



Economic impact disharmony in global biological invasions

Ross N. Cuthbert^{a,*}, Jaimie T.A. Dick^a, Phillip J. Haubrock^{b,c,d}, Daniel Pincheira-Donoso^e, Ismael Soto^b, Elizabeta Briski^f

^a Institute for Global Food Security, School of Biological Sciences, Queen's University Belfast, Belfast BT9 5DL, United Kingdom

^b University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Centre of Aquaculture and Biodiversity of Hydrocenoses, Zátisť 728/II, 389 25 Vodňany, Czech Republic

^c Center for Applied Mathematics and Bioinformatics, Department of Mathematics and Natural Sciences, Gulf University for Science and Technology, Hawally, Kuwait

^d Department of River Ecology and Conservation, Senckenberg Research Institute and Natural History Museum Frankfurt, 63571 Gelnhausen, Germany

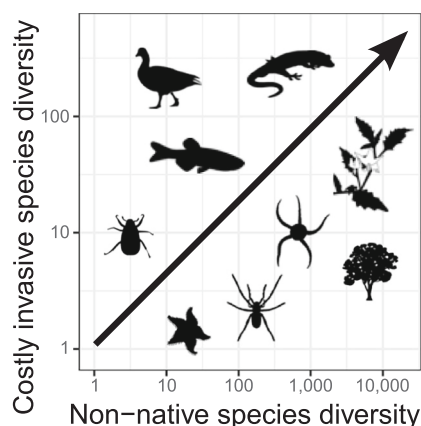
^e School of Biological Sciences, Queen's University Belfast, Belfast BT9 5DL, United Kingdom

^f GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, 24105 Kiel, Germany

HIGHLIGHTS

- More diverse non-native taxa generally include more economically costly species.
- Chordates, nematodes and pathogens are among significantly over-represented taxa.
- Monetary cost magnitude links positively to numbers of costly invasive species.
- Costs are biased towards a few 'hyper-costly' invasive species groups.
- Future invasion rates will continue to harbour new economically costly species.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Damia Barcelo

Keywords:

Biodiversity
Biological invasion
Environmental change
InvaCost
Null model
Socio-economic impact

ABSTRACT

A dominant syndrome of the Anthropocene is the rapid worldwide spread of invasive species with devastating environmental and socio-economic impacts. However, the dynamics underlying the impacts of biological invasions remain contested. A hypothesis posits that the richness of impactful invasive species increases proportionally with the richness of non-native species more generally. A competing hypothesis suggests that certain species features disproportionately enhance the chances of non-native species becoming impactful, causing invasive species to arise disproportionately relative to the numbers of non-native species. We test whether invasive species with reported monetary costs reflect global numbers of established non-native species among phyla, classes, and families. Our results reveal that numbers of invasive species with economic costs largely reflect non-native species richness among taxa (i.e., in 96 % of families). However, a few costly taxa were over- and under-represented, and their composition differed among environments and regions. Chordates, nematodes,

* Corresponding author.

E-mail address: r.cuthbert@qub.ac.uk (R.N. Cuthbert).

<https://doi.org/10.1016/j.scitotenv.2023.169622>

Received 25 October 2023; Received in revised form 21 December 2023; Accepted 21 December 2023

Available online 28 December 2023

0048-9697/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

and pathogenic groups tended to be the most over-represented phyla with reported monetary costs, with mammals, insects, fungi, roundworms, and medically-important microorganisms being over-represented classes. Numbers of costly invasive species increased significantly with non-native richness per taxon, while monetary cost magnitudes at the family level were also significantly related to costly invasive species richness. Costs were biased towards a few ‘hyper-costly’ taxa (such as termites, mosquitoes, cats, weevils, rodents, ants, and asters). Ordination analysis revealed significant dissimilarity between non-native and costly invasive taxon assemblages. These results highlight taxonomic groups which harbour disproportionately high numbers of costly invasive species and monetary cost magnitudes. Collectively, our findings support prevention of arrival and containment of spread of non-native species as a whole through effective strategies for mitigation of the rapidly amplifying impacts of invasive species. Yet, the hyper-costly taxa identified here should receive greater focus from managers to reduce impacts of current invasive species.

1. Introduction

The introduction and establishment of non-native species outside of their native range is a major driver of environmental erosion that is rapidly expanding across ecosystems, societies, and economies globally (Pyšek et al., 2020; Diagne et al., 2021). As globalisation fuels non-native species introductions, biological invasion rates are expected to continue without sign of saturation facilitated by emerging trade and transport links that enable more introduction pathways (Seebens et al., 2017, 2018, 2021; Bonnamour et al., 2021; Haubrock et al., 2023a). In addition, rapid climate and habitat changes are likely to further facilitate the success of non-native species post-introduction (Carlton et al., 2017; Ricciardi et al., 2021; Liu et al., 2023). Despite such large-scale expansion of biological invasions, the majority of impacts resulting from them are caused by a fraction of highly impactful non-native species (hereafter, “invasive species”), whereas only around 1 % of global biodiversity currently has an invasion history (Briski et al., 2023). This relatively small share of global species richness that has been introduced by humans outside of their native range indicates a large-scale source pool for potential future invasions, and therefore, for increasing introductions to result in increasing numbers of impactful invasive species. Whether the numbers of invasive species will increase proportionally, or disproportionately with increasing numbers of non-native species, however, remains unknown. To inform efficient management planning and strategy, it is crucial to understand and predict invasive species groups which are disproportionately successful and most likely to have negative impacts.

Recent studies have examined whether global taxonomic richness reflects the richness of non-native species (Liebhold et al., 2016, 2021; Briski et al., 2023). These analyses have found that, while the invasion rates of many taxa are well-predicted by their respective global species richness, several taxa are significantly over- or under-represented in non-native assemblages compared to expectations based on their total species richness — termed ‘invasion disharmony’ (Liebhold et al., 2021). At the global level across all taxa, Briski et al. (2023) found that non-native taxa directly or indirectly associated with intentional introductions (e.g., agriculture, aquaculture, or pet trade) were particularly over-represented. These lineages include chordates, vascular plants, red and green algae, segmented worms, and bryozoans. Furthermore, non-native species richness trends in relation to global species richness have been shown to differ across levels of taxonomic hierarchy (i.e., phylum, class, and family), and across geographic regions (i.e., continents), and environments (i.e., terrestrial, freshwater, and marine habitats). These variations are attributed to differing taxonomic resolution and research efforts (Briski et al., 2023). However, while impact assessments are critical for management decisions, no studies have yet examined whether costs can be predicted by non-native taxonomic species richness. Addressing that gap will indicate whether certain taxa are over- or under-represented in terms of negative impact occurrence, thereby helping to direct management efforts towards the most harmful invasive groups while identifying potentially understudied taxa.

Monetary costs represent a uniquely universal, quantitative metric to

compare the magnitude of impacts caused by invasive species. The recent release of the *InvaCost* database (Diagne et al., 2020) has enabled global syntheses of the socio-economic impacts of biological invasions. This database compiles and standardises monetary costs associated with invasive species at unprecedented scales (Diagne et al., 2020, 2021; Ahmed et al., 2023). Resulting studies have found that invasive species have caused costs at the global level well in excess of US\$ 1 trillion over the last five decades (Diagne et al., 2021). However, studies have also identified substantial knowledge gaps in the reporting of costs from invasive species, with capacities and efforts biased towards regions such as North America (Hudgins et al., 2023), terrestrial environments (Cuthbert et al., 2021a), and taxa such as insects and mammals (Diagne et al., 2021). Furthermore, cost contributions differ by several orders of magnitude among individual species, with the largest share of invasion costs contributed by a relatively small number of so-called ‘hyper-costly’ invasive taxa, such as mosquitoes, rats, cats, and other notorious invaders (Cuthbert et al., 2021b; Heringer et al., 2021; Soto et al., 2022).

To inform management planning and prioritisation as well as to promote sustainable development, it is imperative to understand whether certain taxonomic groupings of non-native species are more likely to contribute economically costly species, and whether the magnitude of economic costs relates to non-native species richness. However, no studies have examined whether non-native richness is predictive of costly species or their impact magnitude. Two competing hypotheses have been formulated to explain the non-native-invasive species relationship. The first hypothesis posits that the richness of invasive species increases proportionally with the richness of non-native species more generally (i.e., the richness of invasive species is a “fractal” function of the richness of non-native species). This suggests that as invasion rates continue (Seebens et al., 2021), the numbers of socio-economically impactful invasions will concomitantly rise, with risk balanced among taxa. The alternative hypothesis suggests that certain features (e.g., demographic resilience, ‘fast pace’ life histories, association with primary economic sectors) disproportionately enhance the chances of invasive species becoming impactful, leading them to arise disproportionately relative to the numbers of non-native species (i.e., the increasing richness of invasive species is not a function of increases in non-native species). If costly invasions do not resemble non-native species richness due to disproportionate contributions from a few over-represented taxa, it may be pertinent to prioritise these taxa in management efforts owing to their impact disharmony.

Here, we develop a null hypothesis analogous to neutral theory (Hubbell, 2001), which posits that all non-native species have an equal likelihood of causing socio-economic impacts. Based on this theory and that of random sampling from a larger community (Preston, 1948), costly invasive species should be a representative subset of global non-native species richness among taxonomic groups. We define species richness as the number of species per taxon and define “invasive species” on the basis of the presence of an economic cost, while noting that various definitions for “invasive” exist (Haubrock et al., 2023b). We suppose that taxa with large reported numbers of non-native species should have a commensurately high richness of invasive species causing impact. Reciprocally, relatively species-poor non-native species groups

should have a rare assemblage of costly invasive species. We therefore expect that richer non-native species groups will generally harbour higher numbers of costly invasive species and therefore larger economic impact. However, owing to uneven research efforts and known capacities for certain taxa to impact primary socio-economic activity sectors (Cuthbert et al., 2021b; Turbelin et al., 2023), we further hypothesise that several taxonomic groups with costly invasive species will be disproportionately represented compared to global non-native species richness. We thus use one of the largest compilations of non-native species richness globally (Briski et al., 2023), alongside the *InvaCost* database (Diagne et al., 2020), to compare compositions of non-native and costly invasive species, as well as the magnitude of their monetary costs. Moreover, we examine whether these trends are contingent on the taxonomic level, environment type, and geographic region examined, to account for potential differences within and among these contexts.

