Models of Information Spread in Structured Populations

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Abstract—**This paper presents a birth-death model of diffusion processes on graphs, making use of the full population state space consisting of 2^N binary valued vectors together with a Markov process on this space with transition matrix defined by the edge weight matrix of the given population graph. A set of master equations is derived that allows computation of fixation probabilities for any given initial distribution of new information. The transition matrix of the Markov process gives information about most likely initial states, and preferred starting states. A simple example illustrates the apparently paradoxical fact that some population structures allow enhancement of fixation probabilities relative to random drift only for limited values of fitness (or, e.g., rumor believability). In addition, an exact solution is given for complete bipartite graphs. Results obtained are compared to results obtained from a probabilistic voter model update scheme. In addition, the edge-weight matrix of the population graph defines a graph Laplacian that provides information as to increasing or decreasing polarization in a population and this is illustrated with simple examples.**

I. INTRODUCTION

The spread of information in a heterogeneous population is a topic of major interest in a number of fields of study and various models have been devised to better understand how information spreads in structured populations. Such models are very general, applying equally to the spread of rumors and innovations, the spread of computer viruses, and the spread of genetic mutations, to mention only a few cases.

In developing a mathematical approach to this question, populations are represented by directed or undirected graphs with internal population structure coded into an edge weight matrix that specifies interaction probabilities between population members. Different modeling paradigms are used to describe the nature of these interactions, including birth-death, death-birth, voter models, probabilistic voter models, and game-theoretic versions of these. The major emphasis in this paper is on the birth-death paradigm but a probabilistic voter model will be briefly discussed.

A significant quantity to determine is the fixation probability. This is the probability that if an innovation (rumor, virus, genetic mutation, new invention) is introduced at a single vertex in the population graph, it will proceed to become fixed in the population. The Australian statistician Patrick Moran utilized a birth-death model to find the fixation probability for a mutant gene introduced into an initially genetically and structurally homogeneous population in 1958 [1]; but, while the spread of a mutation in homogeneous populations has been studied for over 50 years, the effect of population structure received far less attention until the work of Lieberman, Hauert, & Nowak highlighted its importance [2].

It is now clear that population structures can exert a strong influence, either suppressing or enhancing the effects of selection/retention on fixation probability relative to the original Moran process, and evolutionary dynamics on directed and undirected graphs has become a major focus of research attention [e.g., 3,4,5,6,7]. Much of this effort has been directed to the study of fixation probabilities for single mutants randomly introduced into an otherwise genetically homogeneous population but the mathematical form used applies equally well to other processes of information spread and fixation. This work shows that population structure can enhance or suppress selection relative to drift [8,9,10,11] and that whether selective effects are enhanced or suppressed may depend on both fitness and initial placement of the mutation/innovation [12,13,14].

II. THE BIRTH-DEATH MORAN PROCESS

These models involve a graph in which a member of a population, who either does or does not possess a particular characteristic (e.g., a mutant gene, a particular belief or opinion, an innovative practice, a disease), occupies each vertex. Vertices occupied by population members possessing this characteristic are labeled 1 and those occupied by members not possessing it are labeled 0. The distinguishing characteristic is assumed to have a fitness r ($0 \leq r$) as compared to the fitness 1 of the normal population. The birth-death process is a discrete time process in which, at each iterate, a vertex is chosen at random, biased by fitness, to "reproduce." Following on this choice, a vertex adjacent to the reproducing vertex is chosen to die and be replaced by a copy of the reproducing vertex. This choice is made according to the edge weight probabilities for outgoing edges of the reproducing vertex. Edges can be directed or undirected and the edge from vertex i to vertex j is labeled by the probability that *if* vertex i is chosen for reproduction

then vertex j will be chosen for death. If the population size is N then, at any given time, there will be m "mutants" and N - m normal population members. The Moran process is a biased random drift Markov process on the state space $\{0,1,\dots,N\}$, where the state m indicates a population state with m mutants and N – m normals. States 0 and N are absorbing states. If $p_{m,m-1}$ and $p_{m,m+1}$ are the respective probabilities of state transitions m → m – 1 and m → m + 1, the size (N+1)×(N+1) Markov transition matrix has the form

$$P = \begin{pmatrix} 1 & 0 & 0 & 0 & \cdots & 0 & 0 & 0 \\ p_{1,0} & p_{1,1} & p_{1,2} & 0 & \cdots & 0 & 0 & 0 \\ 0 & p_{2,1} & p_{2,2} & p_{2,3} & \cdots & 0 & 0 & 0 \\ & & & & \vdots & & & \\ 0 & 0 & 0 & 0 & \cdots & p_{N-1,N-2} & p_{N-1,N-1} & p_{N-1,N} \\ 0 & 0 & 0 & 0 & \cdots & 0 & 0 & 1 \end{pmatrix}$$

(1)

Thus, if x_k is the probability of reaching fixation (state N) from state k then

$$x_0 = 0$$
$$x_k = p_{k,k-1}x_{k-1} + p_{k,k}x_k + p_{k,k+1}x_{k+1}$$
$$x_N = 1$$

