Natural Models for Evolution on Networks*

George B. Mertzios[†] Sotiris Nikoletseas[‡] Christoforos Raptopoulos[§]
Paul G. Spirakis[¶]

Abstract

Evolutionary dynamics has been traditionally studied in the context of homogeneous populations, mainly described by the Moran process (Moran, *Proceedings of the Cambridge Philosophical Society*, 54:60–71, 1958). Recently, this approach has been generalized in (Lieberman et al., *Nature*, 433:312–316, 2005) by arranging individuals on the nodes of a network (in general, directed). In this setting, the existence of directed arcs enables the simulation of extreme phenomena, where the fixation probability of a randomly placed mutant (i.e., the probability that the offspring of the mutant eventually spread over the whole population) is arbitrarily small or large. On the other hand, undirected networks (i.e., undirected graphs) seem to have a smoother behavior, and thus it is more challenging to find suppressors/amplifiers of selection, that is, graphs with smaller/greater fixation probability than the complete graph (i.e., the homogeneous population). In this paper we focus on undirected graphs. We present the first class of undirected graphs which act as suppressors of selection, by achieving a fixation probability that is at most one half of that of the complete graph, as the number of vertices increases. Moreover, we provide some generic upper and lower bounds for the fixation probability of general undirected graphs. As our main contribution, we introduce the natural alternative of the model proposed in (Lieberman et al., *Nature*, 433:312–316, 2005). In our new evolutionary model, all individuals interact *simultaneously* and the result is a compromise between aggressive and non-aggressive individuals. We prove that our new model of mutual influences admits a *potential function*, which guarantees the convergence of the system for any graph topology and any initial fitness vector of the individuals. Furthermore, we prove fast convergence to the stable state for the case of the complete graph, as well as we provide almost tight bounds on the limit fitness of the individuals. Apart from being important on its own, this new evolutionary model appears to be useful also in the abstract modeling of control mechanisms over invading populations in networks. We demonstrate this by introducing and analyzing two alternative control approaches, for which we bound the time needed to stabilize to the "healthy" state of the system.

Keywords: Evolutionary dynamics, undirected graphs, fixation probability, potential function, Markov chain, fitness, population structure.

1 Introduction

Evolutionary dynamics has been well studied (see [4, 10, 17, 25, 27–29]), mainly in the context of homogeneous populations, described by the Moran process [21, 23]. In addition, population dynamics has been extensively studied also from the perspective of the strategic interaction in evolutionary game theory, cf. for instance [13–16, 26]. One of the main targets of evolutionary game theory is evolutionary dynamics (see [14, 30]). Such dynamics usually examines the propagation of mutants with a given *fitness* in a population, whose initial members (resident individuals) have different fitnesses. In fact, "evolutionary stability" is the case where no mutant can invade and dominate the population. The evolutionary models and the dynamics we consider here belong to this framework. In addition, however, we consider structured populations (i.e., in the form of an undirected graph) and we study how the underlying graph structure affects the evolutionary dynamics. We study in this paper two kinds of evolutionary dynamics. Namely, the "all or nothing" case (where either the mutant takes over the whole graph or dies out) and the "aggregation" case (more similar in spirit to classical evolutionary game theory, where the mutant's fitness aggregates with the population fitness and generates eventually a homogeneous crowd with a new fitness).

In a recent article, Lieberman, Hauert, and Nowak proposed a generalization of the Moran process by arranging individuals on a connected network (i.e., graph) [19] (see also [24]). In this model, vertices correspond

*A preliminary conference version of this work appeared in *Proceedings of the 7th Workshop on Internet & Network Economics (WINE), Singapore, December 2011, pages 290–301.*

[†]School of Engineering and Computing Sciences, Durham University, UK. Email: `george.mertzios@durham.ac.uk`
[‡]Computer Technology Institute and University of Patras, Greece. Email: `nikole@cti.gr`
[§]Computer Technology Institute and University of Patras, Greece. Email: `raptopox@ceid.upatras.gr`
[¶]Computer Technology Institute and University of Patras, Greece. Email: `spirakis@cti.gr`

to individuals of the population and weighted edges represent the reproductive rates between the adjacent vertices. That is, the population structure is translated into a network (i.e., graph) structure. Furthermore, individuals (i.e., vertices) are partitioned into two types: *aggressive* and *non-aggressive*. The degree of (relative) aggressiveness of an individual is measured by its *relative fitness*; in particular, non-aggressive and aggressive individuals are assumed to have relative fitness 1 and $r \geq 1$, respectively. This modeling approach initiates an ambitious direction of interdisciplinary research, which combines classical aspects of computer science (such as combinatorial structures and complex network topologies), probabilistic calculus (discrete Markov chains), and fundamental aspects of evolutionary game theory (such as evolutionary dynamics).

In the model of [19], one *mutant* with relative fitness $r \geq 1$ is introduced into a given population of *resident* individuals, each having relative fitness 1. At each time step, an individual is chosen for reproduction with a probability proportional to its fitness, while its offspring replaces a randomly chosen neighboring individual in the population. Once u has been selected for reproduction, the probability that vertex u places its offspring into position v is given by the weight w_{uv} of the directed arc $\langle uv \rangle$. Note that for every vertex u, the weights w_{uv} of the several directed arcs $\langle uv \rangle$ may be different to each other. This process stops when either all vertices of the graph become mutants (*fixation* of the graph) or they all become non-mutants (*extinction* of the mutants). Several similar models have been previously studied, describing for instance influence propagation in social networks (such as the decreasing cascade model [18, 22]), dynamic monopolies [6], particle interactions (such as the voter model, the antivoter model, and the exclusion process [1, 12, 20]), etc. However, the dynamics emerging from these models do not consider different fitnesses for the individuals.

The *fixation probability* f_G of a graph $G = (V, E)$ is the probability that eventually fixation occurs, i.e., the probability that an initially introduced mutant, placed uniformly at random on a vertex of G, eventually spreads over the whole population V, replacing all resident individuals. One of the main characteristics in this model is that at every iteration of the process, a "battle" takes place between aggressive and non-aggressive individuals, while the process stabilizes only when one of the two teams of individuals takes over the whole population. This kind of behavior of the individuals can be interpreted as an *all-or-nothing* strategy, in the following sense: if the underlying undirected graph is connected, the vertices become eventually either all mutants (fixation of the graph) or all non-mutants (extinction of the mutants in the graph).

Consider a directed graph, in which for every two vertices u, v, if the directed arc $\langle uv \rangle$ exists then the directed arc $\langle vu \rangle$ exists as well, and additionally $w_{uv} = w_{vu}$. Such a graph is called a *symmetric directed* graph [19]. Note here that symmetric directed graphs do not coincide with undirected graphs. Indeed, in an undirected graph, although for every arc $\langle uv \rangle$ the arc $\langle vu \rangle$ exists as well, it may be that the weights of these two arcs are different, i.e., $w_{uv} \neq w_{vu}$. Lieberman et al. [19] proved that the fixation probability for every symmetric directed graph is equal to that of the complete graph (i.e., the homogeneous population of the Moran process), which tends to $1 - \frac{1}{r}$ as the size n of the population grows. Moreover, exploiting vertices with zero in-degree or zero out-degree ("upstream" and "downstream" populations, respectively), they provided several examples of *directed* graphs with arbitrarily small and arbitrarily large fixation probability [19]. Furthermore, the existence of directions on the arcs leads to examples where neither fixation nor extinction is possible (e.g., a graph with two sources).

In contrast, general *undirected* graphs (i.e., when $\langle uv \rangle \in E$ if and only if $\langle vu \rangle \in E$ for every u, v) appear to have a smoother behavior, as the above process eventually reaches fixation or extinction with probability 1. Furthermore, the coexistence of both directions at every edge in an undirected graph seems to make it more difficult to find *suppressors* or *amplifiers* of selection (i.e., graphs with smaller or greater fixation probability than the complete graph, respectively), or even to derive non-trivial upper and lower bound for the fixation probability on general undirected graphs. This is the main reason why only little progress has been made so far in this direction and why most of the recent work focuses mainly on the exact or numerical computation of the fixation probability for very special cases of undirected graphs, e.g., the star and the path [7–9].

Our contribution. In this paper we overcome this difficulty for undirected graphs and we provide for the fitness values $1 < r < \frac{4}{3}$ the first class of undirected graphs that act as suppressors of selection in the model of [19], as the number of vertices increases. This is a very simple class of graphs (called *clique-wheels*), where each member G_n has a clique of size $n \geq 3$ and an induced cycle of the same size n with a perfect matching between them. We prove that, when the mutant is introduced to a clique vertex of G_n, then the probability of fixation tends to zero as n grows. Furthermore, we prove that, when the mutant is introduced to a cycle vertex of G_n, then the probability of fixation when $1 < r < \frac{4}{3}$ is at most $1 - \frac{1}{r}$ as n grows (i.e., bounded by the value of the homogeneous population of the Moran process). Therefore, since the clique and the cycle have the same number n of vertices in G_n, the fixation probability f_{G_n} of G_n is at most $\frac{1}{2}(1 - \frac{1}{r})$ as n increases (for instance it is necessary that $\frac{n}{\log^7 n} > 1$), i.e., G_n is a suppressor of selection. Furthermore, we provide for the model of [19] the first non-trivial upper and lower bounds for the fixation probability in general undirected graphs. In particular, we first provide a generic upper bound depending on the degrees of some local neighborhood. Second, we present another upper and lower bound, depending on the maximum ratio between the degrees of two neighboring vertices.

As our main contribution, we introduce in this paper the natural alternative of the *all-or-nothing* approach of [19], which can be interpreted as an *aggregation* strategy. In this aggregation model, all individuals interact *simultaneously* and the result is a compromise between the aggressive and non-aggressive individuals. Both of these two alternative models for evolutionary dynamics coexist in several domains of interaction between individuals, e.g., in biology (natural selection vs. mutation of species). With this new model, we try to capture systems like those described in [30], where the intrusion of a mutant generates a new a-posteriori population type which is the result of the aggregation of residents and mutants. However, the difference of our model from the models of [30] is that our interactions take into account the underlying graph structure and the locality of the invaders. In particular, another motivation for our models comes from biological networks, in which the interacting individuals (vertices) correspond to cells of an organ and advantageous mutants correspond to viral cells or cancer. Regarding the proposed model of mutual influences, we first prove that it admits a *potential* function. This potential function guarantees that for any graph topology and any initial fitness vector, the system converges to a stable state, where all individuals have the same fitness. Furthermore, we analyze the long-term behavior of this model for the complete graph. In particular, we prove fast convergence to the stable state, as well as we provide almost tight bounds on the *limit fitness* of the individuals.

Apart from being interesting on its own, this new evolutionary model also enables the abstract modeling of new control mechanisms over invading populations in networks. We demonstrate this by introducing and analyzing the behavior of two alternative control approaches. In both scenarios we periodically modify the fitness of a small fraction of individuals in the current population, which is arranged on a complete graph with n vertices. In the first scenario, we proceed in phases. Namely, after each modification, we let the system stabilize before we perform the next modification. In the second scenario, we modify the fitness of a small fraction of individuals at each step. In both alternatives, we stop performing these modifications of the population whenever the fitness of every individual becomes sufficiently close to 1 (which is considered to be the "healthy" state of the system). For the first scenario, we prove that the number of *phases* needed for the system to stabilize in the healthy state is logarithmic in $r-1$ and independent of n. For the second scenario, we prove that the number of *iterations* needed for the system to stabilize in the healthy state is linear in n and proportional to $r\ln(r-1)$. Related recovery control mechanisms have been studied also in the context of epidemic spreading in the SIR and SIS models (see e.g. [2, 3, 5, 11]).

