

Optimal conservation strategy in fluctuating environments with species interactions: Resource-enhancement of the native species versus extermination of the alien species

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Abstract

Alien species are often a major threat to native species. We consider optimal conservation strategies for a population whose viability is affected both by an alien species (such as a competitor, a predator, or a pathogen) and by random fluctuations of the environment (e.g. precipitation, temperature). We assume that the survivorship of the native population can be improved by providing resources such as food and shelter, and also by an extermination effort that decreases the abundance of the alien species. These efforts decrease the extinction probability of the native population, but they are accompanied by economic costs. We search for the optimal strategy that minimizes the weighted sum of the extinction probability and the economic costs over a single year. We derive conditions under which investment should be made in both resource-enhancement and extermination, and examine how the optimal effort levels change with parameters. When the optimal strategy includes both types of efforts, the optimal extermination effort level turns out to be independent of the density and economic value of the native species, or the variance of the environmental fluctuation. Furthermore, the optimal resource-enhancement effort is then independent of the density of the alien species. However, the parameter dependencies greatly change if one of the efforts becomes zero. We also examine the situation in which the impact of the alien species is uncertain. The optimal extermination effort increases with the uncertainty of this impact except when the cost of extermination is very high.

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1. Introduction

Invasions of alien species form a major threat to biodiversity (Williamson, 1996). Since alien species can be competitors (Goergen and Daehler, 2001) or predators (Diamond, 1989), they often threaten the viability of native species. There have been several experimental and theoretical studies on how to manage alien species in order to mitigate their harm (Watson et al., 1992; Hone, 1994; Ruiz and Carlton, 2003; Byers et al., 2002; Higgins et al., 2000;

Hastings et al., in press; Ruiz and Carlton, 2003; Arriaga et al., 2004; Travis and Park, 2004). For example, Taylor and Hastings (2004) calculated the optimal control strategy for an invasive grass, *Spartina alterniflora* under budget limitation.

In addition to species interactions, plant and animal populations are often affected by environmental and demographic fluctuations. There are several theoretical studies on optimal resource-enhancement strategies with incomplete information on these factors (Yokomizo et al., 2003a, b, 2004; Bretagnolle and Inchausti, 2005). In a previous paper, we studied the optimal level of resource-enhancement effort in the presence of environmental fluctuations (Yokomizo et al., 2003a). We assumed that resource-enhancement effort improves the survivorship of

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an endangered population, but it is accompanied by a cost. The optimal strategy is the one that minimizes the weighted sum of the extinction probability and the economic cost of conservation. We examined how the optimal resource-enhancement effort level depends on effort effectiveness, the magnitude of environmental fluctuation, and the length of the conservation period. In a subsequent study, we considered a situation in which the exact population size is unknown, but some information (a cue) about it is available (Yokomizo et al., 2003b). Accuracy of the cue can be improved by a monitoring effort. Yokomizo et al. (2003b) calculated optimal levels of resource-enhancement and assessment efforts. Yokomizo et al. (2004) extended these results to multiple-year optimization using stochastic dynamic programming. However, none of these models explicitly considers effects of interactions between species, which is the subject of the current study.

Consider a native species threatened by an alien population which reduces the survivorship or the reproductive rate of the focal species. There may be several alternative ways to reduce the extinction risk of the focal species. For instance, its survivorship can be improved, by providing their resources, such as food and shelter, or by diminishing or exterminating the alien species (Caughley and Gunn, 1995). An illustrative example is given by an endangered native species in California, USA, Least Bell’s Vireo (*Vireo bellii pusillus*) (Kus, 1998, 1999). An invasive species, the Brown-headed cowbird (*Molothrus ater*), parasitizes broods of Vireo, thus decreasing its reproductive success. Resource enhancement is aimed at creating or restoring habitats of Vireo, whereas extermination effort consists of removing cowbird eggs from nests of Vireo and of trapping adult cowbirds. Both types of effort entail costs.

The management decision concerning these efforts must also consider effects of stochasticity caused by environmental fluctuations on population dynamics. Currently, there are no general guidelines on how to select the optimal strategy among multiple types of efforts under the constraint of limited economic costs. In this paper, we derive such guidelines for a single year time scope. We focus on the conditions under which both efforts should be positive. First we study the situation in which the per capita impact of the alien species is known, and then we generalize this to cases where this impact can only be estimated with a limited accuracy.

2. The model

We consider the situation illustrated in Fig. 1. A population of a focal species lives in a fluctuating environment and is threatened by an alien species. The management goal is to protect the focal population. Even if the initial density is large, the population may go extinct if the environmental conditions are very unfavorable and/or the alien species has a large negative effect on survivorship of the focal species.

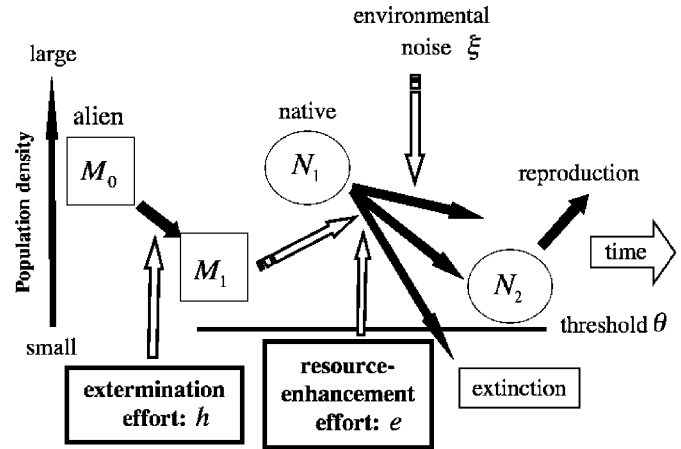


Fig. 1. Scheme of the model (see text).

The population density of the native species is at its minimum just before the reproductive stage. We assume that the population goes extinct when the density drops below a threshold value. The extinction probability is large when the alien population is large and the focal population is small. To mitigate the extinction risk, we can invest in resource-enhancement effort and in extermination effort. Resource-enhancement effort, e.g. by supplying food or shelter, improves the survivorship of the native population directly. In contrast, extermination effort has an indirect positive effect on the focal population, by decreasing the density of the harmful alien population. Since both these efforts are accompanied by economic costs, there may be intermediate optimal levels. The optimal effort levels are chosen based on the initial density of the focal and alien species, before the magnitude of environmental fluctuation of the year becomes known. To simplify the analysis, we assume that the conservation period is 1 year.

2.1. Population dynamics

Let N_1 and M_0 be the densities of the focal population and the alien population respectively at the beginning of the year (see Fig. 1). The density of the alien population after extermination stage, is given by

$$M_1 = M_0 \exp[-a_e - f_h h], \tag{1}$$

where a_e , f_h and h are the decrease in the logarithmic density due to mortality, the effectiveness of extermination effort, and the extermination effort level, respectively.

We assume that the survivorship of the focal population fluctuates randomly and that the survivorship of the focal population decreases with the density of the alien species. Let $\exp[-a_n + \xi - kM_1]$ be the survivorship of the focal species until reproduction. Here, $-a_n$ is the mean decrease in the logarithmic population density, ξ is a random environmental variable following a normal distribution with mean zero and variance σ_ξ^2 , and k is the per capita impact of the alien species.

After investment in extermination effort, we may choose to invest in resource-enhancement effort to improve the survivorship of the focal species. Let e be magnitude of the resource-enhancement effort and let f_e be its effectiveness. The density of the focal population after the risky period is

$$N_2 = \begin{cases} N_1 \exp[-a_n + f_e e - kM_1 + \zeta] & \text{if } -a_n + f_e e - kM_1 + \zeta \leq 0, \\ N_1 & \text{if } -a_n + f_e e - kM_1 + \zeta > 0. \end{cases} \quad (2)$$

For simplicity of the analysis, we here assume that the survivorship of the alien population is not affected by random environmental changes, or by resource-enhancement effort. We denote the initial logarithmic population density by $z = \ln N_1$. The population becomes extinct when $z - a_n + f_e e - kM_1 + \zeta$ becomes lower than a threshold value θ .

