Research Article

Fixation Probabilities on Complete Star and Bipartite Digraphs

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This paper exactly formulates the kth-order fixation probabilities on complete star digraphs (CSDs), which extend the results from Broom and Rychtář (2008). By applying these probability formulae, some asymptotic properties on CBDs are analyzed, and certain CSDs are determined to be amplifiers of selection for arbitrary relative fitness larger than 1, while all the CSDs are proved to be amplifiers of selection for fixed relative fitness slightly larger than 1. A numerical method for fixed population structure (by solving a linear system) is developed to calculate the fixation probabilities on complete bipartite digraphs (CBDs), and some conjectures are finally given through simulations.

1. Introduction

As a newly emerging branch of population dynamics, evolutionary graph theory studies the evolution of structured populations and explores the effect of population structure on evolutionary dynamics [1–6]. Primarily, evolutionary dynamics were investigated on homogeneous infinite populations however, populations in the real world are neither infinite nor homogeneously mixed [2]. In recent years, there is a growing interest in the investigation of evolutionary dynamics on spatial structures or populations with certain nonhomogeneous structure [5, 7–10]. The study of evolutionary dynamics on graphs was popularized by Lieberman et al. [4]. In this framework, the structure of a population is modeled by a weighted digraph on vertices $1, 2, \ldots, N$, which are occupied by individuals (residents and mutants). The graph can describe the architecture of cells in a multicellular organism and represent spatial structure among animals or plants in an ecosystem [8]. Moreover, graphs can also represent relationships in a social network of humans, which means that the dynamics describes cultural selection and the spread of new inventions and ideas. It is supposed

that every individual of the population occupies a unique vertex of the graph. In each iteration, a random individual i is chosen for reproduction with a probability proportional to its fitness, and the resulting offspring will occupy an adjacent vertex j with the probability w_{ij}, which represents the weight on edge $\langle i, j \rangle$, if any. The *intrinsic weights* of a digraph are defined this way: for a vertex i with l outgoing edges, let $w_{ij} = 1/l$ if edge $\{i, j\}$ exists. In this paper, we focus our attention on the structures of this kind of digraphs with intrinsic weights.

Consider a homogeneous population on a weighted graph whose individuals all have baseline fitness 1. Each individual is chosen as the reproducing one with probability proportional to its fitness. Suppose k new mutants with relative fitness r (the new mutant called advantageous if $r > 1$, while disadvantageous if $0 < r < 1$) are introduced by placing them on k randomly chosen vertices of the graph. These mutants have a certain chance of fixation, that is, to generate a lineage that takes over the population. It is an issue in population dynamics to find the kth-order fixation probability, that is, the fixation probability of k mutants, in a population [7, 11, 12].

An unstructured population can be modeled by a complete digraph where all edges have the same weight. The evolution of an unstructured population is often modeled by the *Moran process*, whose kth-order fixation probability is

$$\rho_k^{(M)}(N; r) = \frac{(1 - 1/r^k)}{(1 - 1/r^N)}, \tag{1.1}$$

where resident individuals have fitness 1, while mutants have relative fitness r. The Moran process defines a balance between natural selection and random drift. Lieberman et al. [4] gave the approximation of the first-order fixation probability for stars with large size N by

$$P = \frac{(1 - 1/r^2)}{(1 - 1/r^{2N})}. \tag{1.2}$$

Broom and Rychtář [7] obtained the exact average fixation probability for a mutant, given by $\varrho = [n^2 r / (nr + 1) + r/(n + r)] / [(n + 1)[1 + n/(n + r) \sum_{j=1}^{n-1} ((n + r)/(r(nr + 1)))^j]]$, which recovers (1.2) because for large N we derive $\varrho \approx 1/(1 + \sum_{j=1}^{n-1} 1/r^{2j}) = (1 - 1/r^2)/(1 - 1/r^{2n})$, where n represents the total size of a star except the central individual. In this paper, we further extend these results by deriving the explicit kth-order fixation probability on complete star digraphs (there exists a center vertex which connects each other vertex by two directed edges) as follows:

$$\varrho = \frac{n^2 r / (nr + 1) + r/(n + r)}{(n + 1) \left[1 + n/(n + r) \sum_{j=1}^{n-1} ((n + r)/r(nr + 1))^j \right]}. \tag{1.3}$$

The *temperature* of a vertex is defined as the sum of all weights that lead into that vertex, that is, the temperature of vertex j is given by $T_j = \sum_{j=1}^{N} w_{ij}$ [8]. If all the vertices have the same temperature, then a graph is isothermal. It is known that a structured population has the same first-order fixation probability as the corresponding Moran process if and only if the structure is an isothermal digraph [8]. A structure is referred to as an *amplifier of selection* (resp., suppressor of selection) if the first-order fixation probability of one advantageous

mutant on this structure is greater than (resp., less than) that for the corresponding Moran process. An important issue in evolutionary graph theory is to answer whether a given structure is an amplifier of selection or a suppressor of selection [4, 13, 14].

This paper proceeds as follows. In Section 2, we formulate the exact kth-order fixation probability on complete star graphs, then apply it to answer whether a given complete star graph is an amplifier of selection or not. In Section 3, we obtain the first-order fixation probability on complete bipartite digraphs (all vertices are divided into two sets, and each vertex is connected to every vertex in the other set by a directed edge) by solving a linear system through numerical methods, and pose several conjectures based on the simulations results.

In this paper, we further develop the theory of evolutionary processes on graphs first developed by Lieberman et al. [4], by following the approach of proving analytical results for simple systems in a similar way to Broom and Rychtář [7]. Some useful results advance the formal underpinnings of the modeling of evolution on graphs, since nearly no attempt is made to prove general theoretical results in studies of evolution on graphs.

2. On Complete Star Digraphs

In this section, we obtain explicit formulae for the kth-order fixation probabilities on complete star digraphs and explore their properties and applications in nature and society.

2.1. Basic Concepts and Notations

A *complete star digraph* (CSD) is a digraph with a single central vertex such that (I) there exists an edge from the center vertex to each peripheral vertex; (II) there exists an edge from each peripheral vertex to the center vertex; (III) there exist no other edges. Therefore, a CSD of size N, denoted by $\mathcal{S}_N$, is a digraph with vertex set $\mathcal{V} = \{1, 2, \ldots, N\}$ and directed edge set $\mathcal{E} = \{\langle 1, j \rangle, \langle j, 1 \rangle \mid j = 2, \ldots, N\}$. Figure 1 illustrates one CSD with intrinsic weights. Note that the term "CSD" means "CSD with intrinsic weights" in the sequel.

The kth-order *fixation probability* on $\mathcal{S}_N$ is denoted by $\rho_k(N; r)$, which represents the probability of the event that these k mutants generate a lineage that takes over the whole population.

For technical reasons, we need the following notations in the sequel.

The configuration of a population on $\mathcal{S}_N$, at time t, is depicted by a vector $\Theta(t) = (\theta_1(t), \theta_2(t))$, where $\theta_1(t) = 1$ or 0 if a mutant occupies the central vertex or not, respectively, and $\theta_2(t)$ denotes the number of mutants occupying vertices $2, \ldots, N$. The total number of mutants at time t is denoted by $\theta(t)$, that is, $\theta(t) = \theta_1(t) + \theta_2(t)$. The probability of the event that the mutants finally fixate by starting with $\Theta(0) = (k_1, k_2)$, is denoted by $\rho_{k_1,k_2}(N; r)$ abbreviated to ρ_{k_1,k_2} (without ambiguity).

2.2. Explicit Fixation Probability Formulae

Before exactly formulating the kth-order fixation probability, the following two necessary lemmas are presented.
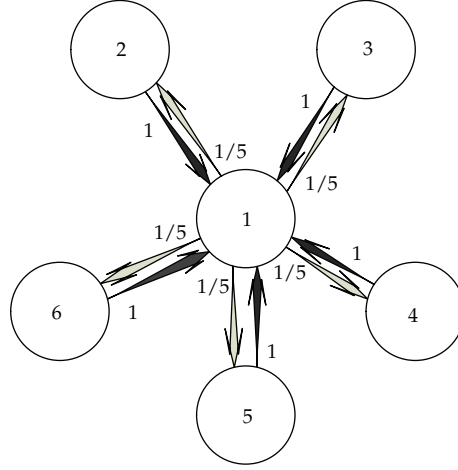
Figure 1: One complete star digraph $\mathcal{S}_6$ with intrinsic weights, the central vertex is indexed 1.

