

About some background problems for ecological modelling

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Abstract

In current publication some key problems in ecological modeling are discussed. In particular, problem of choosing and constructing of mathematical model for the description of population dynamics, and problem of using of models for prognosis were considered. For some considered problems possible ways for its solutions are presented.

Keywords time series, models with continuous and discrete time

Introduction

In nature various population processes influencing on conditions of human habitat can be observed. Agricultural pests may have strong influence on quantity and quality of food supplies. Outbreaks of forest insect pests can lead to disturbance of normal functioning of sectors of modern economics. Dynamics of rodents has strong influence on appearance and spread of various diseases, and so on. This list of examples can easily continue. There is a lot of commercial species of plants and animals, and their dynamics are of special interest for human's life. Finally, there are a lot of various intra-organisms cell processes (in particular, cancer growth processes), and analyses of these processes are of extreme importance for human health.

Changing of number of cells, insects, or fishes etc in time are different variants of population processes. Within the limits of every concrete situation there are various laws of functioning of one or other system, various laws for birth and death processes of individuals, various laws of self-limitation and so on. At the same time for the description of different processes we use one and the same mathematical models. And in the base of used models it is possible to find very close ideas, assumptions, and imaginations about functioning of considered systems. Even the search of new types of mathematical models which can give better description for considering processes, is practically realizing in one and the same direction.

Different parts of modern science which analyze close population processes can be rather isolated. This isolation can lead to funny situations when one and the same equation (model) in closed scientific domains has different names. If model with discrete time and fractional-linear function in right-hand side is used for the description of fish population dynamics it has the name “Beverton – Holt model” (Beverton, Holt, 1957). If this model is used for the description of insect population dynamics it has the name “Skellam model” (Skellam, 1951). It arouses a suspicion that a lot of researches didn’t open and read a book by V.A. Kostitzin (1937) where this model was presented on first pages. Existence of local terminologies in various parts of modern science (it is obvious that it hasn’t a direct relation to model names only) leads to problems in exchanging of ideas, results, problems etc. between specialists.

It is possible to point out some other initial conditions which can lead to appearance of similar problems. It can be based, for example, on conditions of existing education. It isn’t a secret that biologists don’t like to use mathematical models for the description of population processes. This dropping can be based on the following objective facts – mathematicians cannot give answers on some basic and important questions. For example, what kind of mathematical model we have to use for the description of population dynamics? What’s the best – models with discrete or continuous time? What does it mean from the biological point of view that we can differentiate population size? What’s the best statistical criterion for the estimation of model parameters and why? Partly some of these questions we will consider below.

On the other hand, mathematicians don’t like to use existing biological datasets for checking suitability of their models for the description of population dynamics. It depends on quality of existing models, and on common opinion that biological datasets have very low level of precision. In a result of it mathematicians prefer to construct new and new models, to provide deep analyses of models, and to present interpretations of obtaining results. Statisticians don’t like to work with non-linear ecological models – rather simple models contain big number of parameters, non-linear functions, time lag coefficients etc. In most cases it leads to serious problems in searching of the best estimations of model parameters using empirical datasets.

At the same time a big number of most interesting and important problems (first of all, from practical point of view) is in between ecology, modeling, and statistics. But before this combining we have to consider some important problems pointed out above.

Some words about very old discussion...

All deterministic models using in ecological modeling can be conditionally divided on two big groups. If birth process is of the continuous type and in population generations are overlapping, ordinary differential equations (ODEs, ODEs with time lag, integral-differential equations etc.) are usually used for the description of population dynamics (Bazykin, 1985; Brauer, Castillo-Chavez, 2001; Kostitzin, 1937; Nedorezov, 1986, 1987; Svirezhev, 1987; Smith, 1974 and others). If birth process in population has a discrete nature (it can be observed, for example, for insect populations with one-year generations), and generations don't overlap, then recurrence equations are used for the description of population dynamics (Pielou, 1977; Isaev et al., 1979, 1980, 1984, 2001; Hanski, 1999; Kot, 2001; Nedorezov, Utyupin, 2011 and others). Even in a case when generations overlap and birth process has a discrete nature, recurrence equations of systems of recurrence equations are usually used for the description of population dynamics (for example, Leslie model and Leslie – Lefkovitch model of population dynamics with age structure; Leslie, 1945, 1948; Lefkovitch, 1965; Logofet, 1993, 2005, 2008).

In every concrete situation the natural question arises – what kind of mathematical model we have to choose for solution one or other population problem and why? What kind of model will give us best description of the dynamics of considering object? Is it possible to say, for example, that for description of insect population dynamics or fish population dynamics we have to use recurrence equations only?

