

Diffusion Approximation for a Metapopulation Model with Habitat Dynamics

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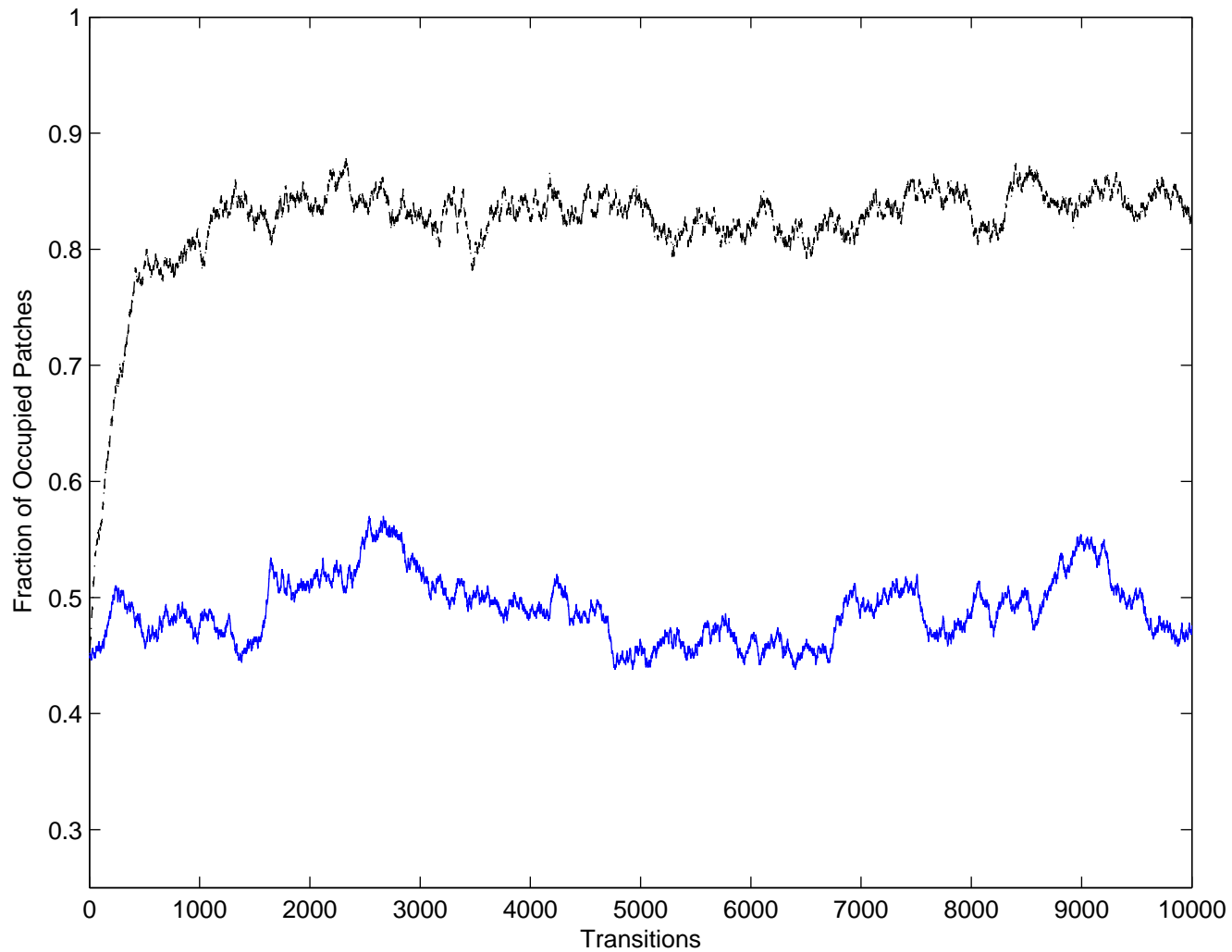
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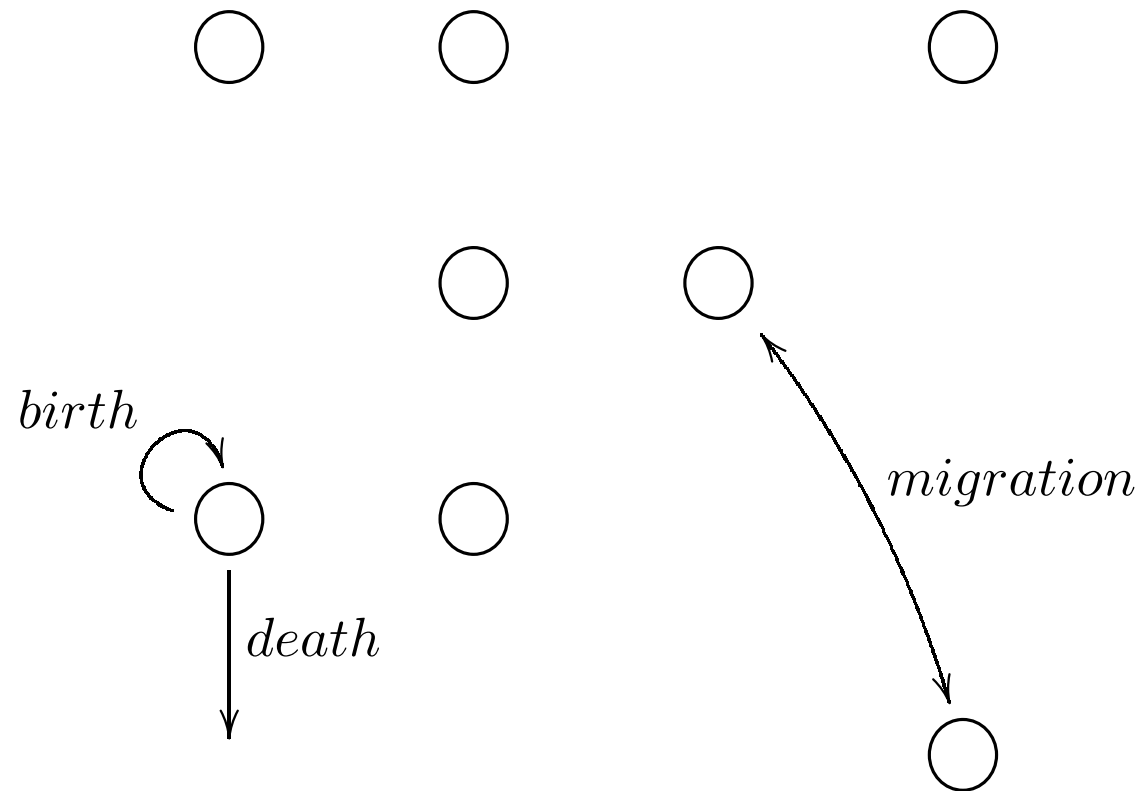
and

ARC Centre of Excellence for Mathematics and Statistics of Complex Systems

Introduction



A Metapopulation



The Model

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- Let M be the total number of patches in the network.
- Let $n(t)$ be the number of occupied patches at time t .
- Let $m(t)$ be the number of suitable patches at time t .
- Assume $\{(m(t), n(t)), t \geq 0\}$ is a Markov chain taking values in $S = \{(m, n) : 0 \leq n \leq m \leq M\}$.

