A Review of Evolutionary Graph Theory With Applications to Game Theory

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Abstract

Evolutionary graph theory (EGT), studies the ability of a mutant gene to overtake a finite structured population. In this review, we describe the original framework for EGT and the major work that has followed it. This review looks at the calculation of the "fixation probability" - the probability of a mutant taking over a population and focuses on game-theoretic applications. We look at varying topics such as alternate evolutionary dynamics, time to fixation, special topological cases, and game theoretic results. Throughout the review, we examine several interesting open problems that warrant further research.

Keywords: evolutionary dynamics; structured population; game theory; fixation probability; time to fixation

1. Introduction

Evolutionary graph theory (EGT), introduced by [23], studies the ability of a mutant gene to overtake a finite structured population. The reproduction of the individuals in the population is modeled as a stochastic process. The structure of the population is represented as a directed, weighted

graph called an *evolutionary graph* (EG). Since its introduction, numerous results on EGT, both analytical and experimental, have been produced. Additionally, several extensions to the model have been proposed, including game-theoretic ones. The application of EGT to game theory has provided researchers new insight about the evolution of cooperation and other game-theoretic concepts in structured populations. In this review, we present the original model of [23] and various extensions. We also summarize major results in EGT (both analytical and experimental), including those relating to game theory. Throughout this review, we pose several open questions in EGT that would be relevant for future research.

This review is organized as follows. In Section 2, we introduce the original model, discuss computation of fixation probability, and describe the standard game theoretic extensions. This is followed by a presentation of results concerning the computation of the fixation probability in Section 3 for graphs of certain topologies - including the large class of undirected EG's. We then turn to the related problem of mean time to fixation in Section 4. Then we describe how some of the results relating to fixation probability change under alternative model dynamics in Section 5. We then survey more advanced game theoretic extensions in Section 6. Finally, in Section 7, we present other major extensions to EGT including the study of bi-level EG's and EG's whose topology change over time.

2. The Model

Consider a population of N individuals where there is no specified graph-structure relating them to each other (this is known as a *well-mixed* population). The *Moran Process* of [29] is a stochastic process used to model evolution in such a population. It is defined as follows. At each time-step a randomly selected individual is chosen to reproduce. Then, a second individual is chosen at random to die – replaced by a duplicate of the first individual. If all of the members of the population are identical (termed *residents* with fitness 1), and a mutant is introduced at random in the population (with fitness r, where $r = 1$ is the special case of *neutral drift*), the probability that the mutant will eventually overtake the population is known as the *fixation probability* (the opposite event - that all mutants die out - is called *extinction* and a population with a lower fixation probability is deemed more *evolutionarily stable* as it is resistant to invasion by a mutant). This

probability, ρ_1, arising from this N original Moran Process, is often termed the *Moran probability* and can be solved for exactly (see equation 1).

$$\rho_1 = \frac{1 - 1/r}{1 - 1/r^N} \tag{1}$$

In the original work that introduced EGT [23], Lieberman et al. generalize the model of the Moran Process by specifying relationships between the N individuals of the population in the form of a directed, weighted graph. We shall use the symbol V to denote the set of individuals. We can think of these individuals as vertices in a graph. The edges of the graph are specified by the adjacency matrix $W = [w_{ij}]$, where for vertices v_i, v_j, the quantity w_{ij} specifies the weight of the directed edge from v_i to v_j. As this is an evolutionary graph (EG), w_{ij} corresponds to the probability that, if v_i is selected to reproduce then it replaces v_j (note that for all v_i, $w_{ii} = 0$). Hence, for any given v_i, $\sum_j w_{ij} = 1$. The earlier work of [46] proves that, in such a structure if $\forall v_i, v_j \in V$ we have $w_{ij} = w_{ji}$, then the fixation probability for a randomly placed mutant is ρ_1. A similar result was proved in [24]. In [23], this result is extended for a wider variety of EG's where $\forall v_i$, $\sum_j w_{ij} = \sum_j w_{ji}$. This type of EG is known as *isothermal*. Consider the following theorem.

Theorem 1 (Isothermal Theorem [23]). *An EG is isothermal iff the fixation probability of a randomly placed mutant is ρ_1.*

Hence, for EG's that are not isothermal, the fixation probability of the evolutionary process is not only dependent on the fitness of the mutant (as in the Moran Process), but also on the structure of the graph.

2.1. Properties of Fixation Probability

Many researchers (such as [9] and [26]) have studied the problem of computing the probability of fixation given that a certain subset of vertices are mutants. If the mutants inhabit set $C \subseteq V$, then this probability is written P_C. As the calculation of the fixation probability (ρ) for an EG is determined based on a uniformly picked vertex, we have the following relationship between ρ and P:

$$N \cdot \rho = \sum_i P_{\{v_i\}} \tag{2}$$

Note that although these two problems are closely related, they have rather different intuitions. The fixation probability ρ provides insight into a graph

of a certain topology. For example, researchers often refer to graphs with a low value for ρ as being "evolutionary stable" as the toplogy of the graph seems to be resistant to a mutant invasion. The fixation probability P_C on the other hand tells us something about a set of vertices C. For example, identifying a certain subset C of a graph that has a higher fixation probability may cause a user to take a certain action regarding those vertices (dependent on the domain).

If the graph is not isothermal, but if we are under neutral drift, fixation probability P_C is additive. This was proven for the special case of undirected graphs in [8] and proved for general, weighted, directed graphs by the authors of this review in [45].

Theorem 2 (Additive Under Neutral Drift [45]). *When $r = 1$ for disjoint sets $C, D \subseteq V$, $P_C + P_D = P_{C \cup D}$.*

This additive result says that, under neutral drift, determining a subset of indivdiuals in the population that maximize fixation probability is not (polynomially) harder than determining the fixation probability. Further, when we fix the topology of the graph, we find that for some subset of vertices C, that the fixation probability under neutral drift is a lower bound for the fixation probability when $r > 1$.

Theorem 3 (Neutral Drift as a Lower Bound [45]). *For a given set C, let $P_C^{(1)}$ be the fixation probability under neutral drift and $P_C^{(r)}$ be the fixation probability calculated using a mutant fitness $r > 1$. Then, $P_C^{(1)} \leq P_C^{(r)}$.*

By Theorem 2 and Equation 2, we observe that under neutral drift $\rho = 1/N$ regardless of the topology of the graph - even with directed and weighted edges. Hence, Theorem 3 tells us that for $r > 1$ we have $\rho \geq 1/N$. This particular observation is independently noted in [20]. In [25] the authors observe in their experiments that fixation probability monotonically increases with r. Based on these observations and Theorem 3, we have the following conjecture.

Conjecture 2.1. *Fixation probability is montonic in r.*

This conjecture seems natural and is supported by experimental results. However, a formal proof is currently lacking.

2.2. The Complexity of Computing Fixation Probability

As we can appeal to the Moran probability only in the case of an isothermal graph, we must resort to other calculations to determine ρ or P. Using the following set of constraints, we can solve directly for any P_C (hence, ρ as well by Equation 2).

$$P_C = \frac{\sum_{v_i \in C} \sum_{v_j \notin C} (r \cdot w_{ij} \cdot P_{C \cup \{v_j\}} + w_{ji} \cdot P_{C - \{v_i\}})}{\sum_{v_i \in C} \sum_{v_j \notin C} (r \cdot w_{ij} + w_{ji})}. \tag{3}$$

These constraints originally appeared in [43] for the case of an undirected EG, but applies to the general case as it follows directly from the rules of dynamics. However, the number of constraints and variables is equal to the number of mutant-resident formations in the graphs, which is intractable for large N. In fact, [23] presents a decision problem related to computing the fixation probability that is claimed to be as hard as any problem in the complexity class NP (the class of nondeterministic polynomial time computable problems). In [9, 8] the authors attempt to reduce the number of constraints by finding automorphisms in the graph. Based on automorphism, the authors are able to calculate the exact number of possible mutant-resident formations (MRF's). Since this number gives the size of the system of linear equations for the fixation probability and in general increases with the difficulty of solving this system, the measure may be a useful indicator in deciding whether to undertake an analytical approach to solving for the fixation probability on a given graph. The authors then show that even in the special case of undirected EG's, if the graph contains a vertex of degree of at least 3, that there is a non-zero probability that the dynamics will evolve to any of the MRF's (except in the trivial cases where $C = V$ or $C = \emptyset$).[1] We note that for the general case, this still leads to an intractable number of constraints. Further, finding graph automorphisms is also a non-trivial problem in the general case (see [50] for the latest complexity results on graph automorphism).

We note that the problem proven to be NP-hard by [23] is actually more general than a standard computation or ρ using their model. As for an upper bound on complexity, Equation 3 only tells us that this problem can

[1]There is the exception of an alternating state where every edge connects a mutant-resident pair. This state cannot be reached if it exists. We would like to thank an anonymous reviewer for pointing this out.

be solved in exponential time. Hence, the issue of finding a tight bound on the complexity for computing fixation probability is still an open problem.

Open Problem 2.1. *What is the computational complexity of determining ρ in an arbitrary evolutionary graph?*

Open Problem 2.1 is important to the study of evolutionary graph theory as virtually all current work in this area is perofrmed with simulation. Often, it has been found that this approach does not scale well for large graphs. Properly identifying the complexity class of this problem may provide insight into the development of a more efficient and scalable approach, perhaps broadening the appeal of this paradigm.

What about the computational complexity of finding P_C - the fixation probability given seet $C \subseteq V$ are mutants and the rest are residents? Clearly, as $\rho = \frac{\sum_{v_i \in V} P_{\{v_i\}}}{N}$, solving N instances of P_C can give us ρ. However, a reduction going in the opposite direction seems less likely, so it is possible that determining P_C may be more difficult than finding ρ.

Despite the computational difficulty of determining the fixation probability in the general case, there are several special classes of EG's where we have analytical solutions (or at least good approximations). We review many of these special cases in the next section. To address the issue of computation of the fixation probability in the general case (i.e., to confirm analytical approximations), most work we review resorts to simulation methods via Markov Chain Monte Carlo (MCMC). These simulations generally rely on a direct application of the model we have already described (see [43] for a pseudocode algorithm). However, as the size of the graph increases, even such simulations may become impractical. In [4], the authors address the issue of increasing the speed of such simulations. Their main technique for the general case is to stop the simulation early if the number of mutants in the population exceed a certain threshold (hence that particular simulation would be considered to have reached fixation). They determine this threshold by finding the conditional probability that mutants spread to M vertices in the graph given that extinction eventually occurs. The authors plot the probability distribution density of this function compared to M and determine for several types of networks (including E-R graphs) of size 10^3, that if $M > 10^2$ then this probability drops to 10^{-5} – which is lower than the estimated standard error of a MCMC simulation by several orders of magnitude (the authors show that the estimated standard error for populations of 10^4

to 10^6 have associated standard errors of at least 10^{-4}). Hence, the outcome of any simulation where the number of mutants exceeds 100 is considered equivalent to fixation. The authors showed that for networks with 10^3 and 10^4 vertices, and showed it provided a significant speed-up of up to 100 times, depending on the size of the network.

