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Managing the impact of invasive species: the value of knowing the density–impact curve

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Abstract. Economic impacts of invasive species worldwide are substantial. Management strategies have been incorporated in population models to assess the effectiveness of management for reducing density, with the implicit assumption that economic impact of the invasive species will also decline. The optimal management effort, however, is that which minimizes the sum of both the management and impact costs. The relationship between population density and economic impact (what we call the "density–impact curve") is rarely examined in a management context and could take several nonlinear forms. Here we determine the effects of population dynamics and density–impact curves of different shapes on optimal management effort and discover cases where management is either highly effective or a waste of resources. When an inaccurate density–impact curve is used, the increase in total costs due to over- or underinvestment in management can be large. We calculate the increase in total costs incurred if the density–impact curve is incorrect and find that the greater the maximum impact caused by an invasive species, the more important it is not only to reduce its density, but also to know the shape of the density–impact relationship accurately. Lack of information regarding the relationship between density and economic impact causes the most acute problems for invaders that cause high impact at low density, where management typically will be too little, too late. For species that are only problematic at high density, ignorance of the density–impact curve can lead to overinvestment in management with little reduction in impact.

Key words: *cost of impact; density dependence; invasive species; modeling economic impact of pests and their control; stochastic dynamic programming; value of information; weed management.*

Introduction

Invasive species have substantial negative environmental and economic impacts worldwide (U.S. Congress 1993, Manchester and Bullock 2000, Sinden et al. 2004). While studies of population dynamics are necessary to determine ecologically appropriate strategies for reducing invader population density (e.g., Buckley et al. 2001, 2007, Taylor and Hastings 2004, Shea et al. 2006), there are only a few studies in which optimal management strategies are derived with explicit consideration of the relationship between ecological or economic impact of invaders and their population density (Finnoff et al. 2005, Whittle et al. 2007). This makes it unclear how one management strategy compares with another in relation to the total costs of both management and impact (Regan et al. 2006).

Commonly, insufficient information exists to describe the relationship between density of an invasive population and economic impacts (Parker et al. 1999). Where this has been explored, both linear and nonlinear relationships between density and cost of impact have been found (Medd et al. 1985, Bobbink and Willems 1987, Standish et al. 2001, Alvarez and Cushman 2002, Hester et al. 2006). It is likely that the optimal management effort for an invasive species that minimizes costs due to management and impact will depend on the shape of the relationship between density and economic impact, what we call here the "density–impact curve." Management strategies that incorporate this curve thereby consider the cost–benefit ratio for reductions in density, however, this has not been well examined. For example Whittle et al. (2007) assume that the impact of an invader is proportional to the invaded area, i.e., that impact of an invader has constant per capita costs. Finnoff et al. (2005) apply a particular nonlinear density–impact curve for management of zebra mussels (*Dreissena polymorpha*) but do not examine the dependence of management strategies on the shape of the density–impact curve.

If the per capita economic impact of an invader is a function of its population density, the reduction in impact of removing one individual will depend on the population density at that time. In Fig. 1 we propose three basic nonlinear shapes that the density–impact

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curve might take (curves I, II, and IV) and contrast them with curve III, which shows economic impact as directly proportional to population density (linear). In curve I (low-threshold curve), the impact remains high until the population density becomes very small. In contrast, in curve IV (high-threshold curve) the impact remains low and then increases dramatically only when the population density becomes very large. Curve II is an S-shaped curve with the impact rapidly increasing at an intermediate population density.

As an example of the low-threshold curve (I), trade restrictions can be applied to grain crops if a certain threshold level of weed-seed contaminant is detected (Davis et al. 1999). Above this threshold the density of the contaminant is irrelevant for trade purposes and a significant reduction in impact of the weed can only be achieved if the density of seed contaminants can be reduced below the threshold for trade restriction. In this case a management effort initiated at high population density would have a negligible effect on the economic impact, but the same effort close to the threshold could substantially reduce the economic impact. Seed contamination by wild radish *Raphanus raphanistrum* (Panetta et al. 1988) is an example of a species that has a density–impact curve with a low threshold (see Fig. 1) as even a low density of the weed results in maximal economic costs. In contrast, the weed species Paterson's curse (*Echium plantagineum*) is an example of an invasive species with a high-threshold density–impact curve (curve IV, see Fig. 1) (Seaman et al. 1989). Paterson's curse is toxic to livestock, which avoid the weed at low density, hence the impact is small until the population density becomes large. Diverse linear and nonlinear high- and low-threshold density–impact relationships have been reported for several species (e.g., Nava-Camberos et al. 2001, Parsons et al. 2005, Brown et al. 2007). Moreover, the form of the density–impact curve could even vary within a species between different habitats, among different stakeholders, or with different measures of impact (Robinson et al. 2005).

Economic costs of impact could include the loss of crop or livestock production due to competition or toxicity (Piggin and Sheppard 1995), loss of markets due to breaches in trade restrictions caused by product contamination (Panetta et al. 1988), loss of valued ecosystem services due to altered ecosystem function and species loss (D'Antonio and Vitousek 1992, Mack and D'Antonio 1998), depreciation in land value due to obligatory control measures or land-use restriction, and loss of tourism revenue due to iconic native species loss, restricted access, or loss of aesthetic values (Serbesoff-King 2003). These are distinct from the costs of management to reduce population density (and hence impact) of the invader.

