Evolutionary Games on Graphs

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Abstract—Game theory provides a useful framework for studying evolution. By considering the population to be nodes on a graph, defining interactions to be weighted connections, graphs have been used to study populations. Game theory can be put to use in this representation of the population as graphs to understand nuances of evolution and evolutionary dynamics. This framework of evolutionary games on graphs has been reviewed in this report. Extensions to current models, to better mimic natural contexts have been proposed.

Index Terms—Evolution, Game Theory, Graphs, Evolutionary Dynamics

I. INTRODUCTION

EVOLUTION is the change in heritable characteristics of populations over generations [1]. It is the explanation for the wide array of behaviors and morphologies observed in life forms.

Rightly put by Dobzhansky, "Nothing in biology makes sense except in the light of evolution". Hence, the study of evolution has been of the utmost priority.

There are 3 major forces that drive evolution of a population: selection, genetic drift, and migration. A combination of these forces have successfully explain all observed natural phenomenon relating to evolution.

Migration is the movement of populations, groups or individuals. Migration can cause geographical barriers between populations, changing the fitness landscape of the population and the potential evolutionary paths could diverge.

Genetic Drift is the variation in the relative frequency of different genotypes in a small population, owing to the chance disappearance of particular genes as individuals die or do not reproduce. [1]

Natural selection was proposed by Charles Darwin, in 1859 [2]. The basic premise is that, mutations arise randomly in individuals, conferring a change in 'fitness', i.e. the rate of survival and reproduction. The individuals with highest fitness pass on their traits. On the population scale, this mechanism results in a gradual change in the morphology/behavior. In the late twentieth century, mathematicians, and computer scientists took particular interest in evolution through natural selection, as it was the ultimate optimization game of Life. One of these approaches which gained popularity among ecologists and evolutionary biologists was the use of game theory to understand Evolution, as proposed by Dr. J. M. Smith and Dr. G. H. Pierce [3].

Each trait could be considered a strategy, with its payoff being the 'fitness' it provides to the animal. With this perspective of strategies and payoffs, Evolution could be viewed

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in the light of game theory. It was initially proposed to understand cooperation in societies. Over time, researchers turned their interest to dynamics of evolution, that is, how a stable equilibrium is adopted, given an initial population. Evolutionary Game Theory has found applications in explaining other evolutionary phenomenon too.

Games on Graphs

In the mid-twentieth century, game theorists were exploring applications in communication and social networks [4]. Graphs proved to be very useful in analyzing such games. Mathematicians had already extensively studied graphs and their properties, establishing a repertoire of theorems that could have applications in game theory on graphs [5].

Evolutionary Games on Graphs

With the establishment of graphs in game theory, Dr. Martin Nowak, a mathematician-turned-biologist used the perspective of games on graphs to view evolution [6].

A graph is a collection of nodes and the edge weights between them. A population can be defined by the individuals that make up the population and the interactions between them. Therefore, a population can be modelled as a graph.

Using this representation of the population as a graph, and defining update rules for defining the state of the graph at the nest iteration, changes can be induced in the population. Hence, appropriate update methods can be used to model evolution. Some such popular update methods will be discussed in the next section.

II. PREVIOUS WORK

There are many different kinds of games that can be played on graphs, such as evolutionary games, social networking, cop and robber pursuit games, chip-firing games and so on [6].

Our focus in this paper is on evolutionary games. We look at how evolution in a population takes place through mutation, and how it can be represented as a game on a weighted graph.

A. Model

A population of N individuals is represented on a weighted graph G with N nodes. The individuals of the population are represented by the nodes of the graph. The edges of the graph, e_{ij} denote the strength of the connection between two individuals i and j.

A 2×2 payoff matrix, A, is defined. It tells the payoffs that two individuals get when they interact with each other, depending on whether they are residents or mutants.
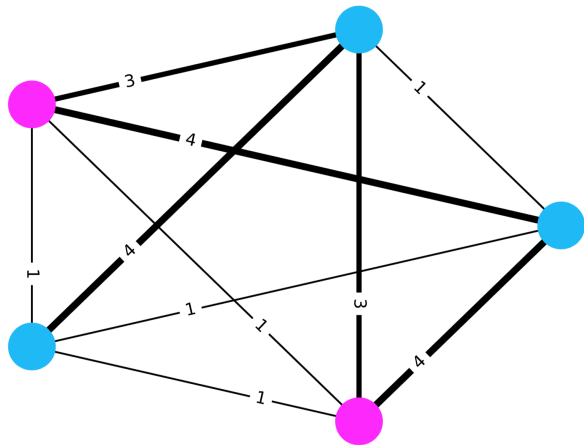
Fig. 1. Graph of a population of 5 individuals: 3 residents (blue) and 2 mutants (pink)

