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HETEROGENEOUS POPULATION**

by

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Evolution of Cooperation in the Snowdrift Game with Incomplete Information and Heterogeneous Population

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Abstract

Differently from previous studies of tag-based cooperation, we assume that individuals fail to recognize their own tag. Due to such incomplete information, the action taken against the opponent cannot be based on similarity, although it is still motivated by the tag displayed by the opponent. We present stability conditions for the case when individuals play unconditional cooperation, unconditional defection or conditional cooperation. We then consider the removal of one or two strategies. Results show that conditional cooperators are the most resilient agents against extinction and that the removal of unconditional cooperators may lead to the extinction of unconditional defectors.

Keywords: cooperation, snowdrift game, replicator dynamics, evolution, similarity.

1 Introduction

The emergence of cooperation has been widely studied in many branches of science. In a well-mixed homogeneous population in which players select either to cooperate or defect, the prisoner's dilemma leads to the extinction of cooperation. Using the standard replicator dynamics, pure defection is the only asymptotically stable state, hence natural selection reduces the average fitness of the population [9]. Other classes of games may lead to cooperation. In the class of coordination games, cooperators survive and take over the entire population in the long run as long as their proportion in the population at the initial conditions is above a threshold given by the Nash equilibrium in mixed strategies. Asymptotic stability in the snowdrift game (class of anti-coordination games) results in a polymorphic population in which both defectors and cooperators survive and coexist. Cooperation can also emerge through other mechanisms such as kin selection [5, 9] in which donors and recipients of cooperation are genetically related, direct reciprocity [15, 9] such as in the iterated prisoner's dilemma with the use of the tit-for-tat strategy and indirect reciprocity where individuals who cooperate are more likely to receive cooperation [10, 9]. Other forms of promoting cooperation can be found in the prisoner's

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dilemma in regular lattices and networks or through group selection [9]. The use of punishment as in [16] may also lead to the extinction of defectors, although punishment is a form of reciprocity.

Contrasting with reciprocity, cooperation can also emerge based on similarity. In [12, 14] a well-mixed population of heterogeneous individuals is modelled. In [12] heterogeneity stems from individuals having a tag and a tolerance threshold, both randomly drawn from a uniform distribution $[0, 1]$. Individual i cooperates with j as long as j 's tag is similar enough to i 's tag, i.e., $|\tau_i - \tau_j| \leq T_i$. Evolution is modelled numerically. Differently from the iterated prisoner's dilemma, the same pair of players is unlikely to meet again. In [14] the same problem is analytically modelled using only two tags (blue, red) and two forms of cooperation (unconditional cooperators and conditional cooperators, i.e., cooperate if the opponent displays the same tag), which combined lead to four strategies. In [13] unconditional defectors are also considered. In such models all individuals can see the opponents' tags as well as they know their own tag (type).

However, in some environmental sciences and behavioural research contexts such assumptions do not hold completely. In the experiment carried out by [3], domestic fowls are artificially marked at random at the back of their necks resulting in their inability to identify their own type while they are able to identify their opponent. Depending on the opponent being tagged or not, the player may behave differently. Although the action taken is motivated by the opponent's tag, it is not based on similarity. A theoretical model of such experiment using a hawk-dove game with finite population is proposed in [7]. In this paper, we investigate the evolution of tag-based cooperation in the same context.

As in [14], individuals are assigned one of two tags, a type-*I* or type-*II* individual. On the other hand, they cannot condition their strategy on their own type as they fail to recognize it. By contrast they recognize their opponent's type and can thus choose a different action for the two types of opponent. This leads to four possible pure strategies: cooperate (defect) against both types and cooperate (defect) against the first type and defect (cooperate) against the second type. The first two strategies are non-discriminating: individuals are programmed to play the same action against any type of opponent, while the last two are discriminating. Thus individuals playing non-discriminating strategies are either unconditional cooperators or unconditional defectors while individuals playing discriminating strategies are conditional cooperators.

In order to adapt the model to the context of the experiment in [3], we introduce some important assumptions that differ from [12, 14]. We assume that the new offspring are randomly assigned their tag in such a way that the proportion of each tag in the population is kept constant over time. The allocation of tag is thus completely independent of the strategy an offspring is programmed to play, as in [2]. Hence, offspring inherit strategies but not tags. Also, we use standard replicator dynamics, eliminating the probability of mutations happening. The latter is similar to the replicator in [14]

without the drift towards cooperation. In particular we eliminate from the dynamics the so-called “tides of tolerance” found in both [12, 14].

