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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 ten 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.

2 1. Introduction

3 When modelling population evolution we are concerned with the spread of heritable
4 characteristics in successive generations. The type of model that is used depends upon whether
5 the population size is assumed to be finite or infinite. The majority of classical evolutionary
6 models (see for example [1, 2]) use infinite populations, although finite population models are
7 also well established, the most important models being those in [3, 4]. These models are stochastic,
8 and are solved using classical Markov chain methodology [5, 6, 7]. See also [8, 9] for an extension
9 to evolutionary games in finite populations.

10 The populations in the models described above, however, were “well-mixed”, i.e. every
11 individual was equally likely to encounter every other individual. Real populations of course
12 contain structural elements, such as geographical location or social relationship, which mean that
13 some pairs individuals are more likely to interact than others. In such circumstances we need to
14 be able to identify distinct individuals (or at least distinct classes of individuals), and considering
15 finite populations is perhaps more natural than infinite ones (although finite structures each
16 containing an infinite number of individuals, so called “island models”, were considered in [10]).
17 In [11] the modelling ideas of [3] were extended to consider such structured populations based
18 upon graphs, known as evolutionary graph theory. This has proved very successful, spawning a
19 large number of papers (for example [12, 13, 14, 15, 16, 17, 18, 19]). For informative reviews see
20 [20, 21].

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

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

41 2. The Model

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

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

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

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

$$54 \quad F_n(S) = \begin{cases} 1 & n \notin S, \\ r \in (0, \infty) & n \in S, \end{cases}$$

55
56 is the fitness of I_n . Here the fitness r of a type A individual is given relative to the fitness of a type
57 B individual assumed to be 1.

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

60 The replacement events may be restricted in the sense that not all individuals can replace
61 one another. To enforce such restrictions, [11] imposed a replacement structure using a weighted
62 directed graph given by the tuple (D, w) where $D = (V, E)$ is a directed graph, with sets V of
63 vertices and E of directed edges, and w is a map that assigns a weight to each edge such that
64 $w : V \times V \rightarrow [0, \infty) : (i, j) \mapsto w_{ij}$. Each vertex $n \in V$ represents I_n therefore $V = \{1, 2, \dots, N\}$ so
65 $|V| = N$. We assume that $(i, j) \in E$ if and only if $w_{ij} > 0$, which indicates that I_i can replace I_j .
66 Note that we allow $w_{ii} > 0$ and therefore I_i can replace itself. All the information contained within
67 the weighted digraph (D, w) is conveniently summarised by the $N \times N$ weighted adjacency
68 matrix $\mathbf{W} = (w_{ij})$ and therefore we will refer to (D, w) using \mathbf{W} , which we call the *replacement*
69 *matrix*.

70 The replacement events are stochastic which means that there is a probability $\tau_{ij} =$
71 $\tau_{ij}(\mathbf{F}(S), \mathbf{W})$ associated with (a copy of) I_i replacing I_j . There are several potential *evolutionary*
72 *dynamics on graphs* that govern how the probability is determined. There three main types of
73 dynamics that are summarised below, see also [21]. We use the convention that I_i is chosen for
74 birth and I_j is chosen for death.

- 75 (i) *Birth-Death (BD)*: I_i is chosen first then I_j . We have that $i \in V$ is chosen with probability
76 b_i and then $(i, j) \in E_i$ is chosen with probability d_{ij} , where E_i are all edges starting in
77 vertex i . d_{ij} is used to signify that there is ‘replacement by death’. Finally, $\tau_{ij} = b_i d_{ij}$.
78 (ii) *Death-Birth (DB)*: I_j is chosen first then I_i . We have that $j \in V$ is chosen with probability
79 d_j and then $(i, j) \in E_j$ is chosen with probability b_{ij} , where E_j are all edges ending in
80 vertex j . b_{ij} is used to signify that there is ‘replacement by birth’. Finally, $\tau_{ij} = d_j b_{ij}$.
81 (iii) *Link (L)*: I_i and I_j are chosen simultaneously. In this case $(i, j) \in E$ is simply chosen with
82 probability τ_{ij} .

83 For each type of these dynamics, the natural selection can, through the fitness parameter, influence
84 either the choice at birth (resulting in adding “B”) or at death (adding “D”). It yields 6 kinds of
85 evolutionary dynamics on graphs summarized in Table 2. These dynamics have been extensively
86 studied, in particular, see [27] for a detailed comparison of them. Of these, the BDB and LB
87 dynamics were used in [11].

88 (a) The fixation probability

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

91 Given that the replacement events are random, the transitions between the states of the
92 population are described by a stochastic process, which we denote \mathcal{E} . The properties of \mathcal{E}
93 can be investigated once the state transition probabilities of moving from state S to S' ,

94 $P_{SS'} = P_{SS'}(*, \mathbf{W}, r)$, are calculated using the replacement probabilities as follows:

$$95 \quad P_{SS'} = \begin{cases} \sum_{i \notin S} \tau_{ij}(\mathbf{F}(S), \mathbf{W}) & \text{if } S' = S \setminus \{j\} \text{ for some } j \in S, \\ \sum_{i \in S} \tau_{ij}(\mathbf{F}(S), \mathbf{W}) & \text{if } S' = S \cup \{j\} \text{ for some } j \notin S, \\ \sum_{\substack{i, j \in S \\ \vee i, j \notin S}} \tau_{ij}(\mathbf{F}(S), \mathbf{W}) & \text{if } S' = S. \end{cases}$$

96
97 The transition probabilities, $P_{SS'}$, satisfy the Markov property because they only depend upon
98 the state S , that is, the probability of transitioning from the present state to another state is
99 independent of any past and future state of the population. The stochastic process $\mathcal{E}_{*, \mathbf{W}, r}$ with
100 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
101 Markov chain $\mathcal{E}_{*, \mathbf{W}, r}$ is part of the class of evolutionary Markov chains described in [28].

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

$$106 \quad \rho_S^A = \sum_{S' \subset \{1, 2, \dots, N\}} P_{SS'} \rho_{S'}^A \quad (2.1)$$

107
108 with boundary conditions $\rho_{\emptyset}^A = 0$ and $\rho_{\mathcal{N}}^A = 1$.

109 As demonstrated in [27], LB and LD dynamics may differ in time scale but they yield the
110 same fixation probabilities when fitness is constant (which is our case). Thus, for our purposes
111 the dynamics are the same and we will thus consider them together and denote them by L.

112 Fixation probability is not the only measure for evolutionary success and we can look at the
113 fixation time [29, 30] as well.

