

Emergence of Chaos, Diffusive Chaos and Strange Attractors in Evolving Volterra Ecosystems

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Abstract

This paper begins with an introduction to the emergence of chaos in a game of evolution proposed recently (Dubois, 1998). The law of conservation of materials in nutrients and populations is used as an environmental closure. Malthusian growth is so transformed to a Pearl-Verhulst map. The game of evolution deals with the competition between a species with its successive mutants. Such a population with random mutations evolves when the ratio birth rate/death rate of a mutant increases. Chaos appears in such an evolving ecosystem.

In this paper, several new basic models of nutrients and population interaction are presented and simulated.

Firstly, a second order Pearl-Verhulst is proposed: a second time derivative term is added to the classical Pear-Verhulst model. This term permits to control the velocity of propagation of a population by spatial diffusion. With low value of the diffusion coefficient, the population front is followed by a spatial uniform concentration of the population. For higher values of the diffusion coefficient bifurcations then chaos appear in the spatial structure of the population. This is what we already called a "diffusive chaos" (Dubois, 1996, 1998).

Secondly, this second order Pearl-Verhulst can show either the classical chaos either a strange attractor similar to Hénon's attractor (1976). The final states in the bifurcation depends on the initial conditions: this system has a memory of its initial conditions, and the system goes to different attraction basins.

Thirdly, the nutrients N - population P interaction model is complicated in adding an intermediate state P^* for the population: P^* is the satiated population and only non satiated population P can take nutrients. Surprisingly, such an ecosystem has memory but also anticipatory properties similar to the incursive model of the Pearl-Verhulst given before (Dubois, 1996). Such a system depends on the initial conditions and show a strange attractor similar to the Hénon attractor.

Keywords: chaos, population propagation, second order Pearl-Verhulst map, Hénon attractor, memory and anticipatory population.

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1 Introduction to the Emergence of Chaos in a Game of Evolution

This paper will consider very simple ecological systems represented by the growth of a biological population constrained by a quantity of nutrients. Indeed, the conservation law of the total materials in the ecosystem is a constraint noted "C" given by the sum of the nutrients and the populations.

Let us consider explicitly the nutrients $N(t)$ for the growth of a population $P(t)$ with a Malthusian growth, the discrete equations are given by

$$N(t+\Delta t) = N(t) - \alpha \cdot \Delta t \cdot N(t) \cdot P(t) + \beta \cdot \Delta t \cdot P(t) \quad (1a)$$

$$P(t+\Delta t) = P(t) + \alpha \cdot \Delta t \cdot N(t) \cdot P(t) - \beta \cdot \Delta t \cdot P(t) \quad (1b)$$

where t is the time and Δt the time step, α is the birth rate, β the death rate of the population $P(t)$, and the growth rate is a function of the quantity of nutrients $N(t)$. From the conservation law of materials, it is assumed that the dead population is recycled to nutrients so that the total quantity of materials is represented by the control parameter C (Dubois, 1998):

$$N(t+\Delta t) + P(t+\Delta t) = N(t) + P(t) = C \quad (2a)$$

$$N(t) = C - P(t) \quad (2b)$$

The total quantity of materials C is a global constraint which gives rise to a non-linear saturation in the growth rate of the population. Indeed, in replacing $N(t)$ given by eq. 2b in eq. 1b, we obtain the following equation

$$P(t+\Delta t) = P(t) + \alpha \cdot C \cdot \Delta t \cdot P(t) - \alpha \cdot \Delta t \cdot P(t)^2 - \beta \cdot \Delta t \cdot P(t) \quad (3a)$$

which is a form of the Pearl (1924) -Verhulst (1847) models. For a constant constraint $C=1$ and parameters $\Delta t=\beta=1$, eq. 3a is

$$P(t+1) = \alpha \cdot P(t) \cdot (1 - P(t)) \quad (3b)$$

which is the well-known Pearl-Verhulst map which gives rise to chaos (May, 1976; Mandelbrot, 1983). Populations with a low birth rate $0 < \alpha < 1$, disappear $P(t)=0$, populations with $1 < \alpha < 3$ have a stable stationary state $P(t) = 1 - 1/\alpha$ and populations for which $3 < \alpha < 4$, show bifurcations and then a chaotic behaviour.

For a system with two species P_1 and P_2 , the equations with nutrients N are

$$N(t+\Delta t) = N(t) + \Delta t \cdot (\beta_1 \cdot P_1(t) + \beta_2 \cdot P_2(t) - \alpha_1 \cdot N(t) \cdot P_1(t) - \alpha_2 \cdot N(t) \cdot P_2(t)) \quad (4a)$$

$$P_1(t+\Delta t) = P_1(t) + \Delta t \cdot (\alpha_1 \cdot N(t) \cdot P_1(t) - \beta_1 \cdot P_1(t)) \quad (4b)$$

$$P_2(t+\Delta t) = P_2(t) + \Delta t \cdot (\alpha_2 \cdot N(t) \cdot P_2(t) - \beta_2 \cdot P_2(t)) \quad (4c)$$

where α and β are the birth and death rates respectively. The dead populations are recycled to nutrients, the total quantity of materials being a constraint C:

$$N(t+\Delta t) + P_1(t+\Delta t) + P_2(t+\Delta t) = N(t) + P_1(t) + P_2(t) = C \quad (4d)$$

$$N(t) = C - P_1(t) - P_2(t) \quad (4e)$$

In taking $\alpha_1 = \alpha_2 = \alpha/2$ and $\beta_1 = \beta_2 = \beta/2$, the addition of the two populations $P(t) = P_1(t) + P_2(t)$ by eqs. 4b-c gives the previous eq. 2b for one population. This means that the population $P(t)$ can be split into two populations $P_1(t)$ and $P_2(t)$ with the same birth and death rates.

When these rates change, in replacing eq. 4e of $N(t)$ in the last two eqs. 4b-c, we obtain

$$P_1(t+\Delta t) = P_1(t) + \Delta t. [\alpha_1.P_1(t).(C-P_1(t)) - \alpha_1.P_1(t).P_2(t) - \beta_1.P_1(t)] \quad (4f)$$

$$P_2(t+\Delta t) = P_2(t) + \Delta t. [\alpha_2.P_2(t).(C-P_2(t)) - \alpha_2.P_1(t).P_2(t) - \beta_2.P_2(t)] \quad (4g)$$

where the effective growth rate of the populations shows a Pearl-Verhulst saturation and an effective competing term between the two populations appears as $a.P_1(t).P_2(t)$ as in the Volterra (1931) model.

Let us now consider the following game of evolution (Dubois, 1998).

Let us start with a very elementary system with one nutrient $N(t)$ and one species $P_1(t)$ evolving with time t for which $C = P_1(t) + N(t) = 1$ (in taking $C = 1$ and $\Delta t = 1$):

$$P_1(t+1) = P_1(t) + \alpha_1 P_1(t)(1 - P_1(t)) - \beta_1 P_1(t) \quad (5)$$

In taking $\alpha_1 = 3$ and $\beta_1 = 2$, for example, the population stabilises to the value $P_1 = 1 - \beta_1/\alpha_1 = 1/3$. If a small part of the species $\Delta P_1 = P_{12}$ gives rise to random mutations at a time T which have the effect to change the growth and decay rates to the values $\alpha_2 = \alpha_1 + \Delta\alpha_1$ and $\beta_2 = \beta_1 + \Delta\beta_1$ where $\Delta\alpha_1$ and $\Delta\beta_1$ can be separately positive, null or negative values, this mutant species P_{12} will compete for the nutrient with the rest of the original species $P_{11} = P_1 - P_{12}$ so that

$$C = P_{11}(T+t) + P_{12}(T+t) + N(T+t) = 1 \quad (5b)$$

The new system can be described by

$$P_{11}(T+t+1) = P_{11}(T+t) + \alpha_1 P_{11}(T+t)(1 - P_{11}(T+t) - P_{12}(T+t)) - \beta_1 P_{11}(T+t) \quad (5c)$$

$$P_{12}(T+t+1) = P_{12}(T+t) + \alpha_2 P_{12}(T+t)(1 - P_{11}(T+t) - P_{12}(T+t)) - \beta_2 P_{12}(T+t) \quad (5d)$$

Different evolutions are depending on the values of the mutations (Dubois, 1998):

1. If $\alpha_2 = \alpha_1$ and $\beta_2 = \beta_1$, there is no evolution.
2. If $\alpha_2/\beta_2 < \alpha_1/\beta_1$, the mutant population P_{12} disappears.
3. If $\alpha_2/\beta_2 > \alpha_1/\beta_1$, the mutant population P_{12} increases and the original population P_{11} disappears. This is a phenomenon of succession which is important during evolution. In this case, the original species shows three phases: growth, stabilisation (maturity) and decay, and the mutant species increases and reaches a biomass value $P_{12} = 1 - \beta_2/\alpha_2$ greater than the biomass of the original population.

