Continuous approximations for the fixation probability of the Moran processes on star graphs

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Abstract

We consider a generalized version of the birth-death (BD) and death-birth (DB) processes introduced by [12], in which two constant fitnesses, one for birth and the other for death, describe the selection mechanism of the population. Rather than constant fitnesses, in this paper we consider more general frequency-dependent fitness functions (allowing any smooth functions) under the weak-selection regime. For a large population structured as a star graph, we provide approximations for the fixation probability which are solutions of certain ODEs (or systems of ODEs). For the DB case, we prove that our approximation has an error of order $1/N$, where $N$ is the size of the population. These approximations are obtained in the same spirit of [7] albeit with quite different techniques. The general BD and DB processes contain, as special cases, the BD-* and DB-* (where * can be either B or D) processes described in [10] — this class includes many examples of update rules used in the literature.

1 Introduction

1.1 Background

The use of stochastic processes to understand the evolutionary dynamics goes back at least to Galton [22], who devised a process to model the extinction of aristocratic
family names, and that today bears his name. Early in the twentieth century, Wright
and Fisher introduced a stochastic process that was a watershed in the study of mathemati-
cal population genetics — now known as the Wright-Fisher (WF) process [21, 24].

Later on, in the early sixties, Moran devised a simplified process as alternative to the
WF process: a birth-death process now known as the Moran process [16]. The Moran
process considers a finite well-mixed population where each individual can interact
with every other individual, with two types (or traits), and such that mutations are
not considered. As a result, two homogeneous states turn out to be absorbing, i.e.,
the dynamics eventually reaches one of them — when this happens we say that the
corresponding type has fixed. This can also be considered as a special case of the
Kimura class of processes studied in [8], and for processes in this class an important
issue is the computation of the fixation probability — i.e. the probability that a given
type will fix conditional on the current state of the population.

Although the original Moran process only considers constant fitnesses, the more
recent versions involve frequency dependent fitnesses — cf. [13, 6, 1, 14, 18, 20, 21].
The classical Moran process and other models that assume well-mixed populations can
be seen as an interacting population dynamics on complete graphs, in which any pair
of individuals can be in interaction with each other. However when the interactions are
restricted to certain pairs of individuals, this can be generalized to the spatial model,
where the interaction can only occur between two neighbours in a given graph.

The use of well-mixed populations has been studied as early as the results in [9, 17,
2]. In 2005, [13] brought the study of population dynamics on graphs to the mainstream
of evolutionary game theory.

The computation of the fixation probability in this framework is more involved
though — [13] identified the class of isothermal graphs, which are a subset of regular
graphs for which the fixation probability can be calculated in a similar way to the
complete graph. Due to this difficulty, [13] studied the fixation probability when there
is only one mutant in a star graph (invasion probability), and found an approximation
when the fitness is constant and the number of leaves is large. [3] found the exact
formula for the invasion probability in a star graph and its asymptotics revisiting the
asymptotic results in [13]. The latter computation was amended in [5]. The exact
formula for the fixation probability for any initial state was later given in [15].

In addition, comparing an evolutionary process on a graph (and its invasion prob-
ability) with the related process on the complete graph, [13] introduced the notion of
accelerator or suppressor graphs, and proved that the star graphs with the BD update
mechanism are accelerators of evolution, i.e. they amplify the rate of the natural selec-
tion. Nevertheless, later on, [12, 11] proved that the DB processes on the star graphs
are evolutionary suppressors rather than accelerators.

The aim of this work is to provide continuous approximations for the fixation prob-
ability in star graphs, when the population is large — this is much in the spirit of [2],
but the techniques used here will be quite different. Instead of constant fitnesses as in
[12] or linear function as in evolutionary game theory, in this paper we consider much
more general frequency-dependent fitness functions (one for birth and one for death)
that can be any smooth functions under the weak-selection regime. It should be em-
phasized that although continuous approximations are provided, no infinite population
limit is considered here.

1.2 Outline

The paper is organized as follows. Section 2 presents the preliminaries, sets the problem and also contains the statement of our main result, that is, a continuous approximation for the fixation probability of star graphs in the DB process with error of order $1/N$. In Section 3 we find continuous approximation candidates for both BD and DB processes. In Section 4 we prove, in the case of the DB process, that the continuous approximation candidate found in Section 3 approximates with error of order $1/N$. Section 5 presents different numerical examples showing that the approximations found in Section 3 for both DB and BD processes, are very close to the fixation probability. Finally, in Section 6 we analyze the asymptotic qualitative behavior of a structured population as a star graph when the fitness is a linear function given by a pay-off matrix, and we also analyze the invasion probability.

1.3 On the notations used

In the following, we write $M = [m_{ij}]$ to denote a matrix in $\mathbb{R}^{n \times n}$, and $M^t$ for the transpose of $M$. We also write $|\cdot|$ for the vector infinity norm in $\mathbb{R}^n$ and $\|\cdot\|$ to denote the corresponding matrix norm, which is given by $\|M\| = \max_{1 \leq i \leq n} \sum_{j=1}^n |m_{ij}|$, i.e., the maximum absolute row sum of the matrix. It will be convenient to regard a vector $v$ as a matrix in $\mathbb{R}^{n \times 1}$, whose entries will be written as $v_{i1} := v_i$. Also, we denote by $I_n$ the $n \times n$ identity matrix. We drop the subscript when it is clear.

2 Evolutionary dynamics in graphs

2.1 Preliminaries

Consider a finite population of $N$ individuals divided into two types (traits), $A$, the wild-type or resident, and $B$, the mutant. Assume that each sub-population is homogeneous, i.e. there is no advantage of any particular individual with respect to others with the same type. The number of individuals is always assumed to be constant. The population is structured, which means that each individual may interact, in different ways, with other individuals in the population according to the geometric structure of a graph that represents the interaction pattern of a given population.

More precisely, let $G = (V, E)$ be a finite, simple (without loops and parallel edges), undirected and connected graph, where $V$ is the set of vertices and $E$ is the set of edges. One unique individual lives at each vertex of the graph $G$, and the vertices $i$ and $j$ are connected if an interaction is possible between the individuals living at them. In other words, each individual only interacts with its neighbours. A special case of this, namely the classical Moran process, is the model for which interactions are allowed for every pair of individuals, i.e., the underlying graph is complete. For simplicity, we call an individual sited at the vertex $i$ the individual $i$. 

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Let \( \varphi_1^A, \varphi_2^A : [0, 1] \rightarrow \mathbb{R}_+ \) be frequency dependent fitness functions (\( \varphi_1^A, \varphi_2^A \in C^\infty \)) such that \( \varphi_1^A(x) \) and \( \varphi_2^A(x) \) represent the birth fitness and the death fitness (or death propensity) of type \( A \), respectively, when there exist \( (1-x)N \) individuals of type \( A \) in the population for \( x \in \{0, 1/N, 2/N, \ldots, 1\} \). In order to balance selection and stochastic drift when the population is large, we assume that we are in the weak-selection regime, i.e., we let \( \varphi_1^B, \varphi_2^B : [0, 1] \rightarrow \mathbb{R}_+ \) be functions such that

\[
\varphi_i^B(x) = \varphi_i^A(x) + \frac{\rho_i(x)}{N},
\]

for \( i = 1, 2 \), where \( \rho_i : [0, 1] \rightarrow \mathbb{R}_+ \) in \( C^\infty \), and \( \varphi_1^B(x) \) and \( \varphi_2^B(x) \) represent the birth fitness and the death fitness of type \( B \), respectively, when there exist \( xN \) individuals of type \( B \) in the population for \( x \in \{0, 1/N, 2/N, \ldots, 1\} \). In what follows, it will be convenient as a simplification device to define \( \varphi_i : [0, 1] \rightarrow \mathbb{R}_+ \) by

\[
\varphi_i(x) := \frac{\varphi_i^B(x)}{\varphi_i^A(x)} = 1 + \frac{\psi_i(x)}{N},
\]

where \( \psi_i(x) = \rho_i(x)/\varphi_i^A(x) \), for \( i = 1, 2 \). Then, in practice, we consider that the fitness functions for \( B \) are \( \varphi_1 \) and \( \varphi_2 \), and the fitness functions for \( A \) are both equal to 1.

### 2.2 Simple stochastic processes on a graph

A simple stochastic process is intuitively taken as one where each population update consists of two events: the birth of a single individual and the death of a single individual. The order of these events does matter and the difference may be quite significant in non-complete graphs. We follow [12], and consider a general BD and DB process allowing for selection both on birth and death. This formulation contains as special cases the BD-* and DB-* (where * can be either B or D) processes described in [10], which in turn include many examples of update rules used in the literature.

