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Managing biological invasions: the cost of inaction

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2 **Managing biological invasions: the cost of inaction**

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39

40

41 **Abstract**

42 Ecological and socio-economic impacts from biological invasions are rapidly escalating
43 worldwide. While effective management underpins impact mitigation, such actions are often
44 delayed, insufficient or entirely absent. Presently, management delays emanate from a lack of
45 monetary rationale to invest at early invasion stages, which precludes effective prevention.
46 Here, we provide such rationale by developing a conceptual model, based on logistic growth,
47 to quantify the cost of inaction towards invasive alien species under varying time delays and
48 management efforts. Further, we apply the resulting model to management and damage data
49 from a relatively data-rich genus (*Aedes* mosquitoes). Our model confirms that rapid
50 management interventions following invasion drastically minimise costs, and that higher
51 management investments lead to much steeper cost declines. Further, we identify a ‘runaway’
52 point beyond which costs of inaction slowly approach saturation. Any management action
53 during this phase can be considered severely delayed, resulting in substantial losses. For
54 *Aedes*, we estimated that a management delay of just 20 years could have accrued additional
55 costs of at least US\$ 842 million in 40 years, whereas in the case of no management, inaction
56 costs could have been approximately three-fold higher, totalling US\$ 2433 million. These
57 results highlight the need for more timely management of invasive alien species by
58 demonstrating how early investments rapidly reduce long-term economic impacts.

59

60 **Keywords:** InvaCost, invasive alien species, logistic growth, socio-economic impacts,
61 prevention and biosecurity, long-term management

62

63 1 Introduction

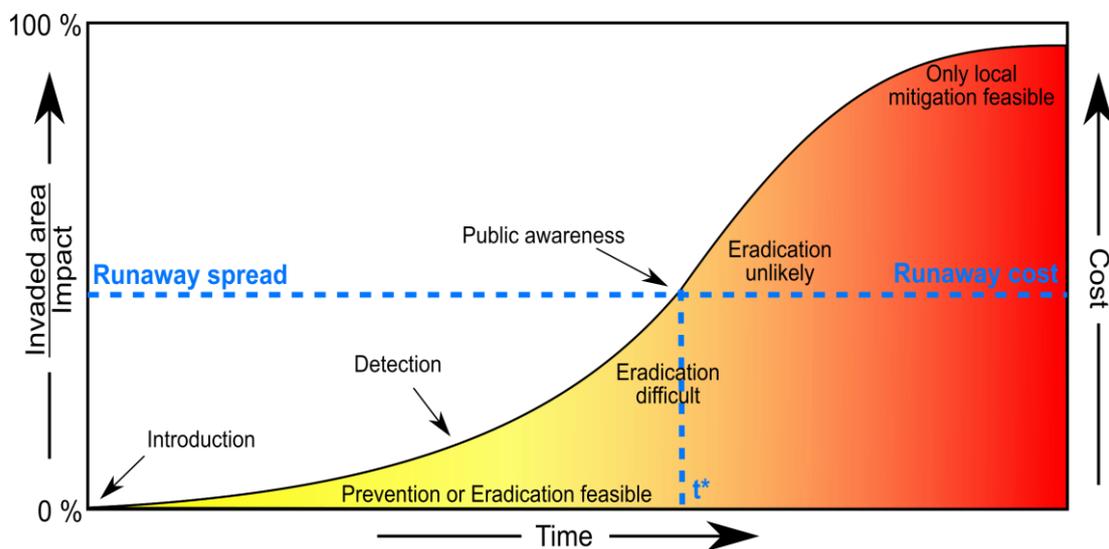
64 Among the countless non-native species that are present worldwide and continue to be
65 introduced (Seebens et al., 2017), a subset of those negatively impact native biodiversity and
66 ecosystems in their novel range, compromise human and social wellbeing and continue to
67 expand their distributions (Walsh et al., 2016; Blackburn et al., 2019; Diagne et al., 2021).
68 Notably, invasive alien species (IAS) can have dramatic impacts on ecosystems (e.g., Shabani
69 et al., 2020; Bellard et al., 2017; Ricciardi & MacIsaac, 2011), multiple sectors of the
70 economy such as agriculture, fisheries and forestry (Paini et al., 2016; Holmes et al., 2009;
71 Haubrock et al., *this special issue*), human health (Shepard et al., 2011; Schaffner et al., 2020)
72 and human and social well-being (Pejchar & Mooney, 2009; Jones, 2017). Even though a lot
73 of these impacts are not yet fully understood or quantified (Vilà et al., 2010; Kumschick et
74 al., 2015; Crystal-Ornelas & Lockwood, 2020), the scientific consensus is that IAS impacts
75 — albeit varying in their nature — are massive, growing, and constitute a major driver of
76 biodiversity loss and global change (Simberloff et al., 2013; IPBES 2019; Pyšek et al., 2020;
77 Seebens et al., 2017). As a result, resource management agencies and conservation
78 practitioners worldwide are continuously working to develop management tools — legal,
79 institutional and methodological — to respond to new invasions through the prevention or
80 limitation of spread and the mitigation of impacts (e.g., Hoffmann & Broadhurst, 2016; Jones
81 et al., 2016).

82 There are, however, several aspects hindering the effective management of invasive
83 populations (Courchamp et al., 2017). In particular, the justification of management
84 expenditures is a challenge, as management is costly, IAS are numerous and budgets are
85 limited. Even though it is generally assumed that early responses are more cost-effective
86 (Leung et al., 2002; Timmins & Braithwaite, 2002; Russell et al., 2015), in practice, applied
87 management is often delayed (if implemented at all). The situation is exacerbated by the
88 observation that the IAS proliferation (and hence any noticeable effect from it) is often
89 delayed due to time lags and long transients that are inherent for the invasion dynamics
90 (Crooks, 2005; Francis et al., 2021). Meanwhile, unless these intrinsic time lags are taken
91 into account (and control actions are applied early accordingly), the IAS management is
92 likely to be inefficient (Francis et al., 2021). Preventative management in particular can be
93 seen as a riskier strategy than waiting to control IAS after establishment, because neither its
94 effectiveness, nor the eventual invasion of a given IAS, can be predicted with high certainty
95 (Finnoff et al., 2007). Indeed, although acting sooner can minimize the total amount of
96 money spent in the long-term, in the absence of an adequate appraisal of their ecological and
97 economic impacts, the cost of inaction may be implicitly assumed to be zero, particularly
98 when responding to ecosystem-based impacts with less tangible damage costs. In a system
99 where impacts are not necessarily borne by the same societal entities as those who fund
100 management actions, immediate spending always needs to be strongly justified. In addition,
101 in the existence of budget limitations and multiple other conservation needs, it is always
102 tempting to wait for impacts to be demonstrated, to be realised or even to be severe before
103 investing in management. As such, allocating budgets to the management of populations that
104 have not yet shown tangible, strong impacts may be difficult to justify for decision makers.

105 For biological invasions, there is presently a lack of such justification to invest in early-
 106 stage management actions. Thus, the objective of this study is to provide quantitative support
 107 for early investment by showing that management becomes increasingly costly with
 108 implementation delay. We focus on a theoretical demonstration, but use both mathematical
 109 modelling and empirical data from the InvaCost database — the most comprehensive and up-
 110 to-date dataset of costs caused by IAS globally (Diagne et al., 2020a, 2020b).

111 Our central hypothesis and model assumption is that the cumulative costs of both
 112 damage and management of IAS follow a logistic curve with time. This assumption follows
 113 the well-accepted “invasion curve” (Leung et al., 2002; Lodge et al., 2016), which predicts
 114 that the area invaded by an IAS initially increases slowly, but then accelerates, and eventually
 115 reaches a plateau (Fig. 1). While the precise shape of the curve may depend on case-specific
 116 details (e.g. on the environmental properties), we mention here that the logistic growth of the
 117 invaded area is shown theoretically in the context of metapopulation dynamics (Amarasekare
 118 1998). If we assume that impact is proportional to the area invaded (Parker et al., 1999), the
 119 costs associated with a single IAS should follow a similar logistic curve.

120 While no one model can describe all invasion impact patterns perfectly, we show the
 121 utility of the invasion curve for describing the cost cumulation patterns of individual IAS.
 122 Further, we use the fitted curves to derive parameters for cost growth rates and cost carrying
 123 capacities, which allow a quantification of the cost of delayed management for any given
 124 management delay period. In this way, we provide a framework for the valuation of foregone
 125 damage costs, which can be used as an imperative to manage species invasions as proactively
 126 as possible.



127
 128 **Figure 1.** The classical invasion curve. This relationship displays a generalized invasive alien population
 129 response over time, after its introduction and establishment into a new environment. As the population expands
 130 and spreads, the area invaded (reported as a percentage of its total invaded area), its impact (damage costs), and
 131 its management costs increase following a logistic curve. Management costs, invaded area, and impact all grow
 132 at increasing rates until t^* , where they reach their maximum rates (which we call the ‘runaway’ point, see
 133 section 3.5). Adapted from Invasive Plants and Animals Policy Framework, Victorian government, 2010.

134 2 Datasets and logistic growth of invasion costs

135 At the time of initiating the study, the InvaCost database includes 9,823 entries from
136 systematic and opportunistic literature searches conducted primarily in English, and
137 altogether in 15 languages (Diagne et al., 2020b; Angulo et al., 2021). This database captures
138 reported economic costs associated with IAS in their novel range (incurring costs from
139 management, damage and losses), including species that may become established in the
140 future (incurring costs from prevention and early detection and rapid response) in a specific
141 area. These data are described with a number of key database descriptors (over 60 in the
142 latest InvaCost version 3.0, see <https://doi.org/10.6084/m9.figshare.12668570> for complete
143 details) and standardised against a single currency (2017 US\$). These descriptors include,
144 among other things, the cost type (“Type of cost merged”), which groups costs into three
145 distinct categories: (a) “Damage” referring to damages or losses incurred by the invasion (e.g.
146 costs for damage repair, resource losses, medical care), (b) “Management” comprising any
147 expenditures dedicated to prevent, limit and/or mitigate invasion impacts (e.g. monitoring,
148 prevention, control, education, eradication) and (c) “Mixed” including indistinguishable
149 damage and management costs (cases where reported costs were not clearly separable from
150 the aforementioned cost types categories). We considered all types of damage costs, but only
151 post-invasion management costs, in order to eliminate preventative management. This was
152 done using the “Management_type” column of the database by selecting the “Post-
153 invasion_management” category therein. We further filtered our dataset to examine only
154 costs incurred at larger scales, using only “Country” and “Site” spatial scales from the
155 “Spatial_scale” column, and focussed on only costs deemed to be of “High” reliability in the
156 “Method_reliability” column. We also removed any extrapolated (unobserved) costs by
157 limiting our search to “Observed” costs in the “Implementation” column.

