The path integral formula for the stochastic evolutionary game dynamics

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Abstract – Although the long-term behavior of stochastic evolutionary game dynamics in finite populations has been fully investigated, its evolutionary characteristics in a limited period of time is still unclear. In order to answer this question, we introduce the formulation of the path integral approach for evolutionary game theory. In this framework, the transition probability is the sum of all the evolutionary paths. The path integral formula of the transition probability is expected to be a new mathematical tool to explore the stochastic game evolutionary dynamics. As an example, we derive the transition probability for stochastic evolutionary game dynamics by the path integral in a limited period of time with the updating rule of the Wright-Fisher process.

Introduction. – Undoubtedly, Darwin’s natural selection theory, including Kimura’s neutral selection theory, is the most basic theoretical foundation for understanding the evolution. In the 1970s, in order to reveal the evolutionary mechanism of animal behavior, including human behavior, Maynard Smith and Price developed the evolutionary game theory with evolutionarily stable strategy (ESS) as the core concept [1–3]. According to the definition of ESS (or evolutionary stability), an ESS is a strategy such that, when all members of the population adopt it, then any mutant strategy cannot invade successfully the population under the influence of natural selection [3]. In evolutionary game theory, the evolutionary game dynamics (e.g., replicator equation based on matrix games, called also replicator dynamics) mainly focus on the time evolution of the frequencies of different strategies in the population [4,5]. The stability of replicator equation and its relationship with evolutionary stability have been fully studied and, for example, an asymptotically stable state of replicator equation must correspond to an ESS [4]. Furthermore, the demographic stochasticity of evolutionary game dynamics in finite populations, also called the stochastic evolutionary game dynamics, has also been analyzed by many scholars using the Moran process or Wright-Fisher process [6,7]. Specifically, the stochastic evolutionary game dynamics based on the Prisoner’s Dilemma game in a finite population and the impact of weak selection on this process have also been used to explain the evolutionary emergence of cooperation, called the one-third law [7,8].

However, we can see that so far, all the studies on stochastic evolutionary game dynamics have only involved the long-term behavior of the system. So, a more challenging question is how we should characterize the evolution of the system in a limited period of time, which involves the possible evolutionary path of the system. In fact, for understanding the more real stochastic evolutionary game dynamics in finite populations, the evolutionary characteristics of the system in a limited period of time may be more important than its long-term behavior, especially, whether the evolutionary path of system will be affected by the selection intensity. This also implies that the effect of different selection intensities on the evolutionary path of system may provide a way to establish a theoretical bridge between Darwin’s natural selection and Kimura’s neutral selection [9].
Path-integral technique was introduced by Feynman for quantum physics and has been proved to be a very powerful tool in various areas of physics, both computationally and conceptually [10–12]. Recent years have witnessed a lot of efforts to develop a similar path integral formulation for the theory of the diffusion process. And such a formulation can supply a calculational technique that may be fruitful in dealing with nonlinear systems [10,12]. The path integral formulations have been applied to population genetics. For example, Rouhani and Barton [13] used path integral to approximate the probability of shifting between selective optima in the context of quantitative trait evolution. The path integrals have also been used to examine fitness flux [14] and Muller’s ratchet [15]. Schraiber [16] introduced the path integral formalism to study the Wright–Fisher process with selection in population genetics. All these studies imply that the path integral may provide a more effective method for a deeper understanding of the mechanism of evolutionary dynamics. In this paper, we introduce the evolutionary path of a two-strategy game dynamics in a finite population, which can be portrayed by calculating transition probability taking advantage of the path integral. It is necessary to point out that we here present a possible theoretical way to show why the evolutionary characteristics of the system in a limited period of time (i.e., evolutionary path) can be described by the path integral. This theoretical framework may provide a new perspective for revealing the mechanisms determining the evolutionary path in the stochastic evolutionary game dynamics.

The transition probability for evolutionary game dynamics in the path integral. –

The framework of the path integral for evolutionary game dynamics. We start by considering a two-strategy stochastic evolutionary game. The fitness (or payoff) of two strategies A and B depends on the composition of the population and is given by the payoff matrix

\[
\begin{pmatrix}
A & B \\
A & (a & b) \\
B & (c & d)
\end{pmatrix}
\]

