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RESEARCH ARTICLE

Optimal strategies for utilizing host plant distributions to slow the spread of plant pests

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Abstract

1. Invasive species are spreading globally, threatening ecosystems, biodiversity, agriculture and human health. When efforts to prevent the establishment of invasive species fail and eradication is not possible, containment becomes necessary to slow or stop the spread of established invaders. A major question is, therefore, how to allocate treatments across space and time to contain populations cost-effectively.
2. Here, we examine how to optimize strategies for slowing the spread of the spongy moth (*Lymantria dispar*) in North America by utilizing gaps with lower densities of host plants. Around these gaps, managers can apply both bio-pesticides and mating disruption using synthetic pheromones to disrupt male mate-finding. We develop a spatially explicit model of the moth's population dynamics, and we develop a novel algorithm that finds the optimal spatial allocation of the two methods across landscapes with heterogeneous host-plant distributions.
3. Our results show that combining pesticide application and mating disruption around host-plant gaps significantly improves cost efficiency: Optimal treatment allocates mating disruption to low moth-density regions nearer the moth-free area and pesticides to higher moth-density regions nearer the invasion front, with minimal spatial overlap in treatments.
4. *Synthesis and applications*. Containment of invasive species can be made markedly more cost-effective by prioritizing landscape features that naturally impede spread. Targeting treatments around host-plant gaps supports a clear operational rule: use mating disruption where densities are low to prevent establishment and concentrate pesticides where densities are high to suppress the advancing front, avoiding costly overlap. More broadly, the algorithm provides a general framework for computing optimal, landscape-specific containment allocations over space.

KEYWORDS
bioeconomic modelling, cost efficiency, invasive species, natural barrier, optimal control, population dynamics, spatial dynamics

1 | INTRODUCTION

Increasing globalization of trade and travel has led to numerous introductions of non-native plant pests across the globe. Many of these pests, such as the spongy moth (*Lymantria dispar*), emerald ash borer (*Agrilus planipennis*) and the chestnut blight pathogen (*Cryphonectria parasitica*), have caused severe ecological and economic impacts, including the decimation of entire tree genera in invaded regions (Lovett et al., 2016). Similarly, agricultural pests such as the codling moth (*Cydia pomonella*) and the cotton bollworm (*Helicoverpa armigera*) have driven a significant rise in pesticide usage worldwide (Perrings, 2007). To combat these challenges, governments have implemented intensive biosecurity measures to prevent the introduction and establishment of invasive pests (Hulme, 2011). These efforts often focus on the interception of pests at borders, surveillance for new pest incursions and rapid eradication of nascent populations. However, despite their success in reducing pest introductions, many species continue to establish and spread in new regions. Once establishment occurs, containment becomes one of the few viable options for managing invasive species, aiming to limit their range expansion and mitigate impacts (Grice et al., 2013; Liebhold & Kean, 2019).

A key factor influencing both invasion success and containment efficacy of plant pests is the spatial distribution of host plants. Invasive herbivores and pathogens often spread more rapidly in landscapes where host plants are abundant, whereas areas with sparse or discontinuous host availability can naturally impede invasions (Rigot et al., 2014). In particular, fragmentation of host plant habitat can slow or even halt pest spread by creating 'gaps' that the invader struggles to cross (Barron et al., 2020; Epanchin-Niell et al., 2022; Fischer & Lindenmayer, 2007; Metz & Tobin, 2022; With, 2002; With & King, 1999). Empirical studies of the spongy moth invasion front have found higher moth densities in regions with higher host-plant densities (Bigsby et al., 2011; Liebhold et al., 1997; Nesslage et al., 2007). Likewise, in agricultural systems, monocultures of crop hosts provide concentrated resources that fuel pest outbreaks, whereas greater plant diversity or dispersed cropping can reduce pest pressure by diluting host availability (Altieri et al., 2024). These patterns demonstrate that host-plant density and configuration fundamentally shape invasion dynamics across forests, farms and rangelands. Managers may thus slow an invader's spread by exploiting naturally occurring host-sparse areas as barriers.

In this study, we address the critical challenge of integrating multiple control methods over space to cost-effectively slow the spread of invasive pests, focussing on the spongy moth (*Lymantria dispar*), a destructive North American forest pest subject to a strong Allee effect. This insect species has been established in eastern North America for over 150 years and has been gradually expanding its range. Since 1999, the USDA Forest Service has implemented a large programme aimed at slowing the spread of this species in order to delay the accrual of impacts following recurrent outbreaks of established populations (Coleman, 2023). This barrier zone project focusses on populations along the species' expanding population front, a region where host tree densities vary considerably (Morin et al., 2005). Despite this variation, the programme operates across the action area by implementing a largely uniform management decision procedure (Tobin et al., 2004).

We present a novel spatially explicit optimization framework that simultaneously considers host plant distribution, pesticide application and mating disruption, to maximize containment effectiveness while minimizing costs. Specifically, we examine how to strategically leverage naturally occurring host-plant gaps by explicitly optimizing the spatial arrangement and intensity of treatments around these natural barriers. In particular, we investigate which types of host-density gaps are more effective barriers to pest spread (e.g. narrow gaps with very few host plants versus wider gaps with intermediate host-plant densities; Figure 1). The presence of host plant gaps, whether created naturally of by active removal, directly limits pest reproduction and survival by reducing access to critical resources (Barron et al., 2020; Robinet et al., 2020; Sun et al., 2023). Moreover, fragmenting habitats can induce Allee effects, where low population densities hinder pest persistence and spread (Courchamp et al., 2008). When combined with mating disruption and pesticide application, host manipulation has the potential to significantly enhance containment efforts. We examine how spatial arrangements of interventions can exploit ecological dynamics, such as Allee effects and dispersal limitations, to slow the spongy moth's spread.