A general BD process in a structured population is defined as follows. At each step, an individual \( i \) is selected from the population to reproduce with probability proportional to its birth fitness, and an individual among the neighbours of \( i \), say \( j \), is selected to die with probability proportional to its death fitness among all neighbours of \( i \). Upon a selection event for \( i \) and \( j \), the individual \( j \) dies and is replaced by an offspring of individual \( i \). Given a population of \( N \) individuals structured as a graph \( G = (V, E) \), with \( k \) mutants, the probability that a new mutant appears in the BD process is

\[
P_{BD}(k \rightarrow k + 1) = \frac{\varphi_1(\frac{k}{N})}{k\varphi_1(\frac{k}{N}) + N - k} \sum_{i \in K} \frac{d_i - n_i}{n_i \varphi_2(\frac{k}{N}) + d_i - n_i},
\]

where \( K \subset V \) is the set of mutant vertices in \( G \), \( d_i \) is the degree of vertex \( i \), and \( n_i \) is the number of mutant neighbours of vertex \( i \). Likewise, the probability that a new wild-type appears in the BD process is

\[
P_{BD}(k \rightarrow k - 1) = \frac{1}{k\varphi_1(\frac{k}{N}) + N - k} \sum_{i \in V \setminus K} \frac{n_i \varphi_2(\frac{k}{N})}{n_i \varphi_2(\frac{k}{N}) + d_i - n_i}.
\]
The mechanism of a general DB process in a structured population is the opposite of the BD process. At each step, first an individual \( i \) is selected from the population to die with probability proportional to its death fitness, and then an individual among the neighbours of \( i \), say \( j \), is selected, to reproduce, with probability proportional to its birth fitness among all neighbours of \( i \). Upon a selective event, individual \( i \) dies and is replaced by an offspring of individual \( j \). Given a population of \( N \) individuals structured as a graph \( G \) with \( k \) mutants, the probability that a new mutant appears in the DB process is

\[
P_{DB}(k \to k + 1) = \frac{1}{k \varphi_2(\frac{k}{N}) + N - k} \sum_{i \in V \setminus K} \frac{n_i \varphi_1(\frac{k}{N})}{n_i \varphi_2(\frac{k}{N}) + d_i - n_i},
\]

and the probability that in the DB process a new wild-type appears is

\[
P_{DB}(k \to k - 1) = \frac{\varphi_2(\frac{k}{N})}{k \varphi_2(\frac{k}{N}) + N - k} \sum_{i \in K} \frac{d_i - n_i}{n_i \varphi_1(\frac{k}{N}) + d_i - n_i}.
\]

As we mentioned before, in the general BD and DB processes, the two homogeneous states are absorbing, so the dynamics eventually reaches one of them and when this happens we say that the corresponding type has fixed. The fixation probability is the probability that a given type will fix given the current state of the population. The BD and DB processes with constant birth and death fitness functions were studied in \[12\]. In this paper, we consider general frequency-dependent birth and death fitness functions in \( C^\infty \). We develop a method to estimate the fixation probability of BD and DB processes for populations on finite star graphs.

A star graph with \( N \) vertices is a connected undirected simple graph that has only one vertex of degree \( N - 1 \), called the center, while all the other vertices, leaves, have degree one. Since the permutations on leaves give isomorphic graphs, the dynamics of the process can be described by the number of mutants at the leaves and the type of the individual living at the center. In the BD process, we denote by \( p_{1,x}^{DB,N} \) (resp. \( p_{2,x}^{DB,N} \) in the DB process) the fixation probability of type \( B \) when the initial state of the process is the star graph with a mutant, \( B \), living at its center and \( xN \) mutants living at its leaves. Similarly, denote by \( p_{2,x}^{BD,N} \) (resp. \( p_{2,x}^{DB,N} \) in the DB process) the fixation probability of \( B \) when the initial state is the star graph with a wild-type, \( A \), at its center and \( xN \) mutants living at its leaves. In the sequel, by removing the superscripts “BD” and “DB” in a statement, an equation, etc., we mean it is true for both BD and DB process. We have \( 2N \) recursive equations

\[
\begin{align*}
p_{1,x}^N &= a_x(\overline{z})p_{2,x}^N + b_x(\overline{z})p_{1,x+\overline{z}}^N \\
p_{2,x}^N &= c_x(\overline{z})p_{2,x-\overline{z}}^N + d_x(\overline{z})p_{1,x}^N
\end{align*}
\]

for \( x \in \{0, \overline{z}, 2\overline{z}, \ldots, 1 - \overline{z}\} \) and \( \overline{z} = 1/N \), with boundary conditions \( p_{2,0}^N = 0 \) and \( p_{1,1-\overline{z}}^N = 1 \), where \( a_x, b_x, c_x, d_x \) are continuous functions on \( z \in [0, \delta] \), \( \delta > \overline{z} \) defined...
for the BD process as

\[ a_{x}^{BD}(z) := \frac{1 - z + xz\psi_2(x + z)}{1 + xz\psi_2(x + z) + z^2\psi_1(x + z)}, \]

\[ b_{x}^{BD}(z) := \frac{z + z^2\psi_1(x + z)}{1 + xz\psi_2(x + z) + z^2\psi_1(x + z)}, \]

\[ c_{x}^{BD}(z) := \frac{z(1 + z\psi_2(x))}{(1 + z\psi_1(x))(1 - z + xz\psi_2(x)) + z(1 + z\psi_2(x))}, \]

\[ d_{x}^{BD}(z) := \frac{(1 + z\psi_1(x))(1 - z + xz\psi_2(x))}{(1 + z\psi_1(x))(1 - z + xz\psi_2(x)) + z(1 + z\psi_2(x))}, \]

and for DB process as

\[ a_{x}^{DB}(z) := \frac{z(1 + z\psi_2(x + z))}{1 + xz\psi_1(x + z) + z^2\psi_2(x + z)}, \]

\[ b_{x}^{DB}(z) := \frac{1 - z + xz\psi_1(x + z)}{1 + xz\psi_1(x + z) + z^2\psi_2(x + z)}, \]

\[ c_{x}^{DB}(z) := \frac{(1 + z\psi_2(x))(1 - z + xz\psi_1(x))}{(1 + z\psi_2(x))(1 - z + xz\psi_1(x)) + z(1 + z\psi_1(x))}, \]

\[ d_{x}^{DB}(z) := \frac{z(1 + z\psi_1(x))}{(1 + z\psi_2(x))(1 - z + xz\psi_1(x)) + z(1 + z\psi_1(x))}. \]

If the process is not in the absorbing states, it eventually jumps to another state in finite time. So by considering transition probabilities conditioned on jumping to another state, we can construct a new Markov chain. More precisely, the transition probability of jumping to a neighbour for the new Markov chain is the conditional probability of jumping to that neighbour provided a jump occurs. We denote by \( L \) the conditional transition probability matrix on the star graph with dimension \( 2N \times 2N \).

For each fixed \( N \), \( L \) is defined as follows

\[
L_{ij} = \begin{cases} 
1, & \text{if } i = j = 1 \text{ or } i = j = 2N; \\
a_{i-1\pi}(\pi), & \text{if } j = i - 1 \text{ and } 2 \leq i \leq N; \\
b_{i-1\pi}(\pi), & \text{if } j = N + i \text{ and } 2 \leq i \leq N; \\
a_{i-N-1\pi}(\pi), & \text{if } j = i - N \text{ and } N + 1 \leq i \leq 2N - 1; \\
b_{i-N-1\pi}(\pi), & \text{if } j = i + 1 \text{ and } N + 1 \leq i \leq 2N - 1; \\
0, & \text{otherwise}.
\end{cases}
\]

where \( a_x, b_x, c_x \) and \( d_x \) are defined in (2) for the BD process and in (3) for the DB.
process. Also, we define $M := L - I$ and denote by

$$ F = \begin{bmatrix}
  p_{2,0}^N \\
  p_{2,\pi}^N \\
  \vdots \\
  p_{2,N-\pi}^N \\
  p_{1,0}^N \\
  p_{1,\pi}^N \\
  \vdots \\
  p_{1,N-\pi}^N 
\end{bmatrix} $$

the fixation probability vector. Note that, $LF = F$ and so $MF = 0$.

We are now ready to state the main theorem of this paper whose proof is given in Section 4.

