

Evolutionary dynamics on graphs - the effect of graph structure and initial placement on mutant spread

M. Broom · J. Rychtář · B. Stadler

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Abstract We study how the outcome of evolutionary dynamics on a heterogeneous undirected graph depends on where the mutant is introduced to the graph, relating in particular to the degree of the vertex where the mutant is introduced, and which vertices are its neighbours. We explore which types of graphs are conducive to mutant fixation and which are not. We give explicit formulae for fixation probabilities in the case of random drift (with mutants of fitness 1, identical to the resident population). For a general mutant fitness r , we give approximations of relative fixation probabilities in terms of the fixation probabilities of neighbours which will be useful for considering graphs of relatively simple structure but many vertices, for instance of the small world network type, and compare our approximations to simulation results. In general, the smaller the degree of a vertex, the higher the fixation probability of a mutant introduced at this vertex. When the mutant starts at a vertex of degree d , then its fixation probability in the graph is proportional to d^{-2} for small $r \approx 0$ and proportional to d^{-1} for $r \approx 1$. We also find an approximation to the fixation probability when r is large. Finally we discuss the implications of our results for more complicated graphs, including evolving graphs.

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M. Broom
Department of Mathematics, University of Sussex, Brighton BN1 9RF, UK
Tel: +44 1273 877243
E-mail: M.Broom@sussex.ac.uk

J. Rychtář
Department of Mathematics and Statistics, University of North Carolina Greensboro, NC27402, USA
Tel: +1 336 334 5836
E-mail: rychtar@uncg.edu

B. Stadler
Department of Computer Science, University of North Carolina Greensboro, NC27402, USA
Tel: +1 336 256 1112
E-mail: bstadle@uncg.edu

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1 Introduction

Evolutionary dynamics models have traditionally considered only homogeneous populations. Population structure, however, can be important and this was demonstrated particularly in [10]. A variety of other papers have considered this idea in different contexts, see for example [4, 8, 13]. Following [10] we consider a model where each vertex represents an individual in the population, and individuals can reproduce into neighbouring vertices.

In homogeneous populations the probability of fixation in a population with N individuals (and so N vertices) is given by the Moran probability [12]

$$P_{Moran} = \frac{1 - 1/r}{1 - 1/r^N} \quad (1)$$

where resident individuals have baseline fitness 1 and mutants have fitness r (each individual being chosen as the reproducing individual with probability proportional to its fitness). The formula (1) holds for regular graphs (graphs where every vertex has the same degree), and for no others [10]; using a different reasoning, this observation was also made in [2].

The evolutionary dynamics on a graph with N vertices leads generally to a system of the order of 2^N equations [2]. This means that one often has to resort to numerical methods, as in [17–19]. The three exceptional types of graphs where the dynamics yields significantly simpler system of equations are regular graphs (yielding N equations, solved in [10]), star graphs ($2N$ equations, solved in [2]), and line graphs ($N^2/4$ equations, progress on an analytical solution made in [2]). In this paper, we give the analytic solution of the dynamics for any type of graph with non-advantageous mutants ($r = 1$).

Besides the mutant’s fitness, there are two main factors that may potentially influence the fixation probability - the local structure around the vertex where the mutant is introduced, and then the global structure of the graph. In this paper we explore both factors, using a theoretical analysis and simulation results. We focus on the degree and on the “temperature” (see [10]) of the vertex to capture the local structure and on the variation of these within a graph to understand the global one. We compare regular graphs, small world networks, line graphs and star graphs.

For a regular graph, the starting position has no influence on the fixation probability [2, 10]. In the star, the mutant does significantly better when it starts on the boundary; and similarly, starting at the end of the line guarantees the highest fixation probability on the line [2]. Here we show that when a mutant has approximately the same fitness as a resident, then the fixation probability if starting at a given vertex is proportional to the inverse of the degree of the vertex. We also generalize the formula for an arbitrary fitness to approximate the relative fixation advantage between mutants introduced at any two vertices of the graph.

The introduced approximation methods have the benefit of extending to larger more complex graphical systems, such as the small world networks of [5, 7, 14, 15, 21].

