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Evolutionary dynamics of the continuous iterated Prisoner's dilemma

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Abstract

The iterated prisoner's dilemma (IPD) has been widely used in the biological and social sciences to model dyadic cooperation. While most of this work has focused on the discrete prisoner's dilemma, in which actors choose between cooperation and defection, there has been some analysis of the continuous IPD, in which actors can choose any level of cooperation from zero to one. Here, we analyse a model of the continuous IPD with a limited strategy set, and show that a generous strategy achieves the maximum possible payoff against its own type. While this strategy is stable in a neighborhood of the equilibrium point, the equilibrium point itself is always vulnerable to invasion by uncooperative strategies, and hence subject to eventual destabilization. The presence of noise or errors has no effect on this result. Instead, generosity is favored because of its role in increasing contributions to the most efficient level, rather than in counteracting the corrosiveness of noise. Computer simulation using a single-locus infinite alleles Gaussian mutation model suggest that outcomes ranging from a stable cooperative polymorphism to complete collapse of cooperation are possible depending on the magnitude of the mutational variance. Also, making the cost of helping a convex function of the amount of help provided makes it more difficult for cooperative strategies to invade a non-cooperative equilibrium, and for the cooperative equilibrium to resist destabilization by non-cooperative strategies.

Finally, we demonstrate that a much greater degree of assortment is required to destabilize a non-cooperative equilibrium in the continuous IPD than in the discrete IPD. The continuous model outlined here suggests that incremental amounts of cooperation lead to rapid decay of cooperation and thus even a large degree of assortment will not be sufficient to allow cooperation to increase when cooperators are rare. The extreme degree of assortment required to destabilize the non-cooperative equilibrium, as well as the instability of the cooperative equilibrium, may help explain why cooperation in Prisoner's Dilemmas is so rare in nature.
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Keywords: Discrete iterated prisoner's dilemma; Continuous iterated prisoner's dilemma; Noisy iterated prisoner's dilemma; Generosity; Cooperation

1. Introduction

The iterated prisoner's dilemma (IPD) has been widely used in the biological and social sciences to model dyadic reciprocity. In the discrete version of the IPD, during each interaction players engage in a standard prisoner's dilemma game in which they have only two options in each iteration: cooperate or defect. In continuous IPDs, in each iteration players' contributions vary along a continuum ranging from pure defection to pure cooperation. When a player increases her contribution level, her payoff decreases, but the average payoff of the pair increases.

Although the continuous IPD seems to be a better model of many real-world situations, it has been subject to much less analysis. Killingback and Doebeli (2002), employing analysis and simulations, consider a model of linear payoff-based strategies in a continuous IPD, and find that cooperation can evolve as long as the initial set of strategies meets a threshold value of cooperativeness. Killingback and Doebeli note that payoff-based strategies have the ability to compensate for nonlinear cost and benefit functions. While the model examined in this paper does not consider payoff-based strategies, making the cost of helping a convex function of the amount of help provided does not change the qualitative nature of our results.

Bendor et al. (1991) organized a tournament of computer strategies in a noisy continuous prisoner's dilemma, and concluded that the strategies that did best

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tended to be generous. Tit-for-Tat (TFT) was found to fare relatively poorly. Bendor, Kramer, and Stout attributed the superior performance of the generous strategies to their ability to avoid spiraling downwards into rounds of mutual recrimination after encountering exogenous error terms. (Wahl and Nowak 1999a, b) examined a version of the continuous IPD, considering strategies of the form $y = kx+d$, where x is the contribution from the other player, and y is the contribution to the other player. Based on a combination of computer simulation and analytical results, they concluded that cooperative strategies that resisted invasion had the characteristics of being optimistic (made high initial offers of x_o), generous (offered more cooperation than the partner did in the previous round) and uncompromising (offered full cooperation only if the partner did). However, cooperation in the continuous IPD with noise was found to be evolutionarily unstable: cooperative strategies were prone to invasion by more cooperative strategies, which in turn were invaded by defectors.

While these results are plausible, they are based mainly on simulations. By focusing on a model of the noisy continuous IPD with a more limited strategy set, we have obtained analytical results that shed some additional light on the dynamics of the continuous IPD. We demonstrate that in a model of the noisy continuous IPD based on a family of reflecting strategies (i.e. with a 'memory' of one move), the following propositions hold:

(1) The non-cooperative equilibrium is an evolutionarily stable strategy (ESS); that is, no other strategy can invade this equilibrium without positive assortment.
(2) A much higher degree of assortment is required to destabilize the non-cooperative equilibrium than in the case of the discrete IPD.
(3) The strategy that achieves the highest payoff when paired against itself is a generous (but not maximally generous) strategy.
(4) This generous strategy is an attractor for a certain neighborhood of the reciprocation parameter; that is, perturbations within the neighborhood will tend toward the equilibrium point.
(5) Any strategy type can drift in against the cooperative equilibrium point, and thus a combination of uncooperative and overly generous types drifting in can destabilize the equilibrium point.
(6) Noise of small magnitude has no effect on this generous strategy, even when negatively (or positively) biased. Error terms of larger magnitude have no effect if their distribution is symmetric.
(7) The function of generosity is to increase contributions to the most efficient level, rather than counteract the corrosiveness of noise.
(8) Allowing the cost of helping to be a convex function of the amount of help provided makes it more difficult for marginally cooperative strategies to invade a non-cooperative equilibrium, and makes it harder for the cooperative equilibrium to resist destabilization by non-cooperative strategies.

In addition, computer simulation with a single-locus, infinite alleles model with Gaussian mutation (Kimura and Crow, 1964) reveals that three general outcomes result from destabilization of the cooperative equilibrium: low mutation rates lead to cyclical polymorphisms of non-cooperative and cooperative types; greater mutation rates lead to collapse of the cooperative equilibrium; finally, higher mutation rates lead to stable polymorphisms containing a spectrum of non-cooperative and cooperative types.

Because the strategy set investigated in this model is more limited than those employed by Bendor et al. (1991); Wahl and Nowak (1999a, b), not all of these results may be applicable to their models. Nonetheless, our model seems to elucidate characteristics of more complicated models that do not readily lend themselves to analysis.

