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Eradication of Invading Insect Populations: From Concepts to Applications

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Abstract

Eradication is the deliberate elimination of a species from an area. Given that international quarantine measures can never be 100% effective, surveillance for newly arrived populations of nonnative species coupled with their eradication represents an important strategy for excluding potentially damaging insect species. Historically, eradication efforts have not always been successful and have sometimes been met with public opposition.

But new developments in our understanding of the dynamics of low-density populations, the availability of highly effective treatment tactics, and bioeconomic analyses of eradication strategies offer new opportunities for developing more effective surveillance and eradication programs. A key component that connects these new developments is the harnessing of Allee effects, which naturally promote localized species extinction. Here we review these developments and suggest how research might enhance eradication strategies.

INTRODUCTION

Biological invasions, the movement and establishment of species outside their native ranges, are occurring in large numbers around the world, mostly as unwelcomed by-products of international trade and travel (77). The Insecta, the world's most diverse taxon, not surprisingly comprise the majority of animal invasions worldwide. Invasive insect pests can profoundly affect agricultural productivity, forest resources, human health, and a wide range of natural ecosystem services (15, 103, 106).

Biological invasions comprise four conceptual stages: arrival, establishment, spread, and impact (69). Invasions begin with the arrival of a nonnative species to a previously uninhabited area. Most arriving populations vanish without intervention; however, some succeed in growing to self-sustaining levels, thereby considered established, and initiate spread into adjacent regions. Although most nonnative organisms that establish in new habitats are benign and rarely noticed (5), some cause economic and ecological impacts that exceed those in their native habitat.

To prevent the arrival of nonnative species, governments may impose quarantine measures to restrict the movement of certain goods, or require that imported material receive treatments such as fumigation (52). Cargo and passengers arriving at ports of entry or border crossings may be subject to inspection to prevent accidental pest introductions. Despite the best efforts of governments, these measures can never block the arrival of all nonnative insect species; continual increases in global trade and passenger movement may overwhelm mitigation measures.

Here we address the roles of surveillance and eradication in the management of recently established, nonnative insects. Eradication represents the deliberate elimination of an invading species from an area (67) and is facilitated by early detection of invasion events. Surveillance systems to detect newly established populations can involve area-wide deployment of traps, visual searches, and reports by concerned citizens (54). Eradication is typically not attempted for most newly detected insect populations because they are not detected early enough for eradication to be practical, treatments for accomplishing eradication are not available, or the costs of eradication outweigh the species' anticipated impacts. For some species, however, eradication can be sensible if it prevents future extensive direct and indirect impacts (84, 100).

Eradication can be controversial. A large proportion of initial establishments occur in urban or suburban areas where inter- and intracountry movement of goods and people first occurs (23). Consequently, eradication programs are often conducted in residential areas, where insecticide use, aerial applications, removal of host plants, and other treatments may evoke a negative response among residents (74, 81). Despite hundreds of successful insect eradication projects (57, 121), skepticism of government programs and presumed failure are common beliefs (22, 80). Some scientists have publically questioned whether eradication is technically feasible (21, 25, 89). In part, skepticism reflects the historical lack of scientific theory behind eradication, the scarcity of research on the population biology of insect eradication since the early work by Knipling (59), and the seemingly impossible feat of eliminating every individual in a population.

Establishment:

reproduction and growth of a nonnative population to a level at which extinction is no longer likely

Prevention:

operation of a biosecurity system to preclude new organism incursions, through quarantine and inspection

Treatment: a method contributing to eradication by either culling individuals or suppressing mating

Surveillance:

post-border survey for the presence of nonnative populations

Eradication: the deliberate extinction of a species from a given region

Pest Risk

Assessment:

assessment of the potential of a species to invade and create impacts

Several previous reviews have addressed insect eradication (79, 80, 89, 92). These earlier works generally focused on selected case studies, and all preceded modern developments in bioeconomics, surveillance, eradication technologies, and the population biology of eradication. Recent advances in our understanding of the dynamics of sparse populations are essential for developing successful and economically efficient strategies for eradicating nonnative insect pests. Contemporary work on bioeconomics has identified the crucial role of economic considerations in the selection of surveillance and eradication strategies. Here we review past insect eradication efforts, describe advances in theory and technology, and identify key research needs to further progress the science of eradication.

