Ecological Applications

Research article

Predicting future damage costs of non-native species using combined dynamical and cost-density equations

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Open Research Statement

All data are freely available in the INVACOST R package, downloadable from the Comprehensive R Archive Network https://cran.r-project.org/package=invacost, and the R package code is open-source and available on github at https://github.com/Farewe/invacost. The version of the package used in this manuscript (v4.1) is stored on Zenodo (Leroy et al. 2022; 10.5281/zenodo.6653232). All MATLAB codes used to generate Figures 2, 3, and 4 in this manuscript are publicly available on GitHub (https://github.com/daa119/Predicting-future-damage-costs) and Zenodo (https://doi.org/10.5281/zenodo.15255501).

Abstract

Biological invasions threaten biodiversity, economic stability, and public health, and are exacerbated by intensive global trade and transport. The economic costs of these invasions have reached US$ trillions globally and are expected to continue increasing. However, while past invasion costs have been described across various contexts, there are few robust projections of future costs, limiting effective management planning. We developed a mathematical framework for predicting future economic damage caused by biological invasions, combining cost-density relationships with a density-time function based on logistic population growth. We tested the model on five non-native mammal species with wide-ranging negative impacts on biodiversity, agriculture, health, and infrastructure globally, using country-specific data from Japan: Pallas' squirrel *Callosciurus erythraeus*, small Indian mongoose *Herpestes javanicus* (synonym *Urva auropunctata*), nutria *Myocastor coypus*, masked palm civet *Paguma larvata*, and raccoon *Procyon lotor*. All species-specific impacts followed a similar S-shaped, high-threshold cost curve over time, characterised by time lags between low impact at low densities and subsequent exponential cost growth and saturation, with varying intrinsic growth rates and sensitivities to resource availability. Our model returned accumulated costs up to 2050 varying over several orders of magnitude, from \$0.43 million (*H. javanicus*) to \$88 million (*P. larvata*), with the highest rates of increase for *P. larvata* (up to 55%) and *H. javanicus* (78%). Under business-as-usual management, our approach identifies thresholds beyond which damages escalate rapidly — for all species, costs begin to surge 40 to 80 years after the first record of the species, with 90% of expected long-term damages incurred within 10 to 20 years — except for *H. javanicus*, which takes approximately 35 years. For managers, these results highlight the importance of timely interventions, underscoring the need for tailored management strategies considering species-specific dynamics, socio-economic contexts, and the speed of cost escalation. We demonstrate that cost dynamics can be reliably forecasted even at early-stage invasions before economic impacts surge. Therefore, early-stage cost dynamics can predict future trajectories of existing and emerging invasions, helping inform proactive management prioritisation. Our predictions equip policymakers and resource managers with improved foresight to anticipate and mitigate future economic burdens of non-native species.

Key words: biological invasions; non-native species; economic costs; impact projections; invasion management; damage modelling; logistic growth; *InvaCost*

A Japanese translation of the abstract is available in Appendix S1.

Introduction

The global expansion of non-native species is driving biodiversity loss worldwide, having contributed to at least 60% of recorded extinctions (Simberloff et al. 2013; Bellard et al. 2016, 2022). The introduction rate of non-native species is also increasing, with 200 species introduced to areas outside their native range annually (IPBES 2023), driven mainly by trade and transportation networks that link previously isolated biological communities (Seebens et al. 2017, 2018, 2020). Biological invasions generally follow four main stages: transport, introduction, establishment, and spread; however, a non-native species' impacts can appear as soon as the species is introduced to a novel environment, as they interact with native species, modify environments, and/or exploit available resources (Blackburn et al. 2011; Soto et al. 2024a).

There are 13 main biodiversity-impact mechanisms identified for non-native species, including direct effects such as competition, predation, or disease transmission, and passive impacts such as toxicity (when consumed) or induced biofouling (Blackburn et al. 2014). These impacts can operate at various ecological scales, ranging from populations to ecosystems/habitats, as well as on socio-economic systems (Blackburn et al. 2014; Carneiro et al. 2025). For instance, non-native species can adversely affect native populations by reducing their population sizes or causing local extinctions (Bellard et al. 2016; Vanbergen et al. 2017). Non-native species also alter both biotic and abiotic interactions within ecosystems, which can initiate cascades that disrupt ecological dynamics, ecosystem structure and function, and even promote more invasions (Stigall 2010; Walsh et al. 2016; Vanbergen et al. 2017; Bucciarelli et al. 2019). Furthermore, non-native species can negatively impact human health by acting as vectors or reservoirs for various pathogens and parasites (Roy et al. 2023), causing direct physical harm through venoms or toxins, or by exacerbating allergies (Juliano and Lounibos 2005; Schaffner et al. 2020; Roy et al. 2023).

In addition to the severe ecological and health repercussions of non-native species, they are also responsible for a growing economic burden across economic sectors, such as agriculture, forestry, and fisheries (Bradshaw et al. 2016; Diagne et al. 2021; Ahmed et al. 2023; Turbelin et al. 2024). Monetary cost assessments of biological invasions help to promote more sustainable global management actions that result in better environment and health outcomes (Soto et al. 2023a), even though many countries struggle to prevent and/or manage invasions (Early et al. 2016; Bradshaw et al. 2024). Although most countries have set targets to manage biological invasions, 45% of countries do not invest at all in the management of non-native species (IPBES, 2023). There is also a lack of international coordination in management, with most countries acting independently and with predominantly reactionary approaches (Cuthbert et al. 2022b). This historical neglect of non-native species management erroneously stems from a perception that the costs of intervention outweigh the potential benefits, in part owing to a lack of damage cost synthesis and insufficient forecasting (Heikkilä 2011; Carneiro et al. 2024). However, early investment in management strategies, such as biosecurity, is often more cost-effective than long-term control measures (Leung et al. 2002; Cuthbert et al. 2022b; Bradshaw et al. 2024). Most invasion cost assessments have so far been descriptive (Ahmed et al. 2023), and there is accordingly an urgent need to move towards predictive analyses of costs through space and time with accessible models. In particular, with rapidly escalating impacts, identifying the temporal dynamics of costs could inform the necessary timings for management interventions across invasion stages to circumvent severe impacts, while enabling forecasting of future cost trajectories for existing and emerging invasions.

A major challenge to management is that the impacts of non-native species are dynamic as populations shift in abundance or range (Parker et al. 1999; Dickey et al. 2020; Soto et al. 2024b). In some cases, these populations exhibit boom-bust dynamics, where an initial rapid increase in population size is followed by a decline or stabilisation due to resource depletion, natural enemies, or other ecological factors (Copp 2007; Strayer et al. 2017). These fluctuations further complicate predictions of long-term impacts and the effectiveness of control measures. The dynamics are often non-linear and influenced by delays in detecting the presence of non-native species or their impacts that hinder the implementation of control measures (Soto et al. 2023b). Indeed, negative impacts can be initially slow to accrue owing to time lags in demographic processes as the new species adapt to novel environmental conditions before expanding rapidly (Haubrock et al. 2022; Robeck et al. 2024), leading to a 'cost of inaction' from delayed management (Ahmed et al. 2022b). While invasion dynamics have previously been characterised in terms of establishment and spread (e.g., the sigmoidal 'invasion curve'; Haubrock et al. 2022), the interplay between economic damage and the population dynamics of invasive species under changing environmental and economic conditions is still poorly understood. Indeed, broad-scale studies on invasion costs frequently present only aggregated and static monetary estimates, and neglect the temporal dynamics and complex types of costs associated with management and damage (Ahmed et al. 2023b). While more recent cost assessments explicitly consider temporal dynamics, few studies have forecasted the economic impacts of biological invasions (Henry et al. 2023; Tarkan et al. 2024), particularly while accounting for the invasion dynamics of the species involved. This often leads to broad generalisations that are not always useful to managers because such predictions ignore variation in cost dynamics among taxonomic groups and contexts.

To promote timely actions that reduce future impacts, it is necessary to develop robust impact predictions. Ahmed et al. (2022) previously developed a modelling framework linking invasion costs to population dynamics. Here, we advance this framework to predict future costs at the species level by developing a model that integrates cost-density relationships with a density-time function based on continuous logistic growth. The model only requires a time series of cost estimates to predict future cost patterns as well as the population dynamics of the target population. By relying solely on damage cost data, it avoids the need for detailed ecological or demographic inputs, making it both simple and broadly applicable across a wide range of non-native species and contexts. In doing so, the temporal economic cost patterns can be used to retrace the population dynamics of non-native species linked to impact, which are fundamentally governed by their intrinsic growth rates and carrying capacities. We test this model on five non-native mammals for which we have extensive data on damage costs from Japan: Pallas' squirrel *Callosciurus erythraeus*, small Indian mongoose *Herpestes javanicus*, nutria *Myocastor coypus*, masked palm civet *Paguma larvata*, and raccoon *Procyon lotor*. All five species cause severe monetary and ecological costs by outcompeting native species, preying on wildlife, overgrazing, and spreading diseases (Nagayama et al. 2020; Watari et al. 2021; Katahira et al. 2022; Tatemoto et al. 2022; Doi et al. 2024). Assuming a business-as-usual management scenario, by quantifying thresholds in temporal dynamics of costs and projecting potential future damages up to 2050, we provide timescales for stakeholders to implement management strategies that address both current invasions and prepare for future threats. Given the need for cost efficiency in the presence of constrained management budgets, these dynamic predictions can help optimise and prioritise investments for individual invasions. This straightforward model also permits prediction of future cost dynamics, based on initial cost data before rapid growth, as well as for future impacts of well-established invasive populations.

