

# Workshop Random Spatial Models from Physics and Biology

WIAS, 16 – 19 March 2005

## List of titles and abstracts

**Wolfgang Angerer** On limit laws for two-type branching processes

We consider a two-type branching process with exponential life-time distribution of particles. It is assumed that particles of the first kind spawn particles of both types, whereas the others only branch into particles of the second type. By considering the statistics of arrival times of particles of the first kind in the population, we obtain a decomposition of the process which yields a number of new results about the probability distribution of the total number of particles at any given instant. The construction also allows one to derive the probability distribution of the number of particle families of given size, which has applications in some areas of mathematical biology.

**Ellen Baake** How T-cells use large deviations to recognize foreign antigens

Our immune system faces the difficult task of having to react to foreign antigens while avoiding reactions to self antigens; this discrimination must be extremely reliable, otherwise dangerous autoimmune reactions may occur.

The talk will explain how this may be accomplished on the basis of the stochastic nature of the interactions between T cell receptors and antigens. On the biological side, we use the mechanism recently proposed by van den Berg and Rand (2001). On the mathematical side, we rely on the theory of large deviations, and collaboration with Frank den Hollander.

**Reinhard Bürger** Intraspecific Competition and Sympatric Speciation

A multilocus model of a quantitative trait is investigated, in which the trait is under frequency-dependent selection and mediates assortative mating. The purpose of the analysis is the identification of conditions that lead to competitive divergence and the establishment of reproductively isolated clusters in the population. This may be interpreted as sympatric speciation. In our model, there are parameters that independently determine the strength of assortment, the costs of being choosy, and the strength of frequency-dependent selection. The latter results from intraspecific competition for a unimodal resource spectrum. Sufficiently strong competition leads to disruptive selection on the phenotypes. Two modes of assortative mating are analyzed in detail, one without costs of being choosy, the other with such costs. Loci contribute additively to the trait. We show that if assortative mating is costly, divergence never occurs. Instead, with

moderately or strong assortment, convergence to one of the monomorphic state occurs. In the absence of costs, competitive divergence can occur if frequency dependence and assortment are both strong enough. Even then, the evolutionary outcome depends on the initial conditions. A population with little initial variation is likely to evolve to a monomorphic state because they are locally stable if assortment is strong. The evolutionary outcome depends in a distinctive non-linear way on the strength of assortment. With moderately strong assortment, there is always less variation maintained than with weak or very strong assortment. Further, the role of linkage and of asymmetric selection on the phenotypes is explored. The consequences for ecologically driven sympatric speciation are discussed.

**Nicolas Champagnat** A microscopic interpretation for a Markov jump process of evolution

We consider an interacting particle Markov process for Darwinian evolution in an asexual population, involving a linear birth rate, a density-dependent logistic death rate and a probability of mutation at each birth event. We introduce a renormalization parameter  $K$  scaling the size of the population, which leads, when  $K \rightarrow \infty$  to a deterministic dynamics. By combining in a non-standard way the limits of large population and of small mutations, we show that a time scale separation between the birth and death events and the mutation events occurs and that the interacting particle microscopic process converges to the biological model of evolution known as the “trait substitution sequence of adaptive dynamics”, which describes Darwinian evolution as a Markov jump process in the trait space.

**Andrej Depperschmidt** A spatial discrete time branching model with local interactions

We consider a discrete state model of the evolution of a lattice based population model with discrete generations. The parameter of the offspring distribution, which is given by the Poisson-distribution, depend on the local density. We show for certain parameters survival and extinction results for this process. The proofs seem to be applicable to competing populations.

**Alison Etheridge** Evolution in spatially continuous problems

Many organisms live in two dimensions. Over local scales, they may be restricted to discrete demes, scattered over a continuous habitat, or distributed in some more complex pattern. Regardless of these local details, the population may appear more or less continuous when viewed over a larger scale. To describe the evolution of such populations, we require a simple model which can approximate a wide variety of local structures in terms of a few parameters. In this talk we describe some of the mathematical problems associated with the search for such a model.

**Steven Evans** Escherichia coli, superprocesses, and quasistationary distributions

In recent, yet-to-be-published experiments, Eric Stewart and his collaborators have shown that when the bacterium *E. coli* divides, genetic damage appears to be segregated preferentially into one of the daughter cells. David Steinsaltz and I are working on a model that describes how the spread of genetic damage across individuals will change as the population evolves. Mathematically, this model is a Dawson-Watanabe superprocess with a spatially varying branching mechanism and a spatial motion that is a one-dimensional diffusion with killing. Analysing the long-term behaviour of such a process involves recent work of ours on quasistationary distributions of killed one-dimensional diffusions.

**Jean-François Le Gall** Conditioned Brownian trees

We consider a Brownian tree consisting of a collection of one-dimensional Brownian paths started from the origin, whose genealogical structure is given by the Continuum Random Tree (CRT). This Brownian tree may be generated from the Brownian snake driven by a normalized Brownian excursion, and yields a convenient representation of the so-called Integrated Super-Brownian Excursion (ISE), which can be viewed as the uniform probability measure on the tree of paths. We discuss different approaches that lead to the definition of the Brownian tree conditioned to stay on the positive half-line. We also establish a Verwaat-like theorem showing that this conditioned Brownian tree can be obtained by re-rooting the unconditioned one at the vertex corresponding to the minimal spatial position. In terms of ISE, this theorem yields the following fact: Conditioning ISE to put no mass on  $] - \infty, -\varepsilon[$  and letting  $\varepsilon$  go to 0 is equivalent to shifting the unconditioned ISE to the right so that the left-most point of its support becomes the origin. One motivation for this work comes from the relations between planar maps and well-labelled trees, which are discrete versions of our conditioned Brownian trees. This lecture is based on a joint work with Mathilde Weill.

