


Effect of the degree of an initial mutant in Moran processes in structured populationsJavad Mohamadichamgavi * and Jacek Miękisz †*Institute of Applied Mathematics and Mechanics, University of Warsaw, 02-097 Warsaw, Poland* (Received 23 June 2023; accepted 15 March 2024; published 11 April 2024)

We study effects of the mutant's degree on the fixation probability, extinction, and fixation times in Moran processes on Erdős-Rényi and Barabási-Albert graphs. We performed stochastic simulations and used mean-field-type approximations to obtain analytical formulas. We showed that the initial placement of a mutant has a significant impact on the fixation probability and extinction time, while it has no effect on the fixation time. In both types of graphs, an increase in the degree of an initial mutant results in a decreased fixation probability and a shorter time to extinction. Our results extend previous ones to arbitrary fitness values.

DOI: [10.1103/PhysRevE.109.044406](https://doi.org/10.1103/PhysRevE.109.044406)**I. INTRODUCTION**

Extinction and fixation of phenotypes and behaviors in animal and human populations are important features of evolutionary processes. The classical model here is the Moran process in populations of fixed finite sizes, consisting of individuals equipped with one of two phenotypes [1]. Namely, an individual is chosen proportional to its fitness and it gives birth to an offspring who inherits its phenotype and replaces a randomly chosen individual. Such a birth-death process (also called an invasion process) is a Markov chain with two absorbing states: homogeneous populations with only one phenotype present. One may also consider death-birth Moran process, where an individual is chosen with a probability inversely proportional to its fitness and is replaced by a randomly chosen individual [2–5].

Here we will study fixation probability and expected fixation and extinction times of mutants in birth-death Moran processes on graphs. In such processes, offspring replace neighbors of ancestors. The study of fixation probabilities on graphs was initiated by Lieberman, Hauert, and Nowak [6]. Since then there appeared many papers on Moran processes on graphs [7–35]. They have shown that the structure of the population can have a significant impact on the evolutionary dynamics and can affect fixation probability and fixation time.

In particular, Antal, Redner, and Sood [9] studied fixation probability on degree-heterogeneous power-law graphs. They considered various dynamics and derived approximate analytical formulas for the dependence of the fixation probability on the degree of an initial mutant. In particular, for the birth-death process (biased invasion process) in the case where fitness of a mutant is very close to that of a resident, they showed that the fixation probability of a mutant is inversely proportional to its degree. In the follow-up paper [10], they studied fixation time in the neutral case. For similar results see also Ref. [19].

The effect of the placement of an initial mutant was also studied by Broom, Rychtář, and Stadler [13]. The authors derived a useful analytical approximation of fixation probability as a function of the degree of the initial mutant for some small graphs. Their findings revealed that initial mutants with fewer connections had a greater advantage, resulting in a higher probability of fixation.

Here we present results of stochastic simulations and use a mean-field-type approximation to derive analytical formulas for the fixation probability on Erdős-Rényi (ER) [36] and Barabási-Albert (BA) [37,38] graphs which agree with stochastic simulations for any fitness values. We also derive formulas for fixation and extinction time for arbitrary fitness values.

We have extended results of Refs. [9,10,19] to models with arbitrary fitness values. In particular, we compared our approximate formula for the fixation probability to that in [9], see Appendix B. In general, we showed that the initial placement of a mutant has a significant impact on the fixation probability and extinction time, while the degree of the initial mutant has no effect on the fixation time. In both types of graphs, an increase of the degree of the initial mutant results in a decreased probability of the mutant taking over the entire population and a shorter time to extinction.

In the two graphs with the same size and average vertex degree, for an initial mutant with the same degree, the fixation probability in the Erdős-Rényi graph is higher than in the Barabási-Albert one. However, due to the presence of hubs, the average fixation probability in the Barabási-Albert graph is higher.

In Sec. II, we present our model, a Markov chain of the Moran process on graphs. In Sec. III, we present results of stochastic simulations and derive analytical results. Further analysis of extinction time is contained in Sec. IV. Discussion follows in Sec. V.

II. MODELS AND METHODS

We will study here the Moran process on two random graphs, the ER [36] and the scale-free BA one [37,38]. We

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build the ER graph by putting with probability p an edge between every pair of $N = 500$ vertices. It follows that the average degree of vertices (the average number of neighbors) is equal to $\alpha = p(N - 1)$. The BA network is built by the preferential attachment procedure. We start with m_o fully connected vertices and then we add $N - m_o$ vertices, each time connecting them with m already available vertices with probabilities proportional to their degrees. If $m_o = \alpha + 1$ and $m = \alpha/2$, then we get a graph with the average degree equal to α . It is known that such a graph is scale-free with the probability distribution of degrees given by $p(k) \sim k^{-3}$ [37–39].

Individuals—mutants with a constant fitness r and residents with a constant fitness 1—are located on the vertices of a graph. At every time step of the process, an individual is chosen with a probability proportional to its fitness and then gives birth to an offspring who inherits its phenotype and replaces a randomly chosen individual. Such a Markov chain with 2^N states has two absorbing ones: homogeneous populations with only one type of individuals present. We start our process with one mutant in the population of residents. We are interested in fixation probability, expected time to fixation and extinction of mutants, denoted respectively by ρ_1^f , e_i^f , and e_1^e . To find such quantities, we performed stochastic simulations.

We simulate the Moran process on graphs with $N = 500$ vertices. For every k , we randomly place an initial mutant on one of the nodes of the degree k and perform 10 000 Monte Carlo simulations until the population reaches one of two absorbing states. To get fixation probability, we divide the number of times the process ends in the all-mutant state by 10 000. Finally, we calculate an average fixation (extinction) time for some chosen k 's.

It is impossible to get rigorous analytical expressions for fixation and extinction probabilities and times for Moran processes on graphs. The situation is much simpler in well-mixed populations [40,41]. Then the Moran process becomes a Markov chain with $N + 1$ states corresponding to the number of mutants or more precisely, a random walk on $\{0, \dots, N\}$ with state-dependent probabilities of moving to the right, $p_{i \rightarrow i+1}$, to the left, $p_{i \rightarrow i-1}$, and not moving, $1 - p_{i \rightarrow i+1} - p_{i \rightarrow i-1}$. Such a model is well known in the context of the gambler's ruin problem. It is easy to see that here we have that $p_{i \rightarrow i+1} = r p_{i \rightarrow i-1}$ where r is the fitness of the mutant. For the fixation probability starting from i mutants, one gets that

$$\rho_i^f = \frac{1 - \frac{1}{r^i}}{1 - \frac{1}{r^N}}. \quad (1)$$

For the fixation probability on graphs, to take into account a degree of an initial mutant, we derive some approximate expressions for transition probabilities up to three mutants and then use the elementary conditional probability formula and the fixation probability ρ_3^f from (1) to obtain an analytic expression for the fixation probability as a function of a degree of the initial mutant. In that way we passed from the full Markov chain with 2^N states to the one with $N + 1$ states corresponding to the number of mutants.

In the following section, we derive analytic expressions for the fixation probability and expected fixation and

extinction times and compare them with results of stochastic simulations.

