

Short Course on Stochastic Differential Equations in Population Biology

Course Syllabus

Course Description

Stochastic differential equations (SDEs) provide an important mathematical framework for modeling biological populations subject to environmental fluctuations and other forms of random variation. They have become increasingly useful in population biology, ecology, epidemiology, and related areas of mathematical biology.

This short course is intended as an introduction to SDEs for students whose main background is in differential equations, dynamical systems, or mathematical biology. No previous course in stochastic differential equations is assumed.

The course will emphasize both the basic mathematical ideas behind SDEs and their applications to population models. We will begin with elementary probability and Brownian motion, then introduce Itô stochastic integrals, Itô's formula, and basic SDE theory. These tools will subsequently be applied to stochastic population models to study positivity, extinction, persistence, stationary distributions, multispecies interactions, invasion rates, invariant measures, ergodicity, and stochastic persistence.

The emphasis will be on developing intuition and learning the main techniques needed to begin reading research papers on stochastic population dynamics.

Course Format

The course consists of **five lectures**, each approximately **two hours**.

Each lecture will combine:

- basic definitions and intuition;
- mathematical derivations;
- worked examples;
- biological interpretations;
- short exercises and discussion;
- connections with current research in stochastic population dynamics.

The lectures are designed so that students can follow the course without previous training in SDEs.

Intended Audience

The course is primarily intended for graduate students and researchers in

- differential equations;
- dynamical systems;

- mathematical biology;
- population dynamics;
- ecology and epidemiology,

who would like to develop a working knowledge of stochastic differential equations and their applications.

Prerequisites

Students should be familiar with ordinary differential equations, elementary multivariable calculus, and basic linear algebra.

A previous course in probability theory is helpful but **not required**. The probability concepts needed for the course will be introduced in the preliminary lecture.

No previous knowledge of stochastic calculus is assumed.

Learning Objectives

By the end of the course, students should be able to:

1. understand the basic probabilistic concepts needed for stochastic differential equations;
2. understand Brownian motion and its fundamental properties;
3. interpret an Itô stochastic differential equation;
4. work with Itô stochastic integrals and apply Itô's formula;
5. solve and analyze several elementary SDEs explicitly;
6. understand existence, uniqueness, positivity, and nonexplosion of solutions;
7. formulate stochastic versions of classical population models;
8. distinguish deterministic growth rates from stochastic long-term growth rates;
9. analyze extinction and persistence in simple stochastic population models;
10. understand stationary distributions and invariant probability measures;
11. formulate and analyze stochastic competition, predator–prey, and epidemic models;
12. understand the role of invasion rates in multispecies stochastic systems;
13. understand the basic ideas of Markov processes, generators, ergodicity, and stochastic persistence;
14. acquire sufficient background to begin reading research literature on stochastic population dynamics.

Lecture 0. Preliminaries: Probability Foundations for SDEs

Main Goal

To introduce the minimum amount of probability theory needed to begin studying stochastic differential equations.

Topics

We will review or introduce:

- deterministic versus stochastic models;
- random experiments and sample spaces;
- events and probability measures;
- random variables;
- discrete and continuous random variables;
- probability distributions;
- expectation and variance;
- covariance and correlation;
- normal distributions;
- conditional probability and conditional expectation;
- independence;
- sequences of random variables;
- basic convergence concepts;
- stochastic processes;
- sample paths;
- filtrations and information;
- adapted stochastic processes;
- martingales;
- Gaussian processes;
- random walks;
- scaling limits and the motivation for Brownian motion.

Special attention will be given to concepts that will appear repeatedly in later lectures.

Biological Motivation

Environmental variables such as temperature, rainfall, food availability, and habitat quality fluctuate randomly. We will discuss how random variables and stochastic processes provide mathematical descriptions of these fluctuations.

Lecture 1. Brownian Motion, Itô Calculus, and Basic SDE Models

Main Goal

To develop the basic language and computational tools of stochastic differential equations.

Topics

We will study:

- definition and properties of Brownian motion;
- Brownian increments;
- quadratic variation;
- why Brownian motion is not differentiable in the ordinary sense;
- motivation for stochastic integration;
- construction and interpretation of the Itô integral;
- elementary properties of the Itô integral;
- Itô isometry;
- martingale properties of stochastic integrals;
- Itô's formula;
- comparison between the ordinary chain rule and Itô's formula;
- scalar stochastic differential equations

$$dX_t = b(X_t) dt + \sigma(X_t) dB_t;$$

- drift and diffusion coefficients;
- geometric Brownian motion;
- explicit solutions;
- moments and distributions;
- stochastic exponential growth;
- stochastic logistic growth;
- Ornstein–Uhlenbeck processes;

- existence and uniqueness of SDE solutions;
- introduction to Euler–Maruyama numerical approximation;
- brief comparison of Itô and Stratonovich formulations.

Population Biology Examples

We will compare the deterministic exponential growth model

$$\frac{dx}{dt} = rx$$

with the stochastic model

$$dX_t = rX_t dt + \sigma X_t dB_t,$$

and examine how environmental noise changes the long-term population growth rate.

Lecture 2. Positivity, Extinction, Persistence, and Stationary Distributions

Main Goal

To learn fundamental techniques for determining the long-term behavior of one-dimensional stochastic population models.

