



Knowledge needs in economic costs of invasive species facilitated by canalisation

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Academiceditor:S.McDermott|Received18September2022|Accepted28November2022|Published19December2022

Citation: Balzani P, Cuthbert RN, Briski E, Galil B, Castellanos-Galindo GA, Kouba A, Kourantidou M, Leung B, Soto I, Haubrock PJ (2022) Knowledge needs in economic costs of invasive species facilitated by canalisation. NeoBiota 78: 207–223. https://doi.org/10.3897/neobiota.78.95050

Abstract

Canals provide wide-ranging economic benefits, while also serving as corridors for the introduction and spread of aquatic alien species, potentially leading to negative ecological and economic impacts. However, to date, no comprehensive quantifications of the reported economic costs of these species have been done. Here, we used the InvaCost database on the monetary impact of invasive alien species to identify the costs of those facilitated by three major canal systems: the European Inland Canals, Suez Canal, and Panama Canal. While we identified a staggering number of species having spread via these systems, monetary costs have been reported only for a few. A total of \$33.6 million in costs have been reported from species linked to European Inland Canals (the fishhook waterflea *Cercopagis pengoi* and the zebra mussel *Dreissena polymorpha*) and \$8.6 million linked to the Suez Canal (the silver-cheeked toadfish *Lagocephalus sceleratus*, the lionfish *Pterois miles*, and the nomad jellyfish *Rhopilema nomadica*), but no recorded costs were found for species facilitated by the Panama Canal. We thus identified a pervasive lack of information on the monetary costs of invasions facilitated by canals and highlighted the uneven distribution of costs.

Keywords

aquatic environment, habitat connectivity, inequality, InvaCost, invasive alien species, monetary costs

Introduction

Aquatic invasive alien species (IAS) are a major threat to biodiversity and ecosystem functioning (Ricciardi and Rasmussen 1999; Molnar et al. 2008; Strayer 2010), as well as human health (Galil 2018; Souty-Grosset et al. 2018). New alien species continue to be introduced at increasing rates (Seebens et al. 2017), and the share that becomes invasive brings considerable and increasing economic costs (Diagne et al. 2021a). Recently, an open database which compiled the economic costs of biological invasions (Diagne et al. 2020) has allowed quantification across a variety of geographical regions (e.g. Haubrock et al. 2022a), ecosystems (e.g. Cuthbert et al. 2021) taxa (e.g. Angulo et al. 2022) and languages (Angulo et al. 2021).

Aquatic IAS spread through multiple vectors and pathways, intentionally or unintentionally, through either active or passive transport. For example, they can escape from confinement (Lockwood et al. 2013), be unintentionally translocated as contaminants or parasites of a certain goods item (e.g. food, plants, timber; Lockwood et al. 2013), through hull fouling (Sylvester and MacIsaac 2010; Sylvester et al. 2011) or ballast waters of ships (Briski et al. 2012, 2013). Also, breaching biogeographical barriers allows new or additional species invasions (Gollasch et al. 2006; Kourantidou et al. 2015; Kaiser and Kourantidou 2021) or the further spread of IAS to secondary invaded areas from primary 'stepping stones' (Bertelsmeier and Keller 2018). For example, roads and railways represent important corridors for IAS (Hulme 2009), also increasing their propagule pressure (Woodford et al. 2013).

One of the most important pathways that allow the spread of IAS are canals connecting geographically-isolated aquatic systems (e.g. Asth et al. 2021), such as the trans-isthmian Suez and Panama Canals, and the cross continental North Sea-to-Black Sea Rhine-Main-Danube Canal. These highly trafficked strategic canals connect transport networks of critical economic and socio-political value, mainstays of global trade and globalisation (Amato 2020). They considerably reduce travel time and distance (therefore also CO₂ emissions), as well as operating costs to shippers and consumers, thus increasing commerce and economic growth (e.g. Lloyd 2018; Park et al. 2020; Cordoba 2022). Nonetheless, these economic benefits are counterbalanced by facilitated introduction and spread of IAS in goods, vessels, and in water due to increased connectivity. If established, IAS can have detrimental ecological consequences, as well as negative economic impacts (Bij de Vaate et al. 2002; Leuven et al. 2009; Galil et al. 2017; Turbelin et al. 2021).

This paper aims to quantify the known economic costs associated with IAS considered to have been facilitated by canals, enabling active (i.e. self-moving species) or passive (i.e. hitchhiker species) spread of these species. For this study, we focused on three major canal systems: Suez, Panama, and European Inland Canals (Fig. 1), as

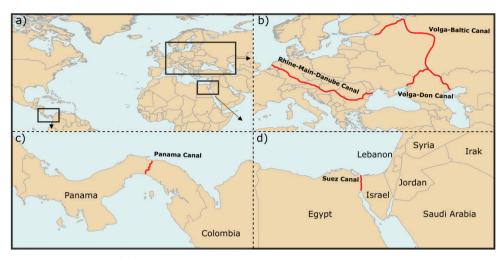


Figure 1. Locations of the main canal systems studied (**a**) the European Inland Canals (**b**), the Panama Canal (**c**), and the Suez Canal (**d**). Red lines represent single canals. As for the European Inland Canals, only the three major canals (the Rhine-Main-Danube Canal, the Volga-Don Canal, and the Volga-Baltic Canal) are represented, for simplicity.

these represent major circumventions of important biogeographical barriers, and for which greater information is available. In particular, we hypothesised that (i) the Suez Canal majorly contributed to IAS economic costs, that (ii) these costs are not evenly distributed among countries of the same canal system, and that (iii) these costs are attributed to different taxa in different canal systems.

