

# Modelling the damage costs of invasive alien species

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## Research Article

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1 *Research Article*

2 **Modelling the damage costs of invasive alien species**

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33 **Abstract**

34 The rate of biological invasions is growing unprecedentedly, threatening ecological and  
35 socioeconomic systems worldwide. Quantitative understandings of invasion temporal  
36 trajectories are essential to discern current and future economic impacts of invaders, and then  
37 to inform future management strategies. Here, we examine the temporal trends of cumulative  
38 invasion costs by developing and testing a novel mathematical model with a population  
39 dynamical approach based on logistic growth. This model characterises temporal cost  
40 developments into four curve types (I - IV), each with distinct mathematical and qualitative  
41 properties, allowing for the parameterization of maximum cumulative costs, carrying  
42 capacities and growth rates. We test our model using damage cost data for eight genera  
43 (*Rattus*, *Aedes*, *Canis*, *Oryctolagus*, *Sturnus*, *Ceratitis*, *Sus* and *Lymantria*) extracted from the  
44 InvaCost database – which is the most up-to-date and comprehensive global compilation of  
45 economic cost estimates associated with invasive alien species. We find fundamental  
46 differences in the temporal dynamics of damage costs among genera, indicating they depend  
47 on invasion duration, species ecology and impacted sectors of economic activity. The fitted  
48 cost curves indicate a lack of broadscale support for saturation between invader density and  
49 impact, including for *Canis*, *Oryctolagus* and *Lymantria*, whereby costs continue to increase  
50 with no sign of saturation. For other taxa, predicted saturations may arise from data  
51 availability issues resulting from an underreporting of costs in many invaded regions.  
52 Overall, this population dynamical approach can produce cost trajectories for additional  
53 existing and emerging species, and can estimate the ecological parameters governing the  
54 linkage between population dynamics and cost dynamics.

55 **Keywords:** biological invasions; cost modelling; InvaCost; logistic growth; non-native  
56 species; population dynamics; resource damages; socioeconomic impacts

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## 66 **1 Introduction**

67 The introduction, establishment and spread of invasive alien species (IAS) continues to erode  
68 biodiversity across biogeographic regions (Simberloff et al. 2013, Bellard et al. 2016). Global  
69 translocations of IAS are accelerating (Seebens et al. 2017, 2020), owing to globalisation-  
70 mediated intensification of trade and transport networks that increasingly interconnect novel  
71 species pools across historically separated areas (Seebens et al. 2018). The process of  
72 biological invasion is characterised by several discrete stages: transport, introduction,  
73 establishment and spread, with invasion success being impeded by geographical, biological  
74 and/or ecological features at each stage (Blackburn et al. 2011).

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

86 Despite the huge threat of IAS to biodiversity, human health and national economies, the  
87 capacity to prevent and manage invasions has remained poorly developed in many countries  
88 (Early et al. 2016). The limited international coordination for establishing management  
89 measures is even more striking. In particular, management has long been given low priority,  
90 most probably because it was assumed that such costs would be high relative to the potential  
91 benefits they could confer (Heikkilä 2011). However, management investments at early  
92 invasion stages, such as biosecurity, can prove more cost-effective than long-term control  
93 (Leung et al. 2002). Nonetheless, a variety of mitigation actions are conducted in managed  
94 areas worldwide (Veitch and Clout 2002, Rumlerová et al. 2016), but only limited  
95 information on IAS-associated costs exists under specific regional, taxonomic, or activity  
96 sector contexts, as well as over temporal scales. As a result, hitherto, the few large-scale  
97 studies of invasion costs have merely represented monetary totals (e.g. Pimentel et al. 2000,

98 2005) without accounting for the temporal dynamics or the complex typology of costs (e.g.  
99 management and damages). Therefore, so far it has not been possible to decipher how  
100 invasion costs are evolving over time, as well as how these trajectories might differ among  
101 taxonomic groups or invaded habitats. Yet, the impacts of IAS are not necessarily constant  
102 across a spatiotemporal context, and are likely to evolve when IAS populations grow and/or  
103 expand (Parker et al. 1999, Dickey et al. 2020), or because of lags in species detection that  
104 govern the deployment of control measures. For economic damages in particular, the extent  
105 to which costs track population dynamics remains poorly understood, while such information  
106 on cost dynamics is crucial to design, prioritize and adapt management actions (Diagne et al.  
107 2020a). Indeed, studies highlighting IAS economic cost trajectories could help divert more  
108 funds to biosecurity and other management actions, or set IAS management priorities to  
109 mitigate further damages. Especially, identifications of IAS for which damage costs are yet to  
110 saturate, *versus* those that have plateaued with time, could inform more efficient management  
111 measures among species.

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

125 Parker et al. (1999) presented a basic framework for understanding how species abundance,  
126 severity of damage, and the size of their invaded range relate to their total impact. In its  
127 original formulation, the authors assumed a constant *per capita* impact over time for a pest  
128 with a given range size, where impact is related only to abundance and species spread.  
129 However, the empirical support for this model is equivocal, as there are likely many scenarios

130 where *per capita* costs are not constant over time. Damages can vary from one year to the  
131 next, and this variance can depend on the taxonomic and trophic groups considered  
132 (Lehmann et al. 2020). In particular, differential *per capita* IAS impacts at different  
133 population densities can substantially modulate the extent of the ecological impacts of a  
134 given IAS population from one year to the next. Also, the trophic requirements and climate  
135 sensitivity of the IAS, in particular for insects, may greatly change along their ontogeny  
136 (Stockhoff 1993). Finally, a variety of synergies (Beggel et al. 2016, Zenni et al. 2020) and  
137 lags (Aikio et al. 2010, Coutts et al. 2017) may complicate the temporal trend of *per capita*  
138 IAS costs, and have so far lacked consideration.

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

## 160 **2 Methods**

### 161 ***2.1 Density-time function based on logistic growth***

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

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

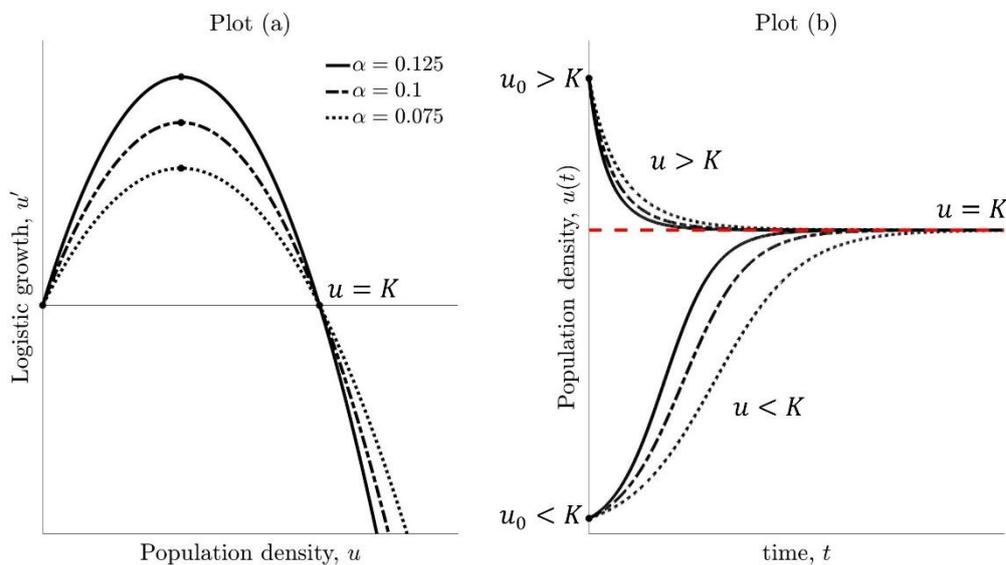
164 where  $u = u(t)$  is the time-dependent population density,  $u'(t)$  is the rate of change in  
 165 density with respect to time, and  $f(u)$  is the *per capita* growth rate. For many populations  
 166 (including IAS), the growth is bounded, a consequence of the fact that resources are usually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

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

171 where  $\alpha$  is the intrinsic growth rate. This equation can be readily solved to obtain:

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

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



174  
 175 **Figure 1.** (a) Logistic growth given by equation (2). (b) Population density as a function of  
 176 time given by equation (3).

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

## 191 **2.2 Accumulated cost as a function of IAS population density (cost-density functions)**

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

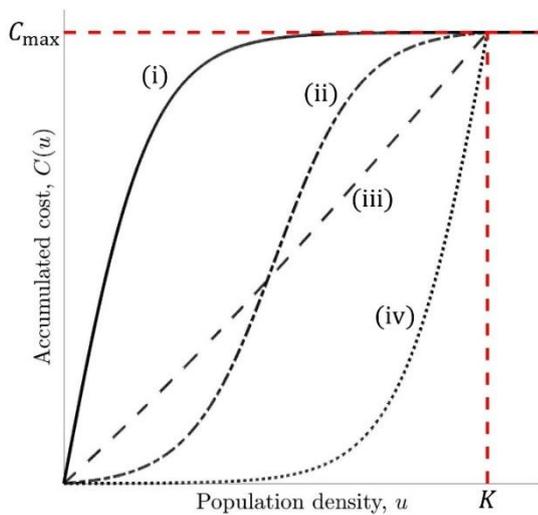
$$199 \quad C(u) = AC_{\max} \left[ \frac{1}{\frac{1-B}{B} \exp\left(-\frac{u}{s_2 K}\right) + 1} - B \right] \quad (4)$$

with

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

200 where  $C_{\max}$  is the maximum accumulated cost of impact,  $K$  is the carrying capacity,  $s_1, s_2$  are  
201 the curve shape parameters which lie between 0 and 1 inclusive, and  $A, B, s$  are parameters  
202 that are expressed in terms of these shape parameters. Note that this model choice is

203 supported by its frequent use by other authors when assessing impacts (see for e.g. Jackson et  
 204 al. 2015, Vander Zanden et al. 2017, Roberts et al. 2018, Sofaer et al. 2018).



205  
 206 **Figure 2.** Illustration of the four types of cost-density functions. Type (i) Low-threshold  
 207 curve with shape parameters  $s_1 = 0, s_2 = 0.1$ , Type (ii) S-shaped (sigmoidal) curve  $s_1 =$   
 208  $0.5, s_2 = 0.1$ , Type (iii) Linear curve  $s_1 = 1, s_2 = 1$  and Type (iv) High-threshold curve  $s_1 =$   
 209  $1, s_2 = 0.1$ .

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

- 212     ▪ For the Type (i) low threshold curve, the accumulated cost increases relatively fast at  
 213     low IAS population densities, and remains high at intermediate/larger densities.
- 214     ▪ For the Type (ii) S-shaped curve, the accumulated cost increases much faster at  
 215     intermediate values of IAS population density in comparison to Type (iii).
- 216     ▪ The Type (iii) linear curve presents a directly proportional relationship.
- 217     ▪ For the Type (iv) high threshold curve, the accumulated cost remains modest at low  
 218     IAS population densities, but increases rapidly for larger densities.

219 In the case  $u > K$ , one may expect annual costs to remain constant and of a considerable  
 220 magnitude, in which case the accumulated costs will grow linearly with time. However, for  
 221 this study, we assume that the threshold density has not been reached, so that  $u < K$ . Given  
 222 this, the cost-density function in equations (4)-(5) applies with limiting behaviour  $C \rightarrow C_{\max}$   
 223 as  $u \rightarrow K$ . Here,  $C_{\max}$  represents a ‘localized’ maximum accumulated cost as spatial aspects  
 224 are not accounted for. This provides an adequate description for scenarios where the IAS has  
 225 stopped spreading (i.e. reached its bioclimatic niche limits) (Barnett 2001, Aplin et al. 2011).

226 Also, in a more realistic scenario, annual damage costs may continue during this phase, but  
227 these costs can be expected to be several orders of magnitude smaller than the largest annual  
228 cost, and the total cost is likely driven more by management costs, which we do not consider.  
229 As a result, the increase in the accumulated cost would be negligible, and therefore can be  
230 considered at a ‘near’ saturation level, i.e. with constant  $C_{\max}$ .

