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Optimizing the use of suppression zones for containment of invasive species

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Abstract
Despite efforts to prevent their establishment, many invasive species continue to spread and threaten food production, human health, and natural biodiversity. Slowing the spread of established species is often a preferred strategy; however, it is also expensive and necessitates treatment over large areas. Therefore, it is critical to examine how to distribute management efforts over space cost-effectively. Here we consider a continuous-space bioeconomic model and we develop a novel algorithm to find the most cost-effective allocation of treatment efforts throughout a landscape. We show that the optimal strategy often comprises eradication in the yet-uninvaded area, and under certain conditions, it also comprises maintaining a "suppression zone," an area between the invaded and the uninvaded areas, where treatment reduces the invading population but without eliminating it. We examine how the optimal strategy depends on the demographic characteristics of the species and reveal general criteria for deciding when a suppression zone is cost effective.

KEYWORDS
barrier zone, bioeconomics, containment, cost-effectiveness, invasive species, optimal control, suppression zone

INTRODUCTION

Harmful invasive species of various taxa are steadily accumulating in virtually every world region, causing damage to agriculture, biodiversity, and human health and infrastructure. Therefore, the search for strategies to manage invasive species takes on increasing significance (Mack et al., 2000; Mooney & Hobbs, 2000; Sala et al., 2000). Virtually all invasions proceed through sequential stages, which include transport, arrival, establishment, and spread (Blackburn et al., 2011; Williamson, 2006). At each of these stages, specific measures (e.g., import prohibitions, inspection, eradication) can be implemented to mitigate invasions. Several economic analyses have shown that interventions to prevent the initial transport or establishment of species ("prevention") are typically the most efficient (Leung et al., 2002; Olson & Roy, 2002; Simberloff, 2003). However, such preventions are not always successful, and the establishments of some nonnative species are inevitable (Catford et al., 2012). In these cases, an alternative is containment, which refers to limiting the spread of established species into surrounding uninvaded regions (Grice et al., 2020; Hulme, 2006; Liebhold & Kean, 2019). Containment may either slow or completely stop the spread of the invasive species, and studies have shown that it may be an overall optimal strategy for minimizing the impacts of nonnative species, depending upon the spatial extent of the invasion (Epanchin-Niell, 2017; Sharov & Liebhold, 1998).

In practice, actions taken to contain the spread of nonnative species can be classified into three categories: (1) limiting dispersal; (2) surveillance and eradication of nascent populations; and (3) suppression zones. Measures that focus on directly limiting the dispersal of the species into uninvaded areas reduce propagule pressure and thereby slow the species' range expansion. One method for limiting dispersal is the placement of barriers, such as: (1) the infamous "rabbit-proof fence" that was erected to prevent invasions by rabbits and other mammalian pests from Western Australia (Cooke, 2014); and (2) the construction of dams in southern Spain to prevent the upstream movement of the nonnative crayfish species *Procambarus clarkia* (Dana et al., 2011). Another method to limit dispersal is the implementation of domestic quarantines that prohibit the transport of commodities that function as vectors of invading species. This includes prohibitions on the intentional movement of invasive plants (Carter, 2000) or the transport of plants that are potentially contaminated with plant pests (Withrow et al., 2015).

The second containment strategy focuses on the surveillance of newly established populations in uninvaded areas, followed by the eradication of these populations (Figure 1A). For example, the rubber vine, *Cryptostegia grandiflora*, is widely established in northwest Queensland, Australia, but beyond a designated line, isolated patches are searched for and eradicated (Cherry et al., 2006). More generally, many containment programs may identify a "barrier zone" surrounding the invaded area; because dispersal from the invaded area is limited to the barrier zone, surveillance and eradication efforts are focused or completely limited to this zone (Dane Panetta, 2012; Panetta & Cacho, 2014). But in other cases, such as the containment of *Lymantria dispar*, in the USA, surveillance and eradication may be focused both in a barrier zone and more distant regions where invading propagules may be accidentally transported by humans (Liebhold et al., 2021).

The third strategy that is applied for the containment of invasive species is the use of a "suppression zone" at the margin of the invaded area. Specifically, target populations are suppressed to indirectly reduce propagule pressure in surrounding uninvaded regions (Figure 1B). An example is the regional containment strategy for blackberry, *Rubus fruticosus*, in Victoria, Australia, in which invasive plant patches are searched-out and controlled at the margin of the invaded area (Grice et al., 2013). Suppression at the margin is carried out in addition to surveillance and eradication of satellite populations in the uninvaded area.

Containment is typically relatively expensive, and complicated to coordinate across large regions, and in the end, it may not be effective (Dane Panetta, 2012). Therefore, a central question is how to contain invasive species cost-effectively; namely, how to manage the established invader such that the annual cost of treatment is minimized.

Most previous bioeconomic studies on invasive species have considered nonspatial models, focusing on optimal strategies for eradication from a target area (Blackwood et al., 2012; Lampert & Liebhold, 2021; Taylor & Hastings, 2004) or optimal strategies for controlling the species at a low density to mitigate its negative effects (Barrett, 2004; Bomford & O'Brien, 1995; Clark, 2010). At the same time,

