Universality of weak selection

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Weak selection, which means a phenotype is slightly advantageous over another, is an important limiting case in evolutionary biology. Recently, it has been introduced into evolutionary game theory. In evolutionary game dynamics, the probability to be imitated or to reproduce depends on the performance in a game. The influence of the game on the stochastic dynamics in finite populations is governed by the intensity of selection. In many models of both unstructured and structured populations, a key assumption allowing analytical calculations is weak selection, which means that all individuals perform approximately equally well. In the weak selection limit many different microscopic evolutionary models have the same or similar properties. How universal is weak selection for those microscopic evolutionary processes? We answer this question by investigating the fixation probability and the average fixation time not only up to linear but also up to higher orders in selection intensity. We find universal higher order expansions, which allow a rescaling of the selection intensity. With this, we can identify specific models which violate (linear) weak selection results, such as the one-third rule of coordination games in finite but large populations.

I. INTRODUCTION

In evolutionary game theory the outcome of strategic situations determines the evolution of different traits in a population [1]. Typically, individuals are hardwired to a set of strategies. The performance in an evolutionary game determines the rate at which strategies spread by imitation or natural selection. Due to differences in payoff, different strategies spread with different rates under natural selection. In infinitely large well-mixed populations this is described by the deterministic replicator dynamics [2–5]. In this set of nonlinear differential equations the intensity of selection, which determines how payoff affects fitness, only changes the time scales but not the direction of selection or the stability properties. In finite populations fluctuations cannot be neglected [6–9]. The dynamics becomes stochastic: selection drives the system into the same direction as the corresponding deterministic process, but sometimes the system can also move into another direction. The strength of selection determines the interplay between these two forces. The absence of selective differences is called neutral selection: moving into one direction is as probable as moving into any other, independent of the payoffs. If selection acts, the transition probabilities become payoff dependent and thus asymmetric. The asymmetry can be the same in each state (constant selection) or state dependent (frequency dependent selection). In general, under frequency dependent selection the probability that one strategy replaces another can be fairly complicated. However, under the assumption of weak selection, some important insights can be obtained analytically [9–16]. It has to be pointed out that these results do, in general, not carry over to stronger selection.

Weak selection describes situations in which the effects of payoff differences are small, such that the evolutionary dynamics are mainly driven by random fluctuations. This approach has a long-standing history in population genetics [17,18]. In evolutionary biology, a phenotype is often found to be slightly advantageous over another phenotype [19,20]. Further, a recent experiment suggests that some aspects of weak selection are reflected in human strategy updating in behavioral games [21]. In the context of evolutionary game dynamics, however, weak selection has only recently been introduced by Nowak *et al.* [9]. The definition of weak selection is unambiguous in the case of constant selection, but there are different ways to introduce such a limit under frequency dependent selection [22].

In the simplest case, frequency dependence can be introduced by an evolutionary game between two types A and B. In a one shot interaction (where strategies are played simultaneously) a type A interacting with another type A receives payoff a, two interacting B types get d each. Type A interacting with B gets b, whereas B obtains c. This symmetric 2×2 game can be described by the payoff matrix

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

Let i denote the number of A individuals in a population of constant size N. Under the assumption of a well-mixed population, excluding self-interactions, the average payoffs for individuals of either type are given by

$$\pi_A = a\frac{i-1}{N-1} + b\frac{N-i}{N-1}, \qquad (2)$$

$$\pi_B = c\frac{i}{N-1} + d\frac{N-i-1}{N-1}. \qquad (3)$$

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These expectation values are the basis for the evolutionary game. In the continuous limit $N \to \infty$, the state of the system is characterized by the fraction of A individuals $x = i/N$. The dynamics are typically given by the replicator dynamics $\dot{x} = x(1-x)(\pi_A - \pi_B)$, which has the trivial equilibria $\hat{x}=0$ and $\hat{x}=1$. Additionally, there can be a third equilibrium between 0 and 1, given by $x^* = (d-b)/(a-b-c+d)$. In finite populations, the probabilistic description does not allow the existence of equilibrium points anymore. Moreover, the invariance of the replicator dynamics under rescaling of the payoff matrix [5] is lost in finite population models. Typically, the average payoffs are mapped to the transition probabilities to move from state i to other states; only $i=0$ and $i=N$ are absorbing states. When only two types compete and there is only one reproductive event at a time this defines a birth-death process. The transition probabilities from i to $i+1$ and from i to $i-1$ are then denoted by T_i^+ and T_i^-, respectively. They determine the probability of the process to be absorbed at a certain boundary, usually called fixation probability, as well as the average time such an event takes, termed average fixation time.

An important result of evolutionary game dynamics in finite populations under weak frequency dependent selection is the one-third rule. It relates the fixation probability of a single type A individual, ϕ_1, to the position of the internal equilibrium x^* in a coordination game, i.e., when $a>c$ and $d>b$. If selection is neutral, we have $\phi_1 = 1/N$. If the internal equilibrium is less than $1/3$, $x^* < 1/3$, then $\phi_1 > 1/N$. Originally, this weak selection result has been found for large populations in the frequency dependent Moran process [9]. Subsequently, the one-third rule has been derived from several related birth-death processes [23–25] and also for the frequency dependent Wright-Fisher process [26,27], which is still a Markov process, but no longer a birth-death process. In a seminal paper, Lessard and Ladret showed that the one-third rule is valid for any process in the domain of Kingman's coalescence [28], which captures a huge number of the stochastic processes typically considered in population genetics. Essentially, this class of processes describes situations in which the reproductive success is not too different between different types. Thus, the generality of the one-third rule under linear weak selection is well established. Here, we ask a slightly different question: To which order can two birth-death processes be considered as identical under weak selection? Some authors have considered higher weak selection orders for specific processes [29–31]. We investigate two classes of birth-death processes, a general pairwise imitation process motivated by social learning and a general Moran process based on reproductive fitness. In this light, we also discuss cases which violate the one-third rule.

The paper is organized in the following way. In Sec. II we compute the weak selection expansion of the fixation probability in a general case of our two classes of birth-death processes. In Sec. III, we perform the same calculations for the significantly more complicated fixation times. In Sec. IV we discuss our analytical results and conclude. Some detailed calculations can be found in Appendixes A and B.