Fig. 2. Birth-Death update method

$$A = \begin{array}{c} \\ \mathcal{R} \\ \mathcal{M} \end{array} \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{array}{c} \mathcal{R} \quad \mathcal{M} \\ \\ \end{array}$$

Depending on the values of a, b, c and d, this matrix could be of the form of Prisoner's Dilemma, Hawk and Dove, Full cooperation, or Stag Hunt. [7]

For a prisoner's dilemma, a, b, c, d are R, S, T, P. Here R denotes the *reward* for mutual cooperation, S, the payoff of the *sucker* being exploited, T, for *temptation* to exploit the other player, and P, the *penalty* for mutual defection.

The *fixation probability* of a mutant species is defined as the probability that it can invade the resident population starting from just one individual. The fixation probability of species $\mathcal{M}$ is

$$\rho_{\mathcal{M}} = \Pr\big[(\mathcal{M}, \mathcal{R}, \mathcal{R}, \mathcal{R}, \ldots, \mathcal{R}) \to (\mathcal{M}, \mathcal{M}, \mathcal{M}, \mathcal{M}, \ldots, \mathcal{M})\big]$$

The payoff f_i of individual i is defined as

$$f_i = \sum_{j \in G} e_{ij} a_{ij}$$

Here a_{ij} is the ijth entry in the payoff matrix A.

B. Moran Process

A simple model to describe finite populations is the Moran process. It is a simple stochastic process which captures genetic drift and natural selection to an extent.

It assumes no interactions between any two individuals of the population. In each time-step, one individual is randomly selected to reproduce, and one individual is randomly selected to die. It is possible for the same node to be selected both reproduction and death.

If there are N individuals in the population, with i mutants, then the probability that in the next step, there are $i+1$ mutants is
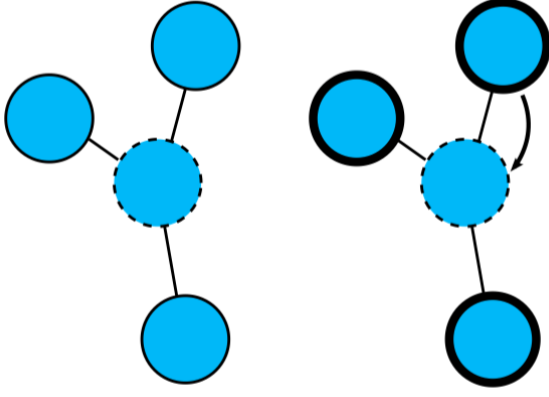
$$\Pr(i \to i+1) = \frac{i}{N} \frac{N-i}{N}$$

This is because there is a $\frac{i}{N}$ probability that a mutant will be chosen to reproduce, and $\frac{N-i}{N}$ probability that a resident will be chosen to die.

Similarly, the probability for one mutant decreasing is:

$$\Pr(i \to i-1) = \frac{N-i}{N} \frac{i}{N}$$

The probability of the third case is

$$\Pr(i \to i) = 1 - \Pr(i \to i+1) - \Pr(i \to i+1)$$
$$= 1 - 2 \cdot \frac{(N-i)i}{N^2}$$
$$= \left(\frac{N-i}{N}\right)^2$$

If we start with one mutant, then the probability that all individual become mutants eventually is the fixation probability, and can be computed using the above three equations.[8] We get:

$$\rho_{\mathcal{M}} = \frac{1}{N}$$

The Moran process is not very realistic as it ignores any interaction between individuals. Two update methods: Birth-Death, and Death-Birth, have been suggested. These take into account the fitness of each node, which directly affects the probability of being selected for reproduction and death. These are more complex than the Moran process, but better mimic life as we see it in nature. The fittest nodes are more likely to survive and reproduce, whereas the less fit ones have a higher chance of dying.

C. Update Methods

Update methods are necessary for the population to evolve. The update methods describe the rules according to which individuals in the population will reproduce or die.

1) Birth-Death (BD): A vertex i is chosen at random with probability distribution proportional to f_i from the graph to reproduce.

$$s_i = \frac{f_i}{\sum_{k \in G} f_k}$$

One of the neighbors, j, of i is selected to die with probability distribution inversely proportional to e_{ij}.

