Population Ecology of Insect Invasions and Their Management*

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Annu. Rev. Entomol. 2008. 53:387–408

The *Annual Review of Entomology* is online at ento.annualreviews.org

This article's doi:
10.1146/annurev.ento.52.110405.091401

0066-4170/08/0107-0387$20.00

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Key Words

Allee effect, establishment, nonindigenous species, spread, stratified dispersal

Abstract

During the establishment phase of a biological invasion, population dynamics are strongly influenced by Allee effects and stochastic dynamics, both of which may lead to extinction of low-density populations. Allee effects refer to a decline in population growth rate with a decline in abundance and can arise from various mechanisms. 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 spread phase of invasions results from the coupling of population growth with dispersal. Reaction-diffusion is the simplest form of spread, resulting in continuous expansion and asymptotically constant radial rates of spread. However, spread of most nonindigenous insects is characterized by occasional long-distance dispersal, which results in the formation of isolated colonies that grow, coalesce, and greatly increase spread. Allee effects also affect spread, generally in a negative fashion. Efforts to slow, stop, or reverse spread should incorporate the spread dynamics unique to the target species.

INTRODUCTION

Geographical barriers such as oceans, mountain ranges, and glaciers have compartmentalized the world's biota into disjunct communities during the ~400 million years of insect evolution. As continents separated or collided, climates changed, and oceans receded, species ranges have constantly shifted, sometimes with the result that species were introduced into communities where they had previously not evolved. But these changes have been relatively slow. Increases in the world's human population over the last 1000 years have brought about changes in our behavior that have greatly accelerated the breakdown of barriers to species movement. For example, the conquest of far reaches of the world by Europeans was accompanied by movements of various species both intentionally (e.g., introduction of domestic species such as the honey bee) and accidentally (e.g., inadvertent movement of species, such as cockroaches, hitchhiking on vessels) (21). More recent sophistication of human societies has resulted in remarkable increases in worldwide movement of humans and their goods. This mobility has unfortunately resulted in a rapid acceleration of introductions of insect species beyond their native ranges (31, 62, 69, 108, 121).

Arrival: transport of a nonindigenous species to new areas outside of its native range

Establishment: growth of a population to sufficient levels such that natural extinction is highly unlikely

Spread: expansion of the nonindigenous species' range into new areas

Many intentionally introduced insects are generally considered beneficial, and most accidentally introduced insect species rarely reach high population levels and are seldom noticed. However, a highly conspicuous minority of nonindigenous species sometimes become particularly abundant and cause considerable ecological, economic, and evolutionary impacts (85, 100, 129). The reasons why populations of alien species sometimes explode and the characteristics of their impacts are not covered in this review. Instead, we focus here on the basic population processes that operate during the invasion process and how this information can be applied to develop effective strategies for mitigating invasions.

Table 1 The three successive invasion phases with corresponding management activities

Invasion phase	Management activities
Arrival	International quarantines Inspection
Establishment	Detection Eradication
Spread	Domestic quarantines Barrier zones

Biological invasions can be broken down into three distinct population processes: arrival (the process by which individuals are transported to new areas outside of their native range), establishment (the process by which populations grow to sufficient levels such that extinction is highly unlikely), and spread (the expansion of an invading species' range into new areas) (25, 74, 92, 119) (**Table 1**). Here we concentrate on population processes operating during the establishment and spread phases. We then discuss management activities associated with the establishment and spread phases and clarify how knowledge of population processes can be used in the selection of effective strategies. The arrival phase is an equally important phase of the invasion process but mostly does not involve population processes; readers are encouraged to consult other sources (34, 52, 81, 149, 127) that have investigated invasion pathways and arrival processes.

ESTABLISHMENT

While rising levels of world trade and travel have resulted in an ever-increasing arrival of alien species, most of them have failed to establish (124, 146). The establishment phase thus represents a critical period during which populations grow and expand their distribution such that extinction is highly unlikely. Founder populations typically are small and consequently are at great risk of extinction. Generally, the smaller the founder population, the less likely is establishment (79, 84). This is conceptually illustrated by historical records of introductions of natural enemies as part of biological control programs, in which establishment frequencies are consistently higher from releases of large numbers of individuals (6, 35, 50).

Much of what we know about the population biology of low-density invading populations is extracted from a rich literature on the population ecology of rare species (i.e., conservation biology). All populations are affected by stochastic abiotic influences (e.g., weather), but low-density populations are particularly influenced by such effects. We can mathematically represent the generational change in population density as

$$N_{t+1} = f(N_t) + \varepsilon_t, \qquad 1.$$

where N is population density in year t or $t + 1$, $f(N_t)$ is a function that encompasses birth and death processes, and ε_t is variation due to stochasticity. In addition to environmental stochasticity, all populations are affected by demographic stochasticity, which refers to random variation in birth and death processes (32). The important result of demographic and environmental stochasticity is that low-density populations (e.g., newly founded invading populations) can be driven to extinction purely due to inimical random variation. However, there is another factor contributing to the extinction of low-density populations that must also be considered: Allee effects.

