Diffusion Approximations for Ecological Models

by

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Zen Maxims for Survival in a Modern University

Those not relevant to my talk

- Don't be irreplaceable; if you can't be replaced, you can't be promoted.
- Give a man a fish and he will eat for a day; teach him how to fish, and he will sit in a boat and drink beer all day.
- If you lend someone $20, and never see them again, it was probably worth it.
- If you tell the truth, you don't need a good memory.
- A closed mouth gathers no foot.

Zen Maxims for Survival in a Modern University

Those relevant to my talk

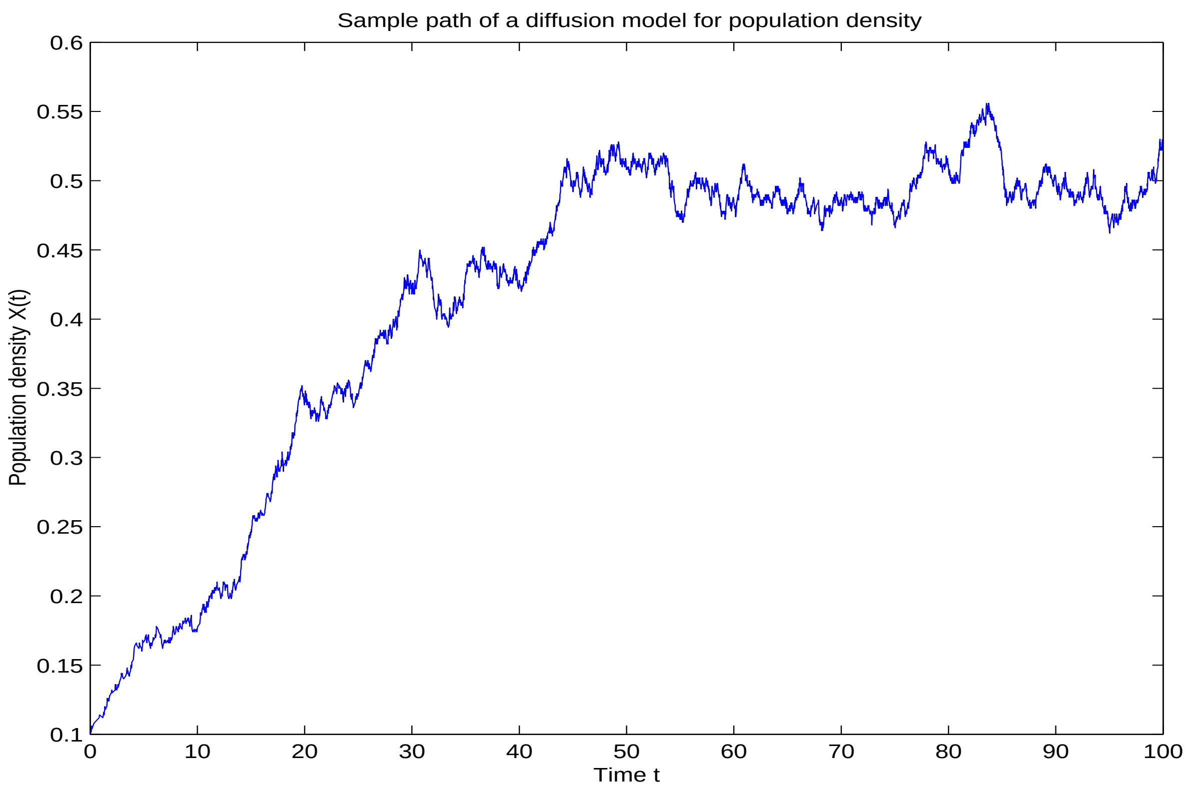
- Good judgement comes from bad experience, and a lot of that comes from bad judgement.

- It may be that your sole purpose in life is simply to serve as a warning to others.

- Before you criticize someone, you should walk a mile in their shoes; that way, when you do criticize them, you'll be a mile away and you'll have their shoes.

DIFFUSION APPROXIMATIONS

Technical definition. A *diffusion process* is a continuous-time (strong) Markov process whose sample path $X(t)$ is an almost-surely continuous function of t.



Diffusion processes are usually realised as approximations of jump processes (in discrete or continuous time) by way of a limiting procedure involving space-time scaling: $\Delta x \sim \sqrt{\Delta t}$.

Why are they useful models? They are popular in ecological modelling because their parameters can be estimated simply from very little data, and they offer explicit expressions for important quantities of interest, such as the expected time to extinction.

Difficulties. Formulae arising from diffusion models are frequently used in situations where this is clearly inappropriate:

- The underlying process, which the diffusion is approximating, might not itself be appropriate for modelling the system in question.
- The approximation procedure is often not well understood, and its physical meaning not taken into account.
- The diffusion approximation might provide estimates that are at variance with the underlying model.

