Article:
Mobilia, M (2013) Evolutionary games with facilitators: When does selection favor cooperation? Chaos, Solitons and Fractals, 56. pp. 113-123. ISSN 0960-0779

https://doi.org/10.1016/j.chaos.2013.07.011

Evolutionary games with facilitators: When does selection favor cooperation?

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We study the combined influence of selection and random fluctuations on the evolutionary dynamics of two-strategy ("cooperation" and "defection") games in populations comprising cooperation facilitators. The latter are individuals that support cooperation by enhancing the reproductive potential of cooperators relative to the fitness of defectors. By computing the fixation probability of a single cooperator in finite and well-mixed populations that include a fixed number of facilitators, and by using mean field analysis, we determine when selection promotes cooperation in the important classes of prisoner's dilemma, snowdrift and stag-hunt games. In particular, we identify the circumstances under which selection favors the replacement and invasion of defection by cooperation. Our findings, corroborated by stochastic simulations, show that the spread of cooperation can be promoted through various scenarios when the density of facilitators exceeds a critical value whose dependence on the population size and selection strength is analyzed. We also determine under which conditions cooperation is more likely to replace defection than vice versa.

Keywords: Evolutionary games; dynamics of cooperation; social dilemmas; fixation; population dynamics.

PACS numbers: 05.40.-a, 02.50.-r, 87.23.Kg, 87.23.Ge

1. Introduction

Evolutionary game theory (EGT) [1–6] provides a suitable framework to model the evolution of cooperative behavior, which is a problem of paramount importance [7]. EGT is traditionally concerned with the dynamics of competing species (strategies) in infinitely large populations where each species' reproductive potential (fitness) varies with the population composition. The selection pressure is thus "frequency-dependent" and the deterministic evolution is described in terms of ordinary differential (replicator) equations [1–5]. The classic notion of evolutionary stable strategy (ESS) is related to the stability of the fixed points of the underlying replicator equations: a strategy is evolutionary stable if the fitness of those adopting it is always higher than the fitness of a small fraction of mutants with an alternative strategy. As an important consequence of frequency-dependent selection, the fitness optimization at an individual level may cause the reduction of the population's average fitness. This yields a "social dilemma", as in the celebrated prisoner's dilemma game where the best strategy for each player is to defect even if mutual cooperation would benefit the whole population [4–6, 8]. Cooperation dilemmas can arise in other simple models, like the two-strategy snowdrift and stag-hunt games [4–6]. The attempt to explain the cooperative behaviors observed in experiments [9, 10] has motivated the investigation of various mechanisms (kin and group selection, reciprocity, local interactions) that could possibly promote the spread of cooperation [11–22].

When the size of the population is finite, evolution is known to be affected by demographic noise. The dynamics is thus often modeled in terms of continuous-time Markov chains and characterized by the notion of fixation probability [4–6]. This concept refers to the possibility that a "mutant type" takes over the entire population and is closely related to the important concept of evolutionary stability in finite populations (ESS_N) put forward by Nowak and collaborators [23]. These authors proposed that in two-player games a given strategy (say D) is evolutionary stable in a finite population if, in addition to having a higher fitness than the alternative strategy (say C), the selection also opposes the replacement of D by C. As a direct consequence, when the fixation probability of the mutant type C is higher than in the absence of selection, the evolution favors C replacing D [4–6, 23].

In this work, we consider the evolutionary dynamics of three important classes of two-strategy games, namely the prisoner's dilemma (PD), snowdrift (SD) and stag-hunt (SH) games, where the pure strategies are "cooperation" (C) and "defection" (D) and the former is supported by the presence of a number of "cooperation facilitators" in the population. The facilitators participate in the dynamics by enhancing the fitness of cooperators relative to the reproductive potential of defectors [24]. Here, our goal is to analyze the interplay in finite populations between selection, demographic fluctuations and facilitators in these paradigmatic classes of evolutionary games. In fact, it is important to understand whether selection favors cooperation, and in particular when it promotes the replacement of defectors by cooperators [1, 2, 4–6, 23]. For instance, while selection always opposes cooperation in the classic PD games (no facilitators), it has been found that cooperation can spread in a special class of PD games with facilitators [24]. For PD, SD and SH games, we here investigate the circumstances and scenarios under which selection and the presence of facilitators favor cooperation at the expense of defection, and how these conditions are influenced by the population size and se-

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lection intensity. To understand when the evolutionary dynamics promotes the spread of cooperation, we determine the critical fraction of facilitators in the population above which selection favors the replacement of defection by cooperation, as well as the density of facilitators necessary for selection to favor cooperation invading defection. We also identify the conditions under which cooperation is more likely to replace defection than vice versa.

The structure of this paper is the following: In the next section, we define the prisoner's dilemma, snowdrift and stag-hunt games in the presence of cooperation facilitators. Section 3 is dedicated to the study of the dynamics in finite populations and to the calculation of the fixation probability. The circumstances under which selection favors the invasion and the replacement of defection by cooperation are studied in Section 4-6. Our conclusions are presented in Section 7.

2. Evolutionary games with cooperation facilitators

We study the evolutionary dynamics of two-strategy games, that can be interpreted as social dilemmas, in the presence of cooperation facilitators. More specifically, we consider a *finite* and well-mixed (spatially homogeneous) population consisting of N individuals, j of which are cooperators (C's) and k are defectors (D's). The population is also comprised of a fixed number ℓ of "cooperation facilitators" that enhance the expected payoff of $\mathsf{C}-$players relative to the average of defectors (see below) [24]. The pairwise interaction between C's and D's is embodied in the payoff matrix and we distinguish three classes of games: the (i) *prisoner's dilemma* (ii) *snowdrift*, (iii) and *stag-hunt* games [1–6, 8, 25–29].

(i) The paradigmatic model of cooperation dilemma is the *prisoner's dilemma* (PD) game whose generic features are conveniently captured by the following payoff matrix [1–6, 8] with three parameters:

$$\begin{array}{c} \\ \mathsf{C} \\ \mathsf{D} \end{array} \begin{array}{c} \begin{array}{cc} \mathsf{C} & \mathsf{D} \end{array} \\ \begin{pmatrix} b-c & -c \\ b & d-c \end{pmatrix} \end{array}, \tag{1}$$

where $b > c > 0$ and $b > d > 0$. The parameters b and c respectively represent the benefit and the cost of cooperation and, in the context of PD games, $r \equiv c/b$ is referred to as the "cost-to-benefit ratio" [24]. Hence, when one player defects and the other cooperates, the latter is "exploited" and receives a payoff $-c$ while the former gets b. The payoff for mutual defection is given by $d-c$ and can be either non-negative ($c \leq d$) or negative ($c > d$), but always less than the payoff $(b-c)$ for mutual cooperation and superior to the exploitation payoff $(-c)$. To simplify our analysis, we shall always consider that b, c, d are all of order $O(1)$. Defection is the only strict Nash equilibrium (NE) of the classic ($\ell = 0$) PD games and a cooperation dilemma arises from the fact that each individual favors defection, even though cooperation enhances the overall payoff of the population. In the presence of a fixed number $\ell = N - j - k$ of cooperation facilitators, the expected payoffs of cooperators and defectors, respectively $\pi_{\mathsf{C/D}}$, are inferred from (1) according to the general principles of EGT, yielding (by excluding self-interactions) [24]:

$$\begin{aligned} \pi_{\mathsf{C}} &= (b-c)\left(\frac{j+\ell-1}{N-1}\right) - c\left(\frac{N-\ell-j}{N-1}\right) \\ \pi_{\mathsf{D}} &= b\left(\frac{j}{N-1}\right) + (d-c)\left(\frac{N-\ell-j-1}{N-1}\right). \end{aligned} \tag{2}$$

As facilitators enhance π_{C} by $b\ell/(N-1)$ and π_{D} by $(c-d)\ell/(N-1)$, their presence supports cooperation relative to defection (since $b > c-d$), see also (7)-(9). The population average payoff is given by $\bar{\pi} = (j\pi_{\mathsf{C}} + k\pi_{\mathsf{D}})/N$. The fixation properties of the special subclass of PD games with facilitators and $c = d$ was studied in Ref. [24].