Lemma 2.1. *Consider a CSD of size $N \geq 3$ and denote by r the relative fitness of a mutant. Then for $k = 1, \ldots, N - 1$, the difference equation system holds:*

$$\mathbf{p}_k = \mathbf{A}\mathbf{p}_{k-1} \tag{2.1}$$

where $\mathbf{p}_k = (\rho_{1,k}, \rho_{0,k})^T \in \mathbb{R}^2$, *and*

$$\mathbf{A} = \begin{pmatrix} \alpha & 1 - \alpha \\ \alpha\beta & 1 - \alpha\beta \end{pmatrix}, \tag{2.2}$$

with $\alpha := 1 + (N-1)/r$, $\beta := r(N-1)/[r(N-1)+1]$.

Proof. This proof proceeds by calculating some conditional probabilities and by the total probability formula. Let $\Theta(0)$, at time $t = 0$, represent the initial configuration of a population on $\mathcal{S}_N$, $\Theta(1)$ represent the new configuration after one step-time, and $k = \theta(0) = \theta_1(0) + \theta_2(0)$ represent the initial total number of mutants. Then two cases are discussed with respect to $\Theta(0)$.

Case 1. (The initial configuration $\Theta(0) = (1, k-1)$). In order to reduce the k mutants by one, a resident individual must be selected to reproduce and, meanwhile the center mutant (staying at vertex 1) has to be chosen for death, whose conditional on the resident's selection, happens with probability 1. Therefore, the conditional probability of going from $\Theta(0) = (1, k-1)$ to $\Theta(1) = (0, k-1)$ is given by

$$\mathbf{Pr}\{\Theta(1) = (0, k-1) \mid \Theta(0) = (1, k-1)\} = \frac{(N-k)}{(rk + N - k)}. \tag{2.3}$$

On the other hand, to increase ω by one, the center mutant has to be chosen for reproduction, and one resident individual connected to the center vertex must be selected

to die. Thus the conditional probability of going from $\Theta(0) = (1, k - 1)$ to $\Theta(1) = (1, k)$ is given by

$$\mathbf{Pr}\{\Theta(1) = (1, k) \mid \Theta(0) = (1, k - 1)\} = \frac{r(N - k)}{[(rk + N - k)(N - 1)]}. \qquad (2.4)$$

By employing (2.3) and (2.4), the probability of the event that the configuration stays unchanged is given by

$$\mathbf{Pr}\{\Theta(1) = (1, k - 1) \mid \Theta(0) = (1, k - 1)\}$$

$$= 1 - \frac{(N - k)}{(rk + N - k)} - \frac{r(N - k)}{[(rk + N - k)(N - 1)]}. \qquad (2.5)$$

Case 2. (The initial configuration $\Theta(0) = (0, k)$). On the one hand, in order to increase k by one, the center individual has to be replaced by a new mutant produced by another. Therefore, the probability of going from $\Theta(0) = (0, k)$ to $\Theta(1) = (1, k)$ is given by

$$\mathbf{Pr}\{\Theta(1) = (1, k) \mid \Theta(0) = (0, k)\} = \frac{rk}{(rk + N - k)}. \qquad (2.6)$$

On the other hand, to reduce k by one, the center resident individual has to be chosen for reproduction and its offspring must replace one mutant. Therefore, the probability of going from $\Theta(0) = (0, k)$ to $\Theta(1) = (0, k - 1)$ is given by

$$\mathbf{Pr}\{\Theta(1) = (0, k - 1) \mid \Theta(0) = (0, k)\} = \frac{k}{[(rk + N - k)(N - 1)]}. \qquad (2.7)$$

It follows from (2.6) and (2.7) that the probability of the configuration remaining unchanged is

$$\mathbf{Pr}\{\Theta(1) = (0, k) \mid \Theta(0) = (0, k)\}$$

$$= 1 - \frac{rk}{(rk + N - k)} - \frac{k}{[(rk + N - k)(N - 1)]}. \qquad (2.8)$$

By the total probability formula, we derive that for $k = 1, \ldots, N - 1$,

$$\rho_{1,k-1} = \mathbf{Pr}\{\Theta(1) = (0, k - 1) \mid \Theta(0) = (1, k - 1)\}\rho_{0,k-1}$$

$$+ \mathbf{Pr}\{\Theta(1) = (1, k) \mid \Theta(0) = (1, k - 1)\}\rho_{1,k} \qquad (2.9)$$

$$+ \mathbf{Pr}\{\Theta(1) = (1, k - 1) \mid \Theta(0) = (1, k - 1)\}\rho_{1,k-1},$$

$$\rho_{0,k} = \mathbf{Pr}\{\Theta(1) = (1, k) \mid \Theta(0) = (0, k)\}\rho_{1,k}$$

$$+ \mathbf{Pr}\{\Theta(1) = (0, k - 1) \mid \Theta(0) = (0, k)\}\rho_{0,k-1} \qquad (2.10)$$

$$+ \mathbf{Pr}\{\Theta(1) = (0, k) \mid \Theta(0) = (0, k)\}\rho_{0,k}.$$

Plugging (2.3)–(2.8) into (2.9)-(2.10) and simplifying the results, we deduce

$$\rho_{1,k} = \alpha\rho_{1,k-1} + (1-\alpha)\rho_{0,k-1}, \tag{2.11}$$

$$\rho_{0,k} = \beta\rho_{1,k} + (1-\beta)\rho_{0,k-1}, \tag{2.12}$$

where $\alpha := 1 + (N-1)/r, \beta := r(N-1)/[r(N-1)+1]$.

By substituting (2.11) into (2.12) and rearranging the terms, we get

$$\rho_{0,k} = \alpha\beta\rho_{1,k-1} + (1-\alpha\beta)\rho_{0,k-1}. \tag{2.13}$$

Equation on (2.1) follows by combining (2.11) and (2.13). $\qquad\square$

Lemma 2.2. *Let N and r be given. Then for $1 \le k \le N-1$, the following hold*

$$\rho_{1,k-1} = \frac{\left[\beta - (\alpha-1)\alpha^{k-2}(1-\beta)^{k-1}\right]}{\left[\beta - (\alpha-1)\alpha^{N-2}(1-\beta)^{N-1}\right]},$$

$$\rho_{0,k} = \frac{\left[\beta\left(1 - \alpha^k(1-\beta)^k\right)\right]}{\left[\beta - (\alpha-1)\alpha^{N-2}(1-\beta)^{N-1}\right]}. \tag{2.14}$$

Proof. We solve the linear difference equation system (2.1) in view of the standard technique given in Elaydi [15]. The matrix $\mathbf{A}$ in (2.2) has two real eigenvalues $\lambda_1 = 1,\ \lambda_2 = \alpha(1-\beta)$.