2 | METHODS

2.1 | Model: Population dynamics

We consider a one-dimensional grid of L connected sites (Figure 2). Each site has a fixed density of host plants, $H_i\,(i = 1, 2, \ldots, L)$—a number between 0 and 1 characterizing the overall density in site i, incorporating tree numbers and sizes. The population density of the invasive species, $n_i(t)$, can vary over both space, i, and time, t. We assume that the population is established on the right side of the grid (where i is close to L), but has not yet invaded sites on the left side of the grid (where i is closer to 1). The manager can apply two treatment methods to stop the invasive species' spread from right to left: apply pesticides that remove a certain portion of the population, or release synthetic pheromones that limit males' ability to find females (mating disruption). The manager can determine the locations and magnitudes of these two methods: We denote R_i and F_i as the annual spending (USD) on pesticide application and mating disruption per hectare, respectively, in site i. We consider strategies that stop the spread of the invasive species and ultimately lead to a stationary (non-changing) spatial distribution. Accordingly, we assume that the manager uses the same strategy every year: The values of R_i and F_i vary across sites but do not change over time.

To model the dynamics on $n_i(t)$, we consider the spread of the spongy moth in North America as a case study. The spongy moth is a univoltine insect that follows an annual cycle during which the new generation displaces the previous one. This insect species naturally

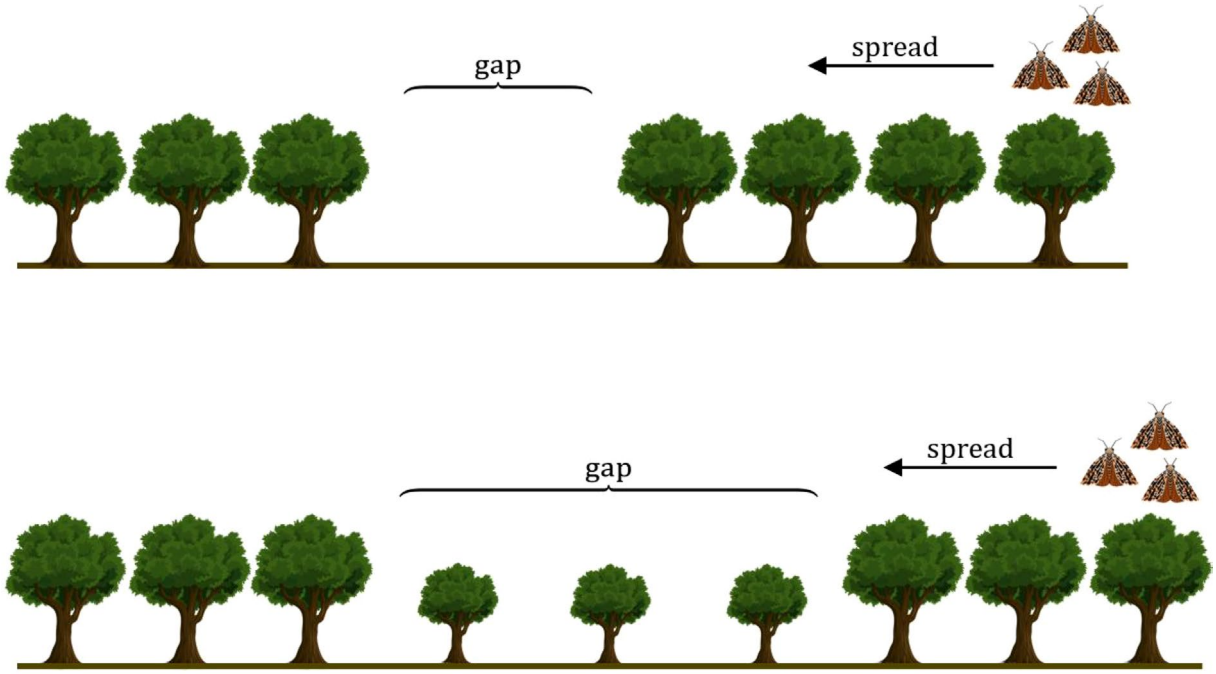

FIGURE 1 Which gap is more effective in slowing the spread? Gaps with lower densities of host plants can assist in slowing the spread of the spongy moth. Some gaps may be narrower with almost no host plants (top), while other gaps may be wider with some intermediate density of host plants (bottom). When managers use pesticides and mating disruption to slow the moth's spread, which gap would be more effective in reducing the cost of treatment?

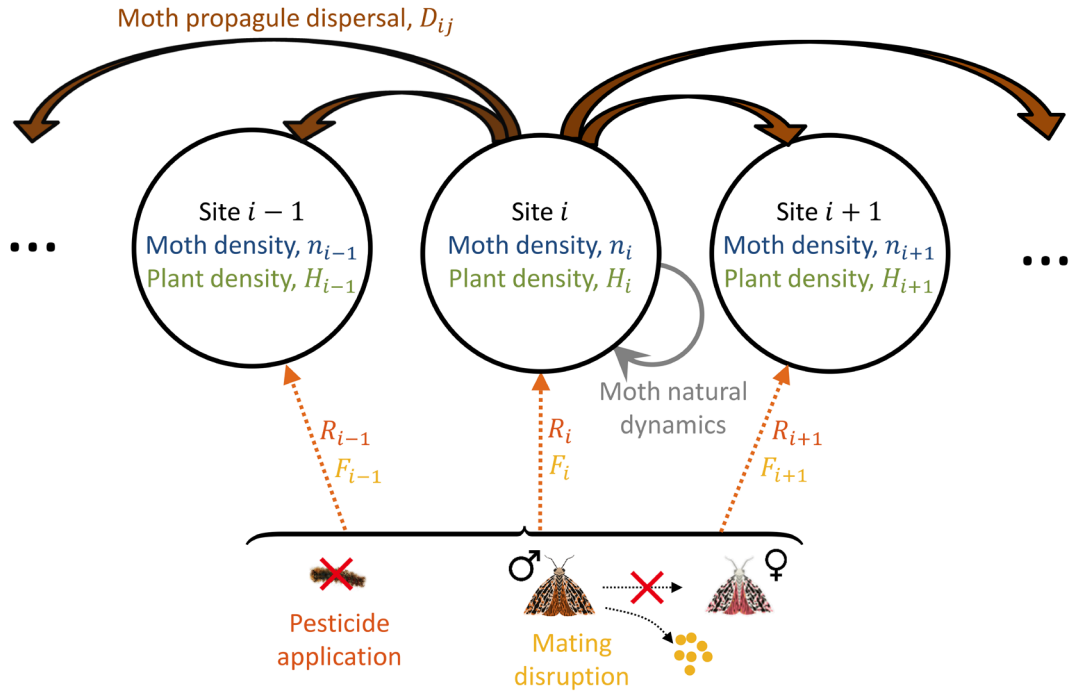

FIGURE 2 Illustration of the model. We consider L sites. Propagules from each site can disperse to nearby sites (brown arrows). The moth population in each site, n_i, also has intrinsic birth-death dynamics that are affected by three site-specific quantities: Host-plant density, H_i and the manager's investments in pesticide application, R_i, and mating disruption, F_i (Equation 1).