Materials and methods

Study systems choice

Canals directly connect distinct biogeographic provinces (as in the case with the Suez and Panama Canals) or contiguous seas in the case of the Kiel and the Corinth Canals, whose biota may intermingle freely. While the latter two can be considered of regional importance (in Germany and Greece, respectively), the former two are globally important. Indeed, the Suez Canal connects the Red Sea with the Mediterranean Sea, while the Panama Canal connects the Atlantic Ocean (Caribbean Sea) with the (eastern) Pacific Ocean, allowing ships to avoid circumnavigating Africa and South America, respectively, and reducing travel by thousands of nautical miles. The Suez Canal, a marine sea-level canal, was officially opened as early as 1869 and was recently doubled by creating a new lane (the 'New Suez Canal', functionally opened in 2016; Bereza et al. 2020), but also by widening and deepening the old canal, to increase its traffic capacity. Following the obstruction of the Suez Canal due to the grounding of a container ship

in March 2021 (Ruiz et al. 2022), the Suez Canal Authority accelerated \$10 billion project plans to further extend and enlarge the canal (https://www.maritime-executive. com/article/suez-canal-sets-new-record-for-traffic-volume; https://www.reuters.com/ business/suez-canal-expansion-due-finish-july-2023-sca-chairman-2022-01-16/). The Panama Canal, a freshwater canal -30 m above sea level, was opened in 1914 and due to the increase in traffic, just like with the Suez Canal, it was recently (2016) expanded and a new set of larger locks was installed, doubling its capacity (Wang 2017). In Europe, the situation is more complicated, with canals connecting multiple water bodies, thus forming a dendritic inland network system of connected major European rivers that ultimately link northern and southern European seas. The major and longest canal-river connections are the Rhine-Main-Danube, Volga-Don and Volga-Baltic Canals, which together with other minor systems form the European Inland Canals connecting the North and Baltic Seas with the Black, Azov and Caspian Seas, crossing all over Europe (Jażdżewski 1980; Bij de Vaate et al. 2002). Among these, the Rhine-Main-Danube Canal, completed in 1992, is the southernmost and longest one and has a particularly high economic importance (Bij de Vaate et al. 2002; Leuven et al. 2009).

Cost data sourcing and filtering

For each canal (Suez, Panama, and European Inland Canals), a detailed list of established IAS reported in the literature to have spread through these pathways, either actively or passively, was compiled by reviewing published papers and datasets (Suppl. material 1: table S1). To analyse the costs of these species, we used data from the InvaCost database, which includes costs from sources written primarily in English (Diagne et al. 2020), but also sources from 21 additional languages (Angulo et al. 2021). InvaCost compiles cost data resulting from systematic searches on the Web of Science, Google Scholar and Google search engine, and opportunistic contacts with experts and stakeholders. Each recorded cost entry was characterised by various descriptors as explained in more detail in Diagne et al. (2020) and in the online database repository (https://doi.org/10.6084/m9.figshare.12668570). InvaCost is a dynamic database that allows new cost entries to be corrected and added as they develop or are reported over time.

The most recent version of InvaCost (4.1 as of January 2022) includes 13,553 cost entries (i.e. rows of data entries with monetary costs) of IAS extracted from published peer-reviewed and grey literature. Although there may be costs that have not been captured (e.g. unpublished or outside the search languages), InvaCost offers the most up-to-date compilation of invasion costs and, therefore, constitutes the best tool available to draw parallels with the current state-of-the-art in cost reporting and associated knowledge gaps. However, considering the dynamic nature of the database, the results are subject to changes in the future as new monetary cost data become available for different species, countries, sectors of the economy, and other factors or as the existing cost data are further refined for accuracy. All costs published in the literature and included in the database were converted to 2017 US\$ values (see Diagne et al. 2020).

For this analysis, we filtered cost entries in the InvaCost database by selecting those IAS that were reported to have been facilitated in their invasion as a result of the construction of selected canals (Suez, Panama, and European Inland Canals). Further, we filtered these IAS' costs by the countries involved in these three canal systems. Since costs of aquatic IAS are often under-reported (Cuthbert et al. 2021; Haubrock et al. 2022b), we included not only the countries crossed by the canals, but also those adjacent and those alongside the same water body of the two ends of the canals (i.e. all the countries bordering the North, Baltic, Black, and Mediterranean Seas; Suppl. material 1: table S2), as they could be affected by the further natural spread of the IAS (e.g. Galil et al. 2017).

Global cost descriptions

To describe the costs of IAS facilitated by the canals over time, we used the expandYearlyCosts function of the 'invacost' package (v0.3-4; Leroy et al. 2020) in R version 4.1.1 (R Core Team 2020). This function facilitates consideration of the temporal dimensions of the data, with the estimated costs per year being expanded in line with the length of time over which costs were reported or expected to have occurred as indicated by each respective publication included in the InvaCost database (Diagne et al. 2020) (i.e. the length of time between the Probable_starting_year_adjusted and Probable ending year adjusted columns). For example, the starting and ending years of a cost could reflect the period of which a control measure was implemented against an invasive population, or a period of reported resource damages to a fishery, as per the information in the cost source document (Diagne et al. 2020). To obtain a comparable cumulative total cost for each estimate over the period during which costs were incurred for each invasion, we multiplied each annual estimate by the respective duration (in years). Therefore, the analyses were conducted based on these 'expanded' entries to reflect the likely duration of the costs as reported in each study analysed. This means that costs covering several years (e.g. \$10 million between 2001 and 2010) are divided according to their duration (i.e. \$1 million for each year between 2001 and 2010). Finally, the cumulative costs of the invasion were estimated based on their classification across the following cost descriptors (i.e. columns) included in the database:

i. Method_reliability: indicating the perceived reliability of cost estimates based on the publication type and estimation method. Costs are considered to be of low reliability in those cases where they were derived from grey literature and/or are lacking documented, repeatable or traceable methods. On the other hand, costs are considered of high reliability if they come from peer-reviewed articles, official documents, or grey literature but with a fully documented, repeatable and traceable method (Diagne et al. 2020). While we acknowledge that this binary classification does not capture the widely varying methodologies of underlying studies, it provides a practical, reproducible and objective means of cost assessment and filtering;

