Optimal control of spatial-dynamic processes: the case of biological invasions

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Abstract:

This study examines the spatial nature of optimal bioinvasion control. We develop and parameterize a spatially explicit two-dimensional model of species spread that allows for differential control across space and time, and we solve for optimal control strategies. We find that the qualitative nature of optimal strategies depend in interesting ways on aspects of landscape and invasion geometry. For example, we show that reducing the extent of exposed invasion edge, through spread, removal, or strategically employing landscape features, can be an optimal strategy because it reduces long-term containment costs. We also show that optimal invasion control is spatially and temporally "forward-looking" in the sense that strategies should be targeted to slow the spread of an invasion in the direction of greatest potential long-term damages. These and other novel findings contribute to the largely nonspatial literature on optimally controlling invasions and to understanding control of spatial-dynamic processes in general.

Keywords: invasive species; spatial-dynamic processes; spatial spread; reaction-diffusion; management; cellular automaton; eradication; containment; spatial control; integer programming

1. Introduction

Much of the economic research on bioinvasion management has framed the issue as a pest control problem, in which the population density of the invader is controlled. This literature has generally focused on the aggregate pest population, without consideration of its spatial characteristics (e.g., Pannell [20], Deen *et al.* [6], Saphores [27]). However, a critical feature of the invasive species problem is that invasions unfold over time and space. Invasions generally begin with the arrival of just one or a few individuals to a region. The population density of the invader may then increase at the arrival site by reproduction. In addition, the population may spread over space by dispersal, so that the initial population of invaders can eventually impact locations far from the site of initial colonization. Bioinvasions are thus characterized by spatial-dynamic processes, rather than by simpler dynamic processes.[1] Although spatial-dynamics of invasion spread has been a subject of empirical and theoretical study for many decades [e.g., 30], it only recently has been considered by economists in their research [17; 34].

Existing research on optimally controlling spreading invasions has primarily employed spatially implicit models of invasion spread, providing insights about how invasion characteristics, such as costs, damages, and invasion size, affect the optimal timing and amount of control (e.g., Sharov & Liebhold [28], Eiswerth & Johnson [7], Olson & Roy [18], Potapov *et al.* [23], Wilen [34], and Olson & Roy [19]).[2] However, few studies have explicitly considered the spatial characteristics of bioinvasions and hence there is less understanding about *where* to allocate optimal control efforts or the effect of spatial characteristics of the invasion or landscape

[1] The concept of spatial-dynamic processes was introduced by Sanchirico and Wilen [24] to discuss harvesting from metapopulations. Articles by Wilen [34] and Smith, Sanchirico, and Wilen [32] discuss existing work on the economics of spatial-dynamic processes with particular focus on renewable resources.

[2] With spatially implicit models, the state variable generally measures the size or extent of invasion and varies across time as a function of itself and the quantity of control; space is not indexed. This approach reduces the spatial-dynamic invasion problem to a simpler dynamic problem that can be used to identify how control should be applied over time. However, without explicit spatial consideration, controls cannot be applied differentially across space and spatial aspects of the invasion or control cannot be examined.

on optimal control choices.[3] This paper addresses these spatial aspects of invasion control, which are important for on-the-ground management of invasions. In addition, this paper contributes insights to the general problem of controlling spatial-dynamic processes.

In this study we show how basic economic parameters of the bioinvasion problem (e.g., cost, damages, discount rate) and spatial characteristics of the invasion and landscape influence the nature of optimal control in the more general spatial-dynamic setting. Our most interesting findings demonstrate the manner in which boundaries and geometry[4] of both the invasion and the landscape matter. For example, the location of an invasion relative to the boundaries of its potential range affects both the prospective damages and control costs, thereby affecting optimal control policies and the net present value of the invasion. In addition, small changes in the spatial configuration of the initial invasion, including shape and contiguity, can change the qualitative nature of optimal controls. This is often because the extent of the exposed invasion edge determines long-term containment costs. We find that the length of the exposed invasion front optimally can be reduced by employing landscape features and/or altering the shape of the initial invasion through spread or removal. We also show how optimal policies exhibit classic "forward-looking" behavior that characterizes optimal dynamic problems. In spatial-dynamic problems, however, optimal policies not only anticipate impacts over time, but they also look forward over space to determine where and when to apply various controls. In general, invasion

[3] Brock and Xepapadeas [3] derived modified Pontryagin Maximum Principle conditions applicable to continuous in time and space diffusion processes. One of their examples described a linear bioinvasion problem that they showed has Most Rapid Approach features, in which it is optimal to use extreme controls, do nothing, or hold the pest at a steady state. Potapov and Lewis [22] modeled optimal spread prevention in a network, in which dispersal between pairs of network nodes depended on the distance between the nodes. They approximated the dynamic optimal control problem with a simpler static problem. They found that, at equilibrium, the landscape can be fully or partially invaded, and in a partially invaded equilibrium, control efforts are concentrated along the invasion front. They also showed that if lakes are clustered, it could be optimal to prevent spread between clusters.
[4] Here we are referring to geometry in the mathematical sense that concerns size, shape, and relative position (i.e., location).

control is targeted to slow the spread of an invasion in the direction of greatest potential local or long-term damages, or in the direction where the costs of achieving control are low.

Our approach tackles the problem of optimal control of a spatial-dynamic bioinvasion process by stripping the problem to its essential features. We employ a spatially explicit, two dimensional invasion spread model that allows for differential control over both time and space. We model species spread with a cellular automaton model on a grid, in which each cell in the grid is invaded or not in each time period and spread occurs between adjacent cells at each time step.[5] This model approximates the basic pattern predicted with a reaction-diffusion process, which predicts a constant radial or linear rate of spread and provides a good description of observed spread patterns for a variety of species [10; 34].[6] Without control efforts, the invasion spreads to fill the entire landscape. However, control actions can be employed to prevent spread of the invasion between adjacent cells and to clear already invaded cells. Each control action is associated with a cost, and combinations of control actions can be used to eradicate, contain, or slow an invasion.

The simplicity of this discrete spatial spread model and the control options we allow provides important benefits. First, the model's specification enables reasonably fast solutions to the spatial-dynamic optimal control problem using integer programming, despite its high dimensionality.[7] In more general spatial-dynamic problems, high-dimensionality limits the size of the problem that can be solved [13; 22], thus limiting the questions that can be addressed. A

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[5] We use the term spread to refer to the process by which uninvaded cells become invaded through dispersal from already invaded locations. This process accounts for both reproduction and dispersal.

[6] Mathematically, reaction-diffusion equations describe how the concentration of one or more substances distributed in space changes under the influence of two processes: local reactions in which the quantity of the substances can change and diffusion which causes the substances to spread out in space. When modeling the spread of biological invasions or other organisms, the reaction process characterizes the species population growth. Thus, reaction-diffusion processes represent the combined processes of reproduction and dispersal.

[7] Even under the constraint of binary invasion states (i.e., each cell in the landscape grid is either invaded or uninvaded in each time period), the size of this optimization problem grows exponentially with the number of grid cells in the landscape and the number of time periods.

second benefit of the model's simplicity is that the intuition is more readily apparent from results. In more complex models it is difficult to identify what factors drive the outcomes; here we can identify specific assumptions and initial conditions that influence control strategies, and why.

To identify and illustrate the role of economic parameters and invasion and landscape geometry in determining optimal control policies, we run a number of comparative spatial-dynamic "experiments" in which we vary one aspect of the invasion while holding all other characteristics of the invasion constant.[8] We then compare the optimal control results across the different scenarios and use these to synthesize a better understanding of invasive species control in a spatially explicit landscape.

In the next section we describe the invasion spread model, economic model, and solution approach. In section 3 we describe the results of our comparative spatial-dynamic "experiments" and derive features of optimal policies for a number of specific spatial-dynamic problems, with an eye toward deriving general qualitative properties of these systems. In section 4, we summarize and discuss results in the context of existing literature. We conclude in section 5 by highlighting some general principles about controlling spatial-dynamic processes that we have deduced from our bioinvasion case study.

