Limit theorems for discrete-time metapopulation models

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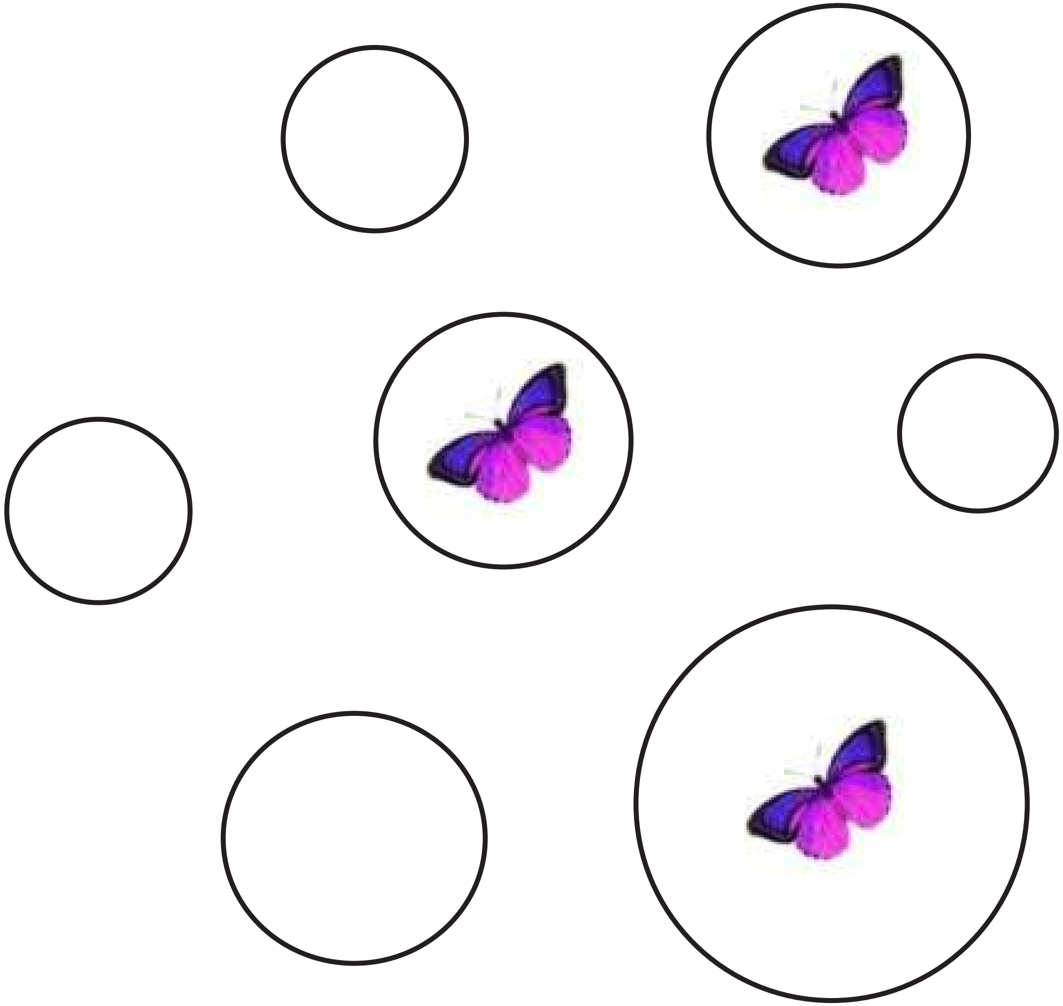
Metapopulations



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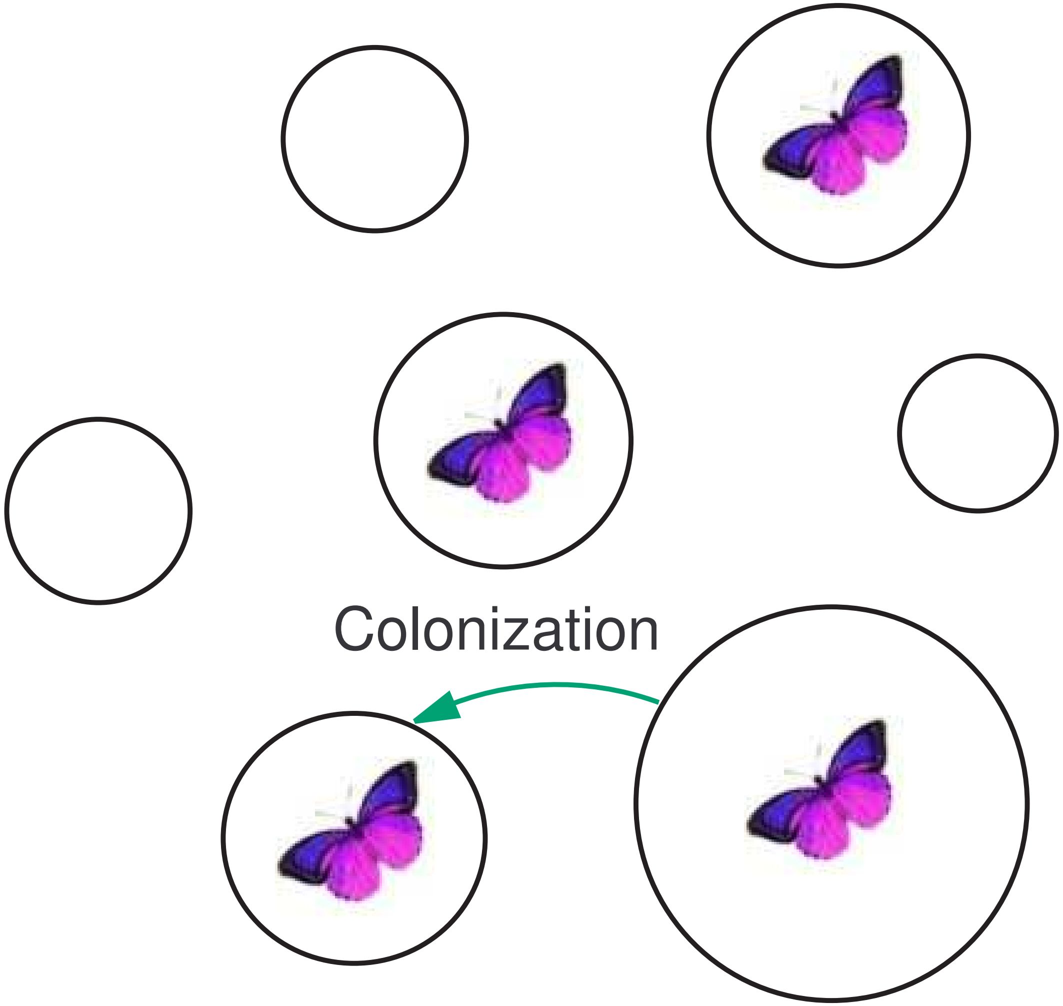

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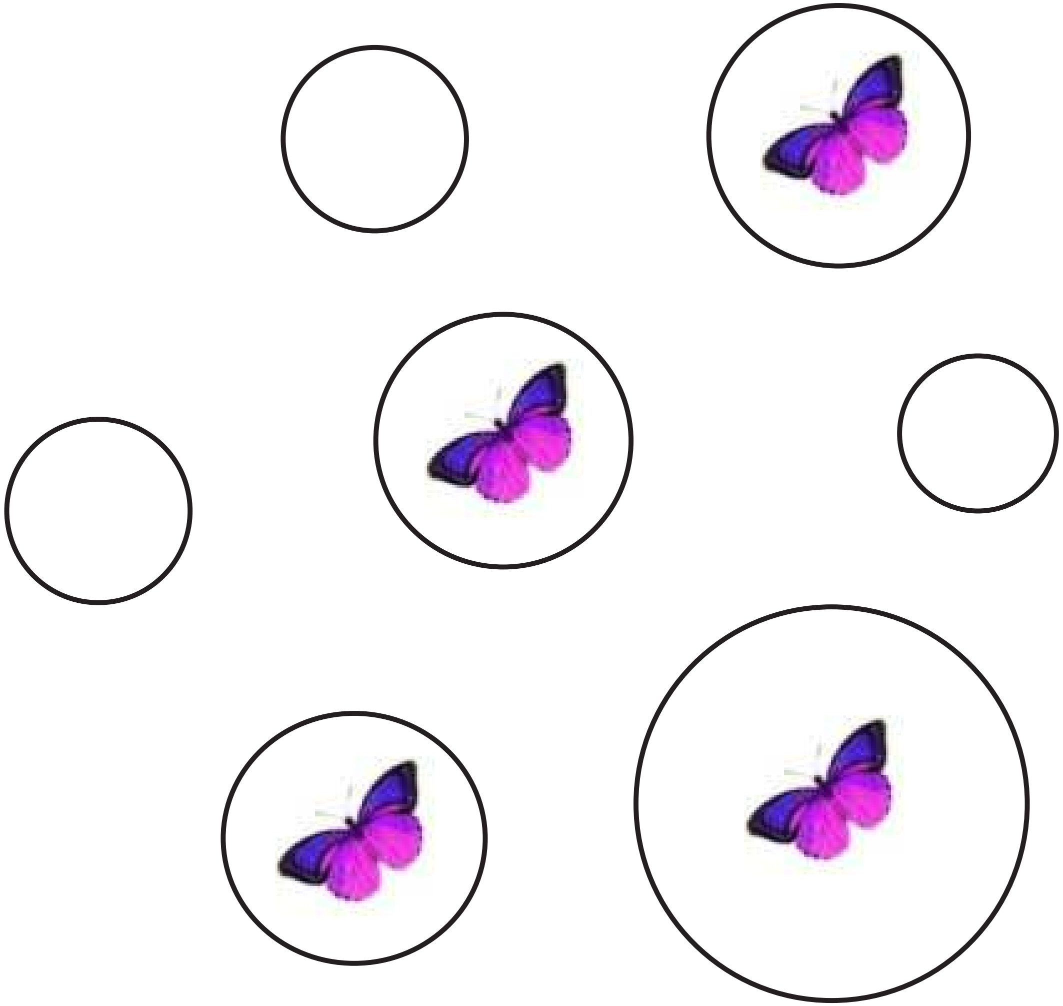

