EVOLUTIONARY BEHAVIOR IN A TWO-LOCUS SYSTEM

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Abstract. In this short note we study a dynamical system generated by a two-parametric quadratic operator mapping 3-dimensional simplex to itself. This is an evolution operator of the frequencies of gametes in a two-locus system. We find the set of all (a continuum set) fixed points and show that each fixed point is non-hyperbolic. We completely describe the set of all limit points of the dynamical system. Namely, for any initial point (taken from the 3-dimensional simplex) we find an invariant set containing the initial point and a unique fixed point of the operator, such that the trajectory of the initial point converges to this fixed point.

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1. Introduction

In this paper following [2, page 68] we define an evolution operator of a population assuming viability selection, random mating and discrete non-overlapping generations. Consider two loci \( A \) (with alleles \( A_1, A_2 \)) and \( B \) (with alleles \( B_1, B_2 \)). Then we have four gametes: \( A_1B_1, A_1B_2, A_2B_1, \) and \( A_2B_2 \). Denote the frequencies of these gametes by \( x, y, u, \) and \( v \) respectively. Thus the vector \((x, y, u, v)\) can be considered as a state of the system, and therefore, one takes it as a probability distribution on the set of gametes, i.e. as an element of 3-dimensional simplex, \( S^3 \). Recall that \((m-1)\)-dimensional simplex is defined as

\[
S^{m-1} = \{ x = (x_1, ..., x_m) \in \mathbb{R}^m : x_i \geq 0, \sum_{i=1}^{m} x_i = 1 \}.
\]

Following [2, Section 2.10] we define the frequencies \((x', y', u', v')\) in the next generation as

\[
W : \begin{align*}
x' &= x + a \cdot (yu - xv) \\
y' &= y - a \cdot (yu - xv) \\
u' &= u - b \cdot (yu - xv) \\
v' &= v + b \cdot (yu - xv),
\end{align*}
\]

where \( a, b \in [0, 1] \).

It is easy to see that this quadratic operator, \( W \), maps \( S^3 \) to itself. Indeed, we have \( x' + y' + u' + v' = 1 \) and each coordinate is non-negative, for example, we check it for \( y' \):

\[
y' = y - a \cdot (yu - xv) = y(1 - au) + axv \geq y(1 - au) \geq 0,
\]

these inequalities follow from the conditions that \( x, y, u, v, a \in [0, 1] \), and therefore, we have \( 0 \leq au \leq 1 \).

The operator \( W \), for any initial point (state) \( t_0 = (x_0, y_0, u_0, v_0) \in S^3 \), defines its trajectory: \( \{ t_n = (x_n, y_n, u_n, v_n) \} \) as

\[
t_n = (x_n, y_n, u_n, v_n) = W^n(t_0), n = 0, 1, 2, ...
\]
Here $W^n$ is the $n$-fold composition of $W$ with itself:

$$W^n(\cdot) = W(W(W(\ldots (W(\cdot)))) \ldots).$$

**The main problem** in theory of dynamical system (see [1]) is to study the sequence $\{t_n\}_{n=0}^{\infty}$ for each initial point $t_0 \in S^3$.

In general, if a dynamical system is generated by a nonlinear operator then complete solution of the main problem may be very difficult. But in this short note we will completely solve this main problem for nonlinear operator (1.1).

**Remark 1.** Using $1 = x + y + u + v$ (on $S^3$) one can rewrite operator (1.1) as

$$x' = x^2 + xy + xu + (1 - a)xy + ayu$$

$$y' = xy + y^2 + (1 - a)yu + axy + yuv$$

$$u' = xu + (1 - b)yu + u^2 + bxv + uv$$

$$v' = (1 - b)xy + yv + by + uv + v^2.$$ (1.2)

Note that the operator (1.2) is in the form of quadratic stochastic operator (QSO), i.e., $V : S^{m-1} \rightarrow S^{m-1}$ defined by

$$V : x'_k = \sum_{i,j=1}^{m} P_{ij,k} x_i x_j,$$

where $P_{ij,k} \geq 0$, $\sum_k P_{ij,k} = 1$.

The operator is not studied in general, but some large class of QSO’s are studied (see for example [3], [4], [5], [6], [7] and the references therein). But the operator (1.1) was not studied yet.