2.2. Criterion for optimality

The extinction probability is decreased by resource-enhancement and extermination efforts. However, both efforts incur a cost. We assume that the economic costs of resource-enhancement effort and extermination effort are $c_e e$ and $c_h h$, respectively, where c_e and c_h are cost coefficients. We search for the effort levels that minimize the weighted sum of extinction risk and economic costs:

$$F = w \left[\begin{array}{c} \text{Extinction risk} \\ \text{of the population} \end{array} \right] + \left[\begin{array}{c} \text{Economic costs} \\ \text{of conservation} \end{array} \right] \rightarrow \text{minimum},$$

where the probability of extinction is multiplied by a positive constant w indicating the economic value of the population. This can be rewritten as

$$\min_{e \geq 0, h \geq 0} E[w\chi[z - a_n + f_e e - kM_1 + \zeta \leq \theta] + c_e e + c_h h], \quad (3)$$

where $\chi[A]$ is an indicator function, which is 1 if event A occurs, and 0 otherwise. We can rewrite total cost as

$$F(e, h) = w \int_{-\infty}^{-z+a_n+\theta-f_e e+kM_1} \exp[-a_e-f_h h] \Phi(x) dx + c_e e + c_h h, \quad (4)$$

where $\Phi(x) = e^{-x^2/2\sigma_\zeta^2} / \sqrt{2\pi\sigma_\zeta^2}$ denotes the probability density function of a normal distribution with mean 0 and variance σ_ζ^2 . The total cost $F(e, h)$ is a function of resource-enhancement effort level e and extermination effort level h . We will now derive the optimal effort levels e^* and h^* that minimize Eq. (4). In the following, we first consider the case where the influence of the alien species k is known. Later we discuss the situation where k is unknown.

3. Optimal resource-enhancement and extermination: mathematical analysis

For convenience we introduce the notation:

$$\begin{aligned} X &= z - a_n - \theta, & Y &= kM_0 e^{-a_e}, \\ \beta_e &= wf_e / (c_e \sqrt{2\pi\sigma_\zeta^2}), & \beta_h &= wf_h / (c_h \sqrt{2\pi\sigma_\zeta^2}), \\ \zeta_e &= \sqrt{\sigma_\zeta^2 \log \beta_e^2}, & \zeta_h &= \sqrt{\sigma_\zeta^2 \log(Y\beta_h)^2}. \end{aligned} \quad (5)$$

Thus, X represents the difference between the expected log-density of the focal species just before reproduction and the extinction threshold. Y indicates the decrease in the log-density of the focal species due to the alien species. In the following we will refer to Y as the effect of the alien species.

The partial derivatives of F with respect to e and h are

$$\frac{\partial F}{\partial e} = -w\Phi(-X - f_e e + Y \exp[-f_h h])f_e + c_e, \quad (6a)$$

$$\frac{\partial F}{\partial h} = -w\Phi(-X - f_e e + Y \exp[-f_h h])Y \exp[-f_h h]f_h + c_h. \quad (6b)$$

The conditions for the optimal effort levels to be positive, and the formulas for the optimal effort levels are derived in Appendix A. Results are summarized in Fig. 2. When $\beta_e \leq 1$, $\partial F/\partial e \geq 0$ for all $e \geq 0$ and $h \geq 0$. When $Y\beta_h \leq 1$, $\partial F/\partial h \geq 0$ for all $e \geq 0$ and $h \geq 0$ (see Appendix A).

The parameter space can be divided into five regions (A–E), based on the signs of the partial derivatives. In regions C and D, F has two extrema. One of these corresponds to the minimum (see Appendices A and B). We denote the location of the local minimum of F by (\hat{e}, \hat{h}) and the optimal effort levels which correspond to a global minimum in $e \geq 0, h \geq 0$ by (e^*, h^*) . In region C there are parameter combinations where (\hat{e}, \hat{h}) lies in the positive quadrant, whereas in region D \hat{h} is always negative. Thus, only in region C there are situations where both optimal effort levels are positive.

In all of the regions other than C, at least one of the optimal effort levels is zero. In region A both efforts should be zero. In region B, optimal resource-enhancement effort is zero, but h^* may be positive, and equal to $\hat{h}(0)$, the optimal value of h when $e = 0$. For high X -values, both effort levels should be zero. For small values of X the value of h^* is determined by comparing the values of $F(0, 0)$ and $F(0, \hat{h}(0))$. When $F(0, 0)$ is smallest, $h^* = 0$, otherwise it is positive and $h^* = \hat{h}(0)$.

In region C, it is possible that both e^* and h^* are positive. In that case their values are (see Appendix A):

$$e^* = \hat{e} = \frac{1}{f_e} (-X + f_e c_h / f_h c_e + \zeta_e), \quad (7a)$$

$$h^* = \hat{h} = \frac{1}{f_h} \log[Y\beta_h / \beta_e]. \quad (7b)$$

In Eq. (7a), ζ_e is an increasing function of the economic value of the population w and the efficiency of

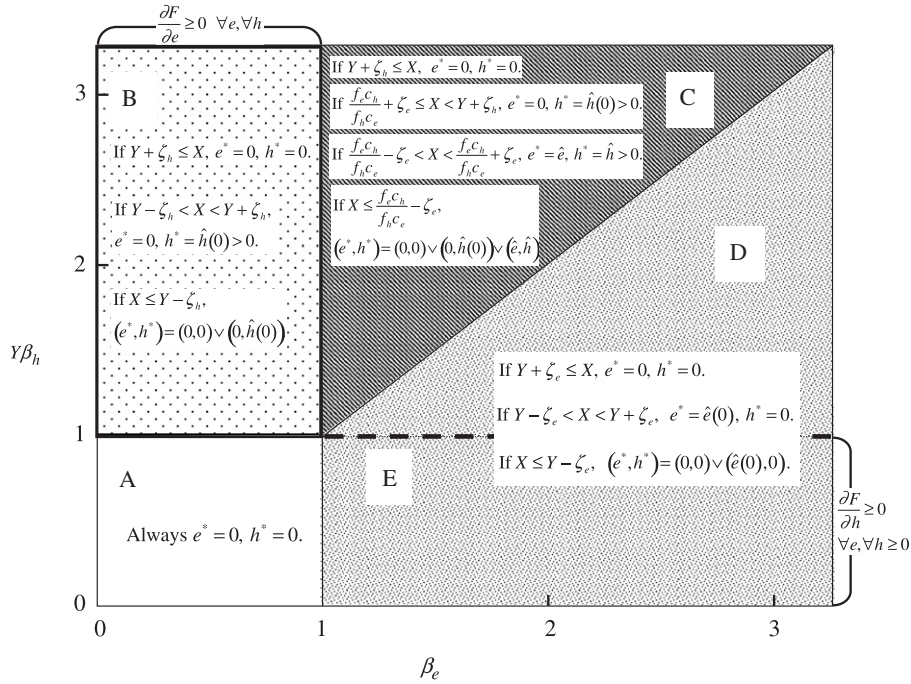


Fig. 2. The optimal resource-enhancement and extermination effort levels. The parameter space is divided into 5 regions based on the existence of extrema and the signs of the partial derivatives (see Appendix A).

resource-enhancement effort f_e , and a decreasing function of the cost of unit resource-enhancement effort c_e . ζ_e has a peak at an intermediate level of the variance of the noise σ_ξ^2 . Furthermore, in this region it cannot happen that $e^* > 0$ whereas $h^* = 0$ (see Appendix A). For small values of X we have to determine the values of e^* and h^* by comparing $F(0, 0)$, $F(0, \hat{h}(0))$, and $F(\hat{e}, \hat{h})$. The smallest value corresponds to the optimum.

In regions D and E, optimal extermination effort is zero, but resource-enhancement effort can be positive. In that case, e^* equals $\hat{e}(0)$, the e -value at which $F(e, 0)$ has its minimum:

$$\hat{e}(0) = \frac{1}{f_e}(Y - X + \zeta_e). \tag{8}$$

For low X -values, the optimal value of e is determined by comparing the values of $F(0, 0)$ and $F(\hat{e}(0), 0)$.

Now, from the summary of these results in Fig. 2, we can derive necessary conditions for $e^* > 0$ and for $h^* > 0$:

$$e^* > 0 \Rightarrow \beta_e > 1 \text{ and } X < \min \left\{ Y + \zeta_e, \frac{f_e c_h}{f_h c_e} + \zeta_e \right\},$$

$$h^* > 0 \Rightarrow Y \beta_h > \max(1, \beta_e) \text{ and } X < Y + \zeta_h, \tag{9a}$$

where ζ_h is an increasing function of the economic value of the population w and the efficiency of extermination effort f_h , and a decreasing function of the cost of unit extermination effort c_h . ζ_h has a peak at an intermediate level of the variance of the noise σ_ξ^2 . Furthermore, from Eq. (9a) we derive the necessary condition for both positive

effort levels as follows:

$$e^* > 0, h^* > 0 \Rightarrow X - \zeta_e < \frac{f_e c_h}{f_h c_e} < Y. \tag{9b}$$

This inequality implies that the both efforts become positive when (I) density of focal species, X is small, (II) effect of the alien species Y is large, and (III) ratio of cost-efficiency between resource-enhancement and extermination effort $f_e c_h / f_h c_e$ is moderate level.

