TITLE: Placing invasive species management in a spatiotemporal context

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Abstract

Invasive species are a worldwide issue, both ecologically and economically. A large body of work focuses on various aspects of invasive species control, including how to allocate control effort to eradicate an invasive population as cost-effectively as possible. There are a diverse range of invasive species management problems, and past mathematical analyses generally focus on isolated examples, making it hard to identify and understand parallels between the different contexts. In this paper we use a single spatiotemporal model to tackle the problem of allocating control effort for invasive species when supressing an island invasive species, and for long-term spatial suppression projects. Using feral cat suppression as an illustrative example, we identify the optimal resource allocation for island and mainland suppression projects. Our results demonstrate how using a single model to solve different problems reveals similar characteristics of the solutions in different scenarios. As well as illustrating the insights offered by linking problems through a spatiotemporal model, we also derive novel and practically applicable results for our case studies. For temporal suppression projects on islands, we find that lengthy projects are more cost-effective and that rapid control projects are only economically cost-effective when population growth rates are high or diminishing returns on control effort are low. When suppressing invasive species around conservation assets (e.g., national parks or exclusion fences), we find that the size of buffer zones should depend on the ratio of the species growth and spread rate.

KEYWORDS: Optimal control theory; partial differential equation; spatial control; suppression; invasive alien species; resource allocation; cat management; *felis catus*

Introduction

Invasive species are an ecological (Gurevitch and Padilla 2004, Duraiappah et al. 2005) and economic (Pimentel et al. 2005) catastrophe. Given the disparity between the scale of the problem and the resources available for management (Pimentel et al. 2005, McCarthy et al. 2012), decision makers need to identify and employ cost-effective management strategies. While there has been substantial research published on invasive species management (Epanchin-Niell and Hastings 2010), important gaps remain, particularly concerning general management strategies. Many recommendations are problem-specific and do not give general insights that could support rapid decision-making for new problems, even when these new problems are similar to those already treated in the existing literature (Higgins et al. 2000, Burnett et al. 2007, Hyder et al. 2008).

Many recommendations have limited applicability because the models that support them make strong, context-specific simplifications. Increasing the complexity and realism of a model makes it harder to analyse and interpret mathematically, so it is reasonable to use a model which is just complex enough to be able to answer the question at hand. One of the most common simplifications to make is to only consider the temporal aspect of a problem (Courchamp et al. 2003, Zhang et al. 2006, Hastings et al. 2006, Kern et al. 2007, Hauser et al. 2007, Baxter et al. 2008, Blackwood et al. 2010, Rout et al. 2013), or only its spatial aspect (Neubert 2003, Hauser and McCarthy 2009, Baker and Bode 2013). However, invasive species control problems are inherently spatiotemporal, since the abundance of an invasive population, and the implementation of a management project, change in both space and time. Temporal models and spatial models are therefore different aspects of a more general problem. Posing a problem initially in a spatiotemporal framework, before making the relevant temporal or spatial assumption, makes it easier to see how specific problems and their solutions fit together. Moreover, by providing an explicit and mechanistic link between the two dimensions of the problem, a spatiotemporal framework offers general and synthetic insights into efficient invasive species management.

As well as revealing parallels between the spatial and temporal cases, spatiotemporal models can directly help solve management problems that are either spatial or temporal. Data about invasive species populations and their management are often either spatial or temporal. Two common types are time series data (e.g., control effort and abundance through time; Terauds et al. 2014) and long-term spatial data (e.g., the effect of ongoing baiting programs on equilibrium predator abundance; Thomson et al. 2000). There are also data which do not fall into either of these categories and are inherently spatiotemporal (e.g., the speed of travelling invasion waves; Phillips et al. 2007). A spatiotemporal modelling framework can synthesise the information contained in these different data, allowing them to contribute to a shared understanding of the ecosystem. Even if simplification later removes either the spatial or temporal aspects of the model, data gained from using the full spatiotemporal model can still be used to make predictions. For example, spatial data can be used to estimate the effectiveness of a spatial allocation of control effort for a mainland suppression project; this information can then be used to inform the temporal scheduling of an island suppression project. Throughout this paper we take this approach: we identify the parameters of a shared spatiotemporal model, and then solve for the optimal resource allocation for either a purely spatial or temporal problem.

Although our spatial or temporal examples are chosen to emphasise the synthetic benefits of a shared spatiotemporal framework, the results we derive provide useful insights into each of our case-studies and provide substantial advances on previous research. Previous work on optimising temporal aspects of invasive species suppression uses bioeconomic models and optimisation techniques that omit fundamental processes. For example, some models assume that growth rates and removal costs do not vary with the density of the invasive population

(Hastings et al. 2006), even though density dependent population dynamics are an essential element of population dynamics (Pearl 1927, Hixon and Johnson 2001) and removal costs are notoriously dependent on population densities (Cacho et al. 2010). Additionally, some previous studies look for cost-efficient suppression strategies over fixed time periods (Higgins et al. 2000, Baxter et al. 2008), even though managers might reasonably want to suppress the species in the shortest possible time, or conversely at a minimum cost, regardless of project length.

Compared to the temporal aspects of invasive species management, much less attention has been paid to the spatial allocation of resources. When an invasive species population becomes well established in a broad landscape, which makes eradication infeasible (Lodge et al. 2006), managers often pursue long-term spatial control. That is, they aim to minimise the incurred environmental or economic damage by suppressing the population to a lower equilibrium abundance across a section of the landscape, particularly in or around a high-value asset (e.g., a national park, predator-proof fence, or the location of a population of endangered species). Although it is known that ongoing control can suppress invasive species populations in a region (Saunders and McLeod 2007), and there exist guidelines for the spatial control of particular species, there is a marked lack of generalised theoretical guidance available for the best spatial distribution of effort (Epanchin-Niell and Hastings 2010).

In this paper we illustrate how a spatiotemporal framework to model invasive species dynamics can provide shared guidance to a range of different management problems, using a case study of feral cat (*felis catus*) management as an example throughout. This addresses a number of the shortcomings present in previous work, including those identified above. We use published results about the growth rate, spread rate and poison baiting efficacy to estimate each of the parameters in our model. Using this model we solve for the optimal allocation of resources through time for invasive species suppression on an island, and we solve for the optimal long-term spatial allocation of resources to suppress an invasive species within a landscape. We use optimal control theory (Pontryagin 1987, Lenhart and Workman 2007) to identify the optimal effort distribution in space or time. In each case, we explain how the problem relates to our central spatiotemporal equation and how to apply optimisation methods.

Model

We use a reaction-diffusion partial differential equation to model the spatial and temporal dynamics of the invasive species. Reaction-diffusion dynamics capture the essential elements of invasive species dynamics: dispersal, density-dependent population growth, and response to control efforts. These models can capture this range of dynamics with a minimum number of parameters and are mathematically tractable. This makes them a good choice for informing a wide range of invasive species control problems. We modify the standard reaction-diffusion equation (Fisher 1937, Okubo and Levin 2001, Hastings et al. 2005) by adding a term which allows for invasive species control (Baker and Bode 2013). This equation models the abundance, N, of the invasive species at position X and time t:

$$\frac{\partial N}{\partial t} = D\nabla^2 N + rN\left(1 - \frac{N}{k}\right) - N(\mu E)^q. \qquad (1)$$

The first term on the right hand side describes dispersal, which we model as random movement (diffusion) which is controlled by the *diffusivity*, D. The ∇^2 operator allows the model to work in any number of dimensions (and alternative coordinate systems, such as Cartesian or polar); in a one dimensional landscape, such as a thin peninsula, $\nabla^2 = \frac{\partial^2}{\partial x^2}$. The second term in Eq. (1) is locally density-dependent population growth, which we model using the logistic growth. The parameters r and k denote the population's intrinsic growth rate and carrying capacity respectively.

