

## Review

## Universal scaling for the dilemma strength in evolutionary games

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**Abstract**

Why would natural selection favor the prevalence of cooperation within the groups of selfish individuals? A fruitful framework to address this question is evolutionary game theory, the essence of which is captured in the so-called social dilemmas. Such dilemmas have sparked the development of a variety of mathematical approaches to assess the conditions under which cooperation evolves. Furthermore, borrowing from statistical physics and network science, the research of the evolutionary game dynamics has been enriched with phenomena such as pattern formation, equilibrium selection, and self-organization. Numerous advances in understanding the evolution of cooperative behavior over the last few decades have recently been distilled into five reciprocity mechanisms: direct reciprocity, indirect reciprocity, kin selection, group selection, and network reciprocity. However, when social viscosity is introduced into a population via any of the reciprocity mechanisms, the existing scaling parameters for the dilemma strength do not yield a unique answer as to how the evolutionary dynamics should unfold. Motivated by this problem, we review the developments that led to the present state of affairs, highlight the accompanying pitfalls, and propose new universal scaling parameters for the dilemma strength. We prove universality by showing that the conditions for an ESS and the expressions for the internal equilibria in an infinite, well-mixed population subjected to any of the five reciprocity mechanisms depend only on the new scaling parameters. A similar result is shown to hold for the fixation probability of the different strategies in a finite, well-mixed population. Furthermore, by means of numerical simulations, the same scaling parameters are shown to be effective even if the evolution of cooperation is considered on the spatial networks (with the exception of highly heterogeneous setups). We close the discussion by suggesting promising directions for future research including (i) how to handle the dilemma strength in the context of co-evolution and (ii) where to seek opportunities for applying the game theoretical approach with meaningful impact.

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## 1. Introduction

### 1.1. Advances in the research of cooperation in social dilemmas

The evolution of cooperation is a basic conundrum in biological systems because unselfish, altruistic actions apparently contradict Darwinian selection [1]. Nevertheless, cooperative behavior is ubiquitous among living organisms, from bacterial colonies to animal and human societies [2–6]. Archetypal examples include vampire bats sharing a meal of blood [7], social animals emitting alarm calls to warn of predators in the vicinity [8], fish inspecting predators preferably in pairs [9], and monkeys grooming each other [10], to name a few. It is noticeable that, in all these examples, cooperative entities make a sacrifice – they help others at a cost to themselves. Exploiters, or cheaters, reap the benefits and forgo costs. Starting from the mid 20th century, a wealth of models and mechanisms have been proposed to explain how a cooperative trait can survive and even thrive [6,11–15]. In particular, the mathematical framework of evolutionary game theory has become essential to overcome the benefit disadvantage in the face of exploitation [11,16]. Moreover, evolutionary game theory generates important insights into the evolution of cooperation, many of which have been found applicable across a myriad of scientific disciplines [15,17–20].

With the advent of new analytical methodologies, many contributions have been made to the proposition of reciprocal altruism and its underlying mechanisms. The pioneering research of Dawes [21] found that natural selection favors defection in a well-mixed population playing the prisoner's dilemma game (PD, perhaps the most famous metaphor for the problem of cooperation) [22–26]. However, if everybody defects, the mean population payoff is lower than if everybody cooperates, thus creating a social dilemma. Resorting to a more technical description, PD is characterized by a Nash equilibrium in which all players are defectors, although the population of cooperators is Pareto efficient [27]. Subsequently, more scenarios have been identified that avoid the inevitability of a social downfall embodied in the well-mixed PD. One such scenario is the chicken game (CH) (also the snowdrift game (SD) or the hawk–dove game (HD)) [28,29], in which mutual defection is individually less favorable than a cooperation–defection pair. Accordingly, CH allows for a stable coexistence of cooperators and defectors in a well-mixed population (namely, the number of cooperator–defector pairs increases). The stag hunt game (SH) [30,31], which together with PD and CH comprises the standard trio of the most investigated social dilemmas [32–36], offers even more support for cooperative individuals in the sense that the interest of mutual cooperation exceeds the benefit of exploitation or cheating. Yet, cooperation in SH can also be compromised by the fact that mutual defection is individually more beneficial than being an exploited cooperator. This game, therefore, has two Nash equilibriums in which all players are either cooperators or defectors.

A research field that has been evolving in parallel with evolutionary game theory is network science, which provides a comprehensive framework for understanding the dynamical processes on networks [37]. Early blending of the two theories happened with the investigation of social dilemmas on a square lattice. In their pioneering work, Nowak and May [38] unveiled that considering spatial topology via the nearest neighbor interactions enabled cooperators to survive by forming clusters and thus minimizing exploitation by defectors. Afterwards, the role of a wide variety of spatial structures in evolutionary games was explored [26,39–73]. Remarkably, heterogeneous networks, such as small-world and scale-free networks [33,74–99], strongly support cooperation in the above-mentioned social dilemmas. Recently proposed multilayer architectures also enrich the impact of spatial topology on the evolution of cooperation [100–107]. Moreover, an even larger realm of evolutionary games (e.g. rock-paper-scissors [108–114], public goods [115–125], and ultimatum [126–131] games) is currently being investigated in conjunction with spatially structured populations. These achievements link to the phenomena (e.g. the emergence of phase transitions [132–135], percolation [136–140], pattern formation [109,141–143], and self-organizing behavior [144]) or the analytical methods (e.g. the mean-field method [42,145] and the pair approximation [25,146,147]) of statistical physics.

Aside from the theoretical studies of equilibriums in well-mixed and networked populations, an important generator of progress has been identifying scenarios that can offset the unfavorable outcome of social dilemmas and stimulate the evolution of cooperation. Well-know examples include tit-for-tat or win-stay-lose-shift strategies [148–151], voluntary participation [115,121,152–154], memory [45,65,155,156], age structure [157–159], social diversity and preference [160–165], heterogeneous action [85,166–171], partner selection [172–174], and punishment and reward [175–180]. Furthermore, the mobility of players [181–195], times scales in evolutionary dynamics [36,196], the role of the finite population size [197–200], and the impact of noise and uncertainty [201–205] have also been thoroughly investigated. Lately, the co-evolution schemes [35,80,81,158,206–219], which involve the joint adjustment of individual strategies and network topology (or the updating rules), emerged as another potential promoter of cooperation (refer to [220] for a comprehensive review).

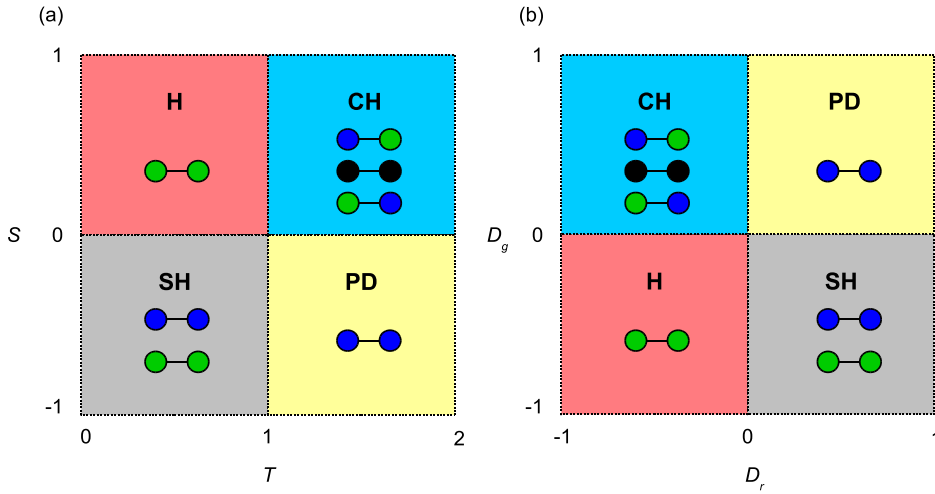


Fig. 1. Schematic representation of social dilemmas in (a)  $T$ – $S$  and (b)  $D_g$ – $D_r$  parameter diagrams. The diagrams can be divided into four regions (denoted by different colors) corresponding to prisoner's dilemma (PD), stag hunt (SH), chicken (CH), and harmony (H) games. In these games, two strategies exist: cooperation, C, and defection, D. The Nash equilibrium of each game is denoted by different strategy pairs, where green, blue, and black circles indicate cooperative, defective, and mixed strategies, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Despite the wide range of achievements so far, much of the progress has recently been attributed to five mechanisms: direct reciprocity, indirect reciprocity, kin selection, group selection, and network reciprocity [221], all of which are described in the subsequent sections. These promising mechanisms differ considerably between themselves, yet they also have one fundamental trait in common. To some extent, their purpose is to reduce the opponent's anonymity relative to the primitive, well-mixed situation [222–239].

### 1.2. Existing dilemma strength and potential pitfalls

Given that the fundamental interactions between individuals are of the pairwise nature, 2-player, 2-strategy games (i.e.  $2 \times 2$  games) are broadly considered as an archetype. Each interaction in a  $2 \times 2$  game requires that two players simultaneously adopt one of the two binary strategies, cooperation (C) or defection (D). In the most basic setup, both players receive a reward,  $R$ , for mutual cooperation and a punishment,  $P$ , for mutual defection. If, however, one chooses C and the other D, the latter gets the temptation payoff,  $T$ , while the former is left with the sucker's payoff,  $S$ . The described game can be divided into four classes according to the payoff ranking (see Fig. 1 for more details). Furthermore, as suggested by Ref. [240], pairwise games can also be classified based on gamble-intending (GID) and risk-averting (RAD) dilemmas, defined by  $D_g = T - R$  and  $D_r = P - S$ , respectively. If  $D_g$  is positive, both players should be inclined to exploit each other. By contrast, if  $D_r$  is positive, players should refrain from the exploitation. When both  $D_g$  and  $D_r$  are positive, the game is a prisoner's dilemma (PD), whereby D dominates C. When the two parameters are negative, we deal with the harmony (H) game, whereby C dominates D (i.e. no dilemma exists). If, however,  $D_g$  is positive and  $D_r$  is negative, we face the so-called chicken (CH, also snowdrift (SD) or hawk–dove (HD)) game, which has an internal (polymorphic) equilibrium. Finally, if  $D_g$  is negative and  $D_r$  is positive, the game, characterized by bi-stability, is called the stag hunt (SH) game (see Fig. 1 for a schematic illustration). Based on these considerations, the replicator dynamics and its internal equilibrium are fully determined by  $D_g$  and  $D_r$  instead of the original parameters  $R$ ,  $T$ ,  $S$ , and  $P$ . Therefore,  $D_g$  and  $D_r$  are useful in quantifying the dilemma strength in games with an infinite, well-mixed population.

However, a recent work [241] reveals that  $D_g$  and  $D_r$  alone may be insufficient for indicating the dilemma strength when a specific reciprocity mechanism is introduced into pairwise games. In Fig. 2 we show the equilibrium fraction of cooperators in a social dilemma on a lattice network of degree  $k = 8$  (simulation details can be found in Section 4.1). Although three illustrated games have the same  $D_g$  and  $D_r$ , the equilibrium fraction of cooperators is completely different, depending on the value of  $R - P$ . The larger the value of  $R - P$ , the higher the equilibrium fraction

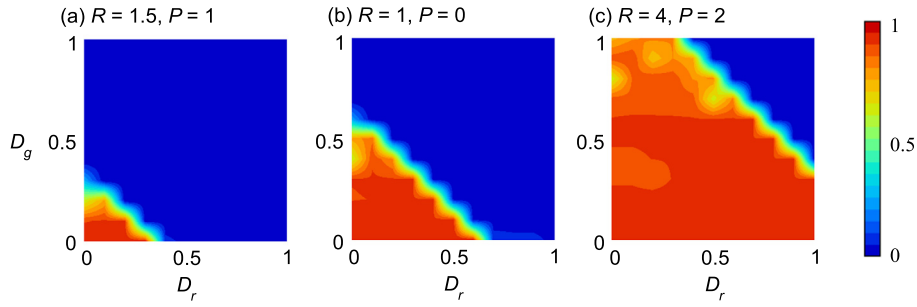


Fig. 2. Equilibrium fraction of cooperators in  $D_r$ – $D_g$  diagrams for (a)  $R = 1.5$ ,  $P = 1$ , (b)  $R = 1$ ,  $P = 0$ , and (c)  $R = 4$ ,  $P = 2$ . Games are played on an 8-neighbor lattice with the Moore neighborhood. Applied strategy updating rule is Imitation Max (IM, see Eq. (22)).