2. Methods

2.1 Spread model

We employ a deterministic, discrete time, cellular automaton model to represent the spread of an invasive species. The landscape is represented as a grid of square cells that comprises the total potential extent of contiguous invasion. Each cell is labeled by its row *i* and

[8] Comparative statics methods vary a parameter and determine how equilibrium solutions to static problems change. Comparative dynamics methods vary a parameter and examine how an optimal dynamic solution path changes; we vary parameters and examine how the full spatial-dynamic solution changes, a technique appropriately termed comparative spatial-dynamics.

column j in the landscape grid, and each cell can take on one of two states: invaded ($x_{i,j} = 1$) or uninvaded ($x_{i,j} = 0$). In the absence of any human intervention, the species spreads from invaded cells to adjacent, uninvaded cells in each time period, based on rook contiguity. Thus, if cell (i,j) were invaded at time t, cells (i,j), (i,j+1), (i,j-1), (i+1,j), and (i-1,j) would be invaded in the next time period. In each subsequent time step, all cells sharing a contiguous border with an invaded cell also become invaded. This model does not allow for long distance dispersal and implicitly assumes absorbing landscape boundaries by defining a finite landscape and a binary invasion status for each cell.

The size and shape of the landscape grid reflect the potential area that a species can invade, which is determined by biotic or abiotic constraints and can be predicted using ecological niche modeling [8; 21]. In addition, an appropriate combination of cell size and time unit must be selected to model specific species. This choice of grid cell size and time interval are closely linked, because the model assumes that the invasion spreads into adjacent uninvaded space at a rate of one grid cell per unit time.

2.2 Economic model

Landscape-level damages at each point in time are directly proportional to the number of invaded grid cells, with marginal (and average) damages equaling d per cell invaded. Spread of the invasion into an uninvaded cell can be prevented in each time period by applying control along all boundaries that the uninvaded cell shares with cells that already are invaded. Thus, the cost of excluding invasion from a cell increases with the number of adjacent (rook contiguous) invaded cells and equals *invaded_neighbors*b*, where b is the cost of preventing invasion along each boundary for one time period and *invaded_neighbors* is the number of invaded adjacent cells ($0 \leq$ *invaded_neighbors* ≤ 4). Additionally, once a cell has been invaded, it remains invaded unless the invasion is removed from the cell at a cost *e*. For a cleared cell to remain uninvaded in the following time periods, adjacent invaded borders require control at a cost *b* per invaded border per time period. If the entire landscape has been cleared, there are no subsequent control costs.

To parameterize this model, economic parameters must be scaled to match the biological model. Specifically, damages and costs are tied to the size of the cell and should be scaled accordingly. Similarly, the discount rate must be scaled to match the unit of time. By separately parameterizing removal costs *e* and spread prevention costs *b*, this model allows flexibility in specifying control costs based on species characteristics. For many species, such as for plants with long-lived seed banks, spread prevention is much less costly than removal, and this can be reflected in the choice of cost parameters.

2.3 Solution approach

Optimal control of the invasion requires minimizing the present value of the sum of control costs and invasion damages across space and time. We formulate this optimization problem as an integer programming problem as follows:

Minimize: $$\sum_{t\in T, t>0} \beta_t * \left(\sum_{(i,j)\in C} x_{i,j,t} d + \sum_{(i,j)\in C} y_{i,j,t} e + \sum_{(i,j,k,l)\in N} z_{i,j,k,l,t} b \right) \quad (1)$$

subject to:

$$x_{i,j,0} = \underline{x}_{i,j} \qquad \forall (i,j)\in C \quad (2)$$

$$y_{i,j,0} = 0 \qquad \forall (i,j)\in C \quad (3)$$

$$z_{i,j,k,l,0} = 0 \qquad \forall (i,j,k,l)\in N \quad (4)$$

$$x_{i,j,t} \geq x_{i,j,t-1} - y_{i,j,t} \qquad \forall (i,j)\in C, t\in T, t\geq 1 \quad (5)$$

$$x_{i,j,t} \geq x_{k,l,t-1} - z_{i,j,k,l,t} - y_{i,j,t} \qquad \forall (i,j,k,l)\in N, t\in T, t\geq 1 \quad (6)$$

$$x_{i,j,t} \in \{0,1\} \qquad \forall (i,j) \in C, t \in T \tag{7}$$

where

$(i,j) \in C$ indexes cells by row i and column j, and C is the set of all cells in the landscape

$(i,j,k,l) \in N$ indexes pairs of neighboring cells, where $(i,j) \in C$ is the reference cell, $(k,l) \in C$ is one of its neighbors, and N is the set of all neighboring cell pairs

$t \in T$ indexes time, where $T = \{0,1,2,...,T_{\max}\}$

$x_{i,j,t} \in \{0,1\}$ is the state of cell (i,j) at time t, where $x_{i,j,t} = 1$ if the cell is invaded and $x_{i,j,t} = 0$ otherwise

$y_{i,j,t} \in \{0,1\}$ is a binary choice variable indicating if invasion is removed from cell (i,j) at time t, where $y_{i,j,t} = 1$ if the cell is cleared and $y_{i,j,t} = 0$ otherwise

$z_{i,j,k,l,t} \in \{0,1\}$ is a binary choice variable indicating if control efforts are applied along the border between cell (i,j) and cell (k,l) at time t to prevent spread from cell (k,l) to cell (i,j), where $z_{i,j,k,l,t} = 1$ if the border is controlled and $z_{i,j,k,l,t} = 0$ otherwise

$\underline{x}_{i,j} \in \{0,1\}$ is the initial state (t=0) of invasion for cell (i,j)

β_t is the discount factor at time t (t>0), where $\beta_t = (1+r)^{1-t}$ and r is the discount rate

d is the damage incurred per time period for each cell that is invaded

e is the cost of removing invasion from a cell

b is the cost per time period of preventing invasion along a border between neighboring cells

Equation (2) establishes the initial state of the landscape by defining which cells are invaded at t=0. Equations (3) and (4) specify that control efforts do not begin until the first time period. Condition (5) requires that a cell that was invaded in the previous time period remains invaded in the current time period unless removal efforts are applied. Equation (6) requires that cell (i,j) become invaded at time t if it had an invaded neighbor in the previous time period, unless invasion is removed from cell (i,j) or control is applied along the invaded border; this condition must hold for cell (i,j) with each of its neighbors. Individually, constraints (5) and (6) provide necessary conditions for a cell to be uninvaded at time t; together, constraints (5) and (6) provide sufficient conditions for a cell to be uninvaded at time t. Specifically, an uninvaded cell (i,j) will become invaded at time t+1 unless all of the borders it shares with invaded cells at time t are controlled at time t+1 or removal efforts are applied to cell (i,j) at time t+1. An invaded cell (i,j) at time t remains invaded at time t+1 unless removal efforts are applied to it at time t+1.

For infinite time horizon problems, this system achieves a steady state equilibrium in which the proportion of invaded landscape ranges from none to all and a positive level of control is applied to landscapes that are partially invaded. In fact, with an infinite time horizon, time consistency requires that the system has reached this equilibrium if the invasion landscape remains unchanged between two time periods. In contrast, for a finite time horizon, the system can reach and maintain a steady state equilibrium for many time periods, but can depart from the steady state towards the end of the time horizon. An infinite time horizon problem can be solved with a finite time horizon specification by choosing an appropriate terminal condition or salvage value. However, specifying an appropriate terminal value is difficult because it depends on the equilibrium state of the system. To deal with this difficulty, the equilibrium solution can be "locked in" using constraints after the equilibrium has been reached, and a salvage value terminal function can be added based on the resulting solution. Here we employ an infinite time horizon, so we add the following constraints to the model defined above:

$$y_{i,j,t} = y_{i,j,t\_mid} \qquad \forall (i,j) \in C, t \in T, t > t\_mid \tag{8}$$

$$z_{i,j,k,l,t} = z_{i,j,k,l,t\_mid} \qquad \forall (i,j,k,l) \in N, t \in T, t > t\_mid \tag{9}$$

$$x_{i,j,t} = x_{i,j,t\_mid} \qquad \forall (i,j) \in C, t \in T, t > t\_mid \tag{10}$$

where 1< *t_mid*<*Tmax*. We choose *t_mid* and *Tmax* large enough for an equilibrium to reached at *t*<*t_mid* and maintained. We calculate the terminal value as:

$$\sum_{t=T+1}^{\infty} \beta_t * \left(\sum_{(i,j)\in C} x_{i,j,T} d + \sum_{(i,j)\in C} y_{i,j,T} e + \sum_{(i,j,k,l)\in N} z_{i,j,k,l,T} b \right) \tag{11}$$

and include this value in the objective function.

2.4 Model implementation

This binary integer programming problem was programmed in Zimpl (Zuse Institute Mathematical Programming Language, version 2.08) and solved using SCIP (Solving Constraint Integer Programs, version 1.1.0).[9] To reduce the number of parameters, we scaled damages *d* to 1, and measured costs *b* and *e* as units of damage; this rescaling (i.e., nondimensionalization) imposes no loss of generality. We set *Tmax*=100 and *t_mid*=50 for all optimizations; this achieved and maintained steady states for all invasions considered.