Furthermore, $\eta_1 = (1,1)^T$ and $\eta_2 = (\alpha-1, \alpha\beta)^T$ are eigenvectors of $\mathbf{A}$ corresponding to λ_1, λ_2, respectively. Denote

$$\mathbf{D} = \begin{pmatrix} 1 & \alpha-1 \\ 1 & \alpha\beta \end{pmatrix}, \tag{2.15}$$

and its inverse matrix

$$\mathbf{D}^{-1} = \left[\frac{1}{(1-\alpha+\alpha\beta)}\right]\begin{pmatrix} \alpha\beta & 1-\alpha \\ -1 & 1 \end{pmatrix}. \tag{2.16}$$

Through the method of diagonalizing matrix $\mathbf{A}$, we make the variable change:

$$\begin{pmatrix} \rho_{1,k} \\ \rho_{0,k} \end{pmatrix} = \mathbf{D}\begin{pmatrix} x_k \\ y_k \end{pmatrix}, \tag{2.17}$$

and thus

$$
\begin{pmatrix} x_k \\ y_k \end{pmatrix} = \mathbf{D}^{-1}\mathbf{A}\mathbf{D}\begin{pmatrix} x_{k-1} \\ y_{k-1} \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & \alpha(1-\beta) \end{pmatrix}\begin{pmatrix} x_{k-1} \\ y_{k-1} \end{pmatrix}
$$
$$
= \begin{pmatrix} 1 & 0 \\ 0 & \alpha^k(1-\beta)^k \end{pmatrix}\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}.
$$

(2.18)

Therefore,

$$
\begin{pmatrix} \rho_{1,k} \\ \rho_{0,k} \end{pmatrix} = \mathbf{D}\begin{pmatrix} 1 & 0 \\ 0 & \alpha^k(1-\beta)^k \end{pmatrix}\mathbf{D}^{-1}\begin{pmatrix} \rho_{1,0} \\ \rho_{0,0} \end{pmatrix}
$$
$$
= \frac{\rho_{1,0}}{(1-\alpha+\alpha\beta)}\begin{pmatrix} \alpha\beta - (\alpha-1)\alpha^k(1-\beta)^k \\ \alpha\beta - \alpha^{k+1}\beta(1-\beta)^k \end{pmatrix}.
$$

(2.19)

Particularly, we know

$$
1 = \rho_{1,N-1} = \left[\frac{\rho_{1,0}}{(1-\alpha+\alpha\beta)}\right] \times \left[\alpha\beta - (\alpha-1)\alpha^{N-1}(1-\beta)^{N-1}\right],
$$

(2.20)

which implies

$$
\rho_{1,0} = \frac{(1-\alpha+\alpha\beta)}{\left(\alpha\beta - (\alpha-1)\alpha^{N-1}(1-\beta)^{N-1}\right)}.
$$

(2.21)

Equation on (2.14) follows from substituting (2.21) into (2.19). The proof is complete. □

Next, we present the main theorem of this section.

Theorem 2.3. *Let r and $N > 2$ be given. Then for each $k = 1,\dots,N-1$, the explicit kth-order fixation probability on $\mathcal{S}_N$ is given by*

$$
\rho_k(N;r) = \frac{r^N[r(N-1)+1]^{N-k-2}}{\left[r^N(r(N-1)+1)^{N-2} - (N-1+r)^{N-2}\right]}
$$
$$
\times \left[(r(N-1)+1)^k - \left(\frac{k}{r^k}\right)(N-2)\left(r^2-1\right)(N-1+r)^{k-2}\right.
$$

(2.22)

$$
\left. -\left(\frac{(N-1+r)}{r}\right)^k\right].
$$

Proof. In light of (2.21), we derive

$$\rho_k(N;r) = \frac{k}{N\rho_{1,k-1}} + \left(\frac{1-k}{N}\right)\rho_{0,k}$$

$$= \frac{k/N\alpha^{k-2}(1-\beta)^{k-1}\left[\alpha^2\beta(1-\beta) - (\alpha-1)\right] + \beta\left[1 - \alpha^k(1-\beta)^k\right]}{\beta - (\alpha-1)\alpha^{N-2}(1-\beta)^{N-1}}. \tag{2.23}$$

By substituting α and β (see Lemma 2.1) into this equation, we have

$$\rho_k(N;r) = \Big\{k/N\ [1+(N-1)/r]^{k-2}\ [1/(r(N-1)+1)]^{k-1}\Big[(1+(N-1)/r)^2\ (r(N-1))$$

$$/\left((r(N-1)+1)^2\right) - (N-1)/r\Big] + r(N-1)/(r(N-1)+1)$$

$$\Big[1 - (1+(N-1)/r)^k/(r(N-1)+1)^k\Big]\Big\}/\Big[(r(N-1))/(r(N-1)+1)$$

$$-(N-1)/r[1+(N-1)/r]^{N-2}/(r(N-1)+1)^{N-1}\Big]$$

$$= \Big[r^{N-1}(r(N-1)+1)^{N-1}\Big]\Big\{k(N-1)\left(r^2-1\right)(2-N)(N+r-1)^{k-2}$$

$$/\Big[r^{k-1}(r(N-1)+1)^{k+1}\Big] + r(N-1)/\left((r(N-1)+1)^{k+1}\right)\Big[(r(N-1)+1)^k$$

$$-((r+N-1)/r)^k\Big]\Big\}/\Big\{(N-1)\Big[r^N(r(N-1)+1)^{N-2} - (r+N-1)^{N-2}\Big]\Big\}$$

$$= r^N[r(N-1)+1]^{N-k-2}/\Big[r^N(r(N-1)+1)^{N-2} - (N-1+r)^{N-2}\Big]$$

$$\times\Big[(r(N-1)+1)^k - \left(k/r^k\right)(N-2)\left(r^2-1\right)(N-1+r)^{k-2}$$

$$-((N-1+r)/r)^k\Big]. \tag{2.24}$$

The proof is complete.   □

Particularly, for the case $k = 1$, (2.22) becomes

$$\rho_1(N;r) = \frac{r^{N-1}(r^2-1)(r(N-1)+1)^{N-3}}{\Big[r^N(r(N-1)+1)^{N-2} - (N-1+r)^{N-2}\Big]}$$

$$\times\left[\frac{(N^2+(r-3)(N-1))}{(N-1+r)}\right]. \tag{2.25}$$

Here we point out that (2.25) is just the same as the formula $\varrho = [n^2 r/(nr+1) + r/(n+r)]/[(n+1)[1 + n/(n+r)\sum_{j=1}^{n-1}((n+r)/(r(nr+1)))^j]]$, which is given in Broom and Rychtář [7], because

$$\varrho = \frac{n^2 r/(nr+1) + r/(n+r)}{(n+1)\left[1 + n/(n+r)\sum_{j=1}^{n-1}((n+r)/(nr^2+r))^j\right]}$$

$$= \frac{n^2 r/(nr+1) + r/(n+r)}{(n+1)\left[1 + \left[r^{n-1}(nr+1)^{n-1} - (n+r)^{n-1}\right]/\left[(r^2-1)(r(nr+1))^{n-1}\right]\right]}$$

$$= \frac{\left[n(n+1)r^2 + (n+1)(n^2-n+1)r\right](r^2-1)\left[r(nr+1)\right]^{n-1}}{(nr+1)(n+r)(n+1)\left[r^{n+1}(nr+1)^{n-1} - (n+r)^{n-1}\right]} \tag{2.26}$$

$$= \frac{r^{N-1}(r^2-1)\left[r(N-1)+1\right]^{N-3}}{r^N\left[r(N-1)+1\right]^{N-2} - \left[N-1+r\right]^{N-2}}$$

$$\times \left(N^2 + (r-3)(N-1)\right)(N-1+r) = \rho_1(N;r),$$

where n represents the number of all individuals except the central one, that is, $n = N - 1$.

2.3. Applications and Properties of the Fixation Probability

Theorem 2.3 allows us to calculate the fixation probability for a given CSD, so here we use it to answer whether a given CSD is an amplifier of selection or not. We have the following result.

Theorem 2.4. $\mathcal{S}_3$, $\mathcal{S}_4$, $\mathcal{S}_5$, $\mathcal{S}_6$, $\mathcal{S}_7$, $\mathcal{S}_8$, $\mathcal{S}_9$, and $\mathcal{S}_{10}$ are all amplifiers of selection.

