
Conflict, Competition, Cooperation & Complexity:

Using Evolutionary Game Theory to model realistic populations

<http://web.evolbio.mpg.de/cccc16/>

**Max Planck Institute
for Evolutionary Biology, Plön
January 13th-15th, 2016**



Max-Planck-Institut für
Evolutionsbiologie, Plön

1 General information

1.1 Travel

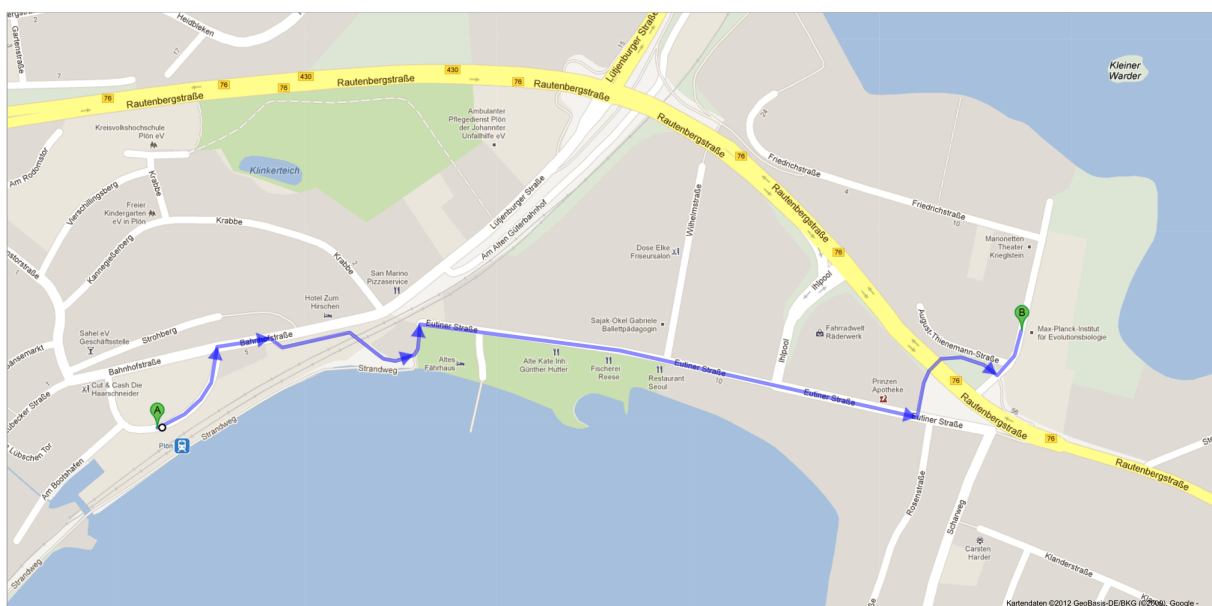
You can reach Plön from Hamburg airport by public transport via Kiel or via Lübeck. We recommend to check out your individual travel plan on the official website of DB: http://www.bahn.de/p_en/view/index.shtml.

- via Kiel: From 07:15, an hourly shuttle-bus departs from Hamburg airport to Kiel. Tickets can be bought directly in the bus: http://www.bahn.de/autokraft/view/angebot/kielius_en/kielius-ueb.shtml.

From Kiel train station you can take the train to Lübeck or Lüneburg which also stops in Plön. The journey from Hamburg airport to Plön via Kiel takes a little more than 2 hours.

- via Lübeck: From Hamburg airport on Platform 2 take the Train S1 to Hamburg central station. In Hamburg Airport you can also find ticket machines from *DB*, where you can buy your ticket for the whole trip to Plön.

From Hamburg central station you then take the train to Lübeck which usually departs from platform 6. In Lübeck you have to change into the train to Kiel which also stops in Plön. The journey via Lübeck takes between 2 and 3 hours.



