

# Biological invasions in Singapore and Southeast Asia: data gaps fail to mask potentially massive economic costs

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## Abstract

The impacts of invasive alien species are well-known and are categorised as a leading contributor to biodiversity loss globally. However, relatively little is known about the monetary costs incurred from invasions on national economies, hampering management responses. In this study, we used published data to describe the economic cost of invasions in Southeast Asia, with a focus on Singapore – a biodiversity-rich, tropical island city state with small size, high human density and high trade volume, three factors likely to increase invasions. In this country, as well as in others in Southeast Asia, cost data were scarce,

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with recorded costs available for only a small fraction of the species known to be invasive. Yet, the overall available economic costs to Singapore were estimated to be ~ US\$ 1.72 billion in total since 1975 (after accounting for inflation), which is approximately one tenth of the total cost recorded in all of Southeast Asia (US\$ 16.9 billion). These costs, in Singapore and Southeast Asia, were mostly linked to insects in the family Culicidae (principally *Aedes* spp.) and associated with damage, resource loss, healthcare and control-related spending. Projections for 11 additional species known to be invasive in Singapore, but with recorded costs only from abroad, amounted to an additional US\$ 893.13 million, showing the potential huge gap between recorded and actual costs (cost records remain missing for over 90% of invasive species). No costs within the database for Singapore – or for other Southeast Asian countries – were exclusively associated with proactive management, highlighting that a shortage of reporting on the costs of invasions is mirrored by a lack of investment in management. Moreover, invasion cost entries in Singapore were under-reported relative to import levels, but total costs exceeded expectations, based on land area and population size, and to a greater extent than in other Southeast Asian countries. Therefore, the evaluation and reporting of economic costs of invasions need to be improved in this region to provide efficient data-based support for mitigation and management of their impacts.

### **Abstract (Chinese)**

**外来物种入侵新加坡和东南亚：数据缺乏不能掩盖潜在巨大的经济损失** 众所周知，外来物种入侵的影响是导致全球生物多样性降低的一个重要因素。然而，对于外来物种入侵造成国家经济损失知之甚少，从而阻碍了有效的管理响应。在这项研究中，我们使用已发表的数据揭示外来物种入侵东南亚造成的经济损失，重点关注新加坡：一个生物多样性丰富的热带岛屿城市国家，面积小、人口密度高、进出口贸易量大，这三个因素可能会增加入侵。新加坡和东南亚的其他国家一样缺乏外来物种入侵造成经济损失的数据，只有一小部分已知的入侵物种造成经济损失的记录。然而，自1975年以来，外来物种入侵在新加坡造成经济损失估计约为17.2亿美元（考虑到通货膨胀），约占整个东南亚经济损失（169亿美元）的十分之一。外来物种入侵在新加坡和东南亚的造成的经济损失主要与蚊科（Culicidae）昆虫（主要是伊蚊）有关，与其造成的直接伤害、资源损失、医疗保障和防治的开支有关。根据在其他国家造成损失的经验，估算另外11种在新加坡入侵物种造成了8.9313亿美元的经济损失，这一结果表明记录和实际损失之间的巨大差距（超过90%的入侵物种的缺乏造成经济损失的记录）。在新加坡或其他东南亚国家的数据库中，没有外来入侵物种造成经济损失的记录，因此缺乏前瞻性的管理措施。这突出表明，对于入侵物种造成经济损失报告的短缺与管理投资缺乏是一致的。此外，相对于进口水平，新加坡的入侵物种造成的经济损失是被低估的，根据土地面积和人口规模，总的经济损失超过了预期，远远高于其他东南亚国家。因此，在这个地区需要加强对入侵物种造成经济损失的评估和报告，从而为减轻和管理其影响提供有效的数据支持。

### **Abstract (Malay)**

**Penaklukan spesies di Singapura dan Asia Tenggara: jurang data gagal untuk menutup kos ekonomi yang berpotensi besar).** Kesan buruk spesies asing invasif diketahui ramai dan dikategorikan sebagai penyumbang utama kehilangan biodiversiti di peringkat global. Walau bagaimanapun, tindak balas pengurusan terhalang kerana kekurangan maklumat tentang penilaian kewangan yang timbul daripada penaklukan spesies asing invasif terhadap ekonomi negara. Dalam kajian ini, kami menggunakan data yang telah diterbitkan untuk menggambarkan kos ekonomi penaklukan spesies di Asia Tenggara, dengan fokus pada Singapura – sebuah negara pulau tropika yang kaya dengan biodiversiti, mempunyai saiz kecil, kepadatan manusia yang tinggi dan jumlah perdagangan yang tinggi, tiga faktor yang berkemungkinan meningkatkan penaklukan spesies. Di negara ini, dan juga di negara-negara lain di Asia Tenggara, data kos masih

kekurangan, dengan kos yang sedia ada cuma untuk sebilangan kecil spesies yang diketahui invasif. Namun, keseluruhan kos ekonomi yang tersedia untuk Singapura dianggarkan ~ US\$ 1.72 bilion secara keseluruhan sejak tahun 1975 (setelah memperhitungkan inflasi), yang merupakan kira-kira sepersepuluh daripada jumlah kos yang dilaporkan di seluruh Asia Tenggara (US\$ 16.9 bilion). Kos ini, di Singapura dan Asia Tenggara, kebanyakannya berkaitan dengan serangga dalam keluarga Culicidae (terutamanya, *Aedes* spp.) dan berkaitan dengan kerosakan, kehilangan sumber daya, penjagaan kesihatan dan perbelanjaan yang berkaitan dengan kawalan. Jangkaan untuk 11 spesies tambahan yang diketahui invasif di Singapura, tetapi hanya dengan menggunakan kos yang dilaporkan dari luar negara, berjumlah US\$ 893.13 juta tambahan, menunjukkan potensi adanya jurang besar antara kos yang direkodkan dan yang sebenar (laporan kos masih tiada untuk lebih daripada 90% invasif spesies). Kos dalam pangkalan data untuk Singapura – atau untuk negara-negara Asia Tenggara lain – tidak dikaitkan secara eksklusif dengan pengurusan proaktif. Ini menunjukkan bahawa kekurangan laporan tentang kos penaklukan spesis dicerminkan oleh kekurangan pelaburan untuk pengurusan. Lebih-lebih lagi, kemasukan kos penaklukan spesis di Singapura kurang dilaporkan berkaitan dengan tahap import, tetapi jumlah kos melebihi jangkaan, berdasarkan keluasan tanah dan saiz penduduk, dan di tahap yang lebih tinggi daripada negara-negara Asia Tenggara yang lain. Oleh itu, penilaian dan pelaporan kos ekonomi penaklukan spesis perlu ditingkatkan di rantau ini untuk memberikan sokongan berasaskan data yang efisien untuk mengurangkan dan menguruskan kesan buruk akibat spesis asing invasif.

### Abstract (French)

**Invasions biologiques à Singapour et en Asie du Sud-Est: les lacunes dans les données ne masquent pas des coûts économiques potentiellement énormes.** Les impacts des espèces exotiques envahissantes (EEE) sont bien connus et sont classés comme l'un des principaux contributeurs à la perte de biodiversité à l'échelle mondiale. Cependant, on en sait relativement peu sur les coûts monétaires induits par les invasions sur les économies nationales, qui entravent les décisions de gestion. Dans cette étude, nous avons utilisé des données publiées pour décrire le coût économique des invasions en Asie du Sud-Est, en mettant l'accent sur Singapour - une ville-état insulaire tropicale riche en biodiversité de petite taille, avec une densité humaine et un volume commercial élevés; trois facteurs susceptibles d'augmenter les invasions. Dans ce pays, ainsi que dans d'autres en Asie du Sud-Est, les données sur les coûts étaient rares, les coûts enregistrés n'étant disponibles que pour une petite fraction des espèces réputées envahissantes. Pourtant, les coûts économiques globaux disponibles pour Singapour ont été estimés à au moins ~ 1,72 milliard de dollars américains, soit environ un dixième du coût total enregistré dans toute l'Asie du Sud-Est (16,9 milliards de dollars américains). Ces coûts, à Singapour et en Asie du Sud-Est, étaient principalement liés aux insectes de la famille des Culicidae (principalement *Aedes* spp.) et associés aux dommages, à la perte de ressources, aux soins de santé et aux dépenses liées au contrôle. Les projections pour 11 espèces supplémentaires connues pour être envahissantes à Singapour, mais avec des coûts enregistrés uniquement en provenance de l'étranger, se sont élevées à 893,13 millions USD supplémentaires, montrant l'énorme écart potentiel entre les coûts enregistrés et réels (les enregistrements de coûts restent manquants pour plus de 90% des espèces envahissantes). Aucun coût dans la base de données pour Singapour - ou pour d'autres pays d'Asie du Sud-Est - n'était exclusivement associé à une gestion proactive, ce qui souligne qu'un manque de rapports sur les coûts des invasions se traduit par un manque d'investissement dans la gestion. De plus, les entrées de coûts d'invasion à Singapour ont été sous-déclarées par rapport aux niveaux d'importation, mais les coûts totaux ont dépassé les attentes fondées sur la superficie des terres et la taille de la population, et dans une plus grande mesure que dans d'autres pays d'Asie du Sud-Est. Par conséquent, l'évaluation et la communication des coûts économiques des invasions doivent être améliorées dans cette région pour fournir un soutien efficace basé sur des données pour l'atténuation et la gestion de leurs impacts.