Fig. 3. Death-Birth update method

$$t_j = \frac{1/e_{ij}}{\displaystyle\sum_{e_{ik}>0} 1/e_{ik}}$$

The offspring takes the place of j.

A condition for the fixation probability of residents to be greater than the fixation probability of mutants is given by:

$$\rho_{\mathcal{R}} > \rho_{\mathcal{M}} \iff a + c > b + d$$

Here a, b, c, d are the entries of the payoff matrix A.

2) Death-Birth (DB): A vertex j is chosen at random uniformly to die.

$$t_j = \frac{1}{N}$$

One of its neighbours, i is chosen at random with probability proportional to $f_i e_{ij}$ to take place of j.

$$s_i = \frac{f_i e_{ij}}{\displaystyle\sum_{e_{kj}>0} f_k e_{kj}}$$

D. Random Mutations

In [6], the authors discuss about random mutations. Reproduction doesn't have 100% fidelity. We assume that random mutations take place with probability u.

If the parent is a resident, $\mathcal{R}$, then the offspring is

$$\begin{cases} \mathcal{R} & \text{with probability } 1 - u \\ \mathcal{M} & \text{with probability } u/2 \\ \mathcal{R} & \text{with probability } u/2 \end{cases}$$

In this case, the system does not achieve a constant steady state, but the expected ratio of residents to mutants is constant.

E. Mean Absorption Time

In [9], the authors studied dynamics on complete graphs. They calculated the *mean absorption time*: the time it takes for either the mutant or the resident to get absorbed by the other by solving equations for transition probabilities recursively with finite time steps.

For simpler computation, all edge weights are assumed to be 1, i.e. $e_{ij} = 1$ for all i, j. That is, the Moran process is followed. Let there be i mutants in the population, and $N - i$ residents. Then the average fitness of a resident is

$$\mu_i = \frac{ib + (N - i - 1)a}{N - 1}$$

and the average fitness of a mutant is

$$\nu_i = \frac{(i - 1)d + (N - i)c}{N - 1}$$

.

For a complete graph, the fixation probability of mutants is obtained by solving the system of equations for $i \in G$:

$$\begin{aligned} \Pr(i \to N) = {} & \Pr(i \to i + 1)\Pr(i + 1 \to N) \\ & + (1 - \Pr(i \to i + 1) - \Pr(i \to i - 1))\Pr(i \to N) \\ & + \Pr(i \to i - 1)\,\Pr(i - 1 \to N) \end{aligned}$$

Here,

- $\Pr(0 \to N) = 0$, because once all individuals are residents, there is no way of getting more mutants.
- $\Pr(N \to N) = 1$, because once all individuals are mutants, they have fixated and will always remain mutant.

The probability that given i mutants in a time-step, there are $i + 1$ mutants or $i - 1$ mutants in the next time-step is given by

$$\Pr(i \to i + 1) = \frac{i(N - i)\nu_i}{(N - 1)(i\nu_i + (N - i)\mu_i)}$$

and

$$\Pr(i \to i - 1) = \frac{i(N - i)\mu_i}{(N - 1)(i\nu_i + (N - i)\mu_i)}$$

respectively.

This is useful in finding the mean time to absorption. Let T_i denote the time-steps it takes for the population to become either all mutants or all residents starting from i mutants. Then all T_i satisfy this system of equations:

$$\begin{aligned} T_i = {} & \Pr(i \to i + 1)T_{i+1} \\ & + (1 - \Pr(i \to i + 1) - \Pr(i \to i - 1))T_i \\ & + \Pr(i \to i - 1)T_{i-1} + 1 \end{aligned}$$

Solving this gives the mean time T_i to absorption in a given population. The boundary conditions here are that $T_0 = T_N = 1$, since the population has already been absorbed.

