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The limits of weak selection and large population size in evolutionary game theory

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Abstract Evolutionary game theory is a mathematical approach to studying how social behaviors evolve. In many recent works, evolutionary competition between strategies is modeled as a stochastic process in a finite population. In this context, two limits are both mathematically convenient and biologically relevant: weak selection and large population size. These limits can be combined in different ways, leading to potentially different results. We consider two orderings: the wN limit, in which weak selection is applied before the large population limit, and the Nw limit, in which the order is reversed. Formal mathematical definitions of the Nw and wN limits are provided. Applying these definitions to the Moran process of evolutionary game theory, we obtain asymptotic expressions for fixation probability and conditions for success in these limits. We find that the asymptotic expressions for fixation probability, and the conditions for a strategy to be favored over a neutral mutation, are different in the Nw and wN limits. However, the ordering of limits does not affect the conditions for one strategy to be favored over another.

Keywords Game theory · Social behavior · Moran process · Selection strength

Mathematics Subject Classification 91A22 · 92D15 · 60J20

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1 Introduction

Evolutionary game theory (Maynard Smith 1982; Maynard Smith and Price 1973; Hofbauer and Sigmund 1998; Weibull 1997; Broom and Rychtár 2013) is a framework for modeling the evolution of behaviors that affect others. Interactions are represented as a game, and game payoffs are linked to reproductive success. Originally formulated for infinitely large, well-mixed populations, the theory has been extended to populations of finite size (Taylor et al. 2004; Nowak et al. 2004; Imhof and Nowak 2006; Lessard and Ladret 2007) and a wide variety of structures (Nowak and May 1992; Blume 1993; Ohtsuki et al. 2006; Tarnita et al. 2009; Nowak et al. 2010; Allen and Nowak 2014).

Calculating evolutionary dynamics in finite and/or structured populations can be difficult—in some cases, provably so (Ibsen-Jensen et al. 2015). To obtain closed-form results, one often must pass to a limit. Two limits in particular have emerged as both mathematically convenient and biologically relevant: large population size and weak selection. The weak selection limit means that the game has only a small effect on reproductive success (Nowak et al. 2004). With these limits, many results become expressible in closed form that would not be otherwise.

Often one is interested in combining these limits. However, a central theme in mathematical analysis is that limits can be combined in (infinitely) many ways. It is therefore important, when applying the large-population and weak-selection limits, to be clear how they are being combined. As a first step, Jeong et al. (2014) introduced the terms Nw *limit* and wN *limit*. In the Nw limit, the large population limit is taken before the weak selection limit, while in the wN limit the order is reversed. Informally, in the Nw limit, the population becomes large "much faster" than selection becomes weak, while the reverse is true for the wN limit. While there are infinitely many ways of combining the large-population and weak-selection limits, the Nw and wN limits represent two extremes in which one limit is taken entirely before the other.

Here we provide formal mathematical definitions of the wN and Nw limits, which were lacking in the work of Jeong et al. (2014). We then apply these limits to the Moran process in evolutionary game theory (Moran 1958; Taylor et al. 2004; Nowak et al. 2004). We obtain asymptotic expressions for fixation probability under these limits, and show how these expressions differ depending on the order in which limits are taken. We also analyze criteria for evolutionary success under these limits. Our results are summarized in Table 1 and Fig. 1. We show how these limits shed new light on familiar game-theoretic concepts such as evolutionary stability, risk dominance, and the one-third rule. We also formalize and strengthen some previous results in the literature (Nowak et al. 2004; Antal and Scheuring 2006; Bomze and Pawlowitsch 2008).

Our paper is organized as follows. First we describe the model and define the wN and Nw limits. We then consider the case of constant fitness as a motivating example. Finally, we present the results of our analysis, first for the wN limit and then the Nw limit. For each limit, we derive the fixation probability for a strategy, as well as determine two conditions that measure the success of that strategy. The first condition compares the strategy's fixation probability to that of a neutral mutation. The second compares the fixation probability of one strategy to the other.

Table 1 Summary of results

	wN limit	Nw limit
ρ_A	$\frac{1}{N}+\frac{w}{6}(a+2b-c-2d)+o(w)$	$\begin{cases} o(w) & b \le d \\ o(w) & b > d \text{ and } a+b < c+d \\ (b-d)w+o(w) & b > d \text{ and } a+b > c+d \\ \frac{b-d}{2}w+o(w) & b > d \text{ and } a+b = c+d \end{cases}$
$\rho_A > \frac{1}{N}$	$a+2b > c+2d$, or $(a+2b = c+2d$ and $b > c)$	$(b > d$ and $a+b \ge c+d)$, or $(b = d$ and $a > c)$, or $(b = d, a = c$ and $b > c)$
$\rho_A > \rho_B$	$a+b > c+d$, or $(a+b = c+d$ and $b > c)$	$a+b > c+d$, or $(a+b = c+d$ and $b > c)$

The asymptotic expansions of the fixation probability of strategy A (ρ_A) and the conditions for which this fixation probability is larger than that of a neutral mutation ($\rho_A > \frac{1}{N}$) are different in the wN and Nw limits. In contrast, conditions for the fixation probability of strategy A to be larger than that of strategy B ($\rho_A > \rho_B$) are the same in both limits

2 Model

In the Moran process (Moran 1958; Taylor et al. 2004; Nowak et al. 2004), a population of size N consists of A and B individuals. Interactions are described by a game

$$\begin{array}{c c} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array}. \tag{1}$$

The fitnesses of A and B individuals are defined, respectively, as expected payoffs:

$$\begin{aligned} f_A(i) &= \frac{a(i-1)+b(N-i)}{N-1}, \\ f_B(i) &= \frac{ci+d(N-i-1)}{N-1}, \end{aligned} \tag{2}$$

where i indicates the number of A individuals. Each time-step, an individual is chosen to reproduce proportionally to its fitness, and an individual is chosen with uniform probability to be replaced.

This process has two absorbing states: $i = N$, where type A has become fixed, and $i = 0$, where type B has become fixed. The fixation probability of A, denoted ρ_A, is the probability that type A will become fixed when starting from a state with a single A individual ($i = 1$). Similarly, the fixation probability of B is denoted ρ_B and defined as the probability that type B will become fixed when starting from a state with single B individual ($i = N-1$). The fixation probability of A can be calculated as (Taylor et al. 2004)

$$\rho_A = \frac{1}{1+\sum_{k=1}^{N-1}\prod_{j=1}^{k}\frac{f_B(j)}{f_A(j)}}. \tag{3}$$

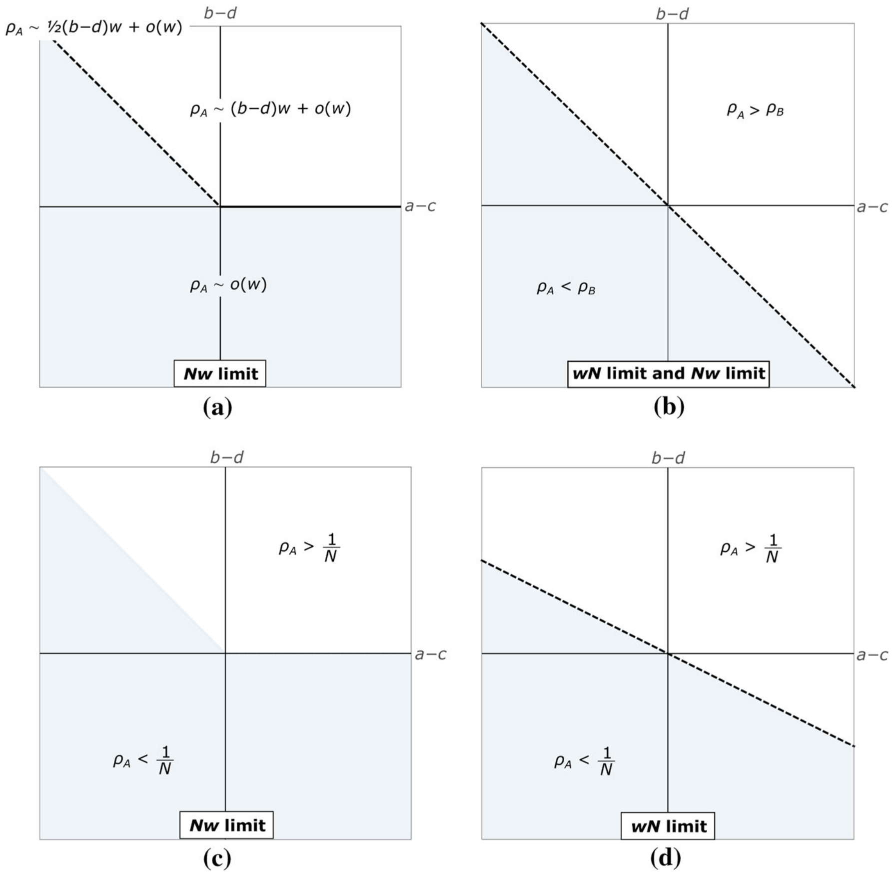

Fig. 1 Summary of our results. **a** Asymptotic expressions for ρ_A under the Nw limit in different parameter regions. The *dashed line* indicates the border case $a + b = c + d$. **b** In both the wN limit and Nw limit, $\rho_A > \rho_B$ if $a + b > c + d$. **c** The order of limits matters when comparing the fixation probability of A (ρ_A) with that of a neutral mutation ($1/N$). In the Nw limit, $\rho_A > 1/N$ if $b > d$ and $a + b \geq c + d$. **d** In the wN limit, $\rho_A > 1/N$ if $a + 2b > c + 2d$

The ratio of fixation probabilities is given by

$$\frac{\rho_A}{\rho_B} = \prod_{j=1}^{N-1} \frac{f_A(j)}{f_B(j)}. \tag{4}$$

For weak selection, we use the rescaled payoffs $F_A(i) = 1 + wf_A(i)$ and $F_B(i) = 1 + wf_B(i)$ in place of the original payoffs $f_A(i)$ and $f_B(i)$, respectively. This is equivalent to replacing the original game matrix (1) with the transformed matrix

$$\begin{pmatrix} 1 + wa & 1 + wb \\ 1 + wc & 1 + wd \end{pmatrix}. \tag{5}$$

Above, the parameter $w > 0$ quantifies the strength of selection. A result is said to hold *under weak selection* if it holds to first order in w as $w \to 0$ (Nowak et al. 2004).

