Coevolution of competing systems: cooperation and inhibition

José M. Albornoz*, Antonio Parravano†

April 17, 2009

Abstract

Using a set of heterogeneous competing systems with intra-system cooperation and inter-system unfair competition, we show how the coevolution of the system parameters (degree of cooperation and unfair competition) depends on the external supply of resources. This kind of interaction is found in social, economic, ecological and biochemical systems; as an illustration we consider the competition between drug-selling gangs. The model consists of a set of units (individuals, machines or enzymes) grouped in a number of systems (organizations, factories or glycosomes), each one composed by a fixed number of units that can be organized in three configurations: isolated (monomers), cooperating in couples (dimers), and cooperating in groups of four (tetramers). The units working in cooperating configurations increase their ability to obtain the resources (customers, raw material or substrates). The supply of resources can be polluted by the systems through inhibitors. When an unit absorbs an inhibitor, its function is blocked during a period of time. When the blocked unit belongs to dimers or tetramers, all units in the group are also inhibited to acquire the resource. Two parameters characterize each system: the fraction of monomers and the range of the average production in which the system is allowed to produce inhibitors. By using a genetic algorithm, we observe that the evolution of the parameters of the systems maintains its long term average values for low and high supply rates, but tends to display global evolutive transitions when the supply of raw material lies between abundance and scarcity.

*Departamento de Electrónica y Comunicaciones, Facultad de Ingeniería, Universidad de Los Andes, Mérida 5101, Venezuela.

†Centro de Física Fundamental, Facultad de Ciencias, Universidad de Los Andes, Mérida, Venezuela. Corresponding author: parravan@ula.ve

1 Introduction

There are many situations in which the global performance of a set of competing systems, measured in some way, is below its maximum possible value due to the "unfair" competition among the systems. Generally, in complex systems the competing components use different strategies that may consume part of the available resources in order to reduce the performance of the others. In these situations there is a global cost but the collateral effect is to favor the apparition of new strategies that tend to increase the diversity and complexity in these systems. This is the case in some social and economic systems [1, 2, 3, 4, 5] and in ecological and biochemical systems [6, 7, 8, 9, 10]. For example, Axelrod [1, 2] considers an evolutionary approach to social norms based on a n-person Prisoner's dilemma. In this norms game the players can defect (getting a payoff and hurting each of the other players) but can be punished if seen by other player. The evolution of the player's strategy (the boldness and the vengefulness) is driven by the selection of the strategies giving the best scores; however, the maximum global score (no one defects) is rarely observed.

There are many situations in which there is an interplay between risk and profit. In some cases, the risk and the profit depend on the degree of organization within a competing system: a greater degree of organization usually results in a greater profit but on the other hand it also may increase potential losses in case of unfair competence. Consider for instance the various drug-selling gangs that coexist in the poorest neighborhoods of a large city [11, 12]. Each gang controls a territory that can expand or contract, but let us assume that it mantains its size (e.g. 10x10 blocks). The gangs compete to sell drugs to a limited number of customers (the resource). The customers prefer to buy in the safest, easiest and quickest possible way and the gangs try to sell as much as they can by using strategies to attract the largest possible fraction of the consumers in the city. The model presented here considers two types of strategies: intra-system cooperation and inter-system aggression. In the gangs example, the degree of intra-gang cooperation can be associated to the various ways in which the gang members are distributed in their territory. The dealers can aggregate in a few intersections or can distribute themselves in as many intersections as dealers in the gang. Busy corners (as well as shopping centers) offer an environment in which customers can buy drugs in an easy and quick way; besides, the presence of other customers gives the impression of a relatively safe place. Inter-system aggressions can be associated with the violence between gangs. In our model aggression has a cost for the aggressor and causes more damage to units working in cooperation than to isolated units. The shooting of a rival drug-dealer immediately stops

drug sales at the crime scene. During the next days or weeks, the police is patrolling the area, scaring away habitual customers who choose to buy drugs in other safer places. If the shooting occurs in a busy corner, where several drug-dealers are simultaneously dealing with customers, income losses per shooting are larger compared to the one-dealer one-corner case. On the other hand, the attacking gang pays a cost in several ways: money to buy guns and/or hire mercenary aggressors, demand of dealers for higher wages because of the added risk, etc.

Here we consider a stylized model to analyze the coevolution of the strategies of systems competing for limited resources [13]; specifically, we study the coevolution of intra-system cooperation and inter-system aggression. Our model consist of $N_g \times N_e$ identical units organized in N_g systems with N_e elements per system. This type of systems is found in cells, where enzymes are grouped within specialized organelles; similarly, in the industrial sector, machines are grouped in factories, or, as in the gang example, drug dealers are grouped in gangs. The systems compete to acquire the resources (substrates, raw material or customers) supplied to the system at a rate $\dot{S}$ and at the same time are allowed to produce inhibitors that reduce the performance of others. The cooperation among associated units increases the efficiency to bind substrate when they are arranged in oligomers, as in the case of enzymes [14]. Inhibitors reduce the efficiency by blocking the unit during a period of time as in the case of the occupation by an inhibitor of the active site where a substrate is bound to the enzyme [14]. The performance (i.e. the production rate) of a system depends on its comparative ability to acquire the resources, which in turn depends on the configuration of the units in the system. In absence of inhibitors, the production rate is greater in systems with cooperating units than in systems with units working in isolation. However, when inhibitors are present, the number of units blocked per inhibitor depends on the working configuration of the units.

In real systems the strategies used by its components to survive and reproduce are in general very sophisticated and are the result of evolution. Models like the one presented below help to understand how the ambient conditions and the interaction between the systems drive the evolution of the model parameters; in our case, the fraction of units working in isolation and the conditions to release inhibitors.

The model is presented in Sec. 2. In Sec. 3 we consider a set of competing systems including four types of systems with different cooperating configurations; two cases are considered: when the inhibitors are externally supplied and when the inhibitors are produced by the systems. In Sec. 4 a genetic algorithm is used to allow the evolution of the system strategies. Conclusions are given in Sec. 5.