disperses in the spring when silk-producing first-instar larvae are carried by the wind to distant trees. Egg masses are laid in the late summer and are occasionally accidentally transported by humans to new locations. Scarcity of host plants limits the ability of first instars to find a host tree to feed on. Accordingly, we consider the following dynamics of the spongy moth population:

$$n_i(t+1) = H_i \exp(-\alpha R_i) \sum_{j=1}^{L} D_{ji} b(n_j(t), F_j), \quad (1)$$

where $\alpha > 0$ is the efficiency of pesticides (higher α implies that a higher fraction of the population is removed per USD investment), D_{ji} is the portion of propagules dispersing from site j to site i (or remaining in site i if $j = i$), and $b(n_i, F_i)$ is a birth function, determining how many propagules are born in a site with n_i individuals, F_i units of synthetic pheromones, and no pesticides (see Table 1: List of symbols).

We assume that dispersal is homogeneous and symmetric, namely, D_{ji} depends only on the distance between j and i, that is $D_{ji} = D_{|j-i|}$, and decreases as $|j - i|$ increases. Specifically, we examine both Gaussian and long-range dispersal kernel matrices (Nathan et al., 2012):

$$D_{ji} = \frac{1}{\sqrt{2\pi}\sigma} \exp\left(\frac{(j-i)^2}{2\sigma^2}\right), \quad (2a)$$

$$D_{ji} = \frac{1}{\pi\sigma} \cdot \frac{1}{1 + (j-i)^2/\sigma^2}, \quad (2b)$$

TABLE 1 Variables and parameters used in the model.

Symbol	Interpretation	Units	Range
State variables			
$n_i(t)$	Pest population density at site i in year t	Density	$n_i \geq 0$
H_i	Host plant density at site i	Unitless	$0 \leq H_i \leq 1$
Control variables			
R_i	Investment in bio-pesticides at site i	USD/(ha × year)	$R_i \geq 0$
F_i	Investment in mating disruption at site i	USD/(ha × year)	$F_i \geq 0$
Parameters			
α	Efficiency of pesticides per investment	(ha × year)/USD	$\alpha > 0$
D_{ji}	Dispersal from j to i	Unitless	$0 \leq D_{ji} \leq 1$
σ	Characteristic dispersal length	km	$\sigma > 0$
r	Baseline growth rate	$(\text{year})^{-1}$	$r > 1$
k	Carrying capacity	Density	$k > 0$
m_0	Probability that a given male finds a given female without mating disruption	Unitless	$0 \leq m_0 \leq 1$
λ	m_0 times the number of males in one unit of n_i per site	Unitless	$\lambda \geq 0$
β	Efficiency of mating disruption per investment	ha × year/USD	$\beta > 0$

where σ is the characteristic dispersal length. In turn, the birth function is given by

$$b(n_i, F_i) = r n_i \left(1 - \frac{n_i}{k}\right) P(n_i, F_i), \quad (3)$$

where r is the base growth rate, k is proportional to the carrying capacity, and $P(n_i, F_i)$ is the probability that a female is found by a male (Blackwood et al., 2012; Lampert & Liebhold, 2021). We assume that males search for females independently from each other, and the probability that a given male finds a given female without mating disruption is given by $m = m_0$. In the presence of mating disruption at site i, this probability declines with F_i and is given by $m_i = m_0 / (1 + \beta F_i)$, where β is the efficiency per unit cost of the synthetic pheromone flakes. In turn, we denote K as the number of males per site in a single unit of population density, such that Kn_i is the number of males in site i. Assuming that each male searches for females independently of other males, the probability that a female is not found by any male can be approximated by the probability of having zero occurrences of an event with probability m_i out of Kn_i lotteries. This Binomial coefficient can be approximated by the Poisson coefficient of a Poisson distribution with mean $Kn_i m_i$. Accordingly, P is given by

$$P(n_i, F_i) = 1 - \exp\left(\frac{\lambda n_i}{1 + \beta F_i}\right), \quad (4)$$

where $\lambda = K m_0$. This relationship is characterized by a strong Allee effect in which, below a threshold density (Allee threshold), populations decrease toward extinction, whereas above the threshold, populations increase in the absence of treatment (Tobin et al., 2009). Specifically, the Allee threshold is given by the population density $0 < n < k$ that satisfies $rnP(n, 0) = 1$, which implies $n = (2/\lambda) \ln(r/(r-1))$ (Lampert & Liebhold, 2021). The parameter λ determines the strength of the Allee effect: Larger λ implies a higher probability that females are found, implying a weaker Allee effect with a lower Allee threshold.

2.2 | Model: Management objective

Given the existing spatial distribution of host plants, the manager needs to choose the spatial distribution of the pesticides and mating disruption. We assume that the spread of the invasive species must be stopped, and we find how the manager could minimize the total cost subject to this constraint (Lampert & Liebhold, 2023). We consider various host-plant distributions, H_i, and for each, we use an optimization algorithm that finds the most cost-effective spatial distribution of pesticide application and mating disruption that stops the population spread (Appendix S1: Numerical Methods (Supporting Information)). Specifically, the objective is to find the distribution of treatments (R_i and F_i for all i) that minimizes the annual cost of treatment (ACT), given by

$$\text{ACT} = \sum_{i=1}^{L} (R_i + F_i), \quad (5)$$

subject to the following constraints: (1) the population's spread stops, with the density n_i approaching a stationary distribution that stays below the Allee threshold for every site $i \leq L_0$, where the dynamics of $n_i(t)$ are given by Equations (1–4); (2) the species is contained but not eradicated, and no treatment is applied on the right side of the grid where the population is established ($R_i = F_i = 0$ if $i \geq L_1$); and (3) treatments are not negative ($R_i \geq 0$ and $F_i \geq 0$ for all i). We then compare various host-plant distributions, and we examine the resulting cost efficiency of each distribution, under optimal use of pesticides and mating disruption.