(ii) *Snowdrift* (SD) games are the prototypes of evolutionary models exhibiting mixed evolutionary stable strategy. The features of these anti-coordination games are aptly captured by the following payoff matrix [1–6, 25–27]:

$$\begin{array}{c} \\ \mathsf{C} \\ \mathsf{D} \end{array} \begin{array}{c} \begin{array}{cc} \mathsf{C} & \mathsf{D} \end{array} \\ \begin{pmatrix} b-c & d-c \\ b & -c \end{pmatrix} \end{array}, \tag{3}$$

where we consider that $b > c + d > 0$, with $c > 0$ and $d > 0$. In its classic version ($\ell = 0$), SD games are characterized by an evolutionary stable (non-strict NE) mixed strategy where C is played with frequency $c/(c+d)$.

When a fixed number ℓ of cooperation facilitators is present in the population, the expected payoffs of cooperators and defectors are inferred from (3):

$$\begin{aligned} \pi_{\mathsf{C}} &= (b-c)\left(\frac{j+\ell-1}{N-1}\right) + (d-c)\left(\frac{N-\ell-j}{N-1}\right) \\ \pi_{\mathsf{D}} &= b\left(\frac{j}{N-1}\right) - c\left(\frac{N-\ell-j-1}{N-1}\right), \end{aligned} \tag{4}$$

where the presence of facilitators enhances π_{C} by $(b-d)\ell/(N-1)$ and π_{D} by $c\ell/(N-1)$, and therefore promotes cooperation relative to defection (since $b-d > c$).

(iii) *Stag-hunt* (SH) games are the prototype of social contrast and trust games. Many features of these coordination games are suitably captured by the simple payoff matrix [1–6, 28–31]:

$$\begin{array}{c} \\ \mathsf{C} \\ \mathsf{D} \end{array} \begin{array}{c} \begin{array}{cc} \mathsf{C} & \mathsf{D} \end{array} \\ \begin{pmatrix} b & -c \\ b-c & d-c \end{pmatrix} \end{array}, \tag{5}$$

where $b > c > d > 0$. In the absence of facilitators, SH games are characterized by two strict pure NEs and by a non-strict NE corresponding to a mixed strategy in which C is played with frequency $d/(c+d)$.

In the presence of ℓ cooperation facilitators, the expected payoff of cooperators and defectors are obtained

from (5):

$$\pi_{\mathsf{C}} = b\left(\frac{j+\ell-1}{N-1}\right) - c\left(\frac{N-\ell-j}{N-1}\right) \quad (6)$$
$$\pi_{\mathsf{D}} = (b-c)\left(\frac{j}{N-1}\right) + (d-c)\left(\frac{N-\ell-j-1}{N-1}\right),$$

where the presence of facilitators enhances π_{C} by $(b+c)\ell/(N-1)$ and π_{D} by $(c-d)\ell/(N-1)$, and therefore supports cooperation relative to cooperation.

For further convenience, it is useful to write the difference $\delta\pi(j)$ between the expected payoffs of defectors and cooperators for the three types of games (PD, SD and SH) as

$$\delta\pi(j) = \pi_{\mathsf{D}}(j) - \pi_{\mathsf{C}}(j) = \alpha\,(j/N) + \beta_\ell, \quad (7)$$

with

$$\alpha = \begin{cases} (c-d)\frac{N}{N-1} & \text{(PD)} \\ (c+d)\frac{N}{N-1} & \text{(SD)} \\ -(c+d)\frac{N}{N-1} & \text{(SH)} \end{cases} \quad (8)$$

and

$$\beta_\ell = \begin{cases} \frac{dN-(b+d-c)\ell+(b-d)}{N-1} & \text{(PD)} \\ \frac{b-dN-(b-c-d)\ell}{N-1} & \text{(SD)}, \\ \frac{dN-(b+d)\ell+b+c-d}{N-1} & \text{(SH)} \end{cases} \quad (9)$$

where we have used (2), (4), (6). Since facilitators enhance π_{C} relative to π_{D}, we notice that for all the above games $\delta\pi(j)$ and β_ℓ are decreasing functions of ℓ.

3. Dynamics, cooperation fixation probability and evolutionary stability

In a population of finite size N, the evolutionary dynamics is generally described by a continuous-time birth-death process [4, 6, 32–34], where at each time step a pair of individuals is randomly drawn to interact and the competition between the strategies, specified by the underlying payoff matrix, is encoded in the transition rates: if one picks a cooperator-defector pair, one of these individuals is randomly chosen for reproduction proportionally to its expected payoff (or fitness) and the other is replaced by the newborn offspring. In each elemental move, the population composition evolves from a state with j cooperators to a state consisting of $j \pm 1$ individuals of type C. The underlying Markov chain is fully specified by the transition rates $T_j^{\pm}$ for the moves $j \to j \pm 1$, respectively, with $T^{\pm}_{j=N-\ell} = T^{\pm}_{j=0} = 0$ to account for the absorbing states $j = 0$ (no cooperators) and $j = N - \ell$ (no defectors) [24]. More specifically, we here consider the transition rates [6, 24, 26, 35–38]:

$$T_j^{\pm} = \frac{j(N-\ell-j)}{N(N-1)}\,\frac{1}{1+e^{\pm\{f_{\mathsf{D}}(j)-f_{\mathsf{C}}(j)\}}}. \quad (10)$$

In these expressions $j(N-\ell-j)/N(N-1)$ accounts for the probability of picking a cooperator-defector pair. The probability that a C reproduces and replaces a D is proportional to $[1+e^{\{f_{\mathsf{D}}(j)-f_{\mathsf{C}}(j)\}}]^{-1}$ (and similarly for D reproducing at the expense of C). This corresponds to the evolution according to the so-called comparison pairwise "Fermi process" (FP) [5, 6, 26–31, 35–38], where f_{C} and f_{D} respectively denote the cooperators and defectors fitness. These quantities are commonly chosen to be proportional to the difference between the C/D's expected payoffs and the average population payoff [6, 24, 26–30]:

$$f_{\mathsf{C/D}}(j) = 1 - s + s[\pi_{\mathsf{C/D}}(j) - \bar{\pi}(j)], \quad (11)$$

where the parameter $0 \le s \le 1$ accounts for the selection strength ($s = 0$ and $s = 1$ respectively correspond to the weak and strong selection limits) and the $1 - s$ is a baseline fitness contribution [6, 26, 28–31]. It has to be noted that $f_{\mathsf{C/D}}(j)$ vary with the population composition ("frequency-dependent selection" [1–6]) and, as before, it is useful to write the difference between f_{D} and f_{C} as $\delta f(j) = f_{\mathsf{D}} - f_{\mathsf{C}} = (s/N)[\alpha j + N\beta_\ell]$. It is also worth mentioning that other microscopic update rules, like the Moran process (MP) [4–6, 25, 26, 30, 31, 34, 39, 40], can also be chosen. The choice of the FP is made to simplify the analysis [(10) only depends on $\delta f(j)$], but it is noteworthy that the FP and MP are known to generally lead to qualitatively similar dynamics and, in the biological relevant case of weak selection intensity ($s \ll 1$), they even predict quantitatively similar results [6, 24, 26, 30, 31, 34].