In a finite size (N) and well-mixed population, the expected payoffs are \(\frac{a(j-1)+b(N-j)}{N-1}\) for A-type and \(\frac{c(j)+d(N-j-1)}{N-1}\) for B-type with \(x = j/N\) being the frequency of the strategy A. As Nowak et al. [17], we take a selection intensity parameter \(\omega (0 \leq \omega \leq 1)\) and the expected payoffs are therefore given by

\[
\begin{align*}
  f_j &= (1 - \omega) + \omega \frac{a(j-1)+b(N-j)}{N-1}, \\
  g_j &= (1 - \omega) + \omega \frac{c(j)+d(N-j-1)}{N-1}.
\end{align*}
\]

For large N, the fitness can be approximatively denoted by

\[
\begin{align*}
  f(x) &= (1 - \omega) + \omega[ax + b(1 - x)], \\
  g(x) &= (1 - \omega) + \omega[cx + d(1 - x)].
\end{align*}
\]

We then shall derive the calculation method for the transition probability for events which occur successively in time. Given an initial probability distribution, the statistics of the evolutionary process can be completely calculated in terms of its transition probability. The transition probability, denoted as \(p(z,t|z_0,t_0)\), is defined as the probability of a transition from one point in the system state space, \(z_0\), at the initial time \(t_0\) to another point in the state space, \(z\), after a limited period of time \(t - t_0\), where \(t > t_0\). Here, “state” can be a measurement of any property of an entity, such as the frequency of a gene, allelle, genotype, phenotype, group of individuals and so on [18]. In such a transition, all the possible paths connecting these two points play roles, each of them realizing a sample function and therefore having a definite possibility. It is natural to postulate that the probability of the overall transition is a sum of all intermediate possibilities from \((z_0,t_0)\) to \((z,t)\) [11],

\[
p(z,t|z_0,t_0) = \sum_{all \ paths} \phi[Z(t)],
\]

where \(\phi[Z(t)]\) is the contribution from a state trajectory \(Z(t)\) (as shown in fig. 1), and “all paths” means of course all possible paths satisfying \(z(t_0) = z_0\) and \(z(t) = z\). The “sum” in eq. (4) can be realized as a functional integral over the space of all possible paths (hence the name “path integral”) with a probability distribution on the path space as its integrand.
The path integral formula for the stochastic evolutionary game dynamics

The transition probability of an evolutionary path. As shown in fig. 2, the initial point is \((z_0, t_0)\), and the final point is \((z, t)\). It is possible to find the system state, \(z_1\), at some time between the time \(t_0\) and \(t\). Then the transition probability along any path between \((z_0, t_0)\) and \((z, t)\) can be written. All alternative paths for the allele frequency from \(z_0\) to \(z\) can be labeled by specifying the position \(z_1\) through which the allele frequency passes at time \(t_1\). Then the transition probability for the system state going from \(z_0\) to \(z\) can be computed. The transition probability to go from \(z_0\) to \(z\) is the sum, over all possible values of \(z_1\), of the transition probability to go from \(z_0\) to \(z_1\) and then from \(z_1\) to \(z\). Thus, the transition probability from \(z_0\) to \(z\) through \(z_1\) can be written as [11,12]

\[
P(\{z, z_1, z_0\}) = p(z, t|z_1, t_1)p(z_1, t_1|z_0, t_0),
\]

where the symbol \(\{\cdots\}\) represents a evolutionary path \(z_0, z_1, \ldots, z\). Similarly, it is possible to make two divisions in all the paths: one at \(t_1\), and the other at \(t_2\). That is because it is easy for biologists to obtain the timely state \(z_2\) at the time \(t_2\) between the time \(t_1\) and \(t\). Then the transition probability going from \(z_0\) to \(z\) can be written as

\[
P(\{z, z_2, z_1, z_0\}) = p(z, t|z_2, t_2)p(z_2, t_2|z_1, t_1)p(z_1, t_1|z_0, t_0).
\]

This means that we look at the frequency which goes from \(z_0\) to \(z\) as if it went first from \(z_0\) to \(z_1\), then from \(z_1\) to \(z_2\), and finally from \(z_2\) to \(z\). The transition probability taken over all such paths that go from \(z_0\) to \(z\) is obtained by integrating this product over all possible values of \(z_1\) and \(z_2\).