Methods

Continuous-time logistic growth model

A general class of models for the population growth of a single species over continuous time can be expressed as:

$$\frac{du}{dt} = uf(u),\ u(0) = u_0 \tag{1}$$

where $u(t)$ represents the population density (e.g., number of individuals per unit area) as a function of time t, and u_0 is the initial population density. The function $f(u)$ represents the per-capita growth rate, which typically depends on population density. For many species, especially at high population densities, $f(u)$ decreases as u increases (known as *compensation*; Herrando-Pérez et al. 2012; Bradshaw and Herrando-Pérez 2023), reflecting the ecological reality that growing populations are ultimately limited by an average, long-term environmental carrying capacity K.

One of the simplest and most widely used models capturing this density feedback is the logistic growth model (Bradshaw and Herrando-Pérez 2023). In this model, the per-capita growth rate decreases linearly with increasing population density, illustrating the competition for limited resources (e.g., food, space, or mates) that intensifies as population size grows. The per-capita growth rate in the logistic model is given by:

$$f(u) = \alpha\left(1 - \frac{u}{K}\right) \qquad (2)$$

where $\alpha > 0$ is the maximum intrinsic growth rate under ideal conditions and no environmental constraints, and $K > 0$ is the environmental carrying capacity — the maximum population density that the environment can sustain without degradation or resource depletion. As population density approaches K, growth rate declines to zero (i.e., resulting in temporal stability in population size).

The logistic growth model is described by:

$$\frac{du}{dt} = \alpha u\left(1 - \frac{u}{K}\right),\ u(0) = u_0 \qquad (3)$$

but can be written in a more convenient form if we introduce a variable to define the re-scaled population density as $z = u/K$, where $0 < z < 1$. The equation then becomes:

$$\frac{dz}{dt} = \alpha z(1 - z),\ z(0) = \frac{1}{\gamma} \qquad (4)$$

which can be solved to express the re-scaled population density at any time t:

$$z(t) = \frac{1}{1 + (\gamma - 1)\exp(-\alpha t)} \qquad (5)$$

where $\gamma = K/u_0$ is an environmental scaling factor that represents the relationship between initial population density u_0 and carrying capacity K, reflecting how environmental resources or limitations scale with initial population size. If α remains constant, carrying capacity becomes directly proportional to initial population density, indicating stable ecological conditions, such as consistent resource availability or habitat quality. In this case, growth slows as the population approaches K due to compensation. This shift moves the model from one where both K and u_0 influence population dynamics to one where their ratio (γ) is the main driver. By focusing on γ, the model captures how environmental factors interact with initial population density to shape growth. An increase in γ reflects more abundant resources or optimal conditions, while a lower γ indicates resource limitation.

The logistic model effectively describes population growth in resource-limited environments by balancing intrinsic growth potential and environmental constraints. Equation 5 shows that when population density is much smaller than carrying capacity ($u_0 << K$), the population grows exponentially. However, as $u(t)$ approaches K (i.e., $z(t) \to 1$), the growth rate slows, and the population stabilises around K. This is a common feature in many ecological systems, where populations initially exhibit rapid growth when resources are abundant, but eventually stabilise at or near K (Brook and Bradshaw 2006). While widely applicable across species, it assumes a constant carrying capacity, but does not account for environmental fluctuations, potential Allee effects (Courchamp et al. 1999) at low population densities, or dynamic factors influencing stationarity (Bradshaw and Herrando-Pérez 2023).

While other growth models also provide exact solutions to equation 1 we focus on the continuous (*cf.* discrete) logistic growth model because it is simple, widely understood, and not prone to issues of parameter identifiability when tested against empirical data (Clark et al. 2010, Simpson et al. 2022). This is particularly important because failure to account for parameter identifiability can result in unreliable or imprecise parameter estimates, potentially leading to incorrect interpretations of the mechanisms involved (Clark et al. 2010). Moreover, its ability to describe the basic pattern of population growth, saturation, and stabilisation makes it a baseline choice for many ecological applications.

Cost-density relationships

Cost-density curves have been previously used to relate the density of non-native species to the cost or impact on socio-ecological systems (e.g., Yokomizo et al. 2009). In many cases, managers assume that impact increases proportionally with invader density, especially when the exact density-impact relationship is unknown (Elgersma and Ehrenfeld 2011); however, ecological impacts often follow non-linear patterns (Jackson et al. 2015). In practice, the connection between the ecological impacts of a non-native species and its population density exhibits both linear and non-linear patterns (e.g., Nava-Camberos et al. 2001; Finnoff et al. 2005; Laverty et al. 2017; Moroń et al. 2019; Bradley et al. 2019). However, research that explicitly links these relationships to the monetary costs resulting from non-native species impacts is scarce, albeit there have been some attempts to address the gap (Ahmed et al. 2022a).

To characterise the diverse forms of cost-density relationships — where the total incurred accumulated damage cost C depends on the (re-scaled) population density z, we adopted a framework based on functional types proposed by Yokomizo et al. (2009), expressed as:

$$C(z) = AC_{\max}\left(\frac{1}{\frac{1-B}{B}\exp\left(-\frac{z}{s_2}\right)+1} - B\right),\ 0 < z < 1 \tag{6}$$

where

$$A = \frac{1+\exp(-s)}{1-B(1+\exp(-s))}, B = \frac{1}{1+\exp\left(\frac{s_1}{s_2}\right)} \text{ and } s = \frac{1-s_1}{s_2} \tag{7}$$

and where $C_{\max}$ represents the maximum potential cost, s_1 and s_2 are shape parameters constrained between 0 and 1, and A, B, and s shape the cost-density curve (Figure 1). This model is well-suited to density-cost dynamics due to its use in evaluating ecological and economic impacts (e.g., Jackson et al. 2015; Vander Zanden et al. 2017; Roberts et al. 2018; Sofaer et al. 2018). It was specifically applied to capture the temporal dynamics of invasion-related economic costs across several genera, revealing distinct types of cost curves and showing how variation in invasion duration, species' ecology, and data availability influence cost patterns and guide management strategies (Ahmed et al. 2022a).

The parameter $C_{\max}$ assumes no further spatial spread of the non-native species within the study area, implying that its current distribution reflects a stable ecological or climatic equilibrium (e.g., Barnett 2001; Aplin et al. 2011). This assumption is reasonable for species that appear to have saturated their potential range, and from an intertemporal perspective, reaching this bound may reduce long-term management costs by limiting the need for sustained control efforts. While annual damage costs can still accrue beyond this density, they are typically lower than during the phase of rapid population growth (Ahmed et al. 2022b). As the population density stabilises near its ecological limit, total costs approach a saturation point, asymptote at or near $C_{\max}$, potentially reflecting ecological or socio-economic adaptation or habituation to the invader's presence within a given area; however, additional costs can still arise through range expansion or dispersal into new regions (Simberloff and Gibbons 2004; Strayer et al. 2006). At that stage, the impact of additional population growth on costs diminishes, shifting the focus from preventing further spread to mitigating the ongoing negative economic and ecological impacts. Management (e.g., maintenance removals — e.g., Venning et al. 2021), which we do not include in this analysis, becomes the primary driver of sustained costs once the species reaches its ecological limit.

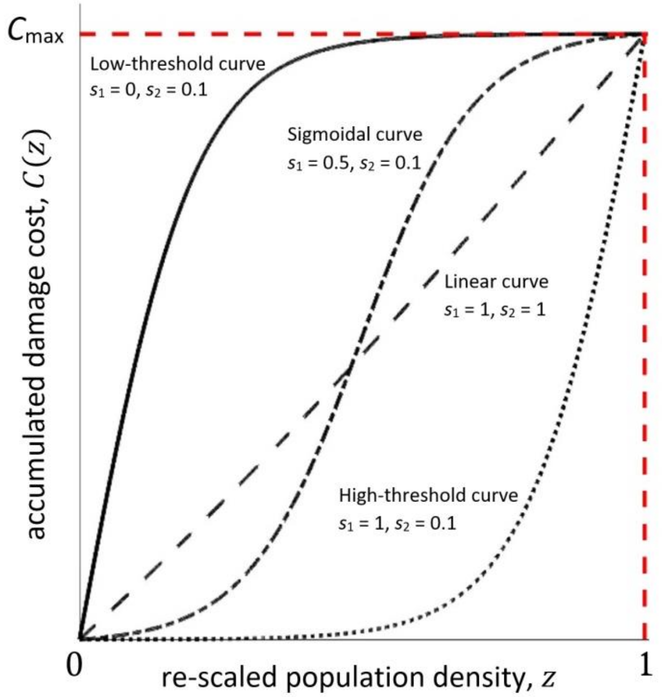

Figure 1 Illustration of the four types of cost-density curves: Low-threshold curve with shape parameters $s_1 = 0$, $s_2 = 0.1$, sigmoidal curve with $s_1 = 0.5$, $s_2 = 0.1$, linear curve with $s_1 = 1$, $s_2 = 1$ and high-threshold curve with $s_1 = 1$, $s_2 = 0.1$. Adapted from Figure 2 in Ahmed et al. (2022a).

