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 formulate a WKB (Wentzel-Kramers-Brillouin) based theory to study fixation in evolutionary games under non-vanishing selection. Within this approach, we accurately account for large fluctuations and compute the mean times and probability of fixation for finite selection intensity w, *beyond* the weak selection limit. The power of our theory is demonstrated on prototypical models of cooperation dilemmas with multiple absorbing states. Our predictions compare excellently with numerical simulations, and we show that our method is superior to the Fokker-Planck approach and has a broader applicability for *finite* w.

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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* (ESFP) [2]. ESFP is closely related to the concept of *fixation* [2, 3], referring to the possibility for mutants to take over (fixate) an entire population of wild species. 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 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]) and it is thus desirable to understand the combined influence of non-vanishing selection and random fluctuations. In this Letter, we study fixation under non-vanishing selection in EGT. As exact results for the fixation probability and mean fixation times (MFTs) are rarely available and often unwieldy (see e.g. [2, 3, 7]), there is need to develop general and reliable methods to treat the evolutionary dynamics. Here, we formulate a dissipative version of the WKB theory [8] that allows us to accurately account for large fluctuations, not aptly captured [9, 10] by the Fokker-Planck approximation (FPA) [7]. In particular, we generalize the WKB method to account for systems with *multiple* absorbing states. Our method is illustrated for two classes of prototypical models of cooperation dilemmas (see below), 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 $\mathsf{A}-$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 $\mathsf{B}-$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 species B ("wild type"). Their respective average payoffs (per individual) are $\Pi_A(n) = (n/N)a + [(N-n)/N]\,b$ and $\Pi_B(n) = (n/N)c + [(N-n)/N]\,d$, while the population mean payoff is $\bar{\Pi}(n) = [n\Pi_A(n) + (N-n)\Pi_B(n)]\,/N$. For infinite ($N \to \infty$) 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 (RD), given by the rate equation $\dot{x} = x(\Pi_A - \bar{\Pi})$ [1, 2]. 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 RD, x^* is stable in ACG and unstable in CG, whereas $x = 0$ and $x = 1$ are unstable fixed points in ACG and stable 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:

$$dP_n(t)/dt = T^+_{n-1}P_{n-1} + T^-_{n+1}P_{n+1} - [T^+_n + T^-_n]P_n. \quad (1)$$

Here, an individual chosen proportionally to its fitness produces an identical offspring which replaces a randomly chosen individual [11], and the total population size N is conserved. Thus, in the master equation (1), the reaction rates for the birth/death transitions $n \to n \pm 1$ are given by $T_n^{\pm} = \chi^{\pm}(f_A(n), f_B(n))\, n(N-n)/N^2$. Here, $\chi^{\pm}$ are (positive definite, well-behaved) functions of the fitness of each species, $f_A(n) = 1 - w + w\Pi_A(n)$ and $f_B(n) = 1 - w + w\Pi_B(n)$, and satisfy $\chi^+(Nx^*) = \chi^-(Nx^*)$ (to recover the properties of the RD when $N \to \infty$ [1–3]). The fitnesses are comprised of a baseline contribution [the constant $(1-w)$] and a term accounting for selection [*i.e.* $w\Pi_A(n)$ for $f_A(n)$], while the parameter $0 \le w \le 1$ measures the selection intensity [2, 3]. Thus, the latter is weak for $w \to 0$, when $T_n^{\pm} \propto n(N-n)/N^2$, and strong for $w \to 1$, when the baseline fitness becomes negligible. As $n \in [0, N]$ and $n = 0$ and $n = N$ are absorbing, the boundary conditions to Eq. (1) are $T^{\pm}(0) = T^{\pm}(N) = 0$.