2. Materials and methods

2.1. Data sources

We used two datasets compiling (i) the global established non-native species richness among phyla, classes, and families (Briski et al., 2023; Supplementary Data 1), and (ii) the global economic costs of these taxonomic groups (*InvaCost* database, Diagne et al., 2020; Supplementary Data 2). Global established non-native species richness was compiled from various data sources (Meyer, 2000; Lambert, 2002; Paulay et al., 2002; Hewitt, 2002; Hewitt et al., 2004; Wonham and Carlton, 2005; Carlton and Eldredge, 2009; Eldredge and Carlton, 2015; Campbell et al., 2016; Casties et al., 2016; NEMESIS, 2017, 2020; U.S. Geological Survey, 2017; Sturtevant et al., 2019; Bailey et al., 2020; Richardson et al., 2020; Schwindt et al., 2020) in Briski et al. (2023). The *SinAS* database from Seebens (2021) formed the basis for this global non-native species list, which was supplemented with the aforementioned sources. Information on geographic region and habitat type invaded was then added for each species entry (Briski et al., 2023). Global assessments of monetary costs from invasive species were extracted from the latest *InvaCost* database version (v4.1; Diagne et al., 2020). The *InvaCost* search protocol consisted of various non-native species and economic cost synonyms, applied across Web of Science, Google Scholar, and the general Google search engine, alongside additional opportunistic data collection from targeted stakeholders (Diagne et al., 2020). *InvaCost* also contains data in at least 22 non-English languages (Angulo et al., 2021). The taxonomy within both of these data sources was aligned using the standards set by the Global Biodiversity Information Facility (gbif.org), selecting the most recently accepted taxonomy at the time of processing. Full information on the search processes and data processing can be found in the two original data source publications (Diagne et al., 2020; Briski et al., 2023).

2.2. Filtering steps

Data in Briski et al. (2023) were aggregated such that the numbers of unique non-native species were summed per phylum, class, and family. The invasive species with reported costs in *InvaCost* were filtered to ensure that only species-specific (i.e., not unspecific or shared costs among multiple species) data entries were retained. We then removed duplicate species such that each species represented a row of data. We considered a species as invasive when it had any monetary cost reported. However, for analyses of actual monetary cost values, we further filtered the data such that only “High” reliability (“Method_reliability” column) and “Observed” (“Implementation” column) costs were retained (Diagne et al., 2020). This ensured that the quantified costs per species in *InvaCost* were from peer-reviewed, official, or reproducible sources (i.e., ‘High’ reliability), while representing costs that were actually incurred (i.e., ‘Observed’) and not potentially occurring. Cost aggregations used

sums from the “Raw_cost_estimate_2017_USD_exchange_rate” column, and therefore costs reported here are in 2017 US\$ to ensure the comparability (Diagne et al., 2020).

2.3. Data analyses

The taxonomic invasion cost coverage was compared to global non-native species richness for phyla, classes, and families. Numbers of taxa with and without reported costs across these taxonomic levels were aggregated into a 2×3 contingency table (i.e., reported/unreported costs \times phyla/classes/families) and analysed using a Pearson Chi-square test. We therefore assessed whether taxonomic data gaps were contingent on the taxonomic level assigned.

We examined whether the numbers of costly invasive species were a representative proportional subset of global non-native species richness. We aggregated and compared the top 15 taxa in terms of numbers of species between costly invasive species and global non-native species, for phyla, classes, and families. In a separate analysis, we then statistically identified outlier taxa by creating a null model of expected costly invasive species richness relative to global non-native species richness (Liebhold et al., 2016). This null model assumed that the distribution of costly invasive species among taxonomic groupings would reflect that of non-native species richness. We generated a region around this null model to represent the probability of a given taxon with costs being over- and under-represented, illustrated by the taxon falling inside or outside of the region. The region was calculated using the upper and lower quantiles of a binomial distribution with a Bonferroni correction for the numbers of taxa per taxonomic level, whereby $(1-\alpha/m) \times 100\%$ of the distribution lay within the boundary, with m the richness of taxa compared (Liebhold et al., 2016). We assumed an α of 0.05 and included only taxa with at least one costly invasive species, while removing rows where numbers of costly invasive species exceeded non-native species richness. We then repeated this analysis by partitioning species between aquatic and terrestrial realms across the databases, with “aquatic” taxa also including semi-aquatic organisms which are associated with water for feeding or reproduction, or which have an aquatic life history stage (Cuthbert et al., 2021a). We further examined patterns of representation across geographic regions (North America, South America, Europe, Africa, Asia, Australia and New Zealand, and Pacific Islands) between the two databases.

We fit a series of non-parametric models to examine the predictive-ness of global non-native species richness for costly invasive species across phyla, classes, and families. We first fit binomial generalised linear models to test if the occurrence of a costly invasive species in a given taxon was predicted by global non-native species richness for that taxon. We fit the explanatory variable of non-native species richness on a log-scale to avoid complete separation. Then, we used a quasi-Poisson generalised linear model to test whether counts of costly non-native species were predicted by global non-native species richness, including taxa with at least one costly invasive species. The quasi-Poisson family was selected as the most suitable for count data, and as it can handle overdispersion and correct for inflated variance. Kruskal-Wallis tests were then used to examine whether the magnitude of aggregated monetary costs per taxon was related to the global richness of non-native species or costly invasive species, since monetary costs violated assumptions of linear modelling; locally estimated scatter smoothing was used to visualise the trend. We further partitioned the family-level data into ‘hyper-costly’ (\geq US\$ 1 billion per in total) and ‘costly’ ($<$ US\$ 1 billion in total) taxa, and examined whether global non-native species richness or costly invasive species richness on a log-scale explained this binary split using binomial generalised linear models.

To further characterise differences between costly invasive and non-native assemblages among families, we used a redundancy ordination analysis. This included the two species groups (non-native and invasive) as well as geographic regions (North America, South America, Europe, Africa, Asia, Australia and New Zealand, and Pacific Islands). The

analysis was based on Hellinger transformation values, which is a method of normalising data for ordination (Oksanen et al., 2022). We plotted the redundancy analysis after ordination on two axes, thereby indicating compositional similarities or dissimilarities among assemblages. To evaluate the significance of the groups and regions, we computed a permutation test ($n = 9999$ permutations). All analyses were done in R version 4.3.1 (R Core Team, 2023) and figures were made in ggplot2 (Wickham, 2016).

3. Results

3.1. Overview and data gaps

Out of 37,270 established non-native species globally across phyla, 860 invasive species (2.31 %) had reported monetary costs. Global non-native species were reported across 55 phyla, 156 classes, and 2698 families. At phylum, class, and family levels, 47 %, 68 %, and 88 % of these non-native taxa had no reported monetary costs, respectively (Fig. 1). Gaps in cost data increased significantly towards lower taxonomic groupings (Chi-square test: $\chi^2 = 106.71$, $df = 2$, $p < 0.001$).

The 15 richest non-native phyla, classes, and families often overlapped between non-native species and costly invasive species groups (Fig. 2). Therefore, costly invasive species tended to come from taxa with greater numbers of non-native species. However, several prominent costly taxa did not have commensurate ranking in terms of non-native species richness. Among phyla, Proteobacteria, Pisuviridota, Kitrinoviridota, Oomycota, and Negarnaviridota were among the top 15 richest costly invasive species groups while not being among the richest non-native taxa (Fig. 2a, b). With classes, Chromadorea, Gammaproteobacteria, Sordariomycetes, and Dothideomycetes featured among the richest costly invasive taxa, but were not among the richest non-native taxonomic groups (Fig. 2c, d). For families, Chrysomelidae, Formicidae, Tephritidae, Cerambycidae, Asparagaceae, Cactaceae, and Polygonaceae were included among the richest costly invasive species groups, but not the top 15 non-native families in terms of species richness (Fig. 2e, f).

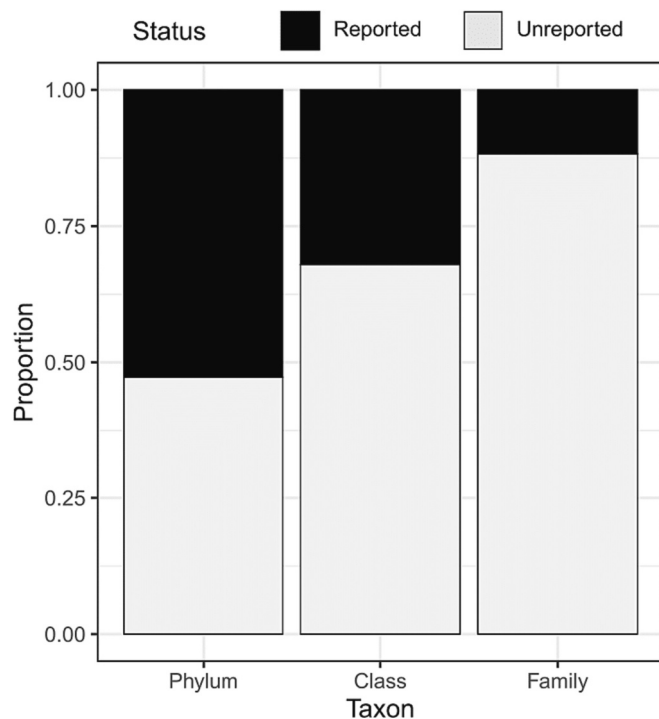


Fig. 1. Proportion of non-native taxonomic groups with reported monetary impacts among phyla, classes, and families.