We used comparative spatial-dynamic "experiments" to elucidate the role of economic parameters and invasion and landscape characteristics in determining the optimal control strategy. Focal characteristics included: border control costs and removal costs, discount rate, landscape size and shape, and initial invasion size, location, and shape. For each focal characteristic, we ran optimizations for different levels of the characteristic while holding all other aspects of the

[9] SCIP is a framework for constraint integer programming based on the branch-and-bound procedure to solve optimization problems [1]. Branching divides the initial problem into smaller subproblems that are easier to solve, and the best of all solutions found in the subproblems yields the global optimum. Bounding avoids enumeration of all (exponentially many) solutions of the initial problem by eliminating subproblems whose lower (dual) bounds are greater than the global upper (primal) bound.

invasion constant. We solved optimizations for a wide array of starting conditions, and we present a subset of these simulations to illustrate key findings.

3. Results

Optimal control strategies for invasions varied dramatically across invasion, landscape, and economic characteristics. Optimal policies ranged from no control to complete eradication. In between these two extremes, optimal policies included: eradication of part of the invasion and containment or abandonment of the rest, immediate complete containment, partial containment that allowed some spread prior to complete containment, and partial containment followed by abandonment of control efforts. For all scenarios examined, clearing or eradication efforts were optimally completed in the first time step.

3.1 Economic parameters

We found, as expected, that high control costs or low damages reduce the amount of optimal control.[10] Optimal policy switches from eradication to less intensive control actions with increasing marginal (average) eradication costs, and shifts from containment to abandonment of the invasion with increasing border control costs and high eradication costs. In addition, the net present value of costs and damages of an optimally controlled invasion with particular physical characteristics is non-decreasing in each control cost parameter. We also found, without having firm prior expectations, that high discount rates cause a shift away from eradication and containment, with a more pronounced effect on the optimality of eradication.[11]

[10] Because we normalized marginal damages to one and scaled control costs accordingly, the effect of an increase in marginal damages is represented in our optimizations as a reduction in control costs. Specifically, a doubling of per unit damages is modeled as halving border control and removal costs.

[11] The shift away from eradication occurs because eradication costs are incurred early in an invasion and therefore are not affected by the discount rate, whereas the benefits from eradication (avoided future damages) are discounted. The effects of discounting on the optimality of containment are less pronounced because containment costs are incurred in perpetuity and therefore are discounted similarly to damages. Nevertheless, high discount rates reduce the optimality of containment because the benefits of containment are the greatest in the future when the invasion would be most widespread without control. Consequently, discounting reduces the benefits of containment by

3.2 Landscape size

Figure 1 illustrates optimal control strategies for a 3 by 3 cell invasion in three different sized landscapes. The figure shows that control efforts are justified at higher marginal (average) control costs for larger landscapes, a result that is intuitive. The result illustrates that optimal policies are spatially forward-looking in the sense that, while the size of the landscape does not affect the costs of control, larger landscapes face higher *potential* damages from spread so that higher early levels of control are justified.

3.3 Invasion size and control delay

We found that controlling small invasions is optimal across a wider range of control costs than controlling large invasions with similar characteristics. Analagously, inadvertent delay of control (e.g., by late discovery) reduces the likelihood for eradication or containment to be optimal. Figure 2 shows this for an invasion spreading in a 15 by 15 landscape. The first panel in the figure represents invasion by a single cell at the center of the landscape and shows that it is optimal to contain or eradicate even when costs are relatively high. The second and third panels respresent larger invasions of five and thirteen cells, where the invasions correspond to a single cell invasion that has (inadvertently) spread for one and two time steps, respectively, before initiation of control. Thus, Figure 2 illustrates both the effects of invasion size and of control delays on optimal control policies, and shows that it is optimal to abandon control of larger invasions over wider ranges of control costs.[12]

Figure 3 shows the landscape-wide net present value of controlling a single cell invasion in a 15 by 15 landscape, where optimal control begins immediately or is delayed one or two time

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relatively more than it reduces the costs. Thus, high discount rates increase the likelihood that abandonment, as opposed to containment, is optimal.

[12] In this example, a range of control strategies is employed for controlling the larger invasions, including slowing and partial eradication.

periods, corresponding to the scenario depicted in Figure 2. The results are shown for three different eradication costs and graphed as a function of border control costs. The net present value of costs and damages increases with control delays, even for low marginal (average) border control and eradication costs, because the size of the invasion, in terms of invaded area and the extent of invasion edge, increases rapidly without control. This demonstrates the importance of finding invasions early. In fact, the costs of delayed control are informative about the value invasion search policies. Only in the case of very high border control and eradication costs, for which abandonment is optimal even for small invasions (shown in right side of Fig. 3c), does delay cause no additional losses.

3.4 Landscape shape

In addition to landscape size, landscape shape has significant effects on the optimal policy of an invasion because landscape boundaries affect control costs and damages by constraining invasion spread. Figure 4 illustrates the optimal control policies for a 2 by 2 cell invasion spreading in three different shaped landscapes. All three rectangular landscapes have equal area (256 cells), but vary in length and width. The figure shows that eradication or containment is optimal across a larger range of economic parameters for invasions occuring in the compact (i.e. square) landscape (Fig. 4a) than in increasingly narrow landscapes (Fig. 4b,c). Narrow landscapes confine the spread of species more than compact landscapes, so damages accrue more slowly, resulting in lower potential total damages.

The particular shape of the landscape, beyond length and width, also affects optimal control policies. For example, nonconvexities in the landscape, including constrictions and expansions, can alter optimal control strategies by affecting the cost of controlling the invasion (Fig. 5) or by affecting the spread rate of the invasion (Fig. 6).

Figure 5 illustrates how landscape geometry can be employed strategically to reduce long-term containment costs. In this scenario, complete containment in the first time period is not optimal because the extent of exposed invasion edge is large. Instead, optimal policy slows the growth of the invasion along the center of the invasion front, and then contains the invasion when it reaches the landscape constriction. This control policy slows the invasion along the region of the invasion front that has the greatest potential long-term growth of damages (because it is spreading towards the largest extent of uninvaded area), and delays complete containment until landscape features constrain long-term costs.

Landscape geometries that contain areas with potentially large rates of damage accumulation, as illustrated in Figure 6, also can lead to interesting strategic containment of an invasion. In this scenario, the invasion is spreading along a narrow section of the landscape towards a region where the landscape becomes wider (and future damages from spread become larger). The narrow section of the landscape confines the invasion to spread at a rate of four cells per time period, and neither containment nor eradication is optimal because of the costs of control are high relative to the avoided damages. However, if the invasion were to spread beyond the narrow region of the landscape, the rate of damage accumulation would increase rapidly because the invasion would spread in three directions rather than one. Consequently, optimal policy contains the invasion when it reaches the end of the constricted region, at which point the containment costs remain the same (control along just four borders) but the avoided damages increase.

3.5 Invasion location

Figure 7 illustrates optimal control policies for invasion of a single cell in a 15 by 15 cell landscape at three different locations. From top to bottom, the panels in Figure 7 represent an invasion beginning at the center, at an edge, and in the corner of the landscape, respectively. In this example, containment is optimal across a larger range of border control costs for invasions occurring more distally, while eradication occurs optimally across a greater range of marginal eradication costs for invasions occurring more centrally. However, the relationship between invasion location and control costs varied across scenarios we examined.

We found that the effect of invasion location on optimal control policy is ambiguous because invasion location affects long-term damages and costs of control in opposing ways. An invasion beginning near an edge takes longer to fully invade the landscape than an invasion that begins near the center because the furthest reaches of the landscape are more distant and the growth of the invasion is constrained by the landscape boundaries. Thus, although an uncontrolled invasion will eventually spread throughout the landscape regardless of its starting location, the net present value of potential damages from an invasion beginning near an edge are lower, which reduces the range of total control costs for which eradication or containment of non-central invasions is optimal.

