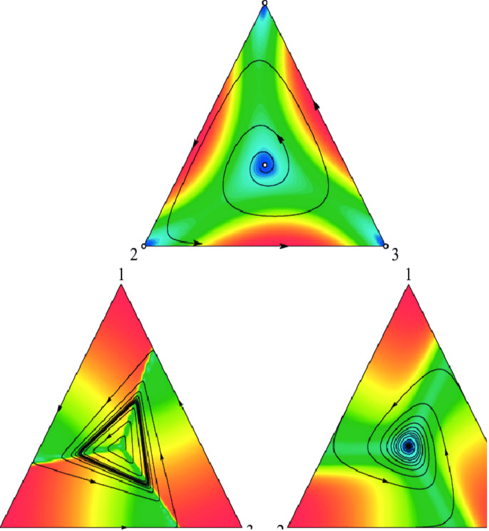

Applications of Evolutionary Game Theory and Non-linear Dynamics to Biological Systems

Team-F

IIT Bombay

Non-Linear Dynamics in Biology

Our Project: Studying three way oscillatory model of co-evolution with mutations.

PHYSICAL REVIEW E **91**, 052907 (2015)

Nonlinear dynamics of the rock-paper-scissors game with mutations

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(Received 11 February 2015; published 11 May 2015)

We analyze the replicator-mutator equations for the rock-paper-scissors game. Various graph-theoretic patterns of mutation are considered, ranging from a single unidirectional mutation pathway between two of the species, to global bidirectional mutation among all the species. Our main result is that the coexistence state, in which all three species exist in equilibrium, can be destabilized by arbitrarily small mutation rates. After it loses stability, the coexistence state gives birth to a stable limit cycle solution created in a supercritical Hopf bifurcation. This attracting periodic solution exists for all the mutation patterns considered, and persists arbitrarily close to the limit of zero mutation rate and a zero-sum game.

DOI: 10.1103/PhysRevE.91.052907 PACS number(s): 05.45.−a, 87.23.Cc, 87.18.−h

Introduction

What is game theory? - decision making
Evolution/animal behavior
Lets look into how it's usually discussed - everyday behavior - game of chess - individual players make decisions - affects not just decision maker, but everyone playing the game - THIS IS WHERE GAME THEORY COMES INTO PLAY!
We try to predict the behaviors we expect to see when the individuals are actually playing this game. But - what does all this have to do with evolution?
Evolutionary theory - individuals who have the best fit for environment - most likely to survive, and their differentiating gene would eventually become more common.

Important aspect relating to game theory, ie, influence by other players - is the reproduction part - can't happen in isolation. Environment too! We need to understand how the organism fits it not only into its physical but also its social environment - might need to coordinate with other organisms to find food, escape predators, raise young. Essentially - fitness of the organism depends on how it's behavior matches up with the behavior of another animals in the group - we're now talking in terms of game theory - life is the game!

EGT:Evolutionary Game Theory

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.

RPS

The emergence of oscillatory (or quasi-oscillatory) behavior is one of the most appealing and debated phenomena that often characterizes co-evolution in population dynamics. Oscillatory dynamics has notably been observed in predator–prey and host–pathogen systems.
Our aim is to study the oscillatory dynamics of rock–paper–scissors games with mutations look at how that this favors the long-lasting co-evolution of all species. Rock–paper–scissors (RPS) games—in which rock crushes scissors, scissors cut paper, and paper wraps rock helps understand the co-evolutionary dynamics of different biological systems, such as the cyclic dominance observed in some communities of lizards. Another popular example is the cyclic competition between three strains of Escherichia coli.

RPS payoff Matrix

In their essence, all variants of the RPS game aim at describing the co-evolutionary dynamics of three species, say A, B and C. We say that A dominates over C, which outcompetes B, which outgrows A and thus closes the cycle. In EGT, the interactions are specified in terms of a payoff matrix P. Generically, the cyclic dominance of RPS games is captured by the following payoff matrix P.

