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Misapplied management makes matters worse: Spatially explicit control leverages biotic interactions to slow invasion

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Abstract

A wide range of approaches has been used to manage the spread of invasive species, yet invaders continue to be a challenge to control. In some cases, management actions have no effect or may even inadvertently benefit the targeted invader. Here, we use the mid-20th century management of the Red Imported Fire Ant, *Solenopsis invicta*, in the US as a motivating case study to explore the conditions under which such wasted management effort may occur. Introduced in approximately 1940, the fire ant spread widely through the southeast US and became a problematic pest. Historically, fire ants were managed with broad-spectrum pesticides; unfortunately, these efforts were largely unsuccessful. One hypothesis suggests that, by also killing native ants, mass pesticide application reduced competitive burdens thereby enabling fire ants to invade more quickly than they would in the absence of management. We use a mechanistic competition model to demonstrate the landscape-level effects of such management. We explicitly model the extent and location of pesticide applications, showing that the same pesticide application can have a positive, neutral, or negative effect on the progress of an invasion, depending on where it is applied on the landscape with respect to the invasion front. When designing management, the target species is often considered alone; however, this work suggests that leveraging existing biotic interactions, specifically competition with native species, can increase the efficacy of management. Our model not only highlights the potential unintended consequences of ignoring biotic interactions, but also provides a framework for developing spatially explicit management strategies that take advantage of these biotic interactions to work smarter, not harder.

KEYWORDS

competition model, disturbance, invasional interference, native–invader interactions, optimal management, red imported fire ant (*Solenopsis Invicta*)

INTRODUCTION

Found in almost every ecosystem worldwide (Vitousek et al., 1997), nonnative species are implicated in species extinctions, significant alterations of ecological community structure and changes in evolutionary trajectories (Mack et al., 2000). In addition to ecological harm, invasive species are estimated to cause significant economic costs, which are incurred not only from the direct effects of invaders, but also indirectly from human attempts to manage invaders and mitigate their harm (Cuthbert et al., 2022; Diagne et al., 2021; Mack et al., 2000; Pimentel et al., 2005; Roy et al., 2023). Cases of successful eradication and control campaigns (Simberloff, 2009) show it is possible to remove invaders entirely or to reduce their impact. Despite some notable successes, however, invasive species continue to be challenging to control (Mack et al., 2000). There are many instances in which management actions have failed to make a difference or have even made the problem worse (Mack et al., 2000). To describe these unintentional adverse effects, we employed the terms "wasted effort" and "counterproductive effort" throughout this paper (we refer to these as "ineffective" or "failed" management as well).

Management of the red imported fire ant, *Solenopsis invicta*, in the southeastern United States (US) serves as a case study for wasted effort. The fire ant was accidentally introduced to the US from Argentina around 1940 through a shipping port in Mobile, Alabama and, after its establishment, it quickly spread (Buren et al., 1974). Fire ants proved to be problematic in many regards, affecting native ant communities (Holway et al., 2002; Porter & Savignano, 1990), agriculture (Vinson, 1997), human health (Vinson, 1997), wildlife (Allen et al., 2006), and infrastructure (Gutrich et al., 2007; Vinson, 1997), with total economic costs exceeding US $16 billion between 1960 and 2020 (Cuthbert et al., 2022). In an attempt to minimize fire ant spread and associated damage, a series of fire ant eradication and control campaigns were funded by the US Congress and southern state governments starting in 1957. These campaigns included aerial and ground applications of heptachlor and dieldrin. In 1962, the standard eradication treatment was switched to Mirex bait, which was applied to more than 140 million acres (equaling approximately 46 million acres of land, because many areas received repeat applications) (Williams et al., 2001). The campaign failed to eradicate fire ants and experts have questioned whether it slowed the invasion at all (Callcott & Collins, 1996; Davidson & Stone, 1989; Morrison, 2000).

Understanding why management fails is critical for effective invasive species control going forward (Abdelkrim et al., 2007). Although these management failures have been studied on a case-by-case basis (e.g., Abdelkrim et al., 2007; Amos et al., 2016; Hoffmann, 2011), there are fewer general theories for understanding the ecological factors which may lead to failed management (see Pearson et al., 2016 for a weed management example and Hoffmann, 2011; Myers et al., 2000; Simberloff, 2009 for eradication examples). Here, we explore one possibility: management actions with off-target effects that harm native species in addition to invaders could reduce native populations, alleviating competitive burdens on the invader and inadvertently assisting invasion. Ecological theory and mathematical models have been used to guide invasive species management, including by identifying better ways to target control resources (e.g., Moody & Mack, 1988; Pepin et al., 2022; Shea et al., 2010). Here, we present a simulation model with similar aims. We demonstrate the possibility of wasted or counterproductive management effort, using the US fire ant invasion as a case study. We use our model to explain one potential mechanism behind such failures and identify spatially explicit management strategies that may serve as effective alternatives.

METHODS

Mechanistic model

The model description follows the Overview, Design concepts, Details (ODD) protocol as outlined by Grimm et al. (2006, 2010).

Purpose

This model was developed to explore one potential mechanism for failed management of an invasive species that is established on and spreading across a landscape. In particular, we focused on the case where strong competition from native species provides a barrier to invader spread but cannot prevent establishment. As such, we modeled ways to slow this spread, potentially "buying time" for the development of alternative control strategies. The main purpose of this model is to understand the effects of disrupting this native–invader competition with management (that affects both natives and invaders), and the potential for such management to lead to wasted or counterproductive effort (i.e., either no effect, or adverse effects).

