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Alien Species as Agents of Global Change

Ecology and Management of the Gypsy Moth in North America as a Case History

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Abstract - Throughout evolutionary history, water and land barriers served to isolate the world's biota into distinct compartments. With the advent of greater human mobility and world trade, these barriers are breaking-down and alien species are increasingly being transported into new habitats. Many alien species have had devastating impacts on their new environment resulting in huge changes in ecosystem processes and properties. In this paper I provide an overview of the population biology of invasions, highlighting the three principal phases of every invasion: arrival, establishment and spread. Furthermore, I demonstrate that for each invasion phase, there is a corresponding phase of management activities aimed at retarding the invasion. Finally, I illustrate the three invasion phases using the gypsy moth, *Lymantria dispar*, in North America as a case history.

I Introduction

From an evolutionary perspective, humans are a small and perhaps insignificant group. But despite this insignificance, our populations have grown to remarkably high levels on almost every continent and major landform. The increases in the world's human population have been quite closely linked to the ability of humans to alter their environment. During the primordial phases of human development, modifications of our habitat were fairly benign and had rather insignificant effects on the biotic and abiotic environments. However, over the last 100 years, we have begun to affect our surroundings in much more dramatic ways. Throughout the world, we have left substantial impacts on our surroundings and disrupted numerous ecosystems. These changes have drastically affected the immense services that natural ecosystems provide the world's population [1, 2].

When considered as a global aggregate, these anthropogenic effects are substantial and are referred to as "global change". These changes are of considerable concern and importance because they affect biological and abiotic properties at the global level and thus the entire world population is affected. Most interest in sources of global change involves anthropogenic changes to the atmosphere, such as release of CFCs causing ozone depletion and increases in CO_2 and methane, but other major concerns include land use changes and habitat fragmentation [3]. These primary causes may result in secondary effects such as climate change and diminished biodiversity.

Only recently has the problem of biological invasions become recognized as another important agent of global change [4, 5]. The concept that biological invasions might be considered a recurrent problem at all was first recognized less than 50 years ago by Elton [6] who documented many instances in which species accidentally transported from one continent to another had erupted to very high densities, often at the expense of native species. Since then numerous studies of invasions by non-indigenous organisms have been shown to cause dramatic changes in ecosystem functions and properties (e.g., biodiversity, nutrient cycling, disturbance regimes) and these changes may be manifest as important biotic and abiotic changes at the global level [4, 7, 8].

Although biological invasions are a problem throughout the world, the deciduous forests of temperate northeastern North America have been affected by alien insects and diseases particularly frequently and intensely over the last 75 years [9, 10]. During the early 1900s the chestnut blight, caused by the exotic fungal pathogen *Cryphonectria parasitica*, caused the virtual elimination of American chestnut, *Castanea dentata*, which was previously one of the most dominant species in the eastern U.S. [11]. Similarly, Dutch elm disease (caused by the fungal pathogen, *Ophiostoma ulmi*) and beech bark disease (a disease complex caused by the beech scale, *Cryptococcus fagisuga*, and the fungal pathogen, *Nectria coccinea* var. *faginata*) have greatly diminished their host tree species in North America [12, 13]. The gypsy moth, *Lymantria dispar*, was introduced to North America in 1869 and subsequently caused millions of hectares of defoliation in oak-dominated forests [10]. Numerous other alien insects and diseases have arrived more recently and are likely to cause further changes to this forest region.

Considerable research has been conducted on the population biology of the invasion process and this work offers some useful concepts for the development of strategies for mitigating current and future invasions. Below we describe the invasion process and illustrate its component processes using the gypsy moth in North America as a case history.

II The Invasion Process

We present here a conceptual overview of the population processes operating during biological invasions. At least three processes underlie all invasions: arrival, establishment, and spread [14, 15]. The recognition of distinct phases of invasions is important because managing the different aspects should use different approaches. Quarantines are the primary method of preventing new invasions. Detection and eradication are the primary approach to preventing or reversing population establishment. Barrier zones are the primary method used to limit range expansion after a population has established.

TABLE I
The three principal invasion phases

Phase	Description	Management activities
Arrival	Founding members of the population are transported to the new area.	Quarantine
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

A. *Arrival*

Many paleontological studies indicate that, as the world's climate has changed, species have typically shifted their ranges in order to track their optimal habitat [16]. However, most historical range shifts were slow, occurring over thousands of years, and large geographical features, such as oceans and mountain ranges, served to isolate the world's biota. This fragmentation of the world's land masses is thought to have greatly enhanced global biodiversity.

