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SOLVING THE LEVINS' PARADOX IN THE LOGISTIC MAP OF POPULATION GROWTH

Evaldo Araújo de Oliveira[1], *Vicente Pereira de Barros*[2], *Roberto André Kraenkel*[3]

[1]Instituto de Matemática e Estatística, Universidade de São Paulo, São Paulo, Brazil, evaldo@vision.ime.usp.br
[2]Instituto de Ciências Ambientais e Desenvolvimento Sustentável, Universidade Federal da Bahia, Barreiras, Brazil
[3]Instituto de Física Teórica, Universidade Estadual Paulista, São Paulo, Brazil

Abstract: We introduce a method to improve maps by adding prior informations and/or constraints. The method starts from an initial map model, wherefrom a likelihood function is defined which is regulated by a temperature-like parameter. Then, the new constraints are added by the use of Bayes rule in the prior distribution. We applied the method to the logistic map of population growth of single species. We show that the population size is limited for all ranges of parameters, allowing thus to overcome difficulties in interpretation of the concept of carrying capacity known as the Levins' paradox.

keywords: Population Dynamics, Logistic Model.

1. INTRODUCTION

Since the very beginnings of the studies of what is now called *population biology*, by Thomas Malthus in 1798, the development of mathematical methods to adequately express the biological concepts has been a central point of the theory. Differential equations, maps and stochastic processes are a few of the modern methods employed, allowing the results to be put in analogy to systems in the physical sciences, a well as with the economical theory [2].

Malthusian theory is based on a constant rate of compound interest, implying an exponential population growth. The underlying hypothesis is that the population is unchecked, that is, there are no limitations to its growth. To overcome this population explosion, P. F. Verhulst proposed to adjust the intrinsic rate of increase, defined as $R_t = (N_{t+1} - N_t)/N_t$ and constant in the Malthusian model, by a nonlinear factor $R_t = r\,(1 - N_t/K)$, with r being the *growth rate*, N_t the population density and K *the carrying capacity*.

Although the Verhulst model[1] overcomes the problem of explosive growth, conceptual problems arise in the interpretation of the carrying capacity K. A criticism consists in what is known as *Levins' paradox* [4]. This paradox appears when we have a negative growth rate and an initial population greater than the carrying capacity ($N_t > K$). In this case, instead of reductions in the population size, since a negative r means a death rate greater then the birth, the logistic model presents unbounded growth.

Some authors work out a new definition of carrying capacity. Gabriel et al. [3] discussed this scenario using a restriction for the region of validity of the equation model. First, these authors showed that setting K in function of r, in such a way that K and r have the same sign, would be enough to solve the Levins' paradox. But, this gauge would bring difficulties to interpret K, since a negative carrying capacity makes no sense. Therefore, in a second step, the authors redefined the carrying capacity as $K_\infty = \lim_{t\to\infty} N_t$ in such way that K_∞ is greater then zero for $r > 0$ and zero for $r < 0$, keeping K as a simple model parameter with $\mathrm{sign}(K) = \mathrm{sign}(r)$.

Although this procedure solves the mathematical paradox and in this way has been useful in practice, we are indeed changing the concept of the carrying capacity. It gives us the population of a species that is supported, given the mount food supply, habitat, and other resources available within an environment. Of course, this capacity can be depredated by the population or improved by planed acts. But this changing (improvement or depredation) can also be developed by the environment independent of the population actions. Therefore, it is interesting to search by another solution that takes account more realistic properties of the observed systems. In this direction, we propose a new method to improve map equations taking account some prior information.

2. THE METHOD

Given a map $m_{t+1} = m_t + f(m_t)$ and some constraints involving $\Delta m_t \equiv m_{t+1} - m_t$ and parameters from $f(...)$, the proposal is to write the constraints as a prior probability distribution and obtain a new map by averaging the variable of interest over the probability of Δm_t be given by $f(m_t)$ times the prior.

The probability of Δm_t given m_t is defined by the Boltzmann factor $L(\Delta m_t|m_t) \propto \exp\{-\beta V\}$, with β been an inverse temperature parameter (related to noise) and V a function of $\Delta m_t - f(m_t)$. The constraints are introduced by a prior distribution, which represents the knowledge state from empirical source or what it is expected from the model. In

[1]Known as *logistic model*.