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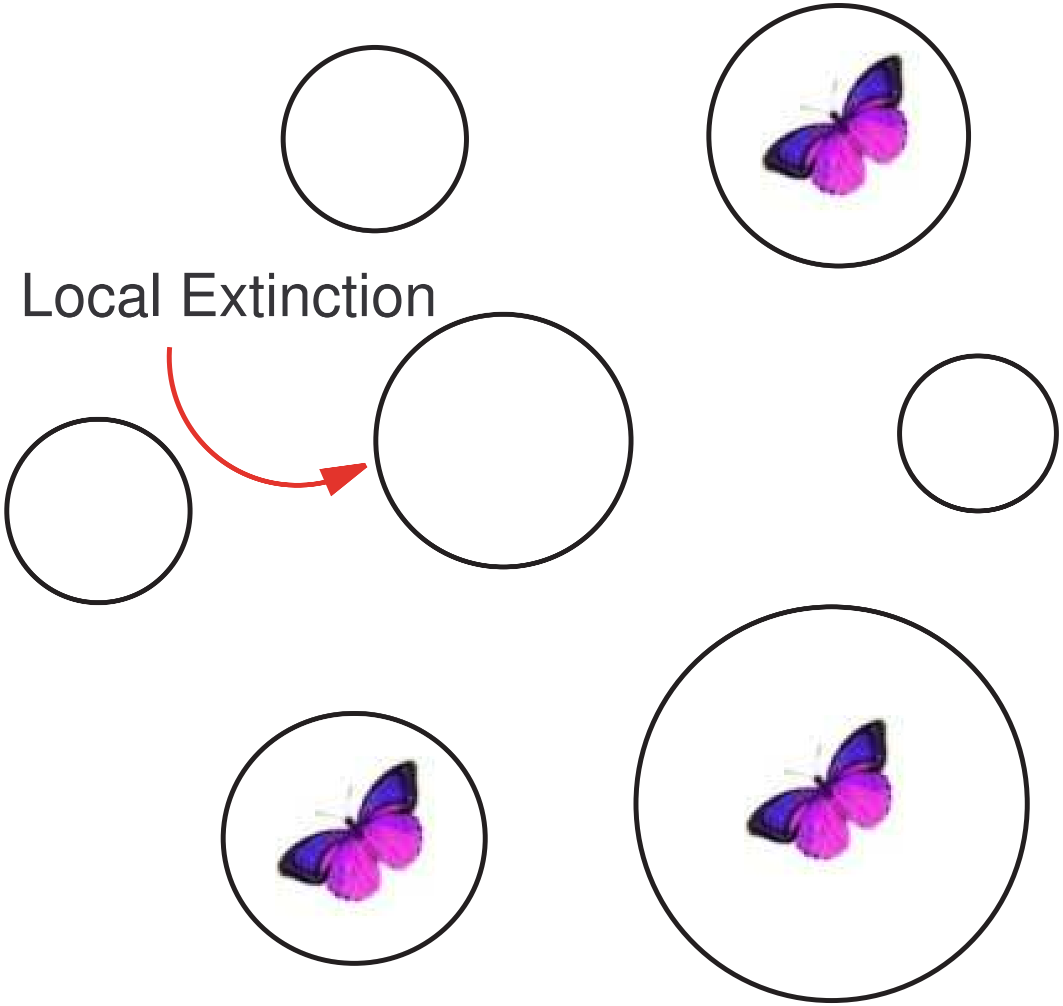

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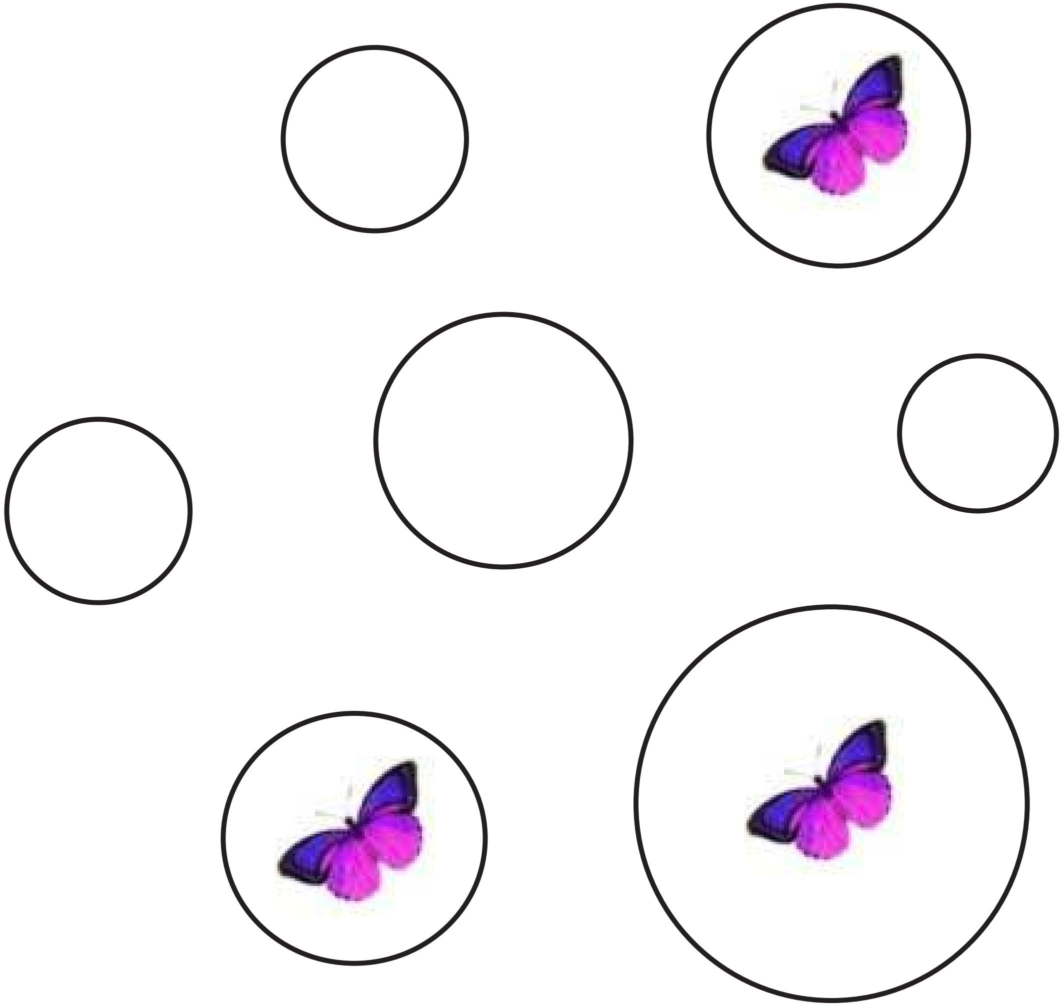