For example, $\alpha_2 = 3$ and $\beta_2 = 1$, which means that the mutant population shows a smallest mortality and its biomass is given by $P_{12} = 1 - 1/3 = 2/3$. Now if a new mutation occurs, a new species will succeed to the old one if $\alpha_3/\beta_3 > \alpha_2/\beta_2$. For example, $\alpha_3 = 4$ and $\beta_3 = 1$, which means that the mutant population shows a greater growth rate. But here a new phenomenon occurs: the population shows chaos and its average biomass is again greater than the preceding one: $P_{13} = 1 - 1/4 = 3/4$.

Let us remark that in the reality, the number of mutations to reach the chaos must be more than two, but the final state is always the same.

The general law is that the species evolves so that its biomass increases: evolution tends to maximise the biomass and at the same time, goes to chaos where the system becomes then locally unpredictable.

But the things are a little more complicated. Indeed, from the chaos theory, there is no solution for a new mutation $\alpha_4/\beta_4 > 4$ with $\alpha_4 > 4$ and $\beta_4 < 1$. The solution is that the mutations diminish the turnover of the dynamics of populations. So, a mutant species P_{14} with $\alpha_4 = 2$ and $\beta_4 = 0.4$ so that $\alpha_4/\beta_4 = 5$, will replace the chaotic species and its biomass will be higher $P_{14} = 1 - 0.4/2 = 0.8$.

The evolution goes thus to the continuation of the maximisation of the biomass but with a slower dynamics and chaos disappears. At the limit case, a mutant species with $\alpha_5 = 2$ and $\beta_5 = 0$ will give the maximum biomass $P_{15} = 1$.

A numerical simulation of this game of evolution is given in Dubois (1998).

Is it possible to have species without mortality or at least with a very low mortality? Yes, the brain cells, called neurons have such a property: once the neural network is created, these neurons live during all the life of the organism (some neurons died and perhaps some new neurons can appear but this is not significant). What can we say about these cells which are the elementary parts of the brain: these cells are at the top of

the evolution. The neurons have realised the dream of the evolution: maximise the biomass and the immortality for only one category of cells (no diversity).

Remark 1: With a weak or null mortality, the growth parameter is limited by the value $\beta = 2$, at the edge of chaos, because there is no more nutrient.

Remark 2: For some values of the parameters this is possible to obtain the coexistence of a species and its mutant species.

There is another possible solution for $\alpha_4/\beta_4 > 4$ for which the dynamics is faster than in the preceding case (diminution of the turnover). If the mutation is incursive, there will be a change in the structure of the equation of the species instead of a simple change in the values of its growth and decay values.

The competition between a recursive species P_{13} and the mutant incursive species P_{14} given by the equation system (Dubois, 1998):

$$P_{13}(t+1) = P_{13}(t) + \alpha_3 N(t) P_{13}(t) - \beta_3 P_{13}(t) \quad (6a)$$

$$P_{14}(t+1) = P_{14}(t) + \alpha_4 N(t) P_{14}(t) - \beta_4 P_{14}(t) \quad (6b)$$

$$N(t+1) = [N(t) - \alpha_3 N(t) P_{13}(t) + \beta_3 P_{13}(t) - \beta_4 P_{14}(t+1)] / [1 + \alpha_4 P_{14}(t+1)] \quad (6c)$$

This system obeys the conservation of materials given by

$$C = N(t) + P_{13}(t) + P_{14}(t+1) = 1 \quad (6d)$$

For example, the chaotic species P_{13} is computed with $\alpha_3 = 4$ and $\beta_3 = 1$ and the mutant incursive species is computed with $\alpha_4 = 4.1$ and $\beta_4 = 1$. The mutant species replaces the other (See the simulation in Dubois, 1998).

So, the mutant incursive population P_{14} obeys the incursive equation:

$$P_{14}(t+1) = P_{14}(t) + \alpha_4 P_{14}(t)(1 - P_{14}(t+1)) - \beta_4 P_{14}(t) \quad (7)$$

which can be transformed to the recursive equation:

$$P_{14}(t+1) = [P_{14}(t) + \alpha_4 P_{14}(t) - \beta_4 P_{14}(t)] / [1 + \alpha_4 P_{14}(t)] \quad (7a)$$

which is an equation of the Michaelis–Menten–Monod type (see Odum, 1983, for such models).

Let us notice that J. Monod (1942) shows experimentally that the growth of bacteria follows such a similar law.

In conclusion, I demonstrated that with a simple model that some natural effects of evolution can be modeled and simulated.

Are the dynamics shown here Darwinian or Lamarckian processes?

When random changes in the parameters gives rise to new species by competition, the process is similar to the Darwinian natural selection of the fittest. The "fittest" means in this game of evolution "the more stable population" with the maximisation of the biomass which leads to chaos and then a diminution of the dynamics of the population and immortality with the disappearance of chaos. Neurons seem to be such evolutive cells with a slow dynamics.

When a structural change in the equation of evolution occurs, the incursive solution is rather similar to a catastrophic process. E. C. Zeeman (1972–1977) proposes a Lamarckian evolution complementary to a Darwinian one.

In my game of evolution, the incursive solution suppresses the chaos and at the same time, the dynamics of the population can increase beyond the possibilities of chaos in maximising also the biomass (see also Odum, 1983, for the maximum biomass related to Lotka (1925) maximum power principle). Growth in a Michaelis–Menten–Monod way plays a central role in ecological models (Odum, 1983).

This game of evolution is evidently too simple to be realistic and must be based also on other evolutionary basic models, but its results are rather surprising and not obvious at all.

Thus, in this paper, I will consider other evolutionary basic models which show different chaotic behaviours with the emergence of strange attractors.

2 A Second Order Pearl–Verhulst Population

The Pearl–Verhulst eq. 3a

$$P(t+\Delta t) = P(t) + \alpha.C. \Delta t.P(t) - \alpha. \Delta t.P(t)^2 - \beta. \Delta t.P(t) \quad (3a)$$

with $\beta.\Delta t = 1 = C = 1$, can be rewritten as

$$P(t+\tau) = (\alpha/\beta).P(t)[1 - P(t)] \quad (8)$$

where $\tau = 1/\beta$. This equation gives rise to bifurcations and chaos. The successive bifurcations correspond to a discrete oscillatory system of successive periods 2, 4, 8, etc for increasing values of α , then to chaos.

Classically, this map (8) corresponds to the following differential continuous Pearl–Verhulst equation

$$dP(t)/dt = \alpha.P(t)[1 - P(t)] - \beta P(t) \quad (9)$$

for which no oscillatory solution exists.

In fact, we can deduce this differential equation in expanding $P(t+\tau)$ in Taylor's series in the following way

$$P(t+\tau) = P(t) + \tau dP(t)/dt \quad (10)$$

so

$$P(t) + \tau dP(t)/dt = (\alpha/\beta).P(t)[1 - P(t)] \quad (11a)$$

or

$$dP(t)/dt = \alpha.P(t)[1 - P(t)] - \beta.P(t) \quad (11b)$$

This equation can be called a first order Pearl–Verhulst differential equation.

A second order differential equation can be deduced in expanding $P(t+\tau)$ to the second order in Taylor's series as

$$P(t+\tau) = P(t) + \tau dP(t)/dt + (\tau^2/2)d^2P(t)/dt^2 \quad (12)$$

and then the differential equation is written as

$$P(t) + \tau dP(t)/dt + (\tau^2/2)d^2P(t)/dt^2 = (\alpha/\beta).P(t)[1 - P(t)] \quad (13a)$$

or

$$dP(t)/dt + (1/2\beta)d^2P(t)/dt^2 = \alpha.P(t)[1 - P(t)] - \beta.P(t) \quad (13b)$$

which is a non-linear damped oscillator with a damping factor equal to 2β :

$$d^2P(t)/dt^2 + 2\beta dP(t)/dt = 2\alpha\beta.P(t)[1 - P(t)] - 2\beta^2.P(t) \quad (13c)$$

In the game of evolution, we have seen that the population evolves in increasing the ratio α/β , so when β decreases, the damping effect will diminish, and when α increases, the frequency of oscillations will increase.

These oscillatory properties could correspond to a new evolutive effect for populations.

A similar evolutionary property of populations was pointed out by Jiri Slechta (1995), who pointed out the importance of the acceleration term for the population dynamics. He argued that this acceleration is the missing link to the derivation of the Darwin evolutionary dynamics. For him, the acceleration term is related to environmental properties. In my model, the acceleration term comes from an intrinsic property of population: a temporal delay in the reaction dynamics. Indeed, let us show in the following section that the second order Pearl-Verhulst model is similar to the classical Pearl-Verhulst model with a time lag.