Notation. In an undirected graph $G = (V, E)$, the edge between vertices $u \in V$ and $v \in V$ is denoted by $uv \in E$, and in this case u and v are said to be *adjacent* in G. If the graph G is directed, we denote by $\langle uv \rangle$ the arc from u to v. For every vertex $u \in V$ in an undirected graph $G = (V, E)$, we denote by $N(u) = \{v \in V \mid uv \in E\}$ the set of neighbors of u in G and by $\deg(u) = |N(u)|$. Furthermore, for any $k \geq 1$, we denote for simplicity $[k] = \{1, 2, \ldots, k\}$.

Organization of the paper. We discuss in Section 2 the two alternative models for evolutionary dynamics on graphs. In particular, we formally present in Section 2.1 the model of [19] and then we introduce in Section 2.2 our new model of mutual influences. In Section 3 we first provide generic upper and lower bounds for the fixation probability in the model of [19] for arbitrary undirected graphs. Then we present in Section 3.3 the first class of undirected graphs which act as suppressors of selection in the model of [19], when $1 < r < \frac{4}{3}$ and as the number of vertices increases. In Section 4 we analyze our new evolutionary model of mutual influences. In particular, we first prove in Section 4.1 the convergence of the model by using a potential function, and then we analyze in Section 4.2 the long-term behavior of this model for the case of a complete graph. In Section 5 we demonstrate the use of our new model in analyzing the behavior of two alternative invasion control mechanisms. Finally, we discuss the presented results and further research in Section 6.

2 All-or-nothing vs. aggregation

In this section we formally define the model of [19] for undirected graphs and we introduce our new model of mutual influences. Similarly to [19], we assume that the underlying graph is connected and that for every edge uv of an undirected graph $w_{uv} = \frac{1}{\deg u}$ and $w_{vu} = \frac{1}{\deg v}$, i.e., once a vertex u has been chosen for reproduction, it chooses one of its neighbors uniformly at random.

2.1 The model of Lieberman, Hauert, and Nowak (an all-or-nothing approach)

Let $G = (V, E)$ be a connected undirected graph with n vertices. In the model of [19], an individual is chosen for reproduction with a probability proportional to its fitness. Thus, if S denotes the current set of mutants, the probability that a particular mutant is selected for reproduction equals

$$\frac{r}{|S| \cdot r + n - |S|}. \tag{1}$$

Thus, using (1), we can describe this process of [19] by a Markov chain with state space $\mathcal{S} = 2^V$ (i.e., the set of all subsets of V) and transition probability matrix P, where for any two states $S_1, S_2 \subseteq V$,

$$P_{S_1,S_2} = \begin{cases} \frac{1}{|S_1|r+n-|S_1|} \cdot \sum\limits_{u \in N(v) \cap S_1} \frac{r}{\deg(u)}, & \text{if } S_2 = S_1 \cup \{v\} \text{ and } v \notin S_1, \\ \frac{1}{|S_1|r+n-|S_1|} \cdot \sum\limits_{u \in N(v) \setminus S_2} \frac{1}{\deg(u)}, & \text{if } S_1 = S_2 \cup \{v\} \text{ and } v \notin S_2, \\ \frac{1}{|S_1|r+n-|S_1|} \cdot \left(\sum\limits_{u \in S_1} \frac{r \cdot |N(u) \cap S_1|}{\deg(u)} + \sum\limits_{u \in V \setminus S_1} \frac{|N(u) \setminus S_1|}{\deg(u)} \right), & \text{if } S_2 = S_1, \\ 0, & \text{otherwise.} \end{cases} \tag{2}$$

Notice that in the above Markov chain there are two absorbing states, namely $\emptyset$ and V, which describe the cases where the vertices of G are all non-mutants or all mutants, respectively. Since G is connected, the above Markov chain reaches with probability 1 one of these two absorbing states, i.e., it either reaches the state $\emptyset$ or the state V. If we denote by h_v the probability of absorption at state V, given that we start with a single mutant placed initially on vertex v, then by definition $f_G = \frac{\sum_v h_v}{n}$. Note that h_v depends on the graph G, as well as on the particular vertex v. Generalizing this notation, let h_S be the probability of absorption at V given that we start at state $S \subseteq V$, and let $h = [h_S]_{S \subseteq V}$. Then, it follows that vector h is the unique solution of the linear system $h = P \cdot h$ with boundary conditions $h_\emptyset = 0$ and $h_V = 1$.

Observe that the state space $\mathcal{S} = 2^V$ of this Markov chain has size 2^n, i.e., the matrix $P = [P_{S_1,S_2}]$ in (2) has dimension $2^n \times 2^n$. To the best of our knowledge, most prior work on computing fixation probabilities of undirected graphs has been restricted to graphs with a high degree of symmetry, which reduces the size of the linear system, for example to regular graphs, stars, paths, and graphs with a small number of vertices [7–10, 19, 24]. In particular, for the case of regular graphs, the above Markov chain is equivalent to a birth-death process with $n-1$ transient (non-absorbing) states, where the forward bias at every state (i.e., the ratio of the forward probability over the backward probability) is equal to r. In this case, the fixation probability is equal to

$$\rho = \frac{1}{1 + \sum_{i=1}^{n-1} \frac{1}{r^i}} = \frac{1 - \frac{1}{r}}{1 - \frac{1}{r^n}}, \tag{3}$$

cf. [24, Chapter 8]. It is worth mentioning that, even for the case of paths, there is no known exact or approximate formula for the fixation probability [9].

2.2 An evolutionary model of mutual influences (an aggregation approach)

The evolutionary model of [19] constitutes a sequential process, in every step of which only two individuals interact and the process eventually reaches one of two extreme states. However, in many evolutionary processes, all individuals may interact simultaneously at each time step, while some individuals have greater influence to the rest of the population than others. This observation leads naturally to the following model for evolution on graphs, which can be thought as a smooth version of the model presented in [19].

Consider a population of size n and a proportion $\alpha \in [0, 1]$ of newly introduced mutants with relative fitness r. The topology of the population is given in general by a directed graph $G = (V, E)$ with $|V| = n$ vertices, where the directed arcs of E describe the allowed interactions between the individuals. At each time step, *every* individual $u \in V$ of the population influences every individual $v \in V$, for which $\langle uv \rangle \in E$, while the degree of this influence is proportional to the fitness of u and to the weight w_{uv} of the arc $\langle uv \rangle$. Note that we can assume without loss of generality that the weights w_{uv} on the arcs are normalized, i.e., for every fixed vertex $u \in V$ it holds $\sum_{\langle uv \rangle \in E} w_{uv} = 1$. Although this model can be defined in general for directed graphs with arbitrary arc weights w_{uv}, we will focus in the following on the case where G is an undirected graph and $w_{uv} = \frac{1}{\deg(u)}$ for all edges $uv \in E$.

Formally, let $V = \{u_1, u_2, \ldots, u_n\}$ be the set of vertices and $r_{u_i}(k)$ be the fitness of the vertex $u_i \in V$ at iteration $k \geq 0$. Let $\Sigma(k)$ denote the sum of the fitnesses of all vertices at iteration k, i.e., $\Sigma(k) = \sum_{i=1}^n r_{u_i}(k)$. Then the vector $r(k+1)$ with the fitnesses $r_{u_i}(k+1)$ of the vertices $u_i \in V$ at the next iteration $k+1$ is given by

$$[r_{u_1}(k+1), r_{u_2}(k+1), \ldots, r_{u_n}(k+1)]^T = P(k) \cdot [r_{u_1}(k), r_{u_2}(k), \ldots, r_{u_n}(k)]^T, \tag{4}$$

i.e.,

$$r(k+1) = P(k) \cdot r(k). \tag{5}$$

In the latter equation, the elements of the square matrix $P(k) = [P_{ij}(k)]_{i,j=1}^{n}$ depend on the iteration k and they are given as follows:

$$P_{ij}(k) = \begin{cases} \frac{r_{u_j}(k)}{\deg(u_j)\Sigma(k)}, & \text{if } i \neq j \text{ and } u_i u_j \in E, \\ 0, & \text{if } i \neq j \text{ and } u_i u_j \notin E, \\ 1 - \sum_{j \neq i} P_{ij}(k), & \text{if } i = j. \end{cases} \tag{6}$$

Note by (5) and (6) that after the first iteration, the fitness of every individual in our new evolutionary model of mutual influences equals the expected fitness of this individual in the model of [19] (cf. Section 2.1). However, this correlation of the two models is not maintained in the next iterations and the two models behave differently as the processes evolve.

In particular, in the case where G is the complete graph, i.e., $\deg(u_i) = n-1$ for every vertex u_i, the matrix $P(k)$ becomes

$$P(k) = \begin{bmatrix} 1 - \frac{r_{u_2}(k)+\ldots+r_{u_n}(k)}{(n-1)\Sigma(k)} & \frac{r_{u_2}(k)}{(n-1)\Sigma(k)} & \cdots & \frac{r_{u_n}(k)}{(n-1)\Sigma(k)} \\ \frac{r_{u_1}(k)}{(n-1)\Sigma(k)} & 1 - \frac{r_{u_1}(k)+r_{u_3}(k)+\ldots+r_{u_n}(k)}{(n-1)\Sigma(k)} & \cdots & \frac{r_{u_n}(k)}{(n-1)\Sigma(k)} \\ \cdots & \cdots & \cdots & \cdots \\ \frac{r_{u_1}(k)}{(n-1)\Sigma(k)} & \frac{r_{u_2}(k)}{(n-1)\Sigma(k)} & \cdots & 1 - \frac{r_{u_1}(k)+\ldots+r_{u_{n-1}}(k)}{(n-1)\Sigma(k)} \end{bmatrix}. \tag{7}$$

The system given by (5) and (6) can be defined for every initial fitness vector $r(0)$. However, in the case where there is initially a proportion $\alpha \in [0,1]$ of newly introduced mutants with relative fitness r, the initial condition $r(0)$ of the system in (4) is a vector with αn entries equal to r and with $(1-\alpha)n$ entries equal to 1.

Observation 1 *Note that the recursive equation (5) is a* non-linear *equation on the fitness values $r_{u_j}(k)$ of the vertices at iteration k.*

Since by (6) the sum of every row of the matrix $P(k)$ equals one, the fitness $r_{u_i}(k)$ of vertex u_i after the $(k+1)$-th iteration of the process is a convex combination of the fitnesses of the neighbors of u_i after the k-th iteration. Therefore, in particular, the fitness of every vertex u_i at every iteration $k \geq 0$ lies between the smallest and the greatest initial fitness of the vertices, as the next observation states.

Observation 2 *Let $r_{\min}$ and $r_{\max}$ be the smallest and the greatest initial fitness in $r(0)$, respectively. Then $r_{\min} \leq r_{u_i}(k) \leq r_{\max}$ for every $u_i \in V$ and every $k \geq 0$.*

Degree of influence. Suppose that initially αn mutants (for some $\alpha \in [0,1]$) with relative fitness $r \geq 1$ are introduced in graph G on a subset $S \subseteq V$ of its vertices. Then, as we prove in Theorem 5, after a certain number of iterations the fitness vector $r(k)$ converges to a vector $[r_0^S, r_0^S, \ldots, r_0^S]^T$, for some value r_0^S. This *limit fitness* r_0^S depends in general on the initial relative fitness r of the mutants, on their initial number αn, as well as on their initial position on the vertices of $S \subseteq V$. Visually, if mutants and non-mutants would be encoded by different colors such as blue and red, respectively, then the limit fitness r_0^S could be thought as a mixture of these two colors, i.e., as the "degree of purple color" that all the vertices obtain after sufficiently many iterations, given that the mutants are initially placed at the vertices of S. In the case where the αn mutants are initially placed with *uniform* probability to the vertices of G, we can define the *limit fitness* r_0 *of* G as

$$r_0 = \frac{\sum\limits_{S \subseteq V,\ |S| = \alpha n} r_0^S}{\binom{n}{\alpha n}}.$$

For a given initial value of r, the bigger is r_0 the stronger is the effect of natural selection in G.

