Hamilton's rule and kin competition in a finite kin population

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ABSTRACT

Kin selection means that individuals can increase their own inclusive fitness through displaying more altruistically toward their relatives. So, Hamilton's rule says kin selection will work if the coefficient of relatedness exceeds the cost-to-benefit ratio of the altruistic act. However, some studies have shown that the kin competition due to the altruism among relatives can reduce, and even totally negate, the kin-selected benefits of altruism toward relatives. In order to understand how the evolution of cooperation is influenced by both kin selection and kin competition under a general theoretical framework, we here consider the evolutionary dynamics of cooperation in a finite kin population, where kin competition is incorporated into a simple Prisoner's Dilemma game between relatives. Differently from the previous studies, we emphasize that the difference between the effects of mutually and unilaterally altruistic acts on kin competition may play an important role for the evolution of cooperation. The main results not only show the conditions that Hamilton's rule still works under the kin competition but also reveal the evolutionary biological mechanism driving the evolution of cooperation in a finite kin population.

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1. Introduction

As pointed out by Nowak, cooperation means that selfish replicators forgo some of their reproductive potential to help one another, but natural selection implies competition and therefore opposes cooperation unless a specific mechanism is at work (Nowak, 2006a,b; Tanimoto, 2021). Moreover, in order to show a general theoretical framework, Nowak also summarized the five rules for the evolution of cooperation, which are kin selection, direct reciprocity, indirect reciprocity, network reciprocity and group selection, respectively (Nowak, 2006b). Kin selection theory developed by Hamilton (Hamilton, 1964a,b; Maynard Smith, 1982) is one of the most important theoretical mechanisms for driving the evolution of cooperation behavior (Maynard Smith, 1982; Nowak, 2006a). This theory says that: individuals are predicted to behave more altruistically and less competitively toward their relatives, because they share a relatively high proportion of their genes; and, consequently, by helping a relative to reproduce, an individual passes its gene to the next generation (Hamilton, 1964a,b; Maynard Smith, 1982). In order to show this succinctly, based on the Prisoner's Dilemma (PD) game (i.e., a cooperator is

someone who pays a cost, c, for another individual to receive a benefit, b, and a defector has no cost and does not deal out benefits) (Maynard Smith, 1982; Nowak, 2006a) and the concept of Hamilton's inclusive fitness (Hamilton, 1964a,b), the inclusive payoff matrix for the pairwise interactions between relatives can be given by $\begin{pmatrix} (1+r)(b-c) & rb-c \\ b-rc & 0 \end{pmatrix}$, where ($i$) for simplicity and without loss of generality, it is assumed that the coefficient of relatedness between all relatives is the same, denoted by r; and (ii) the entry $(1+r)(b-c)$ (or $rb-c$) is the inclusive payoff of an individual displaying cooperation (C) against an individual displaying C (or defection (D)), and $b-rc$ (or 0) is the inclusive payoff of an individual displaying D against an individual displaying C (or D) (Maynard Smith, 1982; Nowak, 2006a). Therefore, cooperation will be favored by natural selection if $rb - c > 0$ (where the term $rb - c$ can be used as a measure of kin selection advantage), or the coefficient of relatedness must exceed the cost-to-benefit ratio of the altruistic act: $r > c/b$ (Nowak, 2006a). This is called the Hamilton's rule, and it provides a fundamental logic for explaining the conflicts of interest between relatives. Of course, we also note that some studies considered the limitations of the concept of inclusive fitness (Nowak et al., 2010; Allen et al., 2013).

Although Hamilton's rule (or kin selection theory) has been successfully used to explain why relatives more tend to cooperate with each other (Nowak, 2006a), the kin competition (i.e., competition

between relatives) caused by the altruistic action among relatives and its effect on kin selection have also been investigated by many studies (Frank, 1998; Grafen, 1984; Hamilton, 1964a, 1972; Platt and Bever, 2009; Queller, 1992, 1994, Taylor, 1992a,b; West et al., 2002). The basic idea behind these studies is that kin competition can reduce, and even totally negate, the kin-selected benefits of altruism toward relatives (Grafen, 1984; West et al., 2002). For example, Hamilton pointed out that limited dispersal of individuals from the natal group (population viscosity) would increase the relatedness between interacting individuals, and so would be an important factor favoring altruism (Hamilton, 1964a, 1971, 1972, 1975). However, limited dispersal of individuals may also increase relatedness between potential competitors, which opposes altruism (Hamilton, 1971, 1975; Platt and Bever, 2009). Thus, a fundamental question is, what is the net effect of these two opposing forces? (West et al., 2002). Some studies have shown that a lower level of dispersal can favor altruism, but, at the same time, this effect can also be cancelled by the increased kin competition (Queller, 1992; Taylor, 1992a).

