Stochastic models for population networks

III: Discrete-time patch occupancy models

[Deterministic and Gaussian approximations]

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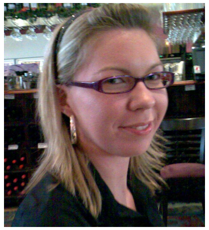

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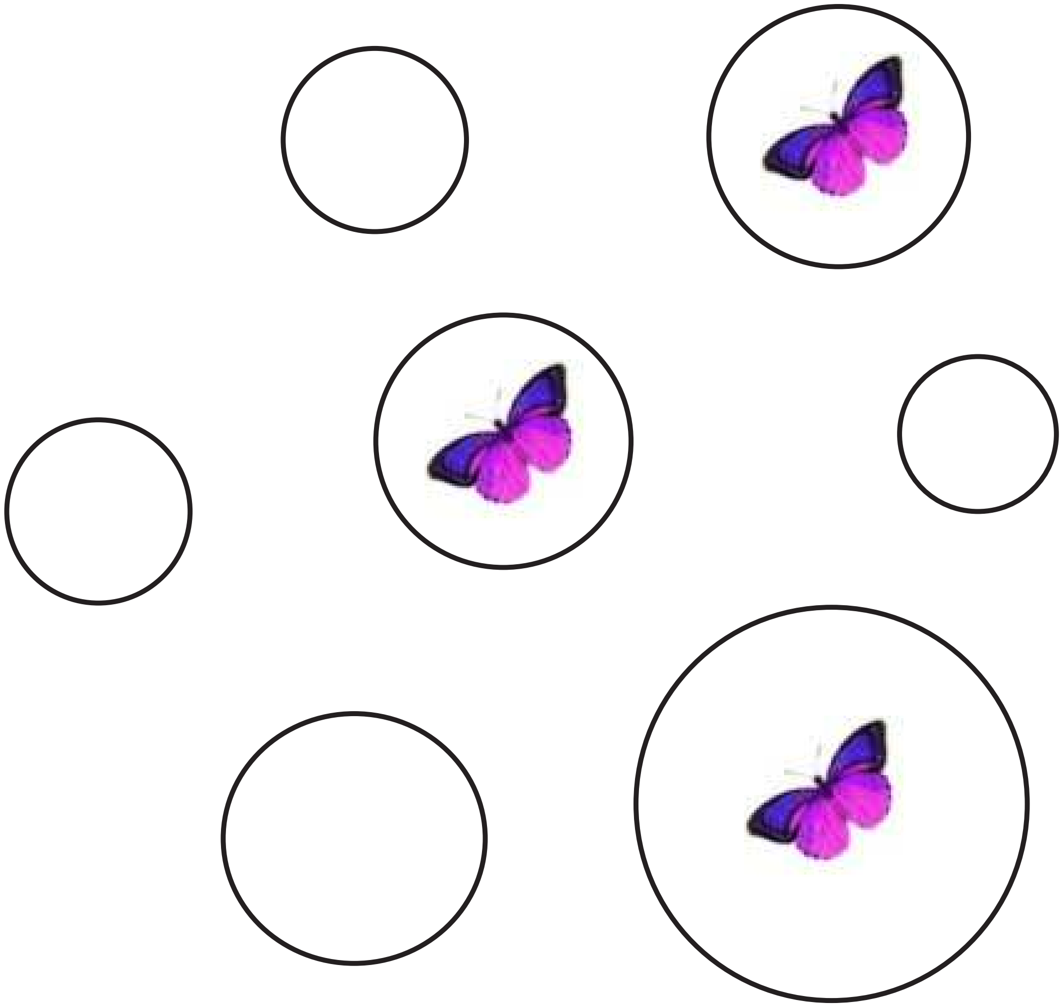
Metapopulations



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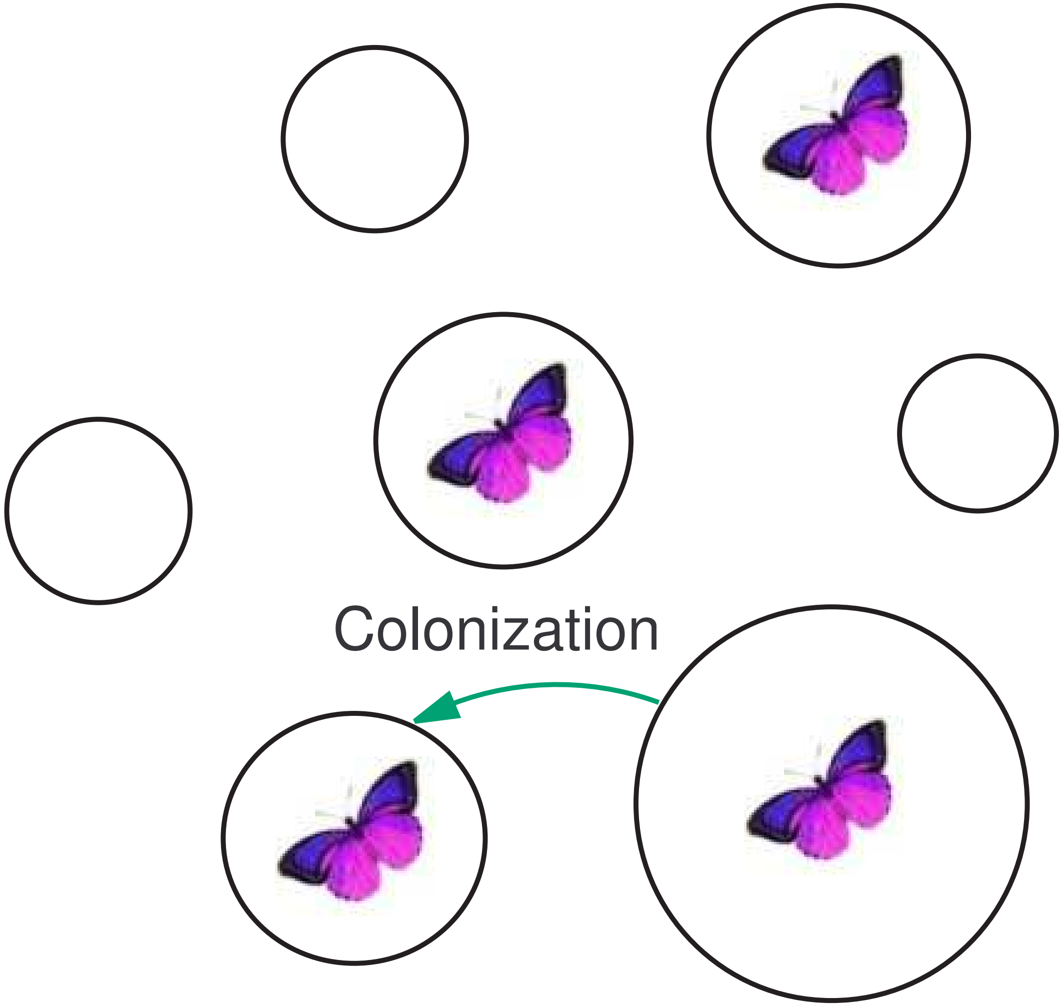

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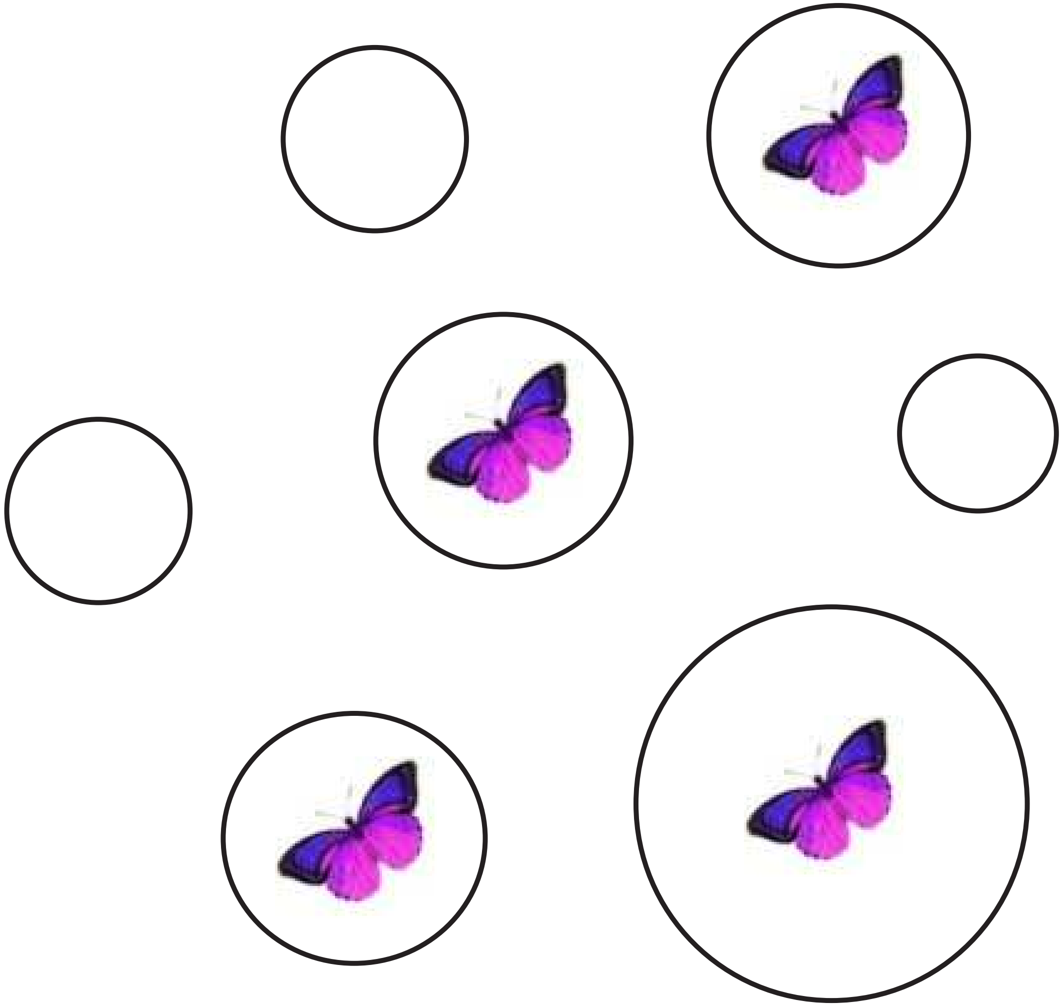

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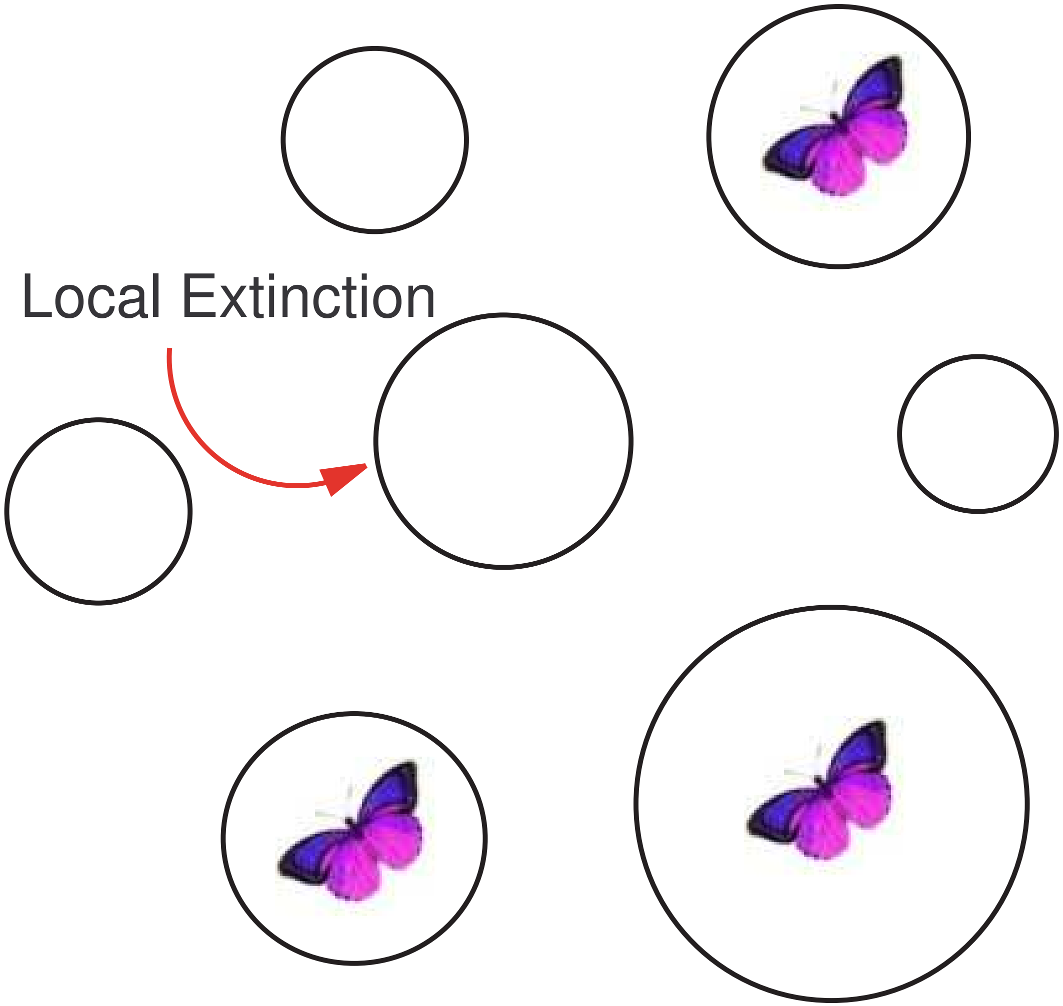
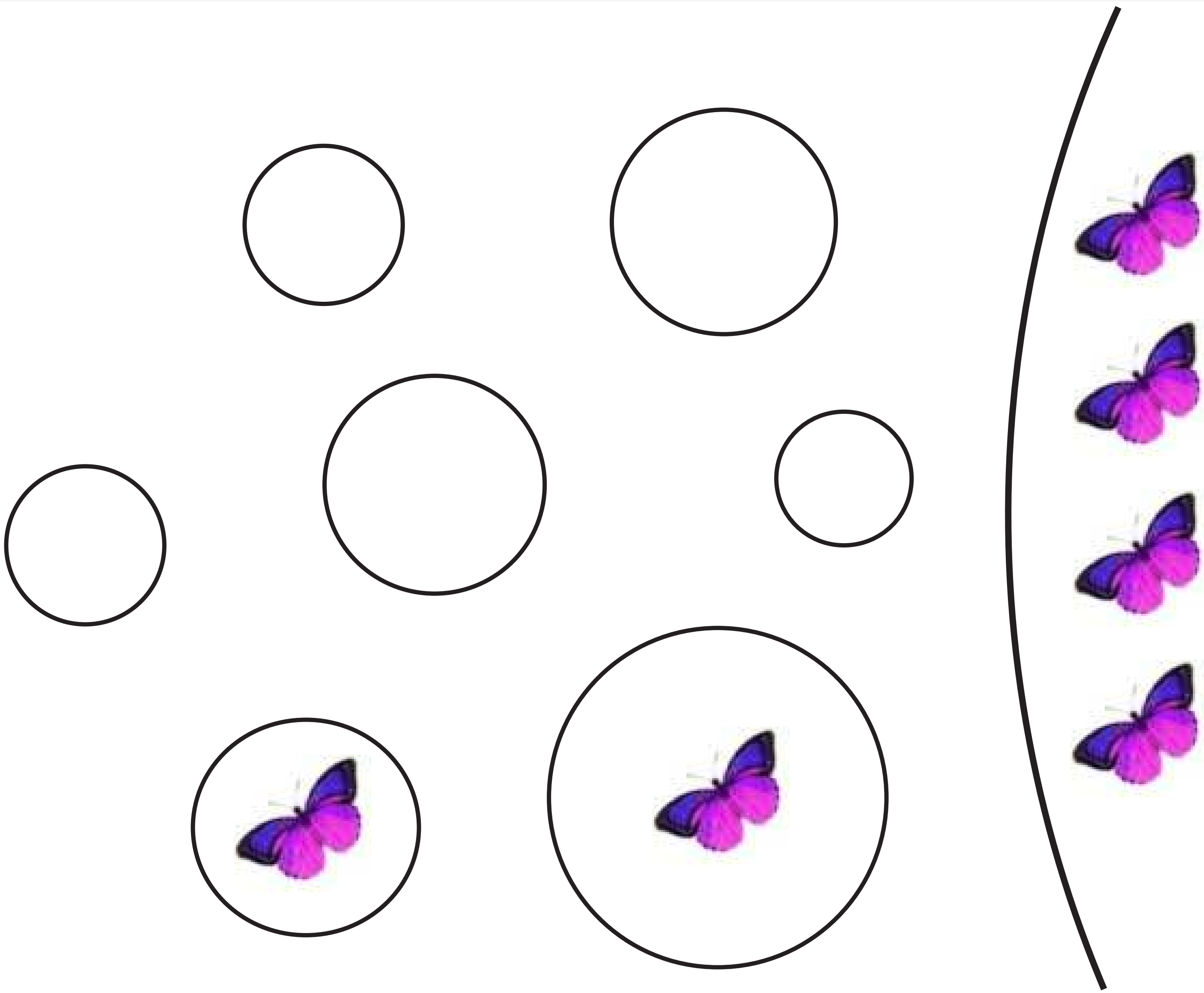


