
Probabilistic methods in population biology

Spring school, March 27–31, 2023, TU Darmstadt

Mini Courses:

Alison Etheridge
Jan Swart

Invited Speakers:

Félix Foutel-Rodier
Nic Freeman
Andreas Greven

Organization:

Frank Aurzada
Volker Betz
Matthias Meiners



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1 General Information

1.1 Accommodation

The participants are recommended to stay in one of the following hotels, located in walking distance (15 minutes) to the lecture venue.

BEST WESTERN Darmstadt Mitte
Grafenstraße 31, 64283 Darmstadt
Tel: +49-6151-28100 info@hotel-darmstadt.bestwestern.de

HOTEL WELCOME
Karolinenplatz 4, 64289 Darmstadt
Tel: +49-6151-3914-0 info.dar@welcome-hotels.com

HOTEL FELIX
Kasinostraße 4, 64293 Darmstadt
Tel: +49-6151-3973720 darmstadt@felix-hotels.de

For directions please see the map on the back cover.

1.2 Registration

On Monday morning, starting from 8am, registration is possible in the lobby of the lecture hall.

1.3 Lecture Hall

Location: Technische Universität Darmstadt. The registration and all lectures will take place in building S2|08, Hochschulstraße 4, 64289 Darmstadt in lecture hall S2|08/171. In the lecture hall, there are two large blackboards and two projectors.

1.4 Map & Points of Interest

The map can be found on the back cover.

1.5 Public Transportation

The closest bus and tram stops to the venue of the workshop are **Schloss** (trams: S2, S3, S9) and **Willy-Brandt-Platz** (trams: S4, S5, S6, S7, S8). Both stops are within 10 minutes walking distance to the lecture hall.

1.6 Food & Beverage

Cheap and plain food can be purchased at the TU Darmstadt Refectory-Canteen (“Mensa”), Alexanderstr. 4, building S1111, Monday to Friday 11:15 to 14:15. Additionally, there are lots of good restaurants and bistros near TU Darmstadt. Please dial +49 6151 preceding the number given below.

Name	Address	Phone	Cuisine	Opening
Ratskeller	Marktplatz 8	26444	German	10:00 - 01:00
Pizzeria da Nino	Alexanderstr. 29	24220	Italian	18:00 - 23:00
Haroun's	Friedensplatz 6	23487	Oriental	11:00 - 22:30
Wellnitz	Lauteschlägerstr. 4	6699255	Bistro	12:00 - 24:00
Cafe Extrablatt	Marktplatz 11	5998820	Bistro	08:30 - 23:30
Ristorante Sardegna	Kahlerstraße 1	23029	Italian	11:30 - 14:45

1.7 Conference Dinner

On Tuesday, March 28, 2023, there will be a conference dinner at the Restaurant *Indian Spicy*, Alexanderstraße 33, 64283 Darmstadt starting at 18:30, Tel: +49-6151-2730978

1.8 Free Afternoon

On Wednesday, March 29, 2023, there will be a free afternoon.

1.9 Contact Information

If you have any questions concerning the workshop, please feel free to contact one of the local organizers or the technical support:

- Prof. Dr. Frank Aurzada
Office: S2-15, Room 341
Phone: +49 6151 - 16 23375
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Acknowledgements

Financial support by the Department of Mathematics at Justus-Liebig-Universität Giessen and the Department of Mathematics at Technische Universität Darmstadt is acknowledged.



Programme

Time	Monday	Tuesday	Wednesday	Thursday	Friday
08:00	Registration				
09:00	Etheridge	Swart	Etheridge	Swart	Swart
10:30	Coffee break	Coffee break	Coffee break	Coffee break	Coffee break
11:00	Swart	Etheridge	Swart	Etheridge	Etheridge
12:30	<i>Lunch</i>	<i>Lunch</i>	<i>Lunch</i>	<i>Lunch</i>	<i>Lunch</i>
14:00	Invited talk Foutel-Rodier	Invited talk Freeman		Invited talk Greven	<i>End of Workshop</i>
15:00	<i>Coffee break</i>	<i>Coffee break</i>		Coffee break	
15:30	Contributed talk: Baumdicker	Short talks: Jovanović		Short talks: Wenzel	
16:00	<i>Coffee break</i>	Courau	<i>Free Afternoon</i>	Sinzger-D'Angelo	
16:15	Short talks: Dai Pra	Ocello		Povar	
	Klippel	Courau		Jacobi	
	Esser	Callegaro	Roth		
	Meier				
	Bauer				
	Reception	18:30 Dinner	<i>Excursion</i>		