- ii. Implementation: whether the cost estimate was incurred in the invaded area (observed; e.g. a cost directly incurred from investment in managing an invasive species, or an invasion-driven decline in a native fishery that resulted in a realised loss of income) or whether it was extrapolated or predicted over time within or beyond the actual distribution area of the IAS (potential), and thus not empirically incurred (Diagne et al. 2020). We emphasise that costs were compiled in InvaCost based on the information in each cost document (i.e. we did not extrapolate or predict cost estimates independently here, and simply compiled reported costs). For example, potential costs may include estimated reductions in fisheries income because of an invasion (Scheibel et al. 2016), known local costs that are extrapolated to a larger system than the one in which they occur (Oreska and Aldridge 2011), and costs extrapolated over several years based on estimates from a shorter period (Leigh 1998);
- iii. Type_of_cost_merged: grouping of costs into categories: (i) damage referring to damages or loss incurred by the invasion (i.e. costs of repairing damage, losses of resources, medical care), (ii) management including expenditure related to control (i.e. surveillance, prevention, management, eradication), (iii) and mixed including mixed cost of damage and control (cases where the reported costs were not clearly distinguishable);
- iv. Impacted_sector: the activity, societal or market sector that was affected by the cost. Seven sectors are described in the database: agriculture, authorities-stakeholders (official structures allocating efforts to manage biological invasions), environment, fishery, forestry, health, public and social welfare, and diverse (Diagne et al. 2020).

To analyse the costs of invasive alien species that were facilitated by canals (European Inland Canals, Suez Canal, and Panama Canal), we extracted species lists from several publications (see Suppl. material 1: table S1) and selected neighbouring countries for which invasions are likely to be facilitated by canals (Suppl. material 1: table S2). We then searched the InvaCost database (4.1) for these species in the respective countries and analysed the obtained data following the protocol and criteria described (Diagne et al. 2020; Leroy et al. 2020; Angulo et al. 2021).

Results

A total of 34 established species for the European Inland Canals, 411 for the Suez Canal, and 98 for the Panama Canal were listed to have been facilitated in their introduction and spread by these canals. In the InvaCost database, we identified in total 19 database entries: 8 for European Inland Canals and 11 for Suez. By way of contrast, no recorded costs were available for Panama. After expansion, these entries resulted in 34 annualised cost entries, encompassing 5 species (the fishhook waterflea *Cercopagis pengoi* and the zebra mussel *Dreissena polymorpha* for the European Inland Canals and the silver-cheeked toadfish *Lagocephalus sceleratus*, the lionfish *Pterois miles*, and the nomad jellyfish *Rhopilema nomadica* for the Suez Canal) for a total of \$42.2 million

(\$33.6 for European Inland Canals and \$8.6 for Suez). The most surprising result is that costs were recorded for only a few species facilitated by the three canals (9% for European Inland Canals, 0.5% for the Suez Canal, and none for the Panama Canal), and this seems not to depend upon the choice of the countries that could be affected by canal-facilitated invaders, but by the general lack of costs reported for those species. Indeed, only a few cost records associated with the listed species were present in the entire InvaCost database (12% for European Inland Canals, 5% for Panama, and 1% for Suez), even for distant countries.

Fig. 2 summarises the recorded costs for European Inland Canals and Suez Canal. There was a clear difference between the two sites in the taxa associated with the costs. In European Inland Canals, all costs were attributed to invertebrates, specifically almost all to molluscs (*Dreissena polymorpha*, \$33.3 million) and just \$0.3 million to crustaceans (*Cercopagis pengoi*). In the case of the Suez Canal, most costs were attributed to vertebrates (*Lagocephalus sceleratus* and *Pterois miles*, \$8.6 million) with two very high-cost entries recorded and the remainder belonging to Cnidaria (*Rhopilema nomadica*, about \$59,000).

Our analysis also revealed an uneven distribution of the recorded costs. Out of the total 26 countries investigated for the European Inland Canals, only the United Kingdom (\$33.3 million), Finland (about \$146,000), Russia (about \$74,000), and Denmark (about \$58,000) reported costs associated with canal-facilitated invasive species. Similarly, only Turkey (\$5.5 million), Cyprus (\$3.1 millions), and Israel (about \$59,000) reported economic costs associated with the Suez Canal, out of the total 23 countries considered. Despite the low number of recorded costs, most of them were attributed to the high reliability category (\$31.5 million for the European Inland Canals and \$8.2 million for the Suez Canal) rather than the low reliability one (\$2.1 million for the European Inland Canals and about \$459,000 for the Suez Canal).

The total costs were differently attributed to observed and potential costs in the two canal systems. In European Inland Canals, about \$16.4 million of observed costs were recorded against about \$17.2 million of potential costs (though this latter result is mostly due to a single very high potential cost recorded). In contrast, in the Suez Canal, costs were mostly associated with observed entries (\$8.2 million, with two very high costs recorded) rather than potential costs (\$0.4 million). As for the type of costs, the recorded costs for the European Inland Canals were mostly attributed to management (\$31.4 million), followed by damage (\$2.1 million), and mixed (about \$55,000). The recorded costs for the Suez Canal, instead, were mainly associated with damage (\$5.5 million) and management (\$3.1 million). The invasive species associated with the European Inland Canals were recorded to impact multiple sectors: authorities-stakeholders (\$24.4 million), environment (\$1.9 million), and fishery (about \$220,000). Moreover, additional costs were recorded for other sectors (diverse: \$6.9 million). Similarly, the invasive species facilitated by the Suez Canal had recorded impacts on authorities-stakeholders (about \$0.5 million), fishery (\$6.2 million, with two very high reported costs), and public and social welfare (\$1.9 million).