Parker et al. (1999) suggest that insights into prioritization and management of invasives might be gained through looking at the feasibility of management together with impact (see also Thomas and Reid 2007).

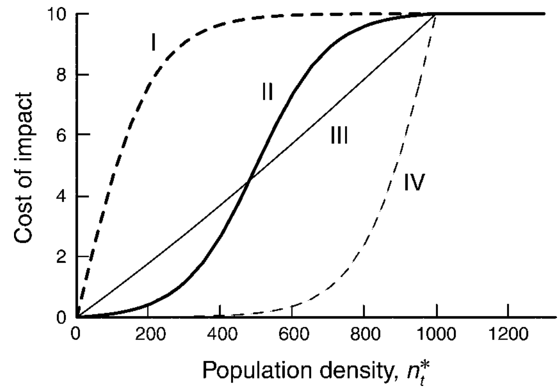

FIG. 1. Four potential relationships between the cost of impact and population density with population density on the x-axis and cost of impact on the y-axis: I, low-threshold curve; II, S-shaped curve; III, linear curve; IV, high-threshold curve. For all curves the maximum cost of impact is $M = 10$; parameter values for individual curves are: I, $u = 0$, $\beta = 0.1$, II, $u = 0.5$, $\beta = 0.1$; III, $u = 1$, $\beta = 1$; and IV, $u = 1$, $\beta = 0.1$. The same line formats are used to refer to these curves throughout all figures.

Here we develop a theoretical framework to formalize and extend the concept of managing for reduced impact by examining how the optimal management effort for an invasive species varies under both ecological and economic parameter sets. We determine how the effectiveness of management depends on the relationship between the cost of impact and population density of the invader (density–impact relationship). The optimal management strategy depends on the management objective (Yokomizo et al. 2003*b*, Nicholson and Possingham 2006). Managers have limited budgets and need to prioritize allocation of resources. Overinvestment wastes money on management that is unnecessary or ineffective at reducing impact and underinvestment wastes money by incurring a cost of impact that outweighs the saving on management costs. Our management objective is to minimize the total costs of the invasive species, including both management and impact costs.

Environmental fluctuations can lead to larger or smaller population sizes than those predicted using a deterministic model, which in turn could lead to under- or overinvestment in management efforts. We determine the effect of environmental fluctuation on optimal management effort using a stochastic mortality function, an approach similar to that used to calculate optimal conservation effort levels for an endangered population in fluctuating environments (Yokomizo et al. 2003*a*, 2004, 2007).

We use a simple stochastic density-dependent population model for a univoltine insect or annual plant population without a seed bank and with nonoverlapping generations (we refer to the invasive species using the generic term "pest" to include insects or plants). We assume that the population is eradicated if it drops

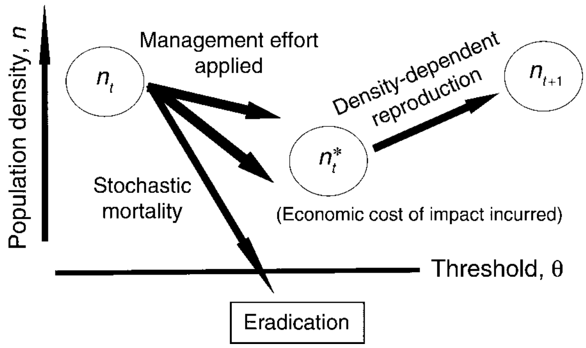

FIG. 2. Schematic depiction of the model showing the sequential timing of stochastic mortality, management, impact costs, and density-dependent reproduction. All of these processes take place within one time step; n_t is density of the population at year t, and n_t^* is population size after management has been conducted.

below a specified eradication threshold. We explore how ecological parameters (magnitude of environmental fluctuations in mortality, population density, strength of density dependence, and eradication threshold) and economic or management parameters (maximum economic impact, time-horizon of management activities, and discount rate) determine the optimal management strategy for the four different density–impact curves in Fig. 1. The discount rate is used to discount future costs in relation to current costs. We use a common currency for impact costs and management costs in order to derive optimal management investment for different density–impact relationships. We determine the cost incurred from misspecification of the density–impact curve to guide prioritization of research on the cost of impact, and, finally, we determine the performance of a fixed annual budget for different density–impact curves.

MODEL DEVELOPMENT

We consider a situation where a population of an invasive species has already established and been detected. For simplicity, we assume a pest population without overlapping generations. The population model is illustrated in Fig. 2. In the first phase of the annual cycle, time t, the density of the population, n_t, decreases due to mortality which changes each year with environmental variance (e.g., precipitation or temperature). Management can be implemented simultaneously with natural mortality to reduce the density of the population. We assume that economic costs (impact) caused by the invader increase monotonically with invader density up to a threshold population density level at which costs of impact reach a maximum level (Fig. 1). In order to reduce these economic impacts we can invest in management efforts to reduce pest density. After management has occurred there is a density-dependent reproductive stage. The pest population density is at its minimum at the beginning of the reproductive stage. We assume that the population is eradicated when the density drops below a threshold value θ; this assumption enables us to assess the dependence of our results on how difficult a species is to eradicate.