**Abstract (Spanish)**

**Invasiones biológicas en Singapur y el sudeste asiático: la falta de datos no logra enmascarar costos económicos potencialmente masivos.** Los impactos de las especies invasoras son bien conocidos y se caracterizan por ser uno de los principales contribuyentes para la pérdida de la biodiversidad a nivel global. No obstante, se conoce relativamente poco sobre el impacto monetario que las invasiones provocan en las economías de las naciones, lo cual obstaculiza las respuestas de manejo. En el presente estudio, se emplearon datos publicados para describir los costes económicos de las especies invasoras en el sudeste asiático, con un enfoque en Singapur –una pequeña ciudad isleña tropical con alta riqueza biológica, alta densidad poblacional y un alto volumen del mercado; tres factores que se asocian con el incremento de invasiones biológicas–. En este país, como en otros del sudeste de Asia, los datos sobre los costes son escasos, donde los registros de costes disponibles representaron solo una fracción de las especies que se conocen como invasoras. No obstante, los datos sobre los costes económicos disponibles en general se estimaron al menos en ~ US \$1.72 mil millones en Singapur, lo cual corresponde aproximadamente a una onceava parte de los costes reportados en todo el sudeste de Asia (US \$16.9 mil millones). Los costes identificados en Singapur y el sudeste asiático se asociaron principalmente con insectos de la familia Culicidae (principalmente *Aedes* spp.) y se asociaron con gastos por daños, pérdida de recursos, cuidado de la salud, y aquellos relacionados con el control. Las proyecciones para las 11 especies adicionales que se sabe que son invasoras en Singapur, pero con registros superficiales en sus costes, alcanzaron un total de US \$893.13 millones, mostrando un gran vacío potencial entre la información registrada y los costes actuales (los registros mantienen una ausencia sobre los costes del 90% de las especies invasoras). Ningún coste en la base de datos de Singapur –o para otro país sudasiático– se asoció exclusivamente con manejo proactivo, destacando que la escasez de información sobre los costes de las invasiones se refleja en la falta de inversión en el manejo. Además, las entradas de los costes de invasoras se mostraron inferiores a los niveles de importación en Singapur, pero los costes totales superaron las expectativas basadas en la extensión del área y el tamaño de la población, y en mayor medida que en otros países del sudeste de Asia. Por lo tanto, es necesario mejorar la evaluación y la presentación de informes sobre los costes económicos de las invasiones en esta región a fin de proporcionar un apoyo eficaz basado en datos para la mitigación y el manejo de sus impactos.

**Keywords**

Ecosystem services, imports, InvaCost, monetary impact, tropics, socioeconomic sectors

**Introduction**

Biological invasions cause significant ecological impacts around the world, posing profound impediments to conservation efforts and potentially driving marked socioeconomic costs (Hulme et al. 2009; Early et al. 2016; Seebens et al. 2017). Invasive species are amongst the main drivers of biodiversity loss worldwide (Malcolm and Markham 2000; Stigall 2010; Bellard et al. 2016; Haubrock et al. 2021). In a socioeconomic context, invasions can directly affect human health, damage goods and services, compromise public and social welfare and impact agriculture (Bradshaw et al. 2016; Paini et al. 2016; Jones 2017; Shackleton et al. 2019). Yet, disproportionately few economic resources are allocated to remediate the large-scale consequences of such invasions in different parts of the world (Hulme et al. 2009; Scaler, 2010; Early et al. 2016). One

of the reasons underlying this discrepancy is undoubtedly related to the limited knowledge and societal awareness of their actual impacts (Courchamp et al. 2017).

Whilst the ecological impacts of invasive species are well-described (see, for example, Gurevitch and Padilla 2004; Didham et al. 2005; Cuthbert et al. 2019a, 2020; Mofu et al. 2019), relatively few studies have synthesised monetary aspects associated with biological invasions (but see Pimentel et al. 2005 for the USA; Kettunen et al. 2009 for Europe; Oreska and Aldridge 2011 for the UK; Gren et al. 2009 for Sweden; Hoffmann and Broadhurst 2016 for Australia; Xu et al. 2006 for China). Yet, highlighting the economic costs of invasions can actually represent a key awareness-building tool for both the general public and authorities, as well as an efficient way for motivating policies, guiding decision-making and prioritising management actions towards invasive species (Dana et al. 2014; McConnachie et al. 2016; Hiatt et al. 2019; Diagne et al. 2020a). Such economic costs might relate to a large variety of impacts, through damage directly or indirectly driven by invaders (e.g. Shwiff et al. 2010), to different types of expenditure dedicated to preventing, controlling or eradicating invasions (e.g. Hoffmann and Broadhurst 2016). Nonetheless, the scarcely reported economic costs are spatially, temporally and taxonomically fragmented (Diagne et al. 2020a), leading to a lack of a holistic understanding of the monetary aspects of invasions. This represents a major challenge for decision-making as invasions represent an ever-increasing trans-boundary socio-ecological challenge (Lovell et al. 2006; Marbuah et al. 2014; Diagne et al. 2020a). Particularly, while regional estimates have highlighted the diversity of costs (e.g. Pimentel et al. 2000, 2005; Kettunen et al. 2009; Nghiem et al. 2013), limited spatial resolution has resulted in piecemeal financial commitments to tackle the growing economic problem of invasions at relevant scales. More detailed and comparable information on specific costs is urgently needed at the government-level, where budgets are established and managed.

As an international travel and trade hub with numerous introduction pathways, Singapore is a country facing high risk of biological invasions (Yeo and Chia 2010; Seebens et al. 2013; Wong 2018) and may thus be a particularly useful example for such nationally-scaled cost estimation. Thus, Singapore is outstanding amongst other Southeast Asian countries due to its very dynamic economic connectivity, despite a relatively small surface area. Singapore is a highly urbanised and densely populated, but biodiverse, tropical island city state, centrally located within Southeast Asia (Tan et al. 2010; Ng et al. 2011; World Bank 2019). The few publications reporting costs of invasive species in Singapore have suggested they might be important (Nghiem et al. 2013), yet costs have lacked synthesis. At least 142 non-native animal species have been reported in Singapore (Yeo and Chia 2010), including species listed on several 'worst invasive alien species' lists (e.g. IUCN).

Recently, the available literature on economic costs of invasive species globally was compiled in the InvaCost database (Diagne et al. 2020b) with the aim of generating the means to fill knowledge gaps on invasion costs worldwide. Using data available from this database, we synthesised and described the available information on economic costs of invasions in Southeast Asia, focusing on Singapore in particular.

We specifically investigated (a) how recorded costs and species are characterised across Southeast Asian countries and (b) Singapore as a more detailed example or case study to describe recorded costs impacting its economy, according to (i) taxa, (ii) cost types and (iii) activity sectors. We also deciphered whether the level of reliability of estimates may impact the financial burden of invaders. Furthermore, we extrapolated additional costs for invaders reported in Singapore, but with unknown costs there. Finally, we correlated invasion costs with importation levels, surface area and population size amongst countries to assess the specificities of Southeast Asian countries. We hypothesised that the costs of invasive species in Singapore are underestimated and yet substantial, as are probably those of other Southeast Asian countries.