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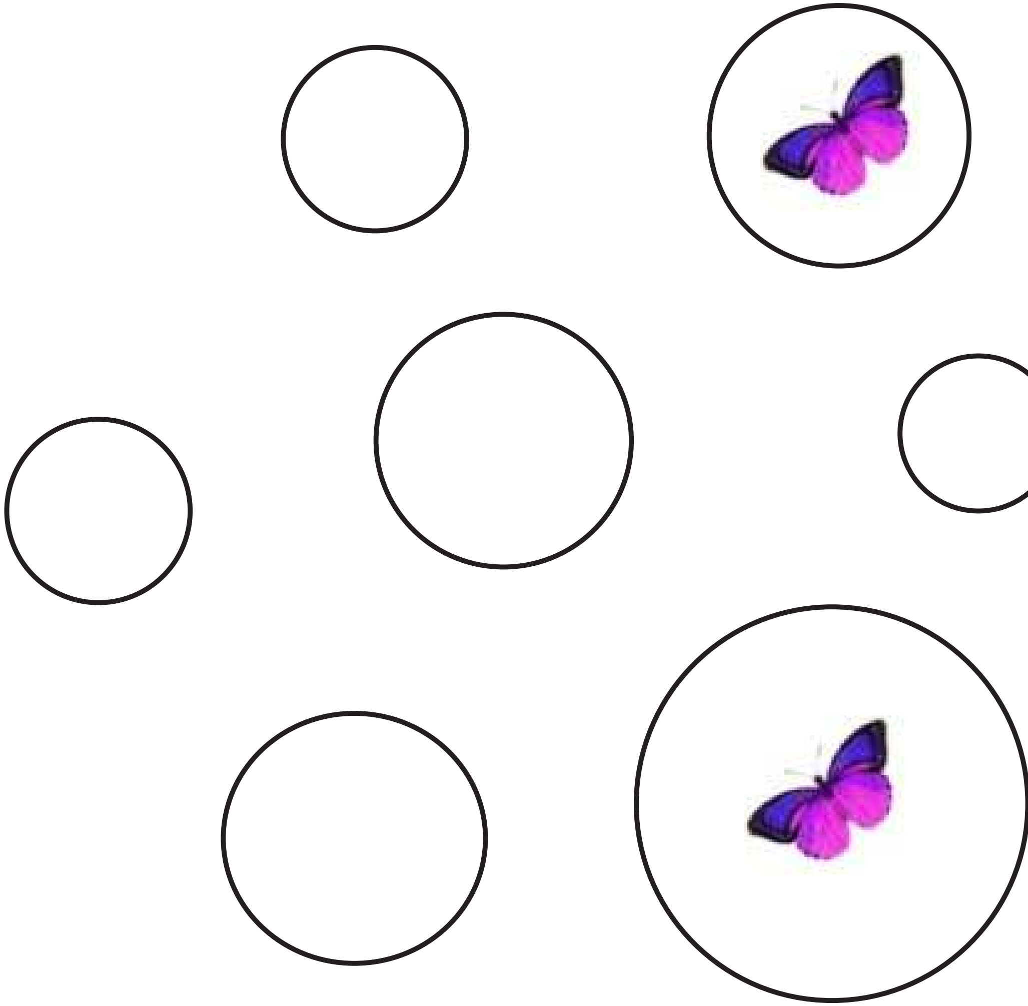

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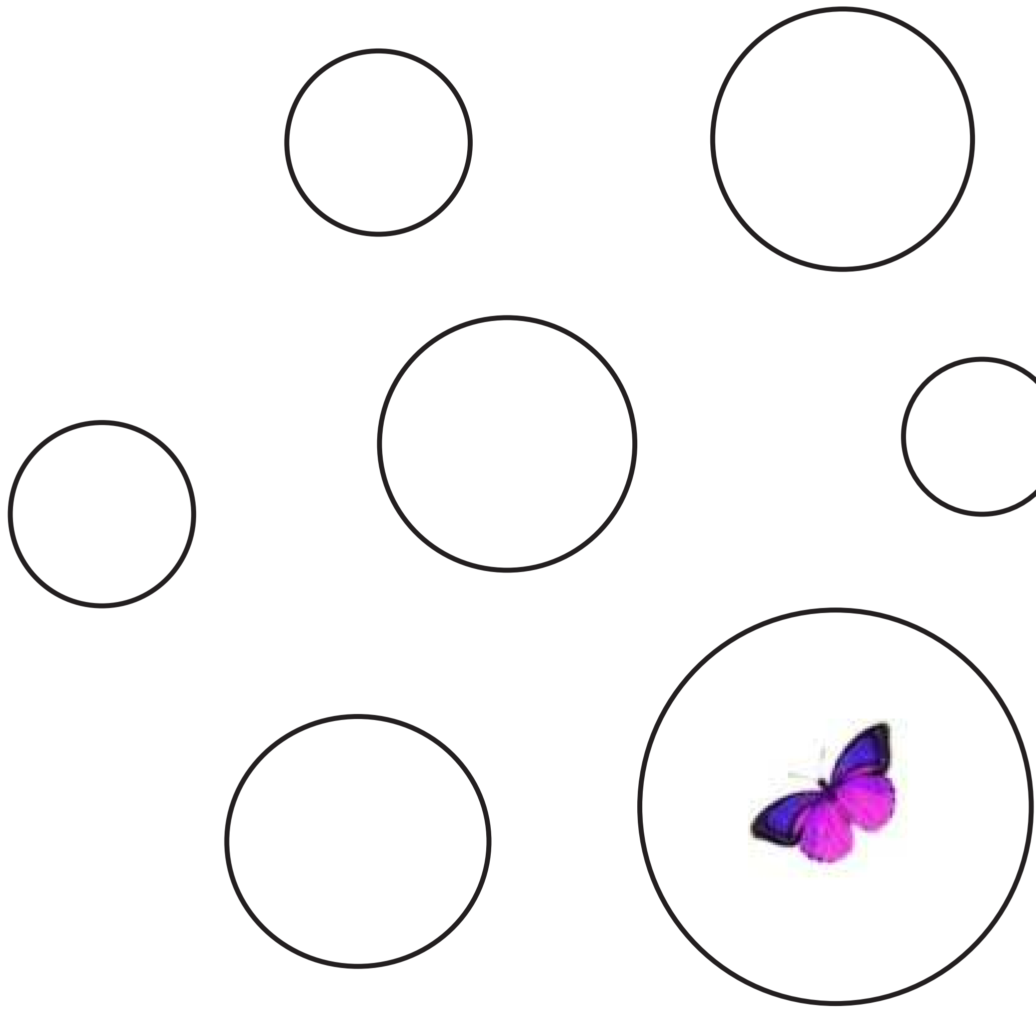

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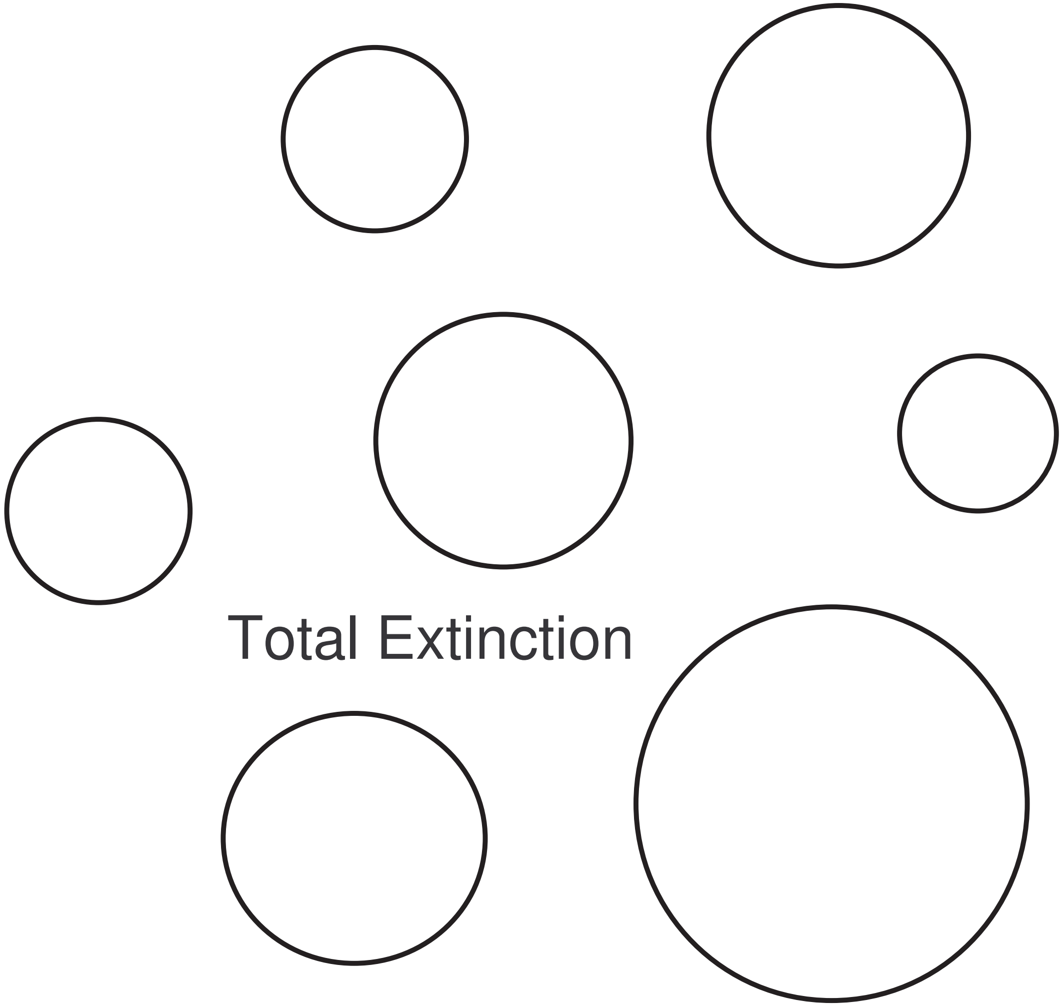