Transition Rates

Stochastic logistic model

$$q((m, n), (m, n + 1)) = c \frac{n}{M} (M - n)$$

$$q((m, n), (m, n - 1)) = en$$

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Transition Rates

Stochastic logistic model **with varying carrying capacity**

$$q((m, n), (m, n + 1)) = c \frac{n}{M} (\textcircled{m} - n)$$

$$q((m, n), (m, n - 1)) = en$$

Transition Rates

A metapopulation model with habitat dynamics

$$q((m, n), (m, n + 1)) = c \frac{n}{M} (m - n)$$

$$q((m, n), (m, n - 1)) = en$$

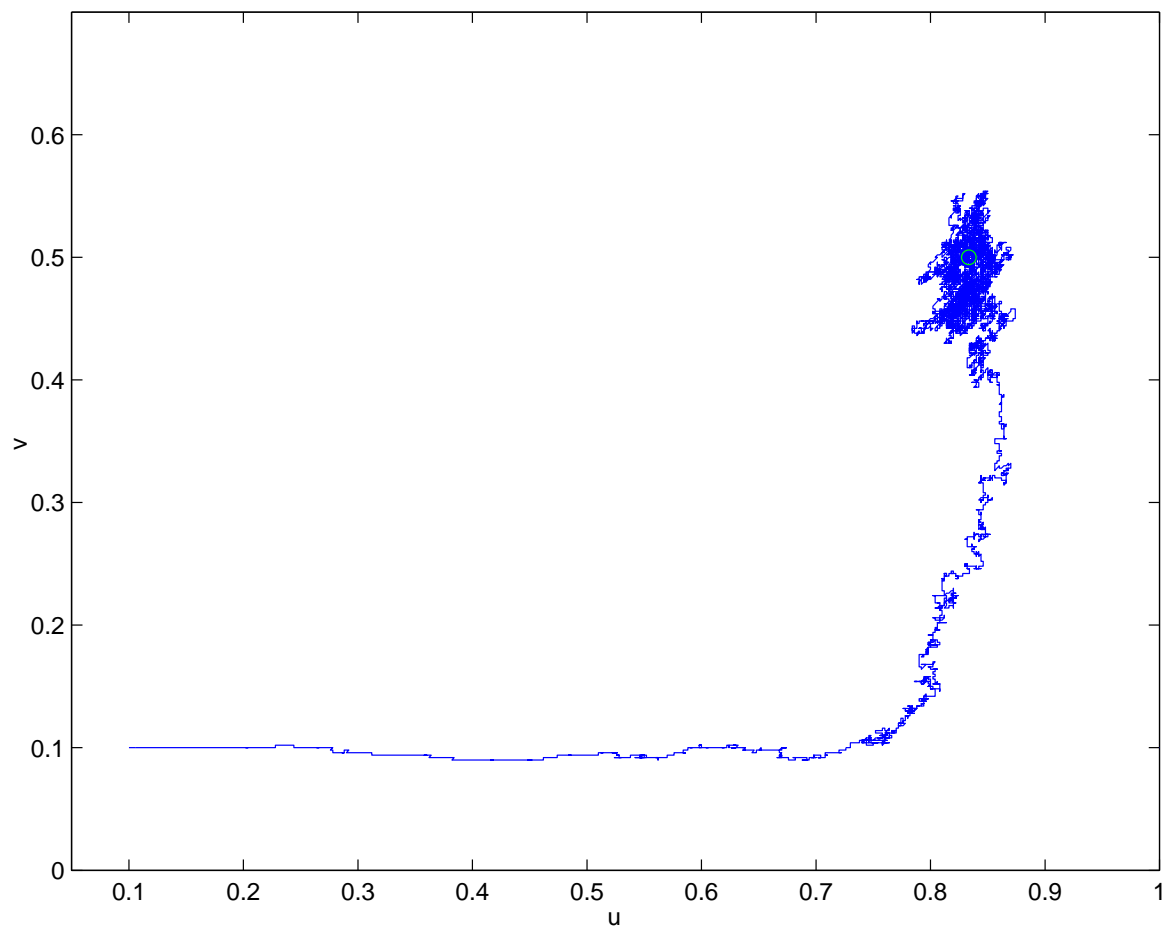
$$q((m, n), (m + 1, n)) = r(M - m)$$

$$q((m, n), (m - 1, n)) = s(m - n)$$

$$q((m, n), (m - 1, n - 1)) = sn.$$

A Simulation

$$u(t) = \frac{m(t)}{M}, v(t) = \frac{n(t)}{M}, M = 500, c = 0.6, e = 0.1, r = 0.5, s = 0.1.$$



Applications

- All metapopulations - natural fluctuations.

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- Metapopulations occupying successional habitats.
- Any fragmented population whose habitat experiences independent, exogenous disturbances;
Many species of butterfly*.

* Hanski, I.A. and Gaggiotti (Eds.) (2004) *Ecology Genetics and Evolution of Metapopulations*. Academic Press, London.

Applications

- All metapopulations - natural fluctuations.
- Metapopulations occupying successional habitats.
- Any fragmented population whose habitat experiences independent, exogenous disturbances;
Many species of butterfly.
- Standard population modelling - a stochastic logistic model with varying carrying capacity.

Density Dependence

- Results of Kurtz* and Barbour**

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

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

**Barbour, A.D. (1976) Quasi-stationary distributions in Markov population processes. *Adv. in Appl. Probab.* 8, 296-314.

Density Dependence

- Results of Kurtz and Barbour allow us to establish:
 1. A unique deterministic approximation to a suitably scaled version of the original process,

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Density Dependence

- Results of Kurtz and Barbour allow us to establish:
 1. A unique deterministic approximation to a suitably scaled version of the original process,
 2. A bivariate normal approximation to the state probabilities of the original process, and
 3. For how long this normal approximation is an adequate approximation to the original process.

What is Density Dependence?

Definition

A one-parameter family of Markov chains $\{P_\nu, \nu > 0\}$ with state space $S_\nu \subset \mathbb{Z}^D$ is called density dependent if there exists a set $E \subseteq \mathbb{R}^D$ and a continuous function $f : E \times \mathbb{Z}^D \rightarrow \mathbb{R}$, such that

$$q_\nu(k, k + l) = \nu f\left(\frac{k}{\nu}, l\right), \quad l \neq 0.$$

Remark. Thus, the family of Markov chains is density dependent if the transition rates of the corresponding “density process” $X_\nu(\cdot)$, defined by

$$X_\nu(t) := \frac{P_\nu(t)}{\nu}, \quad t \geq 0,$$

depend on the present state k only through the density k/ν .

What is Density Dependence?

If we take M , the total number of patches in the metapopulation network, as our index parameter and define the scaled process $x_M(t) = \{u(t), v(t)\} = \{m(t)/M, n(t)/M\}$ and its state space $E = \{(u, v) : 0 \leq v \leq u \leq 1\}$, then we may define a continuous function $f : E \times \mathbb{Z}^2 \rightarrow \mathbb{R}$ by