The relationship between the re-scaled population density z of non-native species and the damage costs they incur can be described broadly using four functional types, each reflecting a distinct pattern of cost accumulation as density increases (Figure 1). The low-threshold curve shows a sharp rise in costs at low densities, followed by a plateau where costs remain consistently high despite additional population growth. In contrast, the sigmoidal curve exhibits a steep escalation in costs at intermediate densities, with costs rising more sharply than in the linear relationship, where costs increase directly in proportion to population density. The high-threshold curve exhibits relatively lower costs at low densities, but experiences a surge once the population exceeds a density threshold. In this particular case, the cost-density function given by equations 6 and 7 can be reduced to:

$$C(z) = \frac{2C_{\max}}{\exp\left(\frac{1}{s_2}(1-z)\right)+1}, \; 0 < z < 1. \qquad (8)$$

Temporal damage cost dynamics

To link the damage cost C to time, we combined the logistic growth model (equation 5) with the cost-density relationship (equations 6–7):

$$C(z) = AC_{\max}\left(\frac{1}{\frac{1-B}{B}\exp\left(-\frac{z}{s_2}\right)+1} - B\right),\ z(t) = \frac{1}{1+(\gamma-1)\exp(-\alpha t)},\ 0 < z < 1 \tag{9}$$

with shape parameters A and B defined as in equation 7. The damage cost function $C(z)$ depends on the shape parameters s_1 and s_2, while population dynamics are governed by the intrinsic growth rate α and the environmental scaling factor γ. By integrating ecological and economic dynamics, this temporal model illustrates how damage costs evolve as the population of non-native species grows and stabilises. It enables researchers and policymakers to predict not only the immediate financial impacts of an invasion, but also how these costs will change over time. This approach is useful because it makes it possible to analyse trends in costs over time as a function of the growth of the species, helping to develop better-informed, long-term management strategies. By considering how population growth slows as the species approaches equilibrium, it helps in forecasting the ongoing economic burden and guiding resource allocation for prevention and control.

Identifying thresholds

We propose several thresholds for management along the damage cost curve to determine when non-native species reach densities beyond which the economic and ecological consequences rise precipitously. The high-threshold damage cost function in equation 8 can be normalised by introducing a re-scaled cost variable $\hat{C} = C/C_{max}$ that lies between 0 and 1, and expressed as:

$$\hat{C}(z) = \frac{2}{\exp\left(\frac{1}{s_2}(1-z)\right)+1},\ 0 < z < 1, \tag{10}$$

(Appendix S2). We define the density beyond which costs begin to escalate rapidly as when the rate of change of normalised cost with density is > 1. To identify that density, we set $d\hat{C}/dz = 1$. Thus, the threshold density z_{thresh} can be derived from equation 10:

$$z_{\text{thresh}} = 1 - s_2\log_e\left[\left(\frac{1}{s_2} - 1\right) + \sqrt{\left(\frac{1}{s_2} - 1\right)^2 - 1}\right]. \tag{11}$$

For example, when $s_2 = 0.1$, $z_{\text{thresh}} = 1 - \frac{1}{10}\log_e\left(9 + 4\sqrt{5}\right) \approx 0.71$ and occurs at time t_{thresh}:

$$t_{\text{thresh}} = -\frac{1}{\alpha}\log_e\left[\frac{1}{\gamma-1}\left(\frac{1}{z_{\text{thresh}}} - 1\right)\right]. \tag{12}$$

The normalised threshold cost is $\hat{C}(z_{\text{thresh}}) = 1 - \frac{2}{5}\sqrt{5} \simeq 0.106$ (equations 10 and 11), i.e., for each species, the accumulated damage cost at the threshold point is approximately 10% of $C_{\max}$.

In terms of actual variables, recall that $z = u/K$, so it follows that the true threshold density u_{thresh} is directly proportional to each species' carrying capacity K, given by $u_{\text{thresh}} \approx 0.711K$. Beyond this point, the marginal damage cost (i.e., the rate of change of accumulated damage cost with respect to population density; $\mathrm{d}C/\mathrm{d}u$) exceeds the average cost per unit density across the full ecological range ($C_{\max}/K$). Ecologically, this represents a transition point: below u_{thresh}, costs accumulate slowly, but beyond it, even small increases in invader density can drive disproportionately large increases in economic damage. The threshold therefore marks the onset of rapid cost escalation, and serves as a warning point for timely management intervention.

Consider the accumulated damage cost reaching a proportion ε of the long-term potential cost $C_{\max}$. If we set $\hat{C}(z) = \varepsilon$ in equation 10, the corresponding saturation population density z_{sat} is:

$$z_{\text{sat}} = 1 - s_2 \log_e\left(\frac{2}{\varepsilon} - 1\right) \tag{13}$$

which occurs at time:

$$t_{sat} = -\frac{1}{\alpha}\log_e\left[\frac{1}{\gamma - 1}\left(\frac{1}{z_{sat}} - 1\right)\right], \tag{14}$$

(Appendix S3). To define the concept of 'near' saturation, we set $\varepsilon = 0.9$, so that the density z_{sat} and the corresponding time t_{sat} are the point where damage costs reach 90% of their maximum value $C_{\max}$, determined from equations 13 and 14. Similarly, 'half' (mid) saturation occurs when $\varepsilon = 0.5$, where z_{mid} and t_{mid} correspond to 50% of $C_{\max}$. We use different subscripts to distinguish between these cases. For $s_2 = 0.1$, the threshold densities are $z_{\text{mid}} = 1 - \frac{1}{10}\log_e 3 \approx 0.89$ and $z_{\text{sat}} = 1 - \frac{1}{10}\log_e\left(\frac{11}{9}\right) \approx 0.98$, corresponding to densities proportional to K, given as $u_{\text{mid}} \approx 0.89K$ and $u_{\text{sat}} \approx 0.98K$, respectively. These density thresholds depend on the curve shape parameter of the high-threshold curve (s_2), whereas the times at which these occur depend also on ecological parameters (α, γ) that govern the population dynamics of the species under consideration.

Model demonstration using randomly generated damage cost data

To demonstrate model applicability, we provide a heuristic example illustrating the damage cost dynamics for two hypothetical non-native species. We randomly generated annual costs independently from a uniform distribution between \$0 and \$1 million for ten consecutive years (time $t = 0$ to $t = 9$ years), and then cumulatively summed these to produce the input data for model fitting using equation 9. As a demonstration, we only considered the high-threshold cost-density curve with shape parameters $s_1 = 1$, $s_2 = 0.1$ (Figure 1). For that scenario, we used the non-linear regression function fitnlm in MATLAB to fit the model to the generated cost data and estimated the best-fitting parameters; long-term accumulated cost $C_{\max}$, environmental scaling factor γ, and intrinsic growth rate α.

We also consider a second scenario assuming the same $C_{\max}$ and γ, but with a reduced population growth ($\alpha/2$). We identified indicative points along the damage cost trajectories, such as the threshold (point prior to rapid cost escalation), midpoint (when costs reach 50% of $C_{\max}$), and near-saturation (when costs reach 90% of $C_{\max}$). We determined these points based on population-density thresholds (equations 11 and 13) and the ecological parameters α and γ (equations 12 and 14).

Data filtering and extraction

The year of first record for each species is taken from the *Standardising and Integrating Alien Species* database; SinAS v2.4.1 (Seebens et. al. 2020), except for *Paguma larvata*, which is listed as pre-19th Century. This exception reflects historical uncertainty about the species' origin in Japan. During the Edo period (1603–1868), illustrations appeared to depict civet-like animals, leading some to think the species was native. However, recent genetic studies have confirmed that *P. larvata* is non-native (Endo et al. 2020). In fact, the exact date of introduction is unknown, but it is now widely thought that the civet was brought to Japan from Taiwan sometime in the 1930s or 1940s. The earliest reliable field record of civet capture dates to 1943 in Shizuoka (Nawa 1965), supporting the conclusion that *P. larvata* should be considered a 20th-Century introduction.

We extracted cost data from the *InvaCost* database version 4.1 — the most comprehensive database of invasive species costs — via the invacost R package (Leroy et al. 2022). We applied a suite of filters to ensure cost records were highly reliable and comparable across species. First, we subsetted costs to those with a non-missing start and end date ('Probable_starting_year_adjusted'/ 'Probable_ending_year_adjusted') and a non-missing value in 2017 US dollars ('Raw_cost_estimate_2017_USD_exchange_rate'). We then used the *expandYearlyCosts* function in the invacost R package to convert costs incurred over multiple years to constant annual values for each cost record that spanned the entire period over which each referenced publication recorded costs. For example, a cost record spanning 2000 to 2009 of

$1 million would be converted to 10 records of $100,000 for the years 2000 through 2009, respectively. While this may misrepresent growing costs over time due to underlying population growth, we did not wish to self-impose a more complex temporal pattern, and note that many cost reports used in this study are given separately for each year, and did not require expanding. We then subsetted data to only those annual costs that were incurred from 1960 through 2022. We applied this cut-off to focus on more recent and reliable cost data. The specific choice of this year is somewhat arbitrary, as invasion pathways and impact processes likely did not change abruptly in 1960. However, data reported after this period are generally more consistent in terms of valuation methods and sectoral detail. As argued in related publications using these data, setting a temporal threshold helps improve comparability and reduces bias caused by historical undersampling and varying economic contexts (Diagne et al. 2021).

We further restricted data to cost records relating to *observed* damage costs that are considered to be highly reliable, using the 'Type_of_cost_merged', 'Implementation' and 'Method_reliability_refined' columns respectively in *InvaCost*. We therefore excluded from our analysis management costs, costs combining damage and management, potential costs, and costs with limited reliability. As a final filter to ensure costs were on a comparable geographical scale under similar socio-economic contexts, we restricted cost records to those reported in Japan using the 'Official_country' column. While filtering to a single country reduced the cost entries included to those coming from a single publication, this set of cost records was the only example of consistent temporal cost reporting of invasive species in the same location over time, highlighting the need for analogous studies in other countries to determine the generality of our findings and/or drivers of discrepancies across regions.

We only model *observed* accumulated damage costs over time. Therefore, we did not include any earlier costs that went unreported — particularly those predating 1960 — in our analysis. As a result, our model probably underestimates the true long-term economic impact of these species. However, because costs tend to rise slowly in the early stages of invasion and escalate sharply only after reaching a threshold density, these missing early costs are likely small in magnitude relative to the peak costs. Thus, while our estimates might slightly understate total accumulated costs, the overall trajectory and main escalation patterns are unlikely to be qualitatively affected. Moreover, this temporal pattern — where annual costs start low, peak, and then decline, forming a bell-shaped curve — has been observed for several non-native species (e.g., *Aedes* spp.;

Ahmed et. al. 2022b), supporting the assumption that early-stage costs typically contribute only a small proportion of long-term damages.