Since r_0^S is a convex combination of r and 1, there exists a value $f_{G,S}(r) \in [0,1]$, such that $r_0^S = f_{G,S}(r) \cdot r + (1 - f_{G,S}(r)) \cdot 1$. Then, the value $f_{G,S}(r)$ is the *degree of influence* of the graph G, given that the mutants are initially placed at the vertices of S. In the case where the mutants are initially placed with uniform probability at the vertices of G, we can define the degree of influence of G as

$$f_G(r) = \frac{\sum\limits_{S \subseteq V,\ |S| = \alpha n} f_{G,S}(r)}{\binom{n}{\alpha n}}.$$

Number of iterations to stability. For some graphs G, the fitness vector $r(k)$ reaches *exactly* the *limit fitness vector* $[r_0, r_0, \ldots, r_0]^T$ (for instance, the complete graph with two vertices and one mutant not only reaches this limit in exactly one iteration, but also the degree of influence is exactly the fixation probability of this simple graph). However, for other graphs G the fitness vector $r(k)$ converges to $[r_0, r_0, \ldots, r_0]^T$ (cf. Theorem 5 below), but it never becomes equal to it. In the first case, one can compute (exactly or approximately) the number of iterations needed to reach the limit fitness vector. In the second case, given an arbitrary $\varepsilon > 0$, one can compute the number of iterations needed to come ε-close to the limit fitness vector.

3 Analysis of the all-or-nothing model

In this section we present analytic results on the evolutionary model of [19], which is based on the sequential interaction among the individuals. In particular, we first present non-trivial upper and lower bounds for the fixation probability, depending on the degrees of vertices. Then we present for $1 < r < \frac{4}{3}$ the first class of undirected graphs that act as suppressors of selection in the model of [19], as the number of vertices increases.

Recall from the preamble of Section 2.2 that, similarly to [19], we assumed that $w_{uv} = \frac{1}{\deg u}$ and $w_{vu} = \frac{1}{\deg v}$ for every edge uv of an undirected graph $G = (V, E)$. It is easy to see that this formulation is equivalent to assigning to every edge $e = uv \in E$ the weight $w_e = w_{uv} = w_{vu} = 1$, since also in this case, once a vertex u has been chosen for reproduction, it chooses one of its neighbors uniformly at random. A natural generalization of this weight assignment is to consider G as a complete graph, where every edge e in the clique is assigned a non-negative weight $w_e \geq 0$, and w_e is not necessarily an integer. Note that, whenever $w_e = 0$, it is as if the edge e is not present in G. Then, once a vertex u has been chosen for reproduction, u chooses any other vertex v with probability $\frac{w_{uv}}{\sum_{x \neq u} w_{ux}}$.

Note that, if we do not impose any additional constraint on the weights, we can simulate multigraphs by just setting the weight of an edge to be equal to the multiplicity of this edge. Furthermore, we can construct graphs with arbitrary small fixation probability. For instance, consider an undirected star with n leaves, where one of the edges has weight an arbitrary small $\varepsilon > 0$ and all the other edges have weight 1. Then, the leaf that is incident to the edge with weight ε acts as a source in the graph as $\varepsilon \to 0$. Thus, the only chance to reach fixation is when we initially place the mutant at the source, i.e., the fixation probability of this graph tends to $\frac{1}{n+1}$ as $\varepsilon \to 0$. Therefore, it seems that the difficulty to construct strong suppressors lies in the fact that unweighted undirected graphs can not simulate sources. For this reason, we consider in the remainder of this paper only unweighted undirected graphs.

3.1 A generic upper bound approach

In the next theorem we provide a generic upper bound of the fixation probability of undirected graphs, depending on the degrees of the vertices in some local neighborhood. In the next theorem, the quantities Q_u and Q_{uv} depend also on the graph G, however we avoid writing Q_u^G and Q_{uv}^G, respectively, in order to keep the notation as simple as possible.

Theorem 1 *Let $G = (V, E)$ be an undirected graph. For any $uv \in E$, let $Q_u = \sum_{x \in N(u)} \frac{1}{\deg x}$ and $Q_{uv} = \sum_{x \in N(u) \setminus \{v\}} \frac{1}{\deg x} + \sum_{x \in N(v) \setminus \{u\}} \frac{1}{\deg x}$. Then*

$$f_G \leq \max_{uv \in E} \left\{ \frac{r^2}{r^2 + rQ_u + \frac{Q_u Q_{uv}}{2}} \right\}. \tag{8}$$

Proof. For the proof we construct a simple Markov chain $\tilde{\mathcal{M}}$, in which the probability of reaching a specific absorbing state is at least the probability of fixation in the original Markov chain. Then, in order to provide an upper bound of the fixation probability in the original Markov chain, we provide an upper bound on the probability of reaching this specific absorbing state in $\tilde{\mathcal{M}}$.

Let u be a choice for the initial vertex that maximizes the probability of fixation. Furthermore, assume that we end the process in favor of the mutants when the corresponding Markov chain describing the model of [19] reaches three mutants. To favor fixation even more, since u maximizes the fixation probability, we assume that, whenever we reach two mutants and a backward step happens (i.e., a step that reduces the number of mutants), then we backtrack to state u (even if vertex u was the one that became non-mutant). Finally, given that we start at vertex u and we increase the number of mutants by one, we assume that the neighbor v of u, which maximizes the forward bias of the state $\{u, v\}$, becomes a mutant. Imposing these constraints (and eliminating self loops), we get a Markov chain $\tilde{\mathcal{M}}$, shown in Figure 1, that dominates the original Markov chain. That is, the probability that $\tilde{\mathcal{M}}$ reaches the state of three mutants, given that we start at u, is an upper bound of the fixation probability f_G of G.

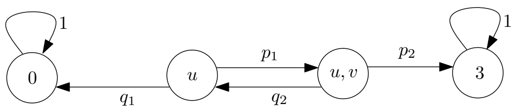

Figure 1: The Markov chain $\tilde{\mathcal{M}}$.

For the Markov chain $\tilde{\mathcal{M}}$, we have that

$$q_1 = \frac{\sum_{x\in N(u)} \frac{1}{\deg x}}{r + \sum_{x\in N(u)} \frac{1}{\deg x}} = \frac{Q_u}{r+Q_u} = 1 - p_1,$$

where $N(u)$ is the set of neighbors of u. Also,

$$\begin{aligned} q_2 &= \frac{\sum_{x\in N(u)\setminus\{v\}} \frac{1}{\deg x} + \sum_{x\in N(v)\setminus\{u\}} \frac{1}{\deg x}}{r(1-\frac{1}{\deg u}) + r(1-\frac{1}{\deg v}) + \sum_{x\in N(u)\setminus\{v\}} \frac{1}{\deg x} + \sum_{x\in N(v)\setminus\{u\}} \frac{1}{\deg x}} \\ &= \frac{Q_{uv}}{r(2-\frac{1}{\deg u}-\frac{1}{\deg v}) + Q_{uv}} = 1 - p_2. \end{aligned}$$

Let now $\tilde{h}_u$ (resp. $\tilde{h}_{uv}$) denote the probability of reaching three mutants, starting from u (resp. starting from the state $\{u, v\}$) in $\tilde{\mathcal{M}}$. We have that

$$\begin{aligned} \tilde{h}_u &= p_1\tilde{h}_{uv} = p_1(p_2 + q_2\tilde{h}_u) \Leftrightarrow \\ \tilde{h}_u &= \frac{p_1p_2}{1-p_1q_2} = \frac{r^2}{r^2 + rQ_u + \frac{Q_uQ_{uv}}{2-\frac{1}{\deg u}-\frac{1}{\deg v}}} \leq \frac{r^2}{r^2 + rQ_u + \frac{Q_uQ_{uv}}{2}}. \end{aligned}$$

This completes the proof of the theorem. ■

Consider for instance a bipartite graph $G = (U, V, E)$, where $\deg u = d_1$ for every vertex $u \in U$ and $\deg v = d_2$ for every vertex $v \in V$. Then any edge of E has one vertex in U and one vertex in V. Using the above notation, consider now an arbitrary edge $uv \in E$, where $u \in U$ and $v \in V$. Then $Q_u = \frac{d_1}{d_2}$ and $Q_{uv} = \frac{d_1-1}{d_2} + \frac{d_2-1}{d_1}$. The right side of (8) is maximized when $d_1 < d_2$, and thus in this case Theorem 1 implies that $f_G \leq \frac{r^2}{r^2+r\frac{d_1}{d_2}+\frac{d_1}{2d_2}\left(\frac{d_1-1}{d_2}+\frac{d_2-1}{d_1}\right)}$. In particular, for the star graph with $n+1$ vertices, we have $d_1 = 1$ and $d_2 = n$. But, as shown in [19], the fixation probability of the star is asymptotically equal to $1 - \frac{1}{r^2}$, whereas the above bound gives $f_{\text{star}} \leq \frac{r^2}{r^2+r\frac{1}{n}+\frac{n-1}{2n}} = 1 - \frac{1}{2r^2+1+o(1)}$.

3.2 Upper and lower bounds depending on degrees

In the following theorem we provide upper and lower bounds for the fixation probability of undirected graphs, depending on the maximum ratio between the degrees of two neighboring vertices.

Theorem 2 *Let $G = (V, E)$ be an undirected graph, where $\frac{\deg(v)}{\deg(u)} \leq \lambda$ whenever $uv \in E$. Then, the fixation probability f_G of G, when the fitness of the mutant is r, is upper (resp. lower) bounded by the fixation probability of the clique for mutant fitness $r_1 = r\lambda$ (resp. for mutant fitness $r_2 = \frac{r}{\lambda}$). That is,*

$$\frac{1-\frac{\lambda}{r}}{1-\left(\frac{\lambda}{r}\right)^n} \leq f_G \leq \frac{1-\frac{1}{r\lambda}}{1-\left(\frac{1}{r\lambda}\right)^n}.$$

Proof. For an arbitrary state $S \subseteq V$ of the Markov Chain (that corresponds to the set of mutants in that state), let $\rho_+(S)$ (resp. $\rho_-(S)$) denote the probability that the number of mutants increases (resp. decreases). In the case where G is a clique, the forward bias $\frac{\rho_+(S)}{\rho_-(S)}$ at state S is equal to r, for every state S [19, 24]. Then,

$$\rho_+(S) = \sum_{\{uv\in E \mid u\in S,\ v\notin S\}} \frac{r}{n-|S|+r|S|}\frac{1}{\deg(u)} \tag{9}$$

and

$$\rho_-(S) = \sum_{\{uv\in E \mid u\in S,\ v\notin S\}} \frac{1}{n-|S|+r|S|}\frac{1}{\deg(v)}. \tag{10}$$

Now, since by assumption $\frac{\deg(v)}{\deg(u)} \leq \lambda$ whenever $uv \in E$, it follows that

$$\frac{1}{\lambda} \cdot \sum_{\{uv \in E \ \mid \ u \in S, \ v \notin S\}} \frac{1}{\deg(v)} \leq \sum_{\{uv \in E \ \mid \ u \in S, \ v \notin S\}} \frac{1}{\deg(u)} \leq \lambda \cdot \sum_{\{uv \in E \ \mid \ u \in S, \ v \notin S\}} \frac{1}{\deg(v)}. \tag{11}$$

By (9), (10), and (11) we get the following upper and lower bounds for the forward bias at state S.

$$\frac{r}{\lambda} \leq \frac{\rho_+(S)}{\rho_-(S)} \leq r\lambda. \tag{12}$$

Notice that the upper and lower bounds of (12) for the forward bias at state S are independent of S. Therefore, the process stochastically dominates a birth-death process with forward bias $\frac{r}{\lambda}$, while it is stochastically dominated by a birth-death process with forward bias $r\lambda$ (cf. equation (3)). This completes the proof of the theorem. ■

3.3 The undirected suppressor

In this section we provide the first class of undirected graphs (which we call *clique-wheels*) that act as suppressors of selection when $1 < r < \frac{4}{3}$, as the number of vertices increases. In particular, we prove that for these values the fitness r the fixation probability of sufficiently large members of this class is at most $\frac{1}{2}(1-\frac{1}{r})$, i.e., the half the fixation probability of the complete graph, as $n \to \infty$. An example of a clique-wheel graph G_n is depicted in Figure 2(a). This graph consists of a clique of size $n \geq 3$ and an induced cycle of the same size n with a perfect matching between them. We will refer in the following to the vertices of the inner clique as *clique vertices* and to the vertices of the outer cycle as *ring vertices*.