2 Evolutionary dynamics on graphs

Let $G = (V, E)$ be an undirected graph, where V is the set of vertices and E is the set of edges. We assume that the graph is finite, connected and simple, i.e. no vertex is connected to itself and there are no parallel edges. We study evolutionary dynamics as described in [10], see also [16]. We treat the dynamics as a discrete time Markov chain. At the beginning, a vertex is chosen at random and replaced by a mutant with fitness r , all remaining vertices having fitness 1. At subsequent steps, a randomly chosen individual replicates with a probability proportional to its fitness and its offspring replaces an individual at a randomly chosen neighbouring vertex. The process stops when there are no mutants or no original residents in the graph. Each state of the dynamics is described by a set $C \subset V$, a set of vertices inhabited by mutants. The transition probabilities of the above Markov chain are determined by a) the probability that a given vertex will be selected for reproduction and b) the probability that, once selected, it places its offspring into another given vertex.

Let $f_i \in \{1, r\}$ be the fitness of an individual at vertex i ; $f_i = r$ means that the individual is a mutant, $f_i = 1$ means that it is a resident. An individual at i is selected for reproduction with probability

$$s_i = \frac{f_i}{\sum_{j \in V} f_j}.$$

The graph structure is represented by a matrix $W = (w_{ij})$, where w_{ij} is the probability of replacing a vertex j by a copy of a vertex i , provided vertex i was selected for reproduction,

$$w_{ij} = \begin{cases} d_i^{-1}, & \text{if } i \text{ and } j \text{ are connected,} \\ 0, & \text{otherwise,} \end{cases}$$

where d_i is the degree of the vertex i , i.e. the number of edges incident to the vertex i .

Let P_C denote the probability of mutant fixation given that mutants currently inhabit a set C . The rules of the dynamics yield, see [2, 16],

$$P_C = \frac{\sum_{i \in C} \sum_{j \notin C} (r w_{ij} P_{C \cup \{j\}} + w_{ji} P_{C \setminus \{i\}})}{\sum_{i \in C} \sum_{j \notin C} (r w_{ij} + w_{ji})} \quad (2)$$

with $P_\emptyset = 0$ and $P_V = 1$. This system has a unique solution following [2].

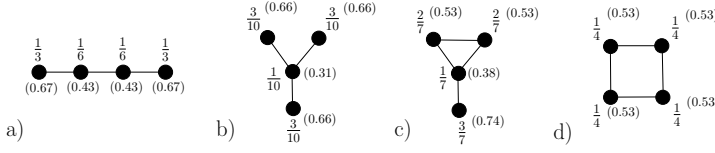


Fig. 1 The fixation probabilities of mutants with $r = 1$ placed in the line, star, lollipop and circle of 4 vertices. The numbers in parenthesis are fixation probabilities for mutants with $r = 2$.

3 Random drift, the case when $r = 1$

Theorem 1 For the case of a random drift, $r = 1$, the solution of (2) is given by

$$P_C = \frac{\sum_{i \in C} d_i^{-1}}{\sum_{k \in V} d_k^{-1}}. \quad (3)$$

Proof The fact that (3) solves the system (2) can be checked by direct substitution. Also, by the uniqueness of the solution of the system (2), (3) is the only solution.

Here we provide the derivation of the formula (3). First assume that, for disjoint sets $C, D \subset V$,

$$P_{C \cup D} = P_C + P_D. \quad (4)$$

Then (2) becomes

$$\sum_{i \in C} \sum_{j \notin C} w_{ji} P_{\{i\}} = \sum_{i \in C} \sum_{j \notin C} w_{ij} P_{\{j\}}$$

which is satisfied if, for all i, j ,

$$w_{ji} P_{\{i\}} = w_{ij} P_{\{j\}}$$

Consequently, whenever vertices i and j are connected,

$$\frac{P_{\{i\}}}{P_{\{j\}}} = \frac{d_j}{d_i} \quad (5)$$

Let us assume that (5) holds even for edges that are not connected. Since

$$1 = P_V = \sum_{j \in V} P_{\{j\}} = P_{\{i\}} \sum_{j \in V} \frac{d_i}{d_j},$$

we get

$$P_{\{i\}} = \left(\sum_{k \in V} \frac{d_i}{d_k} \right)^{-1}. \quad (6)$$

The formula (3) then follows from (6) and (4).