114 (b) The Moran Process

115 The Moran process [3], a stochastic birth-death process on finite fixed homogenous population,
116 can be reconstructed as $\mathcal{E}_{\text{BDB}, \mathbf{W}_H, r}$ for a constant replacement matrix

$$117 \quad \mathbf{W}_H = (1/N)_{i, j}. \quad (2.2)$$

118
119 For any $r \in (0, \infty)$ and any $S \subset \{1, \dots, N\}$, the fixation probability for this process, or *Moran*
120 *probability*, is given by

$$121 \quad \rho_S^A = \begin{cases} \frac{1 - r^{-|S|}}{1 - r^{-N}} & \text{if } r \neq 1, \\ |S|/N & \text{if } r = 1. \end{cases}$$

122
123 We are interested in characterizing graphs (and evolutionary dynamics) that yield the same
124 fixation probabilities as the homogeneous matrix \mathbf{W}_H given in (2.2). We note that for this matrix
125 all of the transition probabilities τ_{ij} take the same value independent of i, j or the dynamics, and
126 consequently the fixation probability under each of the dynamics is the same.

127 (c) Classes of Graphs/ Matrices

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

$$129 \quad W = \{\mathbf{W} : \text{for every } i, j, \text{ there is } n \text{ such that } (\mathbf{W}^n)_{i, j} > 0\}.$$

130
131 This definition means that \mathbf{W} is strongly connected as for any pair of vertices i and j , there is
132 a path (of length n) going from i to j . Unless specified otherwise, we will consider admissible
133 replacement matrices only.

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

$$136 \quad T_n^- = \sum_{j=1}^N w_{jn} \quad \text{and} \quad T_n^+ = \sum_{j=1}^N w_{nj}.$$

137
 138 \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
 139 $i, j \in V$. \mathbf{W} is called *right stochastic* if $T_n^+ = 1$, for all $n \in V$ and it is called *left stochastic* if $T_n^- = 1$,
 140 for all $n \in V$. The sets of all circulations, isothermal matrices, right stochastic matrices, and left
 141 stochastic matrices, respectively are denoted by W_C, W_I, W_R , and W_L respectively.

142 The set C_N denotes the sets of matrices representing *cycles* of length N , more specifically, for
 143 $(w_{ij}) \in C_N$ we have $w_{ii} = 1/2$ for $i = 1, 2, \dots, N$, $w_{i_1 i_2} = \dots = w_{i_n i_{n+1}} = \dots = w_{i_{N-1} i_N} = w_{i_N i_1} =$
 144 $1/2$ for some permutation i_1, i_2, \dots, i_N of the sequence $1, 2, \dots, N$, and $w_{ij} = 0$ otherwise.

145 We also define the maps $f_R : W \rightarrow W_R, f_L : W \rightarrow W_L$, and $f' : W \rightarrow W$ respectively, by

$$146 \quad f_R((w_{ij})) = \left(\frac{w_{ij}}{\sum_n w_{in}} \right), \quad f_L((w_{ij})) = \left(\frac{w_{ij}}{\sum_n w_{nj}} \right), \quad \text{and} \quad f'((w_{ij})) = \left(\frac{w_{ij}}{\sum_{n,k} w_{nk}} \right).$$

147
 148 Note that f_R preserves right stochastic matrices and f_L preserves left stochastic matrices.
 149 Moreover, $f_R(\mathbf{W}) = f_L(\mathbf{W})$ for all $\mathbf{W} \in W_I$. Also, since f' simply involves multiplying \mathbf{W} by
 150 the constant $1/\sum_{n,k} w_{nk}$, it implies that $\mathbf{W} \in W_C \Leftrightarrow f'(\mathbf{W}) \in W_C$.

151 When the dynamics $*$, matrices \mathbf{W}_1 and \mathbf{W}_2 , and fitness r are given, we say that an
 152 evolutionary Markov chain $\mathcal{E}_{*, \mathbf{W}_1, r}$ is ρ -*equivalent* to $\mathcal{E}_{*, \mathbf{W}_2, r}$ if for every $S \subset \{1, \dots, N\}$,
 153 $\rho_S^A(*, \mathbf{W}_1, r) = \rho_S^A(*, \mathbf{W}_2, r)$, in which case we write $\mathbf{W}_1 \sim_{*, r} \mathbf{W}_2$.

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

$$156 \quad M_* = \{\mathbf{W} : \mathbf{W} \sim_{*, r} \mathbf{W}_H \text{ for all } r > 0\}.$$

158 3. Results

159 The map f_R preserves the equivalence classes of BDB and BDD dynamics, f_L preserves the
 160 equivalence classes of DBB and DBD dynamics and f' preserves the equivalence classes for link
 161 dynamics. Specifically, as one can see from the proofs in the Appendix, for any \mathbf{W} and any $r > 0$

$$162 \quad \mathbf{W} \sim_{\text{BDB}, r} f_R(\mathbf{W}), \quad (3.1)$$

$$163 \quad \mathbf{W} \sim_{\text{BDD}, r} f_R(\mathbf{W}),$$

$$164 \quad \mathbf{W} \sim_{\text{DBD}, r} f_L(\mathbf{W}),$$

$$165 \quad \mathbf{W} \sim_{\text{DBB}, r} f_L(\mathbf{W}),$$

$$166 \quad \mathbf{W} \sim_{L, r} f'(\mathbf{W}).$$

167
 168 We thus obtain the following results, which completely specify the graphs which are equivalent
 169 to the homogeneous matrix \mathbf{W}_H for each of our evolutionary dynamics.

170 **Proposition 1** (Link). $M_L = W_C$. More precisely, the following statements are equivalent:

- 171 (a) \mathbf{W} is a circulation.
- 172 (b) For all $r > 0$, $\mathbf{W} \sim_{L, r} \mathbf{W}_H$.
- 173 (c) There is $r > 0$ such that $\mathbf{W} \sim_{L, r} \mathbf{W}_H$.

174 We note that $W_C = f'^{-1}(W_C) = \{\mathbf{W} : f'(\mathbf{W}) \in W_C\}$ and thus, similarly to Proposition 2
 175 below, Proposition 1 can be written as $M_L = f'^{-1}(W_C)$.

176 **Proposition 2** (BDB and DBD). $M_{BDB} = f_R^{-1}(W_C)$ and $M_{DBD} = f_L^{-1}(W_C)$. More precisely, the
177 following statements are equivalent:

- 178 (a) $f_R(\mathbf{W})$ is a circulation.
179 (b) For all $r > 0$, $\mathbf{W} \sim_{BDB,r} \mathbf{W}_H$.
180 (c) There is $r > 0$ such that $\mathbf{W} \sim_{BDB,r} \mathbf{W}_H$

181 The equivalent conditions for DBD are similar to the above for BDB but f_R is replaced by f_L .

182 **Proposition 3** (BDD and DBB). $M_{BDD} = f_R^{-1}(\{\mathbf{W}_H\} \cup C_N)$ and $M_{DBB} = f_L^{-1}(\{\mathbf{W}_H\} \cup C_N)$.
183 More precisely, the following statements are equivalent:

- 184 (a) $f_R(\mathbf{W}) = \mathbf{W}_H$ or $f_R(\mathbf{W}) \in C_N$.
185 (b) For all $r > 0$, $\mathbf{W} \sim_{BDD,r} \mathbf{W}_H$.

