

Fixation of competing strategies when interacting agents differ in the time scale of strategy updatingJianlei Zhang,^{1,2,3} Franz J. Weissing,² and Ming Cao³¹*Department of Automation, College of Computer and Control Engineering, Nankai University, People's Republic of China*²*Theoretical Biology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, The Netherlands*³*Network Analysis and Control Group, Institute for Industrial Engineering, University of Groningen, The Netherlands*

(Received 10 May 2016; revised manuscript received 2 August 2016; published 19 September 2016)

A commonly used assumption in evolutionary game theory is that natural selection acts on individuals in the same time scale; e.g., players use the same frequency to update their strategies. Variation in learning rates within populations suggests that evolutionary game theory may not necessarily be restricted to uniform time scales associated with the game interaction and strategy adaptation evolution. In this study, we remove this restricting assumption by dividing the population into fast and slow groups according to the players' strategy updating frequencies and investigate how different strategy compositions of one group influence the evolutionary outcome of the other's fixation probabilities of strategies within its own group. Analytical analysis and numerical calculations are performed to study the evolutionary dynamics of strategies in typical classes of two-player games (prisoner's dilemma game, snowdrift game, and stag-hunt game). The introduction of the heterogeneity in strategy-update time scales leads to substantial changes in the evolution dynamics of strategies. We provide an approximation formula for the fixation probability of mutant types in finite populations and study the outcome of strategy evolution under the weak selection. We find that although heterogeneity in time scales makes the collective evolutionary dynamics more complicated, the possible long-run evolutionary outcome can be effectively predicted under technical assumptions when knowing the population composition and payoff parameters.

DOI: [10.1103/PhysRevE.94.032407](https://doi.org/10.1103/PhysRevE.94.032407)**I. INTRODUCTION**

How cooperation among nonrelatives can persist in the face of cheating remains a fundamental, profound, and broad-ranging unsolved question in evolutionary biology [1–3]. Evolutionary game theory is the mathematical framework that has provided the deepest insight into this issue [4–6]. Several approaches or frameworks have been proposed in the analysis of strategy evolution and a popular one is the integration of the microscopic patterns of interactions among individuals into the evolutionary setting [7,8]. Furthermore, coevolution of interaction patterns and cooperative behavior has also been identified as a key factor that may enhance or hinder altruism [9–11]. In spite of exciting progresses that have been reported in the past, there are still situations of great practical relevance that remain less explored, and one of them is the role played by time scales when individuals interact and update their strategies [12,13].

Time scales may be associated to different temporal dynamics in evolutionary games, and is a key component in the evolution dynamics. In the general gaming study, there are two time scales in the game dynamics: one is interaction time scale determining how frequently the individuals interact with game partners, and the other is strategy-selection time scale that signifies how frequently they renovate their strategies [14–19]. Many evolutionary game studies make the additional assumption that selection occurs much more slowly than the interaction between individuals. However, this may not always be the case. For instance, experimental studies show that the time scale of selection is much closer to the time scale of interaction in cultural evolution or social learning. Notwithstanding this, the pace at which selection acts on the population is crucial for the appearance and stability of cooperation. How to separate the selection action from the game interaction thus certainly deserves needful attention.

Besides, the majority of the literature does not distinguish the two scales that much and tends to discuss them at the same time by assuming that each round of interaction is always followed by a round of updating, in which individuals can change their current strategies according to different rules.

The time scales associated with game interaction and strategy updating of individuals may be subject to more deliberate rules, with a view to the personal preferences [20–22]. For instance, conservative players prefer the slow strategy adaptations, since they perceive that frequent strategy updating may bring unknown or costly hazard. In contrast, risk-seeking agents are inclined toward seeking new profitable strategies frequently, irrespective of the possible failure in boosting profits. Thus, the role of behavioral preferences in gaming populations should not be disregarded, especially when the cooperative behaviors and dilemma are common phenomena in social systems. In this sense, a deep understanding of it is therefore demanding. Motivated by this fact, we allow individuals to retain heterogeneous time scales associated with game interaction and strategy updating. Our objective here is to understand better what aspects of individual heterogeneity in time scales can influence the strategy evolution outcomes in the played evolutionary games. In short, we aim to elaborate on the influence of expanding the homogeneity of time to binary choices of fast-updating and slow-updating, among pure-strategy agents on cooperation evolution. As mentioned, several simulation works on this topic have been established especially in spatial populations; however, the lack of theoretical results motivates us to make a complementary contribution in studying cooperative problems mathematically.

From the perspective of individual intelligence, including the fact that individuals may have different capabilities to update their strategy frequently [23–27], we focus on the heterogeneity in how often an individual updates her strategy after repeatedly interacting with the peers. Our goal is thus

to understand better how updating frequency may affect strategic competition and thereby promote or inhibit altruistic behaviors.

As a first cut, we assume the overall population can be divided into two groups, and the individuals in one update faster than those in the other. When the updating dynamics of the fast and slow groups can be completely decoupled, we give closed-form approximations for the fixation probabilities of strategies in their groups and such predictions are validated by simulations for the prisoner’s dilemma, snowdrift, and stag-hunt games. Further analyses are carried out for populations under weak selection as well. All the theoretical computation and simulation results reveal that heterogeneity in strategy-update time scales indeed leads to much richer evolutionary outcomes. The different strategy composition of one group always influences the evolution of the other group; the extent to which the influence is exerted depends on the game payoffs and the relative sizes of the groups.

