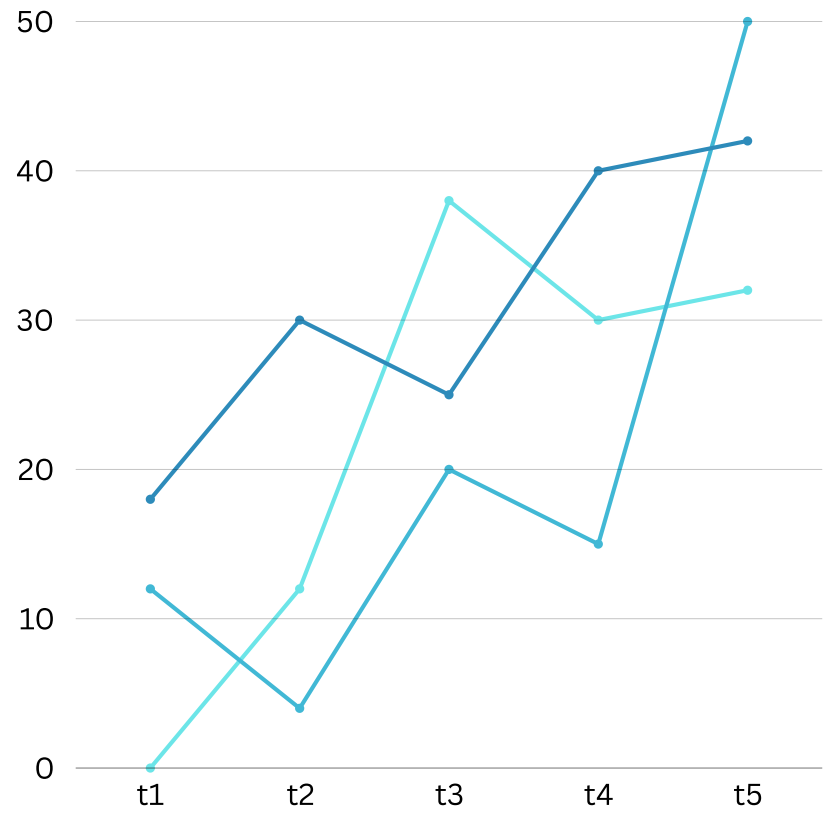
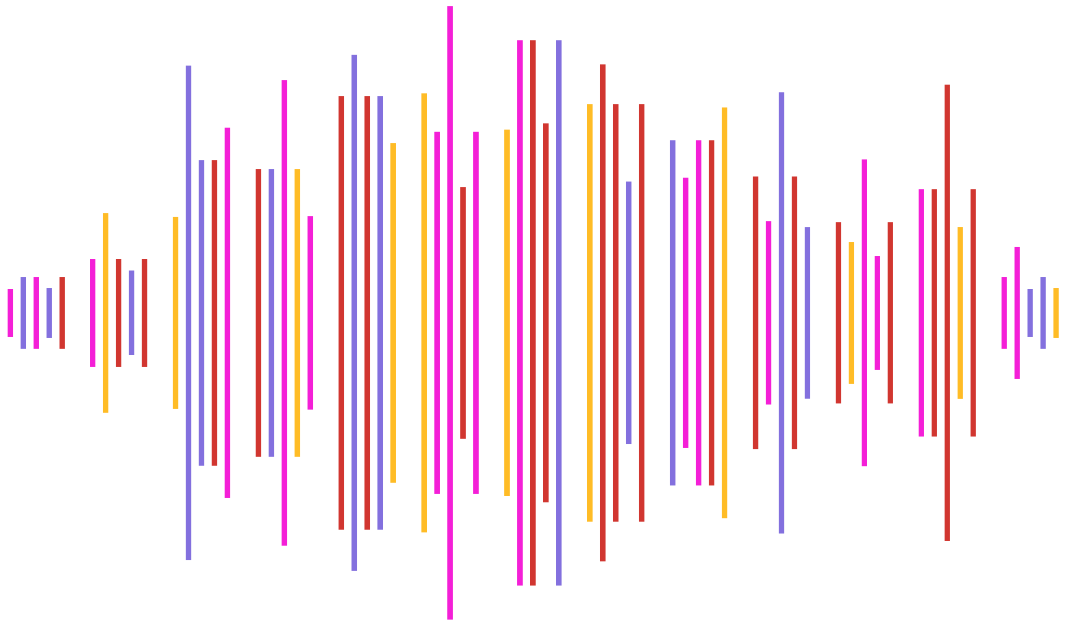
# Introduction to stochastic calculus for population dynamics




