Eradicating down the food chain: optimal multispecies eradication schedules for a commonly encountered invaded island ecosystem

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Summary

1. Islands are global hotspots of both biodiversity and extinction. Invasive species are a primary threat, and the majority of islands have been invaded by more than one. Multispecies eradications are essential for conserving the biodiversity of these islands, but experience has shown that eradicating species at the wrong time can be disastrous for endemic species.

2. Managers not only have to decide how to eradicate each invasive species, they need to determine when to target each species, and how to control multiple species with a limited budget. We use dynamic control theory to show that, when resources are limited, species should be eradicated in a particular order (an eradication schedule). We focus on a common invaded island ecosystem motif, where one invasive predator consumes two prey species (one endemic, one invasive), and managers wish to eradicate both invasives while ensuring the persistence of the endemic species. We identify the optimal eradication schedule for this entire class of problem. To illustrate the application of our solution, we also analyse a particular case study from California’s Channel Islands.

3. For any island ecosystem that shares this motif, managers should begin by allocating all of their resources towards invasive predator control. Only later should resources be shifted towards controlling the invasive prey. This shift should ideally be gradual, but an abrupt shift is very close to optimal. The Channel Islands case study confirms these findings. Targeting both species simultaneously is substantially suboptimal.

4. We reach the robust conclusion that the same eradication schedule should be applied to any island with this ecosystem motif, even if the ecosystem contains different species to the Channel Islands case study.

5. Synthesis and applications. Although very numerous, the world’s invaded island ecosystems could be described by a limited range of invaded ecosystem motifs. By calculating robust optimal eradication schedules for each motif, the approach defined in this study could offer rapid decision-support for a large number of future conservation projects where specific data are scarce.

Key-words: alien invasive species, decision theory, introduced species, optimal control strategy

Introduction

Islands have high levels of both endemism and threat, a combination that has led to their consistent identification as global conservation priorities (Myers et al. 2000; Kreft et al. 2008; Kier et al. 2009). The introduction of invasive species to islands, especially foxes, cats, rodents and ungulates, has already caused many extinctions and represents a major ongoing threat (Blackburn et al. 2004; Vié, Hilton-Taylor & Stuart 2009; Nogales et al. 2013). Removing these invasive species can help avoid extinctions on islands (Brooke, Hilton & Martins 2007; Aguirre-Muñoz et al. 2008; Nogales et al. 2013). Island eradications deliver high return on investment because their relatively small area increases the probability of eradication success.
and their isolation ensures that re-invasion will be rare (Harris et al. 2011). As a result, island eradications have improved the viability of threatened species in a number of documented projects (McGeoch et al. 2010).

Many islands have been invaded by more than one species, and managers often target multiple species for eradication. Among islands where eradications have taken place, 39% targeted more than one species (Fig. 1a; DIHSE 2015). Additionally, the majority of successful species eradications (54%) occurred on islands where multiple species have been eradicated. Except in cases where all the invasive species can be targeted by the same control method (e.g. poison baiting that controls all rodent species), multispecies eradications generally proceed with one species being eradicated after another. Such prioritized eradication may be able to remove multiple invaders, but it can also have undesired consequences through altered community interactions, or ‘trophic cascades’ (Courchamp, Chapuis & Pascal 2003; Innes & Saunders 2011). For example, removing invasive predators can often lead to a rapid increase of invasive herbivores and a decline in native vegetation (Bergstrom et al. 2009), or an increase in mesopredator abundance and a decrease in endemic prey density (Rayner et al. 2007).

The eradication of invasive herbivores can increase the abundance of invasive plants, which can outcompete native plant species (Atkinson 1996). The removal of an invasive prey species can temporarily increase consumption of an endemic prey species due to prey switching (Courchamp, Chapuis & Pascal 2003).

