Mixing Times in Evolutionary Game Dynamics

Andrew J. Black,[1,2,*] Arne Traulsen,[3,†] and Tobias Galla[2,‡]

[1]*School of Mathematical Sciences, The University of Adelaide, Adelaide, South Australia 5005, Australia*
[2]*Theoretical Physics, School of Physics and Astronomy, University of Manchester, Manchester M13 9PL, United Kingdom*
[3]*Max-Planck-Institute for Evolutionary Biology, August-Thienemann-Strasse 2, 24306 Plön, Germany*

Without mutation and migration, evolutionary dynamics ultimately leads to the extinction of all but one species. Such fixation processes are well understood and can be characterized analytically with methods from statistical physics. However, many biological arguments focus on stationary distributions in a mutation-selection equilibrium. Here, we address the mixing time required to reach stationarity in the presence of mutation. We show that mixing times in evolutionary games have the opposite behavior from fixation times when the intensity of selection increases: in coordination games with bistabilities, the fixation time decreases, but the mixing time increases. In coexistence games with metastable states, the fixation time increases, but the mixing time decreases. Our results are based on simulations and the Wentzel-Kramers-Brillouin approximation of the master equation.

How long does it take for a stochastic many-particle system to reach its stationary distribution? This question goes beyond traditional equilibrium statistical physics and requires a theory for nonequilibrium systems. Significant progress has been made over the last decades, but developing a more complete theory is still very much a work in progress. Many nonequilibrium systems lack an energy or Lyapunov function; any theoretical analysis has to start from the microscopic dynamics itself. Such approaches have been applied successfully to off-equilibrium phenomena in physics [1] but also to a number of applications in adjacent disciplines including epidemiology, biological transport, and pattern formation; and to agent-based models in economics and of social phenomena [2–5].

For stochastic processes with absorbing states, our opening question can be answered—at least to some extent. Absorbing states are those in which the system gets "trapped," so that a full dynamic arrest occurs. Systems with absorbing states exhibit new types of phase transitions, universality classes, and complexity, previously unknown in physics [6,7]. They are relevant in social systems, where an absorbing state may correspond to a uniform consensus, and in evolutionary biology where they describe fixation of a trait. Stochasticity can also drive individual phenotypes to extinction in evolutionary game dynamics. In the absence of mutation, a given phenotype is never reintroduced once it has become eliminated from the population. Addressing the question of equilibration times then amounts to calculating the time to fixation [8,9].

The purpose of our work is to develop a similar approach for evolutionary systems with mutation. In such systems there are no absorbing states and thus no fixation. Still, they reach a stationary distribution at asymptotic times. In order to characterize the approach to stationarity we consider what is referred to as the *mixing time* in the theory of Markov processes [10]. This is the time needed for the probability distribution over states to approach its stationary shape up to some small distance ε. The use of Markov processes is common in evolutionary game theory [11], game learning, and equilibrium selection [12,13]. We go beyond the study of equilibria, and focus on the transients of Markov chains and study mixing times in evolutionary games. Mixing times have been considered in the context of Markov-chain Monte Carlo methods [10], and recently in game dynamical learning [14], but, to our knowledge, they have not been discussed for evolutionary processes. We here introduce the basic concepts, analyze mixing times in 2×2 evolutionary games, and show how methods from quasiclassical physics can be used for analytical approximations. Our analysis is based on computer simulations and analytical approximations using the Wentzel-Kramers-Brillouin (WKB) method [15,16]. While we focus on specific instances of evolutionary dynamics, we expect that these tools can describe the nonequilibrium dynamics of a large class of individual-based models.

