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Minimizing invader impacts: Striking the right balance between removal and restoration

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Abstract

Invasive species can cause severe damage in their introduced range; this damage often persists even after removal of the invader. In order to efficiently allocate a limited budget between invader removal and restoration of habitat from which the invader has been removed, it is vital to quantify the impacts of the invasion within an economic context. Here we develop optimal management strategies for biological invasions, which minimize both the direct economic costs of removal and restoration, and the ecological costs of present and future damage caused by the invasion. We demonstrate how this can be formulated as a linear programming problem, enabling the fast and efficient computation of optimal solutions. Using a simple example, we outline some general principles for the optimal control of an invader that damages its environment. Notably, we show that the most effective strategies often switch the priority of removal and restoration over time, and outline the conditions under which restoration is prioritized over removal. The proportion of total funds allocated to restoration will depend on the annual budget, the persistence of damage, and the relative costs of damage, removal and restoration.

Keywords: Invasion; Control; Eradication; Restoration; Linear programming

1. Introduction

The invasion of exotic species outside of their native range can have a strong negative impact on ecosystem function and services (e.g., Liebhold et al., 1995; Williamson, 1996), and attempts to control or reverse their spread can be difficult and costly (Byers et al., 2002; Pimentel et al., 2005). Invasive species often leave lasting damage which persists long after their removal: an example of this is the invasion of exotic cordgrass species (*Spartina* spp.) along the Pacific coast of the USA. Open mudflat is converted into dense *Spartina* meadows, reducing foraging opportunities for many shorebird species and radically changing the benthic community composition (Levin et al., 2006). The dense root mass of *Spartina* accumulates sediment, changing the tidal height (Rosso et al., 2006) and even after control efforts, the resulting elevated mudflat persists and supports a very different vegetative community (J.G. Lambrinos, pers. comm.).

Two ways in which human intervention can mitigate the impact of an established invasion are to remove the invader (for example through eradication or trapping), and in areas from which the invader has been removed, to restore habitat damaged by prior occupation by the invader (for example through reintroduction of native species). While the former intervention is effective at slowing or preventing the invader from occupying new sites, the latter is often necessary to restore previously invaded sites to their prior condition over ecologically relevant timescales. Given the constraints of a limited budget, one of the most important questions facing conservation planners following an initial removal effort is whether to invest in further removal, or in restoration of sites from which the invader has been removed, but which remain damaged.

There have been many attempts to devise optimal control strategies for invasive species using mathematical models (Higgins et al., 1997; Moody and Mack, 1998;

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Eisworth and Johnson, 2002; Byers et al., 2002; Leung et al., 2002; Taylor and Hastings, 2004; Leung et al., 2005; Finnoff et al., 2005). Most of these approaches incorporate some degree of nonlinearity, either in the intrinsic population dynamics of the invader (reflecting that eventually competition for space and resources will slow the rate of population expansion), via the relationship between the control budget and the impact of control, or through interactions between different economic agents. However, the incorporation of nonlinearity into the model to be optimized requires solution by truly computationally intensive methods from stochastic dynamic programming (Bellman and Dreyfuss, 1962). This becomes problematic over long time horizons due to the 'curse of dimensionality' (Bellman, 1961), which means that the population of the invasive species can only be described by a relatively small set of discrete states; dealing with a large number of states is a problem which is still challenging even for current computer power.

While density dependent effects are eventually certain to be important in population regulation, many species expanding into a new range exhibit density-independent growth over many generations. Examples include the expansion of the Collared Dove (*Streptopelia decaocto*) in Western Europe (Hudson, 1965), and the spread of invasive *Spartina alterniflora* in Willapa Bay, WA (Civille et al., 2005), which has been exponential for almost a century. Under the assumption that the effects of density dependence on the initial growth of the invader are small, the population dynamics can be described by a linear model. This has the advantage that the types of calculation required for the optimization are greatly simplified, while the conceptual clarity of the simpler model hones our intuition as to why certain control strategies are optimal. Moreover, by the time density dependence is important, control measures based on removal are highly unlikely to be effective. Surprisingly, few studies have employed linear models to describe the dynamics and control of invasive species (but see Buhle et al., 2005; Hastings et al., 2006).

The aim of this paper is to provide some general guidelines on the allocation of a finite control budget between invader removal and restoration of previously invaded sites. We seek to minimize the total cost of the invasion; we evaluate this total cost by defining explicitly the costs of present and future ecological damage in invaded and controlled areas, and expenditure on removal and restoration. We show how to formulate this as an optimization problem for an exponentially growing population, in a form which can be solved rapidly and efficiently using linear programming (Dantzig, 1963), and briefly illustrate how to expand the approach for an age- or stage-structured population. We compare the optimal strategy derived from linear programming to an *ad hoc* strategy which always prioritizes removal over restoration. We find numerous cases in which always prioritizing removal is not optimal: depending on the life-history and economic parameters, a strategy that switches to prioritizing restoration, or even non-intervention, can be the optimal solution. The optimal strategy will always perform at least as well as a fixed strategy, due to its flexibility to switch among removal, restoration and non-intervention in different time steps; linear programming enables us to calculate exactly when such switches should occur. The biological and economic conditions under which habitat restoration may be prioritized over invader eradication are outlined in Section 5.

2. Model and methods

2.1. Model

Here we present a discrete-time population model to describe the dynamics of the area occupied by an invader in the early (density-independent) phase of expansion, and of the damaged area left after removal of the invader. Control takes the form of invader removal, or restoration of areas from which the invader has previously been removed. Verbally, the model works as follows (see also Fig. 1). The area occupied by the invader after t years of removal and regrowth is denoted by N_t, and the resulting damaged area remaining after t years of restoration and natural recovery is denoted by D_t. In year $t+1$, there is a control period during which the area of the invader removed is H_{t+1} and the damaged area restored is R_{t+1}. After the control period, the invader increases the area it occupies by a factor L (the population growth rate). The damaged area is updated to include the area of the invader just removed, and following natural recovery, a fraction P remains damaged.

The dynamics of the invaded and controlled areas in year $t+1$ are therefore described by

$$N_{t+1} = L(N_t - H_{t+1}) \qquad (1)$$

and

$$D_{t+1} = P(D_t - R_{t+1} + H_{t+1}). \qquad (2)$$

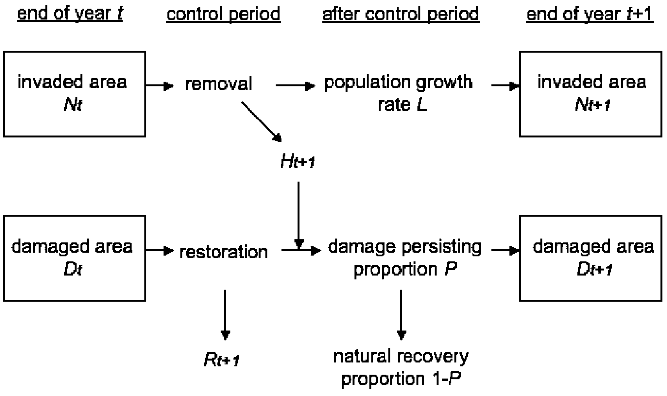

Fig. 1. Schematic of the model structure, showing the area occupied by each habitat state (invaded and damaged: boxes) and the processes that cause changes in these areas (invader removal and subsequent population growth; restoration and subsequent natural recovery of damaged areas: arrows).