Mainland-island configuration



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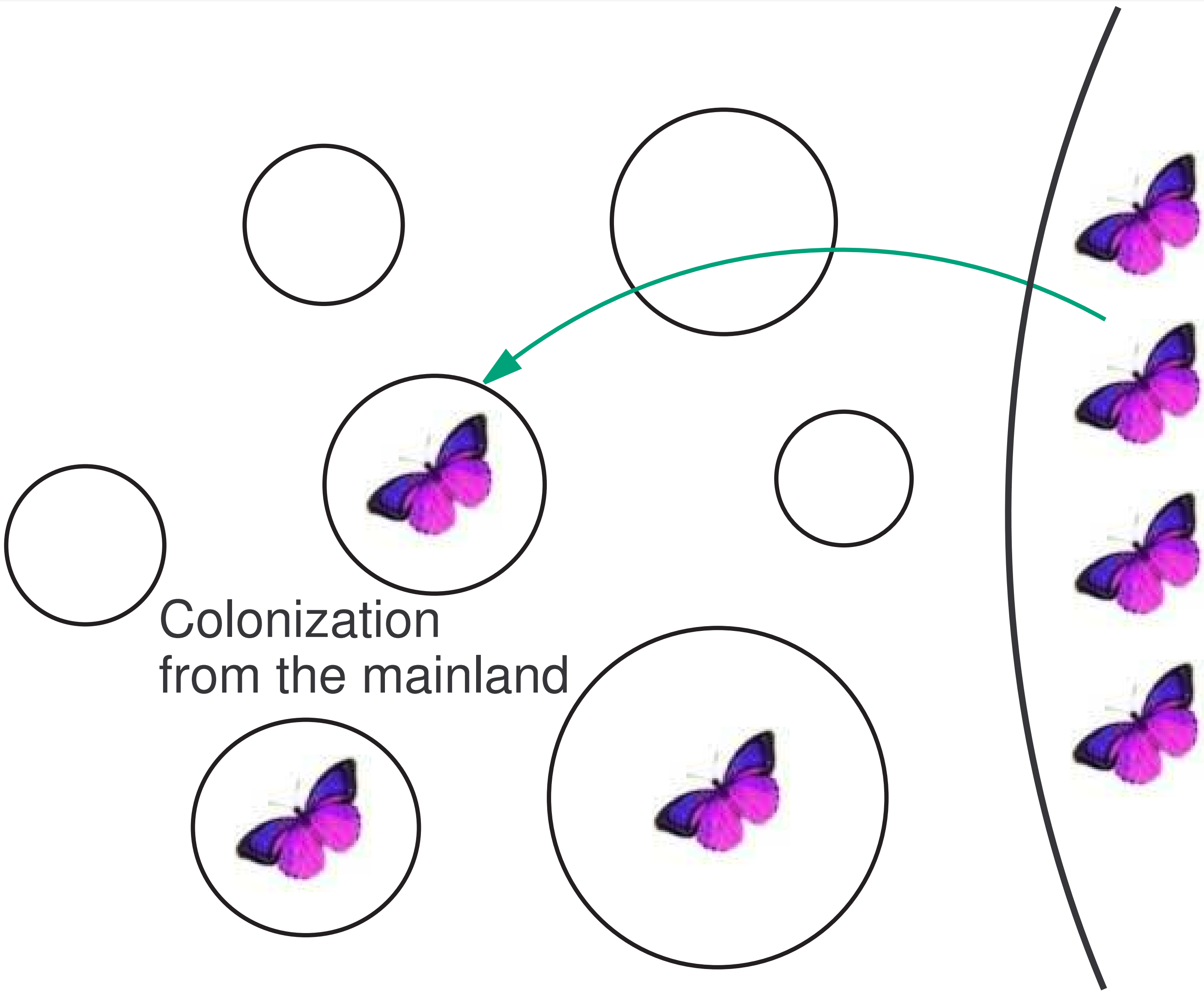


Metapopulations

- 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).

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

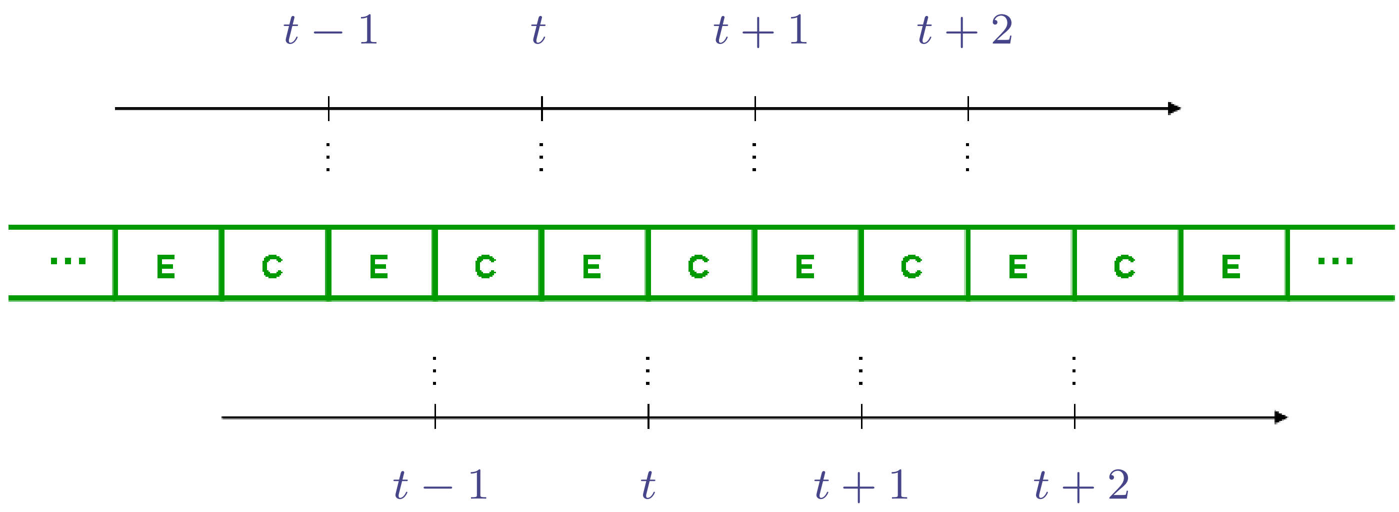
Patch-occupancy models

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.

EC versus CE

$$P = EC$$



$$P = CE$$

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:

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

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

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.

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

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Other possibilities include $c_i = c(1-(1-c_1/c)^i)$ and $c_i = 1-\exp(-i\beta/J)$.

Patch-occupancy models

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 $C \sim \mathit{Bin}(J - i, d + ic/J)$.

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We obtained explicit results for the Mainland-Island model $\ldots$

J-patch Mainland-Island models

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 $q = (1-e)c$

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Define sequences (p_t) and (q_t) by

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

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

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 $B_1 \sim \textit{Bin}(i, p_t)$ and $B_2 \sim \textit{Bin}(J - i, q_t)$. The limiting distribution of n_t is $\textit{Bin}(J, q^*)$.

J-patch Mainland-Island models

We saw that

$$\mathsf{E}(n_t|n_0 = i) = ip_t + (J - i)q_t = ia^t + Jq_t$$

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

and

$$\mathsf{Var}(n_t|n_0 = i) = ip_t(1 - p_t) + (J - i)q_t(1 - q_t)$$

$$= ia^t(1 - a^t)(1 - 2q^*) + Jq_t(1 - q_t)$$

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$$\begin{aligned}\mathsf{Var}(n_t|n_0 = i) &= ip_t(1 - p_t) + (J - i)q_t(1 - q_t) \\ &= ia^t(1 - a^t)(1 - 2q^*) + Jq_t(1 - q_t)\end{aligned}$$
$$(\;\to Jq^*(1 - q^*) \text{ as } t \to \infty).$$

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 $x_0^{(J)} := i^{(J)}/J \to x_0$. Then, . . .

Mainland-Island models: $J \to \infty$

As $J \to \infty$,

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

and

$$J\,\mathsf{Var}(X_t^{(J)}) \to x_0 p_t (1 - p_t) + (1 - x_0) q_t (1 - q_t).$$

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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 $\sqrt{J}(X_t^{(J)} - x_t) \xrightarrow{D} Z_t$, where $Z_t \sim \mathsf{N}(a^t z_0, v_t)$ and

$$v_t = x_0 p_t (1 - p_t) + (1 - x_0) q_t (1 - q_t).$$

Mainland-Island models: $J \to \infty$

We can do better . . .

Theorem $(X_{t_1}^{(J)}, X_{t_2}^{(J)}, \dots, X_{t_n}^{(J)}) \xrightarrow{P} (x_{t_1}, x_{t_2}, \dots, x_{t_n})$, for any finite sequence of times t_1, t_2, . . . , 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, ..., 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 $\sqrt{J}(x^{(J)}_0 - x_0) \to z_0$.