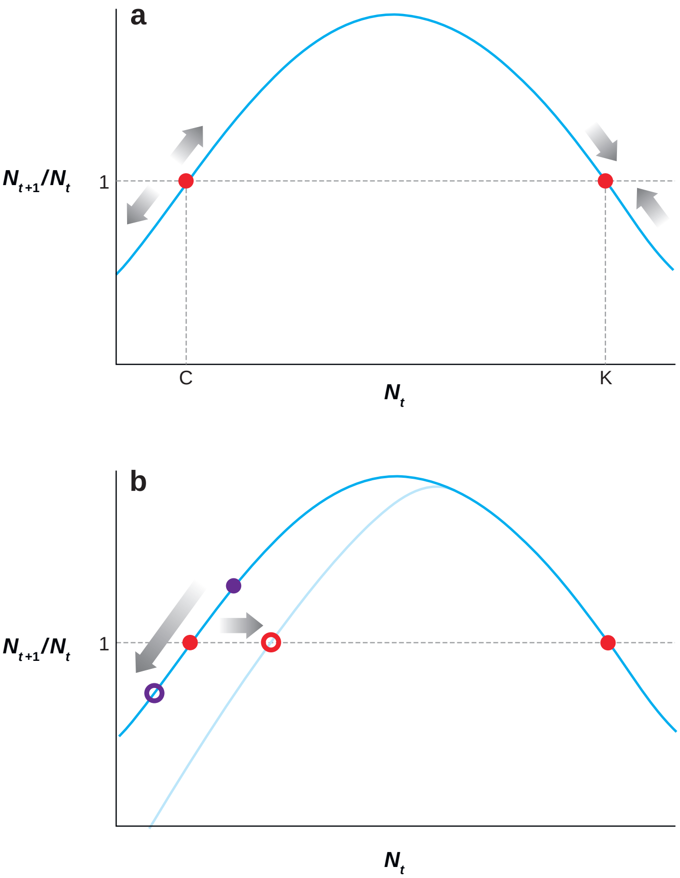

Figure 1

Schematic representation of the Allee effect. 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*) Illustration of equilibria. When density is less than C, the Allee threshold, it will decrease toward extinction. When density exceeds C, it will increase toward K, the carrying capacity. When populations exceed the carrying capacity, they will decrease. (*b*) Illustration of eradication strategies. The first strategy is to reduce the population density (*solid purple dot*) to a density that is below the Allee threshold. In the second strategy, the Allee threshold (*solid red dot*) is increased to a level that exceeds the population density. Both strategies result in population extinction.

Allee Effects

Warder Allee (1) studied animal ecology and is generally thought to be among the first to recognize the concept that animal populations must be composed of some minimum number of individuals to remain viable. Certain processes may lead to decreasing net population growth with decreasing density, and thus there may exist a threshold below which low-density populations are driven toward extinction (**Figure 1*a***). This phenomenon is known as the Allee effect (19, 24), and it has been identified as critical to understanding patterns of extinction from the perspective of conservation biology (128). Of late, there has been growing recognition of its importance during the establishment phase of biological invasions (26, 68, 133).

Causes of Allee effects include failure to locate mates (8, 50), inbreeding depression (66), the failure to satiate predators (39), and the lack of cooperative feeding (17). In many

Allee effect: decreased population growth correlated with decreasing abundance cases, Allee effects arise from several causes, although multiple sources of Allee effects do not necessarily act additively and instead may interact in complex ways (9). The rate at which invading populations arrive at a specific location, called propagule pressure, also may influence the importance of Allee effects on establishment. Leung et al. (68) provided a model for estimating the propagule pressure necessary to achieve establishment for a given Allee effect. Drake & Lodge (27) extended this model to clarify the important role of both the numbers initially arriving and the numbers arriving subsequent to initial colonization; establishment is strongly enhanced by the numbers arriving during both periods. Considerable field data collected for a variety of species support the importance of propagule pressure on establishment (42, 50, 82).

Given the tremendous variation in life history among insect species, there is undoubtedly considerable variation in the role and magnitude of Allee effects during the invasion process. Understanding this role and strength, particularly during the establishment phase, can thus be of critical importance to understanding why some species are more invasive than others.

Variation in Allee Dynamics

Because most insects reproduce sexually, difficulty in mate-finding at low densities can greatly contribute to an Allee effect (8, 50, 115, 126, 144), despite the fact that many insect species have evolved highly efficient mate location systems (e.g., sex pheromones). Consequently, many invasions may fail when founder population densities are so low that males and females are unable to locate each other. Indeed, the efficiency of mate-finding behavior can influence the strength of Allee effects (8). Another determinant is the seasonal synchrony of adult male and female emergence; species with pronounced protandry (males precede females) and variation in developmental times are likely to exhibit stronger Allee effects (12, 106).

The ability to reproduce asexually and other forms of reproductive behavior can also affect the strength that the Allee effect imposes on populations during establishment. Parthenogenic invasive species, such as the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America (80) and fundatrices of the soybean aphid (*Aphis glycines*) (141), would obviously not be affected by difficulties associated with mate-finding at low densities (26), but these organisms could still be subjected to an Allee effect from an alternative mechanism. Arrhenotoky (production of only males by unmated females) leads to diminished Allee effects compared with normal, obligate sexual reproduction but greater effects compared with thelytoky (production of only females by unmated females) and other forms of parthenogenesis (50). Because founding populations of an invading species often suffer from a lack of genetic diversity, organisms that reproduce sexually could be more prone to extinction from an Allee effect induced through inbreeding. This lack of genetic diversity may also limit the establishment success of invaders, although a notable exception is the Argentine ant (*Linepithema humile*), for which reduced genetic variability likely enhanced its invasion success (138). There is little information on the genetics of invading insects, but a review by Lee (67) highlights the importance of the genetic architecture of a founding population and establishment success.

Insects also differ in their strategy of exploiting host plants. Some insects use cooperative feeding behaviors, in which aggregation of individuals increases the ability of populations to overcome host defenses and successfully establish themselves, as is the case in tree-killing bark beetles (104). Larval aggregations, especially neonates or younger larvae of several species, are better able to exploit tough food resources because large groups are more efficient at initializing feeding sites (17, 40). The lack of cooperative feeding, such as when founder populations arrive in low numbers, can thus be a source of

Allee effects in such species. A good example of this is the European spruce bark beetle (*Ips typographus*), which is the most destructive tree-killing bark beetle in Europe (16). This species is common in Europe, and there have been many accidental introductions into North America. In fact, it has been intercepted by port inspectors in the United States 286 times from 1985 to 2001 (44). Despite this intense propagule pressure and the presence of many suitable host trees, this species has never become established in North America. This failure can likely be attributed to the biology of the species, namely that it is only able to colonize live trees through the aggregation of large numbers of adults that collectively act in concert in overcoming host tree defenses (111).