III. APPLICATIONS

We used established results in literature to model the behavior of cooperative breeding and societal thresholds for effective vaccination using the aforementioned tools.
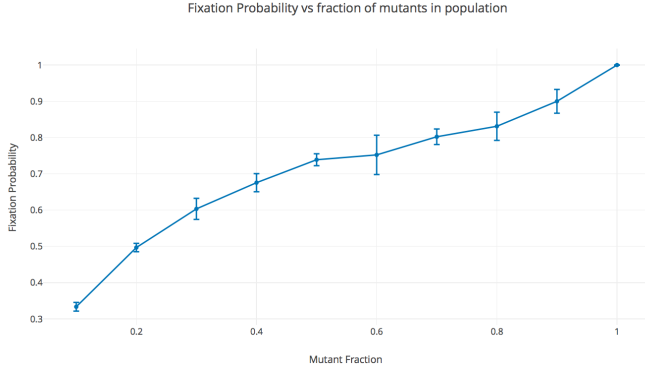
Fig. 4. Results of Simulation. Plot of Fixation Probability vs Fraction of Mutants in Initial Population

Fig. 5. Effect of Herd Immunity on Spread of diseases in a population (Source: Wikimedia Commons)

A. Cooperative Breeding

Parental care is a costly behavior. In many animal societies, such as birds and bats, individuals reduce the cost by engaging in cooperative breeding. Multiple females lay eggs in a single nest and take care of the offspring together, thereby sharing costs of rearing offspring.

Being a cooperative society, there is scope for cheating in the population. The cheats in this case would be those who lay their eggs in the nest, but do not participate in taking care of the offspring.

There is a limit to the number of mutants in the society, before cooperation is no longer a viable strategy, and the society crumbles.

Indicating residents to be individuals who cooperate and mutants to be the cheaters in the society, we used evolutionary games on graphs to understand the carrying capacity of cheaters in this cooperation.

We estimated the values of a, b, c, d for the matrix to be:

$$A = \begin{matrix} & \begin{matrix} \mathcal{R} & \mathcal{M} \end{matrix} \\ \begin{matrix} \mathcal{R} \\ \mathcal{M} \end{matrix} & \begin{pmatrix} 1 & 0.5 \\ 2 & 0 \end{pmatrix} \end{matrix}$$

In a system with cooperators only, benefit is defined to be 1. If a resident interacts with a mutant, the resident has 2 eggs to take care of, and the probability that its brood will reach maturity is assumed to be 0.5. If two mutants interact, the egg will receive no care, and payoff to both parties is 0. If a mutant interacts with a resident,

Keeping the threshold of fixation probability as 0.5, we estimate the threshold of the (Figure 4) fraction of mutants in the population for cooperative breeding to continue to be 0.2, i.e. 20%.

Cooperative breeding is believed to be the precursor strategy to brood parasitism, a behavior wherein eggs are laid in nests of other birds. This behavior is of particular interest to evolutionary biologists, and ethologists for the exemplary mimicry and strategies adopted by the species involved.

Current brood parasites are believed to have evolved from cheats in cooperative breeding. Our analysis supports the feasibility of this hypothesis.
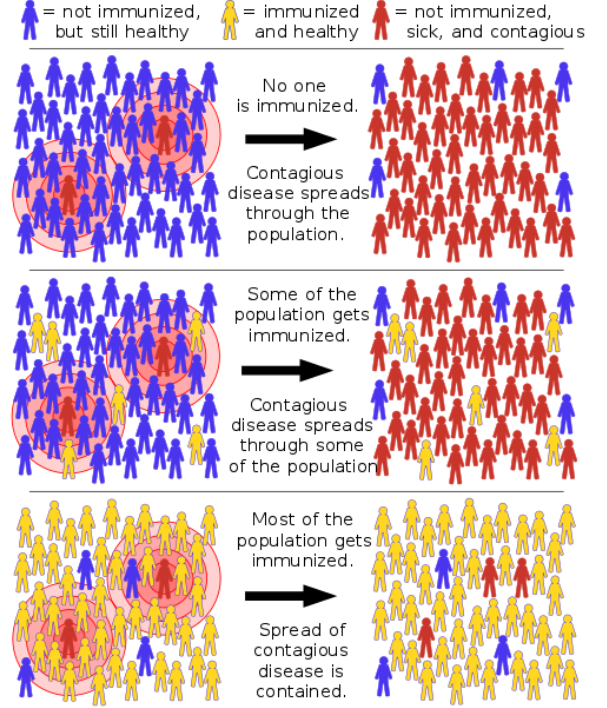
B. Herd Immunity

Herd immunity is a form of indirect protection from infectious disease that occurs when a large percentage of a population has become immune to an infection, thereby providing a measure of protection for individuals who are not immune.

While designing vaccination programs, in order for the program to be successful, it is important to understand the threshold of herd immunity.

