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Bioeconomic synergy between tactics for insect eradication in the presence of Allee effects

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Preventing the establishment of invading pest species can be beneficial with respect to averting future environmental and economic impacts and also in preventing the accumulation of control costs. Allee effects play an important role in the dynamics of newly established, low-density populations by driving small populations into self-extinction, making Allee effects critical in influencing outcomes of eradication efforts. We consider interactions between management tactics in the presence of Allee effects to determine cost-effective and time-efficient combinations to achieve eradication by developing a model that considers pesticide application, predator augmentation and mating disruption as control tactics, using the gypsy moth as a case study. Our findings indicate that given a range of constant expenditure levels, applying moderate levels of pesticides in conjunction with mating disruption increases the Allee threshold which simultaneously substantially decreases the time to eradication relative to either tactic alone. In contrast, increasing predation in conjunction with other tactics requires larger economic expenditures to achieve similar outcomes for the use of pesticide application or mating disruption alone. These results demonstrate the beneficial synergy that may arise from nonlinearities associated with the simultaneous application of multiple eradication tactics and offer new prospects for preventing the establishment of damaging non-native species.

Keywords: Allee effect; eradication; management cost; interaction of control tactics

1. INTRODUCTION

Given the immense impacts caused by certain non-native species, there is often considerable benefit derived from their exclusion. Intervention early in the invasion process is generally the most cost-efficient approach and consequently there may be considerable benefit derived from international quarantines, commodity treatments (e.g. fumigation), inspection of cargo and other approaches to minimize arrival [1,2]. Expenditure of relatively modest sums to achieve pest exclusion generally is dwarfed by the savings that come from preventing the accumulation of impacts once pests are established.

Unfortunately, closure of all invasion pathways is not possible and given trends of increasing world trade, it can be expected that potential pest species will continue to arrive and some fraction will establish [3,4]. When arrival cannot be prevented, the best alternative is often detection and eradication. Here, bioeconomic analyses

indicate considerable benefit of detecting, delimiting and extirpating newly founded populations early when their size and geographical extent are still small [5,6]. As a population persists and grows, the cost of eradication increases and the probability of success decreases [7]. Though it is not possible to eradicate all newly invaded species, like pest exclusion, it is often economically desirable because of the prevention of impact accumulation that can be expected should the invading population be allowed to run its course [5,6].

Here, we define eradication as the total elimination of a species from a given area. Given the perceived difficulty of eliminating all individuals of a species, the practicality of eradication has often been questioned [8,9]. However, recent population studies indicate that low-density populations of a variety of species are governed by Allee effects [10–12] and this may facilitate eradication ([13–15]; see electronic supplementary material, S1). Allee effects may arise from a variety of mechanisms (e.g. mate-location failure, failure to overcome host defences, failure to satiate predators) and create a population threshold, below which population growth rate is negative [16,17]. Consequently, eradication may not require directly eliminating

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all individuals in a population; instead, it may only be necessary to reduce the population below the Allee threshold, and extinction will proceed without further intervention. While culling (e.g. application of a pesticide) can be viewed as reducing the population size, it can also be considered as part of the net reproductive rate, which may act to shift any existing Allee threshold to a higher level (see electronic supplementary material, S1). Other tactics (e.g. mating disruption, sterile male releases) may not involve killing any individuals but instead may directly strengthen an existing Allee effect; such tactics also will cause an upward shift in the Allee threshold (see electronic supplementary material, S1). Eradication is facilitated by increasing the Allee threshold above the current population size [14,15].

There is a long history of attempts to eradicate insect pest populations but not all of these efforts have been successful [7,18]. The tactic that has been the most widely used in insect eradication efforts has been the application of pesticides. Less frequently, eradication has been attempted using mating disruption, mass trapping or release of sterilized males. Each of these four methods may be considered as methods that increase the strength of pre-existing Allee effects and serve to eradicate populations via shifting the Allee threshold to higher levels ([15,19,20]; see electronic supplementary material, S1).

Over the last 50 years, the field of insect pest management has been dominated by the concept of integrated pest management (IPM) [21]. In part, this theory focuses on the benefit arising from the simultaneous implementation of two or more tactics to control populations. Though IPM is usually applied to the management of widely established pest species, the concept of applying multiple control tactics also applies to eradication as many successful eradication programmes have simultaneously used two or more control tactics. For example, the painted apple moth, *Teia annortoides*, was eradicated from Auckland, New Zealand via multiple applications of the bacterial pesticide *Bacillus thuringiensis* along with the release of sterilized males [22].

