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A simple approach to optimal control of invasive species

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Abstract

The problem of invasive species and their control is one of the most pressing applied issues in ecology today. We developed simple approaches based on linear programming for determining the optimal removal strategies of different stage or age classes for control of invasive species that are still in a density-independent phase of growth. We illustrate the application of this method to the specific example of invasive *Spartina alterniflora* in Willapa Bay, WA. For all such systems, linear programming shows in general that the optimal strategy in any time step is to prioritize removal of a single age or stage class. The optimal strategy adjusts which class is the focus of control through time and can be much more cost effective than prioritizing removal of the same stage class each year.

Keywords: Biological invasions; Eradication; Linear programming; *Spartina alterniflora*

1. Introduction

Invasive species have large and widespread impacts, resulting in high ecological and economic costs (Elton, 1958; Anonymous, 1993; Perrings et al., 2002; Hulme, 2003; Pimentel et al., 2005). Given this, there have been a number of attempts to help determine the most effective control strategies for invasive species (Moody and Mack, 1988; Byers et al., 2002; Secord, 2003; Leung et al., 2002; Taylor and Hastings, 2004; Buhle et al., 2005; Saphores and Shogren, 2005). A full treatment of the problem would require nonlinear models, and would therefore fall within the realm of dynamic programming (Bellman and Dreyfuss, 1962; Mangel and Clark, 1988). However, this approach is computationally intensive, meaning that population sizes can be described only by a relatively small number of discrete states, rather than as continuous variables. This is particularly problematic when attempting to devise control strategies for species over a relatively long time horizon. Another alternative approach would be to phrase the problem in continuous time and use methods from optimal control (e.g., Clark, 1990), but this formalism also leads to complex mathematical problems since solutions are difficult to obtain numerically for all but the simplest cases. There is, therefore, a pressing need to develop an approach to the control of stage-structured invasions that is amenable to simple calculations.

Under the assumption that in the early stages of an invasion, the population dynamics can be described by a linear (i.e., density independent) model, we use linear programming (Dantzig, 1963) to determine optimal control strategies, greatly simplifying the kinds of calculations required. We use this framework to derive some general principles for the optimal design of physical (rather than biological) control strategies for invasive species that focus on removal, not changing the life history. We further illustrate the application of this approach with the specific example of *Spartina alterniflora* Loisel., a saltmarsh grass that is native to the Atlantic and Gulf coasts, but invasive on the Pacific Coast of North America (Civille et al., 2005). Using parameters appropriate for this species (Taylor et al., 2004), we show how a strategy which adjusts the classes that are the focus of control through time can be much more cost effective or efficient than prioritizing removal of the same stage class each year.

Linear models of population dynamics have been extensively studied (Caswell, 2001) and used to consider

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the effects of changes in the parameters describing survival, growth rates and reproduction on the dynamics of a population. However, the problem of control of an invading species, especially at an early stage, can be different, by focussing on elimination by removal rather than on reducing the growth rate of the species so it decreases through time. Rather than looking at the well-studied question of how changes in the parameters can change the population growth rate from positive to negative, we shall instead focus on the very different problem of the effect of removal of individuals from various stage classes on population levels. Here, we will demonstrate how to pose the problem in a form suitable for solution by linear programming. We can then determine an optimal answer to the question of how to deploy resources for removal of an invasive, either by minimizing costs required to achieve a desired outcome, or by producing the most desirable outcome in the face of limited resources (expenditures) (Shogren and Tschirhart, 2005).

2. Methods

The dynamics of a linear age- or stage-structured population with k classes in the absence of control are described by the classic equation (Caswell, 2001):

$$N_{t+1} = LN_t, \tag{1}$$

where the entries l_{ij} in the $k \times k$ matrix L give age- or stage-specific growth and survival rates and fecundities. Given the focus on invasion of a plant, we describe the current state of the system by the amount of area occupied by individuals of different ages. Thus, N_t is a vector of length k where the jth entry is the area occupied by individuals of age or stage j. The area removed by control at the start of year $t+1$ is denoted by the vector H_{t+1} of size k, so that with control, the dynamics are given by

$$N_{t+1} = L(N_t - H_{t+1}). \tag{2}$$

Therefore, if the initial population is N_0, the population after T years of control is given by

$$N_T = L^T N_0 - \sum_{i=1}^{T} L^{T+1-i} H_i, \tag{3}$$

i.e., the population size is found by considering how what is removed in a given year propagates linearly and represents a missing portion in future years.