The success of strategy A is quantified in two ways (Nowak et al. 2004). The first, $\rho_A > 1/N$, is the condition that selection will favor strategy A over a neutral mutation (a type for which all payoff matrix entries are equal to 1). The second condition compares the two fixation probabilities. If $\rho_A > \rho_B$, we say that strategy A is favored over strategy B.

3 Limit definitions

We provide here formal mathematical definitions of the wN limit, in which the weak selection is applied prior to taking the large population limit, and the Nw limit, in which these are reversed. We define what it means for a statement to hold true, as well as for a function to have a particular asymptotic expansion, in each of these limits.

First, we define a statement to be true in the wN limit if it holds for all sufficiently large N and all sufficiently small w, where N must be fixed first and w may depend on N. The formal statement is as follows:

Definition 1 Statement $S(N, w)$ is True *in the wN limit* if

$$(\exists N^* \in \mathbb{N}).(\forall N \geq N^*).(\exists w^* > 0).(\forall w,\ 0 < w < w^*).(S(N, w) \text{ is True}).$$

Second, we define what it means for two functions to be asymptotically equivalent to first order in w in the wN limit:

Definition 2 For functions $f(N, w)$ and $g(N, w)$, we say that $f(N, w) \sim g(N, w) + o(w)$ *in the wN limit* if and only if

$$f(N, w) = g(N, w) + wR(N, w),$$

where $\lim_{N\to\infty} \lim_{w\to 0} R(N, w) = 0$.

In words, f and g must differ by w times a remainder term that disappears as first $w \to 0$ and then $N \to \infty$.

Third, we formalize what it means for a statement to be true in the Nw limit. As in the wN limit, it must hold for all sufficiently large N and all sufficiently small w, but here w must be fixed first and N may depend on w.

Definition 3 Statement $S(N, w)$ is True *in the Nw limit* if

$$(\exists w^* > 0).(\forall w,\ 0 < w < w^*).(\exists N^* \in \mathbb{N}).(\forall N \geq N^*).(S(N, w) \text{ is True}).$$

Finally, we define what it means for two functions to be asymptotically equivalent to first order in w in the Nw limit. The only difference from Definition 2 is that the order of limits is reversed:

Definition 4 For functions $f(N, w)$ and $g(N, w)$, we say that $f(N, w) \sim g(N, w) + o(w)$ *in the* Nw *limit* if and only if

$$f(N, w) = g(N, w) + wR(N, w),$$

where $\lim_{w \to 0} \lim_{N \to \infty} R(N, w) = 0$.

4 Example: constant fitness

We illustrate the difference between the Nw and wN limits using the special case of constant fitness. In this case, the payoffs to A and B are set to constant values $f_A = 1 + s$ and $f_B = 1$, independent of the population state i, where $s > -1$ is the selection coefficient of A. The fixation probability of A is (Moran 1958)

$$\rho_A = \frac{1 - (1+s)^{-1}}{1 - (1+s)^{-N}}. \tag{6}$$

In the limits of large population size ($N \to \infty$) and weak selection ($s \to 0$), the asymptotic expansion of ρ_A is different depending on the order in which the limits are taken (Fig. 2). (Note that in the constant-fitness case, selection strength can be quantified by $|s|$ rather than w.) In the wN limit, we have

$$\rho_A \sim \frac{1}{N} + \frac{s}{2} + o(s), \tag{7}$$

whereas in the Nw limit,

$$\rho_A \sim \begin{cases} 0 & \text{if } s \leq 0 \\ s + o(s) & \text{if } s > 0. \end{cases} \tag{8}$$

The asymptotic expressions (7) and (8) hold in the sense specified by Definitions 2 and 4, respectively. Note that ρ_A is linear in the wN limit and piecewise-linear in the Nw limit. Moreover, the slope of ρ_A with respect to s in the wN limit is the average of the two corresponding slopes in the Nw limit (see also Fig. 2d, e).

Although the asymptotic expressions (7) and (8) differ under the two limit orderings, the conditions for the success of type A are the same. This is because, for any $s > -1$ and $N \geq 2$, type A is favored over a neutral mutation ($\rho_A > 1/N$), according to Eq. (6), if and only if $s > 0$. Likewise, A is favored over B ($\rho_A > \rho_B$) if and only if $s > 0$. Since these conditions apply to arbitrary s and N, they remain valid under any limits of these parameters.

5 Results

Having motivated our investigation using the case of constant selection, we now consider an arbitrary payoff matrix (1). We analyze the wN limit first, followed by the Nw limit.

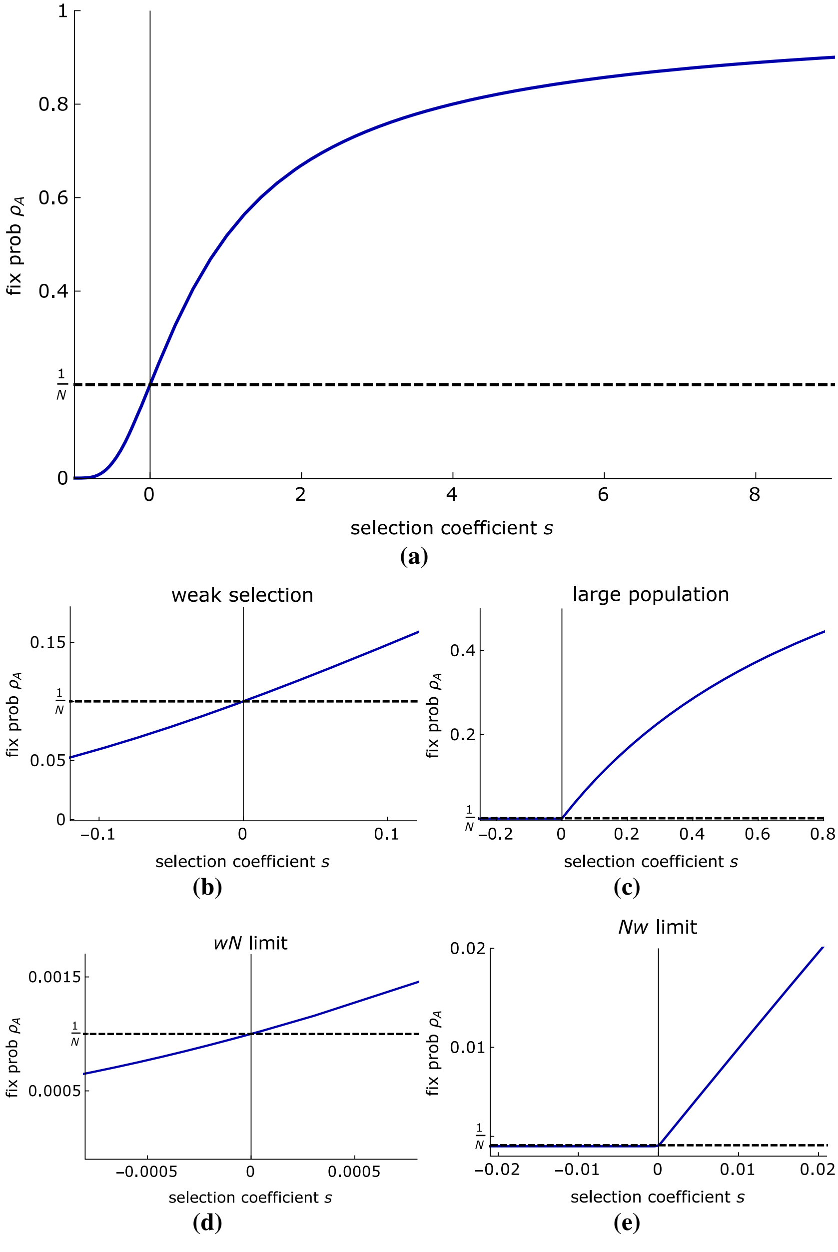

Fig. 2 Fixation probability versus selection coefficient for constant selection. **a** Fixation probability ρ_A, given by Eq. (6), is an increasing function of the selection coefficient s. **b** When selection is weak ($|s| \ll 1$), fixation probability is approximately linear in s. **c** For large population size ($N \to \infty$), fixation probability goes to zero for $s \leq 0$, and there is a corner in the graph at $s = 0$. **d** In the wN limit, weak selection is applied first followed by large population size, resulting in $\rho_A \sim 1/N + s/2 + o(s)$. **e** In the Nw limit, the limit $N \to \infty$ is applied first followed by weak selection. The result is a piecewise-linear function which is zero for $s \leq 0$ and has slope 1 for $s > 0$. Population size is $N = 5$, 10, 10^3, 10^3, and 10^4 in panels **a**–**e**, respectively

5.1 wN Limit

In the wN limit we first apply weak selection and then consider large population size. Results for ρ_A are presented first, followed by conditions for success.

Theorem 1 *In the wN limit,*

$$\rho_A \sim \frac{1}{N} + \frac{w}{6}(a + 2b - c - 2d) + o(w). \tag{9}$$

This theorem formalizes a result of Nowak et al. (2004), and can also be considered a special case of Eq. (92) of Lessard and Ladret (2007).

Proof We apply weak selection to the fitnesses in Eq. (2):

$$\begin{aligned} F_A(i) &= 1 + w\frac{a(i-1) + b(N-i)}{N-1}, \\ F_B(i) &= 1 + w\frac{ci + d(N-i-1)}{N-1}. \end{aligned} \tag{10}$$

Substituting Eq. (10) for $f_A(i)$ and $f_B(i)$ in (3) and taking a Taylor expansion about $w = 0$ gives

$$\rho_A = \frac{1}{N} + \frac{w}{6N}\left(N(a + 2b - c - 2d) - (2a + b + c - 4d)\right) + wQ(N, w), \tag{11}$$

where $\lim_{w\to 0} Q(N, w) = 0$. We regroup,

$$\rho_A = \frac{1}{N} + \frac{w}{6}(a + 2b - c - 2d) + wR(N, w),$$

defining the remainder term as $R(N, w) = Q(N, w) - \frac{1}{6N}(2a + b + c - 4d)$. By taking the limit of $R(N, w)$ as first $w \to 0$ and then $N \to \infty$, we find that

$$\begin{aligned} \lim_{N\to\infty}\lim_{w\to 0} R(N, w) &= \lim_{N\to\infty}\lim_{w\to 0}\left(Q(N, w) - \frac{1}{6N}(2a + b + c - 4d)\right) \\ &= \lim_{N\to\infty}\left(-\frac{1}{6N}(2a + b + c - 4d)\right) \\ &= 0. \end{aligned}$$

By Definition 2, $\rho_A \sim \frac{1}{N} + \frac{w}{6}(a + 2b - c - 2d) + o(w)$ in the wN limit. □

5.1.1 Conditions for success

Theorem 2 *In the wN limit, $\rho_A > \frac{1}{N}$ if and only if one of the following holds:*

(i) $a + 2b > c + 2d$

(ii) $a + 2b = c + 2d$ *and* $b > c$.

