Special feature

Population dynamics of forest-defoliating insects

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INTRODUCTION

Are population cycles and spatial synchrony a universal characteristic of forest insect populations?

Abstract Foliage-feeding forest insects have served as model systems in the study of animal populations for more than 50 years. Early studies emphasized identification of "key" mortality agents or density-dependent sources of mortality. However, these efforts became burdened by rhetorical ambiguity, and population ecologists are increasingly focusing on characterizing population behavior and identifying the processes that generate that behavior. Two types of behavior seem to be common in forest insect populations: periodic oscillations ("population cycles") and spatial synchrony (synchronous fluctuations over large geographic areas). Several population processes (e.g., host–pathogen interactions) have been demonstrated to be capable of producing periodic oscillations, but the precise identity of these processes remains uncertain for most forest insects and presents a challenge to future research. As part of these efforts, a greater emphasis is needed on the use of statistical methods for detecting periodic behavior and for identifying other types of population behavior (e.g., equilibrium dynamics, limit cycles, transient dynamics). Spatial synchrony appears to be even more ubiquitous in forest insect populations. Dispersal and regional stochasticity ("Moran effect") have been shown to be capable of producing synchrony, but again more research is needed to determine the relative contribution of these processes to synchrony observed in natural populations. In addition, there is a need to search for other types of time–space patterns (e.g., traveling waves, spiral waves) in forest insect populations and to determine their causes.

Key words Population dynamics · Periodic oscillations · Outbreak · Nonlinear dynamics

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Introduction

Royama (1992) states that the ultimate question in population dynamics is "Why do animal populations fluctuate as they do?" Throughout the twentieth century, foliage-feeding forest insects have served well as model systems for answering this question. Most of these insects exist in habitats that are relatively free of anthropogenic disturbance and thus lend themselves as suitable subjects for long-term studies. Long-time series are the "bread and butter" in the field of population dynamics because many dynamic patterns only become evident after 20 or more years of data collection. Foliage-feeding forest insects are also valuable model systems because they are relatively easy to sample and the habitat is rarely destroyed by their feeding, even during outbreaks.

The seven papers in this special feature present syntheses of the current knowledge on the population dynamics of some of the most widely studied foliage-feeding insects. If these papers are contrasted with earlier studies of forest insect dynamics over the past several decades, it becomes clear that during this period there has been an evolution of approaches to the field of animal population ecology. The objective has always been to elucidate the mechanisms behind the dynamics of selected species, but the specific questions have varied.

Early scientists (e.g., Varley and Gradwell 1960; Morris 1963) focused on identifying the most "important" factors responsible for changes in population density. The approach most commonly taken was to collect life table data and apply specialized statistical procedures (e.g., "key-factor analysis"; Varley and Gradwell 1960) to identify specific causes of mortality that explained the largest portion of variation in change in density. Although great advances were made by this work, this approach is rarely applied in contemporary studies because of the ultimately nebulous definition of what makes a certain type of mortality "important" (Royama 1996).

As these efforts tapered off, an increasing emphasis was placed on identifying the existence and causes of population

regulation. Although the beginnings of the controversy over the importance of regulation date back to early writings by Nicholson (1933) and Andrewartha and Birch (1954), the search for factors responsible for regulation intensified in the 1970s and 1980s. Considerable effort went into searching for mortality agents that acted in a density-dependent fashion and were thus capable of regulating populations (DenBoer 1986; Stilling 1987).

Although considerable interest still exists in the search for density-dependent agents, there appears to be growing consensus that the question of regulation versus no regulation is moot (Wolda 1995; Murray 1998; Turchin 1999). It appears that much of the controversy about the role of density dependence in population regulation was created by a lack of consensus about definitions and assumptions. As Turchin (1999) pointed out, "Once you translate what you mean by 'density dependence' and 'regulation' into mathematical terms, the formal methods of mathematical proof will tell you whether the second is a logical consequence of the first or not."

As interest in population regulation fades, many studies increasingly focus on population behavior (e.g., population cycles) rather than regulation. The search for processes responsible for certain aspects of population behavior is not new. For example, Anderson and May (1980) proposed that host–pathogen interactions were responsible for population cycles of many forest insect species. Berryman (1996) argued that host–parasitoid interactions are a more likely explanation of forest insect population cycles. Many of the papers presented in this special section also focus on identifying the processes responsible for population behavior (e.g., population cycles). As such, they illustrate the shift of interest to population behavior rather than population regulation.