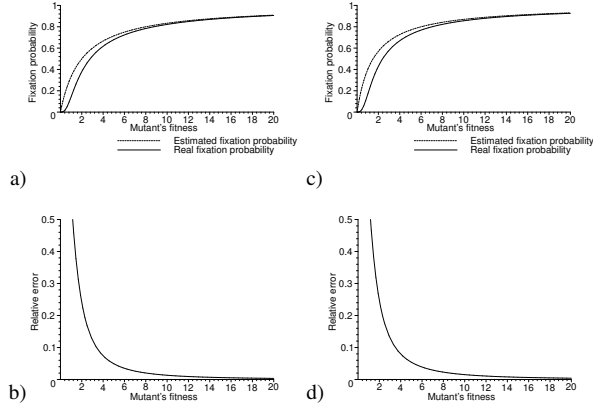


Fig. 2 Comparison of fixation probabilities of mutants starting in the center of the lollipop with 4 vertices (a-b) and on an interior vertex of the line of 4 vertices (c-d) using the formula for large values of r . Real values and values estimated by formula (8) are plotted.

4 Advantageous mutants where $r \gg 1$.

In this section we study the dynamics for very advantageous mutants. When $C = \{i\}$, (2) reads

$$P_{\{i\}} = \frac{\sum_{j \neq i} r w_{ij} P_{\{i,j\}}}{\sum_{j \neq i} (r w_{ij} + w_{ji})}$$

which implies that

$$P_{\{i\}} \sum_{j \neq i} (r w_{ij} + w_{ji}) = \sum_{j \neq i} r w_{ij} P_{\{i,j\}}. \quad (7)$$

When r is very large, we shall assume that the mutants will win with probability 1 as soon as there are at least two mutants in the graph. With this in mind, (7) yields

$$\begin{aligned} r &= \sum_{j \neq i} r w_{ij} \approx \sum_{j \neq i} r w_{ij} P_{\{i,j\}} \\ &= P_{\{i\}} \sum_{j \neq i} (r w_{ij} + w_{ji}) = (r + T_i) P_{\{i\}} \end{aligned}$$

where $T_i = \sum_{j \neq i} w_{ji}$ is the temperature of the vertex i . Consequently,

$$P_{\{i\}} \approx \frac{r}{r + T_i} \quad (8)$$

We see from Figure 2 that the approximation (8) works well when r is sufficiently large, for example of the order of 10 for line or lollipop graphs.

5 The effect of starting position on mutant's advantage

We can see from formula (3) that even for the case of random drift, the graph structure can influence the selection process. If the vertex has low degree, i.e. only a few edges are going into it, a mutant has an advantage if it starts there. We investigated this process on a large range of different graphs, including an exhaustive study of every graph with up to 8 vertices (there are 12112 such graphs). The pattern of low degree and mutant advantage was consistent, and the size of that advantage increased with the difference of the degree of a given vertex and the average over the entire graph. In Figure 1 we saw the different fixation probabilities for a single mutant with $r = 1$ and $r = 2$ introduced at the specified vertex for all vertices on the graph, for four graphs with four vertices. It should be noted that for $r = 1$, the mean fixation probability over all vertices is simply $1/N$. Also, notice that as r increases, the fixation probabilities increase more rapidly for mutants placed into vertices with higher degree.

Now, motivated by equation (5), for $r = 1$, we would like to estimate the advantage of a mutant starting at specific vertex i versus another mutant starting at vertex j for an arbitrary value r . We will work with the system (2) in a similar manner to how we did for $r = 1$ in Section 3. The equation (7) derived from (2) will be satisfied if, for every $i \neq j \in V$,

$$(rw_{ij} + w_{ji})P_{\{i\}} = rw_{ij}P_{\{i,j\}}.$$

Interchanging the roles of i and j , we get that, whenever i and j are connected,

$$\frac{rw_{ij} + w_{ji}}{rw_{ij}}P_{\{i\}} = P_{\{i,j\}} = \frac{rw_{ji} + w_{ij}}{rw_{ji}}P_{\{j\}},$$

which yields the **relative fixation advantage formula**

$$\frac{P_{\{i\}}}{P_{\{j\}}} \approx \frac{r + \frac{d_j}{d_i}}{r + \frac{d_i}{d_j}}. \quad (9)$$

For the case $r \approx 0$, we can see that

$$\frac{P_{\{i\}}}{P_{\{j\}}} \approx \left(\frac{d_j}{d_i}\right)^2$$

and it follows that the fixation probability of any vertex is proportional to d^{-2} , where d is the degree of that vertex. For the case $r \approx 1$ we can use (6) or (9) to see that the fixation probability of any vertex is proportional to d^{-1} .