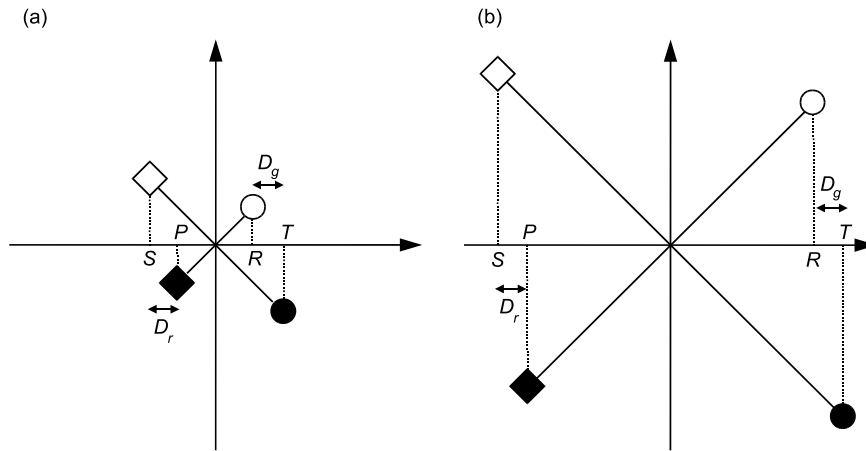


Fig. 3. Two PD games having the same  $D_g$  and  $D_r$ , but different  $R - P$ ; (a) smaller  $R - P$  and (b) larger  $R - P$ .

of cooperators. These results demonstrate that the parameters  $D_g$  and  $D_r$  are insufficient to accurately predict the evolution of cooperation in a pairwise game when a reciprocity mechanism is in place.

What could be the reason for the failure of  $D_g$  and  $D_r$  in estimating the dilemma strength in the presence of reciprocity mechanisms? If  $R - P$  is high relative to  $D_g$  and  $D_r$ , the effect is similar to approaching the limits  $T \rightarrow R$  and  $P \rightarrow S$  (see Fig. 3). The payoff then, as in the Avatamsaka game [242], becomes independent of a player's own decision and is entirely dominated by the opponent's offer. Consequently, in Fig. 3(a) there is less incentive to establish a reciprocal relationship than in Fig. 3(b) because in the former case, getting on the opponent's good side and making it offer  $C$ , secures less gain in terms of the payoff than in the latter case. It would thus seem informative to incorporate  $R - P$  into a new framework for evaluating the dilemma strength of pairwise games in which individuals, abiding by one of the reciprocity mechanisms, repeatedly meet with each other.

Ref. [221] considered the prisoner's dilemma with  $D_g = D_r$ , which, more accurately, is the donor and recipient (D&R) game. In D&R, the dilemma structure is described by two parameters, *benefit* ( $b$ ) and *cost* ( $c$ ) of cooperation. The fraction of cooperators can be expressed as a function of the ratio  $c/b$  regardless of the reciprocity mechanism at work, thus leading to universal scaling for D&R. Assuming  $P = 0$ ,  $R = b - c$ ,  $S = -c$ , and  $T = b$ , one can derive  $c/b = D_g/(R - P + D_r)$ , which contains the contribution of  $R - P$  in addition to  $D_g$  and  $D_r$ . Along this line, it is possible to explain why the equilibrium fraction of cooperators in D&R with any of the five reciprocity mechanisms can be universally evaluated, analogous to Hamilton's rule [243]. However, the shortcoming of this proposal is explicit in that it is ineffective beyond the D&R realm.

To overcome the limitation to D&R, Ref. [241] proposes another set of the universal scaling parameters,  $b/c_c$  and  $b/c_d$ , valid for general PD. This is achieved by considering player's costs,  $c_c$  and  $c_d$ , when the opponent offers  $C$  and  $D$ , respectively. Although a generalization, the idea of Ref. [241] remains restricted to PD and the authors fall short of providing theoretical validation.

Inspired by the described attempts [221,240–242], we set to resolve the issue of the universal scaling parameters for the dilemma strength. In particular, we aim at defining such scaling parameters that can be applied to all  $2 \times 2$  games. This covers the range from an infinite and well-mixed population to a finite and spatially-structured one, irrespective of the reciprocity mechanism in use.

### 1.3. Organization of the review

The remainder of this review is organized as follows. In Section 2, we summarize the existing mathematical apparatus related to the dilemma strength and proceed to propose a new set of the scaling parameters. In Section 3, we focus on the theoretical analysis to prove that the proposed set of parameters is theoretically consistent. We first examine the universal equilibrium state for each of the five reciprocity mechanisms. The universality is further extended to a finite, well-mixed population. To solidify the usefulness of the introduced concepts, we revisit the paradox of cooperation benefits [244] and show that such a paradox is entirely avoided when relying on the new scaling parameters. Augmenting the theoretical analysis, Section 4 deals with the numerical validation of the universality in a spatially structured population. We review frequently used strategy updating rules, spatial interaction networks, and simulation dynamics to finally prove that each of the updating rules produces a nearly identical equilibrium state given the same network. Based on these theoretical and numerical results, we round off the review by summarizing the main findings and by suggesting an outlook in Section 5.

## 2. Dilemma strength and the game structure

We consider a 2-player, 2-strategy ( $2 \times 2$ ) game as a paradigmatic model, which can be further divided into four subclasses (see Fig. 1 for more details). In their basic version,  $2 \times 2$  games consist of bringing together two individuals, asking them to simultaneously adopt one of the two binary strategies, cooperation (*C*) or defection (*D*), and then assigning to each a payoff based on the choices made. According to the description in Section 1.2, the payoffs can be summarized using a matrix notation as follows

$$A = [a_{ij}] = \begin{matrix} & \begin{matrix} C & D \end{matrix} \\ \begin{matrix} C \\ D \end{matrix} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{matrix}. \quad (1)$$

Let us consider an infinite (i.e.  $N \rightarrow \infty$ , where  $N$  is the population size) and well-mixed population, using  $x_i$  to denote the frequency of strategy  $i$ . Then, the expected payoff of this strategy is given by  $f_i = \sum_{j=1}^2 x_j a_{ij}$  and the average payoff of the population can be calculated as  $\varphi = \sum_{i=1}^2 x_i f_i$ . By assuming that the fitness of an individual equals its payoff, the time evolution of the frequency  $x_i$  is given by [16,20]

$$\dot{x}_i = x_i (f_i - \varphi). \quad (2)$$

For simplicity, if  $x$  ( $0 \leq x \leq 1$ ) presents the fraction of strategy *C*, the equilibrium of Eq. (2) becomes one or two of the following three states

$$x^* = 0, 1, \frac{P - S}{R - S - T + P}. \quad (3)$$

The same, however, does not hold in a finite, well-mixed population or a population with any of the reciprocity mechanisms. If the game is depicted using gamble-intending (GID),  $D_g = T - R$ , and risk-averting (RAD),  $D_r = P - S$ , dilemmas [240], the payoff matrix is of the following form

$$A = [a_{ij}] = \begin{matrix} & \begin{matrix} C & D \end{matrix} \\ \begin{matrix} C \\ D \end{matrix} & \begin{pmatrix} R & P - D_r \\ R + D_g & P \end{pmatrix} \end{matrix}. \quad (4)$$

In this situation, the third equilibrium of the right-hand side of Eq. (3) becomes

$$x^* = \frac{D_r}{D_r - D_g}. \quad (5)$$

However, the setup of Eqs. (4) and (5) still cannot predict the equilibrium states of the population with reciprocity mechanisms. To overcome this problem, we introduce a new set of scaling parameters,  $D'_g$  and  $D'_r$ , for the dilemma strength

$$D'_g = \frac{T - R}{R - P} = \frac{D_g}{R - P}, \quad D'_r = \frac{P - S}{R - P} = \frac{D_r}{R - P}. \quad (6)$$

Correspondingly, the payoff matrix is rescaled as

$$A = [a_{ij}] = \begin{matrix} & \begin{matrix} C & D \end{matrix} \\ \begin{matrix} C \\ D \end{matrix} & \begin{pmatrix} R & P - (R - P)D'_r \\ R + (R - P)D'_g & P \end{pmatrix} \end{matrix}. \quad (7)$$

### 3. Theoretical analysis

Taylor and Nowak [222] showed that any of the aforementioned five reciprocity mechanisms could be represented by a suitable transformation of the original payoff matrix in Eq. (1). Inspired by this claim, we perform the same transformation, but then derive the equilibriums of the five mechanisms (via replicator dynamics) using the transformed payoff matrix in Eq. (7). We thus explore if the new scaling parameters  $D'_g$  and  $D'_r$  consistently evaluate the dilemma strength in the presence of the five reciprocity mechanisms. Subsequently, we inspect whether these parameters are also appropriate in the case of a finite, well-mixed population. Finally, we show that  $D'_g$  and  $D'_r$  can prove that the “paradox of cooperation benefits” is not a paradox at all [244].

#### 3.1. Theoretical consistency with the five reciprocity mechanisms

Following Ref. [222], we show how to represent the five reciprocity mechanisms by their respective transformed payoff matrices using the newly introduced dilemma strength parameters,  $D'_g$  and  $D'_r$ . To that end, we also review the basic assumptions behind these mechanisms.

**Direct reciprocity.** If encounters between the same two individuals are repeated, direct reciprocity can emerge and promote the evolution of cooperation [245,246]. In each round, the two players must choose either cooperation or defection. With probability  $w$  their game is extended into another round or with the remaining probability,  $1 - w$ , the game is terminated. Defectors,  $D$ , are assumed to insist on defection in each round, whereas cooperators,  $C$ , select the tit-for-tat behavior; they start with cooperation and then follow the opponent’s previous move, thus embodying the maxim “I help you and you help me.”

**Indirect reciprocity.** Indirect reciprocity is a mechanism based on reputation [247,248]. The decision between cooperation and defection is made depending on what the opponent has done to others as if saying “I help you if you helped someone else.” One way to formalize this idea is to keep track of the opponent’s Image Score (IS). However, the knowledge of IS is not perfect and cannot be known better than with a probability  $q$ . We further assume that a defector,  $D$ , always defects, whereas a cooperator,  $C$ , defects only when the opponent is a confirmed defector or cooperates otherwise. Accordingly, any cooperator happens to cooperate with a defector with the probability  $1 - q$ .

**Kin selection.** Kin selection is a concept originating from the idea that evolutionary games are often played between genetic relatives [243]. A population is characterized by the average relatedness between interacting individuals, which is given by a real number,  $r$  ( $r \in [0, 1]$ ). This parameter then determines the fraction of a player’s own payoff exchanged with the opponent. A cooperator,  $C$ , thus gets  $(S + rT)/(1 + r)$  upon interacting with a defector,  $D$ , who gets  $(T + rS)/(1 + r)$ . Dividing by  $1 + r$  is necessary to keep the payoffs balanced (i.e. equal to  $S + T$ ).

**Group selection.** Group selection takes into account not only competition between individuals but also between groups [249–254]. As in Ref. [255], the population can be subdivided into  $m$  groups and the maximum group size can be set to  $n$ . Individuals play  $2 \times 2$  games with all members of their respective groups, accumulating the payoff,  $F$ , in the process. The fitness of an individual is assumed to be  $1 - \omega - \omega F$ , where  $\omega$  ( $\omega \in [0, 1]$ ) is called the intensity

of selection. In each round, an individual from the entire population is chosen proportional to its fitness to produce an identical offspring, who enters the same group. If the group reaches the maximum size, it splits into two with the probability  $p$ , in which case a randomly selected group simultaneously dies out to prevent the total population from exploding. Alternatively, the group does not divide with the remaining probability,  $1 - p$ , and a random individual within that group has to die. For simplicity, the result presented here is obtained in the limit of weak selection ( $\omega \ll 1$ ), low group splitting rate ( $p \ll 1$ ), and large  $n$  and  $m$ .

