Non-kin selection enhances complexity in cooperation: A unified quantitative law

Xiaoliang Wang[1,2]*, Andrew Harrison[3]*

1 College of Life Sciences, Zhejiang University, Hangzhou 310058, China

2 School of Physical Sciences, University of Science and Technology of China, Hefei 230026, China

3 Department of Mathematical Sciences, University of Essex, Colchester CO4 3SQ, UK

*Correspondence: (X.W.) wxliang@mail.ustc.edu.cn; (A.H.) harry@essex.ac.uk;

Abstract

How cooperation evolves in the presence of selfishness is a core problem in evolutionary biology. Selfish individuals tend to benefit themselves, which makes it harder to maintain cooperation between unrelated individuals and for living systems to evolve towards complex organizations. The general evolutionary model presented here identifies that non-kin selection is the root cause for cooperation between unrelated individuals and can enable and maintain higher complexity of biological organizations (the coexistence of more individuals of different types). The maintained number of genotypes within a cooperation organization is shown to follow a universal exponential law as a quantitative function of the population size and non-kin selection strength, showing a gene-pool-size invariance. Our results highlight that non-kin selection may be a hallmark of biological evolution, and play an important role in shaping life's potentials.

Keywords: Non-kin selection; evolutionary origins; evolutionary theory; biological evolution

1. Introduction

Every level of biological organization involves cooperation among its components. Atoms cooperate (interact) in a DNA structure, genes cooperate (interact) in a cell and animals cooperate (mutually benefit) in a society. The major evolutionary transitions in biology [1] reveal an increasing complexity in cooperation. Many explanations for cooperation [1-29] have been proposed, such as kin selection [4,8,9], group selection [10-13], 'tit-for-tat' strategy [14-16], reciprocity [17-19], policing and punishment [4,20], and biological range expansion [21-23]. However, how higher complexity can be maintained within a cooperating structure has not been explained directly.

Kin selection theory, which is encapsulated in Hamilton's rule [9]: $rb - c > 0$ (r is the genetic relatedness between actor and recipient, b and c are benefits and costs of cooperation, respectively) dominates thinking in current evolutionary biology. The theory argues that cooperation will evolve if the benefits produced by an individual's cooperative behavior lead to individuals with genes that increase their inclusive fitness [9,30]. Such an explanation can only account for the maintenance of cooperation among genetic relatives, especially in animal societies [31-33].

Although many theories and models have also been proposed for cooperation between non-kin [34-36], there are few unified evolutionary models and explanations for the continued cooperation between kin and that between non-kin. Especially, cooperation between non-kin has universally occurred in cooperation between genomes, organelles and even humans [29,34,37]. A unified evolutionary theory is important as it can help to reveal the evolutionary rules for all organisms. Furthermore, how and which factors influence biological complexity is unclear. There is an obvious lack of a quantitative theory to determine the functional

relationship.

We develop a general evolutionary model here, based on a quantitative individual-based approach (stepping stone model) [38-41], to explain the maintenance of cooperation between both related and unrelated individuals. We find non-kin selection can enable and maintain higher complexity in cooperation. We also identify a scale-invariant exponential function that characterizes the complexity in cooperation.

2. Models and methods

The evolutionary model is based on the stepping stone model (SSM) for well-mixed finite populations (i.e. we do not consider the spatial structure of the population), which is based on stochastic processes. The SSM is characterized by the branching process, which is based on fate decisions of individuals.

The design of the evolutionary model is established in the context of social games between a cooperator group and a defector group (Fig. 1). Gene pools in our model continually supply new members for corresponding groups (e.g. through the reproduction of other individuals). The evolutionary dynamics of the model is designed as the following: in each round of the game (time step), the winning side has a chance to add one new member from the gene pool into its group, and the losing side will remove one old member from its group (the total number of individuals within the whole population is thus conserved, i.e. finite populations). After one side completely takes over the whole population, the updating continues. During this process, in each round of updating, one new member is selected from the gene pool into the population, and at the same time one old member in the population is removed.
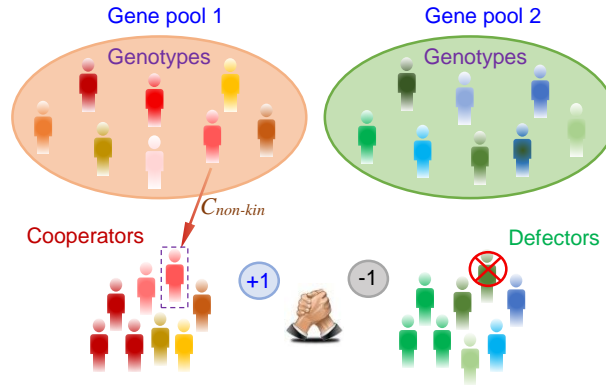

Figure 1. Illustration of the evolutionary model for social games (illustrated with humans): the gene pool acts as the external environmental resources that can supply sufficient new members for the cooperation organization, corresponding to the fact that all elements composing organisms growing on the earth are selected from external environmental resources.