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

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

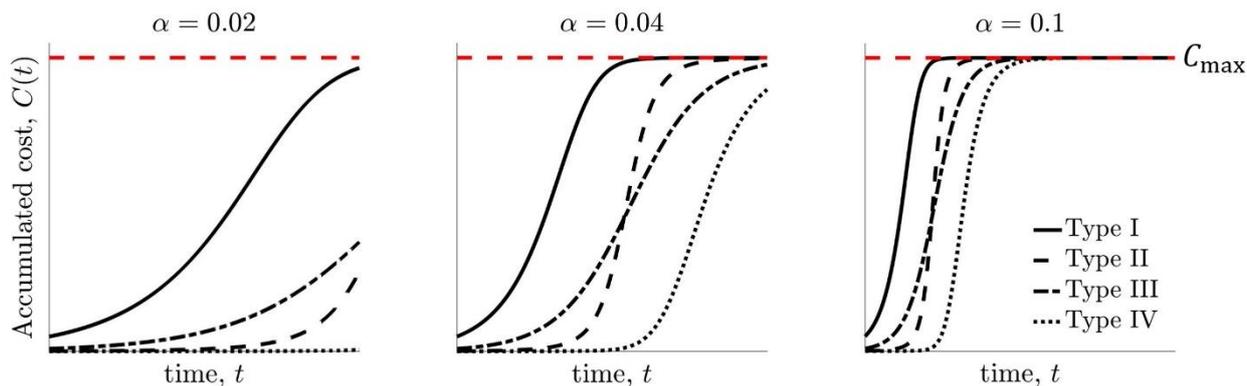
236 We note that the model assumes that the accumulated damage cost remains constant over  
237 time given a fixed IAS density. This may be reasonable on a short time scale, but in the long-  
238 term, the damage cost for a given IAS density may change, e.g. due to economic growth  
239 (Haubrock et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

240 In an ecological context, Type (i) costs may be common for species whose impacts are  
241 roughly equivalent across all abundance levels, reaching near-maximal accumulated costs at  
242 relatively small densities. At the other extreme, Type (iv) costs correspond to species whose  
243 damages are only felt once they have reached very high abundance (Yokomizo et al. 2009).  
244 As an illustration, fouling species who require high densities in order to block pipes, such as  
245 zebra mussels, may be described by Type (iv) (Elliott et al. 2005). Conversely, highly  
246 voracious novel predators introduced in insular communities, such as the feral cat (*Felis*  
247 *catus*) (Hilton and Cuthbert 2010) may rather behave as Type (i). Indeed, these predators  
248 have been able to have deleterious impacts on native fauna that begin even at low densities,  
249 and that do not appear to saturate until near maximal densities. Alternatively, species could  
250 show linear relationships with cost (Type iii) if *per capita* impacts are density-independent.  
251 This can be expected in situations where competition is low while resources are high. This  
252 form has been found for instance for the balsam fir sawfly (*Neodiprion abietis*, Parsons et al.  
253 2005). Most often, linear relationships have been suggested as being common in nature (see  
254 for e.g. Elgersma and Ehrenfeld 2011, Panetta and Gooden 2017). Finally, relationships could  
255 be sigmoidal (Type ii) if density plays both a positive and negative role, which would be  
256 expected if intraspecific competition limits impacts at high density, while Allee effects limit

257 impacts at low density. This form is predicted in models of invasive rodent grazing impacts  
 258 on crops (Brown et al. 2007).

259 **2.3 Accumulated cost as a function of elapsed time since the introduction of IAS (cost-time**  
 260 **functions)**

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



263  
 264 **Figure 3.** Accumulated cost models (I) – (IV) over time since the introduction of IAS,  
 265 corresponding to each functional Type (i) – (iv), respectively, (see Figure 2), presented for  
 266 different values of intrinsic growth rate  $\alpha$ . Line styles are the same as in Figure 2.

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

$$C(t) \approx AC_{\max} \cdot \frac{B(1-B)}{s_2K} \cdot u_0 e^{\alpha t}, \quad (7)$$

276 which demonstrates that all cost models (I - IV) allow for a rapid increase in damage costs  
 277 that arise due to the rapid spread of the IAS shortly after its initial introduction. This is a  
 278 direct result of the fact that logistic growth in the population assumes that the species density  
 279 grows exponentially on a short time scale, which is normally the case for successful invaders

280 during the early phases of the invasion (Shigesada 1997, Crooks 2005). Nonetheless,  
281 ‘invasion debt’ can result in considerable lag times between invader arrival and perceived  
282 impact (Essl et al. 2011).

#### 283 ***2.4 Data collection and processing***

284 Cost data were extracted from the InvaCost database (2419 entries; Diagne et al. 2020b,  
285 <https://doi.org/10.1038/s41597-020-00586-z>) as well as another related data source from  
286 searches made in non-English documents (5,212 entries; Angulo et al. 2020; available at  
287 <https://doi.org/10.6084/m9.figshare.12928136>). Literature sources were obtained *via*  
288 systematic searches in online repositories (Web of Science, Google Scholar and Google  
289 search engine). We gathered additional cost information through contacting experts and  
290 searching specific literature databases of the countries/languages considered, and contacting  
291 official national managers or researchers that could provide cost data. All cost entries were  
292 standardized to a common currency and year for comparability (2017 US\$). This process also  
293 considered an inflation factor based on the Consumer Price Index of 2017 relative to the year  
294 of the cost estimation. All information on the compilation and standardization of data  
295 recorded in InvaCost are detailed in Diagne et al. (2020b). Also, we provide the Appendix A1  
296 for presenting the categories used for each descriptive variable, which corresponds to a  
297 specific column in the InvaCost database (Diagne et al. 2020b).

298 For analyses implemented in the present study, we extracted entries for all species within the  
299 following focal genera: *Rattus* (rats), *Aedes* (mosquitoes), *Canis* (dogs), *Oryctolagus*  
300 (rabbits), *Sturnus* (starlings), *Ceratitis* (fruit flies), *Sus* (pigs) and *Lymantria* (moths). They  
301 were chosen as they comprised some of the richest data, and represented various taxonomic  
302 groups and therefore contrasted life history traits, especially concerning invasion dynamics.  
303 For those genera, the costs entries selected were those estimated at the country level, i.e. not  
304 provided at supra-national or site scales (Table 1; see Appendix A2 for a distribution map of  
305 total economic costs (US\$ million) at the country level). For this purpose, we filtered these  
306 genera using the “Genus” column, and only incorporated entries at the *Country* level within  
307 the “Spatial\_scale” column. We excluded any cost estimates that were considered to have  
308 *Low* reliability (i.e. not sourced from official/peer-reviewed material or not reproducible;  
309 “Method\_reliability” column), and any costs that were *Potential* (i.e. predicted or  
310 extrapolated), rather than actually *Observed* (“Implementation” column) (Diagne et al.  
311 2020b).

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

320 All reported costs were summed across species and countries within a given year to obtain a  
 321 global accumulated cost for each genus over time (see also Appendix A2). Table 1 shows the  
 322 number of independent references used to produce each genus' cost curve, as well as the  
 323 number of unique years for which a total cost could be calculated (i.e. the number of non-  
 324 repeated years for which cost data were available from InvaCost across all references). We  
 325 excluded those cost values from the dataset that reported comparatively very high costs, i.e.  
 326 any cost value that was greater than  $Q_3 + 1.5 \times IQR$  was removed (see Table 1), where  $Q_3$  is  
 327 the upper quartile and  $IQR$  is the interquartile range of the dataset. A single outlier was found  
 328 for the genera *Ceratitis* and *Sus*, while three and five outliers were found for *Lymantria* and  
 329 *Oryctolagus*, respectively. We found no outliers for the other considered genera.

330 **Table 1.** A list of the eight genera used to create cost curves. The years in which extreme  
 331 costs (outliers) occurred, and the corresponding cost values are given for each genus, where a  
 332 blank space indicates that no outliers were found. The number of independent references  
 333 indicates how many separate publications within the InvaCost database were used to create  
 334 the cost curve for that genus, while the number of independent years is the unique cost-year  
 335 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) <i>Rattus</i>	1998 – 2010			6	6
(b) <i>Aedes</i>	1977 – 2017			34	25
(c) <i>Canis</i>	1979 – 2014			7	6
(d) <i>Oryctolagus</i>	1955 – 2019	1953	432.01	16	31
		1996	733.77		
		2001	1938.07		

		2003	518.50		
		2010	433.09		
(e) <i>Sturnus</i>	2000 – 2016			6	5
(f) <i>Ceratitidis</i>	1999 – 2007	1981	13.50	5	5
(g) <i>Sus</i>	1982 – 2016	2017	2293.53	10	9
(h) <i>Lymantria</i>	1933 – 2020	1981	3355.99	8	39
		2002	2203.89		
		2004	368.50		

336

337 We modelled the accumulated cost data (US\$ million) using the four different types of  
338 accumulated cost models (I - IV). The first reported year of damage cost was taken as the  
339 initial year, corresponding to time  $t = 0$ , which is measured in years thereafter. For example,  
340 the time period for *Rattus* is from 1998 ( $t = 0$ ) to 2010 ( $t = 12$ ). The non-linear regression  
341 curve fitting tool ‘fitnlm’ from MatLab was used to identify which model optimally fitted  
342 the data, and selected it based on the highest squared correlation coefficient ( $r^2$ ) or lowest  
343 root mean square error (*RMSE*). Once the best fitting model was found, we reported the  
344 corresponding model parameters for each genus; specifically, the maximum accumulated cost  
345  $C_{\max}$ , carrying capacity  $K$  and the intrinsic growth rate  $\alpha$ .

### 346 **3 Results**

347 We found fundamental differences among taxa in the nature of their cost accumulations over  
348 time, reflected in different best-fitting model types (Figure 4). Of the eight genera assessed,  
349 *Rattus* was best described by model Type I, *Canis* by model Type II, *Oryctolagus*, *Sturnus*  
350 and *Ceratitidis* by model Type III, and lastly *Aedes*, *Sus*, and *Lymantria* by model Type IV  
351 (Table 2, Figure 4). Models for each taxon were associated with a very high  $r^2$  ( $\geq 0.952$ ),  
352 indicating an extremely close model fit with the cost data, with the exception of *Sturnus* and  
353 *Canis*, with still high  $r^2$  values (Table 2). The shaded areas in Figure 4 represent confidence  
354 regions providing the range of predicted cumulative costs. Note that lower confidence levels  
355 were used for those genera with higher data variability, and comparatively, a smaller number  
356 of reported costs (Tables 1, 3).

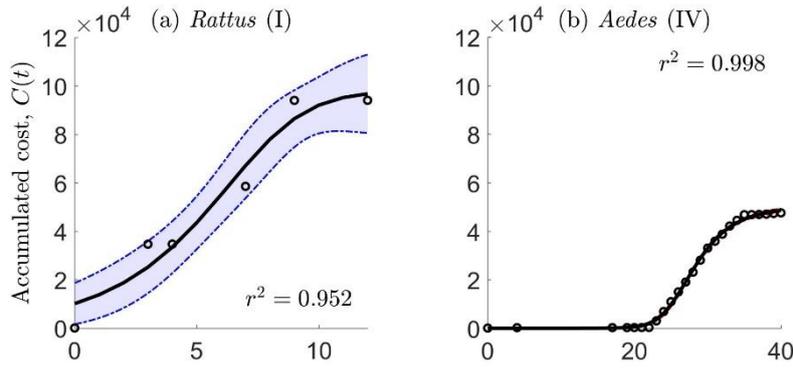
357 *Rattus* (Type I) costs were transitioning to the saturation phase, whilst *Canis* (Type II) costs  
358 were found to be accelerating. Nonetheless, within model types, curvatures differed  
359 substantially in their cost accumulation phases (see Figure 4). Among the Type III model fits,  
360 we found *Oryctolagus* in the early phase with gradually increasing accumulated costs,

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

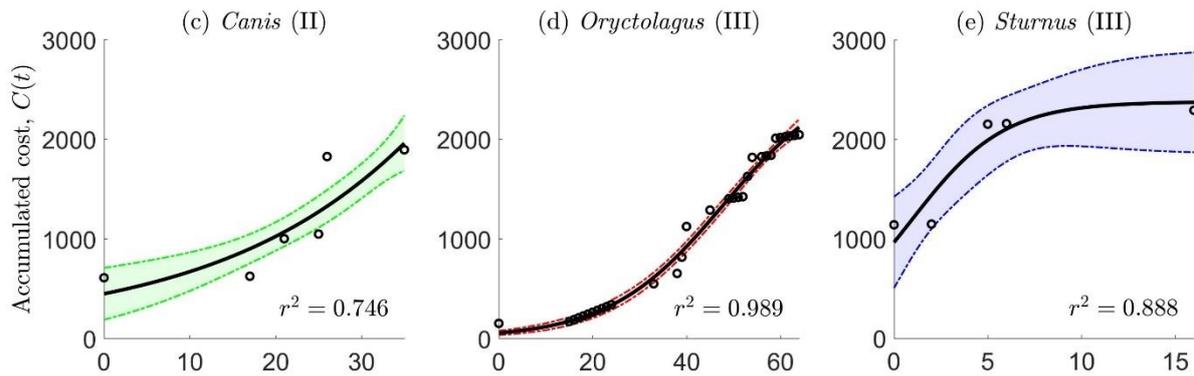
366 Marked differences in the magnitude of costs were also exhibited within and between model  
367 types (Table 2), with *Rattus* exceeding all other genera, by far, in the total amount of  
368 damages incurred (i.e. greatest  $C_{\max}$ ), followed by *Aedes*, with approximately half the *Rattus*  
369 total cost. In general,  $C_{\max}$  was one magnitude higher for *Rattus*, *Aedes* and *Canis* when  
370 compared to the other taxa (Table 2). Accumulated maximum costs of *Oryctolagus*, *Sturnus*,  
371 *Ceratitidis* and *Sus* were predicted to be similar in value, ranging in between US\$ 2,375 and  
372 2,774 million (2007), whereas the maximum cost for *Lymantria* was slightly higher (US\$  
373 4,075 million) (Table 2).

