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Coexistence of competing strategies in evolutionary games

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Chapter 4

Strategy Updating with Multiple Time Scales in Evolutionary Games

This chapter investigate the roles of diversity of time scales in the evolution of public goods games. When applying evolutionary game theory to the analysis of evolutionary dynamics of large populations, a standard assumption is that natural selection acts on individuals in the same time scale, e.g. players use the same frequency to update their strategies. 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. 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). We show that heterogeneity in strategy-update time scales leads to dramatic changes in the dynamics of strategies. We give an approximation formula for the fixation probability of mutant types in finite populations and study the outcome of evolution under weak selection. We find that heterogeneity in time scales enriches the evolutionary dynamics and under simplifying conditions, the more complicated possible outcomes can be surprisingly effectively predicted when knowing the population composition and payoff parameters.

4.1 Introduction

How cooperation among non-relatives can persist in the face of cheating remains a fundamental, profound and broad-ranging unsolved question in evolution-

ary biology (Hardin 1968, Axelrod 1984, Heckathorn 1996). Evolutionary game theory is the mathematical framework that has provided the deepest insight into this issue (Grim 1995, Gintis 2000, Doebeli and Hauert 2005). Several approaches have been used in the analysis of strategy evolution and one popular approach is the integration of the microscopic patterns of interactions among individuals into the evolutionary setting (West et al. 2007, Nowak 2006). Furthermore, coevolution of interaction patterns and cooperative behavior has also been identified as a key factor that may enhance or hinder altruism (Henry et al. 2011, Perc and Szolnoki 2010, Gross and Blasius 2008b). 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.

Time scales may be associated to different temporal dynamics in evolutionary games. The most important two are how often the players interact and how frequent they update their strategies (Sánchez and Cuesta 2005, Iñiguez et al. 2011, Chowdhury et al. 2003, Roca et al. 2006b, Rong et al. 2010, Wu et al. 2009). In fact, the majority of the literature does not distinguish the two that much and tend 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 strategy according to different rules.

In this study, motivated by the fact that individuals may have different capabilities to update their strategy frequently (Bastolla et al. 2005, Claussen and Traulsen 2008, Frank and Sarkar 2010, Lehman and Tilman 2000, Perc and Szolnoki 2008), we focus on the heterogeneity in how often an individual updates its 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 the groups and such predictions are validated by simulations for Prisoner's dilemma, snowdrift and stag-hunt games. Further analysis are carried out for populations under weak selection as well. All the theoretical computation and simulation re-

sults 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 main body of this chapter is organized as follows. Section 4.2 introduces the basic game model and analyzes the evolutionary dynamics of the strategies under different updating time scales. Section 4.3 discusses the implications of the analytical results for the three typical types of two-player games. Section 4.4 investigates the model under weak selection. Finally, we make concluding remarks.

4.2 Evolutionary dynamics with different strategy-update frequencies

4.2.1 Setup of the evolutionary dynamics

Consider a finite well-mixed population of N individuals that are playing a two-player game, where each player can make an option from two 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 -players. The payoffs are summarized in the following payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix}. \end{array} \quad (4.1)$$

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. Now and then at the end of a game round, an individual is chosen randomly to update its strategy. To be more concrete, when just finishing round t , the chosen updating individual chooses randomly another individual from the population to compare their strategies; if the strategies are the same, the updating individual keeps its strategy and otherwise if the strategies are different, say the updating individual plays A

and its chosen comparing individual plays B , the updating individual switches its strategy according to the probability given by the Fermi function

$$p(t) = \frac{1}{1 + e^{-\omega(\pi_B(t) - \pi_A(t))}}, \quad (4.2)$$

where the constant ω is called the *intensity of selection* since $\omega \rightarrow \infty$ leads to strong selection where the probability for selecting fitter individual is 1 and when $\omega \ll 1$, the update reduces to the Moran process under weak selection (Nowak et al. 2004). Obviously, one only needs to swap the positions of π_A and π_B on the righthand side of (2) to compute $p(t)$ if at t the updating individual plays B and its comparing individual plays A .