II. PROBABILITIES OF FIXATION

A birth-death process is characterized by the transition probabilities from each state i to its neighboring states, T_i^+

and T_i^-. We assume that this Markov chain is irreducible on the interior states and we exclude mutations or spontaneous switching from one type to another. Thus, the process gets eventually absorbed at $i=0$ or N. For any internal state, the probability to hit $i=N$ starting from $0<i<N$, ϕ_i, fulfills the recursion equation $\phi_i = (1 - T_i^+ - T_i^-)\phi_i + T_i^- \phi_{i-1} + T_i^+ \phi_{i+1}$ [32–34]. This recursion can be solved explicitly, respecting the boundary conditions $\phi_0 = 0$ and $\phi_N = 1$. For a single A individual in populations of B, the probability to take over the population is [32–34]

$$\phi_1 = \frac{1}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^{k} \frac{T_i^-}{T_i^+}}. \qquad (4)$$

In any model of neutral selection, the transition probabilities of the Markov chain fulfill $T_i^-/T_i^+ = 1$, and hence the respective fixation probability of a single mutant amounts to $1/N$.

In this section we focus on the weak selection approximation of Eq. (4). We do this for two different approaches to evolutionary game theory: imitation dynamics and selection dynamics. In the former case, strategy spreading is based on pairwise comparison and imitation, in the latter it results from selection proportional to fitness and random removal. The most prominent examples are the Fermi process and the Moran process, respectively.

A. Pairwise comparison

In a pairwise comparison process, two individuals are chosen randomly to compare their payoffs from the evolutionary game [Eqs. (2) and (3)]. One switches to the other strategy with a given probability (see Fig. 1). If selection is neutral, this probability is constant. If selection acts, the larger the payoff difference, the higher the probability that the worse imitates the better. But typically there is also a small chance that the better imitates the worse. Otherwise, only the strategy of the more successful individual is adopted. This would lead to a dynamics that is stochastic in the time spent in each interior state but deterministic in direction [24]. Thus, given that all interior states are transient, the fixation probabilities are either 0 or 1, and there is no basis to discuss a weak selection limit.

Selection is parametrized by the intensity of selection $\beta \geq 0$. As a first example we consider the Fermi process [24,35,36]. Let the two randomly selected individuals X and Y have payoffs π_X and π_Y. Then X adopts Y's strategy with probability $g_{\text{Fermi}}(\pi_Y - \pi_X) = 1/(1 + e^{-\beta(\pi_Y - \pi_X)})$. Thus, the transition probabilities of an evolutionary game with payoffs [Eqs. (2) and (3)] are given by

$$T_i^{\pm} = \frac{i}{N} \frac{N-i}{N} \frac{1}{1 + \exp^{\mp \beta(\pi_A - \pi_B)}}. \qquad (5)$$

The probability to stay in state i is $1 - T_i^- - T_i^+$. The Fermi process is closely related to the Glauber dynamics [37]. If we define individuals' energy as the exponential function of payoff, then the Fermi process can be mapped onto the Ising
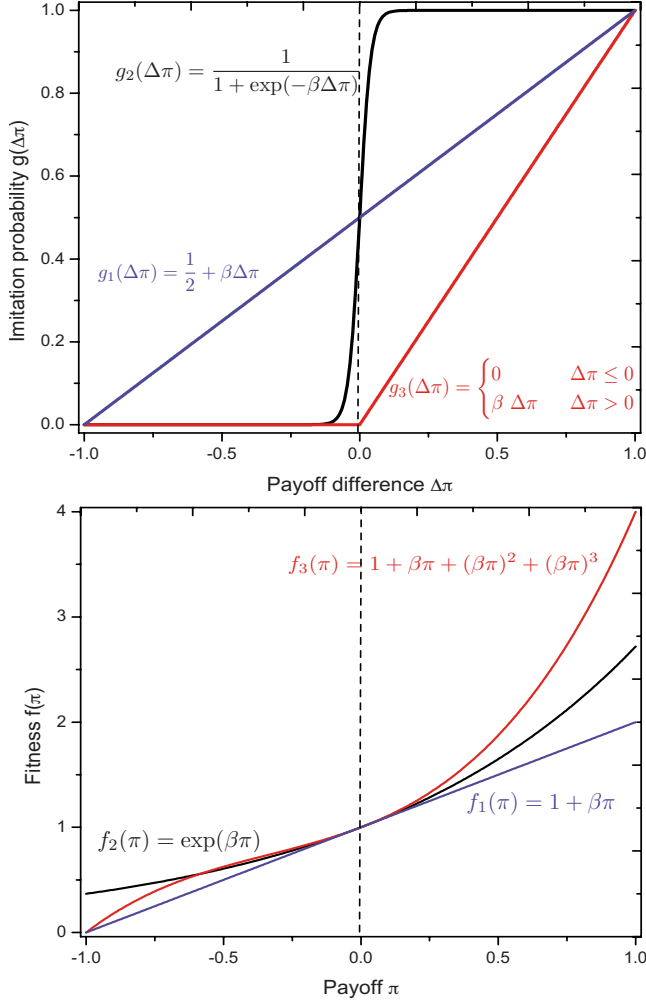
FIG. 1. (Color online) Upper panel: pairwise comparison processes are characterized by the probability $g(\Delta\pi)$ to imitate the strategy of someone else based on the payoff difference $\Delta\pi$. With increasing payoff difference, the imitation probability becomes higher, $g'(\Delta\pi)\geq 0$. Weak selection implies a Taylor expansion at $\Delta\pi=0$. Thus, it can only be invoked for functions that are differentiable in 0. The figure shows three examples of imitation probability functions, $g_1(\Delta\pi)$ is a linear function (selection intensity $\beta=0.5$), and $g_2(\Delta\pi)$ is the Fermi function ($\beta=50$). For the imitation function $g_3(\Delta\pi)$, a meaningful weak selection limit does not exist since $g_3(\Delta\pi)$ is not differentiable in 0. Because $g_3(\Delta\pi)=0$ for $\Delta\pi<0$, the associated stochastic process would be stochastic in time but deterministic in direction. All through the paper, we focus on imitation functions that are differentiable in 0. Lower panel: Moran processes are characterized by a payoff to fitness mapping $f(\pi)$. Fitness is a nondecreasing function of the payoff, $f'(\pi)\geq 0$. The figure shows three examples for payoff to fitness mappings (selection intensity $\beta=1$ for all three functions).

model. The Fermi process has the comfortable property that the ratio of transition probabilities simplifies to $T_i^-/T_i^+ = e^{-\beta(\pi_A-\pi_B)}$, such that the products in Eq. (4) can be replaced by sums in the exponent. Defining $u=(a-b-c+d)/(N-1)$ and $v=(Nb-Nd-a+d)/(N-1)$, such that $\pi_A-\pi_B=ui+v$, leads to

$$\phi_1(\beta) = \frac{1}{1+\sum\limits_{k=1}^{N-1}\exp\left\{-\beta\left[k^2\frac{u}{2}+k\left(\frac{u}{2}+v\right)\right]\right\}}. \quad (6)$$

For large N, the sum can be replaced by an integral, leading to a closed expression [24]. For weak selection, $N\beta\ll 1$, Eq. (6) can be approximated by

$$\phi_1 \approx \frac{1}{N} + \frac{(N-1)[(N+1)u+3v]}{6N}\beta. \quad (7)$$

This can also be obtained directly from $T_i^-/T_i^+\approx 1-\beta(\pi_A-\pi_B)$. The fixation probability under weak selection is greater than in the neutral case if the term linear in β is positive, $Nu+u+3v>0$. In particular, for a coordination game in a large population, this implies $x^*<1/3$. Thus, natural selection favors the mutant strategy if the invasion barrier is less than one-third, which is the well-known one-third rule [9,24,25,28,30]. It holds when the fixation probability in a large but finite population can be approximated up to linear order in selection intensity.