In 1980s, Grafen first incorporated the effect of kin competition on kin selection into Hamilton's rule, and he developed a concise theoretical and logical framework as an extension of Hamilton's rule (Grafen, 1984). Grafen's model includes all individuals whose fitness is affected by an altruistic act, which is given by $r_{xy}b - c - r_{xe}d > 0$ (for convenience, we call it Grafen's inequality), where r_{xy} is the altruist's relatedness to the beneficiary of its altruism (i.e., r in standard Hamilton's rule), r_{xe} is the altruist's relatedness to the individuals who suffer the increased competition from the beneficiary (and possibly reduced competition from the altruist), and d is the general decrement in fitness associated with the altruistic act (Grafen, 1984). The basic idea behind Grafen's inequality is that as the altruist becomes more related to the competitors of the beneficiary (increasing r_{xe}) and/or the altruistic act increases the general level of competition (increasing d), the kin selection advantage in being altruistic is reduced (Grafen, 1984; Queller, 1994; West et al., 2002). Moreover, Queller pointed out that Hamilton's rule is equivalent to Grafen's inequality, as long as relatedness is measured at the correct scale (Queller, 1994; West et al., 2002). In fact, in order to incorporate competition between relatives into empirical studies of kin selection, some methodologies and ecological factors influencing kin selection and kin competition have also been considered by many studies (West et al., 2002; Platt and Bever, 2009). For example, Taylor presented a simple patch-structured model of the evolution of cooperation wherein cooperation increases the competition for space experienced by the progeny of a cooperator (Platt and Bever, 2009; Taylor, 1992b; West et al., 2002), etc.

However, as a basic theoretical framework, we are more interested in: (*i*) whether Grafen's basic idea can be illustrated using PD game between relatives; (*ii*) whether Grafen's inequality could be considered to be a sufficient and necessary condition for the evolution of cooperation in a kin population; and (*iii*) what the evolutionary biological mechanism driving the evolution of cooperation is under the kin selection and kin competition. When we put Grafen's inequality in the framework of PD game between relatives (where, for simplicity and without loss of generality, we still assume that the coefficient of relatedness between all relatives is the same, denoted by r), we can see that Grafen's inequality is only associated with an interaction between a cooperator and a defector (i.e., the term $rb - c - rd$ in Grafen's inequality is the inclusive payoff of an individual displaying C against an individual displaying D), and this also implies that the inclusive payoff of an individual displaying D should be $b - rc - rd$ when it plays against an individual displaying C. However, Grafen's inequality doesn't directly indicate (or define) how the interaction between a pair of cooperators will affect the competition between relatives.

Notice that an interaction between a pair of cooperators contains two altruistic acts. Thus, similar to the basic idea behind Grafen's inequality (Grafen, 1984), we can use $\widetilde{d}$ to denote the general decrement in fitness (or payoff) associated with an interaction between a pair of cooperators, where $\widetilde{d}$ should be reasonably defined to be in the interval $d \leqslant \widetilde{d} \leqslant 2d$ since, in general, the effect of a mutually altruistic act on kin competition should be larger than the effect of an unilaterally altruistic act, but should be less than the sum of the effects of two independent unilateral altruistic acts. For example, mutually altruistic acts may be more conducive to increasing carrying capacity (Platt and Bever, 2009). This implies that the effect of a mutually altruistic act on kin competition should not be regarded as a simple addition of the effects of two unilaterally altruistic acts. Based on this definition, the inclusive payoff of an individual displaying C can be given by $(1 + r)(b - c) - r\widetilde{d}$ when it plays against an individual displaying C. All of these assumptions and definitions based on PD game between relatives lead to a natural question: if the standard Hamilton's rule holds (i.e., $r > c/b$), how does kin competition that is associated with both interactions between a pair of cooperators and between a cooperator and a defector influence the evolutionary dynamics of cooperation behavior in a kin population?

In this study, based on PD game between relatives with kin competition, we will show that for the evolution of cooperation in a finite kin population, Grafen's inequality should be only a sufficient condition but not a necessary condition, or kin selection advantage could still work even if Grafen's inequality does not hold. We will also show that under kin selection and kin competition, what mechanism drives the evolution of cooperation in a finite kin population.

2. A PD game between relatives with kin competition

As shown in the Introduction, when we incorporate the effect of kin competition into a PD game between relatives, the inclusive payoff matrix can be given by

$$\begin{pmatrix} (1 + r)(b - c) - r\widetilde{d} & rb - c - rd \\ b - rc - rd & 0 \end{pmatrix}, \tag{1}$$

where the entry $(1 + r)(b - c) - r\widetilde{d}$ (or $rb - c - rd$) is the inclusive payoff of an individual displaying C against an individual displaying C (or D), and $b - rc - rd$ (or 0) the inclusive payoff of an individual displaying D against an individual displaying C (or D). For this inclusive payoff matrix, we assume that: (*i*) the coefficient of relatedness between all individuals is the same, denoted by r (Maynard Smith, 1982; Nowak, 2006a); (*ii*) the standard Hamilton's rule always holds (i.e., $rb - c > 0$); (*iii*) both parameters d and $\widetilde{d}$ are positive and $d \leqslant \widetilde{d} \leqslant 2d$; and (*iv*) the occurrence of pairwise interactions is random. We note that some studies have proposed the concept of universal dilemma strength in symmetric two-phenotype reciprocal games and proved that this concept can be successfully applied to the classification of payoff matrix structures (Wang et al., 2015; Ito and Tanimoto, 2018; Arefin et al., 2020). However, we here mainly focus our attention on the effect of kin competition on the evolution of cooperation in a PD game.

