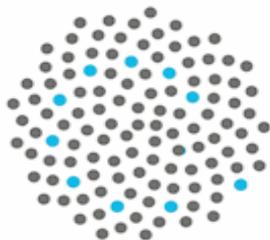


From rabbits in Canberra to convergence in $D[0, t]$: Part II

Phil Pollett

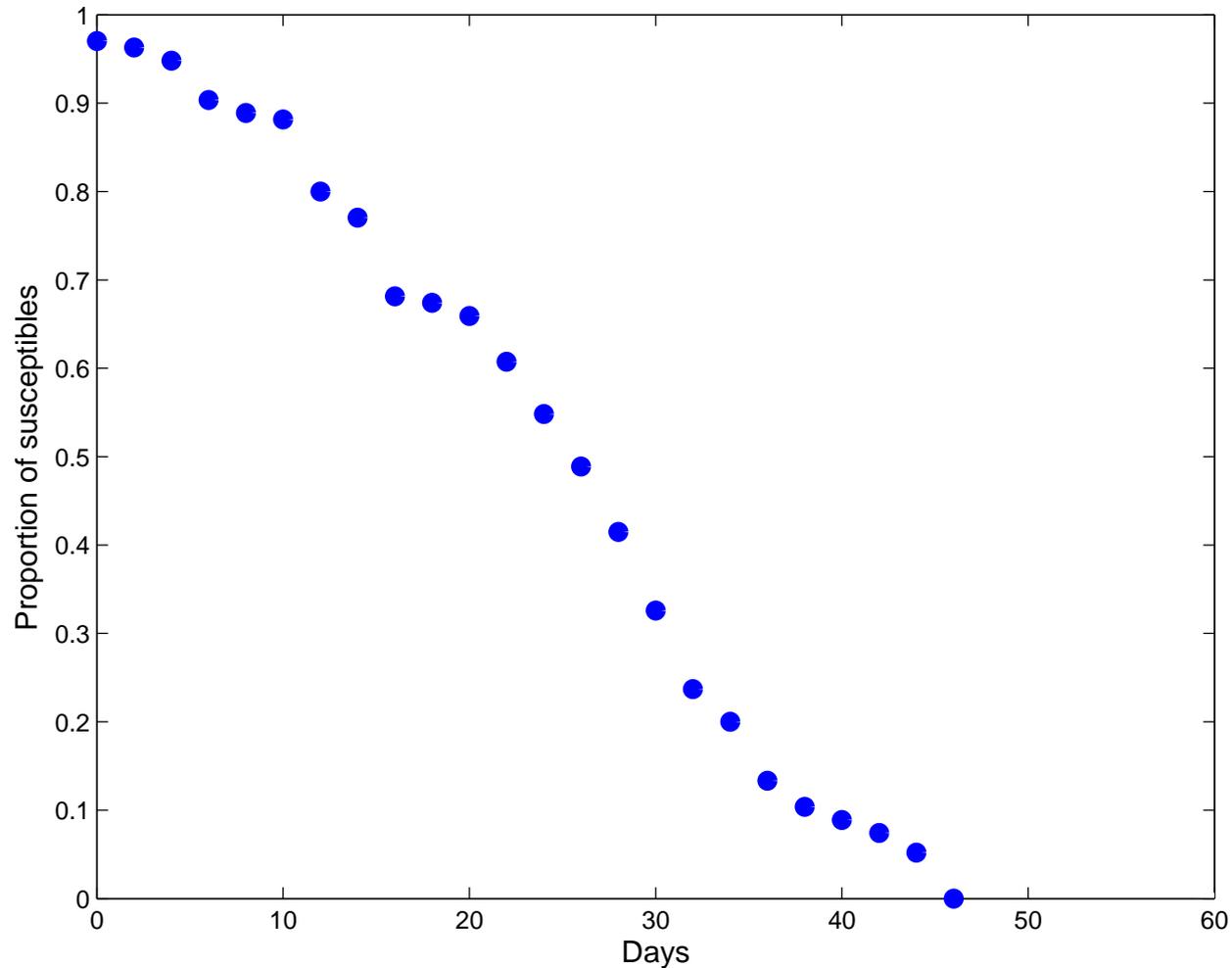
Department of Mathematics and MASCOS

University of Queensland



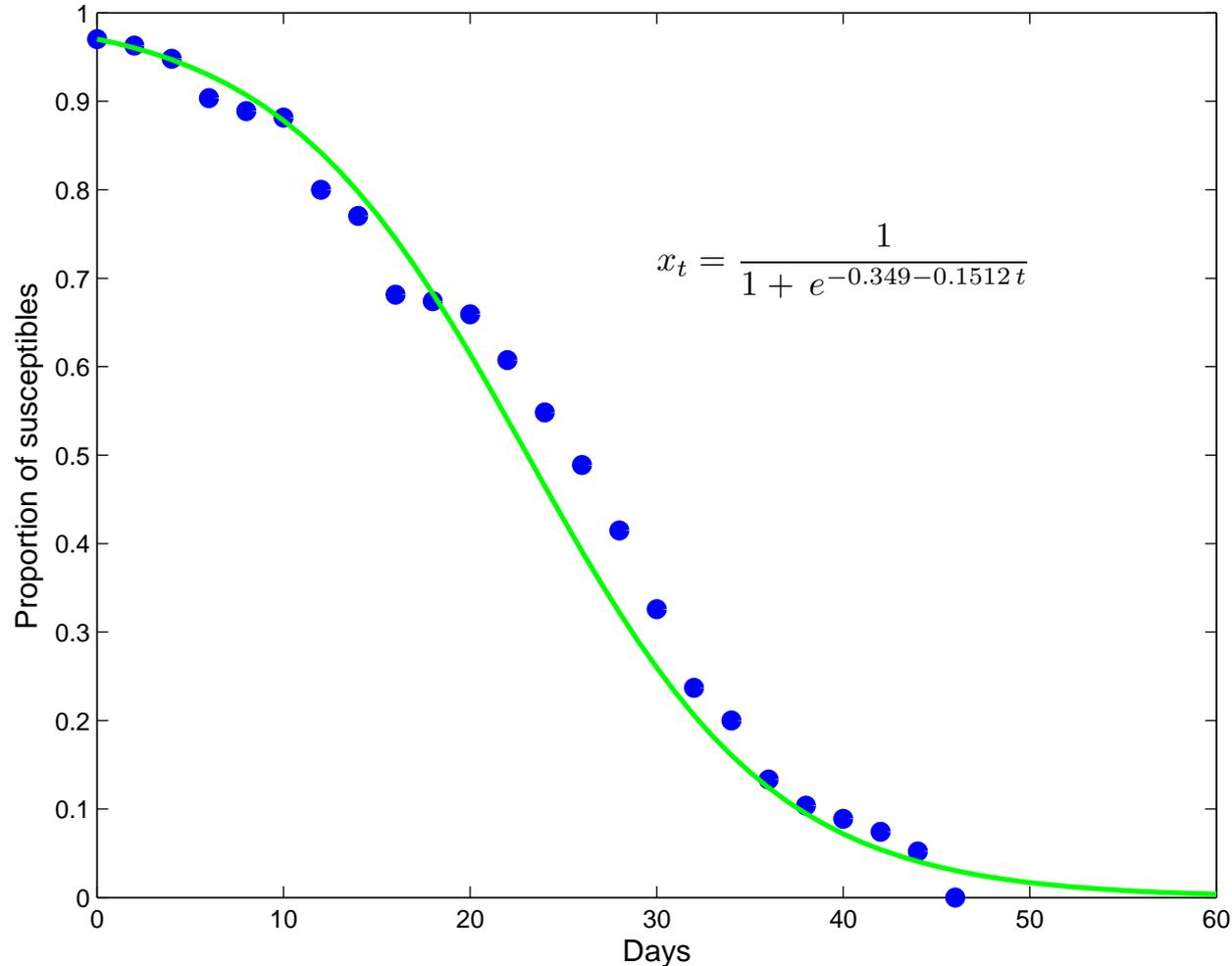
AUSTRALIAN RESEARCH COUNCIL
Centre of Excellence for Mathematics
and Statistics of Complex Systems

Recapitulation - Rabbits in Canberra



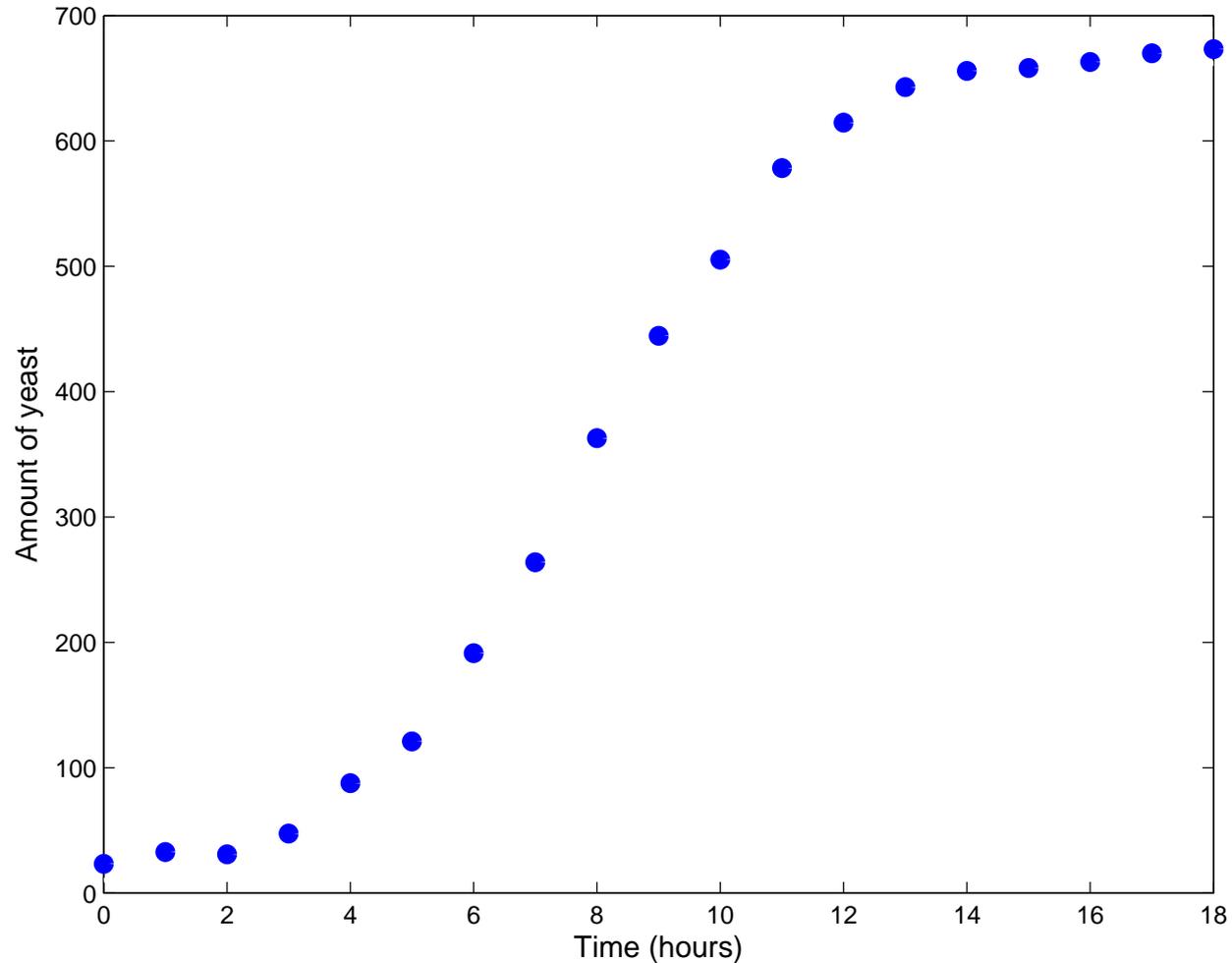
Williams, R.T., Fullagar, P.J., Kogon, C. and Davey, C. (1973) Observations on a naturally occurring winter epizootic of myxomatosis at Canberra, Australia, in the presence of Rabbit fleas (*Spilopsyllus cuniculi* Dale) and virulent myxoma virus, *J. Appl. Ecol.* 10, 417–427.

Recapitulation - Rabbits in Canberra



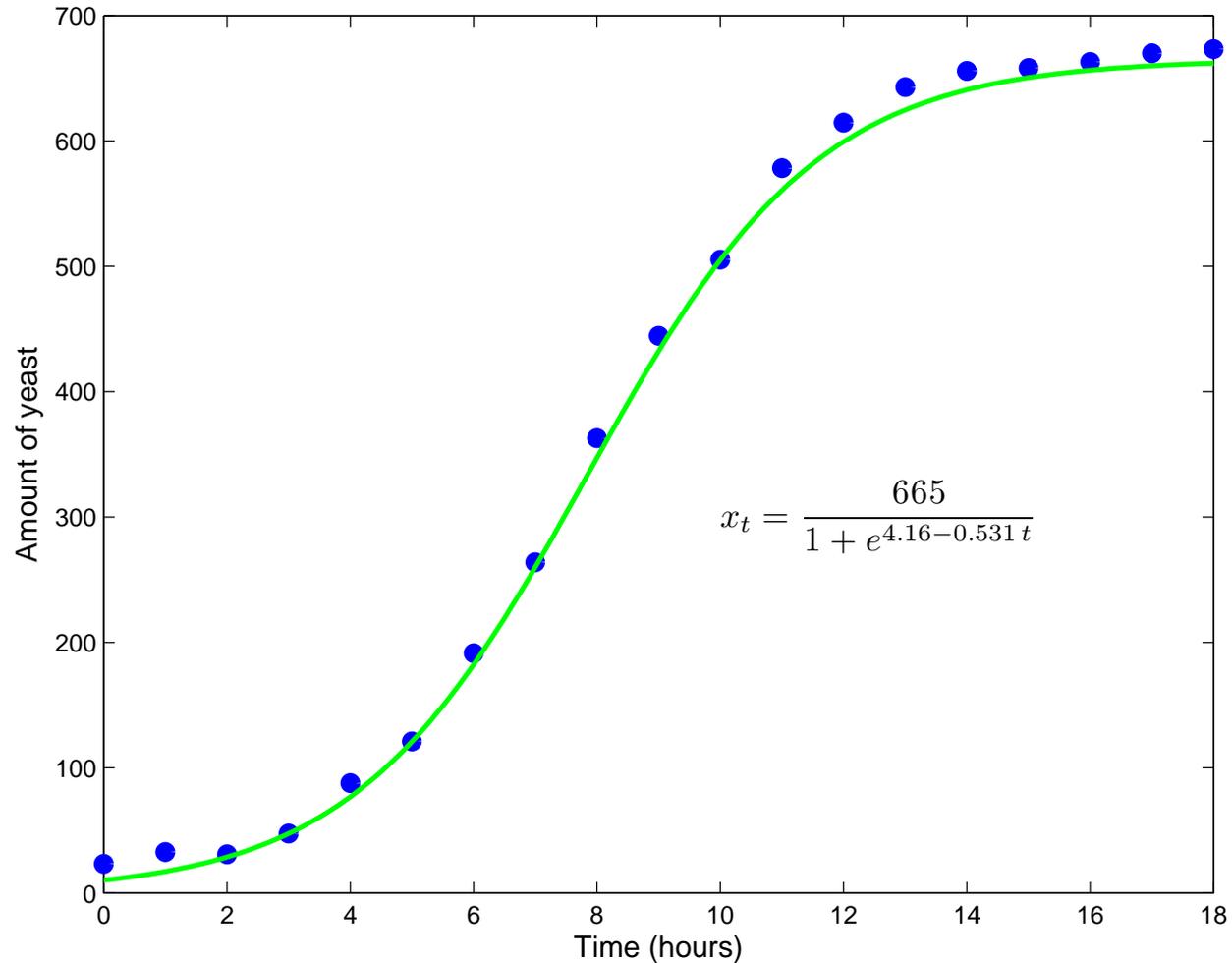
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Recapitulation - Growth of yeast