During games between cooperator and defector groups, the chance to add one new member for both sides is proportional to the current fitness of these two competition groups. The fitness of each side is calculated as: $w_C = \sum_{i=1}^{N_{gety}} w_{gety,i}$, $w_D = \rho(1-f)$. Here, $w_{gety,i}$ is the fitness of cooperators with the genotype i, N_{gety} is the total number of cooperator genotypes in the gene pool, ρ is the resultant fitness of defectors and f is the frequency of all cooperators in the whole population.

Throughout the whole evolutionary process, the removed member is randomly selected from the group with the probability proportional to its abundance in that group, while the newly added member is chosen randomly from the gene pool with the relative reproduction probability (fitness). In the model, the reproduction probability of the cooperator genotype i is expressed as:

Kin selection   **Non-kin selection**

$$w_{gety,i} = (1 - \Delta)\rho f_{gety,i} + b \left[(1 - C_{non\text{-}kin}) \cdot f_{gety,i} + C_{non\text{-}kin} \frac{\left(f - f_{gety,i}\right)}{N_{gety}} \right] \quad (1)$$

where Δ is the cost of cooperation [42], and $f_{gety,i}$ is the frequency of cooperator genotype i in the whole population. b is the additional benefits that a cooperator obtains from kin selection or non-kin selection. When only kin selection acts, cooperators can get the additional benefits only from those with the same genotypes (i.e. relatives). When non-kin selection acts, the additional benefits can be got from those cooperators with different genotypes (non-kin). $C_{non\text{-}kin} \in [0, 1]$ is the coefficient which can be used to tune the non-kin selection strength.

Accordingly, the selection probability (relative fitness) of the genotype i from the gene pool is:

$$P_{gety,i} = \frac{w_{gety,i}}{w_C} \quad (2)$$

$$\sum_{i=1}^{N_{gety}} P_{gety,i} = 1 \quad (3)$$

From Eqs. (1) and (2), we can see that when $C_{non\text{-}kin} = 1$, the newly added member can be selected with a probability that is genetically independent of old members in the group, i.e. non-kin selection. When $C_{non\text{-}kin} = 0$, the addition of new members will completely depend on corresponding old genetically related members, i.e. kin selection. The main model parameters are listed in Table 1.

Table 1: Parameters defined in the model.

Parameter	Description	Value/Range
$C_{non\text{-}kin}$	Non-kin selection strength	0 ~ 1
N	Population size of cooperator group	1 ~ 1500 [41]
N_{gety}	Number of genotypes in gene pool	1 ~ 100

The whole evolutionary process is implemented as follows. Initially, there are $N/2$ defector members and $N/2$ cooperator members with N_{gety} genotypes in the population, and the number of each cooperator genotype is equal (we do not consider defector genotypes). At time step $\tilde{t}$, the number and frequency of genotype i in the whole population are $n_{gety,i}(\tilde{t})$ and $f_{gety,i}(\tilde{t})$, and the total number of cooperators is n_C. We label these genotypes with integers 1, 2, 3, ⋯, N_{gety}.

During social games, we first use the following binomial distribution function to generate an integer 1 or -1 denoting the winning side:

Winning side	1 (cooperators)	-1 (defectors)
Probability	$\dfrac{w_C}{w_C + w_D}$	$\dfrac{w_D}{w_C + w_D}$

If the result is -1, defectors win this round of game, which means cooperators will remove one old member from its group. This process is finished by generating an integer i between 1 and N_{gety} with a N distribution function as:

Genotype	1	2	$\cdots$	N_{gety}
Probability	$f_{gety,1}(\tilde{t})$	$f_{gety,2}(\tilde{t})$	$\cdots$	$f_{gety,n}(\tilde{t})$

Then the number of this genotype at next time step will become $n_{gety,i}(\tilde{t}+1) = n_{gety,i}(\tilde{t}) - 1$, and the total number of cooperators will become $n_C(\tilde{t}+1) = n_C(\tilde{t}) - 1$.

If the output of games between cooperators and defectors is 1, cooperators win this round of game and have a chance to add one new member from the external gene pool. We then use a N distribution function to generate an integer $j \in [1, N_{gety}]$ to denote the new member to be added into the group. The selection probability of the integer j is $P_{gety,j}$ expressed as Eq. (2). So the number of this genotype at next time step will become $n_{gety,j}(\tilde{t}+1) = n_{gety,j}(\tilde{t}) + 1$, and the total number of cooperators will become $n_C(\tilde{t}+1) = n_C(\tilde{t}) + 1$.

After one side takes over the population, we use the same way to generate two integers i and $j \in [1, N_{gety}]$ to respectively indicate the old member to be removed and the new member to be added. So the number of genotypes i and j at next time step will become $n_{gety,i}(\tilde{t}+1) = n_{gety,i}(\tilde{t}) - 1$ and $n_{gety,j}(\tilde{t}+1) = n_{gety,j}(\tilde{t}) + 1$.