When all four strategies are available the dynamics leads to a set of neutrally stable fixed points in which all strategies generally survive (see [2]). Here we consider the effect of removing one pure strategy (an extinction when the population suffers some natural shock). If it is a discriminating strategy, neutral stability remains. By contrast if it is a non-discriminating strategy, asymptotic stability can be achieved. One single discriminating strategy survives, driving the other strategies to extinction. The frequency of cooperation differs from the one in the homogeneous population game (no tags). Two direct consequences of such results are (i) by removing all unconditional cooperators from the population, the extinction of unconditional defectors can be achieved (and vice-versa) under specific conditions leading to a monomorphic population of only conditional cooperator individuals, (ii) conditional cooperators are more resilient against extinction than individuals who do not discriminate. In [14], using standard replicator dynamics, the inexistence of unconditional defectors does not lead to the extinction of unconditional cooperators. Most initial conditions lead to fixed points where the latter survive although selection generally favours a larger proportion of conditional cooperators. Back to our model, when a second strategy is removed, the result that only discriminating strategies are able to survive alone still holds.

The paper is organized as follows: Section 2 presents the snowdrift game for the heterogeneous population with all four pure strategies available in the population. In Section 3 the analysis is extended for the game when one strategy is removed from the population at the initial conditions and we compare our results with those of the snowdrift game played by a homogeneous population as well as those of previous studies on similarity-based cooperation. In Section 4 a second strategy is suppressed. Section 5 concludes.

2 Evolutionary snowdrift game with heterogeneous population

Two individuals have to choose among two actions, cooperate (C) or defect (D). Following [4] or [6] the game payoff matrix (see also [16]) is given by:

$$\begin{array}{cc}
 & \begin{array}{cc} C & D \end{array} \\
 \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} (b - c/2, b - c/2) & (b - c, b) \\ (b, b - c) & (0, 0) \end{pmatrix}
 \end{array}$$

where b is the benefit of cooperation, c its cost. In the prisoner’s dilemma the cost of cooperation is larger than the benefit: $b < c$, and defect is always a dominant strategy. Still both individuals are better off if both cooperate than if both defect: $c < 2b$. In the snowdrift game the benefit of cooperation is larger than its cost, $b > c$. If an individual cooperates with probability α while her

opponent cooperates with probability β the individual's expected payoff is given by $u(\alpha, \beta)$ with

$$u(\alpha, \beta) = \beta b + [(b - c) - (b - c/2)\beta]\alpha = \beta b + (b - c/2)(a - \beta)\alpha \text{ where } a = \frac{b - c}{b - c/2} \quad (1)$$

An individual's best response is to cooperate if the opponent cooperates with probability $\beta < a$, to defect if $\beta > a$ and is indifferent between defection and cooperation if $\beta = a$. The equilibrium is when both individuals cooperate with probability a .

Cooperation at equilibrium has a larger probability than defection ($a > 1/2$) if the benefit of cooperation is relatively large with respect to its cost, i.e., if $b > (3/2)c$. We will refer to *large benefits of cooperation* if $b > (3/2)c$ and *small benefits of cooperation* if $b < (3/2)c$.

Consider a very large well-mixed population with bilateral encounters between individuals programmed to play pure strategies (cooperate or defect) in the snowdrift game. In this homogeneous population there is one asymptotically stable state where the proportion of cooperators (i.e., the frequency with which cooperation emerges) equals a . Now assume that the population is heterogeneous: it is composed of two different types of individuals, type- I and type- II , where an over time fixed proportion x ($0 < x < 1$) of the individuals is of type- I . We assume that one type is more numerous than the other: $x \neq \frac{1}{2}$. Given the very large population, at any bilateral encounter between two individuals the probabilities of the four possible encounters can be written as

$$p(I, I) = x^2; p(I, II) = p(II, I) = x(1 - x); p(II, II) = (1 - x)^2 \quad (2)$$

A strategy is denoted $\alpha = (\alpha_I, \alpha_{II})$ where α_I is the probability of cooperating when the opponent is of type- I , α_{II} is the probability of cooperating when the opponent is of type- II . There are four pure strategies $(1, 1)$, $(1, 0)$, $(0, 1)$, and $(0, 0)$ that we denote CC , CD , DC , and DD respectively. Generic pure strategies will be denoted by i, j . A strategy is non-discriminating if $\alpha_I = \alpha_{II}$ (as pure strategies CC and DD) discriminating if $\alpha_I \neq \alpha_{II}$ (as pure strategies CD and DC). Hence, unconditional cooperators (defectors) play CC (DD) while conditional cooperators play either CD or DC .