The rest of the paper is organized as follows. Section II introduces the basic game model and analyzes the evolutionary dynamics of the strategies under different updating time scales. Section III discusses the implications of the analytical results for the three typical types of two-player games. Section IV investigates the model under weak selection. Finally, in Sec. V we make concluding remarks.

II. EVOLUTIONARY GAME DYNAMICS FOR INDIVIDUALS WITH DIFFERENT STRATEGY-UPDATE FREQUENCIES

A. Setup of the model

We consider a finite and well-mixed population of N individuals who are playing a two-player game, where each player can make a choice from two available strategies, A (e.g., cooperation) and B (e.g., defection). An A player interacting with another A player receives the payoff a , and otherwise when interacting with a B player, obtains b . Similarly, a B player receives c when playing with an A player and d with another B player. The payoffs are summarized in the following payoff matrix:

$$\begin{array}{cc} & \begin{array}{c} A \\ B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array} \quad (1)$$

The game is played round after round, and we use $\pi_A(t)$ and $\pi_B(t)$, $t = 0, 1, 2, \dots$, to denote the average payoffs of A and B players in round t , respectively. After game playing in each game round, an individual is chosen randomly to update its strategy. To be more concrete, when just finishing round t , the chosen individual randomly select another individual from the population to compare their strategies; if they hold the same strategy, the focal player keeps her current strategy in the next game round and otherwise if the strategies are different, say the focal agent is an A player and her chosen partner is a B player, the focal agent will switch her strategy according to the probability given by the Fermi function,

$$p(t) = \frac{1}{1 + e^{-w[\pi_B(t) - \pi_A(t)]}}, \quad (2)$$

where the constant w is called the *intensity of selection* since $w \rightarrow \infty$ leads to strong selection where the probability for selecting fitter individual is 1 and when $w \ll 1$, the update reduces to the Moran process under the weak selection [28]. Obviously, one only needs to swap the positions of π_A and π_B on the righthand side of Eq. (2) to calculate $p(t)$ if at t the updating individual plays B and its comparing individual plays A .

Here it is worth referring to the scope of strategy updating, from where the focal player can select the referable players for strategy updating. Since our motivation is based on the individual intelligence and heterogeneity, the strategy updating in pairs of players is closely related to the gaming surroundings around them. Considering the employed Fermi function that decides the switching probability between players adopting different strategies, the payoffs and strategies are the key components in it. In this sense, an implicit assumption in our work is that the available information needs to be known to the focal player, when she chooses some partner for strategy updating. It is reasonable to assume that there is a positive correlation between the individuals’ ability to spread their own strategy and gaining other individuals’ strategy information. For example, the fast individuals can only obtain other fast individuals’ information, due to the poorer ability of the slow players to spread their information.

Accordingly, we assume that the whole population consists of two subpopulations and an updating individual only chooses a referable agent from her group: one is called the *fast group*, since one individual is chosen randomly from this group to update every round, and the other is called the *slow group*, since a member from this group is chosen to update her strategy every $s \geq 1$ rounds. Therefore, when $s = 1$, the overall population is homogeneous in the strategy-update frequencies and when $s \rightarrow \infty$ the update processes of the fast and slow groups are completely decoupled. We call s the *time scale* of the strategy updating actions and thus when $s > 1$, the overall population is heterogeneous in the time scales of individuals’ updates. To keep the analysis tractable and emphasize the most relevant features of the results, we focus on investigating analytically the case when $s \rightarrow \infty$; in Figs. 4–6, we show through simulations that when s takes other values, the main conclusions of the paper still hold.

B. Calculation of the fixation probabilities

Since A and B , respectively, denote the available strategies in the employed two-strategy game here, the average payoffs π_A and π_B in the gaming population are calculated as follows. We assume that in the current round there are M fast individuals, or equivalently $N - M$ slow ones, in the population. Let j be the number of A players in the fast group and i be that in the slow group. Then

$$\begin{aligned} \pi_A &= \frac{j+i-1}{N-1}a + \frac{N-j-i}{N-1}b, \\ \pi_B &= \frac{j+i}{N-1}c + \frac{N-j-i-1}{N-1}d. \end{aligned} \quad (3)$$

So for the fast players, in the next round, the number of A players will change according to the following

probabilities:

$$\begin{aligned} T_j^+(t) &= \frac{j}{M} \frac{M-j}{M} \frac{1}{1 + e^{-\omega(\pi_A - \pi_B)}}, \\ T_j^-(t) &= \frac{j}{M} \frac{M-j}{M} \frac{1}{1 + e^{\omega(\pi_A - \pi_B)}}, \end{aligned} \quad (4)$$

where T_j^+ denotes the probability to increase by one and T_j^- to decrease by one. One can check that the sum of T_j^+ and T_j^- is always $\frac{j}{M} \frac{M-j}{M}$, which is exactly the probability that the updating individual and its comparing individual have different strategies. The ratio

$$\chi_j = \frac{T_j^-}{T_j^+} = e^{-w(\pi_A - \pi_B)} \quad (5)$$

determines the *fixation probability* ϕ_j [28], which in this problem setup is the probability that all the fast players use A strategy in the end; more precisely,

$$\phi_j = \frac{\sum_{k=1}^{j-1} \left(\prod_{m=1}^k \chi_m \right)}{\sum_{k=1}^{M-1} \left(\prod_{m=1}^k \chi_m \right)}. \quad (6)$$

