standardised all the cost entries on an annual basis for the defined period of their occurrence. Hence, for example, a cost entry initially reported for a six-year period was transformed to six cost entries, with the total cost divided by six to get a yearly cost that was repeated for each of the six cost entries. We processed the database using the R package *invacost* (Leroy et al., 2020).

2.2. Trend identification and meta-regression modelling

To answer our first research question as to whether costs are increasing beyond what we expect due to increasing research effort, we investigated both trends in costs and cost reporting (i.e. research effort) of IAS over time and across space, environments and taxa. For this, we used a two-step procedure. In the first step of the analysis, we used a Mann–Kendall trend test (Kendall, 1949; Mann, 1945) to identify broad monotonic trends (i.e. the trends' slopes; S-statistic) in (a) the number of publications that reported IAS costs and (b) the cumulative costs (US$ 2017) of IAS across geographic regions, primarily at continental scales (Africa, Asia, Europe, North America, Oceania, South/Central America later referred to as South America). Our focus on broader geographic scales of analysis meant that we relied on potentially variable country-level trends in economic impacts, but this was a stronger test of broadscale directionality in cost patterns, since increased noise would be expected to dampen any largescale effects. We further focused on the case of Europe and differences among European countries as the InvaCost database contains abundant cost data from various European countries (Haubrock et al., 2021a, 2021b). Further, species invasions are not stopped by political boundaries (Liu et al., 2021), making it important to assess whether the countries within one continent could similarly react to surging invasions in order to jointly reduce invasion impacts. We used the S-statistic and its variance as a comparable effect size (Kendall, 1948) of the trend, as recently utilised in similar meta-analytical approaches using ecological time series (Daufresne et al., 2009; Pilotto et al., 2020). Concomitant to our hypothesis, we expected the strength of the trends of monetary cost to be steeper than those of the corresponding underlying research effort. To address our second and third research questions concerning whether long-term trends in IAS costs are different across geographic regions and to what extent trends are driven by different taxonomic groups, we compared slopes across regions and the contributions of different taxonomic groups to the respective trends (Pilotto et al., 2020). We further separated temporal autocorrelation (noise) in order to better capture the temporal trend (signal) in publications and cumulative costs by using auto- and cross-covariance and correlation functions (Venerables and Ripley, 2002) to identify serially correlated time series. We accounted for temporal autocorrelation within the time series using models of auto-covariance based on correlation functions (Venerables and Ripley, 2002) and applying the modified Mann–Kendall (Hamed and Rao, 1998) variance correction. We used the S-statistic (i.e., the time-series slope) provided by the Mann-Kendall test and its variance to quantify the effect size (i.e., slope) of each trend (Kendall, 1948). Then, we classified trends in cost reporting by considering whether they were 'significantly positive', 'positive but non-significant', 'stationary' (i.e., not trending positive nor negative), 'negative but non-significant', and lastly 'significantly negative'. The level of significance at which the null-hypothesis was rejected was set at $p \leq 0.05$.

In the second part of the analysis, we used the same approach to investigate trends in the magnitude of costs over time as a function of regional and taxonomic origin of the inferred IAS costs, using individual time-series for each species/reporting country combination. This was done to (i) increase the resolution and number of considered trends, thus representing both a proxy of research effort and a correction of monetary costs (i.e., correcting the increase by greater research effort), (ii) identify whether broader scale spatial trends were masking variability in trend magnitudes and directions at smaller scales, and (iii) identify differences across environments and taxonomic groups. For this, we kept taxonomic resolution (i.e., focusing at the species level) constant for each time series throughout the entire study period to ensure comparability. We identified trends in monetary costs over time via the Mann-Kendall trend test. We then used the *metafor* R package to fit a mixed-effect meta-analytic model that takes into account the variance of each species and country combination with random slopes (i.e., the origin of individual costs; Viechtbauer, 2010; Viechtbauer and Viechtbauer, 2015). The analysis was performed without intercepts, forcing the linear regression to pass through the origin, thus making the assumption that costs initiate at zero. We explored heterogeneity of trends (I^2) following the approach by Higgins and Thompson (2002) as implemented in the *metafor* R package and investigated how trends (specifically their slope and associated increase) differed across geographic regions (i.e., locations in which costs were incurred), environments (aquatic, terrestrial, semi-aquatic), and taxonomic classes. These explanatory variables showed little collinearity ($|r| < 0.5$) and were thus all retained as predictors.