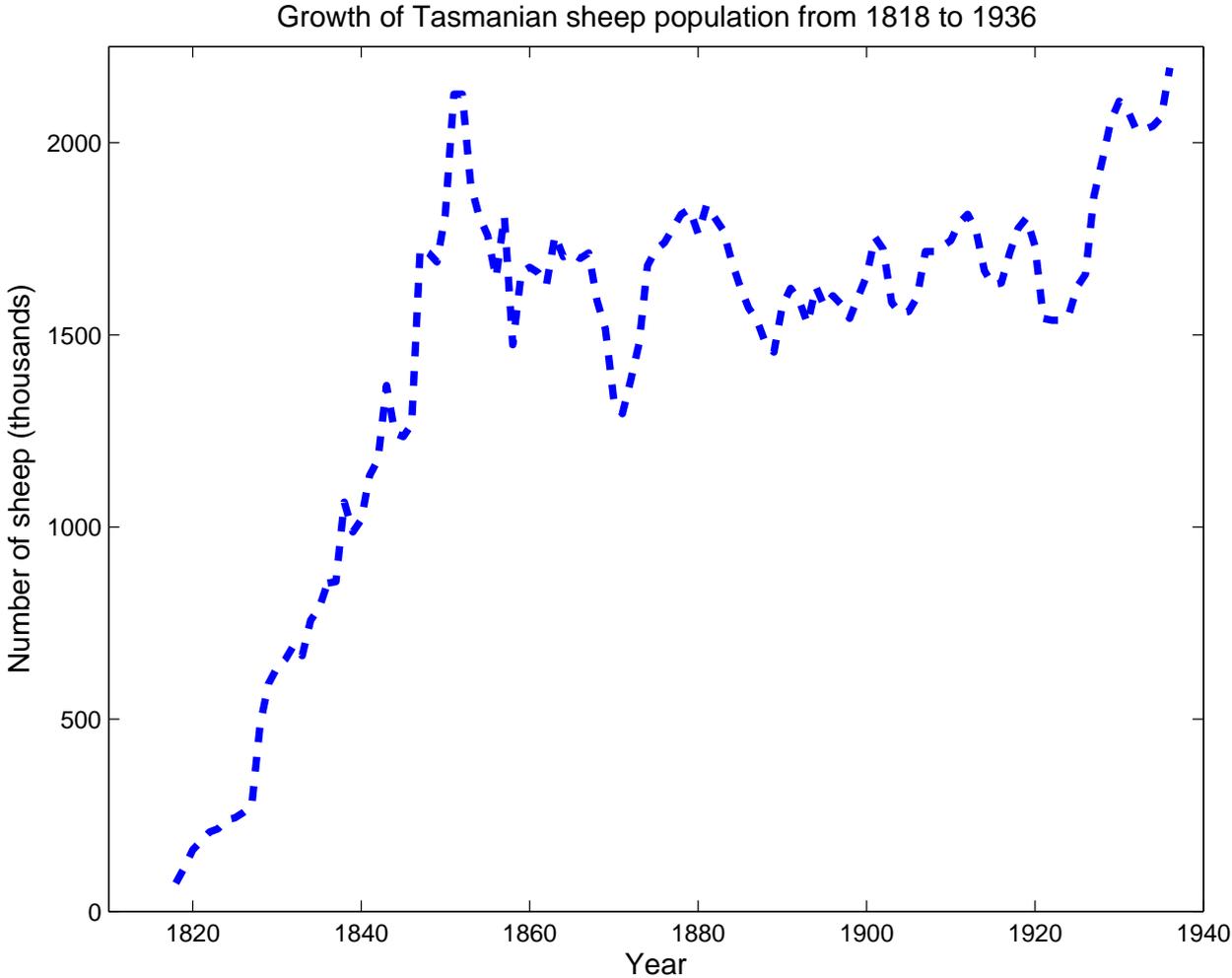
Carlson, T. (1913) *Über Geschwindigkeit und Grosse der Hefevermehrung in Wurze*. *Biochemische Zeitschrift* 57, 313–334.

Recapitulation - Growth of yeast



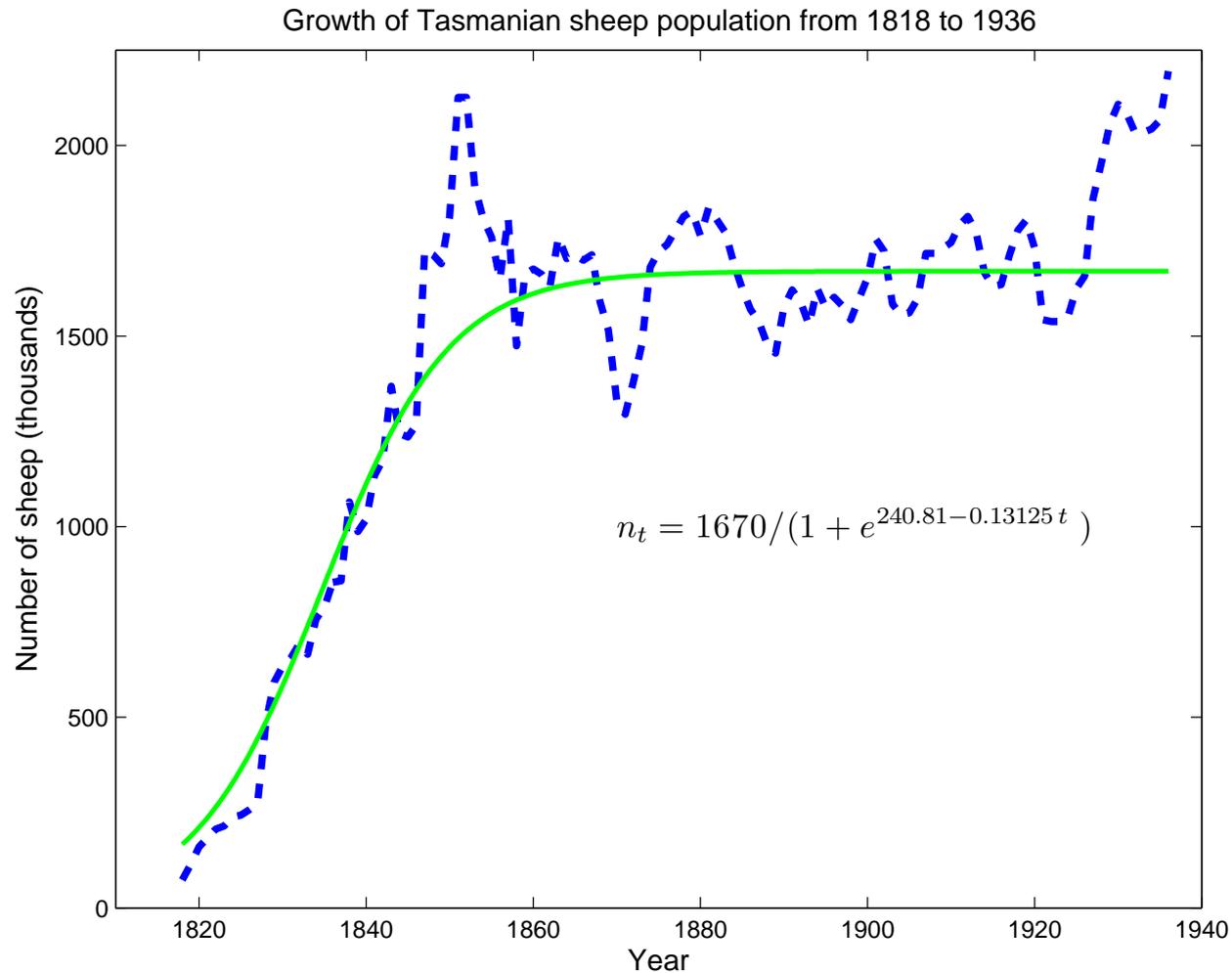
Carlson, T. (1913) *Über Geschwindigkeit und Grosse der Hefevermehrung in Wurze*. *Biochemische Zeitschrift* 57, 313–334.

Sheep in Tasmania



Davidson, J. (1938) On the growth of the sheep population in Tasmania, *Trans. Roy. Soc. Sth. Austral.* 62, 342–346.

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Recapitulation - The Verhulst-Pearl model

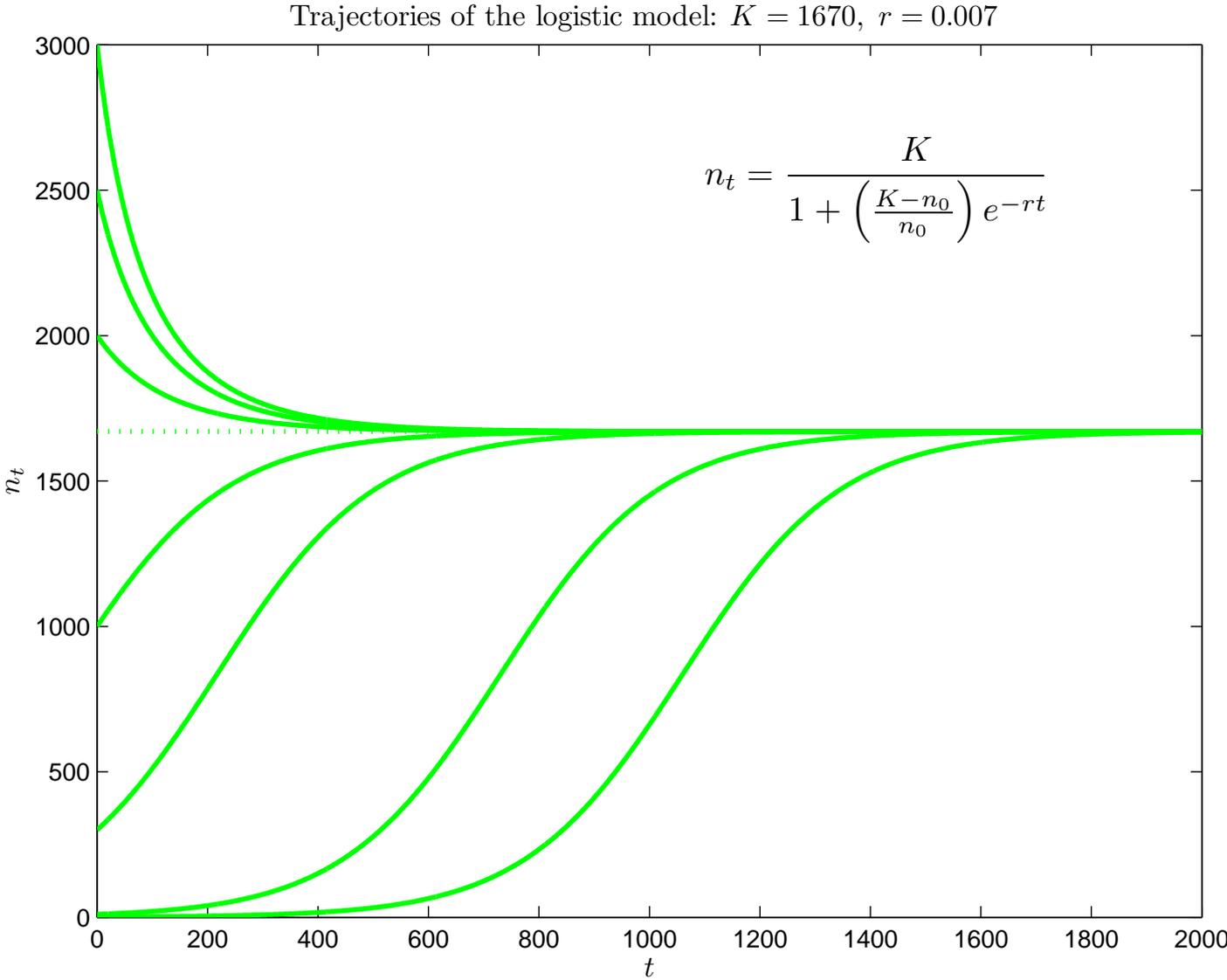
$$\frac{dn}{dt} = rn(1 - n/K).$$

Here r is the growth rate with unlimited resources and K is the “natural” population size (the carrying capacity).

Integration gives

$$n_t = \frac{K}{1 + \left(\frac{K-n_0}{n_0}\right) e^{-rt}} \quad (t \geq 0).$$

Recapitulation - The Verhulst-Pearl model



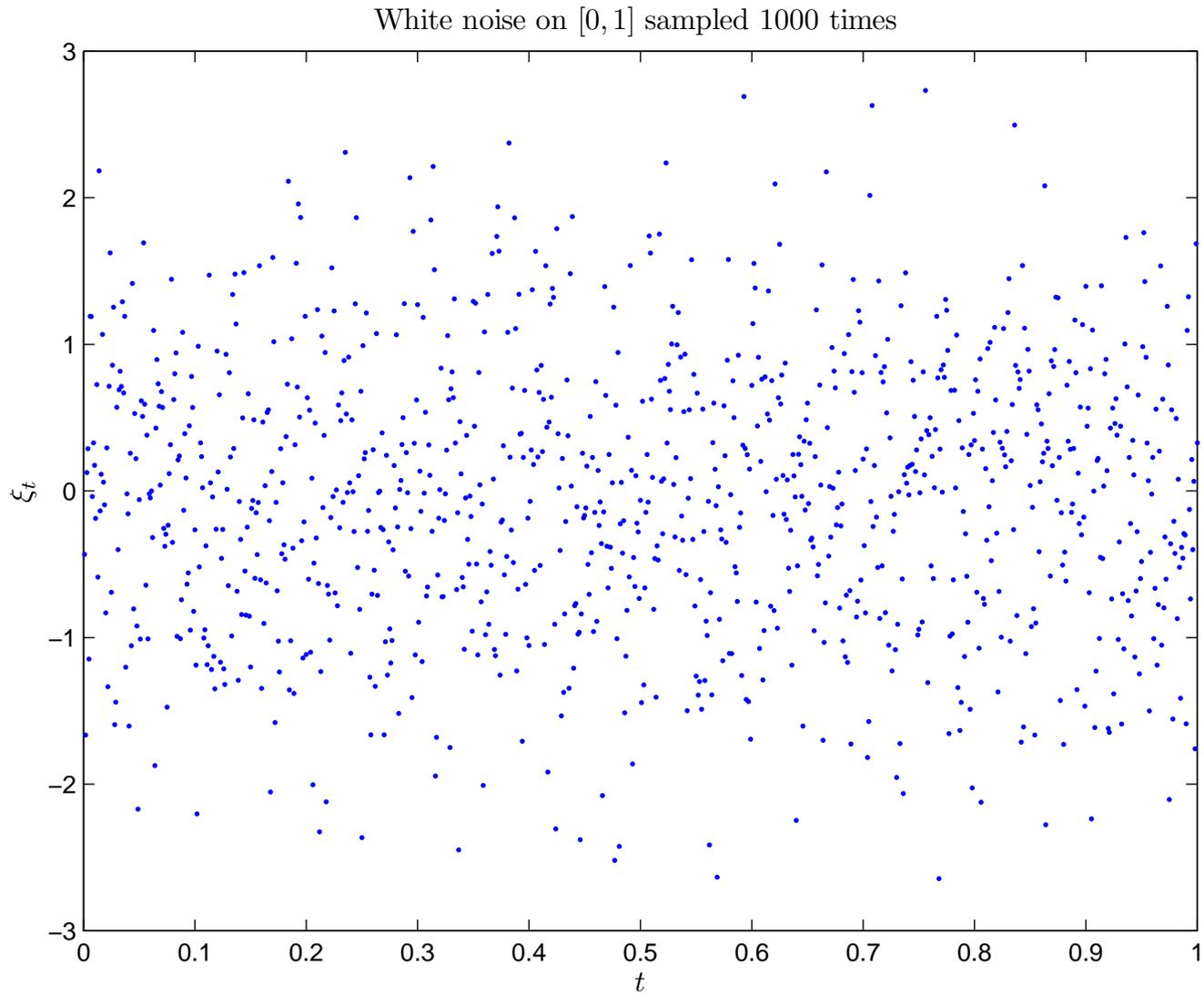
Recapitulation - Adding noise

$$n_t = \frac{K}{1 + \left(\frac{K-n_0}{n_0}\right) e^{-rt}} + \text{something random}$$

