Journal of Theoretical Biology 360 (2014) 163–171

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Punishment does not promote cooperation under exploration dynamics when anti-social punishment is possible

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HIGHLIGHTS

- Punishment has been proposed as a driver of the evolution of cooperation.
- Recent experiments have shown, however, that defectors sometimes punish cooperators.
- Models suggest that cooperation fails if defectors are also allowed to punish.
- We explore the effect of allowing anti-social punishment when mutation is common.
- We find that punishment does not promote cooperation.

ARTICLE INFO

Article history:
Received 26 July 2013
Received in revised form
29 April 2014
Accepted 30 June 2014
Available online 8 July 2014

Keywords:
Cooperation
Anti-social punishment
Mutation rates
Evolutionary dynamics

ABSTRACT

It has been argued that punishment promotes the evolution of cooperation when mutation rates are high (i.e. when agents engage in ‘exploration dynamics’). Mutations maintain a steady supply of agents that punish free-riders, and thus free-riders are at a disadvantage. Recent experiments, however, have demonstrated that free-riders sometimes also pay to punish cooperators. Inspired by these empirical results, theoretical work has explored evolutionary dynamics where mutants are rare, and found that punishment does not promote the evolution of cooperation when this ‘anti-social punishment’ is allowed. Here we extend previous theory by studying the effect of anti-social punishment on the evolution of cooperation across higher mutation rates, and by studying voluntary as well as compulsory Public Goods Games. We find that for intermediate and high mutation rates, adding punishment does *not* promote cooperation in either compulsory or voluntary public goods games if anti-social punishment is possible. This is because mutations generate agents that punish cooperators just as frequently as agents that punish defectors, and these two effects cancel each other out. These results raise questions about the effectiveness of punishment for promoting cooperation when mutations are common, and highlight how decisions about which strategies to include in the strategy set can have profound effects on the resulting dynamics.

1. Introduction

The evolution of cooperation is a central topic of interest across the natural and social sciences (Antal et al., 2009; Apicella et al., 2012; Axelrod, 1984; Capraro, 2013; Chudek and Henrich, 2011; Dal Bó, 2005; Dal Bó and Fréchette, 2011; Fudenberg and Maskin, 1990; Hauert and Doebeli, 2004; Hauert et al., 2002a; Helbing and Yu, 2009; Herrmann et al., 2008; Jacquet et al., 2011; Janssen et al., 2010; Levin, 2006; Milinski et al., 2002; Nowak and Sigmund, 1992, 1993, 1998; Nowak and May, 1992; Ostrom, 1990; Perc and Szolnoki, 2010; Peysakhovich and Rand, 2013; Rand et al., 2009b, 2012, 2013; Rapoport and Chammah, 1965; Rockenbach and Milinski, 2006; Seinen and Schram, 2006; Sigmund, 2010; Skyrms,

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http://dx.doi.org/10.1016/j.jtbi.2014.06.041

1996; Skyrms and Pemantle, 2000; Tarnita et al., 2009; Traulsen and Nowak, 2006; van Veelen et al., 2012; Wedekind and Milinski, 2000; Yoeli et al., 2013). Five mechanisms for the evolution of cooperation have been proposed: direct and indirect reciprocity, spatial selection, kin selection, and multi-level selection (Nowak, 2006; Rand and Nowak, 2013). Adding any of these interaction structures to a prisoner's dilemma can result in cooperation being favoured over defection, as can relaxing the social dilemma by making participation optional (Hauert et al., 2002a). In recent years, the idea that individuals pay a personal cost to impose costs on others has gained increasing attention. Behavioural experiments have shown that individuals are willing to pay to punish others, and that this costly punishment often (although not always) results in an increase in cooperation (Almenberg et al., 2011; Dreber et al., 2008; Espín et al., 2012; Fehr and Gächter, 2000, 2002; Fehr and Fischbacher, 2004; Gächter et al., 2008; Gurerk et al., 2006; Herrmann et al., 2008; Janssen et al., 2010; Ostrom et al., 1992; Rand et al., 2009b; Rockenbach and Milinski, 2006; Sefton et al., 2007; Sutter et al., 2010; Ule et al., 2009; Yamagishi, 1986). Complimenting this empirical work is a body of literature using evolutionary game theory to explore the co-evolution of punishment and cooperation (Boyd and Richerson, 1992; Boyd et al., 2003; Fowler, 2005; Hauert et al., 2007; Helbing et al., 2010; Isakov and Rand, 2011; Nakamaru and Iwasa, 2005, 2006; Ohtsuki et al., 2009; Rand et al., 2009a; Sigmund et al., 2001, 2010; Traulsen et al., 2009). These papers typically examine evolutionary outcomes when the ability to pay to punish defectors is added to one of the mechanisms for the evolution of cooperation: costly punishment is not itself a mechanism for the evolution of cooperation, but must be combined with reciprocity, spatial structure, group selection or voluntary participation.

The existence of a darker form of punishment, however, has begun to challenge the positive role of punishment suggested by much of this work. Numerous experimental studies have shown that some people also engage in 'anti-social punishment' directed at cooperators (Cinyabuguma et al., 2006; Ellingsen et al., 2012; Gächter and Herrmann, 2009, 2011; Gächter et al., 2010; Herrmann et al., 2008; Nikiforakis, 2008; Peysakhovich et al., 2014; Rand and Nowak, 2011; Sylwester et al., 2013). Because this anti-social punishment was seen as unlikely, it was excluded *a priori* from most previous theoretical models. Given the empirical evidence of anti-social punishment, however, it is important to re-evaluate previous models of the co-evolution of cooperation and punishment (Dreber and Rand, 2012).