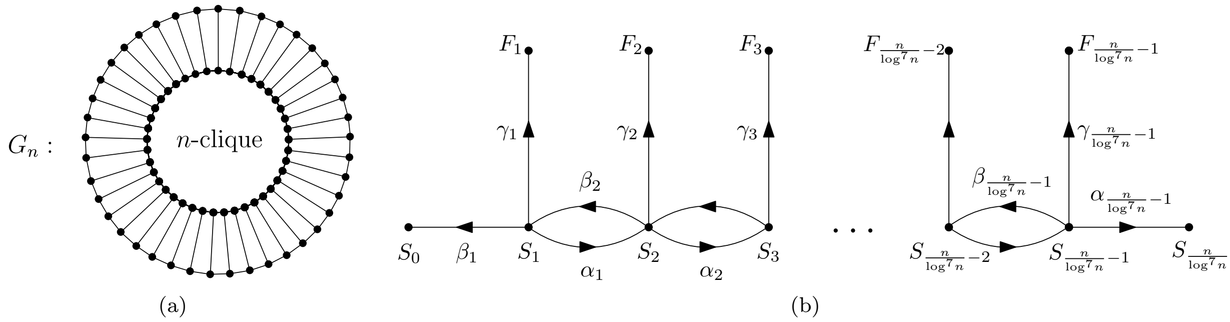

Figure 2: (a) The clique-wheel graph G_n and (b) the state graph of a relaxed Markov chain for computing an upper bound of $h_1 = h_{\text{clique}}$.

Denote by h_{clique} (resp. h_{ring}) the probability that all the vertices of G_n become mutants, given that we start with one mutant in the clique (resp. with one mutant in the ring). We first provide in the next lemma an upper bound on h_{clique}.

Lemma 1 *For any* $r \in \left(1, \frac{4}{3}\right)$,

$$h_{\text{clique}} \leq \frac{7}{6n\left(\frac{4}{3r} - 1\right)} + o\left(\frac{1}{n}\right).$$

Proof. Denote by S_k the state, in which exactly $k \geq 0$ clique vertices are mutants and all ring vertices are non-mutants. Note that S_0 is the empty state. Denote by F_k the set of states where at least one ring vertex of G_n and exactly $k \geq 0$ clique vertices are mutants. With a slight abuse of notation, we refer in the remainder of the proof to F_k as being one state rather than a set of states. Furthermore, for every $k \geq 0$, denote by h_k (resp. by h_{F_k}) the probability that, starting at the state S_k (resp. F_k), we eventually reach the full state (i.e., the state where all vertices are mutants). Note that $h_0 = 0$ and $h_1 = h_{\text{clique}}$, since S_0 is the empty state and S_1 is the state with only one mutant in the clique. In order to compute an upper bound of h_1, we define a relaxation $\overline{\mathcal{M}}$ of the Markov process, in which, once we are in the state $S_{\frac{n}{\log^7 n}}$ or in any of the states F_k, where $k \geq 1$, then we move to the full state (i.e., the state where all vertices are mutants) with probability 1. That is, in the Markov chain $\overline{\mathcal{M}}$, $h_{\frac{n}{\log^7 n}} = 1$ and $h_{F_k} = 1$ for every $k \geq 1$. It is then clear that the value of h_1 in $\overline{\mathcal{M}}$ is greater than or equal to the value of h_1 in the original Markov chain. The Markov chain $\overline{\mathcal{M}}$ is depicted in Figure 2(b), where we eliminated self loops and we omitted (for simplicity of the figure) the transitions of the Markov chain to the full state.

For any $k = 1, \ldots, \frac{n}{\log^7 n} - 1$ in this Markov chain,

$$h_k = \alpha_k h_{k+1} + \beta_k h_{k-1} + \gamma_k, \tag{13}$$

where

$$\begin{aligned}
\alpha_k &= \frac{r^{\frac{k(n-k)}{n}}}{r^{\frac{k(n-k+1)}{n}} + k\left(\frac{1}{3} + \frac{n-k}{n}\right)}, \\
\beta_k &= \frac{k\left(\frac{1}{3} + \frac{n-k}{n}\right)}{r^{\frac{k(n-k+1)}{n}} + k\left(\frac{1}{3} + \frac{n-k}{n}\right)}, \\
\gamma_k &= \frac{r^{\frac{k}{n}}}{r^{\frac{k(n-k+1)}{n}} + k\left(\frac{1}{3} + \frac{n-k}{n}\right)}.
\end{aligned} \tag{14}$$

Notice now by (14) that

$$\frac{\beta_k}{\alpha_k} = \frac{\frac{4}{3}n - k}{r(n-k)} > \frac{4}{3r} > 1, \tag{15}$$

since $r \in \left(1, \frac{4}{3}\right)$ by assumption. Furthermore, since $\frac{1}{1-\frac{1}{\log^7 n}} \leq \frac{7}{6}$ for sufficiently large n, it follows that for every $k = 1, 2, \ldots, \frac{n}{\log^7 n} - 1$,

$$\frac{\gamma_k}{\alpha_k} = \frac{1}{n-k} \leq \frac{7}{6n}, \tag{16}$$

Now, since $\alpha_k + \beta_k + \gamma_k = 1$, (13) implies by (15) and (16) that

$$\begin{aligned}
h_{k+1} - h_k &= \frac{\beta_k}{\alpha_k}(h_k - h_{k-1}) - \frac{\gamma_k}{\alpha_k}(1 - h_k) \\
&\geq \frac{4}{3r}(h_k - h_{k-1}) - \frac{7}{6n}.
\end{aligned}$$

Thus, since $h_0 = 0$ and $h_k \geq h_{k-1}$ for all $k = 1, \ldots, \frac{n}{\log^7 n}$, it follows that for every k,

$$\begin{aligned}
h_{k+1} - h_k &\geq \left(\frac{4}{3r}\right)^k (h_1 - h_0) - \frac{7}{6n} \cdot \sum_{i=0}^{k-1} \left(\frac{4}{3r}\right)^i \\
&= \left(\frac{4}{3r}\right)^k h_1 - \frac{7}{6n} \cdot \frac{\left(\frac{4}{3r}\right)^k - 1}{\frac{4}{3r} - 1}.
\end{aligned}$$

Consequently, since $h_{\frac{n}{\log^7 n}} = 1$ in the relaxed Markov chain, we have that

$$\begin{aligned}
1 - h_1 &= \sum_{k=1}^{\frac{n}{\log^7 n}-1} (h_{k+1} - h_k) \\
&\geq \sum_{k=1}^{\frac{n}{\log^7 n}-1} \left[\left(\frac{4}{3r}\right)^k h_1 - \frac{7}{6n} \cdot \frac{\left(\frac{4}{3r}\right)^k - 1}{\frac{4}{3r} - 1}\right] \Rightarrow \\
h_1 \sum_{k=0}^{\frac{n}{\log^7 n}-1} \left(\frac{4}{3r}\right)^k &\leq 1 + \frac{7}{6n\left(\frac{4}{3r} - 1\right)} \sum_{k=0}^{\frac{n}{\log^7 n}-1} \left[\left(\frac{4}{3r}\right)^k - 1\right],
\end{aligned}$$

and thus

$$h_1 \leq \frac{7}{6n\left(\frac{4}{3r} - 1\right)} + \frac{1}{\sum_{k=0}^{\frac{n}{\log^7 n}-1} \left(\frac{4}{3r}\right)^k}.$$

This completes the proof of the lemma, since $\frac{4}{3r} > 1$. ■

The next corollary follows by the proof of Lemma 1.

Corollary 1 *Starting with one mutant in the clique, the probability that at least one ring vertex becomes a mutant, or that we eventually reach $\frac{n}{\log^7 n}$ mutants in the clique, is at most $\frac{7}{6n\left(\frac{4}{3r}-1\right)} + o\left(\frac{1}{n}\right)$.*

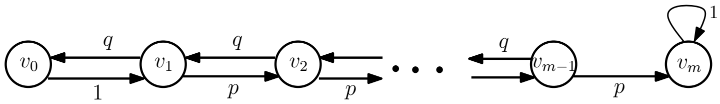

Figure 3: The Markov chain $\mathcal{M}$.

In the remainder of this section, we will also provide an upper bound on h_{ring}, thus bounding the fixation probability f_{G_n} of G_n (cf. Theorem 4). Consider the Markov chain $\mathcal{M}$ that is depicted in Figure 3. Our analysis will use the following auxiliary lemma which concerns the expected time to absorption of this Markov chain.

Lemma 2 *Let $p \neq q$ and $p + q = 1$. Then, as m tends to infinity, the expected number of steps needed for $\mathcal{M}$ to reach v_m, given that we start at v_1, satisfies*

$$\mu_1 = \begin{cases} e^{m \ln \frac{q}{p} + o(m)} & \text{if } p < q \\ \frac{m}{p-q} + o(m) & \text{if } p > q \end{cases}.$$

Proof. For $i = 0, 1, \ldots, m$, let μ_i denote the expected number of steps needed to reach v_m, given that we start at v_i. Clearly, $\mu_m = 0$ and $\mu_0 = 1 + \mu_1$. Furthermore, for $i = 1, \ldots, m-1$, it follows that

$$\mu_i = 1 + p\mu_{i+1} + q\mu_{i-1},$$

i.e.,

$$\begin{aligned} \mu_{i+1} - \mu_i &= \frac{q}{p}(\mu_i - \mu_{i-1}) - \frac{1}{p} \\ &= \left(\frac{q}{p}\right)^i (\mu_1 - \mu_0) - \frac{1}{p} \sum_{j=0}^{i-1} \left(\frac{q}{p}\right)^j \\ &= -\left(\frac{q}{p}\right)^i - \frac{1}{q-p} \left(\left(\frac{q}{p}\right)^i - 1\right). \end{aligned}$$

Consequently, we have that

$$\begin{aligned} \sum_{i=1}^{m-1} [\mu_{i+1} - \mu_i] &= -\mu_1 \Leftrightarrow \\ \mu_1 &= \sum_{i=1}^{m-1} \left[\left(1 + \frac{1}{q-p}\right)\left(\frac{q}{p}\right)^i - \frac{1}{q-p}\right] \Leftrightarrow \\ \mu_1 &= \left(1 + \frac{1}{q-p}\right) \frac{\left(\frac{q}{p}\right)^m - \frac{q}{p}}{\frac{q}{p} - 1} - \frac{m-1}{q-p}. \end{aligned}$$

Thus, for large m, this completes the proof of the lemma. ■

Denote in the following by $\mathcal{M}_1$ the Markov chain of the stochastic process defined in [19] (see Section 2.1 for an overview), when the underlying graph is the clique-wheel G_n, cf. Figure 2(a). The next definition will be useful for the discussion below.