Proof. Combining (1.1) and (2.25) and simplifying, we find that it suffices to confirm that for $r > 1$ and $N = 3, 4, \ldots, 10$, the inequality $\rho_1(N;r) > \rho_1^{(M)}(N;r)$ holds, which is equivalent to $J(N,r) > 0$, where

$$J(N,r) := (r+1)\left(r^N - 1\right)\left[N^2 + (r-3)(N-1), r(N-1)+1\right]^{N-3}$$
$$- (N-1+r)\left[r^N(r(N-1)+1)^{N-2} - (N-1+r)^{N-2}\right]. \tag{2.27}$$

By certain algebraic calculations, it is easy to derive

$$J(3,r) = r^3 - r^2 - r + 1 = (r-1)^2(r+1) > 0,$$

$$J(4,r) = 12r^5 + 4r^4 - 8r^3 - 24r^2 - 4r + 20 = (r-1)^2\left(12r^3 + 28r^2 + 36r + 20\right) > 0,$$

$$J(5,r) = 144r^7 + 72r^6 + 9r^5 - 63r^4 - 288r^3 - 252r^2 + 135r + 243 \tag{2.28}$$

$$= (r-1)^2\left(144r^5 + 360r^4 + 585r^3 + 747r^2 + 621r + 243\right) > 0.$$

Table 1

N	$J(N,r)/(r-1)^2$
6	$2000r^7 + 5200r^6 + 8640r^5 + 12096r^4 + 14928r^3 + 14160r^2 + 8992r + 3104$
7	$32400r^9 + 86400r^8 + 145800r^7 + 205800r^6 + 265825r^5 + 318075r^4 + 317225r^3$
	$+243475r^2 + 139125r + 46625$
8	$605052r^{11} + 1642284r^{10} + 2802996r^9 + 3981348r^8 + 5160960r^7 + 6340608r^6$
	$+7402608r^5 + 7540272r^4 + 6332004r^3 + 4444596r^2 + 2468988r + 823500$
9	$12845056r^{13} + 35323904r^{12} + 60813312r^{11} + 86804480r^{10} + 112842688r^9$
	$+138883248r^8 + 164923857r^7 + 188867315r^6 + 194198613r^5 + 171318455r^4$
	$+133184793r^3 + 91162491r^2 + 50328733r + 16777159$
10	$306110016r^{15} + 850305600r^{14} + 1473863040r^{13} + 2112117120r^{12}$
	$+2752004160r^{11} + 3392000064r^{10} + 4032000000r^9 + 4672000000r^8$
	$+5268953280r^7 + 5440222400r^6 + 4946130304r^5 + 4076784000r^4$
	$+3098682560r^3 + 2109150400r^2 + 1162256640r + 387420416$
$\vdots$	$\vdots$

By using Maple 10, we derive the polynomials $J(N,r)/(r-1)^2$ for $N = 6,7,\ldots,10$, as shown in Table 1.

   It follows directly from Table 1 that $J(N,r) > 0$ holds for $N = 6,7,8,9,10$, which along with (2.28) leads to this result.
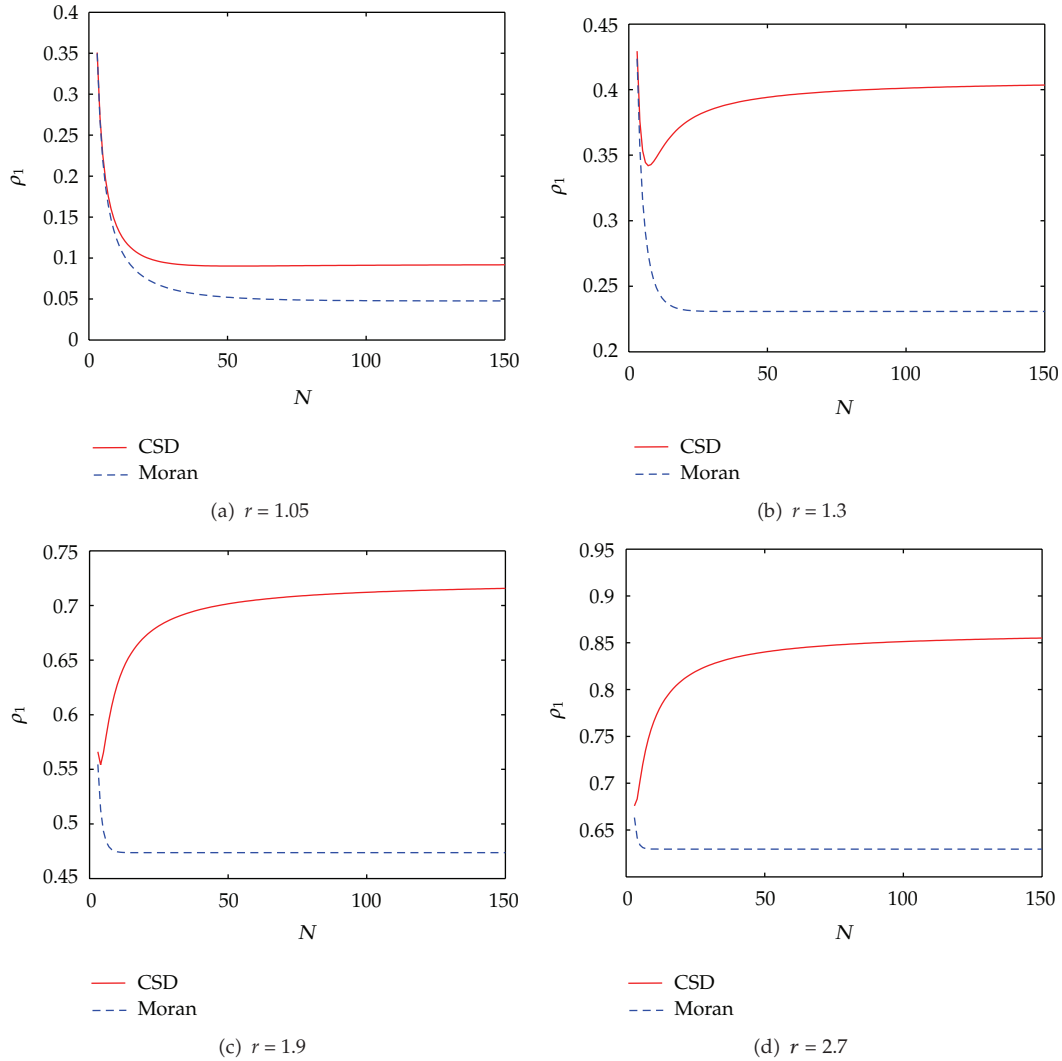
   By (2.28) and Table 1, we guess that for $N \geq 3$ and (2.27) have the following form:

$$J(N,r) = (r-1)^2 \sum_{j=0}^{2N-5} a_j r^j, \quad N \geq 3, \tag{2.29}$$

where each a_j $(j = 0,1,\ldots,2N-5)$ is a nonnegative integer. However, it seems very difficult to prove this inequality in its general form even by the mathematical softwares, since we confront complicated polynomials as N increases, as shown in Table 1. $\square$

   Another utility of **Theorem 2.3** is to study the asymptotic properties of the fixation probabilities on complete star digraphs. For that purpose, we rewrite (2.22) in the following form:

$$\rho_k(N;r) = \left[1 + \frac{1}{(r(N-1))}\right]^{-k}$$

$$\times \left\{ \left[1 + \frac{1}{(r(N-1))}\right]^k - \frac{1}{r^{2k}}\left(1 + \frac{r}{(N-1)}\right)^k - \frac{k(N-2)(r^2-1)}{\left((N-1)^2 r^{2k}\right)\left(1 + \frac{r}{N-1}\right)^{k-2}} \right\}$$

$$\Big/ \left[1 - \frac{1}{r^{2N-2}}\left(1 + \left(\frac{r-1}{r}\right)\right)\Big/\left(\left(N-1+\frac{1}{r}\right)\right)^{N-2}\right]. \tag{2.30}$$

(a) $r = 1.05$

(b) $r = 1.3$

(c) $r = 1.9$

(d) $r = 2.7$

Figure 2: First-order fixation probabilities of CSDs and Moran process with N by fixing relative fitness r.