Following these filters, we identified five mammal species: *C. erythraeus*, *H. javanicus* (now accepted as a synonym of *Urva auropunctata*), *M. coypus*, *P. larvata*, and *P. lotor*. The reclassification of the small Indian mongoose reflects recent taxonomic revisions informed by phylogenetic studies, which reassigned the species from the genus *Herpestes* to *Urva* to represent its evolutionary relationships more accurately. This change has been widely adopted since around 2018 (Veron and Jennings 2017). However, we refer to the species as *Herpestes javanicus* throughout, because it is the name listed in the *InvaCost* database, ensuring consistency with the source data. We re-checked database entries to ensure concordance in recorded cost timing and the timing noted in the associated report, and corrected any discrepancies. We aggregated annual cost records by year and species and calculated cumulative costs from the first year of filtered cost records by each species to the final year of their costs within our window of 1960 to 2022. Thus, we obtained country-level accumulated damage costs by summing all reported costs across species and countries within a given year for each species over time.

Model fitting

To model and predict the damage costs associated with the five non-native mammal species, we used observed damage cost data expressed in millions of US dollars (2017 value) to fit the damage cost model based on the continuous-time logistic growth model (equation 9). We analysed each species over a period defined by the first and last reported years of damage cost data after the database had been filtered. We designated the starting year of the time series as $t = 0$, allowing for a consistent relative timeline for each species (e.g., *C. erythraeus* from 2001–2018, or $t = 0$ to $t = 17$). The damage cost model is parameterised by the maximum accumulated cost ($C_{\max}$), the environmental scaling factor (γ), and the intrinsic growth rate (α). The initial rescaled population density is $z(0) = 1/\gamma$, and is therefore not an independent parameter but determined directly from the estimated value of γ. We estimate these population dynamical parameters by fitting the model directly to the damage cost time series. As such, the only required inputs are the damage cost data, the timing of reported costs, and a prior specification of the cost–density relationship (Figure 1). We are not fitting the density component of the function to species-specific population estimates over time, as is typically done in discrete-time logistic models.

We used the non-linear regression tool fitnlm in MATLAB to fit the cost data and determine the best-fit model parameter set ($C_{\max}$, γ, α) for each species, while considering each of the four cost–density relationships separately. We note that cumulative cost data can introduce statistical autocorrelation, as each point is not independent of previous values. However, our approach is based on fitting a mechanistic model of cumulative impact, where the model structure inherently reflects this accumulation. As such, independence is not a required assumption for our fitted parameters, though model diagnostics and confidence intervals are reported to account for uncertainty. We used the model fitting to predict damage costs for each species from the starting year of observed data up to 2050. We generated predictions with 95% confidence regions to account for uncertainty. For 2050, we reported both the predicted cost and the upper bound of the confidence interval as an estimate of the worst-case scenario. For each species, we identified three key points along the damage cost trajectory: (*i*) the threshold where accumulated costs begin to rise rapidly, (*ii*) the midpoint at which accumulated costs reach half of the potential maximum ($0.5C_{\max}$), and (*iii*) the near-saturation point, at which accumulated costs reach 90% of their maximum value ($0.9C_{\max}$). These estimates provide insights into the temporal dynamics of cost growth, while also highlighting time points for optimum management intervention.

Results

Model demonstration using randomly generated damage cost data

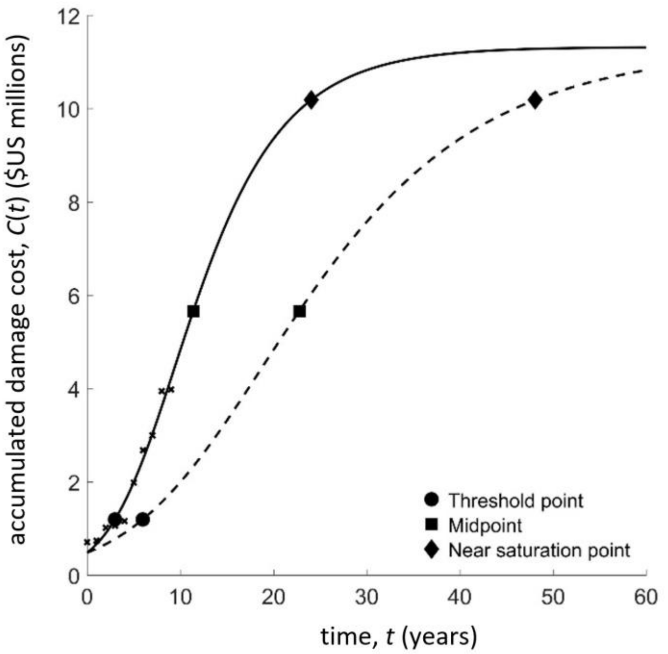

Figure 2 A heuristic example illustrating the damage cost dynamics for two hypothetical non-native species. The damage cost model (equation 9) is fitted to cumulative annual costs that are randomly generated over a 10-year period from $t = 0$ to $t = 9$ (✕). Each annual cost is independently drawn from a uniform distribution ranging between \$0 and \$1 million. For case 1 (solid curve), the estimated best-fitting parameters are: long-term accumulated cost $C_{\max}$ = \$11.32 million, environmental scaling factor $\gamma = 1.62$, and intrinsic growth rate $\alpha = 0.142$, with strong goodness of fit quantified by a root mean-squared error = 0.256, $R^2 = 0.969$. In another scenario, case 2 (dashed line) assumes the same $C_{\max}$ and γ values, but with a halved α (0.071), resulting in a slower cost accumulation. Salient time points are marked along the curves: the threshold (point prior to rapid cost escalation; ●), midpoint (costs reach 50% of $C_{\max}$; ■), and near-saturation (costs reach 90% of $C_{\max}$; ◆). This shows how time milestones can be determined using early-stage cost data, without requiring prior knowledge of their values.

Long-term damage cost dynamics could be effectively predicted from early-stage impacts from invasions using our model (Figure 2). This analysis shows differences in the damage cost-escalation dynamics between the two hypothetical scenarios. In case 1 (solid curve), the damage cost reached \$4.22 million at $t = 9$ years, with a long-term cost projection rising to $C_{\max}$ = \$11.32 million, amounting to an additional \$7.10 million (168.4%) in damages over time. Critical time points occur early: the threshold point (\$1.19 million) is reached at 2.98 years, the midpoint (\$5.66 million) at 11.38 years, and near-saturation (\$10.18 million) at 24.05 years. This delineates a period of rapid cost escalation of 21.07 years (i.e., duration between threshold and near saturation times).

In contrast, case 2 (dashed curve) examines the effect of halving α to 0.071, while keeping $C_{\max}$ and γ the same. As a result, curbing the rate of population growth delays cost escalation, with the threshold now occurring at 5.96 years, the midpoint at 22.76 years, and near saturation at 48.10 years, with the same respective damage cost estimates as in case 1. Consequently, the rapid cost escalation period doubles in duration to 42.14 years.

Although the reliability of non-linear model fitting depends on the quantity and quality of available data, our demonstration uses 10 data points to estimate three parameters. While our model involves combined dynamical and cost-density equations, it remains low-dimensional (i.e., three parameters) and structurally identifiable, enabling stable fitting with relatively few data points. As a guideline, a minimum of three to five data points per parameter is commonly regarded as acceptable when models are well-specified and residuals are well-behaved (Motulsky & Christopoulos, 2004). In this heuristic example, the model fits the generated data closely, and our empirical species-level applications (see later Table 1) are based on similar or larger datasets. These fits are further supported by high goodness-of-fit values and parameter confidence intervals.

Cost-density relationships

For all species we examined, the model fitting resulted in a high-threshold damage cost-density curve (with shape parameters $s_1 = 1$, $s_2 = 0.1$), indicating that the costs associated with non-native mammal species remain low at low population densities but increased rapidly once they surpassed a density threshold (Figure 1; equation 10). This demonstrates that early stages of invasion might not cause large damage, but as populations exceed this threshold, the damage costs rise exponentially as population density increases.

Long-term damage costs and population dynamics

The long-term accumulated cost $C_{\max}$ representing the maximum economic impact varied substantially across species. *Paguma larvata* had the highest $C_{\max}$ at US$83.38 million, and *H. javanicus* had the lowest $C_{\max}$ at US$0.29 million. Other species, such as *P. lotor* (US$62.40 million) and *M. coypus* (US$21.84 million), also had substantial economic impacts (Table 1).

The environmental scaling factor γ (= K/u_0) provides insights into how environmental conditions influence population dynamics, particularly in relation to resource availability. *Procyon lotor* had a high γ of 2.09, indicating its strong capacity to exploit available resources under the given conditions. Similarly, *C. erythraeus* ($\gamma = 1.98$) and *P. larvata* ($\gamma = 1.93$) demonstrated similar potential in their respective environments. However, while high γ values indicate favourable conditions for growth, they do not on their own imply broad ecological adaptability, which depends on other factors such as behavioural plasticity and habitat generalism. In contrast, species such as *H. javanicus* ($\gamma = 1.15$) demonstrate lower environmental scalability, potentially reflecting the isolation of the species to two remote islands.