The expected payoff of an individual playing α while the opponent plays $\beta = (\beta_I, \beta_{II})$ is the sum of the expected payoffs she would obtain in every possible encounter weighted by its probability of occurrence. Therefore the expected payoff of an individual playing α against an opponent playing β , that we denote by $U(\alpha, \beta)$, is given by

$$U(\alpha, \beta) = p(I, I)u(\alpha_I, \beta_I) + p(II, I)u(\alpha_I, \beta_{II}) + p(I, II)u(\alpha_{II}, \beta_I) + p(II, II)u(\alpha_{II}, \beta_{II}).$$

Using (1) and (2) we can rewrite

$$U(\alpha, \beta) = b[x\beta_I + (1 - x)\beta_{II}] + (b - c/2)[a - x\beta_I - (1 - x)\beta_{II}][x\alpha_I + (1 - x)\alpha_{II}]. \quad (3)$$

Note the similarity between this equation and equation (1): α is substituted by $\Psi_\alpha = x\alpha_I + (1 - x)\alpha_{II}$ and β by $\Psi_\beta = x\beta_I + (1 - x)\beta_{II}$. The probability of cooperation (α or β) is substituted by the frequency of cooperation (Ψ_α or Ψ_β).

Now consider that the population is divided into the subgroups that play the four possible pure strategies. A possible state of the population is denoted θ . It gives the proportions of the population using each pure strategy: $\theta = (\theta_{CC}, \theta_{CD}, \theta_{DC}, \theta_{DD})$. Of course for each strategy i we have $0 \leq \theta_i \leq 1$ and $\theta_{CC} + \theta_{CD} + \theta_{DC} + \theta_{DD} = 1$. A state is monomorphic if all population uses one single strategy: $\theta_i = 1$ for some strategy i . Otherwise the state is polymorphic.

In state θ cooperation occurs with frequency $\theta_{CC} + \theta_{CD}$ if the opponent is of type-*I*, and with frequency $\theta_{CC} + \theta_{DC}$ if the opponent is of type-*II*. Indeed those who play *CC* and those who play *CD* cooperate when facing an opponent of type-*I*. For an individual it is as if the opponent was playing $\beta_\theta = (\theta_{CC} + \theta_{CD}, \theta_{DC} + \theta_{CC})$ when the population is in state θ . The individual's expected payoff when playing α is $U(\alpha, \beta_\theta)$ in state θ .

The increase in the proportion of individuals playing pure strategy i is proportional to the payoff gain of the strategy. The population dynamics is governed by replicator dynamics:

$$\dot{\theta}_i = \theta_i [U(i, \beta_\theta) - U(\beta_\theta, \beta_\theta)] \text{ for any } i.$$

This can be rewritten using (3) as

$$\dot{\theta}_{CC} = \theta_{CC}(b - c/2)(a - \Psi_\theta)(1 - \Psi_\theta), \quad (4)$$

$$\dot{\theta}_{CD} = \theta_{CD}(b - c/2)(a - \Psi_\theta)(x - \Psi_\theta), \quad (5)$$

$$\dot{\theta}_{DC} = \theta_{DC}(b - c/2)(a - \Psi_\theta)(1 - x - \Psi_\theta), \quad (6)$$

$$\dot{\theta}_{DD} = \theta_{DD}(b - c/2)(a - \Psi_\theta)(-\Psi_\theta), \quad (7)$$

with

$$\Psi_\theta = \theta_{CC} + x\theta_{CD} + (1 - x)\theta_{DC}. \quad (8)$$

The frequency of cooperation in state θ is given by Ψ_θ . Note that one equation of the system (4-7) is redundant. In [2] the stability of the system is studied when all strategies are available. Their results can be summarized as follows. No monomorphic state is stable. All states θ with $\Psi_\theta = a$ are neutrally stable. In the long run ($t \rightarrow \infty$), the population evolves to a particular neutrally stable state θ which depends on the initial conditions θ_0 . At the neutrally stable states all strategies generally survive. Even if one strategy disappears from the population, the population is still susceptible to be invaded by this strategy. Any natural shock would move the population over time to a different neutrally stable state $\bar{\theta}$ such that $\Psi_{\bar{\theta}} = a$. At the neutrally stable states, the frequency of cooperation is given by a , as happens in the homogeneous snowdrift game.

3 Extinction of one strategy

We now analyze the evolutionary pattern of the population when one of the strategies is removed from the set of strategies, i.e., $\theta_i = 0$ at the initial conditions. This could be the result of extinction driven by a natural shock suffered by the population. In line with [2] we focus the analysis on cases where the system of ordinary differential equations given by (4-7) is hyperbolic at all θ corresponding to a monomorphic population. A first result is that when a discriminating strategy is removed, the population evolves to a neutrally stable state with the same frequency of cooperation as in the game played by a homogeneous population. The proof of the following theorem is given in the Appendix.