The final term describes the effect of management actions: the excess proportional mortality inflicted on the population at each location, due to the control effort E, which may vary in space, time or both. Although this is modelled locally, the impact of control at a location is felt more broadly through the influence of diffusion in the dynamics of Eq. (1). In general, control efforts exhibit diminishing marginal returns on investment: the incremental benefit of applying additional control effort is smaller when the control effort is already large, compared to when the control effort is low (Myers et al. 2000, Fraser et al. 2006, Carrasco et al. 2010b). Put simply: doubling control efforts will remove less than twice the proportion of the invasive population. We use the function $(\mu E)^q$ to model these diminishing marginal returns, though we note that there are many alternatives (e.g., $\log(\mu E + 1)$, or $1 - e^{-\mu E}$). Control efforts are translated into a proportional reduction in the invasive population via the scaling parameter μ, and the diminishing returns parameter q, where $0 < q < 1$ (Baker and Bode 2013). Higher values of q reflect management actions which can be applied at high intensity cost-effectively; low values of q reflect management actions whose marginal returns on investment diminish very quickly and are therefore not cost-effective when applied at high intensity. Control efforts do not always result in a constant proportional reduction in the population. Depending on the control method and species, the proportional reduction may also depend on the species' abundance (Holling 1959). However, constant proportional control is the most parsimonious assumption, and has empirical support for feral cat control (on Macquarie Island; Robinson and Copson 2014).

In general, all of the parameters in Eq. (1) can vary in space and time. For example, D and k may vary depending on the terrain or habitat type (though if the diffusivity varies in space it must be brought inside one derivative, $D\nabla^2 N \rightarrow \nabla \cdot (D\nabla n)$, as ∇D is no longer zero), while r may vary though time. To illustrate that our methods are flexible enough to incorporate such variation, we will consider one example where control effectiveness, μ varies with the season.

Our aim in this paper is to identify optimal resource allocation strategies. As in all optimisation problems, the best distribution of control effort depends on the specific management goals or objectives. Although the precise form of these management objectives will depend on the particular species and location, most can be classified as one of a small set of alternative objectives. The first is to minimise the invasive species population given a budgetary constraint. The second is to reduce the invasive species population below an acceptable threshold, at the lowest possible cost. Finally, managers can jointly minimise the invasive species population and the control costs. Mathematically, this final alternative can be written as:

$$J = (\text{Cost of control effort}) + \omega \times (\text{Invasive species population}). \qquad (2)$$

Here ω is the weighting between spending more on control efforts or tolerating higher invasive species populations; the parameter ω can be interpreted as the cost caused by an individual invasive. One method of calculating this parameter would be to calculate the marginal economic cost of an additional individual from the invasive species (Olson 2006, McIntosh et al. 2009). This third objective allows us to access the optimal solution for the first two objectives: the parameter ω can be adjusted until the either a desired budget constraint has been satisfied, or until the invasive species population reaches its threshold target (Baker and Bode 2013). This objective function assumes that invasive species cause damage proportional to their abundance (Parker et al. 1999). In this paper we focus on scenarios where the aim is to reduce the abundance of the invasive species below a certain threshold at a minimum economic cost, rather than incorporating biodiversity costs explicitly in the objective.

Optimal management involves choosing a distribution of effort through time and space, $E^*(\boldsymbol{X}, T)$, from the literally innumerable range of alternatives. It is important that, when assessing candidate control strategies, an optimal strategy is identified. Although it may not be possible to implement the optimal solution in all circumstances, it provides a valuable yardstick against which to compare alternate strategies. Many previous analyses identify the best option from a finite set of possible strategies (Menz et al. 1980, Higgins et al. 2000, Crespo and Sun 2002, Zhang et al. 2006, Baxter et al. 2008, Cacho and Hester 2011), or restrict the form of the control strategy (e.g., Sharov 2004, Carrasco et al. 2010a). Some restrictions represent legitimate limitations on managers' logistical or physical capabilities (e.g., budgetary constraints) and must be considered. However, other analyses limit the range of feasible control strategies because they apply mathematical optimisation methods which cannot exhaustively search the space of potential solutions. This latter form of *a priori* constraints are not ideal because they preclude unexpected and counter-intuitive management approaches. There are many examples of counter-intuitive solutions to optimisation problems. For instance removing roads from a congested network can actually improve traffic flow (Cohen and Kelly 1990). It is important that we allow for unexpected solutions when assessing invasive species management strategies. *A priori* constraints are also often unnecessary, since there are optimisation methods, such as dynamic programming and optimal control theory (Leonard and van Long 1992), which can find the optimal solution from among all possible strategies.

Parameter identification

The spatiotemporal model is defined by five parameters: D, r, k, μ and q. It would be easiest to estimate these parameters using abundance data that is explicit in space and measured at multiple times, while control effort at various levels is being applied to the population of invasives. However, this type of data is not generally available. In the analyses that follow, we illustrate how to derive parameter values using the example of feral cats in Australia, using information from a range of spatial and temporal experiments and observations (though we note that these values are likely to be specific to Australian semi-arid ecosystems).

Growth rates are one of the most readily available quantities. They can be measured directly, from species traits such as litter size, age of first birth, juvenile survival and lifespan, or from time series analysis. Female feral cats have on average one litter per year with on average 1.75 kittens surviving past twelve weeks (Schmidt et al. 2007). The average feral cat lifespan is approximately 7 years (Hayde 1992). We assume that feral cat populations are approximately half male and half female, so the average increase in cat population per year is $\frac{1.75}{2} - \frac{1}{7} \approx 0.73$. Therefore the growth rate, r, which produces the same yearly increase is $r = \log(1 + 0.73) \approx 0.55$ (Appendix A). The carrying capacity, k, depends strongly on the context. Throughout this paper we will focus on percentage reductions in the population and we re-write Eq. (1), setting $N = nk$. Hence, we describe the invasive population in terms of its density as a proportion of carrying capacity, rather than abundance:

$$\frac{\partial n}{\partial T} = \nabla \cdot (D\nabla n) + rn(1-n) - n(\mu E)^q. \quad (3)$$

Diffusivity can also be measured directly, using observations of dispersing individuals from individual tracking or mark-recapture analyses (see Murray et al. 1986 p. 198), although high-quality data are rare. Diffusivity can also be estimated from measurements of the spread rate of an invasive species following its introduction. The expected spread rate, , c of a species, according to Eq. (4), is $c = 2\sqrt{rD}$ (Murray 2002). Therefore, if the growth rate and spread rate is known, then D can be calculated as:

$$D = \frac{c^2}{4r}. \quad (5)$$

The average spread rate of feral cats across Australia between 1863 and 1890 was 20 – 25km per year (Abbott 2002). Substituting the spread rate into Eq. (5) implies that $D = 182$ to 284 km^2 $year^{-1}$. Alternatively, if diffusivity and the spread rate can be measured directly, then it is possible by rearrangement to infer the growth rate of the species from these two movement quantities.

The control effort parameters μ and q are vital. Estimating them can be difficult, since at least two observations of the effect of control effort on the population are required, with different intensity of control. Eq. (3) can then be solved forwards in time, using the known effort allocation, and candidate values for μ and q (assuming the other parameters are known). The best-estimates of the values will minimise the discrepancy between the solution of Eq. (3) and the measured densities. We estimate the parameters μ and q using the outcome of cat baiting trials. Algar and Burrows (2003) found that cat densities could be reduced by 80-90% from baiting at 100 baits per km^2 on islands. Christensen et al. (2013) repeatedly baited Lorna Glen reserve on the Australian mainland at 50 baits per km^2, and we use their observations from 2003 and 2004. We solve Eq. (3) forwards in time on the islands and on Lorna Glen, using the cat parameter values (with $D = 182$) and identical baiting parameters. As Lorna Glen is on the mainland (rather than an island) we solve Eq. (3) in the surrounding region, though baiting is restricted to Lorna Glen. This allows cats to migrate into Lorna Glen following the first baiting event. We solve for the parameters μ and q which minimise the mean square error between the data and the model: $\mu = 2.21$ and $q = 0.64$. The model parameters are gathered in Table 1.

Temporal suppression problems

In small regions (such as islands, peninsulas and within fenced regions) the abundance, or average density, of the invasive species has a much greater influence on the outcomes of management than its spatial distribution. As a result, we can simplify our general spatiotemporal model to focus only on the temporal aspects of management. We focus on situations where an invasive species is long-established on the island, and managers' main priority is to suppress the population below a threshold, n_T, at minimal cost – i.e. we solve for the most economic cost-effective control strategies, without including damages caused by the invasive species in the objective function.

