General modelling framework: developments, outlook and applications

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Game Theoretical Modelling of Evolution in Structured Populations
NIMBioS
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Outline

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Credits and caveats

- This work is based upon various as yet unpublished ideas of Mark Broom, Karan Pattni and Jan Rychtar.
- It is thus rather speculative, and results may not be completely reliable.
- I will give some indication as to the reliability of each statement as appropriate.
- I have also thrown in a few thoughts gathered during the course of this workshop, which are likely to be even more questionable!

Outline

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General replacement weights

- In Broom et al.[1] (2015) our population evolved using the BDB dynamics $b_i d_{ij}$, where individuals reproduced proportional to fitness, and then replaced a randomly selected groupmate.
- This involved the following weights related to the group size

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

- Combining the above, the population evolved until fixation of one type.

[1]Broom,M., Lafaye, C., Pattni,K. and Rychtář, J. (2015) A study of the dynamics of multi-player games on small networks using territorial interactions *Journal of Mathematical Biology* 71 1551-1574.

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General dynamics

Using these specific weights, we can apply the set of evolutionary dynamics applied to evolutionary graph theory for arbitrary weights, which can be summarised as given below

$$\text{BDB} \qquad b_i = \frac{F_i}{\sum_n F_n},\ d_{ij} = \frac{w_{ij}}{\sum_n w_{in}}$$

$$\text{BDD} \qquad b_i = \frac{1}{N},\ d_{ij} = \frac{w_{ij}F_j^{-1}}{\sum_n w_{in}F_n^{-1}}$$

$$\text{DBD} \qquad d_j = \frac{F_j^{-1}}{\sum_n F_n^{-1}},\ b_{ij} = \frac{w_{ij}}{\sum_n w_{nj}}$$

$$\text{DBB} \qquad d_j = \frac{1}{N},\ b_{ij} = \frac{w_{ij}F_i}{\sum_n w_{nj}F_n}$$

$$\text{LB} \qquad \mathfrak{r}_{ij} = \frac{w_{ij}F_i}{\sum_{n,k} w_{nk}F_n}$$

$$\text{LD} \qquad \mathfrak{r}_{ij} = \frac{w_{ij}F_j^{-1}}{\sum_{n,k} w_{nk}F_k^{-1}}$$

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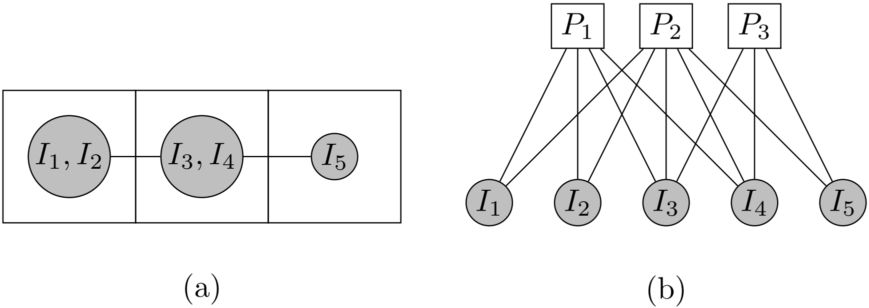
Generalised populations on graphs

- We can consider a population represented by a graph, where each vertex is home to a subpopulation of individuals.
- The population thus behaves like a network of well-mixed populations.
- Each of these populations can have any size, including zero.
- We will be interested in the impact of the subpopulation sizes on important properties of populations.
- There are links to island models of the evolution of populations.

Representation of a generalised population



A model of a population with subpopulations on a graph. a) Individuals of subpopulation Q_m live on place P_m but can visit neighbouring places. b) An alternative visualization on a bi-partite graph where individuals and places are separated.