In the limit of an infinitely large population ($N \to \infty$), with $x \equiv j/N$, $z \equiv \ell/N$ and $T_j^{\pm} \to T^{\pm}(x)$ and $\beta_\ell \to \beta(z)$, the random fluctuations are negligible and the dynamics is aptly described by the mean field rate equation (RE, after proper rescaling of time)

$$(d/dt)x(t) \equiv \dot{x} = T^+(x) - T^-(x) \quad (12)$$
$$= -x(1-z-x)\tanh\left\{\frac{s}{2}(\alpha x + \beta(z))\right\}.$$

This replicator-like equation is characterized by two absorbing fixed points, $x = 0$ (no C's) and $x = 1-z$ (no D's), and possibly by an interior fixed point $x^* = -\beta(z)/\alpha$ corresponding to the coexistence of C's and D's (when $0 < x^* < 1$).

When the population size is finite ($N < \infty$) and random fluctuations cannot be disregarded, the evolutionary dynamics is often characterized by the cooperation fixation probability ϕ_j^{C} which, in the presence of ℓ cooperation facilitators, is the probability that an initial number of j cooperators eventually replace all the defectors, leading to the absorbing state consisting of $N-\ell$ cooperators and ℓ facilitators. This quantity satisfies the (backward) master equation, $j \in [0, N-\ell]$:

$$T_j^-\,\phi^{\mathsf{C}}_{j-1} + T_j^+\phi^{\mathsf{C}}_{j+1} - [T_j^- + T_j^+]\phi_j^{\mathsf{C}} = 0, \quad (13)$$

with $\phi_0^{\mathsf{C}} = 0$ and $\phi^{\mathsf{C}}_{N-\ell} = 1$. With (10), the solution of

(13) reads (see, e.g., [4, 6, 24, 33]):

$$\phi_j^{\mathsf{C}} = \frac{1+\sum_{n=1}^{j-1}\exp\left(\frac{sn}{2N}[\alpha(n+1)+2N\beta_\ell]\right)}{1+\sum_{n=1}^{N-\ell-1}\exp\left(\frac{sn}{2N}[\alpha(n+1)+2N\beta_\ell]\right)}. \quad (14)$$

In particular, the fixation probability of a single cooperator in a sea of $N-\ell-1$ defectors and in the presence of ℓ cooperation facilitators is $\phi_1^{\mathsf{C}} \equiv \phi^{\mathsf{C}}$, with

$$\phi^{\mathsf{C}} = \left[1+\sum_{n=1}^{N-\ell-1}\exp\left(\frac{sn}{2N}[\alpha(n+1)+2N\beta_\ell]\right)\right]^{-1}. \quad (15)$$

Clearly, $\phi^{\mathsf{C}}=1$ when $\ell = N-1$. It has also to be noted that in the absence of selection ($s=0$), the fixation probability of j cooperators for the ensuing neutral dynamics simply reads $\phi_j^{\mathsf{C}} = j/(N-\ell)$, where $N-\ell$ can be interpreted as a population size effectively reduced by the presence of ℓ facilitators.

The notion of fixation probability is particularly important because it is closely related to the concept of evolutionary stability in finite populations [4–6, 23], and it allows to study under which circumstances the spread of cooperation is favored by selection, as proposed by the authors of Ref. [23]. This line of reasoning is readily generalized in the presence of cooperation facilitators: Defection is an evolutionary stable strategy in a population of size N comprising ℓ cooperation facilitators (ESS_N^ℓ) if the following *two conditions* are *simultaneously* satisfied:

i. A single ("mutant") cooperator must have a lower fitness than ("resident") defectors, i.e. $\delta f(1) = (s/N)[\alpha + N\beta_\ell] > 0$.

ii. For $0 \le \ell < N-1$, the fixation probability of a single cooperator has to be lower than in the absence of selection ($s=0$, when there are only random fluctuations), i.e. $\phi^{\mathsf{C}} < (N-\ell)^{-1}$.

The condition (i) ensures that selection opposes the initial spread of cooperation. Furthermore, as the fixation of a strategy can be favored in finite populations even if its initial increase is opposed, the condition (ii) guarantees that selection opposes the replacement of defection by cooperation.

According to Ref. [23] (see also [4, 6]), when any of the above conditions (i), (ii) is violated, defection is not an ESS_N^ℓ. If the condition (i) is satisfied but $\phi^{\mathsf{C}} > (N-\ell)^{-1}$, selection favors the replacement but opposes the invasion of defection by cooperators: in this case, the fixation of C is favored even if the initial increase of C's frequency is opposed. This typically occurs in SH games (see Sec. 6). On the other hand, when the condition (ii) is fulfilled but $\delta f(1) < 0$, selection favors the invasion by cooperators but opposes the replacement of defection by cooperation.

As we are here chiefly interested in determining when selection promotes cooperation in the presence of facilitators, we need to understand when the conditions favoring the invasion and replacement by cooperation are satisfied. With the definitions (8,9) of α and β_ℓ, together with (11) and (14), the *invasion condition* $\delta f(1) < 0$ for which selection favors the invasion of defectors by cooperators reads

$$\alpha + N\beta_\ell < 0, \quad (16)$$

while the *replacement condition* $\phi^{\mathsf{C}} > (N-\ell)^{-1}$ under which selection favors the replacement of defection by cooperation (for $0 \le \ell < N-1$) is

$$N-\ell-1 \;>\; \sum_{n=1}^{N-\ell-1} e^{n\psi_\ell(n)}, \quad \text{with} \quad (17)$$
$$\psi_\ell(n) \;=\; \delta f(1) + s\alpha\left(\frac{n-1}{2N}\right).$$

In the next sections we analyze the implications of the conditions (16) and (17) in PD, SD and SH games. However, since (16) imposes $\delta f(1) < 0$, we can already notice that (17) is automatically satisfied when the invasion condition $\beta_\ell < -\alpha/N$ is fulfilled and $\alpha \le 0$.

Furthermore, in order to understand whether the strategy C is more likely to replace D than vice versa, it may be interesting to compare ϕ^{C} with the probability ϕ^{D} that a single defector D takes over a population consisting of $N-\ell-1$ cooperators C and ℓ cooperation facilitators [4, 6]. Since fixation in either state $j = N-\ell$ or $j=0$ is guaranteed, one has $\phi^{\mathsf{D}} = 1-\phi_{N-\ell-1}^{\mathsf{C}}$ and, with (14), one readily obtains

$$\frac{\phi^{\mathsf{D}}}{\phi^{\mathsf{C}}} \;=\; \exp\left(s\sum_{j=1}^{N-\ell-1}\delta f(j)\right)$$
$$\;=\; \exp\left(\frac{s(N-\ell-1)}{2N}[\alpha(N-\ell)+2N\beta_\ell]\right). \quad (18)$$

As a result, $\phi^{\mathsf{C}} > \phi^{\mathsf{D}}$ when $s>0$ and $\alpha(1-z)+2\beta_\ell < 0$. In large populations ($N \gg 1$), $\beta_\ell \to \beta(z) = -\alpha x^*$ and one finds $\phi^{\mathsf{C}} > \phi^{\mathsf{D}}$ if $x^* < (1-z)/2$ when $\alpha < 0$, which corresponds to C having a larger basin of attraction than D and being risk-dominant [4, 6].

4. When does selection favor cooperation in prisoner's dilemma games with facilitators?

In PD games with ℓ cooperator facilitators the expected payoffs of cooperators and defectors are given by (2), which yields the fitness difference $\delta f(j) = s[\alpha(j/N)+\beta_\ell]$ with $\alpha = (c-d)N/(N-1)$ and $\beta_\ell = [dN-(b+d-c)\ell+(b-d)]/(N-1)$.