Moreover and very curiously, when we add a spatial term to population dynamics with second space derivative, the equation becomes a parabolic equation for which perturbations propagate at an infinite velocity, what is impossible in practice. This property of infinite velocity was pointed out for the heat equation and the Burgers equation in hydrodynamics which are ideal incompressible flows. To avoid such infinite propagation of perturbations in parabolic equations, some authors (Maxwell, 1867, Cattaneo, 1958, Green and Laws, 1972, Vernotte, 1958, Chester, 1963, Kranys, 1966, Müller, 1967, Lambermont and Lebon, 1973, 1976) proposed to add a second order time derivative, so the parabolic equation is transformed to a hyperbolic equation.

3 Diffusive Propagation of a Second Order Pearl-Verhulst Population

Let us consider the Pearl-Verhulst population written in the following form

$$dP(t)/dt + \tau d^2P(t)/dt^2 = \alpha.P(t)[C - P(t)] - \beta.P(t) \quad (14)$$

which corresponds to a delayed equation when τ is small

$$dP(t+\tau)/dt = \alpha.P(t)[C - P(t)] - \beta.P(t) \quad (14a)$$

because

$$P(t+\tau) = P(t) + \tau dP(t)/dt \quad (14b)$$

This means that the growth of the population occurs with a time lag of τ .

The one-dimension spatial diffusion of such a population eq. 14 is given by

$$\partial P(t)/\partial t + \tau \partial^2 P(t)/\partial t^2 = \alpha.P(t)[C - P(t)] - \beta.P(t) + D \partial^2 P(t)/\partial x^2 \quad (15)$$

where D is the diffusion coefficient.

This equation can be written in the following discrete form

$$\frac{[P(x,t+\Delta t) - P(x,t-\Delta t)]/2\Delta t + \tau[P(x,t+\Delta t) - 2P(x,t) + P(x,t-\Delta t)]/\Delta t^2 = \alpha \cdot P(x,t)[C - P(x,t)] - \beta \cdot P(x,t) + D[P(x+\Delta x,t) - 2P(x,t) + P(x-\Delta x,t)]/\Delta x^2 \quad (16)$$

Let us remark that a similar correction to an epidemics equation system was proposed earlier (Dubois and Sabatier, 1998).

A particular case occurs when $\tau = 1/2\beta$ and $\Delta t = 1/\beta$

$$P(x,t+\Delta t) = \Delta t \cdot [\alpha \cdot P(x,t)[C - P(x,t)]] + \Delta t \cdot D[P(x+\Delta x,t) - 2P(x,t) + P(x-\Delta x,t)]/\Delta x^2 \quad (17)$$

which corresponds to the one-dimension spatial diffusion of the Pearl-Verhulst map, as given in the preceding section.

The following numerical simulations of this equation 16 given at Figures 1 to 8, show that the velocity of a population front is related to the time lag τ . When τ increases, the velocity of propagation v of the population front decreases: the velocity v is approximately related to $v \cong \sqrt{D/\tau}$. The values of the parameters are: $\Delta t = 1$, $\alpha = 2$, $C = 1$, $\beta = 1$, $\Delta x^2 = 1$, $D = 0.2$. In these Figures, the space length is 200 and the spatial population front is given after 200 time steps, for different values of τ .

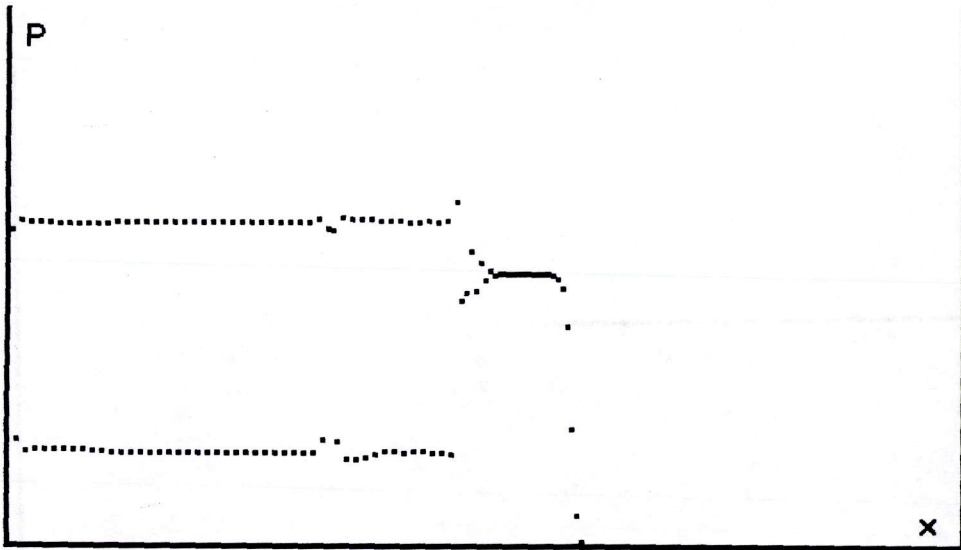


Figure 1: Simulation of eq. 16 for $\tau = 1/3$. A 2-period bifurcation appears.

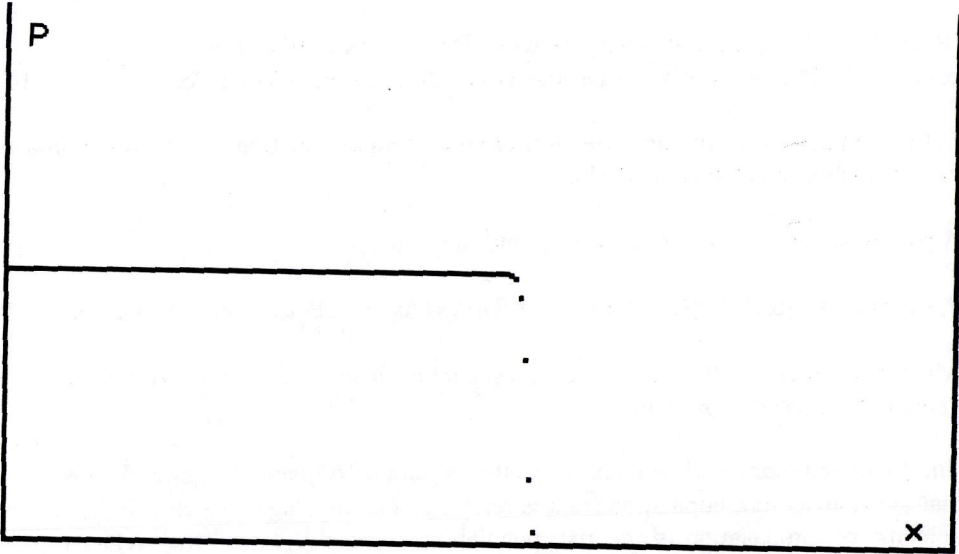


Figure 2: Simulation of eq. 16 for $\tau = 1/2$.

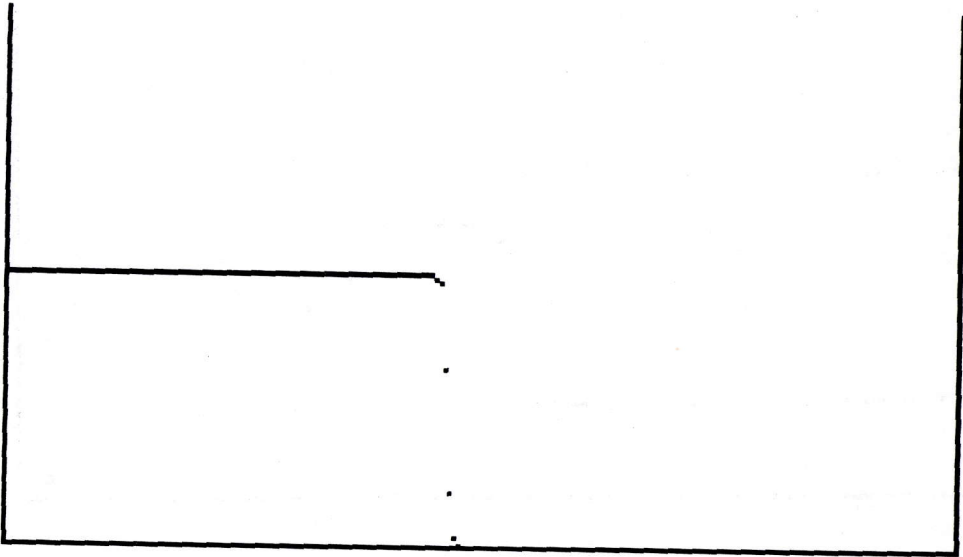


Figure 3: Simulation of eq. 16 for $\tau = 1$.