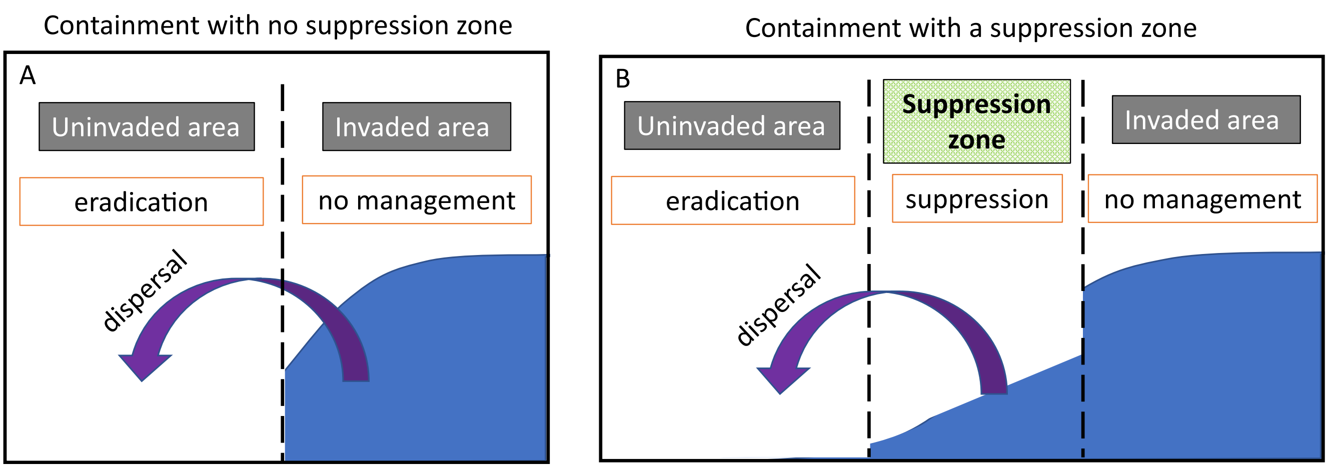

FIGURE 1 Illustration of two strategies for containing an invasive species. (A) Without a suppression zone: in the invaded area, the manager does not suppress the population. Outside the invaded area, in the uninvaded area, the manager eradicates the population. (B) With a suppression zone: in addition to eradication of populations in the uninvaded area, the manager also maintains a "barrier zone", an area where they do not attempt to eliminate the species but still treat it to control it at a lower level to reduce propagule pressure in the uninvaded area.

several bioeconomic studies considered space explicitly, asking how to allocate the suppression efforts throughout a spatially extended landscape. One approach has been to consider two spatial sites, core and periphery, where most studies taking this approach have focused on eradication (Moody & Mack, 1988; Taylor & Hastings, 2004; Wilen, 2007) and some on containment (Panetta & Cacho, 2014). In turn, other bioeconomic studies have considered continuum space models or cellular automatons (Epanchin-Niell, 2017; Higgins et al., 2000). Some of these studies have examined how to allocate treatment efforts over space and time to eradicate an invasive species (Baker, 2017, 2018). Studies focusing on containment have examined what parts of the landscape should be contained (Epanchin-Niell & Wilen, 2012), what is the optimal speed at which the species should be allowed to propagate (Menz et al., 1980; Sharov & Liebhold, 1998), and what is the optimal spatial distribution of treatment efforts (Baker & Bode, 2016; Bonneau et al., 2017; Nishimoto et al., 2021).

In this paper, we focus on the containment of invasive species via their population suppression, either via surveillance and eradication (second strategy) or treatment in a suppression zone (third strategy) or both. Specifically, we examine what is the optimal spatial distribution of treatment efforts that contains the species while minimizing the annual cost. In particular, we examine whether and under what circumstances this optimal strategy comprises a suppression zone. And, if a suppression zone is cost effective, how should it be managed, for example, what should be its size, target population levels, and suppression intensities? We also examine how the optimal strategy depends on the demographic characteristics of the invasive species and its response to the treatment. Note that, while some previous studies have calculated the optimal spatial distribution of treatment efforts to contain a species (Baker & Bode, 2016; Bonneau et al., 2017; Nishimoto et al., 2021), the novelty in our paper is in examining the conditions that determine, based on the characteristics of the system, whether and how to cost-effectively manage a suppression zone.

To answer these questions, we consider a well established continuous-space model, and we develop a novel algorithm to find the optimal distribution of treatment over space. We assume that the decision to stop the species' spread has already been made, but the strategy to achieve this has not been selected. In particular, we compare the containment of invasive plants (Grice et al., 2020) and the containment of invasive animals such as insects (Liebhold & Tobin, 2008), and we examine how changes in demographic parameters affect the optimal treatment in both cases.

METHODS

Model

We consider a population of an invasive species with a density $n(x, t)$ that may vary over space, x, and time, t. The investment in suppression, $A(x, t)$, may also vary over space and time. We consider overlapping generations with continuous-time dynamics. We consider a population that comprises adults and juveniles (e.g., larvae) or seeds, where a fraction γ of the juveniles/seeds disperse before they become adults. For simplicity, we assume that the juveniles become adults relatively quickly, therefore, we can use the single variable n to describe the population density (or the adults' density). (Namely, the adult population dynamics occur on a much slower timescale than the dispersal dynamics.) In turn, the rate of adult mortality in location x and time t is given by $d(n(x, t), A(x, t))$, and the rate of juvenile production is given by $b(n(x, t), A(x, t))$, where this rate incorporates both juveniles' birth and their survival to adulthood. It follows that, for every x and t, the dynamics of $n(x, t)$ are given by (Hutson et al., 2003; Lutscher et al., 2005; Othmer et al., 1988):

$$\frac{dn(x,t)}{dt} = (1-\gamma)b(n,A) - d(n,A) + \gamma\int_{-\infty}^{\infty} b(n(x', t), A(x', t))G(x-x')dx', \quad (1)$$

where $(1-\gamma)$ is the fraction of juveniles that do not disperse, the integral is over space, and $G(x)$ is the dispersal kernel that determines how the juveniles/seeds disperse over space. The shape of G may vary between species and environments, and it depends on the dispersal mechanisms (Nathan et al., 2012).