Note that these conditions are not sufficient, because for very small X the boundary minimum of F may have a lower value than the solutions of $e^* > 0$ or $h^* > 0$. This corresponds to situations in which the density of the focal population is low and, accordingly, the risk of extinction and/or costs of necessary efforts are very high. As a consequence, it is not worth the effort of trying to conserve it anymore. We will refer to this set of X -values as the ‘hopeless zone’. When the conditions in Eq. (9a) hold, e^* can become zero due to this effect when

$$X < \max \left\{ Y - \zeta_e, \frac{f_e c_h}{f_h c_e} - \zeta_e \right\} \tag{10a}$$

and h^* can become zero when

$$X < \max \left\{ Y - \zeta_h, \frac{f_e c_h}{f_h c_e} - \zeta_e \right\}. \tag{10b}$$

However, the boundaries of the hopeless zone may lie much lower than these values. This can only be examined numerically (see the next section).

From Eq. (9a) we see that, regardless of X , e^* will be zero when β_e is smaller than one. From the definition given in Eq. (5), it follows that this happens when the value of the

focal population, w , is small compared to σ_ξ and/or when the ratio of cost to efficiency for resource-enhancement effort c_e/f_e is large. Similarly, Eq. (9a) states that extermination effort should be zero when w is small compared to σ_ξ , when the ratio of cost to efficiency for extermination effort c_h/f_h is large, or when Y is small, i.e. when the alien species has a very low density, or a low impact on the focal species. Furthermore, h^* becomes zero when the ratio $(f_e/c_e)/(f_h/c_h)$ is large compared to Y . $(f_e/c_e)/(f_h/c_h)$ is cost-to-effect ratio of resource-enhancement relative to that of extermination. Thus, if the efficiency of resource-enhancement is high compared to that of extermination, and if the effect of the alien species is small, no extermination effort should be adopted.

When X does not lie in the hopeless zone and β_e exceeds one, the optimal resource-enhancement effort level decreases with X and the cost of the effort, c_e , but increases with w . The optimal resource-enhancement effort has a peak at an intermediate value of the efficiency of the effort, f_e and environmental fluctuation σ_ξ . Further, as long as Y is smaller than β_e/β_h , and X satisfies the condition in Eq. (9a), e^* equals $\hat{e}(0)$ and increases with Y (see Eq. (8)). For larger values of Y , the optimal resource-enhancement effort level equals \hat{e} (see Eq. (7a)) which is independent of Y .

With respect to the optimal extermination level, h^* , we see from Eq. (9a) that the range where $h^* > 0$ increases when ζ_h increases, i.e. with increasing value of the population, w , efficiency of extermination, f_h/c_h , or the effect of the alien species, Y . ζ_h has a peak at an intermediate value of environmental fluctuation σ_ξ^2 . When both extermination and resource-enhancement effort are positive, h^* equals \hat{h} (cf. Eq. (7b)), which increases in Y , and in the ratio of efficiencies of extermination to that of resource-enhancement $\beta_h/\beta_e = (f_h/c_h)/(f_e/c_e)$. The optimal extermination effort has a peak at an intermediate value of the efficiency of the effort f_h and environmental fluctuation σ_ξ^2 .

4. Optimal efforts of resource-enhancement and extermination: numerical analysis

From the analytical results above, we can conclude that the optimal resource-enhancement and extermination levels depend on X , Y , w , σ_ξ^2 , f_e , f_h , c_e , and c_h . We will now explore these dependencies numerically.

4.1. Relationship between total cost and effort levels

Fig. 3a shows the parameter ranges in which resource-enhancement effort and extermination effort are positive or zero for a situation where $Y\beta_h > 1$. The horizontal axis indicates the cost per unit resource-enhancement effort c_e , and the vertical axis is the difference between the expected log-density of the focal species just before reproduction and the extinction threshold, X . Note that, for the chosen parameter values, the situation with $c_e < 0.625$ implies

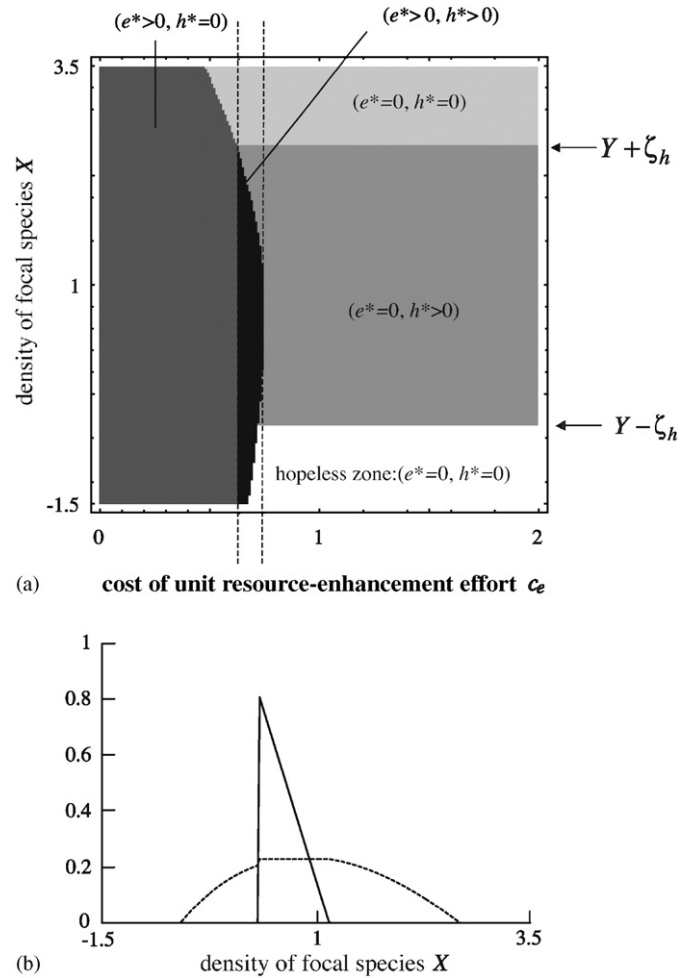


Fig. 3. (a) Parameter regions where optimal resource-enhancement or extermination efforts are positive. The horizontal axis indicates the cost per unit resource-enhancement effort. (b) The optimal resource-enhancement effort (solid lines), and the optimal extermination effort level (broken lines). Parameter values: $w = 5, f_e = 1, f_h = 0.8, c_h = 0.5, \sigma_\xi^2 = 7, Y = 1, c_e = 0.75$ in (b).

$Y\beta_h > \beta_e$, and hence this part corresponds to region D. When $c_e > 0.754, \beta_e < 1$ holds, which corresponds to region B. In-between these two lies region C. The boundaries are indicated by broken lines in Fig. 3a. The white part of the figure depicts the ‘hopeless zone’, where both resource-enhancement effort and extermination efforts are zero in the optimal strategy because it would cost too much to save the population.

Fig. 3b shows the relation between the optimal effort levels and the density of focal species, X , for the case that $c_e = 0.75$. The parameter combinations in Fig. 3b lie in region C. The area with low values of X corresponds to the hopeless zone ($e^* = h^* = 0$). We see that the optimal resource-enhancement effort (solid line) decreases with X . As long as $e^* > 0, h^*$ does not change with X (see also Eq. (7b)). $e^* = 0$ when $X \geq (f_h/c_h)/(f_e/c_e) + \zeta_e$. Note that the boundary for $e^* > 0$ depends on f_h/c_h implying that whether resource-enhancement effort should be adopted depends on the parameter of

