

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

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### 3 **Abstract**

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

18

19 **Key words:** Inclusive fitness, kin selection, altruism, cooperation, Prisoner's dilemma  
20 game

## 21 1 Introduction

22 As pointed out by Nowak, cooperation means that selfish replicators forgo some of their  
23 reproductive potential to help one another, but natural selection implies competition and  
24 therefore opposes cooperation unless a specific mechanism is at work [13, 14, 20]. **More-**  
25 **over, in order to show a general theoretical framework, Nowak also summa-**  
26 **rized the five rules for the evolution of cooperation, which are kin selection,**  
27 **direct reciprocity, indirect reciprocity, network reciprocity and group selec-**  
28 **tion, respectively [14].** Kin selection theory developed by Hamilton [6, 7, 12] is one  
29 of the most important theoretical mechanisms for driving the evolution of cooperation  
30 behavior [12, 13]. This theory says that: individuals are predicted to behave more al-  
31 truistically and less competitively toward their relatives, because they share a relatively  
32 high proportion of their genes; and, consequently, by helping a relative to reproduce, an  
33 individual passes its gene to the next generation [6, 7, 12]. In order to show this succinct-  
34 ly, based on the Prisoner's Dilemma (PD) game (i.e., a cooperator is someone who pays  
35 a cost,  $c$ , for another individual to receive a benefit,  $b$ , and a defector has no cost and  
36 does not deal out benefits) [12, 13] and the concept of Hamilton's inclusive fitness [6, 7],  
37 the inclusive payoff matrix for the pairwise interactions between relatives can be given  
38 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  
39 assumed that the coefficient of relatedness between all relatives is the same, denoted by  $r$ ;  
40 and (ii) the entry  $(1+r)(b-c)$  (or  $rb-c$ ) is the inclusive payoff of an individual displaying  
41 cooperation (C) against an individual displaying C (or defection (D)), and  $b-rc$  (or 0) is  
42 the inclusive payoff of an individual displaying D against an individual displaying C (or  
43 D) [12, 13]. Therefore, cooperation will be favored by natural selection if  $rb-c > 0$  (where  
44 the term  $rb-c$  can be used as a measure of kin selection advantage), or the coefficient of  
45 relatedness must exceed the cost-to-benefit ratio of the altruistic act:  $r > c/b$  [13]. This is  
46 called the Hamilton's rule, and it provides a fundamental logic for explaining the conflicts

47 of interest between relatives. Of course, we also note that some studies considered the  
48 limitations of the concept of inclusive fitness [1,16].

49 Although Hamilton's rule (or kin selection theory) has been successfully used to explain  
50 why relatives more tend to cooperate with each other [13], the kin competition (i.e.,  
51 competition between relatives) caused by the altruistic action among relatives and its effect  
52 on kin selection have also been investigated by many studies [4–6,9,17–19,21,22,26]. The  
53 basic idea behind these studies is that kin competition can reduce, and even totally negate,  
54 the kin-selected benefits of altruism toward relatives [5,26]. For example, Hamilton pointed  
55 out that limited dispersal of individuals from the natal group (population viscosity) would  
56 increase the relatedness competition between interacting individuals, and so would be an  
57 important factor favoring altruism [6,8–10]. However, limited dispersal of individuals may  
58 also increase relatedness between potential competitors, which opposes altruism [8,10,17].  
59 Thus, a fundamental question is, what is the net effect of these two opposing forces? [26].  
60 Some studies have shown that a lower level of dispersal can favor altruism, but, at the  
61 same time, this effect can also be cancelled by the increased kin competition [18,21].

62 In 1980s, Grafen first incorporated the effect of kin competition on kin selection in-  
63 to Hamilton's rule, and he developed a concise theoretical and logical framework as an  
64 extension of Hamilton's rule [5]. Grafen's model includes all individuals whose fitness is  
65 affected by an altruistic act, which is given by  $r_{xy}b - c - r_{xe}d > 0$  (for convenience, we  
66 call it Grafen's inequality), where  $r_{xy}$  is the altruist's relatedness to the beneficiary of its  
67 altruism (i.e.,  $r$  in standard Hamilton's rule),  $r_{xe}$  is the altruist's relatedness to the indi-  
68 viduals who suffer the increased competition from the beneficiary (and possibly reduced  
69 competition from the altruist), and  $d$  is the general decrement in fitness associated with  
70 the altruistic act [5]. The basic idea behind Grafen's inequality is that as the altruist  
71 becomes more related to the competitors of the beneficiary (increasing  $r_{xe}$ ) and/or the  
72 altruistic act increases the general level of competition (increasing  $d$ ), the kin selection  
73 advantage in being altruistic is reduced [5,19,26]. Moreover, Queller pointed out that

