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

Mark Broom [a,*], Chris Cannings [b]

[a] *Department of Mathematics, City University London, Northampton Square, London EC1V 0HB, UK*
[b] *School of Mathematics and Statistics, The University of Sheffield, Hounsfield Road, Sheffield S3 7RH, UK*

## 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.

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## 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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[*] Corresponding author. Tel.: +44 (0) 20 7040 3672.
*E-mail addresses:* mark.broom@city.ac.uk (M. Broom), c.cannings@sheffield.ac.uk (C. Cannings)

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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 network of interactions. Thus the individuals (vertices) in our networks are distinguishable only by the number of links they would like to form with others in the population, and they do not differentiate in any way between those other individuals. They are indifferent to whom they link with. We consider such a dynamic process on a short timescale. We follow a population where individuals have a desired number (or range) of links to other individuals and the process evolves through each trying to achieve its desired number. We do not address the issue of how these desired values arose in the first place, they may well be secondary effects of intrinsic differences between the individuals which might be subject to natural selection. Of course that selective pressure will be affected to some extent by the outcomes resulting from the linking. Each individual will only make a change which improves its number of links, but since all links involve two individuals, the actions of others can make an individual's situation worse, though in the transient phase it may improve it, or leave it unaffected. In Broom and Cannings (submitted for publication) we considered the possible transitions under this process and proved some fundamental results. Here we discuss the Markov chain which results when a probability is associated with the selection of the next individual who attempts to improve their number of links. We are particularly interested in situations where the wishes of the members of the population are incompatible, meaning that the links between the population members are continually changing. We show that the Markov chain associated with what we term the minimal set (involving states where no mutually beneficial addition or removal of a link can occur) is reversible, and so there is always a unique stationary distribution.

## 2. The general model

### 2.1. The graph of the population and graphic deviations

We have some set (the population) $V=\{1,2,\ldots,n\}$ and we consider simple graphs $G=(V,\mathbf{X})$ where $\mathbf{X}$ describes the links (alternatively edges) between pairs of individuals. Whilst the vertices are fixed, the edges evolve. We will consider a random process on the edge set $\boldsymbol{X}$. Thus the state of the process at time $t$ is the edge set $\mathbf{X_t}$. Since the vertices are fixed there is a one to one correspondence between the edge set and the graph, and we will often refer to $\mathbf{X_t}$ as the graph.

At any given time $t$ individual $i$ will have a number of edges $e_{i,t}$ to other individuals. We refer to the vector $\mathbf{e}_t=(e_{1,t},e_{2,t},\ldots,e_{n,t})$ as the *sequence* $\mathbf{e}_t$.

At each time point an individual is chosen and is allowed to add or remove an edge to one other individual in the population. Each vertex has an acceptable range $[m_i,\ M_i]$ of edges to other vertices, where $0\le m_i\le M_i\le n-1$.

If $i$ is selected, and it has a number of edges $e_i<m_i$ (we shall call such a vertex a Joiner) then it forms a new edge, connecting to one of the other vertices it is not connected to at random. If $e_i>M_i$ (we call this a Breaker) then it breaks one of its edges at random. Otherwise, it neither breaks nor creates an edge (we call this a Neutral vertex).

The *distance* between two sequences $\boldsymbol{u}$ and $\boldsymbol{v}$ is $z(\boldsymbol{u},\boldsymbol{v})=\sum_{i=1,n}|u_i-v_i|$.

The *deviation* of individual/vertex $i$ is $\epsilon_i=\max[(m_i-e_i),(e_i-M_i),0]$.

The *deviation* of the above graph $\mathbf{X_t}$ is defined as the sum of the vertex deviations, $\Upsilon_t=\sum_{i=1,n}\epsilon_i$.

Clearly there will be a minimum value of the deviation for any given collection of the ranges $[m_i,\ M_i]$, and this is termed the *score*. There is a set of sequences, and a corresponding set of graphs, which achieve this minimum, and these are termed $J(min)$ and $K(min)$ respectively. In Broom and Cannings (submitted for publication) we proved that there is always a path of allowable moves enabling the process to reach a member of the minimal set, $K(min)$. The set of sequences (graphs) with minimum deviation will of course depend upon the values of the $m_i$ and $M_i$, but we shall just use $J(min)$ ($K(min)$) for notational convenience. Further we proved that, since our process could never increase the deviation of the graph, once $J(min)/K(min)$ is reached, that set cannot be left.

### 2.2. A random process

In Broom and Cannings (submitted for publication) we investigated the possible paths and end states of the process described above. In this paper we consider the random process describing the changing population graph generated when individuals are allowed (in a specific manner) to add and remove edges.

At successive time points, a vertex is chosen at random, with $i$ being selected with probability $p_i>0$, and it changes its number of links according to the process defined above. We thus have a random process which is a homogeneous Markov chain, since the probability of each transition only depends upon the most recent state and not the history of the process.