Recent work in this vein has explored the consequences of including antisocial punishment in various evolutionary scenarios. In the context of prisoner's dilemmas played in lattice-structured populations, adding antisocial punishment prevents cooperative mutants from invading populations of defectors under viability updating (Rand et al., 2010). In the context of stochastic evolutionary dynamics in the limit of low mutation, selection no longer favours cooperation in voluntary (optional) public goods games in the limit of low mutation when antisocial punishment is possible (Rand and Nowak, 2011), unless only defectors, and not loners, can punish cooperators (García and Traulsen, 2012). In the context of group-structured populations, the effectiveness of punishment for promoting cooperation is substantially reduced when antisocial punishment strategies are included (Powers et al., 2012), or when defectors can retaliate when punished (Janssen and Bushman, 2008). Finally, in the context of coordinated punishment, cooperators that punish defectors cannot invade a population of defectors who punish those signalling their intention to punish (McCabe and Rand, in press).

Here we extend this line of work by examining the evolutionary consequences of antisocial punishment in a setting not previously considered: 'exploration dynamics' where the evolutionary process includes a relatively high rate of mutation. A recent model which excludes antisocial punishment has suggested that cooperation can evolve via punishment when mutation rates are high (Traulsen et al., 2009). Frequent mutations serve to maintain all possible strategies at a high frequency in the population, regardless of fitness. In a model where the only possible punishment is targeted at defectors, therefore, mutations maintain a steady supply of punishers. As a result defectors fare poorly and are disfavoured.

We now ask what happens in a model where punishment is not restricted to defectors only. When all forms of punishment are available, high mutation rates lead to a constant supply of individuals of all strategies, including those that punish cooperators. Thus cooperators are punished to the same extent as defectors, and punishment no longer promotes cooperation. We study compulsory and voluntary public goods games. We also follow (García and Traulsen, 2012) and examine voluntary games were loners are exempt from punishment. In all cases, when mutations are sufficiently common, punishment does not promote the evolution of cooperation if anti-social punishment is not excluded.

The rest of the paper is structured as follows. In Section 2, we describe the model and the payoff structure of the compulsory and voluntary public goods games. In Section 3, we describe the dynamics of the evolutionary process and the role of mutation rates. In Section 4, we provide results for the compulsory game. In Section 5, we provide results for the voluntary game. In Section 6, we show results for the effect of varying the intensity of selection in both games. In Section 7, we discuss our findings and conclude.

2. The model

Let N denote the number of individuals in a population playing the public goods game (PGG). The PGG is the multi-player version of the prisoner's dilemma (Hardin, 1968). Each player in a group of n players must decide whether or not to contribute a fixed amount c to the 'common good'. Contributions are multiplied by a factor $r > 1$, and evenly split by all group members, regardless of whether or not they contributed. Thus if x players choose to cooperate, each player receives rcx/n back from the common good. We refer to this game as the compulsory PGG because all players must participate in the PGG.

We also consider a voluntary PGG where participation in the game is not compulsory (Hauert et al., 2002a, 2002b, 2007). Players who choose to abstain from the game receive a constant loner's payoff σ, that is less than the $(r-1)c$ payoff earned by each member of a group where everyone cooperates, but greater than the 0 payoff earned by each member of a group where everyone defects. If all but one player in a group are loners, the game cannot take place and everyone in the group receives the loner's payoff σ.

In both versions of the game, groups of size n are drawn from the population at random in each round to play a PGG. In the compulsory game, individuals choose between C (cooperate) or D (defect). In the voluntary game, a third option – L (loner) – is available. Following the PGG decision, each player is given the option to punish the others in the group: a player's punishment costs her a fee γ for every player she chooses to punish; a punished player incurs a cost β for every punishment she receives ($\beta > \gamma$). Players can condition their punishment decisions on the PGG choice of each potential recipient of punishment.

We describe a strategy as *W-XYZ* (as in (Rand and Nowak, 2011)), where $W \in \{C, D, L\}$ denotes the PGG decision, $X \in \{N = \text{"No"}, P = \text{"Punish"}\}$ denotes whether punishment is directed at cooperators, $Y \in \{N, P\}$ whether it is directed at defectors, and $Z \in \{N, P\}$ whether it is directed at loners. For example, C-NNP is a cooperator strategy that does not punish cooperators and defectors but punishes loners, whereas D-PPP is a defector strategy that punishes all strategies (including others with the same strategy as itself). We now discuss the payoff that each strategy earns when playing against each other strategy for the compulsory and voluntary PGGs. Details of the payoff calculations can be found in Appendix A, and in the Supplementary information of (Rand and Nowak, 2011).

In the compulsory PGG, abstinence from the game (i.e., the loner strategy) is not an option. Thus there are, at most, 8 possible strategies: $W=[C,D]\cdot X=[P,N]\cdot Y=[P,N]$ (to facilitate easier cross-comparison with the voluntary public goods game, we write $Z=[N]$ for all strategies in the compulsory game as loners are non-existent and therefore not punishable).

For the compulsory game, we study three conditions. In the 'No punishment' condition, punishment is not an option for either cooperators or defectors: the only possible strategies are C-NNN and D-NNN. In the 'Pro-social punishment' condition, only punishment of defectors by cooperators is allowed: the possible strategies are C-NNN, C-NPN, and D-NNN. This condition is equivalent to the compulsory game with punishment in (Traulsen et al., 2009). Finally, in the 'Full punishment' condition, all 8 strategies are available; see details in Appendix A.

