

# Replicator - Mutator Evolutionary Dynamics

Vasyl V GAFIYCHUK<sup>†</sup> and Anatoliy K PRYKARPATSKY<sup>‡</sup>

<sup>†</sup> *Institute for Applied Problems of Mechanics and Mathematics, National Academy of Sciences, Naukova St, 3 b, Lviv 79601, Ukraine*  
*E-mail: vagaf@yahoo.com*

<sup>‡</sup> *Dept. of Applied Mathematics at the AGH University of Science and Technology Cracow, Poland, and Institute for Applied Problems of Mechanics and Mathematics National Academy of Sciences, Naukova St, 3 b, Lviv 79601, Ukraine*  
*E-mail: prykanat@cybergal.com, pryk.anat@ua.fm*

*Received September 29, 2003; Accepted February 02, 2004*

## Abstract

We consider the general properties of the quasispecies dynamical system from the standpoint of its evolution and stability. Vector field analysis as well as spectral properties of such system have been studied. Mathematical modeling of the system under consideration has been performed.

## 1 Introduction

This article is devoted to the theoretical study of a self-organization problem of an ensemble of interacting species and to developing a model of a naturally fitted coevolving ecosystem. It is well known since Eigen's work on replicating molecules [1] that the quasispecies approach is very fruitful for modeling the fundamental behavior of evolution (See, for example [2, 4, 5, 6, 7]). Despite a huge amount of papers devoted to this problem, biological evolution is so complex that we are still far from understanding real biological processes of self-organization. The matter is that real experiments and obtained data on the evolution of primitive systems need a comprehensive theoretical description that would allow one to explain these data and put them into a proper context. In this case the central place is given to the investigation of intrinsic properties of a nonlinear system which describes the system evolution. We direct our attention to Eigen's approach and will establish some new but very important mathematical properties of the system which could be useful for modeling many co-evolving ecosystems. In part we will use an approach devised in [8] for describing similar systems evolution.

We start our analysis of quasispecies dynamics in molecular evolution with a discussion of the background of modeling aspects which appear to be very important for further study. The first principle of modeling such types of dynamics is based on a probability consideration of molecular replicator processes, which are well described by the resulting quasispecies concentration vector  $x \in [0, 1]^n$ , where  $n \in \mathbb{Z}_+$  is a number of species, being

normalized by the full probability condition  $\sum_{j=1}^n x_j = 1$ . The latter condition is fundamental to ensuring the full molecular number concentration and will play, in what follows, an important role. Moreover, the set of such vectors  $x \in E^n$  in the Euclidean space  $E^n$  forms the algebraic simplicial submanifold  $S_{n-1} \subset E^n$  on which in reality the studied dynamics holds. For it to be described analytically, it is natural to consider a representative symmetric matrix  $P \in \text{End}E^n$ , such that  $P = f \otimes f$ ,  $\langle f, f \rangle = 1$ , for some vector  $f \in E^n$  modeling the resulting replicator dynamics and simultaneously ensuring two constraints: life on the simplex  $S_{n-1}$  and conservation of the initial molecular system information during its replicator evolution. In general, such a dynamics can be represented in the following form:

$$P(t) = U(t)P(0)V^{-1}(t),$$

with evolution parameter  $t \in \mathbb{R}$ , for some invertible mappings  $V, U : \mathbb{R} \rightarrow GL(E^n)$ , where  $P(0) \in \text{End}E^n$  is an initial molecular dynamics state. Below we consider the symmetric replicator dynamics, whose inverse replicator process matrix  $V \in GL(E^n)$  has to coincide with the forward replicator process matrix  $U \in GL(E^n)$ , that is  $U \equiv V$  holds. As a result, our dynamics is representable as

$$P(t) = U(t)P(0)U^{-1}(t) \tag{1.1}$$

for all moments of time  $t \in \mathbb{R}$ . Assuming smooth dependence of (1.1) on  $t \in \mathbb{R}$ , one easily derives that the following Lax type dynamics

$$dP/dt = [\Lambda, P] \tag{1.2}$$

holds, where by definition, the matrix  $\Lambda = dU/dtU^{-1}$ . For the matrix  $P \in \text{End}E^n$  to conserve its symmetry, the matrix  $\Lambda \in \text{End}E^n$  must be evidently skew-symmetric, that is  $\Lambda = -\Lambda^*$  in  $E^n$ .