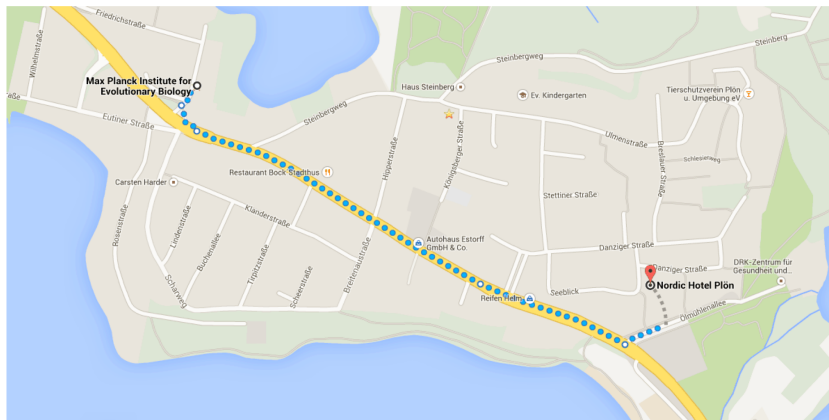
1.2 Hotel information

The address of the Nordic Hotel Plön is Ölmühlenallee 3. You can reach it from the train station either by foot (20 Minutes) or by bus number 331 (stop Fegetasche). For further information about the hotel, you can check their website <http://www.nordic-hotels.com/en/hotels/ploen-nordic-hotel-ploen/>.



Walk 1.2 km, 15 min

Directions from Max Planck Institute for Evolutionary Biology to Nordic Hotel Plön



○ Max Planck Institute for Evolutionary Biology

Use caution - may involve errors or sections not suited for walking

August-Thienemann-Straße 2, 24306 Plön

1. Head south on August-Thienemann-Straße 49 m
2. Turn left toward Rautenbergstraße/B76 70 m
3. Turn left onto Rautenbergstraße/B76 650 m
4. Slight left to stay on Rautenbergstraße/B76 300 m
5. Turn left onto Ölmühlenallee 92 m
i Destination will be on the left

○ Nordic Hotel Plön

Ölmühlenallee 3, 24306 Plön

1.3 Lunch/Coffee

Between the sessions there will be a coffee break with coffee and snacks. Lunch will be provided in the institute.

1.4 Social event / dinner on Thursday

On Thursday there will be conference dinner for all participants:

- Location: "Landgasthof Kasch", Dorfstrasse 60, Timmdorf/Malente
- Meeting time in front of the institute: 17:45
- Dinner includes warm buffet and drinks
- Transfer from the Institute to the restaurant and back to the hotel will be organized

1.5 WiFi

WiFi is accessible for EDUROAM users in the institute. In case you do not have access to eduroam we will provide you with an account for our guest net.

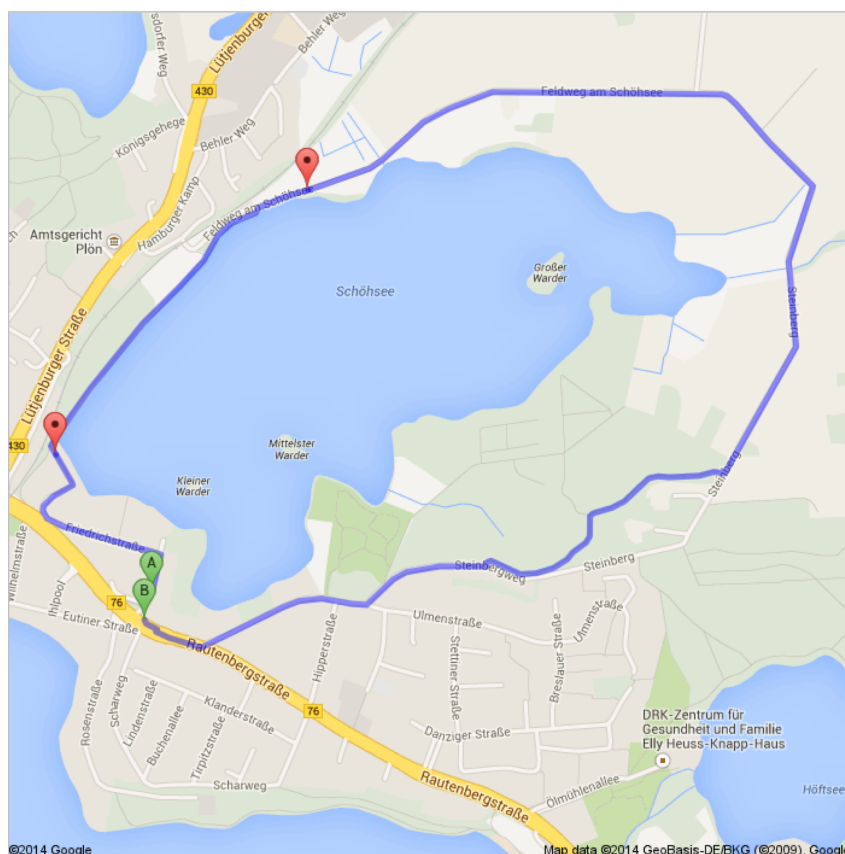
Please ask either Ursula Krützfeldt for help.