In the voluntary PGG, the option to abstain from the public goods game is made available. Loners who abstain from the public goods game receive a constant payoff σ that is independent from the contributions to the common good. There are 24 possible *W-XYZ* strategies: $[C,D,L]\cdot[P,N]\cdot[P,N]\cdot[P,N]$.

For the voluntary game, we study four conditions. In the 'No punishment' condition, punishment is not an option for cooperators, defectors or loners: the possible strategies are C-NNN, D-NNN and L-NNN. In the 'Pro-social punishment' condition, only punishment of defectors by cooperators is allowed: the possible strategies are C-NNN, C-NPN, D-NNN and L-NNN. This condition is equivalent to the voluntary game with punishment in (Traulsen et al., 2009). In the 'Full punishment' condition, all 24 strategies are available. Finally, in the 'Loners alone' condition, loners are not allowed to punish or to be punished. Thus the following 9 strategies are possible: 4 cooperator strategies (C-NNN, C-NPN, C-PNN, C-PPN), 4 defector strategies (D-NNN, D-NPN, D-PNN, D-PPN) and 1 loner strategy (L-NNN). This condition is inspired by García and Traulsen (2012), who propose that cooperation can be sustained if punishment is made available only to players that participate in the PGG. For detailed calculations of the payoffs, see Appendix A.

3. Evolutionary dynamics

We study the transmission of strategies through an evolutionary process. This process may be genetic evolution or social learning. In either case, we assume that strategies with higher payoffs are more likely to survive and reproduce, while strategies with lower payoffs are less likely to do so. Mutations during reproduction lead to the introduction of novel strategies (selected uniformly at random). In the context of social learning, mutations may represent either confusion regarding the strategy of a player you are trying to copy, or experimentation with new strategies.

In many contexts, humans generally avoid using dominated strategies (Camerer, 2003), suggesting that rates of mutation (i.e. random experimentation including with dominated strategies) are not so high. Recent work examining play in economic cooperation games, however, has suggested that intuitions and heuristics (in contrast to rational deliberation) are important for determining cooperative behavior (Rand et al., 2012; Rand et al., 2014). Furthermore, experiments have suggested that a substantial portion of play is non-strategic and random, and has argued that learning in this setting is thus characterized by high mutation rates (Traulsen et al., 2010). Correspondingly, the term 'exploration dynamics' has been introduced to describe dynamics under high mutation rates (Traulsen et al., 2009), which we focus on in the present paper.

We study the evolutionary process as a frequency-dependent Moran process (Nowak et al., 2004) with exponential fitness (Traulsen et al., 2008). In each round, one individual i is picked for reproduction proportional to his/her fitness e^{π_i} (where π_i is the payoff of individual i), while another individual j is chosen with uniform distribution to die, changing his/her strategy. With probability u, a mutation occurs and individual j picks a novel strategy. With probability $1-u$, individual j adopts the strategy of individual i.

We study the evolutionary outcomes over a range of mutation rates using agent-based simulations. We also study the $u\rightarrow 1$ 'high mutation rate' limit analytically (Antal et al., 2009). Here, selection contributes only slightly to the evolutionary dynamics, which are largely dominated by mutation. As a result, all possible strategies are on average almost equally abundant at the same time (unlike the low mutation, weak selection limit where strategies are equally abundant on average but there are never more than two strategies present at the same time). Thus, if there are M strategies, the frequency of strategy s is a perturbation from $1/M$ which is a linear function of the payoff obtained when all strategies are equally abundant (Antal et al., 2009). Specifically, the relative perturbation Δ_s from $1/M$ is given by $\pi_s^* - \left(\sum_j x_j^*/M\right)$, where π_x^* is the expected payoff of strategy x in a population where all strategies have abundance $1/M$. Therefore the strategy that is most common at $u\rightarrow 1$ is the strategy with the highest payoff when $u=1$ (i.e. when all strategies have frequency $1/M$). Note that this result holds regardless of selection strength.

4. Compulsory PGG results

We begin with analytical calculations in the high mutation limit. We ask under what conditions cooperation can be favoured by natural selection. Selection favours cooperation in the high mutation limit if the expected payoff averaged over all cooperative strategies minus the expected payoff averaged over all possible strategies, Δ_C is positive (i.e., if cooperators out-earn non-cooperators on average). Although this is an extreme (and physically unrealistic) limit, it is analytically tractable, and we will subsequently explore how the conclusions generated in the high mutation limit generalize to lower mutation rates using agent based simulations.

Using the no punishment strategy set, we find

$$\Delta_C = -\frac{Fc}{2}.$$

Thus regardless of the payoff parameters, selection disfavours cooperation. Using the pro-social punishment strategy set, however

$$\Delta_C = \frac{D(N,n)N(2\beta-\gamma)}{18} - \frac{Fc}{3}.$$

If punishment is sufficiently effective,

$$\beta > \frac{6F_C + D(N,n)N\gamma}{2D(N,n)N},$$

cooperation can be favoured. Using the full punishment strategy set, however, the result is identical to the no punishment case

$$\Delta_C = -\frac{Fc}{2}$$

Once again cooperation is disfavoured regardless of payoffs, and thus punishment does not promote cooperation.

