Stochastic models for population networks

III: Discrete-time patch occupancy models
[Deterministic and Gaussian approximations]

Phil Pollett

Department of Mathematics
The University of Queensland
http://www.maths.uq.edu.au/~pkp
Collaborators

Fionnuala Buckley (MASCOS)
Department of Mathematics
The University of Queensland

Ross McVinish (MASCOS)
Department of Mathematics
The University of Queensland
Colonization
Metapopulations
Metapopulations

Local Extinction
Mainland-island configuration
Mainland-island configuration

Colonization from the mainland
A metapopulation is a population that is confined to a network of geographically separated habitat patches (for example a group of islands).

Individual patches may suffer local extinction.

Recolonization can occur through dispersal of individuals from other patches.

In some instances there is an external source of immigration (mainland-island configuration).
Many species have life cycles (often annual) that consist of distinct phases, and the propensity for colonization and local extinction is different in each phase. Examples:

The Vernal pool fairy shrimp (Branchinecta lynchi) and the California linderiella (Linderiella occidentalis), both listed under the Endangered Species Act (USA)

The Jasper Ridge population of Bay checkerspot butterfly (Euphydryas editha bayensis), now extinct
There are $J$ patches. We record the number $n_t$ occupied at time $t$ and suppose that $(n_t, t \geq 0)$ is a discrete-time Markov chain taking values in $\{0, 1, \ldots, J\}$ with transition matrix $P = (p_{ij})$.

We assume that colonization (C) and extinction (E) occur in separate distinct phases which are governed by their own transition matrices, $E = (e_{ij})$ and $C = (c_{ij})$. Then, $P = EC$ if the census is taken after the colonization phase or $P = CE$ if the census is taken after the extinction phase.
\[ P = EC \]

\[ P = CE \]
Recall that the number of extinctions when there are \( i \) patches occupied follows a Bin\((i, e)\) law (\(0 < e < 1\)):

\[
e_{i,i-k} = \binom{i}{k} e^k (1 - e)^{i-k} \quad (k = 0, 1, \ldots, i).
\]

\((e_{ij} = 0 \text{ if } j > i.)\) The number of colonizations when there are \( i \) patches occupied follows a Bin\((J - i, c_i)\) law:

\[
c_{i,i+k} = \binom{J - i}{k} c_i^k (1 - c_i)^{J-i-k} \quad (k = 0, 1, \ldots, J - i).
\]

\((c_{ij} = 0 \text{ if } j < i.)\)
Previously we look at two cases.

- \( c_i = (i/J)c \), where \( c \in (0, 1] \) (\( c \) is the maximum colonization potential).

This entails \( c_{0j} = \delta_{0j} \), so that 0 is an absorbing state and \( \{1, \ldots, J\} \) is a communicating class.
Previously we look at two cases.

- $c_i = (i/J)c$, where $c \in (0, 1]$ ($c$ is the maximum colonization potential).

  This entails $c_{0j} = \delta_{0j}$, so that 0 is an absorbing state and $\{1, \ldots, J\}$ is a communicating class.

- $c_i = c$, where $c \in (0, 1]$ (fixed colonization probability—the Mainland-Island configuration).

  Now $\{0, 1, \ldots, J\}$ is irreducible.
Previously we look at two cases.

- \( c_i = (i/J)c \), where \( c \in (0, 1] \) (\( c \) is the maximum colonization potential).
  
  This entails \( c_{0j} = \delta_{0j} \), so that 0 is an absorbing state and \( \{1, \ldots, J\} \) is a communicating class.

- \( c_i = c \), where \( c \in (0, 1] \) (fixed colonization probability—the Mainland-Island configuration).
  
  Now \( \{0, 1, \ldots, J\} \) is irreducible.

Other possibilities include \( c_i = c(1 - (1 - c_1/c)^i) \) and \( c_i = 1 - \exp(-i\beta/J) \).
We might also “combine” the two models and thus account for both internal and external colonization: the number of colonizations when there are \( i \) patches occupied will be \( C \sim Bin(J - i, d + ic/J) \).
We might also “combine” the two models and thus account for both internal and external colonization: the number of colonizations when there are \( i \) patches occupied will be \( C \sim Bin(J - i, d + ic/J) \).

We obtained explicit results for the Mainland-Island model ...
Let $a = p - q = (1 - e)(1 - c)$ $(0 < a < 1)$ and $q^* = q/(1 - a)$, where

- **EC-model:** $p = 1 - e(1 - c)$ and $q = c$
- **CE-model:** $p = 1 - e$ and $q = (1 - e)c$
Let $a = p - q = (1 - e)(1 - c)$ ($0 < a < 1$) and $q^* = q/(1 - a)$, where

- **EC-model:** $p = 1 - e(1 - c)$ and $q = c$
- **CE-model:** $p = 1 - e$ and $q = (1 - e)c$