We encourage you to use our computers (Mac Mini / Windows) to present (we have PDF viewer, Office 2007 on Windows and Keynote 6.2 on Mac OSX). Please

2 Introduction to Plön

Plön is the district seat of the Plön district in Schleswig-Holstein, Germany. It has about 8,700 inhabitants. Plön is almost an island in the middle of 5 different (but mostly connected) lakes. The biggest one, the Grosser Plöner See (Great Plön Lake) has a circumference of almost 40 kms. The town's landmark is Plön Castle, a chateau built in the 17th century on a hill overlooking the town.

The town, nestled as it is in the rolling, wooded lake district of Holstein Switzerland (Holsteinische Schweiz), also has importance in the tourism industry. A morning walk around the Schöhsee behind the Max Planck Institute is recommendable (see below).



3 Program

WEDNESDAY JANUARY 13th

- 9.00 *Welcome*
- 9.30 Hauert
- 10.30 Discussion
- 11.00 **Coffee break**
- 11.30 Krivan
- 12.00 Xu
- 12.30 Revilla
- 13.00 **Lunch**
- 14.30 Garay
- 15.00 Boza
- 15.30 Abou Chakra
- 16.00 Peña
- 16.30 **Coffee break**
- 17.00 The RISE grant - introduction - Mark Broom
- 17.30 Discussion of issues
- 18.00 individual dinner

THURSDAY JANUARY 14th

- 9.00 Leimar
- 10.00 Discussion
- 10.30 **Coffee break**
- 11.00 Candan
- 11.45 Brown
- 12.30 **Extended lunch and research discussions**
- 14.30 Allen
- 15.00 Peeters
- 15.30 Argasinski
- 16.00 **Coffee break**
- 16.30 Further research discussions
- 17.30 Group dinner at Landgasthof Kasch - Transport will be organized

FRIDAY JANUARY 15th

- 9.00 Traulsen
- 9.30 Gallie
- 10.00 Huang
- 10.30 **Coffee break**
- 11.00 Pattni
- 11.30 Broom
- 12.00 Rychtar
- 12.30 Wrap up and lunch snack

Speakers, titles and abstracts

Christoph Hauert *Origin and Structure of Social Networks Based on Cooperative Actions*

Abstract: Societies are built on social interactions. A novel theoretical framework to model dynamic social networks focusses on individual actions instead of interactions between individuals and thereby eliminates the traditional dichotomy between the strategy of individuals and the structure of the population. As a consequence, altruists, egoists and fair types are naturally determined by the local social structures while globally egalitarian networks or stratified structures can arise. Cooperative actions drive the emergence and shape the structure of social networks. This is confirmed in human behavioural experiments. Highly egalitarian social networks readily form based on individual behaviour dominated by egalitarian motives and inequity aversion, which manifests itself in that individuals tend to provide benefits to the less successful while withdrawing benefits from the more successful.