Population dynamics

Let $\exp(-a + \xi_t)$ be the stochastic survivorship at time t, in which $-a$ is the mean decrease in the logarithmic population density and ξ_t is a stochastic variable following a normal distribution with mean zero and variance σ_ξ^2, independent between years. The parameter σ_ξ^2 is a measure of the magnitude of environmental fluctuation. In the model, the level of optimal management effort is chosen based on density of the pest at the start of the time period, before the magnitude of environmental fluctuations on mortality becomes known (see criterion for optimality, below). The population size after this period is

$$n_t^* = \begin{cases} n_t \exp(-a - fe_t + \xi_t) & \text{if } -a - fe_t + \xi_t \le 0 \\ n_t & \text{if } -a - fe_t + \xi_t > 0 \end{cases} \tag{1}$$

where e_t is the level of management effort and f is the effectiveness of the management effort. As this stage includes mortality only, n_t^* never becomes larger than n_t.

At the end of the year, there is a reproductive stage. The population density in the following year is affected by density dependence and approaches or fluctuates around a carrying capacity, Y. We use the density-dependent Hassell model for the dynamics of the species (Hassell 1975):

$$n_{t+1} = \begin{cases} \dfrac{\lambda n_t^*}{(1 + bn_t^*)^k} & n_t^* > \theta \\ 0 & \text{otherwise} \end{cases} \tag{2}$$

where b and k are species-dependent variables that determine the shape of the recruitment function, n_t^* is the population size after management has been conducted, and λ is the per capita population growth rate in the absence of density dependence. The larger b, the smaller the population density in the following year. When population density in the reproductive stage is lower than the eradication threshold θ, population density in the following year becomes 0. When $k < 1$, n_{t+1} monotonically increases with n_t^* (Fig. 3). When $k > 1$ and n_t^* is not small, n_{t+1} decreases with n_t^* (Fig. 3). When $k > 1$ and n_t^* is small, n_{t+1} becomes very large because density dependence is overcompensating. Hence, when $k > 1$, population density in the next year can become large even if we invest in management effort (e.g., Buckley et al. 2001). Let the carrying capacity, Y, be the density at which the population density does not change during the reproductive stage, that is $n_t^* = n_{t+1}$ (Fig. 3). At the carrying capacity, Eq. 2 simplifies to $\lambda = (1 + bY)^k$. To examine how the optimal management strategy depends upon k, we used a fixed value of Y and various values of k in $\lambda = (1 + bY)^k$ (Fig. 3).

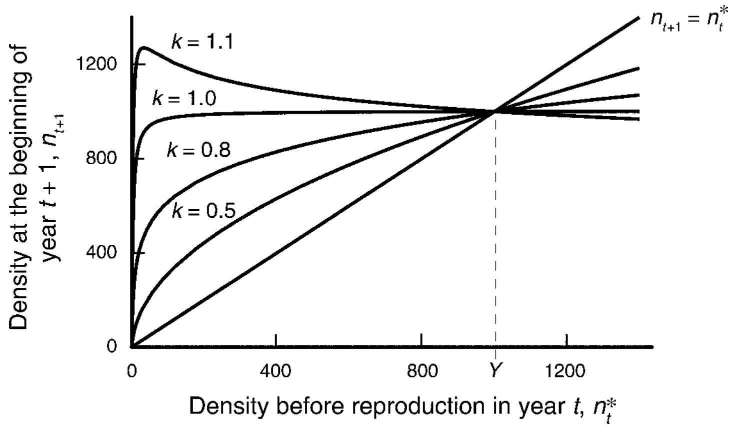

FIG. 3. Density-dependent reproduction for different values of the strength of density dependence, k, with a constant carrying capacity Y. We use the Hassell model for density dependence (Eq. 2).

Criterion for optimality

While in some cases we might expect management effort to lead to reduced economic impacts and for management effort to lead to increased probability of eradication, where these benefits occur they are not achieved without cost. Management effort is accompanied by a cost which we assume is the product of the management effort, e, and the unit cost of management, c. We found the optimal management effort that minimized the sum of the cost of impact and the cost of management over multiple years. We defined this sum as total cost Φ where

$$\Phi = (\text{cost of impact}) + (\text{economic cost of management}).$$

When we choose the management effort in the current year, we need to consider not only the cost of impact caused and the cost of management efforts in this current year but also those in the future. We set a minimized total cost over multiple years Φ^* as follows:

$$\Phi^* = \min_{0 \le e_1, e_2, \ldots, e_T \le E_{\max}} \sum_{\tau=1}^{T} \gamma^{\tau-1} \{E[I_\tau(n_\tau^*)] + cE(e_\tau)\} \quad (3)$$

