

Modelling Forest Insect Dynamics

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Abstract

[Modelling](#) of [population dynamics](#) is the essential part of both research and management of forest pest insects. Forest pest insect models are present in all classes of population models considered in this paper: regression-, theoretical-, non-parametric-, phenology-, and life-system models both of medium and huge size.

Modelling success depends on selection of appropriate complexity level that corresponds to modelling objectives and to available data. Huge models that attempt to integrate all existing knowledge about an insect species and to serve all possible purposes, become obsolete before completion and have unexpectedly limited usage because of the lack of flexibility. Simple models were shown to be efficient in simulation of stationary time-series of population dynamics. However, non-stationary population dynamics usually require more complex models. It seems most beneficial to combine models of different complexity, when complex (but not huge!) models can be used for biological interpretation of simple models.

The shift in forest [pest management](#) objectives from simple (e.g., prevention of defoliation) to complex (e.g., minimization of impact or [slowing the spread](#) of pest population) requires adjustment of modelling strategies. We expect the models to increase in their complexity and scope. The increase in model complexity can be achieved using [object-oriented programming](#) which makes models modular, flexible and re-usable. The cost and time (one year maximum) of model development should not be increased.

Any population model of a forest pest insect that attempts to be realistic should consider spatial dynamics. [Spatial models](#) require different modelling techniques as compared to models of local populations. These include: [geostatistics](#), <http://ftp.mathworks.com/pde.html>, [cellular automata](#), and [metapopulation models](#) in which local populations are considered as individuals. Computers with [parallel processors](#) may become useful for simulation of spatial processes in ecological systems.

Key words: [insects](#), population dynamics, models, forest entomology.

Introduction

Any tactic of forest pest management requires prediction of pest population change over time and/or space. However, the scope of prediction depends on management objectives. The most simple objective -- to prevent defoliation in the current year -- requires information about the area to be treated with pesticide and about the time of sampling and spraying. Two kinds of forecasts are most useful for this management objective: 1) prediction of possible local defoliation from population density samples and 2) prediction of insect development from temperature data.

Current forest pest-management practice is shifting from simple objectives to more complex ones. An example of complex objective is to minimize the impact of pest population on forest ecosystems during

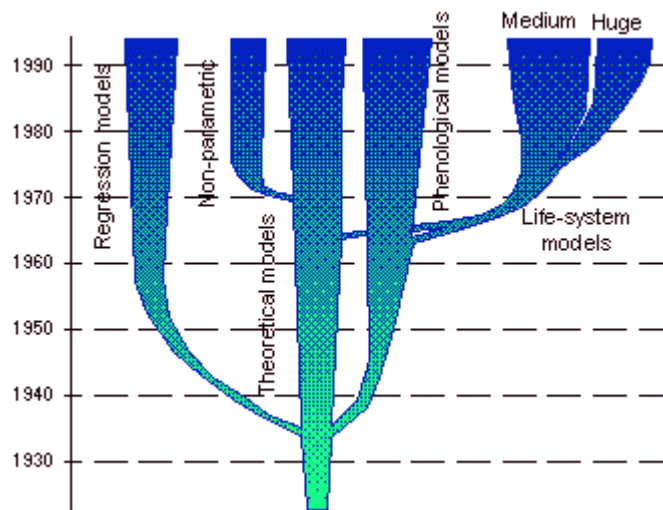
several years. The impact can be changed by silvicultural methods, biological control, or pesticide spraying. Another possible objective is to reduce the spread rate of introduced pest population. These complex objectives require prediction of population change over long time intervals and over large areas. Of course, it is impossible to predict pest abundance at specific location 10 years ahead, but it may be possible to predict the change in average pest population density as a result of some change in environment (e.g., thinning).

Mathematical modelling is the major tool for predicting population dynamics. The changes in pest-management objectives should be followed by a change in modelling methodology. In general, models will become more complex and their temporal and spatial scope will increase. Thus, it is important to reconsider advantages and disadvantages of different kinds of models and to delineate the most promising modelling methodology.