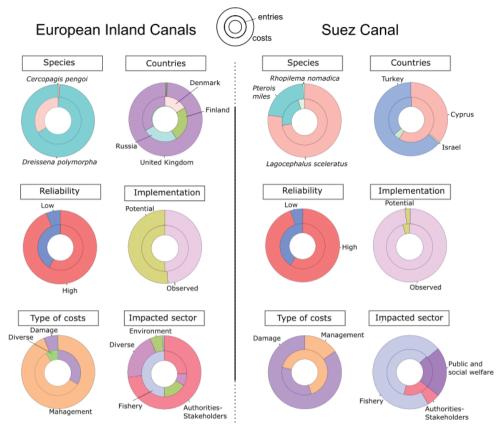


Figure 2. Proportions of monetary costs (outer circle) and cost entries (inner circle) between canals analysed (i.e. European Inland Canals and Suez Canal), according to the cost descriptors studied: species, affected countries, method reliability, implementation, type of costs and impacted sectors.

Discussion

Canals are important corridors for many aquatic IAS, as revealed by the long list of established species that we obtained. The connection of multiple water bodies with distinct ecological communities is well-known to have promoted the spread of numerous invaders (Galil et al. 2008; Leuven et al. 2009; Hulme et al. 2017). These numbers are expected to increase with time, especially after the enlargement of the Suez and the Panama Canals (Galil et al. 2015; Muirhead et al. 2015; Castellanos-Galindo et al. 2020). However, when searching in the InvaCost database for the costs associated with these species, very few entries for very few species (five) were found, even if we opted for an "extensive approach" by including all the countries potentially affected by canal-passing invaders, i.e. not bordering the receiving system directly. This might be unsurprising, as impacts of those species are not well known (hidden below water) or documented in monetary terms, e.g. for the killer shrimp *Dikerogammarus villosus*,

which is widely distributed in Europe (Soto et al. 2022) but only had reported costs from Italy (Tricarico et al. 2010). Also, many of these species could take decades to cause tangible impacts from the moment of their establishment. Moreover, cost data deficiency is common, especially for marine species across many taxa (e.g. Haubrock et al. 2022b; Kouba et al. 2022), countries (e.g. Haubrock et al. 2021a; Renault et al. 2021), and entire regions (e.g. Kourantidou et al. 2021). However, it is very important to stress that this massive lack of data does not mean that there are only a few costs caused by IAS facilitated by the opening of canals, but only that just a few have been recorded or estimated so far. A lack of costs also does not reflect large ecological impacts incurred in these invaded systems, given the challenges for monetisation of environmental effects.

By contrast, the economic benefits arising from commerce through canals such as those examined here can be easily materialised (e.g. Kaluza et al. 2010; Kenawy 2016; Chirosca and Rusu 2021), so that the general perception may be that the benefits far outweigh the drawbacks (Bereza et al. 2020; Cordoba 2022). Indeed, the value from canals includes numerous components that go beyond just income and employment opportunities created locally, but also encompass economic benefits for exporters and consumers of goods at various stages (i.e. from raw materials to consumer goods). Also, some IAS that spread through canals are perceived to have localised benefits, for example for local fisheries (Castellanos-Galindo et al. 2019; van Rijn et al. 2020), without knowledge of their impact. Nevertheless, the results of our analysis show that the data available is insufficient for a trade-off analysis and does not by any means suggest that the benefits of trade facilitated by the canals outweigh the costs of invasions. Since cost-benefit analyses of biological invasions remain difficult, and since beneficiaries are often far removed geographically from the site of environmental damage, this could potentially lead to disparities and social injustices between those parties (countries, stakeholders, economic sectors, and other individuals such as consumers or members of local communities) that benefit from commerce and those that incur the costs of the associated IAS. In turn, this highlights the concepts of environmental accountability, telecoupling and liability from the involved parties at a transnational or even global level (Shafer 2006; Kramarz and Park 2017; Hull and Liu 2018).

Environmental barriers within the respective canal can nevertheless limit the spread of IAS. For example, the Panama Canal is a freshwater canal (mainly composed of Lake Gatun) that marine species need to cross to invade either side. The similar salinity barrier also applies to the Rhine-Main-Danube Canal and the other European Inland Canals, as freshwater conditions in them should prevent the spread of saline species from the Ponto-Caspian region to the North European seas, and the other way around. However, this barrier can halt only stenohaline species actively spreading or fouling the ship hulls, while not impeding biological invasions through ballast waters and sediments (Sylvester and MacIsaac 2010; Briski et al. 2011, 2013). On the other hand, euryoecious species can overcome these barriers. Ponto-Caspian euryhaline taxa have done particularly well in the eastern Baltic Sea because it has low salinity, and many of them have been established in freshwater systems en route from the Ponto-Caspian

region to the North and Baltic Seas (Bij de Vaate et al. 2002). In the case of the Suez Canal, the dissolution of the saltbed of the formerly hypersaline 'Bitter Lakes', which served as an effective barrier up to the 1960s, and the accelerated seawater warming in the Mediterranean, boosted by ever more frequent and severe marine heat waves, have likely enhanced the rate of successful invasions (Biton 2020; Galil et al. 2022). While the overwhelming majority of species traversed the Suez Canal northwards (the so-called Lessepsian migrations), a few species, for which monetary impacts are yet unknown, have been considered to traverse it southwards (anti-Lessepsian migrations; Bos et al. 2020; Azzurro et al. 2022). Considering the economic and socio-political importance of canals, and that the commerce through them cannot be easily impeded, we suggest that prevention and mitigation measures should be undertaken or reinforced by the canal authorities, to reduce the ecological and economic impact of IAS.

