POPULATION MODELS

V.P. Passekov
Division of Modeling Problems, Computing Center of Russian Academy of Sciences, Russia

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Contents

Biographical Sketch

Summary

The paper deals with modeling population phenomena. Two branches of population biology are considered: population genetics and population ecology. The former refers to evolution of population genetic structure in terms of frequencies of genetic types and the latter concerns problems of dynamics of interacting populations in terms of their numbers. The role of mathematics in solving population problems is emphasized. The main factors of microevolution are considered (selection, mutation, and migration) and appropriate models are discussed. Deterministic and stochastic approaches to the description of genetic structure microevolution are presented. Adaptation process and the concept of evolutionary stability are considered with respect to population genetics and population ecology. Models of population growth in discrete and continuous time are given, including age-structure effects. Basic models of population interactions (relation of predator–prey type, competition, symbiosis) are described. The majority of models are given in the framework of difference and ordinary differential equations (ODE). To analyze migration processes, integral equations or partial differential equations (of reaction–diffusion type) are used. Problems of optimal exploitation of renewable biological resource are discussed. Since ecological problems are now central for humankind, development population biology modeling is necessary for sustainable development and the conservation of biodiversity.

1. Construction of Mathematical Population Models and the Main Tasks of Their Study

1.1. Main Branches of Population Biology

Population biology is an area of biology concerning living things on the population level of organization. Among biological sciences, it plays a special role because of population is the least evolving unit. By definition, population represents an arbitrary self reproducing group of (potentially) interbreeding individuals of the same species that occupies a certain area during a rather extended time and which is separated from other similar units by some degree of isolation. The fundamental processes of reproduction and elimination of individuals (through which the main factor of adaptive evolution, natural selection, is realized) happen just in population. Specific for species mutual relations between living organisms and environment take place similarly for groups of similar organisms, i.e., populations.

From the time of Darwin, evolutionary ideas penetrate through all areas of biological researches. According to Darwin's views, (hereditary) individual variability is the basis of evolutionary changes. Evolutionary aspect of population biology is reflected in *population genetics* with its analysis of hereditary variability transformations in a series of generations. Ecological aspects of population biology consist in researches of mutual relations of living organisms with each other and environment. They are reflected in *population ecology* that naturally includes epidemic theory (see *Epidemic Models*). The analysis of problems arising in population biology concerns with theoretical and applied aspects that include dynamics and statics, regularities, problems of stability, forecasting, management, conservation, etc.

1.2. Formation of Mathematical Theory

The solution of the listed problems is based on understanding population phenomena, the basis for the prediction of population transformations. Here the role of mathematical modeling is difficult to overestimate. Both population branches belong to the most formalized areas of biology. One of the first mathematical applications to biology was made here, and many famous mathematicians solved population problems. Therefore, it is possible to say that just here began creation of mathematical biology.

The appearance of mathematical genetics is connected with names of R.A. Fisher, S. Wright, and J.B.S. Haldane at the beginning of the twentieth century. They laid the basis of deterministic and stochastic theories for dynamics of genetic population structure. M. Kimura made significant contribution to the development of stochastic models. At the beginning, the theory was mainly a tool for the creation of general conceptions about evolutionary process and for understanding the mechanisms of selection pressure on genetic structure. At present, due to development of the theory and accumulation of materials, applied aspects and the check of hypotheses on real data (e.g., theoretical explanations of diversity of contemporary populations) more actively take place.

The first attempts at mathematical modeling in ecology began with the study of growth of isolated homogeneous population. The coefficient of population growth in unlimited environment is known as the Malthusian parameter due to the model of exponential growth proposed by T.R. Malthus (1798). The model of selflimited logistic growth was developed by P.F. Verhulst (1848). Here the population converges to equilibrium. Construction of dynamic theory for populations is connected with works of A.G. Lotka (1925) and V. Volterra (1926). Further development of the theory (V.A. Kostitzin, A.N. Kolmogorov, R.G. Leslie), methods of data analysis, and computer modeling allows us to consider mathematical theory of populations as an independent discipline.