This shift in focus by population biologists probably represents a healthy change. The concepts of "important" mortality factors or population regulation impose a level of regularity that may not exist in the complex web of population processes that affect population levels. Characteristics of population behavior, such as population cycles, are emergent properties of population systems. These characteristics can be statistically quantified in field-collected data. In contrast, population regulation is a more nebulous concept, and the search for agents or processes responsible for regulation has become problematic because of a lack of consensus about what regulation is or seemingly intractable problems with statistical tests for density dependence (Wolda and Dennis 1993).

The following special feature papers present syntheses of the present knowledge about the population dynamics of eight foliage-feeding forest insect species. These selected reviews are by no means a random sample of all foliage-feeding forest insects because all these species exhibit outbreak behavior but most forest insect populations remain at largely unnoticeable densities (Mason 1987). Nevertheless, given the information presented here, there are some common characteristics in population behavior shared by most of the species covered. First, most authors concluded that temporal patterns of abundance are characterized by periodic or cyclic behavior. Another feature observed in most of these species was some form of spatial synchrony in the timing of outbreaks across large geographic areas. While population cycles have been widely recognized in many forest insect species for some time (Elton 1927; Myers 1988), spatial synchrony is receiving increased interest and is apparently present in many species (Myers 1998; Williams and Liebhold 2000). Are population cycles and spatial synchrony universal characteristics of all forest insect populations and, if so, what processes produce these patterns? These questions are explored in detail below.

Population cycles

One common feature exhibited by all the species discussed in this special section is the existence of apparent population cycles. Are population cycles a ubiquitous feature of all foliage-feeding forest insects? The answer is probably not. Most of the papers presented here concentrate on the existence and causes of cyclic behavior, but this treatment may overstate the ubiquity of this population behavior. It is quite possible that one of the reasons that these insects were chosen for study was because they exhibit periodicity. Certainly one of the reasons why these insects were studied was because their densities fluctuate considerably, sometimes reaching outbreak densities that have economic and sociological effects. There is little incentive to study insect populations that never reach outbreak levels (Mason 1987). It is also unlikely that an insect species that only sporadically reaches outbreak levels would be the object of a sustained research program. Thus, it appears that periodic outbreak behavior "attracts" the attention of long-term population ecology research, and this bias may result in an overemphasis of outbreak periodicity in insect populations in general.

Given that only insect species that frequently reach outbreak levels will be studied, how many of these exhibit truly periodic behavior? Certainly there is a continuum from some species which exhibit highly periodic behavior to others which exhibit seemingly random temporal distributions of outbreaks. The larch budmoth *Zieraphera diniana* is heralded as an example of a species exhibiting highly regular intervals between outbreaks (Baltensweiler and Fischlin 1988). Other populations, however, such as some North American gypsy moth populations (Williams and Liebhold 1995a), exhibit little or no periodicity. Kendall et al. (1998) reported that only 17% of the 69 insect species they surveyed exhibited significant periodicity. We examined their results more closely and found that 11 of the species that they studied were foliage-feeding forest insects and that 45% of these exhibited significant periodicity, suggesting a greater tendency toward cyclic behavior in this groups. Of course, these types of analyses are constrained by the limited availability of long-time series, and insects sampled in nonforest settings may be subject to more frequent disturbances that might obscure periodic behavior. Nevertheless, these results imply that cyclic behavior is

not universal. We believe that in many cases the visual identification of periodic behavior in population densities may represent a tendency of humans to impose concepts of order in their natural world, even when it does not exist.

Most insect time series are short relative to the length of purported outbreak cycles. Most of the papers in this issue report outbreak cycles ranging from 8 to 12 years. Yet many of the available time series may be only 20–30 years long, or less. During this interval, only two to three outbreaks can be expected to occur, and thus these data would be totally inadequate for testing the existence of regular outbreak cycles. It is our hope that in the future population ecologists will increase their use of statistical tests for detecting periodic behavior.

Several of the papers included in this special section focus on the existence of delayed density-dependent mortality and its role in generating population cycles. This concept has been championed by Turchin (1990) and Berryman (1996). Turchin (1990) analyzed time series of 12 species of forest insects and identified oscillatory behavior and second-order lags in most of these series. He concluded that delayed density dependence may dominate most populations and produce periodic behavior. Similarly, Berryman (1996) pointed out that most forest pest species exhibit periodicity and that delayed density-dependent mortality caused by parasitoids was the most likely cause of these cycles.

