Mutants and Residents with Different Connection Graphs in the Moran Process

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Abstract. The Moran process, as studied by Lieberman, Hauert and Nowak [10], is a stochastic process modeling the spread of genetic mutations in populations. In this process, agents of a two-type population (i.e. mutants and residents) are associated with the vertices of a graph. Initially, only one vertex chosen uniformly at random (u.a.r.) is a mutant, with fitness $r > 0$, while all other individuals are residents, with fitness 1. In every step, an individual is chosen with probability proportional to its fitness, and its state (mutant or resident) is passed on to a neighbor which is chosen u.a.r. In this paper, we introduce and study for the first time a generalization of the model of [10] by assuming that different types of individuals perceive the population through different graphs defined on the same vertex set, namely $G_R = (V, E_R)$ for residents and $G_M = (V, E_M)$ for mutants. In this model, we study the fixation probability, namely the probability that eventually only mutants remain in the population, for various pairs of graphs.

In particular, in the first part of the paper, we examine how known results from the original single-graph model of [10] can be transferred to our 2-graph model. In that direction, by using a Markov chain abstraction, we provide a generalization of the Isothermal Theorem of [10], that gives sufficient conditions for a pair of graphs to have fixation probability equal to the fixation probability of a pair of cliques; this corresponds to the absorption probability of a birth-death process with forward bias r.

In the second part of the paper, we give a 2-player strategic game view of the process where player payoffs correspond to fixation and/or extinction probabilities. In this setting, we attempt to identify best responses for each player. We give evidence that the clique is the most beneficial graph for both players, by proving bounds on the fixation probability when one of the two graphs is complete and the other graph belongs to various natural graph classes.

In the final part of the paper, we examine the possibility of efficient approximation of the fixation probability. Interestingly, we show that there is a pair of graphs for which the fixation probability is exponentially

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small. This implies that the fixation probability in the general case of an arbitrary pair of graphs cannot be approximated via a method similar to [2]. Nevertheless, we prove that, in the special case when the mutant graph is complete, an efficient approximation of the fixation probability is possible through an FPRAS which we describe.

Keywords: Moran process, fixation probability, evolutionary dynamics

1 Introduction

The Moran process [13] models antagonism between two species whose critical difference in terms of adaptation is their *relative fitness*. A *resident* has relative fitness 1 and a *mutant* relative fitness $r > 0$. Many settings in Evolutionary Game Theory consider fitness as a measure of reproductive success; for examples see [3, 7, 14]. A generalization of the Moran process by Lieberman et al [10] considered the situation where the replication of an individual's fitness depends on some given structure, i.e. a directed graph. This model gave rise to an extensive line of works in Computer Science, initiated by Mertzios et al. in [11].

In this work we further extend the model of [10] to capture the situation where, instead of one given underlying graph, each species has its own graph that determines their way of spreading their offsprings. As we will show, due to the process' restrictions only one species will remain in the population eventually. Our setting is by definition an interaction between two players (species) that want to maximize their probability of occupying the whole population.

This strategic interaction is described by an 1-sum bimatrix game, where each player (resident or mutant) has all the strongly connected digraphs on n nodes as her pure strategies. The resident's payoff is the *extinction probability* and the mutant's payoff is the *fixation probability*. The general question that interests us is: what are the pure Nash equilibria of this game (if any)? To gain a better understanding of the behaviour of the competing graphs, we investigate the best responses of the resident to the clique graph of the mutant.

This model and question is motivated by many interesting problems from various, seemingly unrelated scientific areas. Some of them are: idea/rumor spreading, where the probability of spreading depends on the kind of idea/rumor; computer networks, where the probability that a message/malware will cover a set of terminals depends on the message/malware; and also spread of mutations, where the probability of a mutation occupying the whole population of cells depends on the mutation. Using the latter application as an analogue for the rest, we give the following example to elaborate on the natural meaning of this process.

Imagine a population of identical somatic *resident* cells (e.g. biological tissue) that carry out a specific function (e.g. an organ). The cells connect with each other in a certain way; i.e., when a cell reproduces it replaces another from a specified set of candidates, that is, the set of cells connected to it. Reproduction here is the replication of the genetic code to the descendant, i.e. the hardwired commands which determine how well the cell will adapt to its environment, what its chances of reproduction are and which candidate cells it will be able to reproduce on.

The changes in the information carried by the genetic code, i.e. mutations, give or take away survival or reproductive abilities. A bad case of mutation is a cancer cell whose genes force it to reproduce relentlessly, whereas a good one could be a cell with enhanced functionality. A mutation can affect the cell's ability to adapt to the environment, which translates to chances of reproduction, or/and change the set of candidates in the population that should pay the price for its reproduction.

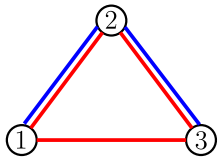
Now back to our population of resident cells which, as we said, connect with each other in a particular way. After lots of reproductions a mutant version of it shows up due to replication mistakes, environmental conditions, etc. This *mutant* has the ability to reproduce in a different rate, and also, to be connected with a set of cells different than the one of its resident version. For the sake of argument, we study the most pessimistic case, i.e. our mutant is an extremely aggressive type of cancer with increased reproduction rate and maximum unpredictability; it can replicate on any other cell and do that faster than a resident cell. We consider the following motivating question: Supposing this single mutant will appear at some point in time on a random cell equiprobably, what is the best structure (network) of our resident cells such that the probability of the mutant taking over the whole population is minimized?

The above process that we informally described captures the real-life process remarkably well. As a matter of fact, a mutation that affects the aforementioned characteristics in a real population of somatic cells occurs rarely compared to the time it needs to conquer the population or get extinct. Therefore, a second mutation is extremely rare to happen before the first one has reached one of those two outcomes and this allows us to study only one type of mutant per process. In addition, apart from the different reproduction rate, a mutation can lead to a different "expansionary policy" of the cell, something that has been overlooked so far.

2 Definitions

Each of the population's individuals is represented by a label $i \in \{1, 2, ..., n\}$ and can have one of two possible types: R (*resident*) and M (*mutant*). We denote the *set of nodes* by V, with $n = |V|$, and the *set of resident(mutant) edges* by $E_R(E_M)$. The node connections are represented by directed edges; A node i has a *type R(M) directed edge* $(ij)_R((ij)_M)$ towards node j if and only if when i is chosen and is of type $R(M)$ then it can reproduce on j with positive probability. The aforementioned components define two directed graphs; the *resident graph* $G_R = (V, E_R)$ and the *mutant graph* $G_M = (V, E_M)$. A node's type determines its fitness; residents have *relative fitness* 1, while mutants have relative fitness $r > 0$.

Our process works as follows: We start with the whole population as residents, except for one node which is selected uniformly at random to be mutant. We consider discrete time, and in each time-step an individual is picked with probability proportional to its fitness, and copies itself on an individual connected to it in the corresponding graph (G_R or G_M) with probability determined by the (weight of the) connection. The probability of i (given that it is chosen) reproducing on j when i is resident(mutant) is by definition equal to some *weight* $w_{ij}^R(w_{ij}^M)$, thus $\sum_{j=1}^n w_{ij}^R = \sum_{j=1}^n w_{ij}^M = 1$ for every $i \in V$. For G_R, every edge $(ij)_R$ has weight $w_{ij}^R > 0$ if $(ij)_R \in E_R$, and $w_{ij}^R = 0$ otherwise. Similarly for G_M. For each graph we then define *weight matrices* $W_R = \left[w_{ij}^R\right]$ and $W_M = \left[w_{ij}^M\right]$ which contain all the information of the two graphs' structure. After each time-step three outcomes can occur: (i) a node is added to the *mutant set* $S \subseteq V$, (ii) a node is deleted from S, or (iii) S remains the same. If both graphs are strongly connected the process ends with probability 1 when either $S = \varnothing$ (*extinction*) or $S = V$ (*fixation*). An example is shown in Figure 1.



$$W_R = \begin{bmatrix} 0 & 1 & 0 \\ \frac{1}{2} & 0 & \frac{1}{2} \\ 0 & 1 & 0 \end{bmatrix} \qquad W_M = \begin{bmatrix} 0 & \frac{1}{2} & \frac{1}{2} \\ \frac{1}{2} & 0 & \frac{1}{2} \\ \frac{1}{2} & \frac{1}{2} & 0 \end{bmatrix}$$

Fig. 1. The 2 graphs combined; the edges of the resident graph are blue and the edges of the mutant graph are red. The respective weight matrices capture all the structure's information, including the weights to each edge. For example, the resident behaviour for node 1 (if chosen) is to reproduce only on node 2, while its mutant behaviour is to reproduce equiprobably on either 2 or 3.

We denote by $f(S)$ the probability of fixation given that we start with the mutant set S. We define the *fixation probability* to be $f = \frac{1}{n}\sum_{u \in V} f(\{u\})$ for a fixed relative fitness r. We also define the *extinction probability* to be equal to $1 - f$. In the case of only one graph G (i.e. $G_R = G_M = G$), which has been the standard setting so far, the point of reference for a graph's behaviour is the fixation probability of the complete graph (called *Moran fixation probability*) $f_{\text{Moran}} = \left(1 - \frac{1}{r}\right) / \left(1 - \frac{1}{r^n}\right)$. G is an *amplifier of selection* if $f > f_{\text{Moran}}$ and $r > 1$ or $f < f_{\text{Moran}}$ and $r < 1$ because it favors advantageous mutants and discourages disadvantageous ones. G is a *suppressor of selection* if $f < f_{\text{Moran}}$ and $r > 1$ or $f > f_{\text{Moran}}$ and $r < 1$ because it discourages advantageous mutants and favors disadvantageous ones.

An undirected graph is a graph G for which $w_{ij} \in E$ if and only if $w_{ji} \in E$. An *unweighted graph* is a graph with the property that for every $i \in V$: $w_{ij} = \frac{1}{deg(i)}$ for every j with incoming edge from i, where $deg(i)$ is the outdegree of node i. In the sequel we will abuse the term *undirected graph* to refer to an undirected unweighted graph.

In what follows we will use special names to refer to some specific graph classes. The following graphs have n vertices which we omit from the notation for simplicity.

- CL as a shorthand for the Clique or complete graph K_n.
- UST as a shorthand for the Undirected Star graph $K_{1,n-1}$.
- UCY as a shorthand for the Undirected Cycle or 2-regular graph C_n.
- CId: as a shorthand for the Circulant graph $Ci_n(1, 2, .., d/2)$ for even d. Briefly this subclass of circulant graphs is defined as follows. For even degree d, the graph CId (see Fig. 2) has vertex set $\{1, 2, \cdots, n\}$, and each vertex i is connected to vertices $\{(i - 1 \pm k) \mod n + 1 : k = 1, \ldots, d/2\}$.

