Economic costs of invasive alien ants worldwide

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Abstract

Invasive ants are amongst the most destructive and widespread invaders across the globe; they can strongly alter invaded ecosystems and are responsible for the displacement of numerous native ant species. Several studies have reported that invasive ants can lead to substantial economic costs. In this study, we search, describe and analyze 1,621 reported costs of invasive ants using the InvaCost database. Economic costs, reported since 1930 for 12 ant species in 27 countries, totaled US$ 56.92 billion. The largest costs were associated with two species, *Solenopsis invicta* and *Wasmannia auropunctata* (US$ 36.91 and 19.91 billion respectively); and two countries, USA and Australia (US$ 28.62 and 27.94 billion respectively). Potential costs (i.e., expected or predicted costs) constituted the vast majority of the reported costs (80.4%). Overall, damage costs amounted to 96.3% of the total cost, impacting mostly the agriculture, public and social welfare sectors, whereas management costs primarily resulted from post-invasion management (US$ 1.78 billion), with much lower amounts dedicated to prevention (US$ 235.62 million). Beside the taxonomic bias, cost information lacked for ~ 77% of the invaded countries per species, and the geographic coverage of costs was only ~ 18% within invaded countries with costs reported. Our synthesis suggests that the global costs of invasive ants are massive but largely underreported, and thus most likely grossly underestimated. We advocate for more and improved cost reporting of invasive ants through better collaborations between managers, practitioners and researchers, a crucial basis for adequately informing future budgets and improving proactive management actions of invasive ants.

Abstract In Spanish -resumen En Español

Las hormigas invasoras están entre las especies más destructivas y más ampliamente extendidas en todo el mundo. Pueden alterar fuertemente los ecosistemas y son responsables de la pérdida de numerosas especies de hormigas nativas en los ecosistemas invadidos. Muchos estudios han mostrado que las hormigas invasoras pueden producir costos económicos importantes. En este estudio, recopilamos, describimos y analizamos 1621 entradas de costos económicos de hormigas invasoras, usando la base de datos InvaCost. Los costes económicos fueron reportados desde 1930, para 12 hormigas invasoras, en 27 países, alcanzando un total de 56.92 mil millones de dólares americanos. Los costes más importantes estaban asociados con dos especies, *Solenopsis invicta* y *Wasmannia auropunctata* (36.91 y $19.91 mil millones respectivamente); y con dos países, Estados Unidos y Australia (28.62 y 27.94 mil millones respectivamente). Los costos potenciales (aquellos esperados o previstos) constituyeron la gran mayoría de los costes reportados (80.4%). Los costes debidos a daños alcanzaron el 96.3% del total, e impactaron sobre todo los sectores de agricultura, y bienestar público y social; mientras que los costes de gestión se invirtieron en su mayoría en la gestión post-invasión (1.78 mil millones de dólares), con mucha menor inversión en prevención (235.62 millones de dólares). Además del sesgo taxonómico, aproximadamente un 77% de los países invadidos por las especies carecieron de reportes de costos económicos, mientras que en los países invadidos con costos reportados, la cobertura geográfica de los costos fue de tan sólo un 18%. Nuestra síntesis sugiere que los

costes globales de las hormigas invasoras son masivos sin embargo muy poco reportados, y por lo tanto gravemente subestimados. Exhortamos entonces, a un mayor y mejor reporte de los costes económicos de las hormigas invasoras a través de una mayor colaboración entre gestores, profesionales e investigadores; lo cual es la base crucial para informar adecuadamente presupuestos futuros así como para mejorar las actuaciones hacia una gestión proactiva de las hormigas invasoras.

Introduction

Social insects, and more particularly ants, are amongst the most impactful invasive alien species (Moller 1996; Holway et al. 2002), with certain characteristics that make them particularly strong invaders, e.g., their super-colonial structure, high reproducibility, and strong ability to monopolize environmental resources to outcompete native species (Passera 1994; Holway et al. 2002; Bertelsmeier et al. 2017; Arnan et al. 2018). The small size of ants, their generalist nesting habits and frequent association with environmental/habitat disturbance (Fournier et al. 2019) favour their easy transport by humans, in addition to facilitating their establishment and subsequent spread (Bertelsmeier et al. 2018). Consequently, over 200 ant species have now established populations outside their native range (Lach et al. 2010; Bertelsmeier et al. 2018). Nineteen of them are recorded in the IUCN list of invasive species (http://www.iucngisd.org/gisd/), with five (the Argentine ant, *Linepithema humile*, the red imported fire ant, *Solenopsis invicta*, the big-headed ant, *Pheidole megacephala*, the little fire ant, *Wasmannia auropunctata*, and the yellow crazy ant, *Anoplolepis gracilipes*) being listed among the “100 of the world’s worst invasive alien species” (Lowe et al. 2000), making this Family unique on that front. In addition, about 20 more species have been proposed as potentially invasive or super-invasive using a trait-based approach (Bertelsmeier et al. 2013; Fournier et al. 2019). It is therefore not surprising that the number of ant species reported as invasive, or exhibiting significant extension in their invaded range, is steadily increasing (e.g., Bertelsmeier et al. 2016; Chifflet et al. 2018, Cordonnier et al. 2020), even more with the ever-increasing increasing globalization and international trade (Bertelsmeier 2021; Seebens et al. 2021).

The consequences of ant invasions are numerous, and they often widely impact native biodiversity and alter local environments (Holway et al. 2002; Lach et al. 2010). Their negative impacts include the displacement of the native ant communities, which scale up to higher trophic levels and affect native vertebrates such as birds, reptiles and amphibians (Allen et al. 2004; Guénard and Dunn 2010; Lach and Hooper-Bui 2010; Alvarez-Blanco et al. 2020, 2021; Bousseyroux et al 2019). Ant invasions also alter ecosystem functions by modifying trophic web dynamics, altering nutrient cycling, or decreasing pollination (e.g., Hansen and Muller 2009; Angulo et al. 2011). Invasive ants also substantially affect human assets (Lard et al. 2002; Motoki et al. 2013) much like invasive insects in general (Bradshaw et al. 2016). Impacts include decreasing agricultural production, infrastructure damage, and affecting human health (Lard et al 2002; Nelder et al. 2006). As a result, economic costs of invasive ant species, including losses and management expenses, are frequently presented as reaching billions of dollars annually. For instance, the estimated total annual cost for the red imported fire ant *S. invicta* initially estimated at US$1 billion annually in the US (Pimentel et al. 2005), amounted to more than US$6 billion annually in

New Zealand (Gutrich et al. 2007), and AU$1.65 billion annually in Australia (Wylie and Janssen-May 2017).

However, economic costs associated with ant invasions have remained poorly reported across multiple-species in the literature, with most relying on red imported fire ants because of their high impacts on health and agriculture, together with the fact that they are among the best scientifically known invasive ants (Sanders and Suarez 2011). Yet, other invasive ant species can also quickly build large populations and become a nuisance, as in the case of the yellow crazy ant or the Argentine ant (Holway et al. 2002), for which reports on economic costs have been restricted primarily to the evaluation of control costs (Hoffmann et al. 2016). Similarly, the little fire ant (*W. auropunctata*) has a painful sting and tends sap-sucking insects, leading to plantations being completely abandoned (Vanderwoude et al. 2015); however, studies evaluating its economic costs are scarce. Also, the African big-headed ant (*P. megacephala*) and the Singapore ant (*Trichomyrmex destructor*) incur substantial economic losses, particularly due to damages to electrical equipment, i.e, they chew through wires which sometimes cause fires (Wetterer 2012), but the quantification of the monetary losses resulting from these damages are rarely published. Moreover, information of the economic costs of other invasive ants is even more fragmented across the literature.