158 For the consistency and comparison in data used, all costs in the original database were
159 ‘expanded’ so that cost entries could be considered on an annual basis. This means that single
160 cost entries spanning multiple years (e.g. \$10 million between 2001 and 2010) were divided
161 into distinct entries according to their duration (e.g. \$1 million for each year between 2001
162 and 2010 corresponding to ten entries in the expanded database). Expansion was done using
163 the *expandYearlyCosts* function of the ‘invaCost’ R package (Leroy et al., 2020), which
164 repeats the annual cost for each database entry according to the estimated time range of
165 impacts provided with each reference in the InvaCost database.

166 To illustrate the logistic growth of economic costs, we used species-specific datasets
167 from the InvaCost database to model the cumulative yearly costs with time. Ideally, we
168 would have shown the applicability of this approach for the majority of IAS. However, we
169 were limited by the number of species with sufficient temporal cost data. Our species-specific
170 approach was thus restricted to genera with both >10 independent post-colonial (after year
171 1500) cost estimates from InvaCost and a lack of large gaps in cost records over time (7
172 genera in total: 3 for damage costs: *Ambrosia*, *Callosciurus*, and *Procyon*, 3 for management
173 costs: *Anoplophora*, *Cenchrus*, and *Salvinia* and 1 genus with adequate records for both
174 damage and management costs: *Aedes*).

175 After establishing that the cumulative damage and management costs of IAS can be
 176 represented by the invasion curve, we formalized the calculation of the cost of management
 177 delay by calculating the total cost of damage and management from the start of the invasion
 178 to any given year, under any given management delay scenario. For illustration purposes, we
 179 applied this calculation to *Aedes* spp. — where management and damage curves are well
 180 defined — under a range of management delay scenarios (Appendix 1).

181 3 Modelling the cost of delayed management

182 Several cost-related terms are used in the following sections, which we highlight here for
 183 ease of interpretation. First, we define the *cumulative cost of management*, *cumulative cost of*
 184 *damage*, and the *total cumulative cost* (*cumulative cost of management* + *cumulative cost of*
 185 *damage*) as the sum of all costs incurred by an IAS since its first reported cost. Second, we
 186 define the *instantaneous cost of damage* and *instantaneous cost of management* as the costs
 187 incurred by a given IAS in a given year or timestep. Third, we define the *marginal cost of*
 188 *damage* and the *marginal cost of management* as the respective change in the cumulative
 189 damage and management costs of a given IAS between two timesteps (which we model as
 190 being equivalent to the *instantaneous costs of damage* and *management*, respectively), and
 191 the *total marginal cost* as the change in the *total cumulative cost* of a given IAS between two
 192 timesteps (i.e., the *total cumulative cost* for this year minus the *total cumulative cost* of the
 193 previous year).

194 3.1 Proactive management

195
 196 We first assume proactive management, i.e. biosecurity measures such as prevention, early
 197 detection and rapid response, which we assume here for the purposes of this modelling
 198 exercise as infallible (i.e., 100% effective at preventing future damage costs by a given IAS).
 199 One of the simplest mathematical formulations of biosecurity is a constant cost per unit time,
 200 I (investment) to prevent the cost of an invasion; which is worth paying if:

$$201 \frac{dB}{dt} = I \tag{1}$$

$$202 \frac{dB}{dt} < \frac{dC}{dt} \Leftrightarrow I < rC \left(1 - \frac{C}{K} \right) \tag{2}$$

203
 204 where B is the unit of biosecurity invested, $C(t)$ is the cumulative damage costs of an
 205 invasive alien species, r is the intrinsic growth rate of damage costs and K is the carrying
 206 capacity of those costs.

207 The difference between the two primitives (i.e., the difference between the investment
 208 cost and the damage cost at time t) is simply the total amount lost in year t by not using
 209 biosecurity. Since solutions for proactive management ($t \leq 0$) are mathematically trivial, we
 210 will only focus on reactive management, i.e., management that starts after an invasion has
 211 started.
 212
 213

214 3.2 Reactive management

215 Following the classical invasion curve (Fig. 1), we hypothesize that the cumulative damage
 216 cost $C(t)$ of an invasive alien species displays logistic growth:

$$217 \quad \frac{dC}{dt} = rC \left(1 - \frac{C}{K}\right), \quad C(0) = C_0 \quad (3)$$

218 and therefore can be modelled using a classical logistic curve as a function of time:

$$219 \quad C(t) = \frac{K}{1 + \left(\frac{K}{C_0} - 1\right)e^{-rt}} \quad (4)$$

220 where C_0 is the initial cumulative damage cost, K is the maximum cost, to which we, for
 221 convenience, refer to as the cost carrying capacity, and r is the intrinsic growth rate of
 222 damage costs.

223 We assume a reactive management action that decreases the impact of an invasion,
 224 and therefore its damage cost. The management itself has an expenditure $M(t - \tau)$ which can
 225 be delayed by τ years. Since the cumulative management cost is expected to also depend on
 226 the invasion stage, it can also be modelled as a logistic curve, with an intrinsic growth
 227 rate r_M that can be different than the growth rate of damage costs. In addition, a reasonable
 228 assumption is that the cumulative management cost is a constant proportion of the damage
 229 cost, and therefore has a cost carrying capacity $K_M = \gamma K$ and an initial management cost
 230 $M(0) = M_0 = \gamma C_0$, where γ is a parameter that quantifies management effort and lies
 231 between 0 and 1 inclusive. Therefore, one can write:

$$232 \quad M(t - \tau) = \gamma \cdot \frac{K}{1 + \left(\frac{K}{C_0} - 1\right)e^{-r_M(t-\tau)}} \cdot H(t - \tau), \quad M(0) = M_0 \quad (5)$$

233 where $H(t - \tau)$ is a unit step function with value 0 if $t < \tau$, $\frac{1}{2}$ if $t = \tau$ and 1 if $t > \tau$ (also
 234 known as the Heaviside function). Note that in eqn. 5, $\tau = 0$ corresponds to a special case
 235 where there is no delay in management with cumulative cost value $M(t)$. Also, with this
 236 formulation, $\gamma = 1$ can be considered as an upper limit where management effort can
 237 theoretically achieve 100% efficiency (i.e., reduce damage costs to zero), at a cost equivalent
 238 to the damage cost. In practice, this value (which implies functional eradication) is rarely
 239 reached even in the case of intensive management efforts.

240 3.3 Cost of inaction

241 If management is introduced at some delayed time τ , the total amount of reduced losses φ is
 242 given by the difference between cumulative damage and management costs:

$$243 \quad \varphi(t, \tau) = C(t) - M(t - \tau) = \frac{K}{1 + \left(\frac{K}{C_0} - 1\right)e^{-rt}} - \gamma \cdot \frac{K}{1 + \left(\frac{K}{C_0} - 1\right)e^{-r_M(t-\tau)}} \cdot H(t - \tau) \quad (6)$$

245 In the case where management is not delayed, the losses amount to:

246 $\varphi(t, 0) = C(t) - M(t) = \frac{K}{1 + \left(\frac{K}{C_0} - 1\right)e^{-rt}} - \gamma \cdot \frac{K}{1 + \left(\frac{K}{C_0} - 1\right)e^{-r_M t}} \cdot H(t)$ (7)

247 We expect the total amount of losses to be greater in the case where management is delayed,
 248 and therefore that $\varphi(t, \tau) > \varphi(t, 0)$ at all times.

249 The ‘cost of inaction’ function (Φ) is the potential savings one can acquire due to earlier
 250 management intervention, i.e., the cost difference between the total losses in eqn. 6-7, written
 251 as:

252 $\Phi(t, \tau) = \varphi(t, \tau) - \varphi(t, 0) = M(t) - M(t - \tau)$ (8)

253

254 which can be expressed as:

255 $\Phi(t, \tau) = \gamma \left(\frac{K}{1 + \left(\frac{K}{C_0} - 1\right)e^{-r_M t}} \cdot H(t) - \frac{K}{1 + \left(\frac{K}{C_0} - 1\right)e^{-r_M (t - \tau)}} \cdot H(t - \tau) \right)$ (9)

256 Note that eqn. 9 depends on the intrinsic growth rate of cumulative management costs r_M , and
 257 not r .

258 3.4 Properties of the cost of inaction function

259 The cost of inaction function (eqn. 9) evaluated at time $t = 0$, with management delay at
 260 some later time $\tau > 0$, reduces to:

261 $\Phi(0, \tau) = \frac{1}{2} \cdot \frac{\gamma K}{1 + \left(\frac{K}{C_0} - 1\right)}$ (10)

262 whereas if management is introduced at $\tau = 0$, then $\Phi(0, 0) = 0$. Also, at some fixed time $t >$
 263 0 , with no management action ($\tau \rightarrow \infty$), one gets:

264 $\Phi(t, \tau \rightarrow \infty) = \gamma \left(\frac{K}{1 + \left(\frac{K}{C_0} - 1\right)e^{-r_M t}} \right)$ (11)

265 and for sufficiently large but finite time, this converges to:

266 $\Phi(t, \tau \rightarrow \infty) = \gamma K$ (12)