3.2. Over- and under-represented taxa

The vast majority of costly taxonomic groups were not significantly over- or under-represented compared to the global richness of non-native species (Fig. 3). Among taxa, 28 % of phyla, 19 % of classes, and 4 % of families were significantly over- or under-represented. Therefore, costly taxa overall were generally well-represented by global non-native species richness.

Among phyla, Chordata, Nematoda, Proteobacteria, Pisuviridota, Kitrinoviridota, and Negarnaviridota were significantly over-represented, whereas Tracheophyta was significantly under-represented compared to the null model (Fig. 3a). Considering classes, Insecta, Mammalia, Chromadorea, Gammaproteobacteria, Sordariomycetes, Stel Paviricetes, and Alsuviricetes were significantly over-represented, whereas Magnoliopsida and Agaricomycetes were significantly under-represented (Fig. 3b). For families, Tephritidae, Xanthomonadaceae, Erebidaceae, Pratylenchidae, Rhinotermitidae, Canidae, Vespidae, and Dreissenidae had significantly more costly species than expected from non-native species richness, while Lamiaceae, Cyperaceae, and Plantaginaceae were significantly under-represented (Fig. 3c).

Similar patterns were found when partitioning families between aquatic and terrestrial environments, because most taxa were well-represented by non-native species richness (Fig. 4). However, the composition of over- and under-represented taxa differed. For aquatic habitats, no costly invasive families were found to be over-represented relative to non-native species richness, but Cichlidae and Cyprinidae were significantly under-represented (Fig. 4a). For terrestrial habitats, contrastingly, Tephritidae, Xanthomonadaceae, Pratylenchidae, Erebidaceae, Canidae, Rhinotermitidae, and Vespidae were over-represented, as well as Sciridae and Gelechiidae, whereas Amaranthaceae was under-represented (Fig. 4b).

Among regions, costly invasive species were again generally well represented by non-native species richness. However, patterns of over- and under-representation of costly invasive species differed among geographic regions according to numbers of non-native species (Fig. 5). In North America, Xanthomonadaceae and Muridae were over-represented, whereas Poaceae and Fabaceae were under-represented (Fig. 5a). In South America, Culicidae were over-represented with Poaceae and Asteraceae under-represented (Fig. 5b). In Europe, no families were over-represented, while Asteraceae, Rosaceae, and Lamiaceae were under-represented (Fig. 5c). In Africa, only Asteraceae was under-represented (Fig. 5d), while in Asia, Gelechiidae and Xanthomonadaceae were over-represented, and Asteraceae, Fabaceae, and Poaceae were under-represented (Fig. 5e). Australia and New Zealand exhibited over-representation by Canidae, Muridae, and Pucciniaceae, whereas Fabaceae was again under-represented (Fig. 5f). Pacific Islands had no over-represented taxa, with Fabaceae and Poaceae under-represented (Fig. 5g).

3.3. Predictiveness of non-native species richness for monetary impacts

Considering costly invasive species occurrence, taxonomic groups with costly invasive species were significantly more likely to come from taxa with greater non-native species richness across all taxonomic levels (binomial generalised linear models: phyla, $z = 2.56$, $p = 0.011$; classes, $z = 5.66$, $p < 0.001$; families, $z = 19.19$, $p < 0.001$). Considering numbers of costly invasive species, richness related significantly positively with non-native species richness at all taxonomic levels (quasi-Poisson generalised linear models: phyla, $t = 6.90$, $p < 0.001$; classes, $t = 9.93$, $p < 0.001$; families, $t = 29.61$, $p < 0.001$) (Fig. 6).

Monetary cost magnitude was less consistently predicted by non-native species richness. The magnitude of monetary cost did not relate significantly to non-native species richness for any taxon (Kruskal-Wallis test: phyla, $\chi^2 = 18$, $df = 18$, $p = 0.456$; classes, $\chi^2 = 33.52$, $df = 36$, $p = 0.587$; families, $\chi^2 = 115.40$, $df = 110$, $p = 0.343$). Similarly, costly

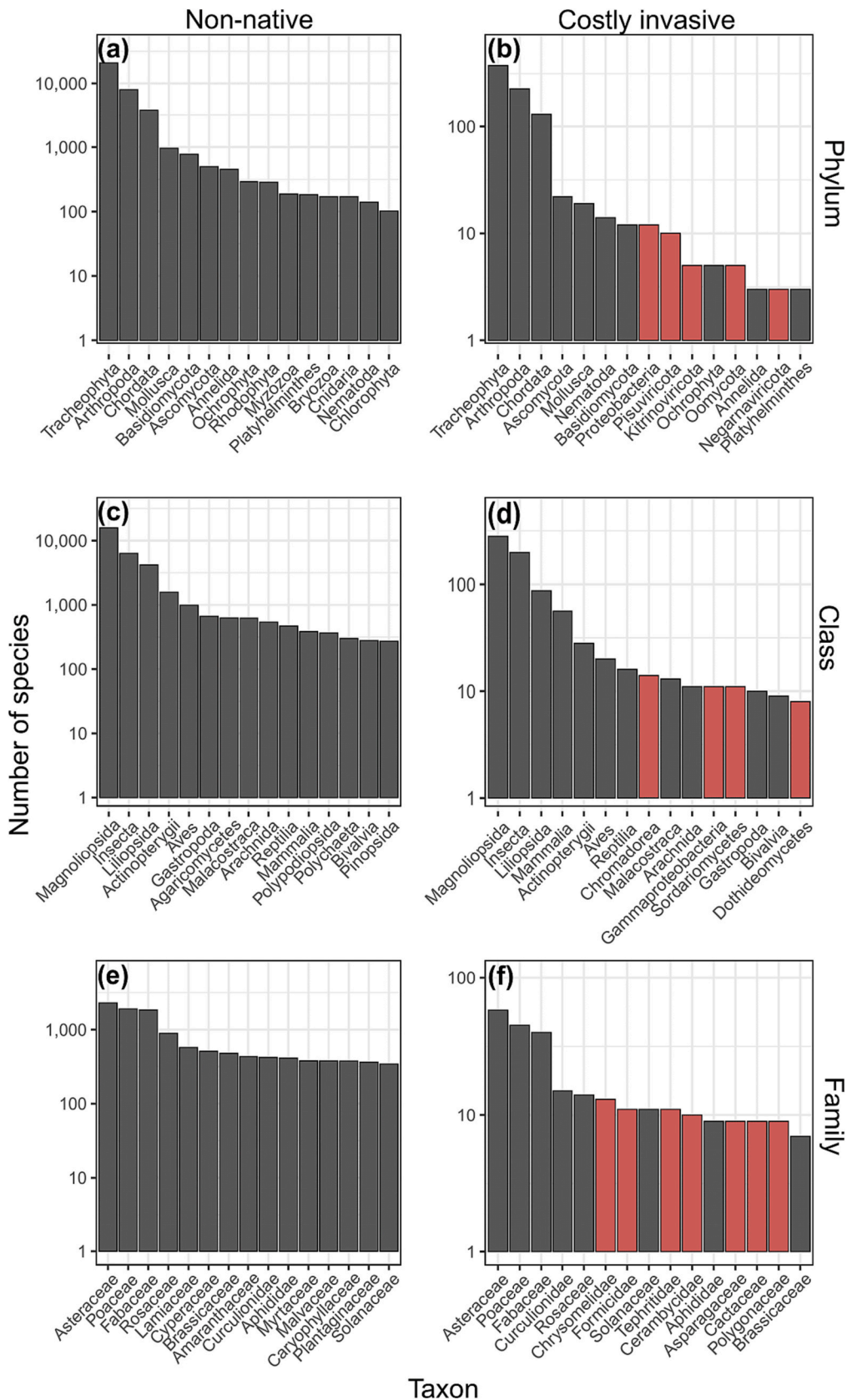


Fig. 2. Top 15 richest taxa among phyla (a, b), classes (c, d), and families (e, f), considering global non-native species (a, c, e) and costly invasive species (b, d, e). Top costly invasive species families which are absent from the top non-native species families are highlighted in red. Note the y-axis is on a log₁₀ scale and differs among subplots.