74 Hamilton's rule is equivalent to Grafen's inequality, as long as relatedness is measured at  
75 the correct scale [19,26]. In fact, in order to incorporate competition between relatives into  
76 empirical studies of kin selection, some methodologies and ecological factors influencing  
77 kin selection and kin competition have also been considered by many studies [17,26]. For  
78 example, Taylor presented a simple patch-structured model of the evolution of cooperation  
79 wherein cooperation increases the competition for space experienced by the progeny of a  
80 cooperator [17,22,26], etc.

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

96 Notice that an interaction between a pair of cooperators contains two altruistic acts.  
97 Thus, similar to the basic idea behind Grafen's inequality [5], we can use  $\tilde{d}$  to denote the  
98 general decrement in fitness (or payoff) associated with an interaction between a pair of  
99 cooperators, where  $\tilde{d}$  should be reasonably defined to be in the interval  $d \leq \tilde{d} \leq 2d$  since,  
100 in general, the effect of a mutually altruistic act on kin competition should be larger than

101 the effect of an unilaterally altruistic act, but should be less than the sum of the effects  
102 of two independent unilateral altruistic acts. For example, mutually altruistic acts may  
103 be more conducive to increasing carrying capacity [17]. This implies that the effect of a  
104 mutually altruistic act on kin competition should not be regarded as a simple addition of  
105 the effects of two unilaterally altruistic acts. Based on this definition, the inclusive payoff  
106 of an individual displaying C can be given by  $(1 + r)(b - c) - r\tilde{d}$  when it plays against  
107 an individual displaying C. All of these assumptions and definitions based on PD game  
108 between relatives lead to a natural question: if the standard Hamilton's rule holds (i.e.,  
109  $r > c/b$ ), how does kin competition that is associated with both interactions between a  
110 pair of cooperators and between a cooperator and a defector influence the evolutionary  
111 dynamics of cooperation behavior in a kin population?

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

## 118 2 A PD game between relatives with kin competition

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

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

121 where the entry  $(1 + r)(b - c) - r\tilde{d}$  (or  $rb - c - rd$ ) is the inclusive payoff of an individual  
122 displaying C against an individual displaying C (or D), and  $b - rc - rd$  (or 0) the inclusive  
123 payoff of an individual displaying D against an individual displaying C (or D). For this  
124 inclusive payoff matrix, we assume that: (i) the coefficient of relatedness between all

125 individuals is the same, denoted by  $r$  [12, 13]; (ii) the standard Hamilton's rule always  
 126 holds (i.e.,  $rb - c > 0$ ); (iii) both parameters  $d$  and  $\tilde{d}$  are positive and  $d \leq \tilde{d} \leq 2d$ ; and  
 127 (iv) the occurrence of pairwise interactions is random. **We note that some studies**  
 128 **have proposed the concept of universal dilemma strength in symmetric two-**  
 129 **phenotype reciprocal games and proved that this concept can be successfully**  
 130 **applied to the classification of payoff matrix structures [2, 11, 25]. However,**  
 131 **we here mainly focus our attention on the effect of kin competition on the**  
 132 **evolution of cooperation in a PD game.**

133 For the evolutionary dynamics of cooperation based on the inclusive payoff matrix in  
 134 Eq. (1), three possible cases are needed to be considered. First, if Grafen's inequality  
 135 holds (i.e.,  $rb - c - rd > 0$ ), then we must have  $((1 + r)(b - c) - r\tilde{d}) - (b - rc - rd) =$   
 136  $rb - c - r(\tilde{d} - d) > 0$  since  $d \leq \tilde{d} \leq 2d$ . This implies that strategy C is always favored  
 137 by natural selection if Grafen's inequality holds. Second, if  $rb - c - rd < 0$  (i.e., Grafen's  
 138 inequality doesn't hold) and  $rb - c - r(\tilde{d} - d) < 0$ , then strategy C can never be favored  
 139 by natural selection. This implies that the kin selection advantage is totally negated  
 140 by the effect of kin competition. Therefore, it is easy to see that only strategy C is an  
 141 evolutionarily stable strategy (ESS) [12, 13] if and only if Grafen's inequality holds; and  
 142 only strategy D is an ESS if and only if  $rb - c - r(\tilde{d} - d) < 0$ . Finally, for the situation  
 143 with  $rb - c - rd < 0$  but  $rb - c - r(\tilde{d} - d) > 0$  (i.e.,  $r(\tilde{d} - d) < rb - c < rd$ ), if we use  $x$  to  
 144 denote the frequency of strategy C in the population, then there must exist a