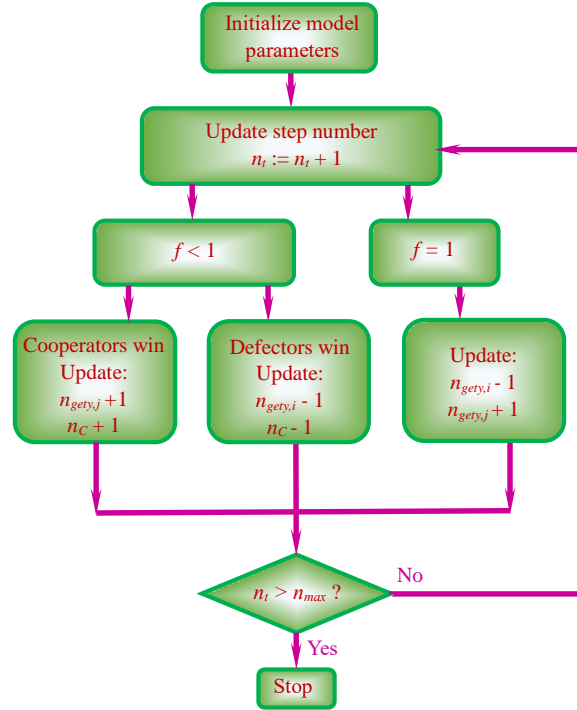The processes above produce the whole evolutionary dynamics of the model, and are presented in Fig. 2.

Figure 2. Illustration of evolutionary dynamics of the model.

3. Results

We first test our evolutionary model for social games between cooperators and defectors. Fig. 3a shows a common knowledge that the presence of defectors who profit from cooperators but pay no costs leads to the evolutionary extinction of cooperation. However, if the cost of cooperation is relatively small, there is a probability for cooperation to evolve due to the chance effect (Fig. 3b). Fig. 3c shows that kin selection only is able to facilitate the evolution of cooperation through providing a group of cooperators with additional benefits, and this facilitation effect is particularly obvious in the presence of smaller cooperation cost and higher benefits resulting from kin selection (Fig. 3d). Simulations and Eq. (1) suggest that cooperation

generally evolves when $b/\rho > \varDelta$, which is approximatively in correspondence to Hamilton's rule.
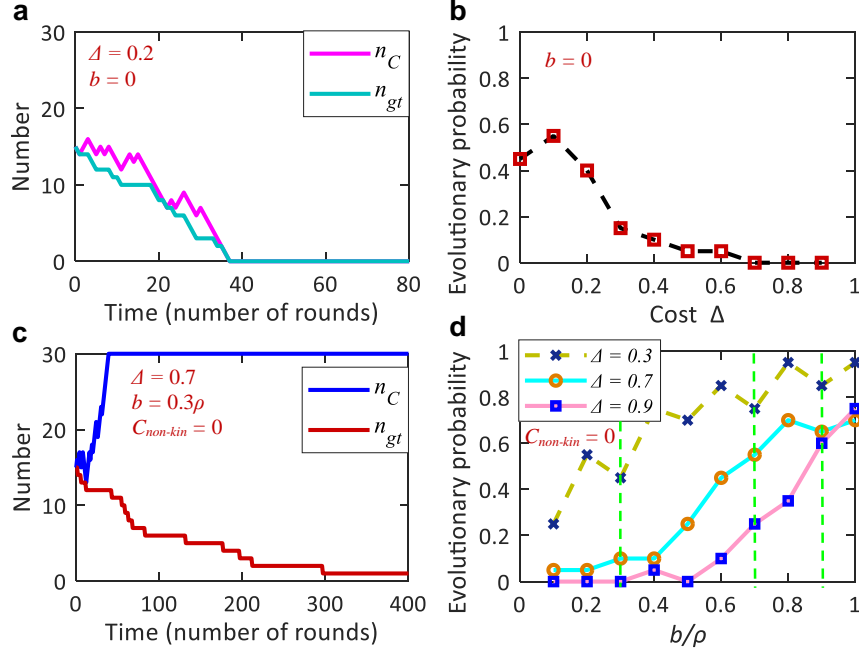

Figure 3. Evolutionary games between cooperators and defectors. (**a**) Evolution of the number of all cooperators and cooperator genotypes in the presence of cooperation cost. (**b**) Evolutionary probability of cooperation under different cost of cooperation. (**c**) Evolution of the number of all cooperators and cooperator genotypes in the presence of cooperation cost and kin selection as well. (**d**) Evolutionary probability of cooperation under different benefits of kin selection. The population size N = 30, and the initial frequency of cooperators within the population is f_0 = 0.5. Initial number of each cooperator genotype is equal, and the total number of cooperator genotypes in the gene pool N_{gety} = 15. Each data point is tested for 20 rounds.

The complexity of a cooperator group is directly characterized by the number of cooperator genotypes within the group. Therefore, we are mainly concerned by how the number of genotypes within the cooperation organization is influenced by model parameters. In our initial simulations, the total number of genotypes in the gene pool N_{gety} is limited to 15. We find that cooperation can be maintained to a large degree among unrelated individuals only if the cooperator group can be continuously supplemented with new cooperator members of genotypes that have little genetic dependence on old cooperator members.