Definition 1 (Ring steps) *A transition of the Markov chain $\mathcal{M}_1$ is called a* ring step *if it results in a change of the number of mutants in the outer ring (i.e., ring vertices).*

We now present some *domination statements* that simplify the Markov chain $\mathcal{M}_1$. More specifically, all these statements will increase the probability of reaching fixation when we start with one mutant in the ring, such that we finally get an upper bound on h_{ring}.

D_1**:** Let v be a vertex on the outer ring, and let v' be its (unique) neighbor in the clique. Let v be a mutant and v' be a non-mutant. We will *forbid* transitions of the Markov chain $\mathcal{M}_1$, where v' places its copy on vertex v.

D_2**:** Fixation is forced when either of the following happens:

A_1**:** The outer ring reaches $\log n$ mutants.
A_2**:** The number of ring steps in order to reach $\log n$ mutants in the ring is more than $\log^2 n$.
A_3**:** The clique reaches n mutants.
A_4**:** A mutant in the clique places a copy of itself on a currently non-mutant of the outer ring.

Let now $\mathcal{M}_2$ be the modified Markov chain after these domination statements are imposed. That is, $\mathcal{M}_2$ is obtained from $\mathcal{M}_1$ by applying the following modifications: (a) We replace each transition $S \to S'$ specified in domination statement D_1 (i.e., where a non-mutant v' in the clique replaces a mutant v in the ring by a copy of it) by a loop $S \to S$ with the same probability. (b) We make a transition from any state specified in domination statement D_2 to the absorbing state V (i.e., the full state, where all vertices are mutants) with probability 1. The following definitions will be useful in what follows.

Definition 2 (Offspring) *If a vertex u places its copy on a vertex v at time t, then we say that v is an* offspring *of u at time t. Furthermore, if a vertex v' is an* offspring *of u, and if v' places its copy on a vertex v'' at time t, then we say that v'' is an* offspring *of u at time t. Moreover, if v is an offspring of u at time t, it remains so until a vertex x places its copy on v at time $t' > t$, where x is* not *an offspring of u.*

Notice in Definition 2 that u is not necessarily a mutant at time t.

Definition 3 (Birth in the clique) *We will say that a vertex v' is* born *in the clique if and only if its (unique) neighbor v in the outer ring is a mutant and makes a transition to the clique (i.e., v places its offspring in v').*

Notice in Definition 3 that, before v' is born in the clique, it is irrelevant whether v' is a mutant or a non-mutant. We only need that v is a mutant. Furthermore, the above definition allows for a specific vertex to be born more than once (i.e., at different time steps). The proof of our main theorem can now be reduced to a collection of lemmas. Lemma 3 concerns the behavior of the ring.

Lemma 3 *Let $\mathcal{B}_1$ be the stochastic process describing the ring steps in Markov chain $\mathcal{M}_2$. Given that we do not have absorption at A_4, then $\mathcal{B}_1$ is a birth-death process with forward bias equal to r. Furthermore, given that we start with a single mutant on the ring, the following hold:*

(1) The probability that the number of mutants in the outer ring reaches $\log n$ before absorption at A_2, A_3 or A_4 is at most $\frac{1-\frac{1}{r}}{1-\left(\frac{1}{r}\right)^{\log n}}$.

(2) The probability that more than $\log^2 n$ ring steps are needed in order to reach $\log n$ mutants in the ring, or to reach absorption in A_2, A_3, or A_4 is at most $O\left(\frac{1}{\log n}\right)$.

Proof. Recall that we do not allow transitions where the clique affects the number of mutants in the outer ring (by the domination statements D_1 and A_4). Then, it can be easily seen that the forward bias of the birth-death process $\mathcal{B}_1$ (i.e., the ratio of the forward probability over the backward probability) is $\frac{\frac{2r}{W}\frac{1}{3}}{\frac{2}{W}\frac{1}{3}} = r$, where W is the sum of the fitness of every vertex in the graph. Thus, part (1) of the lemma follows by equation (3) (for an overview of birth-death processes, see also [23, 24]).

For part (2), let X denote the number of ring steps needed in order to reach $\log n$ mutants in the ring, or to reach absorption in A_2, A_3 or A_4. Then X is stochastically dominated by the number of steps needed for Markov chain $\mathcal{M}$ (cf. Figure 3) to reach v_m, with $m = \log n$ and $p = \frac{r}{r+1}$. Hence, by Lemma 2 and Markov's inequality, we get that

$$\Pr(X \geq \log^2 n) \leq \mathbb{E}[X] \cdot \frac{1}{\log^2 n} \leq \left(\frac{r+1}{r-1}\log n + o(\log n)\right) \cdot \frac{1}{\log^2 n} = O\left(\frac{1}{\log n}\right).$$

This completes the proof of the lemma. ■

The next lemma bounds the number of vertices that are born in the clique (see Definition 3).

Lemma 4 *Given that we start with a single mutant on the ring, the probability that we have more than $\log^7 n$ births in the clique is at most $O\left(\frac{1}{\log n}\right)$.*

Proof. For the proof, we will ignore for the moment what happens in the clique and how the clique affects the ring, since these steps are either forbidden (by D_1) or lead to absorption (by A_4).

Let Y be the number of births in the clique (see Definition 3) that we observe between two ring steps. Notice that at any time before absorption, there will be exactly 2 non-mutants in the outer ring that can perform a ring step (see Definition 1). Furthermore, if the number of mutants in the ring is more than 2, then not all mutants can affect the number of mutants in the ring. We now restrict ourselves, to observe only ring-involved moves (forgetting about the clique), that is, transitions where only vertices of the ring that can cause a ring step or a birth in the clique are chosen. Given that $\mathcal{M}_2$ (i.e., the modified Markov chain) has not been absorbed, the probability that a ring step happens next is

$$p_{step} = \frac{2(1+r)}{2+zr}\frac{1}{3},$$

where z is the number of mutants in the outer ring. Similarly, the probability that a birth in the clique happens next is

$$p_{birth} = \frac{zr}{2+zr}\frac{1}{3}.$$

Consequently, the random variable $Y+1$ is stochastically dominated by a geometric random variable with probability of success

$$p = \frac{p_{step}}{p_{step}+p_{birth}} = \frac{2r+2}{zr+2r+2} \geq \frac{1}{\log n},$$

where in the last inequality we used the observation that at any time before absorption, the number of mutants in the ring is at most $\log n$ because of A_1. But then, by Markov's inequality, we have that

$$\Pr(Y+1 \geq \log^5 n + 1) \leq \frac{\frac{1}{p}}{\log^5 n + 1} \leq \frac{1}{\log^4 n}.$$

But by part (2) of Lemma 3, the probability that there are more than $\log^7 n$ births in the clique before the Markov chain is absorbed is by Boole's inequality at most

$$\log^2 n \Pr(Y \geq \log^5 n) + O\left(\frac{1}{\log n}\right) \leq O\left(\frac{1}{\log n}\right),$$

The last inequality comes from the fact that, in order to get at least $\log^7 n$ births within $\log^2 n$ ring steps, there must be at least $\log^5 n$ births between at least one pair of consecutive ring steps. This completes the proof of the lemma. ∎

The following lemma states that it is highly unlikely that the clique will affect the outer ring, or that the number of mutants in the clique will reach n.

Lemma 5 *Given that we start with a single mutant on the ring, the probability of absorption at A_3 or A_4 is at most $O\left(\frac{1}{\log n}\right)$.*

Proof. For the purposes of the proof, we assign to each birth in the clique a distinct label. Notice that, by Lemma 4, we will use at most $\log^7 n$ labels with probability at least $1 - O\left(\frac{1}{\log n}\right)$. If we end up using more than $\log^7 n$ labels (which happens with probability at most $O\left(\frac{1}{\log n}\right)$ by Lemma 4), then we stop the process and assume that we have reached one of the absorbing states. Furthermore, whenever a mutant v in the clique with label i replaces one of its neighbors with an offspring, then the label of v is inherited by its offspring.

In order for $\mathcal{M}_2$ to reach absorption at A_3, the clique must have n mutants. Since each of these vertices has a label $j \in [\log^7 n]$, there exists at least one label i such that at least $\frac{n}{\log^7 n}$ vertices have label i. Similarly, if $\mathcal{M}_2$ reaches absorption at A_4 and v is the corresponding affected ring vertex, then there exists a label i, such that v has label i. We will call a label i *winner* if there are at least $\frac{n}{\log^7 n}$ vertices in the clique that have label i, or the outer ring is affected by a clique vertex of label i. Clearly, if $\mathcal{M}_2$ reaches absorption at A_3 of A_4, there must be at least one winner.

Recall that, by Corollary 1, the probability that a single mutant in the clique either reaches $\frac{n}{\log^7 n}$ offspring or affects the outer ring is at most $\frac{7}{6n\left(\frac{4}{3r}-1\right)} + o\left(\frac{1}{n}\right)$. Consider now a particular label i. Then, if all the other mutants of the graph that do not have label i (i.e., mutants in the ring or in the clique with label $j \neq i$) had fitness 1, then the probability that i becomes a winner is by Corollary 1 at most $\frac{7}{6n\left(\frac{4}{3r}-1\right)} + o\left(\frac{1}{n}\right)$. The fact that the other mutants that do not have label i have fitness r can only reduce the probability that i becomes a winner. Therefore, considering all different labels $i \in [\log^7 n]$ and using Boole's inequality, we conclude that the probability of reaching absorption at A_3 or A_4 is at most

$$\log^7 n \left(\frac{7}{6n\left(\frac{4}{3r} - 1\right)} + o\left(\frac{1}{n}\right)\right) + O\left(\frac{1}{\log n}\right) = O\left(\frac{1}{\log n}\right),$$

where the term $O\left(\frac{1}{\log n}\right)$ in the left side corresponds to the probability that we have more than $\log^7 n$ labels. This completes the proof of the lemma. ■

Finally, the following theorem concerns the probability of absorption of $\mathcal{M}_2$.

Theorem 3 *For n large, given that we start with a single mutant on the ring, the probability that $\mathcal{M}_2$ is absorbed at A_1 is at most $(1 + o(1))\left(1 - \frac{1}{r}\right)$. Furthermore, the probability of absorption at A_2, A_3, or A_4 is at most $O\left(\frac{1}{\log n}\right)$.*

Proof. The bounds on the absorption at A_1 or A_2 follow from Lemma 3, while the bounds on absorption at A_3 or A_4 follow from Lemma 5. ■

Recall now that $\mathcal{M}_2$ (the modified Markov chain) dominates $\mathcal{M}_1$ (the original Markov chain). Furthermore, recall that the clique-wheel graph G_n has n clique vertices and n ring vertices, and thus the fixation probability of G_n is $f_{G_n} = \frac{1}{2}(h_{\text{clique}} + h_{\text{ring}})$. Therefore, the next theorem is implied by Theorem 3 and Lemma 1.

Theorem 4 *For the Markov chain $\mathcal{M}_1$, and any $r \in \left(1, \frac{4}{3}\right)$, $h_{\text{ring}} \leq (1+o(1))\left(1 - \frac{1}{r}\right)$. Therefore, as $n \to \infty$, the fixation probability of the clique-wheel graph G_n in Figure 2(a) is*

$$f_{G_n} \leq \frac{1}{2}\left(1 - \frac{1}{r}\right) + o(1).$$

The proof of Theorem 4 relies heavily on the bound $r < \frac{4}{3}$ for the fitness r. Unfortunately we could not extend our results to greater values of r; in particular it remains an open question whether the clique wheel graphs act asymptotically as suppressors of selection when $r \geq \frac{4}{3}$.