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

145 such that the expected inclusive payoff of strategy C, denoted by  $\pi_C$ , is larger (or less)  
 146 than the expected inclusive payoff of strategy D, denoted by  $\pi_D$ , if  $x > x^*$  (or  $x < x^*$ ),  
 147 where  $\pi_C$  and  $\pi_D$  are given by

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

148 respectively. Therefore, according to the standard definition of ESS [12], strategies C and  
 149 D are both ESSs if  $r(\tilde{d} - d) < rb - c < rd$ . This shows clearly that strategy C could be  
 150 also an ESS even if Grafen's inequality doesn't hold.

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

### 157 **3 Stochastic evolutionary dynamics of cooperation in a fi-** 158 **nite kin population**

159 Consider a finite kin population with fixed size  $N$  and assume that the selection is weak  
 160 [13, 15]. Without loss of generality, the inclusive fitness of C-strategist, denoted by  $f_C$ ,  
 161 can be defined as  $f_C = (1 - w) + w\pi_C$ , where the parameter  $w$  represents the selection  
 162 intensity with  $w \in [0, 1]$  [13]. Similarly, the inclusive fitness of D-strategist, denoted by  
 163  $f_D$ , is given by  $f_D = (1 - w) + w\pi_D$ .

164 Based on the diffusion approximation of the Moran process [23, 24, 27, 28], we define  
 165 that, at each time step with length  $1/N$ , the transition probability that the system state  
 166 (i.e., the frequency of C in the population) changes from  $x$  to  $x + 1/N$ , denoted by  $\psi^+$ , is  
 167  $\psi^+(x) = x(1 - x)f_C(x) / (xf_C(x) + (1 - x)f_D(x))$ , and, similarly, the transition probability  
 168 that the system state changes from  $x$  to  $x - 1/N$ , denoted by  $\psi^-$ , is  $\psi^-(x) = x(1 -$   
 169  $x)f_D(x) / (xf_C(x) + (1 - x)f_D(x))$ . Let  $\phi(x; t)$  denote the probability density distribution  
 170 that the frequency of C equals exactly  $x$  at time  $t$ . Then, the diffusion approximation of  
 171  $\phi(x; t)$ , or the Fokker-Planck equation of  $\phi(x; t)$ , is given by

$$\frac{\partial \phi(x; t)}{\partial t} = -\frac{\partial}{\partial x} \left[ B^{(1)}(x)\phi(x; t) \right] + \frac{\partial^2}{\partial x^2} \left[ B^{(2)}(x)\phi(x; t) \right], \quad (4)$$



172 where  $B^{(1)}(x) = \psi^+(x) - \psi^-(x)$  and  $B^{(2)}(x) = \psi^+(x) + \psi^-(x)/2N$  [23, 24, 27, 28](the  
173 mathematical derivation is shown in Appendix). Here,  $B^{(1)}(x)$  is called the drift term  
174 (that is due to fitness difference) and  $\sqrt{2B^{(2)}(x)}$  the diffusion term [23, 24, 27, 28]. From  
175 the transition probabilities  $\psi^+(x)$  and  $\psi^-(x)$ , we can see also that both  $x = 0$  and  $x = 1$   
176 are absorbing boundaries [27, 28].

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

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

182 [23, 24, 27, 28](the mathematical derivation is shown in Appendix).

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

### 186 3.1 Fixation probability of strategy C

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

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

191 with the boundary conditions  $u(0, t) = 0$  and  $u(1, t) = 1$  [3]. The ultimate probability  
192  $u(p)$  of fixation of strategy C is defined by  $u(p) = \lim_{t \rightarrow \infty} u(p, t)$ . Since  $x = 1$  is an absorbing  
193 boundary of Eq. (4), the limit  $u(p)$  exists and it is the stationary solution of Eq. (6), i.e.,  
194  $u(p)$  satisfies  $B^{(1)}(p)(du(p)/dp) + B^{(2)}(p)(d^2u(p)/dp^2) = 0$ .