Because we are assuming that the population is uniformly distributed and well-mixed in space, we can consider only the temporal variation in the model by setting $\nabla n = \mathbf{0}$. Hence Eq. (3) becomes

$$\frac{dn}{dt} = rn(1-n) - nE(t)^q, \tag{6}$$

where the effort allocation has been scaled:

$$e(t) = \mu E(t). \tag{7}$$

We assume that the invasive population is initially at its maximum density:

$$n(0) = 1. \tag{8}$$

Reducing the invasive species population below a threshold is equivalent to the general terminal time condition:

$$n(T) \leq n_T \tag{9}$$

where T represents the length of the project. Our objective is to achieve this using as little total effort as possible:

$$\min_{e(t)} J = \min_{e(t)} \int_0^T e(t)dt. \tag{10}$$

This is a special case of Eq. (2), where the integral of control effort, $e(t)$, over the length of the project is the project cost. We do not include the costs of the invasive species (instead, implementing a target density), so we omit the first term of Eq. (2). The optimal solution to this problem is identified using optimal control theory (Appendix B).

Temporal suppression results

The optimal effort allocation, using the cat parameters, for four project lengths is shown using dashed lines in Figure 2a-d. In each case it is optimal to begin the project with relatively low effort, and then to intensify control effort towards the end of the project. When the project length is very long (Figure 1d), the optimal choice is to allocate almost no effort during the initial phase of control. This approach held for every choice of parameters that we tested, although for short projects the effort allocation becomes more uniform (Figure 1a). This accelerating approach to invasive species suppression reflects the high cost-effectiveness of control efforts when the invasive species is abundant. Although it is tempting to apply high control effort while the population is high, as it would result in a quick decrease in the invasive population, diminishing marginal returns of control efforts make this quite cost-ineffective. Initially the invasive species is plentiful, so removals can be achieved cheaply; the per-capita growth rate is low due to density dependence, meaning the population finds it difficult to replace losses. Hence, a small control effort can initially reduce the invasive population economically cost-effectively. As the program progresses, the marginal cost of removing individuals and the per-capita growth rate both increase; these processes work together to require increased control efforts.

As well as changing the relative distribution of control effort, the choice of project length has a significant impact on the total effort required to reduce the population below the threshold (Figure 1e). Total project economic costs must decrease monotonically with increasing project length, since a longer project window still allows a manager to choose a shorter project length. Unsurprisingly, short schedules demand intense control efforts and high total economic costs. This high cost is primarily the result of managers' inability to take full advantage of the cost-effective period of low control at the beginning of the project; longer projects create space for a longer cost-effective suppression phase. This type of slow, accelerating approach would only be appropriate when extra ecological damage caused by the invasive species in the extended project window is minimal.

<Figure 1 about here>

Although increasing the project length reduces the total project cost, there appears to be a lower limit: there is a point where the cost reduction from further increasing the project length becomes essentially zero. We call this point in time, which depends on the parameter values, the "optimal project length". The optimal project length depends on both the population growth rate, r, and the diminishing returns parameter, q (Figure 2). If the growth rate is large, then many new individuals would be produced during the project. Hence, it is advantageous to have a short project. Conversely, if the growth rate is low, then population growth during the project is less of an issue and longer projects become more appropriate. Additionally, the parameter q plays a large role in the optimal project length. If q is large, then control efforts can be applied at very high levels without a significant decrease in control effectiveness. Hence, it is optimal to apply high control efforts to reduce the abundance of the invasive species quickly and prevent the species from having time to repopulate during the project. Otherwise, if q is small, then the marginal benefits of increased control diminishes quickly with increasing effort, making short projects very cost inefficient. Hence, short projects are only cost-effective if the population growth rate is large and the marginal diminishing returns of increased control are small.

<Figure 2 about here>

In this section we assumed that the targeted invasive species was initially at carrying capacity. However, we can use the principle of optimality to calculate the optimal strategy for different initial population sizes from our existing solutions. This principle essentially states that the optimal solution to a smaller problem is contained in the solution to the full problem (Lenhart and Workman 2007). Thus, if we want to find the optimal control strategy for a population of invasives that begins at half its carrying capacity (i.e., $n(0) = 1/2$), we simply find the point along the full optimal control strategy (Figure 1) when the density reaches ½, and follow the remaining section of the optimal control. From the shape of the optimal effort allocation curves in Figure 1, we can see by inspection that the carrying capacity will not strongly influence the optimal strategy. First, the shape of the optimal solution curve is the same: effort needs to increase through time. Second, the total effort required will not change dramatically with larger initial population sizes. The majority of effort is applied to remove the final few invasive individuals, and an initial population at half the carrying capacity will therefore require almost the same amount of effort to suppress to very low density.

Seasonally-varying effectiveness of control

We have so far only considered situations where all of the parameters in Eq. (1) are constant. However, in practice this would rarely be the case. Here we consider a situation where the effectiveness of control efforts varies throughout the year. For example, the willingness of feral cats to consume poison baits is inversely related to the seasonal availability of alternative food sources (Algar et al. 2007, Christensen et al. 2013). Although managers often cope with varying control effectiveness by halting control efforts during periods of low efficacy, this is not necessarily the best response.

To model varying effectiveness we revert to an unscaled version of Eq. (6), which includes the function $\mu(t)$ and therefore allows us to alter control effectiveness through time:

$$\frac{dn}{dt} = rn(1-n) - n \times (\mu(t)E(t))^q. \qquad (11)$$

We choose $\mu(t)$ so that control measures have their full effectiveness for part of the year ($\mu = 1$), which we call the “on-season” and are only partially effective for the rest of the year ($\mu = \mu_0$), which we call the “off-season”. For cats, the on-season would be the relatively short period of late summer to early autumn (Algar et al. 2007). Hence, we set the first three months of each year as the on-season and the remaining nine months as the off-season (as we are considering cat control in the southern hemisphere).

The optimal solution for varying μ_0 is shown in Figure 3, once again using cat baiting parameters. Qualitatively, the shape of the optimal seasonal control is very similar to the optimal control when control effectiveness is constant: the solution for the on-season and off-season sections, taken separately, shows a low-intensity phase followed by a high-intensity phase.

< Figure 3 about here >

There is a simple relationship between the amount of on-season and off-season control (Appendix B):

$$E_{\text{off-season}} = \mu_0^{\frac{q}{1-q}} E_{\text{on-season}}. \qquad (12)$$

Clearly, if $\mu_0 = 0$, then control is completely ineffective in the off-season, and managers would only expend resources during the on-season. However, if controls are partially effective in the off-season, then the off-season effort allocation depends on the diminishing returns parameter (Figure 4). For large values of q, it is optimal to expend almost no control effort during the off-season, as high control effort can be applied quite effectively in the on-season. If q is small on the other hand, then a substantial proportion of the effort allocation should be expended during the off-season, despite its low efficacy.

< Figure 4 about here >

If no control effort is applied during the off-season, then the invasive species is free to replenish. A clear implication of these solutions is that, if possible, it is always good to apply some amount of control effort throughout the year, even during the off-season when they are relatively ineffective.

Long-term spatial control around a conservation asset

Managers often want to suppress invasive species within a region of high conservation value (e.g., national parks), where there are no physical barriers to prevent their entry (cf. Robley et al. 2008). A number of key decisions determine the cost and success of spatial control efforts. These include whether control efforts are limited to within the conservation asset, or extend into the surrounding landscape; whether control effort is applied at a uniform intensity, or varies through space; and whether the effort allocation increases or decreases with proximity to the asset. However, there is no theory available to help determine how these spatial management decisions should be made. Some best practice guidelines recommend uniform control efforts within a *buffer zone* around the conservation asset (Thomson et al. 1992, Saunders and McLeod 2007). The goal of this is to reduce the invasive species population in a large enough region that immigrants will set up a home range that is still distant from the asset. However, plausible alternative spatial management strategies exist. Control intensity could be non-constant within the buffer, increasing in intensity closer to the asset. Managers could also create a “metaphorical fence”: a ring of high intensity control at a distance from the asset (Hayward and Kerley 2009) which aims to prevent any invasive animals reaching the asset. Finally, a combination of a metaphorical fence and high intensity control efforts near the conservation asset could safeguard against individuals who manage to bypass the ring of control.