To exacerbate the issue of underreported costs, a large part of published costs have not been directly observed. For example, earlier estimations of costs of red imported fire ant across a variety of economic sectors in Texas (Lard et al. 2002) have been extrapolated both temporally and spatially across the world, where this invasive ant has expanded far beyond its native range (e.g., Lard et al. 2006; Gutrich et al. 2007; Wylie and Janssen-May 2017; Gruber et al. 2021). More accurate cost reporting through direct estimations can lead invasive ants to gain visibility, and in turn, ensure that managers, stakeholders and practitioners address the serious concerns they represent more effectively - in particular, the ongoing threat to biodiversity (Diagne et al. 2020).

The newly developed InvaCost database (Diagne et al. 2020) is the first comprehensive and standardized compilation of the economic costs associated with biological invasions worldwide. This database provides unique opportunities to thoroughly assess and understand the economic impacts of invasions. Here, we used and enriched this database with additional data to present a detailed and up-to-date, global assessment of the economic costs of invasive ants. Our analyses aimed to: (i) describe the ant species associated with the reported economic costs; (ii) describe the spatial and temporal distribution of reported costs; (iii) highlight the type of costs reported; (iv) decipher the economic sectors impacted by these costs; and (v) identify the potential geographic gaps in the cost reporting.

Methods

Data collection

We used the latest version of the InvaCost database (InvaCost_3.0; 9,823 entries; Diagne et al. 2020, https://doi.org/10.6084/m9.figshare.12668570), consisting of cost data extracted from documents obtained through standardized literature searches (i.e., using ISI Web of Science platform, Google Scholar and the Google search engine) and opportunistic targeted searches (i.e., expert consultations for which data gaps were identified, such as in 10 languages other than English, Angulo et al. 2021). Costs extracted from these sources were converted from local currencies to US$ by correcting the value with the official market exchange rate corresponding to the year of the value and then adjusting to 2017 US$ using inflation factors (Diagne et al. 2020). We extracted data for invasive ant species (selecting for the family Formicidae). Each database entry contains a cost value associated with a unique combination of cost descriptors (see "Data structure" section).

We complemented the InvaCost data by adding costs found from four different targeted searches: (i) in non-English languages, specifically focusing on the economic costs of the 19 invasive ants recognized by the IUCN (http://www.issg.org/database); using the same search strings as those considered in the standardized searches led in the Web of Science platform by Diagne et al. (2020), but with economic terms translated in different languages (Arabic, Chinese, French, German, Greek, Italian, Japanese, Portuguese, Russian, Spanish, and Ukrainian) alongside the scientific names of the 19 ant species; (ii) in the digital database SciELO (Scientific Electronic Library Online) (https://www.scielo.br), which provides access to scientific literature mainly originating from the South American continent, with journal articles usually published in Spanish and Portuguese; (iii) in the bibliographic database FORMIS (http://www.ars.usda.gov/saa/cmave/ifahi/formis), a composition of several ant literature databases, that contains citations for a large proportion of the world's ant literature. More specifically, using EndNote X9, we searched all fields in the database version FORMIS 2018 for each invasive ant species, with the following search items "econom*", "monetary", "dollar", "$", "€", "sterling pound"; (iv) contacting key people (mainly managers and researchers) in relation with invasive ant management programs that we knew of but financial data was either not available or was incomplete. The results of this search, together with the original InvaCost entries, resulted in a total of 643 entries ranging from 1930 to 2084 inclusive of future predictions (herein *raw data*, Online Resource 1 Tab "Raw_data").

Data structure

The *Raw data* contained over 60 descriptive cost variables divided into the following groups (Online Resource 1, tab "Descriptors"): (i) the bibliographic information of the documents where the costs were reported, (ii) the area impacted or where the costs were incurred (e.g., spatial scale, location), (iii) the taxonomy of the focal species, (iv) the temporal extent over which the costs either occurred or were predicted to occur, (v) the typology of each cost reported, and (vi) the economic cost values. To describe the economic costs of invasive ants we used information mainly from the following four cost descriptors: the type of costs, the type of management, the economic sector impacted by invasive ants, and the nature of the implementation of the cost value.

The type of costs (column *type_of_cost_merged*) assigned costs to either "damage" costs (most often corresponding to marketed costs, e.g., the economic losses due to direct and/or indirect impacts of invaders, such as yield loss, medical care, infrastructure damage, or income reduction) or “management” costs (economic resources allocated to actions to avoid the invasion, or to deal with established populations). A third category “diverse/unspecified” grouped costs included in the previous categories or were not specified.

Because we were interested in the types of management actions, we split the “management” category of the previous column using the type of management (column *Management_type*), which categorizes management as: (i) “pre-invasion management”: monetary investments for preventing successful invasions in an area (e.g., early detection); (ii) “post-invasion management”: money spent for managing invasive ants in invaded areas (e.g., control, eradication, monitoring); (iii) “knowledge/funding”: money allocated to all actions and operations that could be of interest at all steps of management at pre- and post-invasion stages (e.g., research, information, education). A “diverse/unspecified” category was assigned when costs included at least two of the above categories (within management), when costs included simultaneously damage and management expenditures or when management costs were unspecified.

The impacted economic sectors (column *economic sector*) were: “agriculture” (e.g., yield losses); “authorities-stakeholders” (governmental services and/or official organizations – such as conservation agencies, forest services that allocate efforts for the management of biological invasions); “health” (costs directly or indirectly related to human medical conditions); and “public and social welfare” (activities, goods or services contributing to human well-being, including local infrastructures such as electrical systems, quality of life such as recreational activities, personal goods such as private properties, public services or market activities). A “diverse/unspecified” category was assigned when costs included at least two categories or were unspecified.

Finally, we also considered the implementation of the costs (column *implementation*) to be important when describing the economic costs of invasive ants (Diagne et al. 2020). This column classifies the cost entries as “observed” if the cost was actually incurred, or “potential” if the cost was expected or predicted to occur beyond the original spatial and/or temporal observation range. While this variable indicates whether the cost was realized or not, the “potential” costs include *per se* different aspects: the temporality of the cost (past/current costs versus predicted or planned costs) and the spatial distribution in relation with the distribution of the invasive species (if the ant is already invading or could invade). However, making clear distinctions within these “potential” costs is beyond the scope of our study.

Data processing

Prior to the analysis, the *raw data* were screened to detect duplicates and overlaps, as a means to avoid overestimating the economic costs of invasive ants. Potential duplicates and overlaps were analysed, and assessed whether to retain or remove some cost entries (see columns “removeForAntProject” and “Comments” in Online Resource 1, where decisions regarding the removal of data are explained). This process accounted for the column *reliability* which evaluates whether the estimation method of the cost was documented, repeatable and/or traceable. As a result, 6 raw costs of “low” reliability were retained as they completed the temporal or spatial patterns (See Online Resource 1) but a total of 41 raw cost entries were removed from the analyses.

