

# Derivation of Stochastic Ordinary and Partial Differential Equations

Ed Allen

NIMBioS Tutorial: Stochastic Models With Biological Applications

University of Tennessee, Knoxville

March, 2011

## ACKNOWLEDGEMENT

I thank all the participants for their time and their interest in stochastic modeling in biology.

I thank Professor Louis Gross and Professor Suzanne Lenhart for requesting and funding this tutorial.

## This Lecture Is Divided Into Several Parts

- (1) A procedure is reviewed for deriving a stochastic ordinary differential equation from an associated discrete stochastic model.
- (2) Stochastic ordinary differential equation systems are derived for several population problems. Equivalence of SDE systems is explained.
- (3) It is shown how stochastic partial differential equation models can be derived. Several examples are presented.

## A Procedure Is Reviewed For Deriving SDEs

- (1) A discrete stochastic model is developed for the random dynamical system. Specifically, for a small time interval, the possible changes with their corresponding transition probabilities are determined.
- (2) The expected changes and the covariance matrix for the changes are determined for the discrete stochastic process.
- (3) A stochastic differential equation model is inferred by similarities in the forward Kolmogorov equations between the discrete and continuous stochastic processes. (Solutions of the discrete model and the SDE approximately satisfy the same probability distribution.)

## The Procedure Is Illustrated For The Birth-Death Process

A simple deterministic model for population growth is:

$$\begin{cases} \frac{dx(t)}{dt} = bx - dx \\ x(0) = x_0 \end{cases}$$

where  $x(t)$  is population at time  $t$  and  $b$  and  $d$  are birth and death rates. The solution is:

$$x(t) = x_0 \exp((b - d)t).$$

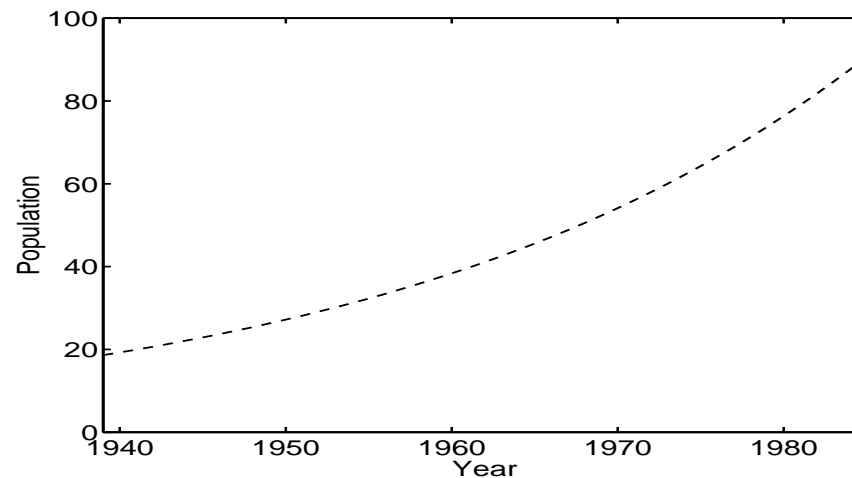


Figure 1: Exponential growth with  $x_0=18$  and  $b - d = .0344$

## But Actual Populations Do Not Grow Smoothly

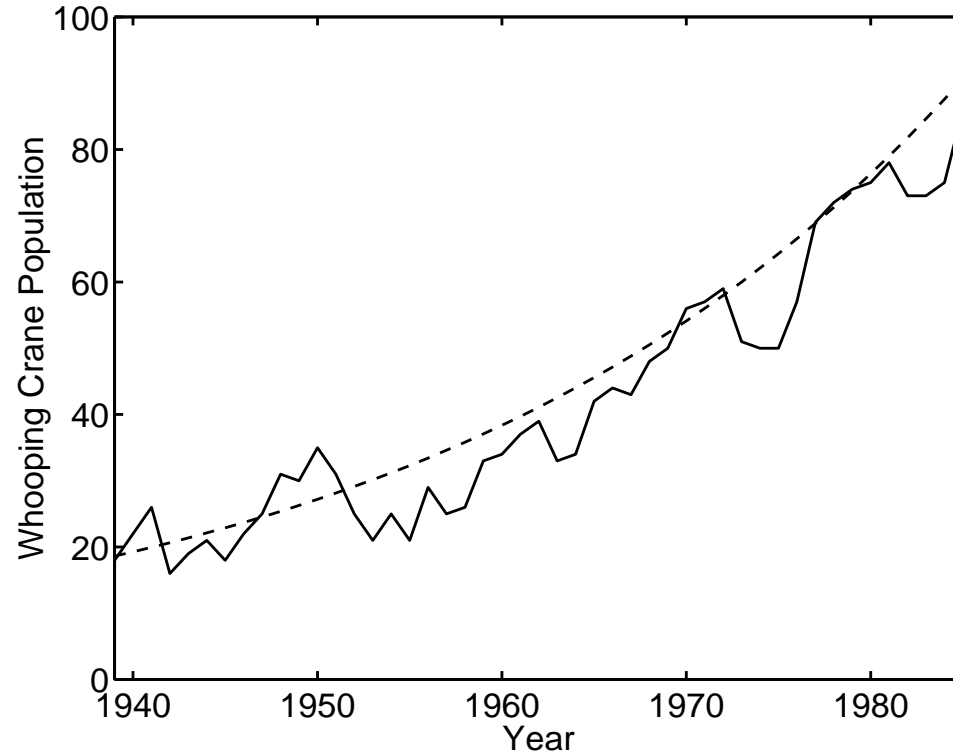


Figure 2: Whooping Crane Population 1939-1985

The population varies in an non-smooth manner due to random births and deaths.

## Considering Random Births And Deaths, A Discrete Stochastic Model Is First Constructed

The random changes in births and deaths are considered for a small time interval  $\Delta t$ .

For interval  $\Delta t$ , three possible changes are a birth, a death, or no change:  $\beta_1 = 1$ ,  $\beta_2 = -1$ , or  $\beta_3 = 0$ .

The probabilities of these changes are:

$$P_1 = bx\Delta t, \quad P_2 = dx\Delta t, \quad P_3 = 1 - (b + d)x\Delta t.$$

Let  $p_k(t) = P(X(t) = x_k)$  be the probability of having  $x_k$  individuals at time  $t$ . Then,

$$p_k(t + \Delta t) = p_k(t)[1 - bx_k\Delta t - dx_k\Delta t] + p_{k-1}(t)[bx_{k-1}\Delta t] + p_{k+1}(t)[dx_{k+1}\Delta t]$$

## Solutions To A Certain SDE Approximately Satisfy The Same Probability Distribution As The Discrete Stochastic Process

For small  $\Delta t$ , the probability distribution approximately satisfies

$$\frac{\partial p(x, t)}{\partial t} = -\frac{\partial(p(x, t)(b - d)x)}{\partial x} + \frac{1}{2}\frac{\partial^2(p(x, t)(b + d)x)}{\partial x^2}.$$

But  $p(x, t)$  is the distribution satisfied by solutions of the SDE:

$$dx(t) = (b - d)x dt + \sqrt{((b + d)x)} dW(t)$$

where  $W(t)$  is a Wiener process.

So, solutions of the discrete stochastic process and the SDE approximately satisfy the same probability distribution.



# An SDE Models The Random Population Growth

The stochastic population model

$$dx(t) = (b - d)x(t)dt + \sqrt{(b + d)x(t)} dW(t)$$

can be solved computationally using:

$$x_{i+1} = x_i + (b - d)x_i\Delta t + \eta_i\sqrt{(b + d)x_i\Delta t} \quad \text{where } \eta_i \sim N(0, 1).$$

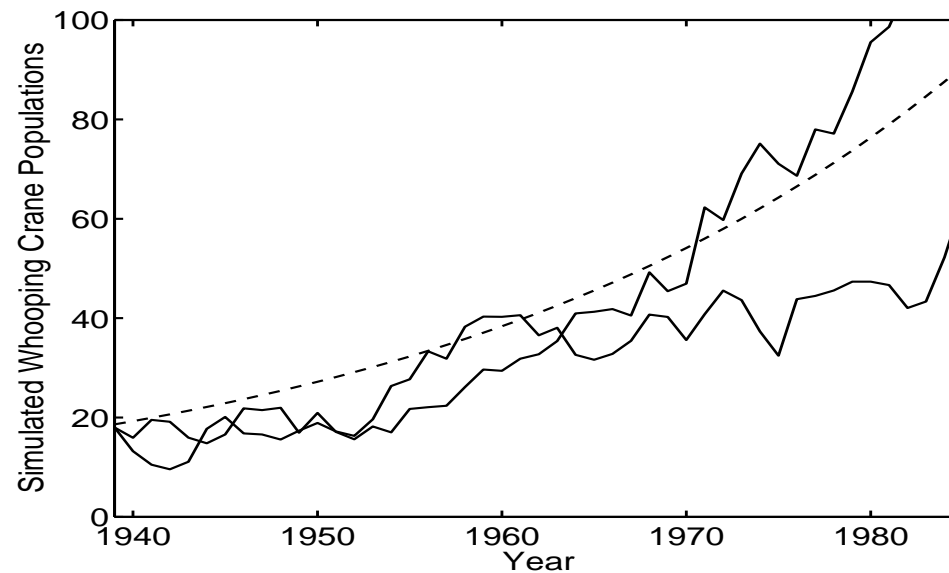


Figure 3: Simulated Whooping Crane Populations 1939-1985

## An SDE Extends An ODE To Include Randomness

The stochastic population model

$$dx(t) = (b - d)x(t)dt + \sqrt{(b + d)x(t)} dW(t)$$

is an SDE model for the birth-death process that can be studied theoretically or computationally.

For example, it immediately yields the standard deterministic ODE model:  $\frac{dy(t)}{dt} = (b - d)y(t)$  where  $y(t) = E(x(t))$ .

The SDE retains the random nature of the actual birth-death process and there are an infinite number of sample path solutions to the SDE. For this problem, the sample paths of the SDE give exact first and second moments to the actual birth-death process. That is,

$$E(x(t)) = a \exp(b - d)t$$

$$\text{Var}(x(t)) = a(b + d)(\exp(2(b - d)t) - \exp((b - d)t))/(b - d).$$

## Multidimensional SDEs For Complicated Problems Can Be Derived By Construction Of A Discrete Stochastic Model

Suppose for small  $\Delta t$  that the discrete stochastic model has mean and covariance matrix for a change  $\Delta \vec{x}$ :

$$\mathbf{E}(\Delta \vec{x}) = \vec{\mu}(\vec{x}(t), t)\Delta t$$

$$\mathbf{E}(\Delta \vec{x}\Delta \vec{x}^T) = V(\vec{x}(t), t)\Delta t.$$

Then, the corresponding SDE system is:

$$d\vec{x}(t) = \vec{\mu}(\vec{x}(t), t)dt + (V(\vec{x}(t), t))^{1/2}d\vec{W}(t)$$

where

$$\vec{x}(t) = [x_1(t), x_2(t), \dots, x_n(t)]^T,$$

$\vec{W}(t) = [W_1(t), \dots, W_n(t)]^T$  is an  $n$ -dimensional Wiener process,

$\vec{\mu}$  is a vector of length  $n$ , and  $V$  is an  $n \times n$  covariance matrix.

## Briefly Summarizing, Discrete Stochastic Processes And Stochastic Differential Equations Are Closely Related

- (1) Solutions of a discrete stochastic process and a stochastic differential equation (SDE) may have approximately the same probability distribution.
- (2) This helps us in deriving a stochastic differential equation by first constructing a discrete stochastic model.

# Consider An SDE For Two Interacting Biological Populations

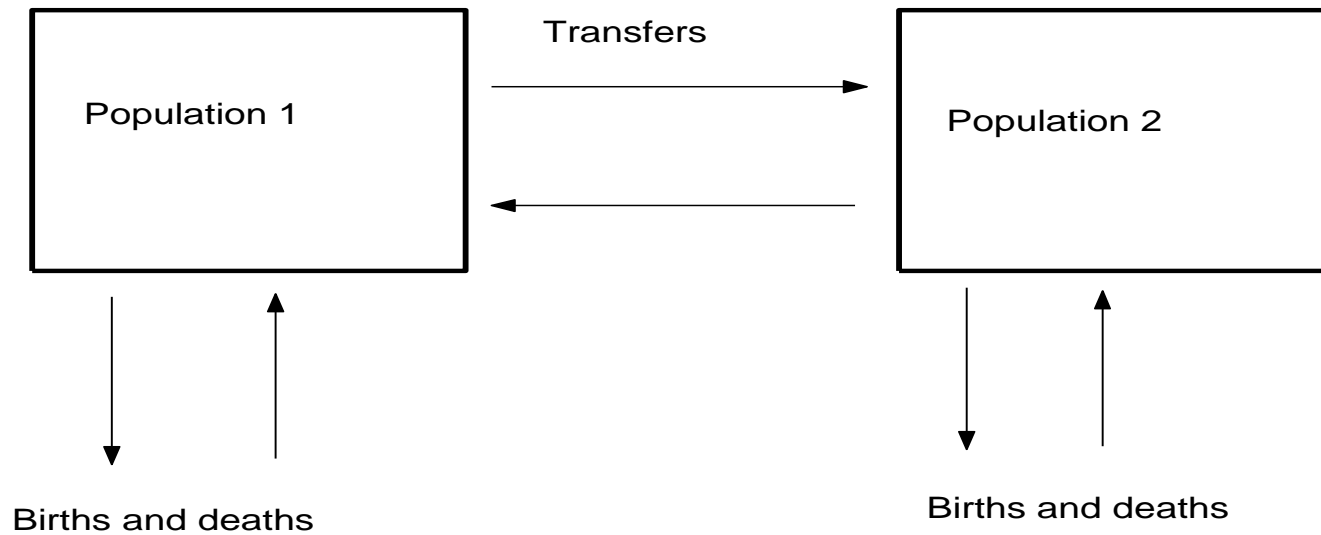


Figure 4: A Diagram Of Two Interacting Populations

## A Discrete Stochastic Model Is First Constructed

Let  $x_1(t)$  and  $x_2(t)$  be the population sizes.