For the evolutionary dynamics of cooperation based on the inclusive payoff matrix in Eq. (1), three possible cases are needed to be considered. First, if Grafen's inequality holds (i.e., $rb - c - rd > 0$), then we must have $\left((1 + r)(b - c) - r\widetilde{d}\right) - (b - rc - rd) = rb - c - r(\widetilde{d} - d) > 0$ since $d \leqslant \widetilde{d} \leqslant 2d$. This implies that strategy C is always favored by natural selection if Grafen's

inequality holds. Second, if $rb - c - rd < 0$ (i.e., Grafen's inequality doesn't hold) and $rb - c - r(\widetilde{d} - d) < 0$, then strategy C can never be favored by natural selection. This implies that the kin selection advantage is totally negated by the effect of kin competition. Therefore, it is easy to see that only strategy C is an evolutionarily stable strategy (ESS) (Maynard Smith, 1982; Nowak, 2006a) if and only if Grafen's inequality holds; and only strategy D is an ESS if and only if $rb - c - r(\widetilde{d} - d) < 0$. Finally, for the situation with $rb - c - rd < 0$ but $rb - c - r(\widetilde{d} - d) > 0$ (i.e., $r(\widetilde{d} - d) < rb - c < rd$), if we use x to denote the frequency of strategy C in the population, then there must exist a

$$x^* = \frac{rd - (rb - c)}{r(2d - \widetilde{d})} \in (0, 1) \tag{2}$$

such that the expected inclusive payoff of strategy C, denoted by π_C, is larger (or less) than the expected inclusive payoff of strategy D, denoted by π_D, if $x > x^*$ (or $x < x^*$), where π_C and π_D are given by

$$\begin{aligned} \pi_C &= x\left((1+r)(b-c) - r\widetilde{d}\right) + (1-x)(rb - c - rd), \\ \pi_D &= x(b - rc - rd), \end{aligned} \tag{3}$$

respectively. Therefore, according to the standard definition of ESS (Maynard Smith, 1982), strategies C and D are both ESSs if $r(\widetilde{d} - d) < rb - c < rd$. This shows clearly that strategy C could be also an ESS even if Grafen's inequality doesn't hold.

However, for more real systems, we are more interested in that for the situation with $r(\widetilde{d} - d) < rb - c < rd$, whether strategy C could be still favored by natural selection in a finite kin population when the initial frequency of C is far less than x^*, or whether Hamilton's rule (i.e. $rb - c > 0$) is still sufficient for strategy C to be favored in a finite kin population even if Grafen's inequality doesn't hold. Furthermore, if the answer is yes, what mechanism drives the evolution of cooperation behavior in a finite kin population?

3. Stochastic evolutionary dynamics of cooperation in a finite kin population

Consider a finite kin population with fixed size N and assume that the selection is weak (Nowak et al., 2004, 2006a). Without loss of generality, the inclusive fitness of C-strategist, denoted by f_C, can be defined as $f_C = (1 - w) + w\pi_C$, where the parameter w represents the selection intensity with $w \in [0, 1]$ (Nowak, 2006a). Similarly, the inclusive fitness of D-strategist, denoted by f_D, is given by $f_D = (1 - w) + w\pi_D$.

Based on the diffusion approximation of the Moran process (Traulsen et al., 2006a,b; Yu et al., 2017; Zheng et al., 2011), we define that, at each time step with length $1/N$, the transition probability that the system state (i.e., the frequency of C in the population) changes from x to $x + 1/N$, denoted by ψ^+, is $\psi^+(x) = x(1 - x)f_C(x)/(xf_C(x) + (1 - x)f_D(x))$, and, similarly, the transition probability that the system state changes from x to $x - 1/N$, denoted by ψ^-, is $\psi^-(x) = x(1 - x)f_D(x)/(xf_C(x) + (1 - x)f_D(x))$. Let $\phi(x; t)$ denote the probability density distribution that the frequency of C equals exactly x at time t. Then, the diffusion approximation of $\phi(x; t)$, or the Fokker–Planck equation of $\phi(x; t)$, is given by

$$\frac{\partial \phi(x; t)}{\partial t} = -\frac{\partial}{\partial x}\left[B^{(1)}(x)\phi(x; t)\right] + \frac{\partial^2}{\partial x^2}\left[B^{(2)}(x)\phi(x; t)\right],$$

where $B^{(1)}(x) = \psi^+(x) - \psi^-(x)$ and $B^{(2)}(x) = (\psi^+(x) + \psi^-(x))/2N$ (Traulsen et al., 2006a,b; Yu et al., 2017; Zheng et al., 2011) (the

mathematical derivation is shown in Appendix). Here, $B^{(1)}(x)$ is called the drift term (that is due to fitness difference) and $\sqrt{2B^{(2)}(x)}$ the diffusion term (Traulsen et al., 2006a,b; Yu et al., 2017; Zheng et al., 2011). From the transition probabilities $\psi^+(x)$ and $\psi^-(x)$, we can see also that both $x = 0$ and $x = 1$ are absorbing boundaries (Zheng et al., 2011; Yu et al., 2017).

Moreover, if the initial frequency of strategy C at time $t = 0$, denoted by p, is considered, then the probability density distribution $\phi(x; t)$ should be rewritten as $\phi(x; p, t)$, i.e., the probability density distribution that the frequency of strategy C equals x at time t if its initial frequency is p. If we regard x as fixed and consider p as a random variable, then the backward Kolmogorov equation of $\phi(x; p, t)$ is given by

$$\frac{\partial \phi(x; p, t)}{\partial t} = B^{(1)}(p)\frac{\partial \phi(x; p, t)}{\partial p} + B^{(2)}(p)\frac{\partial^2 \phi(x; p, t)}{\partial p^2} \tag{5}$$

(Traulsen et al., 2006a,b; Yu et al., 2017; Zheng et al., 2011) (the mathematical derivation is shown in Appendix).

The above Fokker-Planck equation Eq. (4) and backward Kolmogorov equation Eq. (5) provide a basic framework for understanding the effect of kin competition on kin selection advantage (or on evolutionary dynamics of strategy C) in a finite kin population.