Mainland-Island models: $J \to \infty$

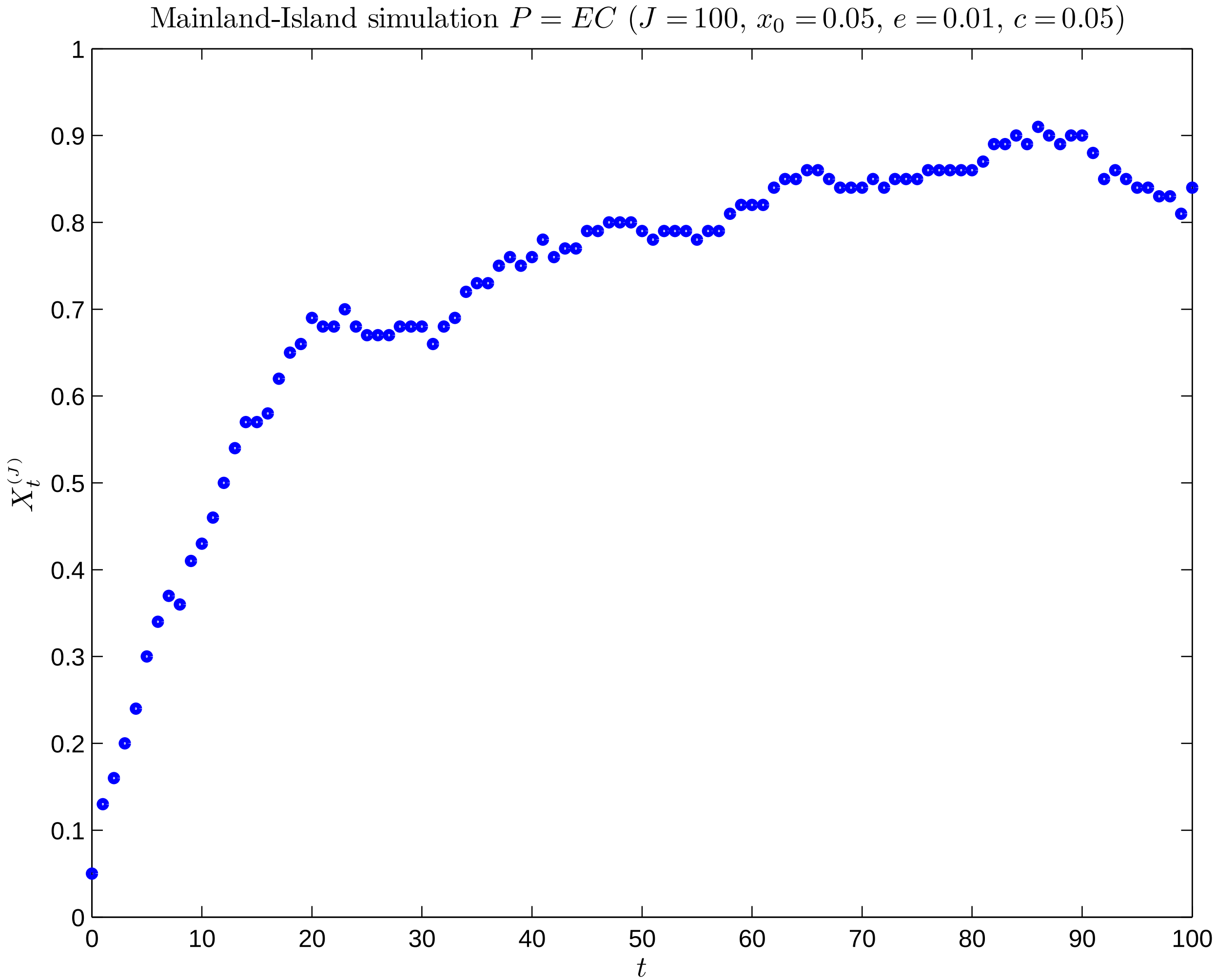
Theorem The finite-dimensional distributions (FDDs) of $(Z_t^{(J)})$ converge to those of the Gaussian Markov chain (Z_t) defined by

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

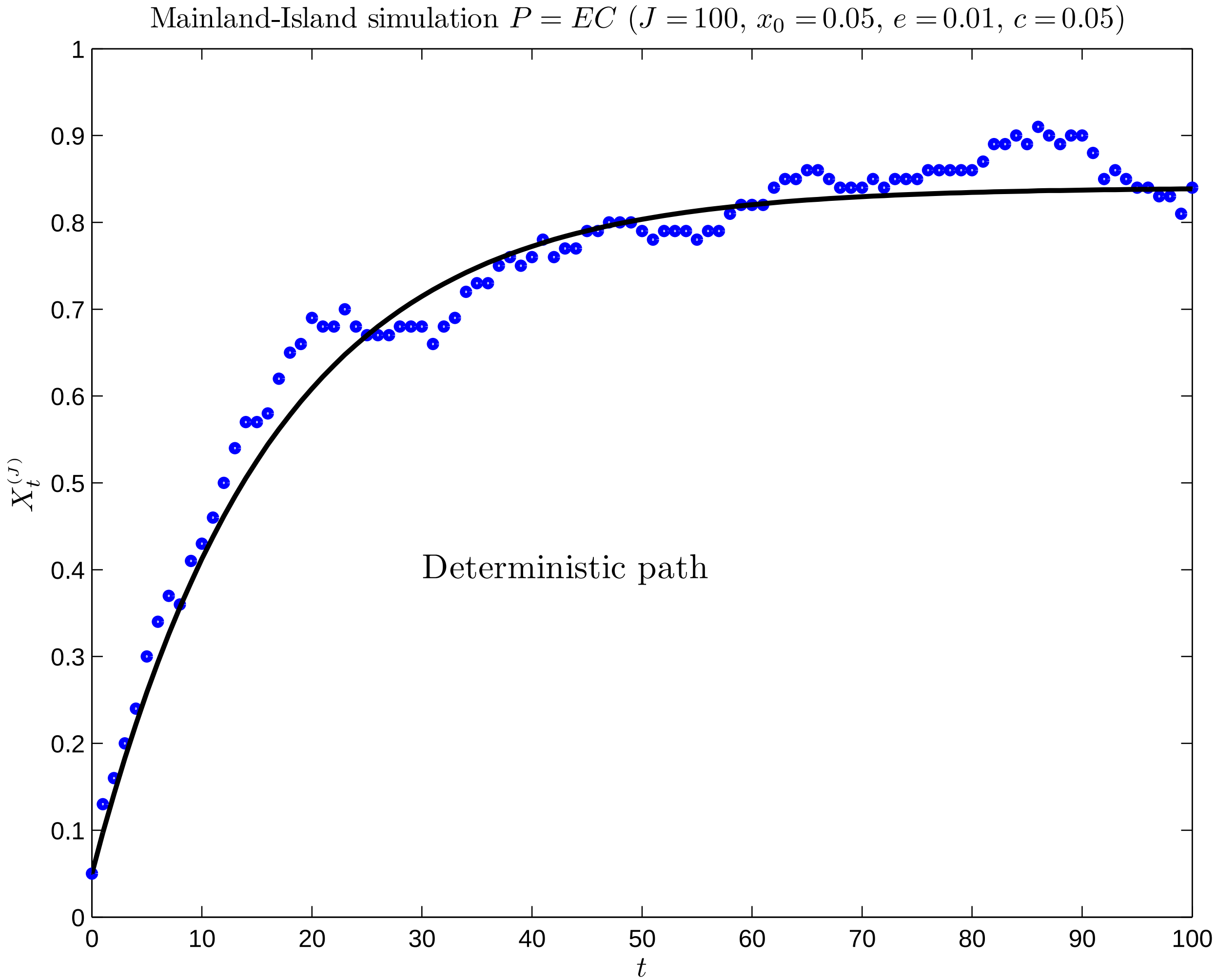
where $a = p - q = (1-e)(1-c)$ and E_t $(t = 0, 1, \dots)$ are independent Gaussian random variables with $E_t \sim \mathsf{N}(0, \sigma_t^2)$, where

$$\sigma_t^2 = x_t p(1-p) + (1-x_t)q(1-q).$$

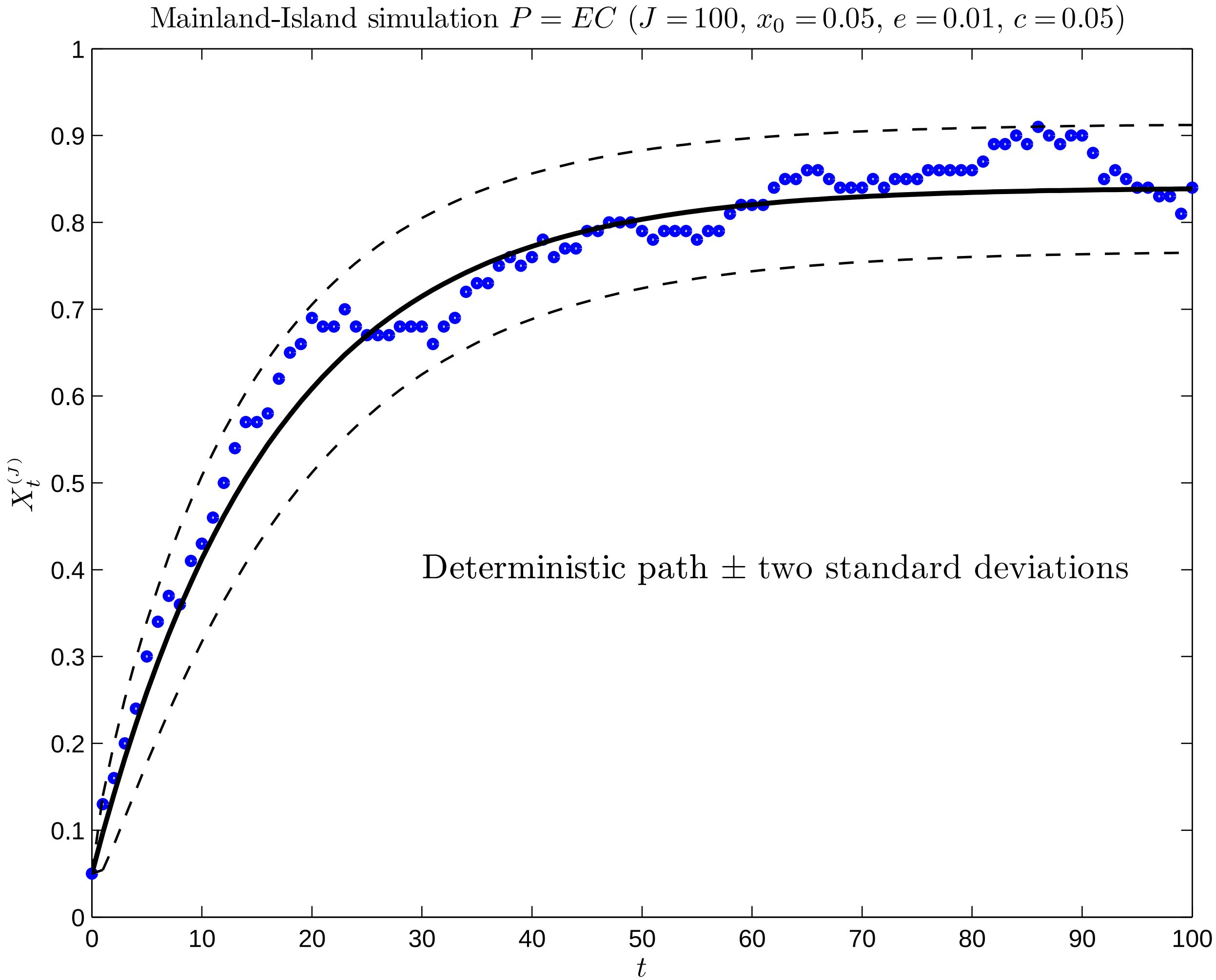
Simulation: $P = EC$



Simulation: $P = EC$ (Deterministic path)



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



Mainland-Island models: $J \longrightarrow \infty$

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 $\sqrt{J}(x_0^{(J)} - q^*) \to z_0$.

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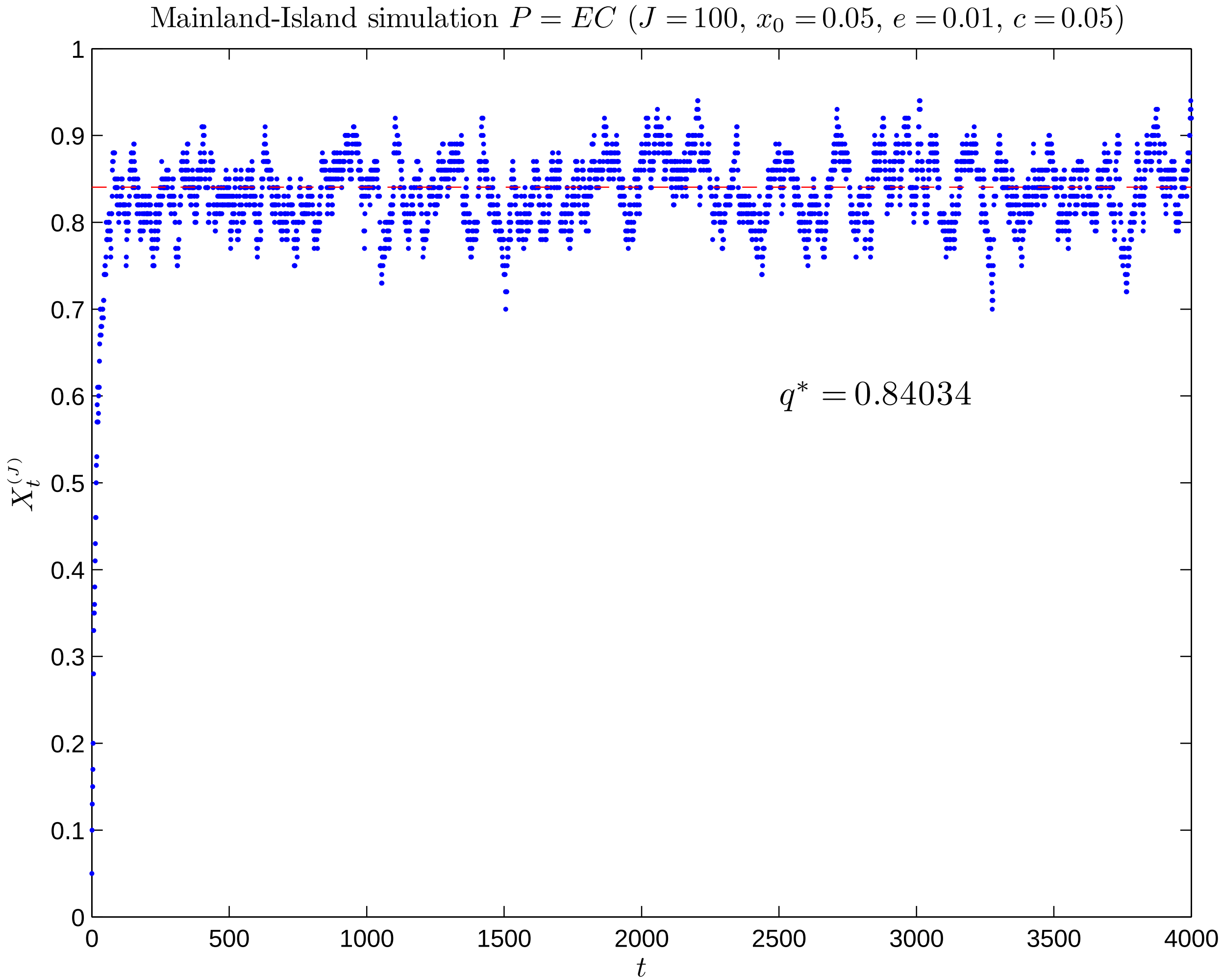
Corollary The FDDs of $(Z_t^{(J)})$ converge to those of the autoregressive (AR-1) process (Z_t) defined by