Can we make general statements based on an expansion of ϕ_1 concerning the probability of switching strategies, $g(\Delta\pi)$? In a general framework, the probability that X switches to the strategy of Y, given the difference in their payoffs, $\Delta\pi=\pi_X-\pi_Y$, is governed by the intensity of selection. We call $g(\Delta\pi)$ the imitation probability function of a general pairwise comparison process. In a well-mixed population, the transition probabilities read

$$T_i^\pm = \frac{i}{N}\frac{N-i}{N}g(\pm\beta\Delta\pi). \quad (8)$$

The larger the payoff difference, the more likely the worse individual switches to the strategy of the better. Therefore, the imitation function is nondecreasing, $g'(\Delta\pi)\geq 0$. Additionally, if the payoffs of the two chosen individuals are equal, the neutral probability of switching is nonzero, $g(0)>0$ (otherwise, the process does not allow a meaningful definition of weak selection because it would always deterministically follow the direction of selection). The fixation probability for this general pairwise comparison process can be expanded to the second order (see Appendix A 1),

$$\phi_1 \approx \frac{1}{N} + C_1\beta + C_2\beta^2, \quad (9)$$

where

$$C_1 = \frac{(N-1)[(N+1)u+3v]}{6N}\frac{2g'(0)}{g(0)} \quad (10)$$

and

$$C_2 = [u^2(N+1)(N+2)+15uv(N+1)+30v^2]$$
$$\times \frac{(N-1)(N-2)}{360}\left(\frac{2g'(0)}{g(0)}\right)^2. \quad (11)$$

C_1 is proportional to the increase of the imitation function at $\Delta\pi=0$ (see Fig. 2). Note that for large N, $C_1>0$ is equivalent to $Nu+3v>0$, which for large N further simplifies to
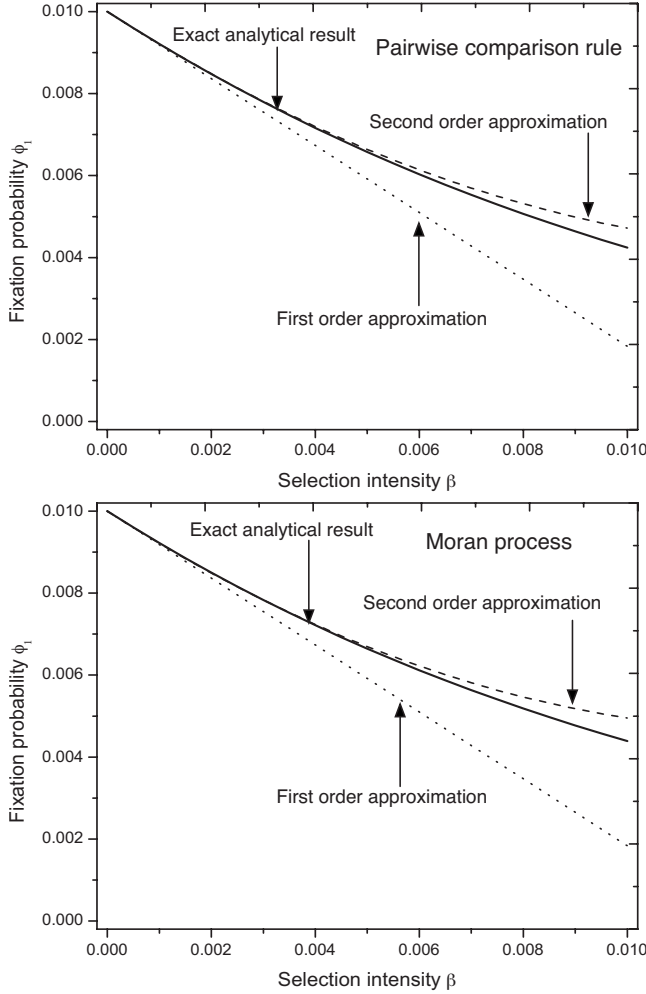
FIG. 2. Approximation of the fixation probability of a single mutant under weak selection. Upper panel: pairwise comparison process with the Fermi function $1/(1+\exp[-\beta\Delta\pi])$ as an imitation function. As shown in the main text, up to the second order the approximation is valid for any imitation function $g(\beta\Delta\pi)$ after appropriate rescaling of the selection intensity β. Lower panel: Moran process with fitness as a linear function of the payoff, $f=1+\beta\pi$. Any other function leads to the same first-order approximation after rescaling of β. However, the second order depends on choice of the function transforming payoff to fitness. Exact analytical results are numerical evaluations of Eq. (4). (Parameters $N=100$, $\beta=1$, $a=4$, $b=1$, $c=1$, and $d=5$ in both panels).

$x^* < 1/3$. Thus, the one-third rule holds for all pairwise comparison processes that fulfill $g'(0)\neq 0$, and $g(0) > 0$. Moreover, C_1 is proportional to $2g'(0)/g(0)$, while C_2 is proportional to the square of this quantity. Thus, $2g'(0)/g(0)$ can be absorbed into the selection intensity by proper rescaling. Therefore, the more rapid the increases of the imitation function at $\Delta\pi=0$, the stronger is the sensitivity of the fixation probability to changes in average payoff. For low switching probabilities in the neutral case, $\Delta\pi=0$, we have a fixation probability that changes rapidly when the payoff difference becomes important, $\Delta\pi\neq 0$. While most previous models have either considered $g(0)=0$ (which lies out of the

scope of our approach because it does not lead to a reasonable definition of weak selection) or $g(0)=0.5$ (which is the default case), some authors have also explored imitation functions with other values of $g(0)$. For example, Szabó and Hauert used the imitation function $g(x)=1/(1+e^{-x+\alpha})$, where α is a constant [38]. In this case $2g'(0)/g(0)=2/[1+\exp(-\alpha)]$; thus, an increase in α is equivalent to an increase in the (small) selection intensity.