It follows from Eq. (3) that

$$\pi_A - \pi_B = \frac{2u(j+i)}{N-1} + \frac{2v}{N-1}, \quad (7)$$

where

$$\begin{aligned} u &= \frac{a - b - c + d}{2} \\ v &= \frac{-a + bN - dN + d}{2}. \end{aligned} \quad (8)$$

Combining Eqs. (5)–(7), we obtain

$$\phi_j = \frac{\sum_{k=1}^{j-1} e^{\frac{-w}{N-1} [k(k+2i+1)u + 2kv]}}{\sum_{k=1}^{M-1} e^{\frac{-w}{N-1} [k(k+2i+1)u + 2kv]}}. \quad (9)$$

By applying the computational technique in Ref. [29], it can be shown that when $u \neq 0$, the fixation probability is approximated by

$$\phi_j = \frac{\text{erf}(\xi_j) - \text{erf}(\xi_0)}{\text{erf}(\xi_M) - \text{erf}(\xi_0)}, \quad (10)$$

where the $\text{erf}(x) = \frac{2}{\sqrt{\pi}} \int_0^x e^{-y^2} dy$ is the Gauss error function [30] and

$$\xi_j = \sqrt{\frac{w}{u(N-1)}} [(j+i)u + v], \quad (11)$$

and that when $u = 0$, the fixation probability is approximated by

$$\phi_j = \frac{e^{\frac{-2wvj}{N-1}} - 1}{e^{\frac{-2wvM}{N-1}} - 1}. \quad (12)$$

Note that the approximation Eqs. (10) and (12) are applicable to any intensity of selection w and any $j \in \{1, \dots, M-1\}$.

Then we shift our attention to the evolution dynamics of slow players. Given the assumption of $s \rightarrow \infty$, when a slow player is chosen to update, the strategic choices of the fast players have already evolved into one of the two absorbing full- A or full- B states. Similarly, we can get the fixation probabilities of strategies in their groups for the slow players if $u \neq 0$,

$$\phi_j = \frac{\text{erf}(\xi_j) - \text{erf}(\xi_0)}{\text{erf}(\xi_{N-\bar{M}}) - \text{erf}(\xi_0)}, \quad (13)$$

where $\bar{M} = 0$ if the fast group evolves into the all- B state and $\bar{M} = M$ otherwise, $\text{erf}(x)$ is still the Gauss error function, and

$$\xi_j = \sqrt{\frac{\omega}{u(N-1)}} [(j + \bar{M})u + v]; \quad (14)$$

when $u = 0$,

$$\phi_j = \frac{e^{\frac{-2\omega v j}{N-1}} - 1}{e^{\frac{-2\omega v (N-M)}{N-1}} - 1}. \quad (15)$$

Synthesizing the fixation probabilities of the fast group described by Eqs. (10) and (12), and that of the slow group described by Eqs. (13) and (15), we can obtain the fixation probabilities for the overall population of N individuals of both fast and slow players. Let n denote the size of the current group of interest, j and i the numbers of A players in the current group and the other group, respectively, and ξ_j , u , and v the same as in Eqs. (10) and (7), respectively. Then the unified expression for the fixation probabilities is that when $u \neq 0$,

$$\phi_j = \frac{\text{erf}(\xi_j) - \text{erf}(\xi_0)}{\text{erf}(\xi_n) - \text{erf}(\xi_0)}, \quad (16)$$

and when $u = 0$,

$$\phi_j = \frac{e^{\frac{-2\omega v j}{N-1}} - 1}{e^{\frac{-2\omega v n}{N-1}} - 1}. \quad (17)$$

Note that i takes its value from $\{0, 1, \dots, N-M\}$ when the current group is the fast group, while i is either 0 or M when the slow group is of interest.

Several well established game models can fully describe the possible cooperative dilemmas in the real social societies, where the degree of conflict between strategies may differ. Using the calculated fixation probabilities, next we will investigate the evolutionary outcomes for three different types of games, where strategy B dominates, A and B coexist, or coordination of A and B is preferred.

III. TYPICAL TWO-PLAYER GAMES

The analytical results have shown that the fixation probabilities depend on not only the initial number of A players, but also the relative sizes of the fast and slow groups. In this section, to further demonstrate this point and, more importantly, to gain insight into how population-level cooperation is influenced, we carry out simulation studies on three typical types of two-player games that are classified according to the structures of the payoff matrix specified in Eq. (1), namely dominance of B ($c > a$ and $d > b$), coexistence of A and B ($a < c$ and

