Strong Bounds for Evolution in Networks*

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Abstract. This work extends what is known so far for a basic model of evolutionary antagonism in undirected networks (graphs). More specifically, this work studies the generalized Moran process, as introduced by Lieberman, Hauert, and Nowak [Nature, 433:312-316, 2005], where the individuals of a population reside on the vertices of an undirected connected graph. The initial population has a single *mutant* of a *fitness* value r (typically $r > 1$), residing at some vertex v of the graph, while every other vertex is initially occupied by an individual of fitness 1. At every step of this process, an individual (i.e. vertex) is randomly chosen for reproduction with probability proportional to its fitness, and then it places a copy of itself on a random neighbor, thus replacing the individual that was residing there. The main quantity of interest is the *fixation probability*, i.e. the probability that eventually the whole graph is occupied by descendants of the mutant. In this work we concentrate on the fixation probability when the mutant is initially on a specific vertex v, thus refining the older notion of Lieberman et al. which studied the fixation probability when the initial mutant is placed at a random vertex. We then aim at finding graphs that have many "strong starts" (or many "weak starts") for the mutant. Thus we introduce a parameterized notion of *selective amplifiers* (resp. *selective suppressors*) of evolution. We prove the existence of *strong* selective amplifiers (i.e. for $h(n) = \Theta(n)$ vertices v the fixation probability of v is at least $1 - \frac{c(r)}{n}$ for a function $c(r)$ that depends only on r), and the existence of quite strong selective suppressors. Regarding the traditional notion of fixation probability from a random start, we provide strong upper and lower bounds: first we demonstrate the non-existence of "strong universal" amplifiers, and second we prove the *Thermal Theorem* which states that for any undirected graph, when the mutant starts at vertex v, the fixation probability at least $(r-1)/(r+\frac{\deg v}{\deg_{\min}})$. This theorem (which extends the "Isothermal Theorem" of Lieberman et al. for regular graphs) implies an almost tight lower bound for the usual notion of fixation probability. Our proof techniques are original and are based on new domination arguments which may be of general interest in Markov Processes that are of the general birth-death type.

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*This work was partially supported by (i) the FET EU IP Project MULTIPLEX (Contract no 317532), (ii) the ERC EU Grant ALGAME (Agreement no 321171), and (iii) the EPSRC Grant EP/G043434/1. The full version of this paper is available at http://arxiv.org/abs/1211.2384

1 Introduction

Population and evolutionary dynamics have been extensively studied [2, 6, 7, 15, 21, 24, 25], mainly on the assumption that the evolving population is homogeneous, i.e. it has no spatial structure. One of the main models in this area is the Moran Process [19], where the initial population contains a single *mutant* with fitness $r > 0$, with all other individuals having fitness 1. At every step of this process, an individual is chosen for reproduction with probability proportional to its fitness. This individual then replaces a second individual, which is chosen uniformly at random, with a copy of itself. Such dynamics as the above have been extensively studied also in the context of strategic interaction in evolutionary game theory [11–14, 23].

In a recent article, Lieberman, Hauert, and Nowak [16] (see also [20]) introduced a generalization of the Moran process, where the individuals of the population are placed on the vertices of a connected graph (which is, in general, directed) such that the edges of the graph determine competitive interaction. In the generalized Moran process, the initial population again consists of a single mutant of fitness r, placed on a vertex that is chosen uniformly at random, with each other vertex occupied by a non-mutant of fitness 1. An individual is chosen for reproduction exactly as in the standard Moran process, but now the second individual to be replaced is chosen among its neighbors in the graph uniformly at random (or according to some weights of the edges) [16, 20]. If the underlying graph is the complete graph, then this process becomes the standard Moran process on a homogeneous population [16, 20]. Several similar models describing infections and particle interactions have been also studied in the past, including the SIR and SIS epidemics [10, Chapter 21], the voter and antivoter models and the exclusion process [1, 9, 17]. However such models do not consider the issue of different fitness of the individuals.

The central question that emerges in the generalized Moran process is how the population structure affects evolutionary dynamics [16, 20]. In the present work we consider the generalized Moran process on arbitrary finite, undirected, and connected graphs. On such graphs, the generalized Moran process terminates almost surely, reaching either *fixation* of the graph (all vertices are occupied by copies of the mutant) or *extinction* of the mutants (no copy of the mutant remains). The *fixation probability* of a graph G for a mutant of fitness r, is the probability that eventually fixation is reached when the mutant is initially placed at a random vertex of G, and is denoted by $f_r(G)$. The fixation probability can, in principle, be determined using standard Markov Chain techniques. But doing so for a general graph on n vertices requires solving a linear system of 2^n linear equations. Such a task is not computationally feasible, even numerically. As a result of this, most previous work on computing fixation probabilities in the generalized Moran process was either restricted to graphs of small size [6] or to graph classes which have a high degree of symmetry, reducing thus the size of the corresponding linear system (e.g. paths, cycles, stars, and cliques [3–5]). Experimental results on the fixation probability of random graphs derived from grids can be found in [22].

