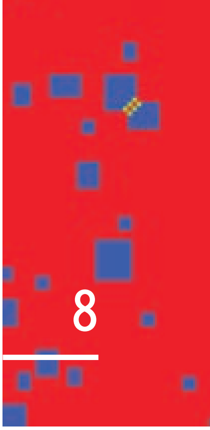


8

EVOLUTIONARY GRAPH THEORY

UP TO NOW we have studied evolutionary dynamics in homogeneous populations, where all individuals are in equivalent positions. Let me now introduce a general framework to analyze the effect of population structure on evolutionary dynamics. We will do this by placing the individuals on the vertices of a graph. The edges of the graph determine competitive interaction. If there is an edge from vertex i to j, then in a genetic setting the offspring of i can replace j. In a cultural setting, some information (an idea) can spread from i to j.

The graph can represent spatial structure among plants or animals in an ecosystem. The graph can also describe the architecture of cells in a multicellular organism, including the cellular differentiation hierarchy. For example, stem cells divide into progenitors, which divide into differentiated cells. The organs of many multicellular animals have such a design, which can delay the onset of cancer (as we shall see in Chapter 12). The graph might also represent relationships in a social network of humans. In this context, the dynamics on the graph describe cultural evolution and the spread of new inventions and ideas. Obviously, human societies are never homogeneous. Individuals in central positions may be more influential than others.

We will ask whether, on the one hand, particular graphs can accelerate the rate of evolution by increasing the fixation probabilities of advantageous mutants. On the other hand, can we find graphs that reduce the fixation probabilities of such mutants? Can certain graphs completely eliminate the effect of selection? Is it possible to characterize all those graphs that have the same evolutionary dynamics (in terms of fixation probability) as unstructured populations? We will assume that the graph does not change on the time scale under consideration. The extension to graphs that change over time is an important task that lies ahead.

This chapter describes first steps into a largely unexplored territory. I have included it in this book because I think that many investigations will follow based on those first steps. The general question of how population structure affects evolutionary dynamics is hugely important and has been a long-standing topic in population genetics. A deeper, mathematical understanding of cultural evolution in human society requires the study of evolutionary dynamics on social networks. Although the main part of this chapter deals with constant selection, the final section looks ahead to games on graphs and states a fascinating result for the evolution of cooperation on graphs.

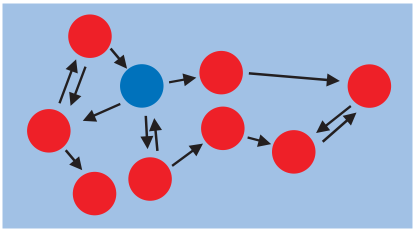
8.1 THE BASIC IDEA

Label all individuals in the population with $i = 1, 2, \ldots, N$. At each time step, a random individual is chosen for reproduction. The probability that the offspring of i replaces j is given by w_{ij}. Hence the process is determined by an $N \times N$ matrix, $W = [w_{ij}]$. Note that all entries of W are probabilities, which means they are numbers between 0 and 1. Moreover, the offspring of any one individual has to go somewhere. Therefore the sum $\sum_{j=1}^{N} w_{ij}$ must be equal to one. The matrix W is stochastic.

We can imagine all individuals occupying the vertices of a graph. If $w_{ij} > 0$, there is an edge from vertex i to j. If $w_{ij} = 0$, there is no edge leading from vertex i to j. The matrix W defines a weighted digraph. Digraphs can have two edges between vertices i and j: one going from i to j; the other one going from j to i (Figure 8.1).

The idea that the offspring of one individual replaces another individual is taken from the Moran process. This process is recovered as the special case

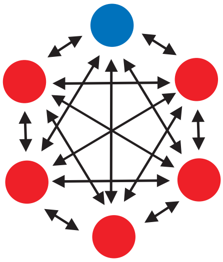
Evolutionary graph theory



1. The individuals occupy the vertices of a graph
2. The edges determine where to place the offspring

Figure 8.1 Evolutionary graph theory is a powerful approach to study the effect of population structure on evolution. The individuals occupy the vertices of the graph. The edges denote reproduction. In each time step, an individual is chosen for reproduction at random but proportional to its fitness. The offspring replaces an adjacent individual with a probability that is proportional to the weight of the edge. We can interpret evolutionary graph theory as describing either genetic reproduction or cultural imitation.