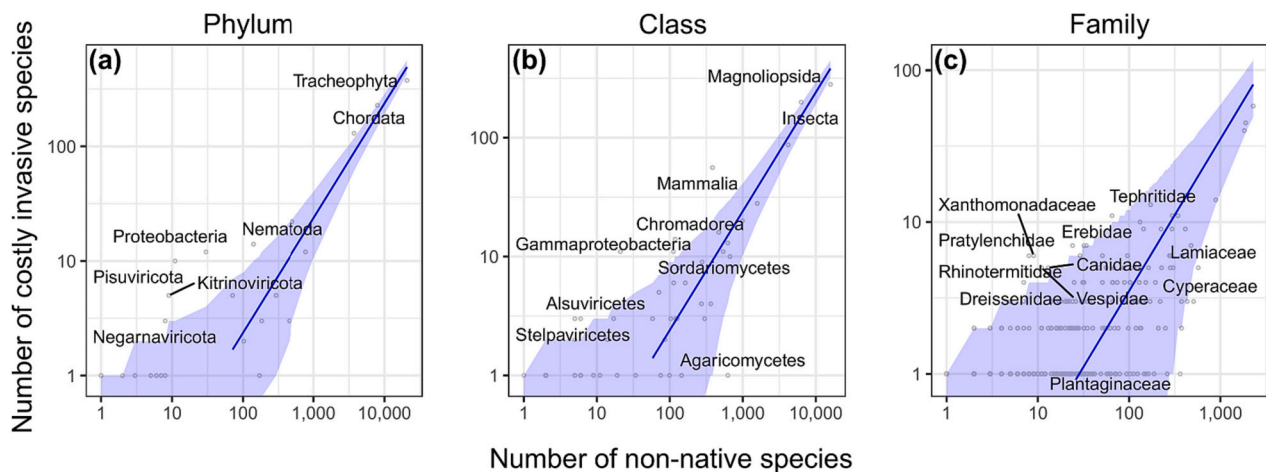


Fig. 3. Costly invasive species richness relative to non-native species richness globally among taxonomic levels: phyla (a), classes (b), and families (c). The solid line represents the expected richness of costly invasive species if their distribution among taxa exactly reflected non-native species richness (i.e., null model). The shaded area represents the upper and lower quantiles of a binomial distribution between these variables, with values Bonferroni-corrected to an α of 0.05 considering the numbers of groups per taxonomic level. Taxonomic names are shown for groups which are outside of this distribution layer. Note that the x- and y-axes are on a \log_{10} scale and differ among subplots.

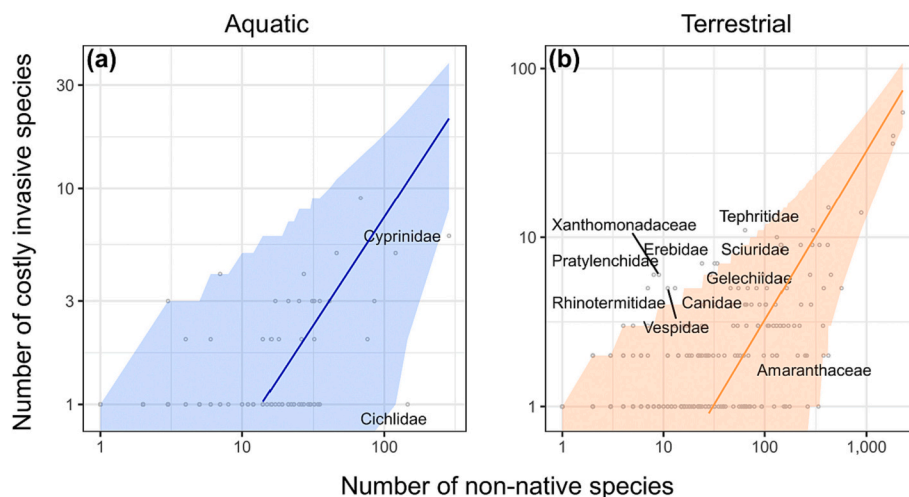


Fig. 4. Costly invasive species richness relative to non-native species richness globally for environments: aquatic (a) and terrestrial (b). The solid line represents the expected richness of costly invasive species if their distribution among taxa exactly reflected non-native species richness (i.e., null model). The shaded area represents the upper and lower quantiles of a binomial distribution between these variables, with values Bonferroni-corrected to an α of 0.05 considering the numbers of groups per taxonomic level. Taxonomic names are shown for groups which are outside of this distribution layer. Note that the x- and y-axes are on a \log_{10} scale and differ among subplots.

invasive species richness did not significantly predict monetary cost magnitude for phyla and classes (Kruskal-Wallis test: phyla, $\chi^2 = 17.11$, $df = 11$, $p = 0.105$, classes, $\chi^2 = 23.59$, $df = 19$, $p = 0.212$). Contrastingly, families with the highest costs came from families with larger numbers of costly invasive species ($\chi^2 = 56.61$, $df = 15$, $p < 0.001$) (Fig. 7a).

Thirty-nine families had total costs exceeding \$1 billion and were deemed 'hyper-costly'. The five costliest families were Rhinotermitidae (5 costly species, \$ 272.6 billion total), Culicidae (4 costly species, \$ 54.6 billion total), Felidae (1 costly species, \$ 47.5 billion total), Curculionidae (15 costly species, \$ 29.6 billion total), and Muridae (4 costly species, \$24.0 billion total). When family-level data were split into 'hyper-costly' (\geq US\$ 1 billion in total) and 'costly' (<US\$ 1 billion in total), 'hyper-costly' families tended to come from richer species groups, although non-native species richness as a predictor marginally lacked statistical clarity in contrast to costly invasive species richness (binomial generalised linear model: non-native species groups, $z = 1.94$, $p = 0.053$;

costly invasive species groups, $z = 5.19$, $p < 0.001$) (Fig. 7b, c).

3.4. Ordination analysis

The family-level composition of non-native and costly invasive species generally fell on opposite sides of the first axis of the ordination space (Fig. 8). The permutation test indicated that this species group divergence was statistically clear ($F_{1,6} = 51.318$, $p < 0.001$), whereas the effect of geographic region was unclear statistically ($F_{6,6} = 2.146$, $p = 0.190$). Therefore, non-native and costly invasive species assemblages within geographic regions were not more similar than those among regions. The pattern of clustering among geographic regions was generally similar between species groups on the second axis.

4. Discussion

Our study provides the first global-scale evidence that economically

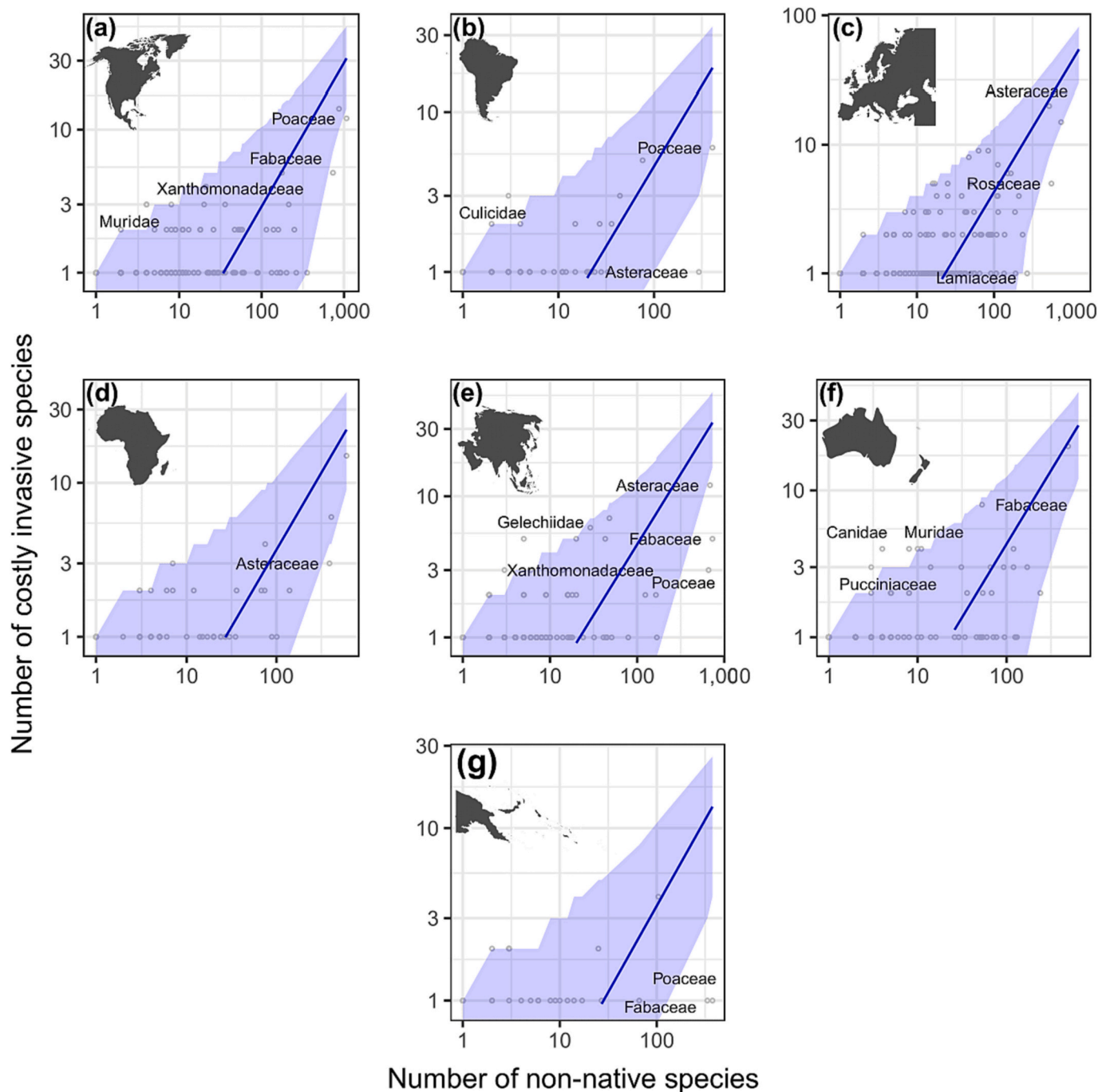


Fig. 5. Costly invasive species richness relative to non-native species richness globally for geographic regions: North America (a), South America (b), Europe (c), Africa (d), Asia (e), Australia and New Zealand (f), and Pacific Islands (g). The solid line represents the expected richness of costly invasive species if their distribution among taxa exactly reflected non-native species richness (i.e., null model). The shaded area represents the upper and lower quantiles of a binomial distribution between these variables, with values Bonferroni-corrected to an α of 0.05 considering the numbers of groups per taxonomic level. Taxonomic names are shown for groups which are outside of this distribution layer. Note that the x- and y-axes are on a \log_{10} scale and differ among subplots.

