



# Sequential interactions—in which one player plays first and another responds—promote cooperation in evolutionary-dynamical simulations of single-shot Prisoner's Dilemma and Snowdrift games

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## ABSTRACT

Cooperation is a central topic in evolutionary biology because (a) it is difficult to reconcile why individuals would act in a way that benefits others if such action is costly to themselves, and (b) it underpins many of the 'major transitions of evolution', making it essential for explaining the origins of successively higher levels of biological organization. Within evolutionary game theory, the Prisoner's Dilemma and Snowdrift games are the main theoretical constructs used to study the evolution of cooperation in dyadic interactions. In single-shot versions of these games, wherein individuals play each other only once, players typically act simultaneously rather than sequentially. Allowing one player to respond to the actions of its co-player—in the absence of any possibility of the responder being rewarded for cooperation or punished for defection, as in simultaneous or sequential iterated games—may seem to invite more incentive for exploitation and retaliation in single-shot games, compared to when interactions occur simultaneously, thereby reducing the likelihood that cooperative strategies can thrive. To the contrary, I use lattice-based, evolutionary-dynamical simulation models of single-shot games to demonstrate that under many conditions, sequential interactions have the potential to enhance unilaterally or mutually cooperative outcomes and increase the average payoff of populations, relative to simultaneous interactions—benefits that are especially prevalent in a spatially explicit context. This surprising result is attributable to the presence of conditional strategies that emerge in sequential games that can't occur in the corresponding simultaneous versions.

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## 1. Introduction

Understanding cooperation is of central importance in evolutionary biology for two main reasons: First, despite the proliferation of cooperation in nature, it is difficult at the outset to reconcile why individuals would act in a way that benefits others if such action is costly to themselves (Axelrod and Hamilton, 1981; Axelrod, 2006). Second, cooperation underpins many of the 'major transitions of evolution' and is essential for explaining the origins of successively higher levels of biological organization (Maynard Smith and Szathmáry, 1997). Consequently, developing theoretical explanations for cooperative behaviour continues to be a priority (Nowak, 2006b).

The Prisoner's Dilemma, and to a lesser extent, the Snowdrift game, are the main theoretical constructs used to study the evolution of cooperation in dyadic interactions (reviewed by Doebeli and Hauert, 2005). In a simplified version of the Prisoner's Dilemma,

cooperators pay a cost,  $c$ , in order to provide a benefit,  $b$ , to their co-player ( $b > c > 0$ ). Defectors do not pay the cost and provide no benefit. Therefore, mutual cooperation garners the 'Reward payoff' of  $R = b - c$  to both participants, mutual defection results in the 'Punishment payoff' of  $P = 0$  to both participants, and unilateral cooperation with a defector yields the 'Temptation payoff',  $T = b$ , to the defector, and the 'Sucker's payoff',  $S = -c$ , to the cooperator ( $T > R > P > S$ ). Because the payoff of a defector is always greater than that of a cooperator regardless of what strategy one's co-player plays, defection dominates cooperation. Moreover, if the payoffs are related to evolutionary fitness (Maynard Smith, 1982), defectors are expected to drive cooperators extinct in large, well-mixed populations (see review of evolutionary game dynamics by Nowak, 2006a).

In the Snowdrift game, both players receive a benefit  $b$ , so long as at least one of them cooperates; otherwise, neither receives a benefit. The total cost of cooperation is  $c$  (again,  $b > c > 0$ ); this cost is split evenly in the case of mutual cooperation or borne entirely by the cooperator in the case of unilateral cooperation. Therefore, in this case,  $R = b - c/2$ ,  $P = 0$ ,  $T = b$ , and  $S = b - c$  ( $T > R > S > P$ ). Un-

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like in the Prisoner's Dilemma, in the Snowdrift game cooperators fare best against defectors and vice versa. As such, evolutionary dynamics predicts that in large, well-mixed populations, cooperators and defectors should coexist with an equilibrium frequency of cooperators of  $(P-S)/(R-S-T+P)$  (Nowak, 2006a). Thus, the mere existence of cooperation does not require special explanation in Snowdrift scenarios, but it is still important to consider mechanisms that may alter its baseline frequency, especially because the average payoff at equilibrium is less than in a population composed of all cooperators (i.e., there is still scope for cooperation to improve; Hauert and Doebeli, 2004).

Both the Prisoner's Dilemma and the Snowdrift game can be further simplified by noting that relative fitness is crucial to evolutionary success, rather than absolute fitness. Thus, the cost-benefit ratio,  $u=c/b$ , can be used to obtain a one-parameter version of the Prisoner's Dilemma where  $R=1$ ,  $P=u$ ,  $T=1+u$ , and  $S=0$ . Similarly, the cost-benefit ratio of mutual cooperation,  $v=c/(2b-c)$ , can be used to frame a one-parameter version of the Snowdrift game where  $R=1$ ,  $P=0$ ,  $T=1+v$ , and  $S=1-v$ . In this version, the equilibrium frequency of cooperators is simply  $1-v$ . Note that  $0 < u < 1$  and  $0 < v < 1$  (Hauert and Doebeli, 2004; Fu et al., 2010).