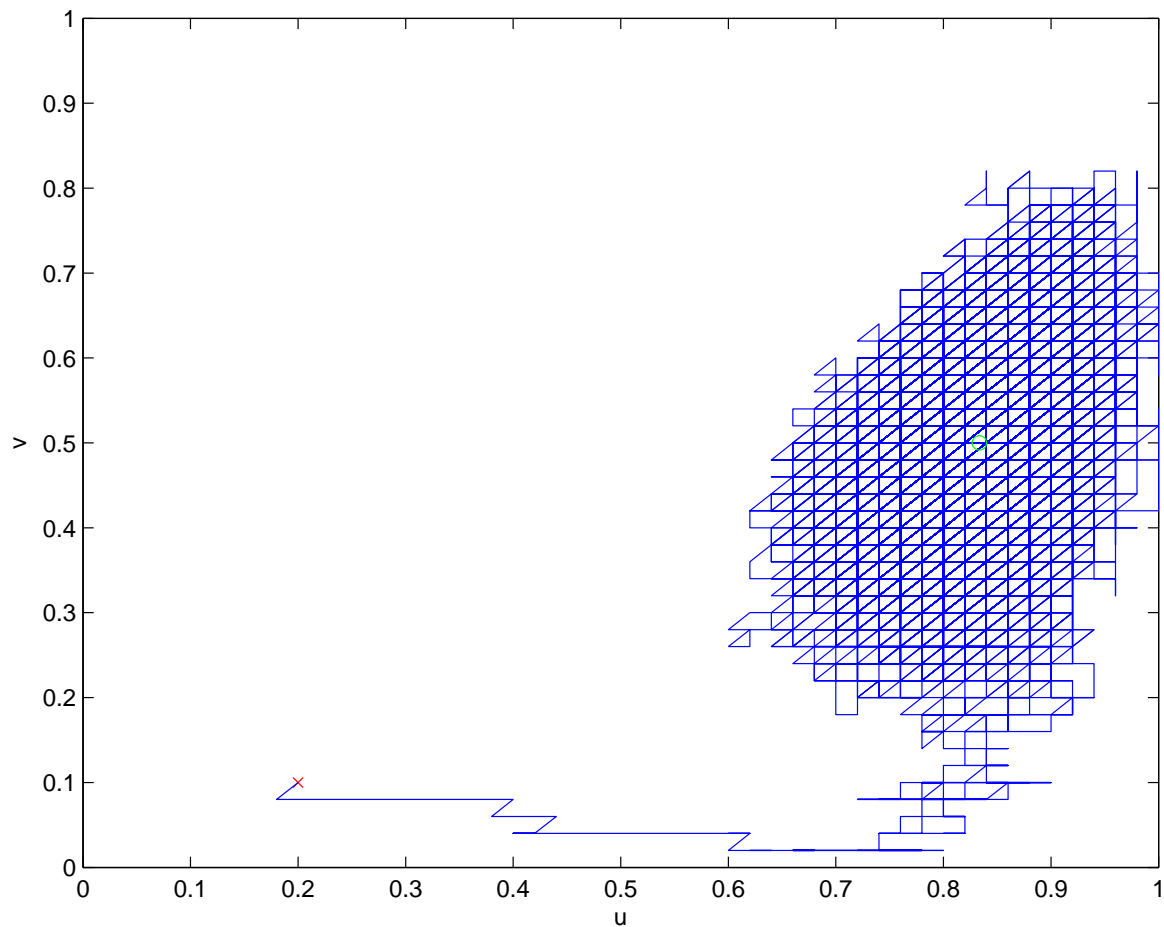
$$f(x, l) = \begin{cases} r(1 - u) & \text{if } l = (1, 0) \\ s(u - v) & \text{if } l = (-1, 0) \\ sv & \text{if } l = (-1, -1) \\ cv(u - v) & \text{if } l = (0, 1) \\ ev & \text{if } l = (0, -1). \end{cases}$$