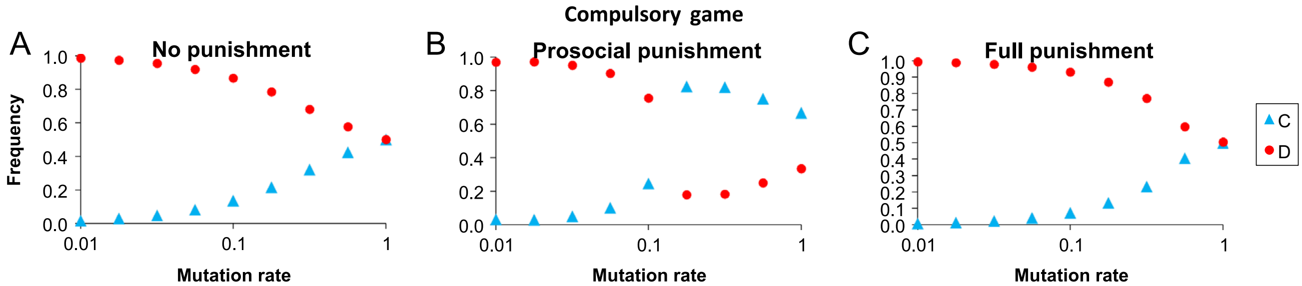

Fig. 1. In the compulsory public goods game, defection dominates when antisocial punishment is allowed. Shown is the frequency of strategies that cooperate (red) and defect (blue) from agent based simulations averaged over 10^7 generations using the no punishment strategy set (a), the prosocial punishment strategy set (b) and the full punishment strategy set (c). Parameters: $N=100$, $n=5$, $r=3$, $\gamma=0.3$, $\omega=\beta=c=1$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

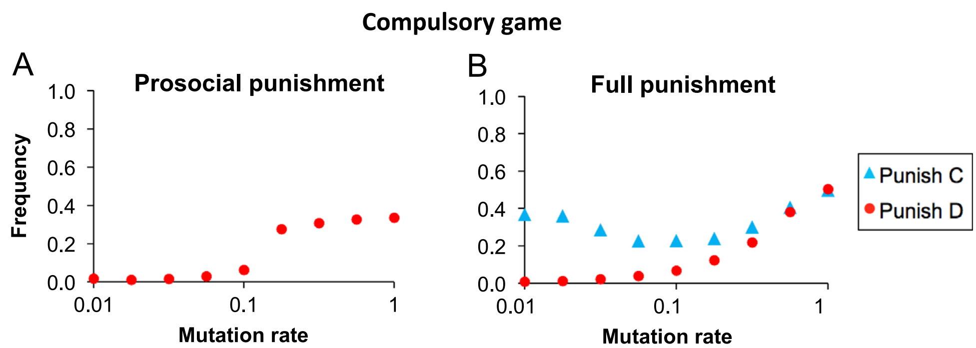

Fig. 2. Punishment is disfavoured by selection in the compulsory public goods game. Shown is the frequency of strategies that punish cooperators (red) and punish defectors (blue) from agent based simulations averaged over 10^7 generations using the prosocial punishment strategy set (a) and the full punishment strategy set (b). Parameters: $N=100$, $n=5$, $r=3$, $\gamma=0.3$, $\omega=\beta=c=1$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

We next explore dynamics outside of the high mutation limit using agent based simulations. We fix $N=100$, $n=5$, $r=3$, $\gamma=0.3$, and $\omega=\beta=c=1$. For each strategy set, we simulate 10^7 generations, and calculate the time-averaged frequency of each strategy over the second half of the simulation (Fig. 1). The simulations show qualitative agreement with the analytical results in the high mutation limit over a wide range of mutation rates: punishment does not promote cooperation when the full punishment strategy set is used. We also note that selection disfavours punishment of any kind (Fig. 2): the aggregate frequency of strategies that punish defectors never rises above neutrally (0.5 in this case) using either the prosocial punishment or full punishment strategy sets, nor does the aggregate frequency of strategies that punish cooperation in the full punishment case.

5. Voluntary PGG results

We again begin with analytical calculations in the high mutation limit, and compare Δ_C across our four voluntary public goods game conditions. Using the no punishment strategy set, we find

$$\Delta_C=\frac{B'(X)}{3}-\frac{\sigma}{3}-\frac{2Fc}{3}.$$

Thus even in the absence of punishment, cooperation can be favoured if the returns on cooperation are sufficiently high:

$$B'(X)>\sigma+2F_C.$$

Using the pro-social punishment strategy set,

$$\Delta_C=\frac{B(X)}{4}-\frac{\sigma}{4}-\frac{Fc}{2}+\frac{D(N,n)N(\beta-\gamma)}{16}.$$

Thus, if the effect of punishment is greater than the cost, $\beta>\gamma$, cooperation is favoured over a larger range of $B'(X)$ values than in the no punishment case: here punishment promotes cooperation (as in (Traulsen et al., 2009)). Using the full punishment strategy set, however, we again obtain a result identical to the no punishment case:

$$\Delta_C=\frac{B'(X)}{3}-\frac{\sigma}{3}-\frac{2Fc}{3},$$

Thus punishment does not promote cooperation when all strategies are possible, as in the compulsory game. Finally, we consider the "loners alone" strategy set, where we find

$$\Delta_C=\frac{B'(X)}{9}-\frac{\sigma}{9}-\frac{5Fc}{9}-\frac{4D(N,n)N(\beta+\gamma)}{81}.$$

As can be seen, punishment inhibits cooperation in this strategy set: Δ_C is decreasing in both β and γ.

Turning to agent based simulations, we use the same parameters as for the compulsory PGG with the additional parameter of $\sigma=1$ (loner's payoff), and simulate over 10^7 generations. We calculate the time-averaged frequencies of all strategies in the second half of the simulation (Fig. 3). The results are similar to those of the compulsory game. Regardless of mutation rate, cooperation is never favoured by selection in the full punishment strategy set where anti-social punishment strategies are included. Similarly, cooperation is disfavoured in the "Loners Alone" strategy set as long as mutation rates are sufficiently large. We also find that punishment of all kinds is disfavoured when mutation rates are sufficiently large (Fig. 4).