Let  $\vec{\Delta x} = (\Delta x_1, \Delta x_2)^T$  be the change in the populations over  $\Delta t$ .

Seven possibilities for  $\vec{\Delta x}$  in time  $\Delta t$ :

$$\begin{aligned} \vec{\eta}_1 &= (-1, 0)^T, & \vec{\eta}_2 &= (-1, 1)^T, & \vec{\eta}_3 &= (0, -1)^T, & \vec{\eta}_4 &= (0, 0)^T, \\ \vec{\eta}_5 &= (0, 1)^T, & \vec{\eta}_6 &= (1, -1)^T, & \text{and } \vec{\eta}_7 &= (1, 0)^T. \end{aligned}$$

The probabilities for these changes are, respectively:

$$\begin{aligned} P_1 &= d_1 x_1 \Delta t, & P_2 &= m_{12} x_1 \Delta t, & P_3 &= d_2 x_2 \Delta t, \\ P_4 &= (1 - b_1 x_1 \Delta t - m_{12} x_1 \Delta t - d_1 x_1 \Delta t - d_2 x_2 \Delta t - m_{21} x_2 \Delta t - p_2 \Delta t), \\ P_5 &= b_2 x_2 \Delta t, & P_6 &= m_{21} x_2 \Delta t, & P_7 &= b_1 x_1 \Delta t. \end{aligned}$$

where  $b_1, d_1, b_2, d_2, m_{12}$ , and  $m_{21}$  are population parameters.

Therefore,

$$E(\vec{\Delta x}) = \sum_{j=1}^7 P_j \vec{\eta}_j = \begin{bmatrix} -d_1 x_1 - m_{12} x_1 + m_{21} x_2 + b_1 x_1 \\ -d_2 x_2 - m_{21} x_2 + m_{12} x_1 + b_2 x_2 \end{bmatrix} \Delta t = \vec{\mu} \Delta t$$

$$E(\vec{\Delta x} \vec{\Delta x}^T) = \begin{bmatrix} d_1 x_1 + m_{12} x_1 + m_{21} x_2 + b_1 x_1 & -m_{12} x_1 - m_{21} x_2 \\ -m_{12} x_1 - m_{21} x_2 & d_2 x_2 + m_{21} x_2 + m_{12} x_1 + b_2 x_2 \end{bmatrix} \Delta t.$$

## An SDE Model Of Two Interacting Populations Is Obtained

$$\text{With } \vec{\mu} = \begin{bmatrix} -d_1x_1 - m_{12}x_1 + m_{21}x_2 + b_1x_1 \\ -d_2x_2 - m_{21}x_2 + m_{12}x_1 + b_2x_2 \end{bmatrix} \quad \text{and}$$

$$V = \begin{bmatrix} d_1x_1 + m_{12}x_1 + m_{21}x_2 + b_1x_1 & -m_{12}x_1 - m_{21}x_2 \\ -m_{12}x_1 - m_{21}x_2 & d_2x_2 + m_{21}x_2 + m_{12}x_1 + b_2x_2 \end{bmatrix}$$

the SDE system obtained for the population dynamics is:

$$d\vec{x}(t) = \vec{\mu}(\vec{x}, t)dt + (V(\vec{x}, t))^{1/2} d\vec{W}(t)$$

where  $\vec{W}(t)$  is the two-dimensional Wiener process.

**Note:** If  $V = 0$ , then the system reduces to a standard deterministic model for the population dynamics.

**Note:** For a single population, the system reduces to

$$dx_1 = (b_1 - d_1)x_1dt + \sqrt{(b_1 + d_1)x_1} dW_1(t).$$

## DERIVATION OF ACCURATE SDE MODELS

In summary, the derivation procedure in deriving an SDE requires three steps:

First, a discrete stochastic model for the process is developed by carefully listing the possible changes along with the corresponding probabilities for a short time step  $\Delta t$ .

Second, the expected change and covariance matrix for the change is calculated for the discrete stochastic process.

Third, the stochastic differential equation system is obtained by letting the expected change divided by  $\Delta t$  be the drift coefficient and the square root of the covariance matrix divided by  $\Delta t$  be the diffusion coefficient.

Note that the derivation procedure provides an Itô SDE rather than, for example, a Stratonovich SDE.



## CALCULATING SQUARE ROOTS OF MATRICES

The derivation procedure produces a term in the SDE system that involves the square root of a symmetric positive definite matrix, that is,  $B = V^{1/2}$ . Solution of the stochastic system involves computation of square roots of matrices.

For a  $2 \times 2$  matrix, the square root can be readily calculated. Indeed,

$$V^{1/2} = \begin{bmatrix} a & b \\ b & c \end{bmatrix}^{1/2} = \frac{1}{d} \begin{bmatrix} a+w & b \\ b & c+w \end{bmatrix},$$

where  $w = \sqrt{ac - b^2}$  and  $d = \sqrt{a + c + 2w}$ . However, for a general  $n \times n$  symmetric positive definite matrix  $V$  with  $n \geq 3$ , there is no formula for  $V^{1/2}$  and it must be calculated numerically.

If  $V$  is put in the canonical form  $V = P^T D P$ , where  $P^T P = I$  and  $d_{ii} > 0$  for  $i = 1, 2, \dots, n$ , then  $V^{1/2} = P^T D^{1/2} P$ . However, for a large matrix, it is computationally intensive to accurately compute all of the eigenvalues and eigenvectors of  $V$  which are needed to determine  $P$  and  $D$ . Fortunately, there are available many numerical procedures for computing  $V^{1/2}$  directly.

## CONSTRUCTION OF EQUIVALENT SDE MODELS IS USEFUL

Often, the square root of the covariance matrix  $B = V^{1/2}$  can be avoided by using an equivalent stochastic system.

Two SDE systems are now studied which are structurally different yet have identical probability distributions. In addition, it can be shown that a sample path solution of one system is also a sample path solution of the other system.

As the SDE models can be interchanged, conceptual or computational advantages possessed by either SDE can be employed in any particular problem.

## EQUIVALENT SDE SYSTEMS

Consider the two Itô SDE systems:

$$d\vec{X}(t) = \vec{f}(t, \vec{X}(t)) dt + G(t, \vec{X}(t)) d\vec{W}(t),$$

and

$$d\vec{X}^*(t) = \vec{f}(t, \vec{X}^*(t)) dt + B(t, \vec{X}^*(t)) d\vec{W}^*(t).$$

where

$$G : [0, T] \times \mathbb{R}^d \rightarrow \mathbb{R}^{d \times m},$$

and

$$B : [0, T] \times \mathbb{R}^d \rightarrow \mathbb{R}^{d \times d}.$$

Let  $\vec{X}(t) = [X_1(t), X_2(t), \dots, X_d(t)]^T$ ,  $\vec{X}^*(t) = [X_1^*(t), X_2^*(t), \dots, X_d^*(t)]^T$ ,  $\vec{W}(t) = [W_1(t), W_2(t), \dots, W_m(t)]^T$ , and  $\vec{W}^*(t) = [W_1^*(t), W_2^*(t), \dots, W_d^*(t)]^T$ , where  $W_i(t)$ ,  $i = 1, \dots, m$  and  $W_j^*(t)$ ,  $j = 1, \dots, d$  are independent Wiener processes and  $m \geq d$ .

Matrices  $G$  and  $B$  are related through the  $d \times d$  matrix  $V$ , where  $V(t, \vec{z}) = G(t, \vec{z})G^T(t, \vec{z})$  and  $B(t, \vec{z}) = V^{1/2}(t, \vec{z})$  for  $\vec{z} \in \mathbb{R}^d$ .

It is shown that solutions to these SDEs have the same probability distribution.

## EQUIVALENT SDE SYSTEMS

Notice that the  $d \times d$  symmetric positive semidefinite matrix  $\mathbf{V}$  has entries

$$v_{i,j}(t, \vec{X}) = \sum_{l=1}^m g_{i,l}(t, \vec{X}) g_{j,l}(t, \vec{X})$$

and  $d \times d$  symmetric positive semidefinite matrix  $\mathbf{B}$  has entries that satisfy

$$v_{i,j}(t, \vec{X}) = \sum_{l=1}^d b_{i,l}(t, \vec{X}) b_{j,l}(t, \vec{X})$$

for  $i, j = 1, \dots, d$ . In component form, these systems can be expressed as

$$X_i(t) = X_i(0) + \int_0^t f_i(s, \vec{X}(s)) ds + \int_0^t \sum_{j=1}^m g_{i,j}(s, \vec{X}(s)) dW_j(s)$$

for  $i = 1, 2, \dots, d$ , where  $f_i$  is the  $i$ th entry of  $\vec{f}$  and  $g_{i,j}$  is the  $i, j$  entry of the  $d \times m$  matrix  $G$  and

$$X_i^*(t) = X_i^*(0) + \int_0^t f_i(s, \vec{X}^*(s)) ds + \int_0^t \sum_{j=1}^d b_{i,j}(s, \vec{X}^*(s)) dW_j^*(s)$$

for  $i = 1, \dots, d$  and  $b_{i,j}$  is the  $i, j$  entry of the  $d \times d$  matrix  $B$ .

## EQUIVALENT SDE SYSTEMS

The solutions to these SDEs possess the same probability distributions; they are equivalent in distribution.

Consider the forward Kolmogorov equation for the probability density function  $p(t, \vec{x})$  associated with the SDE

$$\begin{aligned} \frac{\partial p(t, \vec{x})}{\partial t} = & \frac{1}{2} \sum_{i=1}^d \sum_{j=1}^d \frac{\partial^2}{\partial x_i \partial x_j} \left[ p(t, \vec{x}) \sum_{l=1}^m g_{i,l}(t, \vec{x}) g_{j,l}(t, \vec{x}) \right] \\ & - \sum_{i=1}^d \frac{\partial [p(t, \vec{x}) f_i(t, \vec{x})]}{\partial x_i}. \end{aligned}$$

In particular, if  $\vec{z}_1, \vec{z}_2 \in \mathbb{R}^d$  and  $\vec{z}_1 \leq \vec{z}_2$ , then

$$P(\vec{z}_1 \leq \vec{X}(t) \leq \vec{z}_2) = \int_{z_{1,d}}^{z_{2,d}} \int_{z_{1,d-1}}^{z_{2,d-1}} \dots \int_{z_{1,1}}^{z_{2,1}} p(t, \vec{x}) dx_1 dx_2, \dots dx_d.$$

As the elements of  $V$  satisfy

$$v_{i,j}(t, \vec{x}) = \sum_{l=1}^m g_{i,l}(t, \vec{x}) g_{j,l}(t, \vec{x}) = \sum_{l=1}^d b_{i,l}(t, \vec{x}) b_{j,l}(t, \vec{x}),$$

the two systems have the same forward Kolmogorov equation.

## EQUIVALENT SDE SYSTEMS

In summary, the following result can be proved.

**THEOREM:** Solutions to the two SDE systems possess the same probability distribution. In addition, a sample path solution of one equation is a sample path solution of the second equation.

**Equivalent SDE systems:**

$$d\vec{X}(t) = \vec{f}(t, \vec{X}(t)) dt + G(t, \vec{X}(t)) d\vec{W}(t),$$

and

$$d\vec{X}^*(t) = \vec{f}(t, \vec{X}^*(t)) dt + B(t, \vec{X}^*(t)) d\vec{W}^*(t).$$

where  $G$  is  $d \times m$  and  $B$  is  $d \times d$ ,

$$\vec{X}(t) = [X_1(t), X_2(t), \dots, X_d(t)]^T, \quad \vec{X}^*(t) = [X_1^*(t), X_2^*(t), \dots, X_d^*(t)]^T,$$

$$\vec{W}(t) = [W_1(t), W_2(t), \dots, W_m(t)]^T, \quad \text{and} \quad \vec{W}^*(t) = [W_1^*(t), W_2^*(t), \dots, W_d^*(t)]^T,$$

and where  $V = GG^T$  and  $B = V^{1/2}$ .

