Modelling population processes with random initial conditions

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Starting point

A paper by Bonnie Kegan (US Census Bureau Washington DC) and R. Webster West (now at Texas A&M University) ...

B. Kegan and R.W. West (2005) Modeling the simple epidemic with deterministic differential equations and random initial conditions. *Math. Biosci.* 194, 217–231.

A simple epidemic

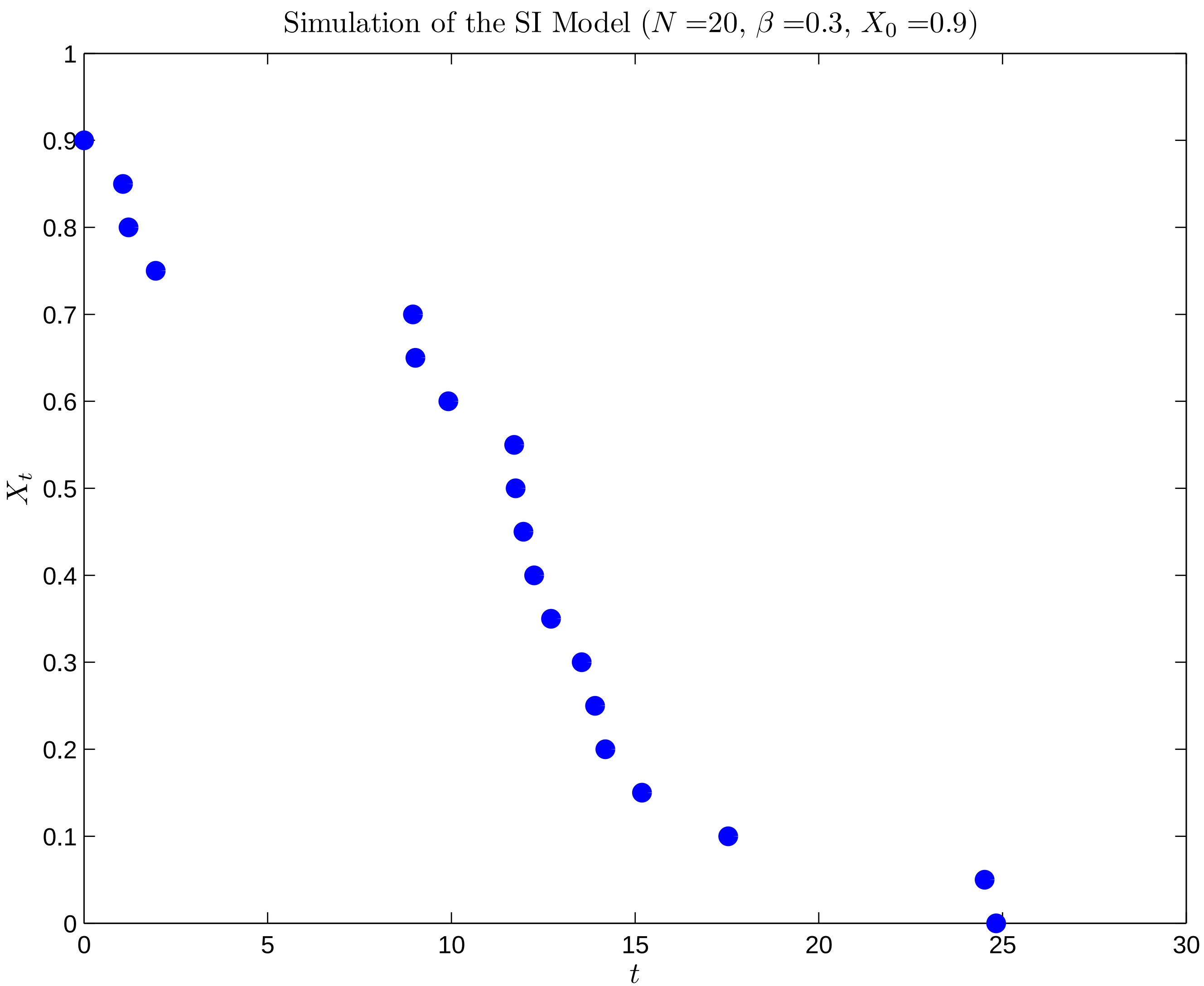
The SI (*Susceptible-Infective*) Model

- N individuals (fixed)
- n_t susceptibles (random process in continuous time)
- $N - n_t$ infectives

Start with a few infectives. Eventually everyone gets the disease. The per-encounter transmission rate β is specified.

Let $X_t = n_t/N$ be the *proportion* of susceptibles.

Proportion of susceptibles



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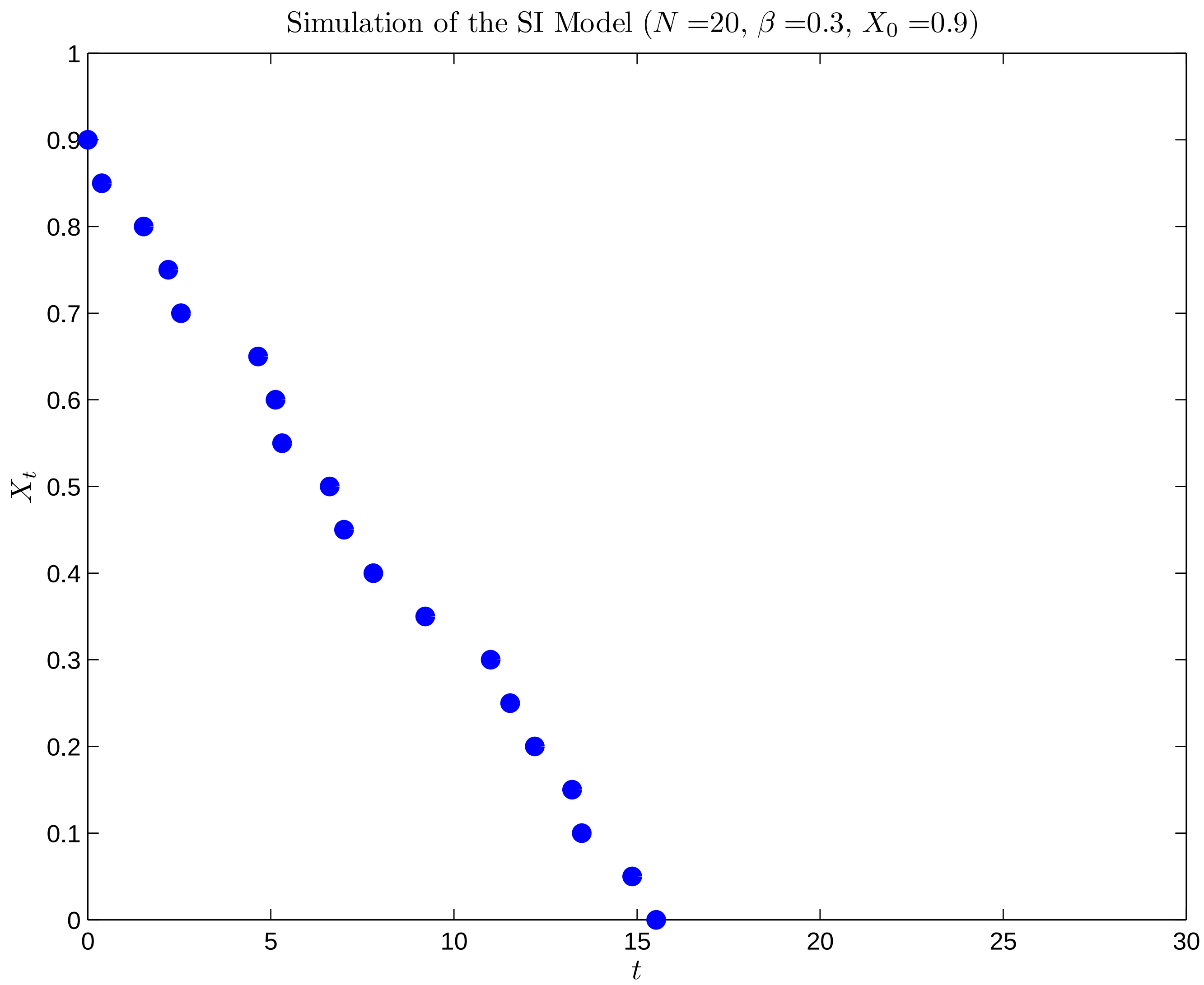

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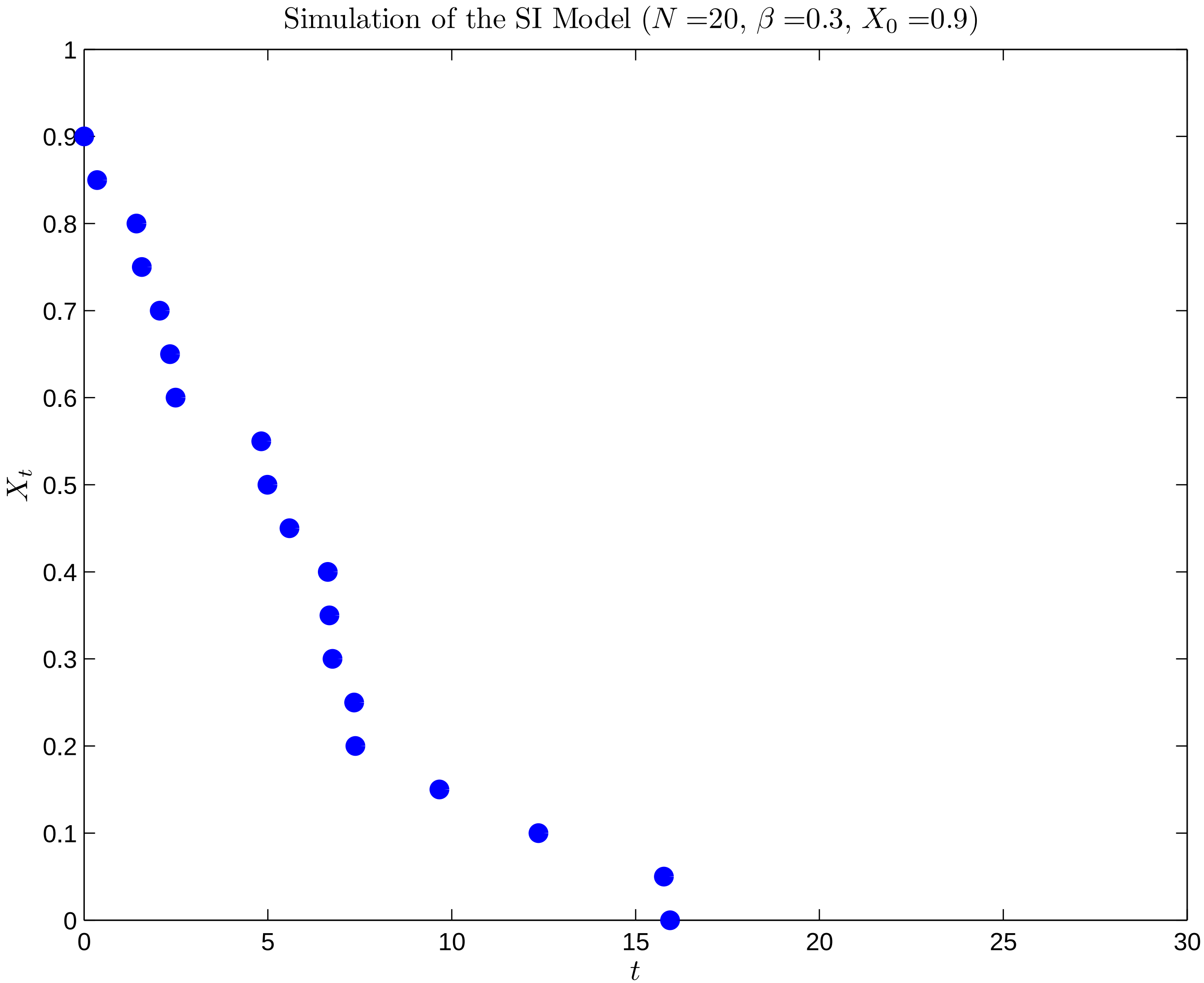

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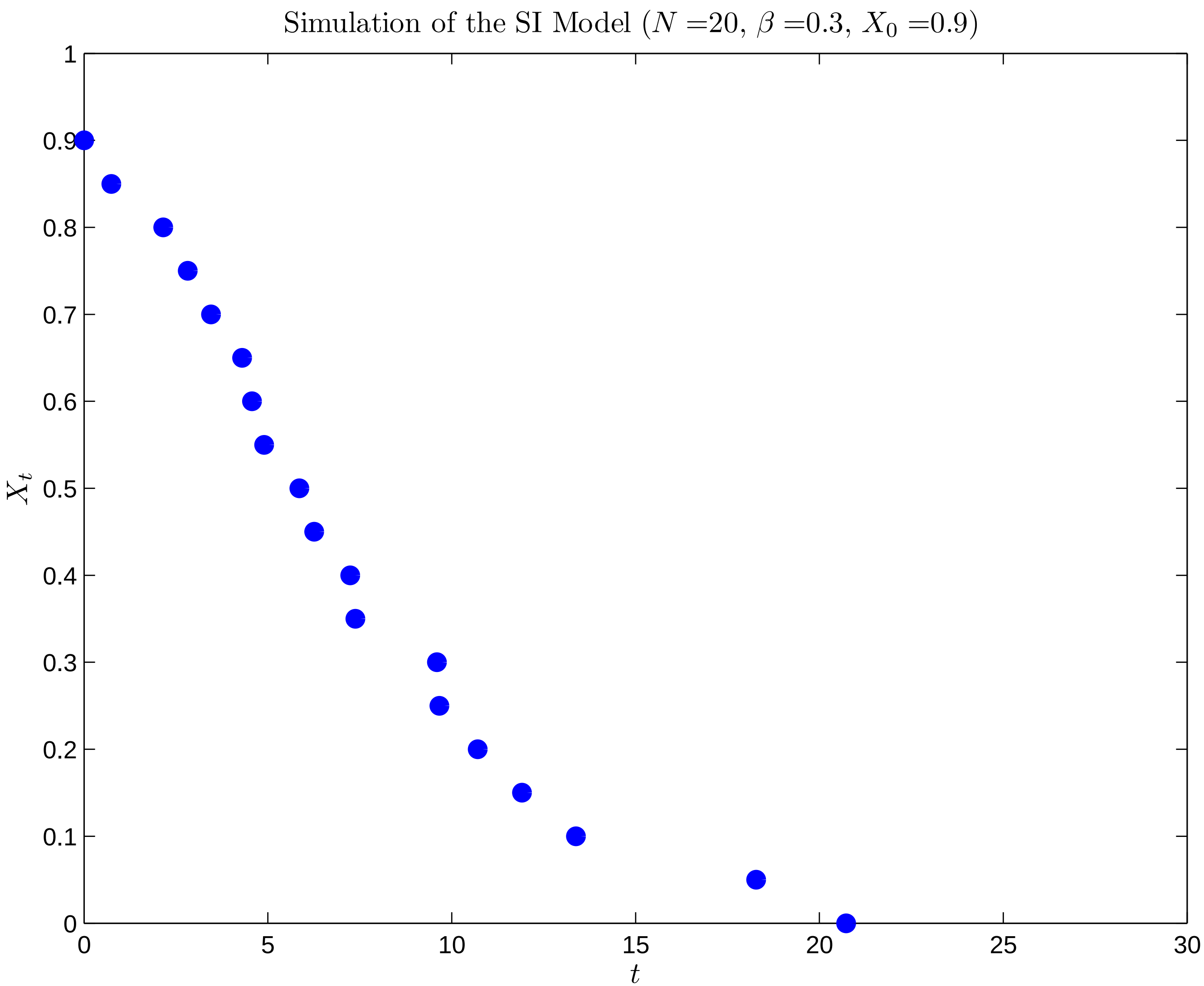

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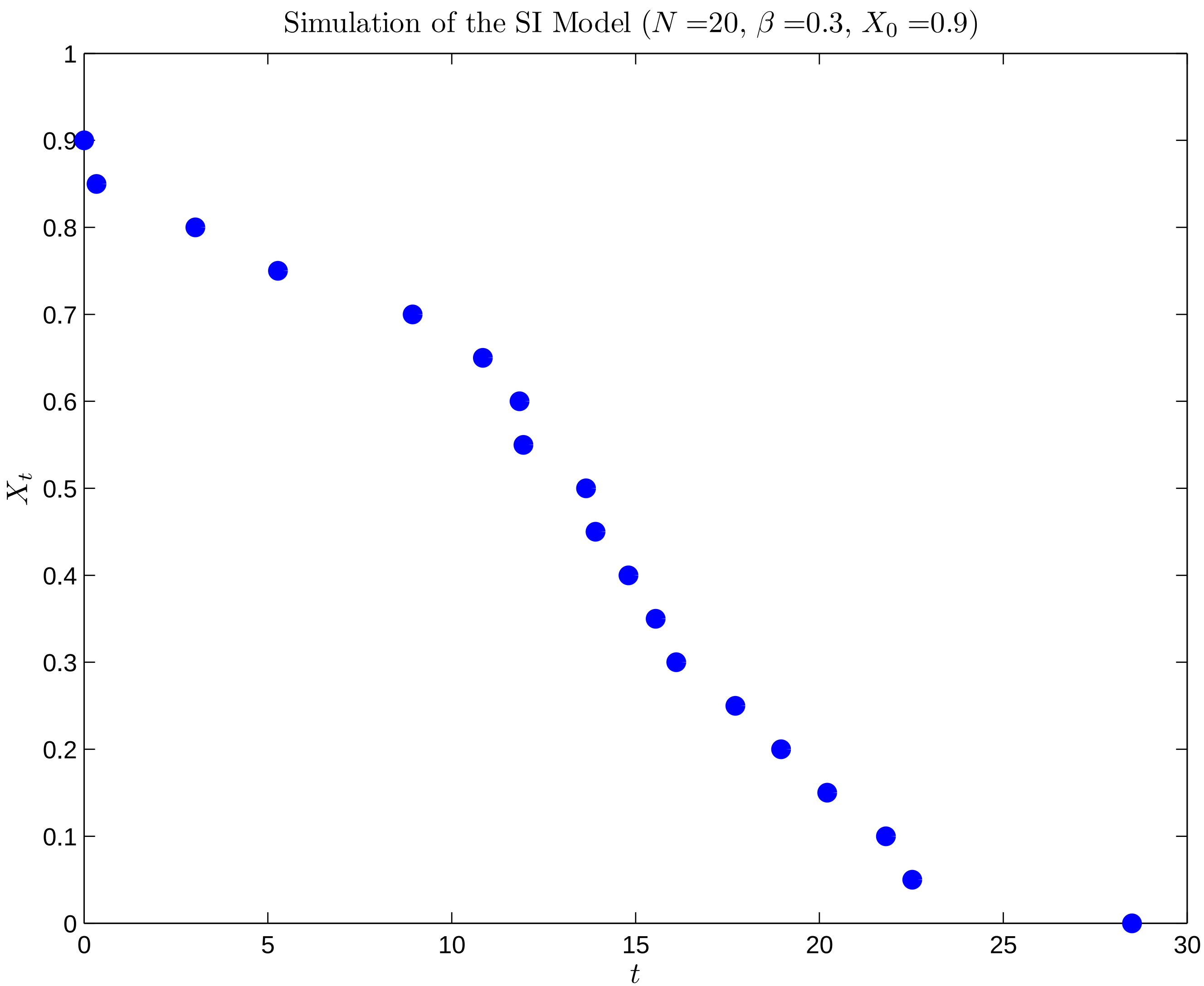