where γ is the discount factor ($0 \le \gamma < 1$; the discount factor reflects the weight placed on future relative to present costs), I_τ is cost of impact in year τ and is a function of management effort in that year, e_τ, and T is the time horizon of the whole management problem. The time horizon determines the period over which the costs are considered and could take a range of values from short (e.g., $T < 3$ years) to long (e.g., $T > 10$ years). We assume that there is a maximum management effort, $E_{\max}$, that can be applied in any year. We obtained the optimal state-dependent management effort for each year using stochastic dynamic programming (SDP). We assumed that the cost of impact is a function of n_t^* which is the population density after management is conducted. We define the cost of impact function $I_t(n_t^*)$ with respect to n_t^* according to Eq. 4 because this function gives general curves of the type in Fig. 1:

$$I_t(n_t^*) = \begin{cases} MC[1/\{1 + \exp[-(n_t^*/Y - u)/\beta]\} - B] & n_t^* \le Y \\ M & n_t^* > Y \end{cases} \quad (4)$$

where $B = 1/(1 + \exp[u/\beta])$ and $C = (1 + \exp[-(1 - u)/\beta])/(1 - B(1 + \exp[-(1 - u)/\beta]))$ in order to set the cost of impact to 0 at $n_t^* = 0$ and to M at $n_t^* = Y$, where M is the maximum cost of impact. We assumed that there is no difference between *functional* forms of the cost of impact when $n_t^* \ge Y$. Fig. 1 shows four different density–impact curves, the shape of which depends on μ and β. We use these curves to examine dependence of the optimal management effort on the impact function. Exploring how these four relationships affect management strategies is the central aim of this paper.

EFFECT OF THE DENSITY–IMPACT CURVE ON OPTIMAL MANAGEMENT EFFORT

Fig. 4 shows the dependence of the optimal management effort in the first year, e_1^*, on density–impact curves under varying economic and population dynamic parameters described in detail below.

Fig. 4a: population density in the first year, n_1

Generally, the optimal management effort increases with population density (Fig. 4a). However for the low-threshold curve (I), the optimal management effort is at its maximum level when the population density is low (see Fig. 4a). At low density, optimal management effort in the low-threshold curve is relatively high due to impacts incurred even when the population density is low, whereas optimal management effort in the other curves becomes 0 due to low-impact costs at low density. For the low-threshold curve ongoing impact and management costs are avoided if the population is eradicated, therefore high management effort is optimal