It is the aim of this chapter to study how the players' strategy-updating frequencies affect the evolutionary dynamics of the overall population. Towards this end, we assume that the whole population consists of two sub-populations and an updating individual only chooses a comparing individual from its own group: one is called the *fast group* since every round one individual is chosen randomly from this group to update, and the other is called the *slow group* since a member from this group is chosen to update 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 the supplementary material of this paper, we show through simulations that when s takes other values, the main conclusions of the chapter still hold. Here, $s \rightarrow \infty$ means that the two groups are decoupled in strategy updating, however players have influences on payoffs of other in the other group.

4.2.2 Analytical analysis for fixation probabilities

We first compute explicitly the average payoffs π_A and π_B . Consider the situation when 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

$$\begin{cases} \pi_A = \frac{j+i-1}{N-1}a + \frac{N-j-i}{N-1}b, \\ \pi_B = \frac{j+i}{N-1}c + \frac{N-j-i-1}{N-1}d. \end{cases} \quad (4.3)$$

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

$$\begin{cases} T_j^+(t) = \frac{j}{M} \frac{M-j}{M} \frac{1}{1+e^{-\omega(\pi_A-\pi_B)}}, \\ T_j^-(t) = \frac{j}{M} \frac{M-j}{M} \frac{1}{1+e^{\omega(\pi_A-\pi_B)}}, \end{cases} \quad (4.4)$$

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

$$\chi_j = \frac{T_j^-}{T_j^+} = e^{-\omega(\pi_A-\pi_B)} \quad (4.5)$$

determines the *fixation probability* ϕ_j (Nowak et al. 2004) which in this problem setup is the probability that all the fast players use A strategy in the end; more precisely

$$\phi_j = \frac{\sum_{k=1}^{j-1} (\prod_{m=1}^k \chi_m)}{\sum_{k=1}^{M-1} (\prod_{m=1}^k \chi_m)}. \quad (4.6)$$

It follows from Eq. (4.3) that

$$\pi_A - \pi_B = \frac{2u(j+i)}{N-1} + \frac{2v}{N-1}, \quad (4.7)$$

where

$$\begin{cases} u = \frac{a-b-c+d}{2} \\ v = \frac{-a+bN-dN+d}{2}. \end{cases} \quad (4.8)$$

Combining Eqs. (4.5)-(4.7), we obtain

$$\phi_j = \frac{\sum_{k=1}^{j-1} e^{\frac{-\omega}{N-1}[k(k+2i+1)u+2kv]}}{\sum_{k=1}^{M-1} e^{\frac{-\omega}{N-1}[k(k+2i+1)u+2kv]}}. \quad (4.9)$$

By applying the computational technique in (Traulsen et al. 2006), it can be shown that when $u \neq 0$, the fixation probability is approximated by the following theorem.

4.2.1. THEOREM. *Under the above process, it holds that*

$$\phi_j = \frac{\text{Erf}(\xi_j) - \text{Erf}(\xi_0)}{\text{Erf}(\xi_M) - \text{Erf}(\xi_0)}, \quad (4.10)$$

where $\text{Erf}(x) = \frac{2}{\sqrt{\pi}} \int_0^x e^{-y^2} dy$ is the Gauss error function (Jeffrey 1979)

$$\xi_j = \sqrt{\frac{\omega}{u(N-1)}} [(j+i)u + v], \quad (4.11)$$

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

$$\phi_j = \frac{e^{\frac{-2\omega v j}{N-1}} - 1}{e^{\frac{-2\omega v M}{N-1}} - 1}. \quad (4.12)$$

Proof:

$$\begin{aligned} \pi_A - \pi_B &= \frac{1}{N-1} [(i+j-1)a + (N-j-i)b - (i+j)c - (N-i-j-1)d] \\ &= \frac{1}{N-1} [(i+j)(a-b-c+d) - a + Nb - Nd + d] \\ &= \frac{(i+j)}{N-1} (a-b-c+d) + \frac{1}{N-1} (-a + bN - dN + d) \end{aligned} \quad (4.13)$$

