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Are the "100 of the world's worst" invasive species also the costliest?

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Abstract Biological invasions are increasing worldwide, damaging ecosystems and socioeconomic sectors. Two decades ago, the "100 of the world's worst" invasive alien species list was established by the IUCN to improve communications , identifying particularly damaging 'flagship' invaders globally (hereafter, *worst*). Whilst this list has bolstered invader awareness, whether *worst* species are especially economically damaging and how they compare to other invaders (hereafter, *other*) remain unknown. Here, we quantify invasion costs using the most comprehensive global database compiling them (InvaCost). We compare these costs between *worst* and *other* species against sectorial, taxonomic and regional descriptors, and examine temporal cost trends. Only 60 of the 100 *worst* species had invasion costs considered as highly reliable and actually observed estimates (median: US$ 43 million). On average, these costs were significantly higher than the 463 *other* invasive species recorded in InvaCost (median: US$ 0.53 million), although some *other* species had higher costs than most *worst* species. Damages to the environment from the *worst* species dominated, whereas *other* species largely impacted agriculture. Disproportionately highest *worst* species costs were incurred in North America, whilst costs were more evenly distributed for *other* species; animal invasions were always costliest. Proportional management expenditures were low for the *other* species, and surprisingly, over twice as low for the *worst* species. Temporally, costs increased more for the *worst* than *other* taxa; however, management spending has remained very low for both groups. Nonetheless, since 40 species had no robust and/or reported costs, the "true" cost of "some of the world's *worst*" 100 invasive species still remains unknown.

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Introduction

Biological invasions are a persistent threat to ecosystems, the biodiversity they support, and the services they provide (Simberloff et al. 2013; Pyšek et al. 2020), with rates of invasion growing rapidly due to globalization (Seebens et al. 2017, 2018; Haubrock et al. 2021a). Myriad invasive alien species (hereafter, invasive species) have been introduced via various pathways between regions (Hulme 2015; Cuthbert et al. 2020). Ecological impacts from invasions have been widespread (Bellard et al. 2016; Dick et al. 2017; Crystal-Ornelas and Lockwood 2020), including native species extinctions (Blackburn et al. 2019), decreased abundances (Bradley et al. 2019), and fitness reductions (Nunes et al. 2019). Prevention of invasions and the spread of established invaders has been suggested to be the most cost-effective means of reducing adverse future effects (Leung et al. 2002).

Effective management strategies are underpinned by communication and outreach to policy makers, stakeholders and the public which improve awareness of—and then actions against—the most impactful invasive species (Courchamp et al. 2017; Lucy et al. 2020). Two decades ago, in response to a lack of specific targets to motivate policy makers and raise public awareness of invasive species, a list of 100 high profile species was compiled by the International Union for the Conservation of Nature (IUCN) Invasive Species Specialist Group (ISSG) of the Species Survival Commission. This list of "100 of the world's worst" invasive species has succeeded to boost awareness of some of the most damaging, distinct and representative invasive species globally, with inclusion in this list based on both the severity of impacts on biodiversity and human activities, and a species' potential to represent important issues in relation to biological invasions (Lowe et al. 2000). As such, species on this list are known to impact upon the structuring and functioning of ecosystems and the biodiversity they support, as well as on key human endeavours. Importantly, absence from the list does not imply lesser impact or lower risk to ecosystems or economies, and the list aims at communicating on biological invasions in general, rather than a subset of species. Of the original 100 species, one taxon, the rinderpest virus, was successfully eradicated a decade ago (World Organisation for Animal Health 2011), resulting in the list being updated with a new 100th

species, the giant salvinia, *Salvinia molesta* (Luque et al. 2013, 2014). The latest list currently comprises 38 plants, 26 invertebrates, 30 vertebrates, five fungi and one micro-organism (Luque et al. 2014).

