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Evolutionary graph theory revisited: when is an evolutionary process equivalent to the Moran process?

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Evolution in finite populations is often modelled using the classical Moran process. Over the last 10 years, this methodology has been extended to structured populations using evolutionary graph theory. An important question in any such population is whether a rare mutant has a higher or lower chance of fixating (the fixation probability) than the Moran probability, i.e. that from the original Moran model, which represents an unstructured population. As evolutionary graph theory has developed, different ways of considering the interactions between individuals through a graph and an associated matrix of weights have been considered, as have a number of important dynamics. In this paper, we revisit the original paper on evolutionary graph theory in light of these extensions to consider these developments in an integrated way. In particular, we find general criteria for when an evolutionary graph with general weights satisfies the Moran probability for the set of six common evolutionary dynamics.

1. Introduction

When modelling population evolution, we are concerned with the spread of heritable characteristics in successive generations. The type of model that is used depends upon whether the population size is assumed to be finite or infinite. The majority of classical evolutionary models (e.g. [1,2]) use infinite populations, although finite

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population models are also well established, the most important models being those in [3,4]. These models are stochastic and are solved using classical Markov chain methodology [5–7]. See also [8,9] for an extension to evolutionary games in finite populations.

The populations in the models described above, however, were 'well-mixed', i.e. every individual was equally likely to encounter every other individual. Real populations of course contain structural elements, such as geographical location or social relationship, which mean that some pairs individuals are more likely to interact than others. In such circumstances, we need to be able to identify distinct individuals (or at least distinct classes of individuals), and considering finite populations is perhaps more natural than infinite ones (although finite structures each containing an infinite number of individuals, the so-called 'island models', were considered in [10]). In [11], the modelling ideas of [3] were extended to consider such structured populations based upon graphs, known as evolutionary graph theory. This has proved very successful, spawning a large number of papers (e.g. [12–19]). For informative reviews, see [20,21].

In an evolving population, we need to consider the mechanism of how the population changes, called the dynamics. Informally, the dynamics specify the way in which heritable characteristics are passed on from one generation to the next. For infinite populations, the classical replicator equation [22] is often used (although there are a number of alternatives), and in the stochastic model of [3] there is a natural replacement dynamics built in. For structured populations, this issue is actually considerably more complex, and the order of births and deaths, and where selection acts, is of vital importance [23,24]. We shall consider a set of dynamics that are commonly used in evolutionary graph theory models. The relationship between dynamics and structure is of key interest because the spread of heritable characteristics is directly dependent upon it. While having essentially no effect on populations with no structure, for constant fitness this relationship potentially yields very different results on graphs. For non-constant fitness, the results will vary for different dynamics even in well-mixed populations [25].

Under some circumstances, it is, however, possible for the dynamics and structure to interact in such a way that the spread of heritable characteristics behaves just as if the population was homogeneous. This was a central theme of the classic paper [11], where two important results, the circulation theorem and the isothermal theorem, were developed that addressed this question (see also [26] for related work). In this paper, we generalize the work of [11] to obtain a complete classification of when the combination of a population structure and dynamics can be regarded as equivalent to a homogeneous population in a precisely defined way, for the six most common evolutionary dynamics and graphs with general weights.

2. The model

We shall first describe the population model of [11], which generalizes the model of [3] by incorporating a replacement structure. The notation used in this paper is summarized in table 1. *The population has a constant size* $N \in \mathbb{Z}$, $N \geq 2$, *consisting of individuals* $I_1, \ldots, I_N$. *Every individual is either of type* A or B.

This implies that there are 2^N different states of the population given by the combination of type A and B individuals. We represent each state by a set S such that $n \in S$ if an individual I_n is of type A. We can easily revert to using the number of type A individuals, $|S|$, if the population is homogeneous. The states $\emptyset$ and $\mathcal{N} = \{1, 2, \ldots, N\}$ have only type B and A individuals, respectively.

Individuals have a constant fitness that may depend upon their type.

The fitness of individuals in state S is thus given by the vector $\mathbf{F}(S) = (F_n(S))_{n=1,2,\ldots,N}$, where

$$F_n(S) = \begin{cases} 1 & n \notin S, \\ r \in (0, \infty) & n \in S \end{cases}$$

is the fitness of I_n. Here the fitness r of a type A individual is given relative to the fitness of a type B individual, assumed to be 1.

Table 1. Summary of notation.

symbol	definition	description
N	$\in \mathbb{Z}^+ \setminus \{0, 1\}$	population size
A, B		the two types of individuals in population
I_n		individual n
S	$= \{n : I_n \text{ of type } A\}$	state of the population
$\mathcal{N}$	$= \{1, 2, \ldots, N\}$	state in which all I_n of type A
r	$\in (0, \infty)$	fitness of a type A individual
$F_n(S)$	$\in \{1, r\}$	fitness of I_n in state S
D	$= (V, E)$	replacement digraph with vertices V where $\lvert V\rvert = N$ and directed edges E
w_{ij}	$\in [0, \infty)$	edge weight such that $w_{ij} > 0$ if and only if $(i, j) \in E$
$\mathbf{W}$	$= (w_{ij})$	*replacement matrix:* $N \times N$ weighted adjacency matrix of tuple (D, w)
T_n^+	$= \sum_{j=1}^{N} w_{nj}$	*out temperature*: sum of all outgoing edge weights of vertex $n \in V$
T_n^-	$= \sum_{i=1}^{N} w_{in}$	*in temperature*: sum of all incoming edge weights of vertex $n \in V$
b_i	$\in [0, 1]$	probability I_i chosen for birth
d_{ij}	$\in [0, 1]$	probability a copy of I_i replaces I_j given I_i was chosen for birth, i.e. replacement by death
d_j	$\in [0, 1]$	probability I_j chosen for death
b_{ij}	$\in [0, 1]$	probability a copy of I_i replaces I_j given I_j is chosen for death, i.e. replacement by birth
$\mathfrak{r}_{ij}$	$\in [0, 1]$	probability a copy of I_i replaces I_j
$P_{SS'}$	$\in [0, 1]$	state transition probability
$\mathbf{S}$	$= (P_{SS'})$	state transition matrix
$\mathcal{E}_{*,\mathbf{W},r}$		stochastic process with state transition matrix $\mathbf{S}$ such that $*$ dynamics are used on graph $\mathbf{W}$ and type A individuals have fitness r
ρ_S^A	$\in [0, 1]$	fixation probability of type A individual given initial state S
W		set of all strongly connected replacement matrices
W_{C}	$\{\mathbf{W} : T_n^+ = T_n^- \; \forall \, n\}$	replacement matrices that are circulations
W_{I}	$\{\mathbf{W} : T_i^+ = T_j^- \; \forall \, i, j\}$	replacement matrices that are isothermal
W_{R}	$\{\mathbf{W} : T_n^+ = 1 \, \forall \, n\}$	right stochastic replacement matrices
W_{L}	$\{\mathbf{W} : T_n^- = 1 \, \forall \, n\}$	left stochastic replacement matrices
C_N		replacement matrices whose digraphs are cycles of length N
f_{R}	$(w_{ij}) \mapsto (w_{ij} / \sum_n w_{in})$	map from W to W_{R}
f_{L}	$(w_{ij}) \mapsto (w_{ij} / \sum_n w_{nj})$	map from W to W_{L}
f'	$(w_{ij}) \mapsto (w_{ij} / \sum_{n,k} w_{nk})$	map from W to W
M_*		replacement matrices for which $\mathcal{E}_*$ is ρ-equivalent to a Moran process when $*$ dynamics are used

During a stochastic replacement event (that happens in an instant), an exact copy of an individual I_i *replaces an individual* I_j.

The replacement events may be restricted in the sense that not all individuals can replace one another. To enforce such restrictions, Lieberman *et al.* [11] imposed a replacement structure using a weighted directed graph given by the tuple (D, w), where $D = (V, E)$ is a directed graph, with sets V of vertices and E of directed edges, and w is a map that assigns a weight to each edge such that $w : V \times V \to [0, \infty) : (i, j) \mapsto w_{ij}$. Each vertex $n \in V$ represents I_n therefore $V = \{1, 2, \dots, N\}$ so $|V| = N$. We assume that $(i, j) \in E$ if and only if $w_{ij} > 0$, which indicates that I_i can replace I_j. Note that we allow $w_{ii} > 0$ and therefore I_i can replace itself. All the information contained within the weighted digraph (D, w) is conveniently summarized by the $N \times N$ weighted adjacency matrix $\mathbf{W} = (w_{ij})$ and therefore we will refer to (D, w) using $\mathbf{W}$, which we call the *replacement matrix*.

The replacement events are stochastic which means that there is a probability $\mathfrak{r}_{ij} = \mathfrak{r}_{ij}(\mathbf{F}(S), \mathbf{W})$ associated with (a copy of) I_i replacing I_j. There are several potential *evolutionary dynamics on graphs* that govern how the probability is determined. There are three main types of dynamics that are summarized below, see also [21]. We use the convention that I_i is chosen for birth and I_j is chosen for death.

(i) *Birth–death* (BD). I_i is chosen first then I_j. We have that $i \in V$ is chosen with probability b_i and then $(i, j) \in E_i$ is chosen with probability d_{ij}, where E_i are all edges starting in vertex i. d_{ij} is used to signify that there is 'replacement by death'. Finally, $\mathfrak{r}_{ij} = b_i d_{ij}$.
(ii) *Death–birth* (DB). I_j is chosen first then I_i. We have that $j \in V$ is chosen with probability d_j and then $(i, j) \in E_j$ is chosen with probability b_{ij}, where E_j are all edges ending in vertex j. b_{ij} is used to signify that there is 'replacement by birth'. Finally, $\mathfrak{r}_{ij} = d_i b_{ij}$.
(iii) *Link* (L). I_i and I_j are chosen simultaneously. In this case, $(i, j) \in E$ is simply chosen with probability $\mathfrak{r}_{ij}$.