We employ $u = \frac{a-b-c+d}{2}$ and $\nu = \frac{-a+bN-dN+d}{2}$, thus

$$\pi_A - \pi_B = \frac{2u(i+j)}{N-1} + \frac{2\nu}{N-1}. \quad (4.14)$$

Because

$$\phi_j = \frac{\sum_{k=1}^{j-1} (\prod_{m=1}^k \chi_m)}{\sum_{k=1}^{M-1} (\prod_{m=1}^k \chi_m)} = \frac{\sum_{k=1}^{j-1} e^{-\frac{\omega}{N-1}[k(k+2i+1)\mu+2k\nu]}}{\sum_{k=1}^{M-1} e^{-\frac{\omega}{N-1}[k(k+2i+1)\mu+2k\nu]}} \quad (4.15)$$

and $x_m = e^{-\omega(\pi_A - \pi_B)}$, we get

$$\phi_j \approx \frac{\int_0^j e^{-\frac{\omega}{N-1}\mu(m+i)^2 - 2\beta m\nu} dm}{\int_0^m e^{-\frac{\omega}{N-1}\mu(m+i)^2 - 2\beta m\nu} dm}. \quad (4.16)$$

By employing $\beta = \frac{\omega}{N-1}$,

$$\int_0^j e^{-\frac{\omega}{N-1}\mu(m+i)^2 - 2\beta m\nu} dm = \int_0^j e^{-\beta\mu(m+i)^2 - 2\beta m\nu} dm. \quad (4.17)$$

If $\mu \neq 0$, let $t = \sqrt{\beta\mu}(m+i)$, then

$$\frac{1}{\sqrt{\beta\mu}} \int_{\sqrt{\beta\mu}i}^{\sqrt{\beta\mu}(k+i)} e^{-t^2 - 2\sqrt{\frac{\beta}{\mu}}\nu t + 2\beta\nu i} dt \quad (4.18)$$

$$= \frac{e^{\frac{\beta}{\mu}\nu^2 + 2\beta\nu i}}{\sqrt{\beta\mu}} \int_{\sqrt{\beta\mu}i}^{\sqrt{\beta\mu}(k+i)} e^{-(t + \sqrt{\frac{\beta}{\mu}}\nu)^2} dt. \quad (4.19)$$

By employing $y = t + \sqrt{\frac{\beta}{\mu}}\nu$,

$$\int_0^j e^{-\frac{\omega}{N-1}\mu(m+i)^2 - 2\beta m\nu} dm \quad (4.20)$$

$$= \frac{e^{\frac{\beta}{\mu}\nu^2 + 2\beta\nu i}}{\sqrt{\beta\mu}} \int_{\sqrt{\beta\mu}(\mu+i\nu)}^{\sqrt{\beta\mu}[(k+i)\mu+\nu]} e^{-y^2} dt \quad (4.21)$$

$$= \frac{e^{\frac{\beta}{\mu}\nu^2 + 2\beta\nu i}}{\sqrt{\beta\mu}} \left(\int_0^{\sqrt{\beta\mu}[(k+i)\mu+\nu]} e^{-y^2} dy - \int_0^{\sqrt{\beta\mu}(i\mu+\nu)} e^{-y^2} dy \right). \quad (4.22)$$

By employing $\beta = \frac{\omega}{N-1}$,

$$\int_0^j e^{-\frac{\omega}{N-1}\mu(m+i)^2 - 2\beta m\nu} dm \quad (4.23)$$

$$= \text{Erf} \left(\sqrt{\frac{\omega}{\mu(N-1)}}(k+i)\mu + \nu \right) - \text{Erf} \left(\sqrt{\frac{\omega}{\mu(N-1)}}i\mu + \nu \right). \quad (4.24)$$

Here,

$$\text{Erf}(x) = \frac{2}{\sqrt{\pi}} \int_0^x e^{-y^2} dy. \quad (4.25)$$

Similarly, we get

$$\int_0^k e^{-\frac{\omega}{N-1}\mu(m+i)^2 - 2\beta m\nu} dm \quad (4.26)$$

$$= \text{Erf}(\varepsilon_k) - \text{Erf}(\varepsilon_0), \quad (4.27)$$

where

$$\varepsilon_n = \sqrt{\frac{\omega}{\mu(N-1)}}[(n+i)\mu + \nu]. \quad (4.28)$$

Hence,

$$\phi_j = \frac{\text{Erf}(\varepsilon_j) - \text{Erf}(\varepsilon_0)}{\text{Erf}(\varepsilon_m) - \text{Erf}(\varepsilon_0)}. \quad (4.29)$$

