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Simulation of chaotic behaviour in population dynamics

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Abstract. In the time evolution of populations, many attractors can be found: fixed points, limit cycles and chaotic regimes. Usually, chaotic behaviour is observed in species which have well defined breeding seasons and a high fertility rate. Different mathematical models have been used in order to simulate those regimes. In this paper, we use the bitstring model introduced to simulate the evolution of age-structured populations — the Penna Model — to simulate a sort of cyclic and chaotic behaviours. In comparison with the standard logistic map, our results show a time changing λ parameter.

PACS. 87.10.+e General, theoretical, and mathematical biophysics (including logic of biosystems, quantum biology, and relevant aspects of thermodynamics, information theory, cybernetics, and bionics) – 05.45.+b Theory and models of chaotic systems – 02.70.Lq Monte Carlo and statistical methods

1 Introduction

The time evolution of a population is governed by some basic parameters: reproduction, environmental constraints and hereditary-mutation. Due to the difficulty of observation of populations in wild or even considering that there is unlikely to isolate the evolution of a specific species, mathematical models constitute an important tool in the study of population dynamics. The first model of population growth was proposed by Linnaeus in 1740. His simple model introduced for the first time the exponential growth. Sixty years later Malthus discussed the problem of food supply, arguing that some environmental restrictions should be added to model the population dynamics and to suppress the indefinite population growth. The idea of many offspring disputing food and the survival of the fittest individuals was used by Darwin (again sixty years after Malthus - 1859) when establishing his concept of Natural Selection [1].

The most known model where these basic assumptions appear is the logistic model for population growth. This model was first introduced by Verhulst in 1844 [2]. In that case, an environmental carrying capacity $N_{\max}$ is introduced and the growth rate of a population is given by

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(1 - \frac{N}{N_{\max}}\right), \tag{1}$$

where r is the intrinsic relative growth rate, *i.e.*, the population growth rate when the environmental effects are negligible. In this continuous process, the final state is always a fixed point. However the discrete version of the logistic model can display a remarkable range of dynamic behaviours: Fixed points, limit cycles and chaos.

Is it possible that some kind of species show such type of chaotic evolution along the time? The *Operophtera brumata* moth is one. The *brumata* is a insect that lives in oaks *Quercus robur* and has a well defined life cycle: Adults emerge from the soil in November/December, reproduce and the larvae form the cocoon in May until the next season, when the process is repeated. In this case, the observed chaotic dynamics of the moth population is produced by a strong competition between environmental factors (weather and predators) and high reproductive rate [1]. Another important ingredient in this case is that this is a species which presents a well defined reproductive period and is therefore better explained through an assumption of discrete time model than a continuous one.

The study of the influence of heredity and mutation on population dynamics started in the '30s [3]. In contrast with other models which had assumed variations in the population size during its evolution, the genetic population theory worked with the perspective of a stable stationary state given by a fixed population: The hypothesis of a balance of selection and mutation. Moreover, the basic calculations have been done taking into account infinite populations. The discussion of extinction scenarios within the theory was proposed by Muller [4], who stated that for an asexual population a progressive genetic deterioration should be observed, with a progressive random loss of better fitted individuals: Muller's ratchet. However, only in

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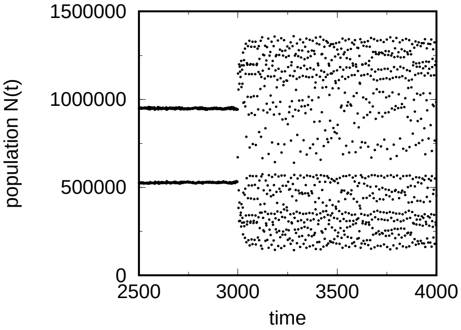

Fig. 1. Evolution of population showing two different regimes: a limit cycle with period 2 and a chaotic regime. The general parameters are: $N_0 = 10^5$, $N_{\max} = 1.5 \times 10^6$, $M = 1$, $T = 6$, $R = 4$. $B = 20$ for $t < 3,000$ and $B = 35$ for $t > 3,000$. This simulation ran up to $t = 20,000$.

the '90s a wide discussion about the problem of extinction due to the accumulation of detrimental mutations began. Lynch and Gabriel [5] pointed out that the accumulation of deleterious mutations is expected to cause a gradual reduction in the population size down to zero, calling the synergistic interaction between fixation of harmful mutations and population reduction mutational meltdown.