It is instructive to first consider the deterministic mean field limit ($N\to\infty$, with $c \neq d$) in which the dynamics is described by the RE (12). The latter is characterized by the system's two absorbing fixed points $x=0$ (no C's) and $x = 1-z$ (no D's). When $0 < -\beta(z)/\alpha < 1$, these are separated by an interior fixed point $x^* = [(b+d-c)z-d]/(c-d)$. A stability analysis of (12) reveals various mean field scenarios:

- If $c > d$ and $z \leq d/(b-c+d)$, there is no interior fixed point and $x = 0$ is the only attractor of the RE (12). This corresponds to the situation where there are no cooperators in the final state.
- If $c > d$ and $d/(b-c+d) < z \leq r$, where $r = c/b$ is the cost-to-benefit ratio, $x^* = [(b+d-c)z-d]/(c-d)$ is the only attractor of the RE (12). In this case, the presence of facilitators leads to the coexistence of cooperators and defectors.
- If $c > d$ and $z > r$, $x = 1-z$ is the only attractor of the RE (12). This corresponds to the situation where (12) predicts that defectors are replaced by cooperators.
- If $c < d$ and $z \leq r$, $x = 0$ is the only attractor of the RE (12).
- If $c < d$ and $r < z \leq d/(b-c+d)$, both $x = 0$ and $x = 1-z$ are stable and separated by the unstable interior fixed point x^*. This situation is characterized by bistability and, depending on whether the initial density of C's is more or less than x^*, the final state will either be $x = 1-z$ or $x = 0$ [2–4, 6].
- If $c < d$ and $z > d/(b-c+d)$, $x = 1-z$ is the only attractor of the RE (12) and this corresponds to the eventual replacement of defectors by cooperators.

It has to be noted that the special case $c = d$ corresponds to the "equals-gains-from-switching" PD game [6] discussed in Ref. [24].

It appears from the above discussion that the existence and stability of x^*, as well as the sign of $c-d$ (payoff for mutual defection), drastically influence the spread of cooperation. In fact, when $z \leq d/(b-c+d)$ there is no interior fixed point in the case $c > d$ whereas x^* exists but is unstable when $c < d$ and $z > r$. According to this mean field picture, we expect that a small number of cooperators will quickly die out if $z \leq d/(b-c+d)$. It is therefore necessary that $z > d/(b-c+d)$ for cooperation to be able to prevail when $N \to \infty$. In fact, when $z > d/(b-c+d)$ and $c < d$ we certainly expect that selection favors cooperation since $x = 1-z$ is then the attractor of (12). The situations where $d/(b-c+d) < z \leq r$ with $c > d$, and $z \leq r$ when $c < d$, are more intriguing because (12) is thus characterized by a stable coexistence fixed point x^* and it is not obvious under which circumstances cooperation will be able to replace defection. In fact, below we show that the replacement of D by C is favored when $z > z^* \equiv \ell^*/N$, where $d/(b-c+d) \leq z^* \leq r$ when $c > d$ and $r \leq z^* \leq d/(b-c+d)$ when $c \leq d$.

Building on the insight gained from the above mean field analysis, we now assess the combined influence of the selection pressure and demographic fluctuations in finite populations, by considering the invasion condition (16) that reads $z > \widetilde{z}$ with

$$\widetilde{z} \equiv \widetilde{\ell}/N = \frac{d}{b+d-c} + \left(\frac{b+c-2d}{b+d-c}\right)\frac{1}{N}, \qquad (19)$$

as well the replacement condition (17) which yields

$$N-\ell-1 \;>\; \sum_{n=1}^{N-\ell-1} e^{n\psi_\ell(n)}, \quad \text{with} \qquad (20)$$

$$\psi_\ell(n) \;=\; \delta f(1) + s\frac{(c-d)(n-1)}{2(N-1)}$$

$$\;=\; s\left[\frac{(c-d)(n+1)}{2(N-1)} + \beta_\ell\right]. \qquad (21)$$

We notice that in the limit $N \gg 1$ the condition $z > \widetilde{z}$ is equivalent to $z > d/(b+d-c)$.

With (18), (8) and (9), one finds that cooperation is more likely to replace defection than vice versa when

$$z > \frac{c+d}{2b+d-c} + \frac{2}{N}\left(\frac{b-c}{2b-c+d}\right). \qquad (22)$$

To analyze when selection favors cooperation in PD games with ℓ cooperators whose expected payoffs is given by (2), one needs to distinguish the cases where the payoff for mutual defection is negative ($c > d$) and non-negative.

4.1. The case of negative payoff for mutual defection ($c > d$)

When there is a negative payoff $d - c < 0$ for mutual defection, $\alpha > 0$ and the replacement condition (20) is generally more stringent than $z > \widetilde{z}$ with (19).

In fact, there is generally an ℓ^*, with $\lfloor\widetilde{\ell}\rfloor \leq \ell^* \leq \lceil Nr\rceil$, such that $\sigma_{\rm PD}(N,\ell) = \sum_{n=1}^{N-\ell-1} e^{n\psi_\ell(n)} - (N-\ell-1) < 0$ when $\ell > \ell^*$ and $s > 0$ [41]. In finite but large populations, when $N(b-c)(c-d) \gg 1$, the replacement condition (20) is therefore satisfied when the density z of facilitators exceeds the critical value $z^* = \ell^*/N$, with $\widetilde{z} \leq z^* \leq r$. Furthermore, with (22) one has $\phi^{\rm C} > \phi^{\rm D}$ in large populations when $x^* > (1-z)/2$ yielding $z > (c+d)/(2b-c+d)$.

One thus distinguishes the following regimes:

- When $z < \widetilde{z}$: Defection is an ESS_N^ℓ.
- When $z > \widetilde{z}$: Defection is no longer an ESS_N^ℓ.
- When $\widetilde{z} < z \leq z^*$: Selection favors the invasion (not the replacement) of defection by cooperation. In this regime a single cooperator is more likely to go extinct than in the absence of selection. When $N(b-c)(c-d) \gg 1$ and $s > 0$, one has $\widetilde{z} \leq z^* \leq r$ ($r = c/b$ is the cost-to-benefit ratio).
- When $z > z^*$: Selection favors both the invasion and replacement of defection by cooperation.
- When $z > (c+d)/(2b-c+d)$ and $N(2b-c+d) \gg 1$: C is more likely to replace D than vice versa.

In PD games with $c > d$ and $z > 0$, *the replacement condition (20) is more stringent than (19) and dictates when*

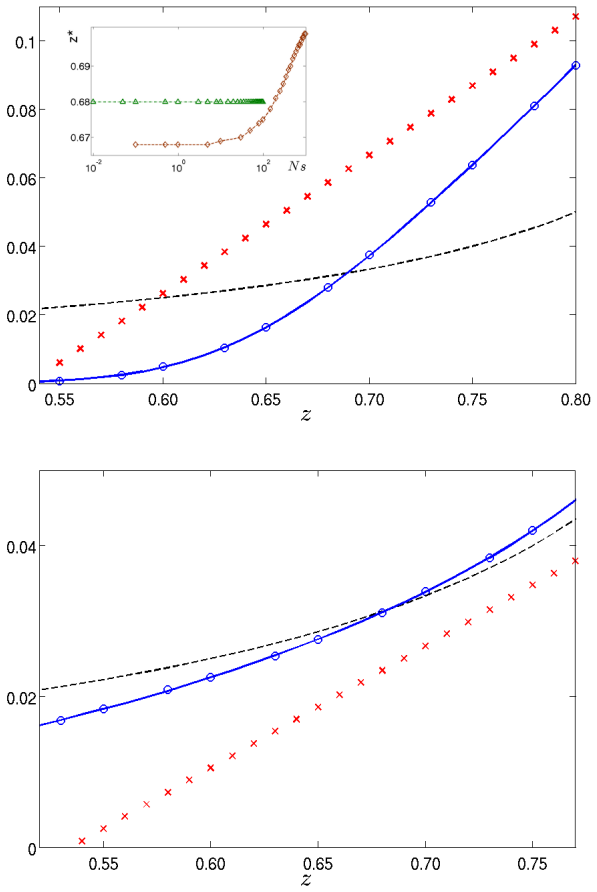

FIG. 1: *(Color online).* ϕ^{C} and $-\delta f(1) > 0$ vs. $z = \ell/N$ in PD games with ℓ facilitators and $N = 100, b = 1, c = 0.8, d = 0.2$. Results of stochastic simulations ($\circ$) for ϕ^{C}, analytical prediction (15) (solid) and $[N(1-z)]^{-1}$ (dashed), while $\times$'s show $-\kappa\delta f(1) > 0$ when $z > \widetilde{z} = 0.535$ [$\kappa = 1$ (top) and $\kappa = 4$ (bottom)]. Top: For strong selection intensity $s = 1$, selection favors the invasion and replacement of D by C when $z > z^* = 0.68$, see text. Bottom: For $s = 0.1$, one also finds $z^* = 0.68$. Inset: z^* vs. Ns with $s = 10^{-4} - 1$, $N = 100$ ($\triangle$) and $N = 1000$ ($\diamond$); we find $z^* \approx 0.684 \pm 0.016$.

selection favors the invasion and replacement of D by C. It is worth noting that the critical value z^* cannot be inferred from the rate equation (12) or from the payoffs (2), but is determined by the nontrivial solution of (20).