2. A model of the continuous iterated Prisoner's dilemma

Consider an iterated game with two players X and Y. X's score for round t, $V_t(X|Y)$, is

$$V_t(X|Y) = x_t - cy_t \tag{1}$$

and Y's score is

$$V_t(Y|X) = y_t - cx_t, \tag{2}$$

where x_t is Y's contribution to X in round t, y_t is X's contribution to Y, and c, the cost of cooperation, is a parameter in the range [0, 1]. Thus, X provides a benefit to Y of x_t at a cost cx_t to X, and Y provides a benefit to X of y_t at a cost cy_t to Y. A contribution of $x_t = 0$ is equivalent to defection and $x_t = 1$ is equivalent to cooperation in a discrete linear prisoner's dilemma in which $b = 1$.

2.1. Parameterization of the strategy space

We consider strategies that condition contributions only on the preceding contribution from the other player; i.e. these strategies have a 'memory' of one, similar to Wahl and Nowak's linear reactive models (1999a, b). Strategies are specified by the values of two parameters. The parameter r represents the rate of reciprocation. Let the range of r be [0, 2]. We wish to define r is such a way that zero designates a non-cooperator, one a strict reciprocator, and two a full cooperator. Accordingly, let X's contribution to Y in round t, denoted as y_t, be defined as

$$y_t = \begin{cases} rx_{t-1}, & 0 \leqslant r \leqslant 1, \\ x_{t-1} + (r-1)(1-x_{t-1}), & 1 < r \leqslant 2. \end{cases} \tag{3}$$

Thus, when r is less than or equal to one, the strategy will return a fraction r of the other player's contribution. When r is greater than one, the strategy will return the other player's contribution, plus a fraction $r-1$ of the difference between 1 (the maximum contribution) and the other

player's contribution. Hence, if r is equal to 2, the strategy will return maximally (i.e. (1) regardless of the other player's contribution. Defining r in this way allows us to map the entire range of contributions $y_t \in [0,1]$ with a continuous function and a single parameter r over the interval [0,2].

The second parameter is $f \in [0,1]$, the first contribution of X to Y.

2.2. Analysis of evolutionary dynamics

Let w be the conditional probability that interaction $t+1$ will take place given that t interactions have already occurred. Let A be a rare invader with reciprocation rate r', and let B be the common type with reciprocation rate r. After some algebra (see Appendix A), we find that the following system of equations characterizes the relative payoffs of all possible pairings of invaders against common types:

$$V(A|B) - V(B|B) = \begin{cases} \frac{fw(r-r')(c-wr)}{(1-w^2r'r)(1-wr)}, & 0 \leqslant r' \leqslant 1, \quad 0 < r \leqslant 1, \\ \frac{w(c-(2-r)w)[f(1-r')(1-w)-(1-r)(1-f(1-w)-r'w)]}{(1-w^2(2-r)r')(1-w)(1-w(2-r))}, & 0 < r' \leqslant 1, \quad 1 \leqslant r \leqslant 2, \\ \frac{w(c-wr)[1+f(r-2)(1-w)-rw+r'(f-1+rw-fw)]}{(1-w)(1-rw)(1-(2-r')rw^2)}, & 1 < r' \leqslant 2, \quad 0 < r \leqslant 1, \\ \frac{(1-f)(r'-r)((2-r)w-c)}{((1-w^2(2-r'))(2-r)(1-w(2-r))}, & 1 \leqslant r' \leqslant 2, \quad 1 < r \leqslant 2. \end{cases} \tag{4}$$

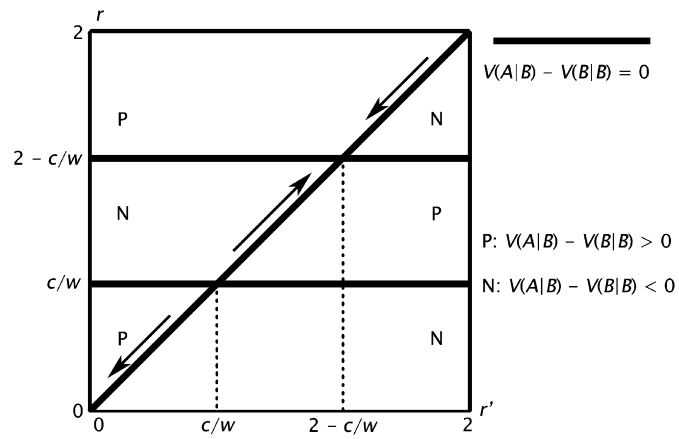

Fig. 1. Payoff map of $V(A|B)-V(B|B)=0$. The thick solid line indicates combinations of r' and r where $V(A|B)-V(B|B)=0$. P indicates that in this region $V(A|B)-V(B|B)>0$ (where P stands for positive), and N indicates $V(A|B)-V(B|B)<0$ (where N stands for negative). The arrows indicate the evolutionary dynamics of this system. The two attractors are $r^*=0$ and $r^*=2-c/w$.

Note the $(1-f)$ term in the last equation of Eq (4). When the invading type A is more generous than the common type B, invaders receive an advantage when the common type makes lower initial contributions of f, because the higher generosity of invading types leads to faster ramping-up of contributions in subsequent rounds of play.

The payoffs given in (4) indicate that there are two critical values of the reciprocation parameter: $r^* = c/w$ and $r^* = 2-c/w$, where c/w is less than 1. As illustrated in Fig. 1, when

$$0 \leqslant r \leqslant c/w, \tag{5}$$

or

$$2 - c/w \leqslant r \leqslant 2, \tag{6}$$

rare, less generous types can always invade the population (i.e. if $r' < r$, then $V(A|B) > V(B|B)$). When

$$c/w \leqslant r \leqslant 2 - c/w, \tag{7}$$

more generous types can always invade the population (i.e. if $r' > r$, then $V(A|B) > V(B|B)$). When r is equal to either of the critical values all rare invading types have the same fitness as the common type.