Presumably, the combination of multiple tactics should result in a higher probability of successful eradication, but little is known about the population response and/or interactions when multiple methods are simultaneously implemented. An important issue that must be considered here is how component Allee effects (both pre-existing and created by a control tactic) might interact to determine the overall demographic Allee effect. A single component Allee effect may negatively interact with other density-dependent processes in ways such that a demographic Allee effect may or may not exist; conversely, two-component Allee effects may positively interact such that the demographic Allee effect, in terms of its Allee threshold, is greater (superadditive) or smaller (subadditive) than the sum of both in isolation [11,23]. Berec *et al.* [23] and Boukal & Berec [19] used simple population models to explore interactions of component Allee effects through the application of multiple tactics for achieving eradication, showing that multiple tactics may interact with superadditivity or subadditivity depending upon combinations of tactics, and also upon parameter conditions [19,23]. However, their results are too general to be directly applicable to any particular biological system or to consider the

inevitable issue of the costs of tactics when evaluating their combined effects [24].

Here, we consider interactions between multiple control tactics with respect to resulting demographic Allee effects, costs and the potential for population eradication. Given that eradication is only an appropriate option when population sizes are very small, empirical measurement of the population-level interactions between tactics is not practical owing to sampling constraints. Therefore, we use a realistic population model to investigate interactions between multiple tactics to quantify both their impacts on the strength of the demographic Allee effect and their cost-effectiveness.

In order to achieve a practical level of realism, we adopted the gypsy moth, *Lymantria dispar*, as a model system. We chose this system because considerable information exists about its population biology; specifically, Allee effects have been well-quantified, arising both from mate-finding failure [13,25,26] and predator satiation [27]. The gypsy moth also makes an excellent model system because eradication has been extensively carried out; though this Eurasian species is widely established in northeastern North America, it has not yet been established in western North America where it has been repeatedly detected and eradicated [28]. We also emphasize that although we parametrize our model according to gypsy moth data, the modelling framework we develop is general and can be easily modified to perform a similar exploration for other pest species, irrespective of the presence of a pre-existing Allee effect in the target species or choices of control tactics.

2. MATERIAL AND METHODS

(a) Population model

We introduce a model parametrized using data from the literature describing the dynamics of low-density gypsy moth populations, but the model can be easily modified to represent any sexually reproducing insect with non-overlapping generations. Although stochasticity may contribute to driving populations to extinction, for the purpose of this work, we solely focus on the direct impact of Allee effects. In particular, we consider a deterministic hybrid modelling approach such that the between-generation (generation time is 1 year for the gypsy moth) population dynamics are modelled in discrete time and the mating season dynamics are described in continuous time. The model tracks densities of insects on a per hectare basis. In this model, we assume that possible control tactics include pesticide application and predator augmentation, which affect larval and pupal survival, respectively, as well as mating disruption via distribution of false pheromone point sources. Here, we outline the discrete-time model of between-generation dynamics; a description of the mating season dynamics can be found in electronic supplementary material, S2.

We assume that during a generation starting at time t , eggs \mathcal{J}_t survive to the pupal stage \mathcal{J}' after undergoing background mortality m_j and mortality owing to pesticide application p . Pesticide efficiency (the proportion of the gypsy moth population killed defined by p) depends on the number of pesticide applications (electronic supplementary material, S3). A fraction W of pupae then avoids predation so that \mathcal{J}'' pupae are ready to emerge. A proportion χ of pupae emerge as females and $1 - \chi$ as males across the mating season, with

Table 1. Parameter values and definitions for the discrete-time model.

parameter	value	definition	unit	reference
m_j	0.05	background larval mortality	yr ⁻¹	—
a	0.404/25	predator attack rate	d ⁻¹ ha ⁻¹	[30]
T	11	length of pupal period	days	[30]
T_h	0.054	predator handling time	day	[30]
λ	546	number of eggs per egg mass	eggs	[31]

eclosion times based on a normal distribution with means μ_M and μ_F and standard deviations σ_M and σ_F for males and females, respectively. This is captured in a continuous-time, mating season model following the spatially implicit approach of Yamanaka & Liebhold [20]. The mating season model describes the dynamics of mate-finding by accounting for interactions between males and females, and captures the mate-finding Allee effect (electronic supplementary material, S2). Moreover, it accounts for mating disruption by false pheromone point sources. Denoted by R , it outputs the number of females that successfully reproduce F_t^m by the end of the mating season (electronic supplementary material, S2). Finally, each of the F_t^m mated females lays one egg mass or λ eggs, time increases by one generation and the life cycle repeats. This results in the basic population model