Spatial control sets long term goals for the invasive populations. We therefore solve for the steady-state solution and set

$$\frac{\partial n}{\partial t} = 0. \tag{13}$$

Eq. (3) then becomes

$$\nabla^2 n = -\frac{r}{D} n(1-n) + n(\mu E)^q. \tag{14}$$

Because we are considering conservation assets within a broader landscape, the natural coordinate system is polar; we re-write Eq. (14)

$$\frac{d^2 n}{d\rho^2} = -\frac{r}{D} n(1-n) + n\big(\mu E(\rho)\big)^q - \frac{1}{\rho}\frac{dn}{d\rho}, \tag{15}$$

where the model is radially symmetric about the conservation asset, and ρ is radial distance from the asset’s centre, which extends to $\rho = l_0$. To justify the use of polar coordinates we must assume that conservation assets will have a fairly regular geometry and can be reasonably well approximated by a circle (although we discuss later how to apply this to irregular geometries). Due to scaling, it is apparent that the only relevant quantity is the ratio of population growth and diffusivity: r/D. This quantity plays a key role in determining the optimal spatial management strategy. When animals are removed from a location in a landscape, a relative *sink* is created: the system will attempt to re-equilibrate either by organisms from nearby locations migrating in, or else by local reproduction. The relative strength of these two processes – encapsulated in the ratio r/D – therefore determines the extent to which local control efforts affect nearby invasive species densities. When the ratio is small (small r or large D), local control efforts have wide-spread consequences; when the ratio r/D is large (large r or small D), the benefits of local control are concentrated locally. This ratio will thereby determine whether managers can achieve superior outcomes by applying control efforts away from their objective (i.e., around the conservation asset), or by applying control efforts at the asset itself.

The objective of control efforts is to minimise the function:

$$\min_{m(\rho)} J_1 = \min_{m(\rho)} \int_0^{l} \rho E(\rho) d\rho + \omega \int_0^{l_0} \rho n(\rho) d\rho. \qquad (16)$$

This equation is analogous to equation (2), where the first term is the total amount of control effort applied, and the second is the total density of predators within the asset, multiplied by ω. Increasing values of ω place greater management emphasis on reducing the invasive species population and less on the control costs. For illustrative purposes in the following figures, we adjust the parameter ω to reduce the invasive species population within the asset to 50% of its carrying capacity; the qualitative form of the optimal solution does not depend on ω.

Spatial control results

Figure 5 shows the spatial distribution of control which optimises the management objective (16) with respect to the governing equation (15) identified using optimal control theory (Appendix C). The optimal distribution of effort is denoted $E^*(\rho)$ and has characteristics that are robust to all possible parameterisations. It is highest at the centre of the conservation asset and decreases beyond the boundary. It is not optimal to distribute control effort across the entire domain (i.e., throughout the region beyond the conservation asset), and it is never optimal to allocate effort uniformly across space (i.e., a constant buffer zone). The optimal baiting distribution results in an invasive species population, $n(\rho)$, which always increases with distance from the asset. The invasive population remains substantially below the carrying capacity for some distance beyond the asset and also for a distance beyond the baited area. Control efforts will unavoidably create a sink within the asset, via a density gradient which draws invasives from the surrounding region. Despite these source-sink dynamics, it is never optimal to transfer all control effort from the conservation asset to the surrounding area in an attempt to pre-emptively remove invasives before they reach the asset (the metaphorical fence approach).

<Figure 5 about here>

Constant buffer zones for an open asset

The optimal solution recommends that control effort should vary smoothly across space, which may be hard to accomplish in practice because more complicated effort allocations will be difficult to implement (Boettiger et al. in press). Managers often apply spatial control in a constant-effort buffer zone around a high value asset, rather than continuously altering effort with distance from the asset (Fleming et al. 2006, Wallach et al. 2009, Sleeman et al. 2009). Here we calculate the optimal buffer zone size and evaluate the cost-effectiveness of this approach, relative to the optimal solution. Although experimentation has been used to determine the best buffer zone size for certain species (Thomson et al. 2000), the results cannot be easily generalised to new species and they have not been assessed relative to an optimal distribution (Metsers et al. 2010). We therefore calculate the optimal buffer zone size using our model, and compare it to the true optimal solution. For comparative purposes, the total control effort applied in the buffer strategy is constrained to be the same as the optimal solution, and the sole decision is thus the radius of the buffer.

The best buffer strategy is very different from the shape of the optimal effort allocation (Figure 5a), and as expected, the optimal solution delivers a better outcome for the same cost. However, the difference in the size of the invasive population is not drastic, as long as the buffer zone is optimally sized; the density of invasives in the conservation asset with the best buffer zone is only about 10% higher than the density resulting from the optimal allocation.

The optimal buffer zone size is defined by a complex implicit relationship between the parameters D, r, l_0 and q and the target invasive species density, and hence no exact solution can be found. Instead we present a close approximation for a target invasive species density of 50% of the environment's carrying capacity (Appendix D):

$$\text{Buffer zone} \approx 100\sqrt{A + B\frac{D}{r}} - l_0 \qquad \textbf{(17)}$$

where

$$A = \left(\frac{l_0 + 0.513}{100} + \frac{0.00671}{q}\right)^2 \text{ and } B = \left(\frac{3.18}{q} - 3.95\right)/10^4. \qquad \textbf{(18)}$$

This equation is based on reducing the invasive species density by 50%, and we are unable to find an approximation for arbitrary invasive species targets. However, we did find that lowering the target invasive species density resulted in a larger optimal buffer zone. For example, if the target density is 10%, the optimal buffer zone was usually 45% to 60% larger than Eq. (17).

Eq. (17) shows that the width of the optimal buffer zone decreases as the size of the conservation asset is increased. This result contrasts current thinking, which assumes that the width of a buffer zone should be independent of the size of the conservation asset, and hence employing a buffer zone around large assets is not feasible (Saunders and McLeod 2007). For very large assets, the optimal buffer zone approaches a fixed width of $0.513 + \frac{0.671}{q}$ km, but only once the area of the asset is in the order 100,000 km^2 –far larger than any intensive invasive control project. Western Shield, the largest conservation program in Australian history, baited 39,000 km^2 for invasives predators. Surprisingly this result has no dependence on either D or r. This is because applying control effort around an asset will only affect the population density a fixed distance into the asset (which depends on D and r). For huge regions, this distance becomes irrelevant compared to the size of the asset.

Optimal Baiting around the Lorna Glen conservation fence

Lorna Glen is an ex-pastoral property in Western Australia's rangelands that was acquired by the Western Australian Government in 2000 (Miller et al. 2010). A small region within Lorna Glen has been fenced, and a number of locally extinct native species have been re-introduced (Bode et al. 2012, Ottewell et al. 2014). The region around the fence is currently poison baited at a uniform density to reduce the number of feral cats which come into contact with the fence, and thus the incursion rate (Bode and Wintle 2010, Tores and Marlow 2012). The size of fenced region is small, relative to the size of Lorna Glen, so we do not include the fenced region in the model. We solve for the cat density across Lorna Glen and seek to minimise it at the location of the fenced region.

The geometry of the property at Lorna Glen is quite different to the circular regions that we have solved so far. We assume that baiting can occur within but not beyond the property, and solve for the cat density in and around Lorna Glen, but outside the fence. To incorporate the irregular geometry of the property we use a *conformal transformation* to map the optimal solution from the circular region to Lorna Glen (Baker and Bode 2013). We also predict the cat density that would result from two reasonable alternatives to the optimal baiting distribution: a buffer zone (Eq. (17)), which in this case should be 19.5km wide, and a constant distribution of bait across the entirety of Lorna Glen (Figure 6)

<Figure 6 about here>

The predator density at the fence perimeter is highest when the bait is distributed at a uniform density across the property. A buffer zone of the optimal width can achieve a 2.6% lower cat density than uniform baiting for the same amount of bait, while the optimal distribution can reduce the cat density by 8.7%, compared to uniform baiting. The size of Lorna Glen is coincidentally quite similar to the optimal buffer zone, so the improvement from switching to a buffer zone from baiting the entire property is relatively small. For the uniform distribution to reduce the cat density at the conservation fence to same density as that the optimal distribution does would require 2.5-3.0 times more bait.