Vlastimil Krivan *Game-theoretic methods for functional response and optimal foraging behavior*

Abstract: We develop a decision tree based game-theoretical approach for constructing functional responses in multi-prey/multi-patch environments and for finding the corresponding optimal foraging strategies. Decision trees provide a way to describe details of predator foraging behavior, based on the predator's sequence of choices at different decision points, that facilitates writing down the corresponding functional response. It is shown that the optimal foraging behavior that maximizes predator energy intake per unit time is a Nash equilibrium of the underlying optimal foraging game. We apply these game-theoretical methods to three scenarios: the classical diet choice model with two types of prey and sequential prey encounters, the diet choice model with simultaneous prey encounters, and a model in which the predator requires a positive recognition time to identify the type of prey encountered. For both diet choice models, it is shown that every Nash equilibrium yields optimal foraging behavior. Although suboptimal Nash equilibrium outcomes may exist when prey recognition time is included, only optimal foraging behavior is stable under evolutionary learning processes.

Fei Xu *Optimal Forager against Ideal Free Distributed Prey*

Abstract: The introduced dispersal-foraging game is a combination of prey habitat selection between two patch types and optimal foraging approaches. Prey's patch preference and forager behavior determine the prey's survival rate. The forager's energy gain depends on local prey density in both types of exhaustible patches and on leaving time. We introduce two game-solution concepts. The static solution combines the ideal free distribution of the prey with optimal-foraging theory. The dynamical solution is given by a game dynamics describing the behavioral changes of prey and forager. We show (1) that each stable equilibrium dynamical solution is always a static solution, but not conversely; (2) that at an equilibrium dynamical solution, the forager can stabilize prey mixed patch use strategy in cases where ideal free distribution theory predicts that prey will use only one patch type; and (3) that when the equilibrium dynamical solution is unstable at fixed prey density, stable behavior cycles occur where neither forager nor prey keep a fixed behavior.

Tomas Revilla *Pollinator foraging flexibility and the coexistence of competing plants*

Abstract: As mutualisms are being increasingly seen under the scope of consumer-resource theory, the issue of consumer choices and their effects on diversity emerges. Here we use optimal foraging theory to study the coexistence between two plants and a common pollinator. Two important details are considered: distinction between plants and plant resources, and pollinator foraging flexibility. When pollinators display fixed preferences, plant coexistence requires pollinator generalism

and weak competition (e.g. for space or nutrients). When pollinator preferences are flexible, positive feedbacks associated with mutualism increase plant competitive asymmetries, making their coexistence more difficult. This is an apparent competition effect. But on the other hand, competition for plant resources (e.g. nectar) promotes pollinator generalism, which helps with plant coexistence. The balance between these two opposite effects depends on the speed of pollinator adaptation relative to the ecological dynamics. We show how population feedbacks and time scales interact, determining the balance between positive and negative effects of mutualism on the stability and diversity of communities.

Jozsef Garay *Evolutionary stability for matrix games under time constraints*

Abstract: In ecology, since actions need different time durations, the time constraints decrease the number of active individuals and so the number of interactions, as well. Based on this, we introduced a matrix game with time constraints, when all different interactions may have different average time durations and different payoffs. We adapt Maynard Smith's evolutionary stability concept for the introduced matrix game under time constraints. The time constraints can change the solution of the prisoners' dilemma game: the cooperator strategy is ESS, if the time durations of defector strategy are long enough. The cooperator strategy is also ESS in the introduced prisoners' sharing game: when the time constraints are given by the original version of prisoners' dilemma and the payoff matrix defines how to share the common plunder, i.e. if the cooperator remains silent, and defector betrays the cooperator, then the cooperator will get the bigger part of plunder.

