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Satisfied-defect, unsatisfied-cooperate: An evolutionary dynamics of cooperation led by aspiration

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Evolutionary game theory has been widely used to study the evolution of cooperation in social dilemmas where imitation-led strategy updates are typically assumed. However, results of recent behavioral experiments are not compatible with the predictions based on the imitation dynamics, casting doubts on the assumption of the imitation-led updates and calling for alternative mechanisms of strategy updates. An aspiration-led update is often considered as an alternative to the imitation-led one. While details of update rules can have significant impacts on the evolutionary outcomes and many variations in imitation-led updates are thus studied, however, few variations exist in aspiration-led updates. We introduce an aspiration-led update mechanism ("Satisfied-Defect, Unsatisfied-Cooperate") that is psychologically intuitive and can yield a behavior richer than the conventional aspiration-led update does in Prisoner's Dilemma games. Using analytical and numerical methods, we study and link the stochastic dynamics of it in well-mixed finite populations and the deterministic dynamics of infinite populations.

I. INTRODUCTION

Explaining cooperation among selfish individuals in social dilemmas is an important problem and has attracted much interest across disciplines including physics [1–4]. The Prisoner's Dilemma (PD) captures the problem of cooperation in the simplest and most challenging form [5]. Two individuals can choose between cooperation and defection. If one defects and the other cooperates, the defector gets a higher payoff than the cooperator does. They get a higher payoff if both cooperate than they do if both defect. Even though they would be better off if both cooperate, individual (rational) reasoning leads to defection in (one-shot) PD games. This illustrates a social dilemma due to the tension between the social optimum and individual interests. In an evolutionary setting, the higher mean payoff of defectors implies more reproductive success (in genetic evolution) and more imitation (in cultural evolution). Cooperation is thus expected to perish. However, cooperation is often observed in real-world social dilemmas.

Various mechanisms in the framework of the evolutionary game theory have been proposed to explain this apparent paradox. For the nongenetic evolution of cooperation, it is typically assumed that successful strategies are spread by payoff-dependent imitation or social-learning [1–4]. Payoff-dependent imitation means that an individual first compares its payoff and that of another individual, and then copies the strategy of the other if the

payoff of the latter is higher. One of the main motivations behind the imitation-based strategy update is that evolutionary game dynamics of the nongenetic evolution becomes formally equivalent to that of the genetic one [6]; similar mathematical models can describe both genetic and nongenetic evolution of cooperation. Although it is less applicable to lower animals that lack cognition capabilities required for social learning, the payoff-dependent imitation is considered adequate for humans and much theoretical work has been developed under this assumption [1–4]. However, doubts have been cast on the imitation-based update and alternatives to it have been called for [7–9]. These are partly due to the recent behavioral experiments on PD games, which showed that humans do not compare payoffs when updating their strategies [8, 10, 11]. Indeed, it is often the case that individuals cannot even perceive the payoff of others in many real-world settings [9].

An alternative to imitation-based social learning would be self-learning. For instance, the aspiration-based mechanism of strategy updates has been extensively investigated [12–21]. According to the aspiration-based update, individuals switch their strategy if the payoffs that they aspire are not met. Unlike the imitation-based update, it does not require any knowledge about the payoffs or strategies of others. Hence, it can be also applicable to the nongenetic evolution of cooperation in lower animals lacking cognitive capacities required for payoff-based imitation. Indeed, aspiration-based strategy updates are often observed in studies of both animal and human behavioral ecology [22–28]. While imitation-based evolutionary dynamics yields cooperation to diminish, aspiration-based dynamics yields the emergence and sustainability

of cooperation even in well-mixed infinite populations.

Since the details of the update rules can have significant influences on the emergence and stabilization of cooperation [29], it is well worth seeking alternative update rules led by aspiration. To our knowledge, however, few alternatives exist in aspiration dynamics. We consider the whole space of aspiration-based update rules, which includes the conventional aspiration-based update. We formulate two psychologically intuitive properties that the desirable update rules should obey. Among all the rules, only one satisfies both properties. We analytically and numerically study the deterministic evolutionary dynamics and the stochastic dynamics of the update rule as well as link them.

II. MODEL DEFINITION

We consider the donation game version of PD games with two (pure) strategies of cooperation (C) and defection (D) in well-mixed populations. A payoff matrix of the game is given by

$$
\begin{array}{c}
\quad\quad C \quad\quad D \\
\begin{array}{c} C \\ D \end{array}
\begin{pmatrix} 1-\rho & -\rho \\ 1 & 0 \end{pmatrix}
\end{array}
\tag{1}
$$

where $\rho \in (0,1)$ denotes the cost of cooperation. In a well-mixed population, any pair of individuals play the game with the same probability. In an infinite population, thus, the mean payoffs of types C and D are

$$
\pi_C(x) = x - \rho, \tag{2}
$$
$$
\pi_D(x) = x \tag{3}
$$

where $x \in [0,1]$ denotes the (relative) abundance or frequency of cooperators in the population. In a finite population, the mean payoffs are given by

$$
\pi_C(i) = \frac{i-1}{N-1} - \rho, \tag{4}
$$
$$
\pi_D(i) = \frac{i}{N-1} \tag{5}
$$

where N denotes the population size and i the number of cooperators.

III. ASPIRATION-BASED STRATEGY UPDATE

We consider the aspiration-based strategy updates where the aspiration level is the same for all individuals of a population. The conventional aspiration-led update can be stated as follows; if one's payoff is higher than (or equal to) the aspiration level (i.e. $\pi \geq A$), then keep the current strategy and otherwise ($\pi < A$), switch it to the other strategy [12, 16–21]. We term this update rule 'Satisfied-Stay, Unsatisfied-Shift' (SSUS), which is a special case of the reinforcement learning [30]. This deterministic rule is often relaxed to be stochastic, which reflects perception errors as well as other uncertainties and

drives the probabilistic change of the population composition. To model the stochastic switching of the strategy, the following probability functions based on Fermi functions are often used

$$
q_{D \to C}(\pi_D, A) = \frac{1}{1 + \exp[-\beta(A - \pi_D)]}, \tag{6}
$$
$$
q_{C \to D}(\pi_C, A) = \frac{1}{1 + \exp[-\beta(A - \pi_C)]} \tag{7}
$$

where $q_{D \to C}$ denotes the probability for switching defection to cooperation, $q_{C \to D}$ the probability for cooperation to defection, β the selection intensity, and A the aspiration level [31]. The lower payoff π than aspiration A, the more likely to switch the strategy; the higher payoff π than aspiration A, the less likely to switch the strategy. As $\beta \to \infty$, the deterministic update rule is recovered.

IV. SATISFIED-DEFECT, UNSATISFIED-COOPERATE

A. Space of strategy update rules

In order to derive an update rule, we explore the whole space of (deterministic) update rules led by aspiration with two strategies C and D. We can encode an aspiration-based update rule as a finite state automaton that has two states of C and D with transitions between them being conditioned on whether $\pi \geq A$ or not. The encoding $(\mathcal{S}_{C+}, \mathcal{S}_{C-}, \mathcal{S}_{D+}, \mathcal{S}_{D-})$ specifies the strategy to be taken $\mathcal{S}_{C+}$ and $\mathcal{S}_{D+}$ given $\pi \geq A$ and the current strategy of C and D, respectively. It also specifies the strategy to be taken $\mathcal{S}_{C-}$ and $\mathcal{S}_{D-}$ given $\pi < A$ and the current strategy of C and D, respectively. For instance, SSUS is encoded as (C, D, D, C) (Table I). In total, there are 2^4 finite state automata of this form. We present two properties that a desirable update rule should obey, each of which is psychologically intuitive.

The first property is conditional switching. The strategy to be taken when 'satisfied' (i.e. $\pi \geq A$) should differ from the one when 'unsatisfied' (i.e. $\pi < A$). This property excludes those rules which yield the same strategy regardless of 'satisfied' or not; e.g. the rule of cooperate-no-matter (C, C, C, C). Among the 16 update rules, four rules satisfy the property of the conditional switching, including SSUS (Table II).

The second property is the selfishness or cost minimization while in satisfaction. For the same outcome of 'satisfied' (i.e. $\pi \geq A$), we assume that individuals prefer defection to cooperation since the latter incurs a cost. For a satisfied cooperator ($\pi_C \geq A$), switching to defection makes sense in that the aspiration is still expected to be met after the switching, but without the cost of cooperation since $\pi_D > \pi_C \geq A$. That is to say, one defects when the aspiration is met. There are four update rules which satisfy the cost-minimization property (Table III).