On the other hand, invasions that occur along an edge of the landscape have lower containment costs because the landscape boundaries prevent spread along the bounded edge at no cost, mediating the effects of lower damages on optimal policy. In the scenario presented in Figure 7, the central invasion (Fig. 7a) does not share any edges with the landscape boundary, whereas the edge and corner invasions (Figs. 7b,c) have one and two edges confined by the landscape boundary, respectively. This reduces the containment costs for these distal invasions by 25 and 50%, respectively, relative to the central invasion.[13]

[13] In general, the relative effect of invasion location on damages and control costs is determined largely by the size of potential landscape and the extent of the invasion that is confined by landscape boundaries. The difference in potential damages from central versus distal invasions is greater in larger landscapes, and more confined invasion edges increase the range of border control costs for which containment is optimal. The range of eradication costs for

We found across all simulations that, for invasions with similar characteristics, the net present value of costs and damages is higher for central invasions than for distal invasions, because central invasions have higher potential damages and higher control costs.

We find also that invasion location can influence control costs even if the initial invasion does not occur immediately adjacent to a landscape boundary. Figure 8 shows the spread of an optimally controlled invasion across four time steps, demonstrating how landscape boundaries are strategically employed. The initial invasion (*t*=0) is a 4 by 4 block of cells located 2 cell widths from the corner of a 15 by 15 cell landscape. Optimal control policy contains the invasion along its central borders, while allowing spread of the invasion towards the corner of the landscape. In time periods 1 through 4, control is applied along the 12, 10, 8, and 10 most central borders of the invaded region, respectively, after which the invasion is contained in perpetuity. This strategy, which confines the invasion using landscape boundaries, reduces the number of exposed borders from 16 to 12, reducing periodic containment costs by 25% for the long-term. In contrast, for an identical invasion located centrally in the landscape, immediate containment is optimal because landscape boundaries cannot be employed to reduce long-term containment costs, and total costs and damages are higher (3696 versus 3176). This provides another illustration of how invasion location affects optimal control policies and the net present value of costs and damages.

Figure 9 provides an example of the effect of invasion location on optimal policy for a two patch invasion, in which one patch occupies a corner cell (the upper left hand patch) and the

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which eradication is optimal is much less mediated by the adjacency of landscape boundaries, because eradication costs depend primarily on the amount of area invaded, rather than the amount of edge. Thus, in most cases central invasions are optimal to eradicate across a larger range of eradication costs than invasions occurring distally (Fig. 7). Furthermore, the cost-effectiveness of eradication relative to containment tends to be higher for more central invasions, because the costs of containing central invasions cannot be reduced by landscape boundaries. This result is illustrated by the steeper line dividing eradication and containment in Figure 7 for the central invasion.

other patch (lower right hand corner) is located one cell width from the opposite corner. A large number of optimal control policies are possible for this invasion depending on the economic parameters. For example, eradication of both patches, containment of both patches, or abandonment of control are optimal policies for situations with low eradication costs, low border control costs, and high control costs, respectively. However, because of the different locations of the two patches relative to the borders, optimal policy applies dramatically different types of control to each patch for small variations in parameter combinations.

For example, the lower right hand patch is more costly to contain (4 exposed edges), so in some circumstances it is optimal to eradicate that patch and perpetually contain the patch that has only 2 exposed edges (Fig 9a). For the same invasion with slightly higher eradication costs, the optimal policy switches so that initial containment of the upper left hand patch is still optimal, but the patch with more exposed borders is neither contained nor cleared (Fig. 9b). Because the invasion is not fully controlled, the invasion spreads, reducing the benefits of containing the upper left hand cell, and eventually all control efforts are optimally abandoned.

Although the landscape boundaries cannot be used to reduce the amount of exposed edge on the lower right hand patch in Figure 9b, the boundaries are employed strategically to slow the invasion. Specifically, optimal policy applies control to the lower right hand patch to direct growth towards the corner. This approach, which was also employed for the invasion in Figure 5, reduces the long-term damages from the invasion by delaying spread in the direction with the highest potential growth. Similarly, in Figure 8, in which a 4 by 4 block of cells is strategically allowed to spread toward the corner in order to reduce the number of exposed edges prior to long-term containment, control efforts also prevent invasion spread centrally, which is the direction of greatest long-term potential growth, and slow the spread of the invasion into the corner. Specifically, in time period 1, control efforts are applied to 12 borders of the invasion, rather than just the 8 central borders, in order to delay damages. These examples illustrate how invasion location within the landscape can affect optimal spatial allocation of control.

3.6 Invasion shape and contiguity

We found that geometric characteristics of the invasion, beyond size and location, affect optimal control policies. In particular, the shape and contiguity of an invasion (holding size constant) affect optimal levels and spatial allocation of control effort. For example, containing a compact invasion, which has a lower edge to area ratio, is optimal over a wider range of border control costs than containing a similar patchy invasion. This is illustrated in Figure 10, which shows the optimal control strategies for a compact 2 by 2 cell invasion and for a patchy invasion of four equidistant cells; both invasions occur near the center of a 15 by 15 cell landscape. In this scenario, the long-term damages from abandoning control are slightly higher for the patchy invasion than for the compact invasion because the patchy invasion spreads faster, but optimal policy mandates abandoning control of the patchy invasion across a larger range of marginal control costs because it has higher containment costs. In particular, across the range of border control costs for which containment of the compact invasion is mandated, optimal management for the patchy invasion may involve containment, spread followed by containment, slowing, and even abandonment. Because containment is more costly for patchy invasions, eradication is optimal across a larger range of marginal (average) eradication costs for patchy invasions than for compact invasions. This is evidenced in Figure 10 by the steeper slope of the line dividing containment and eradication for the patchy invasion.

Clearly, an important feature of invasion geometry is its influence on the invasion edge and the effect of edge length on containment costs. We showed previously that the extent of exposed edge can be reduced by employing landscape boundaries (e.g., Figs. 5 and 8). We also find that optimal policies can reduce the extent of edge by altering the shape of an invasion through clearing cells or allowing spread prior to containment. For example, Figure 11 shows an edgey, nonconvex[14] invasion for which optimal policy combines removal and slowing to reduce the number of exposed edges from 11 to 8 prior to complete containment. Strategic spreading and clearing also was employed to reduce the extent of edge prior to containment for the invasions represented in Figures 1c and 10b. In each case, the approach converts a nonconvex invasion into one that is convex.

We also find that optimal policy sometimes removes nonconvexities from an invasion even when this does not reduce the extent of exposed edge. For example, the "+" shaped, five cell invasion represented in Figure 2b initially has 12 exposed edges. Optimal policy applies control along the outer 4 edges of the invasion in the first time step, allowing the invasion to become a convex block of 9 invaded cells that is contained in perpetuity; twelve exposed borders are maintained. In this example, the benefits of removing nonconvexities depend on relative local spread rates, control costs, and damages in the nonconvex regions. Containment costs depend linearly on the length of exposed edge, whereas the short-term spread rate depends on the number of uninvaded cells bordering the invasion. Nonconvex regions of an invasion have a higher cost of spread prevention because multiple invasion edges need to be controlled to prevent invasion of a single cell. In contrast, convex regions of invasion edge generally have a one to one relationship between control effort and spread prevention, and thus have lower effective control costs. For this reason we find that slowing efforts are generally focused along convex regions of

[14] We use the term convex in the mathematical sense of a convex set. We refer to an invasion as convex if, for every pair of points in the invasion, every point on the straight line segment that joins them also is within the invasion.

the invasion edge, as in Figures 2b, 5, 8, 11, and 12; focusing slowing efforts in this way is most cost effective because it targets areas of high local growth and low relative control costs.

Finally, with respect to non-contiguous (patchy) invasions, our scenarios show that optimal control strategies can vary across invasion patches, but strategies for optimal control of individual patches depend on the entire landscape of the potential invasion (e.g., Figs. 9 and 12). Just as dynamic problems involve choosing an entire time path of decisions that are interdependent, optimal control of a spatial-dynamic system involves simultaneously choosing control efforts across spatially separated patches, because the benefits (avoided future damages) of controlling each patch depend on the control efforts and spread rates at other patches. For example, Figure 12 shows an invasion for which optimal policy requires eradication of one patch and slowing, followed by abandonment, of the other. However, for an identical invasion with slightly higher border control costs (b=16), the benefits of slowing the spread of the large patch are reduced, so that the gains from eradication also are reduced, and eradication of the small patch ceases to be optimal.

4. Summary and Discussion

Our analysis shows that many aspects of an invasion determine the optimal policy, including economic parameters, landscape size and shape, and invasion size, shape, and location. Invasions that are nearly identical can have dramatically different optimal control policies if they differ in any one of these characteristics. An unfortunate consequence of so many factors determining optimal control is that deriving clear and simple rules of thumb for how to best manage all invasions is unlikely. However, we have shown how these factors affect the qualitative nature of optimal control policies, as summarized next, and provided intuition for these results.

