

# Chapter 6

## Evolutionary Graph Theory

### 6.1 Introduction

Evolutionary graph theory (EGT), introduced by Lieberman et al. [17], 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 chapter, we present the original model of [17] and various extensions. We also summarize major results in EGT (both analytical and experimental), including those relating to game theory. For a more comprehensive review of evolutionary graph theory, we suggest the previously-published review of [4], from which this chapter is based.

This chapter is organized as follows. In Sect. 6.2, 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 Sect. 6.3 for graphs of certain topologies—including the large class of undirected EG's. Then we describe how some of the results relating to fixation probability change under alternative model dynamics in Sect. 6.4. We then survey more advanced game theoretic extensions in Sect. 6.5.

## 6.2 Evolutionary Graph Theory Models

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 [23] 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,  $\rho_1$ , arising from this  $N$  original Moran Process, is often termed the *Moran probability* and can be solved for exactly (see Eq. (6.1)).

$$\rho_1 = \frac{1 - 1/r}{1 - 1/r^N} \quad (6.1)$$

In the original work that introduced EGT [17], 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 [32] 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  $\rho_1$ . A similar result was proved in [18]. In [17], 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 6.1 (Isothermal Theorem [17]).** *An EG is isothermal iff the fixation probability of a randomly placed mutant is  $\rho_1$ .*

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.

### 6.2.1 Properties of Fixation Probability

Many researchers (such as [8, 20]) 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 ( $\rho$ ) for an EG is determined based on a uniformly picked vertex, we have the following relationship between  $\rho$  and  $P$ :

$$N \cdot \rho = \sum_i P_{\{v_i\}} \quad (6.2)$$

Note that although these two problems are closely related, they have rather different intuitions. The fixation probability  $\rho$  provides insight into a graph of a certain topology. For example, researchers often refer to graphs with a low value for  $\rho$  as being “evolutionary stable” as the topology 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 [7] and proved for general, weighted, directed graphs[5, 31].

**Theorem 6.2 (Additive Under Neutral Drift [5, 31]).** *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 individuals 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 6.3 (Neutral Drift as a Lower Bound [5, 31]).** *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 6.2 and Eq. (6.2), we observe that under neutral drift  $\rho = 1/N$  regardless of the topology of the graph—even with directed and weighted edges. Hence, Theorem 6.3 tells us that for  $r > 1$  we have  $\rho \geq 1/N$ . This particular observation is independently noted in [15]. In [19] the authors observe in their experiments that fixation probability monotonically increases with  $r$ .

As we can appeal to the Moran probability only in the case of an isothermal graph, we must resort to other calculations to determine  $\rho$  or  $P$ . Using the following set of constraints, we can solve directly for any  $P_C$  (hence,  $\rho$  as well by Eq. (6.2)).

$$P_C = \frac{\sum_{v_i \in C} \sum_{v_j \notin C} (r \cdot w_{ij} \cdot P_{C \cup \{v_j\}} + w_{ji} \cdot P_{C - \{v_i\}})}{\sum_{v_i \in C} \sum_{v_j \notin C} (r \cdot w_{ij} + w_{ji})}. \quad (6.3)$$

These constraints originally appeared in [29] 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, [17] 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 [7, 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  $C = \emptyset$ ).<sup>1</sup> 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 [35] for the latest complexity results on graph automorphism).

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 [29] for a pseudocode algorithm). However, as the size of the graph increases, even such simulations may become impractical. In [3], 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

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<sup>1</sup>There is the exception of an alternating state where every edge connects a mutant-resident pair. This state cannot be reached if it exists.

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.

In change to [5, 31], the authors introduce a novel approach that can quickly compute the fixation probability 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 vertex 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 6.3 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 [18]. While this particular model can also generalize the standard evolutionary graphs of [17]. However, it is unclear if their approximation is still appropriate for arbitrary graphs.

