

Modeling Population Dynamics in Changing Environments

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Abstract

Discrete replicator dynamics view evolution as a coordination game played among genes. While previous models of discrete replicator dynamics do not consider environments that respond to the mixed strategy that a population plays, our model incorporates a feedback-based payoff matrix, which depends on the frequency distribution of alleles. In this model, we construct an environment that is composed of multiple environments with different Nash equilibria. We look at whether the population dynamics converge or whether they exhibit a different behavior, e.g. whether they oscillate and form a stable limit cycle. We provide evidence that with only two Nash equilibria, i.e. two environments, the system will always converge to a fixed point along the line $a + b = 1$. With three Nash equilibria, although we were unable to construct a cyclic behavior, we conjecture that it is possible. Finally, with four Nash equilibria, we give evidence that it is possible for the system to form a stable limit cycle.

1 Introduction

In biology, there is intense scientific interest in evolution and the genetic makeup of populations from generation to generation. On the other hand, game theory studies the relationship between the payoffs of various strategies in a game, the choices a player makes, and the choices other players make. These two fields are linked in evolutionary game theory, where different parts of evolution are modeled with components of a game. Specifically, we look at natural selection with sexual reproduction, where the genetic makeup of the next generation is viewed as the result of a coordination game played among genes. This approach allows us to study properties of biological systems using the machinery of game theory and dynamical systems.

A biological model was developed by Nagylaki [1], whose theorem states that his model of population dynamics about the frequencies of alleles converges under the assumption of weak selection, which assumes that the fitnesses of all genotypes are close to one another. Given the frequency of a genotype in a population and the expected fitness of this genotype, Nagylaki's model describes the next generation's frequency of that genotype. Chastain *et al.* [2] showed that Nagylaki's biological model is equivalent to the Multiplicative Weight Update Algorithm (MWUA) [3] in a repeated coordination game.

By using this connection, Mehta *et al.* were able to show that a reformulation of Nagylaki's model with a discrete MWUA almost always converges to a pure Nash equilibrium [4]. However, Mehta *et al.*'s model are specifically for species that undergo sexual reproduction with no mutation and under static environments. An important question is then the role of mutation and changing environments in the population dynamics. Mehta *et al.*, building on an asexual reproduction model with mutations and changing environments [5], then considered such models with sexual reproduction. Both models use Markov chains to model changing environments. In addition, in both models, without mutation, the species

goes extinct, and, with mutation, the species survives with positive probability.

A question raised by Mehta *et al.* considers what would happen if the environment change depended on population size instead. We consider natural selection with sexual reproduction with changing environments in the style of Weitz *et al.* [6] both with and without mutation. Specifically, our payoff matrix is the sum of multiple payoff matrices, each scaled by a different function of the frequencies of the current generation's alleles.

In all of the previous models, they were able to show convergence of the frequency distribution of alleles. We also look at the long-term behavior of the frequency distribution primarily using numerical simulations for different numbers of payoff matrices. In our models, we see generally that it may be possible for the system not to converge to a fixed point. In order to induce oscillations, we consider payoff matrices with different Nash equilibria and combine them into a single payoff matrix so that points near a Nash equilibrium move away from that Nash equilibria. For one payoff matrix, we see that our model of changing environments degenerates to the static environment model. For two, three, and four payoff matrices, we have the three conjectures, which we have written here in informal language.

Conjecture 1.1. *For a certain class of changing environments, which incorporates two static environments with different Nash equilibria, natural selection with sexual reproduction converges to a fixed point with or without mutation.*

Conjecture 1.2. *For a certain class of changing environments, which incorporates three static environments with different Nash equilibria, natural selection with sexual reproduction converges with or without mutation if the Nash equilibria are all pure.*

If the Nash equilibria are not all pure, it may be possible for our model to not converge.

Conjecture 1.3. *There exists a changing environment, which incorporates four static environments with different Nash equilibria, in which natural selection with sexual reproduction approaches a stable limit cycle.*

In the case with four Nash equilibria, it looks like the stable limit cycle grows and shrinks exponentially with the rate of mutation.

In Section 2, we introduce notation, define terms, and present both related models and our model. In Section 3, we analyze our model and give evidence for our three informal conjectures. We also provide a calculation of the fixed points for the degenerate case. Finally, in Section 4, we discuss our results and provide directions for the future.

2 Preliminaries

2.1 Notation

We denote column vectors as \mathbf{x} and \mathbf{y} , while row vectors are denoted as \mathbf{x}^T and \mathbf{y}^T . The i th coordinate of \mathbf{x} is denoted by x_i . For a matrix A , we define $(A\mathbf{x})_i = \sum_j A_{i,j}x_j$. We let $\mathbf{E}[X]$ denote the expected value of the event X .

2.2 Evolutionary Game Theory

In a game, each player may pick a *strategy*, and the *payoff* is determined by the selected strategies. For two-player games, payoffs for each player are typically represented by a *payoff matrix* W , where each entry $W_{i,j}$ is the payoff for the first player playing their strategy i and the second player playing their strategy j . Players may also choose to randomly play each strategy i with a certain probability x_i , and the distribution of these probabilities is called a *mixed strategy*. A mixed strategy can then be represented as vector \mathbf{x} . If a player picks a single strategy with probability 1, it is called a *pure strategy*.

A pair $(\mathbf{x}^*, \mathbf{y}^*)$ of mixed strategies is a *Nash equilibrium* for two players if

$$\begin{aligned} \forall \mathbf{x} \neq \mathbf{x}^*, \quad (\mathbf{x}^*)^T W \mathbf{y}^* &\geq \mathbf{x}^T W \mathbf{y}^* \\ \forall \mathbf{y} \neq \mathbf{y}^*, \quad (\mathbf{x}^*)^T W \mathbf{y}^* &\geq (\mathbf{x}^*)^T W \mathbf{y}, \end{aligned}$$

where W is the payoff matrix.