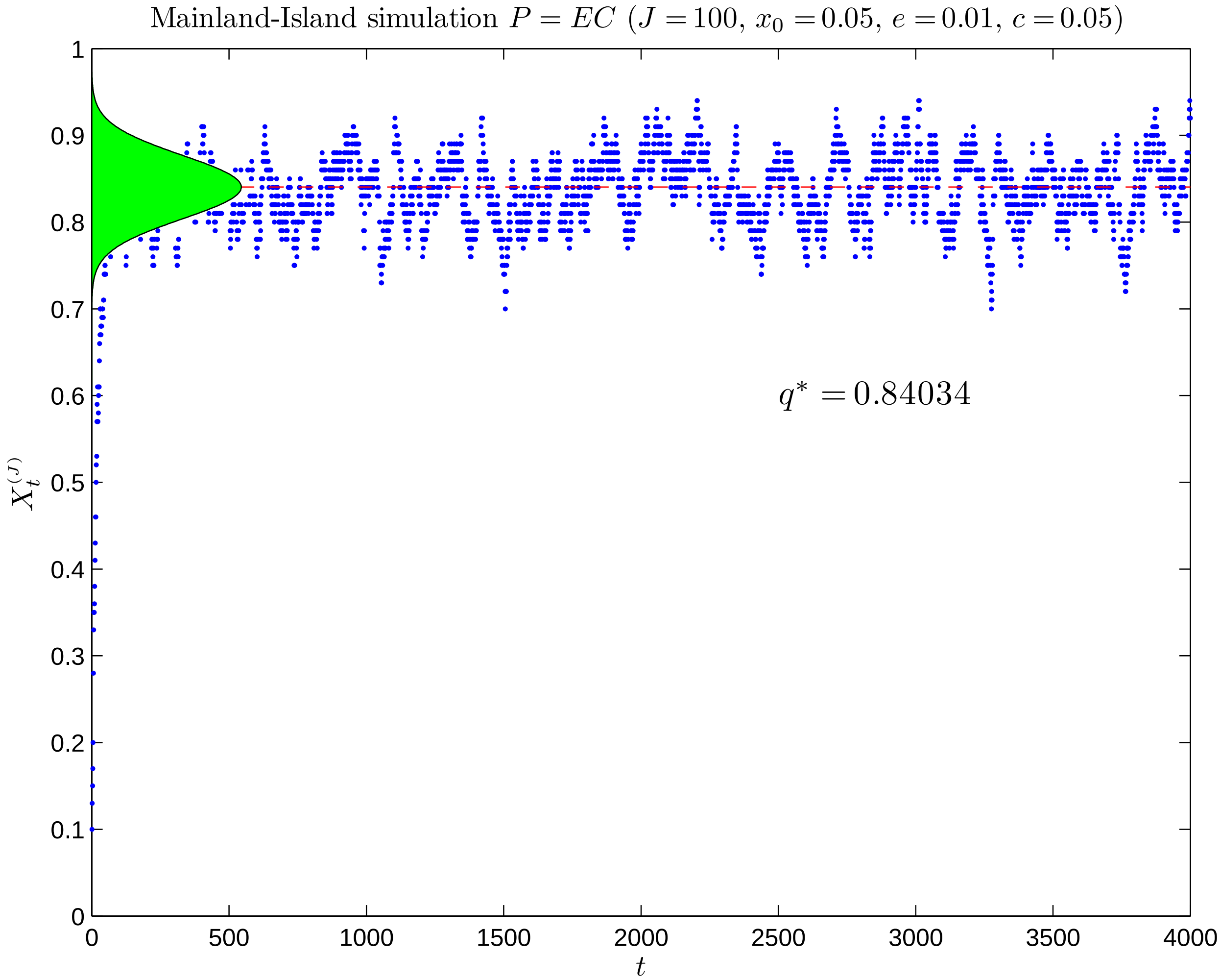
$$Z_{t+1} = aZ_t + E_t \qquad (Z_0 = z_0),$$

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

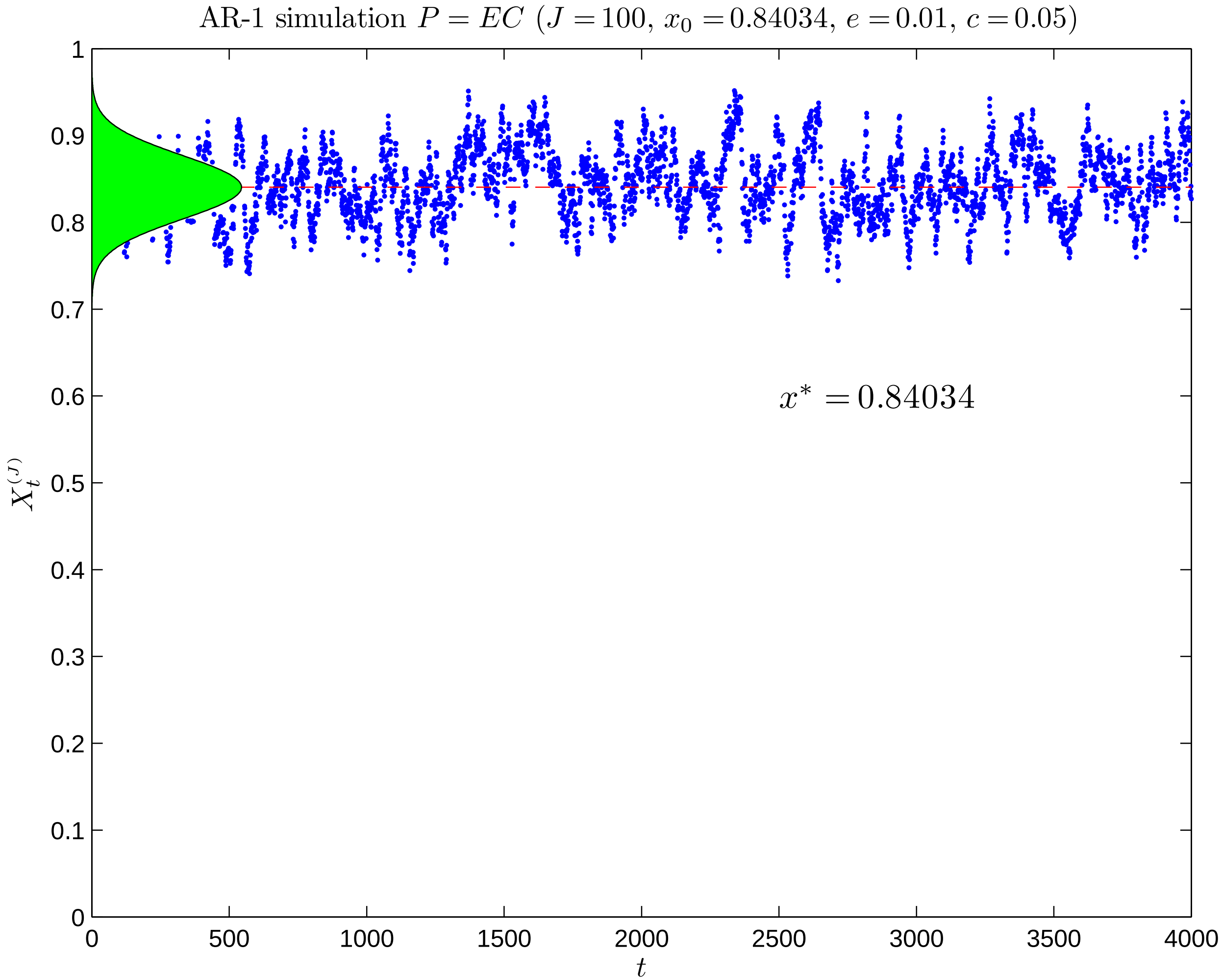
Simulation: $P = EC$



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



AR-1 Simulation: $P = EC$



Gaussian approximations

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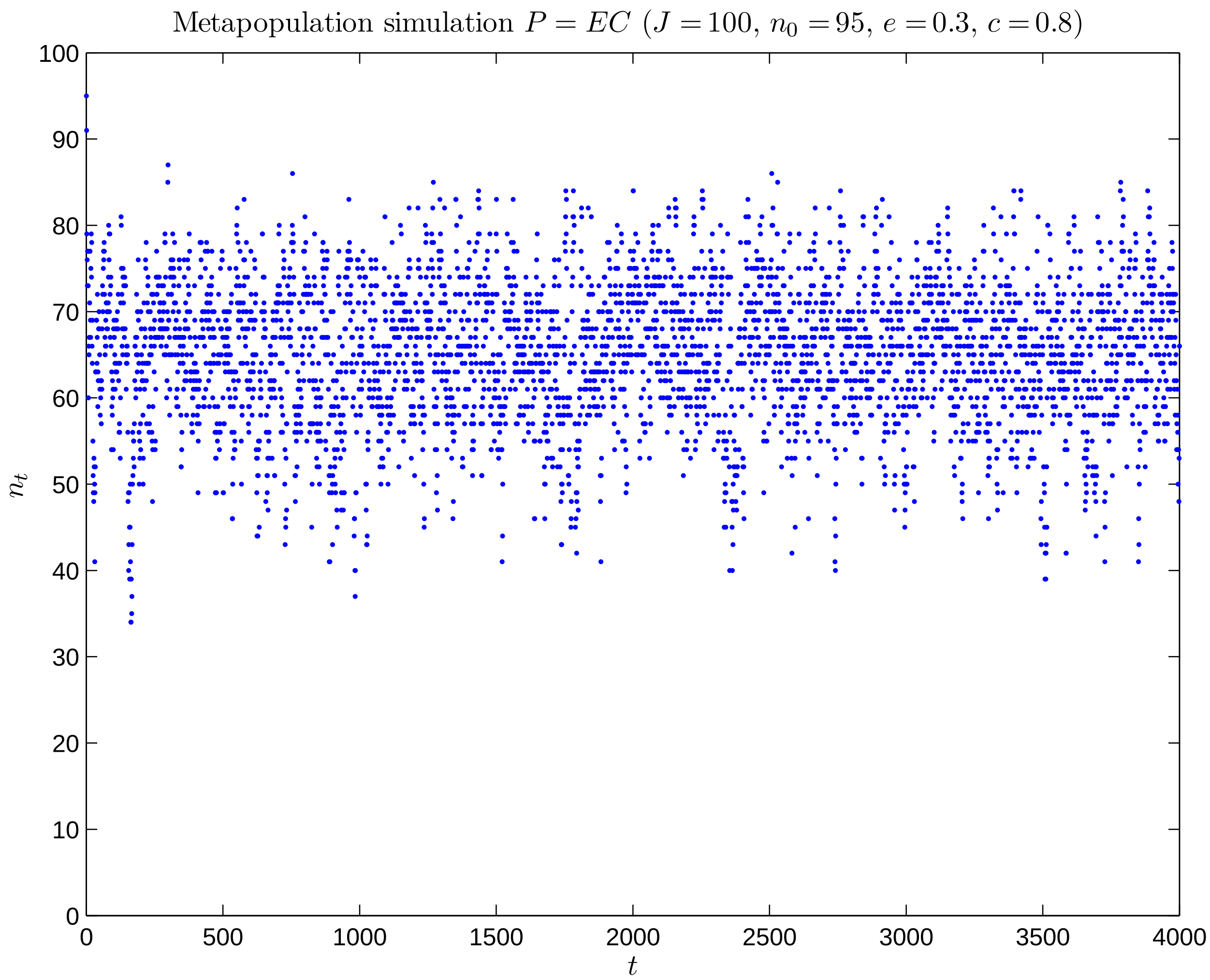
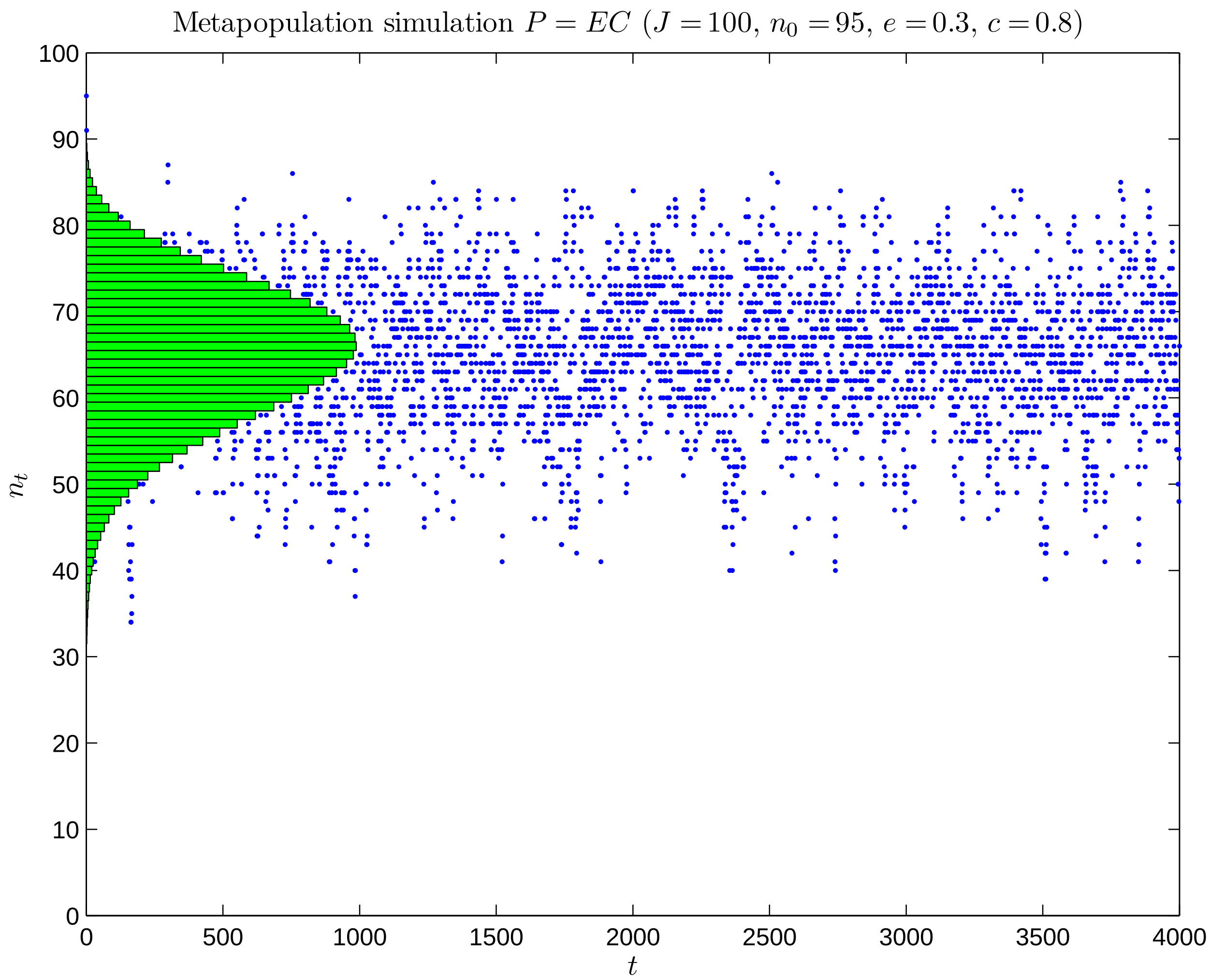
Is there a general theory of convergence for discrete-time Markov chains that share the salient features of the patch-occupancy models presented here?