We consider a well-mixed population of N individuals of type A or B. The state of the system is determined by the number $n \in \{0, \dots, N\}$ of individuals of type A. The payoff matrix and the fitnesses of individuals of the two types in an evolutionary 2×2 game are given by [11]

$$
\begin{array}{cc}
 & \begin{array}{cc} A & B \end{array} \\
\begin{array}{c} A \\ B \end{array} & \begin{array}{cc} a & b \\ c & d \end{array}
\end{array}
\qquad
\begin{aligned}
\Pi_A(n) &= \tfrac{n-1}{N-1}a + \tfrac{N-n}{N-1}b, \\
\Pi_B(n) &= \tfrac{n}{N-1}c + \tfrac{N-n-1}{N-1}d,
\end{aligned}
\tag{1}
$$

if the system is in state n. The parameters a, b, c, and d specify the underlying game. We study the evolutionary dynamics defined by the birth-death process with rates [17]

$$T_n^+ = \frac{1-\mu}{2}[1 + \beta\Delta\Pi(n)]\frac{n(N-n)}{N^2} + \frac{(N-n)^2}{N^2}\frac{\mu}{2},$$

$$T_n^- = \frac{1-\mu}{2}[1 - \beta\Delta\Pi(n)]\frac{n(N-n)}{N^2} + \frac{n^2}{N^2}\frac{\mu}{2}, \quad (2)$$

where $\Delta\Pi(n) = \Pi_A(n) - \Pi_B(n)$, and where T_n^+ is the rate at which an individual of type B is replaced by an individual of type A in state n, and T_n^- is the rate of the opposite event. The parameter $\mu \in [0, 1]$ represents the mutation rate, and $\beta \geq 0$ is the intensity of selection. The probability $P_t(n)$ of finding the system in state n at time t then obeys the master equation

$$\dot{P}_t(n) = T_{n-1}^+ P_t(n-1) + T_{n+1}^- P_t(n+1)$$
$$- (T_n^+ + T_n^-)P_t(n). \quad (3)$$

We denote the asymptotic stationary distribution by $\psi^*(n) = \lim_{t\to\infty} P_t(n)$. Following Ref. [10], the mixing time $t_{\text{mix}}(\varepsilon)$ is defined as $t_{\text{mix}}(\varepsilon) = \min\{t : d(t) \leq \varepsilon\}$ where the variational distance $d(t) = \frac{1}{2}\sum_n |P_t(n) - \psi^*(n)|$ measures the distance of the probability distribution $P_t(\cdot)$ from the stationary distribution $\psi^*(\cdot)$ [10]. The standard choice of the parameter ε is $\varepsilon = \frac{1}{4}$ [10].

In order to characterize the behavior of mixing times in different scenarios, it is useful to first consider the limit of $N \to \infty$. In this case, the fraction of individuals of type A, $x = n/N$, fulfills the deterministic replicator-mutator equation

$$\dot{x} = \beta x(1-x)[(a-c)x - (d-b)(1-x)](1-\mu)$$
$$+ \frac{1-2x}{2}\mu. \quad (4)$$

The number, position, and stability of the fixed points of Eq. (4) generally depend on the parameters β and μ, as well as on the underlying game [11,18].

We first study a symmetric coexistence game, defined by $a = 1, b = 2, c = 2, d = 1$. In this scenario, Eq. (4) has one stable fixed point at $x^* = 1/2$, and no other fixed points. The left panel of Fig. 1 shows the stationary distributions of the resulting Markov chain for different intensities of selection β. With increasing β, the distribution concentrates on the area around the deterministic fixed point. The corresponding mixing times are shown in the right-hand panel, starting the dynamics in a single state, $P_0(n) = \delta_{n,n_0}$, for varying n_0. Increasing the intensity of selection β reduces the mixing time, because mixing is governed by the deterministic flux, which increases with β. For $n_0 \neq \frac{N}{2}$, the mixing time is limited by this term. Note that the fixation time in this game increases exponentially with N, as motion against the deterministic flux is required [9].