The maximum intrinsic theoretical growth rate (α) also varied according to the species. *C. erythraeus* had the highest intrinsic growth rate (0.217), followed by *P. lotor* (0.172), *M. coypus* (0.168), *P. larvata* (0.151), and *H. javanicus* (0.085). The higher this rate, the more abrupt the cumulative costs, which highlights a relationship between the growth rate of the non-native species and the slope of the cumulative cost function. Note that, if the damage cost data already reflect periods during which management interventions were active (e.g., population control or containment), then α is understood as a *realised* or *net* growth rate, that is, the observed population growth under the influence of both ecological conditions and ongoing control measures. In such cases, α captures the combined effects of the population dynamics and existing management actions, rather than a purely unmanaged growth potential.

The re-scaled initial density, $z(0) = u_0/K = 1/\gamma$ (equation 4), represents the proportion of the carrying capacity (K) occupied by the initial population. *Procyon lotor* had the lowest value (0.479), with density $< 0.5K$ at the time of first cost reporting, while *H. javanicus* had the highest (0.868), indicating a population closest to its maximum sustainable size (Table 1; Figure 3).

The model had high goodness of fit across all species (i.e., high R^2 and low root mean-squared errors). Species like *C. erythraeus, M. coypus*, *P. larvata* and *P. lotor* ($R^2 > 0.99$) with low root mean-squared error (Table 1) therefore have reliable cost predictions. *Herpestes javanicus* had a slightly lower $R^2 = 0.935$, with lower goodness of fit due to noisy or incomplete data, and high variability in cost reporting methods in damage impacts. Confidence intervals for $C_{\max}$, γ, and α further validate model precision. Narrow intervals for species like *P. larvata* and *C. erythraeus* reflect high certainty in their estimated impacts, whereas broader intervals for *H. javanicus* indicate greater variability, highlighting the need for additional damage cost records to refine these estimates.

Table 1. Number of independent years with recorded damage costs (*n*), period over which these costs were observed, estimated long-term accumulated cost ($C_{\max}$), environmental scaling factor ($\gamma = K/u_0$, where K = carrying capacity and u_0 = initial population density), maximum intrinsic growth rate (α) with respective 95% confidence intervals in square brackets, and initial re-scaled population density ($z(0) = u_0/K = 1/\gamma$) of the five invasive non-native mammal species in Japan analysed. The model goodness of fit is quantified by the root mean square error (RMSE) and the coefficient of determination (R^2).

Species	*n*	**Cost reporting period**	**Long-term accumulated cost** (US$ million, $C_{\max}$)	**Environmental scaling factor** (γ)	**Intrinsic growth rate** (year^{-1}; α)	**Initial re-scaled population density** $z(0) = 1/\gamma$	RMSE	R^2
Callosciurus erythraeus	16	2001–2017	1.17 [1.08, 1.27]	1.98 [1.80, 2.16]	0.217 [0.185, 0.249]	0.505	0.023	0.996
Herpestes javanicus	9	2000–2017	0.29 [0.13, 0.46]	1.15 [1.07, 1.24]	0.085 [0, 0.201]	0.868	0.014	0.935
Myocastor coypus	18	2000–2017	21.84 [20.99, 22.69]	1.52 [1.50, 1.55]	0.168 [0.156, 0.179]	0.656	0.225	0.999
Paguma larvata	18	2000–2017	83.38 [74.48, 88.28]	1.93 [1.88, 1.97]	0.151 [0.142, 0.161]	0.519	0.509	0.999
Procyon lotor	18	2000–2017	62.40 [57.50, 67.30]	2.09 [1.98, 2.19]	0.172 [0.156, 0.188]	0.479	0.641	0.999

The population density trajectories in Figure 3 illustrate how species-specific growth dynamics can inform ecological strategies and potential management interventions. Species with higher intrinsic growth rates (α), such as *C. erythraeus* ($\alpha = 0.217$), demonstrate rapid potential population growth, quickly saturating their environments.

Higher γ (e.g., *P. lotor*: $\gamma = 2.09$) imply populations starting from a lower baseline relative to K. In contrast, species with lower γ (e.g., *H. javanicus*: $\gamma = 1.15$) begin with densities closer to their carrying capacities, potentially reflecting stable population dynamics constrained by K.

For *C. erythraeus*, *P. larvata*, and *P. lotor*, the first cost was reported for each species at around the same time as the point of inflection, namely where the rate of population density growth began to decline (Figure 3). In contrast, for *H. javanicus* and *M. coypus*, the first recorded cost occurred while their population was already in decline.

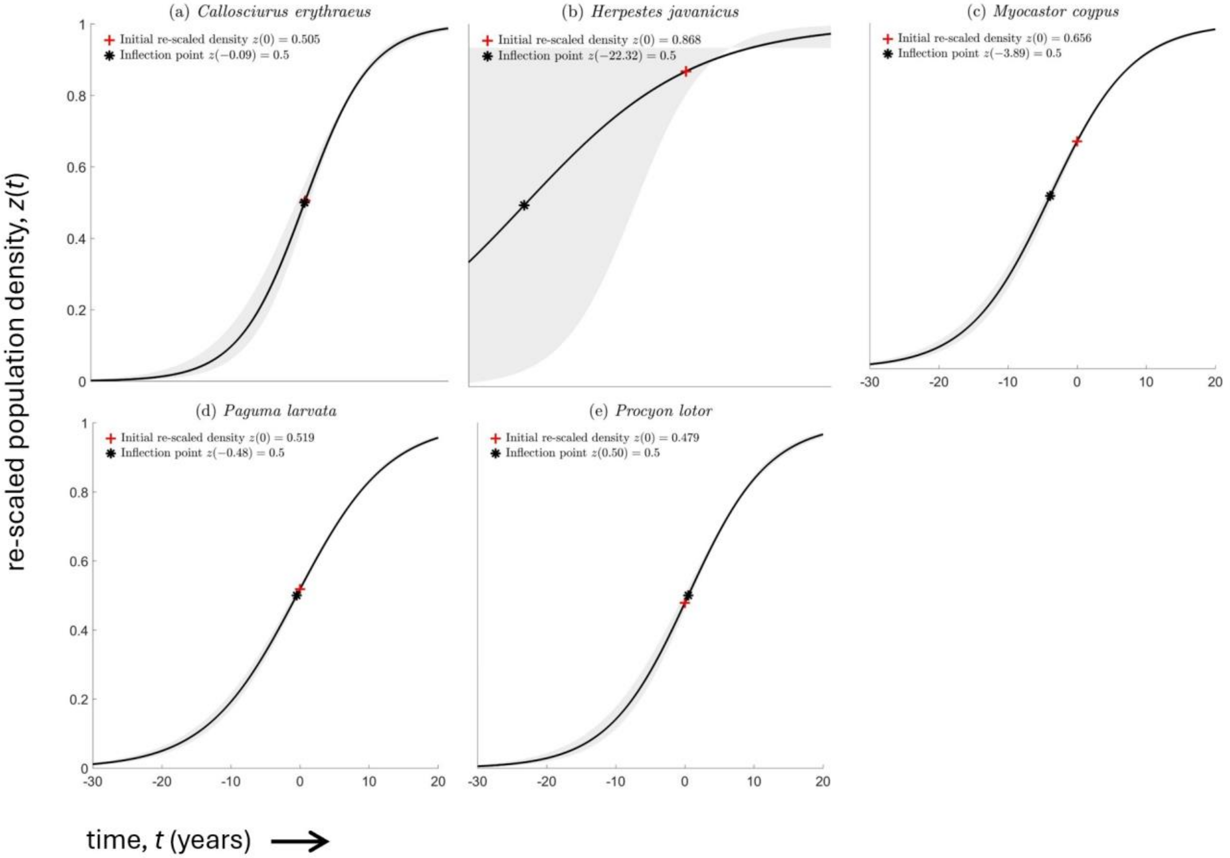

Figure 3 Re-scaled population density plots for the five non-native mammal species from Japan, modelled using the logistic growth model (equation 5). The re-scaled density for each species at the time of first reported cost ($t = 0$) is $z(0) = 1/\gamma = K/u_0$; where K = carrying capacity and u_0 = initial population density; equation 4 (+). Carrying capacity K is reached as the population $z(t)$ approaches 1. The inflection point (✱) indicates a shift from an increasing to a decreasing rate of population density that occurs at half the carrying capacity, or equivalently at $z = 1/2$ at time $t = (1/\alpha)\log_e(\gamma - 1)$. The 95% confidence region is shown (shaded area), plotted using equation 5, with the upper and lower confidence limits of α and γ provided in Table 1. For visualisation purposes, the time axis begins 30 years before the first cost is reported for each species.

Thresholds

Our analysis revealed variability in the timing of escalation of economic impact across the five non-native mammal species (Table 2), reflecting species-specific differences in ecological dynamics, ecological traits, and the associated economic costs, despite similarities in the form of the underlying cost curve. Assuming a business-as-usual management, a few common trends emerged regarding the timing of threshold densities, the speed of cost escalation, and the opportunities for further management interventions.

Callosciurus erythraeus had the shortest duration of rapid cost escalation, with costs rising sharply over just 13.75 years (2005–2019) following a threshold time of 70.05 years. This suggests that once economic impacts began to accelerate, they did so quickly, highlighting the urgency of early intervention for such species. In contrast, *H. javanicus* had a similar threshold time of 78.45 years, but its rapid cost escalation lasted longer at 35.24 years (1988–2024), making it the slowest-escalating species in our dataset.

Myocastor coypus, *P. larvata*, and *P. lotor* had intermediate patterns of cost escalation. *M. coypus* had a threshold time of 62.52 years and a 17.82 year escalation phase (2002–2019), indicating a moderate pace of impact intensification. Meanwhile, *P. larvata* exhibited a near identical threshold time (62.45 years), but a slightly longer escalation period of 19.75 years (2005–2025). On the other hand, *P. lotor* had the shortest threshold time of 43.72 years, with an escalation period of 17.37 years (2006–2023), similar in duration to *M. coypus*.