Whilst the environmental impact of the 100 *worst* species has been well-documented, less is known about the economic impacts of many of these species, and whether those impacts are greater than *other* invasive species absent from the list. In turn, it is also unknown whether investments in management of those species have been bolstered by their inclusion on the list relative to *other* taxa. Overall, the economic importance of the *worst* species remains poorly quantified. More generally, quantifications of economic costs of biological invasions have lagged behind appraisals of invader ecological impacts, with environmental impacts often non-market in nature and thus challenging to quantify with certainty (but see Hanley and Roberts 2019). Nevertheless, over the last two decades, quantifications of invasive species economic impacts have been made at several scales including globally (Cuthbert et al. 2021; Diagne et al. 2021), for the United States (Pimental et al. 2000, 2005) and Europe (Kettunen et al. 2009; Haubrock et al., 2021b), as well as for specific taxonomic groups such as invasive insects (Bradshaw et al. 2016), activity sectors such as agriculture (Paini et al. 2016) and types of cost such as management (Hoffmann and Broadhurst 2016). Across most geographic and taxonomic scales, however, invasion cost estimations have remained diffuse. Additionally, they have lacked standardisation, precluding wider-scale analyses and consideration for the structuring and reliability of estimates where they were reported.

Recently, the InvaCost database has been developed, compiling global economic costs reported from invasive species (Diagne et al. 2020a, b). This database allows for the analysis of invasion costs across a range of taxonomic, spatial, temporal and sectorial scales, with costs comprehensively described against an array of descriptors and standardized against a uniform currency (2017 US$). Here, we employ the InvaCost database to examine the economic costs of "100 of the world's worst" invasive species. Specifically, we aim to determine: (1) what proportion of the world's *worst* invasive species is economic cost information available for; (2) how the total and median costs of the *worst* species compare to those of *other* species; (3) how costs are structured

among socioeconomic sectors, types, environments, taxonomic groups and geographic regions between *worst* and *other* species, and; (4) whether costs of *worst* and *other* species have developed differently over time, and particularly following the publication of the 100 *worst* species list in the year 2000.

Materials and methods

To estimate the economic costs of species within the updated IUCN list "100 of the world's worst" invasive species (Lowe et al. 2000; Luque et al. 2014; GISD 2020), we extracted recorded costs from the latest version of the InvaCost database as of November 2020 (9823 entries in the version 3.0; openly available at https://doi.org/10.6084/m9.figshare.12668570). These data were retrieved via a structured review of publications found in the Web of Science platform, Google Scholar, the Google search engine, and through consultation with invasive species experts and stakeholders in multiple languages (Diagne et al. 2020b; Angulo et al. 2021). Individual cost records were converted to an up-to-date and common currency [i.e., US$ 2017; see Diagne et al. (2020b) for further information on the standardisation procedure]. Finally, each cost entry was depicted by a range of about sixty descriptive fields, allowing cost analyses under different dimensions (see the aforementioned weblink for further details).

We followed several steps to filter the data prior to our analyses. First, we filtered data to include only costs that were of *high* reliability (column: "Method_reliability"), and thus from peer-reviewed literature and official documents, or reproducible sources. Second, we considered only costs that were empirically *observed* (column: "Implementation"), rather than those expected based on predictions from smaller scales. Third, we excluded genera for which species-level information was absent or mixed. The resulting subset contained 5,626 entries (see Supplementary Material 1). We then partitioned the database using the updated list of "100 worst" species (column: "Species") (Luque et al. 2013), with species not captured in that list in InvaCost categorized as *other*. This therefore assigned all entries as one of two categories: *worst* or *other* species. We acknowledge that these filtering steps resulted in the omission of species with only entries of *low* reliability and/or

associated with *potential* cost estimates, but they allowed us to use the most robust data subset that were from more reliable sources and actually observed.

As cost estimates in InvaCost are made under different temporal scales, we annualized the data based on the difference between the "Probable_starting_year_adjusted" (i.e., the year the cost started) and "Probable_ending_year_adjusted" (i.e., the year the cost ended) columns using the *expandYearlyCosts* function of the 'invacost' package (v0.3–4) in R (v4.0.2) (Leroy et al. 2020). Each expanded entry thus corresponded to a single year for which costs were available following this expansion process (i.e., costs spanning multiple years were divided among those same years). Using this expanded database, we examined cost distributions across several descriptors in the database: (*i*) cost type ("Type_of_cost_merged"), (*ii*) impacted activity sector ("Impacted_sector"), (*iii*) environment ("Environment_IAS"), (*iv*) taxonomic grouping ("Kingdom") and (*v*) continent ("Geographic_region"). For (*v*), we also examined the distributions of GDP-qualified costs among regions to account for differences in economic output, by dividing the total costs per region by the respective GDP (using the International Monetary Fund 2021 estimate; https://www.imf.org/external/datamapper/NGDPD@WEO/OEMDC/ADVEC/WEOWORLD). Full description of these variables can be found at https://doi.org/10.6084/m9.figshare.12668570. Two non-parametric Wilcoxon rank sum tests were used to compare (*i*) total and (*ii*) management costs per species between the *worst* and *other* groups.