EXAMPLE

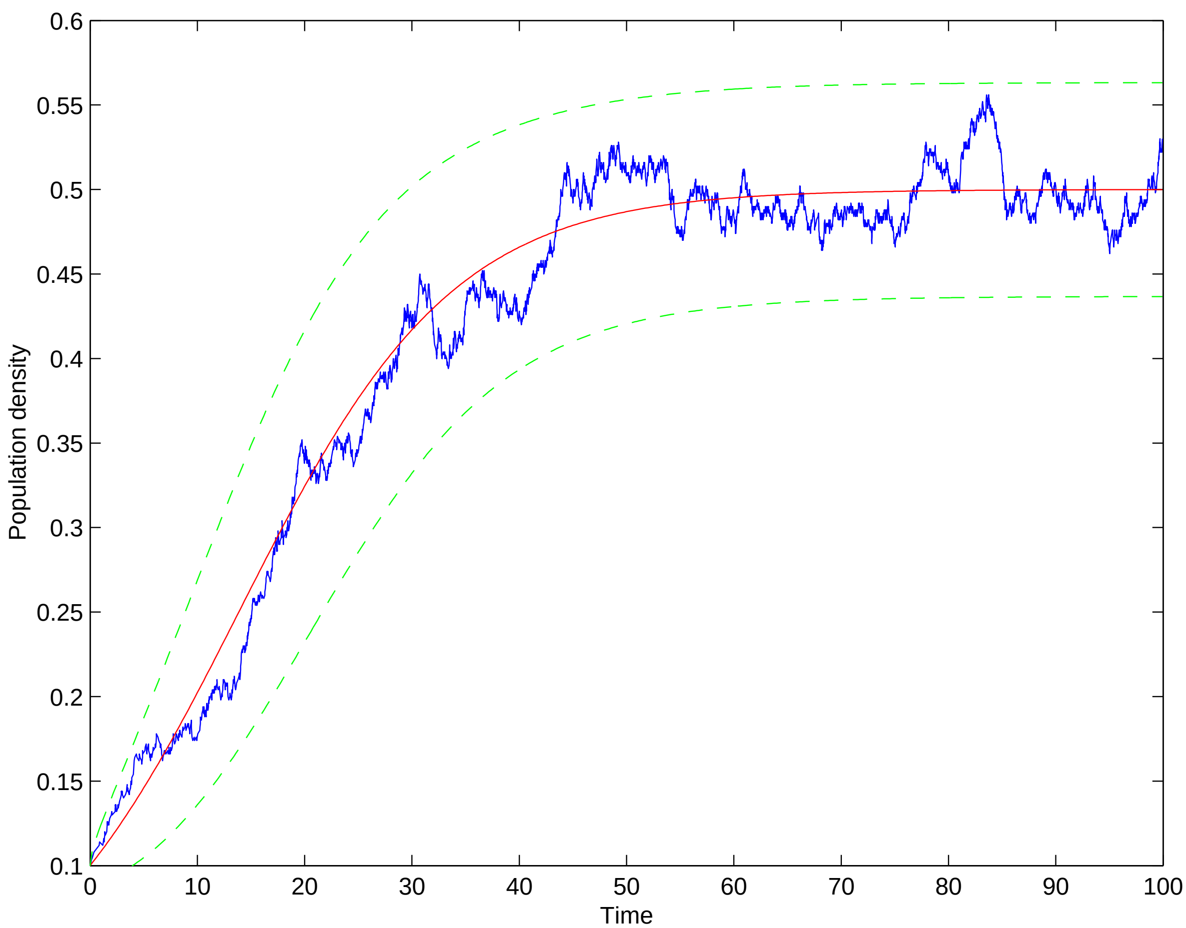
The stochastic logistic model. This model is ubiquitous in the literature on population modelling, but also appears in a variety of different contexts: for example, chemical kinetics, genetics and epidemics. It is a birth-death process $n(t)$ taking values in $S = \{0, 1, \ldots, N\}$ with birth and death rates

$$q(n, n+1) = \frac{\lambda}{N} n(N-n)$$
$$q(n, n-1) = \mu n \,,$$

where N is to be interpretted as the carrying capacity and $\lambda, \mu > 0$. Absorption at state 0 (representing the event of extinction) occurs with probability 1. We will consider the interesting case of positive drift: $\lambda > \mu$.

A diffusion approximation. There is a diffusion approximation for the *density* $X(t) = n(t)/N$, which becomes more and more accurate as N gets large.

Illustration. Here is a simulation of the logistic model, together with its diffusion approximation ($N = 500$, $\lambda = 0.2$, $\mu = 0.1$ and $X(0) = x_0 = 0.1$):



The mean path is shown (solid), with $\pm$ two standard deviations (dashed).