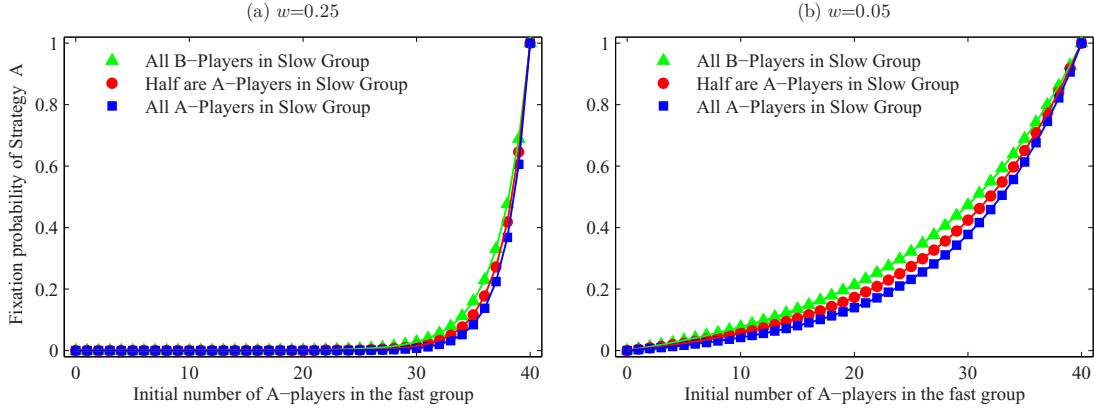


FIG. 1. Fixation probabilities for the game whose dominance strategy is B with different selection intensity: (a) $\omega = 0.25$, and (b) $\omega = 0.05$. The payoff parameter values of the prisoner’s dilemma game: $a = 3$, $b = 1$, $c = 5$, $d = 2$. Here, the horizontal axis means the fixation probability of strategy A in the fast group, while the vertical axis represents the initial number of A players in the fast group. The following settings are the same in Figs. 2 and 3. Simulation results (symbols) coincide perfectly with the approximation results (solid lines). The approximation results are from Eq. (10). Each simulation result corresponds to the average frequency of fixation of A players from 100 independent realizations. Here, the results show that the heterogeneity of time scales on updating has only limited effects on the fixation probabilities.

$b > d$), and a coordination game ($a > c$ and $b < d$). In all the simulations, we take $N = 80$ and $M = 40$.

A. Game with dominating B

Consider the game in which strategy B always dominates, so a B player always obtains a higher payoff than an A player no matter what the fraction of B players is in the population. Thus, it must be true that $c > a$ and $d > b$. A well-known example is the prisoner’s dilemma game (PDG) with $c > a > d > b$, in which a defector is always promised with the highest fitness when facing a cooperator, an exploited cooperator is worse off than a defector playing with another defector, and thus defection is the unique Nash equilibrium [31]. In our simulations, we take $a = 3$, $b = 1$, $c = 5$, $d = 2$, and then A corresponds to cooperation and B defection in a PDG.

We show the results in Fig. 1(a) for $\omega = 0.25$ and Fig. 1(b) for $\omega = 0.05$, which are in perfect agreement with the analytical prediction. It is clear that when the number of A players in the slow group varies, the fixation probability of A players in the fast group changes correspondingly, although the changes are not significant. So the heterogeneity in time scales affects the outcome of the simulated PDG, but not significantly.

B. Game with coexisting A and B

Consider the game in which B is the best reply to A ($c > a$), and at the same time A is the best reply to B ($b > d$). A typical example is the hawk-dove game or the snowdrift game (SDG). For infinite populations, the replicator dynamics predict the stable coexistence of A and B . For simplicity, we take the payoffs in the SDG to be $a = 3$, $b = 2$, $c = 5$, $d = 1$, and then A is to cooperate and B to defect.

Compared with the simulation results for PDG, a substantially different phenomenon takes place for SDG in the evolutionary outcomes that shows the strong influence of time scales. Figure 2 shows that more B players in the slow group lead to much bigger fixation probabilities of A strategy in the

fast group. The reason is rooted in the fact that the more B players in the slow group, the higher payoffs of A players in the fast group, and hence higher chance for having more A players. Again this matches the analytical prediction.

C. Coordination game

Finally, let us discuss coordination games in which $a > c$ and $b < d$, and then A is the best reply to A and at the same time B is the best reply to B . The replicator equation of such systems exhibit bistability: if the fraction of A players is sufficiently high in the beginning, A players will reach fixation; otherwise, B players will dominate. The stronger the intensity of selection, the less likely it is that a single A player can take over a B population. Here, we focus on the stag-hunt game (SHG) as an example of a coordination game. We take $a = 5$, $b = 1$, $c = 3$, $d = 2$ here, where A presents cooperation and B denotes defection.

The evolutionary outcomes depicted in Fig. 3 show a perfect matching between theoretical prediction and simulation. It can be observed that the time scale heterogeneity clearly changes the evolutionary outcomes. For instance, more A players in the slow group lead to a large increment of the A ’s fixation probability in the fast group. The reason is that the more A players in the slow group, the higher payoffs of A players in the fast group, and thus more intensely the strategy A is promoted. The observation that increasing the fraction of one strategy in the slow group benefits the evolution of the same strategy in the fast group merits special attention, since it is the opposite of the results in SDG.

Although our analytical results in the previous section and the simulation results in this section only study the idealized case when $s \rightarrow \infty$, in Figs. 4, 5, and 6 we demonstrate that when s takes its values of 1, 2, 5, 10, 50, and 100, similar conclusions on how the strategy composition of the slow group affects the evolutionary outcome of the fast group are still applicable. This underscores the importance of the insight gained from our analytical prediction and, in fact, now one can always