**Theorem 1.** Let $f_1, f_2, g_1, g_2 : [0, 1] \to \mathbb{R}_+$ be functions defined as

$$ f_1(x) := \frac{x + 1}{2 - \overline{z}}, \quad f_2(x) := \frac{x}{2 - \overline{z}}, $$

$$ g_1(x) := \frac{(1 + x)(1 - \overline{z})}{(2 - \overline{z})^2} \int_0^{1-\overline{z}} 1 + \psi_1(k) - (1 + 2k)\psi_2(k) dk $$

$$ \quad - \frac{x}{2 - \overline{z}} \int_0^x 1 + \psi_1(k) - (1 + 2k)\psi_2(k) dk - \frac{1 + x}{2 - \overline{z}} \int_x^{1-\overline{z}} 1 + (1 - 2k)\psi_2(k) dk $$

and

$$ g_2(x) := \frac{(1 - \overline{z})x}{(2 - \overline{z})^2} \int_0^{1-\overline{z}} 1 + \psi_1(k) - (1 + 2k)\psi_2(k) dk $$

$$ \quad - \frac{x}{2 - \overline{z}} \int_x^{1-\overline{z}} 1 + (1 - 2k)\psi_2(k) dk + \frac{1 - x}{2 - \overline{z}} \int_0^x 1 + \psi_1(k) - (1 + 2k)\psi_2(k) dk. $$

Let $F^{DB}_i$ be a vector such that $F^{DB}_i = f_2((i - 1)\overline{z}) + \overline{z}g_2((i - 1)\overline{z})$ for $1 \leq i \leq N$ and $F^{DB}_{i+N} = f_1((i - N - 1)\overline{z}) + \overline{z}g_1((i - N - 1)\overline{z})$ for $N + 1 \leq i \leq 2N$. Then

$$ \|F^{DB} - F^{DB}\| \leq C\overline{z}, $$

for a constant $C$.

### 3 Finding continuous approximation candidates

First, suppose that there exist smooth functions $q_1, q_2 : [0, 1] \times [0, \delta] \to [0, 1]$ such that

$$ \begin{cases} 
  a_x(z)q_2(x, z) + b_x(z)q_1(x + z, z) - q_1(x, z) = 0 \\
  c_x(z)q_2(x - z, z) + d_x(z)q_1(x, z) - q_2(x, z) = 0 
\end{cases} \quad (4) $$
Since $a_x, b_x, c_x$ and $d_x$ are smooth functions, for a sufficient small $z$, we can use the Taylor series at point $(x, 0)$ and rewrite the first equation in (4) as

$$a_x(0)q_2(x, 0) + b_x(0)q_1(x, 0) - q_1(x, 0) + \left[a_x(0) \frac{\partial q_2}{\partial z}(x, 0) + a_x'(0)q_2(x, 0)\right] z$$

$$+ b_x(0) \left(\frac{\partial q_1}{\partial x}(x, 0) + \frac{\partial q_1}{\partial z}(x, 0)\right) + b_x'(0)q_1(x, 0) - \frac{\partial q_1}{\partial z}(x, 0)\right] z^n$$

$$+ \left[\frac{a_x(0)}{2} \frac{\partial^2 q_2}{\partial x^2}(x, 0) + a_x'(0) \frac{\partial q_2}{\partial z}(x, 0) + \frac{a_x''(0)}{2} q_2(x, 0)\right] z^2$$

$$+ b_x(0) \left(\frac{1}{2} \frac{\partial^2 q_1}{\partial x^2}(x, 0) + \frac{\partial^2 q_1}{\partial x \partial z}(x, 0) + \frac{1}{2} \frac{\partial^2 q_1}{\partial z^2}(x, 0)\right)$$

$$+ b_x'(0) \left(\frac{\partial q_1}{\partial x}(x, 0) + \frac{\partial q_1}{\partial z}(x, 0)\right) + b_x''(0)q_1(x, 0) - \frac{1}{2} \frac{\partial^2 q_1}{\partial z^2}(x, 0)\right] z^3$$

$$+ O(z^4) = 0.$$
Similarly we can write the second equation in (4) as

\[ d_x(0)q_1(x, 0) + c_x(0)q_2(x, 0) - q_2(x, 0) + \left[ d_x(0)\frac{\partial q_1}{\partial z}(x, 0) + d'_x(0)q_1(x, 0) \right. \]
\[ + c_x(0) \left( -\frac{\partial q_2}{\partial x}(x, 0) + \frac{\partial q_2}{\partial z}(x, 0) \right) + c'_x(0)q_2(x, 0) - \frac{\partial q_2}{\partial z}(x, 0) \right] z \]
\[ + \left[ \frac{d_x(0)}{2} \frac{\partial^2 q_1}{\partial z^2}(x, 0) + d'_x(0)\frac{\partial q_1}{\partial z}(x, 0) + \frac{d''_x(0)}{2}q_1(x, 0) \right. \]
\[ + c_x(0) \left( \frac{1}{2}\frac{\partial^2 q_2}{\partial x^2}(x, 0) - \frac{\partial^2 q_2}{\partial x \partial z}(x, 0) + \frac{1}{2}\frac{\partial^2 q_2}{\partial z^2}(x, 0) \right) z^2 \]
\[ + \left[ \frac{d_x(0)}{6} \frac{\partial^3 q_1}{\partial z^3}(x, 0) + \frac{d'_x(0)}{2} \frac{\partial^2 q_1}{\partial z^2}(x, 0) + \frac{d''_x(0)}{2} \frac{\partial q_1}{\partial z}(x, 0) + \frac{d'''_x(0)}{6}q_1(x, 0) \right. \]
\[ + c_x(0) \left( -\frac{1}{6}\frac{\partial^3 q_2}{\partial x^3}(x, 0) + \frac{1}{2}\frac{\partial^3 q_2}{\partial x^2 \partial z}(x, 0) - \frac{1}{2}\frac{\partial^3 q_2}{\partial x \partial z^2}(x, 0) + \frac{1}{2}\frac{\partial^3 q_2}{\partial z^3}(x, 0) \right) z^3 \]
\[ \left. + c'_x(0) \left( \frac{1}{2}\frac{\partial^2 q_2}{\partial x \partial z}(x, 0) - \frac{\partial^2 q_2}{\partial z^2}(x, 0) + \frac{1}{2}\frac{\partial^2 q_2}{\partial z^2}(x, 0) \right) \right] + \frac{c''_x(0)}{2} \left( -\frac{\partial q_2}{\partial x}(x, 0) + \frac{\partial q_2}{\partial z}(x, 0) \right) + \frac{c'''_x(0)}{6}q_2(x, 0) - \frac{1}{6}\frac{\partial^3 q_2}{\partial z^3}(x, 0) \right] z^3 + O(z^4) = 0. \]
3.1 The continuous approximation candidate of the fixation probability for a DB process

In the DB process, the constant term of the Taylor series of both equations in (4) vanishes. For coefficients of first-order, we have

\[
\begin{align*}
q_2(x,0) - q_1(x,0) + \frac{\partial q_1}{\partial x}(x,0) &= 0 \\
q_1(x,0) - q_2(x,0) - \frac{\partial q_2}{\partial x}(x,0) &= 0
\end{align*}
\] (7)

Let \( f_1(x) := q_1(x,0) \) and \( f_2(x) := q_2(x,0) \). Then the system (7) is equivalent to the system of ordinary differential equations (ODEs)

\[
\begin{align*}
f_2(x) - f_1(x) + f_1'(x) &= 0 \\
f_1(x) - f_2(x) - f_2'(x) &= 0
\end{align*}
\] (8)

The sum of two equations in (8) implies \( f_1'(x) = f_2'(x) \). From the first equation we obtain \( f_2(x) = f_1(x) - f_1'(x) \) and substituting in the second equation we get \( f_1'(x) = 0 \). Therefore, \( f_1'(x) = f_2'(x) = k_1 \), for a constant \( k_1 \), i.e., \( f_1(x) = k_1 x + k_2 \) and \( f_2(x) = k_1 x + k_3 \), where \( k_2 \) and \( k_3 \) are constants. Thus, the solution for this system, considering the initial conditions \( f_1(1 - z) = 1 \) and \( f_2(0) = 0 \), is

\[
\begin{align*}
f_1(x) &= \frac{x + 1}{2 - z} \\
f_2(x) &= \frac{x}{2 - z}
\end{align*}
\] (9)