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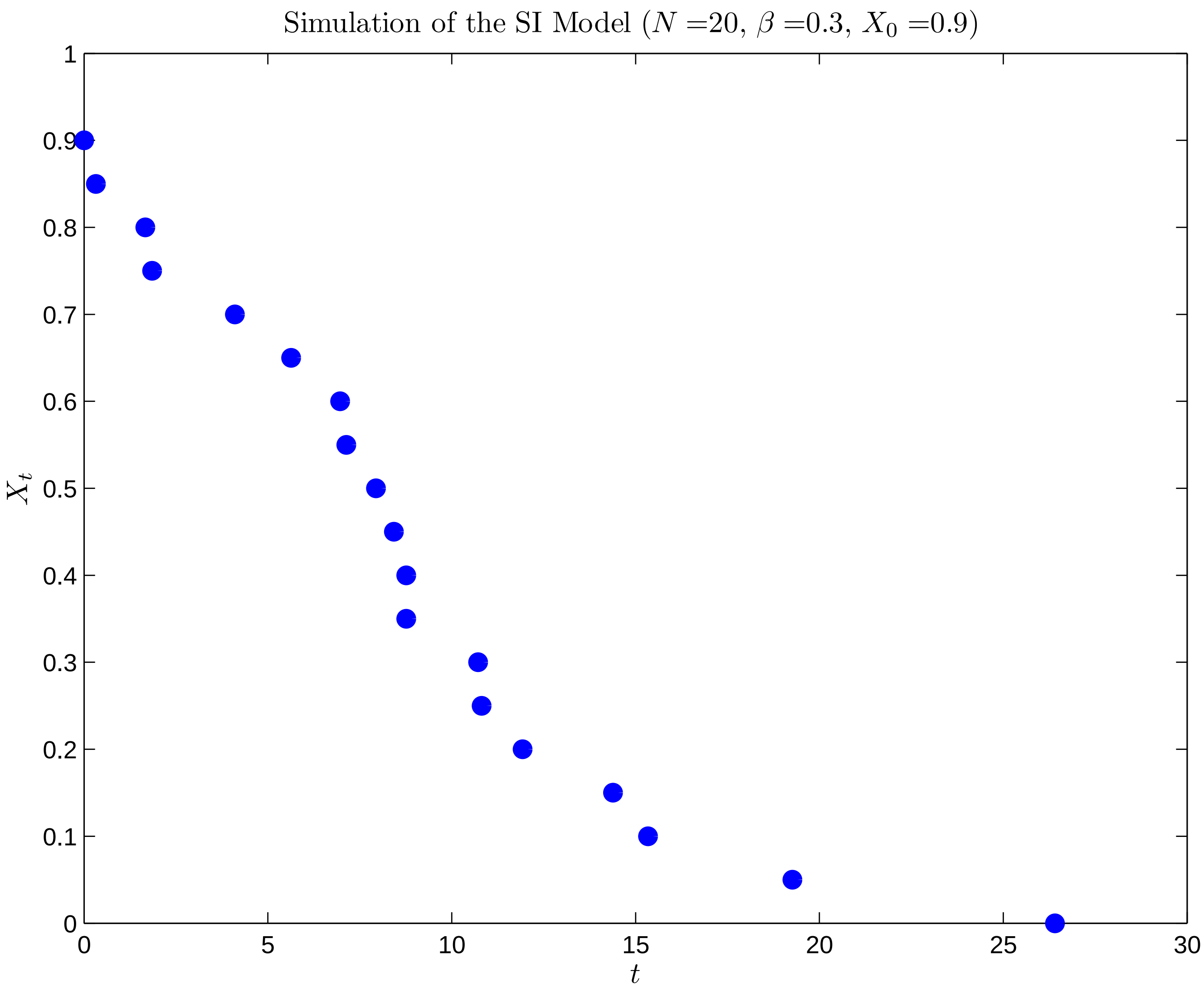
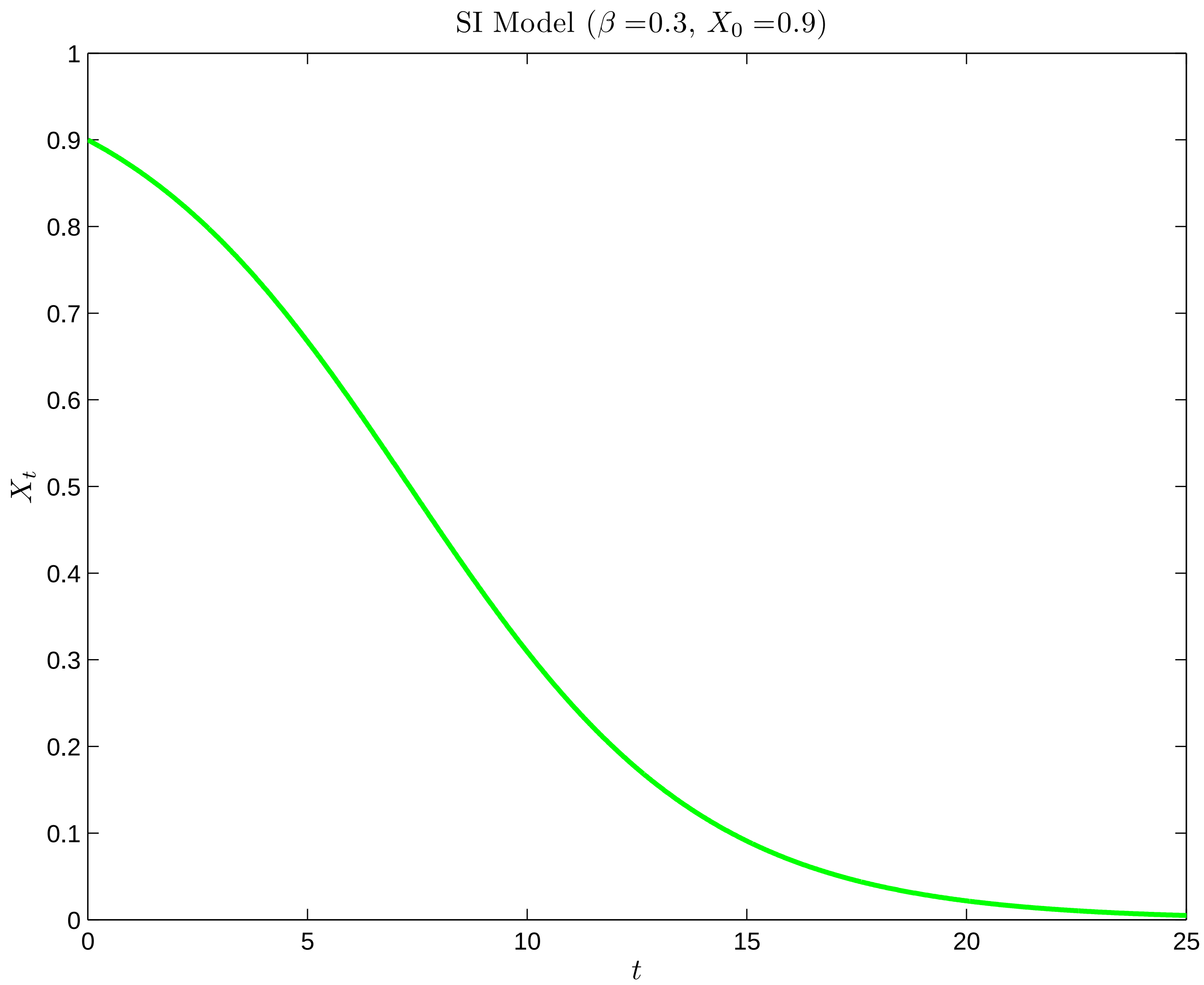


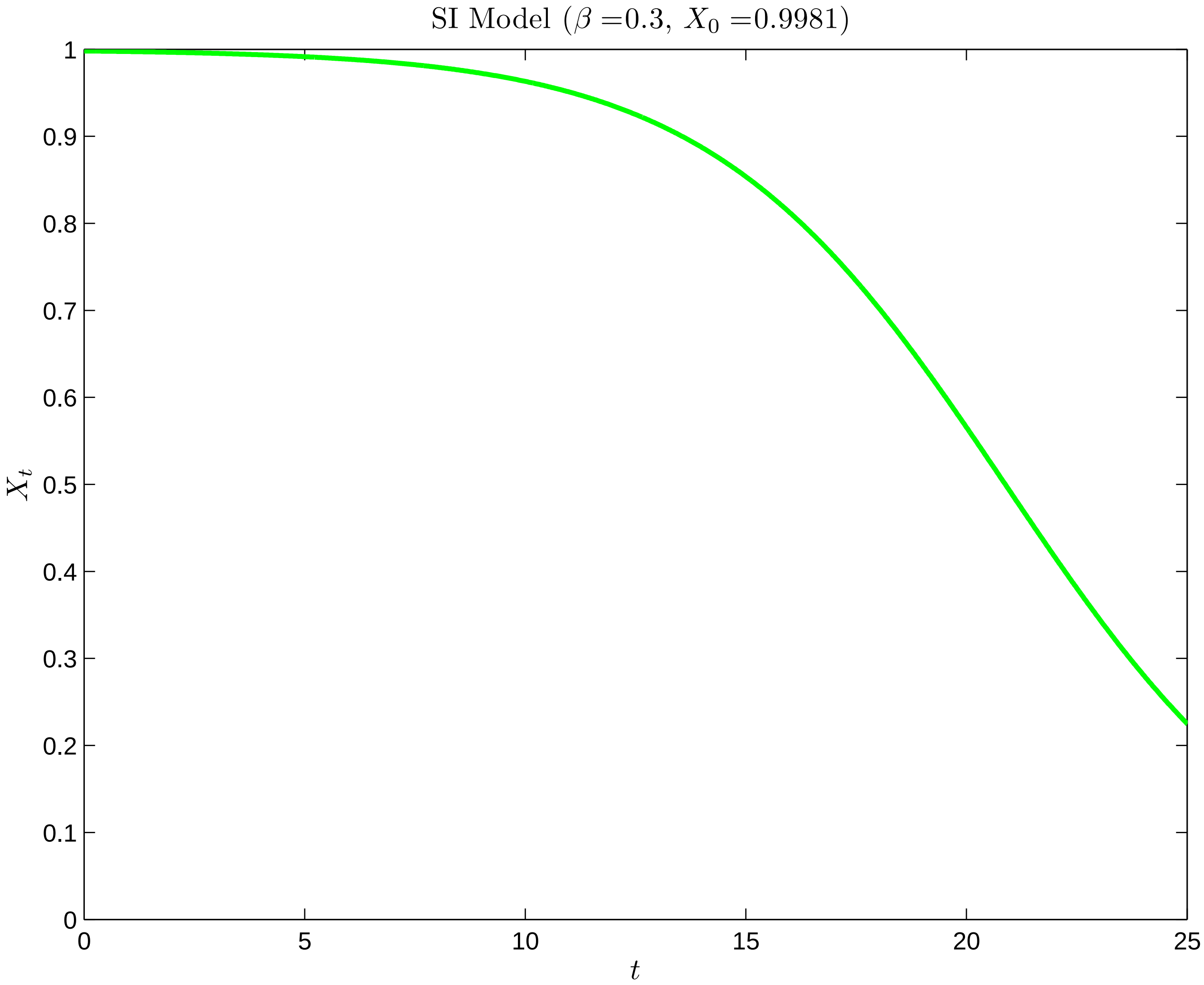
Kegan and West



Kegan and West

- Deterministic dynamics
- Randomness *only* in the initial state

Kegan and West



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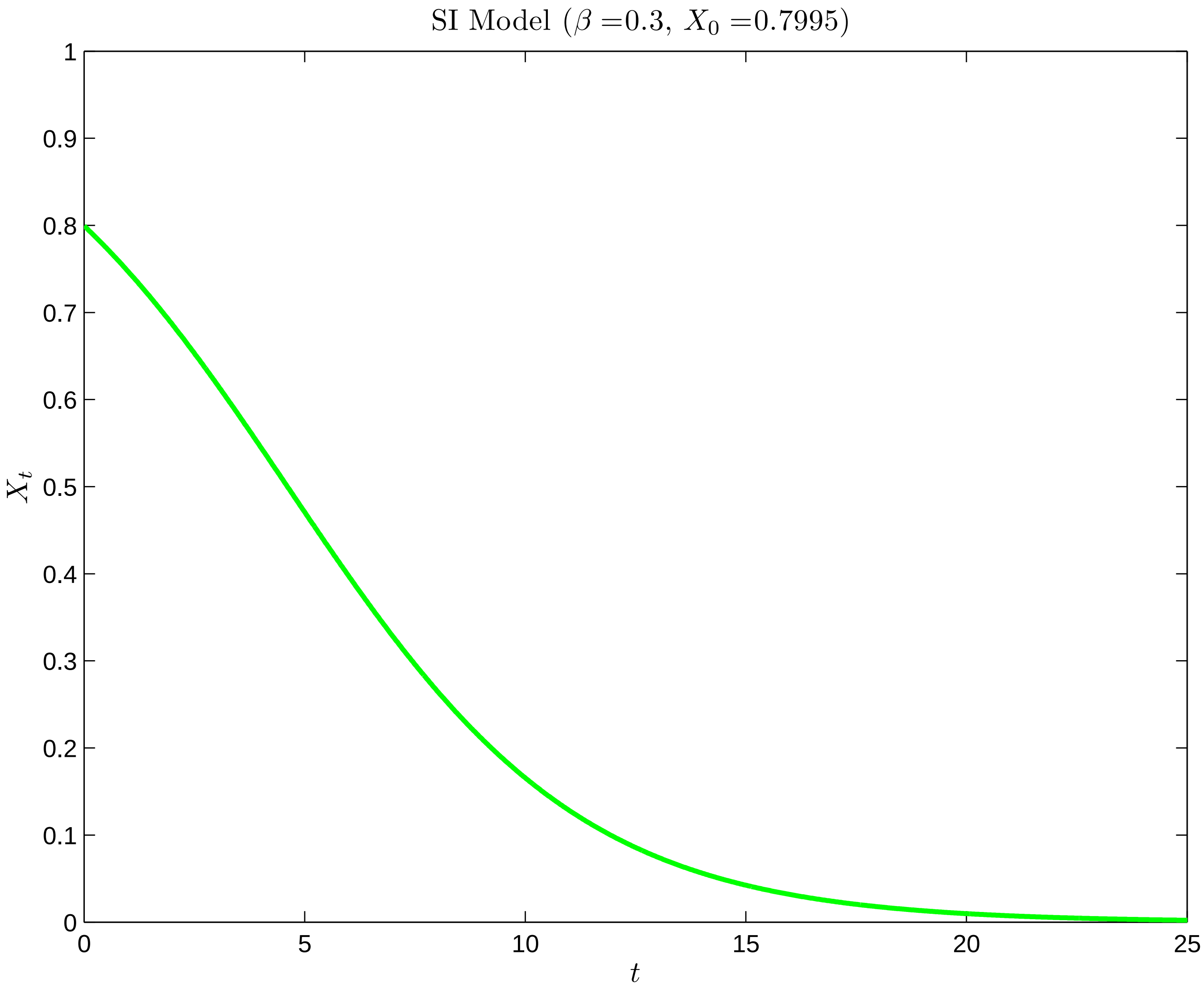

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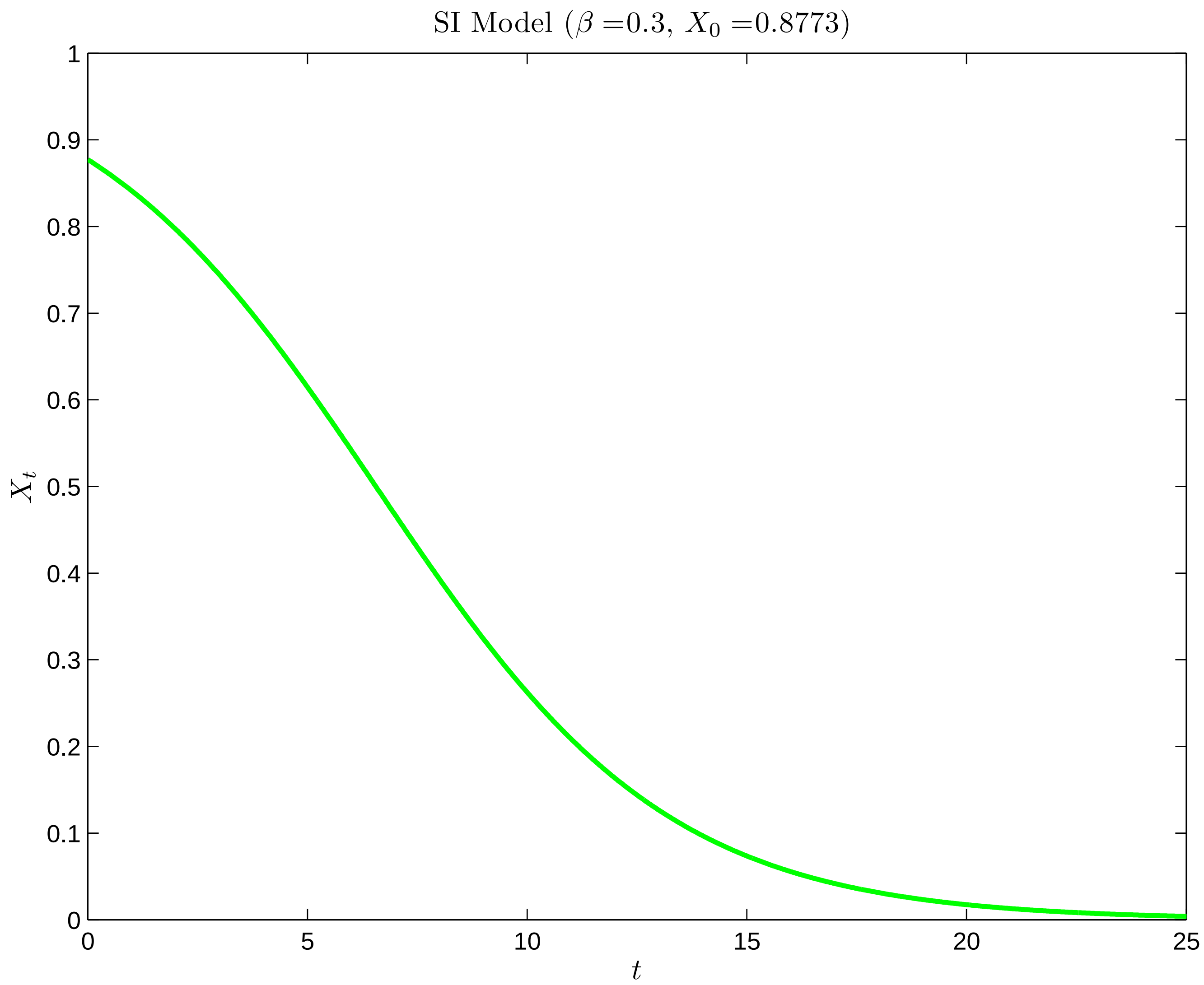

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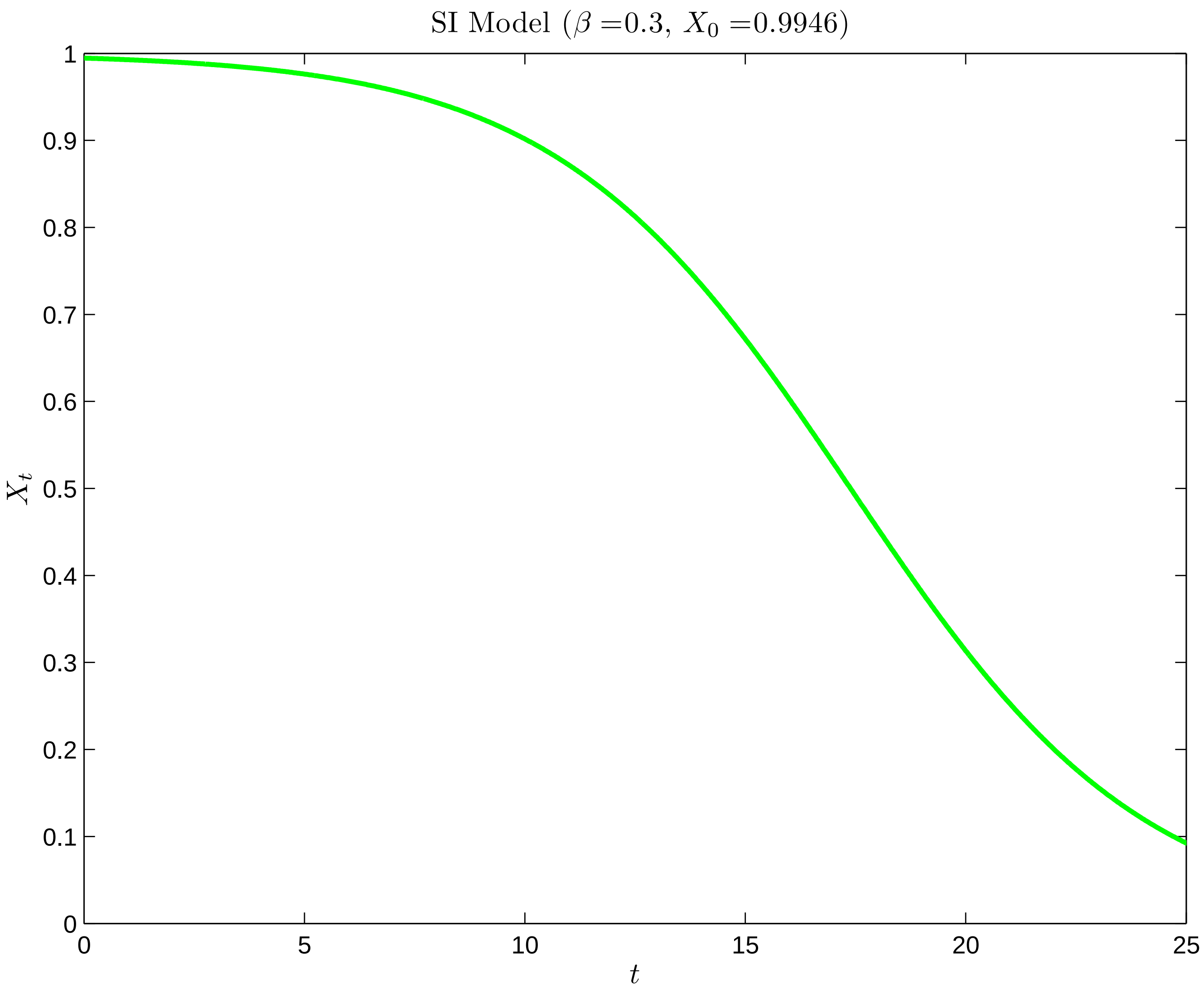