Theorem 1 *When $\theta_{CD} = 0$ or $\theta_{DC} = 0$ (i) no monomorphic state is stable, (ii) all states θ with $\Psi_{\theta} = a$ are neutrally stable.*

Asymptotic stability can never be attained when one discriminating strategy is removed. The population evolves to a weak (neutrally) stable stationary state, susceptible to shocks that move the population away from it to alternative stationary states close enough to ensure neutral stability. Still asymptotic stability is violated. The frequency of cooperation at any neutrally stable state is the same as in the homogeneous game. We illustrate in figure 1 the vector field when $\theta_{CD} = 0$. The figure is drawn for $(\theta_{CC}, \theta_{DC})$. The thick solid straight line in the interior of the state space is the set of neutrally stable states. Its intersections with the boundaries of the state space are $\{(a, 0), (\frac{x-1+a}{x}, \frac{1-a}{x})\}$ if $x > 1 - a$ or $\{(a, 0), (0, \frac{a}{1-x})\}$ if $x < 1 - a$.

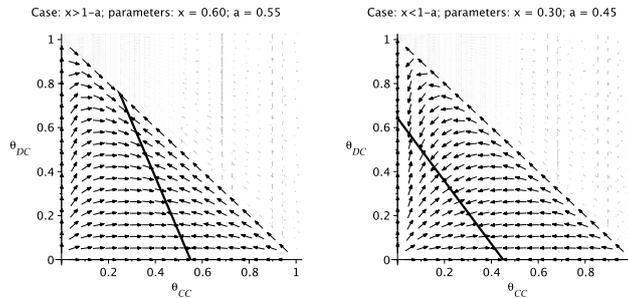


Figure 1: Dynamics when CD is removed. Parameters used: $b - c/2 = 1$; $x = 0.60 \wedge a = 0.55$ (left panel) and $x = 0.30 \wedge a = 0.45$ (right panel).

If instead, a non-discriminating strategy is removed, polymorphism may disappear and the population may evolve to a monomorphic state where the whole population plays a discriminating strategy. In this case all remaining strategies become extinct and asymptotic stability is achieved.

Theorem 2 *In a snowdrift game with large benefits of cooperation, (i) if $\theta_{DD} = 0$, no monomorphic*

state is stable, while (ii) if $\theta_{CC} = 0$, a monomorphic state with discriminating strategy is asymptotically stable for $1 - a < x < a$.

Theorem 3 *In a snowdrift game with small benefits of cooperation, (i) if $\theta_{CC} = 0$, no monomorphic state is stable, while (ii) if $\theta_{DD} = 0$, a monomorphic state with discriminating strategy is asymptotically stable for $a < x < 1 - a$.*

The proof of the theorems is given in the Appendix. Note that the frequency of cooperation is 1 if all individuals always cooperate, 0 if all individuals always defect. At any neutrally stable state the frequency of cooperation is a , as in the homogeneous game.

When a discriminating strategy is removed, none of the remaining strategies is fit enough to drive the other strategies to extinction. Let us illustrate this when $\theta_{CD} = 0$. From (3)

$$\begin{aligned} U(CC, \beta_\theta) - U(DC, \beta_\theta) &= (b - c/2)(a - \Psi_\theta)x \\ U(CC, \beta_\theta) - U(DD, \beta_\theta) &= (b - c/2)(a - \Psi_\theta) \\ U(DC, \beta_\theta) - U(DD, \beta_\theta) &= (b - c/2)(a - \Psi_\theta)(1 - x) \end{aligned}$$

When $\Psi_\theta < a$ cooperation against all individuals is always the best performing strategy ($\dot{\theta}_{CC} > 0$), and defect against all individuals the worst performing strategy ($\dot{\theta}_{DD} < 0$). Cooperation increases its proportion of adoption in the population over time. By contrast when $\Psi_\theta > a$ defecting against all individuals is the fittest strategy and increases its proportion over time, while cooperation against all individuals is the worst performing strategy. The only condition leading to a stable stationary state is when $\Psi_\theta = a$ and a polymorphic neutrally stable state holds.

In fact when one discriminating strategy is removed from the population, the remaining discriminating strategy is always less fit than one of the non-discriminating strategies. The fittest strategy is always one of the non-discriminating strategies but none of them are dominant because they only perform the best when few individuals have adopted them. Once many individuals have adopted a non-discriminating strategy, this strategy always becomes the worst performing strategy, and the proportion of individuals adopting it decreases over time. Thus asymptotic stability cannot be attained and the population evolves to a neutrally stable state in which all strategies available in the population generally survive.