Equation (1) is general and enables the representation of various species and suppression methods. The specific choice of the functions $b(n, A)$ and $d(n, A)$ determines the population dynamics and its response to the suppression. Here we focus on two cases. The first case is motivated by the suppression of large invasive plants contained via the physical removal of adult plants (Grice et al., 2020). In that case, a common assumption in the literature is that the number of individuals removed is proportional to the expenditure on suppression (Blackwood et al., 2010; Lampert et al., 2014, 2018; Taylor & Hastings, 2004). This is because the species is nonmoving and is easily detectable, and therefore, treatment can target those locations where the species is present, regardless of the overall population size. We incorporate this into the model via the following choice of birth and death functions:

$$b(n, A) = rn\left(1 - \frac{n}{k}\right), \tag{2a}$$

$$d(n, A) = \delta n + \alpha A, \tag{2b}$$

where r is the per-capita rate of seed production when the population is small, the term n/k is due to diminished production of seeds at high densities, δ is the natural death rate of adult plants, and α is the amount abated per unit of investment in suppression.

In turn, the second case is motivated by the suppression of invasive insects via insecticide application that eliminates a certain fraction of the population, β, per unit of effort. Insects are often subject to an Allee effect, namely, their populations are less likely to grow if their density is below a certain threshold. Allee effects can arise through various mechanisms, where mate-finding failure at low densities is the most common (Liebhold & Tobin, 2008). Because males search for females independently of one another (Poisson process), we may assume that the probability that a female is found by at least one male is given by $1 - \exp(-\mu n)$, where μ is the probability that a given male finds a given female (Blackwood et al., 2012; Lampert & Liebhold, 2021). Accordingly, we consider:

$$b(n, A) = rn\left(1 - \frac{n}{k}\right)(1 - \exp(-\mu n)), \tag{3a}$$

$$d(n, A) = \delta n + \beta n A. \tag{3b}$$

Note that this equation results in an Allee effect because $d > b$ if n is below a certain Allee threshold, $n < n_a$. Specifically, if k is large ($k \gg 1/\mu$) and $r > \delta$, the Allee threshold without suppression ($A = 0$) is given by:

$$n_a = \frac{1}{\mu}\ln\left(\frac{r}{r - \delta}\right). \tag{4}$$

In turn, the form of the dispersal kernel G depends on the particular species and its dispersal mechanism (Nathan et al., 2012). In particular, it characterizes whether the dispersal is a short-range or a long-range one. Here we consider three widely-used kernel functions (Nathan et al., 2012): (a) an exponentially decaying kernel (short-range), (b) a Gaussian kernel (short-range), and (c) a long-range dispersal kernel:

$$G_1(x - x') = \frac{1}{2\sigma}\exp\left(-\frac{x - x'}{\sigma}\right), \tag{5a}$$

$$G_2(x - x') = \frac{1}{\sqrt{2\pi}\sigma}\exp\left(\frac{(x - x')^2}{2\sigma^2}\right), \tag{5b}$$

$$G_3(x - x') = \frac{1}{\pi\sigma}\cdot\frac{1}{1 + (x - x')^2/\sigma^2}. \tag{5c}$$

While Equations (1–5) define the dynamics of the species, the manager must choose the suppression function $A(x, t)$. We assume that the manager's objective is to contain the invasive species in a certain area (zero spread) while minimizing the annual cost of treatment. We restrict attention to the management in the long run: we assume that the population size, $n(x, t)$, converges to some steady-state population size given by $n^*(x)$, and the manager adopts the same strategy $A(x, t) = A^*(x)$ every year ($n(x, t) \to n^*(x)$ as $t \to \infty$ if $A(x, t) = A^*(x)$). The annual cost of treatment (ACT) is then given by:

$$\mathrm{ACT} = \int_{-\infty}^{\infty} A^*(x)dx. \tag{6}$$

Specifically, the ACT is the rate at which the manager invests in treatment, which we assume does not change over time in the long run; therefore, if we measure time in years, the ACT is the annual cost of treatment.

In turn, we assume that the manager chooses a certain border location, x_0, such that they keep the area where $x < x_0$ uninvaded. Specifically, the manager must keep n^* at zero in the uninvaded area if there is no Allee effect, but if an Allee effect is present, then the manager must keep n^* below the Allee threshold, n_a:

$$n^*(x) \le n_a \;\text{ if }\; x < x_0. \tag{7}$$

We also assume that the manager only contains the species and does not fully eradicate it. Therefore, we restrict attention to cases in which the population is managed only in proximity to the uninvaded area: There exists $x_1 \ge x_0$, such that:

$$A^*(x) = 0 \;\text{ if }\; x > x_1. \tag{8}$$

Finally, note that the population size and the treatment cannot be negative for all x:

$$n(x) \ge 0 \;\text{ and }\; A(x) \ge 0. \tag{9}$$

Therefore, the objective is to find the function $A^*(x)$ that minimizes the ACT (Equation 6), under the constraints that there exist x_1 and t_c such that $A^*(x) = 0$ if $x > x_1$ (Equation 8), $n(x, t) < n_a$ for all $x < x_0$ if $t > t_c$

(Equation 7), and n and A are nonnegative (Equation 9), where the dynamics of $n(x, t)$ are given by Equation (1) with $A = A^*$.

We denote $A^{\mathrm{opt}}(x)$ as the resulting optimal annual suppression, and $n^{\mathrm{opt}}(x)$ as the density distribution at which the species should be contained ($n^* = n^{\mathrm{opt}}$ if $A = A^{\mathrm{opt}}$). If A^{opt} is such that $x_1 = x_0$ ($A^{\mathrm{opt}}(x) = 0$ for all $x > x_0$), the optimal strategy is to have no suppression zone: the manager treats only where $x < x_0$ and abandons the other area. However, if $A^{\mathrm{opt}}(x)$ is such that $x_1 > x_0$ (there exists some area $x_0 < x < x_1$ where $A^{\mathrm{opt}}(x) > 0$ and $n^{\mathrm{opt}}(x) > n_a$), the optimal strategy is to maintain a suppression zone between x_0 and x_1: within the suppression zone, the manager treats the species population, but without aiming to suppress populations to zero; rather, the manager only treats the population in this area as a means to cost-effectively keep the uninvaded area clear.