Indicating residents as vaccinated individuals and non-vaccinated individuals as mutants, Evolutionary Games on Graphs can be used to calculate the threshold for successful vaccinations. The matrix in this case encapsulates the susceptibility to the communicable disease.

$$A = \begin{matrix} & \begin{matrix} \mathcal{R} & \mathcal{M} \end{matrix} \\ \begin{matrix} \mathcal{R} \\ \mathcal{M} \end{matrix} & \begin{pmatrix} 2 & 1 \\ 0 & -2 \end{pmatrix} \end{matrix}$$

Using the above matrix, we calculated that on an average, at least 70% of the population has to be vaccinated for an outbreak to be prevented.

IV. EXTENSIONS

A. Random Mutations

We extend the calculation done in [9] to populations where random mutations are allowed. For simpler computation, we assume that every edge weight is 1, i.e. Moran process is followed.
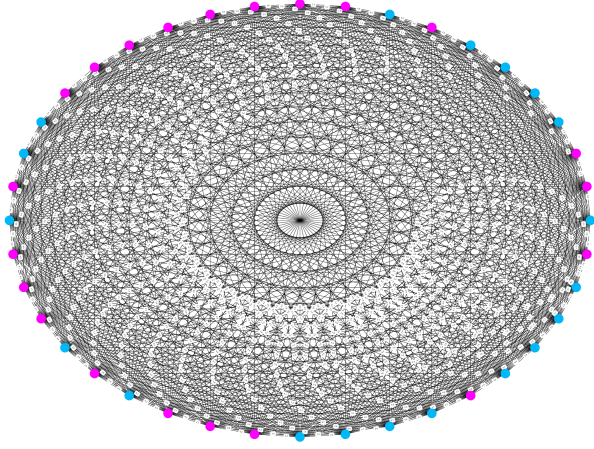
Fig. 6. Graph of a population with 40 individuals. Note that although graphical representation is not efficient, analysis using graphs is.

Let $p_{i,i+1}$ denote the probability that number of mutants changes from i to $i+1$ given that there are no random mutations. The probability that the number of mutants changes from i to $i+1$ in a population of N individuals when random mutations are allowed is:

$$\Pr(i \to i+1) = \left(1 - \frac{u}{2}\right) p_{i,i+1} + \left(\frac{u}{2}\right) p_{i,i-1}$$

Substituting the values of $p_{i,i+1}$ and $p_{i,i-1}$, we get $\Pr(i \to i+1)$ in terms of the basic variables.

$$= \frac{(N-i)c + (i-1)d}{\sum_{i \in G} F_i} \left(\left(1 - \frac{u}{2}\right) \frac{(N-i)}{N-1} \right) i$$
$$+ \frac{ib + (N-i-1)a}{\sum_{i \in G} F_i} \left(\frac{u}{2} \frac{(N-i-1)}{N-1} \right) (N-i)$$

This can be used to the fixation probability, $\rho_{\mathcal{M}} = \Pr(1 \to n)$.

B. Sexual reproduction

The earlier model assumed asexual reproduction.

In most evolutionary contexts, the mode of reproduction is sexual. [10] Although there are some models for incorporating sexual reproduction as an update method, we are proposing a model closer to reality by incorporating a carrying capacity into the model. To our best knowledge, such a model has not been proposed yet.

A node is chosen at random to reproduce. It 'mates' with the neighbor having the highest fitness. Two offsprings are produced. The interaction between them is chosen from the uniform distribution $[0, 1]$. The interactions with parents is set to 0.5. The interactions with other nodes is chosen from the uniform distribution of $[a, b]$ where a and b and the interactions between the parent nodes and the node being considered. Also, every node has a lifespan of 3 iterations, i.e. after three iterations, the node is deleted. If the population exceeds a specified carrying capacity, the nodes with the lowest fitness die off.

We wish to see how stable cooperation strategies with sexual reproduction differ from those with asexual reproduction.

To analyze the payoffs for the defined strategies, a simulation of the population needs was run (Appendix 1), which iterates over multiple generations.

After the population reaches the carrying capacity, an estimate of the fixation probability can be made. Before this state, the stochasticity of the system is beyond the authors' scope of analysis.

Assume that the carrying capacity and the population is N, and there are i mutants at this state.