4.1 Economic factors

Delaying clearing efforts or eradication policies is inefficient because it either enables further spread of the invasion or requires containment effort and accrues more damages.[15] As expected, higher control costs lead to lower optimal levels of control; high border control costs reduce the optimality of containment and high eradication costs reduce the optimality of eradication. Similarly, invasions that produce high damages per area invaded justify higher control efforts to offset damages, a conclusion also supported by previous work (e.g., Sharov and Liebhold [28]).[16] Finally, we find that high discount rates reduce the amount of optimal control, which is consistent with findings by Sharov and Liebhold [28] and Olson and Roy [18].

4.2 Landscape size

All else equal, invasions that have larger potential ranges warrant higher levels of control because potential damages are higher. Thus, knowledge of the potential invasion extent is important for determining optimal policy. Fortunately, the combination of ecological niche modeling and spatial technologies such as geographic information systems have provided methods for predicting the potential ranges of invading species [8; 21]. Nonetheless, managers and policy makers often define potential invasion extent based on political, rather than ecological, boundaries, which can lead to very different control prescriptions.

4.3 Invasion size and delay

Larger invasions are optimal to control over a smaller range of conditions because they cost more to contain or eradicate, have higher long-term damages if contained, and their control

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[15] However, Sharov and Liebhold [28] and Eiswerth and Johnson [7] found that with increasing marginal control costs, removal efforts may be applied over time because high rates of control are penalized. Similarly, Olson and Roy [19] found that stock dependent control costs combined with nonconvexities in the invasion growth function also can lead to optimally delayed eradication.

[16] The pattern of control intensity also depends on how damages vary with the area invaded and on relationships between damages and other characteristics of an invasion, as demonstrated by Olson and Roy [19].

provides fewer benefits because less uninvaded landscape remains to protect.[17] We show that delaying control efforts reduces the value of the system by constraining control options and increasing costs and damages, an intuitive result that is supported by other studies including Smith *et al.* [31], Higgins *et al.* [11], and Taylor and Hastings [33]. Thus, determining and applying optimal control policies to invasions soon after they are detected is important.[18]

4.4 Landscape shape

We are unaware of any other studies that have explicitly examined the effects of landscape shape on optimal control policy. Our results show that invasions in more compact landscapes generally warrant more control because spread is less constrained, resulting in higher long-term damage potential. However, landscape shape also affects the likelihood that an invasion will be located near enough to landscape borders to reduce long-term containment costs. We also showed that nonconvexities in the landscape, such as constrictions and expansions, influence optimal control policies by affecting spread rates and containment costs. These results highlight that current rates of spread may not reflect long-term rates of spread, and optimal control needs to account for long-term spread patterns. Interestingly, landscape nonconvexities are the only situation we found for which delaying the start of control efforts can be optimal.[19]

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[17] These results coincide with findings by Sharov and Liebhold [28] who found that optimal control strategies switch from eradication to slowing to abandonment with increasing initial invasion size for an invasion spreading along a corridor of land. Also, Olson and Roy [18] found that eradication is less likely to be optimal for large invasions that are more costly to eradicate.

[18] Early control of invasions is constrained by the timing of detection, uncertainty about the optimal policy, and possibly lack of knowledge of effective control methods. Early detection of invasions is costly because smaller invasions are more difficult to detect, so an optimal balance between expenditures on detection and costs from delaying control should be found [2; 15]. Also, early in an invasion uncertainty about the damages, spread rate, and potential suitable habitat for an invasion can make determination of optimal policy even more difficult. For some invasions, particularly by novel invaders, effective control strategies may not exist and control may be quite expensive. In these cases, technological innovation may reduce control costs over time. Nonetheless, delaying control is generally costly and optimal control strategies should be identified and applied early on.

[19] Several other studies have found that delaying control can be optimal, but for different reasons. Specifically, Burnett *et al*. [5] and Olson and Roy [19] found that when control costs are stock dependent (i.e., higher marginal control costs for smaller invasions), delaying control to reduce control costs can be optimal. For example, Burnett *et al.* [5] suggested that delaying control is optimal for *Miconia* invasions on some of the Hawaiian islands.

4.5 Invasion location

The role of invasion location on optimal policy has not previously been explored, to the best of our knowledge. The initial location of an invasion affects both optimal control and total costs and damages of an invasion by affecting potential long-term damages and the costs of control. Central invasions face higher potential damages because the invasion can spread through the landscape more rapidly, and control costs may be lower for distal invasions if landscape boundaries can help contain an invasion. Thus, centrally located invasions tend impose higher total costs and damages than distal invasions. Location also influences the optimal spatial allocation of control by determining the direction of greatest potential invasion spread.

4.6 Invasion shape and contiguity

The shape of an invasion affects optimal control policies by affecting containment costs and spread rates. Our results concerning invasion shape and contiguity were distilled from optimizations for a large array of invasion scenarios and can be summarized as follows. First, a greater amount of invasion edge, due to invasion shape, decreases the range of control costs for which containment is optimal, shifting policies toward eradication or abandonment. Second, for non-compact (edgy) invasions, spread or removal prior to containment to reduce the amount of exposed edge may be optimal because it reduces long-term control costs. Third, border control efforts are more likely to be applied along convex regions of an invasion, where local growth rates are higher and relative control costs are lower. Finally, optimal control of patchy invasions depends on the entire landscape, and control efforts can vary across patches based on patch and total invasion characteristics.

4.7 Spatial aspects of control

We have shown that landscape features, such as bottlenecks, can be used strategically to reduce long-term containment costs, contributing to understanding of the role of landscape boundaries in controlling invasions. These boundaries, which are determined by the habitability and porousness of the landscape to the invader, include elevational, temperature, and precipitation gradients, soil types, and water bodies, and should be accounted for when determining optimal control.[20]

Our results regarding the effect of invasion shape on optimal control effort provide insight on improving the use of barrier zones, which have been used to control a variety of invasions, including the boll weevil and gypsy moth. The barrier zone approach applies control efforts along the growing edge of an invasion to slow its spread [28]. Our findings suggest that applying control efforts homogenously along the growing edge can be suboptimal. Instead, it can be better in some situations to apply higher levels of control to convex regions of the growing edge (parts that extend the furthest) and to apply less control along small sections of the growing edge that lag behind the main front. Also, greater amounts of control should be applied to slow the invasion in the direction of greatest long-term potential growth.

Our examination of multi-patch invasions contributes some insight into an unanswered question about where to focus control effort: on large, core patches or on smaller, satellite patches.[21] High-density, established invasions can contribute to invasion expansion both through

[20] For example, an elevationally-constrained invasion spreading in a valley between two mountain ranges may best be contained in a narrow region of the valley. Also, it may be possible to employ restoration to create landscape barriers, because many species more easily invade disturbed ecosystems than diverse or undisturbed systems [e.g., 9; 14]. Creating barriers through restoration of strategic areas in the landscape may reduce the long-term costs of containing invasions that are too widespread to eradicate.

[21] This questions was first addressed in the literature by Moody and Mack [16]. Taylor and Hastings [33] point out that even theoretical frameworks suggest different prioritizations: "the population biology approach suggests that, in general, outliers contribute the most to range expansion and should be removed first, whereas the metapopulation approach suggests prioritizing core populations that supply most of the new propagules."

growth of the main invasion and the creation of new satellite populations. In this study we do not consider long-distance dispersal processes or differential densities among invaded patches, but our results support two points. First, greater amounts of control tend to be optimal for smaller invasions because of eradication and containment costs are lower, suggesting that it may be optimal to focus more control effort on smaller, satellite invasions in some cases. Second, optimal control for each patch of an invasion depends on the entire invasion and landscape, so that patches cannot be considered independently. A blanket strategy or prioritization is thus unlikely to be optimal.

The management of many invasive plants is not regulated because they are classified as too widespread to justify eradication. Our results show, however, that under some circumstances it is optimal to eradicate one patch of an invasion even while allowing other patches to spread. Thus it may be worth controlling small populations that occur far from the main invasion, even when an invasion is widespread. Furthermore, it may be optimal to slow or contain widespread invasions, even when eradication is not justified, especially when large potential for further spread exists.