## Methods

### Data acquisition

Information on the economic cost of invasions in all the Southeast Asian countries (Brunei, Cambodia, East Timor, Indonesia, Laos, Malaysia, Myanmar, Philippines, Singapore, Thailand and Vietnam) was extracted from the InvaCost database (Diagne et al. 2020b; Angulo et al. 2021) concerning the global costs of invasive species, based on published literature, enabling comprehensive quantification of costs associated with invasive species at various spatio-temporal scales. The latest version of the database, as well as a summary of the whole procedure used to build and update it, can be directly accessed at <https://doi.org/10.6084/m9.figshare.12668570>. Briefly, the data in InvaCost were collected following (i) a series of literature searches using the Web of Science platform (<https://webofknowledge.com/>), Google Scholar database (<https://scholar.google.com/>) and the Google search engine (<https://www.google.com/>) and (ii) targeted searches through contacting experts and stakeholders to request potentially unpublished and/or publicly unavailable documents containing cost information. All the retrieved costs were standardised in an up-to-date currency (2017 USD), while also taking into account an inflation factor (Diagne et al. 2020b). We performed descriptive analyses of a subset of this database, by filtering data ('Official\_country' column) to exclusively ascertain invasion costs in each country.

### Cost calculation and description

We considered the total costs of invasions by amalgamating the recorded raw costs (column 'Cost\_estimate\_per\_year\_2017\_USD\_exchange\_rate') per year from our subset. Due to the variability of temporal scales of cost estimates in InvaCost, we annualised the data, based on the difference between the "Probable\_starting\_year\_adjusted" and "Probable\_starting\_year\_adjusted" columns using the "summarizeCosts" function of the 'invaCost' package (v.0.3-4) in R (v.4.0.2) (Leroy et al. 2020). Each expanded entry thus corresponded to a single year for which costs were available following this

expansion process (i.e. costs spanning multiple years were divided amongst those same years). The resulting costs attributed to recorded species were examined according to different descriptive fields of the database (an updated description of these descriptive fields is openly available at <https://doi.org/10.6084/m9.figshare.12668570>):

i. `Method_reliability`: illustrating the perceived reliability of cost estimates, based on the type of publication and method of estimation. Estimates in peer-reviewed publications or official reports or with documented, repeatable and/or traceable methods were designated as “High reliability”; all other estimates were designated as “Low reliability” (Diagne et al. 2020b);

ii. `Implementation`: referring to whether the cost estimate was actually realised in the invaded habitat (“Observed”) or whether it was only predicted to occur (“Potential”);

iii. `Type_of_cost_merged`: grouping of costs according to the categories: (a) “Damage-Loss” referring to damages or losses incurred by invasion (e.g. costs for damage repair, resource losses, medical care), (b) “Management” comprising control-related expenditure (for example monitoring, prevention, management, eradication) and money spent on education and maintenance costs, (c) “Diverse/Unspecified” including mixed damage-loss and management costs (cases where reported costs were not clearly distinguished amongst cost types);

iv. `Impacted_sector`: the activity, societal or market sector that was impacted by the cost (Suppl. material 2); note that individual cost entries not allocated to a single sector were classified under “Mixed” in the “`Impacted_sector`” column. A detailed summary of all descriptors can be found in Suppl. material 1 (see also Diagne et al. 2020b) and the final dataset in Suppl. material 2.

## Temporal dynamics and cost extrapolations

To investigate the temporal dynamics of invasion costs, we used the “`summarizeCosts`” function implemented in the R package ‘`invacost`’ (Leroy et al. 2020). With this method, we calculated the observed cumulative and average annual costs covering the period for which costs were recorded, displaying the changes in invasion costs over time.

As cost information for invasive alien species in Singapore, which we used as an example, was limited (three species; see Results for more details), we also extrapolated potential costs for a few additional known invasive species present in Singapore, but which had recorded costs outside Singapore. For this, we used the most recent comprehensive list of alien animal species in Singapore ( $n = 142$ ; Yeo and Chia 2010). With this information, we first estimated the mean annual cost of the species listed in Yeo and Chia (2010) outside Singapore (at the “country” scale) that was available in InvaCost, assuming the InvaCost database contained recorded cost information for Singapore over the same period (1975–2015). We then applied a correction factor that considers the cost difference between the average costs of all invasive alien species in Singapore and the average costs of all invasive alien species outside Singapore (excluding extreme val-

ues, i.e. the upper and lower 12.5% when implementing the correction factor to cost data). The corrected mean cost of each of these species was then summed to obtain an additional cost of biological invasions not directly available from records in Singapore.

## Southeast Asia and national comparisons

Given Singapore is an economic centre, we compared the available cost information of Singapore – in terms of cost entries and number of recorded species (Liu et al. 2021) – to other available information on invasive alien species costs in Southeast Asian countries recorded in InvaCost (via the aforementioned data processing methods). Furthermore, we compared invasion cost entries with other countries worldwide using a linear regression, based on import value (collected from the International Trade Centre ([https://www.trademap.org/tradestat/Country\\_SelProduct\\_TS.aspx](https://www.trademap.org/tradestat/Country_SelProduct_TS.aspx)) to (i) see how the lack of available data can affect the estimated economic costs and (ii) examine the relationship between trade volume and economic activities with the cost recording of invasive species. We focused on the 50 countries ranking highest in import value, but with recorded data in InvaCost. Further, we collected the data of species that have been introduced in all countries in Southeast Asia (see Results for more details) from the Global Alien Species First Records Database (Seebens et al. 2018; accessed in June 2020).

Finally, we examined the relationships between invasion costs (observed and high reliability costs only) and (i) land area and (ii) human population size using linear regressions (log-transformed) and examined how Singapore compared to other countries globally and in Southeast Asia particularly. Land area and population size per country were obtained using 2020 data from worldometer (<https://www.worldometers.info/world-population/population-by-country/>).

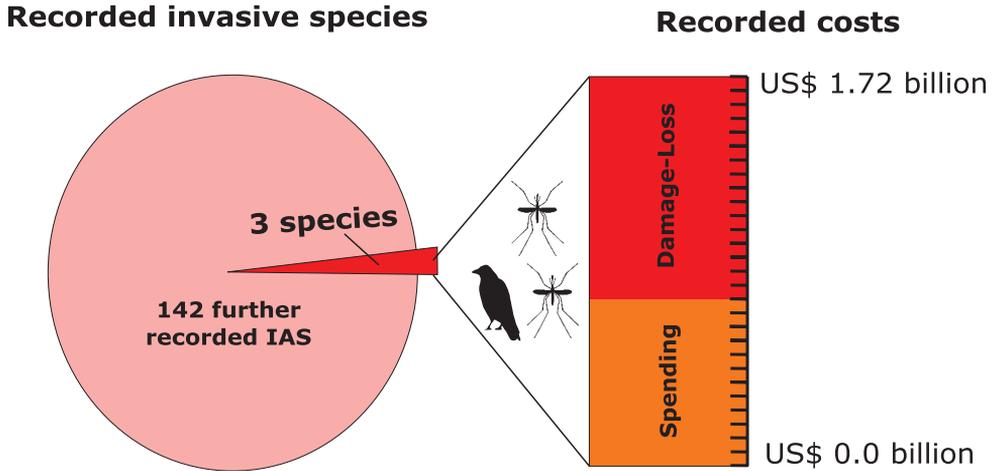
## Results

### Costs across taxa, types and sectors in Singapore

Cost data originated from seven records from six different published sources ( $n = 34$  expanded entries). The recorded costs were found to have occurred after 1975 and amounted to US\$ 1.720 billion in total (Figure 1).

At the taxonomic level, cost estimates were available for species from two families, Culicidae ( $n = 6$  estimates) and Corvidae ( $n = 1$ ). Within Culicidae, *Aedes* spp. drove all of the recorded costs, with four records attributed to *A. aegypti* alone and two as a combination of *A. aegypti* and *A. albopictus*. Although *A. albopictus* is native to Singapore, it was not possible to separate joint cost estimates, which accounted for  $< 0.05\%$  of total Culicidae costs. For Corvidae, the single cost estimate was associated with *Corvus splendens*.