Now, using (9) in the coefficients of second-order, we have

\[
\begin{align*}
\frac{\partial^2 q_2}{\partial z^2}(x,0) + \frac{\partial^2 q_1}{\partial x \partial z}(x,0) - \frac{\partial^2 q_1}{\partial z^2}(x,0) + \frac{x \psi_1(x) - \psi_2(x) - 1}{2 - z} &= 0 \\
\frac{\partial^2 q_1}{\partial z^2}(x,0) - \frac{\partial^2 q_2}{\partial x \partial z}(x,0) - \frac{\partial^2 q_2}{\partial z^2}(x,0) + \frac{\psi_1(x) - x \psi_1(x) - \psi_2(x) + 1}{2 - z} &= 0
\end{align*}
\] (10)

that can be rewritten as

\[
\begin{align*}
g_2(x) + g_1'(x) - g_1(x) &= \frac{1 - x \psi_1(x) + \psi_2(x)}{2 - z} \\
g_1(x) - g_2'(x) - g_2(x) &= \frac{(x - 1) \psi_1(x) + \psi_2(x) - 1}{2 - z}
\end{align*}
\] (11)

for \( g_1(x) := \frac{\partial q_1}{\partial z}(x,0) \) and \( g_2(x) := \frac{\partial q_2}{\partial z}(x,0) \). The solution for (11), with initial condi-
tions $g_1(1 - \overline{z}) = 0$ and $g_2(0) = 0$, is
\begin{equation}
g_1(x) := \frac{(1 + x)(1 - \overline{z})}{(2 - \overline{z})^2} \int_{0}^{1-\overline{z}} 1 + \psi_1(k) - (1 + 2k)\psi_2(k) dk
\end{equation}
\begin{equation}
- \frac{x}{(2 - \overline{z})} \int_{0}^{x} 1 + \psi_1(k) - (1 + 2k)\psi_2(k) dk - \frac{1 + x}{2 - \overline{z}} \int_{x}^{1-\overline{z}} 1 + (1 - 2k)\psi_2(k) dk
\end{equation}
and
\begin{equation}
g_2(x) := \frac{(1 - \overline{z})x}{(2 - \overline{z})^2} \int_{0}^{1-\overline{z}} 1 + \psi_1(k) - (1 + 2k)\psi_2(k) dk
\end{equation}
\begin{equation}
- \frac{x}{2 - \overline{z}} \int_{x}^{1-\overline{z}} 1 + (1 - 2k)\psi_2(k) dk + \frac{1 - x}{2 - \overline{z}} \int_{0}^{x} 1 + \psi_1(k) - (1 + 2k)\psi_2(k) dk.
\end{equation}

Let $\mathbf{F}^{DB}_{i}$ be the vector such that $F_{i}^{DB} = f_{2}(i-1)\overline{z}) + \overline{z}g_{2}(i-1)\overline{z})$ for $1 \leq i \leq N$ and $F_{i} = f_{1}(i - N - 1)\overline{z}) + \overline{z}q_{1}(i - N - 1)\overline{z})$ for $N + 1 \leq i \leq 2N$. In Section 4, we prove that $\mathbf{F}^{DB}_{i}$ is an approximation vector of the fixation probability vector $\mathbf{F}^{DB}$ with error of order $\overline{z}$.

### 3.2 The continuous approximation candidate of the fixation probability for a BD process

In the BD process, the constant term of the Taylor series for (4) are
\begin{equation}
\begin{cases}
-q_{1}(x,0) + q_{2}(x,0) = 0 \\
q_{1}(x,0) - q_{2}(x,0) = 0
\end{cases}
\end{equation}
Therefore, $q_{1}(x,0) = q_{2}(x,0)$. Let $f(x) := q_{1}(x,0)$. Replacing $q_{1}(x,0)$ and $q_{2}(x,0)$ by $f(x)$ in coefficients of first-order, we obtain
\begin{equation}
\begin{cases}
-\frac{\partial q_{1}}{\partial z}(x,0) + \frac{\partial q_{2}}{\partial z}(x,0) = 0 \\
\frac{\partial q_{1}}{\partial z}(x,0) - \frac{\partial q_{2}}{\partial z}(x,0) = 0
\end{cases}
\end{equation}
Thus, $\frac{\partial q_{1}}{\partial z}(x,0) = \frac{\partial q_{2}}{\partial z}(x,0) =: g(x)$, and so the coefficients of second-order are given by
\begin{equation}
\begin{cases}
\frac{1}{2} \left( 2f'(x) - \frac{\partial^{2}q_{1}}{\partial z^{2}}(x,0) + \frac{\partial^{2}q_{2}}{\partial z^{2}}(x,0) \right) = 0 \\
\frac{1}{2} \left( -2f'(x) + \frac{\partial^{2}q_{1}}{\partial z^{2}}(x,0) - \frac{\partial^{2}q_{2}}{\partial z^{2}}(x,0) \right) = 0
\end{cases}
\end{equation}
Let \( h(x) := \frac{\partial^2 q_2}{\partial x^2}(x, 0) \). From any of two equations in \([14]\) we obtain that \( \frac{\partial^3 q_2}{\partial z^3}(x, 0) = h(x) - 2f'(x) \). So, the coefficients of third-order can be written as

\[
\begin{align*}
(1 + \psi_1(x) - x\psi_2(x))f'(x) + &\ g'(x) + \frac{1}{2}f''(x) - \frac{1}{6} \frac{\partial^3 q_1}{\partial z^3}(x, 0) + \frac{1}{6} \frac{\partial^3 q_2}{\partial z^3}(x, 0) = 0 \\
(\psi_1(x) - 1 + (x - 1)\psi_2(x))f'(x) - &\ g'(x) + \frac{1}{2}f''(x) + \frac{1}{6} \frac{\partial^3 q_1}{\partial z^3}(x, 0) - \frac{1}{6} \frac{\partial^3 q_2}{\partial z^3}(x, 0) = 0
\end{align*}
\]

Summing the equations in \([15]\), gives rise to the ODE

\[
(2\psi_1(x) - \psi_2(x))f'(x) + f''(x) = 0,
\]

whose solution, with boundary conditions \( f(0) = q_2(0, 0) = 0 \) and \( f(1 - \bar{x}) = q_1(1 - \bar{x}, 0) = 1 \), is

\[
f(x) = \frac{\int_0^x e^{-\int_0^s (2\psi_1(r) - \psi_2(r))\,dr} \, ds}{\int_0^{1-x} e^{-\int_0^s (2\psi_1(r) - \psi_2(r))\,dr} \, ds}.
\]

Also, letting \( k(x) = \frac{\partial^3 q_2}{\partial z^4}(x, 0) \), from \([15]\) and \([16]\) we have \( \frac{\partial^3 q_2}{\partial z^2}(x, 0) = k(x) + 6f'(x)(x - 1/2)\psi_2(x) - 1 - 6g'(x) \). We continue the analysis one step more for coefficients of fourth-order

\[
\begin{align*}
(1 + \psi_1(x) - x\psi_2(x))\ f'(x) + &\ \frac{1}{2}h'(x) + \frac{1}{2}(1 - x)\psi_2(x)\ f''(x) + \\
\frac{1}{2}g''(x) + &\ \frac{1}{6}f'''(x) - \frac{1}{24} \frac{\partial^4 q_1}{\partial z^4}(x, 0) + \frac{1}{24} \frac{\partial^4 q_2}{\partial z^4}(x, 0) = 0
\end{align*}
\]

Summing the equations in \([18]\), we obtain the ODE

\[
(2\psi_1(x) - \psi_2(x))g'(x) + g''(x) = \frac{1}{2}(1 - 2x)\psi_2(x) f''(x) + \\
\ f'(x) \ (\psi_1(x) + \psi_1(x)(-2x\psi_2(x) + \psi_2(x) - 2) \quad (19)
\]

where the r.h.s. is equal to

\[
\bar{g}(x) = \frac{e^{-\int_0^x 2\psi_1(r) + \psi_2(r)\,dr}}{\int_0^{1-x} e^{-\int_0^s 2\psi_1(r) + \psi_2(r)\,dr} \, ds} \times 
\left( \psi_2(x) + \frac{1}{2}\psi_2^2(x) - 2\psi_1(x) - \psi_1^2(x) + \psi_1'(x) - x\psi_2'(x) \right).
\]
So, the solution for (19) with initial condition \( g(1 - \tau) = g(0) = 0 \) is
\[
g(x) = \int_0^x \left( e^{-\int_0^x (2\psi_1(r) - \psi_2(r))dr} \right) \left( C + \int_0^s \tilde{g}(k)e^{\int_0^k (2\psi_1(r) - \psi_2(r))dr} dk \right) ds,
\]
where
\[
C = \frac{-\int_0^1 - \int_0^x \tilde{g}(k)e^{\int_0^k (2\psi_1(r) - \psi_2(r))dr} dk ds \int_0^1 - \int_0^x e^{-\int_0^k (2\psi_1(r) - \psi_2(r))dr} ds}{\int_0^1 - \int_0^x e^{-\int_0^k (2\psi_1(r) - \psi_2(r))dr} ds}.
\]

In the next sections, we consider the approximate fixation probability vector \( \tilde{F}^{BD} \) such that \( \tilde{F}^{BD}_i = f((i - 1)\tau) + \tau g((i - 1)\tau) \) for \( 1 \leq i \leq N \) and \( \tilde{F}^{BD}_{i+N} = f((i - N - 1)\tau) + \tau g((i - N - 1)\tau) \) for \( N + 1 \leq i \leq 2N \).