More recently, the authors of this review developed a novel approach that can quickly compute the fixation probility in an evolutionary graph (with weights and directions) under neutral drift. We rely on the idea of a *vertex probability* - the probability of a given verterx being a mutant. In the limit of time, these probabilities converge to the fixation probability (for strongly connected graphs). We have shown that this convergence occurs quickly in practice, providing an improvement over MCMC by several orders of magnitude. While this result is for the case of neutral drift, Theorem 3 suggests it may provide good insight for $r > 1$. Further, the quick convergence of our algorithm in practice may also suggest that having a value of $r \neq 1$ may be a source of complexity.

Another recent development is the work of Houchmandzadeh and Vallade who use dynamics to quickly approximate fixation probability in a certain bi-level graph that generalizes the model of [24]. While this particular model can also generalize the standard evolutionary graphs of [23]. However, it is unclear if their approximation is still appropriate for arbitrary graphs. In Section 3.3 we show how this approach can be used to derive the Moran probability (ρ_1). In Section 7.1 we discuss bi-level graphs and discuss their approach further.

2.3. Game Theoretic Extensions

One of the most popular applications of EGT is to game theory. In the game theoretic context, vertices of a graph represent agents and edges represent potential for interaction between them. Interactions between agents are games played that can be described using a normal game theoretic payoff matrix. EGT thus provides a structural component for interactions in populations of agents. Evolutionary game theory, which is concerned with the population-dependent success of game theoretic strategies, has initially mostly focused on well-mixed populations in which interactions between all agents are equally likely. Incorporating EGT to evolutionary game theory can take into account the effect of population structure, which has the capacity to crucially impact evolutionary trajectories, outcomes, and strategy

success. Thus EGT is a welcome tool to explore how many of the results for well-mixed populations are affected by population structure.

In game-theoretic applications of EGT, the evolutionary fitness (f_i) of individual v_i is often related to their game theoretic payoff (P) (based on game-play with neighbors) with something akin to the following equation:

$$f_i = 1 - \mathsf{w} + \mathsf{w} \cdot \mathsf{P} \tag{4}$$

The parameter w relates the payoff acquired from games played to fitness. If $\mathsf{w} = 1$, the payoff acquired is equal to the fitness. If $\mathsf{w} = 0$, the game is irrelevant and we are at neutral drift. An often explored special case is *weak selection*, where $\mathsf{w} << 1$, which reflects the assumption that the game of interest plays only a partial role in the overall fitness of individuals. Using this paradigm, researchers have reached a variety of important conclusions on the effects of population structure on game-theoretic concepts. The inclusion of a game adds a layer of computational complexity to our already difficult problem of determining fixation probability. As with fixation probability computation under fixed fitness, much of the game theoretic work on EGT is done using simulation. Hence, we have the following open problems.

Open Problem 2.2. *Given a two-player game and* w*, what is the computational complexity of determining* ρ *with respect to an arbitrary evolutionary graph?*

Evolutionary game dynamics of finite populations on graphs for a general two-player game between mutants and residents are often considered using the following payoff matrix:

	mutant	resident
mutant	a	b
resident	c	d

(5)

Tarnita et al. [49] consider evolutionary dynamics (under weak selection) on graphs for the general game given by (5) and present a theorem stating that a strategy A (mutant) is favored over strategy B (resident) iff $\sigma a + b > c + \sigma d$, depending on the single parameter σ. "A is favored over B" means that it is more abundant in the stationary distribution of the mutation selection process. The authors show σ to depend on the population structure, update

rule (see Section 5), and mutation rate. Thus the single parameter can be used to quantify the ability of a population structure to promote the evolution of cooperation or to choose efficient equilibria in coordination games. In general, if the combination of update rule and population structure leads to a $\sigma > 1$ (which can but does not necessarily occur for different combinations), individuals of the same strategy type are more likely to interact due to a clustering of strategies [34, 35].

In Section 4 we look at Broom et al. [7] who also study two-player games on graphs, but are mainly concerned time to fixation for a given game. In Section 6 we will review important other works considering various aspects of game theoretic applications of EGT.

3. Determining Fixation Probability for Fixed Fitness

We now turn to the problem of determining fixation probability for some special cases of graphs when the value of r is fixed (i.e., most non-game theoretic work). First we look at computing fixation probabilities for graphs of certain topologies. Then, we look at a very large special case - that of undirected graphs.

3.1. Fixation Probability Calculations for Cetrain Topologies

In [23], the authors examine the fixation probability for a few special cases of EG's to illustrate how fixation can be amplified or suppressed based on the structure of the graph. For example, they define a *one-rooted* graph as a graph with a unique global sourc without incoming edges (i.e., a directed tree, with edges directed toward the leaves, would be such a graph - the unique global source being the root in this case). Hence, for any value of r, if an EG is one-rooted its fixation probability is $1/N$.

Another special case is the EG referred to as a *super-star* (see figure 1). Such a structure, denoted $S^K_{L,M}$ consists of a central vertex, v_{center} surrounded by L leaves. A leaf ℓ, contains M *reservoir vertices*, $r_{\ell,m}$ and $K-2$ ordered chain vertices $c_{\ell,1}, \ldots, c_{\ell,K-2}$. All directed edges are of the form $(r_{\ell,m},\, c_{\ell,1})$, $(c_{\ell,w},\, c_{\ell,w+1})$, $(c_{\ell,K-2}, v_{center})$, and $(v_{center}, r_{\ell,m})$. Denoting the fixation probability of EG $S^K_{L,M}$ as $\rho(S^K_{L,M})$, the following result is given in [23].

$$\lim_{L,M\to\infty} \rho(S^K_{L,M}) = \frac{1 - 1r^K}{1 - 1/r^{K\cdot N}} \tag{6}$$

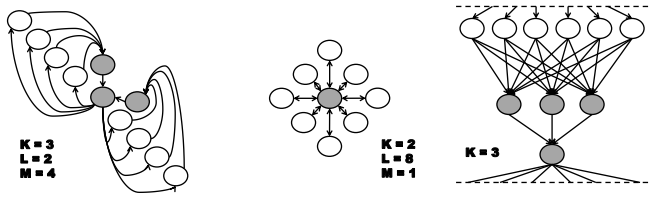

Figure 1: Left: Super-star EG, $K = 3, L = 2, M = 4$. Center: Star EG, $K = 2, L = 8, M = 1$. Right: Funnel EG, $K = 3$.

Because of the role it plays in enhancing fixation, the K parameter is often referred to as the *amplification factor*. If $K = 2$, this is simply referred to as a *star* EG (see figure 1). Another special case, related to the super-star, is the funnel (see figure 1). A generalization of the funnel, known as a *layered network* was studied in [3, 4]. In this type of EG, V can be partitioned into K subsets $V_1, \ldots, V_K$ such that for all $v \in V_i$ there are only outgoing edges to vertices in set $V_{i+1 mod K}$. Barbosa et al. also presents a way to increase the speed of MCMC simulations specific to layered networks in [4]. Their technique involves skipping evolutionary steps where none of the vertices in the graph changes a label. This is done by calculation the probability of a change occurring somewhere in the graph. The tradeoff with this speed-up is the price of calculating this probability compared to the savings. The authors show for layered networks, that this probability can be efficiently computed and yield a 2-3 times speed-up in simulations for K-funnels and random layered networks.

These special cases represent important building blocks for other results. For instance, [7] leverages some of these intuitions to study fixation probability for games on star graphs while the work on bi-level EG's we review in Section 7.1 leverages some of these ideas as well. More recently, this style of analytical calculation of fixation probabilities has been applied to economics in [58] where the authors determine the evolutionary stability of various forms of business, which are modelled as star and bi-level graphs (we discuss this work further in Section 7.1 as well). Analytically finding the value of ρ for certain graph topologies will most likely continue to be an active area of research in EGT, particularly as certain strucutures are identified in nature or other domains. Perhaps an interesting direction would be to use work on the subgraph isomorphism problem [14] to identify structures such as stars and funnels in larger graphs. The presence of such structures may allow us to make statements on the evolutionary stability of the larger graph and/or

compare the probability P_C for certain vertices in the larger graph (i.e., P_C may be higher for a set of nodes located in a star substructure of a larger graph).

3.2. Undirected Evolutionary Graphs

Several works explore a large special case: undirected EG's. In this case, we shall use the symbol E to denote the set of edges. However, it is important to note that the precise definition of this graph is somewhat different than the standard concept of an undirected graph. Specifically, the weights in both directions are not the same. This is defined by [9] as

$$w_{ij} = \begin{cases} d_i^{-1} & \textit{iff } (v_i, v_j) \in E \textit{ or } (v_j, v_i) \in E \\ 0 & \textit{otherwise} \end{cases} \tag{7}$$

where d_i is the degree of v_i. The intuition behind this asymmetric assignment of weights is that if v_i is chosen to reproduce, it replaces one of its neighbors with a uniform probability. In [9], the authors determine a necessary and sufficient condition for an isothermal undirected graph.

Theorem 4 (Undirected Isothermal Theorem [9]). *An undirected EG is isothermal iff it is regular.*

Interestingly, for the undirected case, when $r = 1$ (neutral drift), there is a tractable solution to the constraints specified by equation 3 that is presented in [8].

$$P_C = \frac{\sum_{v_i \in C}(d_i^{-1})}{\sum_{v_j \in V}(d_j^{-1})} \tag{8}$$

Hence, for an undirected graph with $r = 1$, we have $\rho = 1/N$. For the case where a mutant is very advantageous, $r >> 1$, [10] provides us with an approximation for P_C when C is a singleton set (the approximation is based on the assumption that once $|C| \geq 2$, then fixation occurs).

$$P_{\{v_i\}} \approx \frac{r}{r + \sum_{v_j \in V - \{v_i\}} w_{ji}} \tag{9}$$

The authors of [10] conducted an exhaustive study of undirected graphs with 8 vertices and concluded that a low degree of a vertex corresponded with

a more advantageous mutant and this advantage seemed to increase monotonically for vertex v_i with $\frac{\sum_{v_j \in V} d_j}{N} - d_i$. This aligns well with equations 8 and 9. Further, they also provide the following analytical approximation for relative mutant advantage.

$$\frac{P_{\{v_i\}}}{P_{\{v_j\}}} \approx (\frac{d_j}{d_i})^2 \tag{10}$$

The inverse relationship between fixation and the degree of the initial mutant vetex shown by [10] is in strong agreement with the previous work of [1]. It is interesting to note that experimentally, it was observed in [10] that as the relative fitness of the mutant increases, the fixation probabilities increase more rapidly for mutants placed into vertices with higher degree. Some of these results were experimentally verified in [11]. In Section 5, we examine the correlation of the initial mutant's degree to the fixation probability when the dynamics of the evolutionary process is changed via different update rules.