By contrast, when a non-discriminating strategy is removed, a discriminating strategy can be fit enough to drive the other strategies to extinction. Let us illustrate this when $\theta_{CC} = 0$. From (3)

$$\begin{aligned} U(CD, \beta_\theta) - U(DD, \beta_\theta) &= (b - c/2)(a - \Psi_\theta)x \\ U(CD, \beta_\theta) - U(DC, \beta_\theta) &= (b - c/2)(a - \Psi_\theta)(2x - 1) \end{aligned}$$

First consider that $\Psi_\theta < a$. Strategy DD performs the worst, DC becomes the fittest strategy for small proportion of individuals of type- I (i.e., for $x < \frac{1}{2}$) while CD becomes the fittest strategy for

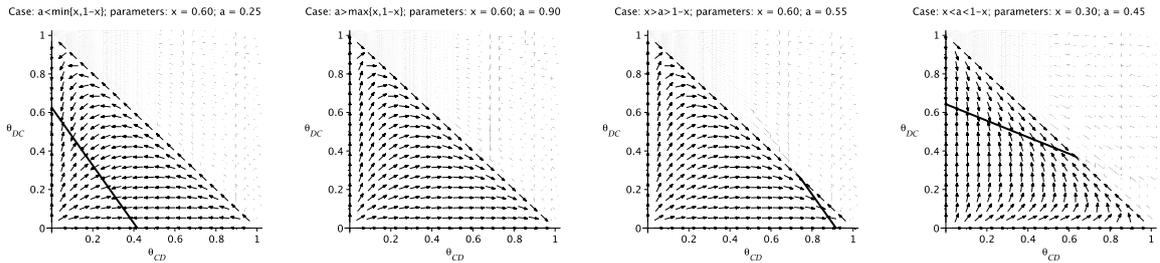


Figure 2: Dynamics when CC is removed. Parameters used: $b - c/2 = 1$; from left to right: $x = 0.60 \wedge a = 0.25$; $x = 0.60 \wedge a = 0.90$; $x = 0.60 \wedge a = 0.55$ and $x = 0.30 \wedge a = 0.45$.

$x > \frac{1}{2}$. Moreover from (5) it can be seen that we can obtain $\dot{\theta}_{CD} = 0$ for $x = \Psi_{\theta}$. Also $\Psi_{\theta} = x > \frac{1}{2}$ is compatible with $\Psi_{\theta} < a$ for large benefits of cooperation ($a > \frac{1}{2}$). Note that in this case the frequency of cooperation is x , which is smaller than a , the frequency of cooperation in the homogeneous game. Similarly from (6) it can be seen that we can obtain $\dot{\theta}_{DC} = 0$ for $\Psi_{\theta} = 1 - x$. Then $\Psi_{\theta} = 1 - x > \frac{1}{2}$ is compatible with $\Psi_{\theta} < a$ for large benefits of cooperation ($a > \frac{1}{2}$). Note that in this case the frequency of cooperation is $1 - x$, again smaller than a . In sum, removing unconditional cooperators leads to the extinction of unconditional defectors under the conditions stated in theorem 2. Still, independently of the asymptotically stable state (be it CD or DC), cooperation is less frequent than in the homogeneous snowdrift game, although cooperation emerges always with a frequency larger than $\frac{1}{2}$. This contrasts with the results found in [12]. In the latter, also for large benefits of cooperation, although the frequency of cooperation is 74% for $\frac{b}{c} \geq \frac{10}{3}$, it decays sharply when the benefit of cooperation decreases below $\frac{b}{c} = 2.5$ (frequency equals only 25% for $\frac{b}{c} = 2$ and equals a residual value of 2% for $\frac{b}{c} = \frac{5}{3}$).

Second consider that $\Psi_{\theta} > a$. Defect against all individuals is the best performing strategy and from (7) it can be seen that $\dot{\theta}_{DD} > 0$. But there is no state $\theta_{DD} \neq 0$ leading to $\dot{\theta}_{DD} = 0$. Whenever $\Psi_{\theta} > a$, there is no asymptotically stable state and the state space necessarily contains a set of neutrally stable states θ with $\Psi_{\theta} = a$ dividing the state space into two regions, one in which $\Psi_{\theta} > a$ holds and the other with $\Psi_{\theta} < a$. On the other hand, when the state space has no neutrally stable state, $\Psi_{\theta} < a$ necessarily holds at any θ . A simulation showing the dynamics for all possible cases when $\theta_{CC} = 0$ is presented in figure 2. In the second left most panel, the state space displays no neutrally stable state and $\theta_{CD} = 1$ is asymptotically stable.

The results of theorems 2 and 3 are further displayed in two diagrams in figure 3 for the case when CC is removed and the population has the same share of individuals playing the three available strategies at the initial conditions, i.e., $\theta_{CD} = \theta_{DC} = \theta_{DD} = 1/3$. For different values of a ranging from 0.01 to 0.99, we have run simulations with 10,000 interactions (enough for the system to achieve a stable state for any value of a) and the diagrams show how the stable states vary with different values of a . In line with theorem 3, there is no asymptotically stable state for $a < 1/2$ and the region

of the diagrams in which small benefits of cooperation hold always displays the coexistence of all three strategies (neutral stability). Asymptotic stability with the survival of a single discriminating strategy necessarily holds within the region where large benefits of cooperation hold. In the left panel, $x = 0.30$ (population composed mainly of type-*II* individuals) and the survival of *DC* alone holds for $a > 1 - x = 0.70$, as stated in theorem 2. In the right panel, $x = 0.85$ and survival of *CD* alone holds for $a > x = 0.85$. The diagrams also display Ψ_θ , which is increasing and equals a until asymptotic stability is achieved.