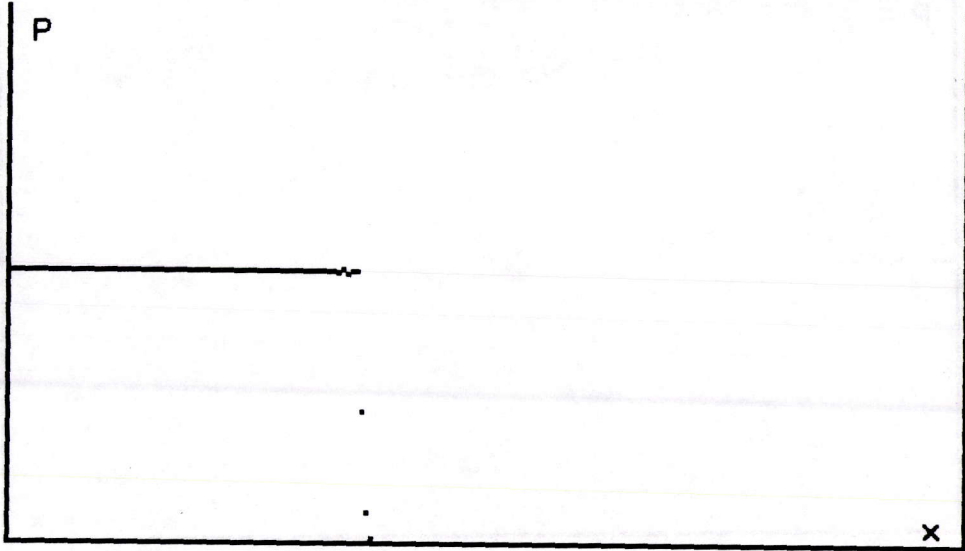


Figure 4: Simulation of eq. 16 for $\tau = 2$.

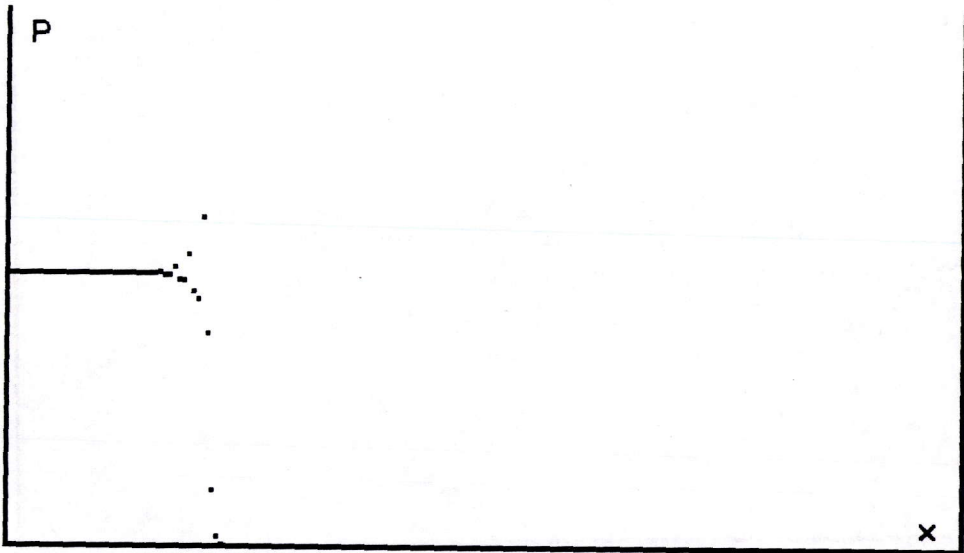


Figure 5: Simulation of eq. 16 for $\tau = 8$.

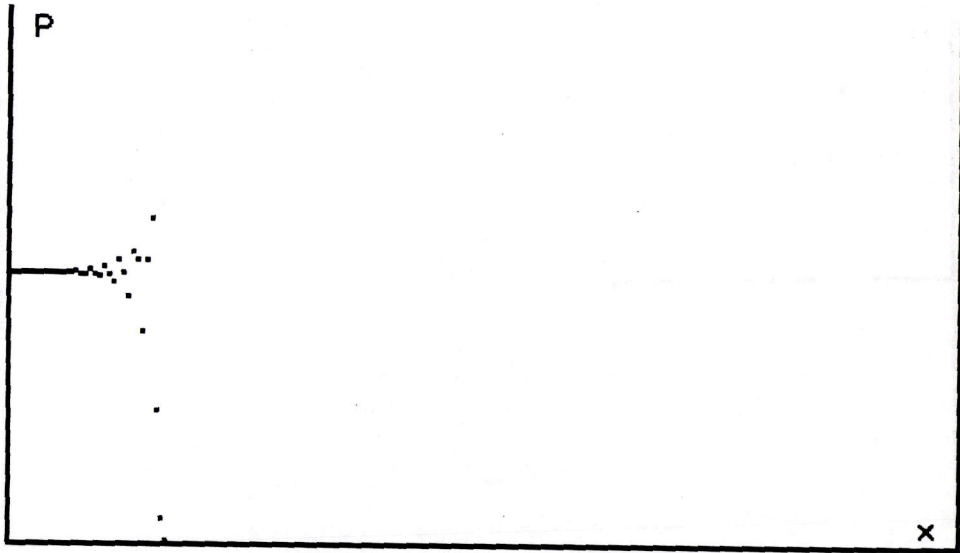


Figure 6: Simulation of eq. 16 for $\tau = 16$.

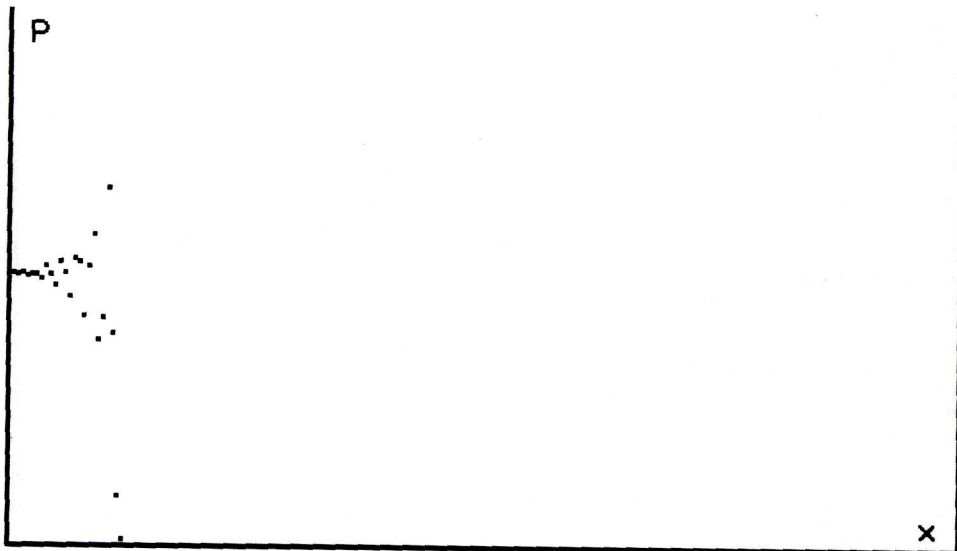


Figure 7: Simulation of eq. 16 for $\tau = 32$.

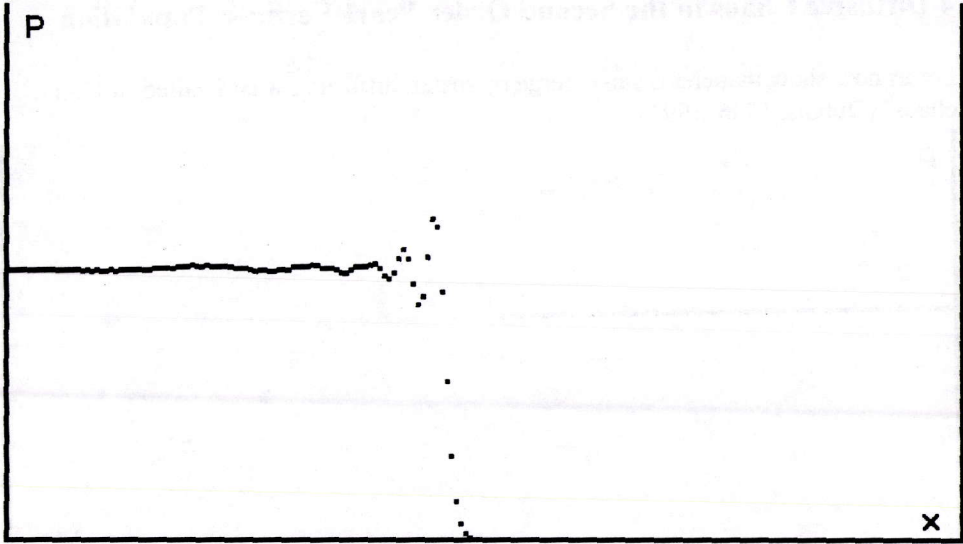


Figure 7a: Simulation of eq. 16 for $\tau = 32$, with a re-scaling of the spatial domain.