## 6.2.2 Game Theoretic Extensions

One of the most popular applications of EGT is 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:

$$f_i = 1 - w + w \cdot P \tag{6.4}$$

The parameter  $w$  relates the payoff acquired from games played to fitness. If  $w = 1$ , the payoff acquired is equal to the fitness. If  $w = 0$ , the game is irrelevant and we are at neutral drift. An often explored special case is *weak selection*, where  $w \ll 1$ , 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.

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:

$$\begin{array}{c|cc} & \text{mutant} & \text{resident} \\ \hline \text{mutant} & a & b \\ \text{resident} & c & d \end{array} \tag{6.5}$$

Tarnita et al. [34] consider evolutionary dynamics (under weak selection) on graphs for the general game given by (6.5) 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  $\sigma$ . “ $A$  is favored over  $B$ ” means that it is more abundant in the stationary distribution of the mutation selection process. The authors show  $\sigma$  to depend on the population structure, update rule (see Sect. 6.4), 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 [24, 25].

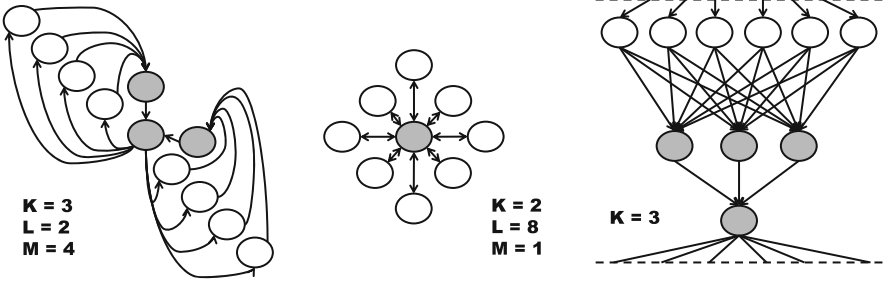
In Sect. 6.5 we will review other important work considering various aspects of game theoretic applications of EGT.

### 6.3 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.

#### 6.3.1 Fixation Probability Calculations for Certain Topologies

In [17], 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



**Fig. 6.1** Left: Super-star EG,  $K = 3, L = 2, M = 4$ . Center: Star EG,  $K = 2, L = 8, M = 1$ . Right: Funnel EG,  $K = 3$

graph. For example, they define a *one-rooted* graph as a graph with a unique global source 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 Fig. 6.1). Such a structure, denoted  $S_{L,M}^K$  consists of a central vertex,  $v_{center}$  surrounded by  $L$  leaves. A leaf  $\ell$ , contains  $M$  reservoir vertices,  $r_{\ell,m}$  and  $K - 2$  ordered chain vertices  $c_{\ell,1}, \dots, c_{\ell,K-2}$ . 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  $S_{L,M}^K$  as  $\rho(S_{L,M}^K)$ , the following result is given in [17].

$$\lim_{L,M \rightarrow \infty} \rho(S_{L,M}^K) = \frac{1/r}{1 - 1/r^{K \cdot N}} \quad (6.6)$$

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 Fig. 6.1). Another special case, related to the super-star, is the funnel (see Fig. 6.1). A generalization of the funnel, known as a *layered network* was studied in [2, 3]. In this type of EG,  $V$  can be partitioned into  $K$  subsets  $V_1, \dots, V_K$  such that for all  $v \in V_i$  there are only outgoing edges to vertices in set  $V_{i+1 \bmod K}$ . Barbosa et al. also presents a way to increase the speed of MCMC simulations specific to layered networks in [3]. 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, [6] leverages some of these intuitions to study fixation probability for games on star graphs while the work on bi-level EG's. More recently, this style

of analytical calculation of fixation probabilities has been applied to economics in [38] where the authors determine the evolutionary stability of various forms of business, which are modelled as star and bi-level graphs. Analytically finding the value of  $\rho$  for certain graph topologies will most likely continue to be an active area of research in EGT, particularly as certain structures are identified in nature or other domains. Perhaps an interesting direction would be to use work on the subgraph isomorphism problem [12] 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).

