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Modelling the damage costs of invasive alien species

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Abstract The rate of biological invasions is growing unprecedentedly, threatening ecological and socioeconomic systems worldwide. Quantitative understandings of invasion temporal trajectories are essential to discern current and future economic impacts of invaders, and then to inform future management strategies. Here, we examine the temporal trends of cumulative invasion costs by developing and testing a novel mathematical model with a population dynamical approach based on logistic growth. This model characterises temporal cost developments into four curve types (I–IV), each with distinct mathematical and qualitative properties, allowing for the parameterization of maximum cumulative costs, carrying

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capacities and growth rates. We test our model using damage cost data for eight genera (*Rattus*, *Aedes*, *Canis*, *Oryctolagus*, *Sturnus*, *Ceratitis*, *Sus* and *Lymantria*) extracted from the InvaCost database—which is the most up-to-date and comprehensive global compilation of economic cost estimates associated with invasive alien species. We find fundamental differences in the temporal dynamics of damage costs among genera, indicating they depend on invasion duration, species ecology and impacted sectors of economic activity. The fitted cost curves indicate a lack of broadscale support for saturation between invader density and impact, including for *Canis*, *Oryctolagus* and *Lymantria*, whereby costs continue to increase with no sign of saturation. For other taxa, predicted saturations may arise from data availability issues resulting from an underreporting of costs in many invaded regions. Overall, this population dynamical approach can produce cost trajectories for additional existing and emerging species, and can estimate the ecological parameters governing the linkage between population dynamics and cost dynamics.

Introduction

The introduction, establishment and spread of invasive alien species (IAS) continues to erode biodiversity across biogeographic regions (Simberloff et al. 2013; Bellard et al. 2016). Global translocations of IAS are accelerating (Seebens et al. 2017, 2021), owing to globalisation-mediated intensification of trade and transport networks that increasingly interconnect novel species pools across historically separated areas (Seebens et al. 2018). The process of biological invasion is characterised by several discrete stages: transport, introduction, establishment and spread, with invasion success being impeded by geographical, biological and/or ecological features at each stage (Blackburn et al. 2011).

By reducing or extirpating native populations (Bellard et al. 2016; Vanbergen et al. 2018), IAS considerably affect biotic and abiotic interactions of recipient communities, with frequent top-down or bottom-up cascading effects (Walsh et al. 2016; Bucciarelli et al. 2018). As such, IAS can compromise ecosystem structure, function and service provisioning (Malcolm and Markham 2000; Stigall 2010; Vanbergen et al. 2018; Blackburn et al. 2019). Moreover, multiple IAS can interact mutualistically (Crane et al. 2020), and can cause a considerable effect on human health through, for example, the vectoring of pathogens and parasites that cause disease (Juliano and Lounibos 2005), or the diffusion of pollen-induced allergies (Schaffner et al. 2020). In turn, the above-mentioned ecological and health impacts of IAS can translate into the accrual of marked economic costs to a diversity of activity sectors (Bradshaw et al. 2016).

Despite the huge threat of IAS to biodiversity, human health and national economies, the capacity to prevent and manage invasions has remained poorly developed in many countries (Early et al. 2016). The limited international coordination for establishing management measures is even more striking. In particular, management has long been given low priority, most probably because it was assumed that such costs would be high relative to the potential benefits they could confer (Heikkilä 2011). However, management investments at early invasion stages, such as biosecurity, can prove more cost-effective than long-term control (Leung et al. 2002). Nonetheless, a variety of mitigation actions are conducted in managed areas worldwide (Veitch and Clout 2002; Rumlerová et al. 2016), but only limited information on IAS-associated costs exists under specific regional, taxonomic, or activity sector contexts, as well as over temporal scales. As a result, hitherto, the few large-scale studies of invasion costs have merely represented monetary totals (e.g., Pimentel et al. 2000, 2005) without accounting for the temporal dynamics or the complex typology of costs (e.g., management and damages). Therefore, so far it has not been possible to decipher how invasion costs are evolving over time, as well as how these trajectories might differ among taxonomic groups or invaded habitats. Yet, the impacts of IAS are not necessarily constant across a spatiotemporal context, and are likely to evolve when IAS populations grow and/or expand (Parker et al. 1999; Dickey et al. 2020), or because of lags in species detection that govern the deployment of control measures. For economic damages in particular, the extent to which costs track

population dynamics remains poorly understood, while such information on cost dynamics is crucial to design, prioritize and adapt management actions (Diagne et al. 2020a). Indeed, studies highlighting IAS economic cost trajectories could help divert more funds to biosecurity and other management actions, or set IAS management priorities to mitigate further damages. Especially, identifications of IAS for which damage costs are yet to saturate, *versus* those that have plateaued with time, could inform more efficient management measures among species.

Much of the current literature on the relationship between the cost of invasions and time comes from optimal IAS control theory (Hastings et al. 2007; Bogich et al. 2008; Epanchin-Niell 2017; Baker et al. 2019). In these studies, the costs under consideration mainly correspond to control efforts, and are tied closely to abundance, with increased control typically diminishing management benefits when IAS abundance becomes small and specimens more difficult to detect. Given that most models have focused on control costs, quantitative understandings of how damage costs relate to invader population dynamics are urgently required. These quantifications will improve the reliability of cost models and extend their scope, where the examination of IAS costs can instead be based on the impacts directly related to damage. Indeed, the exclusion of costs related to preventative measures, surveillance and management, among others (Robertson et al. 2020), which are subject to investment decisions that can differ spatiotemporally irrespective of impact, allows us to assume that the impacts of IAS are synonymous to their damage costs.

Parker et al. (1999) presented a basic framework for understanding how species abundance, severity of damage, and the size of their invaded range relate to their total impact. In its original formulation, the authors assumed a constant *per capita* impact over time for a pest with a given range size, where impact is related only to abundance and species spread. However, the empirical support for this model is equivocal, as there are likely many scenarios where *per capita* costs are not constant over time. Damages can vary from one year to the next, and this variance can depend on the taxonomic and trophic groups considered (Lehmann et al. 2020). In particular, differential *per*

capita IAS impacts at different population densities can substantially modulate the extent of the ecological impacts of a given IAS population from one year to the next. Also, the trophic requirements and climate sensitivity of the IAS, in particular for insects, may greatly change along their ontogeny (Stockhoff 1993). Finally, a variety of synergies (Beggel et al. 2016; Zenni et al. 2020) and lags (Aikio et al. 2010; Coutts et al. 2017) may complicate the temporal trend of *per capita* IAS costs, and have so far lacked consideration.

To provide an urgently needed basis for the quantification of IAS-induced costs, the InvaCost database has recently been developed (Diagne et al. 2020b). This database contains extensive information on the costs (e.g., type of costs, impacted sectors, geographic attributes, reliability of cost estimations, etc.) associated with approximately 340 IAS. In this study, we use this cost information by presenting a dynamical approach to modelling the accumulated damage costs of various IAS with the most resolute records in InvaCost. Global accumulated costs are obtained by summing all reported costs across species and countries within a given year for each genus over time. In doing so, we asked whether the temporal cumulation of costs showed generalities among taxa, or if types of relationships varied given differences in life history traits. Further, we used the model to quantify and compare both cost (maximum cumulated cost) and population (intrinsic growth rate) parameters among the taxa. We addressed this question using the cost-density function proposed by Yokomizo et al. (2009), which presents four possible relationships with distinct properties at different density levels (low threshold, S-shaped, linear and high threshold curves), that relate the cost of impact to population density. We tested the application of our temporal cost model against data extracted from the InvaCost database for eight well-represented genera of interest that spanned a range of damaging invasive animal species: *Rattus* (rats), *Aedes* (mosquitoes), *Canis* (dogs), *Oryctolagus* (rabbits), *Sturnus* (starlings), *Ceratitis* (fruit flies), *Sus* (pigs) and *Lymantria* (moths). This test set allowed the examination of both the differential prioritization of allocated costs and the temporal cost patterns across taxonomic groupings with various life history traits.

Methods

Density-time function based on logistic growth

The temporal population dynamics of a single species can be described by the generic differential equation:

$$u'(t) = uf(u) \tag{1}$$

where $u = u(t)$ is the time-dependent population density, $u'(t)$ is the rate of change in density with respect to time, and $f(u)$ is the *per capita* growth rate. For many populations (including IAS), the growth is bounded, a consequence of the fact that resources are usually limited (e.g., food, habitat etc.). Under such a scenario, the density levels off in the long term, imposing a saturation level known as the carrying capacity K. At a simple level, the corresponding dynamics can be modelled using the logistic equation (Jensen 1975; Lewis et al. 2016), which reads:

$$u'(t) = \alpha u \left(1 - \frac{u}{K}\right) \tag{2}$$

where α is the intrinsic growth rate. This equation can be readily solved to obtain:

$$u(t) = \frac{K}{1 + \left(\frac{K}{u_0} - 1\right)\exp(-\alpha t)} \tag{3}$$

given that the value of the initial density $u_0 = u(0)$ is prescribed (Petrovskii and Li 2006; Lewis et al. 2016).