or perhaps

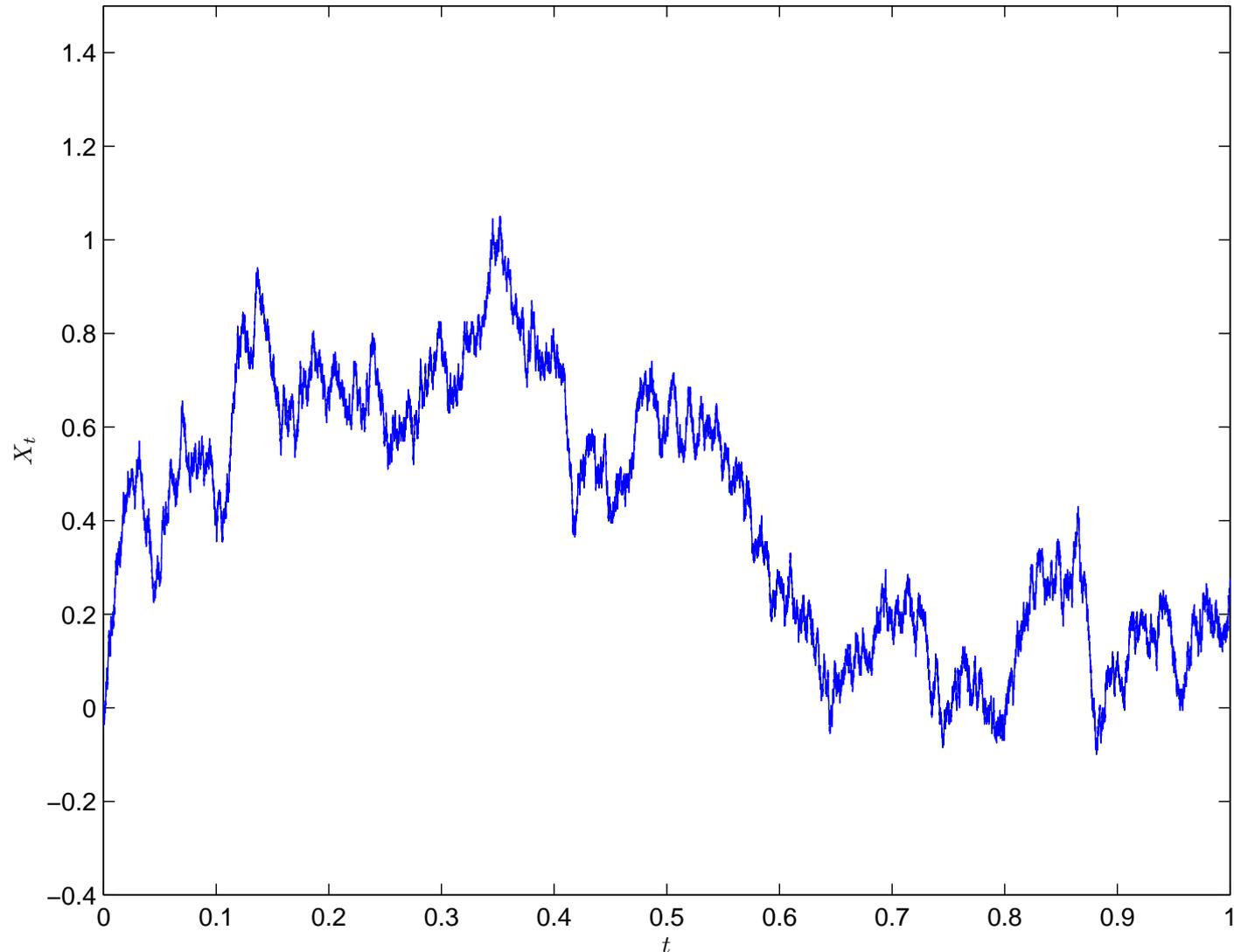
$$\frac{dn}{dt} = rn \left(1 - \frac{n}{K}\right) + \sigma \times \text{noise}.$$

Recapitulation - White noise



Recapitulation - Brownian motion

Random walk simulation: $h = 2.5e-005$, $\Delta = 0.005$



Recapitulation - Langevin equation

In modern parlance, Langevin described the Brownian particle's *velocity* as an *Ornstein-Uhlenbeck (OU) process*.

The *Langevin equation* (for a particle of unit mass) is

$$dv_t = -\mu v_t dt + \sigma dB_t,$$

being Newton's law ($-\mu v = \text{Force} = m\dot{v}$) *plus* noise.

The (strong) solution to this SDE is the OU process:

$$v_t = v_0 e^{-\mu t} + \int_0^t \sigma e^{-\mu(t-s)} dB_s.$$

A different approach

Let's start from scratch specifying a stochastic model with variation being an inherent property: a *Markovian model*.

A different approach

We will suppose that n_t (integer-valued!) evolves as a birth-death process with rates

$$q_{n,n+1} = \lambda n \left(1 - \frac{n}{N}\right) \quad \text{and} \quad q_{n,n-1} = \mu n,$$

where λ is the per-capita birth rate (when N is large), and μ is per-capita death rate. Here N is the *population ceiling* (n_t now takes values in $S = \{0, 1, \dots, N\}$).

I will call this model the *stochastic logistic (SL) model*, though it has many names, having been rediscovered several times since Feller proposed it in 1939.

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I will call this model the *stochastic logistic (SL) model*, though it has many names, having been rediscovered several times since Feller proposed it in 1939.

It shares an important property with the deterministic logistic model: that of *density dependence*.

Density dependence

The Verhulst-Pearl model $\frac{dn}{dt} = rn \left(1 - \frac{n}{K}\right)$ can be written

$$\frac{1}{N} \frac{dn}{dt} = r \frac{n}{N} \left(1 - \frac{N}{K} \frac{n}{N}\right).$$

The state n_t changes at a rate that depends on n_t only through n_t/N .

Density dependence

So, letting $x_t = n_t/N$ be the “population density”, we get

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{E}\right), \quad \text{where } E = K/N.$$

This is a convenient space scaling. We could have set $x_t = n_t/A$, where A is habitat area, and then

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{DE}\right), \quad \text{where } D = N/A.$$

Markovian models

Let $(n_t, t \geq 0)$ be a continuous-time Markov chain taking values in $S \subseteq \mathbb{Z}^k$ with transition rates $Q = (q_{nm}, n, m \in S)$. We identify a quantity N , usually related to the size of the system being modelled.

Definition (Kurtz*) The model is *density dependent* if there is a subset E of \mathbb{R}^k and a continuous function $f : \mathbb{Z}^k \times E \rightarrow \mathbb{R}$, such that

$$q_{n, n+l} = N f_l \left(\frac{n}{N} \right), \quad l \neq 0 \quad (l \in \mathbb{Z}^k).$$

(So, the idea is the same: *the rate of change of n_t depends on n_t only through the “density” n_t/N .*)

*Kurtz, T. (1970) Solutions of ordinary differential equations as limits of pure jump Markov processes, *J. of Appl. Probab.* 7, 49–58.

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Thomas Kurtz (taken in 2003)

Density dependence

Consider the *forward equations* for $p_n(t) := \Pr(n_t = n)$.
Let $q_n = \sum_{m \neq n} q_{nm}$. Then,

$$p'_n(t) = -q_n p_n(t) + \sum_{m \neq n} p_m(t) q_{mn},$$

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and so (formally) $\mathbb{E}(n_t) = \sum_n n p_n(t)$ satisfies

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So if $q_{n,n+l} = N f_l(n/N)$, then

$$\begin{aligned} \frac{d}{dt} \mathbb{E}(n_t) &= - \sum_n \sum_{l \neq 0} N f_l(n/N) n p_n(t) \\ &\quad + \sum_m p_m(t) \sum_{l \neq 0} (m+l) N f_l(m/N) \\ &= \sum_m p_m(t) N \sum_{l \neq 0} l f_l(m/N) = N \mathbb{E} \left(\sum_{l \neq 0} l f_l(n_t/N) \right). \end{aligned}$$

Density dependence

For an arbitrary density dependent model, define $F : E \rightarrow \mathbb{R}$ by $F(x) = \sum_{l \neq 0} l f_l(x)$. Then,

$$\frac{d}{dt} \mathbb{E}(n_t) = N \mathbb{E} \left(F \left(\frac{n_t}{N} \right) \right),$$

or, setting $X_t = n_t/N$ (the *density process*),

$$\frac{d}{dt} \mathbb{E}(X_t) = \mathbb{E} (F(X_t)) .$$

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(But, I *am* hoping for something like that to be true!)

Density dependence

For the SL model we have $S = \{0, 1, \dots, N\}$ and

$$q_{n,n+1} = \lambda n \left(1 - \frac{n}{N}\right) \quad \text{and} \quad q_{n,n-1} = \mu n.$$

Therefore, $f_{+1}(x) = \lambda x (1 - x)$ and $f_{-1}(x) = \mu x$,
 $x \in E := [0, 1]$, and so $F(x) = \lambda x (1 - \rho - x)$, $x \in E$,
where $\rho = \mu/\lambda$.

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where $\rho = \mu/\lambda$.

Now compare $F(x)$ with the right-hand side of the
Verhulst-Pearl model for the density process:

$$\frac{dx}{dt} = r x \left(1 - \frac{x}{E}\right), \quad \text{where} \quad E = K/N. \quad (2)$$

If $K \sim \beta N$ for N large, so that $K/N \rightarrow \beta$, then we may
identify β with $1 - \rho$ and r with $\lambda\beta$, and discover that (2)
can be rewritten as $dx/dt = F(x)$.

Recall that ...

Recall that $(n_t, t \geq 0)$ is a continuous-time Markov chain taking values in $S \subseteq \mathbb{Z}^k$ with transition rates $Q = (q_{nm}, n, m \in S)$, and we have identified a quantity N , usually related to the size of the system being modelled.

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The model is assumed to be *density dependent*: there is a subset E of \mathbb{R}^k and a continuous function $f : \mathbb{Z}^k \times E \rightarrow \mathbb{R}$, such that

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We set $F(x) = \sum_{l \neq 0} l f_l(x), x \in E$.

The density process

We now formally define the *density process* $(X_t^{(N)})$ by $X_t^{(N)} = n_t/N, t \geq 0$. We hope that $(X_t^{(N)})$ becomes more deterministic as N gets large.

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To simplify the statement of results, I'm going to assume that the state space S is finite.

A law of large numbers

The following *functional law of large numbers* establishes convergence of the family $(X_t^{(N)})$ to the unique trajectory of an appropriate approximating deterministic model.

Theorem (Kurtz*) Suppose F is Lipschitz on E (that is, $|F(x) - F(y)| < M_E|x - y|$). If $\lim_{N \rightarrow \infty} X_0^{(N)} = x_0$, then the density process $(X_t^{(N)})$ converges uniformly in probability on $[0, t]$ to (x_t) , the unique (deterministic) trajectory satisfying

$$\frac{d}{ds}x_s = F(x_s), \quad x_s \in E, \quad s \in [0, t].$$

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(If S is an infinite set, we have the additional conditions $\sup_{x \in E} \sum_{l \neq 0} |l| f_l(x) < \infty$ and $\lim_{d \rightarrow \infty} \sum_{|l| > d} |l| f_l(x) = 0$, $x \in E$.)

A law of large numbers

Convergence *uniformly in probability* on $[0, t]$ means that for every $\epsilon > 0$,

$$\lim_{N \rightarrow \infty} \Pr \left(\sup_{s \leq t} |X_t^{(N)} - x_t| > \epsilon \right) = 0.$$

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$$\lim_{N \rightarrow \infty} \Pr \left(\sup_{s \leq t} |X_t^{(N)} - x_t| > \epsilon \right) = 0.$$

The conditions of the theorem hold for the SL model: since $F(x) = \lambda x(1 - \rho - x)$, we have, for all $x, y \in E = [0, 1]$, that

$$|F(x) - F(y)| = \lambda|x - y||1 - \rho - (x + y)| \leq (1 + \rho)\lambda|x - y|.$$

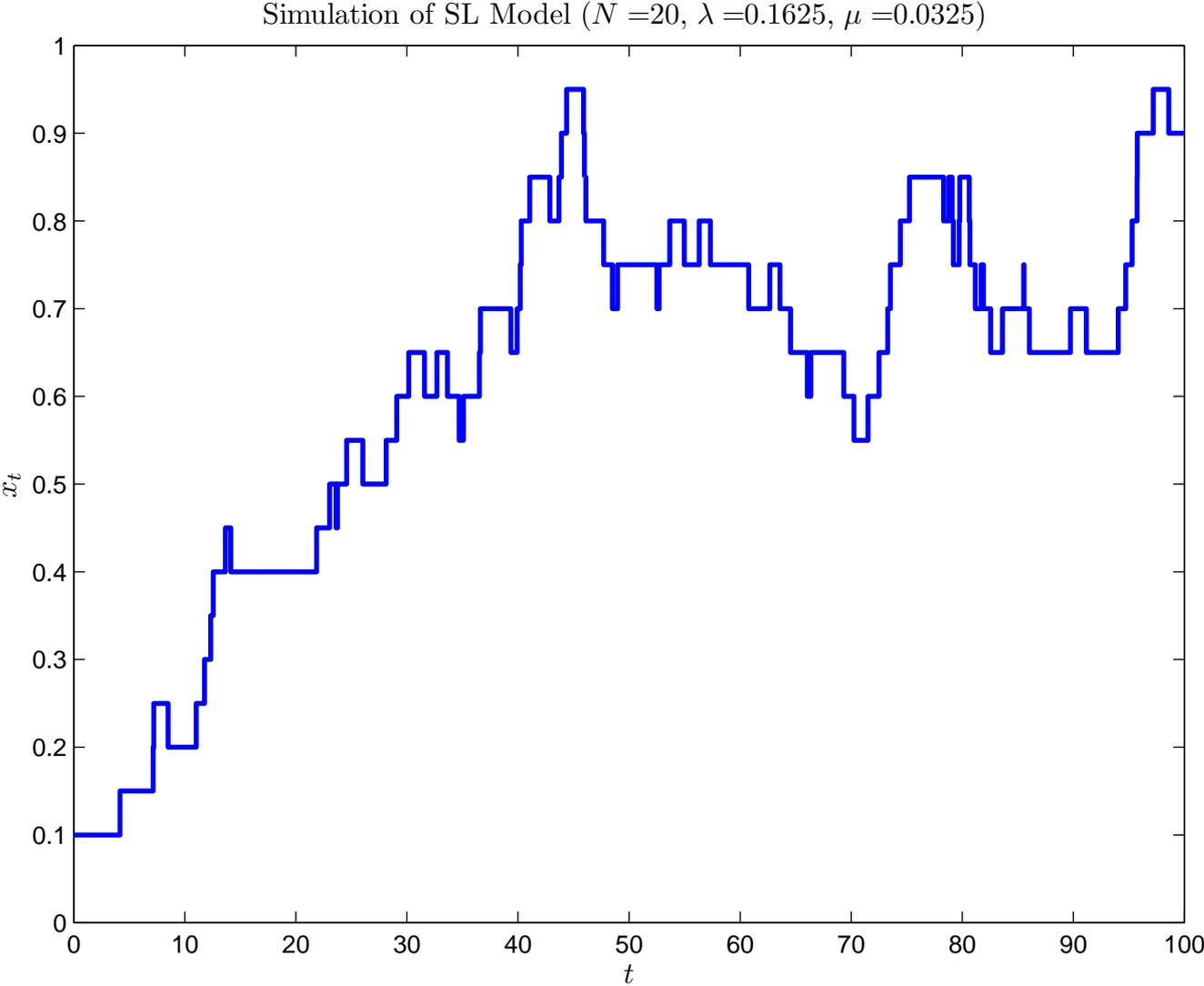
That is, F is Lipschitz on E .