A certain number years ago these questions were in the mid part of discussion in ecological modeling (see, for example, Svirezhev, Logofet, 1978). It is necessary to mark that these questions are very important for practice: models with continuous and discrete time have qualitatively different dynamical regimes even in the cases when models are based on similar biological assumptions. As a good example we can compare two *logistic models*: within the limits of *logistic model with continuous time* (Verhulst model; Verhulst, 1838) regimes with monotonic stabilization of population size at zero or non-zero stable level can be observed only. Within the limits of *discrete logistic model* (Moran, 1950; Ricker, 1954) can be observed as regimes of population stabilization at any level, as various cyclic regimes and chaos. It is assumed that both models are based on one and the same biological background.

Moreover, it looks like common opinion that discrete logistic model is a discrete analog of Verhulst model. In literature (and, in particular, in textbooks) it is possible to find the following

sequence of transformation of Verhulst model which allow obtaining discrete logistic model. Let $x(t)$ be the population size at moment t . Verhulst model has the following form (Verhulst, 1838):

$$\frac{dx}{dt} = x(\alpha - \beta x), \quad (1)$$

where α is a Malthusian parameter (difference between intensity of birth process and intensity of death process in population). This coefficient can be positive or negative (if intensity of death process is bigger than intensity of birth process). Coefficient β in (1) characterizes influence of self-regulative intra-population mechanisms on population dynamics. It is assumed that intra-population competition between individuals can lead to increase of death rate only. Thus, $\beta = \text{const} \geq 0$. It is also assumed that initial population size is non-negative, $x(0) \geq 0$; emigration and immigration are absent in population, and if $x(0) = 0$ then population size becomes identically equal to zero for all $t > 0$.

Let's fix any positive time step $h > 0$. Euler scheme for approximation of derivative gives us the following relation:

$$\frac{x((k+1)h) - x(kh)}{h} = x(kh)(\alpha - \beta x(kh)). \quad (2)$$

Let $x_k = x(kh)$. Taking it into account we can re-write equation (2):

$$x_{k+1} = x_k(\alpha h + 1) - \beta h x_k^2.$$

After linear transformation of variable

$$y_k = \frac{\beta h x_k}{1 + \alpha h},$$

we get the final form for discrete logistic model:

$$y_{k+1} = a y_k (1 - y_k), \quad (3)$$

where $a = 1 + \alpha h$.

Formally speaking, model (3) was deduced from model (1), and, moreover, model (3) looks like model (1). In a result of it there exists common opinion that model (3) is direct discrete analog of Verhulst model (1). But there appears a natural question – why did we use Euler approximation for obtaining equation (3)? We can also use trapezium scheme, Adams – Bethford formula and so on for the approximation of derivative. If we will use Adams formula (Korn, Korn, 1973, page 703, formula (20.8-7)), and cut off it at any finite member we get a *numerical set of analogs for Verhulst*

model. Every discrete analog of Verhulst model will have its own set of dynamical regimes, and its own structure of space of parameters.

If we will use the following approximation of derivative

$$\frac{dx}{dt} \approx \frac{x_{k+1} - x_{k-1}}{2h},$$

after simple transformations we get the following model of population dynamics:

$$x_{k+1} = 2h\alpha x_k - 2h\beta x_k^2 + x_{k-1}.$$

Like discrete logistic model this model can be called a discrete analog of Verhulst model. But this model is more complicated than discrete logistic model – here we have a time lag, and population dynamics depends on population size in two previous time moments.

Thus, this method for obtaining new discrete models (analog of models with continuous time) must be declared as absolutely untenable approach. These mathematical exercises have no relations to population dynamics. Construction of mathematical models must be based on real considering processes we may have in biology, demography and so on. And it cannot be based on sets of various difference schemes using for approximation of differential equations which can be found in modern literature.

As it was pointed out above, in literature it is possible to find the following opinion – if generations in population don't overlap, and/or measurements of population size are discrete in time we *have to use recurrence equations* for the description of population dynamics. In literature it is possible to find other opinion (Gimelfarb et al., 1974, page 91) “...for some problems the use of discrete time is more comfortable than use of continuous time”. But “*more comfortable*” doesn't equal to “*necessary*”.

