

## PhD proposal – 2025

### *Study of the canonical equation of adaptive dynamics and evolutionary branching in regimes with small but frequent mutations*

**Keywords:** applied probability, stochastic modelling of population processes, parameter scalings, adaptive dynamics, population genetics

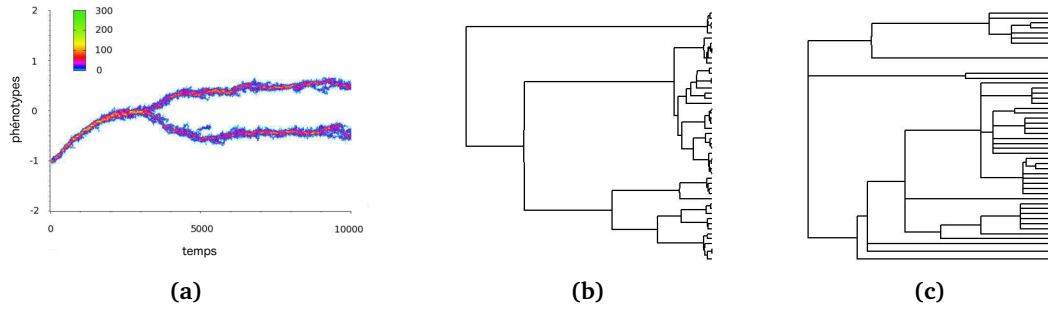
### **Biological and mathematical context**

The biological theory of adaptive dynamics [MGM+96] aims at studying the long term evolution of biological populations taking explicitly into account ecological interactions which drive the selection process. The success of this theory relies on the canonical equation of adaptive dynamics (CEAD) [DL96], a differential equation which describes the approximate long term dynamics of the dominant trait in the population as driven by the gradient of the invasion fitness of mutants, and the evolutionary branching criterion heuristically derived in [MGM+96] which gives conditions on the fitness function under which, after reaching a steady state of the CEAD, the evolutionary process drives the population to diversify from a state with a single dominant trait to states with two (or more) coexisting dominant traits which evolve in opposite directions (Fig. 1(a)). The mathematical analysis of these phenomena relies on parameter scalings applied to stochastic individual-based models, i.e. models which describe each individual event in the population, including births, deaths and mutations. Under a joint scaling of large population and rare mutations, the process converges to the so-called trait substitution sequence (TSS) [CM11], which describes evolution as a succession of random mutant invasions followed by deterministic fast competition phases where unfit traits are eliminated. Applying a scaling of small mutation to the TSS then allows to recover rigorously the CEAD and the evolutionary branching criterion [CM11].

The theory of adaptive dynamics, particularly the toolbox provided by the CEAD and the evolutionary branching criterion, had a strong impact in theoretical ecology. However, there has been some controversy among biologists, particularly about the actual occurrence of evolutionary branching in living populations. The paper [WG05] gathers the main criticisms, among which several deal with the biological assumptions underlying the approximate models, in particular the fact that mutations need to be extremely rare for the approach to work. This motivated the study in [CH25] of a scaling with small but frequent mutations, where the convergence to the CEAD is obtained with a slow-fast analysis involving a fast time scale where the rescaled and centered distribution of traits in the population converges to the centered Fleming-Viot process, and a slow time scale where the mean trait value converges to the CEAD.

The Fleming-Viot process is a well-known process in population genetics, describing the stochastic neutral evolution of population density and support due to births, deaths and mutations. It can be obtained as a scaling limit of a Moran model, so in particular the genealogy between individuals in the Fleming-Viot process is given by the standard Kingman coalescent, in which only two ancestral lines can merge in each coalescence event (Fig. 1(b)). Around the end of the nineties, more general coalescents allowing for multiple mergers [Pit99, Sag99, DK99] (Fig. 1(c)), and the corresponding  $\Lambda$ -Fleming-Viot processes, moved into the focus of probabilists and population geneticists. These genealogies arise

when the population model allows for large reproduction events, that is, offspring numbers in a single reproductive event that can be on the order of the total population size (“skewed offspring distribution”) [MS01]. Species that exhibit such “reproductive sweepstakes”, are certain marine species such as Atlantic cod, and also viruses and fungi. Despite these preliminary works and the relevance of skewed reproduction, the corresponding mechanisms have not yet been incorporated in adaptive dynamics models.