In this paper I want to review the variety of modelling approaches that are applied to forest pest insect populations. I will concentrate on two major problems. The first problem is how to deal with increasing model complexity. Complex models are expensive, difficult to understand and to use. Do we need to continue building these "monsters", or is it better to go back to simple models? The second problem is, how to build space-referenced population models. The way of introducing space into the model depends on the type of model. A series of new space-related modelling approaches introduced into ecology in the past few years is discussed.

Phylogeny of population models

The best way to review methods of insect population modelling is to analyze their "phylogeny".



Theoretical models are relatively simple and represent one or few most important mechanisms of population change. They have been developed for more than a century starting from [exponential](#) and [logistic](#) models. These models were improved and generalized by adding delayed density-dependence, asymmetric population growth, group effect, multiple equilibria and other features (Berryman and Millstein 1990). The major advantage of these models is their simplicity. Model structure is usually very "transparent", and all effects are easy to explain.

The price for using simple models may be the lack of correspondence between model assumptions and

ecological reality (Logan 1994). For example, the exponential model assumes that all individuals reproduce with the same rate r . In real populations, reproduction rate depends on age, weather, habitat and other factors. Nevertheless, exponential model remains useful because it accurately predicts the growth of many populations as if all individuals have equal reproduction rates. This kind of model interpretation can be called "mythological" because model assumptions (the myth) are more important than real processes.

Regression (=empiric) models are based on linear or polynomial relationship between predicted value (e.g., population density) and one or several factors (e.g., temperature, abundance of food or enemies). These models do not represent the mechanisms of population change even at the mythological level. They are used to estimate population density from one or several predictors which may be: population abundance in the previous year, weather parameters, site characteristics, etc. These models are useful for making immediate decisions concerning population treatment. However, they are specific to the data set they were derived from. Any significant change in climate, forest cover, or management strategy may affect the correlation between variables and the validity of regression model may be lost.

Qualitative models can be considered as a subclass of theoretical models. Instead of equations, these models use sets of conditions the equations should satisfy (Berryman and Stenseth 1989). The result is a set of conditions that the trajectory of population change should satisfy. These models have no parameters and are often called "non-parametric". Qualitative models are theoretical tools only. To make a quantitative prediction, the model should be parametrized.

Phenological modeling deserves a special discussion which is beyond the topic of this paper. As a rule, insect development is an autonomous sub-system which can be simulated independently from population dynamics using temperature as input factor.

Life-system models are based on the "life-system" concept (Clark et al. 1967), according to which, population change is driven by the interplay of different ecological processes, and the role of each process is modified by other processes. This concept can be considered as a systems' approach in population ecology (Sharov 1992). Life-system models, in contrast to theoretical models, attempt to handle explicitly all ecological processes that have a significant effect on the population. They often include phenological submodels, and thus, their "phylogenetic roots" are shown both in theoretical and phenological models.

Life-system models are subdivided into two subclasses according to their complexity level. The principal difference between medium and huge models is that huge models are supposed to be universal: they should integrate all available knowledge and satisfy any need for information, while medium models are designed to integrate the most important information, and to satisfy a number of important purposes.

Models of forest pest insects

Forest entomology is one of the major areas of application of population models (Liebhold 1994). All types of models have been used for simulation of forest insect population dynamics.

A series of theoretical models of forest insects has been developed by Berryman and Millstein (1994) in their PAS software. These models are modifications of discrete-time analog of the logistic model. Parameters of these models can be adjusted to fit available data. Other examples of theoretical models are: a spruce budworm model (Morris 1963), a gypsy moth model (Campbell and Sloan 1978), a

southern pine beetle model (Mawby et al. 1989), and a generic model of tree conquest by bark beetles (Stenseth 1989).

Several qualitative models were used to develop classifications of forest pest insect outbreaks (Berryman 1978, Isaev et al. 1984, Berryman and Stenseth 1989).

Examples of medium life-system models are: a model of the winter moth (Varley et al. 1973), a model of the common pine sawfly (Sharov 1991), models of the gypsy moth (Campbell 1981, Sharov and Colbert 1995), and a mountain pine beetle model (Raffa and Berryman 1986).

