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Combining Tactics to Exploit Allee Effects for Eradication of Alien Insect Populations

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ABSTRACT Invasive species increasingly threaten ecosystems, food production, and human welfare worldwide. Hundreds of eradication programs have targeted a wide range of nonnative insect species to mitigate the economic and ecological impacts of biological invasions. Many such programs used multiple tactics to achieve this goal, but interactions between tactics have received little formal consideration, specifically as they interact with Allee dynamics. If a population can be driven below an Allee threshold, extinction becomes more probable because of factors such as the failure to find mates, satiate natural enemies, or successfully exploit food resources, as well as demographic and environmental stochasticity. A key implication of an Allee threshold is that the population can be eradicated without the need and expense of killing the last individuals. Some combinations of control tactics could interact with Allee dynamics to increase the probability of successful eradication. Combinations of tactics can be considered to have *synergistic* (greater efficiency in achieving extinction from the combination), *additive* (no improvement over single tactics alone), or *antagonistic* (reduced efficiency from the combination) effects on Allee dynamics. We highlight examples of combinations of tactics likely to act synergistically, additively, or antagonistically on pest populations. By exploiting the interacting effects of multiple tactics on Allee dynamics, the success and cost-effectiveness of eradication programs can be enhanced.

KEY WORDS Allee effect, biological invasion, density dependence, eradication, invasive species

There has been a steady accumulation of an increasingly wide range of plant-feeding insects in forests, agro-ecosystems, and urban environments postborder and beyond their native range (Levine and D'Antonio 2003, Brockerhoff et al. 2006, Hulme et al. 2008, Aukema et al. 2010). Most species that arrive in a new habitat fail to establish (Williamson and Fitter 1996, Ludsin and Wolfe 2001, Simberloff and Gibbons 2004, Lockwood et al. 2005) or have relatively minor effects in their expanded range (Mack et al. 2000, Aukema et al. 2010). A portion of alien species, however, become invasive with substantial economic and ecological impacts, often increasing the energy footprint of food and fiber production systems because of an increased need for pest management, or irreversibly altering the invaded ecosystem and its biodiversity (Pimentel 2002, Gandhi and Herms 2010, Aukema et al. 2011). High profile invaders such as *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), *Cochliomyia hominivorax* Coquerel (Diptera: Calliphorida), *Adelges tsugae* Annand (Hemiptera: Adelgidae), and *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) cost property owners, local and national government agencies, and private industries billions of dollars annually (Aukema et al. 2010, 2011; Holmes et al. 2010; Kovacs et al. 2011). The distribution of costs from incursions is often contentious.

Preventing the introduction of species has long been recognized as the most effective means to reduce impacts of invaders (Sakai et al. 2001, Hulme et al. 2008, Liebhold and Tobin 2008). Numerous international phytosanitary regulations and agreements, beginning in the United States with the 1912 U.S. Plant Pest Act, have been implemented to reduce risks of inadvertent transport of insects and other organisms through the movement of infested materials (e.g., U.S. Code of Federal Regulations, Title 7, Chapter III, Part 301). Nevertheless, nonnative insects continue to be introduced and newly established species are detected postborder every year (Work et al. 2005, Brockerhoff et al. 2006, Liebhold et al. 2006, McCullough et al. 2006). Given current and projected rates of global trade and travel, it is inevitable that unwanted, nonnative insects will continue to be introduced, and some will establish and ultimately become invasive pests.

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Options available for eradication or, in the event of failure or lack of feasibility, long-term management of invasive insects, depend on biological attributes, hosts and projected impacts of the pest. When an alien species is detected but expected to have little impact, regulatory agencies typically elect to take no action. In New Zealand, for example, an average of one new organism is discovered postborder every week (Kriticos et al. 2005), but eradication programs are rare and mounted only when there is a high probability of expected economic and environmental cost. Decisions to initiate an eradication program are not undertaken lightly, given the significant expense and potential controversy that often accompany such efforts (Kean et al. 2012), particularly so for multi-year projects (Knipling 1979). Moreover, if a nonnative species appears to be established across a large geographic area, eradication is unlikely to be practical (Brockerhoff et al. 2010). Similarly, erroneously declaring success is embarrassing and costly, and undermines future confidence.

Although there are hundreds of cases of successful eradication programs (Kean et al. 2012), there remains considerable pessimism about the feasibility of eradication (Dahlsten and Garcia 1989, Myers et al. 2000). Some failed eradication attempts can be attributed to biological, tactical, resource or political limitations (Myers et al. 1998, Government Accountability Office 2006). The outcomes of some efforts remain ambiguous for reasons ranging from political aversion to an admission of defeat, the difficulty determining when a population is truly eradicated, as well as the potentially embarrassing and costly consequences of erroneously declaring success (Dreistadt 1983, Dreistadt and Weber 1989). To circumvent some of these challenges, previous studies have described probabilistic models used to estimate the confidence that an eradication program was successful given a continual lack of detection in monitoring efforts (Barclay and Hargrove 2005, Kean and Suckling 2005). Ultimately, the damage or potential damage associated with a nonnative species must warrant the investment required to detect and eradicate the population, and viable methods to do so must be available. Given the long-term costs of damage and pest management averted by eradication (Popham and Hall 1958, Klassen 1989, Brockerhoff et al. 2010), eradication should not be discounted as an option, especially if novel approaches can facilitate success. Advances in understanding and technology can generate new tactics or strategies that can be used in programs to eradicate insect pests. For example, identification and synthesis of long-range pheromones and other attractants have provided highly effective detection tools, and facilitated their use as species specific and environmentally benign control tactics (e.g., mating disruption or mass trapping) (Cardé and Minks 1995, El-Sayed 2011).