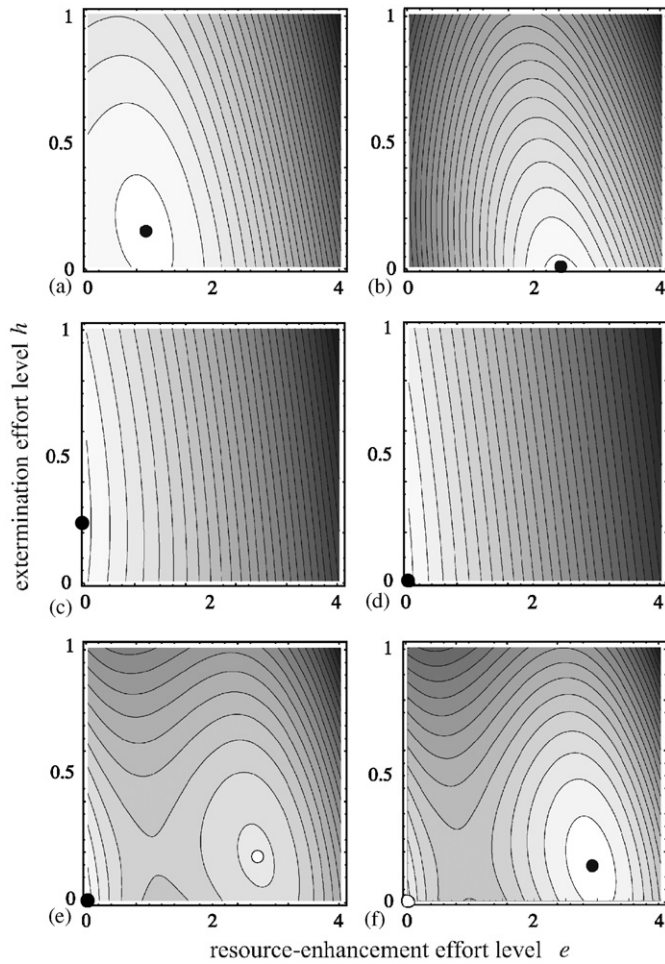


Fig. 4. Contour plots of total cost F . The vertical axis and horizontal axis indicate the extermination effort level and resource-enhancement effort level respectively. A darker shade indicates a higher total cost. Parameter values: $X = 1, c_e = 0.7$ in (a), $X = 1, c_e = 0.5$ in (b), $X = 1, c_e = 1.0$ in (c), $X = 3, c_e = 1.0$ in (d), $X = -1, c_e = 0.72$ in (e), and $X = -1, c_e = 0.7$ in (f). The other parameters are the same as in Fig. 3.

extermination efficiency. In contrast when $e^* = 0, h^*$ is no longer constant, but h^* decreases with X .

Fig. 4 shows the contour plots of total cost F as a function e and h , for specific points in Fig. 3a. The horizontal axis denotes the resource-enhancement effort and the vertical axis denotes the extermination effort. A darker shade indicates high total cost and black circle shows the global minimum of total cost.

Fig. 4a shows the situation with $X = 1$ and $c_e = 0.7$, which lies in region C. For this parameter combination, the total cost is minimized when both effort levels of resource-enhancement effort and extermination effort are positive, because the global minimum of F lies in the positive quadrant.

Fig. 4b shows the situation with $X = 1$ and $c_e = 0.5$, which lies in region D. In this case the total cost has a minimum in $e^* > 0$ but increases monotonically with extermination effort. Hence the optimal resource-enhance-

ment effort is positive, but the optimal extermination effort is zero.

In Fig. 4c, $X = 1$ and $c_e = 1$ and we are in region B. Here, the total cost has a minimum in $h^* > 0$ but increases monotonically with the resource-enhancement effort. Hence extermination effort is positive but resource-enhancement effort is zero at this optimum.

In Fig. 4d, $X = 3$ and $c_e = 1$, a point in region B in the light grey area of Fig. 3a. Here, total cost increases monotonically with resource-enhancement and with extermination effort. Hence optimal resource-enhancement and extermination efforts are both zero.

Fig. 4e shows the case where $X = -1$ and $c_e = 0.72$, which lies in the ‘hopeless zone’ of region C. There is the local minimum at a combination of efforts $e > 0$ or $h > 0$ (shown by a white circle), but the total cost attains its global minimum at $(e, h) = (0, 0)$.

Fig. 4f shows the case where $X = -1$ and $c_e = 0.7$. The total cost at a local minimum at a combination of efforts $e > 0$ or $h > 0$ (shown by a black circle) is smaller than the total at $(e, h) = (0, 0)$.

4.2. Parameter dependence of the optimal effort levels

We now examine the parameter dependence of the optimal strategy. Fig. 5 illustrates the optimal resource-enhancement effort e^* (solid line) and the optimal extermination effort (broken line) as functions of parameters $Y, w, \sigma_\xi^2, f_e, f_h, c_e,$ and c_h . In this section we briefly discuss the parameter dependences. A more detailed discussion including what regions in Fig. 2 is shown in Fig. 5 is given in Appendix C.

(a) Effect of the alien species Y :

The survivorship of focal species decreases with effect of the alien species Y . When Y is small, the survivorship of the native population should be improved by increasing the resource-enhancement effort e , because the extermination effort h does not have much effect. When Y is large, the optimal extermination effort h^* improves the survivorship until the density of the alien population becomes small. Hence h^* increases with Y . For large Y , the optimal resource-enhancement effort e^* is independent of Y . In this region e does not have much effect, because extinction risk is mainly determined by the density of the alien species.

(b) Economic value of the population w :

Either e^* or h^* increases with w . When the density of the alien population becomes small, h does not decrease the extinction probability. Hence in this case h^* becomes constant for large values of w .

(c) Variance of the environmental noise σ_ξ^2 :

Both e and h attain their optima at an intermediate value of σ_ξ^2 . When σ_ξ^2 is very large, extinction risk is mainly determined by the environment, so neither e nor h decrease the extinction probability effectively.

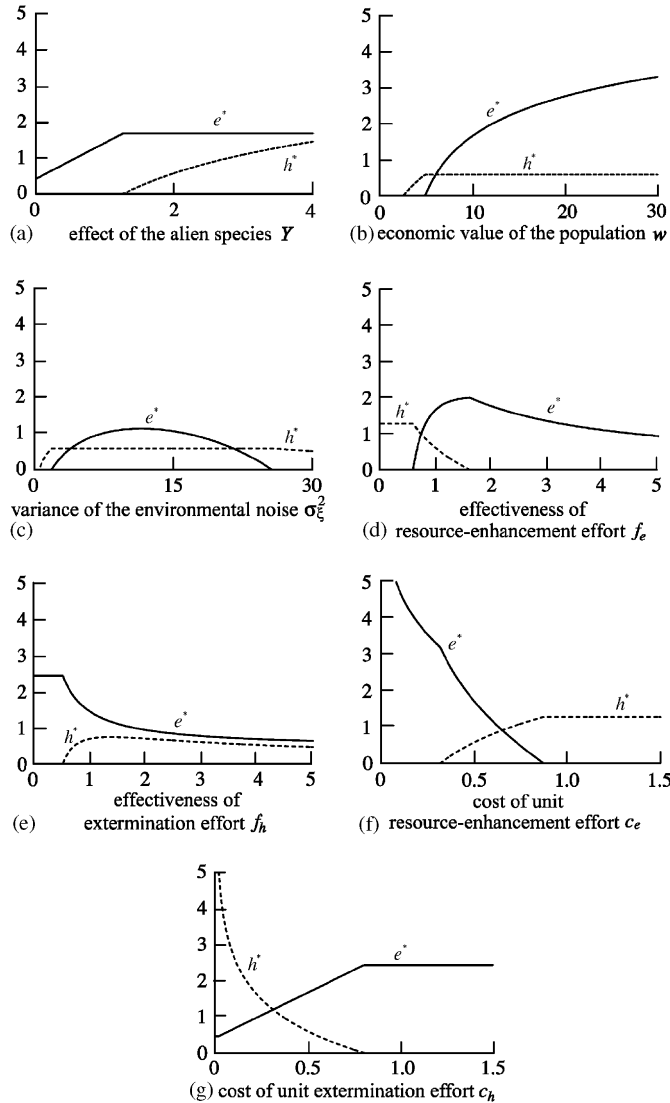


Fig. 5. The optimal resource-enhancement effort (solid lines), and the optimal extermination effort level (broken lines). The horizontal axis indicates (a) Y , (b) w , (c) σ_k^2 , (d) f_e , (e) f_h , (f) c_e , and (g) c_h . Parameter values: $w = 10$ (only in (d) $w = 7$), $X = 3.5$, $Y = 2$, $c_e = 0.5$. The other parameter values are the same as in Fig. 3.

- (d) *Effectiveness of resource-enhancement effort f_e :*
 h^* decreases with f_e . When e improves the survivorship of the native population effectively, we should increase e^* and decrease h^* .
- (e) *Effectiveness of extermination effort f_h :*
 e^* decreases with f_h . When h decreases the density of the alien population more effectively, we should increase h^* and decrease e^* . However since increases in h do not have much effect once the density of the alien species becomes low, at that point investment in e may be needed.
- (f) *Cost of unit resource-enhancement effort c_e :*
 When we need much cost to invest in e , e^* is small. Hence as c_e increases, h^* replaces e^* to keep the extinction probability low.

- (g) *Cost of unit extermination effort c_h :*
 When it costs much to exterminate the alien population, h^* is small. Hence when c_h increases, we should enhance the resource availability of the native population instead of extermination.

