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Exploiting the Achilles Heels of Pest Invasions: Allee Effects, Stratified Dispersal and Management of Forest Insect Establishment and Spread[†]

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Abstract

Given the increasing problem of invasions by forest insects, there is an urgent need to develop effective strategies for managing them. Trends of escalating globalisation impede ongoing efforts to limit the arrival of new species. Consequently, either preventing establishment (through eradication) or limiting the spread of alien species are likely to play increasingly important roles. Here we argue that two traits common to many invading species can be exploited in the design of eradication and containment strategies. The first trait is the Allee effect, in which per capita growth rates decline with decreasing abundance. Allee effects can arise from several different mechanisms and are capable of driving low-density populations to extinction. Strategies to eradicate newly established populations should focus on either enhancing Allee effects or suppressing populations below Allee thresholds such that extinction proceeds without further intervention. The second trait is stratified dispersal, in which occasional long-distance dispersal results in the formation of isolated colonies ahead of the continuously infested range boundary. These colonies grow, coalesce and greatly increase spread rates. An efficient approach to containing the spread of invading species focuses on locating and eradicating these isolated colonies. Thus, Allee effects and stratified dispersal both represent 'weak links' in the invasion process that can be exploited in invasion management strategies.

Keywords: biosecurity; eradication; containment; biological invasion; population ecology.

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Introduction

Invasions by non-indigenous forest insects pose a serious threat to forest ecosystems in virtually every part of the world (Kenis et al., 2009; Langor & Sweeney, 2009; Liebhold et al., 1995). Trends of increasing global trade and travel provide invasion pathways by which species are able to overcome natural barriers to dispersal, such as oceans and mountain ranges, and colonise areas that were previously inaccessible (Levine & D'Antonio, 2003). While most alien forest insects do little harm, a few of them may cause irreparable damage to forest ecosystems. For example, the emerald ash borer, *Agilus planipennis* Fairmaire, appears poised to effect the near total annihilation of the genus *Fraxinus* from the forests of North America (Poland & McCullough, 2006). There has been some success in closing forest pest invasion pathways (e.g. quarantines on solid wood packing material) but these measures are not likely to be 100% effective. More invasions will continue to occur and many of these are likely to have catastrophic ecological and economic consequences (Pimentel et al., 2000; Strong & Pemberton, 2000).

The biological invasion process can be broken down into three distinct phases: **arrival**, the process by which individuals are transported from an area in which they inhabit to one in which they do not; **establishment**, the process by which populations grow to sufficient levels such that extinction is unlikely; and **spread**, the expansion of a population's range (Dobson & May, 1986; Liebhold & Tobin, 2008; Shigesada & Kawasaki, 1997). For each of these stages, there are reciprocal management activities: international quarantines and inspections at the point of export are used to minimise the arrival of species; detection and eradication are used to prevent establishment or create barrier zones; and domestic quarantines at the point of import are used to limit spread (Liebhold & Tobin, 2008). Here, we focus on processes of population ecology operating during the establishment and spread phases.

Although there is a long history of invasion management (e.g. eradication), the scientific foundations for these efforts have often been weak (Myers et al., 2000). Consequently, there is an urgent need to understand the population processes operating during the various stages of an invasion and apply this knowledge in selecting strategies for management. In this paper, we focus on two phenomena characteristic of the population ecology of typical forest insect invaders: Allee effects; and stratified dispersal. We explain why these two traits represent weak links in the invasion process and how management strategies can be designed to exploit them.

Exploiting Allee effects to facilitate eradication

When invading species arrive in a new habitat, they characteristically exist at very low numbers. Considerable research from the field of conservation biology indicates that low-density populations are prone to extinction (Courchamp et al., 2008). Indeed, analyses of historical invasions show that arrival tends to occur at a much higher rate than establishment (Simberloff & Gibbons, 2004; Williamson & Fitter, 1996). Establishment, thus, represents a particularly vulnerable phase for invaders: populations must persist, grow and expand their distribution such that extinction no longer is possible.

One of the dominant causes of extinction in low-density populations is random chance. All populations (both sparse and abundant) are affected by stochastic abiotic effects (e.g. variation in weather conditions), but low-density populations are particularly influenced by such effects. In addition to environmental stochasticity, sparse populations may be strongly affected by demographic stochasticity such as random variation in birth and death processes (Engen et al., 1998). Because small changes in abundance can easily decimate sparse populations to zero, both demographic and environmental stochasticity may cause these populations to become extinct. However, Allee effects likely represent the greatest threat to low-density, newly founded populations.