When $\mu = 0$,

$$\int_0^k e^{-\frac{\omega}{N-1}\mu(m+i)^2 - 2\beta m\nu} dm \quad (4.30)$$

$$= \int_0^k e^{-2\beta m\nu} dm \quad (4.31)$$

$$= -\frac{1}{2\beta\nu}(e^{-2\beta m\nu} - 1). \quad (4.32)$$

That is

$$\phi_j \approx \frac{e^{-\frac{2\omega\nu j}{N-1}} - 1}{e^{-\frac{2\omega\nu m}{N-1}} - 1}. \quad (4.33)$$

□

Note that the approximations Eqs. (4.10) and (4.12) are applicable to any intensity of selection ω and any $j \in \{1, \dots, M-1\}$.

Now we turn our attention to the slow players. Because of the assumption that $s \rightarrow \infty$, when a slow player is chosen to update, the strategic choices of the fast players have already evolved into one of the two absorbing all- A or all- B states. Therefore, following similar steps of deriving the fixation probabilities for fast players, we obtain the fixation probabilities for the slow players, namely when $u \neq 0$,

$$\phi_j = \frac{\text{Erf}(\xi_j) - \text{Erf}(\xi_0)}{\text{Erf}(\xi_{N-M}) - \text{Erf}(\xi_0)}, \quad (4.34)$$

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

$$\xi_j = \sqrt{\frac{\omega}{u(N-1)}} [(j + \bar{M})u + v]; \quad (4.35)$$

when $u = 0$,

$$\phi_j = \frac{e^{\frac{-2\omega v j}{N-1}} - 1}{e^{\frac{-2\omega v(N-M)}{N-1}} - 1}. \quad (4.36)$$

In view of the fixation probabilities for the fast group (4.10) and (4.12) and for the slow group (4.34) and (4.36), we can actually write down 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. (4.10) and (4.8) respectively. Then the unified expression for the fixation probabilities is that when $u \neq 0$,

$$\phi_j = \frac{\text{Erf}(\xi_j) - \text{Erf}(\xi_0)}{\text{Erf}(\xi_n) - \text{Erf}(\xi_0)}, \quad (4.37)$$

and when $u = 0$,

$$\phi_j = \frac{e^{\frac{-2\omega v j}{N-1}} - 1}{e^{\frac{-2\omega v n}{N-1}} - 1}. \quad (4.38)$$

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.

With the calculated fixation probabilities at hand, we are ready to investigate the evolutionary outcomes for three different types of games in which strategy B dominates, A and B coexist, or coordination of A and B is preferred.

4.3 Simulation for typical two-player games

From the analytical analysis in the previous section, it is clear that because of the effect of the time scale, 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 $b > d$) and a coordination game ($a > c$ and $b < d$). In all the simulations, we take $N = 80$ and $M = 40$.

4.3.1 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 (Schelling 1980). 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. 4.1(a) for $\omega = 0.25$ and Fig. 4.1(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 heterogeneity in time scales affects the outcome of the simulated PDG, but not significantly.

4.3.2 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. Fig. 4.2 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.

4.3.3 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 are shown in Fig. 4.3. Again one sees perfect matching between theoretical prediction and simulation. It can be observed that time scale heterogeneity clearly changes the evolutionary outcomes. For instance, more A -players in the slow group lead to large increment of A 's fixation probability. 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 composition 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 the supplementary materials 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 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 popu-

lations under weak selection (payoff trivially influences the fitness of individuals) when $w \ll 1$, since then the approximation in our previous calculation becomes less effective. To address this concern, in the next section, we study the case when $\omega \ll 1$.

4.4 Fixation probability under weak selection

4.4.1 Strategy evolution for fast players

Here, we use the fixation probability of neutral mutants ($1/M$) as a benchmark to verify whether the selection favors A replacing B in the subpopulation of fast players. If $\phi_1 > 1/M$, it means the selection favors A replacing B .

