Reply to "Comment on 'Stochastic dynamics of the prisoner's dilemma with cooperation facilitators' "

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The fixation properties of a simple prisoner's dilemma game in the presence of "cooperation facilitators" have recently been investigated in finite and well-mixed populations for various dynamics [Mobilia, Phys. Rev. E **86**, 011134 (2012)]. In a Comment, Miękisz claims that, for cooperation to be favored by selection in the standard prisoner's dilemma games with facilitators, it suffices that $f_C > f_D$ (where $f_{C/D}$ are the respective fitnesses of cooperators and defectors). In this Reply, we show that, in generic prisoner's dilemma games with ℓ cooperation facilitators, it is generally *not sufficient* that a single cooperator has a higher fitness than defectors to ensure that selection favors cooperation. In fact, it is also necessary that selection promotes the replacement of defection by cooperation in a population of size N, which requires that the fixation probability of a single cooperator exceeds $(N - \ell)^{-1}$. This replacement condition is independent of $f_C > f_D$ and, when the payoff for mutual defection is negative, it is shown to be more stringent than the invasion condition. Our results, illustrated by a series of examples, considerably generalize those reported in the paper [Phys. Rev. E **86**, 011134 (2012)] and in the aforementioned Comment whose claims are demonstrated to be relevant only for a special subclass of prisoner's dilemma games.

The prisoner's dilemma (PD) game is the paradigmatic model of a cooperation dilemma [1]. It illustrates how defection prevails due to individual interest, even though cooperation would benefit the entire population. Yet, many examples of cooperative behavior are commonly observed, and over the years, this has motivated many attempts to generalize the PD and related models, see, e.g., Refs. [3–11] in Ref. [2].

In this context, the dynamics of the prisoner's dilemma game in the presence of ℓ "cooperation facilitators" has recently been investigated in finite and well-mixed (no spatial arrangement) populations [2]. In such a model, cooperators and defectors compete as in the classic PD game [1], but facilitators enhance the reproductive potential (fitness) of cooperators relative to the fitness of defectors. For the sake of simplicity, in Ref. [2], the influence of facilitators on the evolution of cooperation has been studied for the simplest and most convenient ("equal-gains-from-switching") form of PD games (see Refs. [1,3] and Note [16] of Ref. [2]). The ensuing evolutionary dynamics has been investigated in terms of birth-death processes and has been characterized by its fixation properties. In particular, the probability that cooperation prevails over defection and the mean time for such an event to occur have been computed. The fixation probability is particularly important because it is closely related to the notion of evolutionary stability in finite populations [1,4]. In fact, in a well-mixed population of finite size N comprising ℓ cooperation facilitators, selection favors the invasion and replacement of a given strategy, say defection (D), by a mutant type, say cooperation (C), when the following two conditions are fulfilled [2,4,5]:

(i) *Invasion condition*. The fitness of a single cooperator (f_C) is higher than the fitness of defectors (f_D), i.e., $\delta f(1) < 0$ [see Ref. (2)]. This ensures that selection favors the initial spread of cooperation.

(ii) *Replacement condition*. For $0 \leqslant \ell < N - 1$, the fixation probability of a single cooperator (ϕ_1^C) is higher than in the absence of selection pressure, i.e., $\phi_1^C > (N - \ell)^{-1}$ [2]. This

guarantees that selection favors the replacement of defection by cooperation.

When condition (i) is satisfied, but condition (ii) is not fulfilled, selection favors the invasion but not the replacement of D by C. If condition (ii) is satisfied, but condition (i) is not fulfilled, selection favors the replacement (not the invasion) of D by C: The fixation of C is favored even if the initial increase of C's frequency is opposed [1,4].

One of the questions investigated in Ref. [2] concerned the circumstances under which conditions (i) and (ii) are simultaneously satisfied. The author of the Comment [6] claims that, in "standard PD games" with facilitators, selection favors cooperation whenever condition (i) is satisfied. In this Reply, we show that condition (i) is generally *not sufficient* to ensure that selection favors cooperation in prisoner's dilemma games with cooperation facilitators. In fact, below, we show that, in generic PD games with ℓ cooperator facilitators, the replacement condition (ii) can be satisfied or can be violated independently of whether $\delta f(1) < 0$, and it can be more stringent than the invasion condition (i). To establish this result, we revisit some aspects of Ref. [2] by considering the general case of PD games with facilitators.