To avoid such undesirable consequences (Courchamp, Chapuis & Pascal 2003) conservation theorists originally proposed that the eradication of multiple species should be undertaken at the same time (a ‘simultaneous’ approach), on the assumption that this would prohibit any invasive species taking advantage of the removal of another (Zavala-ta, Hobbs & Mooney 2001; Caut et al. 2007; Griffiths 2011; Innes & Saunders 2011; Glen et al. 2013). However, more recent publications have proposed a “trophically strategic” approach (Morrison 2007), whereby eradications are prioritised in a particular sequence that minimises undesired consequences (Morrison 2007, 2011; Innes & Saunders 2011; Glen et al. 2013). There are a number of reasons for trophically strategic approaches. First, the same remoteness that makes islands attractive from an eradication perspective makes them difficult and expensive projects (Courchamp, Chapuis & Pascal 2003; Martins et al. 2006). Simultaneous eradication will place heavy demands on eradication projects that already face the logistical challenges of limited budgets, trained staff and transport. Secondly, simultaneous eradication may be suboptimal even when it is affordable and feasible. For example, if two invasive competitors are controlled simultaneously, the inferior invasive competitor’s population can actually increase if competitive release is sufficiently strong (Caut et al. 2007; Glen et al. 2013). Alternatively, an endangered endemic species might gain the greatest benefit from the rapid removal of its most immediate threatening invasive. Finally, trophically strategic eradications could theoretically make later eradication less difficult or less expensive, if the remaining invasive species become more vulnerable to control (Morrison 2011).

Simultaneous and trophically strategic approaches are extreme examples of ‘eradication schedules’, which describe how finite management resources are distributed through time to the various species being targeted. A schedule defines not just a single decision, but a series of decisions taken in a particular order. While a number of previous studies have contrasted different approaches to multispecies eradications (Courchamp, Langlais & Sugihara 1999; Roemer, Donlan & Courchamp 2002; Courchamp, Woodroffe & Roemer 2003; Fan, Kuang & Feng 2005; Tompkins & Veltman 2006; Zhang, Fan & Kuang 2006; Caut et al. 2007; Russell et al. 2009), they do not consider eradication schedules. First, these analyses do not allow the proportion of funding allocated to each invasive species to change dynamically, instead assuming a constant allocation to each species. Secondly, none of these analyses incorporate the fundamental trade-off in multispecies management: allocating more resources to one invasive species leaves fewer resources for the others.

![Fig. 1.](http://eradicationsdb.fos.auckland.ac.nz) (a) Frequency distribution of the number of species eradicated from 884 islands documented in the Database of Island Invasive Species Eradications (http://eradicationsdb.fos.auckland.ac.nz). Circular marker indicates the number of islands where managers have attempted to eradicate multiple species. (b) General interaction structure (‘motif’) of the invaded three-species ecosystem. Arrows indicate consumption: an endemic prey species is consumed by an invasive predator, which also preys upon an invasive prey species.

Finally, previous analyses only compare a limited number of allocation decisions, which are proposed a priori by the authors. As a result, we cannot be sure that the best option tested is in fact optimal, and we are very unlikely to identify the optimal solution if it is counter-intuitive.

In this study, we outline flexible methods that can identify optimal multispecies eradication schedules with a finite, limited budget, without making any a priori assumptions about the form of the optimal schedule. We apply these methods to invaded island ecosystems that have a particular interaction structure: an ecosystem motif (sensu Milo 2002). The particular ecosystem motif that we consider contains an endemic and an invasive prey species, which are both consumed by an invasive predator (Fig. 1b). We are particularly interested in whether the optimal eradication schedules for this ecosystem motif have consistent and robust features — that is, whether managers should always take the same approach to eradications — since these could provide guidance for managers working on eradication projects where information about the species and the ecosystem is limited. Specifically, we assess whether a tropically strategic approach exists for this ecosystem motif, where the eradication of a particular invasive species should always be prioritized. We then investigate a parameterized case study of this motif from California’s Channel Islands (Roemer, Donlan & Courchamp 2002; Courchamp, Woodroffe & Roemer 2003). We use this example to study the optimal schedule more closely, and to contrast the optimal multispecies eradication schedule with reasonable heuristic approaches (i.e. rules of thumb).

Materials and methods

A multispecies eradication schedule is defined by the amount of resources spent on different eradication actions at each point in time during the project. Throughout this work, we will assume that a different, best-practice control action has been established for each of the invasive species. We thus focus on islands where the target species cannot be controlled by the same method. Managers are faced with a finite annual budget, and at each point in time, they must choose to spend a proportion of that budget on the control action for one invasive species. The remaining budget is automatically allocated towards the other invasive species.