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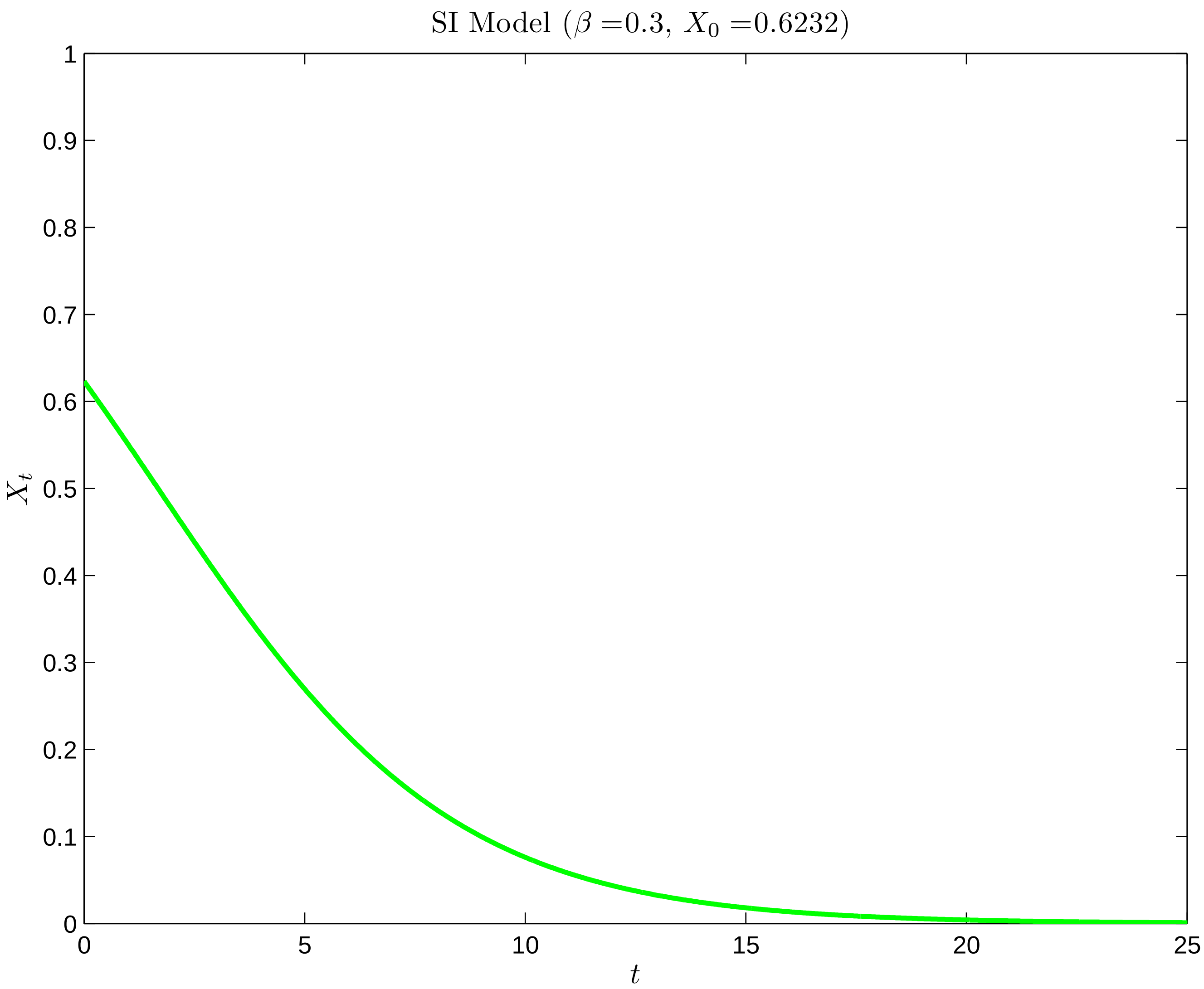

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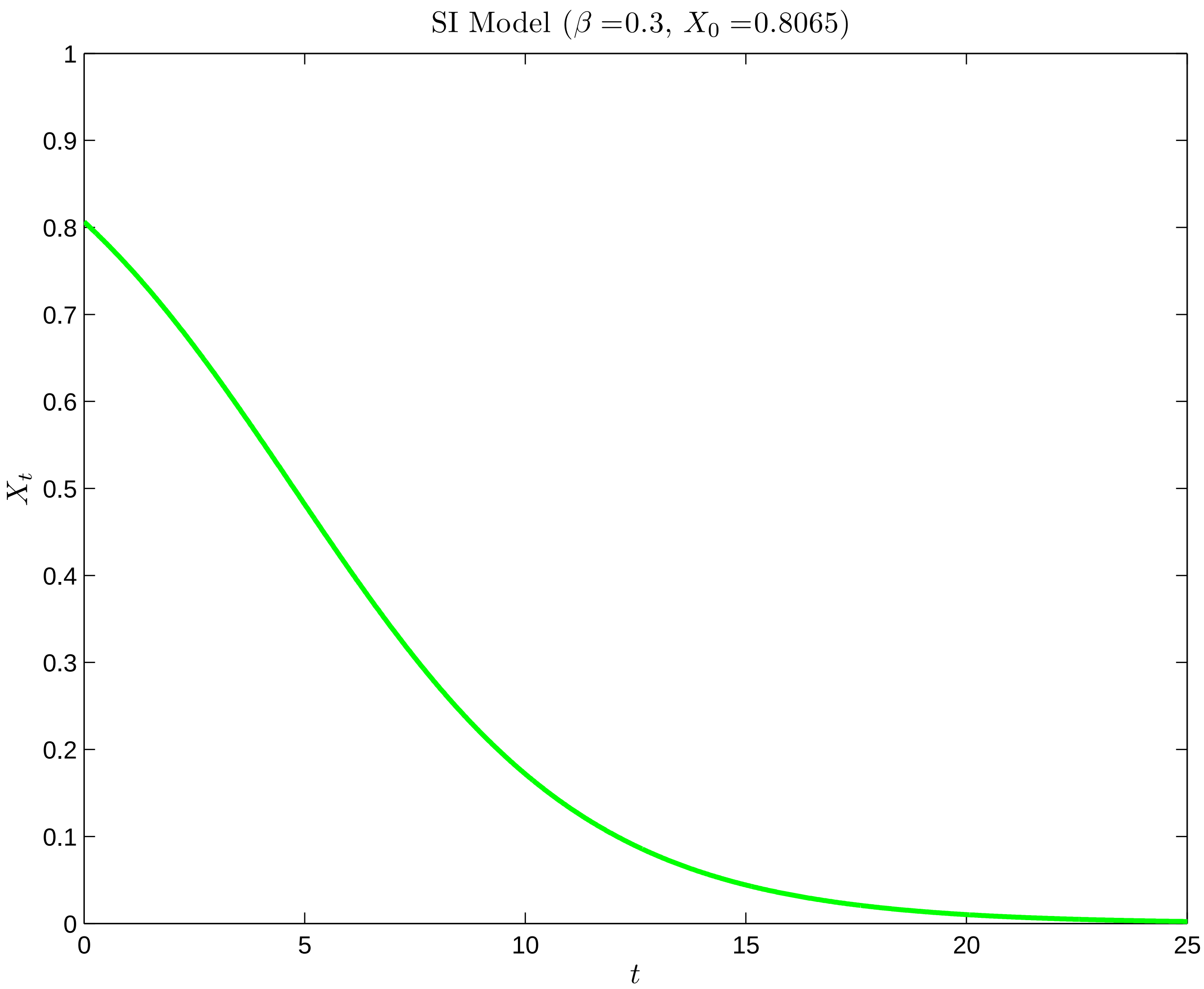

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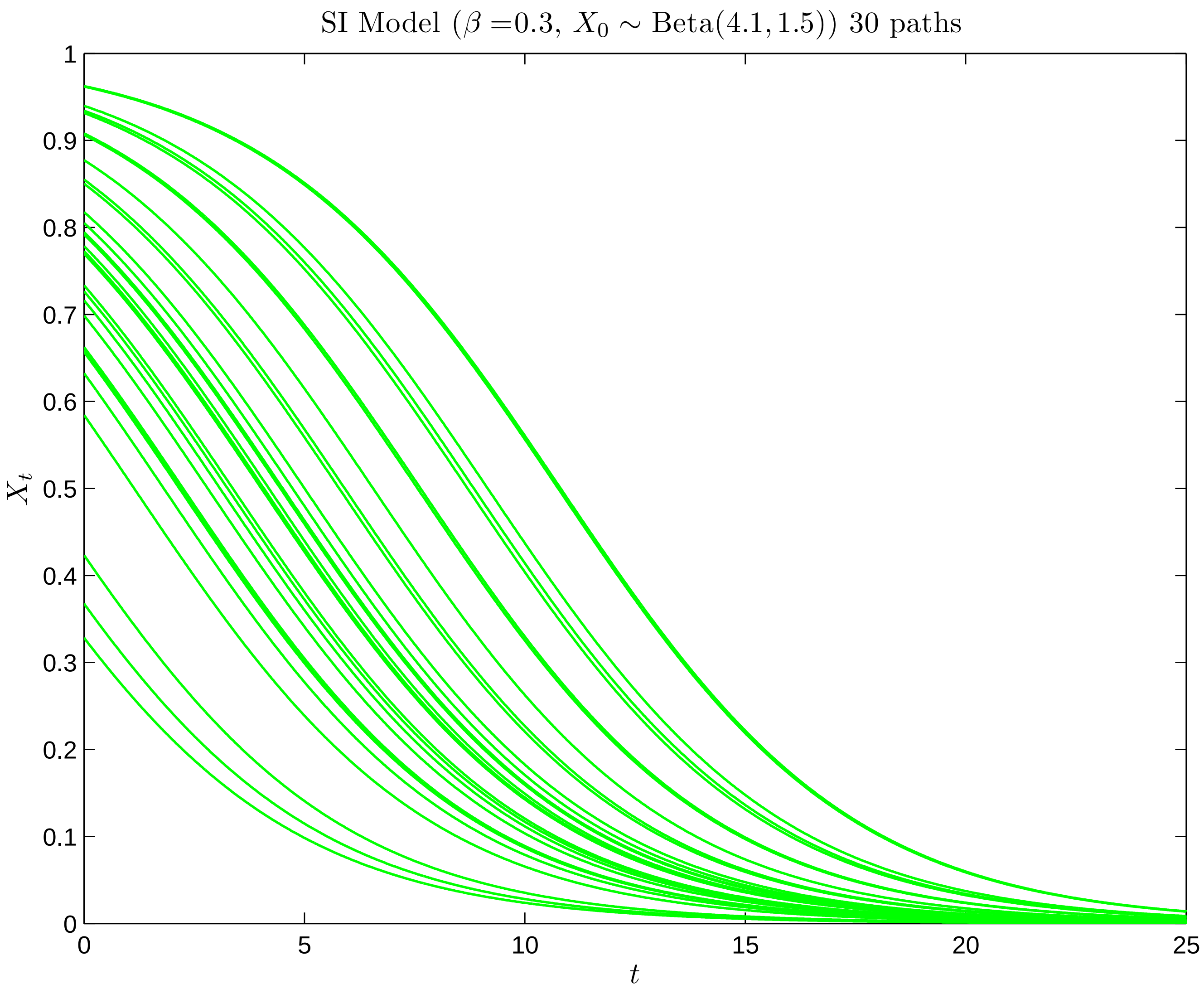
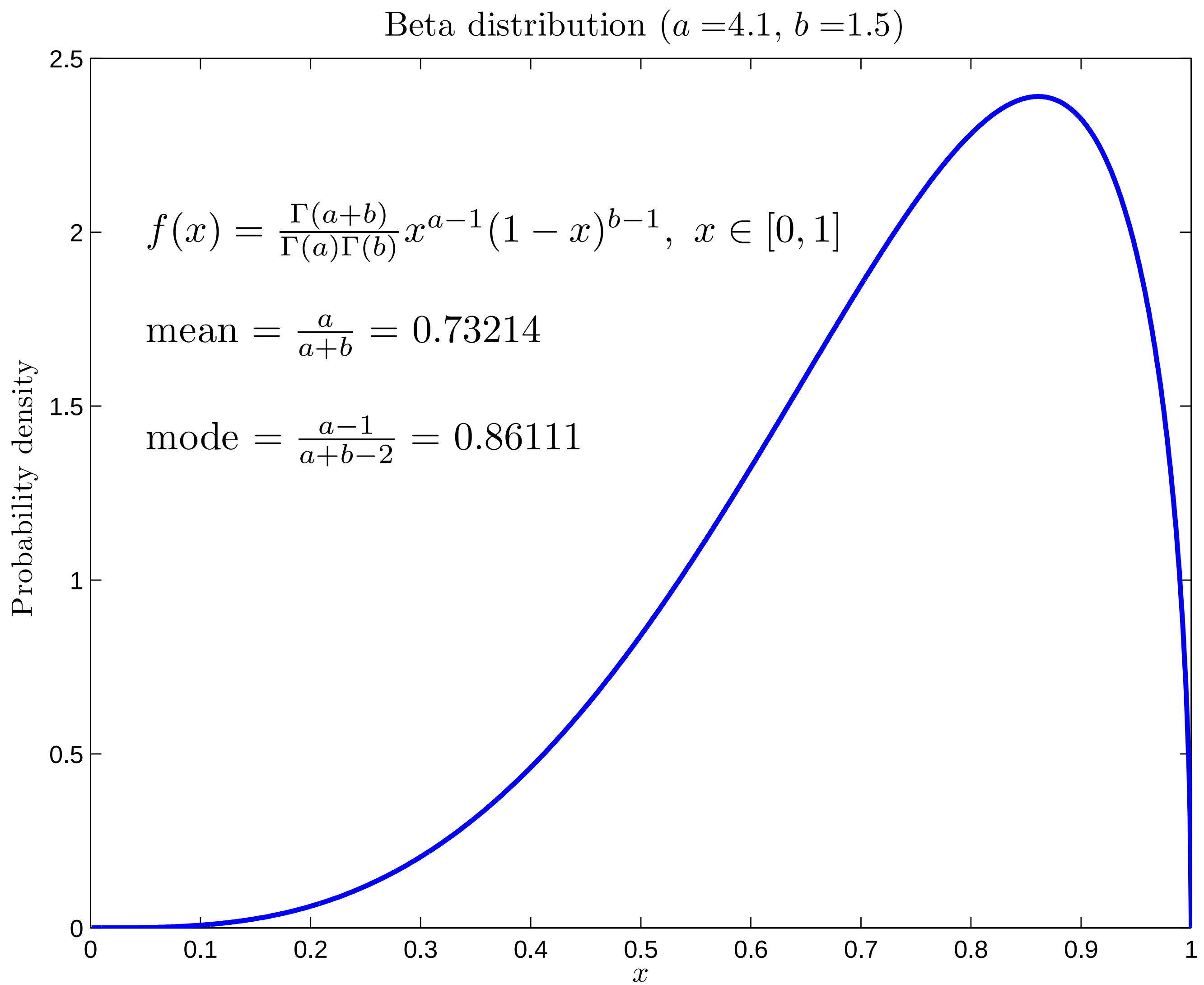
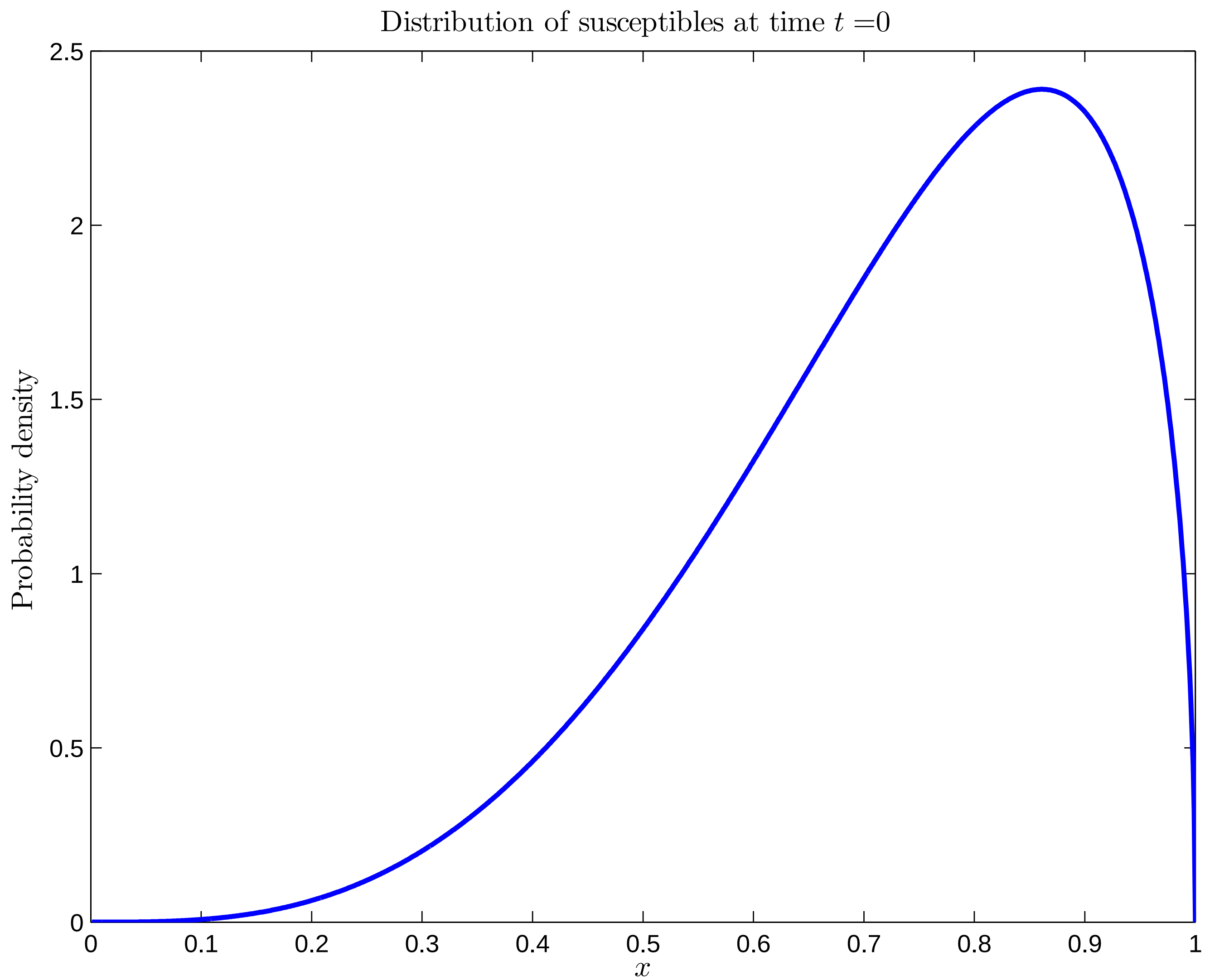


Kegan and West initial distribution



Distribution at time t



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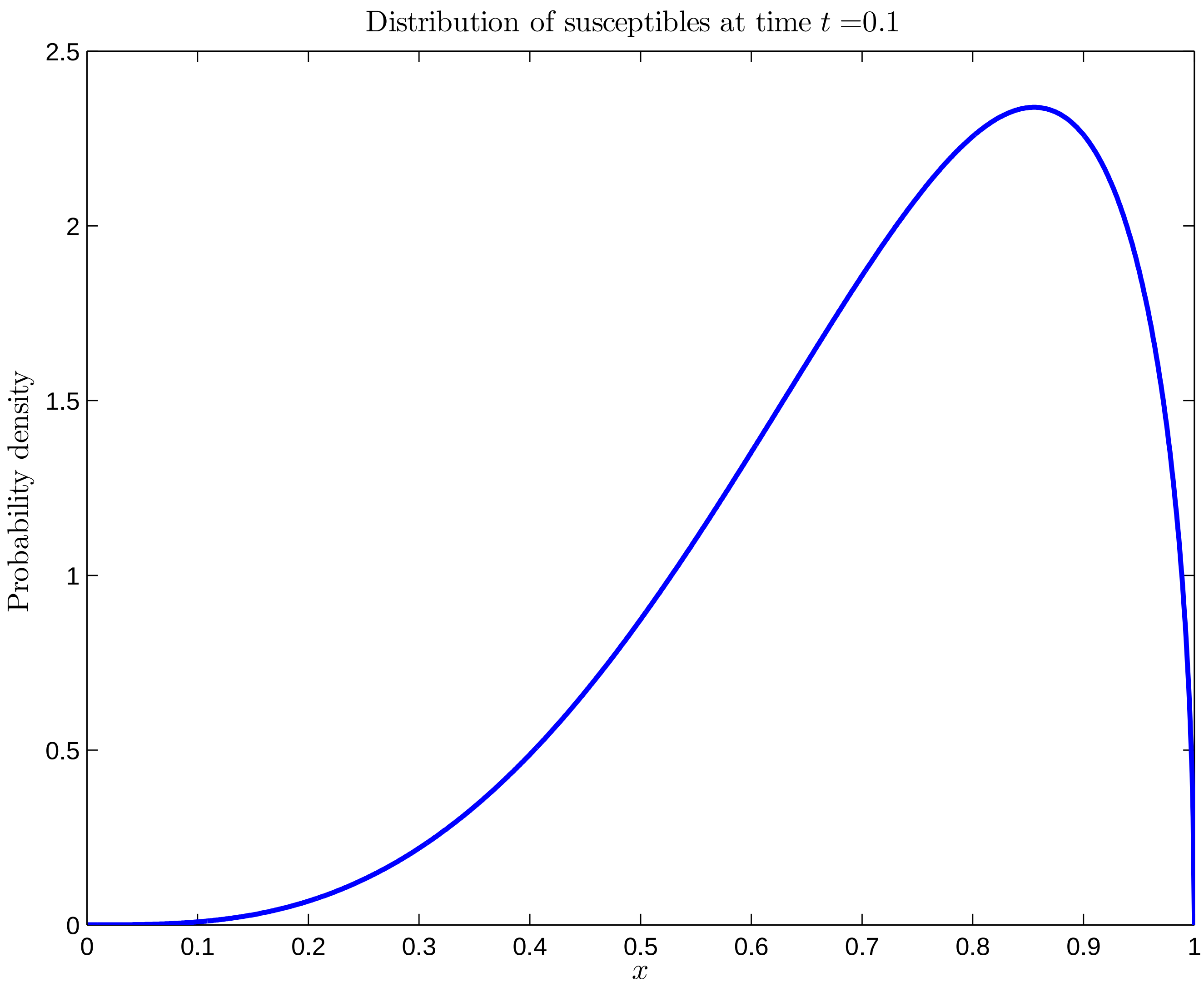