A recent result [8] shows how to construct fully polynomial randomized approximation schemes (FPRAS) for the probability of reaching fixation (when $r \geq 1$) or extinction (for all $r > 0$). The result of [8] uses a Monte Carlo estimator, i.e. it runs the generalized Moran process several times[4], while each run terminates in polynomial time with high probability [8]. Note that improved lower and upper bounds on the fixation probability immediately lead to a better estimator here. Until now, the only known general bounds for the fixation probability on connected undirected graphs, are that $f_r(G) \geq \frac{1}{n}$ and $f_r(G) \leq 1 - \frac{1}{n+r}$.

Lieberman et al. [16, 20] proved the *Isothermal Theorem*, stating that (in the case of undirected graphs) the fixation probability of a regular graph (i.e. of a graph with overall the same vertex degree) is equal to that of the complete graph (i.e. the homogeneous population of the standard Moran process), which equals to $(1 - \frac{1}{r})/(1 - \frac{1}{r^n})$, where n is the size of the population. Intuitively, in the Isothermal Theorem, every vertex of the graph has a *temperature* which determines how often this vertex is being replaced by other individuals during the generalized Moran process. The complete graph (or equivalently, any regular graph) serves as a benchmark for measuring the fixation probability of an arbitrary graph G: if $f_r(G)$ is larger (resp. smaller) than that of the complete graph then G is called an *amplifier* (resp. a *suppressor*) [16, 20]. Until now only graphs with similar (i.e. a little larger or smaller) fixation probability than regular graphs have been identified [3–5, 16, 18], while no class of strong amplifiers/suppressors is known so far.

Our contribution. The structure of the graph, on which the population resides, plays a crucial role in the course of evolutionary dynamics. Human societies or social networks are never homogeneous, while certain individuals in central positions may be more influential than others [20]. Motivated by this, we introduce in this paper a new notion of measuring the success of an advantageous mutant in a structured population, by counting the number of initial placements of the mutant in a graph that guarantee fixation of the graph with large probability. This provides a refinement of the notion of fixation probability. Specifically, we do not any more consider the fixation probability as the probability of reaching fixation when the mutant is placed at a random vertex, but we rather consider the probability $f_r(v)$ of reaching fixation when a mutant with fitness $r > 1$ is introduced at a specific vertex v of the graph; $f_r(v)$ is termed the *fixation probability of vertex v*. Using this notion, the fixation probability $f_r(G)$ of a graph $G = (V, E)$ with n vertices is $f_r(G) = \frac{1}{n} \sum_{v \in V} f_r(v)$.

We aim in finding graphs that have many "strong starts" (or many "weak starts") of the mutant. Thus we introduce the notions of $(h(n), g(n))$*-selective amplifiers* (resp. $(h(n), g(n))$*-selective suppressors*), which include those graphs with n vertices for which there exist at least $h(n)$ vertices v with $f_r(v) \geq 1 - \frac{c(r)}{g(n)}$ (resp. $f_r(v) \leq \frac{c(r)}{g(n)}$) for an appropriate function $c(r)$ of r. We contrast this new

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[4] For approximating the probability to reach fixation (resp. extinction), one needs a number of runs which is about the inverse of the best known lower (resp. upper) bound of the fixation probability.

notion of $(h(n), g(n))$-selective amplifiers (resp. suppressors) with the notion of $g(n)$-*universal amplifiers* (resp. *suppressors*) which include those graphs G with n vertices for which $f_r(G) \geq 1 - \frac{c(r)}{g(n)}$ (resp. $f_r(G) \leq \frac{c(r)}{g(n)}$) for an appropriate function $c(r)$ of r. For a detailed presentation and a rigorous definition of these notions we refer to Section 2.

Using these new notions, we prove that there exist strong selective amplifiers, namely $(\Theta(n), n)$-selective amplifiers (called the *urchin graphs*). Furthermore we prove that there exist also quite strong selective suppressors, namely $(\frac{n}{\phi(n)+1}, \frac{n}{\phi(n)})$-selective suppressors (called the $\phi(n)$-*urchin graphs*) for *any* function $\phi(n) = \omega(1)$ with $\phi(n) \leq \sqrt{n}$.