374 One advantage of the dynamical modelling process is that it can provide information  
375 regarding ecological parameters for taxa at a global scale directly from the cost data (i.e. a  
376 top-down approach). We note that our carrying capacity values should not be interpreted as  
377 the true maximum population density that the species can reach globally, but are reflective of  
378 a proportional maximum. While values of  $K$  require rescaling by some unknown, potentially  
379 disparate constant across taxa in order to be interpretable, our fitted intrinsic growth rates can  
380 be compared directly among taxa if cost-density functions are constant through time. The  
381 highest intrinsic growth rate was found for *Ceratitidis*, with a value  $\alpha = 1.93$  (Table 3), which  
382 explains the comparatively rapid cost accumulation with a quick progression towards the  
383 maximum cost (Figure 4). This was followed by *Sturnus*, *Rattus*, *Aedes* and *Sus*, with a lower  
384 (but similar) value of  $\alpha$  lying between 0.1 and 1, representing slower growth. The remaining  
385 taxa exhibited a much lower intrinsic growth rate with  $\alpha < 0.1$ , which was reflected by a  
386 greater lag or delayed increase in the cost accumulation (Figure 4, Table 3).

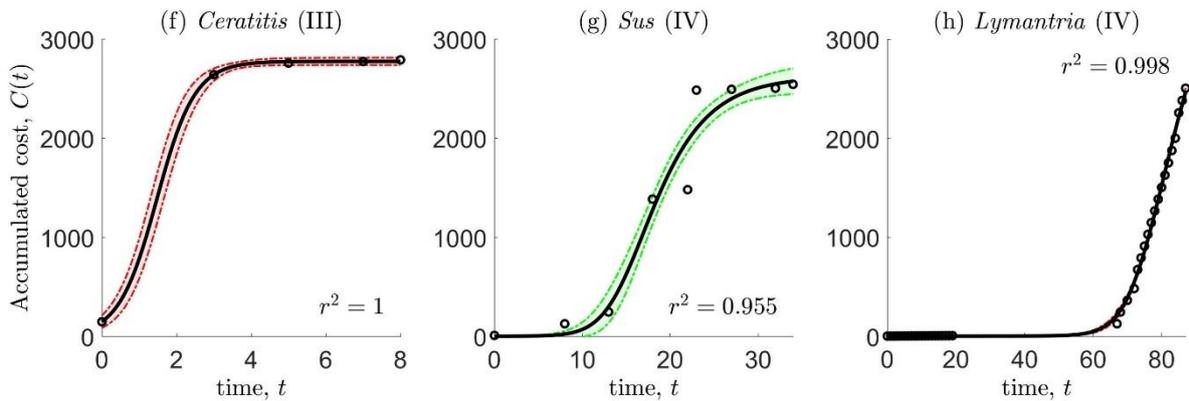
387



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390



391 **Figure 4.** Plot of the best fit accumulated cost model (either Types I - IV) against the cost  
 392 data (US\$ million), with the reported  $r^2$  value. The best fitted model for each is indicated in  
 393 parentheses after the name of each genera; also see Table 2. The shaded areas represent  
 394 confidence regions for the range of predicted cumulative costs with confidence levels 95%  
 395 (red), 80% (blue) and 50% (green) (see Table 3). See Appendix A4 for the corresponding  
 396 plots for each genus with accumulated cost as a function of population density.

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

Genus	Best fit cost model	Coefficient of determination $r^2$	Root mean square error $RMSE$	Maximum accumulated cost $C_{max}$
(a) <i>Rattus</i>	I	0.952	10500	97962
(b) <i>Aedes</i>	IV	0.998	858	49759
(c) <i>Canis</i>	II	0.746	369	11110
(d) <i>Oryctolagus</i>	III	0.989	79.4	2689
(e) <i>Sturnus</i>	III	0.888	275	2375
(f) <i>Ceratitidis</i>	III	1	14.7	2774
(g) <i>Sus</i>	IV	0.955	269	2622
(h) <i>Lymantria</i>	IV	0.998	35.1	4075

400

401 **Table 3.** Confidence intervals for the ecological parameters  $K$  and  $\alpha$ , where smaller  
402 confidence levels were used for those genera with high data variability and relatively smaller  
403 sample size. Confidence levels used are 95% (red), 80% (blue) and 50% (green) –  
404 corresponding to the colour scheme in Figure 4. Note that the lower interval limit for the  
405 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, $\alpha$ (per year)	Confidence interval for $\alpha$
(a) <i>Rattus</i>	80%	48.56	[9.66, 87.46]	0.32	[0.16, 0.48]
(b) <i>Aedes</i>	95%	228.59	[105.81, 351.38]	0.27	[0.25, 0.29]
(c) <i>Canis</i>	50%	5.06	[0, 18.9]	0.02	[0.02, 0.03]
(d) <i>Oryctolagus</i>	95%	42.91	[29.47, 56.36]	0.08	[0.07, 0.09]
(e) <i>Sturnus</i>	80%	2.29	[1.24, 3.35]	0.40	[0.03, 0.77]
(f) <i>Ceratitidis</i>	95%	16.24	[9.37, 23.11]	1.93	[1.69, 2.17]
(g) <i>Sus</i>	50%	7.95	[1.42, 14.48]	0.22	[0.17, 0.28]
(h) <i>Lymantria</i>	95%	252.39	[87.29, 417.69]	0.09	[0.08, 0.1]

406

407 See Appendix A3 for a compiled list of ecological and model shape parameters as they  
408 appear in equations (4) and (5).

#### 409 **4. Discussion**

410 The present study developed and applied a novel mathematical model to examine and predict  
411 the cumulative damage costs of IAS over time. Among eight genera containing notorious  
412 invaders, we report marked differences in cost cumulations. Instances of high costs likely  
413 mirror the widespread distribution of genera which damage infrastructure, agriculture and  
414 represent threats for human health (Meerburg et al. 2009, Luis et al. 2013; Iwamura et al.  
415 2020). Interestingly, the best fitting models, and their underlying parameters, differed among  
416 genera, indicating that the trajectories of cost cumulations can differ substantially among  
417 IAS; these differences can be explained by several factors, potentially including the sectors  
418 that the IAS impact, their abundance, distribution, ecology and their attention from  
419 researchers and other stakeholders that report damages. Furthermore, we determined  
420 differences in intrinsic growth rates of costs among genera due to changes in density,  
421 indicating differential lag time effects in the development of costs at the global scale. The  
422 exponential growth in costs shown by most taxa suggests that management actions could,  
423 reciprocally, result in exponential reductions of these costs below certain population  
424 thresholds. Whilst there are limitations to our approach, including considerations for future  
425 costs in novel invaded regions where species could still be far from  $C_{\max}$  and  $K$ , and while  
426 underlying cost data are poorly available, these models help to elucidate how reported  
427 invasion costs have developed over time among taxa, informing management strategies for  
428 IAS. This potentially includes future IAS without a current invasion history within these focal  
429 genera, given high projected invasion rates in future (Seebens et al. 2020).

#### 430 ***4.1 Cost cumulation model***

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

439 It is important to note that the time of initial cost onset in our model is not the onset of each  
440 genus' invasion. Our cost curve typology is meant to describe only the shape of the accrual of  
441 detected damage costs over time, rather than that of the invasion trajectory from start to

442 finish. In an analogous description of the shape of detected IAS spread trajectories; for  
443 example, Shigesada et al. (1995) defined their spread typology after accounting for a variable  
444 lag phase across species. In the same way, we model only the damage cost accumulation of  
445 IAS after the first report of their economic impacts. Prior to this detection, IAS can be subject  
446 to a variety of factors such as Allee effects and low cost detection effort – especially in the  
447 case of unintentional introductions or species with less of a nuisance status (Hastings et al.  
448 2005), which cause variable lag times between the dates of first introduction of each genus in  
449 our dataset and their first cost detection (see Appendix A5). For instance, *Aedes* spp. have  
450 reported lag times of below 20 years (i.e. initial cost detections less than 20 years after their  
451 known date of first introduction) in their invaded countries, while *Lymantria* spp were  
452 present for 90 years before their impacts were reported in Canada. This difference likely  
453 reflects the nuisance status of mosquitoes in terms of public health (Weber 1979), and the  
454 delay in substantial forestry impacts of *Lymantria* in North America (Pelkki & Sherman  
455 2020).

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

470 Our cost modelling approach accounts for the population dynamics of various genera, and  
471 thus provides a useful framework for investigating temporal cost patterns across various  
472 habitat types and taxonomic groups. By analyzing the shape of the cost-time curves  
473 characterized by model Types (I - IV), we were able to capture how impacts accrue not only  
474 across taxa, but also at different stages of an invasion process. Further, our approach was

475 fitted against actual damage cost data extracted from the most comprehensive database to  
476 date (InvaCost). These data are, however, subject to a series of limitations that likely lead to  
477 an underestimation of reported costs relative to true economic impacts of IAS (Diagne et al.  
478 2020b). Accordingly, the Types of model selected here were inherently influenced by the  
479 nature of underlying data, suggesting that the resolution of cost reporting should be improved  
480 for economic damages globally. Yet, the consistent excellent fits across genera is an  
481 indication of a certain degree of robustness not only of the models but also of the cost data.  
482 More generally, studies on temporally dynamic models of species population growth are  
483 plentiful in the literature (Petrovskii and Li 2006, Kawasaki and Shigesada 2007, Hart and  
484 Avilés 2014, Lohr et al. 2017 etc.); however, very few rely on real cost data, and have instead  
485 focused more on a theoretical examination of optimal control (Yokomizo et al. 2009,  
486 Hastings et al. 2007, Baker et al. 2019).

#### 487 ***4.2 Model Types and maximum accumulated costs***

488 Cost cumulations differed substantially among the genera assessed in the present study,  
489 resulting in their representations over the four model Types. Nonetheless, whilst Types I and  
490 II were displayed solely by *Rattus* spp. and *Canis* spp., respectively, Types III and IV were  
491 more common ( $n = 3$  taxa each). All Types provided an excellent fit to the data ( $r^2 \geq$   
492 0.952), with the exception of *Canis* spp. (Type II) and *Sturnus* spp. (Type III) with still high  
493  $r^2$  values – indicating good fits (see Table 2). The relative commonness of Type III and IV  
494 curves suggests a lack of broadscale support for saturation between invader density and  
495 impact across all genera, as not all displayed an asymptote in cost dynamics. Reciprocally,  
496 this is highly useful for management, as effective actions that reduce invader abundances  
497 could result in an exponential decrease in damage costs from invasions. However, this is less  
498 relevant for species with lower maximum costs, where reductions in costs could be relatively  
499 small in magnitude.

500 The highest accumulated cost was quantified from *Rattus* spp. (Table 2). This is not  
501 surprising as this genus was one of the earliest taxa recognized as an IAS, and has reached  
502 nowadays a widespread, worldwide distribution (CABI 2019). We also note that the costs  
503 would be much higher for *Rattus* spp. should we have included management costs. Because  
504 rat invasions are known to have an extreme detrimental effect on numerous native species  
505 (Atkinson 1985), particularly when introduced to oceanic islands (Shiels et al. 2014, Ruffino  
506 et al. 2015) – in some cases leading to rapid species extinctions (Bell 1978), they have been

507 very extensively managed. In addition to these ecological impacts, these rodents host more  
508 than sixty zoonotic diseases, reducing crop yields and food reserves, and posing a serious  
509 threat to human health (Meerburg et al. 2009, Luis et al. 2013). The next highest accumulated  
510 cost was assigned to *Aedes* spp., which was approximately half of the cost incurred by *Rattus*  
511 spp. (Figure 4, Table 2).

