Modelling evolution in structured populations involving multiplayer interactions

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Outline

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Credits

This work is based upon the papers

- Broom, M. and Rychtar, J. (2012) A general framework for analysing multiplayer games in networks using territorial interactions as a case study *Journal of Theoretical Biology* 302 70-80,
- Broom,M., Lafaye, C., Pattni,K. and Rychtar, J. (2015) A study of the dynamics of multi-player games on small networks using territorial interactions *Journal of Mathematical Biology* (to appear),

and supported by a studentship funded by the City of London Corporation awarded to Karan Pattni.

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Animals' territorial behaviour

- Many animals live alone or in distinct groups on a well-defined territory and forage for food almost exclusively within that territory. Similarly, males of the species may occupy territories for the purposes of mating.
- In either case, territories will often be defended against rivals and so interactions occur at the boundaries of territories. In this scenario, we think of non-overlapping areas with interaction only at the borders.
- Often the area that an animal or group uses for foraging is not exclusive to itself, but can overlap considerably with the territories of others.
- In this case the more general term *home range* is used for the area that an individual or group utilises.
- There will be parts of the environment claimed by two or more individuals/groups and there can be interactions between them, especially over major items of food.

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An example: the territorial behaviour of wild dogs

- Woodroffe, R. 1997. The African Wild Dog: Status Survey and Action Plan. IUCN/SSC Canid Specialist Group, IUCN Publications, Gland Switzerland describes aspects of the territorial behaviour of wild dogs in Africa.
- The size of home ranges varies considerably from site to site, ranging from 500 sq km up to 1500 sq km.
- Packs use smaller areas when they are feeding pups at a den.
- Home range overlap is substantial and varies (from 50% to 80%), see Ginsberg & Macdonald 1990. Foxes, Wolves, Jackals and Dogs - An Action Plan for the Conservation of Canids. IUCN/SSC. Gland, Switzerland.
- There are thus parts of territories where there can be interactions between different dog packs.
- The size of the regions of interaction can vary throughout the year.

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Evolution on graphs

- Within the last ten years, models of evolution have begun to incorporate structured populations using evolutionary graph theory.
- Let $G = (V, E)$ be a simple, finite, undirected and connected graph, where V is the set of vertices and E is the set of edges.
- V represents the set of individuals in the population, and E the connections between pairs of individuals.
- It is usually assumed that individuals are of two different types, residents (R) and mutants (M).
- When pairs of individuals interact, they play a game, with reward a for a mutant against a mutant, b for a mutant against a resident, c for a resident against a mutant and d for a resident against a resident.
- Individuals play a game against all of their neighbours, and their fitness is the average reward from these contests.

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Evolutionary dynamics on graphs

- At the beginning, a vertex is chosen uniformly at random and replaced by a mutant.
- Subsequently at each time step, following the Invasion Process dynamics, an individual is selected to reproduce with probability proportional to its fitness.
- The selected individual then copies itself into a random neighbouring vertex, replacing the individual there.
- We follow the set C of vertices occupied by mutant individuals.
- The states $\emptyset$ and V are the absorbing points of the dynamics, and we are particularly interested in the fixation probability, the probability of the end state being V.

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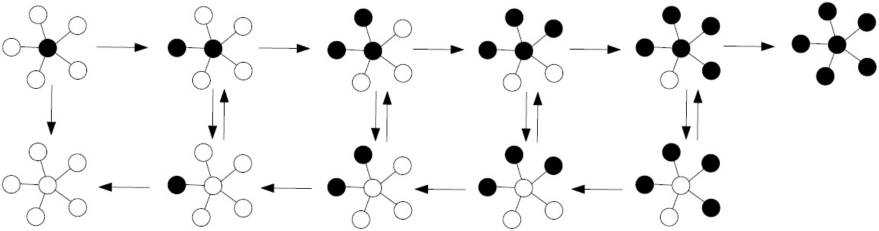
An example graph: the star graph



The distinct states of a star graph with $n = 5$ leaves.

We are typically interested in comparing properties such as the fixation probability of a graph to that of the well-mixed population, where every pair of individuals is connected (i.e. E contains all possible edges).