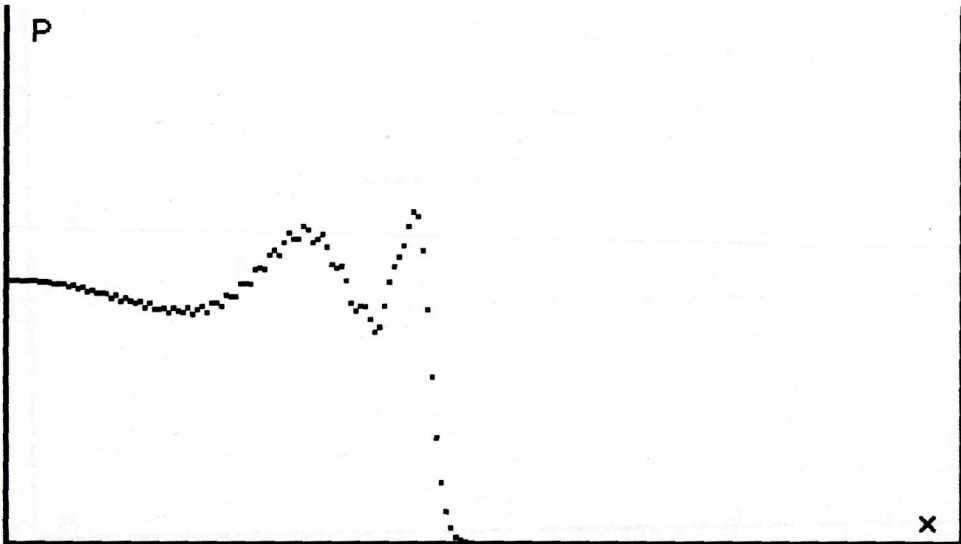


Figure 8: Simulation of eq. 16 for $\tau = 128$, with a re-scaling of the spatial domain.

4 Diffusive Chaos in the Second Order Pearl-Verhulst Population

Let us now show that chaos can emerge by spatial diffusion, what I called "diffusive chaos" (Dubois, 1996, 1998).

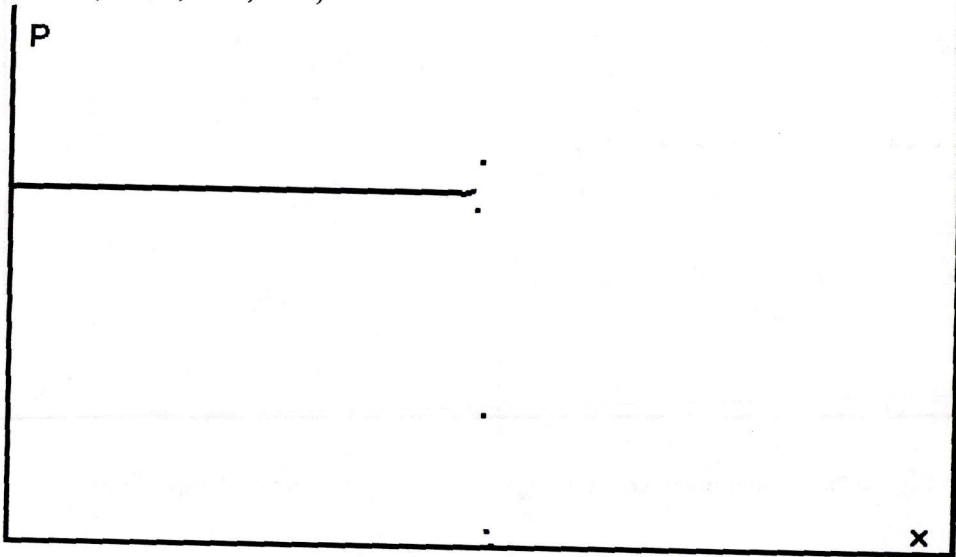


Figure 9: Simulation of eq. 16 for $D = 0.17$.

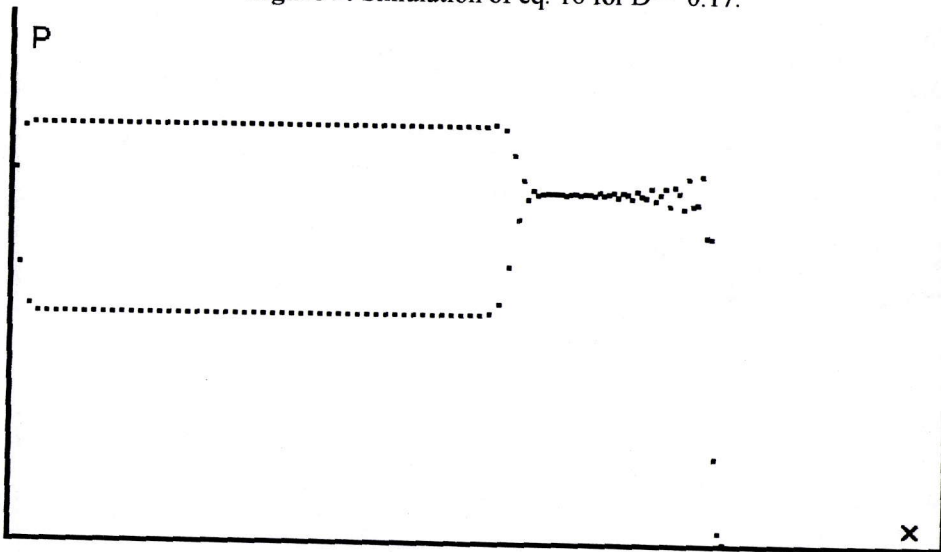


Figure 10: Simulation of eq. 16 for $D = 0.6$.

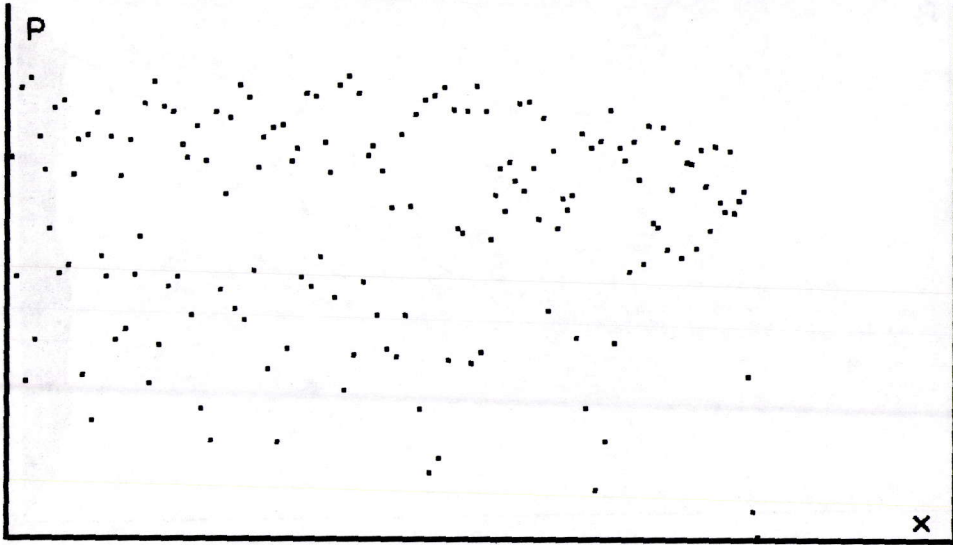


Figure 11: Simulation of eq. 16 for $D = 0.68$.

The Figures 9, 10 and 11 give the numerical simulations of eq. 16 with the parameters $\Delta t = 1$, $\alpha = 2.9$, $C = 1$, $\Delta x^2 = 1$, $\tau = 1$ for 3 different values of the diffusion coefficient D . For low diffusion, a stable homogeneous spatial distribution occurs. A 2-period bifurcation emerges with a higher diffusion and then chaos.

5 Hénon Strange Attractor From Second Order Pearl-Verhulst Map

Without diffusion, the discrete second order Pearl-Verhulst eq. 16 is written as

$$\frac{[P(x,t+\Delta t) - P(x,t-\Delta t)]/2\Delta t + \tau[P(x,t+\Delta t) - 2P(x,t) + P(x,t-\Delta t)]/\Delta t^2 = \alpha \cdot P(x,t)[C - P(x,t)] - \beta \cdot P(x,t)}{(18)}$$

For the following values of the parameters: $\Delta t = 1$, $C = 2.2627$, $\beta = 0.7$ and $\tau = 0.2492307$, this map is similar to the Hénon strange attractor.

The numerical simulations of eq. 18 are given for $\alpha = 0$ to 1.0769, $\alpha = 1$ to 0.0769 with initial conditions $P(0) = 1.48$, $P(-1) = P(0)$ in Figures 12 and 13. With initial conditions $P(0) = 1.48$, $P(-1) = 0$ in Figure 13a. Different initial conditions give different bifurcation diagrams: these equations have a memory of the initial conditions.

Figures 14abc give the first, second and third return maps which are similar to the Hénon strange attractor.