Description of the economic costs of invasive ants

To compare the number of cost entries for each invasive ant species among descriptors, we homogenized all costs recorded on an annual basis using the *expandYearlyCosts* function of the 'invacost' package version 0.3-4 (Leroy et al. 2020) in R version 3.6.3 (R Core Team 2020). This function relies on the duration time of each cost entry provided as the number of years between the cost entry's starting and ending years given in the database. Hence, we obtained comparable annual costs for all cost entries. The *expanded dataset* resulted in 1,621 entries, from which 329 were not considered for reasons explained in the *data processing* section (also see, Online Resource 1, Tab "Expanded_data"). Thus, for our analyses, we considered a total of 1,292 expanded cost entries.

We also calculated the temporal trends of the economic impacts of invasive ant species using the function *calculateRawAvgCosts* from the *invacost package* version 0.3-4 (Leroy et al. 2020) in R version 3.6.3 (R Core Team 2020). This function calculates average annual costs for the whole study period, providing 10-year average costs based on the annualized cost entries calculated.

Other descriptions of the economic costs of invasive ants were formed by using the categorical descriptors in the InvaCost database (see section on *Data structure*), for instance taking into account the nature of the costs (observed vs potential costs) we describe: (i) the magnitude of costs for each invasive ant and the trend of observed costs entries per invasive ant along time; (ii) the geographic distribution of costs by country, splitting the cost in each country by each invasive ant species; (iii) the percentage of each type of cost (damage and the types of management) and we further split the type of cost with the sectors impacted; (iv) and finally, the percentage of each type of management costs (i.e., excluding damages) for each ant species.

Geographic coverage of the economic costs reported for invasive ants

We mapped and compared the geographic locations of the costs reported in the raw database (excluding cost entries marked as "remove") with the invasive range of the ant species with reported costs. In order to obtain geographic coordinates of the costs, we used the column "Location" in the dataset, and the original documents were cross-checked to confirm location; in some cases, more than one location was reported for the same cost entry. Thus, the number of recorded geographic coordinates of the costs reported summed more than the number of cost entries. We then obtained occurrence records of the current invasive distribution of each ant species from both the GBIF (Global Biodiversity Information Facility, https://www.gbif.org), and AntWeb (www.antweb.org). Countries were assigned to geographic coordinates once we removed duplicates and records for which coordinates either fell out of the terrestrial borders or had a 0 (zero) as geographic coordinates.

For each species and invaded country, we calculated the percentage of the number of locations with reported costs in relation to the number of locations found for the species (ant occurrences). Then, we calculated the average percentage of locations with costs per species, referred to as the *geographic coverage* of reported costs per invasive ant species. Locations with various costs were considered only once, and costs at the country level were not considered (in fact, only *S. invicta* in Australia, China, Japan and USA, and *L. humile* in Japan had costs at the country level). Also, ant occurrences in countries within their native range were not considered.

Results

The recorded cost of invasive ant species amounted to US$ 56.92 billion in total with losses amounting to US$ 11.13 billion since 1930 (reported in 697 expanded observed entries) and an additional US$ 45.79 billion until 2084 (reported in 595 expanded potential entries). From the 1,292 cost entries considered, 14% originated from documents written in non-English languages (Japanese, French, Dutch, Chinese, Spanish and Portuguese, listed here by descending number of cost entries); while > 15% were obtained from managers or researchers. By analysing the temporal distribution of annual costs, the mean observed cost of invasive ants between 1930 and 2020 were US$ 120.97 million, while the mean potential costs between 1980 and 2084 were US$ 444.58 million. Most of these costs were documented between 2010 and 2019 (Online Resource 2).

The largest number of cost entries and highest economic costs were reported for *Solenopsis* spp. (721 expanded cost entries, US$ 36.91 billion, Fig. 1a,b), followed by *W. auropunctata* (273 expanded cost entries, US$ 19.91 billion). Although costs were reported for three species of *Solenopsis*, *S. invicta* constituted the most cost entries and economic costs; *S. geminata* was only reported in 8 expanded cost entries for Galápagos Islands (Ecuador) and Ashmore reef (Australia), and the costs for *S. richteri* were reported in the USA but always together with *S. invicta*. *Solenopsis* spp. was the main driver behind the temporal dynamics of the trends in observed costs, in contrast to the rest of the invasive ant species (Fig. 1b). Also, the number of observed cost entries (of *Solenopsis* spp. and to a lesser extent, other ant species) increased with time, suggesting that cost reporting is expected to continue to increase in the near future.

Both *Solenopsis* spp. and *W. auropunctata* had higher ‘potential’ than ‘observed’ costs reported (33.22 *versus* 3.69 and 12.56 *versus* 7.35, respectively, in US$ billion), and this was also the case for *A. octospinosus* (Fig. 1a). The potential costs for *S. invicta* were mainly related to the expected (planned) costs of the eradication program in Australia (Queensland), as well as with the spatial extrapolations of costs to different locations, e.g., some states in the USA or the Pacific Islands. Most of the potential costs for *W. auropunctata* were extrapolations for Hawaii and the Vanuatu Islands; whereas most of the costs for *A. octospinosus* were the planned costs of this species’ future eradication program in Guadeloupe (Carribean oversea territory of France). For other species such as *A. gracilipes* and *L. frauenfeldi*, potential costs were also reported for the ongoing eradication programs in Australia (Queensland and Darwin, respectively). For the remainder of the invasive ants only observed costs were reported.

Most of the economic costs were reported from the USA (403 expanded cost entries, US$ 28.62 billion) and Australia (573 expanded cost entries, US$ 27.94 billion) (Fig. 2). *S. invicta* was associated with the greatest costs incurred, followed by *W. auropunctata*, wherever these species occurred in a country, however, in the case of Australia, *A. gracilipes* ranked as the second costliest. In most of the Pacific islands, *S. invicta* was the only species with reported costs, which were all classified as potential costs since this ant is currently not present there (Fig. 2, Online Resource 3). In countries such as Seychelles, Portugal, Netherlands and Spain, where the lowest costs were documented, all of the monetary losses corresponded to observed costs. No costs were reported from many other regions of the world, such as Africa and almost all of South America (with the exception of the Galápagos Islands in Ecuador).

Most of the economic costs of invasive ants (96.26%) were categorized as damage costs, of which US$ 45.53 billion were potential damages and US$ 9.26 billion were already incurred (Fig. 3a). Management costs amounted to 3.74% of the total costs, with most of the observed management costs (83.63%) assigned to post-invasion management, such as control and eradication (US$ US$ 1.71 billion). In contrast, much lower costs were spent on pre-invasion management actions, such as prevention or early detection (US$ 88.54 million), and for research activities (US$ 28.84 million). When focusing on potential costs, future spending on pre-invasion management actions is expected to be higher than the amount spent on post-invasion actions (US$ 147.08 million vs 70.42 million).

