Mathematics: A Bookkeeping tool or a means of deeper understanding of ecological systems?

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Synopsis

Es wird auf die Beschränkungen von Kompartiment-Modellen eingegangen und ein Modelltyp vorgestellt, der einen Gegenpol zu den klassischen Zustandsvariablen-Modellen bildet, indem versucht wird, der Vielzahl an Freiheitsgraden in natürlichen Systemen durch individuenorientierte Simulation gerecht zu werden und damit ein prinzipielles Problem des Kompartiment-Ansatzes auszuräumen.

mathematical models, simulation

1.   Introduction

The general question concerning the usefulness of mathematical models of biological, and especially ecological, systems, continue to excite interest and controversy. The mathematical modeling of ecological systems is a well-established part of nearly all areas of ecology, particularly population and community ecology. However, many prominent biologists are sceptical of its usefulness.

One critic, Ernst MAYR, considers biology to be at the opposite end of the spectrum from classical mechanics, which is highly amenable to mathematics. His reasons include the extreme complexity of biological systems, the futility of trying to include all relevant variables of a system in a model, and the uniqueness of individual members of species populations.

Arguments and counterarguments about the relevance of mathematics to biological systems were prevalent even in the 18th and 19th centuries. The fact that population statistics were carefully recorded in many towns and cities eventually led observers to note regular patterns and consistencies in the numbers of births, marriages, and deaths. Immanuel KANT, commenting on the demographic tables of J. P. SUSSMILCH, noted:
"Since the free will of man has obvious influence on marriages, births, and deaths, they seem to be subject to no rule by which the number of them could be reckoned in advance. Yet the annual tables of them in the major countries prove that they occur according to laws as stable as (those of) the unstable weather, which we likewise cannot determine in advance, but which, in the large, maintain the growth of plants, the flow of rivers, and other natural events in an unbroken, uniform course" (see PORTER 1986).

Robert CHAMBERS, in his book, Vestiges of Creation, written in the early 1800's, commented on the regularity in population statistics by asserting that "Man is seen to be an enigma only as an individual, in mass, he is a mathematical problem" (see PORTER 1986).

2.   State variable models

These observations of the regularities in human populations stimulated the use of mathematical models both for human and natural populations. Famous examples are the logistic equation of population growth and the Lotka-Volterra equations for interacting populations. These equations and others of their type are called "state variable" population models. In the logistic equation,

$$dN/dt = r(1 - N/K)N, \qquad (1)$$

the state variable N represents the number of individuals, or alternatively the total biomass, of the population, and r and K are constant parameters.

The state variable approach has been most successfully applied to systems that (1) have a small number of variables (that is, number of populations and other components considered as variables), (2) consist of simple individuals that do not have complex ontogenies and behaviors, and (3) have little spatial complexity.

A type of system that usually fulfills these conditions is a laboratory chemostat. As an example of a successful application of state variable equations, consider the model of a simple chemostat system by BORGMANN & al. (1988). The variables are phytoplankton biomass, A, Daphnia biomass, B, and available dissolved phosphorus, N. The authors hypothesized the equations,

$$dA/dt = g_mAN/(K + N) - fAB \qquad (2a)$$
$$dB/dt = feAB - (h + m)B \qquad (2b)$$
$$P_O = N + q_BB + q_AA \qquad (2c)$$

where P_O is total phosphorus in the system and g_m, K, f, e, m, q_A, and q_B are constants. The authors analyzed these equations and compared their qualitative implications with chemostat experiments. They found that the model successfully predicted that,
1. Phytoplankton biomass at steady state should be a function of the harvesting rate of zooplankton, but should be largely independent of the total phosphorus, P_O.
2. Zooplankton biomass is strongly dependent on phosphorus loading rates and is inversely related to the zooplankton harvesting rate.
3. Limit cycle oscillations could occur if nutrient loading is very high (though the complexity of the Daphnia life cycle might have some influence on oscillations also).