It is also interesting to note that the authors of [9] were able to analytically solve for the fixation probabilities for the special case of undirected star graphs ($K = 2$) of L leaf vertices (hence $N = L+1$). Let P_i^0 ($P_i^\emptyset$) denote the fixation of probability given i mutants on the leaves and a the center being a mutant (resp. the center being a resident). [9] derive the following.

$$P_1^0 = \frac{1}{1 + \frac{L}{L+r} \sum_{j=1}^{L-1} \left(\frac{L+r}{r(L \cdot r+1)} \right)^j} \tag{11}$$

$$P_0^0 = \frac{r}{r+L} P_1^0 \qquad P_0^\emptyset = \frac{r \cdot L}{r \cdot L + 1} P_1^0 \tag{12}$$

From this, they derive the following for fixation probability ($\rho_{undir\text{-}star}$).

$$\rho_{undir\text{-}star} = \frac{L \cdot \frac{r \cdot L}{r \cdot L+1} + \frac{r}{r+L}}{(L+1)\left(1 + \frac{L}{L+r} \sum_{j=1}^{L-1} \left(\frac{L+r}{r(L \cdot r+1)} \right)^j \right)} \tag{13}$$

$$\lim_{L \to \infty} \rho_{undir\text{-}star} = \frac{1 - \frac{1}{r^2}}{1 - \frac{1}{r^{2L}}} \tag{14}$$

3.3. Calculating Fixation Probability using Dynamics

Another novel approach to determining fixation probabilities is through the use of dynamics which involves a carefully constructed variation of the Kimura diffusion equation. This approach was introduced by Houchmandzadeh and Vallade for well-mixed populations in [19] and extended to a graphical case (that generalizes the model of [24]) in [20]. Here we illustrate this approach by using it to derive the Moran probability, ρ_1. This particular approach is rooted in the master equation governing a continuous time birth-death stochastic process in a community of fixed size N, when the probability of observing k events in an infinitesimal time interval dt is proportional to Poissonian events dt^k. The transition rates χ, derived from the probability density for the system to change its size from n to m individuals during the infinitesimal period of time as $dt \to 0$, become the weights of the master equation summarized by

$$\chi(n \to n+1) = \chi^+(n), \tag{15}$$

$$\chi(n \to n-1) = \chi^-(n), \tag{16}$$

$$\chi(n \to n+k) = 0 \quad \text{if} \quad |k| > 1. \tag{17}$$

The master equation governing the probability, $P(n,t)$, of observing n individuals at time t and incorporating the transition weight for each observance is given by

$$\frac{\partial P(n,t)}{\partial t} = \chi^+(n-1)P(n-1) - \chi^+(n)P(n) + \chi^-(n+1)P(n-1) - \chi^-(n)P(n). \tag{18}$$

We can generalize problems using the master equation to continuous time Moran processes for haploid populations [20]. As usual, we have a population of N individuals that are either mutants or residents. Individuals in this population die randomly at a rate μ and are immediately replaced with a duplicate of another individual. Also as normal, residents have a fitness of 1 and mutants have a fitness of r. We shall use the symbol s for the value $r-1$ - the difference in fitness between the two. This quantity s will be factored into the duplication probability to decrease or increase the population of individuals carrying the mutant gene by one unit within time step dt. Designating n to be the number of individuals carrying the mutant gene and $(N-n)$ the number of all those who do not, the transition probabilities

become [19]

$$\chi^{-}(n) = \mu n \frac{(N-n)}{N} \tag{19}$$

$$\chi^{+}(n) = \mu n \frac{(N-n)}{N}(1+r) \tag{20}$$

where μn and $\mu(N-n)$ represent the probability per unit of time that either one mutant individual dies and is replaced by a resident individual or vice versa, respectively. The factor $(1+r)$ designates the differing fitness levels of the mutants. Time will be measured in N/μ units so that $\mu/N = 1$.

Because N and μ are fixed, equation 19 and equation 20 can be combined as a function of two parameters allowing a slightly simpler version of equation 18. Thus,

$$\chi(n,s) = \mu n \frac{(N-n)}{N}(1+r) \tag{21}$$

and

$$\frac{\partial P(n,t)}{\partial t} = \alpha(n,r)P(n-1) - \beta(n,r)P(n). \tag{22}$$

where $\alpha(n,r) = \chi(n-1,r) + \chi(n-1,0)$ and $\beta(n,r) = \chi(n,r) - \chi(n,0)$. To transform the discrete master equation 22 into a continuos differential equation for large N, we must set $x = n/N$, $dx = 1/N$, $p(x,t)dx = P(n,t)$, and $\psi(x,r) = \chi(n,r)$. Developing equation 22 by transforming each term into powers of dx yields

$$\frac{\partial p(x,t)}{\partial t} = -\frac{1}{N}\frac{\partial[\alpha(x,r)p(x,t)]}{\partial x} + \frac{1}{2N^2}\frac{\partial^2[\beta(x,r)p(x,t)]}{\partial x^2} + O(dx^3), \tag{23}$$

and can be approximated by the Kimura diffusion equation, such that

$$\frac{\partial p(x,t)}{\partial t} = -Nr\frac{\partial[x(1-x)p(x,t)]}{\partial x} + \frac{\partial^2[x(1-x)p(x,t)]}{\partial x^2}. \tag{24}$$

The neat thing about developing the equation this way is that we do not have to use it as it is an approximation. By deriving Kimura's diffusion equation using the applied transition rates we validate that the method is sound. So instead of resorting to the approximation, we can take a more direct route and extract exact quantities such as the probability generating function (PGF) by letting

$$\phi(z,t) = \sum_n z^n P(n,t), \tag{25}$$

where z is an auxiliary continuos variable. Notice that PGF $\phi(z,t)$ constitutes the most complete information we can have on the given stochastic process. The system will have two absorbing states at $n = 0$ and $n = N$. This will have the added effect of ensuring that $\phi(z,t)$ is a polynomial of degree N for $n < 0$ and $n > N$. Substituting $\phi(z,t)$ into the master equation 22 yields

$$\frac{\partial \phi}{\partial t} = \langle (z^{n+1} - z^n)\chi(n,r)\rangle + \langle (z^{n-1} - z^n)\chi(n,0)\rangle \tag{26}$$

We now turn to the transition rates, $\chi(n,r)$, for the Moran process. Recall that because of the way we measure time, $\mu/N = 1$ and therefore

$$\chi(n,r) = k(r)n(N-n) \tag{27}$$

where $k(r) = 1 + r$. Equation 26 becomes

$$\frac{\partial \phi}{\partial t} = \langle (z^{n+1} - z^n)k(r)n(N-n)\rangle + \langle (z^{n-1} - z^n)k(0)n(N-n)\rangle \tag{28}$$

We can now make use of the identity [19]

$$\langle z^{n+\alpha}k(r)n(N-n)\rangle = k(r)z^{\alpha}z\frac{\partial}{\partial z}\left[N\phi - z\frac{\partial \phi}{\partial z}\right] \tag{29}$$

which when used to evaluate equation 28 yields

$$\begin{aligned}
\frac{\partial \phi}{\partial t} &= (k(r)z^2 - k(r)z + k(0) - k(0)z)\frac{\partial}{\partial z}\left[N\phi - z\frac{\partial \phi}{\partial z}\right] && (30)\\
&= (1-z)(k(0) - k(r)z)\frac{\partial}{\partial z}\left[N\phi - z\frac{\partial \phi}{\partial z}\right] && (31)\\
&= (1-z)(k(0) - k(r)z)\frac{\partial}{\partial z}\left[N\phi - z\frac{\partial \phi}{\partial z}\right] && (32)\\
&= \frac{1}{\sigma}(1-z)(\sigma - z)\frac{\partial}{\partial z}\left[N\phi - z\frac{\partial \phi}{\partial z}\right] && (33)
\end{aligned}$$

where σ is the inverse of the fitness such that $\sigma = k(0)/k(r) = 1/k(r) = 1/(1+r)$. This partial differential equation is well-defined and has the exact same formal structure as the diffusion equation. Notice that it is first order in time t and second order in z. The initial and boundary conditions are specified as well. For the initial condition examine time $t = 0$. There are n_0

individuals with the mutant gene. That means there is a 100% probability of observing n_0 individuals have the mutant gene or $P(n_0, 0) = 1$ and equation 25 becomes

$$\phi(z, 0) = z^{n_0}. \tag{34}$$

Further, because $P(n, t)$ is stochastic we have a boundary in that

$$\phi(1, t) = 1. \tag{35}$$

If $s = 0$, then $k(0) = k(r)$, $\langle n(t) \rangle = n_0$, and

$$\left.\frac{\partial \phi}{\partial z}\right|_{=1} = n_0 \quad \text{if} \quad r = 0. \tag{36}$$

If $r \neq 0$, $z = \sigma$ is a fixed point because

$$\left.\frac{\partial \phi}{\partial t}\right|_{z=\sigma} = 0 \quad \text{if} \quad r \neq 0 \tag{37}$$

which means that

$$\phi(\sigma, t) = \phi(\sigma, 0) = \sigma^{n_0} \tag{38}$$

[20] demonstrate that equation 33 along with initial condition equation 34 and the boundary conditions equation 35 with either equation 36 or equation 38 constitute a well-posed problem.

Fortunately, $\phi(z, t)$ of equation 33 converges to stationary solution $\phi_s(z)$. This stationary solution is found by solving the first order differential equation

$$N\phi_s(z) - z\phi_s^{'}(z) = K \tag{39}$$

where K is a constant. The solution of 39 is

$$\phi_s(z) = c_1 z^N + c_0 \tag{40}$$

If we now use the boundary conditions 35 and 36 when $r = 0$, we can solve for c_1 and c_0. They become

$$c_1 = \frac{n_0}{N}, \qquad c_0 = \frac{N - n_0}{N}. \tag{41}$$

Of course when $r \neq 0$, boundary condition 36 is replaced with 38 and

$$c_1 = \frac{1 - \sigma^{n_0}}{1 - \sigma^N}, \qquad c_0 = \frac{\sigma^{n_0} - \sigma^N}{1 - \sigma^N}. \tag{42}$$

It is interestingly to note that as $r \to 0$, equation 42 converges to equation 41. Note that for relatively small fitness, r, c_1 of equation 42 contains the well-known result for fixation probability for haploid populations, namely the Moran fixation probability result, equation 1 of the previous section.

$$\rho_1 = \frac{1 - 1/r}{1 - 1/r^N} \tag{43}$$

4. Time to Fixation

In this section we explore an area of EGT that has recently seen some interesitng activity: determining the mean time it takes to reach fixation. First we examine this for fixed values of r and then for the case where r depends on the payoff of a two-player game.