Figure 1 Plot (a) shows that there are two steady states found at $u = 0$ (unstable) and $u = K$ (stable), and the maximum growth rate occurs at half the carrying capacity $K/2$ with value $\alpha K/4$. Plot (b) illustrates solution curves to the logistic equation (3), whose dynamics depend on whether the initial density u_0 is less than or greater than K. For very low densities $u \ll K$ and on a short time-scale, the density grows exponentially $u \approx u_0 e^{\alpha t}$, due to local aggregation. For longer times, the density grows much more slowly and exhibits near exponential decay to the carrying capacity due to the negative feedback from intraspecific competition. In the case that $u > K$, the population can no longer be sustained, resulting in a gradual decline. In either case, in the large time limit, the density levels off when the carrying capacity K of the environment is approached. In the absence of any population density data, K is only identifiable up to a constant, since u and K can be re-scaled by any constant to produce the same solution. In contrast, the intrinsic growth rate α is fully identifiable. In our cost modelling approach, we set u_0 equal to 1, which is assumed to be much less than K, as the density of the
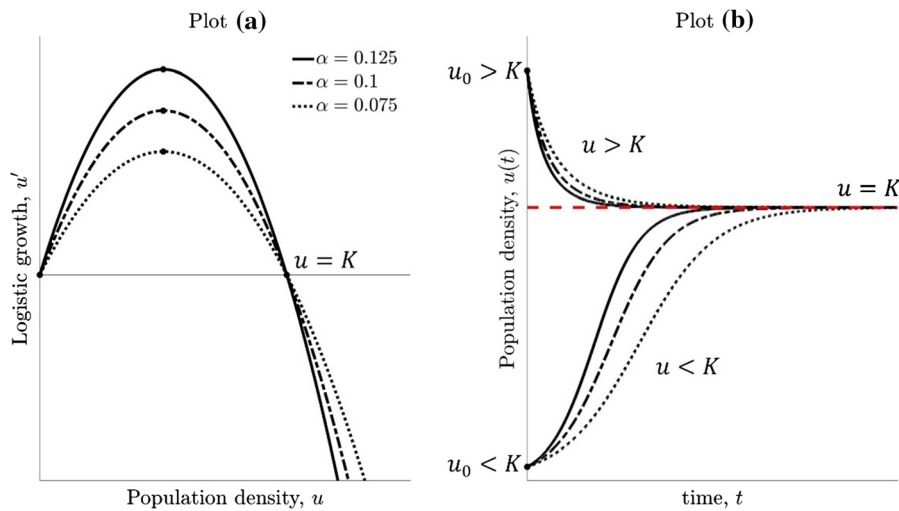
Fig. 1 **a** Logistic growth given by Eq. (2). **b** Population density as a function of time given by Eq. (3)

IAS is usually expected to be relatively low at the time of introduction.

Accumulated cost as a function of IAS population density (cost-density functions)

The relationships between ecological impacts and the population density of an IAS have often been examined (also known as density-impact curves), with both linear and non-linear relationships proposed (Nava-Camberos et al. 2001; Finnoff et al. 2005; Laverty et al. 2017; Bradley et al. 2019; Moroń et al. 2019); however, only a few studies have attempted to link this to the damage costs incurred. For a more thorough investigation of the variety of forms of the cost-density function (i.e., the accumulated cost C as a function of density u), we chose to rely on the functional types proposed by Yokomizo (2009), written as:

$$C(u) = AC_{max} \left[\frac{1}{\frac{1-B}{B} \exp\left(-\frac{u}{s_2 K}\right) + 1} - B \right] \qquad (4)$$

with

$$A = \frac{1 + e^{-s}}{1 - B(1 + e^{-s})}, \ B = \frac{1}{1 + \exp\left(\frac{1}{s_2} - s\right)}, \\ s = \frac{1 - s_1}{s_2} \qquad (5)$$

where C_{max} is the maximum accumulated cost of impact, K is the carrying capacity, s_1, s_2 are the curve shape parameters which lie between 0 and 1 inclusive, and A, B, s are parameters that are expressed in terms of these shape parameters. Note that this model choice is supported by its frequent use by other authors when assessing impacts (see e.g., Jackson et al. 2015; Vander Zanden et al. 2017; Roberts et al. 2018; Sofaer et al. 2018).

Figure 2 illustrates four functional types which express the accumulated cost in terms of IAS population density with distinct behaviours at different density levels.

- For the Type (i) low threshold curve, the accumulated cost increases relatively fast at low IAS population densities, and remains high at intermediate/larger densities.
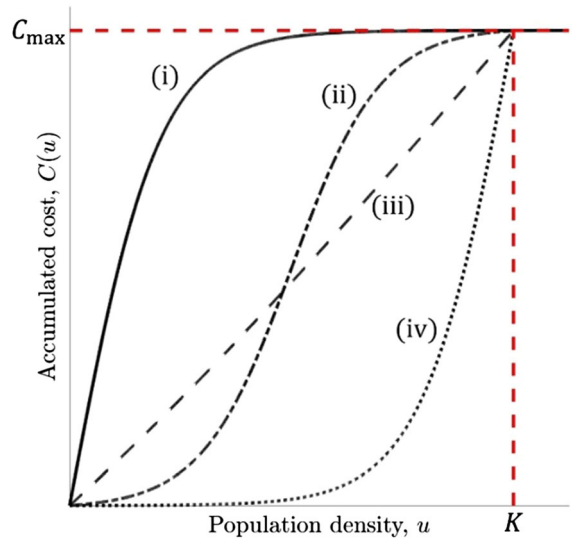
Fig. 2 Illustration of the four types of cost-density functions. Type (i) Low-threshold curve with shape parameters $s_1 = 0, s_2 = 0.1$, Type (ii) S-shaped (sigmoidal) curve $s_1 = 0.5, s_2 = 0.1$, Type (iii) Linear curve $s_1 = 1, s_2 = 1$ and Type (iv) High-threshold curve $s_1 = 1, s_2 = 0.1$

- For the Type (ii) S-shaped curve, the accumulated cost increases much faster at intermediate values of IAS population density in comparison to Type (iii).
- The Type (iii) linear curve presents a directly proportional relationship.
- For the Type (iv) high threshold curve, the accumulated cost remains modest at low IAS population densities, but increases rapidly for larger densities.

In the case $u > K$, one may expect annual costs to remain constant and of a considerable magnitude, in which case the accumulated costs will grow linearly with time. However, for this study, we assume that the threshold density has not been reached, so that $u < K$. Given this, the cost-density function in Eqs. (4)–(5) applies with limiting behaviour $C \to C_{max}$ as $u \to K$. Here, C_{max} represents a 'localized' maximum accumulated cost as spatial aspects are not accounted for. This provides an adequate description for scenarios where the IAS has stopped spreading (i.e., reached its bioclimatic niche limits) (Barnett 2001; Aplin et al. 2011). Also, in a more realistic scenario, annual damage costs may continue during this phase, but these costs can be expected to be several orders of magnitude smaller than the largest annual cost, and the total cost is likely driven more by management costs,

which we do not consider. As a result, the increase in the accumulated cost would be negligible, and therefore can be considered at a 'near' saturation level, i.e., with constant C_{max}.

For all four cost function types, the accumulated cost scales linearly at very low IAS population densities. This is consistent with the concept of invasion debt (Essl et al. 2011). To demonstrate this, consider a species population at low density and relatively large carrying capacity K, so that terms of the order $(u/K)^2$ and higher are negligible and can be omitted. It follows that one can approximate the accumulated cost as follows:

$$C(u) \approx AC_{max} \cdot \frac{B(1-B)}{s_2 K} \cdot u \qquad (6)$$

We note that the model assumes that the accumulated damage cost remains constant over time given a fixed IAS density. This may be reasonable on a short time scale, but in the long-term, the damage cost for a given IAS density may change, e.g., due to economic growth (Haubrock et al. 2021).

In an ecological context, Type (i) costs may be common for species whose impacts are roughly equivalent across all abundance levels, reaching near-maximal accumulated costs at relatively small densities. At the other extreme, Type (iv) costs correspond to species whose damages are only felt once they have reached very high abundance (Yokomizo et al. 2009). As an illustration, fouling species who require high densities in order to block pipes, such as zebra mussels, may be described by Type (iv) (Elliott et al. 2005). Conversely, highly voracious novel predators introduced in insular communities, such as the feral cat (*Felis catus*) (Hilton and Cuthbert 2010) may rather behave as Type (i). Indeed, these predators have been able to have deleterious impacts on native fauna that begin even at low densities, and that do not appear to saturate until near maximal densities. Alternatively, species could show linear relationships with cost (Type iii) if *per capita* impacts are density-independent. This form has been found for a well-known agricultural pest, the balsam fir sawfly (*Neodiprion abietis,* Parsons et al. 2005). Most often, linear relationships have been suggested as being common in nature (see e.g., Elgersma and Ehrenfeld 2011; Panetta and Gooden 2017). Finally, relationships could be sigmoidal (Type ii) if density plays both

a positive and negative role, which would be expected if interference limits impacts at high density, while being by definition low at low density. This form is predicted in models of invasive rodent grazing impacts on crops (Brown et al. 2007).