HISTORICAL ERADICATIONS

The history of insect eradication programs arguably began in 1890 with an expensive and ultimately unsuccessful effort by Massachusetts authorities to eliminate the gypsy moth (*Lymantria dispar*) from the Boston area (28). Since then, there have been at least 750 organized attempts to eradicate insect populations (57). Eradication may be considered for the most economically damaging species but may be practical only for a small subset of them. For example, at least 3,540 nonnative insect species are established in North America (132), but only 63 species have been targeted for eradication (57). Insect eradication has been attempted in at least 92 countries worldwide, but most programs have occurred in North America (48%), Oceania (20%), and Europe (16%) (57, 121).

Of the 672 arthropod eradication programs analyzed by Tobin et al. (121), 395, 110, and 167 were considered successful, failures, or of unknown outcome, respectively. A more recent query of the GERDA database (57) yielded totals of 508, 120, and 132 in these same categories. Such data should be treated with caution, however, because there may be substantial biases in reporting: Successes may be more widely reported than failures, and many small-scale programs may go unreported. The success rate for certain groups, such as tephritid fruit flies, may be particularly high as a consequence of a variety of factors, including the availability of effective surveillance and treatment technologies (114).

The number of insect eradication programs implemented per year has increased dramatically over time (121), perhaps because scientists have developed more effective and efficient tools for detecting and eradicating certain taxa such as Lepidoptera and tephritids (**Table 1**). Eradication of these taxa has become almost routine in some regions. For example, more than 200 programs have targeted 17 species of fruit flies in 31 countries, using male annihilation, the sterile insect technique (SIT), and other methods (114). These programs are generally successful, with no evidence of long-term establishment in most cases examined (for a counterargument, see 87, but also see 42).

Pluess et al. (90, 91) analyzed 136 eradication programs targeting plant pests and weeds and found that the geographic area of the focal infestation significantly affected eradication success. Tobin et al. (121) evaluated 672 programs targeting 130 arthropod species and also identified a negative association between success rate and the size of the area infested. But their analysis indicated that detectability of the target pest was one of the most critical factors associated with eradication success.

Over 80% of the insect eradication attempts recorded by Tobin et al. (121) collectively targeted species of Diptera (41%), Coleoptera (21%), and Lepidoptera (20%). Eradications of Diptera (primarily fruit flies) and Lepidoptera (largely gypsy moths) have had a high success rate undoubtedly because effective and cost-efficient semiochemical lures facilitate early detection and delimitation and because effective treatment tactics such as SIT are available (29, 30, 58). In contrast, the lower

Table 1 Examples of typical characteristics of eradication projects targeting various insect taxa

Taxon	Numbers of programs ^a	Surveillance methods	Treatment tactics	Example species (reference)
Fruit flies (Tephritidae)	213	Food attractant traps, parapheromone traps	Mass trapping, SIT, insecticidal baits, host destruction	Oriental fruit fly (<i>Bactrocera dorsalis</i> complex including <i>Bactrocera papayae</i>) (108) Melon fly (<i>Bactrocera cucurbitae</i>) (60)
Moths (Lepidoptera)	135	Pheromone traps	Microbial pesticides, mating disruption, SIT, host destruction, mass trapping	Painted apple moth (<i>Teia anartoides</i>) (111) Gypsy moth (<i>Lymantria dispar</i>) (44)
Mosquitoes (Culicidae)	64	Larval/pupal visual survey, ovitraps, host attractant traps, light traps	Chemical insecticide treatment of water, SIT	Yellowfever mosquito (<i>Aedes aegypti</i>) (128) Southern saltmarsh mosquito (<i>Aedes camptorhynchus</i>) (55)
Ants (Formicidae)	54	Food attractant traps, visual surveys	Chemical insecticide baits, direct chemical insecticide application	Bigheaded ant (<i>Pheidole megacephala</i>) (50) Argentine ant (<i>Linepithema humile</i>) (102)
Longhorned beetles (Cerambycidae)	43	Visual survey for infested trees, host attractant traps	Host destruction, systemic insecticides	Asian longhorned beetle (<i>Anoplophora glabripennis</i>) (43) Citrus longhorned beetle (<i>Anoplophora chinensis</i>) (125)

^a Accessed from GERDA (57) on February 25, 2015.

Abbreviation: SIT, sterile insect technique.

success rate for Coleoptera reflects the diversity of taxa targeted for eradication and the lack of effective surveillance tools.