A multiplayer public goods game

- Consider the public goods game defined in Broom et al. (2015).

$$R^A_{a,b} = \begin{cases} -1, & a = 1 \\ -1 + \frac{a-1}{a+b-1}v, & a > 1 \end{cases}$$

$$\text{and} \quad R^B_{a,b} = \begin{cases} 0, & a = 0 \\ \frac{a}{a+b-1}v, & a > 0 \end{cases}.$$

- Using the above we followed the evolution of various populations on a graph.

Some early results regarding public goods games

- These consisted of a complete graph where the subpopulations were of sizes 0 up to 12.
- As is commonly the case, only the BDD and DBB type dynamics allow cooperation to evolve.
- The key feature of cooperating populations seems to be the existence of small and stable subgroups.
- We have also developed the concept of the temperature as applied to our framework from Broom et al. (2015), and find a very strong relationship between the fixation probability of a cooperator (defector) and the temperature.

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An independent model with strategic movements

- In a recently submitted paper, Broom and Rychtář consider a model of animal movement following the independent model from previous work.
- We again assume all individuals have no knowledge of the choices of others, so all move independently.
- However this time the movement probabilities are selected strategically.
- Examples include the distribution of foragers over habitats, where the aim could be to maximise food intake and/or minimise the risk from predators.
- How should individuals select their moves, and what distributions are stable?

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Stable occupancy and optimal group size

- Let us assume that the fitness of individuals only depends upon the size of the group that it finds itself in.
- For foraging scenarios small groups are best, as this minimises competition.
- For games involving predation, large groups are often best, due to the “dilution effect”.
- In other scenarios, including those combining the above, intermediate sizes are best.

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Some distributional results

- When smallest group size is optimal, then for a well-mixed population we recover (a finite version of) the habitat selection game.
- When there is some restriction to individual movements, this is not the case (see the following slide).
- When largest group size is optimal, we have a method of generating all stable collections of group sizes, but there may be many of them.
- For well-mixed populations, this reduced to a single group including the whole population.
- For intermediate group sizes the situation is more complex.

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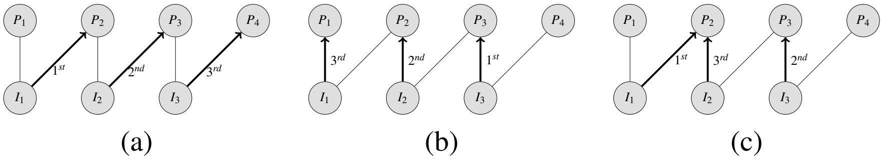
Habitat selection with restricted movement



The habitat selection game with payoffs satisfying
$R_2(1) > R_3(1) > R_4(1) > R_1(1) > R_2(2) > R_3(2)$.
a) and b) show different stable occupancy functions for different orders at which individuals choose their places. c) shows an order under which no stable occupancy is reached.

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A Markov model

- For the independent model, it was assumed that all movements of an individual are independent and identically distributed.
- However, we are also working on population models where movement depends upon the past behaviour of the individual, and often of others.
- For example if at any given time all individuals move independently, and that this depends only upon the last move of the population then we have one version of the Markov model

$$p_{n,m,t}(x_{<t}) = p_{n,m,t}(x_{t-1}) \qquad \forall n, m, t, x_{<t}.$$

- Note that alternatively individuals may not move independently, or they may move independently depending upon their own last move only.

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Public goods games and strategic movements

- We use the same multiplayer public goods game as described above.
- Individuals move according to the types of their groupmates, as a function of $|C| - |D|$, the difference between the number of cooperator and defector groupmates.
- Thus individuals of either type that have many cooperating groupmates remain, those with many defecting groupmates move, to a random new location.
- Fast movement enables cooperators to find other cooperators, but also enables them to be found by defectors.
- Very slow movement prevents cooperators from finding other cooperators.