III. RESULTS

A. Fixation probability

Let ρ_i^f be the fixation probability when initially there are i mutants in the population. We denote by $P_{i \rightarrow j}$ the probability of the transition from the state i to the state j ; of course, for our Moran process, transition probabilities are nonzero only for $|i - j| \leq 1$. From the total probability formula we get

$$\rho_1^f = P_{1 \rightarrow 1} \rho_1^f + P_{1 \rightarrow 2} \rho_2^f, \quad (2)$$

$$\rho_2^f = P_{2 \rightarrow 1} \rho_1^f + P_{2 \rightarrow 2} \rho_2^f + P_{2 \rightarrow 3} \rho_3^f. \quad (3)$$

We substitute (3) into (2) and get

$$\rho_1^f = \frac{P_{1 \rightarrow 2} P_{2 \rightarrow 3}}{(P_{1 \rightarrow 2} + P_{1 \rightarrow 0})(P_{2 \rightarrow 1} + P_{2 \rightarrow 3}) - P_{1 \rightarrow 2} P_{2 \rightarrow 1}} \rho_3^f. \quad (4)$$

For the number of mutants to increase from 1 to 2, the mutant should be chosen for reproduction, and hence

$$P_{1 \rightarrow 2} = \frac{r}{N + r - 1}. \quad (5)$$

For the number of mutants to decrease from 1 to 0, a resident from the mutant's neighborhood with degree k must be selected and its offspring placed in the mutant's location so

$$P_{1 \rightarrow 0} = \sum_{k'} \frac{k}{r + N - 1} \frac{1}{k'} \rho'(k'), \quad (6)$$

where k' is the degree of the selected resident and $\rho'(k')$ is the degree distribution of neighbors of the mutant.

The distribution $\rho'(k')$ of degrees of a node which is connected to a given node is given by $\frac{k' \rho(k')}{\langle k \rangle}$, where $\rho(k')$ is the degree distribution in the graph [42,43]. Therefore

$$P_{1 \rightarrow 0} = \frac{k}{r + N - 1} \frac{1}{\langle k \rangle}. \quad (7)$$

Now we have to calculate $P_{2 \rightarrow 1}$. For this transition, one of the resident neighbors of two mutants must be chosen for the reproduction and replace the mutant. One of them is the first mutant with a degree of k , while the other is a previously mutated node with a degree of k' . We have the following formula:

$$P_{2 \rightarrow 1} = \sum_{k'} \frac{k - 1}{2r + N - 2} \frac{1}{k'} \frac{k' \rho(k')}{\langle k \rangle} + \sum_{k'} \sum_{k''} \frac{k' - 1}{2r + N - 2} \frac{1}{k''} \frac{k' \rho(k')}{\langle k \rangle} \frac{k'' \rho(k'')}{\langle k \rangle}. \quad (8)$$

In this equation, the second moment $\sum_{k'} k'^2 \rho(k')$ appears. After some simplifications we get

$$P_{2 \rightarrow 1} = \frac{1}{2r + N - 2} \frac{1}{\langle k \rangle} \left(k + \frac{\langle k^2 \rangle}{\langle k \rangle} - 2 \right). \quad (9)$$

In the the same way we obtain $P_{2 \rightarrow 3}$,

$$P_{2 \rightarrow 3} = \frac{r}{2r + N - 2} \frac{k - 1}{k} + \sum_{k'} \frac{r}{2r + N - 2} \frac{k' - 1}{k'} \frac{k' \rho(k')}{\langle k \rangle}, \quad (10)$$

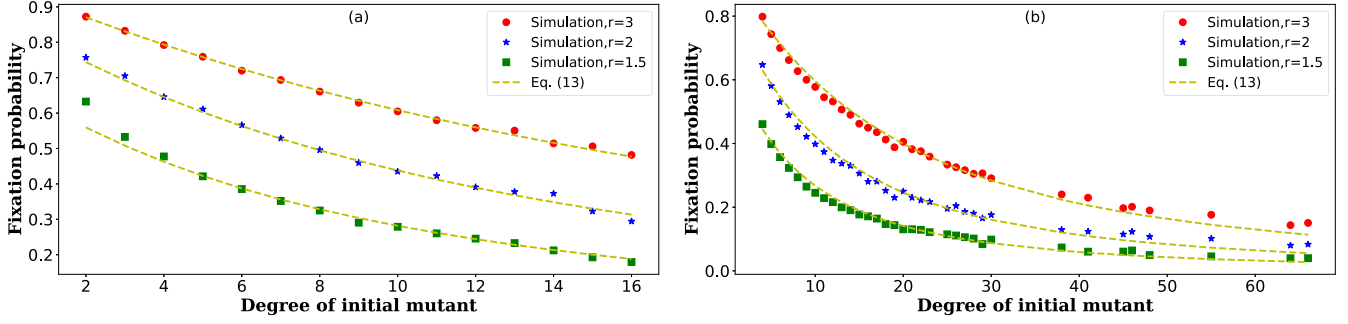


FIG. 1. Fixation probability as a function of a degree of an initial mutant for three fitness values: 3, 2, and 1.5 in (a) ER and (b) BA graphs with the size of 500 and the average degree of 8.

and after some simplifications we have

$$P_{2 \rightarrow 3} = \frac{r}{2r + N - 2} \left(\frac{k-1}{k} - \frac{1}{\langle k \rangle} + 1 \right). \quad (11)$$

This allows us to rewrite (4) as follows:

$$\rho_1^f = \frac{\langle k \rangle^2 r^2 \left(2 - \frac{1}{k} - \frac{1}{\langle k \rangle} \right)}{(r \langle k \rangle + k) \left[r \langle k \rangle \left(2 - \frac{1}{k} - \frac{1}{\langle k \rangle} \right) + \left(k - 2 + \frac{\langle k^2 \rangle}{\langle k \rangle} \right) \right] - r \langle k \rangle \left(k - 2 + \frac{\langle k^2 \rangle}{\langle k \rangle} \right)} \rho_3^f. \quad (12)$$

Now we assume that the effect of an initial mutant is limited to transitions from one-mutant population to two-mutant population and also from two mutants to three mutants. Hence we take ρ_3^f from (1) and get

$$\rho_1^f = \frac{\langle k \rangle^2 r^2 \left(2 - \frac{1}{k} - \frac{1}{\langle k \rangle} \right)}{(r \langle k \rangle + k) \left[r \langle k \rangle \left(2 - \frac{1}{k} - \frac{1}{\langle k \rangle} \right) + \left(k - 2 + \frac{\langle k^2 \rangle}{\langle k \rangle} \right) \right] - r \langle k \rangle \left(k - 2 + \frac{\langle k^2 \rangle}{\langle k \rangle} \right)} \frac{1 - \frac{1}{r^3}}{1 - \frac{1}{r^N}}. \quad (13)$$

To determine the fixation probability of mutants with degree k , we use (13), which requires the knowledge of the average degree $\langle k \rangle$ and the second moment $\langle k^2 \rangle$ of the graph. For the Erdős-Rényi graph with the binomial degree distribution, the average degree is equal to $\langle k \rangle = (N-1)p$ and the second moment $\langle k^2 \rangle = \langle k \rangle \{ \langle k \rangle [1 - 1/(N-1)] + 1 \}$. For the Barabási-Albert graph, the degree distribution follows a power law, resulting in an average degree of $\langle k \rangle = 2m$ and $\langle k^2 \rangle \equiv \langle k \rangle^2 \log N / 4$ [44].

Figure 1 presents the results of stochastic simulations and our analytical approximation for the fixation probability. Our results show a decrease in fixation probability as the initial mutant's degree increases, which agrees with previous findings by Antal, Redner, and Sood [9]. They demonstrated that if fitness of a mutant is close to that of a resident, then the fixation probability is inversely proportional to the degree of the initial mutant. However, comparing our approximation to theirs reveals that their model accurately calculates fixation probability for mutants with fitness close to residents, while our model maintains accuracy across all fitness levels, see Appendix B.

As the degree of the initial mutant increases, it becomes more probable that one of its resident neighbors replaces it. Hence, vertices with a lower number of connections have a higher chance of remaining and progressing toward fixation. In the BA graph, the degree distribution follows a power law, which means that there are a few nodes with very high degrees and many nodes with low degrees. Consequently, in the BA

graph, there may be initial nodes with a high probability of fixation, mainly those with low degrees, and others with very low fixation probabilities, mainly those with high degrees, in contrast to the ER graph where the probability of fixation is more uniform across nodes.