Most of the total observed costs (63.40%) were unassigned to specific economic sectors or affected multiple sectors simultaneously (“diverse/unspecified”) (Fig. 3b). “Agriculture” was thus the specific sector with the greatest observed costs (25.57%). In the case of potential costs more than half impacted “public and social welfare” (52.57%). This general pattern in total costs was strongly driven by damage costs. In relation to (the much smaller) management costs, the greatest impacted sector was “authorities and stakeholders” for both potential and observed costs and for all types of management (pre-invasion and post-invasion management, “knowledge/funding” and “diverse/unspecified”). Post-invasion costs reported a small percentage of potential costs affecting primary sectors such as agriculture (3%) and forestry (0.4%, Fig. 3b).

On considering only management costs, “pre-invasion management” costs constituted a significant part of the total costs only for *Solenopsis* spp., with potential costs forming a higher percentage than observed costs (Fig. 4). These costs were included in a ten year eradication plan in Queensland, Australia, and constituted 59.25% of the total potential costs for this species (this plan also included post-invasion management actions, and “knowledge and funding” actions). For *W. auropunctata* and *A. octospinosus* the cost category “knowledge and funding” was considerable in observed costs (Fig. 4); it constituted 43.19% of observed costs in *Wasmannia* spent in general research, and 31.50% of *Acromyrmex* observed costs spent in research for the optimization of the control strategies in Guadaloupe island). The observed pre-invasion management costs for multiple invasive ants ("Diverse/Unspecified" category) was for biosecurity and the development of educational programs with focus on invasive ants in New Caledonia (France) (Fig. 4).

Taxonomic and geographic coverage in the economic costs of invasive ant species

Although our dataset contained costs for 12 of the 19 invasive ants reported by the IUCN (and none for the other species reported as invasive by other studies), most (99.83%) of the reported costs were only for two species, *S. invicta* and *W. auropunctata*. Yet, even for these two species, many costs are likely missing. For the other 10 species, lower costs were reported. Notably, an analysis at the species-level found that only 19.76% of the locations per country where *S. invicta* occurs (using occurrences in GBIF and AntWeb) have reported costs (Table 1). This outcome was predominantly driven by the USA, where there were a high number of ant occurrences but few reports. Geographic coverage of cost reporting in some other countries was significantly higher, such as in Australia (52.65%, Fig. 5a). It is worth noting that from 18 out of the 20 countries which reported costs on *S. invicta* did not have this species present, since costs were potential there, while other countries reporting observed costs such as New Zealand or Japan had no ant occurrences in the global databases (Table 1; Fig. 5a; Online Resource 4). Similar geographic coverage per country was found for *L. humile* (15.94%) and *P. megacephala* (13.63%), although for *L. humile* costs were reported in 6 out of the 28 invaded countries, they were significantly varied with high reporting in Japan (90.00%) and very low reporting in other countries such as Spain (0.98%), Portugal (0.83%), Australia (0.63%) and the USA (0.13%, Fig. 5c). For *P. megacephala*, costs were reported in only 3 out of the 54 invaded countries and with less variability in the geographic coverage at the country-level (Table 1). For *W. auropunctata* the mean geographic coverage per country was 4.84%, and on comparing to specific countries, it was higher in Australia (12.50%), but lower in Ecuador (3.85%), France (2.03%) and the USA (0.98%, which had the highest number of occurrences for this species) (Fig. 5b). For other species, geographic coverage was higher, although the number of countries with reported costs were low, resulting in a mean geographic coverage of reported costs per country for all invasive ants of 17.65% and a mean percentage of invaded countries without costs of 76.67% (Table 1, Online Resource 5).

Table 1

Geographic coverage of reported costs with respect to ant occurrences. For the countries with reported costs, we compute the geographic coverage (no. of ant occurrences/no. of costs per country, %) and also provide the number of countries with costs (n). The number of invaded countries without costs and corresponding percentage (in parenthesis) is also given. Only ant species present in more than one country were included (See Online Resource 4 for the other species).

	Countries with costs		**Countries**
Species	**geo. coverage**	**n**	**without costs**
Anoplolepis gracilipes	3.15	3	17 (85.00)
Lasius neglectus	30.56	2	12 (85.71)
Lepisiota frauenfeldi	50.00	2	2 (66.67)
Linepithema humile	15.94	6	28 (82.35)
Pheidole megacephala	13.63	3	54 (94.74)
Solenopsis geminata	43.33	2	26 (92.85)
Solenopsis invicta	19.76	20	13 (76.47)
Wasmannia auropunctata	4.84	5	23 (85.18)
Mean	**17.65**		(76.67%)

Discussion

General costs of invasive ant species

Our findings have documented actual costs attributed to ant invasions of at least US$ 11.13 billion between 1930 and 2020 with additional potential costs (expected and/or predicted) of US$ 45.79 billion from 1980 until 2084. Most reported costs were associated with two invasive ant species, *S. invicta*, the red imported fire ant, and *W. auropunctata*, the little fire ant, which mainly occurred in two countries, USA and Australia. Most of the reported costs were associated with damages, in particular, impacting the agriculture and public and social welfare sectors. Management costs constituted only 3.74% of the total amount, the majority of which was spent in post-invasion actions, such as control or eradication. Also, costs were geographically biased: on average 76.67% of invaded countries per species lacked cost reports, and within invaded countries the mean geographic coverage of reported costs per species and country was only 17.65%.

With respect to previous estimates describing invasive ants as causing losses and expenditures reaching > US$ 1 billion annually in specific countries (Pimentel et al. 2005; Gutrich et al. 2007, Wylie and Janssen-

May 2017), our more conservative estimates show that we lose and/or spend annually US$ 121 million due to invasive ant species all around the world. This estimate could increase by US$ 444 million annually when including potential costs (i.e., costs planned, expected or predicted to occur). Note that our annual estimations are on a global scale for all invasive ant species and over the whole time range of available costs (see Online Resource 1). Cost extrapolations to the USA from Pimentel et al. (2005) were examined and not considered as they overlapped with the estimates provided by Lard et al. (2006). More specifically, both articles used data from Texas (Lard et al. 2002) to extrapolate to other US states, and we considered only Lard et al. (2006) which documented the estimation method used and detailed costs for each activity sector.

Information on the economic costs incurred by invasive ants is critically needed as it aids cost-benefit analysis to determine timely management actions. Here, we have shown that incurred costs constituted less than 20% of the total costs reported for invasive ants across the world. Nevertheless, better information on these observed costs can help to further develop predictive models of the monetary impacts of invasive species under different scenarios, thus providing data-oriented suggestions for improved management. In fact, most of the potential costs reported here for invasive ants were extrapolations based on observed data, across both time and space. For example, extrapolations to predict future costs under different management scenarios for *Solenopsis* in Queensland (Australia, Hafi et al. 2014), or for *Wasmannia* in Hawaii (USA, Motoki et al. 2013), or extrapolations to predict costs (past, present or future costs) in other areas where the same ant species invades, such as using the costs caused by *Solenopsis* in Texas to predict costs in other invaded states in the USA (Lard et al. 2006; Gutrich et al. 2007) or in Australia (Wylie and Janssen-May 2017). Also, all the reported costs for *Solenopsis* in the Pacific islands were extrapolated - such areas are expected to be invaded in the near future due to their trade history with other areas where ant invasions are prevalent, such as Australia or China (Gruber et al. 2021). While extrapolation is deemed to be useful, they are by nature highly uncertain; thus, our study highlights the urgent need to provide actual observed costs through accurate monitoring and reporting. Moreover, improved cost reporting by managers, practitioners and researchers can be used to raise awareness on the impacts of ant invasions and in turn, better inform policy makers and enhance public education.