Recall our numerical evaluation of quasi-stationary distributions for the basic J-patch models (described in Lecture 2) $\ldots$.

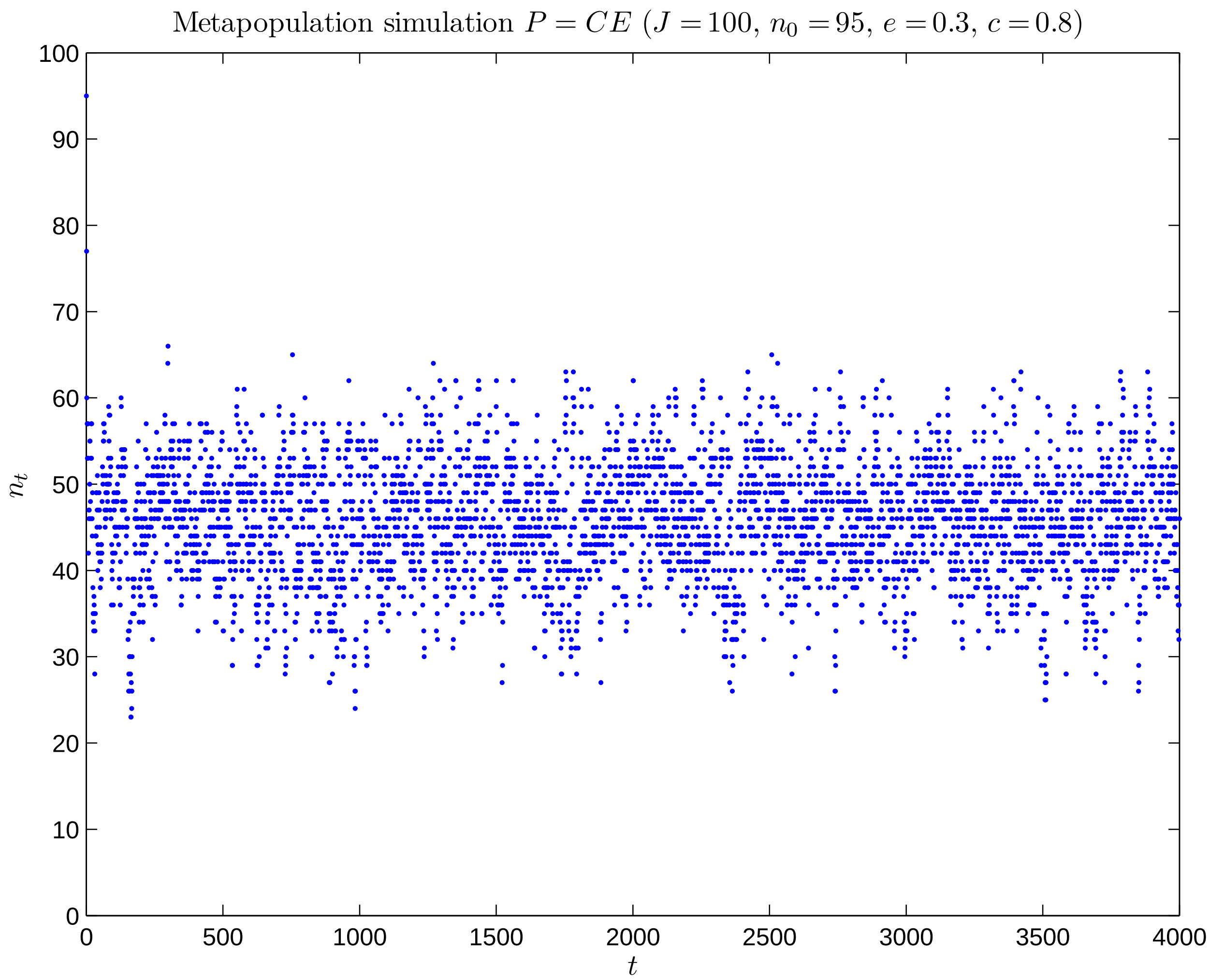
Simulation: $P = EC$



Simulation and qsd: $P = EC$



Simulation: $P = CE$



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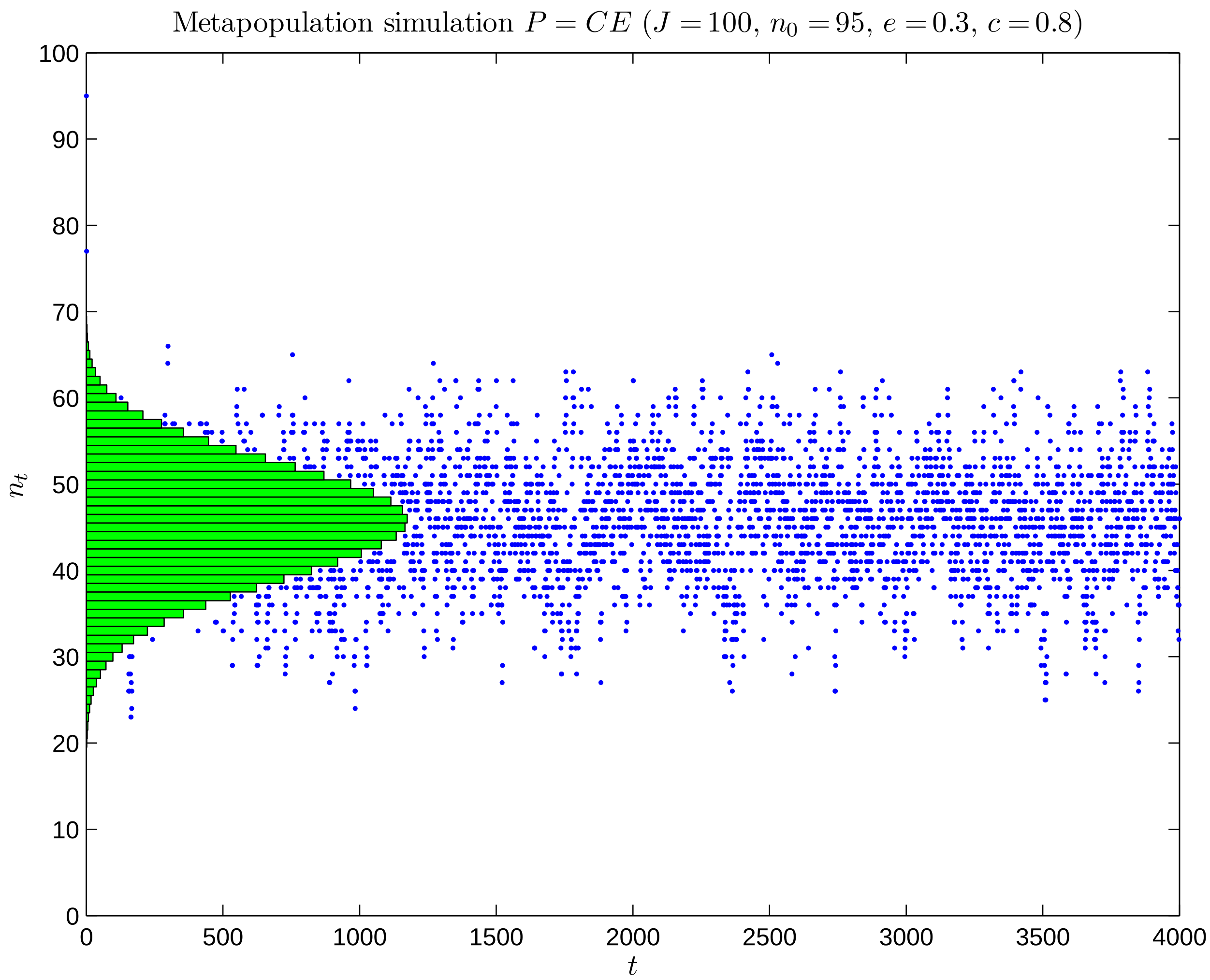

General structure: density dependence

We have a sequence of Markov chains $(n_t^{(J)})$ indexed by J, together with a function f such that

$$\mathsf{E}(n_{t+1}^{(J)}|n_t^{(J)}) = Jf(n_t^{(J)}/J),$$

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

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

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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 $X_0^{(J)} \to x_0$ as $J \to \infty$, then $(X_t^{(J)}) \stackrel{FDD}{\to} (x_t)$, 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

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General structure: density dependence

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

$$\mathsf{E}(Z_{t+1}^{(J)}) = \sqrt{J}\,(\mathsf{E}(X_{t+1}^{(J)}) - f(x_t)) = f'(x_t)\,\mathsf{E}(Z_t^{(J)}) + \cdots,$$

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

General structure: density dependence

Moreover, $J\,\text{Var}(X_{t+1}^{(J)}|X_t^{(J)}) = s(X_t^{(J)})$, suggesting that

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

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

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

If x_{eq} is a *fixed point* of f, and $\sqrt{J}(X_0^{(J)} - x_{\text{eq}}) \to z_0$, then we might hope that $(Z_t^{(J)}) \stackrel{FDD}{\to} (Z_t)$, where (Z_t) is the AR-1 process defined by $Z_{t+1} = aZ_t + E_t$, $Z_0 = z_0$, where $a = f'(x_{\text{eq}})$ and E_t $(t = 0, 1, \dots)$ are iid Gaussian $\text{N}(0, s(x_{\text{eq}}))$ random variables.

Convergence of Markov chains

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

*Karr, A.F. (1975) Weak convergence of a sequence of Markov chains. Probability Theory and Related Fields 33, 41–48.

He considered a sequence of time-homogeneous Markov chains $(X_t^{(n)})$ on a general state space $(\Omega, \mathcal{F}) = (E, \mathcal{E})^{\mathbb{N}}$ 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) $x_n \to x$ in E implies $K_n(x_n, \cdot) \Rightarrow K(x, \cdot)$, then the corresponding probability measures $(\mathbb{P}_n^{\pi_n})$ on $(\Omega, \mathcal{F})$ also converge: $\mathbb{P}_n^{\pi_n} \Rightarrow \mathbb{P}^{\pi}$.

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 $x_n \to x$ in E implies $U_n(x_n, \cdot) \Rightarrow U(x, \cdot)$ and $V_n(x_n, \cdot) \Rightarrow V(x, \cdot)$.

J-patch models: convergence

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 $(X_t^{(J)}, Z_t^{(J)})$.

J-patch models: convergence

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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).

J-patch models: convergence

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 $Z \sim \text{N}(pz, xp(1-p))$.

J-patch models: convergence

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$$y_t = (1-e)x_t \quad \text{and} \quad Y_t = (1-e)Z_t + \text{N}(0, e(1-e)x_t).$$

J-patch models: convergence

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 $C^{(J)} \sim \text{Bin}(J - i^{(J)}, ci^{(J)}/J)$ $(0 < c < 1)$. Thus, $C^{(J)}$ is the number of colonizations starting with $i^{(J)}$ occupied patches. Let $X^{(J)} = x^{(J)} + C^{(J)}/J$ (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 $Z \sim \text{N}((1 + c - 2cx)z, cx(1 - x)(1 - cx))$.

