Population Processes During Establishment and Spread of Invading Species: Implications for Survey and Detection Programs

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Abstract

Three important population processes occur during any biological invasion: arrival, establishment, and spread. Arrival is the process by which individual(s) of the invading organism are transported to their new habitat. Establishment can be considered the opposite of extinction and represents the growth of a newly arrived population sufficient such that extinction is impossible. Spread is the process by which the species expands its range into the new habitat. Because most biological invasions are caused by human activities, these activities are important to understanding the arrival process and the design of detection programs. Establishment is a highly stochastic process and Allee dynamics may be of considerable importance depending upon the life history of the invading species. These characteristics should be incorporated into the timing of responses to positive detection. Population spread is an area of considerable research currently. Early attempts to understand population spread were based upon a simple theory of reaction-diffusion. However, more recent studies indicate that spread often involves two or more forms of stratified dispersal whereby isolated colonies are founded ahead of the expanding population front; these colonies expand and coalesce with the expanding population front. Efforts to monitor spread should incorporate these characteristics.

Introduction

Since the time of Elton's (1958) seminal book on biological invasion, there has been growing attention by ecologists to various aspects of this subject. Because of the tremendous ecological and economic impacts of invasions, this area has drawn the attention of numerous studies focusing on the applied aspects of invasions. But biological invasions also may be considered miniature "ecological experiments" and, therefore, yield new insights into basic problems in ecology (Vitousek et al., 1996). Out of this work has evolved the field of "invasion ecology" that combines the following ecological sub-disciplines: community ecology, population ecology, landscape ecology, animal ecology, and plant ecology. This paper is a general overview of our current state of knowledge on the population ecology of biological invasions.

When considering the population biology of biological invasions, it is possible to recognize three processes underlying all invasions: arrival, establishment, and spread (Dobson & May, 1986) (Table 1). All three phases have been the object of considerable research. These components of the invasion process also are critical to understanding efforts to manage or control invasions: there is a unique correspondence between each stage of the invasion and the strategies for management.

Arrival

For millions of years, the world's biota has evolved in an environment in which the range of individual species was restricted by oceans, mountain ranges, and other barriers to their natural movement. We know that in prehistoric times, the range of many species changed naturally, mostly in response to changes in climate, but these changes were slow and ultimately limited by geographical barriers (Davis, 1987). Over the last century, the rate of new invasions has been increasing continuously (Sailer, 1978; Vitousek et al., 1996). There is little question that the primary reason for this acceleration of invasions is increased human travel and global trade, which have resulted in high rates of accidental transportation of species (e.g., in the ballast of ships) and intentional introductions (e.g., introduced agricultural plant species). Simberloff (1986) noted that patterns of species introductions parallel intercontinental commerce patterns (e.g., most introductions to North America have come from Europe). We also have accelerated the natural rate of biological invasions by

Table 1. The three basic population components of any biological invasion.

Process	Description	Management Approach
Arrival	Transportation of organism to a geographical location outside of its normal range	International quarantine, inspection
Establishment	Population growth to densities such that extinction is impossible due to random change alone	Detection, eradication
Spread	Range expansion	Domestic quarantine, barrier zones (containment)

disturbing habitats. Disturbances do not alter the arrival process but may enhance the establishment of certain species.

The gravity of the problems created by biological invasions was not fully realized until the early 1900s. Before then, most governments had a *laissez faire* attitude about exotic organisms. For example, faya tree, *Myrica faya*, was repeatedly introduced to the Hawai'ian Islands around the turn of the century for the purpose of reforestation (Whiteaker & Gardner, 1992). After it was established extensively, it became clear that this species crowds out native species. It was not until 1912 that the U.S. Congress finally enacted the Domestic Plant Quarantine Act, which gave authority to the U.S. Department of Agriculture to regulate the movement of plant and animal material into and within the United States (Weber, 1930). These and more recent federal quarantine measures were designed to reduce invasions by limiting the arrival process and thus represent a first line of defense.

Establishment

Every seed that falls to the ground does not develop into a reproducing plant. Similarly, many invaders may arrive in a new habitat but few become established. Here we define establishment as the process that results in a population that persists for many generations. Founder populations typically are small and consequently are at great risk of extinction. Generally, the smaller the founder population, the less likely is establishment (MacArthur & Wilson, 1967). It may be possible to identify a "minimum viable population," though establishment is not a deterministic process and in reality the association between population size and establishment is a stochastic[1] relationship. This function reflects many characteristics of the species, such as its intrinsic rate of reproduction, mate location abilities, dispersal, and genetic diversity (Mollison, 1986).