We return now to analyzing the intrinsic structure of our matrix  $P \in \text{End}E^n$ , modeling the replicator dynamics under consideration. From the general form (1.2) one sees that our dynamics possesses a priori so called trace-invariants, namely, all quantities  $SpP^m$  are such for any  $m \in \mathbb{Z}$ , where  $Sp : \text{End}E^n \rightarrow \mathbb{R}$  is the standard matrix trace operator. This fact may be naturally used within our modeling approach. Consider a representative vector  $f \in E^n$  in the following form:  $f = \{\sqrt{x_i} \in \mathbb{R} : i = \overline{1, n}\}$ . Then, the condition  $\langle f, f \rangle = \sum_{j=1}^n x_j = 1$  is satisfied due to the equality  $SpP = \sum_{j=1}^n x_j$  and the fact that the latter quantity is conserved. Since  $P^2 = P$ , all of the other invariants are the same, introducing into the dynamics no additional constraint. Thus, we have naturally imbedded our molecular replicator dynamics initially in the space of concentration vectors  $x \in S_{n-1} \subset E^n$  into the matrix phase space  $\mathcal{P} \ni P$  of symmetric projector mappings of co-dimension one, that is  $P = P^*$  and  $\dim(\text{Im}P) = 1$ . The latter phase space  $\mathcal{P}$  is a Grassmann manifold possessing many important intrinsic mathematical properties, which we shall use to obtain a deeper analysis of the molecular replicator dynamics.

Consider an evolution equation modeling our molecule replicator dynamics in the general matrix Lax type form (1.2), where  $\Lambda(x) = \{\Lambda_{jk} : j, k = \overline{1, n}\}$  is a certain matrix

depending on variables  $x = \{x_i \in \mathbb{R}_+ : i = \overline{1, n}\}$  and  $P = \{\sqrt{x_j x_k} : j, k = \overline{1, n}\}$ . In this case as the matrix  $P$  symmetric, it is evident that the matrix  $\Lambda$  must be skew-symmetric. Below we will focus on processes similar to quasispecies dynamics considered in [1, 2]. Since we will consider  $x \in [0, 1]^n$  as a concentration vector of quasispecies, it has to be nonnegative for all time, so the system (1.1) now is defined on the nonnegative orthant  $\mathbb{R}_+^n = \{x \in \mathbb{R}^n : x_i \geq 0\}$ .

Let us now suppose a system evolves due to the Eigen positive feedback associated with the terms corresponding to the increase of concentrations  $x_j, j = \overline{1, n}$ :

$$dx_j/dt = \sum_{k=1}^n a_{jk} x_k R_k(\mathbf{x}) - F_j(x), \tag{1.3}$$

where an element  $a_{jk}$  expresses the probability that a molecule  $k$  copies into a molecule  $j$  and  $F_j(x)$  denotes the corresponding inverse sink term. In turn the element  $a_{jj}$  gives the probability that a molecule  $j$  replicates faithfully,  $R_k(\mathbf{x})$  is the fitness of the molecules of  $k$  type and characterizes its replication rate.

We have to determine the sink term  $F_j(x), j = \overline{1, n}$ , in order to fulfill the governing condition on the dynamics determined on the  $(n - 1)$  dimensional simplex

$$S_{n-1} = \left\{ x \in \mathbb{R}_+^n : \sum_{i=1}^n x_i = 1 \right\}. \tag{1.4}$$

In order to get the corresponding source term in the equation (1.3) let us determine elements  $\Lambda_{jk}, j, k = \overline{1, n}$  of the skew symmetric matrix  $\Lambda$  in (1.1) as

$$\Lambda_{jk} = \frac{1}{2} \left[ a_{jk} \sqrt{x_k/x_j} R_k(\mathbf{x}) - a_{kj} \sqrt{x_j/x_k} R_j(\mathbf{x}) \right], \tag{1.5}$$