4.1. Time to Fixation for Fixed Fitness

Here, we examine research on time to fixation when the fitness of the mutant and resident is fixed at r and 1 respectively (i.e., not determined by the outcome of a game). In the undirected case, this was explored experimentally in [53], [10], and [42]. Generally, these studies find that certain graph structures which promote fixation (i.e., stars and funnels) also increase time to fixation. In [53], the authors find that stars increase the time to fixation over regular graphs by two orders of magnitude. In [42], the authors examine domination times for lattices. *Domination* in that work refers to a mutant or resident occupying a large fraction of vertices (approaching N) - hence the term 'dominate' is used to describe the results of [42] rather than fixation. They found experimentally that time t_* for mutants to dominate lattices decreases as the dimension of the lattice increases (i.e., a fully-connected graph has a faster time to domination than a square lattice) for several different values of r.

There has also been some work to explore this problem analytically. In [2], the authors provide a method for determining mean time to fixation (and mean time to extinction) in well-mixed populations. This formal method was later adopted by [33] for fixed fitness and [7] for fitness resulting from a two player game (described in the next section). We briefly highlight the most relevant parts of this method as follows. Given a well-mixed population of N individuals, let $0, \ldots, i, \ldots, N$ denote $N + 1$ possible states identified by the number of mutants in each state (analogous to the different configurations

in an evolutionary graph). We will use the notation $P_i, \overline{P_i}$ to denote fixation and extinction probabilities given initial state i. Let μ_i be the the transition probability from state i to state $i-1$ and λ_i be the transition probability from state i to $i+1$. In [2], the authors show the following:

$$P_i = \frac{s_{0,i-1}}{s_{0,N-1}} \tag{44}$$

Where $s_{n,m} = \sum_{k=n}^{m} q_k$ and $q_i = \prod_{j=1}^{i} \frac{\mu_j}{\lambda_j}$. Now we define $P_i^{(t)}, \overline{P_i^{(t)}}$ be the probabilities of entering fixation/extinction at time t. Let t_i (resp. $\overline{t_i}$) be the mean times to fixation (resp. extinction) given state i at time 0. We are concerned with finding t_1 - the probability of fixation given a single mutant invader. Clearly, $P_i = \sum_{t=0}^{\infty} P_i^{(t)}$ and we can obtain the following for the mean time to fixation.

$$t_i = \frac{1}{P_i} \sum_{t=0}^{\infty} t \cdot P_i^{(t)} \tag{45}$$

Additionally, the following recursions hold.

$$P_i^{(t)} = \mu_i P_{i-1}^{(t-1)} + (1-\mu_i-\lambda_i) P_i^{(t-1)} + \lambda_i P_{i+1}^{(t-1)} \tag{46}$$

$$P_i t_i = \mu_i P_{i-1}(t_{i-1}+1) + (1-\mu_i-\lambda_i) P_i(t_i+1) + \lambda_i P_{i+1}(t_{i+1}+1) \tag{47}$$

Through a series of further manipulations and by expression 44, [2] determine the mean time to fixation as follows.

$$t_1 = \sum_{n=1}^{N-1} \frac{s_{0,n-1} s_{n,N-1}}{\lambda_n q_n s_{0,N-1}} \tag{48}$$

Note that [2] rely on determining mean time to fixation based on the transition probabilities (for example, [2] look at when these fixation probabilities are dependent upon game-play, the problem becomes more complex, even for well mixed populations). Further, in a well-mixed population there are $N+1$ states, significantly less than the 2^N possible states for an arbitrary evolutionary graph. Therefore, evolutionary graph theorists focus on reducing the state space (usually by assuming a certain graph topology) and calculating the transition probabilities (μ and λ). If a certain graph topology allows for a tractable number of states, analytical results become apparent.

This method was applied successfully for fixed fineness in [33]. Using the aforementioned described method, they obtain the following result for isothermal evolutionary graphs. Here the notation t_1 refers to the mean time to fixation given a single mutant picked with a uniform probability over the set V.

Theorem 5 (Isothermal Mean Time to Fixation [33]). *For large N in an isothermal structure, the mean time to fixation is:*

$$t_1 = \sum_{n=1}^{N-1} \frac{(r^n - 1)(r^{N-n} - 1)(1 + r)}{(r^N - 1)(r - 1)} \tag{49}$$

Then then show an analogous result for K-star structures.

Theorem 6 (K-Star Mean Time to Fixation [33]). *For large N in a k-star structure, the mean time to fixation is:*

$$t_1 = \sum_{n=1}^{N-1} \frac{(r^{nK} - 1)(r^{(N-n)K} - 1)(1 + r^K)}{(r^{NK} - 1)(r^K - 1)} \tag{50}$$

Though we have analytical results for these special cases, there are still many open questions dealing with mean time to fixation (and extinction). For example, identifying the complexity of calculating the mean time to fixation in the general case has not been addressed. A good complexity analysis may lend some insight into this particular problem. To provide some insight into this general case, we will derive a set of constraints similar to expression 3 earlier in the paper. For a given configuration C of mutant vertices (the remainder of the population being residents), let $\mu_{C,i}$ be the transition probability from C to $C - \{v_i\}$, $\lambda_{C,i}$ be the transition probability from C to $C \cup \{v_i\}$, and γ_C be the probability that C transitions to itself. Hence, we have the following:

$$\mu_{C,i} = \sum_{v_j \notin C} \frac{w_{ji}}{N + r|C| - |C|} \tag{51}$$

$$\lambda_{C,i} = \sum_{v_j \in C} \frac{w_{ji} r}{N + r|C| - |C|} \tag{52}$$

$$\gamma_C = 1 - \left(\sum_{v_i \in C} \mu_{C,i} + \sum_{v_i \notin C} \lambda_{C,i} \right) \tag{53}$$

We can now create an analogous recursion mirroring that of 46 for well-mixed populations where $P_C^{(t)}$ is the probability of entering an all-mutant state at time t given initial set C.

$$\begin{aligned} P_C^{(t)} &= \left(\sum_{v_i \in C} \mu_{C,i} P_{C-\{v_i\}}^{(t-1)}\right) + \gamma_C P_C^{(t-1)} + \left(\sum_{v_i \notin C} \lambda_{C,i} P_{C\cup\{v_i\}}^{(t-1)}\right) \\ P_C t_C &= \left(\sum_{v_i \in C} \mu_{C,i} P_{C-\{v_i\}}(t_{C-\{v_i\}}+1)\right) + \gamma_C P_C(t_C+1) + \\ &\quad \left(\sum_{v_i \notin C} \lambda_{C,i} P_{C\cup\{v_i\}}(t_{C\cup\{v_i\}}+1)\right) \end{aligned}$$

Clearly, as we are dealing with a intractable number of states there are an intractable number of constraints and variables the above expression, making it impractical. Hence, a more practical algorithm is in order if we are to avoid simulation for this problem.

Another option would be to explore mean time to fixation for special cases, such as undirected evolutionary graphs or the case of neutral drift. Another area that is largely unexplored (in the general case) is time-to-fixation under alternate update rules, such as the voter model (although for games on star graphs, we review the work of [15] in the next section).

4.2. Time to Fixation for Games on Graphs

Broom et al. [7] study evolutionary dynamics for general games on several special graph structures: the star, the circle, and the complete graph under a Birth-Death update process (specifically the Invasion Process, see Section 5) while placing an emphasis on the speed of the evolutionary process in their analysis. At each time step, the fitness of an individual is assumed to be the average of the payoffs of games against all its neighbors. The authors analyze and derive exact solutions for the fixation probability of mutants, the mean time to absorption and the fixation time of mutants on the three graph structures considered. The authors find these quantities to differ for the different graph structures and in general depend on population size and graph heterogeneity.

The authors confirm earlier findings that fixation probability usually increases with graph heterogeneity. The time to fixation for mutants was found

to be shortest for the complete graph and longest for the star, confirming the results from the previous section that fixation time generally is longer for graph structures that promote fixation. Fixation times for all graphs explored were also shown to be longest in neutral drift. More interestingly however, using a Hawk-Dove game as an example, the authors show that the variation of the payoff values in the payoff matrix of a game played on graphs plays a crucial role in the behavior of the analyzed quantities. Not only is the fixation probability no longer the same for all regular graphs with N vertices, but also which of the three considered graph types gives the highest mutant fixation probability and the fastest time to fixation/absorption depends on the values of the game's payoff matrix. The authors give several interesting features of the Hawk-Dove game considered regarding the analyzed quantities, but not that these results can be significantly different for a Hawk-Dove game with an alternative payoff matrix.

In general, this work illuminates the fact that discovering and describing (to the extent that they exist) general and consistent patterns in the effects of game payoffs, graph types, and combinations thereof on fixation probability and time to fixation is a challenging but important area for future work. Hadjichrysanthou et al. [15] make a step of progress in this direction by providing general formulae for fixation probability and mean time to absorption for star graphs specifically. The authors provide detailed analysis of these quantities for the fixed fitness case and the Hawk-Dove, Prisoner's Dilemma and coordination games. They find that the time to absorption on star graphs depend crucially on the update process used: while in general Birth-Death processes yield higher fixation probabilities for advantageous mutants, Birth-Death processes take much longer to reach fixation/absorption than Death-Birth processes (see Section 5 for details on these update processes). There is still much room for this type of work on more general graphs:

Open Problem 4.1. *Discover and describe patterns of the effects of a larger variety of graph structures, game payoffs, and their combinations on fixation probability and time to fixation.*

5. Alternate Update Rules

Let us momentarily return to the original model of [23]. At each time-step, some vertex v_i is selected with probability $\frac{f_i}{\sum_{v_j \in V} f_j}$, where f_i is the fitness of v_i and equal to either 1 or r. This is the vertex chosen to reproduce, hence a

Table 1: Different families of update rules.

Update Rule	Intuition
Birth-Death (BD) (a.k.a. Invasion Process (IP))	(1) vetex v_i selected (2) Neighbour of v_i, vetex v_j selected (3) Offspring of v_i replaces v_j
Death-Birth (DB) (a.k.a. Voter Model (VM))	(1) vetex v_i selected (2) Neighbour of v_i, vetex v_j selected (3) Offspring of v_j replaces v_i
Link Dynamics (LD)	(1) Edge (v_i, v_j) selected (2) The offspring of one vetex in the edge replaces the other vetex

'birth' event. The next vertex selected is one of the neighbors of v_i - lets call it v_j and it is selected with probability w_{ij}. This is a 'death' event as v_j is replaced with a duplicate of v_i. Notice that the fitness of v_j is not considered when it is selected. Hence, the fitness bias is on the birth event. This method of selecting vertices v_i and v_j is referred to as an *update rule*. The update rule described in [23] is termed 'birth-death with birth bias' or BD-B updating. Several works address different update rules including: [1, 38, 47, 26, 25]. Overall, we have identified three major families of update rules - birth-death (a.k.a. the invasion process) where the vetex to reproduce is chosen first, death-birth (a.k.a. the voter model) where the vetex to die is chosen first, and link dynamics, where an edge is chosen. We summarize these in table 1.

Note that the three categories of table 1 are very broad as they do not consider fitness-based bias in vetex selection (i.e., the BD-B updating of [23] places the bias on the birth event as the first vertex is chosen with a probability proportional to its fitness). If there is a birth-bias, the individual reproducing is chosen with a probability proportional to its fitness. If there is a death-bias, the individual dying is chosen with a probability inversely proportional to its fitness. We summarize how directionality and bias affect the update rules in table 2. Note that imitation (IM) is also known as *biased link dynamics*.