Two population processes are particularly important when considering establishment: demographic stochasticity and environmental stochasticity. We can mathematically represent the generational change in population density as:

$$N_{t+1} = f(N_t) + \varepsilon 1_t + \varepsilon 2_t \qquad (1)$$

where N_t is population density in year t, $f(N_t)$ is a function that encompasses birth and death processes, å1_t is random variation due to demographic stochasticity, and å2_t is variation due to environmental stochasticity. Demographic stochasticity is random variation in population growth due to variation among individuals in birth and death rates. It is different from environmental stochasticity, which is random variation in birth/death due to temporal variation in the habitat. All populations are affected by environmental stochasticity because of ubiquitous temporal variation in the abiotic environment (e.g., weather). But only low-density populations are affected by demographic stochasticity. When densities are high, variation among individuals averages out to near zero and therefore has little effect on changes in population density. But when densities are low, variation among individuals is proportionally more significant and can dramatically affect changes in density at the population level (Kendall, 1998). The fact that demographic stochasticity affects low-density populations and may lead them to extinction has been recognized as an important issue relating to conservation ecology issues (Stacey & Taper, 1992; Lande, 1993), but has been less widely recognized for its importance in the invasion process.

The important result of demographic and environmental stochasticity is that low-density populations (e.g., newly founded invading populations) are particularly prone to extinction purely as a result of this random variation. However, there is a third source of extinction in low-density populations that should be mentioned: Allee dynamics.

When Warder Allee (1931) wrote his text on animal population ecology, he recognized a phenomenon that exists in populations of certain species: low-density populations are affected by a positive relationship between population growth rate and density (inverse

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[1] Stochastic events or parameters are those governed by probability.

density-dependent mortality). The result of this relationship is that low-density populations are driven toward extinction (Figure 1). This phenomenon, termed the "Allee effect", may result from a multitude of biological mechanisms, e.g., cooperative hunting, predator satiation, and failure to find mates at low densities (Courchamp et al., 1999). The Allee effect has been recognized as critical to understanding patterns of extinction from the perspective of conservation biology (Stephens & Sutherland, 1999), but less is known about its role during biological invasions. Obviously some organisms (e.g., parthenogenetically reproducing aphids) may not exhibit any Allee dynamics but many species (presumably this would include any species that must mate to reproduce) would be expected to exhibit some form of Allee effect at low densities. Hopper and Rousch (1993) used historical data on successes of attempted introductions of varying numbers of individuals of different parasitoid species to show that the successful establishment of these species was explained by Allee dynamics. It is likely that Allee dynamics may be of critical importance to a number of invading species and therefore may be essential to understanding why some species establish more easily than others.

Another population process that affects establishment is dispersal. The ability of an organism to move long distances may enhance its role as an invader from the perspective of arrival and spread. However, from the perspective of establishment, dispersal may, in fact, detract from its ability to invade, because the Allee effect and stochasticity may interact with dispersal in an important manner. We can conclude from the prior discussion that both stochasticity and Allee dynamics may create the existence of a "critical population density threshold" below which establishment is impossible (Figure 1). Obviously, high growth rates allow certain species to exceed such thresholds and overcome these low-density effects. However, dispersal of individuals from their point of recruitment may reverse the effect of population growth and thereby reinforce low-density effects due to stochasticity or Allee effects.

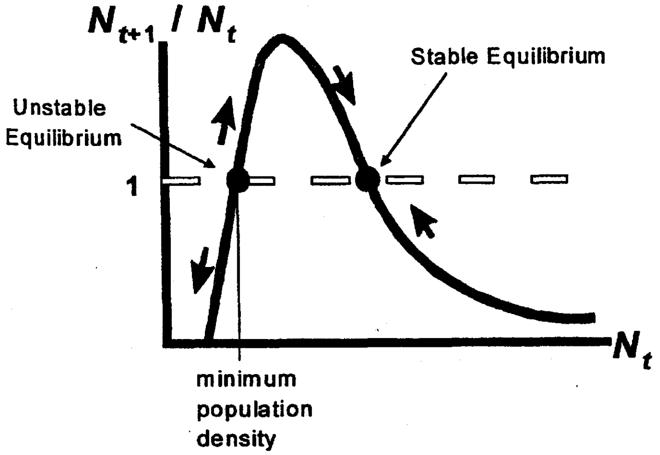

Figure 1. Schematic representation of the Allee effect. Change in population density, N_{t+1}/N_t, is plotted as a function of density at the beginning of the generation, N_t. This relationship determines change in population density f (Nt), shown in equation 1. Note that when density is greater than the minimum population density, it will increase or decrease toward the stable equilibrium, but when it is below this threshold, density will decrease toward extinction.