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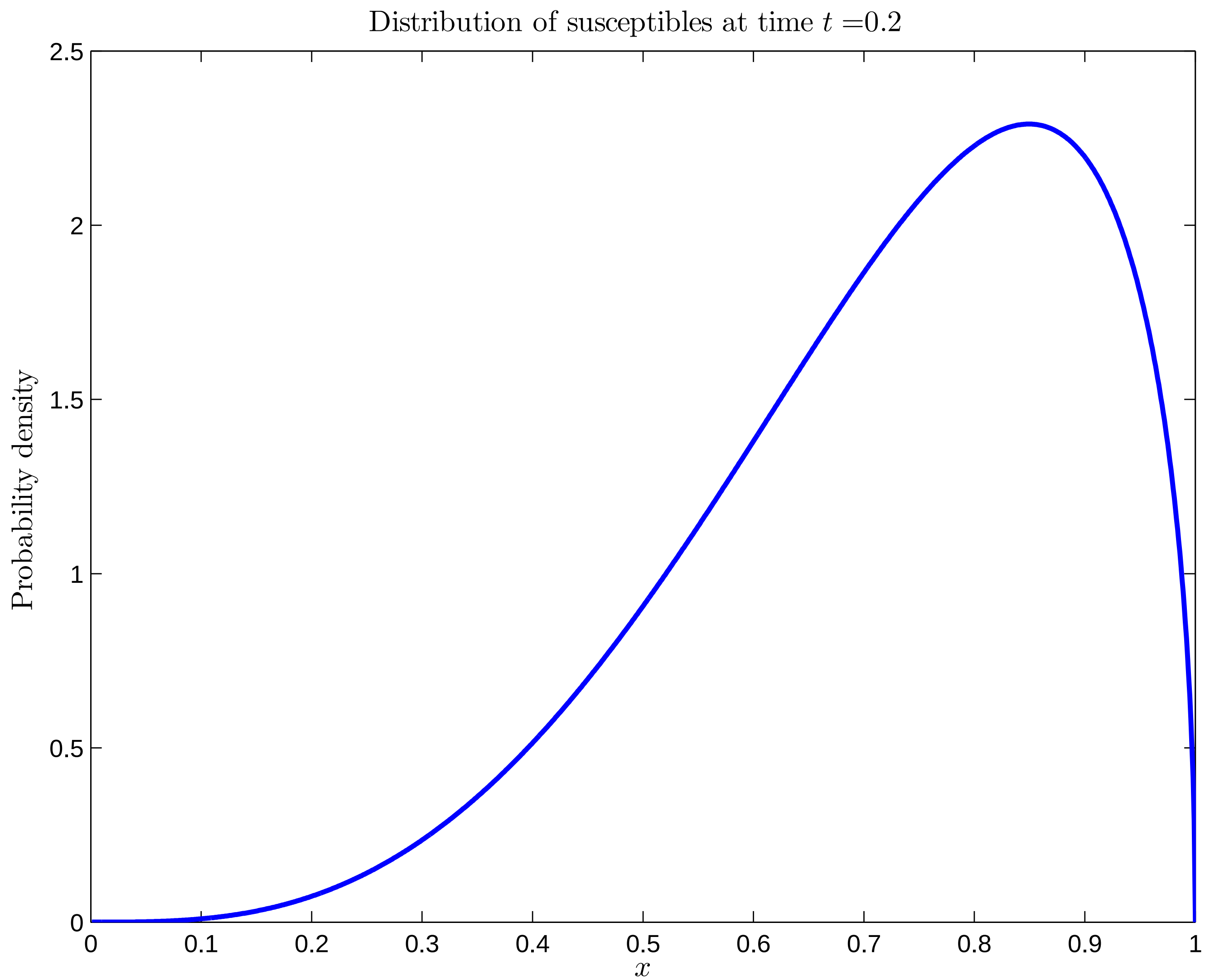

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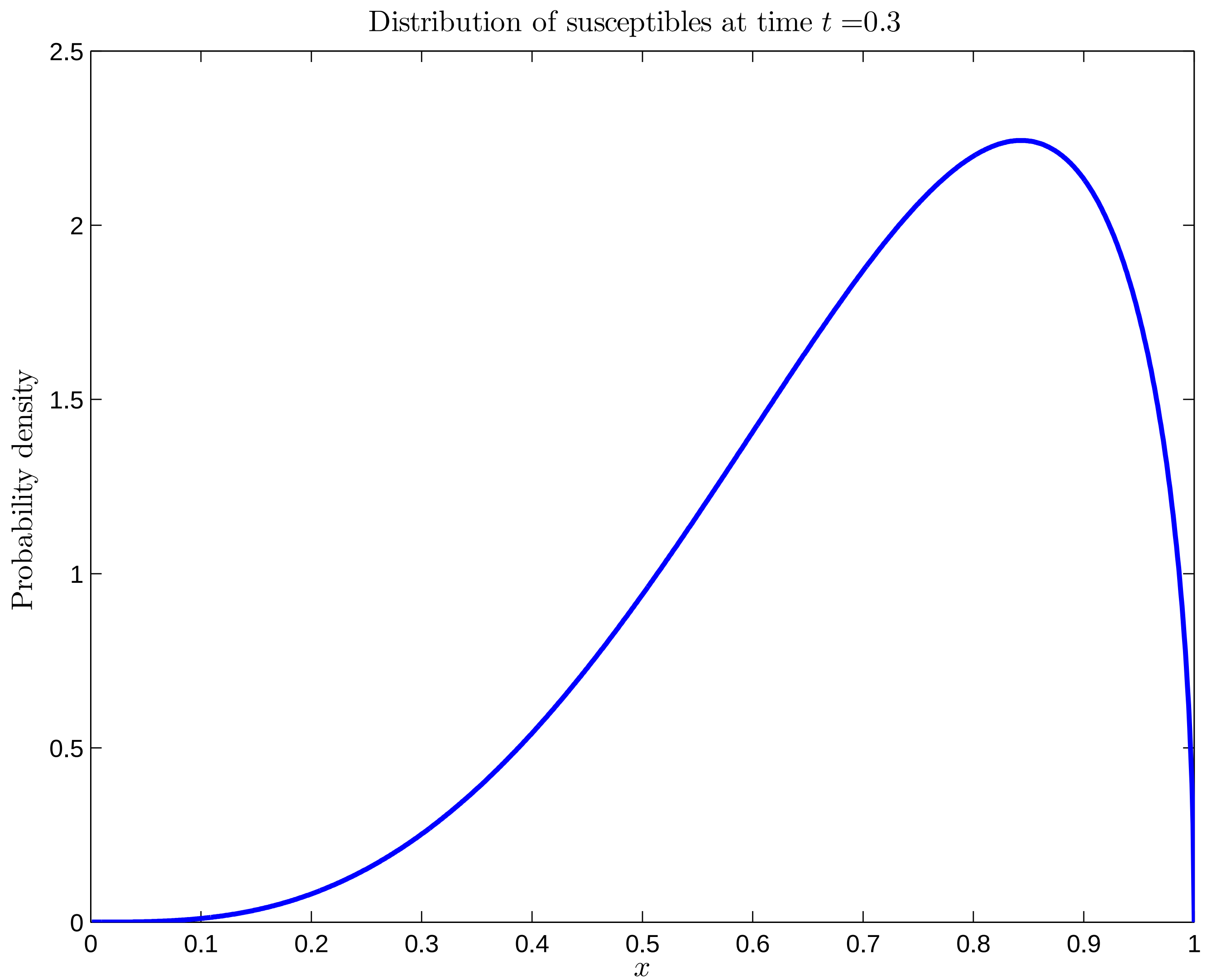

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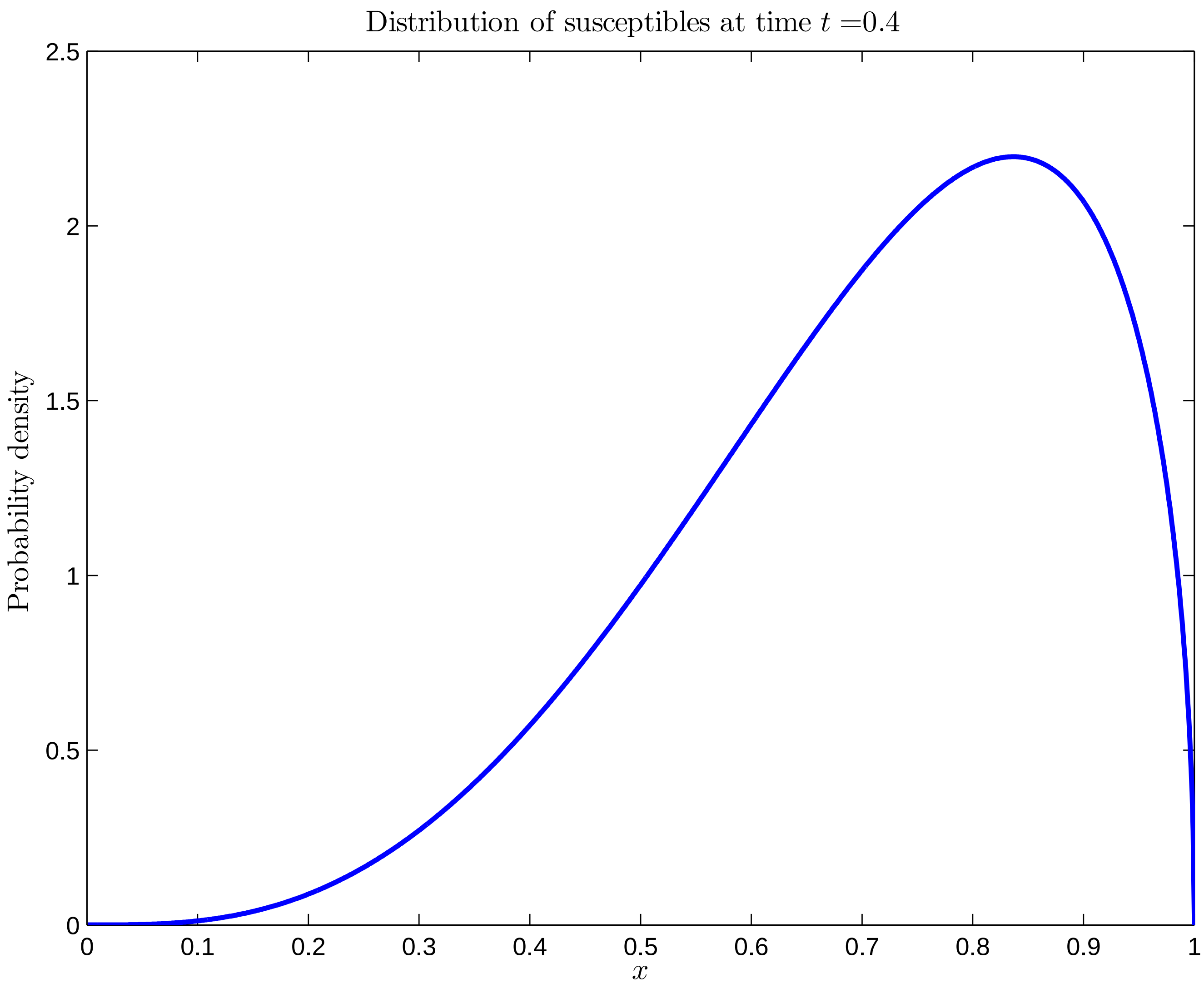

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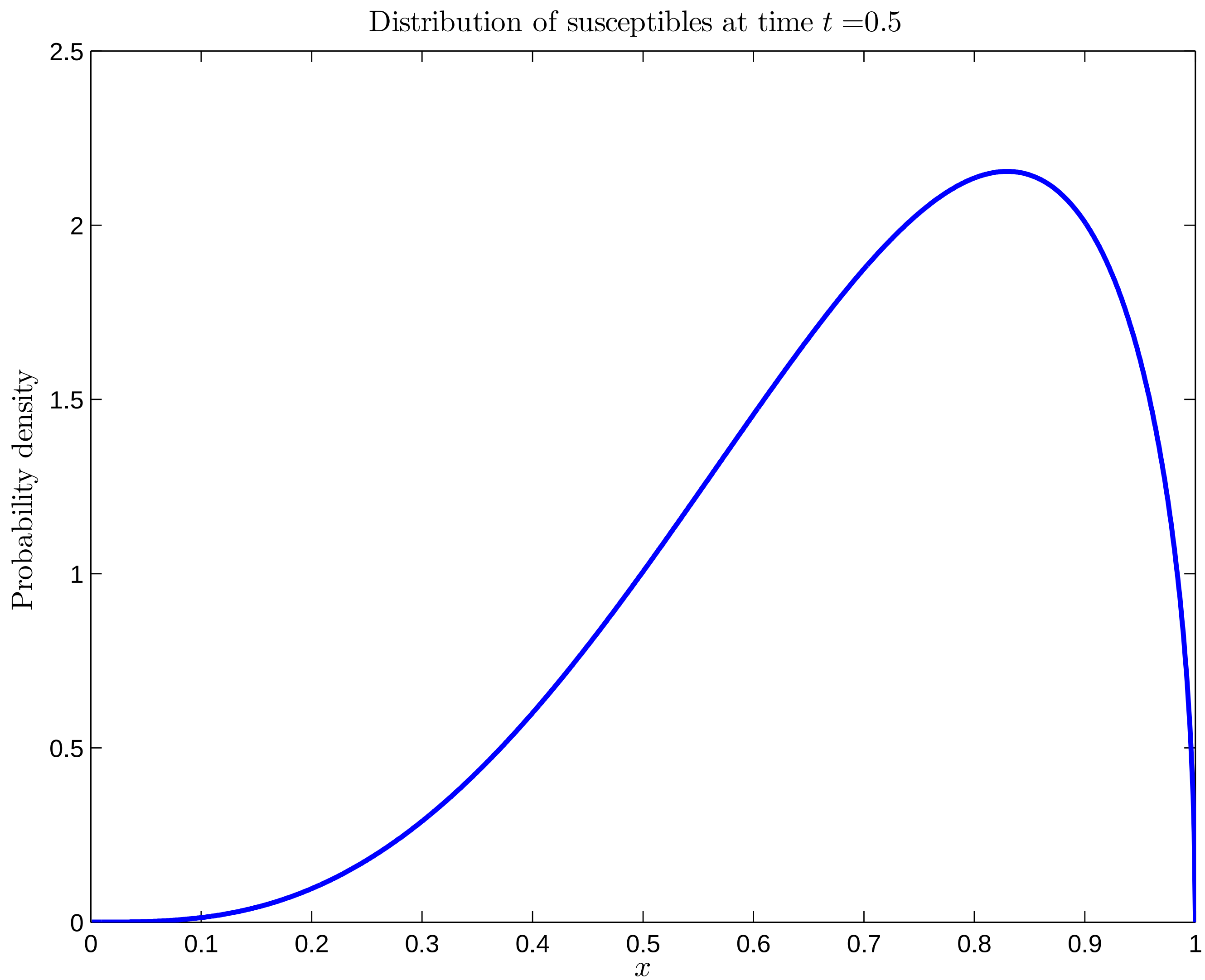

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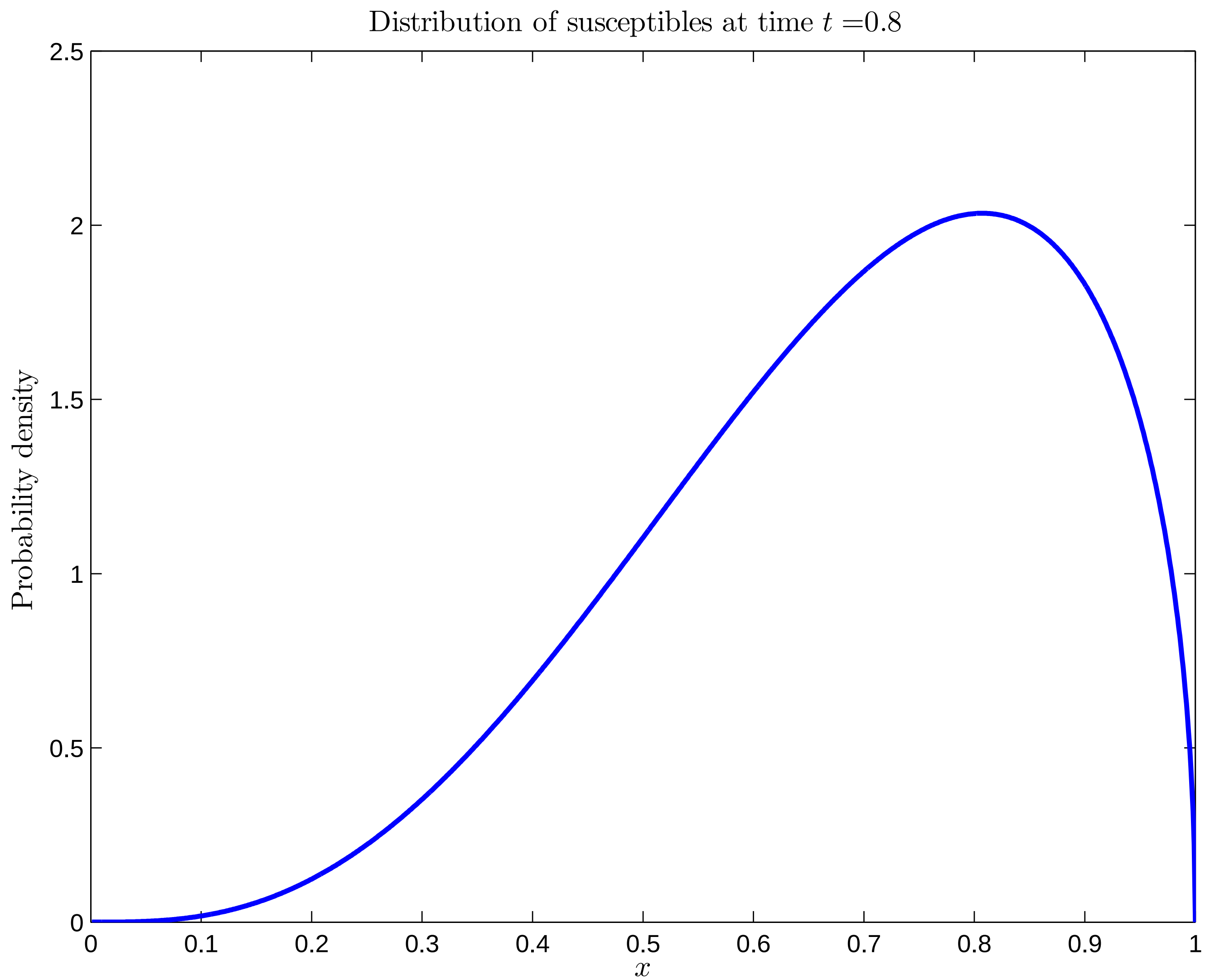

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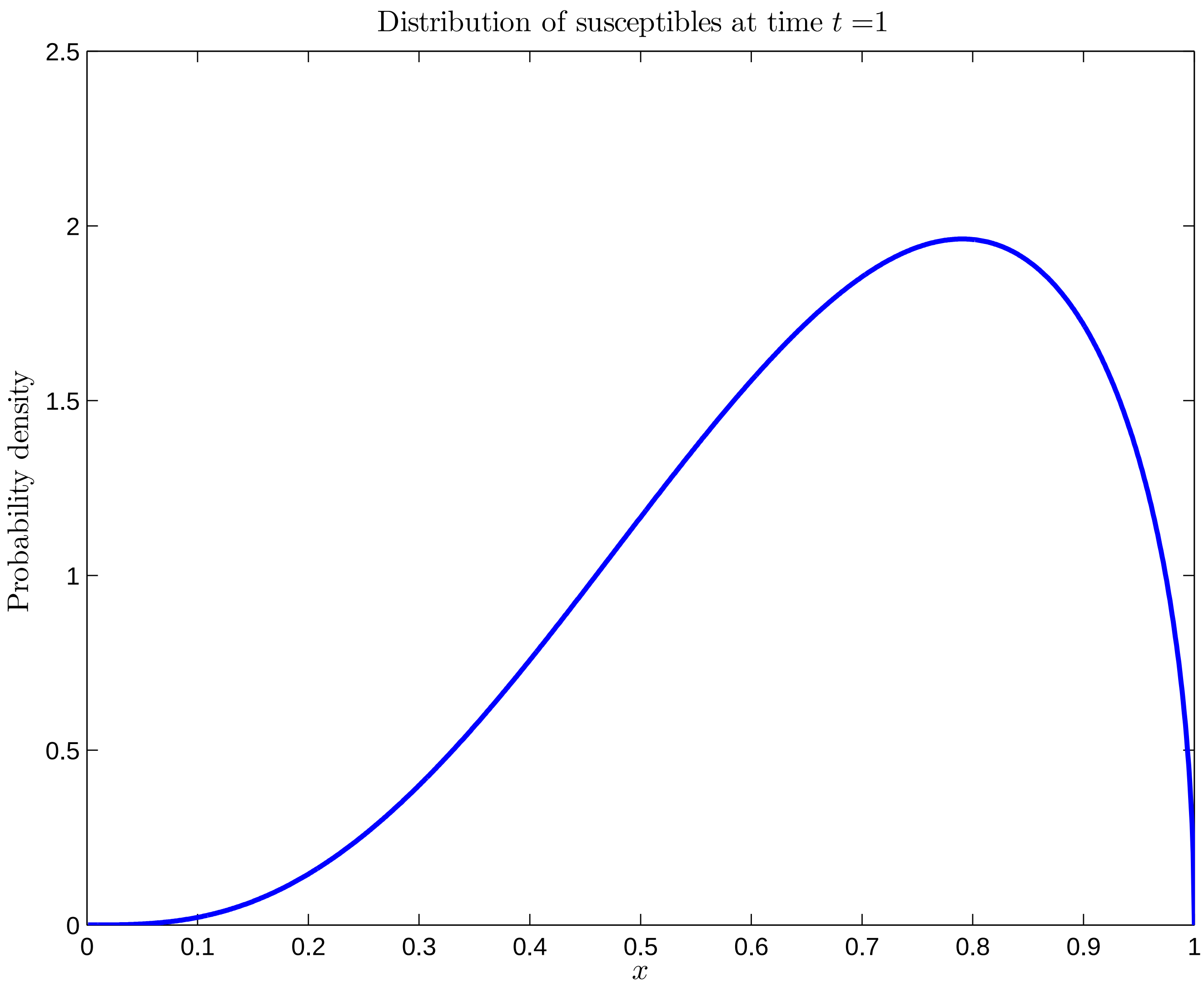

