Why and Why Not Sex?
Multiplicative Update and Evolutionary Theory

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[Project Report]

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Abstract

This project report reviews the paper *"Multiplicative Updates in Coordination Games and the Theory of Evolution"* by Chastain et al., which explores connection between population genetics under weak selection and coordination games. The authors demonstrate that, in this regime, mirrors the multiplicative update dynamics of such games, where genes are players and alleles are strategies. A key finding is that the *mixability* of an allele—its average fitness—is precisely the utility maximized by this evolutionary process, offering a rigorous foundation for the importance of mixability in sexual reproduction. Furthermore, the authors prove, using a technique involving random matrices, that equilibria in these evolutionary games can possess large supports, suggesting that genetic diversity is maintained despite selection for mixability. This work bridges evolutionary theory with concepts from game theory and multiplicative updating, providing a perspective on the fundamental mechanisms driving evolution and the advantage of sex.

Keywords: multiplicative update

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I. INTRODUCTION

A. Developments in the field

B. Organization of the report

II. SET-UP OF THE PROBLEM

A **gene** is defined as a fundamental unit of heredity. Genes exist in variant forms known as **alleles**. The specific combination of alleles an organism possesses for its genes constitutes its **genotype** In the context of this paper, the discussion is focussed on two genes with m and n alleles, resulting in genotypes denoted as ij where $i \in [m]$ and $j \in [n]$. **Recombination** is the process by which offspring inherit a new combination of alleles derived from two parent genotypes in the preceding generation, often through sexual reproduction. In this model, it is assumed that for each gene, an allele is selected from one of the two parent genomes independently and with a probability of one-half, implying no linkage (or correlation) between genes.

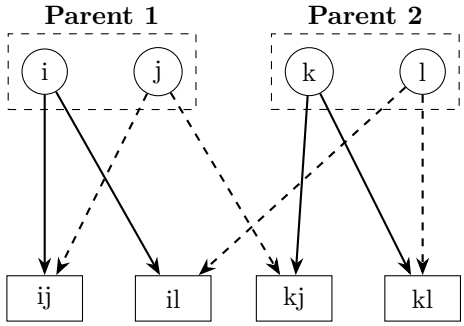

Figure 1: sexual reproduction with recombination

Definition II.1 (Fitness (w_{ij}))**.** The expected number of offspring that a genotype ij produces by mating randomly. It encapsulates the basic genetic parameters of the species. The matrix W of all w_{ij} is often called the **fitness landscape**.

Definition II.2 (Frequency of Genotype (p_{ij}))**.** The proportion of genotype ij in the population. The matrix of p_{ij}'s is the state of the dynamical system. The frequency of genotype ij in generation t is denoted by p_{ij}^t.

Now, the **mean fitness** of all genotypes in the population at generation t, given by $\bar{w}_t = \sum_{ij} p_{ij}^t w_{ij}$. The discussion focusses on study of how the statistical make-up of a population of genotypes changes from generation to generation with Fitness landscape as the background.

Definition II.3 (Marginal Frequency of an Allele)**.** The frequency of a specific allele of a gene in the population, summed over all possible alleles of the other gene(s). For two genes, the marginal frequency of allele i of the first gene is $x_i = \sum_j p_{ij}$, and the marginal frequency of allele j of the second gene is $y_j = \sum_i p_{ij}$. The vectors of these frequencies at time t are denoted by x^t and y^t respectively.

A **game** involves strategic interaction among multiple players, each choosing from a set of **strategies**, where every combination of strategies leads to specific **payoffs** for each player. A coordination game is characterized by the property that all players have the same utility (payoff) for all strategy combination. In this analogy, the **players** are the genes of the organism, and the **strategies** available to each gene are its different alleles. A **mixed strategy** is when the players instead of choosing a pure strategy, choose one at random based on some probability distribution. A mixed strategy for a gene corresponds to the frequency distribution of its alleles in the population. For instance, for a gene with m alleles, the mixed strategy is represented by the vector of allele frequencies $x = (x_1, x_2, ..., x_m)$, where x_i denotes the frequency of the i-th allele.