Understanding this proces has important implications for management. The activity we call "eradication" is aimed at reversing the process of establishment; eradication is forced extinction. It follows from the previous description that eradication is likely to succeed only in situations in which the target population is both low in density and highly restricted in its spatial distribution.

Spread

Once a population is established, its density typically will increase and individuals will disperse into adjoining areas of suitable habitat. For most biological invasions, this spread is the only process that we are able to observe directly; the arrival and establishment phases usually occur without notice by humans. For example, the pine shoot beetle, *Tomicus piniperda*, already was established in six states by the time it was discovered (Haack & McCullough, 1993).

The spread of a species is driven by two processes: population growth and dispersal. As a result most models of population spread have focused on these processes. The simplest and probably the most widely applied model of population spread was developed by Skellam (1951). This model combined Fick's law of diffusion with an exponential model of population growth.

Fick's law assumes random movement (diffusion) and states that the concentration, *C*, of particles is normally distributed across any dimension, *x;* thus, the concentration at any point in time after release at point $x = 0$ is described by:

$$C_{x,t} = \frac{M\, e^{-x^2/4Dt}}{2\sqrt{\pi D t}} \qquad (2)$$

where *t* is the time since the initial release of *M* particles at point $x = 0$ and *D* is the "diffusivity" or "diffusion coefficient" (Okubo, 1980). The diffusion coefficient is constant for any class of particles and set of environmental conditions; *C* is distributed normally at time *t*, with a variance of *Dt*.

The exponential population growth model describes the concept of unlimited population growth:

$$Nt = N_0 e^{rt} \qquad (3)$$

where N_t is the number of individuals at time t and r is the "intrinsic rate of natural increase" (birth rate – death rate under optimal condition; i.e., no crowding) (Varley et al., 1973).

Skellam (1951) combined Fick's law of diffusion with the exponential growth model to obtain a generalized model of the spread of an invading organism:

$$Nx,t = \frac{N_{0,0}\ e^{rt-x^2/4Dt}}{4\pi Dt} \qquad (4)$$

where $N_{x,t}$ is the density of organisms distance, x, from the point of release and time, t, from the time of release of $N_{0,0}$ organisms at time 0. The assumption of random movement in this model implies that the population will spread radially, at an equal rate in all directions (Figure 2A). Skellam (1951) showed that for any detection threshold, T, such that the infested area at any time t is restricted to points where $N_{x,t} > T$, the expansion velocity of the infested front (radial rate of spread), V, is constant and can be described:

$$V = 2 \qquad (5)$$

This model assumes that r and D are constant through time and space during the period of range expansion of the invading organism, an assumption that does not intuitively seem likely (e.g., spatial variation in the habitat may profoundly affect birth/death functions as well as dispersal rates). Nevertheless there has generally been good congruence between predictions of this model and observed rates of spread of most exotic organisms (Levin, 1989; Andow et al., 1990).

Skellam's model assumes a single, continuous form of dispersal and it predicts that range expansion should be a smooth, continuous process (Figure 2A). However some species may be able to disperse in at least two ways. The existence of two forms of dispersal is referred to as "stratified dispersal" (Hengeveld, 1989); in those situations, range expansion will proceed through the formation of multiple discrete, isolated colonies established ahead of the infested front (Shigesada et al., 1995; Shigesada & Kawasaki, 1997). These colonies, in turn, will expand their range and ultimately coalesce. The result of this phenomenon is that range expansion may occur much faster than would occur under a more simple diffusion model.

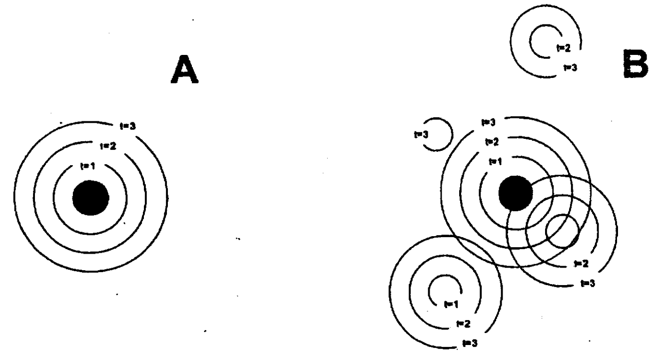

Figure 2. *Schematic representation of range spread between successive generations. The black dot represents the initial range at time 0. A shows spread according Skellam's (1951) diffusion model; B illustrates spread predicted using a stratified dispersal model.*