We illustrate our analyses with the Courchamp, Woodroffe & Roemer (2003) Channel Islands case study, where managers aim to remove populations of an invasive predator, the golden eagle Aquila chrysaetos, and an invasive prey species, feral pigs Sus scrofa, while trying to conserve a population of endemic island foxes Urocyon littoralis. This example clearly illustrates the difficulties involved in multispecies eradications, since the removal of either invasive species will have negative effects on island ecosystem. This parameterized example is only one realization of a more general invaded ecosystem motif (Fig. 1b), where an island that is home to a threatened endemic prey population has been invaded by both a predator and prey species, but where the two prey species do not directly interact. We therefore first consider the optimal eradication schedule for this general invaded ecosystem motif.

MANAGEMENT PROBLEM FOR THE GENERAL ECOSYSTEM MOTIF

Our three-species ecosystem motif comprises two prey species and one predator. One prey species is endemic, with abundance $N_i(t)$ at time $t$; the other prey species and the predator are invasive with abundances denoted $N(t)$ and $P(t)$, respectively. The two prey species do not directly compete, but influence each other indirectly because both are consumed by the predator. Management must distribute a constrained annual budget, $b$, between controlling the predator, $u(t)$, and controlling the invasive prey, $1−u(t)$. This formulation allows the budget to be shared between the two control actions using a single time-dependent ‘control function’, $0≤u(t)≤1$. Note that $u(t)$ allows managers to control only one of the species [if $u(t)=1$ or $u(t)=0$]. The control function therefore defines the allocation schedule and captures the trade-offs associated with a limited management budget.

The ecosystem in Fig. 1b can be described by three coupled differential equations, as defined and explained in Courchamp, Woodroffe & Roemer (2003) and Roemer, Donlan & Courchamp (2002):

$$\frac{dN_i}{dt} = r_iN_i \left[1 - \frac{N_i}{K_i} \right] - m_i \frac{N_i}{\phi N_e + N_i} PNe \quad \text{Eqn 1a}$$

$$\frac{dN}{dt} = r_N \left[1 - \frac{N_i}{K_i} \right] - m_i \frac{N_i}{\phi N_e + N_i} PN_e - \frac{b}{c_N} \left[1 - e^{-\left(1-u(t)\right)t}\right] N_i \quad \text{Eqn 1b}$$

$$\frac{dP}{dt} = \frac{P\left(m_e \phi N_e^2 + m_e \phi N_e^2 \right)}{\phi N_e + N_i} - \theta P - \frac{b}{c_P} \left[1 - e^{-\left(1-u(t)\right)t}\right] P \quad \text{Eqn 1c}$$

where $r_i$ and $r_N$ give the intrinsic growth rates; $m_i$ and $m_e$ indicate the predator attack rates; and $\phi$ and $v$ measure the conversion of consumed prey into new predators. In each case, the subscript refers to either the endemic (e) or the invasive (i) prey species. The rate of natural predator mortality is given by $\theta$. The parameter $\phi$ measures the predator’s preference for the different prey types, with $\phi$-values that are less than one indicating a preference for the invasive prey and $\phi$-values that are larger than one indicating a preference for the endemic prey. The final terms in eqn 1b and 1c incorporate resource-limited invasive control into the equation system of Courchamp, Woodroffe & Roemer (2003) using the control function $u(t)$. The total management budget is denoted $b$, and the parameters $c_N$ and $c_P$ indicate the per-unit-control cost of the two actions, for example the cost per hour of aerial shooting, or the cost of purchasing and distributing poison baits. Finally, $\phi_e$ and $\phi_i$ range between zero and one and indicate the rate at which control spending increases towards its maximum effectiveness, for predator and prey control, respectively. For example, doubling the control effort on a given species does not double the proportion of animals removed (i.e. ‘diminishing returns’). For large $\phi$ values, only small proportions of the annual control budget are needed for the control efforts to be maximally effective.