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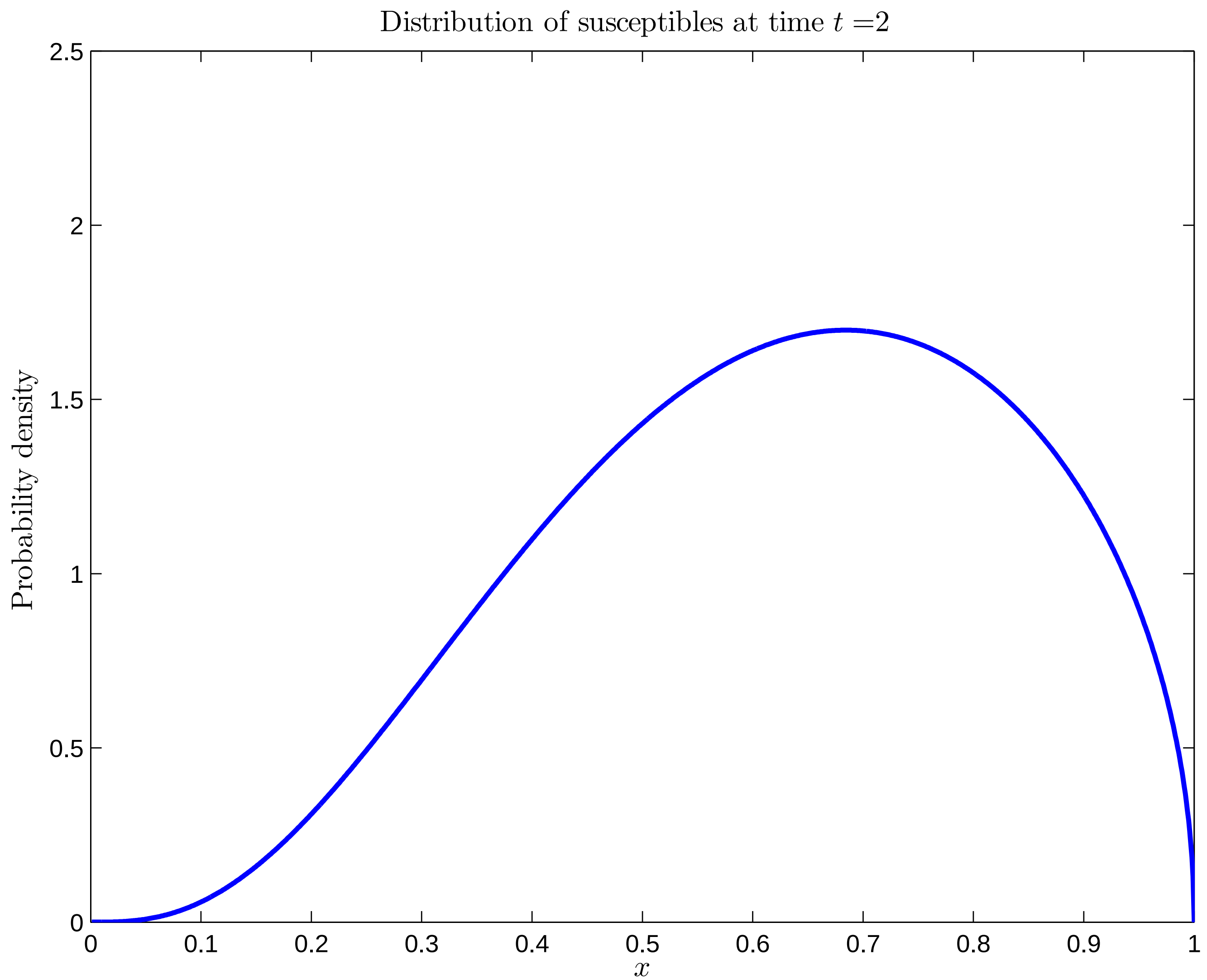

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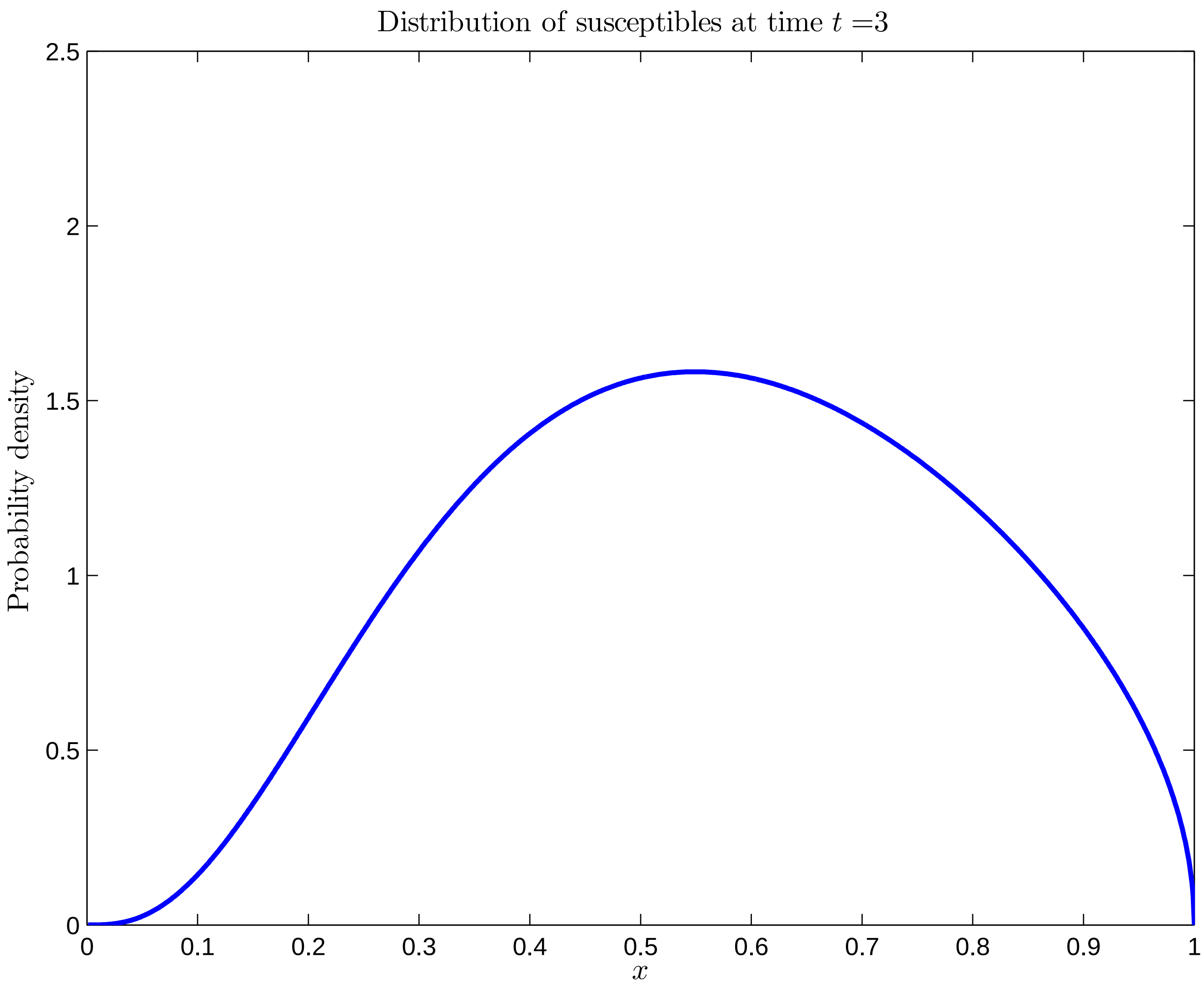

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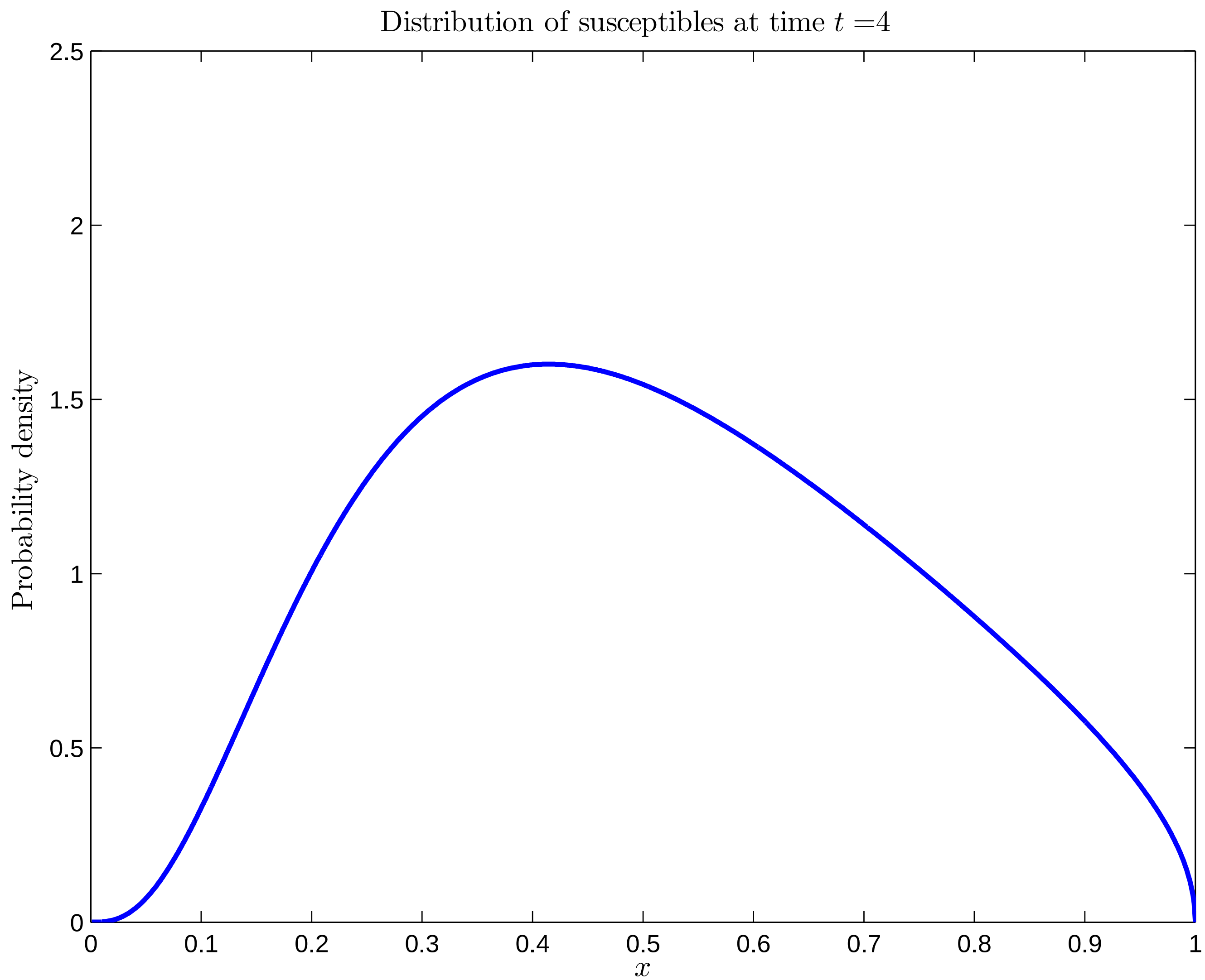

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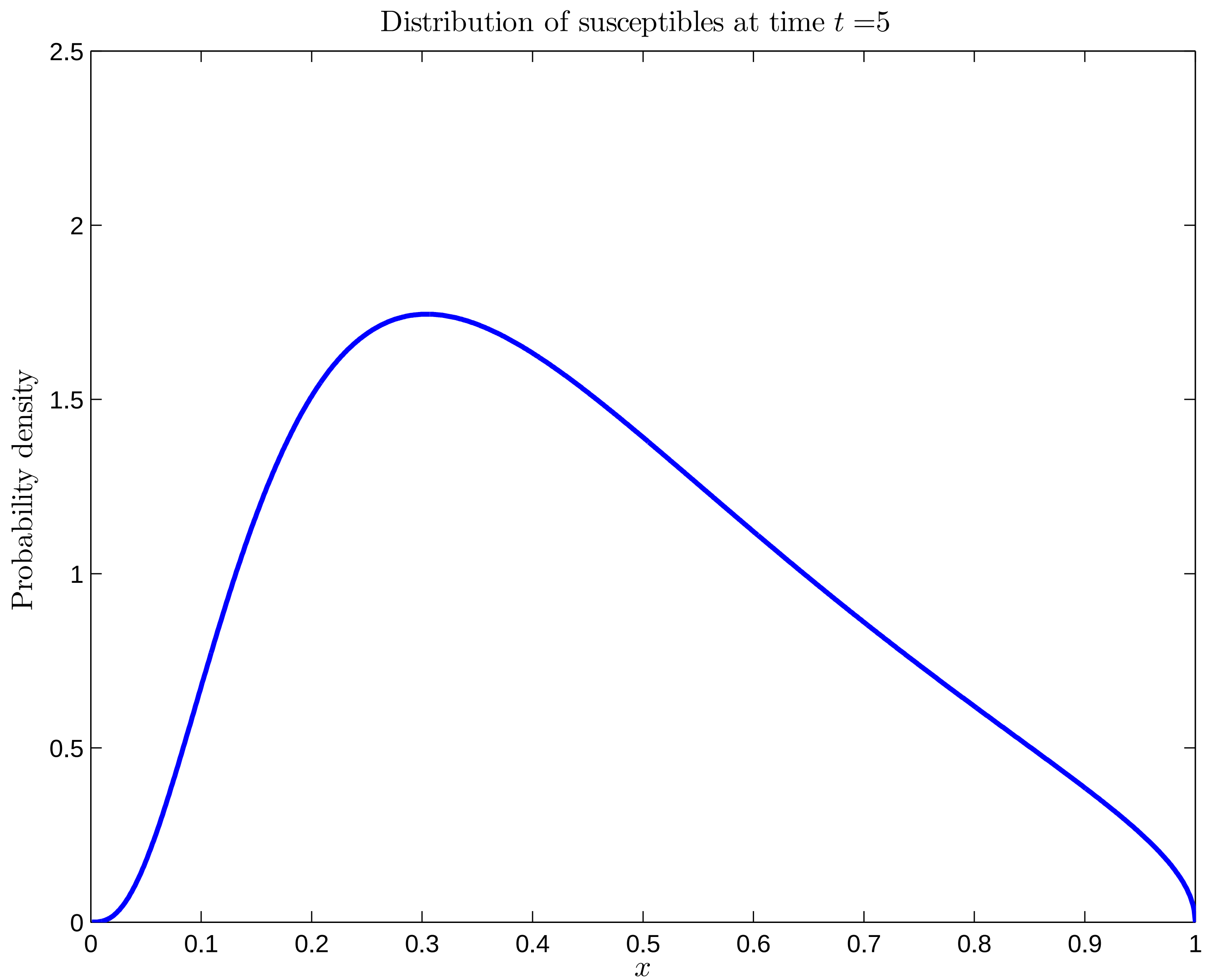

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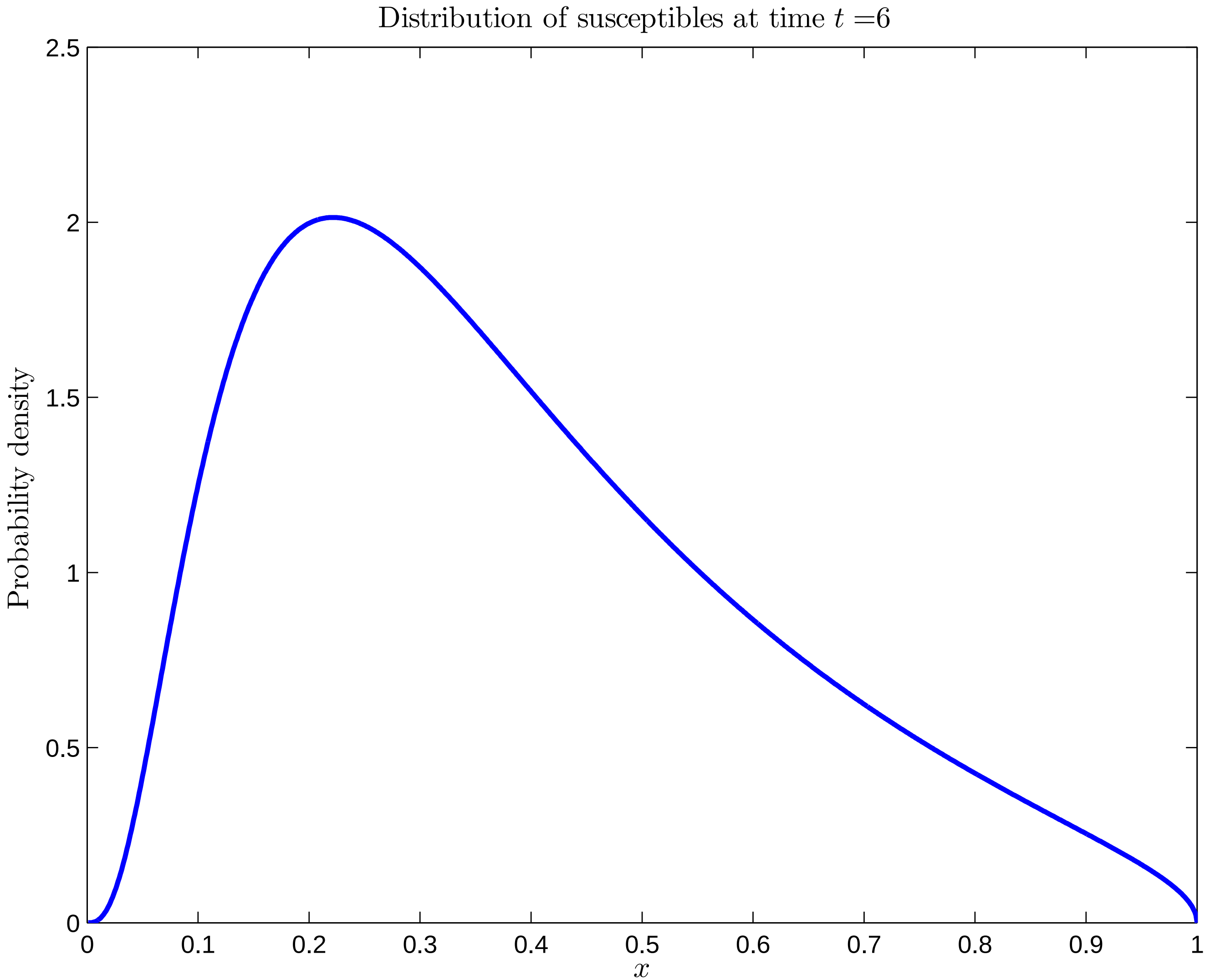

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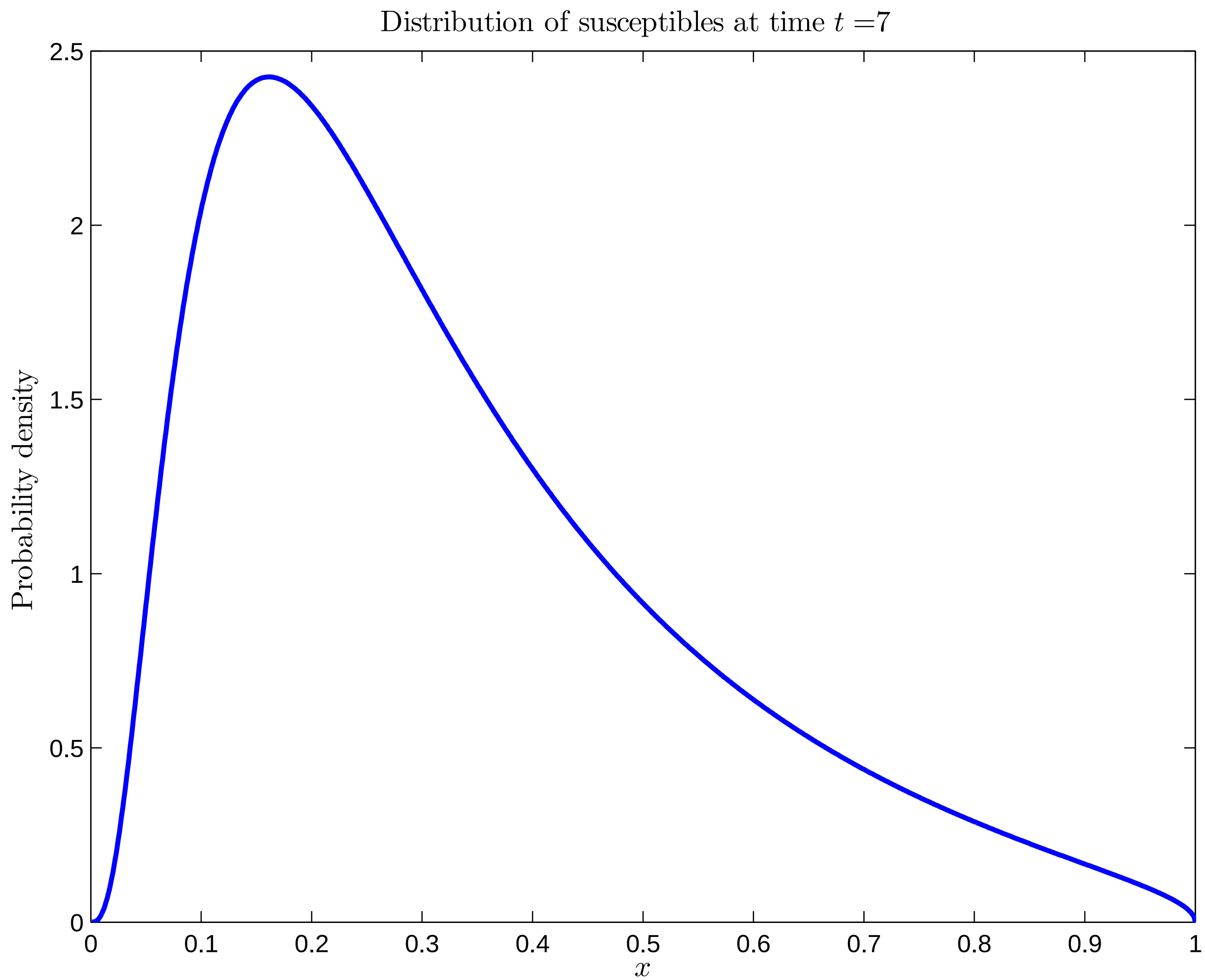