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

535 In contrast, the cost impacts of the remaining genera were found to be one magnitude lower,  
536 with similar cost saturation levels (Table 2). This is primarily due to relatively lower direct  
537 damages to human assets, and the lack of association with disease spread. Nonetheless, these  
538 costs are only lower relative to the costliest species and remain unacceptably high in absolute  
539 value. In addition, these other genera are known to be highly ecologically damaging, yet such

540 damages are more difficult to quantify in economic value than impacts to primary human  
541 sectors (e.g. agriculture) (but see Hanley and Roberts, 2019). It is in fact likely that costs  
542 from these genera, as is also the case for several other taxa, are currently highly  
543 underestimated (Diagne et al., 2020b). This suggests that better cost reporting is required to  
544 more accurately discern the density-impact relationship of IAS, and that this will lead to  
545 higher costs than those reported here.

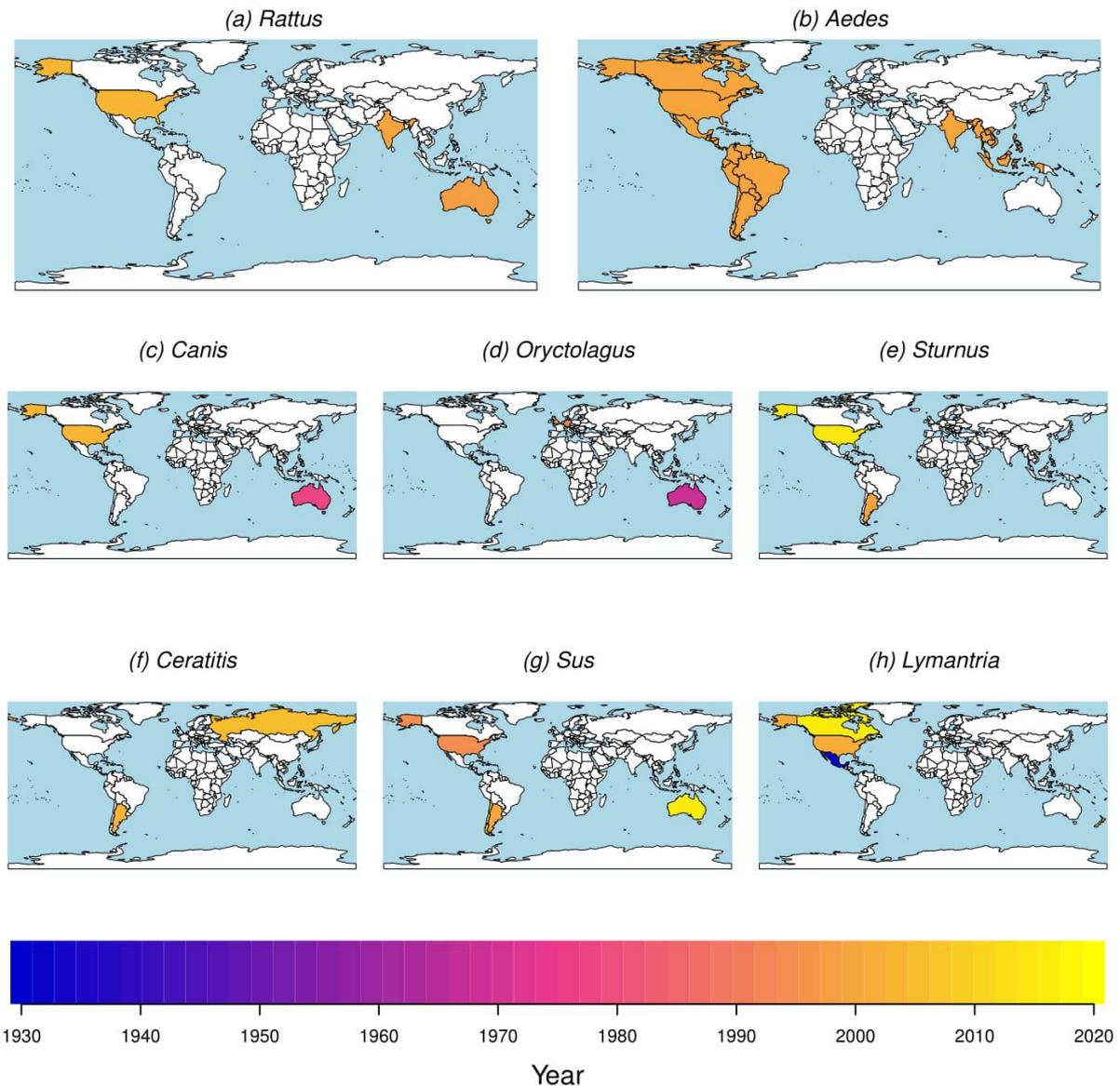
### 546 ***4.3 Cost trajectories***

547 Data permitting, the mathematical model presented could equally be applied locally or  
548 nationally to deduce cost trajectories at finer scales, and to compare different populations of  
549 IAS. For instance, the model we developed was applied in a recent study (alongside other  
550 statistical approaches) to analyze global trends in costs of aquatic IAS (Cuthbert et al. 2020b).  
551 In that vein, populations at an invasion front may exhibit an earlier stage of cost cumulation  
552 as compared with longstanding invader populations. Whilst *Ceratitis* spp. exhibited a  
553 relatively rapid intrinsic growth rate ( $\alpha > 1$ ), other groups such as *Rattus* spp., *Aedes* spp.,  
554 *Sturnus* spp. and *Sus* spp. had intermediate growth rates ( $0.1 < \alpha < 1$ ), whereas growth rates  
555 of genera such as *Canis* spp., *Oryctolagus* spp. and *Lymantria* spp. were much lower ( $\alpha <$   
556  $0.1$ ) (Table 3). These patterns may also relate to the pathways associated with these species,  
557 as well as their life histories (e.g. rapid reproduction) or introduced ranges, with costs arising  
558 from new invaded areas through time (Figure 5). For example, invasions by *Canis* spp.,  
559 *Oryctolagus* spp. and *Lymantria* spp. only occurred recently in the United States and Europe,  
560 and thus time lags in cost development likely emanate from delays in novel invasions,  
561 resulting in lower  $\alpha$ .

562 The rapid intrinsic growth rate of *Ceratitis* spp. reflects a capacity to accrue substantial costs  
563 soon after establishment, with species within this genus known to cause substantial damages  
564 and losses to fruit crops, as well as through the transmission of fruit-rotting fungi (Cayol et al.  
565 1994). For *Aedes* spp., the presence of dormant life stages that are well-adapted to succeed in  
566 urbanized environments through the exploitation of artificial habitats (i.e. artificial  
567 containers) mediates high invasion success (Medlock et al. 2012). This association with  
568 humans, coupled with short generation times and high fecundity, likely caused a relatively  
569 rapid increase in costs. Despite this, an intermediate growth rate in *Aedes* spp. may result  
570 from disparate cost reporting prior to the last two decades for those taxa, whereas taxa with a  
571 higher growth rate (i.e. *Canis* spp.) were reported more recently, reducing delays in modelled

572 population growth rates. Moreover, costs from disease are likely to accrue rapidly once a  
573 given pathogen or parasite is in circulation. Overall, the widespread pancontinental impacts  
574 of *Aedes* spp., and more particularly *A. aegypti* in tropical areas, may have led to a rapid  
575 increase in human health costs. This rapid increase could also be due to concurrent,  
576 analogous trends in urbanization, whereby this species has adapted to perform well in close  
577 association with humans. Similarly, *Rattus* spp. and *Sturnus* spp. can quickly reach high  
578 abundances in urban areas, where populations can spread disease and damage infrastructures,  
579 as well as agricultural enterprises elsewhere (Weber 1979; Linz et al. 2007; Meerburg et al.  
580 2009).

581 In contrast, *Lymantria* spp. costs accrued more slowly, indicating that interest in this species  
582 was subject to a longer lag, or that its impacts to the forestry sector took longer to become  
583 apparent following its invasion (invasion debt). *Lymantria* spp. exhibit just one generation  
584 per year (Doane and McManus, 1981), with spread largely dependent on long-range assisted  
585 movements by humans (e.g. cars or boats) (Hajek and Tobin, 2009). Our data indicate that  
586 the initial reported impacts from this species were relatively small, and increased rapidly only  
587 in the last few decades. However, rather than being an artefact associated with their life  
588 history, this could reflect growing interactions with growing forest industries within its  
589 invaded range (e.g. the United States, Twery 1991; Pelkki & Sherman 2020). Indeed,  
590 *Lymantria* costs accrued only recently in the United States and Canada, following earlier  
591 impacts of a lower magnitude in Mexico (Figure 5). Similarly, *Canis* impacts have been slow  
592 to accrue, but that taxon has been characterized by more recent invasion cost reporting in  
593 North America. Moreover, despite high fecundity, invasions by *Oryctolagus* spp. occurred  
594 only relatively recently within Europe. In contrast, genera such as *Aedes* and *Sus* exhibited  
595 similar timing of cost reporting pan-continently (Figure 5). Finally, *Ceratitidis* is  
596 characterized by very recent and concurrently reported invasion costs in Russia and  
597 Argentina.



598

599 **Figure 5.** Maps illustrating the global temporal distribution (years) in which the first cost was  
600 reported (independent of the magnitude of the respective cost) for each genus. The color  
601 ramp thus corresponds to the year in which the cost was first reported, regardless of its  
602 monetary value. Also see Appendix A2 for a total distribution of costs (US\$ million) at the  
603 country level.

#### 604 **4.4. Synthesis**

605 Understanding the dynamics of cost development at different time scales, from initial cost  
606 accruals to large time saturation levels, is fundamentally required to better inform  
607 stakeholders and scientists of the IAS that require management actions. In this study, we  
608 presented a novel mathematical model which incorporates the dynamical nature of the species

609 population, and demonstrated that it provides a useful framework for the analysis of cost  
610 accumulations. This model can identify genera whose damage costs may escalate rapidly –  
611 thus allowing data-informed prioritization and improved efficiency of control actions. In  
612 situations where costs have saturated relative to population density (such as *Ceratitidis* and  
613 *Sturnus*), large population management expenditures may be necessary to impact cost  
614 trajectories. In contrast, exponential cost trajectories (such as for *Lymantria* and *Oryctolagus*)  
615 suggest that population management could result in exponential damage reductions. Although  
616 many mathematical models have been developed to relate ecological impacts and species  
617 abundances through ‘density-impact’ curves, very few have attempted to provide a direct link  
618 with the incurred costs, and backed them up with empirical cost data. While the costs of IAS  
619 are expected to increase in the forthcoming years, more IAS cost estimations are required in  
620 order to get improved assessments of temporal trends in costs of IAS, in turn ameliorating the  
621 predictive models and ultimately management strategies. Moreover, given cost-density  
622 relationships have been shown to exhibit intraspecific differences among populations (Strayer  
623 2020), improved cost resolution at smaller scales could permit population level comparisons  
624 in cost developments.