4 Analysis of the aggregation model

In this section, we provide analytic results on the new evolutionary model of mutual influences. More specifically, in Section 4.1 we prove that this model admits a *potential function* for arbitrary undirected graphs and arbitrary initial fitness vectors, which implies that the corresponding dynamical systems converge to a stable state. Furthermore, in Section 4.2 we prove fast convergence of the dynamical systems for the case of a complete graph, and we provide almost tight upper and lower bounds on the limit fitness to which the system converges.

4.1 Potential and convergence in general undirected graphs

In the following theorem we prove convergence of the new model of mutual influences using a potential function.

Theorem 5 *Let $G = (V, E)$ be a connected undirected graph. Let $r(0)$ be an initial fitness vector of G, and let $r_{\min}$ and $r_{\max}$ be the smallest and the greatest initial fitness in $r(0)$, respectively. Then, in the model of mutual influences, the fitness vector $r(k)$ converges to a vector $[r_0, r_0, \ldots, r_0]^T$ as $k \to \infty$, for some value $r_0 \in [r_{\min}, r_{\max}]$.*

Proof. Denote the vertices of G by $V = \{u_1, u_2, \ldots, u_n\}$. Let $k \geq 0$. Then (6) implies that for any $i = 1, 2, \ldots, n$, the element $r_{u_i}(k+1)$ of the vector $r(k+1)$ is

$$\begin{aligned} r_{u_i}(k+1) &= \frac{1}{\Sigma(k)} \sum_{u_j \in N(u_i)} \frac{r_{u_j}(k)}{\deg(u_j)} \cdot r_{u_j}(k) + \left(1 - \frac{1}{\Sigma(k)} \sum_{u_j \in N(u_i)} \frac{r_{u_j}(k)}{\deg(u_j)}\right) \cdot r_{u_i}(k) \\ &= r_{u_i}(k) + \frac{1}{\Sigma(k)} \sum_{u_j \in N(u_i)} r_{u_j}(k) \cdot \frac{r_{u_j}(k) - r_{u_i}(k)}{\deg(u_j)}, \end{aligned}$$

and thus

$$\frac{r_{u_i}(k+1)}{\deg(u_i)} = \frac{r_{u_i}(k)}{\deg(u_i)} + \frac{1}{\Sigma(k)} \sum_{u_j \in N(u_i)} r_{u_j}(k) \cdot \frac{r_{u_j}(k) - r_{u_i}(k)}{\deg(u_i)\deg(u_j)}. \tag{17}$$

Therefore, by summing up the equations in (17) for every $i = 1, 2, \ldots, n$ it follows that

$$\begin{aligned} \sum_{u_i \in V} \frac{r_{u_i}(k+1)}{\deg(u_i)} &= \sum_{u_i \in V} \frac{r_{u_i}(k)}{\deg(u_i)} + \frac{1}{\Sigma(k)} \sum_{u_i u_j \in E} \frac{(r_{u_j}(k) - r_{u_i}(k))^2}{\deg(u_i)\deg(u_j)} \\ &\geq \sum_{u_i \in V} \frac{r_{u_i}(k)}{\deg(u_i)}. \end{aligned} \tag{18}$$

Define now the potential function $\phi(k) = \sum_{u_i \in V} \frac{r_{u_i}(k)}{\deg(u_i)}$ for every iteration $k \geq 0$ of the process. Note by Observation 2 that $\Sigma(k) = \sum_{u_i \in V} r_{u_i}(k) \leq n r_{\max}$ is a trivial upper bound for $\Sigma(k)$. Therefore, (18) implies that

$$\begin{aligned} \phi(k+1) - \phi(k) &= \frac{1}{\Sigma(k)} \sum_{u_i u_j \in E} \frac{(r_{u_j}(k) - r_{u_i}(k))^2}{\deg(u_i)\deg(u_j)} \\ &\geq \frac{1}{n r_{\max}} \sum_{u_i u_j \in E} \frac{(r_{u_j}(k) - r_{u_i}(k))^2}{\deg(u_i)\deg(u_j)} > \frac{1}{n^3 r_{\max}} \sum_{u_i u_j \in E} (r_{u_j}(k) - r_{u_i}(k))^2. \end{aligned} \tag{19}$$

Furthermore, note that $r_{\max} \cdot \sum_{u_i \in V} \frac{1}{\deg(u_i)} < n r_{\max}$ is a trivial upper bound for $\phi(k)$. Therefore, since $\phi(k+1) \geq \phi(k)$ for every $k \geq 0$ by (18), it follows that $\phi(k)$ converges to some value ϕ_0 as $k \to \infty$, where $\phi(0) \leq \phi_0 \leq n r_{\max}$. Consider now an arbitrary $\varepsilon > 0$ and let $\varepsilon' = \frac{\varepsilon^2}{n^3 r_{\max}}$. Then, since $\phi(k) \underset{k \to \infty}{\longrightarrow} \phi_0$, there exists $k_0 \in \mathbb{N}$, such that $|\phi(k+1) - \phi(k)| < \varepsilon'$ for every $k \geq k_0$. Therefore, (19) implies that for every edge $u_i u_j \in E$ of G and for every $k \geq k_0$,

$$\begin{aligned} (r_{u_j}(k) - r_{u_i}(k))^2 &\leq \sum_{u_p u_q \in E} (r_{u_p}(k) - r_{u_q}(k))^2 \\ &\leq n^3 r_{\max} \cdot |\phi(k+1) - \phi(k)| \leq n^3 r_{\max} \cdot \varepsilon' = \varepsilon^2. \end{aligned}$$

Thus, for every $\varepsilon > 0$, there exists $k_0 \in \mathbb{N}$, such that $|r_{u_j}(k) - r_{u_i}(k)| < \varepsilon$ for every $k \geq k_0$ and for every edge $u_i u_j \in E$ of G. Therefore, since G is assumed to be connected, all values $r_u(k)$, where $u \in V$, converge to the same value r_0 as $k \to \infty$. Furthermore, since $r_u(k) \in [r_{\min}, r_{\max}]$ by Observation 2, it follows that $r_0 \in [r_{\min}, r_{\max}]$ as well. This completes the proof of the theorem. ■

4.2 Analysis of the complete graph

The next theorem provides an analysis for the limit fitness value r_0 and the convergence time to this value, in the case of a complete graph (i.e., a homogeneous population).

Theorem 6 *Let $G = (V, E)$ be the complete graph with n vertices and $\varepsilon > 0$. Let $\alpha \in [0, 1]$ be the proportion of initially introduced mutants with relative fitness $r \geq 1$ in G, and let r_0 be the limit fitness of G. Then $|r_u(k) - r_v(k)| < \varepsilon$ for every $u, v \in V$, when*

$$k \geq (n-2) \cdot \ln\left(\frac{r-1}{\varepsilon}\right).$$

Furthermore, for the limit fitness r_0,

$$r_0 \leq 1 + \alpha(r-1) + \frac{\alpha(1-\alpha)}{1+\alpha(r-1)} \cdot \frac{(r-1)^2}{2} \tag{20}$$

and

$$\begin{aligned} r_0 &\geq \frac{1 + \alpha(r-1) + \sqrt{(1+\alpha(r-1))^2 + 2\alpha(1-\alpha)(r-1)^2}}{2} \\ &\geq 1 + \alpha(r-1). \end{aligned} \tag{21}$$

Proof. Since G is symmetric, we do not distinguish among the different placements $S \subseteq V$ of the αn initially introduced mutants. Furthermore, at every iteration $k \geq 0$, there exist by symmetry two different fitnesses $r_1(k)$ and $r_2(k)$ for the vertices of S and of $V \setminus S$, respectively. Thus, it suffices to compute only $r_1(k)$ and $r_2(k)$ for every $k \geq 0$. Let $\Delta(k) = r_1(k) - r_2(k)$. Then, $\Delta(0) = r - 1$. It follows now by (4) and (7) that for every $k \geq 0$

$$\begin{aligned} r_1(k+1) &= \left(1 - \frac{(1-\alpha)nr_2(k)}{(n-1)\Sigma(k)}\right) \cdot r_1(k) + \frac{(1-\alpha)nr_2(k)}{(n-1)\Sigma(k)} \cdot r_2(k) \\ &= r_1(k) - \Delta(k)\frac{(1-\alpha)nr_2(k)}{(n-1)\Sigma(k)}. \end{aligned} \tag{22}$$

Similarly,

$$\begin{aligned} r_2(k+1) &= \frac{\alpha n r_1(k)}{(n-1)\Sigma(k)} \cdot r_1(k) + \left(1 - \frac{\alpha n r_1(k)}{(n-1)\Sigma(k)}\right) \cdot r_2(k) \\ &= r_2(k) + \Delta(k)\frac{\alpha n r_1(k)}{(n-1)\Sigma(k)}, \end{aligned} \tag{23}$$

where $\Sigma(k) = \alpha n r_1(k) + (1-\alpha)nr_2(k)$. Subtracting now (23) from (22), it follows that

$$\begin{aligned} \Delta(k+1) &= \Delta(k) - \Delta(k) \cdot \frac{\Sigma(k)}{(n-1) \cdot \Sigma(k)} \\ &= \Delta(k)\frac{n-2}{n-1}, \end{aligned}$$

and thus, since $\Delta(0) = r - 1$, it follows that for every $k \geq 0$

$$\Delta(k) = (r-1) \cdot \left(\frac{n-2}{n-1}\right)^k. \tag{24}$$

Therefore, in particular, $\Delta(k) > 0$ for every $k \geq 0$ if and only if $r > 1$. Let now $\varepsilon > 0$ be arbitrary. Then $|\Delta(k)| \leq \varepsilon$ if and only if

$$\begin{aligned} \left(\frac{n-2}{n-1}\right)^k &\leq \frac{\varepsilon}{r-1} \Leftrightarrow \\ \left(1 + \frac{1}{n-2}\right)^k &\geq \frac{r-1}{\varepsilon}. \end{aligned} \tag{25}$$

However, $\left(1 + \frac{1}{n-2}\right)^{n-2} \to e$ as $n \to \infty$. Thus, for sufficiently large n, (25) is satisfied when $e^{\frac{k}{n-2}} \geq \frac{r-1}{\varepsilon}$, or equivalently when

$$k \geq (n-2) \cdot \ln\left(\frac{r-1}{\varepsilon}\right). \tag{26}$$

Recall by Theorem 5 that $r_1(k) \to r_0$ and $r_2(k) \to r_0$ for some value r_0, as $k \to \infty$, and thus also $\alpha r_1(k) + (1-\alpha)r_2(k) \to r_0$ as $k \to \infty$. Furthermore, it follows by (22) and (23) that

$$\alpha r_1(k+1) + (1-\alpha)r_2(k+1) = \alpha r_1(k) + (1-\alpha)r_2(k) + \frac{\alpha(1-\alpha)}{(\alpha r_1(k) + (1-\alpha)r_2(k))} \cdot \frac{\Delta^2(k)}{n-1}. \tag{27}$$

That is, $\alpha r_1(k) + (1-\alpha)r_2(k)$ is a non-decreasing function of k, and thus $\alpha r_1(k) + (1-\alpha)r_2(k) \geq \alpha r + (1-\alpha)$. Therefore, for every $k \geq 0$,

$$\alpha r_1(k) + (1-\alpha)r_2(k) \leq 1 + \alpha(r-1) + \frac{\alpha(1-\alpha)}{1+\alpha(r-1)} \cdot \frac{1}{n-1}\sum_{k=0}^{\infty} \Delta^2(k). \tag{28}$$