A law of large numbers

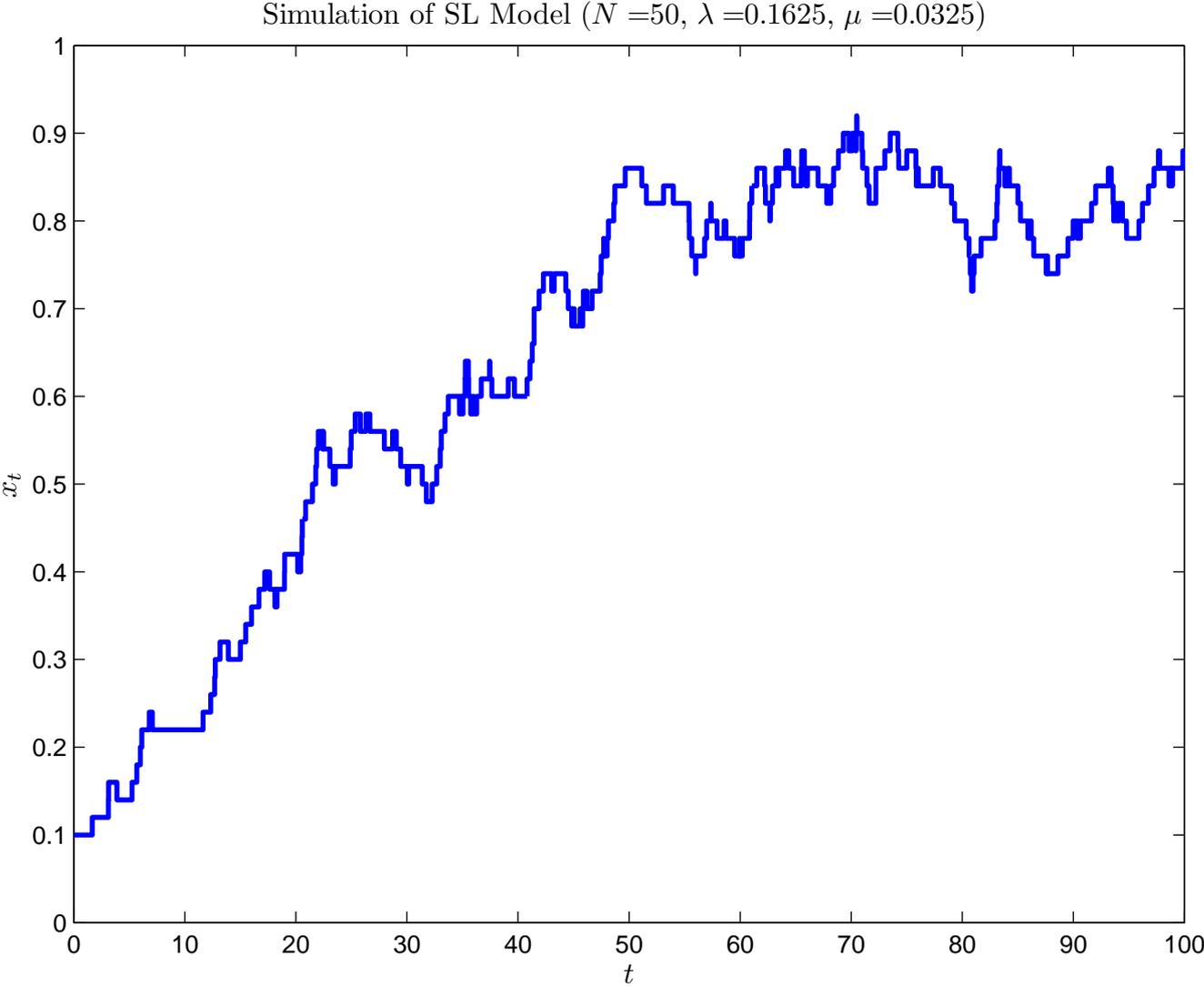
So, provided $X_0^{(N)} \rightarrow x_0$ as $N \rightarrow \infty$, the population density ($X_t^{(N)}$) converges (uniformly in probability on finite time intervals) to the solution (x_t) of the deterministic model

$$\frac{dx}{dt} = \lambda x(1 - \rho - x) \quad (x_t \in E).$$

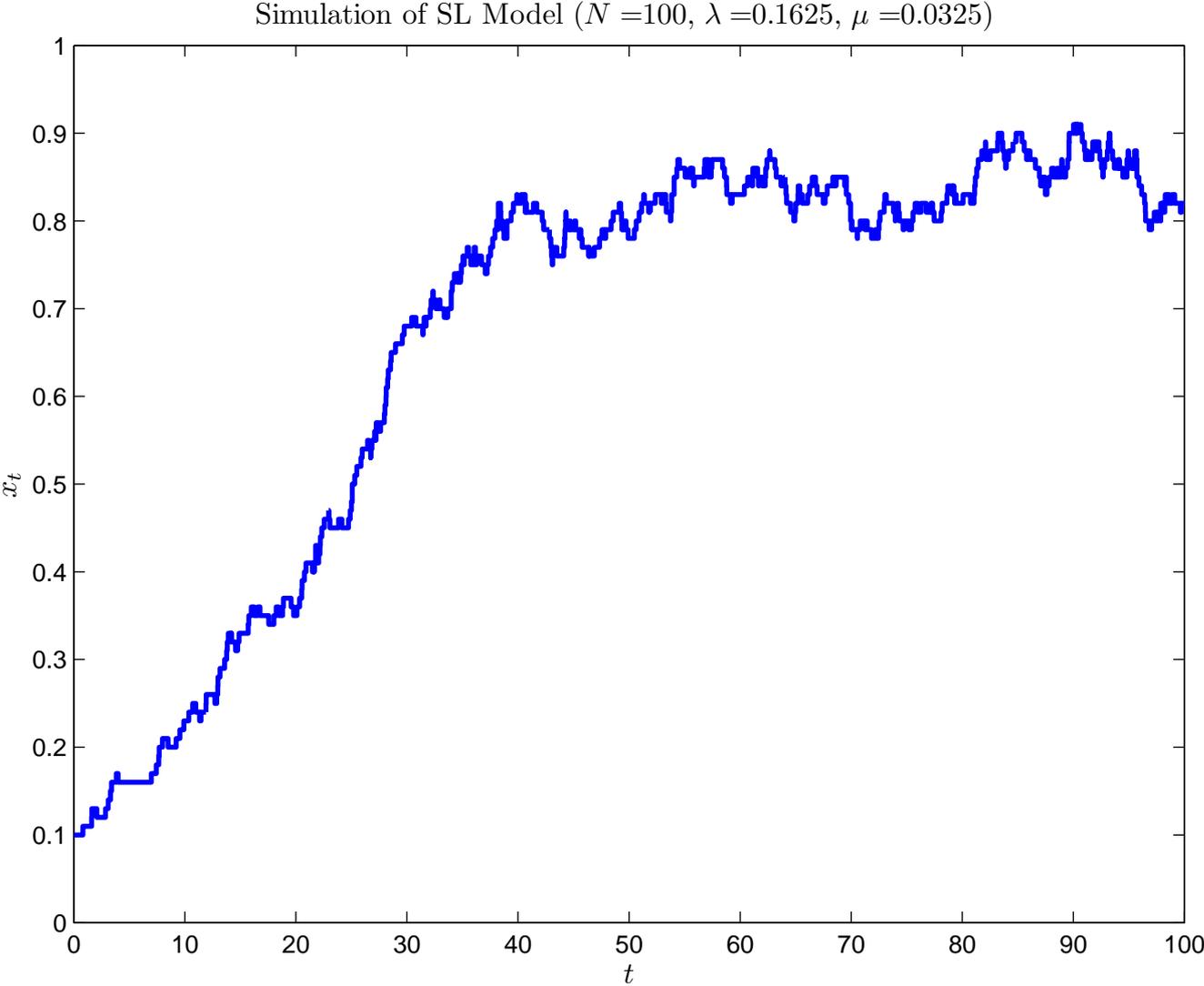
The SL model ($N = 20$)



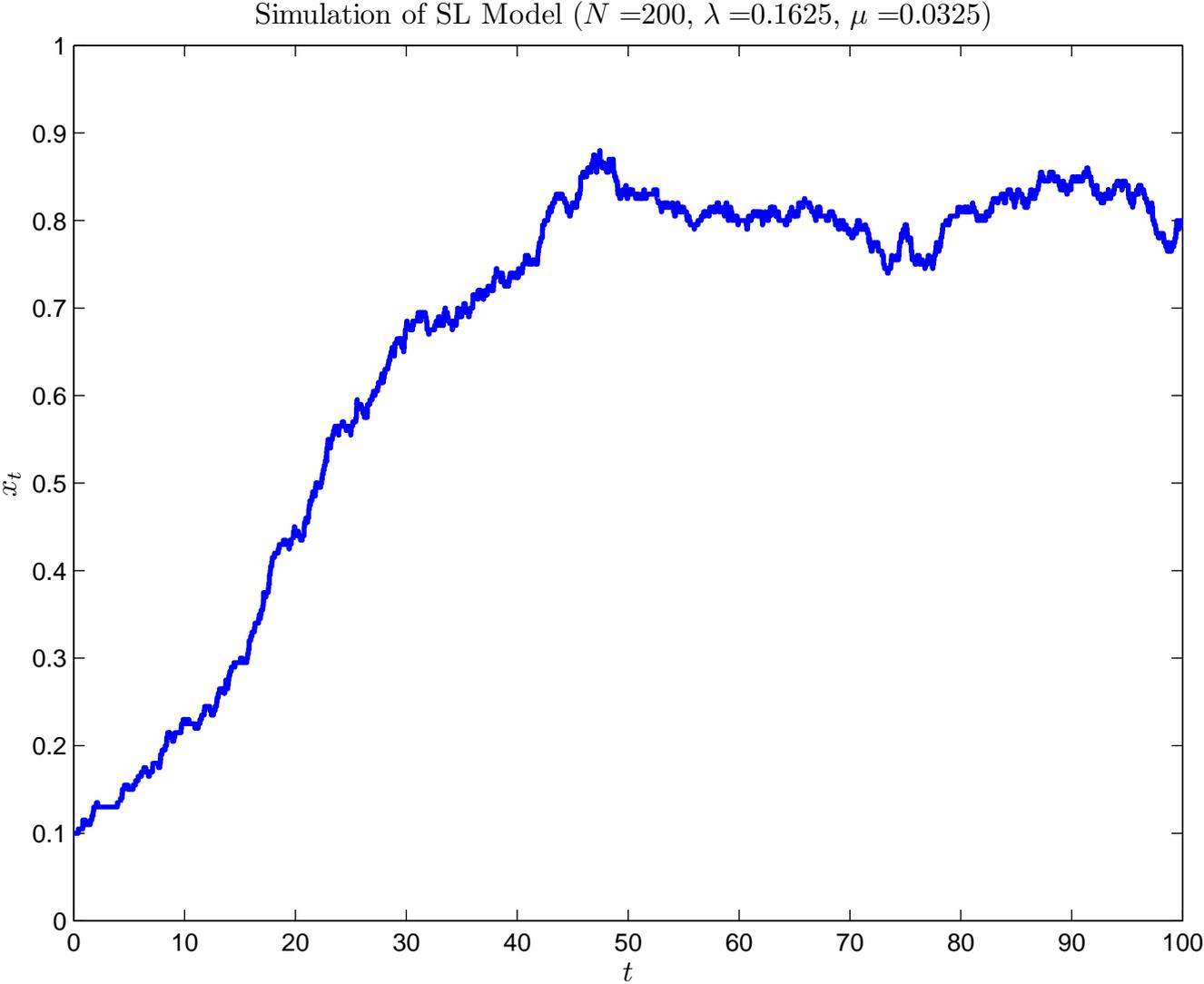
The SL model ($N = 50$)