As described by Chastain *et al.* [2], evolution is related to a game by viewing genes as players. Then we can view alleles, or types, of a gene as its strategies and the frequency distribution of the alleles in the population as its mixed strategy. As an outcome of the game, an organism's ability to reproduce is determined by its payoff from its alleles. A gene's payoff is, thus, interpreted as its fitness and the payoff matrix as the fitness landscape or the environment for the given genes. This determines the distribution of alleles in the next generation. The exact way the payoff matrix determines the number of offspring depends on the model, described in the following sections.

2.3 Population Replicator Dynamics with and without Mutations for Static Environments

We now reintroduce models extensively studied in [7] and [8]. The replicator dynamics model considers population dynamics for a haploid species, which have a single set of chromosomes, with two genes. Let S_1 and S_2 be the set of possible alleles for the first and second gene, respectively. Then an individual can be represented by their alleles $(i, j) \in S_1 \times S_2$. We assume that $n = |S_1| = |S_2|$, so that W is an $n \times n$ matrix. The environment for a species is represented by W , i.e. the fitness of an organism (i, j) can be represented by the entry $W_{i,j}$. Let x_i denote the proportion of the first gene in the population with allele i and y_j as the proportion of the second gene in the population with allele j . Then \mathbf{x} and \mathbf{y} are the probability distributions of the alleles for the first and second gene, respectively.

2.3.1 Model without mutation

For each generation, an organism (i, j) picks another organism (i', j') at random, uniformly from the population, to mate with. The pair have four possible offspring, (i, j) , (i', j) , (i, j') ,

or (i', j') , which each occur with probability $\frac{1}{4}$. In the next generation, let x'_i denote the proportion of offspring with allele i as the first gene and let y'_j denote the proportion of offspring with allele j as the second gene in the next generation. Then the expected value of x'_i is proportional to $x_i x_i (W\mathbf{y})_i + 2 \cdot \frac{1}{2} \cdot x_i (1 - x_i) (W\mathbf{y})_i = x_i (W\mathbf{y})_i$. We can derive a similar result for y'_j . Because \mathbf{x}' and \mathbf{y}' are probability distributions and $\sum_{i=1}^n x_i (W\mathbf{y})_i = \mathbf{x}'^T W\mathbf{y}$ is the average fitness, we can normalize to get

$$\mathbf{E}[x'_i] = x_i \frac{(W\mathbf{y})_i}{\mathbf{x}'^T W\mathbf{y}}, \quad \mathbf{E}[y'_j] = y_j \frac{(W\mathbf{x})_j}{\mathbf{y}'^T W\mathbf{x}}.$$

To define a *deterministic* model for population dynamics, we make the additional assumption that the next generation's frequencies follow the expected value. That is, if we let $(\mathbf{x}(t), \mathbf{y}(t))$ denote the frequencies at time t , then the deterministic model for population dynamics without mutations is

$$\begin{aligned} \forall i \in S_1, \quad x_i(t+1) &= x_i(t) \frac{(W\mathbf{y}(t))_i}{\mathbf{x}^T(t)W\mathbf{y}(t)} \\ \forall j \in S_2, \quad y_j(t+1) &= y_j(t) \frac{(W^T\mathbf{x}(t))_j}{\mathbf{y}^T(t)W\mathbf{x}(t)}. \end{aligned} \tag{1}$$

Another way to interpret this is that the deterministic model essentially represents an infinite population.

2.3.2 Model with mutation

In the model with mutations, an allele i in an individual mutates to another allele i' with probability $\tau < \frac{1}{n}$ for all alleles $i' \neq i$. The allele i does not change with probability $1 - (n-1)\tau$.

As shown in [7], the following model describes the population dynamics with mutations

$$\begin{aligned} \forall i \in S_1, \quad x_i(t+1) &= (1 - n\tau)x_i(t) \frac{(W\mathbf{y}(t))_i}{\mathbf{x}^T(t)W\mathbf{y}(t)} + \tau \\ \forall j \in S_2, \quad y_j(t+1) &= (1 - n\tau)y_j(t) \frac{(W^T\mathbf{x}(t))_j}{\mathbf{y}^T(t)W\mathbf{x}(t)} + \tau. \end{aligned} \tag{2}$$

2.4 Our model

In [7], Mehta *et al.* address the possibility of changing environments by allowing each environment to move randomly to a different possible environment, so that the environments form a Markov chain. However, these environment changes are always completely independent. Instead, we take inspiration from [6] by using a feedback-based payoff matrix, which is defined below. Thus, we update the environment as a function of the frequency distribution of the alleles in the genes.

Given k environments $\{W_i\}$ and a function $\theta_i(\mathbf{x}(t), \mathbf{y}(t))$, we can define the following feedback-based payoff matrix

$$W(t) = \sum_{i=1}^k \theta_i(\mathbf{x}(t), \mathbf{y}(t)) W_i. \quad (3)$$

We wish for no individual to survive all k environments, so we generally construct each environment W_i to have a different Nash equilibrium. We now combine (3) with (1) and (2) to obtain the following models. For changing environments without mutations, a population's mixed strategies are determined by

$$\begin{aligned} \forall i \in S_1, \quad x_i(t+1) &= x_i(t) \frac{(W(t)\mathbf{y}(t))_i}{\mathbf{x}^T(t)W(t)\mathbf{y}(t)} \\ \forall j \in S_2, \quad y_j(t+1) &= y_j(t) \frac{(W(t)^T\mathbf{x}(t))_j}{\mathbf{x}^T(t)W(t)\mathbf{y}(t)}. \end{aligned} \quad (4)$$