(2)

and the single vertex fixation probability is x_1, which is given by

$$\rho = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} \frac{p_{k,k+1}}{p_{k,k-1}}}$$

(3)

For the Moran process

$$p_{m,m-1} = \left(\frac{m}{N}\right)\frac{1}{N-m+rm}, \quad p_{m,m+1} = \left(\frac{N-m}{N}\right)\frac{rm}{N-m+rm}$$

(4)

and a brief calculation yields

$$\rho = \frac{1 - \dfrac{1}{r}}{1 - \dfrac{1}{r^N}}$$

(5)

Any graph with fixation probability given by equation (5) is fixation equivalent to a Moran process--the population structure described by the graph has no influence on fixation probabilities, although it may affect time to fixation.

III. THE EFFECT OF POPULATION STRUCTURE

In their seminal paper, Lieberman, Hauert & Nowak [2] give examples of graphs that suppress fixation probabilities and graphs that enhance fixation probabilities relative to the Moran probability of equation (5) and showed that suppression or enhancement of fixation probability is related to the structure of the edge weight matrix for the population graph. In particular, an edge-weighted graph is said to be *isothermal* if the sum of all weights leading into a vertex is the same for all vertices. The Isothermal Theorem [2] states that a graph with stochastic weight matrix W is fixation equivalent to a Moran process if and only if it is isothermal; or equivalently, if and only if W is doubly stochastic.

In addition to computation of fixation probabilities, other questions relating to information spread in populations have been seriously investigated. Two questions of interest are:

I. What initial node (or set of nodes) leads to the greatest fixation probability?

II. Given an observed distribution of mutants, what is the most likely starting node (or set of nodes) producing this distribution?

The first of these questions becomes significant for inhomogeneous population structures since the fixation probability itself is defined as the average of the fixation probabilities over all nodes, and the fixation probability at different nodes may differ (see Fig. 4b). A graph is fixation equivalent to a Moran process if and only if all single vertex fixation probabilities are equal [2], [15], [16].

The second question is significant for tracing the source of rumors, epidemics, mutations, computer viruses, and other epidemic-like events. Answers to both of these questions arise naturally from an approach via the full state space.

IV. THE STATE SPACE APPROACH

In [17], [18], a state space approach is developed to study computation of birth-death fixation probabilities. Two vectors $\vec{a}(\vec{v}), \vec{b}(\vec{v})$ are defined by $\vec{a}(\vec{v}) = \vec{v} \cdot W, \vec{b}(\vec{v}) = \vec{v}' \cdot W$ where $v_i' = 1 - v_i$ and W is the edge weight matrix describing population interaction structures. Mutant vertices are labeled 1 and normal vertices are labeled 0. For a state vector $\vec{v}$, $a_j(\vec{v})$ is the probability that an edge originating at a mutant vertex terminates at vertex j and $b_j(\vec{v})$ is the probability that an edge originating at a normal vertex terminates at vertex j. For a population of size N, this allows construction of the state transition matrix T = (T_{uv}) on the state space of all length N binary sequences. Confusion between the N vertices of the graphs G and the 2^N elements of the state space is avoided by indexing entities defined on the state space with letters chosen from the latter part of the alphabet (e.g., u,v) while entities referring to vertices of the graph G will be indexed with the letters i, j, and k. State vectors $\vec{u}, \vec{v}$ are also binary numbers and the corresponding indices u and v are set to the denary value of these numbers.

Any set of mutants less than the full state space will go either to extinction or fixation, hence the Markov process with transition matrix T has only two absorbing states: extinction, represented by the vector $\underline{0}$ of all zeros; and, fixation, represented by the vector $\underline{1}$ of all ones. The birth-death (or other) modeling process gives a functional equilibrium between the opposing poles of extinction and fixation. Writing $v = \sum_{i=1}^{N} v_i 2^{N-i}$ and taking x_v as the probability that the corresponding state $\vec{v}$ goes to fixation, the equation $(I - T) \cdot \vec{x} = 0$ for the Markov steady state, with boundary conditions $x_0 = 0$ and $x_{2^N - 1} = 1$, yields the system of master equations

$$\left[N + (r-1)m - r\vec{a}(\vec{v}) \cdot \vec{v} - \vec{b}(\vec{v}) \cdot \vec{v}' \right] x_v -$$

$$r \sum_{i=1}^{N} a_i(\vec{v}) v_i' x_{v+2^{N-i}} - \sum_{i=1}^{N} b_i(\vec{v}) v_i x_{v-2^{N-i}} = 0 \qquad (6)$$

These are linear equations that can be solved by standard packages in Maple, Mathematica, Matlab, and other programs. The catch is that that there are $2^N - 2$ of these equations in an equal number of unknowns. Thus, solution is only possible for small values of N (say N < 20), and even in these cases, exact solutions are likely to be cumbersome. For example, the graph of Fig. 1 represents a cycle with a constriction. Symmetry conditions reduce the 30 equations arising from (6) to 16 equations in 16 unknowns. The fixation probability is given by a ratio of two degree 16 polynomials in the fitness r, with coefficients of up to seven digits in length. It is best represented graphically in terms of the difference between this probability and the corresponding Moran probability on five vertices, as indicated in Fig. 2. The fixation probability for the graph of Figure 1 is greater than that of a Moran process for $1 < r < 2.267235117$. This is a surprising result, showing that the general assumption, that a population structure will always suppress or enhance fixation probability, is wrong.