3.1. Fixation probability of strategy C

We now consider the fixation probability of strategy C under the condition $r(\widetilde{d} - d) < rb - c < rd$. Let $u(p, t)$ denote the probability that strategy C is fixed at time t if its initial frequency is p (i.e., the fixation probability of strategy C at time t with initial frequency p). Similar to Eq. (5), the diffusion approximation of $u(p, t)$ can also be given by

$$\frac{\partial u(p, t)}{\partial t} = B^{(1)}(p)\frac{\partial u(p, t)}{\partial p} + B^{(2)}(p)\frac{\partial^2 u(p, t)}{\partial p^2} \tag{6}$$

with the boundary conditions $u(0, t) = 0$ and $u(1, t) = 1$ (Ewens, 2004). The ultimate probability $u(p)$ of fixation of strategy C is defined by $u(p) = \lim_{t \to \infty} u(p, t)$. Since $x = 1$ is an absorbing boundary of Eq. (4), the limit $u(p)$ exists and it is the stationary solution of Eq. (6), i.e., $u(p)$ satisfies $B^{(1)}(p)(du(p)/dp) + B^{(2)}(p)\left(d^2u(p)/dp^2\right) = 0$.

From some previous studies about the stochastic evolutionary game dynamics in a finite population (Traulsen et al., 2006a,b; Yu et al., 2017; Zheng et al., 2011), for $Nw \ll 1$ (i.e., the selection is weak), the fixation probability $u(p)$ can be given by

$$u(p) = p + \frac{p(1-p)Nw}{2}\left[-(rd - (rb - c)) + \frac{1+p}{3}r(2d - \widetilde{d})\right] \tag{7}$$

(the mathematical derivation is shown in Appendix). In general, for a given initial frequency of strategy C, p, cooperation is considered to be favored by natural selection if the fixation probability of strategy C is larger than its initial frequency, i.e., $u(p) > p$ (Nowak, 2006a). Thus, Eq. (7) implies that for $r(\widetilde{d} - d) < rb - c < rd$ and $Nw \ll 1$, the fixation probability of strategy C is larger than its initial frequency p if $x^* < (1 + p)/3$, or if kin selection advantage satisfies $rb - c > r\left[(1 - 2p)d + (1 + p)\widetilde{d}\right]/3$. Specifically, for $p = 1/N$ with large N, we can see that $u(1/N) > 1/N$ if $x^* < 1/3$ (this is also called the one-third law by Nowak et al. (2004, 2006a)), or if kin selection advantage satisfies

$$rb - c > \frac{r(\widetilde{d} + d)}{3} \tag{8}$$

with $\tilde{d} < 2d$. This result shows clearly that if the above inequality holds, then kin selection advantage could not be totally negated by kin competition even if Grafen's inequality doesn't hold.

On the other hand, let $u\prime(1-p)$ denote the probability that strategy D is fixed at time t if its initial frequency is $1-p$. Then, similar to the analysis of $u(p)$, $u\prime(1-p)$ can be expressed as

$$u\prime(1-p) = (1-p) + \frac{p(1-p)Nw}{2}\left[-\left(r(2d-\tilde{d}) - rd + (rb-c)\right) + \frac{2-p}{3}r(2d-\tilde{d})\right],$$
(9)

and we must have $u(p) + u\prime(1-p) = 1$.

3.2. Mechanism driving cooperation to be favored by natural selection

For the fixation probability of strategy C with $u(1/N) > 1/N$, a further question is what force drives strategy C being favored by natural selection in a finite kin population. In order to answer this question, we consider first the concept of mean effective fixation time (Ewens, 2004; Zheng et al., 2011), and, then, consider the average inclusive fitness about the mean effective fixation time (Ewens, 2004; Zheng et al., 2011).

3.2.1. Mean effective fixation time

Let $\vartheta(t;p)$ denote the probability density function of the time t until one of the boundaries (i.e., $x = 0$ or $x = 1$) is reached given the initial frequency p. Similar to Eq. (5), the diffusion approximation of $\vartheta(t;p)$ also satisfies the backward equation

$$\frac{\partial \vartheta(t;p)}{\partial t} = B^{(1)}(p)\frac{\partial \vartheta(t;p)}{\partial p} + B^{(2)}(p)\frac{\partial^2 \vartheta(t;p)}{\partial p^2}$$
(10)

with boundary conditions $\vartheta(t;0) = \vartheta(t;1) = 0$ (Ewens, 2004).

Since the mean fixation time, defined as $\bar{t}(p) = \int_0^\infty t\vartheta(t;p)dt$, is finite, we have that $t\vartheta(t;p) \to 0$ as $t \to \infty$. Thus,

$$\begin{aligned}
-1 &= -\int_0^\infty \vartheta(t;p)dt \\
&= -[t\vartheta(t;p)]_0^\infty + \int_0^\infty t\frac{\partial \vartheta(t;p)}{\partial t}dt \\
&= 0 + \int_0^\infty t\left[B^{(1)}(p)\frac{\partial \vartheta(t;p)}{\partial p} + B^{(2)}(p)\frac{\partial^2 \vartheta(t;p)}{\partial p^2}\right]dt \\
\Rightarrow & \\
-1 &= B^{(1)}(p)\frac{d\bar{t}(p)}{dp} + B^{(2)}(p)\frac{d^2\bar{t}(p)}{dp^2}
\end{aligned}$$
(11)

with boundary condition $\bar{t}(0) = \bar{t}(1) = 0$. Following Ewens (Ewens, 2004; Zheng et al., 2011), the solution of this equation, $\bar{t}(p)$, can be expressed as