Regarding the traditional measure of the fixation probability $f_r(G)$ of undirected graphs G, we provide upper and lower bounds that are much stronger than the bounds $\frac{1}{n}$ and $1 - \frac{1}{n+r}$ that were known so far [8]. More specifically, first of all we demonstrate the nonexistence of "strong" universal amplifiers by showing that for any graph G with n vertices, the fixation probability $f_r(G)$ is strictly less than $1 - \frac{c(r)}{n^{3/4+\varepsilon}}$, for any $\varepsilon > 0$. This is in a wide contrast with what happens in directed graphs, as Lieberman et al. [16] provided directed graphs with arbitrarily large fixation probability (see also [20]).

On the other hand, we provide our lower bound in the *Thermal Theorem*, which states that for any vertex v of an arbitrary undirected graph G, the fixation probability $f_r(v)$ of v is at least $(r-1)/(r + \frac{\deg v}{\deg_{\min}})$ for any $r > 1$, where $\deg v$ is the degree of v in G (i.e. the number of its neighbors) and $\deg_{\min}$ (resp. $\deg_{\max}$) is the minimum (resp. maximum) degree in G. This result extends the Isothermal Theorem for regular graphs [16]. In particular, we consider here a different notion of *temperature* for a vertex than [16]: the temperature of vertex v is $\frac{1}{\deg v}$. As it turns out, a "hot" vertex (i.e. with hight temperature) affects more often its neighbors than a "cold" vertex (with low temperature). The Thermal Theorem, which takes into account the vertex v on which the mutant is introduced, provides immediately our lower bound $(r-1)/(r + \frac{\deg_{\max}}{\deg_{\min}})$ for the fixation probability $f_r(G)$ of any undirected graph G. The latter lower bound is almost tight, as it implies that $f_r(G) \geq \frac{r-1}{r+1}$ for a regular graph G, while the Isothermal Theorem implies that the fixation probability of a regular graph G tends to $\frac{r-1}{r}$ as the size of G increases. Note that our new upper/lower bounds for the fixation probability lead to better time complexity of the FPRAS proposed in [8], as the Monte Carlo technique proposed in [8] now needs to simulate the Moran process a less number of times (to estimate fixation or extinction).

Our techniques are original and of a constructive combinatorics flavor. For the class of strong selective amplifiers (the urchin graphs) we introduce a novel decomposition of the Markov chain $\mathcal{M}$ of the generalized Moran process into $n-1$ smaller chains $\mathcal{M}_1, \mathcal{M}_2, \ldots, \mathcal{M}_{n-1}$, and then we decompose each $\mathcal{M}_k$ into two even smaller chains $\mathcal{M}_k^1, \mathcal{M}_k^2$. Then we exploit a new way of composing these smaller chains (and returning to the original one) that is carefully done to maintain the needed domination properties. For the proof of the lower bound in the Thermal Theorem, we first introduce a new and simpler weighted process that bounds fixation probability from below (the generalized Moran process is a special case of this new process). Then we add appropriate dummy states to its (exponentially large) Markov chain, and finally we iteratively modify the resulting chain by maintaining the needed monotonicity properties. Eventually this results to the desired lower bound of the Thermal Theorem. Finally, our proof for the non-existence of strong universal amplifiers is done by contradiction, partitioning appropriately the vertex set of the graph and discovering an appropriate independent set that leads to the contradiction.

2 Preliminaries

Throughout the paper we consider only finite, connected, undirected graphs $G = (V, E)$. Our results apply to connected graphs as, otherwise, the fixation probability is necessarily zero. The edge $e \in E$ between two vertices $u, v \in V$ is denoted by $e = uv$. For a vertex subset $X \subseteq V$, we write $X + y$ and $X - y$ for $X \cup \{y\}$ and $X \cap \{y\}$, respectively. Furthermore, throughout r denotes the fitness of the mutant, while the value r is considered to be independent of the size n of the network, i.e. we assume that r is constant. For simplicity of presentation, we call a vertex v "infected" if a copy of the mutant is placed on v. For every vertex subset $S \subseteq V$ we denote by $f_r(S)$ the fixation probability of the set S, i.e. the probability that, starting with exactly $|S|$ copies of the mutant placed on the vertices of S, the generalized Moran process will eventually reach fixation. By the definition of the generalized Moran process $f_r(\emptyset) = 0$ and $f_r(V) = 1$, while for $S \notin \{\emptyset, V\}$,

$$f_r(S) = \frac{\sum_{xy \in E} \left(\frac{r}{\deg x} f(S+y) + \frac{1}{\deg y} f(S-x) \right)}{\sum_{xy \in E} \left(\frac{r}{\deg x} + \frac{1}{\deg y} \right)}$$