**Network reciprocity.** Network reciprocity is closely related to two effects, (i) a limited number of opponents (i.e. diminished anonymity), and (ii) a local adaptation mechanism, whereby a player can only copy a strategy from one of the neighboring players. Based on these effects, we observe that cooperators can form compact clusters even if the conditions do not necessarily favor spreading of the cooperative trait [37]. Over the past two decades, the role of spatial structure and its various cooperation-promoting mechanisms were thoroughly explored in the context of evolutionary games [256–260]. Typically, individuals are represented as the vertices of a graph, whereas edges denote the players who interact with each other. The fitness of an individual is again evaluated as  $1 - \omega - \omega F$ , where  $F$  is the payoff and  $\omega$  ( $\omega \in [0, 1]$ ) denotes the intensity of selection. We select the Death–Birth (DB) updating rule for the evolutionary dynamics [57]. In each round, an individual is randomly selected to die, whereupon the neighbors, proportional to their fitness, engage in a competition for the empty site.

Many other updating rules have been considered for a population on a network (see Section 4) [42]. Among them, the method of pair approximation on regular graphs, though neglecting the long-range interactions, defines a series of deterministic differential equations that specify the time evolution of the expected frequency of cooperators (defectors) [42]. These differential equations produce the standard replicator dynamics with a modified payoff matrix [261].

Starting from the original matrix in Eq. (1) and using the above-mentioned hypotheses, we can derive the following transformed payoff matrices, one for each of the five reciprocity mechanisms

$$\text{Direct reciprocity} \quad \begin{array}{cc} & \begin{array}{c} C \\ D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} \frac{R}{1-w} & S + \frac{wP}{1-w} \\ T + \frac{wP}{1-w} & \frac{P}{1-w} \end{pmatrix} \end{array}, \quad (8)$$

$$\text{Indirect reciprocity} \quad \begin{array}{cc} & \begin{array}{c} C \\ D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & (1-q)S + qP \\ (1-q)T + qP & P \end{pmatrix} \end{array}, \quad (9)$$

$$\text{Kin selection} \quad \begin{array}{cc} & \begin{array}{c} C \\ D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & \frac{S+rT}{1+r} \\ \frac{T+rS}{1+r} & P \end{pmatrix} \end{array}, \quad (10)$$

$$\text{Group selection} \quad \begin{array}{cc} & \begin{array}{c} C \\ D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} (m+n)R & nS + mR \\ nT + mP & (m+n)P \end{pmatrix} \end{array}, \quad (11)$$

$$\text{Network reciprocity} \quad \begin{array}{cc} & \begin{array}{c} C \\ D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S + H \\ T - H & P \end{pmatrix} \end{array}. \quad (12)$$

The term  $H$  in Eq. (12) is defined as follows

$$H = \frac{(k+1)(R-P) - T + S}{(k+1)(k-2)}, \quad (13)$$



Table 1

Conditions for cooperation and defection being an ESS, as well as the interior equilibriums of the five reciprocity mechanisms in terms of the new scaling parameters,  $D'_g$  and  $D'_r$ .

	Cooperation is ESS	Defection is ESS	Interior equilibriums
Direct reciprocity	$\frac{w}{1-w} > D'_g$	$D'_r > 0$	$x^* = \frac{(1-w)D'_r}{(1-w)(D'_r - D'_g) + w}$
Indirect reciprocity	$\frac{q}{1-q} > D'_g$	$D'_r > 0$	$x^* = \frac{(1-q)D'_r}{(1-q)(D'_r - D'_g) + q}$
Kin selection	$r(1 + D'_r) > D'_g$	$r(1 + D'_g) < D'_r$	$x^* = \frac{-r(D'_g + 1) + D'_r}{(1+r)(D'_r - D'_g)}$
Group selection	$\frac{m}{n} > D'_g$	$\frac{m}{n} < D'_r$	$x^* = \frac{nD'_r - m}{n(D'_r - D'_g)}$
Network reciprocity	$k^2 D'_g - k(D'_g + 1) + (D'_r - D'_g) < 0$	$k^2 D'_r - k(D'_r + 1) + (D'_g - D'_r) > 0$	$x^* = \frac{(k^2 - k - 1)D'_r + D'_g - k}{(k^2 - k - 2)(D'_r - D'_g)}$

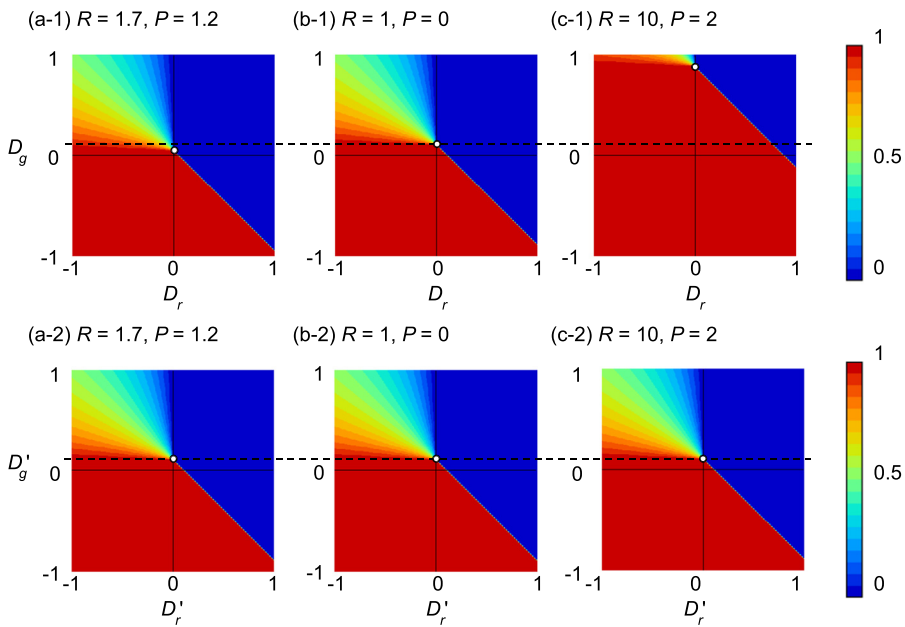


Fig. 4. Equilibrium fraction of cooperators in  $D_r$ – $D_g$  (upper panels) and  $D'_r$ – $D'_g$  (lower panels) diagrams with direct reciprocity. The parameters are (a)  $R = 1.7$ ,  $P = 1.2$ , (b)  $R = 1$ ,  $P = 0$ , and (c)  $R = 10$ ,  $P = 2$ . In all cases the probability of meeting each other in another round is  $w = 0.1$ .

where  $k > 2$  is the degree of the graph. Additionally, the payoff sum of the two interacting players implied by Eq. (10) is exactly the same as that of Eq. (1) (namely,  $R + R$ ,  $P + P$ , and  $S + T$ ).

From Eqs. (8)–(12) we derive, in terms of the new scaling parameters,  $D'_g$  and  $D'_r$ , the set of conditions under which  $C$  and  $D$  are evolutionarily stable strategies (ESS, for details see Table 1). We also find the internal equilibriums (Table 1). Furthermore, using the same equations and starting from the initial fraction of cooperators equal to 0.5, in Figs. 4–8 we show the equilibrium fraction of cooperators in the  $D_g$ – $D_r$  and  $D'_g$ – $D'_r$  diagrams (with different values of  $R - P$ ) for all five reciprocity mechanisms. In these figures, the white circles indicate the boundary points between the four game classes (hereafter four-corners):  $D$ -dominant (PD), polymorphic (CH),  $C$ -dominant (H), and bi-stable (SH). Horizontal dashed line in Figs. 4 and 5 indicates the difference between the four-corners in the case  $R = 1$ ,  $P = 0$  and the point  $D'_g = D'_r = 0$  ( $D_g = D_r = 0$ ), whereas each dashed line in Figs. 6–8 shows the four-corners shifting along the  $D'_g = D'_r$  ( $D_g = D_r$ ) line.

We analyze the effect of direct and indirect reciprocities first. As shown in Figs. 4 and 5, the four-corners undergo an upward shift along the  $D_g$ -axis ( $D'_g$ -axis), reflected in the position of the dashed line. This upward shift implies that, in its weaker region, PD turns into SH, which has a bi-stable equilibrium. In this sense, direct and indirect reciprocities weaken GID ( $D_g = T - R$  or  $D'_g = (T - R)/(R - P)$ ). By contrast, kin selection, group selection, and network



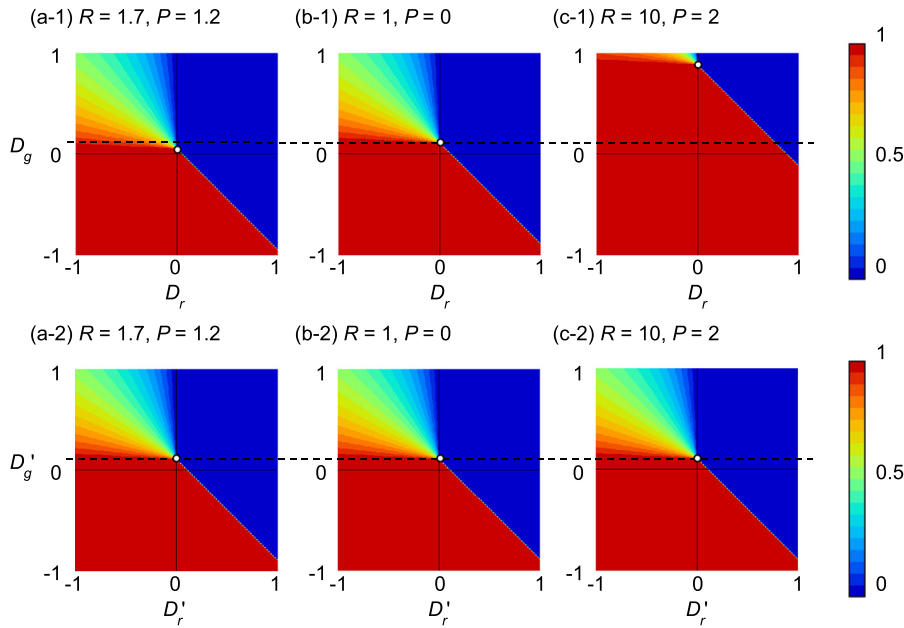


Fig. 5. Equilibrium fraction of cooperators in  $D_r$ – $D_g$  (upper panels) and  $D'_r$ – $D'_g$  (lower panels) diagrams with indirect reciprocity for (a)  $R = 1.7$ ,  $P = 1.2$ , (b)  $R = 1$ ,  $P = 0$ , and (c)  $R = 10$ ,  $P = 2$ . In all cases the probability of knowing the reputation of another individual is  $q = 0.1$ .

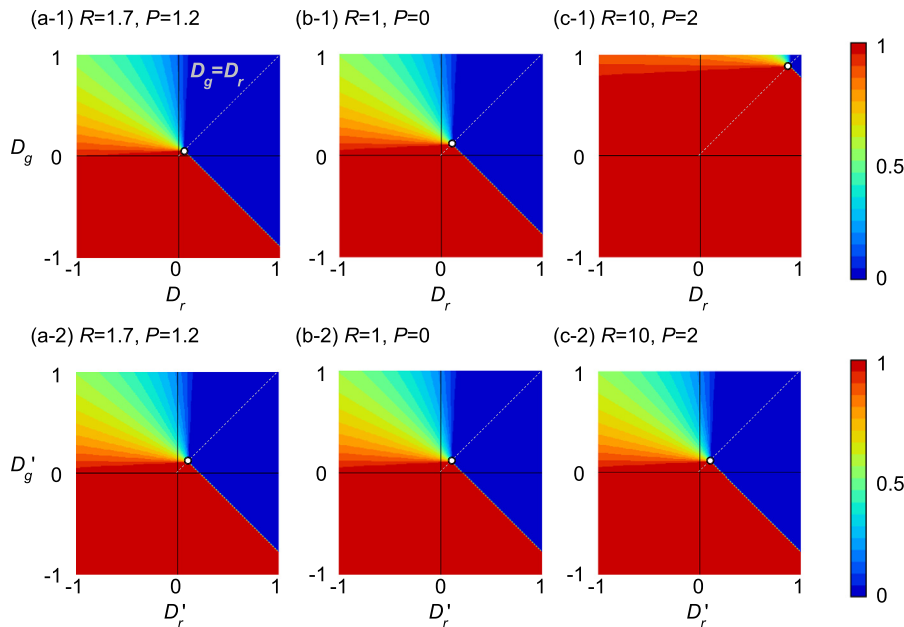


Fig. 6. Equilibrium fraction of cooperators in  $D_r$ – $D_g$  (upper panels) and  $D'_r$ – $D'_g$  (lower panels) diagrams with kin selection for (a)  $R = 1.7$ ,  $P = 1.2$ , (b)  $R = 1$ ,  $P = 0$ , and (c)  $R = 10$ ,  $P = 2$ . In all cases the average relatedness between interacting individuals is  $r = 0.1$ .

reciprocity cause the four-corners to shift diagonally upward and right (i.e. along the  $D_g = D_r$  or  $D'_g = D'_r$  line). This diagonal shift signifies that, in its weaker region, PD turns into either CH, SH, or even H. Thus, kin selection, group selection, and network reciprocity can weaken both GID and RAD.