costly invasive species are largely a proportional subset of non-native species richness. At the family level, 96 % of taxa with costs were well-represented by their respective non-native richness. Therefore, our findings suggest that the numbers of costly invasive species and the magnitude of their economic impacts are likely to rise rapidly in future in concordance with burgeoning rates of biological invasion across taxonomic groups and geographic regions (Seebens et al., 2021). However, a few taxa were significantly over- or under-represented compared to expectations in terms of invasion costs. This economic impact disharmony parallels patterns in invasion success relative to global

biodiversity (Briski et al., 2023). At the phylum level, over-represented taxa included chordates, nematodes, and several groups of pathogenic microorganisms such as viruses and bacteria, suggesting disproportionate levels of impact or research efforts. Furthermore, with the exception of repeated under-representation of several very rich non-native plant taxa in terms of invasion costs, the taxonomic composition of over- and under-representation showed differences between aquatic and terrestrial environments as well as among geographic regions, suggesting that costly invasive species reports are disparate. Despite research biases, these results indicate that there should be a

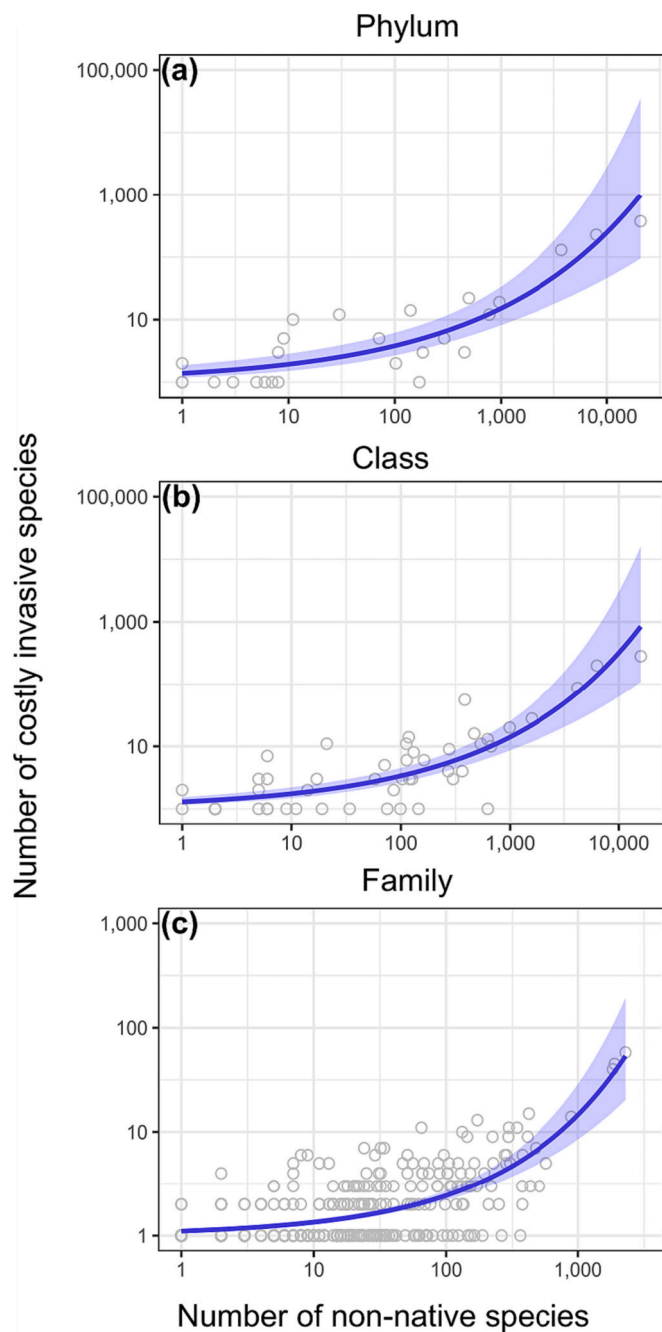


Fig. 6. Costly invasive species richness as a function of non-native species richness for phyla (a), classes (b), and families (c). Lines represent the fit of a quasi-Poisson generalised linear model, with 95 % confidence intervals shaded. Note that the x- and y-axes are on a log₁₀ scale and differ among subplots.

broad focus on prevention of future non-native species across all taxa, while pinpointing several particularly high risk groups for management prioritisation.

4.1. Massively unrealised potential for future impacts

Only 2 % of global non-native species had any reported monetary costs. In turn, only around 1 % of global species richness so far has invaded a non-native region (Briski et al., 2023). This suggests an enormous potential for future invasions and impacts as globalisation continues and new introduction pathways emerge from an extensive unrealised species source pool (Seebens et al., 2018). Indeed, while

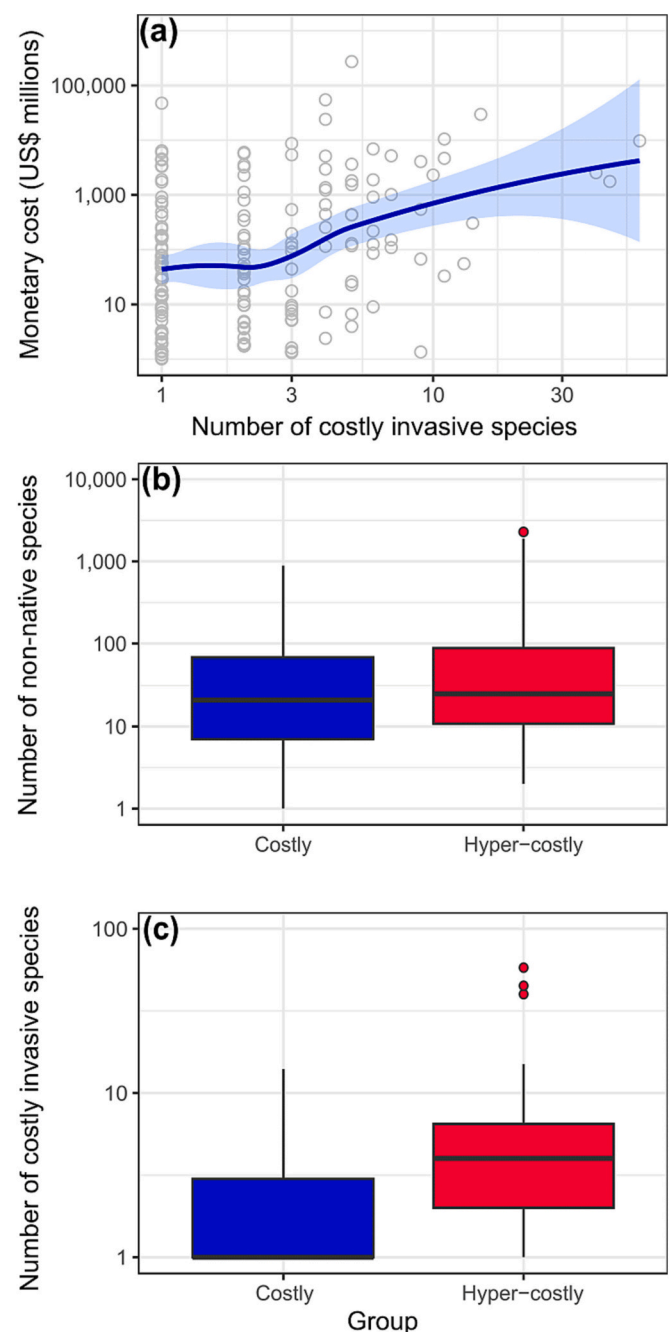


Fig. 7. Monetary cost total magnitudes as a function of numbers of costly invasive species per family. The solid line represents locally estimated scatterplot smoothing with a shaded 95 % confidence interval (a). Comparison of 'hyper-costly' (\geq US\$ 1 billion in total) and 'costly' ($<$ US\$ 1 billion in total) invasive species per family according to non-native species richness (b) and costly invasive species richness (c). In the boxplots, the horizontal bar displays the median, the box gives the interquartile ranges and the whiskers show the largest and smallest values up to 1.5 \times the interquartile range. Note that the y-axes are on a log₁₀ scale and differ among subplots.

current biological invasions can reflect legacies of historical introduction (e.g., colonialism; Lenzner et al., 2022), future invasions will likely arise from a different suite of pathways and vectors which entrain novel taxa, with a correspondingly greater diversity of impacts. In an economic context, this could mean that impacts affect a broader array of activity sectors, or could be exacerbated as patterns of economic activity change. Differences in management prioritisation and strategy could also influence the composition of future impactful invasions. For

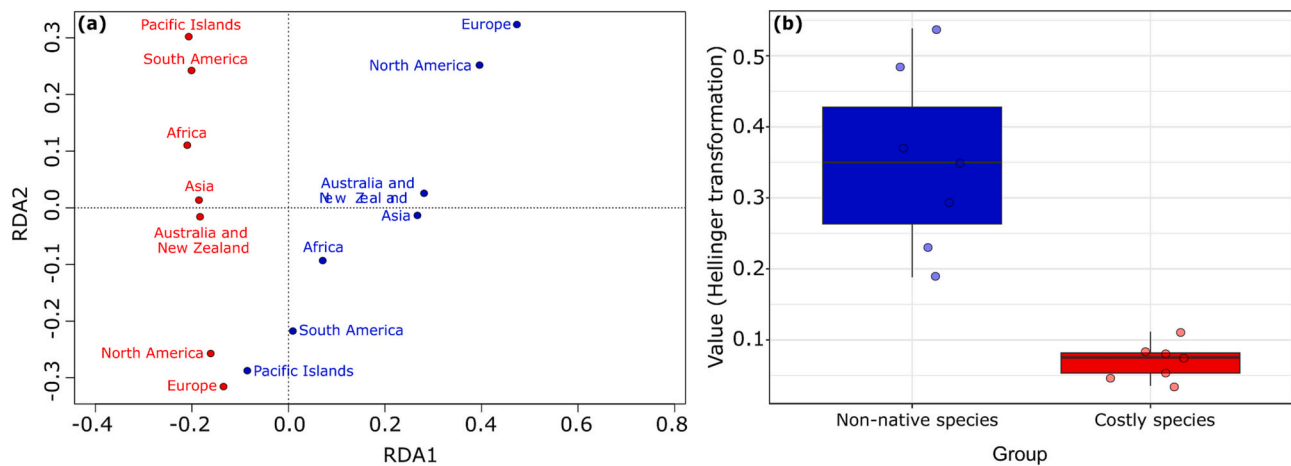


Fig. 8. Results of ordination redundancy analysis on numbers of species per family in each geographic region defined by first two axes, with costly invasive families in blue and non-native families in red (a). Boxplot illustrating the comparative values from Hellinger transformation of costly species and non-native species across geographic regions (b).