2 The model

Consider a set of N_g systems, each one possesing the same number N_e of units. The $N_g \times N_e$ units compete to acquire the available resources that are supplied at a rate $\dot{S}$. The state of each unit is characterized by an integer phase variable $\phi_{i,j}(t)$ where $1 \leq i \leq N_g$ indicates the system, $1 \leq j \leq N_e$ enumerates the units in the system, and t is a discrete time counter. The phase of unit (i, j) evolves in a similar way as the phase of the stochastic automata originally proposed by Mikhailov and Hess [16, 17, 18], but allowing for two additional processes: (i) the unit can bind either to a substrate or to an inhibitor and (ii) units can work in cooperation with one or more units, thus modifying their ability to bind to a substrate or to an inhibitor. The idle state corresponds to the phase $\phi = 0$, where the unit is ready to bind a substrate or an inhibitor. When the unit acquires a substrate the phase changes to $\phi = 1$; afterwards the phase value is increased by one unit in each time step until the unit reaches the maximum phase value $\phi = \tau$; once this happens the unit returns to its original idle state $\phi = 0$. A product is released at a fixed phase $1 < \tau_p < \tau$. When the unit acquires an inhibitor the phase changes from $\phi = 0$ to the negative value $\phi = -\tau_I$; afterwards the phase value is increased by one unit in each time step until the unit reaches its idle state $\phi = 0$. The algorithm to iterate the phase of unit (i, j) is

$$\phi_{i,j}(t+1) = \begin{cases} \phi_{i,j}(t) + 1 & \text{if } \phi_{\mathrm{i,j}}(\mathrm{t}) \neq 0, \\ 0 & \text{if } \phi_{\mathrm{i,j}}(\mathrm{t}) = \tau \\ 1 & \text{if } \phi_{\mathrm{i,j}}(\mathrm{t}) = 0 \text{ with probability } \mathrm{p_{i,j}}, \\ -\tau_I & \text{if } \phi_{\mathrm{i,j}}(\mathrm{t}) = 0 \text{ with probability } \mathrm{q_{i,j}}, \\ 0 & \text{if } \phi_{\mathrm{i,j}}(\mathrm{t}) = 0 \text{ with probability } 1 - \mathrm{p} - \mathrm{q}. \end{cases} \tag{1}$$

The probabilities p and q are given by

$$p_{i,j} = p_0 N_S / \alpha^{\kappa_{i,j}} \quad \text{and} \quad q_{i,j} = p_0 N_I / \alpha^{\kappa_{i,j}}. \tag{2}$$

During a single iteration t the number of substrates N_S and inhibitors N_I changes as they are bound by idle units. In Eq. (2) the parameter p_0 represents the probability that an isolated idle unit binds a substrate when only one substrate is available to be bound. The parameter $\alpha > 0$ controls the cooperativity and the exponent κ is the number of busy units that cooperate with unit j in system i. If an unit is in its inhibited phase ($-\tau_I \leq \phi \leq 0$) the binding probabilities are $p = q = 0$ for the idle units that cooperate with the inhibited unit. When all the units in a cooperative arrangement are in their idle state, $\kappa = 0$ and therefore there is no cooperation; that is, the probability to bind a substrate is the same as if the units were working in isolation. When κ units in a cooperative structure are busy ($1 \leq \phi \leq \tau$) the probabilities p and q of the idle units are increased (if $\alpha < 1$) or decreased

(if $\alpha > 1$) by a factor $\alpha^{-\kappa}$ relative to the isolated case ($\kappa = 0$ or $\alpha = 1$). When a unit binds an inhibitor, it remains inoperative during τ_I iterations. If a unit is inhibited, the other idle units in the cooperative arrangement are also inhibited, however the ones that were processing a substrate continue normally its way toward the idle state. In the following we adopt $\alpha < 1$.

The configuration of cooperative units in a system remains fixed during the simulation; that is, if the units j and $j+1$ of system i are set as a cooperative arrangement these two units remain in cooperation during the complete simulation of one generation. For system i the configuration is characterized by the three parameters M_i, D_i, and T_i giving, respectively, the number of units working in isolation (Monomers), the number of cooperating arrangements of two units (Dimers), and the number of arrangements of four units (Tetramers); all possible configurations satisfy $M_i + 2D_i + 4T_i = N_e$.

At the beginning of a given iteration t the number of substrates in the system is $N_{S,begin}(t) = N_{S,end}(t-1) + \dot{S}$, where $N_{S,end}(t-1)$ is the number of substrates that remained unbound in the previous iteration and $\dot{S}$ is the number of substrates added at the beginning of iteration t. During iteration t, the following procedure is executed: (a) the busy and the inhibited units increase their phase in one unit. (b) an unit (i, j) is selected at random among those in their idle state provided it is not associated to a inhibited one; (c) the selected unit starts its processing cycle with probability $p_{i,j}$, is inhibited with probability $q_{i,j}$, or remains idle with probability $1 - p - q$. If the unit starts its processing cycle the number of substrates in the system N_S decreases by one unit. If an inhibitor is bound, the total number N_I decreases in one unit. If the unit (i, j) does not leave the idle state, it is not selected again during the present iteration. Steps (b) and (c) are repeated until $N_S + N_I = 0$, or until all the units that were idle at the beginning of the iteration t are selected.

The number of products released in a given iteration t by the N_e units in system i is denoted as $\dot{P}_i(t)$ and the total production as $\dot{P} = \sum_1^{N_g} \dot{P}_i$. The mean production rate per unit and per duty cycle in system i is denoted as $\upsilon_i = \tau \dot{P}_i / N_e$ and the corresponding rate for all systems is $\upsilon = (1/N_g) \sum_1^{N_g} \upsilon_i = \tau \dot{P} / N_e N_g$. Since the maximum production rate is $\dot{P} = N_e N_g / \tau$, then $0 \leq \upsilon \leq 1$. In absence of inhibitors, the maximum production is approached when the binding probability is $p \gg 1/\tau$. If $N_e N_g > \tau \dot{S}$ then, $N_{S,end} \sim 0$, the fraction of units in their idle state is $\sim 1 - \tau \dot{S}/(N_e N_g)$, and in average $\dot{P} = \dot{S}$. However, if the configuration of cooperating arrangements in the N_g systems is inhomogeneous, then the production rate $\dot{P}_i$ is also inhomogeneous.

The inhibitors can be introduced by an external source at a rate $\dot{I}_{ext}(t)$

or can be released into the environment by some systems at a rate $\dot{I}_i(t)$. In Sec. 3 and 4 we describe the conditions a system must fulfill to release an inhibitor.

3 Inhomogeneous configurations

Consider a set of $N_g = 20$ systems, each one consisting on $N_e = 120$ units arranged in different cooperative configurations: $M_i = N_e$ for $1 \leq i \leq 5$; $D_i = N_e/2$ for $6 \leq i \leq 10$; $T_i = N_e/4$ for $11 \leq i \leq 15$; and $M_i = 40$, $D_i = 20$, and $T_i = 10$ for $16 \leq i \leq 20$. To quantify the performance of the ith system we evaluate the average production rate $\langle v_i \rangle$ per unit and per duty cycle τ in system i. Let us label these four types of systems as types M, D, T and MDT and their corresponding production rates as $\langle v \rangle_M$, $\langle v \rangle_D$, $\langle v \rangle_T$ and $\langle v \rangle_{MDT}$.