### 6.3.2 Undirected Evolutionary Graphs

Several work explore: 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 Broom and Rychtar [8] as

$$w_{ij} = \begin{cases} d_i^{-1} & \text{iff } (v_i, v_j) \in E \text{ or } (v_j, v_i) \in E \\ 0 & \text{otherwise} \end{cases} \quad (6.7)$$

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 [8], the authors determine a necessary and sufficient condition for an isothermal undirected graph.

**Theorem 6.4 (Undirected Isothermal Theorem [8]).** *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 Eq. (6.3) that is presented in [7].

$$P_C = \frac{\sum_{v_i \in C} (d_i^{-1})}{\sum_{v_j \in V} (d_j^{-1})} \quad (6.8)$$

Hence, for an undirected graph with  $r = 1$ , we have  $\rho = 1/N$ . For the case where a mutant is very advantageous,  $r \gg 1$ , [9] 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).



$$P_{\{v_i\}} \approx \frac{r}{r + \sum_{v_j \in V - \{v_i\}} w_{ji}} \quad (6.9)$$

The authors of [9] conducted an exhaustive study of undirected graphs with eight 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 Eqs. (6.8) and (6.9). Further, they also provide the following analytical approximation for relative mutant advantage.

$$\frac{P_{\{v_i\}}}{P_{\{v_j\}}} \approx \left(\frac{d_j}{d_i}\right)^2 \quad (6.10)$$

The inverse relationship between fixation and the degree of the initial mutant vertex shown by Broom et al. [9] is in strong agreement with the previous work of [1]. It is interesting to note that experimentally, it was observed in [9] 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 [10]. In Sect. 6.4, 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 [8] 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  $P_i^0$  ( $P_i^\theta$ ) denote the fixation of probability given  $i$  mutants on the leaves and the center being a mutant (resp. the center being a resident). Broom and Rychtar [8] derive the following.

$$P_1^0 = \frac{1}{1 + \frac{L}{L+r} \sum_{j=1}^{L-1} \left(\frac{L+r}{r(L+r+1)}\right)^j} \quad (6.11)$$

$$P_0^0 = \frac{r}{r+L} P_1^0 P_0^\theta = \frac{r \cdot L}{r \cdot L + 1} P_1^0 \quad (6.12)$$

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

$$\rho_{undir-star} = \frac{L \cdot \frac{rL}{r \cdot L + 1} + \frac{r}{r+L}}{(L+1) \left(1 + \frac{L}{L+r} \sum_{j=1}^{L-1} \left(\frac{L+r}{r(L+r+1)}\right)^j\right)} \quad (6.13)$$

$$\lim_{L \rightarrow \infty} \rho_{undir-star} = \frac{1 - \frac{1}{r^2}}{1 - \frac{1}{2L}} \quad (6.14)$$

## 6.4 Alternate Update Rules

Let us momentarily return to the original model of [17]. 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 ‘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 [17] is termed ‘birth-death with birth bias’ or **BD-B** updating. Several works address different update rules including: [1, 19, 20, 27, 33]. Overall, we have identified three major families of update rules—birth-death (a.k.a. the invasion process) where the vertex to reproduce is chosen first, death-birth (a.k.a. the voter model) where the vertex to die is chosen first, and link dynamics, where an edge is chosen. We summarize these in Table 6.1.

Note that the three categories of Table 6.1 are very broad as they do not consider fitness-based bias in vertex selection (i.e., the **BD-B** updating of [17] 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 6.2. Note that imitation (**IM**) is also known as *biased link dynamics*.