Gergely Boza *The stability of cooperation in different situations: with reactive investment strategies, in N-person public good games, and with spatial population structure*

Abstract: The vulnerability of cooperative behavior to exploiter or cheater strategies has been studied widely. Our aim is to relax some of the simplifying assumptions of classical game theoretical models inspired by several different biological phenomena. Firstly, often it is more natural to allow continuous and conditional investment strategies. Our aim is to understand factors promoting the emergence and stability of conditional cooperative behavior, regarded as continuous investments performed by individuals with reactive strategies. We will present a rich dynamics depending on the reactivity of investments. Secondly, we will investigate the effect of non-linear payoff-functions in group hunting, motivated by the observation that in many situations achieving the shared goal, such as capturing a prey, depends on the number of cooperators in a sigmoid manner. We demonstrate that cooperation can be stable, even when the proportion of so-called free riders is high in the population, and that division of labor can evolve in such games. Thirdly, we will investigate the effect of spatial population structure on the outcome of different games. Our study unravels a diverse dynamics of social interactions, and offers insights of how cooperative behavior can evolve and be maintained in natural or in human societies.

Maria Abou Chakra *Understanding the emergence and maintenance of mafia behaviour in brood parasites*

Abstract: Interactions between species, whether antagonistic, competitive or mutualistic, can drive the evolution and diversification of species adaptive response. Coevolution between antagonistic species involves constant adaptation and counter adaptation. One well studied example is brood parasitism, where the parasites evade all parental care by laying their eggs in the hosts nest. Parasites are considered as free-riders since they exploit the host in order to increase their own reproductive success. However, in spite of their abilities to defend themselves, some hosts are observed to cooperate with the parasite. Experimental evidence suggests that these hosts accepted a certain degree of parasitism to avoid punishment from the brood parasite. This retaliatory behaviour, the so called mafia behaviour, can emerge if the hosts can condition their response to retaliation. It is such learnt behaviour from a repeated interaction that promotes the evolution of retaliation in our model. Here,

we investigate whether retaliation can be used as a mechanism for the parasite to evade specialization and induce acceptance by the host. Retaliation might be the behaviour which helps parasites invade new ecological niches, and thus, it would be interesting to explore how spatial structure can induce the maintenance of such behaviour despite its inherent costs.

Jorge Peña *Containment and volume orders of spatially structured cooperation*

Abstract: A large body of mathematical and computational work has shown that spatial effects can greatly impact the conditions for the evolution of cooperation. Yet, a systematic comparison between alternative models of spatial structure, associated update rules, and games modelling cooperation is lacking, in particular if we move beyond pairwise interactions or mutations of small effect. Here, we introduce two general approaches to order population structures by their potential to promote the evolution of cooperation in a way that allows comparison across models: the containment order and the volume order. If population structure X is greater than population structure Y in the containment or the volume order, then X can be considered a stronger promoter of cooperation. We provide conditions for establishing the containment order, give general results on the volume order, and illustrate our theory by comparing different models of spatial games and associated update rules. Applying our theory, previously studied models of population structure can be compared and ranked, independently of the particular game representing the cooperative interactions.

Olof Leimar *Genes as cues of relatedness and social evolution in heterogeneous environments*

Abstract: The theory of kin selection explains the evolution of helping when relatives interact. It can be used when individuals in a social group have different sexes, ages or phenotypic qualities, but it does not apply when there is genetic polymorphism in helping. That kind of polymorphism, for instance cheater-cooperator polymorphism in microbes, has attracted much interest. I include these phenomena into a general framework of social evolution. The framework is built on the idea of genetic cues, which means that an individual uses its genotype at a polymorphic locus as a statistical predictor of the current social conditions, including the expected relatedness in a social group.