3.1 External supply of inhibitors

First we consider the case when the system is supplied with a constant rate $\dot{S}$ of substrates and analyze the dependence of $\langle v \rangle_M$, $\langle v \rangle_D$, $\langle v \rangle_T$ and $\langle v \rangle_{MDT}$ on the external supply of inhibitors $\dot{I}_{ext}$. When $\dot{S} = \frac{1}{2} N_e N_g / \tau$ there are enough substrates to maintain half of the units busy; this corresponds to a production rate $\langle v \rangle = 1/2$. The average number of free substrates $N_{S,end}$ depends on p_0 and on the cooperative arrangements in the system. If $p_0 = 1/\tau$ and $N_S = 1$, an isolated unit remains in average half of the time in its idle state. If p_0 is reduced, N_S increases in the same proportion in order to maintain the units working at half velocity. If not all the units work in isolation, the units in cooperative arrangements will be busier than the isolated ones (for $\alpha < 1$). Therefore, in absence of inhibitors one expects $\langle v \rangle_T > \langle v \rangle_D > \langle v \rangle_M$, but these relations change depending on the supply rate of inhibitors $\dot{I}$ and on the blocking time τ_I. The results in Fig. 1 correspond to the case when $\dot{S} = \frac{1}{2} N_e N_g / \tau$. As expected, as $\dot{I}_{ext}$ increases, the performance of the T-systems decreases whereas for the M-systems increases. However, for $\dot{I}_{ext} \geq 1.2$ even the performance of the M-systems decreases because more than half of the units are blocked (i.e. $\tau_I \, \dot{I}_{ext} \, \overline{n}_c \geq \frac{1}{2} N_g N_e$, where $\overline{n}_c \simeq 2$ is the mean number of units in cooperating arrangements). Note that the performance of the MDT systems remains almost constant for $\dot{I}_{ext} < 1.2$.

In order to examine the effect of a non-stationary supply of inhibitors, Fig. 2 shows the average production rates $\langle v \rangle_M$, $\langle v \rangle_D$, $\langle v \rangle_T$ and $\langle v \rangle_{MDT}$ as functions of the unpolluted period τ_{pol}. The supply is $\dot{I}_{ext} = 0$ during $\tau_{pol} - 1$ iterations and in the next iteration the supply is $\dot{I}_{ext} = \tau_{pol}$; that is, the average supply is $< \dot{I}_{ext} >= 1$. In order to reduce synchronization effects

the inhibition time was randomized 10% around its mean value $\tau_I = 5\tau$. Note that as τ_{pol} increases the average production rates tends to the values corresponding to $\dot{I}_{ext} = 0$. When a large number of inhibitors are added in a single iteration ($\tau_{pol} \gg 1$) many idle units in all cooperating arrangements are blocked, and therefore all types of systems reduce their performances during τ_I iterations.

3.2 Internal production of inhibitors

Consider the case in which inhibitors are produced under certain conditions and at a given cost by the systems. We assume that at a given time an inhibitor is released into the environment by system i if the following conditions are fulfilled: (i) at least one of the units in system i has released a product during the present iteration t; (ii) there are no free inhibitors; and (iii) $\overline{v}_{cri} > \overline{v}_i(t) > \overline{v}_{cri}/2$, where $\overline{v}_i$ is the system production averaged during the previous τ_{ave} iterations. The cost of producing an inhibitor is one product. During a given iteration a given system may release more than one inhibitor, but in general, conditions (i) and (ii) limit the release of inhibitors to at most to one per iteration. This corresponds to low intensity conflicts in the drug-gang example.

Fig. 3 shows the average production rates $\langle v_i \rangle$ as function of $\overline{v}_{cri}$ for 20 systems competing to acquire the substrates supplied at a constant rate $\dot{S} = \frac{1}{2} N_e N_g / \tau$. Half of the systems (black lines) have their units ($N_e = 120$) working in isolation (M-systems) and the other half (grey lines) have their units working in cooperative arrangements of four units (T-systems). The curve labelled v_{tot} corresponds to all-systems average production per unit and the curve labelled $\sigma(v_{tot})$ gives its standard deviation. In the region in between the diagonal dashed lines the condition (iii) is fullfilled. The Roman numbers label the 5 different regimes observed in Fig. 3. In regime (I) none of the system production falls in the range $[\overline{v}_{cri}/2, \overline{v}_{cri}]$ and therefore there is no inhibitor production; the cooperation in T-systems results in a better performace than in M-systems. In regime (II) a few M-systems releasing inhibitors (in fact, only one in Fig. 3) are able to substantially reduce the production of T-systems and to increase the production of the remaining non polluting M-systems; however, T-systems perform better than M-systems. Note that the system is self-regulated to mantain the production of the polluting system k close to $\overline{v}_k = \overline{v}_{cri}/2$. In regime (III) all T-systems release inhibitors. The performance of T-systems is reduced because of the cost of producing inhibitors and the blocking of their cooperating units. In this regime the M-systems perform the best, but the system production v_{sys} is reduced by about 10%. In regime (IV) all M-systems release inhibitors

and their performance is higher than T-systems; the disadvantage associated to the cost of releasing inhibitors is over-compensated by the fact that an inhibitor is able to block four units in the T-systems. As in regime (III), the system production υ_{sys} is reduced by about 10%. In regime (V) the T-systems sporadically release inhibitors in such a way that their averaged production rates $\langle \upsilon_i \rangle$ remains close but below $\overline{\upsilon}_{cri}/2$ (note that during the simulation $\overline{\upsilon}_i$ fluctuates around $\langle \upsilon_i \rangle$ and sporadically $\overline{\upsilon}_{cri} > \overline{\upsilon}_i(t) > \overline{\upsilon}_{cri}/2$).

4 Evolution of system parameters

The behavior of the system depends on the arrangement of the units in each system and on the particular conditions at which each system releases inhibitors into the system. The results in Fig. 3 show that small changes in the system parameters can drastically change the distribution of performances. In Fig. 3 we considered that the conditions to release inhibitors were the same for all systems and that there were only two types of systems. Now, we allow heterogeneity in both parameters, that is, systems are characterized by the parameters $(f_M^i, \overline{\upsilon}_{cri}^i)$, where f_M^i is the fraction of the units working in isolation in system i (the rest works in cooperative arrangements of four units), and $\overline{\upsilon}_{cri}^i$ is the value of $\overline{\upsilon}_i$ below which system i may release inhibitors. Note that in Fig. 3 we used the condition $\overline{\upsilon}_{cri} > \overline{\upsilon}_i(t) > \overline{\upsilon}_{cri}/2$ for the release of inhibitors, but now we use $\overline{\upsilon}_i(t) < \overline{\upsilon}_{cri}$. For a given set of system parameters $(f_M^i, \overline{\upsilon}_{cri}^i)$ there is a distribution of the performances $\langle \upsilon_i \rangle$ in a simulation. A change of the parameters f_M or $\overline{\upsilon}_{cri}$ in one of the systems generally results in a redistribution of the performances $\langle \upsilon_i \rangle$ and in a change of the all-systems performance υ_{tot}.