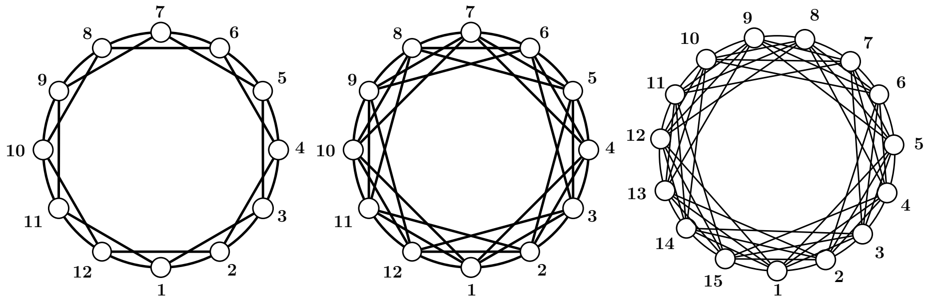


Fig. 2. The classes of 4-regular, 6-regular and 8-regular undirected graphs $CI4$, $CI6$ and $CI8$. Here the number of vertices is $12, 12$ and 15 respectively.

By "*Resident Graph vs Mutant Graph*" we refer to the process with $G_R =$ *Resident Graph* and $G_M =$ *Mutant Graph* and by f_{G_R,G_M} we refer to the fixation probability of that process.

We note that in this paper, we are interested in the asymptotic behavior of the fixation probability in the case where the population size n is large. Therefore, we employ the standard asymptotic notation with respect to n; in particular, r is almost always treated as a variable independent of n. Furthermore, in the rest of the paper, by G_R and G_M we mean graph classes $\{(G_R)_n\}_{n\geq 3}$ and $\{(G_M)_n\}_{n\geq 3}$ respectively, and we will omit the n since we only care about the fixation probability when $n \to \infty$.

3 Our Results

In this paper, we introduce and study for the first time a generalization of the model of [10] by assuming that different types of individuals perceive the population through different graphs defined on the same vertex set, namely $G_R = (V, E_R)$ for residents and $G_M = (V, E_M)$ for mutants. In this model, we study the fixation probability, i.e. the probability that eventually only mutants remain in the population, for various pairs of graphs.

In particular, in Section 5 we initially prove a tight upper bound (Theorem 1) on the fixation probability for the general case of an arbitrary pair of digraphs. Next, we prove a generalization of the Isothermal Theorem of [10], that provides sufficient conditions for a pair of graphs to have fixation probability equal to the fixation probability of a clique pair, namely $f_{\text{Moran}} \stackrel{def}{=} f_{CL,CL} = \left(1 - \frac{1}{r}\right) / \left(1 - \frac{1}{r^n}\right)$; this corresponds to the absorption probability of a simple birth-death process with forward bias r. It is worth noting that it is easy to find small counterexamples of pairs of graphs for which at least one of the two conditions of Theorem 2 does not hold and yet the fixation probability is equal to f_{Moran}; hence we do not prove necessity.

In Section 6 we give a 2-player strategic game view of the process where player payoffs correspond to fixation and/or extinction probabilities. In this setting, we give an extensive study of the fixation probability when one of the two underlying graphs is complete, providing several insightful results. In particular, we prove that, the fixation probability $f_{UST,CL}$ when the mutant graph is the clique on n vertices (i.e. $G_M = CL$) and the resident graph is the undirected star on n vertices (i.e. $G_R = UST$) is $1 - O(1/n)$, and thus tends to 1 as the number of vertices grows, for any constant $r > 0$. By using a translation result (Lemma 1), we can show that, when the two graphs are exchanged, then $f_{CL,UST} \to 0$. However, using a direct proof, in Theorem 4 we show that in fact $f_{CL,UST} \in O\left(\frac{r^{n-1}}{(n-2)!}\right)$, i.e. it is exponentially small in n, for any constant $r > 0$. In Theorem 6, we also provide a lower bound on the fixation probability in the special case where the resident graph is any undirected graph and the mutant graph is a clique.

Furthermore, in Subsection 6.3, we find bounds on the fixation probability when the mutant graph is the clique and the resident graph belongs to various classes of regular graphs. In particular, we show that when the mutant graph is the clique and the resident graph is the undirected cycle, then $1 - \frac{1}{r} - o(1) \leq f_{UCY,CL} \leq \frac{1}{e^{1/r} - o(1)}$, for any constant $r > 2$. A looser lower bound holds for smaller values of r. This in particular implies that the undirected cycle is quite resistant to the clique. Then, we analyze the fixation probability by replacing the undirected cycle by 3 increasingly denser circulant graphs and find that, the denser the graph, the smaller r is required to achieve a $1 - 1/r$ asymptotic lower bound. We also find that the asymptotic upper bound stays the same when the resident graphs become denser with constant degree, but it goes to $1 - 1/r$ when the degree is $\omega(1)$. In addition, by running simulations (which we do not analyse here) for the case where the resident graph is the strongest known suppressor, i.e. the one in [5], and the mutant graph is the clique, we get fixation probability significantly greater than f_{Moran} for up to 336 nodes and values of fitness $r > 2$. All of our results seem to indicate that the clique is the most beneficial graph (in terms of player payoff in the game theoretic formulation). However, we leave this fact as an open problem for future research.

Finally, in Section 7 we consider the problem of efficiently approximating the fixation probability in our model. We point out that Theorem 4 implies that the fixation probability cannot be approximated via a method similar to [2]. However, when we restrict the mutant graph to be complete, we prove a polynomial (in

n) upper bound for the absorption time of the generalized Moran process when $r > 2c\,(1 + o(1))$, where c is the maximum ratio of degrees of adjacent nodes in the resident graph. The latter allows us to give a fully polynomial randomized approximation scheme (FPRAS) for the problem of computing the fixation probability in this case.

4 Previous Work

So far the bibliography consists of works that consider the same structure for both residents and mutants. This 1-graph setting was initiated by P.A.P. Moran [13] where the case of the complete graph was examined. Many years later, the setting was extended to structured populations on general directed graphs by Lieberman et al. [10]. They introduced the notions of amplifiers and suppressors of selection, a categorization of graphs based on the comparison of their fixation probabilities with that of the complete graph. They also found a sufficient condition (in fact [4] corrects the claim in [10] that the condition is also necessary) for a digraph to have the fixation probability of the complete graph, but a necessary condition is yet to be found.

Since the generalized 1-graph model in [10] was proposed, a great number of works have tried to answer some very intriguing questions in this framework. One of them is the following: which are the best unweighted amplifiers and suppressors that exist? Díaz et al. [2] give the following bounds on the fixation probability of strongly connected digraphs: an upper bound of $1 - \frac{1}{r+n}$ for $r > 0$, a lower bound of $\frac{1}{n}$ for $r > 1$ and they show that there is no positive polynomial lower bound when $0 < r < 1$. An interesting problem that was set in [10] is whether there are graph families that are *strong amplifiers* or *strong suppressors* of selection, i.e. families of graphs with fixation probability tending to 1 or to 0 respectively as the order of the graph tends to infinity and for $r > 1$. Galanis et al. [4] find an infinite family of strongly-amplifying directed graphs, namely the "megastar" with fixation probability $1 - O(n^{-1/2} \log^{23} n)$, which was later proved to be optimal up to logarithmic factors [6].

While the search for optimal directed strong amplifiers was still on, a restricted version of the problem had been drawing a lot of attention: which are the tight bounds on the fixation probability of undirected graphs? The lower bound in the undirected case remained $\frac{1}{n}$, but the upper bound was significantly improved by Mertzios et al. [12] to $1 - \Omega(n^{-3/4})$, when r is independent of n. It was again improved by Giakkoupis [5] to $1 - \Omega\left(\frac{1}{\epsilon} n^{-1/3} \log n\right)$ for $r \geq 1 + \epsilon$ where $0 < \epsilon \leq 1$, and finally by Goldberg et al. [6] to $1 - \Omega(n^{-1/3})$ where they also find a graph which shows that this is tight. While the general belief was that there are no undirected strong suppressors, Giakkoupis [5] showed that there is a class of graphs with fixation probability $O(r^2 n^{-1/4} \log n)$, opening the way for a potentially optimal strong suppressor to be discovered.

Extensions of [10] where the interaction between individuals includes a bimatrix game have also been studied. Ohtsuki et al. in [15] considered the generalized Moran process with two distinct graphs, where one of them determines possible pairs that will play a bimatrix game and yield a total payoff for each individual, and the other determines which individual will be replaced by the process in each step. Two similar settings, where a bimatrix game determines the individuals' fitness, were studied by Ibsen-Jensen et al. in [8]. In that work they prove NP-completeness and #P-completeness on the computation of the fixation probabilities for each setting.

5 Markov Chain Abstraction and the Generalized Isothermal Theorem

This generalized process with two graphs we propose can be modelled as an absorbing Markov chain [14]. The states of the chain are the possible mutant sets $S \subseteq V$ (2^n different mutant sets) and there are two absorbing states, namely $\langle \varnothing \rangle$ and $\langle V \rangle$. In this setting, the fixation probability is the average absorption probability to $\langle V \rangle$, starting from a state with one mutant. Since our Markov chain contains only two absorbing states, the sum of the fixation and extinction probabilities is equal to 1.

Transition probabilities. In the sequel we will denote by $X + y$ the set $X \cup \{y\}$ and by $X - y$ the set $X \setminus \{y\}$. We can easily deduce the boundary conditions from the definition: $f(\varnothing) = 0$ and $f(V) = 1$. For any other arbitrary state $\langle S \rangle$ of the process we have:

$$\begin{aligned} f(S) = & \sum_{i \in S, j \notin S} \frac{r}{F(S)} w_{ij}^M \cdot f(S+j) + \sum_{j \notin S, i \in S} \frac{1}{F(S)} w_{ji}^R \cdot f(S-i) + \\ & + \left(\sum_{i \in S, j \in S} \frac{r}{F(S)} w_{ij}^M + \sum_{i \notin S, j \notin S} \frac{1}{F(S)} w_{ij}^R \right) \cdot f(S), \end{aligned} \tag{1}$$

where $F(S) = |S|r + |V| - |S|$ is the total fitness of the population in state $\langle S \rangle$. By eliminating self-loops, we get

$$f(S) = \frac{\sum_{i \in S, j \notin S} r \cdot w_{ij}^M \cdot f(S+j) + \sum_{j \notin S, i \in S} w_{ji}^R \cdot f(S-i)}{\sum_{i \in S, j \notin S} r \cdot w_{ij}^M + \sum_{j \notin S, i \in S} w_{ji}^R}. \tag{2}$$

We should note here that, in the general case, the fixation probability can be computed by solving a system of 2^n linear equations using this latter relation. However, bounds are usually easier to be found and special cases of resident and mutant graphs may have efficient exact solutions.

Using the above Markov chain abstraction and stochastic domination arguments we can prove the following general upper bound on the fixation probability:

Theorem 1. *For any pair of digraphs G_R and G_M with $n = |V|$, the fixation probability f_{G_R,G_M} is upper bounded by $1 - \frac{1}{r+n}$, for $r > 0$. This bound is tight for r independent of n.*

Proof. We refer to the proof of Lemma 4 of [2], as our proof is essentially the same. Briefly, we find an upper bound on the fixation probability of a relaxed Moran process that favors the mutants, where we assume that fixation is achieved when two mutants appear in the population. In their work the resident and mutant graphs are the same and undirected, but this does not change the probabilities of the first mutant placed u.a.r. to be extinct or replicated in our model. Finally, we note that this result is tight, by Theorem 3. □

We now prove a generalization of the Isothermal Theorem of [10].