Accumulated cost as a function of elapsed time since the introduction of IAS (cost-time functions)

The accumulated cost-density function can be expressed explicitly in terms of time $C(t)$ by combining Eq. (4) and the density-time function in Eq. (3).

The four accumulated cost functions, which are now time dependent, i.e., cost models (I)–(IV), see Fig. 3, correspond to each density dependent cost functional Types (i)–(iv), see Fig. 2. These models present distinct qualitative properties depending on the time scale, but more generally, the cost patterns at low/high IAS population densities mimic those seen in Fig. 2. Overall, costs increase monotonically until a maximum level C_{max} is approached, precisely when the IAS density saturates to the carrying capacity. Also, given the accumulated cost as a function of time, crude estimates of the marginal cost can be obtained over some time interval $t_1 < t < t_2$, computed as $C(t_2) - C(t_1)$. In the case of low IAS population densities and on a short time scale, with relatively high carrying capacity, one can obtain from Eq. (6):

$$C(t) \approx AC_{max} \cdot \frac{B(1-B)}{s_2 K} \cdot u_0 e^{\alpha t}, \qquad (7)$$

which demonstrates that all cost models (I)–(IV) allow for a rapid increase in damage costs that arise due to the rapid spread of the IAS shortly after its initial introduction. This is a direct result of the fact that logistic growth in the population assumes that the species density grows exponentially on a short time scale, which is normally the case for successful invaders during the early phases of the invasion (Shigesada 1997; Crooks 2005). Nonetheless, 'invasion debt' can result in considerable lag times between invader arrival and perceived impact (Essl et al. 2011).

Data collection and processing

Cost data were extracted from the InvaCost database (2419 entries; Diagne et al. 2020b, https://doi.org/10.1038/s41597-020-00586-z) as well as another related data source from searches made in non-English
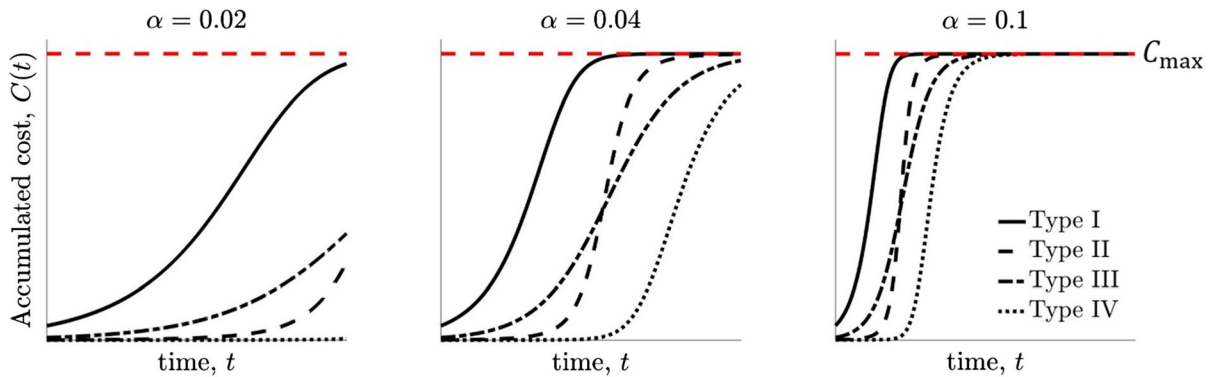
Fig. 3 Accumulated cost models (I)–(IV) over time since the introduction of IAS, corresponding to each functional Type (i)–(iv), respectively (see Fig. 2), presented for different values of intrinsic growth rate α. Line styles are the same as in Fig. 2

documents (5212 entries; Angulo et al. 2020; available at https://doi.org/10.6084/m9.figshare.12928136). Literature sources were obtained via systematic searches in online repositories (Web of Science, Google Scholar and Google search engine). We gathered additional cost information through contacting experts and searching specific literature databases of the countries/languages considered, and contacting official national managers or researchers that could provide cost data. All cost entries were standardized to a common currency and year for comparability (2017 US$). This process also considered an inflation factor based on the Consumer Price Index of 2017 relative to the year of the cost estimation. All information on the compilation and standardization of data recorded in InvaCost are detailed in Diagne et al. (2020b). Also, we provide the Appendix A1 for presenting the categories used for each descriptive variable, which corresponds to a specific column in the InvaCost database (Diagne et al. 2020b).

For analyses implemented in the present study, we extracted entries for all species within the following focal genera: *Rattus* (rats), *Aedes* (mosquitoes), *Canis* (dogs), *Oryctolagus* (rabbits), *Sturnus* (starlings), *Ceratitis* (fruit flies), *Sus* (pigs) and *Lymantria* (moths). They were chosen as they comprised some of the richest data, and represented various taxonomic groups and therefore contrasted life history traits, especially concerning invasion dynamics. For these genera, the cost entries selected were those estimated at the country level, i.e., not provided at supra-national or site scales (Table 1; see Appendix A2 for a distribution map of total economic costs (US$ million) at the country level). For this purpose, we filtered these

genera using the "Genus" column, and only incorporated entries at the *Country* level within the "Spatial_scale" column. We excluded any cost estimates that were considered to have *Low* reliability (i.e., not sourced from official/peer-reviewed material or not reproducible; "Method_reliability" column), and any costs that were *Potential* (i.e., predicted or extrapolated), rather than actually *Observed* ("Implementation" column) based on the database contents at the time of extraction (Diagne et al. 2020b). We note that entries used here may have since been updated in InvaCost v4.0 (for example, *Lymantria* spp. costs in Mexico are now listed as *Potential* rather than *Observed*).

For each entry, we also extracted the timespan associated with the costs recorded using the *expandYearlyCosts* function from the *invacost* R package (Leroy et al. 2020). This function divides the total cost reported by a publication equally across a set of probable starting and ending years, and provides an extended dataset where each entry corresponds to a cost estimate occurring for a single year. Each publication within the InvaCost database acted as an independent reference on reported costs, but the number of years over which the cost was estimated varied across references. Only those genera possessing cost estimates from at least five independent references were considered from the InvaCost database (Table 1).

All reported costs were summed across species and countries within a given year to obtain a global accumulated cost for each genus over time (see also Appendix A2). Table 1 shows the number of independent references used to produce each genus' cost

Table 1 A list of the eight genera used to create cost curves. The years in which extreme costs (outliers) occurred, and the corresponding cost values are given for each genus, where a blank space indicates that no outliers were found. The number of independent references indicates how many separate publications within the InvaCost database were used to create the cost curve for that genus, while the number of independent years is the unique cost-year combination for each genus after all independent references were aggregated

Genus	Time period	Outlier		No. of independent references	No. of independent years associated with costs
		Year(s)	Outlier cost US$ million		
(a) *Rattus*	1998–2010			6	6
(b) *Aedes*	1977–2017			34	25
(c) *Canis*	1979–2014			7	6
(d) *Oryctolagus*	1955–2019	1953	432.01	16	31
		1996	733.77		
		2001	1938.07		
		2003	518.50		
		2010	433.09		
(e) *Sturnus*	2000–2016			6	5
(f) *Ceratitis*	1999–2007	1981	13.50	5	5
(g) *Sus*	1982–2016	2017	2293.53	10	9
(h) *Lymantria*	1933–2020	1981	3355.99	8	39
		2002	2203.89		
		2004	368.50		