4.4.1. THEOREM. *If $\frac{a-b-c+d}{3}[\alpha + 3(1-\alpha)\beta] + (b-d) > 0$ holds, the selection in subpopulation of fast players favors A replacing B .*

Proof: 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

$$\chi_j = \frac{T_j^-}{T_j^+} \approx 1 - \omega(\pi_A - \pi_B) \quad (4.39)$$

which after being substituted to Eq. (4.6) leads to

$$\begin{aligned} \phi_1 &\approx \frac{1}{1 + \sum_{k=1}^{M-1} [1 - \omega(\frac{u}{N-1}k^2 + (\frac{u}{N-1} + \frac{2v}{N-1} + \frac{2ui}{N-1})k)]} \\ &= \frac{1}{M} + \frac{\omega(M-1)}{6M(N-1)} [N(a-b-c+d)(3(1-\alpha)\beta \\ &\quad + \alpha) + 3(b-d)N - 2a - b - c + 4d], \end{aligned} \quad (4.40)$$

where $\alpha = M/N$, $\beta = i/(N-M)$, $u = \frac{a-b-c+d}{2}$ and $v = \frac{-a+b+N-d+N}{2}$. If $\frac{a-b-c+d}{3}[\alpha + 3(1-\alpha)\beta] + (b-d) > 0$, we get $\phi_1 > 1/M$. \square

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 (Ohtsuki, Bordalo and Nowak 2007).

4.4.2 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 , seperately.

Scenario I: fast players converge to all- A

4.4.2. THEOREM. *If $(a - b - c + d)(2\alpha + 1) + 3(b - d) > 0$ holds, the selection in subpopulation of slow players favors A replacing B when the fast subpopulation converges to all- A state.*

Proof: Let j be the number of A -players among slow players. Then the payoffs of strategy A and B for slow players are

$$\begin{cases} \pi_A = \frac{M+j-1}{N-1}a + \frac{N-M-j}{N-1}b, \\ \pi_B = \frac{M+j}{N-1}c + \frac{N-M-j-1}{N-1}d. \end{cases} \quad (4.41)$$

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

$$\begin{cases} T_j^+ = \frac{j}{N-M} \frac{N-M-j}{M} \frac{1}{1+e^{-\omega(\pi_A-\pi_B)}}, \\ T_j^- = \frac{j}{N-M} \frac{N-M-j}{M} \frac{1}{1+e^{+\omega(\pi_A-\pi_B)}}. \end{cases} \quad (4.42)$$

Similarly,

$$\begin{aligned} \phi_j &\approx \frac{1 + \sum_{k=1}^j [1 - \omega(\frac{u}{N-1}k^2 + (\frac{u}{N-1} + \frac{2v}{N-1} + \frac{2u}{N-1}M)k)]}{1 + \sum_{k=1}^{N-M-1} [1 - \omega(\frac{u}{N-1}k^2 + (\frac{u}{N-1} + \frac{2v}{N-1} + \frac{2u}{N-1}M)k)]} \\ &= \frac{j}{N-M} + \frac{\omega(N-M-1)}{6(N-M)(N-1)} [N(a-b-c+d) \\ &\quad (2\alpha+1) + (a-b-c+d)j + 3(b-d)N - 3a + 3d], \end{aligned} \quad (4.43)$$

where α , u and v are the same as in Eq. (4.19).

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

$$(a - b - c + d)(2\alpha + 1) + 3(b - d) > 0. \quad (4.44)$$

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

Scenario II: fast players converge to all- B

4.4.3. THEOREM. *If $(a-b-c+d)(1-\alpha)+3(b-d) > 0$ holds, the selection in subpopulation of slow players favors A replacing B when the fast subpopulation converges to all- A state.*

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

$$\begin{cases} \pi_A = \frac{j-1}{N-1}a + \frac{N-M-j}{N-1}b, \\ \pi_B = \frac{j}{N-1}c + \frac{N-M-j-1}{N-1}d. \end{cases} \quad (4.45)$$

The fixation probability under weak selection reads

$$\begin{aligned} \Phi_j &\approx \frac{1 + \sum_{k=1}^{j-1} [1 - \omega(\frac{u}{N-1}k^2 + (\frac{u}{N-1} + \frac{2v}{N-1})k)]}{1 + \sum_{k=1}^{N-M-1} [1 - \omega(\frac{u}{N-1}k^2 + (\frac{u}{N-1} + \frac{2v}{N-1})k)]} \\ &= \frac{j}{N-M} + \frac{\omega(N-M-1)}{6(N-M)(N-1)} [N(a-b-c+d) \\ &\quad (1-\alpha) + (a-b-c+d)j + 3(b-d)N - 3a + 3d]. \end{aligned} \quad (4.46)$$

Here, α , u and v are the same as in Eq. (4.19).