Theorem 2 (Generalized Isothermal Theorem). *Let $G_R(V, E_R)$, $G_M(V, E_M)$ be two directed graphs with vertex set V and edge sets E_R and E_M respectively. The generalized Moran process with 2 graphs as described above has the Moran fixation probability if:*

1. $\sum_{j\neq i} w_{ji}^R = \sum_{j\neq i} w_{ji}^M = 1$, $\forall i \in V$, *that is, W_R and W_M are doubly stochastic, i.e. G_R and G_M are isothermal (actually one of them being isothermal is redundant as it follows from the second condition), and*
2. *for every pair of nodes $i, j \in V$: $w_{ij}^R + w_{ji}^R = w_{ij}^M + w_{ji}^M$.*

Proof. It suffices to show that in every state S of the Markov chain of the process with $0 < |S| < |V|$ mutants, the probability to go to a state with $|S|+1$ mutants is r times the probability to go to a state with $|S|-1$ mutants (ch.6 in [14]). In our setting, by (1) these probabilities are $\left(r \cdot \sum_{i\in S}\sum_{j\notin S} w_{ij}^M\right)/F$ and $\left(\sum_{i\notin S}\sum_{j\in S} w_{ij}^R\right)/F$ respectively. So, to establish the theorem, it suffices to show that its hypotheses hold if and only if relation (3) holds.

$$\sum_{i\notin S}\sum_{j\in S} w_{ij}^R = \sum_{i\notin S}\sum_{j\in S} w_{ji}^M, \quad \forall \varnothing \subset S \subset V. \tag{3}$$

Consider all the states where only one node i is resident, i.e. $S = V \setminus \{i\}$. Then from relation (3) we get the following set of equations that must hold:

$$\sum_{j\neq i} w_{ji}^M = \sum_{j\neq i} w_{ij}^R = 1, \quad \forall i \in V. \tag{4}$$

Similarly, for all the states where $S = \{i\}$ we get from relation (3):

$$\sum_{j \neq i} w_{ji}^R = \sum_{j \neq i} w_{ij}^M = 1, \quad \forall i \in V. \tag{5}$$

Now, (for general S) the two parts of (3) are:

$$\sum_{i \notin S} \sum_{j \in S} w_{ij}^R = |V| - |S| - \sum_{i \notin S} \sum_{j \notin S} w_{ij}^R \tag{6}$$

$$\text{and} \quad \sum_{i \notin S} \sum_{j \in S} w_{ji}^M = |V| - |S| - \sum_{i \notin S} \sum_{j \notin S} w_{ji}^M, \quad \text{(using (4))}. \tag{7}$$

Thus, by relation (3) it must be: $\displaystyle\sum_{i \notin S} \sum_{j \notin S} w_{ij}^R = \sum_{i \notin S} \sum_{j \notin S} w_{ji}^M, \quad \forall \varnothing \subset S \subset V.$ (8)

Now, consider all the states where only two nodes i and j are resident, i.e. $S = V \setminus \{i, j\}$. Then from relation (8) we get the following set of relations that must hold:

$$w_{ij}^R + w_{ji}^R = w_{ij}^M + w_{ji}^M, \quad \forall i, j \in V. \tag{9}$$

To prove the other direction of the equivalence we show that the sets of relations (4),(9) suffice to make (3) true. If (9) is true, then (8) is obviously true. And, by using (4), the left-hand side of (6) and (7) are equal, thus (3) is true. □

Observe that when $G_R = G_M$ we have the isothermal theorem of the special case of the generalized Moran process that has been studied so far.

6 A Strategic Game View

In this section we study the aforementioned process from a game-theoretic point of view. Consider the strategic game with 2 players; residents (type R) and mutants (type M), so the player set is $N = \{R, M\}$. The action set of a player $k \in N$ consists of all possible strongly connected graphs[4] $G_k(V, E_k)$ that she can construct with the available vertex set V. The payoff for the residents (player R) is the probability of extinction, and the payoff for the mutants (player M) is the probability of fixation. Of course, the sum of payoffs equals 1, so the game can be reduced to a zero-sum game.

The natural question that emerges is: what are the pure Nash equilibria of this game (if any)? For example, for fixed $r > 1$, if we only consider two actions for every player, namely the graphs CL and UST, then from our results from Subsection 6.1, when $n \to \infty$, we get $f_{CL,UST} \to 0$, $f_{UST,CL} \to 1$ and from [1,14], $f_{CL,CL} \to 1 - 1/r$ and $f_{UST,UST} \to 1 - 1/r^2$. Therefore, we get the following bimatrix game:

[4] We assume strong connectivity in order to avoid problematic cases where there is neither fixation nor extinction.

		Player M: CL	Player M: UST
Player R	CL	$1/r$, $1-1/r$	1 , 0
	UST	0 , 1	$1/r^2$, $1-1/r^2$

which has a pure Nash equilibrium, namely (CL, CL). Trying to understand better the behaviour of the two conflicting graphs, we put some pairs of them to the test. The main question we ask in this work is: what is the best response graph G_R of the residents to the Clique graph of the mutants? In the sequel, we will use the abbreviations *pl-R* and *pl-M* for the resident and the mutant population, respectively.

In the proofs of this paper we shall use the following fact from [14]:

Fact 1 *In a birth-death process with state space* $\{0, 1, \ldots, n\}$*, absorbing states* $0, n$ *and backward bias at state* k *equal to* γ_k*, the probability of absorption at* n*, given that we start at* i *is*

$$f_i = \frac{1 + \sum_{j=1}^{i-1} \prod_{k=1}^{j} \gamma_k}{1 + \sum_{j=1}^{n-1} \prod_{k=1}^{j} \gamma_k}.$$

6.1 Star vs Clique

The following result implies (since $(n-4)!^{-1/(n-2)} \to 0$ as $n \to \infty$) that when the mutant graph is complete and the resident graph is the undirected star, the fixation probability tends to 1 as n goes to infinity.

Theorem 3. *If pl-R has the* UST *graph and pl-M has the* CL *graph for* $r > (n-4)!^{-1/(n-2)}$*, then the payoff of pl-M (fixation probability) is lower bounded by* $\frac{1-\frac{1}{n}}{1+\frac{1}{r(n-2)}+\frac{1}{r^2(n-3)}} > 1 - \frac{1}{n} - \frac{1}{r(n-2)} - \frac{1}{r^2(n-3)}$.

Proof. We will find a lower bound to the fixation probability of our process P, by finding the fixation probability of a process P' that is dominated by (has at most the fixation probability of) P. Here is P': Have the undirected star graph $G_R(V, E_R)$ for the residents and the clique graph $G_M(V, E_M)$ for the mutants. We start with a single mutant on a node uniformly at random from the vertex set. If that node is the central one of G_R, then at the next time step it is attacked by a resident with probability 1 and the process ends with the residents occupying the vertex set. If the initial mutant node is a leaf, then the process continues with the following restriction: whenever a mutant node is selected to reproduce on the central node of G_R, instead it reproduces on itself, unless all leaves of G_R are mutants. P' can be modelled as the following Markov chain:

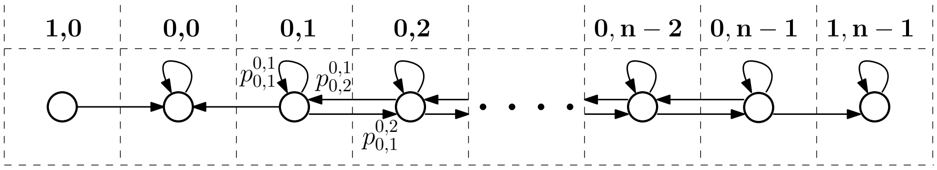


Fig. 3. The Markov chain for process P'.

In Figure 3 we denote by $\langle c, l\rangle$ the state of process P' that has c mutants at the center of G_R (star graph) and l mutants at the leaves of G_R. We also denote by $f_{1,0}$ the fixation probability given that the initial mutant node of process P' is the center of G_R, and by $f_{0,1}$ the fixation probability given that the initial mutant node is a leaf of G_R. Now, the exact fixation probability f' of process P' is:

$$f' = \frac{1}{n} f_{1,0} + \left(1 - \frac{1}{n}\right) f_{0,1} = \left(1 - \frac{1}{n}\right) f_{0,1} \quad \text{, since } f_{1,0} = 0.$$

Now, for a state $\langle 0, i\rangle$ where $1 \le i \le n-1$, the probability of going to state $\langle 0, i-1\rangle$ in the next step is:

$$p_{0,i}^{0,i-1} = \frac{1}{ir + n - i} \cdot \frac{i}{n-1}.$$

For a state $\langle 0, i\rangle$ where $1 \le i \le n-2$ the probability of going to state $\langle 0, i+1\rangle$ in the next step is:

$$p_{0,i}^{0,i+1} = \frac{ir}{ir + n - i} \cdot \frac{n-i-1}{n-1}$$

$$\text{and} \quad p_{0,i}^{0,i+1} = \frac{(n-1)r}{(n-1)r+1} \cdot \frac{1}{n-1} \quad \text{when } i = n-1$$

and the probability of remaining to state $\langle 0, i\rangle$ is: $p_{0,i}^{0,i} = 1 - p_{0,i}^{0,i-1} - p_{0,i}^{0,i+1}$. In our case, where we want the fixation probability given that we start from state $\langle 0, 1\rangle$, by using Fact 1, we get the following:

$$f_{0,1} = \frac{1}{1 + \sum_{j=1}^{n-1} \prod_{k=1}^{j} \gamma_k} \tag{10}$$

From the transition probabilities of our Markov chain, we can see that:

$$\gamma_k = \frac{1}{r} \cdot \frac{1}{n-k-1} \quad \text{, for } 1 \le k \le n-2$$

$$\text{and} \quad \gamma_k = \frac{1}{r} \quad \text{, for } k = n-1.$$

So, from (10) we get:

$$\begin{aligned} f_{0,1} &= \frac{1}{1 + \frac{1}{r(n-2)} + \frac{1}{r^2(n-2)(n-3)} + \frac{1}{r^3(n-2)(n-3)(n-4)} + \cdots + \frac{1}{r^{n-2}(n-2)(n-3)\cdots 1} + \frac{1}{r^{n-1}(n-2)(n-3)\cdots 1}} \\ &\ge \frac{1}{1 + \frac{1}{r(n-2)} + \frac{1}{r^2(n-2)(n-3)} \cdot (n-2)} \qquad \text{, for } r > (n-4)!^{-1/(n-2)} \\ &= \frac{1}{1 + \frac{1}{r(n-2)} + \frac{1}{r^2(n-3)}} \end{aligned}$$

and for the required fixation probability we get:

$$\begin{aligned} f' &= \frac{1 - \frac{1}{n}}{1 + \frac{1}{r(n-2)} + \frac{1}{r^2(n-3)}} \\ &\to 1 \quad \text{as} \quad n \to \infty. \end{aligned}$$

This completes the proof of Theorem 3. □

It is worth noting that, since the game we defined in Subsection 6 is 1-sum, we immediately can get upper (resp. lower) bounds on the payoff of pl-R, given lower (resp. upper) bounds on the payoff of pl-M.