Examples of huge life-system models are: a Western Spruce Budworm Model (Sheehan et al. 1989), a [Gypsy Moth Life System Model](#) (GMLSM) (Sheehan 1989, Sharov and Colbert 1994), and a Southern Pine Beetle (TAMBEETLE) model (Coulson et al. 1989). These models were developed for more than a decade. They gradually evolved increasing their complexity from the "medium" to the "huge" level.

To show the complexity of huge models, I will briefly describe the structure of the GMLSM. Gypsy moth population is considered in a 1-ha forest stand. It is subdivided into portions that correspond to different host tree species and different strata (overstory, understory, boles of trees, and ground level). All ecological processes are considered specifically in each tree species and stratum. Each time step (equal to one or several days), is subdivided into "day" and "night" periods. At night, gypsy moth larvae are feeding, while at day time they rest on the boles or in the litter. Parasitoid behavior also depends on day time. Each gypsy moth cohort is characterized by 40 parameters: including physiological time, sex, stage, host tree species, feeding stratum, total numbers, the proportion of individuals infected by virus and parasitoids, etc. The model also keeps track of the age of viral infection and of parasitoids inside gypsy moth larvae. Gypsy moth cohorts can split and merge due to larval dispersal.

The GMLSM uses more than a thousand parameters and produces ca. one hundred tables and graphs. A user-friendly interface was developed to manage model input and output. The front-end interface for the GMLSM has up to seven hierarchical levels and a field-sensitive help. A graphic interface can be used to display graphs that represent seasonal and long-term dynamics of gypsy moth population. Here are some examples of [input and output screens](#) of the GMLSM.

Simple and complex models

An interesting discussion about complex life-system and simple theoretical models was published in "American Entomologist". Berryman (1991) suggested that "simple theoretical models with parameter values estimated from real data generally will have greater practical utility in management situations because they are cheaper to build, easier to understand and operate, and often more accurate than large biologically explicit models" (p.202). Onstad (1991) agreed that models should be logical and cost-effective, but argued that simple models that ignore essential biological relationships (e.g., age-structure) are heuristically useless. Logan (1994) defended "big ugly models" because only these models can explicitly represent biological causality and, therefore, can be easily interpreted by field ecologists.

I agree with Berryman (1991) that simple models may be more efficient than complex models in prediction of stationary multi-year time series of population dynamics. However, more complex models are usually required for prediction of non-stationary population changes (e.g., seasonal population dynamics, or changes associated with population management or ecosystem management). Non-stationarity means that dynamical rules may change in time (or space) according to some external

factors (human interference, global warming). If there is no experimental data on the effect of some driving factor on population dynamics, then empirical models are useless for predicting non-stationary processes. However, simulation models may be helpful the effect of driving factor on individual population processes (e.g., mortality, reproduction) is known.

Oversimplified models may lose the essential properties of real population systems if they are not based on solid ecological data. For example, Royama (1984) considered the [spruce budworm model](#) (Holling et al. 1977, Casti 1982) non-realistic. This model assumed two stable equilibria that corresponded to endemic and epidemic population densities. Stand maturation was considered as a major factor causing the transition from endemic to epidemic state. It was assumed that outbreak populations were food-limited and that endemic populations were regulated by predation. However, natural populations declined not from food shortage but from diseases and other factors (Royama 1984). In the model, moth migration initiated outbreak spread from epicenters, while in nature there was no evidence of outbreak spread due to moth dispersal.

A similar problem arose with a model of gypsy moth dynamics developed by Campbell and Sloan (1978). They combined data obtained from populations separated in space and time and received a phase plot with two stable equilibria (endemic and epidemic) separated by unstable equilibrium. Liebhold (1992) re-examined the same data set and showed that bimodality hypothesis does not work at the level of local populations.

The third example is the model of host-pathogen population cycles (Anderson and May 1981) which was criticized by Bowers et al. (1993). It was shown that cycles obtained by Anderson and May (1981) resulted from inappropriate arbitrarily chosen parameters. In the case of larch budmoth, host-pathogen interactions alone cannot generate population cycles. The pathogen may still be important in generating population cycles but only if considered together with other ecological processes.

