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The Multilocus Multiplicative Selection Equilibria

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Abstract—The concept of monomial selection is introduced as a natural generalization of the multiplicative selection. It is proven that the equilibrium set of the multilocus multiallele population under monomial selection is generically finite. The result is new even in the multiplicative case. An upper bound for the number of equilibria is given.

Keywords—Monomial selection, Multiplicative selection, Equilibria.

For a population, we consider a set $L = \{1, \dots, l\}$ of autosomal loci with allele genes a_{ik} at the i^{th} locus ($1 \le i \le l$, $1 \le k \le m_i$, $m_i \ge 2$). For each gamete $g = a_{1k_1} \cdots a_{lk_l}$ and each subset $U \subset L$, the corresponding subgamete g_U is the part of g consisting of a_{ik_i} with $i \in U$. In particular, $g_i = a_{ik_i}$ ($1 \le i \le l$). Obviously, $g = g_U g_V$, where V is the subset of those loci which do not belong to U. The partitions $U \mid V$ can be identified with all formally possible crossing-overs. If a crossing-over $U \mid V$ occurs in meiosis then every gamete pair (g, h) produces the recombinant gametes $g_U h_V$ and $h_U g_V$ with equal probabilities $r(U \mid V)/2$, where r is the linkage distribution. The latter is supposed to be fixed in what follows. By definition,

$$r(U \mid V) \ge 0, \qquad \sum_{U|V} r(U \mid V) = 1. \tag{1}$$

A state p of the population on the gamete level is a probability distribution $p(g)$ on the set Γ of all gametes: $p(g) \ge 0$, $\sum p(g) = 1$, where g runs over Γ. Given some fitness values $\lambda(g, h) = \lambda(h, g) \ge 0$, $\lambda(g, g) > 0$, the evolutionary equations under the corresponding selection and random mating are

$$p'(g) = \frac{Q_g(p)}{W(p)}, \qquad g \in \Gamma, \tag{2}$$

where

$$Q_g(p) = \sum_{U|V} r(U \mid V) \sum_{h \in \Gamma} \lambda(g_U h_V, h_U g_V) p(g_U h_V) p(h_U g_V) \tag{3}$$

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and $W(p)$ is the mean fitness,

$$W(p) = \sum_{g,h\in\Gamma} \lambda(g,h)p(g)p(h), \tag{4}$$

see [1, Section 9.5]. In (2), p' means the state in the offspring generation while p is the parental state. The latter is an equilibrium if and only if $p' = p$.

Let us emphasize that $Q_g(p)$ are quadratic forms of p as well as

$$W(p) = \sum_g Q_g(p). \tag{5}$$

We introduce the *monomial selection* by setting

$$\lambda(g,h) = \prod_{i=1}^{l} [\lambda(g_i,h_i)]^{\nu_i} \tag{6}$$

where ν_i are some positive integers. The values

$$\lambda_i\left(a_{ij_i}, a_{ik_i}\right) = \lambda_i\left(a_{ik_i}, a_{ij_i}\right), \qquad 1 \le j_i, \quad k_i \le m_i, \quad 1 \le i \le l \tag{7}$$

are independent positive parameters. If all $\nu_i = 1$, the monomial selection turns into the standard multiplicative selection; cf. [2, Section 9]. In general, the monomial selection is a generalization of the multiplicative selection such that there are some weights ν_i, $1 \le i \le l$, for the contributions of different loci.

The total number of parameters (7) is

$$m = \frac{1}{2}\sum_{i=1}^{l} m_i(m_i+1),$$

while in a general symmetric matrix $(\lambda(h,g))$ the number of independent parameters is much more, namely,

$$M = \frac{1}{2}|\Gamma|(|\Gamma|+1), \qquad |\Gamma| = m_1 m_2 \cdots m_l.$$

For example, if all $m_i = 2$, then $M = 2^{l-1}(2^l+1)$ in contrast to $m = 3l$.

The difference $M - m$ is just the number of independent relations between the fitness values (6).

Now, we bring all the parameters (7) together to a *fitness vector* λ running over the *fitness space* $\mathbf{R}_+^m$. (The latter is the set of all nonzero m-tuples with nonnegative elements.)

THEOREM. *Under monomial selection, the equilibrium set is generically finite, and the total number of equilibria does not exceed* $3^{|\Gamma|-1}$.

The genericity means that the conclusion is true outside a proper algebraic subset of the fitness space.

PROOF. According to (2), the set of equilibria is described by equations

$$p(g)W(p) - Q_g(p) = 0, \qquad g \in \Gamma. \tag{8}$$

In addition,

$$\sum_{g\in\Gamma} p(g) - 1 = 0. \tag{9}$$

Note that (8) implies

$$p(g)Q_h(p) - p(h)Q_g(p) = 0, \qquad g,h \in \Gamma, \tag{10}$$

a system of homogeneous equations of degree 3. In addition, we replace equation (9) by a homogeneous equation of degree 1; namely, we fix a gamete $\gamma \in \Gamma$ and write

$$\sum_{g\in\Gamma} p(g) - \tau p(\gamma) = 0, \tag{11}$$

with a parameter τ.