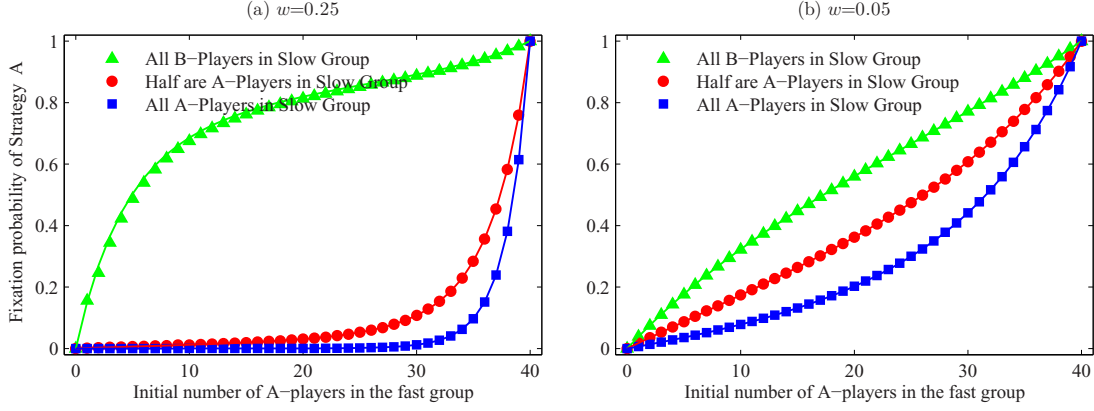


FIG. 2. Evolutionary outcomes for the games where A and B will stably coexist. (a) $\omega = 0.25$, and (b) $\omega = 0.05$. The payoff parameter values of snowdrift game: $a = 3$, $b = 2$, $c = 5$, $d = 1$. Here, the horizontal axis means the fixation probability of strategy A in the fast group, while the vertical axis represents the initial number of A players in the fast group. Results show that the heterogeneity of time scales on updating has significant effects on the fixation of probabilities of strategies in their groups. Specifically, more opposite strategies in the other group promote a strategy to get fixation in its own group.

predict with confidence whether a strategy in the fast group will be promoted or inhibited when facing a slow group of different strategy compositions. One may question, however, whether the conclusions are still applicable for populations under weak selection (payoff trivially influences the fitness of individuals) when $\omega \ll 1$, since then the approximation in our previous calculation becomes less effective. To address this concern, in the next section, we study the case when $\omega \ll 1$.

IV. FIXATION PROBABILITY UNDER WEAK SELECTION

A. Strategy evolution for fast players

For $\omega \ll 1$, our model reduces to the Moran process under weak selection. Then, we address the weak selection approximation as follows. When $\omega \ll 1$, we get

$$\chi_j = \frac{T_j^-}{T_j^+} \approx 1 - \omega(\pi_A - \pi_B), \quad (18)$$

which after being substituted into Eq. (6) leads to

$$\phi_j \approx \frac{1 + \sum_{k=1}^{j-1} \left[1 - \omega \left(\frac{u}{N-1} k^2 + \left(\frac{u}{N-1} + \frac{2v}{N-1} + \frac{2ui}{N-1} \right) k \right) \right]}{1 + \sum_{k=1}^{M-1} \left[1 - \omega \left(\frac{u}{N-1} k^2 + \left(\frac{u}{N-1} + \frac{2v}{N-1} + \frac{2ui}{N-1} \right) k \right) \right]} \quad (19)$$

$$= \frac{j}{M} + \frac{\omega(M-j)j}{6M(N-1)} [N(a-b-c+d)(3(1-\alpha)\beta + \alpha) + (a-b-c+d)j + 3(b-d)N - 3a + 3d], \quad (20)$$

where $\alpha = M/N$, $\beta = i/(N-M)$, $u = \frac{a-b-c+d}{2}$, and $v = \frac{-a+b+N-d+N}{2}$.

Under weak selection, $\phi_j > j/M$ means

$$\frac{a-b-c+d}{3} [\alpha + 3(1-\alpha)\beta] + (b-d) > 0. \quad (21)$$

Note that when $\alpha = 1$, namely the population is homogeneous in their time scales, the above results agree with those for a variety of Moran processes under weak selection [32].

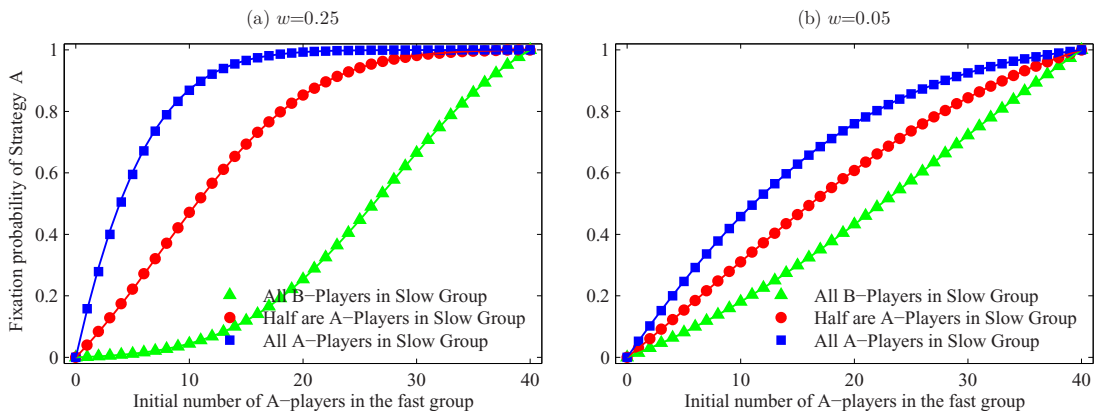


FIG. 3. Evolutionary outcomes for the coordination games. (a) $\omega = 0.25$, and (b) $\omega = 0.05$. The payoff parameter values of stag-hunt game: $a = 5$, $b = 1$, $c = 3$, $d = 2$. Here, the results show that diversity of time scales on updating has significant effects on the fixation probabilities. Different with the results shown in Fig. 2, more opposite strategies in the other group inhibit a strategy to get fixation in its own group.