Now it is straightforward to come up with an imitation function that leads to a violation of the one-third rule, for example, $g(\Delta\pi)=1/(1+\exp\{-\Delta\pi^3\})$. Obviously, $g(\beta\Delta\pi)$ satisfies the conditions $g'(\beta\Delta\pi)\geq 0$, and $g(0)\neq 0$. Further, both the first- and the second-order expansions vanish. Therefore, the fixation probability under weak selection can only be approximated as

$$\phi_1 \approx \frac{1}{N} + C_3\beta^3, \tag{12}$$

where C_3 can be derived in the same way as C_1 and C_2. In special games, the sign of C_3 can also change at $x^*=1/3$, but in general this will not be the case due to the complicated dependence of C_3 on u and v. In more general terms, the one-third rule is not sustained whenever the linear approximation of $g(\beta\Delta\pi)$ vanishes.

B. Moran process

In the frequency dependent Moran process the payoff π, given in Eqs. (2) and (3), is mapped to fitness f, as illustrated in Fig. 1. In each reproductive event, one individual is selected for reproduction (producing an identical offspring) proportional to fitness. To keep the size of the population to the constant value N, a randomly chosen individual is removed from the population subsequently. As in pairwise comparison processes, the state i can at most change by one per time step.

In the simplest case, fitness is a linear function of payoff. With a background fitness of one, the fitnesses of types A and B read $f_A=1+\beta\pi_A$ and $f_B=1+\beta\pi_B$, respectively. The quantity $\beta\geq 0$ serves as the intensity of selection. Note that β is bound such that fitness never becomes negative. The probability that the number of A individuals increases by 1, $i\rightarrow i+1$, is given by

$$T_i^+ = \frac{if_A}{if_A + (N-i)f_B}\frac{N-i}{N}. \tag{13}$$

The other possible transition, $i\rightarrow i-1$, occurs with probability

$$T_i^- = \frac{(N-i)f_B}{if_A + (N-i)f_B}\frac{i}{N}. \tag{14}$$

When selection is neutral, $\beta=0$, we have $T_i^{\pm}=i(N-i)/N^2$. Up to linear order in β the Moran process has the same fixation probability as the Fermi process [Eq. (7)], such that in this approximation the one-third rule is fulfilled. This is because under first-order weak selection, T_i^-/T_i^+ is again a linear function of the payoff difference.

In general, let fitness be *any* non-negative function of the product of payoff and selection intensity, $f(\beta\pi)$, which fulfills $f'(\beta\pi) \geq 0$. For simplicity, we assume that the baseline fitness $f(0)$ is 1. The transition probabilities in a population with types A and B read

$$T_i^+ = \frac{if(\beta\pi_A)}{if(\beta\pi_A) + (N-i)f(\beta\pi_B)} \frac{N-i}{N}, \tag{15}$$

$$T_i^- = \frac{(N-i)f(\beta\pi_B)}{if(\beta\pi_A) + (N-i)f(\beta\pi_B)} \frac{i}{N}. \tag{16}$$

Note that $T_i^-/T_i^+ = f(\beta\pi_B)/f(\beta\pi_A)$. Up to second order in β, the fixation probability of a single A mutant in a population of B is (see Appendix A 2)

$$\phi_1 \approx \frac{1}{N} + D_1\beta + D_2\beta^2, \tag{17}$$

where

$$D_1 = (N-1)\frac{(N+1)u + 3v}{6N}f'(0) \tag{18}$$

and

$$
\begin{aligned}
D_2 = & [u^2(N+1)(N+2) + 15uv(N+1) + 30v^2]\frac{(N-1)(N-2)}{360} \\
& \times f'(0)^2 - [(2a^2 + 4ab + 4cd - 10d^2) + (11d^2 + 2cd - c^2 \\
& - 3b^2 - 6ab - 3a^2)N + (a^2 + 2ab + 3b^2 - c^2 - 2cd \\
& - 3d^2)N^2]\frac{(N-1)}{24N^3}[f'(0)^2 - f''(0)],
\end{aligned} \tag{19}
$$

with u and v as above. Note that the first-order term depends on payoff differences only, but the second-order term also depends on the payoff values directly. An example for such an approximation is shown in Fig. 2. The first-order term D_1 is proportional to the increase in fitness at $\pi=0$, $f'(0)$. The first-order term D_1 is proportional to $Nu+3v$ for large N. Hence, the one-third rule holds for every Moran model for which $f'(0)$ does not vanish under weak selection. Additionally, $f'(0)$ can be absorbed into the selection intensity by rescaling: changing this rate is equivalent to changing the intensity of selection. Note that this is not possible with D_2, where not only the slope but also the curvature of the fitness function at the origin play a role. However, when the exponential fitness function $f = \exp(\beta\pi)$ is employed [39], the second term of Eq. (19) vanishes. This allows us to incorporate $f'(0)$ into the selection intensity even for the second-order term.

Again, we conclude the section with an example where the one-third rule is violated. Consider the fitness function $f(\beta\pi) = 1 + \beta^3\pi^3$, which obviously satisfies $f(0) = 1$, and $f'(\beta\pi) \geq 0$. Both first- and second-order corrections in β vanish, $D_1 = D_2 = 0$. Therefore, the first nontrivial approximation of the fixation probability is

$$\phi_1 \approx \frac{1}{N} + D_3\beta^3. \tag{20}$$

If D_3 changes sign at $x^* = 1/3$, we recover the one-third rule. This is only the case for very special games. In analogy to the previous section, the general one-third rule does not hold anymore.

III. TIMES OF FIXATION

In this section we address the conditional fixation time τ_i^A. In a finite population of $N-i$ individuals of type B and i individuals of type A, τ_i^A measures the expected number of imitation or birth-death events until the population consists of type A only under the condition that this event occurs. In general, the probability $P_i^A(t)$ that after exactly t events the process moved from any i to N, which is the all A state, obeys the master equation $P_i^A(t) = (1 - T_i^+ - T_i^-)P_i^A(t-1) + T_i^- P_{i-1}^A(t-1) + T_i^+ P_{i+1}^A(t-1)$. The average fixation time $\tau_i^A = \sum_{t=0}^{\infty} tP_i^A(t)/\phi_i$ is the stationary first moment of this probability distribution, resulting from a recursive solution of $\phi_i\tau_i^A = (1 - T_i^+ - T_i^-)\phi_i\tau_i^A + T_i^-\phi_{i-1}(\tau_{i-1}^A + 1) + T_i^+\phi_{i+1}(\tau_{i+1}^A + 1)$. In a similar way one can find $\tau_i^B = \sum_{t=0}^{\infty} tP_i^B(t)/(1-\phi_i)$, such that the average total lifetime of the Markov process amounts to $\phi_i\tau_i^A + (1-\phi_i)\tau_i^B$ [32,40,41]. Following Sec. II B we restrict our analysis to the biologically most relevant case $i=1$, which yields [32,40]

$$\tau_1^A = \sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{\phi_l}{T_l^+} \prod_{m=l+1}^{k} \frac{T_m^-}{T_m^+}. \tag{21}$$