Economic activity sectors impacted by invasive ants

The activity sectors incurring the most damages from invasive ants were mainly agriculture, and public and social welfare. Unfortunately, a large part of the documented costs was not detailed to specific economic sectors in the source information, and thus a high proportion of costs had to be classified as diverse or unspecified. Total costs for agriculture amounted US$ 3.61 million for *A. octospinosus* in the French Caribbeans, where this ant is known to be a serious pest (Mikheyev 2008; Celini et al. 2012). Reported economic losses in agriculture have also been reported for *W. auropunctata* in Hawaii (USA) where the nursery floristic exporting sector is expected to be mostly affected (Motoki et al. 2013; Vanderwoude et al. 2015). The most detailed costs in the agriculture sector were reported for *S. invicta* where both damage loss and damage repair as well as control actions have been quantified, affecting different crops, livestock, farm equipment, or the health of farmers or their animals (Lard et al. 2002; Lard et al 2006; Gruber et al. 2021). Agricultural impacts of invasive ants could mainly be attributed to the mutualistic relationship of ants with sap-sucking insects, such as aphids and mealybugs, which directly damage the plants and spread plant diseases (Eubanks 2001). Although some benefits to crops from invasive ants have also been reported, for example *S. invicta* feeding on other pests, such as insects that feed on corn, cotton or sugarcane crops, when all crop types and interactions are considered together, the overall influence of invasive ants in the agricultural sector is overwhelmingly negative (Lard et al 2002; Lard et al. 2006). Also, invasive ants can negatively impact livestock production by making it difficult for animals such as chickens to eat or sleep, and may also kill and eat newly hatched chicks (Wylie and Janssen-May 2017).

Invasive ants widely affect human infrastructure in different ways and to varying degrees, e.g. destroy electrical equipment, cause damages to property (e.g., cars, TV, telecommunication), resulting in high economic losses (Bradshaw et al. 2016). Costs specifically linked to impacts on human health are also frequently reported in the literature, in particular for those invasive ants that bite humans if disturbed, and whose sting can induce anaphylactic or allergic reactions (Boase 2007). For instance, more than 14 million people are stung annually in the US alone (Taber 2000), and of these more than 200,000 people require medical treatment (Holway et al. 2002). In our data, only *S. invicta* was reported as having quantified economic impacts specifically in the health sector in the USA (Lard et al. 2002), while potential medical costs were estimated for the Pacific islands, where outdoor activities are frequent, given that ant invasions could occur in such countries in the near future (e.g. Gruber et al. 2021). However, damage loss caused by *Wasmannia*, assigned to the public and social welfare sector, such as reduced property values or lodging in Hawaii (USA), are due to a reduction in recreational activities in outdoor areas, as this sector is prone to biting and stinging insects (Motoki et al. 2013; Lee et al. 2015). Ant species can also act as pathogen vectors, with some species carrying diseases that can be transmitted to humans, likely causing a wide range of serious infections (Moreira et al 2005). For instance, several ant species collected in Brazilian hospitals showed associated bacterial growth, e.g., the invasive species *Pheidole megacephala* (Fontana et al. 2010). Despite the above implications for health impacts, economic costs are scarcely available, demonstrating yet another important knowledge gap that needs urgent attention.

Economic damages and the costs of management

Although the economic costs of management were substantially lower in comparison with the cost of damages, the literature reports that the management of invasive ants itself is difficult, and can be very expensive (Hoffmann et al. 2010; 2016). However, early responses and other prevention measures implemented to avoid the expansion of early introductions can reduce post-invasion costs and damages, that are in many cases much higher (Leung et al. 2002, 2012; Essl et al. 2020; Diagne et al. 2021). With our data, we found that the already incurred costs of post-invasion management of invasive ants greatly exceed the costs spent for pre-invasion management measures. Clearly current ant invasions should be managed, and budgeting post-invasion management is necessary; however, budgets should also prioritize prevention, as preventing incursions or avoiding further expansion might be more cost effective than eradication attempts (Faulkner et al. 2020). Interestingly, when focusing on potential costs, expected or planned pre-invasion management actions were more expensive than post-invasion actions (US$ 147.08 million vs 70.42 million). Higher post-invasion costs stand for all the species, although it is notable that for *S. invicta* for which US$ 87.81 million are already spent in pre-invasion strategies (versus US$ 1.60 billion spent in post-invasion management), and it is planned to further invest US$ 147.08 million for pre-invasion measures (while only US$ 53.93 million for post-invasion actions) (Janssen 2017).

Many reports of invasive ant control focus on studies from the USA or Australia (Holway et al. 2002; Sanders and Suarez 2011; Hoffmann et al. 2016), which is in line with the fact that higher reported economic costs of invasive ants are found in these regions. Moreover, the spatial coverage of the reported costs of management measures is very similar to the spatial coverage of ant eradication programs reported by Hoffmann et al. (2016), indicating that at least the costs for eradication programs are well reported, although some species for which eradications were described in Hoffmann et al. (2016) had no reported costs (i.e. *Tapinoma melanocephalum*, *Monomorium indicum* or *Myrmecia brevinoda*). For example, in the USA, incurred costs especially concerned with the eradication program of *W. auropunctata* in Hawaii (US$ 10.63 million), and the control strategies in the continent for *S. invicta* (~ US$ 3 billion). Similarly, in Australia the eradication plan of *Solenopsis invicta* in Queensland constituted the majority of observed costs, together with the control and eradication programs of *A. gracilipes* in Queensland, Northern Territory and on Christmas Island (Hoffmann et al. 2016).

Interestingly, costs reported for *L. humile*, which is widely distributed worldwide and causes massive ecological impacts in urban, agricultural and natural environments (Holway et al. 2002; Sanders and Suarez 2011) were much lower than for *Solenopsis* spp., *W. auropunctata* and *A. gracilipes*. Additionally, all costs for this species were incurred and mostly (~ US$ 4 million) in post-invasion management actions, such as eradication programs on the Channel Islands (USA), Norfolk Island (Australia), Tirititi Matangi Island (New Zealand), and mainland Japan. Given the global notoriety of this invasive species it remains unclear why reports have not been produced that estimate its financial implications. Potentially it is because this species became widespread so long ago that focus has instead been given to the other newly arrived or 'horizon' species.

Notably, most of these eradication programs are ongoing, which is in agreement with the increasing trend in the number of reported cost entries for invasive ants worldwide (Fig. 1b) and with the high amount of potential - expected- costs described before. Accordingly, the cost of these programs may not be available as long as they are ongoing. Most of the costs mentioned were obtained directly from the managers of the eradication programs, proving the fundamental importance of the communication between scientists and practitioners and of combining data from different sources and languages (Angulo et al. 2021).