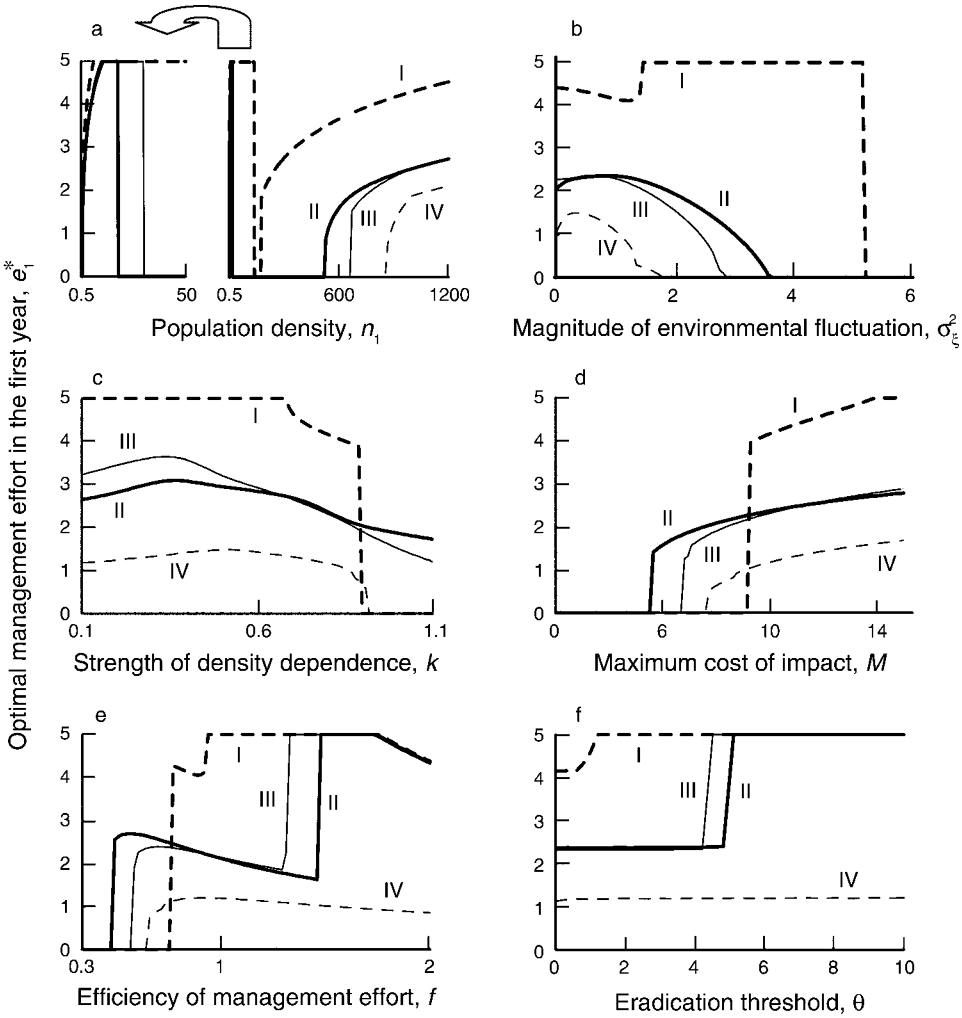

FIG. 4. Dependence of the optimal management effort in the first year, e_1^*, on several economic and demographic parameters. Individual panels (a–f) are described in detail in the text (see *Effect of the density–impact curve on optimal management effort*). Density–impact curves (I–IV) follow Fig. 1. Parameter values are: n_1 (population density in the first year) = 900; M (maximum cost of impact) = 10; Y (carrying capacity) = 1000; f (efficiency of management effort) = 0.8; c (unit cost of management) = 2; magnitude of environmental fluctuation, $\sigma_\xi^2 = 1$; species-dependent variable $a = 0.1$; γ (discount factor) = 0.95; θ (pest-eradication threshold density) = 0.5; species-dependent variable $b = 0.3$; k (strength of density dependence) = 0.8; $E_{\max}$ (maximum management effort) = 5; T (time horizon for whole the management problem) = 5.

when eradication or maintenance at a low density is feasible. For the other curves, only when the population density is very close to 0, and therefore requiring small total effort for eradication, is the optimal management effort at its maximum level (Fig. 4a: inset). The difference in management efforts between the S-shaped (II) and linear curves (III) is largest at intermediate levels of population density. For the high-threshold curve (IV), the optimal management effort is the lowest out of all the curves because impact is low at most population densities.

Fig. 4b: magnitude of environmental fluctuation, σ_ξ^2

Since the mean of $\exp(-a + \xi)$ increases with magnitude of environmental fluctuation σ_ξ^2, we introduce a new parameter $a' = a - \xi$, which follows a normal distribution, to fix the mean of the logarithmic normal distribution, $\exp(-a + \xi)$. Note that mean survivorship is not exactly the same for all σ_ξ^2 because we assume that survivorship $\exp(-a + \xi - fe)$ cannot be larger than 1. From Fig. 4b it can be seen that for small environmental fluctuations, σ_ξ^2, the optimal management effort increases with the magnitude of environmental fluctuation for all density–impact curves other than the low-threshold curve (I), due to high population densities in occasional high survival years. For intermediate values of σ_ξ^2 the optimal management effort for the low-threshold curve (I) reaches the maximum level because occasional low-survival years combined with large management effort enhances the possibility of eradication. For large σ_ξ^2, however, there are decreases in optimal management efforts for all density–impact curves. Large environmental fluctuations either reduce mortality to such an extent that additional management mortality is completely compensated for, or fluctuations increase mortality far beyond that caused by management-induced mortality, making management redundant and a waste of resources.

Fig. 4c: strength of density dependence, k

Strong compensating density dependence (large k) reduces the optimal management effort for all curves (Fig. 4c). When k is large there is rapid density-dependent recovery of the population and the population density at year $t+1$ rebounds quickly even with a large management effort to decease population density n_t^*. Dependence on k is highest for the low-threshold curve. When k is small, density-dependent recovery is slow which enables eradication of the pest with large management effort.

Fig. 4d: maximum cost of impact, M

The optimal management effort increases with the maximum value of impact M as expected (Fig. 4d). When M is large, the cost of the impact is more significant than the cost of management. Therefore high management effort is optimal, especially for the low-threshold curve (I). When M is small, however, the optimal management effort for the low-threshold curve is 0, as management effort is no longer economically viable due to the high cost of reducing only a small impact. It is optimal to invest in management for the S-shaped (II) and linear (III) curves at lower values of M because relatively small management efforts are cost effective at reducing impact, which is not the case for the low-threshold curve.

Fig. 4e: efficiency of management effort, f

When the efficiency of management effort, f, is very small, the optimal management effort, e_1^*, is 0, becoming positive at a different value of f for each curve (Fig. 4e). Less efficient management is more cost effective for the S-shaped (II), linear (III), and high-threshold (IV) curves than for the low-threshold curve (I). This occurs because inefficient management means impact remains high for the low-threshold curve. As high efficiency can reduce overall management effort, e_1^* initially decreases with f. However, e_1^* becomes maximal suddenly at a different higher value of f for each curve as high efficiency makes it possible to eradicate a population with large management effort. For the low-threshold curve e_1^* is maximal even if the value of f is not very large. When efficiency of management increases further, the optimal management effort decreases with f because eradication probability becomes sufficiently large without further management investment.

Fig. 4f: eradication threshold, θ

When the threshold of eradication θ is large, the optimal management effort becomes maximal as it becomes easier to eradicate the pest population (Fig. 4f). Optimal effort for the low-threshold curve (I) becomes maximal at a lower level of θ as compared to the S-shaped (II) and linear (III) curves but the size of the eradication threshold matters little for the high-threshold curve.

Additional considerations: management time horizon, T, and discount factor, γ

Optimal management effort initially increases with the time horizon of management T; however, the optimal management effort quickly reaches a maximal value for all curves, (happening slightly later for the low-threshold curve) except the linear curve. The optimal management effort increases gradually with the discount factor γ as future costs are weighted more highly. More detail and figures are in Appendix A.