These payoffs indicate that this evolutionary system has two attractors. The non-cooperative strategy, $r^* = 0$, is an ESS. When interaction is random, all rare invaders achieve negative payoffs relative to pairings of the common type; i.e., $V(A|0)-V(0|0)<0$ for all $r \in [0,2]$. The value $r^* = 2-c/w$ is an attractor, but not an ESS. When r is in the range $[c/w, 2-c/w]$, populations can always be invaded by more generous mutants, and when it is in the range $[2-c/w, 2]$ populations can be invaded by less generous mutants. Thus, selection will tend to move the population toward the attractor $r^* = 2-c/w$. However, this value is not an ESS because once reached, all values of reciprocation achieve the same fitness as the cooperative equilibrium strategy.

2.3. Explanation of evolutionary dynamics

Natural selection will act to increase the rate of reciprocation, r, if

$$c/w < r \tag{8}$$

and

$$c/w < (2 - r), \tag{9}$$

where c is the cost/benefit ratio, and w is the probability of continued interaction. As is typical in models of reciprocity there is a close relationship between these conditions and Hamilton's rule (1964). See Lehmann and Keller (2006) for a clear discussion.

Expression (8) implies that agents gain from being more generous when the common type's rate of reciprocation, r, weighted by the probability of further interaction, w, exceeds the cost of one's cooperation, c. In other words, agents gain from being more generous when the expected

benefit of a marginal increase in contributions exceeds the cost of contributing. Conversely, strategies gain from being less generous when the other player's rate of reciprocation r, weighted by the probability w of further interaction, is less than the cost c of one's cooperation.

To understand expression (9), recall that for $r>1$, the interaction rule stipulates returning the other agent's contribution from the previous round, plus the residual value of r (i.e. $1-r$) times the difference between the maximum contribution and the other agent's contribution from the previous round. In order to interpret the significance of the factor (2−r) in Eq. (9), let

$$h_{t-1} = 1 - x_{t-1}. \tag{10}$$

Substituting Eq (10) into the definition of X's contribution to Y in round t for $r>1$, Eq (3), yields

$$y_t = 1 - h_{t-1}(2-r) \tag{11}$$

as the response rule for $r>1$. Thus, for $r>1$, the relevant reciprocation factor is now $(2-r)$ rather than r. It follows from Eq. (11) that a rare invader will benefit from continuing to increase its rate of reciprocation r' until the factor $(2-r)$, weighted by the probability of interaction w, equals the cost of cooperation, c. When r increases beyond the equilibrium point $2-c/w$, the factor $(2-r)$, weighted by the probability of interaction w, is less than the cost of cooperation, c, and thus increased generosity is not rewarded. The cooperative equilibrium point is therefore $r* = 2-c/w$, and $r* = c/w$ is an unstable equilibrium point.

The conditions that favor increased or decreased contributions also affect first contributions, since first contributions are essentially special cases of contributions in round $t=1$. Thus, for the reasons mentioned above, when $0 \leqslant r < c/w$ or $2-c/w < r \leqslant 2$, first contributions f tend toward 0, and when $c/w < r < 2-c/w$, first contributions tend toward 1 (see Appendix C for proof). Similarly, over the course of a series of interactions between two players, contributions will tend to either 0 or 1 under the same conditions as for first contributions.

Interestingly, the equilibrium points are unchanged by the addition of small exogenous error terms (i.e. $\varepsilon \ll f$) (see Appendix D for proof). As discussed above, among reflecting strategies, the net condition for increased rate of reciprocation requires that the benefit accrued on round $t+1$ from a small increase in generosity exceed the cost of initiating the small increase in generosity on round t. Small noise terms added to contributions (i.e. errors of implementation, rather than perception) appear both in the benefit on round $t+1$, and in the cost on round t, and hence are subtracted out of the net condition for increased rate of reciprocation. Thus, even if small exogenous error terms are biased negatively, the reciprocation rate r of a given population will still tend to converge on the equilibrium points $r* = 0$ or $r* = 2-c/w$. Of course, if the noise terms are symmetrical, they will also cancel out in the net condition for increased rate of reciprocation.

We studied the effects of convex cost functions by implementing a cost function of the form

$$c(x) = cx^n, \tag{12}$$

where $n>1$. Simulation results indicated that it was more difficult for cooperative strategies to destabilize the non-cooperative equilibrium, and more difficult for the cooperative equilibrium to be sustained against rare non-cooperative invaders. In Figs. 2 and 3, $\mathrm{d}W[r']/\mathrm{d}r'|_{r'=r}$ versus r' are plotted for $r'<1$, and $r'>1$, respectively, where W represents fitness of a rare invader with rate of reciprocation r', against a population with reciprocation rate r, for four different choices of convexity n. Fig. 2 illustrates that as n increases, it is more difficult for marginally cooperative invaders to destabilize a non-cooperative equilibrium. Likewise, Fig. 3 illustrates that as n increases, it is easier for non-cooperative invaders to destabilize a cooperative equilibrium.

2.4. Stability of non-cooperative ESS

The equilibrium behavior in the continuous and discrete IPDs are different in one crucial aspect. In both cases, both pure defection and contingent cooperation are attractors. In the discrete version, relatively low levels of assortative non-random pairing destabilize the non-cooperative equilibrium but not the cooperative (Axelrod and Hamilton, 1981), suggesting that contingent cooperation is the likely

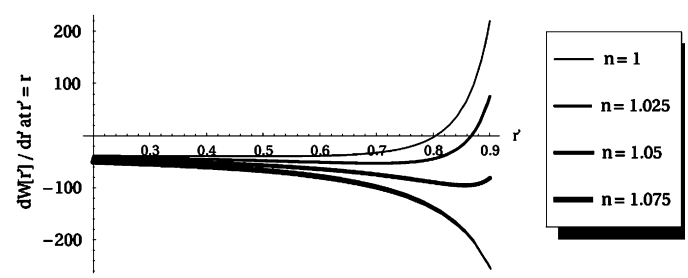

Fig. 2. $\mathrm{d}W[r']/\mathrm{d}r'$ plotted against r', for $r'<1$ and $r'=r$, for four different choices of convexity n. W represents fitness of a rare invader with rate of reciprocation r' in a population with rate of reciprocation r. As n increases, it is more difficult for marginally cooperative invaders to destabilize a non-cooperative equilibrium.

