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Non-linearity and heterogeneity in modeling of population dynamics

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ABSTRACT

The study of population growth reveals that the behaviors that follow the power law appear in numerous biological, demographical, ecological, physical and other contexts. Parabolic models appear to be realistic approximations of real-life replicator systems, while hyperbolic models were successfully applied to problems of global demography and appear relevant in quasispecies and hypercycle modeling. Nevertheless, it is not always clear why non-exponential growth is observed empirically and what possible origins of the non-exponential models are.

In this paper the power equation is considered within the frameworks of inhomogeneous population models; it is proven that any power equation describes the total population size of a frequency-dependent model with Gamma-distributed Malthusian parameter. Additionally, any super-exponential equation describes the dynamics of inhomogeneous Malthusian density-dependent population model. All statistical characteristics of the underlying inhomogeneous models are computed explicitly. The results of this analysis show that population heterogeneity can be a reasonable explanation for power law accurately describing total population growth.

1. Introduction

The study of population growth reveals that the behaviors that follow the power law appear in numerous biological, demographical, ecological and other contexts. In its simplest form, the power equation for population growth generalizes the standard Malthusian equation and has the form

$$\frac{dx}{dt} = kx^p \tag{1.1}$$

Three cases are distinguished: the exponential with $p = 1$, the super-exponential (hyperbolic) with $p > 1$ and the sub-exponential (parabolic) with $p < 1$. Certainly, such simple model can describe a real system only approximately; nevertheless, both sub- and super-exponential growth can be observed in real populations in large domains of values of model variables and parameters.

Well established examples of super-exponential growth apply to global demography [1,2] and some ecological and economic problems [3,4]. Relevance of super-exponential growth model was discussed by Eigen and Schuster ([5], p. 426), who noticed that the quasispecies model can exhibit hyperbolic growth if the growth rate is not a constant but a linear function of the quasispecies concentration.

The most striking peculiarity of the solution to the super-exponential equation is that it has “finite-time singularity”. Indeed, the solution to Eq. (1.1) at $p > 1$ reads

$x(t) \sim 1/(T - t)^{\frac{1}{(p-1)}}$

(see Theorem 3 below for details). Hence, $x(t)$ tends to infinity when t approaches the critical time $T < \infty$, which is determined by initial conditions for (1.1). It is worth noticing that “singularities do not exist in natural and social systems, but the singularities of our approximate mathematical models are usually very good diagnostic of the change of regimes that occur in these systems” [3].

Sub-exponential growth models also have a long (although sometimes “implicit”) history. Schmalhausen [6,7] suggested the following formula to describe the growth for any measurable parameter W of a biological object (such as weight or size of an organism or separate organ):

$$\ln W \cong c + b \ln t \tag{1.2}$$

where b, c are constants, t is the time (or age). This dependence corresponds to the power function

$$\frac{W}{W_0} = \left(\frac{t}{t_0}\right)^b \tag{1.3}$$

and to the equation

$$\frac{dW}{dt} = \frac{b}{t}W. \tag{1.4}$$

Excluding time from (1.4) using (1.3), we obtain

$$\frac{dW}{dt} = bW_0^{1/b}W^{1-1/b} \sim W^{1-1/b} \tag{1.5}$$

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Hence, the Schmalhausen formula has the form of the sub-exponential equation (1.1). The growth coefficient in (1.4) is inversely proportional to time; it is the simplest and universal (but not unique and not always acceptable) explanation of the phenomenon of sub-exponential growth.

Formula (1.3) is closely connected with the *allometric principle*, which postulates a stable relationship between different characteristics x and y of an organism during ontogenesis in the form of the power dependence:

$$y = \alpha x^{\beta}. \tag{1.6}$$

Indeed, if some characteristics of an organism grow according to the formula (1.3) with different b, then excluding time we obtain Eq. (1.6). Allometric relationships allow for the possibility of calculating the mass or volume of organs that are inaccessible for direct measurement, using available data for other organs.

Several interesting attempts were made to substantiate the principle of allometry theoretically. It was shown that allometric relationships (and hence the Schmalhausen formula and sub-exponential equation) are connected with the self-similarity property and the dimensional theory (see, e.g., [8] for applications to models of plant growth).

Eq. (1.2) describes quite well only separate stages of organism development; arbitrary stages of development correspond to different values of the constants. As a result, the Schmalhausen generalized growth formula was rewritten as

$$\ln W_i = c_i + b_i \ln t \quad \text{or} \quad W_i = c_i t^{b_i} \tag{1.7}$$

if $T_i \le t < T_{i+1}$ where c_i, b_i are constants, $i = 1, \dots s$; typically $s = 3$. It was found that unusual wealth of experimental data on the development of quite different biological objects might be approximately described by the generalized Schmalhausen formula [7,9,10]. The underlying model, which implies the generalized Schmalhausen formula (1.7) was suggested and studied in [10,11].