Managers want to identify the optimal eradication schedule, denoted $u^*(t)$. When substituted into eqn 1a−c, this schedule ensures the eradication of both invasive species, but also leaves
the population of threatened endemic prey with the highest possible abundance at the end of the project at time $T$:

$$\max_{0 \leq u(t) \leq 1} N_e(T), \text{ subject to } N_e(T) < 1 \text{ and } P(T) < 1$$  \hspace{1cm} \text{Eqn 2}

We solve for $u^*(t)$ by applying Matlab’s constrained optimization function `fmincon` (Matlab 2012). The eradication schedule is a continuous function, but `fmincon` optimizes over a finite number of control points. We therefore begin by defining an ordered set of 12 equally spaced control points $0 \leq y_i \leq 1$, $i = 1, \ldots, 12$ (additional control points slowed the search process without changing the results). The ‘interior-point’ algorithm of `fmincon` then proposes values for $y_i$, which we turn into a continuous function, $u(t)$ by linear interpolation. This $u(t)$ is used to solve the ecosystem equations (eqn 1a–c) using the forward Euler method, with the three populations initialized at their equilibrium abundances, which we find by solving for the steady state of eqn 1a–c when no eradication efforts are taking place (i.e. $b = 0$). Equation 2 is used to assess the performance of different sets of control points, and `fmincon` automatically searches for the best set of control points, which give $u^*(t)$. Finally, we ensure that the method always converges to the same optimal schedule when we repeat the search from 10 different random initial locations.

**CALCULATING OPTIMAL ERADICATION SCHEDULES FOR THE GENERAL MOTIF**

The values of the ecological and management parameters (Table 1) will depend on the particulars of the eradication project, including the identity of the invasive and endemic species, the island’s location, terrain and environmental conditions. The optimal eradication schedule $u^*(t)$ will therefore also be different for each eradication project. However, different parameter sets may still produce optimal eradication schedules with consistent qualitative features, since the optimal schedule results from the shared ecosystem motif, as well as its parameterization. Such robust qualitative features could represent the ‘trophically strategic’ approaches hypothesized by Morrison (2011) and would help guide management for multispecies island eradications that share the same ecosystem motif, but where data are scarce.

We therefore apply methods inspired by qualitative modelling (Levins 1974; Dambacher, Li & Rossignol 2003; Raymond et al. 2011), to identify a trophically strategic eradication schedule for any management problem that fits our general ecosystem motif. There are two steps in this process. First, we generate 2 million randomly parameterized ecosystem models that are constrained only by the structure of our ecosystem motif (Fig. 1b). Each of these ecosystem models is described by eqn 1a–c, but with a different combination of parameter values, which are selected at random from wide, uniform distributions. To ensure that we can generate almost any realization of our ecosystem motif, we make very few assumptions about the value of these parameters, and where possible choose their bounds to be as wide as possible, informed by the existing literature. The population growth rates are chosen between $0.07 \leq r_e \leq 6.26$ and $0.32 \leq r_i \leq 4.71$, which encompass the growth rates of endemic and invasive species observed in the literature (Hone 1999; Hone, Duncan & Forsyth 2010). The attack rate for each prey species is selected independently and is allowed to vary between very infrequent and frequent ($0.01 \leq m_e, m_i \leq 0.1$). We allow the prey preference parameter to vary substantially, allowing either the invasive or the endemic prey species to be a strongly preferred target of the invasive predator, as well as for the predator to be indifferent ($0.1 \leq \phi \leq 10$). The invasive predator’s conversion efficiency and natural mortality rates are based on the ranges observed by liter-

### Table 1. Parameter values for eqn 1a–c. Point estimates are for the Channel Islands case study; parameter ranges are used for the qualitative modelling