Although different scenarios can be modeled in population dynamics theory [6], up to now Monte Carlo simulations of population dynamics have been mostly given stable stationary configurations when no mutational meltdown occurred. In this paper we show that limit cycles or even a chaotic regime can be obtained in the evolution of a population as described by the Penna model [7]. The Penna model has been introduced to describe the evolution of age-structured populations and important results have been obtained when compared with experimental observations [8,9]. However, up to now, the general belief was that the Penna model could lead only to stable fixed points: a stable population [6,7] or the extinction. Moreover, the case of mutational meltdown was obtained only when all detrimental mutational events were successful disregarding the problem of extinction due to Muller's ratchet effect in small population [8,10]. Even the small oscillations obtained by Puhl *et al.* [11] when studying the prey-predator problem could be damped if the death probability due to environmental factors is divided in two terms: Space restrictions and predators-prey interaction [8]. However, as we are going to show, for some given definitions of the basic parameters a myriad of dynamical behaviours will appear: Limit cycles or chaotic behaviour. First of all, we show that the basic ingredients were present in the basic definition of the population dynamics as given by the original model. After that, we present the results of some simulations and conclude.

2 The model

In the Penna model the genome of an individual is represented by a string of 32 bits. Each bit corresponds to a threatening disease which may appear in a given "year" (the so defined time unit): bit = 1 means the presence of a deleterious mutation and bit = 0 represents a normal allele (allele is any of the various forms a gen can occur). After appearing the disease will act during the entire individual life. The individual that accumulates T mutations dies. Due to environmental restrictions, an individual has the probability

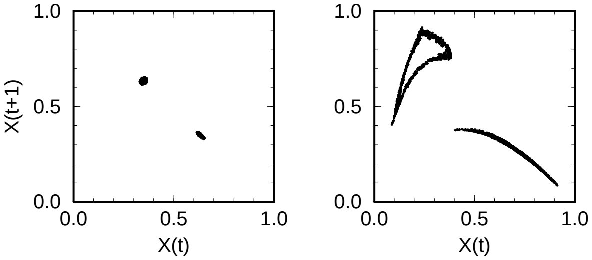

Fig. 2. Return map for the period-2 and chaotic regimes. The chaotic case evolves from the double period when the birth rate is switched from 20 to 35 (at $t = 3,000$).

$$P_\ell(t) = 1 - \frac{N(t)}{N_{\max}} \tag{2}$$

of staying alive from one year to the following. If an individual reaches 32 years it automatically dies. After R years an individual reaches reproductive maturity and produces B offspring per year. The offspring's genome is a copy of its parent genome, apart from M randomly chosen mutations. The mutation procedure is implemented by an OR instruction: only detrimental mutations ($0 \to 1$) are accepted. If the bit was already equal to 1 it remains unchanged.

Although recently some progress has been made in the study of problems involving sexual reproduction [8,12,13], in this paper we will focus our attention only in asexual reproduction.

Initially, a population of N_0 individuals is defined. The evolution of the whole population is given by the following steps: selection, reproduction and mutation events. For each time step — a year — we evaluate $P_\ell(t)$, *i.e.*, a discrete evolution is assumed as discussed above. After that the reproduction takes place for those individuals which are older than R and mutations occur at the birth moment. Thus, the model includes a competition between a parameter which forces the population growth (the birth rate B) and another one which does not allow its indefinite growth (the Verhulst factor). Both parameters depend on the population size $N(t)$. These are the basic ingredients already present in the logistic equation and one can write a generalized logistic equation for the evolution of the population:

$$X(t+1) = \lambda(t) X(t) \left[1 - X(t)\right], \tag{3}$$

where $X(t) = N(t)/N_{\max}$. The intrinsic relative growth rate λ is now a time dependent variable. As is well known

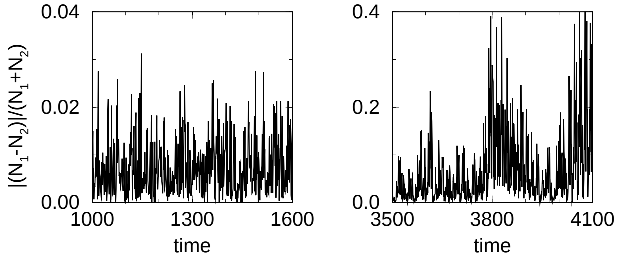

Fig. 3. Relative difference between two initially identical populations evolving in parallel. The plot shows how a small difference will propagate. At left the population evolves following a period-2 attractor and at right a chaotic regime. Note that the difference in the second case is one order of magnitude higher than in the first case.

from the analysis of the discrete logistic equation, in order to obtain different attractors for the dynamics we have to increase λ. Basically it can be done by increasing the birth rate B and the fraction of individuals older than R. The latter is obtained by defining $T > R$. So, only the Verhulst factor will kill individuals before they start reproduction.