186 The equivalent conditions for DBB are similar to the above for BDD but f_R is replaced by f_L .

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

188 Note that unlike in Propositions 1 and 2, Proposition 3 does not contain “any r implies all r ”.
189 In fact, when $r = 1$, there is no selection and thus the dynamics BDB and BDD are the same (and
190 also the dynamics DBB and DBD are the same). Consequently, by Proposition 2,

$$191 \quad \mathbf{W} \sim_{BDD,1} \mathbf{W}_H \Leftrightarrow f_R(\mathbf{W}) \in W_C \Leftrightarrow \mathbf{W} \in M_{BDB},$$

$$192 \quad \mathbf{W} \sim_{DBB,1} \mathbf{W}_H \Leftrightarrow f_L(\mathbf{W}) \in W_C \Leftrightarrow \mathbf{W} \in M_{DBD}.$$

194 (a) Our results in the context of known results

195 For the LB dynamics, Proposition 1 was stated and proved in [11] as the Circulation theorem. For
196 the LD dynamics, Proposition 1 follows from the Circulation theorem and the result of [27] that
197 the fixation probabilities for LB and LD are the same.

198 As shown in Appendix (a), BDB is the same as the LB dynamics for right stochastic matrices
199 (in particular, for BDB dynamics, Proposition 2 can be seen as the Isothermal theorem from [11]).
200 Proposition 2 thus follows from Proposition 1 thanks to (3.1). The natural symmetries between f_R
201 and f_L and BDB and DBD dynamics allow us to extend the Isothermal theorem to DBD dynamics
202 as well (see also [31]).

203 Overall, Propositions 1 and 2 and the occurrence of W_C within them are consistent with the
204 claim made in [11] that the circulation criterion completely classifies all replacement matrices
205 where $\mathcal{E}_{*,\mathbf{W},r}$ is ρ -equivalent to a Moran process.

206 Our most important new result is Proposition 3. It shows that the BDD and DBB dynamics
207 require very strict conditions to yield the Moran process. Either the population structure is
208 homogeneous, or it is a directed cycle. This latter structure is an interesting theoretical example,
209 but is unlikely to apply to real populations, meaning that the homogeneous population is
210 practically the only way to get the Moran process for a realistic population.

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

212 Proposition 3 by definition requires that $w_{ii} > 0 \forall i = 1, 2, \dots, N$. Without such self-loops,
213 $\mathcal{E}_{BDD,\mathbf{W},r}, \mathcal{E}_{DBB,\mathbf{W},r}$ cannot ever be ρ -equivalent to the Moran process. The ability of an
214 individual to replace itself therefore plays an important role in the replacement structure of the
215 population and cannot be discounted. For BD dynamics, when increasing the diagonal weights
216 of \mathbf{W} , the fixation probability decreases for BDB and increases for BDD. For DB dynamics, the
217 increase in fixation probability DBB is greater than that for DBD. For LB dynamics, the fixation
218 probability remains the same.

219 With BDD and DBB evolutionary dynamics on graphs one may encounter the following
220 problems if there are no self-loops. For DBB dynamics, a type A individual with almost infinite
221 fitness still has a fixation probability bounded away from 1 because even type A individuals
222 can be randomly picked for death and replaced by type B individuals [32, page 245]. With self-
223 loops, however, a type A individual will almost always be replaced by itself (or another type A
224 individual) and therefore has a fixation probability approaching 1. Similarly, for BDD dynamics,
225 a type A individual with almost zero fitness does not have near probability 0 of fixating as type
226 A individuals can be randomly picked for birth and replace type B individuals [32, page 245].
227 With self-loops, such an individual will almost always pick itself (or another type A) to replace
228 and therefore its fixation probability is near 0. Thus the inclusion of self-loops removes some
229 problematic features of the BDD and DBB dynamics, and makes them more attractive dynamics
230 to use in models.

231 4. Discussion

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

241 This fixation probability depends upon the fitnesses of the two types of individuals, but
242 can also be heavily influenced by the population structure as given by the weights, and by
243 the evolutionary dynamics used. These effects are commonly observed, although in some
244 circumstances evolution proceeds as if as on a well-mixed population as from the original work of
245 [3], dependent only upon the fitnesses of the two types, and some important results in this regard
246 were already given in [11]. The aim of this paper was to provide a generalised set of conditions
247 for when this would be the case.

248 By defining what is meant by fixation-equivalence to the Moran process, we provided a general
249 result which, independent of the specific dynamics used, helps identify graphs that do not affect
250 the fixation probability. With respect to each of the standard dynamics, we then classified sets of
251 evolutionary graphs that have the same fixation probability as the Moran process (or well mixed
252 population). These sets include graphs that are circulations and therefore generalises the work of
253 [11].

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

260 Presenting evolutionary dynamics on graphs in the way that we have allows one to incorporate
261 a variety of dynamics in their analysis, both of standard type and other definitions. This will
262 improve our understanding of dynamics on graphs in general. We note that the list of dynamics
263 in Table 2 is not exhaustive. For example, [33] used imitation dynamics, which is a class of DBB
264 dynamics with an additional requirement $w_{ii} > 0 \forall i$, and [34] consolidates the BDB and DBD
265 dynamics such that one is chosen with a given probability.

266 In general the inclusion of non-zero self weights, in contrast to many earlier evolutionary
267 graph theory works, allows for a greater flexibility of modelling. We note that this is consistent
268 with the original work of [3], which allowed self-replacement as an integral part of the process.
269 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.

Conflict of interests. We have no competing interests.

Author's contributions. KP developed the original concept in discussion with MB, and carried out the majority of the analysis and writing. MB, JR and LJS have all been closely involved in refining the paper in terms of both analysis and presentation. In particular JR did significant work on the proofs, MB on the Introduction/Discussion and LJS on the scientific presentation. All authors gave final approval for publication.