Define sequences $(p_t)$ and $(q_t)$ by

$$q_t = q^*(1 - a^t) \quad \text{and} \quad p_t = q_t + a^t \quad (t \geq 0).$$
Let \( a = p - q = (1 - e)(1 - c) \) (\( 0 < a < 1 \)) and \( q^* = q/(1 - a) \), where

- **EC-model**: \( p = 1 - e(1 - c) \) and \( q = c \)
- **CE-model**: \( p = 1 - e \) and \( q = (1 - e)c \)

Define sequences \((p_t)\) and \((q_t)\) by

\[
q_t = q^*(1 - a^t) \quad \text{and} \quad p_t = q_t + a^t \quad (t \geq 0).
\]

**Theorem**  Given \( n_0 = i \) patches occupied initially, the number \( n_t \) occupied at time \( t \) has the same distribution as \( B_1 + B_2 \), where \( B_1 \) and \( B_2 \) are independent random variables with \( B_1 \sim Bin(i, p_t) \) and \( B_2 \sim Bin(J - i, q_t) \). The limiting distribution of \( n_t \) is \( Bin(J, q^*) \).
We saw that

\[ E(n_t|n_0 = i) = ip_t + (J - i)q_t = ia^t + Jq_t \]

(\( \rightarrow Jq^* \text{ as } t \rightarrow \infty \))

and

\[ \text{Var}(n_t|n_0 = i) = ip_t(1 - p_t) + (J - i)q_t(1 - q_t) \]

\[ = ia^t(1 - a^t)(1 - 2q^*) + Jq_t(1 - q_t) \]

(\( \rightarrow Jq^*(1 - q^*) \text{ as } t \rightarrow \infty \)).
We saw that

\[ E(n_t|n_0 = i) = ipt + (J - i)qt = ia^t + Jqt \]

\[ (\rightarrow Jq^* \text{ as } t \rightarrow \infty) \]

and

\[ \text{Var}(n_t|n_0 = i) = ipt(1 - pt) + (J - i)qt(1 - qt) \]

\[ = ia^t(1 - a^t)(1 - 2q^*) + Jqt(1 - qt) \]

\[ (\rightarrow Jq^*(1 - q^*) \text{ as } t \rightarrow \infty) \].

Now let \( X_t^{(J)} = n_t / J \) be the proportion of occupied patches at time \( t \). Let \((i^{(J)})\) be a sequence of initial states such that \( x_0^{(J)} := i^{(J)}/J \rightarrow x_0 \). Then, ...
Mainland-Island models: \( J \to \infty \)

As \( J \to \infty \),

\[
E(X_t^{(J)}) \to x_0 p_t + (1 - x_0) q_t
\]

and

\[
J \ Var(X_t^{(J)}) \to x_0 p_t (1 - p_t) + (1 - x_0) q_t (1 - q_t).
\]
Mainland-Island models: \( J \to \infty \)

As \( J \to \infty \),

\[
\mathbb{E}(X_t^{(J)}) \to x_0 p_t + (1 - x_0) q_t
\]

and

\[
J \ Var(X_t^{(J)}) \to x_0 p_t (1 - p_t) + (1 - x_0) q_t (1 - q_t).
\]

Indeed, \( X_t^{(J)} \xrightarrow{P} x_t \), where \( x_t = x_0 p_t + (1 - x_0) q_t \), and, if \( \sqrt{J}(x_0^{(J)} - x_0) \to z_0 \) (the sequence of initial proportions converges to \( x_0 \) at the “correct” rate), then

\[
\sqrt{J}(X_t^{(J)} - x_t) \xrightarrow{D} Z_t, \text{ where } Z_t \sim \mathcal{N}(a^t z_0, v_t)
\]

and

\[
v_t = x_0 p_t (1 - p_t) + (1 - x_0) q_t (1 - q_t).
\]
We can do better …

**Theorem** \( (X^{(J)}_{t_1}, X^{(J)}_{t_2}, \ldots, X^{(J)}_{t_n}) \xrightarrow{P} (x_{t_1}, x_{t_2}, \ldots, x_{t_n}) \), for any finite sequence of times \( t_1, t_2, \ldots, t_n \).
Mainland-Island models: $J \to \infty$

We can do better . . .

**Theorem**  \((X^{(J)}_{t_1}, X^{(J)}_{t_2}, \ldots, X^{(J)}_{t_n}) \xrightarrow{P} (x_{t_1}, x_{t_2}, \ldots, x_{t_n})\), for any finite sequence of times \(t_1, t_2, \ldots, t_n\).