The  $D_g$ – $D_r$  diagrams in Figs. 4–8 show that the larger the value of  $R - P$ , the more obvious the upward shift of the four-corners. However, in the  $D'_g$ – $D'_r$  diagrams, the shift of the four-corners seems unrelated to the value of  $R - P$ . The latter diagrams are, therefore, completely consistent with each scenario, regardless of the difference  $R - P$ . The

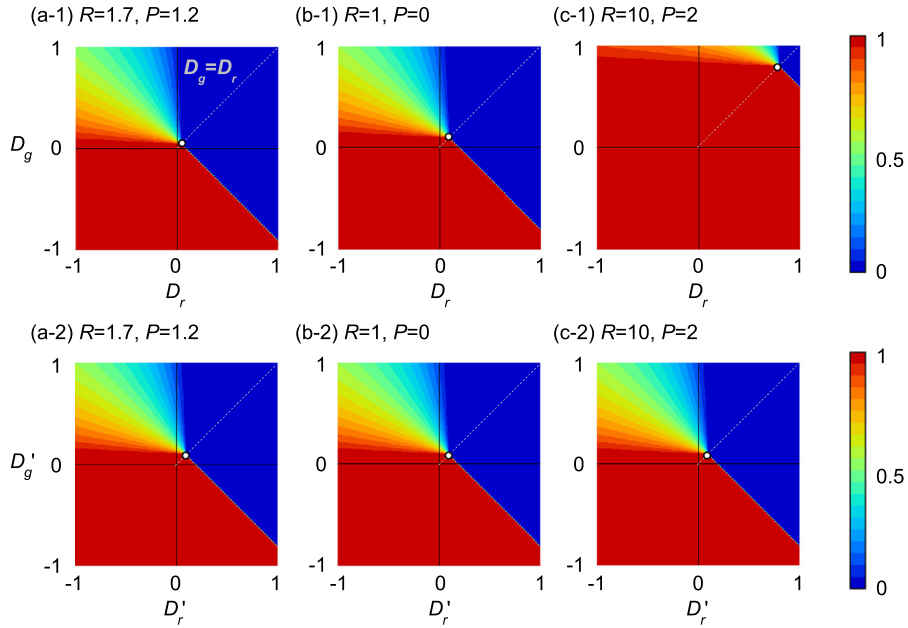


Fig. 7. Equilibrium fraction of cooperators in  $D_r$ – $D_g$  (upper panels) and  $D'_r$ – $D'_g$  (lower panels) diagrams with group selection for (a)  $R = 1.7$ ,  $P = 1.2$ , (b)  $R = 1$ ,  $P = 0$ , and (c)  $R = 10$ ,  $P = 2$ . In all cases the number of groups is  $m = 50$  and the maximum size of a group is  $n = 500$ .

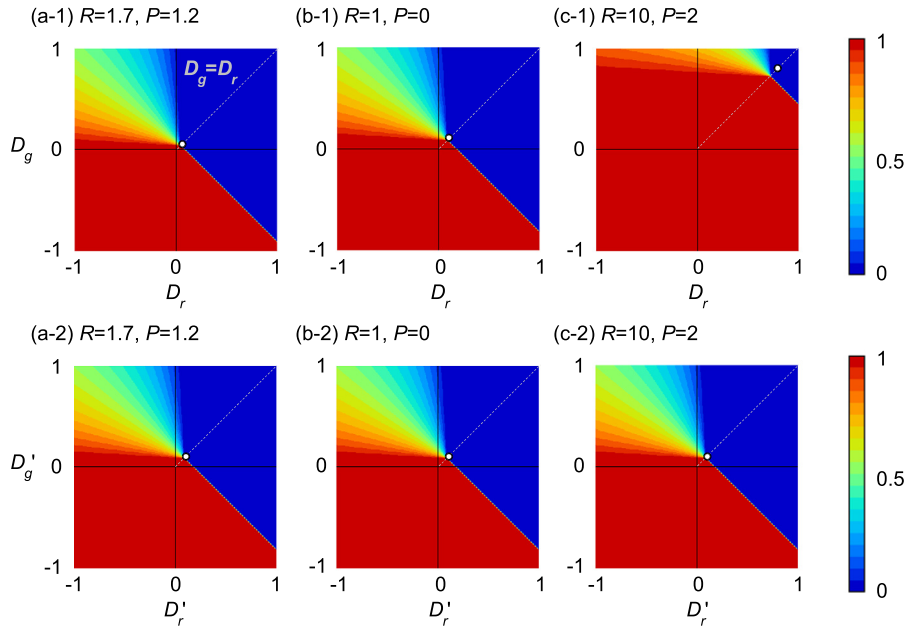


Fig. 8. Equilibrium fraction of cooperators in  $D_r$ – $D_g$  (upper panels) and  $D'_r$ – $D'_g$  (lower panels) diagrams with network reciprocity for (a)  $R = 1.7$ ,  $P = 1.2$ , (b)  $R = 1$ ,  $P = 0$ , and (c)  $R = 10$ ,  $P = 2$ . In all cases the number of neighbors is  $k = 12$ .

new scaling parameters  $D'_g$  and  $D'_r$ , which consider both  $D_g$  and  $D_r$  as well as  $R - P$ , are universally appropriate for evaluating the dilemma strength in any population, irrespective of the reciprocity mechanism.

A careful inspection of Fig. 6 indicates that kin selection has a property that other reciprocity mechanisms do not share. Namely, in some cases the level of cooperation can improve even if  $D'_g$  is increasing. To illustrate this effect better, Fig. 9 shows the equilibrium fraction of cooperators at a fixed  $D'_r$ . In a population obeying kin selection, the payoff of any player is partly determined by the payoff of its opponent (Eq. (10)). Such a mutual dependency enables

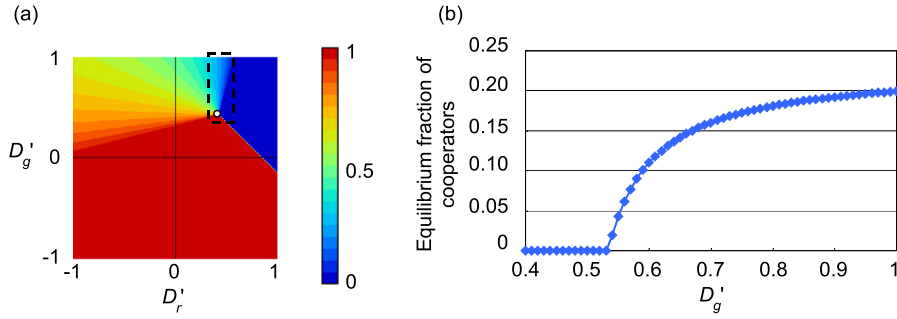


Fig. 9. Equilibrium fraction of cooperators (a) in a  $D'_r$ – $D'_g$  diagram with kin selection and (b) a transect from within the dashed box (constant  $D'_r$ ). The average relatedness between interacting individuals is  $r = 0.3$ .

cooperation instead of defection despite the risk of being exploited, which eventually helps an internal (polymorphic) equilibrium to arise such that both  $C$  and  $D$  players co-exist. Moreover, it is possible that the sum of  $S$  and  $rT$  (i.e. the opponent's contribution) is much greater than  $(1 + r)P$ , thus making a pair of  $C$  and  $D$  better off than a pair of two  $D$ s. Such a possibility arises with the increasing  $r$  and  $T$  (and thus  $D'_g$ ), the latter of which would in other types of games signify that players should exploit each other by choosing  $D$ . A similar, but opposite, phenomenon is observed by fixing  $D'_g$  and decreasing  $D'_r$ , whereby the level of cooperation deteriorates.

### 3.2. Theoretical consistency analysis for a finite, well-mixed population

While the infinite population is an important ingredient in modeling the evolution of the cooperative trait [11], there exist many ways in which the interaction of players may be limited. We examine the case of a finite, well-mixed population in this subsection. The underlying reasoning is that if the proposed universal scaling parameters are applicable to the evolution of cooperation even in a finite, well-mixed population, then their relevance in overcoming social dilemmas is much greater than established so far.

Here, we discuss the so-called fixation probability or, alternatively, the question whether selection favors the mutant's strategy over the resident's strategy [262]. Let us label the finite population size with  $N$ . If the fixation probability of  $C$  ( $D$ ) is greater than  $1/N$ , then the selection favors  $C$  ( $D$ ), which implies that the resident  $D$  ( $C$ ) population will be replaced by a single  $C$  ( $D$ ) mutant in the long term. For the evolutionary dynamics, we consider the Moran process with frequency dependent fitness. In each round, an individual is chosen for reproduction proportional to its fitness and then its offspring replaces another randomly chosen individual. The fixation probability of  $C$  ( $D$ ),  $\rho_C$  ( $\rho_D$ ), is defined as the probability that a single  $C$  ( $D$ ) player in a population of  $N - 1$   $D$  ( $C$ ) players generates a lineage of  $C$ s ( $D$ s), which – instead of going extinct – takes over the entire population. Assuming weak selection ( $\omega \ll 1$ ), both  $\rho_C$  and  $\rho_D$  are given as follows

$$\rho_C \approx \frac{1}{N} \frac{1}{N - (\alpha_C N - \beta_C)\omega/6}, \quad (14.1)$$

$$\rho_D \approx \frac{1}{N} \frac{1}{N - (\alpha_D N - \beta_D)\omega/6}, \quad (14.2)$$

where  $\alpha_C = R + 2S - T - 2P$ ,  $\alpha_D = P + 2T - S - 2R$ ,  $\beta_C = 2R + S + T - 4P$ , and  $\beta_D = 2P + T + S - 4R$ . If  $\rho_C > 1/N$  ( $\rho_D > 1/N$ ) is satisfied, then the selection favors  $C$  ( $D$ ) replacing  $D$  ( $C$ ). These conditions can be expanded into

$$\rho_C > \frac{1}{N} \Leftrightarrow D_g(N + 1) + D_r(2N - 1) + 3(R - P) < 0, \quad (15.1)$$

$$\rho_D > \frac{1}{N} \Leftrightarrow D_r(N + 1) + D_g(2N - 1) + 3(R - P) > 0. \quad (15.2)$$

Expressing Eqs. (15) using only  $D_g$  and  $D_r$  requires the population size to be infinitely large (i.e.  $N \rightarrow \infty$ ). That, of course, would be inconsistent with the premise of a finite population, indicating that the parameters  $D_g$  and  $D_r$  are inappropriate for evaluating the dilemma strength in a finite case. By contrast, the new scaling parameters,  $D'_g$  and  $D'_r$ ,

do not suffer from the same drawback, so that the above inequalities can be rewritten as:

$$\rho_C > \frac{1}{N} \Leftrightarrow D'_g(N+1) + D'_r(2N-1) + 3 < 0, \quad (16.1)$$

$$\rho_D > \frac{1}{N} \Leftrightarrow D'_r(N+1) + D'_g(2N-1) + 3 > 0. \quad (16.2)$$

Therefore, even in the case of a finite, well-mixed population, the fixation probability of either strategy can be evaluated solely using the new scaling parameters.

