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Evolutionary game dynamics of combining the Moran and imitation processes*

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One of the assumptions of previous research in evolutionary game dynamics is that individuals use only one rule to update their strategy. In reality, an individual's strategy update rules may change with the environment, and it is possible for an individual to use two or more rules to update their strategy. We consider the case where an individual updates strategies based on the Moran and imitation processes, and establish mixed stochastic evolutionary game dynamics by combining both processes. Our aim is to study how individuals change strategies based on two update rules and how this affects evolutionary game dynamics. We obtain an analytic expression and properties of the fixation probability and fixation times (the unconditional fixation time or conditional average fixation time) associated with our proposed process. We find unexpected results. The fixation probability within the proposed model is independent of the probabilities that the individual adopts the imitation rule update strategy. This implies that the fixation probability within the proposed model is equal to that from the Moran and imitation processes. The one-third rule holds in the proposed mixed model. However, under weak selection, the fixation times are different from those of the Moran and imitation processes because it is connected with the probability that individuals adopt an imitation update rule. Numerical examples are presented to illustrate the relationships between fixation times and the probability that an individual adopts the imitation update rule, as well as between fixation times and selection intensity. From the simulated analysis, we find that the fixation time for a mixed process is greater than that of the Moran process, but is less than that of the imitation process. Moreover, the fixation times for a cooperator in the proposed process increase as the probability of adopting an imitation update increases; however, the relationship becomes more complex than a linear relationship.

Keywords: evolutionary game dynamics, Moran process, imitation process, fixation probability, fixation time

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1. Introduction

Cooperation is a widespread phenomenon that was studied extensively in social,[1] economic,[2] and biological sciences.[3] Evolutionary game theory[4,5] is one of the most successful frameworks used to discuss this issue. In recent studies, some mechanisms[6] that can promote cooperative evolution were thoroughly developed, such as kin selection,[7] indirect reciprocity,[8] direct reciprocity,[9] multilevel selection,[10] and network reciprocity.[11–13] There are many other factors, including population heterogeneity,[14,15] compassion,[16] and punishment,[17] that influence the evolution of cooperation. During the evolution of cooperation, one of the most interesting open questions[18] relates to how individuals update their strategies based on their knowledge and conception of others and themselves. In the past few years, various approaches were used to study evolutionary game dynamics in finite populations.[19–22] Especially, the standard Moran[22–27] and imitation processes[28–30] are two of the most popular update rules used to describe evolutionary dynamics in a finite population. The standard Moran process was investigated by Taylor *et al.* (2004)[20] and Nowak *et al.* (2004).[25] In the Moran process,[22,25,26] a player is chosen in proportion to their fitness, reproduces, and a randomly chosen player is subsequently replaced by their offspring. The imitation process was introduced by Szabó and Töke.[31] In the imitation process,[28–30,32,33] players focus on comparing payoffs with those of another player in order to evaluate whether or not they should imitate the other player's strategy. If their own payoffs are smaller, they are more likely to imitate strategies successfully. Liu *et al.*[23,27] combined both processes into a mixed process in a grouped population. Zhang *et al.*[34] divided populations into fast and slow groups, and studied population dynamics when interacting individuals differ in terms of the time scale of their updating process. In spite of meaningful progress, there are still some situations of great practical relevance that remain less explored. For instance, previous studies on evolutionary dynamics mostly focus on single update rules. The assumption that every player in a population adopts a single update rule for changing their strategy is idealized and unrealistic. In the real world, due to the influence of environmental factors and individuals' knowledge, individuals are likely to adopt several different update rules with dif-

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ferent probabilities to change (or update) their strategies. In this study, we establish mixed stochastic evolutionary dynamics with two strategies, A (cooperation) and B (defection), by combining the Moran and imitation processes in a finite, well-mixed population. The proposed process can provide insights under the following conditions. Individuals within a population can gain information from other individuals through the internet or by communicating with their neighbors. When individuals update their strategies through the Moran process, they know the strategies and payoffs of each individual in the population, which is equivalent to obtaining information from the internet.[27] When an individual imitates an update strategy, he or she knows the strategy and reward of randomly selected neighbors, which is equivalent to obtaining information through communication with neighbors.[27] In today's society, it is impossible for an individual to rely solely on the internet without communicating with his or her neighbors, or to communicate exclusively with his or her neighbors without going online to obtain information. Motivated by this fact, we build a mixed evolution game model in which each individual updates their strategy based on the imitation process with the probability $\gamma\,(0 \leqslant \gamma \leq 1)$ and on the Moran process with the probability $1-\gamma$. Figure 1 shows the specific mixed evolutionary model. Our objective is to understand how an individual's complex update rules influence the strategy outcomes in evolutionary games.

In the proposed model, we solve the fixation probabilities and fixation times for our stochastic evolutionary process. Fixation probabilities and fixation times[22] are two important concepts in the game dynamics of a finite population. The fixation probability clarifies whether an individual formulates a new strategy (*i.e.* cooperation) and how likely is it that this cooperation takes over the entire population. Fixation times[35,36] generally refer to the unconditional and conditional mean fixation times. The former describe the mean time required for the cooperative process to reach either fixation or extinction. The latter describes the mean time required for the cooperative process to reach fixation. One can see from theoretical analysis that the fixation probability in the established evolutionary game dynamics model is equal to that of two single simple updating models, *i.e.* the Moran and imitation processes. However, fixation times are different from those of the Moran and imitation processes. The evolution of cooperative strategies can be determined intuitively from simulated fixation times. From the fixation probability and fixation times, we highlight the difference between our evolutionary dynamics and the Moran and imitation processes. Thus, we can better understand how a cooperative strategy evolves in this system, where two different update rules are combined.

The remainder of this paper is organized as follows. In Section 2, we introduce a combination of the Moran and imitation processes as a general evolutionary dynamics framework in a finite and well-mixed population. We discuss the analytic expression describing the fixation probability and fixation times in Sections 3 and 4, respectively. Our conclusions are offered in Section 5.

2. Model

We assume a single, well-mixed population of constant size N. We consider two types of strategies, which we call A (cooperation) and B (defection). The game itself is played by two individuals. The payoffs from the game can be written in the following simple matrix:

$$\begin{array}{c} \\ A \\ B \end{array} \begin{array}{c} \begin{array}{cc} A & B \end{array} \\ \begin{bmatrix} a & b \\ c & d \end{bmatrix} \end{array}. \tag{1}$$

A well-mixed population allows interactions between all individuals, which leads to an average payoff, and in turn determines team selection with a special choice of payoff and fitness mapping.[37,38] Under random mating, excluding self-interaction, the expected payoffs to A players and B players are given by[39]

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

$$\pi_B = \frac{ic+d(N-i-1)}{N-1}, \tag{2b}$$

where i is used to denote the current number of A players in the population. Individuals with higher average payoffs produce offspring or are imitated with a higher probability. Thus, reproductive success is based on payoffs from the game. We assume that the degree to which the payoffs contribute to fitness is specified by a parameter $\omega \in [0,1]$ and focus on an exponential payoff-to-fitness mapping.[40] Thus, the fitness of A and B players in terms of exponential mapping is

$$f_A = \mathrm{e}^{\omega\pi_A}, \tag{3a}$$

$$f_B = \mathrm{e}^{\omega\pi_B}. \tag{3b}$$

For $\omega = 0$, selection is neutral and indicates an undirected random walk. Weak selection occurs for $0 < \omega \ll 1$. In the context of evolutionary game theory, the concept of weak selection was introduced by Nowak[25] and refers to the effects of small payoff differences.[41] This describes how selective bias and fluctuations influence each other.