The Moran process is given by the complete graph with identical weights

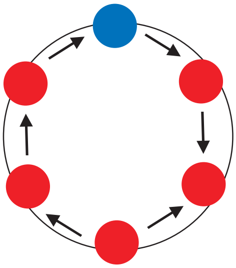


$$\rho = \frac{1-1/r}{1-1/r^n}$$

Figure 8.2 An unstructured population is given by a complete graph: there is an edge between any two vertices. All edges have the same weight. The evolutionary process is equivalent to the Moran process with its well-known fixation probability.

of the complete graph with identical weights, $w_{ij} = 1/N$ for all i and j. The complete graph is defined by the property that all possible edges exist: the offspring of any one individual can replace any other individual (Figure 8.2).

The directed cycle has the same fixation probability as the Moran process



$$\rho = \frac{1-1/r}{1-1/r^n}$$

Figure 8.3 If the graph is a directed cycle, then each individual can place its offspring into the one adjacent place. It is easy to show that the fixation probability of a single mutant with relative fitness r is the same as in the Moran process.

8.2 FIRST OBSERVATIONS

The first question we ask is the following: what is the fixation probability of a new mutant that arises at a random position on a graph?

8.2.1 The Directed Cycle

As a first example, we consider a directed cycle of size N (Figure 8.3). The W matrix is given by

$$W = \begin{pmatrix} 0 & 1 & 0 & \dots & 0 & 0 \\ 0 & 0 & 1 & \dots & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & 0 & 1 \\ 1 & 0 & 0 & \dots & 0 & 0 \end{pmatrix} \tag{8.1}$$

Initially all individuals are of type A. After some time, a mutant B is generated that has relative fitness r. This B individual gives rise to a lineage, which will eventually die out or take over the whole population. Starting from one B mutant, only one cluster of B individuals can emerge. It is not possible for this cluster to break into two or more fragments. This fact makes the calculation of the fixation probability straightforward.

Let m denote the number of B individuals. In order to reduce m by one, the A individual immediately preceding the B cluster in the directed cycle must be chosen for reproduction. Thus the probability to go from m to $m-1$ is given by

$$p_{m,m-1} = \frac{1}{N-m+rm}. \tag{8.2}$$

In order to increase m by one, the B individual at the end of the cluster has to be chosen for reproduction. Therefore the probability of going from m to $m+1$ is given by

$$p_{m,m+1} = \frac{r}{N-m+rm}. \tag{8.3}$$

The ratio of these two probabilities is

$$\gamma_m = \frac{p_{m,m-1}}{p_{m,m+1}} = \frac{1}{r}. \tag{8.4}$$

This quantity is independent of m and identical to what is obtained in the Moran process with constant selection.

From equation (6.13), the fixation probability of a birth-death process is given by

$$\rho = \frac{1}{1+\sum_{k=1}^{N-1}\prod_{m=1}^{k}\gamma_m}. \tag{8.5}$$

Therefore we obtain here

$$\rho = \frac{1-1/r}{1-1/r^N}. \tag{8.6}$$

The fixation probability on a directed cycle is identical to the fixation probability in the Moran process.

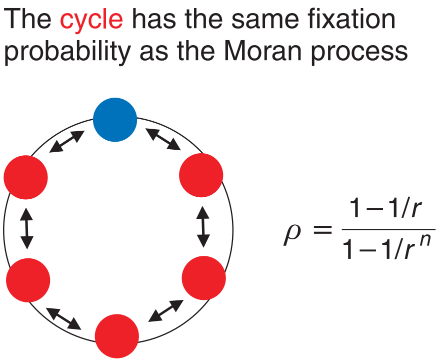


Figure 8.4 If the graph is a cycle, then each individual can place its offspring into any one of the two adjacent places. Again the fixation probability of a single mutant with relative fitness r is the same as in the Moran process.

8.2.2 The Cycle

As a second example, we consider the (bidirected) cycle shown in Figure 8.4. Any two neighbors are connected by two edges: one going in one direction, the other going in the opposite direction. All edges have the same weight. We have

$$W = \begin{pmatrix} 0 & 1/2 & 0 & \dots & 0 & 1/2 \\ 1/2 & 0 & 1/2 & \dots & 0 & 0 \\ 0 & 1/2 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & 0 & 1/2 \\ 1/2 & 0 & 0 & \dots & 1/2 & 0 \end{pmatrix} \tag{8.7}$$

As before, starting from a single B mutant, there can only be one cluster of B. Again it is easy to confirm that

$$p_{m,m-1} = \frac{1}{N-m+rm} \qquad \text{and} \qquad p_{m,m+1} = \frac{r}{N-m+rm} \tag{8.8}$$

Thus the birth-death process on the cycle is described by the same transition matrix as the process on a directed cycle. Hence we obtain the same fixation probability as before.