Law of Large Numbers

$$\frac{1}{N} \sum_{i=1}^N x_i \rightarrow \mu$$

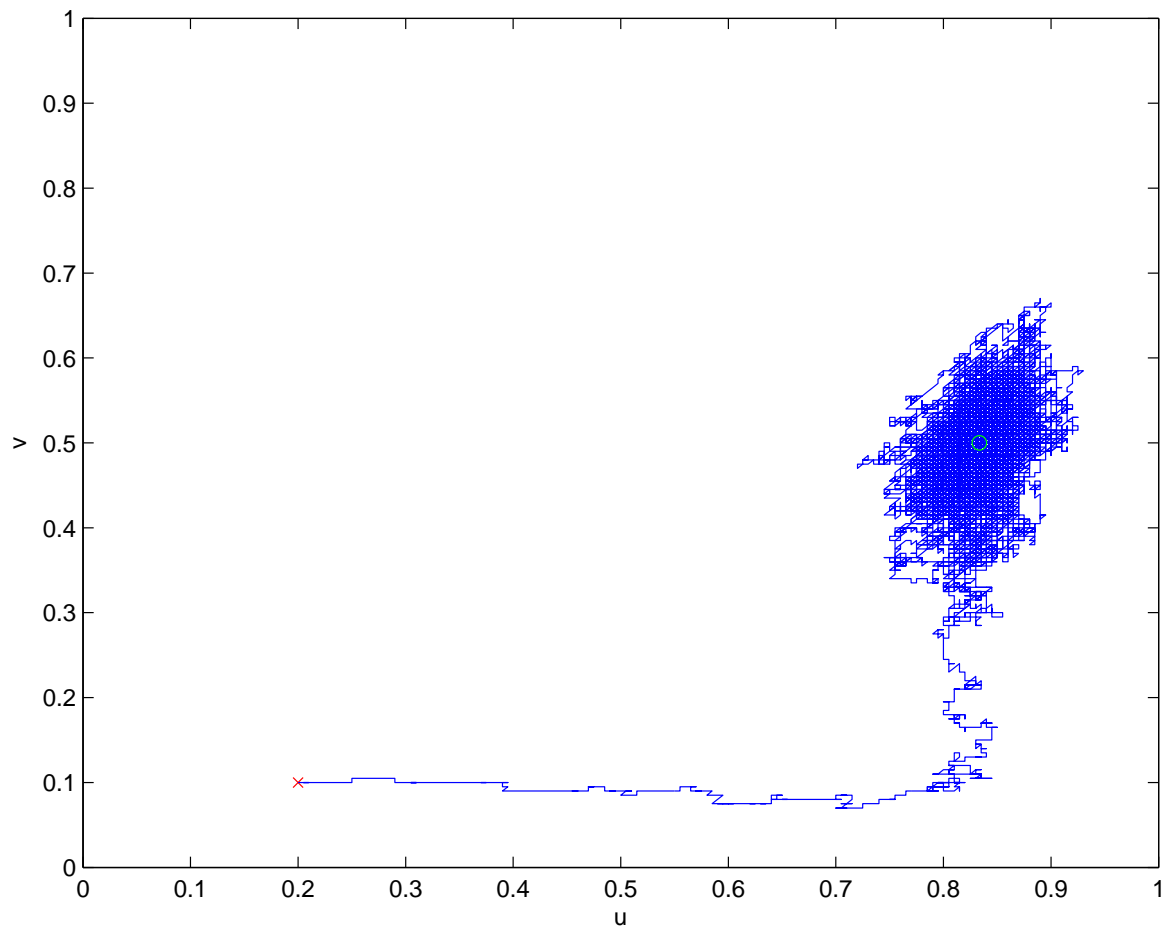
Law of Large Numbers

M=50



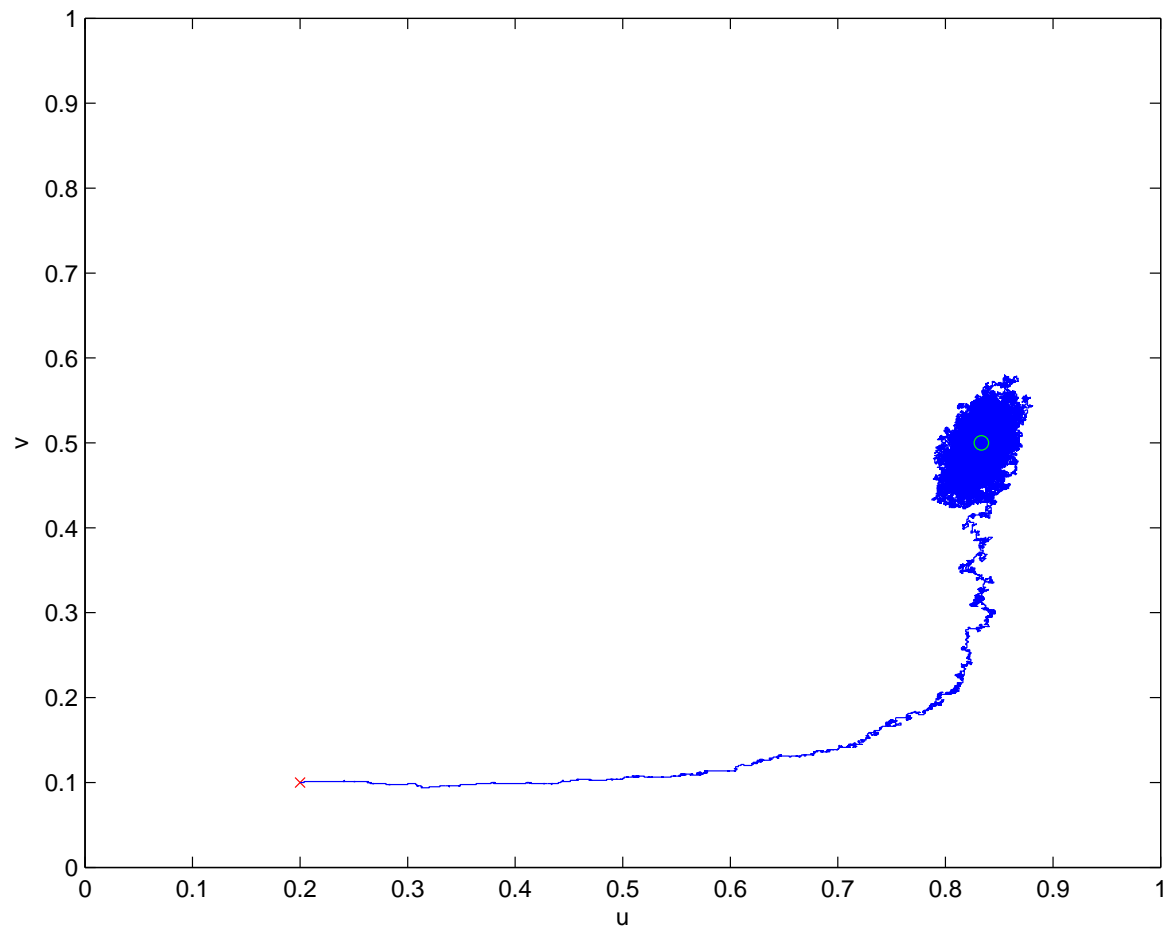
Law of Large Numbers

M=200



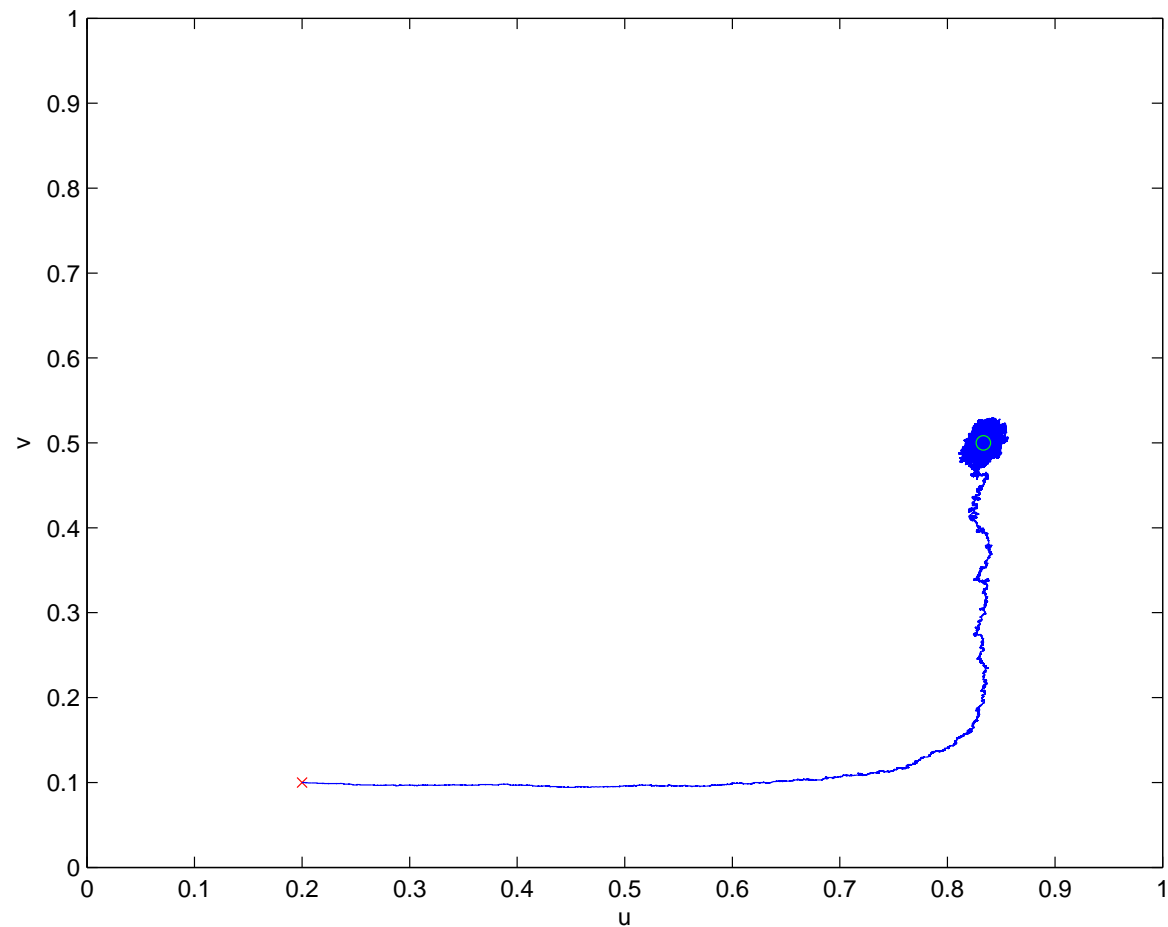
Law of Large Numbers

M=800



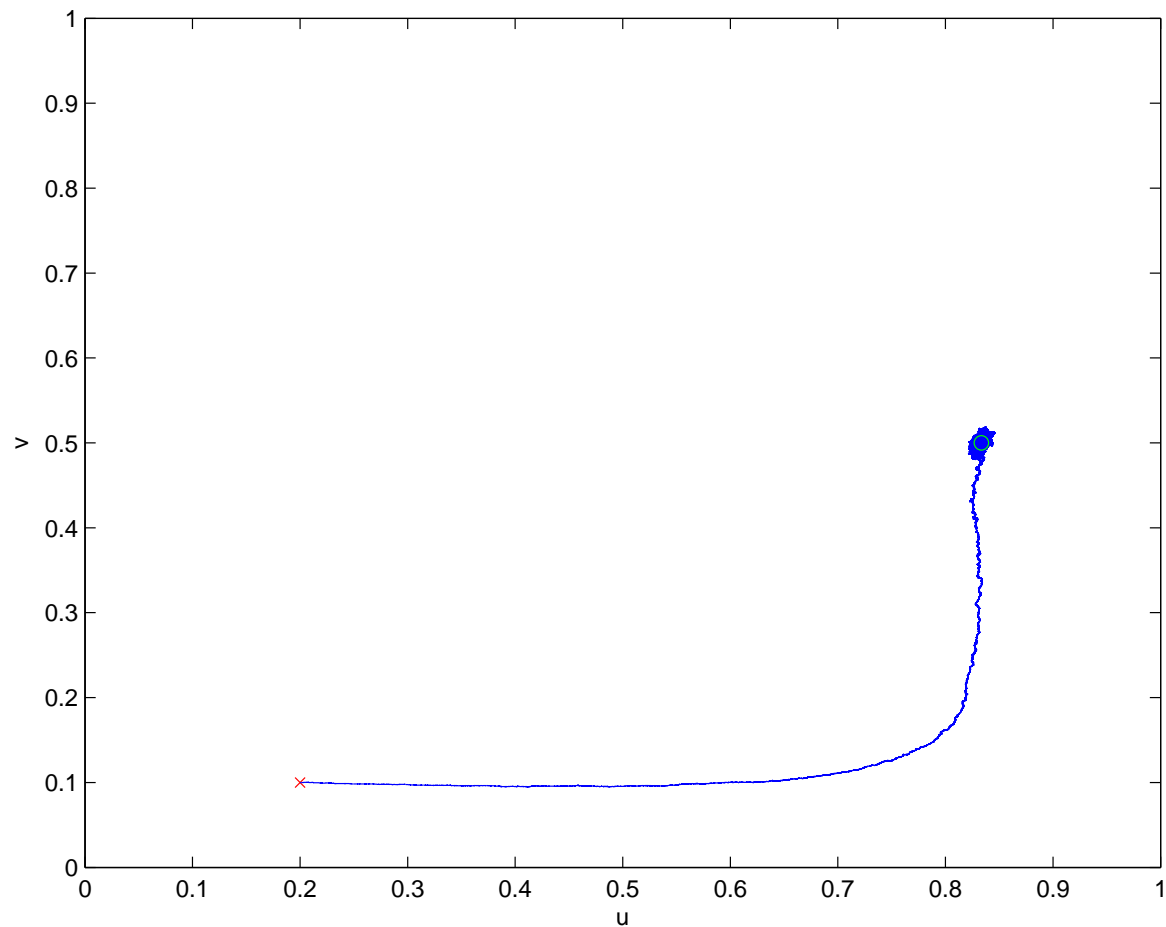
Law of Large Numbers

$M=3200$



Law of Large Numbers

$M=12800$



Law of Large Numbers

$$\frac{m(t)}{M} \rightarrow u(t)$$

$$\frac{n(t)}{M} \rightarrow v(t)$$

where $u(t)$ and $v(t)$ are given by a unique deterministic model.