In the Moran process,[22,25,26] an individual is selected at random with a probability that is proportional to its fitness, and the individual produces an identical offspring. The offspring replaces an individual that is randomly selected for death. The state of the system can change by one (at most) at each time step, and thus the transition probabilities in the standard Moran process are

$$p_{i,i+1}|_{\mathrm{Moran}} = \frac{N-i}{N}\frac{i\mathrm{e}^{\omega\pi_A}}{i\mathrm{e}^{\omega\pi_A}+(N-i)\mathrm{e}^{\omega\pi_B}}, \tag{4a}$$

$$p_{i,i-1}|_{\text{Moran}} = \frac{i}{N}\frac{(N-i)\,e^{\omega\pi_B}}{i e^{\omega\pi_A}+(N-i)\,e^{\omega\pi_B}}, \tag{4b}$$

$$p_{i,i}|_{\text{Moran}} = 1 - p_{i,i+1}|_{\text{Moran}} - p_{i,i-1}|_{\text{Moran}}. \tag{4c}$$

All other entries of the transition matrix are 0.

In the imitation process,[32,42] a randomly chosen individual compares their payoff with that of a second randomly chosen individual; the first individual is more likely to imitate the second individual when the second individual's payoff is higher.[28–30] The state of the system can change by one (at most) at each time step, and thus the transition probabilities are defined as follows:

$$p_{i,i+1}|_{\text{imitation}} = \frac{N-i}{N}\frac{i}{N}\frac{1}{1+e^{-\omega(\pi_A-\pi_B)}}, \tag{5a}$$

$$p_{i,i-1}|_{\text{imitation}} = \frac{N-i}{N}\frac{i}{N}\frac{1}{1+e^{\omega(\pi_A-\pi_B)}}, \tag{5b}$$

$$p_{i,i}|_{\text{imitation}} = 1 - p_{i,i+1}|_{\text{imitation}} - p_{i,i-1}|_{\text{imitation}}. \tag{5c}$$

All other entries of the transition matrix are 0.

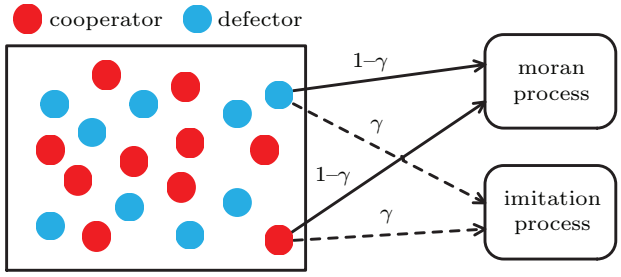


Fig. 1. In our neoteric mixed model, individuals in a finite population play the symmetric 2×2 game. Each individual adopts the Moran rule to change their strategy with probability $1-\gamma$, and adopts the imitation rule to change their strategy with probability γ ($0\le\gamma\le 1$).

Due to the complexity of an individual's environment and their own knowledge, it is natural that individuals change their strategies based on various update rules. Therefore, we no longer assume that individuals update their strategies by relying on a single update rule. Instead, they use two update rules (the Moran process and imitation process) to change policies. Figure 1 shows the details of our model. From Fig. 1, individuals within the proposed model update their strategies based on the Moran process with probability $1-\gamma$ and based on the imitation rule with probability γ. The number of A plays can increase or decrease by exactly one at any time, *i.e.* from i to $i-1$ or $i+1$. Thus, the mixed evolutionary process is a discrete-time Markov chain with state space $\{0,1,\ldots,N\}$, where the states $1,2,\ldots,N-1$ are transient while 0 and N are absorbing. A walk starting at site i is eventually absorbed into either site 0 or N within a finite amount of time and will stay there forever. For convenience, we denote the evolutionary transition probabilities of the mixed process as $p_{i,i\pm1}$. The process stays in state i with probability $1-p_{i,i+1}-p_{i,i-1}$. Therefore, the transition probabilities are

$$p_{i,i+1} = (1-\gamma)\frac{N-i}{N}\frac{i e^{\omega\pi_A}}{i e^{\omega\pi_A}+(N-i)\,e^{\omega\pi_B}} + \gamma\frac{N-i}{N}\frac{i}{N}\frac{1}{1+e^{-\omega(\pi_A-\pi_B)}}, \tag{6a}$$

$$p_{i,i-1} = (1-\gamma)\frac{i}{N}\frac{(N-i)\,e^{\omega\pi_B}}{i e^{\omega\pi_A}+(N-i)\,e^{\omega\pi_B}} + \gamma\frac{N-i}{N}\frac{i}{N}\frac{1}{1+e^{\omega(\pi_A-\pi_B)}}, \tag{6b}$$

$$p_{i,i} = 1 - p_{i,i+1} - p_{i,i-1}. \tag{6c}$$

All other entries of the transition matrix are 0. When $\gamma=0$, this process reduces to the standard Moran process with transition probabilities defined in Eqs. (4a), (4b), and (4c). When $\gamma=1$, this process is the imitation process with transition probabilities defined in Eqs. (5a), (5b), and (5c). We have two absorbing states for mixed evolutionary dynamics without mutation: all individuals are classified as type A or type B.

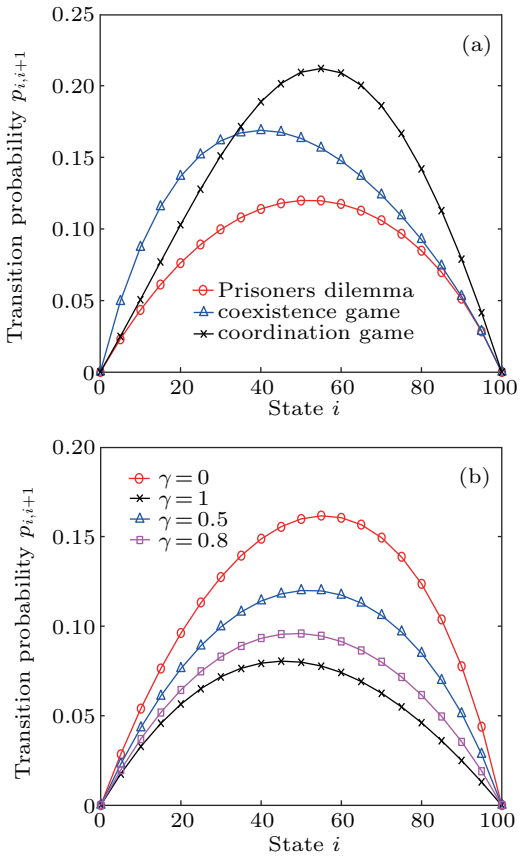


Fig. 2. Transition probabilities with $N=100$ and $\omega=0.005$, where $a=3$, $b=1$, $c=5$, and $d=2$ in the Prisoner's dilemma; for coordination games, $a=3$, $b=2$, $c=5$, and $d=1$; for coexistence games, $a=5$, $b=1$, $c=3$, and $d=2$. Panel (a) shows how transition probabilities vary in three games when $\gamma=0.5$. Panel (b) shows the Prisoner's dilemma as an example. The red and black lines show the transition probabilities $p_{i,i+1}$ in the Moran and imitation processes, respectively. The blue and magenta lines represent the transition probabilities $p_{i,i+1}$ in mixed evolutionary process with $\gamma=0.5$ and $\gamma=0.8$, respectively.

In Fig. 2(a), the transition probabilities in the mixed model for three games are shown with $\gamma=0.5$. According to intuition, different transition probabilities will lead to a difference in the time required to reach fixation in different games. This case will be analyzed in the fourth section. Figure 2(b) shows the transition probabilities in the Prisoner's dilemma

game. We know that the transition probabilities of the Moran process ($\gamma = 0$) are always greater than that of the imitation process and the mixed process. The transition probabilities of the imitation process ($\gamma = 1$) are always smaller than others. The transition probabilities in our process change with γ. All the results from the Prisoner's dilemma game in Fig. 2(b) are also suitable for the coexistence and coordination games. Therefore, changes in the transition probability for those two games are no longer given.