When cooperators within the group can get benefits only from their relatives ($C_{non-kin}$ = 0 in Fig. 4a, i.e. kin selection), new cooperator members will be selected from the gene pool with a strong genetic dependence on the old members within the group (the extreme example is that the new members are reproduced by old members), and the total number of cooperator genotypes within the cooperator group decreases over time. After a long period of evolution, only one of the original fifteen cooperator genotypes survived and took over the whole cooperator population (r = 1), with the others all removed during this process (Fig. 4b). With the emergence and increasing impact of natural non-kin selection (higher non-kin selection strength $C_{non-kin}$, see Eq. 1), more cooperator genotypes can be maintained in the cooperator group as equilibrium points, enhancing the biological complexity (diversity) (Fig. 4a).

If cooperators within the group can get benefits from all cooperators with different genotypes ($C_{non-kin}$ = 1, i.e. non-kin selection acts), new cooperator members can be supplemented with no genetic dependence on the cooperator group (e.g. new members are selected from the gene pool with the equal probability of the

15 genotypes), and the cooperator group can still preserve those original 15 genotypes and maintain the low genetic relatedness among members over a long period of evolution (Fig. 4c). Of course, for animal societies including humans, reproduction of organisms (absolute kin selection) still needs to be involved in all cases (from $C_{non-kin} = 0$ to $C_{non-kin} = 1$) to supply new members as the life span of organisms is limited.
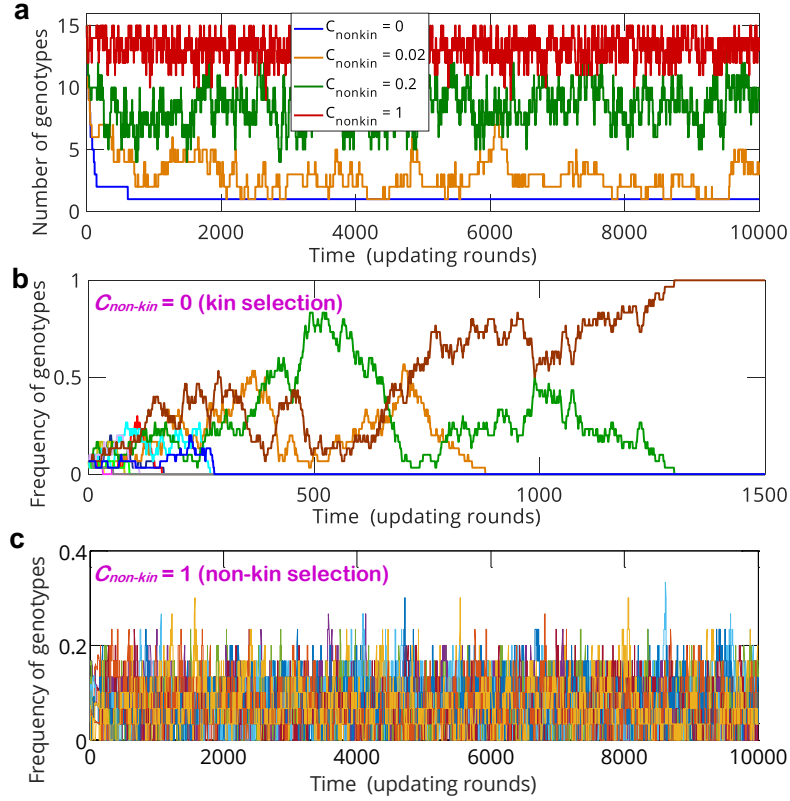

Figure 4. The evolution of social cooperation in well-mixed finite populations. (**a**) Effect of non-kin selection strength $C_{non-kin}$ on the evolution of the total number of cooperator genotypes in the cooperator group: each value of $C_{non-kin}$ can output a specific number of genotypes as an equilibrium point. (**b**), (**c**) Evolution of the frequency distribution of cooperator genotypes within the cooperator group when (**b**) $C_{non-kin} = 0$ and (**c**) $C_{non-kin} = 1$: one colored line represents a specific genotype. Initial frequency of each cooperator genotype within the group is equal, and the total number of cooperator genotypes in the gene pool $N_{gety} = 15$. The population size $N = 30$.
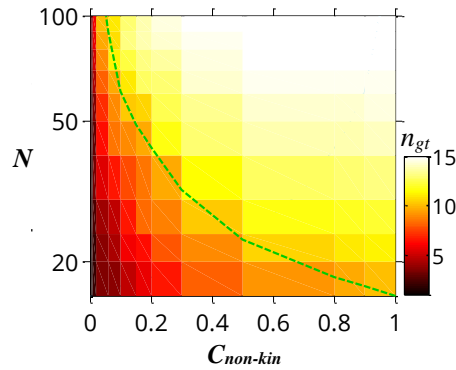

Figure 5. Heat map of the number of maintained cooperator genotypes $n_{gt}(\infty)$ for varying population size N and non-kin selection strength $C_{non-kin}$. Each data point is tested for 10 rounds. Initial frequency of each cooperator genotype within the

group is equal, and the total number of cooperator genotypes in the gene pool N_{gety} = 15.