By letting $r > 1$ and taking limits on both sides of (2.30) in N, then $\rho_k(N;r) \rightarrow 1 - 1/r^{2k}$ as $N \rightarrow \infty$. Lieberman et al. [4] declared this result without rigorous argument. This statement tells us that for sufficiently large N, $\mathcal{S}_N$ is an amplifier of selection because $\lim_{N \to \infty} \rho_1(N;r) = 1 - 1/r^2 > 1 - 1/r = \lim_{N \to \infty} \rho_1^{(M)}(N;r)$.

Figure 2 shows how the first-order fixation probability goes to the limit. For comparative purposes, the first-order fixation probability for the Moran process is also given in this figure. By Theorem 2.4 and a close look at Figure 2, we pose the conjecture: let $r > 1$. Then, $\mathcal{S}_N(N \geq 3)$ is an amplifier of selection.

In the proof of Theorem 2.3, we argue that the conjecture holds for $3 \leq N \leq 10$ by computing some polynomials; however, we confront complex polynomials when N becomes large. Thus, it seems very difficult to generally prove the conjecture. Fortunately, here we derive the following weak but useful result through rigorous reasoning.

Theorem 2.5. *Let $\tau(N) > 0$, depending on N, be sufficiently small. Then for any $r \in (1, 1 + \tau(N))$, $\mathcal{S}_N$ $(N \geq 3)$ is an amplifier of selection.*

Proof. It suffices to prove that for $r \in (1, 1 + \tau(N))$ the following inequality holds:

$$\rho_1(N; r) > \rho_1^{(M)}(N; r), \tag{2.31}$$

which is equivalent to $\rho_1(N; r) > \rho_1^{(M)}(N; r)$ by applying (1.1) and (2.25). We prove this as follows.

Let $f(r) = (r + 1)[N^2 + (N - 1)(r - 3)][r(N - 1) + 1]^{N-3}$, then

$$
\begin{aligned}
f'(r) = {} & f(r) + (N - 1)(r + 1)[r(N - 1) + 1]^{N-3} \\
& + (N - 3)(N - 1)(r + 1)\left[N^2 + (N - 1)(r - 3)\right][r(N - 1) + 1]^{N-4}.
\end{aligned}
\tag{2.32}
$$

It follows from (2.27) that

$$
J(N, r) = \left(r^N - 1\right)f(r) - (N - 1 + r)\left[r^N(r(N - 1) + 1)^{N-2} - (N - 1 + r)^{N-2}\right] \tag{2.33}
$$

whose first- and second-order derivatives in r are, respectively, given by

$$
\begin{aligned}
\frac{\partial J(N, r)}{\partial r} = {} & N r^{N-1} f(r) + \left(r^N - 1\right)f'(r) - r^N[r(N - 1) + 1]^{N-2} \\
& - N(N - 1 + r)r^{N-1}[r(N - 1) + 1]^{N-2} + (N - 1)(N - 1 + r)^{N-2} \\
& - (N - 2)(N - 1)(N - 1 + r)r^N[r(N - 1) + 1]^{N-3}, \\[2mm]
\frac{\partial^2 J(N, r)}{\partial r^2} = {} & N(N - 1)r^{N-2}f(r) + 2N r^{N-1}f'(r) + \left(r^N - 1\right)f''(r) \\
& - 2N r^{N-1}[r(N - 1) + 1]^{N-2} - N(N - 1)(N - 1 + r)\left[r^2(N - 1) + r\right]^{N-2} \\
& - (N - 2)(N - 1)r^2\left[r^2(N - 1) + r\right]^{N-3}[2N(N - 1) + (2N + 1)r] \\
& + (N - 2)(N - 1)\left[(N - 1 + r)^{N-3} - r^N(r(N - 1) + 1)^{N-3}\right] \\
& - (N - 3)(N - 2)(N - 1)^2(N - 1 + r)r^N[r(N - 1) + 1]^{N-4}.
\end{aligned}
\tag{2.34}
$$

Through certain calculations, we derive

$$
\begin{aligned}
f(1) = {} & 2\left[N^2 - 2N + 2\right]N^{N-3}, f'(1) \\
= {} & N^{N-1} + 2(N - 3)(N - 1)\left(N^2 - 2N + 2\right)N^{N-4},
\end{aligned}
\tag{2.35}
$$

which imply

$$\frac{\partial J(N,r)}{\partial r}\Big|_{r=1} = 0, \qquad \frac{\partial^2 J(N,r)}{\partial r^2}\Big|_{r=1} = 2(N-1)(N-2)^3 N^{N-3} > 0. \qquad (2.36)$$

It follows from the Taylor's theorem and the fact $J(N,1) = 0$ that

$$
\begin{aligned}
J(N,r) &= J(N,1) + \frac{\partial J(N,r)}{\partial r}\Big|_{r=1}(r-1) + \frac{1}{2!}\frac{\partial^2 J(N,r)}{\partial r^2}\Big|_{r=1}(r-1)^2 + O\big((r-1)^2\big) \\
&= (N-1)(N-2)^3 N^{N-3}(r-1)^2 + O\big((r-1)^2\big) \\
&= (r-1)^2\big[(N-1)(N-2)^3 N^{N-3} + O(r-1)\big].
\end{aligned}
\qquad (2.37)
$$

Therefore, there exists a small enough $\tau(N) > 0$ such that the inequality $(N-1)(N-2)^3 N^{N-3} + O(r-1) > 0$ holds for arbitrary $r \in (1, 1 + \tau(N))$. The proof is complete. $\qquad\square$

Theorem 2.5 shows that no matter the size of a complete star digraph, it is always an amplifier of selection if the mutant's relative fitness is slightly larger than 1.

In the following, let us examine the asymptotic behavior of $\rho_k(N;r)$ provided that $k = k_N$ depends on N. If $r > 1$ and S_N ($N \geq 3$) is an amplifier of selection, then by taking limits on (2.30), we have (I) if $k_N \to +\infty$, then $\rho_{k_N}(N;r) \to 1$; (II) if $k_N \to k^* < +\infty$, then $\rho_{k_N}(N;r) \to 1 - 1/r^{2k^*}$. The first assertion is interesting because it demonstrates that no matter how slowly the initial number of mutants increases (e.g., proportional to $[\ln \ln N]$) the corresponding fixation probability will always approach one.

When $r = r_N$ depends on N, one may imagine that the asymptotic behavior of $\rho_k(N;r)$ would become much more complex. For example, given k and suppose $r = r_N$. Then we have the assertions: (I) if $r_N \to r^* > 1$, then $\rho_k(N;r_N) \to 1 - 1/(r^*)^{2k}$; (II) if $r_N \to 1$, then $\rho_k(N;r_N) \to 0$. Note that the first assertion follows directly from (2.30). Considering the second assertion, assume that $r_N^N \to \delta > 1$, then it follows from (2.30) that $\lim_{N\to\infty}\rho_k(N;r_N) = \lim_{N\to\infty}(1 - 1/r_N^{2k})/(1 - 1/r_N^{2N-2}) = 0/(1 - 1/\delta^2) = 0$. Finally, in the case $r_N^N \to 1$, the second assertion follows naturally.
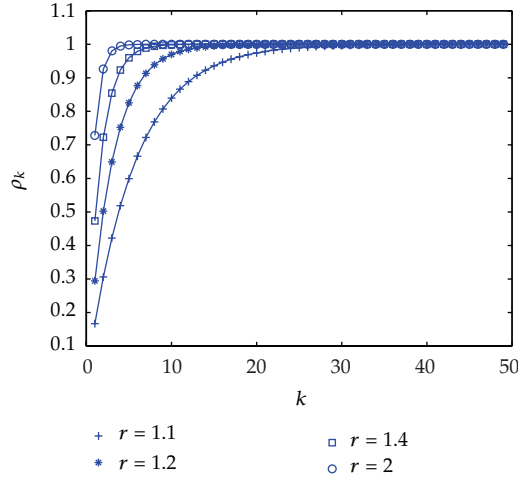
Figure 3 shows that how the kth-order fixation probability changes as the increasing number mutants k.

## 3. Fixation Probabilities on Complete Bipartite Digraphs

This section gives a recursive equation regarding the fixation probabilities on complete bipartite digraphs and obtains some results through a numerical method by simulation.