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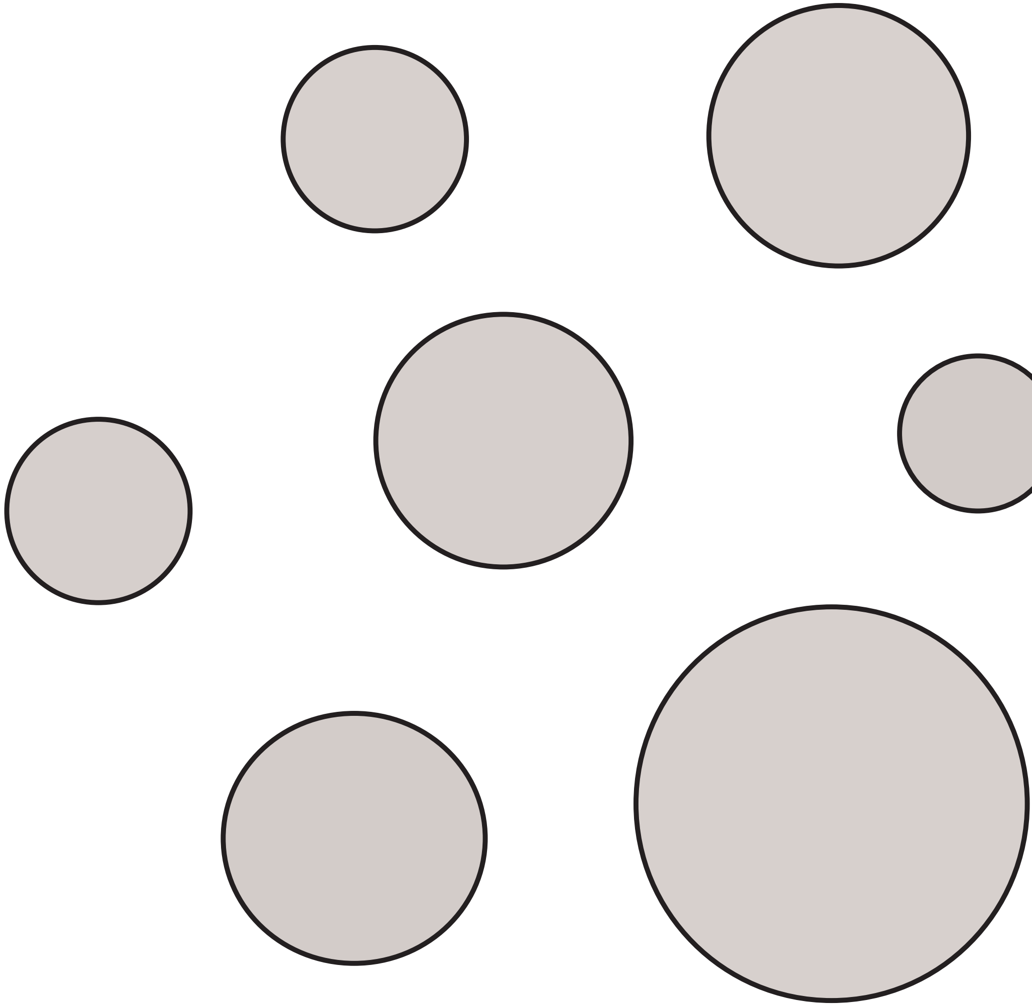
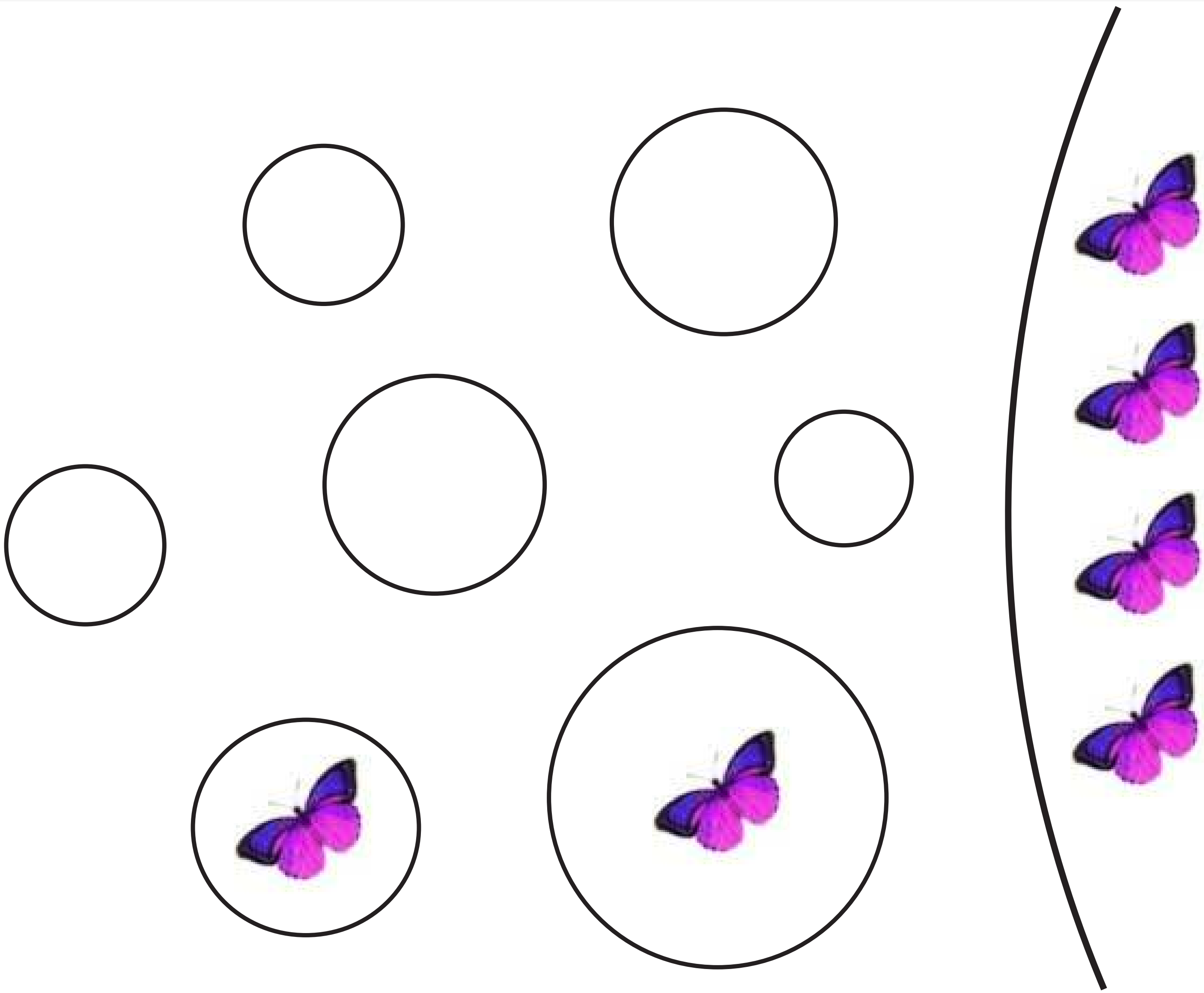