In Fig. 2, we present the distribution of fixation probabilities for a mutant with respect to all initial placements

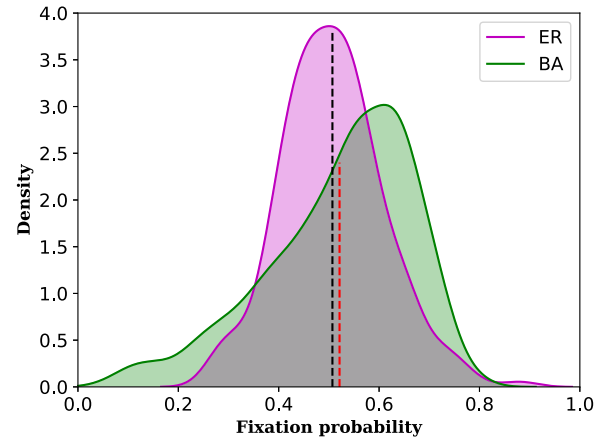


FIG. 2. Distribution of fixation probabilities of a mutant with respect to initial placements on ER and BA graphs with the size of 500 and the average degree of 8. The fitness is 2. Dash lines show the average fixation probability.

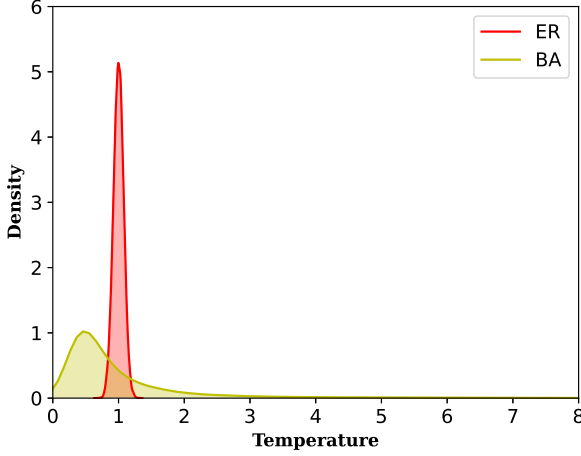


FIG. 3. The distribution of temperatures in ER and BA graphs. The node temperature is simply defined as the inverse of the degree of all nodes leading to that node.

in both graphs of the same size, average degree, and fitness. In ER graphs, fixation probabilities for all vertices are distributed approximately symmetrically around the average fixation probability. In BA graphs, the distribution is asymmetric. Moreover, we see that for $r = 2$, the average fixation probability in the ER graph is approximately 0.5 which is the fixation probability in a well-mixed population, while this value is slightly higher in the BA graph.

This can be understood on the basis of a concept of temperature vertex which is defined as the sum of the inverses of degrees of all neighbors of a given vertex. It was proven in Ref. [6] that for graphs for which all vertices have the same temperature, the so-called isothermal graphs, the average fixation probability is equal to the one in well-mixed populations.

Figure 3 displays the temperature distribution for both graphs with the size of 500 and an average degree of 8. The ER graph exhibits a peak at 1, indicating that nearly all nodes have the same temperature. In contrast to the ER graph, the BA graph's vertices show the large spectrum of temperatures. While there are many vertices with small degrees, leading to higher fixation probabilities, there are only a few vertices with large degrees, leading to low fixation probabilities. Consequently, the average fixation probability in BA graphs is higher than in well-mixed populations and ER graphs.

In Fig. 4, we present the fixation probability for an equal degree of initial placement for both graphs. As shown, the

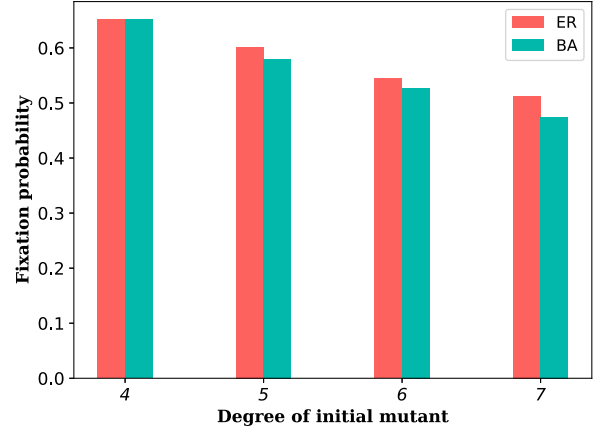


FIG. 4. Fixation probability for various initial mutants with the same degree in ER and BA graphs. The size of the graph is 500 with the average degree of 8 and $r = 2$.

fixation probability of one mutant with the the same degree in both graphs, is slightly higher for the ER graph. However, this does not contradict the observation that the average fixation probability is higher in the BA network. While it is true that the fixation probability for initial mutants with the same degree is higher in ER graphs, there are more nodes with a low degree in BA graphs, which have a higher fixation probability than in ER graphs. As a result, the average fixation probability in BA graphs is greater than that in ER graphs.

B. Fixation time

To derive an analytical expression for the expected value of the fixation time we proceed in an analogous way as for the fixation probability—we use the conditional expected value formula. We follow Antal and Sheuring [2] and obtain an equation for t_i^f , fixation time in populations with i mutants,

$$\rho_1^f t_1^f = P_{1 \rightarrow 1} \rho_1^f (t_1^f + 1) + P_{1 \rightarrow 2} \rho_2^f (t_2^f + 1) \quad (14)$$

and

$$\begin{aligned} \rho_2^f t_2^f &= P_{2 \rightarrow 1} \rho_1^f (t_1^f + 1) + P_{2 \rightarrow 2} \rho_2^f (t_2^f + 1) \\ &\quad + P_{2 \rightarrow 3} \rho_3^f (t_3^f + 1). \end{aligned} \quad (15)$$

We have $\rho_2^f t_2^f$ from (15), we put it into (14) and after some simplifications we get

$$\begin{aligned} t_1^f &= \frac{P_{2 \rightarrow 1} + P_{2 \rightarrow 3}}{\rho_1^f [(P_{1 \rightarrow 0} + P_{1 \rightarrow 2})(P_{2 \rightarrow 1} + P_{2 \rightarrow 3}) - P_{2 \rightarrow 1} P_{1 \rightarrow 2}]} \left\{ \left[\frac{(1 - P_{1 \rightarrow 0} - P_{1 \rightarrow 2})(P_{2 \rightarrow 1} + P_{2 \rightarrow 3}) + (P_{1 \rightarrow 2} P_{2 \rightarrow 1})}{P_{2 \rightarrow 1} + P_{2 \rightarrow 3}} \right] \rho_1^f \right. \\ &\quad \left. + \left[\frac{P_{1 \rightarrow 2}}{(P_{1 \rightarrow 0} + P_{1 \rightarrow 2})} \right] \rho_2^f + \frac{P_{1 \rightarrow 2} P_{2 \rightarrow 3}}{P_{2 \rightarrow 1} + P_{2 \rightarrow 3}} \rho_3^f (t_3^f + 1) \right\}, \end{aligned} \quad (16)$$

where ρ_1^f is given in (13), ρ_2^f in (3), and ρ_3^f in (1).