Maruyama and Kimura [42], Antal and Scheuring [41], as well as Taylor *et al.* [43] showed that the conditional fixation time of a single mutant of either type is the same, $\tau_1^A = \tau_{N-1}^B$. This remarkable identity holds for any evolutionary birth-death process and is thus valid for any 2×2 game and for any selection intensity. However, for $j > 1$ we have $\tau_j^A \neq \tau_{N-j}^B$ unless β vanishes. Since τ_1^A and τ_{N-1}^B are identical up to any order in β, we obtain

$$\left[\frac{\partial^n}{\partial\beta^n}\tau_1^A\right]_{\beta=0} = \left[\frac{\partial^n}{\partial\beta^n}\tau_{N-1}^B\right]_{\beta=0} \tag{22}$$

for any n. This symmetry can help to obtain several properties of the expansion of the conditional fixation time [Eq. (21)], without brute force calculations.

A. Pairwise comparison

Let us first consider the fixation time in the special case of the Fermi process [Eq. (5)]. When the selection intensity vanishes, $\beta = 0$, we have $\tau_1^A(0) = 2N(N-1)$ [13,33]. When selection is weak, $N\beta \ll 1$, the conditional fixation time is approximately $\tau_1^A \approx \tau_1^A(0) + \partial_\beta\tau_1^A(\beta)|_{\beta=0}\beta + \partial_\beta^2\tau_1^A(\beta)|_{\beta=0}\beta^2/2$. For the Fermi process, the first-order term is then given by [13]

$$\left[\frac{\partial}{\partial\beta}\tau_1^A\right]_{\beta=0} = -uN(N-1)\frac{N^2+N-6}{18}, \tag{23}$$

where u stems from $\pi_A - \pi_B = ui + v$ (compare Appendix B 1). The first-order expansion of τ_1^A is only proportional to the i

dependent term u in this special case. This can also be seen from a symmetry argument [41,43]: since $\tau_1^A = \tau_{N-1}^B$, the fixation time does not change under $a \leftrightarrow d$ and $b \leftrightarrow c$. Since u, but not v, is invariant under this exchange of strategy names, τ_1^A can depend under linear weak selection only on u, but not on v. The second-order term of the conditional fixation time for the Fermi process yields

$$\left[\frac{d^2}{d\beta^2} \tau_1^A \right]_{\beta=0} = E_1 u^2 + E_2 uv + E_3 v^2, \tag{24}$$

where

$$E_1 = -\frac{(N-2)(N-1)N}{5400}(180 - 122N + 177N^2 + 59N^3),$$

$$E_2 = -\frac{N^2(6 - 7N + N^3)}{18},$$

$$E_3 = \frac{1}{N}E_2. \tag{25}$$

Now, in contrast to the first-order expansion [Eq. (23)], both u and v enter. An interesting relation is $E_3 = E_2/N$. In the following, we show that this is found for any pairwise comparison process and not only in the special case of the Fermi process.

For general pairwise comparison processes under neutral selection, the conditional fixation time is $\tau_1^A(0) = N(N-1)/g(0)$, where $g(0) > 0$. When selection acts [Eq. (8)], the transition probabilities become dependent on the derivative of the imitation function, $g'(0) \geq 0$. We are now interested in the imitation function's influence on the first- and second-order terms in β. In general, the first-order term in β reads

$$\frac{\partial}{\partial \beta} \tau_1^A = \sum_{|\alpha|=1} \sum_{k=1}^{N-1} \sum_{l=1}^{k} h_\alpha, \tag{26}$$

$$h_\alpha = \left(\frac{\partial^{\alpha_1}}{\partial \beta^{\alpha_1}} \frac{1}{T_i^+} \right) \left(\frac{\partial^{\alpha_2}}{\partial \beta^{\alpha_2}} \phi_l \right) \left(\frac{\partial^{\alpha_3}}{\partial \beta^{\alpha_3}} \prod_{m=l+1}^{k} \frac{T_m^-}{T_m^+} \right), \tag{27}$$

with the multi-index $\alpha = (\alpha_1, \alpha_2, \alpha_3)$, $|\alpha| = \alpha_1 + \alpha_2 + \alpha_3$ (see Appendix B 1 for details of the calculation). The general structure of this term is determined by h_α, which is linear in u and v, as $|\alpha|$ equals 1. Thus, $\partial_\beta \tau_1^A|_{\beta=0} = F_1 u + F_2 v$ is also of this form, where F_1 and F_2 only depend on the population size N. With the same symmetry argument as above, based on [41,43], we can conclude that $F_2 = 0$. This yields

$$\tau_1^A = \tau_{N-1}^B \approx \frac{N(N-1)}{g(0)} + F_1 u \beta. \tag{28}$$

We can now calculate the payoff independent term F_1 for any $g(\Delta\pi)$ from the special case $u = 1$ and $v = 0$, which reads

$$F_1 = -\frac{g'(0)}{g(0)^2} N(N-1) \frac{N^2 + N - 6}{18}. \tag{29}$$

Here, β can be rescaled by $g'(0)/g(0)^2$. Changing $g'(0)$ or $g(0)$ is equivalent to changing the selection intensity appro-

priately. In particular, when $u > 0$, which is true, e.g., for coordination games such as the stag-hunt game [44], the conditional time it takes on average for a mutant type to take over decreases with the intensity of selection. Moreover, for $a > c$ and $b > d$ in combination with $u < 0$, a mutant which is always advantageous over the wild type needs longer to reach fixation than a neutral mutant. This phenomenon, termed stochastic slowdown in [45], occurs in any imitation process since Eq. (28) only depends on u.