An equivalent result was obtained by Bomze and Pawlowitsch (2008).

Proof Under weak selection, it is apparent from Eq. (11) that $\rho_A > 1/N$ if $N(a+2b-c-2d)-(2a+b+c-4d) > 0$ and $\rho_A < 1/N$ if $N(a+2b-c-2d)-(2a+b+c-4d) < 0$. Thus $\rho_A > 1/N$ for sufficiently large N if $a + 2b > c + 2d$ or if $a + 2b = c + 2d$ and $2a + b + c - 4d < 0$. The second condition is equivalent to $a + 2b = c + 2d$ and $b > c$.

For the border case, $a + 2b = c + 2d$ and $b = c$, we take a second-order expansion of ρ_A:

$$\rho_A = \frac{1}{N} - w^2 \frac{(a-b)^2(N+2)(N+1)(N-2)}{240N(N-1)} + \mathcal{O}(w^3).$$

For $N > 2$ and $a \neq b$, the second order term is always negative, which implies that $\rho_A < 1/N$. Lastly, if $a = b = c = d$ then $\rho_A = 1/N$. □

Theorem 3 *In the* wN *limit,* $\rho_A > \rho_B$ *if and only if one of the following holds:*

(i) $a + b > c + d$
(ii) $a + b = c + d$ *and* $b > c$.

Case (i) of this result was stated informally by Nowak et al. (2004).

Proof Substituting Eq. (10) for $f_A(i)$ and $f_B(i)$ into Eq. (4) and taking a Taylor expansion about $w = 0$, we get

$$\begin{aligned}\frac{\rho_A}{\rho_B} &= \prod_{j=1}^{N-1} \frac{N-1+w\left(a(j-1)+b(N-j)\right)}{N-1+w\left(cj+d(N-j-1)\right)} \\ &= 1 + \frac{w}{2}\left(N(a+b-c-d) - 2a + 2d\right) + wQ(N,w),\end{aligned}$$

where $\lim_{w\to 0} Q(N, w) = 0$. Clearly, ρ_A is greater than (less than) ρ_B under weak selection if $N(a + b - c - d) - 2a + 2d$ is positive (negative). The expression is positive for sufficiently large N if $a + b > c + d$ or if $a + b = c + d$ and $a < d$. The second condition is equivalent to $a + b = c + d$ and $b > c$. Lastly, if $b = c$ and $a = d$, then from Eq. (4), $\rho_A = \rho_B$. □

5.2 Nw Limit

In this section, we first determine the limit of ρ_A as $N \to \infty$ (Theorem 4) and then find an asymptotic expression for ρ_A in the Nw limit. We then turn to conditions for success, first in the $N \to \infty$ limit (Theorems 5 and 6) and then the Nw limit.

Theorem 4 *The fixation probability ρ_A has the following large-population limit:*

$$\lim_{N\to\infty} \rho_A = \begin{cases} 0 & \text{if } b \le d \\ 0 & \text{if } b > d,\ a < c \text{ and } I > 0 \\ \frac{(b-d)(c-a)}{b(c-a)+c(b-d)\sqrt{\frac{ac}{bd}}} & \text{if } b > d,\ a < c \text{ and } I = 0 \\ \frac{b-d}{b} & \text{if } b > d,\ a < c \text{ and } I < 0 \\ \frac{b-d}{b} & \text{if } b > d,\ a \ge c, \end{cases} \tag{12}$$

where

$$I = \int_0^1 \ln \tilde{f}(x)dx, \tag{13}$$

and

$$\tilde{f}(x) = \frac{d + x(c-d)}{b + x(a-b)} \text{ for } x \in [0, 1]. \tag{14}$$

Some aspects of this result were obtained by Antal and Scheuring (2006), using a mixture of exact and approximate methods. Our proof confirms the results of Antal and Scheuring (2006) except in the case $b > d$, $a < c$, and $I = 0$, as we detail in the Discussion.

Proof We first establish some basic definitions and results before considering various cases. From Eq. (2), define the function $f\left(\frac{i}{N}, N\right)$ as

$$f\left(\frac{i}{N}, N\right) = \frac{f_B(i)}{f_A(i)} = \frac{d + \frac{i}{N}(c-d) - \frac{d}{N}}{b + \frac{i}{N}(a-b) - \frac{a}{N}}. \tag{15}$$

$\tilde{f}\left(\frac{i}{N}\right)$ of Eq. (14) serves as an approximation to $f\left(\frac{i}{N}, N\right)$ with error:

$$\begin{aligned} \epsilon_N(i) &= f\left(\frac{i}{N}, N\right) - \tilde{f}\left(\frac{i}{N}\right) \\ &= \frac{1}{N} \cdot \frac{ad - bd - \frac{i}{N}(2ad - bd - ac)}{\left[b + \frac{i}{N}(a-b)\right]\left[b + \frac{i}{N}(a-b) - \frac{a}{N}\right]}. \end{aligned} \tag{16}$$

Importantly, $\epsilon_N(i)$ is uniformly bounded in the sense that, for N sufficiently large, there exists a positive constant L such that $|\epsilon_N(i)| \le \frac{L}{N}$ for all $i = 1, \ldots, N$. Specifically, for $N \ge \frac{2a}{\min\{a,b\}}$, we can set

$$L = \frac{2\max\{|ad - bd|, |ac - ad|\}}{(\min\{a, b\})^2}.$$

Therefore, $\lim_{N\to\infty} f(x, N) = \tilde{f}(x)$ uniformly in x.

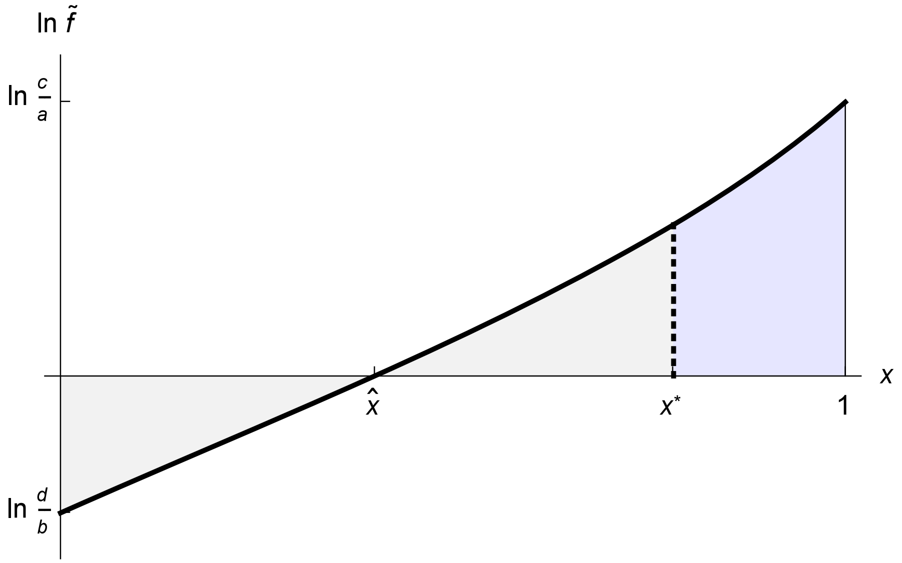

Fig. 3 Plot of $\ln \tilde{f}(x)$ versus x, where $\tilde{f}(x)$ is defined as in Eq. (14). This figure illustrates the case that $b > d, c > a$ and $I > 0$ (the net area under the curve is positive). The point x^* satisfies $\int_0^{x^*} \ln \tilde{f}(x)\, dx = 0$

In our proof, we will make use of some properties of the function $\tilde{f}(x)$. The derivative

$$\frac{d\tilde{f}}{dx} = \frac{bc - ad}{(b + x(a - b))^2}$$

implies that $\tilde{f}(x)$ is monotonic; it is always constant ($bc = ad$), strictly increasing ($bc > ad$), or strictly decreasing ($bc < ad$). Since extrema must occur at the endpoints ($\tilde{f}(0) = d/b$ and $\tilde{f}(1) = c/a$), set

$$\begin{aligned} \tilde{m} &= \min\left\{\tilde{f}(0), \tilde{f}(1)\right\} \\ \tilde{M} &= \max\left\{\tilde{f}(0), \tilde{f}(1)\right\}. \end{aligned} \tag{17}$$

Our proof also makes frequent use of the integral I of Eq. (13), which is evaluated as:

$$I = \ln\left(\frac{b^{\frac{b}{a-b}} c^{\frac{c}{c-d}}}{a^{\frac{a}{a-b}} d^{\frac{d}{c-d}}}\right). \tag{18}$$

An illustration of this integral is given in Fig. 3.

Our overall objective is to investigate the fixation probability of Eq. (3), which can be written

$$\rho_A = \frac{1}{1+S}, \tag{19}$$

where S is the sum defined as

$$S = \sum_{k=1}^{N-1} \prod_{i=1}^{k} f\left(\frac{i}{N}, N\right). \tag{20}$$

Since $\tilde{f}$ is a simpler function than f, we rewrite the product in Eq. (20) as $\prod_{i=1}^{k} \left[\tilde{f}\left(\frac{i}{N}\right) + \epsilon_N(i)\right]$. The bound on $\epsilon_N(i)$ implies that for sufficiently large N,

$$\prod_{i=1}^{k} \left[\tilde{f}\left(\frac{i}{N}\right) - \frac{L}{N}\right] \le \prod_{i=1}^{k} f\left(\frac{i}{N}, N\right) \le \prod_{i=1}^{k} \left[\tilde{f}\left(\frac{i}{N}\right) + \frac{L}{N}\right].$$

Using $\tilde{m}$, the minimum of $\tilde{f}$ given in Eq. (17), we obtain

$$\left(1 - \frac{L}{\tilde{m}N}\right)^k \prod_{i=1}^{k} \tilde{f}\left(\frac{i}{N}\right) \le \prod_{i=1}^{k} f\left(\frac{i}{N}, N\right) \le \left(1 + \frac{L}{\tilde{m}N}\right)^k \prod_{i=1}^{k} \tilde{f}\left(\frac{i}{N}\right). \tag{21}$$

These inequalities allow for the comparison between f and $\tilde{f}$.