The landscape of the maintained number of cooperator genotypes within the population n_{gt} in the space $(C_{non\text{-}kin}, N)$ further demonstrates that the non-kin selection effect is weaker at the smaller population size N (below the dashed line), with fewer genotypes to be maintained (Fig. 5). This is owing to the strong sampling effect arising from the small number of individuals at the low population size [43,44].

To check how the total number of genotypes in gene pool affects our results, we tried varying values of N_{gety}. Fig. 6 shows that for a given population size, the maintained number of genotypes within the group n_{gt} generally increases with N_{gety}, but there is a saturation effect (i.e. n_{gt} has an upper limit) when N_{gety} is beyond a specific value, due to the sampling effect. The emergence of the sampling effect leads to more and more larger deviation of n_{gt} from N_{gety} (see the shadow region in Fig. 6). This result holds for different non-kin selection strength.
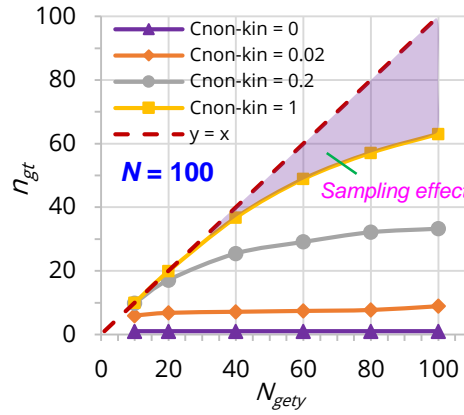

Figure 6. Evolution of n_{gt} as a function of N_{gety} and $C_{non\text{-}kin}$: the shadow region indicates the strength of sampling effect. The population size N = 100. Each data point is tested for 10 rounds.
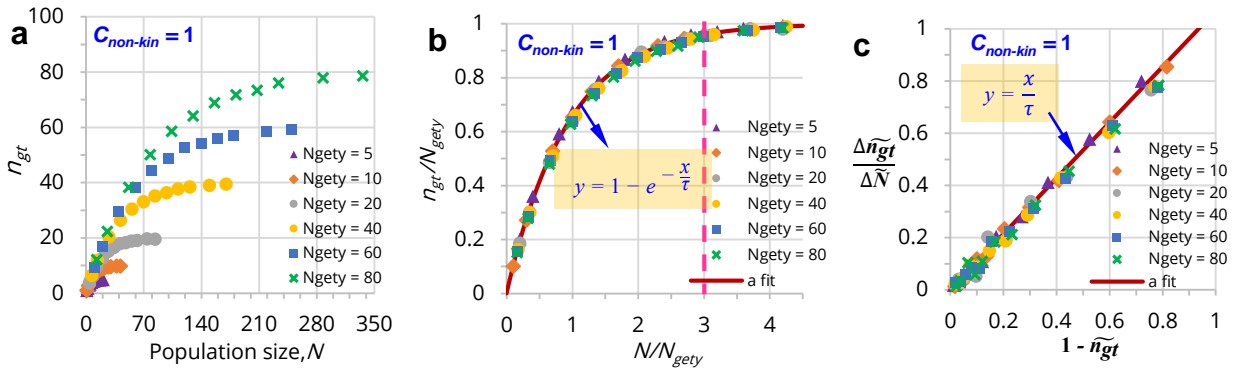

Figure 7. (**a**) Variation of n_{gt} with population size N at different N_{gety}. (**b**) Variation of $\widetilde{n_{gt}}$ with $\widetilde{N}$. (**c**) Variation of the slope of the distribution curve in (**b**) with $1 - \widetilde{n_{gt}}$. $1 - \widetilde{n_{gt}}$ is observed to exponentially decay as $\widetilde{N}$. τ = 0.9354. Non-kin selection strength $C_{non\text{-}kin}$ = 1. Each data point is tested for 10 rounds.

Fig. 6 demonstrates that strong sampling effect exists because the number of individuals within the group is small, which makes a specific genotype hard to persist. To make a population maintain as many genotypes as possible, the population size should be large enough, compared with the number of genotypes to be maintained, as shown in Fig. 7a. Different N_{gety} has distinct n_{gt}-N relations. When both n_{gt} and N are normalized,

however, these relations are observed to collapse to a universal distribution (Fig. 7b). Simulations show that the slope of the distribution curve is proportional to $1 - n_{gt}/N_{gety}$ (Fig. 7c). That is,

$$\frac{d\widetilde{n_{gt}}}{d\widetilde{N}} = \frac{1 - \widetilde{n_{gt}}}{\tau} \quad (4)$$

where $\widetilde{n_{gt}} = n_{gt}/N_{gety}$ and $\widetilde{N} = N/N_{gety}$ are normalized parameters. $\widetilde{n_{gt}}$ can be regarded as the degree of complexity. τ is the characteristic normalized population size, which is related to $C_{non\text{-}kin}$.