Note that (9) was derived, and is more accurate, for pairs of vertices that are neighbours. We can use it for pairs that are not neighbours, yet the approximation may bring additional errors. Also, the approximations generally work well for most values of r , but they are least accurate for mutants which are advantageous with a significant but not overwhelming advantage, for instance $r \approx 2$, and similarly for mutants with $r \approx 1/2$, see the illustrative plots in Figure 3.

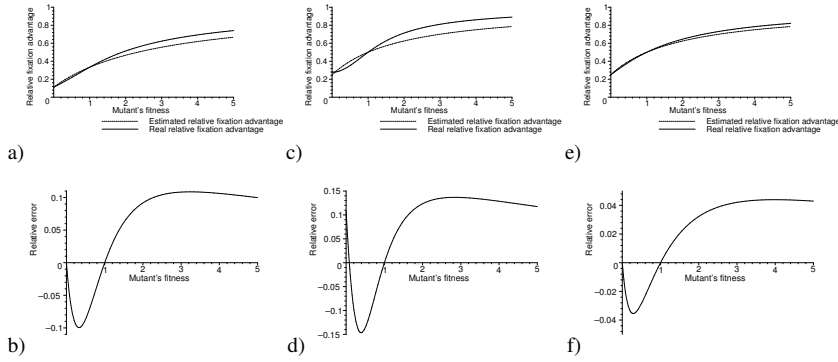


Fig. 3 Comparison of fixation probabilities of mutants on the lollipop with 4 vertices (a-d) and line of 4 vertices (e-f). Real values and values estimated by formula (9) are plotted. a) and b) the central vertex of degree 3 versus the vertex of degree 1 (note that the vertices are neighbours); c) and d) a vertex of degree 2 versus the vertex of degree 1, note that the vertices are not neighbours; e) and f) a central vertex versus an end vertex.

There is an equality in (9) for star graphs [2]. On the other hand, the formula cannot hold exactly in any graph with three vertices i, j, k such that $d_i \neq d_j \neq d_k \neq d_i$ because we would then have

$$\begin{aligned}
 1 &= \frac{P_{\{i\}}}{P_{\{j\}}} \cdot \frac{P_{\{j\}}}{P_{\{k\}}} \cdot \frac{P_{\{k\}}}{P_{\{i\}}} \\
 &= \frac{r^3 + r^2 \left(\frac{d_j}{d_i} + \frac{d_k}{d_j} + \frac{d_i}{d_k} \right) + r \left(\frac{d_k}{d_i} + \frac{d_j}{d_k} + \frac{d_i}{d_j} \right) + 1}{r^3 + r^2 \left(\frac{d_k}{d_i} + \frac{d_j}{d_k} + \frac{d_i}{d_j} \right) + r \left(\frac{d_j}{d_i} + \frac{d_k}{d_j} + \frac{d_i}{d_k} \right) + 1} \\
 &\neq 1
 \end{aligned}$$

In fact we also know that the formula does not hold exactly even when the above does not occur, for example in line graphs [2]. Yet, it is still generally a good approximation and comparing analytical results (for lines, derived by the use of formulae from [2]) and for small graphs (obtained by numerical solution of the system (2)) we can see that the formula (9) in particular approximates well for $r \approx 0$, $r \approx 1$ and $r \approx \infty$.