To get t_3^f we use a well-known technique described in Refs. [16,26]. The time to fixation starting from i mutant is given by the following formula:

$$t_i^f = \sum_{j=1}^{N-1} \frac{\rho_j^f}{\rho_i^f} F_{ij}, \quad (17)$$

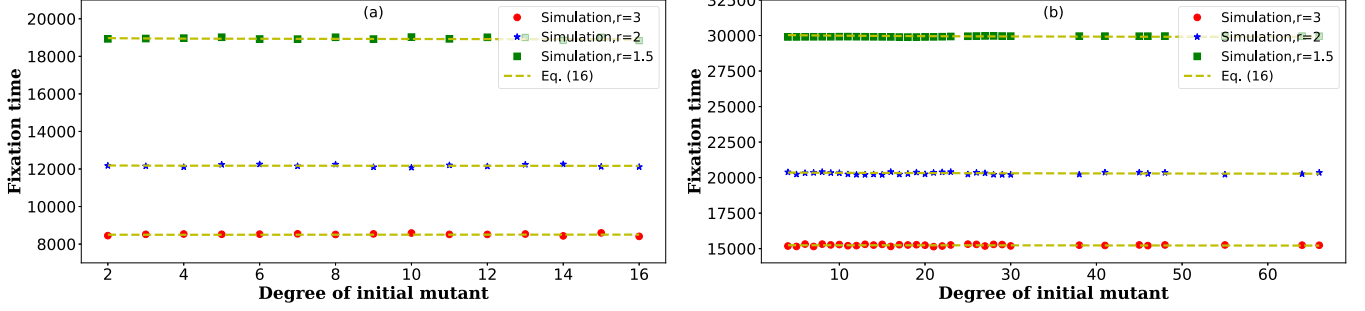


FIG. 5. Fixation time as a function of the degree of an initial mutant for three fitness values, 3, 2, and 1.5, in (a) ER and (b) BA graphs with the size of 500 and the average degree of 8.

where F_{ij} , given in (A6) in the Appendix (A), is the expected number of times, the process which started from i mutants, passes through the state with j mutants before reaching one of the absorbing states and ρ_j^f is the fixation probability starting from j mutants. Values of F_{ij} depend on graphs [see the Appendix (A) for more details].

Figure 5 shows that there is no difference in fixation times for various degrees of an initial mutant. The distribution of fixation times is shown in Fig. 6. We can see that the fixation times are distributed symmetrically around the average fixation time in both graphs. One notable point is that the average fixation time in the BA graph is higher than in the ER one.

C. Extinction time

To find an analytical expression for the extinction time we use a similar approach as we did for the fixation time. Let

$$t_1^e = \frac{P_{2 \rightarrow 1} + P_{2 \rightarrow 3}}{\rho_1^e [(P_{1 \rightarrow 0} + P_{1 \rightarrow 2})(P_{2 \rightarrow 1} + P_{2 \rightarrow 3}) - P_{2 \rightarrow 1} P_{1 \rightarrow 2}]} \left\{ P_{1 \rightarrow 0} + \left[\frac{(1 - P_{1 \rightarrow 0} - P_{1 \rightarrow 2})(P_{2 \rightarrow 1} + P_{2 \rightarrow 3}) + (P_{1 \rightarrow 2} P_{2 \rightarrow 1})}{P_{2 \rightarrow 1} + P_{2 \rightarrow 3}} \right] \rho_1^e \right. \\ \left. + \left[\frac{P_{1 \rightarrow 2}}{(P_{1 \rightarrow 0} + P_{1 \rightarrow 2})} \right] \rho_2^e + \frac{P_{1 \rightarrow 2} P_{2 \rightarrow 3}}{P_{2 \rightarrow 1} + P_{2 \rightarrow 3}} \rho_3^e (t_3^e + 1) \right\}. \quad (20)$$

Here again the idea is that we consider local information and an effect of the initial degree in states 1, 2, and 3 and then we disregard the information about the initial degree. The time to extinction, starting from $i = 3$ mutants is given by the following expression [16,26]:

$$t_3^e = \sum_{j=1}^{N-1} \frac{\rho_j^e}{\rho_3^e} F_{3j}. \quad (21)$$

We present results of stochastic simulations and our analytical approach in Fig. 7. It appears that as the initial mutant's degree increases, extinction time decreases. Essentially, as the initial mutant degree increases, it becomes more likely to select one of its neighbors to replace it. As a result, mutants with higher degrees are more likely to be wiped out in a short period of time. In the BA graph, for two initial mutants with a large difference in degrees, we have completely different extinction times due to the average degree of the network. It is worth noting that for vertices with high

$\rho_i^e = 1 - \rho_i^f$ be the extinction probability starting with i mutants and $P_{i \rightarrow j}$ the transition probability from i to j mutants. We apply the conditional expected value formula for t_i^e , the extinction time from a state with i initial mutants, and get [2]

$$\rho_1^e t_1^e = P_{1 \rightarrow 0} + P_{1 \rightarrow 1} \rho_1^e (t_1^e + 1) + P_{1 \rightarrow 2} \rho_2^e (t_2^e + 1) \quad (18)$$

and

$$\rho_2^e t_2^e = P_{2 \rightarrow 1} \rho_1^e (t_1^e + 1) + P_{2 \rightarrow 2} \rho_2^e (t_2^e + 1) + P_{2 \rightarrow 3} \rho_3^e (t_3^e + 1). \quad (19)$$

These equations for the extinction time are similar to equations we derived for the fixation time. In (18) there is an extra term $P_{1 \rightarrow 0}$ because if the number of mutants reaches zero, then the extinction probability from this state is zero $t_0^e = 0$ and the term $P_{1 \rightarrow 0} \rho_0^e (t_0^e + 1)$ drops out, leaving only the $P_{1 \rightarrow 0}$ term. As before we find $\rho_2^e t_2^e$ from (19) and substitute it into (18) and after some simplifications we get

degrees, the extinction time is almost the same for all values of r . In other words, if the process starts from a hub, then, regardless of r , it will soon become extinct. In Fig. 8, we can see the distribution of extinction times for both graphs. In the ER graph, extinction times are distributed around an average time, while in the BA one, the distribution is more extended. ER graphs exhibit lower average extinction times than BA ones.

In Fig. 9, the extinction time for various initial mutants with equal degrees is presented. Observe that for initial mutants with the same degree, the one in the BA graph exhibits a longer extinction time.

IV. FIXATION AND EXTINCTION TIMES: DISCUSSION

Here we examine in more detail the evolution of a population starting with one mutant. Figures 10 and 11 show the path to extinction and fixation of a mutant in the ER graph with a size of 500 and an average degree of 8. We derive approximate

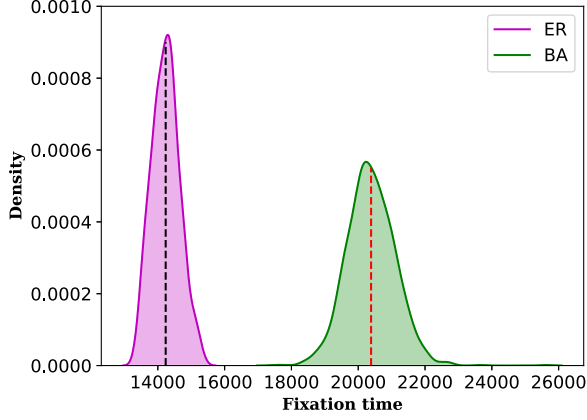


FIG. 6. Distribution of fixation times of a mutant with respect to initial placements on ER and BA graphs with the size of 500 and the average degree of 8. The fitness is 2. Dash lines show the average fixation time.

formulas for the expected number of times the process which started from i mutants, passes through the state with j mutants before reaching fixation and extinction respectively (details of derivation are given in the Appendix A),

$$t_{i,j}^f = \begin{cases} \frac{(r^j - 1)^2 (r^{N-i} - 1) r^{i-j}}{(r-1)(r^N - 1)(r^i - 1) \frac{j}{N-i+rj} \frac{(N-j)(p-\frac{2}{N})}{Np}} & j \leq i \\ \frac{(r^{N-j} - 1)(r^j - 1)}{(r-1)(r^N - 1) \frac{j}{N-i+rj} \frac{(N-j)(p-\frac{2}{N})}{Np}} & j > i \end{cases}, \quad (22)$$

$$t_{i,j}^e = \begin{cases} \frac{(r^j - 1)(r^{N-i} - 1)(r^N - r^j) r^{i-j}}{(r-1)(r^N - 1)(r^N - r^i) \frac{j}{N-i+rj} \frac{(N-j)(p-\frac{2}{N})}{Np}} & j \leq i \\ \frac{(r^N - r^j)(r^{N-j} - 1)(r^i - 1)}{(r-1)(r^N - 1)(r^N - r^i) \frac{j}{N-i+rj} \frac{(N-j)(p-\frac{2}{N})}{Np}} & j > i \end{cases}. \quad (23)$$

