# A dynamic network population model with strategic link formation governed by individual preferences

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## HIGHLIGHTS

- We model the evolution of relationships in a population using graphs.
- The graph changes through time according to the choices of individuals.
- Using Markov chains, we show that the population evolves to a closed class.
- We give a method for finding the stationary distribution over this class.
- We consider some special cases of particular interest.

## ARTICLE INFO

## ABSTRACT

Historically most evolutionary models have considered infinite populations with no structure. Recently more realistic evolutionary models have been developed using evolutionary graph theory, which considered the evolution of structured populations. The structures involved in these populations are typically fixed, however, and real populations change their structure over both long and short time periods. In this paper we consider the dynamics of such a population structure. The timescales involved are sufficiently short that no individuals are born or die, but the links between individuals are in a constant state of flux, being actively governed by the preferences of the members of the population. The process is modelled using a Markov chain over the possible structures. We find that under the specified process the population evolves to a closed class of structures, and we show a method to find the stationary distribution on this class. We also consider some special cases of interest.

## 1. Introduction

### 1.1. Modelling biological populations

Traditional evolutionary models generally consider an infinite population of individuals which is well-mixed in the sense that each pair of individuals is equally likely to interact. This includes the classical game theoretical models of Hamilton (1964a, 1964b, 1967), Maynard Smith and Price (1973), Maynard Smith (1982), Hofbauer and Sigmund (1988, 1998). Whilst real populations are of course finite, the assumption of infinite size is often a reasonable one provided that the population is of sufficiently large size. Such game-theoretical models are concerned with what strategies can evolve and persist within the population. Except at equilibrium values, some strategies have a fitness advantage over others, and this dominates any random effects for a sufficiently large population.

Nevertheless there are some important differences between finite and infinite populations, in particular if there is no such fitness advantage. The classical mathematical genetic models of Fisher (1930) and Wright (1931) dealt with finite well-mixed populations with no selective differences, and were concerned with the speed of the evolutionary process. More recently evolutionary games have also been investigated in finite populations, for example in Taylor et al. (2004). The distinction between a small (relative to the size of the population) invading group which is effectively infinite and a single invading mutant meant that some refinement of the classical concepts of game theory was required.

### 1.2. Evolution on graphs

Real populations, as well as being finite, are not homogeneous, but contain structure. Evolutionary processes have been extended

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to structured populations e.g. Wright (1940), Kimura (1953), Moran (1959), Cannings (1975), in the case of genetic models where populations consisted of a number of sub-populations and interactions between and within populations were different. Recently population structure has been incorporated in a more general manner with the use of graphs, starting with Lieberman et al. (2005). In these models a population consists of $N$ individuals $I_1, \ldots, I_N$. There is a set of indicators $\{x_{ij} : i, j \in \{1, 2, \ldots N\}\}$, and if $x_{ij} = 1$ then individual $i$ influences individual $j$ in some prescribed manner. We can represent the system by a graph $G = (V, X)$, where the set $V$ of vertices correspond to the individuals and the edges correspond to the interactions, there being an edge joining $i$ to $j$ if, and only if, $x_{ij} = 1$. In the case where $x_{ij} = x_{ji}$ for all $i$ and $j$ we will have one or no edge between $i$ and $j$, and the graph is undirected. If we also have $x_{ii} = 0$ for all $i$, then the graph is said to be simple. Throughout the paper we shall assume that our graphs are simple.

In these models the population usually consists of two types of individuals (labelled $A$ and $B$, or resident and mutant) and the state of the population, described by the set of mutant individuals, say, evolves according to an evolutionary dynamics and can be represented as a discrete time Markov chain. The question of whether a mutant placed at a random vertex can invade is addressed, and it turns out that the population structure, i.e. the graph, can have a significant effect on the fixation probability, the probability that the mutant will eventually completely replace the resident population (Antal et al., 2006; Broom and Rychtář, 2008).

In this paper we shall consider networks of individuals represented, as described above, by a simple graph. As described below, the population itself will not evolve, but the connections between individuals will. Of course for real populations both aspects change, see for example Perc and Szolnoki (2010). The emphasis here, in similar spirit to some of the above models, is to fix one aspect (the population) and consider simple models of the other which can be analysed.