The overall estimated cost was mainly caused by *Aedes* spp. with a total of US\$ 1.72 billion split between damage-losses (US\$ 1.14 billion) and management costs (US\$ 578.01 million). For *C. splendens*, the single cost estimate reached US\$ 765.24



**Figure 1.** Relative proportions of known alien species present and recorded costs in Singapore as of 2010 (Yeo and Chia 2010), alongside type categorisations for reported costs.

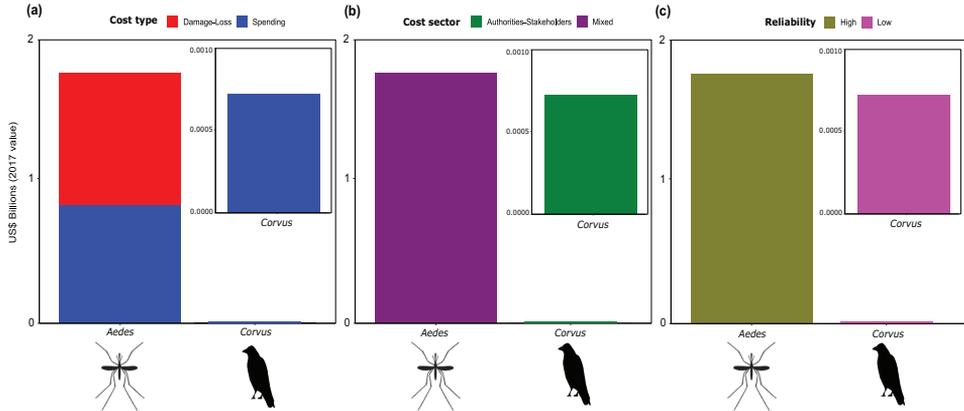
thousand and concerned costs attributed to control-related management efforts (Figure 2a). With respect to the impacted sector, all *Aedes* spp. costs were associated with a combination of impacts on authorities-stakeholders, health and public and social welfare. The single recorded costs for *C. splendens* impacted authorities-stakeholders (Figure 2b). The reported economic costs were associated with terrestrial systems alone and, thus, no costs were documented in aquatic invasions.

From a methodological point of view, all reported costs were classified as “Observed”, i.e. considered as actually occurring and not based on predictions or extrapolations from outside the invaded area. Every documented *Aedes* spp. cost was obtained from accessible peer-reviewed literature and thus deemed “High reliability”. Conversely, the single cost estimate of *C. splendens* was deemed to be of “Low reliability” (Figure 2c). Accordingly, more than 99.9% of costs were deemed “High reliability”.

### Temporal cost accumulations, extrapolations and correlations in Singapore

Costs for invasive species were recorded between 1975 and 2014. These costs tended to increase over time, both in terms of reported costs (1975–1994: n = 2; 1995–2014: n = 32), but also average annual costs (1975–1994: US\$ 1.66 million per year; 1995–2014: US\$ 80.24 million per year), with an annual average cost total of US\$ 41.91 million across the entire period (Suppl. material 3).

Comparing the costs of recorded species in Singapore with their average annual costs per country outside of Singapore, after excluding extreme values (removing 25% extreme values, i.e. the top and bottom 12.5%), costs and expenditure in Singapore were around three times lower than those in the rest of the world. From the 142 species recorded in Yeo and Chia (2010), only an additional 11 were recorded in the InvaCost database (Suppl. material 4). Applying the average annual monetary cost discrepancy



**Figure 2.** Total costs generated by the two genera of invasive species in Singapore with available cost estimates considering **a** cost type **b** impacted sector and **c** reliability of cost estimations.

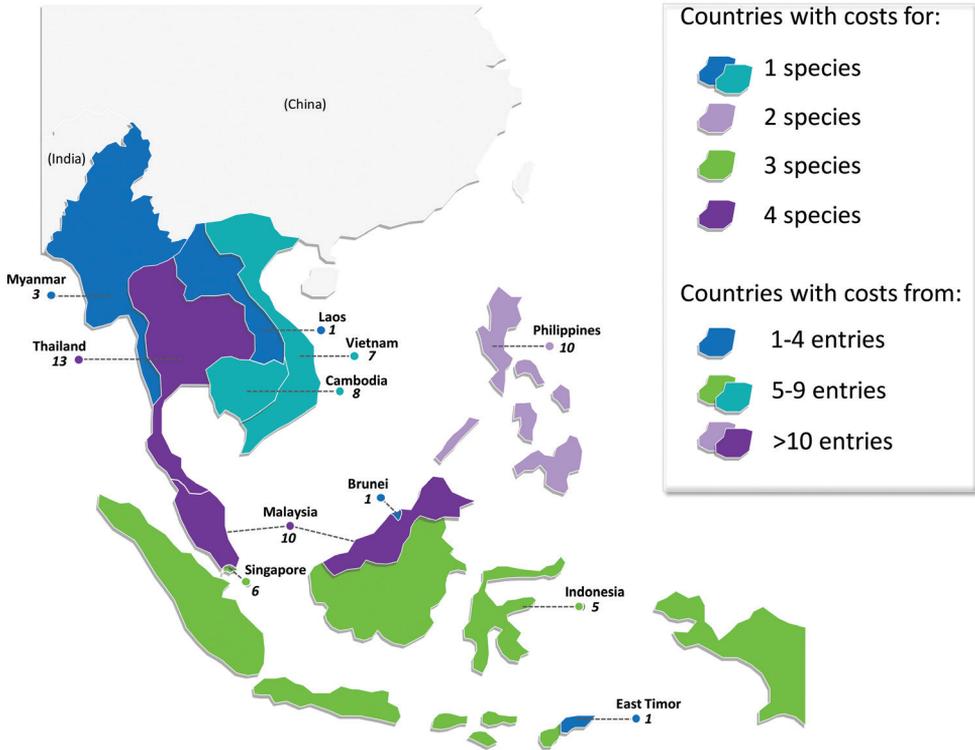
**Table 1.** Comparison of recorded invasive alien species and their costs amongst countries in Southeast Asia. Proportions of species with reported costs, relative to numbers of known reported alien species originating from the Global Alien Species First Records Database (Seebens et al. 2018; accessed in June 2020), are also displayed.

Southeast Asian country	Recorded species	Database entries	Total cost in US\$ billion (2017 value)	Species reported	Proportion of recorded established alien species
Brunei	1 ( <i>Aedes aegypti</i> )	1	0.007	-	-
Cambodia	1 ( <i>Aedes aegypti</i> )	7	0.208	10	10%
East Timor	1 ( <i>Aedes aegypti</i> )	1	0.004	-	-
Indonesia	2 ( <i>Aedes aegypti</i> ; <i>Rattus</i> sp.)	5	3.406	75	2.7%
Laos	1 ( <i>Aedes aegypti</i> )	1	0.054	10	10%
Malaysia	4 ( <i>Aedes aegypti</i> ; <i>Aedes albopictus</i> , <i>Mus musculus</i> , <i>Rattus norvegicus</i> )	10	2.673	36	5.6%
Myanmar	3 ( <i>Aedes aegypti</i> , <i>Mus musculus</i> , <i>Rattus norvegicus</i> )	3	0.152	15	6.7%
Philippines	3 ( <i>Aedes aegypti</i> ; <i>Pomacea canaliculata</i> ; <i>Sternochetus frigidus</i> )	10	3.169	70	4.3%
Singapore	3 ( <i>Aedes aegypti</i> ; <i>Aedes albopictus</i> ; <i>Corvus splendens</i> )	7	1.718	142	2.6%
Thailand	4 ( <i>Aedes aegypti</i> ; <i>Aedes albopictus</i> , <i>Mus musculus</i> , <i>Rattus norvegicus</i> )	13	5.176	45	4.4%
Vietnam	1 ( <i>Aedes aegypti</i> )	6	0.327	20	5%

as a correcting factor to the average annual costs of the 11 invasive species, using the InvaCost data from outside Singapore, resulted in an additional projected annual average cost of US\$ 22.33 million per year and a total of US\$ 893.13 million additional costs considering the period 1975–2015.