3.1. Basic Concepts and Notations

A *complete bipartite digraph* (CBD) is a digraph whose vertices are partitioned into two partite sets so that there is no edge connecting any two vertices in the same partite set, and there is an directed edge connecting each vertex in one partite set to each vertex in the other partite set [16]. A CBD denoted by $\mathcal{B}_{N_1,N_2}$ (here N_1 and N_2 represent the sizes of two partite sets,

Figure 3: The curves of kth-order fixation probability on $\mathcal{S}_{50}$ with respect to k by fixing r. These curves show the values of ρ_k dramatically converge to 1, and they increase as k increases, which is consistent with the fact that the more initial mutants there are, the larger the fixation probability is.
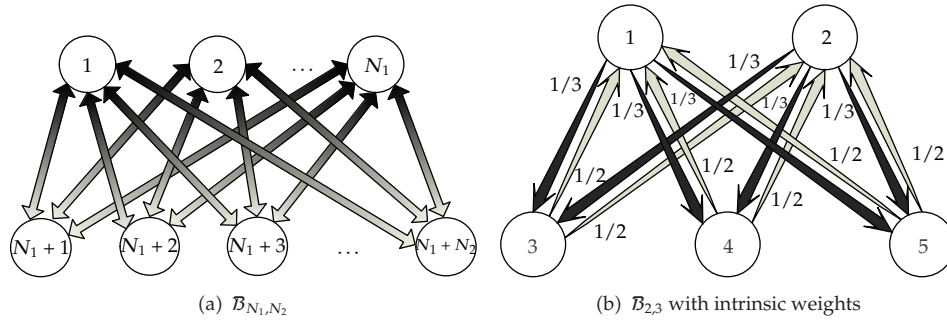
Figure 4: Two complete bipartite digraphs. (a) Shows a general CBD, while (b) shows an unbalanced one with intrinsic weights.

respectively, and due to symmetry, let $N_1 \leq N_2$) is a digraph with vertex set $\mathcal{V} = \{1, 2, \ldots, N\}$ ($N = N_1 + N_2$ is the total size) and edge set $\mathcal{E} = \{\langle i, j \rangle, \langle j, i \rangle \mid i = 1, 2, \ldots, N_1, \; j = N_1 + 1, \ldots, N_1 + N_2\}$. A CBD is *balanced* if its two partite sets have the same size, that is, $N_1 = N_2$, otherwise it is *unbalanced*. The unbalance degree of $\mathcal{B}_{N_1, N_2}$ can be measured by $|N_2 - N_1|$. Figure 4 depicts two CBDs (the second one's unbalance degree is 1). The term "CBD" implies "CBD with intrinsic weights" in the sequel.

Without loss of generality, we suppose here that $N_1 \leq N_2$. Obviously, when $N_1 = 1$, the complete bipartite digraph is just the complete star digraph $\mathcal{S}_{N_2}$. A CBD is an isothermal digraph if and only if it is balanced, thus the first-order fixation probability on a balanced CBD is already known by the isothermal theorem.

For technical reasons, the following notations are needed in the sequel.

Consider a homogeneous population on a CBD where all individuals have fitness 1. Suppose that k new mutants with relative fitness r are introduced by placing them on k randomly chosen vertices. Let $\rho_k(N_1, N_2; r)$ represent the kth-order *fixation probability*, that

is, the probability of the event that these k mutants generate a lineage that takes over the population.

At time t, the configuration of a population on $\mathcal{B}_{N_1,N_2}$ is described by a vector $\Omega(t) = (m_1(t), m_2(t))$, where $m_1(t)$ and $m_2(t)$ represent the number of mutants staying at vertices $1, 2, \ldots, N_1$ and vertices $N_1 + 1, N_1 + 2, \ldots, N_1 + N_2$, respectively.

Let $m(t)$ represent the total number of mutants at time t, that is, $m(t) = m_1(t) + m_2(t)$, and $\rho_{k_1,k_2}(N_1, N_2; r)$ (without ambiguity, ρ_{k_1,k_2}) represent the probability of the event that, starting from $\Omega(0) = (k_1, k_2)$, the mutants finally fixate.

3.2. A Numerical Method

Here we will give an approach for calculating the fixation probability on a CBD and thus three theorems are established as follows.

Theorem 3.1. *Consider a CBD $\mathcal{B}_{N_1,N_2}$ with $N_2 \geq N_1 \geq 2$. Then, we have $\rho_{k_1,k_2}(N_1, N_2; r)$ ($0 \leq k_1 \leq N_1$, $0 \leq k_2 \leq N_2$) satisfying the recursive equation:*

$$\chi_1 \rho_{k_1-1,k_2} + \chi_2 \rho_{k_1,k_2-1} + \chi_3 \rho_{k_1+1,k_2} + \chi_4 \rho_{k_1,k_2+1} = (\chi_1 + \chi_2 + \chi_3 + \chi_4)\rho_{k_1,k_2}, \tag{3.1}$$

where $\chi_1 := k_1(N_2 - k_2)/N_1, \chi_2 := k_2(N_1 - k_1)/N_2, \chi_3 := rk_2(N_1 - k_1)/N_1, \chi_4 := rk_1(N_2 - k_2)/N_2$, and $\rho_{0,0} = 0, \rho_{N_1,N_2} = 1, \rho_{-1,i} = \rho_{j,-1} = \rho_{N_1+1,i} = \rho_{j,N_2+1} = 0, i = 0, 1, \ldots, N_2, j = 0, 1, \ldots, N_1$, are boundary conditions.

Proof. Let $\Omega(0)$, at time $t = 0$, represent the initial configuration of a population on $\mathcal{B}_{N_1,N_2}$ and $\Omega(1)$ represent the new configuration after one step-time. Thus we have $m_1(0) = k_1, m_2(0) = k_2, m(0) = k_1 + k_2$. It is simple to calculate the following conditional probabilities:

$$\mathbf{Pr}\{\Omega(1) = (k_1 + 1, k_2) \mid \Omega(0) = (k_1, k_2)\} = \frac{rk_2(N_1 - k_1)}{(N_1(rk + N - k))},$$

$$\mathbf{Pr}\{\Omega(1) = (k_1, k_2 + 1) \mid \Omega(0) = (k_1, k_2)\} = \frac{rk_1(N_2 - k_2)}{(N_2(rk + N - k))},$$

$$\mathbf{Pr}\{\Omega(1) = (k_1 - 1, k_2) \mid \Omega(0) = (k_1, k_2)\} = \frac{k_1(N_2 - k_2)}{(N_1(rk + N - k))},$$

$$\mathbf{Pr}\{\Omega(1) = (k_1, k_2 - 1) \mid \Omega(0) = (k_1, k_2)\} = \frac{k_2(N_1 - k_1)}{(N_2(rk + N - k))}, \tag{3.2}$$

where $k = k_1 + k_2$, $N = N_1 + N_2$.