The case we modeled generally aligns with hypotheses on the ecological mechanisms that enabled fire ants to invade and rapidly spread through the southeastern US. These hypotheses have been proposed through the large body of empirical work that investigates how fire ant invasion was affected by disturbance and native competition; here we used a mathematical model to extend this evidence base to characterize landscape-level implications of such ecological interactions. Some authors cite the disruption of native ant communities as the key mechanism which enabled *S. invicta* to spread rapidly, based on observational and experimental studies demonstrating competitive superiority and tendency to reinvade disturbed habitats where natives are declining (King & Tschinkel, 2008; Morrison, 2000; Summerlin et al., 1977). Other experiments have suggested that native declines may not be a primary factor in fire ant dominance (Stuble et al., 2011) or that these outcomes may depend on environmental conditions (LeBrun et al., 2012). These hypotheses and our analyses focus on the monogyne form of fire ants (i.e., colonies with one queen), but could also be extended and reparametrized to study polygyne social forms (i.e., colonies that multiple queens), which reach higher colony densities and have different dispersal behavior (Shoemaker & Ascunce, 2010).

Entities, state variables, and scales

We used a one-dimensional coupled map lattice model consisting of 60 homogenous cells and reflecting boundaries, where a single cell represents 1 km^2. Within each cell, we tracked the number of fire ant and native ant colonies in one-year timesteps, following the time it takes for a colony to mature and produce alates (Vinson & Sorensen, 1986). All species of native ants are included as a single population.

Process overview and scheduling

Each year, processes were executed in the following order: natural birth and death processes; dispersal; mortality due to management disturbance; demographic stochasticity. We updated population sizes after each step, and the final population sizes were passed into the next time step.

Design concepts

Following Grimm et al. (2010), we omit design concepts that are not relevant to the model, including objectives, learning, prediction, and sensing.

Basic principles

Traditional Lotka–Volterra competition equations (Lotka, 1924) governed the interaction between fire ant and native ant populations, and thus the birth and death processes for both. Additionally, we conceptualized management (here, pesticide application) as a disturbance, and we structured our assessment of spatially explicit pesticide applications using theory for ecological disturbances (Miller et al., 2011). This theory outlines multiple axes of disturbance (particularly, frequency, intensity, duration, timing, location, extent) (Miller et al., 2021). We tested two key axes of disturbance (spatial location and spatial extent) and conducted sensitivity analyses on a third axis (intensity). In doing so, this model merges competition and disturbance theories in a spatially explicit manner.

Emergence

We expected population sizes within a single cell to follow relatively predictable patterns based on the size of each population and the intensity of the disturbance within that cell. However, this model aimed to characterize properties of landscape-level spread that emerge from dispersal and competition processes across and within individual cells.

Adaptation

Our model assumed that individuals compete and disperse at constant rates; thus, we did not explicitly model adaptive behavior.

Interaction

In our model, fire ant and native ant colonies interact within a given cell through both explicit and implicit competition. Fire ants often become the dominant ant species within their invasive range due to their aggressive foraging and large population sizes (Allen et al., 2004; Morrison, 2000; Wilder et al., 2013). We simplified these competitive interactions into a single value, which describes the effect of one species on the growth of the other, following the Lotka–Volterra competition equations.

Stochasticity

Each component of our model may generate a fractional number of colonies in a single cell, so we used random draws to ensure whole numbers of individual colonies at the end of each time step. This process represents demographic stochasticity (see *Demographic Stochasticity* in the *Submodels* section for details).

Observation

Population sizes of both fire ant and native ant colonies are monitored in each cell and at each time point.

Initialization

Our initial conditions represented a novel invasion by fire ants into a landscape occupied by native ants. Thus, we started the model with native ants at carrying capacity in all cells, and fire ants at 10% of their carrying capacity in only the first cell (i.e., absent in all other cells). We used this setup to generate the initial conditions for our simulations, which characterize the application of pesticides after invaders have begun to establish on the landscape. To model early unconstrained spread, we ran the model without any management until at least one fire ant colony established in the middle cell (i.e., cell 30 of 60 in the one-dimensional landscape). From this set of initial invasions, we randomly selected one to serve as the initial condition for subsequent simulations.

We used 10% of carrying capacity to simulate invasion from low densities while avoiding stochastic fadeout in initialization. Invaders reached carrying capacity in the first cell quickly relative to the establishment of invaders in further cells, so we do not expect our results to be sensitive to this choice. We chose to allow invaders to spread unmanaged over half the landscape to ensure the invader established on the landscape and to allow us to test the effect of large extents of pesticide application. We expected our qualitative conclusions to be robust to the particularities of this choice; tests confirmed this hypothesis. Eradication may be more feasible if invaders occupy only a small portion of the landscape, however this is not our primary question.

Input data

The model does not use input data to represent time-varying processes (Grimm et al., 2010).

Submodels

As discussed in the *Process overview and scheduling* section, our submodels were executed sequentially with asynchronous updating after each step. Here, we present the submodels in the order in which they were executed, and we use the notation t_B, t_D, t_P, t_S to refer to year t after execution of each submodel: natural birth and death processes, dispersal, pesticide-induced mortality, and demographic stochasticity, respectively. We refer to year t after the execution of all submodels without a subscript (i.e., t).