For each type of these dynamics, the natural selection can, through the fitness parameter, influence either the choice at birth (resulting in adding 'B') or at death (adding 'D'). It yields six kinds of evolutionary dynamics on graphs summarized in table 2. These dynamics have been extensively studied, in particular, see [29] for a detailed comparison of them. Of these, the BDB and LB dynamics were used in [11].

(a) The fixation probability

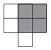
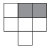
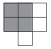
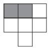
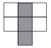
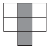
The fixation probability, $\rho_S^A = \rho_S^A(*, \mathbf{W}, r)$, is the probability that the population with initial state S is absorbed in $\mathcal{N}$, where $*$ is the dynamics being used.

Given that the replacement events are random, the transitions between the states of the population are described by a stochastic process, which we denote $\mathcal{E}$. The properties of $\mathcal{E}$ can be investigated once the state transition probabilities of moving from state S to S', $P_{SS'} = P_{SS'}(*, \mathbf{W}, r)$, are calculated using the replacement probabilities as follows:

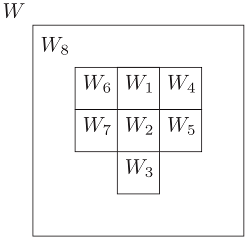
$$P_{SS'} = \begin{cases} \displaystyle\sum_{i \notin S} \mathfrak{r}_{ij}(\mathbf{F}(S), \mathbf{W}) & \text{if } S' = S \setminus \{j\} \text{ for some } j \in S, \\ \displaystyle\sum_{i \in S} \mathfrak{r}_{ij}(\mathbf{F}(S), \mathbf{W}) & \text{if } S' = S \cup \{j\} \text{ for some } j \notin S, \\ \displaystyle\sum_{\substack{i,j \in S \\ \vee i,j \notin S}} \mathfrak{r}_{ij}(\mathbf{F}(S), \mathbf{W}) & \text{if } S' = S. \end{cases}$$

The transition probabilities, $P_{SS'}$, satisfy the Markov property because they only depend upon the state S, that is, the probability of transitioning from the present state to another state is independent of any past and future state of the population. The stochastic process $\mathcal{E}_{*,\mathbf{W},r}$ with state transition matrix $\mathbf{S} = \mathbf{S}(*, \mathbf{W}, r) = (P_{SS'})_{S,S' \subset \{1,2,\dots,N\}}$ is therefore a Markov chain. The Markov chain $\mathcal{E}_{*,\mathbf{W},r}$ is part of the class of evolutionary Markov chains described in [34].

Table 2. List of dynamics together with their definition of M_*.

process	$\mathbb{P}(I_i \text{ replaces } I_j)$	order chosen	$\mathbb{P}$(chosen first)	$\mathbb{P}$(chosen second)	definition of M_*	illustration of M_*
BDB [11,13,14,16,19,27,28]	$\mathfrak{r}_{ij} = b_i d_{ij}$	I_i then I_j	$b_i = \dfrac{F_i(S)}{\sum_n F_n(S)}$	$d_{ij} = \dfrac{w_{ij}}{\sum_n w_{in}}$	$M_{\text{BDB}} = \{\mathbf{W} : f_{\text{R}}(\mathbf{W}) \in W_{\text{C}}\}$ $= f_{\text{R}}^{-1}(W_{\text{C}})$	
BDD [29]	$\mathfrak{r}_{ij} = b_i d_{ij}$	I_i then I_j	$b_i = \dfrac{1}{N}$	$d_{ij} = \dfrac{w_{ij}/F_j(S)}{\sum_n w_{in}/F_n(S)}$	$M_{\text{BDD}} = \{\mathbf{W} : f_{\text{R}}(\mathbf{W}) \in \{\mathbf{W_H}\} \cup C_N\}$ $= f_{\text{R}}^{-1}(\{\mathbf{W_H}\} \cup C_N)$	
DBD [12,13,28,30]	$\mathfrak{r}_{ij} = d_j b_{ij}$	I_j then I_i	$d_j = \dfrac{1/F_j(S)}{\sum_n 1/F_n(S)}$	$b_{ij} = \dfrac{w_{ij}}{\sum_n w_{nj}}$	$M_{\text{DBD}} = \{\mathbf{W} : f_{\text{L}}(\mathbf{W}) \in W_{\text{C}}\}$ $= f_{\text{L}}^{-1}(W_{\text{C}})$	
DBB [16,27,31–33]	$\mathfrak{r}_{ij} = d_j b_{ij}$	I_j then I_i	$d_j = \dfrac{1}{N}$	$b_{ij} = \dfrac{w_{ij}F_i(S)}{\sum_n w_{nj}F_n(S)}$	$M_{\text{DBB}} = \{\mathbf{W} : f_{\text{L}}(\mathbf{W}) \in \{\mathbf{W_H}\} \cup C_N\}$ $= f_{\text{L}}^{-1}(\{\mathbf{W_H}\} \cup C_N)$	
LB [11,13,28]	$\mathfrak{r}_{ij} = \dfrac{w_{ij}F_i(S)}{\sum_{n,k} w_{nk}F_n(S)}$	simultaneous	n.a.	n.a.	$M_{\text{LB}} = \{\mathbf{W} : f'(\mathbf{W}) \in W_{\text{C}}\}$ $= f'^{-1}(W_{\text{C}}) = W_{\text{C}}$	
LD [23]	$\mathfrak{r}_{ij} = \dfrac{w_{ij}/F_j(S)}{\sum_{n,k} w_{nk}/F_k(S)}$	simultaneous	n.a.	n.a.	$M_{\text{LD}} = \{\mathbf{W} : f'(\mathbf{W}) \in W_{\text{C}}\}$ $= f'^{-1}(W_{\text{C}}) = W_{\text{C}}$	

key for illustration of M_*:



$$\begin{aligned}
W_1 &= W_I \cap f_R^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
&= W_I \cap f_L^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
W_2 &= W_I \setminus f_R^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
&= W_I \setminus f_L^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
W_3 &= W_C \setminus W_I \\
W_4 &= (f_R^{-1}(W_C) \setminus W_C) \cap f_R^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
W_5 &= (f_R^{-1}(W_C) \setminus W_C) \setminus f_R^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
W_6 &= (f_L^{-1}(W_C) \setminus W_C) \cap f_L^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
W_7 &= (f_L^{-1}(W_C) \setminus W_C) \setminus f_L^{-1}(\{\mathbf{W_H}\} \cup C_N) \\
W_8 &= W \setminus \textstyle\bigcup_{i=1}^{7} W_i
\end{aligned}$$

The key on the left gives the definition of partitions $W_1, W_2, \ldots, W_8$ of W. The partitions W_i that make up M_* are highlighted for each of the dynamics in the last column. The partition of W, where $\mathcal{E}$ is ρ-equivalent to a Moran process regardless of the standard dynamics being used, is given by $M_{\text{L}} \cap M_{\text{BDB}} \cap M_{\text{BDD}} \cap M_{\text{DBD}} \cap M_{\text{DBB}} \equiv M_{\text{BDD}} \cap M_{\text{DBB}} \equiv W_1$.

The absorbing states of $\mathcal{E}_{*,\mathbf{W},r}$ are $\emptyset, \mathcal{N}$, which means that if the population is in either one of these states then it remains there indefinitely. This property of $\mathcal{E}_{*,\mathbf{W},r}$ can be used to measure the success of a type A individual by calculating the probability that it fixates, that is, everyone in the population is of type A. The fixation probability is then given by solving

$$\rho_S^A = \sum_{S' \subset \{1,2,\ldots,N\}} P_{SS'} \rho_{S'}^A \tag{2.1}$$

with boundary conditions $\rho_\emptyset^A = 0$ and $\rho_\mathcal{N}^A = 1$.

As demonstrated in [29], LB and LD dynamics may differ in time scale but they yield the same fixation probabilities when fitness is constant (which is our case). Thus, for our purposes the dynamics are the same and we will thus consider them together and denote them by L.

We note that the fixation probability is not the only measure for evolutionary success and we can look at the fixation time [35,36] as well.

(b) The Moran process

The Moran process [3], a stochastic BD process on a finite fixed homogeneous population, can be reconstructed as $\mathcal{E}_{\mathrm{BDB},\mathbf{W_H},r}$ for a constant replacement matrix

$$\mathbf{W_H} = \left(\frac{1}{N}\right)_{i,j}. \tag{2.2}$$

For any $r \in (0, \infty)$ and any $S \subset \{1, \ldots, N\}$, the fixation probability for this process, or *Moran probability*, is given by

$$\rho_S^A = \begin{cases} \dfrac{1 - r^{-|S|}}{1 - r^{-N}} & \text{if } r \neq 1, \\ \dfrac{|S|}{N} & \text{if } r = 1. \end{cases}$$

We are interested in characterizing graphs (and evolutionary dynamics) that yield the same fixation probabilities as the homogeneous matrix $\mathbf{W_H}$ given in (2.2). We note that for this matrix all of the transition probabilities $\mathfrak{r}_{ij}$ take the same value independent of i, j or the dynamics, and consequently the fixation probability under each of the dynamics is the same.

(c) Classes of graphs/matrices

The set of all admissible replacement matrices is defined as follows:

$$W = \{\mathbf{W}: \text{ for every } i, j, \text{ there is } l \text{ such that } (\mathbf{W}^l)_{i,j} > 0\}.$$

This definition means that $\mathbf{W}$ is strongly connected as for any pair of vertices i and j, there is a path (of length l) going from i to j. Unless specified otherwise, we will consider admissible replacement matrices only.