<table>
<thead>
<tr>
<th>Ecological parameters</th>
<th>Description</th>
<th>Channel Islands</th>
<th>Bounds used for qualitative modelling</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r_e$ and $r_i$</td>
<td>Intrinsic growth rate of the endemic ($r_e$) and invasive ($r_i$) prey populations</td>
<td>$r_e = 0.32$</td>
<td>$0.07 \leq r_e \leq 6.26$</td>
</tr>
<tr>
<td>$K_e$ and $K_i$</td>
<td>Habitat carrying capacity of endemic ($K_e$) and invasive ($K_i$) prey populations</td>
<td>$K_e = 1544$</td>
<td>$10^2 \leq K_e \leq 10^5$</td>
</tr>
<tr>
<td>$m_e$ and $m_i$</td>
<td>Predator attack rate on endemic ($m_e$) and invasive ($m_i$) prey.</td>
<td>$m_e = 0.086$</td>
<td>$0.01 \leq m_e \leq 0.1$</td>
</tr>
<tr>
<td>$e_e$ and $e_i$</td>
<td>Conversion efficiency of endemic ($e_e$) and invasive ($e_i$) prey.</td>
<td>$e_e = 7.7 \times 10^{-4}$</td>
<td>$0.05 \leq e_e \leq 0.2$</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Natural death rate of the predator</td>
<td>$\theta = 0.09$</td>
<td>$0.01 \leq \theta \leq 0.5$</td>
</tr>
<tr>
<td>$\phi$</td>
<td>Preference of the predator for the endemic prey species</td>
<td>$\phi = 8.1$</td>
<td>$0.1 \leq \phi \leq 10$</td>
</tr>
<tr>
<td>$N_e(0)$</td>
<td>Initial abundance of the three species.</td>
<td>$N_e(0) = 154$</td>
<td>Populations begin at their equilibrium levels</td>
</tr>
<tr>
<td>$N_i(0)$</td>
<td></td>
<td>$N_i(0) = 7561$</td>
<td></td>
</tr>
<tr>
<td>$P(0)$</td>
<td></td>
<td>$P(0) = 25$</td>
<td></td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Management parameters</th>
<th>Description</th>
<th>Value for the channel Islands example</th>
<th>Bounds used for qualitative modelling</th>
</tr>
</thead>
<tbody>
<tr>
<td>$c_N$ and $c_P$</td>
<td>Cost of applying a unit of control effort to the invasive prey ($c_N$) and predator ($c_P$) populations.</td>
<td>$c_N = $100 k</td>
<td>$50 k \leq c_N \leq 150 k$</td>
</tr>
<tr>
<td>$c_N$ and $c_P$</td>
<td>Rate at which control efforts approach maximum effectiveness for prey ($g_N$) and predator ($g_P$) control.</td>
<td>$c_P = $100 k</td>
<td>$50 k \leq c_P \leq 150 k$</td>
</tr>
</tbody>
</table>

Eradicating multiple species from islands

ature reviews (Ricklefs & Miller 1999), 0.05 ≤ ε ≤ 0.2; 0.01 ≤ b ≤ 0.5, although we note that the Channel Islands case study falls slightly outside this range. The carrying capacities of both prey species (Kp and Ks) are selected independently and at random from the range 10^2 to 10^5. We also randomly vary the per-unit cost of the control actions and the rate at which control spending increases in effectiveness, between wide but arbitrary bounds: 0.2 ≤ α_p/α_p ≤ 1.0 and $50 000 ≤ c_P/c_P ≤ $150 000. The annual budget, b, needs to vary between the different parameter sets, since high growth rates and large costs would put eradication beyond the reach of smaller budgets. To ensure that the randomly generated ecosystems are comparable, we choose b at a level that allows both species to be eradicated within the length of time it would take the endemic species to recover from 1% to 90% (T = 6.8/r_p). A randomly generated ecosystem model is only considered in our analyses if all three species can persist (with more than one individual) at equilibrium, in the absence of any eradication efforts (i.e. with b = 0 in eqn 1a–c; Raymond et al. 2011).

The second step is to identify the eradication schedule that satisfies eqn 2 for each of these random ecosystems. We compare the resulting optimal eradication schedules to ascertain whether they approach the eradication in a consistent manner. In particular, we determine whether the optimal funding allocation changes across the project timeline or whether it is constant. If the allocation does change through time, we assess whether the species are eradicated in a consistent, trophically strategic order, and whether the funding allocation between species changes gradually (i.e. there was a period of time when managers were spending resources on both species) or abruptly (i.e. a strictly sequential allocation).

