APPLICATIONS OF NON-LINEAR DYNAMICS AND EVOLUTIONARY GAME THEORY IN BIOLOGICAL SYSTEMS

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ABSTRACT

Evolutionary game theory (EGT) is the application of game theory to evolving populations in biology. It defines a framework of contests, strategies, and analytics into which Darwinian competition can be modelled. EGT explains altruistic behaviours in Darwinian evolution, capturing the interest of economists, sociologists, anthropologists, and philosophers. We aim to use EGT and non-linear dynamics to study the oscillatory dynamics of co-evolution of three species, taking mutations into account. Rock–paper–scissors (RPS) games—in which rock crushes scissors, scissors cut paper, and paper wraps rock help understand the co-evolutionary dynamics of different biological systems, such as the cyclic dominance observed in some lizard communities. Another popular example is the cyclic competition between three strains of Escherichia coli. We have primarily referred to the paper by *D. Toupo and S. Strogatz* [1] and attempted to reproduce its results. However, the aforementioned paper assumed knowledge of the mathematics behind the equations describing the system, and skipped their derivation. For a holistic understanding, we also went through the article by *M. Mobilia* [2] and the book by *S. Strogatz* [3], which cover this math, and have included the same in our report.

I.   INTRODUCTION

The emergence of oscillatory (or quasi-oscillatory) behavior of species' population fractions is one of the most appealing and debated phenomena characterizing co-evolution in population dynamics. Oscillatory dynamics has notably been observed in predator–prey and host–pathogen systems. The popular game of Rock-Paper-Scissors acts as a metaphor in evolutionary biology to describe interactions among three competing species in which each species has an advantage over one of its opponents but not the other. In EGT, these interactions are captured in terms of the payoff matrix P.

According to this matrix, when a pair of players A and B interact: The former gets a negative payoff $-\varepsilon$ while the latter gets a payoff 1. In this case, A is dominated by B and its loss is less than B's gain when $0 < \varepsilon < 1$. Whereas B's gain is higher than A's loss when $\varepsilon > 1$. The parameter ε allows to introduce an asymmetry (when $\varepsilon \neq 1$) in the interactions. When $\varepsilon = 1$, one of the players loses what the other gains and this perfect balance corresponds to a zero-sum game. In addition to the above processes of selection/reproduction, we introduce a third evolutionary mechanism that allows each individual to mutate from one species to another with rate μ:

vs	Rock (A)	Paper (B)	Scissors (C)
Rock (A)	0	$-\varepsilon$	1
Paper (B)	1	0	$-\varepsilon$
Scissors (C)	$-\varepsilon$	1	0

FIG. 1. Payoff Matrix.

$$A \xrightarrow{\mu} \begin{cases} B \\ C \end{cases}, \quad B \xrightarrow{\mu} \begin{cases} A \\ C \end{cases}, \quad C \xrightarrow{\mu} \begin{cases} A \\ B \end{cases}$$

II.   GLOBAL MUTATIONS

Why do we need to consider mutations after all? Let us illustrate this using an analogy with our RPS game. Let x represent the population of players who tends to play rock, y represent the population of players who tend to play paper and z represent the population of players who tend to play scissors.
Suppose the number of players who tend to play scissors increases. As a result:

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1. The players who were playing paper will tend to switch to playing either scissors or rock.
2. Players who were playing rock will tend to use the same strategy as before.
3. Players who were playing scissors will tend to switch to playing rock.
This justifies including mutations in our system.

The equations governing the time evolution of the system are called **replicator equations (REs).**The system described above is modelled using the vector $\mathbf{x}(t)$, whose components x_i are the respective population fractions, with $i\epsilon\{1,2,3\}$, are $x_1 = x(t); x_2 = y(t)$ and $x_3 = z(t)$. Obviously, $x + y + z = 1$ and $\dot{x} + \dot{y} + \dot{z} = 0$. Consequently, the REs read:

$$\dot{x}_i = x_i[(\mathcal{L}(\mathbf{x}))_i - \mathbf{x} \cdot \mathcal{L}(\mathbf{x})] = x_i[f_i(\mathbf{x}) - \phi(\mathbf{x})]$$

Where the dot stands for the time derivative. The important notion of average payoff (per individual) of species i, $f_i(\mathbf{x})$, has been introduced in terms of the payoff matrix as a linear function of the relative abundances: $f(\mathbf{x}) = (\mathcal{L}(\mathbf{x}))$. $\phi(\mathbf{x})$ denotes the population's mean payoff. In this setting, the natural generalization of the replicator equations for the model under consideration is: $\dot{x}_i = x_i[f_i(\mathbf{x}) - \phi(\mathbf{x})] + \mu(1 - 3x_i)$. In order to understand the replicator equations, we must familiarize ourselves with the following jargon:

- **Payoff**: (the advantage for a particular species i over others) $f_i = x_j - \varepsilon x_k$ where x_i has an advantage over x_j but is at loss over x_k. Ex. $f_A = c - \varepsilon b$
- **Mean payoff**: (the mean advantage) $\phi = \sum x_i f_i = a(c - \varepsilon b) + b(a - \varepsilon c) - c(b - \varepsilon a) = (1 - \varepsilon)(ab + bc + ca)$
- Thus the **rate of change of a particular population fraction**: $(x_i) = x_i[f_i - \phi]$ + effects of mutations

Consequently, we arrive at the following system of equations:

$$
\begin{array}{l|l}
\dot{x} = x(f_x - \phi) + \mu(-2x + y + z) & f_x = 1 - x - (\epsilon + 2)y \\
\dot{y} = y(f_y - \phi) + \mu(-2y + x + z) & f_y = (\epsilon + 2)x + (\epsilon + 1)(y - 1) \\
\dot{z} = z(f_z - \phi) + \mu(-2z + x + y) & f_z = y - (\epsilon + 1)x
\end{array}
$$

Solving for ϕ:

$$
\begin{aligned}
\phi &= xf_x + yf_y + zf_z \\
&= \epsilon(x^2 + y^2 - x - y + xy)
\end{aligned}
$$

Hence, the differential equations now stand as:

$$
\begin{aligned}
\dot{x} &= -\epsilon x^3 + (\epsilon - 1)x^2 + x - 2xy - \epsilon xy^2 - \epsilon x^2 y + \mu(1 - 3x) \\
\dot{y} &= -\epsilon y^3 + (2\epsilon + 1)y^2 - (\epsilon + 1)y - \epsilon x^2 y + (2\epsilon + 2)xy - \epsilon xy^2 + \mu(1 - 3y)
\end{aligned}
$$

On solving the equations for $\dot{x} = \dot{y} = \dot{z} = 0$, we get $(\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ as a fixed point for all μ and $(1,0,0), (0,1,0), (0,0,1)$ as fixed points when $u = 0$: these 3 points form a heteroclinic saddle cycle. We consider the case $u > 0$ i.e., species can mutate into each other. The Jacobian for this non linear system is calculated as:

$$
J = \begin{pmatrix} -3\epsilon x^2 + 2(\epsilon - 1)x + 1 - 2y - \epsilon y^2 - 2\epsilon xy - 3\mu & -2x - 2\epsilon xy - \epsilon x^2 \\ -2\epsilon xy + (2\epsilon + 2)y - \epsilon y^2 & -3\epsilon y^2 + (4\epsilon + 2)y - (\epsilon + 1) - \epsilon x^2 + (2\epsilon + 2)x - 2\epsilon xy - 3\mu \end{pmatrix}
$$

Substituting $x = y = z = \frac{1}{3}$, we get:

$$
J = \begin{pmatrix} -\frac{1}{3} - 3\mu & -\frac{\epsilon+2}{3} \\ \frac{\epsilon+2}{3} & \frac{\epsilon+1}{3} - 3\mu \end{pmatrix}
$$

The characteristic polynomial (in λ) is:

$$\lambda^2 - (\frac{\epsilon}{3} - 6\mu)\lambda + 9\mu^2 - \epsilon\mu + \frac{\epsilon^2 + 3\epsilon + 3}{9} = 0$$

We obtain the eigenvalues:

$$\lambda_1, \lambda_2 = (\frac{\epsilon}{6} - 3\mu) \pm \frac{\epsilon + 2}{2\sqrt{3}}i$$

the eigenvalues are imaginary and the real part of the eigenvalues changes sign at $\mu = \frac{\epsilon}{18}$ On calculating the radial velocity $\dot{r}$ by $\dot{r} = \frac{x}{\sqrt{x^2+y^2}}\dot{x} + \frac{y}{\sqrt{x^2+y^2}}\dot{y}$, we observe that $\dot{r} < 0$ for all x, y if $\mu > \frac{\epsilon}{18}$. This means that when the fixed point is stable, we have no limit cycles. Hence we have a **supercritical Hopf Bifurcation** at $\mu = \frac{\epsilon}{18}$.

