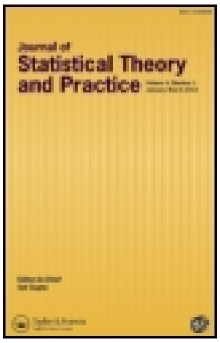

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Evolutionary Dynamics on Graphs - the Effect of Graph Structure and Initial Placement on Mutant Spread

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Evolutionary Dynamics on Graphs - the Effect of Graph Structure and Initial Placement on Mutant Spread

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Abstract

We study the stochastic birth-death process in a finite and structured population and analyze how the fixation probability of a mutant depends on its initial placement. In particular, we study how the fixation probability depends on the degree of the vertex where the mutant is introduced, and which vertices are its neighbours. We find that within a fixed graph, the fixation probability of a mutant has a negative correlation with the degree of the starting vertex. 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. Further, we explore which types of graphs are conducive to mutant fixation and which are not. We find a high positive correlation between a fixation probability of a randomly placed mutant and the variation of vertex degrees on that graph.

AMS Subject Classification: 05C57; 05C82.

Key-words: Birth-death process; Fixation probability; Heterogeneous graphs; Small world networks.

1. Introduction

Evolutionary dynamics has proved to be very influential in the modelling of biological populations. From the simplest models where fitness only depends upon fixed characteris-

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tics, rather than the interactions between the individuals, there has been a huge development of more sophisticated methods of modelling the interactions between individuals including the classical game theoretical models (Bishop and Cannings, 1976; Cressman, 1992; Haigh, 1975; Hofbauer and Sigmund, 1998; Maynard Smith, 1982; Maynard Smith and Price, 1973) and the use of population genetics models (Kimura, 1985; Kimura, 1994).

Such evolutionary dynamics models have traditionally considered only homogeneous populations. Population structure, however, can be important and this was demonstrated particularly by Lieberman, Hauert and Nowak (2005), and a series of related papers have followed, developing these ideas in a number of ways for example investigating game-theoretic models on (usually regular) graphs (Hauert and Doebeli, 2004; Ohtsuki and Nowak, 2006), and considering simple fixed evolution models on irregular graphs (Broom and Rychtář, 2008; Broom, Rychtář and Stadler, 2009). Note that a number of other papers have considered this idea of modelling population structure on graphs in different contexts (Barabási and Albert, 1999; Erdös and Rényi, 1960; Nagylaki and Lucier, 1980).

Following Lieberman, Hauert and Nowak (2005) 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 (Moran, 1958)

$$P_{Moran} = \frac{1-1/r}{1-1/r^N} \tag{1.1}$$

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 (1.1) holds for regular graphs (graphs where every vertex has the same degree), and for no others (Lieberman, Hauert and Nowak, 2005).

The evolutionary dynamics on a graph with N vertices is a birth-death process (see for example Bewernick *et al.* (2007), Crossman, Coolen-Schrijner and Coolen (2009) and references therein) which leads generally to a system of the order of 2^N equations (Broom and Rychtář, 2008; Broom *et al.*, 2010b). This means that one often has to resort to numerical methods, as in Paley, Tarashkin and Elliot (2007), Rychtář and Stadler (2008) and Santos, Pacheco and Lenaerts (2006). The three exceptional types of graph where the dynamics yields significantly simpler system of equations are regular graphs (yielding N equations, solved by Lieberman, Hauert and Nowak (2005)), star graphs ($2N$ equations, solved by Broom and Rychtář (2008)), and line graphs ($N^2/4$ equations, progress on an analytical solution made by Broom and Rychtář (2008)).

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" (Lieberman, Hauert and Nowak, 2005) 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 (Broom and Rychtář, 2008; Lieberman, Hauert and Nowak, 2005). 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 (Broom and Rychtář, 2008).

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 (Bollobás and Chung, 1988; Durrett, 2007; Newman, Barabási and Watts, 2006; Newman and Watts, 1999; Watts and Strogatz, 1998).