## EQUIVALENT SDE SYSTEMS

Consider formulating an SDE model from a random dynamical system consisting of  $d$  components, where  $m \geq d$  distinct independent random changes may occur to the components of the system during a small interval of time.

Two modeling procedures are described for formulating an SDE model.

In the first procedure, the  $m$  changes are collectively considered and means and covariances are determined.

In the second procedure, each change is considered separately.

In both procedures, the number of equations in the SDE model equals the number of components,  $d$ . In addition, the two SDE models are equivalent in that they possess the same probability distribution and a sample path solution of one SDE is also a sample path solution of the other SDE.

## EQUIVALENT SDE SYSTEMS

Consider a stochastic modeling problem that involves  $d$  component processes  $S_1, S_2, \dots, S_d$ ,  $\vec{S} = [S_1, S_2, \dots, S_d]^T$ , where there are a total of  $m \geq d$  possible changes that can occur to at least one of the variables  $S_i$  in a small time interval  $\Delta t$ .

Suppose that the probabilities of these changes can be defined as  $p_j \Delta t \equiv p_j(t, \vec{S}) \Delta t$  for  $j = 1, 2, \dots, m$ , where the  $j$ th change alters the  $i$ th component by the amount  $\lambda_{j,i}$  for  $i = 1, 2, \dots, d$ .

Let  $\vec{r}_j$  represent a random change of the  $j$ th kind:

$$\vec{r}_j = [\lambda_{j,1}, \lambda_{j,2}, \dots, \lambda_{j,d}]^T \text{ with probability } p_j \Delta t.$$

For  $\Delta t$  small,  $(\vec{r}_j)_i$  has approximate mean  $\lambda_{j,i} p_j \Delta t$  and variance  $\lambda_{j,i}^2 p_j \Delta t$ .

An accurate yet simple stochastic model for  $\vec{S}_{n+1}$ , given the vector  $\vec{S}_n$ , is

$$\vec{S}_{n+1} = \vec{S}_n + \sum_{j=1}^m \vec{r}_j$$

for  $n = 0, 1, \dots$



## EQUIVALENT SDE SYSTEMS

In the first modeling procedure, the probability distribution associated with the discrete-time stochastic system is approximately the same as that associated with the SDE system

$$\begin{cases} d\vec{S}(t) = \vec{f}(t, \vec{S}(t))dt + B(t, \vec{S}(t))d\vec{W}^*(t) \\ \vec{S}(0) = \vec{S}_0, \end{cases}$$

where the  $d \times d$  matrix  $B = V^{1/2}$  and  $\vec{W}^*(t)$  is a vector of  $d$  independent Wiener processes.

The vector  $\vec{f}$  and the matrix  $B$  are defined by:

$$E(\Delta\vec{S}) = \sum_{j=1}^m p_j \vec{\lambda}_j \Delta t = \vec{f} \Delta t \quad \text{and} \quad E(\Delta\vec{S}(\Delta\vec{S})^T) = \sum_{j=1}^m p_j \vec{\lambda}_j (\vec{\lambda}_j)^T \Delta t = V \Delta t$$

where  $B = V^{1/2}$ .

## EQUIVALENT SDE SYSTEMS

In the second modeling procedure, the  $m$  random changes are approximated using independent normal variables,  $\eta_j \sim N(0, 1)$ ,  $j = 1, 2, \dots, m$ . For small  $\Delta t$ , the discrete stochastic model is approximated by

$$S_{n+1,i} = S_{n,i} + f_i(t_n, \vec{S}_n)\Delta t + \sum_{j=1}^m \lambda_{j,i} p_j^{1/2} (\Delta t)^{1/2} \eta_j$$

for  $n = 0, 1, \dots$ . This discrete stochastic model is an Euler-Maruyama approximation and converges strongly to the SDE system

$$d\vec{S}(t) = \vec{f}(t, \vec{S}(t)) dt + G(t, \vec{S}(t)) d\vec{W}(t),$$

where the  $i, j$  entry in the matrix  $G$  is  $g_{i,j} = \lambda_{j,i} p_j^{1/2}$ .

This SDE system has  $m$  Wiener processes and the  $d \times d$  matrix  $V = GG^T$  has entries

$$(V)_{i,l} = (GG^T)_{i,l} = \sum_{j=1}^M g_{i,j} g_{l,j} = \sum_{j=1}^M p_j \lambda_{j,i} \lambda_{j,l} = v_{i,l}.$$

Thus, the  $d \times m$  matrix  $G$  satisfies  $V = GG^T$  and the two SDE systems are equivalent.

## EXAMPLE OF EQUIVALENT SDE MODELS

Suppose that there are three chemical species  $S_1, S_2$ , and  $S_3$  interacting through molecular collisions or spontaneously in the four ways described in the table. In the table,  $\mu_1, \mu_2, \mu_3$ , and  $\mu_4$  are reaction rate constants and  $X_1, X_2$ , and  $X_3$  are the number of molecules of species  $S_1, S_2$ , and  $S_3$ , respectively.

Reaction	Probability
$S_1 + S_2 \rightarrow S_3$	$p_1 = \mu_1 X_1 X_2 \Delta t$
$S_3 \rightarrow S_1 + S_2$	$p_2 = \mu_2 X_3 \Delta t$
$2S_2 + S_3 \rightarrow 2S_1$	$p_3 = \mu_3 X_2^2 X_3 \Delta t / 2$
$2S_1 \rightarrow 2S_2 + S_3$	$p_4 = \mu_4 X_1^2 \Delta t / 2$

Possible Change	Probability
$(\Delta \vec{X})_1 = [-1, -1, +1]^T$	$p_1 = \mu_1 X_1 X_2 \Delta t$
$(\Delta \vec{X})_2 = [+1, +1, -1]^T$	$p_2 = \mu_2 X_3 \Delta t$
$(\Delta \vec{X})_3 = [+2, -2, -1]^T$	$p_3 = \mu_3 X_2^2 X_3 \Delta t / 2$
$(\Delta \vec{X})_4 = [-2, +2, +1]^T$	$p_4 = \mu_4 X_1^2 \Delta t / 2$

## EXAMPLE OF EQUIVALENT SDE MODELS

To form the SDE model using the first procedure,  $E(\Delta\vec{X})$  and  $E((\Delta\vec{X})(\Delta\vec{X})^T)$  are computed. Using the tables,

$$\begin{aligned} \vec{f}(X_1, X_2, X_3)\Delta t = E(\Delta\vec{X}) &= \sum_{i=1}^4 p_i(\Delta\vec{X})_i \\ &= \begin{bmatrix} -\mu_1 X_1 X_2 + \mu_2 X_3 + \mu_3 X_2^2 X_3 - \mu_4 X_1^2 \\ -\mu_1 X_1 X_2 + \mu_2 X_3 - \mu_3 X_2^2 X_3 + \mu_4 X_1^2 \\ \mu_1 X_1 X_2 - \mu_2 X_3 - \mu_3 X_2^2 X_3/2 + \mu_4 X_1^2/2 \end{bmatrix} \Delta t \end{aligned}$$

and

$$\begin{aligned} V(X_1, X_2, X_3)\Delta t = E((\Delta\vec{X})(\Delta\vec{X})^T) &= \sum_{i=1}^4 p_i(\Delta\vec{X})_i(\Delta\vec{X})_i^T \\ &= \begin{bmatrix} a + 4b & a - 4b & -a - 2b \\ a - 4b & a + 4b & -a + 2b \\ -a - 2b & -a + 2b & a + b \end{bmatrix} \Delta t \end{aligned}$$

where  $a = \mu_1 X_1 X_2 + \mu_2 X_3$  and  $b = \mu_3 X_2^2 X_3/2 + \mu_4 X_1^2/2$ . It follows that the SDE model for this example problem has the form

$$d\vec{X}(t) = \vec{f}(X_1, X_2, X_3) dt + (V(X_1, X_2, X_3))^{1/2} d\vec{W}^*(t)$$

where  $\vec{W}^*(t) = [W_1^*(t), W_2^*(t), W_3^*(t)]^T$ .

## EXAMPLE OF EQUIVALENT SDE MODELS

Using the second modeling procedure for this example gives the SDE model:

$$\begin{cases} d\vec{X}(t) = \vec{f}(X_1, X_2, X_3) dt + G(X_1, X_2, X_3) d\vec{W}(t) \\ \vec{X}(0) = [X_1(0), X_2(0), X_3(0)]^T, \end{cases}$$

where  $\vec{W}(t) = [W_1(t), W_2(t), W_3(t), W_4(t)]^T$  is a vector of four independent Wiener processes and the  $3 \times 4$  matrix  $G$  has the form

$$G = \begin{bmatrix} -(\mu_1 X_1 X_2)^{1/2} & (\mu_2 X_3)^{1/2} & 2(\mu_3 X_2^2 X_3 / 2)^{1/2} & -2(\mu_4 X_1^2 / 2)^{1/2} \\ -(\mu_1 X_1 X_2)^{1/2} & (\mu_2 X_3)^{1/2} & -2(\mu_3 X_2^2 X_3 / 2)^{1/2} & 2(\mu_4 X_1^2 / 2)^{1/2} \\ (\mu_1 X_1 X_2)^{1/2} & -(\mu_2 X_3)^{1/2} & -(\mu_3 X_2^2 X_3 / 2)^{1/2} & (\mu_4 X_1^2 / 2)^{1/2} \end{bmatrix}.$$

## EXAMPLE OF EQUIVALENT SDE MODELS

To illustrate the agreement between the two SDE models, calculational results using the models were compared with those obtained using a Monte Carlo procedure.

In the Monte Carlo procedure, the molecular process was checked at each small interval of time to see if any reaction occurred. The calculational results for the Monte Carlo procedure are summarized in the table for 5000 sample paths.

The SDE models were numerically solved using the Euler-Maruyama method with 5000 sample paths with the results given in in the table. Also, sample paths calculated using the two SDE models are shown in the figures.

Notice the good agreement between the two SDE models as well as between the SDE models and the Monte Carlo approach.

## EXAMPLE OF EQUIVALENT SDE MODELS

Using Monte Carlo, the following results were obtained at time  $t = 1.0$ .

Chemical Species	$E(X_i)$	$\sigma(X_i)$
$S_1$	<b>79.21</b>	<b>7.28</b>
$S_2$	<b>37.61</b>	<b>5.84</b>
$S_3$	<b>131.19</b>	<b>5.54</b>

Using the SDE models, the following results were obtained at time  $t = 1.0$ .

Model	Chemical Species	$E(X_i)$	$\sigma(X_i)$
<b>First SDE</b>	$S_1$	<b>79.31</b>	<b>7.62</b>
	$S_2$	<b>37.44</b>	<b>6.14</b>
	$S_3$	<b>131.17</b>	<b>6.43</b>
<b>Second SDE</b>	$S_1$	<b>79.39</b>	<b>7.69</b>
	$S_2$	<b>37.47</b>	<b>6.13</b>
	$S_3$	<b>131.09</b>	<b>5.85</b>

In the calculations,  $\mu_1 = 0.02$ ,  $\mu_2 = 0.4$ ,  $\mu_3 = 0.001$ , and  $\mu_4 = 0.03$ . The initial numbers of molecules were  $X_1(0) = X_2(0) = X_3(0) = 100$  and the final time was  $t = 1.0$ .

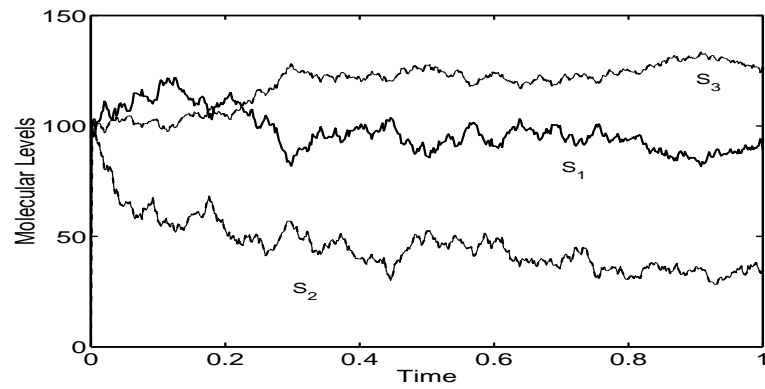


Figure 5: Molecular population levels for one sample path of the first SDE

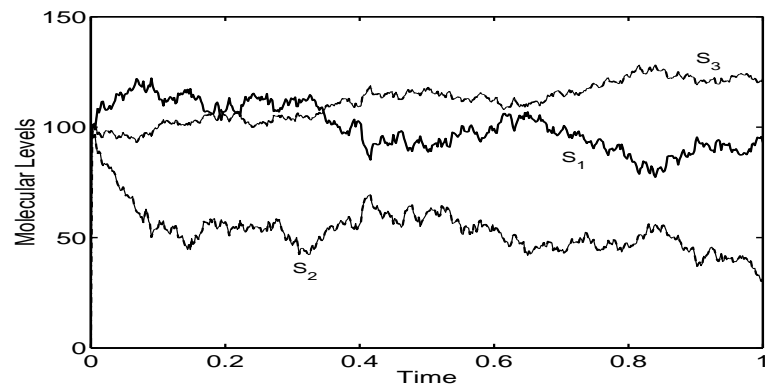


Figure 6: Molecular population levels for one sample path of the second SDE



## PERSISTENCE TIME AND ENVIRONMENTAL VARIABILITY

We briefly consider environmental variability and persistence time for SDE models.