Specification of the approximation. $X(t)$ has an approximate normal $N\left(\mu_t, \sigma_t^2/N\right)$ distribution, where

$$\mu_t = \frac{q x_0}{x_0 + (q - x_0)e^{-\lambda q t}}, \quad t \geq 0,$$

$q = 1 - \rho$, $\rho = \mu/\lambda$ (< 1), and

$$\sigma_t^2 = M_t^2 \int_0^t \left(G(\mu_s)/M_s^2\right) ds,$$

where $G(x) = \lambda x(1 - x) + \mu x$, $0 \leq x \leq 1$, and

$$M_t = \frac{q^2 e^{-\lambda q t}}{(x_0 + (q - x_0)e^{-\lambda q t})^2}.$$

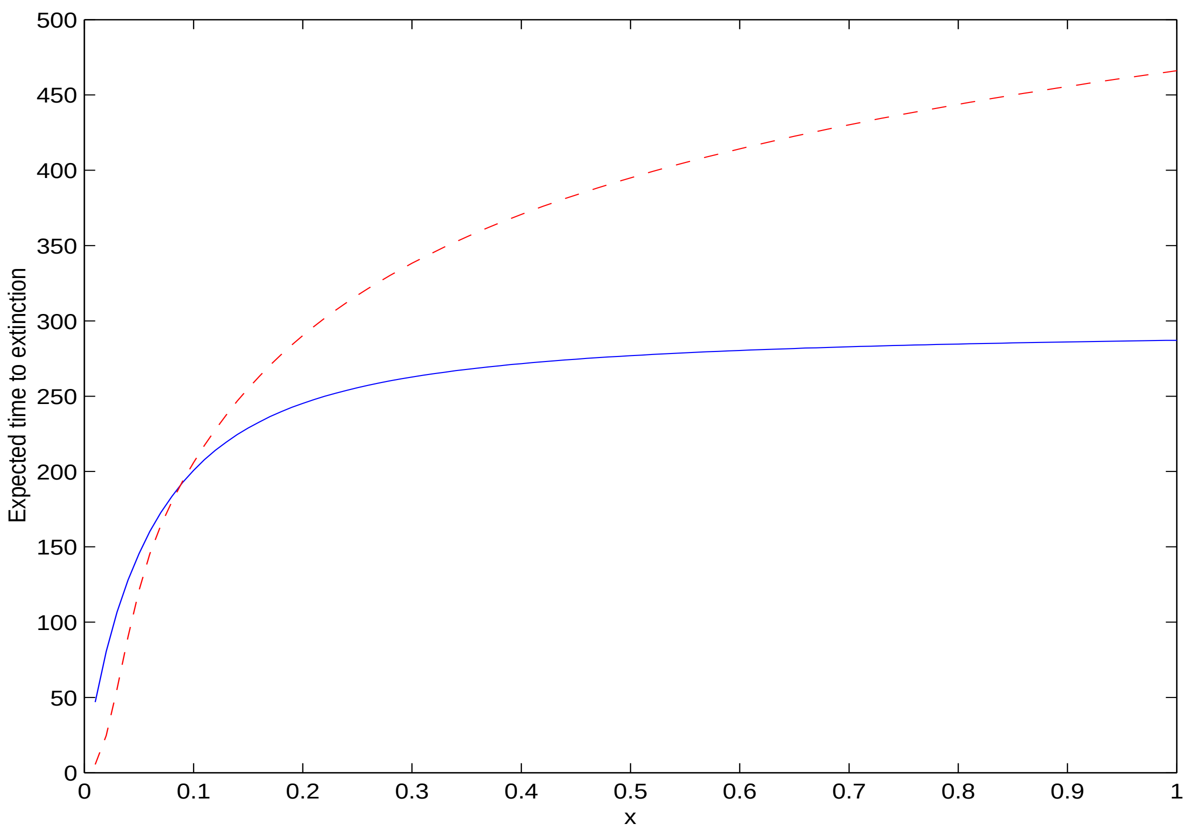
Note that $\sigma_t^2 \to \rho$ and $t \to \infty$.

