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SI on economic costs of invasions - Feeling the pinch: global economic costs of crayfish invasions and comparison with other aquatic crustaceans

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Abstract

Despite voluminous literature identifying invasive species impacts, understandings of monetary costs remain limited. Recently, profound impacts have been attributed to invasive crustaceans, but associated monetary costs lack synthesis. Here, we analyse globally reported costs of invasive freshwater crayfish across taxonomic, spatial and temporal descriptors. Moreover, we compare their cost magnitude to other invasive crustaceans – crabs, amphipods and lobsters. Between 2000 and 2020, crayfish caused US\$ 1.28 billion in reported costs; the vast majority (95%) attributed to Astacidae (principally the signal crayfish *Pacifastacus leniusculus*) and the remainder to Cambaridae. According to reports, crayfish costs mostly impacted European economies (US\$ 1.23 billion), followed by costs reported for North America and Asia. Despite well-known damages caused by invasive crayfish, costs were unreported elsewhere, highlighting knowledge gaps and challenges in cost quantifications. Invasive crayfish costs increased exponentially in the last two decades, averaging at US\$ 61 million per-annum. Invasive crabs caused costs of similar magnitude (US\$ 1.25 billion; US\$ 53 million per-annum) but were mostly confined to North America (95%). Damage-related costs dominated for both crayfish (83%) and crabs (99%), with management spending lacking. Reported economic impacts from amphipods (US\$ 178.8 thousand) and lobsters (US\$ 44.6 thousand) were considerably lower. We identify burgeoning economic costs from these invasive groups yet highlight pervasive knowledge gaps at multiple scales. Further cost reporting is required to better-ascertain the true scale of monetary costs caused by invasive aquatic crustaceans.

Introduction

Owing to their sensitivity to the effects of climate change (Woodward et al. 2010) and a range of other anthropogenic pressures (Strayer 2010; Darwell et al. 2018), freshwater ecosystems have been characterised as the most threatened ecosystems worldwide (Reid et al. 2019). Invasive alien species (IAS) are considered among the strongest drivers of biodiversity decline, as well as disruptors of ecosystem functioning and ecosystem services provisioning (Blackburn et al. 2019; Pyšek et al. 2020), with concerns rising as invasion rates continue to increase (Seebens et al. 2017; 2020; Bailey et al. 2020). Freshwater ecosystems are especially vulnerable to the introduction of alien species (Frederico et al. 2019). Despite the recognition of these ongoing losses and risks, the capacity of various countries to effectively combat and prevent biological invasions remains limited (Early et al. 2016; Faulkner et al. 2020). This can be in part attributed to limited understanding of the magnitude of losses and the expenditure required to avoid those or prevent them from happening in the future.

In recent years, there have been significant advances in understanding the ecological impacts of IAS on recipient aquatic ecosystems (e.g. Jackson 2015; Dick et al. 2017; Bradley et al. 2019; Haubrock et al. 2019b). Whilst frameworks for categorising invader socioeconomic impacts have advanced throughout the years in response to the challenges associated to monetizing socioeconomic impacts (Bacher et al. 2018), the paucity of quantified costs incurred by invasions is weakening the rationale for policy makers to invest the sparse available resources toward prevention, control and eradication. Pimentel et al. (2000; 2005), followed by Kettunen et al. (2009), summarized the costs of IAS on large spatial scales. Despite

the methodological shortcomings of these studies (Charles and Dukes 2008; Cuthbert et al. 2020a), they partly succeeded in raising awareness of IAS-induced costs (Hoffmann and Broadhurst 2016). The existence of information on costs inferred from IAS is of utmost importance; a lack thereof may be misleading for policy making and resource management as well as minimize the awareness and preoccupation regarding IAS. Despite recent efforts to analyze invasion costs of specific taxonomic groups (Bradshaw et al. 2016; Haubrock et al. this issue), across various regions (Crystal-Ornelas et al. in review; Haubrock et al. in press; Liu et al. in review) or habitat types (Cuthbert et al. in review), a detailed collective understanding is still lacking for many taxa and regions. Filling this knowledge gap is critical for informing policy responses, efficiently allocating resources for management and avoiding future losses.

Crayfish are the largest of freshwater invertebrates and among the longest-lived (Souty-Grosset et al. 2006), with almost 700 currently known species (Crandall and De Grave 2017). Owing to their substantial individual size and ability to reach high densities, their omnivorous nature and dominance in trophic interactions and ecosystem engineering (Reynolds and Souty-Grosset 2011), they play important ecological roles (Twardochleb et al. 2013; Lipták et al. 2019; Veselý et al. 2020). Their introduction globally has been mostly for aquaculture, fishery and ornamental purposes (Ackefors 2000; Faulkes 2015; Weiperth et al. 2020), with resulting invasions generally leading to severe ecosystem and socio-economic losses (Lodge et al. 2012; Madzivanzira et al. 2020). In some cases, the entire functioning of freshwater ecosystems has been irreversibly altered by alien crayfish (Lodge et al. 2000; Gherardi 2006). The increasing recognition of severe impacts caused by alien crayfish has attracted increasing research attention about their introduction pathways, risks, ecological interactions and impacts (Gherardi et al. 2011; Haubrock et al. 2019a; South et al. 2019; 2020). Introductions of North American crayfish species are particularly problematic, as they often also vector *Aphanomyces astaci* Schikora (Oomycetes), the causative agent of crayfish plague. This oomycete is included among the IUCN 100 world's worst IAS list (Lowe et al. 2000), given the highly susceptibility and mortality of crayfish species not originating from this continent (Svoboda et al. 2017).

Invasive crayfish species (ICS) are, however, not the only invasive crustaceans with proven impacts on recipient communities (Lodge et al. 2012; Twardochleb et al. 2013). Similar to them, numerous invasive crabs have been recognized as a large threat, with marked adverse ecological and socioeconomic effects. Examples include the Chinese mitten crab *Eriocheir sinensis* Milne-Edwards, 1853 and the European green crab *Carcinus maenas* (Linnaeus, 1758), both listed in the Global Invasive Species Database and among the 100 worst invasive species (Lowe et al. 2000). Amidst their relatively well-established presence in Europe and North America, invasive crabs are also known for their often devastating effects on the invaded environment and native biota (Holdich et al. 1999). Other invasive aquatic crustaceans, such as amphipods for example, have also created large concerns (Cuthbert et al. 2020b). A noteworthy example is the 'killer shrimp' *Dikerogammarus villosus* (Sowinsky, 1894) (e.g. Dick et al. 2002; Taylor and Dunn, 2017).

Despite the recent advances in invasion science confirming the ecological notoriety of ICS as well as other aquatic crustaceans, economic analyses lag behind, and are partly overshadowed by the benefits brought by aquaculture and fishing industries. Direct and indirect costs associated with damages or losses from these taxa therefore remain scarce, resulting in minimal investments into research and management measures. To address this lack of information and highlight existing knowledge gaps in costs of their invasions worldwide, we utilized the InvaCost database, the most recent, comprehensive database of globally reported economic costs of IAS (Diagne et al. 2020a). This database contains detailed information on the costs (e.g. cost types, impacted sectors, regional attributes, cost estimation reliability, etc.) associated with ~ 500 invasive species. In the present study, we use a relevant subset of this database to describe the global costs associated with ICS and other aquatic invasive crustaceans to infer comparisons and understand the magnitude of their impacts. Moreover, we investigate how these costs are structured across space, time, cost types and sectors affected, as well as identify knowledge gaps in cost estimates.