It is easy to observe here that there exists the matrix  $\bar{\Lambda} = \{\frac{1}{2} a_{jk} \sqrt{x_k/x_j} R_k(\mathbf{x}) : j, k = \overline{1, n}\}$ , such that  $\Lambda = \bar{\Lambda} - \bar{\Lambda}^*$ . Substituting expression (1.5) into (1.1) we get that  $F_j(\mathbf{x}) = x_j R_j(\mathbf{x}) \sum_{k=1}^n a_{kj}, j = \overline{1, n}$ . As a result the governing equation for the quasispecies dynamics takes the form:

$$\begin{aligned} dx_j/dt &= \sum_{k=1}^n a_{jk} x_k R_k(\mathbf{x}) - \sum_{k=1}^n \sqrt{x_j x_k} a_{kj} \sqrt{x_j/x_k} R_j(\mathbf{x}) \\ &= \sum_{k=1}^n a_{jk} x_k R_k(\mathbf{x}) - x_j R_j(\mathbf{x}) \sum_{k=1}^n a_{kj} \\ &= \sum_{k \neq j}^n (a_{jk} x_k R_k(\mathbf{x}) - x_j R_j(\mathbf{x})) a_{kj} \end{aligned} \tag{1.6}$$

It is easy to see after summing up equations (1.6) that

$$\sum_j^n dx_j/dt = 0,$$

meaning in this case that the evolution dynamics actually occurs on the simplex (1.4).

It should be mentioned that the system (1.6) is somewhat different from systems considered in a set of papers [2, 3, 4, 5, 6, 7] mainly by sink terms. But only such a form of the sink term ensures the important simplex condition  $\sum_j^n x_j = 1$  for all  $t \in \mathbb{R}$ , without additional constraints involved in the model.

Note here that, the system (1.6) is really representable in the evolution form (1.1) that can be checked easily, and the matrix  $P \in \text{End}\mathbb{R}^n$  is a one-dimensional symmetric projector, that is  $P^2 = P$ ,  $P^* = P$  for  $t \in \mathbb{R}$ , which is important for our further study of the structure of the vector field (1.1) on the corresponding projector matrix manifold  $\mathcal{P}$  [10, 11]. The component vector form of the system (1.6) can be also represented as

$$d\mathbf{x}/dt = AR(\mathbf{x})\mathbf{x} - BR(\mathbf{x})\mathbf{x}. \quad (1.7)$$

with  $A = \{a_{jk} : j, k = \overline{1, n}\}$ ,  $B = \text{diag} \left\{ \sum_{k=1}^n a_{kj} : j = \overline{1, n} \right\}$ , and  $R(\mathbf{x})$ ,  $\mathbf{x} \in S_{n-1}$  being a fitness matrix expression. If the fitness matrix  $R(\mathbf{x})$ ,  $\mathbf{x} \in S_{n-1}$  is diagonal, that is  $R = \bar{R} = \text{diag} \{ \bar{R}_j : j = \overline{1, n} \}$  and does not depend on  $\mathbf{x} \in S_{n-1}$ , the system (1.7) evidently will be linear. Thereby the solution of such a system can be obviously represented as

$$\mathbf{x}(t) = \mathbf{x}(0) \exp[(A - B)\bar{R}]t,$$

where  $x(0) \in S_{n-1}$  is an initial concentration of population of each type.

## 2 Vector field analysis: imbedding into gradient structure

Since our system dynamic flow (1.2) in reality lives on the projector matrix of the Grassmann manifold  $\mathcal{P} \ni P$  [12], all its properties can be naturally extracted from a deeper analysis of its structure on this manifold. In particular, it is important to know where the vector field (1.6) admits the structure of gradient type endowed with some Lyapunov function, ensuring the existence of stable states on the compact Grassmann manifold  $\mathcal{P}$ . In order to study the gradient field structure of the flow (1.1) if any on the projector matrix manifold  $\mathcal{P} \ni P$  let us consider a smooth functional  $\Psi : \mathcal{P} \rightarrow \mathbb{R}$ , whose usual variation is given as