Gaps in the economic data for invasive ants: taxonomy, geography and research

We only have costs reported for the 12 ant species stated, yet most of the costs (76.93% of the cost entries and 99.83% of the economic amount) are for *S. invicta* and *W. auropunctata*, and costs for the rest of highly invasive ants are lacking. Lower or nonexistent costs for other invasive ant species could be due to them being less destructive, or to significant underreporting. Most certainly, a lot of economic costs are neglected, especially of those invasive ant species that are not yet referenced as invasive in the global lists of invasive species, such as *Tetramorium tsushimae* (Steiner et al. 2006), *Cardiocondyla obscurior* (Heinze et al. 2006), *Plagiolepis alluaudi* (Wetterer 2014), *Formica paralugubris* (Frizzi et al. 2018) among others. Although only 19 invasive ant species are referenced in the IUCN database, Lach et al. (2010) already considered that 147 ant species had successfully established populations outside their native range, and 186 species are registered as introduced in the Antweb "Introduced" project in 2020. Moreover, recent studies proposed more than 200 ant species that have established outside of their native range through human-mediated transport (Bertelsmeier et al. 2017), while around ~ 20 more ant species have been identified as potentially invasive based on their life history traits, i.e. at risk of becoming the next invaders such as *Lepisiota canescens* or *Technomyrmex difficilis* (Bertelsmeier et al. 2013; Fournier et al. 2019). The economic costs associated with these species have been, as a consequence, less studied, whereas they could constitute an economic black hole.

Some invasive alien species have even identifiable characteristics leading them to be more susceptible to induce economic costs. For instance, the invasive garden ant *L. neglectus*, which invaded all over Europe from Asia Minor (Espadaler et al. 2007), is an opportunistic species with intensive exploitation of aphids, that could cause massive damage to infested greenhouses (Rey and Espadaler 2005). *Lasius neglectus* ants also have continual presence within homes, inducing food contamination in the catering facilities, and is attracted to electrical installations, light switches, power sockets and electrical security systems, damaging them by its activity (Rey and Espadaler 2005). As a result, this pest species could have an economic impact comparable to the Argentine ant *L. humile*, although the costs reported were much lower given that its geographic expansion is only starting (Espadaler et al. 2007; Ugelvig et al. 2008).

With respect to the geographic coverage of the reported costs even for the most-studied invasive species, many costs are lacking. On average, 77% of the number of invaded countries per species had no reports of costs. Further, when costs were reported in a country, less than 18% of locations on average in those invaded countries had reported costs. In addition, we only mapped occurrence records that were readily available with geographic coordinates compiled for each ant species, which excluded many records that would have increased the gap if included. Beside these taxonomic and geographic gaps, many costs were also ignored in this paper because they were published collectively with other taxa and not only ants. For example, Hequet (2009) presented some costs specifically for *W. auropunctata* in New Caledonia, but other costs linked to population sensitization to invasive alien species or linked to control of *Wasmannia* were considered together with rodent and plant control in isolated islands.

There are certainly many other types of costs related to invasive alien ants that are not recorded in InvaCost, or under-recorded, and that likely contributes to a gross underestimation of their global economic costs. As an example, research grants for scientists studying invasive alien ants are typically not recorded as economic costs and therefore largely absent from the InvaCost database. When asking colleagues worldwide about their research grants on invasive alien ants throughout the last 30 years, we came up with 45 responses providing an estimated US$ 27,000 average per research article (Online Resource 6). If one considers about 4,742 research articles during this period on this topic (with the same keyword search in WoS as described in the Methods, except for the economic components), this suggests that this research grants component alone could be in the order of US$ 127 million (Online Resource 6). This crude estimation does not account for the true cost of a research project (typically a fraction of the money received by researchers), nor the researchers salary (often not included in grants), both of which could significantly increase this estimated amount. This information underlines the existence of substantial additional costs that are not taken into account in the global estimate we provide in this study, and should be considered as an invitation to make publicly available all possible monetary costs related to ant invasions.

The limited cost information that we are reporting also highlights the difficulty to value the impacts caused by invasive ants. Ants most likely hold multiple negative effects, and these impacts may differ from one species to another. Multiple assessment efforts are thus required for improving our understanding of the costs caused by these insects.

In conclusion, we present the most comprehensive assessment of the worldwide economic costs of invasive ants to date. Our description suggests that the global costs of invasive ants are massive, yet largely underreported, and as a result the actual costs are most likely grossly underestimated. We found economic costs documented mainly for two invasive ant species from mainly two countries, despite many other ant species being aggressive invaders worldwide. We also highlight the potential difficulty of obtaining a reliable assessment of the total economic costs incurred by invasive ants and advocate for improved cost reporting from managers, practitioners and researchers. Such efforts will help to understand ant invasions costs at the global scale and in turn, improve management performance and coordination amongst experts from different countries, which is urgently needed as impending ant invasions are expected to increase worldwide.

Declarations

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Conflict of interest

The authors declare that there is no conflict of interest.

Availability of data and material

All data generated and analysed during this study are included in this published article (available in the Online Resource 1).

Code availability

Not available

Author's contributions

EA, FC and CD conceived the idea. BH, PB, YW, DR, FC and EA, searched for data to populate InvaCost. EA carried out the analysis with the help of AT, FC, LBM and CD. EA and MC took lead in writing the original draft, with inputs from all the co-authors. All authors read and approved the final version of the manuscript.

Ethics approval

Not applicable

Consent to participate

Not applicable

Consent for publication

All authors have read and approved the submitted version of the manuscript.

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Figures

Fig. 1. (a) Total economic costs reported for invasive ants (US$, log scale). The total cost per species is expressed in billions (b), millions (m) or thousands (t) with the number of cost entries (given in parenthesis). **(b)** Cumulated number of cost entries. Note that, only species with a high cumulated number of cost entries are presented. A 1mm-scale bar has been added to show species difference in mean worker body size.