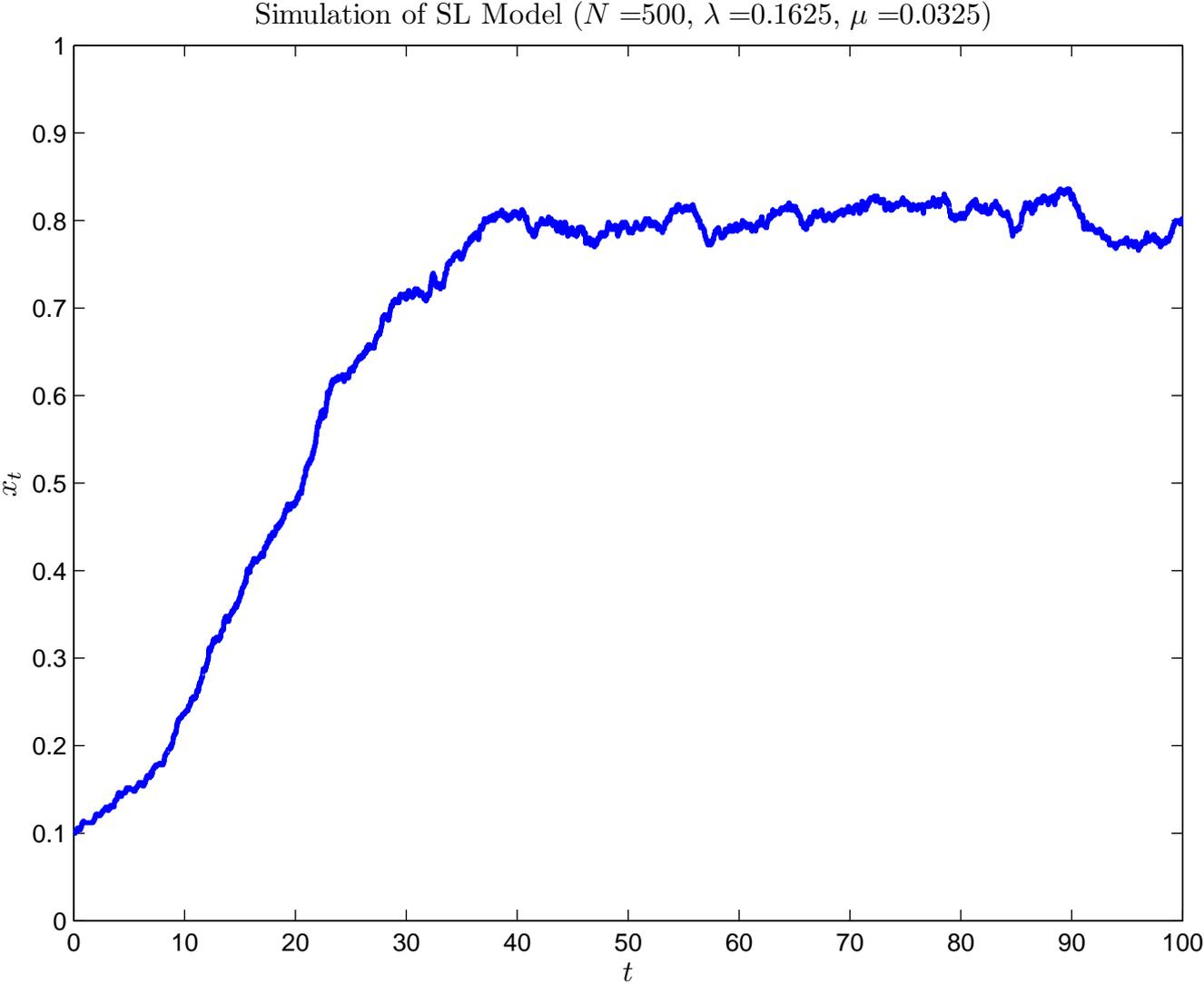
The SL model ($N = 100$)



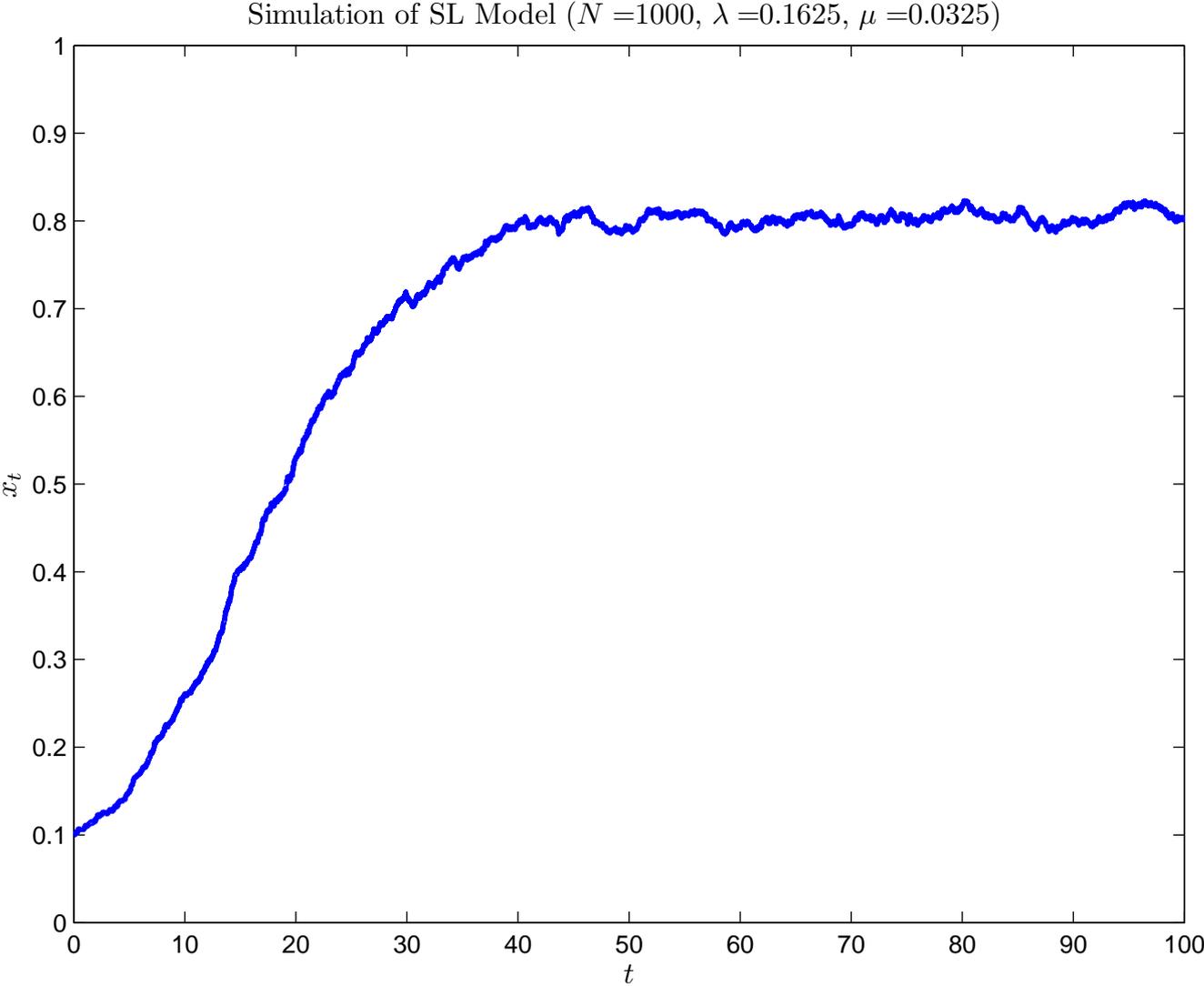
The SL model ($N = 200$)



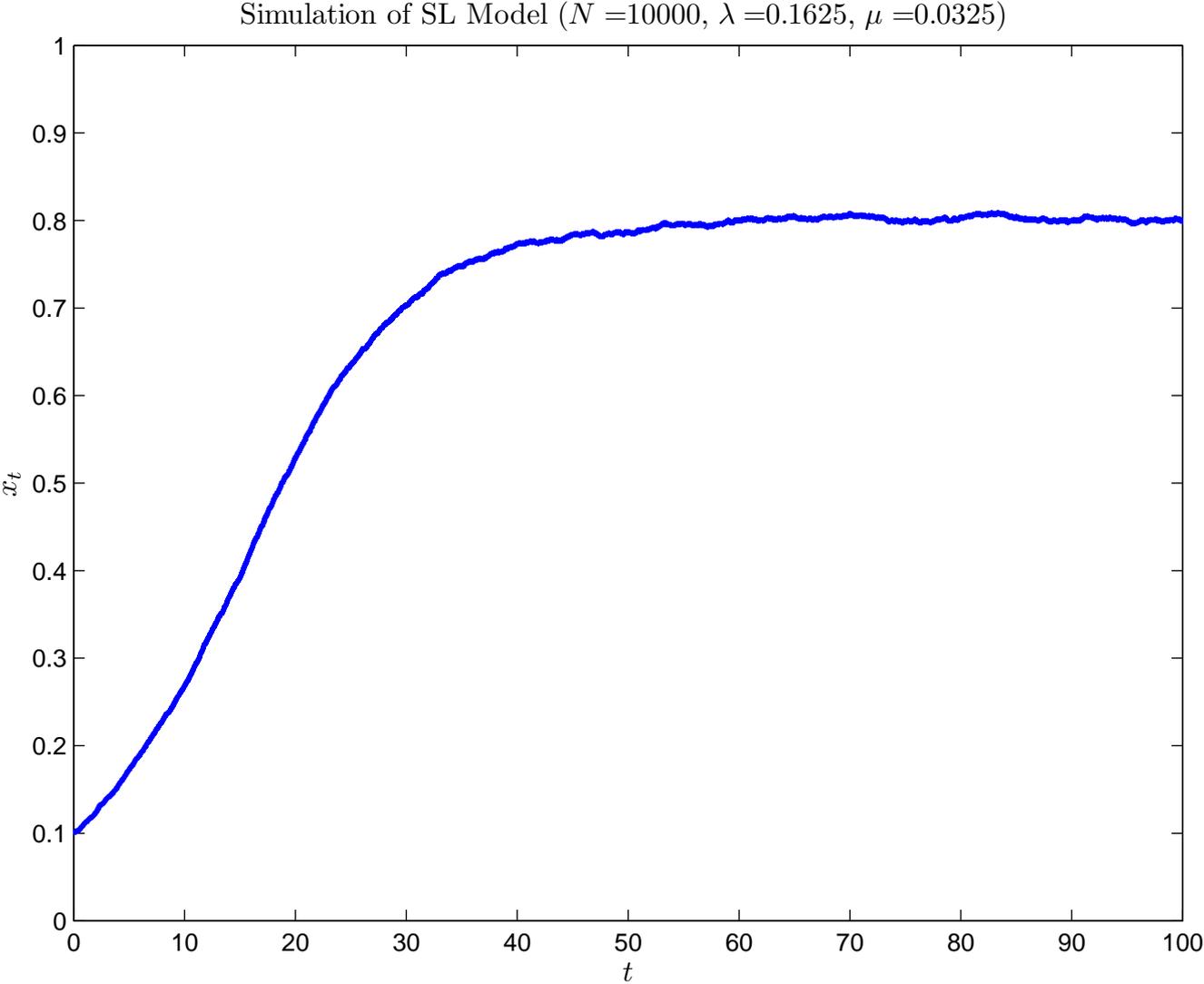
The SL model ($N = 500$)



The SL model ($N = 1000$)

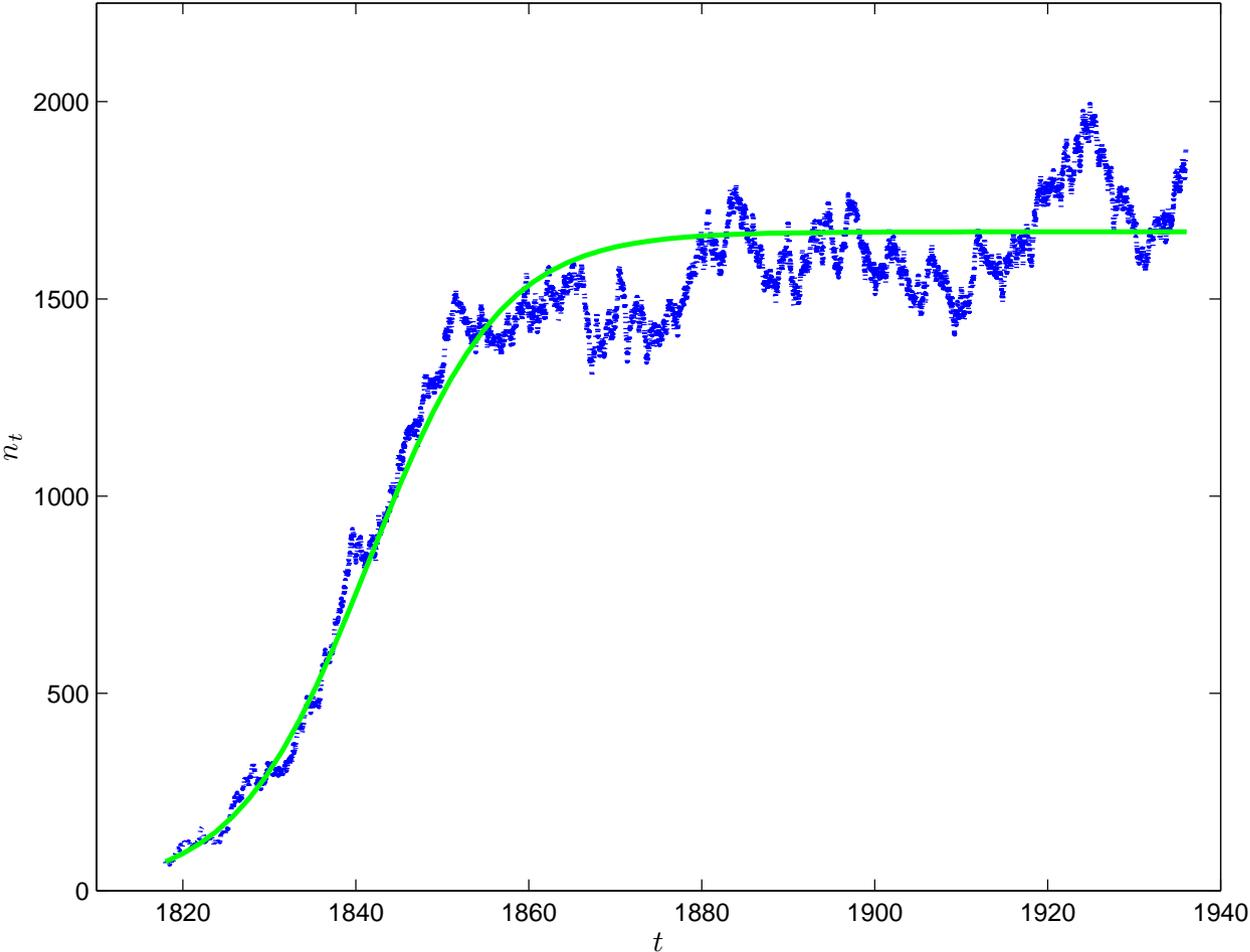


The SL model ($N = 10\,000$)



Simulation of the SL model

Simulation of SL Model ($N = 10000$, $\lambda = 0.78593$, $\mu = 0.65468$, $K = 1670$)



(Solution to the deterministic model is in green)

A central limit law

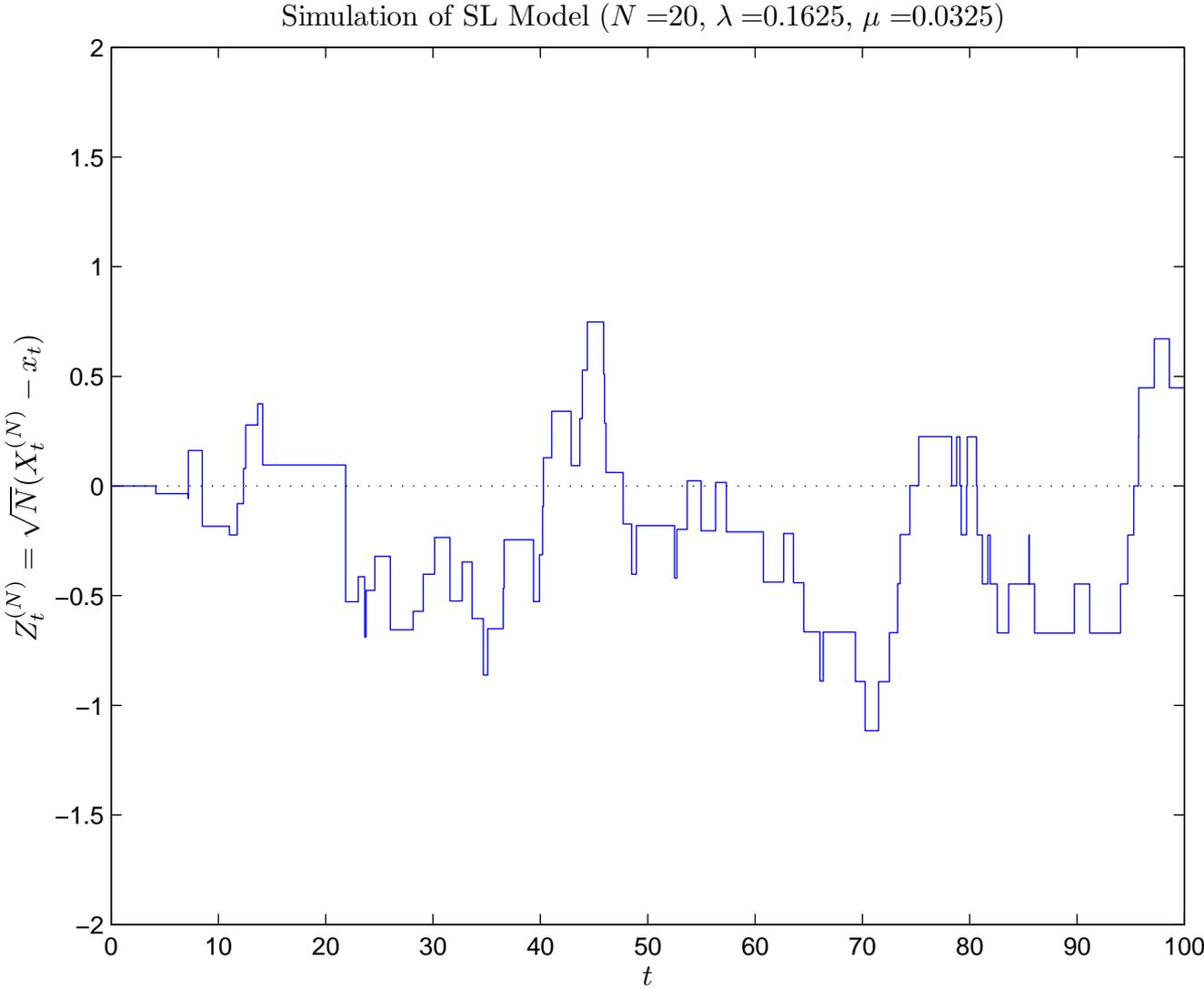
In a later paper Kurtz* proved a *functional central limit law* which establishes that, for large N , the fluctuations about the deterministic trajectory follow a *Gaussian diffusion*, provided that some mild extra conditions are satisfied.