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 by Lieberman, Hauert and Nowak (2005), see also Nowak (2006). 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 (Broom and Rychtář, 2008; Nowak, 2006)

$$P_C = \frac{\sum\limits_{i \in C} \sum\limits_{j \notin C} \left(r w_{ij} P_{C \cup \{j\}} + w_{ji} P_{C \setminus \{i\}} \right)}{\sum\limits_{i \in C} \sum\limits_{j \notin C} \left(r w_{ij} + w_{ji} \right)} \tag{2.1}$$

with $P_\emptyset = 0$ and $P_V = 1$. This system has a unique solution (Broom and Rychtář, 2008).

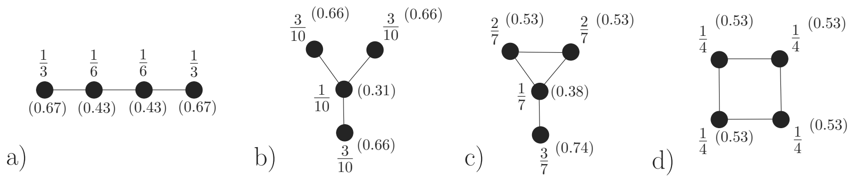

Figure 2.1. The fixation probabilities of mutants with $r = 1$ placed in the line, star, lollypop and circle of 4 vertices. The numbers in parenthesis are fixation probabilities for mutants with $r = 2$.

It was shown in Broom *et al.* (2010b) (see also Shakarian and Roos, 2011) that for the case of random drift, $r = 1$, the solution of (2.1) is given by

$$P_C = \frac{\sum\limits_{i \in C} d_i^{-1}}{\sum\limits_{k \in V} d_k^{-1}}. \tag{2.2}$$

In particular, when $r = 1$, we get

$$\frac{P_{\{i\}}}{P_{\{j\}}} = \frac{d_j}{d_i}. \tag{2.3}$$

Also, the function $C \to P_C$ is, for $r = 1$, an additive probability on the set of graph vertices. However, it will be seen below that it can be considered a nonadditive probability (e.g. Hampel, 2009). The fixation probabilities for a single mutant at each possible starting vertex of several small examples of important graphs are shown in Figure 2.1.

3. Advantageous mutants where $r \gg 1$.

In this section we study the dynamics for very advantageous mutants. When $C = \{i\}$, (2.1) reads

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

which implies that

$$P_{\{i\}} \sum_{j \neq i} (r w_{ij} + w_{ji}) = \sum_{j \neq i} r w_{ij} P_{\{i,j\}}. \tag{3.1}$$

When r is very large, mutants are unlikely to be eliminated, and if they are it is almost certain to happen immediately, before a second mutant appears in the population. Thus in the following calculations 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, (3.1) yields

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

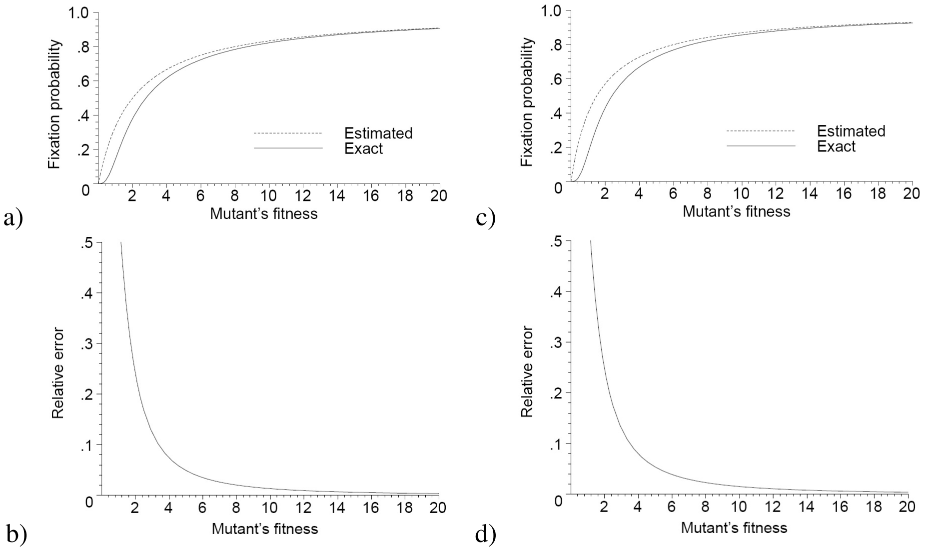

Figure 3.1. Exact versus estimated values of fixation probabilities of mutants starting in the center of the lollypop with 4 vertices (a-b) and on an interior vertex of the line of 4 vertices (c-d). Real values are given by solutions of (2.1) and the estimated values by formula (3.2).