Our understanding of the population ecology of invasive species (Sakai et al. 2001) and in particular, the role of Allee dynamics in biological invasions (Taylor and Hastings 2005, Liebhold and Tobin 2008), has increased in recent years, generating concepts that can be integrated into the design and implementation of operational eradication programs (Tobin et al. 2011). A key concept is that of pest density, which involves knowledge of the number of individuals per unit area. Pest control tactics can be broadly classified as density-independent, such as insecticide applications where a certain proportion of the population is killed, or density-dependent, such as mating disruption, where efficacy is inversely dependent on the absolute density and scarcity plays a role. Tactics could also be used to subdivide or fragment populations, which can then be progressively tackled using the rolling carpet principle (Dyck et al. 2005).

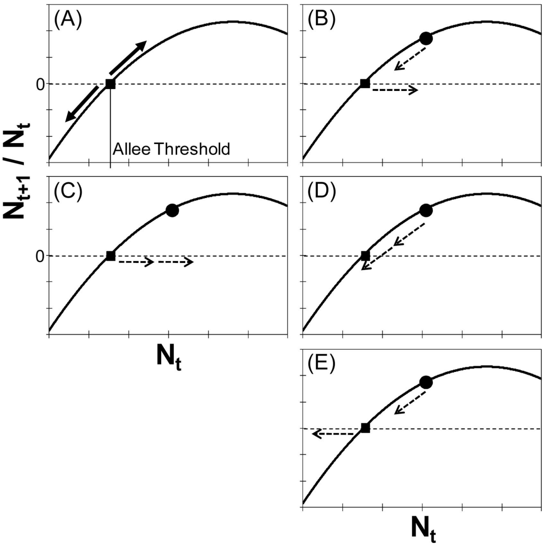

Fig. 1. Allee dynamics resulting from combining treatment tactics (dashed arrows). (A) Representation of Allee dynamics in which the change in population density (N_{t+1}/N_t) is plotted against the initial density (N_t). Initial densities above an Allee threshold (solid square) will lead to a positive rate of population increase until governed by overcrowding dynamics (e.g., a carrying capacity). Initial densities below an Allee threshold will lead to a declining population density and extinction. (B) Synergistically combining a density-independent tactic to reduce population density with one that increases an Allee threshold. (C) Combining two tactics that do not affect density but jointly increase the Allee threshold. (D) Combining two tactics that do not alter the Allee threshold but jointly decrease population density below an Allee threshold. (E) Antagonistic combination of tactics in which one decreases density while another negates an Allee effect.

In many populations, there is a critical population size or density, known as the Allee threshold, below which the per capita population growth rate is negative and the population proceeds toward extinction (Fig. 1A; Courchamp et al. 1999, 2008; Berec et al. 2007). Allee effects may arise from intrinsic biological traits of the organism, or its interactions with its host, natural enemies or other aspects of its environment. Individuals within a sexually reproducing population, for example, are less likely to locate a suitable mate at low than at high densities (Tobin et al. 2009, Rhainds 2010). Some insects, such as mass-attacking bark beetles, rely on high densities to overcome tree defenses and successfully colonize hosts (Raffa and Berryman 1983, Boone et al. 2011), a strategy that is less effective in sparse populations. Moreover, demographic stochasticity alone has been shown to induce an Allee-like effect, which also can challenge the viability of low-density populations (Lande 1998). Allee effects, therefore, function as density-dependent factors affecting population dynamics through altering the rate of population increase (Dennis 1989, Stephens et al. 1999). The application of tactics that reduce the likelihood of mate finding, consequently resulting in a reduced population growth rate, is an example because population density would be reduced over time. Consequences of Allee effects are reflected in unsuccessful classical biological control attempts; successful establishment of natural enemies most often occurred when relatively high densities of organisms are released (Beirne 1975, Stiling 1990, Hopper and Roush 1993, Fagan et al. 2002).