example, ballast water regulations have reduced rates of invasion by aquatic non-native species to the Laurentian Great Lakes by 85 % since 2006 (Ricciardi and MacIsaac, 2022). Whereas, invasions to the Antarctic are likely to accelerate in future with changes to ship activity linked to fishing, tourism, and research (McCarthy et al., 2019). Similarly, introduction rates of certain taxa are anticipated to slow in future (e.g., mammals and fishes), while other taxa are expected to accelerate (e.g., arthropods and birds) (Seebens et al., 2021). Insect production is one specific source which could become a more important contributor of biological invasions in future, owing to an upsurge in edible insect markets (Bang and Courchamp, 2021), whereas regulations could reduce the prevalence of other pathways (e.g., ornamental and horticultural trades; Hulme et al., 2018). Moreover, rapid environmental changes and invasion debts (i.e., delays to invader impact following introduction) could trigger further economic impacts from the thousands of so-far benign non-native species in the near future (Essl et al., 2011; Ricciardi et al., 2021). As global climate change continues to alter habitats and ecosystems, understanding its synergistic effects with invasive species becomes critical. These climatic shifts may either exacerbate the invasion risks by creating more suitable environments for non-native species or, conversely, render some regions less susceptible to certain invasions (Mainka and Howard, 2010). Accordingly, it may take decades for economic impacts to be realised following a biological invasion, and a lack of costs does not preclude future impacts for a given species or higher taxon. Each of the above factors could shift the taxonomic patterns observed here, with disproportionate impacts possible from new groups of costly invasive species.

Invasion costs are scarce for many taxa (Henry et al., 2023), and our analyses are subject to data gaps at multiple levels; just as numbers of non-native species are likely conservative (Briski et al., 2023). Just 53 %, 32 %, and 12 % of taxonomic groups with known non-native species had any reported monetary impacts at phylum, class, and family levels, respectively. It is intuitive that proportional cost gaps increase with taxonomic resolution towards the family level, because — analogous to random sampling theory (Preston, 1948) — there is a smaller pool of non-native species from which economic costs could be reported 'by chance'. Indeed, the mean richness of non-native species per phylum was 678, whereas classes had an average of 238 non-natives, and families only 14. These trends underline that reporting of economic impacts from biological invasion is disparate among taxa (Cuthbert et al., 2021a), and signify a massive potential for economic impacts to accrue in future as existing and emerging invasive species cause harm. Therefore, it can be assumed that richer non-native species groups have a greater likelihood of harbouring impactful invasive species in general.

We further note that our analyses took a conservative stance, whereby a taxon was deemed to be costly if it had *any* reported economic impact at the species-specific level, while it is known that geographic gaps and research biases are pervasive for any individual species and that substantial costs are reported across indistinguishable groups of species (Hudgins et al., 2023).

4.2. Disproportionate representation of a few taxa

Whereas numbers of invasive species with economic impacts and the magnitude of their monetary costs largely reflected the species richness of non-native taxa, a few taxa were always over- or under-represented across taxonomic levels, environments, and geographic regions. Albeit, the composition of these taxa consistently differed. At the coarsest taxonomic level, chordates, nematodes, and pathogenic microorganisms were over-represented compared to global non-native species richness, while vascular plants were under-represented. Chordates are particularly well-studied in invasion science, not least in terms of economic costs, owing to their conspicuous impacts to primary economic sectors such as agriculture as well as their historic association with humans and their introduction vectors (Diagne et al., 2021; Briski et al., 2023). After insects, nematodes are among the costliest invertebrates (Renault et al., 2022), with substantial effects to agriculture and forestry industries, despite their common unintentional introduction (Turbelin et al., 2022). For bacteria and viruses, their prominence could reflect limited research into their invasion status, as well as debate around their consideration as non-native species rather than as emergent taxa which lack clear origin. This means that pathogenic taxa which have a low reported non-native species richness are more likely to have high rates of reported economic impact, such as to the health sector. While parallels between biological invasions and infectious disease are fundamental (Nuñez et al., 2020), we acknowledge that microorganisms are particularly under-represented in non-native species lists (with varying definitions among data sources) and that further research could reveal an enormous species richness of non-native pathogens. Contrastingly, the sole under-representation of vascular plants among phyla largely reflects their very high non-native species richness (van Kleunen et al., 2019), rather than a scarcity of economic impacts, since they still had the largest richness of costly invasive species. This suggests that further research is needed to reveal and report the economic costs of these taxa.

Specific taxa which are over- and under-represented were further elucidated at the class and family levels. Previous studies have similarly found patterns of over- and under-representation (i.e., invasion disharmony) among select taxa from these groups (Liebhold et al., 2016, 2021;

Pyšek et al., 2017; Briski et al., 2023). Considering economic costs, fruit flies (Tephritidae), termites (Rhinotermitidae), moths (Erebidae), lesion nematodes (Pratylenchidae), dreissenid bivalves (Dreissenidae), dogs (Canidae), bacteria (Xanthomonadaceae), and wasps (Vespidae) were significantly over-represented relative to their non-native species richness. Several notorious species within these groups are among the costliest invaders worldwide, such as *Coptotermes formosanus*, *Lymantria dispar*, and *Dreissena polymorpha* (Cuthbert et al., 2021b). Invasive species within these families have well-known impacts which are closely tied to infrastructure and primary socio-economic sectors (agriculture, forestry, and fisheries; Turbelin et al., 2023). For example, invasive fruit flies can negatively affect fruit markets, termites cause severe damage to buildings, moth larval stages impact forestry, dreissenid bivalves damage power plant water intake systems, wild dogs impact livestock, bacteria threaten agricultural produce, and wasps can adversely affect major pollinators (Diagne et al., 2020). This divergence was reinforced by the significant difference between non-native and costly invasive family groups in the redundancy analysis, while regional effects on composition were not statistically clear. Therefore, non-native and costly invasive species were not more similar within than among regions and compositionally had strong variability.

The composition of over-represented taxa versus expectations differed among particular environments and geographic regions, again reflecting that cost information is unavailable among taxa across all contexts or that sample sizes may have been too low for statistical clarity in some cases. This suggests that inferences of over- and under-representation are mediated by context-specific levels of research effort, and that future increases in cost information or elucidation of non-native richness among taxa could potentially resolve inconsistencies and reveal more general trends in impact disharmony. We further note that these inferences included only non-native taxa with at least one costly invasive species, and patterns of under-representation are therefore conservative as many taxa lacked any costly species (e.g., 88 % of families had no reported costs).

4.3. Disparate economic cost reporting

In contrast to patterns of costly invasive species richness, the predictiveness of non-native species richness for monetary cost magnitudes was found to be limited. At all levels, non-native species richness failed to predict the magnitude of invasive species economic costs. This may again largely reflect the disparate nature of economic cost reporting among taxa, whereby single hyper-costly species within a given taxon can obfuscate broad-scale patterns (Cuthbert et al., 2021b; Heringer et al., 2021). Nevertheless, with a larger sample size at the family level, numbers of costly invasive species related significantly positively with their economic cost magnitude. Similarly, the likelihood of a given family with invasion costs being hyper-costly (i.e., total costs exceeding \$1 billion) increased significantly with corresponding costly invasive species richness.

While taxonomic richness of non-native species is a strong predictor of invasion costs among taxa, there are many other variables that mediate socio-economic impact. Natural and social factors such as latitude, environmental match, land area, colonial history, trade patterns, road density, common languages, and research effort influence species-level monetary cost flows among countries (Hudgins et al., 2023). Research effort is particularly likely to influence monetary cost reporting from invasive species, and positive feedback loops could mean that species with already reported impacts have a higher propensity to accrue reported costs in future. Similarly, regions with larger research capacities report higher impacts geographically. These biases are also relevant for terrestrial versus aquatic environments, whereby impacts from aquatic invaders often remain hidden and limited owing to a lack of human assets or monitoring underwater (Cuthbert et al., 2021a). At the level of non-native species richness more broadly, factors such as propagule and colonisation pressures, environmental match, and species

traits influence invasion success, organism visibility, and inclusion of species in non-native taxon lists, alongside differential research efforts among taxa (Briski et al., 2023). In future, as pathways and patterns of economic activity and research directions change (Sardain et al., 2019; Hudgins et al., 2023), the composition of both non-native and costly invasive species could shift considerably.