Denote by T_j^e and T_j^f the expected time it takes a single mutant to take over j nodes in a network before extinction and fixation, respectively. For a single mutant to be fixed, the Moran process must pass through the state with j mutants. Thus, T_j^f is the time needed for a single mutant to be fixed minus the time needed for j mutants to be fixed [35]. Therefore we have

$$\begin{aligned} T_j^f &= t_1^f - t_j^f = \sum_{l=1}^{N-1} t_{1,l}^f - \sum_{l=1}^{N-1} t_{j,l}^f, \\ T_j^e &= t_1^e - t_j^e = \sum_{l=1}^{N-1} t_{1,l}^e - \sum_{l=1}^{N-1} t_{j,l}^e. \end{aligned} \quad (24)$$

We have performed stochastic simulations to see how accurate these analytical formulas are. For t_1^f and t_1^e we use our analytical approximation in (16) and (20). Figures 10(a) and 11(a) show the expected number of times, the population started with one mutant passes through the state with j mutants before fixation and extinction, respectively, while Figs. 10(b) and 11(b) show the value of T_j^f and T_j^e . The results are for the ER network with a size of 500 and an average degree of 8. We present here only results for the ER network, and results for the BA network are the same. We observe that the process before extinction spends most of

its time in states with few mutants. This means that during the process of the extinction of mutants, a few vertices get mutated and if the number of mutants increases, then there is a higher chance of them to be fixed. Therefore, the initial placement of mutants plays an important role in the extinction of mutants. For fixation, unlike extinction, the beginning and the end of the process can have a significant impact on the fixation time. At the beginning of the process when few mutants are available, the probability of choosing them to reproduce is low, so it takes a long time for mutants to increase their number. Furthermore, with fewer residents in the population, it takes longer time to replace them with one of the mutants' offspring at the end of the process. Hence it does not matter where the mutant is initially placed because the start and end of the process are equally important for the fixation time.

We observe that our analytical expressions are less accurate for smaller values of r and are becoming better as r increases. We assumed that the initial mutant degree influences only the probability of transition between one to two and two to three mutants. However, there is a possibility that the number of mutants increases and then decreases again to 1. Hence, the mutant may be different from the starting mutant, leading to an error in our approximation. For large r , there is a low probability that the number of mutants will decrease to 1. Therefore, when there are more mutants, they are more likely to increase rather than decrease their number. Consequently, our approximation is better for larger r .

V. DISCUSSION

To summarize, we examined the impact of the degree of an initial mutant on the fixation probability and fixation and extinction times in Moran processes in structured populations. We performed computer simulations and developed a general mean-field approximation approach on graphs which enabled us to get analytical formulas. In this way we extended to arbitrary fitness values results of Refs. [9,10,19], where the authors provided good approximations for cases with mutant fitness close to that of a resident.

We showed that the fixation probability depends on the vertex degree at which a mutant is introduced. Increasing the degree of the initial mutant makes it more likely for the mutant to be replaced by one of its neighbors. There was no correlation between the degree of the initial mutant and the time it took for the mutant to take over the entire population. The fixation process depends on the entire population, not on the first mutant. We found that, unlike fixation time, extinction time significantly depends on the degree of the first mutant—a mutant with fewer connections needs more time to become extinct. Furthermore, we observed that the extinction time for an initial mutant with a small degree is significantly influenced by its fitness, but as the degree of the first mutant increases, extinction times become independent on the fitness value.

It is important to study the impact of the initial mutant's degree on the fixation probability and fixation and extinction times in frequency-dependent Moran processes of spatial evolutionary games, where fitness is derived from game competitions.

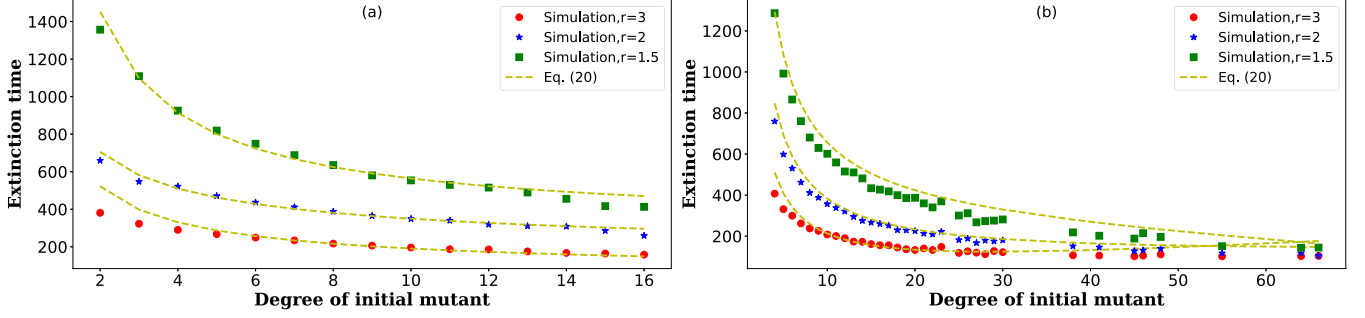


FIG. 7. Extinction time as a function of a degree of an initial mutant for three fitness values, 3, 2, and 1.5, in (a) ER and (b) BA graphs with the size of 500 and the average degree of 8.

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APPENDIX A

We consider here a reduced Markov chain for the Moran process on the graph with $N + 1$ states representing the number i of mutants in the population. The transition matrix can be then written as follows:

$$P_{ij} = p_{i \rightarrow i+1} \delta_{i+1,j} + p_{i \rightarrow i-1} \delta_{i-1,j} + q_i \delta_{i,j}, \quad (\text{A1})$$

where $q_i = 1 - p_{i \rightarrow i+1} - p_{i \rightarrow i-1}$.

Our Markov chain has two absorbing states: $i = 0$ and $i = N$. To calculate absorbing probabilities and expected absorbing times we use the general method described in Ref. [45]. We rewrite the transition matrix as follows:

$$P = \begin{pmatrix} Q & R \\ 0 & I \end{pmatrix}, \quad (\text{A2})$$

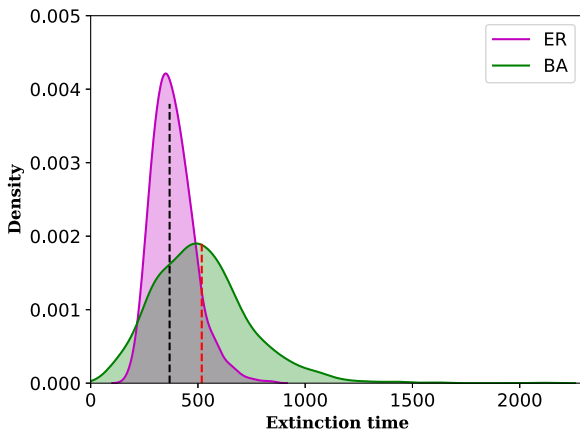


FIG. 8. Distribution of extinction times of a mutant with respect to initial placements on ER and BA graphs with the size of 500 and the average degree of 8. The fitness is 2. The dash lines show the average extinction times.