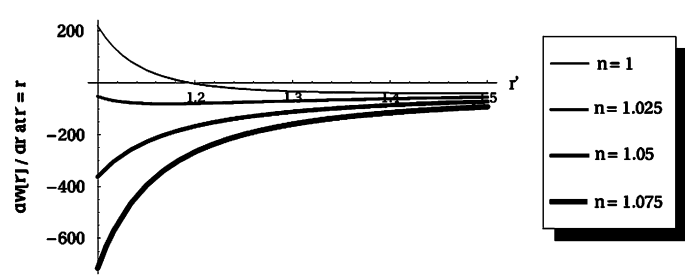

Fig. 3. $\mathrm{d}W[r']/\mathrm{d}r'$ plotted against r', for $r'>1$ and $r'=r$, for four different choices of convexity n. W represents fitness of a rare invader with rate of reciprocation r' in a population with rate of reciprocation r. As n increases, it is easier for non-cooperative invaders to destabilize a cooperative equilibrium.

Table 1
Degree of positive assortment required for successful invasion of rare generous types into a non-cooperative equilibrium in the continuous IPD and the discrete IPD for selected values of c, w, and r'

Parameters	c	0.8	0.5	0.5
	w	149/150	149/150	149/150
	r' of rare invader	0.01	0.01	0.1
Degree of positive assortment required for successful invasion of non-cooperative equilibrium:	Continuous IPD	0.798	0.498	0.474
	Discrete IPD	0.026	0.007	0.007

evolutionary outcome. This is not the case in the continuous game. Suppose that rare invaders have a probability p of being paired with their own type. Then, rare types with rate of reciprocation r' can invade a population in which most individuals have a rate of reciprocation equal to zero when

$$p > \frac{1 - wr'}{1/c - wr'} \tag{13}$$

(see Appendix B for derivation). Compare this to the degree of assortment required for invasion of rare TFT into ALLD in the discrete IPD,

$$p > \frac{1 - w}{1/c - w}. \tag{14}$$

The first inequality (13) approaches the second inequality (14) as r' approaches 1, but Eq (13) is much greater than Eq (14) for small values of r'. Table 1 compares the degree of positive assortment required for successful invasion by rare generous types into a non-cooperative equilibrium in the continuous IPD and the discrete IPD for selected values of c, w, and r' (of the rare invader):

In the continuous case, mutations which lead to only a modest increase in reciprocation require much more assortment to increase than do mutations which have a large effect. A higher degree of assortment is required to jumpstart cooperation in the continuous case than in the discrete case because cooperation diminishes geometrically at a rate wr'. Thus even if interactions go on a long time (so that w is near 1), cooperation only lasts a few time periods when r' is small. Since many situations in nature may correspond to continuous rather than discrete games, and mutations with small effects are often thought to be more likely than mutations with large effects, this fact may have important ramifications for studies of cooperation.

3. Evolutionary dynamics of mixed populations: simulation results

So far we have considered evolutionary dynamics in only simple ecologies. To explore the dynamics of more complex ecologies, we used computer simulations. The simulations utilized a single-locus infinite alleles model (Kimura and Crow, 1964). A population of 8000 unit-memory reflecting strategies, with initial reciprocation rate set at the cooperative equilibrium, $r \approx 2 - c/w$ or 1.2, were randomly paired off, and played continuous iterated prisoner's dilemma games with a probability of termination in each round of $w = 149/150$, yielding an expected game length of $1/(1-w)$ or 150 rounds. The next generation $g+1$ of strategies acquired reciprocation rates by selecting strategies from the previous generation with a probability proportional to the payoffs achieved by the parent strategies in generation g. The reciprocation rates of the offspring in generation $g+1$ were then summed with a Gaussian mutation term with standard deviation s. Resampling was applied to offspring strategies whose reciprocation rates were less than 0 or greater than 2. The cost of cooperation was set at $c = 0.8$, and the simulations were run for 3000 generations.

From this simulation (see Appendix E for detailed results) it was observed that four distinct dynamical outcomes were associated with the mutation parameter s: stable cooperation, cyclical polymorphisms, collapse from the cooperative equilibrium to the uncooperative ESS, and stable polymorphisms. The relationship between s and the dynamical outcomes are summarized in Table 2.

Fig. 4 presents simulation results demonstrating the four ecological types (note that in the case of collapse to the uncooperative ESS, mutation maintains a small non-zero mean that is not perceptible on the scale of this graph).

In order to analyse the evolutionary pathways that lead to these ecological types, we constructed payoff maps (see Figs. 5 through 7). For purposes of illustration, the payoff maps are inset into larger graphs that plot the mean reciprocation rate of the population against generation time, or g. The payoff maps plot expected payoff W of an invading strategy with reciprocation rate r' against a distribution of reciprocation rates for specific choices of g. Reciprocation rate distributions were obtained by sampling 100 individuals from the simulation populations, where $n = 8000$.

As noted in Table 2, simulations with these parameter settings indicate that the cooperative equilibrium is stable when s, the standard deviation of the Gaussian mutation parameter, is in the range [0.002, 0.004].

Table 2
Summary of dynamical outcomes in simulation of continous prisoner's dilemma, with the Gaussian mutation parameter standard deviation s varying from 0.002 to 0.070

Gaussian mutation parameter s, standard deviation	Dynamical outcome
0.002–0.004	Stable cooperation
0.006–0.032	Cyclical polymorphism
0.034–0.058	Collapse to non-cooperative equilibrium
0.060–0.070	Stable polymorphisms

Number of generations $g = 3000$; population size $n = 8000$; cost of cooperation $c = 0.8$; conditional probability of continued interaction $w = 149/150$; and initial $r = 2-c/w \approx 1.2$. Offspring strategies in generation $g+1$ acquired strategies from generation g with a probability proportional to the payoffs achieved by the parent strategies in generation g; the reciprocation rates of the offspring in generation $g+1$ were then summed with a Gaussian mutation term s. For each choice of s, 3 iterations were conducted, except for s in the range [0.028, 0.038], for which 10 iterations were conducted for each choice of s, in order to attain better resolution of transition points.