Let's consider as an example a problem of modeling of insect population dynamics in boreal forests. For big number of species measurements of population sizes/ densities can be provided in autumn when no activities of insects can be observed (Isaev et al., 1980, 1984, 2001; Varley, Gradwell, Hassell, 1973; Vorontsov, 1978). In a result of regular from year to year collection of population densities we get a sequence of non-negative values $x_1^*, x_2^*, \dots, x_N^*$, where N is a number of years or sample size. Taking into account that there are non-overlapping generations, one generation per year, and discrete measurements, researchers describe population dynamics with following difference equation:

$$x_{k+1} = x_k F(x_k), \quad (4)$$

where x_k is population size (density) at k th year, F is a birth coefficient (relative speed of population size changing). For situations when increasing of population size lead to increase of influence of self-regulative mechanisms birth coefficient is usually chose as monotonic decreasing function. In general case this function may have several extreme points.

Existing time series $\{x_k^*\}$, $k = 1, \dots, N$, allow estimating values of parameters of model (4), and in particular, creating of scientifically-based forecast. At the same time some important questions about correct use of discrete models, about effectiveness of these models etc. can arise:

- Let's assume that during a vegetation period of k th year chemical poisons were used for struggle against a pest, i.e. poisons were applied before time moment of population size measurement. Depending on time of applying of poisons (it can be realized as in the beginning of vegetation period as in the end of it) we can get various values of density x_k^* . But how we can estimate a moment for applying of poisons (with the help of model (4)) when effectiveness of used method of population size management has a maximum value? How we can do it if we haven't time between two moments of measurements? Respectively, for fish populations we can conclude that from biological point of view we cannot create a correct problem on optimal catch, about optimal assignment of quotas, and time intervals for catch *in principle*.

- It was pointed out above that function F can be a monotonic decreasing function (see, for example, Varley, Gradwell, Hassell, 1973; Isaev et al., 1984, 1986; Skellam, 1951 and others). What is the result of such a behaviour? Can we say that it is a result of intra-population competition between individuals, or result of specific dependence of productivity on food conditions, or dependence of surviving of individuals on winter conditions, or...? It is impossible to obtain a good answer on these questions because influence of all pointed out mechanisms (moreover, this influence is presented in integral form – like a dependence on conditions between two times of population size measurements) is described in one function F . Such an overload of function F doesn't practically to allow to present substantial biological interpretation of model parameters. Respectively, in most cases this interpretation has a pure declarative character: a priori it is declared that one of parameters describes influence of weather factors on population size changing, second parameter correlates with tension of intra-population competition between individuals, and third parameter is equal to time of search of victims by parasites etc.

This isn't a full list of problems we have or may have when we use discrete models for the description of population dynamics. It is easy to add to this list some more problems, but it doesn't

mean that we don't need to construct new discrete models and use them for fitting of empirical time series. It is important to note that under the certain conditions more complicated models sometimes can be reduced to simpler discrete models (see, for example, Nedorezov, 1986, 1997, 2012 a; Nedorezov, Utyupin, 2011) of the type (4).

Every individual in population can perish at every time moment in a result of impact of various factors (for example, in a result of application of chemical poisons against insect pests). In this occasion death process has a *continuous nature*. In boreal zone for various species appearance of individuals of new generations is realized at any fixed moments (really, during rather short time period). In this sense birth process has a *discrete nature*. Thus, if we describe process of population size decreasing by ordinary differential equations (ODEs), and take into account the discrete nature of birth process we get ODEs with impulses (Kostitzin, 1937; Poulsen, 1979; Aagard-Hansen, Yeo, 1984; Nedorezov, 1986, 1997, 2012 a; Nedorezov, Utyupin, 2011). Such kind of dynamics is typical for big number of biological species which play extremely important role in human activities (Varley, Gradwell, Hassell, 1973; Isaev et al., 1984, 2001; Vorontsov, 1978; Tonnang et al., 2009 a, b, 2012 and others).

First model of that type is presented in book by V.A. Kostitzin (1937). Author analyzed dynamics of insect population which contains individuals of several types – imago, pupae, larva, and egg. Decreasing of population size (individuals of every type) was described by differential equation; transmission from phase to phase (changing of the type of individuals; it was assumed that in model there are non-overlapping generations and non-overlapping phases of insect development), and appearance of individuals of next generations were realized at fixed time moments.

Step by step integration of equations allowed him obtaining the discrete model which is known in modern literature as Skellam model (1951) and Beverton – Holt model (1957). V.A. Kostitzin didn't write that this mathematical object is most suitable for the description of population size dynamics. He reduced model with continuous time to model with discrete time for *ease in analysis*.