Among the 16 finite state automaton, there is only one rule that meets both of the properties, which is

TABLE I. An encoding scheme of an aspiration-based update rule as a finite state automaton that describes transitions between two states of C and D, conditioned on $\pi \geq A$ or not. SSUS is encoded as (C, D, D, C).

$$\begin{array}{c|cc} & \pi \geq A & \pi < A \\ \hline C & \mathcal{S}_{C+} & \mathcal{S}_{C-} \\ D & \mathcal{S}_{D+} & \mathcal{S}_{D-} \end{array} \Longleftrightarrow (\mathcal{S}_{C+}, \mathcal{S}_{C-}, \mathcal{S}_{D+}, \mathcal{S}_{D-}), \qquad \begin{array}{c|cc} & \pi \geq A & \pi < A \\ \hline C & C & D \\ D & D & C \end{array} \Longleftrightarrow (C, D, D, C)$$

TABLE II. Four update rules that satisfy the conditional switching property.

(C, D, C, D), (C, D, D, C), (D, C, C, D), (D, C, D, C)

TABLE III. Four update rules that satisfy the cost-minimization property.

(D, C, D, D), (D, D, D, C), (D, D, D, D), (D, C, D, C).

(D, C, D, C). We name the (D, C, D, C) rule 'Satisfied-Defect, Unsatisfied-Cooperate' (SDUC). The SDUC rule specifies defection to be taken when the aspiration is met ($\pi \geq A$) and cooperation to be taken when the aspiration is not met ($\pi < A$). The switching probabilities of SDUC are given by

$$q_{D \to C}(\pi_D, A) = \frac{1}{1 + \exp[-\beta(A - \pi_D)]}, \qquad (8)$$

$$q_{C \to D}(\pi_C, A) = \frac{1}{1 + \exp[-\beta(\pi_C - A)]}. \qquad (9)$$

Note that it only differs in $q_{C \to D}$, compared to those of SSUS [Eqs. (6) and (7)]. In the next sections, we analyze the evolutionary dynamics of SDUC in infinite and finite populations as well as compare them with those of SSUS.

V. INFINITE POPULATIONS

For a well-mixed infinite population, the mean-field equation of deterministic evolutionary dynamics is given by

$$\frac{dx}{dt} = (1 - x)q_{D \to C} - x q_{C \to D} \qquad (10)$$

where the first term on the right-hand side captures the inflow of individuals switching to cooperation, and the second one, the outflow of those switching from cooperation to defection. At $dx/dt = 0$, we have an equilibrium frequency x^* of cooperators, which satisfies

$$x^* = \frac{q_{D \to C}}{q_{D \to C} + q_{C \to D}}. \qquad (11)$$

Under weak selection $0 < \beta \ll 1$, we can approximate the equilibrium by

$$x^* \approx \left. \frac{q_{D \to C}}{q_{D \to C} + q_{C \to D}} \right|_{\beta=0} + \frac{\partial}{\partial \beta} \left(\frac{q_{D \to C}}{q_{D \to C} + q_{C \to D}} \right) \bigg|_{\beta=0} \beta. \qquad (12)$$

Prior to SDUC, we start with the analysis of SSUS. Although there already exists an analysis of SSUS in an infinite population, it is limited only to the deterministic update, corresponding to the strong selection $\beta \to \infty$ [21]. Our analytical study is based on a stochastic update or weak selection and we numerically study the strong selection cases as well.

A. x^* of SSUS

Under the SSUS rule, at equilibrium, we get

$$x^* = \frac{1 + \exp[-\beta(A - \pi_C)]}{2 + \exp[-\beta(A - \pi_C)] + \exp[-\beta(A - \pi_D)]}. \qquad (13)$$

Under weak selection $\beta \ll 1$, we get

$$x^* \approx \frac{1}{2} + \frac{1}{8}\beta(\pi_C - \pi_D), \qquad (14)$$

which yields

$$x^* \approx \frac{1}{2} - \frac{1}{8}\beta\rho \qquad (15)$$

which is subject to the constraint $0 \leq x^* \leq 1$. The aspiration level A has no impact on x^* that decreases with β and ρ. The condition for cooperation to be more abundant than defection $x^* > 1/2$ is

$$\rho < 0. \qquad (16)$$

However, the condition cannot be met since $0 < \rho < 1$ for PD games. Thus, cooperation cannot be more abundant than defection under SSUS. Only $x^* < 1/2$ holds. Although our analytical derivation of $x^* < 1/2$ is based on the assumption of weak selection $\beta \ll 1$, it also holds well for strong selection $\beta \gg 1$ (Fig. 1). However, the analytical approximation of x^* [Eq. (15)] works well for weak selection β, but not so for strong selection.

B. x^* of SDUC

Under the SDUC rule, at equilibrium, we have

$$x^* = \frac{1 + \exp[-\beta(\pi_C - A)]}{2 + \exp[-\beta(\pi_C - A)] + \exp[-\beta(A - \pi_D)]}. \qquad (17)$$
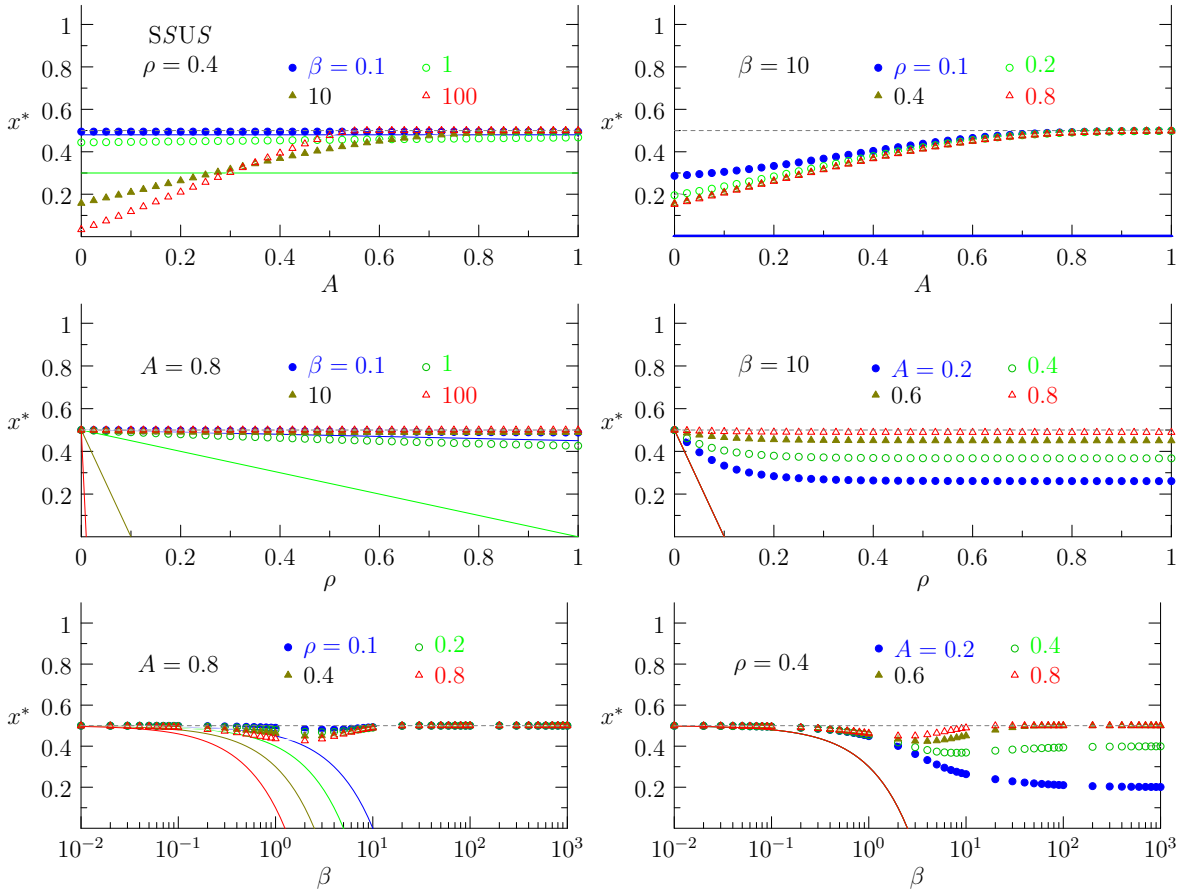
FIG. 1. The equilibrium x^* of SSUS vs. aspiration level A, cost ρ, and selection strength β. The circles and triangles indicate the equilibrium obtained by numerically solving Eq. (13). The solid lines indicates the analytical approximation of x^* by Eq. (15), which works well only for weak selection. The dashed line indicates $x^* = 1/2$.