When the dilemma strength weakens due to the increasing  $R - P$ , selection favors  $D$  rather than  $C$  because inequality (15.2) tends to be more easily satisfied than its counterpart (15.1). At a first glance this may seem paradoxical (see Fig. 2), but the fixation probability quantifies the chance that a mutant can take over the entire population. In an Avatamsaka game [242], characterized by large  $R - P$ , a player's gain is detached from its own decisions and entirely depends on the opponent's choices of  $C$  or  $D$ . Therefore, as  $R - P$  becomes higher, a single  $C$  player in a population of  $N - 1D$  players, will have its payoff suppressed by the consistent choice of  $D$  from its opponents, making the invasion more difficult. The reverse is true for a single  $D$  mutant in a population of  $C$  players.

### 3.3. Is there a real paradox?

Here, we mainly focus on a paradox reported by Németh and Takács [244], who assumed positive assortment and found that higher cooperation benefits enhance the share of cooperators under most, but not all, conditions. The result that the evolution of cooperation could be impeded by higher benefits was named appropriately as the paradox of cooperation benefits. To gain new insights, we revisit this paradox and analyze it using the scaling parameters  $D'_g$  and  $D'_r$ . The analysis consists of two steps. First, we review the model in Ref. [244] and explain what the authors regarded as a paradox. Subsequently, we prove that the paradox disappears with the new scaling parameters, which, in turn, ends up being supportive of the well-known claim that positive assortment is beneficial to the evolution of cooperation [263–266].

#### 3.3.1. Population with positive assortment

We consider an assorted population in which the probability of interacting with players who follow the same strategy is greater than the actual fraction of these players in the population [244]. Let us denote this probability  $\alpha$ . If  $\alpha = 1$ , an individual interacts only with players who rely on the same strategy. By contrast,  $\alpha = 0$ , signifies that an individual interacts with randomly chosen players. In this setup, the average fitness of cooperators ( $f_C$ ) and defectors ( $f_D$ ) is

$$f_C = \alpha R + (1 - \alpha)[xR + (1 - x)S], \quad (17.1)$$

$$f_D = \alpha P + (1 - \alpha)[xT + (1 - x)P]. \quad (17.2)$$

According to the Price equation [267], the conditions in which  $C$  ( $D$ ) becomes ESS and the internal equilibrium are given by

$$\alpha(T - P) > T - R, \quad (18.1)$$

$$\alpha(R - S) < P - S, \quad (18.2)$$

$$x^* = \frac{P - \alpha R - (1 - \alpha)S}{(1 - \alpha)(R + P - S - T)}. \quad (18.3)$$

If  $R - S < T - P$  and  $(P - S)/(R - S) < (T - R)/(T - P)$  hold, then the internal equilibrium  $x^*$  is stable and falls into the region  $[0, 1]$ . If, however,  $R - S > T - P$  and  $(P - S)/(R - S) > (T - R)/(T - P)$ , the equilibrium is still located in the region  $[0, 1]$ , but becomes unstable.

With the help of the new scaling parameters  $D'_g$  and  $D'_r$ , Eqs. (18.1)–(18.3) can be rewritten as:

$$\alpha(1 + D'_g) > D'_g, \quad (19.1)$$

$$\alpha(1 + D'_r) < D'_r, \quad (19.2)$$

$$x^* = \frac{(1 - \alpha)D'_r - \alpha}{(1 - \alpha)(D'_r - D'_g)}. \quad (19.3)$$

Consequently, if  $D'_r < D'_g$  and  $D'_r < \alpha/(1 - \alpha) < D'_g$ , the internal equilibrium  $x^*$  is stable and falls into the region  $[0, 1]$ . If  $D'_r > D'_g$  and  $D'_r > \alpha/(1 - \alpha) > D'_g$ ,  $x^* \in [0, 1]$  becomes unstable.

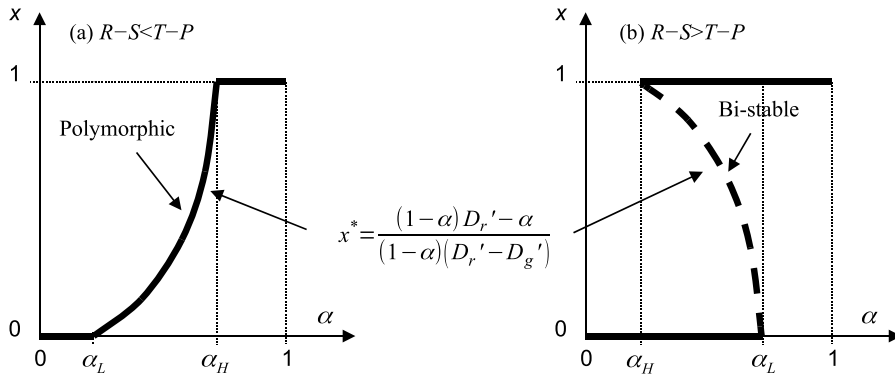


Fig. 10. Equilibrium fraction of cooperators as a function of positive assortment in PD; (a)  $R - S < T - P$  and (b)  $R - S > T - P$ . The dashed line indicates the unstable internal equilibrium point  $x^*$ .

### 3.3.2. The paradox of cooperation benefits suggested by Németh and Takács

Németh and Takács [244] maintain that a paradox may occur when comparing two games with two or more differing payoff elements,  $P$ ,  $R$ ,  $S$ , and  $T$ . To reproduce this paradox, we focus on PD, where the payoffs satisfy the ranking  $T > R > P > S$ . Eqs. (18.1) and (18.2) suggest the following definitions

$$\alpha_H = \frac{T - R}{T - P}, \quad (20.1)$$

$$\alpha_L = \frac{P - S}{R - S}. \quad (20.2)$$

From here the conditions for  $C$  and  $D$  becoming ESS are  $\alpha > \alpha_H$  and  $\alpha < \alpha_L$ , respectively. Fig. 10 shows how the equilibrium curves behave as functions of  $\alpha$  in different situations. If  $R - S < T - P$ , the equilibrium points are  $x = 0$  for  $0 < \alpha < \alpha_L$ , the internal equilibrium  $x^*$  (see Eq. (18.3)) for  $\alpha_L < \alpha < \alpha_H$ , and  $x = 1$  for  $\alpha_H < \alpha < 1$  (Fig. 10(a)). However, when  $R - S > T - P$ , the equilibrium points are  $x = 0$  for  $0 < \alpha < \alpha_H$ ,  $x = 0$  or  $x = 1$  for  $\alpha_L < \alpha < \alpha_H$ , and  $x = 1$  for  $\alpha_L < \alpha < 1$  (Fig. 10(b)).

Next, let us consider two examples: *Game A1* with  $T_A = 7$ ,  $R_A = 3$ ,  $P_A = 1$ , and  $S_A = 0$ ; and *Game B1* with  $T_B = 21$ ,  $R_B = 5$ ,  $P_B = 1$ , and  $S_B = 0$ . Comparing these two examples, we obtain  $\Delta R = R_B - R_A = 2$  and  $\Delta T = T_B - T_A = 14$ . According to Fig. 10(a), both games should have stable internal equilibria  $x^*$ , because they satisfy  $R - S < T - P$ . Interestingly, if we apply  $D_g$  and  $D_r$  as the scaling parameters (not  $D'_g$  and  $D'_r$ ),  $0 < \Delta R < \Delta T$  means that the incentive for selecting  $D$  in *Game B1* is larger than in *Game A1* (because the value  $D_g = T - R$  is larger in *Game B1* than *Game A1*). The equilibrium point of *Game B1* should, therefore, be lower than that of *Game A1*. However, within a certain range of positive assortments,  $\alpha$ , a paradox occurs, whereby cooperation is better off in *Game B1*. This is illustrated in Fig. 11 and relates to the fact that  $\alpha_H(A1) < \alpha_H(B1)$ , whereas  $\alpha_L(A1) > \alpha_L(B1)$ . Németh and Takács [244] regard this outcome to be paradoxical, yet we subsequently demonstrate that the universal scaling parameters,  $D'_g$  and  $D'_r$ , readily resolve the paradox.

### 3.3.3. Explanation of the paradox of cooperation benefits by applying $D'_g$ and $D'_r$

Let us confirm whether the described paradox occurs with the new scaling parameters,  $D'_g$  and  $D'_r$ . Starting from Eqs. (19.1) and (19.2) we define

$$\alpha_H = \frac{D'_g}{1 + D'_g}, \quad (21.1)$$

$$\alpha_L = \frac{D'_r}{1 + D'_r}. \quad (21.2)$$

To simplify the discussion, we consider two other examples: *Game A2* and *Game B2*, such that the scaling parameters of *Game B2* are both larger than those of *Game A2*, i.e.  $D'_g(A2) \leq D'_g(B2)$  and  $D'_r(A2) \leq D'_r(B2)$ . Without making any assumptions regarding the specific payoffs  $T$ ,  $R$ ,  $P$ , and  $S$ , from Eqs. (21.1) and (21.2), it is apparent

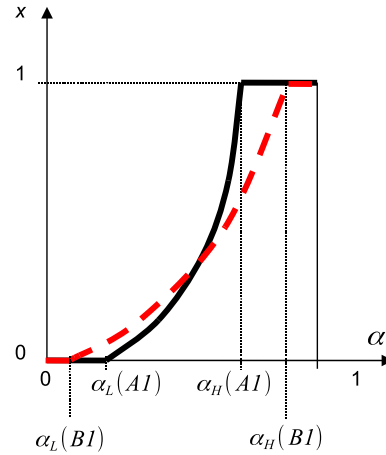


Fig. 11. The paradox of cooperation benefits as a function of positive assortment in PD reported by Németh and Takács [244]. In *Game A1* (black solid line), the payoffs are  $T_A = 7$ ,  $R_A = 3$ ,  $P_A = 1$ , and  $S_A = 0$ , whereas in *Game B1* (red dashed line), the payoffs are  $T_B = 21$ ,  $R_B = 5$ ,  $P_B = 1$ , and  $S_B = 0$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

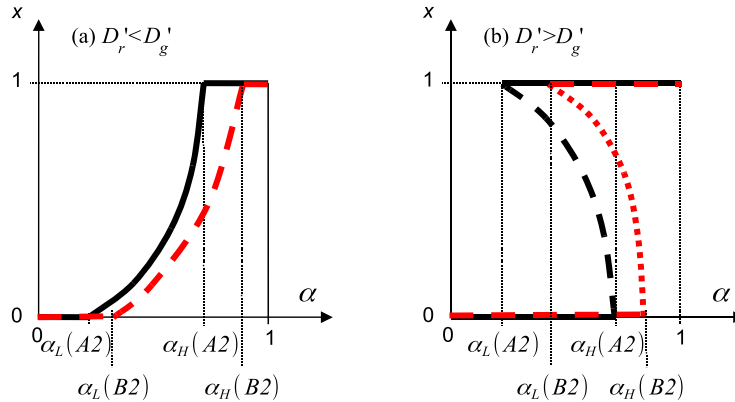


Fig. 12. Equilibrium fraction of cooperators as a function of positive assortment in PD; (a)  $D_r' < D_g'$  and (b)  $D_r' > D_g'$ . The dilemma strength is weaker in the case of *Game A2* than in the case of *Game B2*. Black solid and dashed lines indicate stable and unstable equilibrium points of *Game A2*, respectively. Red dashed and dotted lines indicate stable and unstable equilibrium points of *Game B2*, respectively. The paradox of cooperation benefits never occurs. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

that  $D_r' > -1$  and  $D_g' > -1$  always leads to  $\alpha_L(A2) \leq \alpha_L(B2)$  and  $\alpha_H(A2) \leq \alpha_H(B2)$ . Fig. 12 shows the equilibrium curves when (a)  $D_r' < D_g'$  such that the internal equilibrium  $x^*$  is stable (polymorphic) and (b)  $D_r' > D_g'$ , such that  $x^*$  is unstable (bi-stable). The equilibrium fraction of cooperators in a game with a higher dilemma strength is always lower if the same  $\alpha$  is assumed, proving that there is no paradox. Similar reasoning can be applied to the case  $D_r' \leq -1$  and  $D_g' \leq -1$ . In conclusion, the universal scaling parameters as proposed herein correctly evaluate the dilemma strength and thus resolve the paradoxical viewpoint of Németh and Takács [244].

#### 4. Numerical validation on spatial networks

Thus far, most discussions on the universality of the dilemma strength have been based on a well-mixed population, yet whether the same universality can be achieved in the ubiquitous spatial population remains an open question. Inspired by this question, we examine the effect of spatial networks beyond the above-mentioned regular graph and the Death–Birth (DB) updating rule. In particular, we run a series of numerical simulations to assess the appropriateness of  $D_g'$  and  $D_r'$  as the universal scaling parameters for the dilemma strength under a number of updating rules and topologies.