Some limitations of this study originate from the species and the countries considered. Indeed, in most cases, it can only be presumed that an invader was facilitated by a canal during its spread, especially for species established for a long time, which could have been introduced or spread through other pathways. Other, not easily disentangled, intricacies can also occur. For example, Ponto-Caspian species were sometimes intentionally introduced after canalisation in Europe to stabilise or enrich these new habitats (Arbačiauskas et al. 2010). Also, some IAS further spread from these hubs as secondary, 'stepping stone' invaders (e.g. Gammarus tigrinus, introduced from North America; Rewicz et al. 2019). Moreover, many stowaway species (like those transported via ballast water, or fouling species) have by now become cosmopolitan, being widely and repeatedly translocated. This makes it difficult to attribute them to specific geographic locations, and therefore to follow their spread and their associated costs (e.g. Amphibalanus amphitrite; Wrange et al. 2016). Ultimately, we note that species spreading in the opposite direction, i.e. towards the Ponto-Caspian region or the Red Sea, had no recorded economic costs, likely because movements of alien species from these systems are predominantly unidirectional (e.g. Galil et al. 2015; Cuthbert et al. 2020). However, documented cost flows may also reflect the availability of data, which may be limited due to sources in certain languages not included in InvaCost, inaccessible or very recent literature, or not having been captured in the search terms underlying the database (Diagne et al. 2020; Angulo et al. 2021). As for the countries considered, it should be acknowledged that even those not directly involved through canals can be affected by their facilitation.

Conclusions

Although we tried to be as inclusive as possible, our results underline the paucity of available data. As such, our estimations should be taken with caution, as complex trading relationships and interconnected introduction pathways meant that not all countries invaded as a consequence of canals could be accounted for, i.e. those not immediately bordering the regions linked by canals and those affected by secondary spread (see

fig. 6 in Galil et al. 2021). As the canals considered here are utilised by ships from all over the world, even a very distant country can be affected by hitchhiking species. More focused research is required to elucidate source-sink dynamics for biological invasions and the large-scale effects of pathways and vectors, as well as to quantify the importance of 'stepping stones' for invasion events. In an era of economic uncertainty (Baker et al. 2020), severe economic disparities between those benefiting and those negatively affected will have staggering consequences. Highlighting the magnitude of economic costs and sectors affected due to biological invasions (Cuthbert et al. 2021; Diagne et al. 2021b; Haubrock et al. 2021b) evidences the potential threat to economies and human wellbeing. Here, our results highlight the potential for canals to cause substantial economic costs, in addition to their intended economic benefits, as a result of biological invasions - even for the few species with reported impacts - for which knowledge gaps should be further addressed in future. Thus, we are calling for an increasing effort in (i) identifying the ecological impacts and associated costs of biological invasions in canals and the affected parties, as well as (ii) limiting their staggering increase given the predicted intensification in the use of these infrastructures in the future.

References

- Amato V (2020) The New Routes of Globalization. Containerization, Naval Gigantism and Role of the Suez and Panama Canals. Politics and Knowledge: New Trends in Social Research, 9–19.
- Angulo E, Diagne C, Ballesteros-Mejia L, Adamjy T, Ahmed DA, Akulov E, Banerjee AK, Capinha C, Dia CAKM, Dobigny G, Duboscq-Carra VG, Golivets M, Haubrock PJ, Heringer G, Kirichenko N, Kourantidou M, Liu C, Nuñez MA, Renault D, Roiz D, Taheri A, Verbrugge LNH, Watari Y, Xiong W, Courchamp F (2021) Non-English languages enrich scientific knowledge: The example of economic costs of biological invasions. The Science of the Total Environment 775: 144441. https://doi.org/10.1016/j.scitotenv.2020.144441
- Angulo E, Hoffmann B, Ballesteros-Mejia L, Taheri A, Balzani P, Renault D, Cordonnier M, Bellard C, Diagne C, Ahmed DA, Watari Y, Courchamp F (2022) Economic costs of invasive alien ants worldwide. Biological Invasions 24(7): 2041–2060. https://doi.org/10.1007/s10530-022-02791-w
- Arbačiauskas K, Rakauskas V, Virbickas T (2010) Initial and long-term consequences of attempts to improve fish-food resources in Lithuanian waters by introducing alien peracaridan species: A retrospective overview. Journal of Applied Ichthyology 26: 28–37. https://doi.org/10.1111/j.1439-0426.2010.01492.x
- Asth MDS, Rodrigues RG, Zenni RD (2021) Canals as invasion pathways in tropical dry forest and the need for monitoring and management. Journal of Applied Ecology 58(9): 2004–2014. https://doi.org/10.1111/1365-2664.13950
- Azzurro E, Nourigat M, Cohn F, Ben Souissi J, Bernardi G (2022) Right out of the gate: The genomics of Lessepsian invaders in the vicinity of the Suez Canal. Biological Invasions 24(4): 1117–1130. https://doi.org/10.1007/s10530-021-02704-3