Here, I investigate sequential Prisoner's Dilemma and Snowdrift games, both in spatial and aspatial (well-mixed) populations. The sequential manifestations are different from classic single-shot games where both players play simultaneously, and from iterated games where players play repeatedly (and either simultaneously or alternatingly; e.g., Brauchli et al., 1999 and Nowak and Sigmund, 1994, respectively). Rather, they are single-shot games where one player goes first and the other player responds conditionally based on the first player's opening gambit (see Kun et al., 2006 for an example of a single-shot Snowdrift game without this conditionality, wherein sequential interactions enhanced cooperation in the presence of a synergistic effect of cooperation). In this sense the games investigated here are somewhat similar to the Ultimatum game in that there is a distinct 'proposer' and 'responder' (though unlike here, in the Ultimatum game, the strategy set is different for the first and second player). Theory suggests that asynchrony can alter the relative favourability of different strategies (e.g., Ilcinkas and Pelc, 2008), and experimental results indicate that the sequential Prisoner's Dilemma can lead to substantial levels of cooperation in humans (e.g., Clark and Sefton, 2001). However, allowing one player to respond to the actions of its co-player—in the absence of any possibility of being rewarded for cooperation or punished for defection, and especially in the absence of any sense of the value of 'fair play' or related benefits not strictly accounted for by game payoffs (e.g., Dufwenberg and Kirchsteiger, 2004, Falk and Fischbacher, 2006)—may seem to invite even more incentive and opportunity for exploitation (and retaliation) compared to when interactions occur simultaneously. To the contrary, I use lattice-based simulation models to demonstrate the surprising result that under many conditions, sequential interactions have the potential to enhance unilaterally cooperative and mutually cooperative outcomes and increase the average payoff of populations, relative to simultaneous interactions, even in non-human agents whose fitness is strictly determined by game payoffs and for whom notions of fairness are immaterial. Further, the benefit of sequential interactions in these single-shot games is much greater in the context of spatially structured populations.

## 2. Methods

Interactions take place on a  $200 \times 200$  cell lattice with periodic boundaries. At the start, each of the  $4 \times 10^4$  cells is randomly and independently populated with an individual agent. In sequential games, the agent plays strategy  $i_k^j$  ( $i, j, k \in \{C, D\}$ ), whereby the agent plays  $i$  when playing first,  $j$  when responding to cooperation, and

$k$  when responding to defection. Because each of  $i$ ,  $j$ , and  $k$  have two possible values, there is a total of eight strategies. The payoffs associated with the interactions between these eight strategies are given in Fig. 1a. Note that there are two payoffs associated with every strategy pair, the payoff when an agent plays first, and the payoff when that agent responds to its co-player. Sometimes these two payoffs are the same; for example,  $C_C^D$  is suckered by  $D_C^D$  whether it plays first or second. However, in other instances the two payoffs are different; for example,  $C_C^D$  receives the reward payoff when it plays first against  $C_D^D$ , but it receives the temptation payoff when it plays second. The average payoffs for strategy pairs, assuming an equal probability of playing first or second, are given for the Prisoner's Dilemma and the Snowdrift game in Fig. 1b and c, respectively. The possible average payoffs for some pairs of strategies intersect at  $u=1/2$ ,  $v=1/3$ , or  $v=1/2$ , leading to potentially different patterns of strategy dominance at low versus high values of  $u$  or  $v$  (Fig. 2).

Simultaneous games are equivalent to sequential games that have been constrained to only allow unconditional cooperators,  $C_C^C$ , and unconditional defectors,  $D_D^D$ . In this case, order-of-play has no bearing on the outcome of interactions, and it is exactly as if the players play simultaneously (e.g., see the corners of the payoff matrix, Fig. 1a).

During each time step, a focal individual is selected at random from the lattice. In the spatial version of the model, a competitor is chosen randomly from among the focal individual's four nearest neighbours (von Neumann neighbourhood with periodic boundary conditions; Durrett and Levin, 1994); in the aspatial version of the model, corresponding to well-mixed conditions, the competitor is chosen randomly from the lattice. The focal individual and the competitor each then play the Prisoner's Dilemma or the Snowdrift game, depending on the context, with each of their respective four nearest neighbours (in the spatial version of the model), or with four random individuals (in the aspatial version of the model). In each player-pair, one individual is randomly chosen to play first and its pair-mate is relegated to playing second. Thereafter, the interactions proceed deterministically; players with a particular strategy always play the same thing (i.e., C or D) when playing first or when responding (the latter conditional, but still deterministic, based on what the first player plays), and payoffs are according to Fig. 1a (note that realized payoffs are not averaged with respect to time order, but depend on who plays first and second; but see Section 3.5 for a relaxation of this criterion). In this fashion, the focal individual's and the competitor's average payoffs from the four interactions are computed and defined as  $p_x$  and  $p_y$ , respectively (Hauert and Doebeli, 2004). Three replacement rules are investigated in which replacement occurs either by the replicator rule or one of two Fermi rules (Szabó and Fáth, 2007). When using the replicator rule, if  $p_y > p_x$  a clone of the competitor replaces the focal individual with probability  $(p_y - p_x)/(1+r)$ , where  $r=u$  in the case of the Prisoner's Dilemma, and  $r=v$  in the case of the Snowdrift game (if  $p_y \leq p_x$  the probability of replacement is 0) (Fig. 3a). In the case of the Fermi rule, a clone of the competitor replaces the focal individual with probability  $1/(1 + \exp(-\beta(p_y - p_x)))$ . Different Fermi rules arise from variation in the shape parameter  $\beta$ ; here,  $\beta=2$  or 10, representing low and high levels of payoff-related determinism in replacement, respectively (Fig. 3b). Note that replacement is in series (i.e., one cell at a time, as opposed to in parallel); this type of replacement is often called 'sequential updating', but it should not be confused with the use of the term 'sequential' to refer to sequential games.

The focal individual (or the new focal individual in the case where the original was replaced by a clone of the competitor) is then subject to mutation with probability  $\mu$ . Three levels of mutation are investigated: no mutation ( $\mu=0$ ), low mutation ( $\mu=2.5 \times 10^{-5}$ ), and high mutation ( $\mu=2.5 \times 10^{-3}$ ). If mutation

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