5. Uncertainty concerning the impact of the alien species

So far, we have assumed that the magnitude of the influence of the alien species, k , is fixed and known. In general, however, an accurate knowledge is not available. In this section we examine the optimal efforts for situations where k is a random variable.

Specifically we assume that the probability distribution of k is a uniform distribution with mean μ and variance σ_k^2 , and that k and ξ are independent. Note that, for harmful alien species, k should be positive. We restricted the values of σ_k^2 is less than $\mu/3$ so that k is not negative.

Fig. 6 illustrates how the optimal levels of resource-enhancement effort (solid line) and extermination effort (broken line) change with σ_k^2 . Fig. 6a shows that the

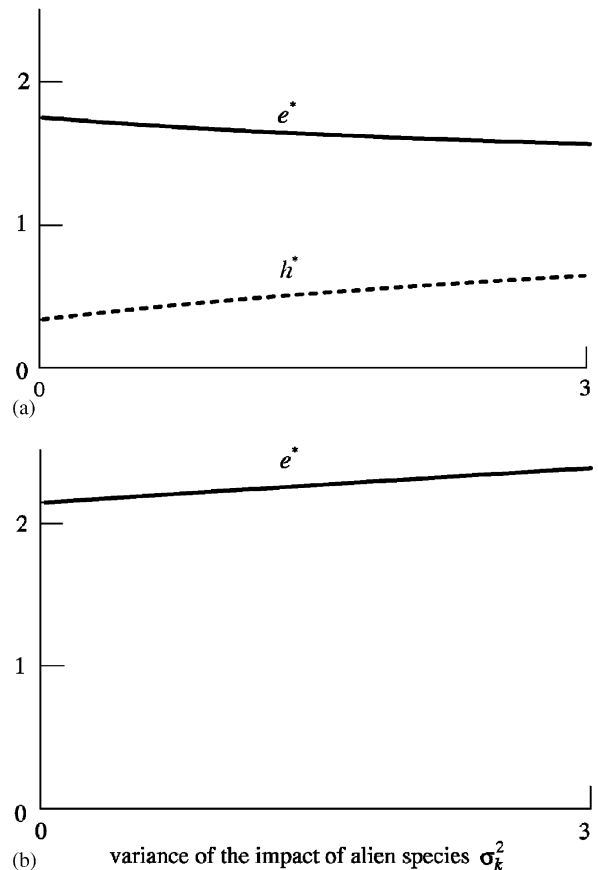


Fig. 6. Dependence of the optimal resource-enhancement effort and extermination effort on uncertainty of influence of the alien population. The solid line indicates the optimal resource-enhancement effort, and the dashed line the optimal extermination effort level. Parameter values: $w = 8$, $X = 3.5$, $f_e = 1.5$, $c_e = 0.5$, $M_0 = 1$, $\mu = 3$, $a_e = 0.5$, $c_h = 0.5$ in (a) and $c_h = 1.5$ in (b). The other parameter values are the same as in Fig. 3.

optimal extermination effort increases with σ_k^2 , whereas the optimal resource-enhancement effort decreases with σ_k^2 . For large σ_k^2 , investing in extermination effort is important, because it diminishes the effect of large k -values, which may drive the focal population to extinction. Fig. 6b shows the situation for large costs of extermination: here $c_h = 1.5$; whereas $c_h = 0.5$ in Fig. 6a. In this case the optimal effort of extermination is zero, and the optimal effort of resource-enhancement increases with σ_k^2 . Now, we should invest more effort in resource-enhancement when the influence of the alien species is highly uncertain, because the extinction probability becomes high. Decreasing the efficiency of extermination has the same effect as increasing its costs (results not shown).

These results show that we should invest more effort in extermination of alien species than in providing resources for the focal species when the uncertainty of the influence of an alien species is large, as long as the optimal strategy is to invest in both. If, however, the optimal extermination effort becomes zero due to large costs and/or low efficiency, we should increase the resource-enhancement effort, to cope with increasing uncertainty of the influence of an alien species.

6. Discussion

We studied the choice of effort of providing food and shelter (resource-enhancement effort) and the effort of suppressing an alien species (extermination effort) to increase survivorship of a focal species in fluctuating environments. The optimal levels of these efforts minimize the total cost defined as the weighted sum of extinction probability and economic costs.

We found that, when both efforts are positive, the optimal resource-enhancement effort depends on the economic value of the population and the density of the focal population, but is independent of the density of the alien population (cf. Eqs. (7a) and (7b)). In the same situation the optimal extermination effort, on the contrary, depends neither on the value of the population nor on the density of the focal population. This result implies that if, due to some unexpected event, the density of the focal species decreases, we should increase only resource-enhancement effort but should keep the extermination level unchanged. In contrast, if for some reason the density of the alien species increases, we should increase the extermination effort, but keep resource-enhancement effort constant.

Concerning whether each of these two kinds of efforts is positive or zero, we have the following conclusion: From Eqs. (7a) and (7b) we see that both the resource-enhancement and extermination effort are positive when $\beta_e/\beta_h = f_e c_h / f_h c_e$ is neither too small nor too large. If one type of the efforts has a very low cost or high effectiveness compared to the other, we should invest only in that type.

Necessary conditions for positive resource-enhancement and extermination efforts are given in Eq. (9a). For low

values of the focal population density, the population is “doomed” and investing in any effort to save the population is not feasible. The upper boundaries for this ‘hopeless zone’ are given in Eqs. (10a) and (10b).

Our numerical analysis further indicates (cf. Fig. 5) that the optimal effort level of resource-enhancement e^* increases with the value of the population (w), the effect of the alien species (Y), and the cost of extermination (c_h). Whereas the increase of e^* with w is monotone, the increase with Y and c_h stops at some point, after which the optimal resource-enhancement level e^* is constant. The optimal resource-enhancement effort decreases with efficiency of extermination (f_h) and the cost of resource-enhancement (c_e). The dependency of e^* on environmental variance (σ_ξ^2) and on the efficiency of resource-enhancement (f_e), however, is not monotonic: e^* attains the maximum at intermediate levels of these parameters. The optimal extermination level h^* increases with Y , w , and c_e . For the latter two parameters (w and c_e), h^* becomes constant after a certain point. h^* decreases with f_e and c_h . It initially increases with σ_ξ^2 and f_h , but shows a slow decline at large values of these parameters.

Next we examined the case in which the magnitude of the impact of the alien species is uncertain. In most situations this parameter is likely to be unknown. Our results show that the ratio of optimal extermination effort to optimal resource-enhancement effort (h^*/e^*) increases with uncertainty of the influence of the alien species, as long as extermination effort is positive ($h^* > 0$). This can be explained by the fact that the harmful effect of the uncertainty in the impact of the alien species can be eliminated effectively by an increased extermination effort. The initial density of an alien population just after invasion is often small, but if its impact is unknown, the extermination effort may be more desirable than effort of resource-enhancement.

In previous papers (Yokomizo et al., 2003a, 2004), we analysed the optimal resource-enhancement effort over multiple years, which minimizes the weighted sum of extinction probability of a focal population and the economic cost of conservation practice. When the conservation period is longer than a single year, resource-enhancement effort in a given year not only reduces the extinction probability in that year, but also contributes to an increase in the density of the focal population afterwards. In the current paper we focus on the problem of a single year only. If we consider the management over a longer period, investing in more extermination effort in the first year can also reduce the density of the alien species in later years. In cases where we can exterminate the alien population completely, we do not need to invest extermination effort in the future. It may be important to exterminate an alien population in the initial stage, right after its invasion. If the alien species is a predator of a native species, its population may increase in the following years in response to a prey increase due to the

resource-enhancement effort. Sinclair et al. (1998) point out that the nature of predation may play a crucial role in the dynamics. Thus, considering multiple-year optimization of resource-enhancement and extermination effort levels will give us a useful insight into the conservation management of focal species jeopardized by alien species. This is an important subject of future theoretical research.

In this study, we did not consider uncertainty in the population size of the native and alien populations. In Yokomizo et al. (2003b, 2004), we considered situations where the size of the native population is not accurately known, and we calculated the optimal monitoring effort, which improves the accuracy of such information. In practice, we often do not have perfect information on the densities of the focal or alien populations, and having more accurate knowledge about the densities of both populations is important for the success of conservation. Thus, another important generalization of the current simple model is to include monitoring effort.

In this paper we assumed that value of the population w has been determined. We can determine this value in several ways (a more detailed explanation is in Yokomizo et al., 2004). One potential method is to determine w based on past conservation policy made by society. An alternative method is to calculate the economic value of the population directly using a contingent valuation method (Jakobsson and Dragun, 2001).