Therefore, eliminating self-loops in the above Markov process,

$$f_r(S) = \frac{\sum_{xy \in E, x \in S, y \notin S} \left(\frac{r}{\deg x} f_r(S+y) + \frac{1}{\deg y} f_r(S-x) \right)}{\sum_{xy \in E, x \in S, y \notin S} \left(\frac{r}{\deg x} + \frac{1}{\deg y} \right)} \tag{1}$$

In the next definition we introduce the notions of *universal* and *selective* amplifiers.

Definition 1. *Let $\mathcal{G}$ be an infinite class of undirected graphs. If there exists an $n_0 \in \mathbb{N}$, an $r_0 \geq 1$, and some function $c(r)$, such that for every graph $G \in \mathcal{G}$ with $n \geq n_0$ vertices and for every $r > r_0$:*

- *$f_r(G) \geq 1 - \frac{c(r)}{g(n)}$, then $\mathcal{G}$ is a class of $g(n)$-*universal amplifiers*,*
- *there exists a subset S of at least $h(n)$ vertices of G, such that $f_r(v) \geq 1 - \frac{c(r)}{g(n)}$ for every vertex $v \in S$, then $\mathcal{G}$ is a class of $(h(n), g(n))$-*selective amplifiers*.*

Moreover, $\mathcal{G}$ is a class of strong universal *(resp.* strong selective*) amplifiers if $\mathcal{G}$ is a class of n-*universal *(resp.* $(\Theta(n), n)$-selective*) amplifiers.*

Similarly to Definition 1, we introduce the notions of *universal* and *selective* suppressors.

Definition 2. *Let $\mathcal{G}$ be an infinite class of undirected graphs. If there exist functions $c(r)$ and $n_0(r)$, such that for every $r > 1$ and for every graph $G \in \mathcal{G}$ with $n \geq n_0(r)$ vertices:*

- *$f_r(G) \leq \frac{c(r)}{g(n)}$, then $\mathcal{G}$ is a class of $g(n)$-*universal suppressors*,*
- *there exists a subset S of at least $h(n)$ vertices of G, such that $f_r(v) \leq \frac{c(r)}{g(n)}$ for every vertex $v \in S$, then $\mathcal{G}$ is a class of $(h(n), g(n))$-*selective suppressors.

Moreover, $\mathcal{G}$ is a class of strong universal *(resp.* strong selective*) suppressors if $\mathcal{G}$ is a class of n-*universal *(resp.* $(\Theta(n), n)$-selective*) suppressors.*

Note that $n_0 = n_0(r)$ in Definition 2, while in Definition 1 n_0 is not a function of r. The reason for this is that, since we consider the fitness value r to be constant, the size n of G needs to be sufficiently large with respect to r in order for G to act as a suppressor. Indeed, if we let r grow arbitrarily, e.g. if $r = n^2$, then for *any* graph G with n vertices the fixation probability $f_r(v)$ tends to 1 as n grows. The next lemma follows by Definitions 1 and 2.

Lemma 1. *If $\mathcal{G}$ is a class of $g(n)$-universal amplifiers (resp. suppressors), then $\mathcal{G}$ is a class of $(\Theta(n), g(n))$-selective amplifiers (resp. suppressors).*

The most natural question that arises by Definitions 1 and 2 is whether there exists any class of strong selective amplifiers/suppressors, as well as for which functions $h(n)$ and $g(n)$ there exist classes of $g(n)$-universal amplifiers/suppressors and classes of $(h(n), g(n))$-selective amplifiers/suppressors. In Section 3 and 4 we provide our results on amplifiers and suppressors, respectively.

3 Amplifier bounds

In this section we prove that there exist no strong universal amplifiers (Section 3.1), although there exists a class of strong selective amplifiers (Section 3.2).