**Gui Araujo**



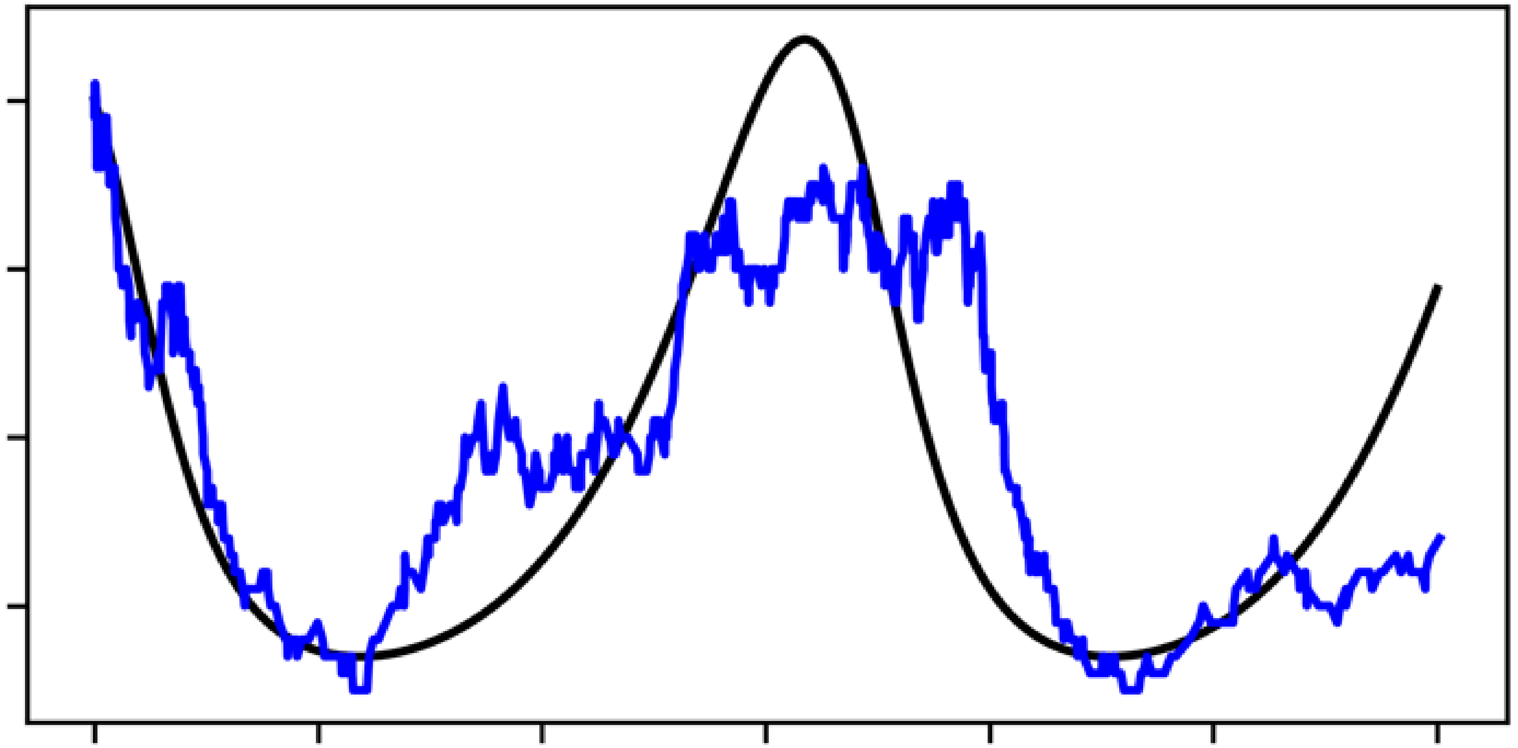
# Introduction

- Stochastic calculus: mathematical assessment of trajectories of random models.

# Introduction

- Stochastic calculus: mathematical assessment of trajectories of random models.

- Uncertainty causes a sample trajectory to have random components, which defines probability distributions associated with the trajectory.