### Southeast Asia and national comparisons

The monetary impact of invasions recorded in Southeast Asia totalled US\$ 16.89 billion between 1960 and 2020. Amongst these, Singapore ranked fifth relative to other countries in terms of reported costs, with two recorded invasive alien species and seven recorded cost entries in InvaCost. Notably, Brunei had the lowest number of recorded

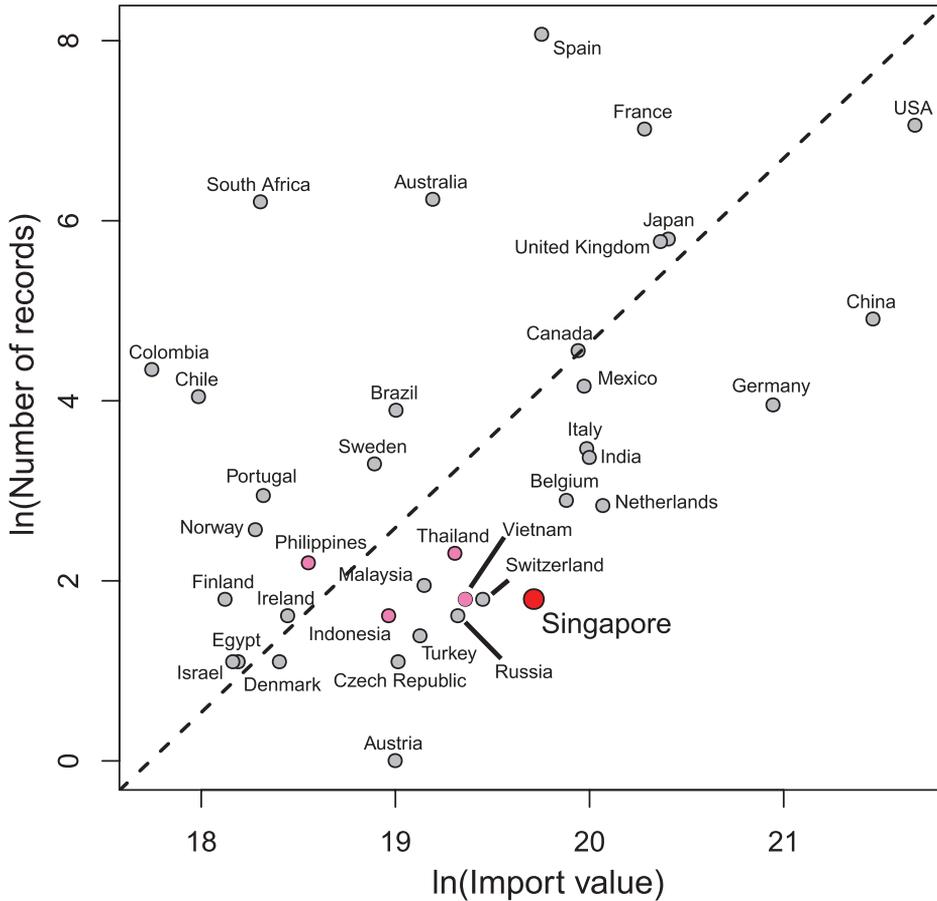


**Figure 3.** Recorded costs and species for Southeast Asian countries.

entries (1), species (1) and costs (US\$ 6.7 million), while Thailand had the highest costs (US\$ 5.2 billion) and most recorded entries (13) according to InvaCost (Table 1), suggesting considerable spatial heterogeneity in the region (Figure 3). In countries where lists of known invasive alien species were available (Liu et al. 2021), all had reported costs for 10% or less of known invasive alien species, with Singapore having the lowest proportion of aliens with costs (< 3%).

We further identified a significant correlation between trade volume and the number of recorded entries in InvaCost (Suppl. material 5). When the number of records from Singapore is related to the volume of trade imports (Figure 4), which has been shown to be strongly related to cost entries (Haubrock et al. 2021b; Kourantidou et al. 2021), the relationship highlights a number of entries 40 times lower than expected. The under-reporting of cost entries in Singapore was considerably more apparent than other high-ranking Southeast Asian countries (i.e. amongst top 50 globally in terms of imports), with Thailand, Vietnam, Malaysia and Indonesia also having fewer records than expected based on imports, but the Philippines having more cost records than expected (Figure 4).

Considering all countries, invasion costs related significantly positively to both land area and population size (Supplement 5). When compared to other countries with costs, Singapore displayed considerably greater costs relative to those variables, even relative to other Southeast Asian nations which mostly clustered together (Figures

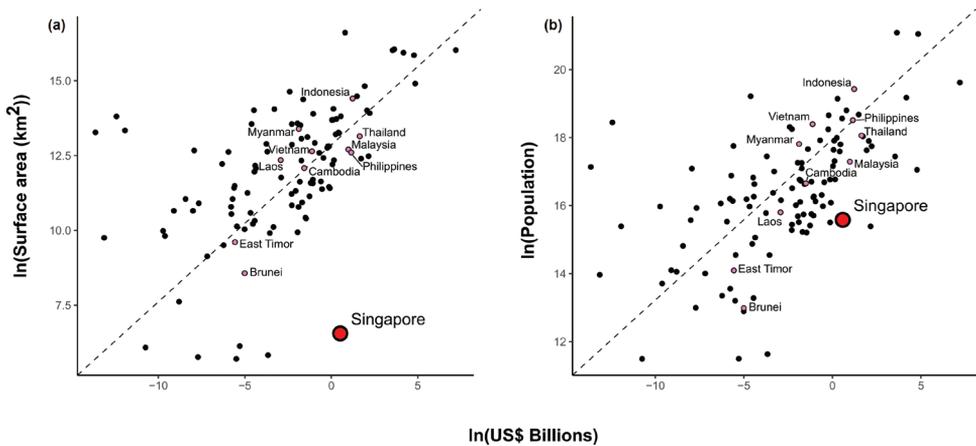


**Figure 4.** Relationship between the import value and the number of records in InvaCost, focusing on the 50 countries ranking highest in both GDP and import values, but with recorded data in InvaCost. Note that all variables are displayed on a ln-scale. Singapore shows a large deficit of records related to expectations from its import value.

5a, b). Indonesia, Myanmar and Vietnam (and Laos in the case of surface area) had lower invasion costs than expected, based on surface area and human population.

## Discussion

The recorded invasion costs in Singapore over the past 40 years have reached US\$ 1.72 billion in total which represents about  $\frac{5}{6}$  of the Ministry of the Environment and Water Resources (S\$ 2.83 billion; US\$ 2.12 billion),  $\frac{2}{3}$  of the Ministry of Trade and Industry (S\$ 3.68 billion; US\$ 2.76 billion) or more than  $\frac{1}{3}$  of the Ministry of National Developments (S\$ 4.8 billion; US\$ 3.67 billion) annual budgets in 2017 (<https://www.singaporebudget.gov.sg>). Despite these costs being high, our study shows that the available entries in the da-



**Figure 5.** Relationships between invasion costs and **a** land area and **b** human population of countries. Note that variables are presented on a  $\ln$ -scale. Each node represents an individual country with costs in InvaCost, while Singapore is highlighted.

tabase were highly fragmentary, with the majority of documented alien animal species in Singapore being absent from the cost estimation (Yeo and Chia 2010). This further puts into perspective overall costs that are already surprisingly high for such a small area, especially when actual costs are expected to be more numerous and thus overall higher than the few recorded costs. Indeed, we show not only that Singapore has few cost entries, but also that it has about 40 times fewer than expected from its trade volume. Contrastingly, comparisons, based on costs relative to land area and human population size, evidenced considerably higher costs in Singapore *pro rata*, based on those variables, with costs comparable to countries approximately 600-times larger and 10-times more populous. These trends were even more marked when compared to relationships amongst other Southeast Asian countries, which were more in line with the global cost pattern.