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

$$P_{\{i\}} \approx \frac{r}{r + T_i} \tag{3.2}$$

We see from Figure 3.1 that the approximation (3.2) works well when r is sufficiently large, for example of the order of 10 for line or lollypop graphs.

4. The effect of starting position on mutant advantage

We can see from formula (2.2) that even for the case of random drift ($r = 1$), 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 the dynamics 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 is consistent, and the size of that advantage increases with the difference of the degree of a given vertex and the average over the entire graph. In Figure 2.1 we see 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 (2.3), 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 (2.1) as done in Broom *et al.* (2010b). The equation (3.1) derived from (2.1) 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**

$$\frac{P_{\{i\}}}{P_{\{j\}}} \approx \frac{r + \frac{d_j}{d_i}}{r + \frac{d_i}{d_j}}. \tag{4.1}$$

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 $r \approx 1$, (4.1) agrees with (2.3) and we see that the fixation probability of any vertex is proportional to d^{-1} in this case.

Note that (4.1) 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 4.1.

There is an equality in (4.1) for star graphs (Broom and Rychtář, 2008). 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, it seems that (4.1) does not hold exactly in any graph other than a star graph. Yet, it is still generally a good approximation to the formula (4.1) and in particular approximates well for $r \approx 0$, $r \approx 1$ and $r \approx \infty$.

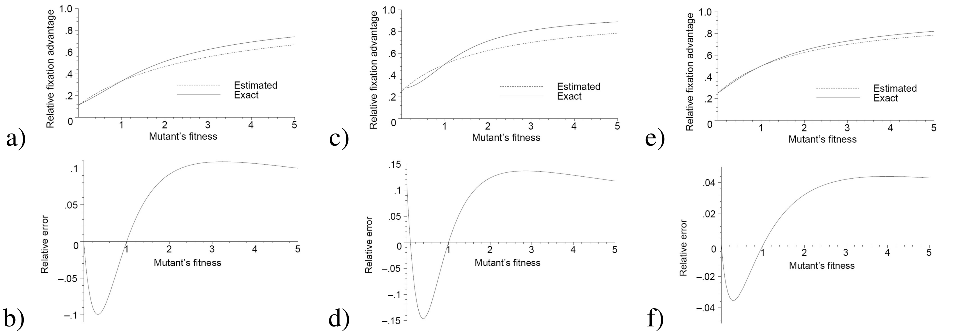

Figure 4.1. Comparison of fixation probabilities of mutants on the lollypop with 4 vertices (a-d) and line of 4 vertices (e-f). Real values and values estimated by formula (4.1) are plotted. a) and b) the central vertex of degree 3 versus the vertex of degree 1 (note that the vertices are neighbours); 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.

5. The effect of graph structure on mutant advantage

We found that $\frac{1}{N}\sum_{v\in V} P_{\{v\}}$, the mean fixation probability of a randomly placed mutant, is positively correlated with the variance of vertex degree in that graph, $\frac{1}{N}\sum_{v\in V}(d_v-\mu)^2$ where $\mu=\frac{1}{N}\sum_{v\in V} d_v$. This is illustrated in Figure 5.1a). The variance of vertex degree is correlated even more strongly with the average fixation probability once we consider graphs with a fixed number of edges only, see for example Figure 5.1b).

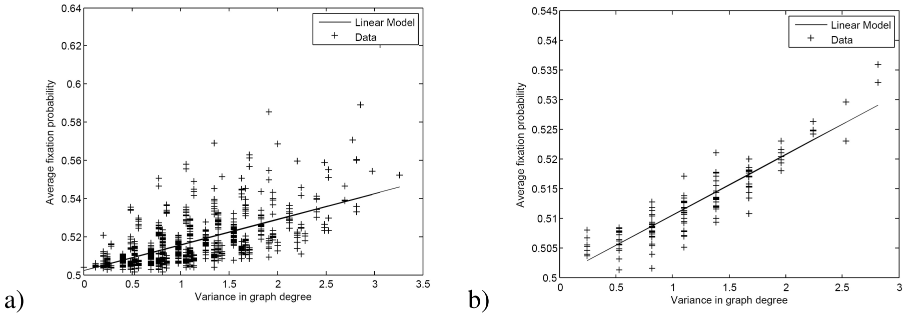

Figure 5.1. Correlation between the mean fixation probability (for $r = 2$) and the variance of vertex degrees in a given graph. a) all connected graphs with 7 vertices, b) all connected graphs with 7 vertices and 12 edges.

