Stochastic models for population networks

III: Discrete-time patch occupancy models

Deterministic and Gaussian approximations

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Metapopulations

Colonization

Local Extinction
**Mainland-island configuration**

Colonization from the mainland

**Metapopulations**

- 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).

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**Accounting for life cycle**

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.

**Patch-occupancy models**

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.
### Patch-occupancy models

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

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

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

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

(\(c_{ij} = 0\) if \(j < i\).)

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### Patch-occupancy models

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 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 \( q = (1 - e)c \)

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

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

and

\[
Var(n_t|n_0 = i) = ip_t(1 - p_t) + (J - i)q_t(1 - q_t)
= ia^t(1 - a^t)(1 - 2q^*) + Jq_t(1 - q_t)
\]

\( \to Jq^*(1 - q^*) \) as \( t \to \infty \).

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

As \( J \to \infty \),

\[
E(X_t^{(j)}) \to x_0p_t + (1 - x_0)q_t
\]

and

\[
J Var(X_t^{(j)}) \to x_0p_t(1 - p_t) + (1 - x_0)q_t(1 - q_t).
\]

Indeed, \( X_t^{(j)} \stackrel{P}{\to} x_t \), where \( x_t = x_0p_t + (1 - x_0)q_t \), 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

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

and

\[
v_t = x_0p_t(1 - p_t) + (1 - x_0)q_t(1 - q_t).
\]

We can do better ...

**Theorem** \( (X_{t_1}^{(j)}, X_{t_2}^{(j)}, \ldots, X_{t_n}^{(j)}) \stackrel{P}{\to} (x_{t_1}, x_{t_2}, \ldots, x_{t_n}) \), for any finite sequence of times \( t_1, t_2, \ldots, t_n \).

For the corresponding central limit law, define the process \( (Z_t^{(j)}, t \geq 0) \) by

\[
Z_t^{(j)} = \sqrt{J}(X_t^{(j)} - x_t)
\]

and suppose that \( \sqrt{J}(x_0^{(j)} - x_0) \to z_0 \).
Mainland-Island models: $J \to \infty$

**Theorem** The finite-dimensional distributions (FDDs) of $(Z(J)^t)$ 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: $P = EC$

Simulation: $P = EC$ (Deterministic path)

Simulation: $P = EC$ (Gaussian approx.)
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 $\sqrt{J} (x_0^{(J)} - q^*) \rightarrow z_0$.

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

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

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

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

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) . . .
Simulation and qsd: $P = EC$

Simulation and qsd: $P = CE$

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

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

General structure: density dependence

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 then define $(X_t^{(J)})$ by $X_t^{(J)} = n_t^{(J)}/J$ and hope that if $X_0^{(J)} 	o x_0$ as $J \to \infty$, then $(X_t^{(J)}) \overset{FDD}{\to} (x_t)$, where $(x_t)$ satisfies $x_{t+1} = f(x_t)$ (the limiting deterministic model).

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 $s$.

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 $(Z_t^{(J)}) \overset{FDD}{\to} (Z_t)$, where $(Z_t)$ is a Gaussian Markov chain with $Z_0 = z_0$. 
General structure: density dependence

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

Formally, by Taylor’s theorem,
\[
f(X^{(j)}_t) - f(x_t) = (X^{(j)}_t - x_t)f'(x_t) + O \left( (X^{(j)}_t - x_t)^2 \right),
\]
and so, since \( \mathbb{E}(X^{(j)}_{t+1}|X^{(j)}_t) = f(X^{(j)}_t) \) and \( x_{t+1} = f(x_t) \),
\[
\mathbb{E}(Z^{(j)}_{t+1}) = \sqrt{J} (\mathbb{E}(X^{(j)}_{t+1}) - f(x_t)) = f'(x_t) \mathbb{E}(Z^{(j)}_t) + \cdots,
\]
suggesting that \( \mathbb{E}(Z_{t+1}) = a_t \mathbb{E}(Z_t) \), where \( a_t = f'(x_t) \).

Moreover, \( J \mathbb{V}(X^{(j)}_{t+1}|X^{(j)}_t) = s(X^{(j)}_t) \), 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 \( E_t \sim N(0, s(x_t)) \).

