Limit theorems for discrete-time metapopulation models

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Metapopulations

Colonization
Metapopulations
Local Extinction
Metapopulations
Total Extinction
Mainland-island configuration

Colonization from the mainland
We record the *number* $n_t$ of occupied patches at each time $t$.

A typical approach is to suppose that $(n_t, t \geq 0)$ is Markovian.
Patch-occupancy models

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Suppose that there are $N$ patches.

Each occupied patch becomes empty at rate $e$ (the *local extinction rate*), colonization of empty patches occurs at rate $c/N$ for each suitable pair ($c$ is the *colonization rate*) and immigration from the mainland occurs that rate $\nu$ (the *immigration rate*).
A continuous-time stochastic model

The state space of the Markov chain \((n_t, t \geq 0)\) is \(S = \{0, 1, \ldots, N\}\) and the transitions are:

\[
\begin{align*}
n &\rightarrow n + 1 \quad \text{at rate} \quad \left( \nu + \frac{c}{N} n \right) (N - n) \\
n &\rightarrow n - 1 \quad \text{at rate} \quad en
\end{align*}
\]
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This an example of Feller’s \textit{stochastic logistic (SL) model}, studied in detail by J.V. Ross.


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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
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There are several ways to model this:

- A quasi-birth-death process with two phases
- A non-homogeneous continuous-time Markov chain (cycle between two sets of transition rates)
- A discrete-time Markov chain
Colonization and extinction phases

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- A discrete-time Markov chain ✔
Recall that there are $N$ patches and that $n_t$ is the number of occupied patches at time $t$. We suppose that $(n_t, t = 0, 1, \ldots)$ is a discrete-time Markov chain taking values in $S = \{0, 1, \ldots, N\}$ with a 1-step transition matrix $P = (p_{ij})$ constructed as follows.
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The extinction and colonization phases are governed by their own transition matrices, $E = (e_{ij})$ and $C = (c_{ij})$.

We let $P = EC$ if the census is taken after the colonization phase or $P = CE$ if the census is taken after the extinction phase.
$P = EC$ \{ 

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\begin{align*}
&\quad \vdots \\
& t - 1 \quad t \quad t + 1 \quad t + 2 \\
&\quad \vdots \\
\end{align*} 

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\cdots & E \quad C \quad E \quad C \quad E \quad C \quad E \quad C \quad E \quad \cdots \\
\cdots & E \quad C \quad E \quad C \quad E \quad C \quad E \quad C \quad E \quad \cdots 
\end{align*}
Assumptions

The number of extinctions when there are \( i \) patches occupied follows a \( \text{Bin}(i, e) \) 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 \( \text{Bin}(N - i, c_i) \) law:

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

\((c_{ij} = 0 \text{ if } j < i.)\)
Thus, we have the following *chain-binomial* structure:

\[ n_{t+1} = \tilde{n}_t + \text{Bin}(N - \tilde{n}_t, c_{\tilde{n}_t}) \quad \tilde{n}_t = n_t - \text{Bin}(n_t, e) \]  \quad \text{(EC)}

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For the CE model (only) it is easy to show that \( n_{t+1} \) has the same distribution as the sum of two *independent* binomial random variables:

\[ n_{t+1} \overset{D}{=} \text{Bin}(n_t, 1 - e) + \text{Bin}(N - n_t, (1 - e)c_{n_t}). \]
Thus, we have the following \textit{chain-binomial} structure:

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    n_{t+1} &= \tilde{n}_t + \text{Bin}(N - \tilde{n}_t, c_{\tilde{n}_t}) \quad \tilde{n}_t = n_t - \text{Bin}(n_t, e) \quad \text{(EC)} \\
    n_{t+1} &= \tilde{n}_t - \text{Bin}(\tilde{n}_t, e) \quad \tilde{n}_t = n_t + \text{Bin}(N - n_t, c_{n_t}). \quad \text{(CE)}
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For the CE model (only) it is easy to show that $n_{t+1}$ has the same distribution as the sum of two \textit{independent} binomial random variables:

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    n_{t+1} \overset{D}{=} \text{Bin}(n_t, 1 - e) + \text{Bin}(N - n_t, (1 - e)c_{n_t}).
\end{equation}

So, $(1 - e)c_i$ is the \textit{effective colonisation probability} when there are $i$ occupied patches.
Examples of $c_i$

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

(This entails $c_{0j} = \delta_{0j}$, so that 0 is an absorbing state and $\{1, \ldots, N\}$ is a communicating class.)
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- $c_i = c$, where $c \in (0, 1]$ is a fixed colonization potential — mainland colonization dominant.

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Other possibilities include $c_i = c_0(1 - (1 - c_1/c_0)^i)$, $c_i = 1 - \exp(-i\beta/N)$ and $c_i = c_0 + (i/N)c$, where $c_0 + c \in (0, 1]$ (mainland and island colonization).
Henceforth we shall be concerned with $X_t^{(N)} = n_t/N$, the *proportion* of occupied patches at time $t$. 
Simulation: EC Model with $c_i = c$

Mainland-Island simulation $P = EC$ ($N = 100$, $x_0 = 0.05$, $e = 0.01$, $c = 0.05$)
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The proportion of occupied patches

Henceforth we shall be concerned with \( X_t^{(N)} = n_t / N \), the \textit{proportion} of occupied patches at time \( t \).

In the mainland-island case \( c_i = c \), the distribution of \( n_t \) can be evaluated explicitly, and we have established large-\( N \) deterministic and Gaussian approximations for \( (X_t^{(N)}) \).

Let

\[ p = 1 - e(1 - c) \quad q = c \]  \quad \text{(EC model)}
\[ p = 1 - e \quad q = (1 - e)c. \]  \quad \text{(CE model)}

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

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

where \(a = p - q = (1 - e)(1 - c)\) (the same for both EC and CE) and \(q^* = q/(1 - a)\).
Let
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where \( a = p - q = (1 - e)(1 - c) \) (the same for both EC and CE) and \( q^* = q/(1 - a) \). Then,
\[ n_t \overset{D}{=} \text{Bin}(n_0, p_t) + \text{Bin}(N - n_0, q_t) \]

(independent binomial random variables).
Mainland-Island $c_i = c$ (Summary)

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where \(a = p - q = (1 - e)(1 - c)\) (the same for both EC and CE) and \(q^* = q/(1 - a)\). Then,

\[ n_t \overset{\mathcal{D}}{=} Bin(n_0, p_t) + Bin(N - n_0, q_t) \quad (\overset{\mathcal{D}}{=} Bin(N, q^*)) \]

\((\text{independent} \ binomial \ random \ variables)\).
Let \( X_t^{(N)} = n_t/N \) be the \textit{proportion} occupied at time \( t \).

If \( X_0^{(N)} \xrightarrow{P} x_0 \), as \( N \to \infty \), then \( X_t^{(N)} \xrightarrow{P} x_t \), where

\[
x_t = x_0 p_t + (1 - x_0) q_t.
\]
Simulation: EC Model with $c_i = c$

Mainland-Island simulation $P = EC$ ($N=100$, $x_0 = 0.05$, $e = 0.01$, $c = 0.05$)
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Let $X^{(N)}_t = n_t/N$ be the proportion occupied at time $t$.

If $X^{(N)}_0 \xrightarrow{P} x_0$, as $N \to \infty$, then $X^{(N)}_t \xrightarrow{P} x_t$, where

$$x_t = x_0 p_t + (1 - x_0) q_t.$$
Let $X_t^{(N)} = n_t/N$ be the proportion occupied at time $t$. If $X_0^{(N)} \xrightarrow{P} x_0$, as $N \to \infty$, then $X_t^{(N)} \xrightarrow{P} x_t$, where

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Now put $Z_t^{(N)} := \sqrt{N} (X_t^{(N)} - x_t)$.  