3.1 Non-existence of strong universal amplifiers

Theorem 1. *For any function $g(n) = \Omega(n^{\frac{3}{4}+\varepsilon})$ for some $\varepsilon > 0$, there exists no graph class $\mathcal{G}$ of $g(n)$-universal amplifiers for any $r > r_0 = 1$.*

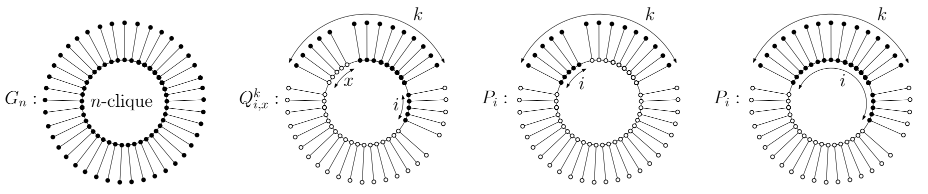
Proof (sketch). The proof is done by contradiction. It involves a surprising partition of the vertices of the graph into three sets V_1, V_2, V_3, where V_1 and V_2 are independent sets, and $N(v) \subseteq V_3$ for every $v \in V_1 \cup V_2$. For the detailed proof we refer to the full paper in the Appendix.

Corollary 1. *There exists no infinite class $\mathcal{G}$ of undirected graphs which are strong universal amplifiers.*

3.2 A class of strong selective amplifiers

In this section we present the first class $\mathcal{G} = \{G_n : n \geq 1\}$ of strong selective amplifiers, which we call the *urchin* graphs. Namely, the graph G_n has $2n$ vertices, consisting of a clique with n vertices, an independent set of n vertices, and a perfect matching between the clique and the independent set, as it is illustrated in Figure 1(a). For every graph G_n, we refer for simplicity to a vertex of the clique of G_n as a *clique vertex* of G_n, and to a vertex of the independent set of G_n as a *nose* of G_n, respectively. We prove in this section that the class $\mathcal{G}$ of urchin graphs are strong selective amplifiers. Namely, we prove that, whenever $r > r_0 = 5$, the fixation probability of any nose v of any graph G_n is $f_r(v) \geq 1 - \frac{c(r)}{n}$, where $c(r)$ is a function that depends only on the mutant fitness r.

Let v be a clique vertex (resp. a nose) and u be its adjacent nose (resp. clique vertex). If v is infected and u is not infected, then v is called an *isolated clique vertex* (resp. *isolated nose*), otherwise v is called a *covered clique vertex* (resp. *covered nose*). Let $k \in \{0, 1, \ldots, n\}$, $i \in \{0, 1, 2, \ldots, n-k\}$, and $x \in \{0, 1, 2, \ldots, k\}$. Denote by $Q^k_{i,x}$ the state of G_n with exactly i isolated clique vertices, x isolated noses, and $k - x$ covered noses. An example of the state $Q^k_{i,x}$ is illustrated in Figure 1. Furthermore, for every $k, i \in \{0, 1, \ldots, n\}$, we define the state P^k_i of G_n as follows. If $i \leq k$, then P^k_i is the state with exactly i covered noses and $k-i$ isolated noses. If $i > k$, then P^k_i is the state with exactly k covered noses and $i - k$ isolated clique vertices. Note that $Q^k_{i,0} = P^k_{k+i}$ and $Q^k_{0,x} = P^k_{k-x}$, for every $k \in \{0, 1, \ldots, n\}$, $i \in \{0, 1, 2, \ldots, n-k\}$, and $x \in \{0, 1, 2, \ldots, k\}$. Two examples of the state P^k_i, for the cases where $i \leq k$ and $i > k$, are shown in Figure 1.



(a) (b) (c) (d)

Fig. 1. (a) The "urchin" graph G_n. Furthermore, the state (b) $Q^k_{i,x}$ and the state P^k_i, where (c) $i \leq k$, and (d) $i > k$.

Let $k \in \{1, 2, \ldots, n-1\}$. For all appropriate values of i and x, we denote by $q^k_{i,x}$ (resp. p^k_i) the probability that, starting at state $Q^k_{i,x}$ (resp. P^k_i) we eventually arrive to a state with $k+1$ infected noses before we arrive to a state with $k-1$ infected noses.

Lemma 2. *Let* $1 \leq k \leq n-1$. *Then* $q^k_{i,x} > q^k_{i-1,x-1}$, *for every* $i \in \{1, 2, \ldots, n-k\}$ *and every* $x \in \{1, 2, \ldots, k\}$.

Corollary 2. *Let* $k \in \{1, 2, \ldots, n-1\}$, $i \in \{0, 1, \ldots, n-k\}$, *and* $x \in \{0, 1, \ldots, k\}$. *Then* $q^k_{i,x} > p^k_{k+i-x}$.

Note by Corollary 2 that, in order to compute a lower bound for the fixation probability $f_r(v)$ of a nose v of the graph G_n, we can assume that, whenever we have k infected noses and i infected clique vertices, we are at state P^k_i. That is, in the Markov chain of the generalized Moran process, we replace any transition to a state $Q^k_{i,x}$ with a transition to state P^k_{k+i-x}. Denote this relaxed Markov chain by $\mathcal{M}$; we will compute a lower bound of the fixation probability of state P^1_0 in the Markov chain $\mathcal{M}$ (cf. Theorem 2).