Selcuk Candan *Title: TBA*

Joel Brown *Using Evolutionary Game Theory to Define, Understand and Treat Cancer*

Abstract: Cancer has variously been defined as a disease of the genes, a disease of unregulated proliferation, and a disease of Darwinian evolution. While elements of all three exist for most cancers, shall focus on the role of natural selection in propelling evolution within the tumor ecosystem, the metastatic process and responses to therapy, particularly the evolution of treatment resistance. In our approach the cancer cells are a unit of selection. They are the players in the games. Their heritable phenotypes are their strategies. The tumor environment, including the associated normal cells, blood vasculature and immune cells set the rules. And the per capita growth rates of clonal lineages of tumor cells are the payoffs. We use a fitness generating function approach to model the evolutionary game that goes on among the tumor cells and between the tumor cells and the cancer therapist. An individual tumor cell's expected fitness is determined by its strategy, the strategy of neighboring tumor cells and the density of tumor cells. Once formulated as an evolutionary game, we can bring all of the tools and mathematics of G-functions and adaptive dynamics to track evolution along adaptive landscapes, characterize convergent stable points (such as ESS, evolutionarily stable minima, NIS, etc.), identify evolutionary branching and speciation, and formulate a lockstep between data and theory. Early examples of this lockstep that we hope to achieve include 1) modelling cancer cell resistance and possible evolutionary double-bind therapies, 2) cancer cell diversification and niche

filling in breast and prostate cancer, 3) group size effects in response to cancer therapy and 3) adaptive therapies for managing communities of tumor cells in prostate cancer.

Ben Allen *Death-Birth Dynamics on Heterogeneous Graphs*

Ronald Peeters *Network characteristics enabling efficient coordination: A simulation study*

Abstract: Using data generated by extensive simulations of a process where individuals interact globally in a coordination game and iteratively imitate the action of the most successful individual in their local neighbourhood, we study the characteristics of the observation network and distribution of initial choices that facilitate (a speedy) convergence to efficient coordination. Knowing these characteristics is crucial when intervening in social network structures with the intention to nudge society to a socially preferred outcome. The most important factor appears to be the share of individuals that are initially seeded with the socially desirable action. Only for a small window of this share, other factors, including the degree distribution in the network and the segregation of individuals using similar actions, have an influence on the dynamic process of achieving efficient coordination. Moreover, networks possessing the properties of a scale-free network are more likely to yield an efficient outcome compared to small-world networks.

Krzysztof Argasinski *Carrying capacity as the selective factor: Towards a mechanistic model of limited population growth based on the "nest site lottery" selection mechanism*

Abstract: We will start from the analysis of the selective consequences of the strategically neutral growth suppression driven by juvenile recruitment survival described by the logistic suppression term $(1-n/K)$. In effect we obtain the selection mechanism called the "nest site lottery" where for each nest site released by a dead adult individual, a single newborn is drawn from the pool of newborn candidates. This frequency dependent selection leads towards the strategy maximizing the number of newborns per adult death. However, multiple strategies can maximize this value. Among them, the strategy with the greatest mortality (which implies the greatest instantaneous growth rate) is selected. This result is important for the discussion about universal fitness measures and which parameters are maximized by natural selection. This is related to the fitness measures R_0 and r , used in life history theory, because the number of newborns per single dead individual equals the lifetime production of newborns R_0 . However the question arise about the correctness of the applied logistic suppression factor. We can show that in this approach the number of recruited newborns can exceed the number of free nest sites. We will build the alternative suppression mechanism based on the availability of free nest sites for newborns. This leads to the simplified (but fully mechanistic) biphasic population growth model free from the inconsistency of classical single phase models (such as the logistic model).

Arne Traulsen *Hidden assumptions in evolutionary games: Strategy sets and mutation kernels*

Abstract: Many models in evolutionary game theory seem to make broad predictions, such as "cooperation evolves if...". Often, these results hinge upon assumptions that are rarely discussed, such as the choice of the strategy set or the mutational distance between different strategies. This talk will present examples in which these assumptions can strongly affect the outcome, focusing on the case of cooperation in repeated games and the evolution of punishment strategies.