3. Results

Globally, both the number of references reporting cost information (S-statistic ± SE: 338.2 ± 107.2; from here on referred to as 'research effort'), and the actual monetary costs of IAS (880.3 ± 207.0) significantly increased over time when pooled across geographic regions. The positive trend in both categories originated from significant increases ($p < 0.001$) across all regions, except for the Sub-Antarctic region (Fig. 1), but considerable heterogeneity (i.e., variation among regional trends) was identified in both costs ($I^2 = 96.7\%$) and research effort ($I^2 = 96.6\%$). Notably, the strength of the globally increasing cost trend was ~2 times stronger than the increase in the research effort, a trend which is consistent across all continents (Fig. 1) yet showed significant and spatially heterogeneous trends (Supplement 2).

When focusing on European countries to compare country-level trends in cost reporting literature and magnitude of costs (by combining costs and cost reporting publications within countries), we found higher spatial resolution cost reporting compared to other continents. We identified low heterogeneity in cost reporting across European countries ($I^2 \leq 1\%$) but higher heterogeneity for monetary costs ($I^2 = 94.9\%$, Fig. 2, Supplement

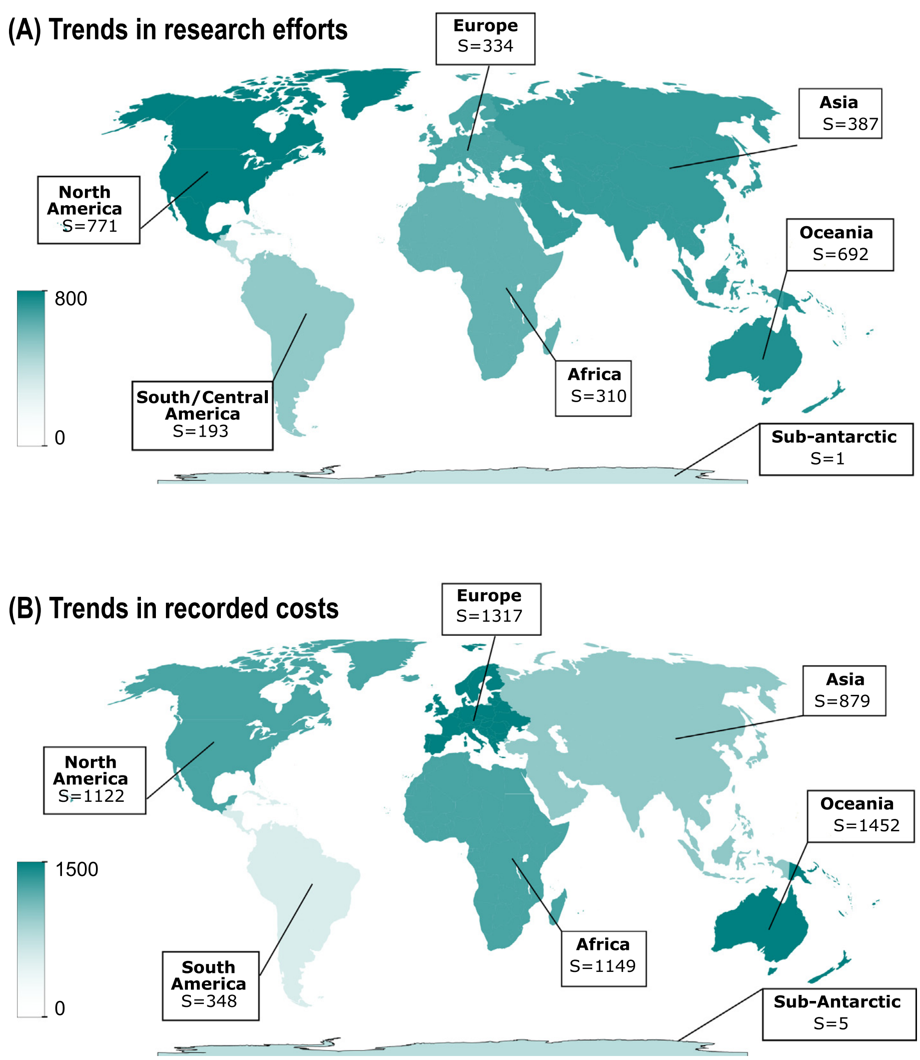

Fig. 1. Trends in research efforts (A) and monetary costs over time (B) incurred per continent according to the Mann-Kendall S-statistic. Strength of the trends (S) is shown as a gradient, from low (light green) to high (dark green).

