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Fixation in Evolutionary Games under Non-Vanishing Selection

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One of the most striking effect of fluctuations in evolutionary game theory is the possibility for mutants to fixate (take over) an entire population. Here, we generalize a recent WKB-based theory to study fixation in evolutionary games under non-vanishing selection, and investigate the relation between selection intensity w and demographic (random) fluctuations. This allows the accurate treatment of large fluctuations and yields the probability and mean times of fixation *beyond* the weak selection limit. The power of the theory is demonstrated on prototypical models of cooperation dilemmas with multiple absorbing states. Our predictions compare excellently with numerical simulations and, for *finite* w , significantly improve over those of the Fokker-Planck approximation.

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INTRODUCTION

Evolutionary game theory (EGT) provides a natural theoretical framework to describe the dynamics of systems where successful types or behaviors, as those arising in biology, ecology and economics [1, 2], are copied by imitation and spread. Evolutionary stability is a crucial concept in EGT and specifies under which circumstances a population is proof against invasion from mutants [1, 2]. This notion was shown to be altered by finite-size fluctuations and led to the key concept of *evolutionary stability in finite populations* [2]. The latter is closely related to the notion of *fixation* [2, 3], referring to the possibility for mutants to take over (fixate) an entire population of wild species individuals. Furthermore, evolutionary dynamics is characterized by the interplay between random fluctuations [4] and selection, that underlies adaptation in terms of the different reproduction potential (fitness) of the individuals. Thus, a parameter was introduced to measure the selection intensity [2]. In this context, the fixation probability of a species has been calculated for a finite two-species population in the weak selection limit of vanishingly small selection intensity [2, 3, 5]. This limit is often biologically relevant and greatly simplifies the analysis (treating selection as a linear perturbation). However, the behaviors obtained under strong and weak selection are often qualitatively different (see e.g. [5, 6]).

In this Letter, we study fixation under non-vanishing selection in EGT and provide a comprehensive analysis of the combined influence of non-vanishing selection and random fluctuations. As exact results for the fixation probability and mean fixation times (MFTs) are rarely available and often unwieldy (see e.g. [2, 3, 7]), our analysis relies on the WKB (Wentzel-Kramers-Brillouin) approximation method [8] directly applied to the underlying master equation [9]. This technique was recently used to treat generic birth-death systems that undergo metastable switching or extinction [10, 11]. Importantly, here we generalize the WKB formalism to systems with *multiple* absorbing states. This theory ac-

curately accounts for the large fluctuations not aptly captured [12, 13] by the Fokker-Planck approximation (FPA) [7]. We illustrate our method on two classes of prototypical models of cooperation dilemmas, the anti-coordination and coordination games, where a coexistence state separates two absorbing states in which the population is composed of only the fixated species while the other goes extinct [1, 2]. We compute the fixation probabilities, the MFTs, as well as the complete probability distribution function (PDF) of population sizes, and show that our theory is superior to the FPA for finite selection strength.

THE MODELS

In EGT, the fitness, or reproduction potential of an individual, is determined by the outcome, called payoff, of its interaction with the others as prescribed by the underlying game [1]. In fact, when two A-individuals interact, both receive a payoff a . If an individual of type A interacts with another of type B, the former receives b while the latter gets a payoff c . Similarly, when two B-individuals interact, both get a payoff d . Now, assume that in a population of size N there are n individuals of type A (“mutants”) and $N - n$ of type B (“wild type”). The respective average payoffs (per individual) are $\Pi_A(n) = (n/N)a + [(N - n)/N]b$ and $\Pi_B(n) = (n/N)c + [(N - n)/N]d$ [14], while the population mean payoff is $\bar{\Pi}(n) = [n\Pi_A(n) + (N - n)\Pi_B(n)]/N$. For infinite ($N \rightarrow \infty$) and well-mixed populations, the density $x \equiv n/N$ of the A species changes according to its relative payoff and obeys the replicator dynamics, given by the rate equation [1, 2]

$$\dot{x} = x(\Pi_A - \bar{\Pi}). \quad (1)$$

Here, we are particularly interested in anti-coordination games (ACG), where $c > a$ and $b > d$, and in coordination games (CG), where $a > c$ and $d > b$. In addition to

the absorbing states $n = 0$ and $n = N$, ACG and CG admit an interior fixed point associated with the *coexistence* of A and B species at a density $x^* = (d-b)/(a-b-c+d)$ of A's. According to the rate equation (1), x^* is an attractor in ACG and a repeller in CG, whereas $x = 0$ and $x = 1$ are repelling fixed points in ACG and attracting in CG.