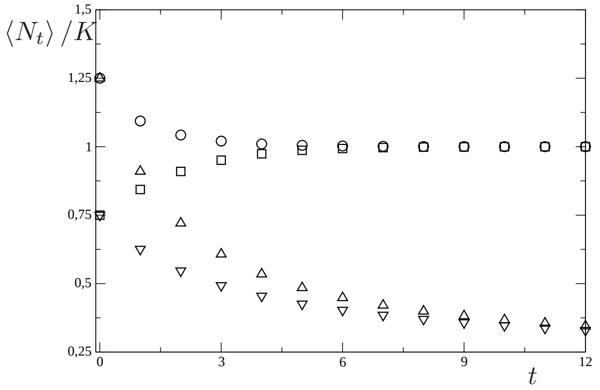

Figure 1 – The evolution of the $\langle N_t \rangle / K$ given by $\langle \Delta N_t \rangle = \langle R_t \rangle \langle N_t \rangle$ and the Eq. (2) with: $r = 0.5$ to circle and square symbols and $r = -0.5$ to triangles.

our case, this information is about the decrease of the population size when $r < 0$ and the convergence to K when $r > 0$. In this direction, we suggest to encode this prior information as

$$p(m_t) = \frac{[1 - \Theta(-r)\Theta(m_t - K)] m_t \exp\{-m_t/\kappa\}/\kappa^2}{1 - \Theta(-r)(1 + K/\kappa)\exp\{-K/\kappa\}} \tag{1}$$

where κ is directly connected with the population in the moment t, i.e. $\langle m_t \rangle = 2\kappa$, and $\Theta(-r)$ is the Heaviside function[2].

The new map for the population growth is then obtained by averaging R_t over the normalized distribution $P(\Delta m_t, m_t) \equiv L(\Delta m_t | m_t) p(m_t)$. Setting $V = -[\Delta m_t - f(m_t)]^2/2$ and $f(m_t) = r(1 - m_t/K)m_t$, the intrinsic rate of increasing is now given by

$$\begin{aligned} \langle R_t \rangle \quad = \quad & r - \frac{r \langle N_t \rangle}{K} \left\{ 1 - \Theta(-r) \frac{2K^2}{\langle N_t \rangle^2} \mathrm{e}^{-2K/\langle N_t \rangle} \right. \\ & \left. \Big/ \left[1 - \Theta(-r) \left(1 + \frac{2K}{\langle N_t \rangle} \right) \mathrm{e}^{-2K/\langle N_t \rangle} \right] \right\} \end{aligned} \tag{2}$$

Once given $\langle R_t \rangle$, not matter how it was calculated, the variation on population is estimated by the product of $\langle R_t \rangle$ by the population today: $\Delta N_t = \langle R_t \rangle N_t$, which produces $\langle \Delta N_t \rangle = \langle R_t \rangle \langle N_t \rangle$.

3. DISCUSSION

For $r > 0$ the equation (2) becomes similar to the Verhulst model and the averaged population goes to the limit of the carrying capacity in finite time. In Fig.(1) a numerical implementation with both $r > 0$ and $r < 0$ illustrates this point.

In the opposite scenario, with a negative growth rate, the population goes to extinction. Of course, the existence time of the population depends on the initial size $\langle N_0 \rangle$, on the growth rate and on the carrying capacity [5]. To illustrate these, consider a simple example: the arriving of a large emigrate population in an population subject to an epidemic.

The first thing to observe is the possibility of two growth rates, one of the native population and another of the foreign one. But, to avoid unnecessary complications it is assumed that the effective grown rate $\bar{r}$ is negative. If the sum of the native plus the foreign population is greater than the carrying capacity, then the total growth rate has to be less than $\bar{r}$ — representing the death due to the disease plus the limitations due to the lack of supplies. Besides, once the lack of supplies will affect the sick individuals more than it would affect the healthy ones, it is expected a total reduction of rate greater than the sum of the rate due the disease plus the rate due to the lack of supplies when $r > 0$. Here the reduction rate is defined as being the absolute value of the growth rate. In the new model (2), if $\langle N_t \rangle \gg K$ and $r < 0$ we have $\langle R_t \rangle \to r - r \langle N_t \rangle (1 - \exp\{-2K/\langle N_t \rangle\})/K$. Recalling that we are considering $r = \bar{r} < 0$, we will have $\langle R_t \rangle < 0$. Besides, in the proposed limit $-\langle N_t \rangle (1 - \exp\{-2K/\langle N_t \rangle\})/K \to 1 + 2\exp\{-2K/\langle N_t \rangle\}$, *i.e.* $\langle R_t \rangle \to 3\bar{r}$. This means that, in the lack of supplies, the death due to diseases is greater than when there is abundance.

Naturally, the major contribution to the reduction rate should comes from r when total population is far from the carrying capacity (less than K) — once it would have abundance. This can be observed in the limit $\langle N_t \rangle \ll K$, that produces $\langle R_t \rangle \to r(1 - \langle N_t \rangle / K)$, *i.e.* the old model is recovered.

This simple example indicates that the present method can be used as a promising tool to improve models, which can be verified in others dynamical population models [1].

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[2] $\Theta(-r) = 1$ for $r < 0$ and zero for $r \geqslant 0$