Recently, however, there have been several challenges to the conclusions of Turchin (1990) and Berryman (1996). Williams and Liebhold (1995b) raised a point made earlier by Royama (1977), that the appearance of inverse lagged correlations in time series does not necessarily imply the existence of a delayed negative feedback (i.e., delayed density-dependent mortality). They showed that these lagged relationships could result from any autocorrelation in an exogenous factor, such as direct density dependence in a generalist predator or autocorrelation in physical conditions (e.g., weather). More recently, Hunter and Price (1998) expanded these criticisms of the use of time-series analysis by Turchin (1990) and Berryman (1996) and suggested that they may overlook the effect of cycles in weather on population dynamics. These papers have resulted in the publication of extended dialogues on this subject (Berryman and Turchin 1997; Williams and Liebhold 1997; Turchin and Berryman 2000; Hunter and Price 2000) that indicate that the interpretation of lagged correlations in time-series data is far from resolved.

Although linear models are capable of producing quasi-periodic behavior, theoretical ecologists have shown that only nonlinear processes are capable of producing truly periodic oscillations (May and Oster 1976; Hastings et al. 1993; Kendall et al. 1999). There are a multitude of nonlinear processes that may produce periodic behavior in theoretical models; these processes include predator–prey, host–pathogen, and maternal effects. As mentioned earlier, observed periodic behavior could also result from quasi-periodicity in some exogenous process such as weather (Williams and Liebhold 1995b; Hunter and Price 1998), or it could be a transient condition as populations progress toward, but never reach, equilibrium dynamics (Hastings and

Higgins 1994). Considering the vast number of potential sources of population cycles, it may be more valuable to consider second-order lag correlations to be diagnostic of periodicity itself rather than any specific mechanism causing periodicity.

We discuss here another example by which quasi-periodic outbreaks may be caused by a mechanism other than delayed density-dependent mortality. There are many examples in population ecology in which dynamics at low densities are governed by processes that are different from those operating at high densities (e.g. Campbell and Sloan 1978). Bimodal dynamics was presented as a conceptual model by Southwood and Comins (1976). More recently, this concept has been expressed mathematically using a self-exciting threshold (SETAR) model (Tong 1990). This is a form of nonlinear time-series model in which the parameters of autoregressive models vary depending on whether the density, N_t, is above or below a threshold, C. Thus a SETAR(2:1,1) model [the notation SETAR(m; p_1, $p_2, \ldots, p_m$) stands for a SETAR model with m regimes, and the order of the jth regime equals p_j] would be described by

$$
\begin{aligned}
N_{t+1} &= a_0 + b_0 N_t + \varepsilon_t \quad N_t \leq C \\
N_{t+1} &= a_1 + b_1 N_t + \varepsilon_t \quad N_t > C
\end{aligned}
\tag{1}
$$

Stenseth et al. (1998a, b) demonstrated that various forms of SETAR models are capable of representing the entire spectrum of dynamic behavior commonly found in ecological systems, including periodic and quasi-periodic behavior. Figure 1 shows the results of simulation using a SETAR(2:0,1) model and illustrates that quasi-periodic outbreak dynamics can be generated by simple processes other than delayed density dependence.

While the seemingly universal nature of population cycles in forest insects is intriguing, population ecologists should exercise caution in their quest for the causes of these cycles. First, the existence of periodic behavior should be quantified statistically before any oscillations are consid-
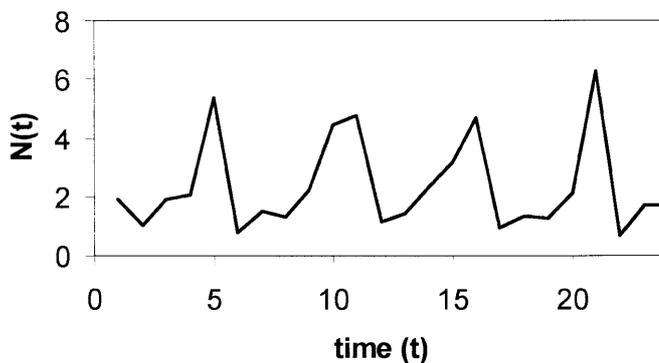

Fig. 1. Simulated time series using a SETAR(2:0,1) model (Tong 1990):

$$
\begin{aligned}
N_{t+1} &= 1.5 + \varepsilon_t \quad N_t \leq 2 \\
N_{t+1} &= 3 - 0.5 N_t + \varepsilon_t \quad N_t > 2
\end{aligned}
$$

where ε_t is a random normal deviate with mean 0 and standard deviation of 0.5

ered regular. Second, ecologists should consider a variety of underlying processes that may generate quasi-periodic population behavior observed in field data. Delayed density-dependent mortality is just one of many types of mechanisms capable of generating oscillations.