Table 2. Year of first species record as listed in the *Standardising and Integrating Alien Species* SinAS database v2.4.1; except for *P. larvata*, where the year is reported in Nawa (1965). Main times along the damage cost curve of the five invasive non-native mammals in Japan, computed from equations 12 and 14, including the threshold time (t_{thresh}), beyond which damage costs begin to escalate rapidly, and the time to half-saturation (t_{mid}) and near-saturation (t_{sat}), when accumulated costs reach 50% and 90% of the potential maximum cost ($C_{\max}$), respectively. These times are measured from the year of the first species record. The rapid cost escalation period is the duration between these times ($t_{\mathrm{sat}} - t_{\mathrm{crit}}$) in years, with the corresponding times in years for each species.

Species	**Year of first record**	**Threshold time** (years; t_{thresh})	**Time to half saturation** (years; t_{mid})	**Time to near saturation** (years; t_{sat})	**Duration of rapid cost escalation** (years; $t_{\mathrm{sat}} - t_{\mathrm{thresh}}$)	**Period of rapid cost escalation**
Callosciurus erythraeus	1935	70.05	75.53	83.80	13.75	2005–2019
Herpestes javanicus	1910	78.45	92.49	113.69	35.24	1988–2024
Myocastor coypus	1939	62.52	69.62	80.34	17.82	2002–2019
Paguma larvata	1943	62.45	70.32	82.20	19.75	2005–2025

Procyon lotor	1962	43.72	50.65	61.09	17.37	2006–2023

Future predictions of damage costs

Among the species we examined, *P. larvata* had the most pronounced absolute increase in economic costs, reflecting its continued period of rapid cost escalation (Table 2). Assuming management follows the prevailing trend, the predicted cost for this species is projected to rise from an estimated US$56.79 million to US$83.18 million (a 46.47% increase). The upper confidence limit suggests an even greater potential rise of 54.94%, reaching US$87.99 million by 2050. Similarly, *P. lotor* is expected to experience a substantial cost increase, with economic impacts growing 36.68%, from US$45.61 million to US$62.34 million. The upper confidence limit suggests a possible 47.32% increase to reach US$67.19 million. In contrast, *C. erythraeus* and *H. javanicus* are projected to have more moderate cost increases. The former is estimated to have a 17.13% rise from US$1.00 million to US$1.17 million, with an upper confidence limit of 26.62% to reach US$1.27 million. *H. javanicus*, while having a relatively lower baseline increase of 19.40% (from US$0.24 million to US$0.29 million), has a substantially larger upper bound projection of 78.37%, indicating a worst-case estimate of US$0.43 million, suggesting potential underestimation of its future impact and greater uncertainty. *Myocastor coypus* followed an intermediate trajectory, with costs expected to rise 17.03% (from US$18.65 million to US$21.83 million). The upper confidence limit indicated an increase of 21.57%, to reach US$22.67 million. Overall, these projections highlight the varying rates of economic escalation among species, with *P. larvata* and *P. lotor* having the most substantial increases, while *C. erythraeus* and *H. javanicus* have more moderate but still important growth. The substantial upper bound increases, particularly for *H. javanicus*, reinforce the importance of considering uncertainty in future cost projections.

Table 3 Predicted economic costs for five non-native mammal species in Japan based on the fitted damage cost model. Includes the estimated costs at the time of the last recorded report, the predicted costs for 2050, and the upper limit of the 95% confidence interval as a worst-case scenario. Percentage increases in costs from the last report to 2050 are presented, including those based on the upper bound estimates.

Species	**Estimated cost at the time of the last cost report** ($US million)	**Predicted cost for 2050** ($US million)	**Predicted cost using the upper confidence limit** ($US million)	**Percentage increase** (%)	**Percentage increase** (%) (upper CI estimate)
Callosciurus erythraeus	1.00	1.17	1.27	17.13	26.62
Herpestes javanicus	0.24	0.29	0.43	19.40	78.37
Myocastor coypus	18.65	21.83	22.67	17.03	21.57
Paguma larvata	56.79	83.18	87.99	46.47	54.94
Procyon lotor	45.61	62.34	67.19	36.68	47.32

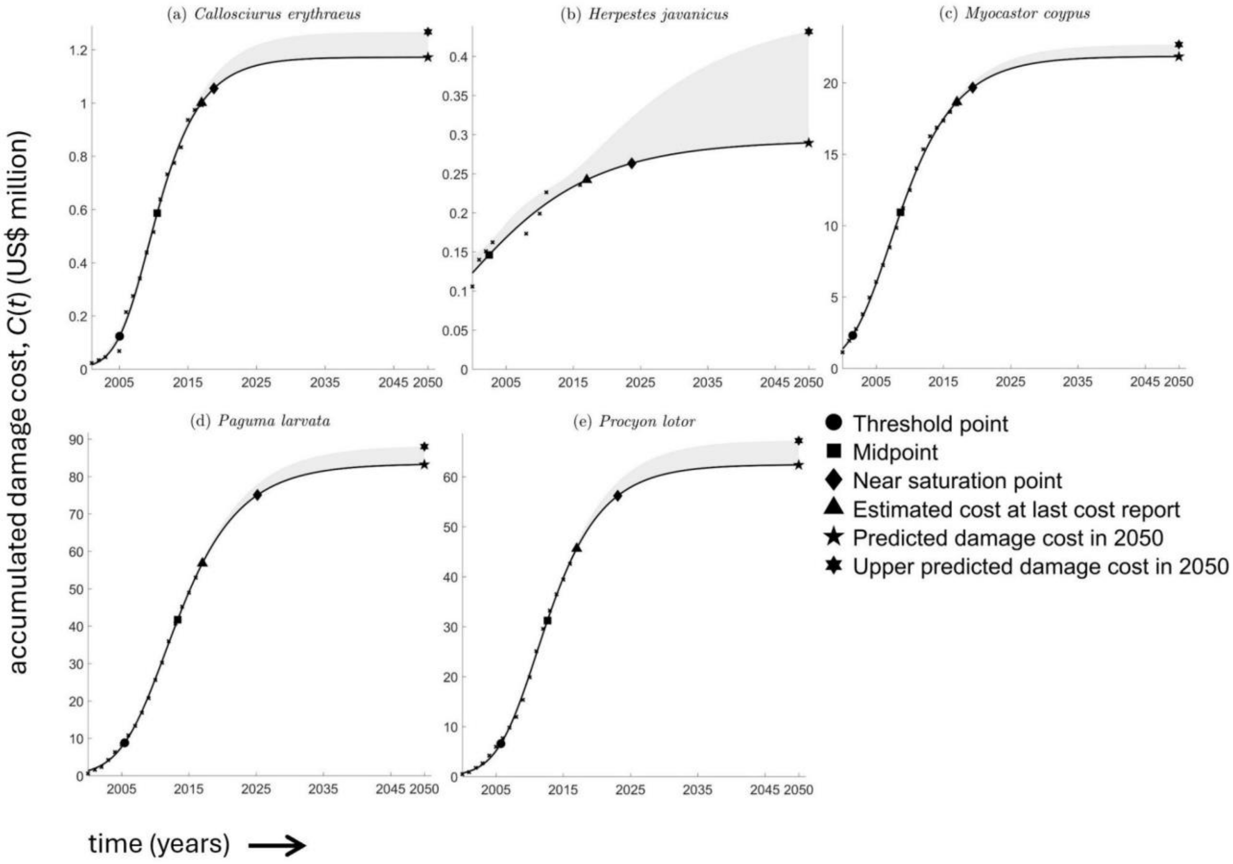

Figure 4 Predicted damage costs over time for five non-native mammal species in Japan (black curves), obtained from fitting the damage cost model (equation 9) against observed cost data (✕). Markers along the cost curves indicate the threshold time (t_{thresh}; ●) beyond which damage costs escalate rapidly, the

midpoint (t_{mid}; ■) when accumulated costs reach half the potential maximum cost ($C_{\max}$), and the time to near saturation (t_{sat}; ◆) when costs reach 90% of $C_{\max}$. The threshold time is not shown for *H. javanicus*, where it occurred before the first recorded cost (i.e., with $t_{\text{thresh}} < 0$), because the damage cost curve is displayed from the point when the first cost was recorded. Other markers include the estimated cost as per the damage cost model when the last recorded cost was reported (▲), and the predicted damage cost in 2050 (★). We only consider the upper 95% confidence region (shaded area) whose upper bound demarcates the temporal cost estimates, used to estimate the 2050 potential cost in a worst case scenario (✶). For illustrative purposes, the vertical cost axis is scaled independently for each species according to its cost magnitude.

Discussion

Our mathematical models forecasting future invasion costs leveraged economic impact data for five candidate invasive mammals in Japan and incorporated both population and cumulative cost dynamics over time. Cost trajectories for all of these non-native species were well-represented by the logistic growth model and conformed to a high-threshold cost-density dynamic, with variable cost magnitudes, intrinsic growth rates, and environmental scalings in relation to resource availability. All the species we examined have already surpassed the threshold year beyond which rapid growth in economic costs ensues, with most also recently surpassing the year of near saturation where > 90% of costs have been incurred. Nevertheless, while these invasions can all be considered at a late stage based on their cost dynamics, our model still forecasts substantial increases of up to 78% by 2050 and absolute sums in the tens of millions of dollars. Moreover, we demonstrate that it can be used where only early-stage cost data are available (i.e., before half the long-term cost is attained) to predict future dynamics. Our model thus presents a framework to characterise non-native mammal populations and their cost dynamics to make future predictions, while identifying threshold times for effective management actions before costs escalate rapidly. In particular, we found that periods of rapid cost escalation are preceded by extensive lag times when population densities and impacts of non-native mammals are low — even if time lags to impact last centuries after introduction, cost escalation to maxima can occur within a few decades. The patterns could inform timely management actions and future impact quantifications for these species in their so-far uninvaded areas, as well as for other closely related non-native species with similar economic impacts.