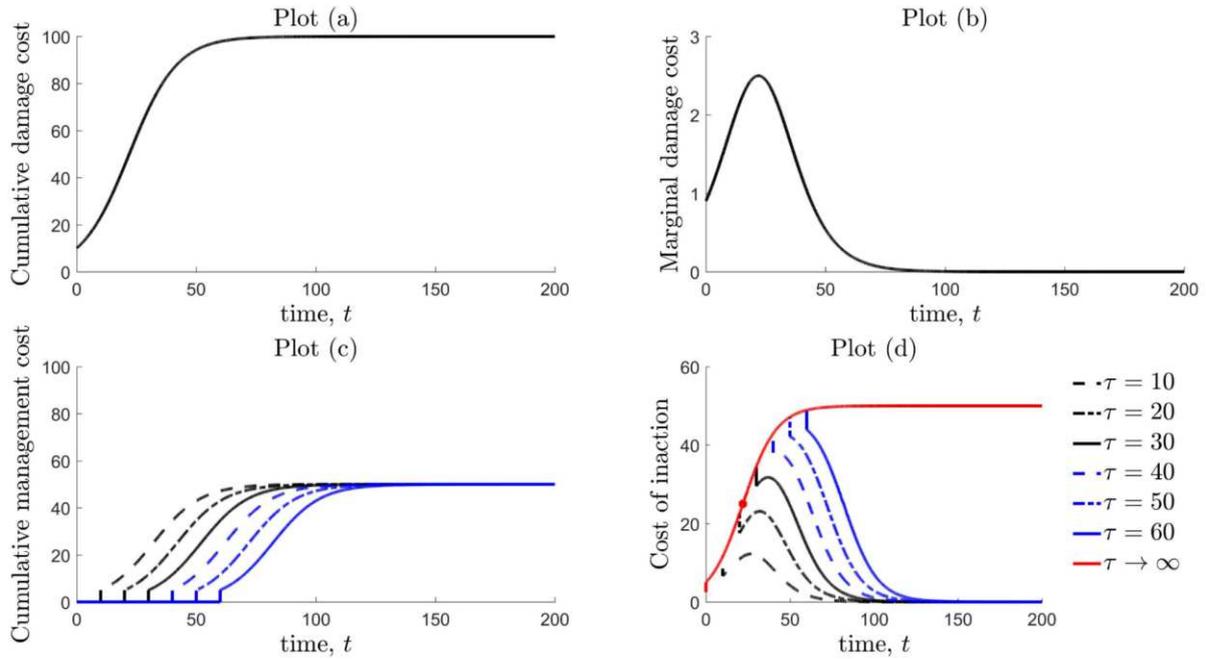
267 which is precisely the level where the cost saturates. Finally, for a fixed but finite
 268 management delay $\tau > 0$, the cost of inaction in the long-term ($t \rightarrow \infty$) reduces to zero i.e.,
 269 $\Phi(t \rightarrow \infty, \tau) = 0$. In summary, the long-term cost dynamics differ depending on whether
 270 management is imposed or not, either leading to null costs (of inaction), or saturating at a
 271 constant level, respectively.

272 3.5 Impacts of management delay and management effort

273 The logistic curve models for cumulative damage and management costs, i.e., eqn. 4-5,
 274 saturate at the cost carrying capacities K and K_M (Fig. 2a,c). The implication is that marginal
 275 damage and management costs decay exponentially in the long-term, eventually reaching
 276 zero (Fig. 2b). In a more realistic scenario, one may expect damage and management costs to
 277 be continuously reported. However, based on empirical findings, these costs appear to be
 278 several orders of magnitude smaller than the corresponding largest reported
 279 damage/management cost, likely due to dwindling effort in cost detection and management,
 280 and saturation of the invisable range (Fig. 1). As a result, any additional contributions to the
 281 cumulative costs of damage and management would be negligible, and therefore can be
 282 reasonably modelled at a ‘near’ saturation level (as demonstrated later for *Aedes* spp. in Fig.
 283 6, see also Ahmed et al., *this special issue*).

284 Fig. 2d illustrates the cost of inaction function $\Phi(t, \tau)$ given by eqn. 9, which
 285 evaluates the difference in cost between two distinct scenarios: one where management is
 286 introduced instantly (at time $\tau = 0$), and one where management is delayed by time τ . In the
 287 special case where no action is taken (considered as a theoretical limit $\tau \rightarrow \infty$, red curve, Fig.
 288 2d), the expenditure continues to accrue and saturates at the carrying capacity of management
 289 costs $K_M = \gamma K$. The red marker in plot (d) is a ‘runaway’ point (or point of inflection, see
 290 Fig. 1) which occurs at time $t^* = \frac{1}{r_M} \ln \left(\frac{K}{c_0} - 1 \right)$ with a corresponding cost of inaction value
 291 at half the management cost carrying capacity i.e., $\Phi^* = \frac{1}{2} K_M = \frac{1}{2} \gamma K$, where the cost
 292 transitions from fast accrual ($t < t^*$) to slower accrual ($t > t^*$).

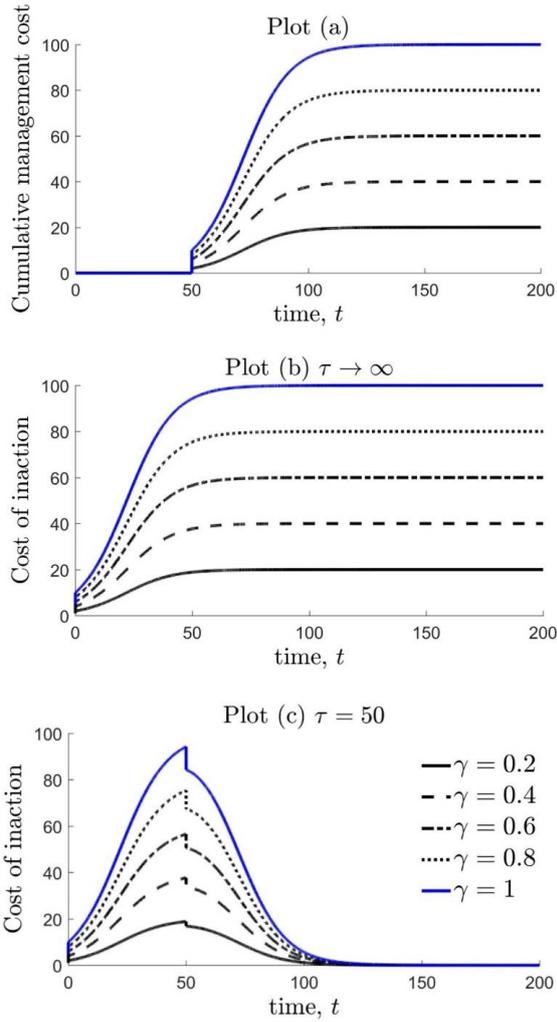
293 In our model, we found that increased delay (larger τ) led to greater expenditures, as
 294 expected. Generally, once management is introduced, the cost of inaction ‘dips’ (due to a
 295 considerable initial management expenditure), and in the long-term, decays exponentially
 296 leading to null costs (of inaction). However, the cost dynamics shortly after management
 297 onset depend heavily on the delay time, specifically when the cost of inaction approaches
 298 saturation. If delayed management is implemented at an early stage, expenditures still may
 299 continue to increase, eventually reaching a peak with subsequent decay (e.g. Fig. 2d for $\tau =$
 300 20). In contrast, if management is implemented after a time where the cost of inaction has
 301 almost saturated, then expenditures will only decrease, and at a much faster rate (e.g. Fig. 2d
 302 for $\tau = 50, 60$). Interestingly, a faster reduction does not outweigh the effects of severely
 303 delayed management, with null expenditures reached much quicker with earlier management.



304

305 **Figure 2:** The impact of management delay. Plot (a) shows cumulative damage costs $C(t)$, which are modelled
 306 using a logistic curve, see eqn. 4. Plot (b) shows the instantaneous damage costs as a function of time (i.e., the
 307 marginal cost for each additional year of damage from eqn. 3). Plot (c) shows cumulative management
 308 costs $M(t - \tau)$, which are proportional to damage costs according to factor γ , and delayed by some time τ , see
 309 eqn. 5. Plot (d) shows the cost of inaction $\Phi(t, \tau)$ over time, see eqn. 9. The red curve illustrates a special case
 310 where no action is ever taken, all others represent different scenarios of increasingly delayed management. The
 311 red marker is the point of inflection or ‘runaway point’. Parameter values in all cases: Damage cost carrying
 312 capacity $K = 100$, Growth rate $r = r_M = 0.1$, Initial damage cost $C_0 = 10$, Management effort $\gamma =$
 313 0.5 , Management cost carrying capacity $K_M = \gamma K = 50$, Management delay τ varied. Figure legend only
 314 applies to plots (c) and (d).

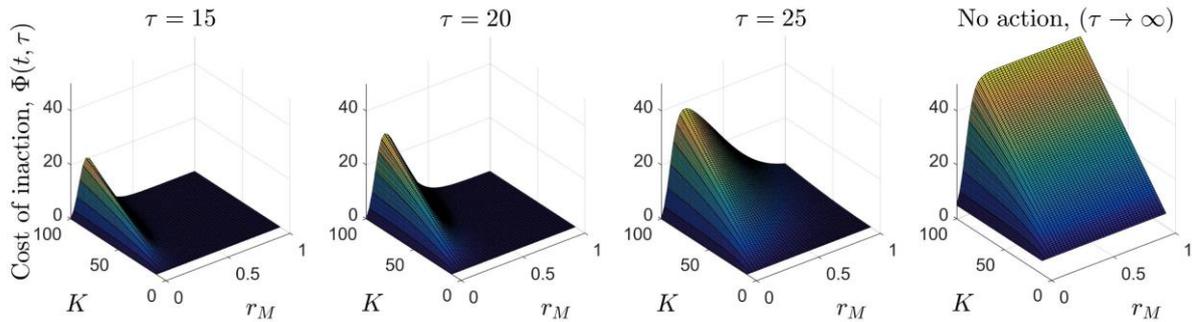
315 We also found that higher management effort γ led to steeper declines in the cost of
 316 inaction after management implementation (Fig. 3). However, increased management effort
 317 led to higher peaks in the cost of inaction due to the relationship between management effort
 318 and management cost.



319

320 **Figure 3:** The impact of management effort. Plot (a) shows management cost curves over time, with a logistic
 321 form and a cost carrying capacity $K_M = \gamma K$, proportional to the damage cost carrying capacity K , with
 322 management effort quantified by parameter γ , see eqn. 5. They are equivalent to plots of Fig. 2c. Plot (b) shows
 323 the associated cost of inaction for an infinite management delay (equivalent to the red curve of Fig. 2d). Plot (c)
 324 demonstrates the impact of management effort on the cost of inaction for a delay of $\tau = 50$. The higher the
 325 management costs, the more costly due to delayed management. Parameter values: Cost carrying capacity $K =$
 326 100 , with management effort γ varied. Intrinsic growth rate $r = r_M = 0.1$, Initial damage cost $C_0 = 10$,
 327 Management delay $\tau = 50$.

328 Upon examining the interactive behaviour of the model parameters (Fig. 4), we found
 329 that longer management delays allowed a wider range of r_M values to lead to large costs,
 330 whereas at low management delays, only small r_M values led to large costs. Across
 331 management delays, larger K values led to greater costs of inaction.



332

333 **Figure 4:** Snapshots of the cost of inaction at time $t = 30$. Management is introduced at different times τ . The
 334 limiting case $\tau \rightarrow \infty$ represents the case where management is not introduced, i.e., no action is taken. Parameter
 335 values: Initial damage cost $C_0 = 10$, Management effort $\gamma = 0.5$.