Mainly the evolutionary aspect of population genetics leads to accent on the analysis of genetic population structure determining hereditary variability. Here choosing state-variables is obvious (numbers or frequencies of genes or genotypes). Usually, only frequencies are considered, and the influence of population size on them is discarded. Formalization of mechanisms of hereditary transformations is also rather evident and is based on universal *Mendelian laws* of genetics repeatedly checked on many diverse objects. Mathematical ecology developed in such a manner that attention was mainly paid to the statics and dynamics of population numbers considered as the main state-variables. In ecological modeling, intraspecies genetic differences between individuals are usually ignored. Mechanisms of ecological interactions are not so evident as in genetics, and their formalization is largely of phenomenological nature. Bringing in principles of natural selection and genetical–evolutionary approaches to quantitative ecology, account of mutual consequences of interspecious interactions both for numbers and genetic structure are realized in conceptions of evolutionary ecology and coevolution theory at present. The current stage of synthesis is still only initial one.

1.3. State Variables. The Main Approaches

Mathematical modeling processes at population level begins from the choice of the main state variables (describing population as a whole) and state space (SS). It is possible to construct a population model without state variables of low level organization, e.g., on the scale where time unit corresponds to generation, intracellular processes proceed in quite different scales. Hierarchy of rates for various variables corresponds to small parameters in dynamic equations. On population time scale inherent in events of birth and death, the mentioned fast processes are important only if they affect fertility and mortality through which they are taken into account.

If changes of population size per generation are small and typical scale of size dynamics considerably exceeds the time of age-structure stabilization, usually population is considered as homogeneous with no age- (and sex-) structure with averaged coefficients of fertility and mortality. Then population state can be described by population number. On larger macroscale, it is possible to trace dynamics of stationary population regimes (determined by changes of environmental parameters) only. Frequently, processes of convergence to stationary regimes are considered as short-term dynamics opposite to long-term macrodynamics including transitions from one regime to another. Here alternation of smooth change periods with fast "jumps" of transition at the loss of stability is typical. Usually, the quantity of critical parameters determining such jumps is small, and the use of simple analytical models for understanding the essence of transformations taken place is perspective.

For deterministic description of dynamics in SS, difference equations (models with nonoverlapping generations or with discrete age-structure) are employed; ordinary differential equations (models with continuous time without age-structure); reaction–diffusion equations, integrodifference and integrodifferential equations (models accounting for movements of individuals and their distribution over habitat); system of first-order partial differential equations (of Liouville) and birth integral equation (models with continuous structures); equations with time-delays (models taking account of hereditary effects or age-structure) are used. The coefficients of these models can be considered as periodic or stochastic functions, etc.

The main tasks of analytical and numerical study of the obtained models include qualitative study (the existence, number and nature of equilibria and limit cycles, existence of chaotic dynamics, etc.) The study of dependence on parameters for the mentioned properties and explicit solution of model equations is very important as well. If stochastic models are employed, these tasks are modified in probabilistic aspect with the use of averages, variances, probabilities of various kind events and distributions of random times of their occurrences, etc.

The rapid development of computer facilities stimulates the development of simulation models. Their distinction consists in extensive description of details for objects under study, i.e., in large number of state variables. Separate blocks and equations of simulation models are developed on the basis of analytical elaboration; parameter estimation is required for objects. Usually, the study of simulation model is based on numerical methods since analytical solution is impossible as a rule. The original euphoria of possibilities of simulation study of complex systems has been replaced by a more sober opinion. It is connected with impossibility of complete numerical investigation for the large number of equations.

In simulation models, large detailing impedes the process of revealing general properties inherent to classes of similar objects. To study general ecological regularities, elementary basic models of a population and two-species communities are useful. Here there is the analogy in approaches of experimenters who carry out model experiments with variation of one factor only. Thus, the main advantage of analytical approach is to reveal general properties and various regimes of community functioning as well as the main mechanisms for qualitative changes of states. Further presentation is devoted to relatively simple analytical models of population biology. Here stability is understood as Lyapunov stability unless stated otherwise.