$$\mathcal{J}' = \mathcal{J}_i m_j p, \quad (2.1)$$

$$\mathcal{J}'' = \mathcal{J}' W(\mathcal{J}', a, T, C, T_h), \quad (2.2)$$

$$F_t^m = R(\mathcal{J}'', \chi, \mu_M, \mu_F, \sigma_M, \sigma_F) \quad (2.3)$$

and

$$\mathcal{J}_{t+1} = \lambda F_t^m \quad (2.4)$$

Predation by generalist predators, primarily rodents, is believed to be the largest source of mortality affecting low-density gypsy moth populations [29,30]. For the predation term $W(\mathcal{J}', a, T, C, T_h)$, we implement the Holling type II functional response estimated by Elkinton *et al.* [30], who fit the required parameters to data collected by experimentally manipulating gypsy moth densities. The predator density was not reported earlier [30], so we assume an intermediate density of 10 predators per hectare based on fig. 3 of Elkinton *et al.* [29]. We assume that predator augmentation increases the predator density relative to this 'baseline' level, which we assign the relative value of $C = 1$. We also assume an observation window of 1 day and find the surviving pupae at the end of each day of the pupal period T (11 days). Then, if \mathcal{J}' is the initial number of pupae, the number \mathcal{J}'_1 that escapes predation during day 1 is

$$\mathcal{J}'_1 = \mathcal{J}' \left(1 - \frac{aC}{1 + aT_h \mathcal{J}'} \right), \quad (2.5)$$

where a is an attack rate, T_h is the handling time and C the relative predator density. At the end of day 2, we similarly have

$$\mathcal{J}'_2 = \mathcal{J}'_1 \left(1 - \frac{aC}{1 + aT_h \mathcal{J}'_1} \right) \quad (2.6)$$

pupae remaining, and after the final (11th) day, we have

$$\mathcal{J}'' = \mathcal{J}'_{10} \left(1 - \frac{aC}{1 + aT_h \mathcal{J}'_{10}} \right) \quad (2.7)$$

adults ready to emerge.

We note that our model considers newly established, low-density pest populations so that exponential growth with no density dependence is a reasonable assumption. Table 1 provides a list of parameters for the discrete-time model, and parameters for the function R representing the mating season model are given in electronic supplementary material, S2.

(b) Summarizing model outcomes

We define the Allee threshold as the critical number of egg masses per hectare below which the population declines towards extinction, and consider a population extinct when the population is completely eliminated by the end of the reproduction season. The threshold of a pre-existing Allee effect may be shifted by the application of control tactics [14,15,19,20,] (see electronic supplementary material, S1). Here, pesticide application is measured as efficiency (proportion of gypsy moth population killed) of the bacterial pesticide *Bacillus thuringiensis* (Bt), predator augmentation is measured as fractional increase of small rodent predators relative to their natural level $C = 1$ (corresponding to 10 rodents per hectare) and mating disruption is measured as the numbers of pheromone flakes released under the assumption that one in every 100 flakes contributes to mating disruption via false trail following (see electronic supplementary material, S3). To compare the efficiency of different control tactics and their combinations, we consider both the annual and total costs of applying each control tactic per hectare. For simplicity, we assume a discount rate of 0 per cent when computing total costs. Plots of each of the annual cost functions can be found in the second row of figure 1, and their rationale is provided in see electronic supplementary material, S4. Finally, we determine the 'optimal cost strategy' for each control tactic (and combination of tactics), which we define here as the strategy with the lowest total cost (annual costs multiplied by years until eradication) under the assumption of constant application of tactics between years.

In the absence of any control tactic, an initial population density of 1.24 egg masses is required for the gypsy moth population to grow (found numerically). For varying levels of intensity of the application of each tactic in addition to every combination of tactics, we find the Allee threshold by simulating our model to determine the minimum number of egg masses needed for a gypsy moth population to have positive growth. We consider low-density populations but for demonstrative purposes, we consider Allee thresholds up to 10 000 egg masses (Allee thresholds greater than this are set to this maximum value). We again note that in the