where Q contains transition probabilities between transient states and R contains transition probabilities from transient states to absorbing ones and I is the identity matrix. $F = (I - Q)^{-1}$ is called the fundamental matrix. It can be shown that F_{ij} is the expected number of times, the process which started from i mutants, passes through the state with j mutants before reaching one of the absorbing states. Then it follows that expected absorption times are given by summations,

$$t_i = \sum_{j=1}^{N-1} F_{ij}. \quad (\text{A3})$$

Expected number of times the process which started from i mutants, passes through the state with j mutants before reaching fixation and extinction respectively can be written as follows [16]:

$$t_{i,j}^f = \frac{\rho_j^f}{\rho_i^f} F_{ij}, \quad t_{i,j}^e = \frac{\rho_j^e}{\rho_i^e} F_{ij}. \quad (\text{A4})$$

Hence expected fixation and extinction times are given by the following expressions:

$$t_i^f = \sum_{j=1}^{N-1} \frac{\rho_j^f}{\rho_i^f} F_{ij}, \quad t_i^e = \sum_{j=1}^{N-1} \frac{\rho_j^e}{\rho_i^e} F_{ij}. \quad (\text{A5})$$

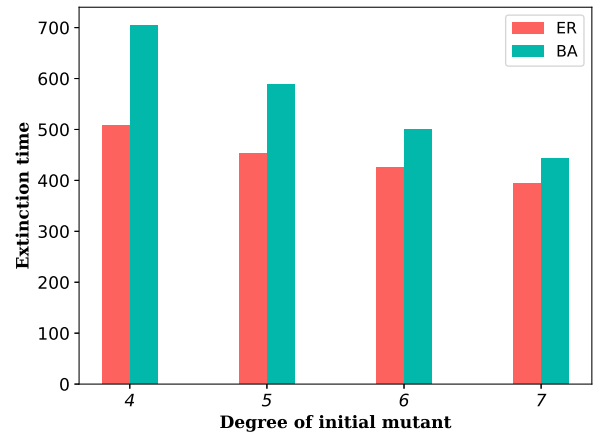


FIG. 9. Extinction time for various initial mutants with the same degree in both networks. The size of the networks is 500, the average degree 8, and $r = 2$.

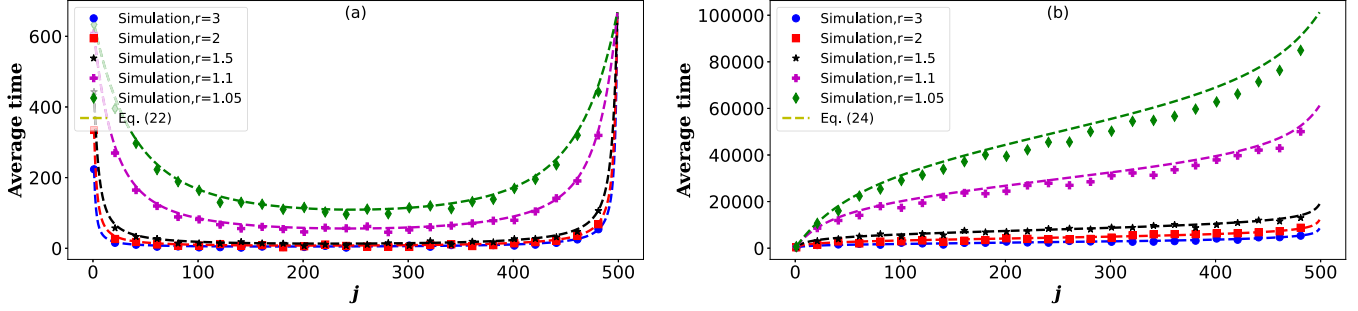


FIG. 10. (a) The expected number of times the population started with one mutant passes through the state with j mutants before fixation, $t_{1,j}^f$, Eq. (22) and (b) the expected time until the number of mutants reaches j from 1, T_j^f , Eq. (17), for various values of r in the ER graph with $N = 500$ and average degree of 8.

Now we turn our attention to graphs. It can be shown that if the Moran process on a graph satisfies the condition $p_{i \rightarrow i+1} = r p_{i \rightarrow i-1}$, then we have [26]

$$F_{ij} = \begin{cases} \frac{(r^j - 1)(r^{N-i} - 1)}{p_{j \rightarrow j-1}(r-1)(r^N - 1)}, & j \leq i \\ \frac{r^{j-i}(r^i - 1)(r^{N-j} - 1)}{p_{j \rightarrow j-1}(r-1)(r^N - 1)}, & i < j \end{cases}. \quad (\text{A6})$$

The authors of Ref. [26] used mean-field techniques and argue that $p_{i \rightarrow i+1} = r p_{i \rightarrow i-1}$ is a good approximation for Erdős-Rényi and Barabási-Albert graphs. We present here their arguments and results.

(i) Erdős-Rényi graph

In the ER graph with N vertices and j mutants, the probability of a mutant being selected for the reproduction is given by $\frac{rj}{rj + N - j}$. Although it may seem that this mutant would have $(N - j)p$ residents in its neighborhood, the population of mutants tends to form clusters, making it likely for a selected mutant to have at least two mutant neighbors. Thus, the probability of a selected mutant being connected to a resident is approximately $(p - \frac{2}{N})$, and the average number of residents connected to a selected mutant is $(N - j)(p - \frac{2}{N})$. Then

$$p_{j \rightarrow j+1} = r p_{j \rightarrow j-1} = \frac{rj}{N - i + rj} \frac{(N - j)(p - \frac{2}{N})}{(N - 1)p}. \quad (\text{A7})$$

(ii) Barabási-Albert graph

Here again, the probability for a mutant to be chosen for the reproduction is $\frac{rj}{rj + N - j}$. For a state with j mutants, I_j represents the average number of edges that connect different

species, also known as interface edges. On average, each mutant (resident) has $\langle k \rangle$ connections, and $\frac{I_j}{j}$ [$I_j/(N - j)$] interface edges. As a result, the probability for a mutant (resident) offspring to replace one of its resident (mutant) neighbors is $\frac{I_j}{m}$ [$\frac{I_j}{m}$]. It follows that

$$p_{j \rightarrow j+1} = r p_{j \rightarrow j-1} = \frac{r I_j}{\langle k \rangle (N - j + r j)}. \quad (\text{A8})$$

In order to find I_j when there are i mutants, it is evident that every resident node has at least m edges and an average of $\frac{I_j}{N - j}$ interface edges. If one resident is changed to a mutant, then the number of mutants increases by 1. Therefore, we can obtain a recursive relationship for the number of interface edges as follows:

$$I_{j+1} = I_j + m - \frac{I_j}{N - j}. \quad (\text{A9})$$

Assuming $I_0 = 0$ we have

$$I_j = m \sum_{i=1}^j \frac{N - j}{N - i}. \quad (\text{A10})$$

APPENDIX B

The effect of the degree of an initial mutant on the fixation probability has been previously studied by Antal, Redner, and Sood [9]. They examined how initial placement impacts fixation probability in various dynamics. In particular, for the birth-death Moran process (biased invasion process) with the mutant fitness equal to 1 and the resident fitness set to $1 - s$,

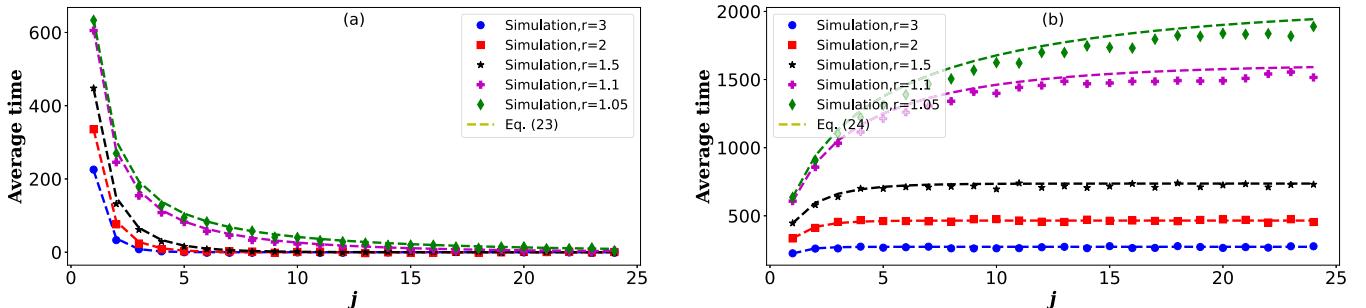


FIG. 11. (a) The expected number of times the population started with one mutant passes through the state with j mutants before extinction, $t_{1,j}^e$, Eq. (23) and (b) the expected time until the number of mutants reaches j from 1, T_j^e , Eq. (17), for various values of r in the ER graph with $N = 500$ and average degree of 8.