For the corresponding central limit law, define the process \((Z^{(J)}_t, t \geq 0)\) by

\[Z^{(J)}_t = \sqrt{J}(X^{(J)}_t - x_t)\]

and suppose that \(\sqrt{J}(x^{(J)}_0 - x_0) \to z_0\).
**Theorem** The finite-dimensional distributions (FDDs) of \((Z_t^{(J)})\) converge to those of the Gaussian Markov chain \((Z_t)\) defined by

\[
Z_{t+1} = aZ_t + E_t \quad (Z_0 = z_0),
\]

where \(a = p - q = (1 - e)(1 - c)\) and \(E_t\) \((t = 0, 1, \ldots)\) are independent Gaussian random variables with \(E_t \sim N(0, \sigma_t^2)\), where

\[
\sigma_t^2 = x_t p(1 - p) + (1 - x_t) q(1 - q).
\]
Simulation: $P = EC$

Mainland-Island simulation $P = EC$ ($J = 100$, $x_0 = 0.05$, $e = 0.01$, $c = 0.05$)
Mainland-Island simulation $P = EC$ ($J = 100$, $x_0 = 0.05$, $e = 0.01$, $c = 0.05$)
Simulation: $P = EC$ (Gaussian approx.)

Mainland-Island simulation $P = EC$ ($J = 100$, $x_0 = 0.05$, $e = 0.01$, $c = 0.05$)

Deterministic path ± two standard deviations
Mainland-Island models: $J \rightarrow \infty$

We can also model the fluctuations about the limiting proportion of patches $q^*$. Let $Z_t^{(J)} = \sqrt{J}(X_t^{(J)} - q^*)$ and suppose that $\sqrt{J}(x_0^{(J)} - q^*) \rightarrow z_0$. 


We can also model the fluctuations about the limiting proportion of patches $q^*$. Let $Z_t^{(J)} = \sqrt{J}(X_t^{(J)} - q^*)$ and suppose that $\sqrt{J}(x_0^{(J)} - q^*) \to z_0$.

**Corollary** The FDDs of $(Z_t^{(J)})$ converge to those of the autoregressive (AR-1) process $(Z_t)$ defined by

$$Z_{t+1} = aZ_t + E_t \quad (Z_0 = z_0),$$

where $a = p - q = (1 - e)(1 - c)$ and $E_t \ (t = 0, 1, \ldots)$ are iid Gaussian $\mathcal{N}(0, \sigma^2)$ random variables with $\sigma^2 = q^*(1 - q^*)(1 - a^2)$. 
Simulation: $P = EC$

Mainland-Island simulation $P = EC$ ($J = 100$, $x_0 = 0.05$, $e = 0.01$, $c = 0.05$)

$q^* = 0.84034$
Simulation: \( P = EC \) (AR-1 approx.)

Mainland-Island simulation \( P = EC \) \( (J = 100, x_0 = 0.05, e = 0.01, c = 0.05) \)

\[ q^* = 0.84034 \]
AR-1 Simulation: \( P = EC \)

\[
\text{AR-1 simulation } P = EC \ (J = 100, x_0 = 0.84034, e = 0.01, c = 0.05)
\]

\[x^* = 0.84034\]
Can we establish deterministic and Gaussian approximations for the basic $J$-patch models (where the distribution of $n_t$ is not known explicitly)?
Can we establish deterministic and Gaussian approximations for the basic $J$-patch models (where the distribution of $n_t$ is not known explicitly)?

Is there a general theory of convergence for discrete-time Markov chains that share the salient features of the patch-occupancy models presented here?
Gaussian approximations

Can we establish deterministic and Gaussian approximations for the basic $J$-patch models (where the distribution of $n_t$ is not known explicitly)?

Is there a general theory of convergence for discrete-time Markov chains that share the salient features of the patch-occupancy models presented here?

Recall our numerical evaluation of quasi-stationary distributions for the basic $J$-patch models (described in Lecture 2) . . .
Metapopulation simulation \( P = EC \) \((J = 100, n_0 = 95, e = 0.3, c = 0.8)\)
Simulation and qsd: $P = EC$

Metapopulation simulation $P = EC$ ($J = 100$, $n_0 = 95$, $e = 0.3$, $c = 0.8$)
Simulation: $P = CE$

Metapopulation simulation $P = CE$ ($J = 100$, $n_0 = 95$, $e = 0.3$, $c = 0.8$)
Simulation and qsd: $P = CE$

Metapopulation simulation $P = CE$ ($J = 100$, $n_0 = 95$, $e = 0.3$, $c = 0.8$)
We have a sequence of Markov chains \( (n_t^{(J)}) \) indexed by \( J \), together with a function \( f \) such that

\[
E(n_{t+1}^{(J)} | n_t^{(J)}) = J f(n_t^{(J)}/J),
\]

or, more generally, a sequence of functions \( (f^{(J)}) \) such that

\[
E(n_{t+1}^{(J)} | n_t^{(J)}) = J f^{(J)}(n_t^{(J)}/J)
\]

and \( f^{(J)} \) converges \textit{uniformly} to \( f \).
We have a sequence of Markov chains \( (n_t^{(J)}) \) indexed by \( J \), together with a function \( f \) such that

\[
E(n_{t+1}|n_t) = J f(n_t/J),
\]

or, more generally, a \textit{sequence} of functions \( f^{(J)} \) such that

\[
E(n_{t+1}|n_t) = J f^{(J)}(n_t/J)
\]

and \( f^{(J)} \) converges \textit{uniformly} to \( f \).
We have a sequence of Markov chains \( (n_t^{(J)}) \) indexed by \( J \), together with a function \( f \) such that