As in [11], for any $\mathbf{W}$ (admissible or not) we define the *in temperature* of I_n, T_n^-, and the *out temperature* of I_n, T_n^+, by

$$T_n^- = \sum_{j=1}^N w_{jn} \quad \text{and} \quad T_n^+ = \sum_{j=1}^N w_{nj}.$$

$\mathbf{W}$ is called a *circulation* if $T_n^+ = T_n^-$, for all $n \in V$ and it is called *isothermal* if $T_i^+ = T_j^-$, for all $i, j \in V$. $\mathbf{W}$ is called *right* stochastic if $T_n^+ = 1$, for all $n \in V$ and it is called *left* stochastic if $T_n^- = 1$, for all $n \in V$. The sets of all circulations, isothermal matrices, right stochastic matrices, and left stochastic matrices, respectively, are denoted by W_C, W_I, W_R and W_L, respectively.

The set C_N denotes the set of matrices representing *cycles* of length N, more specifically, for $(w_{ij}) \in C_N$ we have $w_{ii} = 1/2$ for $i = 1, 2, \ldots N$, $w_{i_1 i_2} = \cdots = w_{i_n i_{n+1}} = \cdots = w_{i_{N-1} i_N} = w_{i_N i_1} = \frac{1}{2}$ for some permutation $i_1, i_2, \ldots, i_N$ of the sequence $1, 2, \ldots, N$, and $w_{ij} = 0$ otherwise.

We also define the maps $f_{\mathrm{R}}: W \to W_{\mathrm{R}}, f_{\mathrm{L}}: W \to W_{\mathrm{L}}$ and $f': W \to W$, respectively, by

$$f_{\mathrm{R}}((w_{ij})) = \left(\frac{w_{ij}}{\sum_n w_{in}}\right), \quad f_{\mathrm{L}}((w_{ij})) = \left(\frac{w_{ij}}{\sum_n w_{nj}}\right) \quad \text{and} \quad f'((w_{ij})) = \left(\frac{w_{ij}}{\sum_{n,k} w_{nk}}\right).$$

Note that f_{R} preserves right stochastic matrices and f_{L} preserves left stochastic matrices. Moreover, $f_{\mathrm{R}}(\mathbf{W}) = f_{\mathrm{L}}(\mathbf{W})$ for all $\mathbf{W} \in W_{\mathrm{I}}$. Also, as f' simply involves multiplying $\mathbf{W}$ by the constant $1/\sum_{n,k} w_{nk}$, it implies that $\mathbf{W} \in W_{\mathrm{C}} \Leftrightarrow f'(\mathbf{W}) \in W_{\mathrm{C}}$.

When the dynamics $*$, matrices $\mathbf{W_1}$ and $\mathbf{W_2}$, and fitness r are given, we say that an evolutionary Markov chain $\mathcal{E}_{*,\mathbf{W_1},r}$ is *ρ-equivalent* to $\mathcal{E}_{*,\mathbf{W_2},r}$ if for every $S \subset \{1, \ldots, N\}$, $\rho_S^A(*, \mathbf{W_1}, r) = \rho_S^A(*, \mathbf{W_2}, r)$, in which case we write $\mathbf{W_1} \sim_{*,r} \mathbf{W_2}$.

We are specifically interested in finding matrices equivalent to the Moran process. For a dynamics $*$, we define

$$M_* = \{\mathbf{W} : \mathbf{W} \sim_{*,r} \mathbf{W_H} \text{ for all } r > 0\}.$$

3. Results

The map f_{R} preserves the equivalence classes of BDB and BDD dynamics, f_{L} preserves the equivalence classes of DBB and DBD dynamics and f' preserves the equivalence classes for link dynamics. Specifically, as one can see from the proofs in appendix A, for any $\mathbf{W}$ and any $r > 0$

$$\left.\begin{aligned} &\mathbf{W} \sim_{\mathrm{BDB},r} f_{\mathrm{R}}(\mathbf{W}),\\ &\mathbf{W} \sim_{\mathrm{BDD},r} f_{\mathrm{R}}(\mathbf{W}),\\ &\mathbf{W} \sim_{\mathrm{DBD},r} f_{\mathrm{L}}(\mathbf{W}),\\ &\mathbf{W} \sim_{\mathrm{DBB},r} f_{\mathrm{L}}(\mathbf{W}),\\ &\mathbf{W} \sim_{\mathrm{L},r} f'(\mathbf{W}). \end{aligned}\right\} \tag{3.1}$$

We thus obtain the following results, which completely specify the graphs which are equivalent to the homogeneous matrix $\mathbf{W_H}$ for each of our evolutionary dynamics.

Proposition 3.1 (Link). $M_{\mathrm{L}} = W_{\mathrm{C}}$. *More precisely, the following statements are equivalent*:

(a) $\mathbf{W}$ *is a circulation.*
(b) *For all* $r > 0$, $\mathbf{W} \sim_{\mathrm{L},r} \mathbf{W_H}$.
(c) *There is* $r > 0$ *such that* $\mathbf{W} \sim_{\mathrm{L},r} \mathbf{W_H}$.

We note that $W_{\mathrm{C}} = f'^{-1}(W_{\mathrm{C}}) = \{\mathbf{W} : f'(\mathbf{W}) \in W_{\mathrm{C}}\}$ and thus, similar to proposition 3.2, proposition 3.1 can be written as $M_{\mathrm{L}} = f'^{-1}(W_{\mathrm{C}})$.

Proposition 3.2 (BDB and DBD). $M_{\mathrm{BDB}} = f_{\mathrm{R}}^{-1}(W_{\mathrm{C}})$ *and* $M_{\mathrm{DBD}} = f_{\mathrm{L}}^{-1}(W_{\mathrm{C}})$. *More precisely, the following statements are equivalent*:

(a) $f_{\mathrm{R}}(\mathbf{W})$ *is a circulation.*
(b) *For all* $r > 0$, $\mathbf{W} \sim_{\mathrm{BDB},r} \mathbf{W_H}$.
(c) *There is* $r > 0$ *such that* $\mathbf{W} \sim_{\mathrm{BDB},r} \mathbf{W_H}$.

The equivalent conditions for DBD are similar to the above for BDB but f_{R} *is replaced by* f_{L}.

Proposition 3.3 (BDD and DBB). $M_{\mathrm{BDD}} = f_{\mathrm{R}}^{-1}(\{\mathbf{W_H}\} \cup C_N)$ *and* $M_{\mathrm{DBB}} = f_{\mathrm{L}}^{-1}(\{\mathbf{W_H}\} \cup C_N)$. *More precisely, the following statements are equivalent*:

(a) $f_{\mathrm{R}}(\mathbf{W}) = \mathbf{W_H}$ *or* $f_{\mathrm{R}}(\mathbf{W}) \in C_N$.
(b) *For all* $r > 0$, $\mathbf{W} \sim_{\mathrm{BDD},r} \mathbf{W_H}$.

The equivalent conditions for DBB are similar to the above for BDD but f_{R} *is replaced by* f_{L}.

In particular, $M_{\mathrm{BDD}} \subset M_{\mathrm{BDB}}$ and $M_{\mathrm{DBB}} \subset M_{\mathrm{DBD}}$. The sets M_* are illustrated in table 2.

Note that unlike in propositions 3.1 and 3.2, proposition 3.3 does not contain 'any r implies all r'. In fact, when $r = 1$, there is no selection and thus the dynamics BDB and BDD are the same (and also the dynamics DBB and DBD are the same). Consequently, by proposition 3.2,

$$\mathbf{W} \sim_{\mathrm{BDD},1} \mathbf{W_H} \;\Leftrightarrow\; f_{\mathrm{R}}(\mathbf{W}) \in W_{\mathrm{C}} \;\Leftrightarrow\; \mathbf{W} \in M_{\mathrm{BDB}},$$

$$\mathbf{W} \sim_{\mathrm{DBB},1} \mathbf{W_H} \;\Leftrightarrow\; f_{\mathrm{L}}(\mathbf{W}) \in W_{\mathrm{C}} \;\Leftrightarrow\; \mathbf{W} \in M_{\mathrm{DBD}}.$$

(a) Our results in the context of known results

For the LB dynamics, proposition 3.1 was stated and proved in [11] as the Circulation theorem. For the LD dynamics, proposition 3.1 follows from the Circulation theorem and the result of [29] that the fixation probabilities for LB and LD are the same.

As shown in appendix Aa, BDB is the same as the LB dynamics for right stochastic matrices (in particular, for BDB dynamics, proposition 3.2 can be seen as the Isothermal theorem from [11]). Proposition 3.2 thus follows from proposition 3.1 thanks to (3.1). The natural symmetries between f_{R} and f_{L} and BDB and DBD dynamics allow us to extend the Isothermal theorem to DBD dynamics as well (see also [37]).

Overall, propositions 3.1 and 3.2 and the occurrence of W_{C} within them are consistent with the claim made in [11] that the circulation criterion completely classifies all replacement matrices where $\mathcal{E}_{*,\mathbf{W},r}$ is ρ-equivalent to a Moran process.

Our most important new result is proposition 3.3. It shows that the BDD and DBB dynamics require very strict conditions to yield the Moran process. Either the population structure is homogeneous, or it is a directed cycle. This latter structure is an interesting theoretical example, but is unlikely to apply to real populations, meaning that the homogeneous population is practically the only way to get the Moran process for a realistic population.