Deterministic Approximation

$$\frac{du}{dt} = r - (r + s)u$$

$$\frac{dv}{dt} = cv(u - v) - (e + s)v$$

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Studied previously by Johnson*.

*Johnson, M.P. (2000) The influence of patch demographics on metapopulations, with particular reference to successional landscapes. *Oikos* 88, 67-74.

Deterministic Approximation

$$\frac{du}{dt} = r - (r + s)u$$

$$\frac{dv}{dt} = cv(u - v) - (e + s)v$$

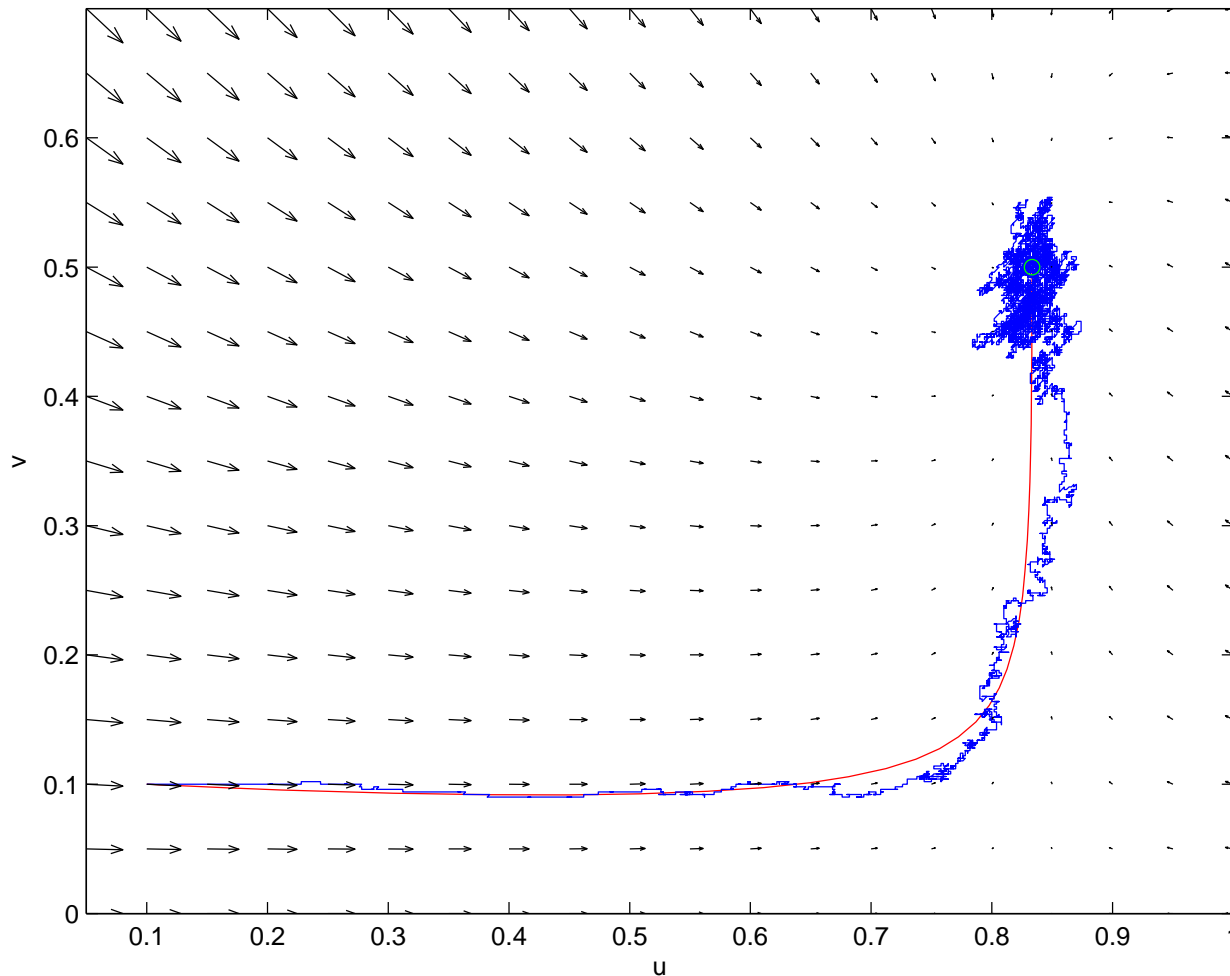
Studied previously by Johnson: has non-trivial fixed point