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

According to the above matrix P, when a pair of A and B players interacts: 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 player 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:

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

REs: Replicator equations

The system described above is modelled using the vector $\mathbf{x}$(t), whose components x_i are the respective population fractions, with $i \epsilon \{A, B, C\}$, are $x_A = x(t); x_B = y(t)$ and $x_C = z(t)$, 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 with mutation is:
$\dot{x}_i = x_i[f_i(\mathbf{x}) - \phi(\mathbf{x})] + \mu(1 - 3x_i)$.

Understanding the REs

1. 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. $f_A = z - \varepsilon y$
2. Mean payoff: (the mean advantage) $\phi = \sum x_i f_i = x(z - \varepsilon y) + y(x - \varepsilon z) - z(y - \varepsilon x) = (1 - \varepsilon)(xy + yz + zx)$
3. Thus the rate of change of a particular population fraction: $\dot{x}_i = x_i[f_i - \phi] + Mutation$

$\therefore$The system of equations is:

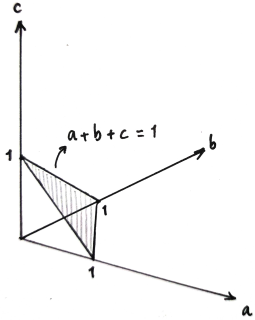
$$\dot{x} = x[z - \varepsilon y + (1 - \varepsilon)(xy + yz + zx)] + \mu(1 - 3x)$$

$$\dot{y} = y[x - \varepsilon z + (1 - \varepsilon)(xy + yz + zx)] + \mu(1 - 3y)$$

$$\dot{z} = z[y - \varepsilon x + (1 - \varepsilon)(xy + yz + zx)] + \mu(1 - 3z)$$

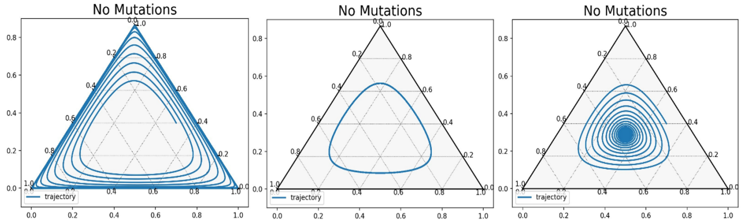
Phase behaviour (without mutation)

In the absence of mutations ($\mu = 0$) the REs admit one interior fixed point, $s^* = (a^*, b^*, c^*) = (1/3, 1/3, 1/3)$ and three absorbing states (1, 0, 0), (0, 1, 0) and (0, 0, 1).



1. When $\varepsilon < 1$, s^* is the system's only attractor, it is globally stable and the trajectories in the phase portrait spiral towards it.
2. When $\varepsilon > 1$, the interior rest point s^* becomes unstable and the flows in the phase portrait form a heteroclinic cycle connecting each of the absorbing fixed points (saddles) at the boundary of the phase portrait. Any fluctuations cause the rapid extinction of two species.
3. When $\varepsilon = 1$, ϕ vanishes (zero-sum game) and the interior rest point s^* is a center. In this case, the quantity a(t)b(t)c(t) is a constant of motion and the trajectories in the phase portrait form closed orbits.

Simulation Results



Having looked at the simpler case of no mutations we now introduce **Global Mutations**.

Note: here onward the variable ε is replaced by $\varepsilon + 1$. This is done in order to increase convenience while programming because the zero sum game now corresponds to $\varepsilon = 0$.

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 fraction of players who tends to play rock, y represent the population fraction of players who tend to play paper and z represent the population fraction of players who tend to play scissors.

Suppose the number of players who tend to play scissors increases. As a result:

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.

