BIOLOGICAL INFORMATION AS THE BASIS FOR STRATEGIES TO MANAGE ALIEN FOREST PEST SPECIES

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SUMMARY

Invasions by destructive alien forest pest species are occurring at an increasing rate. Alien species exhibit a variety of impacts on forest ecosystem processes and some severely limit the sustained management of forests for specific values. In this paper it is discussed the state of knowledge on the population biology operating during the arrival, establishment and spread phases of biological invasion and also how this information can be used to optimize strategies for managing forest pests. In particular, how information on invasion pathways can be used to formulate exclusion strategies. Further it is discussed the role of Allee effects during the establishment and early growth of invading populations and how knowledge of these population processes can be used to optimize the detection and eradication of such populations. Finally is discussed the current state of knowledge on the population biology of range expansion and how this information can be used in programs to contain alien species populations. This review highlights the use of mathematical population biology concepts in predicting invasions and formulating management strategies.

Key words: Forest pests, population biology, mathematic models

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INFORMACIÓN BIOLÓGICA COMO BASE PARA ESTRATEGIAS DE MANEJO DE PLAGAS FORESTALES EXÓTICAS

RESUMEN

Las invasiones por destructivas plagas forestales exóticas están ocurriendo a una tasa creciente. Las especies invasoras provocan diversos impactos sobre los procesos de los ecosistemas forestales y algunas restringen severamente el manejo sustentable del bosque para productos específicos. En el documento se discute el estado del conocimiento sobre como actúa la biologia poblacional durante las fases del ingreso, establecimiento y expansión de la invasión biológica y se discute como usar esta información para optimizar estrategias de manejo de plagas forestales. Particularmente se analiza como la información relacionada con las vías de invasión puede usarse para formular estrategias de exclusión. Adicionalmente se discute el rol del "*efecto Allee*"[2] durante el establecimiento y crecimiento inicial de la población invasora y como el conocimiento de esta población puede usarse para optimizar su detección y erradicación. Finalmente se discute el estado actual del conocimiento sobre la biología de la expansión de la población y como esta información se puede usar en programas para frenar a las poblaciones de especies invasoras. El enfoque destaca el uso de conceptos matemáticos de biologia de poblaciones en la predicción de ataques y formulación de estrategias de manejo.

Palabras clave: Plagas forestales, biología de poblaciones, modelos matemáticos

[2] Efecto atribuido al biólogo estadounidense Warder Allee, que en ecologia de poblaciones relaciona la densidad de la misma con su tendencia a la extinción. (*Nota del Editor*)

INTRODUCTION

In virtually every portion of the world, invasions by destructive alien forest pest species are occurring at an alarmingly increasing rate (Brockerhoff *et al.*, 2006, McCullough *et al.*, 2006). Many of these species have immense impacts on forest ecosystem processes and threaten the sustained management of forests (Liebhold *et al.*, 1995; Vitousek *et al.*, 1996).

Three phases are generally recognized in all biological invasions: arrival, establishment and spread (Shigesada and Kawasaki, 1997; Sakai *et al.*, 2001; National Research Council, 2002) (Table N° 1). Arrival is the process by which an alien species is transported to a novel habitat that is outside of its native range. Establishment refers to the growth of a newly arrived population to a level such that extinction is no longer likely. Spread is the expansion of the newly established population across the range of its nonnative habitat. There are several different types of approaches to managing biological invasions, and each approach corresponds to different stages of the invasion process (Table N° 1). First is discussed the basic biology operating during each invasion phase and then is described how this information can be used to guide management activities.

Table N° 1
THE THREE PRINCIPAL INVASION PHASES

Phase	Description	Management Activities
Arrival	Founding members of the population are transported to the new area.	Quarantine, inspection
Establishment	Founding population grows sufficiently such that extinction is no longer possible.	Detection, eradication
Spread	The species range expands into all habitable portions of the new geographical area.	Barrier zones

ARRIVAL

This phase coincides with the transport of individuals from their original range to a completely new region. In many cases this consists of the transport of a species to a new continent. It is the existence of many new transport mechanisms, known as "invasion pathways," that has lead to problematic increases in numbers of biological invasions over the last 100 years. As such, considerable insight into the causes of invasions can be gained by studying these pathways (Everett, 2000).

An important invasion pathway that has been identified for forest insects is the inter-continental movement of solid wood packing material, which has been implicated in the introduction of several wood-boring insects (Brockerhoff *et al.*, 2006; Haack, 2006). Many other invasion pathways, such as the introduction of infected nursery stock, have been implicated as pathways in the accidental introduction of other exotic forest insect and diseases. Not all invasion pathways involve accidental movement or hitchhiking. Vast numbers of parasitoids and predators have been introduced from other continents as part of classical biological control efforts. Noteworthy examples of pest species that were introduced by individuals who carelessly let them escape include the Africanized bee (Winston, 1992) and the gypsy moth (Liebhold *et* *al*., 1989).