$$\left(\frac{r}{r + s}, \frac{r}{r + s} - \frac{e + s}{c} \right)$$

and persistence condition

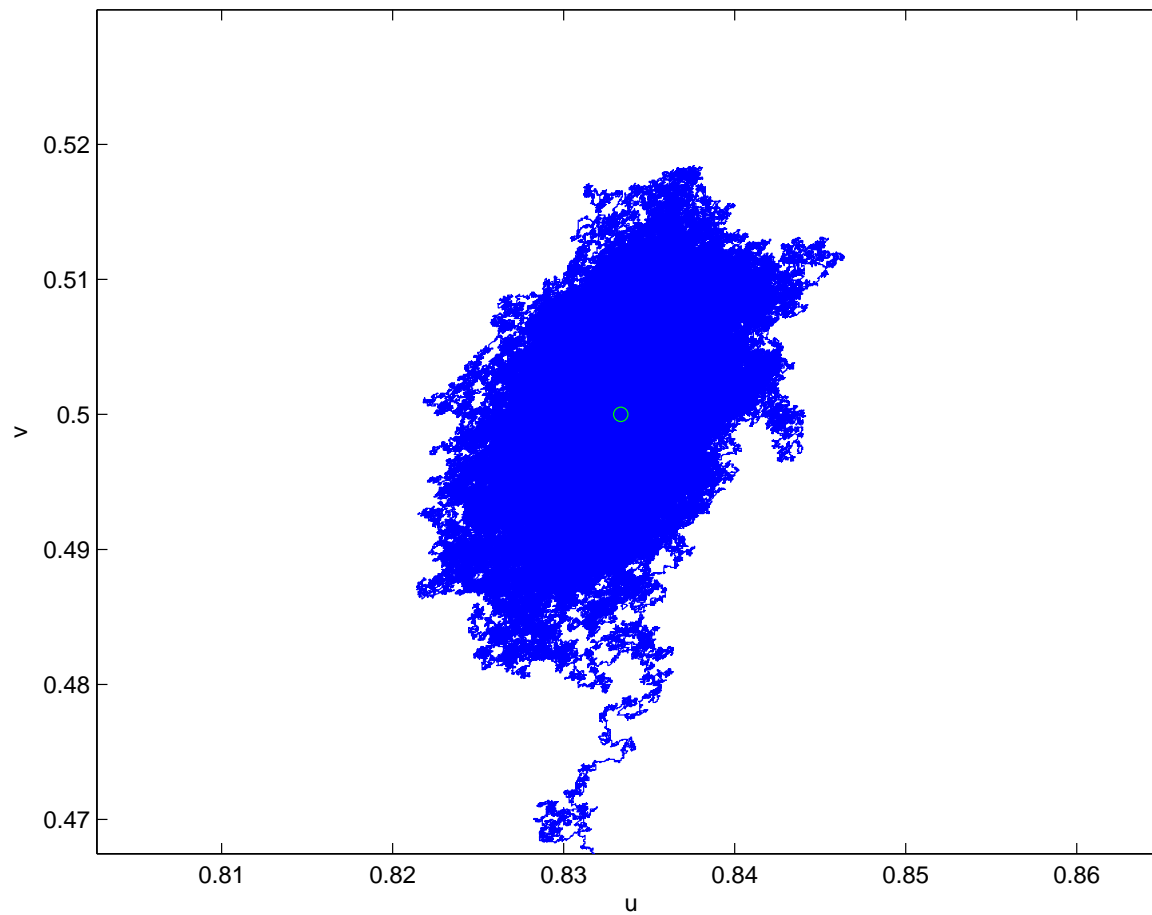
$$\frac{r}{r + s} > \frac{e + s}{c}.$$

Deterministic Model



Variation

M=12800



Normal Approximation

- The second set of results of Kurtz and Barbour allow us to approximate the state-probabilities of the original process, corresponding to the number of suitable and occupied patches, by a normal distribution.

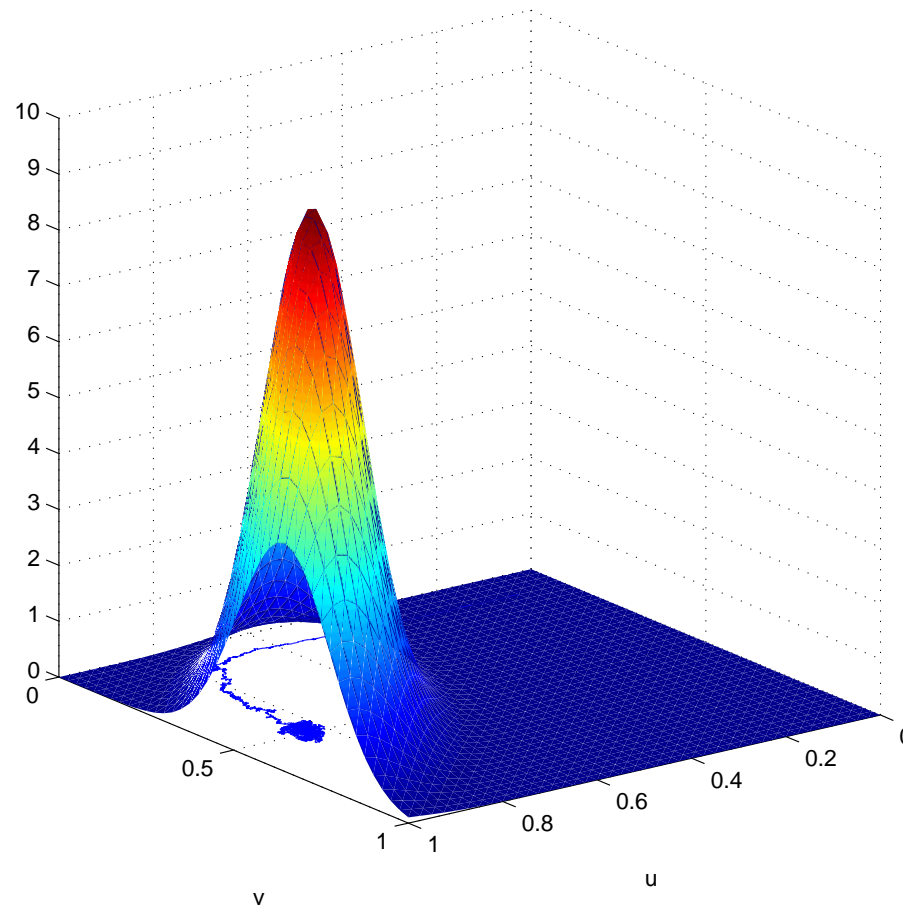
Normal Approximation

- The second set of results of Kurtz and Barbour allow us to approximate the state-probabilities of the original process, corresponding to the number of suitable and occupied patches, by a normal distribution.
- For our model this is a bivariate normal distribution centered at the fixed point of the deterministic model.

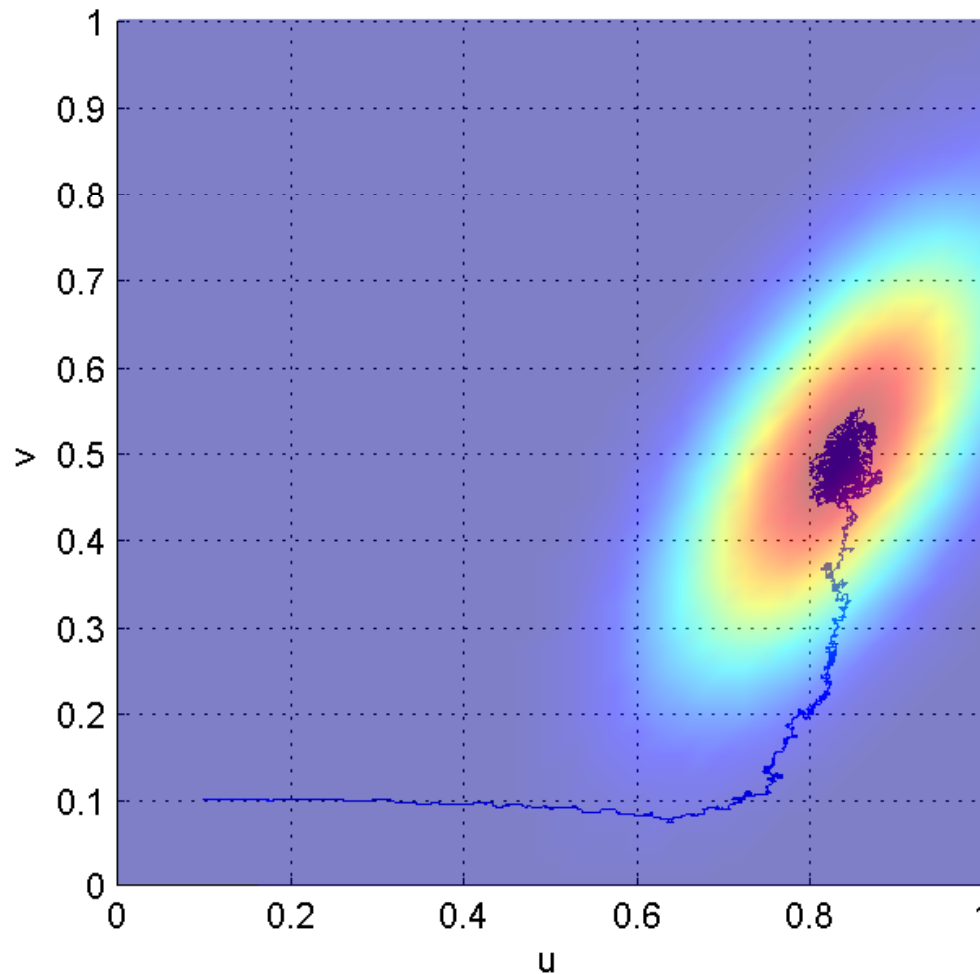
Central Limit Theorem

$$\sqrt{N} \left(\frac{1}{N} \sum_{i=1}^N x_i - \mu \right) \rightarrow N(0, \sigma^2)$$

Normal Approximation - Surface



Normal Approximation - Contours



Variance

- The normal approximation gives the likelihood function and thus provides a framework for statistical inference.