Monday, 27 March 2023

Time	Speaker	Title of Talk
09:00-09:05	Welcome	
09:05-10:35	Alison Etheridge	<i>Mini course</i> <i>Some mathematical models from population genetics</i>
10:35-11:00		–Coffee break–
11:00-12:30	Jan Swart	<i>Mini course</i> <i>Brownian web and Brownian net</i>
12:30-14:00		–Lunch break–
14:00-15:00	Félix Foutel-Rodier	<i>Invited talk</i> <i>Crump-Mode-Jagers processes with interaction as epidemic models</i>
15:00-15:30		–Coffee break–
15:30-16:00	Franz Baumdicker	<i>Contributed talk</i> <i>Using Theoretical Population Genetics to improve Neural Networks for Mutation Rate Estimation</i>
16:00-16:15		–Coffee break–
16:15-16:25	Short talk	Marta Dai Pra
16:25-16:35	Short talk	Andreas Klippel
16:35-16:45	Short talk	Manuel Esser
16:45-16:55	Short talk	Andreas Meier
16:55-17:05	Short talk	Leonard Bauer
17:45-23:00	Reception	–Cheese & Wine–

Tuesday, 28 March 2023

Time	Speaker	Title of Talk
09:00-10:30	Jan Swart	<i>Mini course</i> <i>Brownian web and Brownian net</i>
10:30-11:00		–Coffee break–
11:00-12:30	Alison Etheridge	<i>Mini course</i> <i>Some mathematical models from population genetics</i>
12:30-14:00		–Lunch break–
14:00-15:00	Nic Freeman	<i>Invited talk</i> <i>Weaves, webs and flows</i>
15:00-15:30		–Coffee break–
15:30-15:40	Short talk	Bojana Jovanović
15:40-15:50	Short talk	Philibert Courau
15:50-16:00	Short talk	Antonio Ocello
16:00-16:10	Short talk	Alice Callegaro
18:30-22:00	Conference Dinner	– Restaurant Indian Spicy –

Wednesday, 29 March 2023

Time	Speaker	Title of Talk
09:00-10:30	Alison Etheridge	<i>Mini course</i> <i>Some mathematical models from population genetic</i>
10:30-11:00		–Coffee break–
11:00-12:30	Jan Swart	<i>Mini course</i> <i>Brownian web and Brownian net</i>
		–Free afternoon – Excursion –

Thursday, 30 March 2023

Time	Speaker	Title of Talk
09:00-10:30	Jan Swart	<i>Mini course Brownian web and Brownian net</i>
10:30-11:00		–Coffee break–
11:00-12:30	Alison Etheridge	<i>Mini course Some mathematical models from population genetic</i>
12:30-14:00		–Lunch break–
14:00-15:00	Andreas Greven	<i>Invited talk Forward evolution of genealogies of spatially structured populations</i>
15:00-15:30		–Coffee break–
15:30-15:40	Short talk	Yannic Wenzel
15:40-15:50	Short talk	Mark Sinzger-D'Angelo
15:50-16:00	Short talk	Benjamin Povar
16:00-16:10	Short talk	Dave Jacobi
16:10-16:20	Short talk	Lukas Roth

Friday, 31 March 2023

Time	Speaker	Title of Talk
09:00-10:30	Jan Swart	<i>Mini course Brownian web and Brownian net</i>
10:30-11:00		–Coffee break–
11:00-12:30	Alison Etheridge	<i>Mini course Some mathematical models from population genetic</i>
12:30-14:30		–Lunch, end of the Spring School–

2 List of Talks

2.1 Mini Courses

Alison Etheridge

University of Oxford, UK

Mini course: Some mathematical models from population genetics

Our aim in these lectures is to provide some flavour of the rich variety of mathematical models that arise in the study of the genetics of natural populations and to present some of the main tools that are used to explore their behaviour.