We can continue this process until the time interval is divided into \(L\) intervals (as shown in fig. 1), i.e., \(\Delta t = (t - t_0)/L\). Let the state, which might result from measurement of the coordinate at time \(t_k\), be \(z_k\) (specifically, \(z_n = z, t_n = t\)),

\[
P(\{z\}) = p(z, t|z_{n-1}, t_{n-1})p(z_{n-1}, t_{n-1}|z_{n-2}, t_{n-2})
× \cdots \times p(z_2, t_2|z_1, t_1)p(z_1, t_1|z_0, t_0).
\]

According to the conditional probability of stochastic process, the contribution from a particular path \(\{z\}\) has the measure

\[
\phi[z] = P(\{z\})\Delta\{z\}.
\]

The probability of the overall transition is therefore

\[
p(z, t | z_0, t_0) = \sum_{\{z\}} P(\{z\})\Delta\{z\}.
\]

Eventually, we expect to go the limit \(L \to \infty\), where the nodes of the paths are continuously infinite, and the limit \(\Delta z \to dz\), the transition probability is

\[
p(z, t | z_0, t_0) = \int_R p(z, t|z_{n-1}, t_{n-1})p(z_{n-1}, t_{n-1}|z_{n-2}, t_{n-2})
× \cdots \times p(z_2, t_2|z_1, t_1)p(z_1, t_1|z_0, t_0)Dz = \int_R \prod_{k=1}^n p(z_k, t_k|z_{k-1}, t_{k-1})Dz,
\]

where the integration is to be taken over those ranges of the variables which lie within the region \(R\), i.e., all continuous paths with constraints of \(z_0\) at \(t_0\) and \(z\) at \(t\). As is graphically depicted in fig. 2, division is done once, twice, ..., until \(L\) times between the initial state and the final state. For simplicity, we denote \(Dz = dz_1dz_2 \ldots dz_{n-1}. \quad p(z_k, t_k|z_{k-1}, t_{k-1})\) becomes the transition probability during a very short time, which is the so-called short-time propagator. Since the infinitesimal step could be approximated to one update, this propagator is calculated by recurring one-step update process in the evolutionary game.

The formulation of path integral for the Wright-Fisher process. — Based on the concept of path integral mentioned above, we will explore the integrand in the evolutionary system whose evolutionary way is described by recurring to the Wright-Fisher process to give a typical example. We take the frequency of the strategy \(A, x\), at the time \(t\) as the system states. The probability of a path is a function of a series of the state values \(x_0, x_1, \ldots, x_{n-1}, x_f\). The probability of that path lying in a particular region \(R\) of space-time thus is obtained by integrating the integrand over the region, in which \(x_0, \ldots, x_f \in (0, 1)\). For each update step though the Wright-Fisher process, the new generation is sampled at random from a large population constituted by the offspring of all individuals. The dynamics of this process is given by the corresponding transition probabilities from
Then, according to [24], the short-time propagator would be

\[
T_{x \rightarrow x'} = \left( \frac{N}{j_{x'}} \right) \left( \frac{j_{x'} f(x) - j_{x} f(x)}{j_{x'} f(x) + (N - j_{x}) g(x)} \right)^{j_{x'} x} \pi \tau \sigma^2 \quad \text{for} \quad \| x \| = \| x' \|.
\]

where \( \pi \tau \sigma^2 \) is the transition probability from one state to another state considering all the intermediate states it passed in a limited period — in terms of path integral of such processes which is derived in the following section. In that description, the dynamics then can be formulated by writing down a probability density for observing a complete path of the system step by step [11]. Specifically, the transition probability can be seen as the convolution of an infinite sequence of infinitesimal short time steps. We here will give the evolutionary dynamics in the formula of path integral.

As mentioned above, the transition probability in a short time could be derived from eq. (11), which is the short-time propagator thought as the critical quantity in path integral approach. In the evolutionary process, there are two parts in the transition probability when we consider the effect of selection intensity on the evolutionary dynamics. The former refers to the transition probability including natural selection and the latter refers to the situation which is completely neutral. We take Ito’s formula [12,22,23],

\[
\Delta x_k = x_k - x_{k-1} = \mu(x_{k-1}) \tau + \sqrt{\sigma^2(x_{k-1})}(W_k - W_{t_{k-1}}),
\]

where \( W_k \) is the Wiener process (or Brownian motion). Then, according to [24], the short-time propagator would be

\[
P(x_k, t_k | x_{k-1}, t_{k-1}) = \frac{1}{\sqrt{2\pi(t_k - t_{k-1})\sigma^2(x_{k-1})}} \exp\left[ -\frac{[x_k - x_{k-1} - \mu(x_{k-1})\tau]^2}{2(t_k - t_{k-1})\sigma^2(x_{k-1})} \right].
\]

with \( \tau = t_k - t_{k-1} \).

For one-step update through the Wright-Fisher process, we have

\[
\mu(x) = N(x(1-x) f(x) - g(x))
\]

and

\[
\sigma^2(x) = x(1-x) (f(x) - g(x))^2.
\]

Considering the weak selection and expanding by \( \omega \), we have

\[
\mu(x) = N(x(1-x) f(x) - g(x)) = N\omega \alpha x(1-x)(x - x^*),
\]

where \( \alpha = a - b - c + d, x^* = \frac{d - \nu}{a - b - c + d} \).