To account for fluctuations arising when the population size is finite, the evolutionary dynamics is implemented in terms of fitness-dependent birth-death processes [2, 3] describing, e.g., the evolution of the probability $P_n(t)$ to have n individuals of type A at time t :

$$\frac{dP_n(t)}{dt} = T_{n-1}^+ P_{n-1} + T_{n+1}^- P_{n+1} - [T_n^+ + T_n^-] P_n. \quad (2)$$

Here, an individual chosen proportionally to its fitness produces an identical offspring which replaces a randomly chosen individual [15], and the total population size N is conserved. Thus, in the master equation (2), the reaction rates for the birth/death transitions $n \rightarrow n \pm 1$ are given by $T_n^\pm = \chi^\pm(f_A(n), f_B(n)) n(N-n)/N^2$, where $\chi^\pm(n)$ are functions of the fitness of each species, $f_A(n) = 1 - w + w\Pi_A(n)$ and $f_B(n) = 1 - w + w\Pi_B(n)$. As often in EGT, we focus on systems evolving according to the fitness-dependent *Moran process* (fMP) for which $\chi^+(n) = f_A[(n/N)f_A + (1-n/N)f_B]^{-1}$ and $\chi^-(n) = f_B[(n/N)f_A + (1-n/N)f_B]^{-1}$ [2, 15]. It is worth noticing that $\chi^+(n)$ and $\chi^-(n)$ intersect only at the fixed point value $n = Nx^*$ for $0 \leq n \leq N$, which ensures that the properties of the replicator dynamics (1) are recovered when $N \rightarrow \infty$ [1–3, 16, 17].

The fitnesses $f_A(n)$ and $f_B(n)$ are comprised of a baseline contribution [the constant $(1-w)$] and a term accounting for selection [$w\Pi_A$ for f_A], where the parameter $0 \leq w \leq 1$ measures the selection intensity [2, 3]. The latter is weak for $w \rightarrow 0$, when $T_n^\pm \propto n(N-n)/N^2$, and strong for $w \rightarrow 1$, when the baseline fitness becomes negligible. As $n \in [0, N]$ and $n = 0, N$ are absorbing, the boundary conditions to Eq. (2) are $T_0^\pm = T_N^\pm = 0$.

WKB THEORY OF ANTI-COORDINATION GAMES

Our WKB-based approach is presented in the framework of ACG (e.g. snowdrift and hawk-dove games [1]), where the absorbing states $n = 0$ or $x = 0$ (all B's), and $n = N$ or $x = 1$ (all A's) are separated by the interior attractor x^* [in the language of the rate equation (1)]. However, in the presence of noise x^* becomes *metastable*, which is very naturally accounted by our theory. For $Nx^* \gg 1$, after a short relaxation time t_r , the system settles into a long-lived metastable state whose population size distribution is peaked in the vicinity of Nx^* [13]. This implies that fixation of either species

occurs only in the aftermath of a long-lasting coexistence. At $t \gg t_r$, only the first excited eigenvector of (2), π_n , called the quasi-stationary distribution (QSD), has not decayed and hence determines the shape of the metastable PDF. Indeed, at $t \gg t_r$ the higher eigenmodes in the spectral expansion of $P_n(t)$ have already decayed, and the metastable dynamics of the population sizes PDF satisfies [13]

$$P_n(t) \simeq \pi_n e^{-t/\tau} \quad \text{for } n \in [1, N-1], \quad (3)$$

where $\sum_n \pi_n = 1$. Thus, at $t \gg t_r$ the dynamics of the probabilities to be absorbed at $n = 0$ and $n = N$ satisfies

$$P_0(t) \simeq \phi(1 - e^{-t/\tau}), \quad P_N(t) \simeq (1 - \phi)(1 - e^{-t/\tau}). \quad (4)$$

Here, $\phi^B = \phi$ and $\phi^A = 1 - \phi$ are the fixation probabilities of the B and A species, respectively, τ is the unconditional MFT, and a very strong inequality $\tau \gg t_r$ holds. The fixation probability and MFT are determined by the fluxes into the absorbing states. Therefore, using Eqs. (2) and (4), one obtains

$$\tau = [T_1^- \pi_1 + T_{N-1}^+ \pi_{N-1}]^{-1}, \quad \text{and } \phi = T_1^- \pi_1 \tau. \quad (5)$$

Similarly, the respective *conditional* MFTs of species A and B (conditioned on the fixation of type A and B, respectively) are $\tau^A = [T_{N-1}^- \pi_{N-1}]^{-1}$ and $\tau^B = [T_1^+ \pi_1]^{-1}$. According to Eq. (5), these quantities are determined once we have obtained π_1 and π_{N-1} from the full expression of the QSD that we now compute.