Moreover, we examined the temporal development of average costs, separately considering the *worst* and *other* species groups between 1960 and 2020 (*summarizeCosts* function of the 'invacost' package). For temporal analyses, we also divided each entry by the total numbers of species in the *worst* (total: 60; management only: 58) and *other* (total: 463; management only: 375) groups, respectively, because fewer species were reported in the former. In doing so, we examined whether total costs and management spending per species for the *worst* taxa increased to a greater extent than for *other* species following the publication of the list in the year 2000.

Results

Economic costs were available for 60 of the *worst* 100 invasive species in InvaCost following the aforementioned filters. Outside of this list, cost information for 463 *other* species was available. In total, the 60 *worst* taxa reportedly caused US$ 148.9 billion (*n* = 3,035 expanded database entries; hereon *n*), whereas documented impacts from *other* taxa amounted to US$ 163.2 billion (*n* = 7,484). Average impacts per species of the *worst* taxa (Median: US$ 42.9 million; range: US$ 1 thousand – 43.4 billion) were significantly higher and less varied than *other* invasive species (Median: US$ 534 thousand; range: US$ 4–54.4 billion) (Wilcoxon rank sum test: W = 6891, *p* < 0.001) (Fig. 1a). When considering management costs alone, costs still significantly differed between the two groups, with more investment in management of listed species on average (*worst*, total: US$ 9.0 billion, median: US$ 10.0 million; *other*, total: 23.6 billion, median: US$ 142 thousand) (W = 5008, *p* < 0.001) (Fig. 1b).

The top 10 contributing taxa of the *worst* 100 and of the *other* species for economic impacts are shown separately in Fig. 2, based on the summed impact of each species over the whole period of the cost occurrence. Here, the most damaging *worst* taxa economically included the feral cat, black rat, Formosan termite, red imported fire ant, and leafy spurge, followed by the gypsy moth, wild pig, zebra mussel,

European rabbit, and golden apple snail. Conversely, the top 10 *other* species were dominated by costs from the yellow fever mosquito, boll weevil, annual ragweed, Scleroderris canker and western honey bee, followed by the New World screw-worm fly, Asian blue tick, common pigeon, stable fly and soybean aphid (Fig. 2). The mean cost of the top 10 costliest *worst* species (US$ 13.5 billion) was higher than the top 10 *other* species (US$ 11.7 billion). Yet, these top ten *other* species are on average over four times as costly as the mean from the entire *worst* list (US$ 2.5 billion).

The majority of costs related to damages and losses for both the *worst* (72%) and *other* (61%) species. Despite being in the top 100 and bearing higher average costs, *worst* species management investments were proportionately much lower than for *others* (6% *vs.* 15%) (Fig. 3a, b). The environmental sector was proportionately most impacted by the *worst* species, followed by mixed sectors, public and social welfare, and agriculture (Fig. 3a). Impacts by *other* taxa largely affected agriculture, followed by mixed sectors and authorities-stakeholders (Fig. 3b).