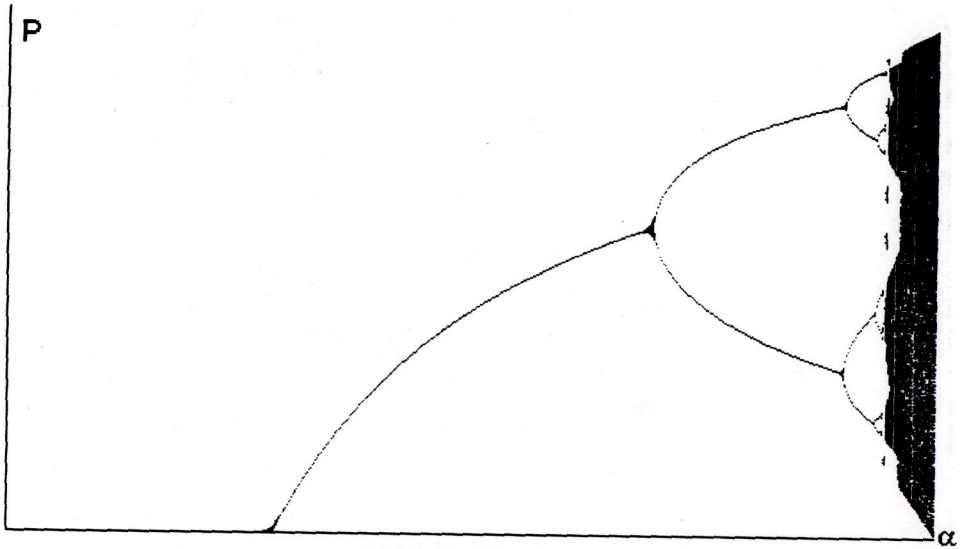


Figure 12: Second order Pearl-Verhulst bifurcation diagram for $\alpha = 0$ to 1.0769, with initial conditions $P(0) = 1.48$, $P(-1) = P(0)$.

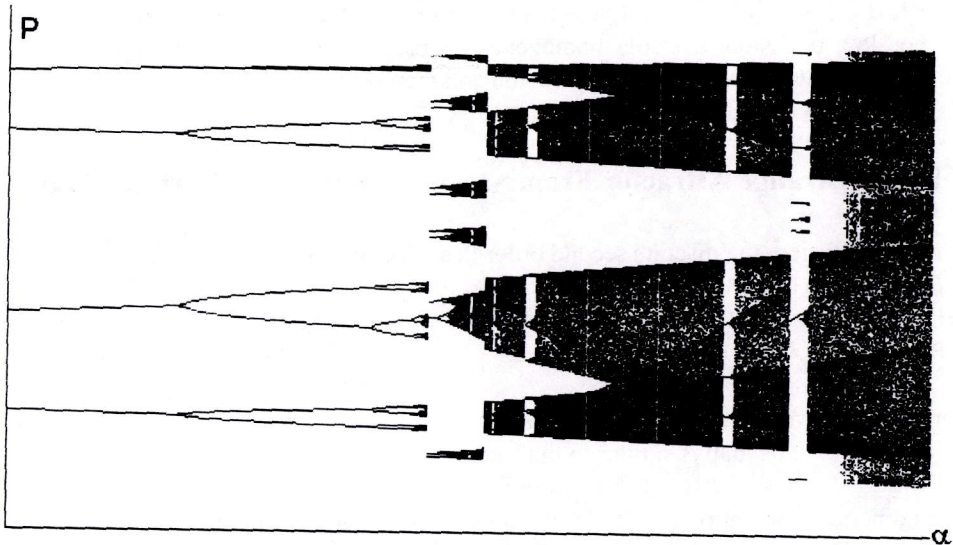


Figure 13 : Second order Pearl-Verhulst bifurcation diagram for $\alpha = 1.0$ to 1.0769 with initial conditions $P(0) = 1.48$, $P(-1) = P(0)$. Look at the specs similar to the specs in the Hénon strange attractor.

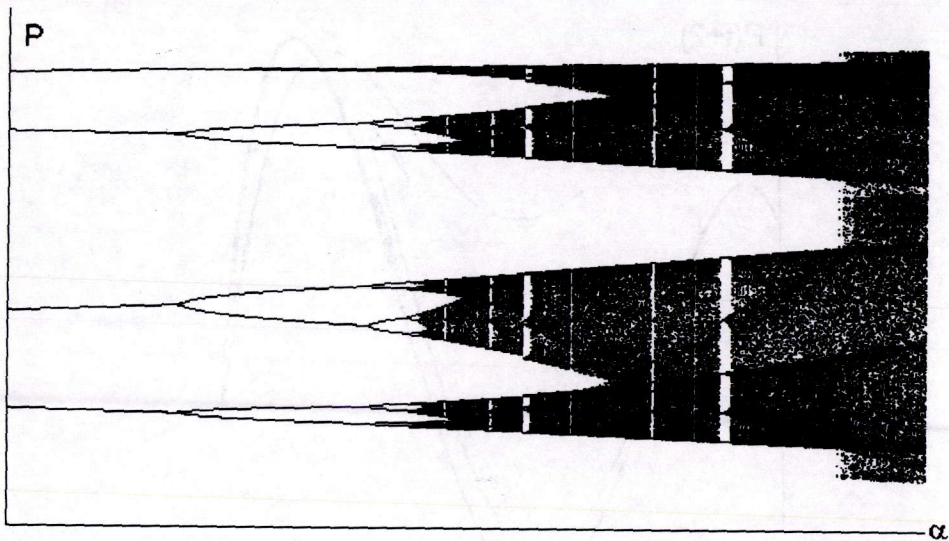


Figure 13a : Second order Pearl-Verhulst bifurcation diagram for $\alpha = 1.0$ to 1.0769 with initial conditions $P(0) = 1.48$, $P(-1) = 0$. The specs disappeared in comparing to Figure 13. Thus this strange attractor has a memory of its initial conditions.

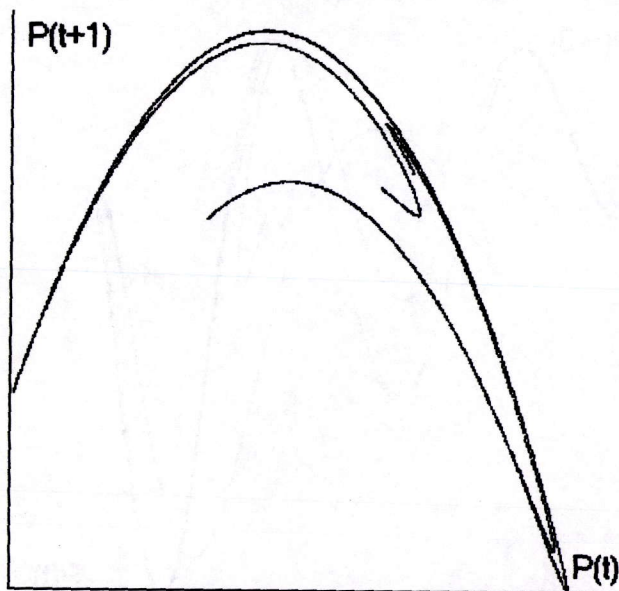


Figure 14a : First return map of eq. 18. This is similar to the Hénon attractor.

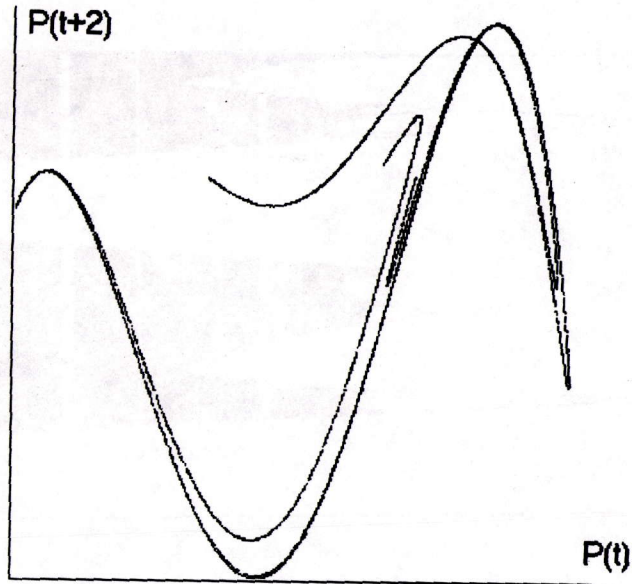


Figure 14b : Second return map of eq. 18.