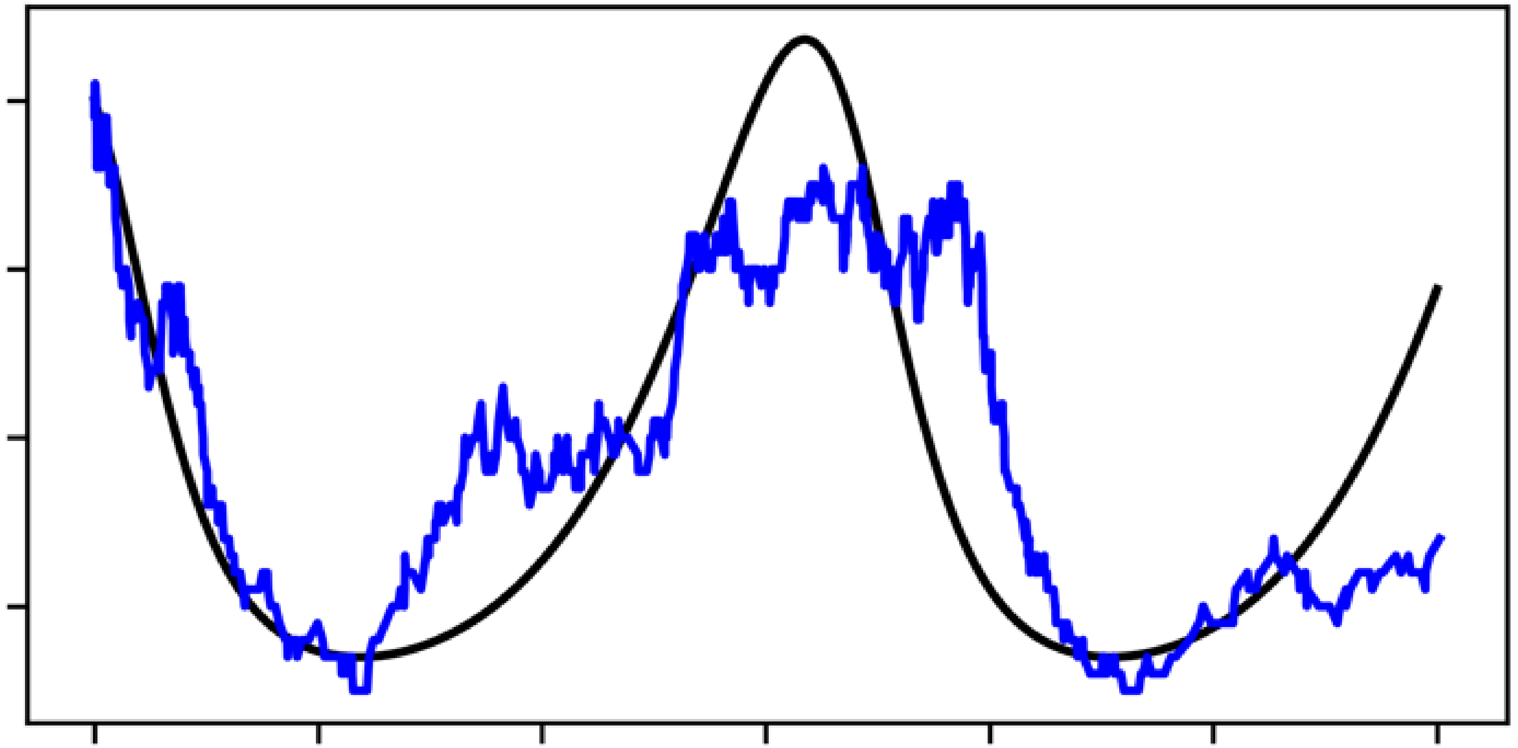


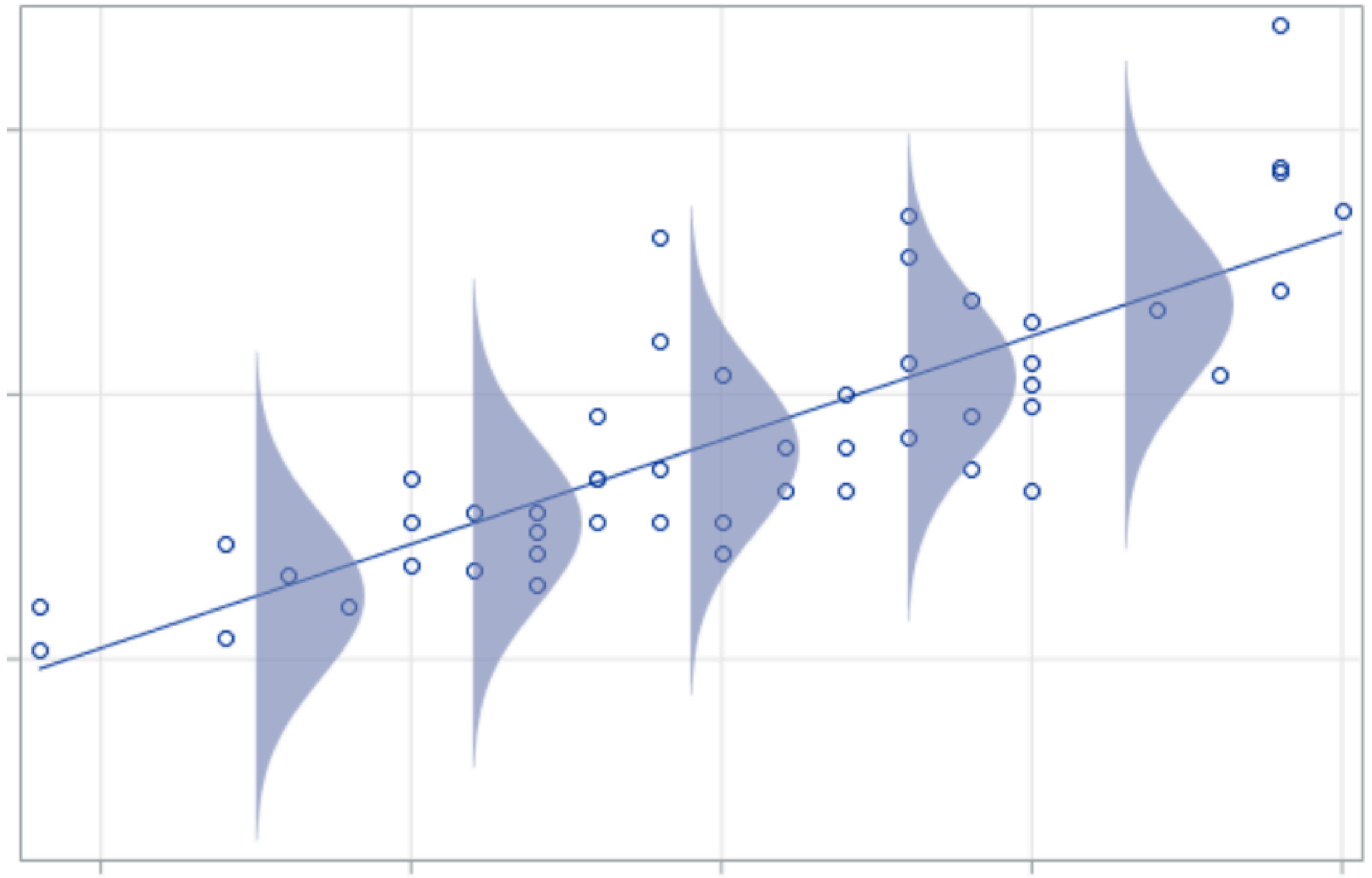
# Introduction

- Stochastic calculus: mathematical assessment of trajectories of random models.

- Uncertainty causes a sample trajectory to have random components, which defines probability distributions associated with the trajectory.

- Then, to each point in time, we can associate a trajectory with a probability distribution, and that distribution evolves as time progresses.





## Markovian models

- All of basic stochastic calculus relies on the study of Markovian models.
- Markovian property: changes in the state of a model depend only on the current state. Then, the propagation of probabilities can condition only on the present and forget about all of the past.

# Markovian models

- All of basic stochastic calculus relies on the study of Markovian models.

- Markovian property: changes in the state of a model depend only on the current state. Then, the propagation of probabilities can condition only on the present and forget about all of the past.

P( future | present, past ) = P( future | present, ~~past~~ )