8.2.3 The Line and the Burst

Let us now consider a linear array as shown in Figure 8.5. From vertex i the offspring can be placed into vertex $i+1$. Vertex N places its offspring onto itself. No edge leads to vertex 1. We have

$$W = \begin{pmatrix} 0 & 1 & 0 & \dots & 0 & 0 \\ 0 & 0 & 1 & \dots & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & 0 & 1 \\ 0 & 0 & 0 & \dots & 0 & 1 \end{pmatrix} \tag{8.9}$$

What is the fixation probability of a randomly placed mutant? The answer is very simple. It is

$$\rho = 1/N. \tag{8.10}$$

With probability $(N-1)/N$ the mutant arises in positions $i = 2, \dots, N$, and its lineage will be eliminated eventually. With probability $1/N$, however, the mutant arises in position $i = 1$, and its offspring lineage will take over the population. The fixation probability is totally independent of the relative fitness, r, of the mutant. Thus the line has a fixation probability that differs from the Moran process.

Another graph that has a different fixation behavior as the Moran process is the "burst," which is also shown in Figure 8.5. There is one central vertex and $N-1$ peripheral vertices. Edges lead from the center to the periphery. We have

$$W = \begin{pmatrix} 0 & 1/(N-1) & 1/(N-1) & \dots & 1/(N-1) & 1/(N-1) \\ 0 & 1 & 0 & \dots & 0 & 0 \\ 0 & 0 & 1 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & 1 & 0 \\ 0 & 0 & 0 & \dots & 0 & 1 \end{pmatrix} \tag{8.11}$$

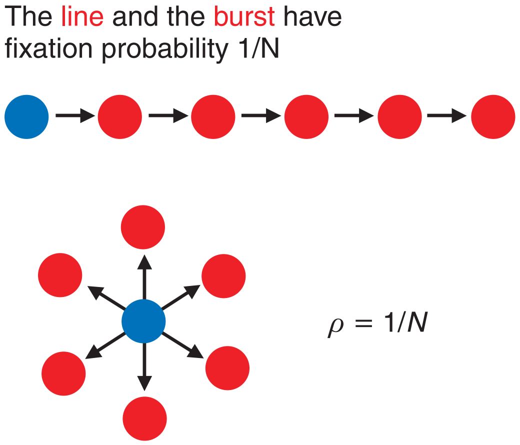


Figure 8.5 Here are two graphs that do not have the same fixation probability as in the Moran process. Both for the "line" and for the "burst," the fixation probability of a randomly placed mutant is $\rho = 1/N$, independent of the fitness of this mutant. In the line, a mutant can only take over the population if it arises in the left-most position. In the burst, the mutant must arise in the central position. These two graphs are suppressors of selection, because all mutants—irrespective of their fitness—have the same fixation probability as a neutral mutant in the Moran process.

A new mutant can only reach fixation if it arises in the center. The chance that a randomly placed mutant originates in the center is $1/N$. Hence the fixation probability is again independent of the relative fitness, r, of the new mutant. The burst and the line have the same fixation probability.

8.2.4 Balancing Drift and Selection

The fixation probability of the Moran process,

$$\rho_M = \frac{1 - 1/r}{1 - 1/r^N}, \tag{8.12}$$

defines a particular balance between natural selection and random drift. If a graph, G, has the same fixation probability as the Moran process, then we say that this graph is ρ-equivalent to the Moran process; it has the same balance of selection and drift.

If, for an advantageous mutant, $r > 1$, the fixation probability on G is greater than the fixation probability in the Moran process, $\rho_G > \rho_M$, then the graph G favors selection over drift. It increases the fixation probability of an advantageous mutant. Therefore graph G is an amplifier of selection.

If, for an advantageous mutant, the fixation probability on G is less than the fixation probability in the Moran process, $\rho_G < \rho_M$, then the graph G favors drift over selection. It reduces the fixation probability of an advantageous mutant. Therefore graph G is a suppressor of selection.

Similarly if, for a disadvantageous mutant, $r < 1$, the fixation probability on G is greater (less) than the fixation probability in the Moran process, then the graph G is a suppressor (amplifier) of selection.

If $\rho_G = 1/N$ for any r, then the graph G is the strongest possible suppressor of selection; it completely eliminates the effect of selection.

We have seen that the cycle and the directed cycle are both ρ-equivalent to the Moran process, whereas the line and the burst completely eliminate selection.

8.3 THE ISOTHERMAL THEOREM

The temperature of a vertex is defined as the sum of all weights that lead into that vertex. The temperature of vertex j is given by

$$T_j = \sum_{i=1}^{N} w_{ij}. \tag{8.13}$$

A vertex with a high temperature will change more often than a vertex with a low temperature. If all the vertices have the same temperature, then a graph is isothermal. We have the following "isothermal theorem": a graph is ρ-equivalent to the Moran process if and only if it is isothermal (Figure 8.6).