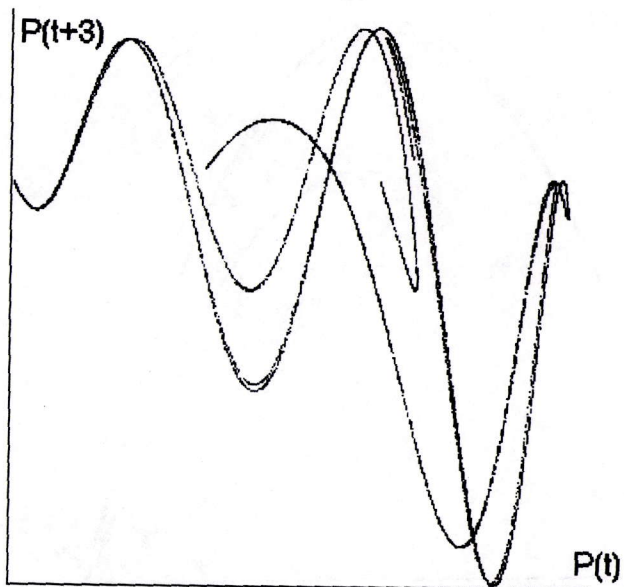


Figure 14c : Third return map of eq. 18.

5 Anticipatory and Memory Effect in a Hénon-like Population

Let us consider the following model

$$dN/dt = -\alpha NP + \gamma P \quad (19a)$$

$$dP^*/dt = +\alpha NP - \beta P^* \quad (19b)$$

$$dP/dt = +\beta P^* - \gamma P \quad (19c)$$

corresponding to



where P^* are satiated P which do not take nutrients: when the satiated P transform to hungry P , they take nutrients. The dead P transform to nutrients: this is a closure condition to have a closed biomass (the nutrients are included to the biomass) system for which

$$N + P^* + P = C \quad (21)$$

where C is the total biomass of the system corresponding to the conservation of the total mass of the ecosystem.

With the closure condition (21), the 3 eqs. 19abc are reduced to the following 2 equations

$$dN/dt = -\alpha NP + \gamma P \quad (22a)$$

$$dP/dt = +\beta(C - N - P) - \gamma P \quad (22b)$$

After some mathematical transformations, we obtain

$$\tau d^2P/dt^2 + dP/dt = \alpha P[C\beta\tau - \gamma\beta\tau/\alpha - P - \tau dP/dt] \quad (23)$$

where $\tau = 1/(\beta + \gamma)$. In this eq. 23, we remark that the growth rate of the P depends on the temporal derivative of P : this is an incursive equation which is an anticipatory effect of the growth of the population.

So eq. 23 can be written as

$$\tau d^2P/dt^2 + (1 + \alpha\tau P)dP/dt = \alpha P[C\beta\tau - \gamma\beta\tau/\alpha - P] \quad (23a)$$

Eq. 23a can be rewritten as

$$d^2P/dt^2 + (\gamma + \beta + \alpha P)dP/dt = \alpha P[C\beta - \gamma\beta/\alpha - (\gamma + \beta)P] \quad (23b)$$

This equation can be written in the following discrete form

$$(\gamma + \beta + \alpha P(t))[P(t+\Delta t) - P(t-\Delta t)]/2\Delta t + [P(t+\Delta t) - 2P(t) + P(t-\Delta t)]/\Delta t^2 = \alpha P(t)[C\beta - \gamma\beta/\alpha - (\gamma + \beta)P(t)] \quad (24a)$$

or

$$P(t+\Delta t) = [(\gamma + \beta + \alpha P(t) - 2/\Delta t)P(t-\Delta t) + 4P(t)/\Delta t + 2\Delta t\alpha P(t)[C\beta - \gamma\beta/\alpha - (\gamma + \beta)P(t)]] / (\gamma + \beta + \alpha P(t) + 2/\Delta t) \quad (24b)$$

The numerical simulations of this eq. 24b was made with the following parameters:

$\Delta t = 1, C = 2, \beta = 1, \gamma = 1$. So eq. 24b becomes

$$P(t+1) = [\alpha P(t)P(t-\Delta t) + 2P(t) + 4\alpha P(t)[1 - P(t)]] / (4 + \alpha P(t)) \quad (25)$$

Figure 15 gives the bifurcation diagram of eq. 25. Figure 16a is an enlargement of the preceding bifurcation diagram. Figure 16 b is the enlarged bifurcation diagram with other initial conditions.

Figures 17a to 17e give the first to the fifth return maps of eq. 25 for $\alpha = 4.305$.

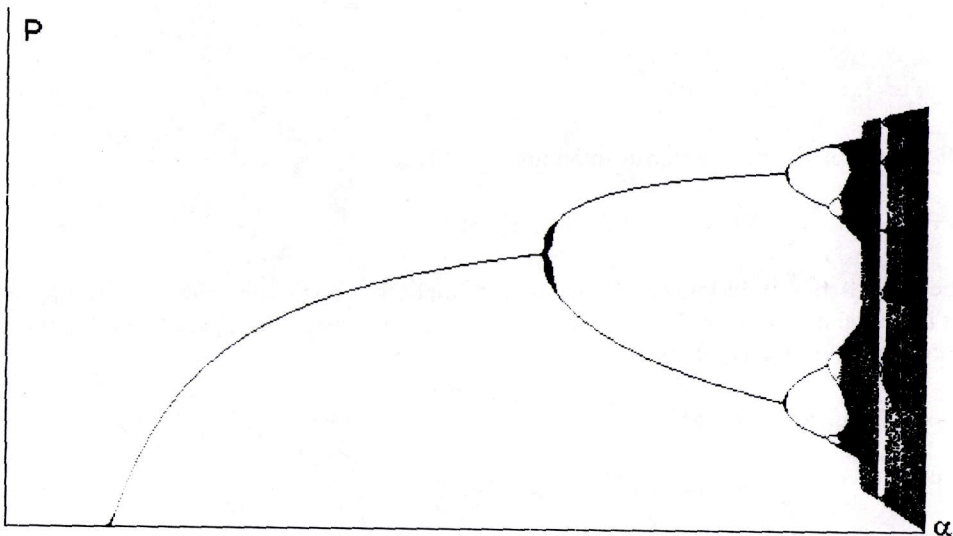


Figure 15 : Bifurcation diagram of eq. 25 for $\alpha=0$ to 4.3.
Initial conditions: $P(0) = 1.48, P(-1) = P(0)$

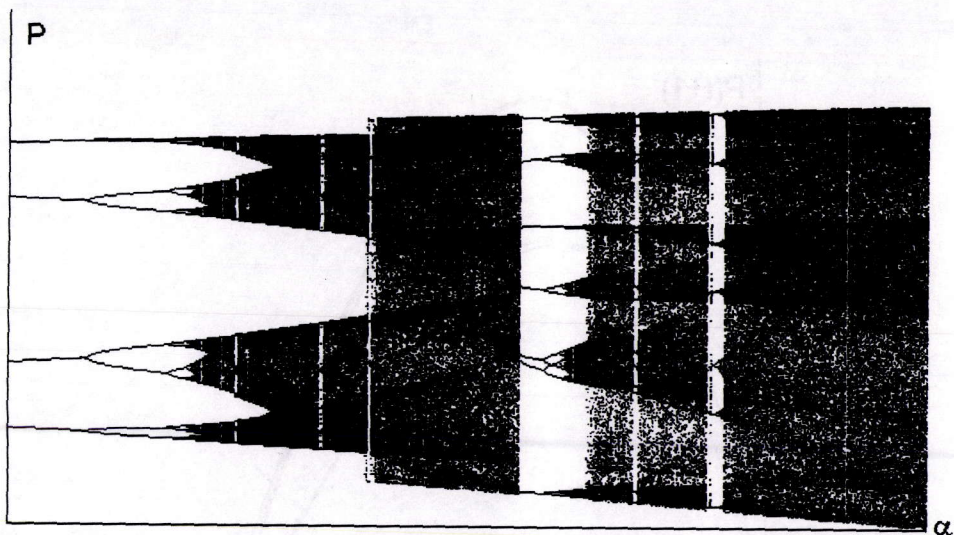


Figure 16a : Bifurcation diagram of eq. 25 for $\alpha = 3.8$ to 4.3 .
 Initial conditions: $P(0) = 1.48$, $P(-1) = P(0)$.