Jenna Gallie *Bet hedging in a real biological system*

Bet hedging – stochastic switching between phenotypes – is a widespread evolutionary adaptation that facilitates survival in changing environments. Here, we describe the emergence of a real-life, microbial bet hedging strategy under laboratory conditions; experimental populations of the bacterium *Pseudomonas fluorescens* SBW25 evolved the ability to persist in a fluctuating environment by rapidly

switching between two distinct colony phenotypes. At the genetic level, a non-synonymous mutation in the central metabolic gene *carB* has been shown to cause colony switching. Present in both phenotypic states, the acquisition of this mutation sets in motion a series of non-genetic, molecular events that ultimately culminates in the phenotypic bifurcation of the population. Together, our results show that natural selection took advantage of pre-existing molecular noise to generate a powerful survival strategy.

Weini Huang *Title: Evolutionary game dynamics under random mutations*

Abstract: Coexistence of multiple phenotypes/genotypes is frequently observed in natural populations. Mutation brings variety, but how this variety is maintained - especially under non-neutral selection - is still a debated question. It has been argued that diversity may arise from frequency dependent interactions among those phenotypes or genotypes. While Evolutionary game theory provides a powerful mathematical framework to study frequency dependent interactions, most game theoretical models focus on mutations between predefined types. This is a constraint for implications in biological populations, where spontaneous mutations are random and their fitness cannot be predefined. Here we present our stochastic models on random mutations in the context of evolutionary game theory. Under frequency dependent selection, diversity increases with selection intensity. This challenges the classical Darwin concept, i.e. selection decreases diversity or high diversity refers to neutral selection - a conclusion valid only if fitness of all phenotypes or genotypes are constant numbers. Meanwhile, we find out that frequency dependent interactions may lead to stochastic fluctuations of total population size, which has a significant impact on the evolutionary outcomes both in small and large populations.

Karan Pattni *Evolutionary graph theory revisited: when is an evolutionary process equivalent to the Moran process?*

Abstract: Evolution in finite populations is often modelled using the classical Moran process. Over the last 10 years, this methodology has been extended to structured populations using evolutionary graph theory. An important question in any such population is whether a rare mutant has a higher or lower chance of fixating (the fixation probability) than the Moran probability, i.e. that from the original Moran model, which represents an unstructured population. As evolutionary graph theory has developed, different ways of considering the interactions between individuals through a graph and an associated matrix of weights have been considered, as have a number of important dynamics. In this talk, we revisit the original paper on evolutionary graph theory in light of these extensions to consider these developments in an integrated way. In particular, we find general criteria for when an evolutionary graph with general weights satisfies the Moran probability for the set of six common evolutionary dynamics.

Mark Broom *Modelling evolution in structured populations involving multiplayer interactions*

Abstract: Within the last ten years, models of evolution have begun to incorporate structured populations, including spatial structure, through the modelling of evolutionary processes on graphs (evolutionary graph theory). One limitation of this otherwise quite general framework is that interactions are restricted to pairwise ones, through the edges connecting pairs of individuals. Yet many animal interactions can involve many individuals, and theoretical models also describe such multi-player interactions. We shall discuss a more general modelling framework of interactions of structured populations, including the example of competition between territorial animals. Depending upon the behaviour concerned, we can embed the results of different evolutionary games within our structure, as occurs for pairwise games such as the Prisoner's Dilemma or the Hawk-Dove game on graphs. For a population to evolve we also need an evolutionary dynamics, and we demonstrate

a birth-death dynamics for our framework. Finally we discuss some examples together with some important differences between this approach and evolutionary graph theory.

Jan Rychtar *Territorial Raider Games*

Abstract: Evolutionary graph theory combines evolutionary games with population structure, induced by the graph. The games on graphs are typically limited to pairwise games occurring on the edges of the graph. Multiplayer games can be important in biological modelling, however, and so recently a new framework for modelling games in structured populations allowing games with arbitrary numbers of players was introduced. We develop this model to investigate the effect of population structure on the level of aggression, as opposed to a well-mixed population for two specific types of graph - circles and complete bi-partite graphs, using a multiplayer hawk-dove game. We find that the graph structure can have a significant effect on the level of aggression, and that a key factor is the variability of the group sizes formed to play the games; the more variable the group size, the lower the level of aggression, in general.

Participants

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