Global Mutations

Following the same procedure as before we calculate the Payoffs (f_i) for each individual species and the Mean Payoff (ϕ).
(using constraints $x + y + z = 1$ and $\dot{x} + \dot{y} + \dot{z} = 0$)

1. $f_x = 1 - x - (\epsilon + 2)y$
2. $f_y = (\epsilon + 2)x + (\epsilon + 1)(y - 1)$
3. $f_z = y - (\epsilon + 1)x$
4. $\phi = \epsilon(x^2 + y^2 - x - y + xy)$

Hence, the differential equations now stand as:
$\dot{x} = -\epsilon x^3 + (\epsilon - 1)x^2 + x - 2xy - \epsilon xy^2 - \epsilon x^2 y + \mu(1 - 3x)$
$\dot{y} = -\epsilon y^3 + (2\epsilon + 1)y^2 - (\epsilon + 1)y - \epsilon x^2 y + 2(\epsilon + 1)xy - \epsilon xy^2 + \mu(1 - 3y)$

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:

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

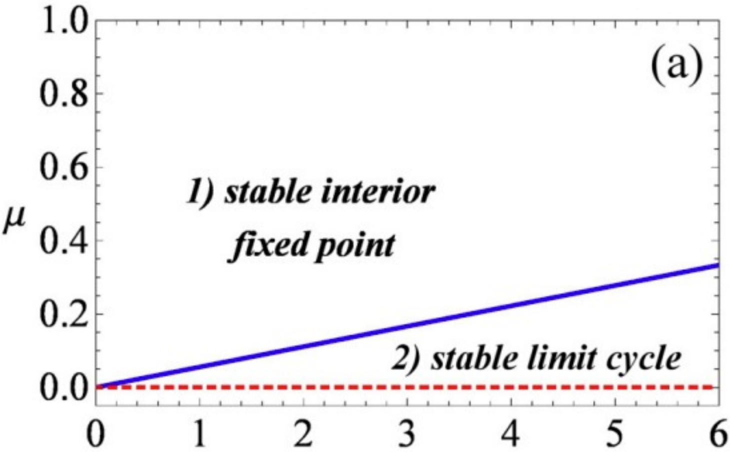
Hopf Bifurcation

We obtain the eigenvalues:

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

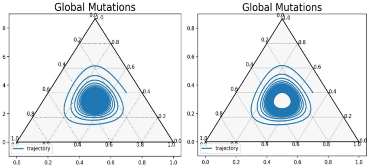
the eigenvalues are imaginary and the real part of the eigenvalues changes sign at $\mu = \frac{\epsilon}{18}$ On calculating the radial velocity $\dot{r}$ by $\dot{r} = \frac{x}{\sqrt{x^2+y^2}}\dot{x} + \frac{y}{\sqrt{x^2+y^2}}\dot{y}$, we observe that $\dot{r} < 0$ for all x, y if $\mu > \frac{\epsilon}{18}$.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

Bifurcation Diagram

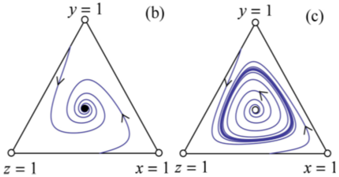


Phase Space Behaviour

Simulation:



Results from paper:



Having addressed global mutations, we now explore **Single Mutations**.

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). We investigate the two cases further.

Single Mutations Case:1

Case 1: $x \to y$

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

$$\dot{x} = x(f_x - \phi - \mu) \tag{1}$$

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

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

Single Mutations Case:1

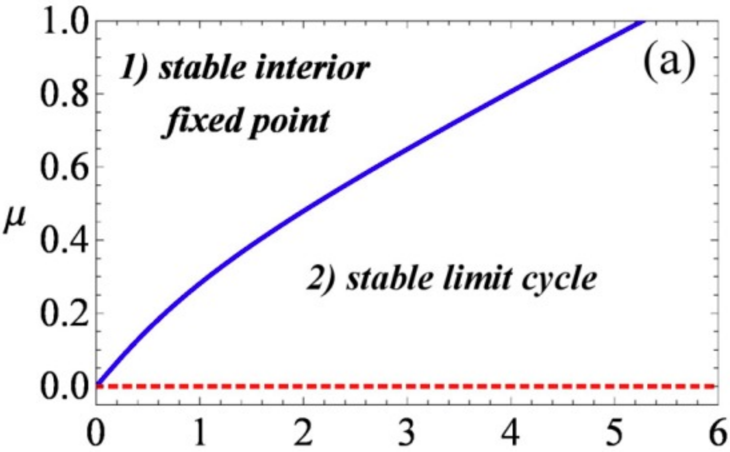
Note that $(x_3, y_3) \to (\frac{1}{3}, \frac{1}{3})$ when $\mu \to 0$. Now, Using linear stability analysis, we infer that the system undergoes a **supercritical Hopf bifurcation** when

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

for small ϵ.