In turn, this enables the comparison of cost efficiencies among various host-plant distributions, by comparing the lowest ACT that results from each distribution. We focus on host-plant distributions that are uniform with $H_i = 1$ over most of the grid, except for a single gap consisting of several consecutive sites with a lower host-plant density, $H_i = H_G$ ($H_G < 1$). We examine variations in both the gap width (i.e. the number of consecutive sites where $H_i = H_G$) and the gap depth (i.e. $1 - H_G$).

2.3 | Parameter estimates

We consider parameter ranges estimated from the literature on the spongy moth in North America. Previous studies have estimated that an application of the bio-pesticide *Bacillus thuringiensis* that costs 54 USD per hectare kills 80% of the larval population (Blackwood et al., 2012). Since we measure R_i in units of USD per site per year, Equation (1) implies that $\alpha = -\ln(2)/54 = 0.03\,(\text{ha} \times \text{year})/\text{USD}$. Previous studies have also estimated that the growth rate r is estimated to be between 2 and 10 (Barron et al., 2020; Elkinton et al., 1996), and the number of males in carrying capacity is in the range of 500 – 1500 egg masses per hectare (Sharov & Liebhold, 1998). Estimates of m_0 are between 0.0052 and 0.17 (Lampert, 2024), implying that λ is between 5 and 170. The efficiency of mating disruption, β, is estimated around $0.08\,(\text{ha} \times \text{year})/\text{USD}$ (Lampert & Liebhold, 2021). The annual windborne dispersal distance of the spongy moth population, determining the standard deviation of the dispersal kernel, σ, ranges from 2.5 to 20 km (Liebhold et al., 1992), while accidental movement by humans can sometimes lead to much longer dispersal distances. In our simulations, each site characterizes 1 km, and the therefore, the ACT is measured in units of USD per year per 10 m strip of land.

2.4 | Numerical methods

To find this optimal, most cost-effective treatment, we developed a novel algorithm that performs a local search over the possible spatial distributions of the moth population density. The algorithm is fully described in Appendix S1: Numerical Methods (Supporting Information) and is demonstrated in Movies 1–3. The complete code of the algorithm's implementation is provided (see the Data and Code Availability Statement section). Although there is no guarantee that the algorithm always finds the most cost-effective solution, it finds at least an approximation to that solution. The algorithm builds on the approach developed in Lampert and Liebhold (2023) and Lampert (2024) for a single treatment method, and we extend it here to account for the simultaneous use of multiple treatment methods over heterogeneous landscapes. This study did not require ethical approval.

3 | RESULTS

3.1 | Each treatment method should be used in distinct sites

Our results indicate that the most cost-effective manner of combining pesticide application and mating disruption is to focus treatments around gaps with lower host plant densities. Several patterns of the optimal distribution of treatments occur throughout the simulations. Most notably, following the optimal solution, both pesticides and mating disruption may be applied, but each in a distinct area (Figures 3 and 4). In particular, although we allow the use of both pesticides and mating disruption in the same site, cost efficiency dictates that each site is treated either solely by pesticides or solely by mating disruption. Specifically, following the optimal solution, pesticides are generally applied in areas where the population density is still higher, while mating disruption is generally applied in areas where the population density is lower, sometimes inside the gap and sometimes in the area on the invasion-free side of the gap. This pattern is general across a wide range of parameters, gap sizes, and dispersal kernels (Figures 3 and 4, Figures S1 and S2). The optimal spatial distribution that we found is the same at all times, and it is capable of stopping the spread of an invader that initially propagates toward the host-plant gap (Figure 5).

3.2 | The optimal gap's width and depth depend on dispersal length and the strength of the Allee effect

The annual cost of pesticide application and mating disruption always decreases when the host gap is either wider or 'deeper', meaning it has a lower density of host plants, which serves as a natural barrier to spread (Figure 6). In all cases, gaps with fewer host plants are more effective. In practice, managers may need to trade-off between wider and deeper natural gaps, even when the total number of missing host plants is similar. For example, managers may have to choose between placing treatments next to a narrow gap with no host plants or next to a wider gap that still contains some host plants. Our results reveal the optimal balance between the gap's width and depth. When dispersal is more localized (Gaussian), containment efficiency is driven mainly by gap depth: For a fixed total density of missing host plants, concentrating those missing hosts into a deeper, narrower gap is more effective than spreading them over a wider, shallower gap (Figures 3 and 6a–c). The Allee effect strengthens this