Numerical analysis

Our model defines an optimal solution, given by the function $A^{\mathrm{opt}}(x)$ that minimizes the annual cost of treatment (minimize ACT, Equation 6), subject to the dynamics (Equation 1) and the constraints (Equations 7 and 8). This treatment function results in a stationary species distribution denoted as $n^{\mathrm{opt}}(x)$. In turn, to find that optimal solution, we developed an algorithm that performs a local search in the space of all possible front shapes (Appendix S1: Figures S1 and S2). To find the optimal treatment, or at least an approximation of that treatment, we developed an algorithm that performs a local search in the space of all possible front shapes. Specifically, the algorithm aims to find the front shape that could be held stationary using the suppression with the lowest ACT. We emphasize that the algorithm performs a local search, where each time it examines a front shape that differs slightly from the previous shapes to look for improvements, and therefore, there is no proof that it converges to the global optimum. However, the fact that the algorithm converges to the same result from various different initial front shapes strengthens the hypothesis that the algorithm's outcome is the global optimum, or at least an approximation that would be difficult to improve further. The algorithm is described here in detail and is demonstrated in Appendix S1: Figures S1 and S2. The algorithm's code is also available as a Supplementary code.

First, note that the reason why $n^{\mathrm{opt}}(x)$ has the shape of a population front is due to our constraints. Specifically, we aim to optimize the ACT in the long run, assuming that the population density function, $n = n^*(x)$, is held stationary using the suppression function $A = A^*(x)$ (i.e., $dn^*/dt = 0$ if $A = A^*$). We assume that $n^*(x) < n_a$ if $x < x_0$ (Equation 7) and that $A^*(x) = 0$ if x is greater than x_1 (Equation 8). Because we consider a species that would spread in the absence of treatment, the constraint in Equation (8) implies that $n^*(x)$ approaches the species' carrying capacity as $x \to \infty$.

In turn, note that for every front shape, $\widehat{n}(x)$, either (1) there exists a unique treatment function $A^*(x)$ that keeps $\widehat{n}(x)$ stationary and satisfies Equations (8) and (9), or (2) such an A^* does not exist. The first step in the algorithm is to build a function that gets $\widehat{n}(x)$ as an input, and returns as an output a function $\widehat{A}(x)$ that equals A^* if it exists; and otherwise, $\widehat{A}(x)$ is a function that satisfies (1) $\widehat{A}(x) \geq 0$ and (2) $d\widehat{n}/dt \leq 0$ if $A = \widehat{A}$. Specifically, to find $\widehat{A}(x)$, the function simulates the natural dynamics (without treatment) for a very short time period, Δt, starting at $n = \widehat{n}$. This results in a density that we denote as n'. Then, for every x, the function finds $A'(x)$ that is needed to suppress the population back from n' to $\widehat{n}$ within a period Δt. Specifically, if $d(n, A)$ is given by Equation (2b), then $A' = (n' - \widehat{n})/(\alpha \Delta t)$. If $d(n, A)$ is given by Equation (3b), then $A' = \ln(n'/\widehat{n})/(\beta \Delta t)$ (the integral of $1/(\beta n \Delta t)$ from $\widehat{n}$ to n'). However, note that we conclude that $A^* = A'$ if and only if $A'(x) \geq 0$ for all x. Otherwise, the front cannot be held stationary using a positive function. Accordingly, the function's output is given by $\widehat{A}(x) = A^*(x)$ for values of x in which $A'(x) \geq 0$ and $\widehat{A}(x) = 0$ for values of x in which $A'(x) < 0$.

In turn, using this function, the algorithm searches locally to find the optimal shape of an invasion front in a continuous-space model by performing a local search in the space of all possible front shapes. Specifically, the algorithm begins with some initial front shape, $\widehat{n}(x)$, that satisfies $\widehat{n}(x) < n_a$ if $x < 0$ (Appendix S1: Figures S1A and S2A). In turn, $\widehat{A}(x)$ is given by the suppression function that is needed to keep $\widehat{n}$ stationary or at least nonincreasing. Next, in each iteration of the algorithm, it slightly changes the shape of $\widehat{n}$ to one that still satisfies Equation (7) and that can be held stationary or nonincreasing using a treatment function $\widehat{A}(x)$ that results in a lower annual cost of treatment (lower ACT, Equation (6)) (Appendix S1: Figures S1B–E and S2B–E). Specifically, the algorithm goes over all values of x from x_0 to some $x_{\max}$. In each location x^* within that range (up to some fine resolution Δx) it examines $n^{\uparrow}$ that differs from $\widehat{n}$ only at $x = x^*$, where $n^{\uparrow}(x^*)$ is between $\widehat{n}(x^*)$ and $\widehat{n}(x^* + \Delta x)$. Similarly, it examines $n^{\downarrow}$ that differs from $\widehat{n}$ only at $x = x^*$, where $n^{\downarrow}(x^*)$ is between $\widehat{n}(x^*)$ and $\widehat{n}(x^* - \Delta x)$. Once the algorithm finds an improvement, it modifies $\widehat{n}$ to the new shape. The algorithm continues until it converges to $\widehat{n}$ and $\widehat{A}$ that cannot be further improved locally, that is, any local changes in $\widehat{n}$ results in $\widehat{A}$ that necessitates a larger ACT (Appendix S1: Figures S1F and S2F). Note that the final result of the algorithm is always a function A^* that keeps $\hat{n}$ stationary and satisfies Equations (8) and (9) (although intermediate stages might include $\hat{A}$ for which $\hat{n}$ declines), a fact that we also verified in all simulations. This is because, if $\hat{A}$ is such that $\hat{n}$ declines, it implies that $\hat{A}$ can be further improved locally by reducing $\hat{n}$ in those locations where $d\hat{n}/dt < 0$.