Mainland-island configuration



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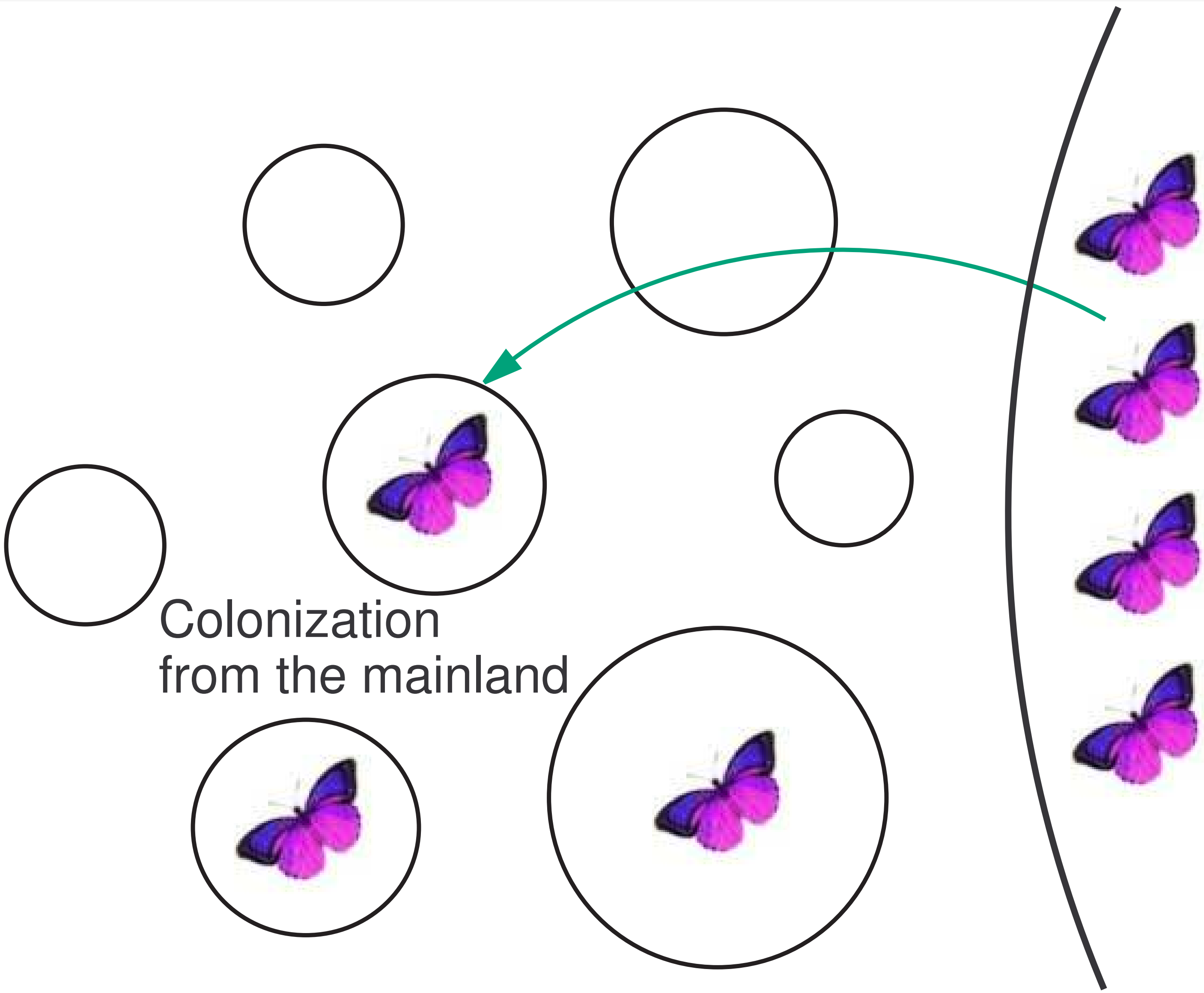

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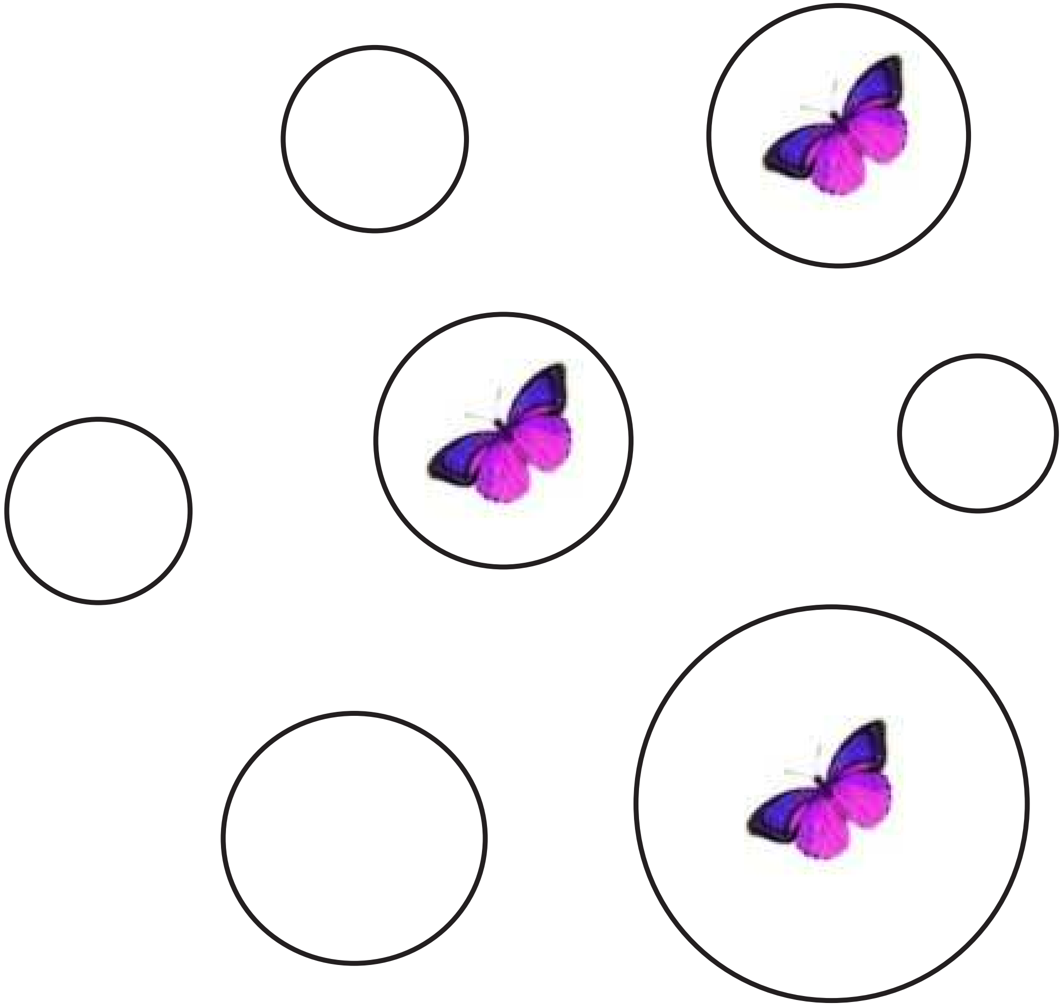

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Suppose that there are N patches.

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 v (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{array}{lll}
n \to n+1 & \text{at rate} & \left(\nu + \dfrac{c}{N} n\right)(N-n) \\
n \to n-1 & \text{at rate} & en
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This an example of Feller's *stochastic logistic (SL) model*, studied in detail by J.V. Ross.

Ross, J.V. (2006) Stochastic models for mainland-island metapopulations in static and dynamic landscapes. *Bulletin of Mathematical Biology* 68, 417–449.

Feller, W. (1939) Die grundlagen der volterraschen theorie des kampfes ums dasein in wahrscheinlichkeitsteoretischer behandlung. Acta *Biotheoretica* 5, 11–40.

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.

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

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.

EC versus *CE*

$$P = EC$$

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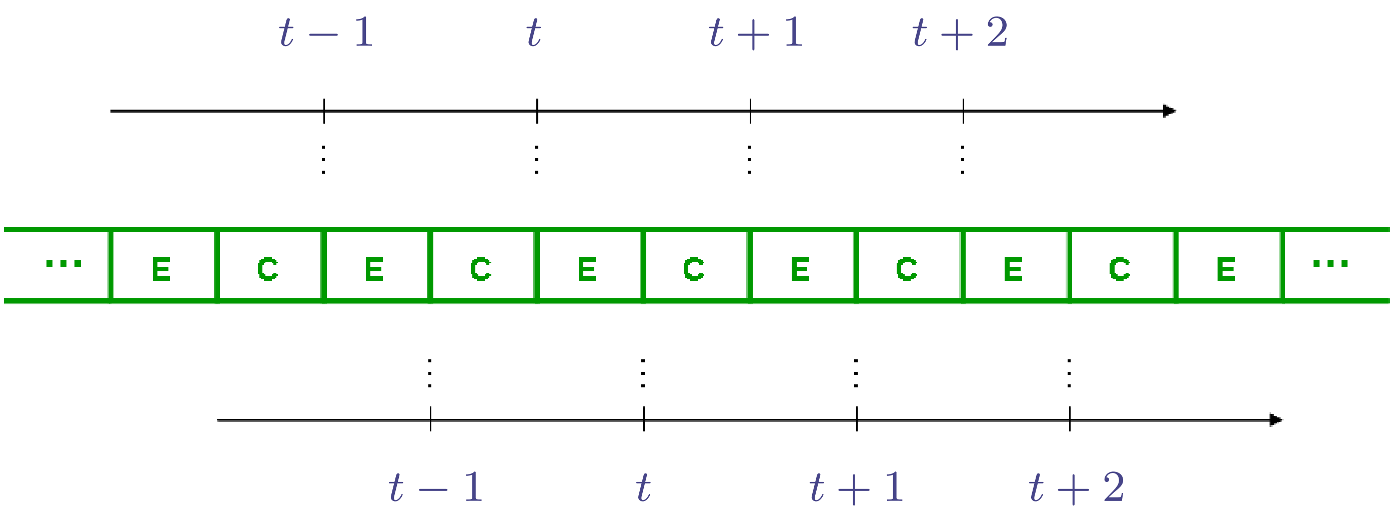

Assumptions

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*$(N - i, c_i)$ law:

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

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

Chain-binomial structure

Thus, we have the following *chain-binomial* structure:

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

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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:

$$n_{t+1} \stackrel{D}{=} \textit{Bin}(n_t, 1 - e) + \textit{Bin}(N - n_t, (1 - e)c_{n_t}).$$

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So, $(1-e)c_i$ is the *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.