2. **The set of limit points**

**Remark 2.** The case $a = b = 0$ is very trivial, so we will not consider this case.

Recall that a point $t \in S^3$ is called a fixed point for $W : S^3 \rightarrow S^3$ if $W(t) = t$.

Denote the set of all fixed points by $\text{Fix}(W)$.

It is easy to see that for any $a, b \in [0, 1]$, $a + b \neq 0$ the set of all fixed points of (1.1) is

$$\text{Fix}(W) = \{ t = (x, y, u, v) \in S^4 : yu - xv = 0 \}.$$ 

This is a continuum set of fixed points.

The main problem is completely solved in the following result:

**Theorem 1.** For any initial point $(x_0, y_0, u_0, v_0) \in S^3$ the following assertions hold

1. If $(x_0 + y_0)(u_0 + v_0) = 0$ then $(x_0, y_0, u_0, v_0)$ is fixed point.
2. If $(x_0 + y_0)(u_0 + v_0) \neq 0$ then trajectory has the following limit:

$$\lim_{n \rightarrow \infty} (x_n, y_n, u_n, v_n) = (A(x_0, u_0)(x_0 + y_0), A(y_0, v_0)(x_0 + y_0), A(x_0, u_0)(u_0 + v_0), A(y_0, v_0)(u_0 + v_0)) \in \text{Fix}(W),$$

where

$$A(x, u) = \frac{bx + au}{(u_0 + v_0)a + (x_0 + y_0)b}.$$ 

**Proof.** We note that for each $\alpha \in [0, 1]$ the following set is invariant:

$$X_\alpha = \{ t = (x, y, u, v) \in S^3 : x + y = \alpha, \ u + v = 1 - \alpha \},$$

i.e., $W(X_\alpha) \subset X_\alpha$. 

Note also that
\[ S^3 = \bigcup_{\alpha \in [0,1]} X^\alpha. \]

The part 1 of theorem follows in the case \( \alpha = 0 \) and \( \alpha = 1 \). Indeed, for \( \alpha = 0 \) we have
\[ X_0 = \{ t = (0,0,u,v) \in S^3 : u + v = 1 \}, \]
and in the case of \( \alpha = 1 \) we get
\[ X_1 = \{ t = (x,y,0,0) \in S^3 : x + y = 1 \}. \]

Note that in both case the restriction of operator on the corresponding set is an id-operator, i.e., all points of the set are fixed points.

Now to prove part 2 we consider the case \( \alpha \in (0,1) \).

Since \( X^\alpha \) is an invariant, it suffices to study limit points of the operator on sets \( X^\alpha \), for each \( \alpha \in (0,1) \) separately. To do this, we reduce operator \( W \) on the invariant set \( X^\alpha \) (i.e., replace \( y = \alpha - x, \ v = 1 - \alpha - u \)):
\[ W^\alpha : \begin{align*} x' &= (1 - a + a\alpha)x + a\alpha u, \\ u' &= (1 - \alpha)bx + (1 - b\alpha)u, \end{align*} \]
where \( a, b \in [0,1], \alpha \in (0,1) \ x \in [0,\alpha], \ u \in [0,1 - \alpha]. \)

It is easy to find the set of all fixed points:
\[ \text{Fix}(W^\alpha) = \{(x,u) \in [0,\alpha] \times [0,1 - \alpha] : (1 - \alpha)x - a\alpha u = 0 \}. \]

The operator \( W^\alpha \) is a linear operator given by the matrix
\[ M^\alpha = \begin{pmatrix} 1 - a + a\alpha & a\alpha \\ (1 - \alpha)b & 1 - b\alpha \end{pmatrix}. \]  

(2.2)

Eigenvalues of the linear operator are
\[ \lambda_1 = 1, \quad \lambda_2 = 1 - (1 - \alpha)a - \alpha b. \]  

(2.3)

For any \( a, b \in [0,1], a + b \neq 0, \alpha \in (0,1) \) we have \( 0 < (1 - \alpha)a + \alpha b < 1 \), therefore, \( 0 < \lambda_2 < 1 \).

