Journal of Theoretical Biology 429 (2017) 105–115

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/jtbi

# Evolutionary dynamics and the evolution of multiplayer cooperation in a subdivided population

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ARTICLE INFO

*Article history:*
Received 6 December 2016
Revised 22 June 2017
Accepted 26 June 2017
Available online 28 June 2017

ABSTRACT

The classical models of evolution have been developed to incorporate structured populations using evolutionary graph theory and, more recently, a new framework has been developed to allow for more flexible population structures which potentially change through time and can accommodate multiplayer games with variable group sizes. In this paper we extend this work in three key ways. Firstly by developing a complete set of evolutionary dynamics so that the range of dynamic processes used in classical evolutionary graph theory can be applied. Secondly, by building upon previous models to allow for a general subpopulation structure, where all subpopulation members have a common movement distribution. Subpopulations can have varying levels of stability, represented by the proportion of interactions occurring between subpopulation members; in our representation of the population all subpopulation members are represented by a single vertex. In conjunction with this we extend the important concept of temperature (the temperature of a vertex is the sum of all the weights coming into that vertex; generally, the higher the temperature, the higher the rate of turnover of individuals at a vertex). Finally, we have used these new developments to consider the evolution of cooperation in a class of populations which possess this subpopulation structure using a multiplayer public goods game. We show that cooperation can evolve providing that subpopulations are sufficiently stable, with the smaller the subpopulations the easier it is for cooperation to evolve. We introduce a new concept of temperature, namely "subgroup temperature", which can be used to explain our results.



## 1. Introduction

Evolutionary game theory has proved to be a very successful way of modelling the evolution of, and behaviour within, populations. The classical models mainly focused on well-mixed populations playing two player games (Maynard Smith, 1982; Maynard Smith and Price, 1973), or alternatively playing games against the entire population (Maynard Smith, 1982). Simple models such as the Hawk-Dove game (Maynard Smith, 1974) and the sex ratio game (Hamilton, 1967) have been used to explain important biological phenomena.

These models were developed to consider finite populations explicitly (Nowak, 2006a, Chapters 6–9) (although see Moran, 1958; 1962 for important earlier non-game theoretic work) and structured populations using the now widespread methodology of evolutionary graph theory originated in Lieberman et al. (2005) (see also Antal and Scheuring, 2006; Broom and Rychtář, 2008; Maciejewski and Puleo, 2014; Voorhees and Murray, 2013, and Allen and Nowak (2014); Shakarian et al. (2012) for reviews). Such population structures can have a profound effect on the result of the evolutionary process even when individuals have a fixed fitness (Lieberman et al., 2005; Masuda, 2009; Pattni et al., 2015). Further, even for a given structure, the rules of the evolutionary dynamics have a significant effect on the evolution of the population.

Previous work has investigated a number of important questions, the most widely considered being how cooperation can evolve. The evolution of cooperation, where individuals make sacrifices to help others, can seem paradoxical within the context of natural selection, especially amongst unrelated individuals. There are a number of ways that mathematical modelling has demonstrated that cooperation can occur (Nowak, 2006b); one key way is through the presence of population structure, which can mean that cooperative individuals are more likely to interact with other cooperators, which makes them resistant to exploitation by defectors (Ohtsuki et al., 2006; Santos and Pacheco, 2005). In particular, this is true for structures where individuals are heterogeneous

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http://dx.doi.org/10.1016/j.jtbi.2017.06.034
0022-5193/

(Santos et al., 2008) allowing hubs or clusters of cooperators to form. The dynamics that one uses are also important; for example Ohtsuki et al. (2006) showed that death-birth or birth-death dynamics with selection on the second event promotes cooperation but not when selection happens in the first event.

One limitation of evolutionary graph theory is that it naturally lends itself to pairwise games, whereas real populations can often involve the simultaneous interaction of many individuals (Domenici et al., 2000; Similä, 1997). Multiplayer games, whilst more common in economic modelling (Binmore, 1992; Harsanyi and Selten, 1988), have become used in increasing frequency within evolutionary games starting with Palm (1984) and Broom et al. (1997) (see also Bukowski and Miekisz, 2004; Gokhale and Traulsen, 2010) and it is important to incorporate these too into the modelling of structured populations. A multiplayer public goods game (Archetti and Scheuring, 2011; 2012; Gokhale and Traulsen, 2014; Wu et al., 2013), (and this type of game is central to our paper too, see Section 2.2) has been used in evolutionary graph theory (Li et al., 2016; 2014; Perc et al., 2013; van Veelen and Nowak, 2012; Zhou et al., 2015), but this typically involves forming an individual and all of its neighbours into a group and allowing them to play a game. Although this is convenient, it is not really natural because there is no mechanism for deciding how individuals spend their time, and so how they share that time with others, either singly or in groups.

More recently a general framework has been developed (Broom et al., 2015; Broom and Rychtář, 2012; 2016; Bruni et al., 2014) which considers the interaction of populations in a more flexible way, where groups of any size can form, with different propensity potentially depending upon a number of factors, including the history of the process. Crucially, the key elements of evolutionary graph theory of population structure, game and evolutionary dynamics occur for this new framework too; this makes it capable of analysing different spatial structures whilst providing the flexibility for different multiplayer interactions. Prior to the current paper, the actual applications of the above framework have been limited. In particular only a single evolutionary dynamics (the BDB dynamics from the current paper) has been used, and only relatively simple populations, which resembled those in evolutionary graph theory (the population consisting of individuals each resident at a unique graph vertex) have been considered.