Although our main focus is spatially distributed populations, we begin with an introduction to the classical Wright-Fisher and Moran models. This provides the opportunity to introduce some terminology and gain some insight into the nature of the approaches that we'll take in the more complicated models that lie ahead. Key concepts will be diffusion approximations, genealogical trees, and the notion of duality.

The next step will be to generalise these models to include spatial structure. This topic has a long and distinguished history, and again we shall begin with classical models due to Kimura, Wright, and Malécot, in which very explicit calculations are possible. However, not only do these models make some very strong assumptions, but in the case of the Wright and Malécot approach to modelling populations evolving in a spatial continuum, in what is arguably the most natural setting of a population evolving in continuous time in a continuous two-dimensional spatial environment, there is a mathematical inconsistency, stemming from what is popularly known as 'the pain in the torus'. Our next model, the spatial Lambda Fleming-Viot process (SLFV) is one way to overcome this. Having introduced the SLFV framework, we use it to investigate the way in which spatial structure interacts with a simple form of natural selection.

Starting with the work of Fisher (1937), the spread of a selectively favoured gene through a population has been modelled through what is now known as the Fisher-KPP equation. A powerful tool in this context has been duality with a spatial branching process. However, natural selection can take many forms, which leads us to consider more general reaction-diffusion equations than the Fisher-KPP equation, and this leads to a slightly different sort of duality. We illustrate with a model of so-called hybrid zones. We uncover the importance of the shape of the domain in which a population evolves, something which we often ignore in our models. If time permits, we shall introduce a final class of models that aims to capture something of the heterogeneity of real populations. Population densities fluctuate in space and time as individuals compete for space and resources. What effect does this have on ancestral lineages?

Jan Swart

UTIA Prague, Czech Republic

Mini course: Brownian web and Brownian net

The Brownian web is a continuum object that can loosely be thought of as a collection of coalescing one-dimensional Brownian motions, starting from each point in space-time. The Brownian net is an extension of the Brownian web that includes branching. The Brownian web and net have been used to study scaling limits of a variety of one-dimensional models, such as (biased) voter models, drainage networks, Potts models, self-repelling random walks, random walks in a random space-time environment, and rough interfaces. There are also interesting links and analogies to topics such as real-trees and oriented percolation. In my course, I will give an introduction to the theory of the Brownian web and net.

2.2 Invited Speakers

Félix Foutel-Rodier

Crump-Mode-Jagers processes with interaction as epidemic models

University of Oxford, UK

Crump-Mode-Jagers processes are population models where the ages at which an individual produces its offspring is allowed to take a general form, creating a complex dependence between the birth times in the population. I will introduce an extension of these objects motivated by epidemiology, where some interaction among individuals is added to account for several important features of epidemics, such as varying contact rate, finite number of susceptible hosts, or behavioral changes. I will present two main results on this model. The first one is a law of large numbers for the age structure of the population, which is reminiscent of a similar result for Crump-Mode-Jagers processes. The second one gives the distribution of the chain of transmissions leading to a typical infection and has interesting consequences for contact-tracing.

This is joint work with Jean-Jil Duchamps and Emmanuel Schertzer.

Nic Freeman

Weaves, webs and flows

University of Sheffield, UK

We consider “weaves” - loosely, a weave is a set of non-crossing cadlag paths that covers $1 + 1$ dimensional space-time. Here, we do not require any particular distribution for the

particle motions. Weaves are a general class of random processes, of which the Brownian web is a canonical example; just as Brownian motion is a canonical example of a (single) random path. It turns out that the space of weaves has an interesting geometric structure in its own right, which will be the focus of the talk. This structure provides key information that leads to an accessible theory of weak convergence for general weaves. Joint work with Jan Swart.

Andreas Greven

Forward evolution of genealogies of spatially structured populations

FAU Erlangen-Nürnberg, Germany

We consider populations of individuals distributed in geographic space and possibly carrying types. The space consists of a discrete set of sites. The population evolves stochastically by birth, death and type changes of individuals. In the limit of infinitely many individuals per site one often obtains diffusion processes. In the individual based version we can introduce the genealogy of the population alive at the current time t , as it evolves in t . Also on the genealogical level we can take the diffusion limit. We explain how to describe the genealogies by equivalence classes of metric measure spaces and to characterize the stochastic processes of genealogies via well-posed martingale problems. This way one obtains strong Markov processes with the Feller property and with cadlag or even continuous path. We focus on the example of spatially interacting (by migration) Fleming-Viot diffusions and super random walks. With the tool of duality we relate the two evolutions, obtaining the genealogy of the super random walk via interacting Feller diffusions driving genealogies of time-inhomogeneous Fleming-Viot genealogies. This is the basis for the ongoing work on ancestral webs, where the genealogy of all individuals ever alive before the time horizon T is studied as stochastic process in T .