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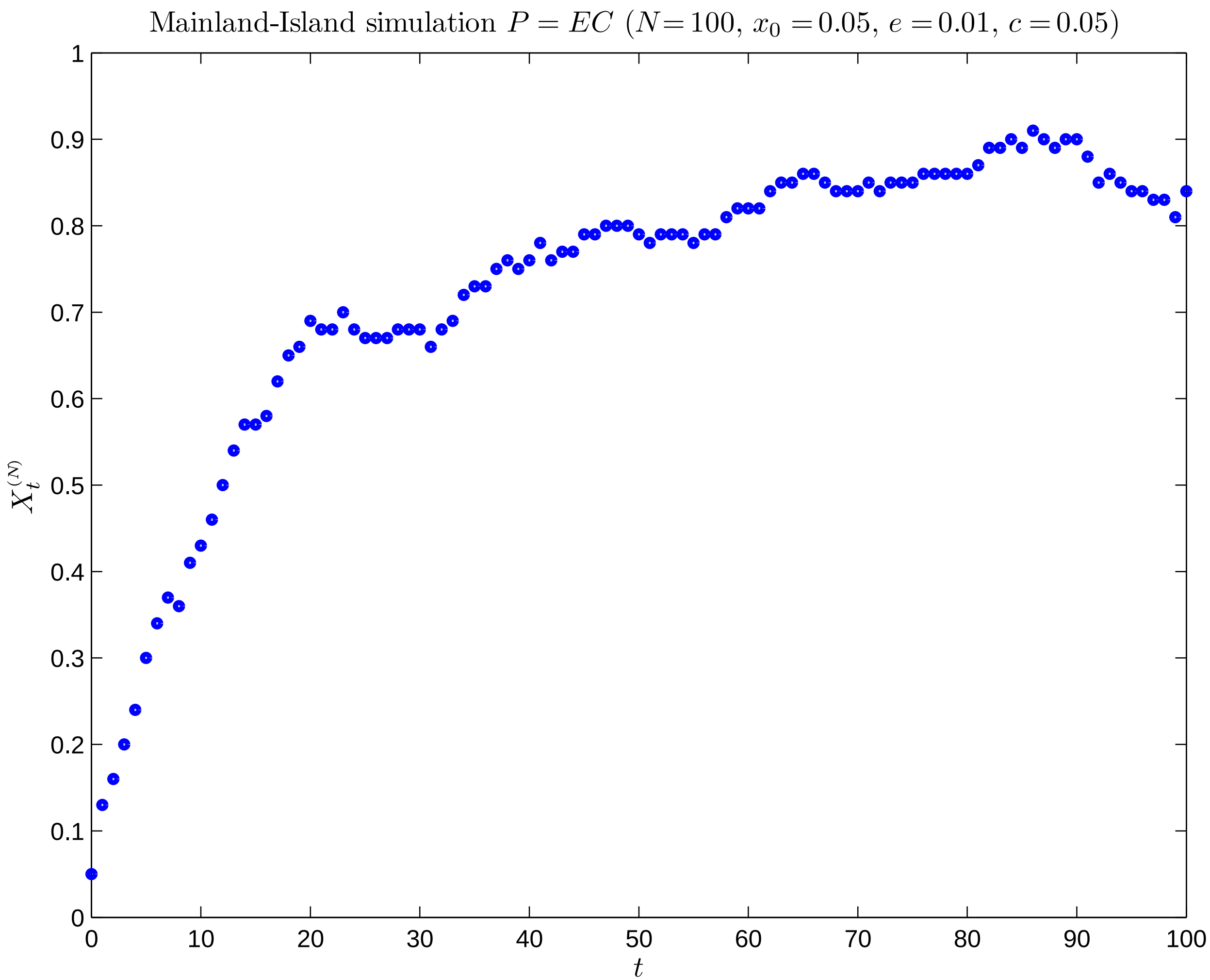
Other possibilities include $c_i = c_0(1-(1-c_1/c_0)^i)$, $c_i = 1-\exp(-i\beta/N)$ and $c_i = c_0 + (i/N)c$, where $c_0 + c \in (0,1]$ (mainland and island colonization).

The proportion of occupied patches

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

Simulation: EC Model with $c_i = c$



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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 $(X_t^{(N)})$.

Buckley, F.M. and Pollett, P.K. (2009) Analytical methods for a stochastic mainland-island metapopulation model. *Ecological Modelling*. In press (accepted 24/02/10).

Mainland-Island $c_i = c$ (Summary)

Let

$$p = 1 - e(1 - c) \qquad q = c \qquad \text{(EC model)}$$

$$p = 1 - e \qquad q = (1 - e)c. \qquad \text{(CE model)}$$

and define sequences (p_t) and (q_t) by

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

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

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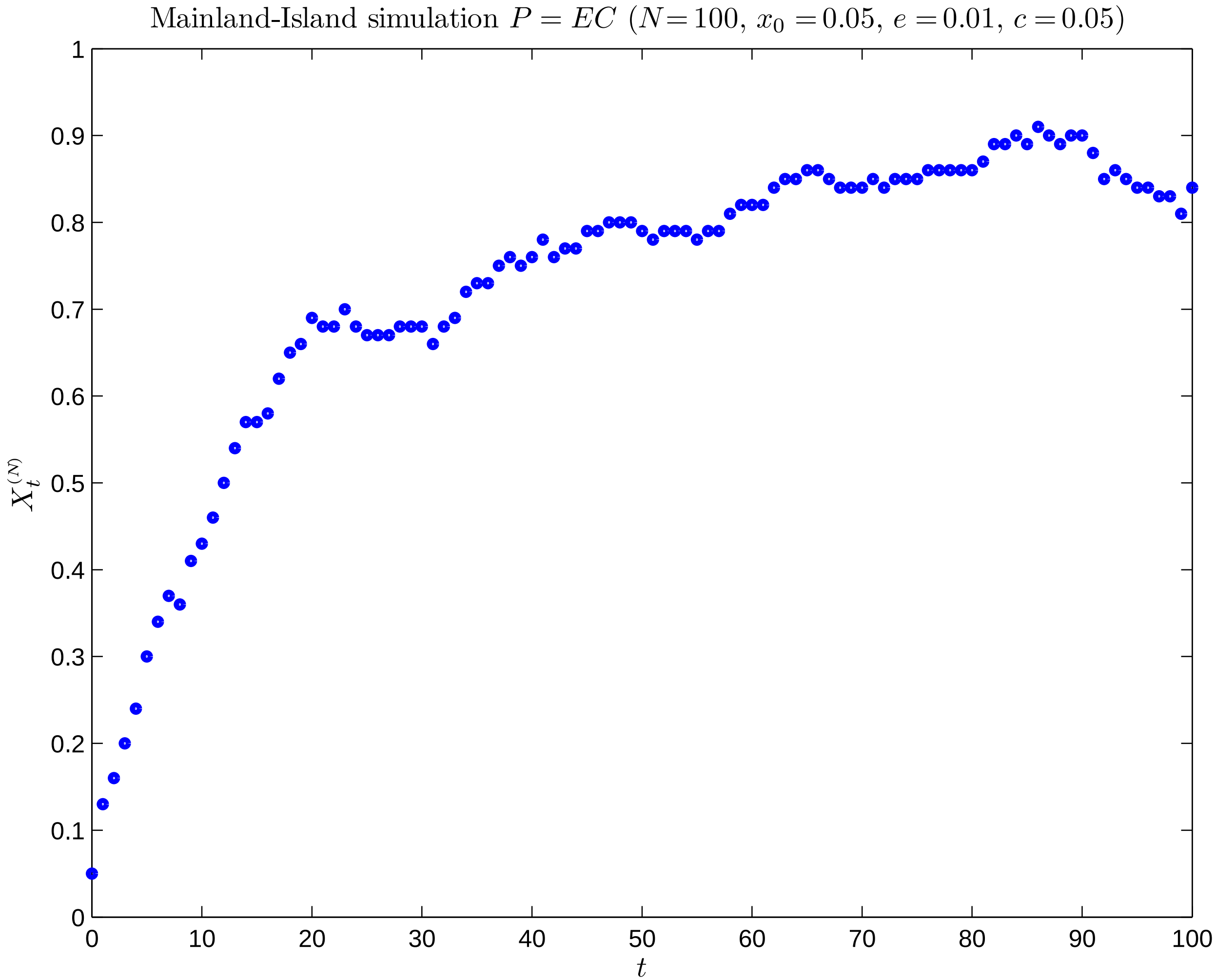
Mainland-Island $c_i = c$ (Summary)

Let $X_t^{(N)} = n_t/N$ be the *proportion* occupied at time t.