Recently we have witnessed a rapid acceleration of range expansions among continents. Increased global movement by humans has facilitated the transfer of thousands of species to vastly new parts of the world. While some movement of species began during early periods of colonial expansion by Europeans, invasions have accelerated dramatically over the last 100 years [17].

Much of the acceleration of invasion rates can be attributed to increases in world trade. Increasingly, commodities are manufactured and consumed in different parts of the world and this has accelerated rates of intercontinental shipping. The major invasion pathways for alien species arrival are thought to be infested plant commodities, ballast water, raw wood packing material, and shipping containers themselves [18]. Of course, there are numerous examples of intentional introductions, especially of plants, birds and fish, that have become damaging invasive pest species.

Quarantine regulations that restrict the movement of certain commodities are probably the most effective tool for limiting invasions. There has been considerable progress in enacting important international quarantines. However, some important invasion pathways, such as ballast water and solid wood packing material remain open and need to be addressed in future quarantine agreements. Unfortunately, global trade agreements often hinder efforts to enact new quarantines. Furthermore, there are some pathways that probably never can be closed.

B. *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. Founder populations typically are small and consequently are at great risk of extinction. Generally, the smaller the founder population, the less likely is establishment. Two population processes are particularly important when considering establishment: stochasticity and Allee dynamics .

Two types of random processes affect the dynamics of virtually all populations. Demographic stochasticity is caused by chance realizations of individual probabilities of death and reproduction in finite populations, and it can have substantial effects in small populations. Environmental stochasticity arises from a nearly continuous series of random perturbations that similarly affect birth and death rates of all individuals in a population, and it is important to both large and small populations. Both types of stochasticity can contribute to population extinction when populations are at very low densities [19].

The "Allee effect" was first described by Allee and colleagues [20] and refers to any process whereby any component of individual fitness is correlated with population size [21]. A multitude of mechanisms can cause this type of density dependence in plant and animal populations, especially at low densities. These mechanisms include failure to locate mates, inbreeding depression, failure to satiate predators, and lack of cooperative feeding [22]. In many cases, this pattern of decreasing per capita growth with decreasing density includes negative growth at very low densities and populations may thereby decline to extinction. The combined influences of Allee dynamics and stochastic processes strongly affect the successful establishment of alien species [23, 24].

Recent studies indicate that by understanding the interaction between stochasticity and Allee dynamics it is possible to optimize strategies to eradicate newly-founded colonies of alien species [25]. This work demonstrates that eradication can typically be achieved simply by reducing populations below some threshold level rather than by eliminating 100% of the population.

C. Spread

Once a population is established, its density typically will increase and individuals will disperse into adjoining areas of suitable habitat. The spread of a species is driven by two processes, population growth and dispersal, and most models of population spread have focused on these processes. The simplest and probably the most widely applied model of population spread was developed in 1951 by Skellam and combines random diffusion with exponential growth [26]:

$$N_{x,t} = \frac{N_{0,0} \quad e^{rt-x^2/4Dt}}{4pDt} \qquad (1)$$

where $N_{x,t}$ is the density of organisms at distance, x, from the point of release and at time, t, from the time of release of $N_{0,0}$ organisms at time 0, D is the "diffusivity" or "diffusion coefficient" that measures dispersal, and r is the "intrinsic rate of natural increase" (birth rate - death rate under optimal condition; i.e., without crowding). The assumption of random movement in this model implies that the population will spread radially at an equal rate in all directions (Fig. 1a). Skellam [26] 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 as:

$$V = 2\sqrt{rD} \qquad (2)$$

There has generally been close congruence between predictions of this model and observed rates of spread of most exotic organisms [27].

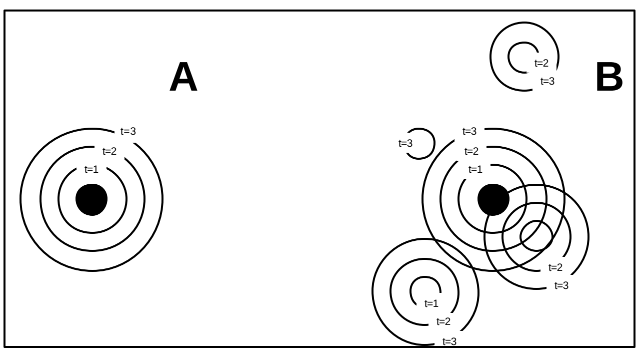

Fig. 1. Schematic representation of range spread between successive generations. The black dot represents the initial range at time 0. A. Spread according Skellam's [26] diffusion model; B. Spread predicted using a stratified dispersal model.