He considered the family of processes $\{(Z_t^{(N)})\}$ defined by

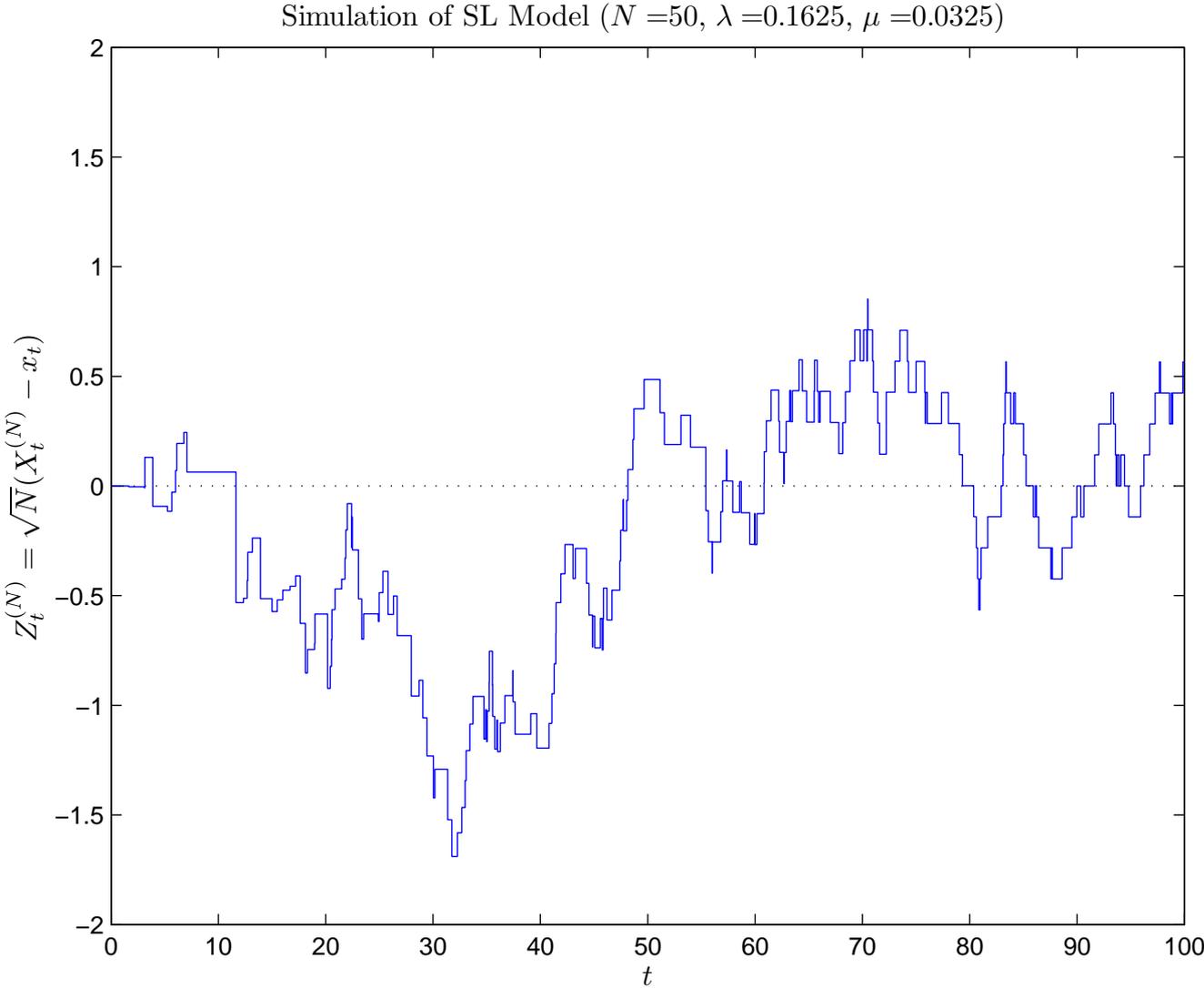
$$Z_s^{(N)} = \sqrt{N} (X_s^{(N)} - x_s), \quad 0 \leq s \leq t.$$

*Kurtz, T. (1971) Limit theorems for sequences of jump Markov processes approximating ordinary differential processes. *J. Appl. Probab.* 8, 344–356.

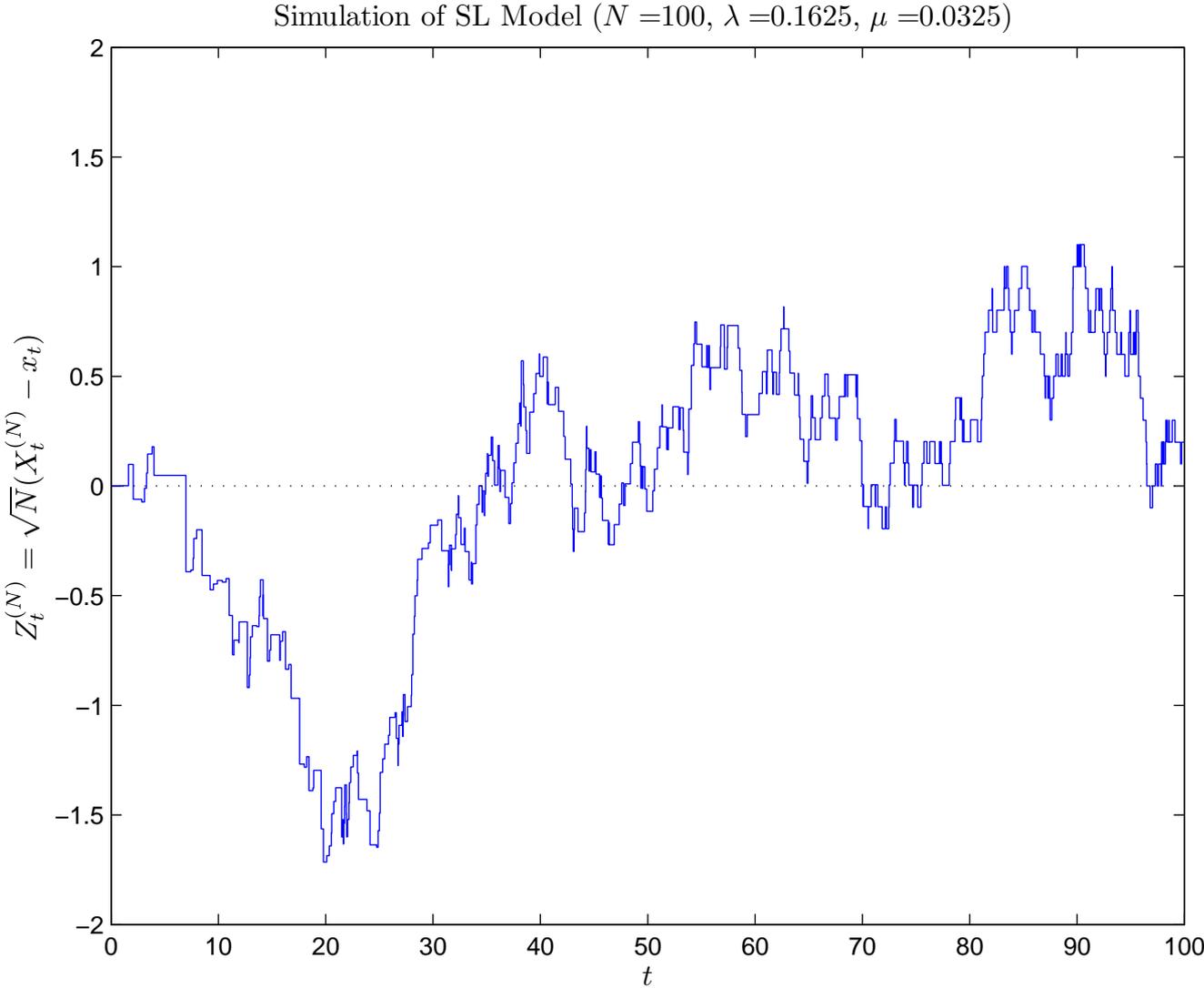
The SL model ($N = 20$)