The sum $\sum_{k=0}^{\infty} \Delta^2(k)$ can be computed by (24) as

$$\sum_{k=0}^{\infty} \Delta^2(k) = (r-1)^2 \cdot \frac{1}{1 - \left(\frac{n-2}{n-1}\right)^2} = (r-1)^2 \frac{(n-1)^2}{2n-3}. \tag{29}$$

Substituting now (29) into (28), it follows that

$$\alpha r_1(k) + (1-\alpha)r_2(k) \leq 1 + \alpha(r-1) + \frac{\alpha(1-\alpha)}{1+\alpha(r-1)} \cdot (r-1)^2 \frac{n-1}{2n-3}. \tag{30}$$

Therefore, since $\frac{n-1}{2n-3} \to \frac{1}{2}$ as $n \to \infty$, and since $\alpha r_1(k) + (1-\alpha)r_2(k) \to r_0$ as $k \to \infty$, it follows by (30) that for sufficiently large n and k,

$$r_0 \leq 1 + \alpha(r-1) + \frac{\alpha(1-\alpha)}{1+\alpha(r-1)} \cdot \frac{(r-1)^2}{2}. \tag{31}$$

Recall by (27) that $\alpha r_1(k) + (1-\alpha)r_2(k)$ is non-decreasing on k, and thus $\alpha r_1(k) + (1-\alpha)r_2(k) \leq r_0$. Therefore, it follows by (27) and (29) that for every $k \geq 0$,

$$\alpha r_1(k) + (1-\alpha)r_2(k) \geq 1 + \alpha(r-1) + \frac{\alpha(1-\alpha)}{r_0} \cdot (r-1)^2 \frac{n-1}{2n-3}.$$

Thus, since $\frac{n-1}{2n-3} \to \frac{1}{2}$ as $n \to \infty$ and $\alpha r_1(k) + (1-\alpha)r_2(k) \to r_0$ as $k \to \infty$, it follows similarly to the above that for sufficiently large n and k,

$$r_0 \geq 1 + \alpha(r-1) + \frac{\alpha(1-\alpha)}{r_0} \cdot \frac{(r-1)^2}{2},$$

and thus

$$r_0^2 - r_0(1+\alpha(r-1)) - \frac{\alpha(1-\alpha)(r-1)^2}{2} \geq 0. \tag{32}$$

Therefore, since $r_0 > 0$, it follows by solving the trinomial in (32) that

$$r_0 \geq \frac{1+\alpha(r-1)+\sqrt{(1+\alpha(r-1))^2 + 2\alpha(1-\alpha)(r-1)^2}}{2}. \tag{33}$$

The statement of the theorem follows now by (26), (31), and (33). ■

The next corollary follows from Theorem 6.

Corollary 2 *Let $G = (V, E)$ be the complete graph with n vertices. Suppose that initially* exactly one *mutant with relative fitness $r \geq 1$ is placed in G and let r_0 be the limit fitness of G. Then $1 + \frac{r-1}{n} \leq r_0 \leq 1 + \frac{r^2-1}{2n}$.*

Proof. Since we have initially one mutant, it follows that $\alpha = \frac{1}{n}$. Then, substituting this value of α in (21), we obtain the lower bound $r_0 \geq 1 + \frac{r-1}{n}$. For the upper bound of r_0, it follows by substituting α in (20) that

$$\begin{aligned} r_0 &\leq 1 + \frac{r-1}{n} + \frac{\frac{1}{n}\frac{n-1}{n}}{\frac{r}{n} + \left(1 - \frac{1}{n}\right)} \cdot \frac{(r-1)^2}{2} \\ &= 1 + \frac{r-1}{n}\left(1 + \frac{n-1}{r+(n-1)} \cdot \frac{r-1}{2}\right) \\ &\leq 1 + \frac{r-1}{n}\left(1 + \frac{r-1}{2}\right) \\ &= 1 + \frac{r^2-1}{2n}. \end{aligned}$$

This completes the proof of the corollary. ■

5 Invasion control mechanisms

As stated in the introduction of this paper, our new evolutionary model of mutual influences can be used to model control mechanisms over invading populations in networks. We demonstrate this by presenting two alternative scenarios in Sections 5.1 and 5.2. In both considered scenarios, we assume that αn individuals of relative fitness r (the rest being of fitness 1) are introduced in the complete graph with n vertices. Then, as the process evolves, we periodically choose a small fraction $\beta \in [0, 1]$ of individuals in the current population and we reduce their current fitnesses to a value that is considered to correspond to the healthy state of the system (without loss of generality, this value in our setting is 1). In the remainder of this section, we call these modified individuals "stabilizers", as they help the population to resist the invasion of the mutants.

5.1 Control of invasion in phases

In the first scenario of controlling the invasion of advantageous mutants in networks, we insert stabilizers to the population in phases, as follows. In each phase $k \geq 1$, we let the process evolve until all fitnesses $\{r_v \mid v \in V\}$ become ε-relatively-close to their fixed point $r_0^{(k)}$ (i.e., until they ε-*approximate* $r_0^{(k)}$). That is, until $\frac{|r_v - r_0^{(k)}|}{r_0^{(k)}} < \varepsilon$ for every $v \in V$. Note by Theorem 5 that, at every phase, the fitness values always ε-approximate such a limit fitness $r_0^{(k)}$. After the end of each phase, we introduce βn stabilizers, where $\beta \in [0, 1]$. That is, we replace βn vertices (arbitrarily chosen) by individuals of fitness 1, i.e., by resident individuals. Clearly, the more the number of phases, the closer the fixed point at the end of each phase will be to 1. In the following theorem we bound the number of phases needed until the system stabilizes, i.e., until the fitness of *every* vertex becomes sufficiently close to 1.

Theorem 7 *Let $G = (V, E)$ be the complete graph with n vertices. Let $\alpha \in [0, 1]$ be the proportion of initially introduced mutants with relative fitness $r \geq 1$ in G and let $\beta \in [0, 1]$ be the proportion of the stabilizers introduced at every phase. Let $r_0^{(k)}$ be the limit fitness after phase k and let $\varepsilon, \delta > 0$, be such that $\frac{\beta}{2} > \sqrt{\varepsilon}$ and $\delta > \frac{4}{3}\sqrt{\varepsilon}$. Finally, let each phase k run until the fitnesses ε-approximate their fixed point $r_0^{(k)}$. Then, after*

$$1 - \frac{\ln\left(\varepsilon + (1+\varepsilon)\frac{1+\alpha}{2}(r-1)\right) - \ln\left(\delta - \frac{4}{3}\sqrt{\varepsilon}\right)}{\ln(1+\varepsilon) + \ln\left(1 - \frac{\beta}{2}\right)}$$

phases, the relative fitness of every *vertex $u \in V$ is at most $1 + \delta$.*

Proof. Consider the first phase, where initially there exist αn mutants with relative fitness r and $(1-\alpha)n$ resident individuals with fitness 1 each. Then, since $r \geq 1$, it follows by (20) for the fixed point $r_0^{(1)}$ after the first phase that

$$\begin{aligned}
r_0^{(1)} &\leq 1 + \alpha(r-1) \cdot \left(1 + \frac{(1-\alpha)(r-1)}{2(1+\alpha(r-1))}\right) \\
&= 1 + \frac{\alpha(r-1)}{2} \cdot \left(1 + \frac{1+(r-1)}{1+\alpha(r-1)}\right) \\
&\leq 1 + \frac{\alpha(r-1)}{2} \cdot \left(1 + \frac{1}{\alpha}\right),
\end{aligned}$$

i.e.,

$$r_0^{(1)} \leq 1 + \frac{1+\alpha}{2}(r-1). \tag{34}$$

Suppose that we let each phase $k \geq 1$ run until the fitnesses ε-approximate their fixed point $r_0^{(k)}$. Note that, at the start of the process, $(1-\alpha)n$ vertices have fitness 1 and αn vertices have fitness r. Similarly, before the kth phase starts, βn vertices have fitness 1 and $(1-\beta)n$ vertices have fitness at most $(1+\varepsilon)r_0^{(k-1)}$. Then, we obtain similarly to (34) that the fixed point $r_0^{(k)}$ at iteration k is in the worst case

$$\begin{aligned}
r_0^{(k)} &\leq 1 + \frac{1+(1-\beta)}{2}\left((1+\varepsilon)r_0^{(k-1)} - 1\right) \\
&= 1 + \left(1 - \frac{\beta}{2}\right)\left((1+\varepsilon)r_0^{(k-1)} - 1\right).
\end{aligned}$$

Therefore

$$(1+\varepsilon)r_0^{(k)} \leq (1+\varepsilon) + (1+\varepsilon)\left(1 - \frac{\beta}{2}\right)\left((1+\varepsilon)r_0^{(k-1)} - 1\right),$$

and thus

$$(1+\varepsilon)r_0^{(k)} - 1 \leq \varepsilon + (1+\varepsilon)\left(1 - \frac{\beta}{2}\right)\left((1+\varepsilon)r_0^{(k-1)} - 1\right).$$

Let now $\lambda = (1+\varepsilon)\left(1 - \frac{\beta}{2}\right)$. Then the last inequality becomes

$$(1+\varepsilon)r_0^{(k)} - 1 \leq \varepsilon + \lambda\left((1+\varepsilon)r_0^{(k-1)} - 1\right)$$

and by induction we have

$$\begin{aligned}(1+\varepsilon)r_0^{(k)}-1 &\leq \varepsilon\sum_{i=0}^{k-2}\lambda^i+\lambda^{k-1}\left((1+\varepsilon)r_0^{(1)}-1\right)\\ &= \varepsilon\frac{1-\lambda^{k-1}}{1-\lambda}+\lambda^{k-1}\left((1+\varepsilon)r_0^{(1)}-1\right).\end{aligned}$$

Therefore, (34) implies that

$$(1+\varepsilon)r_0^{(k)}-1\leq\varepsilon\frac{1-\lambda^{k-1}}{1-\lambda}+\lambda^{k-1}\left(\varepsilon+(1+\varepsilon)\frac{1+\alpha}{2}(r-1)\right). \tag{35}$$

At the end of the kth phase, the relative fitness of each vertex is at most $(1+\varepsilon)r_0^{(k)}$. Now, in order to compute at least how many phases are needed to reach a relative fitness $(1+\varepsilon)r_0^{(k)}\leq 1+\delta$ for every vertex $u\in V$, it suffices by (35) to compute the smallest value of k, such that

$$\varepsilon\frac{1-\lambda^{k-1}}{1-\lambda}+\lambda^{k-1}\left(\varepsilon+(1+\varepsilon)\frac{1+\alpha}{2}(r-1)\right)\leq\delta. \tag{36}$$

Recall now that $\sqrt{\varepsilon}<\frac{\beta}{2}\leq\frac{1}{2}$ by assumption. Therefore $\lambda=(1+\varepsilon)\left(1-\frac{\beta}{2}\right)<(1+\varepsilon)(1-\sqrt{\varepsilon})$, i.e., $\lambda<1$. Thus $1-\lambda^{k-1}<1$ and it suffices from (36) to compute the smallest number k for which

$$\frac{\varepsilon}{1-\lambda}+\lambda^{k-1}\left(\varepsilon+(1+\varepsilon)\frac{1+\alpha}{2}(r-1)\right)\leq\delta. \tag{37}$$

Note now that

$$\begin{aligned}\frac{\varepsilon}{1-\lambda} &= \frac{\varepsilon}{1-(1+\varepsilon)\left(1-\frac{\beta}{2}\right)}\\ &= \frac{\varepsilon}{\frac{\beta}{2}(1+\varepsilon)-\varepsilon}.\end{aligned}$$