In order to analyze $\mathcal{M}$, we decompose it first into the $n-1$ smaller Markov chains $\mathcal{M}_1, \mathcal{M}_2, \ldots, \mathcal{M}_{n-1}$, as follows. For every $k \in \{1, 2, \ldots, n-1\}$, the Markov chain $\mathcal{M}_k$ captures all transitions of $\mathcal{M}$ between states with k infected noses. We denote by F_{k-1} (resp. F_{k+1}) an *arbitrary* state with $k-1$ (resp. $k+1$) infected noses. Moreover, we consider F_{k-1} and F_{k+1} as absorbing states of $\mathcal{M}_k$. Since we want to compute a lower bound of the fixation probability, whenever we arrive at state F_{k+1} (resp. at state F_{k-1}), we assume that we have the smallest number of infected clique vertices with $k+1$ (resp. with $k-1$) infected noses. That is, whenever $\mathcal{M}_k$ reaches state F_{k+1}, we assume that $\mathcal{M}$ has reached state P^{k+1}_{k+1} (and thus we move to the Markov chain $\mathcal{M}_{k+1}$). Similarly, whenever $\mathcal{M}_k$ reaches state F_{k-1}, we assume that $\mathcal{M}$ has reached state P^{k-1}_0 (and thus we move to the Markov chain $\mathcal{M}_{k-1}$).

A decomposition of $\mathcal{M}_k$ into two Markov chains. In order to analyze the Markov chain $\mathcal{M}_k$, where $k \in \{1, 2, \ldots, n-1\}$, we decompose it into two smaller Markov chains $\{\mathcal{M}^1_k, \mathcal{M}^2_k\}$.

In $\mathcal{M}^1_k$, we consider the state P^k_{k+1} absorbing. For every $i \in \{0, 1, \ldots, k\}$ denote by h^k_i the probability that, starting at state P^k_i in $\mathcal{M}^1_k$, we eventually reach state P^k_{k+1} before we reach state F_{k-1}. In this Markov chain $\mathcal{M}^1_k$, every transition probability between two states is equal to the corresponding transition probabilities in $\mathcal{M}_k$.

In $\mathcal{M}^2_k$, we denote by s^k_i, where $i \in \{k, k+1, \ldots, n\}$, the probability that starting at state P^k_i we eventually reach state F_{k+1} before we reach state F_{k-1}. In this Markov chain $\mathcal{M}^2_k$, the transition probability from state P^k_k to state P^k_{k+1} (resp. to state F_{k-1}) is equal to h^k_k (resp. $1-h^k_k$), while all other transition probabilities between two states in $\mathcal{M}^2_k$ are the same as the corresponding transition probabilities in $\mathcal{M}_k$.

Urchin graphs are strong selective amplifiers. We now conclude our analysis by combining the results of Section 3.2 on the two Markov chains $\mathcal{M}_1$ and $\mathcal{M}_2$. In the Markov chain $\mathcal{M}$, the transition from state P^k_0 to the states P^k_k, P^{k-1}_0 is done through the Markov chain $\mathcal{M}_1$, and the transition from state P^k_k to the states P^{k+1}_{k+1}, P^{k-1}_0 is done through the Markov chain $\mathcal{M}_2$, respectively.

In the Markov chain $\mathcal{M}$, the transition probability from state P^k_k to state P^{k+1}_{k+1} (resp. P^{k-1}_0) is s^k_k (resp. $1-s^k_k$). Recall that s^k_k is the probability that, starting at P_k^k in $\mathcal{M}_2$ (and thus also in $\mathcal{M}$), we reach state F_{k+1} before we reach F_{k-1}. Furthermore, the transition probability from state P_0^k to state P_k^k is equal to the probability that, starting at P_0^k in $\mathcal{M}_1$, we reach P_k^k before we reach F_{k-1}. Note that this probability is larger than h_0^k. Therefore, in order to compute a lower bound of the fixation probability of a nose in G_n, we can assume that in $\mathcal{M}$ the transition probability from state P_0^k to P_k^k (resp. P_0^{k-1}) is h_0^k (resp. $1 - h_0^k$).