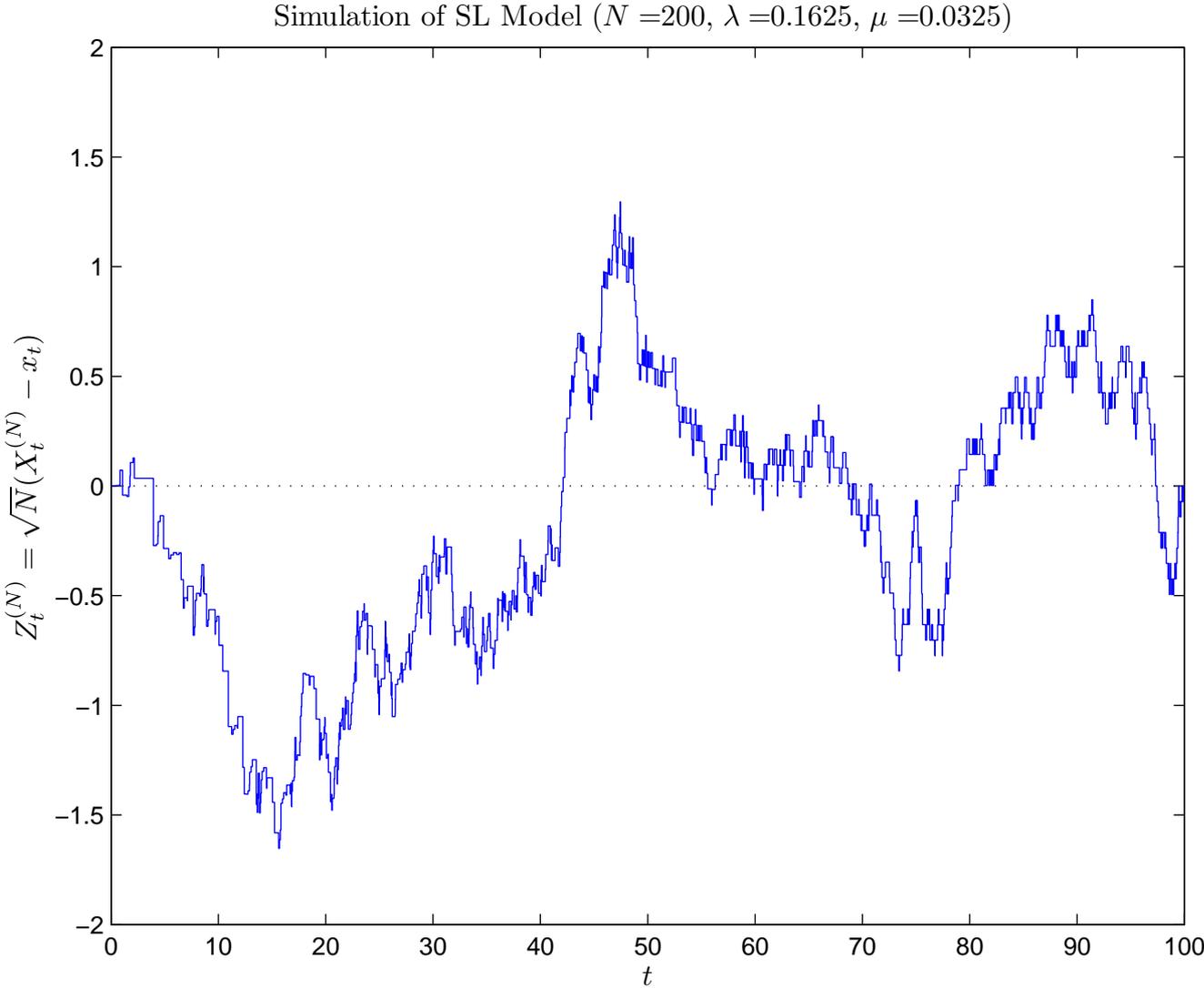
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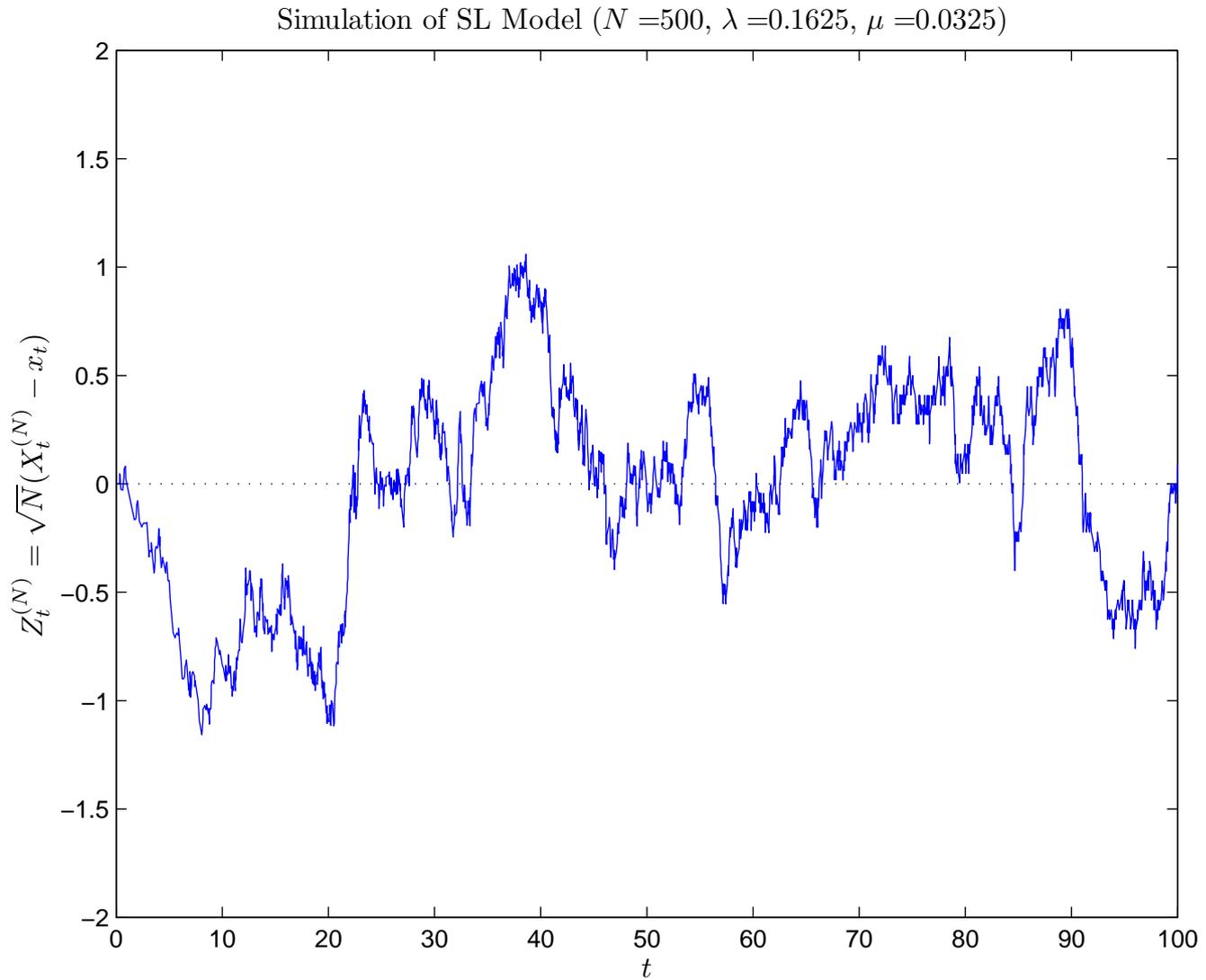
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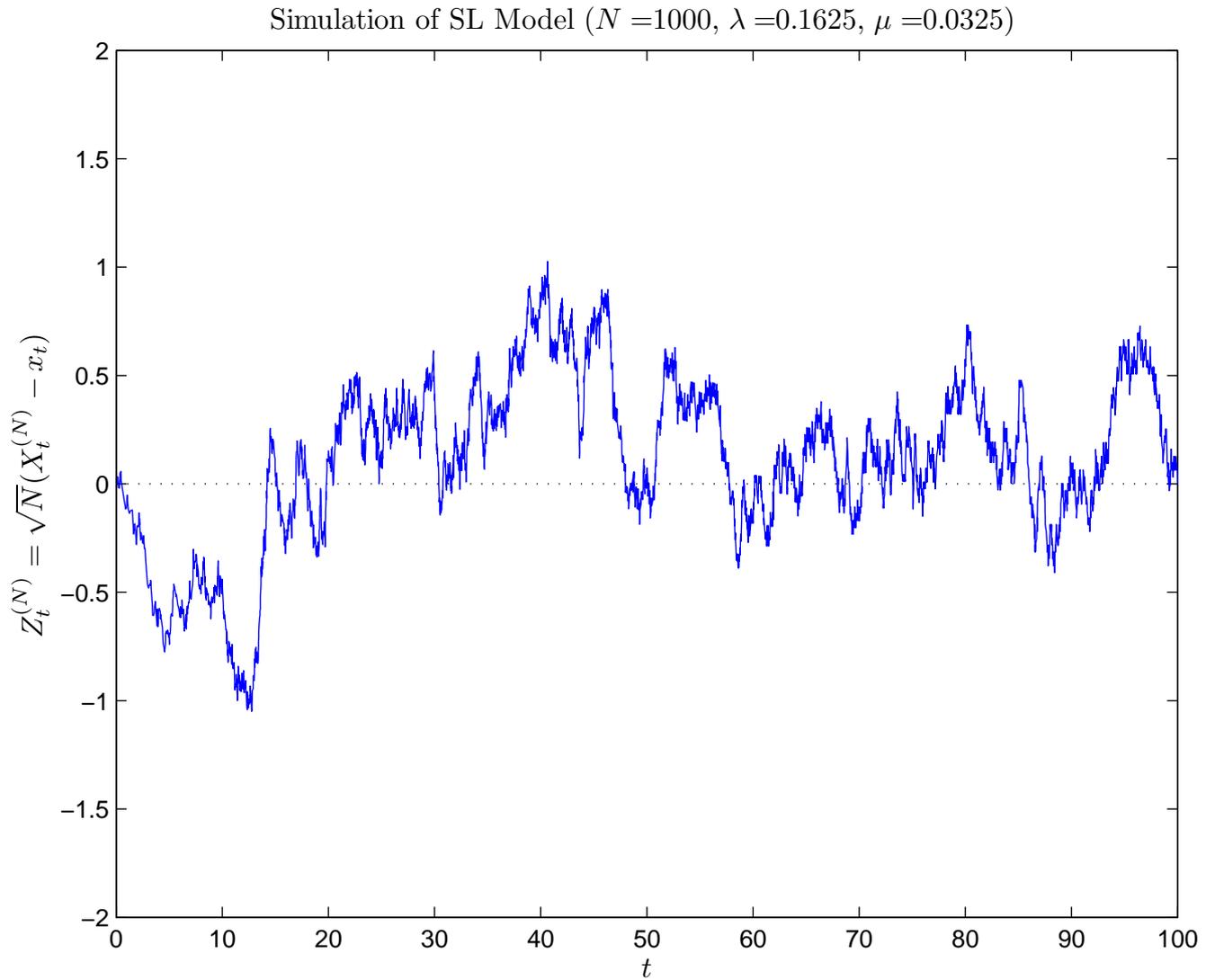
The SL model ($N = 200$)



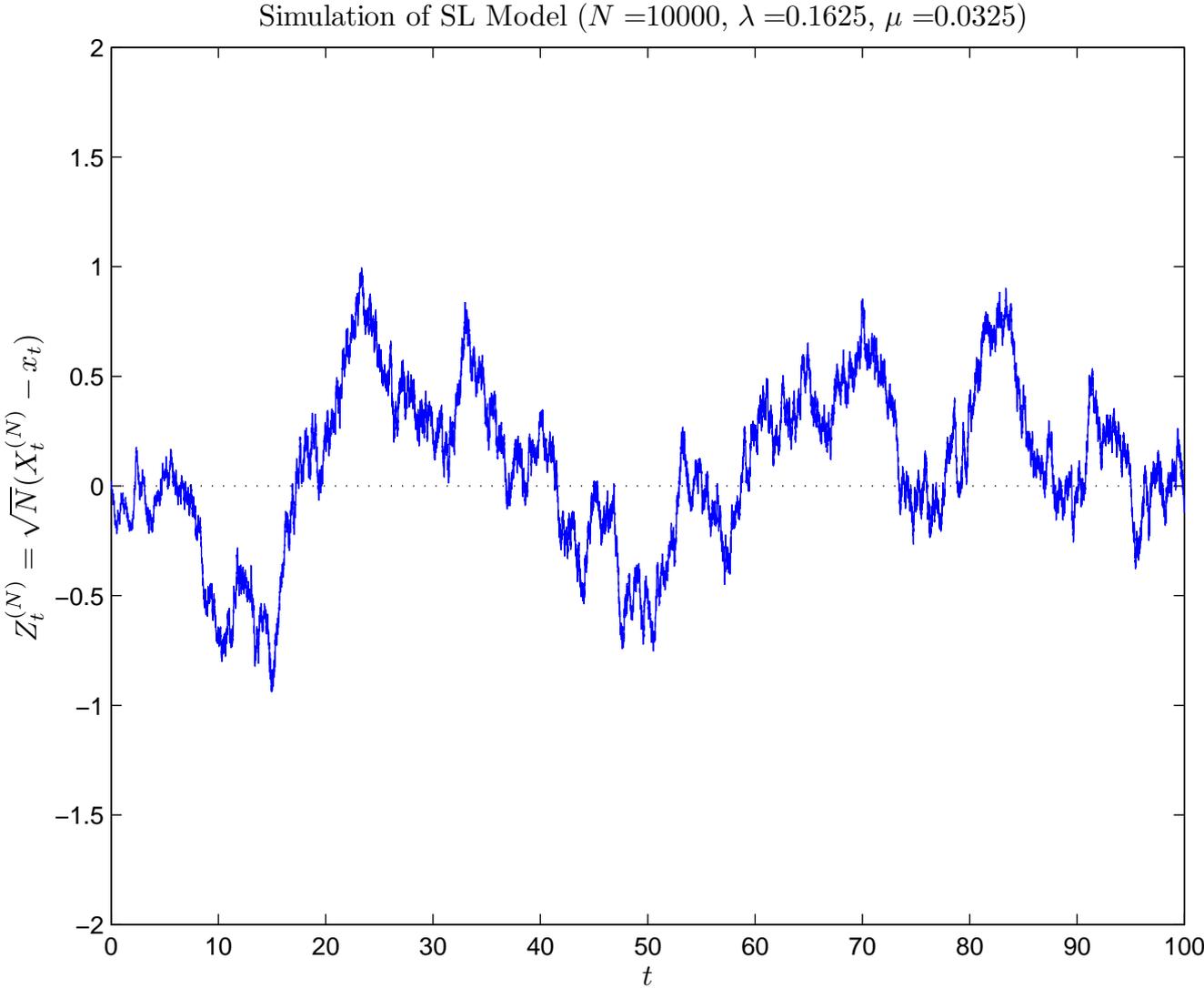
The SL model ($N = 500$)



The SL model ($N = 1000$)

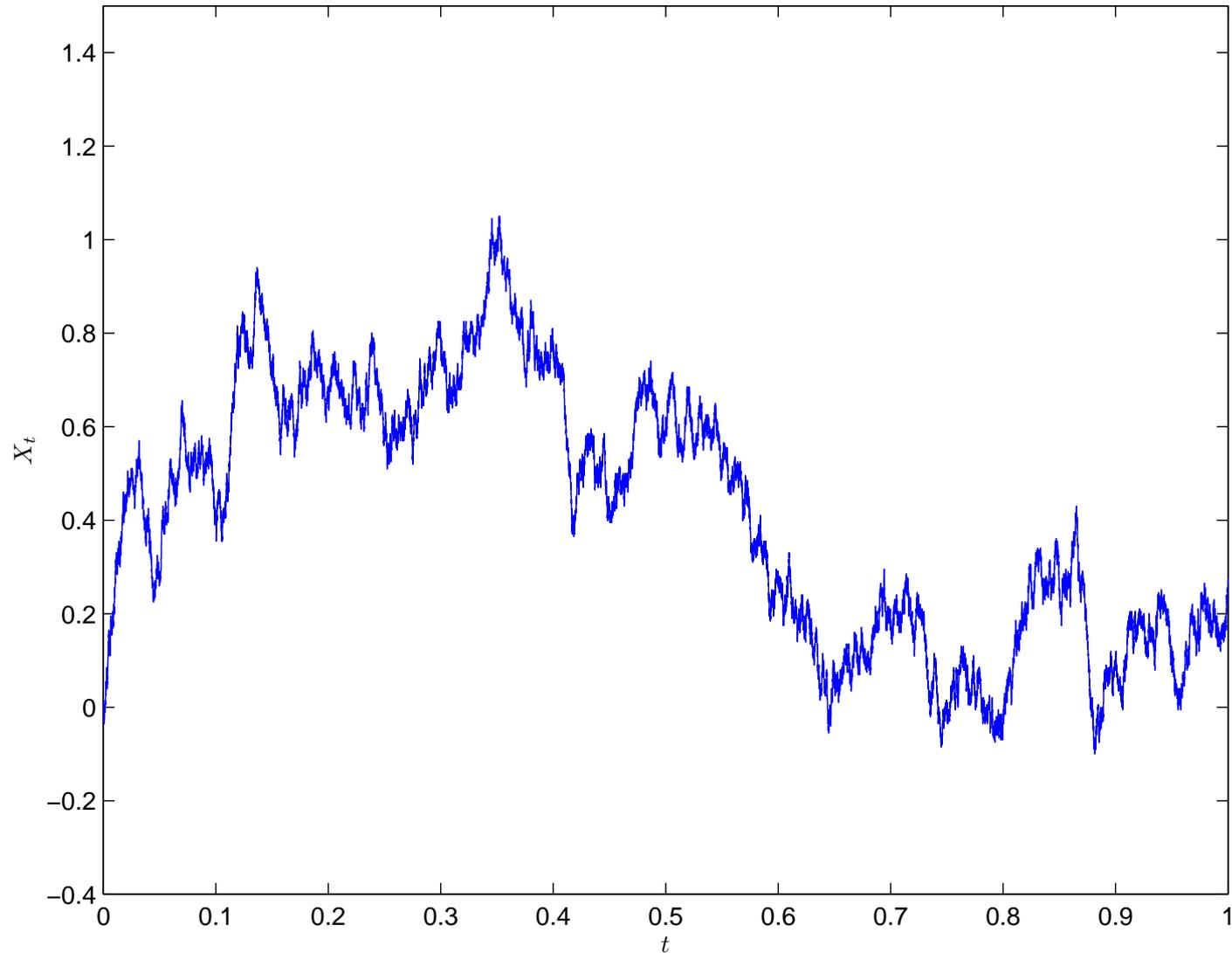


The SL model ($N = 10\,000$)