By (2.1) we define trajectory of an initial point \((x_0,u_0)\) as
\[ (x_{n+1},u_{n+1}) = M^\alpha(x_n,u_n)^T, \quad n \geq 0. \]

(2.4)

Thus
\[ (x_n,u_n) = M^n^\alpha(x_0,u_0)^T, \quad n \geq 1. \]

(2.5)

Therefore we need to find \( M^n^\alpha \). To find it we use a little Cayley-Hamilton Theorem\(^1\) to obtain the following formula
\[ M^n^\alpha = \frac{\lambda_2 \lambda_1^n - \lambda_1 \lambda_2^n}{\lambda_2 - \lambda_1} \cdot I_2 + \frac{\lambda_2^n - \lambda_1^n}{\lambda_2 - \lambda_1} \cdot M^\alpha, \]

where \( I_2 \) is \( 2 \times 2 \) unit matrix and \( \lambda_1, \lambda_2 \) are eigenvalues (defined in (2.3)).

By explicit formula (2.2) we get the following limit
\[ \lim_{n \to \infty} M^n^\alpha = \frac{\lambda_2}{\lambda_2 - \lambda_1} \cdot I_2 - \frac{1}{\lambda_2 - \lambda_1} \cdot M^\alpha = \frac{1}{(1 - \alpha)a + \alpha b} \cdot \begin{pmatrix} ab & \alpha a \\ (1 - \alpha)b & (1 - \alpha)a \end{pmatrix}. \]

Using this limit, for any initial point \((x_0,u_0) \in [0,\alpha] \times [0,1 - \alpha] \) we get
\[ \lim_{n \to \infty} (x_n,u_n) = \lim_{n \to \infty} M^n^\alpha(x_0,u_0)^T = \frac{bx_0 + \alpha u_0}{(1 - \alpha)a + \alpha b} \cdot (\alpha, 1 - \alpha) \in \text{Fix}(W^\alpha). \]  

(2.5)

By (2.4) we obtain

\(^1\)https://www.freemathhelp.com/forum/threads/formula-for-matrix-raised-to-power-n.55028/
Lemma 1. For any initial point \((x_0, y_0, u_0, v_0) \in S^3 \setminus (X_0 \cup X_1)\) there exists \(\alpha \in (0, 1)\) such that \((x_0, y_0, u_0, v_0) \in X_\alpha\) and the trajectory of this initial point (under operator \(W\), defined in (1.1)) has the following limit

\[
\lim_{n \to \infty} (x_n, y_n, u_n, v_n) = \left(A(x_0, u_0)\alpha, A(y_0, v_0)\alpha, A(x_0, u_0)(1 - \alpha), A(y_0, v_0)(1 - \alpha)\right) \in \text{Fix}(W),
\]

where

\[
A(x, u) = \frac{bx + au}{(1 - \alpha)a + ab}.
\]

In this lemma we note that \(\alpha = x_0 + y_0\) and \(1 - \alpha = u_0 + v_0\), therefore, the part 2 of Theorem follows, where limit point of trajectory of each initial point is given as function of the initial point only. Theorem is proved. 

3. Biological interpretations

The results of Theorem 1 have the following biological interpretations:

Let \(t = (x_0, y_0, u_0, v_0) \in S^3\) be an initial state (the probability distribution on the set \(\{A_1B_1, A_1B_2, A_2B_1, A_2B_2\}\) of gametes). Theorem 1 says that, as a rule, the population tends to an equilibrium state with the passage of time.

Part 1 of Theorem 1 means that if at an initial time we had only two gametes then the (initial) state remains unchanged.

Part 2 means that depending on the initial state future of the population is stable: gametes survive with probability

\[
A(x_0, u_0)(x_0 + y_0), A(y_0, v_0)(x_0 + y_0), A(x_0, u_0)(u_0 + v_0), A(y_0, v_0)(u_0 + v_0)
\]

respectively. From the existence of the limit point of any trajectory and from the explicit form of \(\text{Fix}(W)\) it follows that

\[
\lim_{n \to \infty} (y_nu_n - x_nv_n) = 0.
\]

This property, biologically means ([2, page 69]), that the population asymptotically goes to a state of linkage equilibrium with respect to two loci.

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