All submodels were parameterized to reflect the fire ant system in the southeast US. Parameter motivation is discussed briefly for each submodel, and a full list of model parameters can be found in Table 1.

Natural birth and death processes

We modeled within cell dynamics using Euler-type discretized, Lotka–Volterra competition (Case, 2000; Lotka, 1924) with Chesson's (2000) reformulation:

TABLE 1 Model parameter values.

Description	Parameter	Value
Invader carrying capacity	K_I	10,000
Invader intraspecific competition	$\alpha_{II} = 1/K_I$	0.0001
Invader interspecific competition	α_{IN}	0.000308*
Invader intrinsic growth rate	r_I	1.2
Invader max dispersal distance (km)	d_I	5
Invader proportion dispersing	p_I	0.2
Native carrying capacity	K_N	3000
Native intraspecific competition	$\alpha_{\mathrm{NN}} = 1/K_N$	0.000333*
Native interspecific competition	α_{NI}	0.000125*
Native intrinsic growth rate	r_N	1.2
Native max dispersal distance (km)	d_N	2*
Native proportion dispersing	p_N	0.2
Pesticide-induced mortality	$i_t(x)$	1*

Note: Values with an asterisk (*) were included in sensitivity analyses. For α_{IN}, α_{NN}, and α_{NI} we tested changes of 1% and 5% (i.e., $\alpha_{ij} \pm c\alpha_{ij}$ for $c \in \{0.01, 0.05\}$). For d_N and $i_t(x)$, we tested $d_N \in \{1,3,4\}$ and $i_t(x) \in \{0.95, 0.98\}$.

$$N_{(t_B,i)}(x) = N_{(t-1,i)}(x)\left(1 + r_i\left(1 - \alpha_{ii}N_{(t-1,i)}(x) - \alpha_{ji}N_{(t-1,j)}(x)\right)\right), \tag{1}$$

where $N_{(t-1,i)}(x)$ represents the population size in cell x of species i at time $t-1$; r_i is the growth rate of species i; and α_{ij} is the effect of species j on species i. Thus, the term $\alpha_{ii}N_{(t-1,i)}(x)$ represents intraspecific competition and $\alpha_{ij}N_{(t-1,j)}(x)$ represents interspecific competition. We chose parameter values (Table 1) that reflect strong interspecific competition between natives and invaders (Morrison, 2000), based on known equilibria of the Lotka–Volterra competition equations and fire ant carrying capacity. We used a higher carrying capacity for fire ants (monogyne colonies: 10,000 colonies/km^2, or 100 colonies/ha; Allen et al., 2004) than for native ants to reflect field conditions in which fire ants can reach higher colony densities.

Dispersal

Our model assumed that both native and fire ant dispersal follows an exponential dispersal kernel, $K(d_i,y) = \lambda e^{-\lambda y}$ where y represents the distance dispersed, d_i is the maximum dispersal distance, and λ is the exponential rate parameter. We let the maximum dispersal distance for species i be the distance within which 99.9% of dispersal occurs (i.e., we use $\lambda = \log(1-0.999)/-d_i$). Because our model is in discrete space, the proportion of individuals dispersing into the cell y kilometers away is $\kappa(d_i,y) = K(d_i,y) - K(d_i,y-1)$.

Then, the net dispersal in cell x at time t for species i is defined as

$$N_{(t_D,i)}(x) = \sum_{j=1}^{60} \frac{\kappa\left(d_i, |x_j - x|\right)}{n_{|x_j - x|}} p_i N_{t_B}(x_j) - p_i N_{t_B}(x), \qquad (2)$$

where p_i is the percent of alates of species i that disperse within a given year and $N_{(t_B,i)}(x)$ is the population size of species i in cell x after natural birth and death processes. We assume that dispersal is symmetric (i.e., the same number of alates disperse forward and backward from a cell). To accomplish this, we divide the proportion of individuals dispersing, $\kappa\left(d_i, |x_j - x|\right)$, by the number of cells of $|x_j - x|$ distance from the focal cell j; we denote this number of cells as $n_{|x_j - x|}$.We assumed fire ants disperse up to 5 km and further than native ants (Vogt et al., 2000). The proportion of colonies dispersing was roughly calibrated to match observed invasion rates (Appendix S1: Figure S6).

Pesticide-induced mortality

Fire ant and native ant populations were subject to pesticide application after natural birth and death processes and dispersal. We assumed that when pesticides were applied in a cell, they affected native and fire ants equally, where the proportion of colonies killed was based on the intensity of pesticide application in cell x at time t, $i_t(x)$. Thus, after this submodel, the new population size in cell x for species i was $N_{(t_P,i)}(x) = i_t(x) N_{(t_D,i)}(x)$.

Demographic stochasticity

We included demographic stochasticity in our model by rounding $N_{(t_P,i)}(x)$ at each timestep based on a random number drawn from a uniform distribution defined between 0 and 1. If the fractional part of $N_{(t_P,i)}(x)$ was less than the uniform randomly generated number, we rounded all populations down, otherwise we rounded up. We rounded all cells based on a single random number to simulate the difference between "good" and "bad" years.