Skellam's model assumes a single, continuous form of dispersal, and it predicts that range expansion should be a smooth, continuous process (Fig. 1a). 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" [28]; in those situations, range expansion will proceed through the formation of multiple discrete, isolated colonies established ahead of the infested front [15, 29]. These colonies, in turn, will expand their ranges and ultimately coalesce (Fig. 1b). One consequence of this phenomenon is that range expansion may occur much faster than under a simple diffusion model.

III The Gypsy Moth in North America, a Case History

The gypsy moth in North America represents an excellent example of the population biology of invasions. For most alien species, we rarely know the precise circumstances of its arrival, but for the gypsy moth there is very good documentation of its accidental introduction from Europe by an amateur entomologist in 1868 or 1869 near Boston Massachusetts [30]. Starting around 1880, efforts were made to eradicate the species but by 1900 it became clear that these efforts had failed and the species was permanently established in North America. Since 1900, the gypsy moth has slowly expanded its range through much of eastern North America where it is thought to currently occupy slightly less than one third of its potential range (Fig. 2) [31, 32].

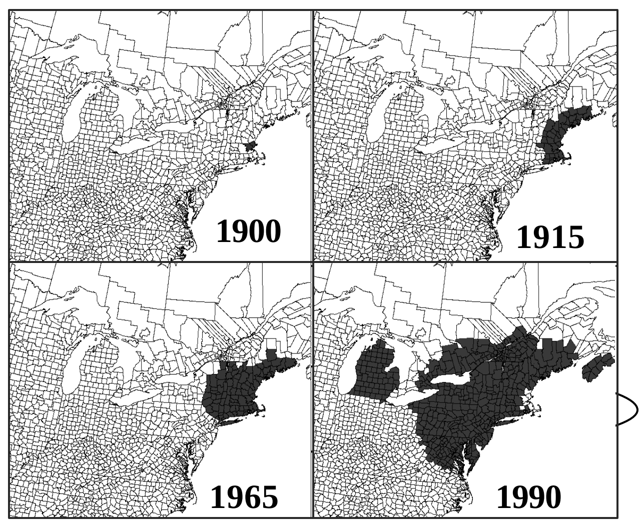

Fig. 2. Historical gypsy moth spread in N. America.

Females in European gypsy moth populations are known to be incapable of flight. Thus, range expansion by the gypsy moth only occurs via short distance dispersal of windborne 1st instar caterpillars and accidental long-distance movement of life stages by humans. This is an excellent example of the stratified dispersal mechanism proposed in theoretical studies [29]. Liebhold et al. [31] estimated that the formation of isolated colonies causes gypsy moth to spread about 10 times faster than if spread only occurred only via the dispersal of 1st instars..

Sharov and Liebhold [33] used data from grids of pheromone traps placed along the expanding population front to quantitatively identify isolated colonies along the expanding gypsy moth population front in Virginia and West Virginia (Fig. 3). They developed a model of gypsy moth spread based upon historical data that documented formation of isolated colonies and their growth. They used this model to identify an optimal strategy for slowing gypsy moth spread via identifying those isolated colonies using grids of pheromone traps and then suppressing them with aerial applications of *Bacillus thuringiensis* or mating disruption tactics.

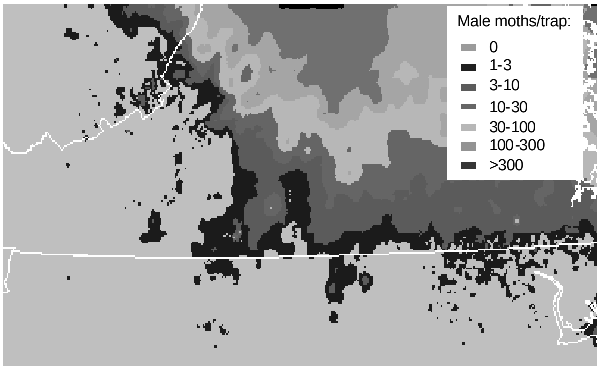

Fig. 3. Interpolated surface of counts of male gypsy moths from pheromone traps deployed on a 1 km grid along the expanding population front (horizontal line is the border between Virginia and North Carolina).

In 1999 a program was put in place by the USDA Forest Service for slowing gypsy moth spread using this strategy [34]. Results to date indicate that the program has been able to reduce spread to less than 50% of previous spread rates. Although millions of dollars are spent on the project every year, it has been shown to be economically beneficial because it postpones the dates at which land managers must begin to expend resources to protect forests from gypsy moth damage.

V. Summary and Conclusions

Better understanding the population ecology of alien species invasions represents a success story for the use of ecological theory. There are many instances in which theoretical models have provided useful information about both the establishment and spread of alien species. As the magnitude of the alien species problem escalates, there will be continued need to develop both analytical and empirical approaches to understanding invasion ecology.

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