The **Multiplicative update scheme** for a mixed strategy is a method to update the probability of following a strategy so as to improve the payoff.

$$x_i^{t+1} = \frac{1}{Z^t} \cdot x_i^t \left(1 + \varepsilon \cdot \sum_j y_j^t \Delta_{ij} \right) \tag{1}$$

where

$$Z^t = \sum_i x_i^t \left(1 + \varepsilon \cdot \sum_j y_j^t \Delta_{ij} \right) = 1 + \varepsilon \sum_i \sum_j x_i^t y_j^t \Delta_{ij} = 1 + \varepsilon \bar{\Delta}^t \tag{2}$$

is the normalization factor to bring x^{t+1} back to the probability setting, and ε is the learning rate. Inserting this into (Eqn. 1) yields

$$x_i^{t+1} = \frac{x_i^t \left(1 + \varepsilon \cdot \sum_j y_j^t \Delta_{ij} \right)}{1 + \varepsilon \bar{\Delta}^t} \tag{3}$$

Nash Equilibrium is a state in a game where no player can improve their payoff by unilaterally changing their strategy, given the strategies of the other players. In our case, it refers to a state of allele frequencies where no single allele of any gene would gain a selective advantage by becoming more frequent, given the current allele frequencies of other genes. A Mixed Strategy Nash Equilibrium occurs when at least one player's optimal strategy involves randomizing over several

of their pure strategies (alleles), with specific probabilities (allele frequencies). The equilibrium is defined by the set of these probability distributions for all players (genes). The equilibrium allele frequencies x^* and y^* constitute a mixed Nash equilibrium of the subgame formed by the alleles that are present in the population (have a non-zero frequency). The **support of an equilibrium** is the set of pure strategies (alleles) that are played with a non-zero probability (have a non-zero frequency in the population) at a given equilibrium.

III. POPULATION DYNAMICS UNDER THE WEAK SELECTION

In a single round of reproduction the frequency of genotypes are updated as follows (shown in [1]):

$$p_{ij}^{t+1} = \frac{1}{\bar{w}_t} w_{ij}(r x_i^t y_j^t + (1-r)p_{ij}^t). \tag{4}$$

The intuition behind the formula is simple

$$p_{ij}^{t+1} \propto \begin{cases} p_{ij}^t & \text{r=0, no recombination} \\ x_i^t y_j^t & \text{r=1, only recombination} \end{cases} \tag{5}$$

In the following sections we are concerned in the only recombination case where,

$$p_{ij}^{t+1} = \frac{1}{\bar{w}_t} w_{ij} x_i^t y_j^t \tag{6}$$

Definition III.1 (Weak Selection)**.** A regime in evolutionary genetics where the fitness values of all genotypes are very close to one another, typically within the interval $[1-s, 1+s]$ for some small $s > 0$, called the **selection strength**. It is a mathematical approximation of Kimura's neutral theory.

Definition III.2 (Wright Manifold)**.** A subset of the space of genotype frequencies where the genotype frequency is a product of the marginal allele frequencies, i.e., $p_{ij} = x_i \cdot y_j$. On the Wright manifold, the population genetic equations take a simpler form as will show next.

Definition III.3 (Linkage Disequilibrium (D_{ij}))**.** The difference between the actual genotype frequency and the expected frequency under the assumption of independence (Wright manifold), defined as $D_{ij} = p_{ij} - x_i \cdot y_j$. It measures the deviation from a product distribution of allele frequencies.

Definition III.4 (Differential Fitness Landscape (Δ_{ij}))**.** Defined as $\Delta_{ij} = \frac{W_{ij}-1}{s}$, where W_{ij} is the fitness of genotype ij and s is the selection strength in the weak selection regime. Thus, Δ_{ij} is in the range $[-1, 1]$.