Recall for two interacting populations that

$$d\vec{x} = \vec{\mu}(t, x_1, x_2) dt + (V(t, x_1, x_2))^{1/2} d\vec{W}(t)$$

where  $\vec{W}(t) = [W_1(t), W_2(t)]^T$ ,  $\vec{\mu}$  and  $V$  are

$$\vec{\mu} = E(\Delta\vec{x})/\Delta t = \begin{bmatrix} b_1x_1 - d_1x_1 - m_{12}x_1 + m_{21}x_2 \\ b_2x_2 - d_2x_2 - m_{21}x_2 + m_{12}x_1 \end{bmatrix}$$

and

$$V = \begin{bmatrix} b_1x_1 + d_1x_1 + m_{12}x_1 + m_{21}x_2 & -m_{12}x_1 - m_{21}x_2 \\ -m_{12}x_1 - m_{21}x_2 & b_2x_2 + d_2x_2 + m_{12}x_1 + m_{21}x_2 \end{bmatrix}.$$

For a single population, this system reduces to

$$dx_1 = (b_1x_1 - d_1x_1) dt + \sqrt{b_1x_1 + d_1x_1} dW_1(t).$$

## EXAMPLE: PERSISTENCE-TIME ESTIMATION

For two interacting populations, the mean persistence time can be defined to be the expected time it takes for the size of either population to reach zero. The mean persistence time can be estimated through numerical solution of the SDE or by solving the backward Kolmogorov differential equation to find the mean persistence time directly.

(1) Individual populations can be simulated by solving the SDE using until one population fails to persist. Averaging many such calculated persistence times yields an estimate for the mean persistence time.

(2) The mean persistence time can also be obtained by solving the backward Kolmogorov equation. Suppose that the size of population 1 cannot exceed  $K_1$  and the size of population 2 cannot exceed  $K_2$ . The reliability function  $R(t, y_1, y_2)$  is the probability that the persistence time is greater than  $t$  with initial populations  $x_1(0) = y_1$  and  $x_2(0) = y_2$ .

## EXAMPLE: PERSISTENCE-TIME ESTIMATION

The reliability function  $R(t, y_1, y_2)$  satisfies the backward Kolmogorov equation:

$$\frac{\partial R}{\partial t} = \sum_{k=1}^2 \mu_k(t, y_1, y_2) \frac{\partial R}{\partial y_k} + \frac{1}{2} \sum_{k=1}^2 \sum_{m=1}^2 v_{km}(t, y_1, y_2) \frac{\partial^2 R}{\partial y_k \partial y_m} \quad \text{with}$$

$$R(0, y_1, y_2) = 1 \quad \text{for } (y_1, y_2) \in (0, K_1) \times (0, K_2)$$

$$R(t, 0, y_2) = 0 \quad \text{for } y_2 \in (0, K_2)$$

$$R(t, y_1, 0) = 0 \quad \text{for } y_1 \in (0, K_1)$$

$$\frac{\partial R(t, K_1, y_2)}{\partial y_1} = 0 \quad \text{for } y_2 \in (0, K_2)$$

$$\frac{\partial R(t, y_1, K_2)}{\partial y_2} = 0 \quad \text{for } y_1 \in (0, K_1).$$

The probability density of persistence times is  $-\frac{\partial R(t, y_1, y_2)}{\partial t}$  and

$T(y_1, y_2) = \int_0^\infty R(t, y_1, y_2) dt$  is the mean persistence time with initial population sizes  $y_1$  and  $y_2$ .

## EXAMPLE: PERSISTENCE-TIME ESTIMATION

As a simple example, consider a single population with birth and death rates  $b(y)$  and  $d(y)$ , respectively, for  $0 \leq y \leq K$ . The corresponding backward Kolmogorov equation is

$$\frac{\partial R}{\partial t} = (yb(y) - yd(y))\frac{\partial R}{\partial y} + \frac{1}{2}(yb(y) + yd(y))\frac{\partial^2 R}{\partial y^2}$$

with  $R(0, y) = 1$  for  $y \in (0, K)$ ,  $R(t, 0) = 0$ , and  $\frac{\partial R(t, K)}{\partial y} = 0$ .

Integrating this equation over time  $t$  from 0 to  $\infty$  yields

$$-1 = (yb(y) - yd(y))\frac{dT(y)}{dy} + \frac{1}{2}(yb(y) + yd(y))\frac{d^2T(y)}{dy^2}$$

with  $T(0) = 0$  and  $T'(K) = 0$ , where  $T(y)$  is the mean persistence time for a population of initial size  $y$ .

## EXAMPLE: PERSISTENCE-TIME ESTIMATION

For a computational comparison, assume that  $K = 20$  and the birth and death rates satisfy

$$yb(y) - yd(y) = \begin{cases} 0 & \text{for } 0 \leq y \leq 10 \\ -1 & \text{for } 10 < y \leq 20 \end{cases} \quad \text{and } yb(y) + yd(y) = 1 \quad \text{for } 0 \leq y \leq 20.$$

The backward equation can be solved exactly to obtain that

$$T(y) = \begin{cases} -y^2 + (21 - e^{-20})y & \text{for } 0 \leq y \leq 10 \\ y + 100 - (19e^{-20} + e^{-40}e^{2y})/2 & \text{for } 10 < y \leq 20. \end{cases}$$

In particular,  $T(5) = 80.0$ ,  $T(10) = 110.0$ , and  $T(15) = 115.0$ . For comparison purposes, the SDE

$$\begin{cases} dx = (b(x)x - d(x)x) dt + \sqrt{(b(x)x + d(x)x)} dW(t) \\ x(0) = y \end{cases}$$

was computationally solved using 10,000 sample paths. The estimates obtained were  $T(5) \approx 80.07$ ,  $T(10) \approx 111.05$ , and  $T(15) \approx 114.01$  indicating good agreement between the SDE calculations and the backward Kolmogorov equation.

## CONSIDER INCLUDING ENVIRONMENTAL VARIABILITY

In the previous SDE models, randomness was caused by randomly varying births, deaths, and interactions. However, the environment also randomly varies affecting the populations.

One way to model the environmental effects would be to include additional variables such as rainfall, predators, competitors, and food supply. Consider the deterministic model for a population of size  $y(t)$ :

$$\frac{dy}{dt} = b(t)y - d(t)y.$$

In a varying environment, the birth and death rates would be functions of additional environmental variables and so,  $b(t) = b(t, v_1, v_2, \dots, v_n)$  and  $d(t) = d(t, v_1, v_2, \dots, v_n)$  where  $v_1, v_2, \dots, v_n$  are  $n$  additional variables. As  $v_1, v_2, \dots, v_n$  vary, the birth and death rates also vary. Hence, an approximate way to include environmental variability, without modeling additional environmental factors, would be to allow the birth and death rates to vary randomly. So, the changes in the environment may produce random changes in a population's birth and death rates that are independent from changes due to demographic variability.

## EXAMPLE: INCLUDING ENVIRONMENTAL VARIABILITY

A discrete stochastic process is now described for the phenomenon.

Let  $y(t)$ ,  $b(t)$ , and  $d(t)$  be the population size, birth rate, and death rate. The changes in these three variables in time  $\Delta t$  are independent under our hypothesis. The possible changes  $\Delta y$ ,  $\Delta b$  and  $\Delta d$  are listed in the table.

Let  $q_b \Delta t$  represent the probability associated with random diffusion of the per capita birth rate. The term  $\pm \beta_b (b_e - b)$  represents the probability associated with drift toward the mean value of  $b_e$ . When  $b(t) \neq b_e$ , where  $b_e$  is the average birth rate in the environment, then the probability of moving closer to  $b_e$  is greater than the probability of moving further away from  $b_e$ .

<b>Change</b>	<b>Probability</b>
$\Delta y_1 = -1$	$p_1 = dy\Delta t$
$\Delta y_2 = 1$	$p_2 = by\Delta t$
$\Delta y_3 = 0$	$p_3 = 1 - (by + dy)\Delta t$
$\Delta b_1 = -\alpha_b$	$p_4 = (q_b - \beta_b(b_e - b))\Delta t$
$\Delta b_2 = \alpha_b$	$p_5 = (q_b + \beta_b(b_e - b))\Delta t$
$\Delta b_3 = 0$	$p_6 = 1 - 2q_b\Delta t$
$\Delta d_1 = -\alpha_d$	$p_7 = (q_d - \beta_d(d_e - d))\Delta t$
$\Delta d_2 = \alpha_d$	$p_8 = (q_d + \beta_d(d_e - d))\Delta t$
$\Delta d_3 = 0$	$p_9 = 1 - 2q_d\Delta t$



## EXAMPLE: INCLUDING ENVIRONMENTAL VARIABILITY

The expected change and the covariance matrix for the change are found as:

$$E(\Delta y) = (b(t) - d(t))y(t)\Delta t$$

$$E((\Delta y)^2) = (b(t) + d(t))y(t)\Delta t$$

$$E(\Delta b) = 2\alpha_b\beta_b(b_e - b(t))\Delta t$$

$$E((\Delta b)^2) = 2\alpha_b^2q_b\Delta t$$

$$E(\Delta d) = 2\alpha_d\beta_d(d_e - d(t))\Delta t$$

$$E((\Delta d)^2) = 2\alpha_d^2q_d\Delta t.$$

For convenience, define  $\beta_1, \beta_2, \alpha_1$ , and  $\alpha_2$  as

$$\beta_1 = 2\alpha_b\beta_b, \quad \beta_2 = 2\alpha_d\beta_d, \quad \alpha_1^2 = 2\alpha_b^2q_b, \quad \text{and} \quad \alpha_2^2 = 2\alpha_d^2q_d.$$

As the covariance matrix is diagonal for this model, the following stochastic differential equation system is obtained:

$$\left\{ \begin{array}{l} dy(t) = (b(t)y(t) - d(t)y(t)) dt + \sqrt{(b(t)y(t) + d(t)y(t))} dW_1(t) \\ db(t) = \beta_1(b_e - b(t)) dt + \alpha_1 dW_2(t) \\ dd(t) = \beta_2(d_e - d(t)) dt + \alpha_2 dW_3(t). \end{array} \right.$$

## EXAMPLE: INCLUDING ENVIRONMENTAL VARIABILITY

The SDE for  $b(t)$  (or  $d(t)$ ) is an Ornstein-Uhlenbeck process and can be solved exactly to yield

$$b(t) = b_e + \exp(-\beta_1 t) \left( -b_e + b(0) + \int_0^t \alpha_1 \exp(\beta_1 s) dW_2(s) \right).$$

This equation implies that, for large time  $t$ , the birth rate  $b(t)$  is approximately normally distributed with mean  $b_e$  and variance  $\alpha_1^2/(2\beta_1)$ . Thus, in this stochastic model, random variations in the environment cause the birth rate (or the death rate) to vary normally about a mean value  $b_e$ .

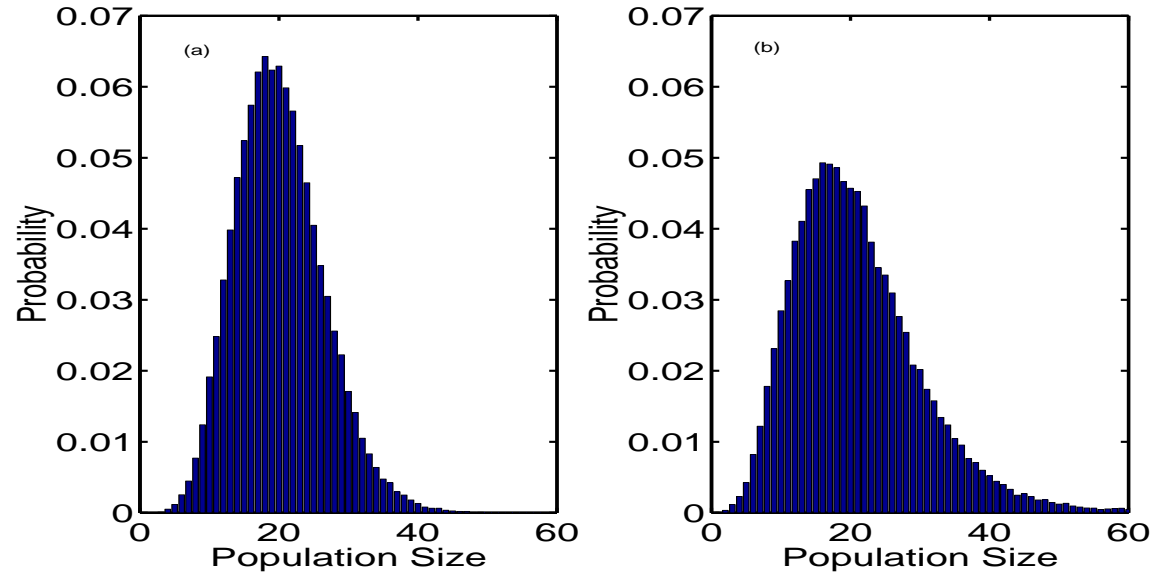


Figure 7: Population distribution at  $t = 1$  for an initial population of size 30 obtained through numerical solution of the SDE system with no environmental variability (a) and with environmental variability (b)

### EXAMPLE: INCLUDING ENVIRONMENTAL VARIABILITY

As a computational example, assume  $\beta_1 = 1 = \beta_2$ ,  $\alpha_1 = 0.5 = \alpha_2$ ,  $b_e = 1$ ,  $d_e = 1.4$ . Suppose that  $y(0) = 30$ ,  $b(0) = b_e$ , and  $d(0) = d_e$ .