About the use and problems of modeling

As it was pointed out above, now we have rather strange situation in modeling of population dynamics. The specificity of current situation can be characterized or described as parallel development of ecology (with ecological theories) and ecological modeling (Isaev et al., 1984,

2001). It isn't a rare opinion among biologists that mathematical modeling is useless part of science and it didn't bring a useful information for solution one or other biological problem.

The real role of modeling isn't so strong like the role of application of statistical methods to solution of biological problems. Moreover, application of non-linear ecological models for solution of various problems meets with serious mathematical problems, and sometimes it meets with unsolved mathematical problems. For example, application of models for preparing of long-term forecast of any species leads to necessity of estimation of model parameters using empirical datasets. In other words, we have to solve *an inverse problem* and to show (or to prove if it is possible) that estimations of model parameters and model are *suitable for the description* of population dynamics. When we talk about suitability of model we assume that following items are truthful: use of existing statistical criterions don't allow us rejecting a hypothesis about Normality of deviations between model and empirical values, there is no serial correlation in a sequence of residuals etc. But this way leads to a set of extremely important problems:

- Diversity of existing statistical criterions which can be used for estimation of model parameters (see, for example, Korn, Korn, 1973; Draper, Smith, 1986, 1987; Wood, 2001 a, b; Bolshev, Smirnov, 1983; McCallum, 2000) can lead to serious incomprehension – what's the best criterion for solution of considering problem and why? Some authors recommend transforming initial samples before estimation of model parameters (in particular, they recommend to use logarithmic transformation; Lakin, 1990; Williamson, 1975). Other specialists don't recommend using non-linear transformations because it can lead to serious changing of final results. Specialists from third group recommend using for discrete models criterions like for one-step regression ahead (without explanations why it is better than two-step regression, three-step regression and so on, or global fitting). Specialists from the fourth group recommend... And this situation will be saved if we cannot say what kind of criterion we have to use in every concrete considering situation.
- It is well-known that inverse problem may have several solutions. For non-linear ecological models loss-function may have several local minima, and every corresponding set of model parameters belongs to "biological zone". Thus, we can get a problem of determination of parameters which are closest to veritable parameters.
- If we found a minimum of loss-function – how we can prove that this minimum is global, and we have best fitting of initial sample? It is possible, for example, in selected part of the space of model parameters to obtain a big number of stochastic points with uniform distribution. For every stochastic point we can find a value of loss-function. If in every point value of loss-function is

bigger than finding minimum, thus, we obtain estimation of probability that in chose part of space of model parameters minimum of function is global. But can we say that this answer is satisfactory result? Some specialists can say yes. Some other specialists will say no. The similar situation we have in selection of significance level – what’s level we have to have for obtaining qualitative biological results? There are no answers on this question – every researcher chooses significance level taking account his or her own experience only.

- Before solution of inverse problem we have to solve the problem with selection of mathematical model – for what kind of model we want to solve the inverse problem? It looks strange but up to current moment we haven’t criterions for choosing a model a’priori (before comparison theoretical and empirical datasets). What’s necessary to do in such a situation? It is obvious that it is impossible to solve inverse problems for thousands and thousands existing models. It is possible to construct a new model – but where is a guarantee that this new model is better than all existing models?

We have to divide between two qualitative different situations. If we want to construct a prognosis of population size changing in time only, and, for example, we are not interested in reaction of population system on any impacts, we have no necessity to use ecological models. For obtaining a good prognosis we can use methods of classic applied statistics. But in a case when we have to have *real values* of population parameters, and to analyze reactions of system on possible external impacts (fishing, use of chemical matters, climatic impacts etc.) we have to use mathematical models.

Does it possible to differentiate a population size?

The wish to use ordinary differential equations for the description of population dynamics had been appeared before than understanding of the fact that using of ODEs leads to appearance of huge set of various critical problems (Volterra, 1931; Lotka, 1920, 1925; Kolmogoroff, 1936; Kostitzin, 1937; Williamson, 1975 and others). In a result of it now we have a rather funny situation – there exists well developed deterministic theory of population dynamics without a good background.

For constructing various forecasts, for preparing computer experiments etc. we have to compare theoretical (model) results with existing time series. We have to estimate model parameters using empirical trajectories. But before this comparison we have to understand what we have to compare and what a background for this comparison is. In other words, can we compare trajectory

of differential equation with trajectory of changing of population size in time, and how we can do it in a correct way?