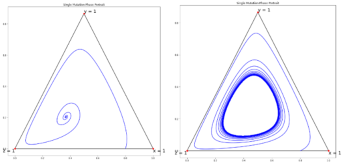
The fixed point (x_3, y_3) is stable for $\mu > \mu_h$. The system exhibits a **stable limit cycle** for $\mu < \mu_h$, which is typical for a supercritical Hopf bifurcation.

Bifurcation Diagram

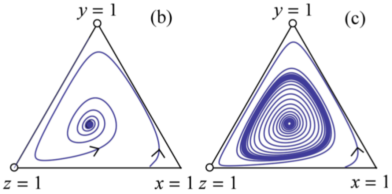


Single Mutations Case:1

Simulations:



Results from paper:



Single Mutations Case:2

Case 2: $y \to x$

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^*):

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

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

and

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

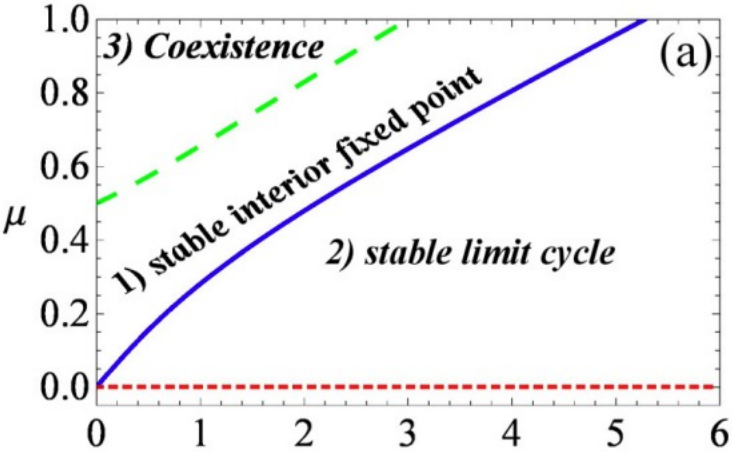
The fixed point (x_4^*, y_4^*) only exists for parameter values above the transcritical bifurcation curve. Linearization about the fixed point yields:

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

The Hopf bifurcation curve is given by:

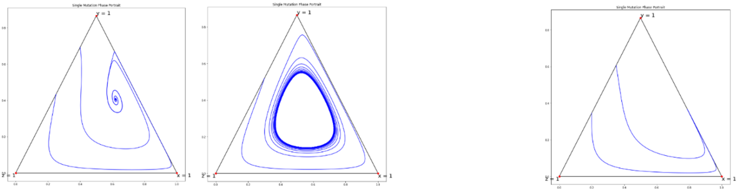
$$\begin{aligned}\mu_h &= \frac{2(\sqrt{\epsilon(\epsilon+2)(4\epsilon(\epsilon+2)+9)+9}-3)-3\epsilon(\epsilon+2)}{7\epsilon} \\ &\approx \frac{\epsilon}{3}-\frac{4\epsilon^3}{27}+\frac{4\epsilon^4}{27}-\frac{4\epsilon^5}{243}+O(\epsilon^6)\end{aligned}$$

Bifurcation Diagram

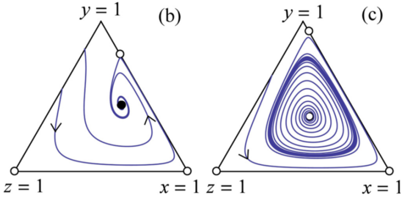


Single Mutations Case:2

Simulations:



Results from paper:



Conclusion

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.

Scope

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.