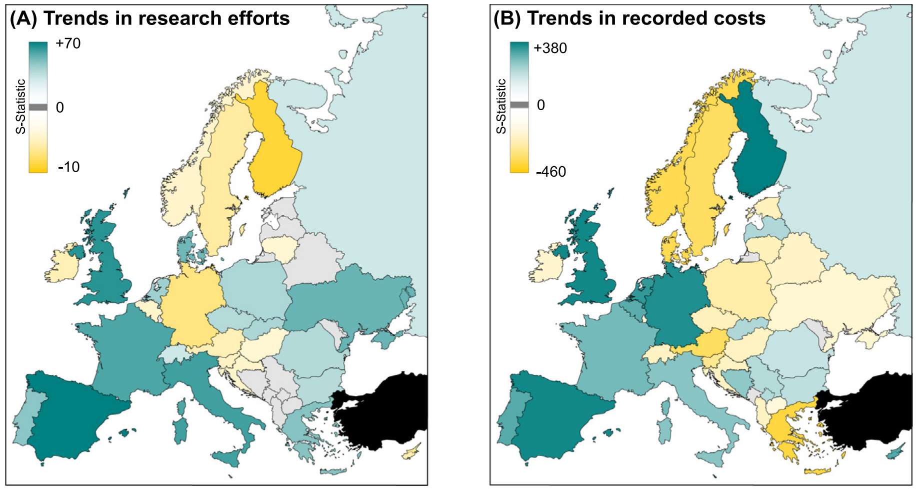

Fig. 2. Trends in the research efforts (A) and monetary costs over time (B) incurred per European country according to the Mann-Kendall S-statistic. Strengths of the trends are shown to distinguish positive (green) or negative (yellow) trends as a gradient, from low (light) to high (dark). Countries with stagnant trends (i.e. a slope of zero) are displayed in dark grey. Countries without available information are shown in light grey and countries that were not included in black.

3). Notably, Italy and Spain were the only countries showing a significant increase in the number of publications over time (Supplement 3a). The monetary costs showed significantly decreasing trends in eight (ordered according to increasing strength of the trend: Czechia, Croatia, Switzerland, Slovenia, Ukraine, Sweden, Austria, Greece) and significantly increasing trends in seven (ordered according to increasing strength of the trend: Malta, Cyprus, Portugal, Netherlands, Spain, Finland, United Kingdom) of the 37 countries for which costs were reported (Supplement 3b). Notably, certain countries also exhibited steeper trends in cost reporting over time (e.g., Norway for monetary costs), but these were non-significant owing to high variances.

3.1. Trends in monetary costs across species and countries

At the level of individual IAS records within different countries (n = 724), costs increased over time across the globe ($p = 0.037$), albeit with a high level of heterogeneity ($I^2 = 94.02\%$). Looking at five kingdoms (namely Animalia, Bacteria, Chromista, Plantae, and viruses) globally, we found that only costs of invasive alien algae (kingdom: Chromista) had significantly positive trends, whereas costs of fungi (kingdom: Fungi) were significant negative predictors (Supplement 4). With regard to classes, we identified herpesvirales (class: Herviviricetes), flatworms (class: Monogenea), oomycotes (class: Oomycetes), brown algae (class: Phaeophyceae), positive-strand RNA viruses (class: Pisoniviricetes), and ferns (class: Polypodiopsida) to positively predict cost trends, whereas ascomycete fungi (class: Dothideomycetes), Basidiomycota (class: Pucciniomycestes), and nematodes (class: Secernentea) were significantly negative predictors (Supplement 4).

This global trend was again driven by specific continents (i.e., Oceania, South and North America). However, the living environment of IAS (i.e., aquatic, terrestrial, semi-aquatic) was not a significant predictor of the global trend (see Supplement 5). In North America ($I^2 = 100.0\%$), the Chromista and Plantae kingdoms as a whole, as well as the classes Magnoliopsida, Mammalia, and Oomycetes, drove the overall trend of cost increase. In South America ($I^2 = 85.18\%$), the Plantae kingdom, specifically the Magnoliopsida class, significantly drove the negative trend in costs, while in Asia ($I^2 = 100.0\%$), the Secernentea class was the only significant driver of the negative trend in costs (Fig. 3; Supplement 6).