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

$$(a-b-c+d)(1-\alpha) + 3(b-d) > 0. \quad (4.47)$$

In this case, natural selection favors a single mutant A to eventually replace a population of B -players. \square

So no matter whether the fast players converge to the absorbing state of all- A or all- B , 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.

Until now, we have shown that when the two subpopulations are decoupled, the timescales in updating play a important role for the evolution of strategies. To verify our theoretical results, we did computer simulations when the two subpopulations are partly decoupled. Here we show the results when the initial numbers of A -players are 1 (green lines), 20 (red lines), 39 (blue lines) and the values of s are 1,

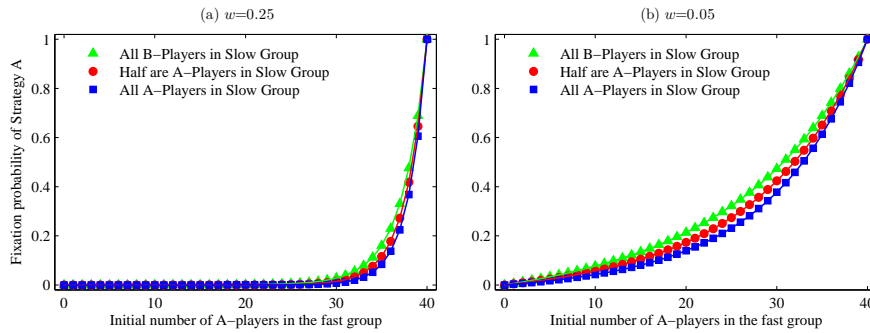


Figure 4.1: Fixation probabilities for the game of dominance of strategy B with different selection intensity: (a) $\omega = 0.25$, and (b) $\omega = 0.05$. The payoff parameter values of Prisoner's Dilemma game are: $a = 3$, $b = 1$, $c = 5$, $d = 2$. The following settings are the same in Figs. 4.2 and 4.3. Computer simulation results (symbols) coincide perfectly with the approximation results (solid lines). The approximation results are from equation (4.10). Each simulation result corresponds to the average frequency of fixation of A -players from 100 independent realizations. Here, the results show that diversity of time scales on updating has only limited effects on the fixation of probabilities.

2, 5, 10, 50, 100. Each datum corresponds to the fraction of fixation of strategy A in 100 independent realizations. We find that the results are very similar for different values of s , so we do not show legends in the following figures. Our simulation results confirmed that our main conclusions in the main text are valid. The values of s do not have significant influences on the fixation probabilities. The fixation probabilities in any real situations are in the range of the two lines corresponding to all A -players and all B -players. Simulation results:

4.5 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,

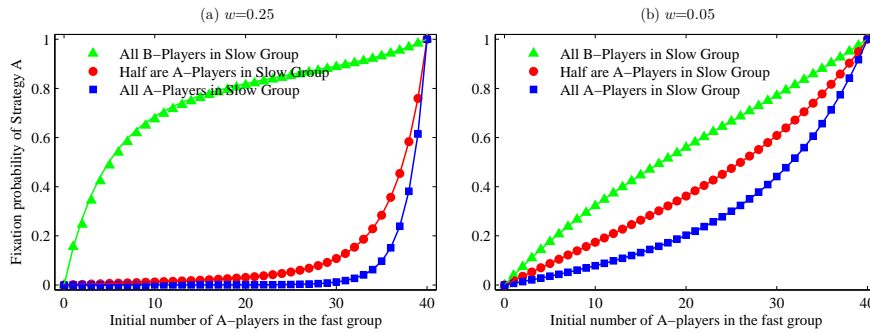


Figure 4.2: Evolutionary outcomes for games with stable coexistence of A and B . (a) $\omega = 0.25$, and (b) $\omega = 0.05$. The payoff parameter values of Snowdrift game are: $a = 3$, $b = 2$, $c = 5$, $d = 1$. Here, the results show that diversity of time scales on updating has significant effects on the fixation of probabilities. Specifically, more opposite strategies in the other group promote a strategy to get fixation in its own group.