We thus wish to consider the Markov chain with transitions defined as follows: (1) For any $\mathbf{x}^*$ which differs from $\mathbf{x}$ in a single entry, where $x_{ij}=0, x^*_{ij}=1$ for some $i,j$,

$$P(\mathbf{X_{t+1}}=\mathbf{x}^*\big|\mathbf{X_t}=\mathbf{x})=\begin{cases} p_i\dfrac{1}{n-1-e_i}+p_j\dfrac{1}{n-1-e_j} & e_i<m_i, e_j<m_j \\ p_i\dfrac{1}{n-1-e_i} & e_i<m_i, e_j\ge m_j \\ p_j\dfrac{1}{n-1-e_j} & e_i\ge m_i, e_j<m_j \\ 0 & e_i\ge m_i, e_j\ge m_j. \end{cases}$$

(2) For any $\mathbf{x}^*$ which differs by $\mathbf{x}$ in a single entry, where $x_{ij}=1, x^*_{ij}=0$ for some $i,j$,

$$P(\mathbf{X_{t+1}}=\mathbf{x}^*\big|\mathbf{X_t}=\mathbf{x})=\begin{cases} p_i\dfrac{1}{e_i}+p_j\dfrac{1}{e_j} & e_i>m_i, e_j>m_j \\ p_i\dfrac{1}{e_i} & e_i>m_i, e_j\le m_j \\ p_j\dfrac{1}{e_j} & e_i\le m_i, e_j>m_j \\ 0 & e_i\le m_i, e_j\le m_j. \end{cases}$$

(3) Similarly for any other $\mathbf{x}^*$, differing from $\mathbf{x}$ in two or more entries,

$$P(\mathbf{X_{t+1}}=\mathbf{x}^*|\mathbf{X_t}=\mathbf{x})=0.$$

The probability of the sequence being unchanged is simply 1 minus the sum of the above probabilities.

### 2.3. The reversibility of the process

We now show that once the population reaches $J(min)$ then the process is a reversible one. This will later allow us to use the detailed balance conditions to find the unique stationary distribution.

**Theorem 1.** *The above described Markov process, when restricted to* $J(min)$, *is reversible.*

**Proof.** We apply Kolmogorov's criterion. A Markov chain is reversible if, and only if, for every finite sequence of states $G_1,G_2,\ldots,G_k=G_1$, the probability of this sequence occurring is equal to the probability of the reverse sequence $G_1=G_k,\ G_{k-1},\ldots,G_1$.

Consider the system when it has reached $K(min)$, and some sequence of states $G_1, G_2, \ldots, G_k = G_1$. All transitions involve one element $x_{ij}$ changing from 0 to 1 or vice versa. Since the process has reached $K(min)$, for any pair of vertices $i$ and $j$ without an edge, at most one can be a Joiner, since otherwise it would be possible to reduce the score further. Similarly, for any pair of vertices with an edge, at most one can be a Breaker. The probability of any transition which involves the move $x_{ij} = 0 \to 1$ (Joiner $i$ selected and forming a link with $j$) is

$$\frac{p_i}{n-1-e_i}$$

and the probability of any transition which involves the move $x_{ji} = 1 \to 0$ (Breaker $j$ selected and breaking a link with $i$) is

$$\frac{p_j}{e_j}.$$

Suppose that in the sequence of changes in $G_1, G_2, \ldots, G_k = G_1$ $x_{ij}$ changes from 0 to 1 $\nu_{ij}$ times (and so it must change from 1 to 0 $\nu_{ij}$ times also), then the probability of the whole sequence occurring is

$$\prod_{i,j} p_i^{\sum_k \nu_{ik}} \prod_{l=1}^{\sum_k \nu_{ik}} \frac{1}{n-1-e_i(l)} p_j^{\sum_k \nu_{kj}} \prod_{l=1}^{\sum_k \nu_{kj}} \frac{1}{e_j(l)},$$

where the elements $e_j(l)$ are the collection of the different numbers of edges connected to $j$ prior to all the increases in that number, and $n-1-e_i(l)$ are the collection of the different numbers of edges absent from $i$ prior to all the increases in this number.

It is clear that when reversing the sequence through the states $G$ vertex $i$ must be selected to form an edge the same number of times as in the original sequence, and must be selected to break an edge the same number of times as in the original sequence, since $x_{ij}$ increases from 0 to 1 the same number of times as it decreases from 1 to 0 in the original sequence, which is the same number of increases from 0 to 1 in the reverse sequence.

It is also clear that following the $e_j(l)$s in the original sequence, every change from $e_j$ to $e_j+1$ must have a corresponding change from $e_j+1$ to $e_j$, which is a change from $e_j$ to $e_j+1$ in the reverse sequence (and similarly for the $n-1-e_i(l)$ terms).

Hence the probability in the reverse direction is identical to that in the original sequence, and so the process is reversible.

In what follows we will not attempt to be systematic in finding all of the results that we can in fullest generality, but will give more restrictive cases of specific interest and show some important results at each stage. A more systematic analysis will be left for later work. We start by restricting each individual to a unique target, before in Section 3 looking at a specific class of target sets.

### 2.4. A unique target

It may be that $m_i = M_i = a_i$, in which case we call $a_i$ the target of $i$, and the sequence $\boldsymbol{a} = (a_1, a_2, \ldots, a_n)$ the target sequence.