There are several other possible extensions of our model. Sabo (2005) showed that fluctuation of predator populations can strongly affect viability of the native population. Our model could be generalized to include such effects. We also did not consider any time delays for resource enhancement effort to take effect and situations in which an alien species decreases the survivorship of native population before the extermination effort. Our study should be considered as a first step towards a general theoretical study on the optimal management strategies for saving focal populations in the presence of other species.

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Appendix A. Derivation of optimal resource-enhancement and extermination effort levels and the condition where optimal effort levels are positive.

From Eqs. (6a) and (6b), we can derive that

$$\begin{aligned} \text{when } \beta_e \leq 1, \quad \frac{\partial F}{\partial e} \geq 0 \quad \forall e, \quad \forall h \geq 0, \\ \text{when } Y\beta_h \leq 1, \quad \frac{\partial F}{\partial h} \geq 0 \quad \forall e, \quad \forall h \geq 0 \end{aligned} \tag{A.1}$$

and when $\beta_e > 1$ and $Y\beta_h > 1$, F has two extrema, at (\tilde{e}, \hat{h}) and (\hat{e}, \hat{h}) , with

$$\tilde{e} = \frac{1}{f_e} (-X + f_e c_h / f_h c_e - \zeta_e), \tag{A.2a}$$

$$\hat{e} = \frac{1}{f_e} (-X + f_e c_h / f_h c_e + \zeta_e), \tag{A.2b}$$

$$\hat{h} = \frac{1}{f_h} \log[Y\beta_h / \beta_e]. \tag{A.2c}$$

In Appendix B it is shown that the extremum at (\hat{e}, \hat{h}) is a minimum.

We are looking for the minimum of F , under the constraints $e \geq 0$ and $h \geq 0$. We will denote this constrained minimum by (e^*, h^*) . A necessary condition for the constrained minimum to be internal is that (\hat{e}, \hat{h}) exists and lies within the considered quadrant of the (e, h) plane. From Eq. (A.2) we can derive:

$$\begin{aligned} \hat{e} > 0 \wedge \hat{h} > 0 & \quad \text{if and only if,} \\ \beta_e > 1, \quad Y\beta_h > 1, \quad Y\beta_h > \beta_e, \quad X < f_e c_h / f_h c_e + \zeta_e. \end{aligned} \tag{A.3}$$

In all other cases, either $e^* = 0$ or $h^* = 0$. To examine this further, we first note that on the basis of the previous results, it is convenient to distinguish the following situations (see Fig. 2 in the main text):

$$\begin{aligned} A : \beta_e \leq 1 \text{ and } Y\beta_h \leq 1, \\ B : \beta_e \leq 1 \text{ and } Y\beta_h > 1, \\ C : \beta_e > 1 \text{ and } Y\beta_h > 1 \text{ and } Y\beta_h > \beta_e, \\ D : \beta_e > 1 \text{ and } Y\beta_h > 1 \text{ and } Y\beta_h \leq \beta_e, \\ E : \beta_e > 1 \text{ and } Y\beta_h \leq 1. \end{aligned} \tag{A.4}$$

We now consider these different sets. First note that from Eq. (A.1) we can conclude that in region A $e^* = h^* = 0$. Further it follows from these equations that in region B, $e^* = 0$. From Eq. (6b), it can be derived that

$$\left. \frac{\partial F}{\partial h} \right|_{e=0} > 0 \text{ if } (Ye^{-f_h h} - X)^2 + 2\sigma_\zeta^2(f_h h - \log Y\beta_h) > 0. \tag{A.5}$$

Let $g_1(h) = (Ye^{-f_h h} - X)^2$ and $g_2(h) = 2\sigma_\zeta^2(f_h h - \log Y\beta_h)$. It is easy to see that $g_2(h)$ increases in h , and furthermore

$$g_1'(h) > 0 \text{ if } h > \frac{1}{f_h} \log \frac{Y}{X}. \tag{A.6}$$

Thus, $g_1(h)$ increases for all $h \geq 0$ if $X > Y$. Otherwise this function has a minimum in $h_{\min} = (1/f_h) \log(Y/X)$, with value $g_1(h_{\min}) = 0$. Furthermore note that

$$\begin{aligned} g_1(0) + g_2(0) < 0 & \quad \text{if } Y - \zeta_h < X < Y + \zeta_h, \\ & \geq 0 \quad \text{otherwise.} \end{aligned} \tag{A.7}$$

We can conclude that

if $X \geq Y + \zeta_h$:
 $g_1(h) + g_2(h) \geq 0 \quad \forall h \geq 0 \Rightarrow F(0, h)$ increases in h . (A.8a)

if $Y \leq X < Y + \zeta_h$:
 $g_1(0) + g_2(0) < 0, g_1'(h) + g_2'(h) > 0$
 $\Rightarrow F(0, h)$ has a maximum at $\hat{h}(0) > 0$. (A.8b)

Note: We use the notation $\hat{h}(0)$ to denote the place where $F(0, h)$ has its minimum. We will not derive an explicit expression for this value.

if $Y - \zeta_h < X < Y + \zeta_h$:
 $g_1(0) + g_2(0) < 0, g_1(h) + g_2(h)$ has a minimum at some $h \geq 0$ with a value less than 0, and increases for h – value.
 $\Rightarrow F'(0, h)$ changes from negative to positive at a value of $h > 0$
 $\Rightarrow F(0, h)$ has a minimum at $\hat{h}(0) > 0$ (A.9a)

if $X \leq Y - \zeta_h$:
 $g_1(0) + g_2(0) \geq 0, g_1(h) + g_2(h)$ has a minimum with value $2\sigma_{\zeta}^2 \left(\log \frac{Y}{X} - \log Y\beta_h \right)$. (A.9b)

In the latter case, depending on the combination of parameter values, there are two possibilities:

if $\frac{1}{\beta_h} < X < Y - \zeta_h$:
 $F(0, h)$ has a maximum at $\hat{h}(0) > 0$ and a minimum at $\hat{h}(0) > 0$. (A.10a)

if $X \leq \frac{1}{\beta_h} \leq Y - \zeta_h$ or $X \leq Y - \zeta_h < \frac{1}{\beta_h}$:
 $F(0, h)$ increases in h . (A.10b)

We can conclude that in region B: $e^* = 0$, and

$X \geq Y + \zeta_h \Rightarrow h^* = 0,$
 $Y - \zeta_h < X < Y + \zeta_h \Rightarrow h^* > 0.$ (A.11)

When $X \leq Y - \zeta_h, h^*$ is determined by comparing the values of $F(0, 0)$ and $F(0, \hat{h}(0))$. When $F(0, 0)$ is the smallest, $h^* = 0$, otherwise it equals $\hat{h}(0)$.

We now turn to region E. From Eq. (A.1) it follows that in this region $h^* = 0$. From Eq. (6a) we can derive that

$\frac{\partial F}{\partial e} \Big|_{h=0} < 0$ for $\tilde{e}(0) < e < \hat{e}(0),$
 ≥ 0 otherwise, (A.12)

where $\tilde{e}(0) = (Y - X - \zeta_e)/f_e$ and $\hat{e}(0) = (Y - X + \zeta_e)/f_e$.

Thus, $F(e, 0)$ has a maximum in $\tilde{e}(0)$ and a minimum in $\hat{e}(0)$. From Eq. (A.12) we can conclude

if $Y - \zeta_e < X < Y + \zeta_e, \tilde{e}(0) < 0 \wedge \hat{e}(0) > 0$
 $\Rightarrow e^* = \hat{e}(0) > 0,$ (A.13a)

if $X \geq Y + \zeta_e, \tilde{e}(0) < 0 \wedge \hat{e}(0) \leq 0$
 $\Rightarrow e^* = 0,$ (A.13b)

if $X \leq Y - \zeta_e, \tilde{e}(0) \geq 0 \wedge \hat{e}(0) > 0.$ (A.13c)

In the last case, e^* can be 0 or positive, depending on which value is the largest: $F(0, 0)$ or $F(\hat{e}(0), 0)$.