The QSD satisfies the quasi-stationary master equation, obtained by substituting Eq. (3) into (2) and neglecting the exponentially small term π_n/τ (to be verified a posteriori):

$$T_{n-1}^+ \pi_{n-1} + T_{n+1}^- \pi_{n+1} - [T_n^+ + T_n^-] \pi_n = 0. \quad (6)$$

For $N \gg 1$, we define the transition rates $\mathcal{T}_\pm(x) = T_n^\pm$ [14] as continuous functions of x , and treat Eq. (6) by employing the WKB ansatz [9–11]

$$\pi_n \equiv \pi_{xN} = \pi(x) = \mathcal{A} \exp[-NS(x) - S_1(x)], \quad (7)$$

where $S(x)$ and $S_1(x)$ are respectively the system's action and its amplitude, and \mathcal{A} is a constant prefactor introduced for convenience. The WKB approximation is here an asymptotic series expansion in powers of $1/N$ based on the exponential ansatz (7) (see, e.g., [9–11]) [18]. Substituting (7) into Eq. (6) yields closed equations for $S(x)$ and $S_1(x)$. To leading order, similarly as in Hamiltonian systems, the action obeys the Hamilton-Jacobi equation $H(x, S') = 0$. In this case, the underlying Hamiltonian is

$$H(x, p) = \mathcal{T}_+(x)(e^p - 1) + \mathcal{T}_-(x)(e^{-p} - 1), \quad (8)$$

where we have introduced the auxiliary momentum $p(x) = dS/dx$ [9–11]. Therefore, to leading order,

the “optimal-path” followed by the stochastic system, from the metastable state to fixation, is $p_a(x) = -\ln[\mathcal{T}_+(x)/\mathcal{T}_-(x)]$, corresponding to the zero-energy trajectory $H(x, p_a) = 0$ with non-zero momentum. The action along $p_a(x)$ is

$$S(x) = -\int^x \ln[\mathcal{T}_+(\xi)/\mathcal{T}_-(\xi)] d\xi. \quad (9)$$

Performing the subleading-order calculations, one obtains $S_1(x) = (1/2)\ln[\mathcal{T}_+(x)\mathcal{T}_-(x)]$ [10, 11]. Imposing the normalization of the Gaussian expansion of the QSD (7) about $x = x^*$, one finds the constant \mathcal{A} , yielding

$$\pi(x) = \mathcal{T}_+(x^*) \sqrt{\frac{S''(x^*)}{2\pi N \mathcal{T}_+(x)\mathcal{T}_-(x)}} e^{-N[S(x)-S(x^*)]}. \quad (10)$$

This expression is valid sufficiently far from the boundaries, where $\mathcal{T}_\pm(x) = \mathcal{O}(1)$ [11], and generally leads to a *non-Gaussian* QSD with systematic deviations from the Gaussian approximation near the tails, as illustrated in Fig. 1(a).

To obtain the full QSD we need to match the WKB result (10) with the solution of Eq. (6) in the vicinity of the absorbing boundaries, where the transition rates can be linearized [11]. For instance, near $x = 0$, $\mathcal{T}_\pm(x) \simeq x\mathcal{T}'_\pm(0)$, so Eq. (6) yields $(n-1)\mathcal{T}'_+(0)\pi_{n-1} + (n+1)\mathcal{T}'_-(0)\pi_{n+1} - n[\mathcal{T}'_+(0) + \mathcal{T}'_-(0)]\pi_n = 0$. Its recursive solution is $\pi_n = (\pi_1/n)(R_0^n - 1)/(R_0 - 1)$, where $R_0 = \mathcal{T}'_+(0)/\mathcal{T}'_-(0)$. Matching this expression with the leading order of Eq. (10) in the vicinity of $x = 0$ yields

$$\pi_1 = \sqrt{\frac{NS''(x^*)}{2\pi} \frac{\mathcal{T}_+(x^*)(R_0 - 1)}{\sqrt{\mathcal{T}'_+(0)\mathcal{T}'_-(0)}}} e^{N[S(x^*)-S(0)]}. \quad (11)$$

