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Evolutionary dynamics of continuous strategy games on graphs and social networks under weak selection

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ABSTRACT

Understanding the emergence of cooperation among selfish individuals has been a long-standing puzzle, which has been studied by a variety of game models. Most previous studies presumed that interactions between individuals are discrete, but it seems unrealistic in real systems. Recently, there are increasing interests in studying game models with a continuous strategy space. Existing research work on continuous strategy games mainly focuses on well-mixed populations. Especially, little theoretical work has been conducted on their evolutionary dynamics in a structured population. In the previous work (Zhong et al., BioSystems, 2012), we showed that under strong selection, continuous and discrete strategies have significantly different equilibrium and game dynamics in spatially structured populations. In this paper, we further study evolutionary dynamics of continuous strategy games under weak selection in structured populations. By using the fixation probability based stochastic dynamics, we derive exact conditions of natural selection favoring cooperation for the death–birth updating scheme. We also present a network gain decomposition of the game equilibrium, which might provide a new view of the network reciprocity in a quantitative way. Finally, we make a detailed comparison between games using discrete and continuous strategies. As compared to the former, we find that for the latter (i) the same selection conditions are derived for the general 2×2 game; especially, the rule $b/c > k$ in a simplified Prisoner's Dilemma is valid as well; however, (ii) for a coordination game, interestingly, the risk-dominant strategy is disfavored. Numerical simulations have also been conducted to validate our results.

1. Introduction

Evolutionary game theory is the study of evolutionary dynamics whenever the fitness of an individual is not constant but depends on interactions with other individuals (Maynard Smith, 1982; Hofbauer and Sigmund, 1998; Nowak, 2006a). Many concepts of evolutionary game theory have their equivalent formulations in mathematical ecology (May, 1973; Hofbauer and Sigmund, 1998). When there is a small number of discrete strategies, the replicator dynamics provides a powerful framework for studying deterministic dynamics in infinitely large, well-mixed populations (Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998; Nowak and Sigmund, 2004). Evolutionary graph theory (Lieberman et al., 2005; Ohtsuki et al., 2006) explores evolutionary dynamics on general population structure or social networks. Especially, Ohtsuki et al. (2006) found a simple rule that specifies evolution of cooperation for 2×2 games on graphs: if the benefit-to-cost ratio of an altruistic act exceeds the average number of neighbors, $b/c > k$, then selection on graphs favors cooperators.In real systems, behavior (or traits in evolutionary ecology) can hardly be expected to have this dramatically discrete nature. Indeed there are considerable evidences that cooperative behavior in nature should be viewed as a continuous strategy, varying over some range, rather than a discrete one (Harrald and Fogel, 1996; Killingback and Doebeli, 2002). Recently, there are increasing interests in studying evolutionary dynamics of games with a continuous strategy space. The first studies on continuous strategy games considered the evolution of degrees of cooperation by interpolating payoffs between discrete outcomes of the Prisoner's Dilemma (PD) (Mar and St. Denis, 1994; Frean, 1996; Harrald and Fogel, 1996). The methods based on the concept of investment are then introduced (Roberts and Sherratt, 1998; Killingback and Doebeli, 2002). When the population is infinite and well-mixed, a widely used analytical method is adaptive dynamics (Hofbauer and Sigmund, 1990;

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Nowak and Sigmund, 1990; Dieckmann and Law, 1996; Metz et al., 1996), which provides tools for studying long-term evolution of continuous strategies in realistic ecological models; when the population is spatially structured, simulation-based methods are mainly used. It remains an open question to analytically study evolutionary dynamics of continuous strategy games on graphs.

In existing work, it has been proved that continuous and discrete strategies are the same in terms of evolutionary game dynamics in a single well-mixed infinite population under the condition that the payoff function of the former is a linear interpolation of the payoff matrix of the latter (Day and Taylor, 2003; Vincent and Cressman, 2000; Meszéna et al., 2001; McGill and Brown, 2007; Tanimoto, 2007). However, in Zhong et al. (2012), we found that under strong selection, continuous and discrete strategies have different equilibria and game dynamics in a well-mixed but finite population when the same payoff function is used. Moreover, in the spatially structured population, such differences become considerable large. By using a statistical test, it illustrated that continuous and discrete strategies are statistically significantly different in terms of the equilibrium. Therefore, it is necessary to pay much more attention to games defined by a continuous strategy.

In this paper, we further study the evolutionary dynamics of continuous strategy games on graphs under weak selection. By extending the fixation probability approach (Imhof and Nowak, 2010) to the structured population, we derive exact conditions for natural selection to favor cooperation. We also present a network gain decomposition to explain the network reciprocity from a quantitative viewpoint. Moreover, we discuss similarity and inconsistency between continuous and discrete strategy games both in theory and by simulation.