For changing environments with mutations, a population's mixed strategies are determined by

$$\begin{aligned} \forall i \in S_1, \quad x_i(t+1) &= (1 - n\tau)x_i(t) \frac{(W(t)\mathbf{y}(t))_i}{\mathbf{x}^T(t)W(t)\mathbf{y}(t)} + \tau \\ \forall j \in S_2, \quad y_j(t+1) &= (1 - n\tau)y_j(t) \frac{(W(t)^T\mathbf{x}(t))_j}{\mathbf{x}^T(t)W(t)\mathbf{y}(t)} + \tau. \end{aligned} \quad (5)$$

Note that when $\tau = 0$, (5) degenerates to (4). Additionally, when $\tau = \frac{1}{n}$, $x_i(t+1) = \tau$ and $y_j(t+1) = \tau$, so the frequency of alleles becomes constant after one time step.

In this paper, we generally look at the case when W is a 2×2 payoff matrix because

most genes only have two alleles.

Because we look at 2×2 payoff matrices, \mathbf{x} and \mathbf{y} are 2×1 vectors, so we let $\mathbf{x} = (a, 1-a)^T$ and $\mathbf{y} = (b, 1-b)^T$. Thus, a mixed strategy of two genes is specified by the ordered pair $(a, b) \in [0, 1]^2$.

We then choose $\theta_i(\mathbf{x}, \mathbf{y}) = f_i(a)g_i(b)$, where f_i and g_i are monotonic continuous surjections from $[0, 1]$ to $[0, 1]$, such that $f_i(0.5) = g_i(0.5) = 0.5$. When testing several values of $\theta_i(\mathbf{x}(t), \mathbf{y}(t))$, we found that the shape of f_i or g_i did not significantly change how the payoff matrix and overall model behaved. For this reason, we typically pick $f_i(a) = a$ or $f_i(a) = 1 - a$ and $g_i(b) = b$ or $g_i(b) = 1 - b$.

For example, given a parameter m , consider $h(x) = m(0.5(2x - 1)^9 + 0.5) + (1 - m)x$.

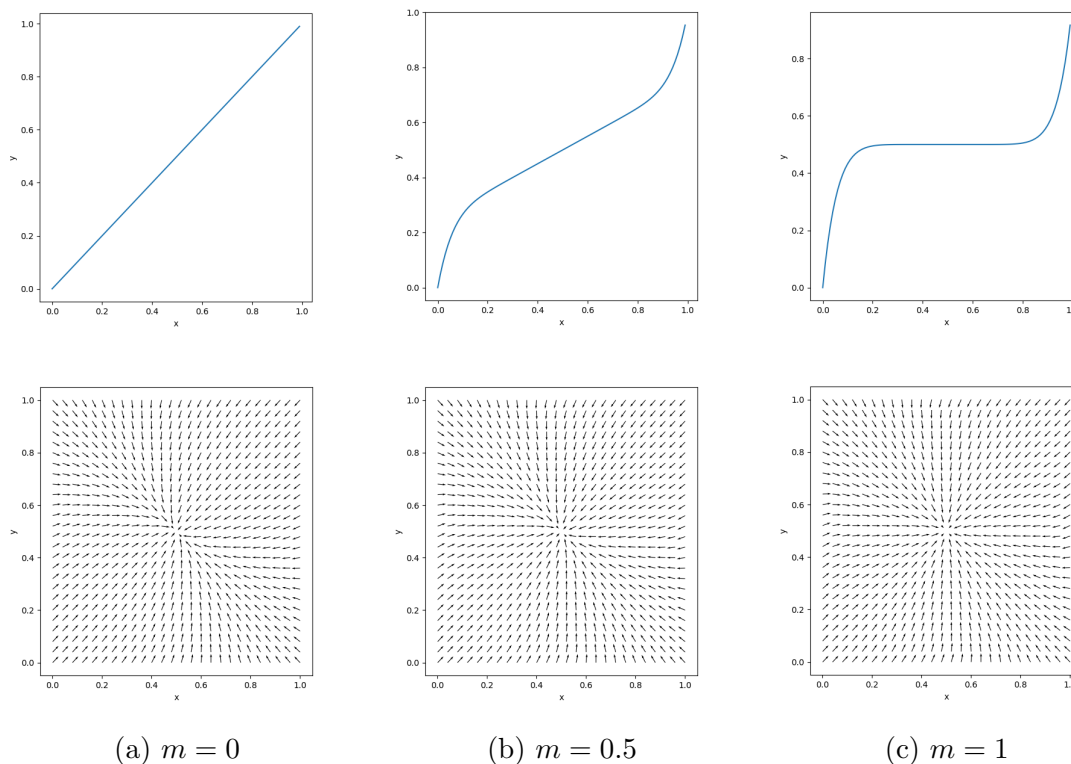


Figure 1: For each of the subfigures, we have a graph of the function $h(x)$ on top and the corresponding phase portrait below it.

Then let

$$W(t) = h(a)h(b) \begin{pmatrix} 1.2 & 0.8 \\ 0.9 & 0.4 \end{pmatrix} + (1 - h(a))(1 - h(b)) \begin{pmatrix} 0.4 & 0.9 \\ 0.8 & 1.2 \end{pmatrix}.$$

We see in Figure 1 that as we vary m , the phase portrait of the model does not change significantly.

3 Characteristics of our Model of Changing Environments

3.1 Degenerate Case: Static Environments

In this section, we look at when $k = 1$. In this case, because of normalization, we may consider our payoff matrix W to be a fixed 2×2 matrix, so $W = \begin{pmatrix} A & B \\ C & D \end{pmatrix}$. Thus, our model describes a static environment. In [4], Mehta *et al.* show that stable fixed points are almost always pure Nash equilibria. Here, we simply calculate all the fixed points for (1).