A similar analysis at $x \simeq 1$ with $R_1 = \mathcal{T}'_-(1)/\mathcal{T}'_+(1)$ gives

$$\pi_{N-1} = \sqrt{\frac{NS''(x^*)}{2\pi} \frac{\mathcal{T}_+(x^*)(R_1 - 1)}{\sqrt{\mathcal{T}'_+(1)\mathcal{T}'_-(1)}}} e^{N[S(x^*)-S(1)]}. \quad (12)$$

Hence, the expressions (10)-(12) provide us with the complete QSD.

FIXATION IN ANTI-COORDINATION GAMES

We now apply the general results obtained in the previous section to study fixation in ACG, when the system follows the fMP. In this case the action given by Eq. (9), becomes

$$S(x) = [B/(B-A) - x] \ln[Ax + B(1-x)] + [D/(C-D) + x] \ln[Cx + D(1-x)], \quad (13)$$

where $A = 1-w+wa$, $B = 1-w+wb$, $C = 1-w+wc$, and $D = 1-w+wd$ [19]. Provided that $N[S(1)-S(x^*)] \gg 1$, and $N[S(0)-S(x^*)] \gg 1$ (which imposes a lower bound

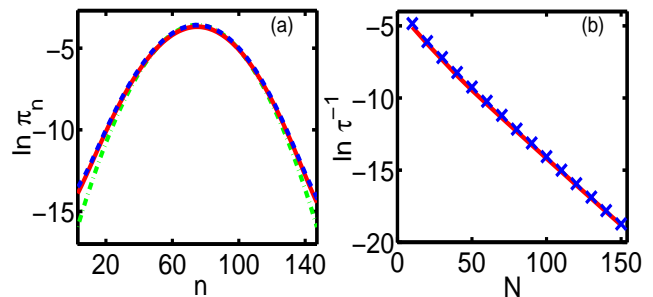


FIG. 1: (*Color online*). (a) $\ln \pi_n$ vs. n (with $N = 150$): theoretical predictions [Eqs. (10)-(13)] (solid) compared with numerical results (dashed) and with the Gaussian approximation of the QSD (dashed-dotted). (b) $\ln \tau^{-1}$ as a function of N : theoretical predictions [Eqs. (5), (11)-(13)] (solid) and numerical results (symbols). Parameters are $a = 0.1$, $b = 0.7$, $c = 0.6$, $d = 0.2$, $w = 0.5$ and the system follows the fMP.

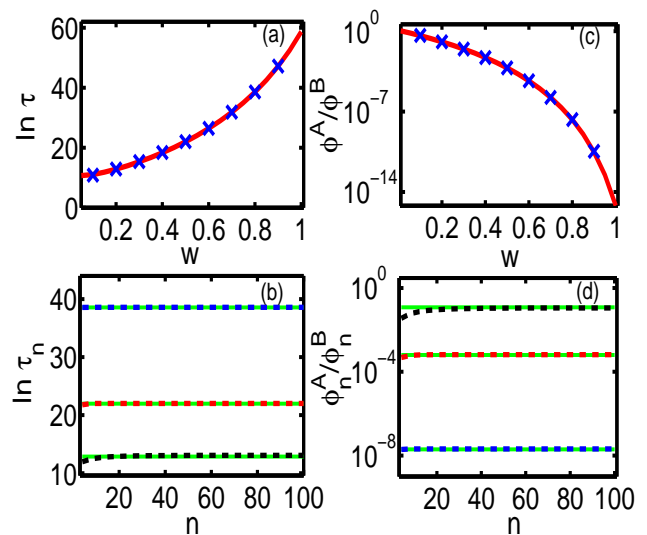


FIG. 2: (*Color online*). (a) $\ln \tau$ vs w : theoretical [Eqs. (5), (11)-(13)] (solid) and numerical results (symbols). (b) Dependence of $\ln \tau$ on the initial number n of A’s, for $w = 0.2$, 0.5 and 0.8 (bottom to top): comparison between theoretical (solid) and numerical (dashed) results. (c) Theoretical [Eq. (14)] (solid) and numerical (symbols) results for the ratio ϕ^A/ϕ^B vs w . (d) Same as in panel (b) for ϕ_c^A/ϕ_n^B (w grows from top to bottom). Parameters are $a = 0.1$, $b = 0.7$, $c = 0.7$, $d = 0.2$, $N = 200$ and the system follows the fMP. In the numerical results of (a) and (c), n is chosen sufficiently large so that fixation does not occur immediately (see text).