SURVEILLANCE

Surveillance surveys are conducted to detect the presence of newly founded populations that are candidates for eradication. Following detection, delimitation surveillance is used to confirm the persistence of the population, delimit its spatial extent, and verify eradication success (**Figure 1**).

Effective surveillance tools (e.g., traps) are crucial for detecting and delimiting newly established populations when they are still small, thereby minimizing the cost of eradication as well as the probability of failure. Many Lepidoptera use long-range sex pheromones, and traps baited with them are generally highly effective tools for detecting and delimiting populations (4, 113). When such pheromones are used as attractants for surveillance, it is virtually impossible for reproductively viable populations to persist for long periods at subdetectable levels if the traps are spaced at distances near males' typical dispersal range; if they are unable to find traps, they will be unable to find mates (122).

Information about chemical communication greatly facilitates surveillance efforts, but such information is not always available prior to the detection of a potentially damaging pest. Effective lures and trapping systems can sometimes be developed in a relatively short time frame, but if attractants cannot be identified and synthesized quickly, there may be alternatives. For example,

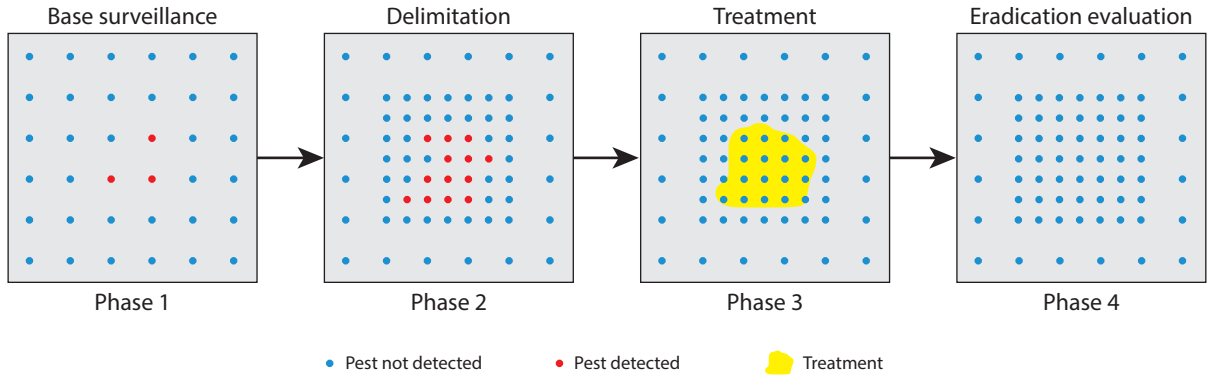


Figure 1

Conceptual surveillance strategy for eradication: base surveillance, delimitation, confirmation of treatment effectiveness, and verification of eradication.

in programs to eradicate the white-spotted tussock moth (*Orgyia thyellina*) and the painted apple moth (*Teia anartoides*) from New Zealand, delimitation was accomplished using traps baited with live females (51, 111).

For species that do not produce long-range sex pheromones or aggregation pheromones, detection and delimitation must rely on less powerful attractants, such as host compounds, or on visual surveys (16, 18). For example, a program to eradicate the Asian longhorned beetle (*Anoplophora glabripennis*) from Chicago (1998–2003) depended on visual surveys by tree climbers and ground crews to identify infested hosts. This process was cumbersome, expensive, and relatively ineffective, especially when trees were newly infested with few signs or symptoms. Consequently, treatments consisting of host removal and application of systemic insecticides could not target trees precisely but instead were applied to all potential host trees within 200 to 800 m of every tree previously determined to be infested (43). Despite these difficulties, the Asian longhorned beetle was ultimately eradicated from Chicago.

When effective tools are available, questions arise about how to best design a surveillance system to optimize detection of newly founded populations small enough to be feasibly eradicated. For example, traps might be spatially deployed in a variety of patterns, from uniform to random. The importance of the spatial arrangement depends on the sensitivity of the trap as well as the budget available for trapping; for example, dynamic trapping arrangements (e.g., rotating grids) can increase the efficiency of surveillance if the traps are sparse relative to the size of target populations (8). At a landscape scale, determining the optimal density of traps requires balancing surveillance costs with costs of eradication (**Figure 2**). Heavy investment in surveillance (i.e., high trap density) increases the likelihood that newly established populations will be detected early, which reduces eradication costs. In contrast, deploying fewer traps is less costly initially but delays detection, resulting in larger populations that are more expensive to eradicate (12, 31, 32, 76).