In [17], [18] a class of graphs called circular flows is defined. This class contains many of the graphs that have been studied in the literature, including cycles, funnels, cascades, and layered networks. Fig. 3 shows a structural schematic of what such graphs are like.
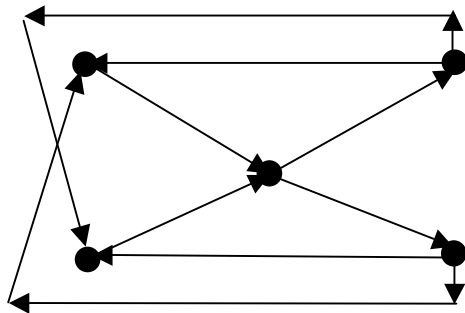
Fig. 1
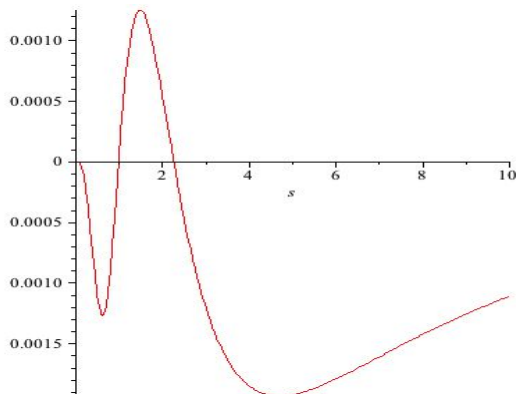N = 5 Cycle of Width 2 With Constriction

Fig. 2
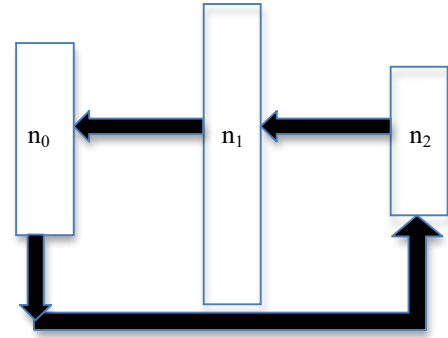Difference between Fixation Probability for Graph of Figure 1 and the Equivalent Moran Probability

Fig. 3
Illustration of a 3-Level Circular Flow

The numbers n_k indicate the number of vertices in the corresponding equivalence classes of vertices while the arrows indicate that each node in class n_{k+1} is connected to every node in class n_k with probability $1/n_k$ (with indices taken mod s+1 where s is the maximum number of classes).

Of particular interest are the complete bipartite graphs $K_{n,m}$, in which there are only two equivalence classes of vertices. Setting $n_0 = n$, $n_1 = m$ the general solution for the fixation probability of these graphs has been found [18]: for the graph $K_{n,m}$ the fixation probability is

$$\rho_{K_{s,n}}(n,m) = \left(\frac{r^{n+m-1}}{nr+m} \right) \left[\frac{(nmr + m^2 - nm + n^2)(mr+n)^{n-s-1}}{P(s,n)} \right] \qquad (7)$$

$$P(n,m) = \frac{r^{n+m}(mr+n)^{m-n} - (nr+m)^{m-n}}{r^2 - 1}.$$

Writing $x_{0,1}$ for the fixation probability for a vertex in the k=1 layer and $x_{1,0}$ for the fixation probability of a vertex in the k = 0 layer,

$$x_{1,0}/x_{0,1} = \left(n^2 + nmr \right) / \left(m^2 + nmr \right) \qquad (8)$$

Thus, if m > n the fixation probability is greater for a vertex located in the k = 1 layer.

If there are k+1 equivalence classes in a circular flow with n_i vertices in the i-th class then this is represented by the k+1 tuple $(n_0, n_1, \ldots, n_k)$. All vertices in each class are equivalent and this symmetry condition reduces the number of equations and unknowns involved to the product of all terms n_s+1, $0 \le s \le k+1$ for k levels [17].