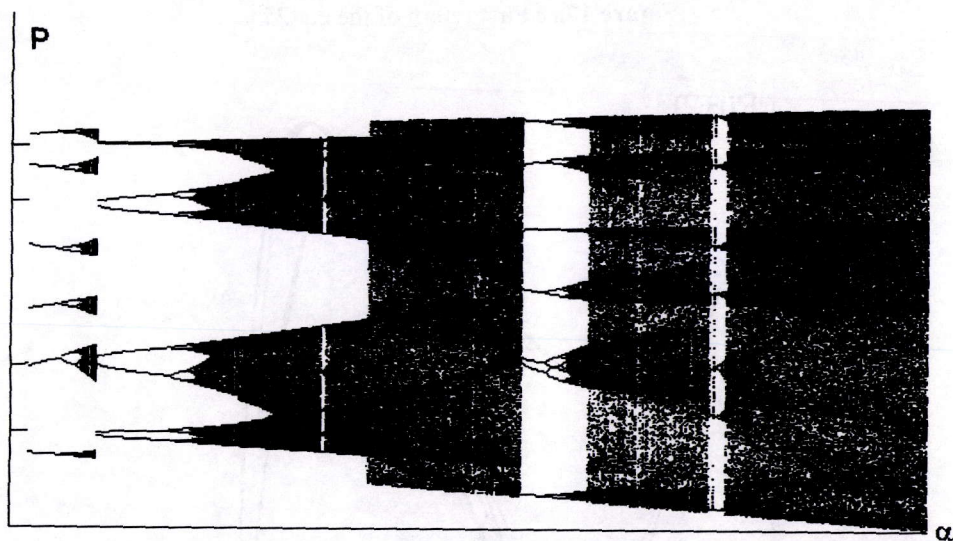


Figure 16b : Bifurcation diagram of eq. 25 for $\alpha = 3.8$ to 4.3 .
 Initial conditions: $P(0) = 0.5$, $P(-1) = 0.5P(0)$.
 Additional bifurcation specs are seen at the left of this figure.
 This anticipatory attractor has a memory of its initial conditions.

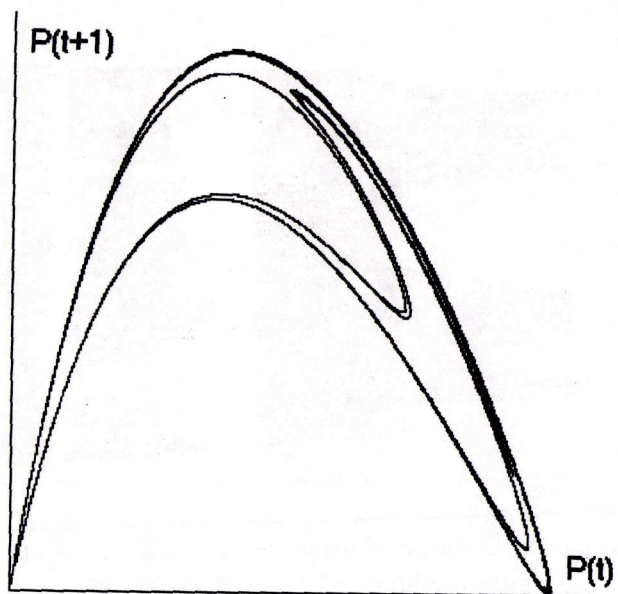


Figure 17a : First return of the eq. 25.

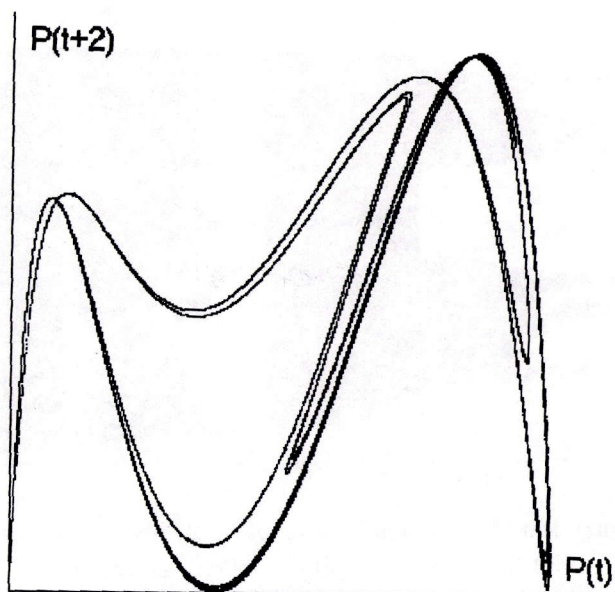


Figure 17b : Second return of the eq. 25.

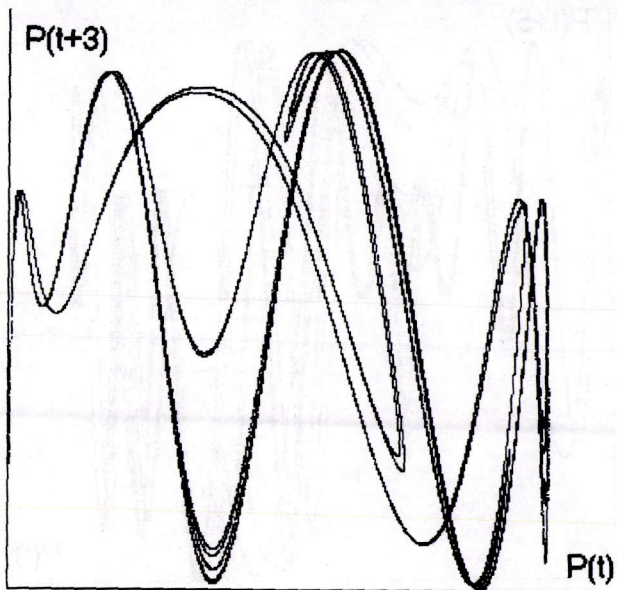


Figure 17c : Third return of the eq. 25.

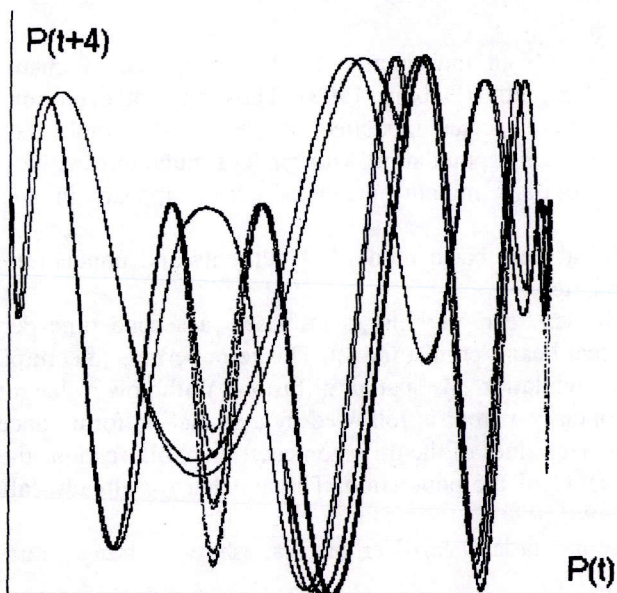


Figure 17d : Fourth return of the eq. 25.

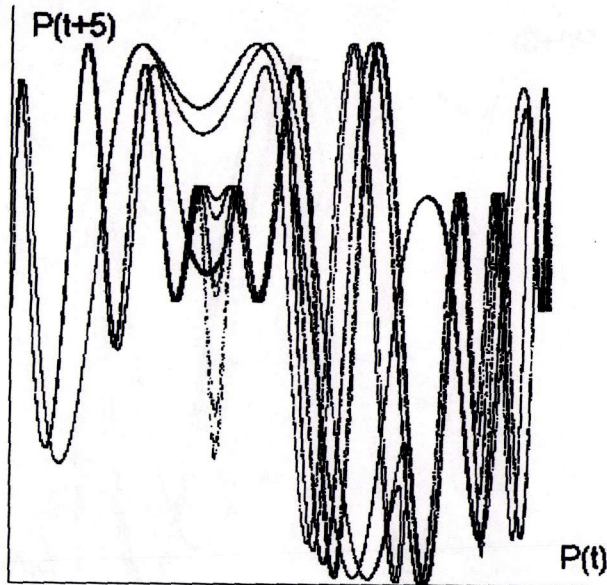


Figure 17e : Fifth return of the eq. 25.

Conclusion

This paper begins with an introduction to the emergence of chaos in a game of evolution proposed recently (Dubois, 1998). This game of evolution deals with the competition between a species modelled by the Pearl-Verhulst equation with its successive mutants. Such a population with random mutations evolves when the ratio birth rate/death rate of a mutant increases. Chaos appears in such an evolving ecosystem.

In this paper, several new basic models of nutrients and population interaction are presented and simulated.

Firstly, a second order Pearl-Verhulst is proposed: a second time derivative term is added to the classical Pear-Verhulst model. This term permits to control the velocity of propagation of a population by spatial diffusion. With low value of the diffusion coefficient, the population front is followed by a spatial uniform concentration of the population. For higher values of the diffusion coefficient bifurcations then chaos appear in the spatial structure of the population. This is what we already called a "diffusive chaos" (Dubois, 1996, 1998).

Secondly, this second order Pearl-Verhulst can show a strange attractor similar to Hénon's attractor (1976).

Thirdly, the nutrients N - population P interaction model is complicated in adding an intermediate state P^* for the population: P^* is the satiated population and only non

satiated population P can take nutrients. Surprisingly, such an ecosystem has memory but also anticipatory properties similar to the incursive model of the Pearl-Verhulst given before (Dubois, 1996). Such a system depends on the initial conditions and show a strange attractor similar to the Hénon attractor with several attraction basins.

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