We now turn to region D. In this region (\hat{e}, \hat{h}) exists. However, note that in this region e^* and h^* cannot both be positive, since that can only happen when this extremum lies in the positive quadrant and, as we can see from Eq. (A.2c) $\hat{h} < 0$ in this region. Thus, at least one of the optimal efforts must be zero. Furthermore, from Eq. (6b) we can derive that

$\frac{\partial F}{\partial h} \Big|_{e=0} = 0$ when $\Phi(-X + Ye^{-f_h h}) = \frac{c_h}{f_h Ywe^{-f_h h(0)}}.$ (A.14)

Substituting this in the other partial derivative Eq. (6a) we find

$\frac{\partial F}{\partial e} \Big|_{e=0} = -\frac{f_e c_h}{f_h Y e^{-f_h h}} + c_e$ (A.15)

and from this it can be derived that

$\frac{\partial F}{\partial e} \Big|_{e=0} > 0$ if $Y\beta_h e^{-f_h h} > \beta_e.$ (A.16)

Thus, since $Y\beta_h \leq \beta_e, F(e, h)$ decreases in e at the point $e = 0$ for all $h \geq 0$. This implies that the combination $e^* = 0, h^* > 0$ cannot occur in region D. The only remaining possibilities are $e^* = 0$ and $h^* = 0$ or $e^* > 0$ and $h^* = 0$. Thus we only have to look at $F(e, 0)$. As a consequence, the conclusions for this region are the same as for region E.

Finally we consider region C. From Eq. (A.3) we see that this is the only region where \hat{e} and \hat{h} can both be positive. Thus, here we may have situations where both e^* and h^* are larger than zero. Furthermore, from Eqs. (6b) and (8) we can derive

$\frac{\partial F}{\partial h} \Big|_{e=\hat{e}(0), h=0} = -w\Phi(-\zeta_e)Yf_h + c_h$ (A.17)

and it can straightforwardly be shown that this is negative when $Y\beta_h > \beta_e$. Therefore, in region C the combination $e^* > 0$ and $h^* = 0$ cannot occur. The only three possibilities are $e^* = 0$ and $h^* = 0, e^* = 0$ and $h^* > 0,$ or both e^* and h^* positive. Furthermore, note that in this region

$\frac{f_e c_h}{f_h c_e} + \zeta_e < Y + \zeta_h.$ (A.18)

From Eq. (7a) we see that, when $(f_e c_h / f_h c_e) + \zeta_e \leq X$, (\hat{e}, \hat{h}) does not lie in the positive quadrant. Hence e^* and h^* cannot both be positive in this situation. The remaining possibility is that $e^* = 0$, whereas h^* can be larger than or equal to zero. This can be determined by considering $F(0, h)$. From Eq. (A.8a) it therefore follows that

$$\text{if } X \geq Y + \zeta_h, \quad e^* = 0, \quad h^* = 0 \tag{A.19}$$

and from Eqs. (A.8b) and (A.9a):

$$\frac{f_e c_h}{f_h c_e} + \zeta_e \leq X < Y + \zeta_h, \quad e^* = 0, \quad h^* = \hat{h}(0) > 0. \tag{A.20}$$

Further, from Eqs. (A.2a) and (A.2b) we see that

$$\begin{aligned} \text{when } \frac{f_e c_h}{f_h c_e} - \zeta_e < X < \frac{f_e c_h}{f_h c_e} + \zeta_e, \quad \tilde{e} < 0 \wedge \hat{e}(0) > 0 \\ \Rightarrow e^* = \hat{e} > 0, \quad h^* = \hat{h} > 0. \end{aligned} \tag{A.21}$$

When $X \leq f_e c_h / f_h c_e - \zeta_e$, we have to determine the values of e^* and h^* by comparing $F(0, 0)$, $F(0, \hat{h}(0))$, and $F(\hat{e}, \hat{h})$.

Appendix B. Proof that a local minimum exists at \hat{e} and \hat{h}

First, we check that the optimal resource-enhancement effort in Eq. (A.2b) extermination effort in Eq. (A.2c) are local minimum using Hessian matrix. The Hessian matrix H of $F(e, h)$ is defined as

$$H = \begin{pmatrix} \frac{\partial^2 F}{\partial e^2} & \frac{\partial^2 F}{\partial e \partial h} \\ \frac{\partial^2 F}{\partial e \partial h} & \frac{\partial^2 F}{\partial h^2} \end{pmatrix}.$$

We must show the following two inequalities to prove the both optimal efforts minimize the total cost:

$$(I) \quad \frac{\partial^2 F}{\partial e^2} \frac{\partial^2 F}{\partial h^2} - \left(\frac{\partial^2 F}{\partial e \partial h} \right)^2 > 0, \tag{B.1}$$

$$(II) \quad \frac{\partial^2 F}{\partial e^2} + \frac{\partial^2 F}{\partial h^2} > 0. \tag{B.2}$$

$$\begin{aligned} \frac{\partial^2 F}{\partial e^2} \frac{\partial^2 F}{\partial h^2} - \left(\frac{\partial^2 F}{\partial e \partial h} \right)^2 &= \frac{w f_h f_e^2}{\sigma_\xi^2} (\Phi(-X - f_e e \\ &+ Y \exp[-f_h h]))^2 (X + f_e e - Y \exp[-f_h h]). \end{aligned}$$

$$\begin{aligned} \frac{\partial^2 F}{\partial e^2} + \frac{\partial^2 F}{\partial h^2} &= w \Phi(-X - f_e e + Y \exp[-f_h h]) \\ &\times \frac{(X + f_e e - Y \exp[-f_h h]) f_e^2}{\sigma_\xi^2} \\ &+ w Y \exp[-f_h h] f_h^2 \Phi(-X - f_e e + Y \exp[-f_h h]) \\ &\times \left\{ \left(\frac{(X + f_e e - Y \exp[-f_h h])}{\sigma_\xi^2} Y \exp[-f_h h] \right) + 1 \right\}. \end{aligned}$$

Since $X + f_e e - Y \exp[-f_h h] = \zeta_e > 0$ at $e = \hat{e}$ and $h = \hat{h}$, Eqs. (B.1) and (B.2) are satisfied. We can conclude that the point (\hat{e}, \hat{h}) corresponds to a local minimum.

In addition, an extremum (\tilde{e}, \hat{h}) corresponds to a local maximum because $(\partial^2 F / \partial e^2)(\partial^2 F / \partial h^2) - (\partial^2 F / \partial e \partial h)^2 < 0$ in which $X + f_e e - Y \exp[-f_h h] = -\zeta_e < 0$ at $e = \tilde{e}$ and $h = \hat{h}$.

Appendix C

C.1. Effect of the alien species Y

Fig. 5a illustrates how the optimal effort levels depend on the decrease in the log-density of the focal species due to the alien species. We chose the parameter set such that $\beta_e > 1$. Thus, when Y is smaller than β_e / β_h , we are in regions D or E. In this case, $Y - \zeta_e < X < Y + \zeta_e$ holds, and $e^* > 0$ and $h^* = 0$. When Y is small, the optimal resource-enhancement effort level $\hat{e}(0)$ is proportional to Y . When Y is larger than β_e / β_h , we reach region C. For the chosen parameter set, $f_e c_h / f_h c_e - \zeta_e < X < f_e c_h / f_h c_e + \zeta_e$. Hence both e^* and h^* are positive. As long as $h^* > 0$, e^* is independent of Y . When Y is large, h^* is much larger than e^* (values not shown in the figure).

C.2. Value of the population w

Fig. 5b illustrates the relation between the optimal effort levels and the (economic) value of the population. We chose the parameter set such that $\beta_e < Y \beta_h$ at any w . Hence, we are in region A, B or C depending on w . If w is small so that $\beta_e < Y \beta_h \leq 1$, we are in region A and no investment in e or h should be made. When $Y \beta_h > 1$ and $\beta_e \leq 1$, h^* increases with w , but e^* is zero, because $Y - \zeta_h < X < Y + \zeta_h$ holds. When w increases, then we reach the situation where $\beta_e > 1$, and e^* becomes positive, because $f_e c_h / f_h c_e - \zeta_e < X < f_e c_h / f_h c_e + \zeta_e$. From that point onwards, h^* is constant, and independent of the value of the population (see Eq. (7b)).

Note that if $Y \beta_h \leq \beta_e$, h^* is zero for any value of w . In that case, we are in regions E or D. e^* is given by Eq. (8) and increases with w .

C.3. Variance of the environmental noise σ_ξ^2

Fig. 5c illustrates the dependence of the optimal effort levels on the variance of the environmental noise. Here, since we chose the parameter set such that $Y \beta_h > \beta_e$, results for regions B and C hold. ζ_e and ζ_h attain their maxima at an intermediate value of σ_ξ^2 . When σ_ξ^2 is small, we are in region C and $Y + \zeta_h \leq X$ is satisfied and both optimal efforts are zero. At larger values of σ_ξ^2 , we reach the situation where $f_e c_h / f_h c_e + \zeta_e \leq X < Y + \zeta_h$, and h^* becomes positive. As σ_ξ^2 increases further, $f_e c_h / f_h c_e + \zeta_e$ becomes larger than X , and the $e^* > 0$ and $h^* > 0$. However, at large values of σ_ξ^2 , β_e becomes less than one. This brings us back to the situation where $h^* > 0$ and $e^* = 0$. Thus, e^* has a peak at an intermediate level of σ_ξ^2 . As long as $e^* > 0$, h^* is independent of σ_ξ^2 (see Eq. (7b)).