Regular graphs (i.e. graphs where the degree variance is 0) are among those least conductive; a graph being described as conductive if its structure is good for allowing the spread of (advantageous) mutants. There are graphs that were even less conductive than regular graphs; in fact there are about 60 graphs among 853 of those with 7 vertices that are less conductive than regular graphs for some $r > 1$. It was observed that the higher r, the smaller the number of graphs that are less conductive than regular ones. In general, if a graph is less conductive than a regular graph for some $r_0 > 1$, then it is less conductive than a regular graph for any $r \in (1, r_0)$ (however, there are a few graphs which are more conductive than a regular graph for relatively large r, but less conductive for intermediate $r > 1$). Figure 5.2 shows two graphs that belong among the least conductive ones for all $r \in (1, 10)$. Moreover, for any $r > 1$, the average fixation probability of a mutant on the least conductive graph (for that specific r) is never less than 99% of the Moran probability, i.e. the average fixation probability of mutants on the regular graphs.

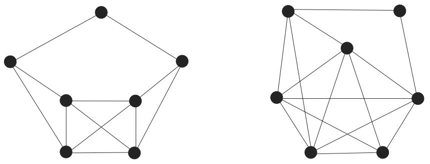

Figure 5.2. Two of the least conductive graphs.

In general a tree structure is very conducive for mutant fixation. Out of these tree graphs, the worst such graphs for mutant fixation are line graphs, although they are still among the best 25% of all graphs. Among graphs with 8 or less vertices, the most conductive graph is the star graph. The star graphs are also highly conductive for graphs with 9 or more vertices; but they are not the most conductive anymore. High variability of the degree of vertices is 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 5.3, which shows the results for the least conductive graphs. The worst performing graph is a circle, a regular graph. This graph is closely followed by two graphs, both of them consisting of a circle and an edge connecting 2 vertices that are not direct neighbours. The surprising result is 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 are in the worst 32 graphs.

Figure 5.4 shows the most conductive graphs among those with 7 vertices and 7 or 8 edges. It should be noted that most graphs look like a star graph and all but one such graph have a property that there is one vertex connected to at least 5 of the remaining vertices.

The structure of the graph can also have a significant effect on the length of the computation between mutant and resident. It is shown in Broom, Hadjichrysanthou and Rychtář (2010a) that in general evolution is slower on the star than on the circle, which is again slower than on the complete graph. They considered both the time to absorption (the time until the population consists only of a single type) and the time to mutant fixation (the time until mutants fixate, conditional upon this occurring) and the pattern was the same, with the

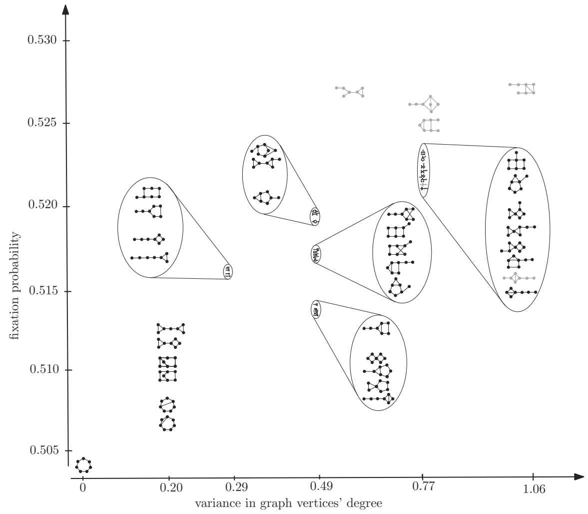

Figure 5.3. Graphs with lowest conductivity (and low variance of vertex degrees) among graphs with 7 vertices and 7 or 8 edges. All such graphs are one rewiring step from one of the three graphs in the lower left corner. The graphs drawn in grey are 2 rewiring steps away. The large ellipses are magnifications of the corresponding smaller ellipses to show the graphs involved clearly. Fixation probabilities are shown for $r = 2$.