Let a' and b' be the frequency for the next generation of the first allele of the first and second gene, respectively. Then we have

$$\begin{aligned} a' &= b \frac{(W\mathbf{y})_1}{\mathbf{x}^T W \mathbf{y}} = \frac{a(bA + (1-b)B)}{a[bA + (1-b)B] + (1-a)[bC + (1-b)D]} \\ b' &= b \frac{(W^T \mathbf{x})_1}{\mathbf{x}^T W \mathbf{y}} = \frac{b(aA + (1-a)C)}{b[aA + (1-a)C] + (1-b)[aB + (1-a)D]}. \end{aligned} \tag{6}$$

If (a, b) is a fixed point, then

$$a' = a \text{ and } b' = b. \tag{7}$$

To solve for the fixed points, we will consider the border and interior cases separately.

Case 1: $a \in \{0, 1\}$ or $b \in \{0, 1\}$

Subcase 1: $a = 0$

Plugging $a = 0$ into (6), we see that $a' = 0 = a$ and $b' = \frac{bC}{bC+(1-b)D}$. To satisfy (7), either $b = 0$ or $C = bC + (1 - b)D$. If $C \neq D$, then $b = 1$. Therefore, when $a = 0$, we have two fixed points $(0, 0)$ and $(0, 1)$.

Subcase 2: $a = 1$

Plugging $a = 1$ into (6), we see that $a' = 1 = a$ and $b' = \frac{bA}{bA+(1-b)B}$. To satisfy (7), either $b = 0$ or $A = bA + (1 - b)B$. If $A \neq B$, then $b = 1$. Therefore, when $a = 1$, we have two fixed points $(1, 0)$ and $(1, 1)$.

The cases for $b = 0$ and $b = 1$ are similar to the first two subcases. Therefore, we have four fixed points on the border: $(0, 0)$, $(0, 1)$, $(1, 0)$ and $(1, 1)$. Also note that points on the boundaries stay on the boundaries.

Case 2: $a \notin \{0, 1\}$ and $b \notin \{0, 1\}$

Plugging (7) into (6), we have that

$$a = a' = \frac{a(bA + (1 - b)B)}{a[bA + (1 - b)B] + (1 - a)[bC + (1 - b)D]}.$$

We can do some algebraic manipulations to solve for b , obtaining

$$b = \frac{D - B}{A - C + D - B}.$$

By a similar process, we obtain

$$a = \frac{D - C}{D - C + A - B}.$$

Therefore, if $(\frac{D-C}{D-C+A-B}, \frac{D-B}{A-C+D-B})$ is in the interior of the unit square, then it is a fixed point. This point was shown to be unstable in [4].

3.2 Inducing Oscillations

By [7], we know that (1) and (2) always converge to a fixed point when W is constant. We look at $W(t)$ of a certain form with $k = 2, 3$, and 4 environments, constructed in such a way that the system looks unlikely to converge.

3.2.1 Two Nash equilibria

We first attempt to induce an oscillation between two strategies under (4) and (5). We construct two environments, $W_1 = \begin{pmatrix} B & D \\ A & C \end{pmatrix}$ and $W_2 = \begin{pmatrix} C & A \\ D & B \end{pmatrix}$, such that B is the largest entry and C is the smallest. We choose the entries of our environments in this way so that there is only one Nash equilibria. Then W_1 and W_2 have Nash equilibria at $(1, 1)$ and $(0, 0)$, respectively. Also, we pick $W(t) = (1 - a)(1 - b)W_1 + abW_2$.

In theory, as the system approaches $(0, 0)$, W_1 is the dominating environment, causing the strategy $(1, 1)$ to be favored. Then the system will tend towards $(1, 1)$, which causes W_2 to dominate. Once W_2 is dominating, the system will once again move towards $(0, 0)$ causing a cycle. However, we found that the system always tended towards a fixed point.

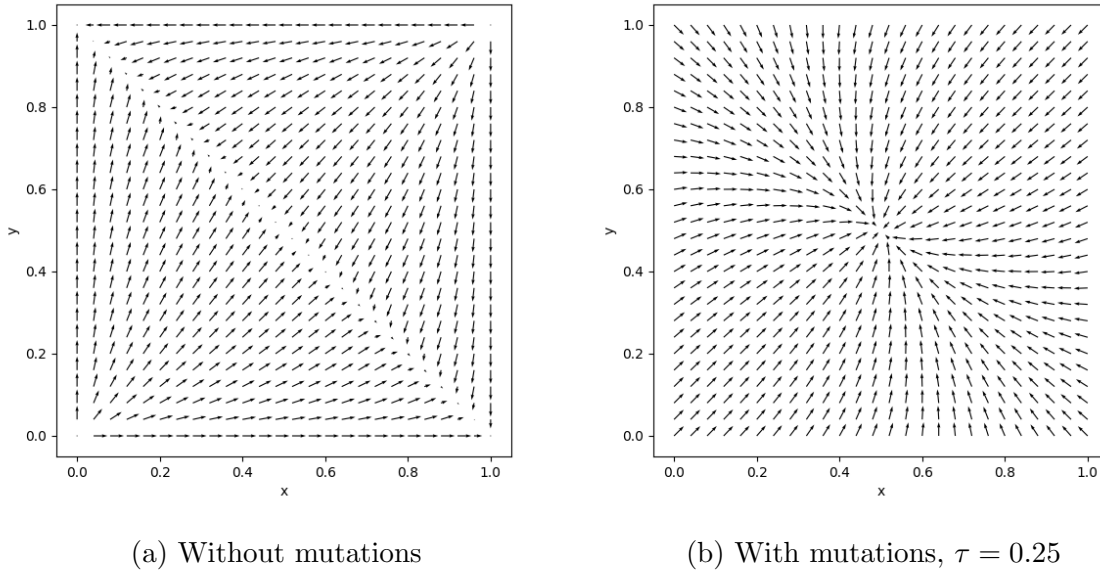


Figure 2: For two Nash equilibria, we set $A = 0.8$, $B = 1.2$, $C = 0.4$, and $D = 0.9$, without and with mutations. We draw the phase portraits.