Definition III.5 (Mixability $(m_t^x(i), m_t^y(j))$)**.** The average fitness of an allele. Specifically, the mixability of allele i of the first gene at time t is $m_t^x(i) = \sum_j y_t^j \Delta_{ij}$, and the mixability of allele j of the second gene at time t is $m_t^y(j) = \sum_i x_t^i \Delta_{ij}$. It represents an allele's ability to function adequately with a broad spectrum of genetic partners.

Consider the evolution of genome frequencies p_{ij}^t in the weak selection regime and the corresponding time series of linkage disequilibria $D_{ij}^t = p_{ij}^t - x_i \cdot y_j$.

Theorem III.1 (Nagylaki [2], [3])**.** For any $t \geq t_0 = 3 \log \frac{1}{s}$ and any i, j

1. $D_{ij}^t = O(s)$;

2. there is a corresponding process $\{\hat{p}_{ij}^t\}$ on the Wright manifold such that:

   (a) $|\hat{p}_{ij}^t - p_{ij}^t| = O(s)$;

   (b) Both processes converge, and there is a one-to-one correspondence between the equilibria of p_{ij}^t and the equilibria of $\hat{p}_{ij}^t$.

Nagylaki's theorem expresses the connection between dynamics in weak selection regime and in the Wright manifold. In order to understand a genotype frequency process in the weak selection regime, one can instead follow a closely related process on the Wright manifold. As we shall see next, it turns out that this simplifies things tremendously and brings about some unexpected connections.

Theorem III.2. Under weak selection with selection strength s, the population genetic dynamics is precisely the multiplicative update dynamics of a coordination game whose payoff matrix is the differential fitness landscape and $\varepsilon = s$.

Proof. We only show the derivation for two genes, the general case being a straightforward generalization.

$$x_i^{t+1} = \sum_j p_{ij}^{t+1} \tag{7}$$

$$= \frac{1}{\bar{w}_t} \sum_j x_i^t y_j^t w_{ij} \tag{8}$$

$$= \frac{x_i^t}{\bar{w}_t} \left(1 + s \sum_j y_j^t \Delta_{ij}\right) \tag{9}$$

$$= \frac{x_i^t \cdot \left(1 + s \sum_j y_j^t \Delta_{ij}\right)}{1 + s \cdot \bar{\Delta}^t} \tag{10}$$

where $\bar{\Delta}^t = \sum_{i,j} x_i^t y_j^t \Delta_{ij}$. This is the multiplicative update dynamic for coordination games (Eqn. 3) with perturbation $\varepsilon = s$. □

Corollary 1 The population genetics dynamics converge asymptotically in the weak selection regime to the genotype with maximal cumulative mixability. More formally, for the i, j that maximizes

$$\frac{1}{T}\left(\sum_{t=1}^{T}\left[m_x^t(i) + m_y^t(j)\right] + s\sum_{t=1}^{T}\left[\left|m_x^t(i)\right| + \left|m_y^t(j)\right|\right]\right), \tag{11}$$

it also holds that:

$$\frac{1}{T}\left(\sum_{t=1}^{T}\left[m_x^t \cdot x^t + m_y^t \cdot y^t\right] - \sum_{t=1}^{T}\left[m_x^t(i) + m_y^t(j)\right] + s\sum_{t=1}^{T}\left[\left|m_x^t(i)\right| + \left|m_y^t(j)\right|\right]\right) \geq 0 \tag{12}$$

in the limit as $T \to \infty$, and thus we do no worse than the best possible i, j pair. This i, j pair also maximizes the cumulative mixability:

$$\frac{1}{T}\sum_{t=1}^{T}\left(2 + s\left(m_x^t(i) + m_y^t(j)\right)\right) \tag{13}$$