Markov property

$$P(X_{t+n} = x | X_t, X_{t-1}, \dots, X_{t-k}) = P(X_{t+n} = x | X_t)$$

## Markovian models

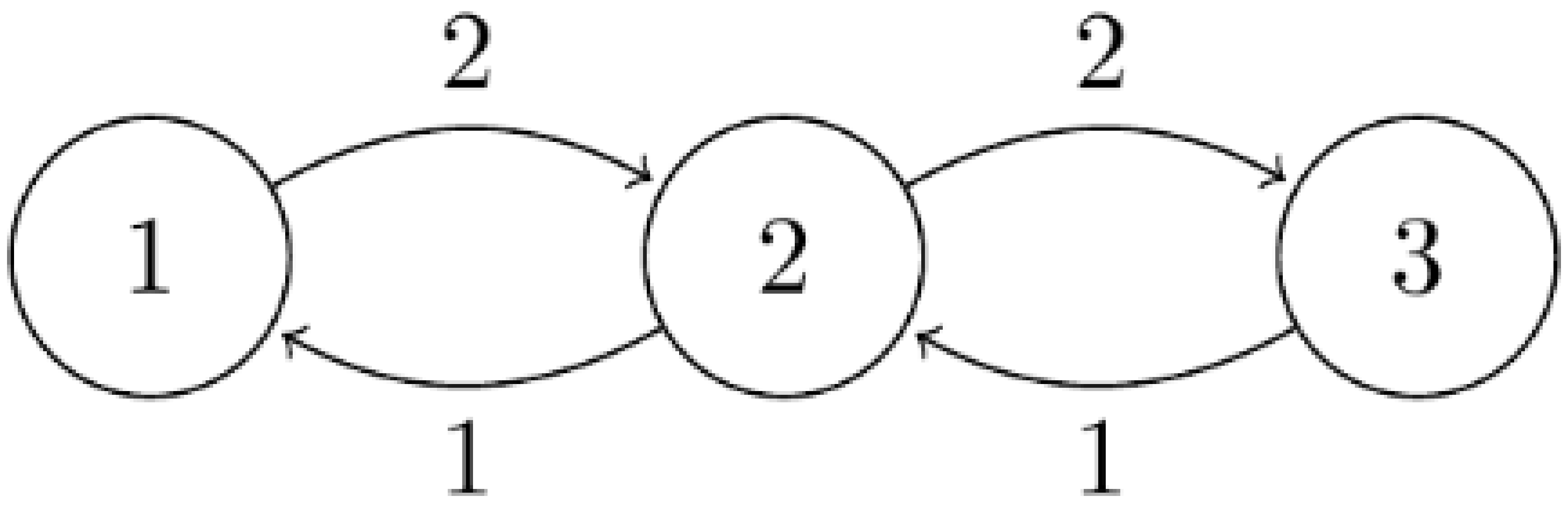
- The formal study of Markovian models is split into 4 categories: discrete x continuous time, and discrete x continuous state space.

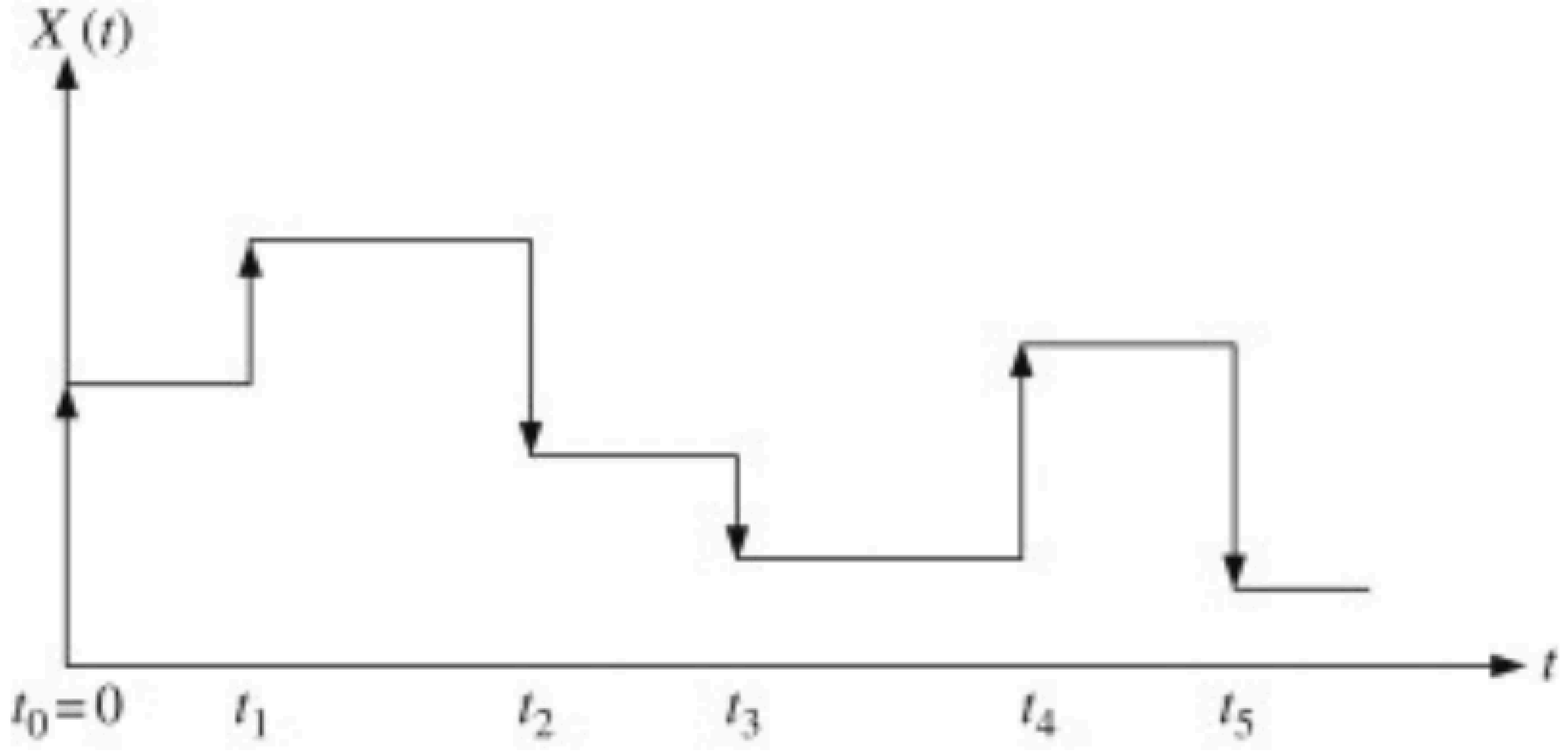
- For population dynamics, the most useful category is continuous time and discrete state space, what we call a Markov jump process.

## Markovian models

- The formal study of Markovian models is split into 4 categories: discrete x continuous time, and discrete x continuous state space.

- For population dynamics, the most useful category is continuous time and discrete state space, what we call a Markov jump process.



# Master Equation of MJPs

- The main goal with a random trajectory is to be able to calculate the probability distributions associated with each possible state at each instant.

# Master Equation of MJPs

- The main goal with a random trajectory is to be able to calculate the probability distributions associated with each possible state at each instant.

- For MJPs, we can derive a master equation as an evolution law for probability densities based on the transition rates between states, $W_{\boldsymbol{n_i},t-dt\to\boldsymbol{n},t}$

$$\frac{d\Pi(\boldsymbol{n},t)}{dt} = \sum_{\boldsymbol{n_i}} \left(W_{\boldsymbol{n_i},\boldsymbol{n}}\Pi(\boldsymbol{n_i},t) - W_{\boldsymbol{n},\boldsymbol{n_i}}\Pi(\boldsymbol{n},t)\right)$$

# Master Equation of MJPs

- The main goal with a random trajectory is to be able to calculate the probability distributions associated with each possible state at each instant.