J-patch models: convergence

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$$y_t = x_t(1 + c - cx_t) \quad \text{and}$$

$$Y_t = (1 + c - 2cx_t)Z_t + \text{N}(0, cx_t(1 - x_t)(1 - cx_t)).$$

J-patch models: convergence

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

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

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

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

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

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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

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

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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J-patch models: convergence

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

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

for any finite sequence of times t_1, t_2, $\ldots$, t_n, 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: $f(x) = (1-e)(1+c-cx)x$

J-patch models: convergence

Theorem If, additionally, $\sqrt{J}(X_0^{(J)} - x_0) \to z_0$, then $(Z_t^{(J)}) \overset{FDD}{\longrightarrow} (Z_t)$, where (Z_t) is the Gaussian Markov chain defined by

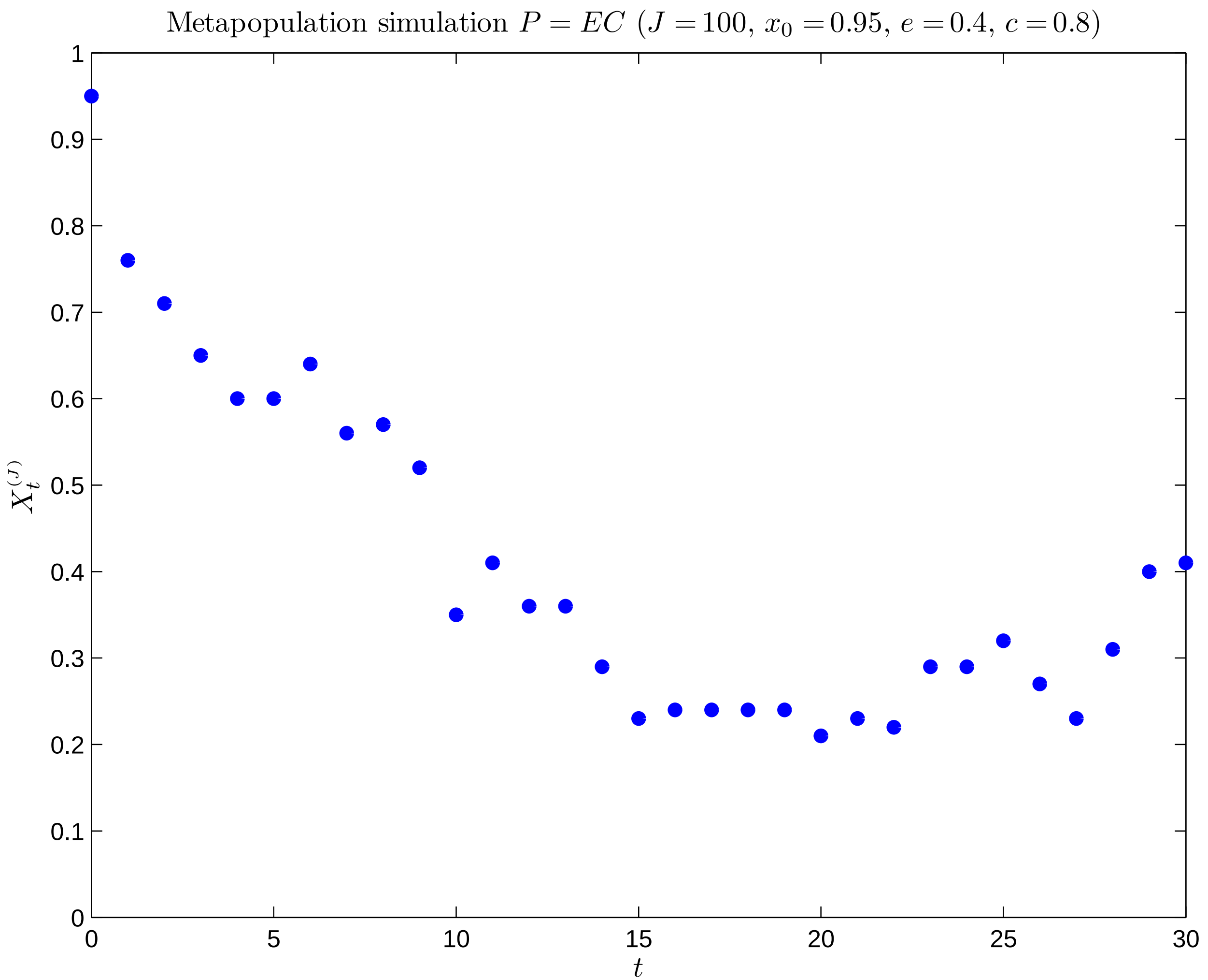
$$Z_{t+1} = f'(x_t)Z_t + E_t \qquad (Z_0 = z_0),$$

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

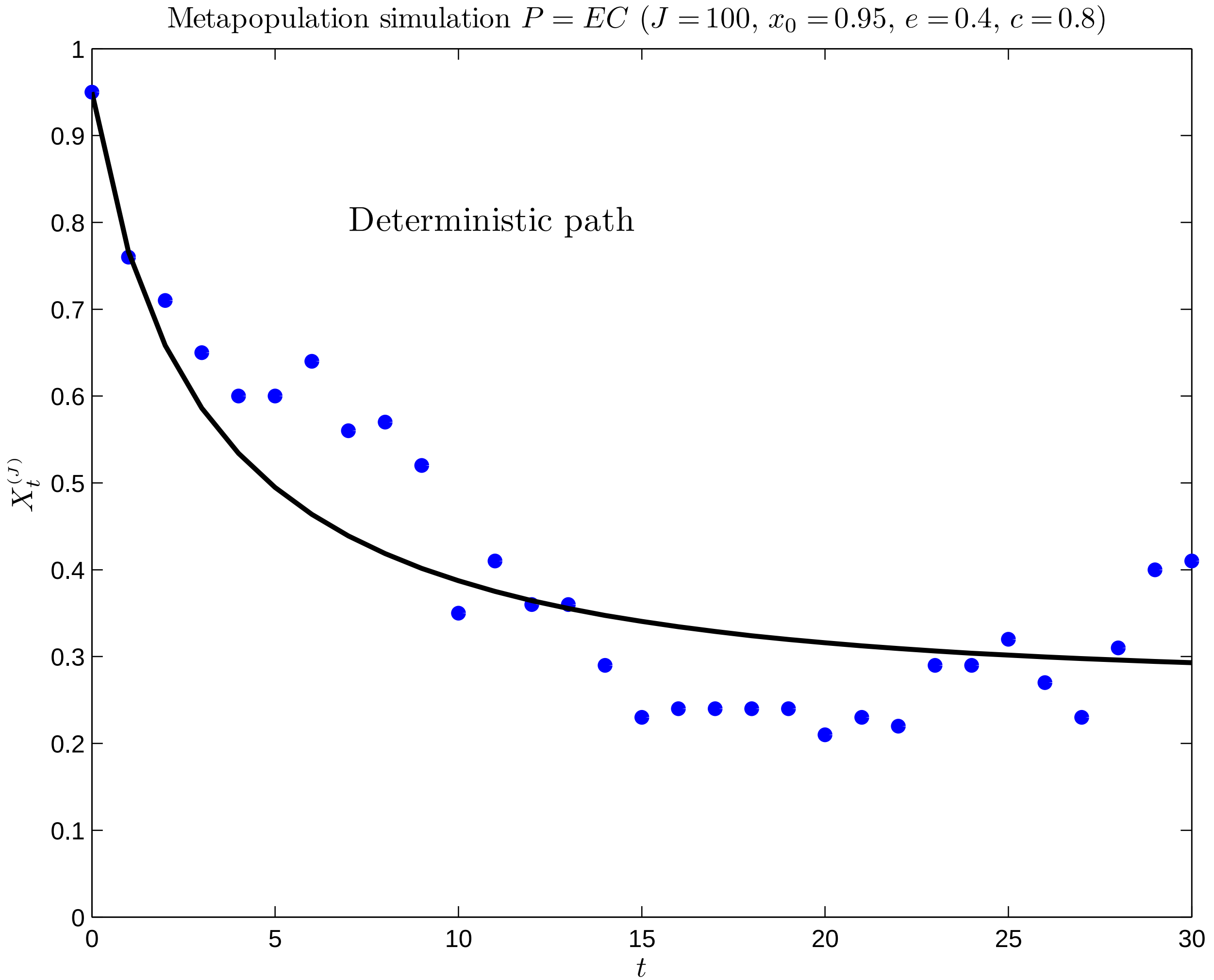
EC-model: $s(x) = (1-e)[c(1-(1-e)x)(1-c(1-e)x) + e(1+c-2c(1-e)x)^2]x$

CE-model: $s(x) = (1-e)[e + c(1-x)(1-c(1-e)x)]x$

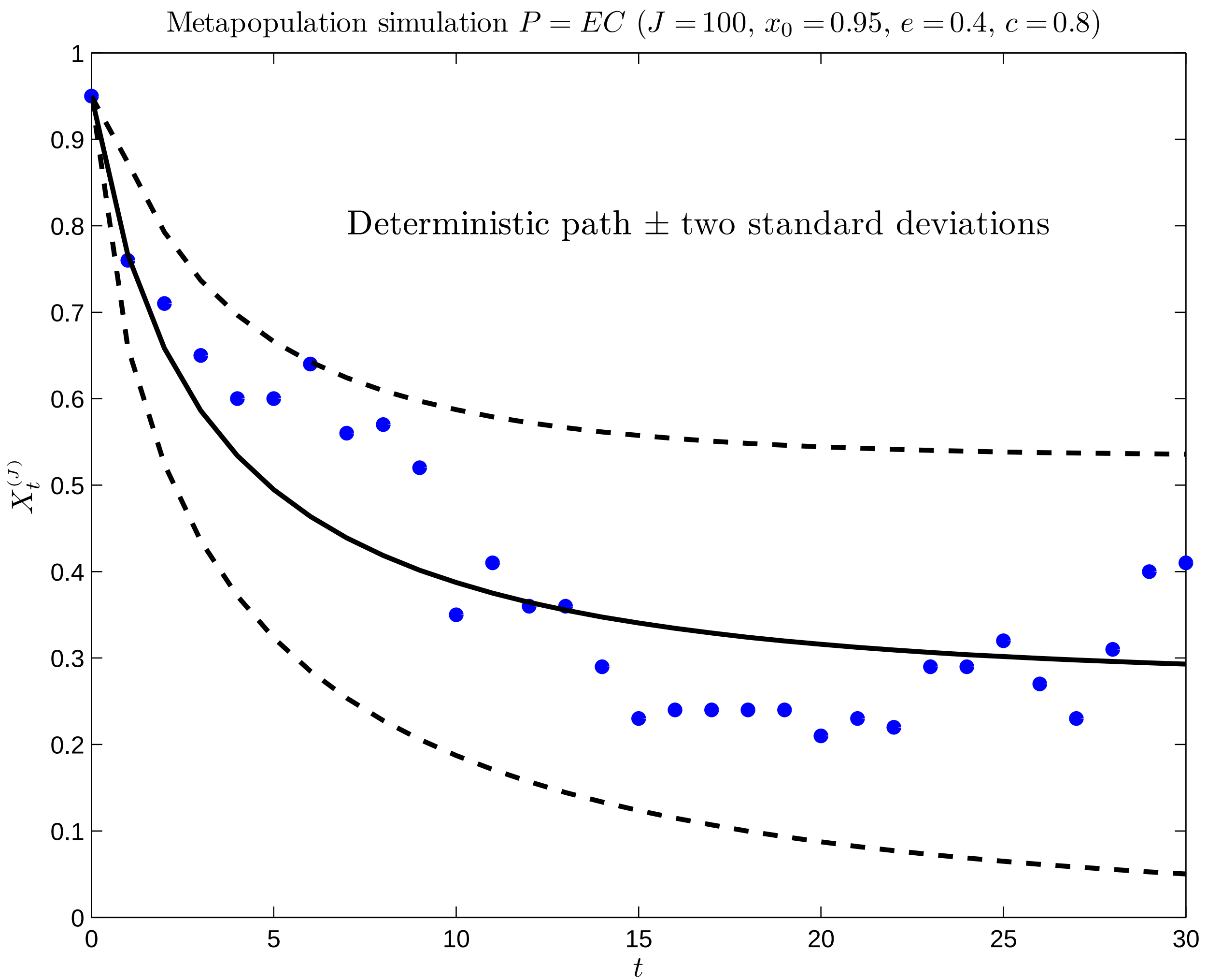
Simulation: $P = EC$



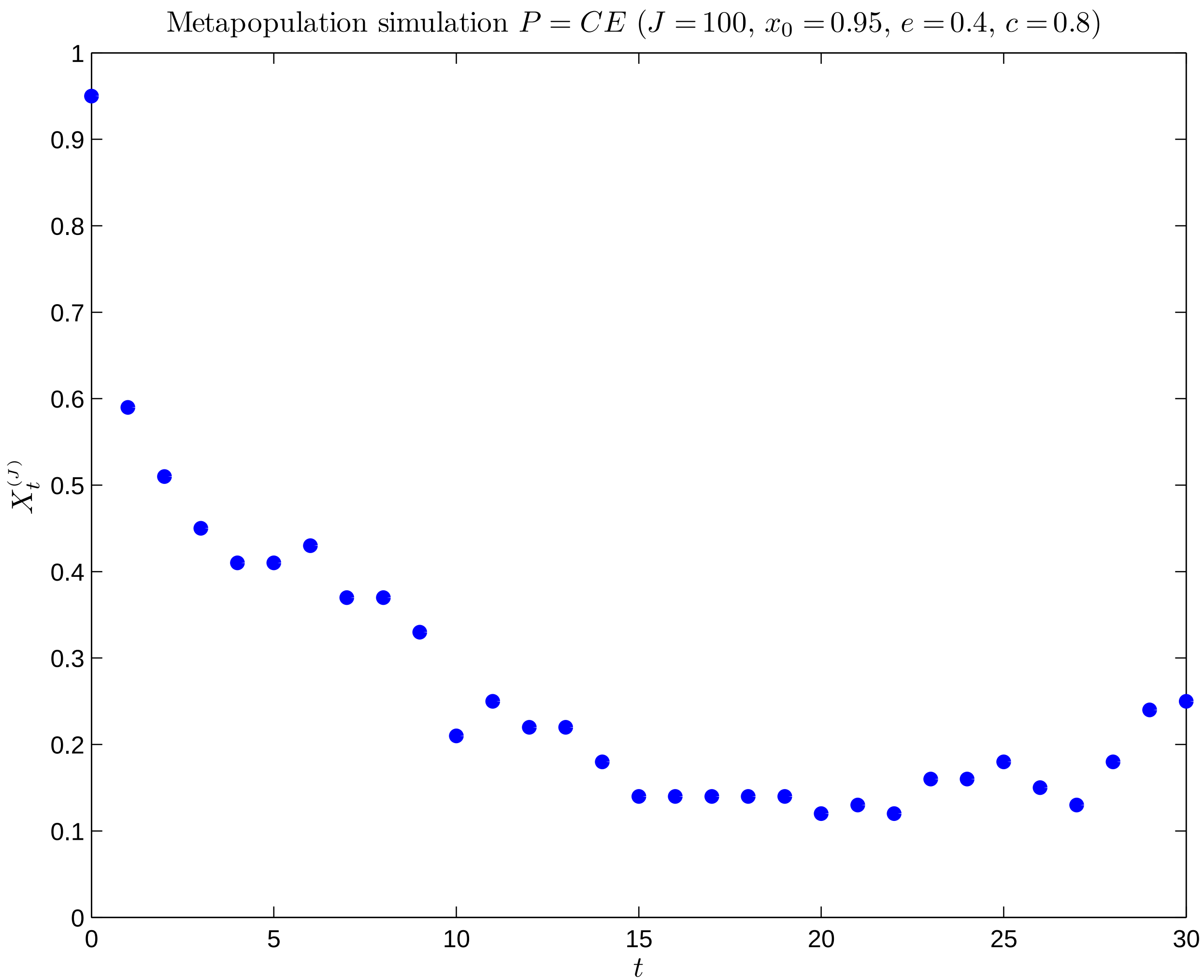
Simulation: $P = EC$ (Deterministic path)