195 From some previous studies about the stochastic evolutionary game dynamics in a  
 196 finite population [23, 24, 27, 28], for  $Nw \ll 1$  (i.e., the selection is weak), the fixation  
 197 probability  $u(p)$  can be given by

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

198 (the mathematical derivation is shown in Appendix). In general, for a given initial fre-  
 199 quency of strategy C,  $p$ , cooperation is considered to be favored by natural selection if the  
 200 fixation probability of strategy C is larger than its initial frequency, i.e.,  $u(p) > p$  [13].  
 201 Thus, Eq. (7) implies that for  $r(\tilde{d} - d) < rb - c < rd$  and  $Nw \ll 1$ , the fixation probability  
 202 of strategy C is larger than its initial frequency  $p$  if  $x^* < (1 + p)/3$ , or if kin selection  
 203 advantage satisfies  $rb - c > r[(1 - 2p)d + (1 + p)\tilde{d}]/3$ . Specifically, for  $p = 1/N$  with  
 204 large  $N$ , we can see that  $u(1/N) > 1/N$  if  $x^* < 1/3$  (this is also called the one-third law  
 205 by Nowak et al. [13, 15]), or if kin selection advantage satisfies

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

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

209 On the other hand, let  $u'(1 - p)$  denote the probability that strategy D is fixed at time  
 210  $t$  if its initial frequency is  $1 - p$ . Then, similar to the analysis of  $u(p)$ ,  $u'(1 - p)$  can be  
 211 expressed as

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

212 and we must have  $u(p) + u'(1 - p) = 1$ .

### 213 3.2 Mechanism driving cooperation to be favored by natural selection

214 For the fixation probability of strategy C with  $u(1/N) > 1/N$ , a further question is what  
 215 force drives strategy C being favored by natural selection in a finite kin population. In

216 order to answer this question, we consider first the concept of mean effective fixation  
 217 time [3, 28], and, then, consider the average inclusive fitness about the mean effective  
 218 fixation time [3, 28].

### 219 Mean effective fixation time

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

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

223 with boundary conditions  $\vartheta(t; 0) = \vartheta(t; 1) = 0$  [3].

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

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

226 with boundary condition  $\bar{t}(0) = \bar{t}(1) = 0$ . Following Ewens [3, 28], the solution of this  
 227 equation,  $\bar{t}(p)$ , can be expressed as

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

228 where

$$t(x; p) = \frac{u'(1-p)}{B^{(2)}(x)H(x)} \int_0^x H(s) ds \quad (13)$$

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

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

230 for  $p \leq x \leq 1$ . Notice that  $H(x) \approx 1$ ,  $B^{(2)}(x) \approx x(1-x)/2N$ ,  $u'(1-p) \approx 1-p$  and  
 231  $u(p) \approx p$  if  $Nw \ll 1$ . Thus, under the weak selection, the mean fixation time  $\bar{t}(p)$  can be  
 232 approximated as

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

233 Here, the integral  $\int_{x_1}^{x_2} t(x; p)dx$  represents the mean time that the frequency of C,  $x$ ,  
 234 spends in the interval  $(x_1, x_2)$  before absorption. Moreover,  $\int_{x_1}^{x_2} \psi^+(x)t(x; p)dx$  represents  
 235 the mean time that the system state jumps from  $x$  to  $x + 1/N$  when  $x$  is in the interval  
 236  $(x_1, x_2)$ , and, similarly,  $\int_{x_1}^{x_2} \psi^-(x)t(x; p)dx$  represents the mean time that the system state  
 237 jumps from  $x$  to  $x - 1/N$  when  $x$  is in the interval  $(x_1, x_2)$ . Notice that  $\int_{x_1}^{x_2} \psi^+(x)t(x; p)dx +$   
 238  $\int_{x_1}^{x_2} \psi^-(x)t(x; p)dx < \int_{x_1}^{x_2} t(x; p)dx$  since the system state doesn't always jump from  $x$  to  
 239  $x \pm 1/N$ . Thus, we can call  $\int_{x_1}^{x_2} (\psi^+(x) + \psi^-(x))t(x; p)dx$  the mean effective time that  $x$   
 240 spends in the interval  $(x_1, x_2)$  [3, 28].