The weak selection approximation of x^* is given by

$$x^* \approx \frac{1}{2} - \left(\frac{\pi_C + \pi_D - 2A}{8} \right) \beta, \qquad (18)$$

which yields

$$x^* \approx \frac{2 + (A + \rho/2)\beta}{4 + \beta}. \qquad (19)$$

Note that the equilibrium frequency x^* of SDUC [Eq. (19)] behaves in manners qualitatively different from that of SSUS [Eq. (15)]. First, x^* increases with A under SDUC, whereas it does not depend on A at all under SSUS. Second, x^* increases with ρ under SDUC, whereas it decreases under SSUS. Third, as β increases, x^* strictly increases, decreases or is constant since $\partial x^*/\partial \beta = 4\left[A - (1-\rho)/2 \right]/(\beta+4)^2$ under SDUC, whereas it only decreases under SSUS. We get cooperation more abundant $x^* > 1/2$ if the following condition is met

$$A > \frac{1-\rho}{2}, \qquad (20)$$

which is feasible. In other words, cooperation can be more abundant than defection under SDUC. The higher

A or ρ, the easier for cooperation to be more abundant. Although we have $x^* < 1$ for any finite β because of the nonzero switching probabilities $q_{D \to C} > 0$ and $q_{C \to D} > 0$ [Eq. (8) and 9], an almost full cooperation $x^* \approx 1$ is feasible if both of the following conditions are met:

$$A > \frac{2 - \rho}{2}, \qquad (21)$$

$$\beta \geq \frac{4}{(\rho + 2A - 2)}, \qquad (22)$$

which are derived by setting the condition for $x^* \geq 1$ from Eq. (19). Although the conditions are derived under weak selection, they work well even for strong selection (Fig. 2). The higher A, ρ, or β, the easier the almost full cooperation occurs. Note that the analytical approximation of x^* [Eq. (19)] works well even for strong selection $\beta \gg 1$ under SDUC, unlike that of SUSS.

VI. FINITE POPULATIONS

The deterministic evolutionary dynamics led by aspiration assumes an infinite population. For a finite pop-
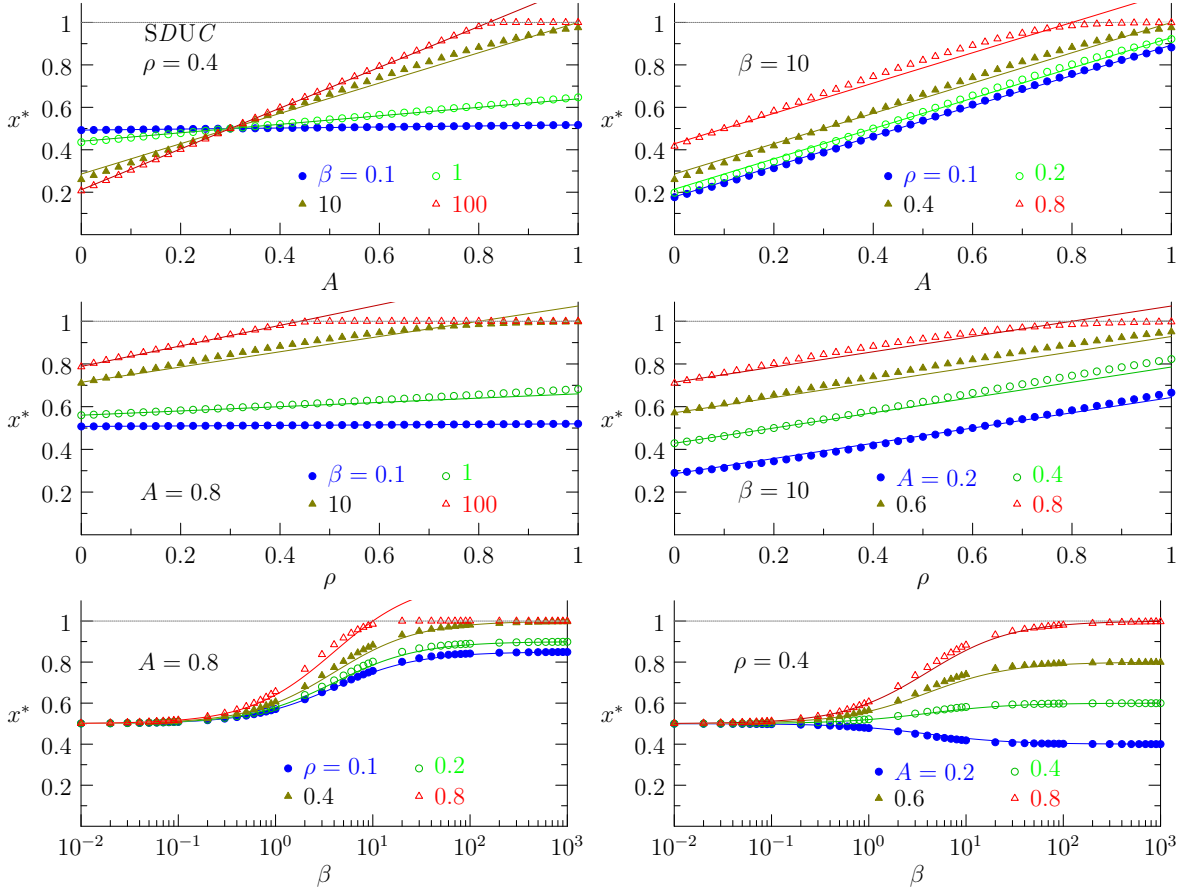
FIG. 2. The equilibrium frequency x^* of SDUC vs. aspiration level A, cost ρ, and selection strength β. The circles and triangles indicate the equilibrium obtained by numerically solving Eq. (17). The solid lines indicates the analytical approximation of the equilibrium by $x^* \approx [2 + (A + \rho/2)\beta] / (4 + \beta)$ [Eq. (19)], which works well even for strong selection $\beta \gg 1$. Where $x^* \approx [2 + (A + \rho/2)\beta] / (4 + \beta) > 1$, it just needs to be capped at $x^* = 1$ since x^* is subject to $0 \leq x^* \leq 1$.

ulation, we have stochastic evolutionary dynamics. We present the stochastic dynamics of SDUC and compare it with that of SSUS. The microprocess at the individual level is modeled as follows: in each time step, an individual is chosen at random, who obtains its payoff in the donation game and switches its strategy with probability $q_{c \to D}$ or $q_{D \to C}$. For a finite population of size N, the state of the population can be specified with the abundance or number of cooperators i. The stochastic dynamics of the finite system can be modeled as a Markov chain of a one-dimensional birth-death process in discrete time. In each time step, the number of cooperators i increases by one with probability T_i^+ (as a defector switches to be a cooperator), decreases by one with probability T_i^- (as a cooperator switches to be a defector), or does not change with probability T_i^0. Only these three events are possible in each time step, i.e., all other transitions have zero probability. The transition probabilities of the Markov chain are given by

$$T_i^+ = \frac{N-i}{N} q_{D \to C}, \qquad (23)$$

$$T_i^- = \frac{i}{N} q_{C \to D}, \qquad (24)$$

$$T_i^0 = 1 - T_i^+ - T_i^-. \qquad (25)$$

Let $(\psi_0, \ldots, \psi_j, \ldots, \psi_N)$ denote the stationary distribution over the abundance or number of cooperators. In general, the stationary distribution of a Markov chain can be obtained as the eigenvector of the transition matrix associated with the largest eigenvalue of 1. For an one-dimensional birth-death process [32–34], the stationary distribution is also given by

$$\psi_j = \begin{cases} \frac{1}{1 + \sum_{k=1}^N \Pi_{i=1}^k T_{i-1}^+/T_i^-} & : j = 0 \\ \frac{\Pi_{i=1}^j T_{i-1}^+/T_i^-}{1 + \sum_{k=1}^N \Pi_{i=1}^k T_{i-1}^+/T_i^-} & : j > 0. \end{cases} \qquad (26)$$

Note that for $j > 0$, we have

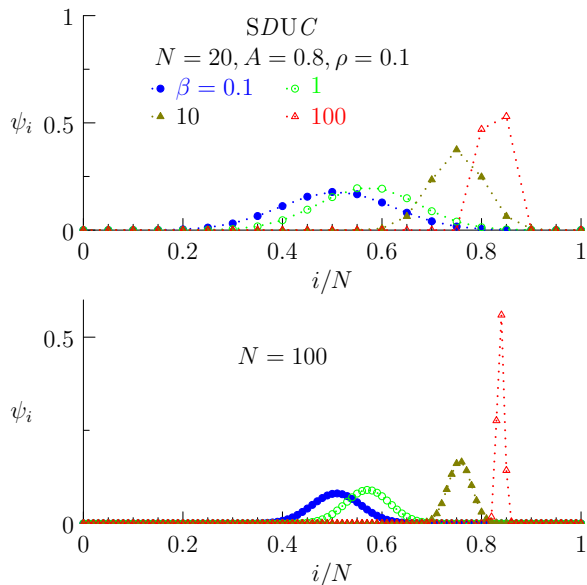$$\psi_j = \psi_0 \Pi_{i=1}^j T_{i-1}^+/T_i^- = \psi_{j-1} T_{j-1}^+/T_j^- \qquad (27)$$

FIG. 3. Stationary distributions ψ_i under SDUC. $A = 0.8, \rho = 0.1$.