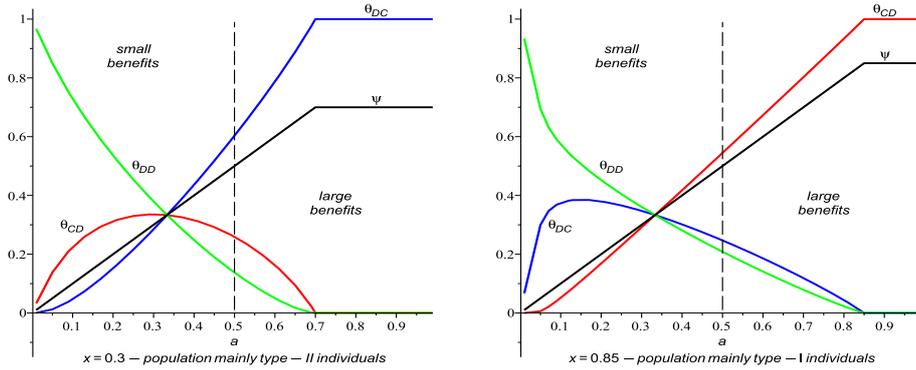


Figure 3: Stable states for different values of a when *CC* is removed (color online).

Before closing this section, consider the case when $\theta_{DD} = 0$. For small benefits of cooperation, the removal of unconditional defectors leads to the extinction of unconditional cooperators under the conditions in theorem 3. Still, the surviving monomorphic population plays cooperation more frequently than in the homogeneous snowdrift game although with a frequency lower than $\frac{1}{2}$ due to the small benefits of cooperation. Our result for $\theta_{DD} = 0$ differs from the typical outcome using standard replicator dynamics in [14] where unconditional defectors do not exist and both conditional and unconditional cooperators end up surviving, although selection tends to favor the individuals who discriminate.

Finally, based on the results so far, individuals who discriminate are more resilient against extinction. This remains true even if a second strategy is suppressed from the population as we show in the next section.

4 Extinction of a second strategy

When a second strategy is removed, only discriminating strategies are able to survive alone and take over the entire population. The following theorem shows that monomorphic states are not stable when only non-discriminating strategies are available:

Theorem 4 *When $\theta_{CD} = 0$ and $\theta_{DC} = 0$ the only asymptotically stable state is polymorphic with $(\theta_{CC}, \theta_{DD}) = (a, 1 - a)$.*

Note that at the asymptotically stable state the frequency of cooperation is $\Psi_{\theta} = a$. When only discriminating strategies are initially possible monomorphic and polymorphic states can be stable. The conditions of stability are given in the next theorem:

Theorem 5 *If $\theta_{CC} = 0$ and $\theta_{DD} = 0$, (i) a monomorphic state with discriminating strategy is asymptotically stable for $\min\{a, 1 - a\} < x < \max\{a, 1 - a\}$ (ii) a polymorphic state $(\theta_{CD}, \theta_{DC}) = (\frac{a+x-1}{2x-1}, \frac{x-a}{2x-1})$ is asymptotically stable for $x < \min\{a, 1 - a\}$ or $x > \max\{a, 1 - a\}$.*

The last result is when we have one non-discriminating strategy and one discriminating strategy. In this case either the discriminating strategy takes over the population or an asymptotically stable (polymorphic) state holds.

Theorem 6 *When the set of possible strategies is composed of one discriminating and one non-discriminating strategy a monomorphic state with the non-discriminating strategy is always unstable. Either a monomorphic state with the discriminating strategy or a polymorphic state is asymptotically stable.*

The proof of the theorems above is straightforward. The state of the population is represented by one single equation of the system (4-7). There are always two isolated fixed points ($\theta_i = 0$; $\theta_i = 1$) corresponding to a monomorphic population and, conditional on the values of the parameters, there may also exist a third isolated fixed point $0 < \theta_i < 1$ corresponding to polymorphism. Asymptotic stability requires $\frac{\partial \theta_i}{\partial \theta_i} < 0$, which always holds either at the fixed point associated with polymorphism or at the fixed point associated with a monomorphic population of conditional cooperators. With only two strategies available, asymptotic stability can hold with polymorphism due to the lower dimension of the state space (\mathbb{R}^1 instead of \mathbb{R}^3 as in section 2 or \mathbb{R}^2 as in section 3).