For some target sequences it is possible for all of the individuals in the population to have precisely the required number of edges, and so if this population state is reached, no individual will want to change and the process that we will describe will come to an end. If this is the case, the sequence is called *graphic* (see e.g. Gould, 1988). Often this is not the case, however. The score of a sequence that we introduced in Section 2.1 is here the distance of the nearest graphic sequence to a specific target sequence. We investigate the score for certain classes of target sequence, and properties of this set of minimal graphs.

We denote the set of graphic sequences by $\boldsymbol{H}$.

The *score* of $\boldsymbol{a}$ is $s(\boldsymbol{a}) = \min_{\boldsymbol{u} \in \boldsymbol{H}} z(\boldsymbol{a}, \boldsymbol{u})$.

The *minimal set* of $\boldsymbol{a}$ is $J(\boldsymbol{a}) = \{\boldsymbol{u} \in \boldsymbol{H} | z(\boldsymbol{u}, \boldsymbol{a}) = s(\boldsymbol{a})\}$.

The set of graphs which yield a minimal score (and so have sequence in $J(\boldsymbol{a})$) is defined as $K(\boldsymbol{a})$.

Following the random process previously defined, there is a path from any sequence to a member of the set of sequences $J(\boldsymbol{a})$ which has positive probability of being followed, and so $J(\boldsymbol{a})$ is an absorbing set, as is the corresponding set of graphs $K(\boldsymbol{a})$. Thus consideration of the process eventually comes down to a consideration of the process within the set $K(\boldsymbol{a})$. We note that it was shown in Broom and Cannings (submitted for publication) that if the target sequence is not graphic, then the set $J(\boldsymbol{a})$ is connected (of course if the target sequence is graphic, then $|J(\boldsymbol{a})| = 1$, so $J(\boldsymbol{a})$ is connected by default).

**Corollary 1.** *For the case with a unique non-graphic target $\boldsymbol{a}$, there is a unique stationary distribution over the sets $J(\boldsymbol{a})$ and $K(\boldsymbol{a})$ which can be found using the detailed balance conditions.*

This result follows immediately from the fact that $J(\boldsymbol{a})$ and $K(\boldsymbol{a})$ are connected, and the process is reversible over this set.

We shall now look at an example. Consider the target sequence $\mathbf{a} = (n-1,\ n-2,\ \ldots, 1,\ 0)$, which we shall refer to as the *arithmetic sequence*. In a subsequent paper we will investigate this target sequence more generally, but for now we shall consider the case with $n=5$ only. It is easy to see that, denoting each vertex by its target score, all of the minimal score graphs have the edges 0–1, 0–2 and 1–2 broken and the edges 2–3, 2–4 and 3–4 formed. Four of the twelve remaining combinations do not lead to minimal score graphs, leading to 8 distinct graphs in total. We show these in Table 1, together with their sequence and their probability in the stationary distribution.

The stationary distribution is found from the transition matrix $\mathbf{M}$, which listing the graphs in the order from Table 1, is given by

$$10 * \mathbf{M} = \begin{pmatrix} 6 & 0 & 2 & 1 & 1 & 0 & 0 & 0 \\ 0 & 8 & 0 & 0 & 1 & 1 & 0 & 0 \\ 2 & 0 & 6 & 0 & 0 & 0 & 1 & 1 \\ 2 & 0 & 0 & 6 & 0 & 0 & 2 & 0 \\ 1 & 1 & 0 & 0 & 6 & 0 & 0 & 2 \\ 0 & 2 & 0 & 0 & 0 & 6 & 0 & 2 \\ 0 & 0 & 1 & 1 & 0 & 0 & 8 & 0 \\ 0 & 0 & 1 & 0 & 2 & 1 & 0 & 6 \end{pmatrix}.$$

## 3. The All or Nothing system

It will be of specific interest to consider graphs with a large score, as this will generally lead to a set $K(\boldsymbol{a})$ with a large number of elements, and a consequently richer structure. Graphs of the form $n_1$ vertices with value $m_1$ and $n_2 = n - n_1$ vertices with value $m_2 < m_1$ have large minimal scores for certain values of

**Table 1**
The steady state probability distribution over the eight minimal score states in the arithmetic case with $n=5$.

| Number | 0–3 | 0–4 | 1–3 | 1–4 | Sequence | Probability |
|---|---|---|---|---|---|---|
| 1 | N | Y | Y | Y | 43 221 | 1/7 |
| 2 | Y | Y | N | Y | 43 212 | 1/7 |
| 3 | N | N | Y | Y | 33 220 | 1/7 |
| 4 | N | Y | Y | N | 33 211 | 1/14 |
| 5 | N | Y | N | Y | 42 211 | 1/7 |
| 6 | Y | N | N | Y | 33 211 | 1/14 |
| 7 | N | N | Y | N | 23 210 | 1/7 |
| 8 | N | N | N | Y | 32 210 | 1/7 |

$m_1$, $m_2$, $n_1$ and $n_2$. For sufficiently large $m_1 - m_2$, minimal scores are achieved when we join all of the $n_1$ vertices to each other, and leave the $n_2$ broken from each other. This leaves each of the $n_1$ with $m_1 + 1 - n_1$ edges to find from links to the $n_2$. Whatever links are added between the two types, the score will then be $n_1(m_1 + 1 - n_1) - n_2 m_2$ if this is positive.