Most reported costs from the *worst* and *other* species came from terrestrial taxa (93% *vs.* 65%), with *other* taxa also comprising high semi-aquatic taxa costs (34%). Reported cost contributions from fully aquatic species were generally low (*worst*: 7%; *other*: 1%). The highest shares of costs were caused by animals in both the *worst* (91%) and *other* (83%)
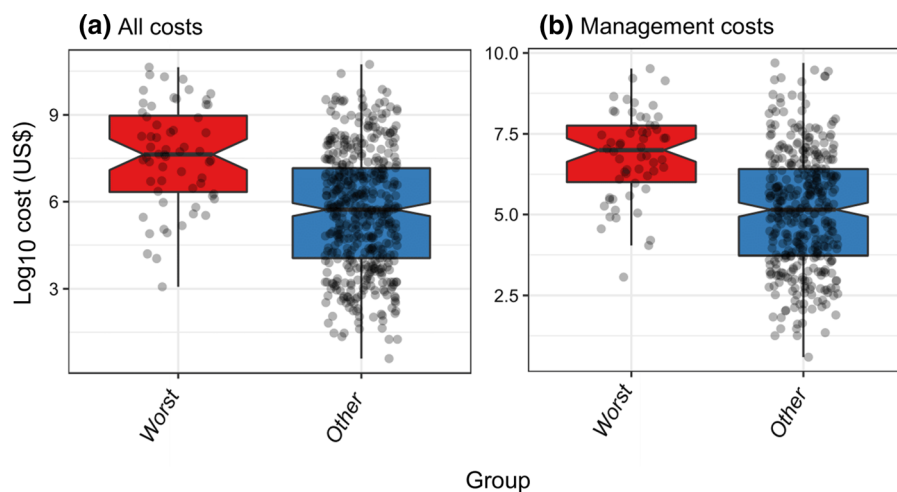

Fig. 1 Boxplots of total (**a**) and management (**b**) costs per invasive species reported in InvaCost, considering listed *worst* and *other* taxa. The box illustrates the median (50%) and

interquartile ranges (25% and 75%) and vertical lines represent minimum and maximum values. Points are costs per species. Note that the costs were transformed onto a log$_{10}$ scale
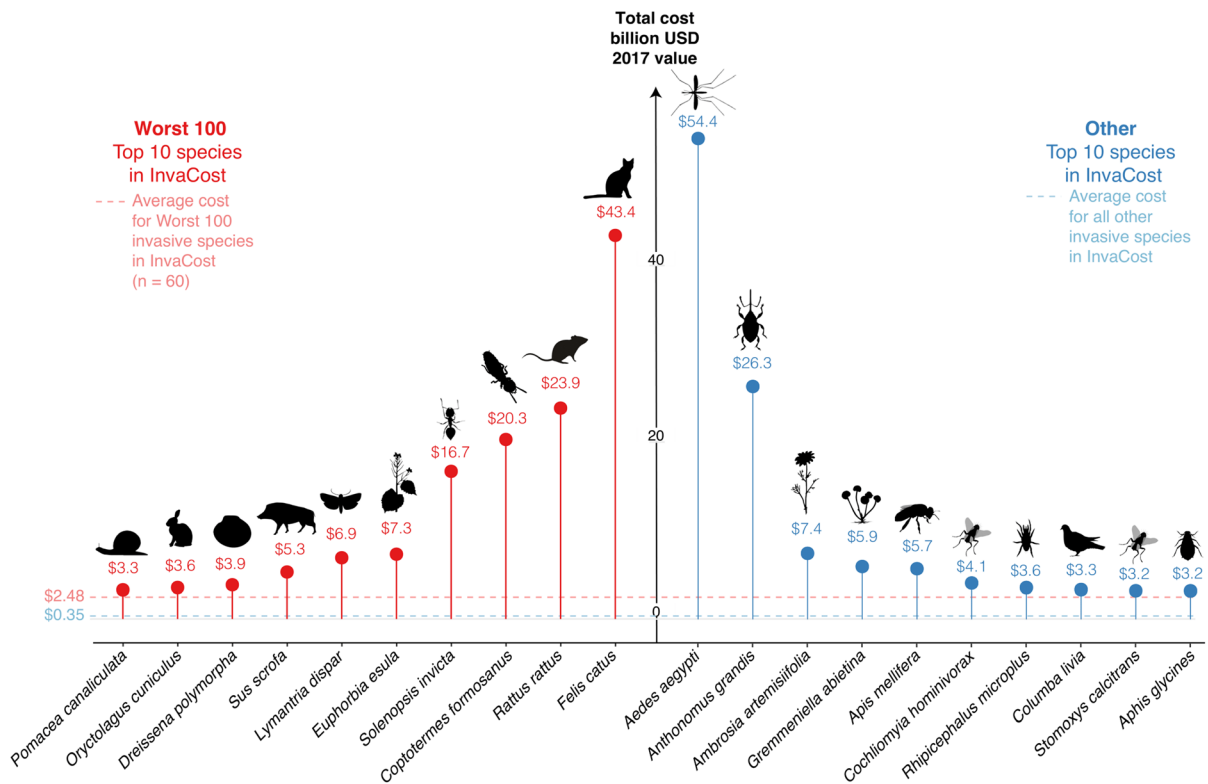
Fig. 2 Total economic costs (billion USD, 2017 value) (1960–2020) for the top ten economically damaging species from the *worst* 100 species (red) and *other* taxa (blue) present in the InvaCost database. Totals were determined across all database entries per species. Horizontal, dashed lines correspond to means from the entire list of each group