Conjecture 3.1. *Two Nash equilibria is not sufficient to induce oscillations and will always converge to a fixed point.*

Evidence. In Figure 2, we see numerically that without mutations, the system will converge to some fixed point on the line $a + b = 1$, and with mutations, the system converges to an interior fixed point, which is near the center. \square

We present some progress towards the proof by showing the following lemma.

Lemma 3.2. *The projection of the trajectory of $(a(t), b(t))$ onto the line $a = b$ converges to a point on the line $a + b = 1$, i.e. $(a, b) = (0.5, 0.5)$.*

We first need some lemmas that show that the projection of the trajectory is monotone and bounded.

Lemma 3.3.

$$(a' - a, b' - b) \cdot (1, 1) = K(1 - a - b),$$

where $K > 0$.

Proof. Let $S = abW_{1,1} + a(1 - b)W_{1,2} + (1 - a)bW_{2,1} + (1 - a)(1 - b)W_{2,2}$.

Then we calculate

$$\begin{aligned} a' - a &= \frac{a(W\mathbf{y})_1}{\mathbf{x}^T W \mathbf{y}} - a = \frac{abW_{1,1} + a(1 - b)W_{1,2}}{abW_{1,1} + a(1 - b)W_{1,2} + (1 - a)bW_{2,1} + (1 - a)(1 - b)W_{2,2}} - a \\ &= \frac{a(1 - a)((B - A)(b(1 - b))(1 - 2a) + (D - C)((1 - a)(1 - b)^2 - ab^2))}{S}. \end{aligned}$$

Similarly,

$$b' - b = \frac{b(1 - b)((B - D)(a(1 - a))(1 - 2b) + (A - C)((1 - b)(1 - a)^2 - ba^2))}{S}.$$

Adding these up and grouping the terms, we obtain

$$\begin{aligned} ((a' - a) + (b' - b))S &= A(b(1 - b)((1 - a)^2 + a^2))(1 - a - b) \\ &\quad + B(2ab(1 - a)(1 - b))(1 - a - b) \\ &\quad - C(b(1 - a)(ba + (1 - b)) + a(1 - b)(ab + (1 - a)))(1 - a - b) \\ &\quad + D(a(1 - a)((1 - b)^2 + b^2))(1 - a - b). \end{aligned}$$

Thus, $(a' - a) + (b' - b)$ has the form $K(1 - a - b)$, and since $S > 0$, we only need to show the following to prove $K > 0$:

$$\begin{aligned} & A(b(1 - b)((1 - a)^2 + a^2)) + B(2ab(1 - a)(1 - b)) + D(a(1 - a)((1 - b)^2 + b^2)) \\ & > C(b(1 - a)(ba + (1 - b)) + a(1 - b)(ab + (1 - a))) \\ & = C(a(1 - a)b^2 + b(1 - b)a^2 + (1 - a)(1 - b)(a + b)). \end{aligned}$$

Because $A, B, D > C$,

$$\begin{aligned} D(a(1 - a)b^2) &> C(a(1 - a)b^2), \\ A(b(1 - b)a^2) &> C(b(1 - b)a^2), \end{aligned}$$

$$A(b(1 - a)) + B(2ab) + D(a(1 - b)) > C(b(1 - a)) + C(2ab) + C(a(1 - b)) = C(a + b),$$

which gives us that $K > 0$. □

Lemma 3.4. $a' + b' < 1$ if $a + b < 1$, $a' + b' > 1$ if $a + b > 1$, and $a' + b' = 1$ if $a + b = 1$.

Proof. Using the same notation as Lemma 3.3, we can calculate

$$\begin{aligned} a' &= \frac{abW_{1,1} + a(1 - b)W_{1,2}}{S}, \\ b' &= \frac{abW_{1,1} + (1 - a)bW_{2,1}}{S}. \end{aligned}$$

Therefore,

$$\begin{aligned} S(1 - a' - b') &= (1 - a)(1 - b)W_{2,2} - abW_{1,1} \\ &= (1 - a)^2(1 - b)^2C - a^2b^2C \\ &= (1 - a - b)((1 - a)(1 - b) + ab)C. \end{aligned}$$

Since $(1 - a)(1 - b) + ab$ is positive, then $1 - a' - b'$ has the same sign as $1 - a - b$. Therefore, $a' + b' < 1$ if $a + b < 1$, $a' + b' > 1$ if $a + b > 1$, and $a' + b' = 1$ if $a + b = 1$. □

Proof of Lemma 3.2. By Lemma 3.3 and Lemma 3.4, the projection of the trajectory is monotone and bounded. Therefore, it must converge to some fixed point. From Lemma 3.3,

we see that the only fixed point lies along the line $a + b = 1$, so the proof is complete. \square

3.2.2 Three Nash equilibria

With three environments, we attempt to oscillate between three of the corners, so we construct $W_1 = \begin{pmatrix} A & B \\ C & D \end{pmatrix}$, $W_2 = \begin{pmatrix} B & D \\ A & C \end{pmatrix}$, $W_3 = \begin{pmatrix} C & A \\ D & B \end{pmatrix}$, such that B is the largest entry and C is the smallest. Then W_1 , W_2 , and W_3 have a Nash equilibrium at $(1, 0)$, $(1, 1)$, and $(0, 0)$, respectively. We let the payoff matrix at each generation be $W(t) = (1 - a)(1 - b)W_1 + a(1 - b)W_2 + abW_3$. In this way, as one environment begins to dominate, meaning that the system approaches its Nash equilibrium, it looks like it would begin to maximize another environment's feedback function in a way that loops through the three Nash equilibria. However, in our simulations, we found that the system always tends towards a fixed point when choosing three corners as Nash equilibria.