$$\delta\Psi(P) := \text{Sp}(D\delta P) \quad (2.1)$$

with a symmetric matrix  $D \in \text{End}E^n$  and  $\text{Sp} : \text{End}E^n \rightarrow \mathbb{R}^1$  being as before the standard matrix trace. Taking into account the natural metrics on  $\mathcal{P}$ , we consider the projection  $\nabla_\varphi\Psi$  of the usual gradient vector field  $\nabla\Psi$  upon the tangent space  $T(\mathcal{P})$  under the following conditions:

$$\varphi(X; P) := \text{Sp}(P^2 - P, X) = 0, \quad \text{Sp}(\nabla\varphi, \nabla_\varphi\Psi) |_{\mathcal{P}} = 0, \quad (2.2)$$

holding on  $\mathcal{P}$  for all  $X \in \text{End}\mathbb{R}^n$ . The first condition is evidently equivalent to  $P^2 - P = 0$ , that is  $P \in \mathcal{P}$ . Thereby we can formulate the following result.

**Statement 1.** *The functional gradient  $\nabla_\varphi\Psi(P)$ ,  $P \in \mathcal{P}$  under the condition (2.2) admits the following commutator Lax type representation:*

$$\nabla_\varphi\Psi(P) = [\Lambda, P]$$

with  $\Lambda \in \text{end}E^n$  being a skew-symmetric matrix satisfying the commutator equation

$$\Lambda = [D, P],$$

where  $D$  is a symmetric matrix.

Consider the projection of the usual gradient  $\nabla\Psi(P)$  upon the tangent space  $T(\mathcal{P})$  of the Grassmann manifold  $\mathcal{P}$  with  $P \in \mathcal{P}$  imbedded into  $\text{End}E^n$ :

$$\nabla_\varphi\Psi(P) = \nabla\Psi(P) - \nabla\varphi(Q; P), \quad (2.3)$$

where  $Q \in \text{End}E^n$  is some still unknown matrix. Taking into account the conditions (2.2), we find that

$$\begin{aligned} \nabla_\varphi\Psi(P) &= D - Q - P(D - Q) - (D - Q)P + PD + DP \\ &= PD + DP + 2PQP, \end{aligned} \quad (2.4)$$

where we made use of the relationships

$$\nabla_\varphi\Psi(P) = D - Q + PQ + QP$$

and

$$P(D - Q) + (D - Q)P + 2PQP = D - Q.$$

Now one can easily see from (2.4) and the second condition in (2.3), that

$$PQP = -PDP \quad (2.5)$$

for all  $P \in \mathcal{P}$ , giving rise to the final result

$$\nabla_\varphi\Psi(P) = PD + DP - 2PDP, \quad (2.6)$$

coinciding exactly with the commutator  $[[D, P], P]$ . Since the matrix

$$\Lambda = \bar{\Lambda} - \bar{\Lambda}^* = DP - PD$$

one gets right away that

$$\bar{\Lambda} = DP + S \quad (2.7)$$

with  $S = S^* \in \text{End}E^n$ . If there exist matrices  $D$  and  $S \in \text{End}E^n$  such that (2.7) is satisfied, then our model will be evidently of gradient type. In particular, the matrix  $D \in \text{End}E^n$  found from (2.7) must satisfy the Volterra criteria  $D'(P) = D'^*(P)$  for any  $P \in \mathcal{P}$  imbedded into  $\text{End}E^n$ .

It should be noted here that the Grassmann manifold  $\mathcal{P}$  is also a symplectic manifold [10, 11] whose canonical symplectic structure is given by the expression:

$$\omega^{(2)}(P) := \text{Sp}(PdP \wedge dPP), \quad (2.8)$$

where  $d\omega^{(2)}(P) = 0$  for all  $P \in \mathcal{P}$ , and the differential 2-form (2.8) is non-degenerate [10, 12] upon the tangent space  $T(\mathcal{P})$ .