3. Fixation probabilities

The following analytical results can be derived based on results from previous studies.[42,43] Let $q_i(t)$ be the probability that the system is found in state i at time t. The master equation[44] of $q_i(t+1)$ is

$$\begin{aligned} q_i(t+1) &= (1-p_{i,i-1}-p_{i,i+1})q_i(t)+p_{i+1,i}q_{i+1}(t) \\ &\quad +p_{i-1,i}q_{i-1}(t). \end{aligned} \tag{7}$$

In a similar fashion, we denote $q_{i,j}(t+1)$ as the probability that capture events, in which the system reaches state j for the first time, are exactly t time steps after the state i. Then, the backward master equation can be written as follows:

$$\begin{aligned} q_{i,j}(t+1) &= (1-p_{i,i-1}-p_{i,i+1})q_{i,j}(t)+p_{i,i+1}q_{i+1,j}(t) \\ &\quad +p_{i,i-1}q_{i-1,j}(t). \end{aligned} \tag{8}$$

After summing over all t, the probability that the system reaches state j at any later time if the system starts in state i is given by

$$\phi_{ij} = \sum_{t=0}^{\infty} q_{i,j}(t). \tag{9}$$

The resulting master equation is

$$\phi_{ij} = (1-p_{i,i-1}-p_{i,i+1})\phi_{ij}+p_{i+1,i}\phi_{i+1,j}+p_{i,i-1}\phi_{i-1,j}. \tag{10}$$

In a finite population, the common concern is the probability of adopting an absorbing strategy A, *i.e.* the probability of ending in state N after beginning in state i. Here, we use ϕ_i to denote this probability. Because this system has two absorbing states, the probability to end in state 0 after starting from i is $1-\phi_i$. In previous studies,[23,32,45] this was defined as

$$\phi_i = \phi_{\mathrm{iN}} = \frac{1+\sum_{j=1}^{i-1}\prod_{m=1}^{j}\frac{p_{m,m-1}}{p_{m,m+1}}}{1+\sum_{j=1}^{N-1}\prod_{m=1}^{j}\frac{p_{m,m-1}}{p_{m,m+1}}}. \tag{11}$$

For a single A individual in the population of B individuals, the probability that individual A takes over the entire population is denoted as the fixation probability:

$$\phi_1 = \frac{1}{1+\sum_{j=1}^{N-1}\prod_{m=1}^{j}\frac{p_{m,m-1}}{p_{m,m+1}}}. \tag{12}$$

3.1. Neutral evolution

Neutral evolution, *i.e.* $\omega = 0$ or the special case of $\pi_A = \pi_B$ for any state i, is the natural benchmark case of a strategy's evolutionary success.[45,46] This leads to the cooperator doing exactly as well as the defector. In the established process, the transition probabilities defined in Eqs. (6a) and (6b) under neutral selection are

$$p_{i,i+1} = \frac{i(N-i)}{N^2}\left(1-\frac{\gamma}{2}\right), \tag{13a}$$

$$p_{i,i-1} = \frac{i(N-i)}{N^2}\left(1-\frac{\gamma}{2}\right). \tag{13b}$$

The probability (13a) is equal to Eq. (13b). Consequently, we have the fraction $p_{i,i-1}/p_{i,i+1} = 1$ for any state i, and from Eq. (12), the fixation probability for a single A individual under neutral selection is

$$\phi_1 = \frac{1}{N}. \tag{14}$$

Thus, the fixation probability under neutral selection in the proposed mixed process is equivalent to that of the Moran and imitation processes.

3.2. Weak selection

The difference between the average payoffs π_A and π_B is defined as follows:

$$\begin{aligned} \pi_A - \pi_B &= \frac{(b-d)N-(a-d)-i(c-d-a+b)}{N-1} \\ &= ui+v, \end{aligned} \tag{15}$$

where

$$u = \frac{a-b-c+d}{N-1}, \tag{16a}$$

$$v = \frac{(b-d)N+d-a}{N-1}. \tag{16b}$$

Under weak selection (*i.e.* as $\omega \to 0$), Taylor expansions of the ratio of transition probabilities up to the first order in ω yields

$$\frac{p_{i,i-1}}{p_{i,i+1}} = \frac{(1-\gamma)\frac{i}{N}\frac{(N-i)\,\mathrm{e}^{\omega\pi_B}}{i\,\mathrm{e}^{\omega\pi_A}+(N-i)\,\mathrm{e}^{\omega\pi_B}}+\gamma\frac{N-i}{N}\frac{i}{N}\frac{1}{1+\mathrm{e}^{\omega(\pi_A-\pi_B)}}}{(1-\gamma)\frac{N-i}{N}\frac{i\,\mathrm{e}^{\omega\pi_A}}{i\,\mathrm{e}^{\omega\pi_A}+(N-i)\,\mathrm{e}^{\omega\pi_B}}+\gamma\frac{N-i}{N}\frac{i}{N}\frac{1}{1+\mathrm{e}^{-\omega(\pi_A-\pi_B)}}} \approx 1-\omega(ui+v). \tag{17}$$

From a prior publication,[27] we can derive

$$\frac{p_{i,i-1}}{p_{i,i+1}} = \frac{p_{i,i-1}|_{\text{Moran}}}{p_{i,i+1}|_{\text{Moran}}} = \frac{p_{i,i-1}|_{\text{imitation}}}{p_{i,i+1}|_{\text{imitation}}}. \tag{18}$$

Although these transition probabilities describing our mixed process are different from those in the Moran and imitation processes, they also yield $p_{i,i-1}/p_{i,i+1} \approx 1-\omega(ui+v)$ under weak selection ($\omega \ll 1$). Thus, the fixation probability in the mixed process with exponential fitness mapping is not affected by the parameter γ. In light of previous research, the fixation probabilities in the mixed process[22] for small ω are given by

$$\phi_1 \approx \frac{1}{N} + \omega \frac{(N-1)}{N} \frac{(N+1)u+3v}{6}. \tag{19}$$

For the general state i, the absorption probabilities under weak selection are also found in prior publications.[22,25,39,47]

$$\phi_i \approx \frac{i}{N} + \omega \frac{i(N-i)}{N} \left(\frac{(N+i)u+3v}{6} \right). \tag{20}$$

Under both neutral and weak selection, the fixation probabilities in this paper are the same as those of the Moran process. Therefore, natural selection favors A replacing B if the fixation probability of a single cooperator under weak selection is higher than $1/N$, *i.e.* $\phi_1 > 1/N$.

When the average fitness values for both types of individuals are equal, *i.e.* $\pi_A = \pi_B$, we can obtain the unstable internal equilibrium for large populations $x^* = (d-b)/(a-c+d-b)$. For $a > c, b > d$, A is the best reply to itself while B is also the best reply to itself. In a large population, selection favors A replacing B if

$$x^* < \frac{d-b}{(d-b)+2(d-b)} = \frac{1}{3}. \tag{21}$$

Thus, if the frequency of A individuals is less than one-third at the unstable internal equilibrium point, the fixation probability of a single A individual will be larger than that of a neutral A individual in a large population under weak selection. The one-third rule holds in our mixed model.

As we all know, the evolutionary stable strategy (ESS)[48,49] is motivated by selection dynamics in infinite populations. However, in a finite population of size N, strategy B is the ESS[45] if selection opposes A invading B and selection opposes A replacing B. $\pi_A < \pi_B$ if selection opposes A invading B, and $\phi_A < 1/N$ if selection opposes A replacing B. Subsequently, strategy B is the ESS if $b(N-1) < c+(N-2)d$ and $a(N-2)+b(2N-1) < c(N+1)+(2N-4)d$ in the proposed mixed process with a finite population of size N.

