Reply to “Comment on ‘Stochastic dynamics of the prisoners dilemma with cooperation facilitators’ ”

Mauro Mobilia

Department of Applied Mathematics, School of Mathematics, University of Leeds, Leeds LS2 9JT, U.K.

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 [M. Mobilia, Phys. Rev. E, 86, 011134 (2012)]. In a Comment, Miekisz 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 \( f_C \) and \( f_D \) are the respective fitnesses of cooperators/defectors). In this Reply, we show that in generic prisoner’s dilemma games with \( \ell \) 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 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 [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.

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

The prisoner’s dilemma (PD) game is the paradigmatic model of 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 [2].

In this context, the dynamics of the prisoner’s dilemma game in the presence of \( \ell \) “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 [1, 3] and note [16] of Ref. [2]). The ensuing evolutionary dynamics has been investigated in terms of birth-death processes and 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 [11-14]. In fact, in a well-mixed population of finite size \( N \) comprising \( \ell \) 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) \textit{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 2]. This ensures that selection favors the initial spread of cooperation.

(ii) \textit{Replacement condition:} For \( 0 \leq \ell < N - 1 \), the fixation probability of a single cooperator \((\phi^C_1)\) is higher than in the absence of selection pressure, i.e. \( \phi^C_1 > (N-\ell)^{-1} \) [2]. This guarantees that selection favors the replacement of defection by cooperation.

When the condition (i) is satisfied, but condition (ii) is not fulfilled, selection favors the invasion but not the replacement of D by C. If the 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, 3].

One of the questions investigated in Ref. [2] concerned the circumstances under which the 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 the 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 \( \ell \) cooperators, selection favors the replacement condition (ii) can be satisfied or 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 Refs. [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 un-
nderstand the interplay between 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 \([5]\),

\[
\begin{pmatrix}
C & D \\
C & b - c & -c \\
D & b & d - c
\end{pmatrix},
\]

where \(b\) and \(c\) are respectively 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 \([2, 6]\) corresponds to \(c = d\) (zero payoff for mutual defection). For our purpose, the expected payoffs of \(C\)'s and \(D\)'s can be identified with the fitnesses of cooperators and defectors, with \(f_C(j) = [(b-c)j + \ell]/(N-1) + c\ell/(N-1)\) and \(f_D(j) = bj/(N-1) + [(d-c)(j-1)/(N-1)]\) \([7]\). The difference \(\delta f(j)\) between \(C\)'s and \(D\)'s fitness thus reads

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

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 processes implemented according to the Fermi update rules \([2, 3]\). The choice of the Fermi process (FP) is here made 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 amendable.

Ref. \([2\), but its analytical treatment is more amendable. In fact, the latter condition says that selection favors the invasion of \(D\) by \(C\) when \(\delta f(1) < 0\), which yields \(z > \tilde{z} = d/(b-c+d) + (b+c-2d)/(b-c+d)N^{-1}\). 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 \(z^* = \ell' N \geq \tilde{z}\) \([5]\). This implies that

\begin{itemize}
  \item[i.] Selection favors the invasion, but not the replacement, of defectors by cooperators when \(z < z^*\). Defection is thus, no longer evolutionary stable as soon as \(z > \tilde{z}\).
  \item[ii.] Selection favors the invasion and replacement of defection by cooperation when \(z > z^*\).
\end{itemize}

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 \((b, r, d, N)\):

<table>
<thead>
<tr>
<th>((b, r, d, N))</th>
<th>(\tilde{z})</th>
<th>(z^*)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1, 0.8, 0.2, 100)</td>
<td>0.5350</td>
<td>0.6800</td>
</tr>
<tr>
<td>(1, 0.8, 0.2, 1000)</td>
<td>0.5035</td>
<td>0.6990</td>
</tr>
<tr>
<td>(1, 0.1, 0.05, 100)</td>
<td>0.0632</td>
<td>0.0700</td>
</tr>
<tr>
<td>(1, 0.1, 0.05, 1000)</td>
<td>0.0537</td>
<td>0.0740</td>
</tr>
</tbody>
</table>

As an example, for the PD game with payoff matrix \([4]\) and \((b, r, d, N) = (1, 0.8, 0.2, 100)\) this shows that the re-
placement 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 $54 \leq \ell \leq 68$. In such a situation, a single cooperater 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 [1] is clearly more stringent than [5] since the exponent on the right-hand-side of [5] is always negative when [1] is satisfied. One can in fact show that in large populations a single cooperater has a higher fixation probability than $(N - \ell)^{-1}$ as soon as the fraction of facilitators is higher than a critical value $z^* \leq \tilde{z} = d/(b-c+d) + [(b+c-2d)/(b-c+d)]N^{-1}$, whereas C has higher fitness than defectors when $z > \tilde{z}$ [5]. This means that, in this case,

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

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

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 $(b, r, d, N)$:

<table>
<thead>
<tr>
<th>$(b, r, d, N)$</th>
<th>$\tilde{z}$</th>
<th>$z^*$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$(1,0.2,0.8,100)$</td>
<td>0.4975</td>
<td>0.4400</td>
</tr>
<tr>
<td>$(1,0.2,0.8,1000)$</td>
<td>0.4998</td>
<td>0.4710</td>
</tr>
<tr>
<td>$(1,0.05,0.1,100)$</td>
<td>0.1033</td>
<td>0.0800</td>
</tr>
<tr>
<td>$(1,0.05,0.1,1000)$</td>
<td>0.0960</td>
<td>0.0860</td>
</tr>
</tbody>
</table>

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 $45 \leq \ell \leq 49$, a single cooperater is more likely to fixate than in the absence of selection, but its fitness is lower than the fitness of 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 $z > \tilde{z}$. In this case ($c < d$) the replacement (not the invasion) of defection is favored when $z^* < z \leq \tilde{z}$. 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 $\tilde{z} = z^*$).*

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].


[3] The payoff matrix [1] with $c = d$ corresponds to “equal-gains-from-switching” PD games and is often used since it is a convenient way to capture many features of the classic PD games. However, this subclass of PD games have special fixation properties since $\delta_f = fc - fb$ [2] is constant, see e.g. A. Traulsen and C. Hauert in Ref. [1].


[7] The fitness $f_{C/D}$ is often defined to be proportional to the expected payoff $\pi_{C/D}$ (see Eq. (2) of Ref. [2]), e.g. with $f_{C/D} = 1 + s\pi_{C/D}$, where $s$ is the selection intensity and $1$ is a baseline contribution. As in Ref. [2], we here set $s = 1$ and, since the rates $T^+$ for the FP depend on $f_8$, $\pi_{C/D}$ can now be identified with $f_{C/D}$. The influence of the selection strength is discussed in Ref. [5].