The negative influence on establishment caused by Allee effects, resulting from any mechanism, tends to be intensified by the propensity of individuals to disperse (50, 126). This is because the populations that found invading populations are spatially isolated. In these populations, emigration is not compensated for by immigration and the result is a net loss due to dispersal, thereby decreasing the population's ability to exceed the Allee threshold. This presents something of a paradox: While dispersal enhances the spread of an invading population (see below), it detracts from its ability to establish.

SPREAD

Spread of a nonindigenous organism is a process by which the species expands its range from a habitat in which it currently occupies to one in which it does not. It can be described in several ways, but most often we estimate spread as an increase in range radius over time, and there can be considerable variability in the spread rates for various species of invading insects (**Table 2**). From an extreme perspective, the transportation of species between continents and their subsequent establishment might be considered as a type of spread. Also, as we describe below, spread is often not continuous but proceeds with populations jumping ahead and forming isolated populations that ultimately coalesce (3, 48, 119). Consequently, there is often

Table 2 Examples of spread rates by invading nonindigenous insects

Order	Species	Area of Invasion	Time Period	Radial rate of spread (km year^{-1})	Reference
Hemiptera	*Adelges tsugae*	N. America	1990–2004	8–13	33
	Cryptococcus fagisuga	N. America	1911–2003	14–15	87
Coleoptera	*Dendroctonus micans*	Europe	1973–1989	15	36
	Popillia japonica	N. America	1920–1940	5–6	119
	Oulema melanopus	N. America	1962–1969	26–90	2
	Lissorhoptrus oryzophilus	Japan	1979–1986	28–470	3
Lepidoptera	*Lymantria dispar*	N. America	1900–2005	3–29	134
	Cameraria ohridella	Europe	2001–2003	17–39	4
	Pieris rapae	N. America	1868–1883	15–170	2
	Phyllonorycter leucographella	Europe	1989–1993	10.3	91
Thysanoptera	*Frankliniella occidentalis*	Europe	1983–2001	209–249	59
Hymenoptera	*Linepithema humile*	N. America	1930–2000	15–67	130
	Solenopsis invicta	N. America	1930–1975	21	13
	Apis mellifera scutellata	S. and Central America	1957–1989	300–500	147
	Sphecophaga vesparum vesparum	New Zealand	1988–1993	1–1.5	5
Diptera	*Pseudacteon tricuspis*	N. America	1999–2001	20	102
	Plecia nearctica	N. America	1940–1975	32	11

Stratified dispersal: two coincident forms of dispersal, a short-distance, continuous form of dispersal coupled with more stochastic dispersal events over long distances

ambiguity between what is considered part of the spread phase and what is considered part of the arrival phase of a new invasion. In maintaining consistency throughout this review, we address the process of spread in reference to the range expansion that follows the initial establishment of a nonindigenous species in a new geographical area. We first describe the process of continuous spread and then introduce the concept of long-distance dispersal. We then examine factors that can influence the rate of spread of invading insects and then conclude this section by reviewing methods of estimating and predicting spread.

Continuous Spread

The continuous spread of nonindigenous species along a population front is generally the result of coupling dispersal with population growth. This was first described in the ecological literature by Skellam (125), whose model specifically combined exponential population growth with diffusive (random) movement. Diffusion has often been applied to describe insect dispersal (54, 94, 107). The magnitude of dispersal is characterized by the diffusion coefficient, D, which can be estimated as the standard deviation of dispersal distances, typically compiled from mark-recapture experiments (54). In Skellam's model, population growth was characterized by r, which is the intrinsic rate of population increase under ideal conditions. Incidentally, Fisher (37) described a model of the spread of an advantageous gene that was identical to Skellam's except that the former adopted logistic growth, which imposes finite limits to growth. Both Skellam's and Fisher's models result in nearly identical patterns of spread (119), and predictions by these models result in continuous range expansion into adjacent areas (**Figure 1*a***). From both models it can be derived that the radial rate of range expansion, V, is asymptotically constant and can be estimated according to

$$V = 2\sqrt{rD}. \qquad 2.$$

Although there are several examples for which Equation 2 has provided spread estimates similar to observed rates of spread (2, 119), there are many cases for which it failed (119). This failure can be attributed to the simplicity of Skellam's biological assumptions and, in particular, to the omission of long-distance dispersal.

Spread Through Long-Distance Dispersal

The spread of insects does not always occur according to simple diffusion; instead, long-range movement of insects, such as through anthropogenic or other mechanisms, may occur with considerable—though unpredictable—frequency. Such leptokurtic, or fat-tailed, dispersal distance distributions can lead to much faster rates of spread than what can be predicted by simple diffusion models (18, 64). Moreover, long-distance dispersal events are more often than not caused by a completely different mechanism than short-distance movement events. The combined processes of short-range and long-range dispersal is called stratified dispersal, and is a major driver of the spread process (48, 119, 120). For example, the spread of the gypsy moth (*Lymantria dispar*) in North America is characterized by stratified dispersal: Short-distance dispersal of airborne first instars on silken threads carries many individuals relatively short distances but humans sometimes accidentally transport life stages long distances, well ahead of the advancing population front (73, 145).

For many nonindigenous insect invaders, anthropogenic movement of life stages is a dominant mode of long-range displacement, though not an exclusive one. Migratory movements of birds have been implicated as the cause of long-distance movement (and consequential spread) of the hemlock woolly adelgid in North America (80). Wind is thought to be the primary mode of long-distance dispersal of the soybean aphid (141). Regardless of the precise mechanisms of stratified