An under-appreciated implication of Allee dynamics is that not every individual must be killed to eradicate a pest population (Liebhold and Bascompte 2003, Liebhold and Tobin 2008), a concept originally derived from conservation programs designed to prevent the extirpation of endangered species (Lande 1988, Courchamp and Macdonald 2001, Courchamp et al. 2008). For those species influenced by Allee effects, a minimum number of individuals is required for a population to remain viable. If an eradication program can drive the pest population below the Allee threshold, eradication can be achieved without the relatively costly efforts to locate and kill the last remaining individuals. Although newly established populations, when detected at low density, tend to be the most amenable to eradication, it is also important to consider the interaction between density and the spatial extent of the population, which could vary between life stages and over time (Vercken et al. 2011). Regardless, when a local population is suppressed below the Allee threshold, extinction becomes increasingly probable. Thus, while Allee effects are the bane of conservation biologists (Courchamp et al. 2008), they can be a benefit in nonnative species management (Tobin et al. 2011). Species subject to strong Allee effects are likely to be more amenable to eradication than species not governed by Allee dynamics or by only weak Allee effects (Liebhold and Tobin 2008). Moreover, Allee effects can affect the rate of spread of invading organisms (Lewis and Kareiva 1993, Taylor et al. 2004, Johnson et al. 2006, Tobin et al. 2007). Programs designed to reduce spread rates are thus more likely to be successful against species subject to Allee dynamics (Sharov and Liebhold 1998, Liebhold et al. 2007). While Allee effects may reduce the final treatment costs in eradication, posttreatment surveillance costs will usually be incurred to demonstrate that eradication has been achieved.

Coupling population theory with a mechanistic understanding of diverse intervention technologies can improve the quality of decisions related to the eradication of nonnative insect species, the cost effective selection and integration of tactics, and the likelihood of success. In this review, we identify and summarize individual tactics that have been or could be used effectively against target pests, and highlight the relevance of Allee dynamics to eradication programs. Where specific case studies related to eradication are limited, we have drawn on relevant examples of tactics used in integrated pest management (IPM) programs, which may also be potentially suitable for use in eradication programs. We then consider the integration of two tactics (for simplicity) within the context of Allee dynamics, and how combinations of tactics can affect the prospect of successful eradication.

Single Tactics

Delimitation Technologies. The ability to efficiently detect and delineate incipient, low-density populations of unwanted organisms is often a key aspect of successful eradication programs (Rejmánek and Pitcairn 2002, Brockerhoff et al. 2010). Traps baited with attractants such as pheromones or host plant volatiles are frequently used in eradication programs, as well as pest management efforts (El-Sayed 2011). Examples include the use of pheromone-baited traps to detect populations of lepidopteran species including European and Asian strains of *L. dispar* in North America (Tobin and Blackburn 2007), and *Orgyia thyellina* Butler (Lepidoptera: Lymantriidae) (Hosking 2003) and *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae) in New Zealand (El-Sayed et al. 2005). Traps baited with pheromone or host plant volatiles have also been widely used to detect or monitor scolytinid bark and ambrosia beetles (Moeck 1970; Borden 1989, 1997). Trap logs or trees that produce attractive volatiles have proved useful in combination with or in the absence of pheromones (Samways 1987; Bakke 1989; McCullough et al. 2009a, b; Smith et al. 2009).

Insecticides. Insecticides can be delivered to an unwanted insect population through a variety of mechanisms, including aerial or ground sprays, trunk injections or soil applications of systemic products, and lure and kill technologies. Historically, broad-spectrum insecticide sprays were widely used in insect eradications (Herms and McCullough 2011), but are rare today given concerns about drift, environmental contamination, exposure, and nontarget effects.

Advances in insecticide formulation and delivery systems can mitigate some risks, and relatively new products may be more acceptable for eradication programs or invasive pest management efforts than sprays of broad spectrum insecticides. Localized applications of insecticide products containing neonicotinoids, avermectin, or azadirachtin applied to ornamental trees via trunk or stem injections, for example, substantially reduce undesirable effects associated with cover sprays (Herms et al. 2009). While selective insecticides and biopesticides are generally preferred for operational programs (Hajek and Tobin 2010), they may be more expensive. Repeated applications may be needed to offset relatively short persistence of some products, such as *Bacillus thuringiensis* Berliner (Bacillales: Bacillaceae) (Garczynski and Siegel 2007). The *kurstaki* strain of *B. thuringiensis* continues to be widely used against *L. dispar* in both eradication and barrier zone management programs in North America (Hajek and Tobin 2010), and was used to successfully eradicate *O. thyellina* (Hosking 2003) and *Teia anartoides* (Lepidoptera: Lymantriidae) from Auckland, New Zealand (Suckling et al. 2007). Although public opposition to the aerial application of *B. thuringiensis* over urban areas can be considerable (Hosking 2003, Hajek and Tobin 2010), the long-term, nontarget impacts of this tactic are generally low (Sample et al. 1996, Glare and O'Callaghan 2000, Herms 2003, Gandhi and Herms 2010). In contrast, aerial applications of the growth regulator diflubenzuron have been shown to have broad-spectrum, persistent impacts on nontarget organisms that can cascade across trophic levels (Martinat et al. 1988, Eisler 1992, Butler et al. 1997). Other IGRs, juvenile hormone analogues, ecdysone agonists, and macrocyclic lactones (such as the spinosyns) are somewhat selective.