The main idea of the proof going forward is to determine under which conditions the sum S diverges and under which conditions the sum converges (and to what value it converges to) as N gets arbitrarily large. To accomplish this, we first split the sum of Eq. (20) as $S = S_1 + S_2$, where S_1 and S_2 are non-negative sums defined as

$$S_1 = \sum_{k=1}^{\lfloor \ln N \rfloor} \prod_{i=1}^{k} f\left(\frac{i}{N}, N\right), \tag{22}$$

$$S_2 = \sum_{k=\lfloor \ln N \rfloor + 1}^{N-1} \prod_{i=1}^{k} f\left(\frac{i}{N}, N\right). \tag{23}$$

Let

$$\begin{aligned}
m_1 &= \min_{1 \le i \le \lfloor \ln N \rfloor} \left\{ f\left(\frac{i}{N}, N\right) \right\}, \\
M_1 &= \max_{1 \le i \le \lfloor \ln N \rfloor} \left\{ f\left(\frac{i}{N}, N\right) \right\}, \\
m_2 &= \min_{\lfloor \ln N \rfloor + 1 \le i \le N-1} \left\{ f\left(\frac{i}{N}, N\right) \right\}, \\
M_2 &= \max_{\lfloor \ln N \rfloor + 1 \le i \le N-1} \left\{ f\left(\frac{i}{N}, N\right) \right\}.
\end{aligned} \tag{24}$$

Since f converges uniformly to the monotonic function $\tilde{f}$,

$$\begin{aligned}\lim_{N\to\infty} m_1 &= \tilde{f}(0) = \frac{d}{b},\\ \lim_{N\to\infty} M_1 &= \tilde{f}(0) = \frac{d}{b},\\ \lim_{N\to\infty} m_2 &= \tilde{m} = \min\left\{\frac{d}{b}, \frac{c}{a}\right\},\\ \lim_{N\to\infty} M_2 &= \tilde{M} = \max\left\{\frac{d}{b}, \frac{c}{a}\right\}.\end{aligned} \tag{25}$$

Useful inequalities obtained from Eqs. (22) and (24) are

$$\begin{aligned}\sum_{k=1}^{\lfloor \ln N\rfloor}\prod_{i=1}^{k} m_1 \le S_1 \le \sum_{k=1}^{\lfloor \ln N\rfloor}\prod_{i=1}^{k} M_1,\\ \sum_{k=1}^{\lfloor \ln N\rfloor} m_1^k \le S_1 \le \sum_{k=1}^{\lfloor \ln N\rfloor} M_1^k.\end{aligned} \tag{26}$$

The geometric series gives

$$\frac{m_1 - m_1^{\lfloor \ln N\rfloor+1}}{1-m_1} \le S_1 \le \frac{M_1 - M_1^{\lfloor \ln N\rfloor+1}}{1-M_1}, \tag{27}$$

as long as $m_1 \neq 1$ and $M_1 \neq 1$, respectively.

Now that we have some basic definitions and results, we pursue $\lim_{N\to\infty}\rho_A$ by considering cases. We first compare b and d. If necessary, we then compare a and c and if further required, consider the sign of I.

1. Case $b < d$ In this case, $\lim_{N\to\infty} m_1 = d/b > 1$ and

   $$\lim_{N\to\infty}\frac{m_1 - m_1^{\lfloor \ln N\rfloor+1}}{1-m_1} = \infty.$$

   It follows from Eq. (27) that $\lim_{N\to\infty} S_1 = \infty$ and consequently, $\lim_{N\to\infty} S = \infty$. Eq. (19) gives $\lim_{N\to\infty}\rho_A = 0$.
2. Case $b = d$
   In this case, $\lim_{N\to\infty} m_1 = d/b = 1$. We will show that the sum $\sum_{k=1}^{\lfloor \ln N\rfloor} m_1^k$ diverges. Fix an arbitrary positive integer B so that

   $$\lim_{N\to\infty}\sum_{k=1}^{B+1} m_1^k = B+1.$$

This implies that for all sufficiently large N,

$$\sum_{k=1}^{B+1} m_1^k > B.$$

In particular, for $\lfloor \ln N \rfloor > B + 1$,

$$\sum_{k=1}^{\lfloor \ln N \rfloor} m_1^k > \sum_{k=1}^{B+1} m_1^k > B.$$

Since B was arbitrary $\sum_{k=1}^{\lfloor \ln N \rfloor} m_1^k$ becomes larger than any positive integer as $N \to \infty$. This proves that

$$\lim_{N\to\infty} \sum_{k=1}^{\lfloor \ln N \rfloor} m_1^k = \infty.$$

From Eq. (26) we conclude that $\lim_{N\to\infty} S_1 = \infty$ and consequently $\lim_{N\to\infty} \rho_A = 0$.

3. Case $b > d$
Under this case $\lim_{N\to\infty} m_1 = \lim_{N\to\infty} M_1 = d/b < 1$. From Eq. (27), S_1 is bounded, and it follows from taking the limit as $N \to \infty$ of Eq. (27) and applying the Squeeze Theorem (Thomson et al. 2001) that

$$\lim_{N\to\infty} S_1 = \frac{d}{b-d}. \tag{28}$$

We now turn our attention to S_2, which requires the consideration of subcases.

(a) Subcase $a > c$
Eq. (25) implies $\lim_{N\to\infty} m_2 < 1$ and $\lim_{N\to\infty} M_2 < 1$. Furthermore, S_2 of Eq. (23) is bounded:

$$\sum_{k=\lfloor \ln N \rfloor+1}^{N-1} m_2^k \le S_2 \le \sum_{k=\lfloor \ln N \rfloor+1}^{N-1} M_2^k$$
$$\frac{{m_2}^{\lfloor \ln N \rfloor+1} - {m_2}^N}{1-m_2} \le S_2 \le \frac{{M_2}^{\lfloor \ln N \rfloor+1} - {M_2}^N}{1-M_2}.$$

Applying the Squeeze Theorem (Thomson et al. 2001),

$$\lim_{N\to\infty} S_2 = 0. \tag{29}$$

Eqs. (28) and (29) together give $\lim_{N\to\infty} S = d/(b-d)$ and by Eq. (19), $\lim_{N\to\infty} \rho_A = (b-d)/b$.

(b) Subcase $a < c$
In this case, $\tilde{f}$ is an increasing function with minimum value of $\tilde{f}(0) = d/b < 1$ and maximum value of $\tilde{f}(1) = c/a > 1$. The behavior of ρ_A depends on the sign of the integral I. Therefore, we must consider subcases to this subcase. An illustration is given in Fig. 3 for the subcase $I > 0$.
  i Subcase $I < 0$
  We will show that $S_2 \to 0$ as $N \to \infty$. Set

$$\tilde{A}_k = \sum_{i=1}^{k} \ln \tilde{f}\left(\frac{i}{N}\right), \tag{30}$$

and

$$\tilde{S_2} = \sum_{k=\lfloor \ln N \rfloor+1}^{N-1} \prod_{i=1}^{k} \tilde{f}\left(\frac{i}{N}\right) = \sum_{k=\lfloor \ln N \rfloor+1}^{N-1} \exp \tilde{A}_k. \tag{31}$$

We will prove $\tilde{S_2} \to 0$ as $N \to \infty$ by first showing that $\exp \tilde{A}_k$ is less than or equal to some constant multiple of e^{kI}, where I is defined in Eq. (13).
Consider the integral $\int_0^{k/N} \ln \tilde{f}(x)\, dx$. Since $\ln \tilde{f}(x)$ is a monotonically increasing function, the left Riemann sum is a lower bound:

$$\begin{aligned}\int_0^{k/N} \ln \tilde{f}(x)\, dx &> \frac{1}{N} \sum_{i=0}^{k-1} \ln \tilde{f}\left(\frac{i}{N}\right) \\ &= \frac{1}{N}\left(\tilde{A}_k + \ln \tilde{f}(0) - \ln \tilde{f}\left(\frac{k}{N}\right)\right).\end{aligned} \tag{32}$$

Furthermore, the maximum value of $\ln \tilde{f}(x)$ is $\ln \tilde{f}(1)$. Substituting this bound into (32) and rearranging, we have that for all $k = 1, ..., N$,

$$\tilde{A}_k < N \int_0^{k/N} \ln \tilde{f}(x)\, dx + \ln \frac{\tilde{f}(1)}{\tilde{f}(0)}. \tag{33}$$

Since $\ln \tilde{f}$ is increasing, the average value of $\ln \tilde{f}(x)$ over intervals $[0, y]$ must be increasing in y. Hence for $y \in [0, 1]$,

$$\frac{1}{y} \int_0^{y} \ln \tilde{f}(x)\, dx \le \int_0^{1} \ln \tilde{f}(x)\, dx = I.$$

Let $y = k/N$ to obtain

$$N \int_0^{k/N} \ln \tilde{f}(x)\, dx \leq kI.$$

Combining with Eq. (33),

$$\tilde{A}_k < kI + \ln \frac{\tilde{f}(1)}{\tilde{f}(0)}. \tag{34}$$

Substitute Eq. (34) into Eq. (31) to obtain

$$\tilde{S}_2 < \sum_{k=\lfloor \ln N \rfloor+1}^{N-1} \frac{\tilde{f}(1)}{\tilde{f}(0)} e^{kI} = \frac{\tilde{f}(1)}{\tilde{f}(0)} \cdot \frac{e^{I(\lfloor \ln N \rfloor+1)} - e^{IN}}{1 - e^{I}}.$$

Therefore since $I < 0$,

$$\lim_{N\to\infty} \tilde{S}_2 = 0. \tag{35}$$

We must now show how $\tilde{S}_2$ relates to S_2. Substitute $\tilde{m} = \tilde{f}(0) = d/b$ into Eq. (21) and sum over k to obtain an upper bound for S_2:

$$\sum_{k=\lfloor \ln N \rfloor+1}^{N-1} \prod_{i=1}^{k} f\left(\frac{i}{N}, N\right) \leq \sum_{k=\lfloor \ln N \rfloor+1}^{N-1} \left(1 + \frac{bL}{dN}\right)^{k} \prod_{i=1}^{k} \tilde{f}\left(\frac{i}{N}\right)$$
$$\leq \left(1 + \frac{bL}{dN}\right)^{N} \sum_{k=\lfloor \ln N \rfloor+1}^{N-1} \prod_{i=1}^{k} \tilde{f}\left(\frac{i}{N}\right).$$