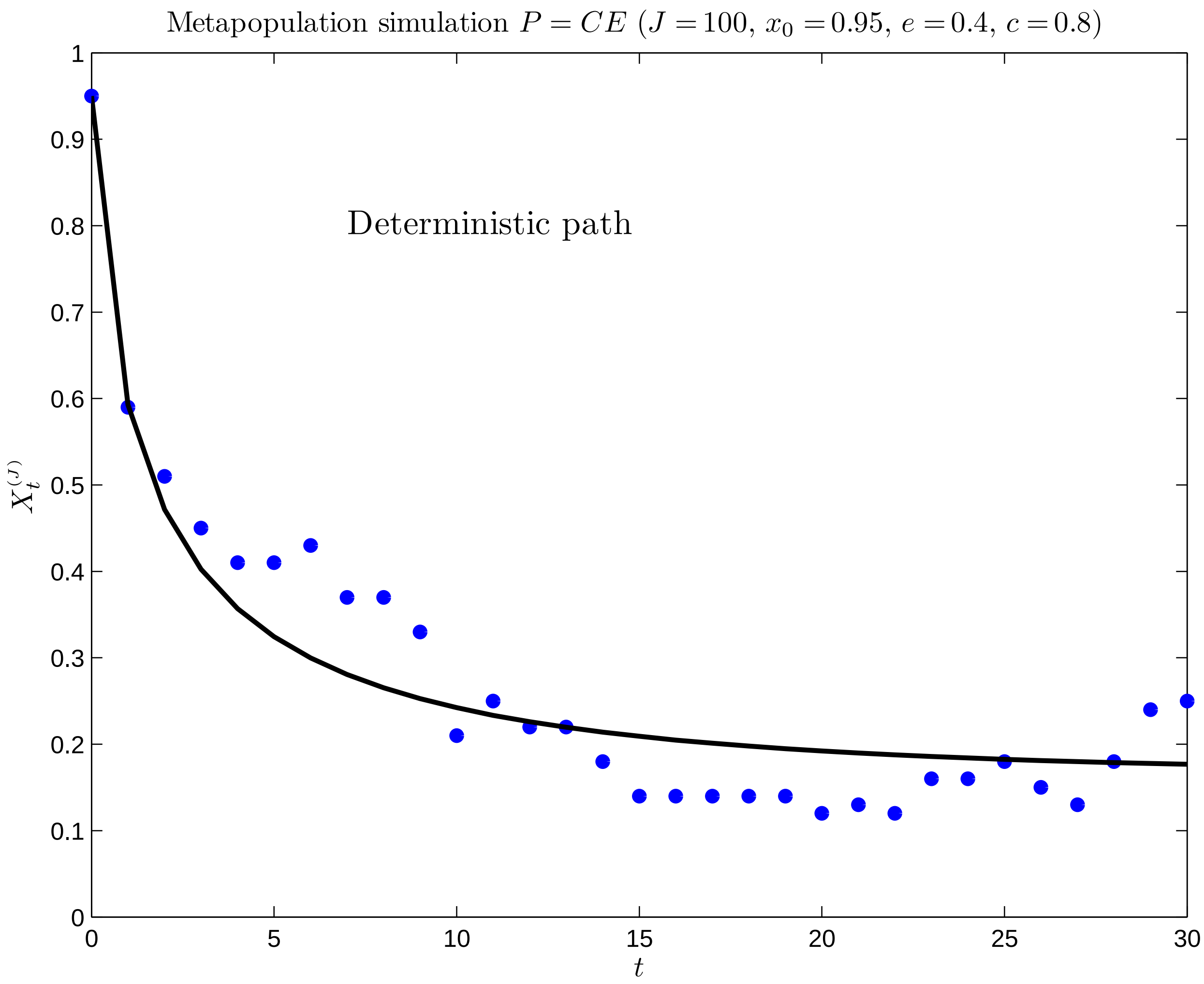
Simulation: $P = EC$ (Gaussian approx.)



Simulation: $P = CE$



Simulation: $P = CE$ (Deterministic path)



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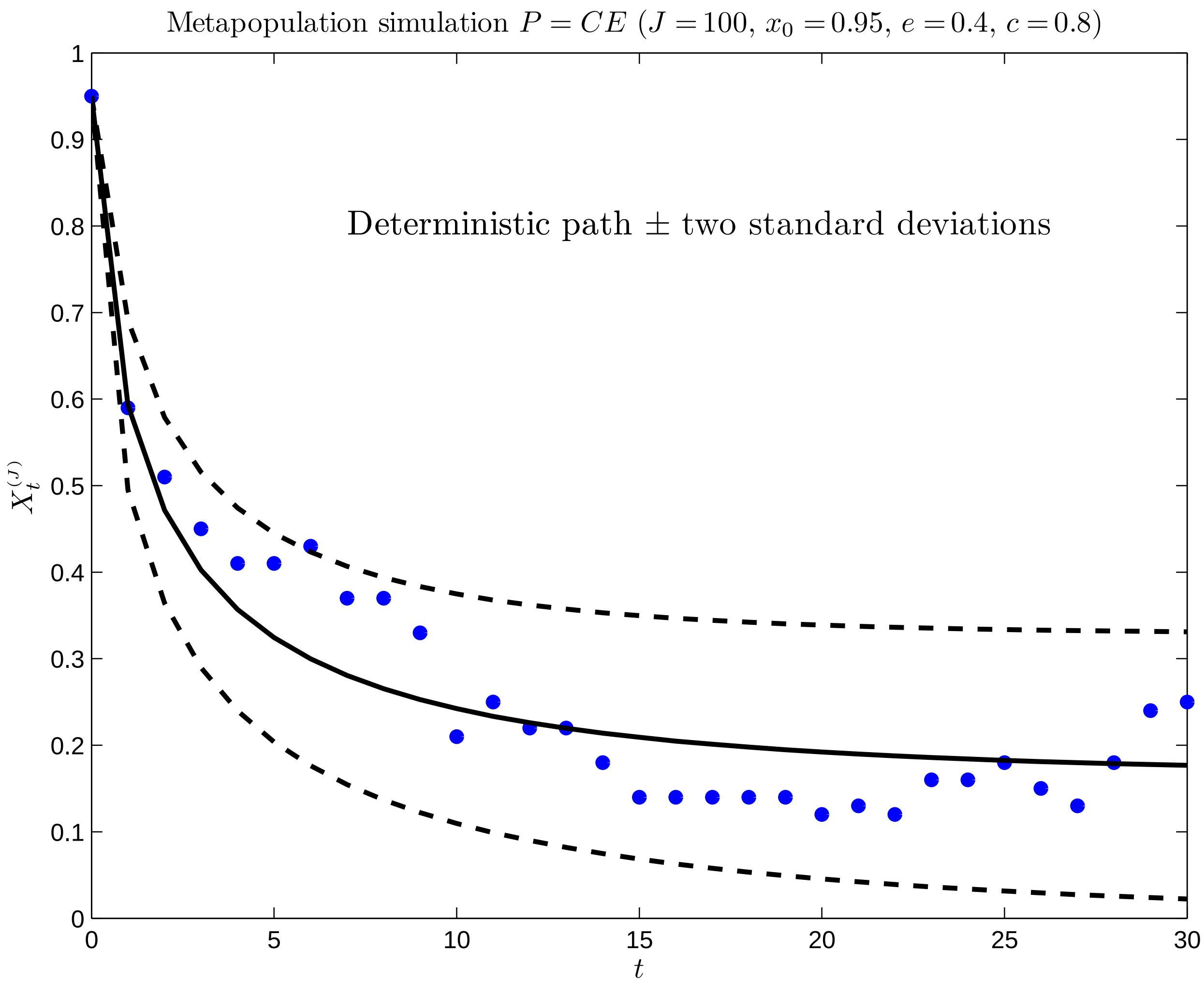

J-patch models: convergence

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

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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.

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J-patch models: convergence

Corollary If $c > e/(1-e)$, so that x^* given above is stable, and $\sqrt{J}(X_0^{(J)} - x^*) \to z_0$, then $(Z_t^{(J)}) \overset{FDD}{\to} (Z_t)$, where (Z_t) is the AR-1 process defined by

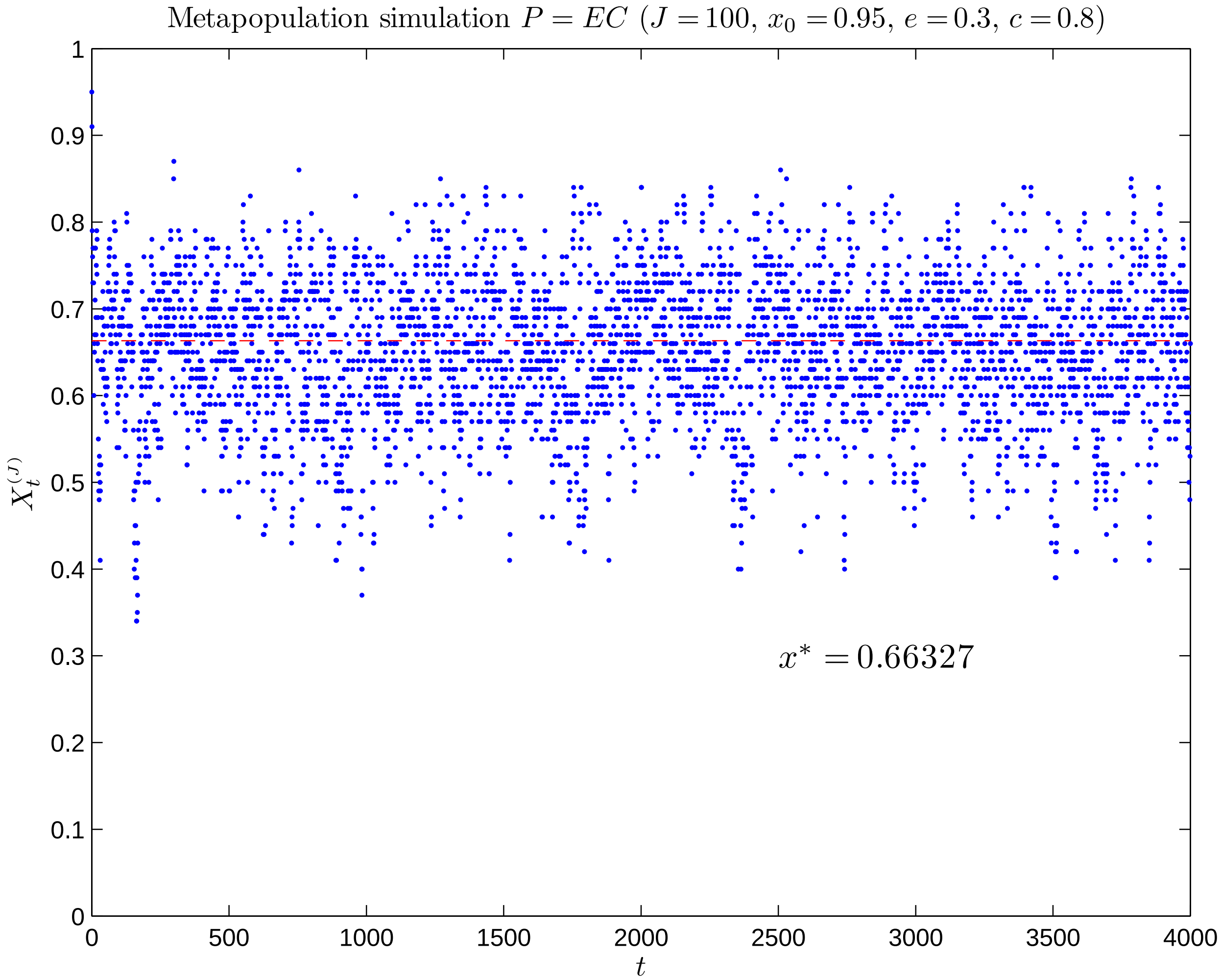
$$Z_{t+1} = (1 + e - c(1-e))Z_t + E_t \qquad (Z_0 = z_0),$$