CALCULATING OPTIMAL ERADICATION SCHEDULES FOR THE CHANNEL ISLANDS CASE STUDY

We construct the optimal eradication schedule for the parameterization given for the Channel Islands study, which involves invasive golden eagles, feral pigs and endemic island foxes. Roemer, Donlan & Cournachamp (2002) and Courchamp, Woodroffe & Roemer (2003) provide estimates for each of the key ecological parameters (Table 1), and we choose arbitrary values for the management parameters because information on per capita control costs and the rate at which control spending increases in effectiveness are unavailable. We assume that the unit cost of the different control actions, c_N and c_P, is equal. Capturing and translocating golden eagles is much more difficult than shooting feral pigs (Roemer, Donlan & Courchamp 2002), and these parameter values mean the initial per capita cost of eagle removal is two orders of magnitude larger than the per capita cost of pig removal (due to the much lower abundance of eagles). We assume the rate at which control spending on either eradication action increases in effectiveness to be the same for the two species (α_p = α_p = 0.75). For these α values, allocating half the budget towards either species removes more than half as many individuals as the entire budget (31%, compared with 52%). Given these cost parameters, we choose a budget that is sufficient to eradicate both the pig and eagle populations within 5 years; the approximate time frame of the Santa Cruz eradication (Morrison 2007). For robustness, we repeat the analyses for budgets that are 50% and 150% of this level. The three populations are initialized at their 2003 levels (Table 1).

After calculating the optimal eradication schedule, we estimate its relative performance in comparison with two sets of reasonable alternatives. Performance is measured by the number of foxes present in the final year of the project, but if either invasive species persists, we consider the performance to equal zero. First, we calculate the performance of constant proportional allocation strategies. These assign a constant proportion u(t) = u_P of the available budget to the eagle population, and the remaining 1 – u_P to pigs, throughout the eradication project. We allow u_P to vary between 0 and 1 in increments of 0.01. Secondly, we calculate the performance of the full range of strictly sequential strategies. Strictly sequential allocation strategies are simple schedules that allocate 100% of the control budget towards one invasive species for a set period of time (0 ≤ t < τ), after which resources are shifted entirely to controlling the other species for the remainder of the project (τ ≤ t ≤ T). The variable τ indicates the point in time when resources are switched from one species to the other. We search through all possible values of τ between 0 and T in increments of 0.1, for both prey-first and predator-first control.

Results

OPTIMAL ERADICATION SCHEDULE FOR THE ECOSYSTEM MOTIF

Of the 2 million random ecosystems generated, the vast majority resulted in one or more of the species rapidly going extinct without any management intervention needed. For example, some parameter sets created endemic prey species with very low growth rates (r_p ≪ 1) that were preferred or commonly attacked by the predator (φ ≫ 1, or m_e ≫ m_i), and so were driven to extinction. These unfeasible ecosystems do not reflect our motif (which we know contains populations of all three species). Nevertheless, we found more than 15 000 where all three species persisted at equilibrium. For each of these ecosystems, we were always able to find a unique optimal eradication schedule that maximized endemic prey numbers, while eradicating both invasive species. These optimal schedules displayed strong and consistent qualitative features, revealing a robust, trophically strategic approach to multispecies eradication for this motif (Fig. 2). This involved the allocation of the majority of control resources towards the invasive predator (i.e. u(t) ≈ 1) for the first 20% of the eradication project. More than 95% of optimal eradication schedules were still allocating almost all of their resources (>99%) towards predator control by the end of the first year. After this initial period, funding was gradually reallocated towards the invasive prey. The optimal schedules often finish the project by spreading control efforts across both invasive species, rather than transferring all the resources to the invasive prey species. The budget allocation proportions at the end of the project varied considerably between the randomly generated ecosystems, but generally allocated between 75% and 100% of the budget to controlling the invasive prey species.

For each random ecosystem model, we also calculated the best strictly sequential eradication strategy, where species are eradicated one by one. Unsurprisingly (given the optimal solution), the predator-then-prey sequence performed
much better than the prey-then-predator sequence. The best predator-then-prey strictly sequential strategy delivered essentially optimal performance, delivering final endemic prey populations that were within 1% of the optimal solution for 98% of the randomly generated ecosystems.