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363 Appendix

364 A. Proofs

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

366 For BDB dynamics we have $\tau_{ij} = b_i d_{ij}$. By definition $\sum_{ij} b_i d_{ij} = 1$, we can therefore write this as
 367 $\tau_{ij} = b_i d_{ij} / \sum_{n,k} b_n d_{n,k}$. Substituting $b_i = F_i / \sum_{m=1}^N F_m$ gives

$$368 \tau_{ij} = \frac{d_{ij} F_i / \sum_{m=1}^N F_m}{\sum_{n,k} (d_{nk} F_n / \sum_{m=1}^N F_m)} = \frac{d_{ij} F_i}{\sum_{n,k} d_{nk} F_n}.$$

369

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

374 (b) Lemma 1 (Forward Bias)

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

$$380 P_S^+ = \sum_{n \notin S} P_{S, S \cup \{n\}} \quad \text{and} \quad P_S^- = \sum_{n \in S} P_{S, S \setminus \{n\}}.$$

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

- 384 • $P_{S, S'} > 0$ only if S and S' differ in at most one element
- 385 • for every $S \neq \emptyset, \{1, \dots, N\}$, there are S^+ and S^- such that $|S^+| = |S| + 1$ and $|S^-| = |S| - 1$
 386 and $P_{S, S^+} > 0, P_{S, S^-} > 0$.

387 Then, the following are equivalent

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

$$389 \rho_S^A = \begin{cases} \frac{1 - c^{-|S|}}{1 - c^{-N}} & \text{if } c \neq 1, \\ |S|/N & \text{if } c = 1 \end{cases}$$

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

$$392 P_S^+ / P_S^- = d.$$

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

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

$$396 r \sum_{a \in S} \sum_{b \notin S} w_{ab} / \sum_{a \in S} \sum_{b \notin S} w_{ba},$$

398 which is what one gets when using Link dynamics, or BDB dynamics if $\mathbf{W} \in W_R$. Note that in
 399 Lemma 1 the forward bias is defined independent of the dynamics and therefore applies to all
 400 dynamics that satisfy the assumptions.

401 *Proof.* “(a) \Rightarrow (b)”: Take any $S \subset \{1, 2, \dots, N\}$. It is known that

$$402 \rho_S^A = \sum_{S'} P_{S, S'} \rho_{S'}^A = P_{S, S} \rho_S^A + \sum_{n \notin S} \left(P_{S, S \cup \{n\}} \rho_{S \cup \{n\}}^A \right) + \sum_{n \in S} \left(P_{S, S \setminus \{n\}} \rho_{S \setminus \{n\}}^A \right)$$

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

$$405 0 = \sum_{n \notin S} \left(P_{S, S \cup \{n\}} \left(\rho_{S \cup \{n\}}^A - \rho_S^A \right) \right) + \sum_{n \in S} \left(P_{S, S \setminus \{n\}} \left(\rho_{S \setminus \{n\}}^A - \rho_S^A \right) \right). \quad (\text{A } 1)$$

406

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

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

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

409

410

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

$$0 = (|S| + 1 - |S|) P_S^+ + (|S| - 1 - |S|) P_S^- \Rightarrow P_S^+ / P_S^- = 1.$$

412

413

414 “(b) \Leftarrow (a)”: The state transition matrix $\mathbf{S} = (P_{S,S'})$ can be scaled to give $\mathbf{S}' = (P'_{S,S'})$ such that
 415 $P'_{S,S} = 0$ 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.
 416 The fixation probability ρ_S^A will be the same whether \mathbf{S}' or \mathbf{S} is used. This is because equation
 417 (2.1) can be rearranged as follows

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

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

419

420

421 Let $\{\mathcal{S}_0, \mathcal{S}_1, \dots, \mathcal{S}_N\}$ be a partition of the states S such that $S \in \mathcal{S}_i$ if $|S| = i$. The probability
 422 $P_{i,j}(S)$ of transitioning from state $S \in \mathcal{S}_i$ to lumped state \mathcal{S}_j with respect to \mathbf{S}' is

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

423

424

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

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

426

427

428 since the forward bias is equal to d . Equation (A 2) satisfies the necessary and sufficient condition
 429 for the Markov chain with state transition matrix \mathbf{S}' to be lumpable with respect to the partition
 430 $\{\mathcal{S}_0, \mathcal{S}_1, \dots, \mathcal{S}_N\}$ (Theorem 6.3.2 page 124, [35]). Let $\hat{\mathbf{S}} = (P_{i,j})$ be the state transition matrix for
 431 this lumped Markov chain then the probability $P_{i,j}$ of transitioning from lumped states \mathcal{S}_i to \mathcal{S}_j
 432 is given by

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

433

434

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

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

438

439

440 In this case,

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

441

442

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

445 (c) Proposition 1 (Link)

446 The following statements are equivalent:

- 447 (a) \mathbf{W} is a circulation.
 448 (b) For all $r > 0$, $\mathbf{W} \sim_{L,r} \mathbf{W}_H$.
 449 (c) There is $r > 0$ such that $\mathbf{W} \sim_{L,r} \mathbf{W}_H$.
 450 (d) For all $r > 0$ and for all $S \subset \{1, 2, \dots, N\}$, the forward bias of $\mathcal{E}_{L,\mathbf{W},r}$ is r , i.e.

$$P_S^+ / P_S^- = r.$$

- 451
 452
 453 (e) There is $r > 0$ such that for all $a \in \{1, 2, \dots, N\}$, the forward bias of the one element set
 454 $S = \{a\}$ is r , i.e.

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

457 *Proof.* For LB dynamics the forward bias is given by

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

460 For LD dynamics the forward bias is given by

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

463 "(a) \Rightarrow (d)": \mathbf{W} is a circulation i.e. $T_n^+ = T_n^-$ for all $n \in \{1, \dots, N\}$ and thus

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

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

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

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

470 "(d) \Rightarrow (e)" is trivial as (d) is much stronger than (e).

471 "(e) \Rightarrow (a)" Let a and r is fixed. By above calculations of the forward bias, we have

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

474 therefore \mathbf{W} is a circulation.

475 "(d) \Rightarrow (b)" follows from Lemma 1.

476 "(b) \Rightarrow (c)" is trivial.