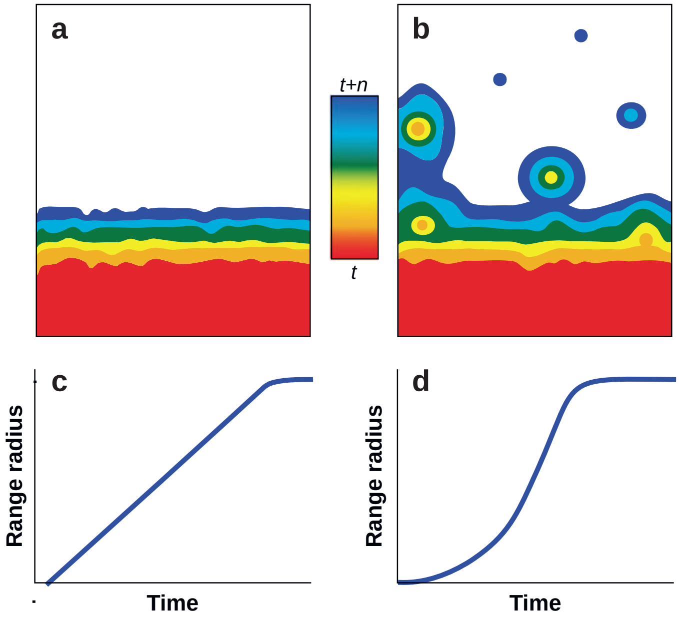

Figure 2

Patterns of spread. (*a*) Hypothetical map of spread under reaction-diffusion. (*b*) Hypothetical spread in the presence of stratified dispersal. (*c*) Hypothetical expansion of the range radius under reaction-diffusion. (*d*) Hypothetical expansion of the range radius under stratified dispersal.

dispersal, its existence has a fundamental effect on spread. The occasional long-range dispersal events initiate isolated colonies ahead of the advancing population front. These colonies grow and can eventually coalesce with the main population, resulting in a much more rapid rate of spread than if long-distance dispersal did not occur (**Figure 2*b***) (48, 119). The ramifications of stratified dispersal can be seen in the invasion dynamics of the Argentine ant, in which the spread from invading colonies with long-distance dispersal was about three times faster than from spread from colonies in which only short-distance dispersal occurred (130). Another fundamental effect is that under spread through simple diffusion (i.e., short-range dispersal only) (125), the rate of spread is constant through time (Equation 2) (**Figure 2*c***), but with stratified dispersal (120) the radial spread rate can (but does not always) accelerate over time (**Figure 2*d***). The mathematics literature has extensively explored traveling wave equations, and these have been widely applied to describe waves of invasion (46). Although traveling wave equations are typically characterized by asymptotically constant wave speeds, there are several situations (such as some cases of long-distance dispersal) in which this does not occur (143).

Ecological examples of the importance of long-distance dispersal and its effects on spread can be found in many invading insects, such as the gypsy moth (114), Argentine ant (130), Africanized honey bee (*Apis mellifera scutellata*) (147), hemlock woolly adelgid (80), emerald ash borer (*Agrilus planipennis*) (7, 88), and horse chestnut leafminer (*Cameraria ohridella*) (41). Several models have been developed that capture spread through stratified dispersal or leptokurtic dispersal kernels (64, 114, 120). However, the most problematic aspect of applying these models is the parameterization of long-distance dispersal. The rarity, and stochasticity, of movement over long distances leads to difficulty in its estimation (139). In a few cases, for which large quantities of detailed records of historical spread exist, it has been possible to directly observe the formation of isolated colonies and quantify the rate at which they form in relation to their distance from the expanding population front (114, 130). These long-distance dispersal events generally decrease in frequency as one moves progressively outward from the population front. Because long-distance dispersal is often caused by human activity, it may be possible to relate long-distance jumps to both distance and ancillary data. For example, Gilbert et al. (41) found that the frequency of jumps in the historical spread of the horse chestnut leafminer in Germany was related not only to distance but also to the local human population density, such that jumps were more common in densely populated areas because of the greater probability of accidental transport. Utilization of local characteristics that affect long-distance dispersal in spread models has been accomplished by the recent application of gravity models, which are based upon Newton's Law of Gravitation. Gravity models consider the site-specific properties of two locations (e.g., their respective population size), the distance between them, and their interaction strength (i.e., more populated locations attract more people and commodities than less populated locations) (10, 88).

Role of Allee Effects

The rate of nonindigenous species spread can be affected by the presence of stochasticity (both environmental and demographic) and Allee effects (53, 57, 64, 70, 133, 137, 142). At the edge of the expanding population front, populations are newly established and generally of low abundance. Given this initial small population size, both stochastic forces and Allee effects can have a pronounced role in limiting the population growth of these newly established populations. Lewis & Karieva (70) modified Skellam's (125) model to incorporate Allee effects at low densities. They showed that spread should still asymptotically reach a constant rate of spread but that this rate may be greatly depressed, depending on the strength of the Allee effect. In the case of a particularly strong Allee effect, spread rate reaches zero, a situation called range pinning, which can prevent a species from invading an otherwise suitable habitat (57). Kot et al. (64) used integrodifference equations, which represent a modeling framework fundamentally different than the reaction-diffusion model of Skellam (125), and observed that Allee effects can sometimes lead to accelerating speeds of invasion.

Isolated colonies born from long-distance dispersal and hence founded well ahead of the population front can likewise be expected to be subjected to Allee effects in a manner similar to newly arrived populations that are in the early stages of establishment (see Establishment, above). Theoretical studies have shown that Allee dynamics can negatively affect the growth and persistence of isolated colonies, thereby limiting spread rates (51, 131). Johnson et al. (53) noted a curious phenomenon of periodically pulsed spread every 3–4 years in historical records of gypsy moth range expansion, and contended that this behavior was caused by an interaction between stratified dispersal and Allee effects. Specifically, they observed that most isolated colonies founded from long-distance dispersal went extinct because of Allee effects, unless populations at the advancing population front were at sufficient levels such that they could found isolated populations that exceeded the Allee threshold. At this point, spread would pulse forward but then stop again until populations once again grew to sufficient levels. For more details of how Allee effects influence spread, the reader should consult Reference 133.

