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Evolution of stinginess and generosity in finite populations

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ABSTRACT

In iterated continuous games, the cooperative investment in a given round is determined by the initial investment and the reciprocation rate, which describe the investment in the first round and the dependence of current investment on the partner's last move, respectively. These two traits usually intertwine during evolution. However, their coevolution is not fully explored. In this paper, we thereby study their coevolution in the iterated continuous public goods games. We find that the reciprocation rate plays a dominant role during the coevolution in both finite and infinite populations. If it exceeds a threshold, a stingy population where individuals invest no more than their partner's last investment evolves to full cooperation, and a generous population where individuals invest more than their partner's last investment decreases to a moderate cooperative state, investing a portion in the first round and then escalating investment in the following rounds. Otherwise, the stingy population evolves to full defection, and the generous one rises to another moderate cooperative state.

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1. Introduction

Cooperation is ubiquitous in the real world. In biological systems, cells cooperate with each other in multicellular organisms. In human society, people cooperate to formulate and run various social organizations (Buss, 1987; Dugatkin, 1997; Eigen and Schuster, 1979; Michod, 1983; Smith and Szathmáry, 1995). However, cooperative behavior can not emerge naturally, since noncooperative individuals, who gain the benefit without the cost of cooperative acts, have higher fitness and thus are favored by natural selection. What leads to the ubiquitousness of cooperation? Nowak (2006) suggested five mechanisms for the evolution of cooperation. As one of the five mechanisms, direct reciprocity, describing the same individuals play a game repeatedly, can establish cooperation among unrelated individuals (André, 2015). It is easy to discover this mechanism in real systems, for example, impalas groom each other (Hart and Hart, 1992; Mooring and Hart, 1992).

Iterated games provide a game theoretic framework for studying the evolution of cooperation through direct reciprocity. In iterated discrete games, individuals have only two possible strategies in each round: cooperation or defection (Fu et al., 2007; Imhof et al., 2005; Imhof and Nowak, 2010; Nowak et al., 2004; Press and Dyson, 2012; Stewart and Plotkin, 2013; 2014). However, coopera-

http://dx.doi.org/10.1016/j.jtbi.2017.03.022 0022-5193/© 2017 Elsevier Ltd. All rights reserved. tion is rarely all-or-nothing in the real world. There is considerable evidence that cooperative investment varies continuously within a certain range. For example, the duration of an allopreening bout for guillemots varies from under a second to over a minute (Roberts and Sherratt, 1998), where the gradually increasing duration means larger and larger amounts of investment. To better depict such situations, iterated continuous games with continuous investments, as natural extensions of the discrete ones, are proposed (Killingback and Doebeli, 2002; Killingback et al., 1999; Le and Boyd, 2007; Roberts and Sherratt, 1998; Takezawa and Price, 2010; Wahl and Nowak, 1999). In iterated continuous games, the amount of contribution in a given round is determined by the initial investment, meaning the investment in the first round, and the reciprocation rate, describing the relation between individuals' investments in two successive rounds. These two traits usually intertwine during the evolution. However, their coevolution is not fully explored. Here, we are aiming to study the coevolution of the initial investment and the reciprocation rate through the iterated two-player continuous public goods game (PGG), in which two players equally share the benefit produced by their total investments and may bear different costs incurred by their own investments in each round (Archetti and Scheuring, 2011; Chen et al., 2012; 2015; Hauert et al., 2006a; Perc et al., 2013; Wu et al., 2014).

In iterated continuous games, strategies stipulate investments in every round. Various strategies have been proposed, such as the "raise-the-stakes" strategy (a player invests a little in the first round and then raises investment with partners that have matched



Journal of Theoretical Biology

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or bettered its last move) (Roberts and Sherratt, 1998), the payoffbased strategy (the investment of a player depends on its own payoff in the last round) (Doebeli and Knowlton, 1998; Killingback and Doebeli, 2002), the autocratic strategy (a player can enforce a unilateral claim to an unfair share of rewards from the partner) (McAvoy and Hauert, 2016; Press and Dyson, 2012), and the reactive strategy (the investment of a player depends on its partner's strategy in the last round) (Nowak and Sigmund, 1990). Specifically, it has been showed that the most successful linear reactive strategies (i.e., the current investment is linearly related to the partner's last investment) invest all in the first round, and then offer more than their partner's last investment, but cooperate fully only if their partner does the same (Wahl and Nowak, 1999). Moreover, Le and Boyd (2007) have proposed a class of piecewise strategies which is constituted by two linear reactive strategies. One of them is the stingy strategy (a player invests no more than what the partner invested in the last round), and the other one is the generous strategy (a player offers more than the partner's last investment). The piecewise functional form ensures that investments always vary within a reasonable range. Moreover, as their names suggest, two typical kinds of investment behavior, stinginess and generosity, can be well characterized by this class of strategies. In this paper, we focus on the stingy and generous strategies proposed by Le and Boyd (2007). However, in contrast to their study, which has only studied the evolution of reciprocation rate and the evolution of initial investment separately, we now analyze the coevolution of these two traits.

Population size usually has a vital effect on evolutionary game dynamics. For iterated discrete games, cooperators are favored by natural selection to replace defectors in finite populations, which does not hold in infinite populations (Imhof et al., 2005; Nowak et al., 2004). Does population size influence evolutionary dynamics for iterated continuous games? Iterated continuous games in infinite populations have been widely studied. However, the corresponding analysis in finite populations has attracted much less attention (André and Day, 2007; Imhof and Nowak, 2010). Motivated by this, we study the evolutionary dynamics of iterated continuous games in both finite and infinite populations. We find that for linear production and remaining functions, the dynamics in finite populations coincides with that in infinite populations. However, when nonlinear production and remaining functions are used, the discrepancy between them arises.