Proof. It holds for the weak selection regime that m_x^t and m_y^t are in the range $[-1, 1]$. Therefore by Theorem 3 in [4]r (and his remark that the same bound holds for our form of the multiplicative update dynamics), we can thus guarantee that, for any pair i and j:

$$\sum_{t=1}^{T} m_x^t \cdot x^t - m_y^t \cdot y^t - \sum_{t=1}^{T} m_x^t(i) + m_y^t(j) + s\sum_{t=1}^{T}\left|m_x^t(i)\right| + \left|m_y^t(j)\right| \geq -\frac{\log n + \log m}{s} \tag{14}$$

Clearly, dividing both sides by T and taking the limit as $T \to \infty$ gives 0 on the RHS. In particular, it will hold for the i and j that maximize m_x and m_y. This shows that as $T \to \infty$, the dynamics converge to the i and j that maximize

$$\frac{1}{T}\sum_{t=1}^{T}\left(2 + s\left(m_x^t(i) + m_y^t(j)\right)\right) \tag{15}$$

□

Corollary 2 The equilibrium achieved by the differential fitness is the same even when different random perturbations are added to it at every generation. Let the differential fitness w_{ij}^t be $\tilde{w}_{ij} + \nu_{ij}^t$, with ν_{ij}^t drawn i.i.d from a zero-mean distribution and bounded almost surely in the interval $[-s(1-|\Delta_{ij}|), s(1-|\Delta_{ij}|)]$. If we run the population genetics dynamics with this fitness, then we will converge to the same equilibrium as when the differential fitness is $\tilde{w}$.

Proof. First we will show that the differential fitness at any point in time is subject to the weak selection regime. For any t, by the almost sure bound on ν_{ij}^t, it can be written in the form

$$1 + s\left(\Delta_{ij} + \frac{\nu_{ij}^t}{s}\right) \tag{16}$$

where $|\nu_{ij}^t/s| \leq 1 - |\Delta_{ij}|$. Therefore, the differential fitness still satisfies weak selection since

$$|\Delta_{ij} + \nu_{ij}^t/s| \leq |\Delta_{ij}| + |\nu_{ij}^t|/s \leq 1 \tag{17}$$

The convergence result from the previous corollary still holds for the dynamics in this case. The i, j that is converged to maximizes:

$$\frac{1}{T}\sum_{t=1}^{T}\left(2 + s\left(\sum_j y_j^t \Delta_{ij} + \sum_i x_i^t \Delta_{ij}\right) + \nu_{ij}^t\right) \tag{18}$$

Because we are analyzing asymptotic behavior at equilibrium, we take the limit $T \to \infty$. In this case, for all i, j,

$$\frac{1}{T}\sum_{t=1}^{T}\nu_{ij}^t = 0 \tag{19}$$

by the strong law of large numbers since $\mathbb{E}[\nu_{ij}^t] = 0$. But then one is simply converging to:

$$\frac{1}{T}\sum_{t=1}^{T}\left(2 + s\left(\sum_j y_j^t \Delta_{ij} + \sum_i x_i^t \Delta_{ij}\right)\right) \tag{20}$$

which is the same as what is being converged to for $\tilde{w}$. Thus it holds for the i, j that maximizes this expression. □

IV. FLIPS AND LARGE SUPPORTS

We just showed that the population dynamics converges. We next show that the equilibria is diverse, i.e. has large support. Under the assumption of weak selection, we assume that the entries of W is are drawn independently from identical non-singular distribution that is centred about 1. By construction, this would mean that entries of Δ are independently identically distributed in $[-1, 1]$.

Recall the update rule for distribution:

$$x_i^{t+1} = x_i^t\left(\sum_j y_{ij}^t W_{ij}\right) = x_i^t\left(W^T y\right)$$

At equilibrium $x_i^{t+1} = x_i^t$, i.e. $W^T y = \mathbb{1}a$ and similarly $Wx = \mathbb{1}b$. We expect x to have large support, which can be specified a sub-matrix of W, say A. We say sub-matrix A is at equilibrium if $Ax = \mathbb{1}a$ and $A^T y = \mathbb{1}a$. One must note that:

1. For equilibrium without extinction state, we look at solutions with $a > 1$.

2. A must be a square matrix.On the contrary assume A is $r \times s$ matrix with $r < s$. Then, the system A^T would be overdetermined. And probability of finding a solution satisfying it is thus zero.