We now suppose that $m_1 = n-1$ and $m_2 = 0$, so that for vertex $i$ either $a_i = 0$ or $a_i = n-1$. Thus we have two types of individuals, which we will denote by *J* and *B*. *J*s want to be linked to as many other individuals as possible, and will be a Joiner unless they are connected to all other individuals, when they are Neutral. When chosen, they will pick a random individual that they are not connected to and form a link to that individual. *B*s want to be linked to as few individuals as possible, and will be a Breaker unless they have no links, when they will be Neutral. When chosen, they will break one of their links at random. If a *J* is chosen which is connected to every other individual, or a *B* which is connected to no individuals, then there is no change in the population.

Examples of systems which include two such types of individuals, one that likes high connectivity and the other low connectivity, may include the following situations. The interactions of parasites and their victims, where such interactions benefit parasites and harm (but do not kill) the victims. Thus parasites are *J*s who want to form as many links as possible, and victims are *B*s who want to avoid all such links. Alternatively an animal population in the breeding season may contain males with territories which include females, and those without. Those without territories want to maximise their interactions with the territories in the hope of gaining a mating opportunity, territory owners want to expel those males. A non-biological case may be advertisers on the web and the recipients of adverts, the advertisers trying to maximise their links and the recipients to minimise them.

### 3.1. Dynamics within the minimal deviation set

We have assumed that $p_i > 0$ so that every individual has some positive probability of selection; thus after sufficient time every *J* will be connected to every other, and no pair of *B*s will be connected, so that the only links that can form or be removed are those between a *J* and a *B*, and the problem reduces to considering a bipartite graph, where the score is always $n_1 n_2$, since e.g. if there are no edges each of the $n_1$ *J*s would have a deficit of $n_2$.

The problem thus reduces to a Markov chain where all pairs of *J*s are linked, no pair of *B*s are linked, and so the states can be represented by an $n_1 \times n_2$ matrix $\boldsymbol{A} = (a_{ij})$ where $a_{ij} = 1$ if $J_i$ is connected to $B_j$, and $a_{ij} = 0$ otherwise. We see an example of the states and transitions of such a Markov chain in Fig. 2 later. Further let $t_i$ be the number of 0s in row $i$ of $\boldsymbol{A}$, and $s_j$ be the number of 1s in column $j$. Clearly

$$\sum_{i=1}^{n_1} t_i + \sum_{j=1}^{n_2} s_j = n_1 n_2.$$

Let us denote the total number of 1s, the number of links, as $l = \sum_{j=1}^{n_2} s_j$.

We shall denote the set of *J*s by $S_J$ and the set of *B*s by $S_B$. Clearly $|S_J| = n_1$, $|S_B| = n_2$ and $S_J \cup S_B = \{1, 2, \ldots, n\}$.

Using Section 2.2 we see the following. If $\boldsymbol{A}$ has $a_{ij} = 1$ for a given pair $(i,j)$ and $\boldsymbol{A}^*$ is identical to $\boldsymbol{A}$ except that $a_{ij} = 0$, then the transition probability from $\boldsymbol{A}$ to $\boldsymbol{A}^*$ is $p_j/s_j$ (clearly $s_j \geq 1$ here as $a_{ij} = 1$).

Similarly, if $\boldsymbol{A}$ has $a_{ij} = 0$ for a given pair $(i,j)$ and $\boldsymbol{A}^*$ is identical to $\boldsymbol{A}$ except that $a_{ij} = 1$, then the transition probability from $\boldsymbol{A}$ to $\boldsymbol{A}^*$ is $p_i/t_i$ (and again $t_i \geq 1$ here as $a_{ij} = 0$).

Any transitions between matrices with more than one difference have zero probability.

There will be no change of state only when (a) a *J* individual $i$ is picked which is already joined to all *B*s so that the $i$th row of $\boldsymbol{A}$ contains only 1s, or (b) a *B* individual $i$ is picked which has no edges so the $i$th column of $\boldsymbol{A}$ contains only 0s.

### 3.2. The stationary distribution

As stated above, since the process is reversible within $J(\boldsymbol{a})$ and $K(\boldsymbol{a})$, it satisfies the detailed balance conditions. This gives us an easy way to find conditions for the unique stationary distribution of the All or Nothing system.

**Theorem 2.** *For the All or Nothing system, the stationary distribution on $J(\boldsymbol{a})$ is given by*

$$P(\boldsymbol{A}) = \frac{\prod_j (s_j!) \prod_i (t_i!)}{(n_2!)^{n_1}} \left( \frac{\prod_{i \in S_J} p_i^{(n_2 - t_i)}}{\prod_{j \in S_B} p_j^{s_j}} \right) P(\boldsymbol{0}).$$

**Proof.** We can use the detailed balance equations to find the relationship between the probabilities of being in states that differ by one entry. If $\boldsymbol{A}$ has $a_{ij} = 1$ for a given pair $(i,j)$ and $\boldsymbol{A}^*$ is identical to $\boldsymbol{A}$ except that $a_{ij} = 0$, then we obtain

$$\frac{P(\boldsymbol{A}) p_j}{s_j} = \frac{P(\boldsymbol{A}*) p_i}{(t_i + 1)} \Rightarrow P(\boldsymbol{A}) = \frac{P(\boldsymbol{A}*) p_i s_j}{p_j (t_i + 1)}.$$