#### 4.1. Setup of spatial networks and updating rules

Of all the  $2 \times 2$  game classes, PD has attracted the greatest interest in both theoretical and experimental studies [131, 268–274]. Therefore, we choose PD for the underlying game structure in all simulations, so that  $0 \leq D_g \leq 1$  and  $0 \leq D_r \leq 1$ , or  $0 \leq D'_g \leq 1$  and  $0 \leq D'_r \leq 1$  with variable  $R - P$ . Each player, indexed by the natural number  $i$ , is represented as a vertex of an interaction graph and initially designated either as a cooperator ( $s_i = C$ , where  $s_i$  is the current strategy of the  $i$ -th player) or a defector ( $s_i = D$ ) with equal probability. We use several types of interaction networks:

- (i) lattice;
- (ii) homogeneous small world network (Ho-SW) generated from a cycle graph by swapping edges randomly in a way that keeps the node degree constant (i.e. an edge is replaced by another edge with probability 0.2, whereupon if node  $i$  was connected to node  $j$  and node  $u$  was connected to node  $v$ , after the replacement  $i$  is connected to  $u$  and  $j$  is connected to  $v$ );
- (iii) Watts–Strogatz’s heterogeneous small world network (He-SW) [275] generated from a cycle graph by rewiring edges randomly in a way that every node may end up having a different degree (i.e. an edge is removed with probability 0.2, but then a shortcut is created in its place to connect one of the nodes of the removed edge with another randomly chosen node) [276];
- (iv) scale-free network (SF) based on the Barabási–Albert algorithm [277].

The size of each network is  $N = 4900$  nodes, where the average node degree is  $\langle k \rangle = 8$  [278].

The game is iterated forward in accordance with the sequential simulation procedure comprised of the following elementary steps. First, each player  $i$  acquires its payoff  $\Pi_i$  by playing the game with all its neighbors (that is, the number of rounds played by the player  $i$  is equal to its degree). After the evaluation of payoffs for the entire population, player  $i$  updates its strategy synchronously. Here, we focus on four different strategy updating rules: Imitation Max, Fermi-PW, Linear-PW, and Roulette.

- (i) Imitation Max (IM): the strategy  $s_i(t)$  of player  $i$  at time step  $t$  will be

$$s_i(t) = s_j(t-1), \quad (22)$$

where  $j$  indicates a player in the  $i$ ’s neighborhood (including  $i$  itself),  $\Omega_i \cup \{i\}$ , whose payoff from the previous round was maximal,  $j = \max\{\Pi_\sigma(t-1), \sigma \in \Omega_i \cup \{i\}\}$ .

- (ii) Fermi-PW (F-PW): player  $i$  randomly chooses one neighbor  $j$  and adopts its strategy  $s_j$  with the following probability

$$W_{s_i \leftarrow s_j} = \frac{1}{1 + \exp[(\Pi_i - \Pi_j)/\tau]}, \quad (23)$$

where  $\tau$  denotes the amplitude of noise or the so-called intensity of selection [26,279]. Limits  $\tau \rightarrow 0$  and  $\tau \rightarrow \infty$  represent completely deterministic and completely random selections of the neighbor’s strategy. Any finite positive value of  $\tau$  incorporates the uncertainties in the strategy adoption. In simulations we use the constant value  $\tau = 0.2$ .

- (iii) Linear-PW (L-PW): the player  $i$  picks up at random one of its neighbors, say  $j$ , and compares the respective payoffs  $\Pi_i$  and  $\Pi_j$ . If  $\Pi_i > \Pi_j$ , player  $i$  keeps its original strategy. Otherwise, player  $i$  copies the strategy of neighbor  $j$  with a probability proportional to the payoff difference

$$W_{s_i \leftarrow s_j} = \frac{\Pi_j - \Pi_i}{\max(k_i, k_j)[\max(R, T, S, P) - \min(R, T, S, P)]}, \quad (24)$$

where  $k_i$  and  $k_j$  are the degree of agents  $i$  and  $j$ , respectively.

- (iv) Roulette (RS): player  $i$  will adopt the strategy of one of its neighbors (including  $i$  itself),  $\Omega_i \cup \{i\}$ , where the adoption probability is given by

$$W_{s_i \leftarrow s_j} = \frac{\Pi_j - \min_{\sigma \in \Omega_i \cup \{i\}} \Pi_\sigma}{\sum_{j \in \Omega_i \cup \{i\}} (\Pi_j - \min_{\sigma \in \Omega_i \cup \{i\}} \Pi_\sigma)}. \quad (25)$$

If all players in the neighborhood  $\Omega_i \cup \{i\}$  have the same payoff, a random adoption will be performed with the uniform probability,  $1/(1 + k_i)$ , where  $k_i$  is the degree of the player  $i$ .

In all simulations, to make sure that the system has reached a stationary state, we waited a transient time of  $t_0 = 10^5$  time steps and then calculated the fraction of cooperators as the average over a time window of additional  $10^4$  time



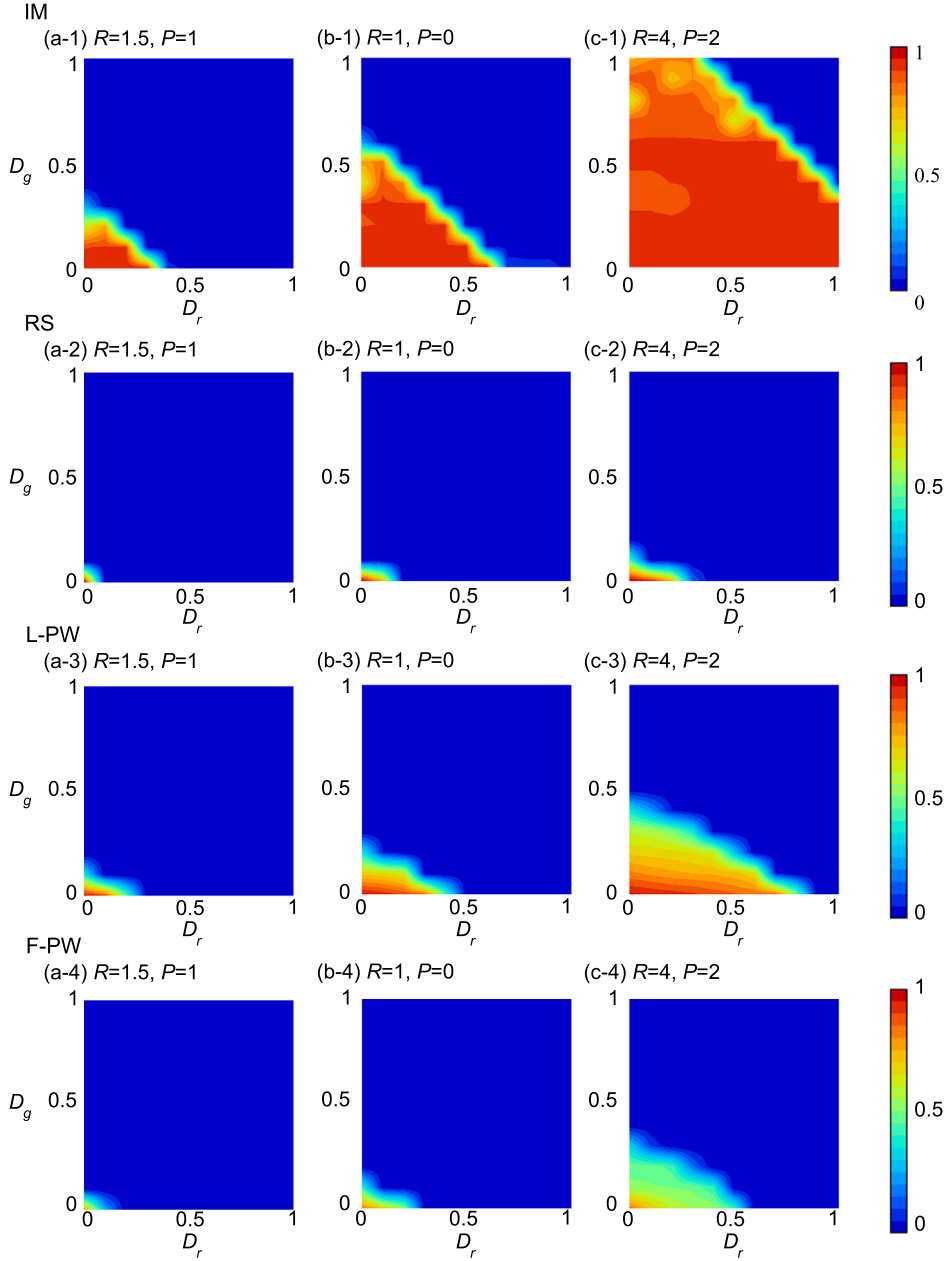


Fig. 13. Equilibrium fraction of cooperators in  $D_r$ - $D_g$  diagrams for (a)  $R = 1.5, P = 1$ , (b)  $R = 1, P = 0$ , and (c)  $R = 4, P = 2$ . Games are played on an 8-neighbor lattice. Considered strategy updating rules include IM (panels in the first row), RS (the second row), L-PW (the third row), and F-PW (the last row).

steps. Fluctuations within the time window were checked if smaller than  $10^{-2}$ , in which case the calculated state was accepted as stationary. If fluctuations exceeded the desired precision we waited for another  $10^4$  time steps and examined the fluctuations once again. To smooth out additional noise caused by the heterogeneity of networks, the final results were averaged over 20 independent realizations of the network topology and the initial conditions.

#### 4.2. Universal scaling and cooperation on spatial networks

Figs. 13–16 show the equilibrium fraction of cooperators in  $D_g$ - $D_r$  and  $D'_g$ - $D'_r$  planes on the lattice and Ho-SW, both of which are homogeneous networks. The equilibrium results in the  $D_g$ - $D_r$  diagram depend on the value of