(Fig. 3). The mean abundance of cooperation is given by

$$\langle X \rangle = \sum_{j=0}^{N} \frac{j}{N} \psi_j. \tag{28}$$

Under weak selection $0 < \beta \ll 1$, the stationary distribution ψ_j can be approximated (to the first order) by

$$\psi_j \approx \psi_j|_{\beta=0} + \frac{\partial \psi_j}{\partial \beta}\bigg|_{\beta=0} \beta. \tag{29}$$

A. $\langle X \rangle$ of SSUS

Under SSUS, a weak selection condition for cooperation to be more abundant than defection $\langle X \rangle > 1/2$ is given by

$$1 - \rho + (-\rho) > 1 + 0, \tag{30}$$

i.e., the sum of payoff entries for cooperation should be larger than that for defection. For the derivation of Eq. (30), see Ref. [20] where the condition for $\langle X \rangle > 1/2$ was analytically derived, but not $\langle X \rangle$ itself. However, the condition of Eq. (30) is equivalent to $\rho < 0$, that is the same as that of infinite populations [Eq. (16)] and cannot be met. Under SSUS, cooperation cannot be more abundant than defection in finite populations nor infinite populations.
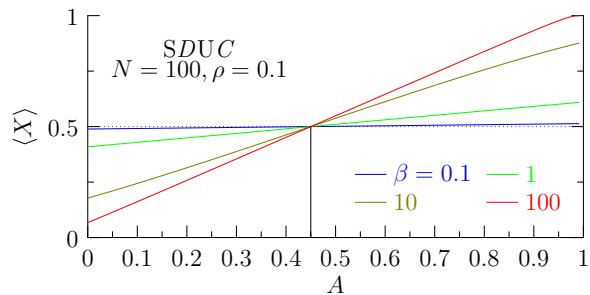

FIG. 4. Mean abundance $\langle X \rangle$ vs. aspiration level A. $\langle X \rangle$ is computed numerically. The horizontal (dotted) line corresponds to $\langle X \rangle = 1/2$ and the vertical line, $A = (1 - \rho)/2 = 0.45$ where $\rho = 0.1$. It clearly demonstrates the validity of Eq. (34) as the condition for $\langle X \rangle > 1/2$, which works well even for strong selection $\beta = 100$.

B. $\langle X \rangle$ of SDUC

Under SDUC, the transition probabilities are given by

$$T_i^+ = \frac{N-i}{N} \frac{1}{1 + e^{-\beta[A-\pi_D(i)]}}, \tag{31}$$

$$T_i^- = \frac{i}{N} \frac{1}{1 + e^{-\beta[\pi_C(i)-A]}}. \tag{32}$$

Under weak selection, we get an analytical approximation of the mean abundance by

$$\langle X \rangle \approx \frac{1}{2} + \frac{1}{8}\left(2A + \rho - 1\right)\beta. \tag{33}$$

For the derivation of Eq. (33), see Appendix A. The condition for cooperation to be more abundant than defection $\langle X \rangle > 1/2$ is then given by

$$A > \frac{1-\rho}{2}. \tag{34}$$

Although the condition [Eq. (34)] is derived under weak selection, it works well for strong selection (Fig. 4). Note that the condition of finite populations [Eq. (34)] is the same as that of infinite populations [Eq. (20)]. Under SDUC, cooperation can be more abundant than defection in both finite and infinite populations under the same condition.

C. Correspondence between stochastic and deterministic dynamics

For infinite populations, the abundance of cooperation is captured by the equilibrium frequency x^* that can be analytically approximated and we straightforwardly derive the condition for $x^* > 1/2$ from it. For finite populations, the abundance of cooperation is captured by the mean $\langle X \rangle$ of the stationary distribution. Although the condition for $\langle X \rangle > 1/2$ was analytically derived, $\langle X \rangle$ itself was not so in the previous work [19, 20]. The lack of

an analytical representation of $\langle X \rangle$ limits further understanding of the aspiration dynamics of finite populations. It also makes it difficult to link the stochastic dynamics of a finite population and the deterministic dynamics of an infinite population [19]. One could consider the latter as a limit case of the former as the population size increases to infinity

In our work, we analytically approximate $\langle X \rangle$ [Eq. (33)], that not only yields the condition for $\langle X \rangle > 1/2$ [Eq. (34)] in a straightforward manner, but also provides further insights on the stochastic dynamics of SDUC in finite populations. According to Eq. (33), for instance, $\langle X \rangle \approx 1/2 + (2A + \rho - 1)\beta/8$ increases with A and ρ. According to Eq. (19), this is qualitatively similar to $x^* \approx [4 + (2A + \rho)\beta]/[2(4 + \beta)]$ in that the latter also increases with A and ρ in infinite populations. However, the analytical approximations Eqs. (33) and (19) of $\langle X \rangle$ and x^* do not match each other whereas numerically computed $\langle X \rangle$ and x^* do so. One way to resolve this incompatibility between the analytical approximations would be to linearize Eq. (19) in β by

$$x^* \approx \frac{1}{2} + \frac{1}{8}\left(2A + \rho - 1\right)\beta. \qquad (35)$$

Then we get

$$\langle X \rangle \approx x^* \approx \frac{1}{2} + \frac{1}{8}\left(2A + \rho - 1\right)\beta \qquad (36)$$

and we analytically establish a quantitative correspondence between the dynamics of finite and infinite populations. However, the correspondence is achieved at a cost of approximation accuracy of Eq. (36), which works well only for weak selection (Fig. 5).

While keeping Eq. (19) that well approximates x^* even for strong selection (Fig. 2), we provide a better alternative in analytically establishing the quantitative correspondence between the dynamics of finite and infinite populations. Rather than the mean $\langle X \rangle$, we capture the abundance of cooperation by the mode of the stationary distribution, i.e., the number (of cooperators) that occurs most frequently where the distribution peaks. Our approximation i^* of the mode satisfies

$$T_{i^*-1}^+/T_{i^*}^- = 1, \qquad (37)$$

which yields

$$\frac{i^*}{N+1} = \frac{1 + e^{-\beta[\pi_C(i^*)-A]}}{2 + e^{-\beta[\pi_C(i^*)-A]} + e^{-\beta[A-\pi_D(i^*-1)]}} \qquad (38)$$

For the derivation of Eq. (37) and 38, see Appendix B. Equation (38) is a finite analog of Eq. (17). Note that i^* is a real number approximation of the (integer) mode $\lfloor i^* \rfloor$, the most frequent number of cooperators in a finite population where $\lfloor i^* \rfloor$ denotes the largest integer that is less than or equal to i^*. In slight abuse of notation, we will write i^* in place of $\lfloor i^* \rfloor$. What we are interested in is the (normalized) mode $\lfloor i^* \rfloor/N$ that is well approximated by i^*/N since $i^*/N - \lfloor i^* \rfloor/N < 1/N$ is negligible for a large N. From Eq. (38) under weak selection $\beta \ll 1$, we get

$$\frac{i^*}{N+1} \approx \frac{1}{2} - \frac{1}{8}\left[\pi_C(i^*) + \pi_D(i^*-1) - 2A\right]\beta, \qquad (39)$$

which yields

$$\frac{i^*}{N+1} \approx \frac{N-1}{4(N-1) + (N+1)\beta}\left[2 + \left(A + \frac{\rho}{2} + \frac{1}{N-1}\right)\beta\right]. \qquad (40)$$

Note that Eqs. (39) and (40) are finite analogs of Eqs. (18) and (19), respectively (Fig. 6). For a large population size N, Eq. (40) is simplified by

$$\frac{i^*}{N} \approx \frac{2 + (A + \rho/2)\beta}{4 + \beta}. \qquad (41)$$

From Eqs. (41) and (19), we have

$$\frac{i^*}{N} \approx x^* \approx \frac{2 + (A + \rho/2)\beta}{4 + \beta}. \qquad (42)$$

Using the analytical approximation of a high accuracy, we are able to link the dynamics of finite populations to that of infinite populations where the mode (of a stationary distribution) of the stochastic dynamics corresponds to the equilibrium frequency of the deterministic dynamics (Fig. 7).