In the figure, the probability distribution of the population size  $y(t)$  is plotted at time  $t = 1.0$ . Two different cases are considered: when there is environmental variability and when there is no environmental variability. It is clear for this example that the variability in the environment spreads out the population size distribution.

## It Is Interesting That Results Of Stochastic Models Can Differ From Deterministic Models

Consider two competing species with populations  $x_1(t)$  and  $x_2(t)$ ,  $x_1(0) = x_2(0) = 15$ , and with birth rates and death rates satisfying:

$$B_1(x_1, x_2) = \frac{5}{6}x_1(t), \quad D_1(x_1, x_2) = \frac{2}{5}x_1(t) + \frac{1}{100}x_1^2(t) + \frac{1}{45}x_1(t)x_2(t)$$
$$B_2(x_1, x_2) = \frac{9}{10}x_2(t), \quad D_2(x_1, x_2) = \frac{3}{4}x_2(t) + \frac{1}{150}x_2^2(t) + \frac{1}{200}x_1(t)x_2(t)$$

The deterministic model for this competition problem is

$$\frac{dx_1}{dt} = B_1(x_1, x_2) - D_1(x_1, x_2), \quad \frac{dx_2}{dt} = B_2(x_1, x_2) - D_2(x_1, x_2)$$

and the SDE model is

$$dx_1 = (B_1(x_1, x_2) - D_1(x_1, x_2)) dt + \sqrt{B_1(x_1, x_2) + D_1(x_1, x_2)} dW_1(t)$$
$$dx_2 = (B_2(x_1, x_2) - D_2(x_1, x_2)) dt + \sqrt{B_2(x_1, x_2) + D_2(x_1, x_2)} dW_2(t).$$

For the deterministic model, population  $x_1$  always out-competes  $x_2$ .

However, for the stochastic model, population  $x_1$  out-competes  $x_2$  only 55% of the time.

## Summarizing The First Part, SDE Models Can Be Derived For Many Biological Problems

- (1) The dynamical system, with time discrete, is studied to determine the different independent changes that occur for a small time interval.
- (2) Appropriate terms are determined for these changes in constructing a discrete-time stochastic model.
- (3) As the time interval approaches zero, the discrete stochastic model leads to a certain stochastic differential equation system. (Solutions of the discrete model and the SDE approximately satisfy the same probability distribution.)

Note that in the derivation procedure, the deterministic and stochastic terms are simultaneously found.

## A Straightforward Procedure Is Described For Deriving SPDEs

It is assumed that the variable of interest randomly varies with time and depends on other variables such as size, position, energy, or age.

(A) A discrete stochastic model is first developed where the problem is discretized in time and in the secondary variables.

(A-1) The dynamical system is studied to determine the different independent random changes that occur.

(A-2) Probabilities are determined for these changes in developing the discrete stochastic model.

(B) As the time interval decreases, the discrete stochastic model leads to a certain SDE system.

(C) Brownian sheets are substituted into the SDE system for the Wiener processes.

(D) The intervals in the secondary variables go to zero and an SPDE model is found that approximates the SDE system.

## To Derive SPDES, Brownian Sheets Are Often Useful

$\int_x^{x+\Delta x} \int_t^{t+\Delta t} \frac{\partial^2 W(x, t)}{\partial x \partial t} dx dt = \eta \sqrt{\Delta x \Delta t}$  is normally distributed with mean 0 and variance  $\Delta x \Delta t$  for any  $t$  and  $x$ .

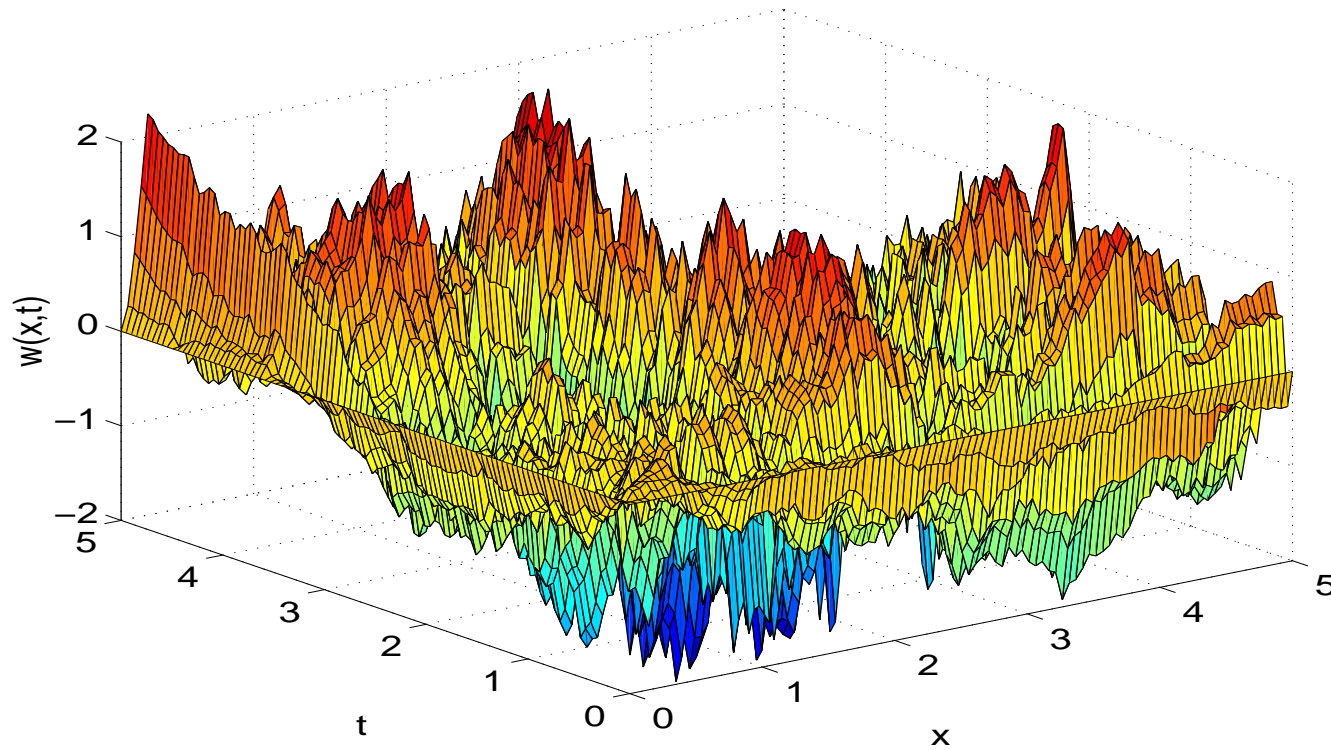


Figure 8: A Brownian Sheet on  $[0, 1] \times [0, 1]$

## Brownian Sheets Can Define Wiener Processes

If  $x_j = x_{min} + (j - 1)\Delta x$  for  $j = 1, 2, \dots, N$ , then the Brownian sheet defines the standard Wiener processes:

$$dW_j(t) = \frac{1}{\sqrt{\Delta x}} \int_{x_j}^{x_{j+1}} \frac{\partial^2 W(x', t)}{\partial t \partial x'} dx' dt \quad \text{for } j = 1, 2, \dots, N.$$

Notice that if  $t_i = (i - 1)\Delta t$  for  $t = 1, 2, \dots, M$ , then

$$\int_{t_i}^{t_{i+1}} dW_j(t') = \sqrt{\Delta t} \eta_{i,j} \quad \eta_{i,j} \sim N(0, 1).$$

Three-dimensional Brownian sheets can also define Wiener processes such as:

$$dW(t) = \frac{1}{\sqrt{\Delta x \Delta y}} \int_x^{x+\Delta x} \int_y^{y+\Delta y} \frac{\partial^3 W(x', y', t)}{\partial t \partial x' \partial y'} dy' dx' dt.$$



## Wiener Processes Parameterized By $x$ Are Also Useful

From a two-dimensional Brownian sheet, an independent one-dimensional Wiener process in  $t$  can be defined for each  $x$  by

$$W^*(t; x) = \lim_{\Delta x \rightarrow 0} \frac{1}{\sqrt{\Delta x}} \int_x^{x+\Delta x} \frac{\partial W(x', t)}{\partial x} dx'$$

where if  $x_1 \neq x_2$ , then the Wiener process  $W^*(t; x_1)$  is independent of the Wiener process  $W^*(t; x_2)$ .

In addition, the integral of the partial derivative of  $f(x, t) \frac{\partial W(t; x)}{\partial t}$  is defined as:

$$\int_x^{x+\Delta x} \frac{\partial}{\partial x} \left[ f(x, t) \frac{\partial W(t; x)}{\partial t} \right] dx = f(x+\Delta x, t) \frac{\partial W(t; x + \Delta x)}{\partial t} - f(x, t) \frac{\partial W(t; x)}{\partial t}.$$

## Several Examples Of Deriving SPDEs Are Presented

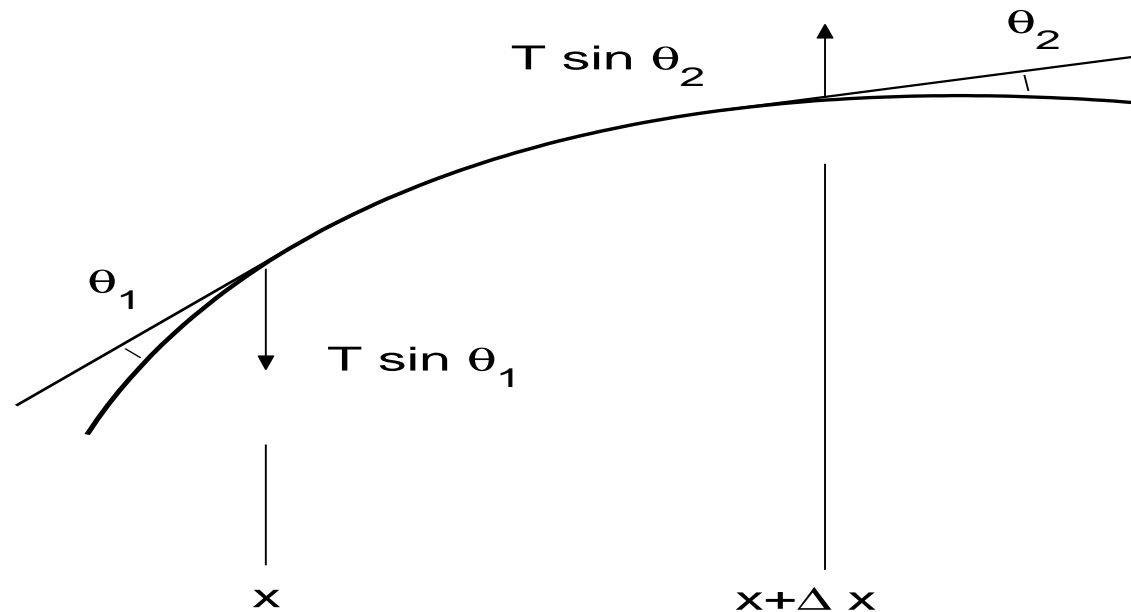
- (A) A stochastic one-dimensional wave equation
- (B) A stochastic one-dimensional transport equation
- (C) Age- and Size-structured stochastic population models
- (D) A stochastic reaction-diffusion equation

## THE CLASSIC PROBLEM OF A RANDOMLY VIBRATING STRING IS CONSIDERED

- (A) A string undergoing random impulses is modeled.
- (B) One could consider the string being hit randomly by sand particles in a dust storm.
- (C) This problem was first considered by J. B. Walsh in 1986 who pointed out that the string displacement could be modeled by an SPDE.