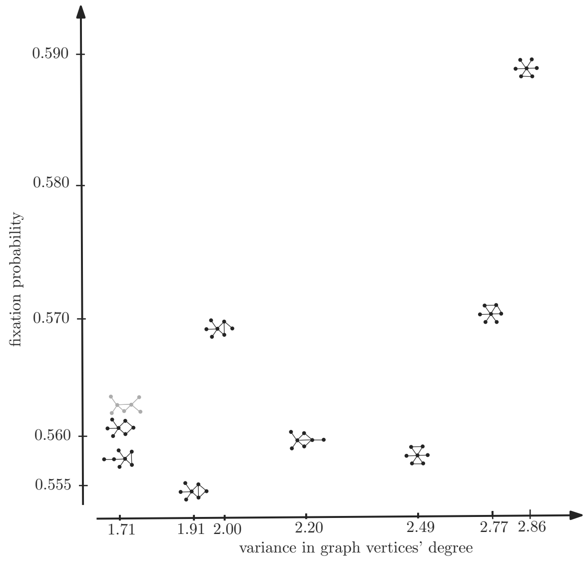

Figure 5.4. Graphs with highest conductivity (and high variance of vertex degrees) among graphs with 7 vertices and 7 or 8 edges. All (except the only one in gray color) such graphs are star like graphs, i.e. with one vertex connected to at least 5 of the remaining vertices. Fixation probabilities are shown for $r = 2$.

times for the star typically an order of magnitude longer. This occurs because all interactions on the star involve the central individual, with most changes occurring with this individual being replaced, and the individuals on the leaves only interacting indirectly through the centre, whereas on the complete graph all individuals can interact with each other. The circle is somewhat inbetween these two extremes in that every individual interacts with exactly two neighbours, and so the fixation/absorption times also take an intermediate value.

6. Interpretations for small world networks and more complex graphical systems

We now return to the small world networks of Bollobás and Chung (1988) and Watts and Strogatz (1998). 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. One way to generate a small world network is to randomly rewire a small number of edges of a regular graph, Watts and Strogatz (1998). We can see from Figure 5.3 and the related discussion, that such a rewiring procedure on graphs with a small number of vertices yields a higher mutant fixation probability than on the regular graph, but this advantage is not great. In fact, regular graphs, even after a slight rewiring, yield a lower fixation probability than most other graph structures. This result was essentially borne out for real small world network graphs from Rychtář and Stadler (2008), where extensive simulations showed an advantage of mutants on small world networks over regular graphs of anything up to about 10%. The formula (4.1) indicates that the more random connections that are 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 (4.1) 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? Three 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. Fan and Chen, 2004). 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 Chan *et al.*, 2003). This type of behaviour is common in real epidemics, for instance, when as soon as someone gets a disease their behaviour may change due 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. Finally, recently deterministic models of graph evolution involving the births and deaths of vertices have been considered by Southwell and Cannings (2010a,b). It would be of particular interest to see how a process of evolution upon a graph that is changing in such a way behaves, especially if, for instance, whether death occurs depends upon the types of the individual at the vertex in question and at its neighbours.

7. Discussion

In this paper we have considered the fortunes of a mutant population within a resident population on a graph, with N vertices 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 in the simple graphs in Figure 2.1.

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 regular graphs, including the complete graph which represents the well-mixed populations generally used in modelling biological populations, are among the worst structures for mutant spread. Other graphs that are not very conductive are the small world networks, again because of their fairly regular structure (e.g. see Figure 5.3).

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 an order of magnitude even for very small graphs.

It should be noted that there are other types of evolutionary dynamics on graphs. For instance Antal, Redner and Sood (2006) investigate and compare three different dynamics both analytically and by simulation, including the one considered here, and find 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. Formula (3.2) may help with an analytical approximation which would enable us to make some qualitative statements about graphs in general. The formula (4.1) is good for estimating the fixation probability for one vertex from the known fixation probability of its neighbour. Multiple usage of (4.1) 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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