WKB theory of ACG. 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 $\mathsf{B}'s$), and $n = N$ or $x = 1$ (all $\mathsf{A}'s$) are separated by the interior stable (in the language of the RD) fixed point x^*. However, in the presence of noise x^* becomes *metastable*, which is very naturally accounted by our theory. We assume that after a short relaxation time t_r, the system settles into a long-lived metastable state whose population size distribution is peaked about $Nx^* \gg 1$ [10, 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 (1), π_n, called the quasi-stationary distribution (QSD), has not decayed and hence determines the metastable PDF [10, 13]. In fact, as $n = 0$ and $n = N$ are absorbing, the metastable PDF decays according to $P_n(t) \simeq \pi_n e^{-t/\tau}$, for $n \in [1, N-1]$, while $P_0(t) \simeq \phi(1 - e^{-t/\tau})$ and $P_N(t) \simeq (1-\phi)(1 - e^{-t/\tau})$. Here, $\phi^B = \phi$ and $\phi^A = 1 - \phi$ are the fixation probabilities of the B and A species, respectively, while $\tau \gg t_r$ is the (unconditional) MFT. As the fluxes into the absorbing states determine both the fixation probability and the MFT, using Eq. (1) for $n = 0$ and $n = N$, one obtains

$$\tau = \left[T_1^- \pi_1 + T_{N-1}^+ \pi_{N-1}\right]^{-1}, \text{ and } \phi = T_1^- \pi_1 \tau. \quad (2)$$

The respective *conditional* MFTs of species A and B (conditioned on the fixation of type A and B, respectively) are $\tau^A = \left[T_{N-1}^- \pi_{N-1}\right]^{-1}$ and $\tau^B = \left[T_1^+ \pi_1\right]^{-1}$. To compute these quantities and those of Eq. (2), it suffices to calculate π_1 and π_{N-1}. Furthermore, the QSD satisfies the quasi-stationary master equation (QSME) [12, 13]: $T_{n-1}^+ \pi_{n-1} + T_{n+1}^- \pi_{n+1} - [T_n^+ + T_n^-]\pi_n = 0$, obtained by substituting $P_n(t) \simeq \pi_n e^{-t/\tau}$ into (1) and neglecting the exponentially small term π_n/τ. For $N \gg 1$, we define the transition rates $\mathcal{T}_{\pm}(x) = T_n^{\pm}$ [14] as continuous functions of x and treat the QSME by the WKB ansatz [8, 12, 13]

$$\pi_n \equiv \pi_{xN} = \pi(x) = \mathcal{A} \exp[-NS(x) - S_1(x)]\,, \quad (3)$$

where $S(x)$ and $S_1(x)$ are respectively the system's action and its amplitude, while $\mathcal{A}$ is a constant prefactor. In fact, introducing the ansatz (3) into the QSME yields closed equations for $S(x)$ and $S_1(x)$. In the leading order, in analogy to Hamiltonian systems, the action obeys the Hamilton-Jacobi equation $H(x, S') = 0$. Here, the underlying Hamiltonian is $H(x,p) = \mathcal{T}_+(x)(e^p - 1) + \mathcal{T}_-(x)(e^{-p} - 1)$ [13], where we have introduced the auxiliary momentum $p(x) = dS/dx$ [8, 12, 13]. 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 [8, 12, 13]. The action along $p_a(x)$ is

$$S(x) = -\int^x \ln\left[\mathcal{T}_+(\xi)/\mathcal{T}_-(\xi)\right]\, d\xi. \quad (4)$$

Performing the subleading-order calculations, one obtains $S_1(x) = (1/2)\ln[\mathcal{T}_+(x)\mathcal{T}_-(x)]$ [12, 13]. Imposing the normalization of the Gaussian expansion of the QSD (3) about $x = x^*$, one finds the constant $\mathcal{A}$, yielding

$$\pi(x) = \mathcal{T}_+(x^*)\sqrt{\frac{S''(x^*)}{2\pi N\, \mathcal{T}_+(x)\mathcal{T}_-(x)}}\, e^{-N[S(x)-S(x^*)]}. \quad (5)$$