According to the classical elimination theory, see, e.g., [3], system (10),(11) has a nontrivial complex solution p if and only if the pair (λ, τ) annihilates all resultants. This condition can be written as a system of algebraic equations

$$R_{i,\gamma}(\lambda,\tau) = 0, \qquad 1 \le i \le i_\gamma, \tag{12}$$

where

$$R_{i,\gamma}(\lambda,\tau) = \sum_{\gamma=0}^{j_{i,\gamma}} R_{ij,\gamma}(\lambda)\tau^j \tag{13}$$

are some polynomials of τ with polynomial coefficients $R_{ij,\gamma}(\lambda)$. Further, we consider two opposite cases. The first of them yields what we need, and the second one leads to a contradiction.

(1) *For each $\gamma \in \Gamma$ at least one of polynomials $R_{ij,\gamma}(\lambda)$ does not identically vanish.*

In this case, the system of equations

$$R_{ij,\gamma}(\lambda) = 0, \qquad 1 \le i \le i_j, \quad 0 \le j \le j_{i,\gamma}, \tag{14}$$

with any $\gamma \in \Gamma$ defines a proper algebraic subset A_γ of the fitness space. The union

$$A = \bigcup_{\gamma\in\Gamma} A_\gamma \tag{15}$$

is also a proper algebraic subset. We prove that *if a fitness vector λ does not belong to A, then the corresponding equilibrium set E_λ is finite.*

Suppose that E_λ is infinite. Then, there exists $\gamma \in \Gamma$ such that the set $\{p(\gamma) : p \in E_\lambda, p(\gamma) \neq 0\}$ is infinite. The set E_λ consists of all nonnegative solutions of (8),(9). If $p \in E_\lambda$ and $p(\gamma) \neq 0$, then p is a nontrivial solution of (10),(11) with $\tau = 1/p(\gamma)$. Hence, $\tau = 1/p(\gamma)$ satisfies all equations (12). We see that every equation (12) has infinitely many solutions τ. Hence, λ annihilates all coefficients $R_{ij,\gamma}(\lambda)$ in (13). By definition of A_γ we have $\lambda \in A_\gamma$, *a fortiori*, $\lambda \in A$. Thus, if $\lambda \notin A$, then E_λ is finite.

(2) *There exists $\gamma \in \Gamma$ such that all $R_{i,\gamma}(\lambda,\tau)$ are identically zero.*

Now for every (λ,τ), system (10),(11) has a nontrivial *complex* solution p. To disprove this, we take $\tau = 0$ and specialize λ as follows.

Let $\lambda_i(a_{ij_i}, a_{ik_i}) = 0$ as long as $j_i \neq k_i$ and let all $\lambda_i(a_{ik_i}, a_{ik_i}) = 1$. By (6), $\lambda(g,g) = 1$ for all g and $\lambda(g,h) = 0$ for $g \neq h$. Note that if $g_U h_V = h_U g_V$, then $g_U = h_U$ and $g_V = h_V$, and hence, $g = h$. For this reason, the interior sum in (3) reduces to $p^2(g)$. The same is true for the whole $Q_g(p)$ because of (1). Thus, (10) becomes

$$p(g)p(h)\left(p(h) - p(g)\right) = 0, \qquad g,h \in \Gamma. \tag{16}$$

Under the restrictions $p(g) \neq 0$ and $p(h) \neq 0$, (16) yields $p(h) = p(g)$; i.e., $p(g)$ is independent of g for $p(g) \neq 0$. Now equation (11) with $\tau = 0$ leads to a contradiction: $\sigma p(g) = 0$ where σ is the number of g such that $p(g) \neq 0$.

If in Case 1, the number of complex solutions of (8),(9) is finite, then it is at most $3^{|\Gamma|-1}$, by Besout's theorem. Indeed, (9) is a linear equation and the sum of all equations (8) is an identity because of (5) and (9). ∎

COROLLARY. *Under multiplicative selection, the equilibrium set is generically finite, and the total number of equilibria does not exceed* $3^{|\Gamma|-1}$.

Certainly, the multiplicative case is the most interesting from a biological point of view. However, the restriction to this case does not change the above proof. In fact, our proof requires the only following properties of the selection patterns:

(1) $\lambda(g,h)$ is a polynomial of $\lambda(g_i,h_i)$, $1 \le i \le l$;
(2) if $\lambda(g_i,h_i)=0$ for some i and some $g_i \ne h_i$, then $\lambda(g,h)=0$.

Thus, our result is valid if $\lambda(g,h)$ is a sum (or even a positive linear combination) of monomial functions. For other recent results on finiteness of the equilibrium set see [4,5].

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