Mechanistic model simulations

Using this model, we tested how fire ant spread was affected by native ant competition and pesticide application, i, across a variety of pesticide application locations. Throughout the text, we characterize each pesticide application as an ordered pair where the first number represents the starting location, and the second number represents the ending location (the difference plus one is the width of the application, or how much "effort" was used). Locations were defined relative to the invader wavefront, or the furthest cell from the origin that contains at least one invader colony. For example, (−4, 2) represents a pesticide application of effort 7, that starts four units behind the wavefront and ends two units ahead. In the 60-cell lattice, we tested all intervention combinations with a starting location between −28 and 2 in increments of two, and with an ending location up to 8 units ahead of the detectable wavefront. In the model, we applied perfectly effective pesticides once in the first year of simulation (i.e., $i_1(x) = 1$).

Given our goal of finding strategies that slow the invasion, we calculated "invasion time" for each pesticide application and a baseline case with no management. "Invasion time" is the average time it took for the invader to reach carrying capacity in every cell across 500 simulations. We then calculated "change in invasion time," or the difference in invasion time between the managed and unmanaged cases. Positive change in invasion time implies a successful intervention, as the managed invasion took longer to reach carrying capacity than the unmanaged invasion. Conversely, unsuccessful strategies are characterized by negative change in invasion time; in these cases, the invader reached carrying capacity faster with management than without (i.e., counterproductive management effort). An invasion time near zero suggests wasted management effort, as the intervention had no effect on invasion time compared with the unmanaged case.

Often, however, native competition or other biotic interactions may be overlooked in the design of management strategies. To reproduce such a situation, we repeated the analysis with no native colonies on the landscape. We also performed sensitivity analyses on our baseline parameters. First, we tested lower disturbance intensities, $i_1(x)$, of 98% and 95% (Oi et al., 2008). As native competitors may differ across geographic locations, we also performed sensitivity analyses on native ant parameters. Specifically, we tested a variety of values for native intraspecific competition (α_{NN}), interspecific competition (α_{NI} and α_{IN}), and native dispersal (d_N). See Table 1 for all values tested. All simulations and analyses were conducted in the R statistical software version 4.2.0 (R Core Team, 2018).

RESULTS

In our model, pesticide application affects how quickly fire ants are established, although the spatial location of the application has a strong impact on the direction and magnitude of the effect. Three qualitatively different management outcomes emerge: applications that increase invasion time and thus achieve management objectives (Figure 1A); applications that do not change invasion time, thereby wasting management effort (Figure 1B); and applications that decrease invasion time, not only wasting effort but making matters worse (Figure 1C).

Applications that decrease invasion time, meaning that management allowed the invasion to proceed more quickly than without intervention, are the worst possible outcome. Many of these counterproductive applications apply pesticides behind and through the invader wavefront, which a priori might seem to be the most useful strategy (Figure 2, shown in orange). For example, strategy (−12, 0) speeds up the invasion by 10.3 years, despite applying pesticide entirely behind the wavefront. These adverse outcomes occur when pesticide applications