The question of the significance of the initial site where an innovation is introduced has been studied in [12], and can be explicitly illustrated with solutions to equations (6). Fig. 4 shows several examples of three level funnel graphs $(n_0, n_1, n_2) = (1,2,n)$. For the (1,2,n) graphs with n < 6 the average fixation probability is enhanced with respect to a Moran process only for limited values of r > 1 (for n ≥ 6 it appears to be enhanced for all r > 1), as indicated in Fig. 4a. Fig. 4b, however, shows the corresponding fixation probabilities for initial placement in the n_0, n_1, and n_2 equivalence classes of vertices. For each case in Fig.4b the lowest curve corresponds to the central n_1 level and the highest curve to the n_2 level while the middle curve corresponds to the n_0 level.
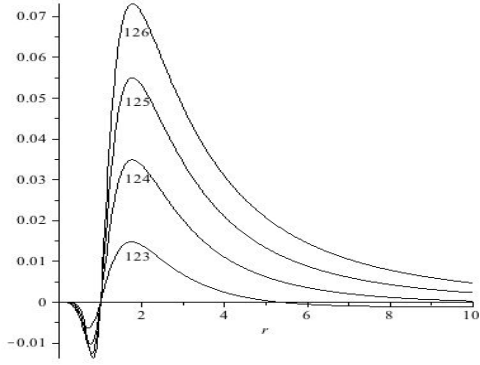
Fig. 4a
Difference between Fixation Probability for Circular Flows (1,2,n)
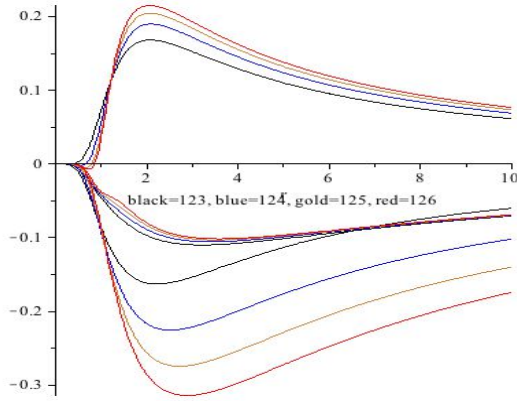and the Equivalent Moran Probability for n = 3 – 6.

Fig. 4b
Single Vertex Fixation Probability Minus Moran Probability for
Circular Flows of Fig. 4a.

This illustrates that for these graphs fixation probability is enhanced relative to a Moran process only if the initial mutant is placed in the n_2 equivalence class.

These sorts of results indicate that if the goal is to enhance the probability an innovation will spread throughout a population careful attention must be paid to where it is introduced.

V. THE STATE TRANSITION MATRIX

Useful results can be obtained by consideration of the state transition matrix T. A state $\vec{u} = (u_1, u_2, ..., u_N)$ defines the binary number $u_1 u_2 ... u_N$. The 2^N population states listed from the top down in numerical order define a $2^N \times N$ matrix S with $S_{ui} = u_i$. As a direct consequence we have:

Lemma 1:

The probability that vertex i will contain a mutant after k iterations, starting from initial state $\vec{u}$, is given by $[T^k S]_{ui}$.

Theorem 1:

Given initial state $\vec{u}$, the probability of fixation is

$$x_u = \lim_{k \to \infty} \left[T^k \cdot S \right]_{ui}.$$

Theorem 2:

Given an initial state $\vec{u}$ and a number of birth-death iterations k, $\left[T^k \right]_{u\underline{1}} \leq x_u \leq 1 - \left[T^k \right]_{u\underline{0}}$.

Lemma 1 and Theorem 2 are reported in different language in [19], [20].

Interpolation of the equation in Theorem 2 yields an estimate for the fixation probability of any initial state $\vec{u}$: set $\Delta_u(k) = 1 - [T^k]_{u\underline{0}} - [T^k]_{u\underline{1}}$ and the linear interpolation estimate fof fixation probability is:

$$est_k(x_u) = \left[T^k \right]_{u\underline{1}} + \frac{\Delta_u(k)}{\left[T^k \right]_{u\underline{0}} + \left[T^k \right]_{u\underline{1}}} \tag{9}$$

This makes it possible to tentatively answer question (II): given that the observed state after k iterations is $\vec{v}$, what are the most likely initial states to produce this observed configuration? The answer is obtained by finding $\max\left\{ T^k_{uv} \big| \vec{u} \in V \right\}$ for sufficiently large values of k. A detail that arises is that for large k these terms may become very small, leaving numerical results vulnerable to rounding errors. This problem can be addressed by dividing each entry of T^k by the appropriate column sum with each iteration.

Let $D(\vec{v}, k) = \sum_{u \in V(H^N)} \left[T^k \right]_{uv}$ and $D(k) = \text{diag}[D(\vec{v}, k)]$.

Then the column entries in $T^k D^{-1}(k)$ will be relative rather than absolute probabilities and these can be computed from $T^{k-1} D^{-1}(k-1)$ as $T^k D^{-1}(k) = [T T^{k-1} D^{-1}(k-1)][D(k) D^{-1}(k-1)]$ where $D(k) D^{-1}(k-1)$ is just the diagonal matrix formed from the column sums of $T T^{k-1} D^{-1}(k-1)$.

VI. SIMULTANEOUS UPDATING

In this section another updating process is considered, a probabilistic voter model, in which at each discrete time the individual at every vertex will change or remain the same with probability determined by the average of the weights assigned to incoming edges of a vertex from other normal and mutant vertices. If the sum of weights of incoming edges from mutant vertices is x while that from normal vertices is y then that vertex will be normal or mutant at the next iteration with probabilities y/(x+y) and x/(x+y).