Discussion

Applying a spatiotemporal framework to invasive species management reveals principles that apply to a range of cases and are robust to model parameterisations. Our analyses reveal that optimal control actions are crucially determined by the process through which the invasive species population recovers from the application of control effort. In the spatial suppression case, a local population of invasives can either recover via local growth, or recover via dispersal from nearby locations. The relative strength of these two processes is governed by the ratio of their associated parameters: r/D (or alternatively, the ratio of growth rate to invasion spread rate: r/c). If this ratio is large, then control effort can be focused close to the important locations in the landscape (e.g., the conservation asset), since it is local population growth that will replace the removed invasives. In contrast, if the ratio is small then control efforts need to extend further into the surrounding region, to reduce the size of nearby populations and thereby to reduce their ability to disperse into the asset. By contrast, in the temporal case, the optimal effort allocation is determined by the ratio of local population growth rate to the diminishing returns on control effort: r/q. When this ratio is large (e.g., if growth rates are high), optimal resource allocation is achieved through intense control over a short period of time. This is because shorter projects give the species less time to reproduce (a particular concern since the population growth rate is high). Additionally, the relatively low diminishing returns parameter means that the high mortality rates required by a short project can be applied without sacrificing cost-effectiveness. In contrast, if this ratio is small (e.g., if the growth rate is low and control efforts exhibit rapidly diminishing returns) a long project would not result in much population recovery, and so greater emphasis can be placed on avoiding the detrimental effects of diminishing returns.

Although spatial and temporal management problems are usually treated separately, the two types of problems can provide insights into each other, provided that they are analysed with a common model. In the most straightforward sense, it allows different data to be used across the problems, which we illustrated using the example of feral cat control. Further to this, real problems rarely fall entirely into either the spatial or temporal category, but knowing the solution to either extreme can help improve our intuition and understanding of mixed problems. For example, the best way to manage a species that is not constrained, but which is spreading fairly slowly, would have elements of both the spatial and temporal solutions. The average intensity of control in the optimal solution would likely increase through time, as we found for the temporal solution, and the distance that control is spread out around the invasion would depend on the spread rate of the species.

Throughout this paper we apply methods that are capable of identifying optimal solutions. Methods that can determine the optimal solution do not rely on us being able to guess the true optimal solution *a priori*, and can therefore reveal counterintuitive solutions. Our analyses reveal two interesting and counter-intuitive results. First, our solutions for spatial effort allocation shows a strong dependence on the ratio of population diffusivity and growth rate, D/r (or equivalently c/r). Although this seems fairly logical, it differs markedly from well-known theoretical results for the spread of invasive species. The speed of an invasion front is $2\sqrt{rD}$ (Murray 2002). Species with faster invasion fronts would seem better equipped to cross baited buffer zones. It would therefore be reasonable to suppose that the radius of buffer zones should depend on the product of the growth rate and diffusivity, rather than the ratio. Second, our analyses of temporal suppression projects show that if the invasive species has a high growth rate, then it is most cost-effective to control that population very rapidly. This is true even though it requires the application of control efforts that are intense enough to be very inefficient (via diminishing marginal returns). However, some might arrive at the opposite conclusion. If an invasive species has a high growth rate, then it would be reasonable to tolerate a longer project timeframe, since the species will recover more rapidly from control efforts, lengthening the removal project.

We chose to use a partial differential equation to model spatiotemporal invasive species for a number of reasons. This type of equation has a long history in ecology (Fisher 1937, Skellam 1951, Okubo and Levin 2001) and in population modelling for management (Neubert 2003, Neubert and Herrera 2008, Miller Neilan and Lenhart 2011). A broad range of methods are available to solve either the full spatiotemporal problem or one dimension at a time (e.g., the ordinary differential equations in our spatial and temporal cases). In the temporal suppression case, our objective did not consider any ongoing environmental damage done by the invasive species. In some cases, this may be an important consideration and this could easily be included in the model. In the spatial case, our model also does not take into account non-local effects of control. Most plausible non-local effects (e.g., baiting will impact individuals at a distance whose home range overlaps the baited area), would operate over spatial scales that are smaller than the regions we have considered. This is not a large assumption, as reaction-diffusion equations are most appropriate at fairly large scales.

Different conservation and ecological contexts would alter our model, which would result in different optimal solutions. These changes may affect the ecological and economic dynamics of the system (Eq. 1). For example, including an Allee effect should divert resources away from the final stages of a temporal suppression project, due to the reduced (and sometimes negative) per-capita growth rate of the species at low density. Including economic discounting would shift resources towards the end of the project, as future actions become relatively cheaper. In some invasive species management projects the invasive species persists at very high densities. This sometimes means that the time spent removing an individual (e.g. removing a plant) is much greater than the search time. To account for this, the control term in our model (i.e., the final term in Eq. 1) could be altered to include a *handling time* via a type II functional response (Holling 1959). More effort would then be required to control an abundant population, such as during the early stages of the project.

Variations on our model could also alter the objective function (Eq. 2). Impacts due to invasive species and invasive species management on endemic species can be included explicitly in models and can be either positive or negative. These can be vital parts of the management problem, altering both the optimal solution and the size of the benefit derived from management (Lampert et al. 2014). For example, the marginal biodiversity damages caused by an invasive species can vary significantly. If an invasive species has been present for very long period, and is no longer in the process of shifting the ecosystem to a new state, it might be acceptable to increase the length of a suppression project to save economic costs.

However, this would generally not be the case for an invasive species which has only recently been introduced, where the ecological impacts of the invasive species are high over short time-frames. Instead, it would be important to control the species faster, and this change would be implemented in the management objective. The resulting optimal control solution would allocate more resources towards the beginning of the project.

In the temporal suppression case, we focus on relatively small insular regions. Provided that they can be effectively quarantined, these areas can be targeted for complete eradication. Insular eradications are an increasingly common type of complete eradications: 1375 vertebrate populations have been targeted with eradication from islands, with 28% of these occurring in the last 10 years (Island Conservation 2012). Our objective function, Eq. (10), only seeks to minimise the control cost. However, during an eradication it would be reasonable to seek to remove individuals as quickly as possible for a variety of reasons, for example: if the invasive species is causing extensive ongoing damage to endemic species (i.e. causing an extinction risk), if there is the potential for a species to become less susceptible to control through time (e.g. cats learning to avoid capture), or for political reasons. However, there are examples of long-term projects that aim to eradicate (e.g. Gardener et al. 2010), and our objective function could be applicable in some of these cases.

Our model does not include stochasticity, but it is possible to think of the solution of differential equations, such as Eq. (1), as the expected outcome of a stochastic system. It is not trivial to formulate a stochastic equation to solve for optimal steady-state spatial control effort. Hence a stochastic formulation is not suitable for unifying the spatial and temporal problems. However, we can assess the performance of our optimal temporal solution for controlling a stochastic invasive population. We constructed a stochastic version of the Ricker model and applied our optimal control strategy (Appendix E). The stochastic model showed very similar behaviour to the deterministic model: even individual realisations follow very similar trajectories to the deterministic model. Of course, if the stochasticity was large enough our solution would perform poorly. Our results should therefore be interpreted carefully when stochastic variation is large.

In all conservation projects, there is a trade-off between gathering more information and delaying a management decision or making a decision more quickly with less information (Grantham et al. 2009). However, care must be taken because if intervention is delayed too long there can be poor outcomes for the species (Lindenmayer et al. 2013). This trade-off exists for the optimal solutions presented in this paper, and in fact, an optimisation that includes a temporal model component is required to solve this trade-off. Although gathering more data would allow more economically cost-effective strategies to be generated, in some cases the delay to gather the data would not be worth the benefits of the improved strategy. In these cases it would be important to conduct value of information analyses to ensure that work to improve control strategy is worth the time and effort.

Many invasive species management questions are strategic, and therefore cannot be easily resolved by experiments. Testing is very expensive since many of the relevant processes operate at very large spatial scales. Further, the outcome of alternative actions can only be observed over long temporal scales, which can result in unacceptable delays (Grantham et al. 2009). Strategic questions are often idiosyncratic (e.g., buffer zone sizes in South Africa might not be optimal for the management of the same species in New Zealand, since animal movement rates vary with habitat type), and experimentation will not be able to compile sufficient comparable replicates. Our case study demonstrates how a general method can be used to quickly gain insight into invasive species control, using only the sort of published data that would be available for many species.

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Ecological Archives material

Appendix A: Continuous and discrete growth rates

Appendix B: Temporal optimal control

Appendix C: Spatial optimal control

Appendix D: Buffer zone approximation to the spatial control problem

Appendix E: Discrete time stochastic model

Table 1

Feral cats (*felis catus*) model parameters for Australian semi-arid ecosystems.