4.8 Some principles of optimal bioinvasion control[22]

Some basic principles that arise from this study are: 1) Protect large areas of uninvaded landscape. For example, small invasions and large landscapes portend larger future damages and thus warrant greater control effort. 2) Reduce the extent of exposed invasion front, by employing landscape features or altering the shape of the invasion through spread or removal, in order to

[22] The generalizability of our results depends upon the extent to which invasion control costs, damages, and spread processes align with our modelling assumptions. In this study we do not allow for long distance dispersal events. However, a constant rate of spread has been shown to provide good approximation of spread patterns for many invaders [29]. For species that exhibit long distance dispersal, eradication would likely be optimal across a greater range of economic parameters, because damages would accrue faster. However, the same qualitative patterns that we found in this study with respect to economic, landscape, and invasion characteristics are likely to hold for invasions with different patterns of spread.

reduce long-term containment costs. 3) Slow the spread of an invasion in the direction of greatest potential local or long-term growth. 5) Do not delay eradication.

5. Conclusions

This paper has two purposes. The first is to provide useful and novel understanding of economically optimal control of bioinvasions. Employing a two dimensional, spatially explicit biological spread model allowed us to examine control strategies that varied across space and time and to identify how the geometry of the invasion and landscape affect the qualitative nature of optimal control policies. As we show, the optimal solution for a spatially explicit optimization problem generates a far richer set of solution characteristics and more nuanced conclusions about how to control bioinvasions than work that treats space only implicitly or does not allow for differentiated control across space. We describe and provide intuition for the wide spectrum of optimal solutions that emerge as we perturb both bioeconomic parameters and landscape and invasion geometry.

The second purpose of this paper is to use the bioinvasion problem as a model case study for learning about a wider class of problems, namely spatial-dynamic problems. Economics has a rich legacy of analysis that addresses the spatial nature of economic activities and that addresses dynamic problems. In contrast, problems driven by spatial-dynamic processes have only recently begun to receive attention.[23] Spatial-dynamic problems are characterized by diffusion or spread processes that generate patterns over space and time. Examples (aside from bioinvasions) include groundwater contamination, epidemics, forest fires, migration and movement, technology adoption, etc. In human-mediated landscapes, economic agents may be affected by these spatial-

[23] This includes work on marine systems by Sanchirico and Wilen [24; 25; 26], Janmaat [12], and Smith, Sanchirico, and Wilen [32], a study on spatial-endogenous fire risk and fuel management by Konoshima and others [13], and work by Brock and Xepapadeas [4]. Wilen [34] and Smith, Sanchirico, and Wilen [32] describe much of the existing work on the economics of spatial-dynamic processes, focusing on renewable resources.

dynamic processes, and they also may affect the patterns that unfold. In a setting in which agents are located over space, a general question arises about how to control spatial-dynamic processes in a manner that maximizes welfare across the whole landscape. As we have shown for the bioinvasion case where spread generates damages, the issue is not only *when* and at *what level* of intensity to initiate controls, but *where*?[24] We have found, in general, that the dynamic parts of the solution (concerned with *when* and at *what level* of intensity to initiate controls) are intertwined in complex ways with, and are not separable from, the spatial part of the solution of *where* to initiate controls.

Some of what emerges from accounting for both space and time reflects our intuition about the dynamic components of the problem, while other features are novel. Most importantly, adding space necessitates concern about *geometric* characteristics of problems in addition to concern about more familiar metrics such as size or quantity. To highlight some of our new findings about bioinvasions that may shed light on the larger class of spatial-dynamic problems, we compare general principles that apply to dynamic problems with some new results that emerge from our consideration of spatial-dynamics:

- In dynamic problems, the index that differentiates decisions (time) runs only forward. In spatial-dynamic problems, the index that identifies decisions is both a time index and a spatial index. Moreover, spatial-dynamic problems run forward in time, but can spread and contract in multiple directions over space.
- The solutions to interesting dynamic problems always involve a dynamic tradeoff such that the optimal control level balances contemporaneous benefits (costs) against the present value of long-term costs (benefits). For example, optimal investment in any period balances the

[24] Spatial-dynamic processes may generate benefits, of course, in which case similar issues would arise in choosing policies that encourage rather than inhibiting spread.

marginal cost of the last unit of investment with the marginal change in the present value of benefits associated with that small change in the capital stock. Importantly, the solution is forward-looking at each date, scanning the complete horizon, adding up the marginal impacts over that horizon (all evaluated along the optimal path), and comparing those anticipated impacts with current marginal costs. Spatial-dynamic problems also are forward-looking but over both time and space. Optimal bioinvasion controls in our problem account for the size and character of the potential space (and hence damages) that lies ahead in both time and space of the advancing invasion front. Directionally-differentiated damages influence the degree of control exerted at any point in time and space. Large prospective damages (either from a large amount of space or from high damages per unit of space) in the path of a spreading front will call forth higher levels of control early and at locations often roughly orthogonal to the path of the front.

- Dynamic optimization solutions depend critically upon the initial state of the system, generally measured by the size of capital or resource level at some starting date. For example, the smaller the initial capital level relative to its steady state level, the larger current optimal investment should be. For spatial-dynamic problems, the geometry of the initial state, as well as its size, matters. As we showed, small variations in shape and location in the landscape can lead to qualitatively different optimal solutions. For example, whether eradication or containment may be optimal depends not only upon basic costs, damages, and discount rate, but also upon how large the initial invasion is relative to the landscape, where it is located, the extent of exposed invasion edge, etc.
- In dynamic problems the optimal decision for any control variable often can be described as an open loop function of time and the initial state. In spatial-dynamic problems, on the other

hand, the optimal control at a site cannot be reduced to an open loop function of time. Instead, optimal control at each point in space depends on its location in space and the state and control levels at other points in space. This was demonstrated in our multi-patch invasion examples, in which the optimal policy at one patch was explicitly interdependent with optimal policies at other patches.

These are just a few of the characteristics that we conjecture may emerge as general properties of solutions of other spatial-dynamic optimization problems. In the end, economists will need to develop new intuition about spatial-dynamic problems by analyzing these and other cases before we can understand what features of the solutions to this class of problems appear to be general, and what features are specific to particular cases.

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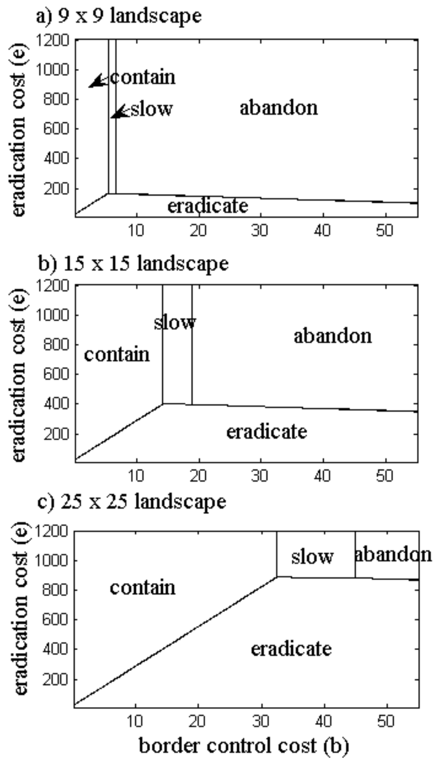


Figure 1. Optimal control strategies for three sizes of landscape (potential invasion range). Parameter space shows how control strategy varies based on eradication and border control costs. The initial invasion is a 3 by 3 block of cells in the center of the landscape. Contain, eradicate and abandon policies all begin in the first time step; slowing policies involve controlling along both exposed edges of each of the four corner cells (a total of 8 edges) for one time period and then abandoning control. (r = 0.05).

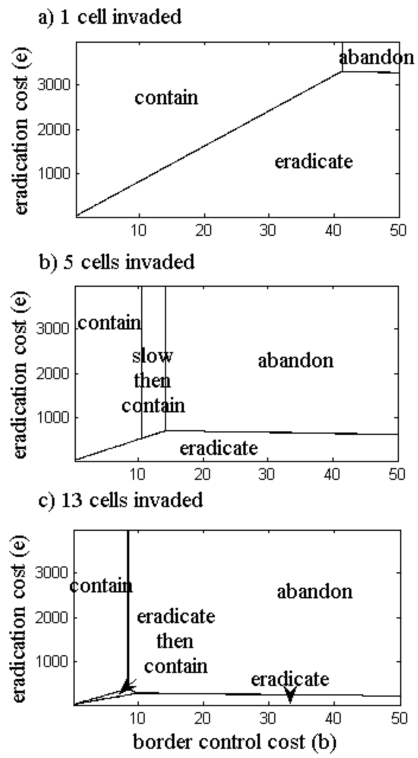


Figure 2. Optimal control strategies for three invasion sizes (inadvertent control delays). Parameter space shows how control strategy varies based on eradication and border control costs for three different invasion sizes in a 15 by 15 cell landscape: a) 1 cell invaded, b) 5 cells invaded (1 central cell and 4 adjacent cells), and c) 13 cells invaded (a 3 by 3 block of cells with an additional cell adjacent to each central edge cell in the block). These invasions represent an initial, single cell invasion with a control delay of a) zero, b) one, and c) two time steps. The slowing strategy in b) contains the invasion along the outer 4 edges of the invasion for 1 time step and then contains the resulting 3 by 3 invasion in perpetuity. The "eradicate then contain" strategy in c) clears the outer 4 cells of the invasion and contains along all borders in the first time period and then contains the resulting 3 by 3 invasion in perpetuity. (r = 0.05).