Following any sequence from $\boldsymbol{0}$ the matrix with all zeros to $\boldsymbol{A}$, we obtain

$$P(\boldsymbol{A}) = \frac{\prod_{j \in S_B} (s_j!)}{\prod_{j \in S_B} p_j^{s_j}} \frac{\prod_{i \in S_J} p_i^{n_2 - t_i}}{\prod_{i \in S_J} n_2!/t_i!} P(\boldsymbol{0}).$$

which rearranges to the stated result. □

We shall now suppose that all *J*s are equally likely to be selected, and the probability that some *J* is selected is $p$, so that $p_i = p/n_1$ for all *J*s. Similarly, all *B*s are equally likely to be selected, and so the probability that some *B* is selected is $q = 1 - p$, with $q_i = (1-p)/n_2$ for *B*s, where we denote the selection probability of a *B* as $q_i$ instead of $p_i$ for convenience. Thus if we are equally likely to select a *J* or a *B*, then $p = 0.5$ and if each individual is equally likely to be selected so that $p_i = q_i = 1/n = 1/(n_1 + n_2)$, then $p = n_1/(n_1 + n_2)$.

As before, if $\boldsymbol{A}$ has $a_{ij} = 1$ for a given pair $(i,j)$ and $\boldsymbol{A}^*$ is identical to $\boldsymbol{A}$ except that $a_{ij} = 0$, then the transition probability from $\boldsymbol{A}$ to $\boldsymbol{A}^*$ is $q/s_j n_2$. If $\boldsymbol{A}$ has $a_{ij} = 0$ for a given pair $(i,j)$ and $\boldsymbol{A}^*$ is identical to $\boldsymbol{A}$ except that $a_{ij} = 1$, then the transition probability from $\boldsymbol{A}$ to $\boldsymbol{A}^*$ is $p/t_i n_1$.

**Theorem 3.** *The stationary distribution on $J(\boldsymbol{a})$ for the equal probability $p_i = p/n_1, q_i = q/n_2$ All or Nothing system is given by*

$$P(\boldsymbol{A}) = \frac{\prod_j (s_j!) \prod_i (t_i!)}{(n_2!)^{n_1}} \left( \frac{p n_2}{q n_1} \right)^l P(\boldsymbol{0}). \tag{1}$$

**Proof.** Using the detailed balance equations again to find the relationship between the probabilities of being in states that differ by one entry, for $\boldsymbol{A}$ which has $a_{ij} = 1$ for a given pair $(i,j)$ and $\boldsymbol{A}^*$ being identical to $\boldsymbol{A}$ except that $a_{ij} = 0$, we obtain

$$P(\boldsymbol{A}) = \frac{P(\boldsymbol{A}*) p n_2 s_j}{q n_1 (t_i + 1)}.$$

Following any sequence from $\boldsymbol{0}$ to $\boldsymbol{A}$ in the same way as in Theorem 2, we obtain the stated result. □

By summing the above terms we can find $P(\mathbf{0})$ to obtain the precise distribution over the states. A problem is that there are $2^{n_1 n_2}$ states and so this number quickly becomes ungovernable.

### 3.3. The total number of edges and a problem of counting

We may be interested in the long term distribution of $L$, the number of 1s, rather than specific states. Considering the matrix with all 1s (so $n_1 n_2$ in total), means that

$$P(L = n_1 n_2) = \frac{(n_1!)^{n_2}}{(n_2)!^{n_1}} \left(\frac{pn_2}{qn_1}\right)^{n_1 n_2} P(L = 0).$$

Note that finding the probability that $L$ takes a particular value is still difficult in general to evaluate, as there are $\binom{n_1 n_2}{l}$ ways to have $l$ 1s, and many different associated probabilities to add. A potential approach would be to consider the possible values of $s_j$ and $t_i$. For any given set of $s_j$s and $t_i$s, we need to

(1) find whether it is attainable (is there any matrix that gives this set?)

(2) if it is attainable, how many matrices will give it. A lower bound is obtained as follows.

Let $k_s(m)$ be the number of $s_j$ values that equal $m$, and $k_t(m)$ be the number of $t_i$ values that equal $m$. Permuting rows and columns gives at least

$$\frac{n_1!}{k_t(0)!k_t(1)!\ldots k_t(n_2)!} \frac{n_2!}{k_s(0)!k_s(1)!\ldots k_s(n_1)!}.$$

(3) How many attainable combinations are there?

If we can answer (1) and (2), does this solve our problem for intermediate values of $n_1$ and $n_2$, or is the remaining number of combinations from (3) still too big?

### 3.4. Particular values of the J selection probability p

For a steady state distribution, the overall probability of increase in $L$ must be balanced by the probability of a decrease in $L$. Since all $J$s are equally likely to be selected, the probability of an increase is simply the probability that a $J$ is selected multiplied by the probability that the $J$ is not already linked to all $B$s, i.e. the row associated with it does not contain all 1s (we shall denote this probability by $P_R$). Similarly the probability that a decrease occurs is the probability that a $B$ is selected multiplied by the probability that its associated column does not contain all 0s (we shall denote this probability by $P_C$). Thus for a steady state we need

$$pE[P_R] = qE[P_C].$$

We shall consider three special cases. Each of the three cases is considered for $n_1 = 3,\ n_2 = 2$ in Table 2.