Leonard Bauer

Infinite rate symbiotic branching with different motion kernels

JGU Mainz, Germany

We are interested in a population with 2 types on the real line. At time 0 we have only mass of type 1 on $(-\infty, 0]$ and only mass of type 2 on $(0, \infty)$. Type 2 mass cant move to the right or left and type 1 moves deterministically according to heat flow and is killed at the interface between type 1 and 2. The killed mass is the driving force of a fair game between type 1 and 2 at the interface. This game pushes the interface to the right when time is passing. We will first have a look at the dynamics of the fair game in one colony and then establish an approximation scheme to introduce the process on the real line. This model fits into the infinite rate symbiotic branching on the real line setting.

Franz Baumdicker

Using Theoretical Population Genetics to improve Neural Networks for Mutation Rate Estimation

Universität Tübingen, Germany

In population genetics, estimating mutation rates or effective population sizes is a crucial task. While optimal linear estimation methods are well-established for low or high recombination rates, intermediate recombination rates present a challenge. Neural networks and machine learning techniques offer promising alternatives to model-based estimation, but their suitability for different applications in population genetics is difficult to evaluate without benchmarks. We present a novel general approach that combines the strengths of theoretical population genetics and neural networks to estimate parameters such as the mutation rate. Our approach features an adaptive reweighting of the loss function based on model-based estimators of the mutation rate, which enables us to adjust the weights of the training data. Our method uses feedforward neural networks to estimate mutation rates based on the site frequency spectrum, and we compare their performance with model-based estimators introduced by Fu, Futschik et al., and Watterson. Remarkably, we demonstrate that a single hidden layer neural network can perform almost as well as model-based estimators for low and high recombination rates while providing a superior estimation method for intermediate recombination rates.

Alice Callegaro

Survival and complete convergence for a branching annihilating random walk
TU München / JGU Mainz, Germany

Branching systems with competition are interacting particle systems which have gained popularity as models for the reproduction of a spatial population with limited environmental resources. We study a branching annihilating random walk (BARW) in which particles move on the lattice and evolve in discrete generations. Each particle produces a poissonian number of offspring which independently move to a uniformly chosen site within a fixed distance from their parent's position. Whenever a site is occupied by at least two particles, all the particles at that site are annihilated. This feature means that the system is not monotone and therefore the usual comparison methods are not applicable. We show that the system survives via coupling arguments and comparison with oriented percolation, making use of carefully defined density profiles which expand in time and are reminiscent of discrete travelling wave solutions. If time allows, I will explain how a refinement of this technique can be employed to show complete convergence for the BARW in certain parameter regimes. The talk is based on a joint work with Matthias Birkner (JGU Mainz), Jiří Černý (University of Basel), Nina Gantert (TU Munich) and Pascal Oswald (University of Basel/JGU Mainz).

Philibert Courau

A model for the genetic architecture of a quantitative trait in an infinite population
Collège de France, Wien Universität, Austria

The infinitesimal model aims at explaining the evolution of complex traits by assuming that a very large number of exchangeable loci interact additively. This means a given genome is characterized by a sequence of genetic values along its chromosomes. Studies typically focus on the law of the sum of these values, generally assumed Gaussian in quantitative genetics, or consider a large but still finite number of loci. Here, we (re-)introduce a mathematical object, which we call a continuous genome, to keep track of the whole genomic structure of an infinite population, and in particular to simulate the genetic value of a chromosomal block which has been submitted to stabilising selection, sex, and mutation.