A genetic algorithm is implemented to analyze the evolution of the system parameters $(f_M^i, \overline{\upsilon}_{cri}^i)$ with $0 \leq f_M^i \leq 1$ and $0 \leq \overline{\upsilon}_{cri}^i \leq 1$. The chromosome of each system is a eight digit binary number; the first four digits give the 16 possible values of the momomer fraction f_M^i $(= 0, 1/15, 2/15, \ldots 15/15)$ and the last four digits give the critical value below which the system may release inhibitors. For the first generation the system parameters are chosen at random. The system parameter N_g, N_e, τ, τ_I, τ_{ave}, and α and the supply of substrates $\dot{S}$ remain fixed for all generations. Each generation consists of t_{sim} iterations of the model. At the end of a generation simulation the system parameters for the next generation (offspring) are set by the following procedure: (i) the performances $\langle \upsilon_i \rangle$ of the N_g systems are ranked in decreasing order. (ii) those systems whose performances are more than one standard deviation above $< \upsilon_{tot} >$ have two offspring and the rest (in decreasing order of performance) have one offspring until the population size N_g is reached.

(iii) Crossover between a random pair of offspring chromosomes occurs with a probability p_{cross}, and offspring mutate with a probability p_{mutate} by changing one of their chromosome digits. The system with the best performance is reproduced always without any change.

Figure 4 shows the results for three different values of the substrate supply rate ($\dot{S} = 1/3$, $1/2$ and $2/3$ of the full occupation value $N_e N_g/\tau$). In each case the evolution for 1500 generations is shown. The tick continuous curve shows the evolution of the mean monomer fraction $f_M = \sum f_M^i/N_g$ of the population, the dotted curve with large fluctuations shows the monomer fraction of the system with performance ranked at half way $(f_M)_{med}$, the dots indicate the monomer fraction of the systems that have released inhibitors during the simulation of a generation, and the almost horizontal tick curve gives the all-systems average production υ_{tot}. As $\dot{S}$ increases (from top to bottom panel in Fig. 4) the average monomer fraction over generations $\overline{f}_M$ decreases, the fluctuations of the monomer fraction of the half ranked system $(f_M)_{med}$ decreases, and the number of systems releasing inhibitors decreases. Note that for $\dot{S} = 2/3$ (bottom panel) $\overline{f}_M$ is small, $(f_M)_{med} \sim 0$ for the majority of generations, and there are few systems releasing inhibitors in each generation.

To estimate the general trends as $\dot{S}$ increases, we performed 5 simulations of 1500 generations for 24 different values of $\dot{S}$ (i.e. $\dot{S} = 1, 2, ..., 24$); the first 100 generation are discarded. Figure 5 shows the average monomer fraction in the five simulations. The continuous curve with error bars corresponds to the average $\overline{f}_M$ of the mean monomer fraction f_M of the population for the 1400×5 generations; the error bars correspond to one standard deviation of the mean monomer fraction f_M. The dashed curve ($\overline{f}_{M,top5}$ vs $\dot{S}$) corresponds to the same average but taking into account only the five systems with best performances in each generation; the dotted curve ($\overline{f}_{M,bot5}$ vs $\dot{S}$) corresponds to the average for the five systems with the worst performances in each generation. Note that as $\dot{S}$ increases $\overline{f}_M$ first increases reaching a maximum around $\dot{S} = 6$ and then decreases. Around the maximum $\overline{f}_{M,top5} > \overline{f}_{M,bot5}$, but the contrary occurs for low and high values of $\dot{S}$. That is, for high and low values of $\dot{S}$ the systems with high monomer fraction tend to have less offspring than systems with low monomer fraction. For very low values of $\dot{S}$ there are many idle units so that inhibitors are not able to reduce the already low system performance because the number of inhibitors released is not enough to block a significant fraction of tetramers. Then, tetrameric configurations are the best strategy to compete to bind the few available substrates.

Figure 5 shows the average $\langle \overline{\upsilon}_{cri} \rangle$ of $\overline{\upsilon}_{cri} = \sum \overline{\upsilon}_{cri}^i/N_g$ in the 5×1400

generations simulated for each of the 24 supply values. The dashed curve ($\langle \overline{v}_{cri,top5} \rangle$) and the dotted curve ($\langle \overline{v}_{cri,bot5} \rangle$) give respectively the corresponding averages for the five systems with best and worst performances. The long dashed diagonal line indicates the average production per cycle per system. As $\dot{S}$ increases the number of systems that reach the condition $\overline{v}_i < \overline{v}^i_{cri}$ decrease; so, for high values of $\dot{S}$, tetrameric configurations perform better.

Figure 6 shows the average $\langle \overline{v}_{cri} \rangle$ of $\overline{v}_{cri} = \sum \overline{v}^i_{cri}/N_g$ in the 5×1400 generations simulated for each of the 24 supply values. The dashed curve ($\langle \overline{v}_{cri,top5} \rangle$) and the dotted curve ($\langle \overline{v}_{cri,bot5} \rangle$) give respectively the corresponding averages for the five systems with best and worst performances. The long dashed diagonal line indicates the average production per cycle per system. As $\dot{S}$ increases, the number of systems that reach the condition $\overline{v}_i < \overline{v}^i_{cri}$ decrease; so, for high values of $\dot{S}$, tetrameric configurations perform better.

Note that the largest values of the dispersion of $\overline{f}_M$ occurs around $\dot{S} = 12$; as shown in the middle panel of Fig. 4. This high dispersion results from the fact that the system has two quasistable states: one of high monomeric fraction and inhibitor production, and other of low monomeric fraction and low inhibitor production. In the drug-selling gangs example, this situation corresponds to extended periods of relative calm, followed by periods of frequent aggressions.

The results shown correspond to a particular choice of model parameters, rules to generate offspring, cooperativity α, conditions to release inhibitors, etc. However, these results show that the interplay between cooperative configurations and the possibility to decrease the production of others by the release of inhibitors result in a rich variety of behaviors. In particular, the model shows that this kind of systems tends to display global evolutive transition when the supply of resources lies in between abundance and scarcity.

5 Summary and Conclusions

We have proposed a model to study the combined effect of competition, cooperation and aggression. The model consists of a set of systems, each one having a number of units that can work with various degrees of cooperation. The systems compete to acquire raw material and can pollute the system with inhibitors.

We first considered a system with four types of systems: M, D, T and MDT-systems, where M, D, and T refer to units working as Monomers, Dimers and Tetramers. We have analyzed the system production of these four types of coexisting systems as a function of the rate at which inhibitors are supplied. If the supply rate of inhibitors is stationary, the T-systems

dominate the consumption of the available resources for low rates whereas at high rates the M-systems dominate the consumption. For a non-stationary supply of inhibitors the performance of the various types of systems depends on the precise time dependence of the supply rate. We have shown results for the case when the supply of inhibitors occurs sporadically but the time average rate remain constant. We have also considered the case in which the systems can release inhibitors into the environment under prefixed conditions and at a given cost. As shown in Fig. 3, when systems are allowed to produce inhibitors, distinct regimes occur.