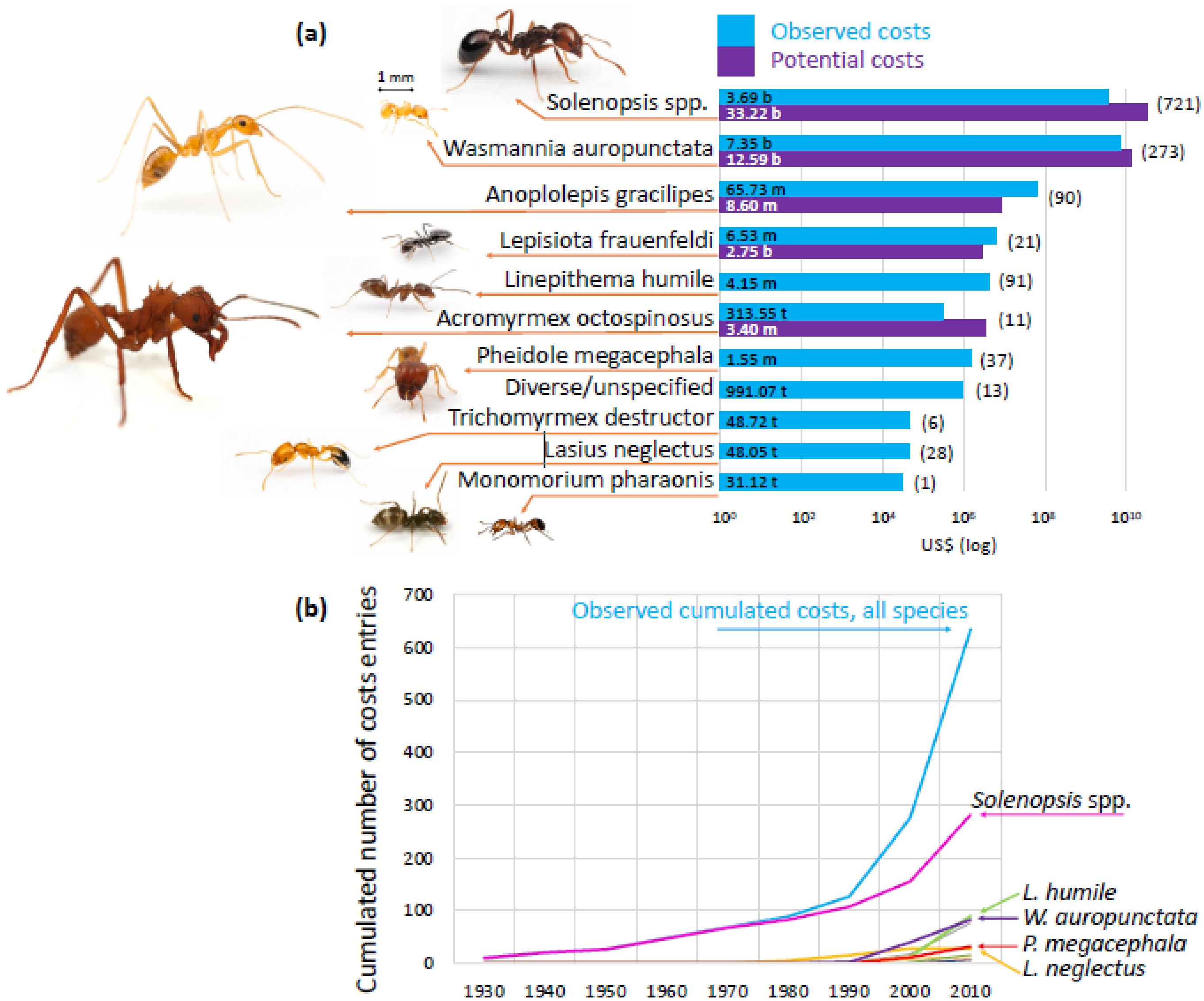

Figure 1

(a) Total economic costs reported for invasive ants (US$, log scale). The total cost per species is expressed in billions (b), millions (m) or thousands (t) with the number of cost entries (given in parenthesis). (b) Cumulated number of cost entries. Note that, only species with a high cumulated number of cost entries are presented. A 1mm-scale bar has been added to show species difference in mean worker body size.

Fig. 2. Global distribution of costs caused by invasive ant species. The brown colour categorical gradient on the countries reflects the countries with the highest (i.e. dark) to lowest (i.e. light) costs; in the absence of any cost reports the countries are coloured in grey. Bar graphs on the green scale represent the economic cost per ant species (log scale) in each country. For each country the total costs (b for billion, m for million, t for thousand) and the number of cost entries (numbers in parenthesis) are added above the bar graph. Circles represent the proportion of observed (blue) and potential (violet) economic costs (outer circle), and number of entries (inner circle). For Ecuador, all costs are reported for Galápagos Islands; for France, all costs are reported for overseas islands; Pacific island countries are grouped. Species codes are: Acr: *Acromyrmex octospinosus*; Ano: *Anoplolepis gracilipes*; Las: *Lasius neglectus*; Lep: *Lepisiota frauenfeldi*; Lin: *Linepithema humile;* Mon: *Monomorium pharaonis*; Phe: *Pheidole megacephala*; Sol: *Solenopsis* spp.; Tri: *Trichomyrmex destructor*; Was: *Wasmannia auropunctata*.

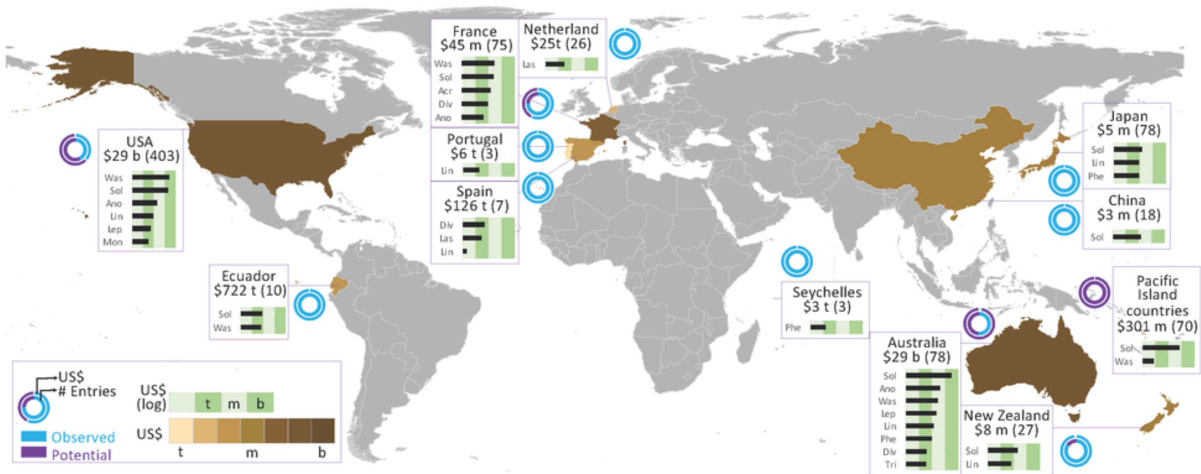

Figure 2

Global distribution of costs caused by invasive ant species. The brown colour categorical gradient on the countries reflects the countries with the highest (i.e., dark) to lowest (i.e. light) costs; in the absence of any cost reports the countries are coloured in grey. Bar graphs on the green scale represent the economic cost per ant species (log scale) in each country. For each country the total costs (b for billion, m for million, t for thousand) and the number of cost entries (numbers in parenthesis) are added above the bar graph. Circles represent the proportion of observed (blue) and potential (violet) economic costs (outer circle), and number of entries (inner circle). For Ecuador, all costs are reported for Galápagos Islands; for France, all costs are reported for overseas islands; Pacific island countries are grouped. Species codes are: Acr: Acromyrmex octospinosus; Ano: Anoplolepis gracilipes; Las: Lasius neglectus; Lep: Lepisiota frauenfeldi; Lin: Linepithema humile; Mon: Monomorium pharaonis; Phe: Pheidole megacephala; Sol: Solenopsis spp.; Tri: Trichomyrmex destructor; Was: Wasmannia auropunctata. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Fig. 3. Distribution of costs between cost type and associated impacted sectors. For the impacted sector, upper (opaque) bars match observed costs and lower (semi-transparent) bars match potential costs.