Table 2: Variations of EGT. v_i and v_j are vertices in a graph that are neighbors, v_i is always chosen first. f_i and f_j are the associated fitness values which both equal 1 in the case of neutral drift.

Update Rule	Special Case	Intuition
Birth-Death (BD)	Unbiased, undirected	offspring of v_i replace v_j
	Directed	Considers v_i's outgoing edges
	Biased-birth (BD-B)	v_i chosen w. prob. proportional to f_i
	Biased-death (BD-D)	v_j chosen w. prob. proportional to f_j^{-1}
Death-Birth (DB)	Unbiased, undirected	offspring of v_j replace v_i
	Directed	Considers v_i's incoming edges
	Biased-birth (DB-B)	v_j chosen w. prob. proportional to f_j
	Biased-death (DB-D)	v_i chosen w. prob. proportional to f_i^{-1}
Link Dyn. (LD)	Unbiased, undirected	one vetex reproduces to replace the other
	Imitation (IM)	least fit vetex dies, replaced by offspring of other vetex
	Pairwise Compar. (PC)	v_j replaces v_i iff $f_j > f_x$, o/w no change
	Directed, unbiased	edge from v_i to v_j, v_i replaces v_j
	Directed, birth biased	edge selected w. prob. proportional to f_i
	Directed, death biased	edge selected w. prob. proportional to f_j^{-1}

Table 3: Relationship between fixation and degree of initial vetex (undirected graphs).

Update Rule	Fixation probability proportional to
BD-B	Inverse of degree of initial vetex
DB-D	Degree of initial vetex
LD	Density of mutant vertices

5.1. Comparing Update Rules in Undirected EG's

For the case on undirected graphs, there are many results based on the initial placement of the mutant have been discovered for several update rules (as we have described for BD-B in the previous section). In [1, 47], the authors study moments of degree distribution, density, and degree-weighted moments and show that the fixation probability is proportional to the average degree-weighted moment for death-birth updating (a.k.a. voter model), the inverse for birth-death (a.k.a. invasion process), and equal to the density (the percentage of the number of vertices in the graph labeled as mutants) for link dynamics, thus independent of the underlying graph in that case. Note that their results for BD-B are in agreement with the finding of [10] described earlier.

As shown in theorem 4, under BD-B, an undirected EG is isothermal iff it is regular. In [1], this is extended to other update rules as follows.

Theorem 7 ([1]). *Evolutionary dynamics under BD-B, DB-D, and LD are equivalent for undirected regular EG's.*

Although there is currently an excellent suit of results for studying evolutionary graphs under various different update rules in the directed case, there has been no work (to the knowledge of the authors) that compares any of these update rules to the synchronous update model described by Santos et al. in [44].[2] At each time-step, all individuals in the population update their labels (i.e., mutant or resident, or strategy if game-play is involved) simultaneously. For each vertex v_i, one of its neighbors (vertex v_j) is selected at $\frac{1}{d_i}$.

[2]Note that the original work of Santos et al. is a model with a game theoretic extension. Here we describe the natural, fixed fitness counterpart for the purpose of examining the update rule. We review this work with respect to its game theoretic results in Section 6.

Then, if and only if $f_j > f_i$, v_i's label is replaced with v_j's label with a probability proportional to $f_j - f_i$ (i.e., $\frac{f_j - f_i}{\max(d_i, d_j) \cdot r}$ for example). There are several interesting aspects about this model. For instance, the fitness of vertices does not play a role in selecting which vertex is born and/or dies. Rather, the fitness determines if a vertex is replaced by a neighbor and the probability at which this happens. Additionally, as all vertices are updated simultaneously, we might conjecture that the evolutionary process occurs faster than in the other update rules. These topics may warrant some further consideration in that synchronous updates may represent some real-world processes more accurately or possibly be used as a proxy for the standard update rules we have already described. Further, the synchronous update model can also easily be extended to the directed case, which we cover for the other update rules in the next section.

5.2. Comparing Update Rules in Directed EG's

Not only does the original model of [23] utilize a directed graph, but many real-world networks can be more accurately modeled as directed graphs than undirected ones. This is the motivation of the work [26, 25]. There are two main conclusions to their work: (1) degree correlation to fixation probability (i.e., using the exact methods of [8] or the mean-field approximation) for undirected graphs does not necessarily hold in the direct case and (2) directed graphs generally suppress fixation more than undirected ones.

In [26], the authors study directed graphs under LD, BD, and DB for $r = 1$. For all three update rules, under $r = 1$, they derive sets of linear constraints using the mean-field approximation (degrees of connected vertices in the EG are uncorrelated). They compare these analytical approximations with experiments and find that, in general, the fixation probability is not only dependent on the degree of the initial vetex but also the global structure of the graph. In fact, often there is no observed relation between degree and fixation. See table 4 for a summary of experimental results compared with the analytical approximations. While [26] mainly considers the case of neutral drift ($r = 1$), they also run some tests with $r = 4$ and claim that fixation increases monotonically with r.

In [25], the authors perform an in-depth comparison on directed and undirected networks for several variants of these rules. He exactly computes fixation probabilities on an exhaustive set of small graphs (with six vertices) and uses Monte-Carlo approximation for randomly generated larger graphs. He found that directed networks tended to suppress more than undirected,

Table 4: Summary of experimental results for directed case with $r = 1$ in [26] illustrating whether experimentally-determined fixation probability results that alighned with the mean-field approximation. d_{in} and d_{out} are the in and out degrees of the initial mutant vetex.

Mean-field approximation	BD: $1/d_{in}$	DB: d_{out}	LD: d_{out}/d_{in}
Asymmetric random	$1/d_{in}$	d_{out}	d_{out}/d_{in}
Asymmetric scale-free	No relation	d_{out}	d_{out}/d_{in}
E-mail	No relation	No relation	No relation
Asymmetric Small World	No relation	No relation	No relation

regardless of update rule. Based on these experiments for small networks, the order of amplification for rules is as follows: BD-B > LD > DB-D > BD-D > DB-B (BD-B was least suppressive and DB-B was the most suppressive). The value of r was set to 4 in these trials. For large graphs (also with $r = 4$), the simulations provided the following ordering: BD-B > BD-D, LD > DB-D > DB-B.

The authors are currently looking at adopting the algorithm of [45] for alternate update rules on directed EG's, which would allow us to obtain more exact and deterministic results on larger graphs(as we would not resort to simulation). This would provide a complement to the work of [25].

6. Further Game Theoretic Extensions

Now that we have described alternate update rules, we shall re-visit our game-theoretic extensions and review some results regarding topics such as cooperation, reciprocity, and evolutionary stability w.r.t. a game on the graph under various update rules.

6.1. Evolutionary Stability on Graphs

Evolutionary stability, describing the ability of a player type comprising a population to be resistant against invasion by another type, is an important concept in evolutionary game theory that has been well studied for well-mixed populations. Ohtsuki et al. [40] analyze evolutionary stability on regular graphs of degree $k > 2$ for the BD, DB, and IM updating rules through pairwise approximation and simulation. Evolutionary stability on graphs means that a small fraction of rare mutants cannot spread, i.e., a

resident strategy evolutionarily stable if it has a selective advantage over an invading strategy (invading at an ϵ fraction of the total population). Ohtsuki et al. provide evolutionary stability conditions for this definition on regular graphs for the different update rules considered, and (on top of the game payoff matrix values) all these conditions depend on the graph degree k. The results are validated through simulations on specific game examples. The important point to consider from these results is that population structure can have crucial impact on the evolutionary stability of strategies, i.e., in the words of "traditional criterion for evolutionarily stable strategies in well-mixed populations is neither necessary nor sufficient to guarantee evolutionary stability in structured populations".

6.2. Regular Graphs and the Replicator Equation

Ohtsuki et al. [38] study evolutionary games on regular graphs of degree k considering the BD, DB, IM, PC update rules[3]. The authors use pair approximation ([28, 27, 22, 17, 51]) to derive a system of ordinary differential equations describing the change in expected frequency of strategies in a game on a graph over time. In the limit of *weak selection* ($w << 1$), the authors show that under the update rules BD, DB, and IM this differential equation is the well-known replicator equation with a transformed payoff matrix. The payoff matrix is the original payoff matrix summed with a payoff matrix describing the local competition of strategies, different for BD, DB, and IM. PC is shown to be equivalent to BD in the model used. This result is applied to the Prisoner's Dillema and the Snow Drift Game on regular graphs. Results for the Prisoner's Dillema coincide with those of [36], showing identical conditions necessary for cooperators to be favored over defectors. Results for the snow drift game qualitatively agree with those of Hauert et al. [18], who observe that spatial structure inhibits cooperation in the snow drift game.

6.3. Evolution of Cooperation and Social Viscosity

Ohtsuki et al. [36] explore the problem of cooperation on a variety of graphs through numerical simulations. The graph types explored are cycles, spatial lattices, random regular graphs, random graphs and scale free networks. Every player plays a game with all its neighbor, where the game

[3]We use the shorter BD and DB notation for the update rules with birth bias BD-B and DB-B. See Table 2.

between two players is given by the payoff matrix (54) below. This game represents a Prisoner's Dilemma game between two players, and gives a kind of Public Goods Game when each player plays the game with all its neighbors. In this game b is called the benefit of the altruistic act and c is the cost of the altruistic cooperation act. A Cooperator that is connected to n Cooperators and m Defectors for receives a payoff of $b\,n - c\,(n + m)$.

	cooperate	defect
cooperate	b - c	- c
defect	b	0

(54)

Ohtsuki et al.'s results suggests that under the DB update rule, a necessary condition for cooperation to arise in the types of graphs explores is that $b/c > k$, where k is the average number of neighbors. This result is derived under the conditions of weak selection and that the number of vertices in the graph is much larger than the average degree. The authors note the close and interesting relation of this result to Hamilton's rule ([16]), which states that kin selection can favor cooperation provided that $b/c > 1/r$, where r is the coefficient of genetic relatedness between individuals. The condition for cooperation fits less well for non-regular graphs, as one would expect due to the larger variance in vertex degrees, but is a good approximation unless the variance in degree distributions of the graph gets too large. Other dynamics explored are IM [4], for which cooperation is favored when $b/c > k + 2$, and BD, for which cooperation is never favored by selection.

Other authors have verified the condition introduced in [36] to hold in a different model with network dynamics. Yang et al. [12] use pair approximation and numerical simulations to deduce cooperation frequencies for social dilemma games (including the Prisoner's Dilemma and Snow-Drift games) on graphs whose structure changes as part of the update rule throughout evolution. The graphs originally are randomly connected with average degree k. The update rule used is a type of DB process which also involves addition and deletion of vertices and edges in the graph: "An individual is selected for reproduction with a probability proportional to his fitness. The offspring

[4]The authors of [36] also note that mathematically, "IM updating can be obtained from DB updating by adding loops to every vertex".

is introduced with the same strategy of his parent and connects to his parent always and other $k-1$ individuals randomly. The offspring replaces a random individual except for his parent. The randomly selected individual with all its links are removed." More recently, the preliminary work of Zhong et al. [57] also confirmed Ohtsuki's rule on a continuous version of the model.