477 "(c) \Rightarrow (e)" follows from Lemma 1. □

478 (d) Proposition 2 (BDB and DBD)

479 More precisely, the following statements are equivalent:

- 480 (a) $f_R(\mathbf{W})$ is a circulation.
 481 (b) For all $r > 0$, $\mathbf{W} \sim_{\text{BDB},r} \mathbf{W}_H$.
 482 (c) There is $r > 0$ such that $\mathbf{W} \sim_{\text{BDB},r} \mathbf{W}_H$.
 483 (d) For all $r > 0$ and for all $S \subset \{1, 2, \dots, N\}$, the forward bias of $\mathcal{E}_{\text{BDB},\mathbf{W},r}$ is r , i.e.

$$484 \quad P_S^+ / P_S^- = r.$$

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

$$488 \quad \frac{\sum_{b \neq a} P_{\{a\},\{a,b\}}}{P_{a,\emptyset}} = r.$$

490 *Proof.* Let $\mathbf{U} = (u_{ij}) = f_R(\mathbf{W}) = (w_{ij} / \sum_n w_{in})$ then for BDB dynamics the forward bias of
 491 $\mathcal{E}_{\text{BDB},\mathbf{W},r}$ is given by

$$492 \quad \frac{P_S^+}{P_S^-} = \frac{\sum_{a \in S} \sum_{b \notin S} \frac{F_a}{n} \frac{w_{ab}}{\sum_n w_{an}}}{\sum_{a \in S} \sum_{b \notin S} \frac{F_b}{n} \frac{w_{ba}}{\sum_n w_{bn}}} = \frac{r \sum_{a \in S} \sum_{b \notin S} u_{ab}}{\sum_{b \notin S} \sum_{a \in S} u_{ba}}$$

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

495 Similarly, with almost identical working as above, when $\mathbf{V} = f_L(\mathbf{W})$, the forward bias of
 496 $\mathcal{E}_{\text{DBD},\mathbf{W},r}$ is the same as forward bias of $\mathcal{E}_{\text{DBD},\mathbf{V},r}$ and is given by

$$497 \quad \frac{P_S^+}{P_S^-} = \frac{\sum_{a \in S} \sum_{b \notin S} \frac{1/F_b}{n} \frac{w_{ab}}{\sum_n w_{nb}}}{\sum_{a \in S} \sum_{b \notin S} \frac{1/F_a}{n} \frac{w_{ba}}{\sum_n w_{na}}} = \frac{\sum_{a \in S} \sum_{b \notin S} v_{ab}}{\frac{1}{r} \sum_{a \in S} \sum_{b \notin S} v_{ba}}.$$

499 and the proof of the Proposition for DBD closely follows the one for BDB given below with \mathbf{U} and
 500 f_R appropriately replaced by \mathbf{V} and f_L .

501 "(a) \Rightarrow (d)": If $\mathbf{U} = f_R(\mathbf{W}) \in W_C$, i.e. if \mathbf{U} is doubly stochastic, then the forward bias (for $S \neq$
 502 \emptyset, \mathcal{N}) is equal to

$$503 \quad \frac{P_S^+}{P_S^-} = \frac{r \sum_{a \in S} \left(\sum_n (u_{an}) - \sum_{k \in S} (u_{ak}) \right)}{\sum_{a \in S} \left(\sum_n (u_{na}) - \sum_{k \in S} (u_{ka}) \right)} = \frac{r \left(|S| - \sum_{a \in S} \sum_{k \in S} u_{ak} \right)}{|S| - \sum_{a \in S} \sum_{k \in S} u_{ka}} = r$$

506 "(d) \Rightarrow (e)" is trivial as (d) is stronger than (e).

507 "(e) \Rightarrow (a)" Let a and r is fixed. By above calculations of the forward bias, we have

$$508 \quad \sum_{a \in S} \sum_{b \notin S} u_{ab} = \sum_{a \in S} \sum_{b \notin S} u_{ba}.$$

509

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

$$511 \quad \sum_{b \notin S} u_{ab} = \sum_{b \notin S} u_{ba} \Rightarrow -u_{aa} + \sum_{i=1}^N u_{ai} = -u_{aa} + \sum_{i=1}^N u_{ia} \Rightarrow 1 = \sum_{i=1}^N u_{ia}$$

513 is true for all $a = 1, 2, \dots, N$ and therefore \mathbf{U} is doubly stochastic and thus $f_R(\mathbf{W})$ is a circulation.514 "(d) \Rightarrow (b)" follows from Lemma 1.515 "(b) \Rightarrow (c)" is trivial.516 "(c) \Rightarrow (e)" follows from Lemma 1. □517 **(e) Proposition 3 (BDD and DBB)**

518 The following statements are equivalent:

519 (a) $f_R(\mathbf{W}) = \mathbf{W}_H$ or $f_R(\mathbf{W}) \in C_N$.520 (b) For all $r > 0$, $\mathbf{W} \sim_{\text{BDD},r} \mathbf{W}_H$.

521 *Proof.* The replacement probabilities $\tau_{ij}(\mathbf{F}(S), \mathbf{W})$ for BDD dynamics can be rewritten as
 522 $\tau_{ij}(\mathbf{F}(S), \mathbf{U})$ where $\mathbf{U} = (u_{ij}) = f_R(\mathbf{W}) = (w_{ij} / \sum_n w_{in})$ by multiplying the numerator and
 523 denominator with $\sum_n w_{in}$ as follows

$$524 \quad \tau_{ij}(\mathbf{F}(S), \mathbf{W}) = \frac{1}{N} \frac{w_{ij}/F_j(S)}{\sum_n w_{in}/F_n(S)} = \frac{1}{N} \frac{w_{ij}/(F_j(S) \sum_n w_{in})}{\sum_n w_{in}/(F_n(S) \sum_n w_{in})} \Rightarrow$$

$$525 \quad \frac{u_{ij}/F_j(S)}{\sum_n u_{in}/F_n(S)} = \tau_{ij}(\mathbf{F}(S), \mathbf{U})$$

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

$$529 \quad \frac{P_S^+}{P_S^-} = \frac{\sum_{a \in S} \sum_{b \notin S} \frac{1}{N} \frac{u_{ab}/F_b}{\sum_n u_{an}/F_n}}{\sum_{a \in S} \sum_{b \notin S} \frac{1}{N} \frac{u_{ba}/F_a}{\sum_n u_{bn}/F_n}} = \frac{\sum_{a \in S} \sum_{b \notin S} \frac{u_{ab}}{\sum_n u_{an}/F_n}}{r \sum_{a \in S} \sum_{b \notin S} \frac{u_{ba}}{\sum_n u_{bn}/F_n}}. \quad (\text{A } 3)$$

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

$$532 \quad b_{ij} = \frac{w_{ij} F_i}{\sum_n w_{nj} F_n} = \frac{w_{ij} F_i / \sum_n w_{nj}}{\sum_n w_{nj} F_n / \sum_n w_{nj}} = \frac{v_{ij} F_i}{\sum_n v_{nj} F_n}$$

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

$$535 \quad \frac{P_S^+}{P_S^-} = \frac{\sum_{a \in S} \sum_{b \notin S} \frac{1}{N} \frac{v_{ab} F_a}{\sum_n v_{nb} F_n}}{\sum_{a \in S} \sum_{b \notin S} \frac{1}{N} \frac{v_{ba} F_b}{\sum_n v_{na} F_n}} = \frac{r \sum_{a \in S} \sum_{b \notin S} \frac{v_{ab}}{\sum_n v_{nb} F_n}}{\sum_{a \in S} \sum_{b \notin S} \frac{v_{ba}}{\sum_n v_{na} F_n}}.$$

537 The proof of the Proposition for DBB closely follows the one for BDD given below with \mathbf{U} and f_R
 538 appropriately replaced by \mathbf{V} and f_L .