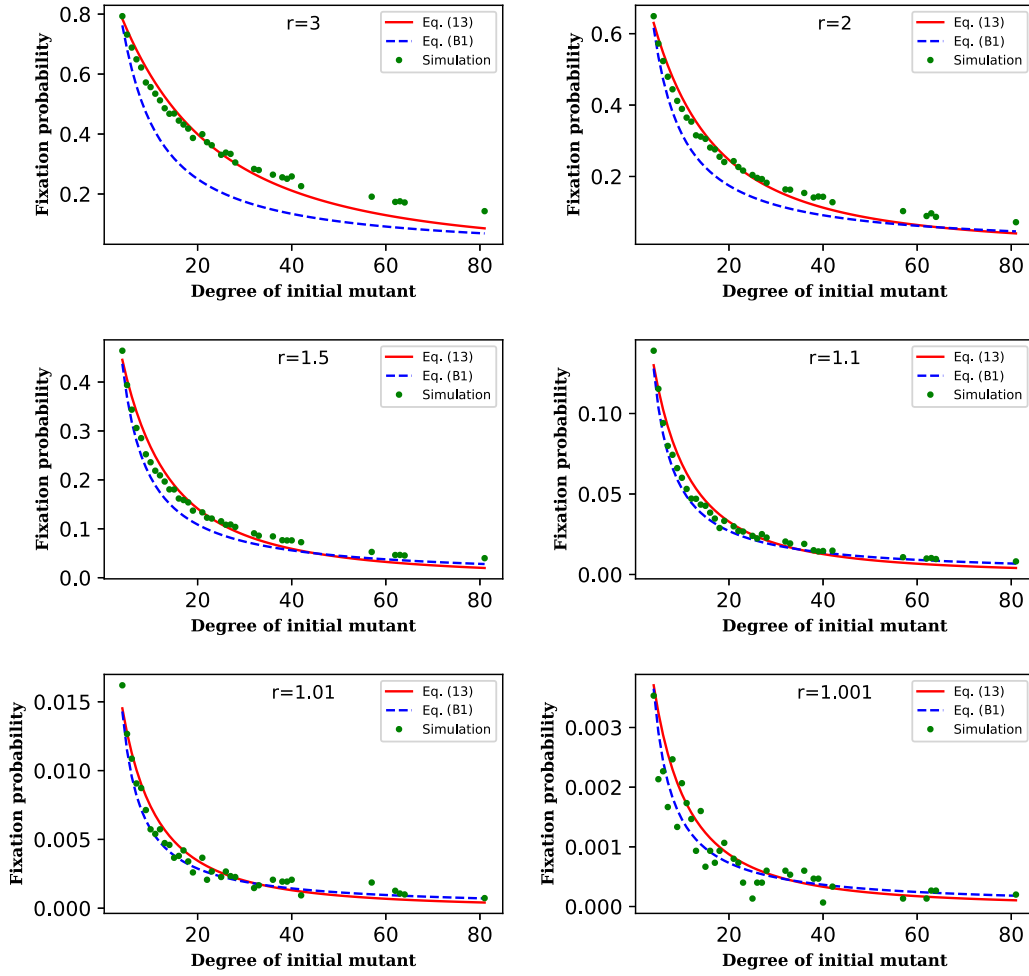


FIG. 12. Fixation probability as a function of the degree of an initial mutant for various fitness values. The red line is our approximation given by (13), the blue dashed line is an approximation given by (B1), and the green dots show the result of simulations. In Eq. (B1) $s = 1 - 1/r$.

the authors derived the following approximate formula for the fixation probability:

$$\rho_1^f(\omega_{-1}) = \frac{1 - e^{-sN\omega_{-1}/(1-s/2)}}{1 - e^{-sN/(1-s/2)}}, \quad (\text{B1})$$

where $\omega_{-1} = \frac{1}{k\mu_{-1}N}$ and $\mu_{-1} = \sum_k \frac{1}{k} \rho(k)$ is the average inverse degree [$\rho(k)$ is the degree distribution] [9].

Figure 12 compares the results of our approximation given in Eq. (13) with Eq. (B1) for various fitness values. We calculated μ_{-1} numerically. To make the connection between the fitness $r = 1 + s > 1$ for mutants and fitness 1 for residents in our paper with Ref. [9], where fitness of mutants is 1 and that of residents $1 - s$, we divide the fitnesses in (B1) by $1 - s$ (fixation probability is invariant under such a scaling).

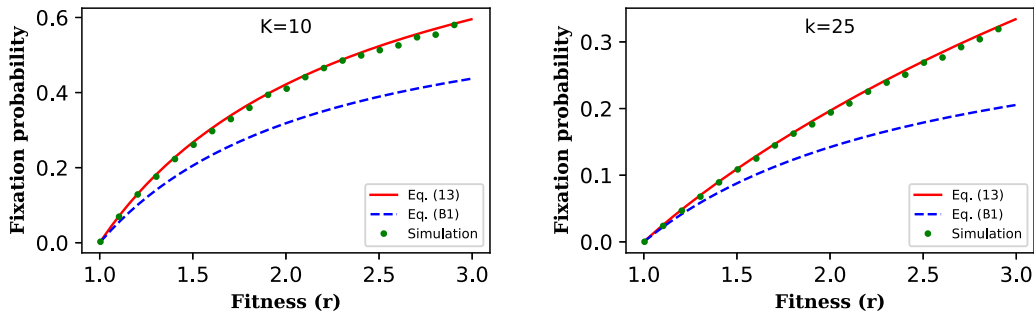


FIG. 13. The fitness effect on fixation probability for an initial mutant with degrees of 10 and 25. The red line is our approximation given by (13), the blue dashed line is an approximation given by (B1), and the green dots show the result of simulations. In Eq. (B1) $s = 1 - 1/r$.

Therefore in (B1), the fitness of mutants is $r = \frac{1}{1-s} > 1$ for $0 < s < 1$ and that of resident is 1. In this way the value of s in (B1) is $1 - \frac{1}{r}$.

We see that our approximation performs well for all values of $s > 0$, while Eq. (B1) is more accurate in cases where r is close to 1 ($s \ll 1$).

For a more direct comparison, we fixed the degree of an initial mutant and varied the fitness r from 1 to 3. Figure 13 shows the results for initial mutants with degrees of 10 and 25. For r close to 1, both approximations perform well. However, as r increases, our approximation in Eq. (13) outperforms Eq. (B1).