Some entomopathogen products such as the *L. dispar* nucleopolyhedrosis virus, commercially registered as Gypchek (Reardon et al. 1996), can be produced economically, and applied over large areas. Efficacy of entomopathogen products varies considerably and could be influenced by temperature, moisture, or other environmental conditions (Ignoffo 1992). Many are highly specific and present little risk to nontarget organisms (Hajek and Tobin 2010), while others, such as the fungal pathogen *Beauveria bassiana*, can affect a relatively broad range of insects (Goettel et al. 1990). Use of some entomopathogen products can also be limited by the need for in vivo production, which requires mass rearing facilities to produce sufficient quantities for application (Reardon et al. 1996). In addition, there are few examples of entomopathogens that effectively control phloem- or wood-boring insects.

Host Destruction. Removal of host plants can be used as a means to reduce populations and limit spread of nonnative pests (Hardee and Harris 2003, Cappaert et al. 2005, Smith et al. 2009). Success of such efforts can depend on the scale, location, economic sector affected, and the ability of regulatory officials to enforce compliance. Early efforts to contain or eradicate *L. dispar* populations in the northeastern United States, for example, included felling and burning infested sections of forests (Herms and McCullough 2011). Destruction of thousands of apple trees across 790 km^2 in Brazil beginning in the late 1990s was credited with substantially reducing populations of *C. pomonella.* This effort received major support from apple growers and the Ministry of Agriculture, with both groups allocating personnel, funds, and equipment to the campaign (Kovaleski and Mumford 2007). In Michigan and Ohio, localized populations of *A. tsugae* became established when infested nursery trees were planted in residential areas, and trees known to be infested were destroyed. Planted and naturally occurring hemlocks in the vicinity of the infested plantings were either destroyed or treated with systemic insecticides over a 3-yr period (Kean et al. 2012). These successful eradication projects affected relatively few landowners and nursery owners, who were generally cooperative with regulatory officials (D.A.H. and D.G.M., unpublished data).

Large-scale projects that encompass host tree destruction, however, frequently engender controversy, and logistical arrangements can be costly and complex, although they have frequently formed a major tactic during eradication programs (Kean et al. 2012). There has often been a role for compensation payments (cash or in kind) in host destruction schemes, that is important for acceptance in some cases. Destruction of infested spruce trees in a Nova Scotia park for *Tetropium fuscum* (F.) (Coleoptera: Cerambycidae) eradication sparked considerable public protest for the loss of amenity value (Henry et al. 2005). Ash tree destruction, designed to ensure infested but asymptomatic trees were eliminated, was used in several projects designed to eradicate localized infestations of *A. planipennis* beginning in 2003 (Herms and McCullough 2011). Although most ash trees in any given project area were relatively small (McCullough and Siegert 2007, Siegert et al. 2010), thousands of trees were removed from forests, riverbanks, residential and urban areas (Cappaert et al. 2005, Stone et al. 2005, Poland and McCullough 2006). Efforts to eradicate *Anoplophora glabripennis* Motschulsky (Coleoptera: Cerambycidae) in the United States and Canada have similarly required destruction of infested or potentially infested host trees (Smith et al. 2009). Most of these programs were centered in urban and residential areas, and sometimes eliminated a substantial portion of the canopy. Public perception and acceptance of the host destruction components in the *A. planipennis* and *A. glabripennis* programs have ranged from supportive to vehement opposition (Smith et al. 2009).

Semiochemical Approaches. One semiochemical approach used for numerous lepidopteran pests is mating disruption, in which large quantities of female moth synthetic sex pheromone are released to disrupt the ability of males to locate calling females (Cardé and Minks 1995, Witzgall et al. 2010). Continual exposure to high levels of pheromones may shut down male searching behavior because of habituation, or males may be simply unable to locate mates, resulting in decreased populations or local extirpation (Yamanaka 2007). This tactic, which has negligible effects on nontarget organisms or the environment, has been effectively used in *L. dispar* eradication programs (Dreistadt and Weber 1989, USDA Forest Service 2010), and is also the preferred control tactic in *L. dispar* barrier zone management (Tobin and Blackburn 2007). Mating disruption has also been evaluated for indigenous lepidopteran defoliators including *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), *Dasychira plagiata* (Walker) (Lepidoptera: Lymantriidae), and *Orgyia pseudotsugata* (McDunnough) (Lepidoptera: Lymantriidae) (El-Sayed

2011), and wood-borers including *Synanthedon* spp. (Lepidoptera: Sesiidae) (Pfieffer et al. 1991, Matsumoto et al. 2007, Leskey et al. 2009). This technology may have utility in eradication programs should these pests become established outside their native range.