539 **(i) If $\mathbf{U} \in C_N$, then $\mathbf{U} \sim_{\text{BDD},r} \mathbf{W}_H$**

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

542 $k_a \neq a$ we have that for all S

$$543 \quad \frac{u_{ab}}{\sum_n u_{an}/F_n(S)} = \frac{u_{ab}}{u_{aa}/F_a(S) + u_{ak_a}/F_{k_a}(S)} = \begin{cases} 0 & \text{if } b \neq k_a, \\ \frac{1/2}{1/2r+1/2} & \text{if } b = k_a. \end{cases}$$

545 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

$$546 \quad \frac{u_{ba}}{\sum_n u_{bn}/F_n(S)} = \frac{u_{ba}}{u_{bb}/F_b(S) + u_{bk_b}/F_{k_b}(S)} = \begin{cases} 0 & \text{if } a \neq k_b, \\ \frac{1/2}{1/2+1/2r} & \text{if } a = k_b. \end{cases}$$

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

$$549 \quad \frac{x/2}{1/2r+1/2} \bigg/ \frac{1}{r} \frac{y/2}{1/2+1/2r} = rx/y$$

551 where x (y) is the number of nonzero u_{ab} (u_{ba}) terms in the numerator (denominator). If we
552 partition the vertices of the digraph of \mathbf{U} into any two sets V_1, V_2 then the number of edges $e(i, j)$
553 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
554 for $a \in S$ and $b \notin S$ the number of nonzero u_{ab}, u_{ba} terms in the numerator and denominator
555 respectively are the same hence $x = y$ and $rx/y = r$ as required. As per Lemma 1, $\mathcal{E}_{\text{BDD}, \mathbf{U}, r}$ is
556 ρ -equivalent to the Moran process.

557 (ii) If $\mathbf{U} \sim_{\text{BDD}, r} \mathbf{W}_{\mathbf{H}}$ for all $r > 0$, then $\mathbf{U} = \mathbf{W}_{\mathbf{H}}$ or $\mathbf{U} \in \mathcal{C}_N$

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

$$559 \quad \sum_{a \in S} \sum_{b \notin S} \frac{u_{ab}}{\sum_n u_{an}/F_n} = \sum_{a \in S} \sum_{b \notin S} \frac{u_{ba}}{\sum_n u_{bn}/F_n} \Rightarrow$$

$$560 \quad \sum_{a \in S} \frac{\sum_{b \notin S} u_{ab}}{\sum_{j \notin S} u_{aj} + \frac{1}{r} \sum_{i \in S} u_{ai}} = \sum_{b \notin S} \frac{\sum_{a \in S} u_{ba}}{\sum_{j \notin S} u_{bj} + \frac{1}{r} \sum_{i \in S} u_{bi}}. \quad (\text{A } 4)$$

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

564 Step 1: Derivation of general state dependent row-sum equation

565 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

$$566 \quad \sum_{a \in S} \frac{1 - U(a, S)}{1 - U(a, S) + U(a, S)/r} = \sum_{b \notin S} \frac{U(b, S)}{1 - U(b, S) + U(b, S)/r} \Rightarrow$$

$$567 \quad \sum_{a \in S} \frac{1}{1 + U(a, S)(1/r - 1)} = \sum_{n=1}^N \frac{U(n, S)}{1 + U(n, S)(1/r - 1)}. \quad (\text{A } 5)$$

568 Equation (A 5) can be written as a Taylor series as follows

$$570 \quad \sum_{a \in S} \sum_{k=0}^{\infty} (-1)^k (1/r - 1)^k [U(a, S)]^k = \sum_{n=1}^N U(n, S) \sum_{k=0}^{\infty} (-1)^k (1/r - 1)^k [U(n, S)]^k \Rightarrow$$

$$571 \quad \sum_{a \in S} \sum_{k=0}^{\infty} (1 - 1/r)^k [U(a, S)]^k = \sum_{n=1}^N \sum_{k=0}^{\infty} (1 - 1/r)^k [U(n, S)]^{k+1} \quad (\text{A } 6)$$

572

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

$$574 \sum_{a \in S} [U(a, S)]^k = \sum_{n=1}^N [U(n, S)]^{k+1}. \quad (\text{A } 7)$$

576 Step 2: The diagonal of \mathbf{U} consists of non-zero elements

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

$$578 u_{aa}^k = \sum_{n=1}^N u_{na}^{k+1}. \quad (\text{A } 8)$$

579 If $u_{aa} = 0$ or 1 then (A 8) implies that all off-diagonal terms in column n are zero which is a
581 contradiction with \mathbf{W} (and thus also $\mathbf{U} = f_R(\mathbf{W})$) being strongly connected, which means that
582 $0 < u_{aa} < 1$.

583 Step 3: The n^{th} column of \mathbf{U} contains m_n nonzero elements, all equal to $1/m_n$

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

$$585 1 = \sum_{n=1}^N u_{na} \left(\frac{u_{na}}{u_{aa}} \right)^k. \quad (\text{A } 9)$$

586 We have that

$$588 \lim_{k \rightarrow \infty} \left(\frac{u_{na}}{u_{aa}} \right)^k = \begin{cases} \infty & u_{na} > u_{aa}, \\ 1 & u_{na} = u_{aa}, \\ 0 & u_{na} < u_{aa}, \end{cases}$$

589 and therefore (A 9) implies that $0 \leq u_{na} \leq u_{aa}$. There must be $n \neq a$ such that $u_{na} = u_{aa}$ as
591 otherwise, by (A 9), we would have $u_{aa} = 1$. Let $C_a = \{i : u_{ia} = u_{aa}\}$. (A 9) becomes

$$592 1 = \left(\sum_{i \in C_a} u_{aa} \right) + \left(\sum_{j \notin C_a} \frac{u_{ja}^{k+1}}{u_{aa}^k} \right) = |C_a| u_{aa} + \left(\sum_{j \notin C_a} \frac{u_{ja}^{k+1}}{u_{aa}^k} \right). \quad (\text{A } 10)$$

593 As $k \rightarrow \infty$, (A 10) implies that $u_{aa} = 1/|C_a|$. Thus, again by (A 10), $u_{ja} = 0$ for all $j \notin C_a$. This
595 means that in column n of \mathbf{U} there should be $m_n = |C_n|$ with $2 \leq m_n \leq N$ nonzero elements,
596 including u_{nn} , that are all equal to $1/m_n$.