These findings are illustrated in Fig. 1 for strong selection strength $s = 1$ and for $s = 0.1$. In Fig. 1, the outcomes of stochastic simulations (obtained with the Gillespie algorithm [42]) perfectly agree with the theoretical expression (15), with $\phi^{\mathsf{C}} > [N(1-z)]^{-1}$ for $z \geq z^*$ and $z^* \leq r$, as predicted by (20). The inset of Fig. 1 illustrates that the critical value $z^* \approx 0.684 \pm 0.016$ is obtained when $Ns = 0.01 - 1000$, which indicates a very weak influence of the selection strength on the value of z^*.

4.2. The case of positive payoff for mutual defection ($c < d$)

When the payoff for mutual defection is positive $d - c > 0$, one has $\alpha < 0$ and $\psi_\ell(n) < 0$ when $z > \widetilde{z}$. The replacement condition (20) is therefore always satisfied when $\delta f(1) < 0$ and (19) is fulfilled. This implies that (16) is more stringent than (20) and *selection favors the invasion and replacement of D by C when* $z > \widetilde{z} = [d + (b + c - 2d)N^{-1}]/(b + d - c)$. Furthermore, proceeding as in Sec. 4.1, one finds that the replacement condition (20) is satisfied when $z > z^*$, where $0 \leq z^* \leq r < \widetilde{z}$. Moreover, with (18) one still finds that $\phi^{\mathsf{C}} > \phi^{\mathsf{D}}$ in large populations when $z > (c + d)/(2b + d - c)$.

The invasion and replacement conditions (19) and (20) are illustrated in Figure 2, where the theoretical prediction (15) perfectly agrees with the results of stochastic simulations, and can be summarized as follows:

- When $z \leq z^*$: Defection is an ESS^{ℓ}_N.
- When $z > z^*$: Defection is no longer an ESS^{ℓ}_N and $r \leq z^* < \widetilde{z}$.
- When $z^* < z < \widetilde{z}$: Selection favors the replacement (not the invasion) of defection by cooperation. In this regime a single cooperator is more likely to fixate than in the absence of selection.
- When $z > \widetilde{z}$: Selection favors both the invasion and replacement of defection by cooperation.
- When $z > (c+d)/(2b+d-c)$ and $N(2b+d-c) \gg 1$: C is more likely to replace D than vice versa.

The inset of Fig. 2 indicates again that the selection intensity has a weak influence on the value of z^*: in Fig. 2, one finds $z^* \approx 0.42 - 0.47$ when $Ns = 0.01 - 1000$.

It is worth noting that in the simple and special case of "equals-gains-from-switching" PD games, with $c = d$, considered in Ref. [24], one has $\widetilde{z} = z^*$ [43] and in this case C is more likely to invade and replace D when $z > r$ and $N \gg 1$, see (22), i.e. when the density of facilitators exceeds the cost-to-benefit ratio.

We have thus shown that in PD games with ℓ cooperator facilitators selection favors the invasion and replacement of defection by cooperation when the fraction of cooperation facilitators exceeds a critical value z^* (with $z > z^* > \widetilde{z}$) imposed by the replacement condition (20) $c > d$. When $c \leq d$, the invasion condition (16) dictates that $z > \widetilde{z}$ (with $\widetilde{z} \geq z^*$) for both the invasion and replacement of defection to be favored.

5. When does selection favor cooperation in snowdrift games with facilitators?

The expected payoffs of SD games with ℓ cooperator facilitators are given by (4) with $b > c + d > 0$. One thus

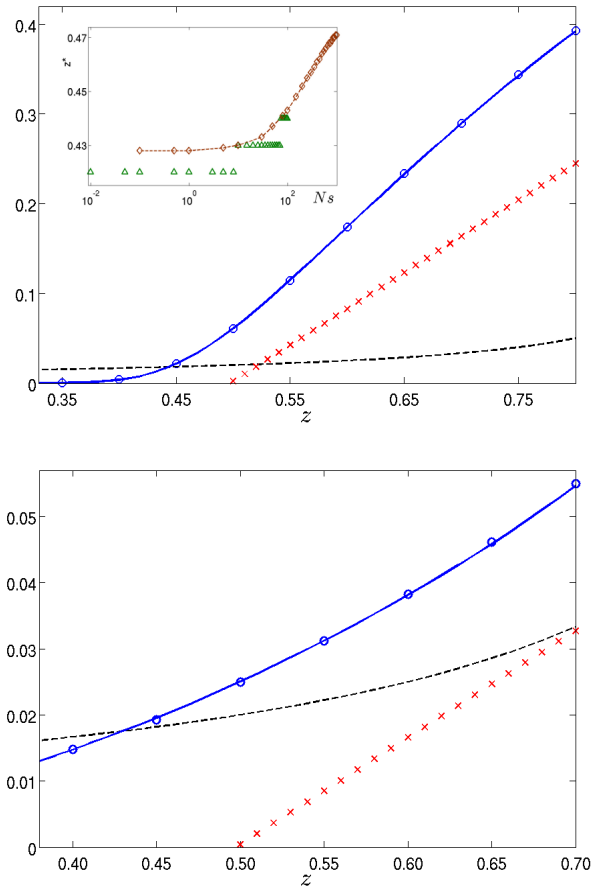

FIG. 2: *(Color online).* As in Fig. 1 with parameters $N = 100, b = 1, c = 0.2, d = 0.8$. Results of stochastic simulations ($\circ$) for ϕ^{C}, analytical prediction (15) (solid) and $[N(1-z)]^{-1}$ (dashed), while $\times$'s show $-\kappa\delta f(1) > 0$ when $z > \widetilde{z} = 0.4975$ [$\kappa = 0.5$ (top) and $\kappa = 1$ (bottom)]. Top: For strong selection intensity $s = 1$, selection favors the replacement of D by C when $z > z^* = 0.44$, see text. Bottom: For selection intensity $s = 0.1$, one has $z^* = 0.43$. Inset: z^* vs. Ns with $s = 10^{-4}-1$, $N = 100$ ($\triangle$) and $N = 1000$ ($\diamond$); we find $z^* \approx 0.42 - 0.47$.

has $\delta f(j) = s[\alpha(j/N) + \beta_\ell]$, with $\alpha = (c+d)N/(N-1)$ and $\beta_\ell = [b - dN - (b-c-d)\ell]/(N-1)$.

It is again instructive to start by considering the mean field dynamics (12) characterized by two absorbing fixed points ($x = 0$ and $x = 1 - z$), as well as a coexistence fixed point $x^* = [d + (b-c-d)z]/(c+d)$ when $z < c/b$. At mean field level, two regimes have to be considered:

- When $z < c/b$, the interior fixed point x^* is the only attractor of (12) that predicts the long-lived coexistence of cooperators and defectors.
- When $z \geq c/b$, the absorbing state $x = 1 - z$ is the only attractor of (12). This corresponds to the situation where cooperation prevails over defection.