curve, as well as the number of unique years for which a total cost could be calculated (i.e., the number of non-repeated years for which cost data were available from InvaCost across all references). We excluded those cost values from the dataset that reported comparatively very high costs, i.e., any cost value that was greater than $Q_3 + 1.5 \times IQR$ was removed (see Table 1), where Q_3 is the upper quartile and IQR is the interquartile range of the dataset. A single outlier was found for the genera *Ceratitis* and *Sus*, while three and five outliers were found for *Lymantria* and *Oryctolagus,* respectively. We found no outliers for the other considered genera.
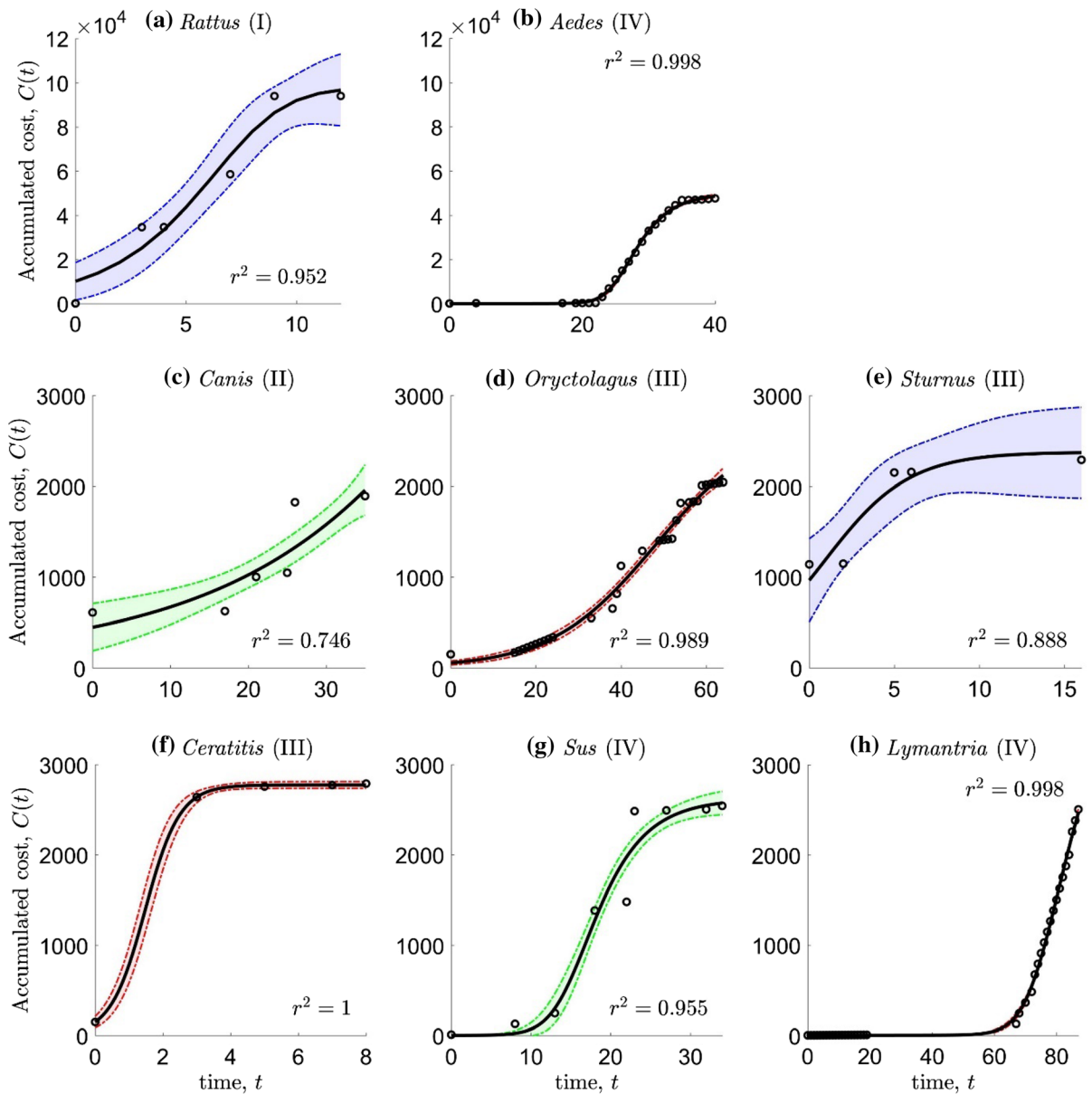
We modelled the accumulated cost data (US$ million) using the four different types of accumulated cost models (I)–(IV). The first reported year of damage cost was taken as the initial year, corresponding to time $t = 0$, which is measured in years thereafter. For example, the time period for *Rattus* is from 1998 ($t = 0$) to 2010 ($t = 12$). The non-linear regression curve fitting tool 'fitnlm' from Matlab was used to identify which model optimally fitted the data, and selected it based on the highest coefficient of determination (r^2) or lowest root mean square error

(*RMSE*). Once the best fitting model was found, we reported the corresponding model parameters for each genus; specifically, the maximum accumulated cost $C_{\max}$, carrying capacity K and the intrinsic growth rate α.

Results

We found fundamental differences among taxa in the nature of their cost accumulations over time, reflected in different best-fitting model types (Fig. 4). Of the eight genera assessed, *Rattus* was best described by model Type I, *Canis* by model Type II, *Oryctolagus*, *Sturnus* and *Ceratitis* by model Type III, and lastly *Aedes*, *Sus*, and *Lymantria* by model Type IV (Table 2, Fig. 4). Models for each taxon were associated with a very high $r^2 (\geq 0.952)$, indicating an extremely close model fit with the cost data, with the exception of *Sturnus* and *Canis*, with still high r^2 values (Table 2). The shaded areas in Fig. 4 represent confidence regions providing the range of predicted cumulative costs. Note that lower confidence levels

Fig. 4 Plot of the best fit accumulated cost model (either Types I–IV) against the cost data (US$ million), with the reported r^2 value. The best fitted model for each is indicated in parentheses after the name of each genera; also see Table 2. The shaded areas represent confidence regions for the range of predicted cumulative costs with confidence levels 95% (red), 80% (blue) and 50% (green) (see Table 3). See Appendix A5 for the corresponding plots for each genus with accumulated cost as a function of population density

were used for those genera with higher data variability, and comparatively, a smaller number of reported costs (Tables 1, 3).

Rattus (Type I) costs were transitioning to the saturation phase, whilst *Canis* (Type II) costs were found to be accelerating. Nonetheless, within model types, curvatures differed substantially in their cost accumulation phases (see Fig. 4, and Appendices A4–A5 for the corresponding population density-time and accumulated cost-density functions). Among the Type III model fits, we found *Oryctolagus* in the early phase with gradually increasing accumulated costs, *Sturnus*

Table 2 The best fit accumulated cost model (either Types I–IV) quantified by the statistical metrics (r^2) and ($RMSE$). We also report the values of the maximum accumulated cost (C_{max} in US\$ million)

Genus	Best fit cost model	Coefficient of determination r^2	Root mean square error $RMSE$	Maximum accumulated cost C_{max}
(a) *Rattus*	I	0.952	10,500	97,962
(b) *Aedes*	IV	0.998	858	49,759
(c) *Canis*	II	0.746	369	11,110
(d) *Oryctolagus*	III	0.989	79.4	2689
(e) *Sturnus*	III	0.888	275	2375
(f) *Ceratitis*	III	1	14.7	2774
(g) *Sus*	IV	0.955	269	2622
(h) *Lymantria*	IV	0.998	35.1	4075

at the transition to reaching the stable plateau, and lastly *Ceratitis* already having reached the plateau phase. Interestingly, this illustrates that the same model type can reflect different stages of the population dynamics depending on the taxa considered (see Appendix A4). Similarly, for Type IV models, *Lymantria* exhibited cost cumulations in an early phase, with a steep increase in costs, whilst *Aedes* and *Sus* were more advanced.

Marked differences in the magnitude of costs were also exhibited within and between model types (Table 2), with *Rattus* exceeding all other genera, by far, in the total amount of damages incurred (i.e., greatest C_{max}), followed by *Aedes*, with approximately half the *Rattus* total cost. In general, C_{max} was one order of magnitude higher for *Rattus, Aedes* and *Canis* when compared to the other taxa (Table 2). Accumulated maximum costs of *Oryctolagus*, *Sturnus*, *Ceratitis* and *Sus* were predicted to be similar in value, ranging in between US\$ 2375 and 2774 million (2007), whereas the maximum cost for *Lymantria* was slightly higher (US\$ 4075 million) (Table 2).

One advantage of the dynamical modelling process is that it can provide information regarding ecological parameters for taxa at a global scale directly from the cost data (i.e., a top-down approach). As a result, we can infer how the population density evolves with time (see Appendix A4). We note that our carrying capacity values should not be interpreted as the true maximum population density that the species can reach globally, but are reflective of a proportional maximum. While values of K require rescaling by some unknown, potentially disparate constant across taxa in order to be

interpretable, our fitted intrinsic growth rates can be compared directly among taxa if cost-density functions are constant through time. The highest intrinsic growth rate was found for *Ceratitis,* with a value $\alpha =$ 1.93 (Table 3), which explains the comparatively rapid cost accumulation with a quick progression towards the maximum cost (Fig. 4). This was followed by *Sturnus*, *Rattus, Aedes* and *Sus*, with a lower (but similar) value of α lying between 0.1 and 1, representing slower growth. The remaining taxa exhibited a much lower intrinsic growth rate with $\alpha < 0.1$, which was reflected by a greater lag or delayed increase in the cost accumulation (Fig. 4, Table 3). See Appendix A3 for a compiled list of ecological and model shape parameters as they appear in Eqs. (4) and (5).