When looking at the Animalia kingdom (based on n = 351 species-specific trends), a small number of classes (n = 6) showed increases: 1) spiders (class: Arachnida), 2) cephalaspis (class: Cephalaspidomorphi), 3) gastropods (class: Gastropoda), 4) insects (class: Insecta), 5) mammals (class: Mammalia), and 6) monogenean flatworms (Class: Monogenea), with the latter two significantly increasing. While only nematodes (class: Secernentea) showed significant declines in costs over time, several other classes (n = 8) showed declining trends: 1) ray-finned fishes (class: Actinopterygii), 2) amphibians (class: Amphibia), 3) tunicates (class: Ascidiacea), 4) birds (class: Aves), 5) bivalves (class: Bivalvia), 6) crustaceans (class: Malacostraca), 7) bristle worms (class: Polychaeta), and 8) reptiles (class: Reptilia). Thus, Monogenea, Mammalia and Secernentea were identified as significantly trend-driving predictors within the Animalia kingdom ($I^2 = 93.6\%$; Supplement 7). Invasive animal species significantly drove the increasing costs in North America, while predicting a significantly negative trend of costs in Asia (Fig. 4A). Invasive plants were found to have stronger effects on global and regional trends compared to invasive animals, significantly driving trends of costs in Africa, South America, Oceania, North America, and Europe. Plants ($I^2 = 47.9\%$), however, were less diverse in terms of recorded classes (n = 8), with only species in the classes of Magnoliopsida and Polypodiopsida being identified as significant contributors to changes in the cost of invasive plants globally (Fig. 4B; Supplement 8); six other plant classes were found to be non-significant positive or negative predictors.

4. Discussion

We found that, while there has been a significant rise in both research effort and reported costs, the increase in costs cannot be explained by increased effort alone. Accordingly, despite the global rise in invasion costs and cost reports through time, costs are rising faster than the rate of reporting, indicating a decoupling of impact and effort. This allows us to conclude that the rise in costs observed is genuine and not driven by growing research effort alone. Yet, our work also highlights that more could be done to explore the link between IAS costs and cost reporting, since our analysis is done simply through pairwise comparisons of S-statistics at continental or global scales. Greater cost reporting efforts are required in many countries to facilitate more granular comparisons of trends.

Invasion science is a relatively new field, which has driven an increase in the awareness of impacts of IAS in the last several decades and has likely led to an increase in efforts to estimate and report their economic impacts. Similarly, rising numbers of biological invasions globally (Seebens et al., 2017, 2021a, 2021b) have likely accelerated the magnitude of economic impact, owing to the arrival of new species with impacts on multiple sectors of the economy, but also the growth of the global economy. Our results show spatially fluctuating, yet increasing costs from IAS globally, indicating a need to consider changes in publication effort across regional and national scales over time; for example, those triggered by shifts in investments