Finally, we have allowed for the evolution of the systems parameters and have found that the interplay between cooperative configurations and the possibility to decrease the production of others by the release of inhibitors result in a rich variety of behaviors. In particular, when the supply of resources lies in between abundance and scarcity, the model displays periods characterized by low degrees of inter-system unfair competence and high degrees of intra-system cooperation followed by periods characterized by high unfair competence and low cooperation. In the competing gangs example, this corresponds to extended periods of relative calm, followed by periods of frequent aggressions.

In the simulations shown here the supply of resources and the number and size of systems are held constant for all generations. However, self-regulatory processes can modify the number and size of the systems and the supply of resources can change in time. In the competing gangs example one expects that the number of costumers per drug-seller evolves in time taking into account the increase of desertions during high violence periods (corresponding to low number of customers per drug-seller) and increase of recruitment during low violence periods (corresponding to high number of customers per drug-seller). Other questions remain open in this study. How the trajectories of the model parameters depend on the selection rules and on the mutation rate, on the size and number of systems and on the ambient conditions? What are the spatio-temporal patterns if the model is extended to a spatially structured environment?

Acknowledgments

This work was supported by Consejo de Desarrollo Científico, Humanístico y Tecnológico of the Universidad de Los Andes, Mérida, under grants No. C-1653-09-05-B and I-1118-08-05-B.

References

[1] R. Axelrod, Amer. Political Sci. Rev. **80** (1986) 1095.

[2] R. Axelrod, *The complexity of coperation. Agent-based models of competition and collaboration* (Princeton University Press, Princeton, NY, 1997).

[3] M.A.R. de Cara, O. Pla and F. Guinea, Eur. Phys. J. **13** (2000) 413.

[4] M. Kuperman, H.S. Wio, Physica A **316** (2002) 592.

[5] G. Szabo, J. Vukov, Phys. Rev. E **69** (2004) 036107.

[6] S.A. Frank, Nature **377** (1995) 520.

[7] Thomas Pfeiffer, Stefan Schuster, Sebastian Bonhoeffer, Science **292** (2001) 504.

[8] R. C. MacLean and I. Gudelj, Nature **441** (2006) 498-501.

[9] J.P. Braselton, P. Waltman, Math. Biosci. **173** (2001) 55.

[10] S.B. Hsu, P. Waltman, Math. Biosci. **187** (2004) 53.

[11] C.B. Block, R. Block, *Street Gang Crime in Chicago*, Research in Brief, National Institute of Justice, Office of Justice Programs, U. S. Department of Justice, 1993.

[12] S.D. Levitt, S.A. Venkatesh, Quarterly Journal of Economics **115** (2000) 755.

[13] E. Pugliese, C. Castellano, M. Marsili, L. Pietronero, Eur. J. Phys. B **67** (2009) 319.

[14] E. Segel, *Enzyme kinetics: behavior and analysis of rapid equilibrium and steady-state enzyme systems* (John Wiley & Sons, New York, 1975).

[15] B. Hess, A.S. Mikhailov, Biophys. Chem. **58** (1996) 365.

[16] A.S. Mikhailov, B. Hess, J. Phys. Chem. **100** (1996) 19059.

[17] P. Stange, A.S. Mikhailov, B. Hess, J. Phys. Chem. B **102** (1998) 6273.

[18] P. Stange, D. Zanette, A.S. Mikhailov, B. Hess, Biophys. Chem. **79** (1999) 233.

[19] A.S. Mikhailov, V. Calenbuhr, 2002. *From Cells to Societies: Models of Complex Coherent Action*. Springer, Berlin, pp. 179-193.

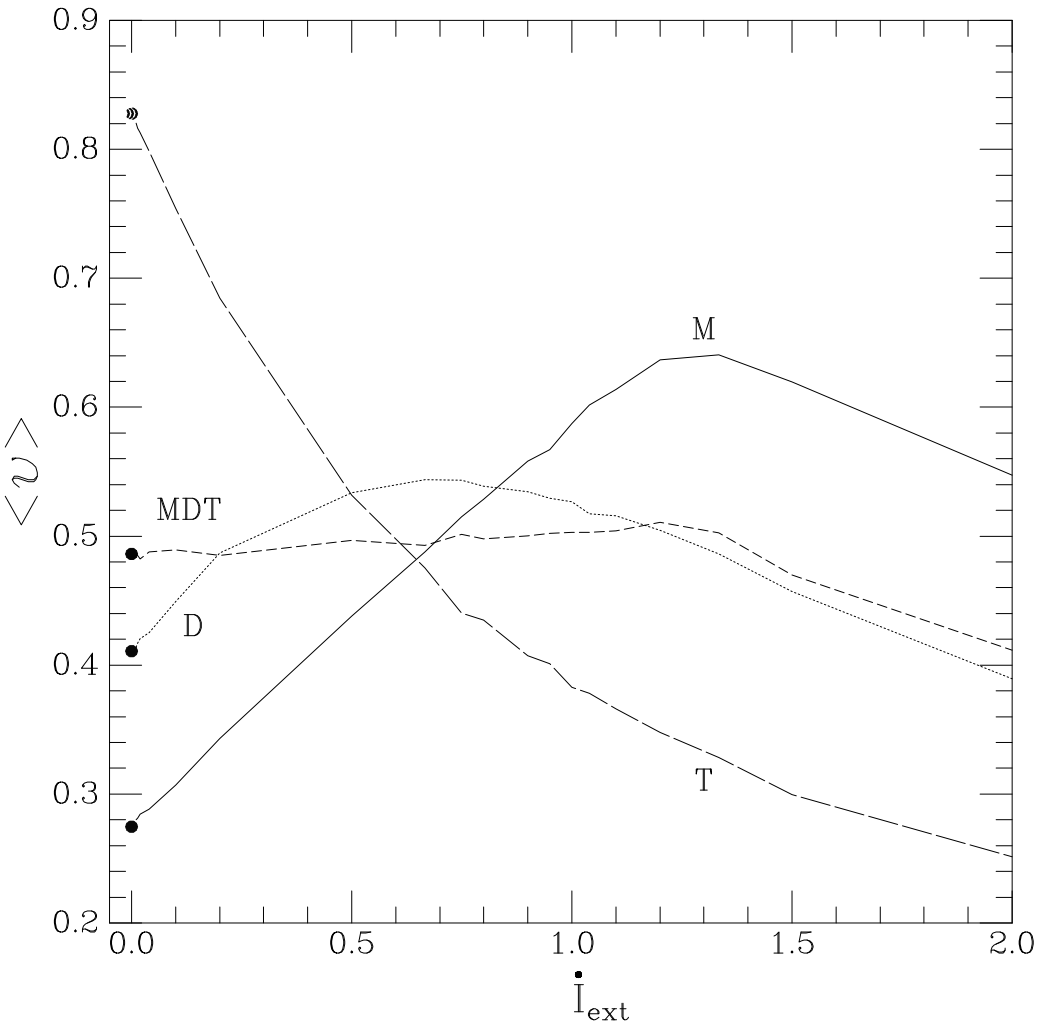

Figure 1: The average production rate $\langle \upsilon \rangle$ per unit and per duty cycle τ for the four types of systems M, D, T and MDT (see text) as function of the external supply rate of inhibitors $\dot{I}_{ext}$. The adopted parameters are $N_e = 120$, $\tau = 100$, $\tau_I = 5\tau$, $p_0 = 1/\tau$ and $\alpha = 1/4$. The substrate supply is kept fixed to $\dot{S} = 12$. A simulation for 200 τ was performed for each value of $\dot{I}_{ext}$.