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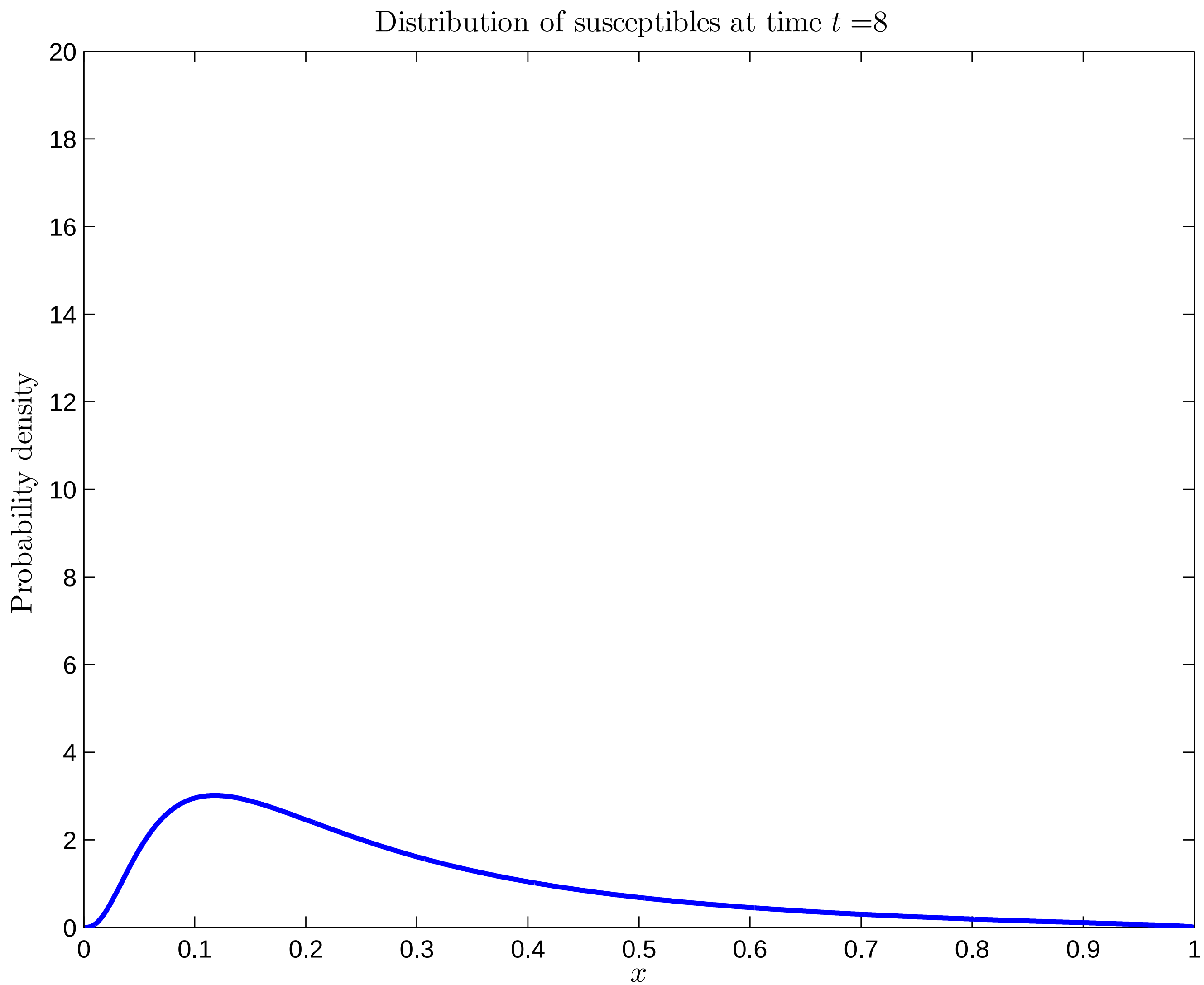

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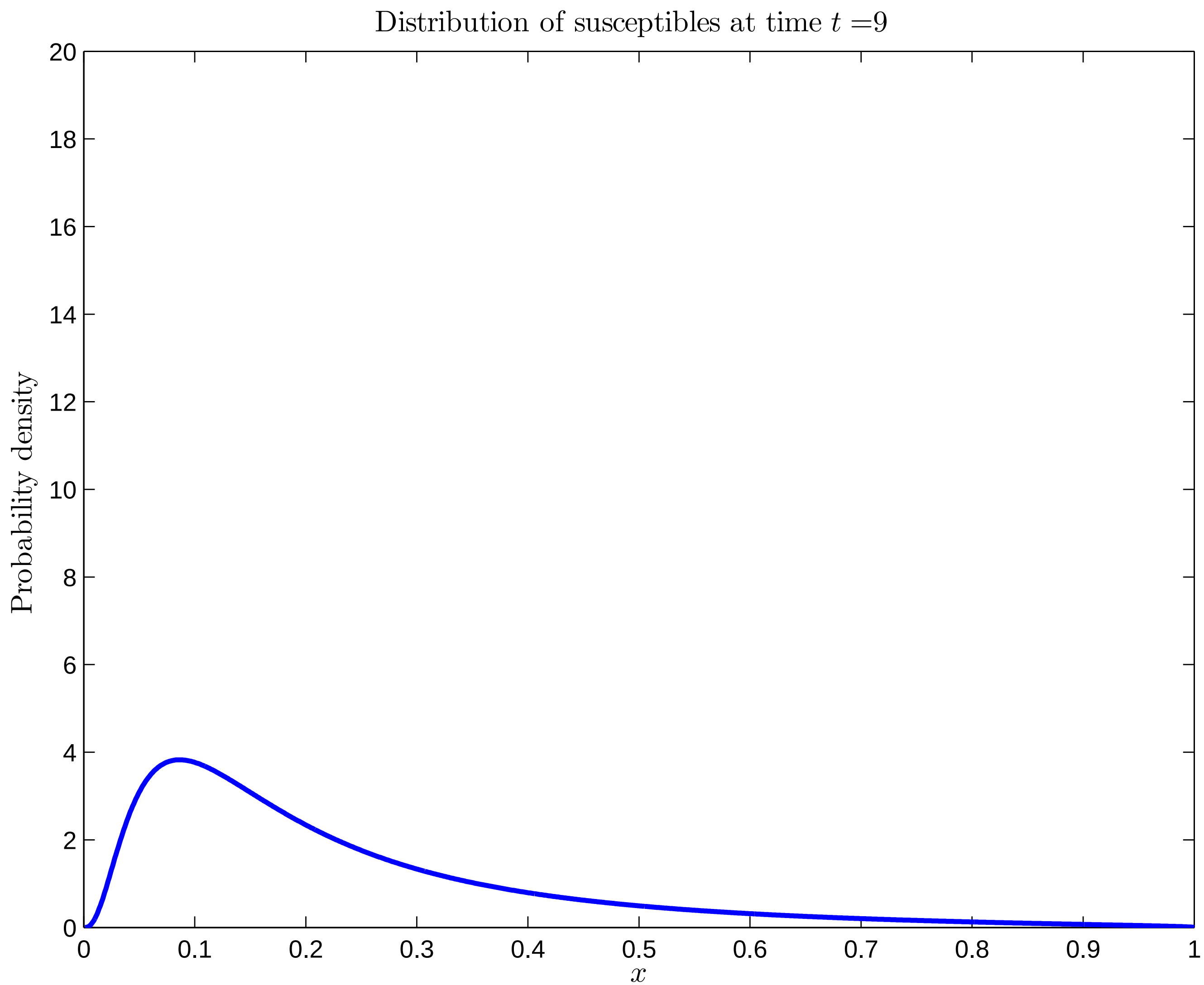

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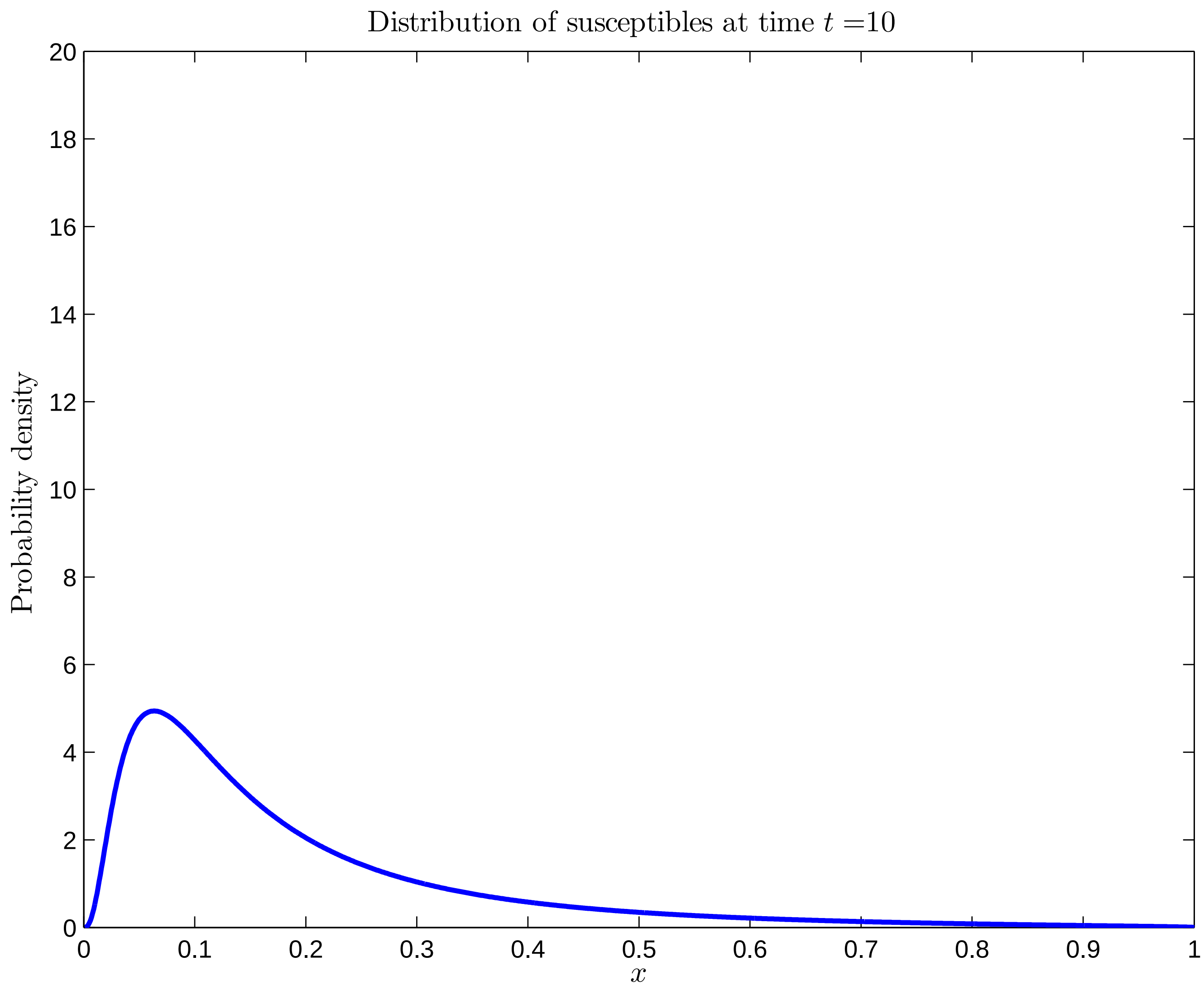

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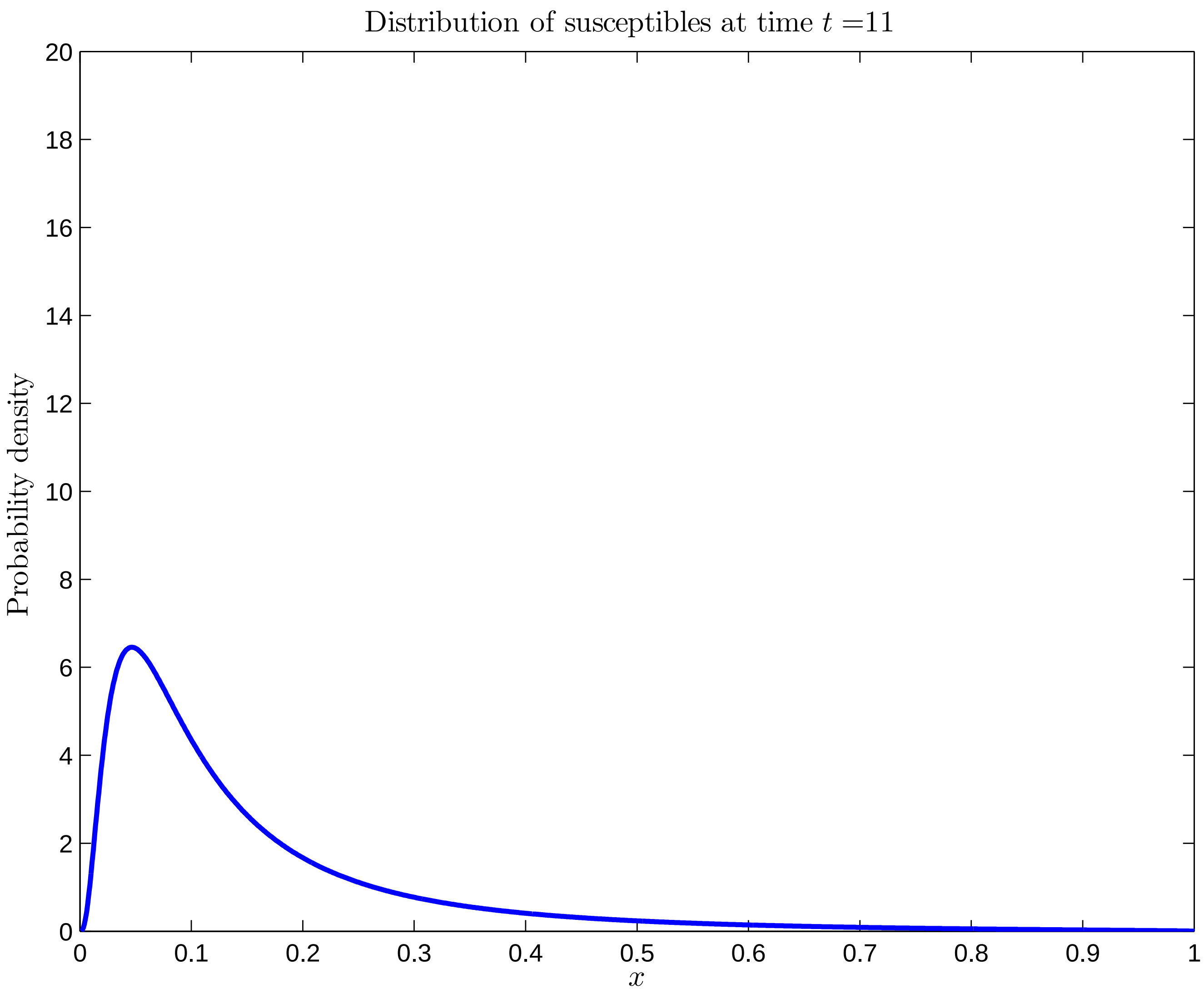

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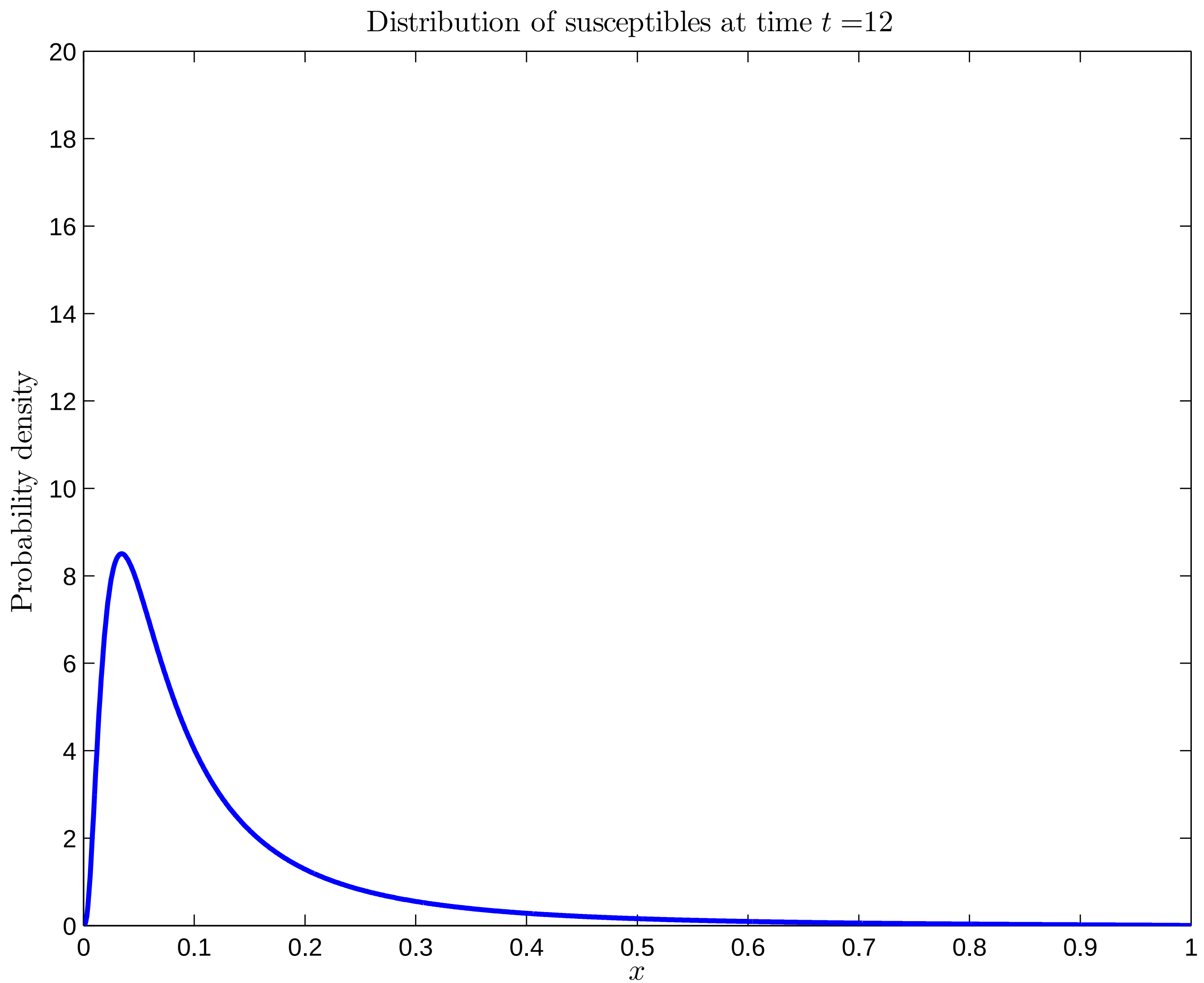

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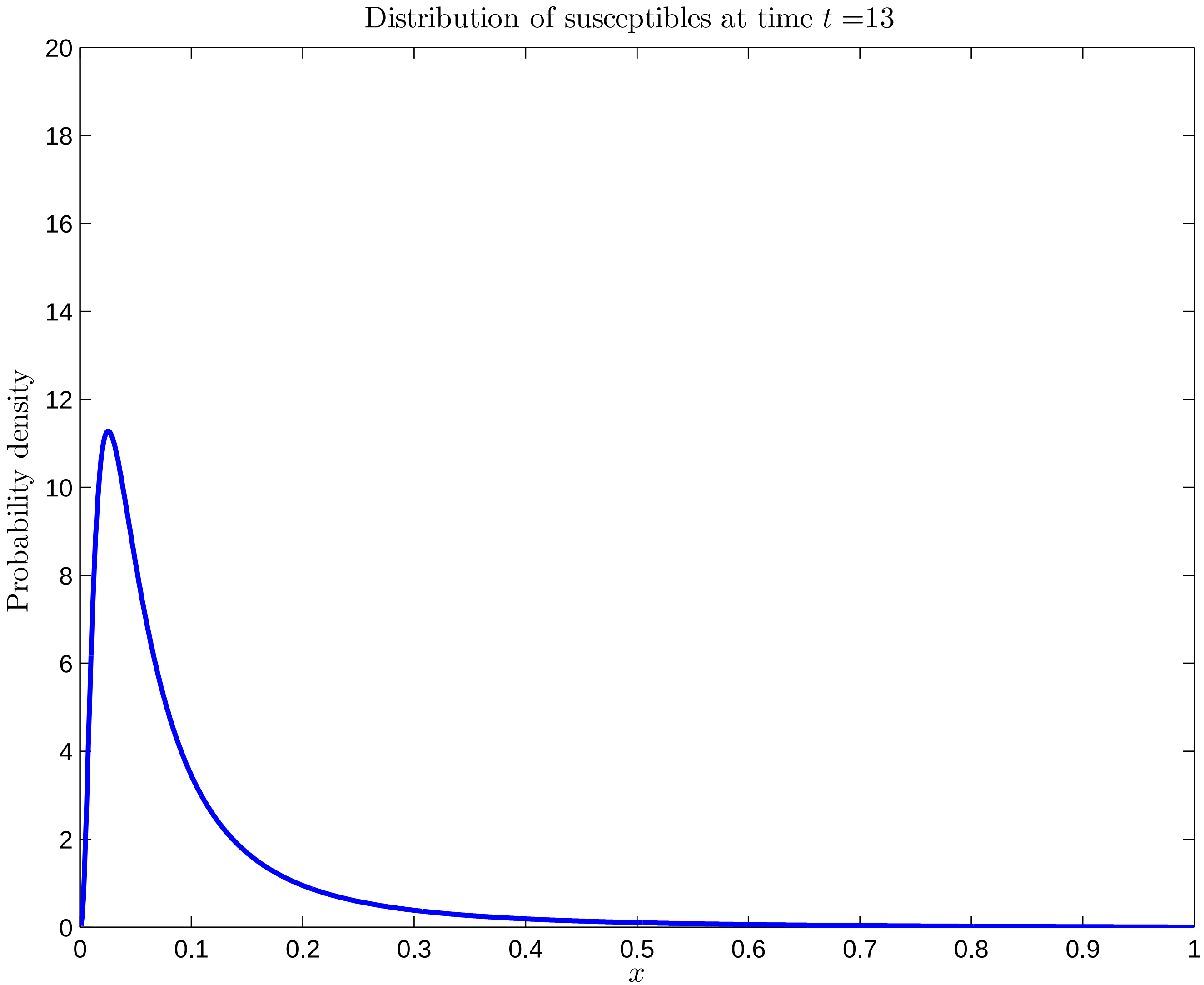