Case (i) $p = n_1/(n_1 + n_2)$, with equal probability for all individuals to be selected, favours the type with the larger number, since $p > q$ if and only if $n_1 > n_2$, as might be expected. There is pressure to move towards all connected (none connected) when $n_1 > n_2$ $(n_1 < n_2)$ until the probability of picking a row (column) which cannot be used is sufficiently large to balance it.

Case (ii) $p = 0.5$ favours the type with the fewest number of individuals, since even though $B$ and $J$s are selected with equal probability, if there were exactly half of the links formed, there is less chance of picking one of these which can then not make/(break) a link for the type with the fewest number of individuals. Thus the mean proportion of links will be slightly less (more) than one half if $n_1 > n_2$ $(n_1 < n_2)$.

Case (iii) the value of $p$ which gives an equal number of 1s and 0s on average. Provided that $n_1 \neq n_2$, then this value will lie between the two values of $p$ given above, and we can find $p$ for special cases computationally.

We note that for $n_1 = n_2$, cases (i)–(iii) are the same.

### 3.5. Equal selection probability for all individuals

We will now consider case (i) above where each individual is selected with equal probability. We will look at some special cases where we can evaluate an exact solution, an approximate solution or at least say something about the form of the solution.

We note that in this case there is a simple duality result. For a given set of edges for $n_1$ $J$s and $n_2$ $B$s, we can reverse the numbers of $J$s and $B$s and replace every edge with a non-edge and every non-edge with an edge, and the probability of obtaining the new graph is identical to the probability of the original (this also works for general $p$ if we replace $p$ by $1-p$, which automatically occurs in case (i)). Thus reversing $n_1$ and $n_2$ in the following yields identical results.

**Theorem 4.** *When $n_1 = 1$, $L$ has a truncated Poisson distribution (maximum value $n_2$) with parameter* 1.

**Proof.** In this case if there are $l$ columns containing a 1, then the row is chosen with probability $1/(n_2 + 1)$ and a column with a 1 entry is chosen with probability $l/(n_2 + 1)$. Thus we obtain

$$p_{k-1}\frac{1}{n_2+1} = p_k \frac{l}{n_2+1} \Rightarrow p_l = \frac{p_{l-1}}{l} \quad l = 1, \ldots, n_2.$$

Thus $p_l = p_0/l!$ which leads to the required truncated Poisson distribution. □

**Theorem 5.** *When $n_2 \gg n_1$ the distribution of $L$ is approximately Poisson $(n_1)$.*

**Proof.** In this case there is pressure to reduce the number of links and we can expect the number to generally be small. For a small number of links $l$, if any row is selected it will be able to add a 1, so that the probability of an increase will be $n_1/(n_1 + n_2)$. Assuming that the small number of 1s are all in different columns (plausible for large $n_2$), then the probability of a decrease is just $l/(n_1 + n_2)$ and so

$$p_{l-1}\frac{n_1}{n_1+n_2} \approx p_l \frac{l}{n_1+n_2} \Rightarrow p_l \approx \frac{n_1 p_{l-1}}{l} \quad l = 1, \ldots, n_2$$

This gives us $p_l \approx n_1^l p_0/l!$, which leads to the stated Poisson distribution. □

For the case $n_1 = n_2$, where this number is large, there is some pressure away from the extremes (the probability of going forward and back is equal if no rows contain all 1s or columns all 0s, but when the number of 1s is small or large, moves towards the middle are increasingly likely). When the number of 1s is approximately $n_1^2/2$, the probability of increasing and decreasing is exactly in balance. Thus the distribution of $X$ is approximately uniform in the region $n_1^2/2 - K < l < n_1^2/2 + K$ for some constant $K$. In fact

**Table 2**
The steady state probability distribution over the values of $L$ when $n_1 = 2,\ n_2 = 3$ for three values of $p$, representing cases (i), (ii) and (iii) respectively.

| State | 0 | 1 | 2 | 3 | 4 | 5 | 6 | Mean |
|---|---|---|---|---|---|---|---|---|
| $p = 0.4$ | 0.1047 | 0.2093 | 0.2442 | 0.2093 | 0.1395 | 0.0698 | 0.0233 | 2.372 |
| $p = 0.5$ | 0.0330 | 0.0989 | 0.1730 | 0.2225 | 0.2225 | 0.1668 | 0.0834 | 3.337 |
| $p = 0.46517$ | 0.0513 | 0.1338 | 0.2037 | 0.2278 | 0.1981 | 0.1292 | 0.0562 | 3.000 |

**Table 3**
The steady state probability distribution over the values of $L$ in the $n_1 = n_2 = 5$ case.

| L | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|---|
| Prob | 0.0003 | 0.0013 | 0.0039 | 0.0085 | 0.0154 | 0.0245 | 0.0350 | 0.0463 | 0.0573 |
| L | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
| Prob | 0.0673 | 0.0753 | 0.0810 | 0.0839 | 0.0839 | 0.0810 | 0.0753 | 0.0673 | 0.0573 |
| L | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | |
| Prob | 0.0463 | 0.0350 | 0.0245 | 0.0154 | 0.0085 | 0.0039 | 0.0013 | 0.0003 | |