$$\bar{t}(p) = \int_0^1 t(x;p)dx,$$
(12)

where

$$t(x;p) = \frac{u\prime(1-p)}{B^{(2)}(x)H(x)}\int_0^x H(s)ds$$
(13)

with $H(x) \equiv \exp\left[-\int_0^x B^{(1)}(z)/B^{(2)}(z)dz\right]$ for $0 \leqslant x \leqslant p$ and

$$t(x;p) = \frac{u(p)}{B^{(2)}(x)H(x)}\int_x^1 H(s)ds$$
(14)

for $p \leqslant x \leqslant 1$. Notice that $H(x) \approx 1, B^{(2)}(x) \approx x(1-x)/2N$, $u\prime(1-p) \approx 1-p$ and $u(p) \approx p$ if $Nw \ll 1$. Thus, under the weak selection, the mean fixation time $\bar{t}(p)$ can be approximated as

$$\begin{aligned}
\bar{t}(p) &= \int_0^p t(x;p)dx + \int_p^1 t(x;p)dx \\
&\approx -2N[(1-p)\ln(1-p) + p\ln(p)].
\end{aligned}$$
(15)

Here, the integral $\int_{x_1}^{x_2} t(x;p)dx$ represents the mean time that the frequency of C, x, spends in the interval (x_1, x_2) before absorption. Moreover, $\int_{x_1}^{x_2} \psi^+(x)t(x;p)dx$ represents the mean time that the system state jumps from x to $x + 1/N$ when x is in the interval (x_1, x_2), and, similarly, $\int_{x_1}^{x_2} \psi^-(x)t(x;p)dx$ represents the mean time that the system state jumps from x to $x - 1/N$ when x is in the interval (x_1, x_2). Notice that $\int_{x_1}^{x_2} \psi^+(x)t(x;p)dx + \int_{x_1}^{x_2} \psi^-(x)t(x;p)dx < \int_{x_1}^{x_2} t(x;p)dx$ since the system state doesn't always jump from x to $x \pm 1/N$. Thus, we can call $\int_{x_1}^{x_2} \left(\psi^+(x) + \psi^-(x)\right)t(x;p)dx$ the mean effective time that x spends in the interval (x_1, x_2) (Ewens, 2004; Zheng et al., 2011).

Let $\bar{\tau}(p)$ denote the mean effective fixation time until one or the other absorbing boundary is reached when the initial frequency of C is p. Then, for $Nw \ll 1$, we have

$$\begin{aligned}
\bar{\tau}(p) &= \int_0^1 \left(\psi^+(x) + \psi^-(x)\right)t(x;p)dx \\
&= \int_0^p \left(\psi^+(x) + \psi^-(x)\right)t(x;p)dx + \int_p^1 \left(\psi^+(x) + \psi^-(x)\right)t(x;p)dx \\
&= 2Nu\prime(1-p)\int_0^p xdx + 2Nu(p)\int_p^1 (1-x)dx \\
&= N\left[p^2 + u(p) - 2pu(p)\right].
\end{aligned}$$
(16)

3.2.2. Average inclusive fitness about the mean effective fixation time

Based on the concept of the mean effective fixation time $\bar{\tau}(p) = \int_0^1 \left(\psi^+(x) + \psi^-(x)\right)t(x;p)dx$, the total inclusive fitness of strategy C about $\bar{\tau}(p)$ is $\int_0^1 f_C(x)(\psi^+(x) + \psi^-(x))t(x;p)dx$, then, the average inclusive fitness of strategy C about $\bar{\tau}(p)$ can be defined as $\bar{f}_{C,\bar{\tau}(p)} = \bar{\tau}(p)^{-1}\int_0^1 f_C(x)(\psi^+(x) + \psi^-(x))t(x;p)dx$ which means the average inclusive fitness of strategy C in the effective fixation process. And, similarly, the average inclusive fitness of strategy D about $\bar{\tau}(p)$ is $\bar{f}_{D,\bar{\tau}(p)} = \bar{\tau}(p)^{-1}\int_0^1 f_D(x)(\psi^+(x) + \psi^-(x))t(x;p)dx$. So, for $Nw \ll 1$, $\bar{f}_{C,\bar{\tau}(p)}$ can be given by

$$\begin{aligned}
\bar{f}_{C,\bar{\tau}(p)} &= \frac{1}{\bar{\tau}(p)}\left[\int_0^p f_C(x)\left(\psi^+(x) + \psi^-(x)\right)t(x;p)dx \right. \\
&\quad \left. + \int_p^1 f_C(x)\left(\psi^+(x) + \psi^-(x)\right)t(x;p)dx\right] \\
&= \frac{2N}{\bar{\tau}(p)}\left[u\prime(1-p)\int_0^p xf_C(x)dx + u(p)\int_p^1 (1-x)f_C(x)dx\right] \\
&= (1-w) + w(rb - c - rd) \\
&\quad + \frac{w}{3}\left((1+r)(b-c) - r\tilde{d} - (rb - c - rd)\right) \cdot \frac{2p^3 + u(p)(1-3p^2)}{p^2 + u(p)(1-2p)} \\
&= (1-w) + w(rb - c - rd) \\
&\quad + \frac{w}{3}\left(b - rc + rd - r\tilde{d}\right) \cdot \frac{2p^3 + u(p)(1-3p^2)}{p^2 + u(p)(1-2p)};
\end{aligned}$$
(17)

and, similarly, $\bar{f}_{D,\bar{\tau}(p)}$ is given by

$$\begin{aligned}
\bar{f}_{D,\bar{\tau}(p)} &= \frac{2N}{\bar{\tau}(p)}\left[u\prime(1-p)\int_0^p xf_D(x)dx + u(p)\int_p^1 (1-x)f_D(x)dx\right] \\
&= (1-w) + \frac{w}{3}(b - rc - rd) \cdot \frac{2p^3 + u(p)(1-3p^2)}{p^2 + u(p)(1-2p)}.
\end{aligned}$$
(18)