For two cases, the specification of the optimal control strategy is relatively obvious. We denote the cost per unit area of removing stage j by c_j, which we assume is fixed over time. Looking just one year ahead (i.e., if $T = 1$), to maximize the area removed LH_t while minimizing the total cost, it is clear that we should remove as much as possible from the age class that has the highest value for $\sum_i l_{ij}/c_j$, then from the next highest, etc. In contrast, for asymptotic, long term, results, it is the reproductive value (Fisher, 1930; Caswell, 2001) that plays the key role, since the reproductive value can be used to determine the contribution of current classes to future population sizes. If we use w_j to denote the reproductive value of age class j, then a simple calculation shows that we should remove as much as possible from the age class that has the highest value for w_j/c_j, then from the next highest, etc.

Since these two quantities clearly can be different we see how the time horizon plays a role. Therefore, we need to understand how to choose the removal amounts in given years that will provide an optimal policy over a fixed time horizon of T years, which we will show can be solved as a linear programming problem. The definition of a linear programming problem (Dantzig, 1963) is that the quantity to be optimized is a linear function of the control variables, that all the control variables are non-negative, and that the constraints can be expressed in terms of linear combinations of the control variables.

We now show how to express our problem as a linear programming problem. The control variables are $H_{t,j}$, the amount of class j that is removed in year t, which must satisfy the usual non-negativity constraint of linear programming,

$$H_{t,j} \geqslant 0. \tag{4}$$

The other constraints that apply in all formulations arise from the requirement that we cannot remove more of any stage class than is already present, i.e. in the tth year of control, $N_{t-1,j} - H_{t,j} \geqslant 0$. From (3) this set of constraints can first be expressed in vector form as

$$\sum_{t=1}^{s} L^{s-t} H_t \leqslant L^{s-1} N_0, \tag{5}$$

where s takes on all values from 1 to T. Thus, in a system with n classes, (5) actually represents nT constraints, and there are nT variables.

Further constraints depend on the specific problem. One might limit the available budget in each year, and it is simple to add discount rates reflecting standard economic principles (Clark, 1990).

As one specific example, we assume that the costs are fixed in every year (for simplicity the same value in each year) and the goal is to minimize the area occupied by the invader at the end of a T year planning horizon. Here, the additional constraints are (one per year)

$$\sum_{j=1}^{n} c_j H_{t,j} \leqslant C \tag{6}$$

and the objective function is to minimize the sum of the components of

$$L^T N_0 - \sum_{i=1}^{T} L^{T+1-i} H_i, \tag{7}$$

producing a problem that can be solved by very simple linear programming algorithms (Press et al., 2002).

The same constraints apply when the goal is eradication by year T at minimal total cost with discount rate, except that the inequality (5) evaluated at $s = T$ now becomes a strict equality, and the objective function is

$$\sum_{t=1}^{T} \sum_{j=1}^{n} c_j e^{-\gamma t} H_{t,j}, \tag{8}$$

where γ is the discount rate.

More generally, we could apply (8) to look at any level of control and, in particular, when the goal is to reduce the invaded area below a threshold. The approach we develop here is quite general and could be used in a variety of problems.

3. Results

Our numerical examples use a simple representation of the dynamics of invasive *Spartina alterniflora* in Willapa Bay, WA. The population is divided into three classes: seedlings, isolated plants (isolates) and agglomerations of plants (meadows). All seedlings mature to become isolates, a fraction of which are absorbed into meadows the following year. Isolated plants grow faster vegetatively than meadows, but meadows have much higher rates of seedling production. The population growth matrix (L) is derived from a linearization of a previous model of invasive *Spartina* (Taylor et al., 2004). All costs are scaled relative to the cost per unit area of the most expensive classes to remove (here, we assume meadows are cheapest to remove, while seedlings and isolates have the same removal cost).

A summary of the model parameters and variables, along with the default parameter values, is given in Table 1.

When the objective is to minimize the population remaining after 10 years of control, the outcome of the optimal strategy is seen to be highly sensitive to the annual budget available for control (Fig. 1a). Moreover, the optimal control strategy is time varying (Fig. 1b), switching from removing the class with the highest reproductive value per unit cost (isolated plants) to that which contributes most to next season's population per unit cost (meadows). The time-varying strategy can perform dramatically better than any fixed strategy, and can even make the difference between control and escape of the invasive (Fig. 1c). Here a fixed strategy constitutes targeting all resources to the removal of a given stage class in any year and then if there are resources remaining after removing all of the given stage class, a second class is prioritized, followed by a third, etc.