Applications of state variable models to gaining insights into ecological systems is not limited to artificial systems such as chemostats. The pelagic zone of some lakes have been modeled with success. For example, it has been found both in models based on reasonable assumptions and in some empirical lake ecosystem studies that,
1. Potential productivity at all trophic levels is set by nutrient supply.
2. Trophic cascades can occur; "a rise in piscivore biomass brings decreased planktivore biomass, increased herbivore biomass, and decreased phytoplankton biomass" (CARPENTER & al. 1985).
3. Sufficient nutrient addition can lead to destabilization of the food web.

Insights of this type have been common enough for relatively simple ecological models to more than justify the attention that has been given them. Yet the dynamics observed in many, if not most, ecological systems, seems to be beyond easy elucidation through traditional modeling approaches. Among the possible reasons for this failure are the following:
1. Spatial complexity. Ecological populations in general are not well mixed. Individuals interact with their neighbors, not with some average of all members of the population implied in most state variable models.
2. Internal structure within populations. The characteristics (feeding, habitat, vulnerability to predation, etc.) change with size and age. Phenotypic variability and growth plasticity often occur.
3. Species complexity. The characteristics of all species present in a natural system cannot be adequately catalogued and represented in a model. It is often the seemingly "obscure" species that become important and cause surprises when external conditions of the system change.

These factors limiting the usefulness of state variable models are much the same as those suggested by MAYR (1988) mentioned earlier. It would be easy to document a number of cases of difficulties for modeling caused by each of these factors. To take just one factor, the complications in dynamics caused by internal structure in populations has been noted by many researchers. PERSSON (1988), for example, showed that in yellow perch populations under certain condition larger or older perch were at a competitive disadvantage in finding prey relative to smaller perch, but that the larger perch could frequently cannibalize the smaller ones. The dynamics that can result from such a complex situation are very difficult to predict and may depend on the precise situation. A single-variable model of the population would have no chance for describing the population dynamics of this system.

3.   Individual-based models

These limitations on the effectiveness of state variable models should make one wary of basing theory exclusively on such models. Many theoretical ecologists, in fact, do not use mathematical models, which they feel to be overly simplistic for the systems they study. Clearly, then there is a need for alternative approaches, and there is active work in this area. One approach is toward the elaboration of state variable models to include internal structure within populations and to include spatial heterogeneity. I will talk more about these models later, but will first make the case for a more radical break from the state variable population models, that is, the development of what have been termed "individual-based" models.

In individual-based models, the variables are not population level quantities such as population size. Instead, the variables are characteristics of the individual organisms within the population (their lengths, weights, ages, conditions, etc.). A model generally contains a changing number of individuals, each of which is kept track of with all its attributes. This means that if, at a given time, there are 1000 individuals in the population and 5 different attributes are followed for each individuals, there are 5000 variables in the model at that time. Such a model can only be evaluated by means of a computer.

The individual-based approach allows one to take into consideration several aspects of populations that are impossible or extremely difficult with state variable models. These include the facts that:
1. Each individual in a biological population is unique, differing in its set of characteristics (age, sex, size, condition, social status, genotype, ...) from all other individuals.
2. Each individual is subject to a different set of experiences and of different local interactions with neighbors.
3. Decision-making by the individual organism, which can depend in complex ways on day-to-day circumstances, should be factored into population behavior.

Despite this, some difficulties in the individual-based approach are obvious. First, the approach seems to be in direct contradiction to the truism mentioned earlier that the individual is essentially unpredictable. The objection is easily dealt with because the approach does no rely on the predictability of particular individuals. Monte Carlo simulations are performed with individuals having some degree of stochasticity, with the idea that the resultant dynamics at more aggregated levels will be properly described.

A second possible objection is that such large, complex simulations are merely bookkeeping procedures and cannot offer the sorts of simple insights that state variable models can. Although it may be difficult to deal with this objection through argument alone, one can make a good argument that in complex ecological situations the individual-based model may be fundamentally much simpler than a state variable model applied to the system. This is because the basic information in an individual-based model can be expressed as a set of rules governing the behavior and physiology of the individuals. These rules will constitute a fixed set of invariants of the model, no matter how many individuals there are or how spatially complex the system is. Given these rules, which may include some assumptions that the individuals will strive to optimize their performance of certain functions, such as survival, growth and reproduction, the individuals will behave accordingly and the behavior of the population or community as a whole will emerge from the collective interactions of the individuals.