D	Diffusivity	182 – 284 $km^2 year^{-1}$
r	Growth rate	0.55 $year^{-1}$
μ	Bait effectiveness	2.21
q	Diminishing returns parameter	0.64

Figure 1

(a-d) The optimal effort allocation (dashed) and corresponding invasive species population (solid) for various project time periods with our cat parameters ($\boldsymbol{r = 0.55}$, $\boldsymbol{q = 0.64}$). (a) To suppress the species to the target density in a short time period (1 year), a high, almost constant effort allocation is required, which results in high total costs. For longer projects (b, c), the effort allocation starts very low and increases through time (although it still remains low compared to short projects). If the project length is further increased (d), the effort allocation has a period with almost zero control, before the allocation is increased. (e) The total effort applied throughout the project for varies time periods for three values of $\boldsymbol{q}$ (0.54, 0.64, 0.74) and $\boldsymbol{r = 0.55}$. The shorter the project time, the higher the costs.

Figure 2

The optimal project length as a function of diminishing returns parameter, $\boldsymbol{q}$, for three values of the population growth rate, $\boldsymbol{r}$. Large values of $\boldsymbol{q}$ make it possible to conduct short projects, while small values require longer projects. Increasing the growth rate, $\boldsymbol{r}$, results in shorter optimal projects.

Figure 3

The optimal effort through time to suppress an invasive species when control measures have limited effectiveness throughout each year, with parameters $r = 0.55$, $q = 0.64$ and $T = 5.25$. The effectiveness of off-season control, relative to on-season, is given by μ_0, and the length of the on-season is 3 months in each year. In the two left-hand figures, $\mu_0 = 0.9$; in the right-hand figures, $\mu_0 = 0.5$.

Figure 4

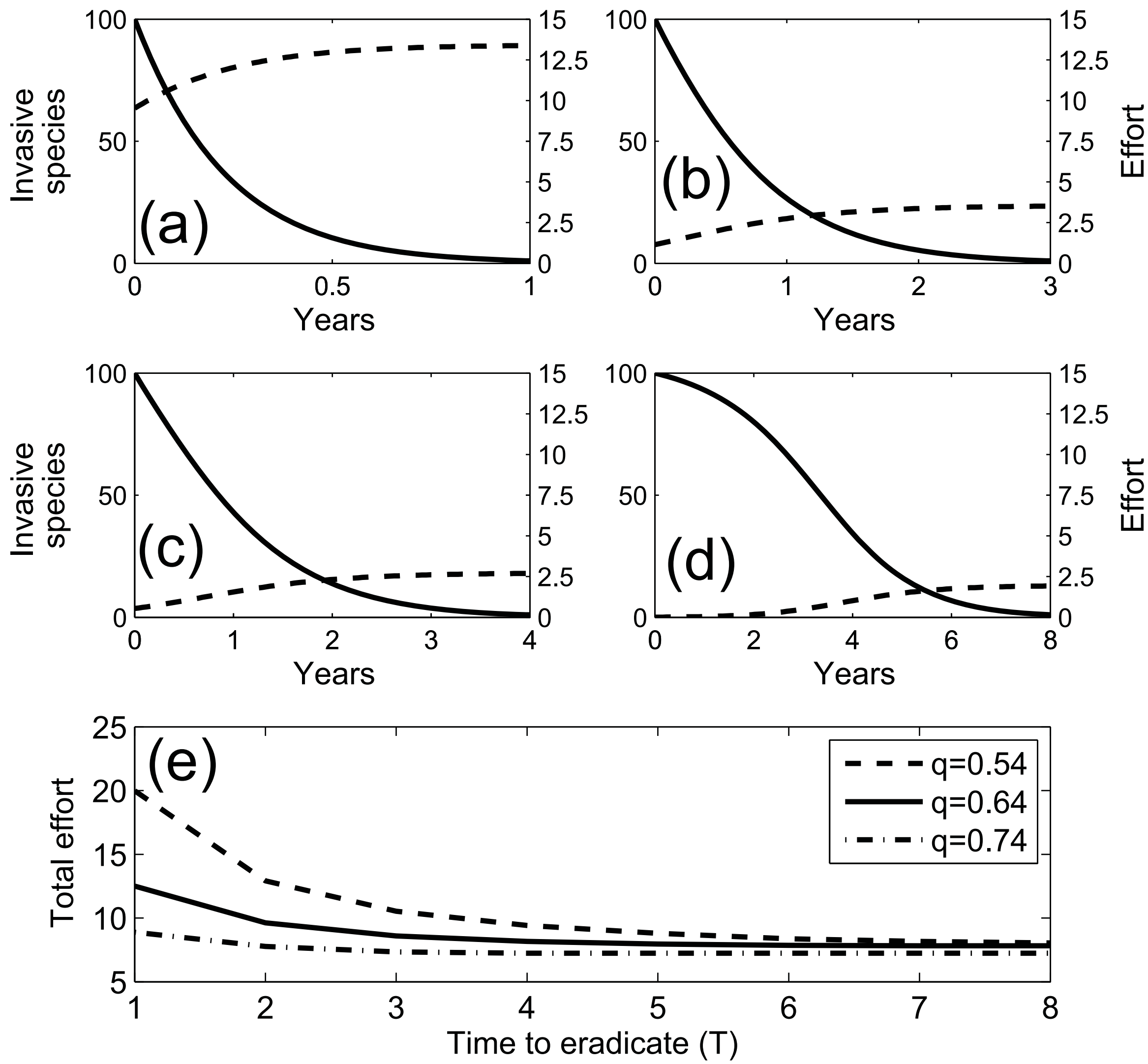
The optimal off-season effort allocation relative to the on-season allocation. The more effective off-season control is, μ_0, the higher effort allocation in the off-season (y-axis). Large values of q result in a greater focus on on-season control activities. This is because the effect of diminishing returns is reduced meaning high intensity control effort can be applied while control efforts are most effective. Other parameter values are the same as in Figure 1.

Figure 5

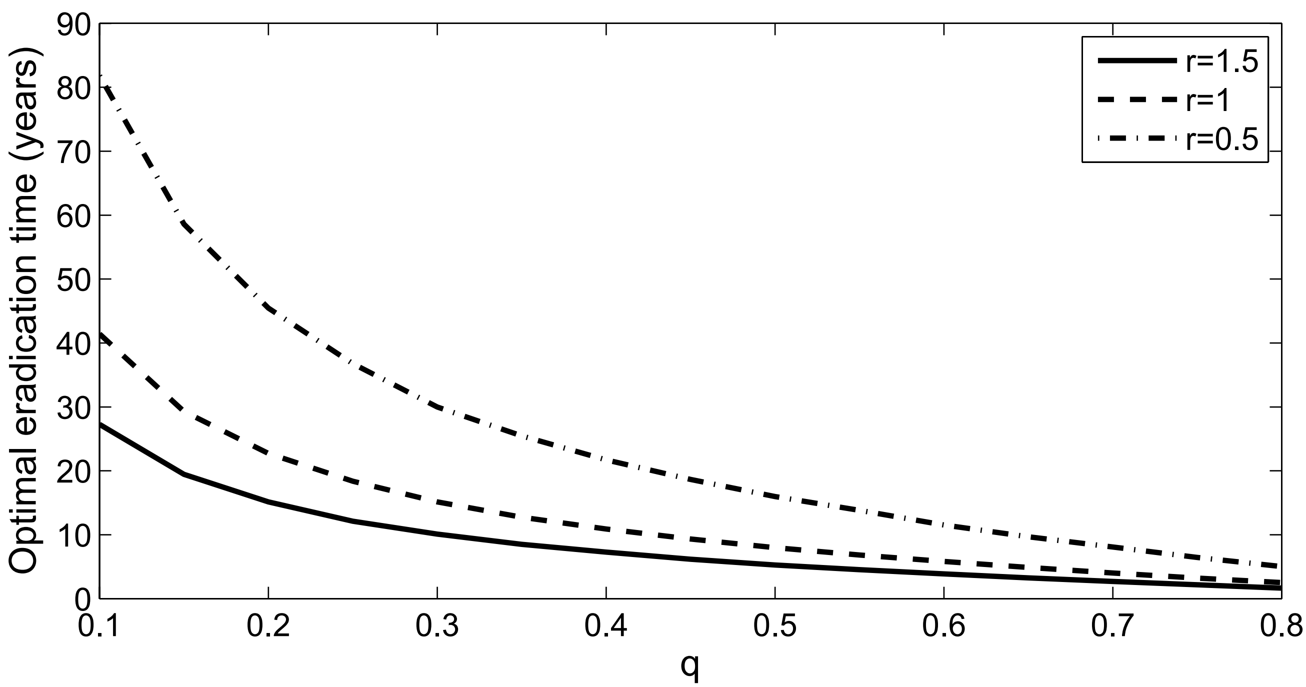
Comparison between the optimal solution and buffer zones for spatial suppression, with parameters $\frac{r}{D} = 5.4 \times 10^{-3}$, $q = 0.63$ $l_0 = 10$km. The grey shading indicates the location of the conservation asset. The optimal effort and corresponding invasive species population are in the dashed black lines, and the solution with a constant buffer zone is the solid black line. The invasive species population is approximately 10% smaller at the edge of the asset when allocating effort optimally, compared to using a buffer zone.