Methods

Data collection and filtering

For the purpose of analyzing global costs of invasive aquatic crayfish, we used data from the InvaCost database (Diagne et al. 2020a), which primarily presents costs from English-written sources. InvaCost is a dynamic database that allows for corrections and additions of new cost entries as they develop or are reported throughout time. The first version of InvaCost comprised 2,419 reported economic costs of IAS retrieved from published peer-reviewed and grey literature (InvaCost v1; as of December 2019). More recently, those data have been supplemented with a search for costs recorded in fifteen of the most widely spoken languages, either as a mother tongue or second language (5,212 cost entries; Angulo et al. 2020), as well as via additional searches (2,374 entries; Ballesteros-Mejia et al. 2020). As of the timing of the writing (November 2020), the latest version of InvaCost (version 3.0, Diagne et al. 2020b; openly available at <https://doi.org/10.6084/m9.figshare.12668570>) consisted of 9,823 cost entries from IAS globally, after resolving duplications, allowing for comprehensive analysis of IAS at different taxonomic, spatial and temporal levels.

In compiling these data, grey and peer-reviewed literature were retrieved from standardised searches in online repositories (Web of Science, Google Scholar and Google search engine). The standardized searches, described in more detail in Diagne et al. (2020a), were enriched by targeted searches aiming at opportunistic collections of material containing cost information on IAS; these searches were performed through national databases, web pages of national institutions, NGOs and other organizations, as well as through contacts with regional national experts (Angulo et al. 2020). The collected material was thoroughly examined to assess relevance, and then scrutinized for collating cost estimates associated with aquatic crustaceans. Every cost entry recorded was described by various descriptors (Supplementary Material 1).

We identified cost entries attributed to invasive freshwater crayfish, based on the “Order” classification by filtering out species belonging to “Decapoda” and thereafter entries belonging to relevant crayfish families (“Astacidae”, “Cambaridae”, “Parastacidae”, and “Cambaroididae”). This resulted in a total of 112 entries. Additionally, to put the costs of invasive crayfish into perspective relative to other invasive crustaceans, we compared them to those of invasive amphipods (Order: Amphipoda; n = 1 species), crabs (Infraorder: Brachyura and Anomura; n = 6), and lobsters (Family: Nephropidae; n = 1), on the basis of reported costs in the InvaCost database. Costs for these groups were extracted using (a) the “Order” column and selecting “Amphipoda”, and (b) the “Family” column and selecting families of crabs and the family “Nephropidae”, respectively. The identified cost entries for all crustaceans thus amounted to 120 entries attributed exclusively to aquatic species.

Temporal cost dynamics, cost descriptors and comparisons across crustacean categories

Deriving the total cumulative cost of invasions over time requires to consider the duration of each reported cost. The duration of each cost entry was inferred from the InvaCost database (columns “Probable starting year adjusted” and “Probable ending year adjusted”; see more details in Diagne et al. 2020b; <http://borisleroy.com/invacost/Readme.html>). When information was missing for the year that the costs started occurring, we conservatively considered the publication year of the original reference as the starting years for costs. In those cases where the last year over which costs occurred was missing, but the cost was listed as ‘highly reliable’ and ‘potentially ongoing’, costs were assumed to continue until 2020 (see *Method reliability* below). Costs in InvaCost were standardized to 2017 equivalent US\$ using the World Bank’s market exchange rate and accounting for inflation through the Consumer Price Index of the year the cost was estimated for in each study. Using the duration time (in years) and the standardized costs in 2017 values (US\$), we annualised the data, with each entry corresponding to a given year. This step made cost entries of different types and durations comparable. For example, a total cost of \$1,000 between the years 2000 and 2009 would correspond to \$100 per year (see <https://doi.org/10.6084/m9.figshare.12668570> for further information). This process allowed us to analyze in a systematic manner the total cumulative cost along the defined period, resulting in 277 cost entries for invasive crayfish species, and considerably less for invasive crab species (n = 71), amphipods (n = 6), and lobsters (n = 2). We provided our final dataset used as a supplement (Supplementary Material 2).

Finally, the invasion costs were analysed based on the following five descriptors (described in more details in Diagne et al. 2020a; see Supplementary Material 1 and Diagne et al. 2020b):

(i) Method reliability: illustrating the perceived reliability of cost estimates based on the type of publication and method of estimation (“High” if costs were described in pre-assessed material (peer-reviewed articles and official reports) or in grey material but with documented, repeatable and traceable methods; and “Low” otherwise); (ii) Implementation: referring to whether the cost estimate was actually realised in the invaded habitat (“Observed”) or whether it was extrapolated based on expectations on costs beyond the invaded habitat and/or predicted over time (“Potential”); (iii) Geographic region:

describing the continental geographic origin of the listed cost; costs that were not attributable to specific regions were categorised as “Diverse/Unspecified”; (iv) Type of cost merged: grouping of costs according to the categories: (a) “Damage-Loss”, referring to damages or losses incurred by invasion (i.e. costs for damage repair, resource losses), (b) “Management costs”, comprising expenditure such as monitoring, prevention, control, eradication and (c) “Mixed” costs, including a mix of categories (a) and (b) which include cases where reported costs were not easily distinguished between damage and control costs; and (v) Impacted sector: the activity, societal or market sector that was impacted by the cost. Individual cost entries not allocated to a single sector were classified under “Mixed” in the “Impacted sector” column.

For the purposes of analysing the economic costs of invasive crayfish and describing trends through time, we used the *calculateRawAvgCosts* function implemented in the R package “invacost” (Leroy et al. in prep; borisleroy.com/invacost/Readme.html). Using this method, we calculated the observed cumulative and average annual costs between the first recorded costs (2000) and last reported costs (2020), considering 5-year intervals.

Last we compared the costs of crayfish invasions to costs of other prominent crustacean invaders (crabs, amphipods, and lobsters) which has helped identify knowledge gaps and biases. Specifically, we focused on comparing how the total costs of these groups varied across species, impacted geographic regions, sectors of the economy, and the type of costs.

Results

Economic costs across taxonomic groups

The total costs of the 277 freshwater crayfish entries amounted to US\$ 1.28 billion, for the period 2000–2020. From this total cost, 94.5% was inferred from Astacidae (US\$ 1.21 billion; n = 159 database entries) and 5.3% from Cambaridae (US\$ 67.8 million; n = 110). Further, eight cost entries were classified as diverse or unspecified. No entries were reported for Parastacidae (crayfish native to the Southern Hemisphere) and Cambaroididae (endangered endemic species from Far-East Asia).

At the genus-level, US\$ 1.21 billion was attributed to the genus *Pacifastacus* (specifically the signal crayfish *P. leniusculus* (Dana, 1852); n = 147), US\$ 54.80 million were attributed to the genus *Faxonius* (34 entries with reported representative species previously attributed to *Orconectes*, see Crandall & De Grave 2017); the rusty crayfish *F. rusticus* (Girard, 1852), the spiny-cheek crayfish *F. limosus* (Rafinesque, 1817), followed by US\$ 13.01 million to the genus *Procambarus* (the red swamp crayfish *P. clarkii* (Girard, 1852); n = 76). Diverse or unspecific costs amounted to US\$ 6.76 million (n = 20).

Economic costs based on method reliability and implementation types

Highly reliable cost entries comprised 99.8% of the documented total cost for freshwater crayfish (as well as 275 of 277 database entries, Fig. 1). Although most entries and cost estimates were classified as ‘High’ reliability, the vast majority of them were ‘Potential’ (US\$ 1.14 billion; 89.1%) rather than ‘Observed’

(10.9% of total costs, US\$ 141 million), implying that most were projected in time and/or space but have not necessarily been borne in practice. Note though that observed costs constituted the majority of database entries (207 out of 277 database entries, Fig. 1).

All invasive crayfish species with recorded costs in InvaCost were native to North America (Fig. 2). The majority of total ('Observed' and 'Potential') reported costs (US\$ 1.23 billion; n = 232) were inferred in Europe, while US\$ 54.8 million (29 database entries) was related to certain parts of North America (specifically Wisconsin, which is north to the native range of rusty crayfish responsible for these costs) and relatively little in Asia (US\$ 292.73 thousand; n = 16) (Fig. 3a). Accordingly, there was a striking absence of cost information for certain regions which include South America, Africa, and Oceania (Figs. 2 and 3).