Thus,

$$S_2 \leq \left(1 + \frac{bL}{dN}\right)^{N} \tilde{S}_2.$$

The limit

$$\lim_{N\to\infty} \left(1 + \frac{bL}{dN}\right)^{N} = e^{bL/d}, \tag{36}$$

together with Eq. (35) gives

$$\lim_{N\to\infty} S_2 = 0. \tag{37}$$

Adding Eqs. (28) and (37), we find $\lim_{N\to\infty} S = d/(b-d)$ and consequently $\lim_{N\to\infty} \rho_A = (b-d)/b$.

ii Subcase $I > 0$

We will show that $S_2 \to \infty$ as $N \to \infty$. Break up S_2 of Eq. (23) so that $S_2 = S_3 + S_4$, where

$$S_3 = \sum_{k=\lfloor \ln N \rfloor+1}^{\lfloor Nx^* \rfloor-1} \prod_{i=1}^{k} f\left(\frac{i}{N}, N\right),$$
$$S_4 = \sum_{k=\lfloor Nx^* \rfloor}^{N-1} \prod_{i=1}^{k} f\left(\frac{i}{N}, N\right), \tag{38}$$

and x^* is defined as the point where $\int_0^{x^*} \ln \tilde{f}(x)\, dx = 0$ (see Fig. 3). Define

$$m_4 = \min_{\lfloor Nx^* \rfloor \le i \le N-1} \left\{ f\left(\frac{i}{N}, N\right) \right\}. \tag{39}$$

This implies the inequality:

$$S_4 \ge \sum_{k=\lfloor Nx^* \rfloor}^{N-1} \prod_{i=1}^{k} m_4 = \sum_{k=\lfloor Nx^* \rfloor}^{N-1} m_4^k = \frac{m_4^{\lfloor Nx^* \rfloor} - m_4^N}{1 - m_4}. \tag{40}$$

Since $\tilde{f}$ is increasing, m_4 has the limit: $\lim_{N\to\infty} m_4 = \tilde{f}(x^*) > 1$. Therefore, $\lim_{N\to\infty} S_4 = \infty$, which implies that $\lim_{N\to\infty} S = \infty$ and $\lim_{N\to\infty} \rho_A = 0$.

iii Subcase $I = 0$

We will show that limit of S_2 as $N \to \infty$ is positive and finite. Let $\hat{x} = (b-d)/(b-d+c-a)$ be the point for which $\tilde{f}(\hat{x}) = 1$ (see Fig. 3). Consider a sequence β_N that satisfies

$$\hat{x} < \lim_{N\to\infty} \frac{\beta_N}{N} < 1,$$

and converges to a limit $\beta = \lim_{N\to\infty} \beta_N/N$. Split S_2 of Eq. (23) at $k = \beta_N$, such that $S_2 = S_5 + S_6$, where S_6 is the right tail-end of the sum. We will show that $S_5 \to 0$ and S_6 approaches a positive constant as $N \to \infty$. Set

$$S_5 = \sum_{k=\lfloor \ln N \rfloor+1}^{\beta_N-1} \prod_{i=1}^{k} f\left(\frac{i}{N}, N\right)$$
$$S_6 = \sum_{k=\beta_N}^{N-1} \prod_{i=1}^{k} f\left(\frac{i}{N}, N\right). \tag{41}$$

To obtain the limit of S_5 we define

$$\tilde{S}_5 = \sum_{k=\lfloor \ln N \rfloor+1}^{\beta_N - 1} \prod_{i=1}^{k} \tilde{f}\left(\frac{i}{N}\right) = \sum_{k=\lfloor \ln N \rfloor+1}^{\beta_N - 1} \exp \tilde{A}_k,$$

where $\tilde{A}_k$ is given in Eq. (30). Set $C = \int_0^\beta \ln \tilde{f}(x)\, dx$. Importantly, $C < 0$ since $\beta < 1$, $I = 0$ and $\ln \tilde{f}(x)$ is monotonic. Similar arguments as in case 3(b)i show that

$$\tilde{S}_5 < \sum_{k=\lfloor \ln N \rfloor+1}^{\beta_N - 1} \frac{\tilde{f}(1)}{\tilde{f}(0)} e^{kC} = \frac{\tilde{f}(1)}{\tilde{f}(0)} \cdot \frac{e^{C(\lfloor \ln N \rfloor + 1)} - e^{C\beta_N}}{1 - e^C}.$$

Since $C < 0$, it follows that

$$\lim_{N\to\infty} \tilde{S}_5 = 0. \tag{42}$$

To relate $\tilde{S}_5$ to S_5, we substitute $\tilde{m} = d/b$ into Eq. (21) to obtain an upper bound for S_5,

$$S_5 \leq \left(1 + \frac{bL}{dN}\right)^N \tilde{S}_5.$$

Consequently, from Eqs. (36) and (42),

$$\lim_{N\to\infty} S_5 = 0. \tag{43}$$

We now turn our attention to S_6 of Eq. (41). Define

$$\begin{aligned} m_6 &= \min_{\beta_N \leq i \leq N-1} \left\{ f\left(\frac{i}{N}, N\right) \right\}, \\ M_6 &= \max_{\beta_N \leq i \leq N-1} \left\{ f\left(\frac{i}{N}, N\right) \right\}, \end{aligned} \tag{44}$$

which have the limits $\lim_{N\to\infty} m_6 = \tilde{f}(\beta) > 1$ and $\lim_{N\to\infty} M_6 = \tilde{f}(1) = c/a > 1$. Rewrite S_6 as

$$\begin{aligned} S_6 &= \left[\prod_{i=1}^{N-1} f\left(\frac{i}{N}, N\right)\right] \left[1 + \sum_{k=\beta_N}^{N-2} \prod_{j=k+1}^{N-1} \left(f\left(\frac{j}{N}, N\right)\right)^{-1}\right] \\ &= \left[\prod_{i=1}^{N-1} f\left(\frac{i}{N}, N\right)\right] \left[1 + \sum_{\ell=1}^{N-\beta_N-1} \prod_{h=1}^{\ell} \left(f\left(\frac{N-h}{N}, N\right)\right)^{-1}\right]. \end{aligned} \tag{45}$$

Denote the second factor on the right-hand side of Eq. (45) by $\hat{S}_6$. From Eq. (44), we have the bounds

$$1 + \sum_{\ell=1}^{N-\beta_N-1} M_6^{-\ell} \le \hat{S}_6 \le 1 + \sum_{\ell=1}^{N-\beta_N-1} m_6^{-\ell}$$
$$1 + \frac{M_6^{-N+\beta_N} - M_6^{-1}}{M_6^{-1} - 1} \le \hat{S}_6 \le 1 + \frac{m_6^{-N+\beta_N} - m_6^{-1}}{m_6^{-1} - 1}.$$

Now taking $N \to \infty$,

$$\lim_{N\to\infty} \frac{M_6}{M_6 - 1} \le \lim_{N\to\infty} \hat{S}_6 \le \lim_{N\to\infty} \frac{m_6}{m_6 - 1}$$
$$\frac{\tilde{f}(1)}{\tilde{f}(1) - 1} \le \lim_{N\to\infty} \hat{S}_6 \le \frac{\tilde{f}(\beta)}{\tilde{f}(\beta) - 1}. \tag{46}$$

Since Eq. (46) is true for all β with $\hat{x} < \beta < 1$, then

$$\lim_{N\to\infty} \hat{S}_6 = \frac{\tilde{f}(1)}{\tilde{f}(1) - 1} = \frac{c}{c - a}. \tag{47}$$

We now analyze the first factor of Eq. (45) by first investigating the integral I. Apply the Extended Trapezoidal Rule (Abramowitz and Stegun 1964) to I:

$$I = \int_0^1 \ln \tilde{f}(x)dx$$
$$= \frac{1}{N}\left[\frac{\ln \tilde{f}(0) + \ln \tilde{f}(1)}{2} + \sum_{i=1}^{N-1} \ln \tilde{f}\left(\frac{i}{N}\right)\right] + \mathcal{O}\left(N^{-2}\right).$$

Recalling that $I = 0$, $\tilde{f}(0) = d/b$ and $\tilde{f}(1) = c/a$, we obtain the asymptotic expansion:

$$\sum_{i=1}^{N-1} \ln \tilde{f}\left(\frac{i}{N}\right) = \ln\sqrt{\frac{ab}{cd}} + \mathcal{O}(N^{-1}). \tag{48}$$

Next we compare the sum in Eq. (48) with $\sum_{i=1}^{N-1} \ln f\left(\frac{i}{N}, N\right)$ by looking at their difference:

$$\begin{aligned}
&\sum_{i=1}^{N-1} \ln f\left(\frac{i}{N}, N\right) - \sum_{i=1}^{N-1} \ln \tilde{f}\left(\frac{i}{N}\right) \\
&\quad = \sum_{i=1}^{N-1} \ln \frac{f\left(\frac{i}{N}, N\right)}{\tilde{f}\left(\frac{i}{N}\right)} \\
&\quad = \sum_{i=1}^{N-1} \ln \Bigg[1 + \frac{1}{N}\left(\frac{a}{b + \frac{i}{N}(a-b) - \frac{a}{N}} - \frac{d}{d + \frac{i}{N}(c-d)}\right) \\
&\qquad\qquad - \frac{1}{N^2}\frac{ad}{\left(d + \frac{i}{N}(c-d)\right)\left(b + \frac{i}{N}(a-b) - \frac{a}{N}\right)}\Bigg].
\end{aligned}$$

As $N \to \infty$, we have the asymptotic expression

$$\begin{aligned}
&\sum_{i=1}^{N-1} \ln f\left(\frac{i}{N}, N\right) - \sum_{i=1}^{N-1} \ln \tilde{f}\left(\frac{i}{N}\right) \\
&\quad = \frac{1}{N}\sum_{i=1}^{N-1}\left(\frac{a}{b + \frac{i}{N}(a-b)} - \frac{d}{d + \frac{i}{N}(c-d)}\right) + \mathcal{O}(N^{-1}).
\end{aligned}$$