Let us assume now that  $\xi : \mathcal{P} \rightarrow \mathbb{R}$  is an arbitrary smooth function on  $\mathcal{P}$ . Then the Hamiltonian vector field  $X_\xi : \mathcal{P} \rightarrow T(\mathcal{P})$  on  $\mathcal{P}$  generated by this function subject to the symplectic structure (2.8) is given as follows:

$$X_\xi = [[D_\xi, P], P] \quad (2.9)$$

where  $D_\xi \in \text{End}E^n$  is a certain symmetric matrix. The vector field  $X_\xi : \mathcal{P} \rightarrow T(\mathcal{P})$  generates on the compact manifold  $\mathcal{P}$  the flow

$$dP/dt = X_\xi(P), \quad (2.10)$$

which is defined globally for all  $t \in \mathbb{R}$ . This flow by construction is evidently compatible with the projector condition  $P^2 = P$ . This means in particular that the condition

$$-X_\xi + PX_\xi + X_\xi P = 0 \quad (2.11)$$

holds on  $\mathcal{P}$ . Thus, it is possible to formulate the following result. Dynamical system (1.2) being considered on the Grassmann manifold  $\mathcal{P}$  can be Hamiltonian that makes it possible to formulate the following statement.

**Statement 2.** *A gradient vector field of the form (2.9) on the Grassmann manifold  $\mathcal{P}$  is Hamiltonian with respect to the canonical symplectic structure (2.8) and a certain Hamiltonian function  $\xi : \mathcal{P} \subset \text{end}E^n \rightarrow \mathbb{R}$ , satisfying conditions*

$$\begin{aligned} \nabla\xi(P) &= [D_\xi, P] - Z + PZ + ZP, \\ \nabla\xi'(P) &= \nabla\xi'^*(P), \quad D_\xi = D \end{aligned}$$

for some matrix  $Z \in \text{End}E^n$  for all  $P \in \mathcal{P} \subset E^n$ .

Consider now the  $(n-1)$ -dimensional simplex  $S_{n-1}$  as a Riemannian space

$$M_g^{n-1} = \{S_{n-1}\}$$

with the metric

$$ds^2(x) := d^2\Psi|_{\mathcal{P}}(x) = \sum_{i,j=1}^n g_{ij}(x) dx_i dx_j|_{\mathcal{P}},$$

where for  $i, j = \overline{1, n}$ ,  $g_{ij}(x) = \frac{\partial^2 \Psi(x)}{\partial x_i \partial x_j}$ ,  $\sum_{i=1}^n x_i = 1$ .

Relative to the metrics on  $M_g^{n-1}$  we can calculate the gradient  $\nabla_g \Psi$  of the function  $\Psi : \mathcal{P} \rightarrow \mathbb{R}$  and set on  $M_g^{n-1}$  the gradient vector field

$$dx/dt = \nabla_g \Psi(x), \tag{2.12}$$

with  $x \in M_g^{n-1}$ ; that is, the condition  $\sum_{i=1}^n x_i = 1$  is satisfied a priori. Having calculated (2.12), we can formulate the next statement.

**Statement 3.** *The gradient vector fields  $\nabla_{\varphi} \Psi$  on  $\mathcal{P}$  and  $\nabla_g \Psi$  on  $M_g^{n-1}$  are equivalent, or in another words, the vector fields*

$$dx/dt = \nabla_g \Psi(x) \tag{2.13}$$

and

$$dP(x)/dt = [[D(x), P(x)], P(x)] \tag{2.14}$$

generate the same flow on  $M_g^{n-1}$ .

As a result from the Hamiltonian property of the vector field  $\nabla_{\varphi} \Psi$  on the Grassmann manifold  $\mathcal{P}$  we obtain result.

**Statement 4.** *The gradient vector field  $\nabla_g \Psi$  (2.12) on the metric space  $M_g^{n-1}$  where  $n = 2m + 1$  is Hamiltonian with respect to the non-degenerate symplectic structure*

$$\omega_g^{(2)}(x) := \omega^{(2)}(P)|_{M_g^{n-1}} \tag{2.15}$$

for all  $x \in M_g^{2m}$  with a Hamiltonian function  $\xi_{\psi} : M_g^{2m} \rightarrow \mathbb{R}$ , where  $\xi_{\psi} := \xi|_{M_g^{n-1}}$ ,  $\xi : \mathcal{P} \rightarrow \mathbb{R}$  is the Hamiltonian function of the vector field  $X_{\xi}$  (2.9) on  $\mathcal{P}$ . Otherwise, if  $n \in \mathbb{Z}_+$  is arbitrary our two flows (2.13) and (2.14) are only Poissonian on  $\mathcal{P}$ .