## RANDOM IMPULSES IN A VIBRATING STRING ARE MODELED

Impulses of magnitude  $\pm\gamma$  randomly occur along a taut string. The probability of an impulse in length  $\Delta x$  in time  $\Delta t$  is  $\lambda\Delta x\Delta t$ . For length  $\Delta x$  the forces are given in the figure:



If  $u(x, t)$  is the string displacement, then

$$T \sin(\theta_1) \approx -T u_x(x, t) \quad \text{and} \quad T \sin(\theta_2) \approx T u_x(x + \Delta x, t).$$

# CONSIDERING THE CHANGES IN MOMENTUM OVER A SMALL TIME INTERVAL LEADS TO AN SDE MODEL

<u>Possible Momentum Change (<math>\Delta M</math>)</u>	<u>Probability</u>
$\Delta t(Tu_x(x + \Delta x, t) - Tu_x(x, t)) + \gamma$	$\lambda \Delta t \Delta x$
$\Delta t(Tu_x(x + \Delta x, t) - Tu_x(x, t)) - \gamma$	$\lambda \Delta t \Delta x$
$\Delta t(Tu_x(x + \Delta x, t) - Tu_x(x, t))$	$1 - 2\lambda \Delta t \Delta x$

## Calculating

$$E(\Delta M) = \Delta t(Tu_x(x + \Delta x, t) - Tu_x(x, t))$$

and

$$E((\Delta M)^2) = 2\gamma^2 \lambda \Delta t \Delta x,$$

it follows that the discrete stochastic model satisfies:

$$M(x, t + \Delta t) - M(x, t) \approx (Tu_x(x + \Delta x, t) - Tu_x(x, t)) \Delta t + \sqrt{2\gamma^2 \lambda \Delta t \Delta x} \eta_{x,t}$$

where  $\eta_{x,t} \sim N(0, 1)$  and  $M(x, t)$  is momentum of length  $\Delta x$  at  $t$ .

## LETTING THE TIME AND THE SPATIAL INTERVALS SHRINK, AN SPDE MODEL IS OBTAINED

As mass  $\times$  velocity = momentum, then

$$M(x, t + \Delta t) - M(x, t) \approx \rho \Delta x (u_t(x, t + \Delta t) - u_t(x, t)).$$

Substituting in this expression, we obtain that

$$\frac{\rho(u_t(x, t + \Delta t) - u_t(x, t))}{\Delta t} = \frac{(Tu_x(x + \Delta x, t) - Tu_x(x, t))}{\Delta x} + \sqrt{\frac{2\gamma^2\lambda}{\Delta t\Delta x}} \eta_{x,t}.$$

This leads directly to the SPDE

$$\rho u_{tt}(x, t) = Tu_{xx}(x, t) + \sqrt{2\gamma^2\lambda} \frac{\partial^2 W(t, x)}{\partial t \partial x}$$

where the diffusion coefficient  $\sqrt{2\gamma^2\lambda}$  has a physical meaning.

# A STOCHASTIC ENERGY-DEPENDENT TRANSPORT EQUATION IS DERIVED

The deterministic time-dependent transport equation has the form:

$$\frac{\partial n(E, t)}{\partial t} = -v\sigma_t(E)n(E, t) + \int_0^{E_{max}} v'\sigma_s(E', E)n(E', t) dE'$$

where

$n(E, t)$  = number of particles at  $t$  of energy  $E$  per unit energy

$v$  = particle speed at energy  $E$

$\sigma_t(E)$  = probability per unit distance of a particle interaction

$\sigma_s(E', E)$  = probability of a change from energy  $E'$  to  $E$

**Note:** An infinite homogeneous medium is assumed.

# TO DERIVE THE SDE MODEL, A DISCRETE ENERGY TRANSPORT EQUATION IS USED

Assuming that

$$n(E, t) \approx \sum_{g=1}^G \chi_g(E) n_g(t) / (\Delta E)_g$$

where  $(\Delta E)_g = E_g - E_{g+1}$  and  $\chi_g(E) = \begin{cases} 1, & E_{g+1} \leq E \leq E_g \\ 0, & \text{otherwise.} \end{cases}$

Then, the discrete energy equations are obtained:

$$\frac{dn_g(t)}{dt} = -v_g \sigma_{a,g} n_g(t) - \sum_{g''=1}^G v_g \sigma_{s,g,g''} n_g(t) + \sum_{g'=1}^G v_{g'} \sigma_{s,g',g} n_{g'}(t)$$

for  $g = 1, 2, \dots, G$ , where, for example,

$$v_g \sigma_{t,g} = \int_{E_{g+1}}^{E_g} v \sigma_t(E) dE / (\Delta E)_g.$$



## AN SDE MODEL CAN NOW BE DERIVED FOR DISCRETE ENERGY TRANSPORT

In deriving an SDE model, all changes in the system are determined for a small time step  $\Delta t$ . This results in a discrete-time stochastic model. A particular SDE model is then inferred from the discrete stochastic model through similarities in the Kolmogorov equations.

For the discrete energy transport equations, there are  $G + G^2$  possible changes in each time interval  $\Delta t$ . Specifically, a particle may be absorbed in group  $g$  with probability  $\sigma_{a,g}v_g\Delta t$  for  $g = 1, 2, \dots, G$  or a particle may scatter from group  $g'$  to group  $g$  with probability  $\sigma_{s,g',g}v_{g'}\Delta t$  for  $g, g' = 1, 2, \dots, G$ .

# A SYSTEM OF DISCRETE ENERGY STOCHASTIC DIFFERENTIAL EQUATIONS IS OBTAINED

The stochastic discrete-energy equations have the form:

$$\begin{aligned}
 dn_g(t) = & -v_g\sigma_{a,g}n_g(t) dt - \sqrt{v_g\sigma_{a,g}n_g(t)} d\hat{W}_g(t) - \sum_{g''=1}^G v_g\sigma_{s,g,g''}n_g(t) dt \\
 & - \sum_{g''=1}^G \sqrt{v_g\sigma_{s,g,g''}n_g(t)} dW_{g,g''}(t) + \sum_{g'=1}^G v_{g'}\sigma_{s,g',g}n_{g'}(t) dt \\
 & + \sum_{g'=1}^G \sqrt{v_{g'}\sigma_{s,g',g}n_{g'}(t)} dW_{g',g}(t) \quad \text{for } g = 1, 2, \dots, G.
 \end{aligned}$$

Next, Brownian sheets are substituted for the Wiener processes.

## Brownian Sheets Are Substituted For The Wiener Processes

The stochastic discrete-energy equations have the form for  $g = 1, 2, \dots, G$ :

$$\begin{aligned}
 dn_g(t) = & \\
 & -v_g\sigma_{a,g}n_g(t) dt - \sqrt{v_g\sigma_{a,g}n_g(t)} \frac{1}{\sqrt{\Delta E_g}} \int_{E_g}^{E_{g+1}} \frac{\partial^2 \hat{W}(E, t)}{\partial E \partial t} dE \sum_{g'=1}^G v_{g'}\sigma_{s,g',g}n_{g'}(t) \\
 & - \sum_{g''=1}^G v_g\sigma_{s,g,g''}n_g(t) dt + \sum_{g'=1}^G v_{g'}\sigma_{s,g',g}n_{g'}(t) dt \\
 & - \sum_{g''=1}^G \sqrt{v_g\sigma_{s,g,g''}n_g(t)} \frac{1}{\sqrt{\Delta E_g \Delta E_{g''}}} \int_{E_g}^{E_{g+1}} \int_{E_{g''}}^{E_{g''+1}} \frac{\partial^3 W(E, E'', t)}{\partial E' \partial E \partial t} dE dE'' \\
 & + \sum_{g'=1}^G \sqrt{v_{g'}\sigma_{s,g',g}n_{g'}(t)} \frac{1}{\sqrt{\Delta E_g \Delta E_{g'}}} \int_{E_g}^{E_{g+1}} \int_{E_{g'}}^{E_{g'+1}} \frac{\partial^3 W(E', E, t)}{\partial E' \partial E \partial t} dE dE'.
 \end{aligned}$$

This equation is divided by  $\Delta E_g$  with  $n_g(t) = n(E_g, t)\Delta E_g$ . Letting the energy intervals go to zero results in an SPDE model.

# THE FINAL SPDE MODEL FOR PARTICLE TRANSPORT HAS AN INTERESTING STRUCTURE

$$\begin{aligned}
 \frac{\partial n(E, t)}{\partial t} = & -v\sigma_a(E)n(E, t) - \sqrt{v\sigma_a(E)n(E, t)} \frac{\partial^2 \hat{W}(E, t)}{\partial E \partial t} \\
 & + \int_0^{E_{max}} v'\sigma_s(E', E)n(E', t) dE' - \int_0^{E_{max}} v\sigma_s(E, E'')n(E, t) dE'' \\
 & + \int_0^{E_{max}} \sqrt{v'\sigma_s(E', E)n(E', t)} \frac{\partial^3 W(E', E, t)}{\partial E' \partial E \partial t} dE' \\
 & - \int_0^{E_{max}} \sqrt{v\sigma_s(E, E'')n(E, t)} \frac{\partial^3 W(E, E'', t)}{\partial E \partial E'' \partial t} dE''
 \end{aligned}$$

where  $\hat{W}(E, T)$  and  $W(E', E, t)$  are independent Brownian sheets.

## SPDEs For Structured Populations Are Derived From Basic Assumptions

(A) The dynamical system, with time and size discrete, is studied to determine the different independent random changes that occur.

(B) Appropriate terms are determined for these changes in developing a discrete-time stochastic model. This model leads to a certain stochastic differential equation system as the time interval decreases.

(C) The stochastic differential equation system then leads to a certain SPDE as the size interval is made smaller.

## A Size-Structured Population Model Is Now Considered

A standard partial differential equation for a size-structured population has the form:

$$\left\{ \begin{array}{l} \frac{\partial u(x, t)}{\partial t} + \frac{\partial(g(x, t)u(x, t))}{\partial x} = -\mu(x, t, P(t))u(x, t), \quad x_{min} < x < x_{max}, \\ g(x_{min}, t)u(x_{min}, t) = \int_{x_{min}}^{x_{max}} \beta(x, t, P(t))u(x, t) dx, \\ u(x, 0) = u_0(x), \quad P(t) = \int_{x_{min}}^{x_{max}} u(x, t) dx, \end{array} \right.$$

where

$u(x, t)$  is the population density at time  $t$  and size  $x$ ,

$\mu$  is the death rate,

$\beta$  is the birth rate,

$g$  is the growth rate of an individual,

$P(t)$  is the total number of individuals in the population,

$x_{min}$  and  $x_{max}$  are the minimum and maximum sizes.

## The Changes Are Now Considered For A Time Interval $\Delta t$

Let  $u_k(t)$  be the population level at time  $t$  of size  $x_{k-1}$  to size  $x_k$ . The changes possible for  $u_k(t)$  are tabulated in Table 1 for  $k > 1$ . Births are added to the first size class and the possible changes are given in Table 2 for  $k = 1$ .

**Table 1 Possible Changes For  $k > 1$**

Possible Change $(\Delta u)_k$	Probability
1	$u_{k-1}g_{k-1}\Delta t/\Delta x$
-1	$u_k g_k \Delta t/\Delta x$
-1	$u_k \mu_k \Delta t$

**Table 2 Possible Changes For  $k = 1$**

Possible Change $(\Delta u)_1$	Probability
1	$\sum_{k=1}^K u_k \beta_k \Delta t$
-1	$u_1 g_1 \Delta t/\Delta x$
-1	$u_1 \mu_1 \Delta t$

Tables 1 and 2 define a discrete stochastic model for a system of  $K$  subpopulations.

## The Discrete Stochastic Model Leads To The Itô Stochastic Differential Equation System As $\Delta t$ Decreases

The discrete stochastic model leads to the Itô system:

$$\begin{aligned}
 du_k(t) = & -\frac{u_k g_k - u_{k-1} g_{k-1}}{\Delta x} dt - u_k \mu_k dt + \sqrt{\frac{u_{k-1} g_{k-1}}{\Delta x}} dW_{k-1}(t) \\
 & - \sqrt{\frac{u_k g_k}{\Delta x}} dW_k(t) - \sqrt{u_k \mu_k} d\hat{W}_k(t)
 \end{aligned}$$

for  $k = 2, 3, \dots, K$  with

$$\begin{aligned}
 du_1(t) = & \sum_{k=1}^K u_k \beta_k dt - \frac{u_1 g_1}{\Delta x} dt - u_1 \mu_1 dt + \sqrt{\sum_{k=1}^K u_k \beta_k} d\tilde{W}(t) \\
 & - \sqrt{\frac{u_1 g_1}{\Delta x}} dW_1(t) - \sqrt{u_1 \mu_1} d\hat{W}_1(t)
 \end{aligned}$$

where  $W_k(t)$ ,  $\hat{W}_k(t)$ , and  $\tilde{W}(t)$ , are independent Wiener processes for  $k = 1, 2, \dots, K$ .