Clearly the most efficient approach to managing the problem is excluding species before they arrive and become established. Once an important invasion pathway has been characterized, this information is of critical importance in formulating international quarantines and inspection programs aimed at excluding certain pest species. Unfortunately there are various economic and political issues that often hamper the implementation of such measures and therefore, government agencies are often not able to keep up with the ever increasing numbers of invasion pathways (Campbell, 2001).

ESTABLISHMENT

Every seed that falls to the ground does not eventually become a tree. Similarly, many invaders may arrive in a new habitat, but few become established and cause inimical economical and environmental effects (Mack *et al*., 2000). 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 and Wilson, 1967; Mollison, 1986). 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 random abiotic influences (e.g., weather), but low-density populations are particularly influenced by both environmental and demographic stochasticity. The important result, particularly when subject to demographic effects, is that low-density populations (e.g., newly founded invading populations) are especially prone to extinction purely as a result of this random variation. However, there is another factor contributing to extinction of low-density populations that must also be considered: Allee dynamics.

Warder Allee (1932) studied animal population ecology, and is generally recognized as the first worker to recognize a phenomenon that exists in low-density populations of most species: certain processes may lead to decreasing net population growth with decreasing density. As a result of this relationship, there sometimes exists a threshold below which low-density populations are driven toward extinction (Figure N° 1). This phenomenon, termed the "*Allee Effect*", may result from a multitude of biological mechanisms, e.g., absence of cooperative feeding, failure to satiate predators, and failure to find mates at low densities (Courchamp *et al*., 1999). The Allee effect has been identified as critical to understanding patterns of extinction from the perspective of conservation biology (Stephens and Sutherland, 1999), and there is growing recognition of its important role during the establishment phase of biological invasions (Drake, 2004; Leung *et al*., 2004; Taylor and Hastings, 2005). The magnitude of Allee effects vary tremendously among species due to variation in life history traits, however virtually every sexually reproducing species can be expected to exhibit an Allee effect at low densities. As such, Allee dynamics may be of critical importance to understanding why some species establish more easily than others.

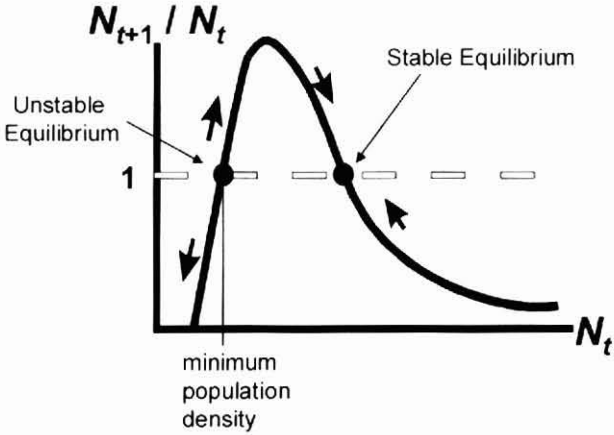


Figure N° 1

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 $f(N_t)$ 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 the establishment process has important implications for management. The activity called "eradication" is aimed at reversing the process of establishment; in other words, eradication is forced extinction (Myers *et al.*, 2000). 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. Liebhold and Bascompte (2003) used an Allee effect model to illustrate the numerical relationships between initial numbers of individuals, the strength of an eradication treatment (% killed), and the probability of population persistence to document the existent of a positive relationship between the initial size of the founder population and the probability of establishment.

SPREAD

Once a population is established, its density typically will increase and individuals will disperse into adjoining areas of suitable habitat. Three phases to the range expansion process are generally recognized (Shigesada and Kawasaki, 1997) (Figure N° 2). Following establishment of the alien population, there is an initial period during which spread accelerates. In the early stages of this phase, populations may remain at extremely low densities and therefore remain undetected for several years (Kean and Barlow, 2000). The bulk of range expansion occurs during the expansion phase. During this phase, the radial rate of spread often increases linearly but in other cases it may accelerate in a nonlinear fashion (Andow *et al.*, 1990). Finally, as the expanding range begins to saturate the geographic extent of suitable habitat, spread declines and ultimately stops.