- Baker SR, Bloom N, Davis SJ, Terry SJ (2020) Covid-induced economic uncertainty (No. w26983). National Bureau of Economic Research, 1–17. https://doi.org/10.3386/w26983
- Bereza D, Rosen D, Shenkar N (2020) Current trends in ship movement via the Suez Canal in relation to future legislation and mitigation of marine species introductions. Management of Biological Invasions 11(3): 476–492. https://doi.org/10.3391/mbi.2020.11.3.09
- Bertelsmeier C, Keller L (2018) Bridgehead effects and role of adaptive evolution in invasive populations. Trends in Ecology & Evolution 33(7): 527–534. https://doi.org/10.1016/j.tree.2018.04.014
- Bij de Vaate A, Jazdzewski K, Ketelaars HA, Gollasch S, Van der Velde G (2002) Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. Canadian Journal of Fisheries and Aquatic Sciences 59(7): 1159–1174. https://doi.org/10.1139/f02-098
- Biton E (2020) Possible implications of sea level changes for species migration through the Suez Canal. Scientific Reports 10(1): 1–16. https://doi.org/10.1038/s41598-020-78313-2
- Bos AR, Ogwang J, Bariche M, Horoiwa M, Megahed M, Ouf A, Yasuda N (2020) Anti-Lessepsian migration rectified: The Comber *Serranus cabrilla* (L. 1758) existed in the Red Sea prior to the Suez Canal opening. Marine Biology 167(9): 1–10. https://doi. org/10.1007/s00227-020-03748-0
- Briski E, Bailey SA, MacIsaac HJ (2011) Invertebrates and their dormant eggs transported in ballast sediments of ships arriving to the Canadian coasts and the Laurentian Great Lakes. Limnology and Oceanography 56(5): 1929–1939. https://doi.org/10.4319/lo.2011.56.5.1929
- Briski E, Wiley CJ, Bailey SA (2012) Role of domestic shipping in the introduction or secondary spread of nonindigenous species: Biological invasions within the Laurentian Great Lakes. Journal of Applied Ecology 49(5): 1124–1130. https://doi.org/10.1111/j.1365-2664.2012.02186.x
- Briski E, Bailey SA, Casas-Monroy O, DiBacco C, Kaczmarska I, Lawrence JE, Leichsenring J, Levings C, MacGillivary ML, McKindsey CW, Nasmith LE, Parenteau M, Piercey GE, Rivkin RB, Rochon A, Roy S, Simard N, Sun B, Way C, Weise AM, MacIsaac HJ (2013) Taxon-and vector-specific variation in species richness and abundance during the transport stage of biological invasions. Limnology and Oceanography 58(4): 1361–1372. https://doi.org/10.4319/lo.2013.58.4.1361
- Castellanos-Galindo GA, Robertson DR, Pacheco-Chaves B, Angulo A, Chong-Montenegro C (2019) Atlantic Tarpon in the Tropical Eastern Pacific 80 years after it first crossed the Panama Canal. Reviews in Fish Biology and Fisheries 29(2): 401–416. https://doi.org/10.1007/s11160-019-09565-z
- Castellanos-Galindo GA, Robertson DR, Sharpe DMT, Torchin ME (2020) A new wave of marine fish invasions through the Panama and Suez canals. Nature Ecology & Evolution 4(11): 1444–1446. https://doi.org/10.1038/s41559-020-01301-2
- Chirosca AM, Rusu L (2021) Statistical and economic analysis of the Rhine-Main-Danube Canal, the bridge between the North Sea and the Black Sea. Journal of Danubian Studies and Research 11: 192–201.
- Cordoba GF (2022) The impact of the Panama Canal transfer on the Panamanian economy. Economics Letters 211: 110208. https://doi.org/10.1016/j.econlet.2021.110208

- Cuthbert RN, Kotronaki SG, Dick JT, Briski E (2020) Salinity tolerance and geographical origin predict global alien amphipod invasions. Biology Letters 16(9): 20200354. https://doi.org/10.1098/rsbl.2020.0354
- Cuthbert RN, Pattison Z, Taylor NG, Verbrugge L, Diagne C, Ahmed DA, Leroy B, Angulo E, Briski E, Capinha C, Catfordk JA, Dalu T, Essl F, Gozlan RE, Haubrock PJ, Kourantidou M, Krameru AM, Renault D, Wasserman RJ, Courchamp F (2021) Global economic costs of aquatic invasive alien species. The Science of the Total Environment 775: 145238. https://doi.org/10.1016/j.scitotenv.2021.145238
- Diagne C, Leroy B, Gozlan RE, Vaissière AC, Assailly C, Nuninger L, Roiz D, Jourdain F, Jarić I, Courchamp F (2020) InvaCost, a public database of the economic costs of biological invasions worldwide. Scientific Data 7(1): 1–12. https://doi.org/10.1038/s41597-020-00586-z
- Diagne C, Leroy B, Vaissière AC, Gozlan RE, Roiz D, Jarić I, Salles J-M, Bradshaw CJA, Courchamp F (2021a) High and rising economic costs of biological invasions worldwide. Nature 592(7855): 571–576. https://doi.org/10.1038/s41586-021-03405-6
- Diagne C, Turbelin A, Moodley D, Novoa A, Leroy B, Angulo E, Adamjy T, Dia CAKM, Taheri A, Tambo J, Dobigny G, Courchamp F (2021b) The economic costs of biological invasions in Africa: A growing but neglected threat? NeoBiota 67: 11–51. https://doi.org/10.3897/neobiota.67.59132
- Galil BS (2018) Poisonous and venomous: marine alien species in the Mediterranean Sea and human health. In: Mazza G, Tricarico E (Eds) Invasive species and human health. CABI, 1–15.
- Galil BS, Nehring S, Panov V (2008) Waterways as Invasion Highways Impact of Climate Change and Globalization. In: Nentwig W (Ed.) Biological Invasions. Ecological Studies, vol. 193. Springer, Berlin, Heidelberg, 59–74. https://doi.org/10.1007/978-3-540-36920-2_5
- Galil BS, Boero F, Campbell ML, Carlton JT, Cook E, Fraschetti S, Gollasch S, Hewitt CL, Jelmert A, Macpherson E, Marchini A, McKenzie C, Minchin D, Occhipinti-Ambrogi A, Ojaveer H, Olenin S, Piraino S, Ruiz GM (2015) 'Double trouble': The expansion of the Suez Canal and marine bioinvasions in the Mediterranean Sea. Biological Invasions 17(4): 973–976. https://doi.org/10.1007/s10530-014-0778-y
- Galil BS, Marchini A, Occhipinti-Ambrogi A, Ojaveer H (2017) The enlargement of the Suez Canal-Erythraean introductions and management challenges. Management of Biological Invasions 8(2): 141–152. https://doi.org/10.3391/mbi.2017.8.2.02
- Galil BS, Mienis HK, Hoffman R, Goren M (2021) Non-indigenous species along the Israeli Mediterranean coast: Tally, policy, outlook. Hydrobiologia 848(9): 2011–2029. https://doi.org/10.1007/s10750-020-04420-w
- Galil BS, Mienis HK, Mendelson M, Gayer K, Goren M (2022) Here today, gone tomorrow the Levantine population of the Brown mussel *Perna perna* obliterated by unprecedented heatwave. Aquatic Invasions 17(2): 174–185. https://doi.org/10.3391/ai.2022.17.2.03
- Gollasch S, Galil BS, Cohen AN (2006) Bridging divides: maritime canals as invasion corridors (Vol. 229). Springer, Dordrecht, 306 pp. https://doi.org/10.1007/978-1-4020-5047-3
- Haubrock PJ, Cuthbert RN, Tricarico E, Diagne C, Courchamp F, Gozlan R (2021a) The recorded economic costs of alien invasive species in Italy. NeoBiota 67: 247–266. https://doi.org/10.3897/neobiota.67.57747