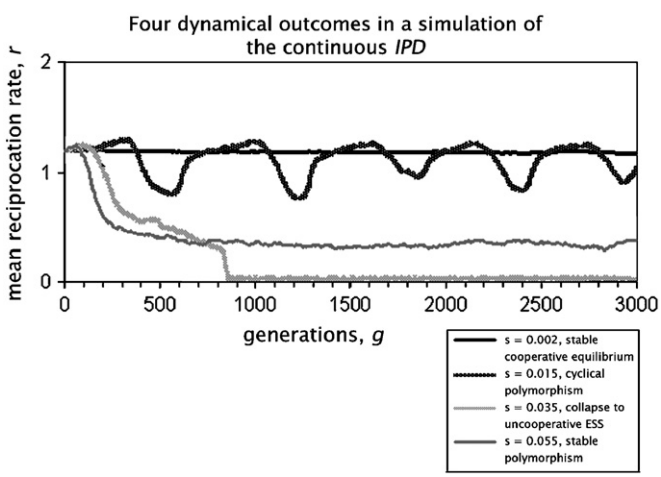

Fig. 4. Continuous *IPD* simulation results of four levels of Gaussian mutation rates, $s = 0.002$, 0.015, 0.035, 0.055. Other parameters: $g = 3000$ generations; population size $n = 10{,}000$; cost of cooperation $c = 0.8$; conditional probability of continued interaction $w = 149/150$; initial $r = 2-c/w \approx 1.2$.

3.1. An example of a cyclical polymorphism of reciprocation types

For mutation standard deviation s in the range [0.006, 0.032], the evolutionary dynamic generally follows a pattern of cyclical polymorphisms, as illustrated in Fig. 5.

The initial population mean reciprocation rate was set at $r^* = 2-c/w \approx 1.2$. After a period of drift, by $g = 300$ the payoff gradient favors strategies with r' less than the mean reciprocation rate (see left inset graph in Fig. 5). Note that the mutation rate parameter standard deviation s permits a proportion of offspring with reciprocation rates less than 1 to come into existence. These types are able to proliferate due to the high payoffs

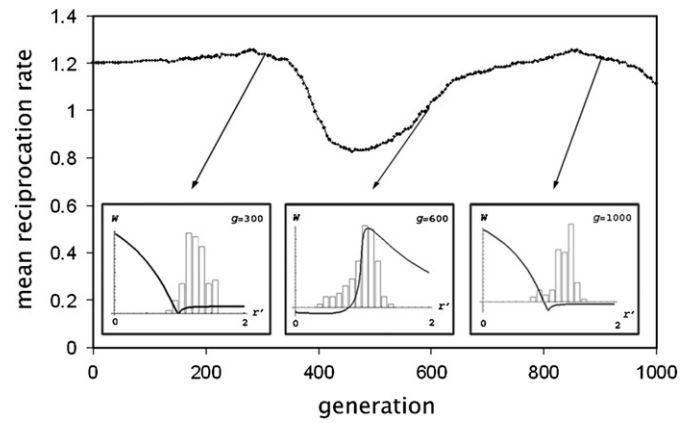

Fig. 5. Simulation illustrating cyclical polymorphisms in a continuous prisoner's dilemma. Gaussian mutation standard deviation $s = 0.015$. Number of generations = 3000, population size $n = 8000$, cost of cooperation $c = 0.8$, conditional probability of continued interaction $w = 149/150$, and initial $r = 2-c/w \approx 1.2$. The main graph plots mean reciprocation rate of the population over generation time g. Inset graphs plot payoff W (bold line) against reciprocation rate r' of a hypothetical invader for a sampled distribution (100 individuals sampled from a population of 8000; represented by bar graph plots) of reciprocation types at $g = 300$ (left inset), $g = 600$ (center inset), and $g = 900$ (right inset).

available to strategies with reciprocation rates less than 1 at $g = 300$.

Between $g = 300$ and 500, the population mean reciprocation rate continues to drop (Fig. 5). After the mean reciprocation rate nears c/w or 0.805, however, the payoff structure switches to favor increasing reciprocation (see middle inset graph in Fig. 5). Thus, the population mean reciprocation rate oscillates around the equilibrium point $r^* = 2-c/w$ or 1.2. This is expected, since, as mentioned in Section 2.2, the equilibrium point $r^* = 2-c/w$ is an attractor with domain of attraction (c/w, 2]. On the other hand, if the mutation rate standard deviation s were sufficiently large, we expect that the population would proceed beyond the domain of attraction of the cooperative equilibrium, causing the entire population to collapse to the non-cooperative equilibrium; this is the case discussed next, in Section 3.2.

3.2. An example of collapse to the non-cooperative equilibrium

For Gaussian mutation standard deviation s in the range [0.034, 0.050], the evolutionary dynamic tends to collapse to the non-cooperative equilibrium, as illustrated in Fig. 6.

As in the previous example in Section 3.1, after starting off at the cooperative equilibrium, the mean population reciprocation rate goes through an initial period of drift, and then the payoff gradient favors decreased reciprocation rates (bold line in left inset graph in Fig. 6). However, the mutation parameter standard deviation s is now sufficiently large to allow a substantial proportion of offspring with reciprocation rates less than c/w to enter the population (see bar graph in left inset graph in Fig. 6); as

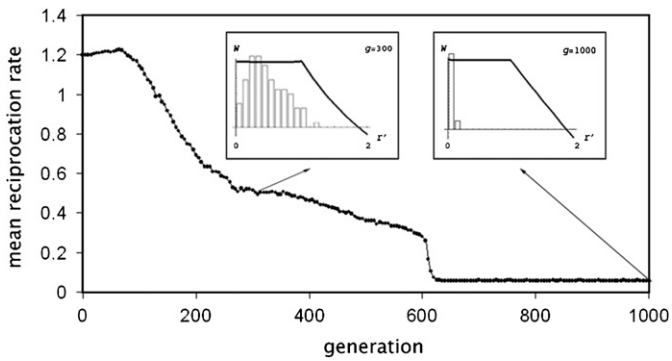

Fig. 6. Simulation illustrating collapse to the non-cooperative equilibrium in the continuous prisoner's dilemma. Gaussian mutation standard deviation $s = 0.045$. Number of generations = 1000, population size $n = 8000$, cost of cooperation $c = 0.8$, conditional probability of continued interaction $w = 149/150$, and initial $r = 2-c/w \approx 1.2$. The main graph plots mean reciprocation rate of the population over generation time g. Inset graphs plot payoff W (bold line) against reciprocation rate r' of a hypothetical invader for a sampled distribution (100 individuals sampled from a population of 8,000; represented by bar graph plots) of reciprocation types at $g = 300$ (left inset) and $g = 1000$ (right inset).