**Andreas Greven** Stochastic spatial population model with selection and mutation

**Bob Griffiths** Importance sampling on coalescent histories in subdivided population models

Likelihood calculations and ancestral inference from molecular data require calculation of the probability of the configuration of types in a sample of genes, or more generally the ability to simulate ancestral histories of genes conditional on the current type configuration in a sample. Importance sampling on entire coalescent histories can be used for likelihood calculations and simulating conditional histories back in time. Transition probabilities of the history chain are known forward in time, but not backward. This talk will discuss constructing

importance sampling transition distributions back in time in subdivided population models where the population frequencies of types of genes are modelled by a Wright-Fisher diffusion process. Construction is from the diffusion process generator. The model corresponds to having a subdivided population coalescent process for a samples' ancestry.

**Martin Hutzenthaler** Ergodic behaviour of branching populations with local competition

We consider a lattice based diffusion model of individuals performing independent random walks and a local population-size dependent branching, which is supercritical below and subcritical above a local carrying capacity. The first question is about extinction/persistence. For sufficiently small carrying capacity we show extinction. We then study the ergodic behaviour of the system in the case of survival. As a result, starting from any homogeneous nontrivial initial law, the process ends up in the unique homogeneous nontrivial invariant measure. For this we employ a very useful self-duality.

**Sylvie Méléard** Stochastic individual models for spatially structured populations with adaptive evolution

We study the dynamics of a spatially structured population describing individuals both characterized by adaptive traits and position. The individuals may reproduce, die or move following a reflected diffusion in a bounded domain. An offspring inherits progenitor's trait except when a mutation occurs and spontaneous mutations may also occur. The death rate depends on the competition between individuals and on their respective positions, which yields interaction between the individuals, characterized both by competition kernel and spatial range. We construct the individual based model as a point process for a fixed spatial interaction range. We study an approximation of this model based on a large population limit and prove that the renormalized point process converges to a weak solution of a nonlinear nonlocal integro-differential equation. Under reasonably smooth assumptions on the coefficients of the diffusion we can prove that this limiting deterministic measure has a density with respect to the Lebesgue measure. Making the spatial interaction range tend to zero, we obtain as final derivation that the sequence of densities converge to the solution of a nonlinear local integro-differential equation.

**Martin Möhle** Coalescent Theory – Simultaneous Multiple Collisions and Sampling Distributions

Recursions for sampling distributions of allele configurations are derived for the situation when the genealogy of the underlying population is modelled by a coalescent process with simultaneous multiple collisions of ancestral lineages. For the Kingman coalescent process with only binary mergers of ancestral lines, the

recursion reduces to that known for the classical Ewens sampling distribution. We solve the recursion for the star-shaped coalescent. The asymptotic behavior of the number  $K(n)$  of alleles (types) for large sample size  $n$  is studied, in particular for the star-shaped coalescent and the Bolthausen-Sznitman coalescent.

**Peter Pfaffelhuber** The evolution of genealogical trees

The typical situation a geneticist faces is to consider genes from a small sample from a large population. The genetic sequences of his/her sample are correlated by common ancestry. A way to describe this is by coalescent-trees which describe the genealogical sample-tree. We want to replace this quite static picture by a dynamical one and study how these sample-trees evolve in time. As a result we derive a tree-valued stochastic process. Applications to various questions in population genetics are possible. As an example we describe how sample-trees relax after a strong reduction in tree-length, e.g. caused by strong selection. The talk is about joint work in progress with Anita Winter and Andreas Greven.

**Wolfgang Stephan** Population Genetics of Adaptation

How do populations adapt to new environments? I am presenting data from our study of *Drosophila melanogaster*. This species is native to Africa, but expanded its habitat to temperate zones around the world after the last ice age (ca. 10 000 years ago). We are testing the hypothesis that this habitat expansion was accompanied by many adaptations. Our approach is based on the hitchhiking effect for discovering selective signatures in the genome. The footprints of selection we are scrutinizing most closely are regions of reduced variation (so-called selective sweeps). In addition, we investigate the pattern of linkage disequilibrium around these sweep regions, using an extension of the basic hitchhiking model by Maynard Smith and Haigh.

**Rongfeng Sun** Renormalization Analysis of Interacting Diffusions

Renormalization analysis has been a powerful tool in the study of interacting diffusions, which arises as the diffusion limit of interacting colonies of population. By identifying the attracting orbits and domains of attraction of the renormalization transform, one can characterize the large space-time scale behavior of the system, which falls into various universality classes. In this talk, we review the basic renormalization scheme and its analysis, and discuss some possible extensions.

**Anton Wakolbinger** Hitchhikers, free-riders and early recombinants: the ancestral partition in a selective sweep

Consider an individual who carries at some genetic locus a new allele which is so advantageous that it fixates in the population in a relatively short time. Then the

ancestry at this selective locus, viewed back from the completion of the selective sweep, is simple: everybody traces back to the founder of the sweep. But what about a neutral locus in the neighbourhood of the selective one? Here, recombination counteracts the hitchhiking of the allele carried by the founder of the sweep.

We derive an approximate sampling formula for the ancestral partition of a sample at the neutral locus. This consists, apart from the original hitchhiking family, of a few singleton free-riders having recombined into the sweep when it is already under way, and, with a small probability, of a (potentially large) family stemming from one recombinant at the onset of the sweep. Principal tools are the structured coalescent in a random background, Yule processes and Polya's urn. This is joint work with Alison Etheridge and Peter Pfaffelhuber.