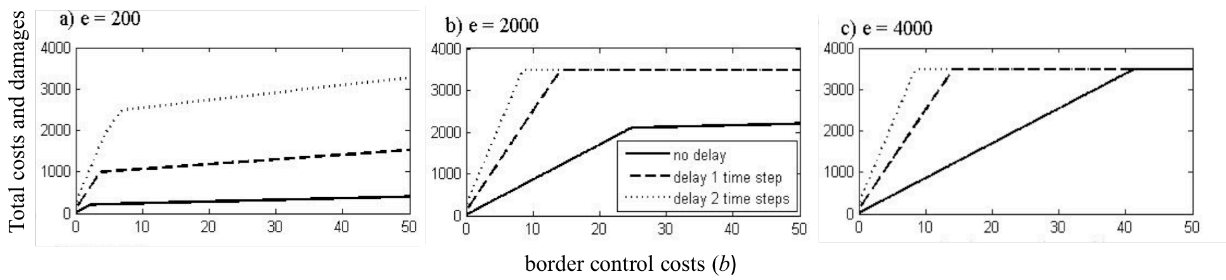


Figure 3. Net present value of costs and damages from optimally controlling an invasion immediately or delaying control by one or two time steps. The initial invasion (t=0) is a single invaded cell at the center of a 15 by 15 landscape. Control begins at t = 1, 2, or 3, for the three lines in each plot. The panels correspond to different marginal eradication costs. (r = 0.05).

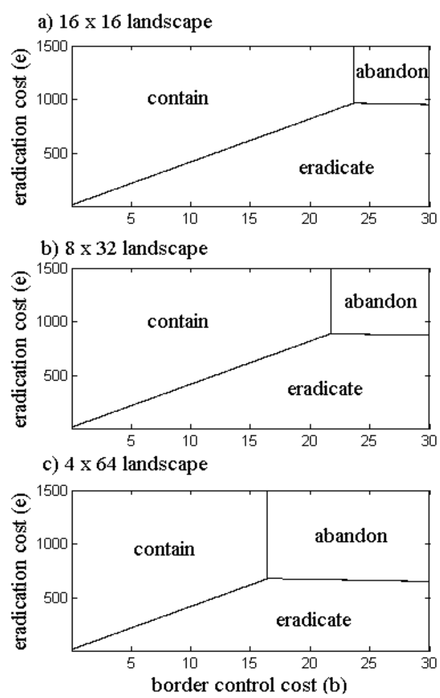


Figure 4. Optimal control strategies for three landscape shapes. Parameter space shows how the optimal control strategy varies based on eradication and border control costs. The three equal-sized landscapes are: a) 16 by 16, b) 8 by 32, and c) 4 by 64, initially invaded by a central 2 by 2 invasion. (r = 0.05).

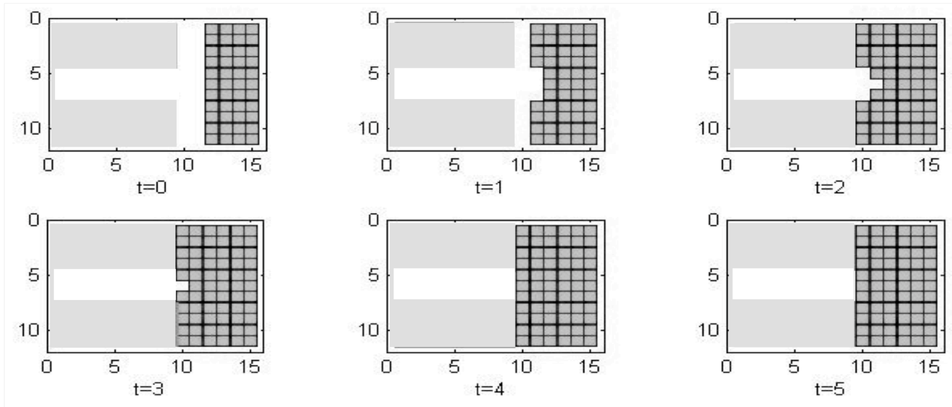


Figure 5. Example of optimal control in a landscape with a constriction. The region is 11 by 15 with two 4 by 9 sections removed (the light grey areas are not invadable). Optimal policy slows the spread of the invasion as it approaches the landscape constriction, where it is ultimately contained in perpetuity. (r = 0.05, b = 7, e = 250).

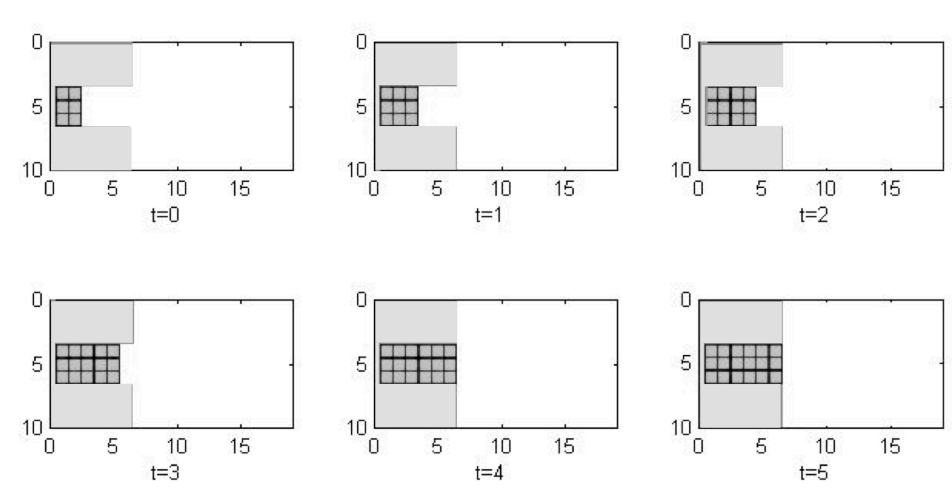


Figure 6. Example of optimal control in a landscape with an expansion. The region is 9 by 18 with two 3 by 6 sections removed (the light grey areas are not invadable). Optimal policy allows the invasion to spread until it reaches the end of the narrow section at time t = 4. Control efforts begin in time period 5 that contain the invasion in perpetuity. (r = 0.05, b = 27, e =250).

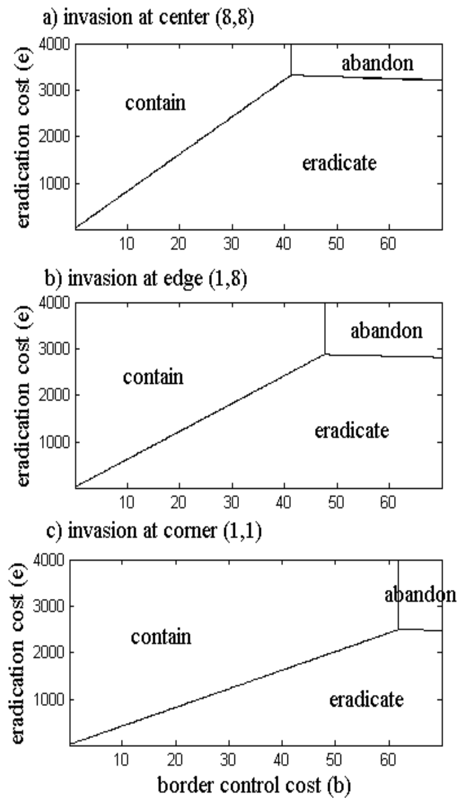


Figure 7. Optimal control strategies for three initial invasion locations. Parameter space shows how the control strategy varies based on eradication and border control costs for a single cell invasion in a 15 by 15 cell landscape located: a) centrally, cell (8,8), b) at an edge (1,8), and c) at a corner, cell (1,1). (r = 0.05).