For an isothermal graph we have $\sum_{i=1}^{N} w_{ij} = \text{constant}$. Since $\sum_{j=1}^{N} w_{ij} = 1$, it follows that $\sum_{i=1}^{N} w_{ij} = 1$. Therefore a graph is ρ-equivalent to the Moran process if and only if W is a doubly stochastic matrix, which means that all rows and all columns sum to one.

Let us prove the isothermal theorem. The configuration of a population on a graph can be described by a binary vector, $\vec{v} = (v_1, \ldots, v_N)$. If the vertex i is occupied by type A, then $v_i = 0$. If the vertex i is occupied by type B, then $v_i = 1$. Therefore the vector $\vec{v}$ describes a two-coloring of the graph. Denote by m the total number of B individuals. Thus $m = \sum_i v_i$. The probability that

The isothermal theorem

The temperature of a vertex is the sum
of all weights leading into that vertex

$$T_j = \sum_i w_{ij}$$

If all vertices have the same temperature,
then the fixation probability is equivalent
to the Moran process

Figure 8.6 The isothermal theorem characterizes all those graphs that have the same fixation probability as the unstructured population (described by the Moran process). The temperature of a vertex determines how often the individual in this vertex will be replaced. A hot vertex changes more often than a cold vertex. If all vertices have the same temperature, then the matrix $W = [w_{ij}]$ is doubly stochastic and the graph is isothermal.

m increases by one is given by

$$p_{m,m+1} = \frac{r \sum_i \sum_j w_{ij} v_i (1 - v_j)}{rm + N - m}. \tag{8.14}$$

The probability that m decreases by one is given by

$$p_{m,m-1} = \frac{\sum_i \sum_j w_{ij} (1 - v_i) v_j}{rm + N - m}. \tag{8.15}$$

The fixation probability is the same as in the Moran process if for any coloring $\vec{v}$ we have

$$\frac{p_{m,m-1}}{p_{m,m+1}} = \frac{1}{r}. \tag{8.16}$$

This is the case if

$$\sum_i \sum_j w_{ij} (1 - v_i) v_j = \sum_i \sum_j w_{ij} v_i (1 - v_j). \tag{8.17}$$

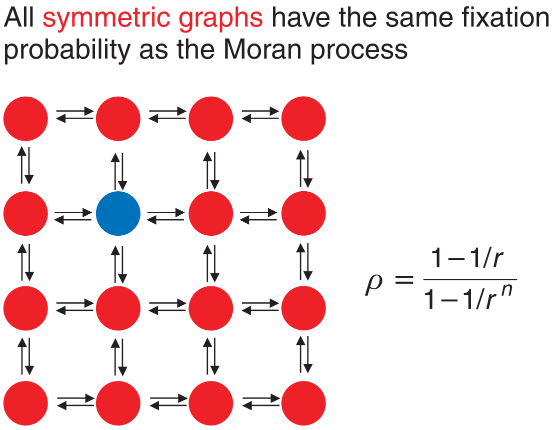


Figure 8.7 A symmetric graph is defined by the property $w_{ij} = w_{ji}$ for all i and j. This means the weight of the connection from vertex i to j is the same as from vertex j to i. It turns out that all symmetric graphs have the same fixation probability as the Moran process. All spatial lattices (square, hexagonal, triangular) are symmetric graphs.

This equality must hold for any vector $\vec{v}$. In particular, it must hold for all vectors of the form $v_k = 1$ and $v_i = 0$ for all $i \neq k$. In this case equation (8.17) reduces to

$$\sum_j w_{kj} = \sum_j w_{jk} \qquad \forall k \tag{8.18}$$

Since $\sum_j w_{kj} = 1$, we have

$$\sum_j w_{jk} = 1 \tag{8.19}$$

and therefore equation (8.18) means that the matrix W is doubly stochastic and the corresponding graph is isothermal.

The cycle and the directed cycle are both isothermal. All symmetric graphs, $w_{ij} = w_{ji}$, are isothermal (Figure 8.7). The cycle is symmetric. Most spatial lattices that have been investigated in evolutionary dynamics are symmetric. But many asymmetric graphs are also isothermal. The directed cycle, for example, is asymmetric but isothermal.