- For MJPs, we can derive a master equation as an evolution law for probability densities based on the transition rates between states, $W_{\boldsymbol{n_i},t-dt\to\boldsymbol{n},t}$

$$\frac{d\Pi(\boldsymbol{n},t)}{dt} = \sum_{\boldsymbol{n_i}} \left( W_{\boldsymbol{n_i},\boldsymbol{n}} \Pi(\boldsymbol{n_i},t) - W_{\boldsymbol{n},\boldsymbol{n_i}} \Pi(\boldsymbol{n},t) \right)$$

- It is based on the conservation of probability mass between in-jumps and out-jumps.

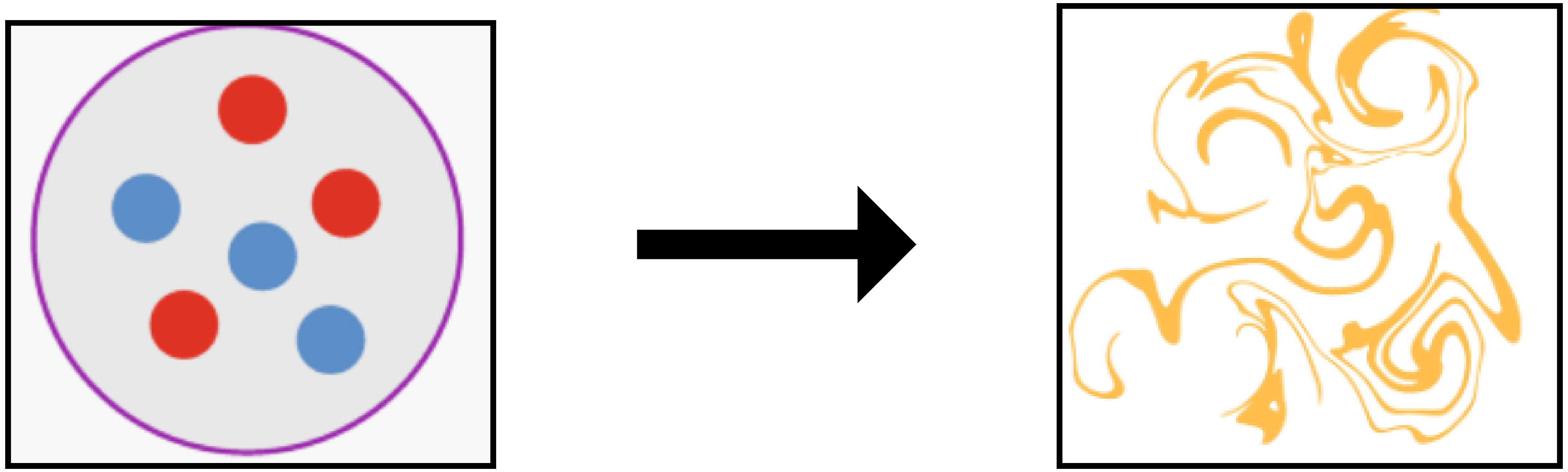
## Population dynamics

- The deterministic equations of population dynamics describe a global context: densities of whole populations being shaped by processes defined solely by rates of change.

# Population dynamics

- The deterministic equations of population dynamics describe a global context: densities of whole populations being shaped by processes defined solely by rates of change.

- To understand the underlying mechanisms promoting those changes, we must shift our model definitions to the individual interactions generating the global-level patterns.



# Population dynamics

- We can work with how frequently events will happen on an individual level, but we can’t define mechanisms that exactly determine individual events.

## Population dynamics

- We can work with how frequently events will happen on an individual level, but we can’t define mechanisms that exactly determine individual events.

- Therefore, we use stochastic calculus to derive evolution laws for trajectories at the individual level.

# Population dynamics

- We can work with how frequently events will happen on an individual level, but we can’t define mechanisms that exactly determine individual events.

- Therefore, we use stochastic calculus to derive evolution laws for trajectories at the individual level.

- We should expect the stochastic individual-level description to match the deterministic global-level description as the system grows infinitely and washes away all uncertainty. As it turns out, we can do it!

## Population dynamics

- We can work with how frequently events will happen on an individual level, but we can’t define mechanisms that exactly determine individual events.

- Therefore, we use stochastic calculus to derive evolution laws for trajectories at the individual level.

- We should expect the stochastic individual-level description to match the deterministic global-level description as the system grows infinitely and washes away all uncertainty. As it turns out, we can do it!

- How is uncertainty washed away? By the **law of large numbers,** uncertainty becomes frequency with infinite numbers.

# Master equation for the logistic model

Model definition

$$\boxed{\begin{array}{c} X \xrightarrow{\omega} 2X \\ X \xrightarrow{\mu} \emptyset \\ 2X \xrightarrow{\gamma} X \end{array}}$$

# Master equation for the logistic model

Model definition

$$X \xrightarrow{\omega} 2X$$

$$X \xrightarrow{\mu} \emptyset$$

$$2X \xrightarrow{\gamma} X$$

Deterministic equation

$$\frac{d\eta}{dt} = \omega\eta - \mu\eta - \gamma\eta^2$$

$$\dot{\eta} = \eta r(1-\eta/K)$$

# Master equation for the logistic model

Model definition

$$X \xrightarrow{\omega} 2X$$

$$X \xrightarrow{\mu} \emptyset$$

$$2X \xrightarrow{\gamma} X$$

Deterministic equation

$$\frac{d\eta}{dt} = \omega\eta - \mu\eta - \gamma\eta^2$$

$$\dot{\eta} = \eta r(1-\eta/K)$$

Equivalencies

$$r = (\omega-\mu)$$

$$K = (\omega-\mu)/\gamma$$

# Master equation for the logistic model

## Model definition

$$X \xrightarrow{\omega} 2X$$

$$X \xrightarrow{\mu} \emptyset$$

$$2X \xrightarrow{\gamma} X$$

## Deterministic equation

$$\frac{d\eta}{dt} = \omega\eta - \mu\eta - \gamma\eta^2$$

$$\dot{\eta} = \eta r(1 - \eta/K)$$

## Equivalencies

$$r = (\omega - \mu)$$

$$K = (\omega - \mu)/\gamma$$

## Master equation

$$\frac{\mathrm{d}\Pi(n,t)}{\mathrm{d}t} = \omega(n-1)\Pi(n-1,t) + \mu(n+1)\Pi(n+1,t) + \frac{\gamma}{\Omega}(n+1)n\Pi(n+1,t)$$

$$-\left(\mathbf{w}n + \mu n + \frac{\gamma n(n-1)}{\Omega}\right)\Pi(n,t).$$

## Stochastic simulation of the ME

- It is impossible to solve the ME for non-trivial systems. However, we can simulate the ME to draw sample trajectories of the model.