## The Itô Stochastic Differential Equation System Can Be Rewritten Using Brownian Sheets

Introduced is a family of one-dimensional Wiener process  $W^*(t; x)$  parameterized by size  $x$ . In addition, a Brownian sheet  $W(x, t)$  is applied. Then,

$$\begin{aligned} \frac{du_k(t)}{dt} = & -\frac{u_k g_k - u_{k-1} g_{k-1}}{\Delta x} - u_k \mu_k + \sqrt{\frac{u_{k-1} g_{k-1}}{\Delta x}} \frac{\partial W^*(t; x_{k-1})}{\partial t} \\ & - \sqrt{\frac{u_k g_k}{\Delta x}} \frac{\partial W^*(t; x_k)}{\partial t} - \sqrt{u_k \mu_k} \frac{1}{\sqrt{\Delta x}} \int_{x_{k-1}}^{x_k} \frac{\partial^2 W(x, t)}{\partial x \partial t} dx \end{aligned}$$

for  $k = 2, 3, \dots, K$  with

$$\begin{aligned} \frac{du_1(t)}{dt} = & \sum_{k=1}^K u_k \beta_k - \frac{u_1 g_1}{\Delta x} - u_1 \mu_1 + \sqrt{\sum_{k=1}^K u_k \beta_k} \frac{dW(t)}{dt} \\ & - \sqrt{\frac{u_1 g_1}{\Delta x}} \frac{\partial W^*(t; x_1)}{\partial t} - \sqrt{u_1 \mu_1} \frac{1}{\sqrt{\Delta x}} \int_{x_1}^{x_2} \frac{\partial^2 W(x, t)}{\partial x \partial t} dx. \end{aligned}$$

## The Size Interval $\Delta x$ Now Approaches Zero Resulting In An SPDE For The Size-Structured Population

Letting  $u_k(t) = u(x_k, t)\Delta x$  and decreasing  $\Delta x$ , then

$$\begin{aligned} \frac{\partial u(x, t)}{\partial t} = & -\frac{\partial(u(x, t)g(x, t))}{\partial x} - u(x, t)\mu(x, t, P(t)) \\ & - \frac{\partial}{\partial x} \left[ \sqrt{u(x, t)g(x, t)} \frac{\partial W^*(t; x)}{\partial t} \right] - \sqrt{u(x, t)\mu(x, t, P(t))} \frac{\partial^2 W(x, t)}{\partial x \partial t} \end{aligned}$$

with

$$\begin{aligned} u(x_{min}, t)g(x_{min}, t) + \sqrt{u(x_{min}, t)g(x_{min}, t)} \frac{\partial W^*(t; x_{min})}{\partial t} = \\ \int_{x_{min}}^{x_{max}} u(x', t)\beta(x', t, P(t))dx' + \sqrt{\int_{x_{min}}^{x_{max}} u(x', t)\beta(x', t, P(t))dx'} \frac{dW(t)}{dt}. \end{aligned}$$

Notice that the SPDE generalizes the original PDE.

## The Population's Age Structure As Well As Size Structure Is Now Considered

A deterministic size- and age-structured partial differential equation is:

$$\left\{ \begin{array}{l} \frac{\partial u(x, y, t)}{\partial t} + \frac{\partial (h(x, y, t)u)}{\partial y} + \frac{\partial (g(x, y, t)u)}{\partial x} = -\mu(x, y, t, P(t))u(x, y, t) \\ h(x, 0, t)u(x, 0, t) = \int_{x_{min}}^{x_{max}} \int_0^{y_{max}} \beta(x', x, y', t, P(t))u(x', y', t) dy' dx' \\ u(x, y, 0) = u_0(x, y), \quad P(t) = \int_{x_{min}}^{x_{max}} \int_0^{y_{max}} u(x, y, t) dy dx \end{array} \right.$$

for  $0 < y < y_{max}$ ,  $x_{min} < x < x_{max}$ , and  $t > 0$  where

$u(x, y, t)$  is the population density,

$\mu(x, y, t, P(t))$  is the death rate for size  $x$  and age  $y$ ,

$\beta(x', x, y', t, P(t))$  is the rate of newborns of size  $x$  born from individuals of size  $x'$  and age  $y'$ ,

$g(x, y, t)$  is the growth rate of an individual,

$h(x, y, t)$  is the age rate of an individual,

$P(t)$  is the total number of individuals,

$h(x, 0, t)u(x, 0, t)$  is the birth rate for newborns of size  $x$ .

## Similar To The Size-Structured Population, A Discrete Stochastic Model Is First Constructed

The time, size, and age intervals are now allowed to approach zero and an SPDE is obtained:

$$\begin{aligned} \frac{\partial u(x, y, t)}{\partial t} = & \frac{\partial(g(x, y, t)u(x, y, t))}{\partial x} - \frac{\partial(h(x, y, t)u(x, y, t))}{\partial y} \\ & - \mu(x, y, t, P(t))u(x, y, t) - \frac{\partial}{\partial x} \left[ \sqrt{g(x, y, t)u(x, y, t)} \frac{\partial^2 W^*(t, y; x)}{\partial y \partial t} \right] \\ & - \sqrt{\mu(x, y, t, P(t))u(x, y, t)} \frac{\partial^3 W(x, y, t)}{\partial x \partial y \partial t} \end{aligned}$$

with

$$\begin{aligned} h(x, 0, t)u(x, 0, t) = & \int_0^{y_{max}} \int_{x_{min}}^{x_{max}} u(x', y', t) \beta(x', x, y', t, P(t)) dx' dy' \\ & + \sqrt{\int_0^{y_{max}} \int_{x_{min}}^{x_{max}} u(x', y', t) \beta(x', x, y', t, P(t)) dx' dy'} \frac{\partial^2 W(x, t)}{\partial x \partial t} \end{aligned}$$

## The SPDEs Are Numerically Solved And Compared With Independent Monte Carlo Computations

The SPDE for a size-structured population is first considered. To obtain a numerical method, the population is divided into size classes and time is discretized. Using an explicit approximation in time gives

$$u_{k,i+1} = u_{k,i} - \frac{u_{k,i}g_{k,i} - u_{k-1,i}g_{k-1,i}}{\Delta x} \Delta t - u_{k,i}\mu_{k,i} \Delta t \\ + \sqrt{\frac{u_{k-1,i}g_{k-1,i}\Delta t}{\Delta x}} \eta_{k-1,i} - \sqrt{\frac{u_{k,i}g_{k,i}\Delta t}{\Delta x}} \eta_{k,i} - \sqrt{u_k\mu_k\Delta t} \hat{\eta}_{k,i}$$

for  $k = 2, 3, \dots, K$  and  $i = 0, 1, 2, \dots$  with

$$\frac{u_{1,i}g_{1,i}\Delta t}{\Delta x} + \sqrt{\frac{u_{1,i}g_{1,i}\Delta t}{\Delta x}} \eta_{1,i} = \sum_{k=1}^K u_{k,i}\beta_{k,i} \Delta t - \sqrt{\sum_{k=1}^K u_k\beta_{k,i}\Delta t} \tilde{\eta}_i$$

where  $\eta_{k,i}, \hat{\eta}_{k,i}, \tilde{\eta}_i \sim N(0, 1)$  are independent normally distributed. (A form of Euler-Maruyama approximation is used.)

## The SPDEs Are Numerically Solved And Compared With Independent Monte Carlo Computations

In the Monte Carlo procedure, the population was divided into 100 size classes and time was divided into 1000 intervals. For each time step, each subpopulation was checked for a death, birth, or size change.

The growth rate, death rate, birth rate, and initial population were assumed to be  $g(x, t) = .5(1 - x)$ ,  $\mu(x, t) = .5$ ,  $\beta(x, t) = 1.5$ ,  $u(x, 0) = 600(1 - x)^2$ . With these parameters, the exact solution to the deterministic size-structured model was  $u(x, t) = 600(1 - x)^2 \exp(t)$ .

### Results For 500 Sample Paths

Avg. Population Level	Standard Dev. in Pop. Level	Average Size	Standard Dev. in Size
330.16 (MC)	20.852 (MC)	.25099 (MC)	.00946 (MC)
331.46 (SPDE)	22.211 (SPDE)	.25063 (SPDE)	.01070 (SPDE)

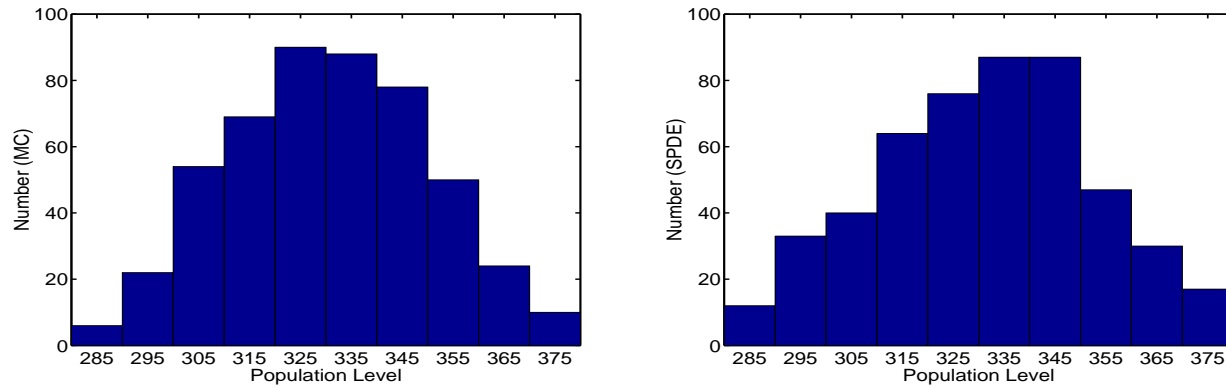


Figure 9: Calculated Distribution of Populations Levels at Time  $t = 0.5$  for 500 Sample Paths Using Monte Carlo (MC) and the Stochastic Partial Differential Equation (SPDE)

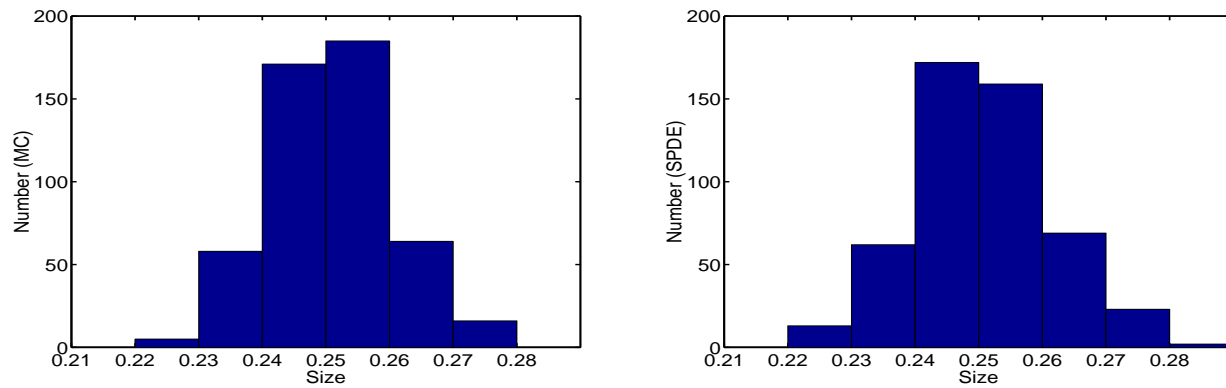


Figure 10: Calculated Distribution of Average Size at Time  $t = 0.5$  for 500 Sample Paths Using Monte Carlo (MC) and the Stochastic Partial Differential Equation (SPDE)

## The Age- And Size-Structured SPDE Was Also Numerically Solved And Compared With Monte Carlo Computations

Integrating the SPDE over a size interval and over an age interval and using an explicit approximation in time yielded the numerical procedure

$$\begin{aligned}
 u_{j,k,i+1} = & u_{j,k,i} - \frac{u_{j,k,i}g_{j,k,i} - u_{j,k-1,i}g_{j,k-1,i}}{\Delta x} \Delta t - \frac{u_{j,k,i}h_{j,k,i} - u_{j-1,k,i}h_{j-1,k,i}}{\Delta y} \Delta t \\
 & - u_{j,k,i}\mu_{j,k,i} \Delta t + \sqrt{\frac{u_{j,k-1,i}g_{j,k-1,i}\Delta t}{\Delta x}} \eta_{j,k-1,i} - \sqrt{\frac{u_{j,k,i}g_{j,k,i}\Delta t}{\Delta x}} \eta_{j,k,i} \\
 & - \sqrt{u_{j,k,i}\mu_{j,k,i}\Delta t} \hat{\eta}_{j,k,i}
 \end{aligned}$$

for  $j = 2, 3, \dots, J$  and  $k = 1, 2, \dots, K$  with

$$\frac{h_{1,k,i}u_{1,k,i}}{\Delta y} = \sum_{k'=1}^K \sum_{j'=1}^J u_{j',k',i}\beta_{j',k',k,i} \Delta t + \sqrt{\sum_{k'=1}^K \sum_{j'=1}^J u_{j',k',i}\beta_{j',k',k,i}\Delta t} \tilde{\eta}_{k,i}$$

where  $\eta_{j,k,i}, \hat{\eta}_{j,k,i}, \tilde{\eta}_{k,i} \sim N(0, 1)$  are independent and  $u_{j,k,i} \approx u(x_k, y_j, t_i)\Delta x\Delta y$  (A type of Euler-Maruyama approximation is used.)