Thus, since $\frac{\beta}{2}>\sqrt{\varepsilon}$ by assumption, it follows that

$$\frac{\varepsilon}{1-\lambda}<\frac{\varepsilon}{\sqrt{\varepsilon}(1+\varepsilon)-\varepsilon}=\frac{\sqrt{\varepsilon}}{1+\varepsilon-\sqrt{\varepsilon}}. \tag{38}$$

However $1+\varepsilon-\sqrt{\varepsilon}\geq\frac{3}{4}$ for every $\varepsilon\in(0,1)$, and thus it follows by (38) that $\frac{\varepsilon}{1-\lambda}<\frac{4}{3}\sqrt{\varepsilon}$. Therefore it suffices from (37) to compute the smallest number k for which

$$\frac{4}{3}\sqrt{\varepsilon}+\lambda^{k-1}\left(\varepsilon+(1+\varepsilon)\frac{1+\alpha}{2}(r-1)\right)\leq\delta.$$

That is,

$$\lambda^{k-1}\leq\frac{\delta-\frac{4}{3}\sqrt{\varepsilon}}{\varepsilon+(1+\varepsilon)\frac{1+\alpha}{2}(r-1)},$$

or equivalently

$$k\geq 1-\frac{\ln\left(\varepsilon+(1+\varepsilon)\frac{1+\alpha}{2}(r-1)\right)-\ln\left(\delta-\frac{4}{3}\sqrt{\varepsilon}\right)}{\ln(1+\varepsilon)+\ln\left(1-\frac{\beta}{2}\right)}.$$

This completes the proof of the theorem. ■

5.2 Continuous control of invasion

In this section we present another variation of controlling the invasion of advantageous mutants, using our new evolutionary model. In this variation, we do not proceed in phases; we rather introduce *at every single iteration* of the process βn stabilizers, where $\beta\in[0,1]$ is a small proportion of the individuals of the population. In the remainder of this section, we assume that at every iteration the βn stabilizers with relative fitness 1 are the same. This assumption provides a worst case bound on the number of iterations needed to get every vertex to fitness at most $1+\delta$. This is because, at each iteration, we select the βn vertices with the smallest fitness and reset their fitness to 1. Since that is the smallest possible change we could make to βn vertices, it takes the longest possible time to reach the fixed point. Note that being able to choose βn non-mutants to reset to fitness 1 means we are only analysing cases where $\alpha + \beta \leq 1$; note however that this is still the interesting case, since this way we investigate how a small number of βn stabilizers (i.e., for a small constant β) impacts on the stabilization process.

Theorem 8 *Let $G = (V, E)$ be the complete graph with n vertices. Let $\alpha \in [0, 1]$ be the proportion of initially introduced mutants with relative fitness $r \geq 1$ in G and let $\beta \in [0, 1]$ be the proportion of the stabilizers introduced at every iteration. Then, for every $\delta > 0$, after*

$$k \geq \left(\frac{r}{\beta}(n-1) - 1\right) \cdot \ln\left(\frac{r-1}{\delta}\right).$$

iterations, the relative fitness of every *vertex $u \in V$ is at most $1 + \delta$.*

Proof. Recall that we assumed for simplicity reasons that at every iteration the βn individuals with relative fitness 1 are the same. Note furthermore that at very iteration k we have by symmetry three different fitnesses on the vertices: (a) the αn initial mutants with fitness $r_1(k)$, (b) the βn stabilizers with fitness 1, and (c) the rest $(1 - \alpha - \beta)n$ individuals with fitness $r_2(k)$, where $1 \leq r_2(k) \leq r_1(k)$ by Observation 2. Note that $r_2(0) = 1$. Let $\gamma = 1 - \alpha - \beta$. Then, we obtain similarly to (22) and (23) in the proof of Theorem 6 that for every $k \geq 0$

$$\begin{aligned} r_1(k+1) &= \left(1 - \frac{(\gamma r_2(k) + \beta)n}{(n-1)\Sigma(k)}\right) \cdot r_1(k) + \frac{\gamma r_2(k) n}{(n-1)\Sigma(k)} \cdot r_2(k) + \frac{\beta n}{(n-1)\Sigma(k)} \\ &= r_1(k) - \frac{1}{(n-1)\Sigma(k)} \left(\gamma n r_2(k)(r_1(k) - r_2(k)) + \beta n(r_1(k) - 1)\right) \end{aligned} \tag{39}$$

and

$$\begin{aligned} r_2(k+1) &= \frac{\alpha r_1(k) n}{(n-1)\Sigma(k)} \cdot r_1(k) + \left(1 - \frac{(\alpha r_1(k) + \beta)n}{(n-1)\Sigma(k)}\right) \cdot r_2(k) + \frac{\beta n}{(n-1)\Sigma(k)} \\ &= r_2(k) + \frac{1}{(n-1)\Sigma(k)} \left(\alpha n r_1(k)(r_1(k) - r_2(k)) - \beta n(r_2(k) - 1)\right), \end{aligned} \tag{40}$$

where $\Sigma(k) = n(\alpha r_1(k) + \gamma r_2(k) + \beta)$. It follows now by (39) and (40) that

$$\begin{aligned} r_1(k+1) - r_2(k+1) &= r_1(k) - r_2(k) \\ &\quad - \frac{(\alpha n r_1(k) + \gamma n r_2(k))(r_1(k) - r_2(k)) + \beta n(r_1(k) - r_2(k))}{(n-1)\Sigma(k)} \\ &= r_1(k) - r_2(k) - \frac{\Sigma(k)(r_1(k) - r_2(k))}{(n-1)\Sigma(k)}, \end{aligned}$$

and thus

$$r_1(k+1) - r_2(k+1) = \frac{n-2}{n-1}(r_1(k) - r_2(k)).$$

Therefore, since $r_2(0) = 1$ and $r_1(0) = r \geq 1$, it follows that for every $k \geq 0$,

$$r_1(k) - r_2(k) = (r-1) \cdot \left(\frac{n-2}{n-1}\right)^k. \tag{41}$$

By substitution of (41) into (39) it follows that

$$r_1(k+1) = r_1(k) - \frac{n}{(n-1)\Sigma(k)} \left(\gamma r_2(k)(r-1)\left(\frac{n-2}{n-1}\right)^k + \beta(r_1(k) - 1)\right). \tag{42}$$

Define now $\Delta(k) = r_1(k) - 1$. Then, it follows by (42) that

$$\begin{aligned} \Delta(k+1) &= \Delta(k) \cdot \left(1 - \frac{\beta n}{(n-1)\Sigma(k)}\right) - \frac{\gamma n r_2(k)}{(n-1)\Sigma(k)}(r-1)\left(\frac{n-2}{n-1}\right)^k \\ &< \Delta(k) \cdot \left(1 - \frac{\beta n}{(n-1)\Sigma(k)}\right). \end{aligned} \tag{43}$$

Note now that $\frac{\beta n}{\Sigma(k)} \geq \frac{\beta}{r}$, and thus (43) implies that

$$\Delta(k+1) \leq \Delta(k) \cdot \left(1 - \frac{\beta}{r(n-1)}\right). \tag{44}$$

Denote now for the purposes of the proof $\lambda = 1 - \frac{\beta}{r(n-1)} = \frac{n-1-\frac{\beta}{r}}{n-1}$. Then, it follows by the system of inequalities in (44) that for every $k \geq 0$

$$\begin{aligned} \Delta(k) &\leq \Delta(0) \cdot \lambda^k \\ &= (r-1) \cdot \lambda^k. \end{aligned} \tag{45}$$

In order to compute at least how many iterations are needed such that $r_1(k) \leq 1+\delta$, i.e., $\Delta(k) \leq \delta$, it suffices by (45) to compute the smallest value of k, such that

$$(r-1) \cdot \lambda^k \leq \delta,$$

i.e.,

$$\begin{aligned} \frac{1}{\lambda^k} = \left(\frac{n-1}{n-1-\frac{\beta}{r}}\right)^k &\geq \frac{r-1}{\delta} \Leftrightarrow \\ \left(1 + \frac{1}{\frac{r}{\beta}(n-1)-1}\right)^k &\geq \frac{r-1}{\delta}. \end{aligned} \tag{46}$$

However, $\left(1 + \frac{1}{\frac{r}{\beta}(n-1)-1}\right)^{\frac{r}{\beta}(n-1)-1} \leq e$ for every $n \geq 1$. Thus (46) is satisfied when

$$e^{\frac{k}{\frac{r}{\beta}(n-1)-1}} \geq \frac{r-1}{\delta},$$

or equivalently when

$$k \geq \left(\frac{r}{\beta}(n-1) - 1\right) \cdot \ln\left(\frac{r-1}{\delta}\right).$$

This completes the proof of the theorem. ■

Observation 3 *The bound in Theorem 8 of the number of iterations needed to achieve everywhere a sufficiently small relative fitness is independent of the proportion $\alpha \in [0,1]$ of initially placed mutants in the graph. Instead, it depends only on the initial relative fitness r of the mutants and on the proportion $\beta \in [0,1]$ of the vertices, to which we introduce the stabilizers. Note that the independence of this bound from α comes from the fact that all terms involving α (via γ and $\Sigma(k)$) were lost between equations (43) and (44) by discarding the substracted term and using $\frac{\beta n}{\Sigma(k)} \geq \frac{\beta}{r}$. As such, the independence from α is a consequence of our analysis and not a fundamental property of the system.*

6 Concluding remarks

In this paper we investigated alternative models for evolutionary dynamics on graphs. In particular, we first considered the evolutionary model proposed in [19], where vertices of the graph correspond to individuals of the population. We provided in this model generic upper and lower bounds for the fixation probability on a general graph G and we presented the first class of undirected graphs (called clique-wheels) that act as suppressors of selection when $1 < r < \frac{4}{3}$. Specifically, we proved that the fixation probability of the clique-wheel graphs is at most one half of the fixation probability of the complete graph (i.e., the homogeneous population) as the number of vertices increases. An interesting open question in this model is whether there exist functions $f_1(r) > 0$ and $f_2(r) < 1$ (independent of the size of the input graph), such that the fixation probability of every undirected graph G with at least two vertices lies between $f_1(r)$ and $f_2(r)$. Another line of future research is to investigate the behavior of the model of [19] in the case where there are more than two types of individuals (*aggressive* vs. *non-aggressive*) in the graph.

As our main contribution, we introduced in this paper a new evolutionary model based on mutual influences between individuals. In contrast to the model presented in [19], in this new model all individuals interact *simultaneously* and the result is a compromise between aggressive and non-aggressive individuals. In other words, the behavior of the individuals in our new model and in the model of [19] can be interpreted as an “aggregation” vs. an “all-or-nothing” strategy, respectively. We prove that our new evolutionary model admits a potential function, which guarantees the convergence of the system for any graph topology and any initial fitnesses on the vertices of the underlying graph. Furthermore, we provide almost tight bounds on the limit fitness for the case of a complete graph, as well as a bound on the number of steps needed to approximate the stable state. Finally, our new model appears to be useful also in the abstract modeling of new control mechanisms over invading populations in networks. As an example, we demonstrated its usefulness by analyzing the behavior of two alternative control approaches. Many interesting open questions lie ahead in our new model. For instance, what is the speed of convergence and what is the limit fitness in arbitrary undirected graphs? What happens if many types of individuals simultaneously interact at every iteration?

Acknowledgment. Paul G. Spirakis wishes to thank Josep Díaz, Leslie Ann Goldberg, and Maria Serna, for many inspiring discussions on the model of [19].

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