In [52], Voelkl and Kasper used evolutionary graph theory to understand the emergence of cooperation in primates. Using social interaction networks derived from empirically observed social interactions, they looked at a two player game with payoff matrix as above (54). The authors use selection intensity equation 4 with $w = 0.01$ to determine fitness. The authors discovered that the structured populations of the primates were more likely to reach fixation than populations of well-mixed individuals.

The authors of [52] also looked at the community structure of the primate interaction networks. For this they leveraged the idea of *modularity* introduced in [31]. Given a partition of vertices in a graph, modularity measures the quality of these partitions - often referred to as "communities". Intuitively, the modularity of a partition increases with the density of edges within communities and decreases with the density of edges outside of communities. Often in work dealing with modularity (such as [30] and [5]) researchers attempt to find an optimal partition. Hence, the modularity of the optimal partition can also be viewed as a property of graph topology. The authors of [52] compare optimal modularity values to fixation probability (ρ, determined by simulation) using linear regression. This led them to the conclusion that 60% of the variance in fixation probability can be accounted for by the modularity of the graph. An interesting direction for future work would be a more detailed examination on the relationship between ρ and optimal modularity based on a wider variety of graphs.

6.4. Graph Heterogeneity and Evolution of Cooperation

Santos et al. [44] investigate the effects of single-scale and scale-free networks on cooperation in the Prisoner's Dillema, Snow-Drift, and Stag-Hunt games through simulations. The update rule used is a type of imitation dynamic in which all vertices update simultaneously in each generation, as follows: for each vertex a random neighbor is chosen, and if that neighbor has achieved a higher payoff, the vertex adopts the strategy of this neighbor with a probability proportional to the payoff difference. The authors find that in degree-heterogeneous graphs cooperation is easier to sustain than in

well-mixed populations and thus identify heterogeneity as a "powerful mechanism for the emergence of cooperation." Additionally, the authors find that the sustainability of cooperation also depends on"detailed and intricate ties" between agents. As evidence of this, scale free networks which exhibit properties like those that emerge from models of growth from preferential attachment (Albert-Barbarasi topology) are shown to produce higher cooperation than random scale-free networks.

Fu et al. [13] devise a framework for the general study of games on arbitrary graphs under weak selection, formulating the game dynamics as a discrete Markov process. Using DB updating and the game of the prisoner's dilemma, they employ their method on random regular graphs and scale-free networks to demonstrate the utility of their framework compared to pair-approximation and simulated data. The authors find a stronger correlation between their approach and the simulated results. They also reach some conclusions on the evolution of cooperation, most notably that under DB updating and weak selection, degree heterogeneous graphs (e.g., scale-free networks) generally impose higher invasion barriers than regular graphs. This extends a result in [1] reporting that a heterogeneous graph is an inhospitable environment for a mutant to evolve in the case of constant selection. Fu et al. show this to be true for weak selection as well. This result seems to be in disagreement with the conclusion of [44], which concludes that graph heterogeneity aids the emergence of cooperation. Fu et al. point out that this conclusion by [44] hinges on the simultaneous appearance of a number of cooperators to overcome the invasion barrier.

6.5. Direct Reciprocity on Regular Graphs

Ohtsuki et al. [37] study reciprocity in the iterated prisoner's dilemma (exhibited by strategies such as Tit-for-Tat) on large, regular graphs through pair approximation for the four update rules BD, DB, IM, and PC under weak selection. The game concerned is again that of payoff matrix (54), but translating the payoffs in the matrix to a repeated game with q probability of playing another iteration and assuming a game between reciprocators playing Tit-for-Tat and Defectors All-D gives the following payoffs:

	cooperate	defect
cooperate	$(b-c)/(1-q)$	- c
defect	b	0

(55)

The authors are particularly concerned with evolutionary stability and "advantageousness" of reciprocators and find that different update rules have a critical effect on these measures. A strategy is termed "advantageous" if a single mutant following the strategy starting in a random position on the graph has a fixation probability greater than the inverse of the population size, meaning that selection favors it over residents. The authors find that the ratio b/c necessary for a cooperator to be advantageous depends only on the probability to play another round in the repeated game (q) and the number of neighbors per individual (k). BD and PC produce identical results, showing evolutionary stability to be harder to achieve for cooperators on graphs compared to well-mixed populations, but it is easier for cooperation to be advantageous. In contrast, DB and IM updating make it easier for cooperation to be both evolutionarily stable and advantageous. In particular, for DB and IM either small k or large q are sufficient for the evolution of cooperation.

6.6. Separate Interaction and Replacement Graphs

Ohtsuki et al. [39] examine the evolution of cooperation in games on regular graphs - again with payoff matrix (54) . However, unlike other work, the graph for the interactions between players in the game (interaction graph H), and the graph among the relationships of who can replace whom (replacement graph G) are separate. The authors consider the case of *weak selection*, where $w << 1$. The authors use BD, DB, and IM updating. The authors consider regular graphs and again use pair approximation for their analysis of fixation probabilites. For DB updating, the authors find the following result, which is verified through experiments: if c and b are the cost and benefit associated with the game, ℓ is the degree of overlap between G and H, and g and h are the degrees of G and H, then the following inequality holds under death-birth updating: $b/c > hg/\ell$. Hence, the authors conclude that, for fixed cost and benefit values, cooperation is less likely to evolve if there is a greater disparity between the interaction and replacement graph, cooperation is maximized when G and H coincide. IM updating leads to $b/c > h(g+2)/\ell$, while BD, as has been shown before, never gives an evolutionary advantage to cooperators.

6.7. Further Work for Game Theoretic Extensions

A main area for future work is the extension of any of the results as described in this section to games with more than two competing strategies

on graphs, as well as for multi-player (> 2) games:

Open Problem 6.1. *Extend results on evolutionary games on graphs to populations with more than two competing strategies and multi-player games.*

However, there are still a significant amount of issues to explored in two-player games. As noted in [35] the benefit-cost payoff matrix (54) used in a number of works described is only a simplified version of the general Prisoner's Dilemma game that has been so important in the study of the evolution of cooperation. Extending results to the general game seems to be of considerable importance to the study of the evolution of cooperation on graphs:

Open Problem 6.2. *Extend results that used the benefit-cost payoff matrix (54) version of the Prisoner's Dilemma to the general Prisoner's Dilemma game payoff matrix.*

In reviewing work on games in EGT, we have noted and important difference in fitness assignment used by different researchers, the effects of which are unclear: While some works have used the average payoff of games on graphs in their fitness computation and resulting analysis (e.g., Broom et al. [7]) others use the total accumulated payoff of games. (e.g., Ohstuski et al. [36] and Santos et al. [44]). There is an important distinction between these on heterogeneous graphs: the former excludes the effect of playing a different amounts of games due to different amounts of neighbors, while the latter does not. It's important to be aware of this difference and it's of high interest to the community to explore to what extent analytical and experimental results are affected by this difference.

Open Problem 6.3. *Explore and understand the effects of using the average vs. accumulated payoff from games played with neighbors for fitness in evolutionary games on graphs.*

On the analysis of reciprocity, while Ohtsuki et al. [37] have considered direct reciprocity in their analyses for regular graphs, as noted by Nowak et al. [35], much more work is needed to work direct and indirect reciprocity into the mathematical frameworks presented by different authors (or a general one) encompassing various update rules and more complex population structures:

Open Problem 6.4. *Incorporate direct and indirect reciprocity into a general mathematical framework for evolutionary games on graphs.*

Concerning punishment and reputation, past work on spatial evolutionary games (e.g., [6]), where the population is structured on a simple grid, has explored the effects of punishment and reputation on the evolution of cooperation. However, the exploration of these mechanisms on general and complex population structures has not yet been explored:

Open Problem 6.5. *Using EGT to explore the effects of punishment and reputation on the evolution of cooperation under the constraints of general, more complex, population structures.*

Generally, we feel there exists a need to incorporate EGT into more evolutionary game theory applications: many existing applications of evolutionary game theory, particularly those in anthropology, economics, and social modeling and prediction could possibly greatly from EGT by using it to account for effects of population structure.

Open Problem 6.6. *Incorporate known or estimated population structures into more existing evolutionary game theoretic applications.*

7. Other Extensions to the Model

There are several other notable extensions to the original model of [23] worth noting. These include scenarios with bi-level graphs, multiple mutants, EG's whose topology changes over time, and other modifications.

7.1. Bi-Level Evolutionary Graphs

Pu Yan Nie introduces bi-level EG's in [32]. In general, a bi-level EG is defined as follows: first, there is an EG representing relationships between communities - with the vertices in this graph representing communities. The work on bi-level EG's often denote the community-level EG as graph B. Each of the m vertices of B is itself an EG of individuals - vertex v_i on graph B is EG A_i. This type of EG has been shown to help describe several biological phenomena. In the bi-level EG's of [32, 56], one of the vertices in graph B is an isothermal EG consisting of n individuals ('leaders'). The remaining $m-1$ vertices in graph B represent single individuals ('followers'). Hence, for the entire graph, $N = n + m - 1$. As only one vertex in graph B represents an

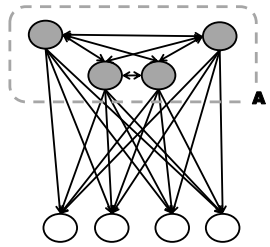

Figure 2: A bi-level EG where the leaders (set A) form an isothermal EG. When they are collapsed into a single vetex, we have a one-rooted EG.

EG, these works use A to refer to the EG consisting of the n leaders. As the structure of A and B are independent, we have the following relationship:

$$\rho(AB) = \rho(A) \cdot \rho(B) \tag{56}$$

where $\rho(AB)$ is the fixation probability of the entire bi-level EG, and $\rho(A), \rho(B)$ are the fixation probabilities of EG's A and B respectively. In [32], graph B is a star formation ($K = 2, M = 1$), with the central vetex being equivalent to EG A. The author shows that for $r \neq 1$ this bi-level graph suppresses fixation more than an isothermal graph, thus helping to explain the evolutionary stability of bi-level structures found in nature. In [56], the authors study a bi-level EG where B is one-rooted and A is equivalent to the root-vetex of B (see figure 2). The one-rooted case reflects hierarchical population structures. The authors show that when the number of followers is identical, that a bi-level EG has a lower fixation probability than a one-rooted EG. They also show that the fixation probability increases when the number of leaders increase (making a bi-level EG of this type with 2 leaders the most stable bi-level EG). They also show that an increase in number of followers decreases fixation probability and that fixation probability for a bi-level EG is closely tied to fitness. The authors apply these theoretical results to biology to help explain why structure occurs in some animal populations. Examples of this include symbiosis (such as the growth of Lichens) and commensalism (i.e., the relationship between clownfish and sea anemone).