Figure 6

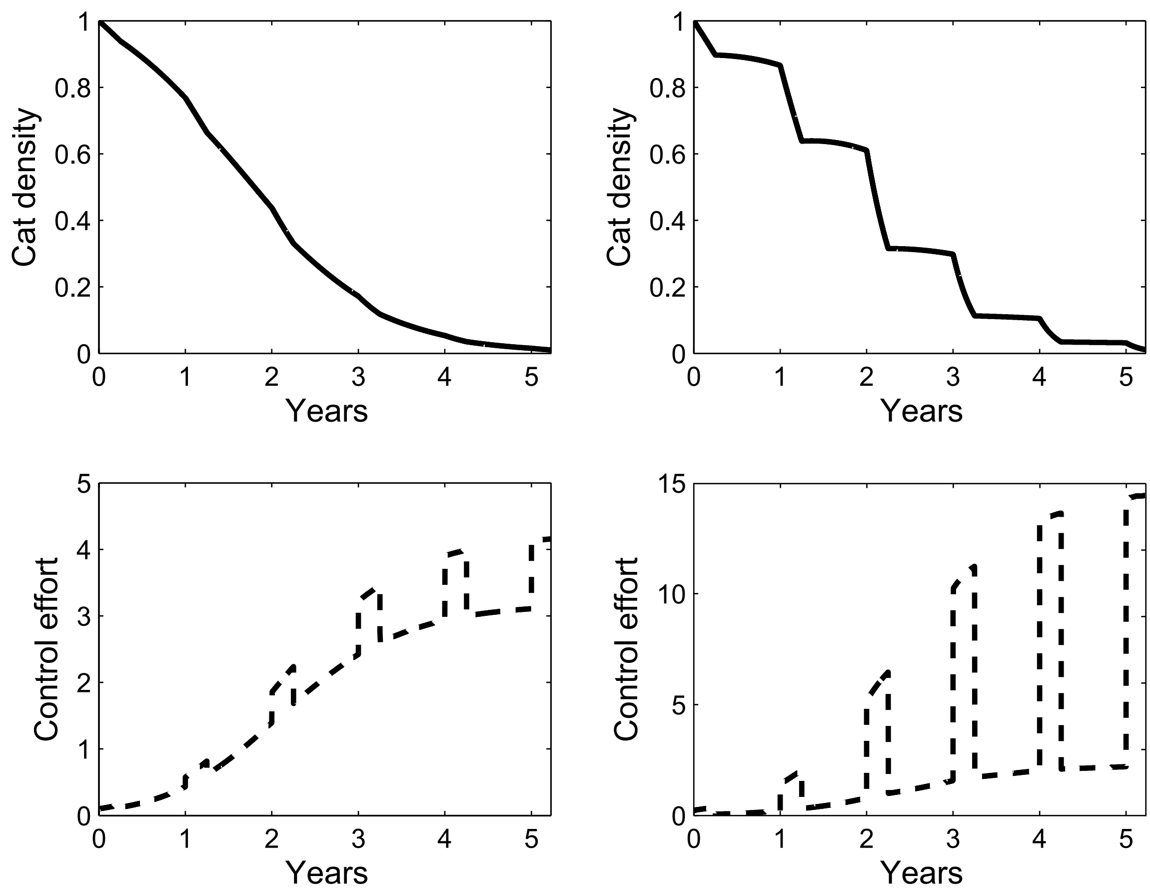
The long term cat density on Lorna Glen with three different baiting strategies, using parameters for feral cats (we chose the lower limit for diffusivity, $D = 182$). The geometry of Lorna Glen is shown in black. The cat density resulting from: (a) optimal baiting, (b) optimal buffer zone and (c) uniform baiting. Both the optimal and buffer zone solutions out-perform uniform baiting in reducing the cat density at the location of the conservation asset. (d) The difference between the cat densities resulting from optimal and uniform baiting. The buffer zone lowers the cat density in a larger region than optimal baiting, but does not lower the density quite as much at the location of the reserve.



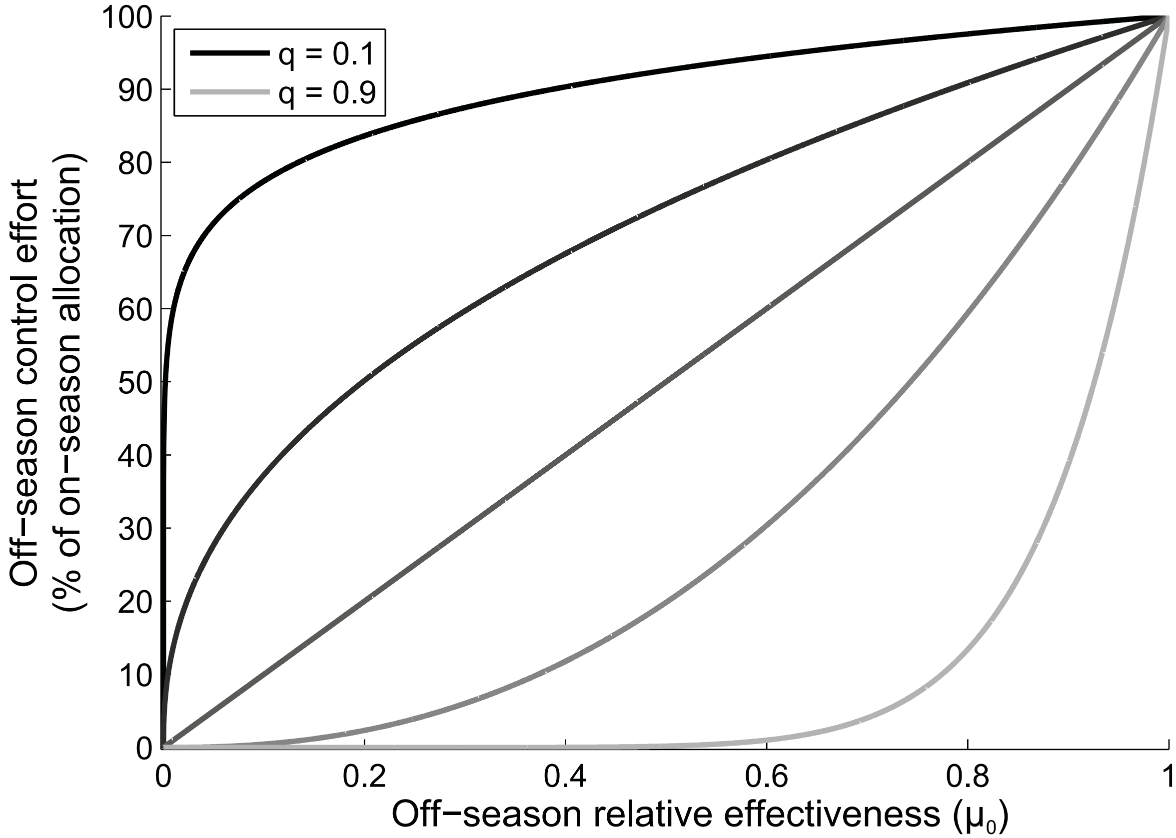
(a)
(b)
(c)
(d)
(e)
Invasive species
Effort
Years
Total effort
Time to eradicate (T)
q=0.54
q=0.64
q=0.74