As with the birth-death process, a Markov transition matrix is constructed which acts on the system state space. If $\vec{u} = (u_1, ..., u_N)$, $\vec{v} = (v_1, ..., v_N)$ are two states the probability of a transition $\vec{u} \to \vec{v}$ is determined in two stages. For given u_j, the probabilities that v_j will be 0 (p_j) or 1 (q_j) are:

$$p_j = (1 - u_j)\left[\frac{ra_j(\vec{u})}{N^*(\vec{u})} \right] + u_j\left[1 - \frac{b_j(\vec{u})}{N^*(\vec{u})} \right]$$

$$q_j = (1 - u_j)\left[1 - \frac{ra_j(\vec{u})}{N^*(\vec{u})} \right] + u_j\left[\frac{b_j(\vec{u})}{N^*(\vec{u})} \right] \tag{10}$$

$$m = \sum_{j=1}^{N} u_j, \quad N^*(\vec{u}) = N - m + rm$$

The $\vec{u} \to \vec{v}$ transition probability is then

$$T_{uv} = \prod_{j=1}^{N} \left[v_j p_j + (1 - v_j) q_j \right] \tag{11}$$

Use of this transition probability allows computation of fixation probabilities. In this case, however, the process is far more computationally expensive and only the simplest examples have been studied. Fig. 5 shows a comparison for the cases of three vertex star and complete graphs.
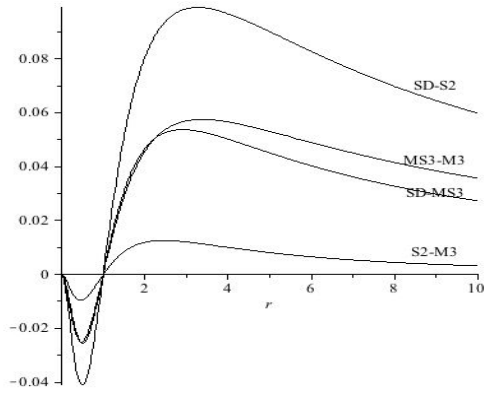
(14)

Fig. 5 Comparison of Simultaneous and Birth-Death Updating
Paradigms on Two Simple Cases

In this figure SD is the fixation probability for a 2-star with simultaneous updating while S2 is the corresponding birth-death fixation probability. Likewise, MS3 is the fixation probability for simultaneous updating on a complete graph with three vertices while M3 is the birth-death fixation probability.

Based on these examples, it appears that fixation probabilities are greater in the simultaneous update paradigm, which may be more appropriate for cases in which information spreads to multiple population members (as with a spam e-mail, for example).

VII. THE GRAPH LAPLACIAN

There is much useful information contained in the graph Laplacian matrix. If the eigenvalues of this matrix are ordered from smallest to largest the first is always 0 and the remaining eigenvalues satisfy $0 \le \lambda_1 \le \lambda_2 \le \dots \le \lambda_{N-1} \le 2$ for an N vertex graph. The number of 0 eigenvalues equal the number of connected components, hence $\lambda_1 > 0$ if and only if the graph is connected. The value of λ_1, called the algebraic connectivity, provides information about the difficulty of cutting the graph into disconnected parts.

Until recently, the graph Laplacian has only been defined for undirected graphs, but recently this has been generalized to the directed case [20].

If W is the edge weight matrix for a directed graph and μ is the steady state solution of $\mu \cdot (I - W) = 0$ then the graph Laplacian is defined as $\Gamma = \mu^{1/2} \cdot (I - W) \cdot \mu^{-1/2}$ where $\mu^{1/2}$ and $\mu^{-1/2}$ are respectively the diagonal matrices with diagonal entries the square roots of the elements of the steady state vector μ. Characteristic equations have been computed for the following graphs:

1. A biased cycle with probability p in the clockwise direction and probability 1-p in the counter-clockwise direction:
2. A k+1 level circular flows $(n_0, \dots, n_k)$.
3. A complete graph in which the vertex set is divided into two components U and V with n vertices in U and m in V. Every vertex in U connects to every other vertex in U with probability p/(n-1) and to every vertex in V with probability (1-p)/m. Every vertex in V connects to every other vertex in V with probability q/(m-1) and to every vertex in U with probability 1/n.
4. A graph similar to case 3 excepting that there is only a single connection between subsets U and V with probability 1-p going in the direction U→V and probability 1-q going in the direction V→U, setting n = |U|-1 and m = |V|-1 (i.e., excluding the distinguished vertex in each subset where the connection occurs).

Cases 3 and 4 are of particular interest in that they provide the possibility of a cut in lines of interaction between sub-populations and thus allow studies of the development or decline of communication among population groups as populations either become polarized, or a consensus (or at least agreement to keep talking) emerges. These two cases are also end points of a sequence in which connections between vertex sets U and V are through subsets: C_U of U and C_V of V.

If p = q = 1 in cases 3 and 4, corresponding to the complete severing of communication between the two subsets of vertices, then the characteristic polynomial reduces to just the product of the polynomials for complete graphs on n and m vertices respectively.