If we add and subtract $(a-b)/(bN)$ to the right-hand side, we obtain a left Riemann sum, which can be replaced as $N \to \infty$ by an integral:

$$\begin{aligned}
&\sum_{i=1}^{N-1} \ln f\left(\frac{i}{N}, N\right) - \sum_{i=1}^{N-1} \ln \tilde{f}\left(\frac{i}{N}\right) \\
&\quad = \frac{1}{N}\sum_{i=0}^{N-1}\left(\frac{a}{b + \frac{i}{N}(a-b)} - \frac{d}{d + \frac{i}{N}(c-d)}\right) - \frac{a-b}{bN} + \mathcal{O}(N^{-1}) \\
&\quad = \int_0^1 \left(\frac{a}{b + x(a-b)} - \frac{d}{d + x(c-d)}\right) dx + \mathcal{O}(N^{-1})
\end{aligned}$$

Evaluate the integral to obtain:

$$\sum_{i=1}^{N-1} \ln f\left(\frac{i}{N}, N\right) - \sum_{i=1}^{N-1} \ln \tilde{f}\left(\frac{i}{N}\right) = \ln\left(\frac{a^{\frac{a}{a-b}}\, d^{\frac{d}{c-d}}}{b^{\frac{a}{a-b}}\, c^{\frac{d}{c-d}}}\right) + \mathcal{O}(N^{-1}). \tag{49}$$

The logarithm can be simplified using the condition $I = 0$. Eq. (18) gives $a^{\frac{a}{a-b}} d^{\frac{d}{c-d}} = b^{\frac{b}{a-b}} c^{\frac{c}{c-d}}$, therefore

$$\ln\left(\frac{a^{\frac{a}{a-b}} d^{\frac{d}{c-d}}}{b^{\frac{a}{a-b}} c^{\frac{d}{c-d}}}\right) = \ln\left(\frac{b^{\frac{b}{a-b}} c^{\frac{c}{c-d}}}{b^{\frac{a}{a-b}} c^{\frac{d}{c-d}}}\right) = \ln\left(\frac{c}{b}\right).$$

Eq. (49) then simplifies to

$$\sum_{i=1}^{N-1} \ln f\left(\frac{i}{N}, N\right) - \sum_{i=1}^{N-1} \ln \tilde{f}\left(\frac{i}{N}\right) = \ln\left(\frac{c}{b}\right) + \mathcal{O}(N^{-1}). \tag{50}$$

Combining Eqs. (48) and (50) yields

$$\begin{aligned}\sum_{i=1}^{N-1} \ln f\left(\frac{i}{N}, N\right) &= \ln\sqrt{\frac{ab}{cd}} + \ln\left(\frac{c}{b}\right) + \mathcal{O}(N^{-1})\\ &= \ln\sqrt{\frac{ac}{bd}} + \mathcal{O}(N^{-1}).\end{aligned}$$

Thus, $\prod_{i=1}^{N-1} f\left(\frac{i}{N}, N\right) = \sqrt{ac/(bd)} + \mathcal{O}(N^{-1})$ and

$$\lim_{N\to\infty} \prod_{i=1}^{N-1} f\left(\frac{i}{N}, N\right) = \sqrt{\frac{ac}{bd}}. \tag{51}$$

Combine Eqs. (47) and (51) with (45) to obtain

$$\lim_{N\to\infty} S_6 = \frac{c}{c-a}\sqrt{\frac{ac}{bd}}. \tag{52}$$

Altogether Eqs. (28), (43) and (52) give

$$\lim_{N\to\infty} S = \lim_{N\to\infty} (S_1 + S_5 + S_6) = \frac{d}{b-d} + \frac{c}{c-a}\sqrt{\frac{ac}{bd}},$$

and from Eq. (19),

$$\lim_{N\to\infty} \rho_A = \frac{(b-d)(c-a)}{b(c-a) + c(b-d)\sqrt{\frac{ac}{bd}}}. \tag{53}$$

(c) Subcase $a = c$
In this case, $\tilde{f}$ is a strictly increasing function with minimum value $\tilde{f}(0) = d/b < 1$ and maximum value $\tilde{f}(1) = c/a = 1$. Thus, $\ln \tilde{f}(x) < 0$ for all $x \in [0, 1)$ implying that $I < 0$. The same argument

used in the case 3(b)i applies here. We obtain the result $\lim_{N\to\infty} \rho_A = (b-d)/b$. □

Theorem 4 gives the large-population limit of ρ_A. We now introduce weak selection to obtain asymptotic expressions for ρ_A in the Nw limit.

Corollary 1 *In the Nw limit,*

$$\rho_A \sim \begin{cases} o(w) & \text{if } b \le d \\ o(w) & \text{if } b > d \text{ and } a+b < c+d \\ \frac{b-d}{2} w + o(w) & \text{if } b > d \text{ and } a+b = c+d \\ (b-d)w + o(w) & \text{if } b > d \text{ and } a+b > c+d. \end{cases} \tag{54}$$

Proof We introduce weak selection according to Eq. (5). The integral I, given in closed form in Eq. (18), has the following expansion as $w \to 0$:

$$I = \frac{w}{2}(c-a+d-b) + \mathcal{O}(w^2). \tag{55}$$

We now separate into the cases of Theorem 4.

1. Case $(b \le d)$ or $(b > d,\ a < c$ and $I > 0)$
   First note that given the expansion of Eq. (55), the condition $(b > d) \wedge (a < c) \wedge (I > 0)$ is equivalent to $(b > d) \wedge (a+b < c+d)$. Since $\lim_{N\to\infty} \rho_A = 0$, $\rho_A \sim o(w)$ by Definition 4.
2. Case $(b > d$ and $a \ge c)$ or $(b > d,\ a < c$ and $I < 0)$
   Using Eq. (55), these two conditions are described by one condition under weak selection: $(b > d) \wedge (a+b > c+d)$. Apply weak selection to $(b-d)/b$ and take $N \to \infty$ to get

   $$\lim_{N\to\infty} \rho_A = \frac{w(b-d)}{1+wb} = w(b-d) + wR(w),$$

   where $\lim_{w\to 0} R(w) = 0$. By Definition 4, $\rho_A \sim (b-d)w + o(w)$.
3. Case $b > d, a < c$ and $I = 0$
   Given Eq. (55), this case under weak selection is equivalent to $(b > d) \wedge (a+b = c+d)$. In particular, we have $b-d = c-a$, which allows the cancellation of a factor of $b-d$ from the numerator and denominator of Eq. (53). Applying weak selection and taking $N \to \infty$ yields

   $$\lim_{N\to\infty} \rho_A = \frac{b-d}{2} w + wR(w),$$

   where $\lim_{w\to 0} R(w) = 0$. By Definition 4, $\rho_A \sim \frac{b-d}{2} w + o(w)$. □

5.2.1 Conditions for success

To determine conditions for success ($\rho_A > 1/N$ and $\rho_A > \rho_B$) in the Nw limit, we must first determine such conditions in the limit of large population size. To do so, we note that

Theorem 5 *$\rho_A > 1/N$ for sufficiently large N if and only if one of the following holds:*

(i) $b > d$ and $a \geq c$
(ii) $b > d$, $a < c$ and $I \leq 0$
(iii) $b = d$ and $a > c$
(iv) $b = d$, $a = c$ and $b > c$

Proof $\rho_A > 1/N$ for sufficiently large N if $\lim_{N\to\infty} N\rho_A > 1$. From Eq. (19), we have the relation

$$\lim_{N\to\infty} N\rho_A = \lim_{N\to\infty} \frac{N}{1+S} = \lim_{N\to\infty} \frac{1}{1/N + S/N} = \left(\lim_{N\to\infty} \frac{S}{N}\right)^{-1}. \tag{56}$$

Consider the following cases.

1. Case ($b > d$ and $a \geq c$) or ($b > d$, $a < c$ and $I \leq 0$)
   From Eq. (12), $\lim_{N\to\infty} \rho_A$ is positive and finite. Thus, $\lim_{N\to\infty} N\rho_A = \infty$.
2. Case $b > d$, $a < c$ and $I > 0$
   Given $S \geq S_4$ and $\lim_{N\to\infty} m_4 = \tilde{f}(x^*) > 1$, where S_4 and m_4 are defined in Eqs. (38) and (39), respectively, we use the inequality of Eq. (40) to obtain

$$\lim_{N\to\infty} \frac{S}{N} \geq \lim_{N\to\infty} \frac{m_4^{\lfloor Nx^*\rfloor} - m_4^N}{N(1-m_4)} = \infty.$$

   Therefore from Eq. (56), $\lim_{N\to\infty} N\rho_A = 0$.
3. Case $b < d$
   Given Eq. (27),

$$S \geq S_1 \geq \frac{m_1^{\lfloor \ln N\rfloor + 1} - m_1}{m_1 - 1}.$$

   Since $\lim_{N\to\infty} m_1 = \frac{d}{b} > 1$,

$$\lim_{N\to\infty} \frac{S}{N} \geq \lim_{N\to\infty} \frac{m_1^{\lfloor \ln N\rfloor + 1} - m_1}{N(m_1 - 1)} = \infty.$$

   Therefore, $\lim_{N\to\infty} N\rho_A = 0$.
4. Case $b = d$
   (a) Subcase $a = b = c = d$
   $f\left(\frac{i}{N}, N\right) = 1$ for all i with $\rho_A = \frac{1}{N}$. Therefore, $\lim_{N\to\infty} N\rho_A = 1$.