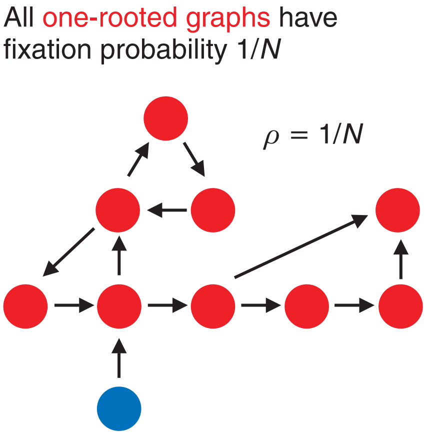


Figure 8.8 It is easy to see that all one-rooted graphs have fixation probability $1/N$ regardless of the fitness of the mutant. Only a mutant that arises in the root generates a lineage that will take over the population. The probability that a randomly placed mutant arises in the root is $1/N$.

The line, however, is not isothermal. The $i = 1$ vertex has temperature 0. The vertices $i = 2, \ldots, N - 1$ have temperature 1. The vertex N has temperature 2. Therefore the line is not ρ-equivalent to the Moran process. The burst is also not isothermal; the central vertex has temperature 0 while all other vertices have temperature 2.

8.4 SUPPRESSING SELECTION

A root is a vertex that has no edge leading into it. A root has zero temperature. If a graph is one-rooted, then it has fixation probability $1/N$. The new mutant must arise at the root, otherwise it cannot take over the whole population. A randomly placed mutant arises at the root with probability $1/N$. Therefore every one-rooted graph completely eliminates selection (Figure 8.8).

If a graph has multiple roots, then any lineage arising from a single mutant can never take over the whole population. If a mutant arises in one of the roots, then it will give rise to a lineage that will never become extinct. Thus, graphs with multiple roots allow the coexistence of different lineages (Figure 8.9).

It is easy to construct suppressors of selection that have a fixation probability of advantageous mutants that is somewhere between $1/N$ and ρ_M. Subdi-

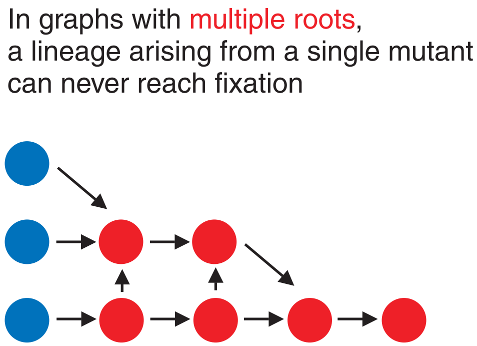


Figure 8.9 If a graph has multiple roots, then the lineage arising from a single mutant can never take over the entire graph. If a mutant arises in a vertex that is not a root, then it can only generate a transient lineage. If a mutant arises in a root, then it will generate a lineage that cannot become extinct. Graphs with multiple roots promote diversity.

vide the population into two compartments with population sizes N_1 and N_2. The total population size is $N = N_1 + N_2$. The first compartment is placed on a complete graph. Edges lead from the first compartment into the second compartment, but not the other way around. The second compartment is on an arbitrary graph with the only constraint that all vertices of the second compartment must be reachable from the first compartment. Thus the first compartment is a source; the second compartment is a sink. The fixation probability of this graph is

$$\rho_G = \frac{1 - 1/r}{1 - 1/r^{N_1}}. \tag{8.20}$$

For advantageous mutants, $r > 1$, we have

$$1/N < \rho_G < \rho_M(N). \tag{8.21}$$

In general, graphs that have small upstream and large downstream populations tend to be suppressors of selection.

8.5 AMPLIFYING SELECTION

The balance between drift and selection, as determined by the fixation probability of the complete graph, can also be tilted toward selection. Consider the

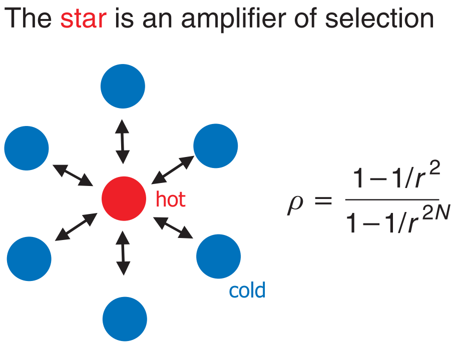


Figure 8.10 It is possible to find graphs that amplify selection over drift. The “star” is a good example. For large N, a mutant with relative fitness r has a fixation probability $\rho = (1-1/r^2)/(1-1/r^{2N})$. Therefore a relative fitness r on a star is equivalent to a relative fitness r^2 in the Moran process. The star is an amplifier of selection.

star structure shown in Figure 8.10. As the population size, N, becomes large, the fixation probability of a randomly placed mutant approaches

$$\rho_M = \frac{1-1/r^2}{1-1/r^{2N}}. \tag{8.22}$$

Hence the star is an amplifier of selection. An advantageous mutant with relative fitness $r > 1$ behaves like an advantageous mutant with fitness r^2 in a standard Moran process. A disadvantageous mutant, $r < 1$, has a probability of fixation that is equivalent to an even greater fitness disadvantage, r^2, in the Moran process.