Now we give the following lemma that connects the fixation probability of a process with given relative fitness, resident and mutant graphs, with the fixation probability of a "mirror" process where the roles between residents and mutants are exchanged.

Lemma 1. $f_{G_R,G_M}(r) \le 1 - f_{G_M,G_R}(\frac{1}{r})$.

Proof. We denote by $f^S_{G_R,G_M}(r)$ the probability of fixation when our population has a set of mutants S with relative fitness $r > 0$, resident graph G_R and mutant graph G_M. We first prove the following:

Claim. $f^S_{G_R,G_M}(r) = 1 - f^{V\setminus S}_{G_M,G_R}(\frac{1}{r})$.

Proof. The probability of fixation for a mutant set S and mutant graph G_M is the same as the probability of extinction of the resident set $V \setminus S$, i.e. one minus the probability of the set $V \setminus S$ conquering the graph. Thus, if we exchange the labels of residents and mutants, the relative fitness of the new residents is 1 and the relative fitness of the new mutants is $1/r$, the new resident graph is G_M, the new mutant graph is G_R and the new mutant set is $V \setminus S$. □

We can now prove Lemma 1 as follows: By the above Claim we have $f^{\{u\}}_{G_R,G_M}(r) = 1 - f^{V\setminus\{u\}}_{G_M,G_R}(\frac{1}{r})$ for every $u \in V$. Since $f^{\{v\}}_{G_M,G_R}(\frac{1}{r}) \leq f^{V\setminus\{u\}}_{G_M,G_R}(\frac{1}{r})$ for every $v \neq u$, we get that $f^{\{u\}}_{G_R,G_M}(r) \leq 1 - f^{\{v\}}_{G_M,G_R}(\frac{1}{r})$. Averaging over all nodes in V we get the required inequality. □

This result provides easily an upper bound on the fixation probability of a given process when a lower bound on the fixation probability is known for its "mirror" process. For example, using Theorem 3 and Lemma 1 we get an upper bound $\frac{1}{n} + \frac{1}{r(n-2)} + \frac{1}{r^2(n-3)}$ for $r > 0$ on the fixation probability of CL vs UST; this immediately implies that the probability of fixation in this case tends to 0. However, as we subsequently explain, a more precise lower bound is necessary to reveal the approximation restrictions of the particular process.

Theorem 4. *If pl-R has the CL graph and pl-M has the UST graph for $r > 0$, then the payoff of pl-M (fixation probability) is upper bounded by $\frac{r^{n-1}}{(n-2)!}$.*

Proof. In order to show this, we give a pair of graphs that yields fixation probability upper bounded by an $o\left(\frac{r^{n-1}}{(n-2)!}\right)$ function. Have the Clique graph $G_R(V, E_R)$ for the residents and the Undirected Star graph $G_M(V, E_M)$ for the mutants; we will call this process P. We will find an upper bound of its fixation probability by considering the following process P' that favors the mutants. Here is P': Have the aforementioned graphs. We start with a single mutant on the central node of G_M. If a mutant is selected to reproduce on a mutant, it reproduces according to the exact same rules of P. If a resident is selected to reproduce on a resident, it also reproduces according to the exact same rules of P. If a resident is selected to reproduce on a mutant, it reproduces according to the exact same rules of P, unless that mutant is the central one; then the resident reproduces on itself, unless all leaves of G_M are residents.

The corresponding Markov chain has $n+1 = |V|+1$ states. A state $\langle i \rangle$, where $i \in \{0, 1, 2, ..., n\}$ is the number of mutants and the only absorbing states are $\langle 0 \rangle$ and $\langle n \rangle$. For state $\langle 1 \rangle$ the probability of going to state $\langle 0 \rangle$ in the next step is:

$$p_1^0 = \frac{n-1}{r+n-1} \cdot \frac{1}{n-1} = \frac{1}{r+n-1}.$$

For a state $\langle i \rangle$, where $i \in \{2, 3, ..., n-1\}$, the probability of going to state $\langle i-1 \rangle$ in the next step is:

$$p_i^{i-1} = \frac{n-i}{ir+n-i} \cdot \frac{i-1}{n-1}.$$

For a state $\langle i \rangle$, where $i \in \{1, 2, ..., n-1\}$, the probability of going to state $\langle i+1 \rangle$ in the next step is:

$$p_i^{i+1} = \frac{r}{ir+n-i} \cdot \frac{n-i}{n-1},$$

and the probability of staying to state $\langle i\rangle$ in the next step is: $p_i^i = 1-p_i^{i-1}-p_i^{i+1}$. In our case, where we want the fixation probability given that we start from state $\langle 1\rangle$, by using Fact 1 we get the following:

$$f_1 = \frac{1}{1+\sum_{j=1}^{n-1}\prod_{k=1}^{j}\gamma_k} \tag{11}$$

From the transition probabilities of our Markov chain, we can see that:

$$\begin{aligned} &\gamma_1 = \frac{1}{r} \\ \text{and} \quad &\gamma_k = \frac{1}{r}\cdot(k-1) \quad \text{, for } 2 \le k \le n-1. \end{aligned}$$

So, from (11) we get:

$$\begin{aligned} f_1 &= \frac{1}{1+\frac{1}{r}1+\frac{1}{r^2}1+\frac{1}{r^3}2+\frac{1}{r^4}3!+\cdots+\frac{1}{r^{n-1}}(n-2)!} \\ &\le \frac{r^{n-1}}{(n-2)!} \\ &\in o\left(\frac{1}{a^n}\right) \quad \text{, where} \quad a>1 \quad \text{is constant.} \end{aligned}$$

This completes the proof of Theorem 4. □

This bound shows that, not only there exists a graph that suppresses selection against the UST (which is an amplifier in the 1-graph setting), but it also does that with great success. In fact for any mutant with constant r arbitrarily large, its fixation probability is less than exponentially small.

In view of the above, the following result implies that the fixation probability in our model cannot be approximated via a method similar to [2].

Theorem 5 (Bounds on the 2-graphs Moran process). *There is a pair of graphs G_R, G_M such that the fixation probability f_{G_R,G_M} is $o\left(\frac{1}{a^n}\right)$, for some constant $a>1$, when the relative fitness r is constant. Furthermore, there is a pair of graphs G'_R, G'_M such that the fixation probability $f_{G'_R,G'_M}$ is at least $1-O\left(\frac{1}{n}\right)$, for constant $r>0$.*

Proof. See Theorem 3 and proof of Theorem 4. □

6.2 Arbitrary Undirected Graphs vs Clique

The following result is a lower bound on the fixation probability.

Theorem 6. *When pl-R has an undirected graph for which $w^R_{xy}/w^R_{yx} \leq c$ for every $(xy) \in E_R$ and pl-M has the CL graph, the payoff of pl-M (fixation probability) is lower bounded by* $\left[\frac{1-\left(\frac{c}{r}\right)^{\log n}}{1-\frac{c}{r}}(1+o(1)) + \frac{\left(\frac{2c}{r}\right)^{\log n} - \left(\frac{2c}{r}\right)^{n}}{1-\frac{2c}{r}}\right]^{-1}$*, for $r > 0$. In particular, for $r > 2c$ the lower bound tends to $1 - \frac{c}{r}$ as $n \to \infty$.*

Proof. Notice that, given the number of mutants at a time-step is $i := |S|$, the probability that a resident becomes mutant is $p_i^{i+1} = \frac{ir}{ir+n-i} \cdot \frac{n-i}{n-1}$, and the probability that a mutant becomes resident p_i^{i-1} is upper bounded by $\frac{\min\{i,n-i\}}{ir+n-i} \max\limits_{(xy)\in E_R} \frac{w^R_{xy}}{w^R_{yx}}$. That is because the maximum possible number of resident-to-mutant edges in G_R at a step with i mutants is achieved when either every mutant has edges in G_R only towards residents, or every resident has edges in G_R only towards mutants; and the most extreme case is when every one of the $\min\{i, n-i\}$ nodes has sum of weights of incoming edges equal to the maximum ratio of degrees of adjacent nodes in G_R, i.e. $c := \max\limits_{(xy)\in E_R} \frac{w^R_{xy}}{w^R_{yx}}$.

This means that the number of mutants in our given process P of an undirected graph vs Clique stochastically dominates a birth-death process P' that is described by the following Markov chain: A state $\langle i \rangle$, where $i \in \{0, 1, 2, ..., n\}$ is the number of mutants on the vertex set and the only absorbing states are $\langle 0 \rangle$ and $\langle n \rangle$. Using Fact 1, we get: $f_1 = 1/\left(1 + \sum_{j=1}^{n-1} \prod_{k=1}^{j} \gamma_k\right)$, where $\gamma_i = p_i^{i-1}/p_i^{i+1}$. From the aforementioned transition probabilities of our Markov chain we have:

$$\gamma_k \leq \begin{cases} \frac{c}{r} \cdot \frac{n-1}{n-k}, & \text{for } k \in \{1, 2, .., \left\lfloor \frac{n}{2} \right\rfloor\} \\ \frac{c}{r} \cdot \frac{n-1}{k}, & \text{for } k \in \{\left\lfloor \frac{n}{2} \right\rfloor + 1, .., n-1\} \end{cases}$$

Now we can calculate a lower bound on the fixation probability of P' using the fact that $\frac{n-1}{n-2} = 1 + \frac{1}{n-2}, \frac{n-1}{n-3} = 1 + \frac{2}{n-3}, \cdots, \frac{n-1}{n-\log n+1} = 1 + \frac{\log n - 2}{n - \log n + 1}$:

$$\begin{aligned} f_1 &= \frac{1}{\left[\sum_{j=0}^{\log n-1} \left(\frac{c}{r}\right)^j\right](1+o(1)) + \left(\frac{c}{r}\right)^{\log n} \frac{(n-1)^{\log n}}{(n-1)\cdots(n-\log n)} + \cdots + \left(\frac{c}{r}\right)^{n-1} \frac{(n-1)^{n-1}}{\left[(n-1)\cdot\dots\cdot\left(\frac{n}{2}+1\right)\right]^2 \cdot \left(\frac{n}{2}\right)}} \\ &\geq \frac{1}{\frac{1-\left(\frac{c}{r}\right)^{\log n}}{1-\frac{c}{r}}(1+o(1)) + \left(\frac{2c}{r}\right)^{\log n} \sum_{j=0}^{n-\log n-1} \left(\frac{2c}{r}\right)^j} \quad , (\gamma_k \text{ is upper bounded by } \frac{2c}{r}) \\ &= \frac{1}{\frac{1-\left(\frac{c}{r}\right)^{\log n}}{1-\frac{c}{r}}(1+o(1)) + \left(\frac{2c}{r}\right)^{\log n} \frac{1-\left(\frac{2c}{r}\right)^{n-\log n}}{1-\frac{2c}{r}}}. \end{aligned}$$

□

From the theorem above it follows that if G_R is undirected regular then the fixation probability of G_R vs CL is lower bounded by $1 - 1/r$ for $r > 2$ and $n \to \infty$, which equals f_{Moran} (defined in Section 2).