The term "Allee effect" is a tribute to the animal ecologist, Warder Allee, who is considered one of the first to recognise that, at low densities, survival and reproduction may often be limited by the lack of conspecifics and that this can lead to population decline (Courchamp et al., 1999; Dennis, 1989). Allee also recognised that decreases in per capita population growth that accompany decreasing density may create population thresholds below which low-density populations are driven toward extinction (Figure 1A). Over the last 20 years there has been growing recognition of the importance of Allee effects in contributing to the extinction, both in the context of conservation of sparse populations and in the context of biological invasions since founder populations of introduced species are generally sparse (Drake, 2004; Leung et al., 2004; Taylor & Hastings, 2005).

Allee effects are ubiquitous and may arise from a variety of mechanisms. These include: failure to locate mates (Berec et al., 2001; Hopper & Roush, 1993; Tobin et al., 2009); inbreeding depression (Lande, 1998); the failure to satiate predators (Gascoigne & Lipcius, 2004); and the lack of cooperative feeding (Clark & Faeth, 1997). Stephens et al. (1999) recognised two terms: "component Allee effect" to refer to the decrease in growth with decreasing density caused by a single mechanism; and "demographic Allee effect" to refer to

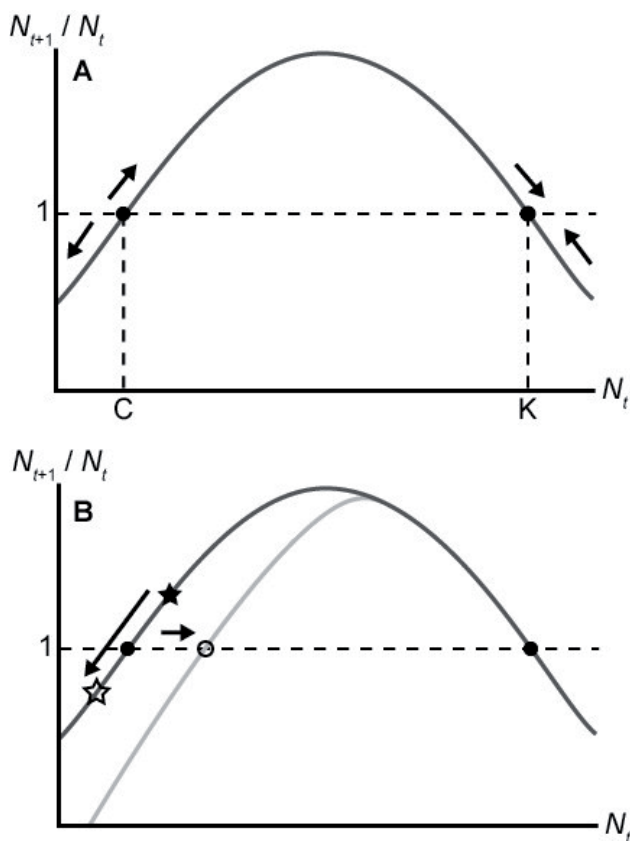


FIGURE 1: Schematic representation of the Allee effect and the influence of eradication strategies, modified from Liebhold and Tobin (2008). Change in population density, N_{t+1} / N_t , is plotted as a function of density at the beginning of the generation, N_t .

A. *Natural Population Dynamics*: the Allee threshold (black circle at C) is defined as the population density below which population growth is less than 1. When the population density is less than C, it will decrease towards extinction. When the population density exceeds C, it will increase toward K, the carrying capacity. When populations exceed the carrying capacity, they will decrease.

B. *Influence of eradication strategies*: the first strategy is to reduce the population density (black star) to a new level (open star) that is below the natural Allee threshold (black circle). In the second strategy, a new, higher Allee threshold created at a new level (open circle) that exceeds the current population density. Both strategies result in population extinction.

decreasing per-capita growth with decreasing density at the population level. In many cases, demographic Allee effects arise from several components, although multiple sources of Allee effects may interact in complex ways and are not necessarily additive (Berek et al., 2007).

Most insects require sex for reproduction. Consequently, failure to locate mates at low densities can limit population growth and contribute to a demographic Allee effect (Berek et al., 2001; Hopper & Roush, 1993; Wells et al., 1998). Despite the evolution of highly efficient mate-location systems (e.g. sex pheromones), males and females may be too distantly located to find each other and mate, and this may ultimately cause a low-density population of invaders to fail to establish. Seasonal asynchrony of adult male and female sexual maturation can also contribute to mate-location failure; species with pronounced protandry (i.e. male emergence precedes that of females) and variation in developmental times are likely to exhibit stronger Allee effects (Calabrese & Fagan, 2004; Robinet et al., 2007, 2008).