Can we construct even more powerful amplifiers? The superstar shown in Figure 8.11 amplifies a selective difference r to r^k, where k is the length of each loop in the graph. As the number of leaves and vertices within each leaf grows, the fixation probability becomes

$$\rho_M = \frac{1-1/r^k}{1-1/r^{2k}}. \tag{8.23}$$

By increasing k, we can guarantee the fixation of any advantageous mutant, $\rho \to 1$ if $r > 1$, and guarantee the extinction of any disadvantageous mutant, $\rho \to 0$ if $r < 1$.

The funnel, shown in Figure 8.12, is another potent amplifier. There are $k+1$ layers, labeled $j = 0, \ldots, k$. Layer 0 contains only a single vertex. Layer

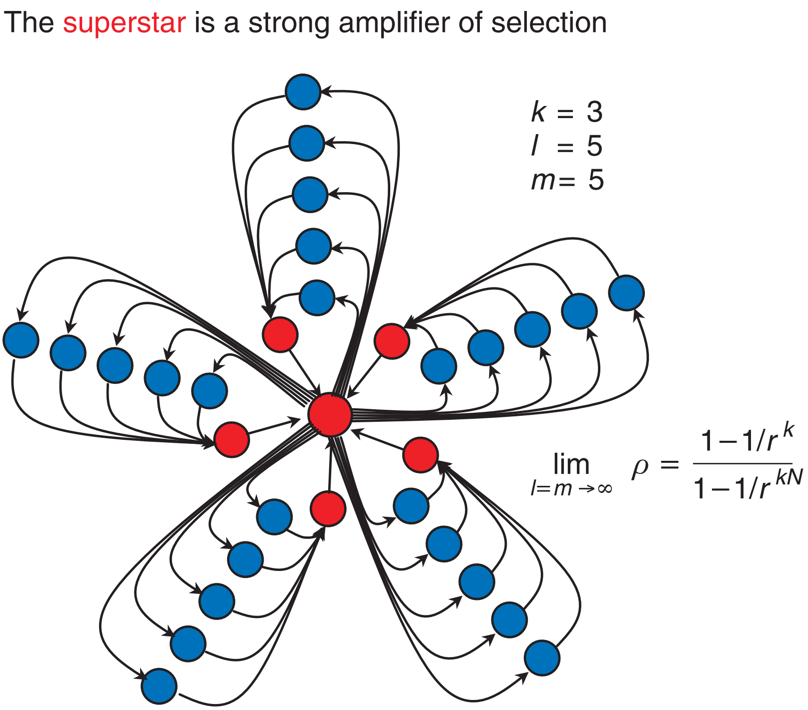

The superstar is a strong amplifier of selection

Figure 8.11 A “superstar” amplifies selection from r to r^k. The parameters l and m denote the number of leaves and the number of loops in a leaf, respectively. The parameter k denotes the length of each loop. The amplification from r to r^k holds in the limit of large l and m. In the limit of large k, the superstar guarantees fixation of any advantageous mutant and elimination of any disadvantageous mutant. The coloring indicates hot vertices (red) and cold vertices (blue).

j contains m^j vertices. All edges that originate from vertices in layer j lead into $j-1$. All edges that originate from the single vertex in layer 0 lead into layer k. As k increases, the fixation probability of any advantageous mutant converges to 1.

Computer simulations show that scale-free networks are mild amplifiers. This is of particular interest because scale-free networks, including small-world networks, have been observed in various circumstances. Scale-free net-