OPTIMAL ERADICATION SCHEDULE FOR THE CHANNEL ISLANDS CASE STUDY

Eradication on the Channel Islands was best approached using the same trophically strategic approach identified for the general ecosystem motif (Fig. 3). All available resources should initially be spent on the control of golden eagles, for just over a year, and thereafter managers should gradually reallocate resources towards feral pig control. After three years, we expect that the eagle population will have been eradicated and so resources should thereafter only be spent on controlling pigs. This decision – to initially ignore the pig population in favour of controlling eagles – allows the population of pigs to grow at the start of the control programme. Although this increase makes pig eradication more difficult, the lower predation pressure allows the fox population to recover as rapidly as possible. The gradual shift of resources away from eagle control is optimal for two related reasons. First, some eagle control needs to continue so that the population is unable to recover and jeopardize both eagle eradication and fox recovery. Secondly, control efforts do not deliver constant marginal benefits, which means management is more efficient, per-dollar, when less is being spent on a given species. Splitting control efforts is therefore generally more cost-effective than targeting one species at a time. Each of these conclusions is robust under all three budget sizes tested (see Fig. S1, Supporting information).

In addition to calculating the optimal eradication schedule for the Channel Islands case study, we determined the relative performance of a series of simple heuristic approaches to multispecies eradication, including all possible proportional and strictly sequential management options. Constant proportional strategies were often unable to eradicate both species. For 61% of the allocation proportions $u_P$ that were tested, either one or both species remained extant by the end of the project. The proportional allocation strategy that best satisfies the management objective (eradication of pigs and eagles;
maximum terminal fox abundance) allocates 34% of the budget to pig control each year and the remaining 66% towards eagles. While this strategy performs the best among all proportional allocations, it compares poorly to the optimal eradication schedule, delivering a 31% smaller fox population at the terminal time.

There are two possible strictly sequential approaches to the Channel Islands case study: controlling pigs first and eagles second and controlling eagles first and pigs second. The first set of options always delivers poor outcomes, since the decision to initially target pigs exposes the fox population to very high levels of eagle predation. The second set of sequential strategies performs much better than the first, particularly the switching times that most closely approximate the optimal solution. The best time to switch from eagle control to pig control is \( t = 1.8 \) years – approximately the time at which the optimal eradication schedule has shifted the majority of funding to pigs (Fig. 3). The resulting fox population after the 5 years for this sequential allocation is within 1% of the fox population achieved by applying the optimal eradication schedule (Fig. S1).

**Discussion**

For our general ecosystem motif, it is always best to begin a multispecies eradication project by directing initial resources towards controlling the invasive predator population until it is significantly reduced; only then should control efforts shift towards the invasive prey species. Near-optimal results can be achieved if managers target the species in sequence, eradicating the predator population first and the invasive prey second.

When facing island ecosystems that have been invaded by multiple species, managers can either prioritize particular species for control, or attempt to eradicate all of the species simultaneously. A simultaneous approach has been justified with the argument that detrimental ecosystem interactions (e.g. trophic cascades) are best avoided by dealing with all species at once. However, such an approach overlooks two crucial factors. First, because conservation budgets are constrained, attempts to manage all species at once result in each receiving less control (with the exception of situations where all species are targeted with the same control action). The best outcomes in conservation are almost always achieved through prioritization (Myers et al. 2000; Bottrill et al. 2008; Kreft et al. 2008; Kier et al. 2009). To paraphrase Friedrich the Great, the manager who tries to eradicate everything, eradicates nothing. Secondly, some combinations of invasive species cause more damage to threatened ecosystems and species than others (Caut et al. 2007; Collins, Latta & Roemer 2009; Raymond et al. 2011). In our case study for example, foxes are more threatened by the presence of eagles alone, than by pigs alone, or by both eagles and pigs. Prioritized eradications give managers the flexibility to be trophically strategic, for example, to expose native species to less harmful combinations of invasive species.