6 The effect of graph structure on mutant's advantage

In [3], the authors investigated a large number of graphs and confirmed the main results of this paper about mutant position and the type of graph which maximises mutant fixation. The mean fixation probability was always at least as large as for the Moran probability yielded by regular graphs. In general a tree structure was very conducive for mutant fixation. Out of these tree graphs, the worst such graphs for mutant fixation were line graphs, although they were still among the best 25% of all graphs. The best such structure was the star graph, followed by star-like graphs. High

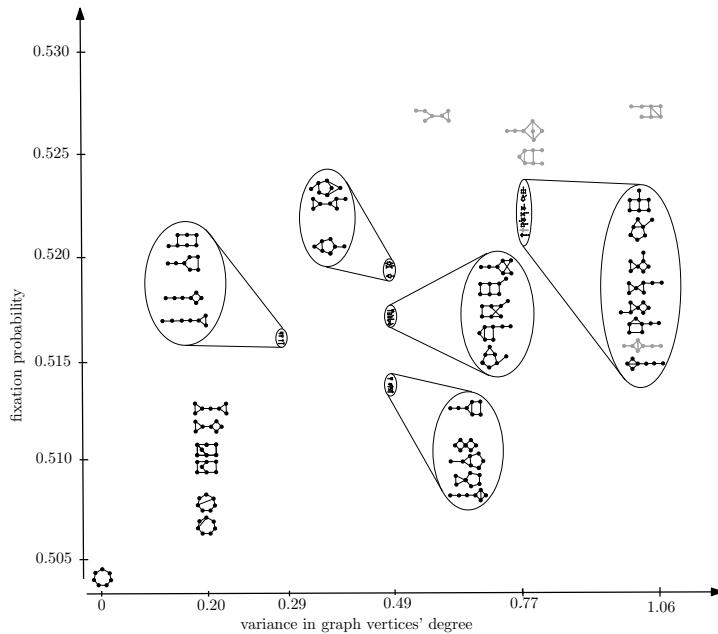


Fig. 4 Small world networks and the influence of variance of vertex degrees on the conductivity of the graph. All graphs with low variance and low conductivity among graphs with 7 vertices and 7 or 8 edges are one rewiring step from one of the three graphs in the lower left corner. The graphs drawn in grey are 2 rewiring steps away. The large ellipses are magnifications of the corresponding smaller ellipses to show the graphs involved clearly. Fixation probabilities shown are for $r = 2$ and obtained by averaging 10^6 simulation runs.

variability of the degree of vertices was the key element associated with high mutant fixation probability.

We now investigate the case of graphs with seven vertices, and in particular those with either seven or eight edges; in total there are 99 such graphs. See Figure 4 where the results for the worst and Figure 5 where the results of the best conductive graphs are depicted, a graph being described as conductive if its structure is good for allowing the spread of mutants. The worst performing graph was a circle, a regular graph. This graph was closely followed by two graphs, both of them consisting of a circle and an edge connecting 2 vertices that were not direct neighbours. The surprising result was that all of the 25 worst conductive graphs could be obtained from one of the worst three graphs by rewiring one single edge (i.e. by selecting an edge and possibly changing one of its endpoints). There are in total 31 graphs that could be obtained by this one step rewiring procedure and all of them were in the worst 32 graphs.

The highest mutant fixation probability is secured by the star-like graphs, which are also the graphs with very high variance in vertex degree.

Another interesting feature is that for some types of graph the relative advantage of an increasingly fit mutant is larger than for others. In Table 1 we see the relative position of the graph in order of its fixation probability for a variety of graphs out of all 853 graphs with seven vertices. Note that the graphs where the probability of