D. Analytical approximations of stationary distributions

The mean and the mode would have a less predictive meaning if the deviation of the stationary distribution is relatively large [35]. To estimate the deviation, under weak selection, we analytically approximate the stationary distribution by

$$\psi_i/\psi_0 \propto \exp\left[-\frac{(i-\mu)^2}{2\sigma^2}\right] \qquad (43)$$

where

$$\mu = \frac{N(N-1)}{4(N-1) + N\beta}\left(2 + \left[A + \frac{\rho}{2} + \frac{1}{2(N-1)}\right]\beta\right), \qquad (44)$$

$$\sigma^2 = \frac{N(N-1)}{4(N-1) + N\beta}. \qquad (45)$$

For the derivation of Eq. (43), see Appendix C. The stationary distribution ψ_i is thus approximated by a normal distribution $\mathcal{N}_{\mu,\sigma}(i)$ of mean μ and standard deviation σ. Note that the mean μ of the normal distribution well approximates the mode i^* of the stationary distribution [Eq. (40)] (Fig. 8). For a large N, Eqs. (44) and (45) are simplified by

$$\frac{\mu}{N} \approx \frac{2 + (A + \rho/2\beta)}{4 + \beta}, \qquad (46)$$

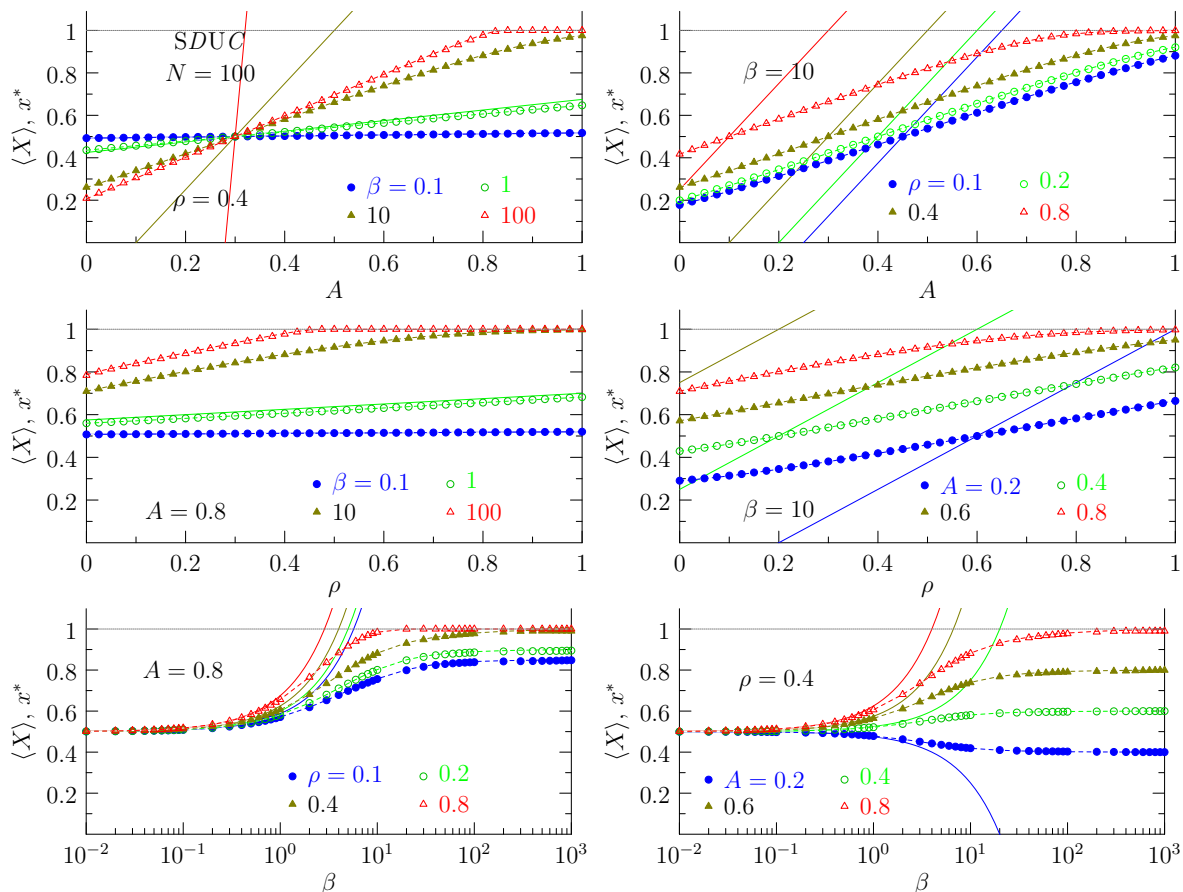$$\frac{\sigma}{N} \approx \frac{1}{\sqrt{N(4+\beta)}}. \qquad (47)$$

FIG. 5. Mean abundance $\langle X \rangle$ of SDUC vs. aspiration level A, cost ρ, and selection strength β. The population size is $N = 100$. The circles and triangles indicate $\langle X \rangle$ numerically obtained. The dashed curves represents the equilibrium frequency x^* in an infinite population, which is obtained by numerically solving Eq. (17) as in Fig. 2. $\langle X \rangle$ and x^* numerically well match each other. The solid curves represent the analytical approximations by Eq. (36), which work well only for weak selection β.
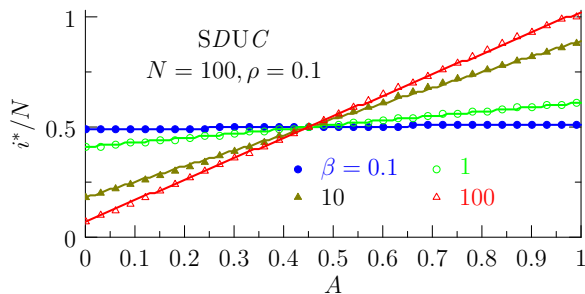

FIG. 6. Mode i^*/N of SDUC vs. aspiration level A. The circles and triangles denote the mode numerically obtained by locating the peak of the discrete distribution ψ_i. The solid curves represent the analytical approximation of the mode by Eq. (40). The analytical approximation well fits the ground truth even for strong selection $\beta = 100$.

Eq. (46) of μ/N well matches Eq. (42) of i^*/N and x^*. Because the standard deviation is relatively small for a large N, the mean and the mode of the distribution have

a predictive meaning. As the population size $N \to \infty$, especially, the (normalized) standard deviation σ/N vanishes with $1/\sqrt{N}$ and the distribution thus converges to a delta function that peaks at x^* where stochastic fluctuations are suppressed (Figs. 9 and 10). In contrast to the previous work [19, 20], we analytically show the link between the stochastic aspiration dynamics of a finite population and the deterministic dynamics of an infinite population, the latter of which is taken as a limit case of the former as the population size increases to infinity.

VII. SUMMARY AND DISCUSSION

Imitation-based strategy updates have been widely used to study the evolution of cooperation in social dilemmas. However, the results of the recent behavioral experiments question the applicability of the imitation dynamics and it is thus well worth considering alternatives such as aspiration dynamics. In PD games, conventional aspiration dynamics yields the coexistence of cooperation and defection at equilibrium in an infinite population and
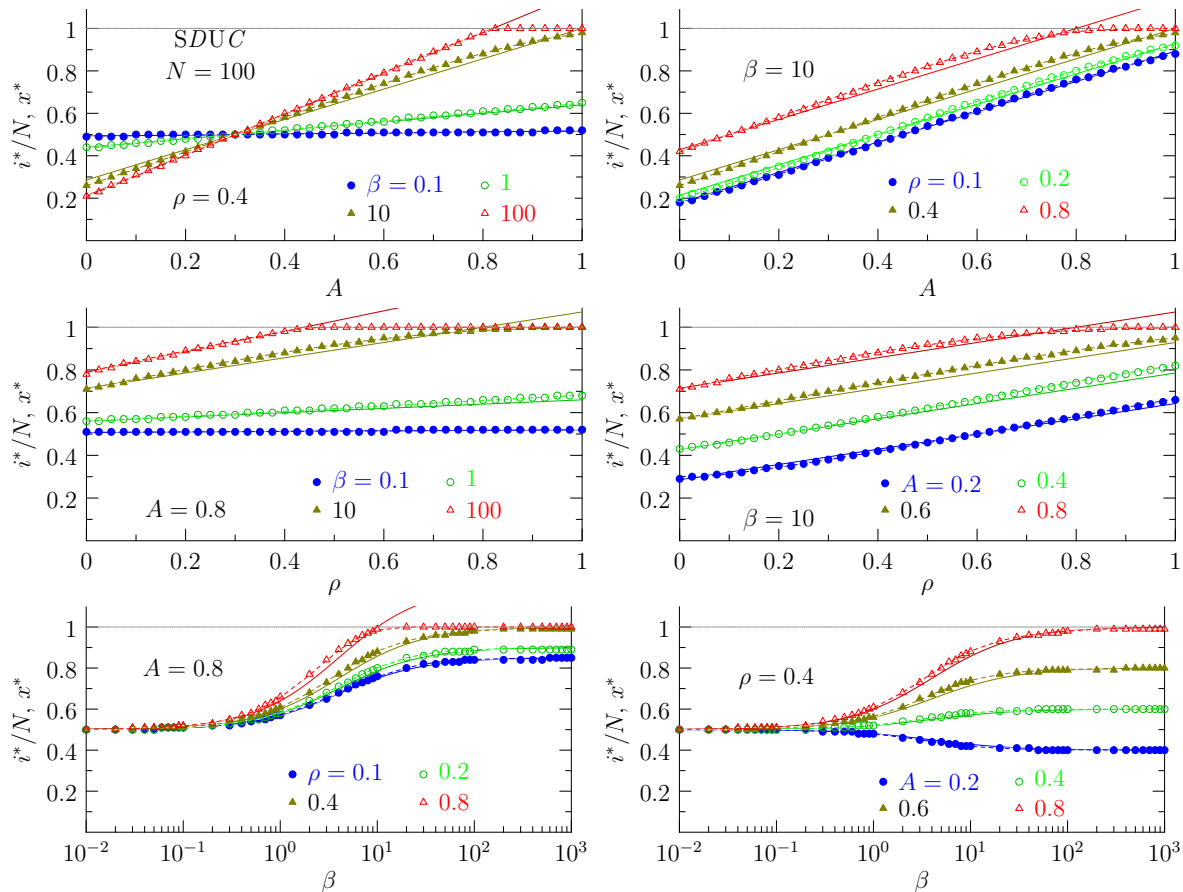
FIG. 7. Mode i^*/N of SDUC vs. aspiration level A, cost ρ and selection strength β. The population size is $N = 100$. The circles and triangles indicate i^*/N numerically obtained. The dashed curves represent the equilibrium frequency x^* in an infinite population, which is obtained by numerically solving Eq. (17) as in Fig. 2. i^*/N and x^* well matches each other. The solid curves represent the analytical approximations by Eq. (42), which work well even for strong selection β.