- Haubrock PJ, Turbelin AJ, Cuthbert RN, Novoa A, Taylor NG, Angulo E, Ballesteros-Mejia L, Bodey TW, Capinha C, Diagne C, Essl F, Golivets M, Kirichenko N, Kourantidou M, Leroy B, Renault D, Verbrugge L, Courchamp F (2021b) Economic costs of invasive alien species across Europe. NeoBiota 67: 153–190. https://doi.org/10.3897/neobiota.67.58196
- Haubrock PJ, Cuthbert RN, Hudgins EJ, Crystal-Ornelas R, Kourantidou M, Moodley D, Liu C, Turbelin AJ, Leroy B, Courchamp F (2022a) Geographic and taxonomic trends of rising biological invasion costs. The Science of the Total Environment 817: 152948. https://doi.org/10.1016/j.scitotenv.2022.152948
- Haubrock PJ, Bernery C, Cuthbert RN, Liu C, Kourantidou M, Leroy B, Turbelin AJ, Kramer AM, Verbrugge LNH, Diagne C, Courchamp F, Gozlan RE (2022b) Knowledge gaps in economic costs of invasive alien fish worldwide. The Science of the Total Environment 803: 149875. https://doi.org/10.1016/j.scitotenv.2021.149875
- Hull V, Liu J (2018) Telecoupling: A new frontier for global sustainability. Ecology and Society 23(4): 41. https://doi.org/10.5751/ES-10494-230441
- Hulme PE (2009) Trade, transport and trouble: Managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46(1): 10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x
- Hulme PE, Bacher S, Kenis M, Kuhn I, Pergl J, Pyšek P, Roques A, Vilà M (2017) Blurring alien introduction pathways risks losing the focus on invasive species policy. Conservation Letters 10(2): 265–266. https://doi.org/10.1111/conl.12262
- Jażdżewski K (1980) Range extensions of some gammaridean species in European inland waters caused by human activity. Crustaceana (Supplement 6): 84–107.
- Kaiser BA, Kourantidou M (2021) Invasive alien species in changing marine arctic economies and ecosystems. CABI Reviews: Perspectives in Agriculture, Veterinary Science. Nutrition and Natural Resources 16: 1–12. https://doi.org/10.1079/PAVSNNR202116022
- Kaluza P, Kölzsch A, Gastner MT, Blasius B (2010) The complex network of global cargo ship movements. Journal of the Royal Society, Interface 7(48): 1093–1103. https://doi.org/10.1098/rsif.2009.0495
- Kenawy E (2016) The economic impacts of the new Suez Canal. IEMed. Mediterranean Year-book, 282–288.
- Kouba A, Oficialdegui FJ, Cuthbert RN, Kourantidou M, South J, Tricarico E, Gozlan RE, Courchamp F, Haubrock PJ (2022) Identifying economic costs and knowledge gaps of invasive aquatic crustaceans. The Science of the Total Environment 813: 152325. https://doi.org/10.1016/j.scitotenv.2021.152325
- Kourantidou M, Kaiser BA, Fernandez LM (2015) Towards Arctic Resource Governance of Marine Invasive Species. In: Heininen L, Exner-Pirot H, Plouffe J (Eds) Arctic Yearbook 2015. Northern Research Forum, Akureyri, Iceland, 175–194.
- Kourantidou M, Cuthbert RN, Haubrock PJ, Novoa A, Taylor N, Leroy B, Capinha C, Renault D, Angulo E, Diagne C, Courchamp F (2021) Economic costs of invasive alien species in the Mediterranean basin. NeoBiota 67: 427–458. https://doi.org/10.3897/neobiota.67.58926
- Kramarz T, Park S (2017) Introduction: The politics of environmental accountability. The Review of Policy Research 34(1): 4–9. https://doi.org/10.1111/ropr.12223
- Leigh P (1998) Benefits and costs of the ruffe control program for the Great Lakes fishery. Journal of Great Lakes Research 24(2): 351–360. https://doi.org/10.1016/S0380-1330(98)70826-3