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- [1] P. A. P. Moran, Random processes in genetics, *Math. Proc. Camb. Philos. Soc.* **54**, 60 (1958).
- [2] T. Antal and I. Scheuring, Fixation of strategies for an evolutionary game in finite populations, *Bull. Math. Biol.* **68**, 1923 (2006).
- [3] M. A. Nowak, *Evolutionary Dynamics: Exploring the Equations of Life* (Harvard University Press, Cambridge, MA, 2006).
- [4] A. Pavlogiannis, J. Tkadlec, K. Chatterjee, and M. A. Nowak, Amplification on undirected population structures: Comets beat stars, *Sci. Rep.* **7**, 82 (2017).
- [5] A. Traulsen, and C. Hauert, Stochastic evolutionary game dynamics, *Rev. Nonlin. Dyn. Complex.* **2**, 25 (2009).
- [6] E. Lieberman, C. Hauert, and M. A. Nowak. Evolutionary dynamics on graphs, *Nature (London)* **433**, 312 (2005).
- [7] H. Ohtsuki and M. A. Nowak, Evolutionary games on cycles, *Proc. R. Soc. B* **273**, 2249 (2006).
- [8] A. Traulsen and M. A. Nowak, Evolution of cooperation by multilevel selection, *Proc. Natl. Acad. Sci. USA* **103**, 10952 (2006).
- [9] T. Antal, S. Redner, and V. Sood, Evolutionary dynamics on degree-heterogeneous graphs, *Phys. Rev. Lett.* **96**, 188104 (2006).
- [10] V. Sood, T. Antal, and S. Redner, Voter models on heterogeneous networks, *Phys. Rev. E* **77**, 041121 (2008).
- [11] M. Broom and J. Rychtář, An analysis of the fixation probability of a mutant on special classes of non-directed graphs, *Proc. R. Soc. A* **464**, 2609 (2008).
- [12] P. M. Altrock, A. Traulsen, and F. A. Reed, Stability properties of under dominance in finite subdivided populations, *J. PLOS Comp. Biol.* **7**, e1002260 (2011).
- [13] M. Broom, J. Rychtář, and B. T. Stadler, Evolutionary dynamics on graphs—the effect of graph structure and initial placement on mutant spread, *J. Stat. Theory Pract.* **5**, 369 (2011).
- [14] P. Shakarian, P. Roos, and A. Johnson, A review of evolutionary graph theory with applications to game theory, *Biosystems* **107**, 66 (2012).
- [15] B. Allen and M. A. Nowak, Games on graphs, *EMS Surv. Math. Sci.* **1**, 113 (2013).
- [16] L. Hindersin and A. Traulsen, Counterintuitive properties of the fixation time in network-structured populations, *J. R. Soc. Interface* **11**, 20140606 (2014).
- [17] S. Tan and J. Lü, Characterizing the effect of population heterogeneity on evolutionary dynamics on complex networks, *J. Sci. Rep.* **4**, 5034 (2014).
- [18] B. Allen and C. E. Tarnita, Measures of success in a class of evolutionary models with fixed population size and structure, *J. Math. Biol.* **68**, 109 (2014).
- [19] W. Maciejewski, Reproductive value in graph-structured populations, *J. Theor. Biol.* **340**, 285 (2014).
- [20] M. Askari and K. A. Samani, Analytical calculation of average fixation time in evolutionary graphs, *Phys. Rev. E* **92**, 042707 (2015).
- [21] B. Adlam, K. Chatterjee, and M. Nowak, Amplifiers of selection, *Proc. R. Soc. A* **471**, 20150114 (2015).
- [22] L. Hindersin and A. Traulsen, Most undirected random graphs are amplifiers of selection for birth-death dynamics, but suppressors of selection for death-birth dynamics, *PLoS Comput. Biol.* **11**, e1004437 (2015).
- [23] F. A. Cuesta, P. G. Sequeiros, and A. L. Rojo, Fast and asymptotic computation of the fixation probability for Moran processes on graphs, *Biosystems* **129**, 25 (2015).
- [24] M. Askari, Z. M. Miraghaei, and K. A. Samani, The effect of hubs and shortcuts on fixation time in evolutionary graphs, *J. Stat. Mech.: Theory Exp.* (2017) 073501.
- [25] F. A. Cuesta, P. G. Sequeiros, and A. L. Rojo, Evolutionary regime transitions in structured populations, *PLoS One* **13**, e0200670 (2018).
- [26] M. Hajhashemi and K. A. Samani, Fixation time in evolutionary graphs: A mean-field approach, *Phys. Rev. E* **99**, 042304 (2019).
- [27] D. Hathcock and S. H. Strogatz, Fitness dependence of the fixation-time distribution for evolutionary dynamics on graphs, *Phys. Rev. E* **100**, 012408 (2019).
- [28] M. Möller, L. Hindersin, and A. Traulsen, Exploring and mapping the universe of evolutionary graphs identifies structural properties affecting fixation probability and time, *Commun. Biol.* **2**, 137 (2019).
- [29] J. Tkadlec, A. Pavlogiannis, K. Chatterjee, and M. A. Nowak, Limits on amplifiers of natural selection under death-birth updating, *PLoS Comput. Biol.* **16**, e1007494 (2020).
- [30] B. Allen, C. Sample, R. Jencks, J. Withers, P. Steinhagen, L. Brizuela, J. Kolodny, D. Parke, G. Lippner, and Y. A. Dementieva, Transient amplifiers of selection and reducers of fixation for death-birth updating on graphs, *PLoS Comput. Biol.* **16**, e1007529 (2020).
- [31] B. Allen, C. Sample, P. Steinhagen, J. Shapiro, M. King, T. Hedspeth, and M. Goncalves, Fixation probabilities in graph-structured populations under weak selection, *PLoS Comput. Biol.* **17**, e1008695 (2021).
- [32] A. McAvoy and B. Allen, Fixation probabilities in evolutionary dynamics under weak selection, *J. Math. Biol.* **82**, 14 (2021).
- [33] M. A. Dehghani, A. H. Darooneh, and M. Kohandel, The network structure affects the fixation probability when it couples to the birth-death dynamics in finite population, *PLoS Comput. Biol.* **17**, e1009537 (2021).
- [34] V. Yagoobi and A. Traulsen, Fixation probabilities in network structured meta-populations, *Sci. Rep.* **11**, 17979 (2021).

- [35] M. Hajihashemi and K. Aghababaei Samani, Path to fixation of evolutionary processes in graph-structured populations, *Eur. Phys. J. B* **94**, 51 (2021).
- [36] P. Erdős and A. Rényi, On random graphs I, *Publ. Math. Debrecen* **6**, 290 (1959).
- [37] A.-L. Barabási and R. Albert, Emergence of scaling in random networks, *Science* **286**, 509 (1999).
- [38] A.-L. Barabási, R. Albert, and H. Jeong, Mean-field theory for scale-free random networks, *Physica A* **272**, 173 (1999).
- [39] R. Durrett, *Random Graph Dynamics* (Cambridge University Press, Cambridge, UK, 2007).
- [40] J. Díaz, L. A. Goldberg, G. B. Mertzios, D. Richerby, M. Serna, and P. G. Spirakis, Approximating fixation probabilities in the generalized Moran process, *Algorithmica* **69**, 78 (2014).
- [41] P. Y. Nie and P. A. Zhang, Fixation time for evolutionary graphs, *Int. J. Mod. Phys. B* **24**, 5285 (2010).
- [42] S. Feld, Why your friends have more friends than you do, *Am. J. Sociol.* **96**, 1464 (1991).
- [43] M. E. J. Newman, S. H. Strogatz, and D. J. Watts, Random graphs with arbitrary degree distributions and their applications, *Phys. Rev. E* **64**, 026118 (2001).
- [44] A. P. Alodjants, A. Yu. Bazhenov, and M. M. Nikitina, Phase transitions in quantum complex networks, *J. Phys.: Conf. Ser.* **2249**, 012014 (2022).
- [45] C. M. Grinstead and J. L. Snell, *Introduction to Probability* (American Mathematical Society, Providence, RI, 1997).