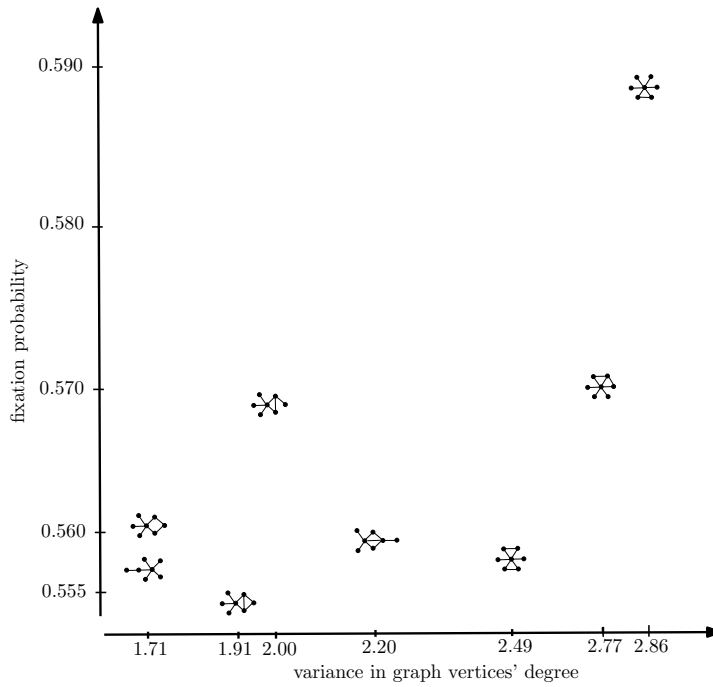


Fig. 5 Star like graphs and the influence of variance of vertex degrees on the conductivity of the graph. Fixation probabilities shown are for $r = 2$ and obtained by averaging 10^6 simulation runs.

Graph	$r = 1.1$	$r = 1.5$	$r = 2$	$r = 10$
	218	268	351	778
	208	333	367	697
	301	465	508	726
	488	379	303	157
	529	435	298	196
	719	558	494	356

Table 1 Order of selected graphs for various values of r , out of 853 graphs, the lower the number the better the mutants do. The top three graphs are becoming relatively less conductive as r increases, the bottom three are becoming relatively more conductive.

mutant fixation increases (relative to others) with increasing r are generally graphs consisting of a single vertex attached to a relatively regular graph (i.e. a vertex with a low degree and very low temperature) while the graphs that worsened are generally two relatively regular graphs connected together (i.e. graphs with low variation in the degree of the vertices).

The structure of the graph can also have a significant effect on the length of the competition between mutant and resident. We considered the process of evolution on graphs with five vertices and with $r = 2$, for the star graph and the complete graph. Recording every replacement (including that on a vertex by an individual of the same type), a thousand graphs of each type were simulated. For the complete graph the mean duration of the contest when the mutant won was 14 (with maximum 58), and was 5 when the mutant lost (with maximum 50), with mutant wins making up about half of the contests. For the star graph the mean duration overall was around 10000 moves, with significantly longer contest lengths when the mutant won and shorter and more variable lengths when the mutant lost. Thus contests for the star graph took approximately a thousand times as long.

7 Interpretations for small world networks and more complex graphical systems

We now return to the small world networks of [5] and [21]. Small world graphs are regular in form with most vertices unconnected, but with a few added random connections which generally make the path length between any two vertices short. From Figure 4 and the related discussion, we can see that our surrogate small world networks have higher mutant fixation probability than the regular graph, but this advantage is not great, and they perform worse in this respect than most other graph structures. This result was essentially borne out for real small world network graphs from [18], where extensive simulations showed an advantage over the Moran probability of anything up to about 10%. This is clearly shown in their Figure 3, reproduced here as Figure 6. The formula (9) indicates that the more random connections added, and thus the greater the variability in the degree of the vertices, the greater the disparity in fixation probability from vertex to vertex, and the greater the potential for mutant fixation on the graph.

In general we can use (9) to make qualitative predictions for more complex graphs by comparing connected vertices, even if the graph is too large and complex for an analytical solution. We can also use the variance in the degree of the vertices of a graph to estimate mutation fixation probability, or at least to obtain an idea of the relative size of such fixation probabilities for different graphs.

All of the above relies on there being a fixed unchanging graph. But what if the graph itself evolves? Two main types of evolving graphs have previously been discussed. Firstly, there are those that evolve at random, independent of any behaviour that is happening on the graph (see e.g. [9]). Under these circumstances, if evolution is slow enough, the situation reduces essentially to what we have described above. However even if that is not the case, we may be able to estimate the variability of the degree of the vertices across the graph at a given time, and still make some statements about the mutant fixation probability. This is particularly the case if some vertices will be prone to low or high degree, and less so if every connection exists or not purely at random. The second type of evolving graph is one that is influenced by the behaviour on the graph itself (see [6]). This type of behaviour is common in real epidemics, for instance, when as soon as someone gets a disease their behaviour may change due