This expression is valid sufficiently far from the boundaries, where $\mathcal{T}_{\pm}(x) = \mathcal{O}(1)$ [13], 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 solution (5) with the solution of the QSME in the vicinity of the absorbing boundaries, where the transition rates can be linearized [13]. For instance, near $x = 0$, $\mathcal{T}_{\pm}(x) \simeq x\mathcal{T}'_{\pm}(0)$, so the QSME 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 $R_0 = \mathcal{T}'_+(0)/\mathcal{T}'_-(0)$ [13]. Matching this expression with the leading order of (5) about $x = 0$ yields

$$\pi_1 = \sqrt{\frac{NS''(x^*)}{2\pi}}\, \frac{\mathcal{T}_+(x^*)\,(R_0 - 1)}{\sqrt{\mathcal{T}'_+(0)\mathcal{T}'_-(0)}}\, e^{N[S(x^*)-S(0)]}. \quad (6)$$

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

$$\pi_{N-1} = \sqrt{\frac{NS''(x^*)}{2\pi}}\, \frac{\mathcal{T}_+(x^*)(R_1 - 1)}{\sqrt{\mathcal{T}'_+(1)\mathcal{T}'_-(1)}}\, e^{N[S(x^*)-S(1)]}. \quad (7)$$

Fixation in ACG. As an application of the results (5)-(7), we study fixation in ACG evolving according to the fitness-dependent Moran process (fMP) [2, 11]. The fMP is often considered in EGT and defined by the transition rates $T_n^{\pm}$ with $\chi^+ = f_A[(n/N)f_A + (1-n/N)f_B]^{-1}$ and

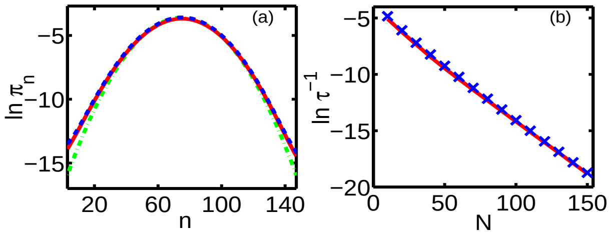

FIG. 1: *(Color online).* (a) $\ln \pi_n$ vs. n (with $N = 150$): theoretical predictions [Eqs. (5)-(8)] (solid) compared with numerical results (dashed) and with the Gaussian approximation of the QSD (dashed-dotted). (b) $\ln \tau^{-1}$ as a function of N: theoretical predictions [Eqs. (2), (6)-(8)] (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.

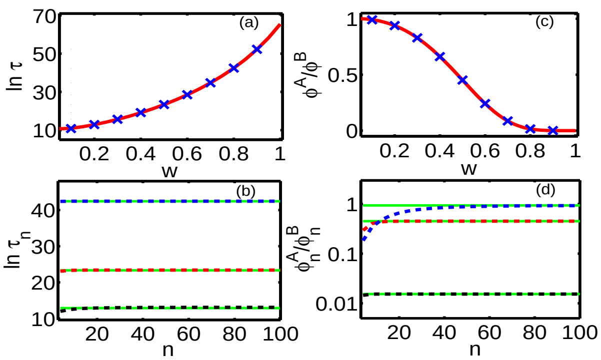

FIG. 2: *(Color online).* (a) $\ln \tau$ vs w: theoretical [Eqs. (2), (6)-(8)] (solid) and numerical results (symbols). (b) Dependence of $\ln \tau$ on the initial number n of A's, for $w = 0.2$, 0.5 and 0.8 (bottom to top): comparison between theoretical (solid) and numerical (dashed) results. (c) Theoretical [Eq. (9)] (solid) and numerical (symbols) results for the ratio ϕ^A/ϕ^B vs w. (d) Same as in panel (b) for ϕ^A/ϕ^B (w grows from top to bottom). Parameters are $a = 0.1$, $b = 0.7$, $c = 0.6$, $d = 0.2$, $N = 200$ 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).