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A limitation of evolutionary graph theory

- One limitation of this otherwise quite general framework is that interactions are restricted to pairwise ones, through the graph edges.
- Many real animal interactions can involve many players, and theoretical models also describe such multi-player interactions.
- We discuss a more general framework of interactions of structured populations focusing on competition between territorial animals.
- We can embed the results of different evolutionary games within our structure, as occurs for pairwise games on graphs.
- Graph models have three elements: graph, game and dynamics. We thus need a more general mode of interaction, potentially multi-player games and an appropriate dynamics.

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The population and its distribution

- We consider a population of N individuals $I_1, \ldots, I_N$ who can move to M distinct places $P_1, \ldots, P_M$.
- Let $X(t) = (X_{n,m}(t))$ be a binary $N \times M$ matrix representing if an individual I_n is at place P_m; i.e.

$$X_{n,m}(t) = \begin{cases} 1, & \text{if } I_n \text{ is at a place } P_m \text{ at time } t, \\ 0, & \text{otherwise.} \end{cases}$$

- We write
  $P(X(t) = x)(x_{<t}) = P(X(t) = x | X(1) = x_1, \ldots, X(t-1) = x_{t-1})$.
- Let $p_{n,m,t}(x_{<t}) = P(X_{n,m}(t) = 1)(x_{<t})$ denote the probability of I_n being at P_m at time t given the history $x_{<t}$.
- The *home range* of an individual I_n is defined by
  $\mathcal{P}_n = \{P_m : p_{n,m,t}(x_{<t}) > 0 \text{ for some } t \text{ and history } x_{<t}\}$.

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Concepts of independence

- The population follows a random process, which can depend upon its entire history. There are simplifications based upon different types of independence. Two important examples are as follows:
- If a given population distribution is independent of the history of the process so that

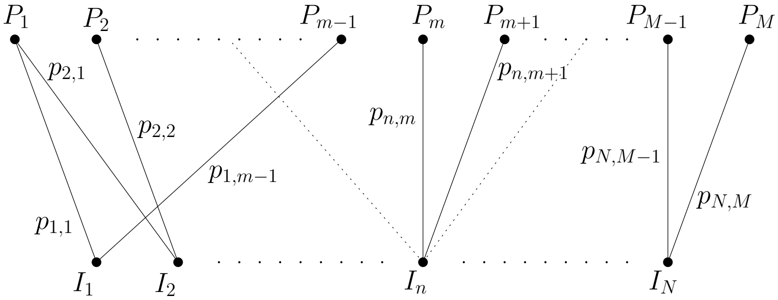
$$P(X(t) = x)(x_{<t}) = P(X(t) = x)$$

we call the model *history-independent*. We call a history independent process *homogeneous* if $P(X(t) = x) = P(X = x)$.
- If the probability of an individual visiting a place depends only upon the individual and the place, but not upon other individuals, the history or the time then

$$p_{n,m,t}(x_{<t}) = p_{n,m} \qquad \forall n, m, t, x_{<t}.$$

In this case we simply call the model *independent*.

A bipartite graph representation of the independent model



The independent model as a bipartite graph. The weight between the vertex representing individual I_n and patch P_m is $p_{n,m}$.

Fitness

- The reward for individual I_n at time t is denoted $R(n, x, t, x_{<t})$.
- If only the current distribution affects the reward, we can use the *mean reward* as the fitness $F_n = \sum_x P(X = x)R(n, x)$.
- The group G of individuals meeting on P_m is $G = \{I_j; x_{j,m} = 1\}$.
- Let $P(X_{\circ,m} = \chi_G)(x_{<t})$ be the probability of group G meeting on P_m at time t. For the independent model we obtain

$$P(X_{\circ,m} = \chi_G) = \prod_{j \in G} p_{j,m} \prod_{j \notin G} (1 - p_{j,m}).$$

- Often the reward to an individual will only depend upon the place that it occupies and the group of individuals on that place so $R(n, x) = R(n, m, \chi_G)$ and

$$F_n = \sum_{m=1}^{M} \sum_{G} P(X_{\circ,m} = \chi_G)(x_{<t})R(n, m, \chi_G).$$

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The territorial interaction model I