Misspecification of Density–Impact Curves

The optimal management effort depends on the shape of the density–impact curve. If we apply an inaccurate density–impact curve, the total realized cost will be larger than those incurred under the correct optimal management investment, defined as the cost of misspecification of the density–impact curve. We will either overinvest in management that is ineffective at reducing impact, or we will underinvest in management incurring impact costs that could have been avoided with more investment. We can express this cost $\hat{\Phi}$ as follows:

$$\hat{\Phi}(u^*, \beta^*, \hat{u}, \hat{\beta}) = \Phi[u^*, \beta^*, e^*(\hat{u}, \hat{\beta})] - \Phi^*[u^*, \beta^*, e^*(u^*, \beta^*)] \qquad (5)$$

where u^* and β^* are the true values which determine the shape of the density–impact curve, and $\hat{u}$ and $\hat{\beta}$ are inaccurate values applied. The total cost Φ is a function of u, β, and e. The management effort $e^*(\hat{u}, \hat{\beta})$ is the optimal management effort under the situation where $u = \hat{u}$ and $\beta = \hat{\beta}$. $\Phi^*[u^*, \beta^*, e^*(u^*, \beta^*)]$ indicates the total costs incurred by applying the optimal management effort obtained previously. When calculating the total cost incurred for the use of an incorrect density–impact curve, $\Phi[u^*, \beta^*, e^*(\hat{u}, \hat{\beta})]$, the optimal management effort $e^*(u^*, \beta^*)$ is not applied; hence $\Phi[u^*, \beta^*, e^*(\hat{u}, \hat{\beta})]$ is larger than $\Phi^*[u^*, \beta^*, e^*(u^*, \beta^*)]$. In most cases we do not have well-described density–impact curves; it is therefore useful to know the implications of applying an inaccurate density–impact curve. In general, when we do not have information on the shape of density–impact curve, we may assume the relationship is linear, i.e., there is a directly proportional relationship between density and impact. Fig. 5 shows the cost incurred by applying the linear curve when the true impact curve is low-threshold (I), S-shaped (II), or high-threshold (IV).

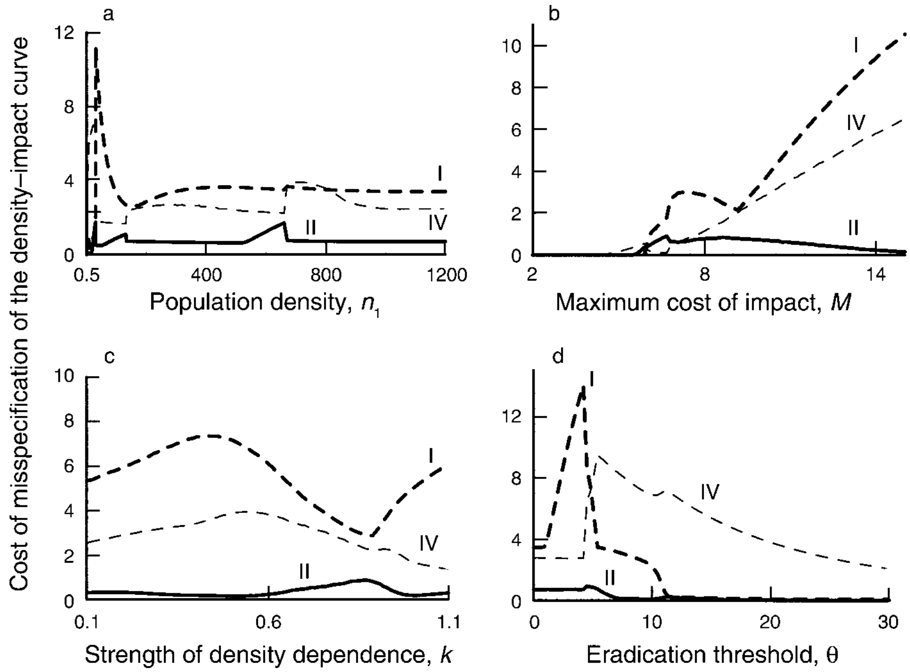

FIG. 5. Dependence of the cost of misspecification on three population measures (population density, density dependence, and eradication threshold) and one economic parameter (maximum cost of impact). Individual panels (a–d) are described in detail in the text (see *Misspecification of density–impact curves*). The parameter values are the same as in Fig. 4.

Fig. 5a: population density in the first year, n_1

The cost caused by misspecification depends little on population density in the first year, n_1, with the exception of the low-threshold curve (I) at low population density, when the cost of misspecification is high (Fig. 5a). Since the management effort e_1^* based on the linear curve (III) is smaller than e_1^* based on the low-threshold curve, we apply too little effort and lose opportunities to eradicate the pest population at low density where eradication is both economically viable and highly beneficial. The cost of misspecification for the S-shaped curve (II) is low due to similarity with the linear curve. The spikes in cost of misspecification at intermediate population densities for the S-shaped and high-threshold curves (IV) are due, respectively, to underinvestment and overinvestment in management. The cost of misspecification for the high-threshold curve is substantial due to recurrent overinvestment in unnecessary management.