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

$$\begin{aligned} \bar{\tau}(p) &= \int_0^1 (\psi^+(x) + \psi^-(x))t(x; p)dx \\ &= \int_0^p (\psi^+(x) + \psi^-(x))t(x; p)dx + \int_p^1 (\psi^+(x) + \psi^-(x))t(x; p)dx \\ &= 2Nu'(1-p) \int_0^p xdx + 2Nu(p) \int_p^1 (1-x)dx \\ &= N \left[ p^2 + u(p) - 2pu(p) \right]. \end{aligned} \quad (16)$$

### 243 Average inclusive fitness about the mean effective fixation time

244 Based on the concept of the mean effective fixation time  $\bar{\tau}(p) = \int_0^1 (\psi^+(x) + \psi^-(x))t(x; p)dx$ ,  
 245 **the total inclusive fitness of strategy C about  $\bar{\tau}(p)$  is  $\int_0^1 f_C(x)(\psi^+(x) + \psi^-(x))t(x; p)dx$ ,**

246 **then**, the average inclusive fitness of strategy C about  $\bar{\tau}(p)$  can be defined as  $\bar{f}_{C,\bar{\tau}(p)} =$   
247  $\bar{\tau}(p)^{-1} \int_0^1 f_C(x)(\psi^+(x) + \psi^-(x))t(x; p)dx$  **which means the average inclusive fitness**  
248 **of strategy C in the effective fixation process.** And, similarly, the average inclusive  
249 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,  
250 for  $Nw \ll 1$ ,  $\bar{f}_{C,\bar{\tau}(p)}$  can be given by

$$\begin{aligned}
\bar{f}_{C,\bar{\tau}(p)} &= \frac{1}{\bar{\tau}(p)} \left[ \int_0^p f_C(x)(\psi^+(x) + \psi^-(x))t(x; p)dx \right. \\
&\quad \left. + \int_p^1 f_C(x)(\psi^+(x) + \psi^-(x))t(x; p)dx \right] \\
&= \frac{2N}{\bar{\tau}(p)} \left[ u'(1-p) \int_0^p x f_C(x)dx + u(p) \int_p^1 (1-x) f_C(x)dx \right] \\
&= (1-w) + w(rb - c - rd) \\
&\quad + \frac{w}{3} \left( (1+r)(b-c) - r\tilde{d} - (rb - c - rd) \right) \cdot \frac{2p^3 + u(p)(1-3p^2)}{p^2 + u(p)(1-2p)} \\
&= (1-w) + w(rb - c - rd) \\
&\quad + \frac{w}{3} \left( b - rc + rd - r\tilde{d} \right) \cdot \frac{2p^3 + u(p)(1-3p^2)}{p^2 + u(p)(1-2p)} ; \tag{17}
\end{aligned}$$

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

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

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

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

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

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

255 i.e.,  $\bar{f}_{C,\bar{\tau}(1/N)} > \bar{f}_{D,\bar{\tau}(1/N)}$  if  $rb - c > r(\tilde{d} + d)/3$ . This result is exactly the same as the  
256 condition that leads to the fixation probability of strategy C,  $u(1/N)$ , being larger than  
257  $1/N$  (see the inequality in Eq. (8)).

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

## 265 4 Discussion

266 In this study, based on the standard PD game between relatives [12,13], the effects of both  
267 kin selection and kin competition on the stochastic evolutionary dynamics of cooperation  
268 in a finite kin population are investigated. Following Grafen's basic idea for the effect of  
269 kin competition on Hamilton's rule [5], we incorporate the kin competition into a PD game  
270 between relatives. However, differently from Grafen's inequality, we here emphasize the  
271 difference between the effects of mutually and of unilaterally altruistic acts on kin com-  
272 petition (i.e., the difference between the effect of an interaction between pair cooperators  
273 and the effect of an interaction between a cooperator and defector). On the other hand,  
274 similar to [13], we also assume that the coefficient of relatedness between all individuals is  
275 the same. Although this assumption is not true, it should be considered to be a reasonable  
276 simplification for revealing how kin competition influences the evolution of cooperation.  
277 Finally, in this study we always assume that the standard Hamilton's rule holds.