(b) Subcase $a = c$ and $a \neq b$
Here

$$\frac{\partial f}{\partial x} = -\frac{(a-b)^2}{N\left(a\left(\frac{1}{N}-x\right)+b(x-1)\right)^2}.$$

Therefore, f is a decreasing function. Let

$$m = \min_{1\leq i\leq N-1}\left\{f\left(\frac{i}{N},N\right)\right\} = f\left(\frac{N-1}{N},N\right) = \frac{a-\frac{a}{N}}{a+\frac{b-2a}{N}},$$
$$M = \max_{1\leq i\leq N-1}\left\{f\left(\frac{i}{N},N\right)\right\} = f\left(\frac{1}{N},N\right) = \frac{b+\frac{a-2b}{N}}{b-\frac{b}{N}}.$$

Then

$$\sum_{k=1}^{N-1} m^k \leq S \leq \sum_{k=1}^{N-1} M^k$$
$$\frac{m^N-m}{N(m-1)} \leq \frac{S}{N} \leq \frac{M^N-M}{N(M-1)} \tag{57}$$

Note that $\lim_{N\to\infty} m = \lim_{N\to\infty} M = 1$. To determine the limit of S/N as $N \to \infty$, requires the derivatives:

$$\frac{dm}{dN} = \frac{a(b-a)}{(Na+b-2a)^2}, \tag{58}$$
$$\frac{dM}{dN} = \frac{b-a}{b(N-1)^2}. \tag{59}$$

Applying L'Hôpital's Rule (Abramowitz and Stegun 1964) and using Eqs. (58) and (59), we obtain the following limits:

$$\lim_{N\to\infty} N(m-1) = \lim_{N\to\infty}\frac{\frac{dm}{dN}}{-N^{-2}} = \frac{a-b}{a},$$
$$\lim_{N\to\infty} N(M-1) = \lim_{N\to\infty}\frac{\frac{dM}{dN}}{-N^{-2}} = \frac{a-b}{b},$$
$$\lim_{N\to\infty} N\ln m = \lim_{N\to\infty}\frac{\frac{1}{m}\frac{dm}{dN}}{-N^{-2}} = \frac{a-b}{a}$$
$$\lim_{N\to\infty} N\ln M = \lim_{N\to\infty}\frac{\frac{1}{M}\frac{dM}{dN}}{-N^{-2}} = \frac{a-b}{b}$$

Therefore,

$$\lim_{N\to\infty} m^N = \lim_{N\to\infty} e^{N\ln m} = \exp\left(\frac{a-b}{a}\right),$$
$$\lim_{N\to\infty} M^N = \lim_{N\to\infty} e^{N\ln M} = \exp\left(\frac{a-b}{b}\right).$$

Take the limit of Eq. (57) to obtain

$$\frac{\exp\left(\frac{a-b}{a}\right)-1}{\frac{a-b}{a}} \le \lim_{N\to\infty}\frac{S}{N} \le \frac{\exp\left(\frac{a-b}{b}\right)-1}{\frac{a-b}{b}}.$$

If $a > b$ (equivalently $b < c$) then $\lim_{N\to\infty} S/N > 1$. If $a < b$ (equivalently $b > c$) then $\lim_{N\to\infty} S/N < 1$. Thus, $\lim_{N\to\infty} N\rho_A > 1$ if $b = d$, $a = c$ and $b > c$ by Eq. (56).

(c) Subcase $a < c$
Set

$$m_7 = \min_{N-\lfloor\ln N\rfloor \le i \le N-1}\left\{f\left(\frac{i}{N}, N\right)\right\}.$$

Note that $\lim_{N\to\infty} m_7 = \tilde{f}(1) = c/a > 1$ given that f converges uniformly to $\tilde{f}$. Then

$$\lim_{N\to\infty}\frac{S}{N} \ge \lim_{N\to\infty}\frac{1}{N}\sum_{k=N-\lfloor\ln N\rfloor}^{N-1} m_7^k$$
$$= \lim_{N\to\infty}\frac{m_7^N - m_7^{N-\lfloor\ln N\rfloor}}{N(m_7-1)} = \infty$$

By Eq. (56), $\lim_{N\to\infty}\rho_A = 0$.

(d) Subcase $a > c$
Here

$$\frac{\partial f}{\partial x} = \frac{b(c-a)+\frac{2ab-b^2-ac}{N}}{N^2\left(b+x(a-b)-\frac{a}{N}\right)^2}.$$

Therefore for $N > \frac{2ab-b^2-ac}{b(a-c)}$, f is strictly decreasing.

Break up the sum S as $S = S_8 + S_9$, where

$$S_8 = \sum_{k=1}^{\lfloor\sqrt{N}\rfloor-1} \prod_{i=1}^{k} f\left(\frac{i}{N}, N\right)$$
$$S_9 = \sum_{k=\lfloor\sqrt{N}\rfloor}^{N-1} \prod_{i=1}^{k} f\left(\frac{i}{N}, N\right).$$

Given $N > \frac{2ab-b^2-ac}{b(a-c)}$, define

$$M_8 = \max_{1\le i\le\lfloor\sqrt{N}\rfloor-1} f\left(\frac{i}{N}, N\right) = f\left(\frac{1}{N}, N\right) = \frac{b+\frac{c-2b}{N}}{b-\frac{b}{N}},$$
$$M_9 = \max_{\lfloor\sqrt{N}\rfloor\le i\le N-1} f\left(\frac{i}{N}, N\right) = f\left(\frac{\lfloor\sqrt{N}\rfloor}{N}, N\right) = \frac{b+\frac{1}{\lfloor\sqrt{N}\rfloor}(c-b)-\frac{b}{N}}{b+\frac{1}{\lfloor\sqrt{N}\rfloor}(a-b)-\frac{a}{N}}.$$

If $c = b$ then $M_8 = 1$ and we have the bound

$$S_8 \le \sum_{k=1}^{\lfloor\sqrt{N}\rfloor-1} M_8^k = \lfloor\sqrt{N}\rfloor - 1.$$

Dividing by N and taking $N \to \infty$ we obtain

$$\lim_{N\to\infty} \frac{S_8}{N} \le \frac{\lfloor\sqrt{N}\rfloor - 1}{N} = 0.$$

If $c \ne b$, we have the bound

$$S_8 \le \sum_{k=1}^{\lfloor\sqrt{N}\rfloor-1} M_8^k = \frac{M_8^{\lfloor\sqrt{N}\rfloor} - M_8}{M_8 - 1}. \tag{60}$$

Note that $\lim_{N\to\infty} M_8 = 1$. We use L'Hôpital's Rule (Abramowitz and Stegun 1964) to determine the limit of S_8/N as $N \to \infty$, which requires the derivative: $\frac{dM_8}{dN} = \frac{b-c}{b(N-1)^2}$. It follows that

$$\lim_{N\to\infty} N(M_8 - 1) = \lim_{N\to\infty} \frac{\frac{dM_8}{dN}}{-N^{-2}} = \frac{c-b}{b},$$
$$\lim_{N\to\infty} \lfloor\sqrt{N}\rfloor \ln M_8 = \lim_{N\to\infty} \frac{\frac{1}{M_8}\frac{dM_8}{dN}}{-\frac{1}{2}N^{-3/2}} = 0.$$

Therefore, $\lim_{N\to\infty} M_8^{\lfloor\sqrt{N}\rfloor} = 1$, and consequently from Eq. (60),

$$\lim_{N\to\infty} \frac{S_8}{N} \leq \lim_{N\to\infty} \frac{M_8^{\lfloor\sqrt{N}\rfloor} - M_8}{N(M_8 - 1)} = 0. \tag{61}$$

We also have an upper bound for S_9:

$$S_9 \leq \sum_{k=\lfloor\sqrt{N}\rfloor}^{N-1} M_9^k \leq \frac{1}{1 - M_9} = \frac{b + \frac{a-b}{\lfloor\sqrt{N}\rfloor} - \frac{a}{N}}{\frac{a-c}{\lfloor\sqrt{N}\rfloor} + \frac{b-a}{N}}$$

Divide by N and take the $N \to \infty$ limit to obtain

$$\lim_{N\to\infty} \frac{S_9}{N} \leq \lim_{N\to\infty} \frac{b + \frac{a-b}{\lfloor\sqrt{N}\rfloor} - \frac{a}{N}}{\sqrt{N}(a - c) + b - a} = 0 \tag{62}$$

Equations (61) and (62) imply $\lim_{N\to\infty} S/N = 0$, and consequently $\lim_{N\to\infty} N\rho_A = \infty$. □

We now apply weak selection to find conditions for which $\rho_A > 1/N$ in the Nw limit.

Corollary 2 *Given the game matrix* (1)*,* $\rho_A > 1/N$ *in the* Nw *limit if and only if one of the following holds:*

(i) $b > d$ *and* $a + b \geq c + d$
(ii) $b = d$ *and* $a > c$
(iii) $b = d, a = c$ *and* $b > c$

Proof In Theorem 5, we found conditions for which $\rho_A > 1/N$ for sufficiently large populations. We introduce weak selection according to Eq. (5). Given the weak selection expansion of I in Eq. (55), Condition (ii) of Theorem 5 becomes $(b > d) \wedge (a < c) \wedge (a + b \geq c + d)$. Note that Condition (i) of Theorem 5 is equivalent to $(b > d) \wedge (a \geq c) \wedge (a + b \geq c + d)$. Therefore, Conditions (i) and (ii) of Theorem 5 together give the one condition $(b > d) \wedge (a + b \geq c + d)$. Conditions (iii) and (iv) of Theorem 5 remain the same under weak selection. □

Finally, we will determine conditions for which $\rho_A > \rho_B$ in the Nw limit by first investigating the large N limit.

Theorem 6 *Given the game matrix* (1)*,* $\rho_A > \rho_B$ *for sufficiently large* N *if and only if one of the following conditions holds:*

(i) $I < 0$
(ii) $I = 0$ *and* $ac < bd$

Proof Eq. (4) with Eq. (15) give

$$\frac{\rho_B}{\rho_A} = \prod_{i=1}^{N-1} f\left(\frac{i}{N}, N\right) \tag{63}$$

Given that $\rho_A > \rho_B$ for sufficiently large N if and only if $\lim_{N\to\infty} \rho_B/\rho_A < 1$, we will find this limit and compare it to 1 for various cases.