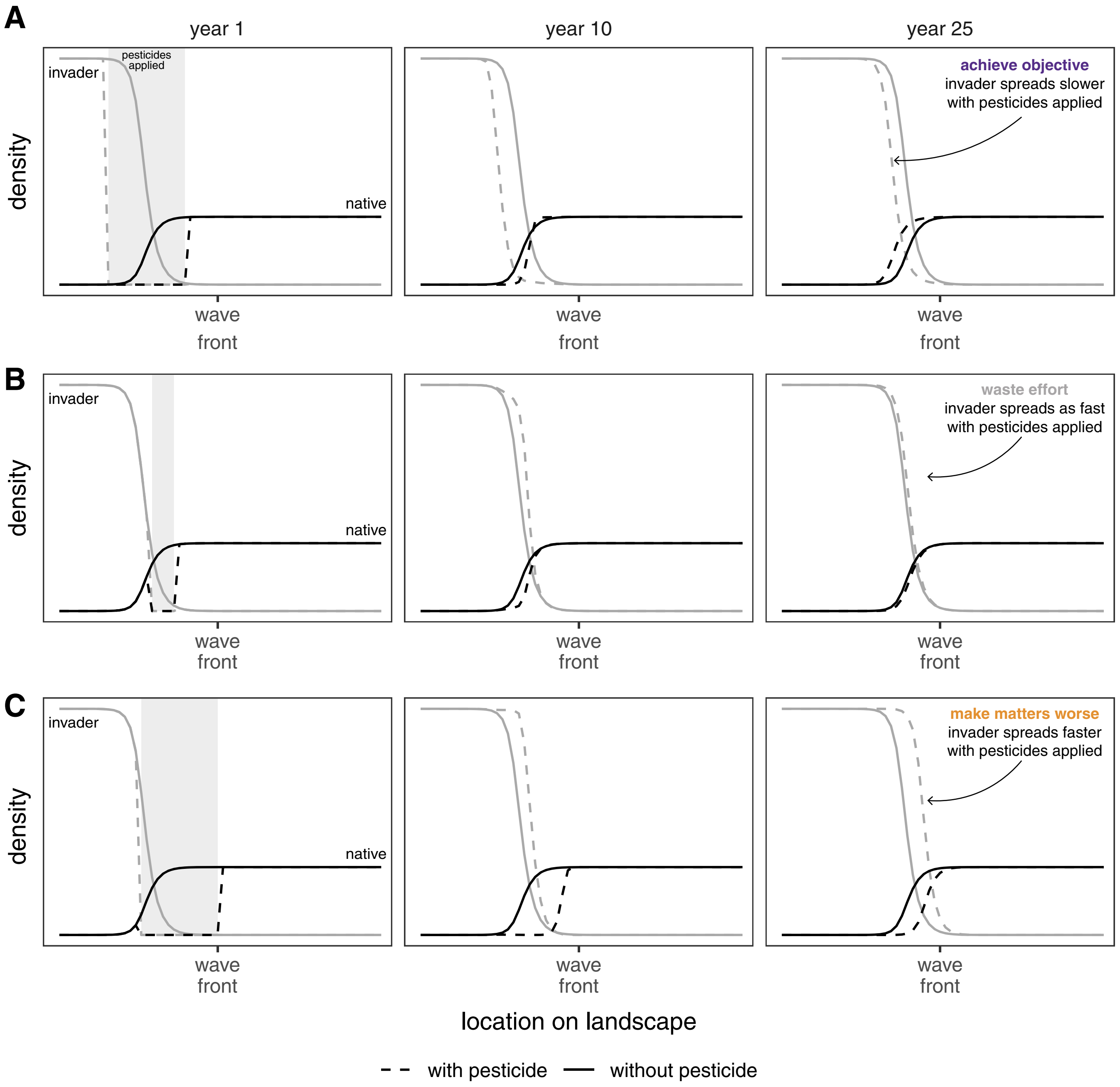

FIGURE 1 Examples of pesticide applications that achieve the objective, waste effort, or make matters worse. Each panel shows invader (gray) and native (black) densities across a one-dimensional landscape at three points in time (1, 10, 25 years). These results compare densities without pesticide (solid lines) to those where pesticide is applied (dashed lines). The "without pesticide" cases are identical in each panel. The locations at which pesticides were applied in year 1 (represented by gray box) change across panels: (A) strategy (−20, −6), (B) strategy (−12, −8), and (C) strategy (−14, 0).