Here, we adopt the same notation as in Ref. [2] and again consider a *finite* and well-mixed population of total size N, comprising j cooperators (C's), k defectors (D's), and $\ell = N - j - k$ cooperation facilitators. In Refs. [2] and [6], cooperators and defectors compete according to a special (equal-gains-from-switching) payoff matrix in which the cost of mutual defection is 0 [3]. Here, to understand the interplay among selection and fluctuations in the presence of facilitators, we consider the generic case of PD games where the payoff for mutual defection is $d - c$ (with $c > 0$), according to the three-parameter PD payoff matrix [5],

$$
\begin{array}{cc}
 & \begin{array}{cc} \mathsf{C} & \quad \mathsf{D} \end{array} \\
\begin{array}{c} \mathsf{C} \\ \mathsf{D} \end{array} &
\left(\begin{array}{cc} b - c & -c \\ b & d - c \end{array} \right),
\end{array} \qquad (1)
$$

where b and c, respectively, are the benefit and cost of cooperation with $b > c > 0$ and $b > d > 0$ and $r \equiv c/b$ is referred to as the "cost-to-benefit ratio." When $c > d$, there is a negative payoff for mutual defection, whereas, the payoff for mutual defection is positive when $c < d$. The special case considered in Refs. [2,6] corresponds to $c = d$ (zero payoff for mutual defection). For our purpose, the expected payoffs of C's and D's here can be identified with the fitnesses of cooperators and defectors with $f_C(j) = [(b-c)(j + \ell - 1)/(N-1)] - ck/(N-1)$ and $f_D(j) = bj/(N-1) + [(d - c)(k-1)/(N-1)]$ [7]. The difference $\delta f(j)$ between D's and C's fitness, thus, reads

$$\delta f(j) = f_D(j) - f_C(j)$$
$$= (c - d)\frac{j}{N-1}$$
$$+ \frac{dN - (b - c + d)\ell + (b - c)}{N-1}, \quad (2)$$

where $\delta f(j)$ varies with j when $c \neq d$ [3], and we note that facilitators support C's by enhancing their reproductive potential relative to D's fitness (since $b - c + d > 0$).

The dynamics is modeled as a continuous-time birth-death process implemented according to the Fermi update rules [2,8]. The choice of the Fermi process (FP) is made here for the sake of concreteness and simplicity (most of the Comment [6] is concerned with the FP). The FP is known to lead to similar dynamics as other processes, such as the Moran model also considered in Ref. [2], but its analytical treatment is more amenable. As in Ref. [2], the rates associated with the transitions $j \rightarrow j \pm 1$ are $T_j^{\pm} = \frac{j(N - \ell - j)}{N(N-1)}[1 + e^{\pm \delta f(j)}]^{-1}$. The fixation probability of a single cooperator in a population consisting of $N - \ell - 1$ defectors is found to be [2,5]

$$\phi_1^C = \left[1 + \sum_{n=1}^{N - \ell - 1} e^{\sum_{j=1}^n \delta f(j)} \right]^{-1}. \quad (3)$$

Clearly, the fixation probability of a single cooperator in a sea of $\ell = N - 1$ facilitators is $\phi_1^C = 1$.

From (2), the invasion condition (i) $\delta f(1) < 0$ is satisfied when the density of cooperation facilitators $z \equiv \ell/N$ (their fraction in the population) is such that $z > \widetilde{z}$, where

$$\widetilde{z} = \frac{d}{b - c + d} + \left(\frac{b + c - 2d}{b - c + d} \right) \frac{1}{N}. \quad (4)$$

Using (3), the replacement condition (ii) $\phi_1^C > (N - \ell)^{-1}$ can be written as

$$N - \ell - 1 > \sum_{n=1}^{N - \ell - 1} \exp \left\{ n \left[\delta f(1) + \frac{(c - d)(n - 1)}{2(N - 1)} \right] \right\}, \quad (5)$$

with $\delta f(1) + \frac{(c-d)(n-1)}{2(N-1)} = d - b(\frac{\ell - 1}{N - 1}) + \frac{(c-d)(n + 2\ell + 1)}{2(N-1)}$. The condition (5) is satisfied when z exceeds a certain critical value $z^* = \ell^*/N$ (i.e., when $z > z^*$, see below).

Three cases need to be distinguished in order to analyze the implications of the conditions (4) and (5) on the dynamics of PD games with cooperation facilitators: (a) $c = d$, (b) $c > d$, and (c) $c < d$.

(a) *Case* $c = d$. This corresponds to the special case of equal-gains-from-switching PD games [3], considered in Refs. [2,6], where the payoff for mutual defection is exactly zero. Since $c = d$, the fitness difference $\delta f(j) = [dN - (b - c + d)\ell + (b - c)]/(N - 1)$ is constant, and (5) simply reads $N - \ell - 1 > \sum_{n=1}^{N - \ell - 1} e^{n \delta f(1)}$. As a consequence, when $z > \widetilde{z} = r + (1 - r)/N$, the invasion condition is satisfied, yielding $\delta f(1) < 0$, and (5) is also fulfilled. As noted in Ref. [6], this means that the condition (17) of Ref. [2] is too restrictive for equal-gains-from-switching PD games: In this special case, selection favors the invasion and replacement of defection by cooperation when $z > \widetilde{z} = z^* = r + (1 - r)/N$. On the other hand, when $z < \widetilde{z}$, neither the invasion nor the replacement conditions are satisfied, and defection is evolutionary stable.