Having addressed global mutations, we now explore **single mutations**.

III.   SINGLE MUTATIONS

Here a particular species mutates into another species at a constant rate μ, which gives rise to very interesting dynamical behaviour. Because of the cyclic symmetry of the rock-paper-scissors game, it suffices to consider only two of the six possible single-mutation pathways. Without loss of generality, we restrict attention to rock(x) $\rightarrow$ paper(y) and paper(y) $\rightarrow$ rock(x). Let us investigate the two cases further.

Case 1: $x \rightarrow y$

When rock mutates into paper, the governing equations get modified as:

$$\dot{x} = x(f_x - \phi - \mu) \tag{1}$$
$$\dot{y} = y(f_y - \phi + \mu) \tag{2}$$

There are 3 **fixed points** of the system: $(0,0)$, $(0,1)$ and an inner fixed point (x_3, y_3) given by

$$x_3 = \frac{(\epsilon+3)A_1 + \epsilon(3\mu + \epsilon^2 + 3\epsilon\mu - 6) - 9}{6(\epsilon(\epsilon+3)+3)}$$

$$y_3 = \frac{-6\mu + A_1 + \epsilon(-3\mu + \epsilon + 3) + 3}{6(\epsilon(\epsilon+3)+3)}$$

where $A_1 = \sqrt{-3\mu^2\epsilon^2 - 6\mu\epsilon(\epsilon(\epsilon+3)+3) + (\epsilon(\epsilon+3)+3)^2}$ Note that $(x_3, y_3) \rightarrow (\frac{1}{3}, \frac{1}{3})$ when $\mu \rightarrow 0$. Using linear stability analysis, we infer that the system undergoes a **supercritical Hopf bifurcation** when

$$u_h = \frac{2(\sqrt{\epsilon(\epsilon+2)(4\epsilon(\epsilon+2)+9)+9} - 3) - 3\epsilon(\epsilon+2)}{7\epsilon} \simeq \frac{\epsilon}{3}$$

for small ϵ. The fixed point (x_3, y_3) is stable for $\mu > \mu_h$. The system exhibits a **stable limit cycle** for $\mu < \mu_h$, which is typical for a supercritical Hopf bifurcation.

Case 2: $y \rightarrow x$

We must note that the dynamics of this case differs qualitatively from the first - the natural tendency is to mutate from rock to paper, because paper has an advantage over rock. The equations describing dynamics for this are:

$$\dot{x} = x(f_x - \phi) + \mu y$$
$$\dot{y} = y(f_y - \phi) - \mu y$$

There are a total of 4 fixed points for this system, as opposed to 3 for the previous case. This happens because the direction of mutation opposes the inherent flow of the system.

A new fixed point (x_4^*, y_4^*) on the boundary line given by $z = 0$ and $x + y = 1$ is created for parameter values in the region above transcritical bifurcation curve. The non-trivial fixed points are given by (x_3^*, y_3^*) and (x_4^*, y_4^*):

$$x_3^* = \frac{6\mu + A_1 + \epsilon(3\mu + \epsilon + 3) + 3}{6(\epsilon(\epsilon+3)+3)}, \quad y_3^* = \frac{(-2\epsilon - 3)A_1 + \epsilon(-3\mu + \epsilon(4\epsilon+15)+21)+9}{6(\epsilon(\epsilon+3)+3)}$$

$$A_1 = \sqrt{-3\mu^2\epsilon^2 - 6\mu\epsilon(\epsilon(\epsilon+3)+3) + (\epsilon(\epsilon+3)+3)^2}$$

and

$$x_4^* = \frac{\epsilon+1+\sqrt{(\epsilon+1)^2 - 4\mu\epsilon}}{2\epsilon}, \quad y_4^* = \frac{\epsilon-1+\sqrt{(\epsilon+1)^2 - 4\mu\epsilon}}{2\epsilon}$$

The fixed point (x_4^*, y_4^*) only exists for parameter values above the transcritical bifurcation curve. Linearization

about the fixed point yields:

$$\mu_{trans} = \frac{\epsilon - \sqrt{\epsilon + 1}}{\sqrt{\epsilon + 1}}$$

The Hopf bifurcation curve is given by:

$$\mu_h = \frac{2(\sqrt{\epsilon(\epsilon + 2)(4\epsilon(\epsilon + 2) + 9) + 9)} - 3) - 3\epsilon(\epsilon + 2)}{7\epsilon}$$

$$\approx \frac{\epsilon}{3} - \frac{4\epsilon^3}{27} + \frac{4\epsilon^4}{27} - \frac{4\epsilon^5}{243} + O(\epsilon^6)$$