In addition, we performed several analyses to examine the hypothesis that at least those solutions demonstrated in Figure 2 are the optimal solutions. First, we examined other modifications to which the algorithm converges, such as slightly changing the entire shape of the front in various directions, and we confirmed that the resulting ACT is higher in all these cases. Second, we repeated the algorithm with various different initial conditions, and we made sure that it always converged to the same solution. Appendix S1: Figures S1 and S2 demonstrate how the algorithm converges to the same solution from different initial choices of the front shape, where Appendix S1: Figure S1 begins with the shape of a front

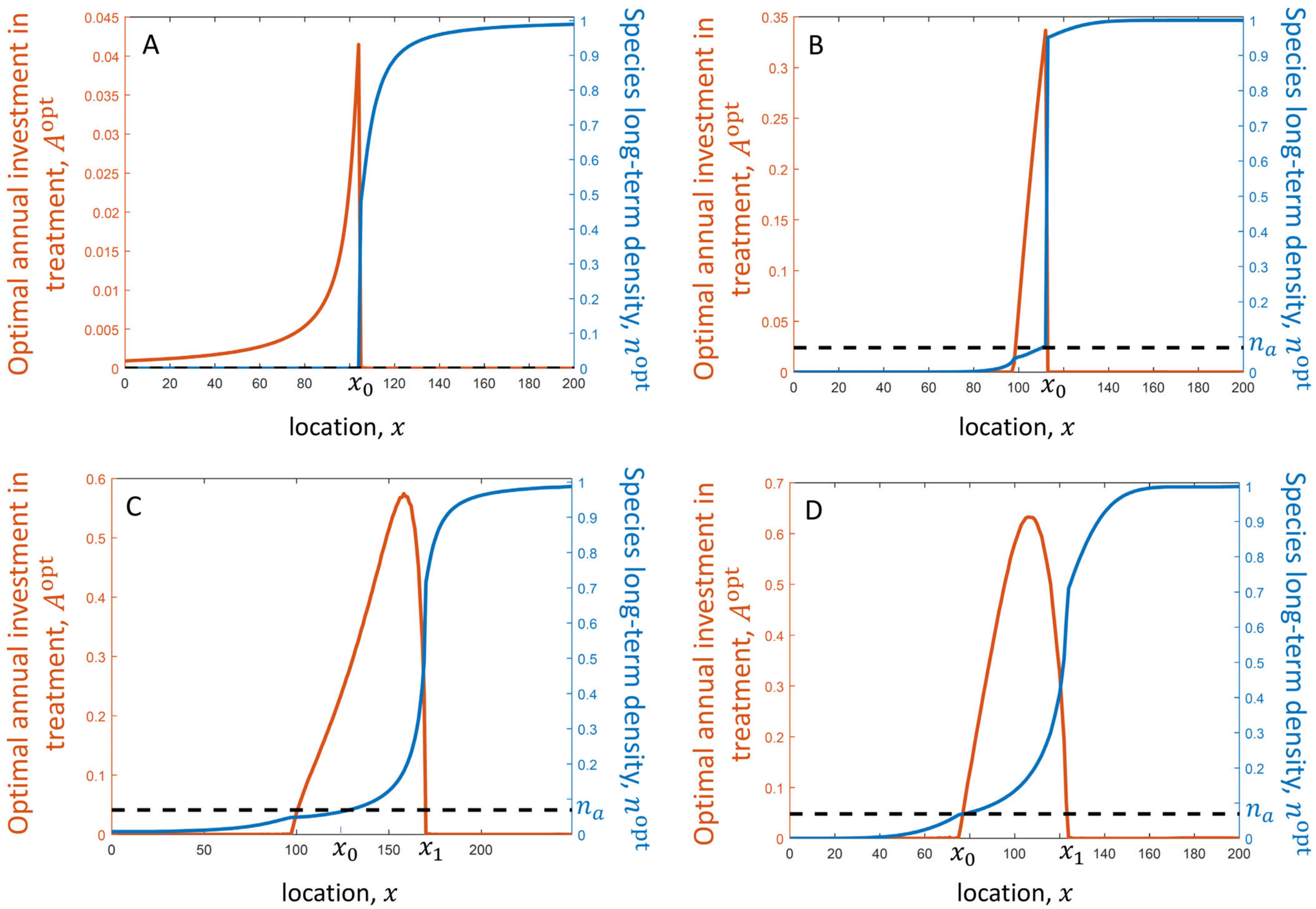

FIGURE 2 A suppression zone is cost effective in some cases. Demonstrated are the optimal suppression functions, $A^{opt}(x)$ (orange), and the corresponding population densities (front's shape), $n^{opt}(x)$ (blue), in four cases. (A, B) The optimal strategy is to have no suppression zone: treatment takes place ($A^{opt}(x) > 0$) only in the uninvaded area ($x < x_0$), which is where (A) $n^{opt}(x) = 0$ or (B) $n^{opt}(x)$ is below the Allee threshold indicated by the black dashed line. Note that the population density declines gradually as x declines in the invaded area because individuals disperse from the invaded area to the uninvaded area. Here, in (A), treatment is additive (the amount removed per dollar invested does not depend on the population size, Equation 2), $G = G_3$, and all individuals disperse ($\gamma = 1$). In (B), treatment removes a certain fraction of the population (F is given by Equation 3), but a large portion of the individuals do not disperse ($\gamma = 0.1$). (C, D) The optimal strategy is to use a suppression zone: managers should treat within a certain area, $x_0 < x < x_1$, in which the population is kept above the Allee threshold ($n^{opt}(x) > n_a$). Managers still keep the population below the Allee threshold in the uninvaded area ($x < x_0$) and abandon treatment in the invaded area ($x > x_1$). Note that, in (D), treatment takes place only in the suppression zone and no treatment is done in the uninvaded area. Here, in both (C) and (D), treatment removes a certain fraction of the species population (F is given by Equation 3), and all individuals disperse ($\gamma = 1$). However, in (C), dispersal in long-range ($G = G_3$), while in (D), dispersal is Gaussian ($G = G_2$). Parameters: (A) F given by Equation (2), $r = 1$, $k = 2$, $\delta = 1$, $\alpha = 10$; (B–D) F given by Equation (3), $r = 2$, $k = 2$, $\delta = 1$, $\beta = 1.61$, $\mu = 10$; (A, C) $G = G_3$, $\sigma = 5$; (B, D) $G = G_2$, $\sigma = 15$; (A, C, D) $\gamma = 1$; (B) $\gamma = 0.1$.

that propagates naturally, and Appendix S1: Figure S2 begins with a piecewise-linear shape.

RESULTS

Our results show that targeting populations in a suppression zone is a cost-effective approach to containment in some cases but not in others. Whether a suppression zone is cost effective or not depends on the suppression methods and the dispersal mechanism. Consider first the case of plant containment in which the number of individuals removed per unit of expenditures on suppression does not depend on the population density (b and d are given by Equation 2). Then, our result shows that the optimal strategy is to have no suppression zone (Figure 2A): the most cost-effective containment strategy is to abandon suppression