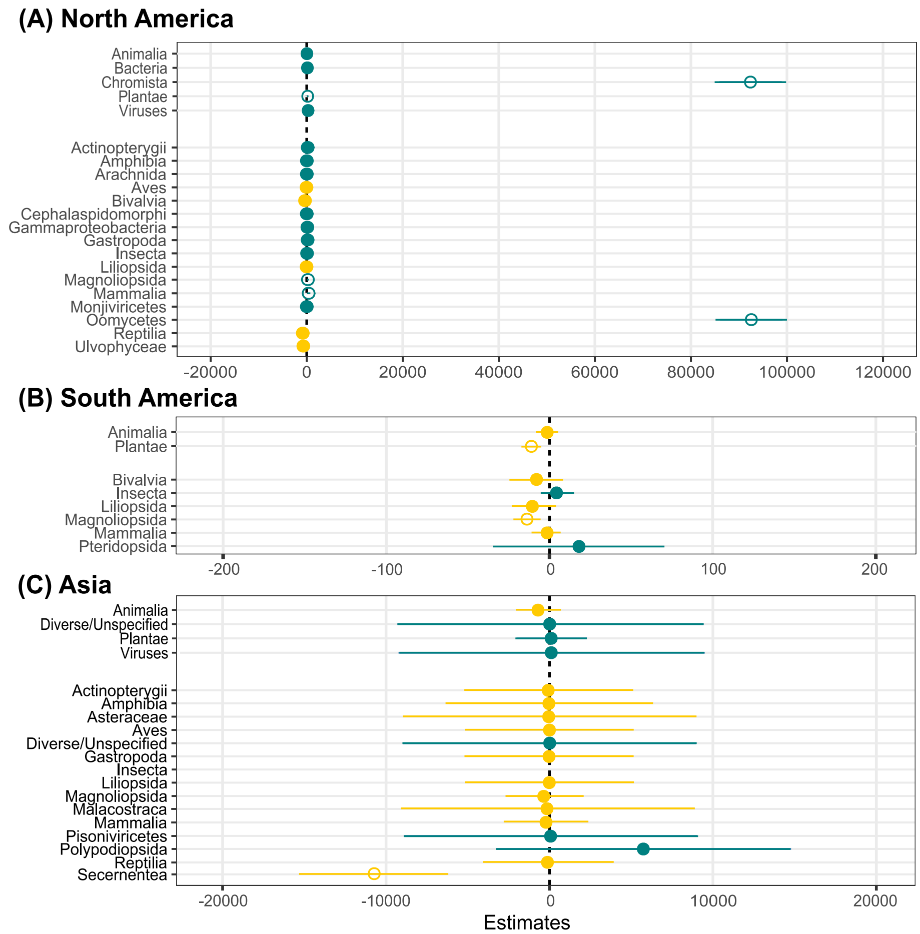

Fig. 3. Forest plots of collated time series from the meta-regression models (S-statistics ± confidence intervals, CI) showing the effective changes of costs for kingdoms and classes within the three continental regions with significant cost trends: (A) Oceania, (B) South America and (C) Asia. Positive and negative trends are displayed in turquoise and yellow, respectively. Significant trends are indicated by empty circles and non-significant trends full circles.

in research and conservation more broadly. We also highlight considerable geographic and taxonomic heterogeneity, showing that increases at the global level have been unevenly distributed, whereby certain countries and taxa have driven the apparent global increase.

When possible, examining our results at finer geographic resolutions allows us to unpack the main drivers of directional trends in costs and research effort. Whereas the relationship between costs, published literature on IAS costs, and scientific attention are linked, the observed trends suggest that there is a steeper increase in the release of publications with cost information in North America and Oceania in particular. These rapid increases are followed by Asia, Europe and Africa, with South/Central America lagging behind. Monetary costs, in contrast, are rising the most rapidly in Oceania, followed by Europe and Africa, North America, Asia and again lastly South/Central America. Furthermore, increases in regional costs were approximately twice as strong as the corresponding regional increase in the reporting of literature. These trends are reinforced by the even more stark difference in IAS-specific literature and monetary costs published at the country scale, whereby the significantly increasing global trend in both categories was driven by Oceania and North America, as well as South America. Historically, both North America and Oceania have been central to invasion science, particularly in terms of research (North America) and management (Oceania) (Veitch and Clout, 2002). In particular, syntheses and analyses of trends of invasion economic impacts in the past largely focused primarily on the United States (Pimentel et al., 2000, 2005), which, together with the country's relatively large research capacity and associate investments in IAS research, could have allowed for more/increasing cost reporting in the following years. Interestingly, we also found a steep increase in monetary costs of invasions in certain regions, such as Africa, but a less rapid increase in publications with cost information. This result suggests that if research effort was higher in these regions, much greater cost increases could have been revealed because costs rise particularly rapidly with each additional publication in these areas (Crystal-Ornelas et al., 2021). If the research capacity in these regions remains similar (low compared to other regions), then they may continue in the future to produce only a few select studies on well-known IAS. While it is likely that knowledge and evidence for additional IAS impacts in these regions exist, the evidence for economic impacts may not be easy to translate to monetary costs or be disseminated through academic channels (Cook et al., 2013). These tend to be limited in the developing part of the world or published in languages different than the ones employed in searches used in constructing the InvaCost database (Angulo et al., 2021; Diagne et al., 2021a, 2021b). These regional increases also fail to account for trends at more granular national scales, where particular countries may exhibit disproportionate contributions to total costs, such as South Africa in the African continent, which is a pioneer with many experts in IAS science (van Wilgen et al., 2020). Data disparities also contributed to our inability to model countries other than Europe at the sub-continental scale, and thus we are unable to discern the potentially highly variable pattern in trends across countries.