Finally, the incorporation of evolutionary insights remains a largely neglected component of current frameworks aimed to predict the pathways that lead certain non-native species to become economically costly (e.g., Le Roux, 2021). We argue that a key first step requires addressing the hypothesis that economically costly species share similar profiles of traits with significant demographic effects (e.g., tendency for ecological generalism, fast life histories). More specifically, we propose the hypothesis that rapid economic (and ecological) impacts will be more likely in species with a trait profile that combines potential for both exaptation (i.e., previously acquired traits that make them demographically viable upon introduction, enabling rapid establishment) and adaptation (i.e., the demographic resilience from traits that facilitated exaptation enhance likelihood for adaptation to remaining environmental demands that could still impact on overall fitness) to the newly introduced environments. The rapid emergence of comprehensive global-scale databases on entire lineages (e.g., Jones et al., 2009; Meiri, 2018; Pincheira-Donoso et al., 2021; Tobias et al., 2022), coupled with machine learning technology for analyses of complex interactions and for accurate predictions, offer unprecedented opportunities to identify species profiles with high potential for rapid economic impacts.

4.4. Future management strategy

Our results reveal that the distribution of economically costly invasive species is largely a subset of global non-native species richness — these findings have significant management implications. Management efforts should seek to reduce invasion rates through proactive preventative measures to dampen future monetary impacts across all taxa which could cause harm, while considering current pathways. Nevertheless, our identification of over- and under-represented taxa points to a need to control the most damaging invasive taxa, as well as to balance research efforts to record monetary costs systematically across a broader suite of taxonomic groups to reduce data gaps and biases. Furthermore, given that our analyses only considered monetary costs as a form of impact, efforts should also be made to standardise and record the effects of invasive species on non-monetary aspects of the socio-economy and environment (Hanley and Roberts, 2019), thereby comparing whether taxa with disproportionate impacts are similar according to ecological and socio-economic effects. If that were the case, management of the same taxa could simultaneously reduce both ecological and socio-economic impacts.

More widely, the overarching implication arising from our findings that economically impactful invasive species are proportional to non-native species is that effective strategies to curb the rapidly expanding economic burden from invasions (Diagne et al., 2021) will require a global and collective agenda of a scale equivalent to the Net Zero emissions agenda (United Nations, 2022). Whereas reactive actions to mitigate the impacts of already costly species remain a critical priority, we suggest that long-term agendas will need to focus on much more ambitious, larger-scale targets similar to climate change goals, which are still missing from key action plans outlined in existing reports (e.g., Kunming-Montreal Global Biodiversity Framework Target 6).

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.169622>.

Ethics and permits

All institutional and national rules for conducting this research were followed, and we did not need special permission to do this research.

CRediT authorship contribution statement

Ross N. Cuthbert: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft. **Jaimie T.A. Dick:** Writing – review & editing. **Phillip J. Haubrock:** Formal analysis, Writing – review & editing. **Daniel Pincheira-Donoso:** Writing – review & editing. **Ismael Soto:** Formal analysis, Visualization, Writing – review & editing. **Elizabeta Briski:** Data curation, Writing – review & editing.

Declaration of competing interest

Ross Cuthbert reports financial support was provided by Leverhulme Trust.

Data availability

The raw data supporting the conclusions of this article are freely available in the Supplementary Material as well as on-line repositories.

Acknowledgements

RNC is funded by a Leverhulme Trust Early Career Fellowship (ECF-2021-001).

References

- Ahmed, D.A., Cuthbert, R.N., Bang, A., Soto, I., Balzani, P., et al., 2023. Recent advances in availability and synthesis of the economic costs of biological invasions. *BioScience* 73, 560–574. <https://doi.org/10.1093/biosci/biad060>.
- Angulo, E., Diagne, C., Ballesteros-Mejia, L., Adamjy, T., Ahmed, D.A., et al., 2021. Non-English languages enrich scientific knowledge: the example of economic costs of biological invasions. *Sci. Total Environ.* 775, 144441 <https://doi.org/10.1016/j.scitotenv.2020.144441>.
- Bailey, S.A., Brown, L., Campbell, M.L., Canning-Clode, J., Carlton, J.T., et al., 2020. Trends in the detection of aquatic non-indigenous species across global marine, estuarine and freshwater ecosystems: a 50-year perspective. *Diversity Distrib.* 26, 1780–1797. <https://doi.org/10.1111/ddi.13167>.
- Bang, A., Courchamp, F., 2021. Industrial rearing of edible insects could be a major source of new biological invasions. *Ecol. Lett.* 24, 393–397. <https://doi.org/10.1111/ele.13646>.
- Bonnamour, A., Gippet, J.M.W., Bertelsmeier, C., 2021. Insect and plant invasions follow two waves of globalisation. *Ecol. Lett.* 24, 2418–2426. <https://doi.org/10.1111/ele.13863>.
- Briski, E., Kotronaki, S.G., Cuthbert, R.N., Bortolus, A., Campbell, M.L., et al., 2023. Does non-native diversity mirror Earth's biodiversity? *Glob. Ecol. Biogeogr.* <https://doi.org/10.1111/geb.13781> in press.
- Campbell, M.L., Hewitt, C.L., Miles, J., 2016. Marine pests in paradise: capacity building, awareness raising and preliminary introduced species port survey results in the Republic of Palau. *Manag. Biol. Invasions* 7, 351–363. <https://doi.org/10.3391/mbi.2016.7.4.05>.
- Carlton, J.T., Eldredge, L.G., 2009. Marine bioinvasions of Hawai'i. The introduced and cryptogenic marine and estuarine animals and plants of the Hawaiian archipelago. *Bishop Museum Bull. Cult. Environ. Stud.* 4 (202 pp).
- Carlton, J.T., Chapman, J.W., Geller, J.B., Miller, J.A., Carlton, D.A., et al., 2017. Tsunami-driven rafting: transoceanic species dispersal and implications for marine biogeography. *Science* 357, 1402–1406. <https://doi.org/10.1126/science.aao1498>.
- Casties, I., Seebens, H., Briski, E., 2016. Importance of geographic origin for invasion success: a case study of the North and Baltic Seas versus the Great Lakes-St. Lawrence River region. *Ecol. Evol.* 6, 8318–8329. <https://doi.org/10.1002/ece3.2528>.
- Cuthbert, R.N., Pattison, Z., Taylor, N.G., Verbrugge, L., Diagne, C., et al., 2021a. Global economic costs of aquatic invasive alien species. *Sci. Total Environ.* 775, 145238 <https://doi.org/10.1016/j.scitotenv.2021.145238>.
- Cuthbert, R.N., Diagne, C., Haubrock, P.J., Turbelin, A., Courchamp, F., 2021b. Are the "100 of the world's worst" invasive species also the costliest? *Biol. Invasions* 24, 1895–1904. <https://doi.org/10.1007/s10530-021-02568-7>.
- Diagne, C., Leroy, B., Gozlan, R.E., Vaissière, A.-C., Aissily, C., et al., 2020. InvaCost, a public database of the economic costs of biological invasions worldwide. *Scientific Data* 7, 277. <https://doi.org/10.1038/s41597-020-00586-z>.
- Diagne, C., Leroy, B., Vaissière, A.-C., Gozlan, R.E., Roiz, D., et al., 2021. High and rising economic costs of biological invasions worldwide. *Nature* 592, 571–576. <https://doi.org/10.1038/s41586-021-03405-6>.
- Eldredge, L.G., Carlton, J.T., 2015. Update and revisions of the marine bioinvasions of Hawai'i: the introduced and cryptogenic marine and estuarine animals and plants of the Hawaiian Archipelago. *Bishop Museum Bull. Cult. Environ. Stud.* 9 (179 pp.).
- Essl, F., Dullinger, S., Rabitsch, W., Hulme, P.E., Hülber, K., et al., 2011. Socioeconomic legacy yields an invasion debt. *Proc. Natl. Acad. Sci. U. S. A.* 108, 203–207. <https://doi.org/10.1073/pnas.1011728108>.
- Hanley, N., Roberts, M., 2019. The economic benefits of invasive species management. *People Nat.* 1, 124–137. <https://doi.org/10.1002/pan3.31>.
- Haubrock, P.J., Balzani, P., Macêdo, R., Tarkan, A.S., 2023a. Is the number of non-native species in the European Union saturating? *Environ. Sci. Eur.* 35, 48. <https://doi.org/10.1186/s12302-023-00752-1>.
- Haubrock, P.J., Cuthbert, R.N., Balzani, P., Briski, E., Cano-Babacil, C., et al., 2023b. Discrepancies between non-native and invasive species classifications. *Biol. Invasions*. <https://doi.org/10.1007/s10530-023-03184-3> in press.
- Henry, M., Leung, B., Cuthbert, R.N., Bodey, T.W., Ahmed, D.A., et al., 2023. Unveiling the hidden economic toll of biological invasions in the European Union. *Environ. Sci. Eur.* 35, 43. <https://doi.org/10.1186/s12302-023-00750-3>.
- Heringer, G., Angulo, E., Ballesteros-Mejia, L., Capinha, C., Courchamp, F., et al., 2021. The economic costs of biological invasions in Central and South America: a first regional assessment. *NeoBiota* 67, 401–426. <https://doi.org/10.3897/neobiota.67.59193>.
- Hewitt, C.L., 2002. Distribution and biodiversity of Australian tropical marine bioinvasions. *Pac. Sci.* 56, 213–222. <https://doi.org/10.1353/psc.2002.0016>.
- Hewitt, C.L., Campbell, M.L., Thresher, R.E., Martin, R.B., Boyd, S., et al., 2004. Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia. *Mar. Biol.* 144, 183–202. <https://doi.org/10.1007/s00227-003-1173-x>.
- Hubbell, S.P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.
- Hudgins, E., Cuthbert, R.N., Haubrock, P.J., Taylor, N.G., Kourantidou, M., et al., 2023. Unevenly distributed biological invasion costs among origin and recipient regions. *Nat. Sustain.* 6, 1113–1124. <https://doi.org/10.1038/s41893-023-01124-6>.
- Hulme, P.E., Brundu, G., Carboni, M., Dehnen-Schmutz, K., Dullinger, S., et al., 2018. Integrating invasive species policies across ornamental horticulture supply chains to prevent plant invasions. *J. Appl. Ecol.* 55, 92–98. <https://doi.org/10.1111/1365-2664.12953>.
- Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., et al., 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90, 2648. <https://doi.org/10.1890/08-1494.1>.
- Lambert, G., 2002. Nonindigenous ascidians in tropical waters. *Pac. Sci.* 56, 291–298. <https://doi.org/10.1353/psc.2002.0026>.
- Le Roux, J., 2021. *The Evolutionary Ecology of Invasive Species*. Academic Press.
- Lenzner, B., Latombe, G., Schertler, A., Seebens, H., Yang, Q., et al., 2022. Naturalized alien floras still carry the legacy of European colonialism. *Nat. Commun.* 6, 1723–1732. <https://doi.org/10.1038/s41559-022-01865-1>.
- Liebholt, A.M., Yamanaka, T., Roques, A., Augustin, S., Chown, S.L., et al., 2016. Global compositional variation among native and non-native regional insect assemblages emphasizes the importance of pathways. *Biol. Invasions* 18, 893–905. <https://doi.org/10.1007/s10530-016-1079-4>.
- Liebholt, A.M., Turner, R.M., Blake, R.E., Bertelsmeier, C., Brockerhoff, E.G., et al., 2021. Invasion disharmony in the global biogeography of native and non-native beetle species. *Divers. Distrib.* 27, 2050–2062. <https://doi.org/10.1111/ddi.13381>.
- Liu, D., Semenchuk, P., Essl, F., Lenzner, B., Moser, D., et al., 2023. The impact of land use on non-native species incidence and number in local assemblages worldwide. *Nat. Commun.* 14, 2090. <https://doi.org/10.1038/s41467-023-37571-0>.
- Mainka, S.A., Howard, G.W., 2010. Climate change and invasive species: double jeopardy. *Integr. Zool.* 5, 102–111. <https://doi.org/10.1111/j.1749-4877.2010.00193.x>.
- McCarthy, A.H., Peck, L.S., Hughes, K.A., Aldridge, D.A., 2019. Antarctica: the final frontier for marine biological invasions. *Glob. Chang. Biol.* 25, 2221–2241. <https://doi.org/10.1111/gcb.14600>.
- Meiri, S., 2018. Traits of lizards of the world: variation around a successful evolutionary design. *Glob. Ecol. Biogeogr.* 27, 1168–1172. <https://doi.org/10.1111/geb.12773>.
- Meyer, J.-Y., 2000. Preliminary Review of the Invasive Plants in the Pacific Islands (SPREP Member Countries) by the South Pacific Regional Environment Programme. Accessed in February 2017; Available at: www.sprep.org.ws.
- National exotic marine and estuarine species information system (NEMESIS), 2017. California non-native estuarine and marine organisms (Cal-NEMO) database. Accessed in February 2017; Available at: <https://invasions.si.edu/nemesis/calnemom/overview>.
- National exotic marine and estuarine species information system (NEMESIS), 2020. Chesapeake Bay introduced species database. Accessed in October 2020; Available at: <https://invasions.si.edu/nemesis/chesapeake.html>.
- Núñez, M., Pauchard, A., Ricciardi, A., 2020. Invasion science and the global spread of SARS-CoV-2. *Trends Ecol. Evol.* 35, 642–645. <https://doi.org/10.1016/j.tree.2020.05.004>.
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., et al., 2022. *vegan: Community Ecology Package* (R package version 2.6-4).
- Paulay, G., Kirkendale, L., Lambert, G., Meyer, C., 2002. Anthropogenic biotic interchange in a coral reef ecosystem: a case study from Guam. *Pac. Sci.* 56, 403–421. <https://doi.org/10.1353/psc.2002.0036>.
- Pincheira-Donoso, D., Harvey, L.P., Cotter, S.C., Stark, G., Meiri, S., et al., 2021. The global macroecology of brood size in amphibians reveals a predisposition of low-fecundity species to extinction. *Glob. Ecol. Biogeogr.* 30, 1299–1310. <https://doi.org/10.1111/geb.13287>.
- Preston, F.W., 1948. The commonness, and rarity of species. *Ecology* 29, 254–283. <https://doi.org/10.2307/1930989>.
- Pyšek, P., Pergl, J., Essl, F., Lenzner, B., Dawson, W., et al., 2017. Naturalized alien flora of the world: species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. *Preslia* 89, 203–274. <https://doi.org/10.23855/preslia.2017.203>.

- Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., et al., 2020. Scientists' warning on invasive alien species. *Biol. Rev.* 96, 1511–1534. <https://doi.org/10.1111/brev.12627>.
- R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Renault, D., Angulo, E., Cuthbert, R.N., Haubrock, P.J., Capinha, C., et al., 2022. The magnitude, diversity, and distribution of the economic costs of invasive terrestrial invertebrates worldwide. *Sci. Total Environ.* 835, 155391 <https://doi.org/10.1016/j.scitotenv.2022.155391>.
- Ricciardi, A., MacIsaac, H.J., 2022. Vector control reduces the rate of species invasion in the world's largest freshwater ecosystem. *Conserv. Lett.* 15, e12866 <https://doi.org/10.1111/conl.12866>.
- Ricciardi, A., Iacarella, J.C., Aldridge, D.C., Blackburn, T.M., Carlton, J.T., Catford, J.A., Dick, J.T., Hulme, P.E., Jeschke, J.M., Liebhold, A.M., Lockwood, J.L., 2021. Four priority areas to advance invasion science in the face of rapid environmental change. *Environ. Rev.* 29 (2), 119–141.
- Richardson, D.M., Foxcroft, L.C., Latombe, G., Le Maitre, D.C., Rouget, M., et al., 2020. The biogeography of South African terrestrial plant invasions. In: Van Wilgen, B.W., Measey, J., Richardson, D.M., Wilson, J.R.U., Zengeya, T. (Eds.), *Biological Invasions in South Africa*. Springer, Berlin.
- Sardain, A., Sardain, E., Leung, B., 2019. Global forecasts of shipping traffic and biological invasions to 2050. *Nat. Sustain.* 2, 274–282. <https://doi.org/10.1038/s41893-019-0245-y>.
- Schwindt, E., Carlton, J.T., Orensanz, J.M., Scarabino, F., Bortolus, A., 2020. Past and future of the marine bioinvasions along the Southwestern Atlantic. *Aquat. Invasions* 15, 11–29. <https://doi.org/10.3391/ai.2020.15.1.02>.
- Seebens, H., 2021. SInAS database of alien species occurrences (2.4.1). Zenodo. <https://doi.org/10.5281/zenodo.5562892>.
- Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., et al., 2017. No saturation in the accumulation of alien species worldwide. *Nat. Commun.* 8, 14435. <https://doi.org/10.1038/ncomms14435>.
- Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., et al., 2018. Global rise in emerging alien species results from increased accessibility of new source pools. *Proc. Natl. Acad. Sci.* 115, E2264–E2273. <https://doi.org/10.1073/pnas.1719429115>.
- Seebens, H., Bacher, S., Capinha, C., Dawson, W., Dullinger, S., et al., 2021. Projecting the continental accumulation of alien species through to 2050. *Glob. Chang. Biol.* 27, 970–982. <https://doi.org/10.1111/gcb.15333>.
- Soto, I., Cuthbert, R.N., Kouba, A., Capinha, C., Turbelin, A., et al., 2022. Global economic costs of herpetofauna invasions. *Sci. Rep.* 12, 10829. <https://doi.org/10.1038/s41598-022-15079-9>.
- Sturtevant, R.A., Mason, D.M., Rutherford, E.S., Elgin, A., Lower, E., et al., 2019. Recent history of nonindigenous species in the Laurentian Great Lakes; an update to Mills et al., 1993 (25 years later). *J. Great Lakes Res.* 45, 1011–1035. <https://doi.org/10.1016/j.jglr.2019.09.002>.
- Tobias, J.A., Sheard, C., Pigot, A.L., Devenish, A.J.M., Yang, J., et al., 2022. AVONET: morphological, ecological and geographical data for all birds. *Ecol. Lett.* 25, 581–597. <https://doi.org/10.1111/ele.13898>.
- Turbelin, A.J., Diagne, C., Hudgins, E.J., Moodly, D., Kourantidou, M., et al., 2022. Introduction pathways of economically costly invasive alien species. *Biol. Invasions* 24, 2061–2079. <https://doi.org/10.1007/s10530-022-02796-5>.
- Turbelin, A.J., Hudgins, E.J., Catford, J.A., Cuthbert, R.N., Diagne, C., et al., 2023. Biological Invasions as Burdens to Primary Economic Sectors. In review. <https://doi.org/10.21203/rs.3.rs-2444595/v1>.
- , 2017. Nonindigenous Aquatic Species Database. Gainesville, Florida. Accessed in March 2017; Available at: <https://nas.er.usgs.gov/queries/SpeciesList.aspx?group=&state=WA&Sortby=1#>.
- United Nations, 2022. Net Zero Commitments by Businesses, Financial Institutions, Cities and Regions. United Nations' High-Level Expert Group on the Net Zero Emissions Commitments of Non-State Entities.
- van Kleunen, M., Pyšek, P., Dawson, W., Essl, F., Kreft, H., et al., 2019. The Global Naturalized Alien Flora (GloNAF) database. *Ecology* 100, e02542. <https://doi.org/10.1002/ecy.2542>.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.
- Wonham, M.J., Carlton, J.T., 2005. Trends in marine biological invasions at local and regional scales: the Northeast Pacific Ocean as a model system. *Biol. Invasions* 7, 369–392. <https://doi.org/10.1007/s10530-004-2581-7>.