If \( x_{eq} \) is a fixed point of \( f \), and \( \sqrt{J}(X^{(j)}_0 - x_{eq}) \rightarrow z_0 \),
then we might hope that \( (Z^{(j)}_t) \overset{FDD}{\rightarrow} (Z_t) \), where \( (Z_t) \) is the AR-1 process defined by \( Z_{t+1} = a_t Z_t + E_t \), \( Z_0 = z_0 \),
where \( a = f'(x_{eq}) \) and \( E_t \) \( (t = 0, 1, \ldots) \) are iid Gaussian \( N(0, s(x_{eq})) \) random variables.

Convergence of Markov chains

We can adapt results of Alan Karr∗ for our purpose.


He considered a sequence of time-homogeneous Markov chains \( (X^{(n)}_t) \) 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 \( (\mathbb{P}^n) \) on \( (\Omega, \mathcal{F}) \) also converge: \( \mathbb{P}^n \Rightarrow \mathbb{P}^\pi \).

Convergence of Markov chains

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 inhomogeneous Markov chain with 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 \( x_n \rightarrow x \) 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 \((X_t^{(J)}, Z_t^{(J)})\).

**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 \(Z_t\)).

**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 \(C^{(J)} \sim \text{Bin}(J - i^{(J)}, c) / J\) \((0 < c < 1)\). 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
\[
X^{(J)} \xrightarrow{P} x(1 + c - cx),
\]
and, if \(\sqrt{J}(x^{(J)} - x) \to z\), then
\[
\sqrt{J}(X^{(J)} - x(1 + c - cx)) \xrightarrow{D} Z,
\]
where \(Z \sim N((1 + c - 2cx)z, cx(1 - x)(1 - cx))\). Therefore,
\[
y_t = x_t(1 + c - cx_t) \quad \text{and} \quad Y_t = (1 + c - 2cx_t)Z_t + N(0, cx_t(1 - x_t)(1 - cx_t)).
\]

**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 \(Z \sim N(pz, xp(1 - p))\). Therefore,
\[
y_t = (1 - e)x_t \quad \text{and} \quad Y_t = (1 - e)Z_t + N(0, e(1 - e)x_t).
\]

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 \(Z_{t+1} = a(x_t)Z_t + N(0, s(x_t))\).

We find that \(a(x) = f'(x)\), as expected.
**J-patch models: convergence**

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

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

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

\[
s(x) = \frac{c(1 - e)x(1 - (1 - e)x)(1 - c(1 - e)x)}{1 + c - 2c(1 - e)x}
\]

\[
= \frac{(1 - e)/c\{1 - (1 - e)x\}(1 - c(1 - e)x) + e(1 - c - 2c(1 - e)x)^2}{x}.
\]

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**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

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

\[
\cdots = (1 - e)[e + c(1 - x)(1 - c(1 - e)x)]x.
\]

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**Theorem** For either of the J-patch state-dependent models, if \( X_0^{(J)} \to x_0 \) as \( J \to \infty \), then

\[
(X_t^{(J)}, X_{t+1}^{(J)}, \ldots, X_{t+n}^{(J)}) \to (x_t, x_{t+1}, \ldots, x_{t+n}),
\]

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:** \( f(x) = (1 - e)(1 + c - cx)x \)

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**Theorem** If, additionally, \( \sqrt{J}(X_0^{(J)} - x_0) \to z_0 \), then

\( (Z_t^{(J)}) \to (Z_t) \), 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

**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 $P = EC$ ($J = 100$, $x_0 = 0.95$, $c = 0.8$)

Simulation: $P = EC$ (Deterministic path)

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

Simulation: $P = EC$ (Gaussian approx.)

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

Simulation: $P = CE$

Metapopulation simulation $P = CE$ ($J = 100$, $x_0 = 0.95$, $e = 0.4$, $c = 0.8$)
### J-patch models: convergence

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

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. **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 $\sqrt{J}(X^{(J)}_0 - x^*) \to z_0$, then $(Z^{(J)}_t) \xrightarrow{FDD} (Z_t)$, 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

- **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 $P = EC$ ($J = 100$, $x_0 = 0.95$, $e = 0.3$, $c = 0.8$)

**simulation**

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

**AR-1 simulation**

$P = EC$ ($J = 100$, $x_0 = 0.66327$, $e = 0.3$, $c = 0.8$)

$P = CE$ ($J = 100$, $x_0 = 0.46429$, $e = 0.3$, $c = 0.8$)

**AR-1 simulation**

$P = CE$ ($J = 100$, $x_0 = 0.46429$, $e = 0.3$, $c = 0.8$)