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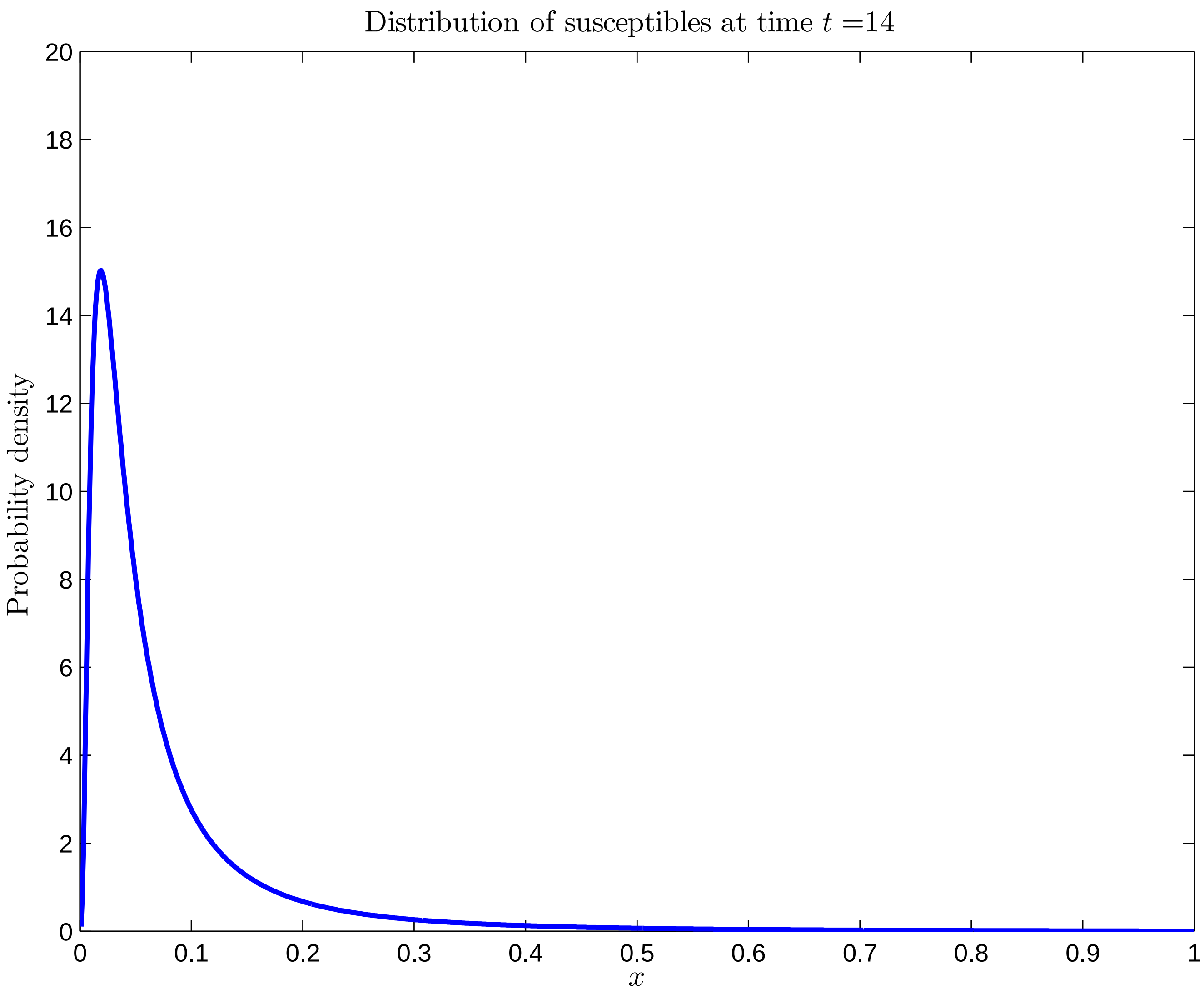

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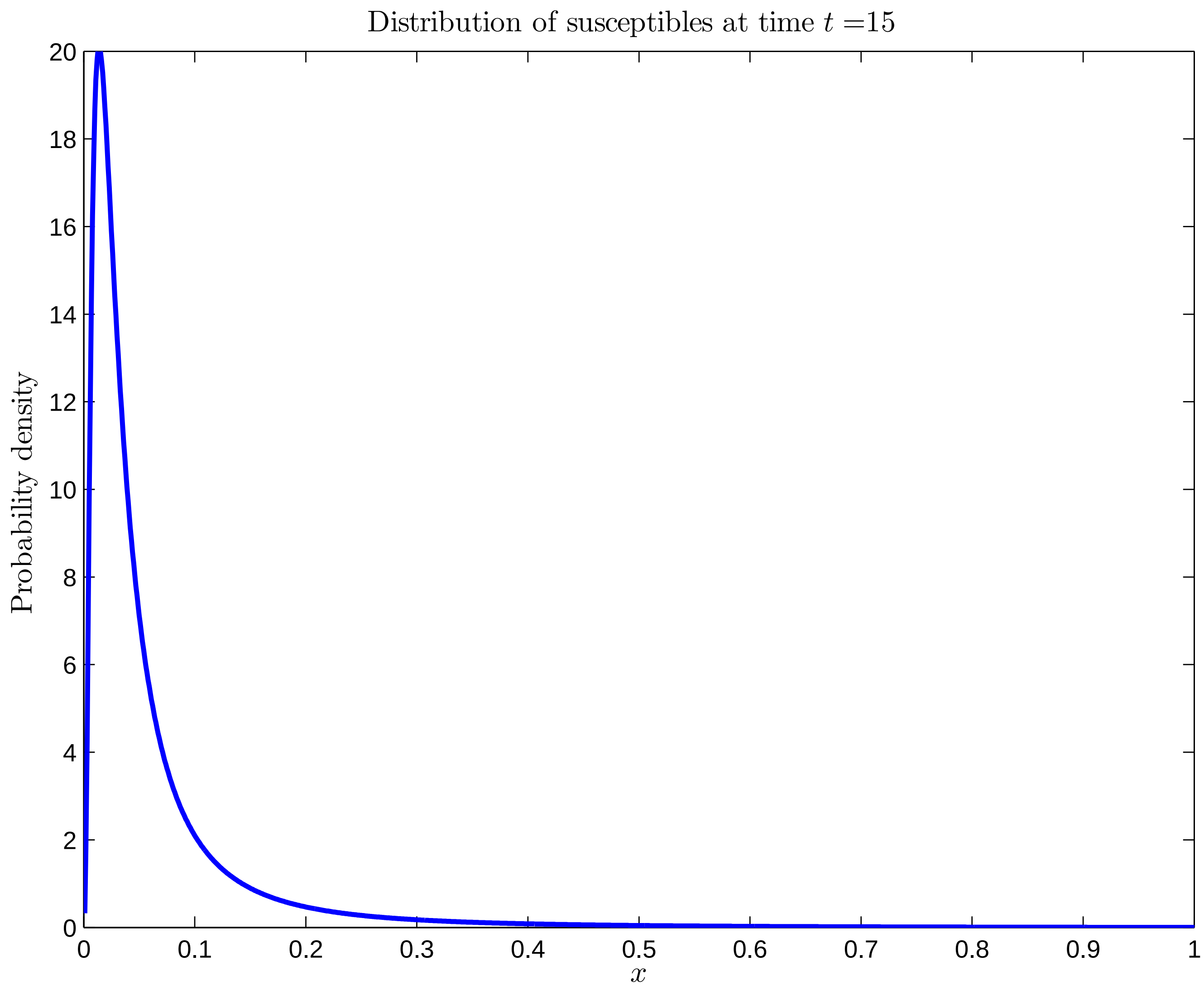

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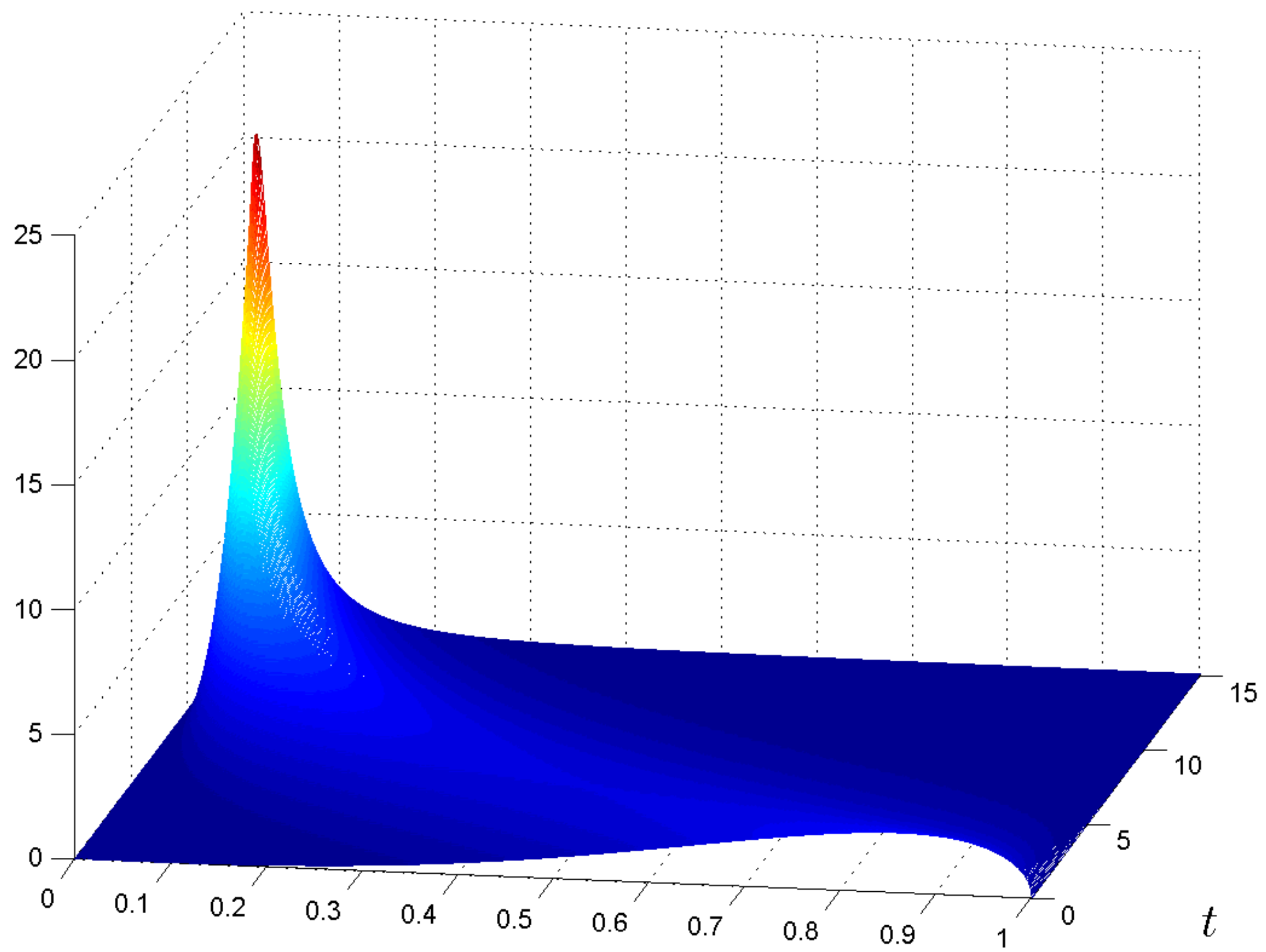

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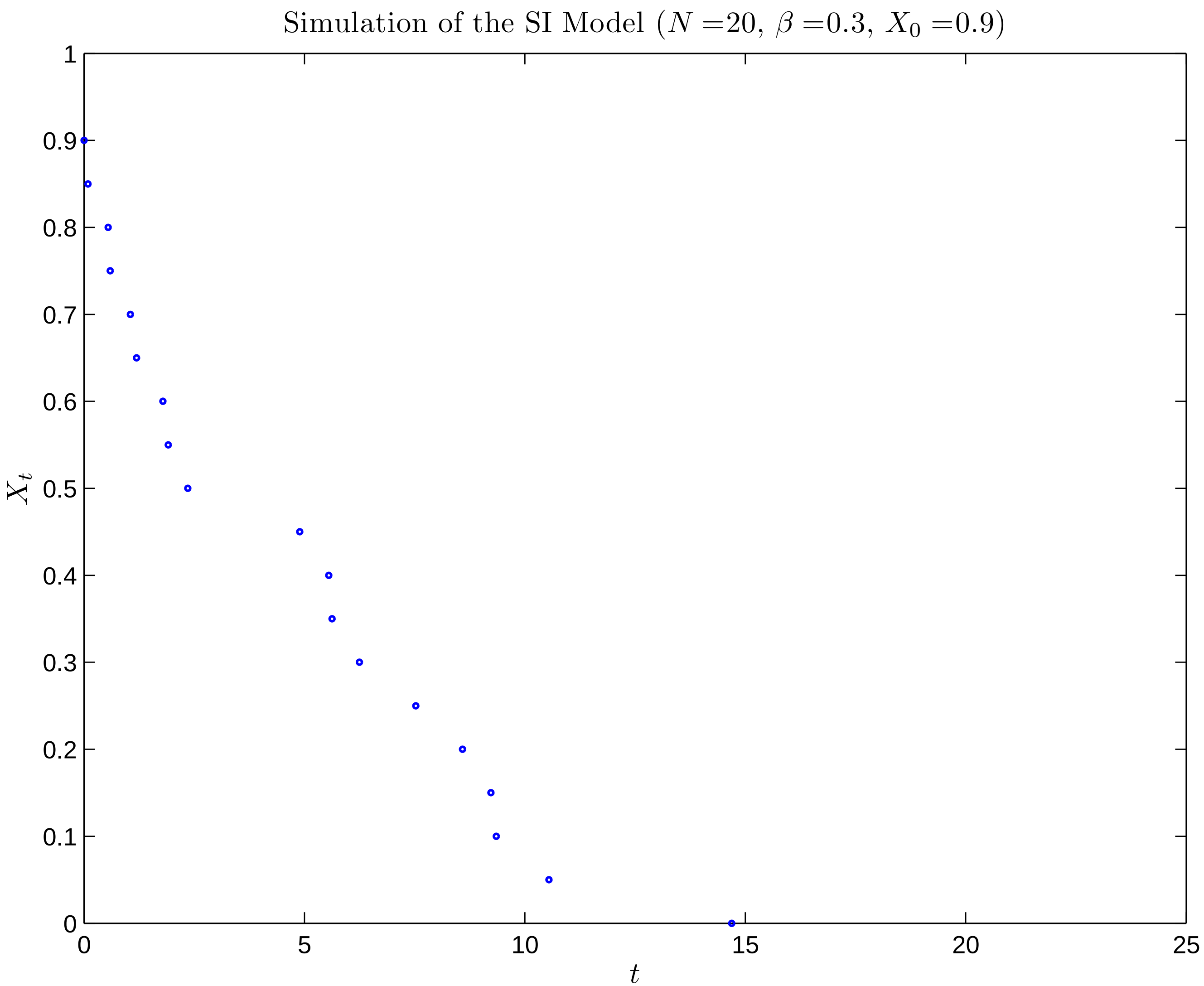

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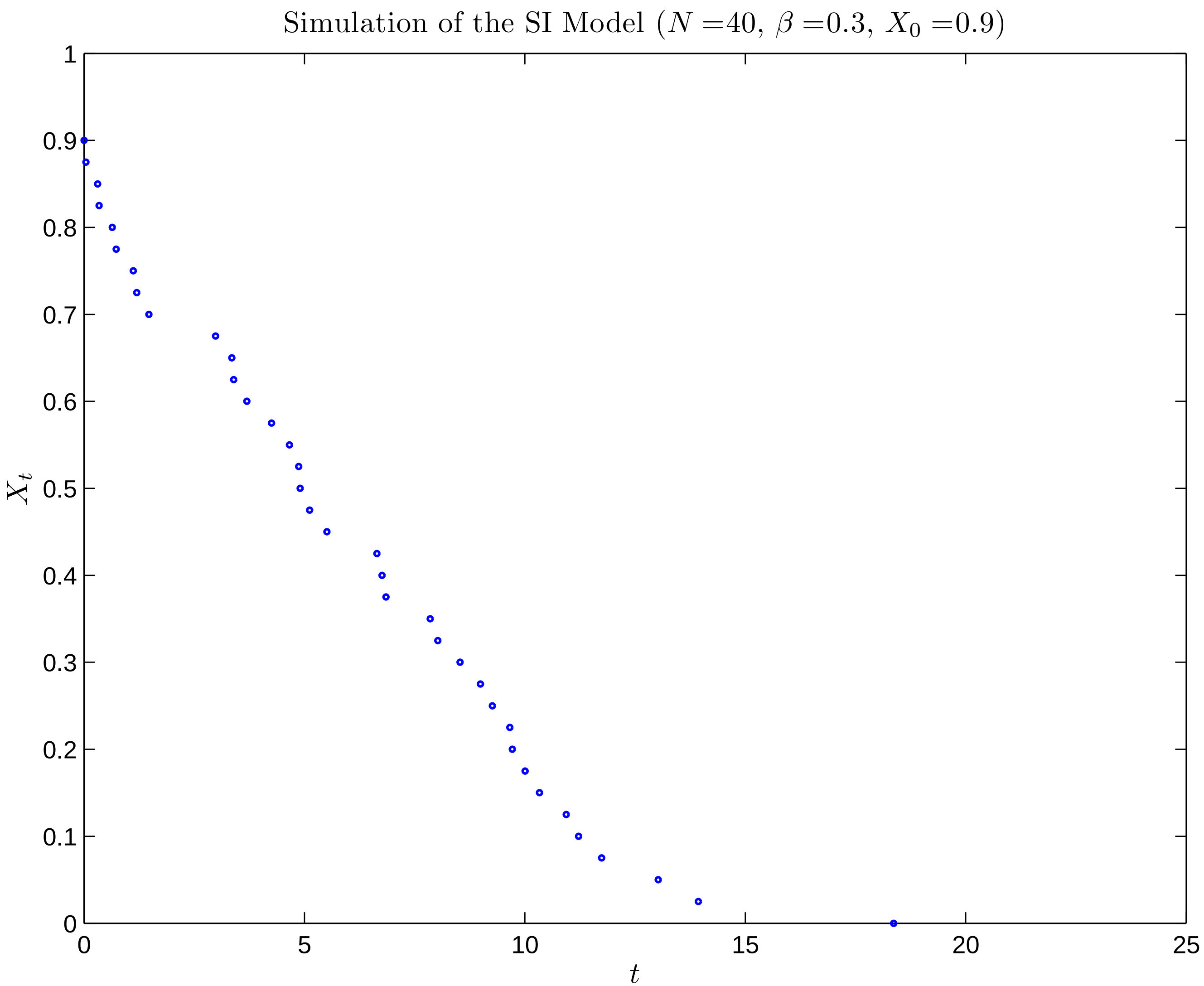