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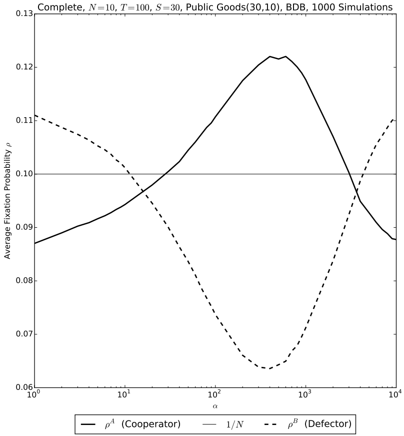
Some preliminary results



In the figure, the higher the parameter α, the less individuals move. We see that cooperation can evolve for intermediate movement.

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Modelling territoriality in animal populations

- This is the most natural application of our methods.
- We could consider boundary conflicts or incursions into the territory of other individuals or groups, such as in the territory raider model.
- Alternatively individuals may travel to different habitats to forage, where they interact, for example as in seabird colonies.
- Here the structure represents a physical location, and movements are physical movements.
- Short term movements, where animals return to a den or roost might be modelled using the independent model. For animals that move over larger territories, such as wild dogs, the Markov model might be more appropriate.

Modelling the evolution of cancer

- In recent years we have seen the development of the modelling of cancer as an evolutionary process.
- The players of the evolutionary game are the cancer cells, within the environment of the body.
- Thus our population structure could represent human organs.
- Then we need to develop the appropriate structure for any given scenario.
- External intervention in the form of treatment would then adjust some of the model parameters.

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Modelling complex human or animal social interactions

- A further potential development of our framework is the interaction of human or animal groups.
- Here places are not necessarily physical, but represent an action related to a position in society, for example in a dominance hierarchy.
- Movement then represents interactions between individuals.
- A static structure of permanent relationships, but with ever changing meetings, could be represented by the independent model.
- For societies with evolving relationships, then Markov or more complex models would be needed.

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NIMBios thoughts I: investigating other properties

- For some populations, the distribution of a quasi-stationary equilibrium (especially its mean) may be more appropriate than fixation probability (or time).
- For example this could be useful for the multi-player Hawk Dove game.
- Associated with this we could consider the population variance.
- We could consider alternative properties that evolve, e.g. according to the Price equation.
- We might have multiple types of individuals with different cooperative levels.

NIMBioS thoughts II: some ideas for spatial distributions

- The spread of wild pig populations.
- Here the pigs‘ spread is mainly due to human action, which can move them between different areas, bypassing those between them.
- Competing plant root systems.
- Plants send roots into neighbouring sites to compete with their neighbours. The population structure can potentially have a great effect on the root density, and consequently on fitesses.
- This is very similar to the army territorial raider game.

NIMBioS thoughts III: less stochasticity

- Making some framework parts non- (or “less”) stochastic.
- Groups can be more permanent, with within and between group competition.
- The presence of a structure, allowing individuals to interact locally (for example with their own offspring), helps cooperative behaviour to occur, and already relates to the above.
- Non-stochastic dynamics can occur, for example using tipping points.
- This is perhaps an extreme example, but nevertheless may sometimes approximate stochastic processes.

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Outline

1. Credits
2. A full set of evolutionary dynamics
3. Strategic movements in structured populations
4. Non-independent movements
5. Applications to real populations
6. NIMBioS thoughts
7. **Some conclusions**

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Conclusions I

- We have now developed our framework to include:
  - a range of dynamics
  - subpopulations
  - strategic movements
  - history-dependent movement
- This starts to open up a range of potential applications.
- These include diverse situations such as animal territoriality, cancer modelling, and human or animal social interactions.

Conclusions II

- From this workshop we have also discovered a number of additional ideas, including the following.
- Following different evolutionary properties to the standard fixation probability/ time.
- Additional spatial type models, using human intervention or applications of the army model.
- Ideas for considering more permanent groups.

Conclusions III

- We will continue to work in some of these areas, in particular continuing with our current partially developed models.
- We hope that you will also be interested in using these ideas and those of the various workshop speakers in your own work.
- We would be particularly interested in hearing about any examples where you do this.
- We are still at the relatively early stages of developing the modelling framework, and so any ideas on this are also welcome!