The rest of this paper is organized as follows: The next section describes the related work. Section 3 describes our model. Section 4 introduces the fixation probability based stochastic dynamics for continuous strategy games. Section 5 calculates the fixation probability using pair approximation and diffusion process. Section 6 gives the conditions of natural selection favoring cooperation and the network gain decomposition. The differences between continuous and discrete strategy games are presented in Section 7. The conclusions are drawn in Section 8.

2. Related work

2.1. Evolutionary dynamics in a discrete strategy space

There is always a population of individuals in evolutionary game theory. When the population is assumed to be infinitely large and well-mixed, evolutionary game dynamics can be studied through the replicator equation (Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998; Nowak and Sigmund, 2004). It describes a selection process: those individuals with higher fitness, identified with the payoff resulting from the game, have more offspring and thus their frequency in the population grows.

However, real populations are rarely well-mixed and have a finite number of individuals. To understand evolutionary dynamics in finite-sized populations, we need a stochastic approach (Schaffer, 1988; Kandori et al., 1993; Fogel et al., 1997; Fogel and Fogel, 2011). A vital quantity is the fixation probability that a mutant spreads through the whole population, having arisen from a single individual (Nowak et al., 2004; Taylor et al., 2004; Imhof et al., 2005).

It is of much interest in studying how population structures affect evolutionary dynamics. An evolutionary game with a spatial structure, regular lattices, was initiated by Nowak and May (1992). They showed that a spatial structure helps a cooperative behavior to appear. Evolutionary graph theory is an extension of spatial games to more general population structures and social networks (Lieberman et al., 2005; Ohtsuki et al., 2006; Santos et al., 2008; Fu et al., 2009). The individuals occupy the vertices of a graph, and the edges of a graph determine who interacts with whom. Ohtsuki et al. (2006) studied the evolution of cooperation on a large variety of graphs. They found that selection favors the evolution of cooperation if $b/c > k$, that is, the benefit-to-cost ratio of altruistic act has to exceed the (average) number of neighbors per individual. Furthermore, Tarnita et al. (2009) proved that for a large number of class of evolutionary games on structured populations with two strategies, the condition for a strategy to be selected for in the limit of weak selection could be described entirely by one, real-valued structure coefficient σ. Zhong et al. (2011) studied the coevolution dynamics of both individual strategies and the population structure in the snowdrift game with mixed strategies. They showed that cooperative behavior can be enhanced using a partner switching mechanism. More efforts to explore evolutionary dynamics in structured populations can be found in Nowak et al. (2010) and references therein.

2.2. Evolutionary dynamics in a continuous strategy space

An implicit limitation of traditional game models is that interactions are discrete: each individual can offer only two options, cooperation or defection. Such a discrete strategy seems unrealistic in the real world, since actual provisions might not be discrete but rather continuous. A common example is body size (McGill, 1998). On the assumption that the type of food consumed is proportionate to body size, coevolution of competition is often modeled by assuming the players (species) vary body size or some measure of body size as a strategy to escape competition, e.g. Anolis lizards (Roughgarden, 1974) or Geospiza finches (Grant, 1999). Body size is a continuous strategy since it can take on any value over some reasonable range. It has also found in the context of predator inspection in fish that different degrees of “cooperation” often occur (Dugatkin and Alfieri, 1991) and in the work on allogrooming in impala that the number of grooming bouts delivered varies substantially (Mooring and Hart, 1992; Hart and Hart, 1992).

Although game models in the continuous space seems to be a better model of many real-world situations, it has been subject to much less analysis. The first studies on this issue considered the evolution of degrees of cooperation by interpolating payoffs between discrete outcomes of the classical Prisoner’s Dilemma (PD) (Mar and St. Denis, 1994; Frean, 1996; Harrald and Fogel, 1996). The methods to model variable levels of cooperation are then introduced (Roberts and Sherratt, 1998; Wahl and Nowak, 1999a,b; Killingback and Doebeli, 2002). Roberts and Sherratt (1998) considered a “raise-the-stakes” strategy for the iterated PD and showed that it invades and is stable against a number of alternative strategies. Wahl and Nowak (1999a,b) examined a version of continuous PD, and concluded that cooperative strategies that resisted invasion had the characteristics of being optimistic, generous, and uncompromising. But cooperation in the continuous PD was found to be evolutionarily unstable. Based on the concept of investment, Killingback and Doebeli (2002) considered a model of linear payoff-based strategies in a continuous PD and found that cooperation can evolve as long as the initial set of strategies meet a threshold value of cooperativeness.

Spatial structures based on continuous cooperative investment has also been addressed (Doebeli and Knowlton, 1998; Killingback et al., 1999; Koella, 2000; Ifti et al., 2004; Jiménez et al., 2009). Doebeli and Knowlton (1998) demonstrated that interspecific mutualism could evolutionarily increase in the extent and frequency for iterated interspecific relationships that take place in spatially structured populations. Killingback et al. (1999) extended the work of Doebeli and Knowlton (1998) and considered a continuous PD on spatially structured populations. They showed that