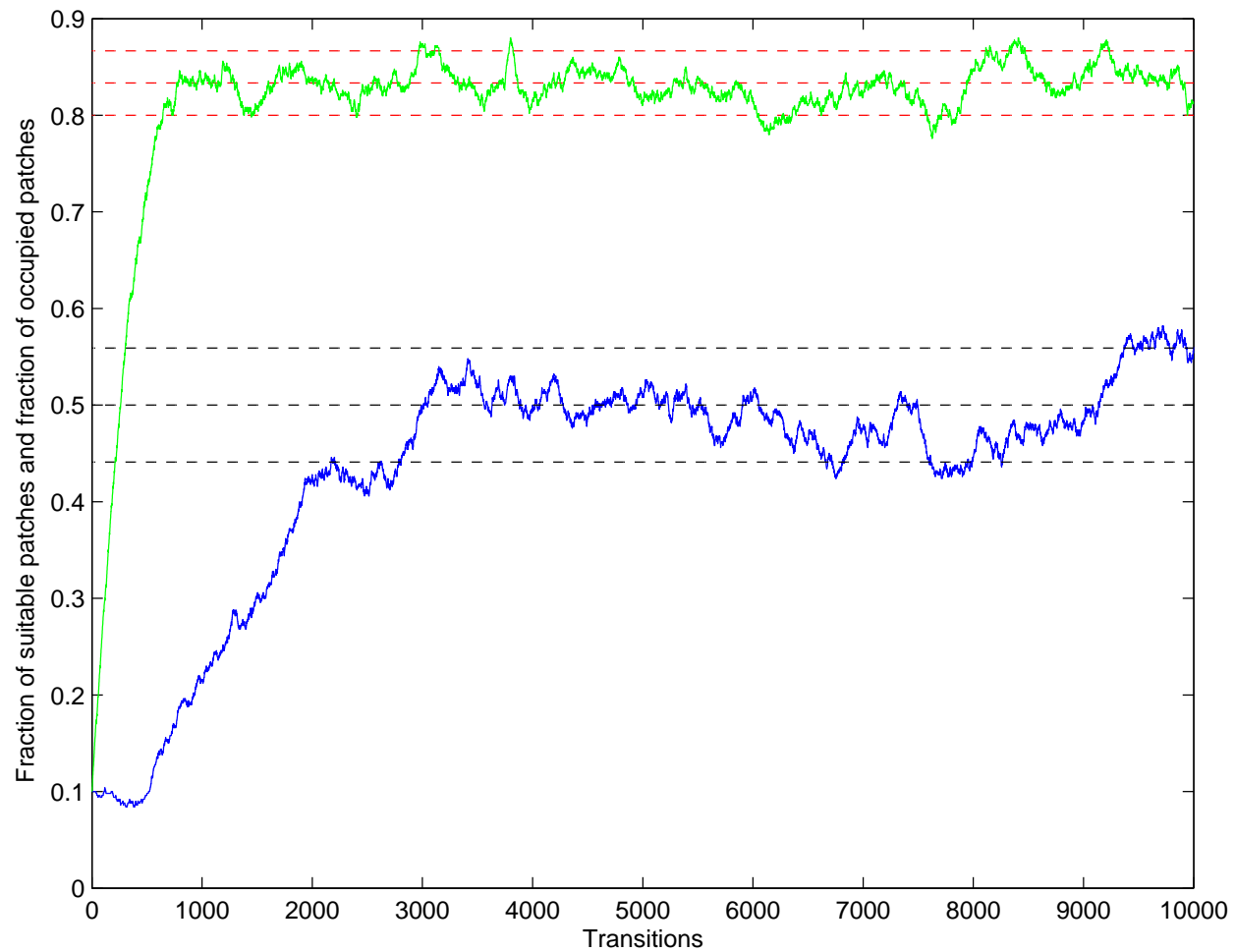
Variance

- The normal approximation gives the likelihood function and thus provides a framework for statistical inference.
- We now have the variance in the number of suitable and occupied patches.

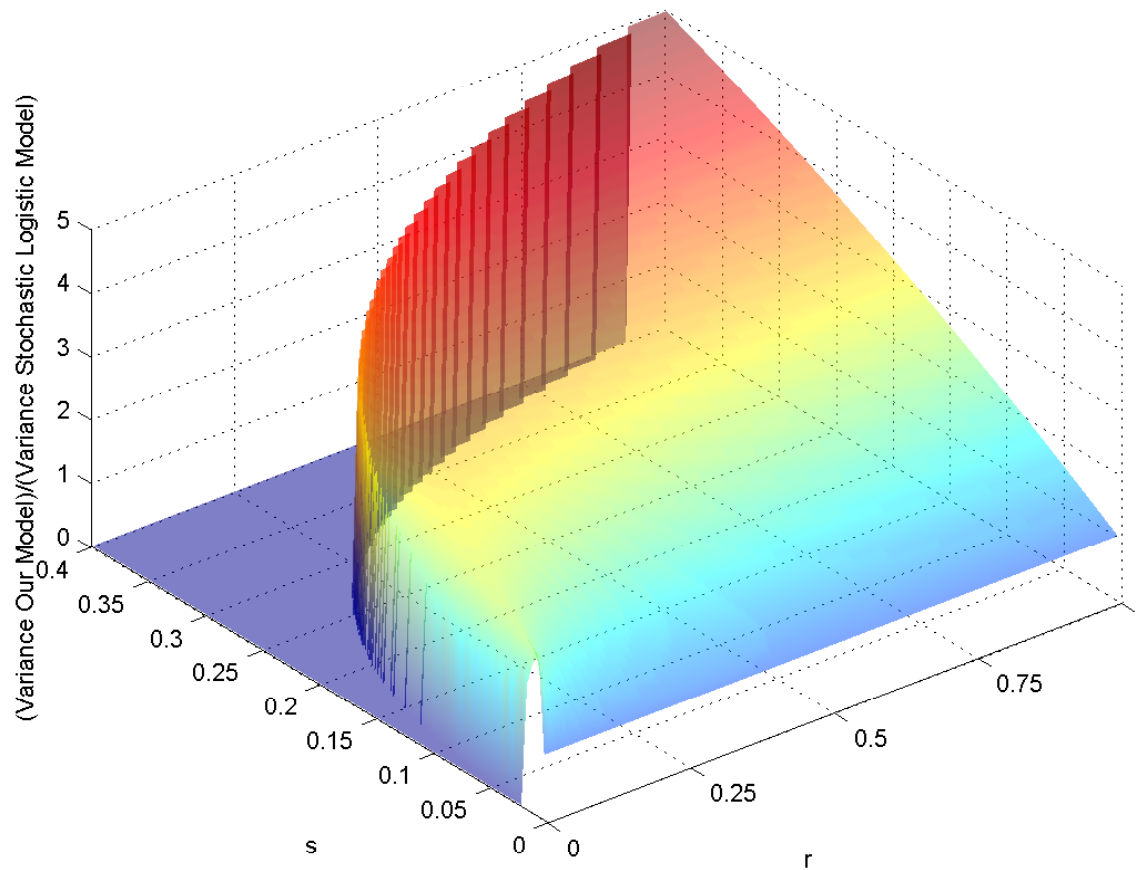
Variance

- The normal approximation gives the likelihood function and thus provides a framework for statistical inference.
- We now have the variance in the number of suitable and occupied patches.
- We can now take into account the variability of the population when making ecological assessments.