### 3 Spectral properties

Consider the eigenvalue problem for a matrix  $P \in \mathcal{P}$ , depending on the evolution parameter  $t \in \mathbb{R}$ :

$$P(t)f = \lambda f, \tag{3.1}$$

where  $f \in \mathbb{R}^n$  is an eigenfunction, and  $\lambda \in \mathbb{R}$  is a real eigenvalue since  $P^* = P$ , i.e. matrix  $P \in \mathcal{P}$  is symmetric. It is seen from the expression  $P^2 = P$  that  $\text{spec}P(t) = \{0, 1\}$  for all  $t \in \mathbb{R}$ . Moreover, taking into account the invariance of  $\text{Sp}P = 1$  we can conclude that only one eigenvalue of the projector matrix  $P(t)$ ,  $t \in \mathbb{R}$ , is equal to 1, all others being equal to zero.

In general, the image  $\text{Im}P \subset \mathbb{R}^n$  of the matrix  $P(t) \in \mathcal{P}$  for all  $t \in \mathbb{R}$  is  $k$ -dimensional,  $k = \text{rank}P$ , and the kernel  $\text{Ker}P \subset \mathbb{R}^n$  is  $(n - k)$ -dimensional, where  $k \in \mathbb{Z}_+$  is a constant, not depending on  $t \in \mathbb{R}$ . As a consequence we establish that at  $k = 1$  there exists a unique vector  $f_0 \in \mathbb{R}^n / (\text{Ker}P)$  for which

$$Pf_0 = f_0. \quad (3.2)$$

Due to the statement above for a projector  $P \in \text{End}E^n$  we can write down the following expansion in the direct sum of mutually orthogonal subspaces:  $E^n = \text{Ker}P \oplus \text{Im}P$ .

Take now  $f_0 \in \mathbb{R}^n$  satisfying the condition (3.2). Then in accordance with (2.13) the next statement holds.

**Statement 5.** *The vector  $f_0 \in E^n$  satisfies the following evolution equation:*

$$df_0/dt = [D(x), P(x)] f_0 + C_0(t)f_0, \quad (3.3)$$

where  $C_0 : \mathbb{R} \rightarrow \mathbb{R}$  is a certain function depending on the choice of the vector  $f_0 \in \text{Im}P$ .

At some value of the vector  $f_0 \in \text{Im}P$  we can evidently ensure the condition  $C_0 \equiv 0$  for all  $t \in \mathbb{R}$ . Moreover one easily observes that for the matrix  $P(t) \in \mathcal{P}$  one has [11] the representation  $P(t) = f_0 \otimes f_0$ ,  $\langle f_0, f_0 \rangle = 1$ , giving rise to the system (1.6) if  $f_0 := \{\sqrt{x_j} \in \mathbb{R}_+ : j = \overline{1, n}\} \in E^n$ .

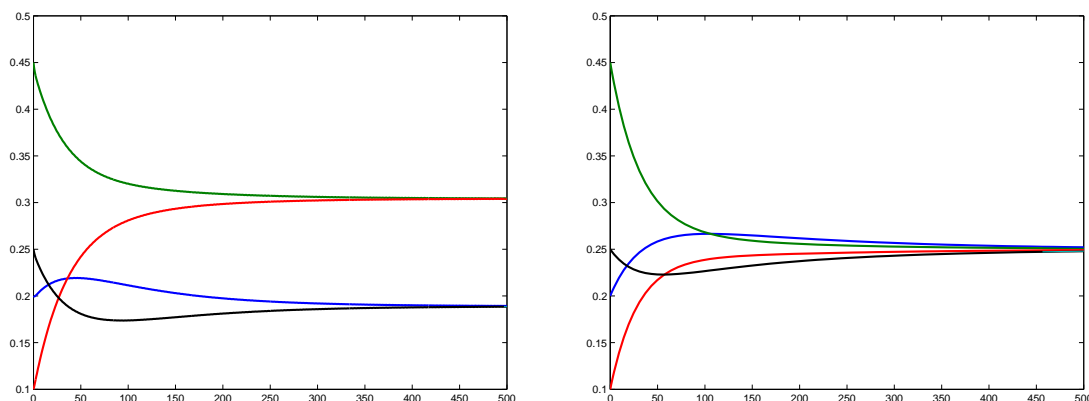
## 4 Discussion of the quasispecies dynamics