6. Intensity of selection

Previous studies have shown that the intensity of selection can play an important role in determining evolutionary outcomes

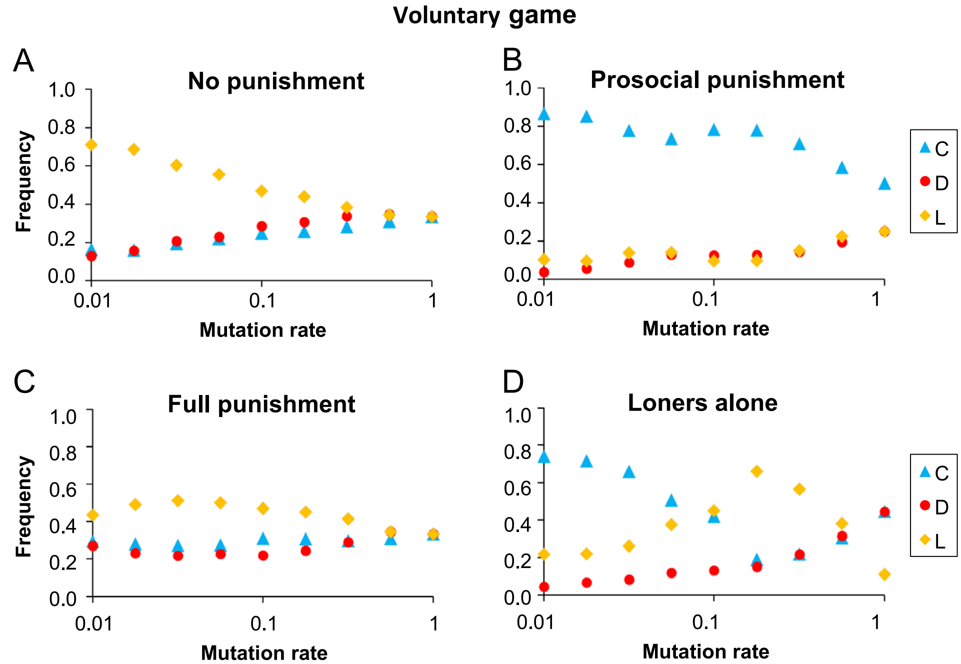

Fig. 3. In the voluntary public goods game with antisocial punishment, cooperation is disfavoured when mutations are common. Shown is the frequency of strategies that cooperate (red), defect (blue) and choose to be loners (yellow) from agent based simulations averaged over 10^7 generations using the no punishment strategy set (a), the prosocial punishment strategy set (b), the full punishment strategy set (c) and the loners alone strategy set (d). Parameters: $N=100$, $n=5$, $r=3$, $\gamma=0.3$, $\omega=\beta=\sigma=c=1$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

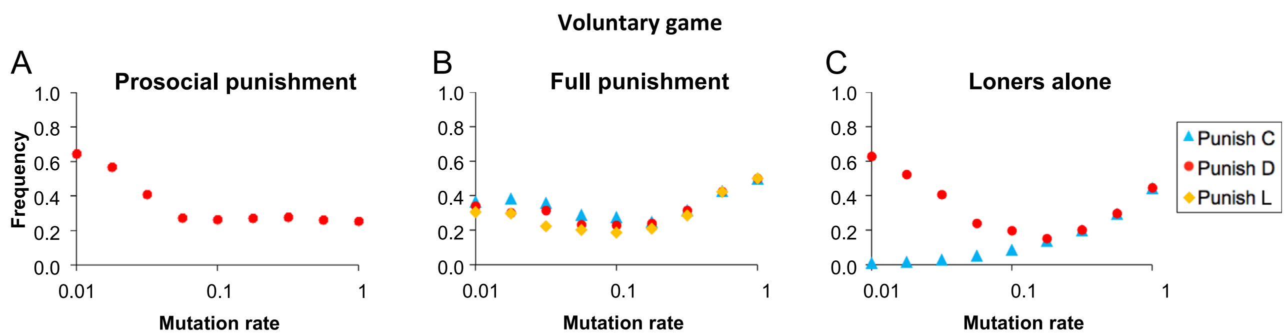

Fig. 4. Punishment is disfavoured by selection in the voluntary public goods game when mutation rates are large. Shown is the frequency of strategies that punish cooperators (red), punish defectors (blue), and punish loners (yellow) from agent based simulations averaged over 10^7 generations using the prosocial punishment strategy set (a), the full punishment strategy set (b), and the loners alone strategy set (c). Parameters: $N=100$, $n=5$, $r=3$, $\gamma=0.3$, $\omega=\beta=c=1$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Manapat et al., 2012; Rand and Nowak, 2012; Wu et al., 2013). In our previous simulations, we held the intensity of selection constant at $w=1$ and varied the mutation rate. Here we demonstrate that our central result, the fact that punishment does not promote cooperation when mutations are common and antisocial punishment is possible, is robust to varying the intensity of selection.

To do so, we fix a fairly high mutation rate of $\mu=10^{-0.5}$ and vary the intensity of selection $w \in [0.1,\ 10]$. For each value of w, we carry out agent based simulations using each of the strategy sets discussed above.

We begin by considering the compulsory PGG (Fig. 5). We find qualitatively equivalent results across intensities of selection: cooperation is favoured only in the prosocial punishment case. The results for the voluntary game are similar (Fig. 6). Again, it is only in the prosocial punishment strategy set that cooperation is ever favoured. In the loners alone strategy set (Fig. 6d), loners become less common when selection is weak, but still defectors are always more common than cooperators. Thus we conclude that our results from Sections 4 and 5 were not unique to the particular intensity of selection used, *w*=*1*.