4 Error estimation for the DB process

This section is devoted to the proof of Theorem 1. First, note that we can rewrite the matrix \( L \) as follows
\[
L = \begin{bmatrix}
1 & 0^t & 0 \\
\alpha & \bar{L} & \beta \\
0 & 0 & 1
\end{bmatrix}
\]
where \( 0 \) is the null vector of dimension \( 2N - 2 \), \( \bar{L} \) is a matrix with dimension \( 2N - 2 \times 2N - 2 \), \( \alpha \) is a vector of dimension \( 2N - 2 \) such that \( \alpha_1 = c_{\tau}, \alpha_N = a_0 \) and \( \alpha_i = 0 \) for all \( i \) different than \( 1 \) and \( N \), and \( \beta \) is a vector of dimension \( 2N - 2 \) such that \( \beta_{N-1} = d_{(N-1)\tau}, \beta_{2N-2} = b_{(N-2)\tau} \) and \( \beta_i = 0 \) for all \( i \) other than \( N-1 \) and \( 2N-2 \).

The following result from [8] shows that there exists a unique fixation probability vector \( \tilde{F}^t = [0 \; \tilde{F}^t \; 1]^t \), where \( \tilde{F} \) is a vector of dimension \( 2N - 2 \), since \( p_{2,0}^N = 0 \) and \( p_{1,1}^N = 1 \).

Proposition 1 (Chalub and Souza [8]). Let \( \tilde{M} = \bar{L} - I \). Then, there exists a unique vector \( \tilde{F} \in \mathbb{R}^{N-2} \), with \( 0 < \tilde{F}_i < 1 \), such that \( \tilde{F}^t = [0 \; \tilde{F}^t \; 1]^t \), with \( M \tilde{F} = 0 \). It satisfies
\[
\tilde{F} = -\tilde{M}^{-1} \beta.
\]

So we are reduced to estimate \( \tilde{F} \). To this end, let \( \tilde{F}^{DB}_{i-1} = \tilde{F}^{DB}_i \) for \( i = 2, \ldots, 2N - 1 \) as defined in Section 3.1. Using Proposition 1 we get
\[
\| \tilde{F} - \tilde{F} \| = \| -\tilde{M}^{-1} \beta - \tilde{F} \| = \| \tilde{M}^{-1} (-\beta - \tilde{M} \tilde{F}) \| \leq \| \tilde{M}^{-1} \| \| \beta + \tilde{M} \tilde{F} \|.
\]

Hence, in order to estimate the error \( \| \tilde{F} - \tilde{F} \| \), we need appropriate upper bounds for \( \| \tilde{M}^{-1} \| \) and \( \| \beta + \tilde{M} \tilde{F} \| \). This is done in Proposition 3 and Proposition 4. To see the details for the DB process, we write \( \tilde{M} = \tau \tilde{M}_0 + \tau^2 \tilde{M}_1 \), where \( \tilde{M}_0 \) is the matrix
defined by

\[
(\widetilde{M}_0)_{ij} = \begin{cases} 
-1/i, & \text{if } i = j; \\
-1 + 1/i, & \text{if } j = i - 1 \text{ and } 2 \leq i \leq N - 1; \\
1, & \text{if } j = N + i \text{ and } 1 \leq i \leq N - 2; \\
1, & \text{if } j = i - N \text{ and } N + 1 \leq i \leq 2N - 2; \\
-1 + 1/i, & \text{if } j = i + 1 \text{ and } N \leq i \leq 2N - 3; \\
0, & \text{otherwise.}
\end{cases}
\]  

(21)

Let \( \tilde{z} \tilde{M}_0 = \tilde{M} \) in the neutral case, i.e. when \( \psi_1 \equiv 0 \) and \( \psi_2 \equiv 0 \). In order to define \( \tilde{M}_1 \) we need Hadamard’s Lemma.

**Lemma 1** (Hadamard’s Lemma [3]). Let \( f : U_{z_0} \subset \mathbb{R} \rightarrow \mathbb{R} \) be a smooth function, where \( U_{z_0} \) is an open neighbourhood of \( z_0 \) and suppose \( f^{(p)}(z_0) = 0 \) for all \( p \) with \( 1 \leq p \leq k \). Then there exist a smooth function \( \tilde{f} : U_{z_0} \rightarrow \mathbb{R} \) such that

\[
f(z) = f(z_0) + (z - z_0)^{k+1}\tilde{f}(z)
\]

for all \( z \in U_{z_0} \). When \( k = 0 \) there are no such \( p \) and the result also holds.

Applying Hadamard’s Lemma to \( a_x(z) - z \), for \( k = 1 \) and \( z_0 = 0 \), we obtain

\[
a_x(z) - z = z^2 \int_0^1 \int_0^1 sa''_x(zsu)dsdu.
\]

Similarity, we rewrite all equations in (3) as

\[
b_x(z) = 1 - z + z^2 \int_0^1 \int_0^1 sb''_x(zsu)dsdu,
\]

\[
c_x(z) = 1 - z + z^2 \int_0^1 \int_0^1 sc''_x(zsu)dsdu,
\]

\[
d_x(z) = z + z^2 \int_0^1 \int_0^1 sd''_x(zsu)dsdu.
\]

Now we can define \( \tilde{M}_1 \) as follows

\[
(\widetilde{M}_1)_{ij} = \begin{cases} 
\int_0^1 \int_0^1 sc''_x(zsu)dsdu \bigg|_{z=\tilde{z}}, & \text{if } j = i - 1 \text{ and } 2 \leq i \leq N - 1; \\
\int_0^1 \int_0^1 sd''_x(zsu)dsdu \bigg|_{z=\tilde{z}}, & \text{if } j = N + i \text{ and } 1 \leq i \leq N - 2; \\
\int_0^1 \int_0^1 sa''_{(i-N)x}(zsu)dsdu \bigg|_{z=\tilde{z}}, & \text{if } j = i - N \text{ and } N < i \leq 2N - 2; \\
\int_0^1 \int_0^1 sb''_{(i-N)x}(zsu)dsdu \bigg|_{z=\tilde{z}}, & \text{if } j = i + 1 \text{ and } N \leq i \leq 2N - 3; \\
0, & \text{otherwise.}
\end{cases}
\]
The next lemma shows there exist an upper bound for $\tilde{M}_1$ that does not depend on $\tilde{z}$.

**Lemma 2.** There exist a constant $C_1$ independent of $\tilde{z}$ such that $\|\tilde{M}_1\| \leq C_1$.

**Proof.** Note that the function inside the integral of each term of matrix $\tilde{M}_1$ is a continuous function. Then, for variables $u, s \in [0, 1]$ and $\tilde{z} < 1$, there exist a maximum value that does not depend on $\tilde{z}$. Therefore, each term of $\tilde{M}_1$ is bounded by a constant independent of $\tilde{z}$ and so, the result follows.

We use the lemma below to find an upper bound for $\|\tilde{M}_0^{-1}\|$ in Proposition 2.