The very few recorded costs were linked principally to the human health sector and mainly driven by mosquitoes, with large incurred costs listed for healthcare and their control. This is mostly related to costs arising from limiting the risk of infectious human diseases, such as Zika, dengue or chikungunya, which are caused by pathogens, vectored principally by *A. aegypti* and *A. albopictus*, as well as losses through direct healthcare costs (Beltrame et al. 2007; Zammarchi et al. 2015). Indeed, mosquitoes are considered as a severe problem in Singapore, underlined by the considerable costs on control and the medical field (Carrasco et al. 2011). These total costs relating to human health in Singapore are significant, considering previous estimation of annual costs on human health and environment in the entirety of Southeast Asia (US\$ 1.85 billion; US\$ 1.4–2.5 billion per year) estimated by Nghiem et al. (2013). Moreover, our extrapolations for species known to be present in Singapore, but with no reported costs there, indicated further economic impacts summing to US\$ 893.13 million over 1975–2014. Although this figure has to be taken with caution, it underlines the magnitude of potentially occurring costs which are not accounted for in published literature. These numbers are still

likely underestimated (Diagne et al. 2021), given that these additional costs stem from just 11 of the 142 known animal invaders in Singapore that were available in InvaCost, with plant species missing entirely. Indeed, information on plant invasions in Singapore and, particularly, with regard to their monetary impacts, are scarce (Meyer 2000), with Yeo and Chia (2010) listing only relatively few invasive examples, such as the water hyacinth *Eichhornia crassipes*, which entered Singapore's waterways and proliferated to a damaging extent. As such, most invaders lack cost information at the Singapore scale, yet also internationally. Nevertheless, this lack of information, although striking, is neither surprising nor different from what is found in similar studies elsewhere. First, we showed that this is a general pattern in the region, with Singapore amongst the countries with most cost entries in Southeast Asia. Second, national or regional studies on the economic costs of biological invasions outside this region also consistently reported only between 2% and 10% of invasive alien species having recorded costs, for example, Argentina (Duboscq-Carra et al. 2020), Asia (Liu et al. 2021), Australia (Bradshaw et al. 2021), France (Renault et al. 2021), Germany (Haubrock et al. 2021c), Mexico (Rico-Sánchez et al. 2021) and United Kingdom (Cuthbert et al. 2021a).

In the context of Southeast Asia, this national bias is even more pronounced; amidst differences in economic activities amongst countries (note that Singapore has the highest GDP per capita in Southeast Asia), the lack of cost information for invasive alien species more broadly across Southeast Asian countries is striking. Singapore had the lowest proportion of known invasive alien species with reported costs, while all Southeast Asian countries had costs for 10% or below in terms of listed invasive alien species. This is also noteworthy in an all-Asia context (Liu et al. 2021), as shown by a lack of cost information in, for example, South Korea (only one 'Unspecified' record), Saudi Arabia (no records), Turkey (no records), Thailand (only records considering *A. aegypti* and *A. albopictus*) and Iran (no records), which are all amongst the 10 countries with the highest GDP in Asia (International Monetary Fund 2019; <https://www.imf.org/>). This suggests that lower economic wealth is likely not to be a determinant of how biological invasions – and their monetary costs – are documented (Nghiem et al. 2013).

Regarding the overall cost estimation, it is possible to overestimate costs if one assumes that the costs repeatedly occurring over time are repeated for a longer duration than it actually occurs (if total duration is not reported). To stay conservative, we assigned a single duration year for cost entries for which such information was missing and the cost was potentially ongoing. Furthermore, it is possible that the annual monetary burden increased over the years due to frequent descriptions of new invaders. In addition, the spatial scale for estimating costs in InvaCost reflect 'site' and/or 'country' level estimates, meaning that the national burden could be higher as some 'regional' costs may not have specified specific countries. Additionally, we show that the relatively large number of alien species present in Singapore (see Yeo and Chia 2010) potentially contributes further costs exceeding those that were recorded in InvaCost. However, one should consider that a) Yeo and Chia (2010) presented detailed information only for animals, excluding plants and microbes in this assessment; and b) the difficulties in quantifying certain types of economic impact – especially concerning ecosystem services and the many forms of damage that occur indirectly (Spangenberg and Settele 2010). For all these reasons, it could

be assumed that the presented costs may represent potentially a massive underestimation of the real economic costs of biological invasions in Singapore and Southeast Asia.

Our work also reveals a considerable taxonomic bias in the reported economic impacts of the 142 reported alien animal species in Singapore. The weighting of costs towards taxa in the database does not reflect the 'true' taxonomic composition of alien species in Singapore. Freshwater fishes and reptiles together make up the majority of alien species in this country (61%) (Yeo and Chia 2010), but no cost data were found for any of these taxa here. Yet, Yeo and Chia (2010) present anecdotal information that several non-native plant species (e.g. the South American water hyacinth, *Eichhornia crassipes*) are likely to have necessitated regular management at various scales, sometimes at considerable (yet unquantified) financial cost. This information, however, mostly relied on Wee and Corlett (1986), who, although most likely being outdated, listed 34 potentially invasive plant species present in Singapore. Nevertheless, these two accounts together are only about one quarter of the 648 species listed by GRIIS (Kwek et al. 2020), underlining the gap of cost reporting for invasive species in Singapore.

Whilst we cannot exclude that some existing cost data may have not been captured by the InvaCost database, this taxonomic discrepancy should be discussed. Singapore has a history of freshwater species introductions (Yeo and Chia 2010; Ng et al. 2010; Liew et al. 2012; Ng and Yeo 2012; Kwik et al. 2013; Ng et al. 2015, 2016a, b). Accidental releases/escapes aside, key drivers of intentional releases can often be cultural (e.g. for aesthetic, recreational or religious reasons; Yeo and Chia 2010). Usually, impacts on aquatic habitats or native communities are less obviously perceived by the public and authorities or are perceived as beneficial for local municipalities (Selge et al. 2011; Kilian et al. 2012). This could partially explain the overall bias towards costs on terrestrial habitats and the lack of information regarding aquatic habitats (Cuthbert et al. 2021b). Yet, as Singapore and many other countries of Southeast Asia are (or include) islands and, in many cases, have extensive and economically-important inland water systems, it is striking that no cost exists here for aquatic invasions. Furthermore, birds are known to be commonly released for religious purposes (Su et al. 2016); however the present study contained costs for just one species, indicating additional knowledge gaps.

Given that management and control costs usually outweigh the costs of prevention and surveillance (Leung et al. 2002), the presence of various introduction pathways in Singapore (Yeo and Chia 2010; Jaafar et al. 2012) raises the concern about how economic costs are related to pathways (Liu et al. 2019). Indeed, this should be evaluated for framing management policies by relevant stakeholders, because currently, Singapore does not have specific management plans in place that address threats from major invasive alien species, but has implemented various surveillance/monitoring programmes (National Parks Board Singapore 2015).

Despite most of the economic costs in Singapore being related to the control of invasive species and the costs of healthcare, it can be assumed that other damage or losses have not yet been estimated. For example, similarly data-poor studies found major costs for agriculture in Argentina or the UK (Duboscq-Carra et al. 2021; Cuthbert et al. 2021a) or forestry in Sweden (Haubrock et al. 2021b). In each case, it seemed clear that these trends were driven by few records, suggesting that a richer

cost record might, in each case, reveal costs for other activity sectors, substantially raising the overall estimates. In Southeast Asia, biological invasions could exert a very significant toll on major economic sectors, such as forestry in Indonesia, agriculture in Vietnam, fisheries in the Philippines or tourism in Thailand. In the case of many invasive species, only with more costs being described can we get a better understanding of the cost distribution for each descriptor. Furthermore, without information on the financial pressures that invasive species apply to an economy, efforts to tackle these, whether through prevention, surveillance or applied control and monitoring efforts, might fail at an underestimated monetary value due to inadequate investments. Given the likely underestimated costs identified for biodiversity-rich Southeast Asian countries and illustrated with Singapore, alongside their rapidly growing population densities, trade volumes and GDP, the need for effective invasive species management and cost reporting is paramount.