Habitat Variability

Another complexity that affects spread is geographical variation in habitat characteristics that affect reproduction or dispersal. The concept of invasibility, which has been applied most frequently to the study of plant invasions, focuses on habitat characteristics that increase or decrease the ability of a nonindigenous species to successfully spread into a new habitat (77). Some of these habitat characteristics that are thought to influence invasion success include the presence or absence of competitors and regulators (20, 97). For insects, there are several examples of both biotic and abiotic factors that vary across habitats and influence spread. Holway (49) reported that Argentine ant spread was greater in areas where elevated soil moisture promoted population growth. Evans & Gregoire (33) found that the hemlock woolly adelgid spread slower in cold climates than in warm climates where winter survival is higher. Sharov et al. (117) reported that the spread of the gypsy moth in Michigan was positively associated with forest susceptibility, but another study over a larger spatial extent failed to quantify a relationship between the success rate of newly establishing gypsy moth colonies and the quality of the habitat (145). Because geographical variation in long-distance dispersal can profoundly affect spread rates (41), and the establishment of isolated colonies formed through long-distance dispersal is subject to Allee effects, any variation in the habitat that affects Allee dynamics (e.g., ability to find mates and satiation of predators) can be expected to affect spread. Tobin et al. (137) analyzed historical data on the spread of the gypsy moth and detected considerable geographical and temporal variation in the strength of Allee effects, and they were furthermore able to document that there was a strong negative correlation between Allee strength and local spread rates. Several theoretical explorations indicate that spread rates are affected by habitat fragmentation and other aspects of the spatial arrangement of favorable habitat (58, 93, 148), but future work is needed to document these phenomena in nature.

Spread Latency

A characteristic observed in many biological invasions is that there is typically a period of time between the arrival of a nonindigenous species and its population growth to sufficient levels such that it is noticed (109). Memmott (82) found that in the year following the release of *Arytainilla spartiophila*, a herbivorous biological control agent, populations typically decreased and then slowly began to increase in following years. The Japanese beetle (*Popillia japonica*) spread slowly following its introduction into North America but then gradually increased its rate of invasion (119). Liebhold and Tobin (75) reported a delay of approximately 12 years from the initial accidental introduction of the gypsy moth into North America until populations were noticed. Several hypotheses have been advanced to explain these time lags. One explanation is the alteration of the habitat by the invader to make it more favorable over a long time period (105). Another hypothesis is the necessity for local adaptation by an invader, which occurs over a prolonged period (67). In some systems, the delay in population expansion is thought to be caused by the accumulation of multiple introductions that provide sufficient genetic diversity for population adaptation and growth (29, 63). In other cases, the delay may merely reflect that it takes time for the founding population to grow to levels sufficient to be detected, especially when the dominance of emigration over immigration acts as a drain on small, isolated populations (55, 119).

Estimation and Prediction of Spread

As part of investigations of specific invasions, there is often a need to forecast future spread, which in turn can be used to predict impacts and facilitate the timing of strategies aimed at minimizing these impacts. There are two conceptual approaches for predicting spread. The first approach involves using available data on life-history traits to parameterize mechanistic models of spread. In the simplest case, this may only involve using estimates of r and D and applying them in Equation 2 to predict the asymptotic radial spread rate. A major problem here is that, as noted above, the spread of most species is more complicated and typically involves both long-range dispersal and Allee effects. Although there are mechanistic models that capture these and other complications, collection of data adequate for parameterization of such models is often impractical. This leads us to the second approach, which is to predict future spread on the basis of empirical estimation of historical spread. Hastings et al. (46) advocated this as a more practical alternative for predicting future spread, even though there are several limitations to this approach as well. First, for invasions that have only recently been discovered, there may not be historical space-time data from which to draw. Second, the assumption that future spread will be the same as past spread does not always hold because spread rates may vary through time.

Several different approaches have been adopted for estimating spread rates from historical data (118, 119, 134). Although it is possible to describe spread in terms of either the rate of radial expansion or in terms of the rate of area increase, the latter is rarely

Detection: use of population surveys to identify the arrival of nonindigenous populations

Eradication: forced extinction of a population

used because the former often (but not always) increases in a linear fashion, whereas the latter more likely increases in a geometric fashion. When spread proceeds as the expansion of a perfect circle, the radius can be estimated simply as

$$\sqrt{\frac{A_t}{\pi}}, \qquad 3.$$

where A_t is the colony area at time t. The radial rate of expansion can thus be estimated according to

$$\frac{\left(\sqrt{A_{t+n}/\pi} - \sqrt{A_t/\pi}\right)}{n}, \qquad 4.$$

where n is the length of the observation period. However, in most cases there are geographical irregularities that limit the invaded habitat (i.e., bodies of water in the case of terrestrial insects), and invasion would not proceed in a perfectly circular fashion. These irregularities can bias estimates formed when using Equation 4. One alternative approach in these situations is to estimate the colony radius as the average of radii emanating from the point of introduction at equal-angle intervals. Radii that intersect irregularities (e.g., oceans) should be excluded when averaging the length of these radii. Because the shape of the invasion front may be irregular, another approach to measuring invasion speed is to simply average the distance between colony boundaries measured at regular intervals along the invasion front (**Figure 3*b***). Several other related methods for estimating spread rates from successive population boundaries have certain desirable features (116, 134), and many of these methods have been greatly facilitated by the use of a geographical information system.

It is important to note that the population front may not be directly measured as a continuous boundary, but instead data may consist of points or areas (e.g., counties) at which the presence or absence of the invading species has been historically recorded (**Figure 3*a***). Such data collected over several years can be converted to a space-time series of boundaries, which can then be used in methods described above to estimate radial rates of spread. Alternatively, the radial spread rate can be estimated as the slope of the linear regression of the distance from the site of introduction as a function of the date of first presence (**Figure 3*c***). For robust time series, this approach yields results comparable to other methods that depend on more extensive space-time distribution data (134). Evans & Gregoire (33) estimated historical spread rates for the hemlock woolly adelgid using Tobit regression, and noted that this approach provided a more unbiased estimate of spread from such space-time data.

It is often likely that historical data may be lacking from which spread rates can be estimated because the early stages of an invasion often go unnoticed. For example, the emerald ash borer was first discovered in North America in 2002 when it had already spread into a large region in Michigan and Ontario, and probably one or two decades after its arrival (101). Thus, the detection of a nonindigenous species in a specific location may not always accurately reflect the time of establishment. In some cases, it may be possible to reconstruct historical space-time invasion histories using specialized methods. This is particularly true for wood-boring insects, because larval galleries and adult emergence holes typically leave a record that can be dated from tree rings. Lu (78) utilized the results of such dendrochronological methods to backdate the timing of initial infestation of the Asian longhorned beetle (*Anoplophora glabripennis*) from a series of trees to reconstruct its spread in New York. Although labor-intensive, this approach is an innovative method of estimating the timing and subsequent spread of nonindigenous wood borers when less-expensive survey tools (i.e., pheromone-baited traps) are unavailable.