\[
E(n_{t+1}^{(J)}|n_t^{(J)}) = J f(n_t^{(J)}/J),
\]

or, more generally, a sequence of functions \( (f^{(J)}) \) such that

\[
E(n_{t+1}^{(J)}|n_t^{(J)}) = J f^{(J)}(n_t^{(J)}/J)
\]

and \( f^{(J)} \) converges *uniformly* to \( f \).
We have a sequence of Markov chains \((n^{(J)}_t)\) indexed by \(J\), together with a function \(f\) such that

\[
E(n^{(J)}_{t+1}|n^{(J)}_t) = J f(n^{(J)}_t / J),
\]

or, more generally, a sequence of functions \((f^{(J)})\) such that

\[
E(n^{(J)}_{t+1}|n^{(J)}_t) = J f^{(J)}(n^{(J)}_t / J)
\]

and \(f^{(J)}\) converges \textit{uniformly} to \(f\).

We then define \((X^{(J)}_t)\) by \(X^{(J)}_t = n^{(J)}_t / J\) and hope that if \(X^{(J)}_0 \to x_0\) as \(J \to \infty\), then \((X^{(J)}_t) \overset{FDD}{\to} (x_t)\), where \((x_t)\) satisfies \(x_{t+1} = f(x_t)\) (the limiting deterministic model).
General structure: density dependence

Next we suppose that there is a function $s$ such that

$$\text{Var}(n_{t+1}^{(J)} | n_t^{(J)}) = Js(n_t^{(J)}/J)$$

or, more generally, a sequence of functions $(s^{(J)})$ such that

$$\text{Var}(n_{t+1}^{(J)} | n_t^{(J)}) = J s^{(J)}(n_t^{(J)}/J)$$

and $s^{(J)}$ converges \textit{uniformly} to $s$. 
Next we suppose that there is a function $s$ such that

$$\text{Var}(n_{t+1} | n_t) = Js(n_t / J)$$

or, more generally, a sequence of functions $(s^{(J)})$ such that

$$\text{Var}(n_{t+1} | n_t) = J s^{(J)}(n_t / J)$$

and $s^{(J)}$ converges \textit{uniformly} to $s$. 
Next we suppose that there is a function $s$ such that

$$\text{Var}(n_{t+1}^{(J)} | n_t^{(J)}) = J s(n_t^{(J)}/J)$$

or, more generally, a sequence of functions $(s^{(J)})$ such that

$$\text{Var}(n_{t+1}^{(J)} | n_t^{(J)}) = J s^{(J)}(n_t^{(J)}/J)$$

and $s^{(J)}$ converges *uniformly* to $s$. 
Next we suppose that there is a function $s$ such that

$$\text{Var}(n_{t+1}^{(J)}|n_t^{(J)}) = Js(n_t^{(J)}/J)$$

or, more generally, a sequence of functions $(s^{(J)})$ such that

$$\text{Var}(n_{t+1}^{(J)}|n_t^{(J)}) = Js^{(J)}(n_t^{(J)}/J)$$

and $s^{(J)}$ converges uniformly to $s$.

We then define $(Z_t^{(J)})$ by $Z_t^{(J)} = \sqrt{J}(X_t^{(J)} - x_t)$ and hope that if $\sqrt{J}(X_0^{(J)} - x_0) \to z_0$, then $(Z_t^{(J)}) \xrightarrow{\text{FDD}} (Z_t)$, where $(Z_t)$ is a Gaussian Markov chain with $Z_0 = z_0$. 
What will be the form of this chain?
What will be the form of this chain?

Consider the simplest case, \( f(J) = f \) and \( s(J) = s \).
What will be the form of this chain?

Consider the simplest case, \( f^{(J)} = f \) and \( s^{(J)} = s \).

Formally, by Taylor’s theorem,

\[
 f(X_t^{(J)}) - f(x_t) = (X_t^{(J)} - x_t)f'(x_t) + O \left( (X_t^{(J)} - x_t)^2 \right),
\]

and so, since \( \mathbb{E}(X_{t+1}^{(J)}|X_t^{(J)}) = f(X_t^{(J)}) \) and \( x_{t+1} = f(x_t) \),

\[
 \mathbb{E}(Z_{t+1}^{(J)}) = \sqrt{J} \left( \mathbb{E}(X_{t+1}^{(J)}) - f(x_t) \right) = f'(x_t) \mathbb{E}(Z_t^{(J)}) + \cdots,
\]

suggesting that \( \mathbb{E}(Z_{t+1}) = a_t \mathbb{E}(Z_t) \), where \( a_t = f'(x_t) \).
Moreover, $J \Var(X_{t+1}^{(J)}|X_t^{(J)}) = s(X_t^{(J)})$, suggesting that

$$Z_{t+1} = a_t Z_t + E_t \quad (Z_0 = z_0),$$

where $a_t = f'(x_t)$ and $E_t$ ($t = 0, 1, \ldots$) are independent Gaussian random variables with $E_t \sim N(0, s(x_t))$. 
Moreover, $J \operatorname{Var}(X_{t+1}^{(J)}|X_t^{(J)}) = s(X_t^{(J)})$, suggesting that

$$Z_{t+1} = a_t Z_t + E_t \quad (Z_0 = z_0),$$

where $a_t = f'(x_t)$ and $E_t \ (t = 0, 1, \ldots)$ are independent Gaussian random variables with $E_t \sim \mathcal{N}(0, s(x_t))$.