**Figure 1:** (a): Evolutionary branching in a stochastic individual-based population dynamics with mutation and selection. (b) and (c): Kingman- and Beta(1, 1)-coalescent respectively. (c) arises from a highly skewed offspring distribution and allows for multiple mergers, in contrast to (b), which only involves binary mergers.

## Project description

The following PhD project builds upon the work [CH25]. It aims to derive and understand the CEAD in regimes with skewed offspring distribution and under small but frequent mutations. It also aims to study the time scale and conditions for evolutionary branching in a regime with small but frequent mutations.

## Tasks

The first task of the PhD student will be to get familiar with the biological theory of adaptive dynamics [MGM+96, DL96], the mathematical theory of stochastic adaptive dynamics [CM11, CH25] and models of population genetics, including Canning’s model, general coalescent processes and  $\Lambda$ -Fleming-Viot processes [Sag99, MS01, CH23]. The order and the contents of the next tasks can be adapted to the expertise and the interests of the PhD student.

In the second task of the PhD, the student will consider population models with skewed reproduction and CEAD in a similar way as in [MS01], in a frequent mutation regime. We expect that the ancestral structure on the fast time scale should converge to the one of a  $\Lambda$ -Fleming-Viot process. The extension of the averaging technique of [CH25] will require to establish ergodicity properties of centered  $\Lambda$ -Fleming-Viot processes as in [Ch23]. Different limiting CEAD and time scales are expected depending on whether the associated coalescent process comes down from infinity or not.

The third task of the PhD deals with cases where two coexisting traits are initially present in the population. In this case, we expect the convergence to a 2-dimensional CEAD describing the coevolution of the two coexisting traits. This extension of [CH25] requires a proper description of the mean trait and rescaled population distributions around the two dominant traits. We expect that the coevolving centered Fleming-Viot processes that

will be obtained on the fast time-scale become asymptotically independent, so that they both reach their most recent common ancestor fast, but jointly, their most recent common ancestor appears on a much longer time scale.

Finally, the PhD student will study the influence of initial distance between traits in the dimorphic case. The goal is to quantify the minimal initial distance so that we can observe the divergence of the two traits. This divergence will of course occur on a longer time scale than in the previous task. In a nutshell, this task consists in quantifying the threshold below which the fluctuations in the Fleming-Viot process acting on the fast time scale become too large to allow for a divergence between the two traits. This situation can be interpreted as the late phase of evolutionary branching, so we expect to deduce lower bounds on the time scale of evolutionary branching using large deviations estimates on the width of the support of Fleming-Viot processes.

## PhD thesis context

The PhD thesis will take place in the Probability and Statistics team of the Institut Élie Cartan de Lorraine ([IECL](#)) and in the [SIMBA](#) (Statistical Inference and Modeling for Biological Applications) team of [Inria Nancy](#). During the PhD thesis, the student will have the opportunity to discover the world of mathematical research through the life of a dynamic mathematics laboratory, and to attend seminars and working groups in probability and statistics.

This PhD thesis is part of an international project in collaboration with the group of Prof. Jochen Blath (Goethe-Universität Frankfurt, Germany). The PhD student will take part in regular meetings with this group, that will take place either in Nancy or in Frankfurt. Part of the project will be done in collaboration with this group.

## Funding

The PhD project will be funded by the ANR-DFG project NeCoSAD, which is currently under evaluation by the French and German research agencies.

## Advantages

- ▶ Subsidized meals
- ▶ Partial reimbursement of public transport costs
- ▶ Leave: 7 weeks of annual leave + 10 extra days off due to RTT (statutory reduction in working hours) + possibility of exceptional leave (sick children, moving home, etc.)
- ▶ Possibility of teleworking (90 days per year) and flexible organization of working hours
- ▶ Professional equipment available (videoconferencing, loan of computer equipment, etc.)
- ▶ Social, cultural and sports events and activities
- ▶ Access to vocational training
- ▶ Social security coverage

## Skills

The candidate should have skills in stochastic modeling and probability theory. In particular, skills in stochastic models of population dynamics and/or population genetics will be highly appreciated. An affinity or experience with biological applications is also welcome.

## Supervision

The PhD thesis will be supervised by Nicolas Champagnat.

## Contact

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## Application

The application file should be submitted on the [Inria job offer web site](#).

## Bibliography

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