MANAGEMENT OF ESTABLISHMENT

Prevention of establishment requires driving the invading population to extinction. We define eradication as the total elimination of a

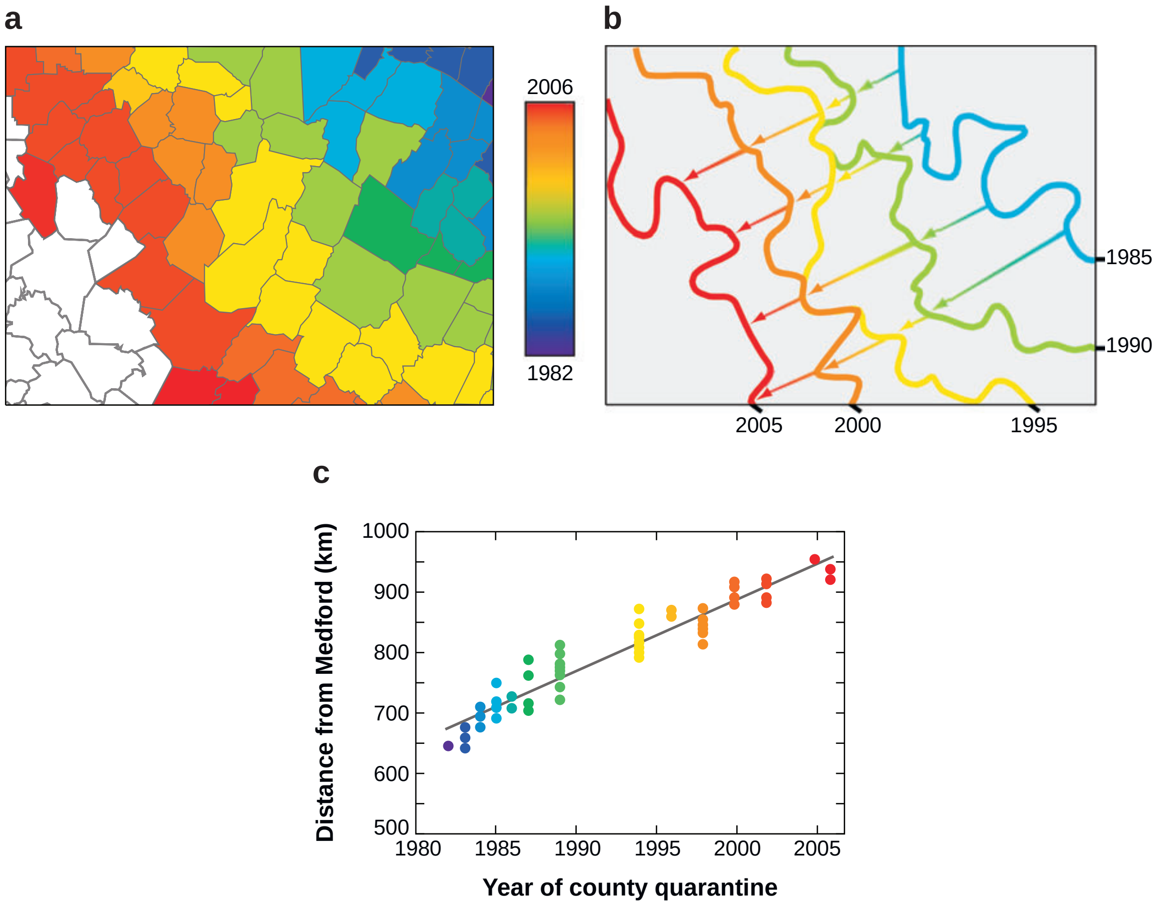

Figure 3

Methods for estimating radial rates of spread (134). (*a*) Example of typical records of the date of establishment by municipality [this example consists of records of gypsy moth invasion by county in portions of West Virginia and Virginia (134)]. (*b*) Estimation of spread rate by averaging distances between yearly boundaries. (*c*) Estimation of the spread rate as the slope of the regression of distance from the initial gypsy moth infestation in Medford, Massachusetts, as a function of time (in this example the slope was estimated as 11.7 km year^{-1}).

species from a geographical area (61, 89, 123). Despite the central role that eradication plays in the management of biological invasions, the entire concept has been controversial for many years (23, 89, 90, 123). One source of this controversy is a belief held by many that it is either impossible or impractical to eliminate every individual in a population (22). Another problem often raised is that eradication is impossible if there is a steady flow of new invaders ready to recolonize an area that is eradicated (15, 90). But perhaps the greatest reason for skepticism is the occurrence of several failed eradication programs, such as efforts to eliminate the red imported fire ant, *Solenopsis invicta*, from the United States (89, 98) [although this same insect was successfully eradicated from New Zealand (110)]. Of course, there are also many examples of highly successful eradication efforts (89, 122, 123). Thus it would appear that there is a need to clarify under what circumstances eradication is a practical option and how it might be most efficiently accomplished. We believe that the basic population processes associated with the establishment process (described above) are critical to these questions.

A common practical problem that is often raised about the eradication concept is the impracticality of killing every individual in a population. An implicit assumption of this argument is that eradication can only occur by eliminating all individuals within the population (22, 61). However, according to our knowledge of the population biology of sparse invading populations (see Establishment, above), most insect species exhibit both stochastic dynamics and Allee effects, and these processes are likely to drive small populations toward extinction without intervention. Thus, the critical strategy in eradication is not necessarily 100% reduction of a population but rather the reduction of a population below some threshold, below which they will proceed toward extinction without further effort (**Figure 2*b***). Liebhold & Bascompte (71) proposed a simple model of stochastic population growth coupled with Allee dynamics to illustrate this concept. They utilized the gypsy moth as a case study to parameterize the model and explored the relationship between population size and the killing power (i.e., % mortality) necessary to achieve eradication. This model explained why there exists a history of success in eradicating sparse gypsy moth populations using only one or two aerial applications of *Bacillus thuringiensis*, a treatment that is considered to achieve only 95% mortality in a best-case scenario (72, 83).