in the invaded area and only eradicate new populations in the uninvaded area. This result is general and holds for all choices of the kernel function and all parameter values if b and d are given by Equation (2). The reason is that the cost per unit of abatement is the same for treatment in either the suppression zone or the uninvaded area (Equation 2). In turn, in the steady-state, only a fraction of the population located at $x > x_0$ eventually arrives at some $x < x_0$ and, therefore, it is less efficient to suppress at $x > x_0$ (Appendix S2).

Conversely, consider the case in which an Allee effect exists and the number of individuals removed per investment is proportional to the population size (b and d are given by Equation 3; e.g., pesticide application to treat insects). In that case, it is more costly to abate the population when its density is low. Our results show that a suppression zone is cost effective if and only if the Allee threshold, n_a, is below a certain level and/or the fraction of individuals that disperse, γ, is above a certain threshold (Figures 2B–D and 3; Appendix S2).

Specifically, if γ is below a certain threshold, the optimal solution is to have no suppression zone (Figure 2B): the most cost-effective containment strategy in this situation is to treat only in the uninvaded area to suppress n below the Allee threshold (eradicate new populations). However, if γ is above that threshold, the optimal solution is to maintain a suppression zone between x_0 and x_1, where the manager treats the invasive species but maintains the species density above the Allee threshold ($A^{\text{opt}}(x) > 0$ and $n^{\text{opt}}(x) > n_a$ if $x_0 < x < x_1$; Figure 2C,D). Specifically, if b and d are given by Equation (3) and $r > \delta$, then a sufficient condition for having a suppression zone as part of the optimal strategy is (Appendix S2):

$$\gamma > 2\frac{n_a}{k}\frac{r}{r-\delta}, \tag{10}$$

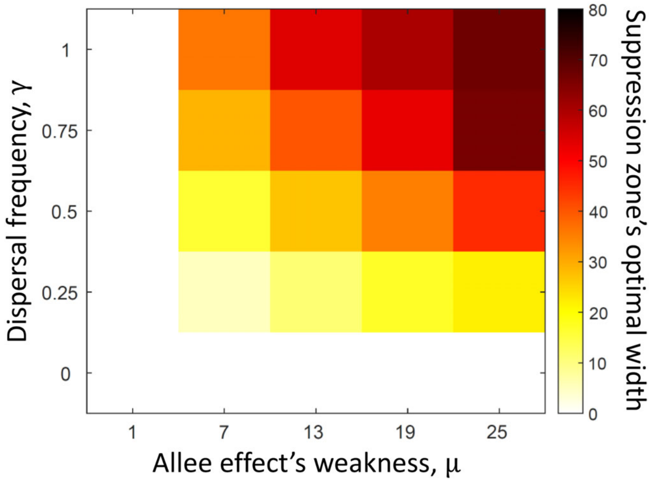

FIGURE 3 The optimal width of the suppression zone is larger (suppression begins further away from the uninvaded area) if the Allee effect is weaker and if the dispersal frequency is larger. Demonstrated are the widths of the suppression zone, assuming that the optimal suppression strategy is used, for various values of the parameters γ (dispersal frequency, Equation (1)) and μ (lower μ implies a stronger Allee effect, Equation 3). Specifically, we assume that the dynamics are given by Equation (1) and F is given by Equation (3), namely, the suppression removes individuals in proportion to the population size. If γ or μ are below a certain threshold, the optimal strategy is to have no suppression zone (therefore the optimal width of the suppression zone is zero). For values of γ and μ above that threshold, the optimal width of the suppression zone increases with the value of these two parameters. Other parameters: $r = 2$, $k = 2$, $\delta = 1$, $\beta = 1.61$, $G = G_3$, $\sigma = 5$.

where n_a is the Allee threshold (Equation 4). Furthermore, following the optimal solution, if a suppression zone exists, its width (size) increases as the portion of juveniles that disperse (γ) increases and as the Allee threshold (n_a) decreases (Figure 3). Specifically, note that without treatment, n approaches a steady density (carrying capacity) given by $n = k(r-\delta)/r$ (Appendix S2). Therefore, the right-hand side of Equation (10) is two times the ratio between the Allee threshold and the carrying capacity.