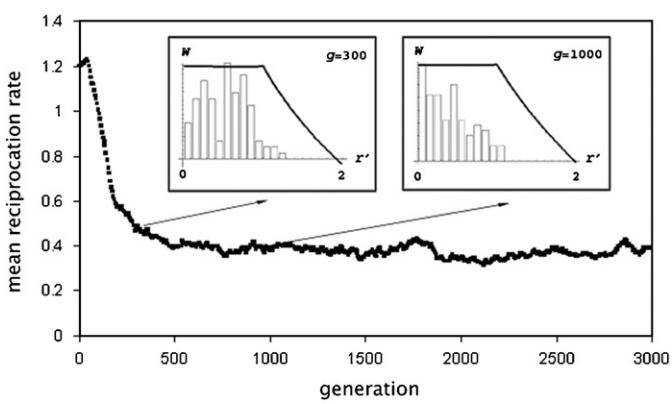

Fig. 7. Simulation illustrating stable polymorphisms in the continuous prisoner's dilemma. Gaussian mutation standard deviation $s = 0.065$. Number of generations $g = 3000$, population size $n = 8000$, cost of cooperation $c = 0.8$, conditional probability of continued interaction $w = 149/150$, and initial $r = 2-c/w \approx 1.2$. The main graph plots mean reciprocation rate of the population over generation time g. Inset graphs plot payoff W (bold line) against reciprocation rate r' of a hypothetical invader for a sampled distribution (100 individuals sampled from a population of 8000; represented by bar graph plots) of reciprocation types at $g = 300$ (left inset) and $g = 1000$ (right inset).

explained in Section 2.2, the non-cooperative equilibrium point $r^* = 0$ is an attractor with domain of attraction $[0, c/w)$. The population is thus driven toward the non-cooperative equilibrium (right inset graph in Fig. 6). The mean reciprocation rate around the non-cooperative equilibrium is non-zero due to constant mutation.

3.3. An example of a stable polymorphism of reciprocation types

Finally, at sufficiently high mutation rates ($s \geqslant 0.060$), a stable polymorphism of cooperative and non-cooperative types is maintained in the population. As in the previous Section 3.2, after starting out approximately at the cooperative equilibrium $r^* = 2-c/w$ or 1.2, the mutation parameter allows offspring with reciprocation rates less than c/w to enter the population, driving the population toward the non-cooperative equilibrium $r* = 0$ (Fig. 7, left inset graph). Unlike the previous case, though, the mutation rate here is large enough to maintain a spectrum of reciprocation types via mutation-selection balance (Fig. 7, right inset graph). In addition, there is a small payoff maximum at $r' = 1$, which enables a limited degree of disruptive selection (Fig. 7, right inset graph).

4. Discussion

4.1. Wahl and Nowak's continuous IPD model

Wahl and Nowak (1999a,b) considered a version of the continuous IPD with strategies of the form $y = kx + d$. They used computer simulations to show that cooperative strategies that apparently resisted invasion were optimistic (made high initial offers of x_o), generous (offered more cooperation than the partner did in the previous round) and uncompromising (offered full cooperation only if the partner did).

The model used here has only parameters, f, the first contribution, and r, the rate of reciprocation, but it employs a more complex piece-wise linear functional form. We believe that this formalization is useful because it represents a continuum of strategy types ranging from complete stinginess ($r = 0$) through balanced reciprocity ($r = 1$) to complete generosity ($r = 2$) with a single parameter. In our view, the piece-wise linear form, though somewhat more complicated mathematically than a single linear response rule, is conceptually simple due to its symmetry, with the response for $r \geqslant 1$ being a mirror image of the response rule for $r < 1$. Instead of reflecting back the amount received in the previous round, generous strategies reflect back the remaining difference between the amount received in the previous round and the maximum contribution. The analytical simplicity gained in our model allows us to make conclusions that are applicable to Wahl and Nowak's model.

In comparing the general instability of the reflecting strategy continuous IPD with the general instability of the discrete IPD, in the case of the discrete IPD, TFT is susceptible to invasion by strategies that perform identically against TFT (such as TF2T), but which have characteristics that distinguish their behavior in other ecologies. Similarly, in the reflecting strategy continuous IPD, uncooperative strategies perform identically against the cooperative equilibrium strategy, but are unmasked in other ecologies.

Wahl and Nowak (1999b) found that cooperation in the continuous IPD with noise was evolutionarily unstable: cooperative strategies were prone to invasion by more cooperative strategies, which in turn were invaded by

defectors. The manner in which Wahl and Nowak model noise is different from our method. Wahl and Nowak consider errors of perception, while we consider errors of implementation. Note that the definitions of perception and implementation errors employed here are different from the definitions employed in models of indirect reciprocity (e.g. Panchanathan and Boyd, 2004). In the simple model presented here, strategies have no capacity to deal with 'knowledge' of their own errors. Thus, errors of perception as defined in the case of indirect reciprocity are not applicable this model. Nonetheless, the overall pattern of our model matches the finding obtained by Wahl and Nowak: namely, the cooperative equilibrium is susceptible to uncooperative strategies that drift in. Our computer simulation indicates that, in single-locus infinite alleles Gaussian mutation models, if the population is destabilized from the cooperative equilibrium, it will then settle into a range of dynamical outcomes, depending on the mutation rate.