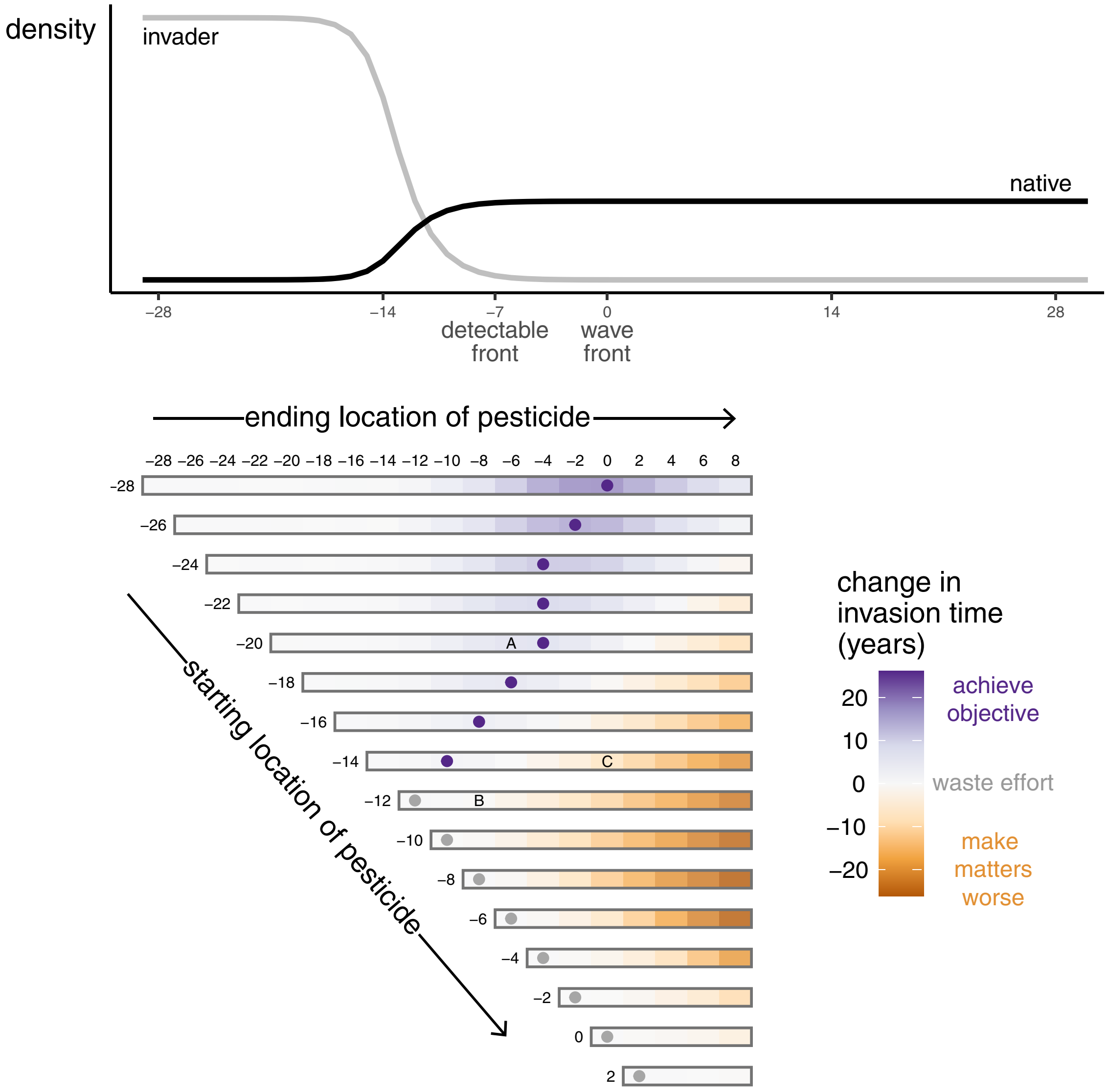

FIGURE 2 Pesticide applications can have positive, neutral, or negative effects on invasion time. (Upper) Invasive ant and native ant densities across the landscape at the time of pesticide application. The *x*-axis shows the location of the "detectable front" and the "wavefront." The "detectable front" is the furthest cell from the origin containing at least 100 colonies/km^2 (the detection threshold) of invasive ants. The wavefront is the furthest cell from the origin that contains any invasive ant colonies. (Lower) Change in invasion time when broad-spectrum pesticide is applied at different locations on the landscape. Each cell represents a distinct range of pesticide application with a unique starting location and ending location: for each row, the first cell represents the starting location and the other cells represent ending locations. For example, the second cell in the upper row represents a pesticide application that started 28 units behind the wavefront and ended 26 units behind the wavefront, whereas the last cell in the upper row represents a pesticide application that started 28 units behind the wavefront and ended 8 units ahead. Cell color shows the expected change in invasion time, where positive values indicate an invasion slower than no-control (purple, achieve objective), values near zero indicate little change in the speed of the invasion (gray, wasted effort), and negative values indicate a faster invasion (orange, make matters worse). The dot in each row shows the optimal ending cell of a pesticide application for the corresponding starting location (i.e., the strategy that yielded the greatest change in invasion time). The dot color represents whether the optimal change in invasion time was greater than 1 year (purple) or between −1 and 1 year (gray). The examples shown in Figure 1 are indicated in the corresponding cell (for example, panel A in Figure 1, which shows strategy (−20, −6), is represented with an "A" in Figure 2).

kill more native than invader populations (mortality ratio <0; Figure 3) and can be caused by both narrow and wide application efforts (spatial extent: 5–33 units). In addition, there are five pesticide application ranges tested here that kill more invaders and still make matters worse: (−20, 4), (−20, 6), (−22, 6), (−22, 8), and (−24, 8).

We classified strategies that did not change invasion time as wasted effort: applications that use resources but do not affect invasion outcomes (Figure 2, shown in gray). Unlike strategies that make matters worse, strategies that waste effort can be caused by pesticide applications with any mortality ratio (i.e., kill more natives, equal natives and invaders, or more invaders). This is because there are two ways a pesticide application may lead to wasted effort (Figure 3). First, the long-term progression of the invasion wave is not affected by interventions that are narrow in spatial extent and are sufficiently ahead or behind the wavefront. For example, the strategies that kill the largest ratio of invaders to natives have very little effect on invasion time (mortality ratio >3, or killing at least 20 times more invaders than natives, Figure 3). This occurs because the disturbed areas are easily recolonized and the wavefront is not affected. Second, there are interventions around the wavefront that serve as a transition between effective and ineffective strategies. For example, the change in invasion time for strategy (−22, 4) is 0.7, but marginally increasing or decreasing the width of that intervention changes the efficacy of that strategy (e.g., change in invasion time for strategy [−22, 2] is 3.8 vs. −5.3 for strategy [−22, 8]). The mortality ratios for these three strategies are not significantly different, all between 0.2 and 0.6, or killing 1.3–1.8 times more invaders than natives.

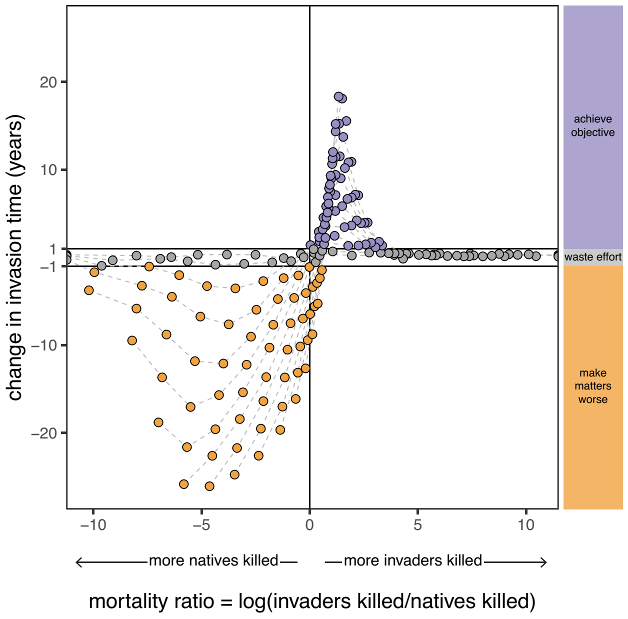

FIGURE 3 Change in invasion time as a function of invader and native pesticide-induced mortality. Each point represents one range of pesticide application with a unique starting and ending location (i.e., each cell in Figure 2). The color of the point shows whether that strategy achieves objective (purple), wastes effort (gray), or makes matters worse (orange) based on the change in invasion time. Mortality ratio is measured as the logarithm of the ratio of invaders killed by pesticide and natives killed by pesticide. A mortality ratio of 0 indicates the same number of invaders and natives killed, a mortality ratio of 5 is equivalent to killing approximately 150 times more invaders than natives, and a mortality ratio of −5 is equivalent to killing approximately 150 times more natives than invaders. Dotted gray lines connect strategies of the same width or "effort."