7. Discussion

We have shown that when cooperators can be the targets of punishment, adding punishment does not promote the evolution of cooperation under exploration dynamics. When all forms of punishment are available, anti-social punishment towards cooperators is as common as traditional punishment of defectors in the high mutation limit. Thus anti-social punishment cancels out the positive effects that pro-social punishment may otherwise provide.

These results emphasize the importance of which strategies are (or are not) included in the strategy set. The choice of strategies is always important. But when agents are selecting strategies at random a substantial fraction of the time (as is the case when mutation rates are not so small), then one's choice of which strategies to include has an especially profound effect on the evolutionary outcomes: even strategies which perform extremely poorly will sometimes be played, and thus can have a substantial impact on the evolutionary outcomes. Thus it is critical to not inadvertently alter one's results by selectively omitting certain strategies (for example, strategies that are possible but seem unlikely based on our observations of the world around us).

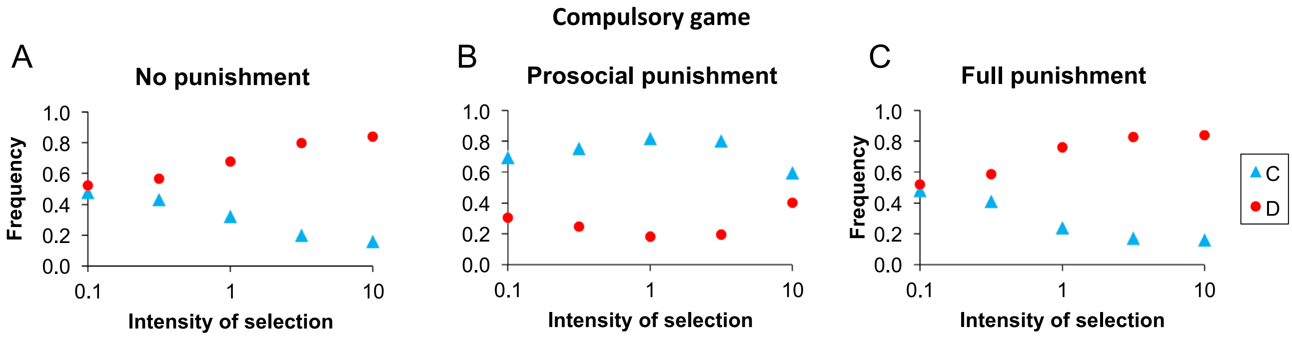

Fig. 5. In the compulsory public games, our results are robust across a wide range of selection strengths, in that cooperation is only favoured when punishment cannot be targeted at cooperators. Shown is the frequency of strategies that punish cooperators (red), punish defectors (blue), and punish loners (yellow) from agent based simulations averaged over 10^7 generations. We show that our results are qualitatively the same for a wide range of selection strengths for the no punishment strategy set (a), the prosocial punishment strategy set (b), and the full punishment strategy set (c). Parameters: $N=100$, $n=5$, $r=3$, $\gamma=0.3$, $\beta=c=1$, $\mu=10^{-0.5}$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