Other semiochemical-based approaches to pest management include mass trapping (Schlyter et al. 2003, El-Sayed et al. 2006) and lure and kill (Foster and Harris 1997, El-Sayed et al. 2009). Both tactics involve the attraction and subsequent removal of individuals from the population. This approach has been used for suppression of native (Silverstein 1981, Borden 1989) and nonnative bark beetles (McCullough and Sadof 1998), and in eradication efforts against *L. dispar* (USDA Forest Service 2010) and *Anthonomous grandis* Boheman (Coleoptera: Curcurlionidae) (El-Sayed et al. 2006). Unfortunately, while phloem- and wood-boring beetles comprise a substantial and increasingly large proportion of new invaders (Aukema et al. 2010), many do not use long range pheromones (Hardie and Minks 1999), including prominent invaders such as *Agrilus planipennis* and *Anoplophora glabripennis* (Cappaert et al. 2005, Smith et al. 2009). Moreover, while mass trapping has the potential to eradicate or suppress low-density, isolated pest populations (El-Sayed et al. 2006, Yamanaka 2007), it can be logistically challenging to use effectively because of low trap efficiency, trap saturation, the lack of trap selectivity, and the need for high trap density and hence high cost. In some cases, pheromones used as kairomones by predators or parasitoids of the target pest have the potential to interfere with biological control if large numbers of natural enemies are also trapped (Herms et al. 1991, Dahlsten et al. 2004).

Semiochemical-based tactics can also be used to disrupt pheromone-based, mass attack behavior of certain bark beetle species that would normally facilitate successful colonization of live host trees (Borden 1989, 1997; Raffa 2001, Boone et al. 2011). For example, at least 40 attacks per square meter of bark surface were required for *Dendroctonus ponderosae* Hopkins (Coleoptera: Curcurlionidae) to overcome tree defenses (Raffa and Berryman 1983). The inability of low-density, founder populations to successfully mass attack hosts in a new environment may explain why *Ips typographus* (L.) (Coleoptera: Curculionidae) has failed to establish outside its native range (Grégoire et al. 2006), despite frequent introductions (Brockerhoff et al. 2006). Potential also exists for semiochemicals to be used in push-pull strategies (Cook et al. 2007), where disruptants or repellant compounds 'push' beetles away from susceptible hosts and 'pull' them toward baited traps or trap trees. Such an approach successfully protected a rare stand of Torrey Pines from *Ips paraconfusus* bark beetles in California (Shea and Neustein 1995) and was used effectively in some stands to deter attack by *D. ponderosae* (Borden et al. 2006).

Sterile Insect Technique. The sterile insect technique (SIT) (Knipling 1959, 1979) has been used in several insect eradication programs and has no adverse effects on nontarget organisms or the environment (Vreysen et al. 2007). Sterility results from the induction of dominant lethal mutations in irradiated sperm or eggs. In operational programs, sterilized insects are released en masse, with the goal of reducing production of viable eggs by the pest. This tactic, however, is density dependent because it is more effective in low-density populations than higher density ones (Knipling et al. 1979) and is therefore most effective at the start or end of a response when the target population is small. Other potential barriers include the ability of sterilized insects to outcompete wild insects for mates, the need to mass rear viable individuals, and the capability to transport sterilized insects of high fitness from rearing facilities to the target population.

SIT played a major role in the successful eradication of *Cochliomyia hominivorax* (Coquerel) (Diptera: Calliphoridae) in the United States, Mexico, and Latin America (Wyss 2000), and has been used against tephritid fruit flies in numerous locations (Hendrichs 2002, Klassen and Curtis 2005). This tactic was also used against *Euscepes postfasciatus* (Fairmaire) (Coleoptera: Curculionidae) in Japan (Moriya and Miyatake 2001). Two large, area-wide SIT programs were used successfully to eradicate *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae) in California and *Cydia pomonella* L. (Lepidoptera: Tortricidae) in British Columbia (Bloem et al. 2007). Smaller programs targeting other Lepidoptera have also been undertaken (Suckling et al. 2007, Vreysen et al. 2007). Public opposition to aerial insecticide applications to eradicate *C. capitata* outbreaks in California and Florida led to the year-round, prophylactic release of sterile flies in these areas beginning in 1994 (Enkerlin 2005). Recent interviews with stakeholders in New Zealand asked for their preference among three treatments tactics used in eradication; the greatest preference was for the sterile insect technique followed by aerial applications of pheromone and lastly aerial applications of *B. thuringiensis* (Gamble et al. 2010).

Biological Control. Classical biological control, the deliberate introduction of nonnative natural enemies of a pest, is rarely compatible with the goal of eradication, in part because approval for release of new agents generally involves relatively long time frames. This process can be especially protracted when foreign exploration, importation, and host specificity studies to avoid detrimental effects to nontarget species are required. However, where it is possible to predict threats from rapid geographic expansion and risk assessment, initiating steps to identify and evaluate natural enemies for potential biocontrol efforts may be prudent as it may be possible to gain prior approval, especially where the biological control agent has been efficacious in previously invaded areas.