## Stochastic simulation of the ME

- It is impossible to solve the ME for non-trivial systems. However, we can simulate the ME to draw sample trajectories of the model.

- The standard procedure is to use the SSA or Gillespie's algorithm. Since naively sorting interactions for each time interval is too demanding, the SSA is based on a simple trick.

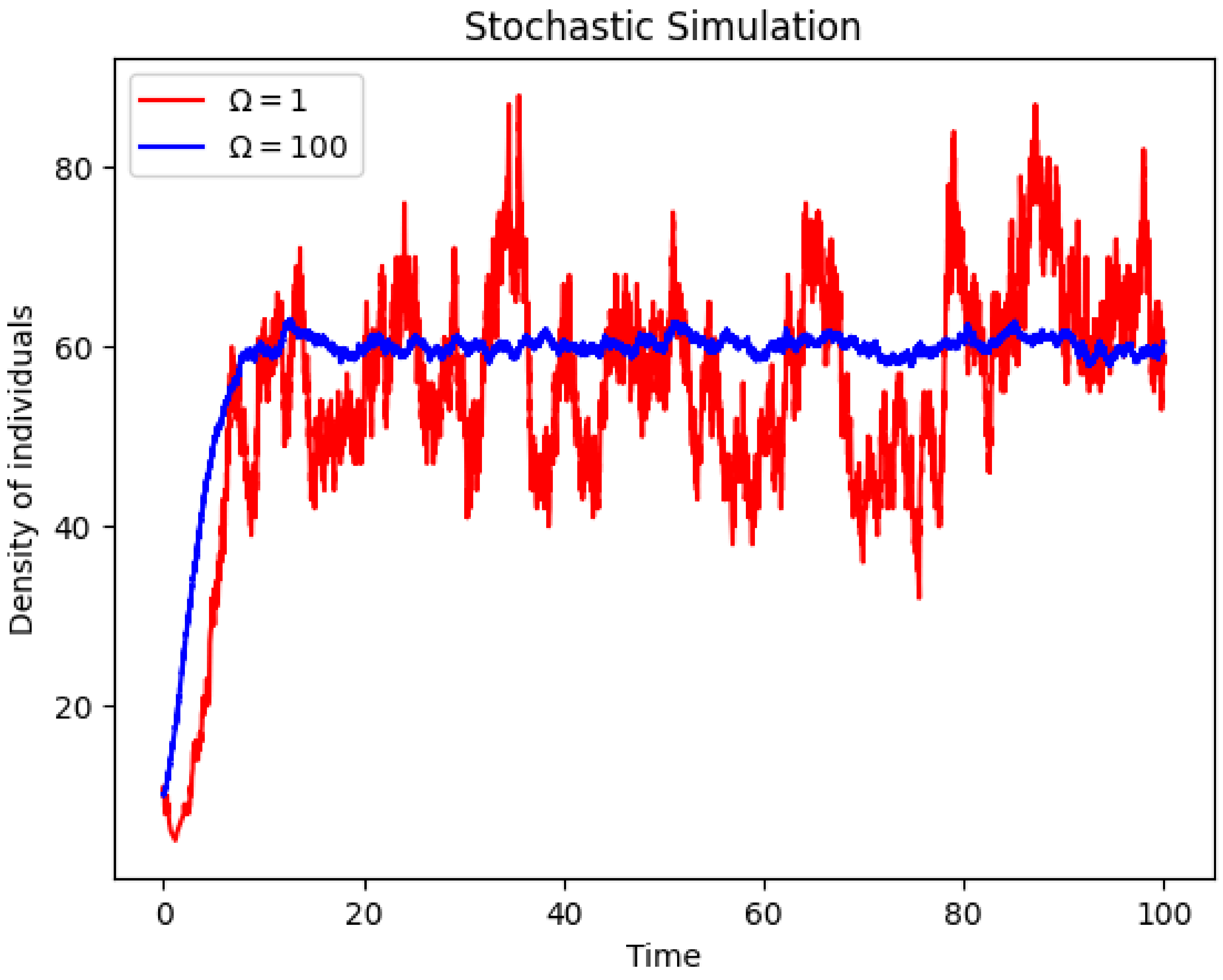