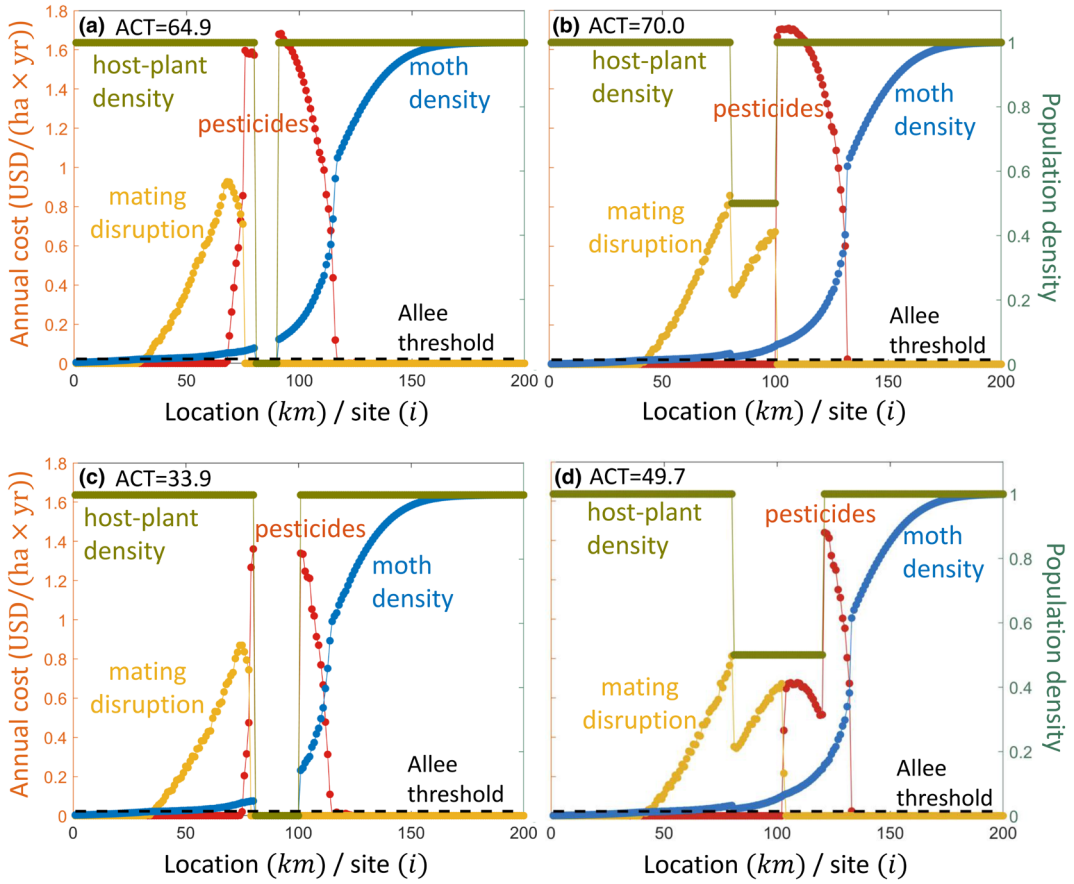

FIGURE 3 Optimal distribution of pesticides and mating disruption exhibits a spatial separation of treatment types. Demonstrated are spatial steady distributions (1) population density, n_i (blue); (2) host-plants density, H_i (green); and (3) optimal intensities of the treatment methods—pesticide application, R_i^{opt} (red) and mating disruption, F_i^{opt} (yellow). Dashed black line shows the Allee threshold. The annual cost of treatment (ACT) is the sum over all treatments in all sites, given in units of USD per year per 10 m strip of land. The distributions of pesticides and mating disruption, as found by our algorithm, are designed to minimize the annual cost of treatment, while ensuring that the spread of the population is stopped and does not propagate further from right to left. We consider a Gaussian dispersal kernel (D_{ij} is given by Equation (2a)). (a) Host plants are absent from a 10 km strip. (b) Half of the host plants are absent from a 20 km strip. (c) Host plants are absent from a 20 km strip. (d) Half of the host plants are absent from a 40 km strip. Each grid cell size represents 1 km. The results show that, in all panels, mating disruption is used only on the left-hand side of the host-plant gap, and there is a clear separation between areas where mating disruption should be used and those where pesticides should be used. Note that, if two gaps have the same total density of host plants absent, the narrower gap is more effective and results in a lower annual cost of treatment (ACT in (a) is lower than in (b); ACT in (c) is lower than in (d)). All parameter values are the same in all four panels: $r = 2\,(\text{year})^{-1}$, $k = 1$, $\lambda = 50$, $\alpha = 0.03\,(\text{ha} \times \text{year})\,/\,\text{USD}$, $\beta = 0.08\,(\text{ha} \times \text{year})\,/\,\text{USD}$, $\sigma = 15$ km.

advantage of deep gaps because pushing densities far below the Allee threshold makes local populations unlikely to persist or contribute to spread. In contrast, when the dispersal kernel has a long tail, the trade-off reverses: among gaps with the same total density of missing host plants, wider gaps are generally more effective and yield a lower annual cost of treatment (Figures 4 and 6d–f).

4 | DISCUSSION

Our study highlights the importance of leveraging variation in host-plant density when integrating multiple strategies to cost-effectively contain the spread of invasive plant pests. We demonstrated how spatial coordination of pesticide and mating disruption treatments with natural barriers of low host-plant density can create cost-effective barriers to pest range expansion. Though it may not be practical to manipulate host density via plant removal in systems such as large landscapes over which spongy moth spread occurs, existing areas with naturally low host plant densities can be leveraged as cost-efficient natural barriers. This approach enables strategic use of landscape features, reducing overall management costs. Similarly, our results demonstrate that aligning control efforts with the spatial layout of host plants significantly improves cost efficiency. The strategic use of host-poor zones is an example of real-world containment programmes that use both treatments and landscape structure to slow pest spread (Barron et al., 2020). Note that, in most invasion management situations (including that of the spongy moth), it is generally prohibitively expensive