A viable strategy for achieving eradication might therefore be the application of a treatment (e.g., insecticide) that kills a sufficient proportion of a population such that the residual population falls below the Allee threshold and extinction proceeds. However, the crucial role played by Allee dynamics suggests an additional strategy, namely the manipulation of population processes such that the Allee threshold is increased (**Figure 2*b***). Examples of this approach are provided by various tactics designed to interfere with mating. Mating disruption (14, 150), mass-trapping (30), and the release of sterile insects (47, 60) are considered methods that reduce the probability of females mating with a fertile male. As such, they represent approaches for manipulating the Allee threshold by increasing it, and consequently they serve to enhance the role that Allee effects can have on low-density populations. It is therefore not surprising that there are many examples of how these methods facilitated successful eradication programs (30, 60). Although Allee effects are also caused by factors other than mating (19), we are not aware of any eradication strategies that have been based upon the manipulation of these other causes of Allee effects, nevertheless this might be a valuable avenue for further research.

Another argument against the concept of eradication is that in areas where a species is removed, reinvasion by the same species may occur, thus negating the eradication effort (89). This argument is furthermore strengthened in areas where propagule pressure is high (e.g., ports of entry), which would obviously make the task of eradication more difficult (27, 68). However, Simberloff (123) argued that while reinvasion detracts from the value of eradication, it does not necessarily make it a futile endeavor. Instead, cost-benefit analyses aimed at evaluating the economic and social benefits of eradication efforts should account for the probability of reinvasion. There are many examples of insect species (e.g., gypsy moth and Mediterranean fruit fly, *Ceratitis capitata*) that are repeatedly eradicated from areas following reinvasion, but the benefits of eradication in these cases vastly outweigh the cost of establishment; thus, eradication is still cost-effective (123). Areas of geographic isolation (e.g., islands) typically have lower rates of reinvasion, making eradication particularly practical. Aside from rates of reinvasion, other factors that should be accounted for in a cost-benefit analysis are the strength of Allee effects (which determines the extinction threshold), the availability and costs (both economic and social) of population suppression measures, and the availability and cost of survey techniques that are effective in low-density populations.

Survey techniques are indeed a critical component of any eradication effort. They are necessary both to delimit the spatial extent of the nascent population (and target suppression) and to evaluate the success of the effort. For some species, chemical attractants are available for use in inexpensive yet effective traps for detecting their presence. However, for other species, such trap tools may not be available, and surveys would have to rely on expensive techniques (e.g., visual examination) to detect and delimit a population. For example, pheromone-baited traps were not available during eradication efforts against the painted apple moth (*Teia anartoides*) in New Zealand; nevertheless, eradication was successfully achieved (at great expense) using traps baited with live females (produced in a rearing facility) as the primary survey tool (56). For pest species of potentially high economic importance but for which highly sensitive survey tools are lacking, it may be beneficial to regularly apply control measures in areas of known high propagule pressure, even in the absence of survey data indicating the presence of a population. For example, sterile male releases are made regularly as prophylactic treatments against establishment of invasive fruit flies in selected urban locations in the United States, Australia, and Japan (47). Nevertheless, the lack of efficient methods for surveying populations can greatly constrain the feasibility of eradication and should always be considered in cost-benefit analyses. Economic issues relating to such cost-benefit analyses are beyond the scope of this review; however, readers are directed to other sources that describe methods for evaluating the economic costs and benefits of both eradication and containment (96, 99, 113).

MANAGEMENT OF SPREAD

Management activities considered here consist of slowing, stopping, or reversing spread. Reversing or stopping spread probably require greater resources than slowing spread so the latter may be the most realistic objective. As is the case for management of establishment, the selection of one, if any, of these options depends on expected socioeconomic benefits as well as the population biology of the target species (113), but we limit our focus here to how population biology affects the selection of spread management strategies. Because spread is a species-specific phenomenon, optimal spread management strategies are likely to vary considerably among different species. In particular, individual species differ widely in the importance of long-range dispersal to spread, and various species may be more or less vulnerable to Allee effects and stochastic forces.

Because spread represents the coupling of dispersal with population growth, its management may focus on reducing dispersal, growth, or some combination of both. To iterate, long-distance dispersal events are typically less common than short-distance dispersal, but they have a greater influence on rates of spread; thus, expending a little effort to minimize long-distance dispersal events may greatly reduce spread. Because long-distance spread is frequently caused by humans, it may sometimes be controlled using domestic quarantines. For example, long-distance spread of exotic wood-boring insects, such as the emerald ash borer, occurs predominantly through the movement of infested firewood or nursery stock (88, 101). The sweetpotato whitefly, *Bemisia tabaci*, is generally spread through the shipment of contaminated plants (95), and the spread of the Asian tiger mosquito (*Aedes albopictus*) in the United States is largely related to the movement of used tires (86). Thus, quarantines that limit the movement of these items may greatly reduce the spread of these species (140). There is a long history of use of domestic quarantines to limit the spread of invading insects and readers should consult Reference 38 for a comprehensive treatment of this tactic. In some systems, other alternatives for reducing spread by mitigating long-distance dispersal may be available.

Delimit: use of surveys to characterize the spatial extent of an isolated alien population

Containment: a strategy designed to reduce the rate of spread of a nonindigenous species

Krushelnycky et al. (65) found that budding dispersal of Argentine ant colonies at the expanding population front could be stopped through pesticide applications, and in some cases, this tactic has completely eliminated spread into adjoining uninfested areas.