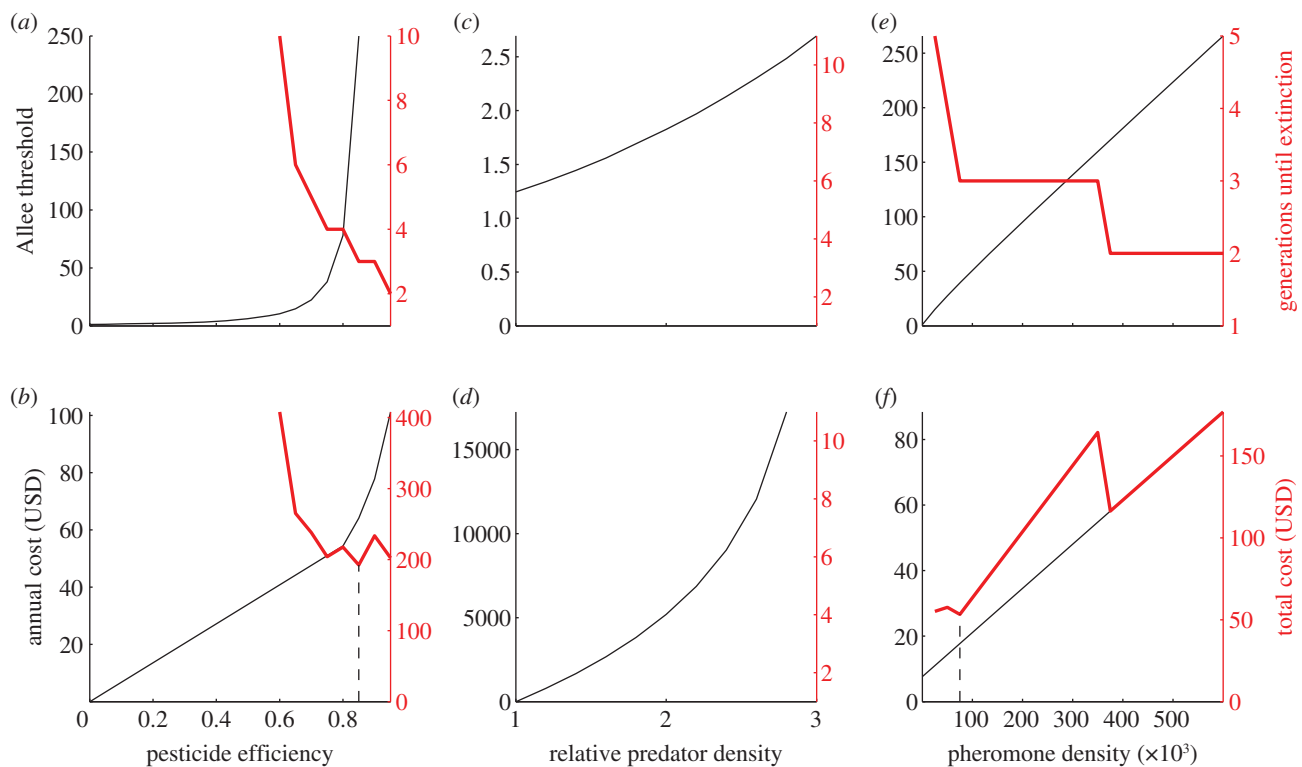


Figure 1. Changes in the Allee threshold after implementing a single control tactic alone. (*a,c,e*) The top row of figures shows the Allee threshold versus intensity of a particular control tactic (in black) in addition to the number of generations until eradication with an initial number of egg mass of 10 (in red). (*b,d,f*) The second row shows the annual costs of achieving that level of effectiveness (black) and the total costs that account for generations until eradication (red). When applicable, the vertical dashed line represents the optimal level of a particular control tactic. From left to right, the figures correspond to pesticide application, predator augmentation and mating disruption.

absence of predator augmentation, all simulations assume the predator density is at its baseline level of $C = 1$ (i.e. 10 rodents per ha) to reflect natural systems.

3. RESULTS

We first determine the effects of control tactics applied individually, and then we describe the relative effects of interacting control tactics. For various levels of each control tactic, we assume that the control is applied at the same level each year; in other words, predator densities are maintained, the same level of pesticide is applied and the same number of pheromone flakes per hectare are released each year. We display the shifted Allee threshold in addition to the number of generations required to achieve population extinction given an initial population size of 10 egg masses per hectare, a realistic value for typical invading populations of the gypsy moth. While a different initial invasion size will affect the quantitative results, the qualitative results are identical (see electronic supplementary material, S5). As our model is deterministic, measuring the time to extinction in this context only makes reasonable sense if the shifted Allee threshold exceeds 10 egg masses. Finally, we show the associated control costs and optimal cost strategy.

(a) *The effects of a single control tactic*

The first tactic we consider is pesticide application, and we display our results in figure 1*a,b*. Low to intermediate levels of pesticide efficiency result in marginal increases in the Allee threshold, but with high levels of pesticide

efficiency, the threshold increases significantly (black line, figure 1*a*). This implies that pesticide application can be effective for eradicating populations when its efficiency is relatively high (>75%). We find that it takes 10 generations to accomplish eradication with 60 per cent pesticide efficiency, five generations with 70 per cent pesticide efficiency and only two generations with 95 per cent pesticide efficiency (red line, figure 1*a*). We also show that annual costs increase linearly when the kill fraction is less than 80 per cent and nonlinearly for larger kill fractions which would indicate limitations on the level of affordable impacts (black line, figure 1*b*). However, when taking into account the number of generations until extinction, the total cost (red line, figure 1*b*) actually decreases with higher pesticide efficiencies by limiting the number of generations requiring management. Moreover, the optimal cost strategy is achieved with a pesticide efficiency of 85 per cent.