4. Fixation times

Another quantity of interest in evolutionary dynamics of finite populations is the average fixation time.[22,32,41,50] Two different fixation times should be considered seriously during the evolutionary process: the unconditional average time and the conditional fixation time.

The unconditional average time to fixation t_1 is the expected time required to reach the absorbing states (either one of the two absorbing states) starting from the initial state $i = 1$. This time t_i is defined as

$$t_i = 1 + p_{i,i-1}t_{i-1} + p_{i,i+1}t_{i+1} + (1 - p_{i,i-1} - p_{i,i+1})t_i. \tag{22}$$

The conditional fixation time t_i^{C} specifies the mean time required to reach the absorbing state N when starting from state i, provided that A is ultimately reached. In order to obtain the value t_i^{C}, it is expedient to start from[22,35]

$$\begin{aligned} \phi_i t_i^{\text{C}} = {} & \phi_{i-1}p_{i,i-1}(t_{i-1}^{\text{C}}+1) + \phi_i(1-p_{i,i-1}-p_{i,i+1})(t_i^{\text{C}}+1) \\ & + \phi_{i+1}p_{i,i+1}(t_{i+1}^{\text{C}}+1). \end{aligned} \tag{23}$$

The solutions to Eqs. (22) and (23) were presented in previous publications, and the specific expressions for the unconditional and conditional fixation times were obtained and given by Eqs. (24) and (25), respectively.

$$t_1 = \phi_1 \sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{1}{p_{l,l+1}} \prod_{m=l+1}^{k} \frac{p_{m,m-1}}{p_{m,m+1}}, \tag{24}$$

$$t_1^{\text{C}} = \sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{\phi_l}{p_{l,l+1}} \prod_{m=l+1}^{k} \frac{p_{m,m-1}}{p_{m,m+1}}. \tag{25}$$

Although the transition probabilities in the proposed mixed process are different from those of the Moran and imitation processes, they also yield $p_{i,i-1}/p_{i,i+1} \approx 1-\omega(ui+v)$ under weak selection (*i.e.* $\omega \ll 1$). Thus, the weak selection approximations for the fixation probabilities ϕ_i in our proposed mixed process and the other two single processes are identical. However, the difference between the transition probabilities under weak selection leads to different unconditional and conditional average times. We give a concrete analysis of the unconditional and conditional average fixation times in the proposed evolutionary process in the following section.

4.1. Neutral selection

Here, we briefly recall the unconditional and conditional mean fixation times in the Moran and imitation processes in finite, well-mixed populations. The unconditional mean fixation time $t_1|_{\text{Moran}}$ and conditional mean fixation time $t_1^{\text{C}}|_{\text{Moran}}$ for a single strategy A individual in the Moran process under neutral selection are given by

$$t_1|_{\text{Moran}} = \frac{1}{N} \sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{2N^2}{l(N-l)} = NH_{N-1}, \tag{26a}$$

$$t_1^{\text{C}}|_{\text{Moran}} = \sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{l}{N} \prod_{m=l+1}^{k} \frac{2N^2}{l(N-l)} = N(N-1), \tag{26b}$$

where the harmonic number is $H_{N-1} = \sum_{l=1}^{N-1} \frac{1}{l}$.

Under neutral selection, the unconditional mean fixation time $t_1|_{\text{Imitation}}$ and the conditional mean time $t_1^{\text{C}}|_{\text{Imitation}}$ for a single strategy A individual in the imitation process are given by

$$t_1|_{\text{Imitation}} = 2NH_{N-1}, \tag{27a}$$

$$t_1^{\text{C}}|_{\text{Imitation}} = 2N(N-1). \tag{27b}$$

For neutral selection, substituting Eqs. (14), (15), and (17) into Eqs. (24) and (25) yields the unconditional and conditional fixation times in our proposed process:

$$t_1 = \phi_1 \sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{1}{p_{l,l+1}}\prod_{m=l+1}^{k}\frac{p_{m,m-1}}{p_{m,m+1}} = \frac{2N}{2-\gamma}H_{N-1}, \tag{28}$$

$$t_1^{\text{C}} = \sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{\phi_l}{p_{i,i+1}}\prod_{m=l+1}^{k}\frac{p_{l,l-1}}{p_{l,l+1}} = \frac{2N(N-1)}{2-\gamma}. \tag{29}$$

The unconditional and conditional mean fixation times in the proposed mixed process are not the same as those in the standard Moran or imitation processes. Those times in a single process are only connected with the population size N. However, in the mixed process, the fixation times also depend on γ.

Although the approximate fixation probabilities ϕ_l in our process are identical to those of the Moran and imitation processes, different transition probabilities for different mixed processes lead to different mean fixation times. In the following section, we will discuss times associated with this mixed evolutionary process under weak selection.

4.2. Weak selection

Calculating the fixation time is quite complicated under weak selection. Therefore, Taylor's first-order expansion approximation is used to approximate the fixation times[19] as follows:

$$t_1 \approx t_1|_{\omega=0} + \omega\cdot\frac{\partial}{\partial\omega}t_1\Big|_{\omega=0}, \tag{30}$$

$$t_1^{\text{C}} \approx t_1^{\text{C}}|_{\omega=0} + \omega\cdot\frac{\partial}{\partial\omega}t_1^{\text{C}}\Big|_{\omega=0}. \tag{31}$$

In Ref. [32], the authors presented specific results for the fixation times under weak selection. The unconditional and conditional average fixation times in the imitation process are

$$t_1|_{\text{Imitation}} \approx 2NH_{N-1} + vN(N-1-H_{N-1})\omega, \tag{32a}$$

$$t_1^{\text{C}}|_{\text{Imitation}} \approx 2N(N-1) + uN(N-1)\frac{N^2+N-6}{18}\omega. \tag{32b}$$

For the Moran process, the unconditional and conditional average fixation times are

$$t_1|_{\text{Moran}} = NH_{N-1} + v\frac{N}{2}(N+1-2H_N)\omega, \tag{33a}$$

$$t_1^{\text{C}}|_{\text{Moran}} = N(N-1) - u\frac{N^2(N^2-3N+2)}{36}\omega. \tag{33b}$$

Calculating the fixation time is quite complicated in the case of weak selection, even for a single simple model, and the same holds for the fixation time in our mixed model. Thus, we also use Taylor's method to approximate the fixation time. The weak selection approximation of the unconditional mean fixation time in our mixed model can be written as follows:

$$\begin{aligned} t_1 \approx\ & \frac{2N}{2-\gamma}H_{N-1} + \left[\frac{N(N-1)}{(2-\gamma)}\frac{(N+1)u+3v}{3}\right]H_{N-1}\omega \\ & - \frac{4(1-\gamma)}{[(2-\gamma)]^2}\left[\frac{N(N-1)u}{2} + Nv(H_N-1)\right]\omega \\ & - \frac{\gamma N}{[(2-\gamma)]^2}\left[(N-1)u + H_{N-1}v\right]\omega \\ & - N\frac{N-1}{(2-\gamma)}\left[\frac{(N+1)u+3v}{3}H_{N-1} - (u+v)\right]\omega. \end{aligned} \tag{34}$$

A detailed calculation can be found in Appendix A. $\gamma = 0$ reduces to the Moran process, and the unconditional mean fixation time in Eq. (34) simplifies to Eq. (33a). On the contrary, $\gamma = 1$ reduces to the imitation process, and the unconditional mean fixation time in Eq. (34) simplifies to Eq. (32a).