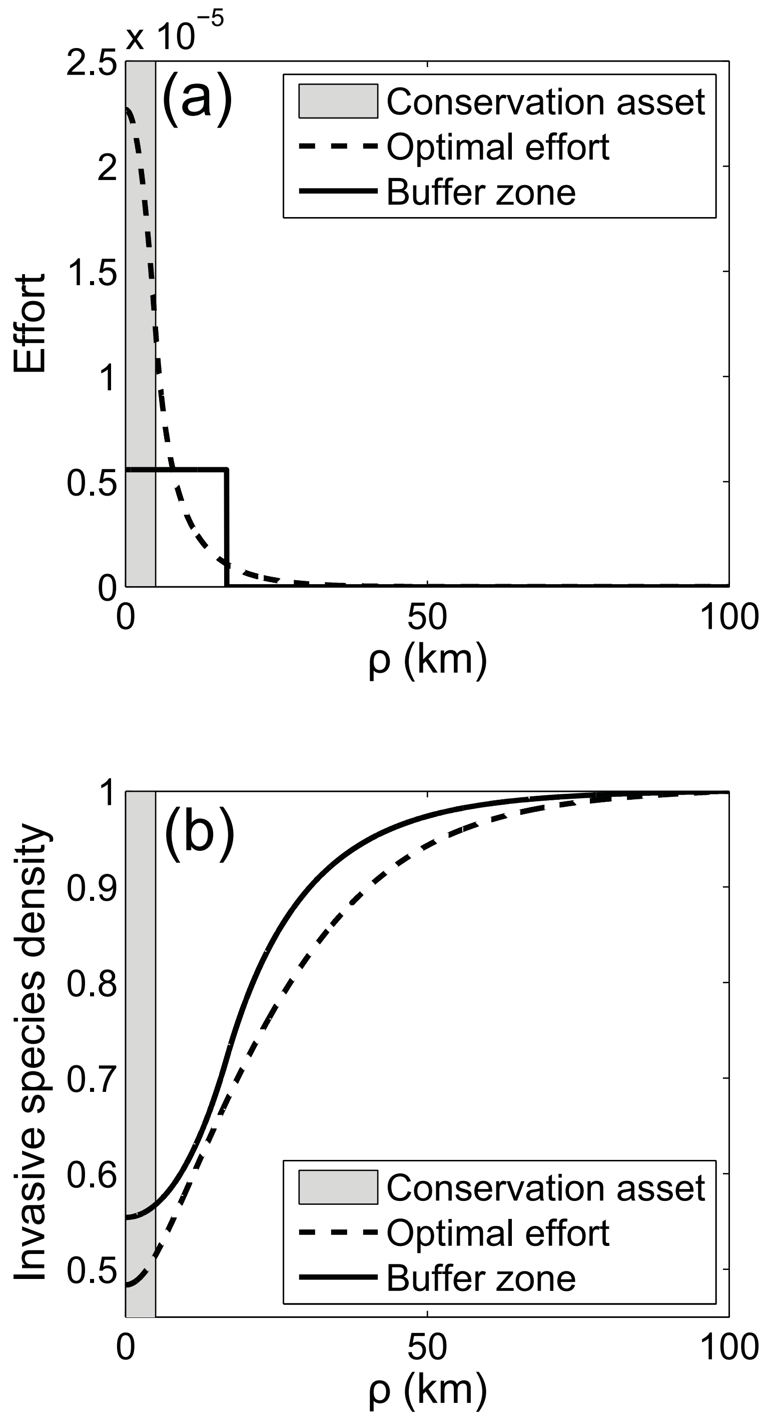
Optimal eradication time (years)
q
r=1.5
r=1
r=0.5
0
10
20
30
40
50
60
70
80
90
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8

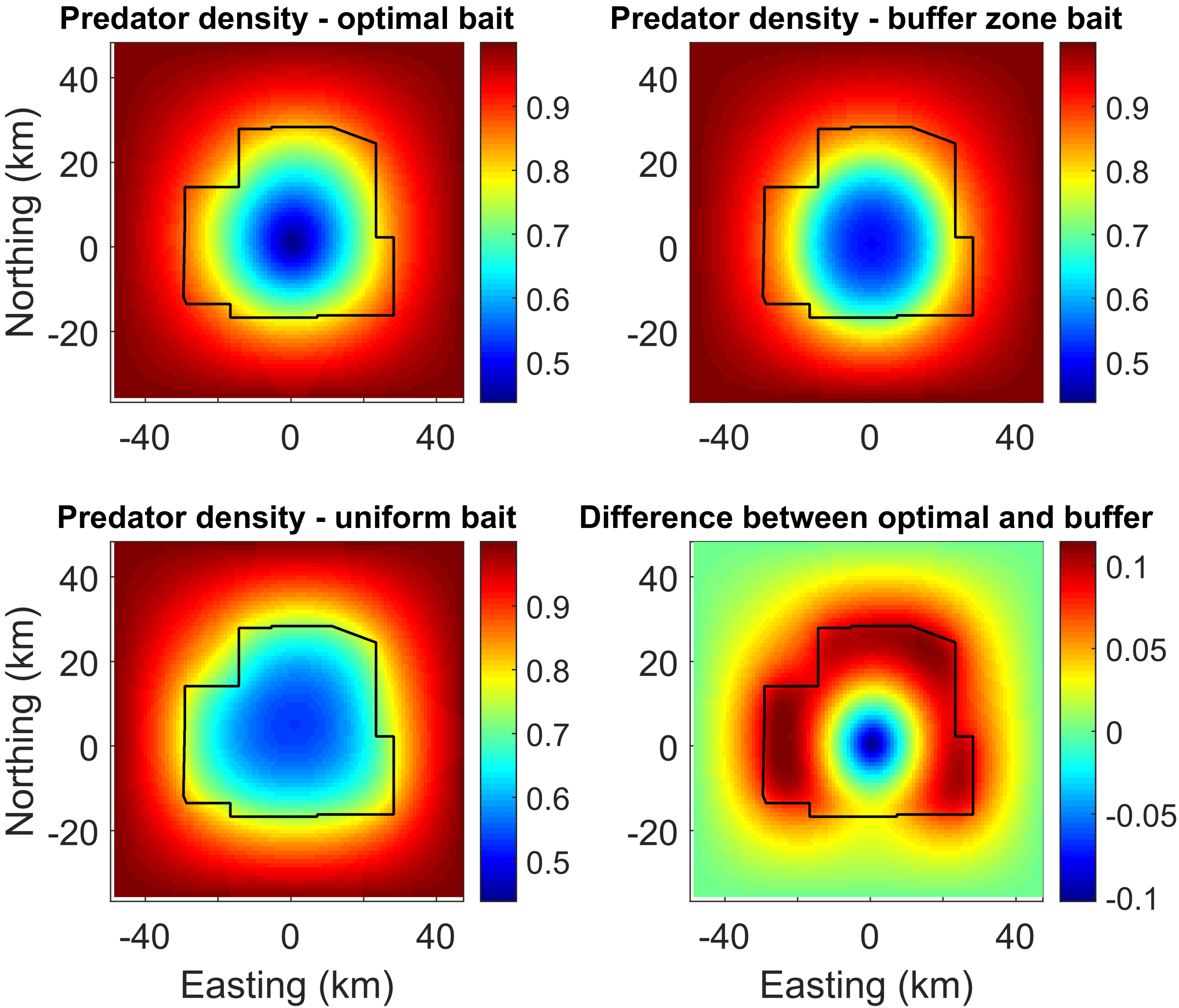


Cat density
Years
Control effort



q = 0.1
q = 0.9
100
90
80
70
60
50
40
30
20
10
0
0
0.2
0.4
0.6
0.8
1
Off−season control effort
(% of on−season allocation)
Off−season relative effectiveness (μ_0)


x 10^−5
2.5
2
1.5
1
0.5
0
Effort
(a)
Conservation asset
Optimal effort
Buffer zone
0
50
100
ρ (km)
1
0.9
0.8
0.7
0.6
0.5
Invasive species density
(b)
Conservation asset
Optimal effort
Buffer zone
0
50
100
ρ (km)



Predator density - optimal bait
Predator density - buffer zone bait
Predator density - uniform bait
Difference between optimal and buffer
Northing (km)
Easting (km)
40
20
0
-20
-40
0.9
0.8
0.7
0.6
0.5
0.1
0.05
-0.05
-0.1