If $x_{eq}$ is a fixed point of $f$, and $\sqrt{J}(X_0^{(J)} - x_{eq}) \rightarrow z_0$, then we might hope that $(Z_t^{(J)}) \overset{FDD}{\longrightarrow} (Z_t)$, where $(Z_t)$ is the AR-1 process defined by $Z_{t+1} = aZ_t + E_t$, $Z_0 = z_0$, where $a = f'(x_{eq})$ and $E_t \ (t = 0, 1, \ldots)$ are iid Gaussian $\mathcal{N}(0, s(x_{eq}))$ random variables.
We can adapt results of Alan Karr* for our purpose.


He considered a sequence of time-homogeneous Markov chains \( \{X_t^{(n)}\} \) on a general state space \((\Omega, \mathcal{F}) = (E, \mathcal{E})^N\) with transition kernels \((K_n(x, A), x \in E, A \in \mathcal{E})\) and initial distributions \((\pi_n(A), A \in \mathcal{E})\).

He proved that if (i) \( \pi_n \Rightarrow \pi \) and (ii) \( x_n \rightarrow x \) in \( E \) implies \( K_n(x_n, \cdot) \Rightarrow K(x, \cdot) \), then the corresponding probability measures \((\mathbb{P}_{\pi_n}^{\pi_n})\) on \((\Omega, \mathcal{F})\) also converge: \( \mathbb{P}_{\pi_n}^{\pi_n} \Rightarrow \mathbb{P}^{\pi} \).
The “adaption” to our two-phase patch-occupancy models is simply to observe that Karr’s main result (his Theorem 1) remains true for a time \textit{inhomogeneous} Markov chain with \textit{alternating} transition kernels: $U, V, U, V, \ldots$.

For a sequence of such chains we will have a sequence of pairs $(U_n, V_n)$. In addition to (i), we check (ii') that $x_n \to x$ in $E$ implies $U_n(x_n, \cdot) \Rightarrow U(x, \cdot)$ and $V_n(x_n, \cdot) \Rightarrow V(x, \cdot)$. 
We follow the above programme for the (time-homogeneous) Markov chain \((X_t^{(J)}, Z_t^{(J)})\), where recall that \(X_t^{(J)}\) is the proportion of occupied patches at time \(t\) and \(Z_t^{(J)} = \sqrt{J}(X_t^{(J)} - x_t)\), where \((x_t)\) is the limiting deterministic trajectory. We apply the adaption of Karr’s results to the two-phase counterpart of \((X_t^{(J)}, Z_t^{(J)})\).
We follow the above programme for the (time-homogeneous) Markov chain \((X_t^{(J)}, Z_t^{(J)})\), where recall that \(X_t^{(J)}\) is the proportion of occupied patches at time \(t\) and \(Z_t^{(J)} = \sqrt{J}(X_t^{(J)} - x_t)\), where \((x_t)\) is the limiting deterministic trajectory. We apply the adaption of Karr’s results to the two-phase counterpart of \((X_t^{(J)}, Z_t^{(J)})\).

**Notation.** In what follows, \(y_t\) is the next state after one phase (E or C) of the limiting deterministic trajectory and \(Y_t\) is the next state of the limiting Gaussian process (the current states being \(x_t\) and \(Z_t\)).
**E-phase.** Let \((i^{(J)})\) be a sequence of integers such that \(i^{(J)} \in \{0, 1, \ldots, J\}\) and \(x^{(J)} := i^{(J)}/J \to x\) as \(J \to \infty\), and suppose that \(B^{(J)} \sim \text{Bin}(i^{(J)}, p)\), where \(p = 1 - e\) (\(0 < e < 1\)). Thus, \(B^{(J)}\) is the number of survivors of the extinction phase starting with \(i^{(J)}\) occupied patches. Let \(X^{(J)} = B^{(J)}/J\). It is easy to see that \(X^{(J)} \xrightarrow{P} px\), and, if \(\sqrt{N}(x^{(J)} - x) \to z\), then \(\sqrt{N}(X^{(J)} - px) \xrightarrow{D} Z\), where \(Z \sim \mathcal{N}(pz, xp(1 - p))\).
**E-phase.** Let \((i^{(J)})\) be a sequence of integers such that \(i^{(J)} \in \{0, 1, \ldots, J\}\) and \(x^{(J)} := i^{(J)}/J \to x\) as \(J \to \infty\), and suppose that \(B^{(J)} \sim \text{Bin}(i^{(J)}, p)\), where \(p = 1 - e\) \((0 < e < 1)\). Thus, \(B^{(J)}\) is the number of survivors of the extinction phase starting with \(i^{(J)}\) occupied patches. Let \(X^{(J)} = B^{(J)}/J\). It is easy to see that \(X^{(J)} \xrightarrow{P} px\), and, if \(\sqrt{N}(x^{(J)} - x) \to z\), then \(\sqrt{N}(X^{(J)} - px) \xrightarrow{D} Z\), where \(Z \sim \text{N}(pz, xp(1 - p))\). Therefore,