From Eq. (4), we can derive that the number of genotypes maintained within a cooperation organization follows a universal exponential function of the form:

$$\widetilde{n_{gt}} = 1 - e^{-\frac{\widetilde{N}}{\tau}} \quad (5)$$

Eq. (5) suggests that the maintained number of genotypes within the population has a N_{gety}-invariant dependence. That is, the normalized number of preserved genotypes within the population is independent of the abundance of the external gene pool. In our study, we observe that both the N_{gety}-invariant dependence and also the function (i.e. Eq. 5) hold for varying $C_{non\text{-}kin}$ (Fig. 8a), suggesting Eq. (5) is a universal function. However, smaller $C_{non\text{-}kin}$ will dramatically increase the characteristic constant τ, as presented in Fig. 8b. Surprisingly, the parameter τ is observed to strictly vary with $C_{non\text{-}kin}$ in a power law, with a power exponent of $-5/8$. From the universal Eq. (5) and also Fig. 8a, we can also derive that to maintain a specific number of genotypes within the population, the population size needs to be at least 3 times larger than the characteristic constant τ.
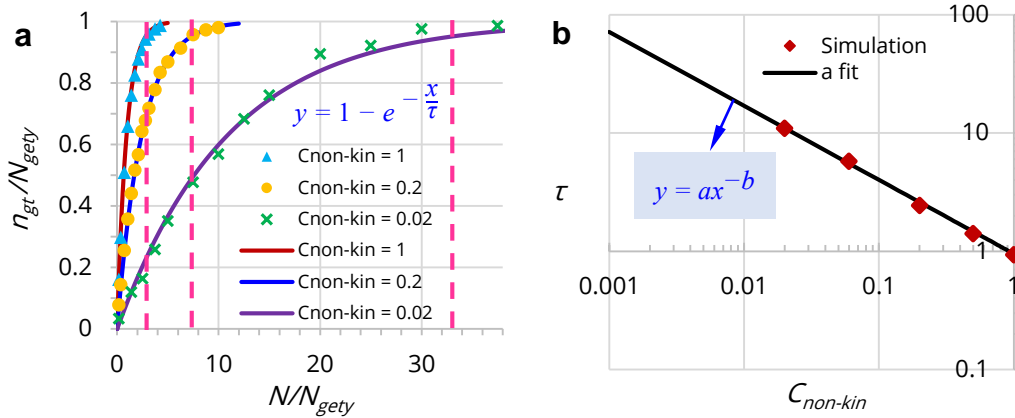

Figure 8. (**a**) Variation of $\widetilde{n_{gt}}$ as a function of $\widetilde{N}$ and varying non-kin selection strength $C_{non\text{-}kin}$. (**b**) Variation of the characteristic constant τ in Eq. (5) as a function of $C_{non\text{-}kin}$: τ varies with $C_{non\text{-}kin}$ in a power law. $a = 0.9539$ and $b = 5/8$. Each data point is tested for 10 rounds.

Taking the power law identified in Eq. (5), we can obtain the following function:

$$\widetilde{n_{gt}} \approx 1 - e^{-\widetilde{N}C_{non\text{-}kin}^{5/8}} \quad (6)$$

i.e.

$$\frac{n_{gt}}{N_{gety}} = 1 - e^{-\frac{N}{N_{gety}}C_{non\text{-}kin}^{5/8}} \quad (7)$$

From Eq. (6), we can see that $\widetilde{n_{gt}}$ increases with both $\widetilde{N}$ and $C_{non\text{-}kin}$. If $C_{non\text{-}kin} = 0$, $\widetilde{n_{gt}}$ will become zero despite the very large population size, which means the genetic diversity within the population will disappear.

Therefore, our theory identifies that the essence of biological complexity or diversity is non-kin selection. If $C_{non\text{-}kin} = 1$, $\widetilde{n_{gt}}$ will vary with $\widetilde{N}$ in a simple exponential law:

$$\widetilde{n_{gt}} = 1 - e^{-\widetilde{N}} \quad (8).$$

Fig. 9 shows the distribution of $\widetilde{n_{gt}}$ for varying $\widetilde{N}$ and $C_{non\text{-}kin}$, which is plotted by the Eq. (6). Fig. 9 exhibits a much similarity with Fig. 5. This suggests that the quantitative law identified here is reasonable.
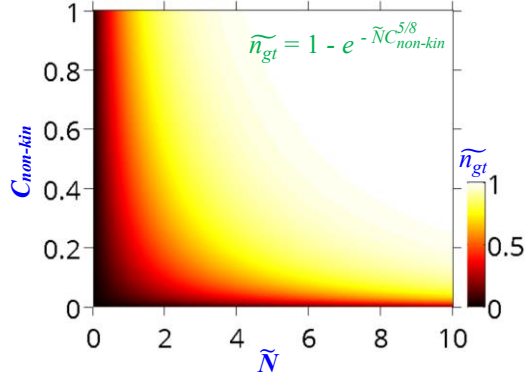

Figure 9. Distribution of $\widetilde{n_{gt}}$ in space ($C_{non\text{-}kin}$, $\widetilde{N}$). Plotted using Eq. (6).