These examples show that realism is important in model development. Huge life-system models are most realistic, and they were expected to yield most accurate and comprehensive predictions. However, huge models of forest pest insect populations had a very limited usage (Liebhold 1994).

The problem of huge models was realized back in 1970's (Lee 1975). The models that were expected to serve too many purposes appeared to be almost useless for any specific purpose. As a rule, specialized models were more advantageous to reach specific objectives than huge generalized models. For example, if we try to analyze gypsy moth phenology using the GMLSM we will come across several problems. First, there are too many model parameters that are not related to gypsy moth phenology. Second, model parameters are formatted in a specific way which may be not appropriate our needs. If we want to use a Weibull distribution of egg hatch time, he will have to enter this distribution by points instead of entering parameters. Third, the format of model output may be incompatible with statistical software which we planned to use for the analysis of simulation results. Fourth, it is difficult to modify model algorithm because the code is large, and additional parameters have to be included into the interface. Fifth, the majority of huge models were developed for more than a decade and it was not rational to wait for their completion. Huge models become obsolete before their completion because the problems they are focused on were solved using other methods or were replaced by other problems. Thus, many researchers prefer to develop their own simple models instead of using huge universal models.

The failure of huge models was caused by two major factors: 1) non-flexibility of model structure and 2) long period of model development, which are side effects of high model complexity. Nobody would argue that a model should be no more complex than is necessary (Onstad 1991, Logan 1994). The problem is to determine what level of realism and complexity is necessary.

This problem cannot be solved by setting the rules how to make models. However, I think it will be useful to set a time limit of one year for development of any kind of model. One year is a long period as compared to the life time of scientific hypotheses. Thus, the models should be developed fast enough to be competitive in scientific world. The time limit of one year can be considered as a constraint on model complexity and as a protection from building huge models, defined above.

If time permits, it may be most beneficial to combine models of different complexity because: 1) the lack of realism in a simple model can be compensated by its comparison with a complex model, and 2) analytical solutions of a simple model may provide insights into the behavior of a complex model. For example, the simple differential equation model for gypsy moth population dynamics was parametrized using several complex models (Wilder et al. 1994). This model demonstrated interesting non-linear dynamics including chaos which would be impossible to analyze using complex models.

When discussing modelling strategies we need to consider possible effects of new technologies on modelling practice. One of the ways to increase modelling efficiency is to use object-oriented programming (Silvert 1993). The philosophy behind object-oriented programming is to build modular code with highly independent parts. Each part of the code specifies a particular "object": its structure, function, and interaction with other objects. Objects are encapsulated, that means the ways of their usage are pre-determined. Thus, any "illegal" interaction is forbidden. Because of encapsulation, object-oriented programs are highly compatible with each other.

The most popular object-oriented language is C++. Besides encapsulation it provides several other advantages. Inheritance and overloading of functions and operators can be used for program modification without re-writing the code. This is often called "code recycling". It is possible to develop a library of standard objects most often used in population modelling (e.g., cohort, population) and then customize these objects for each particular model using inheritance.

Another advantage of object-oriented programming is that parts of the program can be developed independently. There may be almost no central coordination. Complex models may evolve gradually from simple ones without any global project. Thus, there is no need to initiate huge and expensive modelling projects. It is better to continue development of specialized models for specific purposes and see if they will naturally aggregate into bigger models. It will necessary happen if aggregation yields any practical benefit.

Object-oriented methodology may result in reduction of time spent on model development. As a result, more complex models will be possible to build in the time limit of one year, than it was in the past.

Space representation in population models

In the past, the majority of models were focused on local populations which were considered isolated from the rest of the world. If migration was admitted, then it was considered constant or random and was not related to population dynamics in nearby sites. The importance of spatial models is based on the following:

1. Dispersal is important in the dynamics of all insect populations at all spatial scales. Many insects disperse hundreds of miles during one season (Westbrook et al. 1992). But even slow-dispersing populations like gypsy moth in North America cannot be accurately predicted in isolation from neighboring stands (Campbell and Sloan 1978, Gould et al. 1990).