In Europe, the vast majority of total costs were incurred in Sweden (US\$ 1.03 billion; n = 24), followed by the United Kingdom (US\$ 176.75 million; n = 91); the costs in both countries were entirely due to *P. leniusculus*. Monetary impacts in Spain (US\$ 7.63 million; n = 69), Portugal (US\$ 4.11 million; n = 2) and France (US\$ 1.72 million; n = 37) were significantly lower and mostly driven by *P. clarkii*, whereas those incurred in Italy (US\$ 6.29 million; n = 7) were not linked to a specific species (Fig. 3a). Considering only observed costs, US\$ 116.41 million was attributed to Europe and US\$ 24.56 million to North America. Within Europe, 'Observed' costs were reported predominantly in the United Kingdom (US\$ 99.41 million; n = 79), Spain (US\$ 7.63 million; n = 69), Italy (US\$ 6.29 million; n = 7), France (US\$ 1.72 million; n = 37), Portugal (US\$ 1.22 million; n = 1), and Norway (US\$ 145.36 thousand; n = 1) (Fig. 3b).

Economic costs among cost types and impacted sectors

With respect to cost types, 83.2% of crayfish-related costs were attributed to damages or resource losses, and only 12.8% allocated to management expenditures on prevention, control or eradication; very few were classified as mixed (4.0%). Regarding impacted sectors, the majority was, however, classified under "Mixed" sectors (US\$ 1.06 billion; 82.5%; n = 35), followed by impacts to "Authorities-Stakeholders" (US\$ 193.51 million; 15.1%; n = 204), impacts to "Fishery" (US\$ 24.64 million; 1.9%; n = 20), and lastly to the categories "Environment" (US\$ 7.41 million; < 1%; n = 17) and "Agriculture" (US\$ 1.22 million; < 1%; n = 1). Observed costs differed considerably, with 37.8% of costs (US\$ 53.6 million) being attributed to management expenditure, 25.8% (US\$ 36.4 million) to damage-losses, and 36.4% (US\$ 52.3 million) classified as mixed costs (Fig. 4a). The majority of observed costs were attributed to "Authorities-Stakeholders" (US\$ 82.28 million; 58.4%), substantially driven by *P. leniusculus*. This cost was followed by costs to "Fishery" (US\$ 24.64 million; 17.5%), inferred by *F. rusticus*, "Environment" (US\$ 7.41 million; 5.3%) and lastly "Agriculture" (US\$ 1.22 million; <1 %), both majorly induced by *P. clarkii*. Costs attributed to "Mixed" sectors totalled at (US\$ 25.72 million; 18%) (Fig. 4b).

Temporal dynamics of costs

For invasive crayfish, the recorded total cost of US\$ 1.28 billion between 2000 and 2020 (Fig. 5a) amounted to an average annual cost over the entire period of US\$ 61.14 million and to US\$ 6.71 million

when only observed costs were considered. Because the effects of time lags in cost reporting were not incorporated into the analyses, average cost estimates tended to reach a plateau phase in recent years (Fig. 5). Nonetheless, reported costs have increased in the last two decades by two orders of magnitude.

Costs of other crustaceans

The reported costs of invasive crabs summed up to US\$ 1.25 billion, being based on costs for only five species: the *C. maenas* (US\$ 1.19 billion; n = 22), followed by the *E. sinensis* (US\$ 62.79 million; n = 46), the red king crab *Paralithodes camtschaticus* (Tilesius, 1815) (US\$ 915.67 thousand; n = 1), the blue crab *Callinectes sapidus* Rathbun, 1896 (US\$ 20.75 thousand; n = 1), and lastly the flower crab *Portunus pelagicus* (Linnaeus, 1758) (US\$ < 1 thousand; n = 1) (Supplementary material 3a). The majority of crab invasion costs (94.9%) was inferred in North America, with the majority of those (97.4%) reported in Canada and the remaining costs reported in the USA. Significantly fewer costs (< 1%) were reported in Europe (Germany, Norway, and Spain) and Africa (Tunisia) (Supplementary Material 3b). The costs affected primarily the “Fishery” sector (US\$ 1.16 billion; n = 21), with 3% (US\$ 32.19 million; n = 4) of the costs attributed to “Authorities-Stakeholders” and 5% (US\$ 62.79 million; n = 46) classified as “Mixed” costs. Almost all reported total costs (99.9%) were attributed to damage costs, with very few attributed to management (Fig. 6a). In the past 20 years and since the first recorded crab cost in InvaCost, annual costs remained on average at US\$ 53 million. Between 2000 and 2020, crab invasion costs averaged at US\$ 53.10 million per year.

Overall, six expanded costs were inferred to amphipods, specifically the killer shrimp *D. villosus*, summing up to US\$ 178.8 thousand (n = 6). These costs were classified as “Damages and losses”, impacting “Authorities-Stakeholders” solely in Europe (Italy). Lastly, the two recorded costs inferred to marine lobsters (Nephropidae) summed up to US\$ 44.6 thousand. Similar to amphipod costs, costs inferred by Nephropidae predominantly impacted Authorities-stakeholders in Europe (UK), but were attributed to “Management costs” (Fig. 6b).

Discussion

The present study is the first systematic analysis of global economic costs of invasive crayfish species and other aquatic crustaceans. Analysis of several cost descriptors helped identify key trends and knowledge gaps across spatial, taxonomic and temporal scales. Most reported crayfish costs were obtained from peer-reviewed literature and thus deemed “highly reliable”, however, the vast majority were based on predictions or extrapolations arising from relatively few studies. As a result, there was a substantial difference between realized and predicted/expected costs of ICS. We identified four key costly species, *P. clarkii*, *F. rusticus*, *F. limosus* and *P. leniusculus*, with the latter representing the highest costs, while other damaging ICS were absent from the database. The analysis also includes comparison of ICS costs with other invasive crustaceans, namely crabs, amphipods and lobsters.

Spatial biases and persisting knowledge gaps

Documented costs of ICS were found to be dominated by European countries, with comparatively few costs reported in North America, and Asia (Japan), and no costs reported for all other geographic regions, despite the global extent of crayfish invasions (Lodge et al. 2012; Ribeiro 2020). The absence of reported costs for Africa is noteworthy, as continental Africa and associated island nations are recipients of nine crayfish species (Madzivanzira et al. 2020).

Several prominent ICS have long introduction-histories in Europe (Holdich et al. 2009; Kouba et al. 2014). Dedicated research in recent years has enabled inclusion of several crayfish in the list of invasive species of EU concern, the Union list (European Commission 2016). As such, efforts to estimate and report costs in Europe might reflect a proactive stance on behalf of the European Union (European Commission 2014) in trying to understand the costs of ICS and limit their spread. Reported costs for ICS in Europe indicate that Sweden has been affected significantly. On the other hand, information on costs of ICS from South America, Africa, Oceania and Asia (except a few costs in Japan) were entirely absent, but can be expected in the future given the ongoing spread of ICS and targeted research in these regions (Horwitz and Knott 1995; Nunes et al. 2017; Madzivanzira et al. 2020; Oficialdegui et al. 2020b; Haubrock et al. in review). For instance, considering the growing production trends of *P. clarkii* in China in the last few years (global leading production country of crayfish, exceeding one million tonnes per year recently according to FAO 2020a), it is obvious that such a production cannot be reached without side effects. Indeed, this has become recognised as a national food security issue in the country, given that larger areas of agricultural land are permanently flooded, leaving less space for other crops including rice (Ho 2020), but environmental consequences are also indisputable. The lack of reported costs from diverse regions in InvaCost may be attributed to a number of reasons, which may span from the comparably shorter introduction histories, limited attention to aquatic environments, anecdotal reporting, low research effort on this topic and limited available funding, or limited accessibility to relevant cost information. However, this geographical bias is not unique to costs from invaded aquatic environments or ICS (see Early et al. 2016; Cuthbert et al. in review).