Quasispecies dynamics is very interesting for researchers and there are a lot of papers devoted to its computer simulation [2, 4, 5, 6, 7]. In order to single out the characteristic features of the model stated above, let us write down the model typically used for quasispecies dynamics. In vector form such a model can be written as

$$d\mathbf{x}/dt = (AR - \langle R \rangle)\mathbf{x} \quad (4.1)$$

where  $R = \text{diag}\{\bar{R}_j : j = \overline{1, n}\}$  is the diagonal matrix with the Malthusian fitness values,  $\langle R \rangle := \sum_{i=1}^n \bar{R}_i x_i$ . The diagonal elements  $a_{jj}$ ,  $j = \overline{1, n}$ , of the matrix  $A = \{a_{jk} : j, k = \overline{1, n}\}$  correspond to the self-replication process, and nondiagonal - to mutation. In order to fulfill the simplex condition we have to put [2, 4, 5] for each column  $a_{jj} = 1 - \sum_{k=1}^n a_{kj}$ ,  $j = \overline{1, n}$ , hence the column sum will give rise to unity. In contrast to (4.1) in our model (1.6) we do not require such a constraint in order to satisfy the simplex condition.





**Figure 1.** Quasispecies dynamics as a results of computer simulation of the equation (4.1) - a and our model (1.6) - b. Initial conditions:  $\mathbf{x} = (0.2; 0.45; 0.1; 0.25)^T$

The mutation matrix  $A$  in our model has to be nondiagonal. The choice of matrix  $A$  specifies the generation and recombination rates among different molecules in chemical process. A very interesting application of the model stated in the papers [2, 4, 5] is for describing quasispecies evolution. In the framework of this approach the bio-molecules are considered as a bitstrings of length  $L$ . In this case we have  $2^L$  different molecules. As a result the mutation matrix  $A$  is of huge dimension. If we consider bio-molecules with  $L \gg 1$  this approach is not practically feasible. In this case some simplification can be achieved when certain macromolecules are grouped together in such a way that the number of independent variables is reduced to  $L+1$  [9]. In the framework of this approach a certain sequence (master sequence) is chosen beforehand and all other sequences are grouped into error classes, according to their Hamming distance from the chosen one. Sequences which have the same Hamming distance from the master one comprise a one error class. Such reduction of the dimensionality makes it possible to run computer simulations that reveal some features inherent in a real biological process. In this case we can write down the nondiagonal elements  $a_{jk}$  of mutation matrix  $A$  as the probability of mutation at string  $k$  to string  $j$

$$a_{jk} = q^{L-H_{jk}}(1-q)^{H_{jk}} \quad (4.2)$$

where  $q$  is the probability that a particular locus of the chain is copied correctly into the next generation, i.e. the probability of replication,  $(1-q)$  is the probability of mutation,  $L$  is a bit string length, and  $H_{jk}$  is the Hamming distance between string  $j$  and  $k$  and is defined as the number of positions, in which the two sequences differ. In order to note the difference between two models we simulate our model for simplest case  $L = 3$ . The plot of computer simulation with matrix given by formulae (4.2) is presented in Fig.1 (a, b). We can easily see that even with the same initial conditions and matrix replication mutation matrix  $A$  the results of the evolution process for the two models is quite different.

Let us find a stationary frequency distribution in the framework of the derived model (1.6). If we set the right hand side of the equation (1.6) to zero we get for constant fitnesses the next expression

$$x_j = \frac{\sum_{k \neq j}^n a_{jk} x_k \bar{R}_k}{\bar{R}_j \sum_{k \neq j}^n a_{kj}}. \quad (4.3)$$

Analyzing the expression (4.3) one can see that the values of the frequencies do not depend on diagonal elements  $a_{jj}$ ,  $j = \overline{1, n}$ , and the replicator process in this model is determined only by the input given by nondiagonal elements  $a_{kj}$ ,  $k \neq j = \overline{1, n}$ , which is natural from the biological point of view. If the fitness value of some species  $\bar{R}_j$  is much greater than all of the rest fitnesses, the values of  $x_j$  will be chosen less than all the others. In this case the results obtained, for example for a single peak model landscape in the framework of (4.1), which lead to so called “phase transition” and vanishing of the corresponding species, called master species if  $a_{jj} < 1/\bar{R}_j$  may be interpreted in another way [2, 4, 5].