2. Spatial heterogeneity is one of the most important factors in population dynamics (Onstad 1988). Thus, averaging population density over space often leads to confusing results (Flemming 1991, Liebhold 1992).
3. Population management requires space-referenced prediction. Thus, local population models have a limited value for a manager.
4. Several important phenomena like spatial pattern of population change, synchronization of pest outbreaks, spread of invading species can be studied only using spatial models.
5. Local population dynamics are often unstable, and therefore, it is hardly predictable (e.g., population may get extinct). But ensembles of spatially distributed local populations have stable patterns and can be simulated (DeAngelis and Waterhouse 1987).
6. Usually, there are very limited data on individual local populations. Thus, local models are difficult to validate and to use for population prediction. More data can be found on population dynamics over large areas.

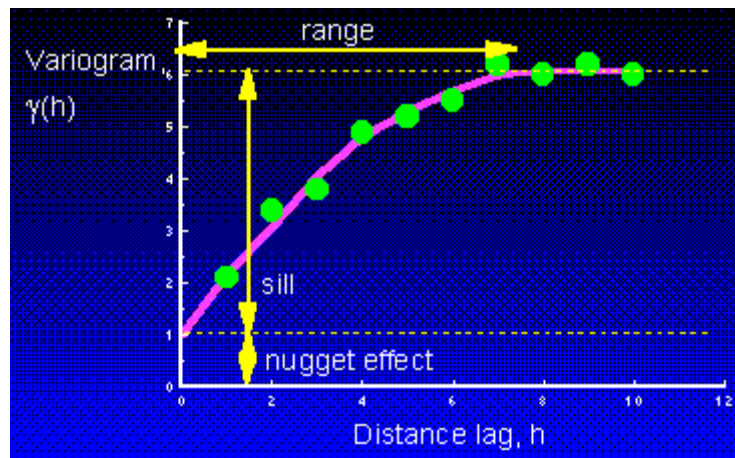
Interest to spatial modelling has increased in the past 3-5 years. A special issue of "Ecology" 1994(1) is devoted to spatial models. In 1991 a special issue of Biological Journal of the Linnean Society was devoted to metapopulation dynamics (metapopulation is a set of local populations that exchange by migrants).

One of the reasons for increased popularity of spatial models is the development of technology that can handle spatial information. Geographic Information Systems (GIS) are able to handle and display large amounts of spatial data. GIS is a basis for a new methodology in ecological studies called "landscape ecology" (Turner 1989). With the help of GIS, pest management is moving to the landscape level (Coulson 1992). Several pest-management expert systems have been developed using GIS, e.g., the gypsy moth expert system (Ravlin et al. 1990, Ravlin 1991) and the southern pine beetle expert system (Coulson et al. 1989a).

Transition of pest-management practice to the landscape level requires spatial population models. It is interesting that spatial models appeared almost in all classes of population models.

Space representation can be introduced into regression models by adding space-related variables. For example, population density in neighboring area was used as a predictor in the model of a bark beetle *Dendroctonus frontalis* (Mawby and Gold 1984). The entire area was subdivided into grid cells, and the future state of each cell was predicted from its previous states as well as from states of neighboring cells. In mathematical sense, this is a cellular automaton. Zhou and Liebhold (1995) used stochastic cellular automata to predict gypsy moth defoliation in Massachusetts. Probability of cell transition between two possible states (defoliated and non-defoliated) was considered as a function of neighborhood cell states.

Recently a new statistical approach, called geostatistics, has been developed for the analysis of spatially referenced data (Isaaks and Srivastava 1989). Geostatistics was originally developed in geology, but now it is widely used in ecology (Rossi et al. 1992, Liebhold et al. 1993). The basic idea of geostatistical methods is to measure spatial dependence between measurements taken at different distances from each other and then to use this information for interpolation, extrapolation, or simulation. Spatial dependence is traditionally measured using a variogram which shows the variance between measurements separated by specific lag-distance.