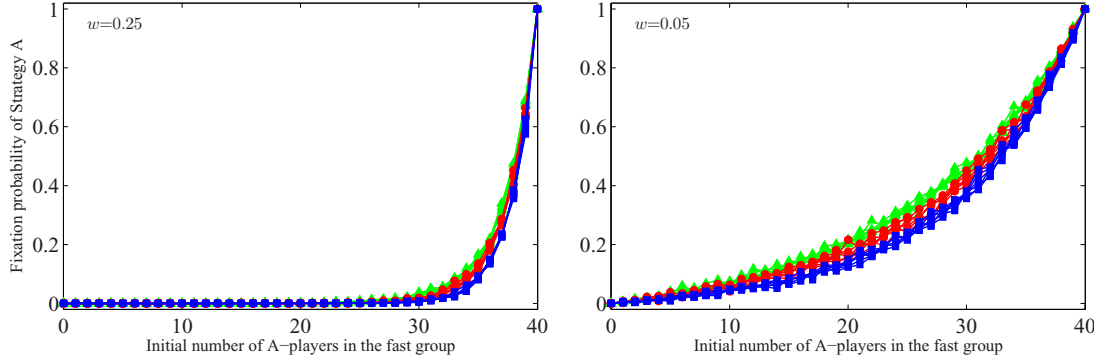


FIG. 4. Simulation results of games whose dominating strategy is B . Here, the horizontal axis means the fixation probability of strategy A in the fast group, while the vertical axis represents the initial number of A players in the fast group. $\omega = 0.25$ and $\omega = 0.05$, respectively. The initial numbers of A players in the slow groups are 1 (green lines), 20 (red lines), and 39 (blue lines) for comparison. Moreover, though a group of values $s = 1, 2, 5, 10, 50, 100$ are used here, the nondistinctive differences between them make it unnecessary to distinguish them with different colors. The simulation results here show notable consistency with the theoretical results in Fig. 1, suggesting the validity of our theoretical analysis.

B. Strategy evolution for slow players

After the fast players have evolved into their absorbing states, the slow players start their evolution processes. We have to carry out our computation for two separate absorbing states of fast players, all- A and all- B , separately.

1. Scenario I: Fast players converge to the all- A state

Now let i be the number of A players among slow players. Then the payoffs of strategy A and B for slow players are

$$\begin{aligned}\pi_A &= \frac{M+i-1}{N-1}a + \frac{N-M-i}{N-1}b, \\ \pi_B &= \frac{M+i}{N-1}c + \frac{N-M-i-1}{N-1}d.\end{aligned}\quad (22)$$

So the probability to have $i+1$ or $i-1$ A players in the slow players in the next game round when having j A players

in the current round are

$$\begin{aligned}T_i^+ &= \frac{i}{N-M} \frac{N-M-i}{M} \frac{1}{1+e^{-\omega(\pi_A-\pi_B)}}, \\ T_i^- &= \frac{i}{N-M} \frac{N-M-i}{M} \frac{1}{1+e^{+\omega(\pi_A-\pi_B)}}.\end{aligned}\quad (23)$$

Similarly,

$$\begin{aligned}\phi_i &\approx \frac{1 + \sum_{k=1}^i [1 - \omega(\frac{u}{N-1}k^2 + (\frac{u}{N-1} + \frac{2v}{N-1} + \frac{2u}{N-1}M)k)]}{1 + \sum_{k=1}^{N-M-1} [1 - \omega(\frac{u}{N-1}k^2 + (\frac{u}{N-1} + \frac{2v}{N-1} + \frac{2u}{N-1}M)k)]} \\ &= \frac{i}{N-M} + \frac{\omega(N-M-1)}{6(N-M)(N-1)} [N(a-b-c+d)(2\alpha+1) \\ &\quad + (a-b-c+d)i + 3(b-d)N - 3a + 3d],\end{aligned}\quad (25)$$

where α , u , and v are the same as in Eq. (19).

Under weak selection, if strategy A performs better than neutral selection [i.e., $\phi_1 > 1/(N-M)$], the following

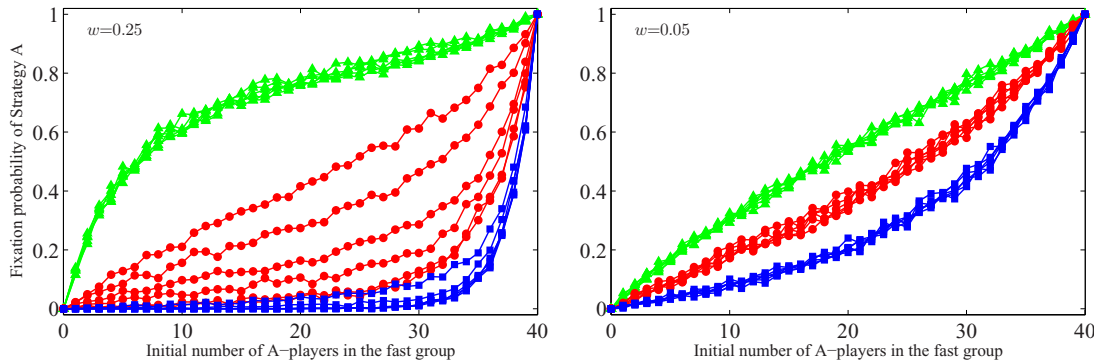


FIG. 5. Simulation results of games where A and B will stably coexist. Here, the horizontal axis means the fixation probability of strategy A in the fast group, while the vertical axis represents the initial number of A players in the fast group. $\omega = 0.25$ and $\omega = 0.05$, respectively. The initial numbers of A players in the slow groups are 1 (green lines), 20 (red lines), and 39 (blue lines) for comparison. Still, we do not distinguish $s = 1, 2, 5, 10, 50, 100$ with different colors. The simulation results here show much consistency with the theoretical results in Fig. 2, suggesting the validity of our theoretical analysis.