Our research results demonstrate that the root cause for the low genetic relatedness between individuals in the biological evolution model we have studied is the non-kin selection effect within various cooperator groups. Therefore, all mechanisms should play a part in cooperation between non-kin through taking non-kin selection. However, we stress that both reciprocity and group selection are not fully equal to non-kin selection. For example, reciprocity may easily lead to cooperation between only kin when kin selection dominates, and it cannot explain well the human altruism where individuals do not benefit themselves at all but show an evident self-sacrifice [34]. The non-kin selection we proposed here is a universal concept, as it can provide a good explanation for any cooperation between unrelated individuals including human altruism and even cooperation between different molecules.

Our evolutionary model can output different genetic relatedness as equilibrium points for each non-kin selection strength. This provides a mechanism to have a hierarchy of stable biological systems with different genetic relatedness.

4. Summary and discussion

Explaining cooperation is the basis to understand the emergence and evolution of complex biological organizations. At present, a prevalent explanation for the evolution of cooperation is kin selection as presented in Hamilton's rule. However, the basic biological evolution towards higher levels has not been explained directly. In this article, using a stochastic individual-based approach, we develop a simple but relatively general evolutionary model to show that when and only when non-kin selection is included, the cooperation between unrelated individuals can be maintained for long periods, suggesting that non-kin selection is the origin of biological complexity (diversity). Our model identifies a unified quantitative law to characterize the complexity in cooperation: the number of genotypes maintained within a cooperation organization follows a universal scale-invariant exponential distribution function, which shows a dependence on both the population size and non-kin selection strength and also an independence on the abundance of genotypes in the external gene pool.

Different from kin selection, group selection and reciprocity, non-kin selection means that to enable and maintain cooperation between unrelated individuals, individuals must actively select the non-self (this can lead to the mutation of organisms, the cooperation between animals, and so on). This requires that individuals have to get out of the genetic dependence. Besides, our general evolutionary model shows that kin selection and non-kin selection are the only two root causes for different degrees of complexity of biological systems. This demonstrates that both group selection and reciprocity are not the root cause, but may be effects of the causes.

Complexity in biological systems can be partly captured by synergetic interactions, which refer to the whole being more than the sum of its parts [45]. Synergy is based on interactions between individuals of different types. Our research reveals that the cooperation complexity originates from non-kin selection between individuals. This may suggest that non-kin selection is the origin of all beings, including the universal synergy effects.

We believe non-kin selection is an important evolutionary force for shaping complex biological organizations. Under the power of natural non-kin selection, the biological attribute of organisms may be gradually dragged from kin selection to the final non-kin selection. The most significant difference between humans and animals may be that we humans have evolved to abandon the absolute kin selection to survive throughout the operation of our lives. Non-kin selection might be a natural law of biological evolution and should be investigated further.

References

1. Szathmary, E. & Smith, J. M. The major evolutionary transitions. *Nature* **374**, 227-232 (1995).

2. Nash, J. F. Equilibrium points in N-person games. *Proc. Natl Acad. Sci. USA* **36**, 48-49 (1950).

3. Smith, J. M. The theory of games and the evolution of animal conflicts. *J. Theor. Biol.* **47**, 209-221 (1974).

4. Nowak, M. A. Five rules for the evolution of cooperation. *Science* **314**, 1560-1563 (2006).

5. West, S. A. et al. Social evolution theory for microorganisms. *Nat. Rev. Microbiol.* **4**, 597-607 (2006).

6. West, S. A., Griffin, A. S. & Gardner, A. Evolutionary explanations for cooperation. *Curr. Biol.* **17**, R661-R672 (2007).

7. Asfahl, K. L. & Schuster, M. Social interactions in bacterial cell-cell signaling. *FEMS Microbiol. Rev.* **41**, 92-107 (2017)

8. Hamilton, W. D. The evolution of altruistic behaviour. *Am. Nat.* **97**, 354-356 (1963).

9. Hamilton, W. D. The genetical evolution of social behaviour, I & II. *J. Theor. Biol.* **7**, 1-52 (1964).

10. Wynne-Edwards, V. C. Animal Dispersion in Relation to Social Behaviour (Oliver and Boyd, Edinburgh, 1962).

11. Wilson, D. S. A theory of group selection. *Proc. Natl Acad. Sci. USA* **72**, 143–146 (1975).

12. Traulsen, A. & Nowak, M. A. Evolution of cooperation by multilevel selection. *Proc. Natl. Acad. Sci. USA* **103**, 10952-10955 (2006).

13. A. Gardner, Group selection (Oxford Bibliographies in Evolutionary Biology, Oxford University Press, 2018).

14. Axelrod, R. The Evolution of Cooperation (Basic Books, New York, 1984).

15. Nowak, M. A. & Sigmund, K. Tit for tat in heterogeneous populations. *Nature* **355**, 250-253 (1992).

16. Nowak, M. A. et al. Emergence of cooperation and evolutionary stability in finite populations. *Nature* **428**, 646-650 (2004).