\[
y_t = (1 - e)x_t \quad \text{and} \quad Y_t = (1 - e)Z_t + \text{N}(0, e(1 - e)x_t).
\]
**C-phase.** Let \((i^{(J)})\) be a sequence of integers such that
\[i^{(J)} \in \{0, 1, \ldots, J\}\] and 
\[x^{(J)} := \frac{i^{(J)}}{J} \rightarrow x\] as \(J \rightarrow \infty\),
and suppose that \(C^{(J)} \sim \text{Bin}(J - i^{(J)}, \frac{ci^{(J)}}{J})\) \((0 < c < 1)\).
Thus, \(C^{(J)}\) is the number of colonizations starting with \(i^{(J)}\) occupied patches. Let 
\[X^{(J)} = x^{(J)} + \frac{C^{(J)}}{J}\] (being the proportion of occupied patches after the colonization phase).
It is easy to prove that
\[X^{(J)} \xrightarrow{P} x(1 + c - cx),\] and, if \(\sqrt{J}(x^{(J)} - x) \rightarrow z\), then
\[\sqrt{J}(X^{(J)} - x(1 + c - cx)) \xrightarrow{D} Z,\] where
\[Z \sim \mathcal{N}((1 + c - 2cx)z, cx(1 - x)(1 - cx)).\]
C-phase. Let \( (i^{(J)}) \) be a sequence of integers such that \( i^{(J)} \in \{0, 1, \ldots, J\} \) and \( x^{(J)} := i^{(J)}/J \to x \) as \( J \to \infty \), and suppose that \( C^{(J)} \sim \text{Bin}(J - i^{(J)}, c i^{(J)}/J) \) \((0 < c < 1)\). Thus, \( C^{(J)} \) is the number of colonizations starting with \( i^{(J)} \) occupied patches. Let \( X^{(J)} = x^{(J)} + C^{(J)}/J \) (being the proportion of occupied patches after the colonization phase). It is easy to prove that
\[
X^{(J)} \overset{P}{\to} x(1 + c - cx), \quad \text{and, if} \quad \sqrt{J}(x^{(J)} - x) \to z, \quad \text{then}
\]
\[
\sqrt{J}(X^{(J)} - x(1 + c - cx)) \overset{D}{\to} Z, \quad \text{where}
\]
\[
Z \sim \mathcal{N}((1 + c - 2cx)z, cx(1 - x)(1 - cx)).
\]
Therefore,
\[
y_t = x_t(1 + c - cx_t) \quad \text{and}
\]
\[
Y_t = (1 + c - 2cx_t)Z_t + \mathcal{N}(0, cx_t(1 - x_t)(1 - cx_t)).
\]
We can thus “build” the limiting deterministic \((x_t)\) trajectory and the limiting Gaussian process \((Z_t)\) for each of our models (EC and CE) by specifying \(f(x)\) such that \(x_{t+1} = f(x_t)\), and \(a(x)\) and \(s(x)\) such that \(Z_{t+1} = a(x_t)Z_t + \mathcal{N}(0, s(x_t))\).

We find that \(a(x) = f'(x)\), as expected.
EC-model. \( f(x) = (1 - e)(1 + c - c(1 - e)x)x \) and

\[
Z_{t+1} = (1 + c - 2c(1 - e)x_t) \left[ (1 - e)Z_t + \mathcal{N}(0, e(1 - e)x_t) \right] + \mathcal{N}(0, c(1 - e)x_t(1 - (1 - e)x_t)(1 - c(1 - e)x_t)),
\]

implying that \( a(x) = (1 - e)(1 + c - 2c(1 - e)x) \) and

\[
s(x) = c(1 - e)x(1 - (1 - e)x)(1 - c(1 - e)x)
\]
\[
+ (1 + c - 2c(1 - e)x)^2 e(1 - e)x
\]
\[
= (1 - e) \left[ c(1 - (1 - e)x)(1 - c(1 - e)x) + e(1 + c - 2c(1 - e)x)^2 \right] x.
\]
**J-patch models: convergence**