Such networks arise naturally in many contexts and there has recently been an explosion of interest in networks in biology, as well as in economics and sociology. In economics we might consider companies which trade with each other and in sociology individuals who are friends or colleagues. In the biological context there are many possible ways in which such a structure might arise. The spatial positions of individuals will naturally define interactions through proximity, whether this be for plants in a fixed position or for territorial animals. The use of networks in biology is by no means new. For example food webs, in which the interaction of predators and prey is illustrated, go back at least to the seminal work of Elton (1927). In social animals there will be dominance interactions and also mutuality ones which can be represented using the above graph idea. Primate social structures can be particularly complex and can influence key behavioural features such as the level of cooperation e.g. Voelkl and Kasper (2009) and Voelkl and Noë (2008). The analysis of observed animal social networks has been discussed in detail in Croft et al. (2009) where various examples can be found, while aspects of the modelling of networks is explored in Newman (2010).

### 1.3. Evolution of graphs

The models that we have described so far have population structure, but it is a fixed one. In real populations over time, and especially as individuals die and are born, the links between individuals and the number of individuals changes, so any graph of contacts will change over time. This was investigated in Southwell and Cannings (2010a, 2010b, 2010c). They considered a population and its interactions at time $t$ represented by the simple graph $G_t = \{V_t, X_t\}$. In their basic model the populations at time $t + 1$ had graph $G_{t+1}$ where $V_{t+1}$ consisted of all of the

individuals in $V_t$ together with one new individual (offspring) for each of these individuals. The set of edges $E_{t+1}$ contained all of the edges of $E_t$ plus additional new edges. Specifically if $(i, j) \in V_t$ and $i^*$ and $j^*$ were the offspring of $i$ and $j$ respectively, then there were eight models generated by the inclusion/exclusion of the edges $(i^*, j^*)$, $(i^*, j) \cup (i, j^*)$ and $(i, i^*) \cup (j, j^*)$. The underlying motivation was that the relationships between individuals in a social population are often, as least partially, inherited e.g. dominance in baboons (see Amboseli Baboon Research Project, 2012). The addition or the removal of vertices through age and/or vertex degree (number of edges) was also incorporated.

### 1.4. The effect of behaviour on graph structure

The above models consider change over a long period of time. Many individuals are born and die and the entire composition of the population changes many times. However, populations can also change in important ways in short periods of time. The basic idea behind our modelling is that within a population animals may show varying degrees of willingness or desire to interact with others, because there are both benefits and penalties attached to such interaction. These benefits and penalties may well vary between individuals, and so we expect, and indeed observe, that individuals have differing behaviours with respect to the establishment and severance of links with others.

This phenomenon has been labelled "sociability" and investigated in various species across a wide evolutionary range. In non-human primates such differences have been found to be stable across time, see for example Capitanio (2002), and references therein. In bottlenose dolphins long term alliances are made between males, see e.g. Wiszniewski et al. (2012), but also relatively labile alliances are often made e.g. Connor et al. (1999). In sheep it was demonstrated that different individuals differed in respect of the closeness they maintained to other members of the flock (Sibbald and Hooper, 2004). Thus as a secondary effect the number of nearest neighbours to whom an individual was linked would vary. Thus a sheep who had more than enough nearest neighbours would happily move away, and in so doing reduce the number of nearest neighbours, and a sheep who had too few such "links" would tend to move towards others and in so doing establish additional links.

Epidemics can be modelled on graphs where individuals move between a number of states, containing at least two types, susceptibles and infectives. Individuals can catch the disease and recover, and in such models there are usually no changes in the population itself. Often the process occurs on a fixed graph and models are similar to the evolutionary processes from Lieberman et al. (2005) etc. However, recent models (Kiss et al., 2010; Funk et al., 2009) have incorporated behavioural changes as a result of epidemics (e.g. knowledge that the disease is prevalent makes individuals reduce their rate of contact) which can have a significant effect upon whether an epidemic spreads.

In all of these examples we see a set of animals with temporary links between various individuals. Of course the probability of a link existing between a pair of individuals will often be affected by the relatedness of those individuals, by their genders and by their position in any dominance hierarchy. There are also likely to be spatial components. In some of the examples, e.g. in the bottlenose dolphin case, the links are reciprocal whereas in others they might be considered to be initiated, or broken, by the action of one of the individuals. Similarly the absence of a connection may benefit one but not the other (e.g. a female and a poor quality male). This falls into the theory of biological markets and partner choice, see Noë (2001) and Noë and Hammerstein (1994).

In this paper we do not attempt to model all of these complexities but instead concentrate on a model which examines only the