on w), the MFTs and fixation probability are obtained from Eqs. (5) and (11)-(13) with $T_1^- = T_{N-1}^+ \simeq N^{-1}$. These results generalize those obtained previously in the limiting cases $Nw \ll 1$ [3, 5] and $w = 1$ (for which $A = a$, $B = b$, $C = c$, and $D = d$) [6]. As illustrated in Fig. 1(b), one finds that the unconditional MFT asymptotically exhibits an exponential dependence on the population size N , $\tau \propto N^{1/2} e^{N(\Sigma - S(x^*))}$, where

the governing exponent $\Sigma \equiv \min[S(0), S(1)]$ is readily obtained from (13). With (10)-(12), this confirms that π_n/τ is indeed exponentially small. For $0 < w < 1$, one finds that Σ increases monotonically with w , as shown in Fig. 2(a). Here (as in our other figures), the theoretical predictions are compared with the numerical solution of the master equation (2) yielding an excellent agreement. It also follows from (5),(11)-(13) that for $N \gg 1$ and small (but not too small) selection intensity, $N^{-1} \ll w \ll 1$, the conditional MFTs grow exponentially as $\tau^A \sim N^{1/2} e^{Nw(a-c)^2/[2(c-a+b-d)]}$, and $\tau^B \sim N^{1/2} e^{Nw(b-d)^2/[2(c-a+b-d)]}$, with $\tau = \tau^A \tau^B / (\tau^A + \tau^B) \sim \min(\tau^A, \tau^B)$.

As our approach assumes that fixation occurs *after* the metastable state is reached, the expressions obtained for the MFTs are *independent* of the initial number n of A's, when $n \gg 1$. This is confirmed in Fig. 2(b) where theory and numerical results agree excellently.

The ratio $\phi^A/\phi^B = \phi^{-1} - 1$ between the fixation probabilities of the A's and B's allows to understand the influence of selection and the interplay between selection and demographic stochasticity. Indeed, with Eqs. (5), and (11)-(13), our theory yields

$$\frac{\phi^A}{\phi^B} = \frac{\pi_{N-1}}{\pi_1} = \sqrt{\frac{BD}{AC}} \left(\frac{C-A}{B-D} \right) \frac{B^{N(\frac{B}{B-A})} D^{N(\frac{D}{C-D})}}{A^{N(\frac{A}{B-A})} C^{N(\frac{C}{C-D})}}. \quad (14)$$

In Fig. 2(c), we show the ratio ϕ^A/ϕ^B and find a nontrivial exponential dependence on w in excellent agreement with numerical calculations. Contrary to the neutral case $w = 0$ (not covered by our theory), where the ratio of fixation probabilities strongly depends on the initial number of A's [2], Eq. (14) predicts that ϕ^A/ϕ^B is independent of the initial condition when the selection strength is finite. Indeed, the numerical results presented in Fig. 2(d) confirm that for $n \gg 1$, the ratio ϕ^A/ϕ^B coincides with (14) and becomes independent of n when w is nonzero (for $w \ll 1$ the convergence requires $n \sim Nx^*$).

WKB THEORY AND FIXATION IN COORDINATION GAMES

As a further illustration of our theory, we accurately compute the fixation probability in CG (*e.g.* stag-hunt game [1]). Here, the fixed point x^* is a repeller while $x = 0, 1$ are attracting, hence there is no metastability and fixation occurs quickly [6]. As a result, with an initial minority of A's, $n < Nx^*$, the fixation of B's is almost certain, and we are interested in calculating the exponentially small probability $\phi_n^A \equiv \phi^A(x)$ that A's fixate. Such a probability satisfies the following equation [2, 3, 6]:

$$T_n^+ \phi_{n+1}^A + T_n^- \phi_{n-1}^A - [T_n^+ + T_n^-] \phi_n^A = 0, \quad (15)$$

which is the stationary backward master equation of this problem [7], with boundary conditions $\phi_0^A = 0, \phi_N^A = 1$.