625 **Appendix**

626 **Appendix A1: Glossary of terms**

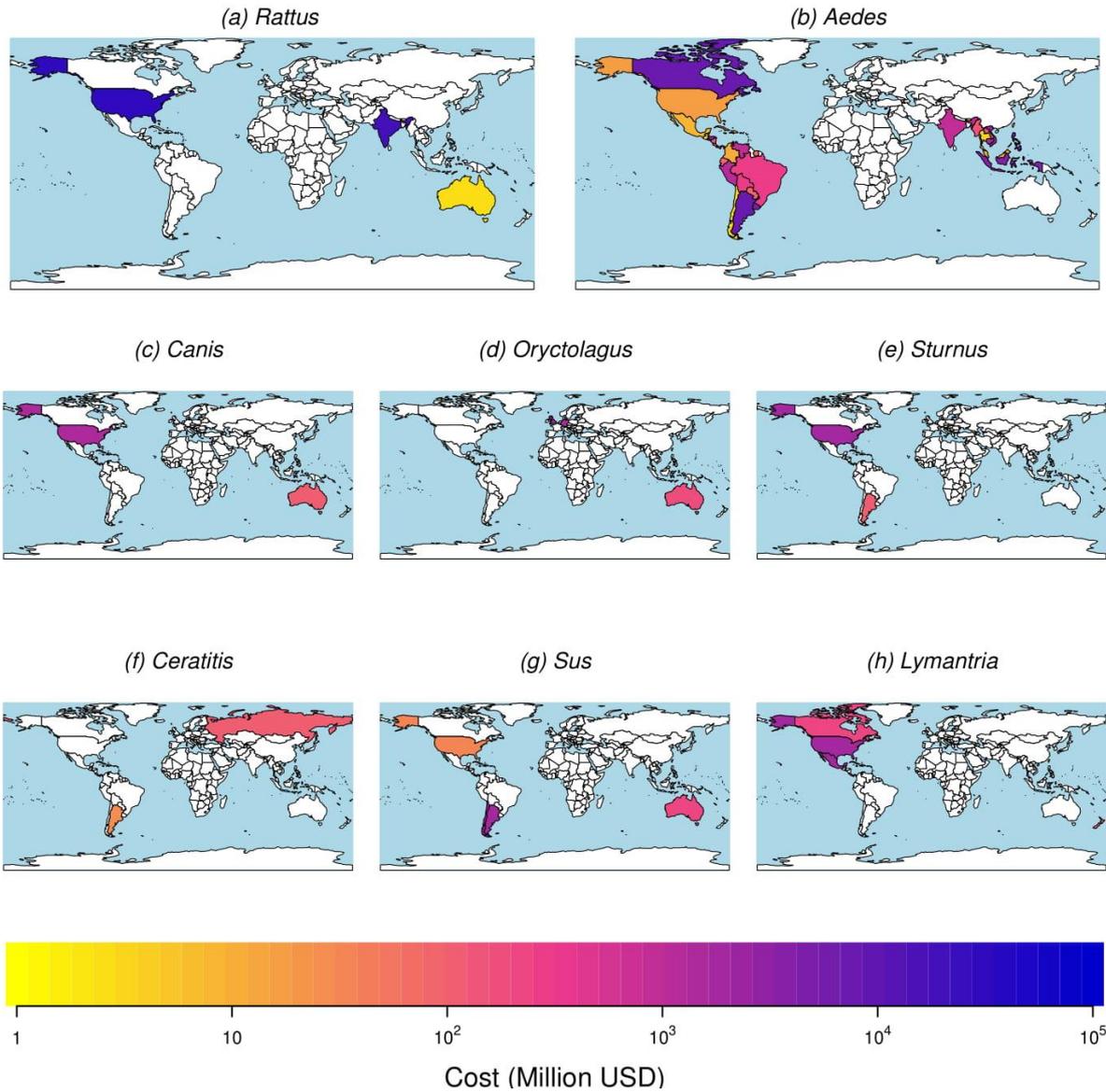
627 Categories used for each descriptive variable that corresponds to a specific column in the  
628 InvaCost database (Diagne et al. 2020b).

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’).
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).

<p>Probable starting year</p> <p>Probable ending year</p>	<p>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.</p>
<p>Spatial scale</p>	<p>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).</p>

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

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



633

634 **Appendix A3: Ecological and model shape parameters**

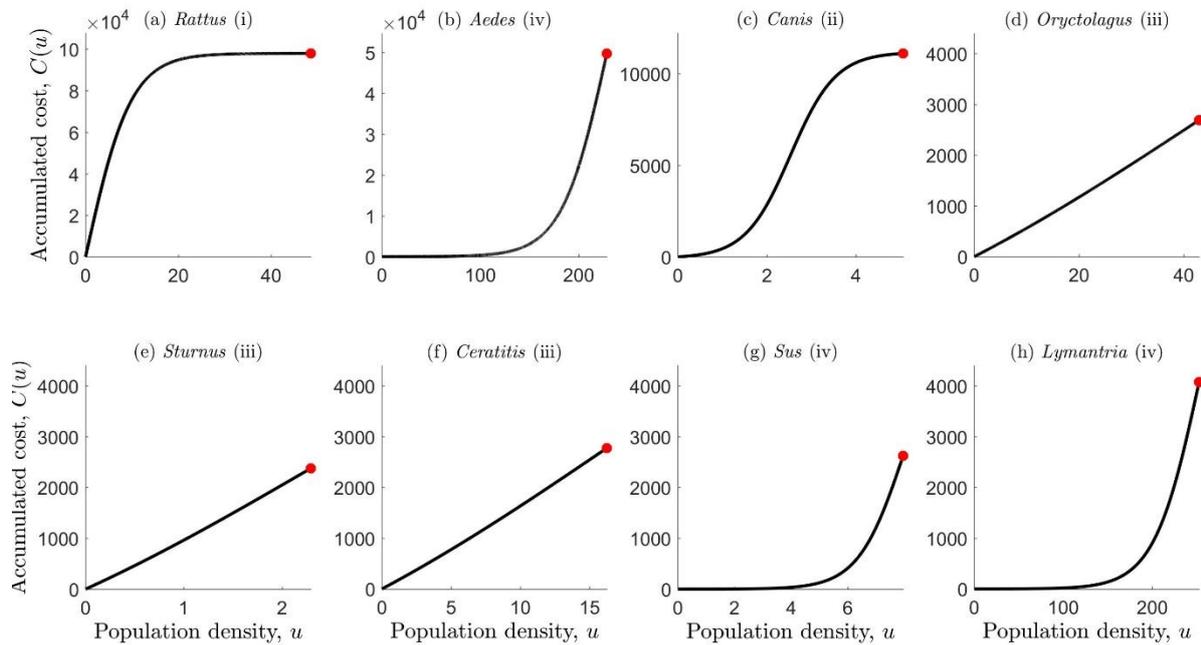
635 Parameter description: Maximum accumulated cost  $C_{\max}$ , Carrying capacity  $K$  (per unit  
 636 area), Intrinsic growth rate  $\alpha$  (per year), Best fit cost model types (I-IV, see Figure 3), Model  
 637 shape parameters ( $s_1, s_2, s, A, B$ , as they appear in equations (4) and (5)).

Genus	$C_{\max}$	$K$	$\alpha$	Best fit cost model type	$s_1$	$s_2$	$s$	$A$	$B$
(a) <i>Rattus</i>	97962	48.56	0.32	I	0	0.1	10	2	0.5
(b) <i>Aedes</i>	49759	228.59	0.27	IV	0.1	0.1	0	2	0
(c) <i>Canis</i>	11110	5.06	0.02	II	0.5	0.1	5	1.0136	0.0067
(d) <i>Oryctolagus</i>	2689	42.91	0.08	III	1	1	0	4.3279	0.2689
(e) <i>Sturnus</i>	2375	2.29	0.40	III	1	1	0	4.3279	0.2689
(f) <i>Ceratitris</i>	2774	16.24	1.93	III	1	1	0	4.3279	0.2689

(g) <i>Sus</i>	2622	7.95	0.22	IV	1	0.1	0	2	0
(h) <i>Lymantria</i>	4075	252.39	0.09	IV	1	0.1	0	2	0

638 **Appendix A4: Accumulated costs as a function of population density**

639 The plots below show the accumulated cost-density functions for each genus. The best fitting  
640 model types (i)-(iv) are indicated, also see Figure 2. The red marker represents the point  
641 where accumulated costs saturate at  $C_{\max}$  precisely when the population density reaches the  
642 carrying capacity  $K$ . The corresponding ecological parameters, including model shape  
643 parameters are given in Appendix A3.



644

645 **Appendix A5: First cost record of each IAS genus in each invaded country, where known.**

646 For reference, the year of first record in InvaCost is provided in order to determine the lag in  
647 cost detection following IAS introduction. Data on first records were obtained from the  
648 sTwist database.

649

Genus	Country	First InvaCost record	First record of invasion	Lag (years)
<i>Aedes</i>	Brazil	2000	1996	4
<i>Aedes</i>	Argentina	2000	1980	20
<i>Canis</i>	USA	1979	1930	49
<i>Canis</i>	Australia	2000	1815	185

<i>Lymantria</i>	USA	1933	1869	64
<i>Lymantria</i>	Canada	2002	1912	90
<i>Oryctolagus</i>	Great Britain	1955	1135	820
<i>Oryctolagus</i>	Australia	1953	1788	165
<i>Oryctolagus</i>	Germany	1970	1149	821
<i>Oryctolagus</i>	United Kingdom	2001	1135	866
<i>Rattus</i>	Australia	1998	1796	202
<i>Rattus</i>	United Kingdom	2010	1751	259
<i>Rattus</i>	Denmark	2002	1725	277
<i>Rattus</i>	USA	2005	1703	302
<i>Sturnus</i>	Argentina	2016	1987	29
<i>Sturnus</i>	Australia	2002	1856	146
<i>Sturnus</i>	USA	2000	1844	156
<i>Sus</i>	Argentina	2017	1910	107
<i>Sus</i>	Australia	1982	1788	194
<i>Sus</i>	Chile	2016	1574	442
<i>Sus</i>	USA	2000	1526	474

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658 **Conflicts of interest/Competing interests**

659 The authors declare that there are no conflicting or competing interests.

660 **Availability of data and material**

661 Underlying data are publicly available in Diagne et al. (2020b - accessible at  
662 <https://www.nature.com/articles/s41597-020-00586-z>) and in online repositories  
663 (<https://doi.org/10.6084/m9.figshare.12668570.v1>;  
664 <https://doi.org/10.6084/m9.figshare.12928136>).

665 The final dataset used for analysis in this paper will be provided on the Dryad digital  
666 repository.

667 **Code availability**

668 Not applicable.

669 **Authors' contributions**

670 All authors conceptualized the study. CD and FC led the collection of data. DAA, EJH and  
671 CD analyzed and visualized the data. DAA developed the cost model and led the writing of  
672 the manuscript. RNC led the interpretation of the results. All authors contributed substantially  
673 to writing the manuscript and approved its submission.

674 **Ethics approval**

675 Not applicable.

676 **Consent to participate**

677 Not applicable.

678 **Consent for publication**

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

680 **References**

- 681 1. Aikio S, Duncan RP, Hulme PE (2010) Lag-phases in alien plant invasions:  
682 separating the facts from the artefacts. *Oikos* 119:370–378
- 683 2. Allmon RA, Sebens KP (1988) Feeding biology and ecological impact of the  
684 introduced nudibranch, *Tritonia plebeia*, New England, USA. *Marine Biology* 99:  
685 375–385
- 686 3. Angulo E, Diagne C, Ballesteros-Meja L, Adamjy T, Ahmed DA et al (2020) Non-  
687 English languages enrich scientific knowledge: the example of economic costs of  
688 biological invasions. *Sci Total Environ* (Under review).
- 689 4. Aplin KP, Suzuki H, Chinen AA, Chesser RT, ten Have J et al (2011) Multiple  
690 Geographic Origins of Commensalism and Complex Dispersal History of Black Rats.  
691 *PLoS ONE* 6(11): e26357

- 692 5. Atkinson IAE (1985) The spread of commensal species of *Rattus* to oceanic islands  
693 and their effect on island avifaunas. In: Moors PJ (ed) Conservation of Island Birds,  
694 vol 3, pp. 35–81, ICBP Cambridge
- 695 6. Baker CM, Diele F, Lacitignola D, Marangi C, Martiradonna A (2019) Optimal  
696 control of invasive species through a dynamical systems approach. *Nonlinear*  
697 *Analysis: Real World Applications* 49:45-70
- 698 7. Barnett SA (2001) *The Story of Rats: Their Impact on Us, and Our Impact on Them*  
699 Allen & Unwin, Crows Nest, NSW, Australia
- 700 8. Beggel S, Brandner J, Cerwenka AF, Geist J (2016) Synergistic impacts by an  
701 invasive amphipod and an invasive fish explain native gammarid extinction. *BMC*  
702 *Ecol* 16:32
- 703 9. Bell BD (1978) The Big South Cape Island rat irruption. In: Dingwall PR, Atkinson  
704 IAE, Hay C (eds) *The Ecology and Control of Rodents in New Zealand Nature*  
705 *Reserves. Information Series, vol. 4, pp. 33–46. Department of Land and Surveys,*  
706 *Wellington*
- 707 10. Bellard C, Thuiller W, Leroy B, Bakkeness M, Genovesi P et al (2013) Will climate  
708 change promote future invasions? *Global Change Biology* 19:3740–3748
- 709 11. Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent  
710 extinctions. *Biol Lett* 12:20150623
- 711 12. Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP et al (2011) A proposed  
712 unified framework for biological invasions. *Trends Ecol Evol* 26:333–339
- 713 13. Blackburn T, Bellard C, Ricciardi A (2019) Alien versus native species as drivers of  
714 recent extinctions. *Frontiers in Ecology and the Environment* 17:203–207
- 715 14. Bogich TL, Liebhold AM, Shea K (2008) To sample or eradicate? A cost  
716 minimization model for monitoring and managing an invasive species. *Journal of*  
717 *Applied Ecology* 45:1134-1142
- 718 15. Boukal D, Berec L (2002) Single-species models of the allee effect: extinction  
719 boundaries, sex ratios and mate encounters. *J Theor Biol* 218:375–394
- 720 16. Bradley BA, Laginhas BB, Whitlock R, Allen JM, Bates AE et al (2019)  
721 Disentangling the abundance-impact relationship for invasive species. *Proceedings of*  
722 *the National Academy of Sciences* 116: 9919–9924
- 723 17. Bradshaw CJ, Leroy B, Bellard C, Roiz D, Albert C et al (2016) Massive yet grossly  
724 underestimated global costs of invasive insects. *Nature communications* 7(1):1-8