This analysis indicates that when the number of facilitators is raised from 0 to c/b, the interior fixed point x^* is an attractor and an initial small density of cooperator increases to reach the value x^*. Furthermore, when the fraction of facilitators $z \geq c/b$, any initial number of cooperators grows and quickly replace all the defector. At mean field level, it is thus clear that a fraction $z \geq c/b$ of facilitators leads to a sustained level of cooperation in SD games. This picture is significantly altered by the demographic fluctuations arising in finite populations, where x^* is metastable [25–27] and a careful analysis has to be carried out to determine under which circumstances the selection favors cooperation replacing defection.

Since the mean field analysis has revealed that in the absence of fluctuations there is a sustained level of cooperation for $z \geq 0$, we need to focus on the replacement condition (17) to understand the combined influence of selection and demographic noise. In fact, the invasion condition (16) here yields $z > \widetilde{z} = -d^{-1} + [(b+c+d)/(b-c-d)]/N$ which simply reduces to $z \geq 0$ and is always satisfied when $N(b-c-d) \gg 1$.

For SD games in the presence of ℓ facilitators, the condition under which cooperation is favored by selection is thus given by (23) which here reads

$$N - \ell - 1 > \sum_{n=1}^{N-\ell-1} e^{n\psi_\ell(n)}, \quad \text{with} \tag{23}$$

$$\psi_\ell(n) = \delta f(1) + s\frac{(c+d)(n-1)}{2(N-1)} = s\left[\frac{(c+d)(n+1)}{2(N-1)} + \beta_\ell\right].$$

One can analyze (23) as in Sec. 4 and distinguish between the cases $c \geq d$ and $c < d$. In fact, from (18) we infer that in large populations $\phi^{\mathsf{C}} > \phi^{\mathsf{D}}$ when $x^* > (1-z)/2$, which yields $z > (c-d)/(2b-c-d)$ when $c \geq d$, whereas C is always more likely to replace D than vice versa when $c < d$.

The more interesting situation arises when $c \geq d$ and $N(b-c) \gg 1$. In this case, *there is a critical fraction of facilitators z^*, with $0 \leq z^* \leq c/b$, above which (23) is satisfied and selection favors C invading and replacing D.* The replacement condition (23) and $\delta f(1) < 0$ for $c \geq d$ are illustrated in Fig. 3, in which an excellent agreement is reported between (15) and stochastic simulations: it is found that $\phi^{\mathsf{C}} > [N(1-z)]^{-1}$ when $z > z^* \geq c/b$ as predicted by (23). The inset of Fig. 3 illustrates that the critical value z^* grows with the selection intensity s and population size N as a monotonic function of the scaling variable Ns.

When $c < d$ and $z < c/b$, the coexistence fixed point is closer to the absorbing state $x = 1 - z$ than to $x = 0$. In this case, when $N(d-c) \gg 1$, *the replacement condition (23) is satisfied for $z \geq 0$, i.e. even in the absence of facilitators, and selection always favors the invasion and replacement of D by C.*

In summary, SD games with ℓ cooperation facilitators are characterized by the following regimes:

- When $z \geq 0$ and $(b-c-d)N \gg 1$: Defection is

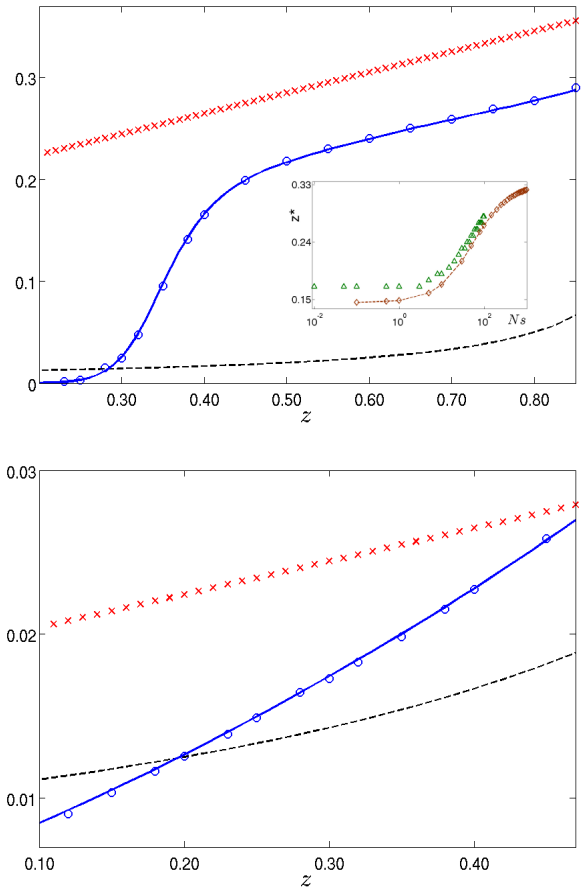

FIG. 3: *(Color online).* ϕ^{C} and $-\delta f(1)$ vs. $z = \ell/N$ in SD games with ℓ facilitators and $N = 100, b = 1, c = 0.6, d = 0.2$. Results of stochastic simulations ($\circ$) for ϕ^{C}, analytical prediction (15) (solid) and $[N(1-z)]^{-1}$ (dashed), while $\times$'s show $-\delta f(1) > 0$ for all values of $z \geq 0$. Top: For $s = 1$, selection favors C replacing D when $z > z^* = 0.28$, see text. Bottom: For $s = 0.1$, we find $z^* = 0.19$. Inset: z^* vs. Ns with $s = 10^{-4} - 1$, $N = 100$ ($\triangle$) and $N = 1000$ ($\diamond$).

never an ESS_N^ℓ since $\delta f(1) < 0$ and the invasion of D by C is favored.

- When $c \geq d$ and $0 \leq z \leq z^*$: Selection favors the invasion (not the replacement) of defection by cooperation. In this regime, the fixation probability of a single cooperator is lower than in the absence of selection ($s = 0$).

- When $c \geq d$ and $z > z^*$, with $N(c-d) \gg 1$: Selection favors the invasion and replacement of defection by cooperation. The critical value $z^* \leq c/b$ is an increasing function of Ns (see inset of Fig. 3).

- When $c \geq d$ and $z > (c-d)/(2b-c-d)$: C is more likely to replace D than vice versa in large populations.

- When $c < d$ and $N(c-d) \gg 1$: Selection favors the invasion and replacement of defection by cooperation even in the absence of facilitators and C is always more likely to replace D than vice versa, i.e. for any $z \geq 0$.

6. When does selection favor cooperation in stag-hunt games with facilitators?

The expected payoffs of SH games (5) with ℓ cooperator facilitators are given by (6), and the fitness difference reads $\delta f(j) = s[\alpha(j/N)+\beta_\ell]$, with $\alpha = -(c+d)N/(N-1)$ and $\beta_\ell = [dN - (b+d)\ell + b + c - d]/(N-1)$.

Useful information is provided by the study of the mean field rate equation (12) characterized by an unstable interior fixed point $x^* = [d-(b+d)z]/(c+d)$ separating the absorbing states $x = 0$ and $x = 1-z$ when $0 \leq z < d/(b+d)$. There are two mean field regimes:

- When $0 \leq z < d/(b+d)$, x^* exists and is unstable, whereas $x = 0$ (no C's) and $x = 1-z$ (no D's) are both stable (bistability). Since $x^* < (1-z)/2$, the state $x = 1-z$ has a larger basin of attraction than $x = 0$ and C is therefore risk-dominant: (12) leads to a state with no D's when $x(0) > x^*$ [4–6, 28–31].