In heterogeneous landscapes, the optimal intensity of surveillance is affected by regional variation, with greater surveillance intensity preferred in regions with higher probabilities of arrival and establishment, higher costs of eradication, and lower surveillance costs (31, 32, 46). For example, intensive surveillance may be appropriate at ports near industrial areas at higher risk for arrival and establishment of certain nonnative insects (4, 94). Other invasive insects tend to establish relatively frequently in urban areas (23), where surveillance is typically less expensive

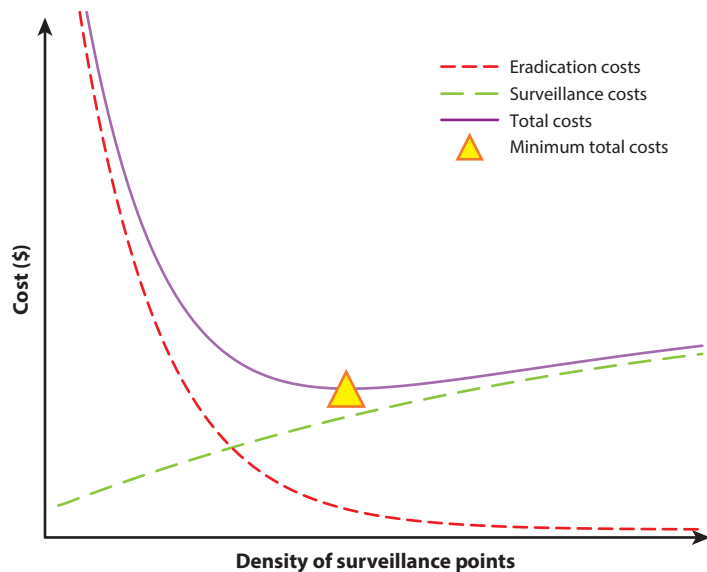


Figure 2

Composite and total costs of invasion as a function of surveillance intensity (density of surveillance points). Total costs are the sum of eradication costs and surveillance costs. Eradication costs decrease with increasing surveillance intensity because invasions are discovered earlier. Optimal surveillance intensity occurs where total costs are lowest (adapted with permission from Reference 32).

than in remote, difficult-to-access environments. Risk-based analyses typically focus more intense surveillance in urban areas and near ports, but some effort should also be allocated to regions with a lower probability of invasion (32).

The rate and method in which an organism spreads, whether through natural dispersal or anthropogenic transport, can affect the likelihood of early detection and delimitation. For example, transport of infested material can result in secondary populations establishing a considerable distance from the main infestation. These satellite populations can challenge eradication efforts, particularly when surveillance tools are relatively inefficient (48).

In addition to detecting and delimiting pest incursions, surveillance helps managers monitor the progress of eradication programs and evaluate success or failure. Demonstrating success is especially problematic because it can be difficult to determine whether a population lingers at subdetectable levels. Several statistical tests have been designed for this purpose. One approach relies only on sighting records, and was originally developed to analyze endangered populations and fossil records, for which survey efficacy is not known (97). These basic tests may be modified to take into account the rate of population decline (107), relative search effort (73), and the reliability of data (63, 118). Another approach, developed by veterinarians for determining whether a region is free from animal diseases (71), has been applied to insect eradications (26, 56). This method relies on estimates of survey tool sensitivity, which may be directly quantified for insect traps (101, 115, 123). It also requires the user to specify a minimum target population size for detection that should ideally correspond to any potential extinction threshold. An additional, Bayesian approach was developed for analyzing vertebrate eradications (93). These methods estimate the declining probability that a population is present at the end of an eradication program, allowing eradication to be declared successful once this falls below some predefined threshold. Alternatively,

Incursion: the post-border occurrence of a new nonnative population

the problem may be reframed in bioeconomic terms such that eradication is declared when the costs of continued monitoring exceed the expected costs of stopping too soon (96). This approach recognizes that the choice of survey and eradication investment is at least in part an economic decision, and the threshold should be reasonably informed by both biology and economics.