The contrast between these two models can be illustrated using the gypsy moth, *Lymantria dispar*, as a case study. Liebhold et al. (1992) used estimates of r and D in Skellam's model (equation 5) to estimate the radial rate of range expansion as ca. 2 km/year. The value of D that Liebhold et al. (1992) used was based on the assumption that dispersal only occurs via windborne dispersal of first instars. However Liebhold et al. also reported that over the period 1965–1990 North American gypsy moth populations actually spread at a rate of ca. 21 km/yr, which was much greater than the value predicted using Skellam's model. They concluded that the greater observed rate of spread was due to a second form of dispersal, namely accidental transportation of life stages, and that this stratified dispersal was the cause of the greater spread rates observed. Sharov and Liebhold (1998a) used historical gypsy moth trapping data to identify isolated colonies ahead of the advancing gypsy moth population front (Figure 2B). These data were used to parameterize a stratified dispersal model that predicted the historically observed 21 km/yr rate of spread.

Numerous plant invasive species spread according to a stratified dispersal model (Shigesada & Kawasaki, 1997). An interesting aspect of this type of spread is that establishment is an important component. Isolated colonies are formed ahead of the expanding population front due to dispersal of propagules (Figure 2B), but the ability of these propagules to successfully found new populations that spread and coalesce is entirely dependent upon their ability to establish successfully. Therefore, all of the population processes that are important to establishment, namely stochasticity and Allee dynamics, may be of critical importance to the spread process. For example, the existence of a strong Allee effect will reduce probabilities of establishment, which, in turn, may reduce rates of spread (Lewis & Kareiva, 1993). Studying the historical spread of the house finch in North America, Veit and Lewis (1996) found that mating success in isolated, low-density populations is low and that this results in a strong Allee effect. Veit and Lewis (1996) modeled this effect and showed that Allee dynamics were of critical importance in explaining observed rates of spread.

Implications for Invasion Management Strategies

Understanding the processes operating during the invasion process is critical to virtually all aspects of managing biological invasions. As shown in Table 1, different invasion management activities correspond to each of the three phases of biological invasions. When contemplating different approaches to managing invasions, one should weigh the costs and benefits of concentrating activities at different stages of the invasion process. For example, Sharov and Liebhold (1998b) developed a general bioeconomic model of invasions and illustrated how it can be used to identify an optimal strategy of eradication versus containment. That model used information about rates of spread, costs of eradication, costs of containment, and economic impacts to compare the costs and benefits of eradication versus containment versus no action. Any strategic decision of this type will be highly dependent on the population biology of the organism of interest. Dispersal, population growth rate, stochasticity, and Allee dynamics are likely to influence the selection of a management strategy. For example, if a given species has a relatively high minimum population-density threshold (Figure 1), it may not be necessary to eradicate populations detected at low levels; or if higher densities are detected, eradication may be accomplished simply via suppression to or below that critical density. The combined action of stochasticity and Allee dynamics may accomplish the final act of eradication with no further intervention.

Population biology also should be considered when evaluating the risk of invasion for any species. The probability that a species will successfully invade a new habitat is a function of its ability to arrive, establish, and spread. Some species may be at great risk to one phase of the invasion process, but be at low risk for another phase. For example, tree-killing bark beetles of the genus *Dendroctonus* may be at high risk of arrival in exotic habitats due to their ability to complete development on raw wood, but they are of low risk to establishment because their ability to colonize and reproduce on hosts requires aggregations of large numbers of individuals (a type of Allee effect).

Finally, the population dynamics of an organism may be of critical importance when designing a detection system. As stated earlier, certain species may have a critical density below which stochasticity and/or Allee dynamics drives them to extinction (Figure 1). The relative level of such a threshold should determine the detection threshold that is necessary for a given species. If that threshold is relatively high, detection devices need not be highly sensitive (e.g., light traps, plant volatile-baited traps) and the traps need not be spaced too densely. However, when the critical-density threshold is relatively low, a more sensitive detection system (e.g., sex pheromone baited traps) may be required. In some cases, it may be difficult to obtain and use a species' life-history traits to predict these demographic relationships, but some information usually is available to make these distinctions at a coarse level. These relationships highlight the need to collect more information about the population biology of candidate alien species. Often, little is known about the population ecology of isolated, low-density populations of most species. These considerations underscore the need for additional research.

References

Allee, W.C. 1931. Animal Aggregations. A Study in General Sociology. University of Chicago Press, Chicago.

Andow, D.A., P.M. Kareiva, S.A. Levin and A. Okubo. 1990. Spread of invading organisms. Landscape Ecology 4:177–188.