Allee effects may also arise when various types of co-operative behaviours (not related to mate-finding) are limited at low population levels. For example, predation can be expected to contribute a component Allee effect in any small invading population (Gascoigne & Lipcius, 2004). At high population densities, there is 'safety in numbers' whereby predators become satiated before all the insects in a population have been consumed. Obviously, this leads to an increase in insect survival. Another example is that many insect species exhibit co-operative feeding, in which an aggregation of individuals increases the ability of a population to overcome host defences and successfully establish itself, as is the case in tree-killing bark beetles (Raffa & Berryman, 1983). This benefit may not apply at low population numbers, however.

Because Allee effects are a common cause of extinction of invading populations, it makes sense that efforts to prevent establishment should be designed to enhance Allee effects. Eradication is defined as the total elimination of a species from a geographical area (Knipling, 1979; Simberloff, 2003). Even though eradication has played a crucial role in the management of biological invasions, the concept has often been the subject of controversy (DeBach, 1964; Myers et al., 1998, 2000; Simberloff, 2003). It has been argued that eradication is not a realistic goal because it is either impossible or impractical to eliminate every individual in a population (Dahlsten et al., 1989). Perhaps the greatest reason for skepticism is the occurrence of several failed eradication programmes, such as efforts to eliminate the imported fire ant, *Solenopsis invicta* Buren (Perkins, 1989), and the gypsy moth, *Lymantria dispar* (L.), (Forbush & Fernald, 1896; Spear, 2005) from the United States. However, there are also many

examples of highly successful eradication efforts (Myers et al., 1998; Simberloff, 2001, 2003, 2009). Thus, there is a critical need to clarify when and where eradication is practical and to understand the basic population processes associated with eradication.

We submit that the long-held notion that eradication can only occur by eliminating all individuals within a population (Dahlsten et al., 1989; Knipling, 1979) is false. There is ample evidence that most insect species exhibit both stochastic dynamics and Allee effects at low densities, and that these processes are likely to drive extremely small populations toward extinction without intervention (Liebhold & Bascompte, 2003; Drake, 2004). As a result, the success of eradication is not dependent on achieving complete elimination of a population but rather the reduction of a population below some threshold, beyond which it will proceed toward extinction without further effort (Figure 1B). The concept of achieving eradication through the suppression of populations below the Allee (extinction) threshold was suggested by Liebhold and Bascompte (2003) who used a simple model of stochastic population growth coupled with Allee dynamics. They applied this model to invading gypsy moth populations as a case study to parameterise their model and explored the relationship between population size and the “killing power” (i.e. % mortality) necessary to achieve eradication. Their results showed that, when densities of invading populations were suppressed below the Allee threshold, most populations became extinct without further intervention. This concept explains the consistent success that has been achieved in eradicating sparse gypsy moth populations using only one or two aerial applications of *Bacillus thuringiensis* Berliner, a treatment that is considered to achieve, at most, 95% mortality only under ideal conditions (Hajek & Tobin, 2009; Liebhold & McManus, 1999; Miller, 1990).

Eradication can thus be accomplished through the application of any treatment (e.g. pesticide) that kills a sufficient proportion of a population such that the residual population falls below the Allee threshold and extinction proceeds. An alternative to suppressing populations below the natural Allee threshold is the strategy of artificially manipulating the Allee threshold. Certain population processes may be altered such that the new Allee threshold exceeds the current population level and therefore the population decreases toward extinction (Figure 1B). Examples of population process manipulations that increase the strength of Allee effects are various treatments that interfere with mating such as mating disruption (Yamanaka, 2007), mass-trapping (El-Sayed et al., 2006), and the release of sterile insects (Klassen & Curtis, 2005). Such methods have been used in several successful eradication programmes even though no individuals are actually killed (El-Sayed et al., 2006; Klassen & Curtis, 2005). Yamanaka and Liebhold (2009) provide a spatially

implicit model that contrasts the efficacy of these three methods for achieving eradication by manipulating the Allee effect. Though never attempted, other approaches that do not involve altering mating success (such as increasing host-defence responses) could also be used to manipulate the Allee threshold and thereby achieve eradication. In theory, any treatment that increases mortality or reduces reproductive output can be expected to reduce population growth (i.e. decrease along the y-axis in Figure 1B) and potentially reduce the population size below the Allee threshold (C in Figure 1A, defined here as the population density below which population growth is less than 1) and consequently drive the population to extinction.