A similar difference between cost reporting and magnitude of monetary costs was also apparent in Europe, where directionality and strength of trends in cost reporting and actual costs did not coincide across countries. This is despite cost data in Europe being relatively abundant and IAS research generally being well-developed. However, Europe is also very diverse in terms of GDP, population density, and other factors such as

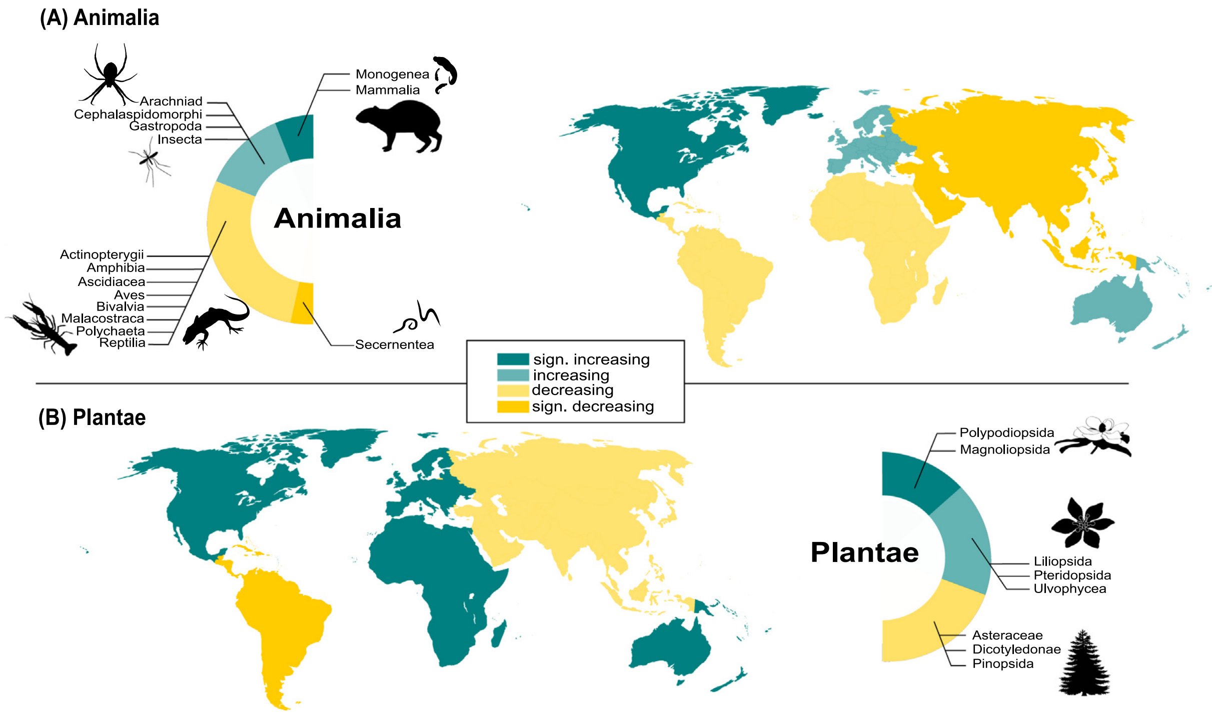

Fig. 4. Trends for invasive alien species within (A) the Animalia and (B) Plantae kingdoms, showing the breakdown in the trend of monetary costs across continental regions and classes.

strong connectivity across countries that may increase cross-cutting awareness of IAS costs (Haubrock et al., 2022). It is therefore no surprise that the majority of European countries display varying trends in both publication effort and costs over time. This trend could also be explained by national-scale differences, as we found only two countries (Spain and Italy) to express a significant increase in cost reporting literature, while several countries indicated a significant increase in costs (e.g., Finland, UK, Spain, Portugal and The Netherlands). However, the faster accrual for Spain may be a database-driven artefact because: (i) while compiling InvaCost, non-English literature (especially in Spanish) constituted a considerable subset of the currently available data (Angulo et al., 2021), and (ii) out of the 75 references included in the InvaCost database for Spain, 80% (60) were obtained through targeted efforts (e.g., consultations with environmental managers from all regions in the country; Angulo et al., 2021); including several grey literature sources. This may also partly reflect the differences in targeted searches when building the database, which was also influenced by the linguistic capacity of the database creators (Angulo et al., 2021), as opposed to other countries (e.g., Eastern European and Balkan countries) for which targeted searches were absent. Nevertheless, these gaps also highlight that the actual availability of cost information may be even higher among seemingly understudied regions due to a lack of publicly available literature or literature in English, possibly implying even higher costs and likely steeper increases in costs compared to those reported here.