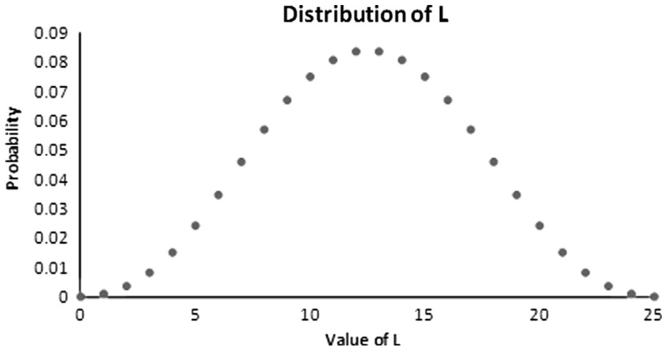

**Fig. 1.** The probability distribution of the total number of links $L$ for the case with $n_1 = n_2 = 5$ (see also Table 3).

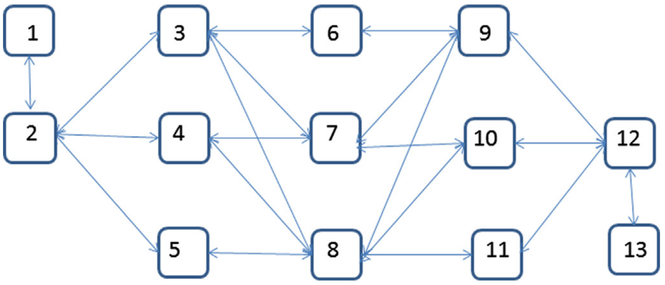

**Fig. 2.** The possible transitions between the 13 states for the case $n_1 = 2$ and $n_2 = 3$. Writing states in terms of the number of links to each individual, with $J$ individuals listed first, we have the following correspondence: 1=11 000, 2=21 100, 3=31 110, 4=22 110, 5=22 200, 6=41 111, 7=32 111, 8=32 210, 9=42 211, 10=33 211, 11=33 220, 12=43 221, 13=44 222.

**Table 4**
The steady state probability distribution over the states in the $n_1 = n_2 = 2$ case. The states in row one are defined as (in order) the number of $B$s connected to; neither $J$, only $J_1$, only $J_2$, both $J$s. The entries in row 2 are the number of states in the original notation that are equivalent to the corresponding new form.

| State | 2000 | 1100 | 1010 | 1001 | 0200 | 0110 | 0101 | 0020 | 0011 | 0002 |
|---|---|---|---|---|---|---|---|---|---|---|
| No. orig. | 1 | 2 | 2 | 2 | 1 | 2 | 2 | 1 | 2 | 1 |
| Prob. | 2/17 | 2/17 | 2/17 | 2/17 | 1/34 | 2/17 | 2/17 | 1/34 | 2/17 | 2/17 |

**Table 5**
The steady state probability distribution over the values of $L$ in the $n_1 = n_2 = 2$ case.

| L | 0 | 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|
| Prob. | 2/17 | 4/17 | 5/17 | 4/17 | 2/17 |

calculations and simulations show that $K$ is quite small and this flat region is thus narrow, and the probabilities tail off quickly. The case with $n_1 = n_2 = 5$ is shown in Table 3 and Fig. 1.

We finally briefly consider two of the simplest cases, starting with $n_1 = 2,\ n_2 = 2$.

We can summarise any case with exactly two rows by four numbers: the number of columns with no 1s, the number with a 1 in row 1 only, the number with a 1 in row 2 only, and the number with a 1 in both rows. Each of these will represent a number of states in the original form. For the case with two columns there are 10 different states (7, allowing a swap between row 1 and row 2). The probabilities for the states are shown in Table 4. Reducing just to considering $L$ this gives Table 5.

For the case with three columns, $n_1 = 2,\ n_2 = 3$ ,there are 20 different states (13, allowing a swap between row 1 and row 2). The possible transitions between the states are shown in Fig. 2. The probabilities for the states are given in Table 6. Reducing to just considering $L$ this gives the $p = 0.4$ row from Table 2.

## 4. Discussion

The modelling of finite populations with structure has become increasingly common, following Lieberman et al. (2005). In such models the members of the population are represented by the vertices of the graph, and the links between them by the graph edges. Generally evolution happens on the graph, but the graph itself does not change (see Southwell and Cannings, 2010a, 2010b, 2010c for a model where a population and its graph evolves in a deterministic way).

In this paper we have considered a population where the individuals themselves do not change, but links between individuals change through time as a result of direct actions by the population members, where each individual has a preferred total number of links (a single number, or a range of allowable numbers). Transitions follow a Markov chain on the set of edges of the graph, where a transition to a new state occurs when an individual forms or breaks a link to another individual, as it tries to achieve its preferred number of links. For any given graph there is an associated sequence which is the collection of the number of links for each individual. Possible scenarios where this process is relevant are those of biological partner selection (Noë and Hammerstein, 1994; Noë, 2001), sociability (Capitanio, 2002; Connor et al., 1999; Sibbald and Hooper, 2004; Wiszniewski et al., 2012) and behavioural responses to epidemics (Kiss et al., 2010; Funk et al., 2009), as we have discussed in the Introduction.