278 For the main results of this paper, we first show that based on the inclusive payoff  
279 matrix in Eq. (1) and the standard definition of ESS [12], the strategy C is the unique  
280 ESS if Grafen's inequality holds (i.e.,  $rb - c - rd > 0$ ); only strategy D is an ESS if  
281  $rb - c - r(\tilde{d} - d) < 0$ ; and strategies C and D are both ESSs if  $r(\tilde{d} - d) < rb - c < rd$ .  
282 So, strategy C could be also an ESS even if Grafen's inequality doesn't hold. Secondly,  
283 in order to reveal the evolutionary dynamics of cooperation in a finite kin population

284 with fixed size  $N$ , we show that for the situation with large  $N$  and weak selection, if the  
285 inclusive payoff matrix in Eq. (1) satisfies condition  $r(\tilde{d} - d) < rb - c < rd$ , then, when  
286 the initial frequency of strategy C is  $1/N$ , the fixation probability of strategy C is larger  
287 than  $1/N$  if and only if  $rb - c > r(\tilde{d} + d)/3$ . This result not only exactly matches Nowak et  
288 al.'s one-third law [13, 15] but also shows clearly that strategy C still could be favored by  
289 natural selection even if Grafen's inequality doesn't hold. Finally, based on the concept of  
290 mean effective fixation time, we show that the evolutionary biological mechanism driving  
291 cooperation to be favored by natural selection in a finite kin population is that the average  
292 inclusive fitness of strategy C about the mean effective fixation time is larger than the  
293 average inclusive fitness of strategy D about the mean effective fixation time. All these  
294 results clearly indicate that, even in the simplest case, Grafen's inequality should be only  
295 a sufficient condition, not a necessary condition, for the evolution of cooperative behavior  
296 in a kin population.

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

## 301 Appendix

### 302 Derivation of Eq. (4)

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

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

304 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

305 at  $x$  and  $t$ , which are

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

306 Notice that

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

307

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

308 and

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



309 Then the right hand of Eq. (A1),

$$\begin{aligned}
& \phi(x - 1/N; t)\psi^+(x - 1/N) + \phi(x + 1/N; t)\psi^-(x + 1/N) \\
& - \phi(x; t)\psi^-(x) - \phi(x; t)\psi^+(x) \\
\approx & \phi(x; t)\psi^+(x) + \phi(x; t) \left[ -\frac{\partial}{\partial x}\psi^+(x)\frac{1}{N} + \frac{\partial^2}{\partial x^2}\psi^+(x)\frac{1}{2N^2} \right] \\
& - \psi^+(x)\frac{\partial}{\partial x}\phi(x; t)\frac{1}{N} + \left[ \frac{\partial}{\partial x}\phi(x; t) \right] \left[ \frac{\partial}{\partial x}\psi^+(x) \right] \frac{1}{N^2} \\
& + \psi^+(x)\frac{\partial^2}{\partial x^2}\phi(x; t)\frac{1}{2N^2} \\
& + \phi(x; t)\psi^-(x) + \phi(x; t) \left[ \frac{\partial}{\partial x}\psi^-(x)\frac{1}{N} + \frac{\partial^2}{\partial x^2}\psi^-(x)\frac{1}{2N^2} \right] \\
& + \psi^-(x)\frac{\partial}{\partial x}\phi(x; t)\frac{1}{N} + \left[ \frac{\partial}{\partial x}\phi(x; t) \right] \left[ \frac{\partial}{\partial x}\psi^-(x) \right] \frac{1}{N^2} \\
& + \psi^-(x)\frac{\partial^2}{\partial x^2}\phi(x; t)\frac{1}{2N^2} \\
& - \phi(x; t)\psi^-(x) - \phi(x; t)\psi^+(x) \\
= & \phi(x; t) \left[ \frac{\partial(\psi^-(x) - \psi^+(x))}{\partial x}\frac{1}{N} \right] + (\psi^-(x) - \psi^+(x))\frac{1}{N}\frac{\partial\phi(x; t)}{\partial x} \\
& + \frac{\partial^2(\psi^-(x) + \psi^+(x))\phi(x; t)}{\partial x^2}\frac{1}{2N^2} \\
& + \left[ \frac{\partial}{\partial x}\phi(x; t) \right] \left[ \frac{\partial}{\partial x}(\psi^-(x) + \psi^+(x)) \right] \frac{1}{N^2} \\
& + (\psi^-(x) + \psi^+(x))\frac{1}{2N^2}\frac{\partial^2}{\partial x^2}\phi(x; t) \\
= & \frac{1}{N}\frac{\partial}{\partial x} [(\psi^-(x) - \psi^+(x))\phi(x; t)] + \frac{1}{2N^2}\frac{\partial^2}{\partial x^2} [(\psi^-(x) + \psi^+(x))\phi(x; t)] . \quad (\text{A6})
\end{aligned}$$