The usefulness of the individual-based models in representing types of dynamics beyond easy reach of the state variable models can best demonstrated through examples.

Example 1: Forest Stand Dynamics

The individual-based approach to describing succession in forests is the "gap phase" model, which represents the dynamics of a forest as follow:
1. The death of canopy trees periodically open up environmental patches, or gaps that can be colonized by seedlings.
2. Seedling establishment, growth and competition for light, water, and nutrients by individual plants can be modeled explicitly, individual by indidividual, inside the gap, using knowledge of the physiological properties of the plants.
3. The use of many Monte Carlo runs for individual gaps, and a knowledge of the frequency of gap formation, give one a statistical picture of the changing forest community.

SHUGART (1984) and others have used this modeling approach to make many general and specific predictions that have been verified by observation.

Example 2: Fish Population Recruitment

Predicting the number of recruits in a fish population given the number of eggs laid at an earlier time is a fundamental problem in fisheries ecology and one that has eluded state variable models. The individual-based approach is able to model the internal dynamics of the population, which depends critically on the size-frequency distribution of individuals through time. An individual-based model has been developed that follows the dynamics of a fish cohort from eggs to yearlings in order to calculate recruitment to the yearling class (DE-ANGELIS & al. 1991).

The model simulates the foraging, growth, and exposure to mortality of young-of-the-year fish on daily time steps according to a set of physiological and behavioral rules subject to stochasticity. Only some representative fraction of the fish in the population are actually simulated. Prey in several size classes are modeled as state variable populations, whose densities can be affected by grazing by the fish. Other environmental characteristics, such as temperature and predator density, can also be specified through time.

The individual-based fish recruitment model has been used to make predictions at two different levels; generic predictions relevant to a type of situation (e. g., smallmouth bass, Micropterus dolomieue, in a small northern temperate lake) and specific predictions relevant to a specific lake in a given year. Among the general results of the model is the prediction that a nonlinear humped relationship can exist between the number of eggs laid in a particular year and the number of yearling recruits the next year. The humped nature of the relationship results from the fact that high egg densities lead to stunting of growth and high winter mortality.

Example 3: Wood Stork Breeding Colony

An individual-based model has been developed by WOLFF (submitted) to attempt to predict the reproductive success of a colony of wood storks in a wetlands (Everglades of Florida). The model simulates the activities of all the adult of the colony on 15-minute time intervals as well as the growth of their offspring. A set of rules is prescribed for the physiology and behavior of the adults and nestlings. The model adults forage in a landscape of 25.600 1/4 by 1/4 km cells, while the food availability in each of the cells can vary from day to day.

The wood stork colony model has been used to relate various scenarios of landscape change through the growing season (water depth and hence food availability) to the number of nestlings reaching the fledgling stage.

4. Discussion

The objective of this paper hast not been to assert the superiority of the individual-based approach, but to indicate that there may be types of ecolotical problems for which it is better suited than the state variable approach. The individual-based approach lends itself well to problems in which individuals in a population may have complex life cycles and live in a complex environment, as long as the physiology and behavior of the individuals can be specified by a set of rules.

It is reasonable to ask whether one has only the choice of these two dichotomous approaches or whether intermediate sorts of models can also be developed. There are, in fact, a range of models that can be termed intermediate between the two described model types. State variable models have been eleborated to take into account size and age structure of populations. Leslie matrix models (see CASWELL 1989) and McKendrick - von Foerster model (see METZ & DIEKMANN 1988) are examples of these. State variable models can also be elaborated to include spatial extent and heterogeneity, by dividing a region into subregions and keeping track of the fractions of various populations in different subregions as a function of time.

Each of the types of models discussed in this paper has advantages and disadvantages. Comprehensive analyses of the limitations of each model type and of which types are most valid and useful for given ecological problems are urgently needed.

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