groups, with relatively few contributions from plants (*worst*: 9%; *other*: 10%) (Fig. 3c, d). Considering average costs per species in taxonomic kingdoms, *worst* species had higher costs than *other* species for animals (US$ 3.6 billion *vs*. 0.7 billion), plants (US$ 745.6 million *vs*. 63.6 million) and chromists (US$ 53.2 million *vs*. 44.7 million), but not fungi (US$ 0.1 billion *vs*. 1.2 billion) or viruses (US$ < 1 million *vs*. 328.1 million).

Cost contributions from the *worst* taxa were very imbalanced among regions, being substantially highest in North America (Fig. 3c). Conversely, whilst costs from *other* taxa were also predominated in North America, cost contributions in Asia, Europe, Africa and South America were proportionally much higher than the *worst* taxa, but Oceania was lower (Fig. 3d). Even when qualifying cost contributions by GDP (excluding mixed continents and Antarctic-Subarctic), North America contributed the highest share of *worst* taxa total costs (45%), followed by Oceania (32%). For *other* taxa, however, Africa contributed the

highest share of GDP-qualified costs (29%), followed by North America (25%) and South America (21%).

Between 1960 and 2000, US$ 9.5 million was spent on the *worst* species per year per species, and this number increased one order of magnitude, to US$ 100 million per year per species after 2000. For *others*, US$ 1.7 million was spent per year before 2000 and US$ 11.8 million per species after. Accordingly, total costs for the *worst* species increased more markedly after 2000 (11-fold) than *other* species (seven-fold) (Fig. 4a; Figure S1).