Courchamp, F., T. Clutton-Brock and B. Grenfell. 1999. Inverse density dependence and the Allee effect. Trends in Ecology and Evolution, 14(10):405–410.

Davis, M.B. 1987. Invasions of forest communities during the holocene: beech and hemlock in the Great Lakes region. Symposium British Ecological Society 26:373–393.

Dobson, A.P. and R.M. May. 1986. Patterns of invasions by pathogens and parasites. In: Ecology of Biological Invasions of North America and Hawaii, H.A. Mooney and J.A. Drake (eds.). Ecological Studies 58. Springer-Verlag, New York, pp. 68–76.

Elton, C.S. 1958. The Ecology of Invasions by Animals and Plants. Methuen, London, 181 pp.

Haack, R.A. and D.G. McCullough. 1993. Update on the pine shoot beetle. Michigan Christmas Tree Journal 36:20–21.

Hengeveld, R. 1989. Dynamics of Biological Invasions. Chapman & Hall, London.

Hopper, K.R. and R.T. Roush. 1993. Mate finding, dispersal, number released, and the success of biological control introductions. Ecological Entomology 18:321–331.

Kendall, B.E. 1998. Estimating the magnitude of environmental stochasticity in survivorship data. Ecological Applications 8:184–193.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911–927.

Levin, S.A. 1989. Analysis of risk for invasions and control programs. In: Biological Invasions: a Global Perspective, J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson (eds.). SCOPE 37. Wiley, Chichester, U.K., pp. 425–435.

Lewis M.A. and P. Kareiva. 1993. Allee dynamics and the spread of invading organisms. Theoretical Population Biology 43:141–158.

Liebhold, A.M., J. Halverson and G. Elmes. 1992. Quantitative analysis of the invasion of gypsy moth in North America. Journal of Biogeography 19:513–520.

MacArthur, R.H. and E.O. Wilson. 1967. The Theory of Island Biogeography. Monographs in Population Biology 1. Princeton University Press, Princeton.

Mollison, D. 1986. Modeling biological invasions: chance, explanation, prediction. Philosophical Transactions of the Royal Society of London, Biological Sciences 314:675–693.

Okubo, A. 1980. Diffusion and Ecological Problems: Mathematical Models. Biomathematics 10. Springer-Verlag, Berlin.

Sailer, R.I. 1978. Our immigrant insect fauna. Bulletin of the Entomological Society of America 24:3–11.

Sharov, A.A. and A.M. Liebhold. 1998a. Model of slowing the spread of the gypsy moth (Lepidoptera: Lymantriidae) with a barrier zone. Ecological Applications 8:1170–1179.

Sharov, A.A. and A.M. Liebhold. 1998b. Bioeconomics of managing the spread of exotic pest species with barrier zones. Ecological Applications 8:833–845.

Shigesada, N. and K. Kawasaki. 1997. Biological Invasions: Theory and Practice. Oxford University Press, Oxford, U.K.

Shigesada, N., K. Kawasaki and Y. Takeda. 1995. Modeling stratified diffusion in biological invasions. American Naturalist 146:229–251.

Simberloff, D. 1986. Introduced insects: A biogeographic and systematic perspective. In: Ecology of Biological Invasions of North America and Hawaii, H.A. Mooney and J.A. Drake (eds.). Ecological Studies 58. Springer-Verlag, New York, pp. 3–26.

Skellam, J.G. 1951. Random dispersal in theoretical populations. Biometrika 38:196–218.

Stacey, P.B. and M. Taper. 1992. Environmental variation and the persistence of small populations. Ecological Applications 2:8–29.

Stephens, P.A. and W.J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends in Ecology and Evolution, 14(10):401–405.

Varley, G.C., G.R. Gradwell and M.P. Hassell. 1973. Insect Population Ecology. University California Press, Berkeley.

Veit, R.R. and M.A. Lewis. 1996. Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. American Naturalist 148:255–274.

Vitousek, P., C.M. D'Antonio, L. Loope and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist 84:468–478.

Weber, G.A. 1930. The Plant Quarantine and Control Administration: Its History, Activities and Organization. Brookings Institute for Government Research Service Monograph of the U.S. Government No. 59. Washington, DC, 198 pp.

Whiteaker, L.D. and D.E. Gardner. 1992. Firetree (*Myrica faya*) distribution in Hawai'i. In: Alien Plant Invasions in Native Ecosystems of Hawaii: Management and Research, C.P. Stone, C.W. Smith and J.T. Tunison (eds.). University of Hawaii Cooperative National Park Research Studies Unit, Honolulu, pp. 225–240.

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