**EC-model.** \( f(x) = (1 - e)(1 + c - c(1 - e)x)x \) and

\[
Z_{t+1} = (1 + c - 2c(1 - e)x_t)[(1 - e)Z_t + \text{N}(0, e(1 - e)x_t)] \\
+ \text{N}(0, c(1 - e)x_t(1 - (1 - e)x_t)(1 - c(1 - e)x_t)),
\]

implying that \( a(x) = (1 - e)(1 + c - 2c(1 - e)x) \) and

\[
s(x) = c(1 - e)x(1 - (1 - e)x)(1 - c(1 - e)x) \\
+ (1 + c - 2c(1 - e)x)^2 e(1 - e)x \\
= (1 - e)[c(1 - (1 - e)x)(1 - c(1 - e)x) + e(1 + c - 2c(1 - e)x)^2]x.
\]
EC-model. \( f(x) = (1 - e)(1 + c - c(1 - e)x)x \) and

\[
Z_{t+1} = (1 + c - 2c(1 - e)x_t)[(1 - e)Z_t + \mathcal{N}(0, e(1 - e)x_t)] \\
+ \mathcal{N}(0, c(1 - e)x_t(1 - (1 - e)x_t)(1 - c(1 - e)x_t)),
\]

implying that \( a(x) = (1 - e)(1 + c - 2c(1 - e)x) \) and

\[
s(x) = c(1 - e)x(1 - (1 - e)x)(1 - c(1 - e)x) \\
+ (1 + c - 2c(1 - e)x)^2 e(1 - e)x \\
= (1 - e)[c(1 - (1 - e)x)(1 - c(1 - e)x) + e(1 + c - 2c(1 - e)x)^2]x.
\]
**J-patch models: convergence**

**CE-model.** \( f(x) = (1 - e)(1 + c - cx)x \) and

\[
Z_{t+1} = (1 - e)[(1 + c - 2cx_t)Z_t + \mathcal{N}(0, cx_t(1 - x_t)(1 - cx_t))] + \mathcal{N}(0, e(1 - e)x_t(1 + c - cx_t)),
\]

implying that \( a(x) = (1 - e)(1 + c - 2cx) \) and

\[
s(x) = e(1 - e)x(1 + c - cx) + (1 - e)^2cx(1 - x)(1 - cx)
\]

\[
\cdots = (1 - e)[e + c(1 - x)(1 - c(1 - e)x)]x.
\]
**J-patch models: convergence**

**CE-model.** \( f(x) = (1 - e)(1 + c - cx)x \) and

\[
Z_{t+1} = (1 - e)[(1 + c - 2cx_t)Z_t + \mathcal{N}(0, cx_t(1 - x_t)(1 - cx_t))] \\
+ \mathcal{N}(0, e(1 - e)x_t(1 + c - cx_t)),
\]

implying that \( a(x) = (1 - e)(1 + c - 2cx) \) and

\[
s(x) = e(1 - e)x(1 + c - cx) + (1 - e)^2cx(1 - x)(1 - cx) \\
\cdots = (1 - e)[e + c(1 - x)(1 - c(1 - e)x)]x.
\]
**CE-model.** \( f(x) = (1 - e)(1 + c - cx)x \) and

\[
Z_{t+1} = (1 - e)[(1 + c - 2cx_t)Z_t + N(0, cx_t(1 - x_t)(1 - cx_t))] \\
+ N(0, e(1 - e)x_t(1 + c - cx_t)),
\]

implying that \( a(x) = (1 - e)(1 + c - 2cx) \) and

\[
s(x) = e(1 - e)x(1 + c - cx) + (1 - e)^2cx(1 - x)(1 - cx) \\
\cdots = (1 - e)[e + c(1 - x)(1 - c(1 - e)x)]x.
\]
**Theorem** For either of the $J$-patch state-dependent models, if $X_0^{(J)} \to x_0$ as $J \to \infty$, then

$$
(X_{t_1}^{(J)}, X_{t_2}^{(J)}, \ldots, X_{t_n}^{(J)}) \overset{P}{\to} (x_{t_1}, x_{t_2}, \ldots, x_{t_n}),
$$

for any finite sequence of times $t_1, t_2, \ldots, t_n$, where $(x_t)$ is defined by the recursion $x_{t+1} = f(x_t)$ with

**EC-model:** $f(x) = (1 - e)(1 + c - c(1 - e)x)x$

**CE-model:** $f(x) = (1 - e)(1 + c - cx)x$
**Theorem**  If, additionally, $\sqrt{J}(X_0^{(J)} - x_0) \to z_0$, then $(Z_t^{(J)}) \xrightarrow{FDD} (Z_t)$, where $(Z_t)$ is the Gaussian Markov chain defined by

$$Z_{t+1} = f'(x_t)Z_t + E_t \quad (Z_0 = z_0),$$

where $E_t \ (t = 0, 1, \ldots)$ are independent Gaussian random variables with $E_t \sim \mathcal{N}(0, s(x_t))$ and

- **EC model**: $s(x) = (1 - e)[c(1 - (1 - e)x)(1 - c(1 - e)x) + e(1 + c - 2c(1 - e)x)^2]x$
- **CE model**: $s(x) = (1 - e)[e + c(1 - x)(1 - c(1 - e)x)]x$
Simulation: $P = EC$

Metapopulation simulation $P = EC$ ($J = 100$, $x_0 = 0.95$, $c = 0.4$, $c = 0.8$)
Simulation: \( P = EC \) (Deterministic path)

![Graph showing the simulation of a metapopulation with parameters \( J = 100, x_0 = 0.95, e = 0.4, c = 0.8 \).](image)

- **Deterministic path**

  - \( P = EC \) (Deterministic path)

  - Parameters: \( J = 100, x_0 = 0.95, e = 0.4, c = 0.8 \)
Simulation: $P = EC$ (Gaussian approx.)