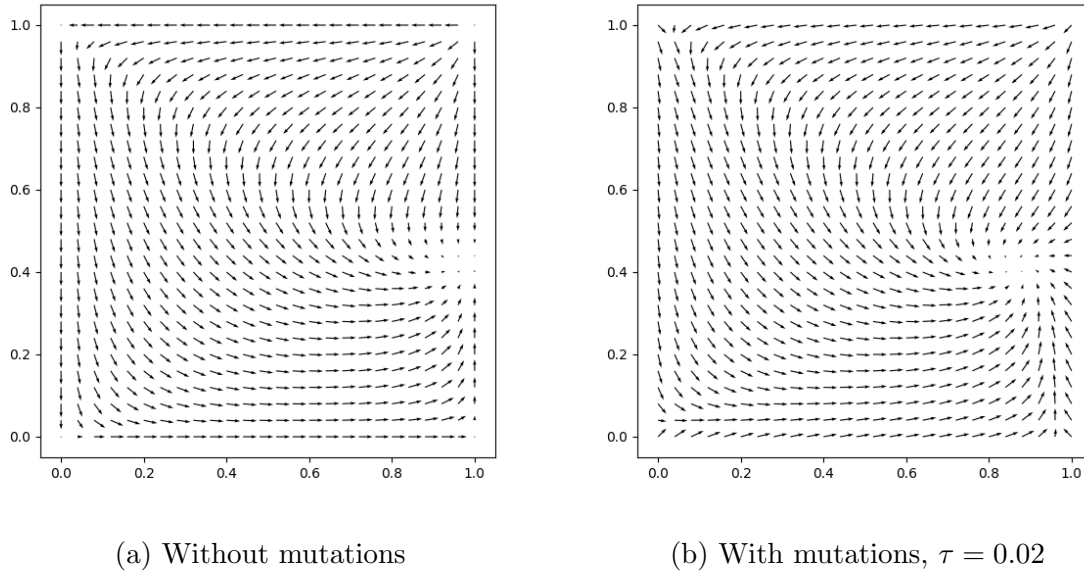


Figure 3: For three Nash equilibria without mutations, we set $A = 0.8$, $B = 1.2$, $C = 0.4$, and $D = 0.9$, without and with mutations. We draw the phase portraits.

Conjecture 3.5. *Inducing oscillations with three Nash equilibria is possible (but not by choosing three corners).*

Evidence. It is unclear whether or not we can induce an oscillation using only three Nash equilibria, but we believe that it may be possible by considering using Nash equilibria which are not on the corners. In particular, we note that [8] was successful in inducing oscillations in a similar type of problem with three Nash equilibria by creating a Rock-Paper-Scissors game, which uses a 3×3 payoff matrix instead.

When the Nash equilibria are the corners, in Figure 3, we see numerically that without mutations, the system converges to a fixed point on the border, and with mutations, the system converges to an interior fixed point near the border. \square

3.2.3 Four Nash equilibria

With four Nash equilibria, we conjecture that we are able to induce an oscillation. We construct four environments, $W_1 = \begin{pmatrix} A & B \\ C & D \end{pmatrix}$, $W_2 = \begin{pmatrix} B & D \\ A & C \end{pmatrix}$, $W_3 = \begin{pmatrix} D & C \\ B & A \end{pmatrix}$, $W_4 = \begin{pmatrix} C & A \\ D & B \end{pmatrix}$, such that B is the largest entry and C is the smallest. Then W_1, W_2, W_3 , and W_4 have a Nash equilibrium at $(1, 0)$, $(1, 1)$, $(0, 1)$, and $(0, 0)$, respectively. We let the payoff matrix at each generation be $W(t) = (1-a)(1-b)W_1 + a(1-b)W_2 + abW_3 + (1-a)bW_4$. Note that the model is constructed in a similar way so that the system generally moves counterclockwise about some fixed point.

Conjecture 3.6. *There exists a stable limit cycle, which grows and shrinks exponentially in terms of τ .*

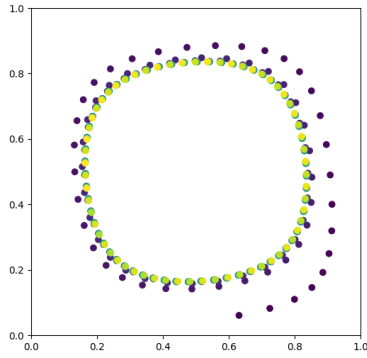
Evidence. In Figure 4(a) and 4(b), we see that the system orbits around a limit cycle counterclockwise after a sufficient amount of time, despite where the system initializes. In Figure 4(c), we see that the system roughly oscillates between the four corners.

We would like to show that there exists a continuous curve C_1 , such that at every point on C_1 , the trajectory points out, and another continuous curve C_2 that surrounds C_1 , such that at every point on C_2 , the trajectory points in. The existence of C_1 and C_2 supports the conjecture that the limit cycle exists. In Figure 4(d), we picked $(a - 0.5)^4 + (b - 0.5)^4 = 10^{-30}$ as the curve C_1 for $\tau = 0.02$. Then applying (5) to a large number of points on the curve, we found numerically that they all point out in this case, suggesting the existence of a limit cycle.