The variance increases (spatial dependence decreases) with increasing distances among sample points. The principal geostatistical method is kriging, which uses weighted average of sample measurements to estimate the value at non-sampled points. For each estimation, the weights are calculated from expected spatial dependence between estimated point and sampled points. Hohn et al. (1993) used 3-dimensional kriging in space and time to predict gypsy moth-caused defoliation in Massachusetts.

Phenological models can be easily transformed to the spatial scale because weather data-bases are already spatially dependent. For example, the gypsy moth expert system includes a phenological simulator which operates at the landscape level (Schaub et al. 1992). Gypsy moth development is first simulated for extreme elevations and then interpolated to intermediate elevations. The model generates the map of insect stages for any selected date. This is particularly important for management purposes because the map allows to develop a treatment schedule for different areas.

Spatial theoretical models can be classified into three categories: 1) diffusion models, 2) cellular automata, and 3) metapopulation models.

Diffusion-based models are based on the partial differential equation:

$$\frac{\partial N}{\partial t} = D \left(\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right) + f(N)$$

where N is population density, t is time, x is space, and f(N) is the rate of local population growth as a function of N (Fisher 1937, Skellam 1951, Okubo 1980). For exponential (or logistic) local population growth, the model predicts a travelling wave of spreading population which moves with velocity of:

$$v = \sqrt{4rD}$$

where r is population growth rate, and D is diffusion coefficient (Skellam 1951). A review of diffusion-based models can be found in (Holmes et al. 1994).

Skellam's model and its modifications were applied to the spread of a variety of species (Kareiva 1983, Andow et al. 1990, Dwyer 1992). In many cases a good correspondence was found between actual and estimated spread rates. However, in other cases there was no good agreement between a model and reality. For example, Liebhold et al. (1992) estimated expected spread rate of gypsy moth as 2.5 km/year, while in reality it varied from 7.61 to 20.78 km/year since 1966.

The major problem in diffusion models is to incorporate different kinds of variability. Shigesada et al. (1986) discussed population spread in heterogeneous environment. Goldwasser et al. (1994) analyzed the effect of individual variability in dispersal on population spread rate.

Cellular automata can be used in theoretical models if the rules of cell transition have biological interpretation in terms of ecological processes such as population growth, dispersal, etc. For example, Molofsky (1994) developed a model that simulates the formation of spatial patterns in a population.

Metapopulation models do not specify implicit spatial relations between local populations. A metapopulation is usually considered as a set of local populations that occupy habitat patches, which distances to each other are not specified. The majority of metapopulation models assumes an equilibrium between colonization and extinction rates (Levins 1969, Hanski 1991).

A new type of metapopulation models was suggested by Shigesada et al. (1995). They considered the spread of invading population as a result of establishment and growth of new populations far from the leading edge. The model is similar to the model of age-structured population as if local populations are individuals. This model can be applied to the populations that are spreading much faster than it is predicted by the Skellam's model.

Introduction of spatial domain into life-system models considerably increases their complexity. As a result, computation time becomes a problem. One of the solutions is to simulate the dynamics of local populations simultaneously using parallel processors (Smith 1991, Costanza and Maxwell 1991). However, parallel processing technology is not available to the majority of researchers because the hardware remains very expensive. Thus, life-system models seldom incorporate space dimension. An example of spatial life-system model is the model of microsporidia transmission in gypsy moth populations (Onstad et al. 1993). This kind of models may become more numerous when supercomputers with parallel processors will be more available.

Conclusions

1. Forest entomology is one of the most important application areas of population modelling.
2. Model complexity depends on objectives and available data. However, it is not rational to develop huge models which become obsolete prior to their completion. I suggest a time limit of one year for development of any models.
3. I expect the increase in average model complexity because forest pest management objectives become more complex. Object-oriented programming can enhance modelling efficiency so that the cost and time spent on model development will not increase.
4. Population models of forest pest insects cannot be considered realistic if they ignore spatial processes. Among the rapidly developing methods of spatial modelling are: geostatistics, cellular automata, and metapopulation models.

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