When comparing only management spending between the groups per species, the *worst* species received a three-fold increase in investment post-2000 compared to pre-2000 (US$ 1.5 million and then 4.5 million), while *other* species had approximately a two-fold increase (US$ 713 thousand and then 1.6 million) (Fig. 4b; Figure S1). However, numbers of unexpanded (i.e., before being annualised) cost entries increased less for the *worst* species (ten-fold) than for
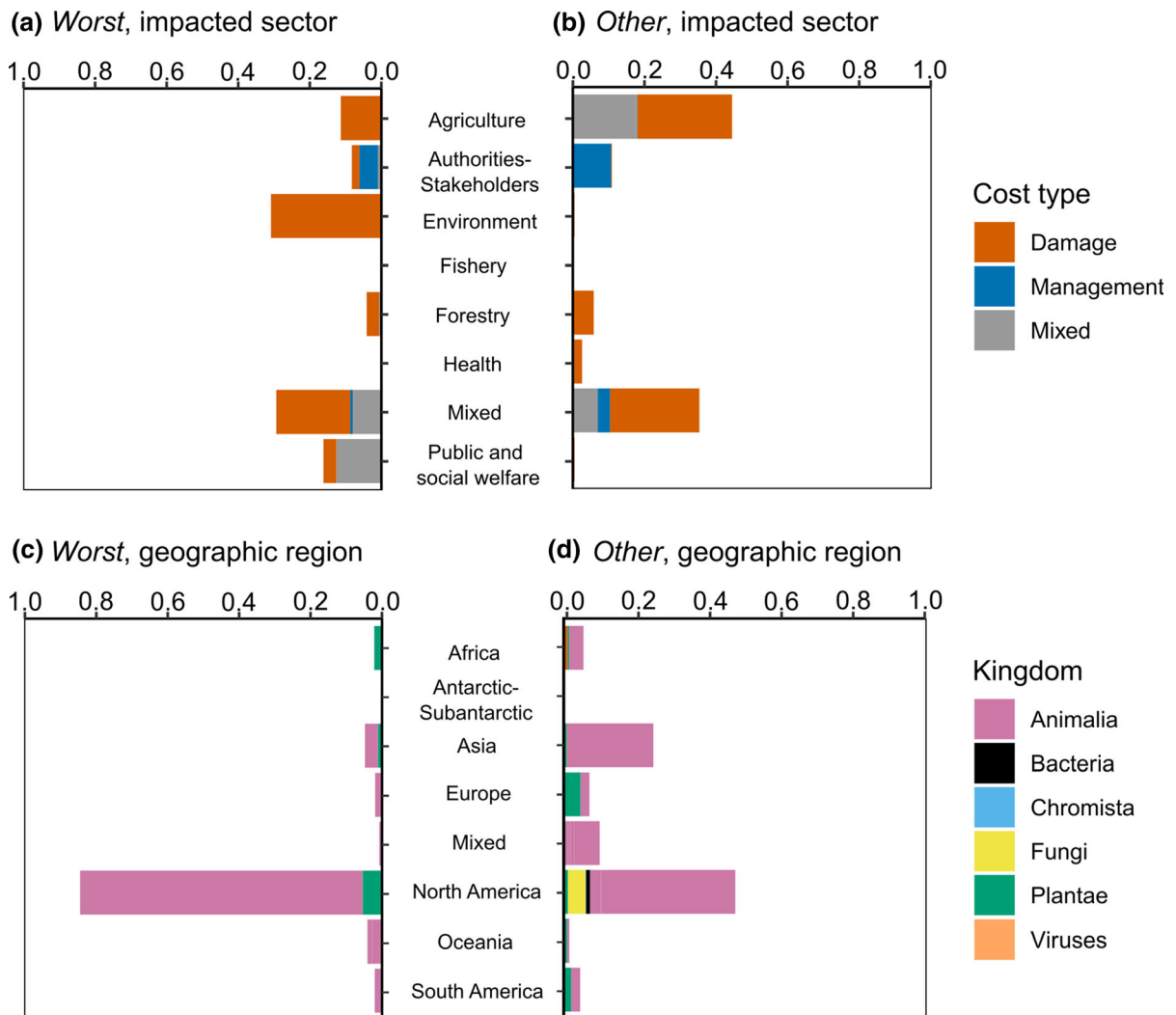
(a) *Worst*, impacted sector

(b) *Other*, impacted sector

(c) *Worst*, geographic region

(d) *Other*, geographic region

Fig. 3 Proportions of total costs among *worst* (**a**, **c**) and *other* (**b**, **d**) invasive species available in InvaCost, across socioeconomic sectors and cost types (**a**, **b**) and geographic regions and taxonomic kingdoms (**c**, **d**)

other species (36-fold) before and after 2000 (publication year).

Discussion

Despite almost two decades of heightened visibility of invaders within the "100 of the world's worst" invasive species list (Lowe et al. 2000; Luque et al. 2014), over one third lacked robust economic costs. Nonetheless, average economic impacts of the 60 *worst* invasive species significantly exceeded that of all *other* reported invasive species. Admittedly,

inclusion of invasive species on this list may have contributed to increasing the economic costs reported for these taxa, with *worst* costs increasing 11-fold and *others* seven-fold after the list was published; but they seem more economically damaging based on the available data. Nonetheless, management spending only increased towards the *worst* species slightly more (three-fold) than *others* (two-fold) after 2000, and thus management investments have been outweighed by increasing damage costs from invasion for both groups.