1.4. Space of States

In simple cases, population state is described by the vector $\mathbf{N} = \{N_i\}$ of numbers (biomasses, densities, i.e., numbers per area unit) of various type individuals. Usually, $\{N_i\}$ are considered as continuous variables. Since they are nonnegative, SS is (say, *n*-dimensional) nonnegative orthant

$$\mathrm{R}_+^n = \{\mathbf{N}: N_i \geq 0,\ i = 1,...,n\}.$$

It is possible to describe population state in terms of total number $N = \sum N_i$ and structure **p** (frequencies for various type individuals). Vector $\mathbf{p} = \{p_i = N_i/N\}$ of frequencies for types belongs to $(n - 1)$-dimensional simplex S_n:

$$S_n = \{\mathbf{p}:\ p_i \geq 0,\ i = 1, ..., n,\ \sum_{i=1}^{n} p_i = 1\}. \tag{1}$$

It is possible to analyze only independent $n - 1$ coordinates on simplex, discarding, e.g., the latter, $p_n = 1 - \sum_{i=1}^{n-1} p_i$.

If spontaneous generation of any type individuals is impossible, the model usually is written as

$$(N_i)' = f_i(\mathbf{N}, t)N_i,\ \ f_i \geq 0,\ \ i = 1, ..., n,\ \ \mathbf{N} \in \mathrm{R}_+^n.$$

Here the prime refers to varibles at the next generation (more generally, at the next time step).

These equations give the model of *self reproducing system* with nonoverlapping generations. In terms of total size *N* and structure **p**, the model is

$$N' = \sum f_i\,(N,\mathbf{p},t)N_i = (\sum f_i(N,\mathbf{p},t)p_i)N = f(N,\mathbf{p},t)N, \tag{2a}$$

$$(p_i)' = (f_i(N,\mathbf{p},t)/f(N,\mathbf{p},t))p_i, \quad N \neq 0. \tag{2b}$$

Here subsystem for structure **p** is separated if there exists a factorization

$$f_i(\mathbf{N},t) = \tilde{\mathrm{f}}(N,\mathbf{p},t)\hat{\mathrm{f}}_i(\mathbf{p},t),$$

where $\tilde{\mathrm{f}}$ and $\hat{\mathrm{f}}_i$ are some co-factors. ODE model of self reproducing system is

$$dN_i/dt = f_i(\mathbf{N},t)N_i, \; i = 1,\dots,n, \quad \mathbf{N} \in \mathrm{R}^n_+. \tag{3}$$

In terms of total number N and structure **p**, the model is written as

$$dN/dt = \sum f_i\,(N,\mathbf{p},t)N_i = (\sum f_i(N,\mathbf{p},t)p_i)N = f(N,\mathbf{p},t)N, \tag{4a}$$

$$dp_i/dt = p_i(f_i(N,\mathbf{p},t) - f(N,\mathbf{p},t)), \; N \neq 0. \tag{4b}$$

Subsystem (4b) is separated if

$$f_i(\mathbf{N},t) = f_i(N,\mathbf{p}\,,t) = \tilde{\mathrm{f}}(N,\mathbf{p},t) + \hat{\mathrm{f}}_i(\mathbf{p},t) \tag{5}$$

for some terms $\tilde{\mathrm{f}}$ and $\hat{\mathrm{f}}_i$. For infinite dimensional generalizations of finite-dimensional models, population states are described by distribution functions over space, age, genetic types, etc.

Structures of many equations of population genetics and ecology are similar since they include the same type of nonlinearity due to pair interaction terms. It is the consequence of pairwise sex cells (*gametes*) fusion at fertilization to produce an offspring *genotype* (genetic constitution) in genetics and of the pair encounters of individuals leading to species number changes in ecology. For example, equations for community structure in Lotka–Volterra ecological model and in genetic model of selection are formally the same. Population models and chemical reaction kinetics models are similar because of analogy in principle of pair encounters and the law of mass action.

The basic property of an abstract population is its reproduction in time. Therefore, modeling has common features for populations of any nature (economical objects, cells, etc.). In particular, dynamics of selfreplicating macromolecules in models of prebiotic evolution is described by the same equations as in genetic models.