Discussion

The present study developed and applied a novel mathematical model to examine and predict the cumulative damage costs of IAS over time. Among eight genera containing notorious invaders, we report marked differences in cost cumulations. Instances of high costs likely mirror the widespread distribution of genera which damage infrastructure, agriculture and represent threats for human health (Meerburg et al. 2009; Luis et al. 2013; Iwamura et al. 2020). Interestingly, the best fitting models, and their underlying parameters, differed among genera, indicating that the trajectories of cost cumulations can differ substantially among IAS; these differences can be explained by several factors, potentially including the

Table 3 Confidence intervals for the ecological parameters K and α, where smaller confidence levels were used for those genera with high data variability and relatively smaller sample size. Confidence levels used are 95% (red), 80% (blue) and 50% (green)—corresponding to the colour scheme in Fig. 4. Note that the lower interval limit for the carrying capacity for *Canis* was negative and thus cut off at zero

Genus	Confidence level	Carrying capacity, K (per unit area)	Confidence interval for K	Intrinsic growth rate, α (per year)	Confidence interval for α
(a) *Rattus*	80%	48.56	[9.66, 87.46]	0.32	[0.16, 0.48]
(b) *Aedes*	95%	228.59	[105.81, 351.38]	0.27	[0.25, 0.29]
(c) *Canis*	50%	5.06	[0, 18.9]	0.02	[0.02, 0.03]
(d) *Oryctolagus*	95%	42.91	[29.47, 56.36]	0.08	[0.07, 0.09]
(e) *Sturnus*	80%	2.29	[1.24, 3.35]	0.40	[0.03, 0.77]
(f) *Ceratitis*	95%	16.24	[9.37, 23.11]	1.93	[1.69, 2.17]
(g) *Sus*	50%	7.95	[1.42, 14.48]	0.22	[0.17, 0.28]
(h) *Lymantria*	95%	252.49	[87.29, 417.69]	0.09	[0.08, 0.1]

sectors that the IAS impact, their abundance, distribution, ecology and their attention from researchers and other stakeholders that report damages. Furthermore, we determined differences in intrinsic growth rates of costs among genera due to changes in density, indicating differential lag time effects in the development of costs at the global scale. The exponential growth in costs shown by most taxa suggests that management actions could, reciprocally, result in exponential reductions of these costs below certain population thresholds. Whilst there are limitations to our approach, including considerations for future costs in novel invaded regions where species could still be far from $C_{\max}$ and K, and while underlying cost data are poorly available, these models help to elucidate how reported invasion costs have developed over time among taxa, informing management strategies for IAS. This potentially includes future IAS without a current invasion history within these focal genera, given high projected invasion rates in future (Seebens et al. 2021).

Cost cumulation model

The assessments were restricted to the calculation of the economic cost resulting from damages, which represent valuable indicators of the impact of biological invasions (US Congress 1993; Williamson 1998). Conversely, management costs may be more disparately reported, due to changeable investment priorities, research focuses and governmental policies. As such, the costs due to IAS projected here are underestimates, especially since we excluded uncertain damage cost types (i.e., predictions and low reliability costs), management costs, and additional filtering steps that omitted costs above or below the country-level scale, and notwithstanding additional gaps in underlying cost reporting.

It is important to note that the time of initial cost onset in our model is not the onset of each genus' invasion. Our cost curve typology is meant to describe only the shape of the accrual of detected damage costs over time, rather than that of the invasion trajectory from start to finish. In an analogous description of the shape of detected IAS spread trajectories; for example, Shigesada et al. (1995) defined their spread typology

after accounting for a variable lag phase across species. In the same way, we model only the damage cost accumulation of IAS after the first report of their economic impacts. Prior to this detection, IAS can be subject to a variety of factors such as Allee effects, variable spread rates, and low cost detection effort—especially in the case of unintentional introductions or species with less of a nuisance status (Hastings et al. 2005), which cause variable lag times between the dates of first introduction of each genus in our dataset and their first cost detection (see Appendix A6). For instance, *Aedes* spp. have reported lag times of below 20 years (i.e., initial cost detections less than 20 years after their known date of first introduction) in their invaded countries, while *Lymantria*. spp were present for 90 years before their impacts were reported in Canada. This difference likely reflects the nuisance status of mosquitoes in terms of public health (Weber 1979), and the delay in spread and subsequent substantial forest impacts of *Lymantria* in North America (Aukema et al. 2011).

The assumption of logistic growth was justified by its explanatory power in the context of biological invasions (Lewis et al. 2016). In particular, it successfully models a common invasion scenario, where population expansion decreases as resources become scarce, and levels off when the carrying capacity of the environment is reached. Alternatives to this growth model exist, such as the more complicated forms: 'generalized logistic growth' (Tsoularis and Wallace 2002) or the 'Allee effect' (Dennis 2002; Boukal and Berec 2002; Courchamp et al. 2008). Also, in more complex scenarios, population dynamics can exhibit marked 'boom' and 'bust' dynamics, where the invader density can reach high levels, but then substantially decline to lower levels—which has been observed for a variety of species (Allmon and Sebens 1988; Creed and Sheldon 1995; Williamson and Fitter 1996; Zaitsev and Marnaev 1997). Lastly, other species have been observed to exhibit oscillatory behaviors (Ross and Tittensor 1986; Elkinton and Liebhold 1990). These more complex dynamics and associated alternative functional forms should be considered when the fit of a simpler model is poor, which was not the case in our study.

Our cost modelling approach accounts for the population dynamics of various genera, and thus provides a useful framework for investigating temporal cost patterns across various habitat types and taxonomic groups. By analyzing the shape of the cost-time curves characterized by model Types (I)–(IV), we were able to capture how impacts accrue not only across taxa, but also at different stages of an invasion process. Further, our approach was fitted against actual damage cost data extracted from the most comprehensive database to date (InvaCost). These data are, however, subject to a series of limitations that likely lead to an underestimation of reported costs relative to true economic impacts of IAS (Diagne et al. 2020b). Accordingly, the Types of model selected here were inherently influenced by the nature of underlying data, suggesting that the resolution of cost reporting should be improved for economic damages globally. Yet, the consistent excellent fits across genera is an indication of a certain degree of robustness not only of the models but also of the cost data. More generally, studies on temporally dynamic models of species population growth are plentiful in the literature (Petrovskii and Li 2006; Kawasaki and Shigesada 2007; Hart and Avilés 2014; Lohr et al. 2017 etc.); however, very few rely on real cost data, and have instead focused more on a theoretical examination of optimal control (Yokomizo et al. 2009; Hastings et al. 2007; Baker et al. 2019).

Model Types and maximum accumulated costs

Cost cumulations differed substantially among the genera assessed in the present study, resulting in their representations over the four model Types. Nonetheless, whilst Types I and II were displayed solely by *Rattus* spp. and *Canis* spp., respectively, Types III and IV were more common ($n = 3$ taxa each). All types provided an excellent fit to the data ($r^2 \geq 0.952$), with the exception of *Canis* spp. (Type II) and *Sturnus* spp. (Type III) with still high r^2 values—indicating good fits (see Table 2). The relative commonness of Type III and IV curves suggests a lack of broadscale support for saturation between invader density and impact across all genera, as not all displayed an asymptote in cost dynamics. Reciprocally, this is highly useful for management, as effective actions that reduce invader abundances could result in an exponential decrease in damage costs from invasions. However, this is less relevant for species with lower maximum costs, where reductions in costs could be relatively small in magnitude.

The highest accumulated cost was quantified from *Rattus* spp. (Table 2). This is not surprising as this genus was one of the earliest taxa recognized as an IAS, and has reached nowadays a widespread, world-wide distribution (CABI 2019). We also note that the costs would be much higher for *Rattus* spp. should we have included management costs. Because rat invasions are known to have an extreme detrimental effect on numerous native species (Atkinson 1985), particularly when introduced to oceanic islands (Shiels et al. 2014; Ruffino et al. 2015)—in some cases leading to rapid species extinctions (Bell 1978), they have been very extensively managed. In addition to these ecological impacts, these rodents host more than sixty zoonotic diseases, reducing crop yields and food reserves, and posing a serious threat to human health (Meerburg et al. 2009; Luis et al. 2013). The next highest accumulated cost was assigned to *Aedes* spp., which was approximately half of the cost incurred by *Rattus* spp. (Fig. 4, Table 2).