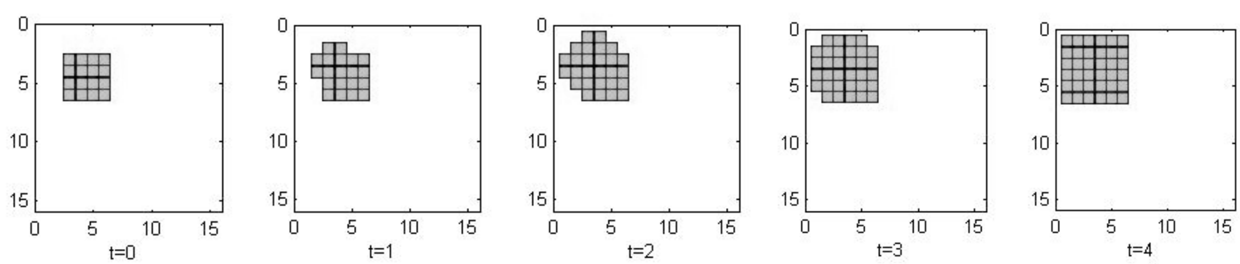
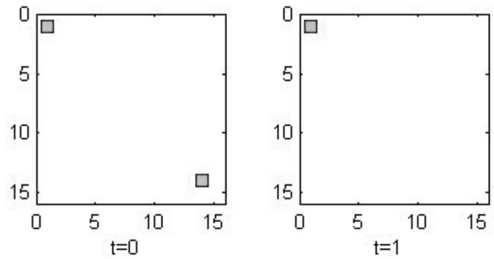


Figure 8. Optimal control of an invasion in a 15 by 15 cell landscape by a 4 by 4 patch of cells near a corner of the landscape. (r = 0.05, b = 10, e =230).

a)



b)

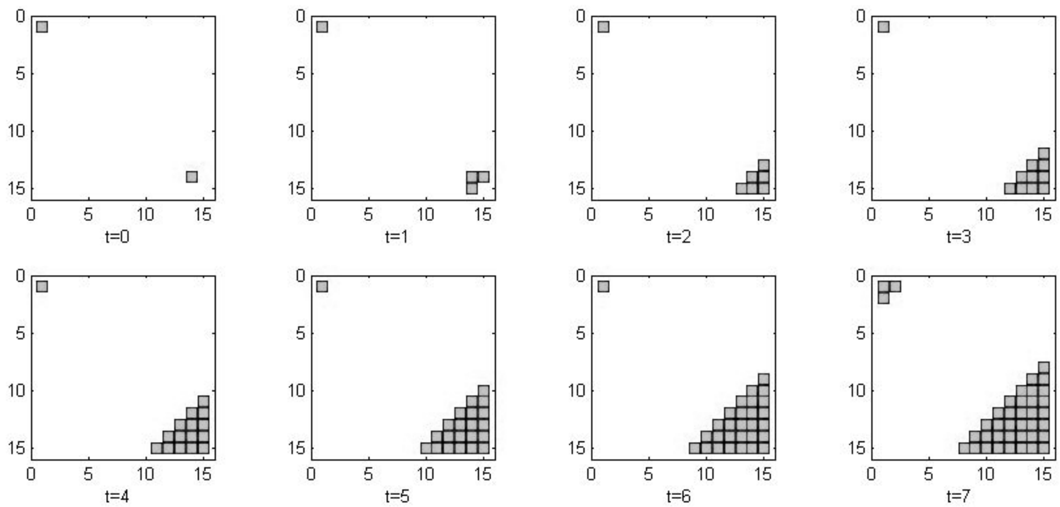


Figure 9. Optimal control of a 2 patch invasion in a 15 by 15 cell landscape for 2 different eradication costs. Invasion begins in cells (1,1) and (14,14) (in a corner and near a corner, respectively). In scenario (a) the optimal policy eradicates the cell in the lower right hand corner in the first time period and contains the invasion in the upper left hand corner in perpetuity. (r = 0.05, b = 27, e =1600). With slightly higher eradication costs in scenario (b), the optimal policy slows the invasion for the first 6 time periods and abandons control over the whole landscape at time t = 7. (r = 0.05, b = 27, e =1800).

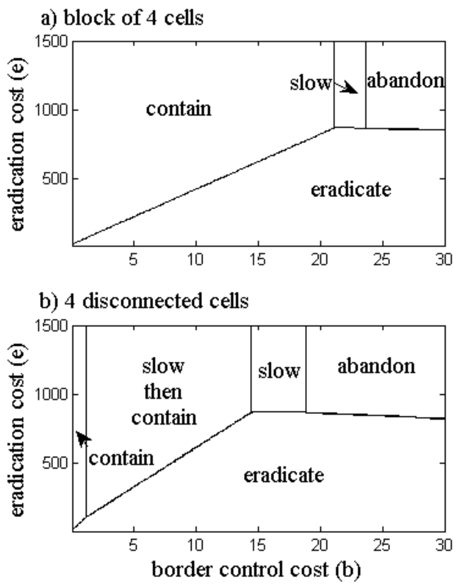


Figure 10. Optimal control strategies for two invasions that differ in contiguity. Parameter space shows how the optimal control strategy varies based on eradication and border control costs for invasion by: a) 4 contiguous or b) 4 equidistant, noncontiguous cells in a 15 by 15 landscape. The initial invasion occurs near the center of the landscape as: a) a block of 4 cells ((8,8), (8,9), (9,8), (9,9)), and b) 4 separated cells ((7,7), (7,9), (9,7), (9,9)). (r = 0.05).

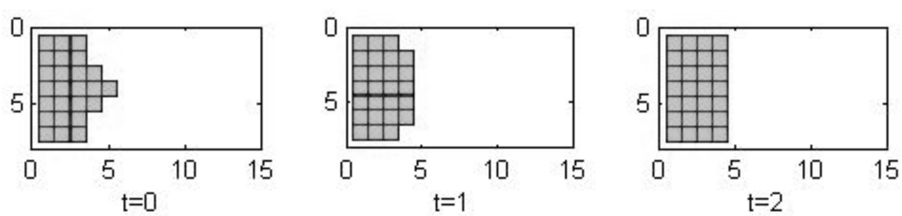


Figure 11. Optimal control of an invasion in a 7 by 14 cell landscape by a patch of cells with local concavities. The optimal policy eradicates one cell and slows the spread in the first time period, partially contains the invasion in t = 2, and contains the invasion in perpetuity beginning in the third time period. (r = 0.05, b = 7, e = 83).

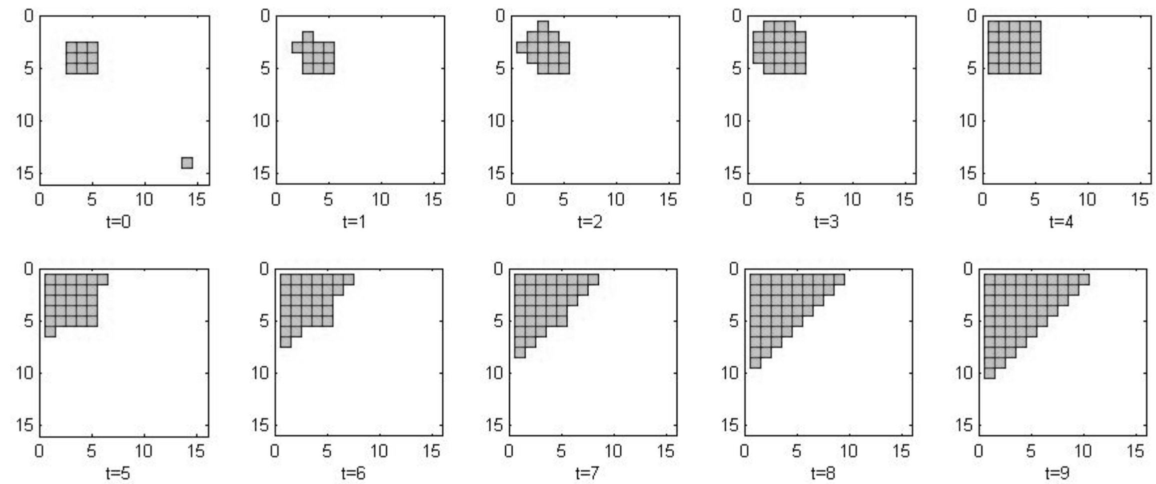


Figure 12. Optimal control of an invasion in a 15 by 15 cell landscape by a small (1 cell) and large (9 cells) patch. Optimal policy eradicates the small patch and slows the spread of the larger patch by directing spread into the corner of the landscape. Eventually the invasion spreads to fill the entire landscape. (r = 0.05, b = 14, e =450).