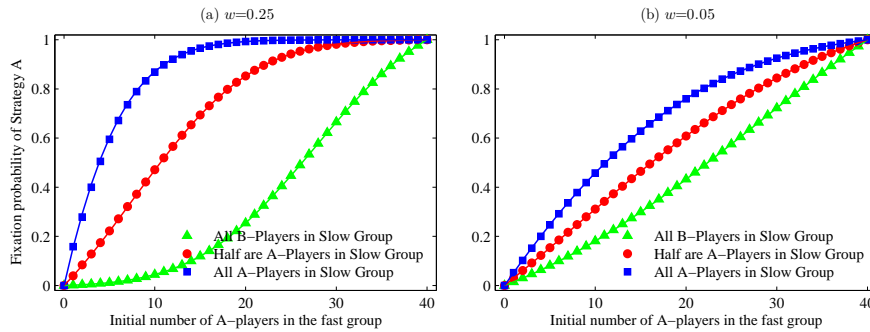


Figure 4.3: Evolutionary outcomes for coordination games. (a) $\omega = 0.25$, and (b) $\omega = 0.05$. The payoff parameter values of Stag-hunt game are: $a = 5$, $b = 1$, $c = 3$, $d = 2$. Here, the results show that diversity of time scales on updating has significant effects on the fixation of probabilities. But, unlike the results shown in Fig. 4.2, more opposite strategies in the other group inhibit a strategy to get fixation in its own group.

by introducing a crucial parameter s as the ratio between time scales of fast and low players, we are enabled to provide closed-form approximation for the evolutionary

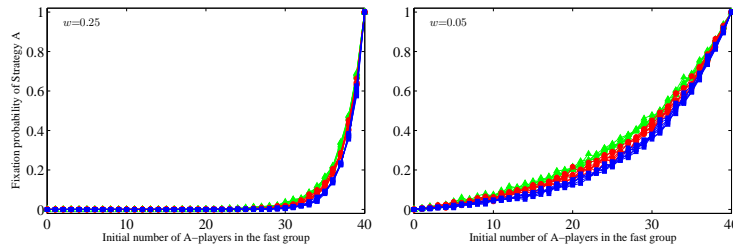


Figure 4.4: Simulation results of games with dominance of B.

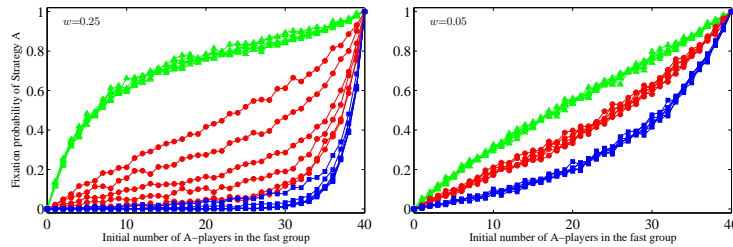


Figure 4.5: Simulation results of games with coexistence of A and B .

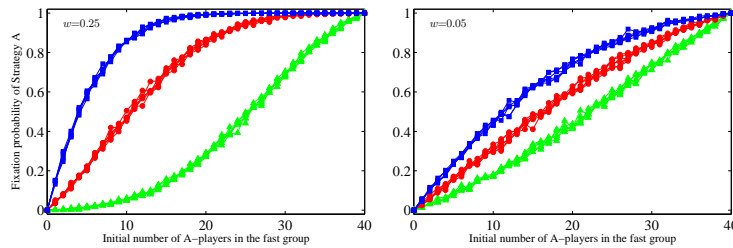


Figure 4.6: Simulation results of coordination games.

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 change 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 lends itself to multiple extensions. Up to now we have limited our study to the situation where only two types of players are considered, while multiple types are often 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. Our model certainly does not explain all aspects of time scales in the context of evolutionary game theory and alternative definitions of time scales deserve further attention to look for plausible explanations for the individual heterogeneity and ultimately the persistence of cooperation.