3 Results and conclusions

Although we did many different simulations, in the following we show only our main results. Figure 1 shows a detail in the evolution of a population (where we did not plot the initial transient). Starting with $N_0 = 10^5$ individuals, firstly we obtain a period-2 evolution. Notice that this period-2 evolution is permanent and the same results have been obtained for larger populations. The general parameters are: $N_{\max} = 1.5 \times 10^6$, $B = 20$, $R = 4$, $T = 6$ and $M = 1$. The simulations started with individuals with half of the genome randomly filled with detrimental mutations. We assume, following previous works [14], that the final state does not depend upon the initial configuration of the genomes. Thus, we assumed a much higher B value than the usual ones and worked with $T > R$ instead of $T < R$ of earlier publications.

After $t = 3,000$ we switch the birth rate to $B = 35$, now introducing a strong competition between the number of offspring and the environmental carrying capacity. With these conditions, a small population in a given year can generate a large population in the next one, almost reaching the maximum environmental capacity, as can be seen in the right part of Figure 1. After that — in the year that follows — environmental restrictions will reduce the population by nearly an order of magnitude. The chaotic regime arises in this scenario. It is very difficult to obtain a chaotic regime starting with a population with all the individuals with the same age. During the transient period sometimes occurs the extinction of the entire population. So, we let the system reach a stationary state and then turn the dial, changing parameters.

Figure 2 shows the return map for the period-2 (at left) and chaotic (at right) regimes. In each map were plotted the last 2,000 points of the 9,000 obtained in our simulations. Due to small fluctuations, two spots are obtained in the period-2. In this case we used $N_{\max} = 1.5 \times 10^5$ and $N_0 = 10^4$. These two spots give rise to the two attractors shown in the right part of the figure. Along the time the population jumps from one part to the other, showing the characteristics of a period-2 regime.

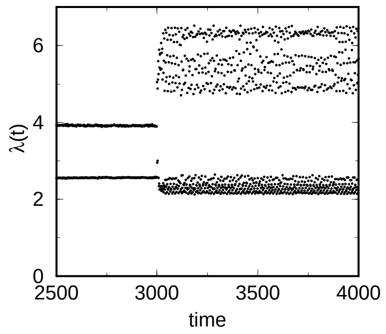

Fig. 4. Evolution of $\lambda(t)$ with time. This value has been obtained from the same simulation as shown in Figure 1.

In order to better understand the difference between the two regimes, we studied how a small change produced in one of the initially identical populations will propagate along the time. This is similar to the study of spread of damage done in many problems [15]. The process was done as follows: First we ran a simulation up to a specific maximum time (usually $t_{\max} = 10,000$). After that, we repeated this simulation, starting with exactly the same set of parameters. At a pre-defined time step ($t = 1,000$ for period-2 and $t = 3,500$ for chaotic regime) we remove an individual from the population of the second simulation. For period-2 we started with $N_0 = 10^4$, keeping $N_{\max} = 1.5 \times 10^5$ and for the chaotic regime we used $N_0 = 10^5$ and $N_{\max} = 1.5 \times 10^6$. Having the two populations, we calculated the relative difference between their sizes: $|(N_1 - N_2)|/(N_1 + N_2)$. The results are shown in Figure 3. For period-2 dynamics a residual difference remains indefinitely. This difference, as one can see, is always less than or of the order of 2%. For the chaotic case, the difference grows rapidly showing strong changes. Sometimes this difference is greater than 60%. We did not measured the difference in the age-structure of the populations.

Finally, Figure 4 show the evolution of $\lambda(t)$ as defined in equation (6). This parameter does not have a constant value, even for the period-2 case. It is interesting to report that this type of non-fixed value and non-periodic value — for the chaotic regime — is also obtained in real populations, as the case of the moth cited above [1].

In conclusion, in contrast to earlier assumptions, we have shown that the Penna model can exhibit all the basic behaviours found in the dynamics of real populations. A chaotic regime was obtained trough the competition between a high reproductive rate and environmental restrictions. This situation can be considered for populations with well defined reproductive period. If we change continuously the P_ℓ parameter accompanying the population growth, the chaotic regime will disappear, as one obtains in the solution of the continuous logistic equation. An interesting aspect observed in the different regimes is that the intrinsic relative growth rate is not a constant parameter, but a time-changing one. It follows the period of the attractor. For the chaotic case the same type of behaviour has been observed. Further investigations on the characterization of the attractor and on the intrinsic relative growth rate are in progress and the results will be published elsewhere.

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