For the second-order term in the expansion in β we can write

$$\frac{\partial^2}{\partial \beta^2} \tau_1^A = \sum_{|\alpha|=2} \sum_{k=1}^{N-1} \sum_{l=1}^{k} h_\alpha, \tag{30}$$

where h_α is of the form $G_1 u^2 + G_2 uv + G_3 v^2$. Thus, $\partial_\beta^2 \tau_1^A|_{\beta=0}$ is also of this form, where the G_i's only depend on N. Again, we consider the transformations $a \leftrightarrow d$ and $b \leftrightarrow c$ which correspond to exchanging the names of the strategies. For the transformed game, we obtain $\partial_\beta^2 \tau_{N-1}^B|_{\beta=0} = G_1 u^2 + G_2 u\tilde{v} + G_3 \tilde{v}^2$ with $\tilde{v} = (Nc - Na - d + a)/(N-1)$. Using Eq. (22), we obtain $G_2 u(v - \tilde{v}) + G_3(v^2 - \tilde{v}^2) = 0$. With $v + \tilde{v} = -Nu$, we then get $G_3 = G_2/N$—the symmetry discussed above for a special case holds for any imitation function. Eventually, the second-order term in β for general imitation probability is given by

$$\frac{\partial^2}{\partial \beta^2} \tau_1^A = G_1 u^2 + G_2 uv + \frac{G_2}{N} v^2. \tag{31}$$

The special cases $u = 1, v = 0$, as well as $u = 0, v = 1$, allow us to compute G_1 and G_2 explicitly. Thus, we have (see Appendix B 1)

$$G_1 = -\frac{(N-2)(N-1)N}{5400}(180 - 122N + 177N^2 + 59N^3)$$
$$\times \left\{ \frac{2[g'(0)]^2}{g(0)^3} \right\} - \frac{N^2(N-1)(2N-1)}{6}\left[\frac{g''(0)}{g(0)^2} \right], \tag{32}$$

$$G_2 = -\frac{N^2(6 - 7N + N^3)}{18}\left\{ \frac{2[g'(0)]^2}{g(0)^3} \right\} - N^2(N-1)\frac{g''(0)}{g(0)^2}. \tag{33}$$

Obviously, Eq. (31) does not allow a rescaling of the intensity of selection. Instead, the properties of the imitation function enter in a more intricate way. An example of this approximation is shown in Fig. 3.

B. Moran process

To close this section, we consider the Moran process, where selection at birth is proportional to fitness and selection at death is random. For neutral selection $\beta = 0$, it is well known that $\tau_1^A(0) = N(N-1)$ [13,33,41]. When selection is weak $\beta \ll 1$, the conditional mean fixation time is approximately $\tau_1^A \approx \tau_1^A(0) + \partial_\beta \tau_1^A|_{\beta=0}\beta$. For the Moran process with linear fitness function, $f_A = 1 + \beta \pi_A$, we have $\partial_\beta \tau_1^A|_{\beta=0} = -uN^2(N^2 - 3N + 2)/36$ (compare [13,43]). The first-order
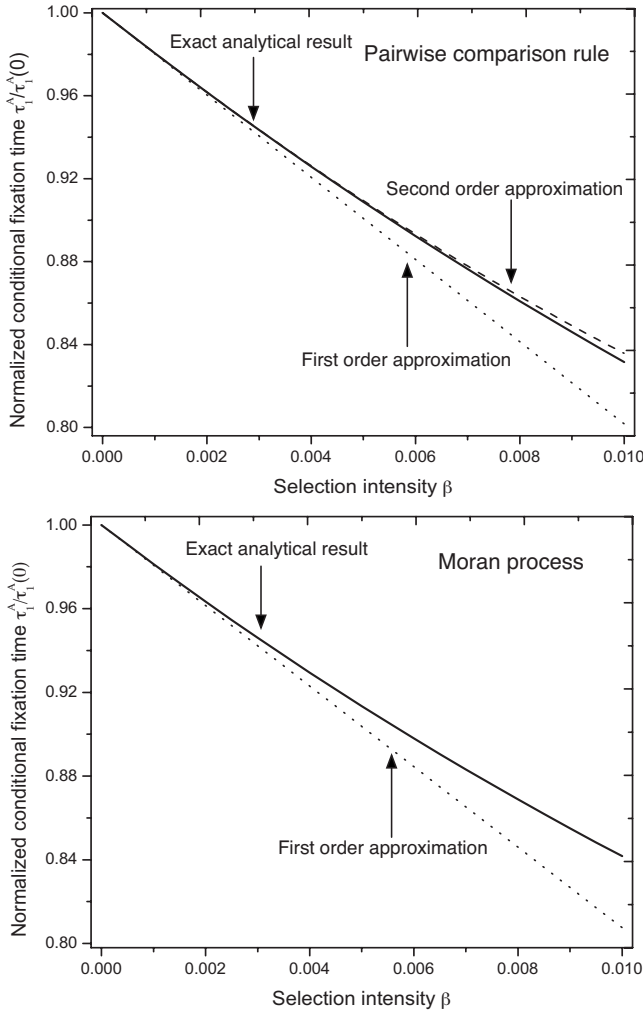
FIG. 3. Weak selection approximation of the conditional fixation time of a single mutant, the exact result is given in Eq. (21). Upper panel: the approximations are shown for the Fermi process, but they would be identical up to the second order for any other pairwise comparison process after appropriate rescaling of the selection intensity. Lower panel: for any Moran process the first-order approximation is independent of the precise function mapping payoff to fitness (here it is linear). Any higher order approximation depends on the details of the function. Note that the first-order approximation in the two panels is not identical due to a difference in the dependence on population size N (same parameters as in Fig. 2).

expansion of τ_1^A again depends only on u, but not on v. This can be shown based on [41,43] or explicitly [13].

With general fitness mapping $f(\beta\pi)$ with transition rates (15) and (16), we have

$$\left[\frac{\partial}{\partial\beta}\tau_1^A(\beta)\right]_{\beta=0} = -f'(0)N^2\frac{N^2-3N+2}{36}u, \qquad (34)$$

which allows a rescaling of the intensity of selection when τ_1^A is approximated up to linear order.

With general fitness function $f(x)$, it becomes unwieldy to calculate higher order terms in β. However, the general

calculations are similar to that of the general pairwise comparison rules. Equation (19) reveals that already the second-order expansion of the fixation probability ϕ_1 with general fitness mapping is tedious in form. Thus, the equivalent terms for the fixation time τ_1^A are even more complicated and do not lead to further insight in this case. Since it would be only an academic exercise to calculate them, we do not give them explicitly here. It is clear that the weak selection approximation is not universal over a large class of processes in second order in the fixation times.

IV. DISCUSSION

In the past years, weak selection has become an important approximation in evolutionary game theory [9–15]. Weak selection means that the game has only a small influence on evolutionary dynamics. In evolutionary biology and population genetics, the idea that most mutations confer small selective differences is widely accepted. In social learning models, it refers to a case where imitation is mostly random, but there is a tendency to imitate others that are more successful. Since weak selection is the basis of many recent results in evolutionary dynamics [10,11,46–48], it is of interest how universal these results are. It has been shown that they are remarkably robust and the choice of evolutionary dynamics has only a small impact in unstructured populations [28,49]. In structured populations, however, the choice of evolutionary dynamics can have a crucial impact on the outcome [11,47,50–54]. For example, for a prisoner's dilemma on a graph under weak selection, cooperation may be favored by a death-birth process while it is never favored by a birth-death process. In a well-mixed population, however, the transition probabilities for those two processes are identical; thus, they lead to the same result. However, in general, spatial structure has a less pronounced effect under weak selection than under strong selection [53,54].