IV. RESULTS

Using Python, we have plotted the phase space behavior for the cases of no mutations (FIG.1), global mutations (FIG.2), and single mutations (FIG. 3 and FIG. 4). For FIGs. 2,3 and 4, we have depicted our simulations in part (a) on the left and results from the paper in part (b), on the right. FIG.1 was not in the paper. The codes have been hyperlinked [4].
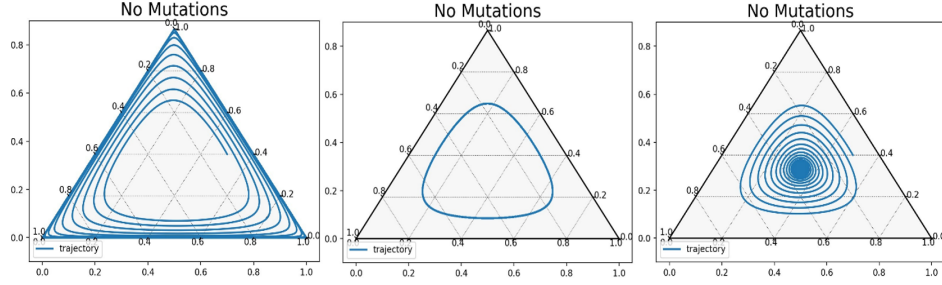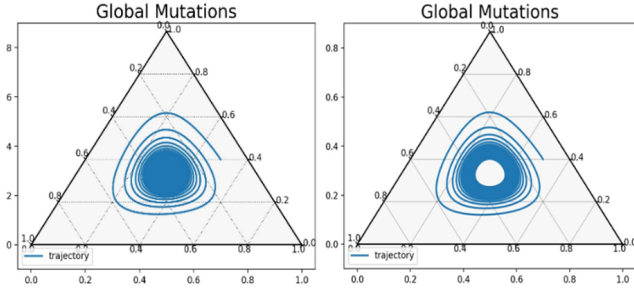

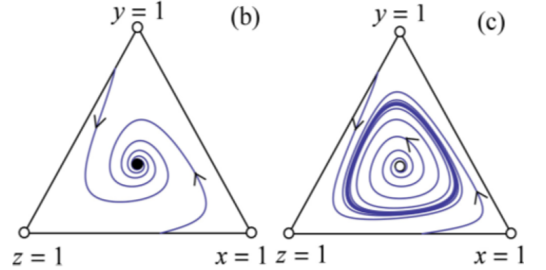FIG. 1. No mutations ($\mu = 0$)

FIG. 2a. Global mutations (ours)

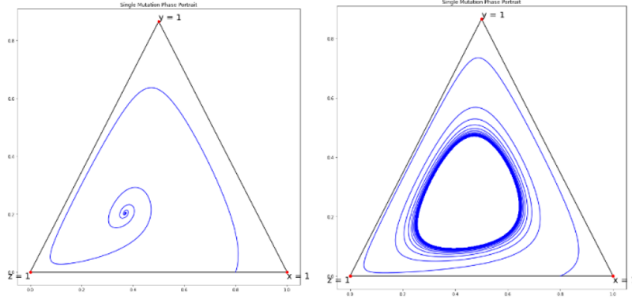FIG. 2b. Global mutations (paper) [1]