Taxonomic biases

Whilst overall costs of ICS were found to be substantial, the underlying cost quantification presented covers only a small subset of species from a few regions. For instance, *P. leniusculus* accounted for the largest share of the total cost, however, these were inferred only from northern European countries where targeted Plan Actions were developed to prevent reduction of native noble crayfish *Astacus astacus* (Linnaeus, 1758) stocks (Bohman and Edsman 2011). The second most costly crayfish invader in Europe, *P. clarkii*, was reported primarily in southern parts of the continent, where the majority of invaded habitats are found. These burgeoning costs of *P. clarkii* (US\$ 13.01 million) were estimated on the basis of 76 observations. The fact that this species is particularly widespread in Europe (Kouba et al. 2014), and already present in 40 countries of four continents with the potential for further spread (Oficialdegui et al. 2020b), highlights the knowledge gap in costs at a broader spatial but also temporal scale. Other high-profile ICS that are also listed by the EU as prominent invaders (European Commission 2016) but with no invasion costs reported, include *F. virilis* and the parthenogenetic marbled crayfish *P. virginalis* Lyko, 2017.

The latter has a high spread potential (Hossain et al. 2018) and can be expected to cause considerable damage in the near future (Feria and Faulkes 2011). Additionally, cost data for some members of the Parastacidae family are lacking, despite their ubiquitous presence in substantial pathways such as aquaculture and pet trade (e.g. yabby *C. destructor* (Clark, 1936) and redclaw *C. quadricarinatus* (von Martens, 1868); Souty-Grosset et al. 2006; Madzivanzira et al. 2020; Haubrock et al. in review).

Given these knowledge gaps, the presented costs in our study are mostly driven by *P. leniusculus*, inferred from damage-losses and control actions. The vast majority of these costs were the result of extrapolations, possibly indicating a lack of empirical reporting effort and monitoring. This bias is noteworthy and worrisome, as applied management efforts are seemingly not dedicated to several high-risk species, e.g. *P. clarkii* (Gherardi et al. 2011; Souty-Grosset et al. 2016) or other emerging invasive ones (e.g. *C. quadricarinatus* and *P. virginialis*). For instance, dense burrowing has been signalled as especially problematic, affecting irrigation ditches and causing water leakages, but management is only scarcely conducted and is inherently challenging in cryptic aquatic ecosystems (Kouba et al. 2016; Haubrock et al. 2019b). Further, ICS cause significant damages to hydraulic and irrigation systems, but information about the associated costs are largely missing (Tricarico et al. 2018; Madzivanzira et al. 2020). This could suggest a lack of management efforts on widely established ICS, and especially among Southern European countries. Note though that insufficient management could be attributed to the limited capacity to implement widespread management actions when ICS are so diffused (see management section below), and/or possibly a lack of adequate funding for such interventions.

The overall cost (categorized as damage-losses) impacted various sectors such as “Fisheries”, “Environment” and “Public and social welfare”. Only two recorded costs are reported for crayfish plague, specifically in Norway (US\$ 72.8 million: diverse/unspecified; US\$ 2 million). Costs associated with this pathogen are therefore heavily underestimated, as exemplified by numerous rapid population extinctions of native crayfish across Europe (Svoboda et al. 2017). Occurrence of chronically infected European native crayfish populations is a relatively rare and poorly understood phenomenon (Svoboda et al. 2017; Mojžišová et al. 2020; Ungureanu et al. 2020). The pathogen is currently also known from further regions harbouring equally susceptible native crayfish in: South America (Peiró et al. 2016), Indonesia (Putra et al. 2018), and Japan (Martin-Torrijos et al. 2018; Mrugała et al. 2017), posing a threat to their remaining populations. Recent research efforts have focused on, the role of crabs (Schrimpf et al. 2014; Svoboda et al. 2014b; Tilmans et al. 2014) and shrimp (Mrugała et al. 2019; Putra et al. 2018; Svoboda et al. 2014a) as alternative hosts of this pathogen.

Temporal biases

Considering temporal trends, a complete lack of costs reported prior to 2000 indicates a large knowledge gap in how ICS have historically impacted human well-being and ecosystems. This is despite the long history of freshwater crayfish introductions worldwide and more than 150 years of crayfish plague outbreaks in Europe (Holdich et al. 2009; Kouba et al. 2014). In the case of *P. clarkii*, which is a costly and prominent invader especially in Southern Europe, most studies concerning its impact were not published

until the end of 1990s, albeit being introduced in the 1970s (Oficialdegui et al. 2020b). This lag in bringing crayfish invasions to the attention of the scientific community and managers raises questions about ICS awareness, policies, perceptions and funding available for research prior to 2000. Given current invasion rates globally (Seebens et al. 2017) and future projections (Seebens et al. 2020), the high likelihood that known costs are broadly underestimated and poorly monetized along with trends over the past two decades, we expect that future research may shed more light on the true costs of ICS.

Data deficiencies in invaded regions as a whole can have knock-on effects, especially on cost reporting and estimation of potential costs. For example, the Upper Zambezi catchment has been invaded by *C. quadricarinatus* through multiple introductions since 2001 (Madzivanzira et al. 2020). There are known impacts of this invasion upon fisheries conferred through scavenging behaviours (Weyl et al. 2017; Madzivanzira et al. 2020) as well as consumptive effects on juvenile fish affecting recruitment (Madzivanzira et al. in review). The challenge can be attributed to poor or outdated assessments of the impacted fisheries which limits an understanding of their values and therefore the costs triggered by the invasion. This conundrum likely applies to other species and countries, such as *P. clarkii* in Kenya (Lowery and Mendes 1977), *C. quadricarinatus* in Mozambique (Chivambo et al. 2019), and *P. virginalis* in Madagascar (Andriantsoa et al. 2019). Indicatively, the 30% gill net catch reduction attributed to invasive crayfish in Zambian floodplains results in an estimated deficit of US\$ 128.33 per household which needs to be compensated for by increased fishing effort over time (Turpie et al. 1999). This cost, however, can be seen as a lower-bound estimate and highlights the challenges involved in valuing with confidence through time the damages caused by invasions. Even larger challenges apply to quantifying and valuing the loss in ecosystem services and the many forms of damage that occur indirectly (Pejchar and Mooney 2009; Spangenberg and Settele 2010; Schröter et al. 2014; Temel et al. 2018).

Costs of other aquatic crustaceans

Based on the reported costs of ICS, and considering that this taxonomic group remains largely understudied, it is not unreasonable to assume that costs for other related taxonomic groups such as invasive crabs or amphipods are also greatly underestimated. Having identified only five invasive crabs and one invasive amphipod species with reported costs (plus only two entries associated with invasive lobsters) indicates that there likely remain substantial knowledge gaps.

In comparison to other invasive crustaceans, ICS and invasive crabs dominated in terms of reported costs (being several magnitudes higher), although the number of reported costs was also several magnitudes higher in ICS than for invasive crabs. Indeed, costs of crabs were similar in magnitude, amidst originating from merely six unexpanded database entries (in contrast to the 114 unexpanded crayfish entries in InvaCost). This bias is noteworthy, because (a) commercial fisheries in marine environments are typically of much larger scale and commercial value compared to freshwater commercial fisheries and the same applies to commercial fisheries for marine vs. freshwater crustaceans (FAO 2020b) and (b) crab species recorded in InvaCost affect mainly the marine fishery sector. Invasion costs were not reported for many notorious and widespread invasive crabs, such as the *C. maenas*, Asian shore crab *Hemigrapsus*

sanguineus (De Haan 1853) and the Harris mud crab *Rhithropanopeus harrisi* (Gould, 1841), which have marked economic and ecological impacts via predation on shellfish resources, spatially overlapping and causing costs to other commercial fisheries (Grosholz et al. 2000; Lohrer 2001; Zaitsev and Öztürk 2001; Boyle et al. 2010). Also, impacts of invasive crabs in poorly explored aquatic ecosystems such as Arctic marine waters remain challenging due to limited understanding of baseline values and therefore costs of expanding crab invasions (Kourantidou et al. 2015; Kaiser and Kourantidou, in review). The snow crab *Chionoecetes opilio* (O. Fabricius, 1788) in the Barents Sea is one such prominent example which continues to grow at the cost of several benthic species (Kaiser et al. 2018). Commercial interest in harvesting this species may also hinder progress towards understanding their costs (Kourantidou and Kaiser 2019a). The red king crab *Paralithodes camtschaticus* is yet another example of high-impact invasion in Arctic waters which owing to its high commercial value is primarily managed as a commercial fishery rather than an invasion in Norway and exclusively as a commercial fishery in Russia, with ecosystem damages often downplayed (Kourantidou and Kaiser 2019b). Similarly, to other species, the present InvaCost database does not sufficiently cover the multiple costs associated to bycatches in spatially overlapping fisheries, predation and degradation upon native species (Skonhoft and Kourantidou, in review) or costs spent for baseline and restoration research (Kourantidou and Kaiser, in review). InvaCost is a living database that continues to be improved as reported costs become available.