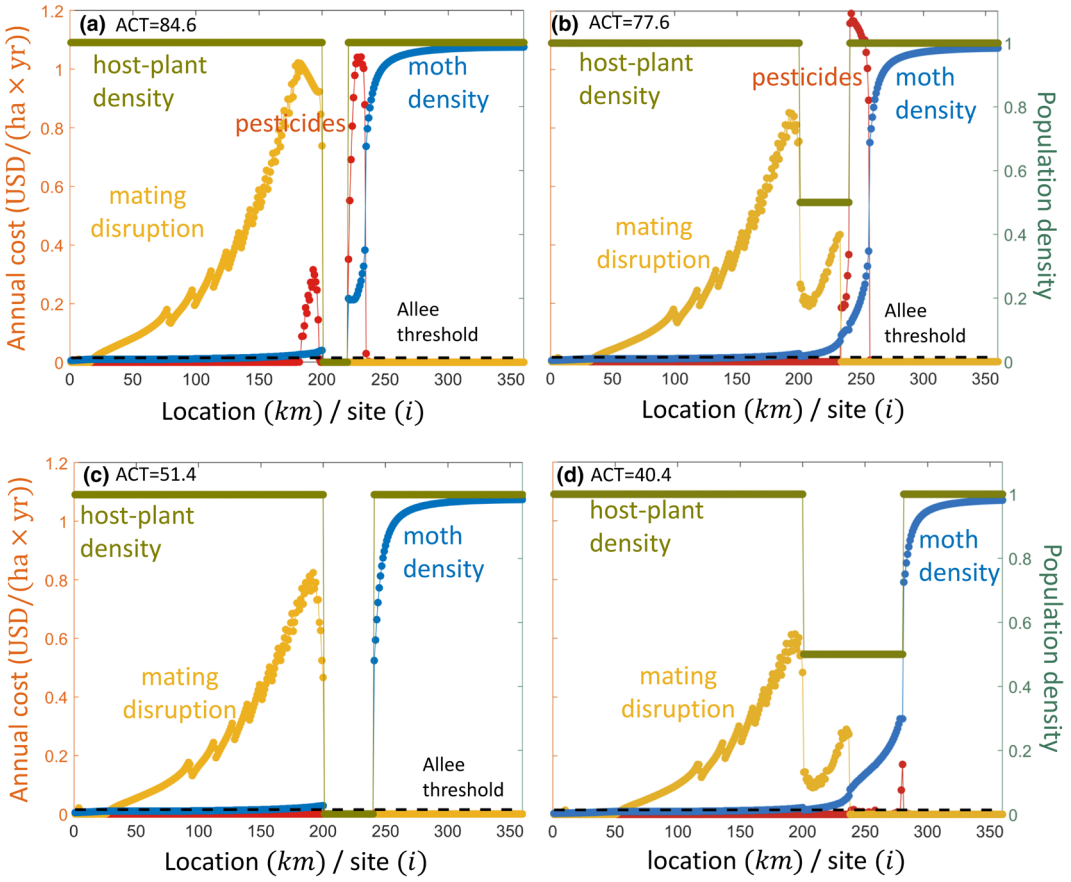

FIGURE 4 Optimal distribution of pesticides and mating disruption exhibits a spatial separation of treatment types – long-range dispersal. As in Figure 3, demonstrated are spatial steady distributions (1) population density, n_i (blue); (2) host-plants density, H_i (green); and (3) optimal intensities of the treatment methods—pesticide application, R_i^{opt} (red) and mating disruption, F_i^{opt} (yellow). The annual cost of treatment (ACT) is the sum over all treatments in all sites, given in units of USD per year per 10 m strip of land. Here, in contrast to Figure 3, we consider a dispersal kernel with a long tail. Each panel shows the optimal solutions for a different host-plant distribution: (a) Host plants are absent from a 20 km strip; (b) Half of the host plants are absent from a 40 km strip. (c) Host plants are absent from a 40 km strip. (d) Half of the host plants are absent from an 80 km strip. Each grid cell size represents 1 km. As in Figure 3, mating disruption is used only on the left-hand side of the host-plant gap, and there is a clear separation between areas where mating disruption should be used and those where pesticides should be used. Here, in contrast to Figure 3, if two gaps have the same total density of host plants absent, the wider gap is more effective and results in a lower annual cost of treatment (ACT in (a) is higher than in (b); ACT in (c) is higher than in (d)). Parameter values are the same as those in Figure 3, except the dispersal kernel that is given by Equation (2b) with $\sigma = 4$ km.

to remove hosts over very large areas. Thus, the use of host removal as a tactic would be limited to situations where spread is being managed over very small spatial scales (Barron et al., 2020). However, the results presented here on the effect of host gaps on the optimization of containment strategies remain valuable for guiding the containment of herbivorous insects, including the spongy moth, under various natural spatial configurations of host densities.

Our results also emphasize the necessity of using pesticides and mating disruption to complement the use of host plant gaps. In areas where host-plant density is reduced, these methods can prevent pest persistence and limit their dispersal beyond the gap. Our results revealed that the optimal placement of treatments often requires spatial segregation, with pesticides used closer to higher pest densities and mating disruption focused on areas with lower pest densities (Figures 3 and 4). This is consistent with previous studies showing that pesticide application is more cost-effective for controlling high-density populations, whereas mating disruption is more cost-effective for managing low-density populations (Lampert & Liebhold, 2021). This strategy is also consistent with the finding that the effective operational use of mating disruption for containment of the spongy moth is largely limited to moderate to low moth populations (Onufrieva et al., 2019). However, while previous studies suggested that the timing of using each treatment method should be density-dependent (Lampert & Liebhold, 2021), here the results indicate that the location where each method is targeted should also be density-dependent, and accordingly, depend on the distance from the host plant gaps.

In turn, the role of Allee effects is also important in understanding containment success. Fragmenting host plant availability not only reduces pest reproduction but also enhances the likelihood that local populations fall below the Allee threshold and collapse in