- When $z \geq d/(b+d)$, the absorbing state $x = 1-z$ is the only attractor of (12) whereas $x = 0$ is unstable and there is no interior fixed point. This situation corresponds to C prevailing over D.

The mean field analysis reveals that the absorbing states are stable in SH games and separated by the unstable coexistence fixed point x^* when the fraction of facilitators is raised from 0 to $z = d/(b+d)$. In this situation, a small number of cooperators would quickly die out under the mean field dynamics (12) and it is necessary that $z \geq d/(b+d)$ for cooperation to be able to spread in infinitely large populations.

In the absence of facilitators ($\ell = 0$), SH games are always characterized by the bistability of C and D (two strict NEs) and, under weak selection and in populations of large but finite size ($Ns \ll 1$ and $N \gg 1$), it has been shown that selection favors the the replacement of D by C when $x^* < 1/3$, which here means $c > 2d$, i.e. when the basin of attraction of C is more than twice that of D (the so-called "1/3-rule") [4, 6, 23, 28, 30].

In SH games with cooperation facilitators, the invasion condition $\delta f(1) < 0$ (16) leads to $z > \widetilde{z}$, where

$$\widetilde{z} = \frac{d}{b+d} + \left(\frac{b-2d}{b+d}\right)\frac{1}{N}, \tag{24}$$

which coincides with the mean field requirement $z > d/(b+d)$ when $N \to \infty$. Moreover, the replacement

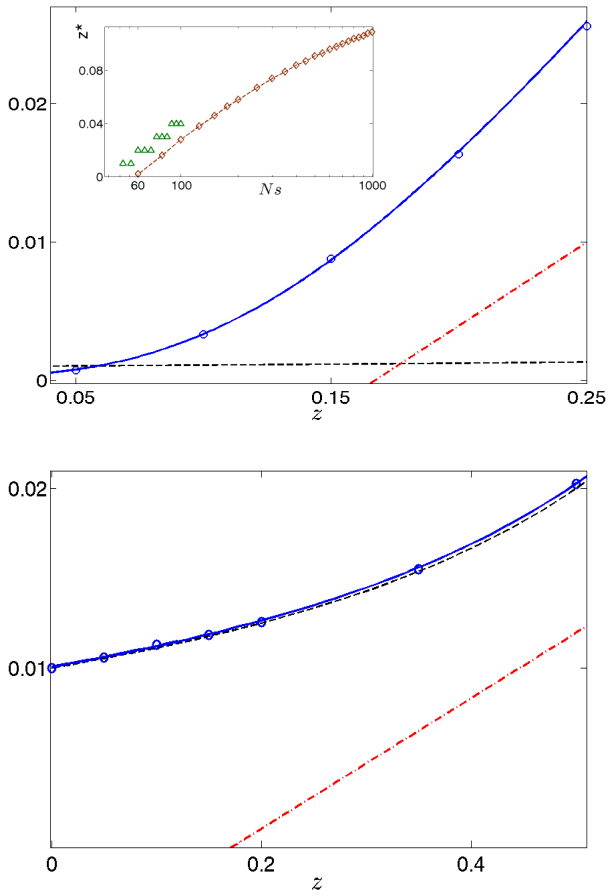

FIG. 4: *(Color online).* ϕ^{C} and $-\delta f(1) > 0$ vs. $z = \ell/N$ in SH games with ℓ facilitators and $b = 1, c = 0.8, d = 0.2$. Here, $x^* = 0.2 - 1.2z$. Results of stochastic simulations ($\circ$) for ϕ^{C}, analytical prediction (15) (solid) and $[N(1-z)]^{-1}$ (dashed); while the dashed-dotted lines show $-\kappa\delta f(1) > 0$ when $z > \widetilde{z}$ [$\kappa = 1$ (top) and $\kappa = 30$ (bottom)]. Top: When $s = 0.2$ and $N = 1000$, $\widetilde{z} \approx 0.167$, and selection favors C replacing D when $z > z^* \approx 0.059$. Bottom: When $s = 0.1$ and $N = 100$, selection always favors the replacement of defection and $\widetilde{z} \approx 0.172$. Inset: z^* vs. Ns with $s = 10^{-4} - 1$, $N = 100$ ($\triangle$) and $N = 1000$ ($\diamond$); when $Ns \lesssim 60$, the replacement condition (25) is satisfied even when $\ell = 0$, see text.

condition (17) yields

$$N - \ell - 1 \; > \; \sum_{n=1}^{N-\ell-1} e^{n\psi_\ell(n)}, \quad \text{with} \tag{25}$$

$$\begin{aligned} \psi_\ell(n) &= \delta f(1) - s\frac{(c+d)(n-1)}{2(N-1)} \\ &= s\left[-\frac{(c+d)(n+1)}{2(N-1)} + \beta_\ell\right]. \end{aligned}$$

Since $z > \widetilde{z}$ guarantees $\delta f(1) < 0$ and thus $\psi_\ell(n) < 0$, it is clear that (25) is satisfied when the invasion condition (16) is fulfilled: *$z > \widetilde{z}$ is therefore more stringent than (25) and dictates that selection favors the invasion and replacement of defection by cooperation when the density of facilitators in the population exceeds (24).* As a consequence, the replacement condition (25) is satisfied when $z > z^*$, with $z^* \leq \widetilde{z}$. Furthermore, with (18), (8) and (9), we find that $\phi^{\mathsf{C}} > \phi^{\mathsf{D}}$ when $x^* < (1-z)/2 - [(b+c+d)/(c+d)]/(2N)$. In large populations ($N(c+d) \gg 1$) this yields $x^* < (1-z)/2$, a condition which is here always satisfied, and therefore in SH games (5) C is always risk-dominant and more likely to replace D than vice versa.

Guided by the above mean field analysis and discussion of the 1/3-rule, in our analysis we distinguish the case where the selection strength is finite, with $N \gg 1$ and $Ns \gg 1$, from the situation where the population size is large (but finite) and the selection intensity is weak ($N \gg 1$ and $Ns \ll 1$).

When $N \gg 1$ and $Ns \gg 1$, there is a critical density of facilitators z^*, with $0 < z^* \leq \widetilde{z}$ above which (25) is satisfied: *selection favors the replacement of defection by cooperation when $z > z^*$.* This is illustrated in Figs. 4 and 5 (top) where the results of stochastic simulations for ϕ^{C} coincide with the prediction (15) and it is confirmed that (25) is satisfied when $z > z^*$, with $0 < z^* \leq \widetilde{z}$, while both (16) and (25) are satisfied when $z > \widetilde{z}$. The critical value z^* grows with s and admits $\widetilde{z}$ as an upper-bound. In the insets of Figs. 4 and 5 the dependence of z^* on s and N is shown to be given by monotonically growing functions of the scaling variable Ns.

When the coexistence fixed point x^* is close to the absorbing state $x = 0$ and $Ns \ll 1$ one finds that selection favors the replacement of defection even in the absence of facilitators, as illustrated in Fig. 4 (bottom). This can be rationalized by generalizing the 1/3-rule in the presence of facilitators [4, 6, 23, 28, 30]. In fact, for large populations and weak selection, when $N(1-z) \gg 1$ and $Ns \ll 1$, one can write $\sum_{n=1}^{N-\ell-1} e^{n\psi_\ell(n)} = N(1-z)\,[1 + (Ns/6)(1-z)\,\{2d - c - z(3b - c + 2d) + \mathcal{O}(Ns)\}]$. The replacement condition (25) thus becomes

$$z > \frac{2d - c}{3b - c + 2d}. \tag{26}$$

Hence, *when $c > 2d$ the replacement of defectors is favored by (weak) selection for any $z \geq 0$, i.e. even in the absence of facilitators, while $z^* = (2d-c)/(3b-c+2d)$ when $c < 2d$.* The result (26) can also be rewritten as the following condition on the location of the unstable coexistence fixed point:

$$x^* < 1/3 - (z/9)[1 + (c/d)], \tag{27}$$

where terms of order $\mathcal{O}(z^2)$ have been neglected and the 1/3-rule is recovered when $z = 0$. We infer from the inset of Fig. 4, that when $Ns \gtrsim 60$ a density $z > z^*$ of facilitators is necessary to favor the replacement of defection. In Fig. 5 (bottom), selection is found to (slightly) favor the replacement of defectors by cooperators when $z > z^* \approx 0.06 - 0.07$ in good agreement with (26,27).