Next, we address a symmetric coordination game with parameters $a = 2$, $b = 1$, $c = 1$, $d = 2$. In this case, Eq. (4) has an unstable fixed point at $x_1 = \frac{1}{2}$ and two stable
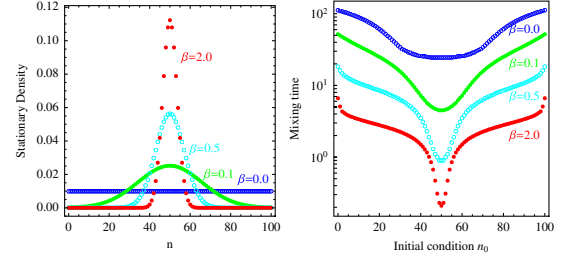

FIG. 1 (color online). Symmetric coexistence game in a population of $N = 100$ individuals. Left: Stationary distributions of the stochastic dynamics [Eq. (3)]. Right: Mixing time ($\varepsilon = 1/4$) when the stochastic process is started from a Dirac distribution at $P_0(n) = \delta(n - n_0)$. The mutation rate is $\mu = 1/101$, leading to a uniform stationary distribution at $\beta = 0$.

fixed points x_2 and x_3 near $x = 0$ and $x = 1$, respectively. Figure 2 shows the bimodal stationary distributions and mixing times for this game. With increasing β, the distribution becomes sharply peaked around the stable fixed points. For a localized initial condition the mixing process requires motion against the deterministic flow. Hence, mixing is governed by stochastic effects, and the analytical computation of mixing times is far from straightforward. When the system is started near a stable fixed point, it will quickly tend to a quasistationary distribution (QSD) around that fixed point. The probability will then slowly leak over to the other side on a time scale exponentially slow in N. Thus, the mixing times increase with increasing intensity of selection, whereas fixation times decrease with β [9]. We can exploit this separation of time scales to calculate the mixing time analytically, similar to the problem of calculating the mean switching time between quasistationary states.

Let us assume that we start to the left of the unstable fixed point, $x_1 = n_1/N$. The time-dependent ansatz we use for the probability distribution is

$$\psi^{\text{leak}}(n) = \begin{cases} \psi^*(n)(1 + e^{-Et}) & n < n_1 \\ \psi^*(n)(1 - e^{-Et}) & n > n_1, \end{cases} \quad (5)$$
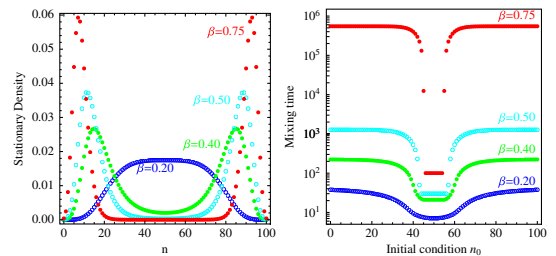

FIG. 2 (color online). Symmetric coordination game in a population of $N = 100$ individuals. Left: Stationary distribution of the master equation, Eq. (3). Right: Mixing time ($\varepsilon = 1/4$) as a function the position of the Dirac distribution from which the dynamics is started. The mutation rate is $\mu = 1/101$, leading to a flat stationary distribution for $\beta = 0$.

where $-E < 0$ is the eigenvalue of the slowest decaying mode of the problem. The validity of this ansatz can be verified numerically, it holds on an exponentially long time scale in N. Calculating the variational distance between the ansatz of Eq. (5) and the stationary distribution, we find $t_{mix}(\varepsilon) = -E^{-1}\ln[2\varepsilon]$ such that the problem reduces to finding the eigenvalue $-E$. Based on Eq. (5), the current through the central fixed point is given by $J(t) = \frac{d}{dt}\sum_{n<n_1}\psi^{leak}(n) = -(E/2)e^{-Et}$. Thus we can find E from the initial current, $J(0) = -E/2$. Calculating the mixing time then reduces to determining the escape current in a bistable potential [19].