336 4 Empirical results

337 4.1. Damage and Management curves

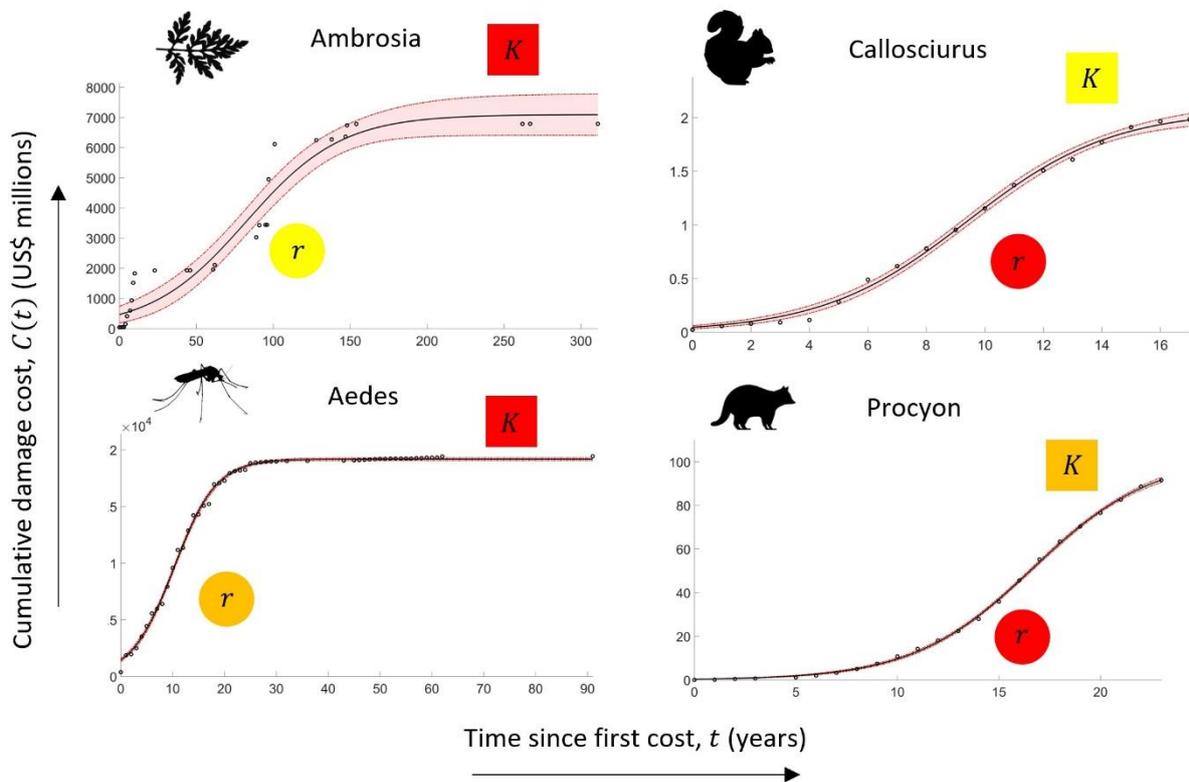
338 All of our logistic fits were very strong across genera ($R^2 > 0.9$, Table 1). We found that
 339 raccoons (*Procyon*) and squirrels (*Callosciurus*) had the highest r values, while longhorn
 340 beetles (*Anoplophora*) and *sandburs* (*Cenchrus*) had the highest r_M values (Fig. 5). *Aedes*,
 341 *Anoplophora* and *Ambrosia* spp. reached very high damage and/or management costs.
 342 *Anoplophora* had both high r_M and K_M values. While all economic impact data are subject to
 343 time lags in invasion and detection (Crooks, 2005), we found greater support for lagged
 344 occurrence of damage costs compared to management costs when collating InvaCost data
 345 with the sTwist database for first records of invasions (Seebens et al., 2020, Table 1). The
 346 initial damage cost is found to be significantly lower than the cost carrying capacity (approx.
 347 10% or lower), and varies across genera. This does not hold for initial management costs,
 348 which can be relatively much higher, for e.g. *Salvinia* (*floating fern*). The “cost lag” column
 349 provides the time between the first known record of the IAS anywhere outside of its native
 350 range (from the sTwist Database, Seebens et al., 2020) and the first record within InvaCost.

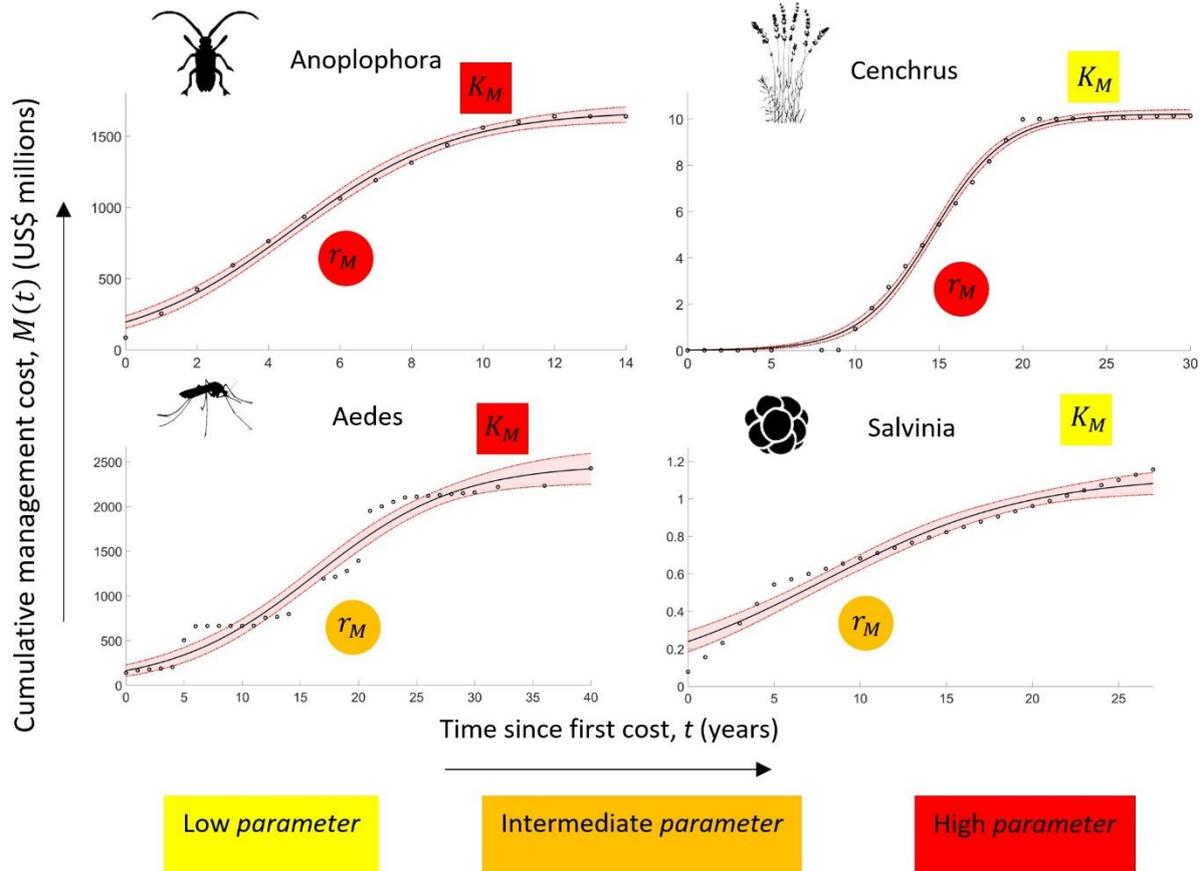
351 **Table 1.** Logistic modelling results for (A) cumulative damage costs and (B) cumulative management costs.
 352 Note that these costs were modelled separately without assuming proportionate cost carrying capacities. Growth
 353 rates: low $r, r_M < 0.1$ (yellow), intermediate $0.1 < r, r_M < 0.3$ (orange), high $r, r_M > 0.3$ (red). Cost carrying
 354 capacity: low $K, K_M < 100$ (yellow), intermediate $100 < K, K_M < 1000$ (orange), high $K, K_M > 1000$ (red).
 355 The “# estimates” column provides the number of independent cost references provided in the InvaCost
 356 database with which the curves were derived. The parameter values are rounded to two decimal places, but the
 357 initial cost to carrying capacity ratio is computed using values to a higher degree of accuracy, see Appendix 2.

358

Genus	Cost intrinsic growth rate	Cost carrying capacity	Initial cost	Initial cost to carrying capacity ratio (%)	Cost lag (year) Time of cost onset after introduction (years)	#No. of independent cost estimates	Coefficient of determination R^2

		r	K	C_0	C_0/K (%)			
A. Cumulative damage costs	<i>Ambrosia</i>	0.03	7094.85	463.61	6.53	0	196	0.941
	<i>Callosciurus</i>	0.40	2.07	0.05	2.21	66	32	0.997
	<i>Aedes</i>	0.24	19183.48	1450.54	7.56	0	134	0.997
	<i>Procyon</i>	0.34	102.35	0.36	0.35	33	21	0.999
		r_M	K_M	M_0	M_0/K_M (%)			
B. Cumulative management costs	<i>Anoplophora</i>	0.44	1679.51	194.26	11.57	0	13	0.994
	<i>Cenchrus</i>	0.46	10.21	0.01	0.12	8	106	0.996
	<i>Aedes</i>	0.16	2474.19	163.11	6.59	0	97	0.966
	<i>Salvinia</i>	0.17	1.13	0.24	21.23	0	13	0.956