- Consider a scenario where there are three individuals I_1, I_2, I_3 and each can move freely within a territory in a shape of a square.
- The individual's territories overlap, creating six distinct places $P_1, \dots, P_6$.
- Assuming the territories are relatively small and that individuals roam freely and randomly, we may assume that at any given time, the probability of an individual being on a place within its own territory is proportional to the area of the place.
- We thus get an independent model with

$$(p_{n,m}) = \begin{pmatrix} \frac{1}{2} & \frac{1}{4} & \frac{1}{4} & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{4} & \frac{1}{2} & \frac{1}{4} & 0 \\ 0 & \frac{1}{4} & \frac{1}{4} & 0 & \frac{1}{4} & \frac{1}{4} \end{pmatrix}.$$

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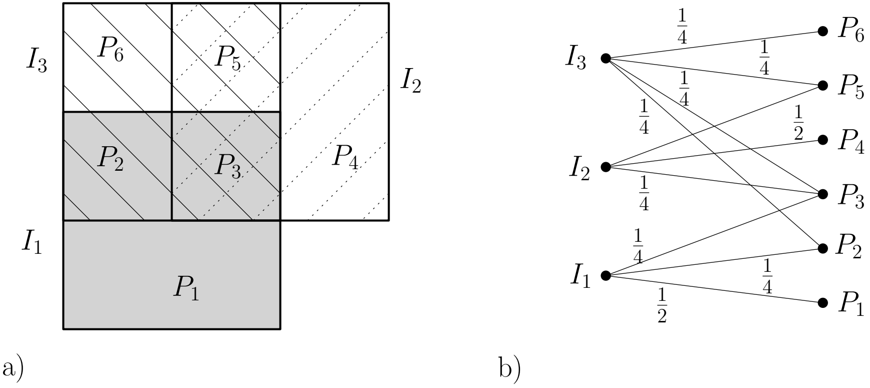
The territorial interaction model II



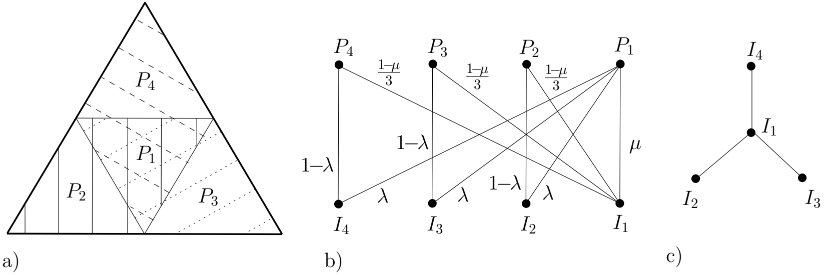
The territory of I_1 is the grey square, the territory of I_2 is the square with dotted lines, the territory of I_3 is the square with solid lines.

The territorial raider model I

- Now, consider a special case of the territorial interaction model. Individuals $I_1, \ldots, I_N$ each occupy their own place $P_1, \ldots, P_N$.
- We consider an example of a star graph with four individuals.
- Each leaf individual has probability of moving to the centre λ. The centre individual has probability of staying in the centre is μ, going to each leaf with equal probability $(1-\mu)/3$ otherwise.
- In particular we consider a specific class with a single *home fidelity* parameter h, where $\mu = h/(h+3)$ and $\lambda = 1/(h+1)$.
- We thus have the following probabilities of movement

$$(p_{n,m}) = \begin{pmatrix} \frac{h}{h+3} & \frac{1}{h+3} & \frac{1}{h+3} & \frac{1}{h+3} \\ \frac{1}{h+1} & \frac{h}{h+1} & 0 & 0 \\ \frac{1}{h+1} & 0 & \frac{h}{h+1} & 0 \\ \frac{1}{h+1} & 0 & 0 & \frac{h}{h+1} \end{pmatrix}.$$

The territorial raider model II



a) Individual I_n lives in place P_n but can raid neighbouring places. The territory of I_1 is the whole triangle, the territory of I_2 is the rhombus encompassed by full lines etc; b) representation as a general independent model; c) visualization as multi-player interactions on a graph.

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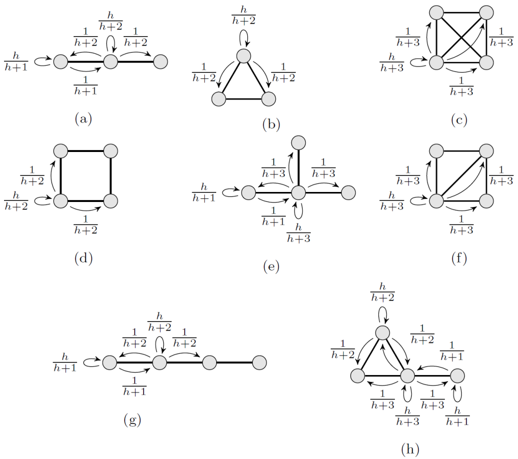
The territorial raider model III

The population structures and movement probabilities for small graphs on 3 and 4 vertices. (a) 3 vertex line, (b) triangle, (c) 4 vertex complete graph, (d) 4 vertex “circle", (e) 4-vertex star, (f) diamond (g) 4 vertex line, (h) paw.