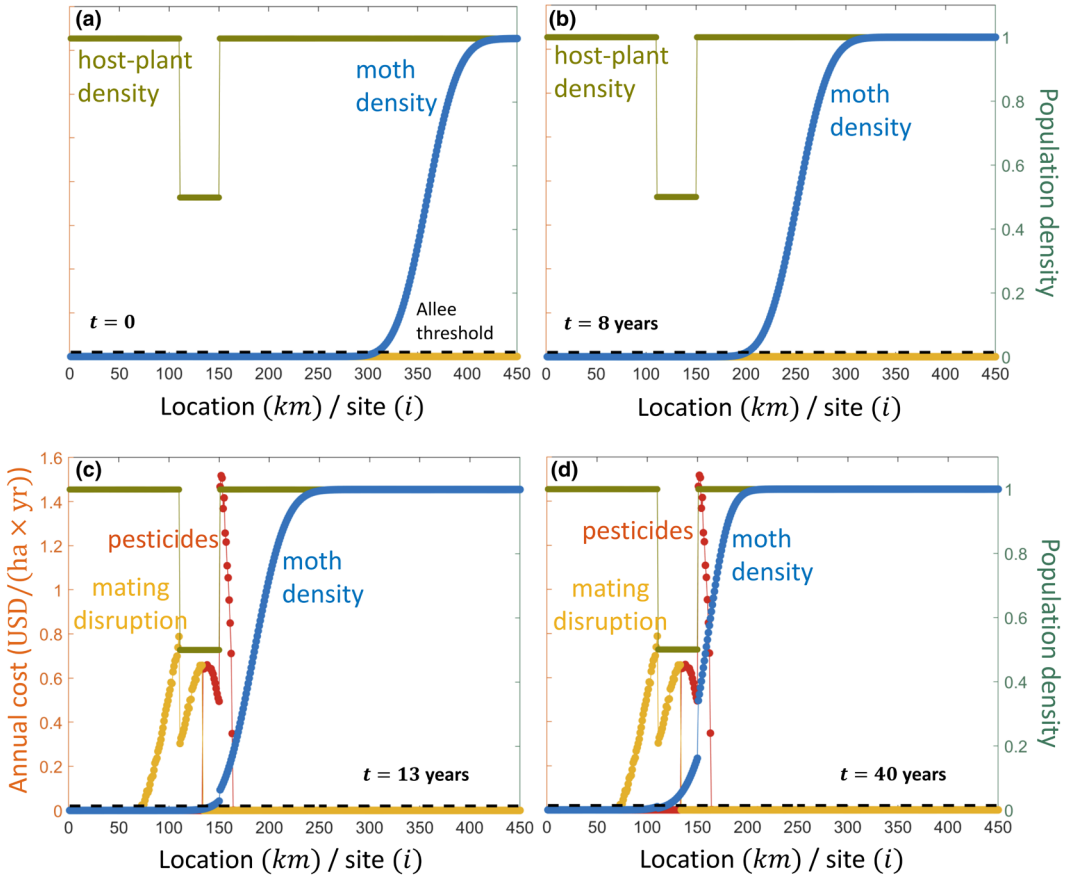

FIGURE 5 The moth approaches the host-plant gap and is stopped by the treatment. Demonstrated are the dynamics of the moth population. (a,b) the population is initially located on the right side of the grid, and it propagates towards the host-plant gap. (c, d) The treatment is applied near the host-plant gap and stops the population spread. Parameters: D_{ji} is given by Equation (2a), $r = 2$ (year)$^{-1}$, $k = 1$, $\lambda = 50$, $\alpha = 0.03$ (ha × year) / USD, $\beta = 0.16$ (ha × year) / USD, $\sigma = 15$ km.

low-density areas. Our findings align with previous studies that highlight the interaction between dispersal limitations and Allee effects in shaping population dynamics (Courchamp et al., 2008; Lewis & Kareiva, 1993). Importantly, the strength of the Allee effect influences the optimal intensity and spatial configuration of host plant removal, with stronger Allee effects allowing for wider, less intensive removal zones (Figure 6, Figure S2).

Our findings demonstrate the importance of strategic spatial planning, showing that optimized placement and intensity of control methods can significantly reduce containment costs. Previous studies have also emphasized the value of spatially optimizing management, and found that concentrating efforts in key barrier zones or high-risk areas outperforms uniform control strategies (Barron et al., 2020). The insights gained here, such as the superior performance of narrow, well-defined host gaps over diffuse low-host areas as barriers when dispersal is Gaussian, can guide managers in prioritizing certain landscape features or control zones. We anticipate that these principles are transferable to other invasive pests and ecosystems, especially where host resources are patchy. Ultimately, strategies that exploit the spatial structure of both the pest population and its host resources offer promising avenues to slow the spread of invasive species and pests.

Our methodology is generalizable and can be used to study more broadly how to manage invasive species and pests around natural barriers. To name but a few examples, in Europe, the Pyrenees mountains act as a barrier to the northward spread of the pinewood nematode (*Bursaphelenchus xylophilus*); the tallest peaks block most infested beetles while lower-elevation passes allow some to cross, creating corridors where intensified monitoring and control are prioritized (Haran et al., 2015). In Australia, an arid 'waterless' corridor is being used to stall the invasion of cane toads by sealing leaky water tanks and removing artificial ponds along a 150-km stretch with little natural water. Authorities created a dry gap in which toads struggle to survive, thereby stopping their westward spread (Phiddian, 2024). Likewise, barriers are also used to limit the spread of aquatic invasive species (Jones et al., 2021). Across these examples, the pattern is consistent: leveraging a landscape's natural "gaps" or unfavourable zones, and fortifying them with targeted interventions, can help slow an invader's spread. This highlights the potential generalizability of the methods demonstrated here, suggesting that our methods can be used in the future for various similar case studies.

While the model described here captures key aspects of how geographical heterogeneity in host cover affects spread and the optimal allocation of treatments in containment programs, it does