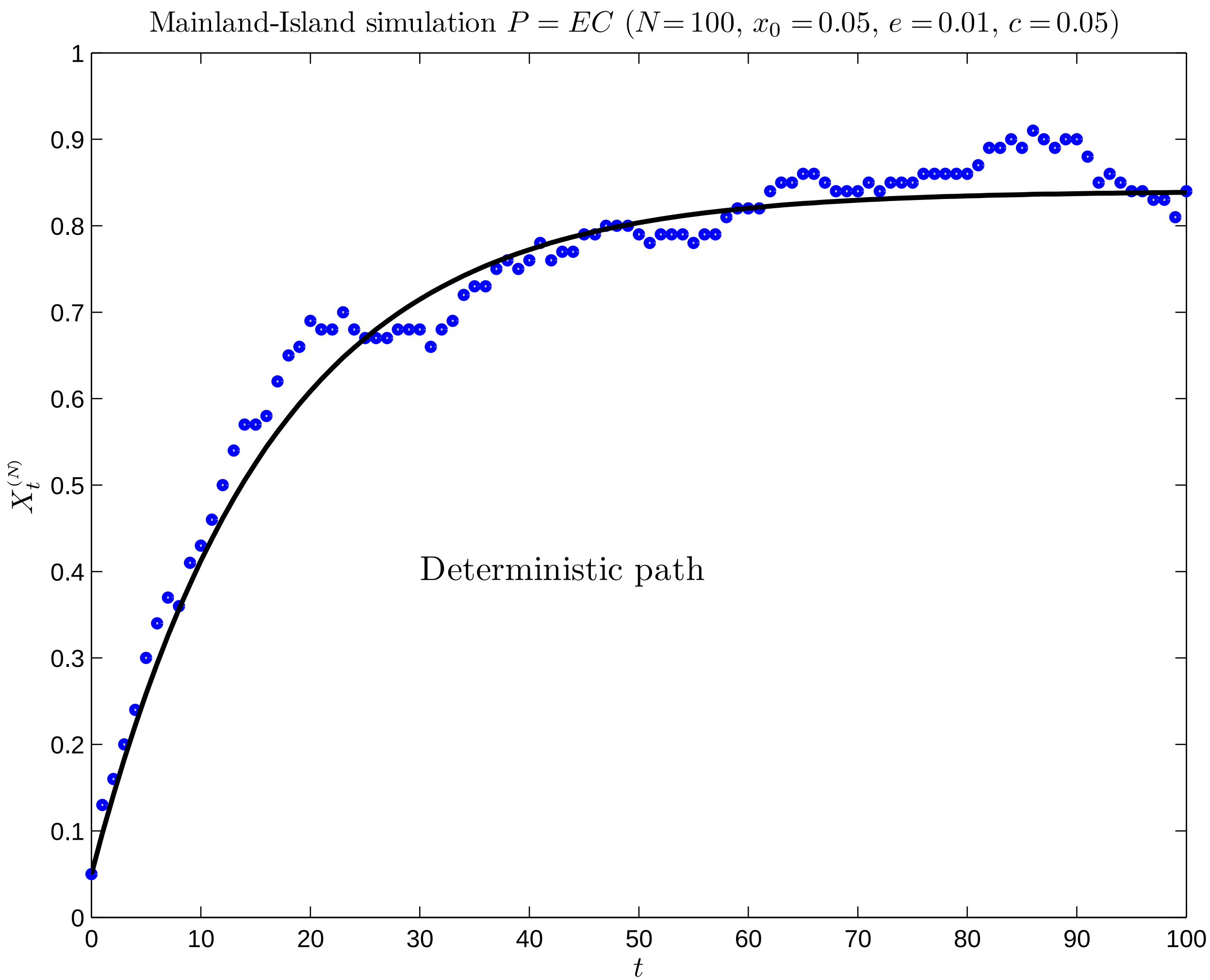
If $X_0^{(N)} \xrightarrow{P} x_0$, as $N \to \infty$, then $X_t^{(N)} \xrightarrow{P} x_t$, where

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

Simulation: EC Model with $c_i = c$



Simulation: EC Model (Deterministic path)



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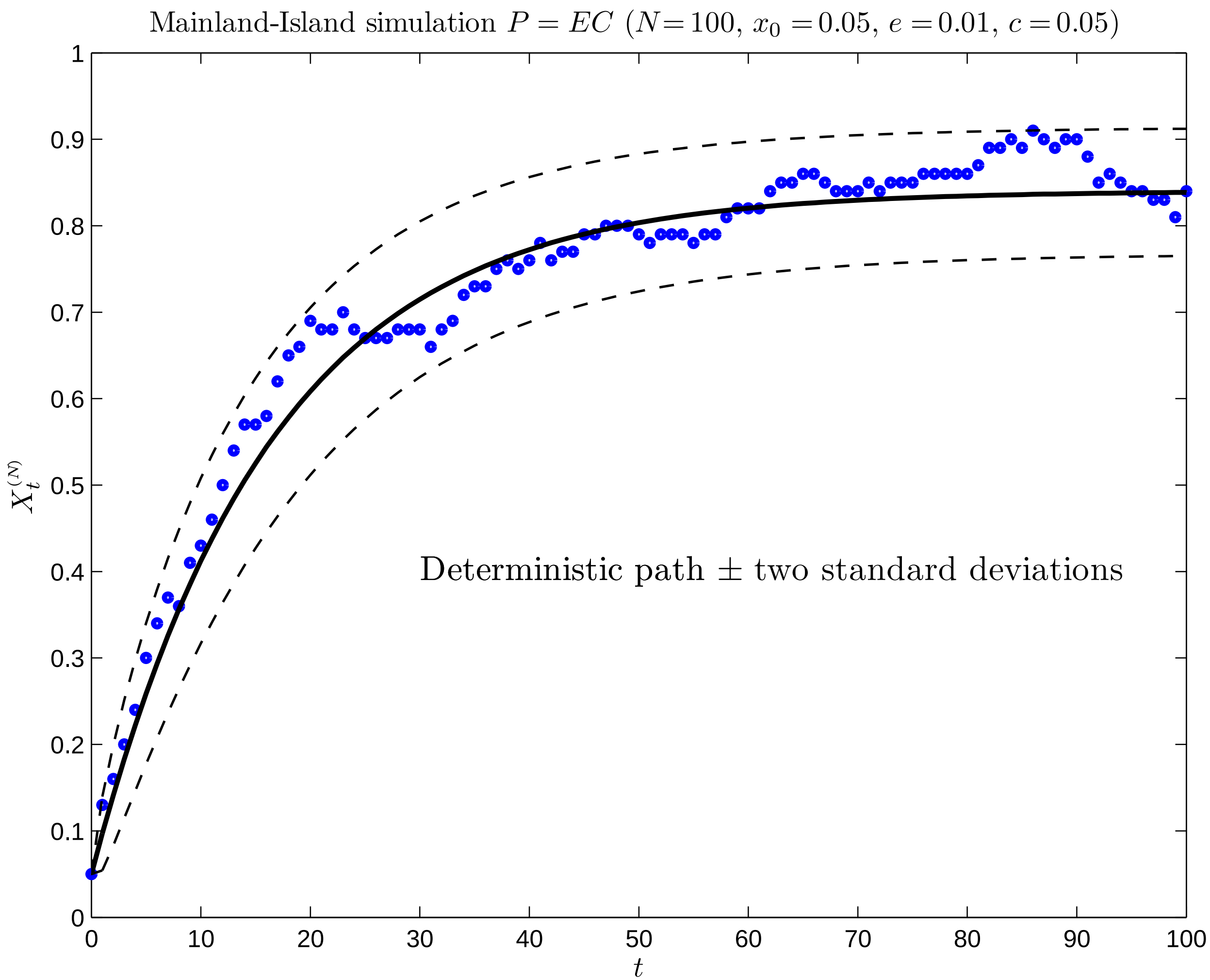
Now put $Z_t^{(N)} := \sqrt{N}(X_t^{(N)} - x_t)$. Then, if $Z_0^{(N)} \xrightarrow{D} z_0$, $Z_t^{(N)} \xrightarrow{D} \mathrm{N}(a^t z_0, V_t)$, where

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

Simulation: EC Model (Gaussian approx.)