FIG. 3a. Single mutations $x \rightarrow y$ (ours)
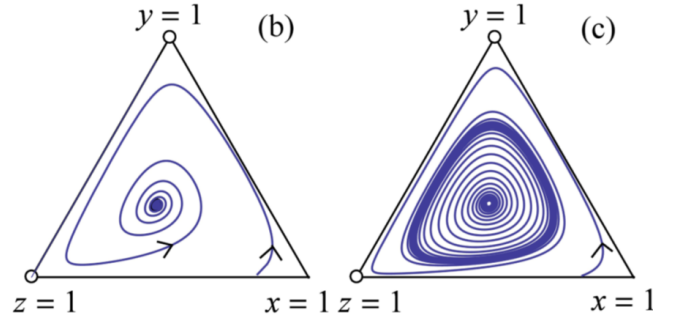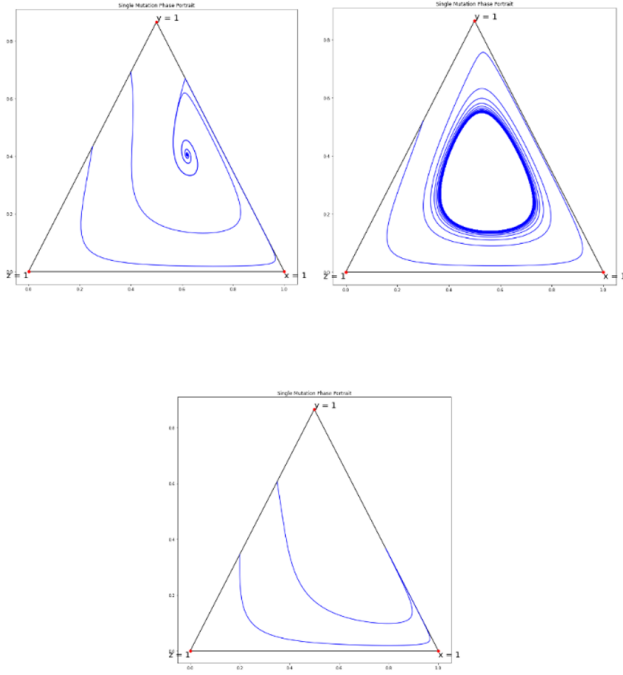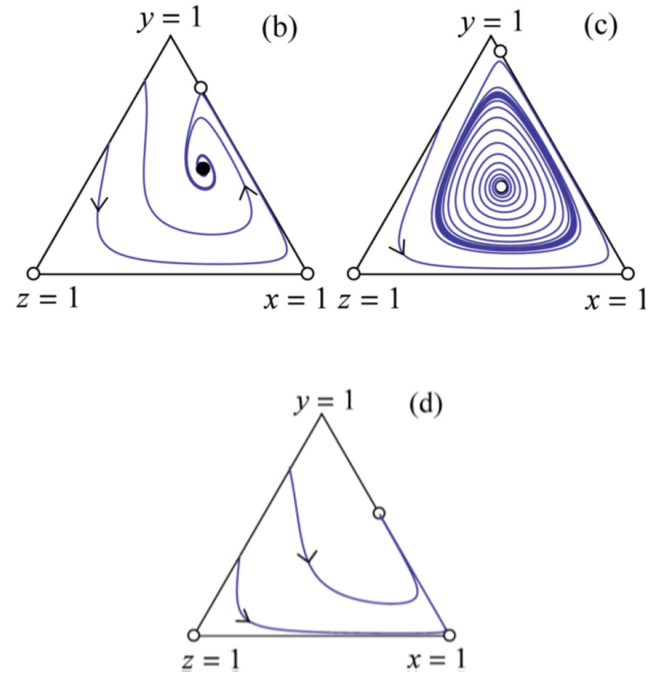

FIG. 3b. Single mutations $x \rightarrow y$ (paper) [1]

FIG. 4a. Single mutations $y \to x$ (ours)

FIG. 4b. Single mutations $y \to x$ (paper)[1]

V. CONCLUSION AND OPEN QUESTIONS

Our analysis of the Replicator-Mutator equations describing interactions and mutations in the biological system, has revealed a rich and diverse phase space behaviour - existence of **cyclic dominance, co-existence states, stable limit cycles and Hopf bifurcations**, to name a few. A common feature observed for a wide class of mutation patterns, is the existence of stable limit cycle solutions. For such mutation patterns, a tiny rate of mutation and a miniscule departure from a zero-sum game is enough to destabilise the co-existence state of the Rock-Paper-Scissors game and to set it into self-sustained oscillations.

However it remains an open question, as to whether limit cycles exist for *all* patterns of mutation. In the most general case, the rates and pathways of mutation will be a function of several parameters. Another shortcoming in our results, is that the Replicator-Mutator equations have been derived considering the system of the three species to be completely isolated - the effect of the surrounding environment has been completely neglected. It will be interesting to investigate the dynamics of the system in more realistic scenarios, where the effects of environment and variable mutation rates are considered. Such investigations will undoubtedly open the doors to new frontiers in EGT and Population Dynamics.

[1] Mauro Mobilia. Oscillatory dynamics in rock–paper–scissors games with mutations. *Journal of Theoretical Biology*, 264(1):1–10, 2010.
[2] H Strogatz Steven and R Strogatz. Nonlinear dynamics and chaos: with applications to physics, biology, chemistry, and engineering, 1994.
[3] Danielle FP Toupo and Steven H Strogatz. Nonlinear dynamics of the rock-paper-scissors game with mutations. *Physical Review E*, 91(5):052907, 2015.