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Now put $Z_t^{(N)} := \sqrt{N}(X_t^{(N)} - x_t)$. Then, if $Z_0^{(N)} \xrightarrow{D} z_0$,

$Z_t^{(N)} \xrightarrow{D} N(a^t z_0, V_t)$, where

$$V_t = x_0 p_t (1 - p_t) + (1 - x_0) q_t (1 - q_t).$$
Mainland-Island simulation \( P = EC \) (\( N = 100 \), \( x_0 = 0.05 \), \( e = 0.01 \), \( c = 0.05 \))

Deterministic path \( \pm \) two standard deviations
Can we establish deterministic and Gaussian approximations for the basic $N$-patch models (where the distribution of $n_t$ is not known explicitly)?
Simulation: EC Model with $c_i = (i/N)c$
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Is there a general theory of convergence for discrete-time Markov chains that share the salient features of the patch-occupancy models presented here?
We have a sequence of Markov chains \((n_t^{(N)})\) indexed by \(N\), together with functions \((f_t)\) such that

\[
E(n_{t+1}^{(N)} | n_t^{(N)}) = N f_t(n_t^{(N)}/N).
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We have a sequence of Markov chains \((n^{(N)}_t)\) indexed by \(N\), together with functions \((f_t)\) such that

\[
E(n^{(N)}_{t+1} | n^{(N)}_t) = N f_t(n^{(N)}_t / N).
\]

We then define \((X^{(N)}_t)\) by \(X^{(N)}_t = n^{(N)}_t / N\). We hope that if \(X^{(N)}_0 \xrightarrow{D} x_0\) as \(N \to \infty\), then \((X^{(N)}_t) \xrightarrow{FDD} (x_t)\), where \((x_t)\) satisfies \(x_{t+1} = f_t(x_t)\) (the limiting deterministic model).
Next we suppose that there are functions \((s_t)\) such that

\[
\text{Var}(n_{t+1}^{(N)} | n_t^{(N)}) = N s(n_t^{(N)} / N).
\]
General structure: density dependence

Next we suppose that there are functions \( (s_t) \) such that

\[
\mathcal{N} \text{Var}(X_{t+1}^{(N)}|X_t^{(N)}) = s(X_t^{(N)}).
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We then define \((Z_t^{(N)})\) by

\[
Z_t^{(N)} = \sqrt{N}(X_t^{(N)} - x_t).
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Next we suppose that there are functions \((s_t)\) such that

\[
\text{Var}(Z_{t+1}^{(N)} \mid X_t^{(N)}) = s_t(X_t^{(N)}).
\]

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Next we suppose that there are functions \( (s_t) \) such that

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\text{Var}(n_{t+1}^{(N)} | n_t^{(N)}) = N s_t(n_t^{(N)}/N).
\]

We then define \( (Z_t^{(N)}) \) by \( Z_t^{(N)} = \sqrt{N} (X_t^{(N)} - x_t) \). We hope that if \( \sqrt{N}(X_0^{(N)} - x_0) \xrightarrow{D} z_0 \), then \( (Z_t^{(N)}) \xrightarrow{FDD} (Z_t) \), where \( (Z_t) \) is a Gaussian Markov chain with \( Z_0 = z_0 \).
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Consider the time-homogeneous case, $f_t = f$ and $s_t = s$. 
General structure: density dependence

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Consider the time-homogeneous case, \( f_t = f \) and \( s_t = s \).

Formally, by Taylor’s theorem,

\[
f(X_t^{(N)}) - f(x_t) = (X_t^{(N)} - x_t)f'(x_t) + \cdots
\]

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

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

suggesting that \( \mathbb{E}(Z_{t+1}) = a_t \mathbb{E}(Z_t) \), where \( a_t = f'(x_t) \).
We have

$$\text{Var}(X_{t+1}^{(N)}) = \text{Var}(E(X_{t+1}^{(N)}|X_t^{(N)})) + E(\text{Var}(X_{t+1}^{(N)}|X_t^{(N)})).$$