Note that for every $k \in \{2, \ldots, n-1\}$ the infected vertices of state P_0^k is a strict subset of the infected vertices of state P_k^k. Therefore, in order to compute a lower bound of the fixation probability of state P_0^1 in $\mathcal{M}$, we can relax $\mathcal{M}$ by changing every transition from state P_{k-1}^{k-1} to state P_k^k to a transition from state P_{k-1}^{k-1} to state P_0^k, where $k \in \{2, \ldots, n-1\}$. After eliminating the states P_k^k in $\mathcal{M}'$, where $k \in \{1, 2, \ldots, n-1\}$, we obtain an equivalent birth-death process $\mathcal{B}_n$. Denote by p_1 the fixation probability of state P_0^1 in $\mathcal{B}_n$, i.e. p_1 is the probability that, starting at state P_0^1 in $\mathcal{B}_n$, we eventually arrive to state P_n^n. For the next theorem we use the lower bounds of Section 3.2.

Theorem 2. *For any $r > 5$ and for sufficiently large n, the fixation probability p_1 of state P_0^1 in $\mathcal{B}_n$ is $p_1 \geq 1 - \frac{c(r)}{n}$, for some appropriate function $c(r)$ of r.*

We are now ready to provide our main result in this section.

Theorem 3. *The class $\mathcal{G} = \{G_n : n \geq 1\}$ of urchin graphs is a class of strong selective amplifiers.*

4 Suppressor bounds

In this section we prove our lower bound for the fixation probability of an arbitrary undirected graph, namely the *Thermal Theorem* (Section 4.1), which generalizes the analysis of the fixation probability of regular graphs [16]. Furthermore we present for every function $\phi(n)$, where $\phi(n) = \omega(1)$ and $\phi(n) \leq \sqrt{n}$, a class of $(\frac{n}{\phi(n)+1}, \frac{n}{\phi(n)})$-selective suppressors in Section 4.2.

4.1 The Thermal Theorem

Consider a graph $G = (V, E)$ and a fitness value $r > 1$. Denote by $\mathcal{M}_r(G)$ the generalized Moran process on G with fitness r. Then, for every subset $S \notin \{\emptyset, V\}$ of its vertices, the fixation probability $f_r(S)$ of S in $\mathcal{M}_r(G)$ is given by (1), where $f_r(\emptyset) = 0$ and $f_r(V) = 1$. That is, the fixation probabilities $f_r(S)$, where $S \notin \{\emptyset, V\}$, are the solution of the linear system (1) with boundary conditions $f_r(\emptyset) = 0$ and $f_r(V) = 1$.

Suppose that at some iteration of the generalized Moran process the set S of vertices are infected and that the edge $xy \in E$ (where $x \in S$ and $y \notin S$) is activated, i.e. either x infects y or y disinfects x. Then (1) implies that the probability that x infects y is higher if $\frac{1}{\deg x}$ is large; similarly, the probability that y disinfects x is higher if $\frac{1}{\deg y}$ is large. Therefore, in a fashion similar to [16], we call for every vertex $v \in V$ the quantity $\frac{1}{\deg v}$ the *temperature* of v: a "hot" vertex (i.e. with high temperature) affects more often its neighbors than a "cold" vertex (i.e. with low temperature). It follows now by (1) that for every set $S \notin \{\emptyset, V\}$ there exists at least one pair $x(S), y(S)$ of vertices with $x(S) \in S$, $y(S) \notin S$, and $x(S)y(S) \in E$ such that

$$f_r(S) \geq \frac{\frac{r}{\deg x(S)} f_r(S + y(S)) + \frac{1}{\deg y(S)} f_r(S - x(S))}{\frac{r}{\deg x(S)} + \frac{1}{\deg y(S)}} \tag{2}$$

Thus, solving the linear system that is obtained from (2) by replacing inequalities with equalities, we obtain a lower bound for the fixation probabilities $f_r(S)$, where $S \notin \{\emptyset, V\}$. In the next definition we introduce a weighted generalization of this linear system, which is a crucial tool for our analysis in obtaining the Thermal Theorem.

Definition 3. (the linear system L_0) *Let $G = (V, E)$ be an undirected graph and $r > 1$. Let every vertex $v \in V$ have weight* (temperature) *$d_v > 0$. The linear system L_0 on the variables $p_r(S)$, where $S \subseteq V$, is given by the following equations whenever $S \notin \{\emptyset, V\}$:*

$$p_r(S) = \frac{r d_{x(S)} p_r(S + y(S)) + d_{y(S)} p_r(S - x(S))}{r d_{x(S)} + d_{y(S)}} \tag{3}$$

with boundary conditions $p_r(\emptyset) = 0$ and $p_r(V) = 1$.