Fig. 5b: maximum cost of impact, M

Although the total cost Φ increases with M, the cost of misspecification for the S-shaped curve (II) becomes close to 0 at large M (Fig. 5b) as when M is large, the optimal management efforts in the S-shaped and linear curves (III) are very similar. The cost of misspecification rises rapidly with M for the high- and low-threshold curves due to overand underinvestment in management, respectively.

Fig. 5c: strength of density dependence, k

For $k < 1$ the cost of misspecification for the low-threshold curve (I) first increases and then decreases strongly with k (Fig. 5c). The merit of investing in large management efforts becomes small due to stronger density-dependent recovery and optimal management efforts for the low-threshold and linear (III) curves converge. However the cost of misspecification for the low-threshold curve increases sharply when k is larger than 1. For $k > 1$ the optimal management efforts for the low-threshold and linear curves are 0 and moderate, respectively. Due to overcompensating density dependence, for the low-threshold curve, investing an inaccurate moderate level of management effort results in a large population density in the following year, large economic cost of the effort, and no decrease in impact.

Fig. 5d: eradication threshold, θ

When θ is small (i.e., the population is difficult to eradicate), the cost of misspecification for the low- and high-threshold curves is large (Fig. 5d). Since eradication is very beneficial for the low-threshold curve (I), application of the linear curve (III) results in a lower-than-necessary management effort, especially when eradication is difficult. On the other hand, since eradication is a waste of management effort for the high-threshold curve (IV), misspecification results in overinvestment in management and consequent waste of resources.

Performance of Fixed Annual Budget for Different Density–Impact Curves

We have calculated the optimal management effort needed to minimize the total costs incurred in managing the impact of an invasive species over the specified time period, T. However there are cases where we invest a fixed annual budget R in a management effort every year over that time period; for example budgets are commonly set by governments or granting agencies for fixed yearly expenditure over 3–5 years. If the amount of the annual budget is fixed, the cost of impact over multiple years depends on the amount of the annual budget. We calculated the reduction of cost of impact by management effort under a fixed annual budget, $\Psi(R)$, and assumed that we could not carry over the annual budget from year to year:

$$\Psi(R) = \sum_{\tau=1}^{T} \gamma^{\tau-1}[E(I_\tau \mid e_\tau = 0) - E(I_\tau \mid e_\tau = R/c)] \quad (6)$$

where R is an annual budget and R/c represents invested management effort in each year. The reduction in cost of impact is summed over all years up to the time horizon T, taking into account the discount factor γ. The reduction in impact in any particular year of budget allocation is the difference between the expected impact with no management effort, $E(I_\tau \mid e_\tau = 0)$, and the expected impact when the fixed annual budget is spent on management effort, $E(I_\tau \mid e_\tau = R/c)$.

Fig. 6 shows reduction of impact depending on the management budget, $\Psi(R)$. As expected the reduction in impact increases with the amount of budget for small budgets and becomes asymptotic for large budgets. Each curve becomes asymptotic at a different value of R. For the low-threshold curve (I), we cannot reduce the impact when the annual budget is not sufficiently large; hence investing a small budget is not efficient. With the other curves we can reduce the impact efficiently even if only a small budget is available. This result shows that it is important to understand the shape of density–impact curves even when the annual budget is fixed.

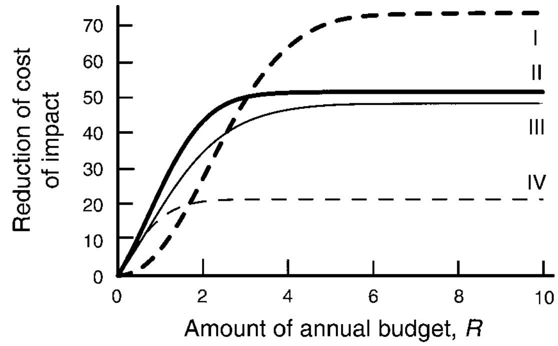

Fig. 6. Efficiency of budget investment is shown as the reduction in cost of impact as a function of investment of a fixed annual budget in management effort for each of the density–impact curves (I–IV) from Fig. 1. The parameter values are the same as in Fig. 4.

Discussion

The general theoretical model presented here demonstrates the importance of knowing the shape of the density–impact curve when devising effective management strategies, especially for invaders with high maximum impact and high impact at low density. We have shown that the optimal management effort largely depends on the density–impact curve, and misspecification of the density–impact curve causes unnecessary impact cost or wasted management effort. Thomas and Reid (2007) point out that the density–impact relationship also has consequences for the effectiveness of weed control by biocontrol agents. Due to computational limitations, we used a general population model to explore the dependence of the optimal management strategy on a suite of ecological and economic parameters. Density–impact curves should be incorporated into other species-specific analytical or simulation management models as appropriate. For mathematical and computational convenience we used restrictive assumptions of no seed bank and a univoltine or annual organism; however the limitations of the particular demographic model used here could easily be avoided in alternative tactical modeling frameworks. The generality of our results can be extended if we use the eradication-threshold parameter as a proxy for the effects of different life histories, e.g., a species with a seed bank can be considered as difficult to eradicate.