So, since $N \text{Var}(X_{t+1}^{(N)}|X_t^{(N)}) = s(X_t^{(N)}),$

$$\text{Var}(Z_{t+1}^{(N)}) = N \text{Var}(X_{t+1}^{(N)}) = N \text{Var}(f(X_t^{(N)})) + E(s(X_t^{(N)}))$$

$$\sim a_t^2 N \text{Var}(X_t^{(N)}) + E(s(X_t^{(N)})) \text{ (where } a_t = f'(x_t))$$

$$= a_t^2 \text{Var}(Z_t^{(N)}) + E(s(X_t^{(N)})),$$

suggesting that $\text{Var}(Z_{t+1}) = a_t^2 \text{Var}(Z_t) + s(x_t).$
We have

$$\text{Var}(X_{t+1}^{(N)}) = \text{Var}(\mathbb{E}(X_{t+1}^{(N)}|X_t^{(N)})) + \mathbb{E}(\text{Var}(X_{t+1}^{(N)}|X_t^{(N)})).$$

So, since $N \text{Var}(X_{t+1}^{(N)}|X_t^{(N)}) = s(X_t^{(N)})$,

$$\text{Var}(Z_{t+1}^{(N)}) = N \text{Var}(X_{t+1}^{(N)}) = N \text{Var}(f(X_t^{(N)})) + \mathbb{E}(s(X_t^{(N)}))$$

$$\sim a_t^2 N \text{Var}(X_t^{(N)}) + \mathbb{E}(s(X_t^{(N)})) \text{ (where } a_t = f'(x_t))$$

$$= a_t^2 \text{Var}(Z_t^{(N)}) + \mathbb{E}(s(X_t^{(N)})),$$

suggesting that $\text{Var}(Z_{t+1}) = a_t^2 \text{Var}(Z_t) + s(x_t)$.

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And, since \((Z_t)\) will be Markovian, we might hope 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 \(E_t \sim N(0, s(x_t))\).
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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 \(\sqrt{N}(X_0^{(N)} - x_{eq}) \rightarrow z_0\), then we might hope that \((Z_t^{(N)}) \xrightarrow{FDD} (Z_t)\), where \((Z_t)\) is the AR-1 process defined by \(Z_{t+1} = a Z_t + E_t, Z_0 = z_0\), 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 \((\mathbb{P}^{\pi_n})\) on \((\Omega, \mathcal{F})\) also converge: \(\mathbb{P}^{\pi_n} \Rightarrow \mathbb{P}^\pi\).
**Theorem**  For the \( N \)-patch models with \( c_i = (i/N)c \), if \( X_0^{(N)} \xrightarrow{D} x_0 \) as \( N \to \infty \), then

\[
(X_{t_1}^{(N)}, X_{t_2}^{(N)}, \ldots, X_{t_n}^{(N)}) \xrightarrow{D} (x_{t_1}, x_{t_2}, \ldots, x_{t_n}),
\]

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

\[
f(x) = (1 - e)(1 + c - c(1 - e)x)x \\
f(x) = (1 - e)(1 + c - cx)x
\]

(\( \text{EC model} \))

(\( \text{CE model} \))
Theorem  If, additionally, \( \sqrt{N}(X_0^{(N)} - x_0) \xrightarrow{D} z_0 \), then 
\( (Z_t^{(N)}) \xrightarrow{FDD} (Z_t) \), 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 \( E_t \sim N(0, s(x_t)) \) and 

\[
s(x) = (1 - e)[c(1 - (1 - e)x)(1 - c(1 - e)x) + e(1 + c - 2c(1 - e)x)^2]x \quad \text{(EC model)}
\]

\[
s(x) = (1 - e)[e + c(1 - x)(1 - c(1 - e)x)]x \quad \text{(CE model)}
\]
Metapopulation simulation $P = EC$ ($N = 100, x_0 = 0.95, e = 0.4, c = 0.8$)
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Simulation: EC Model (Gaussian approx.)