The intuition behind this result is as follows. First, the reason why it might be more effective to treat further away from the uninvaded area is that suppression is more efficient at large densities: According to the dynamics we consider here (Equation 3), the number of individuals abated per unit of treatment is proportional to n (Equation 3b). In turn, in the uninvaded area, n is below the Allee threshold ($n \leq n_a$), whereas in the invaded area, n is closer to the population's carrying capacity. Therefore, the larger the ratio between n_a and the carrying capacity is, the more efficient it is to treat outside the invaded area. Second, if more individuals disperse from the uninvaded area to the invaded area, the more beneficial it is to treat in the uninvaded area. Therefore, a larger γ implies a higher efficiency of treating outside the invaded area.

Note that the optimal solution sometimes dictates targeting populations only in the suppression zone (Figure 2D), but sometimes it dictates treating populations in both the suppression zone and the uninvaded area (Figure 2C). Also, note that the improvement achieved by using the more cost-effective treatment strategy could be significant. For example, with the parameters used in Figure 2C, if the manager uses a suppression function that keeps the front in a shape of a propagating front, the ACT is greater by 228% compared with the optimal solution (Appendix S1: Figure S1). If the manager uses a suppression function that keeps the front with a piecewise-linear shape (Appendix S1: Figure S2A), the ACT is greater by 440% compared with the optimal solution (Appendix S1: Figure S2).

DISCUSSION

We examined how to optimally stop the spread of an invasive species, focusing on how to distribute the efforts to suppress the species over space to minimize the ACT. We presented a broad analysis that provides managers with insight into the biological and logistic characteristics. To do that, we considered a continuous-space model that also enables the suppression intensity to vary continuously over space. Such a model introduces a computational challenge, and we overcame this challenge by developing a novel algorithm.

We showed that containment often necessitates the eradication of populations that disperse to uninvaded areas. Furthermore, in some cases, it may be cost effective to also suppress the species in a "suppression zone," located along the edge of the invaded area; in this area, the population is being suppressed but not eliminated. We show that if the cost of abatement does not depend on the population size, such as the case with the abatement of some large invasive plants (Lampert et al., 2014; Taylor & Hastings, 2004), then it is not cost effective to use a suppression zone (Figure 2A). Conversely, if the cost of abatement is proportional to the population size, such as the case with insecticide applications (Dent & Binks, 2020), and if the fraction of individuals that disperse is relatively large (Equation 10), then maintaining a suppression zone is cost effective (Figure 2C,D).

In practice, there are few instances in which suppression zones have been implemented, except with some invasive plants (Grice et al., 2013). Therefore, our results show that there may be new opportunities to improve current strategies in some cases by implementing a suppression zone, either in parallel to a barrier zone (Figure 2C) or alone (Figure 2D). In particular, when considering insect populations, the number of individuals abated due to pesticide treatments is generally proportional to the insect population density (i.e., relatively few individuals are killed when low-density populations are treated). In these situations, containment may be more effective when the eradication of satellite populations is coupled with the suppression of populations at the periphery of the invaded area. The benefit of this suppression is greatest for target species that exhibit strong Allee effects. In the presence of Allee effects, very small satellite populations are likely to go extinct with little intervention (Lewis & Kareiva, 1993; Liebhold & Bascompte, 2003), and therefore, suppression of peripheral populations may result in the founding of smaller satellite populations that are more likely to become extinct. This result provides another example of how the existence of the Allee effect offers unique opportunities for managing invasions (Tobin et al., 2011). A particularly instructive example of containment targeting an insect invasion is the case of the spongy moth, *Lymantria dispar*, in the USA, where satellite populations are detected and eradicated in a barrier zone to slow the spread of this species (Tobin & Blackburn, 2007). Given that strong Allee effects are known to be present in this insect (Tobin et al., 2009), our analysis suggests that greater efficiency of this program might be achieved via suppression of populations at the periphery of the invaded region.

We did not compare the costs and benefits of containment as an overall strategy, but there have been previous studies showing that expenditures made to slow or stop spread sometimes outweigh the costs of no action (Epanchin-Niell & Wilen, 2012; Sharov & Liebhold, 1998). While it is commonly held that intervening in the early stages of invasion (i.e., prevention of arrival) is more cost effective than interventions later on (Leung et al., 2002; Lodge et al., 2006), there are reasons to question this dogma. In many species, there are long delays between establishment and the accumulation of impacts, and such lags mean that costs associated with impacts may be small when discounted back to the time of arrival, which corresponds to the timing of prevention (Epanchin-Niell & Liebhold, 2015). Such effects will tend to favor the adoption of interventions that are timed in later stages of invasions, such as the management of spread. Taken together, these factors point toward increased consideration of containment and refinement of containment strategies as part of future efforts to manage biological invasions.

Our study has several limitations that could be addressed in future studies. First, real-world invasion spread is stochastic and, therefore, the distribution of invading populations at the periphery of the invasion front is often patchy (Shigesada & Kawasaki, 1997). Consequently, suppression efforts are not being applied uniformly and survey efforts are required to locate populations to be eradicated. We do not explicitly address the optimal allocation of resources between survey and suppression although this topic has already received attention in the literature (Epanchin-Niell et al., 2012; Hauser & McCarthy, 2009). Second, we do not address the allocation of efforts toward direct control of the dispersal of propagules into the uninvaded area (e.g., using barriers or quarantines), but operational containment programs may carry out these efforts in addition to implementing an eradication zone and suppression zone. Third, while we focused on invasions that need to be stopped, a more general question is how to optimally slow the spread of an invasion, allowing propagation at nonzero speeds (Sharov & Liebhold, 1998). Finally, we found the optimal long-term management profile, A^{opt}, at least approximately, but more work is needed to identify optimal management during the initial phase until n approaches n^{opt}, as well as the optimal choice of x_0 that would minimize the initial cost of treatment plus the prolonged cost of damage. Nevertheless, although A^{opt} is the optimal treatment only in the long run, it is sufficient for stopping the spread of a propagating front that initially has a shape that differs from n^{opt} (Figure 4), and this result holds for all cases demonstrated in Figure 2.