The characteristic polynomials are listed in Table I, setting x = $\lambda - 1$ with λ an eigenvalue of Graph Laplacian. Case 1 is given in terms of a recursion relation; all others are explicit formulas.

TABLE I
CHARACTERISTIC POLYNOMIALS OF CASES 1-4

Case	Characteristic Polynomial
1	$\displaystyle\sum_{s=0}^{(N-1)/2} C_s(N) p^s (1-p)^s x^{N-2s} + p^N + (1-p)^N$ $\qquad$ *N odd* $\displaystyle\sum_{s=0}^{(N-2)/2} C_s(N) p^s (1-p)^s x^{N-2s} - K^N$ $\qquad$ *N even* $C_{2k}(N) = C_{2k}(N-1) - C_{2k-1}(N-2)$ $C_{2k+1}(N) = C_{2k+1}(N-1) - C_{2k}(N-2)$ $C_0(N) = 1,\ C_1(N) = -N$ $K^N = \left[p^{N/2} - (1-p)^{N/2} \right]^2\ N = 0 \bmod 4$ $K^N = \left[p^{N/2} + (1-p)^{N/2} \right]^2\ N = 2 \bmod 4$
2	$x^{N-k-1}\left[x^{k+1} + (-1)^k \right],\quad N = \displaystyle\sum_{s=0}^{k} n_s$
3	$\left(x - p/(n-1) \right)^{n-1} \left(x - q/(m-1) \right)^{m-1} \left[x^2 + (p+q)x + p+q-1 \right]$
4	$\left(x - \dfrac{1}{n} \right)^{n-1} \left(x - \dfrac{1}{m} \right)^{m-1} \left\{ \left[x^2 - p'q' \right]\left(x - \dfrac{n-1}{n} \right)\left(x - \dfrac{m-1}{m} \right)\right.$ $\left. - \dfrac{p}{n}\left(x - \dfrac{m-1}{m} \right)x - \dfrac{q}{m}\left(x - \dfrac{n-1}{n} \right)x + \dfrac{pq}{nm} \right\}$ $p' = 1-p,\ \ q' = 1-q$

A measure of the degree of communication between separate sets of vertices can be defined in terms of the eigenvalues of the graph Laplacian, although an exact general form for this is still being investigated. If λ_1 is

found to be decreasing in time, for example, it may suggest increasing polarization in the represented population.

For the graph of case 3 a relatively easy measure is obtained: there are n-1 eigenvalues equal to (n+p)/n, m-1 eigenvalues equal to (m+q)/m and two remaining eigenvalues of 0 and 2-p-q (recalling x = λ-1). This suggests use of the 2-p-q eigenvalue, although a measure incorporating both the magnitude and direction of communication bias requires knowledge of both the relative magnitudes of p and q, and the norm of the two dimensional vector $\vec{b} = (2-p-q)(1-p, 1-q)$, given by

$$|\vec{b}| = (2-p-q)\sqrt{2-2(p+q)+p^2+q^2} \qquad (11)$$

Fig. 6 gives a plot of this norm for 0≤p,q≤1. In this figure p = 1 corresponds to no communication from the subset U of the population to the subset V, while q = 1 corresponds to no communication from V to U. Thus the communication bias goes in the direction determined by the relative sizes of p and q while the magnitude of bias is given by (11). If p > q, for example, then the population subset U is favored (i.e., there is a greater degree of contact from V to U than in the other direction). In Fig. 6 it is clear that the greatest degree of communication between subsets U and V occurs when p = q = 0, i.e., when there is no within subset communication and the graph is a complete bipartite graph. Likewise, there is no communication between U and V when p = q = 1.

As an extension of this idea, dynamical interactions can be posited, leading to the coefficients p and q varying in time. In this case, the degree of communication between subsets U and V will follow a path on the surface of Fig. 6.

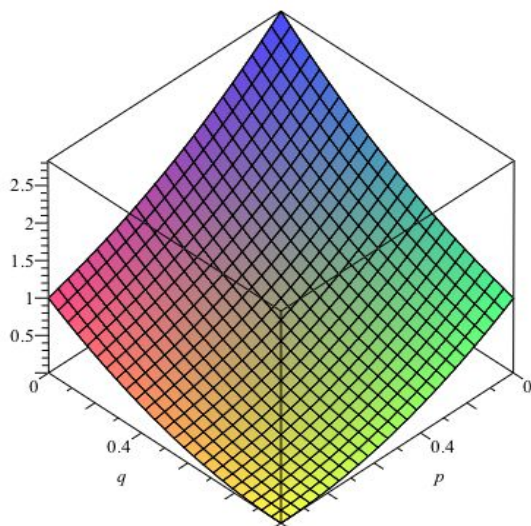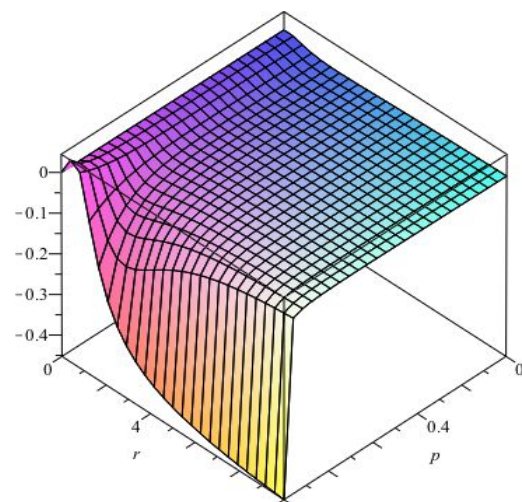Fig. 7 shows plots of the fixation probabilities for case 3 as a function of p and r, with q = 1/2 and n = m = 3.