This implies that the difference between $\bar{f}_{C,\bar{\tau}(p)}$ and $\bar{f}_{D,\bar{\tau}(p)}$, denoted by $\Delta\bar{f}_{\bar{\tau}(p)} = \bar{f}_{C,\bar{\tau}(p)} - \bar{f}_{D,\bar{\tau}(p)}$, can be expressed as

$$\Delta\bar{f}_{\bar{\tau}(p)} = w(rb - c - rd) + \frac{wr(2d-\tilde{d})}{3} \cdot \frac{2p^3 + u(p)(1-3p^2)}{p^2 + u(p)(1-2p)}.$$
(19)

For $p = 1/N$ with large N, we have the approximation

$$\Delta\bar{f}_{\bar{\tau}(1/N)} \approx w\left(rb - c - \frac{r(\tilde{d}+d)}{3}\right),$$
(20)

i.e., $\bar{f}_{C,\tau(1/N)} > \bar{f}_{D,\tau(1/N)}$ if $rb - c > r(\widetilde{d} + d)/3$. This result is exactly the same as the condition that leads to the fixation probability of strategy C, $u(1/N)$, being larger than $1/N$ (see the inequality in Eq. (8)).

Therefore, for the mechanism driving cooperation to be favored by natural selection, Eq. (20) not only shows clearly the connection between the terms $\Delta\bar{f}_{\tau(1/N)}, rb - c$ (kin selection advantage) and $r(\widetilde{d} + d)/3$ (effect of kin competition on kin selection) but also deeply reveals the force driving the fixation probability of strategy C to be larger than its initial frequency. Specifically, for $Nw \ll 1$ and $r(\widetilde{d} - d) < rb - c < rd$, if $rb - c > r(\widetilde{d} + d)/3$, then $\bar{f}_{C,\tau(1/N)} > \bar{f}_{D,\tau(1/N)}$ leads to $u(1/N) > 1/N$, i.e., the fundamental evolutionary biology mechanism behind $u(1/N) > 1/N$ is $\bar{f}_{C,\tau(1/N)} > \bar{f}_{D,\tau(1/N)}$.

4. Discussion

In this study, based on the standard PD game between relatives (Maynard Smith, 1982; Nowak, 2006a), the effects of both kin selection and kin competition on the stochastic evolutionary dynamics of cooperation in a finite kin population are investigated. Following Grafen's basic idea for the effect of kin competition on Hamilton's rule (Grafen, 1984), we incorporate the kin competition into a PD game between relatives. However, differently from Grafen's inequality, we here emphasize the difference between the effects of mutually and of unilaterally altruistic acts on kin competition (i.e., the difference between the effect of an interaction between pair cooperators and the effect of an interaction between a cooperator and a defector). On the other hand, similar to Nowak (2006a), we also assume that the coefficient of relatedness between all individuals is the same. Although this assumption is not true, it should be considered to be a reasonable simplification for revealing how kin competition influences the evolution of cooperation. Finally, in this study we always assume that the standard Hamilton's rule holds.

For the main results of this paper, we first show that based on the inclusive payoff matrix in Eq. (1) and the standard definition of ESS (Maynard Smith, 1982), the strategy C is the unique ESS if Grafen's inequality holds (i.e., $rb - c - rd > 0$); only strategy D is an ESS if $rb - c - r(\widetilde{d} - d) < 0$; and strategies C and D are both ESSs if $r(\widetilde{d} - d) < rb - c < rd$. So, strategy C could be also an ESS even if Grafen's inequality doesn't hold. Secondly, in order to reveal the evolutionary dynamics of cooperation in a finite kin population with fixed size N, we show that for the situation with large N and weak selection, if the inclusive payoff matrix in Eq. (1) satisfies condition $r(\widetilde{d} - d) < rb - c < rd$, then, when the initial frequency of strategy C is $1/N$, the fixation probability of strategy C is larger than $1/N$ if and only if $rb - c > r(\widetilde{d} + d)/3$. This result not only exactly matches Nowak et al.'s one-third law (Nowak et al., 2004, 2006a) but also shows clearly that strategy C still could be favored by natural selection even if Grafen's inequality doesn't hold. Finally, based on the concept of mean effective fixation time, we show that the evolutionary biological mechanism driving cooperation to be favored by natural selection in a finite kin population is that the average inclusive fitness of strategy C about the mean effective fixation time is larger than the average inclusive fitness of strategy D about the mean effective fixation time. All these results clearly indicate that, even in the simplest case, Grafen's inequality should be only a sufficient condition, not a necessary condition, for the evolution of cooperative behavior in a kin population.

Finally, we would like to say that although the study of this paper is only based on a simple theoretical model, it provides a possible explanation for understanding how the kin competitions caused by unilateral altruistic acts and by mutual altruistic acts work together in the evolution of cooperation.

CRediT Author statement

Qiao-Qiao Hea: Conceptualization and formal analysis. **Xiu-Deng Zheng:** Conceptualization and formal analysis. **Ruth Macecd:** Conceptualization and formal analysis. **Yi Tao:** Conceptualization and formal analysis. **Ting Ji:** Conceptualization and formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Author contribution: T.J., Q-Q.H., Y.T., X-D.Z. and R.M. conceptualized the project and discussed its significance; Q-Q.H., X-D.Z. and Y. T. did the mathematical analysis; Q-Q.H., T.J. and Y.T. wrote the paper.