Topics

We will discuss:

- local and global solutions;
- stopping times;
- explosion times;
- positivity of population solutions;
- logarithmic transformations;
- Lyapunov functions;
- generators of diffusion processes;
- Dynkin’s formula;
- martingale estimates;
- stochastic logistic equations;
- almost-sure growth rates;
- extinction criteria;
- persistence in mean;
- stochastic permanence;

- threshold phenomena caused by environmental noise;
- stationary probability distributions;
- derivation of stationary densities;
- the Fokker–Planck viewpoint;
- Gamma-type stationary distributions for stochastic logistic models;
- calculation of stationary means and variances;
- interpretation of stochastic thresholds.

A basic model studied in detail will be

$$dX_t = X_t(a - bX_t) dt + \sigma X_t dB_t.$$

Applying Itô's formula to $\log X_t$ gives

$$d \log X_t = \left(a - bX_t - \frac{\sigma^2}{2} \right) dt + \sigma dB_t.$$

This example illustrates one of the central ideas of the course:

environmental noise can change the effective long-term growth rate of a population.

Lecture 3. Multispecies Stochastic Population Models

Main Goal

To extend the one-species theory to interacting biological populations.

Topics

We will introduce:

- multidimensional Brownian motion;
- covariance matrices;
- correlated environmental noise;
- multidimensional SDEs;
- multidimensional Itô's formula;
- positivity and invariant coordinate planes;
- stochastic Lotka–Volterra systems;
- two-species competition models;
- stochastic predator–prey systems;
- simple stochastic epidemic models;

- boundary population dynamics;
- resident species and invading species;
- stochastic invasion rates;
- calculation of invasion rates using boundary stationary distributions;
- extinction versus coexistence scenarios;
- effects of noise on deterministic coexistence;
- biological interpretation of stochastic thresholds;
- Lyapunov functions for multidimensional systems.

For example, we will consider stochastic competition models of the form

$$\begin{aligned}dX_1(t) &= X_1(t)(r_1 - a_{11}X_1(t) - a_{12}X_2(t))dt + \sigma_1 X_1(t)dB_1(t), \\dX_2(t) &= X_2(t)(r_2 - a_{21}X_1(t) - a_{22}X_2(t))dt + \sigma_2 X_2(t)dB_2(t).\end{aligned}$$

We will examine how the ability of one species to invade the stationary population of another can determine long-term coexistence or exclusion.

Lecture 4. Markov Processes, Invariant Measures, Ergodicity, and Stochastic Persistence

Main Goal

To introduce the dynamical-systems viewpoint needed for more advanced research on stochastic population models.

Topics

We will study:

- the Markov property;
- transition probabilities;
- transition semigroups;
- Feller processes;
- infinitesimal generators;
- Dynkin's formula;
- backward and forward Kolmogorov equations;
- invariant probability measures;
- occupation measures;
- Krylov–Bogoliubov averaging;

- tightness;
- Lyapunov conditions for recurrence;
- ergodic invariant measures;
- ergodic theorems;
- boundary invariant measures;
- invasion rates associated with boundary measures;
- stochastic persistence;
- extinction;
- persistence through average Lyapunov functions;
- weighted invasion-rate conditions;
- relation between deterministic persistence and stochastic persistence.

We will conclude with a brief introduction to more advanced stochastic population models, including:

- stochastic differential equations with switching;
- jump processes and Lévy noise;
- stochastic delay equations;
- stochastic reaction–diffusion equations;
- spatial stochastic population models;
- stochastic epidemic systems;
- stochastic models in changing environments.

These topics may provide starting points for future reading projects and research.

Textbooks and References

The lectures will primarily draw on the following introductory references:

B. Øksendal, *Stochastic Differential Equations: An Introduction with Applications*, Springer.

This is a standard introductory text on Brownian motion, Itô integrals, Itô's formula, stochastic differential equations, diffusion processes, and stochastic calculus.

X. Mao, *Stochastic Differential Equations and Applications*, Horwood Publishing.

This text is particularly useful for existence, uniqueness, stability, Lyapunov methods, positivity, and long-term behavior of stochastic differential equations.

For applications to biological stochastic models, additional references and selected research papers will be introduced during the course when appropriate.

Approach to the Course

Because this is an introductory short course, the emphasis will not be on developing a complete measure-theoretic probability theory.

Instead, we will focus on

Probability intuition $\rightarrow$ Itô calculus $\rightarrow$ SDEs $\rightarrow$ population models $\rightarrow$ long-term dynamics.

Important formulas will generally be derived rather than simply stated, and simple examples will be used before more abstract results are introduced.

Students are encouraged to ask questions throughout the lectures.

Exercises

Short exercises will be suggested after each lecture. These will mainly involve:

- applying Itô's formula;
- solving elementary SDEs;
- computing expectations and long-term growth rates;
- determining extinction or persistence thresholds;
- analyzing stochastic logistic models;
- computing simple invasion rates;
- interpreting mathematical results biologically.

The exercises are intended to reinforce the lecture material rather than serve as formal examinations.

Overall Goal

The purpose of this short course is not to cover all aspects of stochastic differential equations. Rather, it is to provide a solid entry point for researchers and graduate students in differential equations, dynamical systems, and mathematical biology.

After completing the course, students should have enough background to continue studying more advanced topics in stochastic differential equations and, in particular, to begin reading research papers on stochastic population dynamics.