The work on bi-level EG's is extended in [55] where the authors consider bi-level EG's where the mutant has a different fitness depending on the level of the graph. The model is described as follows. In this work, each vertex of B is associated with an EG. Hence, vertices $v_1, \ldots, v_i, \ldots, v_m$ in EG B are associated with EG's $A_1, \ldots, A_i, \ldots, A_m$. Each of these groups has n_i

individuals and adjacency matrix W_i (B has adjacency matrix W_0). The fixation probability of a mutant with fitness r taking over one of these groups is $\rho(W_i, n_i, r)$. For graph B, the fitness of the mutant is r_0 and the fixation probability for B is written $\rho(W_0, m, r_0)$. The authors study the case where the levels of the graph and r, r_0 are independent. For the overall bi-level EG, the authors obtain the following fixation probability (denoted $\rho(W, n, m, r, r_0)$ where $W = \{W_0, \ldots, W_m\}$).

$$\rho(W, n, m, r, r_0) = \frac{\sum_{i=1}^{m} n_i \cdot \rho(W_i, n_i, r)}{\sum_{i=1}^{m} n_i} \cdot \rho(W_0, m, r_0) \tag{57}$$

What if the fitness of one level of the population is dependent on the other? Regretfully, this has not been addressed with the current work on bi-level evolutionary graphs and provides us with the following open problem.

Open Problem 7.1. *Computing the fixation probability for a bi-level EG when r, r_0 are not independent ([55] assumes independence).*

Further, we also note that the stochastic evolutionary process on a bi-level graph takes place on the entire graph (i.e., graphs A and B at the same time scale). Essentially, a bi-level EG is a special case of an evolutionary graph as defined in [23]. What happens when the two levels of the graph evolve at different time scales? To study this, we would most likely view the stochastic process on the two graph structures - A and B separately. Such an addition would seem to add another layer of complexity to the problem. Additionally, game theoretic extensions to bi-level graphs have also not yet been considered. This would also likely go hand-in-hand with studying the fixation probability of bi-level graphs under different model dynamics.

It turns out that the earlier model of [24] is also an evolutionary graph. In that model, there are m islands whose relationship is specified in graph B. This specifies the migration pattern between islands. Each island has n individuals in a well mixed population (i.e., $n = n_1 = n_2 = \ldots = n_m$ and each A_i is a complete, undirected graph). In [24], the author uses birth-death updating and assumes that progeny in an island descend only from local individuals. The recent work of [20] explores this model without this assumption and under both birth-death and death-birth dynamics. It is interesting to note that their model is both a generalization and a special case of the original model of [23]. As this model specifies a particular bi-level graph, it is a special case. However, by setting $n = 1$ we can encode

an arbitrary evolutionary graph. Adopting the technique of [19] for well-mixed populations, (see Section 3.3) the authors develop an approximation technique for fixation probability under this model. For $r > 1$, they show that the approximation is valid when $n \cdot m \cdot (r-1)$ is approximately greater than 1. However, it is unclear how this approach can scale, particularly as m increases - all of the experiments in [20] had $m \leq 5$ (the experiments where the approximation performed the best had $n = 50$). Not only is the scalability of this approach an area for future work, but the issue of the topology of the A_i graphs as well. Can the same approach be used for an arbitrary bi-level graph?

In [55], the authors describe several anecdotal applications of bi-level EG's. or example, describe several species whose populations resemble a non-hierarchical bi-level EG where both upper and lower level structures are isothermal including the budgerigar of Oceania and the aptenodytes fosteri (emperor penguins) of Antarctica. However, in [58] the authors take a step further toward a real-world application by using bi-level EG's and star EG's to examine the stability of various types of business forms. Specifically, they look at corporations with individual decisions (CID's), multi-person decision corporations (MDC's), and stock corporations (SC's). They model CID's as 1-level star graphs and MDC's and SC's are modeled as bi-level graphs. They find that, under reasonable conditions, MDC's have a higher fixation probability than CID's, which have a higher fixation probability than SC's. Hence, by through the lens of EGT, SC's represent the most stable organizational structure for business.

7.2. Multiple Mutants

In [41], the authors discuss the issue of *clonal interference* where two different lineages in a population compete with each other. In such a case, multiple mutations exist in a population. Hence, the authors of this work extend the model of [23] to allow for this case. These mutants are referred to as type-1 and type-2 mutants. The authors are primarily concerned with determining the fixation probability of the type-2 mutants. The authors view the population of individuals as two disjoint sets. The first set defined by the authors is the set of type-1 mutants which is referred to as the *resident mutant population* (RMP). The authors use use m_1 to denote the cardinality of this set. The second set is the set of residents in the population which are referred to as the *wild type population* (WTP). There are $N - m_1$ individuals in this set. To obtain the fixation probability of the type-2 mutant ($\rho^{(2)}$),

the authors consider the fixation probability of the type-2 mutants within the WTP and RMP populations. As the probability that a type-2 mutant occurs in the WTP and RMP populations are $(N - m_1)/N$, m_1/N respectively, the authors derive the following equation for the fixation probability of the type-2 mutant:

$$\rho^{(2)} = \frac{(N - m_1) \cdot \rho^{(2)}_{WTP}}{N} + \frac{m_1 \cdot \rho^{(2)}_{RMP}}{N} \tag{58}$$

where $\rho^{(2)}_{WTP}$ is the fixation probability of a type-2 mutant in the WTP and $\rho^{(2)}_{RMP}$ is the fixation probability of the type-2 mutant in the RMP. The authors come up with analytical approximations of fixation probabilities for the type-2 mutants in the cases of lines and fully-connected graphs. These approximations work well in the cases where $m_1 >> 1$ and r is high. For a lines, they obtain $\frac{m_1 \cdot (1-1/r)}{N} + \frac{(N-m_1)^2}{2 \cdot N^2} \cdot (1 - 1/r)$ and for a fully-connected graph they obtain $\frac{N-m_1}{N} \cdot \frac{1}{m_1+1} + \frac{m_1}{N} \cdot \left(1 - \frac{N+(r-1)m_1}{Nr^2}\right)$ The authors perform simulation experiments that aligned well with these analytical results. Hence, they were able to demonstrate that topology and the population of the type-1 mutants figures significantly into fixation probability calculations in real populations.

7.3. EG's that Change Over Time

In [3], the authors modify the original formulation of [23] by examining a simple class of graphs that change over time [3]. Specifically, they look at layered networks. They find, through experimental simulation, that their growth structure also substantially increases the fixation probability. In future work, the authors intend to explore a more general framework for dynamic graphs.

In [10], the authors conjecture results for undirected graphs that change over time for BD-B. They conjecture that existing BD-B results still hold if the graph changes more slowly than it evolves. They also suspect that even if the graph does not change slowly, that existing BD-B results will still provide 'good' estimates.

Overall, studying fixation probability on a graph whose topology changes over time is an area ripe for new research. For example, preferential attachment has been observed in graph-structured with evolving topologies and essentially states that vertices of high degree are more likely to increase

their connections as time progresses [21]. Now consider birth-death updating, where the results described in the previous sections show that fixation probability is inversely proportional to its degree. So, under preferential attachment with birth-death updating, do new mutant vertices whose degree increases end up suppressing evolution as they connect to more residents? How do the time scales of the topology evolution with the evolution of the mutant trait affect each other? Further, would alternate methods of graph evolution, such as the biologically-inspired models of [48] affect fixation (i.e., as compared to preferential attachment)?

7.4. Further Extensions

In [42], the authors examine the model of [23] under birth-death updating on graphs where vetex connectivity is fixed - specifically lines, square lattices, cubic lattices, and fully-connected graphs. They then extend the model to allow offspring to not be perfect clones of their parents. Further, in their model, the offspring of a parent subject to a mutation with a probability of μ and increase the fitness with a probability p, or decrease it with probability $1 - p$. The calculation of the new fitness for the offspring is based on a previously studied model. They examined their asexual model experimentally on graphs with $250,000$ vertices and the results showed that the equilibrium fitness of the population was correlated with the dimensionality of the lattice - specifically that more connected graphs had a higher level of equilibrium fitness. No saturation was observed for the fully connected graph in this case. The authors also examined a modification to the model allowing for sexual reproduction with multiple genes per vetex. For sexual reproduction, the equilibrium fitness increased not only with the dimension of the lattice, but also with the population.

In [54], the authors study EGT in the case where the fitness of the mutant changes with its frequency. For example, the fitness of cancer cells changes with frequency which often causes a failure in therapy. Given a population of size N, they assume N different values of r – each associated with a different number of mutants in the population. They assume $r_1 \leq r_2 \leq \ldots \leq r_N$ and obtain analytical approximation for the fixation probabilities of super-stars and isothermal EG's.

In [53], the authors consider a 'local' version of the Moran process where the update rules are dependent upon a *deme*. In this work, a deme (indexed the same way as the vertices in v) corresponds to the neighborhood of a given vertex. In this case, [53] adds the requirement that for each vetex v_i,

$w_{ii} > 0$ (note that this type of self-loop is not permitted in the original mode of [23]). At each step, a row W_i of the matrix is chosen with a probability $1/N$. Next, a vetex v_j is selected s proportional to the fitness of all vertices in the deme. Finally, the vetex to be replaced is selected based on the outgoing edge weights of v_j. The authors experiment with this process on star and Kawachi-style small world networks to find that this process achieves the Moran probability for fixation.

8. Conclusion

In this paper we have described *evolutionary graph theory*, which was first introduced in [23] and generalizes the classic Moran process of [29]. We have described the original model, the major results and extensions, and applications to game theory. While this is still a relatively new tool for fields such as biology, physics, game theory, and computer science, the number of publications on the topic seems to be steadily increasing each year - hence resulting in this review. Our view is that there is great potential with EGT for a variety of applications, and that represents the next wave of research in this area. Applied work such as [58] for economics and [52] in biology most likely represent just the beginning of a new trend. However as EGT becomes more operational, many new questions arise. First, how can the model be adjusted for certain applications? Second, can we learn the model and/or mutant fitness from historical data? Third, many real-world applications utilize large data sets, for example, a data set LiveJournal social network data set consists of over 4 million vertices and over 6 million edges.[5] Can procedures for calculating fixation probability and time to fixation be scaled for these large data-sets? There are multiple directions in which EGT can be taken. We are very excited about the possibilities due to the large problem-space.