(b) The importance of self-loops in BDD and DBB dynamics

Proposition 3.3 by definition requires that $w_{ii} > 0 \;\forall i = 1, 2, \ldots, N$. Without such self-loops, $\mathcal{E}_{\mathrm{BDD},\mathbf{W},r}, \mathcal{E}_{\mathrm{DBB},\mathbf{W},r}$ cannot ever be ρ-equivalent to the Moran process. The ability of an individual to replace itself therefore plays an important role in the replacement structure of the population and cannot be discounted. For BD dynamics, when increasing the diagonal weights of $\mathbf{W}$, the fixation probability decreases for BDB and increases for BDD. For DB dynamics, the increase in fixation probability DBB is greater than that for DBD. For LB dynamics, the fixation probability remains the same.

With BDD and DBB evolutionary dynamics on graphs, one may encounter the following problems if there are no self-loops. For DBB dynamics, a type A individual with almost infinite fitness still has a fixation probability bounded away from 1 because even type A individuals can be randomly picked for death and replaced by type B individuals [38, p. 245]. With self-loops, however, a type A individual will almost always be replaced by itself (or another type A individual) and therefore has a fixation probability approaching 1. Similarly, for BDD dynamics, a type A individual with almost zero fitness does not have near probability 0 of fixating as type A individuals can be randomly picked for birth and replace type B individuals [38, p. 245]. With self-loops, such an individual will almost always pick itself (or another type A) to replace and therefore its fixation probability is near 0. Thus, the inclusion of self-loops removes some problematic features of the BDD and DBB dynamics, and makes them more attractive dynamics to use in models.

4. Discussion

In this paper, we have considered an evolutionary graph theory model of a population involving general weights and a variety of evolutionary dynamics based upon the work of Lieberman *et al*. [11], which was a development of the classical population model of Moran [3]. In such populations, the population size is fixed at all times and at successive discrete time points one replacement event occurs. Like the aforementioned papers, we consider two types of individuals, where fitness depends upon type but no other factors (i.e. there are no game-theoretic interactions). In particular, the single most important property of such a process is the fixation probability, the probability that a randomly placed mutant individual of the second type will eventually completely replace the population of the first type.

This fixation probability depends upon the fitnesses of the two types of individuals, but can also be heavily influenced by the population structure as given by the weights, and by the evolutionary dynamics used. These effects are commonly observed, although in some circumstances evolution proceeds as if as on a well-mixed population as from the original work of Moran [3], dependent only upon the fitnesses of the two types, and some important results in this regard were already given in [11]. The aim of this paper was to provide a generalized set of conditions for when this would be the case.

By defining what is meant by fixation-equivalence to the Moran process, we provided a general result which, independent of the specific dynamics used, helps identify graphs that do not affect the fixation probability. With respect to each of the standard dynamics, we then classified sets of evolutionary graphs that have the same fixation probability as the Moran process (or well-mixed population). These sets include graphs that are circulations and therefore generalizes the work of Lieberman *et al*. [11].

An important new result shows that the set of weights for which we obtain fixation equivalence to the Moran process for the BDD and DBB dynamics is very restricted, and so that for most populations with any structure this equivalence will not hold for these dynamics. We note also that the inclusion of non-zero self weights w_{ii} eliminates some problematic features of these two dynamics (i.e. that individuals with 0 fitness could fixate or those with infinite fitness could be eliminated) and so improves the applicability of these dynamics.

Presenting evolutionary dynamics on graphs, in the way that we have, allows one to incorporate a variety of dynamics in their analysis, both of standard type and other definitions. This will improve our understanding of dynamics on graphs in general. We note that the list of dynamics in table 2 is not exhaustive. For example, Ohtsuki & Nowak [27] used imitation dynamics, which is a class of DBB dynamics with an additional requirement $w_{ii} > 0 \ \forall i$, and Zukewich *et al*. [39] consolidates the BDB and DBD dynamics such that one is chosen with a given probability.

In general, the inclusion of non-zero self-weights, in contrast to many earlier evolutionary graph theory works, allows for a greater flexibility of modelling. We note that this is consistent with the original work of Moran [3], which allowed self-replacement as an integral part of the process. For well-mixed populations, it does not matter much whether this possibility is included or not (at least for sufficiently large populations with intermediate fitness values), and it is likely that it has often been excluded for reasons of convenience because of this without the ramifications being fully considered in many later works. It is thus important to consider whether to include such self weights when modelling spatial structure using evolutionary graph theory.

Data accessibility. There is no supporting data for this article.

Authors' contributions. K.P. developed the original concept in discussion with M.B., and carried out the majority of the analysis and writing. M.B., J.R. and L.J.S. have all been closely involved in refining the paper in terms of both analysis and presentation. In particular, J.R. did significant work on the proofs, M.B. on the Introduction/Discussion and L.J.S. on the scientific presentation. All authors gave final approval for publication.

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Appendix A. Proofs

(a) BDB is the same as LB for right stochastic matrices

For BDB dynamics, we have $\mathfrak{r}_{ij} = b_i d_{ij}$. By definition $\sum_{ij} b_i d_{ij} = 1$, we can therefore write this as $\mathfrak{r}_{ij} = b_i d_{ij} / \sum_{n,k} b_n d_{n,k}$. Substituting $b_i = F_i / \sum_{m=1}^{N} F_m$ gives

$$\mathfrak{r}_{ij} = \frac{d_{ij} F_i / \sum_{m=1}^{N} F_m}{\sum_{n,k} (d_{nk} F_n / \sum_{m=1}^{N} F_m)} = \frac{d_{ij} F_i}{\sum_{n,k} d_{nk} F_n}.$$

If $\mathbf{W}$ is right stochastic, i.e. $\sum_{n=1}^{N} w_{in} = 1$ for all $i = 1, 2, \ldots N$, for BDB dynamics we have that $d_{ij} = w_{ij} / \sum_{n=1}^{N} w_{in} = w_{ij}$ giving $\mathfrak{r}_{ij} = w_{ij} F_i / \sum_{n,k} w_{nk} F_n$ which is the LB dynamics as required. We also have that DBD is the same as LD for left stochastic matrices. The explanation follows the same procedure as above.

(b) Lemma A.1 (Forward Bias)

The key lemma A.1 stated below is used in the proofs of all propositions, and it relies heavily on the notion of *forward bias* of state S which is then given by the ratio of the probabilities of a forward transition to a backward transition from S. A forward and backward transitions from S occurs when the number of type A individuals increase and decrease by one, respectively, which happen with probability

$$P_S^+ = \sum_{n \notin S} P_{S, S \cup \{n\}} \quad \text{and} \quad P_S^- = \sum_{n \in S} P_{S, S \setminus \{n\}}.$$

Lemma A.1 (Constant Forward Bias). *Let $\mathcal{E}$ be an evolutionary process on states $S \subset \{1, 2, \ldots, N\}$ with transition probabilities $P_{S,S'}$ that satisfy*

(1) *$P_{S,S'} > 0$ only if S and S' differ in at most one element,*
(2) *for every $S \neq \emptyset, \{1, \ldots, N\}$, there are S^+ and S^- such that $|S^+| = |S| + 1$ and $|S^-| = |S| - 1$ and $P_{S,S^+} > 0, P_{S,S^-} > 0$.*

Then, the following are equivalent:

(a) *There is a constant $c > 0$ such that for all $S \subset \{1, 2, \ldots, N\}$*

$$\rho_S^A = \begin{cases} \dfrac{1 - c^{-|S|}}{1 - c^{-N}} & \text{if } c \neq 1, \\[2ex] \dfrac{|S|}{N} & \text{if } c = 1, \end{cases}$$

(b) *$\mathcal{E}$ has constant forward bias, that is, there is a constant d such that for all $S \subset \{1, 2, \ldots, N\}$*

$$\frac{P_S^+}{P_S^-} = d.$$

Moreover, if either (a) *or* (b) *hold, then $c = d$.*

Note that a similar result is given in [11,20] where the forward bias is explicitly defined as

$$\frac{r \sum_{a \in S} \sum_{b \notin S} w_{ab}}{\sum_{a \in S} \sum_{b \notin S} w_{ba}},$$

which is what one gets when using Link dynamics, or BDB dynamics if $\mathbf{W} \in W_{\mathrm{R}}$. Note that in lemma A.1 the forward bias is defined independent of the dynamics and therefore applies to all dynamics that satisfy the assumptions.