Also, by Lemma 1 and the above theorem, when $G_R = CL$, G_M is an undirected graph with $w^M_{xy}/w^M_{yx} \leq c$ for every $(xy) \in E_M$, and relative fitness $r < \frac{1}{2c}$, then the upper bound of the fixation probability tends to $\frac{c}{r}$ as $n \to \infty$.

6.3 Circulant Graphs vs Clique

In this subsection we give bounds for the fixation probability of CId vs CL. We first prove the following result that gives an upper bound on the fixation probability when G_R is the CId graph as described in Section 2 and G_M is the complete graph on n vertices.

Theorem 7. *When mutants have the CL graph, if residents have a CId graph and $d \in \Theta(1)$, then the payoff of pl-M (fixation probability) is upper bounded by $\left[e^{\frac{1}{r}} - \frac{1}{r^n}\frac{1}{n!}\frac{1}{1-\frac{1}{r}}\right]^{-1}$ for $r > 1$ and $\left[e^{\frac{1}{r}} - \frac{1}{r^n}\frac{1}{n!} - o(1)\right]^{-1}$ for $r \leq 1$. In particular, for constant $r > 0$ the upper bound tends to $e^{-\frac{1}{r}}$. If $d \in \omega(1)$, then the upper bound is $\left(1 - \frac{1}{r}\right)\left[1 - \frac{1}{r^{g(n)}} - o(1)\right]^{-1}$, for $r > 0$, where $g(n)$ is a function of n such that $g(n) \in \omega(1)$ and $g(n) \in o(d)$. The bound improves as $g(n)$ is picked closer to $\Theta(d)$ and, in particular, for $r > 1$ it tends to $1 - \frac{1}{r}$.*

Proof. We will bound from above the payoff of the mutant (i.e. the fixation probability) of our process P, by finding the fixation probability of a process P' that dominates (has at least the fixation probability of) P. The dominating process P' is the least favorable for the residents. Here is P': Have the CId graph for the residents, as defined in Section 2 in the more general case where the number of its vertices does not concern us, and the clique graph for the mutants. We start with a single mutant on a node (w.l.o.g. we give it label $j = 1$) uniformly at random from the vertex set. Throughout the process, if a resident is selected to reproduce on a resident, it reproduces according to the exact same rules of P. If a mutant is selected to reproduce on a mutant, it reproduces according to the exact same rules of P. However, if a mutant is selected to reproduce on a resident, it obeys to the following restriction: it can only reproduce on a resident that is connected to the maximum number of mutants possible (equiprobably, but it does not really matter due to the symmetry of the produced population). If a resident is selected to reproduce on a mutant when the number of mutants is $i \in \{1, 2, ..., n-1\}$, then the last among the i mutants that was inserted becomes resident, thus preserving the minimality of the probability of the residents to hit the mutants (see Figure 4).

It is easy to see that process P' allocates the mutants in a chain-like formation that allows residents to "hit" the mutants with the smallest possible number of resident edges. In other words, if we consider the mutant set S and the resident set $V \setminus S$, in every step of the process the number of resident edges on the cut $(S, V \setminus S)$ of G_R is minimum. This process is the worst the residents could deal with.

Due to the symmetry that our process P' brings on the population instances, the corresponding Markov chain has $n + 1 = |V| + 1$ states, as every state with the same number of mutants can be reduced to a single one. A state $\langle i \rangle$, where $i \in \{0, 1, 2, ..., n\}$ is the number of mutants and the only absorbing states are $\langle 0 \rangle$ and $\langle n \rangle$. After careful calculations we get that, for a state $\langle i \rangle$, where

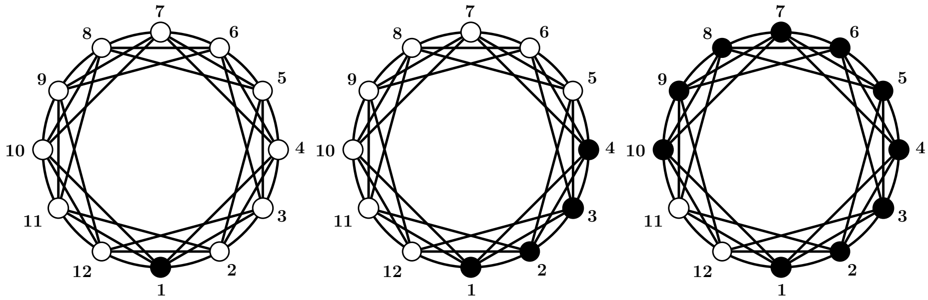


Fig. 4. Three instances of process P'. Only the resident graph $G_R = CId$ is shown. White nodes are residents and black nodes are mutants. Here $d = 6$ and $n = 12$.

$i \in \{1, 2, ..., n-1\}$, the probability of going to state $\langle i-1 \rangle$ in the next step is:

$$p_i^{i-1} = \begin{cases} \frac{1}{ir+n-i} \cdot i\left(1 - \frac{i-1}{d}\right), & \text{for } i \in \{1, 2, .., \frac{d}{2}+1\} \\ \frac{1}{ir+n-i} \cdot \frac{1}{2} \cdot \left(\frac{d}{2}+1\right), & \text{for } i \in \{\frac{d}{2}+2, .., n-\frac{d}{2}\} \\ \frac{1}{ir+n-i} \cdot \left[\frac{1}{2} \cdot \left(\frac{d}{2}+1\right) - \frac{1}{d} \cdot \left(i-n+\frac{d}{2}\right)\left(i-n+\frac{d}{2}+1\right)\right], & \text{for } i \in \{n-\frac{d}{2}+1, .., n-1\} \end{cases}$$

the probability of going to state $\langle i+1 \rangle$ in the next step is:

$$p_i^{i+1} = \frac{ir}{ir+n-i} \cdot \frac{n-i}{n-1}.$$

and the probability of staying to state $\langle i \rangle$ in the next step is: $p_i^i = 1 - p_i^{i-1} - p_i^{i+1}$. In our case, where we want the fixation probability given that we start from state $\langle 1 \rangle$, by using Fact 1 we get the following:

$$f_1 = \frac{1}{1 + \sum_{j=1}^{n-1} \prod_{k=1}^{j} \gamma_k} \tag{12}$$

If ***d* is constant**: from the transition probabilities of our Markov chain, we can see that:

$$\gamma_k \geq \frac{1}{r} \cdot \frac{n-1}{k(n-k)} \quad \text{, for } 1 \leq k \leq n-1.$$

So, from (12) we get:

$$
\begin{aligned}
f_1 &= \frac{1}{1+\frac{1}{r}\frac{n-1}{n-1}+\frac{1}{r^2}\frac{(n-1)^2}{2(n-1)(n-2)}+\frac{1}{r^3}\frac{(n-1)^3}{3!(n-1)(n-2)(n-3)}+\cdots+\frac{1}{r^{(n-1)}}\frac{(n-1)^{(n-1)}}{[(n-1)!]^2}} \\
&\le \frac{1}{1+\frac{1}{r}+\frac{1}{r^2}\frac{1}{2}+\frac{1}{r^3}\frac{1}{3!}+\cdots+\frac{1}{r^{(n-1)}}\frac{1}{(n-1)!}} \\
&= \frac{1}{e^{\frac{1}{r}}-\left[\frac{1}{r^n}\frac{1}{n!}+\frac{1}{r^{(n+1)}}\frac{1}{(n+1)!}+\cdots\right]} \\
&= \frac{1}{e^{\frac{1}{r}}-\frac{1}{r^n}\frac{1}{n!}\left[1+\frac{1}{r}\frac{1}{n+1}+\frac{1}{r^2}\frac{1}{(n+1)(n+2)}+\cdots\right]} \\
&\le \frac{1}{e^{\frac{1}{r}}-\frac{1}{r^n}\frac{1}{n!}\left[1+\frac{1}{r}+\frac{1}{r^2}+\cdots\right]}, \text{ for } r>1, \text{ or } \le \frac{1}{e^{\frac{1}{r}}-\frac{1}{r^n}\frac{1}{n!}-o(1)}, \text{ for constant } r\le 1 \\
&= \frac{1}{e^{\frac{1}{r}}-\frac{1}{r^n}\frac{1}{n!}\frac{1}{1-\frac{1}{r}}}, \text{ for } r>1, \quad \text{or} \quad = \frac{1}{e^{\frac{1}{r}}-\frac{1}{r^n}\frac{1}{n!}-o(1)}, \text{ for constant } r\le 1 \\
&\to \frac{1}{e^{\frac{1}{r}}} \quad \text{as} \quad n\to\infty.
\end{aligned}
$$

If $\boldsymbol{d \in \omega(1)}$ **and** $\boldsymbol{d \in O(n)}$: take a function $g(n) \in \omega(1)$ and $g(n) \in o(d)$. Then, from the transition probabilities of our Markov chain and (12) we get:

$$
\begin{aligned}
f_1 &\le \frac{1}{1+\sum_{j=1}^{d/2+1}\prod_{k=1}^{j}\gamma_k} \le \frac{1}{1+\sum_{j=1}^{g(n)}\prod_{k=1}^{j}\gamma_k} \\
&\le \frac{1}{1+\frac{1}{r}+\frac{1}{r^2}\left(1-\frac{1}{d}\right)+\frac{1}{r^3}\left(1-\frac{1}{d}\right)\left(1-\frac{2}{d}\right)+\cdots+\frac{1}{r^{g(n)-1}}\left(1-\frac{1}{d}\right)\left(1-\frac{2}{d}\right)\cdots\left(1-\frac{g(n)-2}{d}\right)} \\
&\le \frac{1}{\left[1+\frac{1}{r}+\frac{1}{r^2}+\frac{1}{r^3}+\cdots+\frac{1}{r^{g(n)-1}}\right]-o(1)} \\
&= \frac{1}{\frac{1-\frac{1}{r^{g(n)}}}{1-\frac{1}{r}}-o(1)} \\
&\to 1-\frac{1}{r} \quad \text{when} \quad r>1 \quad \mathit{as} \quad n\to\infty.
\end{aligned}
$$

This completes the proof of Theorem 7. $\square$

We also show that our upper bound becomes tighter as d increases. In particular, we prove the following lower bounds:

Theorem 8. *When mutants have the CL graph, if residents have the UCY (degree d=2) or a graph of the class CId for degree d=4,6 or 8, then the payoff of pl-M (fixation probability) is lower bounded by* $\left[\frac{1-\left(\frac{1}{r}\right)^{\log n}}{1-\frac{1}{r}}(1+o(1))+\frac{\left(\frac{c}{r}\right)^{\log n}-\left(\frac{c}{r}\right)^{n}}{1-\frac{c}{r}}\right]^{-1}$*, where* $c=\frac{d+2}{d}$ *for* $r>0$*. In particular, for* $r>c$ *the lower bound tends to* $1-\frac{1}{r}$ *as* $n\to\infty$*.*

Proof. We prove one by one each of the cases: *UCY vs CL*, *CI4 vs CL*, *CI6 vs CL* and *CI8 vs CL*.

