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Abstract. We introduce a new method to improve Markov maps by means of a Bayesian approach. 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 a 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.

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, as well as with the economical theory [1].

The 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. In 1838, P. F. Verhulst proposed a mathematical model describing the self-limited growth of a biological population, where the saturation tends to halt exponential growth, driving the population size to an equilibrium. Verhulst proposed essentially 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:

$$R_t = r \left(1 - \frac{N_t}{K}\right),$$

(1)
with $r$ being the growth rate and $K$ the carrying capacity. This concept models the self-interaction of a species and accounts for the intra-species competition.

Equation (1) is called logistic model and recovers the Malthusian model by setting $K$ to infinity, which means an unlimited capacity. Besides, $r > 0$ means a total growth rate greater than the total reduction rate and the opposite for $r < 0$.

Although the logistic model 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 [2]. 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 on the population size, since a negative $r$ means a death rate greater then the birth, the logistic model presents unbounded growth.

Much effort has been made to overcome this problem, as for example, to model a population in the limit of the carrying capacity by analyzing the effect of processes such as culling or sterilization, but avoiding the problematic set of parameters $r$ and $K$ [3]. Another usual procedure is to define new constants in nondimensional quantities in the logistic equation [4] and be free of the paradox, but left with no clear interpretation of the constant in front of the nonlinear term.

In this direction, some authors work out a new definition of carrying capacity. Gabriel et al. [5] discussed this scenario using a restriction for region of validity of the equation. 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, again, 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

$$K_{\infty} = \lim_{t \to \infty} N_t, \text{ with } N_0 > 0$$

having as consequence

$$K_{\infty} = \begin{cases} \text{constant, for } r > 0 \\ 0, \text{ for } r < 0 \end{cases}$$

and kept $K$ as a simple model parameter with $\text{sign}(K) = \text{sign}(r)$.

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 (e.g. when the population acts as plague) or improved by planed acts. But this changing (improvement or depredation) can also be developed by the environment independent of the population actions, e.g. the introduction of a lethal virus in the environment that interacts only with the specie observed or its resources. Therefore, it is interesting to search by another solution that takes account more realistic properties of the observed systems. In this sense, a interesting approach would be the probability theory.

Usually, the application of probability theory is recommended when we have to deal with assertions in the absence of complete information. But in the Bayesian Theory, probabilities can be interpreted as an extension of the logic [6, 7] and be can used to incorporate information on deterministic models.

2. Adding informations by the Bayes Theorem

Given a map $N_{t+1} = N_t + f(N_t)$, parameters from $f(\ldots)$ and some constraints involving $\Delta N_t \equiv N_{t+1} - N_t$, the proposal is to incorporate these constraints in a prior probability distribution and obtain a new map by averaging the variable of interest over the probability of $\Delta N_t$ be given by $f(N_t)$ times the prior.
This procedure is different from usual application of Bayesian theory, which is applied to analysis of experimental or observational data. Here, the idea is not to fit some experimental data set, but to use the concept of probability in the Bayesian theory to improve a given map by adding new constraints. We thus discuss the model instead of the data. However, the main essence of the Bayesian Theory — the concepts and distinction between the prior, the likelihood and the posterior distributions — is required at all moment as in typical subjective probability models.

Here the likelihood is used to set the probability of observing a variation $\Delta N_t$ on the population given the actual state $N_t$ and the chosen model defined by $\Delta N_t = f(N_t)$, i.e. $L \equiv P(\Delta N_t|N_t)$. On the other hand, the constraints which represent the prior informations, is embedded in the prior distribution over $N_t$. Thus, by using the Bayes theorem, the joint distribution $P(\Delta N_t, N_t) = P(\Delta N_t|N_t)P(N_t)$ is calculated and the model update by averaging the variable of interest, e.g. $R_t = g(\Delta N_t, N_{t+1})$, over $P(\Delta N_t, N_t)$.

The rest of this article is divided in two sections. In section (3) we describe the new method by applying it on the Verhulst model, wherefrom the main equations are developed and implemented. In section (4), we discuss the results as well as the method to improve map models, showing that our approach is free of the Levins’ paradox and gives a bounded population in a natural way in all parameter ranges.

3. Improving the Verhulst model

The main point in the Verhulst model is to consider the rate of increase $R_t = \Delta N_t / N_t$ as a function of population size and some parameters. Is also in it, the rate of increase, that the Levins’ paradox is found. Therefore, if we want to improve the Verhulst model, a good point to start is $R_t$.

As mentioned, the proposal is to consider that the map models the average behavior of population, which suggest to change $R_t$ by $\langle R_t \rangle$, where $\langle ... \rangle$ means $\int ... P(\Delta N_t, N_t) d\Delta N_t dN_t$ and $P(\Delta N_t, N_t)$ is obtained by the Bayes’ Theorem [8]:

$$P(\Delta N_t, N_t) = L(\Delta N_t|N_t)p(N_t),$$

where $P(\Delta N_t, N_t)$ is the probability to observe $\Delta N_t$ and $N_t$, $L(\Delta N_t|N_t)$ is the likelihood and $p(N_t)$ is the prior distribution.