Proof. '(a) ⇒ (b)': Take any $S \subset \{1, 2, \ldots, N\}$. It is known that

$$\rho_S^A = \sum_{S'} P_{S,S'}\rho_{S'}^A = P_{S,S}\rho_S^A + \sum_{n\notin S}(P_{S,S\cup\{n\}}\rho^A_{S\cup\{n\}}) + \sum_{n\in S}(P_{S,S\setminus\{n\}}\rho^A_{S\setminus\{n\}})$$

and using $P_{S,S} = 1 - P_S^+ - P_S^-$ gives

$$0 = \sum_{n\notin S}(P_{S,S\cup\{n\}}(\rho^A_{S\cup\{n\}} - \rho_S^A)) + \sum_{n\in S}(P_{S,S\setminus\{n\}}(\rho^A_{S\setminus\{n\}} - \rho_S^A)). \tag{A 1}$$

For $c \neq 1$, equation (A 1) simplifies to

$$0 = \frac{1 - c^{-|S|-1} - 1 + c^{-|S|}}{1 - c^{-N}}P_S^+ + \frac{1 - c^{-|S|+1} - 1 + c^{-|S|}}{1 - c^{-N}}P_S^- \Rightarrow$$

$$\frac{P_S^+}{P_S^-} = \frac{c^{-|S|} - c^{-|S|+1}}{c^{-|S|-1} - c^{-|S|}} = \frac{1 - c}{c^{-1} - 1} = c.$$

For $c = 1$, equation (A 1) simplifies to

$$0 = (|S| + 1 - |S|)P_S^+ + (|S| - 1 - |S|)P_S^- \Rightarrow \frac{P_S^+}{P_S^-} = 1.$$

'(b) ⇐ (a)': The state transition matrix $\mathbf{S} = (P_{S,S'})$ can be scaled to give $\mathbf{S}' = (P'_{S,S'})$ such that $P'_{S,S} = 0$ and $P'_{S,S'} = P_{S,S'}/(1 - P_{S,S}) = P_{S,S'}/(P_S^+ + P_S^-)$ where S is a non-absorbing state. The fixation probability ρ_S^A will be the same whether $\mathbf{S}'$ or $\mathbf{S}$ is used. This is because equation (2.1) can be rearranged as follows:

$$\rho_S^A = \sum_{S'} P_{SS'}\rho_{S'}^A \Rightarrow \rho_S^A = P_{SS}\rho_S^A + \sum_{S':S'\neq S} P_{SS'}\rho_{S'}^A \Rightarrow$$

$$\rho_S^A(1 - P_{SS}) = \sum_{S':S'\neq S} P_{SS'}\rho_{S'}^A \Rightarrow \rho_S^A = \sum_{S':S'\neq S} \frac{P_{SS'}}{P_S^+ + P_S^-}\rho_{S'}^A.$$

Let $\{\mathcal{S}_0, \mathcal{S}_1, \ldots, \mathcal{S}_N\}$ be a partition of the states S such that $S \in \mathcal{S}_i$ if $|S| = i$. The probability $P_{i,j}(S)$ of transitioning from state $S \in \mathcal{S}_i$ to *lumped state* $\mathcal{S}_j$ with respect to $\mathbf{S}'$ is

$$P_{i,j}(S) = \begin{cases} 0 & j \neq i \pm 1, \\ \dfrac{1}{d+1} & j = i - 1, \\ \dfrac{d}{d+1} & j = i + 1 \end{cases} \quad \text{for } i = 1, 2, \ldots, N-1. \tag{A 2}$$

This can be easily verified, for example, take $j = i - 1$ then

$$P_{i,i-1}(S) = \sum_{S'\in\mathcal{S}_{i-1}} P'_{S,S'} = \sum_{S'\in\mathcal{S}_{i-1}} \frac{P_{S,S'}}{P_S^+ + P_S^-} = \frac{P_S^-}{P_S^+ + P_S^-} = \frac{1}{1+d}$$

since the forward bias is equal to d. Equation (A 2) satisfies the necessary and sufficient condition for the Markov chain with state transition matrix $\mathbf{S}'$ to be lumpable with respect to the partition $\{\mathcal{S}_0, \mathcal{S}_1, \ldots, \mathcal{S}_N\}$ (Theorem 6.3.2, p. 124, [40]). Let $\hat{\mathbf{S}} = (P_{i,j})$ be the state transition matrix for this lumped Markov chain then the probability $P_{i,j}$ of transitioning from lumped states $\mathcal{S}_i$ to $\mathcal{S}_j$ is given by

$$P_{i,j} = P_{i,j}(S).$$

The state transition matrix $\hat{\mathbf{S}}$ describes a random walk with absorbing barriers and therefore the probability ρ_i^A of type A individuals fixating when the population starts in lumped state $\mathcal{S}_i$ is calculated using the methods in [5] to give

$$\rho_i^A = \frac{1+\sum_{j=1}^{i-1}\prod_{k=1}^{j}(P_{k,k-1}/P_{k,k+1})}{1+\sum_{j=1}^{N-1}\prod_{k=1}^{j}(P_{k,k-1}/P_{k,k+1})}.$$

In this case,

$$\rho_i^A = \begin{cases} \dfrac{1-d^{-i}}{1-d^{-N}} & d \neq 1, \\ \dfrac{i}{N} & d = 1 \end{cases}$$

as $P_{k,k-1}/P_{k,k+1} = 1/r$ for $k = 1, 2, \ldots, N-1$. By definition, $\rho_S^A = \rho_i^A$ where $i = |S|$ as required. ■

(c) Proposition 3.1 (Link)

The following statements are equivalent:

(a) **W** is a circulation.
(b) For all $r > 0$, $\mathbf{W} \sim_{\mathrm{L},r} \mathbf{W_H}$.
(c) There is $r > 0$ such that $\mathbf{W} \sim_{\mathrm{L},r} \mathbf{W_H}$.
(d) For all $r > 0$ and for all $S \subset \{1, 2, \ldots, N\}$, the forward bias of $\mathcal{E}_{\mathrm{L},\mathbf{W},r}$ is r, i.e.

$$\frac{P_S^+}{P_S^-} = r.$$

(e) There is $r > 0$ such that for all $a \in \{1, 2, \ldots, N\}$, the forward bias of the one element set $S = \{a\}$ is r, i.e.

$$\frac{\sum_{b\neq a} P_{\{a\},\{a,b\}}}{P_{a,\emptyset}} = r.$$

Proof. For LB dynamics, the forward bias is given by

$$\frac{P_S^+}{P_S^-} = \frac{\sum_{a\in S}\sum_{b\notin S}(w_{ab}F_a/\sum_{n,k} w_{nk}F_n)}{\sum_{a\in S}\sum_{b\notin S}(w_{ba}F_b/\sum_{n,k} w_{nk}F_n)} = \frac{r\sum_{a\in S}\sum_{b\notin S} w_{ab}}{\sum_{a\in S}\sum_{b\notin S} w_{ba}}.$$

For LD dynamics, the forward bias is given by

$$\frac{P_S^+}{P_S^-} = \frac{\sum_{a\in S}\sum_{b\notin S}(w_{ab}/F_b/\sum_{n,k} w_{nk}/F_k)}{\sum_{a\in S}\sum_{b\notin S}(w_{ba}/F_a/\sum_{n,k} w_{nk}/F_k)} = \frac{r\sum_{a\in S}\sum_{b\notin S} w_{ab}}{\sum_{a\in S}\sum_{b\notin S} w_{ba}}.$$

'(a) ⇒ (d)': **W** is a circulation i.e. $T_n^+ = T_n^-$ for all $n \in \{1, \ldots, N\}$ and thus

$$\sum_{a\in S}\sum_{b\notin S} w_{ab} = \sum_{a\in S}\left(\sum_{n} w_{an} - \sum_{k\in S} w_{ak}\right) = \sum_{a\in S}\left(T_a^+ - \sum_{k\in S} w_{ak}\right) \Rightarrow$$

$$\sum_{a\in S}\sum_{b\notin S} w_{ab} = \sum_{a\in S}\left(T_a^- - \sum_{k\in S} w_{ka}\right) = \sum_{a\in S}\left(\sum_{n} w_{na} - \sum_{k\in S} w_{ka}\right) \Rightarrow$$

$$\sum_{a\in S}\sum_{b\notin S} w_{ab} = \sum_{a\in S}\sum_{b\notin S} w_{ba}.$$

Note that $\sum_{a\in S}\sum_{b\notin S} w_{ab} \neq 0$ because **W** is admissible and represents a strongly connected graph. Thus, the forward bias for both LB and LD is equal to r.

'(d)⇒(e)' is trivial as (d) is much stronger than (e).

'(e)⇒(a)' Let a and r be fixed. By above calculations of the forward bias, we have

$$\sum_{b\notin S=\{a\}} w_{ab} = \sum_{b\notin S=\{a\}} w_{ba} \Rightarrow -w_{aa} + \sum_{i=1}^{N} w_{ai} = -w_{aa} + \sum_{i=1}^{N} w_{ia} \Rightarrow \sum_{i=1}^{N} w_{ai} = \sum_{i=1}^{N} w_{ia}$$

therefore $\mathbf{W}$ is a circulation.

'(d)⇒(b)' follows from lemma A.1.

'(b)⇒(c)' is trivial.

'(c)⇒(e)' follows from lemma A.1. ■

(d) Proposition 3.1 (BDB and DBD)

More precisely, the following statements are equivalent:

(a) $f_{\mathrm{R}}(\mathbf{W})$ is a circulation.
(b) For all $r > 0$, $\mathbf{W} \sim_{\mathrm{BDB},r} \mathbf{W_H}$.
(c) There is $r > 0$ such that $\mathbf{W} \sim_{\mathrm{BDB},r} \mathbf{W_H}$.
(d) For all $r > 0$ and for all $S \subset \{1, 2, \dots, N\}$, the forward bias of $\mathcal{E}_{\mathrm{BDB},\mathbf{W},r}$ is r, i.e.

$$\frac{P_S^+}{P_S^-} = r.$$

(e) There is $r > 0$ such that for all $a \in \{1, 2, \dots, N\}$, the forward bias of $\mathcal{E}_{\mathrm{BDB},\mathbf{W},r}$ of the one element set $S = \{a\}$ is r, i.e.

$$\frac{\sum_{b\neq a} P_{\{a\},\{a,b\}}}{P_{a,\emptyset}} = r.$$

Proof. Let $\mathbf{U} = (u_{ij}) = f_{\mathrm{R}}(\mathbf{W}) = (w_{ij}/\sum_n w_{in})$ then for BDB dynamics the forward bias of $\mathcal{E}_{\mathrm{BDB},\mathbf{W},r}$ is given by

$$\frac{P_S^+}{P_S^-} = \frac{\sum_{a\in S}\sum_{b\notin S}(F_a/\sum_n F_n)(w_{ab}/\sum_n w_{an})}{\sum_{a\in S}\sum_{b\notin S}(F_b/\sum_n F_n)(w_{ba}/\sum_n w_{bn})} = \frac{r\sum_{a\in S}\sum_{b\notin S} u_{ab}}{\sum_{b\notin S}\sum_{a\in S} u_{ba}}$$

and therefore the forward bias of $\mathcal{E}_{\mathrm{BDB},\mathbf{W},r}$ is the same as forward bias of $\mathcal{E}_{\mathrm{BDB},\mathbf{U},r}$.