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## References

- Angulo E, Diagne C, Ballesteros-Mejía L, Akulov EN, Dia CAKM, Adamjy T, Banerjee A-K, Capinha C, Duboscq VG, Dobigny G, Golivets M, Heringer G, Haubrock PJ, Kirichenko N, Kourantidou M, Liu C, Nuñez M, Renault D, Roiz D, Taheri A, Watari Y, Xiong W, Courchamp F (2021) Non-English languages enrich scientific data: the example of the costs of biological invasions. *Science of the Total Environment* 775: e144441. <https://doi.org/10.1016/j.scitotenv.2020.144441>
- Bellard C, Genovesi P, Jeschke JM (2016) Global patterns in threats to vertebrates by biological invasions. *Proceedings of the Royal Society B: Biological Sciences* 283: e20152454. <https://doi.org/10.1098/rspb.2015.2454>
- Bradshaw CJ, Leroy B, Bellard C, Roiz D, Albert C, Fournier A, Courchamp F (2016) Massive yet grossly underestimated global costs of invasive insects. *Nature Communications* 7: 1–8. <https://doi.org/10.1038/ncomms12986>

- Bradshaw CJA, Hoskins AJ, Haubrock PJ, Cuthbert RN, Diagne C, Leroy B, Andrews L, Page B, Cassey P, Sheppard AW, Courchamp F (2021) Detailed assessment of the reported economic costs of invasive species in Australia. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The economic costs of biological invasions around the world*. *NeoBiota* 67: 511–550. <https://doi.org/10.3897/neobiota.67.58834>
- Courchamp F, Fournier A, Bellard C, Bertelsmeier C, Bonnaud E, Jeschke JM, Russell JC (2017) Invasion biology: specific problems and possible solutions. *Trends in Ecology and Evolution* 32: 13–22. <https://doi.org/10.1016/j.tree.2016.11.001>
- Cuthbert RN, Dickey JW, Coughlan NE, Joyce PW, Dick JT (2019a) The Functional Response Ratio (FRR): advancing comparative metrics for predicting the ecological impacts of invasive alien species. *Biological Invasions* 1–5. <https://doi.org/10.1007/s10530-019-02002-z>
- Cuthbert RN, Bacher S, Blackburn TM, Briski E, Diagne C, Dick JT, Haubrock PJ, Lenzner B, Courchamp F (2020) Invasion costs impacts and human agency: Response to Sagoff 2020. *Conservation Biology* 34(6): 1579–1582. <https://doi.org/10.1111/cobi.13592>
- Cuthbert RN, Bartlett AC, Turbelin AJ, Haubrock PJ, Diagne C, Pattison Z, Courchamp F, Catford JA (2021) Economic costs of biological invasions in the United Kingdom. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The economic costs of biological invasions around the world*. *NeoBiota* 67: 299–328. <https://doi.org/10.3897/neobiota.67.59743>
- Cuthbert RN, Pattison Z, Taylor NG, Verbrugge L, Diagne C, Ahmed DA, Leroy B, Angulo E, Briski E, Capinha C, Catford JA, Dalu T, Essl F, Gozlan RE, Haubrock PJ, Kourantidou M, Kramer AM, Renault D, Wasserman RJ, Courchamp F (2021b) Global economic costs of aquatic invasive alien species. *Science of the Total Environment* 775: e145238. <https://doi.org/10.1016/j.scitotenv.2021.145238>
- Dana ED, Jeschke JM, García-de-Lomas J (2013) Decision tools for managing biological invasions: existing biases and future needs. *Oryx* 48: 56–63. <https://doi.org/10.1017/S0030605312001263>
- Diagne C, Catford JA, Essl F, Nuñez MA, Courchamp F (2020a) What are the economic costs of biological invasions? A complex topic requiring international and interdisciplinary expertise. *NeoBiota* 63: 25–37. <https://doi.org/10.3897/neobiota.63.55260>
- Diagne C, Leroy B, Gozlan RE, Vaissière A-C, Assailly C, Nuninger L, Roiz D, Jourdain F, Jarić I, Courchamp F (2000b) InvaCost, a public database of the economic costs of biological invasions worldwide. *Sci Data* 7: e277. <https://doi.org/10.1038/s41597-020-00586-z>
- Didham RK, Tylianakis JM, Hutchison MA, Ewers RM, Gemmill NJ (2005) Are invasive species the drivers of ecological change?. *Trends in Ecology and Evolution* 20: 470–474. <https://doi.org/10.1016/j.tree.2005.07.006>
- Duboscq-Carra VG, Fernandez RD, Haubrock PJ, Dimarco RD, Angulo E, Ballesteros-Mejia L, Diagne C, Courchamp F, Nuñez MA (2021) Economic impact of invasive alien species in Argentina: a first national synthesis. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The economic costs of biological invasions around the world*. *NeoBiota* 67: 329–348. <https://doi.org/10.3897/neobiota.67.63208>
- Early R, Bradley BA, Dukes JS, Lawler JJ, Olden JD, Blumenthal DM, Sorte CJ (2016) Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications* 7: e12485. <https://doi.org/10.1038/ncomms12485>

- Gren M, Isacs L, Carlsson M (2009) Costs of alien invasive species in Sweden. *AMBIO: A Journal of the Human Environment* 38: 135–140. <https://doi.org/10.1579/0044-7447-38.3.135>
- Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution* 19(9): 470–474. <https://doi.org/10.1016/j.tree.2004.07.005>
- Haubrock PJ, Pilotto F, Innocenti G, Cianfanelli S, Haase P (2021a) Two centuries for an almost complete community turnover from native to non-native species in a riverine ecosystem. *Global Change Biology* 27(3): 606–623. <https://doi.org/10.1111/gcb.15442>
- 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 (2020) Economic costs of invasive alien species across Europe In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The economic costs of biological invasions around the world*. *NeoBiota* 67: 153–190. <https://doi.org/10.3897/neobiota.67.58196>
- Haubrock PJ, Cuthbert RN, Sundermann A, Diagne C, Golivets M, Courchamp F (2021) Economic costs of invasive species in Germany. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The economic costs of biological invasions around the world*. *NeoBiota* 67: 225–246. <https://doi.org/10.3897/neobiota.67.59502>
- Hiatt D, Serbesoff-King K, Lieurance D, Gordon DR, Flory SL (2019) Allocation of invasive plant management expenditures for conservation: Lessons from Florida USA. *Conservation Science and Practice* e51. <https://doi.org/10.1111/csp2.51>
- Hoffmann BD, Broadhurst LM (2016) The economic cost of managing invasive species in Australia. *NeoBiota* 31: 1–1. <https://doi.org/10.3897/neobiota.31.6960>
- Hulme PE, Pyšek P, Nentwig W, Vilà M (2009) Will threat of biological invasions unite the European Union? *Science* 324: 40–41. <https://doi.org/10.1126/science.1171111>
- Jaafar Z, Yeo DCJ, Tan HH, O’Riordan RM (2012) Status of estuarine and marine non-indigenous species in Singapore. *Raffles Bulletin of Zoology Supplement No 25*: 79–92.
- Jones BA (2017) Invasive species impacts on human well-being using the life satisfaction index. *Ecological Economics* 134: 250–257. <https://doi.org/10.1016/j.ecolecon.2017.01.002>
- Kettunen M, Genovesi P, Gollasch S, Pagad S, Starfinger U, ten Brink P, Shine C (2009) *Technical support to EU strategy on invasive alien species (IAS)* Institute for European Environmental Policy (IEEP) Brussels, 44 pp.
- Kilian JV, Klauda RJ, Widman S, Kashiwagi M, Bourquin R, Weglein S, Schuster J (2012) An assessment of a bait industry and angler behavior as a vector of invasive species. *Biological Invasions* 14: 1469–1481. <https://doi.org/10.1007/s10530-012-0173-5>
- Kourantidou M, Cuthbert RN, Haubrock PJ, Novoa A, Taylor NG, Leroy B, Capinha C, Renault D, Angulo E, Diagne C, Courchamp F (2021) Economic costs of invasive alien species in the Mediterranean basin. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The economic costs of biological invasions around the world*. *NeoBiota* 67: 427–458. <https://doi.org/10.3897/neobiota.67.58926>
- Kwek Yan C, Yeo Chong Jinn D, Chia C, Tan Tiang Wah H, Lim Kok Peng K, Heok Hui T, Koh Siang T, Wong LJ, Pagad S (2020) *Global Register of Introduced and Invasive Spe-*