In summary, selection favors the invasion and replacement of defection by cooperation in stag-hunt games in

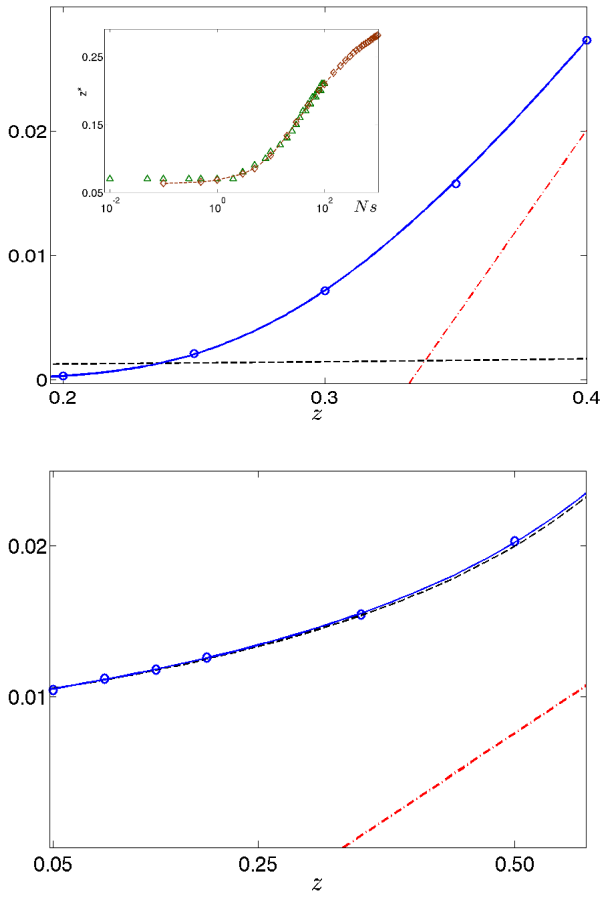

FIG. 5: *(Color online).* As in Fig. 4 with parameters $b = 1, c = 0.8, d = 0.5$. Here, $x^* = (5/13)(1 - 3z)$. Results of stochastic simulations ($\circ$) for ϕ^{C}, analytical prediction (15) (solid) and $[N(1-z)]^{-1}$ (dashed); while the dashed-dotted lines show $-\kappa\delta f(1) > 0$ when $z > \widetilde{z}$ [$\kappa = 1$ (top) and $\kappa = 30$ (bottom)]. Top: When $s = 0.2$ and $N = 1000$, $\widetilde{z} \approx 0.33$, and selection favors C replacing D when $z > z^* \approx 0.24$. Bottom: When $s = 0.001$ and $N = 100$, one has $z^* \approx 0.06$ and $\widetilde{z} \approx 0.33$, see text. Inset: z^* vs. Ns with $s = 10^{-4} - 1$, $N = 100$ ($\triangle$) and $N = 1000$ ($\diamond$).

the presence of ℓ facilitators when the invasion condition $z > \widetilde{z}$, with (24), is satisfied, and one distinguishes the following scenarios:

- When$Ns \gg 1$ and $z \leq z^*$: Defection is an ESS_N^ℓ.
- When $Ns \gg 1$ and $z > z^*$: Defection is no longer an ESS_N^ℓ. The critical density of facilitators z^* is an increasing function of Ns, with $0 < z^* \leq \widetilde{z}$.
- When $z^* < z \leq \widetilde{z}$: Selection favors the replacement (not the invasion) of defection by cooperation. In this regime, the fixation probability of a single cooperator is higher than in the absence of selection ($s = 0$). When $Ns \ll 1$ (weak selection) and $N(1-z) \gg 1$, $z^* = (2d - c)/(3b - c + 2d)$ if $c < 2d$, while selection favors the replacement of defectors even when $z = 0$ if $c > 2d$.
- When $z > \widetilde{z}$: Selection favors both the invasion and replacement of defection by cooperation.
- When $N(c + d) \gg 1$ and $z \geq 0$ C is always risk-dominant in SH games (5) with cooperation facilitators, and more likely to replace D than vice versa ($\phi^{\mathsf{C}} > \phi^{\mathsf{D}}$).

7. Conclusion

We have studied the combined influence of random fluctuations and selection pressure on the evolutionary dynamics of three classes of two-strategy games in the presence of cooperation facilitators. More precisely, we have considered the evolution of the prisoner's dilemma (PD), snowdrift (SD) and stag-hunt (SH) games in a well-mixed population of size N comprising ℓ cooperation facilitators. These are individuals enhancing the cooperators' reproductive potential (relative to defectors' fitness). By computing the exact cooperation fixation probability and by analyzing the mean field dynamics, we have investigated the circumstances under which selection favors the invasion and replacement of defection by cooperation. Invasion is favored when cooperators have a higher fitness than defectors, whereas selection favors the replacement of defectors when the fixation probability of a single cooperator is higher than $(N - \ell)^{-1}$ obtained under neutral dynamics. We have also determined the conditions under which cooperation is more likely to replace defection than vice versa. Interestingly, the invasion and replacement conditions lead to various scenarios when the fraction of facilitators present in the population varies. In PD and SD games, selection favors the replacement of defection by cooperation when the density of facilitators exceeds a critical value z^* that depends on the model's parameters and admits the cost-to-benefit ratio as an upper-bound. Selection also favors cooperators invading defectors in PD games with negative payoff for mutual defection when the density of facilitators exceeds z^*. When the payoff for mutual defection is positive in PD games, selection favors both the replacement and invasion of cooperation by defection when cooperators have higher fitness than defectors. In SD games, defection is generally not evolutionary stable in large populations and selection favors its invasion and replacement by cooperation when the density of facilitators is greater than z^*. In large populations, the critical value z^* is found to display a weak dependence on the population size N and selection strength s in PD games, whereas in SD and SH games z^* grows nontrivially with the scaling variable Ns. In SH games, the invasion and replacement of defection is favored whenever cooperators have a higher fitness than defectors. We have also generalized the so-called 1/3-rule and shown that in SH games the replacement of defection under weak selection occurs when the unstable mean field coexistence fixed point is

below a critical threshold that depends on the density of facilitators.

These findings show that the presence of cooperation facilitators can drastically alter the dynamics of paradigmatic models of social dilemmas via various scenarios, and can possibly be seen as an alternative mechanism to try and explain examples of cooperative behavior. It would be interesting to investigate the influence of cooperation facilitators on the evolution of spatially structured populations on complex networks, a subject that has recently received much attention, see e.g. [5, 44–46].

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[41] Since $\psi_\ell(n)$ given by (21) increases with n and decreases with ℓ, while $\psi_{\lfloor\widetilde{\ell}\rfloor}(n) \geq 0$ and $\psi_{\lceil Nr\rceil}(n) \leq 0$ when $N(b-c)(c-d) \gg 1$, one obtains $\sigma_{\rm PD}(N, \lfloor\widetilde{\ell}\rfloor) > 0$

and $\sigma_{\rm PD}(N, \lceil Nr \rceil) < 0$. One therefore generally has $\sigma_{\rm PD}(N, \ell) < 0$ for $\ell > \ell^*$, where $\lfloor \widetilde{\ell} \rfloor \leq \ell^* \leq \lceil Nr \rceil$, as confirmed in Figs. 1 and 2.

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