An alternative to limiting dispersal is reducing population growth. There are two approaches available: suppression of isolated colonies formed through long-distance dispersal, or suppression of populations at or behind the advancing population front. In most cases, the latter strategy may not be practical because of the shear magnitude of the area that must be suppressed. One exception to this is the effort in the United States to reverse the spread of the boll weevil (*Anthonomus grandis grandis*), which feeds primarily on cotton (45). But the success of this program may be attributed at least partially to its narrow host range, and for such invaders, the area where suppression must be targeted is likely to be smaller than that for polyphagous insects. Moreover, it may also be feasible, especially in the case of agricultural pests such as the boll weevil, to suppress populations simply by not planting its host crop for one or more years.

The other approach, suppressing outlying colonies, may be the most efficient strategy for reducing spread in most cases. The spread of several nonindigenous plant species is also dominated by long-distance dispersal, and theoretical studies indicated that the reversal of plant spread can most efficiently be achieved by first suppressing outlying isolated populations and then progressing efforts proximally (43, 132). Sharov & Liebhold (114) proposed a generalized model of slowing spread of an invading species by locating a barrier zone at the expanding population front. Within this zone, most isolated colonies formed through long-distance dispersal are eradicated. The benefit of this strategy is that the treatment of relatively small areas (isolated colonies) has a large, negative impact on spread. This strategy has been applied in the management of the gypsy moth spread in the United States using an approximately 100-km-wide barrier zone along its advancing front. The annual cost of this program is roughly $12 million, and gypsy moth spread has been reduced by over 60% (112, 135).

As with the management of establishment, a prime prerequisite to the success of any spread management effort is the availability of practical methods for detecting low-density populations. This is particularly crucial for strategies that focus on finding and eradicating isolated populations formed through long-range dispersal because densities of such populations are often low. Much of the credit for the success of gypsy moth containment efforts is attributed to the availability of pheromone-baited traps that are inexpensive yet highly sensitive for detecting low-density populations (135). For insects for which such survey methods are not available (e.g., the emerald ash borer), a containment strategy may not be practical.

The second prerequisite to successful management is the availability of control tactics that are effective at low densities. Ideally, at least some of the available control tactics should have minimal adverse nontarget and environmental impacts so that they may be applied in all potential habitats. A crucial consideration once again is the Allee effect. As previously mentioned, eradication can be achieved either by suppressing a population below the Allee threshold or by increasing the Allee threshold (**Figure 2*b***). This logic also applies to the management of spread, in particular to the eradication of isolated colonies formed by long-distance dispersal. The sterile male technique is one approach to increasing the Allee threshold and it has been successfully applied in efforts to stop or reduce the spread of invading insect species such as the Mediterranean fruit fly, the melon fly (*Bactrocera cucurbitae*), and the Mexican fruit fly (*Anastrepha ludens*) (60). Mating disruption is another approach to increasing the Allee threshold and is currently the primary treatment used in the current gypsy moth containment program (136).

One approach that has rarely been considered for management of spread but holds promise is classical biological control. Several models of spread that incorporate Allee effects indicate that introduction of predators or other natural enemy species can slow, stop, or even reverse the spread of their hosts (35, 97). Natural enemy population need not directly cause an Allee effect themselves, although a failure to satiate predators is a mechanism of an Allee effect. The impact of natural enemies on the growth of host populations can still enhance the negative effect of Allee effects on spread. Clear examples of this phenomenon in field populations are not common except for the work of Elkinton et al. (28), who provided convincing evidence that introduction of the generalist tachinid parasitoid, *Compsilura concinnata*, to North America in the late 1800s caused the spread of the browntail moth (*Euproctis chrysorrhoea*) to reverse, and currently, its range is limited to only a few isolated coastal locations. While introduction of generalist natural enemy species is inadvisable due to nontarget effects, the introduction of specialist species may hold potential for reducing the spread of certain nonindigenous species.

CONCLUSIONS

Given the increasing rates of nonindigenous species arrival and establishment, even though only a minority become destructive pests, there is little question that this is a problem out of control. Although technological and socioeconomic advances have facilitated spectacular increases in world trade and travel, these advances have unfortunately not been accompanied by the development of effective strategies for excluding the accidental transport of exotic pests. Because of the onslaught of invaders, eradication and containment are increasingly being attempted in response to these invasions. Unfortunately, the design of many of these programs has relied more heavily on intuition and optimism rather than on scientific principles (90, 122).

Over the past 10 years there has been an explosion of literature on the population ecology of biological invasions (76, 103), with many examples of how mathematical ecology can make useful predictions that have substantial applied value. Despite these advances, there still is a disconnect between the science and management of invasions. In this review we have attempted to bridge this gap by summarizing the science of invasion population ecology, and then illustrating how this information can be applied in developing effective management strategies. In particular, the important role of Allee dynamics presents a potential weak link during the establishment phase, and even during the spread phase, that can be exploited in the design and implementation of eradication and containment programs.

The field of invasion biology is still growing, and over the next decades, there likely will be important new advances in understanding the dynamics of the invasion process. But, in addition to the scientific challenges that invasions pose to population ecologists, there remain important challenges to pest management specialists in utilizing scientific information in management efforts. Thus, one of the important steps to bringing the nonindigenous species problem back under control will be to increase communication between scientists and pest management specialists to develop and apply science-based strategies.

SUMMARY POINTS

1. All biological invasions proceed through the arrival, establishment, and spread phases; specific management strategies can be implemented to mitigate each phase.

2. During the establishment phase, population dynamics are affected by population processes that are unique to low-density populations. The most critical of these are Allee effects and stochasticity.
3. Efficient strategies to eradicate invading populations capitalize on Allee effects by reducing populations below Allee thresholds or enhancing Allee effects.
4. Nonindigenous species spread is driven by the coupling of population growth with dispersal. While some species spread in a spatially continuous manner, most exhibit stratified dispersal, which results in discrete jumps that generally increase the rate of spread.
5. Efforts to contain or slow spread rates are most efficient if they target isolated newly established, low-density populations that arise through long-distance dispersal.
6. Allee dynamics affect these isolated populations; thus efforts for limiting spread should exploit the Allee effect.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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Annual Review of Entomology

Volume 53, 2008

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