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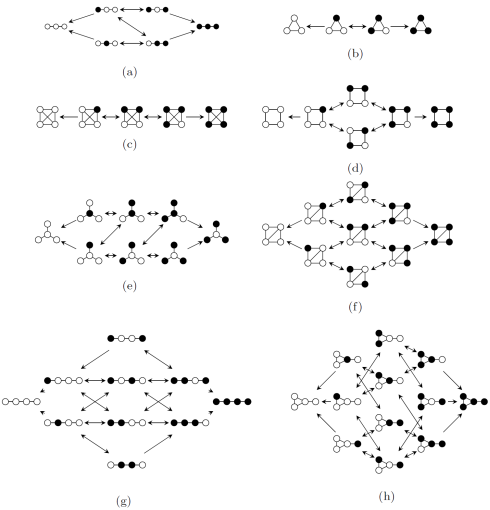
The territorial raider model IV

The transition graphs for small graphs on 3 and 4 vertices.



(a) (b) (c) (d) (e) (f) (g) (h)

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An evolutionary dynamics I

- Let b_i denote the probability an individual I_i is selected for reproduction where, $b_i = F_i / \sum_k F_k$.
- Let d_{ij}, for $i \neq j$, denote the probability that I_j is replaced by a copy of I_i given I_i is selected for reproduction.
- We calculate d_{ij} by considering all possible places P_m and all possible groups $G \subset \{1, 2, \ldots, N\}$ involving both individuals i and j; weighted by $\chi(m, G)$, the probability of the group G meeting at place P_m, and by a factor $(|G| - 1)^{-1}$ representing the fact that in a group G, an individual I_i could replace any one of $|G| - 1$ other individuals.

$$d_{ij} = \sum_{m=1}^{N} \sum_{G:i,j \in G} \frac{\chi(m, G)}{|G| - 1}, \text{ where}$$

$$\chi(m, G) = \prod_{k \in G} p_{km} \prod_{k' \notin G} (1 - p_{k'm}).$$

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An evolutionary dynamics II

Letting $P_{SS'}$ denote the transition probability from state S to state S' in the dynamic process of our game, for $S \neq S'$ we have

$$P_{SS'} = \begin{cases} \sum_{i \notin S} b_i d_{ij}; & \text{if } S' = S \setminus \{j\} \text{ for some } j \in S \\ \sum_{i \in S} b_i d_{ij}; & \text{if } S' = S \cup \{j\} \text{ for some } j \notin S \\ 0; & \text{otherwise} \end{cases}$$

and we set

$$P_{SS} = 1 - \sum_{S' \neq S} P_{SS'}.$$

An evolutionary dynamics III

- The *temperature* of the I-vertex I_j is

$$T_j = \sum_{i \neq j} d_{ij}.$$

- Let ρ_S^A be the probability that A fixates from state S, where

$$\rho_S^A = \sum_{S' \subset \{1,2,\ldots,N\}} P_{SS'} \rho_{S'}^A$$

  with boundary conditions $\rho_\emptyset^A = 0$, $\rho_V^A = 1$.
- The mean fixation probability of A, ρ^A, is defined as

$$\rho^A = \sum_i \frac{T_i}{\sum_j T_j} \rho_{\{i\}}^A.$$

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An example game

- We consider a multi-player game with strategies Hawk and Dove, competing for a single reward, value V, where each individual has a "background" reward R irrespective of their strategy.
- If all individuals in a fighting group are Doves, they split the reward, so each receives the reward divided by the number in the group.
- If there are any Hawks, all the Doves flee and get 0, all the Hawks fight and one of them receives the reward, and all of the others receive a cost C.
- Thus if we denote $R^D_{a,b}(R^H_{a,b})$ the reward for a Hawk (Dove) within a group with a Hawks and b Doves (including itself), we get

$$R^H_{a,b} = R + \frac{V-(a-1)C}{a}, \quad R^D_{a,b} = \begin{cases} R; & \text{if } a > 0 \\ R + \frac{V}{b}; & \text{if } a = 0 \end{cases}.$$