- 725 18. Brown PR, Huth NI, Banks PB, Singleton GR (2007) Relationship between  
726 abundance of rodents and damage to agricultural crops. *Agriculture, ecosystems and*  
727 *environment* 120(2-4):405-415
- 728 19. Bucciarelli GM, Suh D, Lamb AD, Roberts D, Sharopton D et al (2018). Assessing  
729 effects of non-native crayfish on mosquito survival. *Conserv Biol* 33:122–131
- 730 20. CABI (2019) *Rattus rattus* (black rat). In: *Invasive Species Compendium*.  
731 Wallingford, UK: CAB International. [www.cabi.org/isc](http://www.cabi.org/isc)
- 732 21. Cayol JP, Causse R, Louis C, Barthes J (1994) Medfly *Ceratitis capitata* Wiedemann  
733 (Dipt., Trypetidae) as a rot vector in laboratory conditions. *Journal of Applied*  
734 *Entomology* 117:338–343
- 735 22. Courchamp F, Berek L, Gascoigne J (2008) *Allee Effects in Ecology and*  
736 *Conservation*. Oxford University Press
- 737 23. Coutts SR, Helmstedt KJ, Bennett JR (2017) Invasion lags: the stories we tell  
738 ourselves and our inability to infer process from pattern. *Divers Distrib* 24(2):244–  
739 251
- 740 24. Crane K, Coughlan NE, Cuthbert RN, Dick JTA, Kregting L et al (2020) Friends of  
741 mine: An invasive freshwater mussel facilitates growth of invasive macrophytes and  
742 mediates their competitive interactions. *Freshwater Biol* 65:1063–1072
- 743 25. Creed RP, Sheldon SP (1995) Weevils and watermilfoil: did a North American  
744 herbivore cause the decline of an exotic plant? *Ecological Applications* 5:1113–1121
- 745 26. Crooks JA (2005) Lag times and exotic species: The ecology and management of  
746 biological invasions in slow-motion. *Écoscience* 12(3):316-329
- 747 27. Cuthbert RN, Cunningham EM, Crane K, Dick JTA, Callaghan A et al (2020a) In for  
748 the kill: novel biosecurity approaches for invasive and medically important mosquito  
749 species. *Management of Biological Invasions* 11(1):9–25
- 750 28. Cuthbert RN, Pattison Z, Taylor NG, Verbrugge L, Diagne C et al (2020b) Global  
751 economic costs of aquatic invasive alien species. *Science of the Total Environment*  
752 (in press)
- 753 29. Dennis B (2002) Allee effects in stochastic populations. *Oikos* 96(3):389 – 401
- 754 30. Diagne C, Catford JA, Essl F, Nuñez MA, Courchamp F (2020a) What are the  
755 economic costs of biological invasions? A complex topic requiring international and  
756 interdisciplinary expertise. *NeoBiota* 63:25–37

- 757 31. Diagne C, Leroy B, Gozlan RE, Vaissière AC, Assailly C et al. (2020b) InvaCost, a  
758 public database of the economic costs of biological invasions worldwide. *Sci Data*  
759 7:277
- 760 32. Dickey JWE, Cuthbert RN, South J, Britton JR, Caffrey J et al (2020) On the RIP:  
761 Using the Relative Impact Potential metric to assess the ecological impacts of  
762 invasive alien species. *NeoBiota* 55: 27-60
- 763 33. Doane CC, McManus ML (1981) The gypsy moth: research towards integrated pest  
764 management. USDA Forestry Service Technical Bulletin No. 1585
- 765 34. Early R, Bradley B, Dukes J, Lawler J, Olden J et al (2016) Global threats from  
766 invasive alien species in the twenty-first century and national response capacities.  
767 *Nature Communications* 7(12485)
- 768 35. Elgersma KJ, Ehrenfeld JG (2011) Linear and non-linear impacts of a non-native  
769 plant invasion on soil microbial community structure and function. *Biol Invasions*  
770 13:757–768
- 771 36. Elkinton JS, Liebhold AM (1990) Population dynamics of gypsy moth in North  
772 America. *Annual Review of Entomology* 35:571–596
- 773 37. Elliott P, Aldridge DC, Moggridge GD, Chipps M (2005) The increasing effects of  
774 zebra mussels on water installations in England. *Water and Environment Journal*  
775 19(4): 367-375
- 776 38. Epanchin-Niell RS (2017) Economics of invasive species policy and management.  
777 *Biol Invasions* 19:3333–3354
- 778 39. Essl F, Dullinger S, Rabitsch W, Hulme PE, Hulber K et al (2011) Socioeconomic  
779 legacy yields an invasion debt. *Proc Natl Acad Sci USA* 108:203–207
- 780 40. Finnoff DC, Shogren JF, Leung B, Lodge DM (2005) The importance of bioeconomic  
781 feedback in invasive species management. *Ecological Economics* 52:367–381
- 782 41. Hanley N, Roberts M (2019) The economic benefits of invasive species management.  
783 *People Nat* 1:124-137
- 784 42. Hajek AE, Tobin PC (2009) North American Eradications of Asian and European  
785 Gypsy Moth. In: Hajek AE, Glare TR, O’Callaghan M (eds) *Use of Microbes for*  
786 *Control and Eradication of Invasive Arthropods. Progress in Biological Control*, vol 6.  
787 Springer, Dordrecht
- 788 43. Hart E, Avilés L (2014) Reconstructing local population dynamics in noisy  
789 metapopulations: The role of random catastrophes and Allee effects. *PLoS One*  
790 9:e110049

- 791 44. Hastings, A., Cuddington, K., Davies, K. F., Dugaw, C. J., Elmendorf, S., Freestone,  
792 A., ... & Thomson, D. (2005). The spatial spread of invasions: new developments in  
793 theory and evidence. *Ecology Letters*, 8(1), 91-101.
- 794 45. Hastings A, Richard JH, Taylor CM (2007) A simple approach to optimal control of  
795 invasive species. *Theoretical population biology*. 70:431-5
- 796 46. Haubrock PJ, Turbelin AJ, Cuthbert RN, Novoa A, Taylor NG et al (2021) Economic  
797 costs of invasive alien species across Europe. *NeoBiota*, in press.
- 798 47. Heikkilä J (2011) Economics of biosecurity across levels of decision-making: a  
799 review. *Agronomy for Sustainable Development*, Springer Verlag/EDP  
800 Sciences/INRA 31(1) pp.119-138
- 801 48. Hilton GM, Cuthbert RJ (2010) The catastrophic impact of invasive mammalian  
802 predators on birds of the UK Overseas Territories: a review and synthesis. *Ibis* 152(3):  
803 443-458
- 804 49. Iwamura T, Guzman-Holst A, Murray KA (2020) Accelerating invasion potential of  
805 disease vector *Aedes aegypti* under climate change. *Nat Commun* 11:2130
- 806 50. Jackson MC, Ruiz-Navarro A, Britton JR (2015) Population density modifies the  
807 ecological impacts of invasive species. *Oikos* 124:880–887
- 808 51. Jensen, A (1975) Comparison of Logistic Equations for Population Growth.  
809 *Biometrics* 31(4):853-862
- 810 52. Juliano SA, Lounibos LP (2005) Ecology of invasive mosquitoes: effects on resident  
811 species and on human health. *Ecol lett* 8(5):558–574
- 812 53. Kawasaki K, Shigesada N (2007) An integrodifference model for biological invasions  
813 in a periodically fragmented environment. *Japan Jour Ind App Math* 24:3–15
- 814 54. Laverty C, Green KD, Dick JTA, Barrios-O'Neill D, Mensink, PJ et al (2017)  
815 Assessing the ecological impacts of invasive species based on their functional  
816 responses and abundances. *Biol Invasions* 19:1653–1665
- 817 55. Lehmann P, Ammunét T, Barton M, Battisti A, Eigenbrode SD et al (2020) Complex  
818 responses of global insect pests to climate warming. *Front Environ Ecol* 18(3):141-  
819 150
- 820 56. Leroy B, Kramer AM, Vaissière AC, Courchamp F, Diagne C (2020). Analysing  
821 global economic costs of invasive alien species with the *invacost* R package. *bioRxiv*  
822 2020.

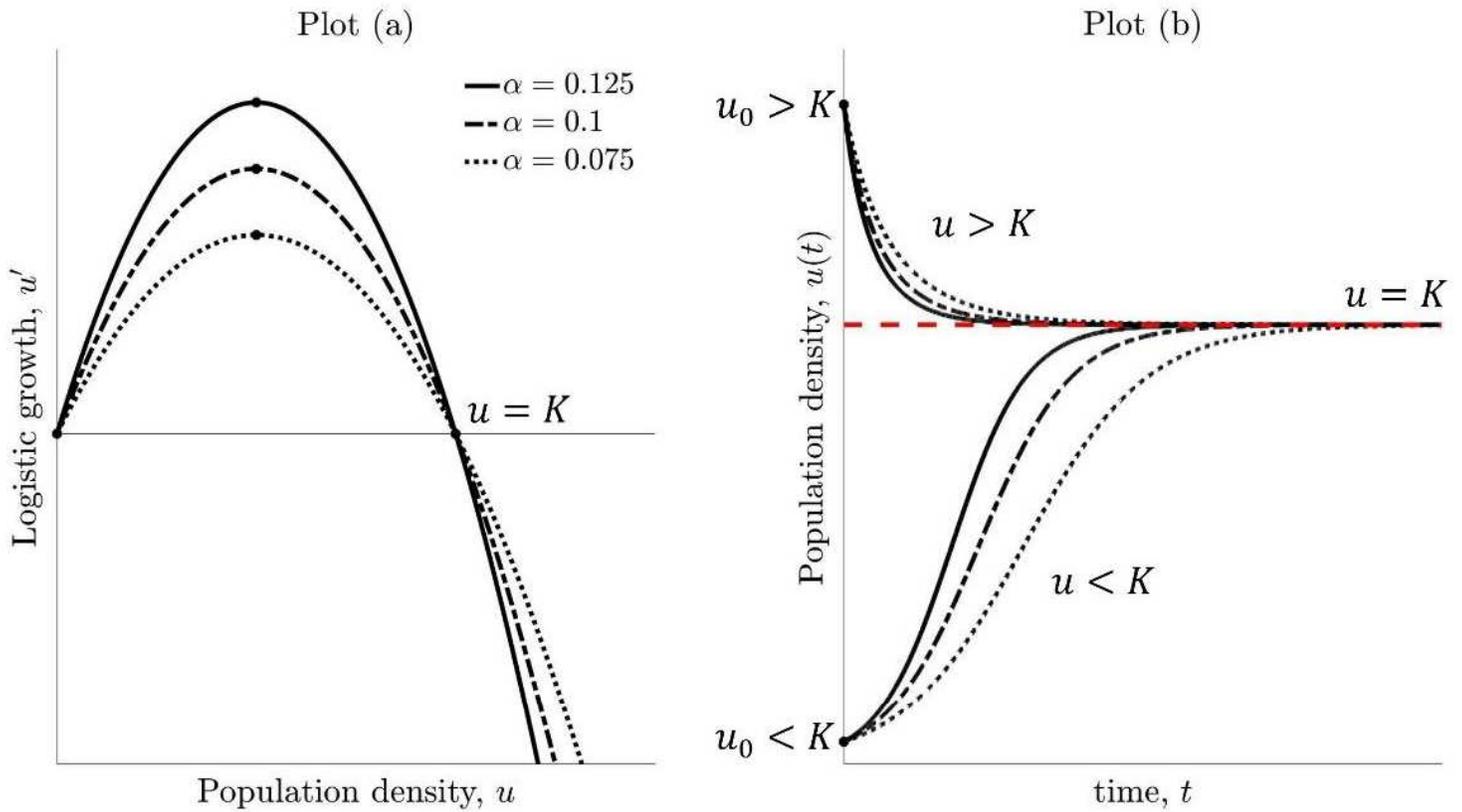
- 823 57. Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA et al (2002) An ounce of  
824 prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proc R  
825 Soc London B 269(1508):2407-2413
- 826 58. Lewis M, Petrovskii SV, Potts, J (2016) The Mathematics Behind Biological  
827 Invasions. Springer.
- 828 59. Linz GM, Homan HJ, Gaukler SM, Penry LB, Bleier WJ (2007) European starlings: a  
829 review of an invasive species with far-reaching impacts. Managing Vertebrate  
830 Invasive Species: Proceedings of an International Symposium. USDA/APHIS/WS,  
831 National Wildlife Research Center, Fort Collins, CO
- 832 60. Lohr CA, Hone J, Bode M, Dickman CR, Wenger A et al (2017) Modeling dynamics  
833 of native and invasive species to guide prioritization of management actions.  
834 Ecosphere 8:e01822
- 835 61. Luis A, Hayman DT, O'Shea T, Cryan P, Gilbert AT et al (2013) A comparison of  
836 bats and rodents as reservoirs of zoonotic viruses: are bats special? Proc R Soc  
837 London B 280:20122753
- 838 62. Malcolm J, Markham A (2000) Global warming and terrestrial biodiversity decline.  
839 Washington, DC: WWF
- 840 63. Medlock JM, Hansford KM, Schaffner F, Versteirt V, Hendrickx G et al (2012) A  
841 review of the invasive mosquitoes in Europe: ecology, public health risks, and control  
842 options. Vector-Borne Zoonot 12:435– 447
- 843 64. Meerburg B, Singleton GR, Kijlstra A (2009) Rodent-borne diseases and their risks  
844 for public health. Crit Rev Microbiol 2009(35):221–270
- 845 65. Moroń D, Skórka P, Lenda M, Kajzer-Bonk J, Mielczarek L et al (2019) Linear and  
846 non-linear effects of goldenrod invasions on native pollinator and plant populations.  
847 Biol Invasions 21:947–960
- 848 66. Nava-Camberos U, Riley DG, Harris MK (2001) Density–yield relationships and  
849 economic injury levels for *Belmisia argentifolia* (Homoptera: Aleyrodidae) in  
850 cantaloupe in Texas. Journal of Economic Entomology 94:180–189
- 851 67. Panetta F, Gooden B (2017) Managing for biodiversity: impact and action thresholds  
852 for invasive plants in natural ecosystems. NeoBiota 34:53–66
- 853 68. Parker I, Simberloff D, Lonsdale W, Goodell K, Wonham M (1999) Impact: Toward  
854 a framework for understanding the ecological effects of invaders. Biological  
855 Invasions 1:3 – 19