We have addressed the question as to what extent two evolutionary processes can be considered as identical by investigating the fixation probability and the fixation time. For any given 2×2 payoff matrix, we have considered two classes of evolutionary processes: pairwise comparison and Moran processes. An interesting special case is the Moran process with exponential fitness mapping, which is equivalent to the Fermi process (a special case of the pairwise comparison rule) in terms of fixation probabilities.

For the fixation probability, the first-order term in the selection intensity always has the same form, given that it does not vanish. In addition, regardless of the choice of imitation functions, two pairwise comparison processes are always identical up to second-order weak selection in the fixation probabilities. For the Moran processes, an equivalent statement does not hold. Recently, a paper has shown that in 3×3 games under weak selection, the Fermi update rule can be quite different from the Moran process and the local update rule (an imitation process with linear imitation function [23]), while the Moran process and the local update rule are

more similar to each other [55]. Our result shows that for weak selection in 2×2 games, these three processes can be mapped to each other by an appropriate rescaling of the intensity of selection.

For the first-order approximation of the average fixation time, there are differences in the dependence on the system size, but all processes depend on the game in the same way. This follows from a symmetry in fixation times [41,43]. For higher orders in the intensity of selection, a simple rescaling of the selection intensity does not exist for the fixation times and a general statement on the relation between two processes cannot be made.

The robustness of weak selection results, i.e., the invariance to changes of the underlying stochastic process, found in the linear approximation is remarkable but follows from basic assumptions on evolutionary dynamics. Moreover, the universality of weak selection breaks down when higher order terms are discussed.

APPENDIX A: THIRD ORDER EXPANSION OF THE FIXATION PROBABILITIES

Here, we expand the fixation probability ϕ_1 for general birth-death processes up to the third order. Let $\gamma_i = T_i^- / T_i^+$ and

$$\left[\frac{\partial^s}{\partial \beta^s} \gamma_i \right]_{\beta=0} = p_{si}. \tag{A1}$$

Note that the first index of p_{si} refers to the order of the derivative and the second index gives the position in state space. We expand Eq. (4) to the third order under weak selection $\gamma_i \approx 1 + p_{1i}\beta + p_{2i}\beta^2/2 + p_{3i}\beta^3/6$. Hence, we have

$$\prod_{i=1}^{k} \gamma_i \approx 1 + \underbrace{\sum_{j=1}^{k} p_{1j}\beta}_{L_{1k}} + \underbrace{\left[\sum_{j=1}^{k} (p_{2j} - p_{1j}^2) + (\sum_{j=1}^{k} p_{1j})^2 \right] \frac{\beta^2}{2}}_{L_{2k}}$$

$$+ \underbrace{\left[\sum_{j=1}^{k} p_{3j} + 3 \left(\sum_{j=1}^{k} p_{1j} \right) \left(\sum_{s=1}^{k} p_{2s} \right) - 3 \sum_{j=1}^{k} p_{1j}p_{2j} \right] \frac{\beta^3}{6}}_{L_{3k}}. \tag{A2}$$

Then, the fixation probability can be written as

$$\phi_1 \approx \left(N + \beta \underbrace{\sum_{k=1}^{N-1} L_{1k}}_{Q_1} + \frac{\beta^2}{2} \underbrace{\sum_{k=1}^{N-1} L_{2k}}_{Q_2} + \frac{\beta^3}{6} \underbrace{\sum_{k=1}^{N-1} L_{3k}}_{Q_3} \right)^{-1} \tag{A3}$$

$$\approx \frac{1}{N} - \frac{Q_1}{N^2}\beta + \left[\frac{Q_1^2}{N^3} - \frac{Q_2}{2N^2} \right]\beta^2 - \left[\frac{Q_1^3}{N^4} - \frac{Q_1 Q_2}{N^3} + \frac{Q_3}{6N^2} \right]\beta^3. \tag{A4}$$

This now serves as a starting point for our particular processes with certain choices of $\gamma_i = T_i^- / T_i^+$ and particular p_{si} resulting from this.

1. General pairwise comparison process

For general switching probabilities in a pairwise comparison process, we have

$$p_{1i} = -\frac{2g'(0)}{g(0)}\Delta\pi_i, \tag{A5}$$

$$p_{2i} = \left(\frac{2g'(0)}{g(0)}\Delta\pi_i \right)^2, \tag{A6}$$

$$p_{3i} = -2\frac{6[g'(0)]^3 - 3g(0)g'(0)g''(0) + g(0)^2 g'''(0)}{g(0)^3}(\Delta\pi_i)^3. \tag{A7}$$

Inserting these quantities into Eqs. (A2) and (A3) leads to

$$Q_1 = -\frac{2g'(0)}{g(0)}\sum_{k=1}^{N-1}\sum_{i=1}^{k}\Delta\pi_i, \tag{A8}$$

$$Q_2 = \left(\frac{2g'(0)}{g(0)} \right)^2 \sum_{k=1}^{N-1} \left(\sum_{i=1}^{k}\Delta\pi_i \right)^2, \tag{A9}$$

$$Q_3 = 2\frac{6[g'(0)]^3 + 3g(0)g'(0)g''(0) - g(0)^2 g'''(0)}{g(0)^3}$$
$$\times \sum_{k=1}^{N-1}\sum_{i=1}^{k}(\Delta\pi_i)^3 - \frac{24(g'(0))^3}{g(0)^3}$$
$$\times \sum_{k=1}^{N-1} \left(\sum_{i=1}^{k}\Delta\pi_i \right) (\sum_{s=1}^{k}(\Delta\pi_s)^2). \tag{A10}$$

Here, Q_1 and Q_2 have been calculated in the main text. Note that they only depend on $g'(0)/g(0)$, whereas Q_3 also depends on higher order derivatives of the imitation function. Thus, two pairwise comparison processes that are identical in first order are also identical in second order. Only in third order, differences start to emerge.