Reposted costs of invasive amphipods were attributed exclusively to *D. villosus*. This notorious Ponto-Caspian invader has been shown to have marked impacts on a diverse range of prey types, including crayfish eggs/juveniles and fish eggs/larvae, with a greater feeding efficiency than native analogues towards vertebrates and invertebrates (Bollache et al. 2008; Taylor and Dunn 2017; Roje et al. 2021). Invasions by *D. villosus* can result in the extirpation of native species from freshwaters (Gergs and Rothhaupt 2015), and once established, populations can dominate native communities in terms of biomass and abundance (Josens et al. 2005; van Riel et al. 2006). Globally, only 27 alien species of gammarids have been reported, and these principally originate from the Ponto-Caspian region (Cuthbert et al. 2020b), with 96% of recognised gammarid invaders, thus lacking costs, as exemplified by the 'demon shrimp' *D. haemobaphes* (Eichwald 1841) having similar ecological effects as *D. villosus* (Constable and Birkby 2016).

Invasion perception and management implications

Despite their significance for socio-economic well-being and their susceptibility to change, aquatic invasions have overall received less attention (Maclsaac et al. 2011; Lynch et al. 2020; Cuthbert et al. in review). Often, both invaders and their impacts are challenging to monitor, which can lead to a series of knock-on effect time delays between impact reporting and management interventions (Beric and Maclsaac 2015), thus reducing the efficacy of preventative biosecurity measures (Coughlan et al. 2020), and hampering the understanding of their costs (Hanley and Roberts 2019). Crustaceans, however, have received comparatively substantial public attention, perhaps because of their prominent role in aquatic ecosystems or their popularity as food items (Kawai et al. 2015). The introduction of alien crustaceans,

however, has not only induced a considerable native to alien species turnover (Kouba et al. 2014), but has also led to the loss of cultural heritages and traditions (Edsman 2004; Swahn 2004; Kataria 2007).

Public perceptions are of special consideration in the context of management responses (Höbart et al. 2020) and directly affect reporting of costs from invasions. Similar to other invasions, aquatic invasions may bring benefits (King et al. 2006; Christie et al. 2019), despite their harmful properties. Commercial and recreational fisheries for introduced crustaceans also contribute to a higher perceived value of these invasive species (Kourantidou and Kaiser 2019a). In low-income areas, they are often valued as a cheap source of protein or may contribute to regional economies (Andriantsoa et al. 2020; Haubrock et al. in review), resulting in limited recognition of costs (especially indirect ones) and possibly limited interest to understand impacts and identify related costs (Kourantidou and Kaiser 2019b). In Sweden, for example, the native crayfish *A. astacus* was largely extirpated by competition with the invasive *P. leniusculus* and transmission of the crayfish plague pathogen (Bohman and Edsman 2011), which itself has caused considerable monetary impact. As a result, the original source of income was largely replaced by *P. leniusculus* having a lower market price. The Swedish example, however, highlights how the almost complete loss of a native species (i.e. a considerable environmental and cultural damage-loss), along with costly spread control, created additional management costs. Similar substitutions towards the consumption of the introduced *P. virginialis* were also reported in Madagascar (Andriantsoa et al. 2019; 2020). Stakeholder interests at odds for certain species with perceived benefits may trigger conflicts in resource management (Zengeya et al. 2017; Oficialdegui et al. 2020a; Kourantidou and Kaiser 2019a; 2019b).

Reporting of invasion costs (foremost management and research related) relies on managers and stakeholders to have reached the end of a pathway which eventually leads to management interventions (Latombe et al. 2017). Pathways which lead up to applied management can vary but ultimately, they involve a risk assessment (e.g. Hawkins et al. 2015; Bacher et al. 2018), a classification of invasion status (e.g. Blackburn et al. 2011) and a choice of appropriate management intervention (see Robertson et al. 2020). However, formal risk assessments, specifically for crayfish species, are lacking (but see Roy et al. 2019; Yonvitner et al. 2020; Haubrock et al. in review). This could be due to either a data deficiency in evidence for crayfish impact assessments (such as in South Africa; Weyl et al. 2020) and/or due to the intensive nature of compiling contextually relevant impact assessments. Nevertheless, recent national horizon scanning exercises have ranked invasive crayfishes, crabs and amphipods as among the top ten risky species across all habitat types (Lucy et al. 2020).

Management intervention or cost reporting may be hindered in some cases due to public perceptions, stakeholder interests at odds and backlash, or lack of perceived necessity for management. Further, it is generally well-established in the literature that investment into control and management can lower damage-losses (Leung et al. 2002). In this study, total damages and resource losses were found to be an order of magnitude higher than control or management costs, suggesting the need for more proactive rather than reactive responses. However, management costs were dominant when considering empirically observed costs alone for ICS. Nonetheless, management attempts have largely failed at developing tools

to hinder the spread or successfully eradicate widely established populations of invasive aquatic crustaceans (Gherardi et al. 2011; Stebbing et al. 2014; Haubrock et al. 2018). Indeed, feasible eradications are only possible under a narrow range of specific conditions (rather small, isolated localities) and with the use of drastic measures like long-term dewatering or application of non-selective biocides which may negatively affect the entire aquatic biota (Lidova et al. 2019; Manfrin et al. 2019; Peay et al. 2019; Chadwick et al. 2020). Therefore, effective management interventions may be impractical in many e.g. African or Asian systems because of their broad geographical expanse, besides their high costs. This is further underlined by the high cost and scale-specific methods used to control aquatic IAS in the USA or Europe (i.e. the use of rotenone, dewatering and draw-down methods). Furthermore, some management or control interventions may have unexpected adverse outcomes (Závorka et al. 2020; Loureiro et al. 2018). Developing effective means of introduction and spread prevention is therefore of key importance as crustacean invaders can lead to long-term persisting and growing invasion costs (Krieg and Zenker 2020).

Conclusion

In this study, we highlight that there is an exponentially increasing trend in reported costs of ICS since recording started in 2000. However, the currently available information is generally highly fragmented both spatially and taxonomically. Our analysis sheds light on several limitations and knowledge gaps in economic impacts of crayfish and other crustacean invasions. A better understanding of impacts, past and ongoing costs of ICS is therefore urgently needed to allow national and regional authorities to invest in appropriate policies and measures that can help mitigate those in the future. Considering the lack of reported costs across many invaded regions, despite well-known impacts of some ICS, the estimates provided in this study are probably very conservative. Nonetheless, despite being a rather small group taxonomically with only a few species having triggered invasions, the economic losses at a global level are substantial. Likewise, only five crab species represent significant invasion costs while amphipods are almost overlooked in this regard, indicating the dire need of investigating the true costs of invasive crustaceans. The costs identified along with the knowledge gaps highlighted in this study call for more effort to understand the impacts of invasive aquatic crustaceans on primary sectors as well as social and human wellbeing. A more thorough understanding of the positive values associated with crustacean invasions can help advance management and identify suitable compromises in those cases where stakeholder interests are conflicting.