- 856 69. Parsons K, Quiring D, Piene H, Moreau G (2005) Relationship between balsam fir  
857 sawfly density and defoliation in balsam fir. *Forest ecology and management*, 205(1-  
858 3):325-331
- 859 70. Pelkki M, Sherman G (2020) Forestry's Economic Contribution in the United States.  
860 Forest Products Society. *Forest Prod J* 70(1):28–38
- 861 71. Petrovskii SV, Li BL (2006) Exactly solvable models of biological invasion.  
862 Chapman Hall/CRC, Boca Raton, FL
- 863 72. Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs  
864 of nonindigenous species in the United States. *BioScience* 50:53–65
- 865 73. Pimentel D, Zuniga R, Morrison S (2005) Update on the environmental and economic  
866 costs associated with alien invasive species in the united states. *Ecological Economics*  
867 15:273–288
- 868 74. Roberts CP, Uden DR, Allen CR, Twidwell D (2018) Doublethink and scale  
869 mismatch polarize policies for an invasive tree. *PLoS ONE* 13(3):e0189733
- 870 75. Robertson PA, Mill A, Novoa A, Jeschke JM, Essl F et al (2020) A proposed unified  
871 framework to describe the management of biological invasions. *Biological Invasions*  
872 22(9):2633-2645
- 873 76. Roiz D, Wilson AL, Scott TW, Fonseca DM, Jourdain F et al (2018) Integrated Aedes  
874 management for the control of Aedes-borne diseases. *PLoS neglected tropical*  
875 *diseases* 12(12):e0006845
- 876 77. Ross J, Tittensor AM (1986) The establishment and spread of Myxomatosis and its  
877 effect on rabbit populations. *Philos Trans R Soc B* 314:599–606
- 878 78. Ruffino L, Zarzoso-Lacoste D, Vidal E (2015) Assessment of invasive rodent impacts  
879 on island avifauna: methods, limitations and the way forward. *Wildl Res* 42:185–195
- 880 79. Rumlerová Z, Vilà M, Pergl J, Nentwig W, Pyšek P (2016) Scoring environmental  
881 and socioeconomic impacts of alien plants invasive in Europe. *Biol Invasions*  
882 18:3697–3711
- 883 80. Schaffner U, Steinbach S, Sun Y, Skjøth CA, de Weger LA et al (2020) Biological  
884 weed control to relieve millions from Ambrosia allergies in Europe. *Nat Commun*  
885 11:1745
- 886 81. Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE et al (2017) No  
887 saturation in the accumulation of alien species worldwide. *Nature Communications*  
888 8:14435

- 889 82. Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE et al (2018) Global rise  
890 in emerging alien species results from increased accessibility of new source pools.  
891 PNAS 115:E2264–E2273
- 892 83. Seebens H, Bacher S, Blackburn TM, Capinha C, Dawson W et al (2020) Projecting  
893 the continental accumulation of alien species through to 2050. *Global change biology*.
- 894 84. Shiels AB, Pitt WC, Sugihara RT, Witmer GW (2014) Biology and impacts of Pacific  
895 island invasive species. 11. *Rattus rattus*, the black rat (Rodentia:Muridae). *Pacific*  
896 *Science* 68(2)
- 897 85. Simberloff D, Martin J, Genovesi P, Maris V, Wardle DA et al (2013) Impacts of  
898 biological invasions: what's what and the way forward. *Trends Ecol Evol* 28:58–66
- 899 86. Shigesada N, Kawasaki K (1997) *Biological Invasions: Theory and Practice*. Oxford  
900 Univ. Press, Oxford
- 901 87. Shigesada N, Kawasaki K, Takeda Y (1995). Modeling stratified diffusion in  
902 biological invasions. *Am. Nat*, 146(2): 229-251.
- 903 88. Sofaer HR, Jarnevich CS, Pearse IS (2018) The relationship between invader  
904 abundance and impact. *Ecosphere* 9:e02415
- 905 89. Stigall A (2010). Invasive species and biodiversity crises: testing the link in the late  
906 devonian. *PLoS One* 5:e15584
- 907 90. Stockhoff BA (1993) Ontogenic change in dietary selection for protein and lipid by  
908 gypsy-moth larvae. *J Insect Physiol* 39:677–686
- 909 91. Strayer DL (2020) Non-native species have multiple abundance–impact curves.  
910 *Ecology and Evolution*. 10(13):6833–6843
- 911 92. Tsoularis A, Wallace J (2002) Analysis of logistic growth models. *Mathematical*  
912 *Biosciences*. 179:21–55 PMID: 12047920
- 913 93. Twery MJ (1991) Effects of defoliation by gypsy moth. In: Gottschalk KW, Twery  
914 MJ, Smith SI eds 1991. *Proceedings, USDA Interagency Gypsy Moth Research*  
915 *Review, 1990*. GTR-NE-146. Radnor, PA: USDA Forest Service, Northeastern  
916 Forest Experiment Station. 152p.
- 917 94. US Congress, Office of Technology Assessment (1993) *Harmful Non-indigenous*  
918 *Species in the United States*. Washington, DC
- 919 95. Vanbergen AJ, Espíndola A, Aizen MA (2018) Risks to pollinators and pollination  
920 from invasive alien species. *Nat Ecol Evol* 2:16–25

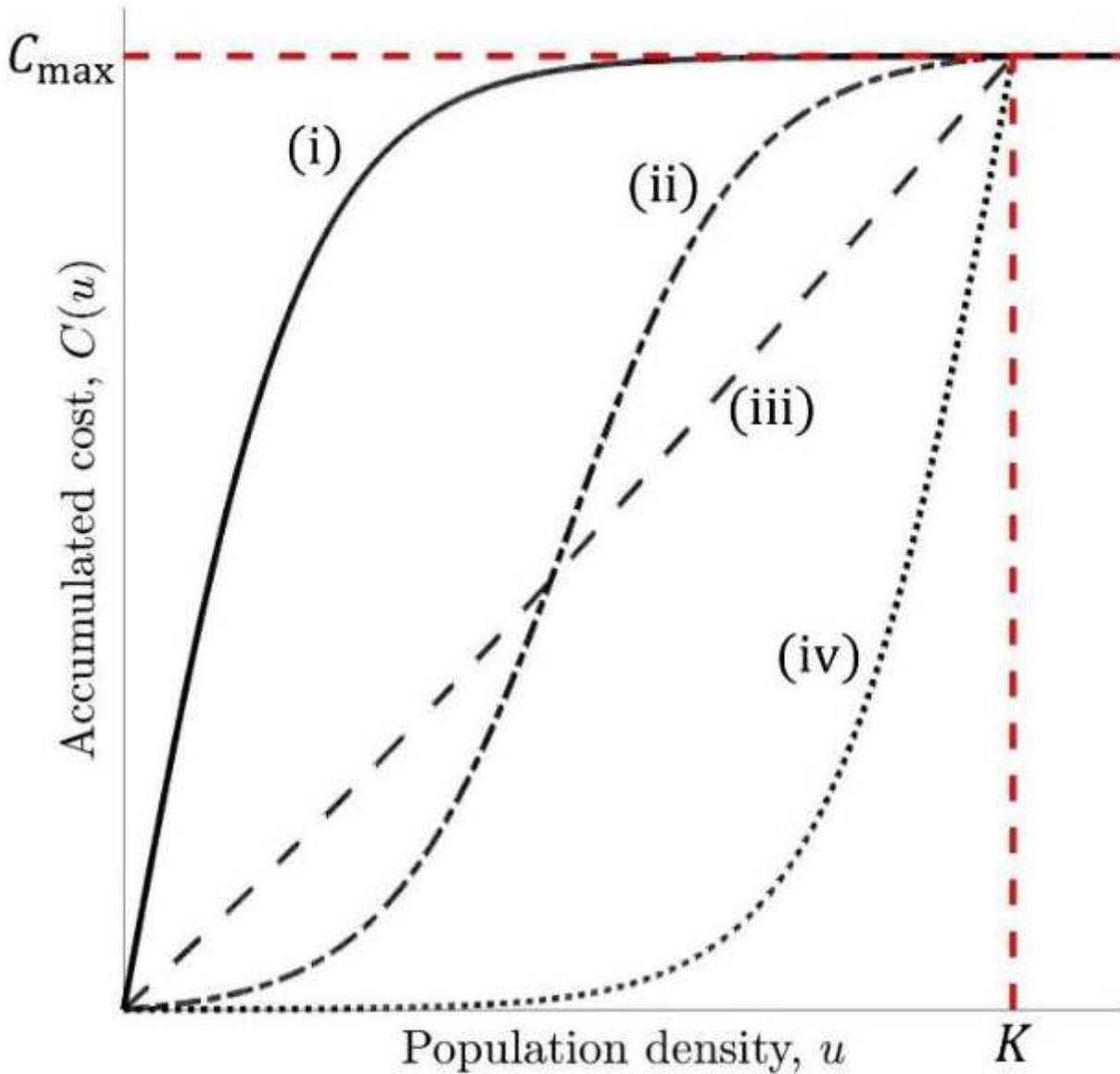
- 921 96. Vander Zanden MJ, Hansen GJ, Latzka AW (2017) A framework for evaluating  
922 heterogeneity and landscape-level impacts of non-native aquatic species. *Ecosystems*  
923 20:477–491
- 924 97. Vazquez-Prokopec GM, Chaves LF, Ritchie SA, Davis J, Kitron U (2010) Unforeseen  
925 costs of cutting mosquito surveillance budgets. *PLoS neglected tropical diseases*  
926 4(10): e858
- 927 98. Veitch CR, Clout MN (2002) *Turning the Tide: the Eradication of Invasive Species.*  
928 Gland, Switzerland and Cambridge UK: IUCN Species Specialist Group
- 929 99. Walsh JR, Carpenter SR, Zanden MJV (2016) Invasive species triggers a massive loss  
930 of ecosystem services through a trophic cascade. *Proc Nat Acad Sci* 113:4081–4085
- 931 100. Weber WJ (1979) *Health hazards from pigeons, starlings and English*  
932 *sparrows.* Thomson Publications: California
- 933 101. Williamson MH, Fitter A (1996) The characters of successful invaders.  
934 *Biological Conservation* 78:163–170
- 935 102. Williamson M (1998) Measuring the impact of plant invaders in Britain. In:  
936 Starfinger U, Edwards K, Kowarik I, Williamson M (eds) *Plant Invasions: Ecological*  
937 *Consequences and Human Responses*, pp 57–68. Backhuys, Leiden, The Netherlands
- 938 103. Yokomizo H, Possingham H, Thomas M, Buckley Y (2009) Managing the  
939 impact of invasive species: the value of knowing the density - impact curve.  
940 *Ecological Applications* 19(2):376 – 386
- 941 104. Zaitsev Y, Marnaev V (1997) *Biological Diversity in the Black Sea: A Study*  
942 *of Change and Decline.* United Nations Publications, New York
- 943 105. Zenni RD, da Cunha WL, Musso C, de Souza JV, Nardoto GB et al (2020)  
944 Synergistic Impacts of Co-Occurring Invasive Grasses Cause Persistent Effects in the  
945 Soil-Plant System after Selective Removal. *Funct Ecol* 34:1102–1112