Note also that q is an equilibrium point, which is asymptotically stable ($\mu_t \to q$). It can be shown that

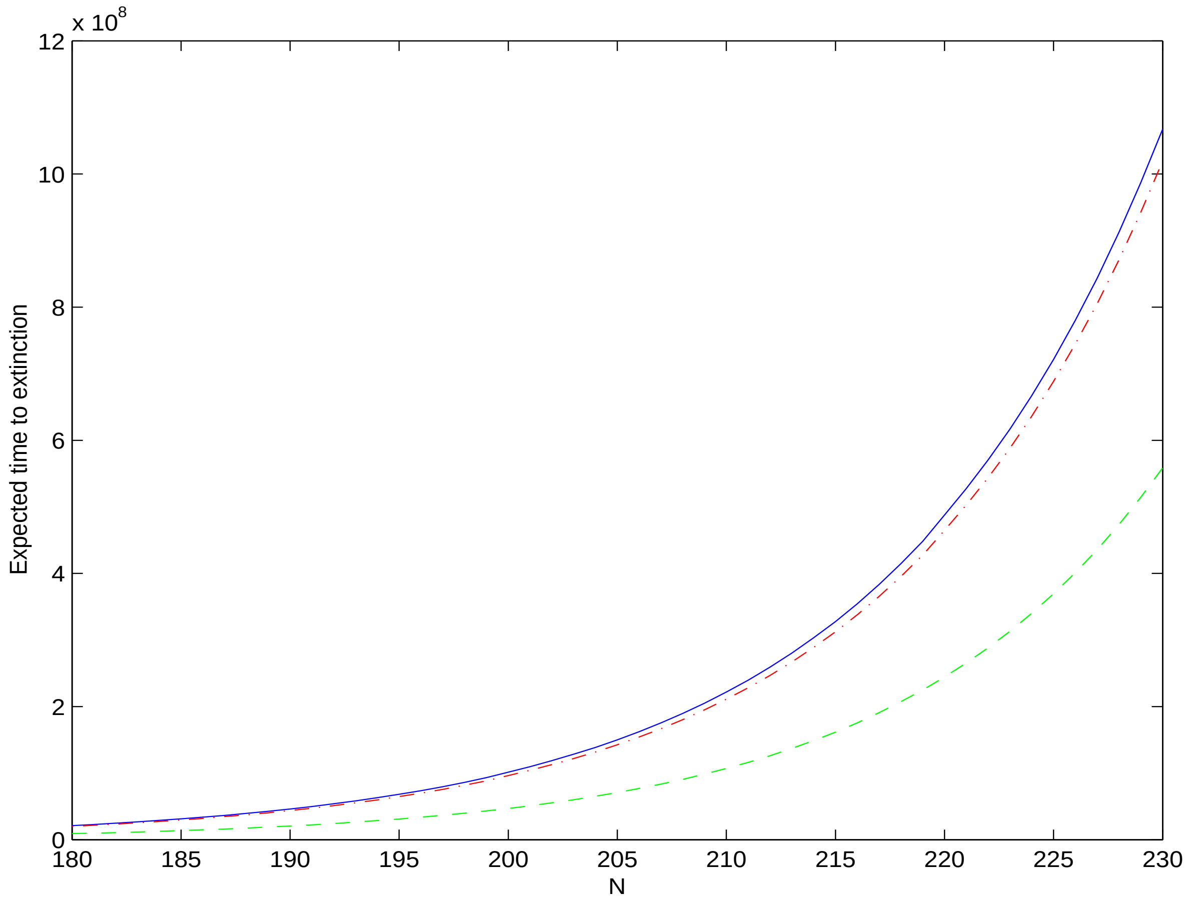
$$\sigma_t^2 = \rho(1 - e^{-2\lambda q t}) + O(|x_0 - q|),$$

for x_0 near q.

Extinction times. The diffusion approximation accurately models the density $X(t)$, but how good is it in predicting extinction times? Let τ_i be the expected time to extinction starting in state i.



The approximation (dashed) for τ_i is show, together with the exact values (solid) obtain directly from the logistic model ($N = 100$, $\lambda = 0.1111$, $\mu = 0.1$, $n(0) = n_0 = i$, $x_0 = x = i/N$).



Shown is the diffusion approximation (dashed) for τ_i, the exact values (solid) and a large-N asymptotic expansion (dash-dot):

$$\tau_i \sim \frac{\rho(1-\rho^i)}{\mu(1-\rho)^2}\left(\frac{e^{-(1-\rho)}}{\rho}\right)^N \sqrt{\frac{2\pi}{N}}.$$

($\rho = 0.1538$, $\mu = 0.1$, $x_0 = 0.05$, and $n_0 = i = [0.05 \times N]$.)

PAPER IN THE PROCEEDINGS

We identify a class of Markovian models (called *asymptotically density dependent* models) that permit a diffusion approximation through a simple limiting procedure. This procedure allows one to immediately identify the most appropriate approximating diffusion and to decide whether the diffusion approximation is appropriate for describing the population in question. Result are presented in a form that most easily permits their direct application to population models.

Additionally, results are presented that allow one to assess the accuracy of diffusion approximations by specifying for *how long* and *over what ranges* the underlying Markovian model is faithfully approximated.

The logistic model is considered in detail. In addition to diffusion approximations, several exact methods are presented, which are useful outside this context.