**Lemma 3** (Stoyan and Tako [19]). Let $K \in \mathbb{R}^{n \times n}$ be a matrix with non-positive off-diagonal elements, i.e. $K_{ij} \leq 0$ for $i \neq j$, and suppose there exists a positive vector $r > 0$ with $Kr > 0$, then

$$
\|K^{-1}\| \leq \frac{\|r\|}{\min_{i=1, \ldots, n} (Kr)_i}.
$$

**Proposition 2.** Let $\tilde{M}_0$ be the matrix defined in (21). Then $\|\tilde{M}_0^{-1}\| \leq 1$.

**Proof.** First note that each off-diagonal element of the matrix $-\tilde{M}_0$ is non-positive. Now, consider the vector $r$ such that $r_j = \tilde{z}(N - 1 - (N - 1 - j)^2/(N - 1))$ for $j = 1, \ldots, N - 1$ and $r_j = \tilde{z}(N - 1 - (j - N)^2/(N - 1))$ for $j = N, \ldots, 2N - 2$. Then $(-\tilde{M}_0 r)_i = 1$ for $i = 1, \ldots, 2N - 2$. Also, $\|r\| = \tilde{z}(N - 1)$. Therefore, from Lemma 3 $\|\tilde{M}_0^{-1}\| \leq 1$.

We are now ready to find upper bounds for $\|\tilde{M}^{-1}\|$ and $\|\beta + \tilde{M}\tilde{F}\|$ in the following propositions.

**Proposition 3.** There exists a constant $C$, independent of $\tilde{z}$, for which

$$
\|\tilde{M}^{-1}\| \leq C/\tilde{z}.
$$

**Proof.** Note that $\tilde{M}^{-1} = \tilde{z}^{-1}(I+\tilde{z}\tilde{M}_0^{-1}\tilde{M}_1)^{-1}$. Using Proposition 2 and Lemma 2, and for a sufficiently small $\tilde{z}$ (big $N$), we have

$$
\|\tilde{z}\tilde{M}_0^{-1}\tilde{M}_1\| \leq \tilde{z}\|\tilde{M}_1\| \leq C_2 < 1.
$$

Therefore, from a property of Neumann series,

$$(I + \tilde{z}\tilde{M}_0^{-1}\tilde{M}_1)^{-1} = \sum_{i=0}^{\infty} (-\tilde{z}\tilde{M}_0^{-1}\tilde{M}_1)^i.$$

Thus,

$$
\|\tilde{M}^{-1}\| \leq \tilde{z}^{-1}\|(\tilde{M}_0 + \tilde{z}\tilde{M}_1)^{-1}\| \\
\leq \tilde{z}^{-1}\sum_{i=0}^{\infty} \|(\tilde{z}\tilde{M}_0^{-1}\tilde{M}_1)^i\| \\
= \tilde{z}^{-1}\frac{1}{1-C_2} < \tilde{z}^{-1}C.
$$

$\Box$
Proposition 4. With the notation as in (20), there exists a constant $C_2$ that does not depend on $\gamma$, such that
\[
\|\beta + \tilde{M}\tilde{F}\| \leq \gamma^2 C_2.
\]
Proof. In order to simplify computations, we write $a_x(z) = z + z^2 \gamma_{a_z}$, $b_x(z) = 1 - z + z^2 \gamma_{b_z}$, $c_x(z) = 1 - z + z^2 \gamma_{c_z}$ and $d_x(z) = z + z^2 \gamma_{d_z}$, where $\gamma_{a_z}$, $\gamma_{b_z}$, $\gamma_{c_z}$ and $\gamma_{d_z}$ can be deduced from equations in (22). Also we remind the reader that $f_1(x) = (x+1)/(2-\gamma)$, $f_2(x) = x/(2-\gamma)$, and $g_1(x)$ and $g_2(x)$ are defined in Subsection 3.1. For $2 \leq i \leq N - 2$ and $x = \gamma i$, $(\beta + \tilde{M}\tilde{F})_i$ is equal to
\[
c_x(\gamma)(f_2(x-\gamma) + \gamma g_2(x-\gamma)) - (f_2(x) + \gamma g_2(x)) + d_x(\gamma)(f_1(x) + \gamma g_1(x))
\]
\[
= (1 - \gamma + \gamma^2 \gamma_{c_z}) \left( \frac{x - \gamma}{2 - \gamma} + \gamma g_2(x - \gamma) \right) - \left( \frac{x}{2 - \gamma} + \gamma g_2(x) \right)
\]
\[
+ (\gamma + \gamma^2 \gamma_{d_z}) \left( \frac{x + 1}{2 - \gamma} + \gamma g_1(x) \right)
\]
\[
= \gamma (g_2(x - \gamma) - g_2(x)) + \gamma^2 \left( \frac{1}{2 - \gamma} - g_2(x - \gamma) + \frac{x}{2 - \gamma} \gamma_{c_z} + g_1(x) + \frac{x + 1}{2 - \gamma} \gamma_{d_z} \right)
\]
\[
+ \gamma^3 \left( g_2(x - \gamma) - \frac{\gamma_{c_z}}{2 - \gamma} - \gamma_{d_z} g_1(x) \right) \leq \gamma (g_2(x - \gamma) - g_2(x)) + \gamma^2 C_1
\]
where $C_1$ is a constant that is independent of $\gamma$. It is not hard to see that $g_2(x - \gamma) - g_2(x) = \gamma g(x)$, where $g(x)$ is a continuous function and so $g_2(x - \gamma) - g_2(x) \leq \gamma C_2$, for $x \in [0,1]$. Also,
\[
(\beta + \tilde{M}\tilde{F})_1 = -(f_2(\gamma) + \gamma g_2(\gamma)) + d_\gamma(\gamma)(f_1(\gamma) + \gamma g_1(\gamma)) \leq -\gamma g_2(\gamma) + \gamma^2 C_3,
\]
and we can deduce that $g_2(\gamma) \leq \gamma C_4$. Finally, $(\beta + \tilde{M}\tilde{F})_{N-1}$ is equal to
\[
c_{1-\gamma}(\gamma)(f_2(1 - 2\gamma) + \gamma g_2(1 - 2\gamma)) - (f_2(1 - \gamma) + \gamma g_2(1 - \gamma)) + d_{1-\gamma}(\gamma)
\]
\[
\leq \gamma (g_2(1 - 2\gamma) - g_2(1 - \gamma)) + \gamma^2 C_5.
\]
Therefore, $(\beta + \tilde{M}\tilde{F})_i \leq \gamma^2 C_6$, for $1 \leq i \leq N - 1$. Similarly, for each $N \leq i \leq 2N - 2$, we have $(\beta + \tilde{M}\tilde{F})_i \leq \gamma^2 C$. Thus, the result follows.

Proof of Theorem 1. Using Propositions 3 and 4 in (20), and recalling that $\tilde{F}_1 = 0$ and $\tilde{F}_{2N} = 1$, we conclude that the approximation of the fixation probability vector given by $\tilde{F}$ is of order $\gamma$ and so Theorem 1 holds.

5 Numerical examples

In this section we present some numerical examples indicating that our approximation, given in Section 3 for both the BD and the DB processes is quite close to the fixation probability vector even for small $N$. In Figure 1 we can see examples in the BD process with the same fitness functions and different $N$ — as the larger $N$, the better our approximation. We can also observe the same for the DB process in Figure 2. Other examples comparing different fitness functions are presented in Figures 3 and 4.
Figure 1: The continuous approximation (in blue) compared to the exact fixation probability for a population structured as a star graph in the BD process, for $N = 20, 40, 60, 100$. In green, we have the fixation probability of a population structured as a star with a resident in the center, and in orange, we have the fixation probability when the center is a mutant. In these examples, $\psi_1(x) = 2(x - 0.5)$ and $\psi_2(x) = x + 1$.

6 Additional results

6.1 Equivalences

In the BD process, [7] showed that an approximation of the fixation probability for a large population structured as a complete graph is equal to

$$\phi(x) = \frac{\int_x^1 e^{-\int_0^y (\psi_1(r) - \psi_2(r)) dr} dy}{\int_0^1 e^{-\int_0^y (\psi_1(r) - \psi_2(r)) dr} dy}.$$  \hspace{1cm} (23)

and this is a solution of the ODE

$$(\psi_1(x) - \psi_2(x)) f'(x) + f''(x) = 0.$$  \hspace{1cm} (24)

In the BD process, our approximation of the fixation probability for the star graph is quite similar to (23); the difference is that we have a constant 2 multiplying the function $\psi_1$. Let $w = 1 - x$ and $\overline{\psi}(w) := 1 - f(1 - w)$ be the approximation of the fixation probability for type A. Then from [21], in the complete graph we have

$$(\psi_2(1 - w) - \psi_1(1 - w)) \overline{\psi}(w) + \overline{\psi}'(w) = 0.$$

Therefore, in the complete graph, computing the approximation of the fixation probability for type A is equivalent to considering the birth fitness function of $B$ as the death
Figure 2: The continuous approximation (in blue) compared to the exact fixation probability (in orange) for a population structured as a star graph when the center is a resident, in the DB process. When the center is a mutant, the continuous approximation and the exact fixation probability are given in gray and green, respectively. The fitness functions are $\psi_1(x) = 2(x - 0.5)$ and $\psi_2(x) = x + 1$, for $N = 20, 40, 60, 100$.