Compared with the unconditional mean fixation time, the only difference is the fixation probability ϕ_l instead of ϕ_1. The linear term in the weak selection expansion of ϕ_l is given in Eq. (35). This is similar to the unconditional mean time, and corresponding details for this calculation can be found in Appendix B.

$$\begin{aligned} t_1^{\text{C}} \approx\ & \frac{2N(N-1)}{2-\gamma} + \frac{N^2(N-1)}{18(2-\gamma)}\left[(4N+1)u+9v\right]\omega \\ & - (N-2)\frac{N(N-1)}{18(2-\gamma)}\left[(5N+3)u+9v\right]\omega \\ & - \frac{1}{(2-\gamma)^2}\left[4(1-\gamma)\left(\frac{N(N+1)(N-1)u}{6} + \frac{N(N-1)}{2}v\right)\right. \\ & \left. + \gamma N\left(\frac{N(N-1)u}{2} + (N-1)v\right)\right]\omega, \end{aligned} \tag{35}$$

$\gamma = 0$ reduces to the Moran process, and the conditional mean fixation time in Eq. (35) simplifies to Eq. (33b). On the contrary, $\gamma = 1$ reduces to the imitation process, and equation (35) simplifies to Eq. (32b).

The unconditional mean fixation times (Eqs. (32a) and (33a)) in both simple models are only related to the constant v, which describes the average payoff difference between strategies A and B. Meanwhile, the conditional mean fixation times (Eqs. (32b) and (33b)) in both simple models are only related to the slope u of the average payoff difference between strategies A and B. Equations (34) and (35) show that the two fixation times in our proposed model are much more complicated than any one of those in the simple models because they are related to v and u.

4.3. Numerical analysis

To observe changes in fixation times more directly, we performed theoretical simulations based on Eqs. (24) and (25). Now we consider the Prisoner's dilemma game,[51] in which strategy B (defection) always has a higher payoff ($c > a, d > b$) and is always dominant, regardless of the fraction of strategy A (cooperation). The Prisoner's dilemma is a coexistence game[34] in which both strategies A and B produce the highest payoffs when interacting with the other strategy ($a < c, b > d$). In coordination games, both strategies A and B produce the highest payoffs when interacting with their own types ($a > c, b < d$). A cannot invade B during a coordination game with a well-mixed population, and *vice versa*.

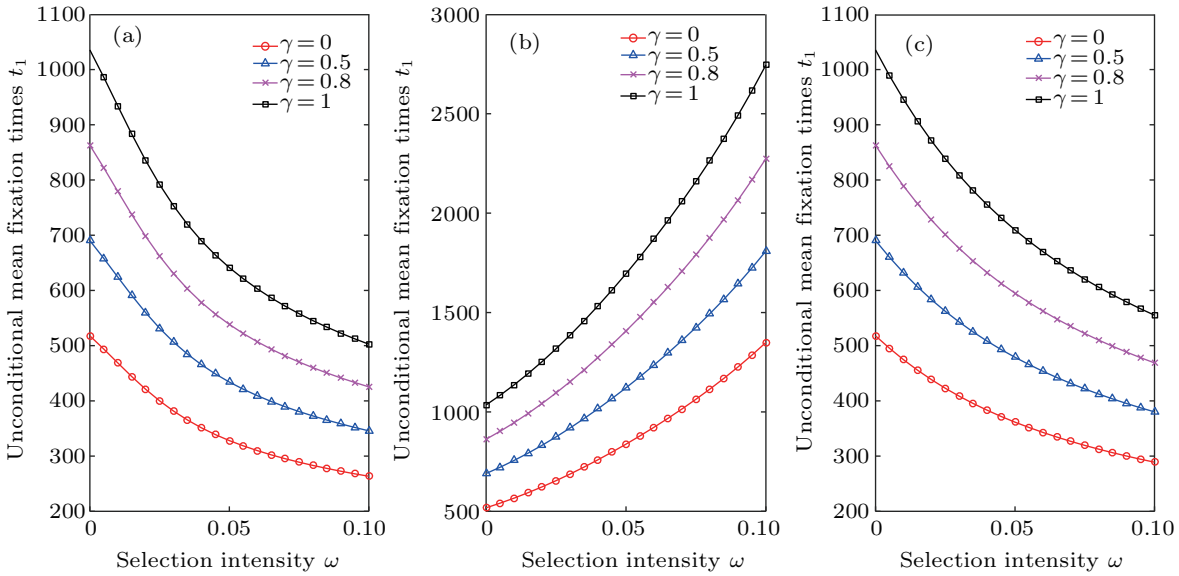


Fig. 3. Theoretical unconditional mean fixation times for a strategy A individual (a single cooperator) with $N = 100$. (a) Unconditional mean fixation time in the Prisoner's dilemma with $a = 3$, $b = 1$, $c = 5$, and $d = 2$. (b) Unconditional mean fixation time in coexistence games with $a = 3$, $b = 2$, $c = 5$, and $d = 1$. (c) Unconditional mean fixation time in coordination games with $a = 5$, $b = 1$, $c = 3$, and $d = 2$. The red and black lines show the Moran and imitation processes, respectively. The blue and magenta lines show our proposed process with $\gamma = 0.5$ and $\gamma = 0.8$, respectively.

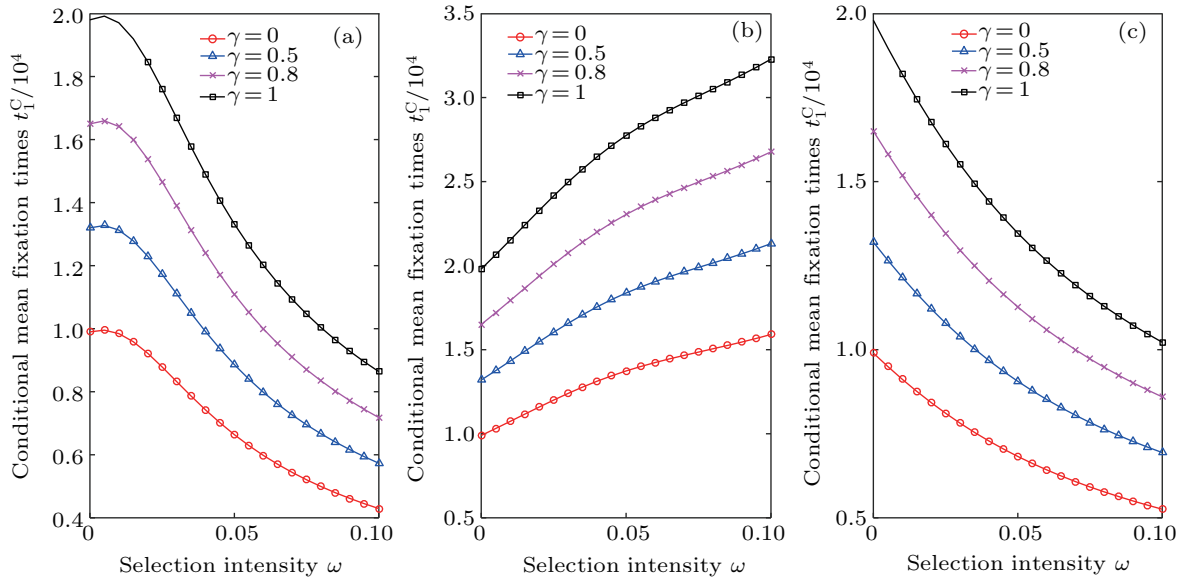


Fig. 4. Theoretical conditional mean fixation times for a strategy A individual with $N = 100$. (a) Prisoner's dilemma results with $a = 3$, $b = 1$, $c = 5$, and $d = 2$. (b) Coexistence game results with $a = 3$, $b = 2$, $c = 5$, and $d = 1$. (c) Coordination game results with $a = 5$, $b = 1$, $c = 3$, and $d = 2$. The red and black lines show changes in the unconditional mean fixation times in the standard Moran process and imitation process, respectively. The blue and magenta lines show changes in the unconditional mean fixation times in our proposed process with $\gamma = 0.5$ and $\gamma = 0.8$, respectively.