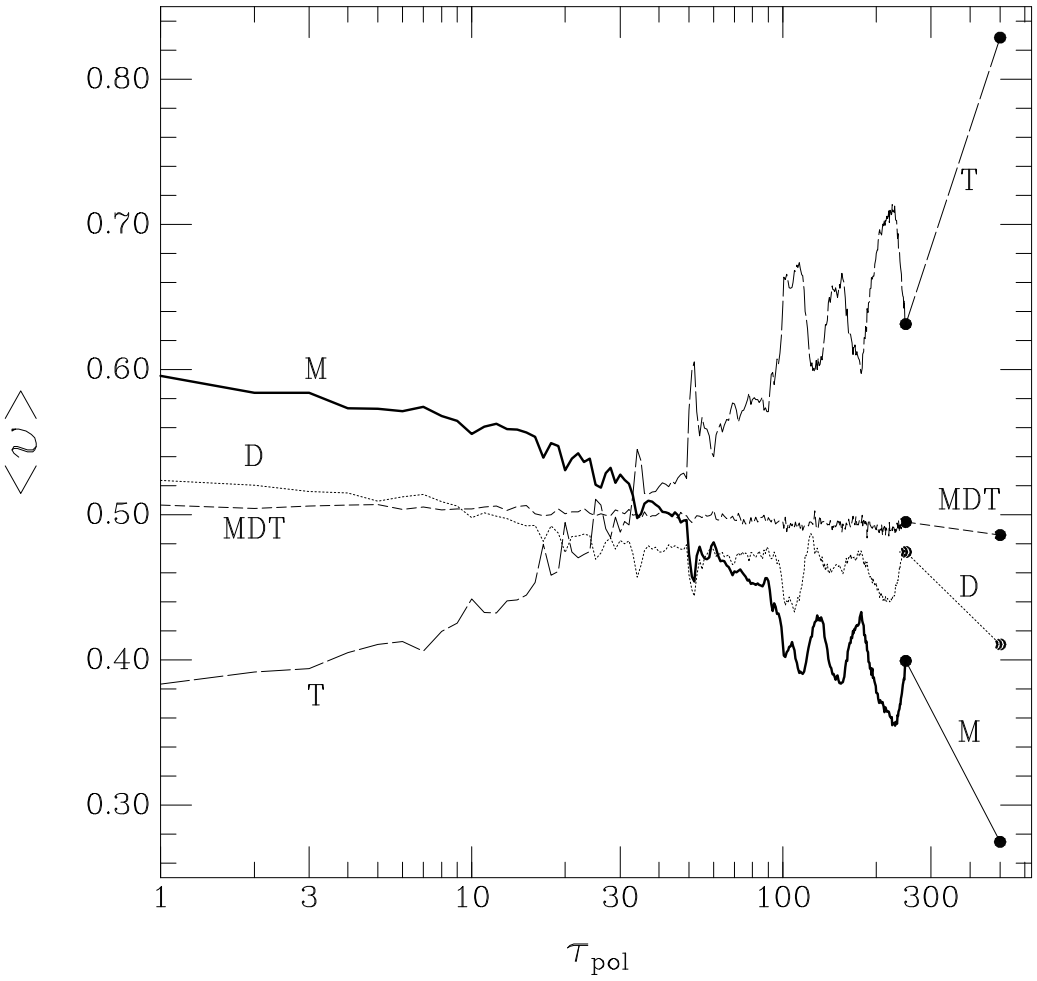

Figure 2: The average production rates for the four types of systems M, D, T and MDT as a function of unpolluted period τ_{pol} for $< \dot{I}_{ext} >= 1$. Model parameters as in Fig. 1.