In summary, when the environmental variance is very small, the population is relatively safe. Hence we do not need to invest much in e or in h . In contrast when the environmental variance is very large, e does not affect extinction probability effectively. This is why e^* has a maximum at a moderately large variance of the environmental noise. This finding was reported also by Yokomizo et al. (2003a, b, 2004), who studied a situation without species interaction. On the other hand, h^* is not affected very strongly by σ_ξ^2 . At very high values, it starts to decrease slowly.

C.4. Effectiveness of resource-enhancement effort f_e

Fig. 5d illustrates the relation between the optimal effort levels and the effectiveness of e . Because we chose the parameter set such that $Y\beta_h > 1$, results for regions B–D hold. When f_e is small, $\beta_e < 1$ holds, and $Y - \zeta_h < X < Y + \zeta_h$ satisfied. Hence (see results for region B, Fig. 2) $h^* > 0$, but $e^* = 0$. As long as $e^* = 0$, h^* is independent of f_e . When f_e increases, we reach the situation where $\beta_e > 1$ and $Y\beta_h > \beta_e$, and we enter region C. In the considered case, $f_e c_h / f_h c_e - \zeta_e < X < f_e c_h / f_h c_e + \zeta_e$ is also satisfied. Hence e^* and h^* are positive. From Eq. (7b) we see that h^* decreases with f_e .

At larger values of f_e , $Y\beta_h \leq \beta_e$ holds, and we reach region D. In region D, $h^* = 0$. Since $Y - \zeta_e < X < Y + \zeta_e$ is satisfied, $e^* > 0$ at very large values of f_e . e^* has a peak at an intermediate level of f_e . This result shows that, when e is not effective, e is replaced by h .

C.5. Effectiveness of extermination effort f_h

Fig. 5e shows how the optimal effort levels depend on the effectiveness of h . Here since we chose the parameter set satisfying $\beta_e > 1$, results for regions C–E hold. When f_h is so small that $Y\beta_h \leq \beta_e$, we are in regions D or E, and $h^* = 0$. In this case, $Y - \zeta_e < X < Y + \zeta_e$ is satisfied. Hence $e^* > 0$. This implies that, if we cannot exterminate the alien species efficiently, we should invest in e . When f_h is so large that $Y\beta_h > \beta_e$, we are in region C. Since $f_e c_h / f_h c_e - \zeta_e < X < f_e c_h / f_h c_e + \zeta_e$, $e^* > 0$ and $h^* > 0$. When h becomes more effective, h^* initially increases but then gradually decreases with f_h for a very large f_h .

C.6. Cost of unit resource-enhancement effort c_e

The dependence of the optimal effort levels on cost of unit resource-enhancement effort is shown in Fig. 5f. Here because we chose the parameter set such that $Y\beta_h > 1$, results for regions B–D holds. When c_e is small, $Y\beta_h \leq \beta_e$ and $Y - \zeta_e < X < Y + \zeta_e$ are satisfied. Hence only e^* should be positive (cf. results for region D, see Fig. 2). β_e and ζ_e are both decreasing functions of c_e . When c_e increases, $Y\beta_h > \beta_e$ is satisfied and we reach region C. Initially, $f_e c_h / f_h c_e - \zeta_e < X < f_e c_h / f_h c_e + \zeta_e$ is satisfied. Then e^* and h^* are both positive. When c_e becomes very large, $\beta_e \leq 1$,

and only e^* is positive. Thus, if it costs much to improve the survivorship of the focal species by e , we should mitigate extinction risk by exterminating the alien species.

C.7. Cost of unit extermination effort c_h

Fig. 5g indicates the dependence of the optimal effort levels on the cost of unit extermination effort. Since we chose the parameter set such that $\beta_e > 1$, results for regions C and D hold. When c_h is small, $Y\beta_h > \beta_e$ and $f_e c_h / f_h c_e - \zeta_e < X < f_e c_h / f_h c_e + \zeta_e$ are satisfied. Then both of e^* and h^* are positive. In this case e^* increases with c_h . When c_h increases further, however, we reach the situation where $Y\beta_h \leq \beta_e$, and $Y - \zeta_e < X < Y + \zeta_e$, and only e^* is positive. From that moment on, e^* becomes independent of c_h .

Thus, if extermination involves large costs (c_h is large), h^* is replaced by e^* , i.e. if h involves large costs, we should instead improve the survivorship of the focal population by enhancing their resource availability.

References

- Arriaga, L., Castellanos, A.E., Moreno, E., Alarcon, J., 2004. Potential ecological distribution of alien invasive species and risk assessment: a case study of buffel grass in arid regions of Mexico. *Conserv. Biol.* 18, 1504–1514.
- Bretagnolle, V., Inchausti, P., 2005. Modelling population reinforcement at a large spatial scale as a conservation strategy for the declining little bustard (*Tetrax tetrax*) in agricultural habitats. *Anim. Conserv.* 8, 59–68.
- Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson, I.A.E., Seastedt, T.R., Williamson, M., Chornesky, E., Hayes, D., 2002. Directing research to reduce the impacts of nonindigenous species. *Conserv. Biol.* 16, 630–640.
- Caughley, G., Gunn, A., 1995. Conservation biology in theory and practice. Blackwell Science, Massachusetts, (459pp.).
- Diamond, J.M., 1989. Conservation biology 900 kiwis and a dog. *Nature*, 338, 544.
- Goergen, E., Daehler, C.C., 2001. Reproductive ecology of a native Hawaiian grass (*Heteropogon contortus*; poaceae) versus its invasive alien competitor (*Pennisetum setaceum*; poaceae). *Int. J. Plant Sci.* 162, 317–326.
- Hastings, A., Hall, R.J., Taylor, C.M., in press. A simple approach to optimal control of invasive species. *Theor. Popul. Biol.*, in press.
- Higgins, S.L., Richardson, D.M., Cowling, R.M., 2000. Using a dynamic landscape model for planning the management of alien plant invasions. *Ecol. Appl.* 10, 1833–1848.
- Hone, J., 1994. Analysis of Vertebrate Pest Control. Cambridge University Press, New York, (270pp.).
- Jakobsson, K.M., Dragun, A.K., 2001. The worth of a possum: valuing species with the contingent valuation method. *Environ. Resour. Econ.* 19, 211–227.
- Kus, B.E., 1998. Use of restored riparian habitat by the endangered Least Bell's Vireo (*Vireo bellii pusillus*). *Restoration Ecol.* 6, 75–82.
- Kus, B.E., 1999. Impacts of brown-headed cowbird parasitism on productivity of the endangered Least Bell's Vireo. *Stud. Avian Biol.* 18, 160–166.
- Ruiz, G.M., Carlton, J., 2003. Invasive Species: Vectors and Management Strategies. Island Press, Washington, (484pp.).
- Sabo, J.L., 2005. Stochasticity, predator-prey dynamics, and trigger harvest of nonnative predators. *Ecology* 86, 2329–2343.
- Sinclair, A.R.E., Pech, R.P., Dickman, C.R., Hik, D., Mahon, P., Newsome, A.E., 1998. Predicting effects of predation on conservation of endangered prey. *Conserv. Biol.* 12, 564–575.

- Taylor, C.M., Hastings, A., 2004. Finding optimal control strategies for invasive species: a density-structured model for *Spartina alterniflora*. *J. Appl. Ecol.* 41, 1049–1057.
- Travis, J.M.J., Park, K.J., 2004. Spatial structure and the control of invasive alien species. *Anim. Conserv.* 7, 321–330.
- Williamson, L., 1996. *Biological invasions*. Chapman & Hall, London, (256pp.).
- Yokomizo, H., Yamashita, J., Iwasa, Y., 2003a. Optimal conservation effort for a population in a stochastic environment. *J. Theor. Biol.* 220, 215–231.
- Yokomizo, H., Haccou, P., Iwasa, Y., 2003b. Conservation Effort and Assessment of Population Size in Fluctuating Environments. *J. Theor. Biol.* 224, 167–182.
- Yokomizo, H., Haccou, P., Iwasa, Y., 2004. Multiple-year optimization of conservation effort and monitoring effort for a fluctuating population. *J. Theor. Biol.* 230, 157–171.
- Watson, J., Warman, C., Todd, D., Laboudallon, V., 1992. The Seychelles magpie robin *Copsychus sechellarum*: ecology and conservation of an endangered species. *Biol. Conserv.* 61, 93–106.