$\chi^- = f_B[(n/N)f_A + (1-n/N)f_B]^{-1}$. Here, using Eq. (4), the action (with $A = 1 - w + wa$, $B = 1 - w + wb$, $C = 1 - w + wc$, and $D = 1 - w + wd$ [15]), reads

$$S(x) = [B/(B-A) - x]\ln[Ax + B(1-x)] + [D/(C-D) + x]\ln[Cx + D(1-x)]. \quad (8)$$

Provided that $N[S(1) - S(x^*)] \gg 1$, and $N[S(0) - S(x^*)] \gg 1$ (which imposes a lower bound on w), the MFTs and fixation probability are obtained from Eqs. (2) and (6)-(8) 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 $\Sigma \equiv \max[S(0), S(1)]$ is readily obtained from (8). 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 (1) yielding excellent agreement. It also follows from (2),(6)-(8) that for $N \gg 1$ and small (but not too small) selection intensity, $N^{-1} \ll w \ll 1$, the MFTs grow exponentially as $\tau^A \sim N^{1/2} e^{Nw(a-c)^2/[2(c-a+b-d)]}$, and $\tau^B \sim N^{1/2} e^{Nw(b-d)^2/[2(c-a+b-d)]}$. 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. This is confirmed in Fig. 2(b), showing a comparison between analytical and numerical results for $w > 0$, and $n \gg 1$.

The ratio $\phi^A/\phi^B = \phi^{-1} - 1$ allows to understand the influence of selection by comparing the fixation probability of A's and B's. Using Eqs. (2,6-8), our theory yields

$$\frac{\phi^A}{\phi^B} = \frac{\pi_{N-1}}{\pi_1} = \sqrt{\frac{BD}{AC}} \left(\frac{C-A}{B-D}\right) \frac{B^{N\left(\frac{B}{B-A}\right)} D^{N\left(\frac{D}{C-D}\right)}}{A^{N\left(\frac{A}{B-A}\right)} C^{N\left(\frac{C}{C-D}\right)}}. \quad (9)$$

In Fig. 2(c), we show the ratio ϕ^A/ϕ^B as a function of the selection strength w and find a nonlinear dependence characterized by a sigmoid shape, in excellent agreement with numerical calculations. Contrary to the neutral case ($w = 0$) [2], not covered by our theory, (9) is independent of the initial condition. In fact, the numerical results of Fig. 2(d) confirm that the ratio ϕ^A/ϕ^B becomes independent of n (with $n \gg 1$) and coincides with (9) when $w > 0$ (for $w \ll 1$ the convergence requires $n \sim Nx^*$).

WKB theory and fixation in CG. 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 unstable while $x = 0, 1$ are stable. Thus, with an initial minority of A's, $n < Nx^*$, the fixation of B's is almost certain, while there is an exponentially small probability ϕ_n^A that A's fixate. This probability satisfies $T_n^+ \phi_{n+1}^A + T_n^- \phi_{n-1}^A - [T_n^+ + T_n^-]\phi_n^A = 0$, with boundary conditions $\phi_0^A = 0, \phi_N^A = 1$ [2, 3, 6]. It is convenient to introduce $\mathcal{P}_n \equiv \phi_{n+1}^A - \phi_n^A \simeq d\phi_n^A/dn = (1/N) d\phi^A(x)/dx$, satisfying $\mathcal{P}_0 = \phi_1^A$ and $\mathcal{P}_{N-1} = 1 - \phi_{N-1}^A$. Here, we use the WKB theory to treat the equation $\mathcal{T}^+(x)\mathcal{P}(x) - \mathcal{T}^-(x)\mathcal{P}(x - 1/N) = 0$ for $\mathcal{P}(x) \equiv \mathcal{P}_n$, and recover the asymptotically exact results [6, 16]. Using the ansatz $\mathcal{P}(x) = \mathcal{A} e^{-N\mathcal{S}(x)}$, in the leading order one has $\mathcal{T}_+(x) - \mathcal{T}_-(x) e^{\mathcal{S}'(x)} = 0$, whose solution is $\mathcal{S}(x) = -S(x)$ [given by Eq. (4)]. (Here $\mathcal{S}_1(x)$, the subleading correction omitted in the ansatz for $\mathcal{P}(x)$, is found to be a constant [16]). Normalizing $\sum_{n=0}^{N-1} \mathcal{P}_n \simeq N \int_0^1 \mathcal{P}(x) dx = 1$, and assuming that the main contribution arises from the Gaussian region around x^*, one obtains the amplitude $\mathcal{A} \simeq \sqrt{|S''(x^*)|/(2\pi N)} e^{-NS(x^*)}$. The fixation probability, $\phi^A(x) \simeq N \int_0^x \mathcal{P}(x') dx'$, is therefore given by

$$\phi^A(x) = \sqrt{N|S''(x^*)|/(2\pi)} \int_0^x e^{N[S(x') - S(x^*)]} dx'. \quad (10)$$