When the goal of control is eradication at minimum cost (Fig. 1d), the timing of control is highly sensitive to the size of the economic discount rate relative to the population growth rate; essentially, higher discount rates shift the timing of control towards the end of the time frame.

There have been two previous attempts to model *Spartina* control (Taylor and Hastings, 2004; Grevstad, 2005). The former employs a nonlinear stage-structured model and uses a genetic algorithm to find optimal control strategies, while the latter tests the effects of a discrete set of control strategies on a spatially explicit model. Both reach the conclusion that under most circumstances, the most effective control strategy is to prioritize removal of isolates. This is under the assumption that the costs of removing meadows and isolates are equal, in which case isolates have the greatest short- and long-term contributions to population growth per unit cost and, hence, the optimal control strategy predicted by this model would be the same. However, isolates are typically located further offshore than meadows, and are consequently exposed for shorter periods at low tide, so that the cost per unit area of control over a growing season is likely to be higher for isolates. In this situation, the switching strategy adopted by the linear program can perform significantly better than prioritizing isolates.

Table 1
Model parameters and variables

Symbol	Definition (and default value)
N_t	Population size in year t
H_t	Area removed in year t
L	Matrix of population growth, $\begin{pmatrix} 0 & 0.0000646 & 0.0177 \\ 1 & 1.115 & 0 \\ 0 & 0.265 & 1.107 \end{pmatrix}$
N_0	Initial population size (km^2), $\begin{pmatrix} 0.00008226 \\ 0.01186 \\ 0.005977 \end{pmatrix}$
T	Number of years of control (10)
c	Relative cost per km^2 of removal of each stage class, $\begin{pmatrix} 1 \\ 1 \\ 0.4 \end{pmatrix}$
C	Maximum annual budget
γ	Annual discount rate

4. Discussion

We have shown that optimal control strategies, based on removal rather than change of life histories, for invasive species can be determined using linear programming. This has three important consequences. First, it is known (Dantzig, 1963) that the optimal solution to a linear programming problem lies at a vertex (of the constraints). This leads to the immediate conclusion that an optimal control strategy in any given year will always be to invest the maximum effort possible into the removal of a single stage class, only investing resources in other classes if the first class has been completely removed. Second, in general, a problem that requires a solution over time like the one we have posed would fall in the class of dynamic programming problems which are difficult to solve numerically. In contrast, the solution of linear programming problems is very easy, and even quite large problems (with many years and many age or stage classes) can be solved very rapidly numerically (minutes or less on a typical personal computer) to very high accuracy. Thus, this approach is potentially of use in the design and implementation of practical management strategies under alternate assumptions about costs of control and estimates of life history parameters of different stage classes. Third, the general approach presented here can give valuable insights into why certain control strategies are more efficient than others. Such insights can help us understand the results of more complex models which incorporate a greater degree of biological realism for specific systems (e.g., Buckley et al., 2003).

Clearly, there are limitations to our approach. We have limited ourselves to regions where the population dynamics can be described by a linear model. Explicit consideration of spatial aspects is outside the realm of our approach as presented here. When the population is so large that density dependence starts to play a role, a different approach is needed, but in these cases the kind of control approach we advocate is likely to be of less importance. Similarly, if an invasive exhibits a strong Allee effect (negative growth rates at low densities), a different approach to designing management strategies might be more useful. However, weak Allee effects (arising, for example, through slower growth rates for seedlings) can be described by a model (Taylor and Hastings, 2004) that would be amenable to an analysis like that presented here. Our approach is sufficiently flexible to deal with other constraints arising from the biology. For example, if the different stage classes of the invasive occur together, a spatially structured model in which control targets specific