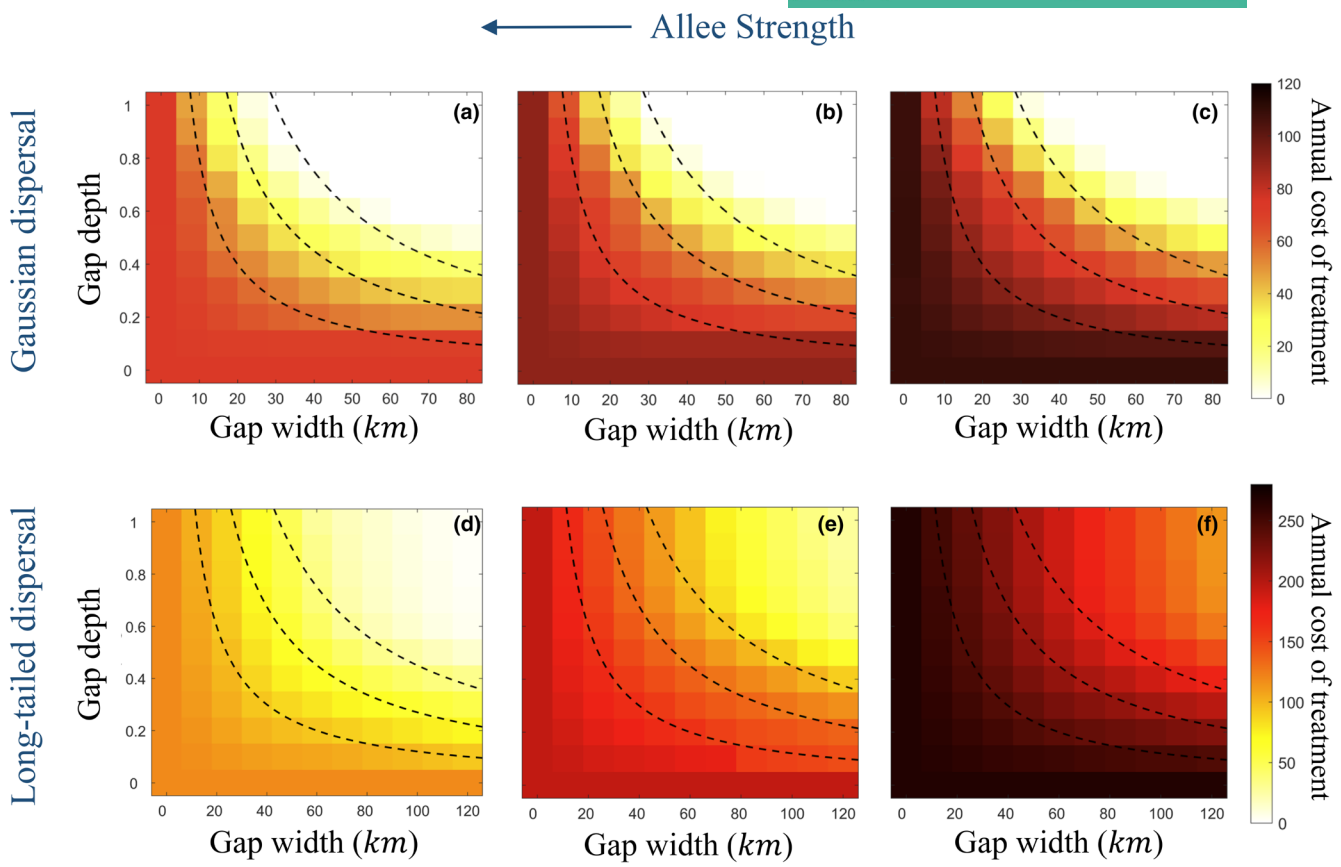

FIGURE 6 The annual cost of treatment (ACT) decreases when (1) the host-plant gap is wider, (2) the gap has a lower density of host plants, and (3) the Allee effect is weaker. Each panel shows the annual cost of treatment (ACT; colour bar), with lighter colours indicating lower (better) ACT values, for various gap widths (number of consecutive sites with a lower host-plant density; *x*-axis) and gap depth (density of host plants that are absent at each site along the gap, $1 - H_i$; *y*-axis). Panels correspond to different strengths of the Allee effect ($\lambda = 50$, $\lambda = 100$, $\lambda = 200$) and different dispersal kernels (Equations (2a) and (2b)). The other parameter values are the same as in Figure 3 (panels (a–c)) and Figure 4 (panels (d–f)). Along each black dashed line, the total density of absent host plants in the gap is identical. Along these lines, if dispersal is Gaussian (a–c), the optimal gap is deeper rather than wider, whereas if dispersal is long-range (d–f), the optimum occurs at an intermediate width.

make several simplifying assumptions. First, while in reality there are many characteristics of forest habitats (e.g. forest structure, age, species composition) that can affect the dynamics of herbivorous insect populations, we only considered host density. This choice was motivated by the ubiquitous evidence that herbivorous insect populations are modulated by the 'resource concentration hypothesis' (Hambäck & Englund, 2005), but we acknowledge that populations are affected by other forest characteristics. Second, we focused on simple, one-dimensional gaps. However, the two-dimensional structure may be important, especially for gaps that the spongy moth can circumvent by moving around them. Third, we focussed only on gaps with uniform population densities, but our methodology applies more broadly to non-uniform gaps that can be examined in future studies. Fourth, we assume that dispersal occurs as propagules disperse with the wind. While this assumption well-characterizes the spongy moth, other variations of the model could better apply to species where adults migrate. Fifth, our model is deterministic, which results in the same containment treatment each year. However, real-world dynamics are stochastic, and spongy moth dispersal is stratified (Shigesada & Kawasaki, 1997). Therefore, in practice, treatment locations and intensities could vary annually and depend on stochastic events occurring in a particular year, which necessitates ongoing surveillance and monitoring. Sixth, we used a simplified model for the moth's population dynamics, while in reality its dynamics could be affected by predation, parasitoids and pathogens.

We selected the spongy moth as a case study, in part because this species is widely studied and consequently data are available for selecting realistic population parameters. But this species was also selected because it is currently the focus of a large, area-wide programme to slow its spread in the United States, termed 'Slow the Spread' (Coleman, 2023). Across the spongy moth's expanding invasion front, there exists considerable spatial variation in habitat (Morin et al., 2005). This variation can be quantified at a range of spatial scales and is caused by various factors, including variation in land use cover (e.g. large gaps created by agricultural land use) and variation in forest tree species composition (densities of host and non-host tree species) both of which are driven by local- and

landscape-level variation in climate and soils. Decisions on the spatial allocation of treatments and surveys are made yearly based on survey results processed using a decision procedure (Tobin et al., 2004). Currently, this procedure does not incorporate information about the spatial distribution of host trees. While the analysis provided here is still not yet specific enough to be incorporated into the procedure, we believe that certain rules of thumb revealed here are applicable more broadly (such as spatial segregation is needed between pesticide application and mating disruption) and that our results provide a baseline that future studies could use to improve the efficiency of the Slow the Spread programme and other invasive species management programmes by incorporating information on the spatial distribution of susceptible forests.

AUTHOR CONTRIBUTIONS

Adam Lampert designed research, developed the model, performed analysis, wrote the paper; Andrew M. Liebhold designed research, wrote the paper.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicting interests.

DATA AVAILABILITY STATEMENT

No external datasets were used in this study. All parameter values needed in order to reproduce the results are given in Methods: parameter estimates and in the relevant figure legends. The algorithm is described in Appendix S1: Numerical Methods (Supporting Information). The code is published on the open repository Zenodo, https://doi.org/10.5281/zenodo.17828882 (Lampert, 2025). All the results in this manuscript are reproducible using the archived code.

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SUPPORTING INFORMATION

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

Appendix S1. Numerical methods.

Figure S1: When dispersal depends on host-plant density, the optimal distribution of treatments still exhibits a spatial separation of treatment types.

Figure S2: For various strengths of the Allee effect, the optimal distribution of treatments exhibits a spatial separation of treatment types.

Movie 1. The algorithm converges to the optimal solution—deep gap, Gaussian kernel. The movie demonstrates how the algorithm iterates towards more cost-effective solutions until it approaches the optimal solution (at least approximately). At each configuration, the combination of pesticides (red) and mating disruption (yellow) would keep the population from propagating leftward. At each iteration, the algorithm updates the distribution of the species (blue) to one that results in a lower annual cost of treatment (ACT). Parameters are the same as those in Figure 3.

Movie 2. The algorithm converges to the optimal solution—wide gap, Gaussian kernel. The movie demonstrates how the algorithm iterates towards more cost-effective solutions until it approaches the optimal solution (at least approximately). Parameters are the same as those in Figure 3 and Movie 1, where only the distribution of host-plants differs from Movie 1.

Movie 3. The algorithm converges to the optimal solution—wide gap, long-tail kernel. The movie demonstrates how the algorithm iterates toward more cost-effective solutions until it approaches the optimal solution (at least approximately). Parameters are the same as those in Figure 4.

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