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

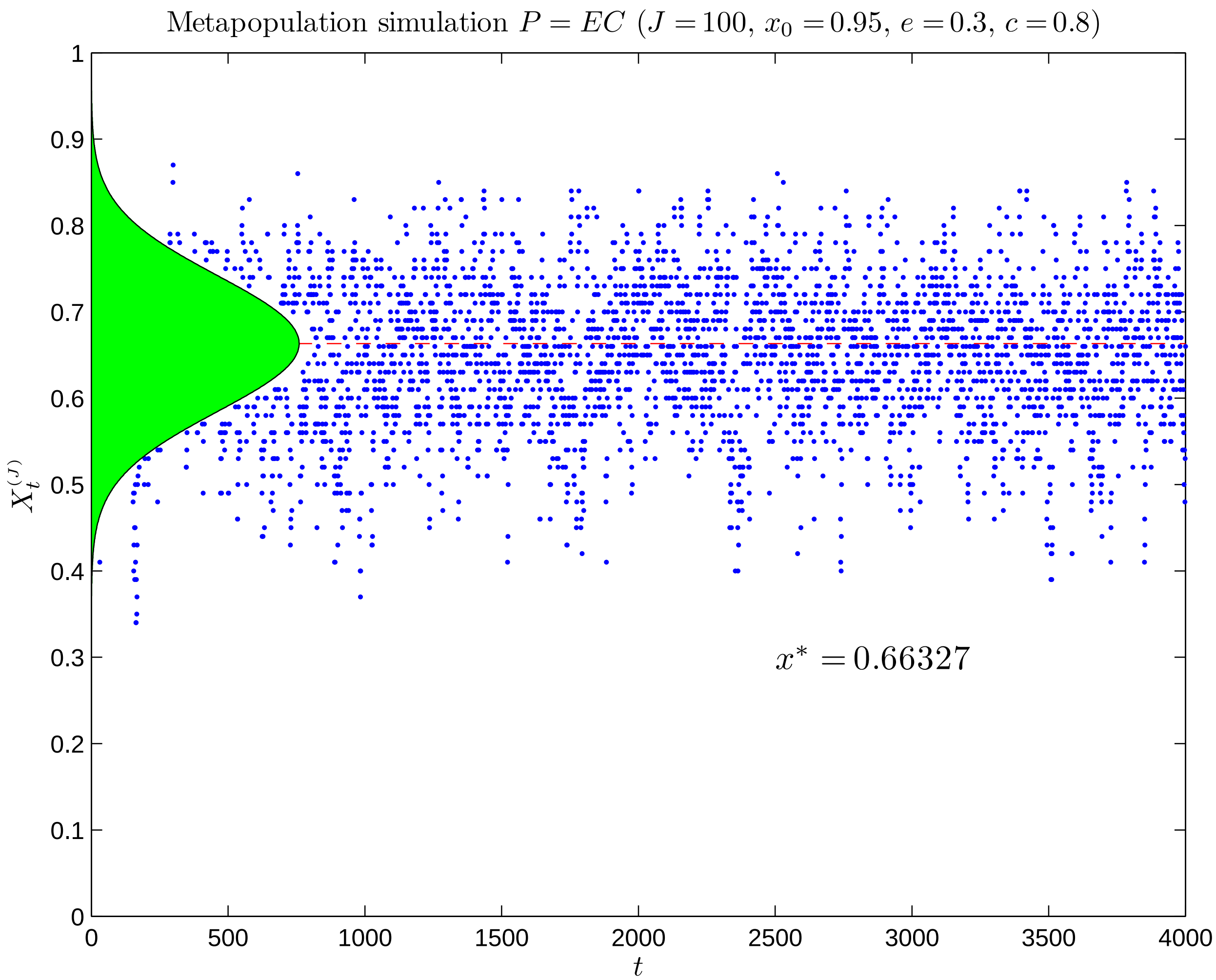
EC-model: $\sigma^2 = (1-e)[c(1-(1-e)x^*)(1-c(1-e)x^*) + e(1+c-2c(1-e)x^*)^2]x^*$

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

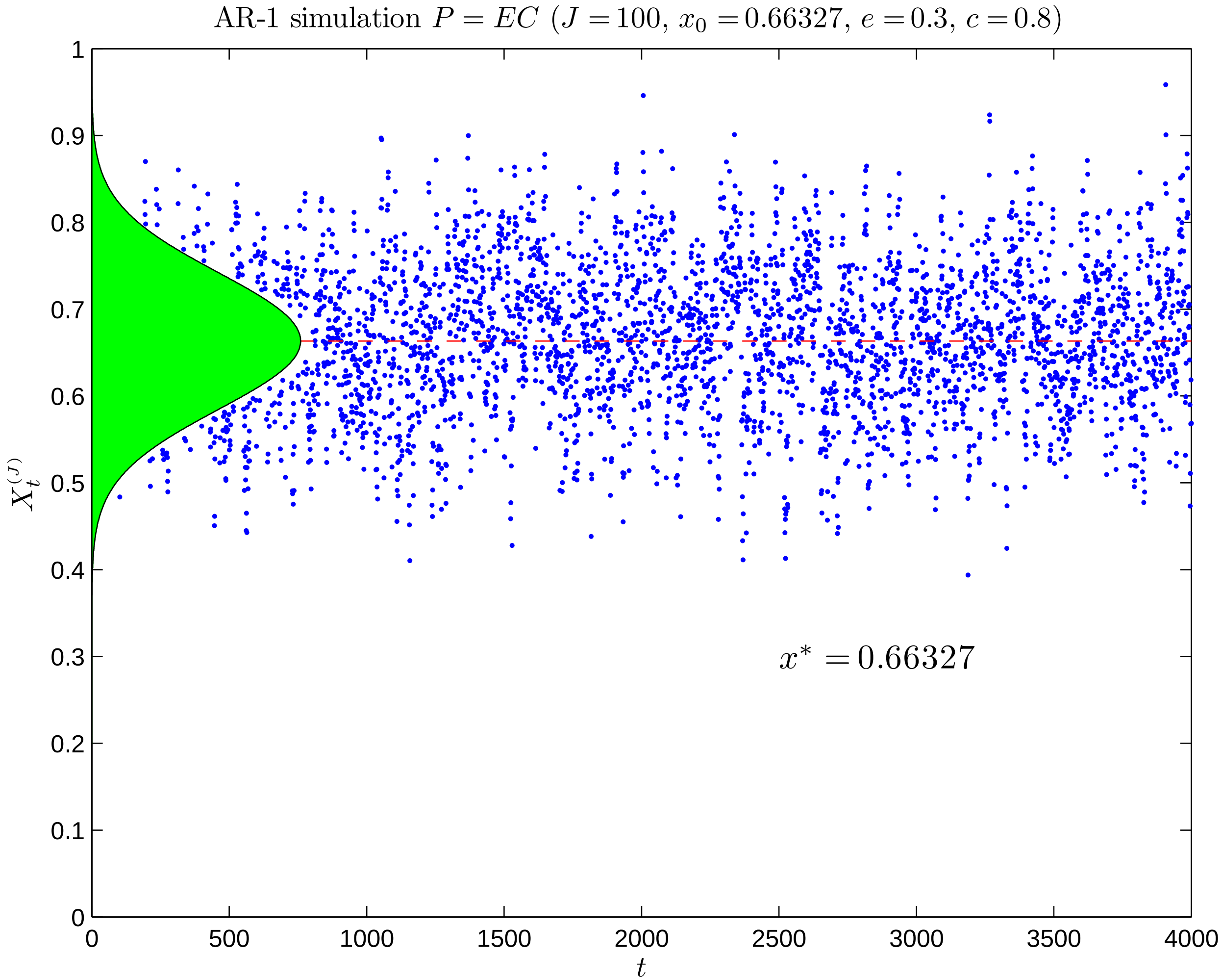
Simulation: $P = EC$



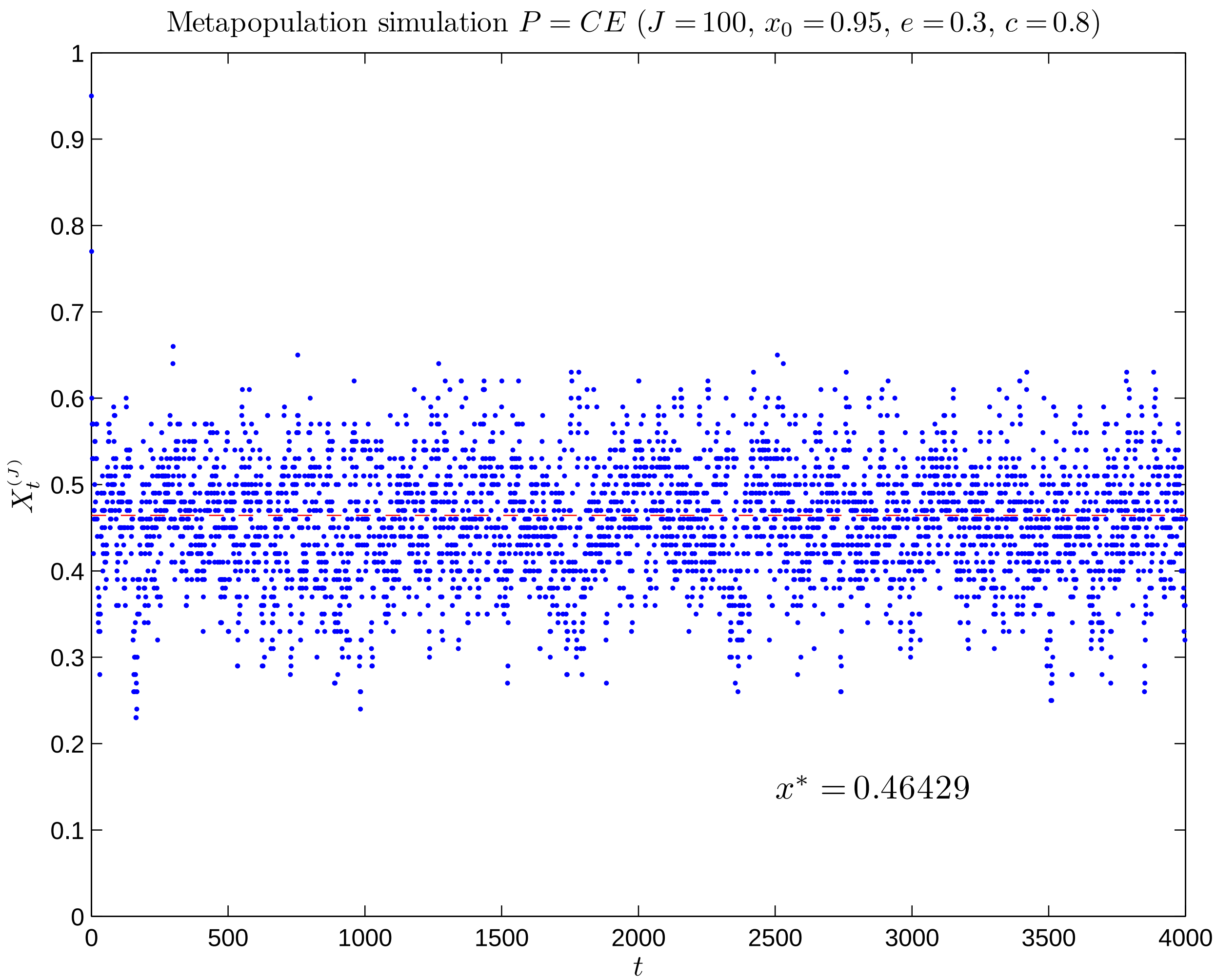
Simulation: $P = EC$ (AR-1 approx.)



AR-1 Simulation: $P = EC$



Simulation: $P = CE$



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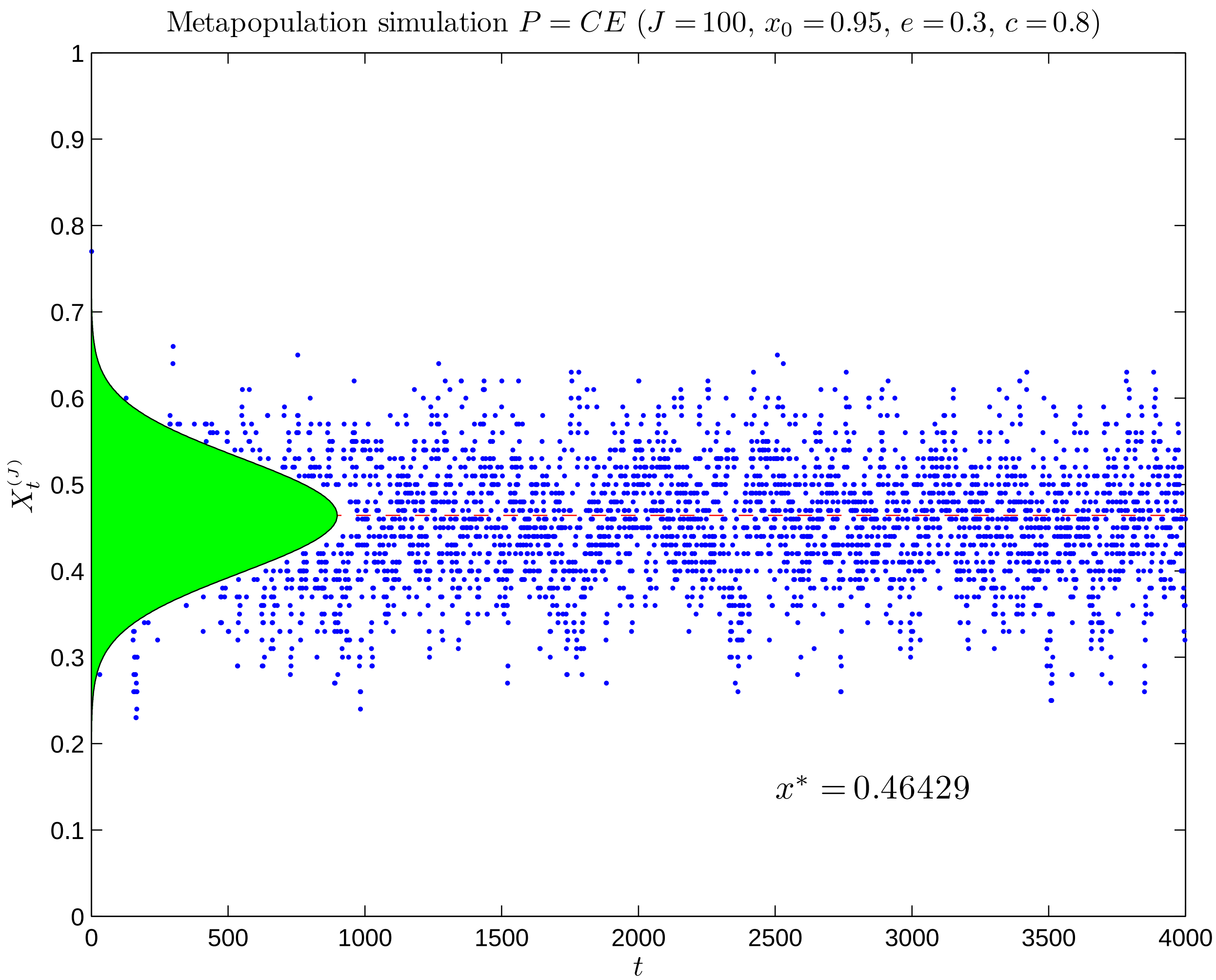

AR-1 Simulation: $P = CE$