Natural enemies can presumably mediate Allee effects in populations of their prey (Gascoigne and Lipcius 2004, Gregory and Courchamp 2010, McLellan et al. 2010), which could have application in eradication programs, but empirical examples are rare. Introduction of the generalist parasitoid *Compsilura concinnata* (Meigen) (Diptera: Tachinidae) into North America

Table 1. Potential outcomes when combining tactics (A and B) hypothesized to be density-dependent (DD) or density-independent (DI) in insect eradication compared with single tactics alone

Combination type	Quality of interaction	Examples
Synergistic	AB > A + B	1. Inundative biocontrol (DD) + SIT (DD) 2. Mating disruption (DD) + SIT (DD) 3. Transgenic host plants (DI) + SIT (DD) 4. Insecticides (DI) + mass trapping (DD) 5. Insecticides (DI) + mating disruption (DD) 6. Mating disruption (DD) + lure and kill (DD) (when using different semiochemicals)
Additive	AB = A + B	1. Insecticides (DI) + host destruction (DI) 2. Selective insecticides (DI) + innundative biocontrol (DI) 3. Two insecticides targeting different life stages (DI)
Redundant	AB = A or B	1. Broad-spectrum insecticide (DI) + innundative biocontrol (DD) 2. Broad-spectrum insecticide (DI) followed by selective insecticide (DI) 3. Mating disruption (DD) + lure and kill (DD) (same semiochemical)
Antagonistic	AB < A + B	1. SIT (DD) and mass trapping (DD) (trap saturation) 2. Broad-spectrum insecticides (DI) + biocontrol (DD) (pest resurgence through natural enemy mortality)

for *L. dispar* control has been credited with causing local extinctions and dramatically reducing remaining populations of the invasive *Euproctis chrysorrhoea* (L.) (Lepidoptera: Lymantriidae) in areas of the northeastern United States (Elkinton et al. 2006). Unfortunately, this parasitoid also attacks many nontarget Lepidoptera species in North America (Parry 2009), and may be responsible for major declines in native saturniid populations (Boettner et al. 2000). Release of the parasitoid *Bessa remota* (Aldrich) (Diptera: Tachinidae) is believed to have caused the extirpation of its target host, *Levuana iridescens* Betheune-Baker (Lepidoptera: Zygaenidae), in Fiji (Hoddle 2006). Inundative release of native or previously established parasitoids or predators could also presumably act to suppress or limit spread of a localized pest population. The use of natural enemies for biocontrol, however, is more often a strategy for long-term management of nonnative species and restoration of ecosystems degraded by invasive species (Hoddle 2004). Although such releases have rarely played a role in eradication efforts, biological control could potentially act synergistically in combination with other tactics such as egg parasitism with releases of sterile females (Cossentine and Jensen 2000, Carpenter et al. 2004).

Multiple Tactic Combinations

When developing an eradication strategy for an insect pest, it could be tempting to simply deploy all available tactics as rapidly as possible within financial constraints. Indeed, a primary challenge in eradication is the availability of sufficient funds to achieve success (Brockerhoff et al. 2010, Kean et al. 2012). Potential interactions between tactics used either simultaneously or sequentially can be positive or negative (Knipling 1979, Barclay 1992) and warrant consideration when an eradication strategy is developed. Understanding and incorporating Allee effects (Fig. 1A; Allee 1938, Stephens et al. 1999) into operational programs can strongly influence costs and success of eradication efforts. Because there could be many causes of an Allee effect (Courchamp et al. 2008), multiple control tactics can be combined to exploit different causes of an Allee effect or to act synergistically on one cause of an Allee effect. Indeed, recent work has suggested that multiple causes of an Allee effect are not necessarily additive, but instead may interact in a complex way (Berec et al. 2007). Thus, identifying the most efficient combinations of tactics to use against populations subject to Allee dynamics can facilitate successful eradication. Regardless of the tactics used, both the efficiency and potential success of eradication can be enhanced by considering the interactions between or among tactics. We consider the following categories of tactic interactions: synergistic, additive, redundant, and antagonistic (Table 1; Fig. 1).

Synergystic Interaction. Combining two (or more) tactics to generate a synergistic interaction is ideal, regardless of whether Allee dynamics are exploited (Fig. 1B–C) or not (Fig. 1D) (Barclay and Li 1991). Several options for combining treatment tactics to specifically enhance or exploit an Allee effect are listed in Table 1. Synergistic effects could be achieved by combining a density-independent tactic that reduces pest density with a density-dependent tactic that increases the Allee threshold (Fig. 1B; Berec et al. 2007). This interaction is particularly relevant for eradication because it can enhance program effectiveness by increasing the benefit-to-cost ratio. For example, mating disruption with pheromone application can be an effective, density-dependent tactic at low population densities, but is generally ineffective at higher densities because of visual mate location (Roelofs et al. 1970, Cardé and Minks 1995, Sharov et al. 2002, Yamanaka 2007). Insecticide applications or host removal are both density-independent tactics that can be used at higher pest densities, but removing a sufficient number of individuals to drive a population below an Allee threshold may not be cost-effective or practical. Decreasing pest density with insecticides followed by pheromone applications to disrupt mating of surviving adults can act synergistically by reducing the overall population density and concurrently increasing the Allee threshold (Fig. 1B).