597 Step 4: m_n is the same for all n

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

$$599 (u_{ii} + u_{ij})^k + (u_{ji} + u_{jj})^k = \alpha \frac{1}{m_i^{k+1}} + \beta \frac{1}{m_j^{k+1}} + \gamma \left(\frac{1}{m_i} + \frac{1}{m_j} \right)^{k+1} \quad (\text{A } 11)$$

600 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 $1/m_i$
602 is adjacent to $1/m_j$ in columns i and j respectively. More precisely, α is the cardinality of the
603 set $K_{ij}^i = \{n : u_{ni} = 1/m_i, u_{nj} = 0\}$, β is the cardinality of the set $K_{ij}^j = \{n : u_{ni} = 0, u_{nj} = 1/m_j\}$
604 and γ is the cardinality of the set $K_{ij}^{ij} = \{n : u_{ni} = 1/m_i, u_{nj} = 1/m_j\}$.

605 Since $C_i = K_{ij}^i \cup K_{ij}^{ij}$ and $C_j = K_{ij}^j \cup K_{ij}^{ij}$, we have that $m_i = \alpha + \gamma$ and $m_j = \beta + \gamma$. Since
606 $K_{ij}^i, K_{ij}^j, K_{ij}^{ij}$ are disjoint, we have $\alpha + \beta + \gamma \leq N$. Now, consider the different possibilities we
607 can have on the left-hand side of equation (A 11).

608 **Case 1:**

609 $u_{ii} = 1/m_i, u_{ij} = 0$ in row i and $u_{ji} = 1/m_i, u_{jj} = 1/m_j$ in row j . Thus $\alpha, \gamma \geq 1$ and therefore
 610 equation (A 11) gives

$$\begin{aligned}
 611 \quad \frac{1}{m_i^k} + \left(\frac{m_i + m_j}{m_i m_j}\right)^k &= \frac{\alpha}{m_i^{k+1}} + \frac{\beta}{m_j^{k+1}} + \gamma \left(\frac{m_i + m_j}{m_i m_j}\right)^{k+1} \Rightarrow \\
 612 \quad \frac{1}{(\alpha + \gamma)^k} + \left(\frac{\alpha + \beta + 2\gamma}{(\alpha + \gamma)(\beta + \gamma)}\right)^k &= \frac{\alpha}{(\alpha + \gamma)^{k+1}} + \frac{\beta}{(\beta + \gamma)^{k+1}} + \gamma \left(\frac{\alpha + \beta + 2\gamma}{(\alpha + \gamma)(\beta + \gamma)}\right)^{k+1} \Rightarrow \\
 613 \quad \frac{(\beta + \gamma)^k + (\alpha + \beta + 2\gamma)^k}{[(\alpha + \gamma)(\beta + \gamma)]^k} &= \frac{\alpha(\beta + \gamma)^{k+1} + \beta(\alpha + \gamma)^{k+1} + \gamma(\alpha + \beta + 2\gamma)^{k+1}}{[(\alpha + \gamma)(\beta + \gamma)]^{k+1}} \Rightarrow \\
 614 \quad (\beta + \gamma)^k + (\alpha + \beta + 2\gamma)^k &= \frac{\alpha(\beta + \gamma)^{k+1} + \beta(\alpha + \gamma)^{k+1} + \gamma(\alpha + \beta + 2\gamma)^{k+1}}{(\alpha + \gamma)(\beta + \gamma)} \Rightarrow \\
 615 \quad (\beta + \gamma)^k + (\alpha + \beta + 2\gamma)^k &= \frac{\alpha(\beta + \gamma)^k}{\alpha + \gamma} + \frac{\beta(\alpha + \gamma)^k}{\beta + \gamma} + \frac{(\alpha\gamma + \beta\gamma + 2\gamma^2)(\alpha + \beta + 2\gamma)^k}{\alpha\beta + \alpha\gamma + \beta\gamma + \gamma^2} \Rightarrow \\
 616 \quad \frac{\gamma(\beta + \gamma)^k}{\alpha + \gamma} &= \frac{\beta(\alpha + \gamma)^k}{\beta + \gamma} + \frac{(\gamma^2 - \alpha\beta)(\alpha + \beta + 2\gamma)^k}{\alpha\beta + \alpha\gamma + \beta\gamma + \gamma^2}.
 \end{aligned}$$

618 As $k \rightarrow \infty$, we get $(\beta + \gamma)^k \neq (\alpha + \gamma)^k \pm (\alpha + \beta + 2\gamma)^k$ since $\alpha + \beta + 2\gamma > \beta + \gamma, \alpha + \gamma$ hence
 619 we want $\gamma^2 = \alpha\beta$ to get rid off $(\alpha + \beta + 2\gamma)^k$. This implies that $\beta + \gamma = \alpha + \gamma \Rightarrow \alpha = \beta \Rightarrow \alpha =$
 620 $\beta = \gamma$ giving $m_i = m_j$.

621 **Case 2:**

622 $u_{ii} = 1/m_i, u_{ij} = 1/m_j$ in row i and $u_{ji} = 0, u_{jj} = 1/m_j$ in row j . This case is symmetrical to
 623 Case 1 and therefore we get that $\alpha = \beta = \gamma$ giving $m_i = m_j$.

624 **Case 3:**

625 $u_{ii} = 1/m_i, u_{ij} = 1/m_j$ in row i and $u_{ji} = 1/m_i, u_{jj} = 1/m_j$ in row j . Thus $\gamma \geq 2$ and therefore
 626 equation (A 11) gives

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

633 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
 634 we want $2\alpha\beta + \alpha\gamma + \beta\gamma = 0 \Rightarrow \alpha, \beta = 0$ giving $m_i = m_j$.

635 **Case 4:**

636 $u_{ii} = 1/m_i, u_{ij} = 0$ in row i and $u_{ji} = 0, u_{jj} = 1/m_j$ in row j . Thus $\alpha, \beta \geq 1$ and therefore
 637 equation (A 11) gives

$$\begin{aligned}
 638 \quad 1/m_i^k + 1/m_j^k &= \frac{\alpha}{m_i^{k+1}} + \frac{\beta}{m_j^{k+1}} + \gamma \left(\frac{m_i + m_j}{m_i m_j}\right)^{k+1} \Rightarrow \\
 639 \quad \frac{1}{(\alpha + \gamma)^k} + \frac{1}{(\beta + \gamma)^k} &= \frac{\alpha}{(\alpha + \gamma)^{k+1}} + \frac{\beta}{(\beta + \gamma)^{k+1}} + \gamma \left(\frac{\gamma + \beta + 2\gamma}{(\alpha + \gamma)(\beta + \gamma)}\right)^{k+1} \Rightarrow
 \end{aligned}$$