Therefore, the probability that the configuration does not change is given by

$$
\begin{aligned}
\mathbf{Pr}\{\Omega(1) = (k_1, k_2) \mid \Omega(0) = (k_1, k_2)\} \\
= 1 - \mathbf{Pr}\{\Omega(1) = (k_1 + 1, k_2) \mid \Omega(0) = (k_1, k_2)\} \\
- \mathbf{Pr}\{\Omega(1) = (k_1, k_2 + 1) \mid \Omega(0) = (k_1, k_2)\} \\
- \mathbf{Pr}\{\Omega(1) = (k_1 - 1, k_2) \mid \Omega(0) = (k_1, k_2)\} \\
- \mathbf{Pr}\{\Omega(1) = (k_1, k_2 - 1) \mid \Omega(0) = (k_1, k_2)\}.
\end{aligned}
\tag{3.3}
$$

By the total probability formula, we derive

$$
\begin{aligned}
\rho_{k_1,k_2} = \mathbf{Pr}\{\Omega(1) = (k_1 + 1, k_2) \mid \Omega(0) = (k_1, k_2)\}\rho_{k_1+1,k_2} \\
+ \mathbf{Pr}\{\Omega(1) = (k_1, k_2 + 1) \mid \Omega(0) = (k_1, k_2)\}\rho_{k_1,k_2+1} \\
+ \mathbf{Pr}\{\Omega(1) = (k_1 - 1, k_2) \mid \Omega(0) = (k_1, k_2)\}\rho_{k_1-1,k_2} \\
+ \mathbf{Pr}\{\Omega(1) = (k_1, k_2 - 1) \mid \Omega(0) = (k_1, k_2)\}\rho_{k_1,k_2-1} \\
+ \mathbf{Pr}\{\Omega(1) = (k_1, k_2) \mid \Omega(0) = (k_1, k_2)\}\rho_{k_1,k_2}.
\end{aligned}
\tag{3.4}
$$

Note that $\rho_{0,0} = 0$, $\rho_{N_1,N_2} = 1$ and $\rho_{-1,i}, \rho_{j,-1}, \rho_{N_1+1,i}, \rho_{j,N_2+1}$, $i = 0, 1, \ldots, N_2$, $j = 0, 1, \ldots, N - 1$ are meaningless, thus we assume $\rho_{-1,i} = \rho_{j,-1} = \rho_{N_1+1,i} = \rho_{j,N_2+1} = 0$, $i = 0, 1, \ldots, N_2$, $j = 0, 1, \ldots, N - 1$. Then (3.1) follows immediately by plugging (3.2) and (3.3) into (3.4) and simplifying. The proof is complete. □

Theorem 3.2. *For $1 \leq k \leq N - 1$, the following holds*

$$
\rho_k(N_1, N_2; r) = \frac{\sum_{k_1 = \max\{k,N_2\} - N_2}^{\min\{k,N_1\}} \binom{N_1}{k_1}\binom{N_2}{k-k_1}}{\binom{N_1+N_2}{k}\rho_{k_1,k-k_1}(N_1, N_2; r)}.
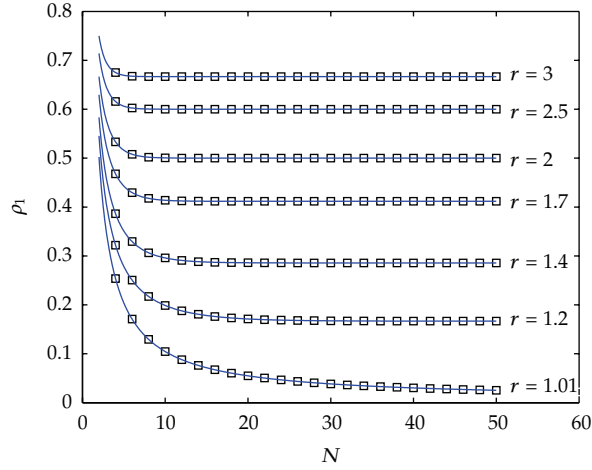\tag{3.5}
$$

Particularly,

$$
\rho_1(N_1, N_2; r) = \frac{N_2}{(N_1 + N_2)_{\rho_{0,1(N_1,N_2;r)}}} + \frac{N_1}{(N_1 + N_2)_{\rho_{0,1(N_1,N_2;r)}}}.
\tag{3.6}
$$

Sketch. The randomness of the initial configuration of mutants gives

$$
\mathbf{Pr}\{\Omega(0) = (k_1, k - k_1)\} = \frac{\binom{N_1}{k_1}\binom{N_2}{k-k_1}}{\binom{N_1+N_2}{k}},
\tag{3.7}
$$

where k_1 represents the number of mutants staying at vertices $1, 2, \ldots, N_1$.

Figure 5: Comparisons between the first-order fixation probability (FOFP) of CBDs and that of the Moran process with different fixed r. The lines and little rectangles represent the FOFPs of the Moran process and CBDs over N, respectively. This figure shows that FOFPs of CBDs are always equal to those of the corresponding Moran process with the same size N.

Equation on (3.5) follows from this equation and the following total probability formula:

$$\rho_k(N_1, N_2; r) = \sum_{k_1=\max\{k,N_2\}-N_2}^{\min\{k,N_1\}} \mathbf{Pr}\{\Omega(0) = (k_1, k - k_1)\}\rho_{k_1,k-k_1}(N_1, N_2; r). \tag{3.8}$$

From the above theorems, calculating $\rho_1(N_1, N_2; r)$ reduces to solving the difference equation system (3.1) with $(N_1 + 1)(N_2 + 1) - 2 = N_1 N_2 + N_1 + N_2 - 1$ variables, because $\rho_{0,0}, \rho_{N_1,N_2}$ are known. It is known [17] that solving a linear system in n variables with the *Gaussian elimination method* would take $O(n^2)$ time. So, we have the result.

**Theorem 3.3.** $\rho_1(N_1, N_2; r)$ *is numerically obtainable in* $O(N_1^2 N_2^2)$ *time.*

In the best case $\rho_1(1, N_2; r)$ *is computed in* $O(N_2^2)$ *time, whereas in the worst case* $\rho_1(N_1, N_1; r)$ *consumes up to* $O(N_1^4)$ *calculation time.*

3.3. Numerical Experiments

Based on the theory established above, this section aims to experimentally reveal how a CBD, affects the first-order fixation probability (3.6) of an advantageous mutant. The experiments are done using *Matlab*.

At first sight, $\rho_1(N_1, N_2; r)$ depends on three parameters. However, we will focus our attention on how ρ_1 is affected by N_1 and N_2 because these two parameters characterize the CBD. Therefore, we will fix the fitness r in the subsequent experiments.

Experiment 1. To verify the theory's correctness and guarantee the effectiveness of the following experiments, this experiment illustrates (see **Figure 5**) that the fixation probability

(a) $r = 1.1$

(b) $r = 1.3$

(c) $r = 2$

(d) $r = 2.5$
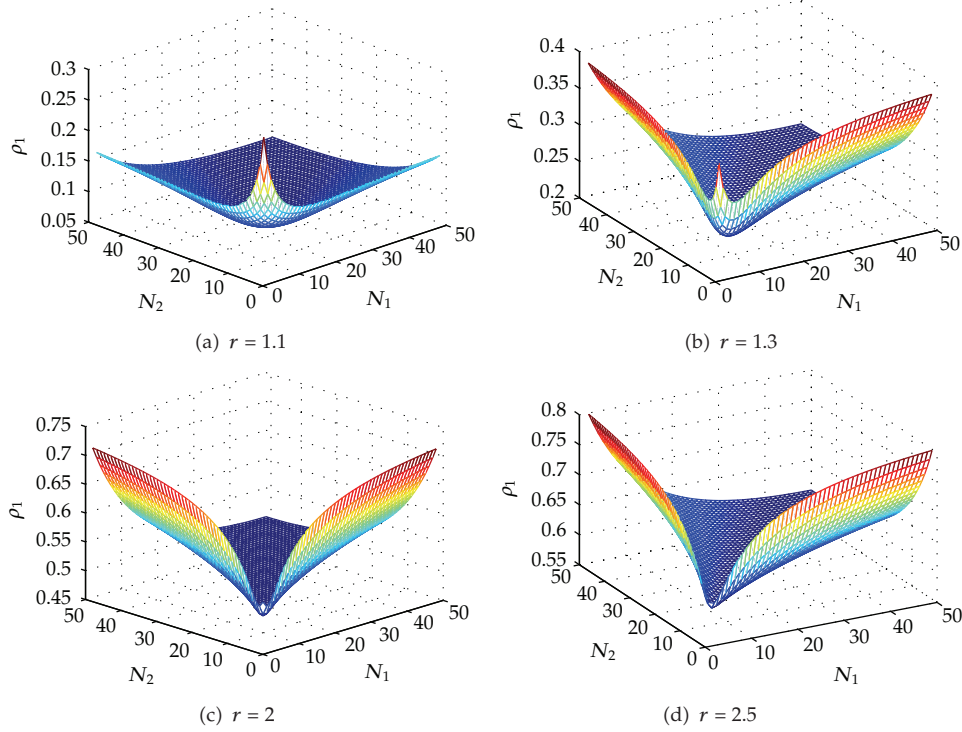
Figure 6: The lattice graphs of ρ_1 with respect to N_1, N_2 by fixing r. Note that the figures are symmetric due to the symmetry of CBDs.

of balanced CBDs is equal to that of the corresponding Moran process. Here, the isothermal theorem of Lieberman et al. [4] is referenced.

