

Parallel Session

# Evolutionary Dynamics VII

## EVOLUTIONARY DYNAMICS AND THE EVOLUTION OF MULTIPLAYER COOPERATION IN A SUBDIVIDED POPULATION

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Joint work with Prof. Mark Broom (City, University of London) and Prof. Jan Rychtář (University of North Carolina at Greensboro).

*Keywords:* Evolutionary Graph Theory, Multiplayer Games.

The classical models of evolution have been developed to incorporate structured populations using evolutionary graph theory and, more recently, a new framework has been developed to allow for more flexible population structures which potentially change through time and can accommodate multiplayer games with variable group sizes. In this paper we extend this work in three key ways. Firstly by developing a complete set of evolutionary dynamics so that the range of dynamic processes used in classical evolutionary graph theory can be applied. Secondly, by building upon previous models to allow for a general subpopulation structure, where all subpopulation members have a common movement distribution. Subpopulations can have varying levels of stability, represented by the proportion of interactions occurring between subpopulation members; in our representation of the population all subpopulation members are represented by a single vertex. In conjunction with this we extend the important concept of temperature (the temperature of a vertex is the sum of all the weights coming into that vertex; generally, the higher the temperature, the higher the rate of turnover of individuals at a vertex). Finally, we have used these new developments to consider the evolution of cooperation in a class of populations which possess this subpopulation structure using a multiplayer public goods game. We show that cooperation can evolve providing that subpopulations are sufficiently stable, with the smaller the subpopulations the easier it is for cooperation to evolve. We introduce a new concept of temperature, namely “subgroup temperature”, which can be used to explain our results.

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## EVOLUTIONARY DYNAMICS IN THE TWO-LOCUS TWO-ALLELE MODEL WITH WEAK SELECTION

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*Keywords:* Selection, Recombination, Epistasis, Equilibrium structure, Index theory.

Two-locus two-allele models are the simplest models to explore the role of epistasis for a variety of important evolutionary problems, including the maintenance of polymorphism. However, due to the mathematical complexity arising from the fact that epistasis generates linkage disequilibrium, few general insights have emerged. Here, we study a simpler problem by assuming that linkage disequilibrium can be ignored. This is a valid approximation if selection is sufficiently weak relative to recombination. The central point in our analysis is the inference of the number and stability of fully polymorphic equilibria from the boundary flow, i.e., from the dynamics at the four marginal single-locus subsystems. For general fitness matrices, this is rather difficult, however, for many specific classes of fitness schemes, including additive fitnesses, purely additive-by-additive epistasis, multilinear epistasis, and the symmetric viability model, we obtain complete characterizations of the possible equilibrium structures. The key mathematical ingredient for this is index theory. The specific form of epistasis has both a big influence on the possible boundary flows as well as on the internal equilibrium structure admitted by a given boundary flow.

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**THE WRIGHT-FISHER MODEL FOR EXPONENTIALLY GROWING POPULATIONS**

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*Keywords:* Wright-Fisher process, Genetic drift, Mutation, Coexistence, Albinism.

The Wright-Fisher process is widely used in population genetics to model the evolution of allele frequencies under the influence of genetic drift and its interactions with mutation and selection. Current understanding of the Wright-Fisher process is largely based on its properties for populations of constant size. As the human population has been growing exponentially since the advent of agriculture approximately 500 generations ago, it is of considerable interest to investigate how the predictions of the model change for exponentially growing populations.

In this work we use simulations and analysis of the Wright-Fisher process and a diffusion equation that approximates it to explore the fate of a mutation occurring in an exponentially growing population. In particular we show that instead of a mutant allele necessarily converging to either extinction or fixation, as occurs in constant populations, it may coexist indefinitely with native alleles. The probability of coexistence increases with the population growth rate, while the expected frequency of a coexisting allele decreases. This implies that population growth alone is sufficient to account for the indefinite maintenance of several alleles at a locus.

To illustrate these results we consider a particular mutation of the *OCA2* gene that is the cause of the high frequency of albinism among the Bantu-speaking people of sub-Saharan Africa. Archaeological and linguistic evidence suggest that this mutation occurred over 3,000 years ago, before the spread of Bantu-speakers from the area of what is now Cameroon. We show that observed frequencies of albinism among these populations are consistent with the mutation occurring at that time in a population with an (effective) size of a few hundred. It is therefore not necessary to invoke factors such as selection pressure or cultural differences to account for persistence of albinism, although these may also play a role.

The consequences of the indefinite coexistence of alleles for the evolution of genetic diversity will be discussed in the talk “Genetic diversity in rapidly growing populations” presented by Mark Roberts.

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## GENETIC DIVERSITY IN RAPIDLY GROWING POPULATIONS

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*Keywords:* Genetic Diversity, Heterozygosity, Genetic Drift, Mutation.

Theoretical population genetics is founded on mathematical models which predict that genetic drift causes alleles either to go extinct or replace all other alleles at the same locus. In the absence of new mutations every member of a population becomes homozygous at each locus and all alleles at a locus will eventually be descended from the same ancestral allele. When a steady input of mutations creating new types of alleles is added to the model an equilibrium is created at which the loss of diversity due to genetic drift balances the creation of diversity through mutation.

These predictions are usually illustrated by models in which the population size is constant, but they are regarded as holding much more widely. In this work we confirm that they do indeed continue to hold if the population growth is constrained, in a sense we make precise. However none of the predictions hold for models in which populations grow rapidly, such as are appropriate for the observed exponential growth of human populations. In particular we show that for such rapidly growing populations the eventual outcome is that every allele in the population is unique. The timescale over which this increase in diversity occurs is typically of the order of thousands of generations, but significant effects are observable over much shorter periods. These include the ‘excess of rare variants’ that has been observed in both genomic data and simulations of the genetic history of human populations.

This talk is a sequel to that on “The Wright-Fisher model for exponentially growing population” presented by Peter Nabutanyi and will focus particularly on the evolution of heterozygosity in the ‘infinite allele’ model for the interaction of drift and mutation.

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## Evolutionary Dynamics VII

INFORMATION GEOMETRY AND ITS APPLICATION  
TO THE WRIGHT-FISHER POPULATION WITH  
RECOMBINATION

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*Keywords:* Wright–Fisher model, Recombination, Fisher information metric, Equilibrium states, Mutual information.

In this talk, I will give out a brief introduction to Information Geometry and how to apply it in the context of population genetics. In particular, I will give out a geometrical interpretation for the Ohta–Kimura formula [2] and discuss its generalizations for linkage equilibria in Wright–Fisher models with several loci. The state space associated with the Ohta–Kimura model is simply a Riemannian manifold of constant positive curvature. Furthermore, the equilibria states for recombination can be interpreted geometrically as a product of spheres. In the case of only two loci, I will derive the long-term behaviour of the mutual information between these two loci. This is a joint work with Jürgen Jost and Julian Hofrichter.

**Acknowledgements:** J.H. and T.D.T. have been supported by scholarships from the IMPRS “Mathematics in the Sciences” during earlier stages of this work. T.D.T. was also partially supported by the Vietnam Institute for Advanced Studies in Mathematics (VIASM).

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