a nontrivial stationary distribution in a finite population. In contrast, imitation dynamics yields the extinction of cooperation in a well-mixed infinite population and fixation in a finite population.

The details of the update rules can have significant impacts on the evolutionary outcomes and numerous variations in imitation dynamics have been studied such as birth-death, death-birth, Moran process, pairwise comparison, imitate-the-best, etc. To our knowledge, however, few variations exist in aspiration dynamics. There are additional reasons to seek alternative mechanisms of strategy updates in aspiration dynamics. Although aspiration-led strategy updates are often observed in studies of both animal and human behavioral ecology, not all of them comply with the conventional aspiration-led update by SSUS. Being conditioned on the current strategy as well as the payoff-aspiration difference, SSUS yields a different strategy depending on the current strategy. When the aspiration level is met, for instance, some individuals (continue to) cooperate while others defect according to SSUS. In animal behavior, however, a strategy update is often conditioned on only the payoff-aspiration difference, but not the current strategy. In

the variance-sensitive foraging behavior of animals, for example, whether animals choose a variance-averse strategy or a variance-prone strategy is entirely conditioned on whether an aspiration level is met or not, but not on the current strategy [36, 37]. SSUS is a kind of reinforcement learning that assumes humans to do less or abandon the strategy diminishing in value and switch to the other strategy potentially more rewarding. However, humans sometimes show an opposing tendency, trying harder at what they have been doing rather than less [38–40]. In the context of aspiration-led strategy updates, this implies that individuals do not necessarily switch the current strategy even if the aspiration is not met, contrary to SSUS.

With these motivations behind, we search the whole space of strategy update rules led by aspiration to derive a rule that meets the desirable properties. Previously, a space of conditional cooperative strategies was searched to derive desirable strategies in imitation dynamics [41]. Rather than a space of strategies in imitation dynamics, we search a space of strategy update mechanisms in aspiration dynamics and introduce SDUC as an alternative to SSUS. Depending on the payoff-aspiration dif-
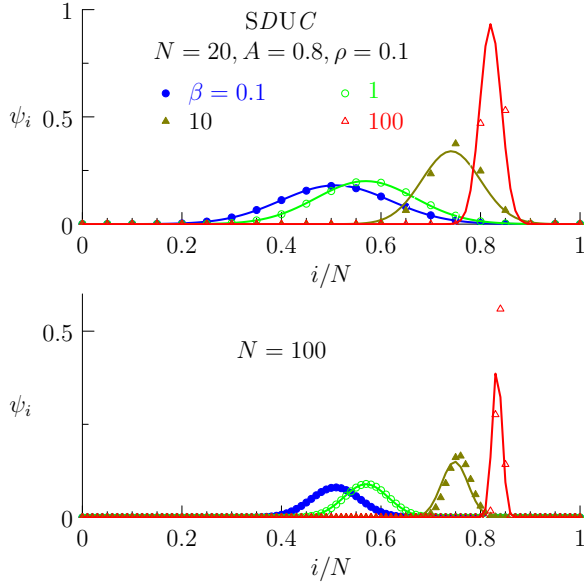
FIG. 8. The stationary distributions ψ_i are well approximated by the normal distributions $\mathcal{N}_{\mu,\sigma}(i)$. The circles and triangles indicate ψ_i that is numerically obtained. The solid curves indicate the normal distributions $\mathcal{N}_{\mu,\sigma}(i)$.
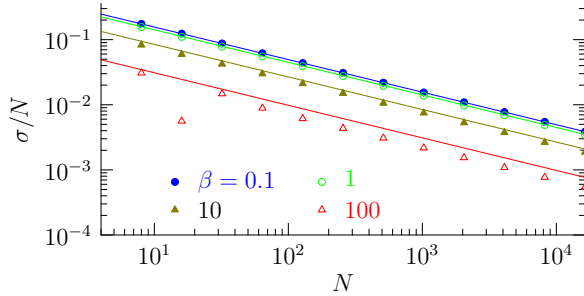

FIG. 9. Normalized standard deviation σ/N vs. population size N. The solid curves denote analytical approximation of the deviation [Eq. (45)]. The circles and the triangles denote the deviation numerically computed. The deviation decreases as the population size increases.
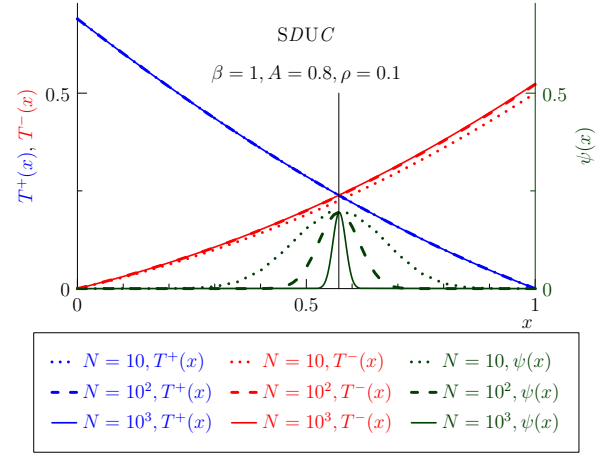

FIG. 10. The transition probabilities and the stationary distribution over $x = i/N$ where $T^+(x) = T_i^+, T^-(x) = T_i^-$ and $\psi(x) = \psi_i$. The vertical line indicates the location of the equilibrium x^* of the deterministic dynamics, which well matches the mode i^*/N of the stationary distributions as well as $x = x^*$ such that $T^+(x^*) = T^-(x^*)$. For visual clarity, the graphs of distributions $\psi(x)$ are scaled such that each of them has the same height at the mode.

ference, SDUC specifies which strategy to "take", while SSUS specifies whether to "switch" the current strategy. SDUC seems psychologically intuitive in that individuals opt for the costly pro-social action of cooperation only when they are in need and opt against it otherwise.

For an infinite population, we get an analytical approximation of the abundance of cooperation at equilibrium for SSUS and SDUC, respectively. From the equilibrium abundance, we can straightforwardly derive the condition that yields more abundant cooperation than defection. SDUC is simpler than SSUS in that the strategy update of SDUC is conditioned on the payoff-aspiration difference but not on the current strategy, whereas SSUS is conditioned on both. However, SDUC yields more variety in the evolutionary outcomes of PD games than

SSUC does, the latter of which only yields cooperation to be less abundant. SDUC can yield cooperation more abundant than defection and vice versa. SDUC can even lead to almost full cooperation.

For a finite population, the previous works analytically derived the condition for more abundant cooperation, but not the abundance of cooperation itself [19, 20]. The lack of the analytical representation of the abundance limits further understanding of aspiration dynamics of finite populations and causes difficulty in linking the dynamics between finite and infinite populations. In our work, we derive the analytical representations of the abundance of cooperation as well as the stationary distributions in finite populations for SDUS. From the analytical representations, we straightforwardly derive the condition for more abundant cooperation and link the stochastic dynamics of finite populations to the deterministic dynamics of infinite populations, the latter of which is considered as a limit case of the former as the population size increases to infinity.