## Stochastic simulation of the ME

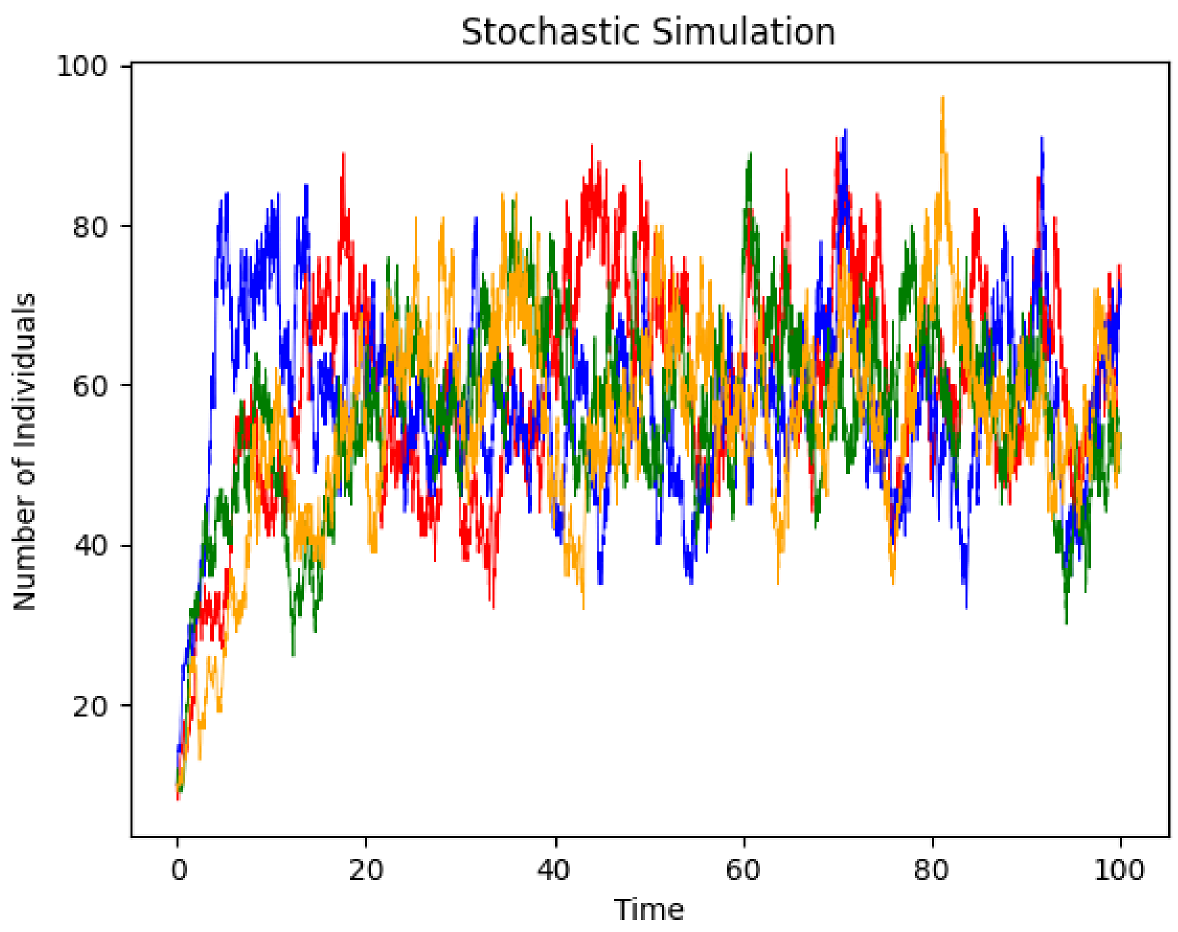
- It is impossible to solve the ME for non-trivial systems. However, we can simulate the ME to draw sample trajectories of the model.

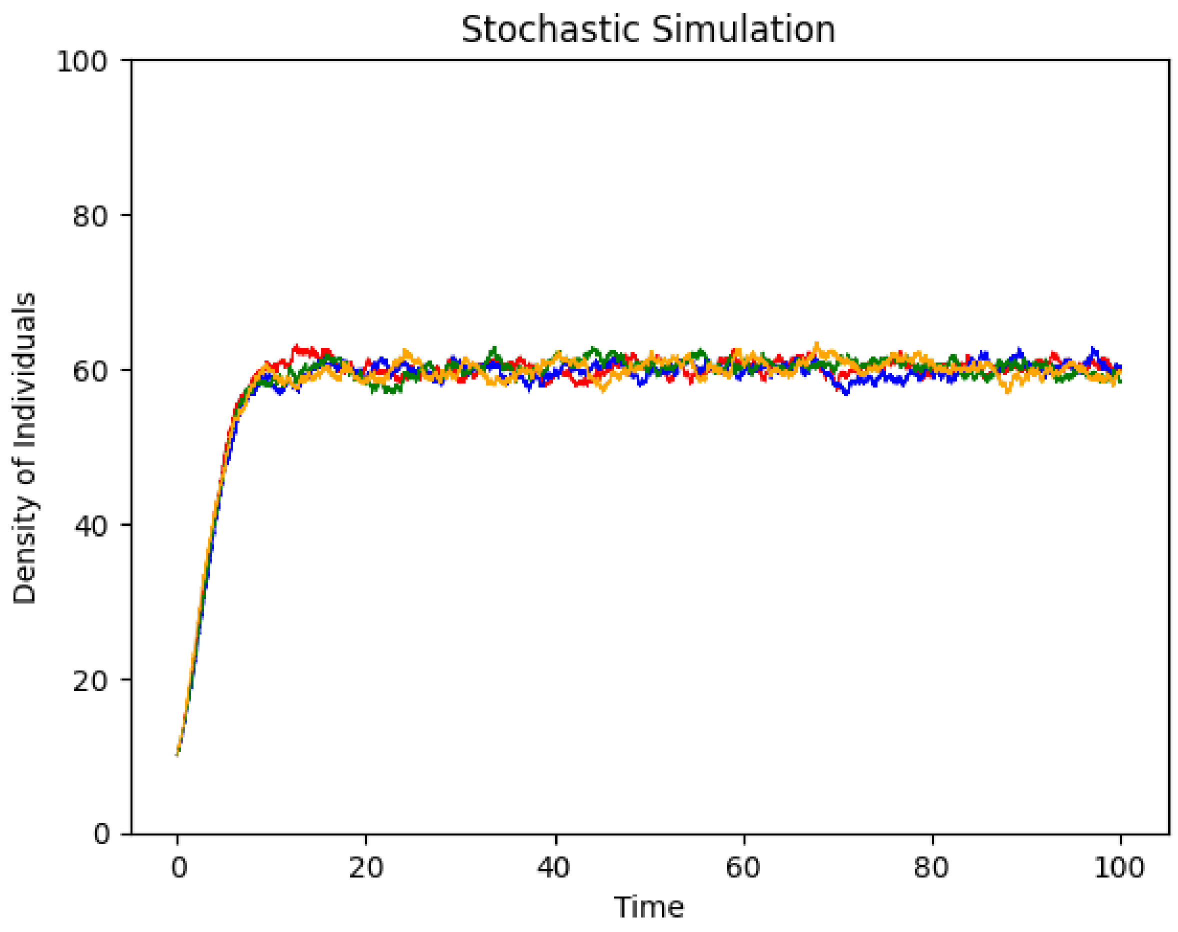
- The standard procedure is to use the SSA or Gillespie's algorithm. Since naively sorting interactions for each time interval is too demanding, the SSA is based on a simple trick.