We will first look at the product of $\tilde{f}$-terms and then compare it to the product of f-terms. Since $\tilde{f}$ is monotonic, the left and right Riemann sums, $\frac{1}{N}\left(\tilde{A}_{N-1} + \ln \tilde{f}(0)\right)$ and $\frac{1}{N}\left(\tilde{A}_{N-1} + \ln \tilde{f}(1)\right)$, respectively, serve as bounds for the definite integral I (where $\tilde{A}_{N-1}$ is defined in Eq. (30)). This implies

$$NI - \ln \tilde{M} \le \tilde{A}_{N-1} \le NI - \ln \tilde{m}, \tag{64}$$

where the minimum, $\tilde{m}$, and maximum, $\tilde{M}$, of $\tilde{f}$ are defined in Eq. (17). Keeping in mind that $\prod_{i=1}^{N-1} \tilde{f}\left(\frac{i}{N}\right) = \exp\left(\tilde{A}_{N-1}\right)$, exponentiate Eq. (64) to obtain

$$\frac{e^{NI}}{\tilde{M}} \le \prod_{i=1}^{N-1} \tilde{f}\left(\frac{i}{N}\right) \le \frac{e^{NI}}{\tilde{m}}.$$

Combining this with the inequality of Eq. (21), which compares f to $\tilde{f}$, and using Eq. (63), we obtain

$$\left(1 - \frac{L}{\tilde{m}N}\right)^{N-1} \frac{e^{NI}}{\tilde{M}} \le \frac{\rho_B}{\rho_A} \le \left(1 + \frac{L}{\tilde{m}N}\right)^{N-1} \frac{e^{NI}}{\tilde{m}}.$$

Thus, if $I > 0$ then $\lim_{N\to\infty} \rho_B/\rho_A = \infty$. If $I < 0$ then $\lim_{N\to\infty} \rho_B/\rho_A = 0$. The only case left to consider is $I = 0$. In this case, Eq. (51) implies that $\lim_{N\to\infty} \rho_B/\rho_A = \sqrt{ac/(bd)}$. If $ac > bd$ then the limit is greater than 1, if $ac < bd$ then the limit is less than 1, and if $ac = bd$ then the limit equals 1. □

Corollary 3 *Given the game matrix* (1), $\rho_A > \rho_B$ *in the* Nw *limit if and only if one of the following holds:*

(i) $a + b > c + d$
(ii) $a + b = c + d$ *and* $b > c$

Proof We introduce weak selection according to Eq. (5). Given the weak selection expansion of integral I in Eq. (55), $I < 0$ implies $a + b > c + d$ and $I = 0$ implies $a + b = c + d$. Furthermore, the inequality $ac < bd$ is

$$(1 + wa)(1 + wc) < (1 + wb)(1 + wd),$$

which reduces as $w \to 0$ to

$$a + c < b + d. \tag{65}$$

Thus, Condition (i) of Theorem 6 becomes $a + b > c + d$ and Condition (ii) becomes $a + b = c + d$ and $b > c$ (equivalently $a + b = c + d$ and $a < d$) in the Nw limit. □

6 Discussion

In the analysis of evolutionary models, the limits of large population size and weak selection are biologically relevant and mathematically convenient. We have analyzed the effect of combining these limits, in different orders, on the fixation of strategies in the Moran process with frequency dependence. Our results (summarized in Table 1) show that the Nw and wN limits yield different asymptotic expressions for fixation probability, as well as different conditions for a strategy to have larger fixation probability than a neutral mutation. Interestingly, however, the conditions are the same for $\rho_A > \rho_B$.

To understand the relationship between the Nw and wN results, it is helpful to rewrite them in terms of two payoff differences:

$$\alpha = a + b - c - d = \lim_{N\to\infty} \left(f_A\left(\tfrac{N}{2}\right) - f_B\left(\tfrac{N}{2}\right)\right)$$
$$\beta = b - d = \lim_{N\to\infty} \left(f_A(1) - f_B(1)\right).$$

In words, α is the payoff difference when both types are equally abundant, while β is the payoff difference when A is rare, with both differences taken in the large-population limit. These quantities relate to familiar concepts in evolutionary game theory: If $\beta < 0$ then B is an *evolutionary stable strategy* (ESS; Maynard Smith and Price, 1973), whereas the sign of α determines which of the two types is *risk dominant* (Harsanyi and Selten 1988; Nowak et al. 2004).

In the Nw limit, for a A-mutant to be favored in the sense $\rho_A > 1/N$ in the Nw limit requires that both α and β are positive. This means that A must have a payoff advantage both when rare and when 50% abundant. A deficiency in either of these two situations will prevent A from reaching fixation when the large-population limit is taken first. In contrast, for the wN limit, it is only necessary that the sum $\alpha + \beta = a + 2b - c - 2d$ be positive, effectively averaging over the two situations. Thus, when the weak-selection limit is taken first, a selective disadvantage in one situation is not prohibitive, and can be compensated for by an advantage in the other.

The condition $a + 2b > c + 2d$ for $\rho_A > 1/N$ in the wN limit is an instance of the one-third law of evolutionary game theory (Nowak et al. 2004; Ohtsuki et al. 2007; Bomze and Pawlowitsch 2008; Lessard and Ladret 2007; Lessard 2011; Zheng et al. 2011). This rule can be understood as stating that type A is favored to invade (in the sense $\rho_A > 1/N$ in the wN limit, excluding borderline cases) if and only if A has a payoff advantage when comprising one-third of the population. Previous works (Traulsen et al. 2006b; Wu et al. 2010) have shown that the one-third law breaks down away from the regime $Nw \ll 1$; correspondingly, we do not find any one-third law in the Nw limit. In light of our results, the one-third condition $a + 2b > c + 2d$ can be interpreted as a superposition of the separate conditions $\alpha > 0$ and $\beta > 0$, which are jointly necessary in the Nw limit but which only need be satisfied in sum ($\alpha + \beta > 0$) in the wN limit.

Our other results can also be expressed in terms of the payoff differences α and β. The asymptotic expressions for fixation probability, Eqs. (9) and (54), can be written as

$$\rho_A \sim \frac{1}{N} + \frac{w}{6}(\alpha + \beta) + o(w) \qquad (wN \text{ limit})$$
$$\rho_A \sim \theta(\alpha) \max\{\beta, 0\} w + o(w) \qquad (Nw \text{ limit}).$$

Above, $\theta(x)$ is the Heaviside step function:

$$\theta(x) = \begin{cases} 0 & x < 0 \\ \frac{1}{2} & x = 0 \\ 1 & x > 0. \end{cases}$$

The success condition $\rho_A > \rho_B$ reduces to $\alpha > 0$ in both limit orderings, and is therefore equivalent (up to borderline cases) to the statement that type A is risk-dominant (Harsanyi and Selten 1988; Nowak et al. 2004).

Our analysis of the Nw limit required us to first examine the large-population limit of ρ_A. Our results in Theorem 4 confirm the earlier results of Antal and Scheuring (2006), except in the borderline case $b > d$, $a < c$ and $I = 0$, for which

$$\lim_{N \to \infty} \rho_A = \frac{(b-d)(c-a)}{b(c-a) + c(b-d)\sqrt{\frac{ac}{bd}}}.$$

Antal and Scheuring obtained $\lim_{N \to \infty} \rho_A = (b-d)/2b$. These results differ, for example, for the payoff matrix

$$\begin{pmatrix} e & 2e \\ 4 & 4 \end{pmatrix},$$

which satisfies $b > d$, $a < c$, and $I = 0$. The difference arises from Antal and Scheuring's replacement of the sum $\tilde{A}_k$, defined in our Eq. (30), by its integral approximation.

Here we have focused on the Moran model of a well-mixed population with overlapping generations. The Nw and wN limits can also be applied to other models, where they may lead to novel questions or shed new light on existing results. Instead of Moran updating, one can consider Wright–Fisher updating (Fisher 1930; Wright 1931; Imhof and Nowak 2006), in which generations are non-overlapping. In the case of a constant selection coefficient $s > 0$, Haldane (1927) obtained the well-known approximation $\rho \approx 2s$. We expect that this approximation will be asymptotically exact in the Nw limit. For the wN limit, results of Imhof and Nowak (2006) imply

$$\rho \sim \frac{1}{N} + s + o(s)$$

for constant selection, and more generally,

$$\rho_A \sim \frac{1}{N} + \frac{w}{3}(a + 2b - c - 2d) + o(w)$$

for an arbitrary 2×2 matrix game (1). The pairwise-comparison process is another model of evolutionary game dynamics for which some limit results have been derived (Traulsen et al. 2005, 2006a, 2007; Wu et al. 2010, 2013, 2015). The Moran, Wright–Fisher, and pairwise comparison models all fall into a class of exchangeable selection models considered by Lessard and Ladret (2007), who derived general results that we can now recognize as pertaining to the wN limit. Finally, one can consider structured populations in which individuals occupy vertices of a graph (Ohtsuki et al. 2006; Szabó and Fáth 2007; Allen and Nowak 2014). For the case of the cycle (Ohtsuki and Nowak 2006), the wN and Nw limits were studied by Jeong et al. (2014), although without formal definitions and without considering borderline cases. For regular graphs of degree greater than two, there are results that appear to pertain to the wN limit (Ohtsuki et al. 2006; Chen 2013; Allen and Nowak 2014), but the Nw limit remains open.

Our results were obtained via exact computation of fixation probabilities according to Eq. (3). Alternatively, one can use the diffusion approximation (Kimura 1964; Helbing 1996; Traulsen et al. 2006a, b; Bladon et al. 2010), in which a finite-population process is approximated by a stochastic differential equation of Langevin form,

$$\dot{x} = a(x) + b(x)\xi, \tag{66}$$

where x represents the frequency of type A, ξ is uncorrelated Gaussian white noise with variance 1, and both $a(x)$ and $b(x)$ vanish at the endpoints $x = 0, 1$. The first term of Eq. (66) represents directional selection, while the second represents random genetic drift. The Moran, Wright–Fisher, and pairwise comparison models can all be approximated this way. In the diffusion context, the product Nw appears to determine how the dynamics behave under the large-population and weak-selection limits. If $Nw \to \infty$ as $N \to \infty$ and $w \to 0$, the second term in Eq. (66) vanishes and the dynamics become deterministic (Traulsen et al. 2005). If instead $Nw \to 0$, stochasticity is preserved (Traulsen et al. 2006b). An important question, still under active investigation (Lessard and Ladret 2007; Saakian and Hu 2016), is to determine conditions under which the diffusion approximation is asymptotically exact.

The Nw and wN limits represent two extremes out of the infinitely many ways to combine the large-population and weak-selection limits. In the most general case, one considers an arbitrary sequence of pairs $\{(w_j, N_j)\}_{j=1}^{\infty}$ such that $w_j \to 0$ and $N_j \to \infty$ as $j \to \infty$. It may be supposed that results for other limiting schemes will lie between the Nw and wN extremes in some sense. Based on results from the diffusion approximation (Traulsen et al. 2006b) and other approaches (Lessard and Ladret 2007), it appears plausible that the Nw results extend to all limits with $Nw \to \infty$ and the wN results extend to all limits with $Nw \to 0$, but we have not shown this formally.

Finally, we caution that results obtained in the weak selection limit—either alone or combined with other limits—do not always extend to stronger selection (Wu et al. 2010, 2013). Indeed, when there are more than two strategies, it is possible to find one ranking of strategies for both the weak selection and strong selection limits, but a different ranking for intermediate selection strengths (Wu et al. 2013). Such results underscore the need to assess selection strength when applying evolutionary game-theoretic results to biological populations.

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