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, 33], 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

**Table 6.1** Different families of update rules

Update rule	Intuition
Birth-Death (BD) (a.k.a. Invasion process (IP))	(1) vertex $v_i$ selected
	(2) Neighbour of $v_i$ , vertex $v_j$ selected
	(3) Offspring of $v_i$ replaces $v_j$
Death-Birth (DB) (a.k.a. Voter model (VM))	(1) vertex $v_i$ selected
	(2) Neighbour of $v_i$ , vertex $v_j$ selected
	(3) Offspring of $v_j$ replaces $v_i$
Link dynamics (LD)	(1) Edge $(v_i, v_j)$ selected
	(2) The offspring of one vertex in the edge replaces the other vertex

**Table 6.2** Variations of EGT

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 vertex reproduces to replace the other
	Imitation (IM)	Least fit vertex dies, replaced by offspring of other vertex
	Pairwise Compar. (PC)	$v_j$ replaces $v_i$ iff $f_j > f_i$ , 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 $f_j^{-1}$

$v_i$  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

**Table 6.3** Relationship between fixation and degree of initial vertex (undirected graphs)

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

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 [9] described earlier (Table 6.3).

As shown in Theorem 6.4, under BD-B, an undirected EG is isothermal iff it is regular. In [1], this is extended to other update rules as follows.

**Theorem 6.5 ([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 [30]. 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  $\frac{1}{d_i}$ . 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.

Not only does the original model of [17] 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 [19, 20]. There are two main conclusions to their work: (1) degree correlation to fixation probability (i.e., using the exact methods of [7] 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 [20], 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 vertex but also the global structure of the graph. In fact, often there is no observed relation between degree and fixation. See Table 6.4 for a summary of experimental results compared with the analytical approximations. While [20] 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 [19], 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, 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.

**Table 6.4** Summary of experimental results for directed case with  $r = 1$  in [20] illustrating whether experimentally-determined fixation probability results that aligned with the mean-field approximation

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

$d_{in}$  and  $d_{out}$  are the in and out degrees of the initial mutant vertex

## 6.5 Further Game Theoretic Results

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.

### 6.5.1 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. [28] 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  $\varepsilon$  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”.

### 6.5.2 Regular Graphs and the Replicator Equation

Ohtsuki et al. [27] study evolutionary games on regular graphs of degree  $k$  considering the BD, DB, IM, PC update rules.<sup>2</sup> The authors use pair approximation [14, 16, 21, 22, 36] 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* ( $w \ll 1$ ), 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,

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<sup>2</sup>We use the shorter BD and DB notation for the update rules with birth bias BD-B and DB-B. See Table 6.2.

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 [26], showing identical conditions necessary for cooperators to be favored over defectors.

### 6.5.3 Evolution of Cooperation and Social Viscosity

Ohtsuki et al. [26] 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 neighbors, where the game between two players is given by the payoff matrix (6.15) 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  $bn - c(n + m)$ .

	cooperate	defect	
cooperate	$b - c$	$-c$	(6.15)
defect	$b$	$0$	

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 [13], 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,<sup>3</sup> for which cooperation is favored when  $b/c > k + 2$ , and BD, for which cooperation is never favored by selection.

### 6.5.4 Graph Heterogeneity and Evolution of Cooperation

Santos et al. [30] investigate the effects of single-scale and scale-free networks on cooperation in the Prisoner's Dillema, Snow-Drift, and Stag-Hunt games through

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<sup>3</sup>The authors of [26] also note that mathematically, "IM updating can be obtained from DB updating by adding loops to every vertex".

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. [11] 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 [30], which concludes that graph heterogeneity aids the emergence of cooperation. Fu et al. point out that this conclusion by Santos et al. [30] hinges on the simultaneous appearance of a number of cooperators to overcome the invasion barrier.

## 6.6 Conclusion

In this chapter, we have described *evolutionary graph theory*, which was first introduced in [17] and generalizes the classic Moran process of [23]. We have described the original model, the major results and extensions, and applications to game theory. A somewhat recent trend in the area of evolutionary graph theory is applied work such as [38] for economics and [37] in biology most likely represent just the beginning of a new trend. Further, the desire to add realism to diffusion models extends beyond EGT and is currently an active topic relating to nearly every model in this book. In the next chapter, we review some empirical results toward this end.

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