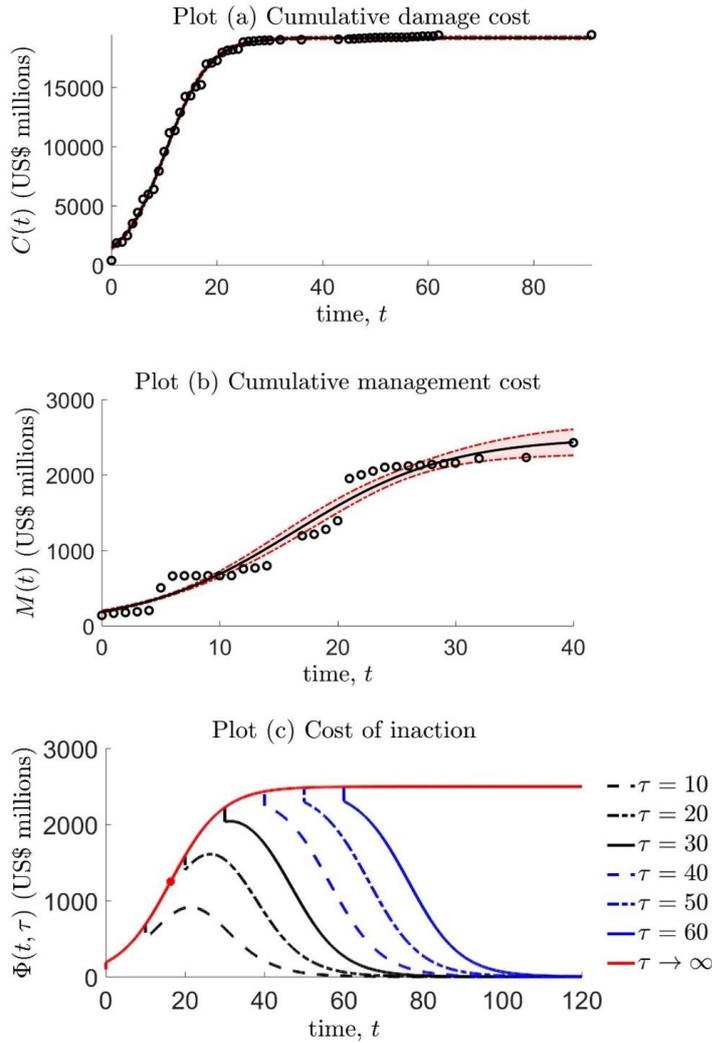


360

361 **Figure 5.** Model fitting of cumulative damage costs (top) and cumulative management costs (bottom) using a
 362 logistic curve, for different invasive alien species. The red shaded areas around the curves represent 95%
 363 confidence regions indicating the range of predicted cumulative costs. The estimated logistic model fit
 364 parameters are given in Table 1. The range for low/intermediate/high parameter values are given in the caption
 365 of Table 1 using the same colour scheme. High values of the intrinsic growth rate (r or r_M) illustrate species for
 366 which costs increase rapidly; high values of the cost carrying capacity (K or K_M) illustrate species for which
 367 costs eventually saturate at high values. Dots represent annual total costs. Note that the scales differ across
 368 subplots.

369 4.2 Case study for *Aedes* spp.

370 We illustrate the utility of our model in its ability to calculate the net present benefit of acting
 371 immediately, in terms of the foregone losses for each year of management delay, using the
 372 genus for which we have good empirical data on both damage and management costs over
 373 time (*Aedes* spp.; see Appendix 1 for detailed calculations). *Aedes* have many decades of
 374 damage cost data that display clear saturation at a very high cost, with an intermediate cost
 375 intrinsic growth rate (Fig. 6a). The management costs to date for this genus are much lower
 376 (we estimate a management effort of $\gamma = 0.13$), but also generally tend to follow a logistic
 377 curve (Fig. 6b). By synthesizing the outputs of both of these models, we can calculate the
 378 cost of inaction at the global scale for any given management delay using eqn. 9 (see Fig. 6c).



379

380 **Figure 6:** Plot (a) Cumulative damage cost for *Aedes*. Parameters: Initial damage cost $C_0 = 1450.54$, cost
381 carrying capacity $K = 19183.48$, intrinsic growth rate $r = 0.24$, coefficient of determination $R^2 = 0.997$. Plot
382 (b) Cumulative management cost for *Aedes*. Parameters: Initial management cost $M_0 = \gamma C_0 = 188.86$, cost
383 carrying capacity $K_M = \gamma K = 2497.63$, where $\gamma = 0.13$ quantifies management effort, intrinsic growth rate
384 $r_M = 0.15$, $R^2 = 0.965$. Red shaded area represents a 95% confidence region. Plot (c) shows the cost of inaction
385 for *Aedes*, with management delay τ . The red marker is the runaway point which occurs at $(t^*, \Phi^*) =$
386 $(16.33, 1248.86)$. Note that the estimated parameters for management costs differ from those reported in Table
387 1, as here it is assumed that cost carrying capacities are directly proportional. Also, the parameter values
388 reported here are rounded to two decimal places, but all computations use estimated parameter values to a
389 higher degree of accuracy, see Appendix 2.

390 For instance, after 40 years from the first reported damage cost, total costs incurred due to
391 this genus following a 20-year management delay would amount to \$17.6B worldwide, while
392 immediate management would lead to only \$16.7B in costs. The cost of inaction is the
393 difference between these two costs, estimated at ~\$842M. In contrast, the cost of inaction in
394 the case of no management action can be significantly higher, approximately three-fold
395 totalling \$2433M, and in the long-term saturating to \$2497M. See Appendix 1 for details of
396 the calculation, with accurate parameter values listed in Appendix 2. We further estimate a
397 ‘runaway point’ at $t^* = 16.3$ years, that is the transition point beyond which the cost of
398 inaction begins to accrue at a slower rate, eventually saturating at a maximum value which is

399 precisely the long-term cost in the scenario where the genus is never managed. As such, the
400 greatest cost reduction comes from managing in the first ~15 years after its arrival. With this
401 modelling framework, we can estimate multi-billion dollar additional global costs for
402 neglecting to begin management of mosquito invasions.

403 **5 Implications for management**

404 Our work highlights that failing to begin managing an invasion can quickly lead to immense
405 costs. Under the assumptions of our model, in the absence of any management, the cost of
406 inaction itself has a logistic shape (see red curve in Fig. 2d), as has been shown for damage
407 costs across a range of genera and habitat types considered in the InvaCost database (Ahmed
408 et al., *this special issue*). Therefore, the cost of inaction increases exponentially prior to a
409 certain threshold time, after which it eventually saturates at a high level. This means not only
410 that IAS costs can quickly increase to unbearable amounts, but also that they may initially be
411 deceitfully slow to accrue, therefore not signaling to policy makers the urgency to invest in
412 management. Indeed, during this initial time period, the willingness to allocate funds to IAS
413 management may be low due to the lack of perceived risk or impact detection (Finnoff et al.,
414 2007). However, as we have shown here, these costs can inflate suddenly and potentially
415 overwhelm major sectors of the economy.

416 Our work defines a crucial window of management opportunity — before the
417 inflection point of the cost of inaction curve in the absence of management. Prior to this
418 ‘runaway point’, the cost of inaction grows substantially from a small value, meaning that the
419 cost paid each year for management delays quickly becomes very large (solid line, Fig. 2d).
420 Beyond this point, the growth in the cost of inaction slows, and in the long-term reaches a
421 constant maximum, implying that each successive year of waiting has the same maximum
422 cost. As such, we can show that when management is less costly than damage ($\gamma < 1$): (i)
423 initiating management at any time can reduce the total cost of a given IAS over a long-time
424 horizon, but importantly, (ii) there is a critical time window within which initiating
425 management action can lead to large savings over short time horizons.

426 The exact length of this window of opportunity depends not only on the cost of
427 management, but also on the damage and management cost curve parameters K and r_M . In
428 turn, these parameters are inherently affected by, for example, the taxonomic grouping of
429 IAS. We found that larger-bodied IAS such as raccoons (*Procyon*) and squirrels
430 (*Callosciurus*), and those that could easily be transported as hitchhikers such as *Anoplophora*
431 and *Cenchrus*, had higher r values. This may reflect their greater dispersal ability, or capacity
432 to become entrained in anthropogenic vectors to spread. While empirical data limitations
433 meant that we were only able to fit parameters to a small number of genera, we predict that
434 other rapidly spreading invaders, such as ballast water/hull contaminants (e.g. mollusks and
435 copepods; Lin et al., 2020) may have high cost growth rates r . In contrast, genera similar to
436 *Aedes* and *Ambrosia* spp. that may not necessarily disperse rapidly at continental scales, but
437 have potential for triggering significant costs, could exhibit high cost carrying capacities K in
438 spite of low cost growth rates. We found that *Anoplophora* had high r and K values,
439 suggesting it has both a large capacity for damage and a fast growth in costs. These patterns

440 would likely be similar for the fall armyworm (*Spodoptera frugiperda*), which has spread
441 rapidly throughout Africa and Asia with high economic impacts (Abrahams et al., 2017).
442 Other species we suspect will show this pattern are the Asian hornet *Vespa velutina* and the
443 lionfish *Pterois volitans*, as they are among the fastest spreaders in terrestrial and marine
444 realms, respectively, and are also known to have very high management and/or damage
445 impacts (Barbet-Massin et al., 2020; Diagne et al., 2020).

446 However, we acknowledge that many IAS may not have any reported economic costs
447 at all, let alone costs that conform to a logistic curve. IAS impacts are often hard to quantify
448 and monetize (Charles & Dukes, 2008), with many economic losses therefore going
449 unreported due to a suite of biases or limited capacity to capture them (Bellard & Jeschke,
450 2016). The data we selected for this analysis were chosen based on the availability of
451 consistent cost reporting through time by multiple independent sources. While this resulted in
452 a limited sample of IAS suitable for our analysis, this approach was necessary given the lack
453 of cost information for most species at sufficient temporal resolution. Although this work
454 should serve primarily as a theoretical demonstration, where estimated, the costs of inaction
455 were found to be striking. An additional limitation of this study is that, with the exception of
456 the parameterization of management effort for *Aedes* (equivalent to 13% of the damage
457 costs), it does not consider management efficiency. Future research should address this flaw
458 and focus on empirical validation, where the suitability of this model is tested across multiple
459 taxa, habitats, and costs from different sectors of the economy. This calls for more effort into
460 estimating and reporting costs in a standardized way (Diagne et al., 2021). Although it may
461 seem intuitive that management is cost-efficient at preventing higher damage costs, we
462 recognize that it can be dependent on the efficiency of management. However, it is currently
463 impossible with the (poor) data available to factor in management efficiency in a reliable
464 manner. Such an endeavour would require data on the damage cost of species under very
465 similar conditions of management and lack of management, which do not exist to our
466 knowledge.

467 While we were limited in the data and species suitable for our analysis, it is important
468 to acknowledge how this may have impacted our results. Firstly, given the general tendency
469 to research and record species with higher costs for both management and damage, our data
470 are likely skewed to highly damaging species and species requiring costly management. For
471 the same reason, we may have not fully captured the initial, lower costs of each genus.
472 Further, due to lags in IAS detection along with their impacts (Essl et al., 2011), the actual
473 occurrence of impacts is likely somewhat earlier on the timelines, compared to the ones we
474 report in this study, and is variable across species and invaded countries (proxied by ‘cost
475 lag’ column of Table 1, Seebens et al., 2020). Furthermore, our cost saturation estimations
476 could reflect delays in more contemporary cost reporting, and do not preclude the possibility
477 of future spikes in cost due to range expansions of these IAS (Louppe et al., 2019) or
478 advances in cost quantification methods, and should therefore be interpreted with caution.
479 Finally, the costs incurred are subject to country-level differences considering, for example,
480 the importance of certain industries (Paini et al., 2016), the different research capacity, effort
481 and funding landscapes, the suitability of habitat for each IAS (Parker 1999), and other
482 socioeconomic or environmental factors across countries.