The nature of costs of the *worst* and unlisted *other* may be explained by several factors. First, the lack of
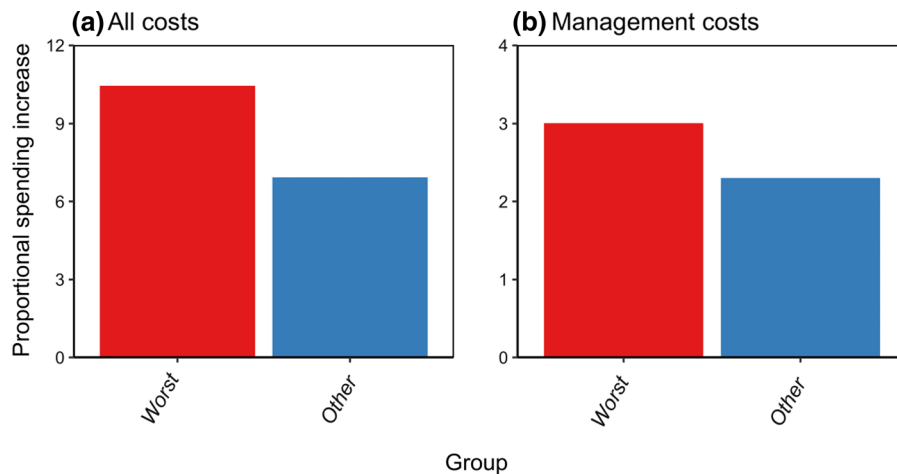
Fig. 4 Proportional increase in invasion costs between *worst* and *other* taxa over time per species, post-2000 relative to pre-2000 (year when 100 *worst* species list was published), considering all costs (**a**) and management costs only (**b**). For example, a proportional increase of 10 corresponds to a ten-fold increase in costs between pre-2000 and post-2000

robust invasion costs, especially for 40% of the 'flagship' 100 species listed, illustrates a broader, pervasive issue surrounding robust invasion cost estimations. The vast majority of invasive species have not been examined for economic costs (e.g., Gren et al. 2009; Haubrock et al., 2021b; Liu et al. 2021), with cost quantifications remaining lackluster relative to ecological impact appraisals (Crystal-Ornelas and Lockwood 2020). Therefore, improved invasion cost estimation is required for invasive species more generally, with no published estimates of economic impact for the majority of known aliens (*ca.* 14,000 species; Cuthbert et al. 2021). Second, the differences in cost structuring of *worst* and *other* species costs may be further attributed to underlying criteria for species being listed. Impacts on biodiversity were a key criterion for inclusion on the list (Lowe et al. 2000), with such impacts often non-market in nature and thus challenging to quantify in monetary terms (but see Hanley and Roberts 2019). Indeed, impacts to the environment sector were particularly marked in the *worst* compared to *other* taxa (31% *vs.* < 1%). Similarly, whilst impacts on human activities were also considered when selecting species, such impacts may also frequently be non-market in nature (e.g., certain recreational activities) and thus equally challenging to quantify holistically. Nonetheless, management investments, which should comprise a high proportion of costs for species with few market

impacts, were very low overall (*worst*: 6%; *other*: 15%).

Third, differences in costs may be an artefact of the filtering and averaging strategies employed in the present study. Indeed, as we solely considered species-specific, observed, highly reliable costs, to minimise irrelevant cost estimates considering cost data associated with non-robust estimation methods and/or not actually observed. However, when the reliability and implementation filters are removed, the number of *worst* species increases to just 68. Several of the most economically damaging species were not considered for the IUCN *worst* species list, given the necessity of a broad taxonomic range for the list. Indeed, 90 of the *other* species exceeded the median cost of the *worst* (US$ 43 million). This particularly negated inclusion of several known economically-damaging congenerics, such as the yellow fever mosquito *Aedes aegypti* and brown rat *Rattus norvegicus*, which imparted marked costs but were already represented at the genus level by another species (*Aedes albopictus* and *Rattus rattus*) and therefore were not listed in the *worst* 100 as a rule. Importantly, this also reflects the caveat that the enlisting of a given species does not imply that it is any more damaging than *others* (Lowe et al. 2000; Luque et al. 2014). Furthermore, it indicates that inclusion of species on such a list is not a prerequisite for management expenditure.

Data gaps mean that our results should be cautioned in terms of species comparisons and that they are

likely underestimates for both *worst* and *other* groups. A lack of costs, or complete absence, for certain taxa in the InvaCost database does not equate to a lack of impact. It may be that these impacts are more difficult to quantify in monetary terms in certain sectors (e.g. environmental), located in countries with a lower capacity to study invasions, or in habitats that are more difficult to monitor. As such, even species with the lowest reported economic costs on the *worst* list (e.g. red-vented bulbul *Pycnonotus cafer* and chytrid fungus *Batrachochytrium dendrobatidis*) or those without costs at all (e.g. common wasp *Vespula vulgaris*, fire tree *Morella faya* and common malaria mosquito *Anopheles quadrimaculatus*) could have substantial costs that are as of yet undocumented. Likewise, this applies to the *other* taxa, whereby the vast majority of known invasive species lack economic cost studies. As such, low costs likely reflect knowledge gaps rather than a lack of impact for many taxa.