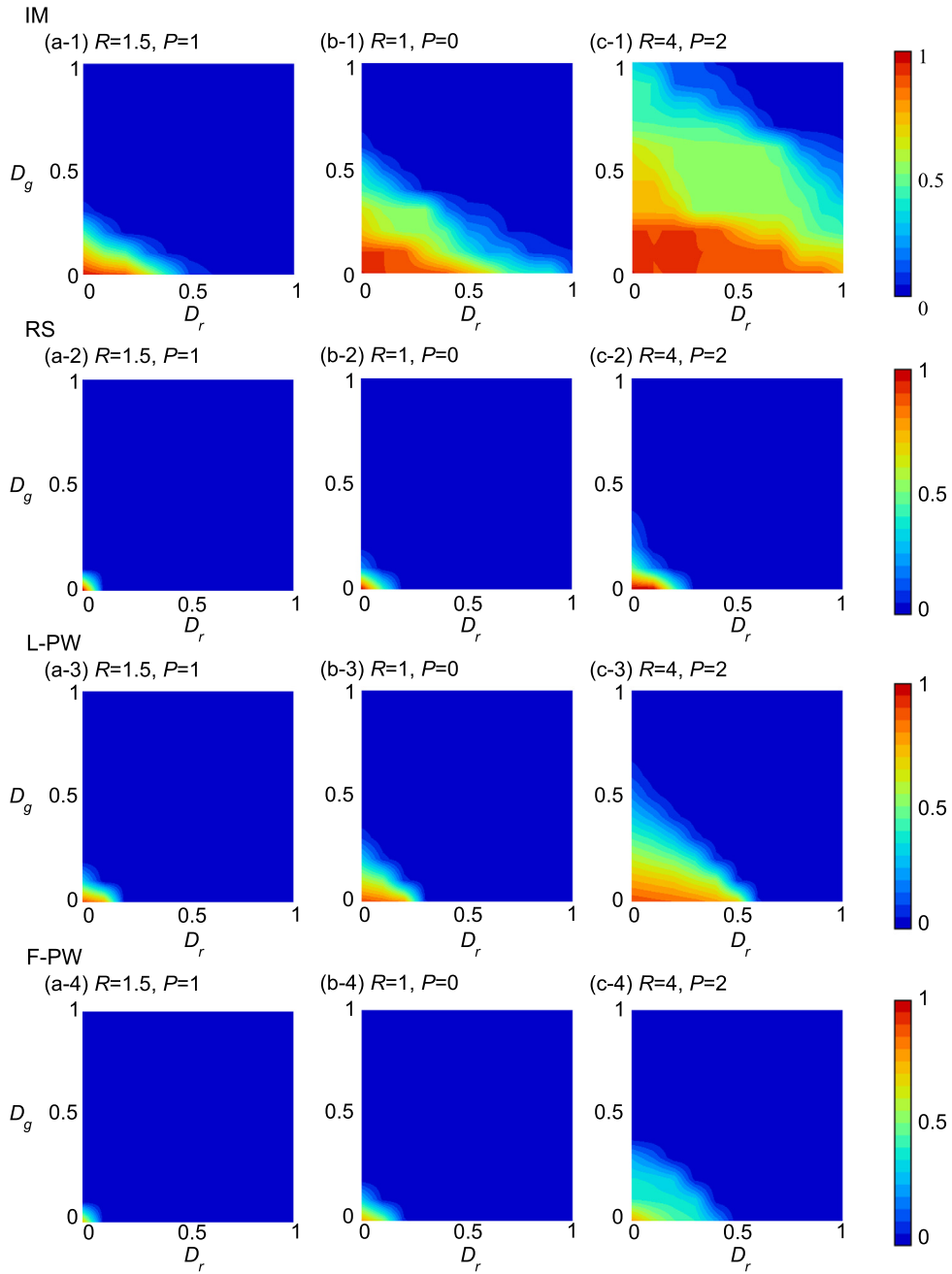


Fig. 14. Equilibrium fraction of cooperators in  $D_r$ – $D_g$  diagrams for (a)  $R = 1.5$ ,  $P = 1$ , (b)  $R = 1$ ,  $P = 0$ , and (c)  $R = 4$ ,  $P = 2$ . Games are played on an 8-neighbor Ho-SW. Considered strategy updating rules include IM (panels in the first row), RS (the second row), L-PW (the third row), and F-PW (the last row).

$R - P$  regardless of the updating rule (Figs. 13 and 14). However, if the  $D'_g$ – $D'_r$  is chosen, the situation changes: the equilibrium fraction of cooperators is nearly identical for all updating rules, irrespective of the values of  $R - P$  (Figs. 15 and 16). The results thus validate that the scaling parameters  $D'_g$  and  $D'_r$  are more suitable than  $D_g$  and  $D_r$  as the scaling parameters for the dilemma strength.

Interestingly, with the F-PW rule contours differ somewhat between games even if the parameters  $D'_g$  and  $D'_r$  are implemented. The reason is that, unlike other rules, F-PW contains an additional parameter,  $\tau$ , which acts as

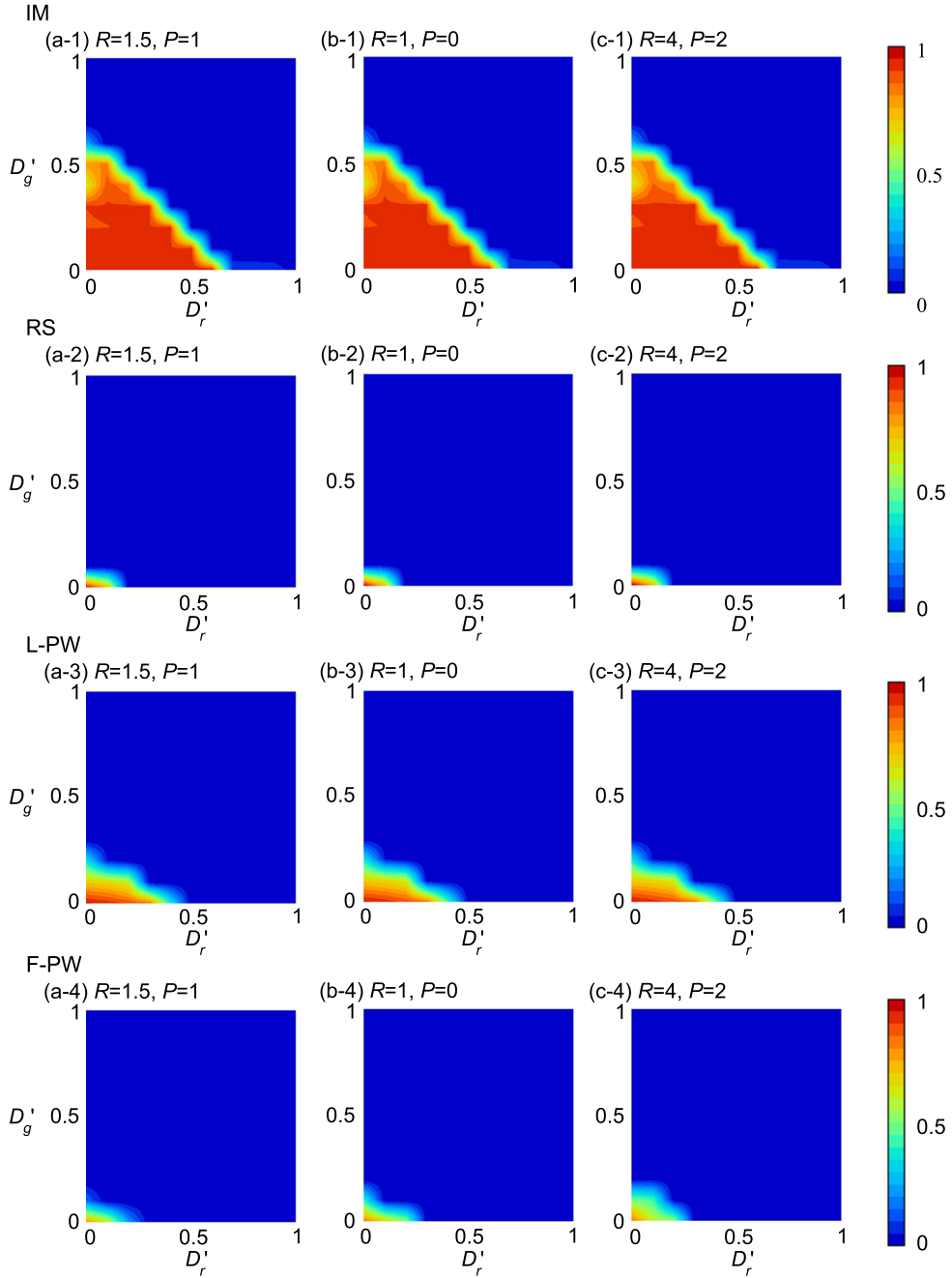


Fig. 15. Equilibrium fraction of cooperators in  $D'_r$ - $D'_g$  diagrams for (a)  $R = 1.5$ ,  $P = 1$ , (b)  $R = 1$ ,  $P = 0$ , and (c)  $R = 4$ ,  $P = 2$ . Games are played on an 8-neighbor lattice. Considered strategy updating rules include IM (panels in the first row), RS (the second row), L-PW (the third row), and F-PW (the last row).

the intensity of selection [280,281]. When using the Fermi function, increasing  $R - P$  causes the payoff difference between players to increase, which cannot be compensated by a constant  $\tau$ . Consequently, the adoption probability in Eq. (23) depends on  $R - P$ . The most direct adjustment to overcome such a difficulty is to rescale the intensity of selection,  $\tau$ , by replacing it with  $\tau' = \tau(R - P)$ . Fig. 17 shows the equilibrium result with this new intensity of selection. Regardless of  $R - P$ , the equilibrium fraction of cooperators remains the same. Moreover, this particular solution helps answering the question why other updating rules that depend on the payoff difference (namely, L-PW

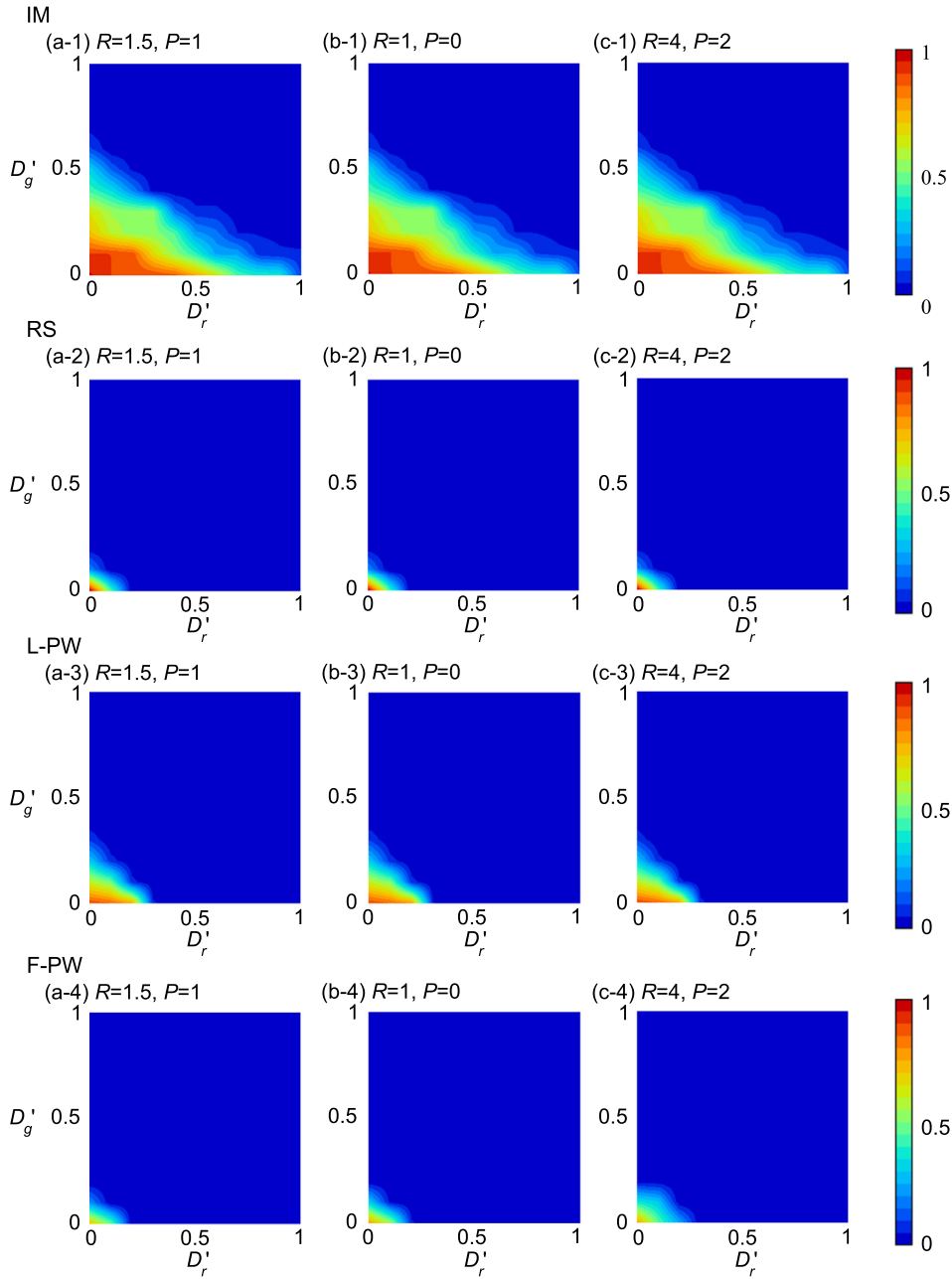


Fig. 16. Equilibrium fraction of cooperators in  $D'_r$ – $D'_g$  diagrams for (a)  $R = 1.5$ ,  $P = 1$ , (b)  $R = 1$ ,  $P = 0$ , and (c)  $R = 4$ ,  $P = 2$ . Games are played on an 8-neighbor Ho-SW. Considered strategy updating rules include IM (panels in the first row), RS (the second row), L-PW (the third row), and F-PW (the last row).

and RS) do not require any adjustments. The reason is that the associated adoption probabilities (Eqs. (24) and (25)), contain payoff differences in their denominators, both of which inherently depend on the value of  $R - P$ . For this reason, L-PW and RS produce identical contours in  $D'_g$ – $D'_r$  diagrams.