Despite pesticide application strategies with neutral or detrimental effects on invasion time, the same amount of effort can achieve the management objective when applied to a different location on the landscape (Figure 2, shown in purple; Figure 4; Appendix S1: Figure S1). Of all the locations for pesticide we considered, the most effective strategy slows the invasion by 18.3 years; this application starts 28 units behind and ends at the wavefront. However, misidentifying the wavefront by 7 units behind the actual front (here, because of a detection limit of 100 colonies) reduces the efficacy of this application by more than half, slowing the invasion by only 7.1 years. Strategies that achieve the management objective generally kill more invaders than natives (Figure 3), spatially targeting locations with high densities of invaders and few natives.

Designing pesticide application strategies without considering native competition thus can lead to significant

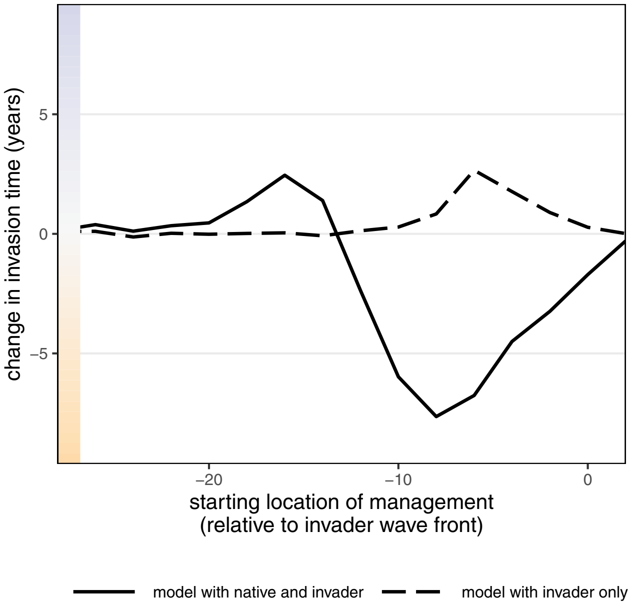

FIGURE 4 Optimal allocation with and without native competition considered in management design. For all control strategies considered over a width of seven cells, change in invasion time across starting locations for a model that includes native competition (solid) and a model that only considers the invader (dashed). See Appendix S1: Figure S1 for results from strategies of varying width.

wasted or counterproductive effort (Figure 4). In an invader-only model, the best strategy for pesticide application over a width of seven cells starts six units behind and sprays through the wavefront (i.e., strategy [−6, 0]); this reflects common intuition about where to focus pesticide applications (as discussed above). Yet, in the model that includes native competition, this strategy leads to the worst outcomes (invasion time speeds up by 6.8 years). In fact, for pesticide application over a width of seven cells, all locations that are effective in the invader-only model are counterproductive in the native–invader model.

These results depend on native competitive ability (Appendix S1: Figure S2) and maximum native dispersal distance (Appendix S1: Figure S3). Stronger native interspecific competition (i.e., with the invader) and weaker native intraspecific competition (i.e., with other natives) both increase the magnitude of counterproductive effort possible (e.g., speed up invasion by 46 years when native interspecific competition is increased by 5%, compared with 26 years in the base case). Similar, but less strong, results occur when the efficacy of pesticide application is decreased (i.e., the proportion of colonies killed by pesticide, Appendix S1: Figure S4).

DISCUSSION

Inappropriate invasive species management wastes resources and can further harm ecosystems. Here, we demonstrate one way in which management could fail: invaders can spread more quickly when management harms natives and inadvertently disrupts native–invader competition. The fire ant invasion in the US may serve as an example, where broad-spectrum pesticides were applied to vast swaths of land disrupting native communities and failing to control (and possibly even accelerating) fire ant spread. In the fire ant system, this hypothesis has been supported primarily by experimental and observational studies (King & Tschinkel, 2008; Morehart et al., 2022; Morrison, 2000; Summerlin et al., 1977); here, our results extend this evidence base, illustrating the landscape-level ramifications of disrupting native–invader competition and, more generally, illuminate one mechanism that could lead to failed or ineffective management.

The conclusions of our study are closely tied to important concepts from invasion biology. In our model, effective management regimes target areas around the wavefront with high invader densities and few natives. By targeting these areas, successful pesticide applications simultaneously accomplish two tasks: (1) reduce invader propagule pressure and prevent invaders from establishing new populations, and (2) maintain native populations and avoid release of invaders from their competitors. All strategies that do the opposite and kill more natives than invaders have counterproductive outcomes. However, killing more invaders than natives does not guarantee success. Strategies that apply pesticide around the wavefront can waste effort or even make matters worse by enabling, rather than preventing, invader recolonization. For example, there were five pesticide applications that killed more invaders than natives, but still made matters worse; in these cases, invaders recolonized the disturbed area more quickly and therefore still benefited from the pesticide application. Moreover, strategies that apply pesticides relatively far behind the invader wavefront do not affect long-term landscape-level dynamics, because invaders can also easily recolonize these areas. Thus, the most successful strategies will leverage both the mortality-inducing effect of pesticides and the competition provided by natives. These insights may also pertain to other invader systems, and in the future, spatially targeted control campaigns could be employed to avoid wasted or counterproductive effort (especially where invader-specific control strategies do not exist).