In this paper we further develop the general theory of the framework originated in Broom and Rychtář (2012). We first show how to represent subpopulations using a reduced graphical representation within our structure, which will then allow us to potentially consider larger populations with a richer structure than previously. We then demonstrate how to apply a standard set of evolutionary dynamics to consider a range of evolutionary processes. This is vital since, as mentioned above, dynamics can have a big effect on the outcome of evolution within other models, including evolutionary graph theory, and as we will see, this is certainly also true for our work. Finally we use these new tools to consider the evolution of cooperation using a multiplayer public goods game (Archetti and Scheuring, 2011; Szolnoki and Perc, 2010a; 2010b; van Veelen and Nowak, 2012) and show that cooperation can occur when both the structure and evolutionary dynamics act together in favour of the cooperators.

The paper is structured as follows: in Section 2 the model framework is described, including how to incorporate subpopulations. In Section 3 a standard set of evolutionary dynamics to be used with our model are defined. In Section 4 we introduce and discuss the important concepts of fixation probability and temperature. In Section 5 we study the evolution of cooperation in our model with subpopulations. Section 6 is then a general discussion.

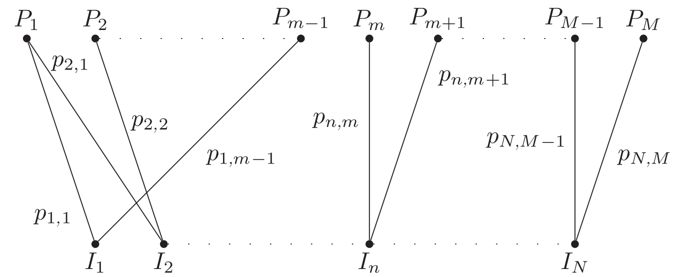


**Fig. 1.** The fully independent model from Broom and Rychtář (2012). There are $N$ individuals who are distributed over $M$ places such that $I_n$ visits place $P_m$ with probability $p_{nm}$. Individuals interact with one another when they meet, for example, $I_1$ and $I_2$ can interact with one another when they meet in $P_1$.

## 2. A framework for modelling evolution in structured populations

A framework for modelling the movement of individuals was presented in Broom and Rychtář (2012). This is a very general and flexible methodology, the details of which are not necessary for the current paper. Below we describe the fully independent version of this framework in which individuals move independently of each other and independently of the population's history (any past movements), and a version of the fully independent model called the territorial raider model as introduced in Broom and Rychtář (2012) and further developed in Broom et al. (2015). We then develop a generalization of this model, which then forms the basis of much of the work in this paper, although we note that Section 3 in particular is more general. Important terms used in the current paper are given in Table 1.

### 2.1. The population structure

We begin by introducing the fully independent model. Consider a population made up of $N$ individuals $I_1, \ldots, I_N$ who can move around $M$ places $P_1, \ldots, P_M$. The probability of individual $I_n$ being at place $P_m$ is denoted by $p_{nm}$; see Fig. 1 for a visual representation using a bi-partite graph. When individuals move around they form groups. Let $\mathcal{G}$ denote any group of individuals, then the probability $\chi(m, \mathcal{G})$ that group $\mathcal{G}$ forms in place $P_m$ is given by

$$\chi(m,\mathcal{G}) = \prod_{i\in\mathcal{G}} p_{im} \prod_{j\notin\mathcal{G}} (1-p_{jm}). \tag{2.1}$$

We can show from Eq. (2.1) that

$$1 = \sum_m \sum_{\substack{\mathcal{G} \\ n\in\mathcal{G}}} \chi(m,\mathcal{G}) \quad \forall n. \tag{2.2}$$

This follows intuitively from the fact that individual $I_n$ has to be present in some place $P_m$ in some group $\mathcal{G}$ at any given time. The mean size of an individual's group (see also Bruni et al., 2014) is given by

$$\bar{G} = \sum_m \sum_{\mathcal{G}} \frac{\chi(m,\mathcal{G})|\mathcal{G}|^2}{\sum_m \sum_{\mathcal{G}} \chi(m,\mathcal{G})|\mathcal{G}|} = \sum_m \sum_{\mathcal{G}} \frac{\chi(m,\mathcal{G})|\mathcal{G}|^2}{N} \tag{2.3}$$

where the simplification of the denominator follows from Eq. (2.2).

When a group of individuals is formed they will then interact with one another. In particular, individual $I_n$ will receive a payoff that depends upon the group $\mathcal{G}$ it is present in and the place $P_m$ occupied by this group. This is denoted as $R_{n,m,\mathcal{G}}$ and was referred to in Broom and Rychtář (2012) as a *direct group interaction payoff* because individual $I_n$ only interacts with other individuals with whom it is directly present (Broom and Rychtář, 2012 allowed for a more general class of payoff but this is the only type we will consider, and hence will just refer to it as the payoff). Individual $I_n$'s