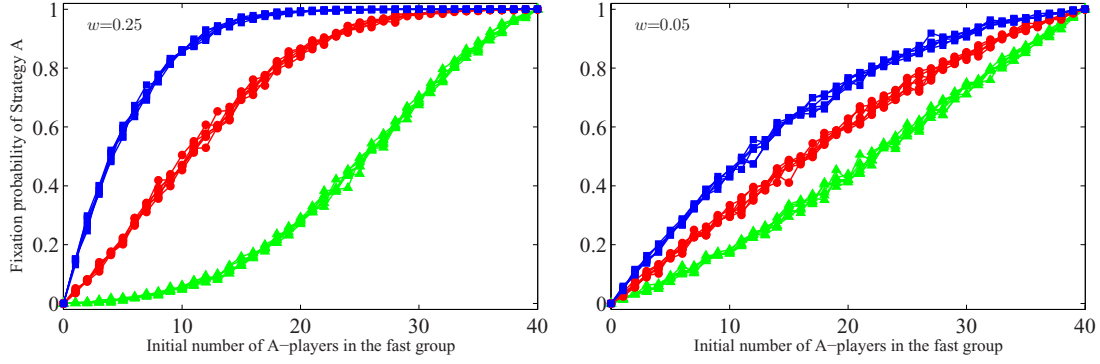


FIG. 6. Simulation results of the coordination games. Here, the horizontal axis means the fixation probability of strategy A in the fast group, while the vertical axis represents the initial number of A players in the fast group. $\omega = 0.25$ and $\omega = 0.05$, respectively. The initial numbers of A players in the slow groups are 1 (green lines), 20 (red lines), and 39 (blue lines) for comparison. The simulation results here show notable consistence with the theoretical results in Fig. 3, suggesting the validity of our theoretical analysis.

condition should be satisfied:

$$(a - b - c + d)(2\alpha + 1) + 3(b - d) > 0. \quad (26)$$

Thus, natural selection favors a single mutant A to eventually replace a population of B players.

2. Scenario II: Fast players converge to the all- B state

In this case, the payoffs for playing A or B in slow players are

$$\begin{aligned} \pi_A &= \frac{i-1}{N-1}a + \frac{N-M-i}{N-1}b, \\ \pi_B &= \frac{i}{N-1}c + \frac{N-M-i-1}{N-1}d. \end{aligned} \quad (27)$$

The fixation probability under weak selection reads

$$\begin{aligned} \Phi_i &\approx \frac{1 + \sum_{k=1}^{i-1} \left[1 - \omega \left(\frac{u}{N-1} k^2 + \left(\frac{u}{N-1} + \frac{2v}{N-1} \right) k \right) \right]}{1 + \sum_{k=1}^{N-M-1} \left[1 - \omega \left(\frac{u}{N-1} k^2 + \left(\frac{u}{N-1} + \frac{2v}{N-1} \right) k \right) \right]} \\ &= \frac{i}{N-M} + \frac{\omega(N-M-1)}{6(N-M)(N-1)} [N(a-b-c+d)(1-\alpha) \\ &\quad + (a-b-c+d)i + 3(b-d)N - 3a + 3d]. \end{aligned} \quad (28)$$

Here, α , u , and v are the same as in Eq. (19).

Under weak selection, strategy A performs better than neutral selection, if

$$(a - b - c + d)(1 - \alpha) + 3(b - d) > 0. \quad (30)$$

In this case, natural selection favors a single mutant A to eventually replace a population of B players. So no matter which absorbing state (all- A or all- B) the fast players converge to, the evolutionary outcome of the slow players is always affected by the relative sizes of fast and slow players, which is further scaled by the payoffs.

V. SIMULATIONS

To verify our theoretical results shown in the main text, we also establish computer simulations under the assumption that the two subpopulations (fast or slow) are partly decoupled. The specific results are about the dependence of the fixation probability of strategy A on the initial number of A players in the fast group, the initial number of A players in the slow group,

the s , and the ω . In the given figures, each datum corresponds to the fraction of fixation of strategy A in the 100 independent realizations.

Though a group of values $s = 1, 2, 5, 10, 50, 100$ are used here, the nondistinctive differences between them make it unnecessary to distinguish them with different colors. The values of s do not have significant influences on the fixation probability of strategy A in the fast groups. One main conclusion provided by the simulation results is that our theoretical analysis is valid. In our calculation of fixation probability of the strategy, we assume that when a slow player is chosen to update, the strategic choices of the fast players have already evolved into one of the two absorbing full- A or full- B states. Even without the restrictive assumption just mentioned, the same conclusions have again been validated through simulation results.

VI. CONCLUSION

The origin of cooperation has been one of the hot spots in evolutionary biology for decades with natural selection in its kernel. In fact, selection frequencies may vibrate in a population. Our theoretical model is largely different from previous studies by introducing individual heterogeneity in their strategy-update time scales. Herein, by introducing a crucial parameter s as the ratio between time scales of fast and slow players, we are enabled to provide closed-form approximation for the evolutionary outcome of fast and slow groups when $s \rightarrow \infty$. One crucial step is that under the simplifying condition, the fast players always enter their absorbing states before the slow players start to update. This condition can be easily removed when one is only interested in simulation study and in fact our simulation results have indicated that the conclusion in the paper still holds when the fast and slow strategy-updating dynamics are coupled.