For all asymptotically stable points in theorems 4, 5 and 6, the frequency of cooperation equals (differs from) that of the homogeneous snowdrift game whenever asymptotic stability corresponds to a polymorphic (monomorphic) population. Differently from theorems 2 and 3, the existence of asymptotic stability associated with a monomorphic population is not conditional on the size of the benefit of cooperation.

5 Conclusion

In this paper, we have studied how frequent cooperation emerges in the context of a snowdrift game played by a heterogeneous population composed of two types of players and incomplete information

with regard to players' own type. We have considered the case in which not all four pure strategies are available in the population. When one pure strategy has been removed two core results are: when a discriminating strategy is not played by the population, neutral stability persists but, if instead, a non-discriminating strategy is not played, asymptotic stability can be achieved. When asymptotic stability holds, it is always for a monomorphic state with a discriminating strategy, implying the extinction of both unconditional cooperators and defectors. Frequency of cooperation however differs from the one obtained in the game played by a homogeneous population. For small (large) benefits of cooperation, cooperation emerges at a frequency lower (greater) than $\frac{1}{2}$, however more (less) often than in the homogeneous population case.

Appendix

In order to find the stable states, we start by looking for the system fixed points, i.e., the solutions of the system of equations (4-7). Then the eigenvalues of the Jacobian matrix (evaluated at the fixed points) are computed. Recall that the condition for asymptotic stability is that the eigenvalues are all negative. The entries of the Jacobian matrix are for any $i \neq j$

$$\begin{aligned} \frac{\partial \dot{\theta}_i}{\partial \theta_i} &= (b - c/2) \left[(a - \Psi_{\theta}) (\eta_i - \Psi_{\theta}) + \theta_i (2\Psi_{\theta} - \eta_i - a) \frac{\partial \Psi_{\theta}}{\partial \theta_i} \right] \\ \frac{\partial \dot{\theta}_i}{\partial \theta_j} &= (b - c/2) \theta_i (2\Psi_{\theta} - \eta_i - a) \frac{\partial \Psi_{\theta}}{\partial \theta_j} \\ \text{with } \eta_i &= \begin{cases} 1 & \text{if } i = CC \\ x & \text{if } i = CD \\ 1 - x & \text{if } i = DC \\ 0 & \text{if } i = DD \end{cases} \end{aligned} \quad (9)$$

Theorem 1

Proof. First consider that strategy $\theta_{CD} = 0$. The population dynamics is governed by equations (4) and (6) and the frequency of cooperation (8) can be rewritten as $\Psi_{\theta} = \theta_{CC} + (1 - x)\theta_{DC}$. A state can be represented by $\theta = (\theta_{CC}, \theta_{DC})$ as $\theta_{DD} = 1 - \theta_{CC} - \theta_{DC}$. There are three isolated fixed points $(1, 0)$, $(0, 1)$, $(0, 0)$, and all θ such that $\Psi_{\theta} = \theta_{CC} + (1 - x)\theta_{DC} = a$ are non-isolated fixed points. We compute the Jacobian matrix $\Omega(\theta)$ using (9)

$$\Omega(\theta) = \begin{pmatrix} \frac{\partial \dot{\theta}_{CC}}{\partial \theta_{CC}}(\theta) & \frac{\partial \dot{\theta}_{CC}}{\partial \theta_{DC}}(\theta) \\ \frac{\partial \dot{\theta}_{DC}}{\partial \theta_{CC}}(\theta) & \frac{\partial \dot{\theta}_{DC}}{\partial \theta_{DC}}(\theta) \end{pmatrix}$$

that we evaluate at the isolated fixed points. We obtain

$$\Omega((1, 0)) = (b - c/2)(1 - a) \begin{pmatrix} 1 & 1 - x \\ 0 & x \end{pmatrix}$$

$$\Omega((0, 0)) = (b - c/2)a \begin{pmatrix} 1 & 0 \\ 0 & 1 - x \end{pmatrix}$$

and

$$\Omega((0,1)) = (b - c/2)(1 - a - x) \begin{pmatrix} -x & 0 \\ 1 & 1 - x \end{pmatrix}$$

Both eigenvalues of the first two matrices are positive. In consequence, state $(0,0)$ and state $(1,0)$ are unstable. The eigenvalues of the third matrix are of opposite signs: state $(0,1)$ is a saddle point. Neutral stability is achieved for θ such that $\Psi_\theta = a$. Indeed the set of neutrally stable states always divides the state space into two regions with $\theta_{CC} = 1$ in one region and $\theta_{DD} = 1$ in the other. Therefore the vector field flows from these two sources towards stationary states θ such that $\Psi_\theta = a$. When $\theta_{DC} = 0$, the dynamics is similar: we also obtain that neutral stability is achieved for all θ such that $\Psi_\theta = a$. ■