Figure 3: Our approximation (in blue) compared to the exact fixation probability for the BD process, for $N = 40$. In green, we have the fixation probability of a population structured as a star with a resident in the center, and in orange, we have the fixation probability when the center is a mutant. On the left, $\psi_1(x) = 10(x - 0.5)$ and $\psi_2(x) = 0$, and on the right, $\psi_1(x) = 0$ and $\psi_2(x) = -10(x - 0.5)$.

However, in the star graph we can not do the same, since we have the constant 2 multiplying $\psi_1$. 
Figure 4: The continuous approximation (in blue) compared to the exact fixation probability (in orange) for a population structured as a star graph when the center is a resident, in the DB process. When the center is a mutant, the continuous approximation and the exact fixation probability are given in gray and green, respectively. On the left, \( \psi_1(x) = 10(x - 0.5) \) and \( \psi_2(x) = 0 \), and on the right, \( \psi_1(x) = 0 \) and \( \psi_2(x) = -10(x - 0.5) \), for \( N = 100 \).

### 6.2 Fitness functions given by 2-player games

Note that in the DB process, if instead of \( \varphi_1^A = 1 \) and \( \varphi_1^B = 1 + \psi_1/N \), we consider \( \varphi_1^A = 1 + \psi_1^A/N \) and \( \varphi_1^B = 1 + \psi_1^B/N \), the system of ODEs (11) does not change and (11) reduces to

\[
\begin{align*}
\frac{dg_1(x)}{dx} - g_1(x) &= \frac{-x(\psi_1^B(x) - \psi_1^A(x)) + \psi_2^B(x) - \psi_2^A(x) + 1}{2 - \overline{z}}, \\
\frac{dg_2(x)}{dx} &= \frac{(x - 1)(\psi_1^B(x) - \psi_1^A(x)) + \psi_2^B(x) - \psi_2^A(x) - 1}{2 - \overline{z}}.
\end{align*}
\]

(25)

Summing the equations gives us

\[
g_1'(x) - g_2'(x) = \frac{1}{2 - \overline{z}} \left[ -(\psi_1^B(x) - \psi_1^A(x)) + 2(\psi_2^B(x) - \psi_2^A(x)) \right].
\]

Therefore, (11) is equivalent to (25) for \( \psi_1 = (\psi_1^B - \psi_1^A) \) and \( \psi_2 = (\psi_2^B - \psi_2^A) \). Now, suppose that the fitness of the individual occupying the center is different from the fitness of those occupying the leaves. More explicitly, let \( \varphi_1^A(x) = 1 + \psi_1^A(x)/N \) (respectively, \( \varphi_1^B(x) = 1 + \psi_1^B(x)/N \)) be the birth fitness function for an individual of type \( A \) (resp., \( B \)) when it occupies one of the leaves, and let \( \varphi_1^{CA}(x) = 1 + \psi_1^{CA}(x)/N \) (resp., \( \varphi_1^{CB}(x) = 1 + \psi_1^{CB}(x)/N \)) when it occupies the center, in a population with \( xN \) individuals of type \( B \). Similar notation can be easily defined for the death fitness functions. As a result (11) reduces to

\[
\begin{align*}
\frac{dg_1(x)}{dx} - g_1(x) &= \frac{-x(\psi_1^B(x) - \psi_1^A(x)) + \psi_2^C(x) - \psi_2^A(x) + 1}{2 - \overline{z}}, \\
\frac{dg_2(x)}{dx} &= \frac{(x - 1)(\psi_1^B(x) - \psi_1^A(x)) + \psi_2^B(x) - \psi_2^C - 1}{2 - \overline{z}}.
\end{align*}
\]

(26)

Thus, (25) is a particular case of (26), when \( \psi_2^C = \psi_2^A(x) \) and \( \psi_2^B = \psi_2^B(x) \).
This is similar for the BD process. If instead of \( \psi^A_i = 1 \) and \( \psi^B_i = 1 + \psi_i/N \) we consider \( \varphi^A_i = 1 + \psi^A_i/N \) and \( \varphi^B_i = 1 + \psi^B_i/N \), then (16) is equivalent to

\[
[2(\psi^B_1(x) - \psi^A_1(x)) - (\psi^B_2(x) - \psi^A_2(x))] f'(x) + f''(x) = 0. \tag{27}
\]

Also, in the case that the individuals at the center and the leaves have different fitness functions, (16) is equivalent to

\[
[(\psi^B_1(x) - \psi^A_1(x)) + (\psi^B_1(x) - \psi^A_1(x)) - (\psi^B_2(x) - \psi^B_2(x))] f'(x) + f''(x) = 0. \tag{28}
\]

So, (27) is a particular case of (28), when \( \psi^CA = \psi^A(x) \) and \( \psi^CB = \psi^B(x) \).

Now, consider the case in which the fitnesses are linear functions of the frequencies, determined by 2-player games with weak-selection, i.e. let \( P_1, P_2, P_3 \) and \( P_4 \) be four \( 2 \times 2 \) positive pay-off matrices corresponding to four different games

|     | \( A \) | \( B \) |
|-----|--------|--------|
| \( A \) | \( a \) | \( b \) |
| \( B \) | \( c \) | \( d \) |

|     | \( A \) | \( B \) |
|-----|--------|--------|
| \( A \) | \( \bar{a} \) | \( \bar{b} \) |
| \( B \) | \( \bar{c} \) | \( \bar{d} \) |

where \( (P_i)_{11} \) indicates the benefit when an individual of type \( A \) plays against another individual of type \( A \), \( (P_i)_{12} \) is the benefit when an individual of type \( A \) plays against an individual of type \( B \), \( (P_i)_{21} \) indicates the benefit when an individual of type \( B \) plays against an individual of type \( A \) and finally, \( (P_i)_{22} \) is the benefit when an individual of type \( B \) plays against another individual of type \( B \). For \( i = 1, 2 \) and \( J \) indicating one of the types \( A, B, CA \) or \( CB \), define the fitness function \( \varphi^i_J = 1 + \psi^i_J \) by letting

\[
\begin{align*}
\psi^1_A(x) &= ax + b(1 - x), & \psi^1_B(x) &= cx + d(1 - x), \\
\psi^2_A(x) &= \bar{a}x + \bar{b}(1 - x), & \psi^2_B(x) &= \bar{c}x + \bar{d}(1 - x), \\
\psi^CA(x) &= \bar{a}x + \bar{b}(1 - x), & \psi^CB(x) &= \bar{c}x + \bar{d}(1 - x), \\
\psi^CA(x) &= \bar{a}x + \bar{b}(1 - x) \text{ and } \psi^CB(x) &= \bar{c}x + \bar{d}(1 - x). \tag{29}
\end{align*}
\]

Letting \( \psi_1 = (\psi^B_1 - \psi^A_1), \psi_2 = (\psi^B_2 - \psi^A_2), \psi_{1C} = (\psi^CB - \psi^CA) \) and \( \psi_{2C} = (\psi^CB - \psi^CA) \), we get

\[
\begin{align*}
\psi_1(x) &= \gamma(x - x^*), & \psi_2(x) &= \bar{\gamma}(x - \bar{x}^*), \\
\psi_{1C}(x) &= \bar{\gamma}(x - \bar{x}^*), & \psi_{2C}(x) &= \bar{\gamma}(x - \bar{x}^*), \tag{30}
\end{align*}
\]

where \( \gamma = (-a + b + c - d), x^* = \frac{b - d}{\gamma}, \bar{x}^* = \frac{\bar{b} - \bar{d}}{\bar{\gamma}} \), \( \bar{\gamma} = (-a + \bar{b} + \bar{c} - \bar{d}), \bar{x}^* = \frac{\bar{b} - \bar{d}}{ar{\gamma}} \)
If $\gamma < 0$ and $0 < x^* < 1$, we have the coexistence case. If $\gamma > 0$ and $0 < x^* < 1$, the game is called coordination (or continuation game), when the two types have the same or corresponding fitnesses. If $\psi_1 > 0$, it is said that type $B$ dominates type $A$, and if $\psi_1 < 0$, type $A$ dominates type $B$. The same nomenclature is used for all games with equivalent relations. Observe that, in the BD process, we can define the birth fitness $\psi_1$ as a function corresponding to the sum of two games determined by $P_1$ and $P_3$. Similarly, in the DB process, we can define the death fitness $\psi_2$ as a function related to the sum of two games given by $P_2$ and $P_4$.