Marta Dai Pra

Xi-coalescents arising from structured populations undergoing bottlenecks
HU Berlin, Germany

Ancestry models can be used for predicting genetic diversity of a population, which can then be compared to observed data. In population genetics most theory and statistical tests have been developed using the classical Wright–Fisher model and the Kingman coalescent. Nevertheless, organisms having a genealogy not well described by the Kingman coalescent are not rare. One example populations with large variation in population size, that might rather be described by a multiple merger coalescent. We present a spatially structured model undergoing localized, recurrent bottlenecks, and describe their ancestral lines. Depending on the severity and the length of the bottleneck, we derive as scaling limits different structured Xi-coalescents featuring simultaneous multiple mergers and migrations.

Manuel Esser

Metastability and multi-scale analysis of individual-based population models
Universität Bonn, Germany

The biological theory of adaptive dynamics aims at studying the interplay between ecology and evolution through the modeling of the basic mechanisms: heredity, mutations and competition. A rigorous derivation of the theory was achieved over the last two decades in the context of stochastic individual-based models. These Markov processes are driven by microscopic interactions between single individuals and evolve over time towards traits of higher fitness. The typical evolutionary behaviour can be studied by looking at limits of large populations and rare mutations. This talk introduces multiple scaling parameters and gives an overview of time scales that are involved in the above model. We will then focus on the parameter regime of moderately rare mutations, where multiple new mutant traits are present at the same time. In this setting we can distinguish three important time scales:

Ecological interactions between well-established subpopulations, like the competition for resources, can change the composition of the overall population within a short time of order one. This is related to classical Lotka-Volterra dynamics and leads to equilibrium states between the larger traits.

Short-range mutations and the initial exponential growth of small mutant populations can be witnessed on a logarithmic time scale.

Finally, long-range mutations - in particular those that need to traverse a large fitness valley - are quite rare and occur on an even more accelerated time scale.

Looking at the limiting jump-processes for the short- and long-range mutations, respectively, we see that the first one is deterministic, while the later one again shows a random

nature and can be seen as metastable transitions between so-called evolutionary stable conditions. I will outline the main ideas of constructing the limiting multi-scale processes and then demonstrate some interesting phenomena in the case of easy examples. The talk is based on an ongoing collaboration with Anna Kraut and previous works of Anton Bovier, Lorene Coquille and Charline Smadi.

Dave Jacobi

Superbrownian Motion with Dormancy

TU Berlin, Germany

The majority of species exhibit a behaviour called Dormancy, in which the individuals switch into a state of low metabolic activity, that protects them from harsh environmental conditions and in this way increases their chance of survival. Therefore models from mathematical population biology have to incorporate this phenomenon. We will extend the classical Superbrownian Motion, which is a measure-valued branching markov process, to model Dormancy and retrieve a process that we will call on/off Superbrownian Motion. This process has many interesting properties, that are often closely related to classical Superbrownian Motion, but at the same time exhibit new and different behaviour. We will go on a short trip around on/off Superbrownian Motion and some related model.

Bojana Jovanović

Dynamical analysis of a stochastic delayed epidemic model with lévy jumps and regime switching

University of Niš, Serbia

In this work a delayed stochastic SLVIQR epidemic model, which can be applied for modeling the new coronavirus COVID-19 after a calibration, is derived. Model is constructed by assuming that transmission rate satisfies the mean-reverting Ornstein-Uhlenbeck process and, besides a standard Brownian motion, another two driving processes are considered: a stationary Poisson point process and a continuous finite-state Markov chain. For the constructed model, the existence and uniqueness of positive global solution is proven. Also, sufficient conditions under which the disease would lead to extinction or be persistent in the mean are established and it is shown that constructed model has a richer dynamic analysis compared to existing models. In addition, numerical simulations are given to illustrate the theoretical results.

Andreas Klippel

tba

TU Darmstadt, Germany

tba

Andreas Meier

Long-range voter model on the real line

JGU Mainz, Germany

In the voter model on \mathbb{Z} a countable number of people (called voters) have two opinions, say 0 or 1, and each voter is placed at a site of \mathbb{Z} . Each person has an exponential distributed clock. If the clock rings the voter adopts the opinion of a randomly chosen neighbour. It is well known that this process satisfies a moment duality with a coalescing random walk. We are interested in a situation where an uncountable number of voters is placed on the real line and we allow that they adopt their opinion of other voters that are far away. Hence we think of a measure valued process satisfying a moment duality relation with a coalescing system of symmetric α -stable processes with $\alpha \in (1, 2)$. Such a process has been constructed by Steven N. Evans in 1997 where he allows more general coalescing mechanisms and infinitely many opinions. In the talk I will introduce the process and talk about some fractional properties. This is joint work in progress with my supervisor Achim Klenke and with Leonid Mytnik.