The three panels in Fig. 3 show results for the Prisoner's dilemma, coexistence, and coordination games. Different combinations of update rules result in different updating rates in the three games. In the Moran process ($\gamma = 0$), a cooperator takes the least time to reach the homologous state (all A individuals or all B individuals), and thus their update rate is the fastest. Contrary to the Moran update process, the imitation process ($\gamma = 1$) takes the longest time to reach the homol-

ogous state, thus the update rate is the slowest. This is because the transition probability in the Moran process is greater than that in the imitation process, as shown in Fig. 2. The time required for the mixed update process to reach the homologous state is between that of the two simple update processes. The unconditional mean time becomes longer as γ increases because less information is known. However, this growth is not linearly related to γ. This is consistent with our intuition. Moreover, this analysis indicates that the behavior of the unconditional fixation times in the mixed process is not just the average value of the values from the two pure processes. Even if $\gamma = 0.5$, the time required for the mixed update process to reach the homologous state is closer to the time required under the Moran process. This conclusion is also suitable for the conditional fixation time, as shown in Fig. 5.

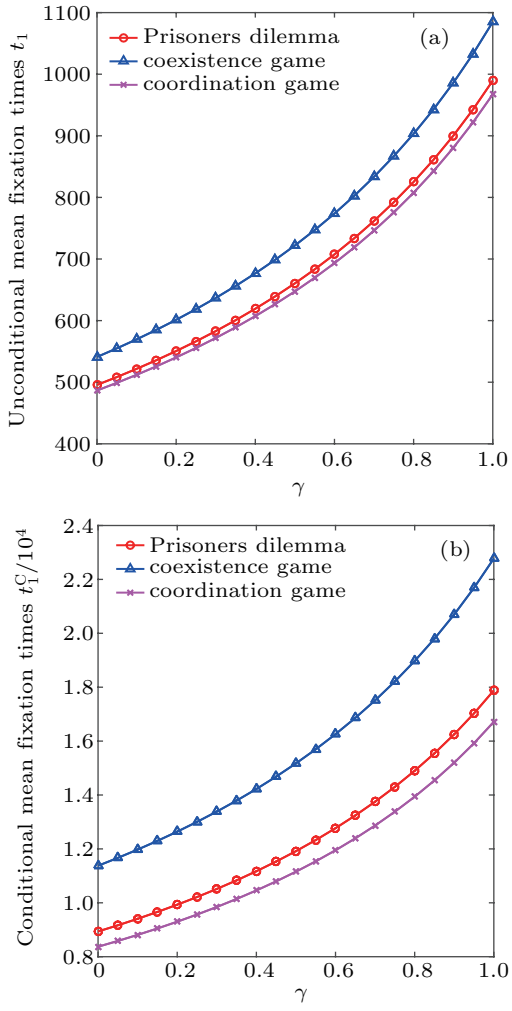


Fig. 5. (a) Unconditional mean fixation times and (b) conditional mean fixation times for a strategy A individual with $N = 100$ and $\omega = 0.005$. The red, magenta, and blue lines show fixation times from the Prisoner's dilemma, coordination, and coexistence games, respectively. For the Prisoner's dilemma, $a = 3$, $b = 1$, $c = 5$, and $d = 2$; for coordination games, $a = 3$, $b = 2$, $c = 5$, and $d = 1$; for coexistence games, $a = 5$, $b = 1$, $c = 3$, and $d = 2$.

Figure 4 shows the conditional mean fixation time for a single cooperator with respect to the selection intensity ω. Figures 4(a), 4(b), and 4(c) show results from the Prisoner's dilemma, coexistence, and coordination games, respectively. One can see from Fig. 3 and Fig. 4 that the conditional mean fixation time is always greater than the unconditional mean fixation time under the same conditions. In the Prisoner's dilemma and coordination games, the conditional fixation time decreases with selection intensity ω, while in the coexistence game, this time increases with selection intensity.

Figure 5 shows that the conditional and the unconditional mean fixation times change as γ increases under weak selection for any type of game. When the individual only adopts the Moran process update strategy, the time required for a single cooperator to reach fixation in a finite population is the shortest. As γ increases, both types of fixation times increase at a faster rate. Coexistence games reach an internal equilibrium, which leads to the coexistence of two strategies. Therefore, two strategies are not apt to encroach on each other throughout the population, and thus the time required to reach the homologous state is the longest compared to the other two games. A single cooperator requires more time to reach fixation in the coexistence game than in the Prisoner's dilemma and coordination games, regardless of γ. The coordination game consists of two boundary equilibrium points, and thus populations are more likely to reach the homologous state. Furthermore, cooperation can accelerate as long as the probability of using the Moran rule increases, *i.e.* full cooperation is reached sooner when the probability that the individual adopts the Moran rule is greater. This applies in any type of game.

5. Conclusion

In this study, we apply mixed evolutionary dynamics to a finite population while considering the Moran and imitation processes, which are two of the most popular update rules used to describe evolutionary dynamics in a finite population. Our theoretical model is largely different from those published previously as it introduces two different update rules for each individual. Under the same conditions, the transition probability in the mixed process is always between those of the two single processes, and the transition probability in the Moran process is greater than that of the imitation process. Based on the transition probability, we studied the fixation probability and fixation times. The fixation probability result agrees with that of a single process, but the fixation time is not equal to that of a single process. The proposed model can be characterized in terms of the fixation times, which are nonlinearly connected with the probability of adopting the imitation rule. Accordingly, the Moran and imitation processes are two special cases of our proposed dynamic model. The simulated mean fixation times provide some insight into how cooperative strategies evolve. The simulated mean fixation times provide some insight into how cooperative strategies evolve. Cooperation increases as the probability that an individual uses the Moran

rule increases. In a real society, human beings are complex and are influenced by a variety of environmental factors. It is possible to update strategies according to several different rules. Therefore, we can also study the evolutionary dynamics of a population based on a mixture of other update strategies, such as the aspiration update rule, pair comparison update rule, and so on.

Appendix A. Unconditional mean fixation time

We calculated linear corrections for the unconditional mean fixation time t_1 in our proposed process in detail. The specific calculations here are equivalent to those in a previous publication.[32] The first-order expansion of the unconditional mean fixation time can be written as follows:

$$t_1 = \phi_1 \sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{1}{p_{l,l+1}}\prod_{m=l+1}^{k}\frac{p_{m,m-1}}{p_{m,m+1}} \approx t_1|_{\omega=0} + \omega\cdot\left[\frac{\partial}{\partial\omega}t_1\right]\Big|_{\omega=0}. \tag{A1}$$

The first term can be seen in Eq. (28). Our goal here is to compute the linear term $\left[\frac{\partial}{\partial\omega}t_1\right]\Big|_{\omega=0}$.