The results for the Channel Islands case study reflected the general motif. Managers should begin by spending their entire effort on controlling the population of golden eagles first, before gradually shifting the effort towards the eradication of pigs. Previous analyses of the Channel Islands ecosystem could not determine how eradication should proceed if resources were limited, since targeting either eagles or pigs first would produce undesirable consequences (Courchamp, Woodroffe & Roemer 2003; Collins, Latta & Roemer 2009). Approximating the gradual optimal solution with a strict sequence of eradications – first eagles and then pigs – produces outcomes that are effectively indistinguishable from the optimal solution. This approximation is an attractive rule of thumb and should be used in preference to the more gradual optimal solution, since a strict sequence will be more straightforward to implement than a continuous transition and will likely be more robust to stochasticity in the population dynamics and control effort. We note that the optimal solution is still useful to know, because it allows us to verify the effectiveness of the simple rule of thumb. Since a lengthy search period is required before eradication can be declared, the rule of thumb suggests that eradication of the prey species should begin once predator control (rather than search effort) ceases.

While our results will hold for any ecosystem that shares the qualitative structure shown in Fig. 1a, they still depend on a set of assumptions. We based our model of the invaded ecosystem motif on the case study on the Channel Islands described by Courchamp, Woodroffe & Roemer (2003), which uses a three-species model. Clearly, these three species are only the most directly relevant of the many species present on these islands. In fact, the population viability of the endemic island fox has also been approached using an ecosystem model that contained native skunks (Roemer, Donlan & Courchamp 2002). The presence of additional and dynamically important species (endemic or invasive) could alter our recommendations. Our optimization methods are flexible enough to incorporate additional species, but there is always a risk that the introduction of additional dynamical variables (in this case, species) will create problems with predictability and sensitivity to initial conditions. In addition to parametric uncertainty, the structure of our model (e.g. the logistic functional form of the intrinsic prey growth functions) is uncertain, although it is based on ecologists’ best understanding of the population dynamics. It is possible that different functional forms for the population equations will result in very different dynamics (see Wood & Thomas 1999 for an extreme example) and thus a different optimal allocation schedule. Similarly, although islands are relatively small ecosystems, their dynamics are internally heterogeneous (Rayner et al. 2007), a structural difference that could be included in future analyses. Finally, our model does not consider the influence of stochasticity in either the population dynamics or the control effectiveness. A deterministic model (eqn 1a–c) can be considered as the average outcome of a
stochastic system, but further analysis will be required to assess whether our general deterministic eradication schedule is robust to stochasticity.

The qualitative form of our optimal control schedule (Fig. 2) is independent of the model’s economic and ecological parameterization. The priority given to predator eradication is not the result of the predator’s preference for the endemic prey species, how fast its population grows, or how expensive it is to control. Our conclusions are therefore unaffected by the parametric uncertainty that is common to ecological management questions (Regan, Colyvan & Burgman 2002), and a decision about which species to target first for eradication can therefore be taken without additional information. Our findings result only from the qualitative structure of the interaction network and from the form of the objective function. Any multispecies eradication project that shares these two qualities will therefore also share the general form of the optimal eradication schedule. As a consequence, our conclusions are applicable to also share the general form of the optimal eradication schedule. Any multispecies eradication project that shares these two qualities will therefore also share the general form of the optimal eradication schedule. Any multispecies eradication project that shares these two qualities will therefore also share the general form of the optimal eradication schedule.

Our general methods – qualitative modelling ideas applied to the control of dynamical systems – could readily be applied to the control of different invaded ecosystem motifs. Important and common motifs include islands that contain a single endemic prey species and two invasive predators (e.g. seabirds, rats and mice; Caut et al. 2007), or an invasive super-predator, an invasive mesopredator and an endemic prey (Courchamp, Chapuis & Pascal 2003; Le Corre 2008). These two motifs are common to a great number of invaded islands across the globe (Le Corre 2008). A small number of common invaded ecosystem motifs would likely describe a large proportion of the world’s invaded islands. Conservation managers require broad guidelines on how to approach invaded island ecosystems when simultaneous eradication is not possible and information is scarce (Possingham et al. 2001; Le Corre 2008). A taxonomy of the most common ecosystem motifs and a matching set of qualitative optimal eradication schedules would be a valuable contribution to the theory of island conservation.

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Data accessibility

Data have not been archived because this article does not contain data.

References


Eradicating multiple species from islands


Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Optimal eradication schedules for the Channel Islands case study, for three different eradication budgets.