$$\begin{aligned}
640 \quad & \frac{(\beta + \gamma)^k + (\alpha + \gamma)^k}{[(\alpha + \gamma)(\beta + \gamma)]^k} = \frac{\alpha(\beta + \gamma)^{k+1} + \beta(\alpha + \gamma)^{k+1} + \gamma(\alpha + \beta + 2\gamma)^{k+1}}{[(\alpha + \gamma)(\beta + \gamma)]^{k+1}} \Rightarrow \\
641 \quad & (\beta + \gamma)^k + (\alpha + \gamma)^k = \frac{\alpha(\beta + \gamma)^{k+1} + \beta(\alpha + \gamma)^{k+1} + \gamma(\alpha + \beta + 2\gamma)^{k+1}}{(\alpha + \gamma)(\beta + \gamma)} \Rightarrow \\
642 \quad & (\beta + \gamma)^k + (\alpha + \gamma)^k = \frac{\alpha(\beta + \gamma)^k}{\alpha + \gamma} + \frac{\beta(\alpha + \gamma)^k}{\beta + \gamma} + \frac{\gamma(\alpha + \beta + 2\gamma)^{k+1}}{\alpha\beta + \alpha\gamma + \beta\gamma + \gamma^2}. \\
643
\end{aligned}$$

644 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.

645 **Conclusion from all the cases above**

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

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

652 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
653 are m nonzero elements in row x of \mathbf{U} . Consider the state $S = \mathcal{R}_x \setminus \{y\}$ for $y \in \mathcal{R}_x \setminus \{x\}$. For this
654 S (as well as any other state), we have that

$$\left. \begin{array}{l} \text{if } n \in S \text{ then } 1/m \\ \text{if } n \notin S \text{ then } 0 \end{array} \right\} \leq U(n, S) \leq \frac{\min(m, |S|)}{m}.$$

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

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

660 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
661 $U(n, S)$ 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
662 left-hand side and right-hand side of equation (A 12) should always be equal to one. Therefore,
663 as $k \rightarrow \infty$, we require that

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

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

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

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

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

673 Since $\lambda'_S(m - 1) = m$ there exist m rows j_1, j_2, \dots, j_m such that $U(j_n, S) = (m - 1)/m$, that is,
674 $u_{j_n a} = 1/m \forall a \in S$. This means that $\mathcal{C}_a = \{j_1, j_2, \dots, j_m\} \forall a \in S$ hence $\mathcal{C}_a = \mathcal{C}_{a'}$ for all $a, a' \in S$.

675 **Step 6: $m = 2$ or $m = N$**

676 By contradiction, assume that $2 < m < N$. We can consider another state $S' = \mathcal{R}_x \setminus \{z\}$ such
677 that $z \in \mathcal{R}_x \setminus \{x, y\}$. We then have that $i_{\max} = m - 1$ in equation (A 12) because $|S'| = m - 1$
678 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 $x \in S, S'$
679 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
680 vertices $i \in \mathcal{R}_x$ are disconnected from $j \in \mathcal{N} \setminus \mathcal{R}_x$ and we therefore have disconnected graphs,
681 a contradiction. \square

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}	$= \{1, 2, \dots, N\}$	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 $ V = 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.
τ_{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.

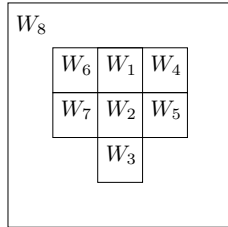
Table 1: Notation used in this paper.

Table 2: List of dynamics used in this paper together with their definition of M_* .

Process	$\mathbb{P}(I_i \text{ replaces } I_j)$	Order chosen	$\mathbb{P}(\text{Chosen first})$	$\mathbb{P}(\text{Chosen second})$	Definition of M_*	Illustration of M_*
BDB [11, 13, 14, 16, 19, 33, 36]	$\tau_{ij} = b_i d_{ij}$	I_i then I_j	$b_i = \frac{F_i(S)}{\sum_n F_n(S)}$	$d_{ij} = \frac{w_{ij}}{\sum_n w_{in}}$	$M_{\text{BDB}} = \{\mathbf{W} : f_R(\mathbf{W}) \in W_C\}$ $= f_R^{-1}(W_C)$	
BDD [27]	$\tau_{ij} = b_i d_{ij}$	I_i then I_j	$b_i = \frac{1}{N}$	$d_{ij} = \frac{w_{ij}/F_j(S)}{\sum_n w_{in}/F_n(S)}$	$M_{\text{BDD}} = \{\mathbf{W} : f_R(\mathbf{W}) \in \{\mathbf{W}_H\} \cup C_N\}$ $= f_R^{-1}(\{\mathbf{W}_H\} \cup C_N)$	
DBD [12, 13, 36, 37]	$\tau_{ij} = d_i b_{ij}$	I_j then I_i	$d_j = \frac{1/F_j(S)}{\sum_n 1/F_n(S)}$	$b_{ij} = \frac{w_{ij}}{\sum_n w_{nj}}$	$M_{\text{DBD}} = \{\mathbf{W} : f_L(\mathbf{W}) \in W_C\}$ $= f_L^{-1}(W_C)$	
DBB [16, 33, 38, 39, 40]	$\tau_{ij} = d_i b_{ij}$	I_j then I_i	$d_j = \frac{1}{N}$	$b_{ij} = \frac{w_{ij} F_i(S)}{\sum_n w_{nj} F_n(S)}$	$M_{\text{DBB}} = \{\mathbf{W} : f_L(\mathbf{W}) \in \{\mathbf{W}_H\} \cup C_N\}$ $= f_L^{-1}(\{\mathbf{W}_H\} \cup C_N)$	
LB [11, 13, 36]	$\tau_{ij} = \frac{w_{ij} F_i(S)}{\sum_{n,k} w_{nk} F_n(S)}$	Simultaneous	N/A	N/A	$M_{\text{LB}} = \{\mathbf{W} : f'(\mathbf{W}) \in W_C\}$ $= f'^{-1}(W_C) = W_C$	
LD [23]	$\tau_{ij} = \frac{w_{ij}/F_j(S)}{\sum_{n,k} w_{nk}/F_k(S)}$	Simultaneous	N/A	N/A	$M_{\text{LD}} = \{\mathbf{W} : f'(\mathbf{W}) \in W_C\}$ $= f'^{-1}(W_C) = W_C$	

Key for Illustration of M_* :

W



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

The key on the left gives the definition of partitions W_1, W_2, \dots, 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 $M_L \cap M_{\text{BDB}} \cap M_{\text{BDD}} \cap M_{\text{DBD}} \cap M_{\text{DBB}} \equiv M_{\text{BDD}} \cap M_{\text{DBB}} \equiv W_1$.