$$\left[\frac{\partial}{\partial\omega}t_1\right]\Big|_{\omega=0} = \left[\sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{\phi_1}{p_{l,l+1}}\prod_{m=l+1}^{k}\frac{p_{m,m-1}}{p_{m,m+1}}\right]'\Big|_{\omega=0} = \sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{1}{p_{l,l+1}}\frac{\partial\phi_1}{\partial\omega}+\phi_1\frac{\partial}{\partial\omega}\frac{1}{p_{l,l+1}}\right]\Big|_{\omega=0} - \sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{\phi_1}{p_{l,l+1}}\sum_{m=l+1}^{k}(um+v)\right]\Big|_{\omega=0}, \tag{A2}$$

where we apply

$$\left[\prod_{m=l+1}^{k}\frac{p_{m,m-1}}{p_{m,m+1}}\right]_{\omega=0} = 1$$

and

$$\left[\frac{\partial}{\partial\omega}\prod_{m=l+1}^{k}\frac{p_{m,m-1}}{p_{m,m+1}}\right]_{\omega=0} = -\sum_{m=l+1}^{k}(um+v).$$

For the fixation probabilities in Eq. (20) under weak selection, we obtain

$$\frac{\partial\phi_1}{\partial\omega} = \frac{N-1}{N}\frac{(N+1)u+3v}{6}, \tag{A3}$$

$$\phi_1|_{\omega=0} = \frac{1}{N}. \tag{A4}$$

By referring to the transition probability in Eqs. (6a), (6b), and (6c), we obtain

$$p_{l,l+1}|_{\omega=0} = (1-\gamma)\frac{N-l}{N}\frac{l}{N}+\gamma\frac{N-l}{N}\frac{l}{N}\frac{1}{2} = \frac{N-l}{2N}\frac{l}{N}(2-\gamma), \tag{A5}$$

$$\left[\frac{\partial}{\partial\omega}\frac{1}{p_{l,l+1}}\right]\Big|_{\omega=0} = \frac{\partial}{\partial\omega}\frac{1}{(1-\gamma)\frac{N-l}{N}\frac{l}{l+(N-l)\mathrm{e}^{-\omega(\mu l+v)}}+\gamma\frac{N-l}{N}\frac{l}{N}\frac{1}{1+\mathrm{e}^{-\omega(\mu l+v)}}}\Bigg|_{\omega=0} = -\frac{N[4(1-\gamma)(N-l)+\gamma N](\mu l+v)}{[(2-\gamma)]^2(N-l)l}. \tag{A6}$$

Thus,

$$\frac{1}{p_{l,l+1}}\cdot\frac{\partial\phi_1}{\partial\omega} = \frac{N(N-1)[(N+1)u+3v]}{3l(N-l)(2-\gamma)}, \tag{A7}$$

$$\phi_1\cdot\frac{\partial}{\partial\omega}\frac{1}{p_{l,l+1}}\Big|_{\omega=0} = -\frac{[4(1-\gamma)(N-l)+\gamma N](\mu l+v)}{4[(1-\frac{1}{2}\gamma)]^2(N-l)l}. \tag{A8}$$

Equation (A3) can now be written as follows:

$$\frac{\partial}{\partial\omega}t_1 = \underbrace{\sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{N(N-1)}{l(N-l)(2-\gamma)}\frac{(N+1)u+3v}{3}\right]}_{K_1} - \underbrace{\sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{[4(1-\gamma)(N-l)+\gamma N](\mu l+v)}{[(2-\gamma)]^2(N-l)l}\right]}_{K_2} - \underbrace{\sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{2N}{l(N-l)(2-\gamma)}\sum_{m=l+1}^{k}(um+v)\right]}_{K_3}. \tag{A9}$$

We can now calculate the terms K_1, K_2, and K_3 in Eq. (A9):

$$K_1 = \sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{N(N-1)}{l(N-l)(2-\gamma)}\frac{(N+1)u+3v}{3}\right] = \sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{1}{(N-l)}\frac{N(N-1)}{l(2-\gamma)}\frac{(N+1)u+3v}{3}\right] = \left[\frac{N(N-1)}{(2-\gamma)}\frac{(N+1)u+3v}{3}\right]H_{N-1}, \tag{A10}$$

$$K_2 = \sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{[4(1-\gamma)(N-l)+\gamma N](\mu l+v)}{[(2-\gamma)]^2(N-l)l}\right] = \sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{1}{(N-l)}f_1 = \sum_{l=1}^{N-1}f_l$$

$$= \sum_{l=1}^{N-1}\left[\frac{[4(1-\gamma)(N-l)+\gamma N](\mu l+\nu)}{(2-\gamma)^2 l}\right]$$
$$= \frac{4(1-\gamma)}{(2-\gamma)^2}\left[\frac{N(N-1)u}{2}+Nv(H_{N-1}-1)\right]$$
$$+\frac{\gamma N}{(2-\gamma)^2}[(N-1)u+H_{N-1}v], \quad \text{(A11)}$$

$$K_3 = \sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{2N}{l(N-l)(2-\gamma)}\sum_{m=l+1}^{k}(um+v)\right]$$
$$= \sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{2N}{l(N-l)(2-\gamma)}(f_k-f_l)\right]$$
$$= \frac{2}{(2-\gamma)}\left[\underbrace{\sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{f_k}{l}}_{Q_1}+\underbrace{\sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{f_k}{N-l}}_{Q_2}\right.$$
$$\left.-\underbrace{\sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{f_l}{l}}_{Q_3}-\underbrace{\sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{f_l}{(N-l)}}_{Q_4}\right]$$
$$= \frac{N(N-1)}{(2-\gamma)}\left[\frac{(N+1)u+3v}{3}H_{N-1}-(u+v)\right], \quad \text{(A12)}$$

where we use the function

$$\sum_{m=l+1}^{k}(um+v) = f_k - f_l, f_m = m(m+1)\frac{u}{2}+mv \quad \text{(A13)}$$

and

$$\sum_{k=l}^{N-1} f_k = \sum_{k=l}^{N-1} k\left[(k+1)\frac{u}{2}+v\right] = \frac{u}{2}\sum_{k=l}^{N-1}k^2+(\frac{u}{2}+v)\sum_{k=l}^{N-1}k$$
$$= \frac{N-l}{6}\left(N^2+Nl+l^2-1\right)u$$
$$+\frac{N-l}{2}(N+l-1)v. \quad \text{(A14)}$$

Equations (A13) and (A14) can be used to calculate the terms Q_1, Q_2, Q_3, and Q_4:

$$Q_1 = \sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{f_k}{l} = \sum_{l=1}^{N-1}\frac{1}{l}\sum_{k=l}^{N-1}f_k$$
$$= \frac{1}{6}\sum_{l=1}^{N-1}\frac{N(N-1)(N+1)u+3N(N-1)v}{l}$$
$$-\frac{1}{6}\sum_{l=1}^{N-1}[(l^2-1)u-3(l-1)v]$$
$$= \frac{N(N-1)}{6}[(N+1)u+3v]H_{N-1}$$
$$-\frac{N-1}{36}(N-2)[(2N+3)u+9v], \quad \text{(A15)}$$

$$Q_2 = \sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{f_k}{N-l} = \sum_{l=1}^{N-1}\frac{1}{N-l}\sum_{k=l}^{N-1}f_k$$
$$= \frac{N-1}{6}\sum_{l=1}^{N}[(N+1)u+3v]+\frac{Nu+3v}{6}\sum_{l=1}^{N-1}l+\frac{u}{6}\sum_{l=1}^{N-1}l^2$$
$$= \frac{N-l}{6}\left[(11N^2-N-6)u+9(3N-2)v\right], \quad \text{(A16)}$$

$$Q_3 = \sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{f_l}{l} = \sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[(l+1)\frac{u}{2}+v\right]$$
$$= \frac{N-1}{12}N[(N+4)u+6v], \quad \text{(A17)}$$

$$Q_4 = \sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{f_l}{(N-l)} = \sum_{k=1}^{N-1}f_k$$
$$= \frac{N-1}{6}N[(N+1)u+3v]. \quad \text{(A18)}$$

Inserting Eqs. (A10), (A11), and (A12) into Eq. (A2), we obtain an approximation of the linear term $\left[\frac{\partial}{\partial\omega}t_1\right]\Big|_{\omega=0}$. Combining this with Eq. (31) leads to the unconditional mean fixation time under weak selection (Eq. (35)).