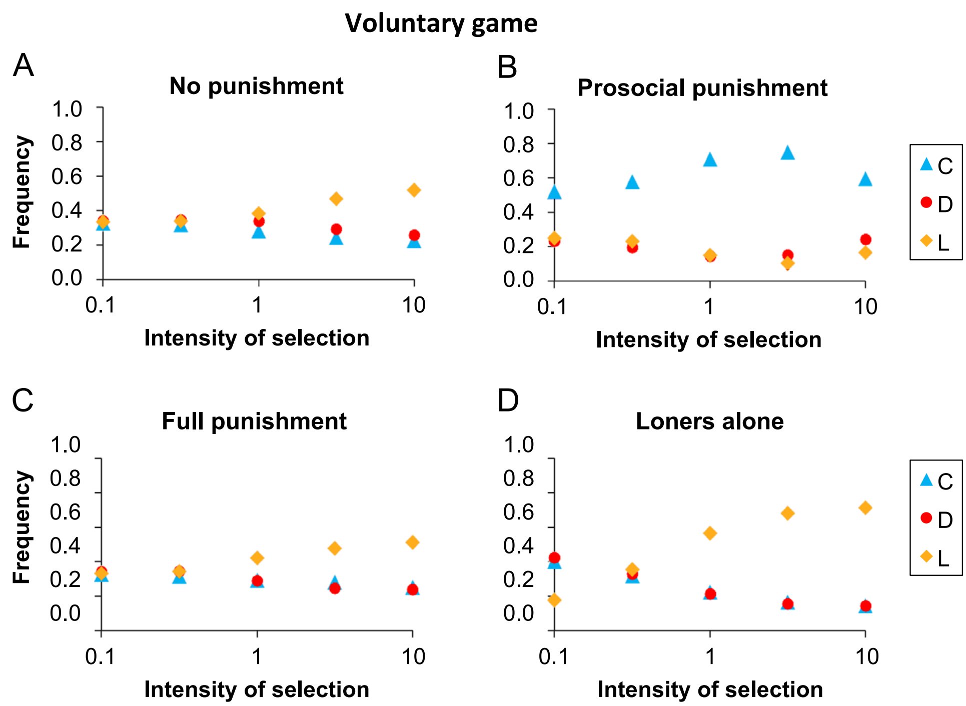

Fig. 6. For the voluntary public goods games, varying the selection strength does not alter our main result that cooperation is only favoured when punishment cannot be targeted at cooperators. Shown are the results using the no punishment strategy set (a), the prosocial punishment strategy set (b), the full punishment strategy set (c) and the loners alone strategy set (d), where the frequency of strategies that punish cooperators (red), punish defectors (blue), and punish loners (yellow) are averaged over 10^7 generations. Parameters: $N=100$, $n=5$, $r=3$, $\gamma=0.3$, $\beta=c=1$, $\mu=10^{-0.5}$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Our findings are consistent with previous work on anti-social punishment in the low mutation limit using the same payoff structures we studied here (Rand and Nowak, 2011). The extension to higher mutation rates is of substantial interest because it has been suggested that such mutation rates are a form of 'exploration' and innovation that play an important role in human learning (Traulsen et al., 2009; Traulsen et al., 2010). Under these circumstances of high mutation, evolutionary dynamics may favour qualitatively different strategies compared to when mutation is rare (Antal et al., 2009). We see this in our results when considering the voluntary public goods game in which loners are not allowed to punish or be punished. This concept of 'leaving the loners alone' is an effective mechanism for promoting cooperation in the low mutation limit (García and Traulsen, 2012). We show here, however, that when mutations are sufficiently common, punishment does not promote cooperation even when loners are left alone. On the contrary, punishment actually inhibits cooperation (by giving the non-punished loners an advantage over both cooperators and defectors). Determining how the mutation threshold at which cooperators are no longer favoured varies with the game parameters is an important direction for future work.

In sum, we have shown that punishment does not promote cooperation when mutations are common unless cooperators are protected from punishment. These results add to a growing body of literature using evolutionary game theory that calls into question the positive role of peer punishment in the evolution of cooperation (Dreber and Rand, 2012; Janssen and Bushman, 2008; Powers et al., 2012; Rand and Nowak, 2011; Rand et al., 2009a, 2010).

Acknowledgements

We thank Julián García and Arne Traulsen for helpful comments and suggestions. O.P.H. is grateful to the department of

Organismic and Evolutionary Biology at Harvard for fellowship support. Funding from the John Templeton Foundation is gratefully acknowledged.

Appendix A

Calculation of voluntary public goods game payoffs

The payoff of strategy s in the PGG δ_1 is determined as follows. If $i_C+i_D<1$, then there are not enough non-loners for the public goods game to occur, and so $\delta_1=\sigma$ regardless of the strategy of player s. Otherwise,

$$\delta_1 = rc\frac{i_C}{i_C+i_D} - cs_C$$

The payoff of strategy s from being punished is given by the following equation:

$$\delta_2 = -\beta(sc(i_{pC}-s_{pC}) + s_{D(i_{pD}-s_{pD})} + s_L(i_{pL}-s_{pL})).$$

The payoff of strategy s from paying to punish others δ_3 is given by the following equation:

$$\delta_3 = -\gamma(s_{pC}(i_C-s_C) + s_{pD}(i_D-s_D) + s_{pL}(i_L-s_L)).$$

The total payoff of strategy s is then given by the following equation:

$$P_s = \delta_1+\delta_2+\delta_3$$

Thus far we have calculated the payoff of a particular strategy playing the PGG with punishment in a group with a particular set of $n-1$ other players. To calculate the expected (average) payoff of a strategy s in a population of size N, we must now consider the average group composition. Let X_i be the total number of players in the population of size N using strategy i, $i\in[1,\ 24]$. A randomly sampled group of size n has a specific composition given by the multivariate hypergeometric distribution

$$H(\boldsymbol{I},\boldsymbol{X}) = \frac{\binom{X_1}{i_1}\binom{X_2}{i_2}\cdots\binom{X_{24}}{i_{24}}}{\binom{N}{n}}$$

where $\boldsymbol{I}=(i_1,i_2,\ldots,i_{24})$ and $\boldsymbol{X}=(X_1,X_2,\ldots,X_{24})$. The average payoff π_s for strategy s is then $\sum_{i_1}\sum_{i_2}\ldots\sum_{i_{24}}\boldsymbol{H}(\ldots)P_s$.