483 It is also worth noting that while our analysis was done on selected species and the
484 costs that were available for those, it is likely that in many cases biosecurity measures and
485 other proactive measures can be rendered even more cost effective when several species are
486 managed simultaneously. For instance, airport quarantine and interception services deal with
487 very large lists of potential invaders such as insect species, with only marginal costs for each
488 additional species (Lougheed et al., 2007). Aquatic biosecurity measures such as *Check*
489 *Clean Dry* campaigns similarly target a range of taxa indiscriminately (e.g., bivalves,
490 crustaceans and macrophytes; Anderson et al., 2015; Shannon et al., 2018; Coughlan et al.,
491 2020). Transport legislation such as wood-packing material treatment protocol ISPM15 can
492 also help minimize IAS risk at that pathway level (Leung et al., 2014).

493 **6 Conclusion**

494 Mathematical modelling is an important part of the theoretical ecology toolbox as
495 well as of ecological research more generally; it also plays an important role in informing
496 ecosystem managers, decision-makers and stakeholders. There are many well-documented
497 cases where even simple, conceptual models made a direct and significant impact on
498 ecosystem management, in particular helping to find an efficient and cost-saving strategy
499 (DeAngelis et al., 2021). In studies on biological invasion, mathematical models have been
500 used efficiently for a few decades aiming to identify different invasion scenarios, to reveal
501 the effect of various factors on invasion success and thus to facilitate understanding of the
502 phenomenon (Hengeveld, 1989; Shigesada and Kawasaki, 1997; Lewis et al., 2016).
503 Economic issues such as losses and associated costs have been a focus of modelling studies
504 too (e.g. see Marten and Moore, 2011), although this line of research, in our opinion, remains
505 under-developed.

506 The present study, for the first time, presents a conceptual model which monetizes the
507 cost of inaction concerning IAS management. While the cost of inaction is often implicitly
508 assumed to be zero, here we show that it can take on a very high value. We hope that this
509 conceptual demonstration can help motivate the collection of necessary data that allow for
510 more comprehensive empirical estimates of the cost of inaction. We have demonstrated the
511 suitability of this approach for a suite of genera which have both damage and management
512 costs that closely resemble logistic growth through time. Parameterizing these curves alone
513 helps to understand the rate at which the costs of each IAS is accruing, and the estimated total
514 cumulative cost of these IAS in the future. Further, we have confirmed, using our relatively
515 data-rich *Aedes* spp. case study, that more rapid management interventions and higher
516 management efforts can greatly reduce inaction costs — at the near-billion US\$ scale over
517 two decades for this genus alone. Moreover, our cautionary identification of ‘runaway’ points
518 should motivate timely management prior to the closing of IAS windows of opportunity for
519 efficient and effective control. We expect our results to help resource managers justify early
520 action, even if initially costly, and accordingly decision makers to fund it, in order to
521 simultaneously increase efficiency, efficacy and decrease overall costs.

522 **Declarations**

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534 **Conflict of interest**

535 The authors have declared that no competing interests exist.

536 **Availability of data and material**

537 The data used in this work come from publicly available databases
538 (sTwist:<https://zenodo.org/record/3925164#.YDv-dS3b0Wo>; InvaCost:
539 <https://doi.org/10.6084/m9.figshare.12668570>). Derived data used for curve parameterization
540 are provided at <https://github.com/emmajhudson/InvaCost>.

541 **Code availability**

542 Code and derived data are provided at <https://github.com/emmajhudson/InvaCost>.

543 **Authors' contributions**

544 Conceptualization - DAA, EJH, RNC, MK, PJH, BLb, CL, BLn, FC

545 Dataset (conception, finalisation) - CD, FC

546 Analyses - DAA, EJH

547 Methodology - DAA, EJH, BLn, FC

548 Writing - All authors

549 Visualizations - DAA, PJH, FC

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699 **Appendix 1.** Example calculation of the cost of inaction for *Aedes* (mosquitoes).

700 **Example** What is the total amount of savings (cost of inaction) for *Aedes* at $t = 40$ years, if
701 management were to be introduced at $\tau = 0$, instead of being delayed by $\tau = 20$ years?

702 The cumulative damage cost from *Aedes* at $t = 40$ years is $C(40) = 19169.73$ \$US
703 millions, see Fig. 6a.

704 If we consider a scenario where management is introduced at $\tau = 0$ (i.e., at the same time
705 when damage costs begin to cumulate), then at $t = 40$, damage costs would have potentially
706 reduced by $M(40) = 2433.09$ \$US millions, see Fig. 6b.

707 Therefore, the total amount of reduced losses is then the difference between these costs, and
708 can be computed from eqn. 7:

709 $\varphi(40,0) = C(40) - M(40) = 16736.64$ \$US millions.

710 Now consider another scenario where management is introduced at some delayed time $\tau =$
711 20 , in this case the damage cost at $t = 40$ would have reduced by $M(20) = 1591.07$ \$US
712 millions. The total amount of reduced losses is then: $\varphi(40,20) = C(40) - M(20) =$
713 17578.66 \$US millions.

714 As expected, the cumulative cost of damages incurred is greater in the latter scenario where
715 management is delayed.

716 The cost of inaction which is the potential savings one can acquire, is the difference of these
717 losses, where management is applied earlier or delayed:

718 $\Phi = \varphi(40,20) - \varphi(40,0) = M(40) - M(20) = 842.02$ \$US millions, see also Fig. 6c.

719 Note that this can be directly calculated from eqn. 9.

720 In contrast, the cost of inaction at $t = 40$ years (in the case where no action is taken) is
721 $\Phi(40, \tau \rightarrow \infty) = 2433.09$, and in the long-term saturates to 2497.71 \$US millions.

722 Note that the parameter values reported in the caption of Fig. 6 are rounded to two decimal
723 places for brevity, whereas the above calculation utilised estimated parameters to a higher
724 degree of accuracy, see Appendix 2.

Appendix 2.

Table S1. List of parameters used across equations and their definitions.

Parameter	Description	Parameter values used for the cost of inaction calculation for <i>Aedes</i> spp. in Section 4.2 and Appendix 1, to a higher degree of accuracy
K	Cost carrying capacity for cumulative damage costs (US\$ millions)	19183.48098446320
C_0	Initial damage cost (US\$ millions)	1450.537256354340
r	Intrinsic growth rate for cumulative damage costs (per year)	0.243593284247693
γ	Management effort; lies between $\gamma = 0$ (no management effort) and $\gamma = 1$ (maximum management effort) inclusive.	0.130201583626750
$K_M = \gamma K$	Cost carrying capacity for cumulative management costs (proportional to cost carrying capacity for cumulative damage costs, US\$ millions)	2497.719603650754
$M_0 = \gamma C_0$	Initial cumulative management cost (proportional to initial cumulative damage cost, US\$ millions)	188.8622478869361
r_M	Intrinsic growth rate for cumulative management costs (per year)	0.153294868601048
τ	Management delay (year)	$\tau = 0$ or 20

Figures

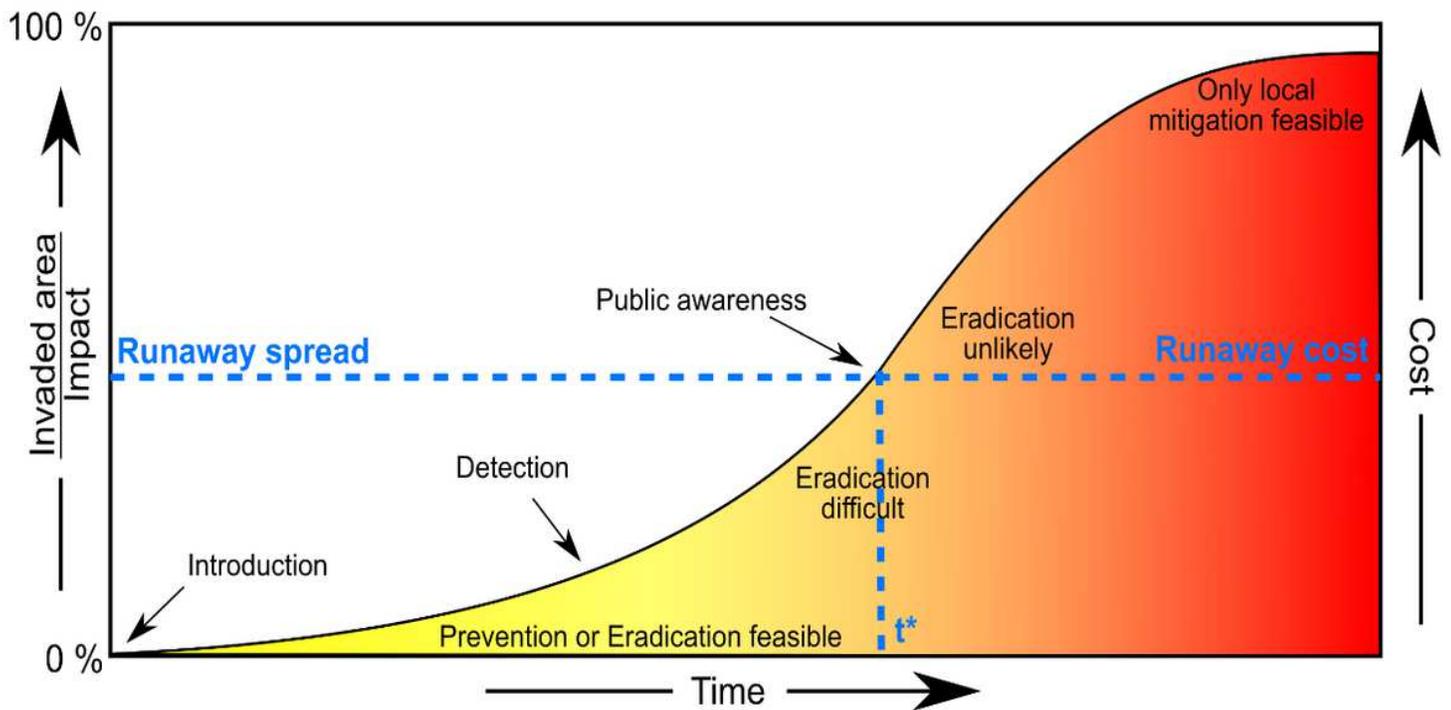


Figure 1

The classical invasion curve. This relationship displays a generalized invasive alien population response over time, after its introduction and establishment into a new environment. As the population expands and spreads, the area invaded (reported as a percentage of its total invaded area), its impact (damage costs), and its management costs increase following a logistic curve. Management costs, invaded area, and impact all grow at increasing rates until t^* , where they reach their maximum rates (which we call the 'runaway' point, see section 3.5). Adapted from Invasive Plants and Animals Policy Framework, Victorian government, 2010.