Fig. 7a Fixation Probability Minus Moran Fixation Probability for Case 3 With n = m = 3, q = 2/5
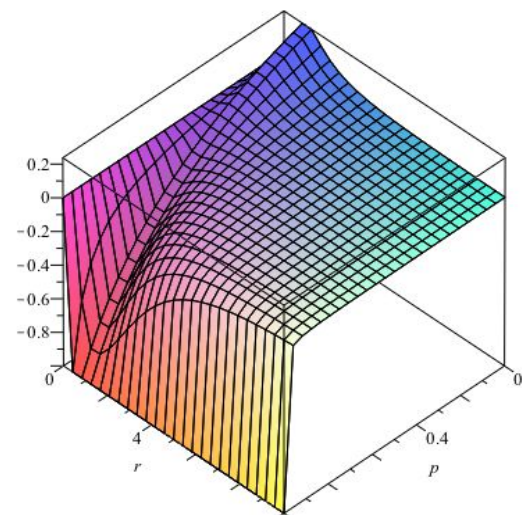
Fig. 7b U Minus V Fixation Probabilities
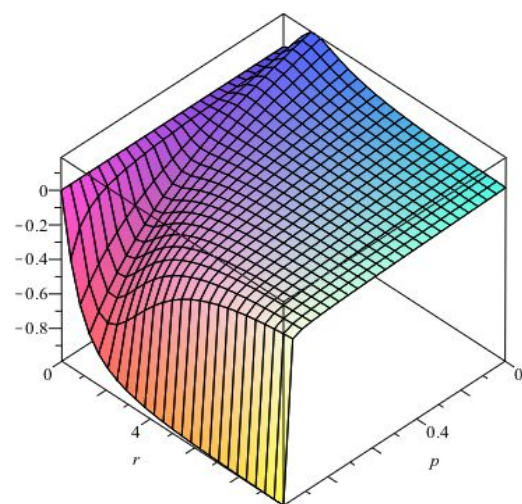

Fig. 6 Plot of $|\vec{b}|$ From Case 3

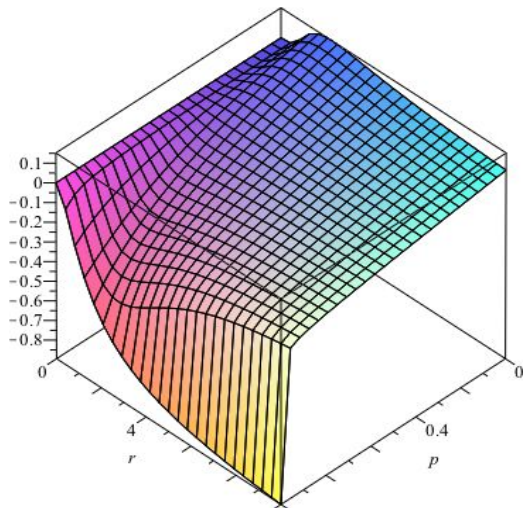Fig. 7c Fixation Probability for Case 3 With Two Vertices of U Set to One Minus That for Two Vertices of V Set to One.

Fig. 7d Fixation Probability for Case 3 With a Single Vertex in U Minus That With a Single Vertex in V Set to One.

Fig. 8b Fixation Probability if Initially U is all Zeros, V is All Ones.