Model demonstration using randomly generated damage cost data

While the example cases are based on long-term observed cost dynamics (i.e., multi-decadal), we heuristically demonstrated that future cost trajectories can be predicted with only early-stage (i.e., sub-decadal) cost data. This underpins the applicability of our approach for managers, where future forecasts can be made even using initial impact reportings with different assumptions for underlying parameters. This further highlights that early management actions that aim to control population growth can influence ecological and economic outcomes, particularly when aiming to reduce the intermediate-term damage costs of non-native species. Even with randomness in the input cost data, the model reliably captures the future damage cost dynamics, and moreover, key time milestones such as threshold, midpoint or near saturation points can be identified from early-stage cost data alone. Thus this offers a robust framework for anticipating critical ecological thresholds and prioritising proactive strategies. While the long-term cost remains unchanged by design among the two scenarios considered, early management intervention effectively gives practitioners more time to mitigate intermediary damage impacts.

Cost-density relationships

All five mammal species we examined had a high-threshold damage cost-density relationship, where damage costs stayed low at low population densities but increased rapidly once exceeding a threshold density. Ecologically, this pattern reflects a common scenario in the invasion dynamics of many species (e.g. Soto et al. 2023b). At low densities, non-native species might not immediately disrupt ecosystems due to their limited interaction with native species or resources (Sofaer et al. 2018; Spear et al. 2021). Their ecological impacts can be subtle, with minimal competition, predation, or habitat alteration — this could reflect lag times to impact or 'sleeper populations', whereby effects rise rapidly due to environmental changes or the arrival of new genotypes (Spear et al. 2021). However, as a population grows and its density increases, the effects of non-native species can become more pronounced, resulting in greater competition for resources, predation pressure on native species, and changes in habitat structure (Bradley et al. 2019). Ecologically, this indicates that non-native mammal populations must cross a threshold size before their impacts escalate and become severe, which could be, in turn, linked to species-specific life history traits. Economically, this threshold corresponds to an accumulated damage cost of approximately 10% of the species' long-term potential cost ($C_{\max}$), providing a quantifiable benchmark for identifying the onset of cost escalation. The reasons for high-threshold damage may be explained by considering environmental heterogeneity within the landscape. Landscapes consist of natural environments (e.g. forests and rivers) and areas of human activity (e.g. agricultural areas, human settlements, etc.) where economic damage can occur. If the population growth is dependent on the natural environment, the population will inconspicuously increase in the natural environment without causing economic damage until a certain density is reached (delayed impact). After that, when a certain density point is exceeded, some individuals will spread into human activity areas, causing economic damage. Furthermore, if a population that invades an area of human activity becomes familiar with humans, the per-capita impact will increase, resulting in a non-linear increase in impact with density. In fact, these five species mainly depend on resources in the natural environment for food and shelter, although they also feed on agricultural crops (Ohdachi et al. 2018). In Japan, the proportion of natural environment areas is high (e.g., 70% of the land area is forested), and therefore, in order to spread their populations over a wide area, they need to increase in natural environments. In human activity areas, there are known cases of Pallas' squirrels and raccoons being fed by humans, raccoons and civets settling in human houses, indicating becoming less fearful of humans. It is also important to view these cost dynamics in the context of management interventions, as some species such as the small Indian mongoose have been successfully eradicated from parts of Japan. For example, following a long-term intensive trapping programme initiated in 2000, the mongoose was declared eradicated from Amami-Oshima Island in 2024, after population estimates declined from > 6,000 to near-zero (Fukasawa et al., 2013a; Barun et al., 2011). This eradication not only resulted in the recovery of native species (Fukasawa et al. 2013b; Watari et al. 2013), but is also expected to lead to a complete reduction in future damage costs incurred in these fully managed areas (Watari et al., 2021; Yamada & Sugimura, 2004).

Overall, for the five species we examined, there was a strong density threshold above which economic costs increased sharply. This threshold can be explained by the constraints of food and space resources and the ability of non-native species to exploit them (Faria et al. 2025). This confirms the results of Bodey et al. (2025) who argued that the magnitude of the costs for non-native mammals is related to reproductive output alongside predation and herbivory, and therefore to the density of the invasive population. These differential cost magnitudes and population density trajectories illustrate the importance of understanding species-specific growth dynamics. For species with rapid intrinsic growth rates such as *C. erythraeus* and *P. lotor*, population control measures need to be implemented early to prevent their populations from reaching densities that would result in substantial ecological and economic damage. For slower-growing species such as *M. coypus*, which might reflect a constraint on area-wide distribution expansion based on the discontinuity of the potential habitat due to its water-dependence, the delayed onset of damage provides a longer window for intervention (including containment), but this should not be misinterpreted as a reason to delay action indefinitely. The longer-term impact of these species, if left unmanaged, can still be considerable, especially in sensitive or highly impacted ecosystems.

The high-threshold damage cost-density curve provides valuable insights into the need for timely management to prevent populations from reaching sizes where the economic and ecological impacts become disproportionately large. While the high-threshold curve employed here suggests a generalisable invasion cost dynamic, previous cost models at the coarser genus level found a mixture of types (low-threshold, sigmoidal, linear), albeit with the high-threshold curve being the most common cost-density relationship across genera (Ahmed et al. 2022a). However, unlike previous assessments, we controlled for country-level differences in cost reporting and socio-economic activity by harnessing a time series of impacts from a single country and study, which, while specific to Japan, provides a controlled context for understanding broader trends. While it is speculative to claim that this pattern characterises most mammalian invasions based on only five species, the consistency of the high-threshold curve as an adequate descriptor of the cost-density relationship — despite the species' differing in their ecological traits, range sizes, and impacts — suggests that it is not atypical.

Variability of interspecific long-term costs

Our study highlights the considerable variability in the long-term economic impacts of non-native mammalian species. The large range in maximum cost underscores the need for species-specific assessments when considering the ecological and economic consequences of non-native species. These results corroborate the skewed distribution of costs among non-native species, with global impacts dominated by the negative impacts caused by a few high-profile taxa (Cuthbert et al. 2022a; Soto et al. 2022; Jiang et al. 2022). They further emphasise the complexity of managing biological invasions and provide insights into how ecological characteristics, such as growth rates and environmental adaptability, influence the economic burdens that non-native species impose over time (Bodey et al. 2025).

Ecologically, the high magnitude costs caused by *P. larvata* was likely linked to the species' broad ecological tolerance, its ability to thrive in various habitats, and its role in transmitting zoonoses, and damaging of agricultural systems (Shimoyama and Tsuji 2024). Likewise, *P. lotor* is highly adaptable and capable of living in urban environments alongside forests and farms, where it disrupts ecosystems by preying on native species, spreading zoonotic diseases, and competing for resources (Salgado 2018). Their increasing presence in urban areas has damaged infrastructure, increased waste management costs, and posed potential public health risks (García et al. 2012; Salgado 2018). Despite the moderate cost projections for *C. erythraeus*, the non-monetisable ecological impacts of this species, including competition with native squirrel populations and damage to trees, still threaten long-term forest health, with cascading effects on ecosystem services such as carbon sequestration and biodiversity conservation (Bertolino and Lurz 2013). *Herpestes javanicus* has caused declines in native vertebrate populations, leading to changes in food-web dynamics and reduced ecosystem resilience (Watari et al. 2008). Its low estimated costs could reflect the species' limited distribution in certain Japanese islands and current management success, but the upper confidence limit suggested that the species could pose a much greater future economic burden if its range expands. In *M. coypus*, burrowing activity can have disproportionately large ecological and economic effects as populations increase, with structural damage to levees, riverbanks, and wetlands scaling non-linearly (Corriale et al. 2006; Dondina et al. 2024). At low densities, burrowing can cause localised erosion, but as population size grows, widespread destabilisation of critical infrastructure could occur, leading to costly repairs and habitat degradation. Similar dynamics might apply to other species with habitat-altering behaviours, where population expansion intensifies impacts beyond simple numerical increases. For other species we assessed, damages could be affected by density feedback, such as where the viability of agricultural crops or integrity of infrastructure (Suzuki and Ikeda 2020; Tamura and Yasuda 2023) can be exacerbated as population sizes pass a threshold that compromises their function. Similarly, for invasive species implicated in zoonotic infections, risks can increase non-linearly with initial invader densities owing to the increasing risk of pathogen transmission as densities (and therefore, individual contact rates) increase.

Threshold densities

The identification of threshold densities in the damage cost curve has implications for understanding the dynamics of the economic impacts of non-native species based on their population dynamics. The variation in the timing of threshold densities across species underscores the need for tailored management strategies. Although each species exerts pressure on ecosystems in unique ways, the fundamental conclusion is clear: early intervention is necessary to avoid reaching threshold points, after which costs rise exponentially. The major implications of our model thresholds are that: (*i*) time lags to cost reporting last decades — even centuries — meaning that initially benign invasions could precipitate substantial economic impacts in the future; (*ii*) there are threshold densities before the rapid escalation of damage costs, where management actions such as rapid eradication should be prioritised to mitigate exponential growth; (*iii*) the rapid cost-growth phase typically lasts 10–20 years within species at the spatial scales we examined; and (*iv*) future cost increases can remain substantial even after the point of saturation is reached, notwithstanding the potential for new invasions or impacted sectors to emerge. These thresholds have clear management implications, corroborating the ‘cost of inaction’ that accrues with management delay over time (Ahmed et al. 2022b). The variation in the duration of rapid cost escalation reflects the broader ecological and economic implications of species invasions — some species require urgent, short-term action, while others present more gradual opportunities for intervention. However, the common theme is the need for early detection and management, particularly for those species with shorter durations of rapid cost escalation where the potential for escalation of costs can be more acute. It is also important to consider the feasibility of management interventions at all impact stages, because actions might not be effective in the absence of appropriate techniques or resources (Robertson et al. 2020).