The likelihood is defined as the Boltzmann factor

$$L \propto \exp\{-\beta V\},$$

with $\beta$ been an inverse temperature parameter (related to noise) and $V$ a function of $\Delta N_t - f(N_t)$. Therefore, using equation (1) as the initial model and considering a quadratic potential function, we obtain

$$V = \frac{1}{2} \left[ \Delta N_t - \left( r - \frac{r}{K} N_t \right) N_t \right]^2$$

and

$$L(\Delta N_t|N_t) = \sqrt{\frac{\beta}{2\pi}} \exp\left\{ -\frac{\beta}{2} \left[ \Delta N_t - \left( r - \frac{r}{K} N_t \right) N_t \right]^2 \right\}.$$  

The prior distribution represents the knowledge from empirical source or what it is expected from the model. In our case, this information is about the decrease of the population size when
$r < 0$ and the convergence to $K$ when $r > 0$. Besides, we can also add constraints to compensate some known limitations from the original map. In this context, we suggest to encode this prior information as

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

(6)

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

\[ \Theta(-r) = \begin{cases} 
1 & \text{for } r < 0 \\
0 & \text{for } r > 0.
\end{cases} \]

(7)

Given the equations (5) and (6), we obtain the posterior distribution by (4) and the next step is to calculate $\langle R_t \rangle$:

\[ \langle R_t \rangle = r \frac{1 - 2\kappa/K + \Theta(-r)(1 + 2\kappa/K)\exp(-K/\kappa)}{1 - \Theta(-r)(1 + K/\kappa)\exp(-K/\kappa)}. \]

(8)

Note that $\langle R_t \rangle$ does not depend on $\beta$ and this comes from its definition, that is linear on $\Delta N_t$. But, when the parameter of interest is a nonlinear function of $\Delta N_t$, $\beta$ can play an important role to take account fluctuations on the map. This flexibility is required when we deal with experimental time-series, that have multiple sources of stochasticity [9]. Naturally, the biological meaning of $\beta$ could be explored in future works.

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: $\Delta N_t = \langle R_t \rangle N_t$. But, in biological problems there exist others events, not considered in the logistic model, which cause some fluctuation on the expected growth. Therefore, if we want to adjust the parameters of the model from experimental data, it is suitable to consider the averaged estimative of the last expression, i.e.

\[ \langle \Delta N_t \rangle = \langle \langle R_t \rangle N_t \rangle = \langle R_t \rangle \langle N_t \rangle. \]

(9)

To compare the resulting model from (9) to the Verhulst model, we rewrite $\kappa$ in terms of $\langle N_t \rangle$ in the equation (8):

\[ \langle R_t \rangle = r \frac{1 - \langle N_t \rangle/K + \Theta(-r)(1 + \langle N_t \rangle/K)\exp(-2K/\langle N_t \rangle)}{1 - \Theta(-r)(1 + 2K/\langle N_t \rangle)\exp(-2K/\langle N_t \rangle)}. \]

(10)

For $r > 0$ the equation (10) becomes similar to (1) and the averaged population goes to the limit of the carrying capacity in finite time. As in the Verhulst model, this time is independent from where the population starts, whether above or below the carrying capacity. In Fig.(1) a numerical implementation with both $r > 0$ and $r < 0$ illustrates this point.

4. Discussion

Considering two trials developed from initial populations $N_0(1)$ and $N_0(2)$ for $r > 0$, the difference between the times at which they become equal $K$ is given by

\[ t_1 - t_2 = \frac{1}{r} \ln \left[ \frac{N_0(2)}{N_0(1)} \right]. \]

(11)

where $t_1$ is the time where $N_t \to K$ from $N_0(1)$ and $t_2$ is the time where $N_t \to K$ from $N_0(2)$.

The initial time is the same in both situations and $N_0(1) < K$ and $N_0(2) > K$. The ratio in the logarithm is always greater than one, but the absolute value of logarithm may be smaller then values of $t_1$ and $t_2$. This means that the accuracy to distinguish when the population achieve the *carrying capacity* is not a good parameter for quantitative statements.
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 [10]. To illustrate these, consider a simple example: the arriving of a large emigrate population in a 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 $r > 0$. In the new model (10), if $\langle N_t \rangle \gg K$ and $r < 0$, $\langle R_t \rangle$ will be proportional to $r$, which implies a dynamics similar to the one of the Malthusian model. Besides, it can be interpreted as if, in the lack of supplies, the death due to diseases was greater than when there is abundance.

Naturally, the major contribution to the reduction rate should come 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 $\langle R_t \rangle \rightarrow r(1 - \langle N_t \rangle / K)$, $i.e.$ the old model is recovered.

While recent works [5] try to solve the Levins’ paradox adjusting the sign of $K$ with $\text{sign}(r)$ or restricting the valid region to $N_t$, the proposed model keeps the meaning of the carrying capacity and allows for initial conditions either above or below the carrying capacity for both $r > 0$ and $r < 0$.

Another important detail is the Bayesian approach used in this paper to obtain a new map with the desired constraints. As the Lagrange multipliers, the prior distribution can be used to restrict the model to some region. In this way, the distribution is built from the geometrical information on the mathematical space induced by variables and parameters of the model.

This simple example indicates that the present method can be used as a promising tool to improve models, what can be verified in others dynamical population models [11]. Besides the application presented here, the method can be also applied to problems of other nature, as for example, is the case of mechanical systems.

Once redefining the Logistic model, the next step is to investigate models where $r$ can change, $i.e.$ with $r \equiv r_t$. The super abundance problems, competition systems or structured populations,
maybe implemented by the method by using another tricks of the Bayesian approach developed
in the study of learning systems [12, 13].

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