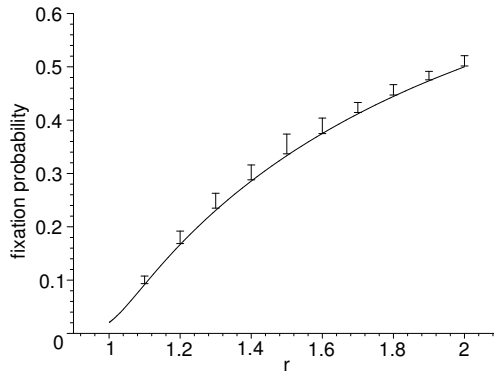


Fig. 6 The fixation probability of mutants on a regular square lattice, given by the formula (1), and on small world networks derived from this underlying graph, where the values for the small world networks are indicated by the top of the vertical lines.

to sickness or deliberate isolation. In the context of evolution on a graph this raises interesting possibilities. We know that mutants with smaller numbers of connections do better. Thus if a mutant could strategically cut connections it would maximise its chances of fixation, provided it did not cut so many that the graph became disconnected. In general the different propensity for mutant-mutant, resident-resident and mutant-resident connections would have a significant effect on the probability of eventual fixation, even if these were not governed strategically. We could use our work here to make some statements about this probability if we could use information on these connections to obtain information on the degrees of connected pairs, or the variability of this degree.

8 Discussion

In this paper we have considered the fortunes of a mutant population within a resident population on a graph, starting with a single mutant. The fixation probability within any graph depends upon the starting position of the mutant with a mutant at a vertex with few connections doing best. When the mutant starts at a vertex of degree d , and its fitness is approximately the same as that of resident individuals, then its fixation probability in the graph is proportional to d^{-1} . This is illustrated clearly in the simple graphs in Figure 1.

Assuming that a mutant is placed in a randomly chosen vertex in a graph, the fixation probability is simply $1/N$ for mutants with $r = 1$. However, if a mutant has superior fitness to the resident population, which will generally be the case for mutants that eventually reach fixation, then the type of graph that it appears on will have a significant effect on its fixation probability. Overall graphs of the tree type (especially stars) are helpful to mutant spread, and those with a regular structure with cycles are not. In general a regular graph, which represents the well-mixed popu-

lations generally used in modelling biological populations, is the worst structure for mutant spread. Another graph that is not conducive is the small world network, again because of its fairly regular structure (e.g. see Figure 4). Whether a graph is conducive or not also depends on the level of mutant advantage, and in Table 1 we see some examples where changing r alters the relative performance of some structures quite dramatically.

Another factor that varies between types of graphs is the time that fixation or elimination of mutants takes. On a well-mixed graph there are more routes to fixation and the contest is resolved far more quickly than on tree-like structures, especially the star, and the difference can be several orders of magnitude even for very small graphs.

It should be noted that there are other types of evolutionary dynamics on graphs. For instance [1] investigates and compares three different dynamics both analytically and by simulation, including the one considered here, and finds different results depending on the dynamics used. In particular they find fixation is more likely if the mutant starts on higher degree nodes in a model called the biased voter model, where the population evolves through one individual dying at random, and its vertex then being occupied by a copy of the individual of one of those connected to it, chosen with probability proportional to its fitness. Thus it is important to think about the dynamics of any particular process.

For graphs with a large number of vertices, it is very hard to analyse them mathematically except in a few special cases, and so simulation is often used. Another purpose of this paper was to come up with an analytical approximation which would enable us to make some qualitative statements about graphs in general. For instance the relative fixation advantage formula (9) gives an indication of the relative size of the fixation probabilities on vertices linked by a small number of intermediate steps and formula (8) indicates that for very advantageous mutants the key for mutant fixation is the temperature of the vertex at which it is introduced. We see in general from Figures 2 and 3 that these approximations are quite good but that there is some degree of error. The formula (9) is good for estimating the fixation probability for one vertex from the known fixation probability of its neighbour. Multiple usage of the formula accumulates mistakes. However if the graph has a small diameter (such as the small world network), the mistake can be bounded since the formula need only be used a few times. We maintain that the results obtained here will be of use in making qualitative analyses of more complex graphs in general, potentially including evolving structures.

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