## The Age- And Size-Structured SPDE Was Also Numerically Solved And Compared With Monte Carlo Computations

In an independent Monte Carlo procedure, the age- and size-structured population was divided into 200 size-age classes and time was divided into 4000 steps. For each time step, each subpopulation was checked for a death, birth, or size change.

The growth rate, death rate, birth rate, and initial population were assumed to be:

$$g(x, y, t) = .5(1 - x)(1 - y),$$

$$\mu(x, y, t) = -1 + 2/(1 - y) - (1 - 2x)(1 - y),$$

$$\beta(x', x, y', t) = 18x(1 - x), \quad u(x, y, 0) = 7200x(1 - x)(1 - y)^2,$$

with  $x_{min} = 0$ ,  $x_{max} = 1$ ,  $y_{min} = 0$ , and  $y_{max} = 1$ .

With these parameter selections, the exact solution to the deterministic PDE is  $u(x, y, t) = 7200x(1 - x)(1 - y)^2 \exp(t)$ .

## Numerical Solution Of The SPDE Compared Well With Monte Carlo Computations

The population levels (total number of individuals), average individual size, and the average individual age at time  $t = 1$  for 500 sample paths are given.

Population Level	Standard Dev. in Pop. Level	Average Size	Standard Dev. in Size
1038.89 (MC)	82.36 (MC)	0.49963 (MC)	0.00404 (MC)
1076.52 (SPDE)	96.53 (SPDE)	0.50180 (SPDE)	0.00599 (SPDE)

Individual Average Age	Standard Dev. in Age
0.26318 (MC)	0.00410 (MC)
0.26855 (SPDE)	0.00570 (SPDE)

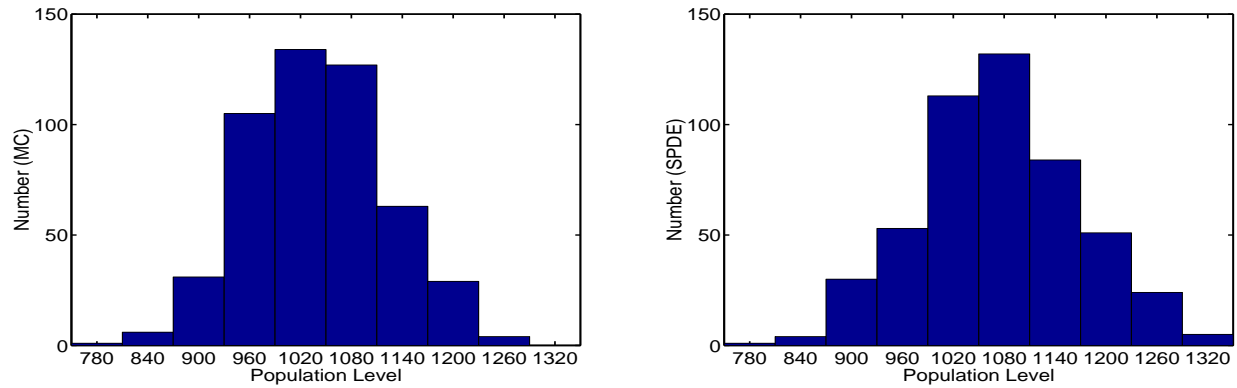


Figure 11: Calculated Distribution of Populations Levels at Time  $t = 1.0$  for 500 Sample Paths Using Monte Carlo (MC) and the Stochastic Partial Differential Equation (SPDE)

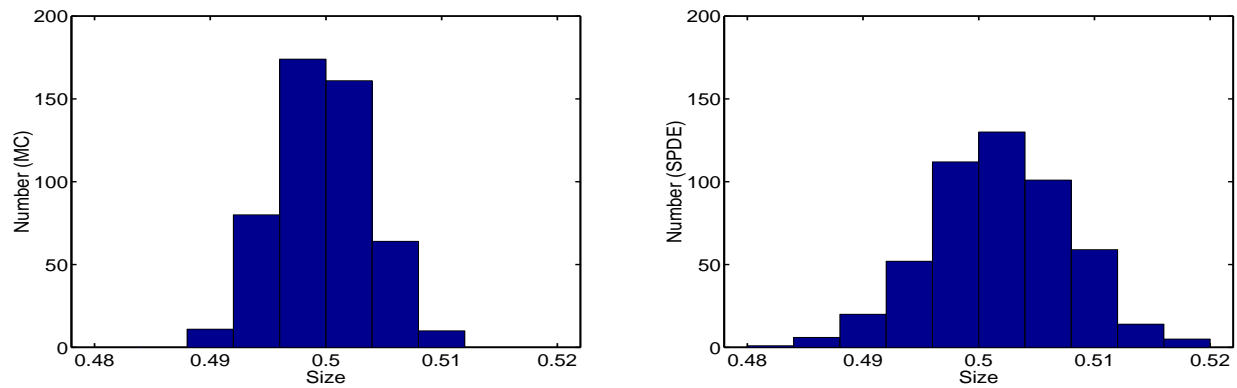


Figure 12: Calculated Distribution of Average Size at Time  $t = 1.0$  for 500 Sample Paths Using Monte Carlo (MC) and the Stochastic Partial Differential Equation (SPDE)

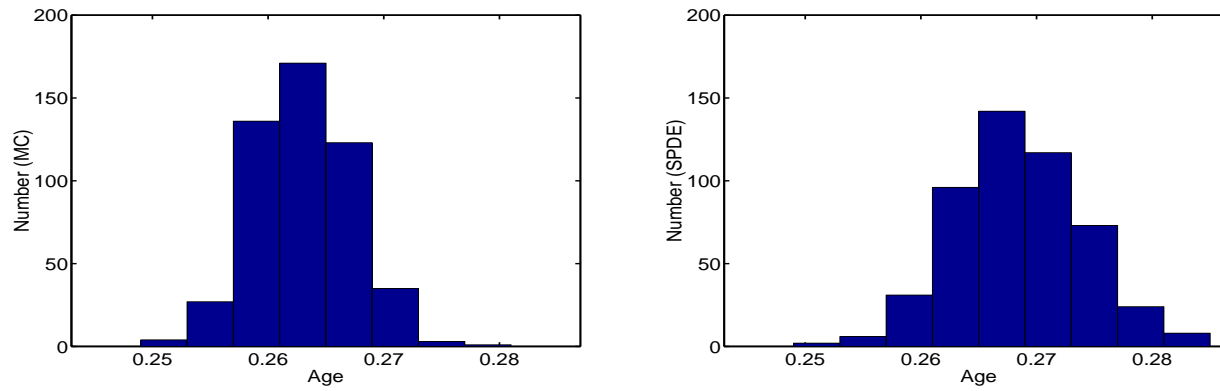


Figure 13: Calculated Distribution of Average Age at Time  $t = 1.0$  for 500 Sample Paths Using Monte Carlo (MC) and the Stochastic Partial Differential Equation (SPDE)

## Consider Now Derivation Of An SPDE For A Reaction-Diffusion Problem

Reaction-diffusion models are useful in population genetics models and in population dynamics models. For example, reaction-diffusion models may be useful in studying competition between two different species in a spatially-varying environment.

A deterministic reaction-diffusion model for two species may have the form:

$$\frac{\partial N_1(t, x)}{\partial t} = D_1(x) \frac{\partial^2 N_1(t, x)}{\partial^2 x} + N_1 b_1(t, x, N_1, N_2) - N_1 d_1(t, x, N_1, N_2)$$

$$\frac{\partial N_2(t, x)}{\partial t} = D_2(x) \frac{\partial^2 N_2(t, x)}{\partial^2 x} + N_2 b_2(t, x, N_1, N_2) - N_2 d_2(t, x, N_1, N_2).$$

**Considered Here Is A Single Population  $N(x, t)$  And The Changes Are Studied For A Time Interval  $\Delta t$**

Let  $N_k(t)$  be the population level at time  $t$  from position  $x_{k-1}$  to position  $x_k = x_{k-1} + \Delta x$ . The changes possible for  $N_k(t)$  are given in the table.

Possible Change $(\Delta N)_k$	Probability
<b>1</b>	$b(t, N_k)N_k$
<b>-1</b>	$d(t, N_k)N_k$
<b>1</b>	$J^+(x_{k-1})\Delta t$
<b>-1</b>	$J^-(x_{k-1})\Delta t$
<b>-1</b>	$J^+(x_k)\Delta t$
<b>1</b>	$J^-(x_k)\Delta t$

where  $b$  and  $d$  denote birth and death rates, respectively, and  $J^+$  and  $J^-$  are right- and left-moving currents.

This table defines a discrete stochastic model for a system of subpopulations.

## An SDE Model Is Obtained For The System Of Subpopulations

The SDE system has the form:

$$\begin{aligned} dN_k(t) = & (b(t, N_k)N_k - d(t, N_k)N_k)dt \\ & + (J^+(x_{k-1}) - J^-(x_{k-1}))dt - (J^+(x_k) - J^-(x_k))dt \\ & + \sqrt{b(t, N_k)N_k + d(t, N_k)N_k} \frac{1}{\sqrt{\Delta x}} \int_{x_{k-1}}^{x_k} \frac{\partial^2 W(t, x)}{\partial t \partial x} dx \\ & + \sqrt{(J^+(x_{k-1}))} \frac{\partial W^+(t; x_{k-1})}{\partial t} - \sqrt{(J^+(x_k))} \frac{\partial W^+(t; x_k)}{\partial t} \\ & - \sqrt{(J^-(x_{k-1}))} \frac{\partial W^-(t; x_{k-1})}{\partial t} + \sqrt{(J^-(x_k))} \frac{\partial W^-(t; x_k)}{\partial t} \end{aligned}$$

where certain Wiener processes and Brownian sheets are used in the expression.

**Now, The Spatial Interval Is Allowed To Approach Zero  
Resulting In An SPDE**

**Substituting**  $N(x_k, t)\Delta x = N_k(t)$ ,  $J^+(x) = -\frac{D}{2}\frac{\partial N(x, t)}{\partial x} + \frac{v}{2}N(x, t)$ ,  
**and**  $J^-(x) = \frac{D}{2}\frac{\partial N(x, t)}{\partial x} + \frac{v}{2}N(x, t)$  **and letting**  $\Delta x$  **approach zero,**  
**then the reaction-diffusion SPDE is obtained:**

$$\begin{aligned} \frac{\partial N(x, t)}{\partial t} &= b(t, N)N - d(t, N)N + \frac{\partial}{\partial x} \left( \frac{D(x)\partial N(x, t)}{\partial x} \right) \\ &+ \sqrt{b(t, N)N + d(t, N)N} \frac{\partial^2 W(t, x)}{\partial t \partial x} \\ &+ \frac{\partial}{\partial x} \left( \sqrt{-\frac{D(x)\partial N(x, t)}{2\partial x} + \frac{v}{2}N(x, t)} \frac{\partial W^+(t; x)}{\partial t} \right) \\ &- \frac{\partial}{\partial x} \left( \sqrt{\frac{D(x)\partial N(x, t)}{2\partial x} + \frac{v}{2}N(x, t)} \frac{\partial W^-(t; x)}{\partial t} \right) \end{aligned}$$



## Good Results Are Obtained Between The SPDE And Monte Carlo Computations

An infinite region  $-\infty < x < \infty$  is considered where the initial population density satisfies  $N(x, 0) = 60 - 120x^2 + 60x^4$  for  $-1 \leq x \leq 1$  and  $N(x, 0) = 0$ , otherwise. Let  $b = d = 0$ . Two cases are considered:  $D = 0.05, v = 1.5$  and  $D = 0.067, v = 2.0$ . The mean number of individuals in the interval  $[-1, 1]$  and the variance are computed at the times  $t = 2.5, 5.0, 10.0, 20.0$ . The results for the SPDE model are compared with Monte Carlo (MC) computations using 4000 paths.

Table: Computational results for the two cases

Time	Mean (SPDE)	Var. (SPDE)	Mean (MC)	Var. (MC)
2.5	57.5	5.74	57.8	5.46
5.0	51.0	9.83	51.6	9.72
10.0	42.3	13.6	43.3	14.2
20.0	33.1	15.8	34.0	16.1
2.5	55.1	7.86	56.0	7.05
5.0	47.6	12.2	49.0	11.5
10.0	38.5	15.7	39.9	14.9
20.0	29.3	16.4	30.7	16.4