Appendix 1. Derivation of Eq. (4)

The master equation of $\phi(x; t)$ with time step length $1/N$ is

$$
\begin{aligned}
\phi(x; t + 1/N) - \phi(x; t) = \quad &\phi(x - 1/N; t)\psi^+(x - 1/N) \\
&+ \phi(x + 1/N; t)\psi^-(x + 1/N) \\
&- \phi(x; t)\psi^-(x) - \phi(x; t)\psi^+(x).
\end{aligned} \tag{A1}
$$

For large N, $\phi(x; t + 1/N)$, $\phi(x \pm 1/N; t)$ and $\psi^\pm(x \mp 1/N)$ have the Taylor series expansions at x and t, which are

$$
\begin{aligned}
\phi(x; t + 1/N) &\approx \quad \phi(x; t) + \tfrac{\partial}{\partial t}\phi(x; t)\tfrac{1}{N}, \\
\phi(x \pm 1/N; t) &\approx \quad \phi(x; t) \pm \tfrac{\partial}{\partial x}\phi(x; t)\tfrac{1}{N} + \tfrac{\partial^2}{\partial x^2}\phi(x; t)\tfrac{1}{2N^2}, \\
\psi^\pm(x \mp 1/N) &\approx \quad \psi^\pm(x) \mp \tfrac{\partial}{\partial x}\psi^\pm(x)\tfrac{1}{N} + \tfrac{\partial^2}{\partial x^2}\psi^\pm(x)\tfrac{1}{2N^2}.
\end{aligned} \tag{A2}
$$

Notice that

$$
\phi(x; t + 1/N) - \phi(x; t) \approx \frac{\partial}{\partial t}\phi(x; t)\frac{1}{N}, \tag{A3}
$$

$$
\begin{aligned}
&\phi(x - 1/N; t)\psi^+(x - 1/N) \\
\approx \quad &\phi(x; t)\psi^+(x) + \phi(x; t)\left[-\tfrac{\partial}{\partial x}\psi^+(x)\tfrac{1}{N} + \tfrac{\partial^2}{\partial x^2}\psi^+(x)\tfrac{1}{2N^2}\right] \\
&-\psi^+(x)\tfrac{\partial}{\partial x}\phi(x; t)\tfrac{1}{N} + \left[\tfrac{\partial}{\partial x}\phi(x; t)\right]\left[\tfrac{\partial}{\partial x}\psi^+(x)\right]\tfrac{1}{N^2} \\
&+\psi^+(x)\tfrac{\partial^2}{\partial x^2}\phi(x; t)\tfrac{1}{2N^2},
\end{aligned} \tag{A4}
$$

and

$$
\begin{aligned}
&\phi(x + 1/N; t)\psi^-(x + 1/N) \\
\approx \quad &\phi(x; t)\psi^-(x) + \phi(x; t)\left[\tfrac{\partial}{\partial x}\psi^-(x)\tfrac{1}{N} + \tfrac{\partial^2}{\partial x^2}\psi^-(x)\tfrac{1}{2N^2}\right] \\
&+\psi^-(x)\tfrac{\partial}{\partial x}\phi(x; t)\tfrac{1}{N} + \left[\tfrac{\partial}{\partial x}\phi(x; t)\right]\left[\tfrac{\partial}{\partial x}\psi^-(x)\right]\tfrac{1}{N^2} \\
&+\psi^-(x)\tfrac{\partial^2}{\partial x^2}\phi(x; t)\tfrac{1}{2N^2}.
\end{aligned} \tag{A5}
$$

Then the right hand of Eq. (A1),

$$\phi(x-1/N;t)\psi^+(x-1/N) + \phi(x+1/N;t)\psi^-(x+1/N)$$
$$-\phi(x;t)\psi^-(x) - \phi(x;t)\psi^+(x)$$
$$\approx \phi(x;t)\psi^+(x) + \phi(x;t)\left[-\frac{\partial}{\partial x}\psi^+(x)\frac{1}{N} + \frac{\partial^2}{\partial x^2}\psi^+(x)\frac{1}{2N^2}\right]$$
$$-\psi^+(x)\frac{\partial}{\partial x}\phi(x;t)\frac{1}{N} + \left[\frac{\partial}{\partial x}\phi(x;t)\right]\left[\frac{\partial}{\partial x}\psi^+(x)\right]\frac{1}{N^2}$$
$$+\psi^+(x)\frac{\partial^2}{\partial x^2}\phi(x;t)\frac{1}{2N^2}$$
$$+\phi(x;t)\psi^-(x) + \phi(x;t)\left[\frac{\partial}{\partial x}\psi^-(x)\frac{1}{N} + \frac{\partial^2}{\partial x^2}\psi^-(x)\frac{1}{2N^2}\right]$$
$$+\psi^-(x)\frac{\partial}{\partial x}\phi(x;t)\frac{1}{N} + \left[\frac{\partial}{\partial x}\phi(x;t)\right]\left[\frac{\partial}{\partial x}\psi^-(x)\right]\frac{1}{N^2}$$
$$+\psi^-(x)\frac{\partial^2}{\partial x^2}\phi(x;t)\frac{1}{2N^2}$$
$$-\phi(x;t)\psi^-(x) - \phi(x;t)\psi^+(x)$$
$$= \phi(x;t)\left[\frac{\partial(\psi^-(x)-\psi^+(x))}{\partial x}\frac{1}{N}\right] + \left(\psi^-(x)-\psi^+(x)\right)\frac{1}{N}\frac{\partial\phi(x;t)}{\partial x}$$
$$+\frac{\partial^2(\psi^-(x)+\psi^+(x))\phi(x;t)}{\partial x^2}\frac{1}{2N^2}$$
$$+\left[\frac{\partial}{\partial x}\phi(x;t)\right]\left[\frac{\partial}{\partial x}(\psi^-(x)+\psi^+(x))\right]\frac{1}{N^2}$$
$$+\left(\psi^-(x)+\psi^+(x)\right)\frac{1}{2N^2}\frac{\partial^2}{\partial x^2}\phi(x;t)$$
$$= \frac{1}{N}\frac{\partial}{\partial x}\left[(\psi^-(x)-\psi^+(x))\phi(x;t)\right] + \frac{1}{2N^2}\frac{\partial^2}{\partial x^2}\left[(\psi^-(x)+\psi^+(x))\phi(x;t)\right].$$