Beyond high levels of awareness and research capacity, European countries may also have a shorter lag time in the reporting of costs, with countries or regions in the Global South and/or the developing world lagging behind in their efforts to record costs of IAS, leading to less steep or stagnating trends. Yet, using species-specific trends led to differing national trends when combining information at the country level (see Supplement 9), likely due to the variability in IAS within each country. We acknowledge, as a possible limitation, that our approach relied on the assumption that potential costs are as equally important as observed costs. We also found minimal differences between our main approach and one restricted to high reliability and observed costs across regions and European countries (Supplement 10). While some regions and European countries showed differences in the velocity of cost increases when relying on highly reliable costs, Africa expressed the steepest increase. On the one hand, this emphasises the relevance and importance of extrapolated costs in recent years, but also shows how realised costs are increasingly considered in Africa (Diagne et al., 2021a, 2021b). This is noteworthy, because invasion biology was not prominent in most countries of Africa until recent years when compared to e.g., Oceania, Europe or North America.

The diverse regional trends, underlying national trends, and differences between them further indicate that the scale of quantification for invasion costs is a key determinant in cost trends. For instance, we found that when combining data across continental regions (for both cost reporting and monetary costs), costs for South America did significantly increase. Yet, when increasing the resolution of underlying time series, we found an overall significant increase in both cost reporting and monetary costs, while no South American country showed a significant increase by itself (Supplement 2). This underlines the benefits of using the highest possible spatial resolution to investigate trends that large-spatial scale analyses may obscure. Regardless of the spatial scale, questionable relationships can arise if publication effort and taxonomic information are not appropriately accounted for. When this is done, the resulting models can provide insight into the taxa contributing to trend variability. In our case, plants and animals exhibited increasing costs, likely due to significant advances in the understanding of their impacts (Pyšek et al., 2008; Crystal-Ornelas and Lockwood, 2020b). However, similar to the aforementioned spatial scale effects, when we downscaled our analysis from kingdoms to classes, there was even more variability in cost and effort trend directions, as smaller sample sizes will have more variable trends. Animals displayed similar differences, with Monogenea and Mammalia significantly increasing and Secernentea significantly decreasing. In South America, no class or kingdom had a significant positive effect on the trajectory of costs over time, but multiple classes suggest a decreasing cost trend, slowing down the generation of costs in South America.

In terms of plant classes, Magnoliopsida comprise one of the overrepresented classes in the global naturalized alien flora (e.g., species belonging to Asteraceae and Fabaceae). Given the role of species biotic traits in driving their invasive characteristics (Pyšek et al., 2017; Schmidt and Drake, 2011), Magnoliopsida's frequent invasive traits, as well as their extensive distribution and high number of impactful species may explain their significant economic damage over time. On the other hand, the trend for Polypodiopsida may be driven by the fact that, although the invasive potential of terrestrial ferns was until recently overlooked, recent studies reveal that ferns have a high invasive potential (Jones et al., 2019; Yanez et al., 2020). Therefore, the increased attention towards these groups in recent years most likely influenced the taxonomic heterogeneity at the class level.

Our results highlight significantly increasing research interest as well as monetary impacts of biological invasions globally over time and also uncovers key regional differences driven by variability in cost reporting across countries and taxa. Since InvaCost is a living database for which new costs are frequently added as they become available, the observed trends only reflect the latest version of the database and are likely to change in the future. Nevertheless, our results suggest that IAS costs and the reporting of those costs are globally increasing, with differing regions accelerating at different velocities and trends being highly diverse. This, in line with recent research (Seebens et al., 2021a, 2021b) suggesting further increases in the future due to more IAS translocations and realisation of costs, highlights the need to intensify research effort and advance our understanding of IAS impacts to the economy to help inform policy.

CRediT authorship contribution statement

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Ross N. Cuthbert: Formal analysis, Conceptualization, Methodology, Writing- Original draft preparation, Visualization.

Emma J. Hudgins: Formal analysis, Conceptualization, Methodology, Writing- Original draft preparation, Visualization.

Robert Crystal-Ornelas: Methodology, Writing- Reviewing and Editing.

Melina Kourantidou: Methodology, Writing- Reviewing and Editing.

Desika Moodley: Writing- Reviewing and Editing.

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Anna J. Turbelin: Data curation, Methodology, Formal analysis, Writing- Reviewing and Editing, Visualization.

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Declaration of competing interest

The authors have no financial/personal interest or belief that could affect their objectivity to declare.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.152948.

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