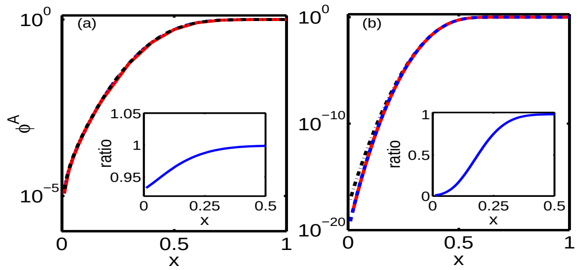

FIG. 3: *(Color online).* The fixation probability $\phi^A(x)$ for the fMP process: theoretical result (10) (solid), numerical calculations (dashed) and FPA (dash-dotted), with $a = 4, b = 0.2, c = 0.3, d = 3.8, N = 100$. Insets: ratio between theoretical results and those of the FPA, see text. (a) For $w = 0.1$, $Nw^2 = 1$ and all curves agree well, with an error of about 7% in the predictions of the FPA for $x \to 0$. (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.

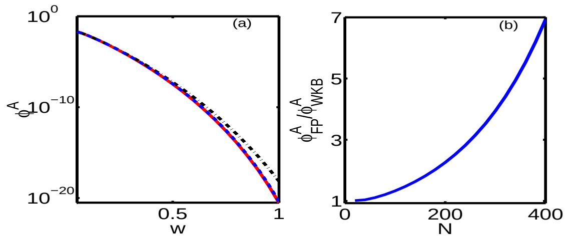

FIG. 4: *(Color online).* (a) Fixation probability $\phi^A(x)$ as function of w: theoretical result (10) (solid), numerical calculations (dashed) and FPA (dash-dotted), for $a = 1$, $b = 0.2$, $c = 0.3$, $d = 0.8$, and $N = 200$. (b) Ratio between the predictions of the FPA and those of our theory vs 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.

Eq. (10) asymptotically coincides with the exact result for $N \gg 1$ and holds for *any* $0 \le x \le 1$ [16]. For the fMP, an analytical expression of $\phi^A(x)$ is readily inferred from (8). In Figs. 3 and 4(a) we find an excellent agreement, for any value of x and w, between theory and numerics.

To compare with the FPA, we rewrite (10) as $\phi^A(x) = \Psi(x)/\Psi(1)$, with $\Psi(x) = \int_0^x dy\, e^{-\int_0^y dz\, \Theta(z)}$ and $\Theta = N \ln\left[\mathcal{T}_+(z)/\mathcal{T}_-(z)\right]$. For the FPA, $\Theta(z)$ is replaced by $\Theta_{\rm FP}(z) = 2Nz\left[\mathcal{T}_+'(x^*) - \mathcal{T}_-'(x^*)\right]/\left[\mathcal{T}_+(x^*) + \mathcal{T}_-(x^*)\right]$ (linear noise approximation) [7]. As a result, for the fMP we find $\Theta(x) - \Theta_{\rm FP}(x) \sim Nw^2(x - x^*)^2$ around x^* [16]. Thus, while it is applicable when $Nw \ll 1$ [3, 5], the FPA is unable to account for fixation, and is plagued by exponentially large errors, for finite w ($w \gtrsim N^{-1/2}$). This is shown in Figs. 3 and 4 where our predictions and those of the FPA are compared for various values of w and N.

Conclusion. We have derived a WKB-based theory that naturally accounts for non-Gaussian behavior and allows the accurate calculation of important large-fluctuation-induced phenomena. With this approach, generalized to account for multiple absorbing states, we have studied fixation in evolutionary games under non-vanishing selection. 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 $w \to 0$ limit (where the FPA holds), our theory agrees excellently with numerical simulations over a broad range of finite selection strength ($0 < w \le 1$), 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 [16]. 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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