We have derived a sequence of approximation formulas that determine the fixation probabilities under a range of initial conditions. The difference in time scales leads to much richer evolutionary dynamics for typical two-player games, which underlines the importance and generality of our findings. We find that time scale diversity has different influences on different game models. Specifically, in the prisoner's dilemma game where only defection is the dominant

strategy, the fixation probabilities of strategies in one group changes only slightly when the composition of strategies of the other group changes. In the snowdrift game, which allows for stable coexistence of cooperators and defectors in well-mixed populations, the corresponding changes are much more significant. In the stag-hunt game, in which each strategy is the best reply to itself, the corresponding changes are again significant, but the promoted strategy is the opposite of that in the snowdrift game. In addition to the approximation results, we study the evolutionary dynamics with different time scales under weak selection.

The result reported here could flexibly lend itself to multiple extensions. In the current model we limited our study to the situation where only two types of players are considered, while multiple types may be more common in practical settings. Thus, investigating what happens in the presence of increasing diversity or even dynamically varying

strategy-update frequencies is an intriguing topic to be studied in the future. Besides, alternative definitions of time scales deserve further attention to look for plausible explanations for the individual heterogeneity and ultimately the persistence of cooperation.

ACKNOWLEDGMENTS

The authors are supported by the Dutch Organization for Scientific Research (NWO) (Grant No. 82301006), the Dutch Technology Foundation (STW) (Grant No. vidi-14134), the European Research Council (Grant No. ERC-StG-307207), and the National Natural Science Foundation of China (Grants No. 61573199, No. 61573200, No. 61603199, and No. 61603201). We also thank the editor and two referees for their valuable comments.

-
- [1] G. Hardin, *Science* **162**, 1243 (1968).
- [2] A. Robert, *The Evolution of Cooperation* (Basic Books, New York, 1984).
- [3] D. D. Heckathorn, *Am. Soc. Rev.* **61**, 250 (1996).
- [4] P. Grim, *J. Theor. Biol.* **173**, 353 (1995).
- [5] H. Gintis, *Game Theory Evolving* (Princeton University Press, Princeton, 2000).
- [6] M. Doebeli and C. Hauert, *Ecol. Lett.* **8**, 748 (2005).
- [7] S. West, A. Griffin, and A. Gardner, *Curr. Biol.* **17**, R661 (2007).
- [8] M. A. Nowak, *Science* **314**, 1560 (2006).
- [9] A. Henry, P. Prałat, and C.-Q. Zhang, *Proc. Natl. Acad. Sci. USA* **108**, 8605 (2011).
- [10] M. Perc and A. Szolnoki, *BioSystems* **99**, 109 (2010).
- [11] T. Gross and B. Blasius, *J. Roy. Soc. Interface* **5**, 259 (2008).
- [12] R. Cong, T. Wu, Y.-Y. Qiu, and L. Wang, *Phys. Lett. A* **378**, 950 (2014).
- [13] Z. Rong, Z.-X. Wu, and G. Chen, *Europhys. Lett.* **102**, 68005 (2013).
- [14] A. Sánchez and J. A. Cuesta, *J. Theor. Biol.* **235**, 233 (2005).
- [15] G. Iñiguez, J. Kertész, K. K. Kaski, and R. A. Barrio, *Phys. Rev. E* **83**, 016111 (2011).
- [16] D. Chowdhury, D. Stauffer, and A. Kunwar, *Phys. Rev. Lett.* **90**, 068101 (2003).
- [17] C. P. Roca, J. A. Cuesta, and A. Sánchez, *Phys. Rev. Lett.* **97**, 158701 (2006).
- [18] Z. Rong, Z.-X. Wu, and W.-X. Wang, *Phys. Rev. E* **82**, 026101 (2010).
- [19] A. Szolnoki, Z. Wang, J. Wang, and X. Zhu, *Phys. Rev. E* **82**, 036110 (2010).
- [20] A. Szolnoki, M. Perc, G. Szabó, and H.-U. Stark, *Phys. Rev. E* **80**, 021901 (2009).
- [21] Z.-X. Wu, Z. Rong, and P. Holme, *Phys. Rev. E* **80**, 036106 (2009).
- [22] A. Szolnoki and G. Szabó, *Europhys. Lett.* **77**, 30004 (2007).
- [23] U. Bastolla, M. Lassig, S. C. Manrubia, and A. Valleriani, *J. Theor. Biol.* **235**, 521 (2005).
- [24] J. C. Claussen and A. Traulsen, *Phys. Rev. Lett.* **100**, 058104 (2008).
- [25] D. M. Frank and S. Sarkar, *PLoS ONE* **5**, e10688 (2010).
- [26] C. L. Lehman and D. Tilman, *Am. Nat.* **156**, 534 (2000).
- [27] M. Perc and A. Szolnoki, *Phys. Rev. E* **77**, 011904 (2008).
- [28] M. A. Nowak, A. Sasaki, C. Taylor, and D. Fudenberg, *Nature* **428**, 646 (2004).
- [29] A. Traulsen, M. A. Nowak, and J. M. Pacheco, *Phys. Rev. E* **74**, 011909 (2006).
- [30] A. Jeffrey, *Mathematics for Engineers and Scientists*, 5th ed. (Chapman and Hall, London, 1996).
- [31] T. C. Schelling, *The Strategy of Conflict* (Harvard University Press, Cambridge, MA, 1980).
- [32] H. Ohtsuki, P. Bordalo, and M. A. Nowak, *J. Theor. Biol.* **249**, 289 (2007).