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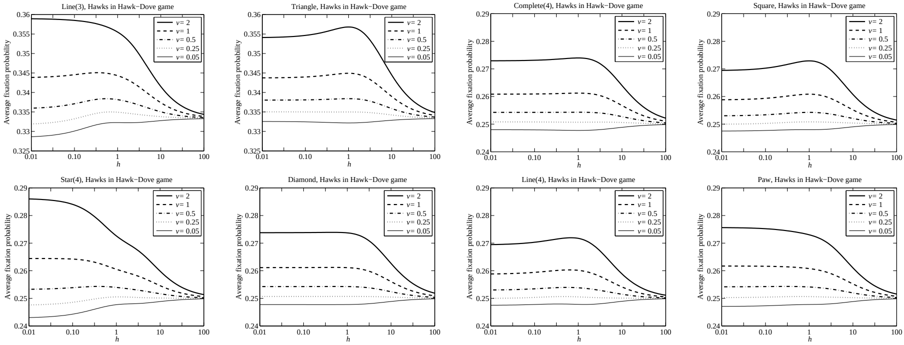
Outline

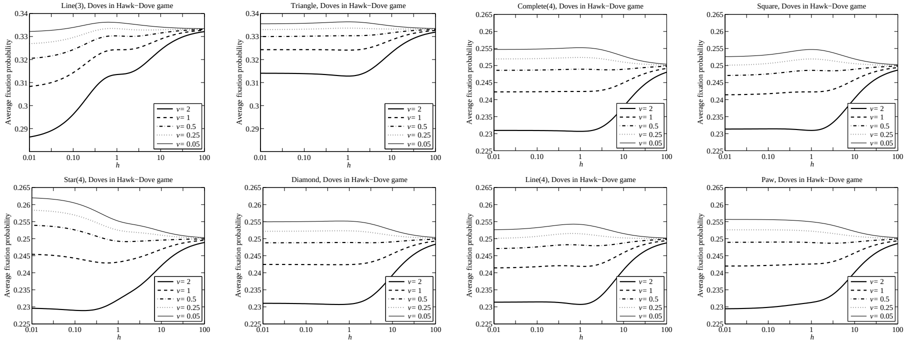
Hawk fixation probability in a Dove population

The fixation probabilities of a single Hawk in a population of Doves for small graphs on 3 and 4 vertices.



Dove fixation probability in a Hawk population

The fixation probabilities of a single Dove in a population of Hawks for small graphs on 3 and 4 vertices.



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Discussion I

- We have developed a new framework for modelling game theoretical interactions in a structured population.
- The framework incorporates three key components: population structure; evolutionary dynamics; evolutionary game.
- A useful area of application of our model is in animal territorial behaviour.
- Different species can exhibit different types of territoriality, and a flexible system of modelling this is required.

Discussion II

- Evolutionary graph theory has made, and continues to make, important contributions to the understanding of the effect of population structure.
- Our framework has some advantages over standard evolutionary graph theory.
- For example, multi-player games can be explicitly modelled in our structure.
- In addition, there is a natural (and more logical) way of converting aggregated game payoffs into fitness.

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Discussion III

- Following a recently accepted paper, we have considered an example which incorporates all three key aspects of our framework.
- In particular we have developed a birth-death dynamics and a natural way to find the fixation probability of a rare mutant for any population structure.
- We have seen that key features of the structure, including the temperature and the mean group size, have a strong influence on the fixation probability.
- For example, high temperature amplifies the influences of the key game parameters like the reward, increasing the fixation probabilities of the fitter individuals, and decreasing the fixation probabilities of the weaker individuals.

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Discussion IV

- An important next step in this work is to more fully incorporate evolutionary dynamics in the new framework.
- In evolutionary graph theory, there are a number of dynamics reflecting different biological scenarios. In particular we need to develop death-birth dynamics, as well as alternative birth-death dynamics.
- Another aspect that needs development is the analysis of more realistic populations.
- This requires larger populations, and also populations that have differing numbers of places and individuals, i.e. which are not "graph-like".
- The above work is ongoing. We note that this research is still in its relatively early stages.

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