Exploiting stratified dispersal to limit invasion spread

Invasion spread is the process by which a species expands its range from a habitat that it currently occupies to one which it does not. In a few species, spread is continuous and simply results from the coupling of random dispersal with population growth. This type of basic spread can be represented by a simple reaction-diffusion model that couples exponential or logistic population growth with diffusive (random) movement (Fisher, 1937; Skellam, 1951). In such models, the magnitude of dispersal is characterised by the diffusion coefficient, D , which can be estimated as the standard deviation of dispersal distances, typically compiled from mark-recapture experiments (Kareiva, 1983). In these simple reaction-diffusion models, population growth is characterised by r , which is the intrinsic rate of population increase under ideal conditions. An interesting characteristic of these models is that the radial rate of range expansion can be shown to be constant and estimated as $2\sqrt{rD}$ (Hastings et al., 2005). Though there are a few species in which simple reaction-diffusion models have accurately predicted observed rates of spread (Andow et al., 1990; Shigesada & Kawasaki, 1997), there are many cases where they have failed (Shigesada & Kawasaki, 1997). The basic problem with these models is that they often are too simple; in particular, they fail to account for long-distance dispersal.

Because many insects are prone toward long-range movement, spread may not always be represented by simple reaction-diffusion. There are several examples indicating that such leptokurtic or “fat-tailed” dispersal distance distributions can lead to much faster rates of spread than those predicted by simple diffusion models (Clark, 1998; Kot et al., 1996). For many species, occasional long-distance dispersal events are frequently caused by accidental movement by humans. For example, movement of firewood is known to be an important pathway facilitating long-distance movement of several forest insect species. For species, such as the emerald ash borer in North

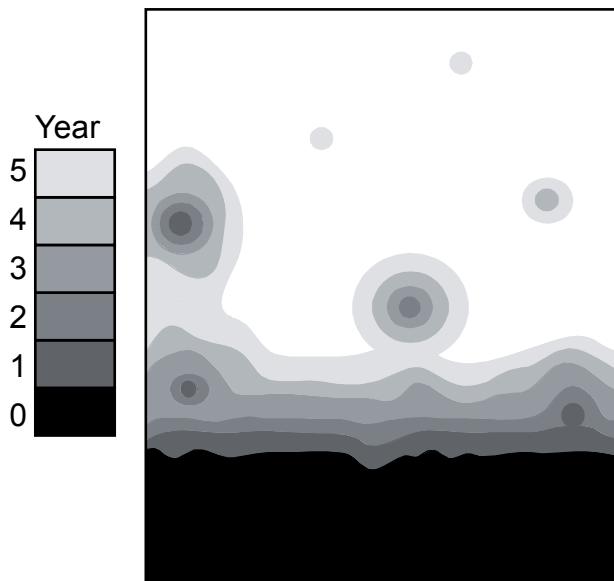


FIGURE 2: Schematic diagram of spread between successive generations (years 0-5) predicted using a stratified dispersal model (Hengeveld, 1989; Shigesada et al., 1995; Shigesada & Kawasaki, 1997). The solid innermost circle represents the initial range at year 1. Figure modified from Liebhold and Tobin (2008).

America, such long distance movement mediated by humans is known to play a key role in invasion spread (Poland & McCullough, 2006). The combined process of short-range- and long-range dispersal is referred to as “stratified dispersal,” and is a major driver of spread dynamics (Figure 2) (Hengeveld, 1989; Shigesada & Kawasaki, 1997; Shigesada et al., 1995). When long-distance dispersal occurs, even at a relatively low rate, it can cause much greater rates of spread than would occur with only short-range dispersal because populations “jump” well ahead of the continuously infested boundary of the expanding species range (Shigesada et al., 1995). These jumps result in isolated populations that grow and ultimately coalesce with the expanding population front. Stratified dispersal is well illustrated by the spread of the gypsy moth in North America: short-distance dispersal of airborne first instars on silken threads carries many individuals relatively short distances but humans inadvertently transport life stages long distances, well ahead of the advancing population front (Hajek & Tobin, 2009; Liebhold et al., 1992; Whitmire & Tobin, 2006). As a result, spread is enhanced by the growth of isolated colonies ahead of the expanding population front and their eventual coalescence with the population front. The rate of gypsy moth spread is largely determined by the rate of formation and growth of these colonies (Sharov & Liebhold, 1998a).