(b) *Case* $c > d$. This corresponds to the case where the payoff of mutual defection $(d - c)$ is negative. In this case, the replacement condition (5) is more stringent than (4). In fact, the latter condition says that selection favors the invasion of D by C when $\delta f(1) < 0$, which yields $z > \widetilde{z} = d/(b - c + d) + [(b + c - 2d)/(b - c + d)]N^{-1}$. However, it can be shown that, in large populations [when $N(b - c)(c - d) \gg 1$], the replacement condition (5) is satisfied only if the fraction of cooperation facilitators in the population exceeds a critical value $z^* = \ell^*/N \geq \widetilde{z}$ [5]. This implies that

   i. Selection favors the invasion but not the replacement of defectors by cooperators when $\widetilde{z} < z \leqslant z^*$. Defection is, thus, no longer evolutionary stable as soon as $z > \widetilde{z}$.

   ii. Selection favors the invasion and replacement of defection by cooperation when $z > z^*$.

For PD games with cooperation facilitators and negative payoff for mutual defection, the replacement condition is more stringent than the invasion condition and dictates when selection favors cooperation. This is illustrated by the examples reported in the following table for various sets of parameters (b, r, d, N):

(b, r, d, N)	$\widetilde{z}$	z^*
$(1, 0.8, 0.2, 100)$	0.5350	0.6800
$(1, 0.8, 0.2, 1000)$	0.5035	0.6990
$(1, 0.1, 0.05, 100)$	0.0632	0.0700
$(1, 0.1, 0.05, 1000)$	0.0537	0.0740

As an example, for the PD game with payoff matrix (1) and $(b, r, d, N) = (1, 0.8, 0.2, 100)$ this shows that the replacement and invasion of defection by cooperation is favored when the population is composed of more than 68 facilitators. Furthermore, selection favors the invasion (not the replacement) when the number of facilitators is $54 \leqslant \ell \leqslant 68$. In such a situation, a single cooperator has a higher fitness than defectors but is more likely to become extinct than under neutral dynamics (when $\delta f = 0$ [2]).

(c) *Case* $c < d$. This corresponds to the case where the payoff of mutual defection is positive (but less than the payoff $b - c$ of mutual cooperation). When $c < d$, the invasion condition (4) is clearly more stringent than (5) since the exponent on the right-hand side of (5) is always negative when (4) is satisfied. One can, in fact, show that, in large populations, a single cooperator has a higher fixation probability than $(N - \ell)^{-1}$ as soon as the fraction of facilitators is higher than a

critical value $z^* \leqslant \widetilde{z} = d/(b-c+d) + [(b+c-2d)/(b-c+d)]N^{-1}$, whereas, C has a higher fitness than defectors when $z > \widetilde{z}$ [5]. This means that, in this case,

    i. Selection favors the replacement but not the invasion of defectors by cooperators when $z^* < z \leqslant \widetilde{z}$. Defection is, thus, no longer evolutionary stable as soon as $z > z^*$.

    ii. Selection favors the invasion and the replacement of defection by cooperation when $z > \widetilde{z}$.

For PD games with cooperation facilitators and positive payoff for mutual defection, the invasion condition is, therefore, more stringent than the replacement condition and dictates when selection favors cooperation. This is illustrated by the examples reported in the following table for various sets of parameters (b,r,d,N):

(b,r,d,N)	$\widetilde{z}$	z^*
$(1, 0.2, 0.8, 100)$	0.4975	0.4400
$(1, 0.2, 0.8, 1000)$	0.4998	0.4710
$(1, 0.05, 0.1, 100)$	0.1033	0.0800
$(1, 0.05, 0.1, 1000)$	0.0960	0.0860

As an example, for the PD game with payoff matrix (1) and $(b,r,d,N) = (1, 0.2, 0.8, 100)$, this shows that the replacement and invasion of defection by cooperation is favored when the population comprises at least 50 facilitators. Furthermore, selection favors the replacement (not the invasion) of defectors by cooperators as soon as there are at least 45 facilitators.

Hence, when the number of facilitators is $45 \leqslant \ell \leqslant 49$, a single cooperator is more likely to fixate than in the absence of selection, but its fitness is lower than the fitness of the defectors.

In conclusion, we have seen that the replacement and invasion conditions are generally two independent (necessary) requirements that need to be satisfied for selection to favor cooperation. When the payoff of mutual defection is negative $(c > d)$, the replacement condition (5) is more stringent than $\delta f(1) < 0$ and dictates that selection favors cooperation when the density of facilitators exceeds a critical value z^*. When there is a positive payoff for mutual defection, the invasion condition $\delta f(1) < 0$ imposes that selection favors the replacement and invasion by cooperation when $z > \widetilde{z}$. In this case $(c < d)$, the replacement (not the invasion) of defection is favored when $z^* < z \leqslant \widetilde{z}$. It is worth noting that, for generic prisoner's dilemma games $(c \neq d)$ with cooperation facilitators, the value z^* saturating (5) cannot be inferred from a simple rescaling of (1). In Ref. [5], it is shown that z^* depends only weakly on the population size and selection strength (when $N \gg 1$). *The relevance of the claims made in the Comment [6] is, therefore, limited to the special case $c = d$ of equal-gains-from-switching PD games (for which $\widetilde{z} = z^*$).*

A detailed analysis of the circumstances under which selection favors the spread of cooperation in three important classes of (symmetric) evolutionary games (prisoner's dilemma, snowdrift, and stag-hunt games) with cooperation facilitators can be found in Ref. [5].

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