Similarly, with almost identical working as above, when $\mathbf{V} = f_{\mathrm{L}}(\mathbf{W})$, the forward bias of $\mathcal{E}_{\mathrm{DBD},\mathbf{W},r}$ is the same as forward bias of $\mathcal{E}_{\mathrm{DBD},\mathbf{V},r}$ and is given by

$$\frac{P_S^+}{P_S^-} = \frac{\sum_{a\in S}\sum_{b\notin S}(F_b^{-1}/\sum_n F_n^{-1})(w_{ab}/\sum_n w_{nb})}{\sum_{a\in S}\sum_{b\notin S}(F_a^{-1}/\sum_n F_n^{-1})(w_{ba}/\sum_n w_{na})} = \frac{\sum_{a\in S}\sum_{b\notin S} v_{ab}}{(1/r)\sum_{a\in S}\sum_{b\notin S} v_{ba}}.$$

and the proof of the proposition for DBD closely follows the one for BDB given below with $\mathbf{U}$ and f_{R} appropriately replaced by $\mathbf{V}$ and f_{L}.

'(a)⇒ (d)': If $\mathbf{U} = f_{\mathrm{R}}(\mathbf{W}) \in W_{\mathrm{C}}$, i.e. if $\mathbf{U}$ is doubly stochastic, then the forward bias (for $S \neq \emptyset, \mathcal{N}$) is equal to

$$\frac{P_S^+}{P_S^-} = \frac{r\sum_{a\in S}(\sum_n(u_{an}) - \sum_{k\in S}(u_{ak}))}{\sum_{a\in S}(\sum_n(u_{na}) - \sum_{k\in S}(u_{ka}))} = \frac{r(|S| - \sum_{a\in S}\sum_{k\in S} u_{ak})}{|S| - \sum_{a\in S}\sum_{k\in S} u_{ka}} = r$$

'(d)⇒(e)' is trivial as (d) is stronger than (e).

'(e)⇒(a)' Let a and r be fixed. By above calculations of the forward bias, we have

$$\sum_{a\in S}\sum_{b\notin S} u_{ab} = \sum_{a\in S}\sum_{b\notin S} u_{ba}.$$

Consider the states $S = \{a\}$ in which there is only one individual of type A then

$$\sum_{b\notin S} u_{ab} = \sum_{b\notin S} u_{ba} \Rightarrow -u_{aa} + \sum_{i=1}^{N} u_{ai} = -u_{aa} + \sum_{i=1}^{N} u_{ia} \Rightarrow 1 = \sum_{i=1}^{N} u_{ia}$$

is true for all $a = 1, 2, \dots, N$ and therefore $\mathbf{U}$ is doubly stochastic and thus $f_{\mathrm{R}}(\mathbf{W})$ is a circulation.

'(d)⇒(b)' follows from lemma A.1.
'(b)⇒(c)' is trivial.
'(c)⇒(e)' follows from lemma A.1. ■

(e) Proposition 3.3 (BDD and DBB)

The following statements are equivalent:

(a) $f_{\mathrm{R}}(\mathbf{W}) = \mathbf{W_H}$ or $f_{\mathrm{R}}(\mathbf{W}) \in C_N$.
(b) For all $r > 0$, $\mathbf{W} \sim_{\mathrm{BDD},r} \mathbf{W_H}$.

Proof. The replacement probabilities $\mathfrak{r}_{ij}(\mathbf{F}(S),\mathbf{W})$ for BDD dynamics can be rewritten as $\mathfrak{r}_{ij}(\mathbf{F}(S),\mathbf{U})$, where $\mathbf{U} = (u_{ij}) = f_{\mathrm{R}}(\mathbf{W}) = (w_{ij}/\sum_n w_{in})$ by multiplying the numerator and denominator with $\sum_n w_{in}$ as follows:

$$\mathfrak{r}_{ij}(\mathbf{F}(S),\mathbf{W}) = \frac{1}{N}\frac{w_{ij}/F_j(S)}{\sum_n w_{in}/F_n(S)} = \frac{1}{N}\frac{w_{ij}/(F_j(S)\sum_n w_{in})}{\sum_n w_{in}/(F_n(S)\sum_n w_{in})} \Rightarrow$$

$$\frac{u_{ij}/F_j(S)}{\sum_n u_{in}/F_n(S)} = \mathfrak{r}_{ij}(\mathbf{F}(S),\mathbf{U})$$

and therefore we have that $\mathbf{W} \sim_{\mathrm{BDD},r} \mathbf{U}$, for all $r > 0$. The forward bias using $\mathbf{U}$ for state S is given by

$$\frac{P_S^+}{P_S^-} = \frac{\sum_{a\in S}\sum_{b\notin S}(1/N)(u_{ab}F_b^{-1}/\sum_n u_{an}F_n^{-1})}{\sum_{a\in S}\sum_{b\notin S}(1/N)(u_{ba}F_a^{-1}/\sum_n u_{bn}F_n^{-1})} = \frac{\sum_{a\in S}\sum_{b\notin S}(u_{ab}/\sum_n u_{an}F_n^{-1})}{(1/r)\sum_{a\in S}\sum_{b\notin S}(u_{ba}/\sum_n u_{bn}F_n^{-1})}. \tag{A 3}$$

Similarly, let $\mathbf{V} = (v_{ij}) = f_{\mathrm{L}}(\mathbf{W}) = (w_{ij}/\sum_n w_{nj})$. Then for DBB dynamics we have

$$b_{ij} = \frac{w_{ij}F_i}{\sum_n w_{nj}F_n} = \frac{w_{ij}F_i/\sum_n w_{nj}}{\sum_n w_{nj}F_n/\sum_n w_{nj}} = \frac{v_{ij}F_i}{\sum_n v_{nj}F_n}$$

and therefore the forward bias when using $\mathbf{V}$ is given by

$$\frac{P_S^+}{P_S^-} = \frac{\sum_{a\in S}\sum_{b\notin S}(1/N)(v_{ab}F_a/\sum_n v_{nb}F_n)}{\sum_{a\in S}\sum_{b\notin S}(1/N)(v_{ba}F_b/\sum_n v_{na}F_n)} = \frac{r\sum_{a\in S}\sum_{b\notin S}(v_{ab}/\sum_n v_{nb}F_n)}{\sum_{a\in S}\sum_{b\notin S}(v_{ba}/\sum_n v_{na}F_n)}.$$

The proof of the proposition for DBB closely follows the one for BDD given below with $\mathbf{U}$ and f_{R} appropriately replaced by $\mathbf{V}$ and f_{L}.

(i) If $\mathbf{U} \in C_N$, then $\mathbf{U} \sim_{\mathrm{BDD},r} \mathbf{W_H}$

If $\mathbf{U} \in C_N$ then there are only two non-zero elements in each row. In particular, in row i of $\mathbf{U}$ we have that $u_{ii}, u_{ik_i} = \frac{1}{2}$ for some $k_i \neq i$. In the numerator of equation (A 3) for $a \in S$, $b \notin S$ and $k_a \neq a$ we have that for all S

$$\frac{u_{ab}}{\sum_n u_{an}/F_n(S)} = \frac{u_{ab}}{u_{aa}/F_a(S) + u_{ak_a}/F_{k_a}(S)} = \begin{cases} 0 & \text{if } b \neq k_a, \\ \dfrac{1/2}{1/2r + 1/2} & \text{if } b = k_a. \end{cases}$$

Similarly, in the denominator of equation (A 3) for $a \in S$, $b \notin S$ and $k_b \neq b$ we have that for all S

$$\frac{u_{ba}}{\sum_n u_{bn}/F_n(S)} = \frac{u_{ba}}{u_{bb}/F_b(S) + u_{bk_b}/F_{k_b}(S)} = \begin{cases} 0 & \text{if } a \neq k_b, \\ \dfrac{1/2}{1/2 + 1/2r} & \text{if } a = k_b. \end{cases}$$

This means that equation (A 3) for all S can be written as

$$\frac{(x/2)/(1/2r + 1/2)}{(1/r)((y/2)/(1/2 + 1/2r))} = \frac{rx}{y},$$

where $x(y)$ is the number of non-zero u_{ab} (u_{ba}) terms in the numerator (denominator). If we partition the vertices of the digraph of $\mathbf{U}$ into any two sets V_1, V_2 then the number of edges $e(i,j)$ and $e(j,i)$ for $i \in V_1$ and $j \in V_2$ are by definition the same because it is a cycle. This means that for $a \in S$ and $b \notin S$ the number of non-zero u_{ab}, u_{ba} terms in the numerator and denominator, respectively are the same hence $x = y$ and $rx/y = r$ as required. As per lemma A.1, $\mathcal{E}_{\mathrm{BDD},\mathbf{U},r}$ is ρ-equivalent to the Moran process.