Lemma IV.1. Let $A = U + sB$, where U is matrix with all entries 1. Then A is an equilibrium if and only if B^{-1} exist with non-negative row and column sums.

Proof. First we show that if A is in equilibrium then B^{-1} exist with positive row and column sums.

$$(U + sB)\,x = \mathbb{1}a \implies Bx = \mathbb{1}\frac{1-a}{s} \implies x = B^{-1}\mathbb{1}\left(\frac{1-a}{s}\right) \tag{21}$$

And similarly for y. Note that $\left(\frac{1-a}{s}\right)$ is positive, thus B^{-1} must ahve positive row and column sums.

Also, from any non-negative solutions of $Bz = \mathbb{1}$ and $B^T w = \mathbb{1}$, we can construct non-negative x and y (with elements summing to 1) as:

$$x_i = \frac{z_i}{\sum_i z_i}; y_i = \frac{w_i}{\sum_i w_i} \text{ and } a = 1 + \frac{s}{\sum_i z_i} > 1$$

□

Consider $S, T \subseteq [n]$ and $\mathcal{I}$ with identity matrix of $n \times n$ dimensions. Then $\forall s \in S$ **flip** the sth $1 \xrightarrow{flip} -1$. Say resulting matrix is $\mathcal{I}_S$. The result of this is for any matrix V of size $n \times n$, the all rows with index $s \in S$ of $\mathcal{I}_S V$ are flipped as compared to that of V. Similarly all columns with index $t \in T$ of $V\mathcal{I}_T$ are flipped as compared to that of V. Consider the following examples of flipping with $S = \{2\}$ and $T = \{3\}$:

$$\underbrace{\begin{bmatrix} 1 & 0 & 0 \\ 0 & -1 & 0 \\ 0 & 0 & 1 \end{bmatrix}}_{\mathcal{I}_S} \cdot \underbrace{\begin{bmatrix} v_{11} & v_{12} & v_{13} \\ v_{21} & v_{22} & v_{23} \\ v_{31} & v_{32} & v_{33} \end{bmatrix}}_{V} = \underbrace{\begin{bmatrix} v_{11} & v_{12} & v_{13} \\ -v_{21} & -v_{22} & -v_{23} \\ v_{31} & v_{32} & v_{33} \end{bmatrix}}_{\mathcal{I}_S V}$$

$$\underbrace{\begin{bmatrix} v_{11} & v_{12} & v_{13} \\ v_{21} & v_{22} & v_{23} \\ v_{31} & v_{32} & v_{33} \end{bmatrix}}_{V} \cdot \underbrace{\begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & -1 \end{bmatrix}}_{\mathcal{I}_T} = \underbrace{\begin{bmatrix} v_{11} & v_{12} & -v_{13} \\ v_{21} & v_{22} & -v_{23} \\ v_{31} & v_{32} & -v_{33} \end{bmatrix}}_{V \cdot \mathcal{I}_T}$$

Lemma IV.2. For every $V \in [-1, 1]^{n \times n}$, there are $S, T \subseteq [n]$ such that $\mathcal{I}_S V \mathcal{I}_T$ has rows and columns with non-negative sum.

Proof. We define an iterative procedure that, starting from V, repeatedly flips the sign of rows or columns with negative sums, and we show that this process must terminate in a matrix with all row and column sums non-negative.