- Idea: 1) sort the time until the next interaction occurs, which is exponentially distributed, since it's the waiting time of a simple Poisson process (between jumps, it's a counting process with a constant rate!). Then, 2) sort which interaction it will be, which is simply weighted according to the transition rates.

# Simulation of the Logistic model



## Fokker-Planck equation

- Is a partial differential equation for probability densities that incorporates drift and diffusion forces acting on continuous state spaces. In the context of MJPs, it is derived as an approximation of the ME.

## Fokker-Planck equation

- Is a partial differential equation for probability densities that incorporates drift and diffusion forces acting on continuous state spaces. In the context of MJPs, it is derived as an approximation of the ME.

- For a 1D state-space, such as the logistic model, with A(x) as the drift function and B(x) as the diffusion function, it's written as:

$$\frac{\partial \Pi(x)}{\partial t} = -\frac{\partial}{\partial x}[A(x)\Pi(x)] + \frac{\partial^2}{\partial x^2}[B(x)\Pi(x)]$$

- If A(x) is positive linear on x and B(x) is constant, the solution is a Gaussian. This is the case of the linear noise approximation, first order of the system size expansion.

# FP for the logistic equation

- Fokker-Planck equation for the logistic model:

$$\frac{\partial \Pi(x)}{\partial t} = -\frac{\partial}{\partial x}[(\omega x - \mu x - \gamma x^2)\Pi(x)] + \frac{1}{2}\frac{\partial^2}{\partial x^2}[(\omega x + \mu x + \gamma x^2)\Pi(x)]$$

# FP for the logistic equation

- Fokker-Planck equation for the logistic model:

$$\frac{\partial \Pi(x)}{\partial t} = -\frac{\partial}{\partial x}[(\omega x - \mu x - \gamma x^2)\Pi(x)] + \frac{1}{2}\frac{\partial^2}{\partial x^2}[(\omega x + \mu x + \gamma x^2)\Pi(x)]$$

- It’s a nonlinear equation with **structured fluctuations.** The system size expansion separates the deterministic solution and considers the noise around it. In this case, the LNA solution becomes a **time-dependent Gaussian.**

$$\frac{n}{\Omega} = \eta + \frac{\xi}{\sqrt{\Omega}}$$

$$\frac{\partial \Pi(\xi)}{\partial t} = -\frac{\partial}{\partial \xi}[(\omega - \mu - 2\gamma\eta)\xi\Pi(x)] + \frac{1}{2}\frac{\partial^2}{\partial \xi^2}[(\omega\eta + \mu\eta + \gamma\eta^2)\Pi(x)] + \mathcal{O}(\Omega^{-1/2})$$

## Langevin equation

- Is a stochastic differential equation that directly models continuous densities as a random variable through the addition of noise on the deterministic model. The 1D Langevin (Ito) equation is:

$$dx = A(x)dt + C(x)dW$$

- A(x) is the deterministic drift function and C(x) is a function modulating the size of the noise. The noise, dW's are independent at each instant and the increments are standardized Gaussian (W is a Wiener process). Each source of noise requires a new W.

## Langevin equation

- Is a stochastic differential equation that directly models continuous densities as a random variable through the addition of noise on the deterministic model. The 1D Langevin (Ito) equation is:

$$dx = A(x)dt + C(x)dW$$

- A(x) is the deterministic drift function and C(x) is a function modulating the size of the noise. The noise, dW's are independent at each instant and the increments are standardized Gaussian (W is a Wiener process). Each source of noise requires a new W.

- This equation is mathematically equivalent to the FP equation, and in practice it can work as a **sample generator** for FP models.

# Langevin equation

- In practice, we integrate A(x) while disturbing the trajectory at each dt with the addition of the noises W as random independent samples from a standard Gaussian distribution N(0,1). The only trick in the numerical integration is that dW transforms to the square root of dt instead of dt, i.e.:

$$dW = \mathcal{N}(0,1)\sqrt{dt}$$

## Langevin equation

- In practice, we integrate A(x) while disturbing the trajectory at each dt with the addition of the noises W as random independent samples from a standard Gaussian distribution N(0,1). The only trick in the numerical integration is that dW transforms to the square root of dt instead of dt, i.e.:

$$dW = \mathcal{N}(0,1)\sqrt{dt}$$

- In the example of the logistic model, the Langevin equation has 3 sources of noise, because there are 3 independent types of individual events generating the logistic global equations:

$$dx = (\omega x - \mu x - \gamma x^2)dt + \sqrt{\omega x}dW_1 + \sqrt{\mu x}dW2 + \sqrt{\gamma x^2}dW_3$$
$$dx = (\omega x - \mu x - \gamma x^2)dt + \sqrt{(\omega x + \mu x + \gamma x^2)}dW$$

# Intrinsic noise x external noise

- **Intrinsic noise:** is randomness arising from the individual-level events due to the low numbers (and more generally finiteness) of individual counts.

# Intrinsic noise x external noise

- **Intrinsic noise:** is randomness arising from the individual-level events due to the low numbers (and more generally finiteness) of individual counts.

- **External noise:** is randomness arising from external sources, not directly linked to the dynamical process. Can be an additional source of noise that is part of the model or coming from fluctuations in the values of model parameters, such as interaction rates.

## Intrinsic noise x external noise

- **Intrinsic noise:** is randomness arising from the individual-level events due to the low numbers (and more generally finiteness) of individual counts.

- **External noise:** is randomness arising from external sources, not directly linked to the dynamical process. Can be an additional source of noise that is part of the model or coming from fluctuations in the values of model parameters, such as interaction rates.

- The noise (or diffusion processes) discussed here are all intrinsic noise naturally arising from the interactions. It’s inescapable for finite systems defined only through transition rates and can be directly derived from the functional structure of interactions. Then, external noise can be independently added on top of it.