UCY vs Clique. We will bound from below the payoff of the mutant (i.e. the fixation probability) of our process P, by finding the fixation probability of a process P'' that is dominated by (has at most the fixation probability of) P. The dominated process P'' is the most favorable for the residents. Here is P'': Have the undirected 2-regular graph $G_R(V, E_R)$ for the residents and the clique graph $G_M(V, E_M)$ for the mutants. Note the way we have numbered the nodes in Figure 5. We start with a single mutant on a node (w.l.o.g. we give it label $j = 1$) uniformly at random from the vertex set. Throughout the process, if a resident is selected to reproduce on a resident, it reproduces according to the exact same rules of P. If a mutant is selected to reproduce on a mutant, it reproduces according to the exact same rules of P. However, if a mutant is selected to reproduce on a resident, it obeys the following restrictions:

– When the number of mutants is $i \in \{1, 2, ..., \lfloor \frac{n}{2} \rfloor\}$, when a resident is chosen to die, the resident with the smallest odd label j becomes mutant.
– When the number of mutants is $i \in \{\lfloor \frac{n}{2} \rfloor + 1, ..., n-1\}$, then the resident that is chosen to die, dies.

If a resident is selected to reproduce on a mutant when the number of mutants is $i \in \{1, 2, ..., n-1\}$, then the last among the i mutants that was inserted becomes resident, thus preserving the maximality of the probability of the residents to hit the mutants (see Figure 5).

It is easy to see that the first $\lfloor \frac{n}{2} \rfloor$ mutants in process P'' are allocated in such a way, so that a mutant is always connected to two residents. Thus, the edges going from residents to mutants are maximized. This is the least favorable allocation for the mutants.

A state $\langle i \rangle$, where $i \in \{0, 1, 2, ..., n\}$ is the number of mutants on the vertex set and the only absorbing states are $\langle 0 \rangle$ and $\langle n \rangle$. For a state $\langle i \rangle$, where $i \in \{1, 2, ..., \lfloor \frac{n}{2} \rfloor\}$, the probability of going to state $\langle i-1 \rangle$ in the next step is:

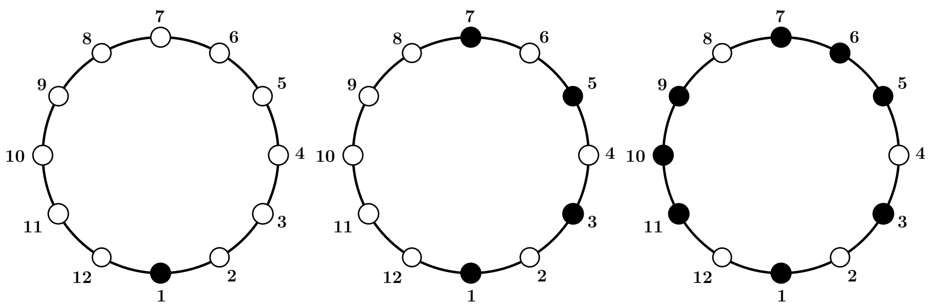


Fig. 5. Three instances of process P''. Only the resident graph $G_R = UCY$ is shown. White nodes are residents and black nodes are mutants.

$$p_i^{i-1} = \frac{i}{ir+n-i},$$

the probability of going to state $\langle i+1 \rangle$ in the next step is:

$$p_i^{i+1} = \frac{ir}{ir+n-i} \cdot \frac{n-i}{n-1}.$$

and the probability of staying to state $\langle i \rangle$ in the next step is: $p_i^i = 1 - p_i^{i-1} - p_i^{i+1}$.

For a state $\langle i \rangle$, where $i \in \{\lfloor \frac{n}{2} \rfloor + 1, ..., n-1\}$, the probability of going to state $\langle i-1 \rangle$ in the next step is:

$$p_i^{i-1} = \frac{n-i}{ir+n-i},$$

the probability of going to state $\langle i+1 \rangle$ in the next step is:

$$p_i^{i+1} = \frac{ir}{ir+n-i} \cdot \frac{n-i}{n-1}.$$

and the probability of staying to state $\langle i \rangle$ in the next step is: $p_i^i = 1 - p_i^{i-1} - p_i^{i+1}$. In our case, where we want the fixation probability given that we start from state $\langle 1 \rangle$, by using Fact 1, we get the following:

$$f_1 = \frac{1}{1 + \sum_{j=1}^{n-1} \prod_{k=1}^{j} \gamma_k} \tag{13}$$

From the transition probabilities of our Markov chain, we can see that:

$$\begin{aligned} & \gamma_k \leq \frac{1}{r} \cdot \frac{n-1}{n-k} \quad \text{, for } 1 \leq k \leq \left\lceil \frac{n}{2} \right\rceil \\ \text{and} \quad & \gamma_k = \frac{1}{r} \cdot \frac{n-1}{k} \quad \text{, for } \left\lceil \frac{n}{2} \right\rceil + 1 \leq k \leq n-1. \end{aligned}$$

So, from (13) we get:

$$f_1 = \frac{1}{1 + \frac{1}{r} + \frac{1}{r^2}\frac{(n-1)^2}{(n-1)(n-2)} + \cdots + \frac{1}{r^{\frac{n}{2}-1}}\frac{(n-1)^{\frac{n}{2}-1}}{(n-1)\cdots\cdots\left(\frac{n}{2}+1\right)} + \frac{1}{r^{\frac{n}{2}}}\frac{(n-1)^{\frac{n}{2}}}{(n-1)\cdots\cdots\left(\frac{n}{2}\right)} + \cdots + \frac{1}{r^{n-1}}\frac{(n-1)^{n-1}}{\left[(n-1)\cdots\cdots\left(\frac{n}{2}+1\right)\right]^2\cdot\left(\frac{n}{2}\right)}}$$

and since $\dfrac{n-1}{n-2} = 1 + \dfrac{1}{n-2}, \quad \dfrac{n-1}{n-3} = 1 + \dfrac{2}{n-3}, \cdots, \dfrac{n-1}{n-\log n+1} = 1 + \dfrac{\log n - 2}{n - \log n + 1},$

$$= \frac{1}{\left[1 + \frac{1}{r} + \frac{1}{r^2} + \cdots + \frac{1}{r^{\log n-1}}\right](1+o(1)) + \frac{1}{r^{\log n}}\frac{(n-1)^{\log n}}{(n-1)\cdots(n-\log n)} + \cdots + \frac{1}{r^{n-1}}\frac{(n-1)^{n-1}}{\left[(n-1)\cdots\cdots\left(\frac{n}{2}+1\right)\right]^2\cdot\left(\frac{n}{2}\right)}}$$

$$\geq \frac{1}{\frac{1-\left(\frac{1}{r}\right)^{\log n}}{1-\frac{1}{r}}(1+o(1)) + \left(\frac{2}{r}\right)^{\log n}\left[1 + \frac{2}{r} + \left(\frac{2}{r}\right)^2 + \cdots + \left(\frac{2}{r}\right)^{n-\log n-1}\right]}$$, since γ_k is upper bounded by

$$= \frac{1}{\frac{1-\left(\frac{1}{r}\right)^{\log n}}{1-\frac{1}{r}}(1+o(1)) + \left(\frac{2}{r}\right)^{\log n}\frac{1-\left(\frac{2}{r}\right)^{n-\log n}}{1-\frac{2}{r}}}$$

$$\to 1 - \frac{1}{r} \quad \text{when} \quad r > 2 \quad as \quad n \to \infty.$$

CI4 vs Clique. We will bound from below the payoff of the mutant (i.e. the fixation probability) of our process P, by finding the fixation probability of a process P'' that is dominated by P. The dominated process P'' is the most favorable for the residents. Here is P'': Have the $CI4$ graph for the residents and the clique graph for the mutants. Note the way we have numbered the nodes in Figure 2. We start with a single mutant on a node (w.l.o.g. we give it label $j = 1$) uniformly at random from the vertex set. Throughout the process, if a resident is selected to reproduce on a resident, it reproduces according to the exact same rules of P. If a mutant is selected to reproduce on a mutant, it reproduces according to the exact same rules of P. However, if a mutant is selected to reproduce on a resident, it obeys the following restrictions:

- When the number of mutants is $i \in \left\{1, 2, ..., \left\lfloor \frac{n}{3} \right\rfloor\right\}$, when a resident is chosen to die, the resident with the smallest label $j = 3m + 1$ for some $m \in \mathbb{N}$ becomes mutant.
- When the number of mutants is $i \in \left\{\left\lfloor \frac{n}{3} \right\rfloor + 1, ..., \left\lfloor \frac{2n}{3} \right\rfloor\right\}$, when a resident is chosen to die, the resident with the smallest label $j = 3m + 2$ for some $m \in \mathbb{N}$ becomes mutant.
- When the number of mutants is $i \in \left\{\left\lfloor \frac{2n}{3} \right\rfloor + 1, ..., n-1\right\}$, then the resident that is chosen to die, dies.

If a resident is selected to reproduce on a mutant when the number of mutants is $i \in \{1, 2, ..., n-1\}$, then the last among the i mutants that was inserted becomes resident, thus preserving the maximality of the probability of the residents to hit the mutants (see Figure 6). Using these rules we have put the mutants to the worst possible allocation, i.e. the probability that they get attacked by residents is maximum in every step of the process. In other words, for every

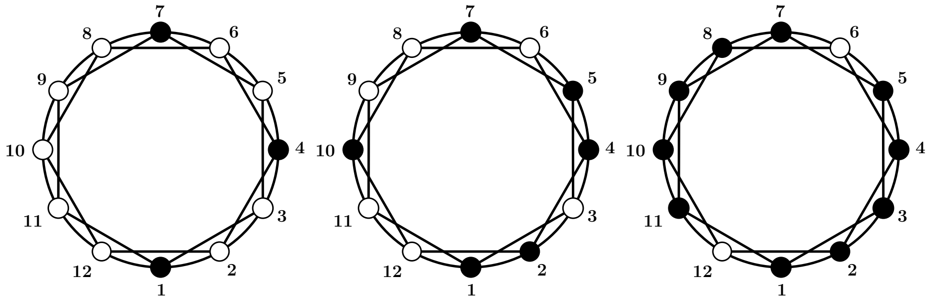


Fig. 6. Three instances of process P''. Only the resident graph $G_R = CI4$ is shown. White nodes are residents and black nodes are mutants.

$k \in \{1, 2, ..., n-1\}$ we have maximized the quotient γ_k as defined in Fact 1. Consequently, we get the following values of γ_k:

- $\gamma_k \leq \frac{1}{r}\frac{n-1}{n-k}$, for $k \in \left\{1, 2, ..., \left\lceil \frac{n}{3} \right\rceil \right\}$,
- $\gamma_k \leq \frac{1}{r}\frac{n}{3}\frac{n-1}{k(n-k)}$, for $k \in \left\{ \left\lceil \frac{n}{3} \right\rceil + 1, ..., \left\lceil \frac{2n}{3} \right\rceil \right\}$,
- $\gamma_k = \frac{1}{r}\frac{n-1}{k}$, for $k \in \left\{ \left\lceil \frac{2n}{3} \right\rceil + 1, ..., n-1 \right\}$.