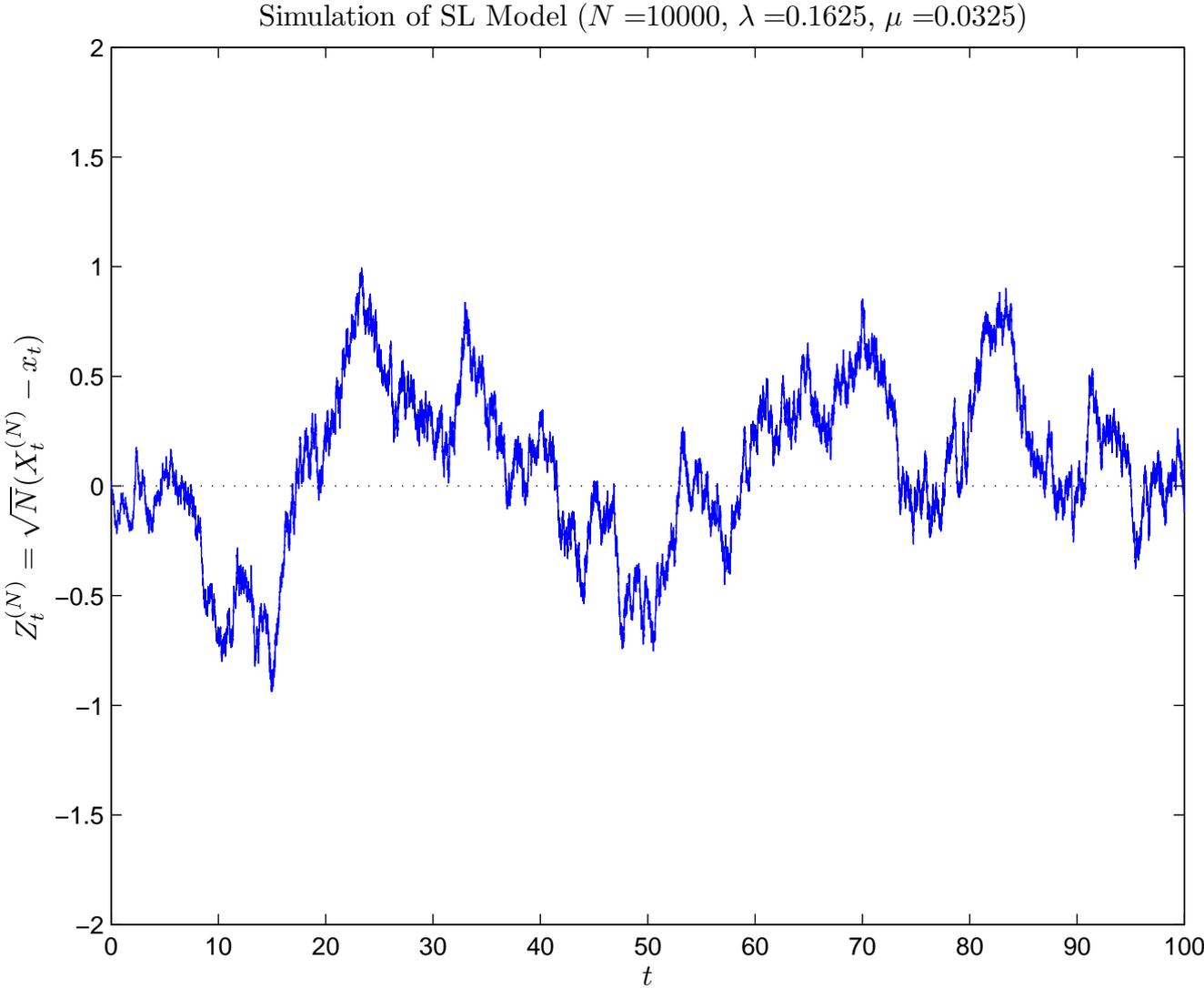


Recapitulation - Brownian motion

Random walk simulation: $h = 2.5e-005$, $\Delta = 0.005$



The SL model ($N = 10\,000$)



A central limit law

Theorem Suppose that F is Lipschitz and has uniformly continuous first derivative on E , and that the $k \times k$ matrix $G(x)$, defined for $x \in E$ by $G_{ij}(x) = \sum_{l \neq 0} l_i l_j f_l(x)$, is uniformly continuous on E .

Let (x_t) be the unique deterministic trajectory starting at x_0 and suppose that $\lim_{N \rightarrow \infty} \sqrt{N} (X_0^{(N)} - x_0) = z$.

Then, $\{(Z_t^{(N)})\}$ converges weakly in $D[0, t]$ (the space of right-continuous, left-hand limits functions on $[0, t]$) to a Gaussian diffusion (Z_t) with initial value $Z_0 = z$ and with mean and covariance given by $\mu_s := \mathbb{E}(Z_s) = M_s z$, where $M_s = \exp(\int_0^s B_u du)$ and $B_s = \partial F(x_s)$, and

$$V_s := \text{Cov}(Z_s) = M_s \left(\int_0^s M_u^{-1} G(x_u) (M_u^{-1})^T du \right) M_s^T .$$

A central limit law

The functional central limit theorem tells us that, for large N , the scaled density process $Z_t^{(N)}$ can be approximated *over finite time intervals* by the Gaussian diffusion (Z_t) .

In particular, for all $t > 0$, $X_t^{(N)}$ has an approximate normal distribution with $\text{Cov}(X_t^{(N)}) \simeq V_t/N$.

We would usually take $x_0 = X_0^{(N)}$, thus giving $\mathbb{E}(X_t^{(N)}) \simeq x_t$.

A central limit law

For the SL model we have $F(x) = \lambda x(1 - \rho - x)$, and the solution to $dx/dt = F(x)$ is

$$x(t) = \frac{(1-\rho)x_0}{x_0 + (1-\rho-x_0)e^{-\lambda(1-\rho)t}}.$$

We also have $F'(x) = \lambda(1 - \rho - 2x)$ and

$$G(x) = \sum_l l^2 f_l(x) = \lambda x(1 + \rho - x) = F(x) + 2\mu x,$$

giving

$$M_t = \exp\left(\int_0^t F'(x_s) ds\right) = \frac{(1-\rho)^2 e^{-\lambda(1-\rho)t}}{(x_0 + (1-\rho-x_0)e^{-\lambda(1-\rho)t})^2}.$$

We can evaluate

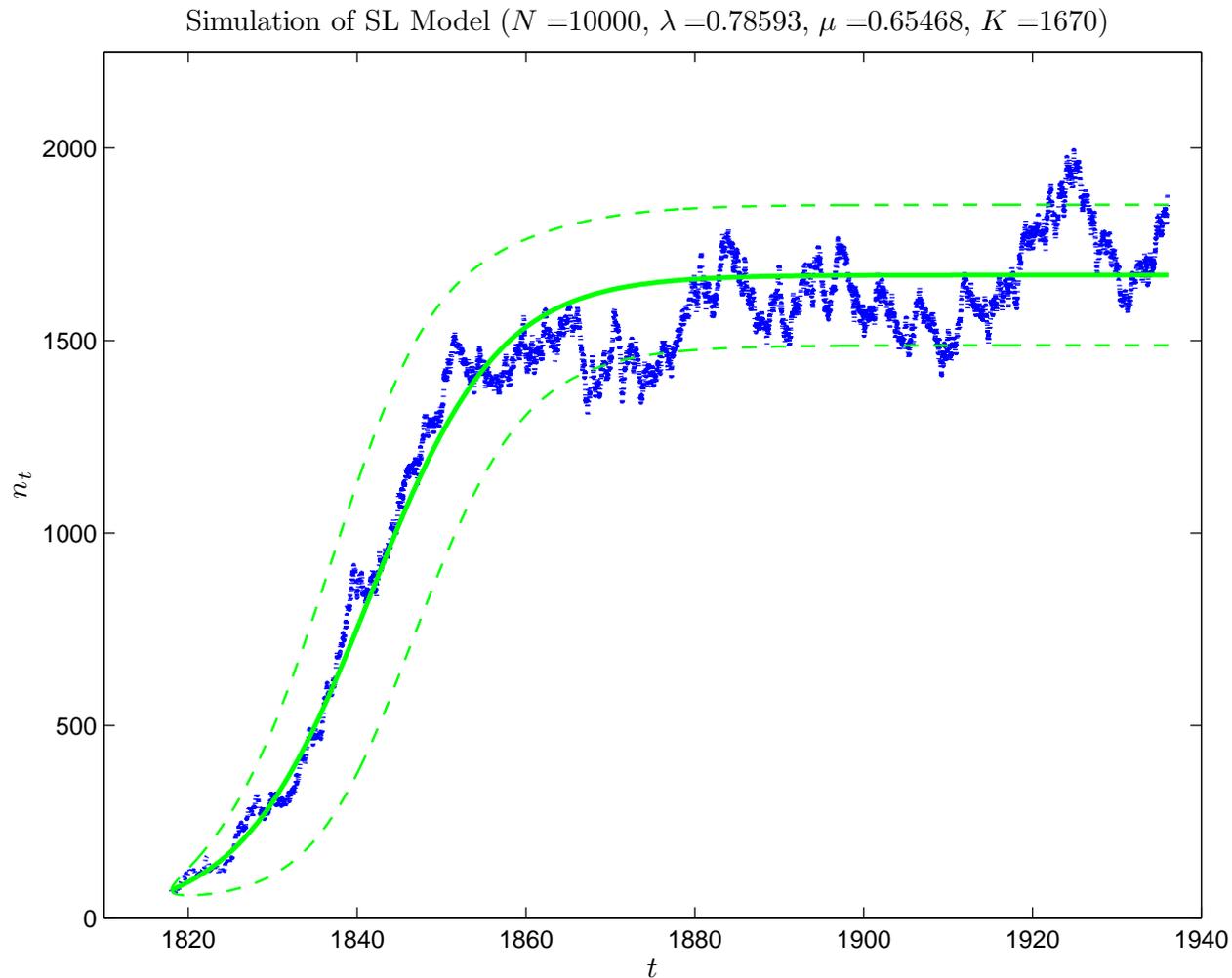
$$V_t := \text{Var}(Z_t) = M_t^2 \left(\int_0^t G(x_s)/M_s^2 ds\right)$$

numerically, or ...

Or ...

$$\begin{aligned} V_t = & x_0 \left(\rho x_0^3 + x_0^2 (1 + 5\rho) (1 - \rho - x_0) e^{-\lambda(1-\rho)t} \right. \\ & + 2x_0 (1 + 2\rho) (1 - \rho - x_0)^2 (\lambda(1 - \rho)t) e^{-2\lambda(1-\rho)t} \\ & - \left. \left((1 - \rho - x_0) [3\rho x_0^2 + (2 + \rho)(1 - \rho)x_0 - ((1 + 2\rho))(1 - \rho)^2] \right. \right. \\ & \quad \left. \left. + \rho(1 - \rho)^3 \right) e^{-2\lambda(1-\rho)t} \right. \\ & \left. - (1 + \rho)(1 - \rho - x_0)^3 e^{-3\lambda(1-\rho)t} \right) / \left(x_0 + (1 - \rho - x_0) e^{-\lambda(1-\rho)t} \right)^4. \end{aligned}$$

The SL model



(Deterministic trajectory plus or minus two standard deviations in green)

The OU approximation

If the initial point x_0 of the deterministic trajectory is chosen to be an equilibrium point of the deterministic model, we can be far more precise about the approximating diffusion.

The OU approximation

Corollary If x_{eq} satisfies $F(x_{\text{eq}}) = 0$, then, under the conditions of the theorem, the family $\{(Z_t^{(N)})\}$, defined by

$$Z_s^{(N)} = \sqrt{N}(X_s^{(N)} - x_{\text{eq}}), \quad 0 \leq s \leq t,$$

converges weakly in $D[0, t]$ to an **OU process** (Z_t) with initial value $Z_0 = z$, local drift matrix $B = \partial F(x_{\text{eq}})$ and local covariance matrix $G(x_{\text{eq}})$. In particular, Z_s is normally distributed with mean and covariance given by $\mu_s := \mathbb{E}(Z_s) = e^{Bs}z$ and

$$V_s := \text{Cov}(Z_s) = \int_0^s e^{Bu} G(x_{\text{eq}}) e^{B^T u} du.$$

The OU approximation

Note that

$$V_s = \int_0^s e^{Bu} G(x_{\text{eq}}) e^{B^T u} du = V_\infty - e^{Bs} V_\infty e^{B^T s},$$

where V_∞ , the stationary covariance matrix, satisfies

$$BV_\infty + V_\infty B^T + G(x_{\text{eq}}) = 0.$$

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We conclude that, for N large, $X_t^{(N)}$ has an approximate Gaussian distribution with

$$\text{Cov}(X_t^{(N)}) \simeq V_t/N.$$

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For the SL model, $\text{Var}(X_t^{(N)}) \simeq \rho(1 - e^{-2\lambda(1-\rho)t})/N.$

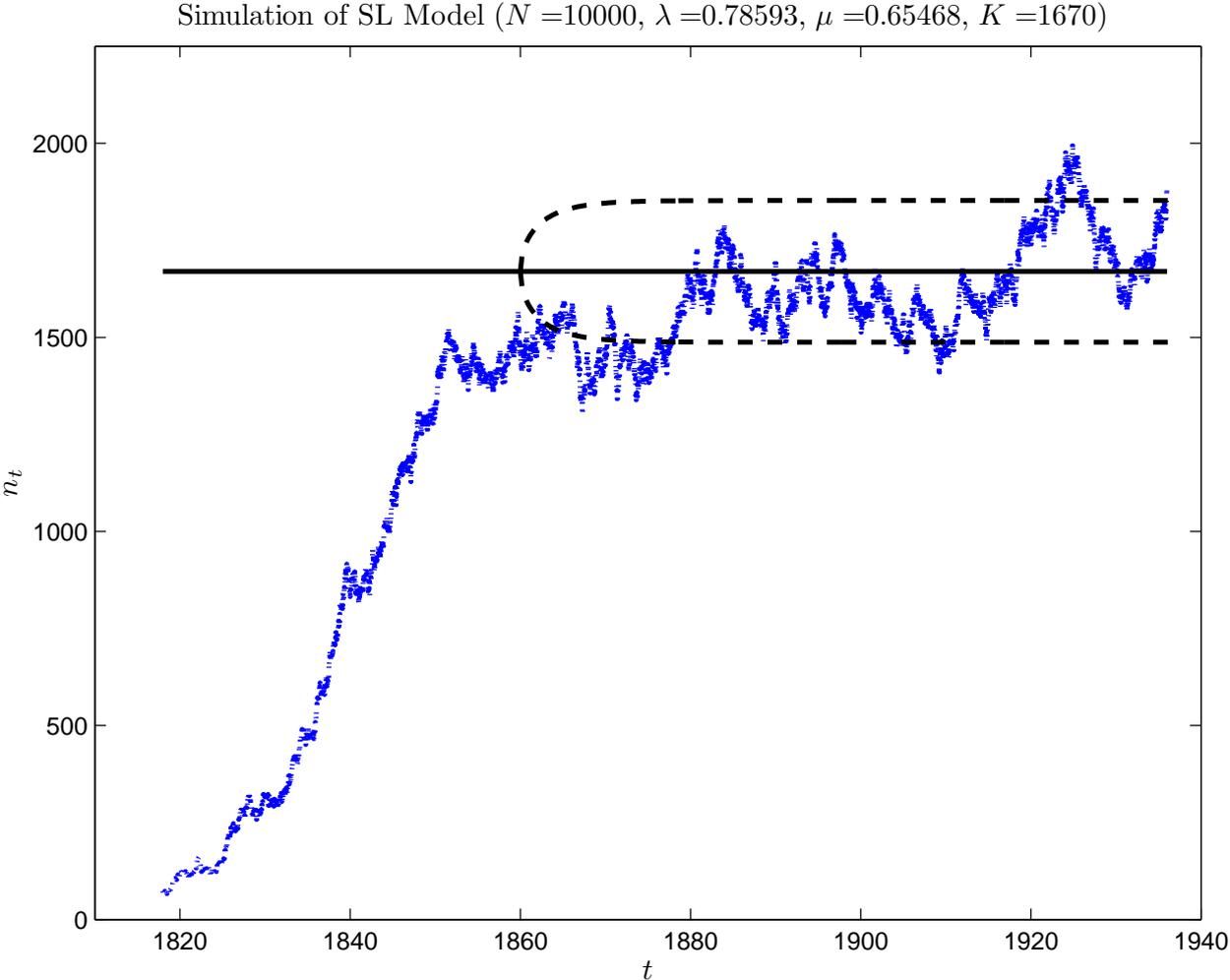
The OU approximation

This brings us “full circle” to the approximating SDE

$$dn_t = -\alpha(n_t - K) dt + \sqrt{2N\alpha\rho} dB_t,$$

where $\alpha = \lambda(1 - \rho)$.

The SL model



(Deterministic equilibrium plus or minus two standard deviations is in black)