Results from the second control tactic, predator augmentation, are shown in figure 1*c,d*. There is a slow increase in the Allee threshold that only reaches approximately twice its initial level even when the predator density is three times the baseline level (black line, figure 1*c*). This small increase in the Allee threshold implies that this control tactic alone would be unlikely to result in successful eradication. This observation is confirmed by observing that for any level of enhanced predation, eradication is not possible (absence of the red line; figure 1*c*). Furthermore, as demonstrated in figure 1*d*, predator augmentation is very costly to implement. To determine whether the attack rate (*a*)

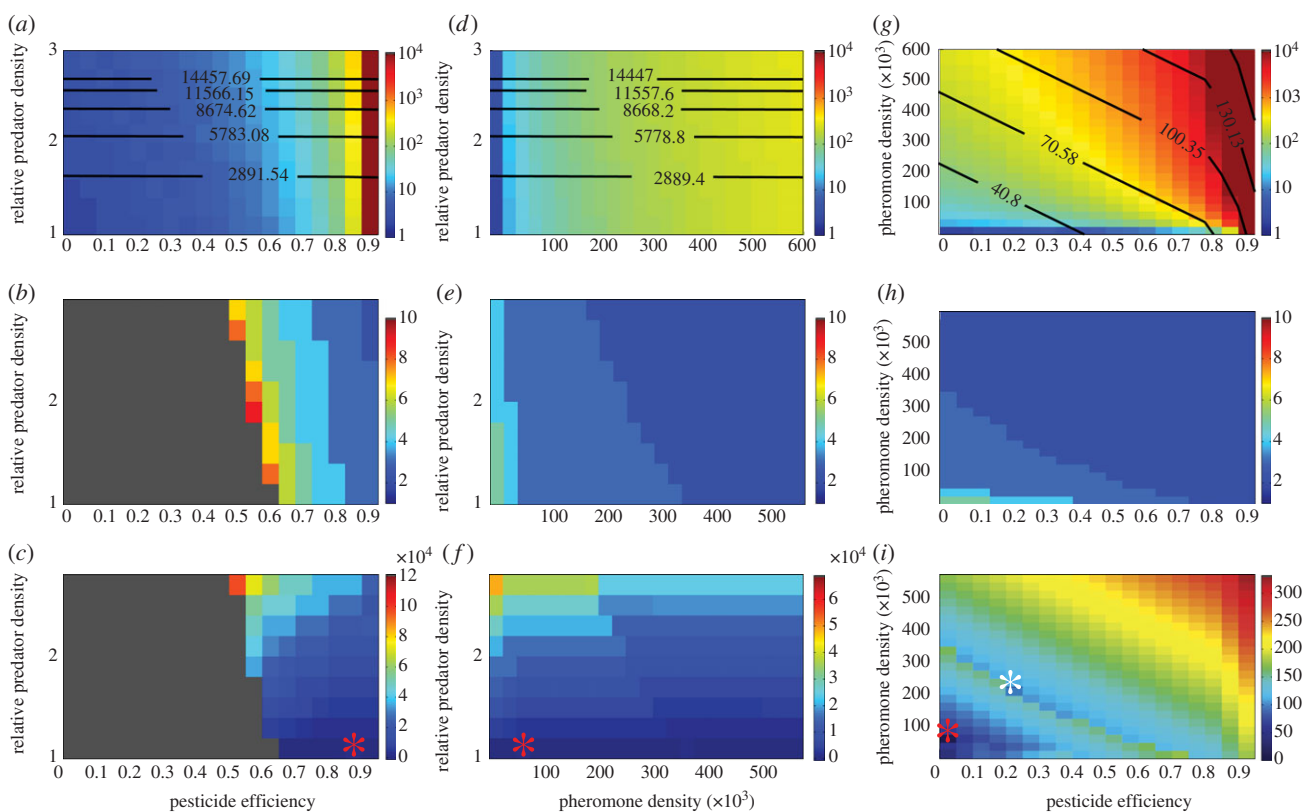


Figure 2. The top row of plots displays the interactions between two control tactics with the colours corresponding to the \log_{10} transform of the Allee threshold. Isoclines showing combinations of control tactics that have equal annual costs per hectare (USD) are overlaid on each of these plots (black lines). In (a,c) the isoclines appear horizontal; however, this is a direct consequence of the costs associated with predator augmentation. The second row indicates the corresponding number of years before extinction for each combination of tactics when the initial population is composed of 10 egg masses, and the bottom row displays the associated total costs. Grey indicates that eradication for a given combination is not feasible. The optimal cost strategy for each combination is indicated by a red star, and the white star represents a combination of pesticides and false pheromone point sources that requires less time than the optimum with only a marginal increase in cost. All simulations assume an initial population size of 10 egg masses.

plays a significant role in these observations, see electronic supplementary material, S5 provides a sensitivity analysis which demonstrates that even with a 100-fold increase in a , the Allee threshold plateaus at approximately 29 egg masses.