EXPLOITING ALLEE EFFECTS

Records of pest interceptions at ports of entry show that many more nonnative species arrive than establish and that the probability of establishment increases with the number of arriving individuals (17). The magnitude of propagule pressure is perhaps the most important determinant of establishment success (68, 105). Conservation biologists have long recognized the important role of stochasticity and Allee effects in the extinction of low-density populations (24, 62). Environmental and demographic stochasticity contribute to extinctions of invading populations and help explain why propagule pressure affects their establishment (27, 65).

The Allee effect, which is the positive relationship between individual fitness and either population size or density, can be a considerable constraint on the persistence of low-density populations (**Figure 3**) (24, 109). Inbreeding depression, reduced ability to overcome host defenses, and failure to saturate or repel natural enemies are among the many causes of Allee effects (7, 61). Perhaps the most ubiquitous cause in sexually reproducing species is failure to locate a mate. Males and females often have difficulty finding each other in low-density populations, even for species that utilize powerful sex pheromones (41).

At the population level, demographic Allee effects represent a decline in the per capita population growth rate as population density decreases. Weak Allee effects indicate a situation in which population growth rate declines with decreasing density but remains positive at all densities. Conversely, Allee effects are considered strong when population growth rate becomes negative at low densities. The latter situation gives rise to the Allee threshold, which is the minimum number of individuals (or density) that must be present to sustain a viable, reproducing population (24) (**Figure 3**).

Allee thresholds have profound implications for eradication programs because eliminating a population does not require killing every last individual. Instead, populations need only be reduced below the Allee threshold and extinction should proceed without further intervention (65, 67, 120) (**Figure 3**). However, the unpredictable rate and severity of stochastic effects coupled with uncertainty in estimating population parameters and size contribute to uncertainty in estimating Allee thresholds (9). Therefore, to ensure success, managers must be conservative in their choice of target population densities when implementing strategies to reduce populations below the Allee threshold. Understanding the role of Allee effects in eradication is also important because certain treatments can be used to intensify existing Allee effects, increase Allee thresholds, or create effects that previously did not exist (67, 120) (**Figure 3**). For example, Allee effects arising from mate-location failure can be strengthened by tactics such as mating disruption, male culling (either traps or lure-and-kill methods), and SIT (13, 67, 117, 131).

TREATMENT TECHNOLOGIES

For more than 125 years, development and adoption of new treatment tools have characterized the evolution of insect eradication. Initially these developments were driven by a need for greater efficiency [e.g., hand removal of gypsy moth eggs in the 1880s was replaced by successively more sophisticated tools, culminating in aerial application of biopesticides in the 1970s (28, 119)], but more new tools are needed to address shifting boundaries in social acceptability. Aerial application of broad-spectrum chemical insecticides was once commonplace but has now been replaced largely

Allee effect:

decreasing individual fitness with decreasing population size or density; if strong enough, Allee effects can drive populations to extinction

Interception:

detection of a nonnative organism at the border or transitional facility

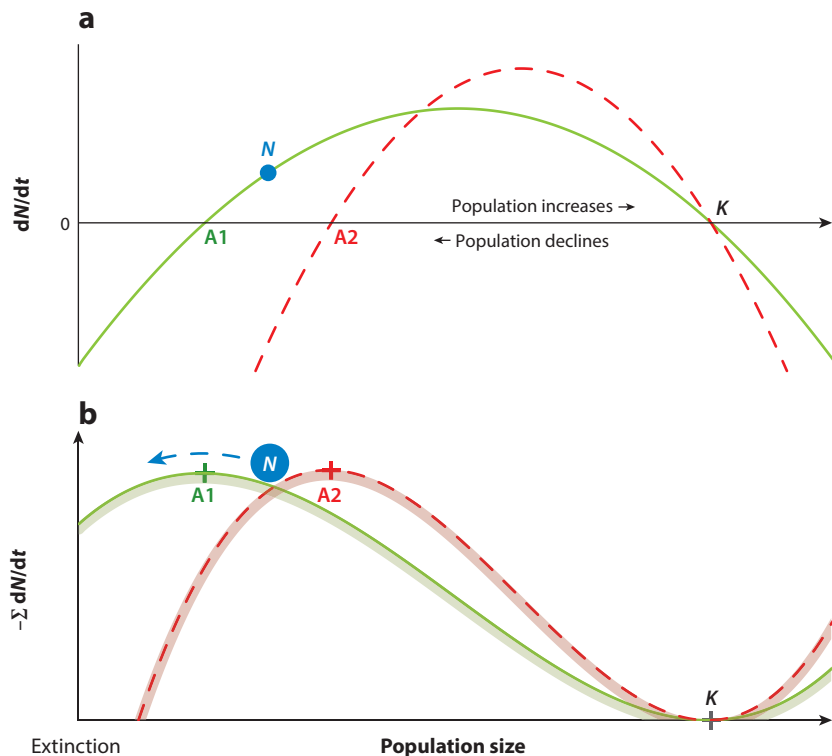


Figure 3

Allee effects and their application to eradication. (a) In the left hand portion of the plot, the presence of an Allee effect is indicated by declining growth with decreasing density. The Allee threshold, A1, occurs where the growth curve crosses 0. Eradication can be achieved by decreasing population size, N , below A1, or by modifying the growth rate function such that the new Allee threshold, A2, exceeds N . (b) The same dynamics, with the population size conceptualized as a rolling ball on a hill (green curve) defined by the cumulative negative rate of change. Here eradication may be achieved by pushing the ball over the brow of the hill (Allee threshold A1) or by modifying the growth curve to change the shape of the hill (red curve). K represents the carrying capacity.

by technologies with fewer impacts on nontarget species (47). The use of insecticides is now much more localized and targeted. For example, systemic insecticides, usually applied to the soil or injected into the base of tree trunks, have been used in eradication programs targeting wood borers such as the Asian longhorned beetle (43). Most ant eradication programs still rely on insecticides, but usage has shifted from spraying contact insecticides to broadcast spreading of insecticidal baits, which have a much lower impact on nontarget species (49). Microbial insecticides, such as *Bacillus thuringiensis* var. *kurstaki* (*Btk*), are more target specific, and these are frequently used in eradication programs targeting Lepidoptera, including incipient populations of gypsy moth in North America (44, 45). In a few instances, inundative releases of parasitoids have been combined with other eradication tactics (114).

Many of the emerging tools for achieving eradication are based on insect sex pheromones, which are species specific and are generally considered to have no adverse impacts on human health or the environment (53). They also typically function to enhance Allee effects by interfering with

mate location and thus intensify one of the main factors that naturally limit establishment of many invading insect species (67). Sex pheromones are often used in mass trapping, a tactic that reduces successful mating and reproduction by removing large numbers of adult insects, usually males. Mass trapping of moderate- to high-density populations is less practical because an extremely high percentage of males must be removed from the area to substantially reduce mating success (98, 130, 131). Mass trapping for eradication is most successful during the early phases of invasion, when population density is low (30, 115).

Mating disruption, another tactic that exploits sex pheromones, has been used in a number of responses targeting Lepidoptera (110, 116). Males are prevented from locating females by saturating the environment with sex pheromones that are applied either from the air or ground by slow-release devices. Unfortunately, this technique disrupts surveillance trapping, which may make it difficult to monitor eradication progress (85).

As an eradication treatment the SIT has virtually no adverse impacts, is perceived as acceptable by residents (38), and has a historical record of success (60, 114). In one of the most well-known eradication programs, SIT was used in the 1960s to eradicate the screwworm (*Cochliomyia bominiivorax*) from the southern United States. Millions of males were reared, sterilized, and released. Their wild mates could not produce viable offspring, resulting in the decline and eventual extirpation of the population (79). Models show that SIT is effective particularly for species in which males, but not females, are capable of multiple matings (6, 131). Unfortunately, facilities for insect mass-rearing and irradiation can be expensive and thus limit the practicality of SIT, particularly if target populations are not small. In addition, technical difficulties of sterilization may constrain the ability of sterilized adults to compete successfully with wild males (99).

Eradication programs sometimes destroy host plants, often in conjunction with other tactics, to control target pest populations. For example, attempts to eradicate the painted apple moth, *Teia anartoides*, from Auckland, New Zealand, combined host plant destruction with *Btk* application and SIT (111). An ongoing effort to eradicate the boll weevil, *Anthonomus grandis grandis*, from the southern United States uses bans on planting cotton, along with other tactics, in combination with host plant destruction (2). Host plant destruction was unsuccessful for eradication of emerald ash borer (*Agrilus planipennis*), in large part because of rapid spread and ineffective methods for delimiting populations (48), but has been a component of successful eradication programs targeting the Asian longhorned beetle (43).