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[5] http://snap.stanford.edu/data/index.html

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References

[1] Antal, T., Redner, S., Sood, V., 2006. Evolutionary dynamics on degree-heterogeneous graphs. Physical Review Letters 96 (18), 188104.
URL http://link.aps.org/abstract/PRL/v96/e188104

[2] Antal, T., Scheuring, I., 2006. Fixation of strategies for an evolutionary game in finite populations. Bulletin of Mathematical Biology 68, 1923–1944, 10.1007/s11538-006-9061-4.
URL http://dx.doi.org/10.1007/s11538-006-9061-4

[3] Barbosa, V. C., Donangelo, R., Souza, S. R., 2009. Network growth for enhanced natural selection. Physical Review E (Statistical, Nonlinear, and Soft Matter Physics) 80 (2), 026115.
URL http://link.aps.org/abstract/PRE/v80/e026115

[4] Barbosa, V. C., Donangelo, R., Souza, S. R., Oct 2010. Early appraisal of the fixation probability in directed networks. Phys. Rev. E 82 (4), 046114.

[5] Blondel, V., Guillaume, J., Lambiotte, R., Lefebvre, E., 2008. Fast unfolding of communities in large networks. Journal of Statistical Mechanics: Theory and Experiment 2008, P10008.

[6] Brandt, H., Hauert, C., Sigmund, K., 2003. Punishment and reputation in spatial public goods games. Proceedings of the Royal Society of London. Series B: Biological Sciences 270 (1519), 1099.

[7] Broom, M., Hadjichrysanthou, C., Rychtar, J., 2010. Evolutionary games on graphs and the speed of the evolutionary process. Proceedings of the Royal Society A 466, 1327–1346.

[8] Broom, M., Hadjichrysanthou, C., Rychtar, J., Stadler, B. T., Apr. 2010. Two results on evolutionary processes on general non-directed graphs.

Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences 466 (2121), 2795–2798.
URL http://rspa.royalsocietypublishing.org

[9] Broom, M., Rychtář, J., May 2008. An analysis of the fixation probability of a mutant on special classes of non-directed graphs. Proceedings of the Royal Society A 464, 2609–2627.

[10] Broom, M., Rychtář, J., Stadler, B., 2009. Evolutionary dynamics on graphs - the effect of graph structure and initial placement on mutant spread. Submitted.

[11] Broom, M., Rychtář, J., Stadler, B., 2009. Evolutionary dynamics on small-order graphs. Journal of Interdisciplinary Mathematics 12 (2), 129–140.

[12] Dong-Ping, Y., Hai, L., Chen-Xu, W., Jian-Wei, S., 2009. Modelling moran process with network dynamics for the evolution of cooperation. Chinese Physics Letters 26 (6).

[13] Fu, F., Wang, L., Nowak, M. A., Hauert, C., Apr. 2009. Evolutionary dynamics on graphs: Efficient method for weak selection. Physical Review E 79 (4).

[14] Garey, M. R., Johnson, D. S., 1979. Computers and Intractability; A Guide to the Theory of NP-Completeness. W. H. Freeman & Co., New York, NY, USA.

[15] Hadjichrysanthou, C., Broom, M., Rychtar, J., 2011. Evolutionary games on star graphs under various updating rules. Dynamic Games and Applications, 1–22.

[16] Hamilton, W., 1964. The genetical evolution of social behaviour. II* 1. Journal of theoretical biology 7 (1), 17–52.

[17] Haraguchi, Y., Sasaki, A., 2000. The evolution of parasite virulence and transmission rate in a spatially structured population. Journal of Theoretical Biology 203 (2), 85–96.

[18] Hauert, C., Doebeli, M., Apr. 2004. Spatial structure often inhibits the evolution of cooperation in the snowdrift game. Nature 428 (6983), 643–6.
URL http://dx.doi.org/10.1038/nature02360

[19] Houchmandzadeh, B., Vallade, M., Nov 2010. Alternative to the diffusion equation in population genetics. Phys. Rev. E 82, 051913.
URL http://link.aps.org/doi/10.1103/PhysRevE.82.051913

[20] Houchmandzadeh, B., Vallade, M., July 2011. The fixation probability of a beneficial mutation in a geographically structured population. New Journal of Physics 13 (7), 073020.
URL http://stacks.iop.org/1367-2630/13/i=7/a=073020

[21] Jeong, H., Neda, Z., Barabasi, A. L., 2003. Measuring preferential attachment in evolving networks. EPL (Europhysics Letters) 61 (4), 567.
URL http://stacks.iop.org/0295-5075/61/i=4/a=567

[22] Keeling, M., 1999. The effects of local spatial structure on epidemiological invasions. Proceedings: Biological Sciences 266 (1421), 859–867.

[23] Lieberman, E., Hauert, C., Nowak, M. A., 2005. Evolutionary dynamics on graphs. Nature 433 (7023), 312–316.
URL http://dx.doi.org/10.1038/nature03204

[24] Maruyama, T., 1974. A simple proof that certain quantities are independent of the geographical structure of population. Theoretical Population Biology 5 (2), 148 – 154.
URL http://www.sciencedirect.com/science/article/pii/0040580974900379

[25] Masuda, N., 2009. Directionality of contact networks suppresses selection pressure in evolutionary dynamics. Journal of Theoretical Biology 258 (2), 323 – 334.

[26] Masuda, N., Ohtsuki, H., 2009. Evolutionary dynamics and fixation probabilities in directed networks. New Journal of Physics 11, 033012.

[27] Matsuda, H., Ogita, N., Sasaki, A., Sato, K., 1992. Statistical mechanics of population. Prog. Theor. Phys 88 (6), 1035–1049.

[28] Matsuda, H., Tamachi, N., Sasaki, A., N., O., 1987. A lattice model for population biology. In: Mathematical Topics in Biology, Morphogenesis and Neuro-sciences. Vol. 71 of Springer Lecture Notes in Biomathematics. pp. 154–161.

[29] Moran, P., 1958. Random processes in genetics. Mathematical Proceedings of the Cambridge Philosophical Society 54 (01), 60–71.

[30] Newman, M. E. J., Jun 2004. Fast algorithm for detecting community structure in networks. Phys. Rev. E 69 (6), 066133.

[31] Newman, M. E. J., Girvan, M., Feb 2004. Finding and evaluating community structure in networks. Phys. Rev. E 69 (2), 026113.

[32] Nie, P. Y., 2008. Evolutionary graphs on two levels. Ars Comb. 86.

[33] Nie, P.-Y., Zhang, P.-A., 2010. Fixation Time for Evolutionary Graphs. International Journal of Modern Physics B 24, 5285–5293.

[34] Nowak, M., May, R., 1992. Evolutionary games and spatial chaos. Nature 359 (6398), 826–829.

[35] Nowak, M., Tarnita, C., Antal, T., 2010. Evolutionary dynamics in structured populations. Philosophical Transactions of the Royal Society B: Biological Sciences 365 (1537), 19.

[36] Ohtsuki, H., Hauert, C., Lieberman, E., Nowak, M. A., May 2006. A simple rule for the evolution of cooperation on graphs and social networks. Nature 441 (7092), 502–505.
URL `http://dx.doi.org/10.1038/nature04605`

[37] Ohtsuki, H., Nowak, M., 2007. Direct reciprocity on graphs. J Theor Biol 247, 462–470.

[38] Ohtsuki, H., Nowak, M. A., November 2006. The replicator equation on graphs. Journal of Theoretical Biology 243 (7), 86–97.
URL `http://dx.doi.org/10.1016/j.jtbi.2006.06.004`

[39] Ohtsuki, H., Pacheco, J., Nowak, M., 2007. Evolutionary graph theory: Breaking the symmetry between interaction and replacement. J Theor Biol 246, 681–694.

[40] Ohtsukia, H., Nowak, M., 2008. Evolutionary stability on graphs. Journal of Theoretical Biology 251, 698–707.

[41] Paley, C., Taraskin, S., Elliott, S., 2010. The two-mutant problem: clonal interference in evolutionary graph theory. Journal of Chemical Biology 3, 189–194, 10.1007/s12154-010-0042-6.
URL http://dx.doi.org/10.1007/s12154-010-0042-6

[42] Paley, C. J., Taraskin, S. N., Elliott, S. R., 2007. Temporal and dimensional effects in evolutionary graph theory. Physical Review Letters 98, 098103.
URL doi:10.1103/PhysRevLett.98.098103

[43] Rychtář, J., Stadler, B., Winter 2008. Evolutionary dynamics on small-world networks. International Journal of Computational and Mathematical Sciences 2 (1).

[44] Santos, F. C., Pacheco, J. M., Lenaerts, T., February 2006. Evolutionary dynamics of social dilemmas in structured heterogeneous populations. PNAS 103 (9), 3490–3494.
URL http://dx.doi.org/10.1073/pnas.0508201103

[45] Shakarian, P., Roos, P., 2011. Fast and deterministic computation of fixation probability in evolutionary graphs. In: CIB '11: The Sixth IASTED Conference on Computational Intelligence and Bioinformatics (accepted). IASTED.

[46] Slatkin, M., May 1981. Fixation probabilities and fixation times in a subdivided population. Evolution 35 (3), 477–488.

[47] Sood, V., Antal, T., Redner, S., 2008. Voter models on heterogeneous networks. Physical Review E (Statistical, Nonlinear, and Soft Matter Physics) 77 (4), 041121.
URL http://link.aps.org/abstract/PRE/v77/e041121

[48] Southwell, R., Cannings, C., 2010. Some models of reproducing graphs: I pure reproduction. Applied Mathematics 1 (3), 137–145.

[49] Tarnita, C., Ohtsuki, H., Antal, T., Fu, F., Nowak, M., 2009. Strategy selection in structured populations. Journal of Theoretical Biology 259, 570–581.

[50] Torán, J., May 2004. On the hardness of graph isomorphism. SIAM J. Comput. 33, 1093–1108.
URL http://dx.doi.org/10.1137/S009753970241096X

[51] Van Baalen, M., 2000. Pair approximation for different spatial geometries. In: The geometry of ecological interactions: simplifying spatial complexity. Cambridge University Press, p. 359387.

[52] Voelkl, B., Kasper, C., 2009. Social structure of primate interaction networks facilitates the emergence of cooperation. Biology Letters 5, 462–464.

[53] Whigham, P. A., Dick, G., 2008. Evolutionary dynamics for the spatial moran process. Genetic Programming and Evolvable Machines 9 (2), 157–170.

[54] Zhang, P., Nie, P., 2009. Evolutionary graphs with frequqnecy dependent fitness. International Journal of Modern Physics B 23 (4), 537–543.

[55] Zhang, P., Nie, P., Hu, D., 2010. Bi-level evolutionary graphs with multi-fitness. Systems Biology, IET 4 (1), 33 –38.

[56] Zhang, P. A., Nie, P. Y., Hu, D. Q., Zou, F. Y., 2007. The analysis of bi-level evolutionary graphs. Biosystems 90 (3), 897–902.

[57] Zhong, W., Zhang, Y., Liu, J., june 2011. Evolutionary dynamics of continuous strategy games on social networks under weak selection: A preliminary study. In: Evolutionary Computation (CEC), 2011 IEEE Congress on. pp. 2514 –2518.

[58] Zhou, A.-n., 2011. Stability analysis for various business forms. In: Zhou, Q. (Ed.), Applied Economics, Business and Development. Vol. 208 of Communications in Computer and Information Science. Springer Berlin Heidelberg, pp. 1–7.