As in the Undirected Cycle vs Clique case, using now the fact that γ_k is upper bounded by $\frac{3}{2r}$, we get:

$$f_1 \geq \frac{1}{\left[1 + \frac{1}{r} + \frac{1}{r^2} + \cdots + \frac{1}{r^{\log n - 1}}\right](1 + o(1)) + \left(\frac{3}{2r}\right)^{\log n} \left[1 + \frac{3}{2r} + \left(\frac{3}{2r}\right)^2 + \cdots + \left(\frac{3}{2r}\right)^{n - \log n - 1}\right]}$$

$$= \frac{1}{\frac{1 - \left(\frac{1}{r}\right)^{\log n}}{1 - \frac{1}{r}}(1 + o(1)) + \left(\frac{3}{2r}\right)^{\log n} \frac{1 - \left(\frac{3}{2r}\right)^{n - \log n}}{1 - \frac{3}{2r}}}$$

$$\to 1 - \frac{1}{r} \quad \text{when} \quad r > \frac{3}{2} \quad as \quad n \to \infty.$$

CI6 vs Clique. We will bound from below the payoff of the mutant (i.e. the fixation probability) of our process P, by finding the fixation probability of a process P'' that is dominated by P. The dominated process P'' is the most favorable for the residents. Here is P'': Have the $CI6$ graph for the residents and the clique graph for the mutants. Note the way we have numbered the nodes in Figure 2. We start with a single mutant on a node (w.l.o.g. we give it label $j = 1$) uniformly at random from the vertex set. Throughout the process, if a resident is selected to reproduce on a resident, it reproduces according to the exact same rules of P. If a mutant is selected to reproduce on a mutant, it reproduces according to the exact same rules of P. However, if a mutant is selected to reproduce on a resident, it obeys the following restrictions:

- When the number of mutants is $i \in \left\{1, 2, ..., \left\lfloor \frac{n}{4} \right\rfloor \right\}$, when a resident is chosen to die, the resident with the smallest label $j = 4m + 1$ for some $m \in \mathbb{N}$ becomes mutant.

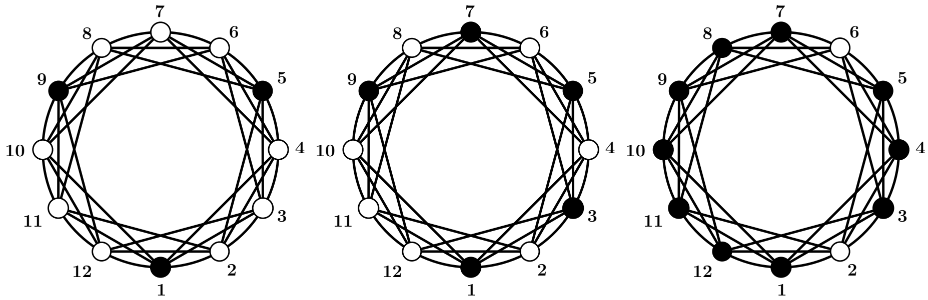


Fig. 7. Three instances of process P''. Only the resident graph $G_R = CI6$ is shown. White nodes are residents and black nodes are mutants.

- When the number of mutants is $i \in \left\{\left\lfloor \frac{n}{4} \right\rfloor + 1, ..., \left\lfloor \frac{2n}{4} \right\rfloor\right\}$, when a resident is chosen to die, the resident with the smallest label $j = 4m + 3$ for some $m \in \mathbb{N}$ becomes mutant.
- When the number of mutants is $i \in \left\{\left\lfloor \frac{2n}{4} \right\rfloor + 1, ..., \left\lfloor \frac{3n}{4} \right\rfloor\right\}$, when a resident is chosen to die, the resident with the smallest label $j = 4m + 2$ for some $m \in \mathbb{N}$ becomes mutant.
- When the number of mutants is $i \in \left\{\left\lfloor \frac{3n}{4} \right\rfloor + 1, ..., n - 1\right\}$, then the resident that is chosen to die, dies.

If a resident is selected to reproduce on a mutant when the number of mutants is $i \in \{1, 2, ..., n-1\}$, then the last among the i mutants that was inserted becomes resident, thus preserving the maximality of the probability of the residents to hit the mutants (see Figure 7). Using these rules we have put the mutants to the worst possible allocation, i.e. the probability that they get attacked by residents is maximum in every step of the process. In other words, for every $k \in \{1, 2, ..., n-1\}$ we have maximized the quotient γ_k as defined in Fact 1. Consequently, we get the following values of γ_k:

- $\gamma_k \leq \frac{1}{r} \frac{n-1}{n-k}$, for $k \in \left\{1, 2, ..., \left\lceil \frac{n}{4} \right\rceil\right\}$,
- $\gamma_k \leq \frac{1}{r} \frac{n/6 + k/3}{k} \frac{n-1}{n-k}$, for $k \in \left\{\left\lceil \frac{n}{4} \right\rceil + 1, ..., \left\lceil \frac{2n}{4} \right\rceil\right\}$,
- $\gamma_k \leq \frac{1}{r} \frac{n/2 - k/3}{k} \frac{n-1}{n-k}$, for $k \in \left\{\left\lceil \frac{2n}{4} \right\rceil + 1, ..., \left\lceil \frac{3n}{4} \right\rceil\right\}$,
- $\gamma_k = \frac{1}{r} \frac{n-1}{k}$, for $k \in \left\{\left\lceil \frac{3n}{4} \right\rceil + 1, ..., n - 1\right\}$.

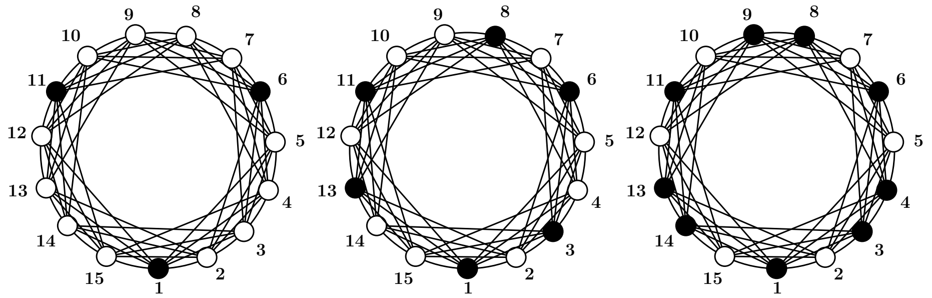


Fig. 8. Three instances of process P''. Only the resident graph $G_R = CI8$ is shown. White nodes are residents and black nodes are mutants.

As in the Undirected Cycle vs Clique case, using now the fact that γ_k is upper bounded by $\frac{4}{3r}$, we get:

$$
\begin{aligned}
f_1 &\geq \frac{1}{\left[1+\frac{1}{r}+\frac{1}{r^2}+\cdots+\frac{1}{r^{\log n-1}}\right](1+o(1))+\left(\frac{4}{3r}\right)^{\log n}\left[1+\frac{4}{3r}+\left(\frac{4}{3r}\right)^2+\cdots+\left(\frac{4}{3r}\right)^{n-\log n-1}\right]} \\
&= \frac{1}{\frac{1-\left(\frac{1}{r}\right)^{\log n}}{1-\frac{1}{r}}(1+o(1))+\left(\frac{4}{3r}\right)^{\log n}\frac{1-\left(\frac{4}{3r}\right)^{n-\log n}}{1-\frac{4}{3r}}} \\
&\to 1-\frac{1}{r} \quad \text{when} \quad r>\frac{4}{3} \quad as \quad n\to\infty
\end{aligned}
$$

CI8 vs Clique. We will bound from below the payoff of the mutant (i.e. the fixation probability) of our process P, by finding the fixation probability of a process P'' that is dominated by P. The dominated process P'' is the most favorable for the residents. Here is P'': Have the $CI8$) graph for the residents and the clique graph for the mutants. Note the way we have numbered the nodes in Fig.2. We start with a single mutant on a node (w.l.o.g. we give it label $j = 1$) uniformly at random from the vertex set. Throughout the process, if a resident is selected to reproduce on a resident, it reproduces according to the exact same rules of P. If a mutant is selected to reproduce on a mutant, it reproduces according to the exact same rules of P. However, if a mutant is selected to reproduce on a resident, it obeys the following restrictions:

- When the number of mutants is $i \in \left\{1, 2, ..., \left\lfloor \frac{n}{5} \right\rfloor\right\}$, when a resident is chosen to die, the resident with the smallest label $j = 5m + 1$ for some $m \in \mathbb{N}$ becomes mutant.
- When the number of mutants is $i \in \left\{\left\lfloor \frac{n}{5} \right\rfloor + 1, ..., \left\lfloor \frac{2n}{5} \right\rfloor\right\}$, when a resident is chosen to die, the resident with the smallest label $j = 5m+3$ for some $m \in \mathbb{N}$ becomes mutant.

– When the number of mutants is $i \in \left\{\left\lfloor \frac{2n}{5} \right\rfloor + 1, ..., \left\lfloor \frac{3n}{5} \right\rfloor\right\}$, when a resident is chosen to die, the resident with the smallest label $j = 5m + 4$ for some $m \in \mathbb{N}$ becomes mutant.
– When the number of mutants is $i \in \left\{\left\lfloor \frac{3n}{5} \right\rfloor + 1, ..., \left\lfloor \frac{4n}{5} \right\rfloor\right\}$, when a resident is chosen to die, the resident with the smallest label $j = 5m + 2$ for some $m \in \mathbb{N}$ becomes mutant.
– When the number of mutants is $i \in \left\{\left\lfloor \frac{4n}{5} \right\rfloor + 1, ..., n-1\right\}$, then the resident that is chosen to die, dies.

If a resident is selected to reproduce on a mutant when the number of mutants is $i \in \{1, 2, ..., n-1\}$, then the last among the i mutants that was inserted becomes resident, thus preserving the maximality of the probability of the residents to hit the mutants (see Figure 8).

Using these rules we have put the mutants to the worst possible allocation, i.e. the probability that they get attacked by residents is maximum in every step of the process. In other words, for every $k \in \{1, 2, ..., n-1\}$ we have maximized the quotient γ_k as defined in Fact 1. Consequently, we get the following values of γ_k:

– $\gamma_k \leq \frac{1}{r}\frac{n-1}{n-k}$, for $k\left\{1, 2, ..., \left\lceil \frac{n}{5} \right\rceil\right\}$,
– $\gamma_k \leq \frac{1}{r}\frac{n/10+k/2}{k}\frac{n-1}{n-k}$, for $k \in \left\{\left\lceil \frac{n}{5} \right\rceil + 1, ..., \left\lceil \frac{2n}{5} \right\rceil\right\}$,
– $\gamma_k \leq \frac{1}{r}\frac{3n/10}{k}\frac{n-1}{n-k}$, for $k \in \left\{\left\lceil \frac{2n}{5} \right\rceil + 1, ..., \left\lceil \frac{3n}{5} \right\rceil\right\}$,
– $\gamma_k \leq \frac{1}{r}\frac{3n/5-k/2}{k}\frac{n-1}{n-k}$, for $k \in \left\{\left\lceil \frac{3n}{5} \right\rceil + 1, ..., \left\lceil \frac{4n}{5} \right\rceil\right\}$,
– $\gamma_k = \frac{1}{r}\frac{n-1}{k}$, for $k \in \left\{\left\lceil \frac{4n}{5} \right\rceil + 1, ..., n-1\right\}$.