Other desirable combinations include two density-dependent tactics that jointly increase the Allee threshold without affecting population density (Fig. 1C), or two density-independent tactics that do not alter the Allee threshold but jointly decrease the population density below an Allee threshold (Fig. 1D). Examples of successful combination of tactics include inundative release of *Trichogramma* egg parasitoids followed by SIT, which acted synergistically to reduce populations of *C. pomonella* (Bleom et al. 1998, Cossentine and Jensen 2000). Carpenter et al. (2004) determined that the combined effect of using both tactics exceeded the effects of deploying each tactic in isolation because the sterile eggs laid by irradiated moths enhanced the parasitoid population. A combination of mating disruption and SIT, two density-dependent tactics, could also be synergistic (Bloem et al. 2007); while no individuals are killed directly, the increased Allee threshold may lead to a decline in the pest population (Fig. 1C). An area-wide eradication program against the cotton pest *P. gossypiella* incorporated mating disruption, insecticides and SIT, a combination that acted synergistically with transgenic cotton (containing *B. thuringiensis*) (Simmons et al. 2007). Releasing parasitoids to attack larval stages of the pest combined with SIT, which acts on the adults could also be synergistic (Barclay and Li 1991). Additional potentially synergistic combinations can be postulated, such as release of a sex pheromone to disrupt mating or achieve mass trapping, coupled with a female attractant-based lure and kill system. At present, most mass trapping systems target males.

Additive Interaction. An additive interaction involves two treatment tactics that act neither synergistically or antagonistically. Two density independent tactics, such as two insecticides that each target a different life stage, likely act in an additive manner because each reduces the population density independently of each other. Although this is a suitable combination of tactics for eradication because the continuous reduction of population density could still render a population below an Allee threshold (Fig. 1D), it requires more effort than synergistic combinations of tactics. Depending upon the circumstance, tactics that generally interact in an additive manner could interact synergistically; for example, application of a selective insecticide application could be synergistic with biological control if the biological control agent displayed nonrandom searching behavior and specifically sought out residual members of the population that were not targeted by the insecticide (Barclay 1987, Barclay and Chao 1991).

Redundant Interaction. To be cost-effective, it is also important to avoid combining tactics that are redundant, where tactics overlap in effect, or supersede each other (Table 1). Examples include the concurrent use of a broad-spectrum and a selective insecticide, two density-independent tactics, or the concurrent use of mating disruption and lure-and-kill, two density-dependent tactics. Although in practice these types of tactic combinations are rarely, if ever, used, it is important to highlight them in our efforts to illustrate the utility of synergistic interactions.

Antagonostic Interaction. Regardless of the tactics used, multiple tactics should not, in principle, interact in an antagonistic manner (Table 1; Fig. 1E). Combinations of tactics can have antagonistic consequences, which clearly would be counterproductive to eradication efforts. For example, if an insecticide application killed predatory insects that would otherwise prey upon any residual pest population, the combination could be considered antagonistic and potentially negate the effect of a predator-driven Allee effect (Fig. 1E; Gascoigne and Lipcius 2004, Gregory and Courchamp 2010, McLellan et al. 2010). A simultaneous combination of SIT and mass trapping could also be counterproductive. Sterile insects would be removed from the population while the efficacy of mass trapping would be reduced if traps were saturated by large numbers of sterile insects. Pest suppression tactics can also interfere with surveillance programs to detect, delimit, or monitor the pest population. Pheromone-baited traps, for example, can be silenced by widespread application of pheromone applied for mating disruption (Thorpe et al. 2007), a critical concern when trap catch data are needed for decision-making (Tobin and Blackburn 2007). While it is also possible that these traps are not silenced through mating disruption but rather indicate treatment efficacy, poorly conceived combinations are still counterproductive and the possible interactions need to be examined carefully. In the case where mass baiting to detect fruit flies also masks the presence of traps to an extent, it could be worthwhile to deploy traps because they can still provide relatively cheap information compared with rearing from randomly sampled host fruits.

In many cases, efficacy of different tactics varies with pest density and combining tactics requires consideration of the spatial distribution of the invasive pest population. In particular, tactics that are density-independent could be used broadly across a pest's spatial distribution, while density-dependent tactics may be effective only in specific areas. To further optimize an eradication strategy, culling, host removal, and other density-independent tactics could be used initially against high density populations within the infested area, followed by implementation of density-dependent tactics, such as mating disruption (Fig. 2).

However, insecticide application combined with biocontrol could function in an additive or possibly synergist manner if, for example, a parasitoid displayed nonrandom searching behavior (Barclay 1987, Barclay and Li 1991). Regardless of the tactics used, both the efficiency and potential success of eradication can be enhanced by considering the interactions between or among tactics.