Metapopulation simulation $P = EC$ ($J = 100$, $x_0 = 0.95$, $e = 0.4$, $c = 0.8$)

Deterministic path $\pm$ two standard deviations
Simulation: \( P = CE \)

Metapopulation simulation \( P = CE \) \((J = 100, x_0 = 0.95, e = 0.4, c = 0.8)\)
Simulation: $P = CE$ (Deterministic path)

Metapopulation simulation $P = CE$ ($J = 100$, $x_0 = 0.95$, $c = 0.4$, $e = 0.8$)
Simulation: $P = CE$ (Gaussian approx.)

Metapopulation simulation $P = CE$ ($J = 100$, $x_0 = 0.95$, $e = 0.4$, $c = 0.8$)

Deterministic path ± two standard deviations
In both cases (EC and CE) the deterministic model has two equilibria, $x = 0$ and $x = x^*$, given by

- **EC-model:**
  $$x^* = \frac{1}{1 - e} \left( 1 - \frac{e}{c(1 - e)} \right)$$

- **CE-model:**
  $$x^* = 1 - \frac{e}{c(1 - e)}$$
In both cases (EC and CE) the deterministic model has two equilibria, $x = 0$ and $x = x^*$, given by

**EC-model:**

$$x^* = \frac{1}{1 - e} \left( 1 - \frac{e}{c(1 - e)} \right)$$

**CE-model:**

$$x^* = 1 - \frac{e}{c(1 - e)}$$

Indeed, we may write $f(x) = x \left( 1 + r \left( 1 - \frac{x}{x^*} \right) \right)$, $r = c(1 - e) - e$ for both models (the form of the discrete-time logistic model), and we obtain the condition $c > e/(1 - e)$ for $x^*$ to be positive and then stable.
In both cases (EC and CE) the deterministic model has two equilibria, $x = 0$ and $x = x^*$, given by

**EC-model:** $x^* = \frac{1}{1 - e} \left( 1 - \frac{e}{c(1 - e)} \right)$

**CE-model:** $x^* = 1 - \frac{e}{c(1 - e)}$

Indeed, we may write $f(x) = x (1 + r (1 - x/x^*))$, $r = c(1 - e) - e$ for both models (the form of the discrete-time logistic model), and we obtain the condition $c > e/(1 - e)$ for $x^*$ to be positive and then stable. **Note:** this is the condition for supercriticality in the corresponding infinite-patch model (Lecture 2).
Corollary  If $c > e/(1 - e)$, so that $x^*$ given above is stable, and $\sqrt{J}(X_0^{(J)} - x^*) \to z_0$, then $(Z_t^{(J)}) \xrightarrow{FDD} (Z_t)$, where $(Z_t)$ is the AR-1 process defined by

$$Z_{t+1} = (1 + e - c(1 - e))Z_t + E_t \quad (Z_0 = z_0),$$

where $E_t \ (t = 0, 1, \ldots)$ are independent Gaussian $N(0, \sigma^2)$ random variables with

**EC-model:** $\sigma^2 = (1 - e)[c(1 - (1 - e)x^*) (1 - c(1 - e)x^*)]$

$$+ e(1 + c - 2c(1 - e)x^*)^2]x^*$$

**CE-model:** $\sigma^2 = (1 - e)[e + c(1 - x^*) (1 - c(1 - e)x^*)]x^*$
Metapopulation simulation $P = EC$ ($J = 100$, $x_0 = 0.95$, $e = 0.3$, $c = 0.8$)

$x^* = 0.66327$
Simulation: $P = EC$ (AR-1 approx.)

Metapopulation simulation $P = EC$ ($J = 100, x_0 = 0.95, e = 0.3, c = 0.8$)

$x^* = 0.66327$
AR-1 Simulation: $P = EC$

AR-1 simulation $P = EC$ ($J = 100$, $x_0 = 0.66327$, $e = 0.3$, $c = 0.8$)

$x^* = 0.66327$
Metapopulation simulation \( P = CE \) \((J = 100, x_0 = 0.95, e = 0.3, c = 0.8)\)

\[ X^{(j)}(t) \]

\[ x^* = 0.46429 \]
Simulation: $P = CE$ (AR-1 approx.)

Metapopulation simulation $P = CE \ (J = 100, \ x_0 = 0.95, \ e = 0.3, \ c = 0.8)$

$x^* = 0.46429$
AR-1 Simulation: $P = CE$

AR-1 simulation $P = CE$ ($J = 100$, $x_0 = 0.46429$, $e = 0.3$, $c = 0.8$)

$x^* = 0.46429$