Experiment 2. Given $r > 1$ and $\mathcal{N}_k = \{2, 3, \ldots, k\}$, we wish to know how ρ_1 depends on N_1 and N_2. For the purpose, we evaluate ρ_1 for each pair (N_1, N_2) with $N_1, N_2 \in \mathcal{N}_{50}$. The resulting $\rho_1 - (N_1, N_2)$ lattice graphs are plotted in **Figure 6**.

Experiment 3. Given N and $r > 1$, it is interesting to know how ρ_1 depends on N_1 (without loss of generality, again let $N_1 \leq N_2$). Thus for each pair (r, N) with $r \in \{1.1, 1.2, 1.4, 1.7, 2\}$ and $N \in \{52, 102\}$, we evaluate ρ_1 for all $N_1 = 2, \ldots, [N/2]$. The resulting $\rho_1 - N_1$ curves are plotted in **Figure 7**, which suggests that ρ_1 declines as N_1 increases, that is,

$$\rho_1(1, N-1; r) > \rho_1(2, N-2; r) > \cdots > \rho_1\left(\left[\frac{N}{2}\right], N - \left[\frac{N}{2}\right]; r\right). \tag{3.9}$$

In particular, ρ_1 attains its maximum and minimum when $N_1 = 1$ and $N_1 = [N/2]$, respectively. This implies that all unbalanced CBDs under consideration are amplifiers of selection. Moreover, the more unbalanced a CBD, the more significantly it will amplify selection. On this basis, we pose the following conjecture.

Conjecture 3.4. *For any $r > 1$ and $N \geq 4$, the inequality chain* (3.9) *holds.*

(a) $N = 52$

(b) $N = 102$
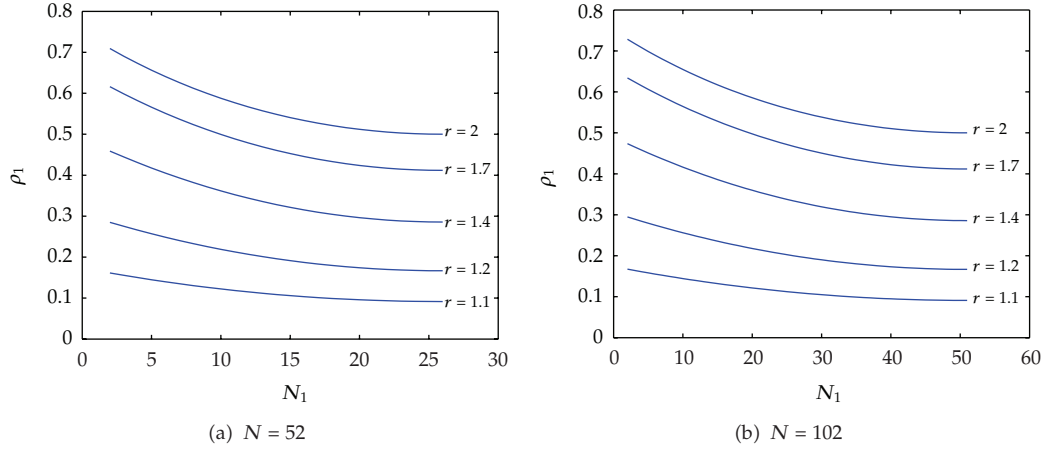
Figure 7: First-order fixation probability over the size of smaller partite set by fixing the total size N.

(a) $r = 1.2$

(b) $r = 1.6$
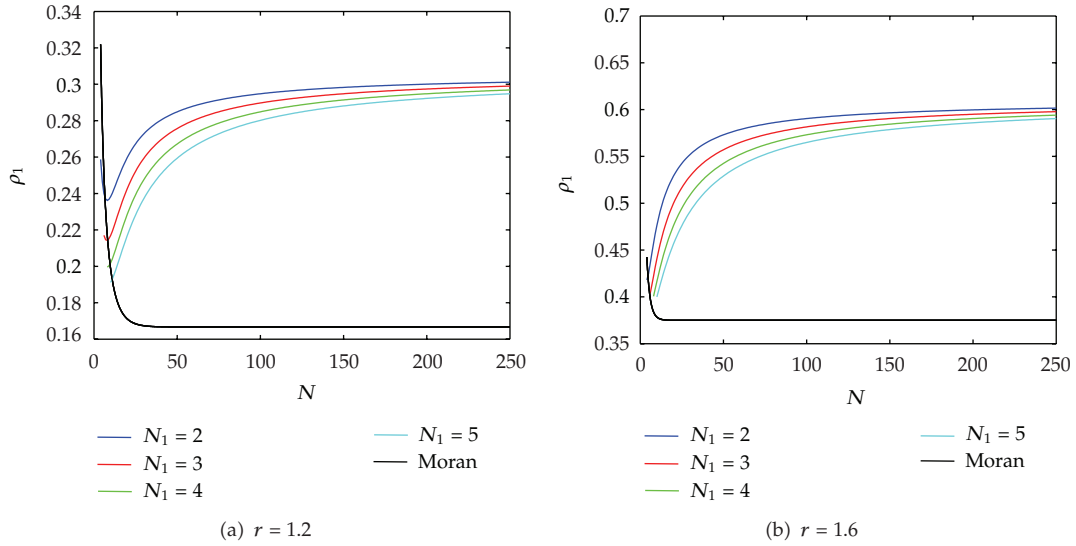
Figure 8: First-order fixation probability over the total population size. This figure shows the phenomenon that for each pair (r, N_1) under consideration, $\rho_1(N_1, N - N_1; r)$ converges. Furthermore, the limit of ρ_1 declines as N_1 increases with fixed r.

Experiment 4. Let $r > 1$ and N_1 be given, we expect to know how ρ_1 depends on N. For that purpose, for each pair (r, N_1) with $r \in \{1.2, 1.6\}$ and $N_1 \in \{2, 3, 4, 5\}$ we compute ρ_1 for $2N_1 \leq N \leq 250$. The resulting $\rho_1 - N$ curves are given in Figure 8. For comparison, then $\rho_1 - N$ curves for the corresponding Moran processes are also depicted in this figure. The following conjecture is posed here.

Conjecture 3.5. *For any $r > 1$ and any positive integer $N_1 \geq 2$, $\rho_1(N_1, N - N_1; r)$ converges. Moreover, the following inequality chain holds:*

$$\lim_{N \to \infty} \rho_1(2, N - 2; r) < \lim_{N \to \infty} \rho_1(3, N - 3; r) < \lim_{N \to \infty} \rho_1(4, N - 4; r) < \cdots. \qquad (3.10)$$

4. Conclusions

This paper derives the explicit formulae for the kth-order fixation probabilities on complete star digraphs and applies them to study some asymptotic properties of populations on CSDs. In order to better understand how the structure of a population affects its evolution, we also chose to study how complete bipartite digraphs affect the first-order fixation probability of an advantageous mutant. For fixed population structure, a method (by solving a linear system) has been proposed to calculate this fixation probability. Numerical experiments have revealed some interesting phenomena, which need a reasonable explanation. After careful consideration, we find that, except isothermal digraphs, rooted digraphs and multiplerooted digraphs, complete star digraphs may be the only digraphs whose kth-order fixation probabilities can be expressed analytically. Therefore, a wise strategy for studying the fixation probabilities on other kinds of structures is to numerically determine them [18]. We are currently working toward this direction and also attempting to modify the model under study to adapt the evolution of the trustworthiness of large-scale distributed systems. It is also worth extending this work to, say, the cooperation on one graph, on a pair of graphs, or on hypernetworks [5, 19–23].

Acknowledgments

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