Many successful eradication programs have combined two or more tactics to eradicate populations (57). In some cases, multiple tactics may target different parts of a single population. For example, a program may apply pesticides to a higher-density core region of an invasion and mating disruption to sparser, peripheral areas (117). Treatments such as habitat destruction may be applied at the periphery of a population to contain it while a different tactic is used to drive resident populations to extinction.

Often, two or more types of treatments are applied in the same area. Certain combinations of tactics may act synergistically in raising the Allee threshold and facilitating eradication, but in other cases, multiple tactics may interfere with each other when applied in the same location (10). Synergy is most likely when a density-independent treatment (e.g., pesticides) is paired with a density-dependent treatment (e.g., mating disruption) (117). Multiple component Allee effects may combine and interact in complex and nonlinear ways to determine an overall demographic Allee effect (7, 24), and such synergistic interactions can be exploited to reduce eradication costs (7, 10, 117). Blackwood et al. (10) used a model to show that insecticides and mating disruption may act synergistically. Ultimately, the benefit of combining tactics is a question of economics. Synergy exists when expenditure on two tactics results in a greater shift in the Allee threshold than spending the same amount on any single tactic (10).

Most successful eradication programs include quarantine measures to limit the transport of potentially infested material to uninfested areas. The life stages of many organisms are cryptic and may be spread accidentally with nursery plants, logs, firewood, produce, and other commodities. If such transport is not curbed, then establishment of secondary populations can further challenge eradication efforts (48, 66).

SOCIAL FACTORS

Despite the generally high efficacy of conventional pesticides, relatively few are desirable for aerial application, particularly over ecologically sensitive or urbanized areas. Microbial pesticides, most notably *Btk* toxins, are considered more acceptable for aerial application over urban areas and are frequently used in programs to eradicate Lepidoptera (45). As part of the 1996–1997 program to eradicate white-spotted tussock moth from Auckland, New Zealand, some residential areas were aerially treated with *Btk* 23 times (51). There is little evidence of adverse effects of aerial *Btk* treatments on human health (86, 88). Concerns exist about the effects of *Btk* treatments on nontarget Lepidoptera (14, 78); however, most eradication treatments are applied over relatively small areas such that immigration might be expected to facilitate rapid recovery of affected species. Indeed, the effects of *Btk* treatments on nontarget populations are generally temporary (39). Moreover, any negative effects of *Btk* on nontarget species must be considered in relation to the possible direct and indirect effects of invasive target on these species (39, 70, 95).

Although removal of host material may be a highly effective eradication treatment in some circumstances, it may face intense opposition by local residents. During the program to eradicate brown spruce longhorn beetle (*Tetropium fuscum*) from Nova Scotia, legal action was taken by residents to suspend the felling and removal of host trees from a park where the infestation was first discovered (75). A similar legal action was taken in Ohio in response to host removal as part of the emerald ash borer eradication program, but was unsuccessful (83).

A misinformed or ill-informed public may fail to recognize the difference between chemical insecticide treatments and semiochemical-based eradication treatments, such as mating disruption and mass trapping, which have little to no effect on human health or on nontarget species. Indeed, this was the case with the aborted eradication program against the light brown apple moth (*Epiphyas postvittana*) in California (2007–2008). When mating disruption was implemented, hundreds of residents complained of impacts on their health and on the health of birds and pets (22), and some scientists argued that eradication was futile (21). Ultimately, this program was canceled (112) despite the lack of convincing evidence of impacts on human health or other nontarget effects (124) and despite subsequent demonstration that mating disruption is efficacious (19).

One lesson learned from the many instances of adverse public reaction to eradication programs is the need for effective outreach and education of local residents (72, 74). In most cases when public opposition thwarted eradication programs, the public lacked information about why eradication was proposed, which tactics would be employed, and how the program would likely affect their lives or communities. In the absence of public outreach, residents are likely to be suspicious, and some will be sympathetic to conspiracy theories and other radical arguments. The successful program to eradicate the painted apple moth from Auckland dedicated approximately one-third of the entire program budget to public outreach (11). Similarly, public support generated by extensive outreach played an important role in the ultimate success of the program to eradicate the Asian longhorned beetle from Chicago (3).