At this point, it is convenient to introduce the auxiliary quantity

$$\mathcal{P}_n \equiv \phi_{n+1}^A - \phi_n^A \equiv \mathcal{P}(x), \quad (16)$$

which is a normalized PDF peaked at x^* . From Eq. (16), the fixation probability ϕ_n^A can be easily obtained, yielding $\phi_n^A = \sum_{m=0}^{n-1} \mathcal{P}_m$. Substituting Eq. (16) into Eq. (15), one arrives at a difference equation for the PDF $\mathcal{P}(x)$ which reads

$$\mathcal{T}_+(x)\mathcal{P}(x) - \mathcal{T}_-(x)\mathcal{P}(x-1/N) = 0. \quad (17)$$

This equation can be treated with the WKB ansatz $\mathcal{P}(x) = \mathcal{A}_{CG} e^{-NS(x) - \mathcal{S}_1(x)}$. To leading order one has $\mathcal{T}_+(x) - \mathcal{T}_-(x)e^{\mathcal{S}'(x)} = 0$, whose solution is $\mathcal{S}(x) = -S(x)$ [where $S(x)$ is given by Eq. (9)]. In the subleading order, after some algebra, one finds $\mathcal{S}_1(x) = (1/2) \ln[\mathcal{T}_+(x)/\mathcal{T}_-(x)]$. Normalizing $\sum_{n=0}^{N-1} \mathcal{P}_n \simeq N \int_0^1 \mathcal{P}(x) dx = 1$, and assuming a main Gaussian contribution arising from $x \simeq x^*$, we find $\mathcal{A}_{CG} \simeq \sqrt{|S''(x^*)|/(2\pi N)} e^{-NS(x^*)}$. In the realm of the WKB approach, we have thus obtained an expression of $\mathcal{P}(x)$ that holds for $0 \leq x \leq 1$. [It can be checked that such a WKB result satisfies Eq. (17) also near the absorbing boundaries [21].] From the expression of $\mathcal{P}(x)$, the fixation probability thus reads

$$\phi_n^A = \sqrt{\frac{|S''(x^*)|}{2\pi N}} \sum_{m=0}^{n-1} \sqrt{\frac{T_m^-}{T_m^+}} e^{N[S(m/N) - S(x^*)]}. \quad (18)$$

Of special interest is the limit of $n \ll Nx^*$ corresponding to the fixation of a few mutants in a sea of wild-type individuals [2]. In this case, it can be shown that Eq. (18) can be well approximated by $\phi^A(x) \simeq \mathcal{P}(x)/[e^{\mathcal{S}'(x)} - 1]$ when $w = \mathcal{O}(1)$, while for small selection $N^{-1} \ll w \ll 1$, $\phi^A(x) \simeq \sqrt{N|S''(x^*)|/(2\pi)} \int_0^x dy e^{N[S(y) - S(x^*)]}$ [21]. A comparison between theory (18) and numerical results, using $S(x)$ from Eq. (13), is shown in Figs. 3 and 4(a) and an excellent agreement is observed.

The WKB theory presented in this section (as well as that dedicated to the ACG) is valid as long as $w \gg N^{-1}$. For small selection intensity, $w \ll 1$ [20], the fixation probability is often computed using the FPA (or diffusion approximation) [3-5], usually considered within the linear noise approximation [7]. Thus, for $N^{-1} \ll w \ll 1$ (and $N \gg 1$), the predictions of the WKB and FPA approximations can be compared (together with results of numerical simulations) to determine their respective domains of validity.

For the purpose of comparison, it is convenient to rewrite both WKB and FPA predictions in the following form: $\phi^A(x) \simeq \Psi(x)/\Psi(1)$, where $\Psi(x) = \int_0^x dy e^{-\int_0^y dz \Theta(z)}$. From Eq. (18), one finds that for the WKB approach the exponent reads $\Theta_{WKB}(z) = N \ln[\mathcal{T}_+(z)/\mathcal{T}_-(z)]$, whereas