Invaders within the *Aedes* genus are some of the fastest-spreading worldwide, producing detrimental impacts to both resident species and ecosystems, and also represent some of the most prominent insect vectors of diseases (e.g., Zika, dengue, chikungunya, and yellow fever) (Juliano and Lounibos 2005). For these insects, the invasion front of the yellow fever mosquito *A. aegypti* is expected to increase significantly in the future (Iwamura et al. 2020), indicating that associated costs will heighten further with climate change. Similarly, the congeneric *A. albopictus*, which produces desiccation-tolerant and freeze-resistant eggs (Medlock et al. 2012; Cuthbert et al. 2020), is likely to continue to spread through pathways such as the used tire and ornamental plant trades in temperate regions, as has occurred in Europe (Medlock et al. 2012). Such invasive range increases are exacerbated by climate change, especially for ectothermic animals (Bellard et al. 2013). Overall, mosquito-borne diseases cause millions of human deaths per year, and therefore sustained control efforts and integrated management programs are of utmost importance to prevent disease outbreaks (Roiz et al. 2018)—with high global economic damages being driven predominantly through healthcare costs. Early preventative measures are the most efficient means for controlling invasive mosquito species (amongst other taxa) as compared with longer term control actions (Leung et al. 2002; Vazquez-Prokopec et al. 2010). Moreover, given our focus on damage costs, these IAS control efforts could reduce longer-term economic damages. Whilst our mathematical model suggested costs from *Aedes* are saturating, we stress that, empirically, costs from such taxa will probably continue to escalate as they invade new areas, as human populations grow, and as novel pathogens emerge. The third most costly genus comprised *Canis* spp., where economic damages accrued as a result of livestock mortality and human medical expenditures associated with feral dog bites (Pimentel et al. 2000).

In contrast, the cost impacts of the remaining genera were found to be one order of magnitude lower, with similar cost saturation levels (Table 2). This is primarily due to relatively lower direct damages to human assets, and the lack of association with disease spread. Nonetheless, these costs are only lower relative to the costliest species and remain unacceptably high in absolute value. In addition, these other genera are known to be highly ecologically damaging, yet such damages are more difficult to quantify in economic value than impacts to primary human sectors (e.g., agriculture) (but see Hanley and Roberts 2019). It is in fact likely that costs from these genera, as is also the case for several other taxa, are currently highly underestimated (Diagne et al. 2020b). This suggests that better cost reporting is required to more accurately discern the density-impact relationship of IAS, and that this will lead to higher costs than those reported here.

Cost trajectories

Data permitting, the mathematical model presented could equally be applied locally or nationally to deduce cost trajectories at finer scales, and to compare different populations of IAS. For instance, the model we developed was applied in a recent study (alongside other statistical approaches) to analyze global trends in costs of aquatic IAS (Cuthbert et al. 2021). In that vein, populations at an invasion front may exhibit an earlier stage of cost cumulation as compared with longstanding invader populations. Whilst *Ceratitis* spp. exhibited a relatively rapid intrinsic growth rate ($\alpha > 1$), other groups such as *Rattus* spp., *Aedes* spp., *Sturnus* spp. and *Sus* spp. had intermediate growth rates ($0.1 < \alpha < 1$), whereas growth rates of genera such as *Canis* spp., *Oryctolagus* spp. and *Lymantria* spp. were much lower ($\alpha < 0.1$) (Table 3). These
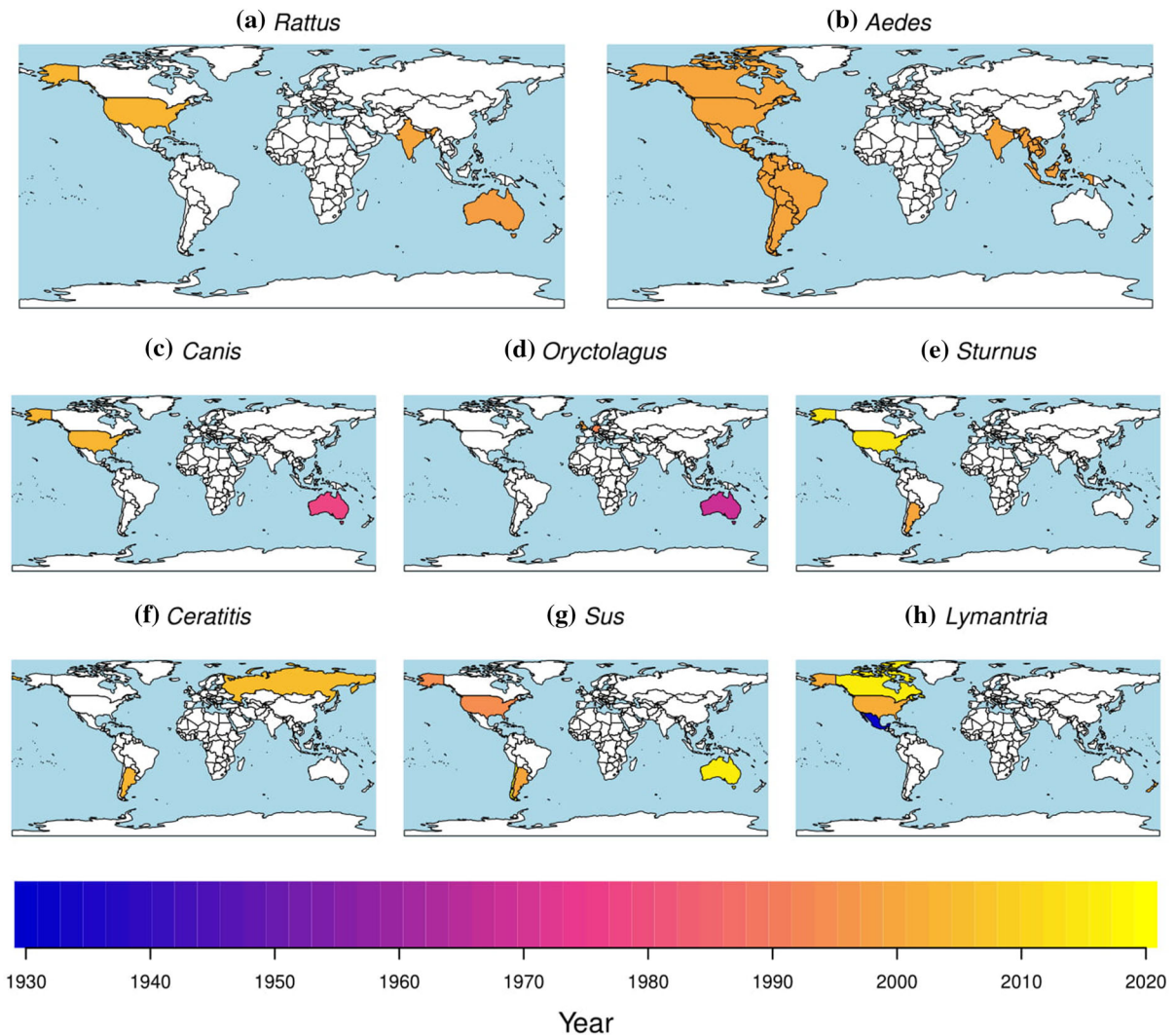
Fig. 5 Maps illustrating the global temporal distribution (years) in which the first cost was reported (independent of the magnitude of the respective cost) for each genus. The color ramp thus corresponds to the year in which the cost was first reported, regardless of its monetary value. Also see Appendix A2 for a total distribution of costs (US$ million) at the country level. These distributional data reflect the state of the Invacost database at the time of analysis. We note that entries used here may have since been updated in InvaCost v4.0 (for example, *Lymantria* spp. costs in Mexico are now listed as *Potential* rather than *Observed*)

patterns may also relate to the pathways associated with these species, as well as their life histories (e.g., rapid reproduction) or introduced ranges, with costs arising from new invaded areas through time (Fig. 5). For example, costs produced from invasions by *Canis* spp., and *Oryctolagus* spp. only occurred recently in the United States and Europe, and thus time lags in cost development likely emanate from delays in novel invasions, resulting in lower α.

The rapid intrinsic growth rate of *Ceratitis* spp. reflects a capacity to accrue substantial costs soon after establishment, with species within this genus known to cause substantial damages and losses to fruit crops, as well as through the transmission of fruit-rotting fungi (Cayol et al. 1994). For *Aedes* spp., the presence of dormant life stages that are well-adapted to succeed in urbanized environments through the exploitation of artificial habitats (i.e., artificial containers) mediates high invasion success (Medlock et al. 2012). This

association with humans, coupled with short generation times and high fecundity, likely caused a relatively rapid increase in costs. Despite this, an intermediate growth rate in *Aedes* spp. may result from disparate cost reporting prior to the last two decades for those taxa, whereas taxa with a higher growth rate (i.e., *Ceratitis* spp.) were reported more recently, reducing delays in modelled population growth rates. Moreover, costs from disease are likely to accrue rapidly once a given pathogen or parasite is in circulation. Overall, the widespread pancontinental impacts of *Aedes* spp., and more particularly *A. aegypti* in tropical areas, may have led to a rapid increase in human health costs. This rapid increase could also be due to concurrent, analogous trends in urbanization, whereby this species has adapted to perform well in close association with humans. Similarly, *Rattus* spp. and *Sturnus* spp. can quickly reach high abundances in urban areas, where populations can spread disease and damage infrastructures, as well as agricultural enterprises elsewhere (Weber 1979; Linz et al. 2007; Meerburg et al. 2009).