A challenge that exists for population ecologists in the future is to expand their characterization of population behavior beyond the presence or absence of cycles. Theoretical ecologists have shown that nonlinear processes are capable of producing a multitude of population behaviors, which include equilibrium dynamics, true periodicity, limit cycles, chaos, and other behaviors (May and Oster 1976; Hastings et al. 1993; Kendall et al. 1999). The challenge for field ecologists is to identify representations of this wider variety of population behaviors in nature and ultimately to identify the mechanisms that produce them.

Spatial synchrony

As Levin (1992) pointed out, space is central to nearly every problem in ecology. Although theoretical ecologists have made great strides to explore the role of space in population dynamics (Hassell et al. 1991; Tilman and Kareiva 1997), field ecologists have been limited in their ability to confirm these theoretical findings in nature because of the technical complexities of spatial data. These technical problems are now being overcome, and one of the seemingly ubiquitous properties of forest insect populations is some degree of spatial synchrony in populations.

Spatial synchrony is the process by which populations in spatially disjunct locations fluctuate in a similar manner. Although this phenomenon has been observed qualitatively for many years (Myers 1988; Shepherd et al. 1988), it has only been measured quantitatively in recent years (Ranta et al. 1995; Bjørnstad et al. 1999; Williams and Liebhold 2000). In the papers forming this special section, spatial synchrony is reported in most of the seven insect species, either qualitatively or quantitatively.

Along with the quest to identify the processes generating population cycles, identification of the process causing spatial synchrony is one of the great challenges facing population ecologists. There has been a tremendous interest in applying this question to a variety of different animal species, and the emergent conclusion from this work is that when populations fluctuate as the result of some endogenous process (e.g., predator–prey cycles), disjunct populations will come into sync either as the result of a small amount of dispersal (of either hosts or predators) among populations or as the result of regional stochasticity ("Moran effect"), most likely as synchronous weather variability (Ranta et al. 1995, 1999; Kendall et al. 2000). The papers in this special section illustrate that it is often difficult to distinguish between dispersal versus regional stochasticity as causes of spatial synchrony (Kendall et al. 2000). Theoretical studies suggest that periodicity itself greatly contributes to the appearance of spatial synchrony; Bjørnstad (2000) reviewed the patterns of spatial synchrony

in several different systems and concluded "Cyclic populations yearn to align themselves." The extent to which spatial synchrony is coupled with cyclic dynamics in forest insects remains unclear, but this question should be addressed in future studies.

Spatial synchrony can be considered just one of many categories of time–space patterns. Theoretical ecologists have demonstrated that relatively simple spatially explicit models are capable of generating a variety of possible spatial patterns (Hassell et al. 1991), although many of these (e.g., "spiral waves") have yet to be identified in natural systems. Closely related to the concept of spatial synchrony is the phenomenon of moving outbreaks or "traveling waves" (Bjørnstad et al. 1999; Lambin et al. 1998). The concept that outbreaks are observed first in certain locations and then "spread" to other areas has been observed qualitatively for several forest insects (Berryman 1987), but work is needed to quantify this phenomenon statistically from field data. It seems likely that both dispersal and regional stochasticity are candidate explanations for this phenomenon, as is the case for spatial synchrony. The identification of time–space patterns in forest insect abundance and understanding the causes of these patterns is a challenge for the future.

Conclusion

Forest insects have served well as model systems for the study of population dynamics. The community of scientists studying these organisms has moved beyond identifying "key" factors and population regulation because these problems were constrained by rhetorical ambiguities. Instead, the focus of forest insect dynamics research has shifted to understanding patterns through time and space. Quasi-periodic oscillations appear to be a common feature in the temporal patterns of abundance of most forest insects, but the reasons for their ubiquity remain uncertain. Spatial synchrony also appears to be a characteristic of the spatial dynamics shared by most forest insects, but its causes also remain uncertain. Understanding these phenomena represents a challenge to those studying forest insect population dynamics. The search for other patterns of abundance through time and space should also be a priority in the future.

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