With a slight abuse of notation, whenever $S = \{u_1, u_2, \ldots, u_k\}$, we denote $p_r(u_1, u_2, \ldots, u_k) = p_r(S)$.

Observation 1 *The linear system L_0 in Definition 3 corresponds naturally to the Markov chain $\mathcal{M}_0$ with one state for every subset $S \subseteq V$, where the states $\emptyset$ and V are absorbing, and every non-absorbing state S has exactly two transitions to the states $S + y(S)$ and $S - x(S)$ with transition probabilities $q_S = \frac{r d_{x(S)}}{r d_{x(S)} + d_{y(S)}}$ and $1 - q_S$, respectively.*

Observation 2 *Let $G = (V, E)$ be a graph and $r > 1$. For every vertex $x \in V$ let $d_x = \frac{1}{\deg x}$ be the temperature of x. Then $f_r(S) \geq p_r(S)$ for every $S \subseteq V$, where the values $p_r(S)$ are the solution of the linear system L_0.*

Before we provide the Thermal Theorem (Theorem 4), we first prove an auxiliary result in the next lemma which generalizes the Isothermal Theorem of [16] for regular graphs, i.e. for graphs with the same number of neighbors for every vertex.

Lemma 3. *Let $G = (V, E)$ be a graph with n vertices, $r > 1$, and d_u be the same for all vertices $u \in V$. Then $p_r(u) = \frac{1 - \frac{1}{r}}{1 - \frac{1}{r^n}} \geq 1 - \frac{1}{r}$ for every vertex $u \in V$.*

We are now ready to provide our main result in this section which provides a lower bound for the fixation probability on arbitrary graphs, parameterized by the maximum ratio between two different temperatures in the graph.

Theorem 4 (Thermal Theorem). *Let $G = (V, E)$ be a connected undirected graph and $r > 1$. Then $f_r(v) \geq \frac{r-1}{r+\frac{\deg v}{\deg_{\min}}}$ for every $v \in V$.*

The lower bound for the fixation probability in Theorem 4 is almost tight. Indeed, if a graph $G = (V, E)$ with n vertices is regular, i.e. if $\deg u = \deg v$ for every $u, v \in V$, then $f_r(G) = \frac{1-\frac{1}{r}}{1-\frac{1}{r^n}}$ by Lemma 3 (cf. also the Isothermal Theorem in [16]), and thus $f_r(G) \cong \frac{r-1}{r}$ for large enough n. On the other hand, Theorem 4 implies for a regular graph G that $f_r(G) \geq \frac{r-1}{r+1}$.

4.2 A class of selective suppressors

In this section we present for every function $\phi(n)$, where $\phi(n) = \omega(1)$ and $\phi(n) \leq \sqrt{n}$, the class $\mathcal{G}_{\phi(n)} = \{G_{\phi(n),n} : n \geq 1\}$ of $(\frac{n}{\phi(n)+1}, \frac{n}{\phi(n)})$-selective suppressors. We call these graphs $\phi(n)$-*urchin graphs*, since for $\phi(n) = 1$ they coincide with the class of urchin graphs in Section 3.2. For every n, the graph $G_{\phi(n),n} = (V_{\phi(n),n}, E_{\phi(n),n})$ has n vertices. Its vertex set $V_{\phi(n),n}$ can be partitioned into two sets $V^1_{\phi(n),n}$ and $V^2_{\phi(n),n}$, where $|V^1_{\phi(n),n}| = \frac{n}{\phi(n)+1}$ and $|V^2_{\phi(n),n}| = \frac{\phi(n)}{\phi(n)+1}n$, such that $V^1_{\phi(n),n}$ induces a clique and $V^2_{\phi(n),n}$ induces an independent set in $G_{\phi(n),n}$. Furthermore, every vertex $u \in V^2_{\phi(n),n}$ has $\phi(n)$ neighbors in $V^1_{\phi(n),n}$, and every vertex $v \in V^1_{\phi(n),n}$ has $\phi^2(n)$ neighbors in $V^2_{\phi(n),n}$. Therefore $\deg v = n+\phi^2(n)-1$ for every $v \in V^1_{\phi(n),n}$ and $\deg u = \phi(n)$ for every $u \in V^2_{\phi(n),n}$.

Theorem 5. *For every function $\phi(n)$, where $\phi(n) = \omega(1)$ and $\phi(n) \leq \sqrt{n}$, the class $\mathcal{G}_{\phi(n)} = \{G_{\phi(n),n} : n \geq 1\}$ of $\phi(n)$-urchin graphs is a class of $(\frac{n}{\phi(n)+1}, \frac{n}{\phi(n)})$-selective suppressors.*

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