An inherent social problem facing many eradication programs is the disconnect between those who bear the costs and those who benefit. For example, when an agricultural pest initially establishes in an urban area, local residents may perceive little motivation to accommodate eradication

treatments. Social scientists have recognized that regional management and eradication of biological invasions can be achieved only if all stakeholders cooperate (34, 36, 129). Coordination may be facilitated by top-down and middle-out approaches that promote education, regulation, incentives, and increased communication among all stakeholders.

A robust economic analysis that compares costs and benefits should always be conducted to assess any proposed eradication program (18). The benefits may be considerable because without eradication a localized population may spread across a large area, potentially accruing massive impacts. However, discounting future anticipated impacts back to the time of eradication diminishes the value of averted damages (33, 35, 84, 100). Ideally, such a cost-benefit analysis should incorporate uncertainty, not only in the likelihood of eradication success, but also in the anticipated damage should the pest become established. Further economic research is needed before methods accounting for such uncertainty can be developed.

FUTURE CHALLENGES

Simberloff (104) argued that eradication of newly founded nonnative species should be attempted more frequently than has historically been the case. In hindsight, the eradication of many established invasive insect pests would have been economically beneficial. Eradication may not have been attempted when these invasions occurred because the magnitude of the potential impacts of the pest were underestimated or perhaps ignored, because surveillance was inadequate to detect invading populations early enough, or because decision makers simply did not appreciate that eradication was a viable option. Recent reviews (90, 121) have demonstrated that insect eradication is feasible in many cases, and we highlight here its importance to enhancing biosecurity efforts.

Researchers can use risk analysis to identify potentially invasive species for which eradication may be practical (64, 82). This presumes, of course, that risks associated with a potentially invasive insect species can be assessed. Although this presumption is true for many insects that are pests in their native range or have become invasive elsewhere, there remain many species that are novel and hence not adequately studied. For example, the emerald ash borer is largely a secondary pest in its native range in China and Korea, where it colonizes severely stressed or dying native ash trees (*Fraxinus* spp.). As such, little to no information on its biology and control was available when it was detected in North America, where it has caused widespread mortality of ash and continues to spread (48).

Development of more effective area-wide surveillance systems for high-risk species should also be a high priority to increase the probability that incursions will be detected early enough so that eradication is feasible. Improved methods are critically needed to facilitate early detection of insect taxa that do not produce long-range pheromones. Even when attractants are available, the efficiency of surveillance programs can be further improved. For example, risk mapping (127) and bioeconomic optimization (31, 32) can ensure that surveillance is carried out over large regions in a cost-effective manner. Opportunities exist to efficiently coordinate surveillance for multiple target species. For example, attractants for several species can often be combined in a single trap (20). Finally, citizen scientists can contribute to national invasive species surveillance systems. Efforts to connect with and more fully exploit this resource are needed (1, 37, 40). Similarly, new treatment tools will be needed for a wider range of invasive species, as social acceptability increasingly defines which tools may be used. Future treatments should ideally be target specific, possibly exploiting target genetics, and should be used in complementary combinations.

More work is needed to better understand the social issues related to eradication. Communication strategies, such as educating stakeholders and encouraging stakeholders to participate and cooperate with eradication programs, would help residential communities understand

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suppression of
biological invasions
through collective
actions offshore, at the
border and postborder

expectations prior to incursions (72, 126). Programs in urban areas are particularly challenging partly because effective, socially acceptable treatments for many insect groups are lacking (38, 110), and better approaches for engaging stakeholders are needed. Thus, both biological and social aspects of eradication warrant further research.

SUMMARY POINTS

1. Insect eradication is feasible and has often been successful.
2. Given current globalization trends, eradication is playing an increasingly important role in nonnative pest exclusion.
3. Knowledge of population dynamics, insect behavior, treatment efficacy, and bioeconomics is key to developing more successful surveillance and eradication programs.
4. Allee effects often dominate the dynamics of invading populations; eradication can be accomplished by reducing a population below the Allee threshold rather than by eliminating every individual.
5. Investment in surveillance programs is crucial to reducing costs and increasing success of eradication efforts.

FUTURE ISSUES

1. Eradication programs often must be carried out in urban settings, which presents particular challenges; more acceptable eradication technologies and new strategies for engagement with the public through better communication are needed.
2. Improved surveillance systems across a wider range of invasive taxa are needed.
3. There is a need to better engage the public in surveillance activities.

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