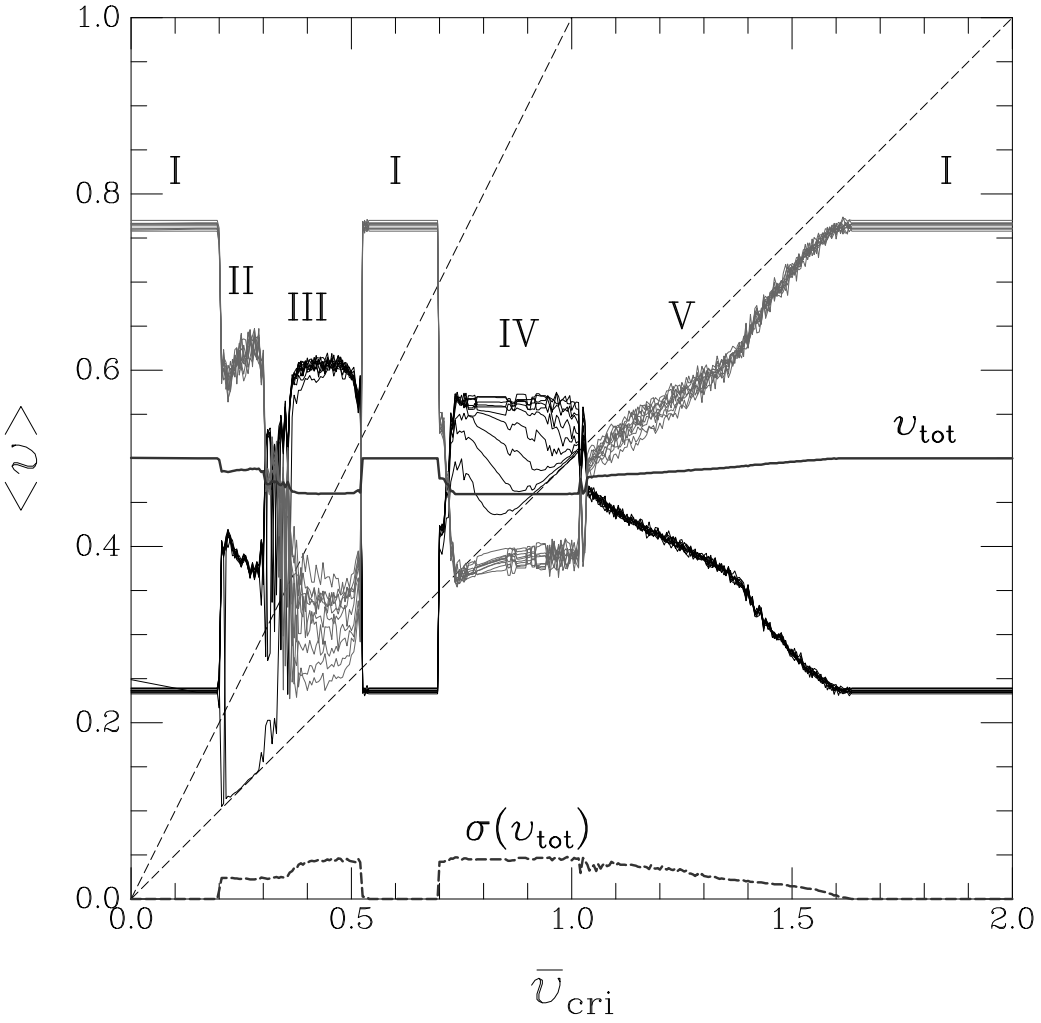

Figure 3: The average production rate $\langle v_i \rangle$ of the 20 competing systems as a function of the critical averaged production $\overline{v}_{cri}$ (see text). The model parameters are the same as in Fig. 1 and $\tau_{ave} = 10\ \tau$. Half of the systems (black curves) have their units working in isolation (M-systems) and the other half (grey curves) have their units working in cooperative arrangements of four units (T-systems). The curve labelled v_{tot} corresponds to the total average production and the curve labelled $\sigma(v_{tot})$ to its standard deviation. In the region in between the two diagonal dashed lines the condition (iii) is fullfilled. The Roman numbers label the 5 different regimes displayed by the systems.

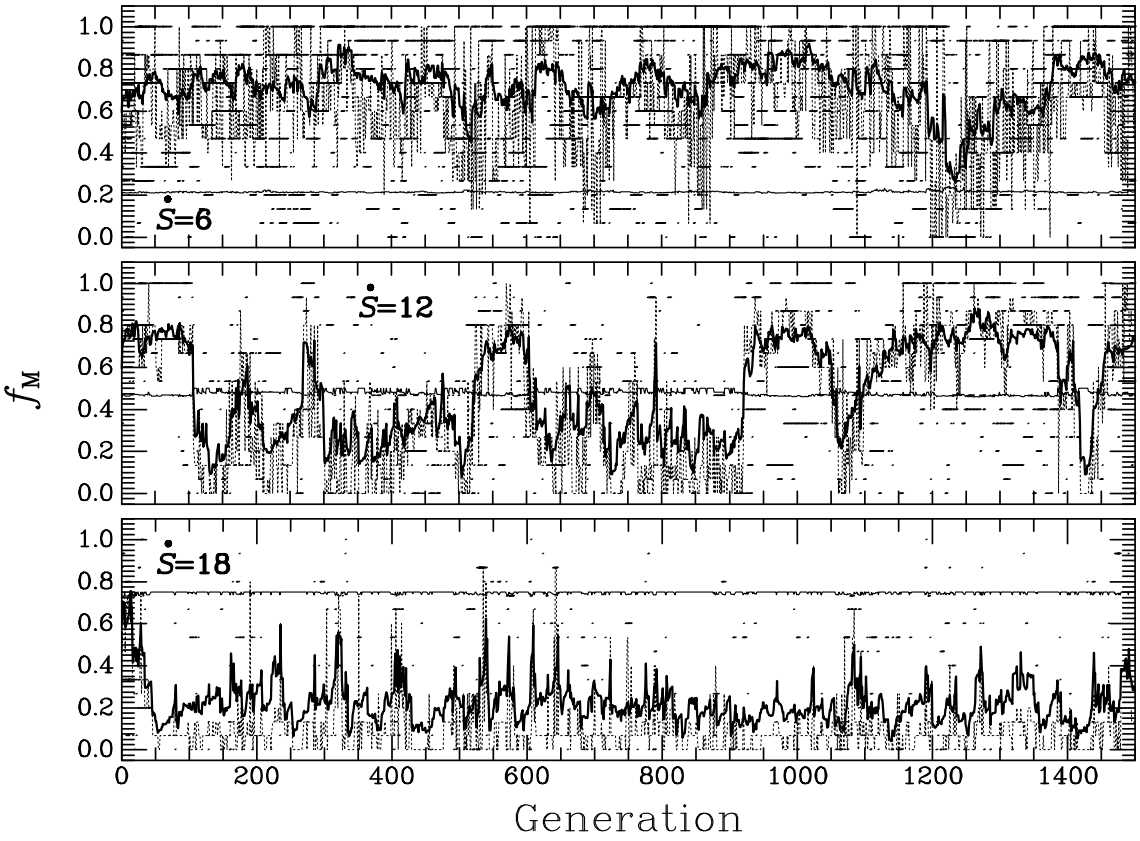

Figure 4: Evolution of the monomer fraction of the population during 1500 generations for the three labelled values of the substrate supply $\dot{S}$. The thick continuous curve shows the evolution of the monomer fraction $f_M = \sum f_M^i / N_g$ of the population, the dotted curve with large fluctuations shows the monomer fraction of the system with performance ranked at half way $(f_M)_{med}$, the dots indicate the monomer fraction of the systems that have released inhibitors during the simulation of a generation, and the almost horizontal thin curve shows the total average production υ_{tot}. The model parameters are $N_g = 20$, $N_e = 120$, $\tau = 100$, $\tau_I = 6\ \tau$, $\tau_{ave} = 10\ \tau$, $p_0 = 1/\tau$, $\alpha = 1/4$, and $p_{cross} = p_{mutate} = 0.05$.