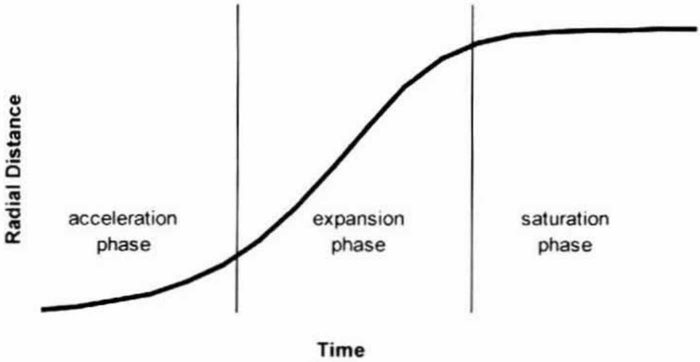
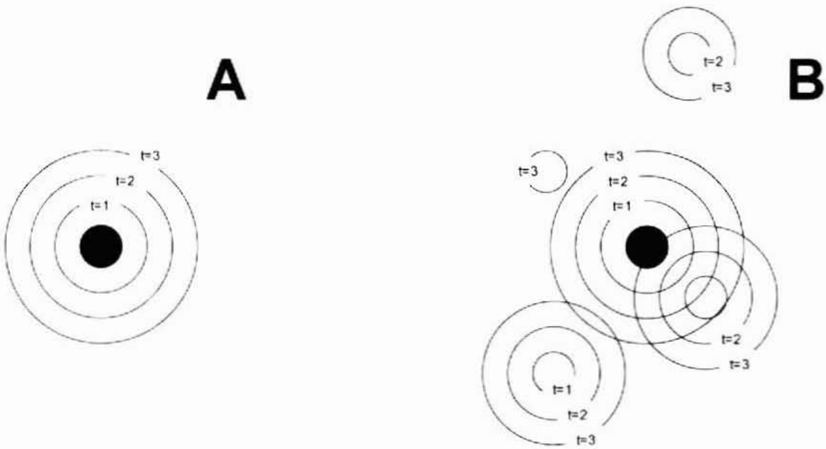


Figure N° 2
GENERALIZED RANGE EXPANSION OF INVADING SPECIES. RADIAL DISTANCE REFERS TO THE DISTANCE FROM THE SITE OF INTRODUCTION TO THE EXPANDING POPULATION FRONT.

The spread of a population 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 random (Gaussian) dispersal with exponential (Malthusian) population growth to model expansion following an initial introduction of individuals. Skellam (1951) used this model to show that the radial rate of expansion of the infested population front (radial rate of spread) should be constant and directly proportional to the square root of the product of the "diffusion coefficient" (a measure of the amount of movement) and the intrinsic rate of increase (this is a measure of population growth under ideal conditions). The assumption of random movement in this model implies that the population will spread radially, at an equal rate in all directions (Figure N° 3a).

Skallam's model makes several simplifying assumptions, such as that movement is random and organisms spread through a homogenous environment. Nevertheless there has generally been some (but not total) congruence between predictions of this model and observed rates of spread of exotic organisms (Andow *et al.*, 1990; Shigesada and Kawasaki, 1997).



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

Figure N° 3
SCHEMATIC REPRESENTATION OF RANGE SPREAD BETWEEN SUCCESSIVE GENERATIONS.

Skellam's model assumes a single, continuous form of dispersal and it predicts that range expansion should be a smooth, continuous process (Figure N° 3a). 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, isolate colonies established ahead of the infested front (Shigesada *et al.*, 1995; Shigesada and 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 diffusion model.

Numerous animal and plant species spread according to a coalescing colony model (Shigesada and 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 N° 3b), 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 and Kareiva, 1993). Veit and Lewis (1996), in studying the historical spread of the house finch in North America, 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 was of critical importance in explaining observed rates of spread.

For practical reasons it may not be economically viable to contain the spread of a species after it is established. Sharov and Liebhold (1998a) proposed a mathematical approach for balancing costs and benefits in evaluation of the practicality of eradication and containment activities. In some cases it may be beneficial to slow the spread of an invading species, without necessarily stopping its spread or totally eradicating it. In programs which attempt to slow the spread of an invading species that spreads via a stratified diffusion process, the optimal approach may be to locate and eradicate isolated colonies before they enlarge (Sharov and Liebhold, 1998b; Taylor and Hastings, 2004, Tobin *et al.*, 2004; Grevstad, 2005).

CONCLUSION

The problem of alien forest pests is increasing in magnitude and given current trends of increasing world trade and travel, it can expected the problem to continue to intensify. While there have been important advances in the understanding of the biology of invasions, there are many processes that are not fully understood. In particular, it is known relatively little about biotic interactions operating during the very early phases of establishment, in part due to the difficulty of sampling very sparse populations. Given the importance of the alien species problem, authors anticipate that research on the biology of invasions to increase resulting in an improvement of our understanding of these processes. Hopefully, the increase in knowledge will lead to new and more effective approaches to limiting this unwanted consequence of globalization.

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