In Fig. 7 the parameter q is set to 2/5 (so the weights connecting vertices in V with all other vertices in U and V are 1/5) while p varies between zero and one. By symmetry, if p = 2/5 the values in Figs. 7b, 7c, and 7d equal zero while they are positive for p < 2/5 and negative for p > 2/5. If p < 2/5 this means that there is a bias in the direction from U to V and vice versa for p > 2/5. Thus the greater fixation probability goes with vertices in the subgroup of vertices that have a greater probability of communicating with the other subgroup. Comparison to Fig. 6 with q = 2/5 shows the increase in communication degree as p decreases from one to zero. Note that in there is a sharp drop in all of the graphs in Fig. 7 at p = 1. This corresponds to no communication from population U to population V hence the fixation probability for any innovation introduced into the U population will be zero, fixation can only occur in this case if the innovation is introduced into the V population. This is illustrated in Fig. 8, which shows the separate fixation probabilities U and V from Fig 7b.
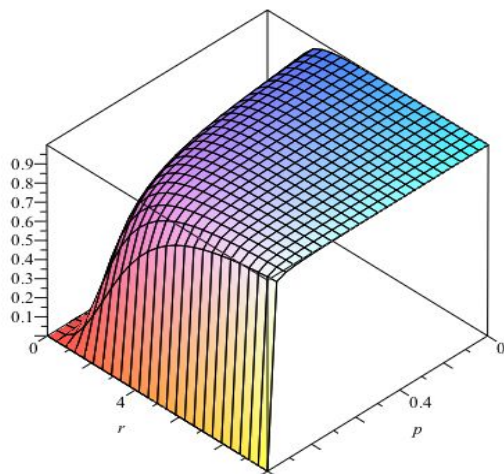
In Fig. 8a the fixation probability drops to zero for p = 1 (i.e., there are no non-zero links from U to V) while in Fig. 8b it rises to one, indicating a certainty of fixation. This is because all of subgroup V shares the innovation but there is no connection from U to V that could cause a change in V, while there are non-zero links from V to U.

VIII. A THERMODYNAMIC ANALOGY

Given a population graph with N vertices and edge weight matrix W, the temperature of vertex j is defined as

$$t_j = \sum_{i=1}^{N} W_{ij}$$ and the probability that a single mutant

introduced at vertex j in an other wise normal population will go extinct in one iteration of a birth-death process is t_j/N. If N is considered as an "effective volume" then t_j/N is analogous to the pressure exerted on vertex j by the population distribution (described by specifying a state $\vec{u}$) and the terms $a_j(\vec{u})/N, b_j(\vec{u})/N$ are analogous to partial pressures exerted on the population member at vertex j by the mutant and normal sub-populations, respectively. This concept shows up in population ecology, for example, with the concept of *propagule pressure* used in studies of the spread of invasive species in an ecosystem [21].

Various entropy measures are useful is studying graph structures [e.g., 22]. Two of use here are the "temperature" entropy, and the fixation entropy. The temperature entropy

$$I_t = -\frac{1}{N} \sum_{j=1}^{N} t_j \log\left(\frac{t_j}{N}\right) \tag{12}$$

provides information about the in degree structure of the graph G. If the fixation probability for a vertex j is ρ_j then the corresponding fixation entropy is

$$I_\rho = -\sum_{i=1}^{N} \frac{\rho_i}{N\rho} \log\left(\frac{\rho_i}{N\rho}\right) \tag{13}$$

where ρ is the average fixation probability (the usual fixation probability of the graph). In [12] analysis of all 853

Fig. 8a Fixation Probability if Initially U is All Ones, V All Zeros.

undirected graphs with seven vertices show finds that the average fixation probability is positively correlated with the variance of the vertex degree, and this carries over to the variance of in degree for directed graphs [18].

IX. DISCUSSION

The value of the Moran process is that it provides a standard for comparison, corresponding to a completely homogeneous population (as represented by a complete graph). The example of Fig. 1 illustrated that fixation probability may be enhanced or suppressed with respect to the Moran probability for only limited values of fitness. To see how surprising this is, suppose that a rumor is introduced into a population with believability r > 1 (i.e., it is more believable than normally held belief). What the example of Fig. 1 (and other similar cases) are saying is that there may be lower and upper bound on believability such that if r is outside this range, the spread of a rumor will be suppressed when compared to its spread in a homogeneous population, even though it is more believable than the belief it is intended to replace.

A point that needs to be discussed is that with the exception of the general cases presented (the fixation probability for the complete biparte graphs, the characteristic polynomials listed in Table I) the graphs studied have very simple structure and can only be considered as toy models for far more complex situations. Nevertheless, toy models can often have value as a means of developing intuition. The graphs of case 3 considered in section VII, for example, would not be expected to apply directly to any real group where different individuals would have different probabilities of interacting, communicating, and influencing others, both in-group and out-group. But it can be considered with the probabilities 1-p and 1-q for influence between the subgroups U and V taken as averages over the respective populations. Likewise, the graphs described by case 4 can represent cases in which the two subgroups U and V have selected single individual representatives to negotiate their group interests.

The value of the state space approach is that it provides immediate results for the fixation probability of any state, not just the average over all single vertex fixation probabilities, as illustrated by the graphs of Fig. 7. The difficulty involved is the large number of equations that are required unless symmetry considerations can be used to reduce this to manageable size, and even in these cases the actual solutions can be unwieldy. These problems can be avoided in part through analysis of the state transition matrix rather than direct solution of (6). This has been discussed in section V where a method to obtain estimates of initial states for observed patterns of innovation is provided.

Nevertheless, it is important to emphasize the need to develop approximation methods. While equation (6) can be solved in principle for any graph, the computational task grows exponentially with the number of vertices and even when exact solutions are obtained they are difficult to grasp unless represented graphically (the solution for R in Fig. 7a, for example, runs to 34 lines with numerical coefficients ranging into the trillions). In this regard, it may be useful to fall back on some of the various information measures that can be defined.

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