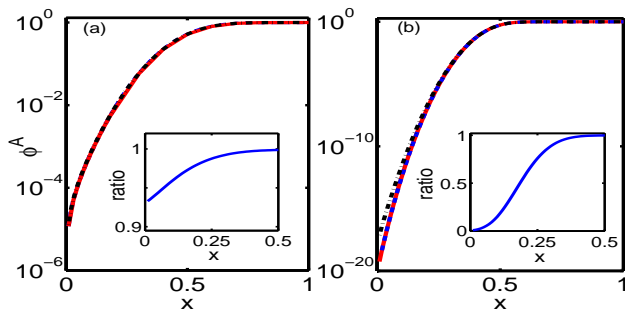


FIG. 3: (*Color online*). The fixation probability $\phi^A(x)$ for the fMP process: theoretical result (18) (solid), numerical calculations (dashed) and FPA (dash-dotted), with $a = 4, b = 0.2, c = 0.3, d = 3.8, N = 100$. Insets: ratio between theoretical results and those of the FPA, see text. (a) For $w = 0.1, Nw^2 = 1$ and all curves agree well, with an error of about 7% in the predictions of the FPA for $x \rightarrow 0$. (b) For $w = 0.75, Nw^2 \gg 1$, the curve obtained from the FPA systematically deviates from the others and yields exponentially large errors.

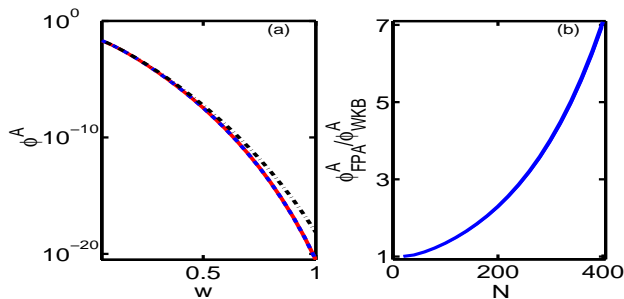


FIG. 4: (*Color online*). (a) Fixation probability $\phi^A(x)$ as function of w : theoretical result (18) (solid), numerical calculations (dashed) and FPA (dash-dotted), for $a = 1, b = 0.2, c = 0.3, d = 0.8$, and $N = 200$. (b) Ratio between the predictions of the FPA and those of our theory vs N , for $w = 0.25, a = 4, b = 0.2, c = 0.3$, and $d = 3.8$. The results of the FPA deteriorate when both w and N increase. In (a) and (b), $n = 10$ thus $x = 10/N$, and the system follows the fMP.

for the FPA one has the exponent $\Theta_{\text{FPA}}(z) = 2Nz [\mathcal{T}'_+(x^*) - \mathcal{T}'_-(x^*)] / [\mathcal{T}_+(x^*) + \mathcal{T}_-(x^*)]$ [7]. Hence, it can be shown that in the vicinity of $x = x^*$, $\Theta_{\text{WKB}}(x) - \Theta_{\text{FPA}}(x) \sim Nw^2(x - x^*)^2$ [21]. Therefore, while the WKB result (18) is accurate for any finite value of w [as shown in Fig. 4(a)], the FPA is unable to account for fixation and yields exponentially large errors when $w \gtrsim N^{-1/2}$. In fact, the predictions of the FPA (within linear noise approximation) are accurate only when the selection intensity satisfies $w \ll N^{-1/2}$, which is a more stringent condition than $w \ll 1$. This is illustrated in Figs. 3 and 4 which display a comparison between our predictions and those of the FPA for various values of w and N .

CONCLUSION

We have studied fixation in evolutionary games under non-vanishing selection and elucidated the nontrivial relation between selection intensity and effects of demographic fluctuations. This has been achieved by generalizing a recent WKB-based theory to account for multiple absorbing states. This approach naturally accounts for non-Gaussian behavior and allows an accurate treatment of large fluctuations. In the framework of models of cooperation dilemmas, we have analytically computed the QSD (shape of the metastable PDF), MFTs and the fixation probabilities *beyond* the weak selection limit. While it does not cover the $w \rightarrow 0$ limit (where the FPA holds), our theory agrees excellently with numerical simulations over a broad range of finite selection strength ($0 < w \leq 1$), where the FPA generally fails. For concreteness, our approach has been illustrated for two classes of (formally solvable) 2×2 games, but is neither restricted to linear payoffs nor to a specific choice of the transition rates [21]. Importantly, our theory can be adapted to study evolutionary processes for which there is no rigorous analytical treatment (e.g. 3×3 games [1]) and help generalize the concept of evolutionary stability.

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