The concept of ‘near saturation’ where damage costs reach 90% of the maximum potential provides another important perspective for management. For species like *M. coypus*, reaching near saturation signals that the species’ impact on the ecosystem is approaching its peak. This stage represents an ideal point for localised management interventions. While it might not always be possible to completely reverse the trajectory, management efforts could aim to reduce the population density below the threshold (z_{thresh}). Ecologists should consider acting at this juncture, even if opportunities were missed at earlier stages, because action can prevent further escalation of costs and reduce the long-term damage. However, species that reach near saturation more slowly require careful and continuous monitoring to ensure that their impacts do not go unchecked, despite impacts being less acute. Given that some of our results are future projections, it would be unwise to neglect further management, particularly considering the potential for new invasions to reset the dynamic and trigger additional costs. The timeframes associated with threshold and near-saturation points highlight the importance of establishing early warning systems for non-native species. These results should further be viewed in the context of the Japanese islands where they were estimated, because invasions into further islands could cause for the high-threshold cost dynamic to repeat several times, with these 'new' subnational invasions not necessarily captured with country-level first records. The same could be said for economic development, as surges in new sectors could provide novel impact opportunities in invasive populations.

Role of management in shaping future damage cost trajectories

Our modelling framework focuses on predicting damage costs over time, assuming implicitly that current management efforts will be the same in the future. This assumption reflects a practical limitation: reliable, disaggregated data on management expenditures are largely absent from the *InvaCost* database. Using the same filters applied to damage costs, only *P. lotor* had reported management costs totalling US$0.07 million between 2014 and 2017, amounting to a negligible 0.60% of the total observed damage cost over the same period. No comparable data were available for the other focal species, although it is likely that variable management is in place. This data gap necessitates a damage-only approach, meaning that our forecasts do not incorporate possible cost reductions associated with current or future control efforts.

Nevertheless, it is well-established that management, particularly when implemented early, can substantially reduce long-term economic impacts. Previous work has shown that delays in management can result in much higher total costs, even when interventions are eventually introduced. For instance, Ahmed et al. (2022b) quantified the cost of inaction using a generalised damage–management model and empirical cost data for *Aedes* mosquitoes, revealing that early action could have reduced long-term losses by billions of dollars. These findings align with a broader literature showing that proactive management is more cost-effective than delayed or reactive responses (Leung et al., 2002; Lodge et al., 2016; Epanchin-Niell 2017; Cuthbert et al., 2022b; Bradshaw et al. 2024).

Because our model does not include management explicitly, the projected damage cost trajectories should be interpreted as baseline estimates under business-as-usual management intervention. Improved management could alter these trajectories, reducing both the rate and magnitude of damage cost accumulation. Conversely, declining or absent management could result in even steeper escalation. The lack of consistent management data thus remains a limitation for forecasting models, not only in this study but across much of the invasion economics literature (Diagne et al., 2021).

Future research directions

While our study provides a useful approach to modelling past dynamics and future trajectories of the economic impacts of non-native species through generalised cost curves, there remain several avenues for improvement. (*i*) One limitation is data completeness and precision, especially for species such as *H. javanicus* where the scarcity of reported damage costs hampers robust inference. This scarcity does not necessarily mean that costs were not incurred, but that they were not systematically reported. Indeed, current reporting of damage costs for many invasions are insufficiently detailed (or entirely absent) for rigorous cost assessments over time. National-level variation in reporting is also important, with a general need for standardisation and expansion of cost reporting to improve model reliability (Diagne et al. 2021; Hulme et al. 2024). (*ii*) Our model currently assumes logistic growth with a fixed carrying capacity, yet ecological systems often display more complex population dynamics, including time-varying growth rates, fluctuating carrying capacities, and non-linear behaviours such as boom–bust cycles or chaotic fluctuations (Strayer et al. 2017; Haubrock et al. 2022). Future extensions could incorporate these complexities using stochastic or non-autonomous growth models. (*iii*) Another important omission is the role of management. Although we focus solely on damage costs, management efforts can substantially alter population trajectories and delay or reduce associated costs (Ahmed et al. 2022b). Improved and standardised reporting of management costs would enhance predictive capacity by allowing models to account for feedback between control efforts and the ensuing damage cost dynamics. This is especially relevant when interpreting the steepness or timing of cost accumulation, which could partly reflect underlying control efforts. Including management expenditure data, where available, could help disentangle the extent to which cost curves reflect ecological spread *versus* suppression effects (Lodge et al. 2006). In the absence of such data, models that incorporate only damage costs, such as the one we present here, provide a useful, albeit conservative, estimate of future impacts under scenarios lacking increased management intervention. (*iv*) At a broader scale, the damage cost model could be adapted for national-level assessments, allowing for country-specific forecasts that guide local policy and resource allocation, especially in regions with high invasion exposure or economic vulnerability (Zenni et al. 2021). Moreover, there is a strong case for modelling feedback loops between biological invasions and societal responses. For instance, the time it takes for a non-native species to reach economic thresholds might allow managers to adapt their interventions, thereby altering the trajectory of costs (Ahmed et al. 2022b). (*v*) Developing dynamic threshold models that evolve with intervention intensity and timing would therefore improve both predictive realism and policy relevance (Seebens et al. 2017; Essl et al. 2020). Because the magnitude of economic costs can reflect a 'lock and key' mechanism between impacted sectors and the invading population's traits (Cuthbert et al. 2025), changes in sectors of economic activity or invader trait changes over time could be further integrated into a dynamic modelling framework to account for modifications in these economic and invasional characteristics. Models could also incorporate trajectories of economic development, because the emergence or intensification of economies might amplify impacts within a given range, even where impacts might otherwise appear to have saturated. Similarly, trait changes in invasive populations, whether through evolution or through environmentally mediated phenotypic plasticity, could reinitiate or exacerbate impacts and require adaptive parameterisation over time (Cuthbert et al. 2025). (*vi*) From a theoretical standpoint, there is also scope to integrate spatio-temporal dynamics using reaction-diffusion models or network-based approaches. These tools can capture the spread of invasive populations across heterogeneous landscapes and identify spatial hotspots of risk (Hastings 1996; Cantrell and Cosner 2003; Volpert and Petrovskii 2025). Addressing these directions will enhance our capacity to anticipate, interpret, and manage the economic risks posed by non-native species in an increasingly interconnected world.

Conclusion

Integrating ecological population dynamics with economic cost modelling can elucidate the latent, non-linear relationships underpinning biological invasions, informing both future impacts and management responses. By centering the focus on future projections, our modelling framework highlights the economic costs expected to escalate in the coming decades, even for species that appear to have stabilised. Anchoring predictions in logistic growth and density feedback-impact thresholds, the framework reveals an ecological reality: non-native species often exhibit prolonged periods of minimal detectable impact before costs escalate abruptly.

These delayed trajectories, driven by time lags in population establishment and resource exploitation, indicate that while the past dynamics provide important insights, the future escalation of costs remains substantial, challenging conventional risk assessments that prioritise immediate threats over long-term projections.

For ecologists, this result underscores the importance of monitoring not just population presence or spread, but also the future thresholds at which invasions transition from ecologically benign to destabilising. The model's reliance on species-specific growth rates and environmental adaptability highlights the interplay between life-history traits and invasion outcomes. For example, fast-growing species require urgent intervention to pre-empt rapid cost surges, while 'slower' invaders might still need long-term vigilance to avoid future saturation of ecological and economic systems, emphasising that even species with slow growth trajectories could drive future costs as they reach their threshold point. These dynamics reinforce the value of mechanistic, trait-based approaches in invasion ecology, moving beyond static impact assessments to capture the temporal cascades of harm expected in the future.

For policymakers and practitioners, our work emphasises that early action, guided by projected ecological thresholds, is not just precautionary, but also economically imperative. Even for population-specific cost trajectories that have reached apparent saturation decades or centuries post-invasion, we show that the potential for future escalation remains substantial, potentially driven by changes in economic activity, new sub-national invasions, or changing population-level traits. By framing invasions as delayed yet exponential threats, the model compels a shift from reactive to anticipatory governance, particularly in regions with high invasion debt. Ultimately, this synthesis of ecological and economic principles provides a universal lens to confront the escalating biodiversity crisis, urging interdisciplinary collaboration to mitigate the profound, yet often irreversible, costs of inaction and the future impacts of biological invasions.

Author contributions

Danish A. Ahmed and Corey J.A. Bradshaw conceived the ideas and designed the methodology; Emma J. Hudgins filtered, extracted and compiled the data from the *InvaCost* database; Danish A. Ahmed and Noor Tahat analysed the data; Danish A. Ahmed, Corey J.A. Bradshaw, Emma J. Hudgins and Ross N. Cuthbert led the writing of the manuscript. All authors contributed to the

ecological interpretation of the findings, and were involved in writing, reviewing, and editing the manuscript.

Statement on inclusion

Our study brings together a global team of researchers, including a scientist based in Japan (Yuya Watari), given the research focus is on the damage costs of non-native species in Japan. Collaboration began at an early stage to ensure that all authors contributed to the study design, analysis, and/or ecological interpretation. Where relevant, we cited literature authored by regional experts and included references to studies published in both English and Japanese, reflecting our effort to acknowledge and integrate local and regional perspectives. In addition, a Japanese-language abstract has been provided in Appendix S1 to enhance accessibility for regional audiences.

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Conflict of Interest

The authors declare no conflicts of interest. There are no financial, personal, or professional affiliations that could be perceived as influencing the work reported in this study.

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