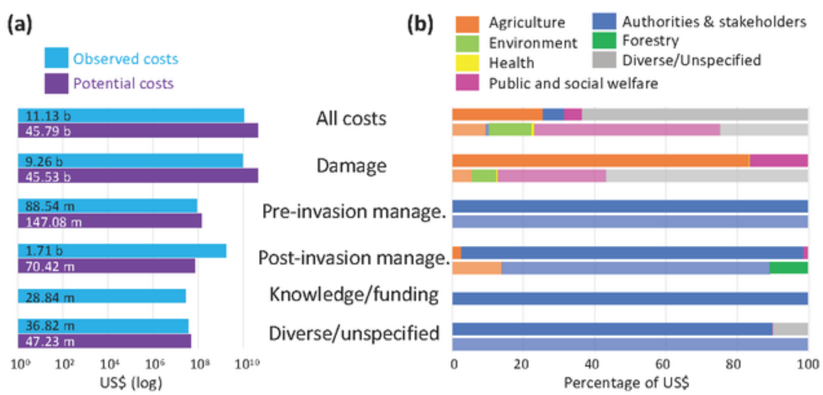

Figure 3

Distribution of costs between cost type and associated impacted sectors. For the impacted sector, upper (opaque) bars match observed costs and lower (semi-transparent) bars match potential costs.

Fig. 4. Distribution of management costs types for each ant species. Upper (opaque) bars match observed costs and lower (semi-transparent) bars match potential costs

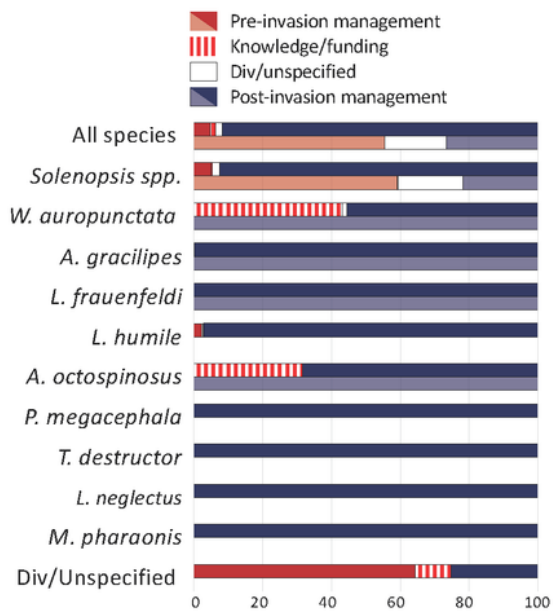

Figure 4

Distribution of management costs types for each ant species. Upper (opaque) bars match observed costs and lower (semi-transparent) bars match potential costs.

Figure 5. Geographic coverage of economic costs reported for (a) *Solenopsis invicta*, (b) *Wasmannia auropunctata*, and (c) *Linepithema humile*. Countries invaded are marked in dark grey. Orange circles represent ant occurrences while green triangles represent locations where costs are reported. For each country, two linked circles represent with their size the total number of ant occurrences (orange) and the total number of cost locations (green); the number of cost entries (n) as well as the US$ is given for each country, in billion (b) or million (m). In (a) Pacific countries are grouped with an ellipse, together with French overseas territories represented by New Caledonia, French Polynesia and Wallis and Futuna.

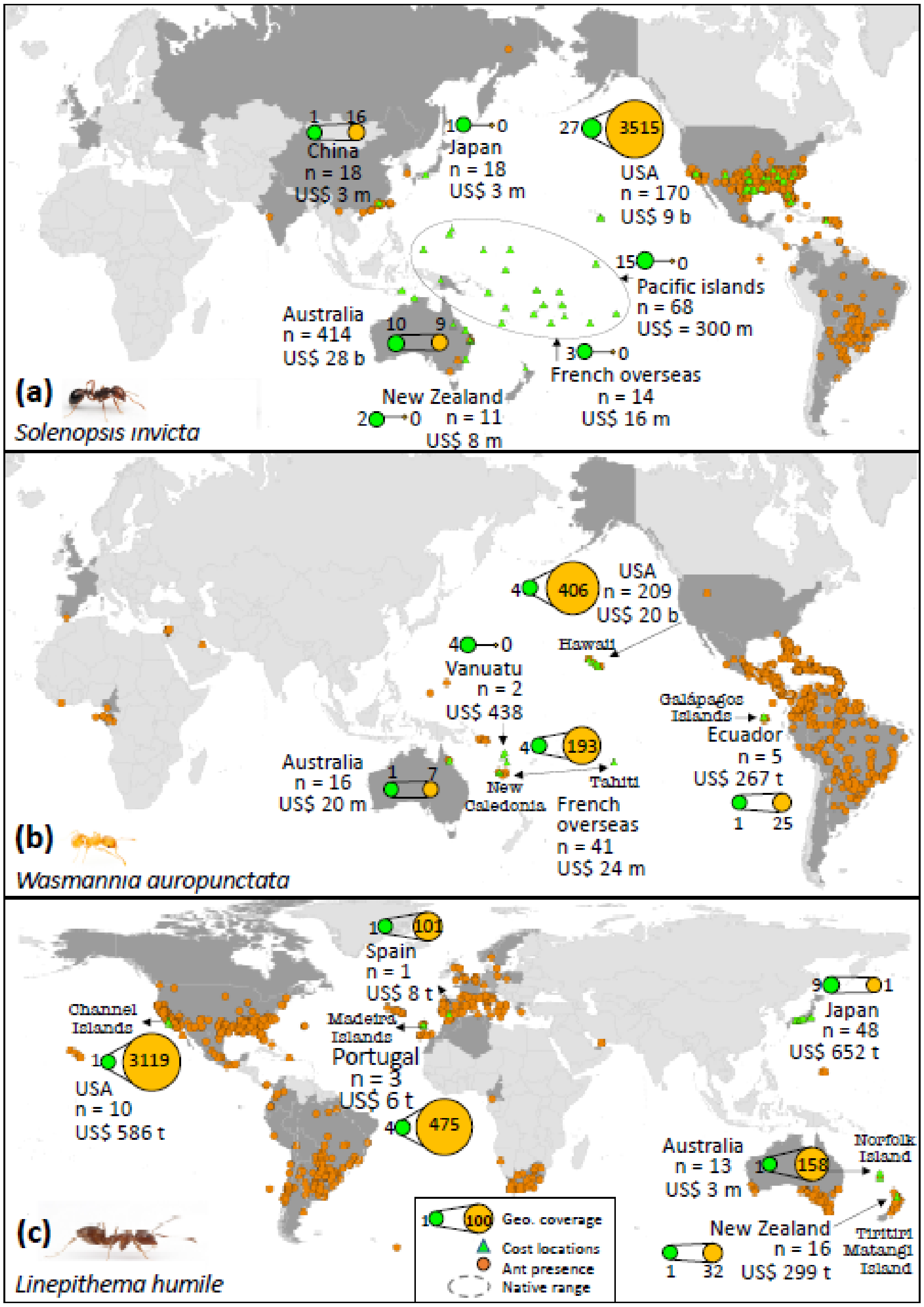

Figure 5

Geographic coverage of economic costs reported for (a) Solenopsis invicta, (b) Wasmannia auropunctata, and (c) Linepithema humile. Countries invaded are marked in dark grey. Orange circles represent ant occurrences while green triangles represent the locations where costs are reported. For each country, two linked circles represent with their size the total number of ant occurrences (orange) and the total number of cost locations (green). For illustrative purposes, the maximum circle size is set to 500, so that a higher number of ant occurrences has the same size. The number of cost entries (n) as well as the cost in US$ is given for each country, in billion (b), million (m) or thousand (t). In (a) Pacific countries are grouped with an ellipse, together with French overseas territories represented by New Caledonia, French Polynesia and Wallis and Futuna. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

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