The funnel is a strong amplifier of selection

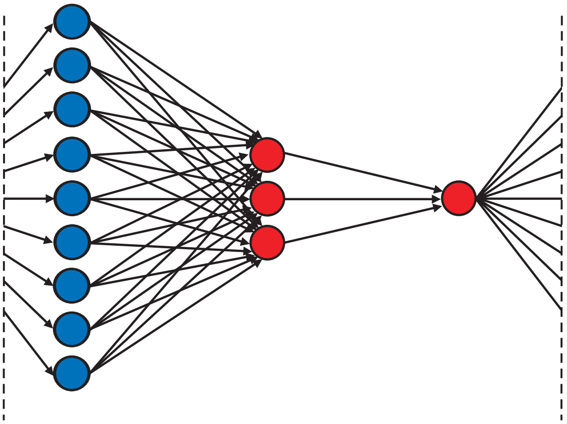


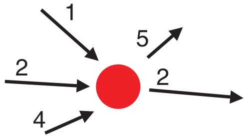
Figure 8.12 The "funnel" is another potent amplifier of selection. There is a single vertex in one layer. All edges leading into that vertex come from a preceding layer with m vertices. All edges leading into that layer come from a preceding layer with m^2 vertices, and so on. All outgoing edges of the single vertex wrap around to lead into the largest layer. In the limit of large m and many layers, the fixation probability converges to one for any advantageous mutant and to zero for any disadvantageous mutant. Again the coloring indicates hot vertices (red) and cold vertices (blue). The superstar and the funnel were invented by Erez Lieberman.

works are defined by the property that they have a degree distribution which is a straight line in a log-log plot. The degree of a vertex is the number of edges connected to this vertex.

8.6 CIRCULATIONS

We can also design a more elegant version of evolutionary dynamics on graphs. Instead of first choosing a vertex for reproduction and then choosing again where to place its offspring, we can simply choose an edge. In this case w_{ij} can be any non-negative number, and W need not be a stochastic matrix. Edge ij is chosen with a probability proportional to w_{ij} multiplied by the fitness of its tail, which is the fitness of the individual at vertex i.

The circulation theorem
The fixation probability is the same as in the Moran process, if and only if the graph is a circulation



Sum over incoming weights = Sum over outgoing weights

Figure 8.13 In an extended approach to evolutionary graph theory, the matrix W is no longer stochastic; instead, the weights w_{ij} are arbitrary non-negative numbers. In each time step, an edge is chosen with a probability proportional to its weight multiplied by the fitness of the individual at its tail. If edge ij is chosen, then the offspring of i will replace j. In this framework, a graph has the same fixation behavior as the Moran process if and only if it is a circulation. A graph is a circulation, if for each vertex the sum of incoming weights equals the sum of outgoing weights. Circulations constitute an important set of graphs that arise in many different contexts.

In this framework, a graph G is ρ-equivalent to the Moran process if and only if it is a circulation (Figure 8.13). A circulation is defined by the property

$$\sum_{j=1}^{N} w_{kj} = \sum_{j=1}^{N} w_{jk} \qquad \forall k = 1, \ldots, N \tag{8.24}$$

This means that for each vertex k, the sum over all weights entering it must equal the sum over all weights leaving it. The proof of this “circulation theorem” is equivalent to that of the “isothermal theorem.” Note that every isothermal graph is a circulation, but not every circulation is isothermal.

8.7 GAMES ON GRAPHS

The next step is to study evolutionary game dynamics on graphs. The general task would be to calculate the fixation probability of a certain strategy, A, competing with another strategy, B. In principle, there can be two different graphs: the interaction graph, H, determines who plays with whom, while the replacement graph, G, specifies the reproductive events (who learns from whom or who is replaced by whose offspring). Classifying all games on all combinations of graphs is a vast (and perhaps even impossible) undertaking. Here I can mention only one specific, though most illuminating, example.

Let us suppose that the replacement graph and the interaction graph are the same, $H = G$, and study the interaction between cooperators, C, and defectors, D. A cooperator helps all of its neighbors. For each neighbor, the cooperator pays a cost, c, and the neighbor receives a benefit, b. Defectors do not provide any help. They have no costs, but they can benefit by receiving help from adjacent cooperators. Each individual occupies the vertex of a graph. The payoffs from all interactions are summed. At first, let us consider regular graphs of degree k: each individual has exactly k neighbors. We consider the case of weak selection: the fitness of an individual is a constant plus w times the payoff. Weak selection means that w is small.

Consider three different update rules for the game dynamics.

1. "Birth-death" process: In each time step, an individual is selected for reproduction proportional to its fitness. The offspring replaces a random neighbor. It turns out that for any choice of the parameter values, b and c, the fixation probability of cooperators, ρ_C, is always less than $1/N$, while the fixation probability of defectors, ρ_D, is always greater than $1/N$:

   $$\rho_C < 1/N < \rho_D. \tag{8.25}$$

   In this "birth-death" process, selection always favors defectors.
2. "Death-birth" process: In each time step, a random individual is chosen to die. The neighbors compete for the empty site proportional to their fitness. In this case, we find that cooperators are advantageous and defectors are disadvantageous, $\rho_C > 1/N > \rho_D$, if

   $$b/c > k. \tag{8.26}$$

   This surprisingly simple rule is the crucial condition for the evolution of cooperation on regular graphs given the "death-birth" update rule.