The possibility of wasted and counterproductive effort extends beyond the specific case modeled here, which depends on strong competition from natives and the ability of invaders to better recolonize disturbed areas. Understanding how other ecological mechanisms could lead to failed management is important. In the fire ant case specifically, detections outside of their known range highlight their potential expansion due to effects of climate change and/or hybridization of fire ants with other more cold-tolerant imported ants (Seltzer et al., 2023; Sutherst & Maywald, 2005). More generally, ecological processes, such as resistance, reinvasion, propagule pressure, or invader succession (Hoffmann, 2011; Lockwood et al., 2005; Myers et al., 2000; Simberloff, 2009), could lead to unsuccessful management efforts. Other dispersal modes (e.g., stratified dispersal; Shigesada & Kawasaki, 1997) and conclusions about how to manage core versus satellite populations (Grevstad, 2005) may also be relevant. Through investigation into these mechanisms and their interaction with biotic forces (including those not considered here, like invader–invader interactions; Simberloff & Von Holle, 1999), we can build a general theory about failed management and obtain a fuller understanding of factors that may lead to wasted or counterproductive effort.

Our model provides a simplified representation of the invasion process. More specific models could be developed to explore the ramifications of additional, real-world complexities or to make recommendations for a specific system, environment, or location. For instance, our one-dimensional model could be extended to two dimensions to more closely reflect landscape dynamics, although we expect this would provide similar qualitative conclusions (Lewis et al., 2006). Furthermore, we modeled a single, contiguous management intervention but, in practice, pesticides are often applied repeatedly and noncontiguously (including the fire ant eradication and control campaign; Williams et al., 2001). Our model can be extended to show how such management interventions affect invasion, complementing other work on disturbance (here, pesticide application) frequency and timing (Miller et al., 2011). For example, a single management intervention would alter the initial conditions of invaders and natives and then our approach could be reapplied to examine the impacts of repeated pesticide applications.

We have also assumed the primary goal of pesticide application is to "slow" the invasion, potentially buying time for the development of alternative control strategies. However, there may be other goals in applying pesticide, and our model can be used to identify spatially explicit management strategies for these alternative objectives as well. Differing objectives may require different management interventions (Probert et al., 2016; Shea et al., 2010), as the same strategy could waste effort with respect to one objective but not another. For example, our model shows strategies that are sufficiently ahead of or behind the wavefront have no effect on invasion time. These strategies, although not effective at a landscape level, may still have positive effects for local control. However, a more difficult trade-off exists for strategies that are locally effective but have negative consequences at the landscape level, or vice versa. Local control may be even more important in areas inhabited by endangered species or areas that have high cultural value. Eradication is another important objective that could be considered in this framework.

Implementation of spatially explicit control strategies would require knowledge of the exact location of the invader wavefront, but surveillance of invasive species can be difficult, especially at low densities (Mehta et al., 2007). In the presence of such uncertainty, one might choose to implement a strategy that is robust to a certain degree of error regarding the location of the wavefront. This "robustness" is another possible objective, which would require careful definition (e.g., to minimize the chance of making matters worse or maximize the chance of native persistence beyond some time period). Future analyses could contrast various objectives, and potentially identify win-win strategies that achieve multiple objectives at the same time.

The conclusions of our model could be validated in multiple ways. Statistical models could pair data on fire ant range expansion (Appendix S1: Figure S6) with data on where, when, and how much pesticide was applied to the landscape. Historical county quarantine records have been used as a proxy for range expansion in other invasions (e.g., spongy moth or hemlock wooly adelgid, Goldstein et al., 2019; Tobin et al., 2015); however, obtaining specific information on pesticide applications from the gray literature may be more difficult. In addition, the model clearly motivates design of experiments at the front of invasion waves; verifying the effects of management disturbances of varying extent, intensity, and location (with respect to the invasion front) would provide a useful test of the hypotheses and intervention recommendations from our model.

Native competition can provide a meaningful barrier to the spread of an invasive species. Our model demonstrates that overlooking such competition may not only waste management effort but in fact make the situation worse. Management will be more successful when carefully targeted to leverage existing biotic interactions. While our results are motivated by, and tailored to, the invasive fire ant, the general approach could be applied to the development of spatial management strategies for other invasive species (see also Pepin et al., 2022). Furthermore, the general insight that relatively subtle shifts in intervention specifications can shift outcomes from beneficial to redundant or the adverse also applies in nonspatial invader management settings. Finally, these ideas have implications for improving the management of threatened and endangered species (e.g., Crouse et al., 1987). In short, identifying maximally effective interventions, and avoiding those that waste resources or make matters worse, will necessarily benefit all subfields of applied ecology.

AUTHOR CONTRIBUTIONS

All authors conceptualized the project. Emily Howerton and Katriona Shea designed the model; implementation and analysis was performed by Emily Howerton. Emily Howerton wrote the original manuscript draft, with editing and revision from all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Howerton, 2023) are available in Zenodo at https://doi.org/10.5281/zenodo.10359711.

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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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