Let $V^{(0)} = V$. At each step t, construct $V^{(t+1)}$ from $V^{(t)}$ as follows:

- If there exists a row i such that the sum of the entries in row i, denoted $\text{row}_i(V^{(t)}) = \sum_{j=1}^{n} V_{ij}^{(t)}$, is negative, then flip row i.
- Else if there exists a column j such that $\text{col}_j(V^{(t)}) = \sum_{i=1}^{n} V_{ij}^{(t)} < 0$, flip column j.
- If no such row or column exists, terminate the process and output $V^{(t)}$.

Define the *total matrix sum* at step t as

$$S_t := \sum_{i=1}^{n} \sum_{j=1}^{n} V_{ij}^{(t)}.$$

Suppose at step t we flip a row i with sum $\sigma = \text{row}_i(V^{(t)}) < 0$. Then flipping row i changes each entry in that row from $V_{ij}^{(t)}$ to $-V_{ij}^{(t)}$, increasing the total sum by $-2\sigma > 0$. Similarly, flipping a column with negative sum increases the total matrix sum by a strictly positive amount.

Since all entries of V lie in the interval $[-1, 1]$, the total matrix sum S_t is upper bounded by n^2. Furthermore, as long as a flip is performed, the increase in S_t is at least $2\sigma_0$, where σ_0 is the minimum absolute value of any negative row or column sum in V at start.

Thus, the process cannot increase the total matrix sum indefinitely, and must terminate after finitely many steps. When it terminates, no row or column has negative sum. Let $S \subseteq [n]$ denote the set of row indices that were flipped, and $T \subseteq [n]$ the set of column indices that were flipped during the process. Then the final matrix is $V' = \mathcal{I}_S V \mathcal{I}_T$, and by construction, every row and column sum in this matrix is non-negative. □

This result allows us to estimate the measure of set of matrices with the required properties. Consider the domain $M = [-1, 1]^{n \times n}$ and subset M^+ which has positive rows and column sum and inverse exist. Now, consider all the flipping of B, i.e. $\mathcal{I}_S B \mathcal{I}_T$. There are $\frac{2^n \times 2^n}{2} = 2^{(2n-1)}$ distinct matrices. The factor two accounts for over-counting as $\mathcal{I}_S B \mathcal{I}_T = \mathcal{I}_{[n]-S} B \mathcal{I}_{[n]-T}$. Now notice that $(\mathcal{I}_S V^{-1} \mathcal{I}_T)^{-1} = \mathcal{I}_S V \mathcal{I}_T$. So, by applying the $2^{(2n-1)}$ transformations ($V \to \mathcal{I}_S V \mathcal{I}_T$) to M^+, we exhaust all matrices of M. Thus probability that a matrix in M is also in M^+ is at least $\frac{1}{2^{(2n-1)}} = 2^{-(2n-1)}$.

This result along with IV.1 now allows us to find the probability of finding the required A. This result is captured in following theorem.

Theorem IV.1 (Diversity)**.** The expected number of $k \times k$ equilibria in $m \times n$ fitness matrix under weak selection regime is at least $2\left(\frac{mn}{4k^2}\right)^k$.

Proof.

$$
\begin{aligned}
&\mathbb{E}(\text{Number of } k \times k \text{ equilibrium matrix }) \\
&= (\text{Number of } k \times k \text{ matrix}) \cdot \mathcal{P}(\text{A is an equilibrium}) \\
&= \tbinom{m}{k} \cdot \tbinom{n}{k} \cdot \mathcal{P}(B^{-1} \in M^{+}) \\
&\geq \left(\frac{mn}{k^2}\right)^k \cdot \mathcal{P}(B^{-1} \in M^{+}) \\
&= \left(\frac{mn}{k^2}\right)^k \cdot 2^{-(2k-1)} \\
&= 2\left(\frac{mn}{4k^2}\right)^k
\end{aligned}
$$

Notice that for $k \leq \frac{\sqrt{mn}}{2}$, this number is exponential in k. □

V. OUTLOOK AND SUMMARY

ACKNOWLEDGMENTS

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