17. Trivers, R. The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**, 35–57 (1971).

18. Ohtsuki, H., Hauert, C., Lieberman, E. & Nowak, M. A. A simple rule for the evolution of cooperation on graphs and social networks, *Nature* **441**, 502-505 (2006).

19. Preussger, D. et al. Reciprocal Fitness Feedbacks Promote the Evolution of Mutualistic Cooperation. *Curr. Biol.* **30**, 1-11 (2020).

20. Sigmund, K., Hauert, C. & Nowak, M. A. Reward and punishment. *Proc. Natl Acad. Sci. USA* **98**, 10757-10762 (2001).

21. Nadell, C. D., Foster, K. R. & Xavier, J. B. Emergence of spatial structure in cell groups and the evolution of cooperation. *PLoS Comput. Biol.* **6**, e1000716 (2010).

22. Van Dyken, J. D. et al. Spatial population expansion promotes the evolution of cooperation in an experimental Prisoner's Dilemma. *Curr. Biol.* **23**, 919-923 (2013).

23. Datta, M. S. et al. Range expansion promotes cooperation in an experimental microbial metapopulation. *Proc. Natl. Acad. Sci. USA* **110**, 7354-7359 (2013).

24. Nowak, M. A. & May, R. M. Evolutionary games and spatial chaos. *Nature* **359**, 826-829 (1992).

25. Griffin, A. S., West, S. A. & Buckling, A. Cooperation and competition in pathogenic bacteria. *Nature* **430**, 1024-1027 (2004).

26. Gore, J., Youk, H. & van Oudenaarden, A. Snowdrift game dynamics and facultative cheating in yeast. *Nature* **459**, 253-256 (2009).

27. Fletcher, J. A. & Doebeli, M. A simple and general explanation for the evolution of altruism. *Proc. R. Soc. B* **276**, 13-19 (2009).

28. Hilbea, C. et al. Evolution of cooperation in stochastic games. *Nature* **559**, 246-249 (2018).

29. Li, A. et al. Evolution of cooperation on temporal networks. *Nat. Commun.* **11**, 2259 (2020).

30. Gardner, A., Griffin, A. S. & West, S. A. Theory of cooperation. In: *eLS*. John Wiley & Sons, **2016**.

31. West, S. A., Gardner, A. & Griffn, A. S. Altruism. *Curr. Biol.* **16**, R482-R483 (2006).

32. Fisher, R. M. Cornwallis, C. K. & West, S. A. Group formation, relatedness, and the evolution of multicellularity. *Curr. Biol.* **23,** 1120-1125 (2013).

33. Kennedy, P. et al. Altruism in a volatile world. *Nature* **555**, 359-362 (2018).

34. Fehr, E. & Fischbacher, U. The nature of human altruism. *Nature* **425**, 785-791 (2003).

35. Goodnight, C. J. Multilevel selection: the evolution of cooperation in non-kin groups. *Popul. Ecol.* **47**, 3-12 (2005).

36. Clutton-Brock, T. Cooperation between non-kin in animal societies. *Nature* **462**, 51-57 (2009).

37. Kay, T. Lehmann, L. & Keller, L. Kin selection and altruism. *Curr. Biol.* **29**, R438-R442 (2019).

38. Moran, P. A. P. Random processes in genetics. *Math. Proc. Cambridge* **54**, 60-71 (1958).

39. Nowak, M. A. & Sigmund, K. Evolutionary dynamics of biological games. *Science* **303**, 793-799 (2004).

40. Blythe, R. A. & McKane, A. J. Stochastic models of evolution in genetics, ecology and linguistics. *J. Stat. Mech. Theory E* **2007**, P07018 (2007).

41. Korolev, K. S. et al. Genetic demixing and evolution in linear stepping stone models. *Rev. Mod. Phys.* **82**, 1691-1718 (2010).

42. Lopez, J. G., Donia, M. S. & Wingreen, N. S. Modeling the ecology of parasitic plasmids. *The ISME Journal* **15**, 2843-2852 (2021).

43. Hallatschek, O. et al. Genetic drift at expanding frontiers promotes gene segregation. *Proc. Natl. Acad. Sci. USA* **104**, 19926-19930 (2007).

44. Hallatschek, O. & Nelson, D. R. Population genetics and range expansions. *Phys. Today* **62**, 42-47 (2009).

45. Wu, B., Arranz, J., Du, J., Zhou, D. & Traulsen, A. Evolving synergetic interactions. *J. R. Soc. Interface* **13**, 20160282 (2016).

Author contributions: X.W. conceived this research, developed models, implemented theoretical calculations and data analysis, and wrote the paper. A.H. evaluated the article, provided revision suggestions and contributed to the writing. All authors participated in discussion.

Conflict of interest: The authors declare no conflict of interest.

Data and Materials Availability

All calculation data and code are available from X.W. upon reasonable request.