Confidence Intervals



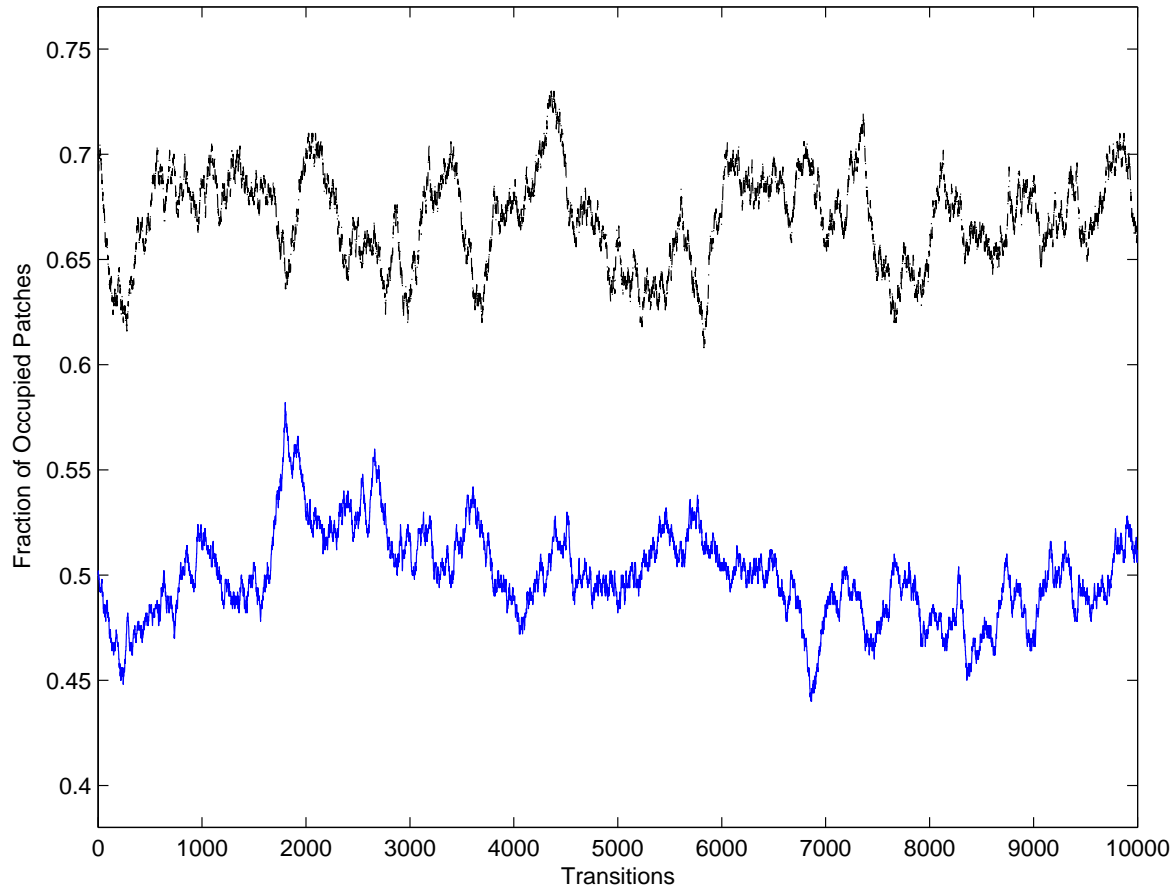
Increase in Variance



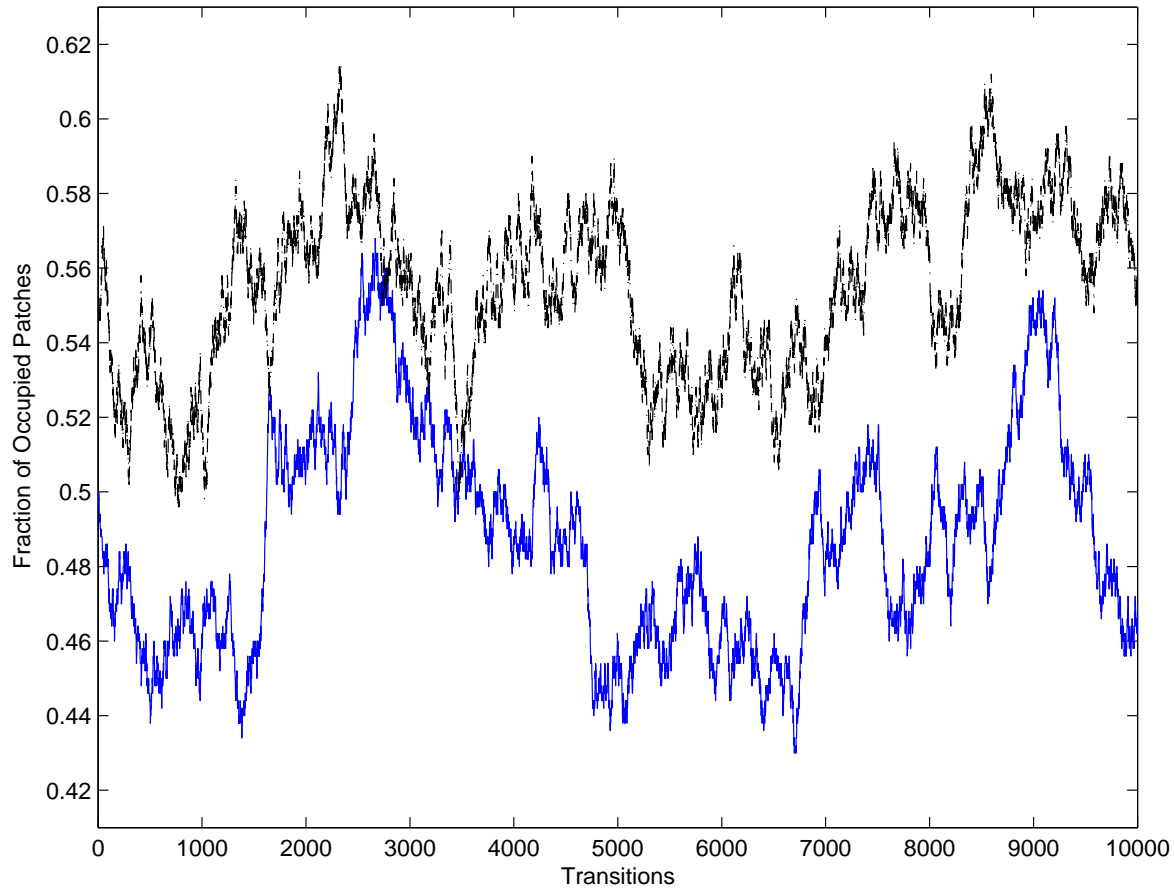
Comparison to Existing Models

<i>Model</i>	<i>FP</i>	<i>PC</i>
New Model	$\left(\frac{r}{r+s}, \frac{r}{r+s} - \frac{e+s}{c} \right)$	$\frac{r}{r+s} > \frac{e+s}{c}$
Stochastic Logistic Model with $e + s$	$1 - \frac{e+s}{c}$	$c > e + s$
SLM with $e + s$ & reduced habitat	$\frac{r}{r+s} \left[1 - \frac{e+s}{c} \right]$	$c > e + s$

Comparison of Models



Comparison of Models



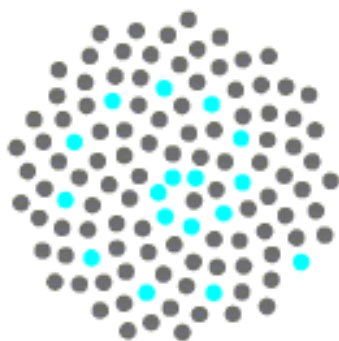
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AUSTRALIAN RESEARCH COUNCIL

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