The effects of varying densities of false pheromone point sources on the Allee threshold, time to extinction and control costs are displayed in figure 1e,f. The Allee threshold and annual costs both increase approximately linearly with density of pheromone sources. Furthermore, mating disruption allows for a faster increase in the Allee threshold when compared with the other control tactics (until pesticide efficiency approaches 80%) at costs of the same order as those associated with pesticide application. In contrast to pesticide application, however, the number of generations until eradication is comparatively insensitive to the density of pheromone point sources for most of its admissible range. Consequently, the optimal cost strategy for false pheromone point source density is to apply only 75 000 sources, and the total cost is lower than the optimal level of pesticide efficiency (53.27 USD compared with 192.37 USD per hectare, respectively).

These results allowed us to determine the most effective single control tactic for increasing the Allee threshold given a particular budget. We find that at low budgets, mating disruption has the greatest effect on the Allee threshold. For slightly higher budgets, pesticide

application becomes the most effective tactic in increasing the Allee threshold.

(b) Interacting control tactics

In this section, we evaluate the interaction between control tactics by computing the Allee threshold for relevant combinations for each pair of the three tactics considered. For each combination of tactics, we display the Allee threshold on a \log_{10} scale to highlight the differences in thresholds for different combinations (figure 2a,d,g). Additionally, we overlay annual cost isoclines (i.e. lines indicating combinations of equal cost) to determine whether, given a fixed cost, the Allee threshold is highest for a combination of tactics or if it achieves its maximum for a single control tactic alone. Finally, we display the number of generations until extinction (figure 2b,e,h) as well as the associated total costs (figure 2c,f,i). In this figure, grey squares represent combinations that will not achieve eradication, and the optimal cost strategy is indicated by a red star. A full summary of the optimal cost strategies is displayed in table 2.

We first consider the interaction between pesticide application and predator augmentation (figure 2a–c). For most fixed annual costs, the highest Allee threshold is obtained by applying both control tactics simultaneously rather than applying either tactic singly (indicated by the

Table 2. Optimal cost strategies for combined tactics.

control tactics	control time (years)	strategy	total cost per hectare (USD)
pesticide and predation	3	85% pest efficiency, no augmentation	192.37
pheromone and predation	3	75 000 pher sources, no augmentation	53.27
pesticide and pheromone	3	no pest, 75 000 pher sources	53.27
pesticide and pheromone	2	20% pest efficiency, 225 000 pher sources	103.09

black lines on figure 2a); the exception to this is at very low costs in which the highest Allee threshold would be obtained using pesticides only. In turn, this increases the range of population sizes for which eradication efforts may be successful (figure 2a,b). However, it is clear that the greatest increases in the Allee threshold result from increasing pesticide efficiency. Moreover, independent of length of control programme, the optimal cost strategy is to obtain pesticide efficiency of 85 per cent and allocate no resources towards predator augmentation as a result of the high costs associated with increasing predator densities (figure 2c and table 2). In general, eradication programmes result in population extinction within around 2–4 years; therefore, the ‘opportunity window’ (range of control combinations achieving eradication within this time frame) enlarges as the budget increases (figure 2b). Although the costs of increasing predator density are much higher than those of pesticide application, investment in increasing the predator density in addition to applying maximal pesticide efficiency increases the chance of eradication by increasing the Allee threshold and decreasing the extinction time. Moreover, larger annual budgets that allow greater augmentation of predator densities may be more environmentally desirable by reducing the number of years of pesticide applications (i.e. lower pesticide impacts on non-target organisms).

Similar to the interaction between pesticide application and predator augmentation, for most fixed annual costs combining release of pheromone sources and predator augmentation increases the Allee threshold and decreases time to extinction relative to the application of each control tactic singly (figure 2d–f). Again, however, the optimal cost strategy with this combination of tactics always uses false pheromone sources in the absence of predator augmentation (figure 2f). There are, however, several quantitative differences. First, except for the lowest values of pheromone point source density, eradication of populations initially composed of 10 egg masses is relatively fast (three or fewer generations) (figure 2e). Further, Allee thresholds with this combination are small only when the pheromone point source density is very low. This implies that in many practical situations where the initial number of egg masses is not large, such as 10 which is used in our case, the ‘opportunity window’ covers a substantial range of the pheromone point source densities, and the appropriate combination of the two tactics may be determined in part based on criteria outside of the scope of our model (e.g. minimizing the impact of a real application of pheromones on public discomfort).