The equation (4.3) can be evidently written as a fixed point problem  $x = \tilde{A}x$ , where  $\tilde{A} = \{a_{jk} \bar{R}_k / (\bar{R}_j \sum_{k \neq j}^n a_{kj}) : k, j = \overline{1, n}\}$  with diagonal elements  $a_{jj} := 0$ ,  $j = \overline{1, n}$ . So, its solution exists if the matrix  $\tilde{A}$  possesses the eigenvalue  $\lambda = 1$ , or the determinant equation  $\det(\mathbf{1} - \tilde{A}) = 0$ , where  $\mathbf{1}$  is the identity matrix, is satisfied identically. But this is true for any matrix  $A$  and arbitrary parameters  $\bar{R}_j \in \mathbb{R}_+$ ,  $j = \overline{1, n}$ . If this equation is not satisfied, the process of reducing some amount of species from the system happens, that is some of frequencies will become exactly zero and the resulting system remains to live on a simplex of lower dimension. The latter situation can be considered as a “phase reduction” naturally related with some threshold values of frequencies found from the determinant equation written above, linked with the notion of “phase transition” used in the above cited articles. This behavior is of great interest for diverse applications since it can be interpreted as a type of simplex reduction  $S_{n-1} \rightarrow S_{n-l}$  for  $1 < l < n$ , taking place in some kinds of replicator dynamics models. Taking into account this aspect of these models and their importance in studying biological replicator and other models, we plan to study them in more detail in the near future.

**Acknowledgements.** The authors are deeply indebted to their friends, in particular Prof. Z. Peradzhynski from Warsaw University, professors J. Myjak, S. Brzywczy and B. Choczewski from AGH University of Science and Technology of Krakow for fruitful and constructive discussions of the replicator dynamics models considered in this paper. The work of A.P. was in part financed through a local WMS AGH grant for which he expresses his thanks.

## References

- [1] Eigen M, Self-organization of matter and the evolution of biological macromolecules, *Naturwissenschaften* **58** (1971), 465–523.
- [2] Eigen M and Schuster P, Stages of Emerging Life - Five Principles of Early Organization, *J.Mol.Evol.* **19** (1982), 47–61.

- 
- [3] Eigen M, McCaskill J and Schuster P, Molecular Quasi-Species, *J.Phys. Chem.* **92** (1988), 6881–6891.
- [4] Luque B, An introduction to Physical theory of Molecular Evolution, *Central European Journal of Physics* **3** (2003), 516–555.
- [5] Schuster P, Evolution at molecular resolution, in: Leif Matsson, ed. Nonlinear Cooperative Phenomena in Biological Systems, World Scientific, Singapore 1998, 86–112.
- [6] Michod R E, Darwinian Dynamics, New Jersey: Princeton University Press, 1999.
- [7] Page K M, Nowak M A, Unifying evolutionary dynamics, *J.Theoret. Biology* **219** (2002), 93–98.
- [8] Prykarpatsky A K and Gafiychuk V V, Replicator dynamical systems and their gradient and Hamiltonian properties, cond-mat/0302493 (2003).
- [9] Swetina J, and Schuster P, Self-Replication with Errors - A Model for Polynucleotide Replication, *Biophys.Chem.* **16** (1982), 329–345.
- [10] Prykarpatsky A K, Mykytiuk I V, Algebraic integrability of dynamical systems on manifolds, the Netherlands: Kluwer Academic Publisher, 1998.
- [11] Prykarpatsky A K, Hentosh O, On some class of gradient dynamical systems associated with a polynomial discrete probability distribution, *Math. Methods & Phys. Mech. Fields* (2003) (in print, in Ukrainian).
- [12] Prykarpatsky A K, Zagrodzinski J A and Blackmore D L, Lax type flows on Grassmann manifolds and dual momentum mappings, *Report on Math. Physics* **95** (1996).