For a constant $\kappa > 0$, indicating the selection intensity, let us now modify our fitness functions by $\phi_J^i = 1 + \kappa \psi_J^i / N$, for $i = 1, 2$, where as before $J$ represents an arbitrary type from the set of types $\{A, B, C, A, B, C\}$. In the case that $\kappa \gg 1$, $\psi_2 = 0$, and $\psi_{1C} = \psi_1$ in (30), we can follow [7] to show that the asymptotic qualitative behavior of a population structured as a star graph is the same as that structured as a complete graph. In fact, for large $N$, if we only consider the leaves, we expect the behavior of the population in the star graph be quite similar to that in the complete graph, as the center of the star has the role of connecting leaves, i.e. leaves interact with each other through the center. Let $\theta_s = s \psi_1$ for $s = 1, 2$, and let $\phi_1(1)$ be the approximate fixation probability for the complete graph given in (23) and $\phi_1(2)$ be our approximation for the star graph. Following the same lines of argument in [7], for the dominance case, if $\theta_s > 0$, $B$ is dominant and

$$\phi_1(\theta_s)(x) = 1 - \exp(-\theta_s(0)x / \kappa) + O(\kappa). \quad (31)$$

In fact, type $B$ dominates in the star graph faster than in the complete graph. Similarly, if $\theta_s < 0$, $A$ is dominant and

$$\phi_1(\theta_s)(x) = \exp(\theta_s(1)(1 - x) / \kappa) + O(\kappa). \quad (32)$$

So, in the star graph, type $A$ dominates slower than in the complete graph. An example is given in Figure 5.

![Figure 5](https://example.com/figure5.png)

Figure 5: Approximations for the fixation probability in the star graph, in blue, and in the complete graph in orange. The fixation probability for the neutral case is given in green. On the left: $N = 1000$, $\kappa = 10$, $\psi_1(x) = (x - 1.5)$ and $\psi_2 = 0$; $A$ dominates. On the right: $N = 1000$, $\kappa = 10$, $\psi_1(x) = (x + 0.5)$ and $\psi_2 = 0$; $B$ dominates.

In the coexistence case, if $\int_0^1 \theta_s(r)dr \ll -\kappa$, the asymptotic approximation is given by (31). If $\int_0^1 \theta_s(r)dr \gg \kappa$, the asymptotic approximation is given by (32). Finally, if
\[ \int_0^1 \theta_s(r) dr \sim \kappa, \]

we have
\[ \phi_{s(i)}^\kappa(x) = \frac{C}{C + \lambda} \exp(\theta_s(1)(1 - x)/\kappa) + \frac{\lambda}{C + \lambda} (1 - \exp(-\theta_s(0)x/\kappa)) + O(\kappa), \] (33)

with \( \theta_s(0) > 0 > \theta_s(1) \), where \( C = \exp(\kappa^{-1} \int_0^1 \theta_s(r) dr) \), and \( \lambda = |\theta_s(1)|/\theta_s(0) \).

In the coordination case, \( \theta \) also has a unique root \( x^* \), with \( \theta'(x^*) > 0 \), and we have
\[ \phi_{s(i)}^\kappa(x) = N\left( \sqrt{\frac{\theta_s'(x^*)}{\kappa}} (x - x^*) \right) - N\left( \sqrt{\frac{\theta_s'(x^*)}{\kappa}} (1 - x^*) \right) + O(\sqrt{\kappa}) \] (34)

where \( N(x) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{x} e^{-y^2/2} dy \) is the normal cumulative distribution function. An example is given in Figure 6.

When \( \kappa = 1 \),
\[ \phi_{s(i)}''(x) = \frac{-s\psi_1(x)e^{-s\int_0^x \psi(r) dr}}{\int_0^x e^{-s\int_0^r \psi(r) dr}} \]
implies that \( A \) is dominant for a convex function \( \phi_s \), and \( B \) is dominant for a concave function \( \phi_s \). If \( \phi_s \) has an inflection point with the concave part coming first (on the left of the inflation point) and the convex part coming next (on the right of the inflation point), the game is a coexistence game. Finally, if \( \phi_s \) has an inflection point with the convex part coming first (on the left) and the concave part coming next (on the right), the game is a coordination game.

In the DB process, if \( \kappa \) is of order less than \( N \), then the behavior of the population does not essentially depend on the fitness functions.

![Figure 6: Approximations for the fixation probability in the star graph, in blue, and in the complete graph in orange, for the BD process. The fixation probability for the neutral case is given in green. On the left: \( N = 1000, \kappa = 10, \psi_1(x) = (0.5 - x) \) and \( \psi_2 = 0 \); we have the coexistence game. On the right: \( N = 1000, \kappa = 10, \psi_1(x) = (x - 0.5) \) and \( \psi_2 = 0 \); we have the coordination game.](image-url)

### 6.3 Invasion probability

Consider the approximate fixation probability vectors given in Section 3. In the DB process, a large population has a high chance to resist against the invasion of a mutant.
occupying a leaf. In fact, the fixation probability of a single mutant starting at a leaf is approximately $1/(2N)$. On the other hand, if a mutant invades the center, it has basically $1/2$ chance to fix. Letting $\rho$ be the probability to choose the center, the invasion probability in the DB process is

$$\rho \left( \frac{N}{2N - 1} + \frac{g_1(0)}{N} \right) + (1 - \rho) \left( \frac{1}{2N - 1} + \frac{g_2(1/N)}{N} \right).$$

In the BD process, however, the approximate fixation probability of a single mutant at the center is of order $N^{-2}$, or more precisely it is equal to $N^{-2} f'(0)$. This is much smaller than this probability in the DB process. On the other hand, the approximate fixation probability of a single mutant at a leaf is $f(1/N)$. Therefore, the approximate invasion probability in the BD process is

$$\rho f'(0) \frac{N}{N^2} + (1 - \rho) f(1/N),$$

where again $\rho$ is the probability to choose the center.

In the BD process for $\psi_1 = r$, constant, and $\psi_2 = 0$, the approximate invasion probability for a uniformly selected mutant site is

$$\frac{e^{-2r(1 - z + e^{2r(-1 + z - 4r\overline{\rho}(\overline{\rho})^{3})})}}{-1 + e^{2r(-1 + \overline{\rho})}}.$$

Thus letting $\overline{\rho} \to \infty$, the limit of the ratio of the invasion probability of a mutant occupying a uniformly chosen site in the star graph to the same probability for the complete graph of the same size is

$$\frac{2e^r}{1 + e^r},$$

which is an increasing function and for $r > 0$, this limit is greater than 1. Therefore, the star is an amplifier of selection. For a general distribution, the limit of the invasion probability in the star over the invasion probability in the complete graph is

$$\frac{2e^r(1 - \rho)}{1 + e^r},$$

as $\overline{\rho}$ tends to zero; see Figure 7 for the plot of (35). From Figure 7 we can see that, for a large population, if the probability $\rho$ of choosing the center is close to zero, then the star is an amplifier of selection. In the contrary, when $\rho$ increases, the star becomes a suppressor. For $\rho = \frac{1}{2} e^r(-1 + e^r)$, we have $\frac{2e^r(1-\rho)}{1+e^r} = 1$.

7 Discussion

In contrast to the previous results in the literature which only consider constant or linear fitness functions, in this paper we provided continuous approximations for the fixation probability of large populations on the star graph considering general frequency-dependent (smooth) fitness functions under the weak-selection regime. In the DB case, we proved that the approximation error is of order $1/N$, where $N$ is the size of the
Figure 7: Plot of the ratio \((35)\) in orange.

population. That is, the larger the population, the smaller the error. Even though for now we can only prove that the approximation error is small for the DB case, many numerical examples including the ones presented in this paper indicate that even for small populations our approximations are quite close to the exact fixation probability for both the DB and BD processes. As applications, we calculated the invasion probability for the star graph, for different initial type-configurations. We also analyzed the asymptotic qualitative behaviour of a population structured as a star graph when the fitness is a linear function given by a pay-off matrix. We specifically determined whether the star graph is an amplifier or a suppressor of selection, when the birth fitness \(\psi_1\) is constant.

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