- Leroy B, Kramer AM, Vaissière AC, Courchamp F, Diagne C (2020) Analysing global economic costs of invasive alien species with the invacost R package. bioRxiv, 1–18. https://doi.org/10.1101/2020.12.10.419432
- Leuven RS, van der Velde G, Baijens I, Snijders J, van der Zwart C, Lenders HJ, bij de Vaate A (2009) The river Rhine: A global highway for dispersal of aquatic invasive species. Biological Invasions 11(9): 1989–2008. https://doi.org/10.1007/s10530-009-9491-7
- Lloyd RA (2018) The Panama Canal as a Determinant of fdi in Panama. Review of Integrative Business and Economics Research 7: 87–102.
- Lockwood JL, Hoopes MF, Marchetti MP [Eds] (2013) Invasion ecology, 2nd edn. Wiley-Blackwell / John Wiley and Sons, 444 pp.
- Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. Frontiers in Ecology and the Environment 6(9): 485–492. https://doi.org/10.1890/070064
- Muirhead JR, Minton MS, Miller WA, Ruiz GM (2015) Projected effects of the Panama Canal expansion on shipping traffic and biological invasions. Diversity & Distributions 21(1): 75–87. https://doi.org/10.1111/ddi.12260
- Oreska MP, Aldridge DC (2011) Estimating the financial costs of freshwater invasive species in Great Britain: A standardized approach to invasive species costing. Biological Invasions 13(2): 305–319. https://doi.org/10.1007/s10530-010-9807-7
- Park C, Richardson HW, Park J (2020) Widening the Panama Canal and US ports: Historical and economic impact analyses. Maritime Policy & Management 47(3): 419–433. https://doi.org/10.1080/03088839.2020.1721583
- R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Renault D, Manfrini E, Leroy B, Diagne C, Ballesteros-Mejia L, Angulo E, Courchamp F (2021) Biological invasions in France: Alarming costs and even more alarming knowledge gaps. NeoBiota 67: 191–224. https://doi.org/10.3897/neobiota.67.59134
- Rewicz T, Grabowski M, Tończyk G, Konopacka A, Bącela-Spychalska K (2019) Gammarus tigrinus Sexton, 1939 continues its invasion in the Baltic Sea: First record from Bornholm (Denmark). BioInvasions Records 8(4): 862–870. https://doi.org/10.3391/bir.2019.8.4.14
- Ricciardi A, Rasmussen JB (1999) Extinction rates of North American freshwater fauna. Conservation Biology 13(5): 1220–1222. https://doi.org/10.1046/j.1523-1739.1999.98380.x
- Ruiz GM, Galil BS, Davidson IC, Donelan SC, Miller AW, Minton MS, Muirhead JR, Ojaveer H, Tamburri MN, Carlton JT (2022) Global marine biosecurity and ship layups: Intensifying effects of trade disruptions. Biological Invasions 24(11): 3441–3446. https://doi.org/10.1007/s10530-022-02870-y
- Scheibel NC, Dembkowski DJ, Davis JL, Chipps SR (2016) Impacts of northern pike on stocked rainbow trout in Pactola Reservoir, south Dakota. North American Journal of Fisheries Management 36(2): 230–240. https://doi.org/10.1080/02755947.2015.1116472
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K,

- Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. Nature Communications 8(1): 1–9. https://doi.org/10.1038/ncomms14435
- Shafer WE (2006) Social paradigms and attitudes toward environmental accountability. Journal of Business Ethics 65(2): 121–147. https://doi.org/10.1007/s10551-005-4606-2
- Soto I, Cuthbert RN, Ahmed DA, Kouba A, Domisch S, Marquez JR, Beidas A, Amatulli G, Kiesel J, Shen LQ, Florencio M, Lima H, Briski E, Altermatt F, Archambaud-Suard G, Borza P, Csabai Z, Datry T, Floury M, Forcellini M, Fruget J-F, Leitner P, Lizée M-H, Maire A, Ricciardi A, Schäfer RB, Stubbington R, Van der Lee GH, Várbíró G, Verdonschot RCM, Haase P, Haubrock PJ (2022) Tracking a killer shrimp: *Dikerogammarus villosus* invasion dynamics across Europe. Diversity & Distributions 00: 1–16. https://doi.org/10.1111/ddi.13649
- Souty-Grosset C, Anastácio P, Reynolds J, Tricarico E (2018) Invasive freshwater invertebrates and fishes: Impacts on human health. In: Mazza G, Tricarico E (Eds) Invasive Species and Human Health. CABI, 91–107. https://doi.org/10.1079/9781786390981.0091
- Strayer DL (2010) Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology 55: 152–174. https://doi.org/10.1111/j.1365-2427.2009.02380.x
- Sylvester F, MacIsaac HJ (2010) Is vessel hull fouling an invasion threat to the Great Lakes? Diversity & Distributions 16(1): 132–143. https://doi.org/10.1111/j.1472-4642.2009.00622.x
- Sylvester F, Kalaci O, Leung B, Lacoursière-Roussel A, Murray CC, Choi FM, Bravo MA, Therriault TW, MacIsaac HJ (2011) Hull fouling as an invasion vector: Can simple models explain a complex problem? Journal of Applied Ecology 48(2): 415–423. https://doi.org/10.1111/j.1365-2664.2011.01957.x
- Tricarico E, Mazza G, Orioli G, Rossano C, Scapini F, Gherardi F (2010) The killer shrimp, *Dikerogammarus villosus* (Sowinsky, 1894), is spreading in Italy. Aquatic Invasions 5(2): 211–214. https://doi.org/10.3391/ai.2010.5.2.14
- Turbelin AJ, Diagne C, Hudgins EJ, Moodley D, Kourantidou M, Novoa A, Haubrock PJ, Bernery C, Gozlan RE, Francis RA, Courchamp F (2021) Species on the move: Stowaways and contaminants cause the greatest economic impacts. Biological Invasions, 1–27. https://doi.org/10.21203/rs.3.rs-440305/v1
- van Rijn I, Kiflawi M, Belmaker J (2020) Alien species stabilize local fisheries catch in a highly invaded ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 77(4): 752–761. https://doi.org/10.1139/cjfas-2019-0065
- Wang M (2017) The role of Panama Canal in global shipping. Maritime Business Review 2(3): 247–260. https://doi.org/10.1108/MABR-07-2017-0014
- Woodford DJ, Hui C, Richardson DM, Weyl OL (2013) Propagule pressure drives establishment of introduced freshwater fish: Quantitative evidence from an irrigation network. Ecological Applications 23(8): 1926–1937. https://doi.org/10.1890/12-1262.1
- Wrange AL, Charrier G, Thonig A, Alm Rosenblad M, Blomberg A, Havenhand JN, Jonsson PR, André C (2016) The story of a hitchhiker: Population genetic patterns in the invasive barnacle *Balanus (Amphibalanus) improvisus* Darwin 1854. PLoS ONE 11(1): e0147082. https://doi.org/10.1371/journal.pone.0147082

Supplementary material I

Knowledge needs in economic costs of invasive species facilitated by canalization

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Data type: tables (word file)

Explanation note: Sources used for the extraction of species for each canal system. Countries considered for each canal system.

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Link: https://doi.org/10.3897/neobiota.78.95050.suppl1