The same relations (1.7) were found when studying the development not only of individuals, but also of populations and communities. A well-known example is the “3/2 power rule” of plant self-thinning and its modifications ([12,13], etc.). Part of the monograph [14] was devoted to systematic applications of formula (1.7) to different characteristics of tree populations and forest communities, such as dynamics of an average diameter of trees, wood stock, etc. Thus it seems that the Schmalhausen formula of sub-exponential growth may be considered as an essential empirical law of developmental biology.

More recent well-known example of sub-exponential population growth applies to some molecular replicator systems. Von Kiedrowski [15] realized that populations of most experimentally studied artificial replicators (typically, oligonucleotides that replicate in vitro via binary ligation) grow approximately according to the parabolic law (Eq. (1.1) with $p = 1/2$) rather than exponentially [16–18]. The principle cause of the sub-exponential growth of these populations appears to be product inhibition, which slows down the reproduction process, compared to the exponential case [16,18,19].

Based on these results, Szathmary and Smith [20] presented a general conceptual model of prebiological evolution of replicators using the power equation (1.1) to describe the concentration of molecules.

The models of biological populations composed of non-exponential *homogeneous* or monomorphic subpopulations (clones) deviate from Darwinian “survival of the fittest”, see [21–25]. Specifically, the models imply “differential survival of the fittest” as $p = 1$, “survival of the common” as $p > 1$, and “survival of everybody” as $p < 1$.

The reason is that non-exponential clones possess some unrealistic properties. The birth rate per individual in model (1.1) is $r = kx^{p-1}$. Then, the birth rate for parabolic model increases indefinitely as the population size decreases and *tends to zero*. It can be easily shown that the birth rate for hyperbolic models increases as the population size increases, and both become infinite at a *finite* time moment. Recall that the birth rate per individual must be bounded for any realistic biological population.

Nevertheless, despite these unrealistic peculiarities of the simplified growth equation (1.1), power law growth appears to be an essential feature of evolving populations that could be even more directly relevant for biological and prebiological evolution than the exponential growth case. Therefore, understanding the laws governing this type of growth is of potential interest for evolutionary studies.

The question arises: what are the possible origins of the non-exponential models and how can we derive them from realistic assumptions? The last problem appears non-trivial because both sub- and super exponential models possess some unrealistic properties described above. To eliminate these peculiarities we need to know where they come from.

The starting point is that heterogeneity is one of the key properties of any real evolving biological system. I show here that model (1.1) can be understood within the frameworks of inhomogeneous population models, and that population heterogeneity can be a reasonable explanation for these growth laws of the total population size.

2. Inhomogeneous or polymorphic population models

Heterogeneity amounts to the existence of differences between individuals that could be subject to natural selection and drift which can operate only if the population is non-homogeneous. The dynamics of distributions of individuals within heterogeneous populations can be described by replicator equations which capture the ”basic tenet of Darwinism” [26,27]. A very high or even infinite system dimensionality is one of the principal difficulties in the study of replicator equations. An effective method for solving a wide class of RE based on the reduction theorem has been recently developed and applied to some well-known and new problems concerning the dynamics of heterogeneous populations and communities [28,29].

For completeness, the main results of the general theory of inhomogeneous population models [28,30] are given here for a particular case of the model, which is sufficient for our purposes. Consider an inhomogeneous population composed of individuals with different Malthusian parameters a; we refer to the set of all individuals having given value of the parameter a as an a-clone and let $l(t, a)$ be the size of a-clone at the moment t. We assume that the growth rate of the population may depend on its total size $N(t)$. Dynamics of such a population can be described by the following model:

$$\frac{dl(t,a)}{dt} = al(t,a)g(N), \quad N(t) = \int_A l(t,a)\,da \tag{2.1}$$

where $g(N)$ is an appropriate function.

Denote $P(t,a) = l(t,a)/N(t)$ to be the current frequency of a given value of the parameter a; the probability density function (pdf) $P(t,a)$ describes the distribution of the parameter a along the population in t moment. We suppose that the initial pdf of the Malthusian parameter a, $P(0,a)$, is given, and its moment generating function (mgf) $M_0(\lambda) = \int_A \exp(\lambda a)P(0,a)\,da$ is known.

In order to solve the problem (2.1), let us define formally the “keystone” auxiliary variable $q(t)$ as the solution to the Cauchy problem

$$\frac{dq}{dt} = g(N), \quad q(0) = 0. \tag{2.2}$$

This equation cannot be solved at this moment, because the population size $N(t)$ is unknown. However, the clone densities and population size can be expressed with the help of the keystone variable