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

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

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

(EC model)

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

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In both cases (EC and CE) the deterministic model has two equilibria, \( x = 0 \) and \( x = x^* \), given by

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\begin{align*}
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\end{align*}
\]

(EC model)

(CE model)

Indeed, we may write \( f(x) = x \left( 1 + r \left( 1 - x / x^* \right) \right) \), \( r = c(1 - e) - e \) 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.
Corollary  If \( c > e/(1 - e) \), so that \( x^* \) given above is stable, and \( \sqrt{N}(X^{(N)}_0 - x^*) \xrightarrow{D} z_0 \), then \( (Z^{(N)}_t) \xrightarrow{FDD} (Z_t) \), 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

\[
\sigma^2 = (1 - e)[c(1 - (1 - e)x^*)(1 - c(1 - e)x^*)] \\
+ e(1 + c - 2c(1 - e)x^*)^2]x^* \quad \text{(EC model)}
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Metapopulation simulation $P = EC$ ($N=100$, $x_0 = 0.95$, $e = 0.3$, $c = 0.8$)

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

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

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- A general theory of convergence for sequences of time-inhomogeneous density-dependent Markov chains.
Recent developments


- A general theory of convergence for sequences of time-inhomogeneous density-dependent Markov chains.

- Analysis of the scheme

\[
\begin{align*}
n_{t+1} &= \tilde{n}_t + \text{Bin}(N - \tilde{n}_t, c(\tilde{n}_t/N)) \quad \tilde{n}_t = n_t - \text{Bin}(n_t, e) \quad \text{(EC)} \\
n_{t+1} &= \tilde{n}_t - \text{Bin}(\tilde{n}_t, e) \quad \tilde{n}_t = n_t + \text{Bin}(N - n_t, c(n_t/N)) \quad \text{(CE)}
\end{align*}
\]

where \( c \) is continuous, increasing and concave, with \( c(0) \geq 0 \) and \( c(x) \leq 1 \).
Recent developments

- Stability analysis of the limiting deterministic model:
  (i) **Stationarity**: $c(0) > 0$.
  (ii) **Evanescence**: $c(0) = 0$ and $c'(0) \leq e/(1 - e)$.
  (iii) **Quasi stationarity**: $c(0) = 0$ and $c'(0) > e/(1 - e)$.
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- Infinite-patch models. If \( c(0) = 0 \) and \( c(x) \) has a continuous second derivative near 0, then

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  This leads to the scheme

  \[
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  n_{t+1} &= \tilde{n}_t + \text{Poi}(m\tilde{n}_t) \quad \tilde{n}_t = n_t - \text{Bin}(n_t, e) \quad \text{(EC)} \\
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  \end{align*}
  \]
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- Analysis of the more general scheme

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    n_{t+1} &= \tilde{n}_t + \text{Poi}(m(\tilde{n}_t)) & \tilde{n}_t &= n_t - \text{Bin}(n_t, e) & \text{(EC)} \\
    n_{t+1} &= \tilde{n}_t - \text{Bin}(\tilde{n}_t, e) & \tilde{n}_t &= n_t + \text{Poi}(m(n_t)), & \text{(CE)}
\end{align*}
\]

assuming \( m(n) = n_0 \mu(n/n_0) \).
Recent developments

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- Analysis of the more general scheme

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\begin{align*}
n_{t+1} &= \tilde{n}_t + \text{Poi}(m(\tilde{n}_t)) & \tilde{n}_t &= n_t - \text{Bin}(n_t, e) \tag{EC} \\
n_{t+1} &= \tilde{n}_t - \text{Bin}(\tilde{n}_t, e) & \tilde{n}_t &= n_t + \text{Poi}(m(n_t)) \tag{CE}
\end{align*}
\]

assuming \(m(n) = n_0 \mu(n/n_0)\). In the limit as \(n_0 \to \infty\) \(X^{(N)}_t := n_t/n_0\) has a deterministic approximation that can exhibit the full range of dynamic behaviour (including chaos).
Ricker dynamics: \( \mu(x) = x \exp(r(1-x)) \)