SSUS and SDUC also yield differences in terms of the relation between cooperation and cost. The abundance of cooperation under SSUS decreases with the cost of cooperation, which also corroborates the outcome of imitation-led evolutionary dynamics [42, 43]. On the other hand, the abundance of cooperation under SDUC increases with the cost, which appears somewhat counterintuitive. When more realistic ecological factors are taken into consideration, however, similar positive correlations between cooperation and cost occur due to the spatial self-organization in imitation-led eco-evolutionary dynamics [44–46]. While the eco-evolutionary dynamics requires additional complexities such as a structured population, a nonconstant population size and movements

of individuals, SDUC yields the positive correlation in a minimal model that assumes only a well-mixed population of a constant size and does not require movements of individuals.

We hope that the introduction of SDUC paves a way of searching for further mechanisms of aspiration-led strategy updates. For instance, the space of possible update rules could be expanded by taking the cost of cooperation into account in addition to the aspiration level.

Appendix A: Derivation of Eq. (33)

We seek the condition that yields cooperation to be more abundant than defection $\langle X \rangle > 1/2$ under weak selection $0 < \beta \ll 1$. According to Eqs. (28) and (29), the mean abundance $\langle X \rangle$ can be approximated by

$$\langle X \rangle = \sum_{j=0}^{N} \frac{j}{N} \psi_j \approx \sum_{j=0}^{N} \frac{j}{N} \left(\psi_j \big|_{\beta=0} + \frac{\partial \psi_j}{\partial \beta} \bigg|_{\beta=0} \beta \right). \tag{A1}$$

The stationary distribution ψ_j is given by Eq. (26):

$$\psi_j = \begin{cases} \frac{1}{1 + \sum_{k=1}^{N} \Pi_{i=1}^{k} T_{i-1}^+/T_i^-} & : j = 0 \\ \frac{\Pi_{i=1}^{j} T_{i-1}^+/T_i^-}{1 + \sum_{k=1}^{N} \Pi_{i=1}^{k} T_{i-1}^+/T_i^-} & : j > 0. \end{cases}$$

We consider only ψ_j for $j > 0$ since $\frac{j}{N}\psi_j$ for $j = 0$ has effectively no contribution to the mean abundance of cooperation $\langle X \rangle = \sum_{j=0}^{N} \frac{j}{N}\psi_j = \sum_{j=1}^{N} \frac{j}{N}\psi_j$.

Let us denote the distribution by $\psi_j = \psi_{\mathcal{N},j}/\psi_{\mathcal{D}}$ where the nominator $\psi_{\mathcal{N},j}$ and the denominator $\psi_{\mathcal{D}}$ are given by

$$\psi_{\mathcal{N},j} = \Pi_{i=1}^{j} T_{i-1}^+/T_i^-, \tag{A2}$$

$$\psi_{\mathcal{D}} = 1 + \sum_{k=1}^{N} \psi_{\mathcal{N},k}. \tag{A3}$$

To derive the condition for $\langle X \rangle > 1/2$ under weak selection, we need to compute

$$\psi_j \big|_{\beta=0} = \frac{\psi_{\mathcal{N},j}}{\psi_{\mathcal{D}}} \bigg|_{\beta=0}, \tag{A4}$$

$$\frac{\partial \psi_j}{\partial \beta} \bigg|_{\beta=0} = \frac{\psi'_{\mathcal{N},j}\psi_{\mathcal{D}} - \psi_{\mathcal{N},j}\psi'_D}{(\psi_{\mathcal{D}})^2} \bigg|_{\beta=0}, \tag{A5}$$

which are to be inserted into Eq. (A1).

From Eqs. (31) and (32),

$$T_i^+ = \frac{N-i}{N} \frac{1}{1 + e^{-\beta[A-\pi_D(i)]}},$$
$$T_i^- = \frac{i}{N} \frac{1}{1 + e^{-\beta[\pi_C(i)-A]}}.$$

We then have

$$T_i^+ \big|_{\beta=0} = \frac{N-i}{2N}, \tag{A6}$$

$$T_i^- \big|_{\beta=0} = \frac{i}{2N}, \tag{A7}$$

$$(T_i^+)' \big|_{\beta=0} = \frac{N-i}{4N}[A - \pi_D(i)], \tag{A8}$$

$$(T_i^-)' \big|_{\beta=0} = \frac{i}{4N}[\pi_C(i) - A], \tag{A9}$$

where $(T_i^+)' = \partial T_i^+/\partial\beta$ and $(T_i^-)' = \partial T_i^-/\partial\beta$. Inserting Eqs. (A6) and (A7) into Eqs. (A2) and (A3), we get

$$\psi_{\mathcal{N},j} \big|_{\beta=0} = C_N^j, \tag{A10}$$

$$\psi_{\mathcal{D}} \big|_{\beta=0} = 2^N, \tag{A11}$$

where $C_N^j = N!/(j!(N-j)!)$ is a binomial coefficient. We get

$$\psi'_{\mathcal{N},j} \big|_{\beta=0}$$
$$= \sum_{i=1}^{j} \left[\frac{(T_{i-1}^+)' T_i^- - T_{i-1}^+ (T_i^-)'}{(T_i^-)^2} \Pi_{k=1,k\neq i}^{j} \frac{T_{k-1}^+}{T_k^-} \right]\bigg|_{\beta=0}, \tag{A12}$$

$$\psi'_{\mathcal{D}} \big|_{\beta=0} = \sum_{j=1}^{N} \psi'_{\mathcal{N},j} \big|_{\beta=0}. \tag{A13}$$

From Eq. (A6) to A9, we get

$$\frac{(T_{i-1}^+)' T_i^- - T_{i-1}^+ (T_i^-)'}{(T_i^-)^2} \bigg|_{\beta=0}$$
$$= \frac{N-(i-1)}{2i}[2A - \pi_C(i) - \pi_D(i-1)], \tag{A14}$$

$$\Pi_{k=1,k\neq i}^{j} \frac{T_{k-1}^+}{T_k^-} \bigg|_{\beta=0} = \frac{i}{N-(i-1)} C_N^j. \tag{A15}$$

Inserting Eqs. (A14) and (A15) into Eq. (A12), we get

$$\psi'_{\mathcal{N},j} \big|_{\beta=0} = \frac{C_N^j}{2} \sum_{i=1}^{j} [2A - \pi_C(i) - \pi_D(i-1)], \tag{A16}$$

$$\psi'_{\mathcal{D}} \big|_{\beta=0} = \sum_{j=1}^{N} \frac{C_N^j}{2} \sum_{i=1}^{j} [2A - \pi_C(i) - \pi_D(i-1)]. \tag{A17}$$

Inserting Eqs. (A10), (A11), (A16), and (A17) into Eqs. (A4) and (A5), we get

$$\psi_j \big|_{\beta=0} = \frac{C_N^j}{2^N}, \tag{A18}$$

$$\frac{\partial \psi_j}{\partial \beta} \bigg|_{\beta=0} = \frac{C_N^j}{2^{2N+1}} \left\{ A2^{N+1}j - 2^N \sum_{i=1}^{j} [\pi_C(i) + \pi_D(i-1)] \right.$$
$$\left. - AN2^N + \sum_{k=1}^{N} C_N^k \sum_{i=1}^{k} [\pi_C(i) + \pi_D(i-1)] \right\} \tag{A19}$$

where $\pi_C(i) + \pi_D(i-1) = 2(i-1)/(N-1) - \rho$ according to Eqs. (4) and (5).

Using

$$\sum_{j=1}^{N} j^3 C_N^j = N^2(N+3)2^{N-3}, \tag{A20}$$

$$\sum_{j=1}^{N} j^2 C_N^j = N(N+1)2^{N-2}, \tag{A21}$$

$$\sum_{j=1}^{N} j C_N^j = N2^{N-1}, \tag{A22}$$

we get

$$\sum_{j=1}^{N} \frac{j}{N} \psi_j \big|_{\beta=0} = \frac{1}{2}, \tag{A23}$$

$$\sum_{j=1}^{N} \frac{j}{N} \frac{\partial \psi_j}{\partial \beta} \Big|_{\beta=0} = \frac{1}{8} \left(2A + \rho - 1 \right). \tag{A24}$$

Then we get

$$\langle X \rangle \approx \sum_{j=1}^{N} \frac{j}{N} \psi_j \big|_{\beta=0} + \sum_{j=1}^{N} \frac{j}{N} \frac{\partial \psi_j}{\partial \beta} \Big|_{\beta=0}$$
$$= \frac{1}{2} + \frac{1}{8} \left(2A + \rho - 1 \right) \beta. \tag{33}$$

Appendix B: Derivation of Eqs. (37) and (38)

From Eqs. (31) and (32), we have

$$T_{i-1}^+/T_i^- = \frac{N-i+1}{i} \frac{1 + e^{-\beta[\pi_C(i)-A]}}{1 + e^{-\beta[A-\pi_D(i-1)]}}. \tag{B1}$$

