Towards a Theory of Insect Epidemiology

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Introduction

Problems in economic entomology are frequently epidemiological in nature; that is, low level (endemic) populations are tolerated by man while population explosions (epidemics or outbreaks) are treated as disasters. This is particularly true in forestry, and forest entomologists have been preoccupied with explaining the causes of insect epidemics.

Entomologists have played a central role in the development of a theory of population regulation and in the controversy surrounding the concept of density-dependence. The result of this bitter controversy was a turn away from theory towards empiricism. Recently, however, there has been a return to theoretical studies based, this time, on a firmer empirical foundation. The present work is an effort to consolidate and extend recent developments towards a theory of insect epidemics based largely on the author’s experience and readings in forest entomology.

Reproduction Theory

The fundamental ideas on density-dependent reproduction in animal populations have been discussed at length in the ecological literature (see the excellent review in Clark et al., 1967). Forest entomologists have played important roles in their development and application. However, it was the fish biologist Ricker (1954) who consolidated these ideas into a comprehensive theory, which he applied to management problems. The basic principle can be stated as follows: Let the realized per capita replacement rate of a population be 

\[ R = \frac{N_{g+1}}{N_g} \]

where \( N_g \) is the density of individuals in the \( g \)th generation. If \( R \) is regulated by density-dependent negative feedback, then \( R \to 0 \) as the population density \( N \to \infty \) (Fig. 1). Under these conditions, there is a density, \( \bar{N} \), where \( R = 1 \), and the population density is in equilibrium because one offspring is produced to replace each parent. Whether the equilibrium point, \( \bar{N} \), is stable or unstable depends on the slope, \( b \), of the replacement function, \( R = f(N) \), in the neighborhood of \( \bar{N} \) (May et al., 1974); i.e.,

\[ b = -\frac{d \ln R}{d \ln N} \]

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Fig. 1. (Upper) The relationship between the per capita replacement rate, \( R \), and population density, \( N \), in a density-dependent system with a single equilibrium point, \( S_i \), occurring at density \( N_i \). (Lower) Growth and equilibration of a population under control of the above density-dependent function, with time in generations, \( g \).

In the example shown in Fig.1, the population attains a stable state after damped oscillations because \( 1 < b < 2 \). If the reproduction curve steepens so that \( b > 2 \), then the oscillations will increase in amplitude and the system is unstable. If \( b < 1 \), then population density approaches equilibrium asymptotically.

The basic concept, as stated above, can be generalized to include positive feedback at very low densities, the so-called "ALLEE effect" (see the broken line in Fig.1, upper). However, as we are presently interested in the problem of epidemics rather than extinction, we will ignore this.

Although the equilibrium point, \( S_i \), is usually stable in natural insect populations\(^1\), it is not necessarily static in space and time. For example, in a heterogenous

\(^1\) It is possible that the equilibrium point, \( S_i \), may be unstable (i.e., \( b > 2 \)) in some natural insect populations, particularly when they are colonizing environments which are more favorable than those in which they evolved. In these cases, Ricker's model may give rise