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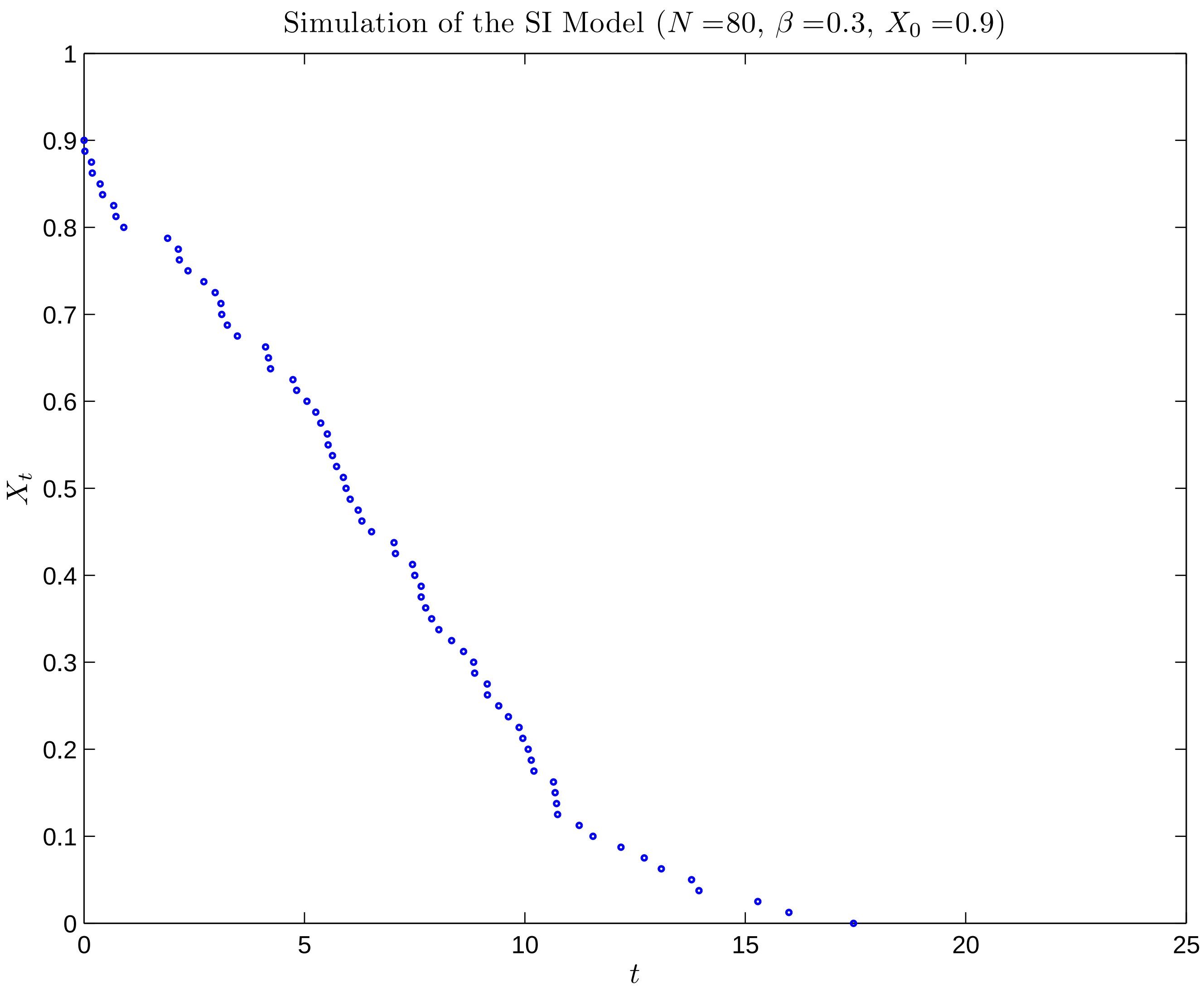

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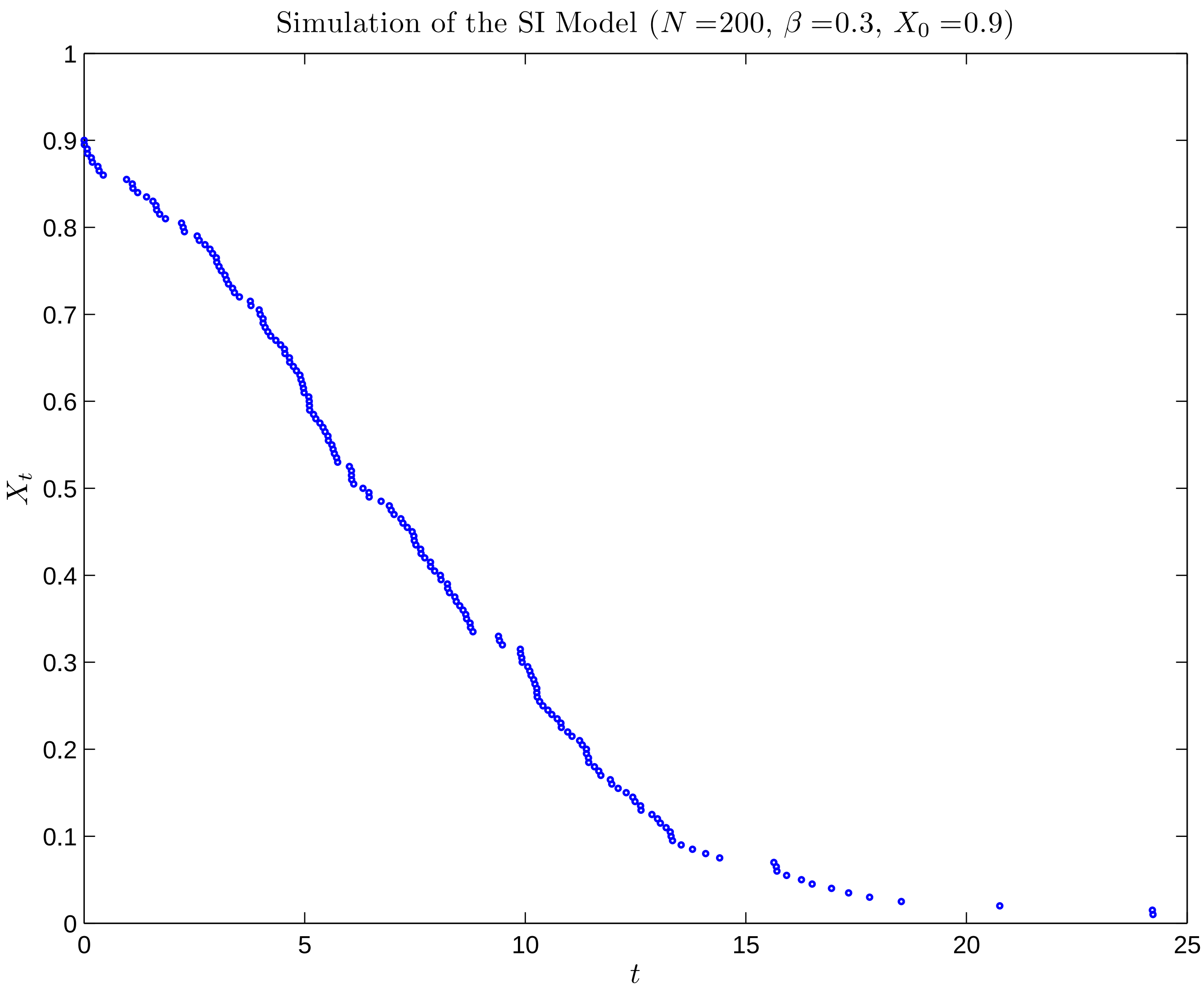

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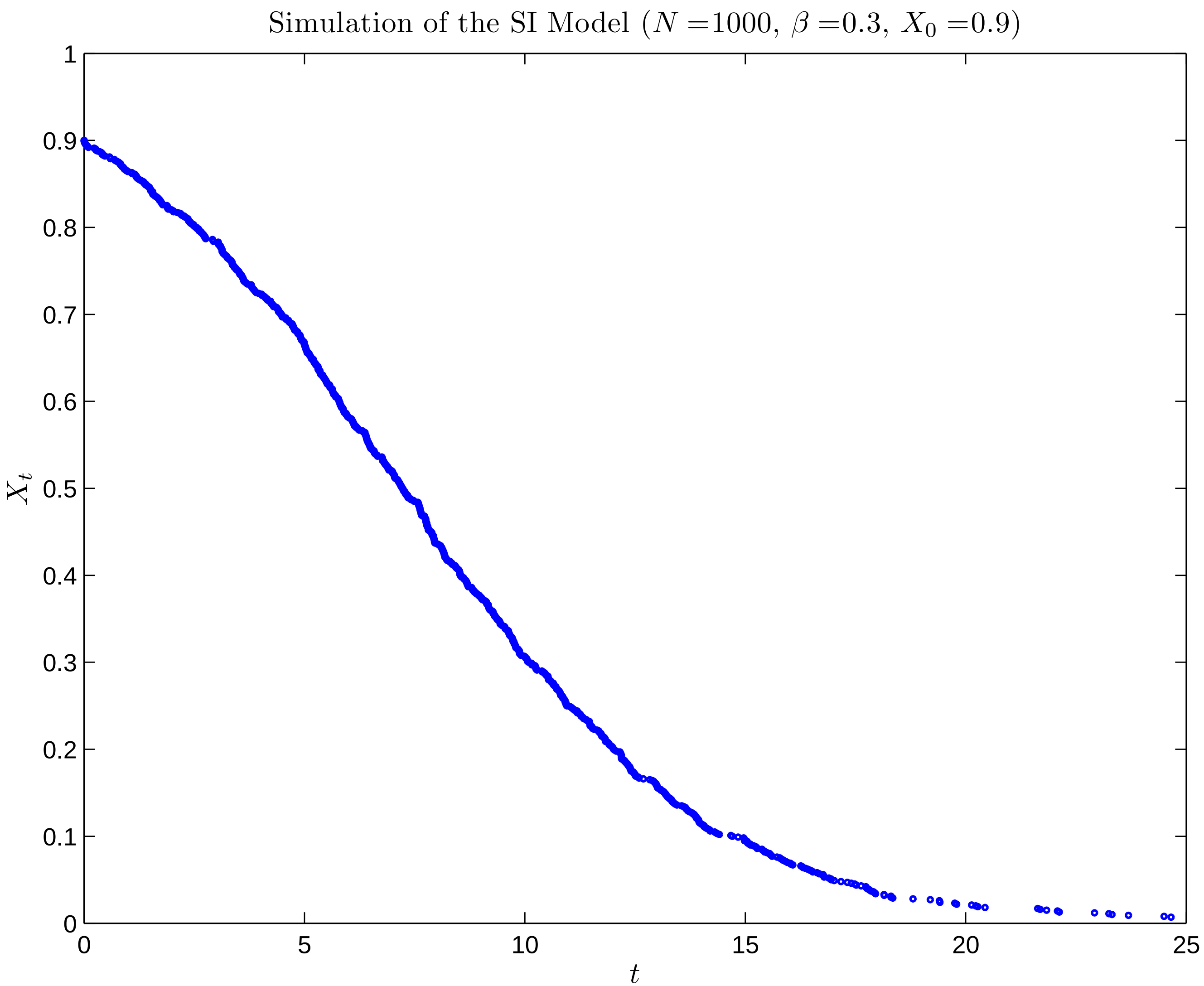

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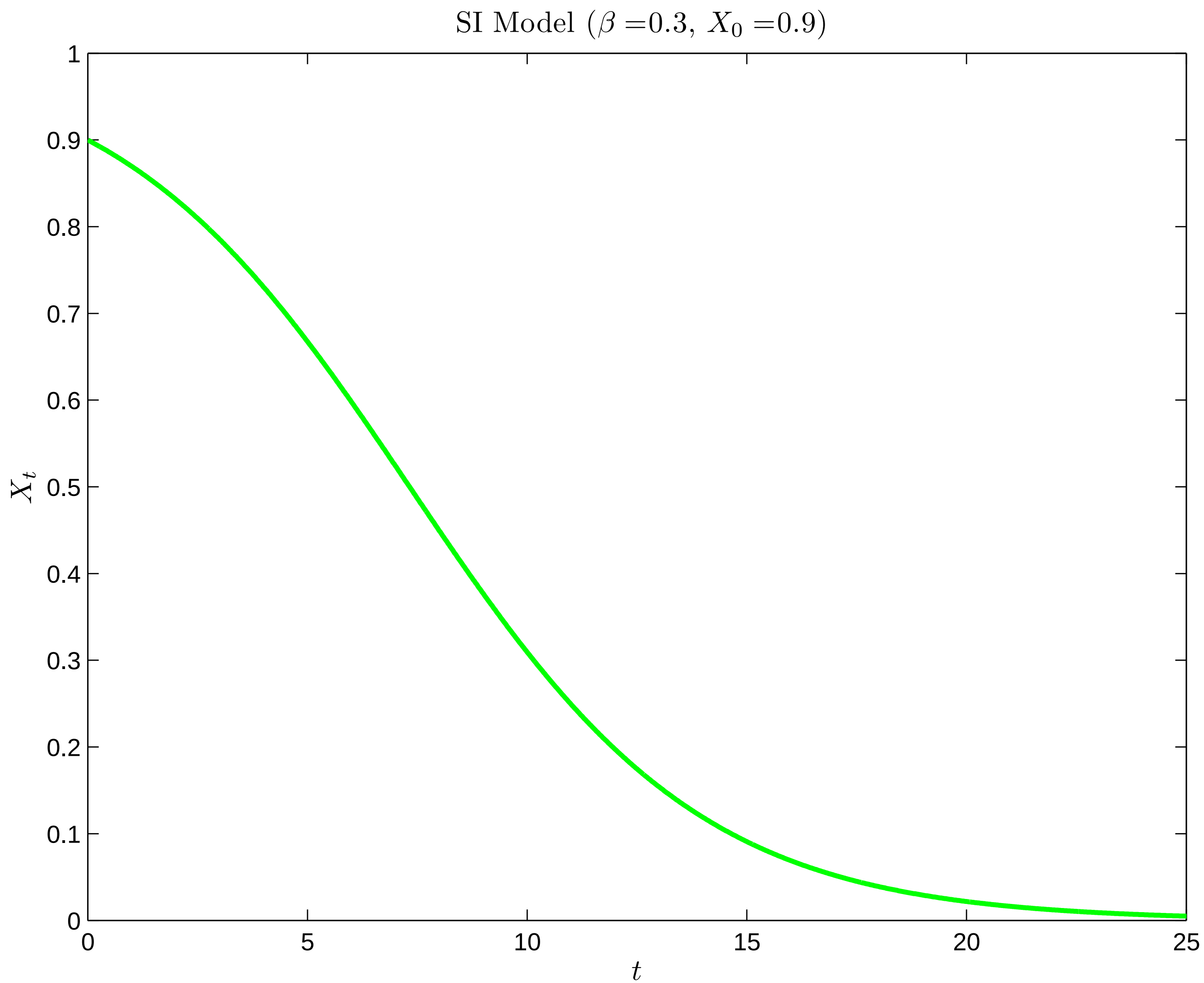

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We can do this (and more) for a very large class of stochastic models called *density dependent Markov chains*.

I will first explain how the Kegan and West approach (mapping an initial distribution) can be extended: *we do not need to evaluate the trajectories explicitly*.

Our population process

Our population process $(n_t,\, t \geq 0)$ is assumed to be a continuous-time Markov chain taking values in a subset S of $\mathbb{Z}^D$.

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It has a (stable and conservative) set of transition rates $Q = (q(m,n),\, m,n \in S)$, so that $q(m,n)$ is the transition rate from m to n for $n \neq m$ and $q(m,m) = -q(m)$, where $q(m) = \sum_{n \neq m} q(m,n)$ $(< \infty)$ is the total rate out of state m.

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For example, in the SI model n_t is the number of susceptibles at time t, $S = \{0, 1, \ldots, N-1\}$, where N is total number of individuals (we assume that there is at least one infective), and $q(n) = q(n, n-1) = (\beta/N)n(N-n)$, where β is the per-contact transmission rate.

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Density dependent models

We suppose that the process is *density dependent* in the sense of Tom Kurtz (1970): there is a parameter N (usually a parameter of the model and often related to the size of the population) with the property that

$$q(n, n+l) = N f\left(\frac{n}{N}, l\right), \quad n, n+l \in S,$$

for suitable functions $f(x, l)$, $x \in E$, where $E \subseteq \mathbb{R}^D$.

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The SI model is density dependent because

$$q(n, n-1) = \frac{\beta}{N} n(N-n) = N\beta \frac{n}{N}\left(1 - \frac{n}{N}\right),$$

and hence $f(x, -1) = \beta x(1-x)$, $x \in E = [0, 1)$.

Step I: Identify the deterministic model

Set $X_t = n_t/N$ and call $(X_t,\, t \geq 0)$ the *density process* (of course X_t would typically *be* a population density).

Set $F(x) = \sum_{l \neq 0} l f\,(x, l)$.

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Theorem 1. For every $\epsilon > 0$,

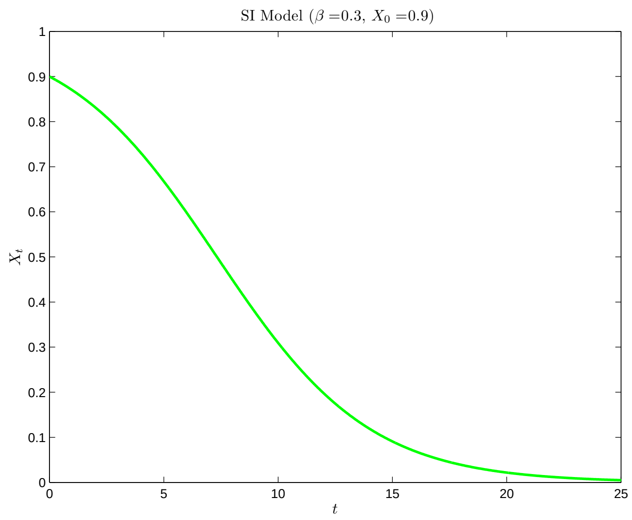
$$\Pr\left(\sup_{0 \leq s \leq t} \left| X_s^{(N)} - x(s) \right| > \epsilon \right) \to 0 \quad \text{as} \quad N \to \infty.$$

Step I: Identify the deterministic model

For the SI model

$$\frac{dx}{dt} = -\beta x(1-x) \qquad x(0) = x_0.$$

$$x(t) = \frac{x_0}{x_0 + (1-x_0)e^{\beta t}} \qquad (t \geq 0).$$



Step II: Map the initial distribution

Think of the initial population density X_0 as being a random variable with a specified probability density function (pdf) f_0.

Write $x(t, x_0)$ for the trajectory starting at x_0.

Determining the action of the map $g_t(x_0) = x(t, x_0)$ (assumed to be injective) on f_0 to obtain a pdf f_t that summaries the effect of random initial conditions in our population: for any $t > 0$,

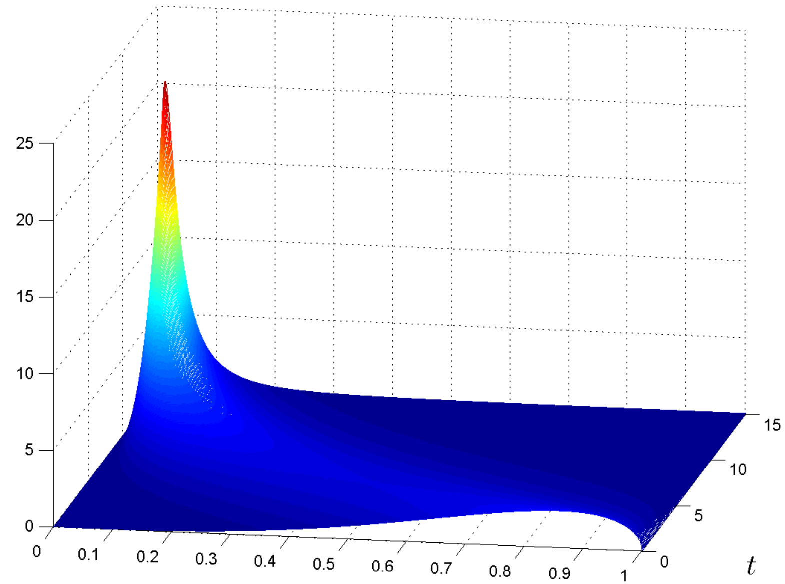
$$f_t(y) = |J_t(y)| f_0\left(g_t^{-1}(y)\right), \quad y \in \mathcal{R}_t,$$

where J_t is the Jacobian of g_t^{-1} and $\mathcal{R}_t = g_t(E)$ is the image of E under g_t.

Step II: Map the initial distribution

For the SI model, $\mathcal{R}_t = E = [0,1)$ for all t, and

$$f_t(y) = \frac{e^{-\beta t}}{(y + (1-y)e^{-\beta t})^2} f_0\left(\frac{y}{y + (1-y)e^{-\beta t}}\right), \qquad y \in [0,1).$$



Step II: Map the initial distribution

For one-dimensional models ($D = 1$) this can be done without evaluating the trajectories explicitly.

We are given

$$\frac{dx}{dt} = F(x) \qquad x(0) = x_0.$$

Let $L(u)$ be the primitive $L(u) = \int^u dw/F(w)$. Suppose L is injective, so that L^{-1} is well defined (it is sufficient that F be everywhere positive or everywhere negative).

Theorem 2.

$$f_t(y) = \frac{F(L^{-1}(L(y) - t))}{F(y)} f_0(L^{-1}(L(y) - t)), \quad y \in \mathcal{R}_t.$$

Step III: Unexplained variation

The following result quantifies the variation not accounted for when random dynamics are ignored.

Theorem 3. For N large,

$$\mathrm{Cov}(X_s) \simeq V_s + \frac{1}{N}\int_E \Sigma_s(x_0) f_0(x_0)\, dx_0,$$

where $V_s = \mathrm{Cov}(x(s, X_0))$ (variation due to initial conditions)

$$\Sigma_s(x_0) = M_s \int_0^s M_u^{-1} G(x(u, x_0))(M_u^{-1})^T \, du \, M_s^T \, ,$$

$M_s = \exp(\int_0^s B_u \, du)$, $B_s = \nabla F(x(s, x_0))$ and $G(x)$ is the $D \times D$ matrix with entries $G_{ij}(x) = \sum_{l \neq 0} l_i l_j f_l(x)$.

Step III: The one-dimensional case

Corollary. Suppose $D = 1$. For N large,

$$\mathrm{Var}(X_s) \simeq V_s + \frac{1}{N} \int_E \Sigma_s(x_0) f_0(x_0)\, dx_0,$$

where $V_s = \mathrm{Var}(x(s, X_0))$ (variation due to initial conditions),

$$\Sigma_s(x_0) = M_s^2 \int_0^s M_u^{-2} G(x(u, x_0))\, du\,,$$

$M_s = \exp(\int_0^s B_u\, du)$, $B_s = F'(x(s, x_0))$ and $G(x) = \sum_{l \neq 0} l^2 f_l(x)$.

For the SI model

$$\Sigma_t = e^{\beta t} x_0 (1 - x_0) \frac{(1-x_0)^2 e^{2\beta t} - (1-2x_0-2\beta t x_0(1-x_0))e^{\beta t} - x_0^2}{(x_0+(1-x_0)e^{\beta t})^4}.$$

Unexplained variation in the SI model