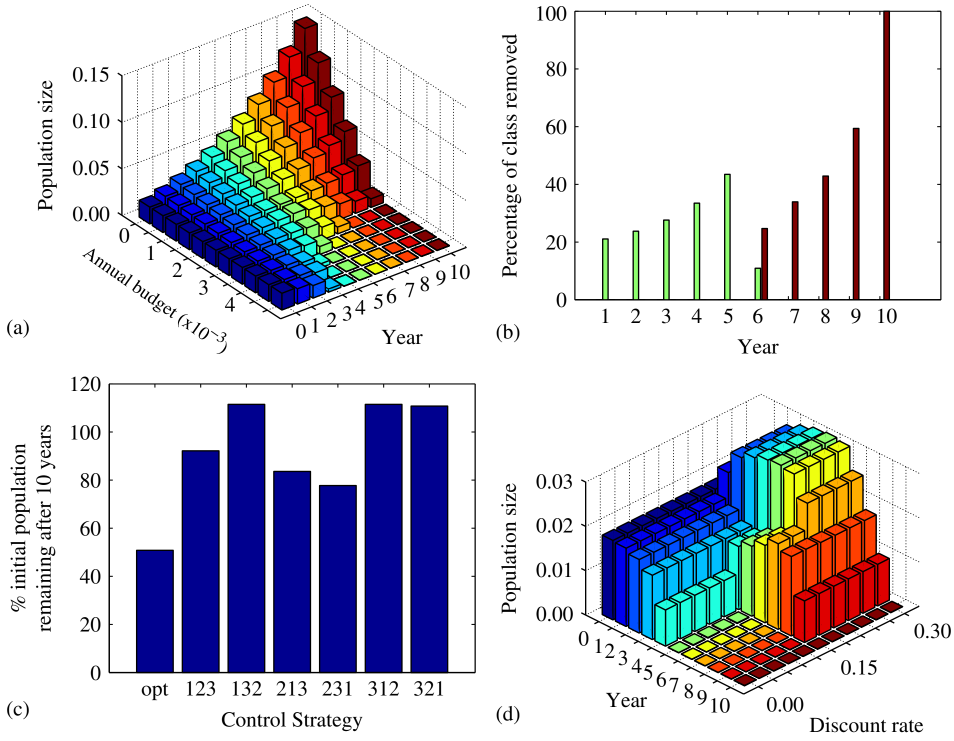

Fig. 1. Optimal control of invasive species. (a) Population size as a function of time and the annual budget allocated to control, when the objective is to minimize the population within 10 years subject to budget constraint. The model parameters and variables are summarized in Table 1. (b) The fraction of each stage class (green for isolates, red for meadows) removed by control in each year under the optimal control strategy. The annual budget, scaled relative to the removal cost of the most expensive class to remove, is $C = 0.0025$ (this corresponds to the removal cost of $2500\,\mathrm{m}^2$ of isolates, approximately 14% of the initial invaded area). (c) Relative performance of the optimal strategy for the above annual budget compared to sequential removal of each of the stage classes (123 denotes a strategy that removes seedlings [1] first, then isolates [2], then meadows [3], etc.). The relative performance is measured by the fraction of the initial population size remaining after 10 years of control. (d) Population size as a function of time and the annual discount rate, when the objective is to eliminate the invasive whilst minimizing total expenditure. The annual budget, $C = 0.004$ (sufficient to remove 22% of the initial area).

patches based on their net reproductive output would be more appropriate.

Our goal here has not been to develop detailed recommendations for a specific invasion, but to begin to develop general principles and to look at the utility of an approach based on linear programming. Although we have used the example of *Spartina alterniflora*, even in this case there are important issues outside the realm of our simple model (e.g., Secord, 2003). It is also useful to compare our results to the ones in Taylor and Hastings (2004) for control of *Spartina* that used other methods appropriate when nonlinearities (density dependence or Allee effects) are included. In particular, the case with Allee effects differs from the case we studied here in that the optimal strategy with Allee effects can be to focus removal on more than one class at a time. Thus, the results for a model without density independence highlight the role played by the Allee effect in the choice of management strategies.

Another key assumption in our model has been that costs are directly proportional to the number removed. Clearly, this may not be the case for several reasons. For example, it might be more costly to remove the last few individuals of a class, in analogy to similar problems in fish harvesting that look at the catch as a function of effort (Clark, 1990). Thus, conclusions about removal of all of a single class may need to be modified if this more realistic assumption is included.

However, our simple approach does provide important general insights and directions for designing control strategies. We have demonstrated that the approach we have used leads to time-dependent control strategies that are in fact more efficient (less costly, or achieving more control at the same cost) than a removal strategy that does not vary with time. Our results correspond to the heuristic concept of first directing control efforts at those age or stage classes with the highest ratio of reproductive value to control cost, and then at the end of a fixed time period directing efforts at those classes with the highest ratio of areas controlled relative to cost. Our work is able to confirm this heuristic control strategy and to determine when (in time) strategy switches should be made, and as well to demonstrate how large the difference in efficacy of control is when the time varying strategy is used. Moreover, the effect of including discount rates can dramatically affect the timing of control. In addition to these general results, we have shown, using the specific example of a *Spartina alterniflora* invasion, that the optimal control strategy can easily be calculated, and potentially is far superior to ad hoc strategies.

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