(ii) If $\mathbf{U} \sim_{\mathrm{BDD},r} \mathbf{W_H}$ for all $r > 0$, then $\mathbf{U} = \mathbf{W_H}$ or $\mathbf{U} \in \mathcal{C}_N$

By lemma A.1, the forward bias (A 3) is equal to r for all $S \subset \{1, \ldots, N\}$ giving

$$\left.\begin{aligned}\sum_{a\in S}\sum_{b\notin S}\frac{u_{ab}}{\sum_n u_{an}/F_n} &= \sum_{a\in S}\sum_{b\notin S}\frac{u_{ba}}{\sum_n u_{bn}/F_n} \Rightarrow\\ \sum_{a\in S}\frac{\sum_{b\notin S}u_{ab}}{\sum_{j\notin S}u_{aj} + (1/r)\sum_{i\in S}u_{ai}} &= \sum_{b\notin S}\frac{\sum_{a\in S}u_{ba}}{\sum_{j\notin S}u_{bj} + (1/r)\sum_{i\in S}u_{bi}}.\end{aligned}\right\} \tag{A 4}$$

Note that if $r = 1$, (A 4) holds for all $\mathbf{U} \in W_{\mathrm{C}}$. From now, we will consider $r \neq 1$ only. For clarity, the remainder of this section of the proof is broken down into the following six steps.

Step 1. Derivation of general state-dependent row-sum equation.

Let $U(a,S) = \sum_{i\in S} u_{ai}$, i.e. $1 - U(a,S) = \sum_{j\notin S} u_{aj}$. Equation (A 4) thus becomes

$$\left.\begin{aligned}\sum_{a\in S}\frac{1-U(a,S)}{1-U(a,S)+U(a,S)/r} &= \sum_{b\notin S}\frac{U(b,S)}{1-U(b,S)+U(b,S)/r} \Rightarrow\\ \sum_{a\in S}\frac{1}{1+U(a,S)(1/r-1)} &= \sum_{n=1}^{N}\frac{U(n,S)}{1+U(n,S)(1/r-1)}.\end{aligned}\right\} \tag{A 5}$$

The above equation can be written as a Taylor series as follows:

$$\left.\begin{aligned}\sum_{a\in S}\sum_{k=0}^{\infty}(-1)^k\left(\frac{1}{r}-1\right)^k[U(a,S)]^k &= \sum_{n=1}^{N}U(n,S)\sum_{k=0}^{\infty}(-1)^k\left(\frac{1}{r}-1\right)^k[U(n,S)]^k \Rightarrow\\ \sum_{k=0}^{\infty}\sum_{a\in S}\left(1-\frac{1}{r}\right)^k[U(a,S)]^k &= \sum_{k=0}^{\infty}\sum_{n=1}^{N}\left(1-\frac{1}{r}\right)^k[U(n,S)]^{k+1}\end{aligned}\right\} \tag{A 6}$$

For equation (A 6) to hold for all r the coefficients of $(1-1/r)^k$ should be same, that is, for all k

$$\sum_{a\in S}[U(a,S)]^k = \sum_{n=1}^{N}[U(n,S)]^{k+1}. \tag{A 7}$$

Step 2. The diagonal of $\mathbf{U}$ consists of non-zero elements.

Consider the state $S = \{a\}$ then equation (A 7) gives

$$u_{aa}^k = \sum_{n=1}^{N} u_{na}^{k+1}. \tag{A 8}$$

If $u_{aa} = 0$ or 1, then (A 8) implies that all off-diagonal terms in column n are zero which is a contradiction with $\mathbf{W}$ (and thus also $\mathbf{U} = f_{\mathrm{R}}(\mathbf{W})$) being strongly connected, which means that $0 < u_{aa} < 1$.

Step 3. The nth column of $\mathbf{U}$ contains m_n non-zero elements, all equal to $1/m_n$.

Since $0 < u_{aa} < 1$, we can divide equation (A 8) by u_{aa}^k giving

$$1 = \sum_{n=1}^{N} u_{na} \left(\frac{u_{na}}{u_{aa}}\right)^k. \tag{A 9}$$

We have that

$$\lim_{k\to\infty} \left(\frac{u_{na}}{u_{aa}}\right)^k = \begin{cases} \infty & u_{na} > u_{aa}, \\ 1 & u_{na} = u_{aa}, \\ 0 & u_{na} < u_{aa}, \end{cases}$$

and therefore (A 9) implies that $0 \le u_{na} \le u_{aa}$. There must be $n \ne a$ such that $u_{na} = u_{aa}$ as otherwise, by (A 9), we would have $u_{aa} = 1$. Let $\mathcal{C}_a = \{i : u_{ia} = u_{aa}\}$. (A 9) becomes

$$1 = \left(\sum_{i\in\mathcal{C}_a} u_{aa}\right) + \left(\sum_{j\notin\mathcal{C}_a} \frac{u_{ja}^{k+1}}{u_{aa}^k}\right) = |\mathcal{C}_a| u_{aa} + \left(\sum_{j\notin\mathcal{C}_a} \frac{u_{ja}^{k+1}}{u_{aa}^k}\right). \tag{A 10}$$

As $k \to \infty$, (A 10) implies that $u_{aa} = 1/|\mathcal{C}_a|$. Thus, again by (A 10), $u_{ja} = 0$ for all $j \notin \mathcal{C}_a$. This means that in column n of $\mathbf{U}$ there should be $m_n = |\mathcal{C}_n|$ with $2 \le m_n \le N$ non-zero elements, including u_{nn}, that are all equal to $1/m_n$.

Step 4. m_n is the same for all n.

Considering state $S = \{i, j\}$ and using $u_{aa} = 1/m_a$, (A 7) can be written as follows:

$$(u_{ii} + u_{ij})^k + (u_{ji} + u_{jj})^k = \alpha \frac{1}{m_i^{k+1}} + \beta \frac{1}{m_j^{k+1}} + \gamma \left(\frac{1}{m_i} + \frac{1}{m_j}\right)^{k+1}, \tag{A 11}$$

where α, β, γ are the number of rows where $1/m_i$ is adjacent to 0, 0 is adjacent to $1/m_j$, and $1/m_i$ is adjacent to $1/m_j$ in columns i and j, respectively. More precisely, α is the cardinality of the set $K_{ij}^i = \{n : u_{ni} = 1/m_i, u_{nj} = 0\}$, β is the cardinality of the set $K_{ij}^j = \{n : u_{ni} = 0, u_{nj} = 1/m_j\}$ and γ is the cardinality of the set $K_{ij}^{ij} = \{n : u_{ni} = 1/m_i, u_{nj} = 1/m_j\}$.

As $\mathcal{C}_i = K_{ij}^i \cup K_{ij}^{ij}$ and $\mathcal{C}_j = K_{ij}^j \cup K_{ij}^{ij}$, we have that $m_i = \alpha + \gamma$ and $m_j = \beta + \gamma$. Since $K_{ij}^i, K_{ij}^j, K_{ij}^{ij}$ are disjoint, we have $\alpha + \beta + \gamma \le N$. Now, consider the different possibilities we can have on the left-hand side of equation (A 11).

Case 1: $u_{ii} = 1/m_i$, $u_{ij} = 0$ in row i and $u_{ji} = 1/m_i$, $u_{jj} = 1/m_j$ in row j. Thus $\alpha, \gamma \ge 1$ and therefore equation (A 11) gives

$$\frac{1}{m_i^k} + \left(\frac{m_i + m_j}{m_i m_j}\right)^k = \frac{\alpha}{m_i^{k+1}} + \frac{\beta}{m_j^{k+1}} + \gamma \left(\frac{m_i + m_j}{m_i m_j}\right)^{k+1} \Rightarrow$$

$$\frac{1}{(\alpha+\gamma)^k} + \left(\frac{\alpha+\beta+2\gamma}{(\alpha+\gamma)(\beta+\gamma)}\right)^k = \frac{\alpha}{(\alpha+\gamma)^{k+1}} + \frac{\beta}{(\beta+\gamma)^{k+1}} + \gamma \left(\frac{\alpha+\beta+2\gamma}{(\alpha+\gamma)(\beta+\gamma)}\right)^{k+1} \Rightarrow$$

$$\frac{(\beta+\gamma)^k + (\alpha+\beta+2\gamma)^k}{[(\alpha+\gamma)(\beta+\gamma)]^k} = \frac{\alpha(\beta+\gamma)^{k+1} + \beta(\alpha+\gamma)^{k+1} + \gamma(\alpha+\beta+2\gamma)^{k+1}}{[(\alpha+\gamma)(\beta+\gamma)]^{k+1}} \Rightarrow$$

$$(\beta+\gamma)^k + (\alpha+\beta+2\gamma)^k = \frac{\alpha(\beta+\gamma)^{k+1} + \beta(\alpha+\gamma)^{k+1} + \gamma(\alpha+\beta+2\gamma)^{k+1}}{(\alpha+\gamma)(\beta+\gamma)} \Rightarrow$$

$$(\beta+\gamma)^k + (\alpha+\beta+2\gamma)^k = \frac{\alpha(\beta+\gamma)^k}{\alpha+\gamma} + \frac{\beta(\alpha+\gamma)^k}{\beta+\gamma} + \frac{(\alpha\gamma+\beta\gamma+2\gamma^2)(\alpha+\beta+2\gamma)^k}{\alpha\beta+\alpha\gamma+\beta\gamma+\gamma^2} \Rightarrow$$

$$\frac{\gamma(\beta+\gamma)^k}{\alpha+\gamma} = \frac{\beta(\alpha+\gamma)^k}{\beta+\gamma} + \frac{(\gamma^2-\alpha\beta)(\alpha+\beta+2\gamma)^k}{\alpha\beta+\alpha\gamma+\beta\gamma+\gamma^2}.$$

As $k \to \infty$, we get $(\beta+\gamma)^k \ne (\alpha+\gamma)^k \pm (\alpha+\beta+2\gamma)^k$ since $\alpha+\beta+2\gamma > \beta+\gamma$, $\alpha+\gamma$ hence we want $\gamma^2 = \alpha\beta$ to get rid off $(\alpha+\beta+2\gamma)^k$. This implies that $\beta+\gamma = \alpha+\gamma \Rightarrow \alpha = \beta \Rightarrow \alpha = \beta = \gamma$ giving $m_i = m_j$.