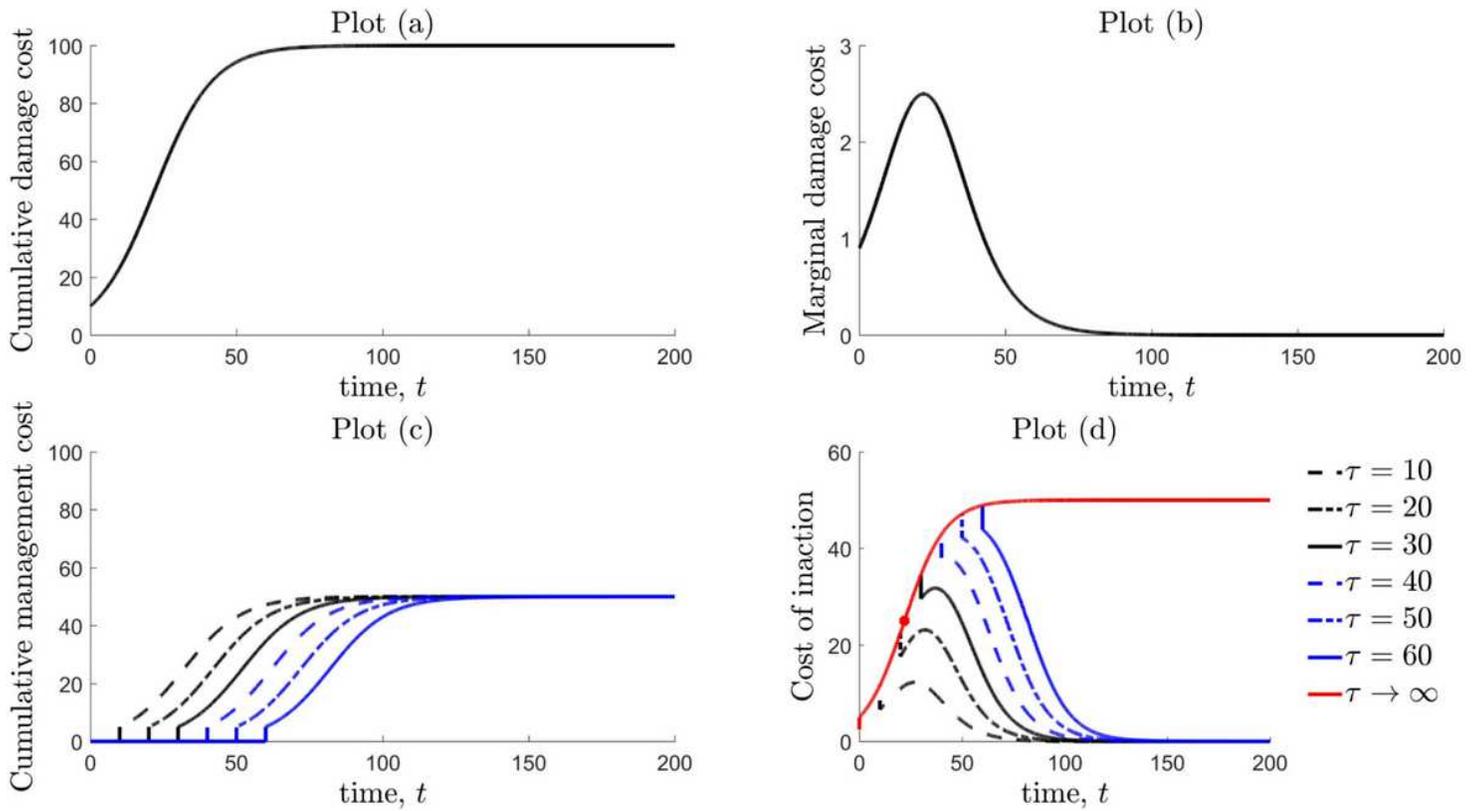


Figure 2

The impact of management delay. Plot (a) shows cumulative damage costs $C(t)$, which are modelled using a logistic curve, see eqn. 4. Plot (b) shows the instantaneous damage costs as a function of time (i.e., the marginal cost for each additional year of damage from eqn. 3). Plot (c) shows cumulative management costs $M(t-\tau)$, which are proportional to damage costs according to factor γ , and delayed by some time τ , see eqn. 5. Plot (d) shows the cost of inaction $\Phi(t,\tau)$ over time, see eqn. 9. The red curve illustrates a special case where no action is ever taken, all others represent different scenarios of increasingly delayed management. The red marker is the point of inflection or 'runaway point'. Parameter values in all cases: Damage cost carrying capacity $K=100$, Growth rate $r=rM=0.1$, Initial damage cost $C_0=10$, Management effort $\gamma=0.5$, Management cost carrying capacity $KM=\gamma K=50$, Management delay τ varied. Figure legend only applies to plots (c) and (d).

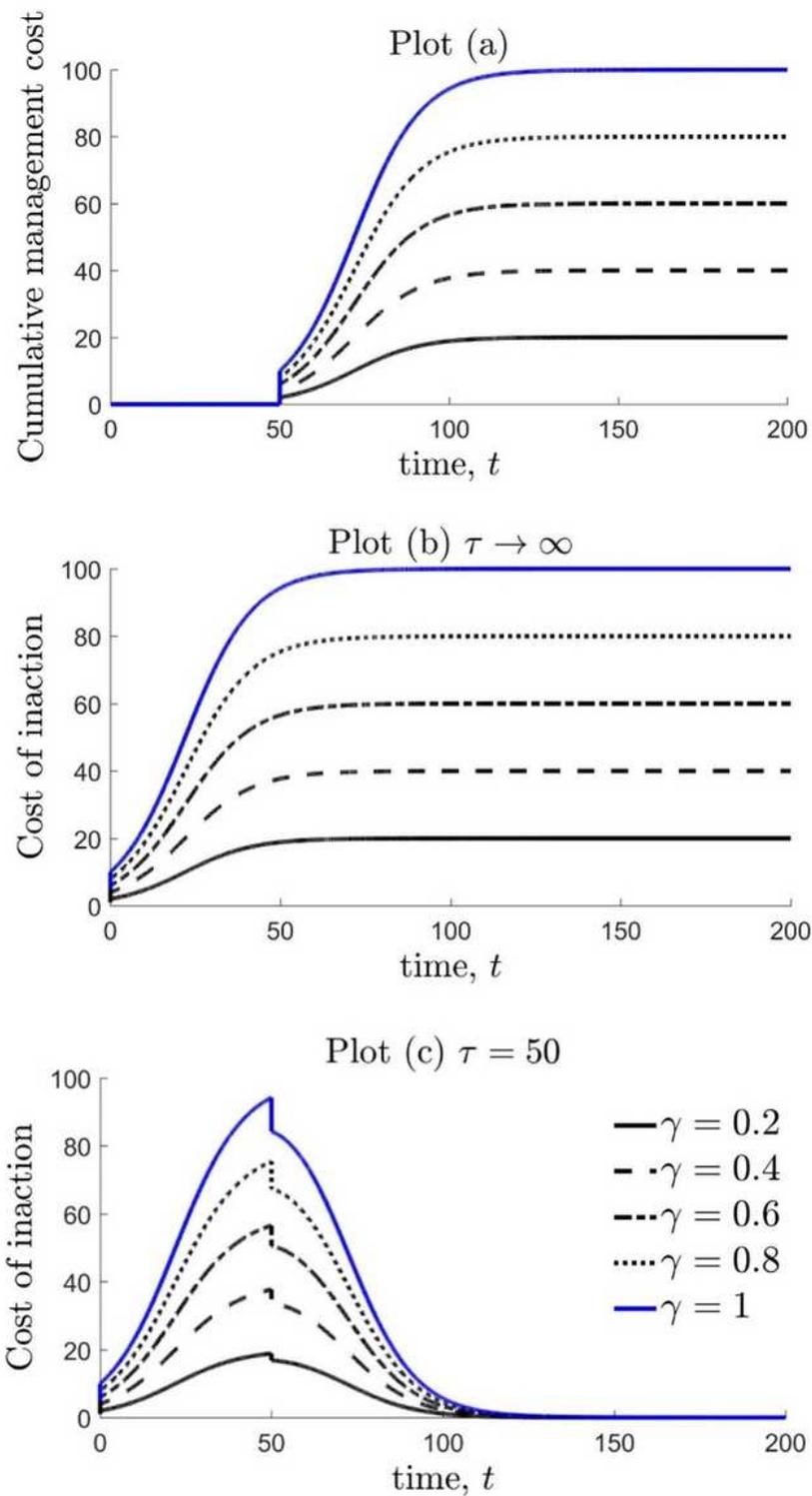


Figure 3

The impact of management effort. Plot (a) shows management cost curves over time, with a logistic form and a cost carrying capacity $KM = \gamma K$, proportional to the damage cost carrying capacity K , with management effort quantified by parameter γ , see eqn. 5. They are equivalent to plots of Fig. 2c. Plot (b) shows the associated cost of inaction for an infinite management delay (equivalent to the red curve of Fig. 2d). Plot (c) demonstrates the impact of management effort on the cost of inaction for a delay of

$\tau=50$. The higher the management costs, the more costly due to delayed management. Parameter values: Cost carrying capacity $K=100$, with management effort γ varied. Intrinsic growth rate $r=r_M=0.1$, Initial damage cost $C_0=10$, Management delay $\tau=50$.