In contrast, *Lymantria* spp. costs accrued more slowly, indicating that interest in this species was subject to a longer lag (Appendix A6), that its spread rates were slower, or that its impacts to its host trees took longer to become apparent following its invasion (invasion debt). *Lymantria* spp. exhibit just one generation per year (Doane and McManus 1981), with spread largely dependent on long-range assisted movements by humans (e.g., cars or boats) (Hajek and Tobin 2009). Our data indicate that the initial reported impacts from this species were relatively small, and increased rapidly only in the last few decades (but see our note in *Methods* about recent database corrections for this genus). However, rather than being an artefact associated with their life history, this could reflect growing interactions with growing urban forests within its invaded range (e.g., the United States, Twery 1991; Aukema et al. 2011). Indeed, *Lymantria* costs accrued only recently in the United States and Canada (Fig. 5). Similarly, *Canis* impacts have been slow to accrue, but that taxon has been characterized by more recent invasion cost reporting in North America. Moreover, despite high fecundity, invasions by *Oryctolagus* spp. occurred only relatively recently within Europe. In contrast, genera such as *Aedes* and *Sus* exhibited similar timing of cost reporting pancontinentally (Fig. 5). Finally, *Ceratitis* is characterized by very recent and concurrently reported invasion costs in Russia and Argentina.

Synthesis

Understanding the dynamics of cost development at different time scales, from initial cost accruals to large time saturation levels, is fundamentally required to better inform stakeholders and scientists of the IAS that require management actions. In this study, we presented a novel mathematical model which incorporates the dynamical nature of the species population, and demonstrated that it provides a useful framework for the analysis of cost accumulations. This model can identify genera whose damage costs may escalate rapidly—thus allowing data-informed prioritization and improved efficiency of control actions. In situations where costs have saturated relative to population density (such as *Ceratitis* and *Sturnus*), large population management expenditures may be necessary to impact cost trajectories. In contrast, exponential cost trajectories (such as for *Lymantria* and *Oryctolagus*) suggest that population management could result in exponential damage reductions. Although many mathematical models have been developed to relate ecological impacts and species abundances through 'density-impact' curves, very few have attempted to provide a direct link with the incurred costs, and backed them up with empirical cost data. While the costs of IAS are expected to increase in the forthcoming years, more IAS cost estimations are required in order to get improved assessments of temporal trends in costs of IAS, in turn ameliorating the predictive models and ultimately management strategies. Moreover, given cost-density relationships have been shown to exhibit intraspecific differences among populations (Strayer 2020), improved cost resolution at smaller scales could permit population level comparisons in cost developments.

Data availability Underlying data are publicly available in Diagne et al. (2020b—accessible at https://www.nature.com/articles/s41597-020-00586-z) and in online repositories (https://doi.org/10.6084/m9.figshare.12668570.v1; https://doi.org/10.6084/m9.figshare.12928136).The final dataset used for analysis in this paper will be provided on the Dryad digital repository.

Declarations

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

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

Appendix A1: Glossary of terms

Categories used for each descriptive variable that corresponds to a specific column in the InvaCost database (Diagne et al. 2020b).

Column title	Description
Cost estimate per year local currency	The 'Raw cost estimate local currency' transformed to a cost estimate per year of the 'Period of estimation' (obtained by dividing the raw cost estimate by the number of years* of the 'Period of estimation')

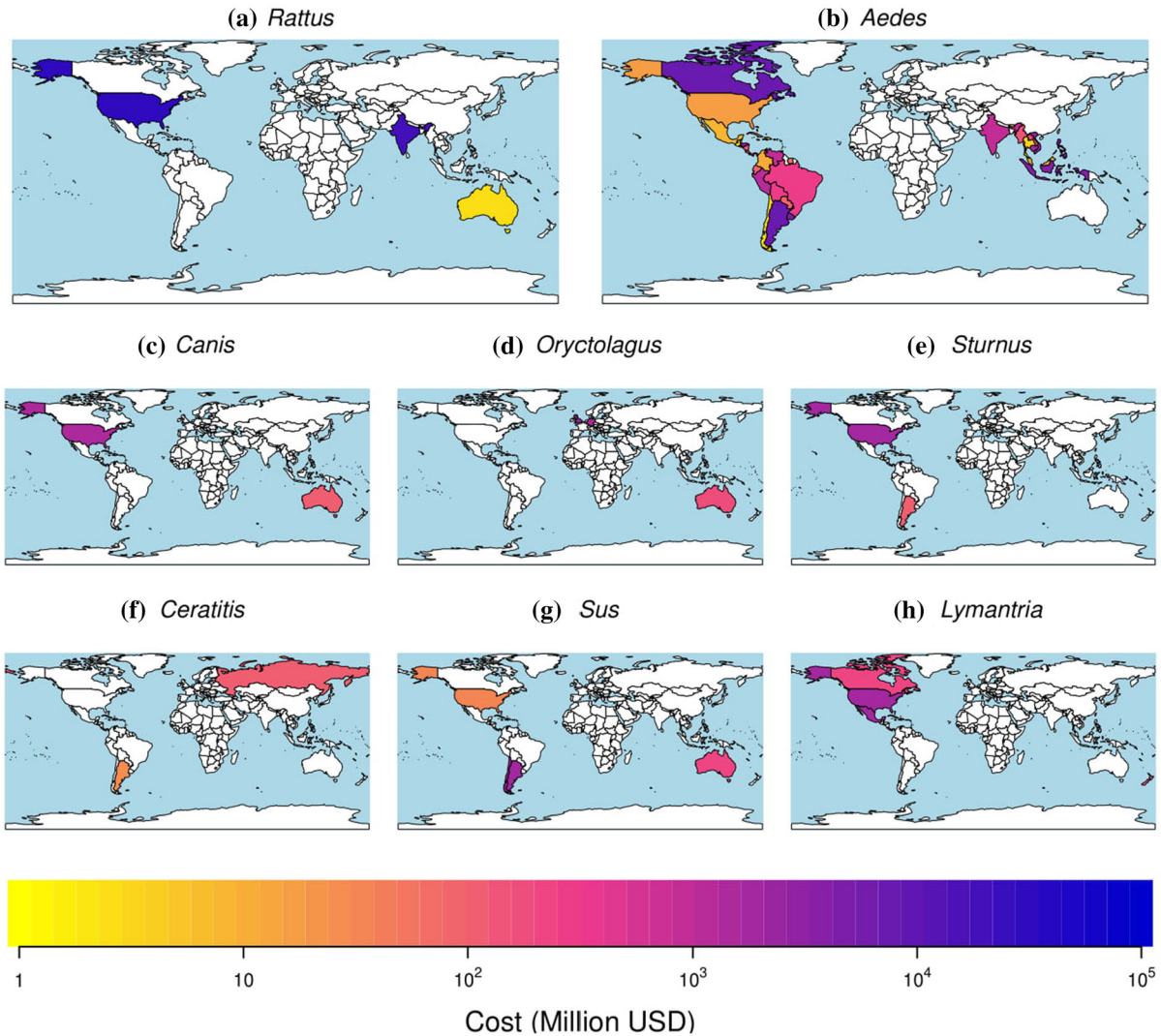| Column title	Description
Impacted sector	The sector impacted by the cost estimate in our socio-ecosystems (e.g., agriculture, health, public and social welfare)
Period of estimation	If provided, the exact period of time covered by the costs estimated, otherwise the raw formulation (e.g., late 90's, during 5 years)
Probable starting year Probable ending year	The year range in which the cost is known or assumed to occur. When not explicitly provided by the authors, we mentioned 'unspecified' in both columns unless the authors provided a clear duration time. In this case, we considered the 'Publication year' as a reference for the probable starting/ending year from which we added/subtracted the number of years* of the 'Period of estimation'. In the case of a cost estimate provided for a one-year period straddling two calendar years, we mentioned the latest year of the cost occurrence in both columns. When vague formulations were used (e.g., early 90's), we still translated them in probable ending/starting year (e.g., 1990–1995). We will harmonise the way these specific cases are dealt with when reviewing and validating new lines proposed by new contributors
Spatial scale	The spatial scale considered for estimating the cost: global (worldwide-scale), intercontinental (sites from two or more geographic regions) continental ('geographic region' level), regional (several countries within a single geographic region), country, site (for cost evaluated at intra-country level, including USA states) and unit (for costs evaluated for a well-defined surface area or entity)

*The number of years of the 'Period of estimation' is the difference between the 'Probable ending year' and the 'Probable starting year'.

Appendix A2: Maps illustrating the distribution of total economic costs (US$ million) at the country level.