Case 2: $u_{ii}=1/m_i,\ u_{ij}=1/m_j$ in row i and $u_{ji}=0,\ u_{jj}=1/m_j$ in row j. This case is symmetrical to Case 1 and therefore we get that $\alpha=\beta=\gamma$ giving $m_i=m_j$.

Case 3: $u_{ii}=1/m_i,\ u_{ij}=1/m_j$ in row i and $u_{ji}=1/m_i,\ u_{jj}=1/m_j$ in row j. Thus $\gamma\geq 2$ and therefore equation (A 11) gives

$$\begin{aligned}
2\left(\frac{m_i+m_j}{m_im_j}\right)^k &= \frac{\alpha}{m_i^{k+1}}+\frac{\beta}{m_j^{k+1}}+\gamma\left(\frac{m_i+m_j}{m_im_j}\right)^{k+1} \Rightarrow\\
2\left(\frac{\alpha+\beta+2\gamma}{(\alpha+\gamma)(\beta+\gamma)}\right)^k &= \frac{\alpha(\beta+\gamma)^{k+1}+\beta(\alpha+\gamma)^{k+1}+\gamma(\alpha+\beta+2\gamma)^{k+1}}{[(\alpha+\gamma)(\beta+\gamma)]^{k+1}} \Rightarrow\\
2(\alpha+\beta+2\gamma)^k &= \frac{\alpha(\beta+\gamma)^{k+1}+\beta(\alpha+\gamma)^{k+1}+\gamma(\alpha+\beta+2\gamma)^{k+1}}{(\alpha+\gamma)(\beta+\gamma)} \Rightarrow\\
2(\alpha+\beta+2\gamma)^k &= \frac{\alpha(\beta+\gamma)^k}{\alpha+\gamma}+\frac{\beta(\alpha+\gamma)^k}{\beta+\gamma}+\frac{(\alpha\gamma+\beta\gamma+2\gamma^2)(\alpha+\beta+2\gamma)^k}{\alpha\beta+\alpha\gamma+\beta\gamma+\gamma^2} \Rightarrow\\
\frac{(2\alpha\beta+\alpha\gamma+\beta\gamma)(\alpha+\beta+2\gamma)^k}{\alpha\beta+\alpha\gamma+\beta\gamma+\gamma^2} &= \frac{\alpha(\beta+\gamma)^k}{\alpha+\gamma}+\frac{\beta(\alpha+\gamma)^k}{\beta+\gamma}.
\end{aligned}$$

As $k\rightarrow\infty$, we get $(\alpha+\beta+2\gamma)^k\neq(\beta+\gamma)^k+(\alpha+\gamma)^k$ since $\alpha+\beta+2\gamma>\beta+\gamma,\ \alpha+\gamma$ hence we want $2\alpha\beta+\alpha\gamma+\beta\gamma=0\Rightarrow\alpha,\beta=0$ giving $m_i=m_j$.

Case 4: $u_{ii}=1/m_i,\ u_{ij}=0$ in row i and $u_{ji}=0,\ u_{jj}=1/m_j$ in row j. Thus $\alpha,\beta\geq 1$ and therefore equation (A 11) gives

$$\begin{aligned}
\frac{1}{m_i^k}+\frac{1}{m_j^k} &= \frac{\alpha}{m_i^{k+1}}+\frac{\beta}{m_j^{k+1}}+\gamma\left(\frac{m_i+m_j}{m_im_j}\right)^{k+1} \Rightarrow\\
\frac{1}{(\alpha+\gamma)^k}+\frac{1}{(\beta+\gamma)^k} &= \frac{\alpha}{(\alpha+\gamma)^{k+1}}+\frac{\beta}{(\beta+\gamma)^{k+1}}+\gamma\left(\frac{\gamma+\beta+2\gamma}{(\alpha+\gamma)(\beta+\gamma)}\right)^{k+1} \Rightarrow\\
\frac{(\beta+\gamma)^k+(\alpha+\gamma)^k}{[(\alpha+\gamma)(\beta+\gamma)]^k} &= \frac{\alpha(\beta+\gamma)^{k+1}+\beta(\alpha+\gamma)^{k+1}+\gamma(\alpha+\beta+2\gamma)^{k+1}}{[(\alpha+\gamma)(\beta+\gamma)]^{k+1}} \Rightarrow\\
(\beta+\gamma)^k+(\alpha+\gamma)^k &= \frac{\alpha(\beta+\gamma)^{k+1}+\beta(\alpha+\gamma)^{k+1}+\gamma(\alpha+\beta+2\gamma)^{k+1}}{(\alpha+\gamma)(\beta+\gamma)} \Rightarrow\\
(\beta+\gamma)^k+(\alpha+\gamma)^k &= \frac{\alpha(\beta+\gamma)^k}{\alpha+\gamma}+\frac{\beta(\alpha+\gamma)^k}{\beta+\gamma}+\frac{\gamma(\alpha+\beta+2\gamma)^{k+1}}{\alpha\beta+\alpha\gamma+\beta\gamma+\gamma^2}.
\end{aligned}$$

As $k\rightarrow\infty$, we get $0\neq(\alpha+\beta+2\gamma)^k$ since $\alpha,\beta\geq 1$ hence we require that $\gamma=0$ to get an equality.

Conclusion from all the cases above

We see that $m_i\neq m_j$ is potentially possible only in Case 4. However, **U** is strongly connected. If one connects i and j by a path $i=i_0,i_1,i_2,\ldots,i_n=j$, then one has $m_{i_k}=m_{i_{k+1}}$ as i_k and i_{k+1} must fall into Case 1, Case 2 or Case 3. Thus $m_i=m_j$. This implies that every column of **U** has $2\leq m\leq N$ non-zero elements, including u_{nn}, that are all equal to $1/m$. This is also true for every row of **U** because it is right stochastic by definition.

Step 5. There exists state S such that $\mathcal{C}_a=\mathcal{C}_{a'}$ for all $a,a'\in S$.

We can define the state $\mathcal{R}_x=\{n:u_{xn}=u_{xx}\}$ then, by definition, $x\in\mathcal{R}_x$ and $|\mathcal{R}_x|=m$ since there are m non-zero elements in row x of **U**. Consider the state $S=\mathcal{R}_x\setminus\{y\}$ for $y\in\mathcal{R}_x\setminus\{x\}$. For this S (as well as any other state), we have that

$$\left.\begin{array}{ll}\text{if } n\in S \text{ then} & \dfrac{1}{m}\\[2ex] \text{if } n\notin S \text{ then} & 0\end{array}\right\}\leq U(n,S)\leq\frac{\min(m,|S|)}{m}.$$

We can therefore write equation (A 7) in the form

$$\sum_{i=1}^{\min(m,|S|)} \lambda_S(i)\left(\frac{i}{m}\right)^k = \sum_{i=0}^{\min(m,|S|)} \lambda'_S(i)\left(\frac{i}{m}\right)^{k+1} \tag{A 12}$$

where $\lambda_S(i)$ is the number of $U(n,S)$ terms equal to i/m for $n \in S$ and $\lambda'_S(i)$ is the number of $U(n,S)$ terms equal to i/m for $n \in \mathcal{N}$, which means that $\lambda'_S(i) \geq \lambda_S(i)$ for $i \neq 0$. The ratio of the left- and right-hand sides of equation (A 12) should always be equal to one. Therefore, as $k \to \infty$, we require that

$$\lambda_S(i_{\max}) = \lambda'_S(i_{\max})\frac{i_{\max}}{m},$$

where $i_{\max}$ is the largest i such that $\lambda_S(i) > 0$.

We have that $i_{\max} = m-1$ in equation (A 12) because $|S| = m-1$ so $U(x,S) = (m-1)/m$. This means that for state S, as $k \to \infty$, we require that

$$\lambda_S(m-1) = \lambda'_S(m-1)\frac{m-1}{m}.$$

As $\lambda_S(m-1)$ is an integer, $\lambda'_S(m-1)$ has to be a multiple of m and the only possible value that satisfies this criteria is $\lambda'_S(m-1) = m$ hence $\lambda_S(m-1) = m-1$.

As $\lambda'_S(m-1) = m$ there exist m rows $j_1, j_2, \ldots, j_m$ such that $U(j_n, S) = (m-1)/m$, that is, $u_{j_n a} = 1/m$ $\forall a \in S$. This means that $\mathcal{C}_a = \{j_1, j_2, \ldots, j_m\}$ $\forall a \in S$ hence $\mathcal{C}_a = \mathcal{C}_{a'}$ for all $a, a' \in S$.

Step 6. $m = 2$ or $m = N$.

By contradiction, assume that $2 < m < N$. We can consider another state $S' = \mathcal{R}_x \setminus \{z\}$ such that $z \in \mathcal{R}_x \setminus \{x, y\}$. We then have that $i_{\max} = m-1$ in equation (A 12) because $|S'| = m-1$ so $U(x, S') = (m-1)/m$. As before, this means that $\mathcal{C}_a = \mathcal{C}_{a'}$ for all $a, a' \in S'$. Since $x \in S, S'$ and $\mathcal{R}_x = S \cup S'$ we have that $\mathcal{C}_a = \mathcal{C}_{a'}$ for all $a, a' \in \mathcal{R}_x$. For $2 < m < N$ this implies that vertices $i \in \mathcal{R}_x$ are disconnected from $j \in \mathcal{N} \setminus \mathcal{R}_x$ and we therefore have disconnected graph, a contradiction. ■

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