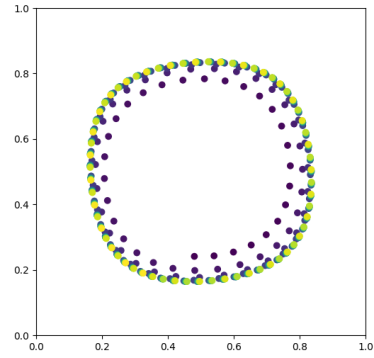
For an analytic proof, note that $(0.5, 0.5)$ is a fixed point because then all the entries of W are equal. Then we could take a sufficiently small neighborhood of points around $(0.5, 0.5)$. We suspect that all points in this neighborhood would be repelled from $(0.5, 0.5)$, which would also show the existence of C_1 .

For C_2 , we consider the boundary of the unit square $[0, 1]^2$. If $a = 0$, then $a' = \tau$. Also, if $a = 1$, then $a' = 1 - \tau$. The cases for $b = 0$ and $b = 1$ are similar. Thus, the system always points inwards for $\tau > 0$. Therefore, we see that we may choose C_2 to be this boundary.

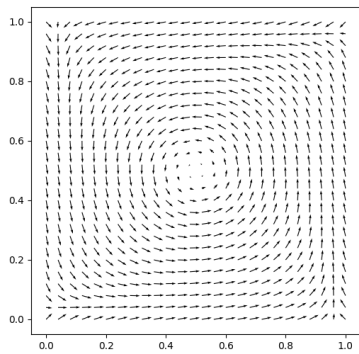
In Figure 5, we note that as τ increases, the curve shrinks in size rapidly. We guess that the rate of decrease is exponential in terms of τ . It is not clear whether the limit cycle eventually shrinks to a single point once τ is large enough or whether the cycle continuously shrinks in size, but we believe the latter to be true. If the former were true, then our numerical evidence for C_1 would not work once τ is larger than some threshold. \square



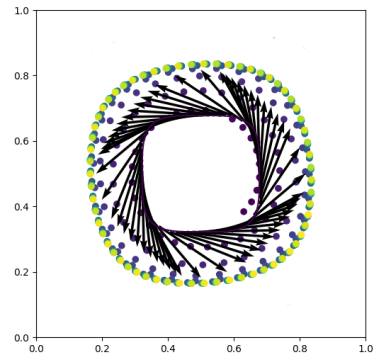
(a) Trajectory When Initialized Outside the Limit Cycle



(b) Trajectory When Initialized Inside the Limit Cycle



(c) Phase Portrait



(d) Direction of Curve Inside Limit Cycle

Figure 4: For four Nash equilibria, we set $A = 0.8$, $B = 1.2$, $C = 0.4$, $D = 0.9$, and $\tau = 0.02$. Note that purple indicates the first timestep, and yellow indicates the last.