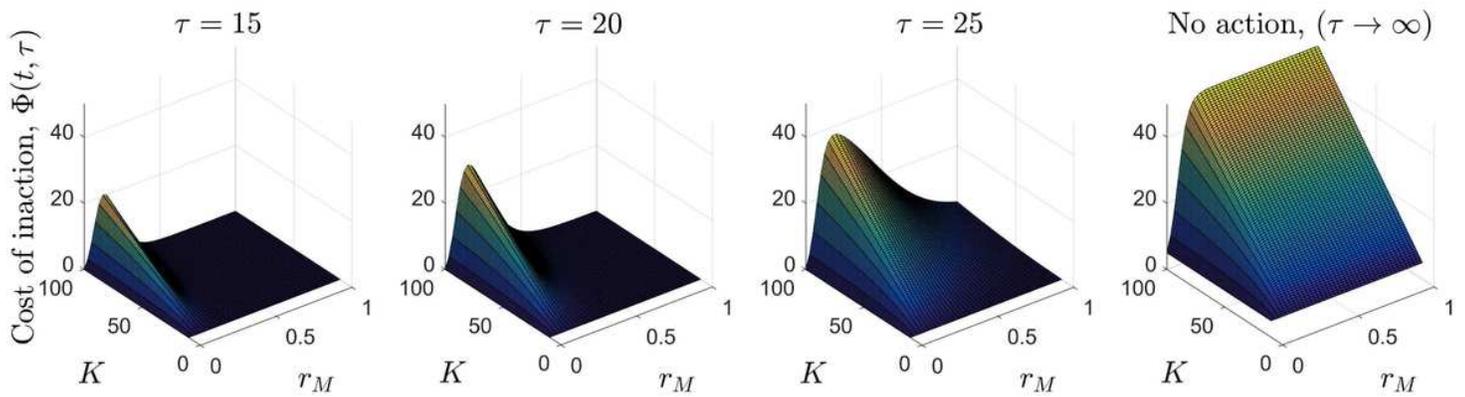


Figure 4

Snapshots of the cost of inaction at time $t=30$. Management is introduced at different times τ . The limiting case $\tau \rightarrow \infty$ represents the case where management is not introduced, i.e., no action is taken. Parameter values: Initial damage cost $C_0=10$, Management effort $\gamma=0.5$.

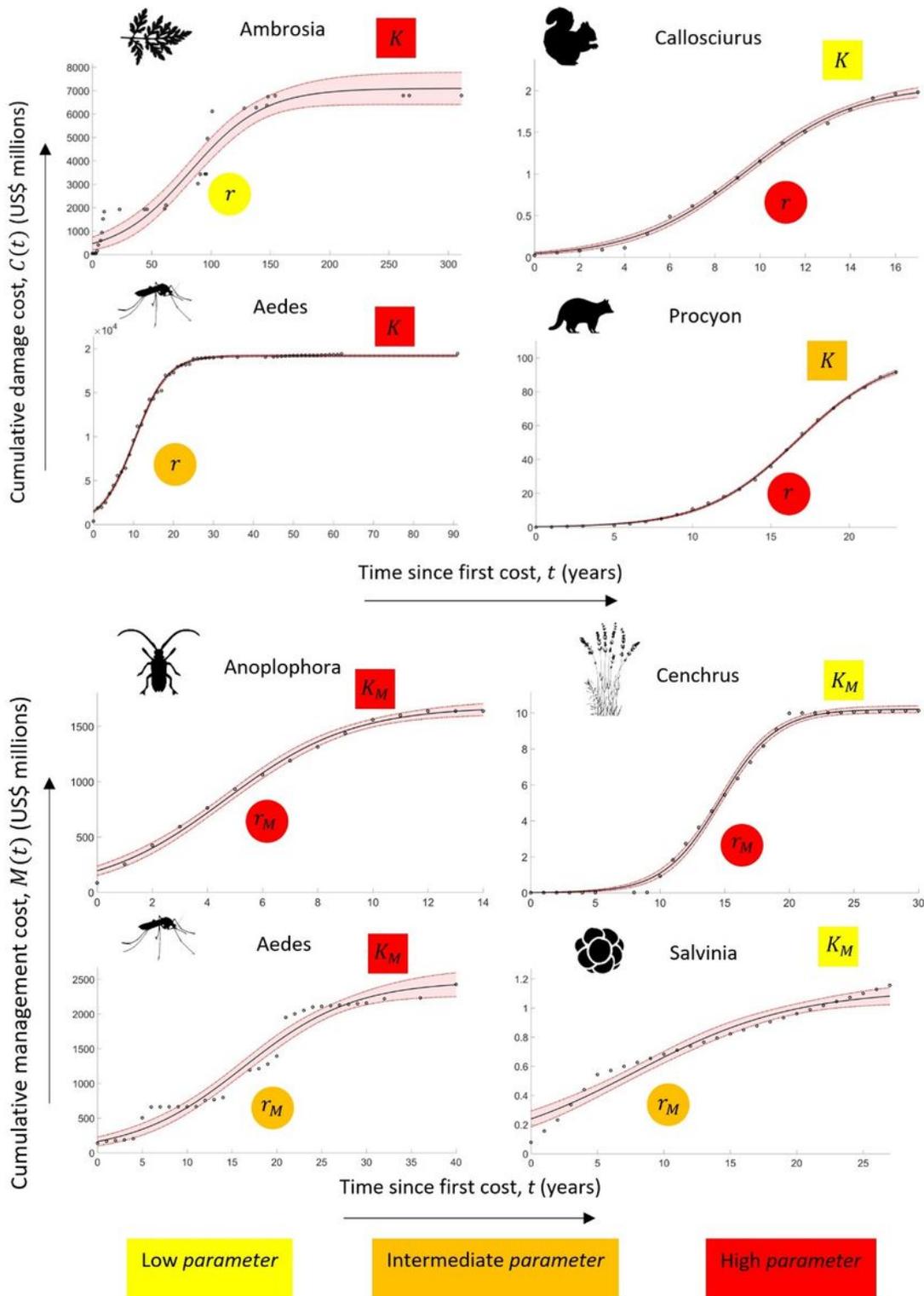


Figure 5

Model fitting of cumulative damage costs (top) and cumulative management costs (bottom) using a logistic curve, for different invasive alien species. The red shaded areas around the curves represent 95% confidence regions indicating the range of predicted cumulative costs. The estimated logistic model fit parameters are given in Table 1. The range for low/intermediate/high parameter values are given in the caption of Table 1 using the same colour scheme. High values of the intrinsic growth rate (r or r_M)

illustrate species for which costs increase rapidly; high values of the cost carrying capacity (K or K_M) illustrate species for which costs eventually saturate at high values. Dots represent annual total costs. Note that the scales differ across subplots.

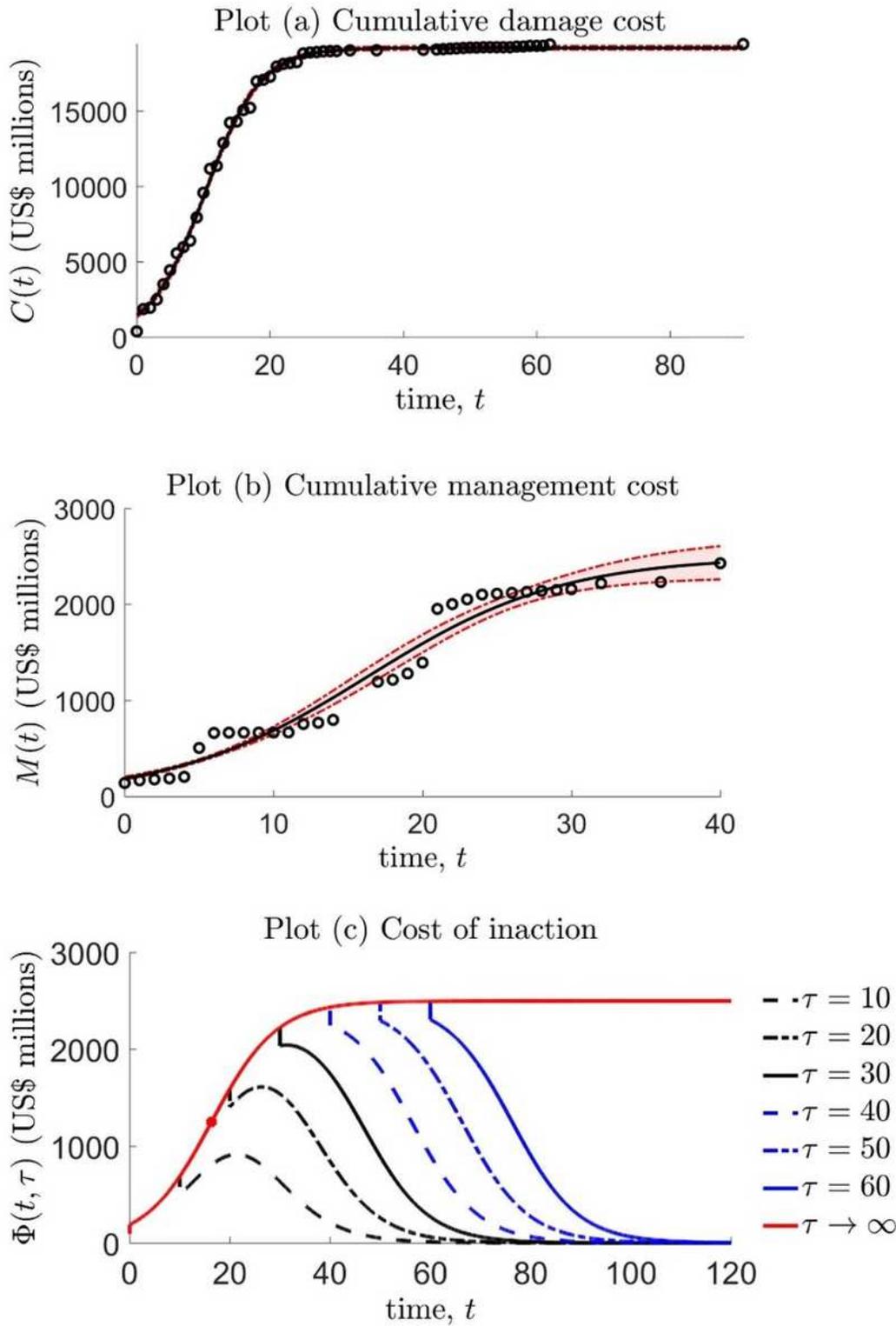


Figure 6

Plot (a) Cumulative damage cost for *Aedes*. Parameters: Initial damage cost $C_0=1450.54$, cost carrying capacity $K=19183.48$, intrinsic growth rate $r=0.24$, coefficient of determination $R^2=0.997$. Plot

(b) Cumulative management cost for Aedes. Parameters: Initial management cost $M_0 = \gamma C_0 = 188.86$, cost carrying capacity $K_M = \gamma K = 2497.63$, where $\gamma = 0.13$ quantifies management effort, intrinsic growth rate $r_M = 0.15$, $R^2 = 0.965$. Red shaded area represents a 95% confidence region. Plot (c) shows the cost of inaction for Aedes, with management delay τ . The red marker is the runaway point which occurs at $(t^*, \Phi^*) = (16.33, 1248.86)$. Note that the estimated parameters for management costs differ from those reported in Table 1, as here it is assumed that cost carrying capacities are directly proportional. Also, the parameter values reported here are rounded to two decimal places, but all computations use estimated parameter values to a higher degree of accuracy, see Appendix 2.