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Discovering the effect of nonlocal payoff calculation on the stabilty of ESS: Spatial patterns of Hawk–Dove game in metapopulations

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ABSTRACT

The classical idea of evolutionarily stable strategy (ESS) modeling animal behavior does not involve any spatial dependence. We considered a spatial Hawk–Dove game played by animals in a patchy environment with wrap around boundaries. We posit that each site contains the same number of individuals. An evolution equation for analyzing the stability of the ESS is found as the mean dynamics of the classical frequency dependent Moran process coupled via migration and nonlocal payoff calculation in 1D and 2D habitats. The linear stability analysis of the model is performed and conditions to observe spatial patterns are investigated. For the nearest neighbor interactions (including von Neumann and Moore neighborhoods in 2D) we concluded that it is possible to destabilize the ESS of the game and observe pattern formation when the dispersal rate is small enough. We numerically investigate the spatial patterns arising from the replicator equations coupled via nearest neighbor payoff calculation and dispersal.

1. Introduction

Evolutionary game theory is a mathematically accessible way of describing different behavioral traits in a population each of which is associated with a pure strategy of the underlying game. The initial focus of evolutionary game theory was on the concept of evolutionarily stable strategies (ESS) which is used to enhance our understanding of the evolution of animal behavior by Maynard Smith (1974) and Maynard Smith and Price (1973). A strategy is defined to be an ESS if a small number of individuals playing a different strategy cannot invade a population playing it. An important question regarding ESS is if such a strategy is attainable. The study by Taylor and Jonker (1978) extended the realm of evolutionary game theory to include dynamics. In other words, they introduced the replicator equations relating the ESS concept with the equilibria of these equations (Hofbauer and Sigmund, 1998). Since then replicator equations are at the core of evolutionary game theory. This classical model describes the evolution of behavioral traits in an infinite population assuming that a given individual is equally likely to interact with any other. Key advances were made by relaxing some of the above mentioned assumptions. In particular, the inclusion of finite populations and spatial structure in evolutionary games have accelerated the progress of the theory.

Stochastic processes have been applied to model evolutionary game dynamics in finite populations (Taylor et al., 2004). There are a variety of microscopic rules describing the game dynamics in finite populations such as birth-death update, death-birth update or pairwise comparison rules (Ohtsuki et al., 2006). These update rules describes a class of Markov chains, transition probabilities of which are assumed to depend on frequencies of phenotypes and game parameters. For many of these processes, replicator equation is not only a limiting deterministic case (Traulsen et al., 2005) but also describes the mean dynamics of the underlying Markov chains.

Considering the fact that natural environments possess a spatial dimension, meaning that individuals have limited mobility and interact with their neighbors, led many scholars to incorporate this important property into the study of evolutionary games. To analyse the effect of spatial structure on evolutionary game dynamics different approaches have been taken in to account: numerical simulations of games on grids (see *e.g.* Nowak et al., 1994; Nowak and May, 1992; Nowak and Sigmund, 2000) or more generaly on graphs (Allen and Nowak, 2014; Szabó and Fath, 2007); and analytical studies of replicator-diffusion equations (see, for example, Ferriere et al., 2000; Hofbauer, 1998; Hofbauer et al., 1997; Hutson and Vickers, 1992). We would like to note that a similar partial differential equation is found as a hydrodynamical limit of the frequency dependent Moran process (Chalub and Souza, 2009). In addition, integro-differential replicator equations taking nonlocal payoff calculation into consideration were obtained as a meso-

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scopic limit of the structured individual based models (see e.g. Aydogmus et al., 2017; Hwang et al., 2013).

Here we let individuals play the Hawk-Dove game, originally developed by Maynard Smith and Price (1973), to describe certain scenarios in animal conflict modeling a contest over a shareable resource. There are two subtypes or morphs of one species with two strategies, Hawk and Dove. Both subtypes first display aggression. The Hawk escalates into a fight until it either wins or is injured (loses), whereas the Dove runs for safety if faced with major escalation. Unless faced with such escalation, the Dove attempts to share the resource.

Rather than taking the continuous space into account as in replicator-diffusion or integro differential equations, we consider a landscape ecology perspective and subdivide the environment into distinct but identical patches with periodic boundaries each of which contains a population of K individuals. We would like to note that stochastic population models considering a collection of patches on which a number of individuals lives were studied by Tilman and Kareiva (1997) and Arrigoni and Pugliese (2002). In evolutionary game theory literature, a similar approach was taken by Hauert and Imhof (2012) to study a finite population of individuals subdivided into demes with the assumption of *local interactions* meaning that individuals interact only with other members of the same deme.

In our dynamical setting we assume that a patch containing two subtypes of the same species is chosen randomly at each time step. Then an individual is drawn from this site with a probability depending on its fitness and replaces a randomly chosen individual from its natal site with probability $1-\mu$ or one of the neighboring sites. Such a process can be seen as a spatial coupling of frequency dependent Moran processes (Taylor et al., 2004) via dispersal. Hence μ identifies the dispersal probability of a newborn. The fitness calculation, on the other hand, has two major components. The first one is the payoff calculation and the other is related to determining the effect of payoffs on fitness.