Substituting for each of the 24 strategies and simplifying gives

$$\pi_{C-NNN} = B'(\boldsymbol{X}) - F'(X_L)c - X_{pC}\beta D(N,n)$$
$$\pi_{C-NNP} = B'(\boldsymbol{X}) - F'(X_L)c - (X_{pC}\beta + X_L\gamma)D(N,n)$$
$$\pi_{C-NPN} = B'(\boldsymbol{X}) - F'(X_L)c - (X_{pC}\beta + X_D\gamma)D(N,n)$$
$$\pi_{C-NPP} = B'(\boldsymbol{X}) - F'(X_L)c - (X_{pC}\beta + (X_D+X_L)\gamma)D(N,n)$$
$$\pi_{C-PNN} = B'(\boldsymbol{X}) - F'(X_L)c - ((X_C-1)\gamma + (X_{pC}-1)\beta)D(N,n)$$
$$\pi_{C-PNP} = B'(\boldsymbol{X}) - F'(X_L)c - ((X_C+X_L-1)\gamma + (X_{pC}-1)\beta)D(N,n)$$
$$\pi_{C-PPN} = B'(\boldsymbol{X}) - F'(X_L)c - ((X_C+X_D-1)\gamma + (X_{pC}-1)\beta)D(N,n)$$
$$\pi_{C-PPP} = B'(\boldsymbol{X}) - F'(X_L)c - ((X_C+X_D+X_L-1)\gamma + (X_{pC}-1)\beta)D(N,n)$$
$$\pi_{D-NNN} = B'(\boldsymbol{X}) - X_{pD}\beta D(N,n)$$
$$\pi_{D-NNP} = B'(\boldsymbol{X}) - (X_L\gamma + X_{pD}\beta)D(N,n)$$
$$\pi_{D-NPN} = B'(\boldsymbol{X}) - ((X_D-1)\gamma + (X_{pD}-1)\beta)D(N,n)$$
$$\pi_{D-NPP} = B'(\boldsymbol{X}) - ((X_D+X_L-1)\gamma + (X_{pD}-1)\beta)()D(N,n)$$
$$\pi_{D-PNN} = B'(\boldsymbol{X}) - (X_{pD}\beta + X_C\gamma)D(N,n)$$
$$\pi_{D-PNP} = B'(\boldsymbol{X}) - (X_{pD}\beta + (X_C+X_D)\gamma)D(N,n)$$
$$\pi_{D-PPN} = B'(\boldsymbol{X}) - ((X_D+X_D-1)\gamma + (X_{pD}-1)\beta)D(N,n)$$
$$\pi_{D-PPP} = B'(\boldsymbol{X}) - ((X_D+X_D+X_L-1)\gamma + (X_{pD}-1)\beta)D(N,n)$$
$$\pi_{L-NNN} = \sigma - X_{pL}\beta D(N,n)$$
$$\pi_{L-NNP} = \sigma - ((X_L-1)\gamma + (X_{pL}-1)\beta)D(N,n)$$
$$\pi_{L-NPN} = \sigma - (X_D\gamma + X_L\beta)D(\mathrm{N},\mathrm{n})$$
$$\pi_{L-NPP} = \sigma - ((X_D+X_L-1)\gamma + (X_{pL}-1)\beta)D(N,n)$$
$$\pi_{L-PNN} = \sigma - (X_C\gamma + X_L\beta)D(N,n)$$
$$\pi_{L-PNP} = \sigma - ((X_C+X_L-1)\gamma + (X_{pL}-1)\beta)D(N,n)$$
$$\pi_{L-PPN} = \sigma - ((X_C+X_D)\gamma + X_{pL}\beta)D(N,n)$$
$$\pi_{L-PPP} = \sigma - ((X_C+X_D+X_L-1)\gamma + (X_{pL}-1)\beta)D(N,n)$$

where X_C is the frequency of cooperators, X_D is the frequency of defectors, X_L is the frequency of loners, X_{pC} is the frequency of players that punish cooperators, X_{pD} is the frequency of players that punish defectors, and X_{pL} is the frequency of players that punish loners, the benefit of the PGG is given by the following equation:

$$B'(\boldsymbol{X}) = \frac{rcX_C}{N-X_L-1}\left(1-\frac{N}{n(N-X_L)}\right) + \frac{\binom{X_L}{n-1}}{\binom{N-1}{n-1}}\left(\sigma + \frac{rcX_C(X_L-n+1)}{n(N-X_L-1)(N-X_L)}\right)$$

The effective cost of contributing is given by the following equation:

$$F'(X_L) = 1 - \frac{r}{n}\frac{N-n}{N-X_L-1} + \frac{\binom{X_L}{n-1}}{\binom{N-1}{n-1}}\left(\frac{r}{n}\frac{X_L+1}{N-X_L-1} + r\frac{N-X_L-2}{N-X_L-1} - 1\right).$$

and

$$D(N,n) = \frac{n-1}{N-1}.$$

If $X_L \geq (N-1)$, then there is never more than 1 loner in a group, the public goods game is never played, and $B(\boldsymbol{X}) = \sigma$ and $F(X_L) = 0$.

These payoff expressions were originally presented in Rand and Nowak (2011), and based on original derivations in Traulsen et al. (2009). We refer readers to these prior publications for further details.

Calculation of compulsory public goods game payoffs

Using the same approach as in the calculation of the payoffs in the voluntary PGG, we define the payoff π_s of each strategy s as a function of the frequencies of cooperators X_C, defectors X_D, punishers of cooperation X_{pC} and punishers of defection X_{pD}

$$\pi_{C-NNN} = B(\boldsymbol{X}) - F(N,n) - X_{pC}\beta D(N,n)$$
$$\pi_{C-NPN} = B(\boldsymbol{X}) - F(N,n) - (X_{pC}\beta + X_D\gamma)D(N,n)$$
$$\pi_{C-PNN} = B(\boldsymbol{X}) - F(N,n) - ((X_{pC}-1)\beta + (X_C-1)\gamma)D(N,n)$$
$$\pi_{C-PPN} = B(\boldsymbol{X}) - F(N,n) - ((X_{pC}-1)\beta + (X_C-1+X_D)\gamma)D(N,n)$$
$$\pi_{D-NNN} = B(\boldsymbol{X}) - X_{pD}\beta D(N,n)$$
$$\pi_{D-NPN} = B(\boldsymbol{X}) - ((X_{pD}-1)\beta + (X_D-1)\gamma)D(N,n)$$
$$\pi_{D-PNN} = B(\boldsymbol{X}) - (X_{pD}\beta + X_C\gamma)D(N,n)$$
$$\pi_{D-PPN} = B(\boldsymbol{X}) - ((X_{pD}-1)\beta + (X_C+X_D-1)\gamma)D(N,n)$$

where $B(\boldsymbol{X}) = (rcX_C)(1-(1/n))(N-1)$ is the payoff from the compulsory public goods game, $F(N,n) = (1-(r/n)((N-n)/(N-1)))c$ is the effective cost of contributing to the compulsory public goods game, and $D(N,n) = (n-1)/(N-1)$.

These payoff expressions are based on the original derivations in Traulsen et al. (2009). We refer readers to these prior publications for further details.

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