Since $T_0^+/T_1^- > 1$, $T_{N-1}^+/T_N^- < 1$, and $T_{i^*-1}^+/T_{i^*}^-$ strictly decreases with real numbers $i^* \in (0, N) \subset \mathbb{R}$,

there is a single real number i^* that satisfies

$$T_{i^*-1}^+/T_{i^*}^- = 1, \tag{37}$$

which yields

$$\frac{i^*}{N+1} = \frac{1 + e^{-\beta[\pi_C(i^*)-A]}}{2 + e^{-\beta[\pi_C(i^*)-A]} + e^{-\beta[A-\pi_D(i^*-1)]}}. \tag{38}$$

Note that i^* is a real number approximation of the mode that is an integer, the most frequent number of cooperators. For integers $i \in [0, N] \subset \mathbb{Z}$, T_{i-1}^+/T_i^- strictly decreases with i. Then we have $T_{i-1}^+/T_i^- > 1$ for $i < \lfloor i^* \rfloor$, $T_{i-1}^+/T_i^- \geq 1$ for $i = \lfloor i^* \rfloor$ and $T_{i-1}^+/T_i^- < 1$ for $i > \lfloor i^* \rfloor$ where $\lfloor i^* \rfloor$ denotes the largest integer that is less than or equal to i^*. Since $\psi_i = \psi_{i-1} T_{i-1}^+/T_i^-$, the discrete distribution ψ_i picks at $i = \lfloor i^* \rfloor$ that is the (integer) mode of the distribution (Fig. 10).

Appendix C: Derivation of Eq. (43)

Under weak selection $\beta \ll 1$, we have

$$\frac{T_{j-1}^+}{T_j^-}$$
$$\approx \frac{N-j+1}{j} \left(1 - \frac{\rho\beta}{2} \right) \exp\left[-\beta \left(\frac{j-1}{N-1} - \rho - A \right) \right]. \tag{C1}$$

Inserting Eq. (C1) into Eq. (27) as well as using $\left(1 - \frac{\rho}{2}\beta\right)^k \approx e^{-k\frac{\rho}{2}\beta}$ and $\frac{N!}{k!(N-k)!}p^k(1-p)^{N-k} \approx \frac{1}{\sqrt{2\pi Np(1-p)}} \exp\left[-\frac{(k-Np)^2}{2Np(1-p)}\right]$ [47], we get

$$\psi_i/\psi_0 \propto \exp\left[-\frac{(i-\mu)^2}{2\sigma^2}\right] \tag{43}$$

where

$$\mu = \frac{N(N-1)}{4(N-1)+N\beta} \left(2 + \left[A + \frac{\rho}{2} + \frac{1}{2(N-1)} \right] \beta \right), \tag{44}$$

$$\sigma^2 = \frac{N(N-1)}{4(N-1)+N\beta}. \tag{45}$$

[1] F. C. Santos and J. M. Pacheco, Physical Review Letters **95**, 098104 (2005).

[2] G. Szabó, J. Vukov, and A. Szolnoki, Physical Review E **72**, 047107 (2005).

[3] H. S. Sugiarto, J. S. Lansing, N. N. Chung, C. H. Lai, S. A. Cheong, and L. Y. Chew, Physical Review Letters **118**, 208301 (2017).

[4] V. Stojkoski, Z. Utkovski, L. Basnarkov, and L. Kocarev, Physical Review E **97**, 052305 (2018).

[5] M. van Veelen, J. García, D. G. Rand, and M. A. Nowak, Proceedings of the National Academy of Sciences **109**, 9929 (2012).

[6] A. Traulsen, D. Semmann, R. D. Sommerfeld, H.-J. Krambeck, and M. Milinski, Proceedings of the National Academy of Sciences **107**, 2962 (2010).

[7] D. Vilone, J. J. Ramasco, A. Sánchez, and M. S. Miguel, Physical Review E **90**, 022810 (2014).

[8] J. Grujić, C. Gracia-Lázaro, M. Milinski, D. Semmann, A. Traulsen, J. Cuesta, Y. Moreno, and A. Sánchez, Scientific Reports **4**, 4615 EP (2014).

[9] G. Cimini and A. Sánchez, Journal of The Royal Society Interface **11** (2014).

[10] C. Gracia-Lázaro, A. Ferrer, G. Ruiz, A. Tarancón, J. Cuesta, A. Sánchez, and Y. Moreno, Proceedings of the National Academy of Sciences 109, 12922 (2012).

[11] G. Cimini and A. Sanchez, Journal of Artificial Societies and Social Simulation 18, 22 (2015).

[12] M. A. Amaral, L. Wardil, M. Perc, and J. K. L. da Silva, Physical Review E 94, 032317 (2016).

[13] X. Liu, M. He, Y. Kang, and Q. Pan, Physical Review E 94, 012124 (2016).

[14] Z.-X. Wu and Z. Rong, Physical Review E 90, 062102 (2014).

[15] T. Płatkowski and P. Bujnowski, Physical Review E 79, 036103 (2009).

[16] X. Chen and L. Wang, Physical Review E 77, 017103 (2008).

[17] G. Szabó and G. Fáth, Physics Reports 446, 97 (2007).

[18] C. P. Roca and D. Helbing, Proceedings of the National Academy of Sciences 108, 11370 (2011).

[19] J. Du, B. Wu, P. M. Altrock, and L. Wang, Journal of The Royal Society Interface 11 (2014).

[20] J. Du, B. Wu, and L. Wang, Scientific Reports 5, 8014 EP (2015).

[21] M. Posch, A. Pichler, and K. Sigmund, Proceedings of the Royal Society of London. Series B: Biological Sciences 266, 1427 (1999).

[22] Y. van Bergen, I. Coolen, and K. N. Laland, Proceedings of the Royal Society of London. Series B: Biological Sciences 271, 957 (2004).

[23] B. G. Galef and E. E. Whiskin, Animal Behaviour 75, 2035 (2008).

[24] C. Grüter, T. J. Czaczkes, and F. L. W. Ratnieks, Behavioral Ecology and Sociobiology 65, 141 (2011).

[25] L. L. Lopes and G. C. Oden, Journal of Mathematical Psychology 43, 286 (1999).

[26] L. L. Thompson, E. A. Mannix, and M. H. Bazerman, Journal of Personality and Social Psychology 54, 86 (1988).

[27] S. Siegel, Psychological Review 64, 253 (1957).

[28] W. Clay Hamner and D. L. Harnett, Journal of Experimental Social Psychology 11, 329 (1975).

[29] G. Szabó, A. Szolnoki, and J. Vukov, EPL 87, 18007 (2009).

[30] T. Płatkowski, Applied Mathematics and Computation 251, 46 (2015).

[31] C. Hauert and G. Szabó, American Journal of Physics, American Journal of Physics 73, 405 (2005).

[32] N. G. van Kampen, Stochastic processes in physics and chemistry, 3rd ed. (Elsevier, Amsterdam, 2007).

[33] C. W. Gardiner, Handbook of Stochastic Methods for Physics, Chemistry, and the Natural Sciences, 3rd ed. (Springer, Berlin, 2004).

[34] R. Mahnke, J. Kaupuzs, and I. Lubashevsky, Physics of Stochastic Processes: How Randomness Acts in Time (WILEY-VCH, Weinheim, 2009).

[35] A. Traulsen, J. M. Pacheco, and M. A. Nowak, Journal of theoretical biology 246, 522 (2007).

[36] T. Caraco, S. Martindale, and T. S. Whittam, Animal Behaviour 28, 820 (1980).

[37] I. S. Lim, P. Wittek, and J. Parkinson, Animal Behaviour 110, 69 (2015).

[38] P. M. Rabbitt, Journal of Experimental Psychology 71, 264 (1966).

[39] D. Laming, Acta Psychologica 43, 199 (1979).

[40] G. Gratton, M. G. H. Coles, and E. Donchin, Journal of Experimental Psychology: General 121, 480 (1992).

[41] C. Hilbe, L. A. Martinez-Vaquero, K. Chatterjee, and M. A. Nowak, Proceedings of the National Academy of Sciences 114, 4715 (2017).

[42] H. Ohtsuki, C. Hauert, E. Lieberman, and M. A. Nowak, Nature 441, 502 (2006).

[43] M. van Baalen and D. A. Rand, Journal of Theoretical Biology 193, 631 (1998).

[44] A. Szolnoki, A. Antonioni, M. Tomassini, and M. Perc, EPL (Europhysics Letters) 105, 48001 (2014).

[45] E. S. Colizzi and P. Hogeweg, BMC Evolutionary Biology 16, 31 (2016).

[46] R. M. Paul E. Smaldino, Jeffrey C. Schank, The American Naturalist 181, 451 (2013).

[47] M. L. Boas, Mathematical Methods in the Physical Sciences, 3rd ed. (John Wiley & Sons, Hoboken, 2005).