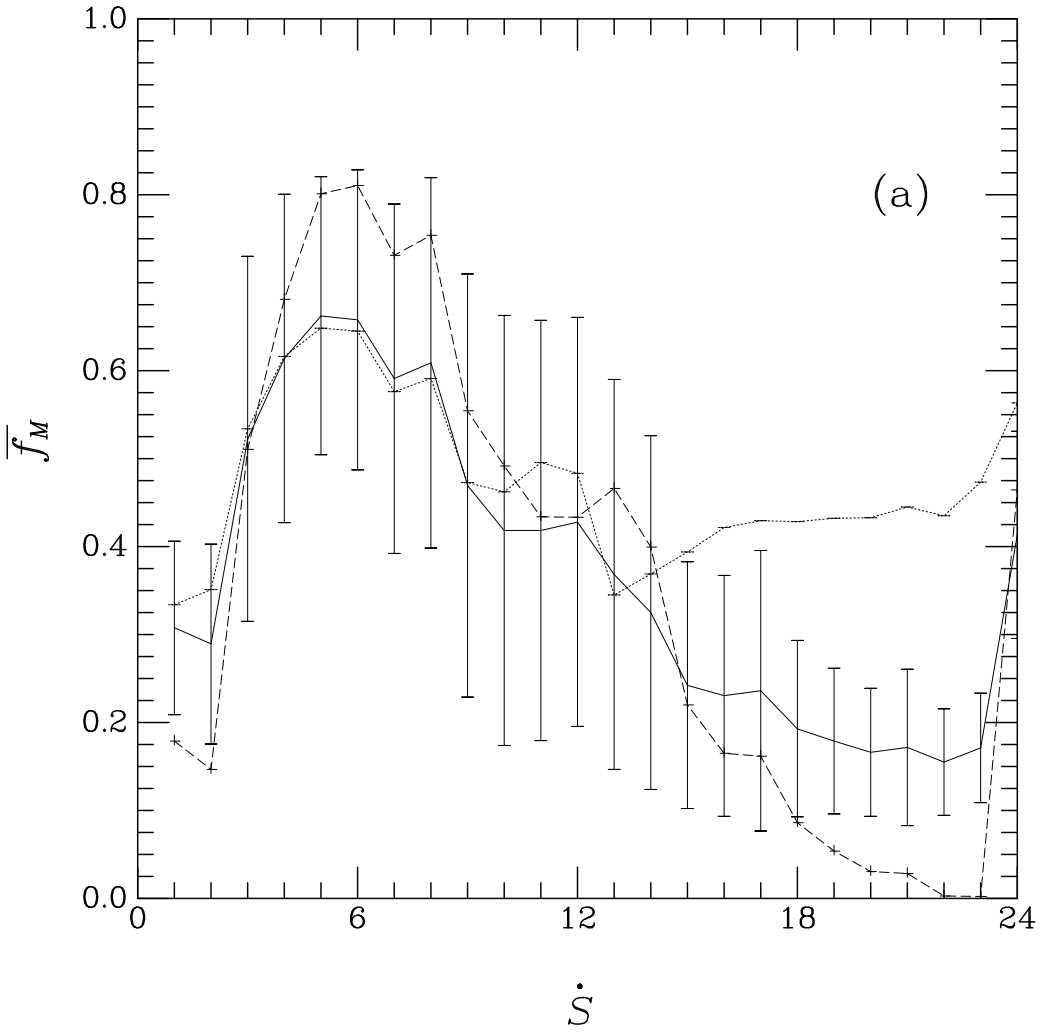

Figure 5: The average $\overline{f}_M$ of the mean monomer fraction f_M of the population for the last 1400 generations in 5 simulations as function of the supply rate $\dot{S}$. The dashed ($\overline{f}_{M,top5}$ vs $\dot{S}$) and the dotted ($\overline{f}_{M,bot5}$ vs $\dot{S}$) curves show respectively the corresponding averages for the five systems with best and worst performances in each generation. Model parameters as in Fig. 4.

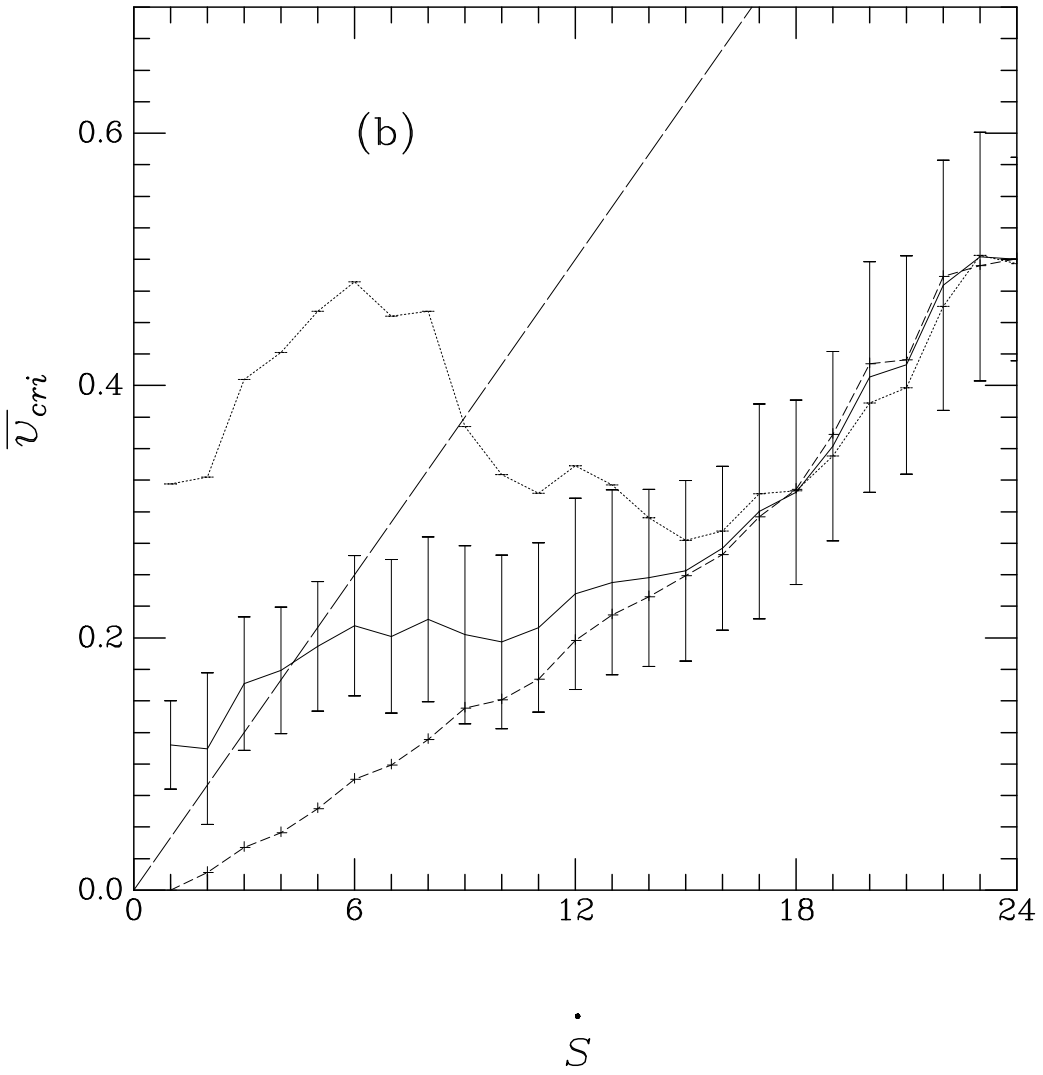

Figure 6: The average $\langle \overline{v}_{cri} \rangle$ of $\overline{v}_{cri} = \sum \overline{v}^i_{cri}/N_g$ in the 5×1400 generations as function of the supply rate $\dot{S}$. The dashed ($\langle \overline{v}_{cri,top5} \rangle$) and the dotted ($\langle \overline{v}_{cri,bot5} \rangle$) curves show respectively the corresponding averages for the five systems with best and worst performances in each generation. The long dashed diagonal line indicates the maximum average production per unit and per cycle. Model parameters as in Fig. 4.