Whilst efforts were made to provide a broad taxonomic breadth in the 100 *worst* list, taxonomic unevenness was also found considering available *worst* and *other* species in respect to economic costs, with both being dominated by animals and from terrestrial environments. We found that costs of groups such as invasive plants are lacking. Nevertheless, the much higher damages and losses incurred overall suggests that greater management investments are required to offset costs from all invasive taxonomic groups, particularly at early invasion stages (Leung et al. 2002). Indeed, management spending increased at a much lower rate than damage costs for both *worst* and *other* invaders. Geographic gaps accompanied taxonomic unevenness, with the highest costs of the *worst* species occurring by far in North America, even when considering GDP, whilst *other* species were more balanced regionally. For example, costs in Asia were five-fold higher proportionally for *other* taxa compared to the *worst*. Overall, these taxonomic and geographic results might reflect wider biases in invasion impact research (Crystal-Ornelas and Lockwood 2020). On the other hand, the diversity of sectors impacted indicates that the listing of the *worst* species was broad in scope.

Temporally, costs generally increased over time per species for both species groups. However, costs of the *worst* species grew more than the *others* before and after the list was published in the year 2000 (11-fold *vs*. seven-fold), but only slightly so for management investment (three-fold *vs*. two-fold). As one of the aims of inclusion of species on the *worst* species list was to increase societal awareness, such an increase in communications does not appear to have succeeded to substantially boost management investments for the *worst* species compared to *other* invaders. Conversely, damage costs have increased at a much greater rate for both the *worst* and *other* species than management. As rates of invasion continue to increase worldwide (Seebens et al. 2017, 2021), it is expected that such costs will continue to rise, and perhaps especially for *other* species as novel invasions might be accompanied with novel economic impacts. Indeed, the fact that only one of the previously listed *worst* species has been successfully eradicated illustrates the challenges and shortcomings of invader management more broadly (Luque et al. 2013). Given the cost effectiveness of early-stage invasion management compared to long-term control (Leung et al. 2002), increased investments should be made to prevent introduction of invasive species—both inside and outside of the list. Such interventions could take several forms depending on the pathway of introduction, such as the implementation of airport checks for alien taxa in transit, more efficacious ballast water regulations or tighter restrictions on the trade of exotic pets.

Overall, whilst the present study compiled available information on economic costs of species included in and excluded from the IUCN "100 of the world's worst" invasive species list, a large share (40%) of *worst* species lacked robust economic cost appraisals. This reflects a wider absence of cost estimation in invasion science—while we acknowledge that the InvaCost data here are not exhaustive. Nonetheless, the proportionate extent of cost reporting (60 of 100 with robust data) for listed species is far higher considering the very low cost reporting for *other*, unlisted species (463 overall, relative to all known invaders worldwide, of *ca*. 14,000 aliens; Cuthbert et al. 2021). Accordingly, our findings suggest that the list effectively increased cost reporting for the *worst* species, or that they are generally better-studied. We again stress that many of those still lack robust monetary appraisals. Moreover, we note that listed *worst* species were often selected on the basis of their economic impacts, and so they may simply be more likely to have reported costs. Despite differences identified here, the "true" economic impact of the 100 *worst* invasive species thus remains

unknown, as well as the cost of invasions more broadly. We therefore encourage more resolute cost reporting to quantify the global extent of invasion costs for all invasive taxa.

Availability of data and material Underlying data are publicly available in Diagne et al. (2020b: accessible at https://www.nature.com/articles/s41597-020-00586-z) and in an online repository (https://doi.org/10.6084/m9.figshare.12668570).The final dataset used for analysis in this paper will be provided as Supplementary Material.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that there are no conflicting or competing interests.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication All authors have seen and approved the manuscript and have consented for publication.

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