4.2. Bendor, Kramer, and Stout's tournament

In Bendor et al.'s (1991) noisy continuous IPD tournament, they found that the most successful strategies were those that were generous, where generosity was defined as $V(TFT|x)-V(x|TFT)$; i.e., a strategy x was deemed generous if x did worse against TFT than TFT playing against x (Bendor et al., 1991, p. 701). While Bendor, Kramer, and Stout's explanation was that generous strategies avoided spiraling into rounds of mutual recrimination in noisy environments (Bendor et al., 1991, p. 706), the preceding analysis suggests that another role of generosity in the noisy continuous IPD is to ramp up contributions to the most efficient level. Moreover, this is true even for continuous IPDs in noise-free environments. Nonetheless, noise may still corrode cooperation for strategies that are sensitive to contribution thresholds, and generosity in perception and implementation may help counteract this tendency, as Bendor, Kramer, and Stout asserted.

4.3. Cooperative dilemmas in nature

The prominence of the discrete IPD in the social and biological sciences has resulted in much focus on reciprocity. However, to date, few examples of reciprocal altruism have been documented among non-primates (Dugatkin, 1997; Hammerstein, 2003). Our analysis of the continuous IPD suggests that two important factors may contribute to the scarcity of solutions to cooperative dilemmas in nature. First, generous invaders are typically neither sufficiently numerous nor sufficiently cooperative to overcome the costs of cooperation. Jumpstarting generosity is easier in the discrete IPD model, but the discrete model applies only to situations with a sharp dichotomy between cooperation and defection. These types of situations are likely to be rare in nature. It is normally held that selection gives rise to complex behavioral adaptations in small steps. The discrete model only permits drastic mutations from an uncooperative to a fully cooperative state. This continuous model suggests that small amounts of cooperation lead to the rapid decay of cooperation, and thus even a large degree of assortment will not be sufficient to allow cooperation to increase when rare.

Second, the generous equilibrium itself is potentially unstable. Depending on the magnitude of the mutation parameter variance, the system is driven to one of four dynamic states: stable cooperation; cyclical polymorphisms; collapse into the non-cooperative equilibrium; or stable polymorphisms maintained principally via mutation-selection balance, and to a lesser degree via disruptive selection.

Mutation has two competing effects. Increasing the mutation rate can allow highly cooperative types to invade a non-cooperative population. However, high mutation rates also encourage the re-invasion of the cooperative equilibrium by non-cooperative types.

Despite the differences in parameterization, the qualitative aspects of our model agree broadly with those of Wahl and Nowak's (1999a) model. We concur that the evolution of cooperation in the continuous IPD is dependent to a large degree on the cost/benefit ratio. We also observe that the mutation rate presents a further wrinkle to the evolution of cooperation. Finally, as the dynamics of this model are sensitive to the choice of parameterization, models of greater generality may help test the validity of the conclusions in this paper.

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Appendix A. Relative payoffs of all possible pairings of strategy types

Let A denote a player with level of reciprocation r', $0 \leqslant r' < 1$, and let B denote a player with level of reciprocation r, $0 \leqslant r < 1$. We wish to show that

$$V(A|B) - V(B|B) = \frac{fw(r-r')(c-wr)}{(1-w^2r'r)(1-wr)}. \tag{A.1.}$$

A and B receive the following contributions:

Round	B's contribution to A	A's contribution to B
1	f	f
2	fr	fr'
3	$fr'r$	frr'
4	fr^2r'	fr'^2r
…	…	…

Weighting each player's contribution each round by a factor of w, and summing to infinity, we obtain

$$V(A|B) = \frac{f((1-c)+w(r-cr'))}{1-w^2r'r}. \quad \text{(A.2.)}$$

Using Eq. (A.2.), we can derive $V(B|B)$, and thus obtain

$$V(A|B) - V(B|B) = \frac{fw(r-r')(c-wr)}{(1-w^2r'r)(1-wr)}, \quad \text{(A.3.)}$$

as desired. Eq. (A.3.) yields the unstable equilibrium point $r^* = c/w$.

The proofs for the other three cases ($r'>1$ and $r<1$, etc.) follow similarly, and are left to the reader.

Appendix B. Degree of positive assortment required for invasion of non-cooperative population by rare marginally generous strategies

Consider two strategies: R, with reciprocation rate $r = 0$, and S, with reciprocation rate $r = \delta$, where δ is small. Let the first contribution be f for both strategies.

$$V(R|R) = f - cf = (1-c)f \quad \text{(B.1.)}$$

$$V(S|R) = f - cf - w\delta fc \quad \text{(B.2.)}$$

$$V(S|S) = f(1-c)/(1-w\delta) \quad \text{(B.3.)}$$

S invades when

$$pV(S|S) + (1-p)V(S|R) > V(R|R). \quad \text{(B.4.)}$$

Substituting Eq. (B.1.), (B.2.), and (B.3.) into (B.4.) yields

$$p > \frac{1-w\delta}{1/c - w\delta}$$

as the required degree of positive assortment for invasion of a non-cooperative population by a marginally generous invader.

Appendix C. First contributions tend toward either 0 or 1

Let A denote a player with first contribution f_1, and let B denote a player with first contribution f_2. The rate of reciprocation for both players is $r<1$. We wish to show that f evolves toward either 0 or 1, depending on r.

A and B receive the following contributions:

Round	B's contribution to A	A's contribution to B
1	f_2	f_1
2	f_1r	f_2r
3	f_2r^2	f_1r^2
…	…	…

Weighting each player's contributions each round by a factor of w, and summing to infinity, we obtain

$$V(A|B) = \frac{f_2(1-cwr+wr-c)}{1-(wr)^2}. \quad \text{(C.1.)}$$

Using Eq. (C.1.), we can derive $V(B|B)$, and thus obtain

$$V(A|B) - V(B|B) = \frac{(f_1-f_2)(wr-c)}{1-(wr)^2} \quad \text{(C.2.)}$$

which is positive if $f_1>f_2$ and $r>c/w$, or $f_1<f_2$ and $r<c/w$.

Similarly, for $r>1$,

$$V(A|B) - V(B|B) = \frac{(f_1-f_2)(w(2-r)-c)}{1-(w(2-r))^2}. \quad \text{(C.3.)}$$

Thus, combining Eqs. (C.2.) and (C.3.)., when $r<c/w$ or $r>2-c/w$, first contributions f will tend toward 0, and when $c/w<r<2-c/w$, first contributions will tend toward 1.