Finally, we examine the evolution of the cooperative trait on heterogeneous He-SW and SF networks. Because we confirmed that the qualitatively identical outcomes are obtained by other updating rules, only IM is considered here. Figs. 18 and 19 show contours for the equilibrium fraction of cooperators in  $D_g$ – $D_r$  and  $D'_g$ – $D'_r$  diagrams. Unfortunately, neither pair of the parameters can guarantee identical contours between games, thus forcing the conclusion

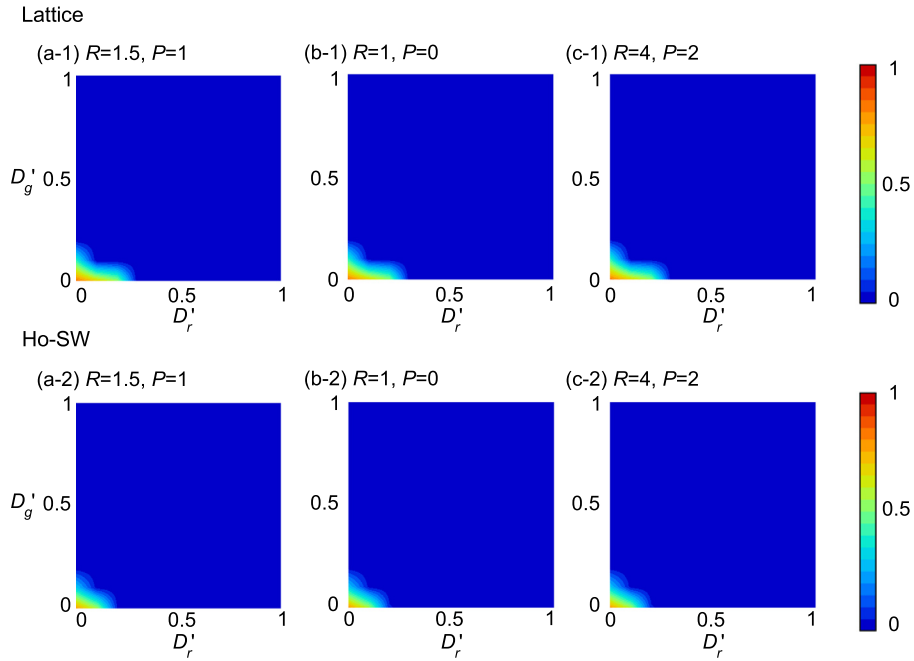


Fig. 17. Equilibrium fraction of cooperators in  $D'_r$ – $D'_g$  diagrams for (a)  $R = 1.5$ ,  $P = 1$ , (b)  $R = 1$ ,  $P = 0$ , and (c)  $R = 4$ ,  $P = 2$ . Games are played on an 8-neighbor lattice (panels in the upper row) and Ho-SW (the lower row). Applied strategy updating rule is F-PW in which the original intensity of selection is rescaled by  $R - P$ .

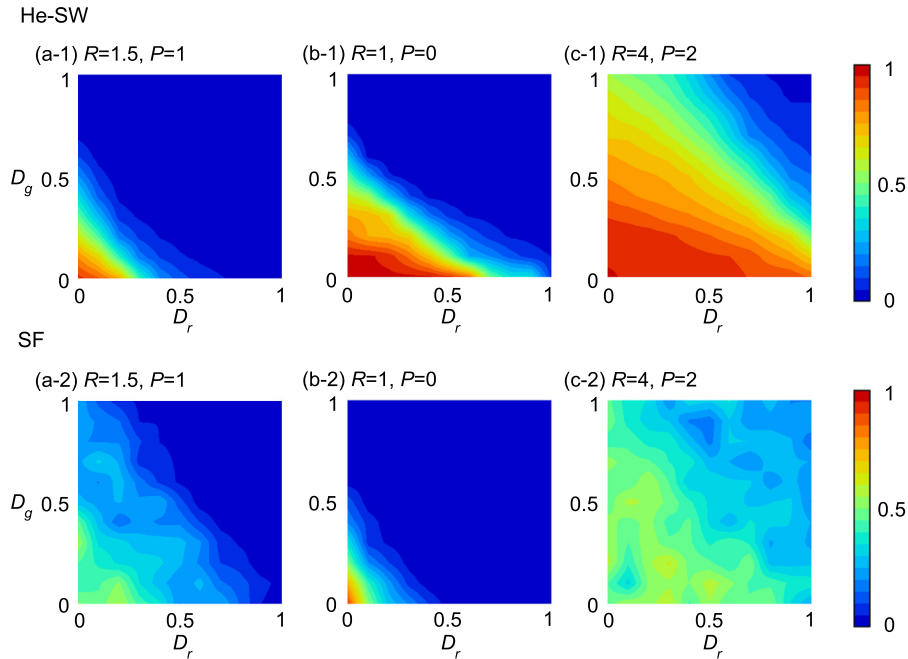


Fig. 18. Equilibrium fraction of cooperators in  $D_r$ – $D_g$  diagrams for (a)  $R = 1.5$ ,  $P = 1$ , (b)  $R = 1$ ,  $P = 0$ , and (c)  $R = 4$ ,  $P = 2$ . Games are played on He-SW (panels in the upper row) and SF (the lower row) with the average node degree ( $k$ ) = 8. Applied strategy updating rule is IM.

that both pairs are inappropriate as the scaling parameters. The failure is particularly noticeable if SF is assumed as the interaction network. Namely, in heterogeneous networks the difference in the number of games played by each agent has a considerable influence on the individual's payoff [83,282]. If the number of games differs greatly (which is

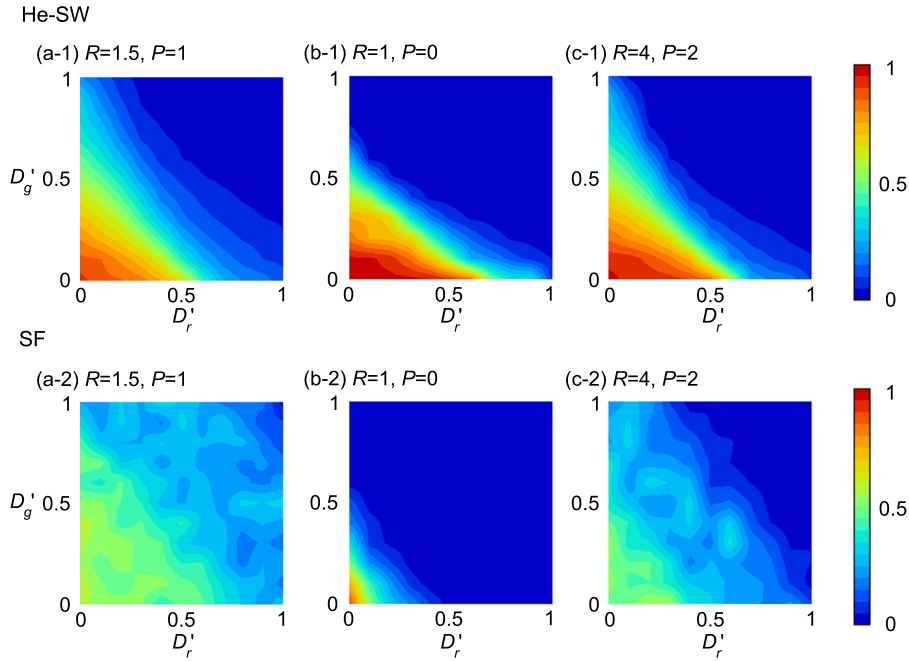


Fig. 19. Equilibrium fraction of cooperators in  $D'_r$ - $D'_g$  diagrams for (a)  $R = 1.5$ ,  $P = 1$ , (b)  $R = 1$ ,  $P = 0$ , and (c)  $R = 4$ ,  $P = 2$ . Games are played on He-SW (panels in the upper row) and SF (the lower row) with the average node degree  $\langle k \rangle = 8$ . Applied strategy updating rule is IM.

closely related to the degree distribution), it is insufficient to consider the dilemma strength on a per-interaction basis. Therefore, a future scaling framework involving the number of neighbors may prove more suitable for analyzing the cooperation evolution on heterogeneous networks.

## 5. Conclusion and future prospects

Universal scaling for the dilemma strength is a fascinating subject that simplifies the underlying structure governing social dilemmas and sheds new light onto our understanding of the emergence of cooperative behavior. For an infinite, well-mixed population, the previously defined sets (the individual payoffs  $R$ ,  $T$ ,  $S$ , and  $P$ , or GID and RAD,  $D_g = T - R$ ,  $D_r = P - S$ ) are appropriate as the scaling parameters. However, if considering a population with social viscosity becomes a priority, predicting the course of the evolutionary dynamics in a simple manner is not possible from these two sets. We showed that a new set of the scaling parameters ( $D'_g = (T - R)/(R - P)$  and  $D'_r = (P - S)/(R - P)$ ) is universally valid irrespective of the reciprocity mechanism at work, both in the context of infinite and finite, well-mixed populations.

In Section 3, we discussed the consistency of  $D'_g$  and  $D'_r$  as quantifiers of the dilemma strength. Inspired by the results in Ref. [222], we demonstrated theoretically that the conditions for an ESS and the expressions for the internal equilibria in a population subjected to any of the five well-known reciprocity mechanisms depend only on  $D'_g$  and  $D'_r$ . Furthermore, an analogous result holds for the fixation probability of the different strategies in a finite, well-mixed population. Subsequently, we have reviewed the so-called paradox of cooperation benefits and highlighted that the paradox disappears if the appropriate scaling parameters (namely,  $D'_g$  and  $D'_r$ ) for the dilemma strength are applied. Therefore, we conclude that the scaling parameters proposed herein are universally effective in evaluating the equilibrium state of cooperation in any population with social viscosity.

In conjunction with the above-mentioned advances, Section 4 examined the universality of the dilemma strength scaling parameters,  $D'_g$  and  $D'_r$ , within the framework of structured populations. This was deemed important because the framework of structured populations incorporates a variety of distinct updating rules and spatial network structures. By means of numerical simulations, we have shown that nearly identical equilibrium outcomes are guaranteed for all updating rules, but not all network structures. The outcome of the evolutionary dynamics on heterogeneous topologies

is dependent on the number of games played by each individual (i.e. the individual's interaction degree), which is not included in the scaling parameters we proposed.

The effort to uncover the intricacies of scaling for the social dilemma strength, in addition to the new findings, also led to, as of yet, unexplored problems that merit further attention. Perhaps the most interesting issue is whether the proposed framework for the dilemma strength remains robust if the game involves a co-evolutionary scenario. The co-evolutionary scenario usually refers to the joint adjustment of the strategy and the updating rule or the interaction topology [34,220,283,284]. A more recent viewpoint [285] is to update both the strategy and the payoff, and thus cause the structure of the underlying game to change dynamically (e.g. from PD to CH or SH along the evolutionary trajectory). This type of a problem definitely constitutes a new challenge to the universality of scaling for the dilemma strength and deserves in-depth exploration. Furthermore, as shown in Section 4, equilibrium contours on heterogeneous networks are non-uniform, meaning that further improvements to the universality of scaling for the dilemma strength is needed to avoid the influence of an individual's interaction degree. Finally, we have not touched upon multiple interaction games, such as the public goods game [116,286–290], which should be regarded as the extensions of pairwise games, and therefore are of importance to the universality of scaling for the dilemma strength considered herein.

Social dilemmas are ubiquitous at the different levels of human and animal interactions, which makes evolutionary game theory applicable across a range of natural and social sciences. In this sense, it is expected that the reviewed dilemma strength is a concept of rather general importance. For example, evolutionary games have proven useful in analyzing traffic jams, where phase transitions between different traffic dilemmas occur [291–294]. Another example is the study of the social function of political concepts such as ideological rigidity [295,296]. A common approach to estimating the dilemma strength may benefit these and many other fields such as public health (behavioral epidemiology [297–308]) or engineering (system optimization [309,310], resource allocation [311], stability analysis [312], and packet routing design [313,314]), all of which, more or less, are influenced by a decision-making process. We reiterate that the aim of this review was to highlight the importance of universal scaling for the dilemma strength via mathematical and physical methods. In hope that our aim was achieved, we also sincerely expect that the outlined directions for the future advancements can accelerate the progress of this beautiful and highly applicable avenue of research.

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