2. Deterministic Models of Population Genetics

The main factor of adaptive evolution is natural selection, other factors are thought of as *neutral* ones. Deterministic microevolutionary factors are referred to as *systematic* factors. The use of deterministic models for the description of population–genetical dynamics is limited by analysis of a small number of loci. It is connected with exponential growth of possible types of gametes as the amount of loci with more than one allele increases. If experimental data on share of such loci are extrapolated to a whole genome, say, of humans, the number of gamete types greatly exceeds the quantity of gametes of people ever lived. The majority of these types never meet in finite population. Further, p_i usually denotes the frequency (concentration) of the *i*-th gamete, p_{ij} is the frequency of genotype formed by *i*-th and *j*-th gametes.

2.1. Model of Population with Nonoverlapping Generations. Hardy–Weinberg Law

Being carefully investigated, the model with nonoverlapping generations is considered as a basic model of population genetics and as the starting point for various applications and generalizations. It assumes synchronous passage of life cycle stages by individuals; annual plants, which leave seeds in autumn and die in winter, are an example. Usually, population state is described at the stage of newborns. The state at the beginning of the following generation is determined by the previous one. Analytically, a transition law is written as the superposition of all transformations during the life cycle. The last stages consist of *haploid* (with one set of chromosomes) gamete production and their independent pairwise fusion (due to *random mating,* or *panmixia)* to give *diploid* (with two sets of chromosomes) offspring. Parents die out and offspring replace them.

In the case of a self reproducing system in continuous time, the dynamic equations are given by (4). Functions $f_i(N,\mathbf{p},t)$ (coefficients of growth, or offspring number per individual for discrete time) are interpreted as current *fitnesses* of genetic types, function $f(N,\mathbf{p},t)$ is *population fitness* or *mean fitness*. In models of mathematical genetics, analysis is usually limited to study of statics and dynamics of structure, neglecting the influence of number on it. Such an approach is justified, e.g., under the assumption of constant (for example, equilibrium) population size or such an abstraction as its infinity. Besides, dynamic equations for structure are separated under condition (5). The analysis of genetic structure dynamics is also simplified in the case of different scales of changes for population number and frequencies of genes. The latter are frequently considered as more conservative variables. The use of small parameters leads to closed equations of zero-order approximation for frequencies.

In the case of random mating in diploid population, independent combination of genotypes in parental pairs and gametes in offspring leads to *Hardy–Weinberg* law (independently published by mathematician G.H. Hardy and physician W. Weinberg in 1908):

At panmixia with no selection and other systematic factors in a large isolated diploid population with nonoverlapping generations, equilibrium for frequencies of *ordered* (by subscripts) *one-locus genotypes* $\{p_{ij}\}$ is reached in the next generation for any initial state. The equilibrium is characterized by independent combination of alleles in genotypes $\{p_{ij} = p_i\, p_j\}$, where $\{p_i\}$ are initial (and constant in time) allele frequencies.

Sex chromosomes X and Y determine sex (usually, XX, XY are female and male, respectively), other chromosomes are called *autosomal*. Y-chromosome practically does not carry loci; loci of X-chromosome are called *sex-linked*. If sex-structure is taken into account, differences in frequencies of autosomal genes and genotypes between sexes disappear in the next generation. Then Hardy–Weinberg law holds. Differences between male and female frequencies of sex-linked genes decrease twice for generation. In the limit, they are equal, and Hardy–Weinberg law holds for females.

Elementary factors of microevolution are selection (the main factor of adaptation), mutation (source of new hereditary material for selection), migration, and random genetic drift (nondirectionally changing genetic structure of population due to sampling effects, see Section 3.1). Modern theory of evolution considers the joint action of the factors.

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Biographical Sketch

Vladimir Passekov is a known specialist in theoretical population genetics and ecological population modeling. He graduated from Moscow State University as a biologist and as a mathematician. His scientific career began at Moscow University and now he works at Computing Center of Russian Academy of Sciences. He is the author of about 80 scientific papers.