As in the Undirected Cycle vs Clique case, using now the fact that γ_k is upper bounded by $\frac{5}{4r}$, we get:

$$
\begin{aligned}
f_1 &\geq \frac{1}{\left[1 + \frac{1}{r} + \frac{1}{r^2} + \cdots + \frac{1}{r^{\log n - 1}}\right](1 + o(1)) + \left(\frac{5}{4r}\right)^{\log n}\left[1 + \frac{5}{4r} + \left(\frac{5}{4r}\right)^2 + \cdots + \left(\frac{5}{4r}\right)^{n - \log n - 1}\right]} \\
&= \frac{1}{\frac{1-\left(\frac{1}{r}\right)^{\log n}}{1-\frac{1}{r}}(1 + o(1)) + \left(\frac{5}{4r}\right)^{\log n}\frac{1-\left(\frac{5}{4r}\right)^{n-\log n}}{1-\frac{5}{4r}}} \\
&\to 1 - \frac{1}{r} \quad \text{when} \quad r > \frac{5}{4} \quad as \quad n \to \infty
\end{aligned}
$$

This completes the proof of Theorem 8. □

By the above two theorems, we get the following:

Corollary 1. *If $G_R = UCY$ (or G_R is one of $CI4$, $CI6$ and $CI8$), $G_M = CL$, and $r > 2$ (respectively $r > \frac{3}{2}$, $r > \frac{4}{3}$ and $r > \frac{5}{4}$), then f_{G_R,G_M} tends to a constant as $n \to \infty$.*

Finally, we note that, by Lemma 1 and the above Corollary, when the resident graph is complete (i.e. $G_R = CL$), the mutant graph is UCY (or one of $CI4$, $CI6$, $CI8$), and the relative fitness satisfies $r < \frac{1}{2}$ (respectively $r < \frac{2}{3}$, $r < \frac{3}{4}$ and $r < \frac{4}{5}$), then the fixation probability is upper bounded by a constant, as $n \to \infty$.

7 An Approximation Algorithm

Here we present a fully polynomial randomized approximation scheme (FPRAS)[5] for the problem UNDIRECTEDVSCLIQUE of computing the fixation probability in the Moran process when the residents have an undirected graph and the mutants have the clique graph with $r > 2c\left(1 + \frac{2}{n-5}\right)$, where c is the maximum ratio of the degrees of adjacent nodes in the resident graph. The following result is essential for the design of a FPRAS; it gives an upper bound (which depends on c, r and is polynomial in n) on the expected absorption time of the Moran process in this case.

Theorem 9. *Let $G_R(V, E_R)$ be an undirected graph of order n, for which $w^R_{xy}/w^R_{yx} \leq c$ for every $(xy) \in E_R$. Let $G_M(V, E_M)$ be the clique graph of order n. For $r \geq 2c\left(1 + \frac{2}{n-5}\right)$ and any $S \subseteq V$, the absorption time τ of the Moran process "G_R vs G_M" satisfies:*

$$\mathbb{E}[\tau | X_0 = S] \leq \frac{r}{r-c} n(n - |S|).$$

In particular, $\mathbb{E}[\tau] \leq \frac{r}{r-c} n^2$.

Proof. We use the following potential function:

$$\phi(S) = |S|$$

for any possible mutant set $S \subseteq V$. We first prove the following intermediate result which states that the number of mutants (potential) strictly increases in expectation when $r \geq 2c\left(1 + \frac{2}{n-5}\right)$, where $c := \max\limits_{(xy)\in E_R} \left(w^R_{xy}/w^R_{yx}\right)$, i.e. the maximum ratio of the degrees of adjacent nodes in the resident graph. We first prove the following lemma:

Lemma 2. *Let $(X_i)_{i\geq 0}$ be a Moran process when the resident graph is a general undirected graph and the mutant graph is the clique. If $r \geq 2c\left(1 + \frac{2}{n-5}\right)$, where $c := \max\limits_{(xy)\in E_R} \left(w^R_{xy}/w^R_{yx}\right)$, then*

$$\mathbb{E}\left[\phi(X_{i+1}) - \phi(X_i) | X_i = S\right] \geq \left(1 - \frac{c}{r}\right) \frac{1}{n} > 0.$$

[5] An FPRAS for a function f that maps problem instances to numbers is a randomized algorithm with input X and parameter $\epsilon > 0$, which is polynomial in $|X|$ and ϵ^{-1} and outputs a random variable g, such that $Pr\{(1-\epsilon)f(X) \leq g(X) \leq (1+\epsilon)f(X)\} \geq \frac{3}{4}$ [9].

Proof. By $F(S)$ we denote the total fitness $|S|r + |V| - |S|$ of a state with mutant set S. For $r \geq 2c\left(1 + \frac{2}{n-5}\right)$ and $\varnothing \subset S \subset V$ we have:

$$\begin{aligned}
&\mathbb{E}\left[\phi(X_{i+1}) - \phi(X_i)|X_i = S\right] = \\
&= \frac{1}{F(S)}\left[\sum_{\substack{xy\in E_M\\ x\in S, y\in V\setminus S}} r\cdot w^M_{xy}\cdot(\phi(S+y) - \phi(S)) + \sum_{\substack{yx\in E_R\\ x\in S, y\in V\setminus S}} w^R_{yx}\cdot(\phi(S-x)-\phi(S))\right] \\
&= \frac{1}{F(S)}\left[\sum_{\substack{xy\in E_M\\ x\in S, y\in V\setminus S}} r\cdot w^M_{xy} - \sum_{\substack{yx\in E_R\\ x\in S, y\in V\setminus S}} w^R_{yx}\right] \\
&\geq \frac{1}{F(S)}\left[\frac{r}{n-1}\cdot|S|(n-|S|) - c\cdot\min\{|S|, n-|S|\}\right],
\end{aligned}$$

where we used the fact that $w^M_{xy} = \frac{1}{n-1}$ for every $(xy) \in E_M$, and $\sum_{\substack{yx\in E_R\\ x\in S, y\in V\setminus S}} w^R_{yx} \leq c\cdot\min\{|S|, n-|S|\}$ as in the proof of Theorem 6.

The maximum value of $F(S)$ is rn, and the minimum of the function in the last brackets is $r - c$ for $r \geq 2c\left(1+\frac{2}{n-5}\right)$. This completes the proof of Lemma 2. □

The expected absorption time can be bounded using martingale techniques. In particular, we employ the following theorem (Theorem 6 of [2]), which was used to bound the absorption time of the process with a single undirected graph.

Theorem 9.A ([2]) *Let $(Y_i)_{i\geq 0}$ be a Markov chain with state space Ω, where Y_0 is chosen from some set $I \subseteq \Omega$. If there are constants $k_1, k_2 > 0$ and a non-negative function $\psi : \Omega \to \mathbb{R}$ such that:*

- *$\psi(S) = 0$ for some $S \in \Omega$,*
- *$\psi(S) \leq k_1$ for all $S \in I$ and*
- *$\mathbb{E}[\psi(Y_i) - \psi(Y_{i+1})|Y_i = S] \geq k_2$ for all $i \geq 0$ and all S with $\psi(S) > 0$,*

then $\mathbb{E}[\tau] \leq k_1/k_2$, where $\tau = \min\{i : \psi(Y_i) = 0\}$.

We can now prove Theorem 9 as follows: Let $(Y_i)_{i\geq 0}$ be the process that behaves identically to the Moran process $(X_i)_{i\geq 0}$ except that, if $Y_j = \varnothing$ then $Y_{j+1} = \{x\}$, where x is a vertex chosen uniformly at random. Setting $\tau' = \min\{i : Y_i = V\}$, we have $\mathbb{E}[\tau|X_0 = S] \leq \mathbb{E}[\tau'|Y_0 = S]$. Putting $\psi(Y) = \phi(V) - \phi(Y) = n - \phi(Y)$, $k_1 = \psi(S) \leq n$, $k_2 = (1 - c/r)/n$ satisfies the conditions of Theorem 9.A - the third condition follows from Lemma 2 for $\varnothing \subset Y_i \subset V$ and $\mathbb{E}[\psi(Y_i) - \psi(Y_{i+1})|Y_i = \varnothing] = \frac{1}{n}\cdot n = 1 > k_2$. The result follows from Theorem 9.A. □

For our algorithm to run in time polynomial in the length of the input, r must be encoded in unary.

Theorem 10. *There is an FPRAS for* UNDIRECTEDVSCLIQUE, *for* $r > 2c\left(1 + \frac{2}{n-5}\right)$.

Proof. We present the following algorithm. First, we find the constant c by checking every edge of the resident graph and exhaustively finding the maximum ratio of adjacent nodes' degrees in $O(n^3)$ time. If and only if our r is greater than $2c\left(1 + \frac{2}{n-5}\right)$, we simulate the Moran process where residents have some given undirected graph and mutants have the clique graph. We compute the proportion of simulations that reached fixation for $N = \lceil 2\epsilon^{-2} \ln 16 \rceil$ simulation runs with maximum number $T = \lceil 8rn^2N(r-c)^{-1} \rceil$ of steps each. In case of simulations that do not reach absorption in the T-th step, the simulation stops and returns an error value.

Also, each transition of the Moran process can be simulated in $O(1)$ time. This is possible if we keep track of the resident and mutant nodes in an array, thus choose the reproducing node in constant time. Further, we can pick the offspring node in constant time by running a breadth-first search for each graph before the simulations start, storing the neighbours of each node for the possible node types (resident and mutant) in arrays. Hence the total running time is $O(n^3 + NT)$, which is polynomial in n and ϵ^{-1} as required by the FPRAS definition.

Now, we only have to show that the output of our algorithm computes the fixation probability to within a factor of $1 \pm \epsilon$ with probability at least $3/4$. Essentially, the proof is the same as in [2] with modifications needed for our setting. For $i \in \{1, 2, ..., N\}$, let Y_i be the indicator variable, where $Y_i = 1$ if the i-th simulation of the Moran process reaches fixation and $Y_i = 0$ otherwise. We first calculate the bounds on the probability of producing an output of error ϵ in the event where all simulation runs reach absorption within T steps. The output of our algorithm is then $g = \frac{1}{N}\sum_{i=1}^{N} Y_i$ while the required function is the fixation probability f. Using Hoeffding's inequality we get:

$$Pr\{|g - f| > \epsilon f\} \le 2e^{-2\epsilon^2 f^2 N} \le 2e^{-f^2 \ln 16/4} < \frac{1}{8}$$

where the latter inequality is because $f \ge 1 - c/r > 1/2$ due to Theorem 6.

Now, by using Theorem 9 and Markov's inequality, the process reaches absorption within t steps with probability at least $1 - \epsilon$, for any $\epsilon \in (0, 1)$ and any $t \ge \frac{r}{r-c} n^2 \frac{1}{\epsilon}$. Therefore, the event that any individual simulation has not reached absorption within T steps, happens with probability at most $1/(8N)$. By taking the union bound, the event of a simulation run not reaching absorption within T steps happens with probability at most $1/8$. Thus, the probability of producing an output g as required, is at least $3/4$. □

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