Eulogy

This article is dedicated to Professor Olaf LF Weyl who passed away suddenly on November 14th, 2020. Prof. Olaf Weyl was a hugely influential scientist, mentor and dear friend, who described our African crayfish work as his 'pet project'. His giant presence, in every way, is sorely missed.

Declarations

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Data availability statement

All the data used in this study was made available as supplementary material.

Conflicts of interest/Competing interests

No conflict of interest has to be declared.

Availability of data and material

The underlying data was provided as supplementary material.

Code availability

The R-code required has been referenced in the related sections within the methods.

Authors' contributions

AK, FJO, PJH, RNC and MK led the writing. PJH analysed data. JS, ET, BL, RG provided valuable insights and further literature. FC created the database. All authors contributed to all aspects of the manuscript production.

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Figures

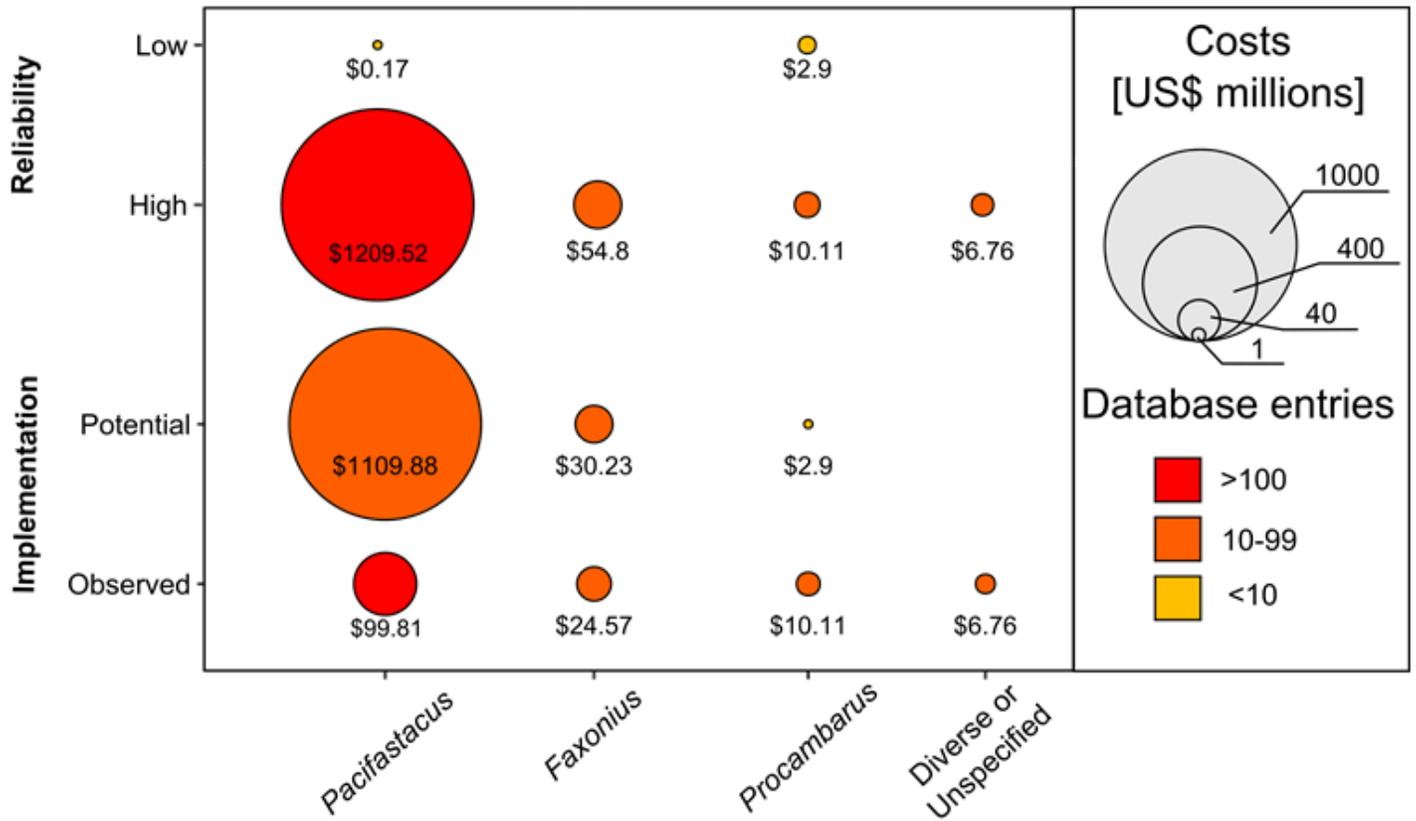


Figure 1

Global costs in US\$ millions (2017 value) of recorded invasive crayfish genera according to method reliability ('Low' vs. 'High') and implementation of cost ('Potential' vs. 'Observed'). Circle sizes depict the total amount of costs in US\$, whereas colouration indicates numbers of entries.

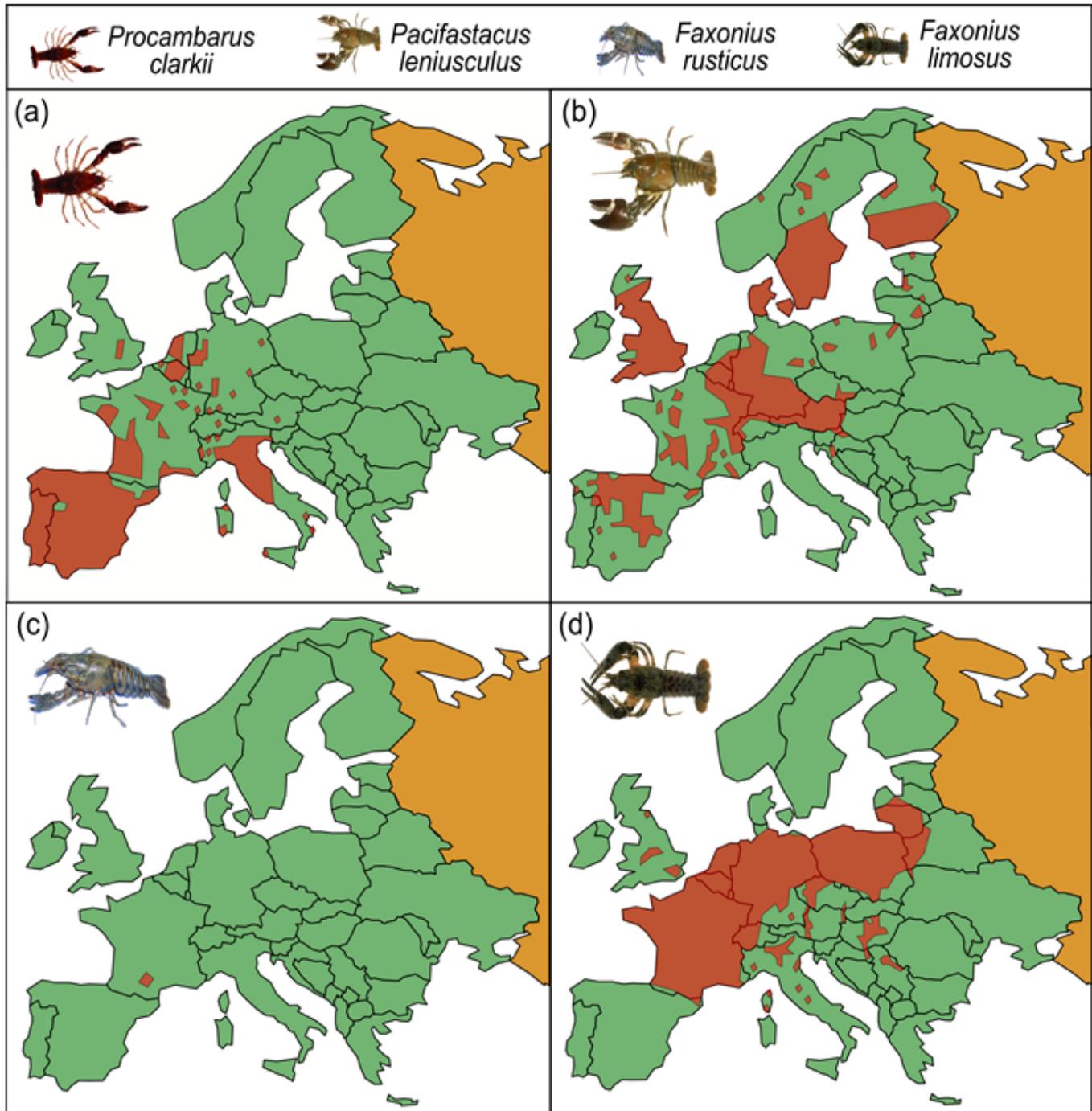


Figure 2

Indicative European distribution (red) of *Procambarus clarkii* (a), *Pacifastacus leniusculus* (b), *Faxonius rusticus* (c), and *Faxonius limosus* (d) (Kouba et al. 2014; Collas and Andrieu 2019). Note that reported costs of rusty crayfish are exclusively from North America. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