We conclude that despite the importance of eradication as a management tool for averting the long-term economic, social and environmental costs of invasive species, fundamental theoretical underpinnings of eradication strategies are not well-developed. The

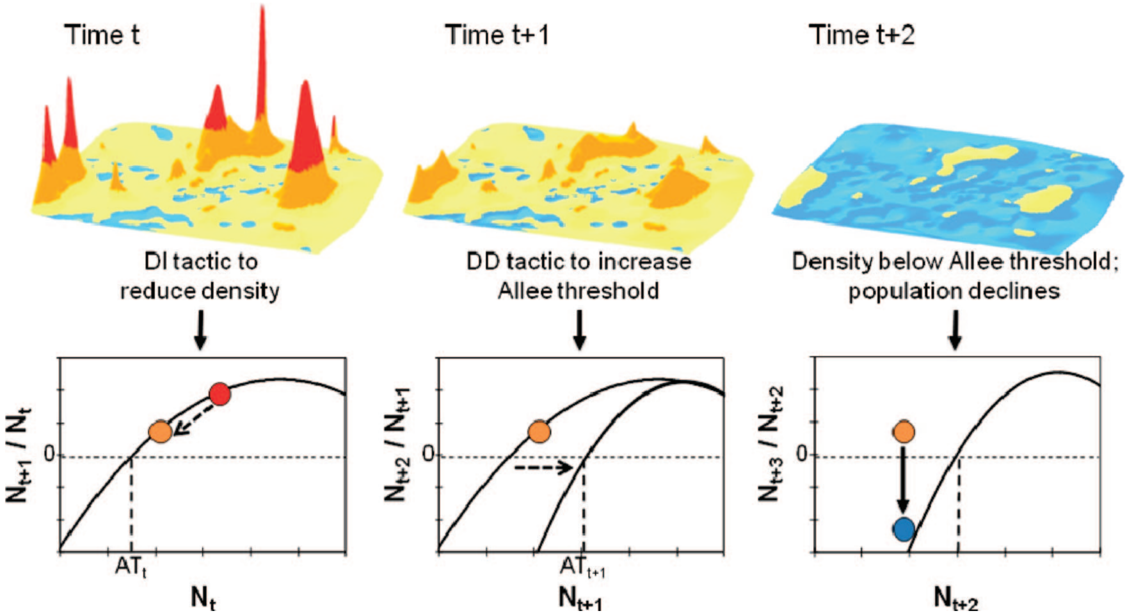

Fig. 2. Combining treatment tactics in space and time. A spatial representation of an insect population, from low (blue) to high (red) densities at time t. High density areas are treated at time t using a density-independent tactic, such as a pesticide, resulting in a decrease in density. At time t + 1, the remaining population is managed using a density-dependent tactic, such as mating disruption, to increase the Allee threshold. At time t + 2, the remaining population density is below the Allee threshold, and the population declines toward extinction.

number of eradication programs has risen steadily as globalization has increased, and hundreds of insect eradication programs have now been documented (Kean et al. 2012). Critics of insect eradication have suggested that such programs seldom succeed (e.g., Myers et al. 2000), perhaps because of a number of high-profile eradication failures. There is evidence, however, that many eradication efforts have indeed been successful, most often at a state or regional rather than continental scales (Kean et al. 2012), although there are prominent examples of successful wide-scale eradiction programs (Klassen 1989, Wyss 2000, Hardee and Harris 2003). It seems clear that insect eradication is more feasible and cost-effective than has been generally recognized (Brockerhoff et al. 2010, Kean et al. 2012).

Advances in population biology have practical implications for eradication programs in the same way that they influence programs designed to conserve and protect rare species from extinction (Courchamp et al. 2008). While the goals are different, the same principles constrain low-density populations of an invasive pest or an endangered species. Understanding and exploiting Allee effects that may facilitate eradication is especially important because resources need not be expended to locate and kill every individual of the target pest (Liebhold and Tobin 2008). Once populations are suppressed below the Allee threshold, extinction is likely to occur without further intervention. Understanding interactions when tactics are combined (Table 1) can reveal desirable and underperforming combinations. Desirable combinations will facilitate efforts to suppress or eradicate pest populations, particularly if synergistic interactions can be achieved and exploited. Ideally, the likely effect of potential tactics used alone and in combinations should be considered early in the development of an eradication strategy and potentially synergistic combinations should be used when and where possible.

We have highlighted how eradication tactics can be combined in strategic and sometimes counter-intuitive ways to simultaneously manipulate pest density and Allee dynamics to achieve eradication. We recognize, however, that eradication of some insect groups is currently more feasible than others. Many lepidopteran defoliators, for example, respond to long-range sex pheromones and remain exposed for much of their life cycle to natural enemies, microbial insecticides or entomopathogens. Unfortunately, there are clear knowledge gaps and limited means to effectively detect, trap or control other groups including sap-feeders and many phloem- and wood-boring species. New strategies and technology to identify and exploit Allee thresholds and synergistic combinations of control tactics are especially needed to deal with these invaders, which comprise a substantial portion of the damaging invasive pests in North America (Langor et al. 2009, Aukema et al. 2010). Benefits associated with implementing control tactics alone or in combinations will need to be evaluated to justify program costs (Barclay and Li 1991), but the prospect of increasing the success of eradication programs is a strong incentive. A greater appreciation and consideration of potential interactions between and among treatments that synergistically exploit Allee dynamics could enhance the success and reduce costs of eradication programs.

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