Low-threshold species (curve I in Fig. 1) will generally be among our worst invaders as their impact is apparent even at low density. However, we identify several scenarios when the cost of management outweighs the benefits obtained in terms of reduction of impact and when the optimal management strategy is to invest nothing in management. For low-threshold species this is when environmental fluctuations are large, density-dependent recovery is rapid, and the cost of impact is low to moderate relative to management costs. In contrast, maximal management investment for low-threshold species is optimal when the population densities are low, density-dependent recovery is slow, and the maximal cost of impact moderate to high. The costs of not recognizing a low-threshold species and managing it as if impact is directly proportional to density are greatest at low population densities, high maximal impact, and when eradication is difficult.

High-threshold species (IV) may not be noticeably apparent as problematic until they achieve high densities, and our model suggests that large investments in management are not necessary unless they are easy to eradicate and/or the maximum cost of impact is large. In fact much of the cost of using the wrong density–impact relationship for these species is due to overinvestment in unnecessary management. Such invasive species might be better targeted for tactical management at high density as the optimal management effort rarely reaches the level of maximum management effort, $E_{\max}$. These general findings should motivate research on the shape of density–impact relationships and the search for generalizations about how that shape differs among species, invaded habitats, and types of impact.

The density–impact curve also affects whether we should attempt eradication as, once the population is eradicated, we no longer need to invest in management effort. Since the impact for the low-threshold curve (I) is the largest among the four curves at all population densities below the carrying capacity, eradication is most justified for this curve. Indeed, the value of knowing the correct curve is particularly great for low-threshold populations at low density where eradication is likely to be more easily achieved. An alternative interpretation is that given impact is so disproportionate to density, management efforts might be better directed at prevention of arrival and establishment (e.g., through quarantine measures) rather than population reduction. On the other hand, there is little benefit in eradication for high-threshold curve (IV) populations as large impact is only apparent at high population density.

It may not be the best option to delay action until we obtain information on the shape of the impact curve (Simberloff 2003). This is especially true for low-threshold populations where management investment is very effective at low densities (i.e., early in an invasion) when lack of data on the shape of the density–impact curve is likely to be greatest. An extension of the current study would be to determine the optimal management effort under uncertainty of the density–impact curve by, for example, assuming a probability distribution for the parameters of the density–impact relationship or information-gap decision theory (Ben-Haim 2001). Information-gap decision theory derives the most robust management option to meet a minimum performance requirement under severe uncertainty (Ben-Haim 2001, Regan et al. 2005). An alternative approach would be to attempt to generalize the characteristics of species or habitats that tend to give rise to different density–impact relationships and apply these generalizations to new problems.

Budgetary constraints often mean limited resources have to be allocated to the management of multiple invasive species over several years. Strategies for the allocation of a budget to minimize the total cost of management and impact of multiple populations would be useful for practitioners. Unfortunately, due to the large number of calculations involved, the SDP (stochastic dynamic programming) approach used here is not well suited to dealing with multiple populations over several years. Furthermore, the results of a single-species problem cannot simply be transferred to a multi-species problem because the single species with the highest optimal management effort is not necessarily a higher priority for management. However, if the annual budgets for each species are fixed, we can obtain optimal allocation of the total budget using a calculation such as that used in Fig. 6, taking into account reduced impact divided by the amount of a fixed annual budget.

In natural ecosystems invasive species can decrease species richness and change ecosystem function (e.g., Costello et al. 2000, Alvarez and Cushman 2002). In order to use our analysis in these cases we need to learn the economic value of species richness or ecosystem functioning to obtain the optimal management effort of the invasive species. It is not straightforward to obtain these values although attempts have been made (Costanza et al. 1997, Edwards and Abivardi 1998). The loss of species and ecosystem function due to invasion could be irreversible and may not necessarily be simple functions of density of invasive species in the current time period. Furthermore, restoration effort may be needed in order to reverse the impacts caused, inflating management costs (Parker et al. 1999).

In our model the density of an invasive population changes but the area occupied does not expand. Impact could, however, increase with the area infested even if the density remains the same. If impact scales with the area infested, a spatial-spread model can be substituted for our population-dynamic model and occupied area–impact curves used. Insights obtained here are applicable to models of dynamics of the infested area if we replace density with the infested area when interpreting results. For the low-threshold curve (I) it might be appropriate to manage to reduce spread (e.g., by using containment or quarantine procedures) if the population density is small, but once the population expands to infest a large area, management effort to reduce spread becomes ineffective. We have also neglected spatial structure; effectiveness or cost of management effort may be different for a uniformly distributed invasive population compared with an aggregated population at the same density.

As we have limited resources for invasive-species management it is crucial to set appropriate management goals (Buckley 2008) in order to avoid spending money on density reductions that are quickly compensated for or ineffective at reducing the detrimental impacts of invasive species. While we focused on the form of the density–impact curve we have also shown that quantifying the magnitude (maximum cost) of impact, M, is also crucial, as total costs and the cost of misspecification for low- and high-threshold curves increase with M. Overall, this study is an important first step towards clarifying the value of knowing not just the population ecology of an invasive species and the magnitude of impact but also the shape of the relationship between invader density and economic impact in making sound management decisions.

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APPENDIX

A figure illustrating parameter dependencies of a management time horizon T and discount factor γ (*Ecological Archives* A019-016-A1).