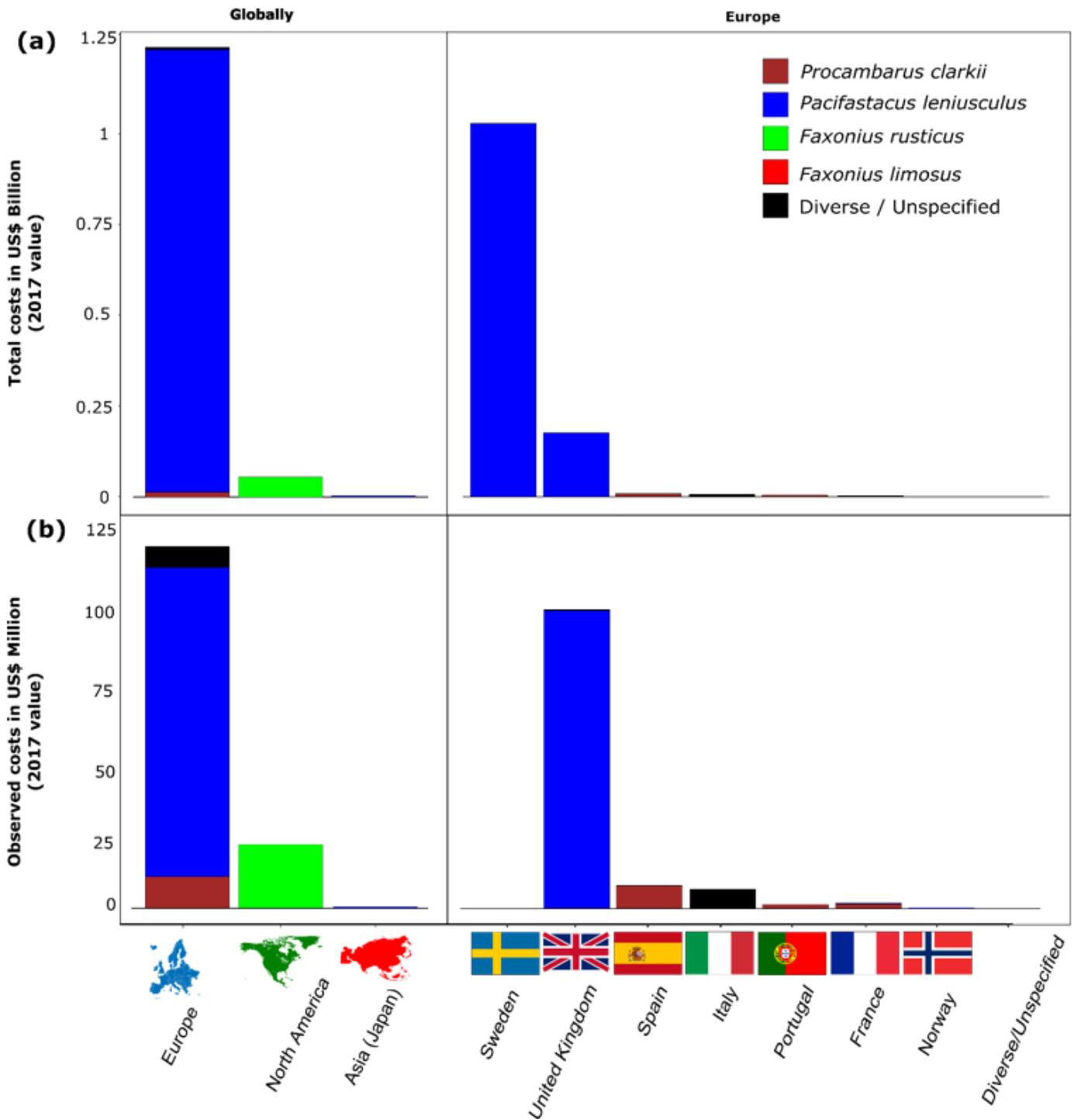


Figure 3

Distribution of total (a) and observed (b) invasive crayfish costs across continents and European countries. Note that subplot (a) is scaled in billions and (b) in millions. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

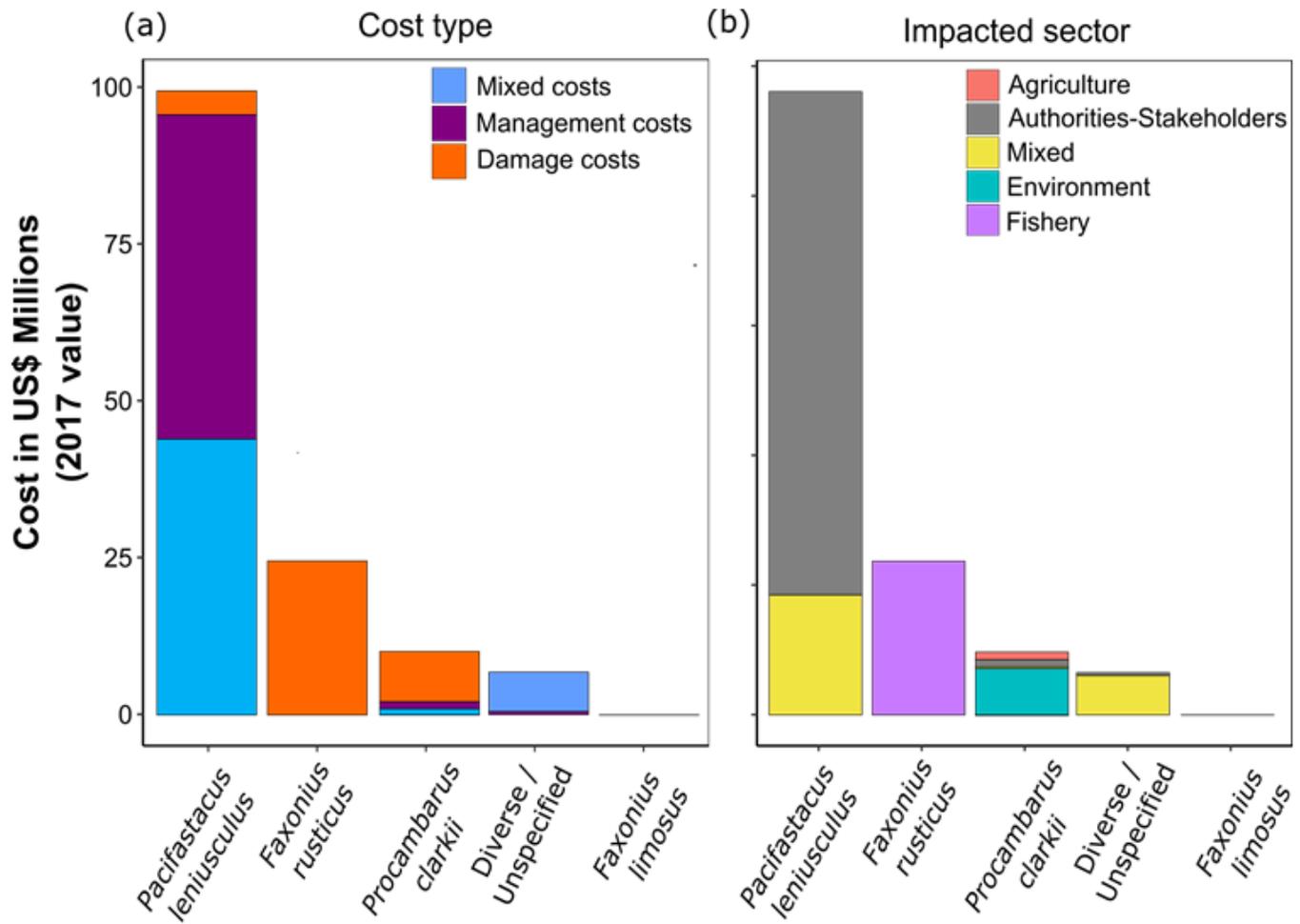


Figure 4

Observed economic cost estimates for invasive crayfish species according to cost type (a) and impacted sector (b).