Then, the transition probability in a short time has been given in eq. (13), which is the short-time propagator thought as the critical quantity in path integral approach. We define two types of transition probability when we consider the effect of selection intensity on the evolutionary dynamics. They are \( p_w(x', t|x_0, t_0) \) and \( p_0(x', t|x_0, t_0) \), respectively [16]. The former refers to the transition probability including natural selection and the latter refers to the situation which is completely neutral. According to eq. (7), they can be written as

\[
p_w(0)(x_f, t_f|x_0, t_0) = \int_0^1 \int_0^1 \cdots \int_0^1 p_w(0)(x_f, t_f|x_{n-1}, t_{n-1}) \times \cdots \times p_w(0)(x_2, t_2|x_1, t_1) p_w(0)(x_1, t_1|x_0, t_0) dx_1 dx_2 \cdots dx_{n-1},
\]

where \( p_w(0)(x_1, t_1|x_0, t_0) \) is the propagator from \( x_0 \) to \( x_1 \) when there is natural selection (and neutral selection), \( p_0(0)(x_2, t_2|x_1, t_1) \) is that from \( x_1 \) to \( x_2 \), and so on.

Thus, the transition probability of a given path, along which the frequency evolves from \( (x_0, t_0) \) to \( (x_f, t_f) \) passing \( x_1, x_2, \ldots, x_n \) is shown as

\[
P_w[\{x\}] = p_w(x_f, t_f|x_{n-1}, t_{n-1}) \times p_w(x_{n-1}, t_{n-1}|x_{n-2}, t_{n-2}) \times \cdots \times p_w(x_2, t_2|x_1, t_1) p_w(x_1, t_1|x_0, t_0)
\]

Similarly, the corresponding formula for the situation not containing the selection intensity (\( \omega = 0 \)) is

\[
P_0[\{x\}] = p_0(x_f, t_f|x_{n-1}, t_{n-1}) \times p_0(x_{n-1}, t_{n-1}|x_{n-2}, t_{n-2}) \times \cdots \times p_0(x_2, t_2|x_1, t_1) p_0(x_1, t_1|x_0, t_0)
\]

with

\[
\begin{align*}
p_0[\{x\}] &= p_0(x_f, t_f|x_{n-1}, t_{n-1}) \times p_0(x_{n-1}, t_{n-1}|x_{n-2}, t_{n-2}) \times \cdots \times p_0(x_2, t_2|x_1, t_1) p_0(x_1, t_1|x_0, t_0) \\
&= \prod_{k=1}^n p_0(x_k, t_k|x_{k-1}, t_{k-1}).
\end{align*}
\]
For these two different types of evolutionary path, we can obtain the probability of a relative selective path which is a selection-driven path conditioned on a totally neutral path (when $\omega = 0$) by normalized processing, that is [16]

$$P^\omega[[x]] \approx \frac{P^\omega[[x]]}{P^0[[x]]},$$  \hspace{1cm} (19)

where $p_w(x_k,t_k| x_{k-1},t_{k-1})$ is the transition probability from $x_{k-1}$ to $x_k$ containing the selection intensity, and $p_0(x_k,t_k| x_{k-1},t_{k-1})$ is the transition probability from $x_{k-1}$ to $x_k$ not including the selection intensity.

Substituting eqs. (17) and (18), eq. (19) can be written as

$$P[[x]] = \prod_{i=1}^{n} \exp \left[ \frac{(x_i - x_{i-1}) \mu(x_{i-1})}{2\sigma^2(x_{i-1})} - \frac{\mu(x_{i-1})^2}{4\sigma^2(x_{i-1})} \right].$$  \hspace{1cm} (20)

For $\tau \to 0$, the summation would be an integral, and $x_1 - x_0$ and $\tau$ become $dx$ and $ds$, respectively. Then, we have

$$\frac{p_w(x_f,t_f|x_0,t_0)}{p_0(x_f,t_f|x_0,t_0)} = \int_{(x_0,t_0)}^{(x_f,t_f)} \frac{\mu(s)}{2\sigma^2(s)} dx \int_{t_0}^{t_f} dt \frac{\mu^2(x)}{2\sigma^2(x)} dx$$

$$= \exp \left[ - \frac{1}{4} \int_{t_0}^{t_f} dt N^2 \omega^2 \alpha^2 x(1-x)(x-x^*)^2 \right] dx$$

$$= \exp \left[ - \frac{1}{4} \int_{t_0}^{t_f} dt N^2 \omega^2 \alpha^2 x(1-x)(x-x^*)^2 \right] dx.$$