These distributional data reflect the state of the Invacost database at the time of analysis. We note that one entry has since been updated in Invacost 4.0

(*Lymantria* spp. costs in Mexico are now listed as *Potential* rather than *Observed*)

(a) *Rattus*

(b) *Aedes*

(c) *Canis*

(d) *Oryctolagus*

(e) *Sturnus*

(f) *Ceratitis*

(g) *Sus*

(h) *Lymantria*

Cost (Million USD)

Appendix A3: Ecological and model shape parameters

Parameter description: Maximum accumulated cost C_{max}, Carrying capacity K (per unit area), Intrinsic growth rate α (per year), Best fit cost model types (I– IV, see Fig. 3), Model shape parameters (s_1, s_2, s, A, B, as they appear in Eqs. (4) and (5)).

Genus	C_{max}	K	α	Best fit cost model type	s_1	s_2	s	A	B
(a) *Rattus*	97,962	48.56	0.32	I	0	0.1	10	2	0.5
(b) *Aedes*	49,759	228.59	0.27	IV	1	0.1	0	2	0
(c) *Canis*	11,110	5.06	0.02	II	0.5	0.1	5	1.0136	0.0067
(d) *Oryctolagus*	2689	42.91	0.08	III	1	1	0	4.3279	0.2689
(e) *Sturnus*	2375	2.29	0.40	III	1	1	0	4.3279	0.2689
(f) *Ceratitis*	2774	16.24	1.93	III	1	1	0	4.3279	0.2689
(g) *Sus*	2622	7.95	0.22	IV	1	0.1	0	2	0
(h) *Lymantria*	4075	252.49	0.09	IV	1	0.1	0	2	0

Appendix A4: Population density as a function of time

The plots below show the population density for each genus as a function of time, given by Eq. (3) which is the solution of the logistic Eq. (2). This solution depends on the intrinsic growth rate α and carrying capacity K with corresponding values given in Appendix A3. The green marker represents the value of the initial density which is fixed as $u_0 = u(0) = 1$ for all genus. Note that the time-period is given in Table 1, where the initial year corresponds to time $t = 0$, and measured in years thereafter.
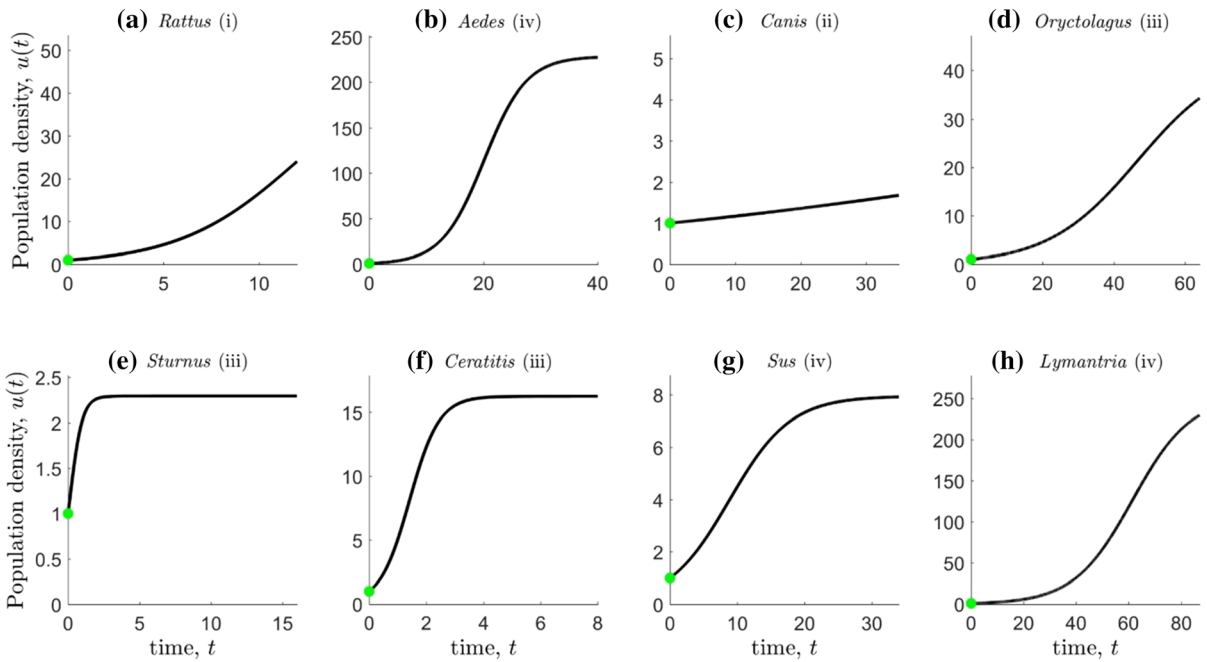
Appendix A5: Accumulated costs as a function of population density

The plots below show the accumulated cost-density functions for each genus. The best fitting model types (i)–(iv) are indicated, also see Fig. 2. The red marker represents the point where accumulated costs saturate at C_{max} precisely when the population density reaches the carrying capacity K. The corresponding ecological parameters, including model shape parameters are given in Appendix A3.
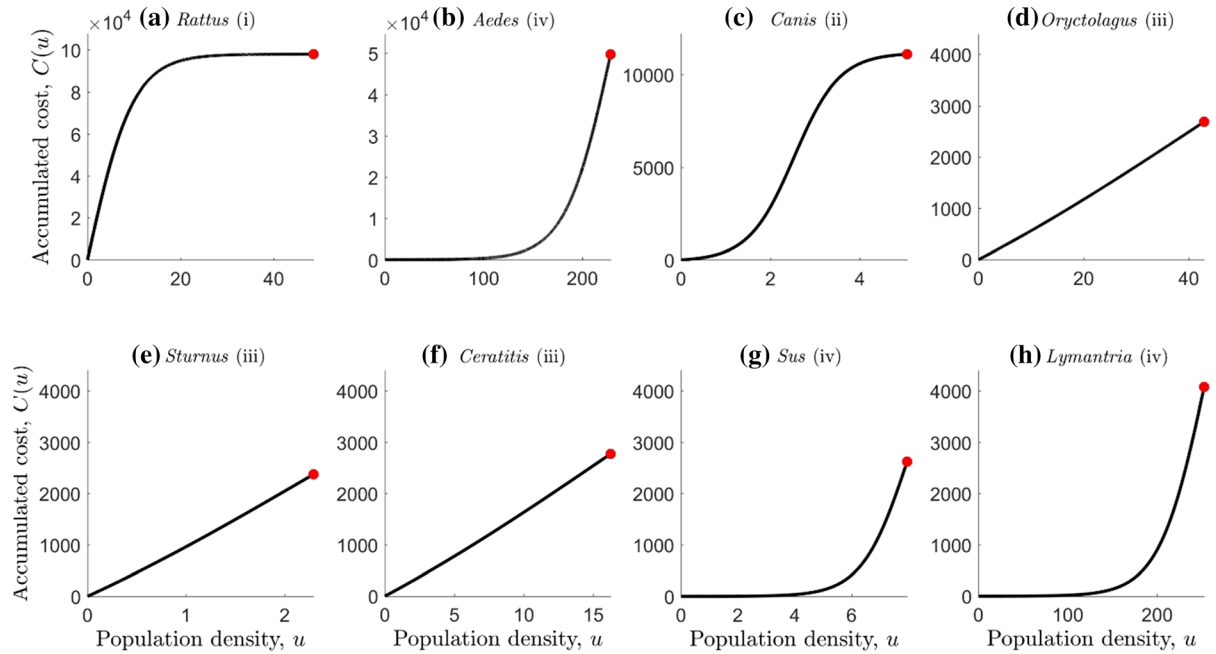
Appendix A6: First cost record of each IAS genus in each invaded country, where known

For reference, the year of first record in InvaCost is provided in order to determine the lag in cost detection following IAS introduction. Data on first records were obtained from the sTwist database, which is the most up-to-date global database for alien species' first records (Seebens et al. 2020).

Genus	Country	First InvaCost record	First record of invasion	Lag (years)
Aedes	Brazil	2000	1996	4
Aedes	Argentina	2000	1980	20
Canis	USA	1979	1930	49
Canis	Australia	2000	1815	185
Lymantria	USA	1933	1869	64
Lymantria	Canada	2002	1912	90
Oryctolagus	Great Britain	1955	1135	820
Oryctolagus	Australia	1953	1788	165
Oryctolagus	Germany	1970	1149	821
Oryctolagus	UK	2001	1135	866
Rattus	Australia	1998	1796	202
Rattus	UK	2010	1751	259
Rattus	Denmark	2002	1725	277
Rattus	USA	2005	1703	302
Sturnus	Argentina	2016	1987	29
Sturnus	Australia	2002	1856	146
Sturnus	USA	2000	1844	156
Sus	Argentina	2017	1910	107
Sus	Australia	1982	1788	194
Sus	Chile	2016	1574	442
Sus	USA	2000	1526	474

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