Appendix B. Conditional mean fixation time

Here, we are interested in finding the approximate conditional mean fixation time t_1^{C} in our proposed process. Deriving the conditional mean fixation time follows a similar process as the unconditional mean fixation time. The first-order expansion of the conditional mean fixation time can be written as follows:

$$t_1^{\mathrm{C}} \approx t_1^{\mathrm{C}}|_{\omega=0} + \omega\cdot\left[\frac{\partial}{\partial\omega}t_1^{\mathrm{C}}\right]\Big|_{\omega=0}. \quad \text{(B1)}$$

The first term can be found in Eq. (29). Our goal here is to compute the linear term $\left[\frac{\partial}{\partial\omega}t_1^{\mathrm{C}}\right]\Big|_{\omega=0}$,

$$\left[\frac{\partial}{\partial\omega}t_1^{\mathrm{C}}\right]\Big|_{\omega=0} = \sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{1}{p_{l,l+1}}\frac{\partial\phi_l}{\partial\omega}+\phi_l\frac{\partial}{\partial\omega}\frac{1}{p_{l,l+1}}\right]_{\omega=0}$$
$$-\sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{\phi_l}{p_{l,l+1}}\sum_{m=l+1}^{k}(um+v)\right]. \quad \text{(B2)}$$

For the fixation probabilities in Eq. (20) under weak selection, we obtain

$$\phi_l \approx \frac{l}{N}+\omega\frac{l(N-l)}{N}\left(\frac{u(N+l)+3v}{6}\right), \quad \text{(B3)}$$

$$\frac{\partial\phi_l}{\partial\omega} = \frac{l(N-l)}{N}\left(\frac{u(N+l)+3v}{6}\right), \quad \text{(B4)}$$

$$\frac{1}{p_{l,l+1}}|_{\omega=0} = \frac{2N^2}{l(N-l)(2-\gamma)}. \quad \text{(B5)}$$

So

$$\frac{1}{p_{l,l+1}}\frac{\partial\phi_l}{\partial\omega}\Big|_{\omega=0} = \frac{l(N-l)}{N}\left(\frac{u(N+l)+3v}{6}\right)\cdot\frac{2N^2}{l(N-l)(2-\gamma)}$$
$$= \frac{N}{(2-\gamma)}\left(\frac{u(N+l)+3v}{3}\right), \quad \text{(B6)}$$

$$\frac{\partial}{\partial\omega}\frac{1}{p_{l,l+1}}\bigg|_{\omega=0}=\frac{\partial}{\partial\omega}\frac{1}{(1-\gamma)\dfrac{N-l}{N}\dfrac{l}{l+(N-l)\,\mathrm{e}^{-\omega(\mu l+\nu)}}+\gamma\dfrac{N-l}{N}\dfrac{l}{N}\dfrac{1}{1+\mathrm{e}^{-\omega(\mu l+\nu)}}}\bigg|_{\omega=0}$$
$$=-\frac{N[4(1-\gamma)(N-l)+\gamma N](\mu l+\nu)}{(2-\gamma)^2(N-l)l}, \tag{B7}$$

$$\phi_l|_{\omega=0}\approx\frac{l}{N}, \tag{B8}$$

$$\phi_l\,\frac{\partial}{\partial\omega}\frac{1}{p_{l,l+1}}\bigg|_{\omega=0}=\frac{[4(1-\gamma)(N-l)+\gamma N](\mu l+\nu)}{(2-\gamma)^2(N-l)}, \tag{B9}$$

$$\phi_l\frac{1}{p_{l,l+1}}\bigg|_{\omega=0}\approx\frac{l}{N}\frac{2N^2}{l(N-l)(2-\gamma)}=\frac{2N}{(N-l)(2-\gamma)}, \tag{B10}$$

$$\left[\frac{\partial}{\partial\omega}t_1^{\mathrm{C}}\right]\bigg|_{\omega=0}=\underbrace{\sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\left(\frac{u(N+l)+3v}{3}\right)\cdot\frac{N}{(2-\gamma)}\right]}_{H_1}$$
$$\underbrace{-\sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{[4(1-\gamma)(N-l)+\gamma N](\mu l+\nu)}{(2-\gamma)^2(N-l)}\right]}_{H_2}$$
$$\underbrace{-\sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{2N}{(N-l)(2-\gamma)}\sum_{m=l+1}^{k}(um+v)\right]}_{H_3}. \tag{B11}$$

We can now calculate the terms H_1, H_2, and H_3 in Eq. (B11):

$$H_1=\sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\left(\frac{u(N+l)+3v}{3}\right)\cdot\frac{N}{(2-\gamma)}\right]$$
$$=\frac{N}{3(2-\gamma)}\sum_{k=1}^{N-1}\sum_{l=1}^{k}[u(N+l)+3v]$$
$$=\frac{N}{3(2-\gamma)}\left[\frac{N(N-1)}{2}(Nu+3v)+\frac{N(N-1)(N+1)}{6}u\right]$$
$$=\frac{N^2(N-1)}{18(2-\gamma)}[(4N+1)u+9v], \tag{B12}$$

$$H_2=\sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{[4(1-\gamma)(N-l)+\gamma N](\mu l+\nu)}{(2-\gamma)^2(N-l)}\right]$$
$$=\frac{1}{(2-\gamma)^2}\left[4(1-\gamma)\sum_{k=1}^{N-1}\sum_{l=1}^{k}(\mu l+\nu)+\gamma N\sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{(\mu l+\nu)}{(N-l)}\right]$$
$$=\frac{1}{(2-\gamma)^2}\left\{4(1-\gamma)\left[\frac{N(N+1)(N-1)u}{6}+\frac{N(N-1)}{2}v\right]+\gamma N\left[\frac{N(N-1)u}{2}+(N-1)v\right]\right\}, \tag{B13}$$

$$H_3=\sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{2N}{(N-l)(2-\gamma)}\sum_{m=l+1}^{k}(um+v)\right]$$
$$=\sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{2N}{(N-l)(2-\gamma)}(f_k-f_l)\right]$$
$$=\frac{2N}{(2-\gamma)}\left\{\frac{N-1}{36}((11N^2-N-6)u+9(3N-2)v)-\frac{N-1}{6}N[(N+1)u+3v]\right\}$$
$$=\frac{N(N-1)(N-2)}{18(2-\gamma)}\{(5N+3)u+9v\}, \tag{B14}$$

where

$$\sum_{m=l+1}^{k}(um+v)=f_k-f_l, \tag{B15}$$

$$f_k=k(k+1)\frac{u}{2}+kv,\ f_l=l(l+1)\frac{u}{2}+lv, \tag{B16}$$

and

$$\sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{1}{N-l}f_l\right]=\frac{N-1}{6}N[(N+1)u+3v], \tag{B17}$$

$$\sum_{k=1}^{N-1}\sum_{l=1}^{k}\left[\frac{1}{N-l}f_k\right]=\sum_{k=1}^{N-1}\frac{1}{N-l}\sum_{k=l}^{N-1}f_k$$
$$=\frac{N-1}{36}((11N^2-N-6)u+9(3N-2)v). \tag{B18}$$

Inserting Eqs. (B12), (B13), and (B14) into Eq. (B11) yields an approximation for the linear term $\left[\dfrac{\partial}{\partial\omega}t_1\right]\bigg|_{\omega=0}$. Combining this approximation with Eq. (32) leads finally to the unconditional mean fixation time (Eq. (35)) under weak selection.

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