- cies - Singapore. Version 1.2. Invasive Species Specialist Group ISSG. Checklist dataset accessed via GBIF.org [2021-02-14]
- Kwik JTB, Kho ZY, Quek BS, Tan HH, Yeo DCJ (2013) Urban stormwater ponds in Singapore: potential pathways for spread of alien freshwater fishes. *BioInvasions Records* 2: 239–245. <https://doi.org/10.3391/bir.2013.2.3.11>
- Leroy B, Kramer A, Vaissière A-C, Diagne C (in prep). *invacost: INVACOST Database With Methods To Analyse Invasion Costs*. R package version 0.3-4. <http://borisleroy.com/invacost/Readme.html>
- Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society of London Series B: Biological Sciences* 269: 2407–2413. <https://doi.org/10.1098/rspb.2002.2179>
- Liew JH, Tan HH, Yeo DCJ (2012) Some cichlid fishes recorded in Singapore. *Nature in Singapore* 5: 229–236.
- Liu X, Blackburn TM, Song T, Li X, Huang C, Li Y (2019) Risks of biological invasion on the belt and road. *Current Biology* 29: 499–505. <https://doi.org/10.1016/j.cub.2018.12.036>
- Liu C, Diagne C, Angulo E, Banerjee A-K, Chen Y, Cuthbert RN, Haubrock PJ, Kirichenko N, Pattison Z, Watari Y, Xiong W, Courchamp F (2021) Economic costs of biological invasions in Asia. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The economic costs of biological invasions around the world*. *NeoBiota* 67: 53–78. <https://doi.org/10.3897/neobiota.67.58147>
- Lovell SJ, Stone SF, Fernandez L (2006) The economic impacts of aquatic invasive species: a review of the literature. *Agricultural and Resource Economics Review* 35: 195–208. <https://doi.org/10.1017/S1068280500010157>
- Malcolm JR, Markham A (2000) *Global warming and terrestrial biodiversity decline*. WWF, Washington.
- Marbuah G, Gren IM, McKie B (2014) Economics of harmful invasive species: a review. *Diversity* 6: 500–523. <https://doi.org/10.3390/d6030500>
- McConnachie MM, van Wilgen BW, Ferraro PJ, Forsyth AT, Richardson DM, Gaertner M, Cowling, RM (2016) Using counterfactuals to evaluate the cost-effectiveness of controlling biological invasions. *Ecological Applications* 26: 475–483. <https://doi.org/10.1890/15-0351>
- National Parks Board Singapore (2015) *Singapore 5<sup>th</sup> National Report to the Convention on Biological Diversity (2010–2014)*.
- Meyer JY (2000) Preliminary review of the invasive plants in the Pacific islands (SPREP Member Countries). *Invasive species in the Pacific: A technical review and draft regional strategy* 85.
- Ng HH, Tan HH, Yeo DCJ, Ng PKL (2010) Stingers in a strange land: South American freshwater stingrays (Potamotrygonidae) in Singapore. *Biological Invasions* 12: 2385–2388. <https://doi.org/10.1007/s10530-009-9663-5>
- Ng TH, Foon JK, Tan SK, Chan MKK, Yeo DCJ (2016b) First non-native establishment of the carnivorous assassin snail *Anentome helena* (von dem Busch in Philippi 1847). *BioInvasions Records* 5: 143–148. <https://doi.org/10.3391/bir.2016.5.3.04>

- Ng TH, Liew JH, Song JZE, Yeo DCJ (2016a) First record of the cryptic invader *Pyrgophorus platyrachis* Thompson 1968 (Gastropoda: Truncatelloidea: Cochliopidae) outside the Americas *BioInvasions Records* 5: 75–80. <https://doi.org/10.3391/bir.2016.5.2.03>
- Ng TH, Tan SK, Yeo DCJ (2015) Clarifying the identity of the long-established globally-invasive *Physa acuta* Draparnaud 1805 (Gastropoda: Physidae) in Singapore. *BioInvasions Records* 4: 189–194. <https://doi.org/10.3391/bir.2015.4.3.06>
- Ng TH, Yeo DCJ (2012) Non-indigenous frogs in Singapore. *Nature in Singapore* 5: 95–102.
- Ng PKL, Corlett RT, Tan HTW (2011) Singapore Biodiversity: An Encyclopedia of the Natural Environment and Sustainable Development. Editions Didier Millet, 552 pp.
- Nghiem LT, Soliman T, Yeo DC, Tan HT, Evans TA, Mumford JD, Carrasco LR (2013) Economic and environmental impacts of harmful non-indigenous species in Southeast Asia. *PLoS ONE* 8(8): e71255. <https://doi.org/10.1371/journal.pone.0071255>
- 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: 305–319. <https://doi.org/10.1007/s10530-010-9807-7>
- Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States, *BioScience* 50: 53–66. [https://doi.org/10.1641/0006-3568\(2000\)050\[0053:EAECON\]2.3.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0053:EAECON]2.3.CO;2)
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52(3) 273–288. <https://doi.org/10.1016/j.ecolecon.2004.10.002>
- 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. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) *The economic costs of biological invasions around the world*. *NeoBiota* 67: 191–224. <https://doi.org/10.3897/neobiota.67.59134>
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Bacher S (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications* 8: e14435. <https://doi.org/10.1038/ncomms14435>
- Seebens H, Gastner MT, Blasius B (2013) The risk of marine bioinvasion caused by global shipping. *Ecology Letters* 16: 782–790. <https://doi.org/10.1111/ele.12111>
- Scalera R (2010) How much is Europe spending on invasive alien species? *Biological Invasions* 12: 173–177. <https://doi.org/10.1007/s10530-009-9440-5>
- Shackleton RT, Shackleton CM, Kull CA (2019) The role of invasive alien species in shaping local livelihoods and human well-being: A review. *Journal of Environmental Management* 229: 145–157. <https://doi.org/10.1016/j.jenvman.2018.05.007>
- Shwiff SA, Gebhardt K, Kirkpatrick KN, Shwiff SS (2010) Potential economic damage from introduction of brown tree snakes *Boiga irregularis* (Reptilia: Colubridae) to the Islands of Hawai'i. *Pacific Science* 64: 1–10. <https://doi.org/10.2984/64.1.001>
- Stigall AL (2010) Invasive species and biodiversity crises: testing the link in the Late Devonian. *PLoS ONE* 5: e15584. <https://doi.org/10.1371/journal.pone.0015584>
- Su S, Cassey P, Blackburn TM (2016) The wildlife pet trade as a driver of introduction and establishment in alien birds in Taiwan. *Biological Invasions* 18: 215–229. <https://doi.org/10.1007/s10530-015-1003-3>

- Tan HTW, Chou LM, Yeo DCJ, Ng PKL (2010) *The Natural Heritage of Singapore* (3<sup>rd</sup> Edn.). Pearson Prentice Hall, 323 pp.
- Wee YC, Corlett RT (1986) *The City and the Forest: Plant Life in Urban Singapore*. Singapore University Press, Singapore.
- Wong D (2018) Singapore retains spot as 5<sup>th</sup> most visited city in the world. *The Straits Times*. <https://www.straitstimes.com/singapore/spore-retains-spot-as-5th-most-visited-city-in-the-world> [27 Sep 2018]
- World Bank World Development Indicators (2019) Population density (people per sq km of land area). [Retrieved from on 10 Dec 2019.]
- Xu H, Ding H, Li M, Qiang S, Guo J, Han Z, Wan F (2006) The distribution and economic losses of alien species invasion to China. *Biological Invasions* 8: 1495–1500. <https://doi.org/10.1007/s10530-005-5841-2>
- Yeo DCJ, Chia CSW (2010) Introduced species in Singapore: an overview. *Cosmos [Journal of the Singapore National Academy of Science]* 6(1): 23–37. <https://doi.org/10.1142/S0219607710000486>

## Supplementary material 1

### **Description of the procedure used for collecting and describing cost data in the InvaCost database (adapted from Diagne et al. 2020)**

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Data type: database description

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Link: <https://doi.org/10.3897/neobiota.67.64560.suppl1>

## Supplementary material 2

### **Database subset**

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Data type: database

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### Supplementary material 3

#### **Annual average costs of biological invasions in Singapore. Note the y-axis is on a $\log_{10}$ scale**

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Data type: database

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Link: <https://doi.org/10.3897/neobiota.67.64560.suppl3>

### Supplementary material 4

#### **Extrapolated annual average costs for those invasive species known to be in Singapore with recorded costs in InvaCost**

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Data type: database

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### Supplementary material 5

#### **Relationships between trade value and recorded cost entries per country in InvaCost, as well as land area and human population with total cost**

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