310 Thus, Eq. (A1) can be approximated as

$$\frac{\partial\phi(x; t)}{\partial t} = -\frac{\partial}{\partial x} \left[ B^{(1)}(x)\phi(x; t) \right] + \frac{\partial^2}{\partial x^2} \left[ B^{(2)}(x)\phi(x; t) \right] , \quad (\text{A7})$$

311 where

$$\begin{aligned}
B^{(1)}(x) &= \psi^+(x) - \psi^-(x) , \\
B^{(2)}(x) &= \frac{\psi^+(x) + \psi^-(x)}{2N} .
\end{aligned} \quad (\text{A8})$$

312 **Derivation of Eq. (5)**

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

$$\begin{aligned}\phi(x; p, t + 1/N) - \phi(x; p, t) &= \psi^+(p)\phi(x; p + 1/N, t) \\ &\quad + \psi^-(p)\phi(x; p - 1/N, t) \\ &\quad - \psi^+(p)\phi(x; p, t) - \psi^-(p)\phi(x; p, t) .\end{aligned}\tag{A9}$$

315 Notice that

$$\begin{aligned}\phi(x; p, t + 1/N) &= \psi^+(p)\phi(x; p + 1/N, t) + \psi^-(p)\phi(x; p - 1/N, t) \\ &\quad + [1 - \psi^+(p) - \psi^-(p)]\phi(x; p, t) .\end{aligned}\tag{A10}$$

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

$$\begin{aligned}\phi(x; p, t + 1/N) - \phi(x; p, t) &\approx \frac{1}{N} \frac{\partial \phi(x; p, t)}{\partial t} , \\ \psi^+(p)[\phi(x; p + 1/N, t) - \phi(x; p, t)] &\approx \psi^+(p) \left[ \frac{1}{N} \frac{\partial \phi(x; p, t)}{\partial p} + \frac{1}{2N^2} \frac{\partial^2 \phi(x; p, t)}{\partial p^2} \right] \\ \psi^-(p)[\phi(x; p - 1/N, t) - \phi(x; p, t)] &\approx \psi^-(p) \left[ -\frac{1}{N} \frac{\partial \phi(x; p, t)}{\partial p} + \frac{1}{2N^2} \frac{\partial^2 \phi(x; p, t)}{\partial p^2} \right] .\end{aligned}\tag{A11}$$

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

$$\frac{\partial \phi(x; p, t)}{\partial t} = B^{(1)}(p) \frac{\partial \phi(x; p, t)}{\partial p} + B^{(2)}(p) \frac{\partial^2 \phi(x; p, t)}{\partial p^2} .\tag{A12}$$

319 **Derivation of Eq. (7)**

320 The solution of equation

$$B^{(1)}(p) \frac{du(p)}{dp} + B^{(2)}(p) \frac{d^2 u(p)}{dp^2} = 0\tag{A13}$$

321 can be expressed as

$$u(p) = \frac{\int_0^p H(s) ds}{\int_0^1 H(s) ds} \quad (\text{A14})$$

322 [3], where for  $Nw \ll 1$  (i.e., weak selection), we have the approximation

$$\begin{aligned} H(s) &\equiv \exp \left[ - \int_0^s \frac{B^{(1)}(z)}{B^{(2)}(z)} dz \right] \\ &= \exp \left[ -2N \int_0^s \frac{w(\pi_C(z) - \pi_D(z))}{2(1-w) + w(\pi_C(z) + \pi_D(z))} dz \right] \\ &\approx \exp \left[ -Nw \int_0^s (\pi_C(z) - \pi_D(z)) dz \right]. \end{aligned} \quad (\text{A15})$$

323 This also implies that

$$\begin{aligned} u(p) &= \frac{\int_0^p e^{-Nw \int_0^s (\pi_C(z) - \pi_D(z)) dz} ds}{\int_0^1 e^{-Nw \int_0^s (\pi_C(z) - \pi_D(z)) dz} ds} \\ &\approx p - Nw \left[ \int_0^p G(s) ds - p \int_0^1 G(s) ds \right], \end{aligned} \quad (\text{A16})$$

324 where

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

325 Therefore, we have that

$$u(p) = p + \frac{p(1-p)Nw}{2} \left[ -(rd - (rb + c)) + \frac{1+p}{3} r(2d - \tilde{d}) \right]. \quad (\text{A18})$$

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