Using replicator-diffusion equations as a modeling tool leads us to the assumption of local interactions (*i.e.* local payoff calculation) as in Hauert and Imhof (2012). In the context of the Hawk-Dove game, this is to say that individuals living at a patch do not compete for the resources with the residents of other sites. This very same assumption, on the other hand, was criticized by Britton (1989) and Doebeli and Killingback (2003) and relaxed by supposing that reproduction and hence population dynamics take place in a habitat patch whose resources are also used by individuals that live and reproduce in neighboring patches through foraging. This relaxation leads us to the fact that individuals from neighboring sites compete for the common resources and hence the payoff calculation for individuals residing in a patch does not depend solely on the local population configuration but also on the weighted average of the frequencies of the morphs in a certain neighborhood of the site. We would like to remark that there is a vast literature on individual based models of evolutionary spatial games taking nonlocal payoff calculation in a neighborhood of a spatial location into account (see, for example, pioneering studies by Nowak and May (1992) and Nowak et al. (1994)). The second major component of fitness calculation is related to the intensity of selection w, a parameter determining the strength of payoffs compared to the baseline fitness. As Ohtsuki and Nowak (2006) point out simple as well as illuminating results arise in the limit of weak selection, $w \ll 1$. This is also the case for our model, hence we assume that the effect of payoffs is small when compared to baseline fitness.

The process considered here is a coupled system of Markov chains taking the spatial structure of the environment into account. This coupling between these chains is through dispersal and nonlocal payoff calculation. We find that the mean field dynamics of this coupled system of Markov chains is a coupled system of replicator equations (CRE). Here, we hypothesized that the magnitude of dispersal probability μ is comparable to that of the small selection parameter $w \ll 1$. This hypothesis is shown to be a requirement to destabilize the ESS of the Hawk–Dove game. In particular, we analyse this limiting deterministic case near the ESS of the underlying Hawk-Dove game and find that small dispersal rate gives rise to spatial pattern formation in 1D and 2D spatial regions with periodic boundaries when the magnitude of the dispersal probability is of order $O(w)$. We would like to note that spatial pattern formation is also possible in the strong selection regime. For a brief discussion and illustration of these patterns, see Appendix C.

The emergence of spatial inhomogeneity is related to the nonlocal (or quasi-local) interactions that are shown to be a mechanism for spatial pattern formation for a number of ecological processes (Aydogmus, 2015; 2017; Britton, 1989; Doebeli and Killingback, 2003; Genieys et al., 2006; Killingback et al., 2013; Kisdi and Utz, 2005; Maruvka and Shnerb, 2006; Utz et al., 2007). In these earlier works it was shown that the spatial inhomegeniety is due to the fluctuating density of a species. Whereas, pattern formation in our model describes the fluctuations in the frequencies of the morphs due to the fact that replicator equations are used to model evolution in phenotype space.

The structure of this article is as follows: In Section 2, we give a detailed description of our stochastic model and relate it to deterministic meanfield equations. In Section 3, we perform a linear stability analysis of the model and investigate the conditions for pattern formation. In Section 4, we study the pattern formation numerically for the nearest neighbor interactions and investigate the effects of patch sizes and neighborhood types. Lastly, we discuss and summarize our findings in Section 5.

2. From coupled Moran process to CRE

In this section we consider a class of two player symmetric games whose payoff matrix is given as follows:

	A	B
A	a	b
B	c	d

Here we consider a landscape ecology perspective and divide the habitat into identical distinct patches each of which contains K individuals. Since our aim is to obtain and analyse the mean dynamics of a stochastic model, we assume that K is large. We denote the set of these patches by S. Each site q in the set S has a dispersal neighborhood denoted by N^q.

Suppose that each individual in the population is either type A or B. At each transition time, a site of origin $q \in S$ is chosen randomly, and the following actions take place in order:

- An individual from the site q is chosen to reproduce according to a frequency dependent probability
- With probability μ, the offspring migrates to one of the neighbouring sites in N^q equally likely and replaces a randomly chosen individual in this site.
- The offspring replaces a randomly chosen individual from the site of origin q with probability $1-\mu$.

Before proceeding to an introduction of our stochastic model, we discuss how to take a nonlocal payoff calculation into account. Suppose that, for any site q, the frequency of type A individuals at time t is given by $\mathcal{X}^q(t) := \mathcal{X}^q$ and denote the vector of these frequencies by $\mathcal{X} = (\mathcal{X}^q)_{q\in S}$. The payoff calculation is directly related to the foraging range of the species denoted by $\mathcal{N}^q$. For the sake of simplicity we suppose that an individual from site q is able to play the game with any individual in her site of origin q or one of its neighboring sites in N^q and collects her payoff. Hence the foraging