As this is a one-step process, exact expressions exist for the mean first passage times [20]. One avenue would be to derive the large N asymptotics for these [9,21,22]. We do not follow this approach, instead we calculate the initial current through the unstable fixed point based on the celebrated WKB approximation. This has two advantages: first, this method is valid for a much wider range of problems, such as those with multiple jumps [23,24], or of higher dimensions [25]; second, the stationary distribution $\psi^*(n)$ is calculated as a by-product. Our approach also complements recent studies which have successfully introduced these methods to evolutionary game theory by calculating fixation times in evolutionary games without mutation [26]. Before we describe the main steps of the calculation, it is useful to expand the transition rates, Eq. (2), into powers of $1/N$ in leading and subleading order. Specifically, we write $T^{\pm}(Nx) = w_{\pm}(x) + u_{\pm}(x)/N$ [24]. We use the WKB ansatz

$$\psi^{WKB}(x) = \exp[-NS(x) - S_1(x)], \qquad (6)$$

where both $S(x)$ and $S_1(x)$ are assumed to be of order N^0. It is important to note the difference between the ansatz of Eq. (5) and the ansatz of Eq. (6). The ansatz of Eq. (5) is valid on exponentially long time scales and about the asymptotes of the distribution and it takes account of the back current through the central fixed point. The ansatz of Eq. (6) is valid everywhere, but only on short time scales. It can therefore be used to calculate the initial current. We proceed by inserting Eq. (6) into Eq. (3), assuming (quasi) stationarity $(\partial_t\psi^{WKB} = 0)$ and expanding the resulting equation into powers of N^{-1} [16,23,24,26]. In lowest order, we find a Hamilton-Jacobi equation,

$$H(x, p) \equiv w_+(x)(e^p - 1) + w_-(x)(e^{-p} - 1) = 0, \quad (7)$$

where $p = \partial_x S$. This constitutes an equation for $S(x)$ and it has two solutions: (i) the activation solution

$$S(x) = \int^x d\xi \ln\left[\frac{w_+(\xi)}{w_-(\xi)}\right] \qquad (8)$$

and (ii) the so-called relaxation solution $S(x) = 0$. In next order, we find the activation solution

$$S_1(x) = \int^x d\xi\left(\frac{u_-(\xi)}{w_-(\xi)} - \frac{u_+(\xi)}{w_+(\xi)}\right) + \frac{1}{2}\ln[w_+(x)w_-(x)], \qquad (9)$$

and the relaxation solution $S_1(x) = \ln[H_p(x, 0)]$, where $H_p = \partial H/\partial p$. In our setup the activation solution describes the behavior of the QSD to the left of $x_1 = 1/2$. The relaxation mode, describing deterministic motion to the right of x_1, will play no significant role in our further analysis.

To complete the calculation two main tasks remain: (i) the activation solution ψ^{WKB} defined by Eqs. (6), (8), and (9) needs to be normalized, and (ii) the QSD needs to be connected to the initial current $J(0)$ through x_1. These tasks can be addressed by performing a Kramers-Moyal expansion of the master equation, Eq. (3), around the unstable fixed point x_1. Writing $f_{\pm}(x) = Nw_{\pm}(x)\psi(x)$ we find

$$\partial_x\left[\sum_{r=\pm 1}\frac{r}{N}f_r(x) - \frac{r^2}{2N^2}f_r'(x)\right] = 0, \qquad (10)$$

where the term in the square bracket is identified as the divergence-free probability current $J(0)$. Further algebraic manipulations then lead to [23]

$$J = \psi^{WKB}(x)H_{px}(x, 0)(x - x_1) - \frac{H_{pp}(x, 0)\partial_x\psi^{WKB}(x)}{2N}, \qquad (11)$$

where $H_{pp} = \partial^2 H/\partial p^2 = w_+ + w_-$ and $H_{px} = \partial^2 H/\partial x\partial p = w_- w_+'/w_+ - w_+ w_-'/w_-$. Rearranging Eq. (11) one has

$$\psi^{WKB}(y) = \frac{J\sqrt{\pi}}{H_{px}\ell}e^{y^2}\mathrm{erfc}(y),$$

$$\text{where } y = \frac{x - x_1}{\sqrt{H_{pp}/(NH_{px})}}. \qquad (12)$$

The final step then consists in matching the asymptote, $\psi^{WKB}(y) = J\sqrt{\pi}e^{y^2}$, valid for $y \ll -1$, with the relaxation-mode solution $\psi^{WKB}(x) = Ae^{-NS(x)-S_1(x)}$. The normalization constant A is obtained from a Gaussian approximation of the relaxation solution about the fixed point x_2 [25].