In this paper, we first investigate the evolution of the initial investment and that of the reciprocation rate given that the other

2. Model

In a well-mixed population of size *N*, any two individuals play the iterated continuous PGG. The next round of game occurs with probability w, $0 \le w \le 1$. The case of w = 0 is the one-shot game, and w = 1 means that individuals will interact infinite rounds. In each round, both individuals are endowed with the same available resource (1 for simplicity), and they invest some of their endowments into a public pool simultaneously. The investment, which takes any value between 0 and 1, is determined by two continuous traits: the initial investment $p \in [0, 1]$ and the reciprocation rate $r \in [0, 2]$. Here, p denotes the amount of investment in the first round, and r quantifies the dependence of an individual's current investment m_k (without loss of generality, we set the present moment as the *k*th round, where k > 1) on its partner's investment in the immediately previous round m'_{k-1} .

A strategy pair (p, r) stipulates the investment in every round. Here, the stingy strategies $S_{p,r}$ with $0 \le r \le 1$ and the generous strategies $G_{p,r}$ with $1 < r \le 2$ are considered. An individual using $S_{p,r}$ invests p in the first round, and then its investment is r times what its partner invested in the previous round, i.e., $m_k = rm'_{k-1}$. When two stingy individuals with $0 \le r < 1$ play against each other, one's investment is always less than the other one's last investment, and their investments non-monotonically decrease to zero as $k \to \infty$. When two stingy individuals with r = 1 play against each other, their investments alternate between their initial investments. It is worth mentioning that $S_{p,1}$ can be viewed as the continuous TFT, and $S_{0,0}$ is identical with ALLD. An individual using $G_{p,r}$ invests p in the first round, and then it invests $(r-1)(1-m'_{k-1})$ more than its partner's last investment, i.e., $m_k =$ $m'_{k-1} + (r-1)(1-m'_{k-1})$. When two generous individuals play the iterated continuous PGG, their investments non-monotonically increase to one as $k \to \infty$. Here, $G_{1,2}$ is identical with ALLC.

The payoff of an individual is accumulated over all rounds. In every round, two individuals get the same public goods. The amount of public goods each individual gets is specified by the production function $g(\bar{m})$, which is an increasing function of the average of two individuals' investments \bar{m} and satisfies g(0) = 0. Besides the public goods, the remaining endowment (the initial endowment 1 minus the cost incurred by the investment) is the other part of an individual's payoff. It is specified by the remaining function h(m) which is a decreasing function of the individual's investment m and meets h(0) = 1 and h(1) = 0. Here, P_{xy} , which denotes the expected payoff for an individual with strategy x playing against an individual with strategy y, is given by

$$P_{xy} = \begin{cases} \sum_{t=0}^{\infty} \left(w^{2t} \left(g \left((rr')^{t} \frac{p+p'}{2} \right) + h (r^{t}r'^{t}p) \right) + w^{2t+1} \left(g \left((rr')^{t} \frac{r'p+rp'}{2} \right) + h (r^{t+1}r'^{t}p') \right) \right), & x = S_{p,r}, \ y = S_{p',r'}; \\ \sum_{t=0}^{\infty} \left(w^{2t} \left(g \left((2-r)^{t} \left(2-r' \right)^{t} \frac{(p-1)+(p'-1)}{2} \right) + h \left((2-r)^{t} \left(2-r' \right)^{t} (p-1) + 1 \right) \right) \right) \\ + w^{2t+1} \left(g \left((2-r)^{t} \left(2-r' \right)^{t} \frac{(2-r')(p-1)+(2-r)(p'-1)}{2} \right) + h \left((2-r)^{t+1} \left(2-r' \right)^{t} (p'-1) + 1 \right) \right) \right), x = G_{p,r}, \ y = G_{p',r'}. \end{cases}$$

$$(1)$$

trait is fixed. Then, their coevolution is studied. We find that the reciprocation rate plays a dominant role during the coevolution. For stingy strategies, if it exceeds a threshold value at the start of evolution, the initial investment and the reciprocation rate increase, and the population evolves to full cooperation, investing all throughout all rounds; otherwise, both of them decrease, and the population evolves to full defection, investing nothing in every round. Whereas for generous strategies, the reciprocation rate above (below) the threshold at the start leads to the decrease (increase) of these two traits. A generous population evolves to full cooperation, or moderate cooperation, investing a portion in the first round and then escalating investment in the following rounds.

3. Results

We use adaptive dynamics to analyze the evolution of the population strategy. Here, the population strategy is $x \in \{p, r, (p, r)\}$, meaning that all the individuals use strategy x, and a mutant with strategy y rarely appears in the population. We assume x and y are of the same type, i.e., they are both stingy or both generous. The adaptive dynamics of x in a finite population of size N is described by (see Appendix A for details):

$$\dot{x} = \frac{\partial}{\partial y}|_{y=x}\rho(y,x) = \frac{(N-1)\frac{\partial}{\partial y}|_{y=x}P_{yx} - \frac{\partial}{\partial y}|_{y=x}P_{xy}}{2NP_{xx}} = D(x), \qquad (2)$$

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