Finally, we consider the interaction between pesticide application and application of false pheromone point sources (figure 2g–i). For a fixed annual budget, these control tactics operate synergistically; substantial increases in the Allee threshold are observed with

combinations of the two tactics (figure 2g). While the optimal cost strategy has a duration of 3 years and requires the application of false pheromone point sources only, eradication can be achieved in just 2 years using a combination of both tactics for a modest increase in cost (103.09 USD versus 53.27 USD). In fact, using both pesticides and false pheromone point sources is cheaper and less time-consuming than using pesticides alone. Regarding the time to extinction, it is always preferable to release some pheromones; except for the lowest values of the pheromone point source density, eradication of populations initially composed of 10 egg masses is relatively fast and takes only two generations at relatively low costs. We note that at high enough budgets, specific mixtures of spending on the two tactics do not substantially differ in their effectiveness; criteria such as environmental safety or non-target effect concerns might then be used to select an appropriate combination.

4. DISCUSSION

Despite the clear benefit of preventing the establishment of pest species, the practicality of insect eradication is often questioned [8,9,18]. Many of these questions revolve around the perception of the difficulty of eliminating every individual in a population. Related to this is the difficulty in sampling very low-density populations to confirm that eradication has been accomplished. At low densities, however, the population dynamics of insect species may be dominated by Allee effects [11,12,14,32] and this as well as other processes occurring at low population sizes, including demographic stochasticity, may eliminate the need for direct removal of all individuals. In particular, the presence of a strong demographic Allee effect will create a density threshold, below which populations will probably decline towards extinction. Thus, eradication should be approached simply with a strategy of forcing a population below its Allee threshold (or raising the Allee threshold above the current population size) [13,15].

In this study, we modelled Allee effects arising from both mate-finding failure and from generalist predators in a well-studied system, in which data are available to mechanistically quantify these interactions. We then applied this model to evaluate the interactions between three management tactics: pesticide spraying, augmentation of natural enemy populations and mating disruption via distribution of false pheromone point sources. All three tactics interact with and intensify component Allee effects that are already present ([19]; see electronic supplementary material, S1).

An important and unique aspect of our study was that we compared various combinations of management tactics in three ways which is only possible because we focused on a specific system for which we were able to estimate the efficacy and cost of each control tactic.

First, we evaluated how various combinations of tactics shift the Allee threshold. Second, we used simulations to determine the number of generations expected before extinction for various combinations of tactics. Finally, we were able to use cost accounting information to model the annual and total expenses associated with these combinations. By focusing on costs and years to extinction, we were able to directly compare the efficacy of these various combinations. Such information is of critical importance in the allocation of resources for achieving eradication efficiently in real applications.

Simulations indicated that both pesticide application and mating disruption were effective when used individually and eradication could be achieved practically (figure 1). There is empirical support for this conclusion. The microbial pesticide *Bacillus thuringiensis* is routinely used to eradicate small, isolated gypsy moth populations in the western USA and virtually all of these programmes have been successful [33]. Mating disruption is used less frequently for eradicating gypsy moth populations, not because of lack of effectiveness, but because of concerns over the fact that treatments shut down captures in pheromone-baited traps that are used to confirm eradication and delimit additional treatments [34]. However, mating disruption is the dominant treatment method used in the gypsy moth slow the spread (STS) programme—a barrier-zone project that slows gypsy moth range expansion by locating and treating isolated gypsy moth populations ahead of the expanding population front [35]. The populations targeted by this programme are isolated colonies, much like those targeted in true eradication projects. Mating disruption has been found to be as effective, or even more effective, in the STS programme than spraying with *B. thuringiensis* [35].

Elevation of gypsy moth mortality via augmentation of small rodent predator populations has been experimentally documented in the field [30] but has never been applied as an operational eradication treatment. Results here indicate that this predation creates relatively small Allee thresholds, and augmentation of predator populations is unlikely to result in eradication when implemented alone (figure 1). In addition, our results indicate that from a cost perspective there is generally little benefit in including predator augmentation in addition to either pesticide application or mating disruption (figure 2).