Theorems 2 and 3

Proof. First consider that $\theta_{CC} = 0$. The population dynamics is governed by (5) and (6) and the frequency of cooperation (8) can be rewritten as $\Psi_\theta = x\theta_{CD} + (1-x)\theta_{DC}$. A state can be represented by $\theta = (\theta_{CD}, \theta_{DC})$ as $\theta_{DD} = 1 - \theta_{CD} - \theta_{DC}$. We compute the Jacobian matrix $\Omega(\theta)$ using (9)

$$\Omega(\theta) = \begin{pmatrix} \frac{\partial \dot{\theta}_{CD}}{\partial \theta_{CD}}(\theta) & \frac{\partial \dot{\theta}_{CD}}{\partial \theta_{DC}}(\theta) \\ \frac{\partial \dot{\theta}_{DC}}{\partial \theta_{CD}}(\theta) & \frac{\partial \dot{\theta}_{DC}}{\partial \theta_{DC}}(\theta) \end{pmatrix}$$

at the isolated fixed points $(1,0)$, $(0,1)$, and $(0,0)$. We obtain

$$\Omega((1,0)) = (b - c/2)(x - a) \begin{pmatrix} x & 1 - x \\ 0 & 2x - 1 \end{pmatrix}.$$

That is, when the benefits of cooperation are large ($a > 1/2$) the eigenvalues are negative if $1/2 < x < a$, i.e., $(1,0)$ is asymptotically stable for $1/2 < x < a$. When the benefits of cooperation are small ($a < 1/2$), $(1,0)$ is unstable or a saddle point. Similarly, we have

$$\Omega((0,1)) = (b - c/2)(1 - a - x) \begin{pmatrix} 1 - 2x & 0 \\ x & 1 - x \end{pmatrix}$$

Thus for large benefits of cooperation $(0,1)$ is asymptotically stable for $1 - a < x < 1/2$, while when the benefits of cooperation are small $(0,1)$ is unstable or a saddle point. By contrast in the Jacobian matrix

$$\Omega((0,0)) = (b - c/2)a \begin{pmatrix} x & 0 \\ 0 & 1 - x \end{pmatrix}$$

the eigenvalues are both positive and $(0,0)$ is unstable. Whenever none of the isolated fixed points is asymptotically stable, all states θ with $\Psi_\theta = a$ are neutrally stable.

Second consider that $\theta_{DD} = 0$. A state can be represented by $\theta = (\theta_{CC}, \theta_{CD})$ as $\theta_{DC} = 1 - \theta_{CC} - \theta_{CD}$. The population dynamics is governed by (4) and (5) and the frequency of cooperation (8) can

be rewritten as (using $\theta_{DC} = 1 - \theta_{CC} - \theta_{CD}$) $\Psi_{\theta} = 1 - x + x\theta_{CC} + (2x - 1)\theta_{CD}$. The Jacobian matrix $\Omega'(\theta)$ using (9) is now

$$\Omega'(\theta) = \begin{pmatrix} \frac{\partial \dot{\theta}_{CC}}{\partial \theta_{CC}}(\theta) & \frac{\partial \dot{\theta}_{CC}}{\partial \theta_{CD}}(\theta) \\ \frac{\partial \dot{\theta}_{CD}}{\partial \theta_{CC}}(\theta) & \frac{\partial \dot{\theta}_{CD}}{\partial \theta_{CD}}(\theta) \end{pmatrix}$$

Evaluated at the isolated fixed points $(1, 0)$, $(0, 1)$ and $(0, 0)$, the Jacobian matrices become

$$\Omega'((1, 0)) = (b - c/2)(1 - a) \begin{pmatrix} x & 2x - 1 \\ 0 & 1 - x \end{pmatrix}$$

$$\Omega'((0, 1)) = (b - c/2)(a - x) \begin{pmatrix} 1 - x & 0 \\ -x & 1 - 2x \end{pmatrix}$$

$$\Omega'((0, 0)) = (b - c/2)(a - 1 + x) \begin{pmatrix} x & 0 \\ 0 & 2x - 1 \end{pmatrix}$$

When the benefits of cooperation are small ($a < 1/2$) we obtain that $(1, 0)$ is unstable, $(0, 1)$ is asymptotically stable for $a < x < 1/2$ and $(0, 0)$ is asymptotically stable when $1/2 < x < 1 - a$. When the benefits of cooperation are large, $(1, 0)$, $(0, 1)$ and $(0, 0)$ are unstable. All states θ with $\Psi_{\theta} = a$ are neutrally stable if there is no asymptotically stable state. ■

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