As the population changes over time, it was proved in Broom and Cannings (submitted for publication) that it gets ever closer to a connected minimal set of sequences (using a distance measure called the deviation, where the graph achieves minimal deviation), and so satisfies the conflicting preferences of the population members as much as possible. In some cases, all preferences may be satisfied so that the number of edges in the graph is within the allowable range for all individuals, and then the process stops. When all individuals have a unique target, this occurs if the sequence of preferences is a graphical sequence, and so can be attained by some graph.

We demonstrated that once the minimal set is reached, the Markov chain is reversible, and so that the detailed balance conditions apply. This then provided a method for finding the stationary distribution for the case where there is a unique target, both over the specific graphs and potentially the sequence of scores (but see Section 3.3) within the population.

**Table 6**
The steady state probability distribution over the states in the $n_1 = 2,\ n_2 = 3$ case. The states in row one are defined as (in order) the number of *B*s connected to; neither *J*, only $J_1$, only $J_2$, both *J*s.

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| State | 3000 | 2100 | 2010 | 2001 | 1200 | 1110 | 1101 | 1020 | 1011 | 1002 |
| Prob. | 18/172 | 18/172 | 18/172 | 12/172 | 9/172 | 12/172 | 12/172 | 9/172 | 12/172 | 6/172 |
| State | 0300 | 0210 | 0201 | 0120 | 0111 | 0102 | 0030 | 0021 | 0012 | 0003 |
| Prob. | 3 /172 | 3/172 | 6/172 | 3/172 | 6/172 | 6/172 | 3/172 | 6/172 | 6/172 | 4/172 |

We considered a specific example, the “All or Nothing” system, where the population was split into two types, *J*s which want to maximise their number of links, and *B*s which want to minimise this number. We found an explicit form for the stationary distribution for the general All or Nothing system, and also for some special cases. One problem we encountered was that the total number of states quickly becomes large, and so in practice it can still be difficult to explicitly write the distribution of *L*, the total number of links (the probability of each graph can be found, but there are too many that correspond to *L* to be added systematically).

We finally considered some special cases of the All or Nothing system where we could avoid the above problem by considering approximate results where either the number of *B*s was much smaller than the number of *J*s, or vice versa, or finding exact results when both numbers were small.

There are a number of potential future developments. In this first paper we concentrated on introducing the random process and some basic results, and then moved to look at the All or Nothing system. A more systematic investigation of the system in its most general case still needs to be carried out, and similarly further investigation of the unique target case in its most general form is needed.

Secondly, currently individuals break or form links to get closer to their ideal values, but they make no choice in relation to which links are formed or broken. It may be that some choices are better than others (e.g. joining to another who is not averse to the link may be better than to one who may subsequently break the link, especially if there is some cost to the act of joining or breaking). Thus such choices could be introduced. This could become particularly complicated, however, if individuals had memories of the previous choices of others, and initially memoryless models would be easiest to consider.

One way for some links to be preferable to others is if individuals prefer to be connected to those also linked to their neighbours, so called “transitivity preferences” e.g. Marvel et al. (2011). A friend of a friend may thus be more likely to be an individual's friend too than a random individual is, and in the extreme limit all connected individuals would form non-overlapping cliques. We could incorporate this into our model by having a target function that included not just the number of links of the individual, but also the links of connected individuals too (though it would be important to consider what an individual would reasonably know about the connections of those it is connected to).

A third possibility is where only some of the possible links are allowed. Thus, we may imagine a spatially distributed population and individuals may only be able to form links with their close neighbours. Thus a similar process to that described in this paper would occur on a reduced edge set of allowable links. This may help with the problem of counting that we encountered in Section 3.3.

Ultimately, it will be of interest to introduce an evolving population into our model, as in many of the models described in the Introduction. We can consider games played across the network so that at any time point an individual plays a game against all of its neighbours, as in standard evolutionary graph theory models. Individuals would receive a payoff determined by (for example) the average of such contests at that timepoint, and so given the distribution of different states on the graph, we can evaluate the expected payoff of both *B*s and *J*s in a system containing $n_1$ *J*s and $n_2$ *B*s. In any situation we can thus compare the fitnesses of both *J*s and *B*s, with the process evolving so that an individual is replaced by one of the other type (because either individuals reproduce or change strategy according to fitness).

As the composition of the population changes, the preferences of the individuals also change, and so the dynamics of the network will alter. Thus there would be a co-evolutionary system where both the occupants of vertices and the edge set of the graph evolve co-dependently (see Rand et al., 2011; Perc and Szolnoki, 2010 for work in this area). What is the long term distribution of *J*s and *B*s? Can there be a number of equilibria? If sophisticated strategies which base their likelihood of forming/breaking links based upon previous games with the individuals concerned (e.g. prefer to connect to cooperators in a Prisoner's Dilemma) are allowed, then they will likely prevail. There are many ways to make our model more realistic (and more complicated), and our priority will be to develop those which allow at least some analysis.

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