In many situations where an alien species has already expanded its range large enough such that eradication is no longer practical, there may still be considerable benefit derived from either stopping or slowing its future spread (Sharov & Liebhold, 1998b). Various attempts have been made for slowing, stopping or even reversing the spread of invading species. In most cases, however, slowing spread may be the only realistic objective because reversing or stopping the spread are too costly. Of course the practicality of managing spread and selection of management strategies will vary considerably between species due to differences in their biology.

Because spread results from the coupling of dispersal with population growth, its management should focus on reducing dispersal, reducing growth, or some combination of both. As described above, long-distance dispersal events, though proportionally less common, are typically the most important determinant of spread rates. Consequently, spending a relatively small amount of effort to minimise long-distance dispersal can greatly reduce spread. Because long-distance dispersal is frequently mediated by humans moving goods contaminated with hitchhiking invaders, domestic quarantines that suppress anthropogenic movement should reduce spread rates, although total compliance may be difficult to achieve. Additional methods for reducing long-distance dispersal may also be effective; e.g. pesticide applications to Argentine ant, *Linepithema humile* (Mayr), colonies budding along an expanding population front have slowed and in some places eliminated spread to adjacent uninfested areas (Krushelnycky et al., 2004).

Another strategy for reducing invasion spread is population suppression using one of two distinct strategies: (i) suppression of isolated colonies formed by long-distance dispersal and (ii) suppression of populations at or behind the advancing population front that serve as source populations for propagules that found new colonies through long-distance dispersal. The latter strategy often may not be practical because of the sheer magnitude of the area that must be suppressed. However, one successful example of the strategy of suppressing populations over large areas behind the advancing population front has been the successful reversal of the spread of the boll weevil, *Anthonomus grandis grandis* Boheman, in the United States (Hardee & Harris, 2003). The alternative of suppressing isolated colonies is described by Sharov and Liebhold (1998b). These authors proposed a generalised model for slowing the spread of an invading species by eliminating isolated colonies that have formed through long-distance dispersal and which are located ahead of the expanding population front. Current efforts to slow the spread of the gypsy moth in the US provide a good example of this strategy. In this programme, a grid of pheromone-baited traps are deployed over an approximate 100-km wide band

along the advancing gypsy moth front to detect newly-founded isolated populations (Tobin et al., 2004). Once located, these colonies are eradicated or suppressed using aerial applications of either microbial pesticides or mating disruption agents. Over the last 10 years, the programme has reduced gypsy moth spread rates by over 60% (Sharov et al., 2002; Tobin & Blackburn, 2007).

Conclusions

The story of the Greek hero Achilles and his vulnerable heel has a convenient applicability to the management of biological invasions. In many ways, biological invasions resemble Achilles, a fierce warrior who left a trail of destruction in his path. Though slightly different, the effects of many invasive species on ecosystem processes can be immense, with some resemblance to the destruction wrought by Achilles. Much of Achilles' ferocity could be attributed to his immortality, achieved by his mother who dipped him in the River Styx as an infant. Unfortunately for Achilles, his immortality was imperfect and he had one spot of vulnerability on his heel where his mother grasped him during his immortalising dunk. This weakness was ultimately his demise as the Trojan prince Paris killed Achilles by sending an arrow into his heel.

Much like the ferocious warrior Achilles, invading species do have their weaknesses. In particular, Allee dynamics cause a potential "weak link" during the establishment phase that can be greatly exploited to achieve successful eradication. Similarly, the fact that many non-native species spread through stratified dispersal provides excellent opportunities for limiting the spread of these organisms through barrier-zone management programmes.

Given that the problem of invading forest insects is growing around the world, steps need to be taken to mitigate the problem. Some progress is being made in reducing rates of arrival of certain alien forest pests. For example, an international standard for phytosanitary measures (ISPM 15) that provides guidelines for the regulation of wood packaging material moving in international trade holds promise for reducing arrivals of woodboring insects (Haack & Patrice, 2009). However, it seems unlikely that all pathways can be completely blocked so new, problematic species will continue to arrive. Consequently, research is needed on effective ways of managing invasions that involve limiting establishment and spread. In searching for more effective management methods, there is hope of finding strategies that exploit the weaknesses of invasions identified here: Allee effects and stratified dispersal. In the future, it is possible that additional weaknesses in invasion processes will be identified and these will offer additional management strategies.

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