Another limitation of our analysis is that we did not consider costs associated directly with surveillance. In real-life containment projects substantial expenditures are made to survey regions both to determine the spatial extent of the invaded range as well as to detect satellite populations (Grice et al., 2020; Liebhold & Kean, 2019). As is the case in eradication (Epanchin-Niell et al., 2012), there will be a trade-off between expenditures on surveillance vs. treatments. Future studies are needed to address such trade-offs in the selection of containment strategies. Another area that could be explored in the future is the integration of containment strategies with "functional eradication" strategies. This term was proposed by Green & Grosholz (2021) to describe situations in which managers choose to suppress populations of an invading species below levels that cause negative impacts across a region. Because such strategies typically contain the spread of invading populations, in addition to population suppression, there is an overlap with the objectives of simple containment. Specifically, the suppression in the suppression zone could also serve a similar role to that of "functional eradication" in that area.

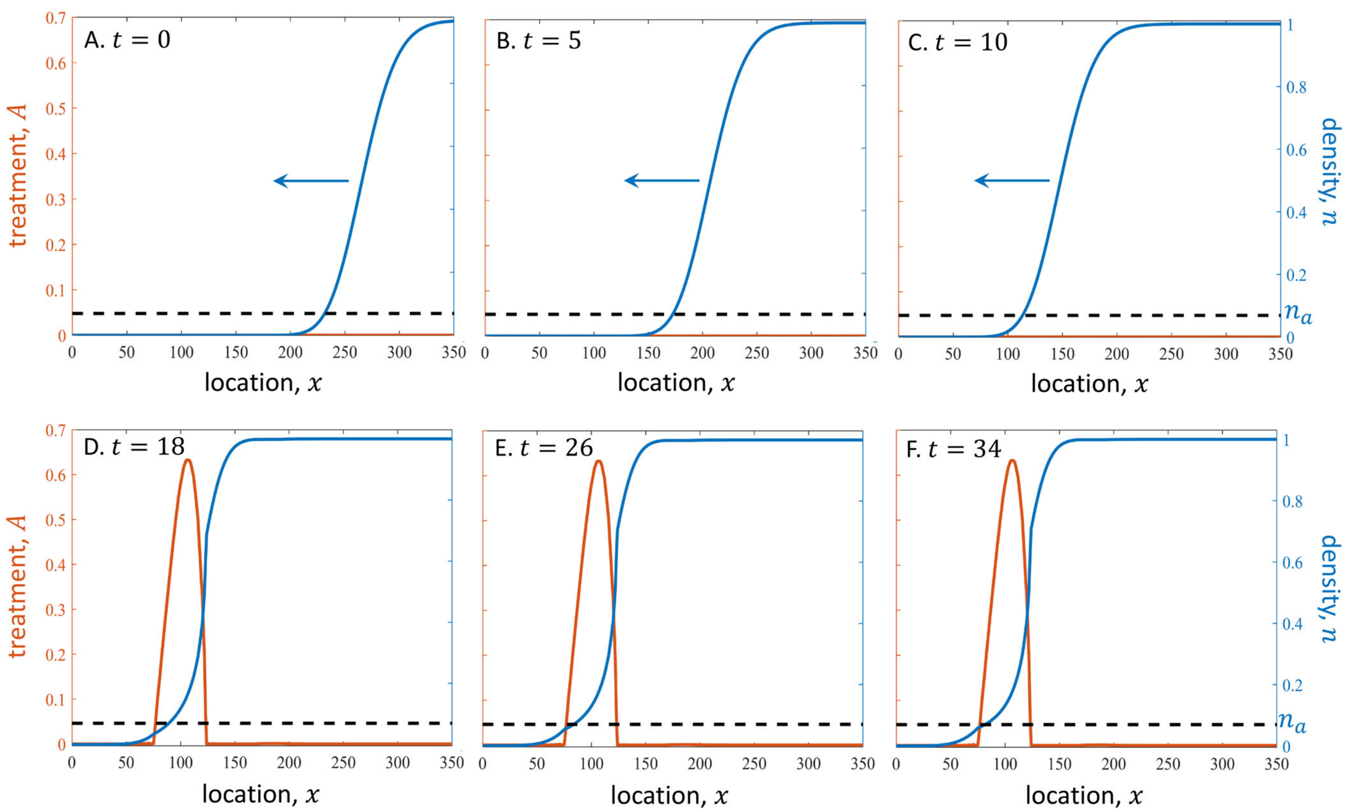

FIGURE 4 The invasive species population initially propagates, but stops after suppression is applied. (A–C) Treatment is not applied ($A = 0$), and the invasion front propagates over time from right to left. (D–F) The treatment $A(x) = A^{\text{opt}}(x)$ is applied, and the invasion front stops and converges to $n(x) = n^{\text{opt}}(x)$. Parameters are the same as in Figure 2D.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Code (Lampert, 2022b) is provided in Zenodo at https://doi.org/10.5281/zenodo.7313577. Simulation results (Lampert, 2022a) are provided in Dryad at https://doi.org/10.5061/dryad.kkwh70s7j.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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