Let us briefly come back to our example of an imitation function that violates the one-third rule, $g(x) = [1 + \exp(-x^3)]^{-1}$. In this case, we have $g(0) = 1/2$,

$g'(0)=g''(0)=0$, and $g'''(0)=3/2$. Thus, both Q_1 and Q_2 vanish and the third-order expansion of the fixation probability is

$$\phi_1 \approx \frac{1}{N} + \frac{N-1}{60N}[(N+1)(3N^2-2)u^3 + 15(N+1)Nu^2v$$
$$+ 30(N+1)uv^2 + 30v^3]\beta^3. \tag{A11}$$

2. Moran processes

For the Moran processes with general fitness functions, we have $p_{1i}=-f'(0)\Delta\pi_i$ and $p_{2i}=2[f'(0)]^2\pi_A\Delta\pi_i-f''(0)(\pi_A+\pi_B)\Delta\pi_i$. Inserting these quantities into Eqs. (A2) and (A3) leads to

$$Q_1 = -f'(0)\sum_{k=1}^{N-1}\sum_{i=1}^{k}\Delta\pi_i,$$

$$Q_2 = \{[f'(0)]^2 - f''(0)\}\sum_{k=1}^{N-1}\sum_{i=1}^{k}(\pi_A^2 - \pi_B^2)$$
$$+ [f'(0)]^2\sum_{k=1}^{N-1}\left(\sum_{i=1}^{k}\Delta\pi_i\right)^2. \tag{A12}$$

Thus, the first- and the second-order expansions of the fixation probability of such processes are given in Eqs. (18) and (19), respectively. In particular, for $f(\pi)=1+\pi^3$, both p_{1i} and p_{2i} vanish and $p_{3i}=-6(\pi_A^3-\pi_B^3)$. In Eq. (A3), this yields

$$\phi_1 = \frac{1}{N} + \underbrace{\frac{1}{N^2}\sum_{k=1}^{N-1}\sum_{i=1}^{k}(\pi_A^3 - \pi_B^3)\beta^3}_{D_3} + o(\beta^3), \tag{A13}$$

where

$$D_3 = [1/60N(N-1)^2][-3c^2d(N-2)(1+N)(2N-1)$$
$$- 3cd^2(N-2)(N+1)(3N-4) + 6a^2b(N-2)(N^2-2N$$
$$+ 2) + a(a^2+3b^2)(N-2)(3N^2-6N+1) - c^3(1+N)$$
$$\times(3N^2-2) + 2b^3(1+N-9N^2+6N^3)$$
$$- d^3(N-2)(29-39N+12N^2)].$$

APPENDIX B: TIMES OF FIXATION

General expressions for the first- and second-order expansions of the fixation time for the birth-death process have been given in Eqs. (26) and (30). Based on these, we show the results for the general pairwise comparison rule first and then discuss the Moran process.

1. General pairwise comparison process

For the first-order term of the fixation time [Eq. (26)], each h_α on the right-hand side is proportional to $g'(0)/g^2(0)$. Thus, the first-order term of the fixation time is of the form $Rg'(0)/g^2(0)$. In particular, when $g(\Delta\pi)$ is the Fermi func-

tion, $g'(0)/g^2(0)$ is 1. Hence, the first order of the fixation time for the Fermi process is R [cf. Eq. (23)]. This leads to the first-order expansion of the fixation time for general pairwise comparison rule [Eq. (29)].

For the second order, we write Eq. (30) explicitly as

$$\frac{\partial^2}{\partial\beta^2}\tau_1^A = \underbrace{\sum_{k=1}^{N-1}\sum_{l=1}^{k}h_{(2,0,0)}}_{K_1} + \underbrace{\sum_{k=1}^{N-1}\sum_{l=1}^{k}h_{(0,2,0)}}_{K_2} + \underbrace{\sum_{k=1}^{N-1}\sum_{l=1}^{k}h_{(0,0,2)}}_{K_3}$$
$$+ 2\underbrace{\sum_{k=1}^{N-1}\sum_{l=1}^{k}h_{(1,1,0)}}_{K_4} + 2\underbrace{\sum_{k=1}^{N-1}\sum_{l=1}^{k}h_{(1,0,1)}}_{K_5} + 2\underbrace{\sum_{k=1}^{N-1}\sum_{l=1}^{k}h_{(0,1,1)}}_{K_6}. \tag{B1}$$

As shown in the main text, the second-order term is of the form $G_1u^2+G_2uv+(G_2/N)v^2$. Letting $u=1$ and $v=0$ leads to

$$K_1 = \frac{N^2(N-1)(2N-1)}{6}\frac{2[g'(0)]^2-g(0)g''(0)}{g(0)^3},$$

$$K_2 = -\frac{N^2(N-2)(N-1)(17+63N+16N^2)}{2700}\frac{2[g'(0)]^2}{g(0)^3},$$

$$K_3 = \frac{N(-120+4N+350N^2-65N^3-290N^4+121N^5)}{1800}$$
$$\times\frac{2[g'(0)]^2}{g(0)^3},$$

$$K_4 = -\frac{N^3(N^2-1)}{12}\frac{2[g'(0)]^2}{g(0)^3},$$

$$K_5 = \frac{N^3(2-3N+N^2)}{9}\frac{2[g'(0)]^2}{g(0)^3},$$

$$K_6 = -\frac{N^2(2+25N-15N^2-25N^3+13N^4)}{180}\frac{2[g'(0)]^2}{g(0)^3} \tag{B2}$$

after some tedious calculations using the identity $\Sigma_{k=1}^{M}\Sigma_{l=1}^{k}=\Sigma_{l=1}^{M}\Sigma_{k=l}^{M}$ [56]. Summing these K_i's leads to G_1 in Eq. (32). On the other hand, letting $u=0$ and $v=1$ yields

$$K_1 = N(N-1)\frac{2[g'(0)]^2-g(0)g''(0)}{g(0)^3},$$

$$K_2 = \frac{N^2(N-1)(N-2)}{18}\frac{2[g'(0)]^2}{g(0)^3},$$

$$K_3 = \frac{N(4N^3-15N^2+17N-6)}{18}\frac{2[g'(0)]^2}{g(0)^3},$$

$$K_4 = -\frac{N^2(N-1)}{2}\frac{2[g'(0)]^2}{g(0)^3},$$

$$K_5 = \frac{N(N-1)(N-2)}{2} \frac{2[g'(0)]^2}{g(0)^3},$$

$$K_6 = -\frac{N^2(N-1)(N-2)}{3} \frac{2[g'(0)]^2}{g(0)^3}. \tag{B3}$$

Adding these K_i's yields G_2/N as in Eq. (33). Thus, the quantities in Eq. (31) are finally derived.

2. Moran processes

For Moran processes, the approach is fully equivalent to pairwise comparison processes. However, the results do not only depend on payoff differences u and v but also on the full payoff matrix with entries a, b, c, and d. This makes the calculations a matter of diligence and leads to quite long expressions, but not to additional insights. Thus, we do not give details of the derivation here.

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