This is the desired path integral formula for the Wright-Fisher model. The first term of the integrand is constant independent of the intermediate states which the gene frequency passed. Once there is a certain selection intensity, it is a fixed value. The interaction of the selection therefore affects the transition probability by the second term of the integrand, which depends on the order, state and time of the interaction. We can also identify the stochastic action of this process through

$$S[x(t)] = -\frac{1}{4} \int_{t_0}^{t_f} dt N^2 \omega^2 \alpha^2 x(1-x)(x-x^*)^2.$$  \hspace{1cm} (22)

**Discussion and conclusion.** In this work, we introduced the path integral formula for the stochastic evolutionary game dynamics and characterized the evolutionary dynamic in a limited period of time. For the stochastic process, we did not take the corresponding Fokker-Planck equation or Langevin equation which mainly describe the stationary dynamics. We instead derived the short-time transition probability (the Feynman propagator), substituted it repeatedly to derive the path integral formula of the transition probability finally. The short-time transition probability is the probability that the strategy frequency changes from one generation to the next generation. As an example, we derive the transition probability for stochastic evolutionary game dynamics by the path integral in a limited period of time with the updating rule of the Wright-Fisher process.

Introducing the path integral approach, we here concentrate our attention on the transition probability in the finite population, which is the probability of the transition from the initial state to the final state in a limited period of time. There is no doubt that the fixation probabilities, the fixation time, and the stationary distribution can be explored to portray the evolutionary dynamics [5,19]. However, the transition probability actually has some special applications for the mediate behaviors. For example, there recently has been growing interest in analyzing samples taken from the same or related populations at different time points by the transition probability [25].

Making use of the transition probability in a limited period of time, the distribution of probability density at a certain time can also be obtained. It has been calculated by some other methods in previous works [21,26,27]. For the Wright-Fisher process without including the selection intensity, the probability density has been calculated by the solution which is obtained based on the Fokker-Planck equation. However, for the situation where the selection intensity as is considered, it is invalid for Fokker-Planck equations to get an analytical approximate solution. Based on the formulation of the transition probability, it is possible to obtain the probability density at a certain time given the probability density at the initial time, whether the selection intensity is included or not. Specifically, the probability density $p(x_f,t_f)$ of the evolution $X(t)$ is then obtained from

$$p(x_f,t_f) = \int_{0}^{t_f} p(x_f,t_f|x_0,t_0)p(x_0,t_0)dx_0,$$  \hspace{1cm} (23)

where $p(x_0,t_0)$ is the initial probability density of $X(t)$ at $t = t_0$. According to the path integral formula we
mentioned, we obtain

\[
p(x_f, t_f) = p(x_0, t_0) \int_R p(x_f, t_f | x_{n-1}, t_{n-1}) p(x_{n-1}, t_{n-1} | x_{n-2}, t_{n-2}) \times \cdots \times p(x_2, t_2 | x_1, t_1) p(x_1, t_1 | x_0, t_0) d\mathbf{x},
\]

where \( R \) is the range of the \( n \)-dimensional state for \( x \) and \( d\mathbf{x} = dx_0 dx_1 dx_2 \cdots dx_{n-1}. \) With the help of the transition probability, on the one hand, the probability density at any time during the evolutionary process, not just the stationary distribution, can be calculated.

As a new method for calculating the transition probability, the path integral can be applied not only when the selection intensity is constant, but also when it is frequency-dependent. We explored the case where the selection intensity is constant and derived the path integral formula as eq. (21), in which the integral with respect to the first term of the integrand can be calculated directly. This integral is independent of the intermediate evolutionary process and it can be regarded as the normalized coefficient. Since eq. (21) is not easily calculated, one could take some approximate approaches in eq. (15). Besides, the more reasonable model to reflect a realistic scenario of natural evolution is that the selection intensity is not constant. For example, it may be a frequency-dependent selection, which has been widely studied in the framework of evolutionary game [28] and eco-evolutionary game [29–31]. It is reasonable to change the constant selection intensity as a function of the state, i.e., \( \omega(x) \) and the path integral in this case will be more complex, the normalized coefficient will be difficult to determine.

In a word, the path integral approach provides a novel insight to study the evolutionary game. One could consider the evolutionary process with eco-evolutionary feedback [29–31], environment fluctuation [32–34], the varying selection intensity [35–37], mutation [38–40] and so on in this framework. And how these factors affect the evolutionary game could be explored in this formula in the future.

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