The probability that a mutant is chosen at random to reproduce is $\frac{i}{n}$. The probability that the node the chosen node mates with is a mutant is the probability that the interaction between the chosen node and a mutant is the highest. Let $\mathcal{M}$ represent the set of interactions of the chosen node with mutants. The cardinality of this set is i if the chosen node is not a mutant. Define Δ as:

$$\Delta = max\{\mathcal{M}\} - min\{\mathcal{M}\}$$

From order statistics, we have that the probability of a mutant with interaction u with the chosen node being the highest interaction as $Nu^{(N-1)}\Delta u$.

Noting that a mutant mating with a mutant gives a mutant and that a resident mating with a mutant gives a mutant with 0.5 probability, we have:

$$\Pr(i \to i+1) = iu^{N-1}\Delta u + 0.5(N-i)u^{N-1}\Delta u$$

The first term captures Mutant-Mutant Matings and the second term captures Resident-Mutant Matings. Simplifying the above expression, we get:

$$\Pr(i \to i+1) = 0.5(N+i)u^{N-1}\Delta u$$

Note that $\langle u \rangle = 0.5$, as interactions are chosen to from U[0,1]. Also, we can average out Δu to be $\langle max\{\mathcal{M}\}\rangle - \langle min\{\mathcal{M}\}\rangle$

For an uniform distribution with i elements ($\mathcal{M}$), from order statistics, we have that

$$\langle max\{\mathcal{M}\}\rangle = \frac{i}{i+1}$$

and

$$\langle min\{\mathcal{M}\}\rangle = \frac{1}{i+1}$$

Therefore,

$$\langle max\{\mathcal{M}\}\rangle - \langle min\{\mathcal{M}\}\rangle = \frac{i-1}{i+1}$$

Hence, $\Pr(i \to i+1)$ is given by:

$$\Pr(i \to i+1) = \frac{(N+i)(i-1)}{2^N(i+1)}$$

The probability $P(i \to i-1)$, that a mutant reduces is given by whether the mutants age is more than the threshold and the relative fitness. As we are considering the state where the population is at its carrying capacity, let us assume that 2 nodes die at each stage. This is given by:

$$\Pr(i \to i-1) = \Pr(\sum_{\mathcal{M}} \mathbb{1}_{(G(m)=3)} = 1) + P_1$$

where P_1 is the probability that the node with lowest fitness is a mutant. Let us define m_1 and m_2 as the 2 lowest elements of $\mathcal{M}$. From order statistics, we have:

$$P_1 = (n-1)(1-u)^{N-1}(m_2 - m_1)$$

m_1 and m_2 are the 2 lowest numbers from a uniform distribution of i numbers. We know that $\langle m_2 - m_1 \rangle = \frac{1}{i+1}$ from order statistics. Hence, in expectation, $\langle P_1 \rangle$ is:

$$\langle P_1 \rangle = \frac{(n-1)}{2^{N-1}(i+1)}$$

Hence,

$$\Pr(i \to i-1) = \frac{i}{N} + \frac{(n-1)}{2^{N-1}(i+1)}$$

We have found the expectation values of probability of increase and decrease in number of mutants, at steady population density, where interactions are defined from an uniform distribution.

V. FUTURE PROSPECTS

We propose to use this framework to probe the following possibilities:

A. Sympatric Speciation

Sympatric speciation implies a divergence of traits in the population without any geographical barriers. Assuming a population with a normal distribution of fitness, we wish to probe the conditions under which the population diverges into two distinct populations (fitness as a curve with two peaks). This is concerned with non-equilibrium states of the game. Such an analysis will reveal possible cooperations that may aid in sympatric speciation.

B. Studying Social Dilemma using games on graphs

The principles of Evolutionary Game Theory can find applications in non-evolutionary scenarios too.

Assuming a population of N individuals and that one of them has to make a decision from an array of decisions and each decision affects the population in a certain way.

An example is: Should Trump pull out of the Iran Deal? What are the possible decisions? How will each decision affect international relations? How will each decision affect his chances of re-election?

This scenario can be modeled using Evolutionary Games on graphs, to find the most suitable decision, by having the matrix indicate the current stance that each node has established for each outcome.

C. Epidemiology

Epidemiology is the study of incidence, distribution and control of diseases. The spread of communicable diseases in a society is heavily reliant on the immunity of individuals and the social interactions between individuals. Hence, evolutionary graph theory can be used to model the spread of diseases and identify the most tactical response causing minimal spread/damage in least time.

VI. SUMMARY

- We characterized evolutionary games on graphs
- We applied existing to two natural systems, cooperative breeding and herd immunity.
- We extended the model for mutations and sexual reproduction to better mimic natural contexts.

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