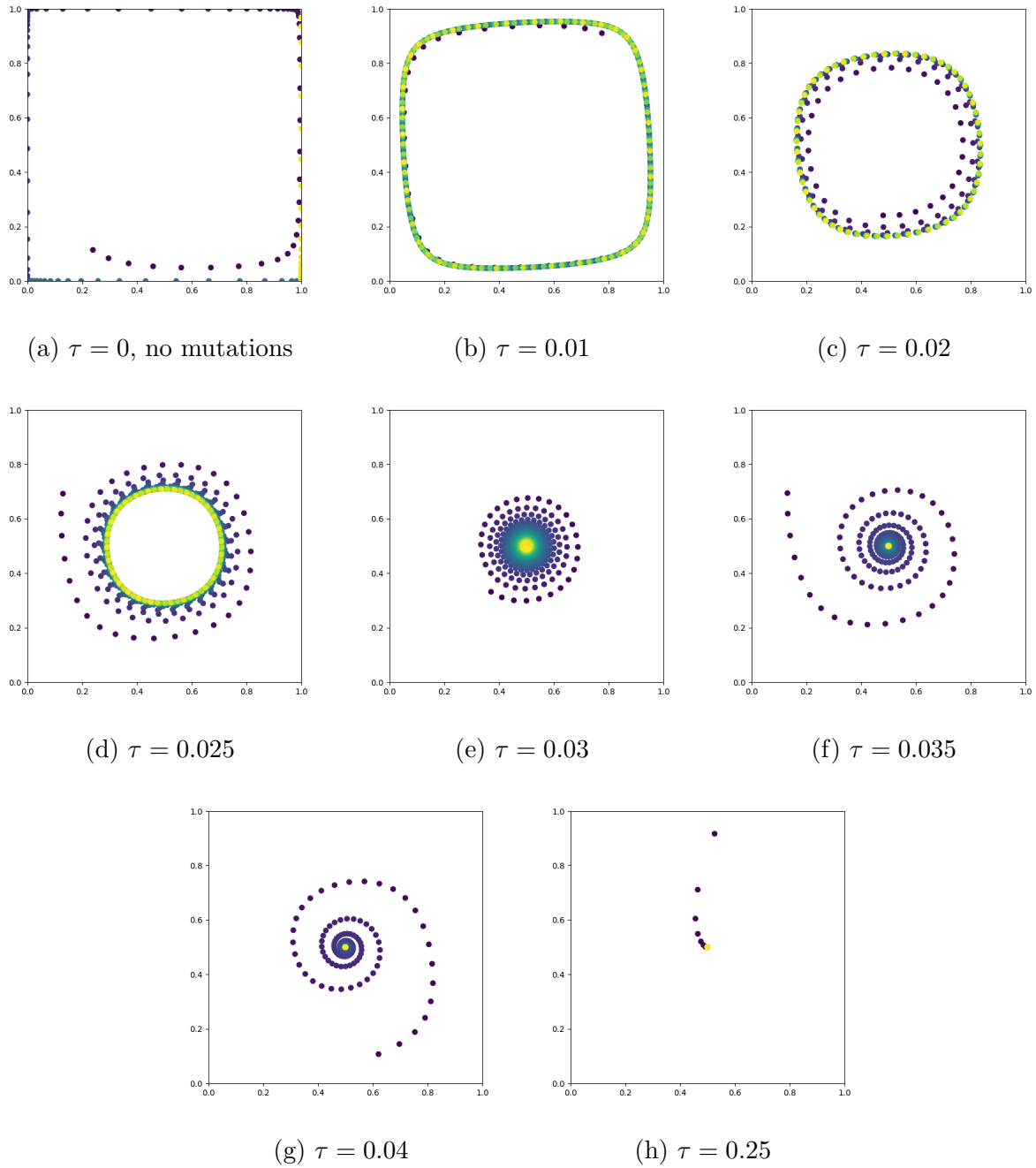


Figure 5: For four Nash equilibria, we set $A = 0.8$, $B = 1.2$, $C = 0.4$, and $D = 0.9$. Note that purple indicates the first timestep, and yellow indicates the last.

4 Conclusion and Future Work

In this paper, we studied various aspects of discrete replicator dynamics and developed a new model that includes changing environments which depends on the allele distribution. In particular, we constructed our model by combining multiple payoff matrices with different Nash equilibria in order to try to find cases where the system does not converge to a fixed point. For two Nash equilibria, we found numerically that the system always converged to a fixed point along the line $a + b = 1$. For three Nash equilibria, we conjecture that because of the Rock-Paper-Scissors game, it may be possible to cause the system to oscillate, but not by choosing only pure Nash equilibria. For four Nash equilibria, we constructed a case in which the system seems to approach a stable limit cycle, whose size changes exponentially with respect to the mutation rate.

Our work also has biological implications. We see that if there are only two environments, the distribution of alleles tends to converge to some fixed point along the middle of the favorable distributions of each environment. For four environments and potentially for three environments, the distribution of alleles does not converge to any single point, and instead exhibits periodic behavior. By viewing a biological problem through the lens of dynamical systems and game theory, we are able to derive new insights into evolutionary behavior and population dynamics.

In creating these models, several questions arise, creating many future directions.

- Can we algebraically solve for the fixed points in our model with changing environments? Can we complete the proof of the existence of a limit cycle? What is the equation for the limit cycle?
- How many Nash equilibria are necessary to induce oscillations? Specifically, does three Nash equilibria work for a 2×2 payoff matrix?

- What if we introduce models that include other biological concepts, like noise and horizontal gene transfer? For example, we could introduce noise by adding some error to each iteration of our model. In some preliminary simulations of this noisy model, it seems like the trajectory with four Nash equilibria stayed within a band around the limit cycle. We can also model horizontal gene transfer, which is a mechanism by which species can pass genetic material among themselves without reproduction, by allowing genes to donate a certain fraction of each of their alleles to each other.
- In [7], Mehta *et al.* look at not only the distribution of genes but also the population size. Mehta *et al.* are able to prove that in their model of changing environments, without mutations, extinction occurs, while with mutations, there is a positive probability of survival. Can we also show something about extinction and survival in our model?

5 Acknowledgments

I would like to express my most sincere gratitude to my mentor, graduate student Mr. YounHun Kim at MIT, who guided me throughout this project and showed me what it means to be a researcher. I would like to thank my brother Mr. Jeffrey Shen for helping me throughout the editing process and making numerous corrections to my paper. Many thanks to my tutor Dr. John Rickert of Rose Hulman, the head math mentor Dr. Tanya Khovanova of MIT mathematics, and RSI alumni Mrs. Emma Smith Zbarsky for their suggestions on my paper. I would like to thank Professor David Jerison, Dr. Ankur Moitra, and Dr. Slava Gerovitch of MIT mathematics for organizing my mentorship. I would not have had this amazing opportunity without my sponsors, Mr. Joshua He, Ms. Zhinuin Xue, and Ms. Audrey Gerson. Thank you to my parents for their endless support. Lastly, I would like to thank the Research Science Institute, Center for Excellence in Education, and the Massachusetts Institute of Technology for giving me the opportunity to conduct this research.

References

- [1] T. Nagylaki, J. Hofbauer, and P. Brunovsky. Convergence of multilocus systems under weak epistasis or weak selection. *Journal of Mathematical Biology*, 1999.
- [2] E. Chastain, A. Livnat, C. Papadimitriou, and U. Vazirani. Algorithms, games, and evolution. *Proceedings of the National Academy of Sciences of the United States of America*, 2014.
- [3] S. Arora, E. Hazan, and S. Kale. The multiplicative weight update method: a meta algorithm and applications. *Theory of Computing*, 2012.
- [4] R. Mehta, I. Panageas, and G. Piliouras. Natural selection as an inhibitor of genetic diversity. Available at <https://arxiv.org/pdf/1408.6270.pdf>, 2014.
- [5] D. Wolf, V. Vazirani, and A. Arkin. Diversity in times of adversity: probabilistic strategies in microbial survival games. *Journal of theoretical biology*, 2005.
- [6] J. S. Weitz, C. Eksin, K. Paarporn, S. P. Brown, and W. C. Ratcliff. An oscillating tragedy of the commons in replicator dynamics with game-environment feedback. *Proceedings of the National Academy of Sciences of the United States of America*, 2016.
- [7] R. Mehta, I. Panageas, G. Piliouras, P. Tetali, and V. V. Vazirani. Mutation, sexual reproduction and survival in dynamic environments. Available at <https://arxiv.org/abs/1511.01409>, 2016.
- [8] J. Hofbauer and K. Sigmund. *Evolutionary Games and Population Dynamics*. Cambridge University Press, Cambridge UK, 1998.