Despite being the most expensive tactic considered here, predator augmentation might be considered in conjunction with the other tactics because both pesticide application and mating disruption usually involve spraying from aircraft, and aerial spraying in eradication programmes often invokes adverse reactions by the public [18]. Furthermore, application of pesticides may be undesirable in locations where there is concern about conservation of non-target species susceptible to pesticides. Though expensive, augmentation of predators can slightly enhance eradication when used in combination with the other tactics, allowing for less use of pesticides or mating-disruption techniques. It is also possible that other types of generalist predators (e.g. arthropods) might be augmented at lower cost with potentially greater impacts. Augmentation of natural enemy populations, also termed ‘conservative biological control’ has been applied for the control of widely established populations, but to our knowledge has never been used as part of a pest

eradication programme. Our results indicate that there may be some merit in pursuing this approach in the context of eradication.

The complexities of tactic interactions for eradication are best illustrated by the various combinations of mating disruption and pesticide application (figure 2). Combined tactic efficacies, measured both by shifts in the Allee threshold and by the time to eradication are characterized by nonlinear surfaces. For eradication programmes spanning 2 years, the optimal combination of tactics requires non-zero expenditures on both types of tactic; this results from the convexity of these surfaces and the manner in which they intersect the largely linear total cost surfaces. Low to moderate expenditures on pesticide application alone tend to be relatively ineffective in terms of time to eradication, and at higher expenditure levels, much higher levels of effectiveness can be obtained by including low-level mating disruption. This extreme nonlinearity of the Allee threshold shift and time to extinction in the response to mating disruption apparently arises out of the demographic interaction with pesticide application because such nonlinearity is not seen in the effectiveness of mating disruption when applied alone (figure 1). This analysis considered a fixed initial invasion size; while the number of generations required for extinction and the corresponding total cost will differ depending on the initial size; this analysis provides an example of the population dynamics for realistic invasions. Moreover, we only display the results of constant application of tactics each year, whereas strategies may optimally change over time depending on the population size. However, consideration of time-varying control strategies is beyond the scope of this paper and our results provide evidence for the benefit of using multiple control tactics in managing pest populations.

The mechanistic model applied here provides insight into how eradication of the gypsy moth can most effectively be conducted. These results have obvious use for management of this economically significant forest pest but may also provide insight for other species. Given similarity in biologies, we anticipate that these results could be extrapolated for development of strategies for eradicating other Lepidoptera species (e.g. eradication of the apple painted moth, *Orgyia anartoides*, from New Zealand; [22]). For species with much different biologies and population behaviours, similar mechanistic models could be constructed to explore eradication strategies. For example, other species might reproduce asexually and thus not exhibit an Allee effect arising from mate-finding, such as is the case with the hemlock woody adelgid *Adelges tsugae*. Additionally, some species, such as the mountain pine beetle *Dendroctonus ponderosae*, exhibit group feeding and this could be simulated, along with tactics designed to enhance this component Allee effect. The efficacy of tactics that either creates an Allee effect or interacts with other Allee effects is difficult to predict qualitatively and population models are of critical importance for predicting success. Kramer *et al.* [12] found that strong Allee effects were present in 30 per cent of terrestrial insect species that have been examined, which could limit the extent to which the approach outlined here could be applied. However, Allee effects may be present in a much larger number of species but they are simply not detected because of the difficulty of sampling low-density populations.

In our gypsy moth case study, we explored interactions between three control tactics. Two of these tactics are commonly used and all can be expected to have a positive effect towards eradication. Previous work considered the interaction of component Allee effects, defining additivity in terms of the Allee threshold of a double Allee effect versus the sum of the Allee thresholds for each Allee effect in isolation [23]. However, we argue that from a management standpoint, a more appropriate definition of additivity between control tactics should be based on maximizing the Allee threshold at a fixed budget level. According to this definition, two control tactics are synergistic (superadditive) if it is optimal to use a combination of tactics rather than one in isolation and they interfere (subadditive) if the Allee threshold when applying a combination of control tactics is lower than the thresholds for each tactic in isolation. Thus, according to this definition, the interactions between all tactics studied here can be identified as synergistic for nearly every annual cost. We again emphasize that while the optimal strategies exclude predator augmentation, the observed synergistic effects favour a combination of tactics at high budgets. However, synergy between tactics cannot be expected to be the case in all systems. In other systems, where various operational control tactics are available, we cannot exclude the possibility that some combinations of tactics might interfere, that is, their interaction would be subadditive, such as mass-trapping combined with release of sterile insects or broad-spectrum insecticides combined with augmentative biological control. Efficiency (or lack thereof) of such presumably subadditive treatment combinations should be explored in future studies.

We argue that our work has more general implications than simply providing insights into the eradication of a particularly important pest. The existence of synergy between control tactics used for eradication may be quite common and could be exploited in the eradication of a variety of other invading pest species. The generality lies in demonstrating the need to consider interactions among different aspects of the population dynamics in determining how control tactics will interact. These insights are only possible by considering a carefully parametrized model as we have done here.

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