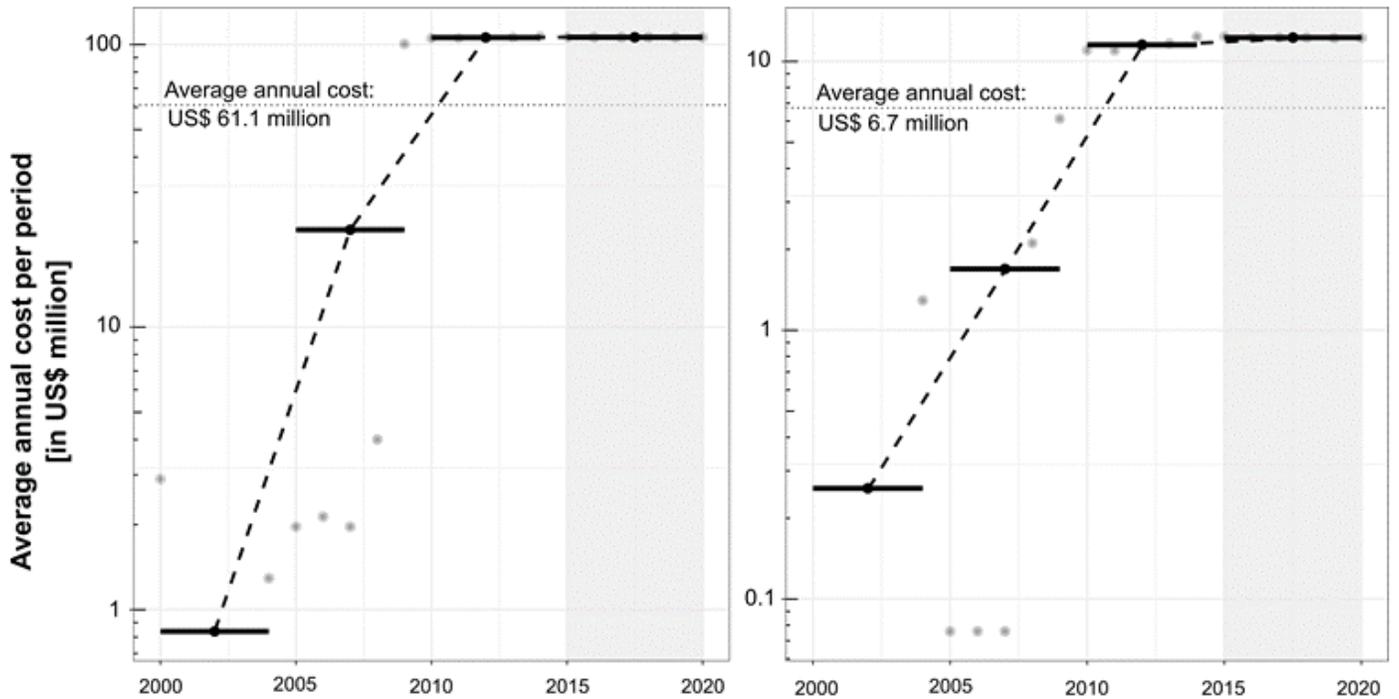


Figure 5

Temporal development of reported cumulative costs (total on the left vs. observed on the right) between 2000 – 2020 of invasive crayfish. Points represent decadal means. Note that the last 5 years indicated in grey are subject to incompleteness in cost reporting and that the y-axes are shown on log10 scales that differ between subplots.

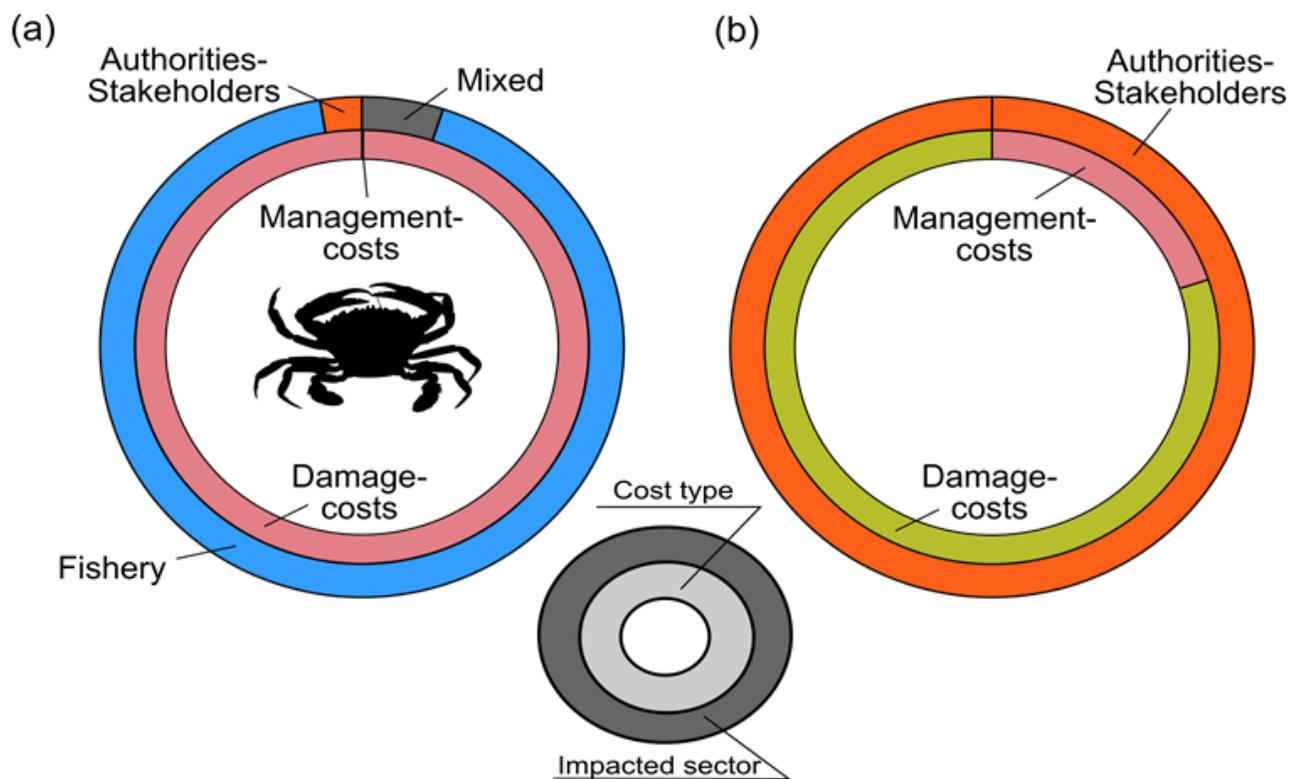


Figure 6

Share of (a) total crab costs vs. (b) total costs of amphipods and lobsters among sectors and cost types.

Supplementary Files

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