Antonio Ocello

Controlled superprocesses and HJB equation in the space of finite measures

Sorbonne Université Paris, France

This talk would give the formalism to consider a class of stochastic control problems where the underlying controlled system is a super diffusion. We prove the existence of these processes as weak scaling limits of controlled branching processes. We derive a dynamic programming principle for our stochastic control problem by their uniqueness in law. This opens the way to a PDE characterization for the associated value function, that relies on the notions of derivations in the space of finite positive measures. We conclude by proving that the value function is a solution to a Hamilton-Jacobi-Bellman PDE in the viscosity sense.

Benjamin Povar

Convergence of local times at 0 of Bienaymé-Galton-Watson processes with immigration

University of Warwick, United Kingdom

We study the joint convergence of Bienaymé-Galton-Watson processes with immigration (BGWI) and its “naive” local times at 0 to the corresponding Continuous Branching Process with immigration (CBI) and its local time at 0. We do this by analysing the structure of excursions from zero and around positive levels; and looking at the convergence of the hitting times of the BGWI to the hitting times of CBI. The research is done jointly with Aleksandar Mijatovic and Gerónimo Uribe Bravo.

Lukas Roth

Split-Merge Process on Graphs

TU Darmstadt, Germany

We look at a basic split-merge process on graphs: given a certain graph with weights on the nodes and edges, at each time step we randomly choose either a node or an edge according to the weights. If an edge is chosen, we merge the corresponding nodes into one node. On the other hand, if a node is chosen, we split this node into two nodes. If we consider a certain type of graphs and update the weights after each merge and split in a certain way, this model is equivalent to the classical split-merge process on intervals (Coagulation-Fragmentation), which is well studied. Like in CF, we can consider a model with continuous weights and a model with discrete weights. We investigate how we can change the type of graphs or the update rules to still get similar results as in the CF model, for example convergence of the discrete model to the continuous one.

Mark Sinzger-D'Angelo

Hawkes process modelling for chemical reaction networks in random environment

TU Darmstadt, Germany

Cellular processes are open systems, situated in a heterogeneous context, rather than operating in isolation. Chemical reaction networks (CRNs) whose reaction rates are modelled as external stochastic processes account for the heterogeneous environment when describing the embedded process. A marginal description of the embedded process is of interest for (i) fast simulations that bypass the co-simulation of the environment, (ii) obtaining new process equations from which moment equations can be derived, (iii) the computation of information-theoretic quantities, and (iv) state estimation. It is known since Snyder's and related works that marginalization over a stochastic intensity turns point processes into

self-exciting ones. While the Snyder filter specifies the exact history-dependent propensities in the framework of CRNs in Markov environment, it was recently suggested to use approximate filters for the marginal description.

By regarding the chemical reactions as events we establish a link between CRNs in linear random environment and Hawkes processes, a class of self-exciting counting processes widely used in event analysis. The Hawkes process can be obtained as a moment closure or as the optimal linear approximation under the quadratic criterion. We show the equivalence of both approaches. Furthermore, we use martingale techniques to provide results on the agreement of the Hawkes process and the exact marginal process in their second order statistics, i.e., covariance, auto- and cross-correlation.

Yannic Wenzel

A multi-locus feedback model for speciation

University of Vienna, Austria

We consider a stochastic meta-population model to study the emergence of genetic incompatibilities between subpopulations.

The genetic distance between two subpopulations is determined by two antagonistic forces: (1) mutations increase the genetic distance and occur at a constant rate, (2) migration events decrease the genetic distance. An important feature of our model is that the migration rate decreases with genetic distance, reflecting greater genetic incompatibility and lower gene flow. Starting from a stochastic model, we consider a deterministic approximation of our model. This allows us to show how the feedback between migration and genetic distance can lead to the formation of distinct species with complex interbreeding structures (ring species, etc.).

3 List of Participants

Alberti, Frederic JGU Mainz, Germany
Aurzada, Frank TU Darmstadt, Germany
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Edelmann, Dominic NCT Heidelberg, Germany
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