Carrying out this procedure the initial current is found to be exponential in N:

$$J(0) = \frac{H_{pp}(x_1)}{4\pi N}\sqrt{S''(x_2)|S''(x_1)|}e^{N[S(x_2)-S(x_1)]+S_1(x_2)-S_1(x_1)}. \qquad (13)$$

Finally the mixing time is

$$t_{mix}(\varepsilon) = \ln(2\varepsilon)/[2J(0)]. \qquad (14)$$

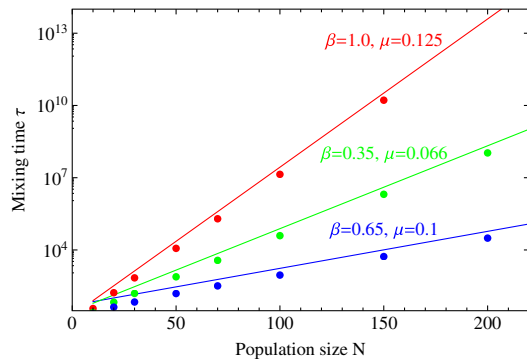Figure 3 shows the mixing times calculated via the WKB method along with direct computation from a

FIG. 3 (color online).   Mixing time ($\varepsilon = 1/4$) for the symmetric coordination game as a function of the population size N. Lines are calculated from Eq. (14); dots are from integration of the master equation.

numerical integration of the master equation. Agreement is generally very good, except for small values of N when the introduction of the continuous variable x as well as the expansion in powers of N^{-1} become inaccurate. The slight offset between the two sets of results is due to the Gaussian approximation made when normalizing the QSD $\psi^{\mathrm{WKB}}(\cdot)$. Better agreement could be obtained by normalizing the distribution numerically. We note that the dependence of $t_{\mathrm{mix}}(\varepsilon)$ on ε is logarithmic, so the impact of a choice different from $\varepsilon = \frac{1}{4}$ is minor.

While the WKB approach can successfully be employed to obtain mixing times, there are limitations to this method. One potential problem is the divergence of the WKB solution $\psi^{\mathrm{WKB}}(x)$ at the boundaries of the system. This does not affect the outcome of our calculation as long as the stable fixed points of the replicator-mutator equation are not too close to the boundaries of phase space, but it does limit the range of β and u for which it is valid. We stress that the ansatz of Eq. (5) still applies, but the eigenvalue E needs to be calculated via a different approach. The methods we have presented lend themselves to generalisation. For example, the assumption of symmetry of the problem can be relaxed, and cases in which the stationary distribution is not symmetric and/or the unstable fixed point is not at $x = 1/2$ can be addressed with relatively minor modifications of the ansatz of Eq. (5) [27].

In summary, we have introduced the concept of mixing times for evolutionary dynamics with mutation. As intensity of selection is increased, the mixing times in coexistence games decrease. In coordination games, one observes the opposite trend. In both cases the behavior of mixing times is opposite to that of fixation times in the corresponding systems without mutation. The concept of mixing times may often be more appropriate for many biological systems than the computation of fixation times, in particular when effects of mutation or immigration cannot be ignored [28]. As shown in our work, tools from theoretical physics can be used to successfully estimate mixing times based on semianalytical considerations.

We expect this to be useful not only for biological systems, but also for models of social dynamics and other interacting many-particle processes.

*andrew.black@adelaide.edu.au
†traulsen@evolbio.mpg.de
‡tobias.galla@manchester.ac.uk

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[27] This is achieved by replacing $1 + e^{-Et}$ in Eq. (5) by $1 + (y^{-1} - 1)e^{-Et}$, where $y = \sum_{n=0}^{n_1} \psi^*(n)$, assuming the dynamics is started to the left of the central fixed point.

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