Appendix D. Small noise terms ($\varepsilon << f$) do not affect the equilibria

Let A denote a player with first contribution $f+\varepsilon$ and reciprocation level r', where ε is a small exogenous implementation error term, and let B denote a player with first contribution f and reciprocation level r. We wish to show that the addition of ε to A's first move will not affect the equilibrium point $r^* = c/w$.

A and B receive the following contributions:

Round	B's contribution to A	A's contribution to B
1	f	$f+\varepsilon$
2	$(f+\varepsilon)r$	fr'
3	$fr'r$	$(f+\varepsilon)r'r$
…	…	…

Weighting each player's contributions each round by a factor of w, and summing to infinity, we obtain

$$V(A|B) - V(B|B) = \frac{(wr-c)(\varepsilon + w(f(r'-r)-\varepsilon r))}{(1-w^2r'r)(1-wr)}. \quad \text{(D.1.)}$$

If $\varepsilon \ll f$, then $r<c/w$, and $r'>r \Rightarrow V(A|B)-V(B|B)<0$. Thus the overall evolutionary dynamics remain unchanged by the addition of an exogenous error term. The equilibrium point $r^* = c/w$ remains unchanged.

The proof for the other case ($r^* = 2-c/w$) follows similarly, and is left to the interested reader.

Appendix E. Dynamical outcomes in a continuous prisoner's dilemma simulation with varying s (standard deviation of the Gaussian mutation parameter)

Table 3 lists the results of simulations of the continuous prisoner's dilemma, with the Gaussian mutation parameter standard deviation s varying from 0.002 to 0.070. This

Table 3
Dynamical outcomes in a continuous prisoner's dilemma simulation with varying s (standard deviation of Gaussian mutation parameter)

Gaussian mutation parameter s, standard deviation	Results from three iterations (except * results, which were run for 10 iterations)
0.002	Stable cooperation (SC)
0.004	SC
0.006	Cyclical polymorphism (CP)
0.008	CP
0.010	CP
0.012	CP
0.014	CP
0.016	CP
0.018	CP
0.020	CP
0.022	CP
0.024	CP
0.026	CP
0.028	*CP × 7 Collapse to non-cooperative ESS (CO) × 3
0.030	*CP × 9, CO × 1
0.032	*CP × 6, CO × 4
0.034	*CO × 4, CP × 6
0.036	*CO × 3, CP × 7
0.038	*CO
0.040	CO
0.042	CO
0.044	CO
0.046	CO
0.048	CO
0.050	CO
0.052	CO
0.054	CO
0.056	CO
0.058	CO × 2 stable polymorphism (SP) × 1
0.060	SP
0.062	SP
0.064	SP
0.066	SP
0.068	SP
0.070	SP

SC indicates stable cooperation; CP indicates cyclical polymorphism; CO indicates collapse to non-cooperative equilibrium; SP indicates stable polymorphism. Number of generations $g = 3000$; population size $n = 8000$; cost of cooperation $c = 0.8$; conditional probability of continued interaction $w = 149/150$; and initial $r = 2-c/w \approx 1.2$. Offspring strategies in generation $g+1$ acquired strategies from generation g with a probability proportional to the payoffs achieved by the parent strategies in generation g; the reciprocation rates of the offspring in generation $g+1$ were then summed with s. For each choice of s, 3 iterations were conducted, except for s in the range [0.028, 0.038], for which 10 iterations were conducted for each choice of s.

table shows that four basic dynamical outcomes resulted: stable cooperation; cyclical polymorphisms; collapse to non-cooperative equilibrium; and finally, stable polymorphisms. Parameters were as follows: number of generations $g = 3000$; population size $n = 8000$; cost of cooperation $c = 0.8$; conditional probability of continued interaction $w = 149/150$; and initial $r = 2-c/w \approx 1.2$. Offspring strategies in generation $g+1$ acquired strategies from generation g with a probability proportional to the payoffs achieved by the parent strategies in generation g; the reciprocation rates of the offspring in generation $g+1$ were then summed with a Gaussian mutation term s. For each choice of s, 3 iterations were conducted, except for s in the range [0.028, 0.038], for which 10 iterations were conducted for each choice of s, in order to attain better resolution of transition points.

References

Axelrod, R., Hamilton, W.D., 1981. The Evolution of Cooperation. Science, New Series 211 (4489), 1390–1396.

Bendor, J., Kramer, R.M., Stout, S., 1991. When in Doubt… cooperation in a noisy Prisoner's dilemma. J. Conflict Resol. 35 (4), 691–719.

Dugatkin, L.A., 1997. Cooperation Among Animals: An Evolutionary Perspective. New York, Oxford University Press.

Hamilton, W.D., 1964. The genetical evolution of social behaviour I and II. J. Theor. Biol. 7, 1–16.

Hammerstein, P., 2003. Why is reciprocity so rare in social animals? A protestant appeal. In: Peter, H. (Ed.), Genetic and Cultural Evolution of Cooperation. MIT Press, Cambridge, MA, pp. 83–94.

Lehmann, L., Keller, L., 2006. The evolution of cooperation and altruism. A general framework and a classification of models. J. Evol. Biol. 19, 1365–1376.

Killingback, T., Doebeli, M., 2002. The continuous Prisoner's dilemma and the evolution of cooperation through reciprocal altruism with variable investment. Am. Nat. 160 (4), 421–438.

Kimura, M., Crow, J., 1964. The number of alleles that can be maintained in a finite population. Genetics 49, 725–738.

Panchanathan, K., Boyd, R., 2004. Indirect reciprocity can stabilize cooperation without the second-order free rider problem. Nature 432, 499–502.

Wahl, L.M., Nowak, M.A., 1999a. The continuous Prisoner's dilemma: I. linear reactive strategies. J. Theor. Biol. 200, 307–321.

Wahl, L.M., Nowak, M.A., 1999b. The continuous Prisoner's dilemma: II. linear reactive strategies with noise. J. Theor. Biol. 200, 323–338.