# Figures



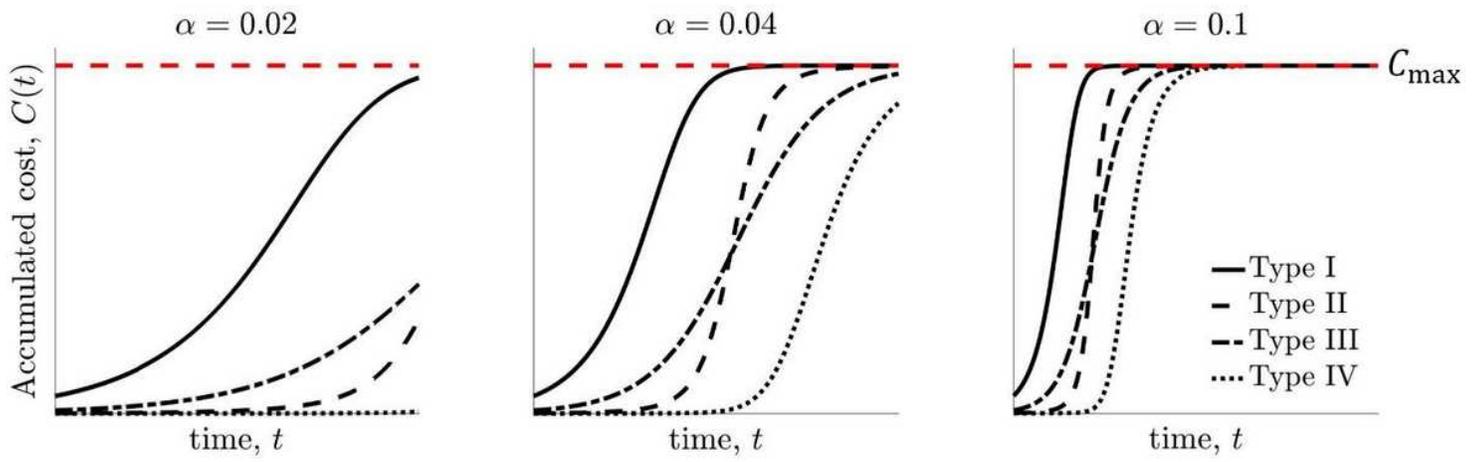
**Figure 1**

(a) Logistic growth given by equation (2). (b) Population density as a function of time given by equation (3).



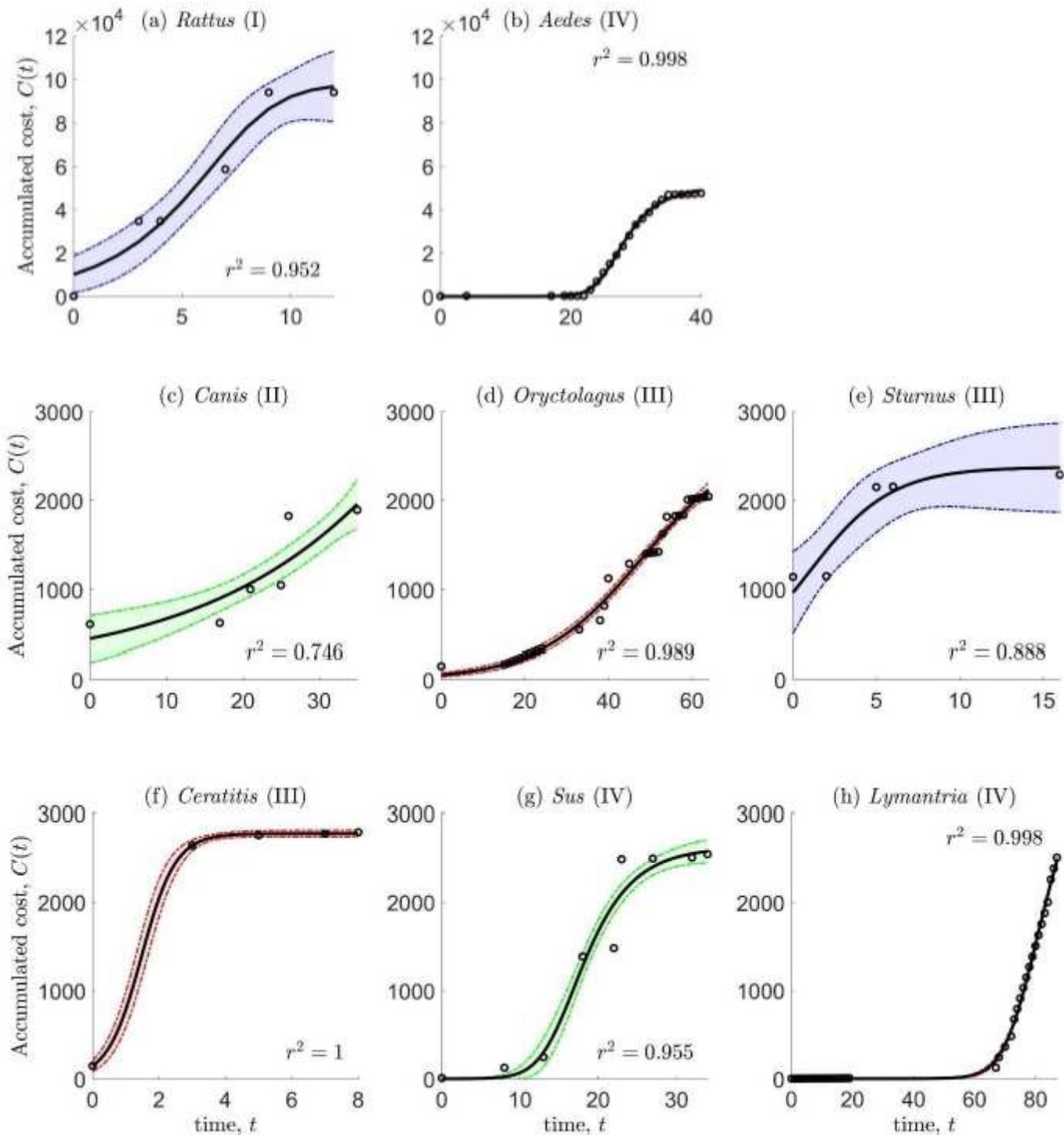
**Figure 2**

Illustration of the four types of cost-density functions. Type (i) Low-threshold curve with shape parameters  $\alpha_1 = 0$ ,  $\alpha_2 = 0.1$ , Type (ii) S-shaped (sigmoidal) curve  $\alpha_1 = 0.5$ ,  $\alpha_2 = 0.1$ , Type (iii) Linear curve  $\alpha_1 = 1$ ,  $\alpha_2 = 1$  and Type (iv) High-threshold curve  $\alpha_1 = 1$ ,  $\alpha_2 = 0.1$ .



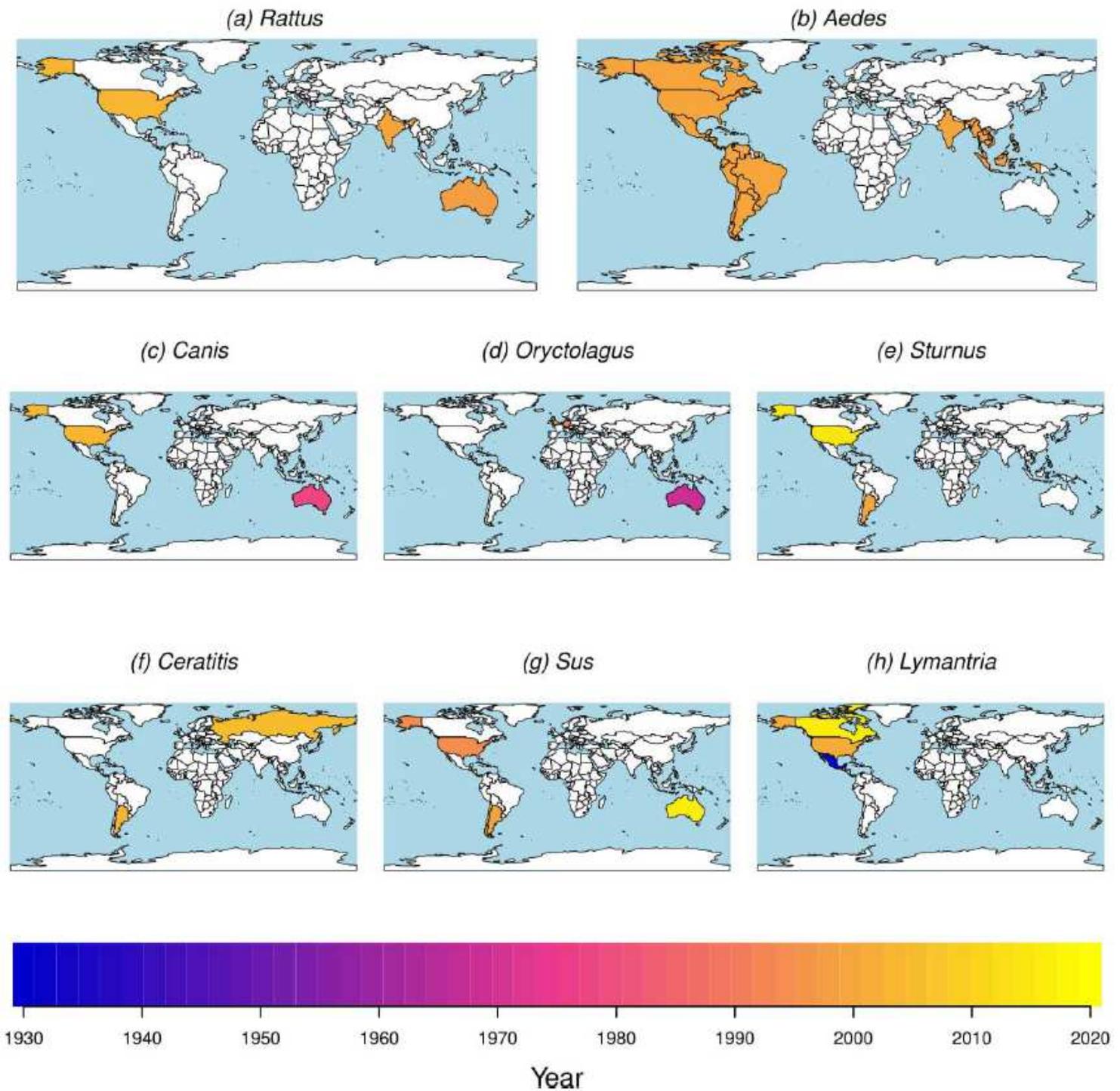
**Figure 3**

Accumulated cost models (I) – (IV) over time since the introduction of IAS, corresponding to each functional Type (i) – (iv), respectively, (see Figure 2), presented for different values of intrinsic growth rate  $\alpha$ . Line styles are the same as in Figure 2.



**Figure 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 A4 for the corresponding plots for each genus with accumulated cost as a function of population density.



**Figure 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. 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.