(A6)

Thus, Eq. (A1) can be approximated as

$$\frac{\partial\phi(x;t)}{\partial t} = -\frac{\partial}{\partial x}\left[B^{(1)}(x)\phi(x;t)\right] + \frac{\partial^2}{\partial x^2}\left[B^{(2)}(x)\phi(x;t)\right],$$

(A7)

where

$$B^{(1)}(x) = \psi^+(x) - \psi^-(x),$$
$$B^{(2)}(x) = \frac{\psi^+(x)+\psi^-(x)}{2N}.$$

(A8)

A.2. Derivation of Eq. (5)

Similar to the master equation of $\phi(x;t)$, the master equation of $\phi(x;p,t)$ about the initial frequency p is given by

$$\phi(x;p,t+1/N) - \phi(x;p,t) = \psi^+(p)\phi(x;p+1/N,t)$$
$$+\psi^-(p)\phi(x;p-1/N,t)$$
$$-\psi^+(p)\phi(x;p,t) - \psi^-(p)\phi(x;p,t).$$

(A9)

Notice that

$$\phi(x;p,t+1/N) = \psi^+(p)\phi(x;p+1/N,t) + \psi^-(p)\phi(x;p-1/N,t)$$
$$+\left[1-\psi^+(p)-\psi^-(p)\right]\phi(x;p,t).$$

(A10)

From the Taylor series expansions at p and t, we have that

$$\phi(x;p,t+1/N) - \phi(x;p,t) \approx \frac{1}{N}\frac{\partial\phi(x;p,t)}{\partial t},$$
$$\psi^+(p)[\phi(x;p+1/N,t) - \phi(x;p,t)] \approx \psi^+(p)\left[\frac{1}{N}\frac{\partial\phi(x;p,t)}{\partial p} + \frac{1}{2N^2}\frac{\partial^2\phi(x;p,t)}{\partial p^2}\right]$$
$$\psi^-(p)[\phi(x;p-1/N,t) - \phi(x;p,t)] \approx \psi^-(p)\left[-\frac{1}{N}\frac{\partial\phi(x;p,t)}{\partial p} + \frac{1}{2N^2}\frac{\partial^2\phi(x;p,t)}{\partial p^2}\right].$$

(A11)

Thus, the backward Kolmogorov equation corresponding to Eq. (A9) can be obtained, which is

$$\frac{\partial\phi(x;p,t)}{\partial t} = B^{(1)}(p)\frac{\partial\phi(x;p,t)}{\partial p} + B^{(2)}(p)\frac{\partial^2\phi(x;p,t)}{\partial p^2}.$$

(A12)

A.3. Derivation of Eq. (7)

The solution of equation

$$B^{(1)}(p)\frac{du(p)}{dp} + B^{(2)}(p)\frac{d^2u(p)}{dp^2} = 0$$

(A13)

can be expressed as

$$u(p) = \int_0^p H(s)ds\bigg/\int_0^1 H(s)ds$$

(A14)

(Ewens, 2004), where for $Nw \ll 1$ (i.e., weak selection), we have the approximation

$$
\begin{aligned}
H(s) &\equiv \exp\left[-\int_0^s \frac{B^{(1)}(z)}{B^{(2)}(z)}\,dz\right]\\
&= \exp\left[-2N\int_0^s \frac{w(\pi_C(z)-\pi_D(z))}{2(1-w)+w(\pi_C(z)+\pi_D(z))}\,dz\right]\\
&\approx \exp\left[-Nw\int_0^s (\pi_C(z)-\pi_D(z))\,dz\right].
\end{aligned}
$$

(A15)

This also implies that

$$
\begin{aligned}
u(p) &= \frac{\int_0^p e^{-Nw\int_0^s(\pi_C(z)-\pi_D(z))dz}ds}{\int_0^1 e^{-Nw\int_0^s(\pi_C(z)-\pi_D(z))dz}ds}\\
&\approx p - Nw\left[\int_0^p G(s)ds - p\int_0^1 G(s)ds\right],
\end{aligned}
$$

(A16)

where

$$G(s) = \int_0^s (\pi_C(z)-\pi_D(z))dz = s(rb-c-rd) + \frac{s^2}{2}r(2d-\widetilde{d}).$$ (A17)

Therefore, we have that

$$u(p) = p + \frac{p(1-p)Nw}{2}\left[-(rd-(rb+c)) + \frac{1+p}{3}r(2d-\widetilde{d})\right].$$

(A18)

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