3. Imitation process: In each time step, a random individual is chosen to update its strategy. It will either stay with its own strategy or imitate a neighbor's strategy proportional to fitness. Therefore the focal individual's own payoff also affects the update dynamics. In this case we find that cooperators are advantageous and defectors are disadvantageous, $\rho_C > 1/N > \rho_D$, if

$$b/c > k + 2. \tag{8.27}$$

For $k = 2$, a regular graph is a cycle. In this case the three results can be obtained from direct calculations. All that is required is to check whether the boundary between a cluster of cooperators moves in favor of the cooperators or the defectors (Figure 8.14). For the "birth-death" process, only the payoff of the two individuals right at the boundary matters. Clearly the defector has a higher payoff than the cooperator. The boundary always moves in favor of the defectors. Selection promotes defection, in this case. For the other two update rules, the payoff of the four individuals that are closest to the boundary determines the outcome. There are always two cooperators and two defectors. Again the defector at the boundary has a higher payoff than the cooperator at the boundary. But the second cooperator has a higher payoff than the second defector. Therefore cooperation could be favored. A simple calculation shows that this is precisely the case, if $b/c > 2$ for the "birth-death" rule and $b/c > 4$ for the imitation rule.

For $k > 2$, the three findings can be obtained via a complicated calculation that uses "pair-approximation." In this technique, one keeps track of the average frequency of cooperators and defectors as well as the average frequency of all pairs, CC, CD, DC, and DD. Strictly speaking, pair approximation is formulated for Bethe lattices (or Cailey trees), where every individual has exactly k neighbors and there are no loops.

The findings were confirmed by computer simulations for lattices and random regular graphs. There is excellent agreement between the simulation results and the calculation that uses pair approximation. Moreover, the simple rules $b/c > k$ and $b/c > k + 2$ also hold for random graphs and scale-free networks.

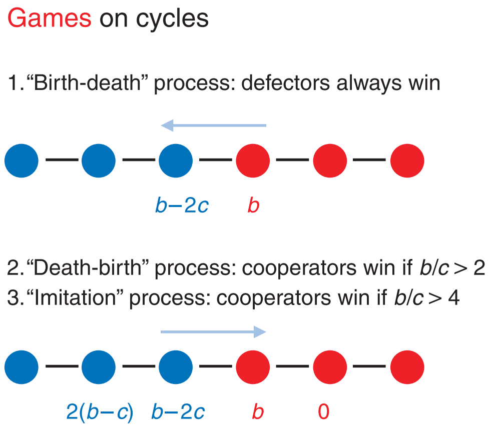


Figure 8.14 Games on graphs can be studied by assuming that individuals interact with their nearest neighbors and thereby accumulate payoff. This figure illustrates the evolution of cooperation on a one-dimensional graph, a cycle. Cooperators pay a cost c for each neighbor. Each neighbor of a cooperator receives benefit b. In the “birth-death” update rule, selection always favors defectors, because only the payoffs of the two individuals at the boundary matter. For the “death-birth” process, the payoff of the next two individuals is also important; in this case, selection favors cooperators provided $b/c > 2$. For the “imitation” process, cooperators win if $b/c > 4$. All calculations are performed in the limit of weak selection and large population size. To calculate the fixation probability of either cooperators or defectors, we only have to analyze whether the boundary between a large cluster of cooperators and a large cluster of defectors moves in one direction or the other, because the lineage arising from one individual always forms a single cluster. A cluster of cooperators (or defectors) cannot break into pieces.

SUMMARY

- Evolutionary graph theory is a powerful approach to study the effect of population structure on evolution.
- The graph can represent the spatial configuration of a population, the differentiation hierarchy of cells in a multicellular organism, or a social network.
- The vertices of the graph are individuals. The (weighted) edges denote reproduction.

- Reproduction can be genetic or cultural. In the first case, the offspring of one individual replaces another individual in an adjacent vertex. In the second case, cultural information spreads from one vertex to the next.
- We study the fixation probability of a randomly placed mutant with relative fitness r.
- If a graph is isothermal, then it has the same fixation behavior as the unstructured population.
- Graphs that are not isothermal can change the balance between drift and selection.
- Amplifiers of selection increase the probability of fixation of advantageous mutants and reduce the probability of fixation of disadvantageous mutants. Suppressors of selection work in the opposite direction.
- The star, superstar, and funnel are amplifiers of selection.
- Scale-free graphs are amplifiers of selection.
- In an extended framework, all graphs that are circulations have the same fixation behavior as the unstructured population.
- We can also study games on graphs. A simple rule for the evolution of cooperation on graphs is $b/c > k$: selection favors cooperation if the benefit-to-cost ratio exceeds the number of neighbors.