It was obvious from the very beginning (Kolmogoroff, 1936; Lyapunov, Bagrinovskaya, 1975) that differentiation of integer-valued variable $x(t)$ (population size) is not allowed (or illegal) operation. Thus, there were several attempts to construct a base for using of models of population dynamics which are systems of ODEs. A.N. Kolmogoroff (1936) assumed that ODEs can be applied for description of population dynamics in a case when population size is rather big. In this case it is possible to create new variables for time and size (it is possible “to compress” variables) – under certain conditions it will allow to use differential equations for approximation of values of new variables.

If we accept Kolmogoroff’s point of view we have also to accept the assumption that deterministic models cannot be used for the description of dynamics of rare populations. Moreover, it isn’t obvious for natural populations what “rather big size of population” is. Even for mass species of forest insects differential equations cannot practically be applied to whole time series – when population is in the zone of stability or in the phase of depression, population size is extremely small (Varley, Gradwell, Hassell, 1973; Isaev et al., 1984, 2001; Vorontsov, 1978).

Finally, if we accept Kolmogoroff’s point of view we have no possibilities to compare model and empirical results, and to use datasets for estimation of model parameters. Additionally, we have no possibilities to use deterministic models for the explanation of population dynamics.

A.A. Lyapunov (Lyapunov, Bagrinovskaya, 1975) assumed that deterministic (mechanistic) models describe changing of averages of population sizes in time. In other words, it isn’t a real population dynamics – it is a mean value of the respective stochastic process. For example, if we consider Galton – Watson process with continuous time (Harris, 1966; Sevastyanov, 1971), dynamics of mean value of particles in population is described by differential equation (Malthus model), and at every time moment we have integer value of number of particles. Similar results can be obtained for birth and death processes (Bharucha-Reid, 1969). Thus, it was assumed that deterministic models describe population dynamics “in average”. But it is impossible to give a strong proof for this idea – there are no possibilities to deduce deterministic models from the respective probabilistic models (more precisely, it is possible for extremely small number of deterministic models).

If we assume that Lyapunov’s assumption is truthful, we get a problem in estimation of model parameters. First of all, there are no probabilistic models which are the bases for deterministic

model. The second, comparison of one of possible stochastic realizations of population process with dynamics of average population size is devoid of any sense. For example, if we have over-critical simple branching process average of population size describes by monotonously increasing exponential function. On the other hand, with positive probability we can get a realization of stochastic process which corresponds to population elimination during finite time. How we can compare this stochastic trajectory with monotonic increasing function? All statistical criterions (see, for example, Draper, Smith, 1976, 1977; Bard, 1974) will show an existence of dependence in time series of deviations between theoretical and empirical results. It means that with big probability we have to reject hypothesis about suitability of considering model for fitting of empirical datasets.

Thus, in both considered above situations we have serious problems with comparison of theoretical and empirical datasets. More precisely, in both situations we haven't a background for using of real datasets for estimation of model parameters. If we want to escape out of the problems of comparison theoretical and real datasets we have to have a common agreement those deterministic models (systems of ODEs or based on systems of ODEs) give us *approximations of real time series*. We can talk about approximation only, and theoretical values are not population sizes or population densities at any time moments. Theoretical values can be equal to population sizes if we have good approximation of initial dataset.

Considering model variable can be called pseudo-size of population or population size – it is important to note that this pseudo-size of population we compare with real time series, and, moreover, for obtaining a good approximation model must describe in a respective manner influence of various regulators on population (like real regulators influence on real population).

Postulating that model variable is a pseudo-size of population, isn't a sufficient condition for providing effective comparison between theoretical and empirical time series. If a priori we assume that population dynamics is pure stochastic process then using of deterministic model for approximation of one realization of this process looks rather strange. But for natural populations we cannot get more than one trajectory in principle.

Additionally we have to assume that population dynamics has a *deterministic nature*. Deviations between trajectories of deterministic model, and, for example, real time series can appear in a result of use of one or other method of measurement (Nedorezov, 2012 a, b). If some deviations of population size from a *deterministic trajectory* appear then ecosystem regulative mechanisms return back the subsystem into previous conditions. In such conditions we can apply differential and recurrence equations for the description of population dynamics.

Assumption about deterministic character of population dynamics is in contradiction with a common imagination about an influence of stochastic factors on population size changing in time. For example, it is possible to point out factorial climatic theory – within the limits of this theory stochastic weather factors are the main regulators of population size changing (Uwarov, 1921, 1931; Isaev et al., 1984, 2001; Varley, Gradwell, Hassell, 1973). But even in a case when weather factors have strong impacts on population fluctuations, influence of ecosystem regulatory mechanisms can be rather effective, and it can give us a background for use of deterministic mathematical models.

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