Gaussian approximations

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

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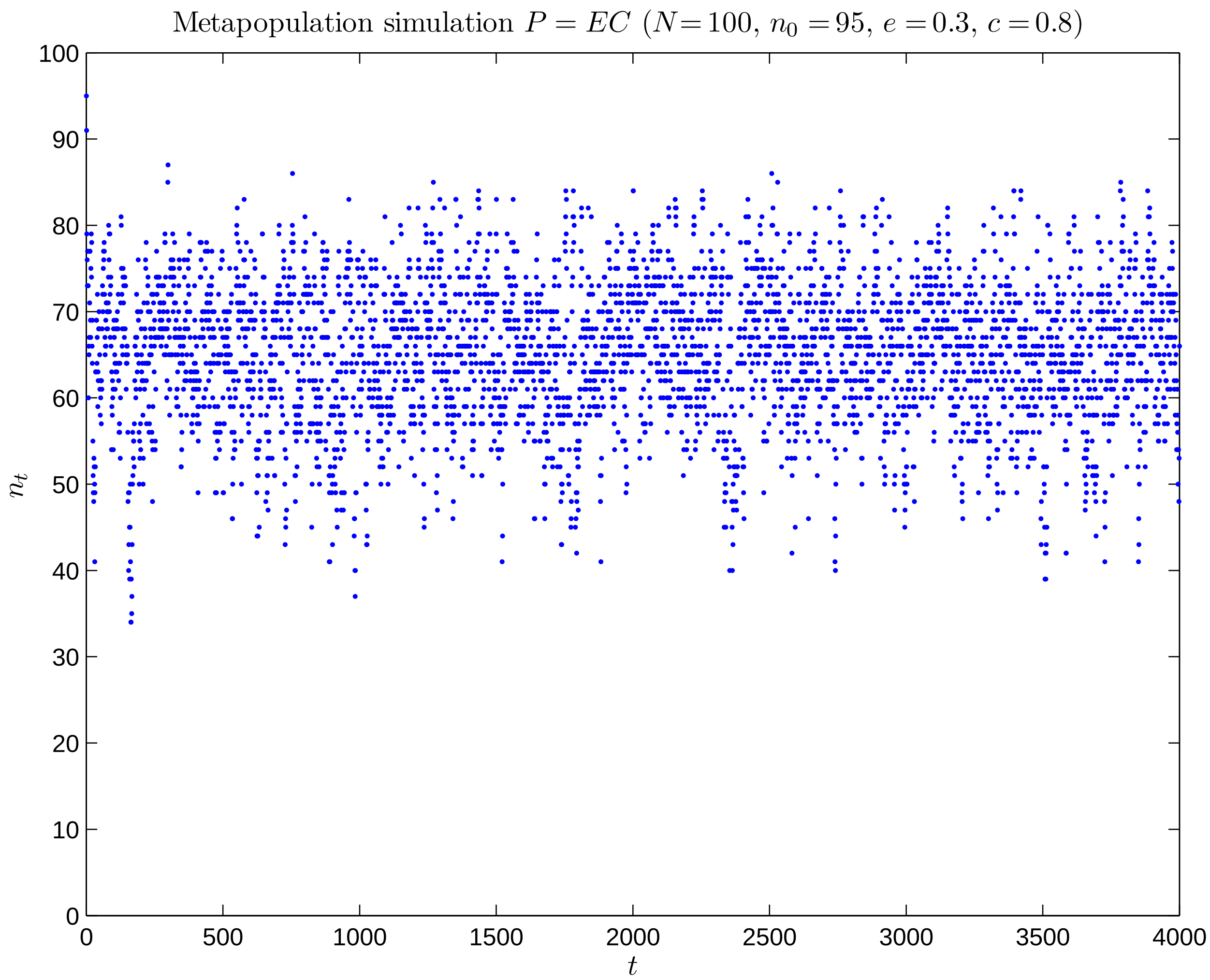

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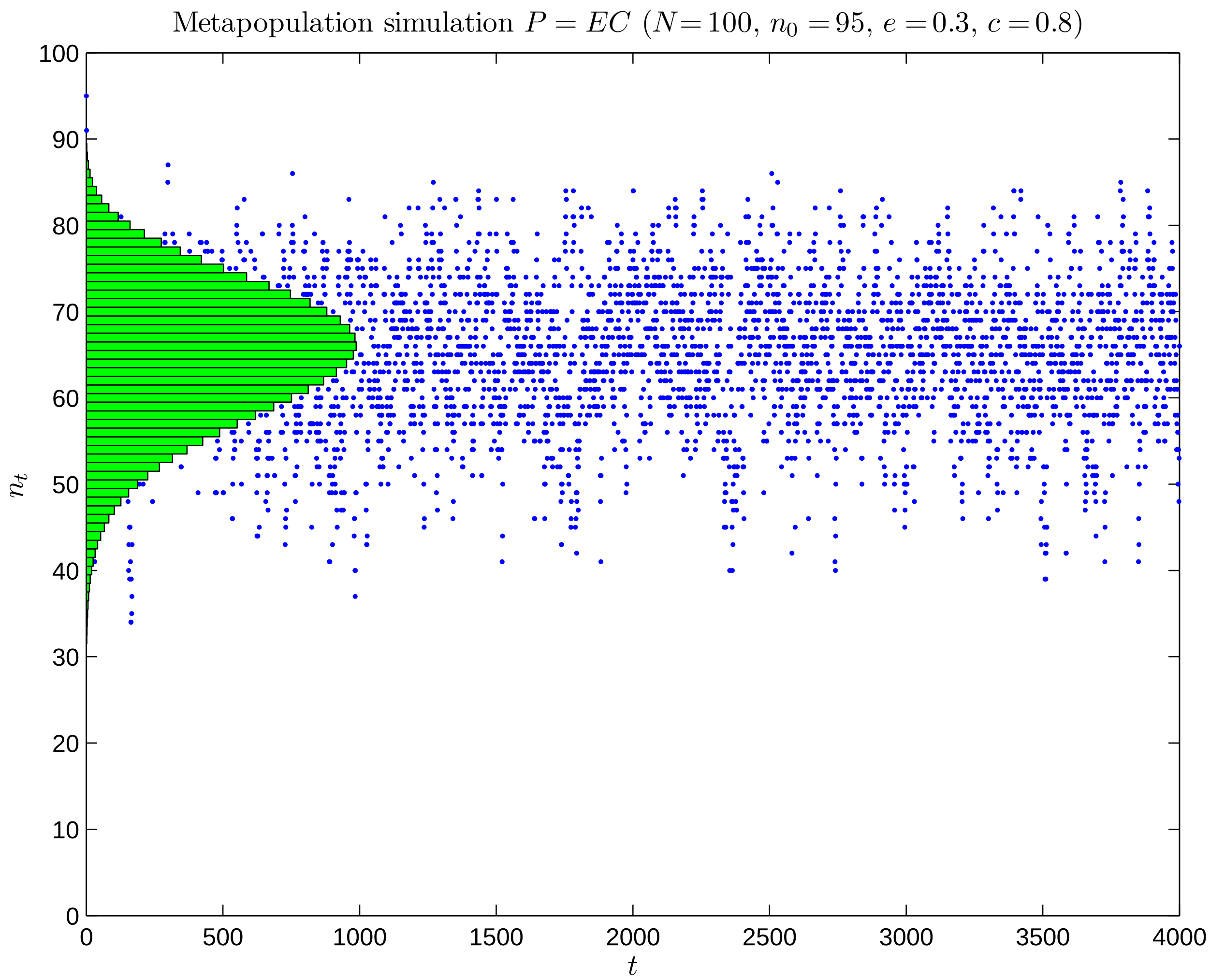

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Is there a general theory of convergence for discrete-time Markov chains that share the salient features of the patch-occupancy models presented here?

General structure: density dependence

We have a sequence of Markov chains $(n_t^{(N)})$ indexed by N, together with functions (f_t) such that

$$\mathsf{E}(n_{t+1}^{(N)} | n_t^{(N)}) = N f_t(n_t^{(N)}/N).$$

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General structure: density dependence

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

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Formally, by Taylor's theorem,

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

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

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

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

General structure: density dependence

We have

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

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

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

$$\begin{aligned}\text{Var}(Z_{t+1}^{(N)}) &= N\,\text{Var}(X_{t+1}^{(N)}) = N\,\text{Var}(f(X_t^{(N)})) + \text{E}(s(X_t^{(N)})) \\ &\sim a_t^2 N\,\text{Var}(X_t^{(N)}) + \text{E}(s(X_t^{(N)}))\ \text{(where } a_t = f'(x_t)\text{)} \\ &= a_t^2\,\text{Var}(Z_t^{(N)}) + \text{E}(s(X_t^{(N)})),\end{aligned}$$

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

And, since (Z_t) will be Markovian, $\ldots$

General structure: density dependence

And, since (Z_t) will be Markovian, we might hope 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 $E_t \sim \mathrm{N}(0, s(x_t))$.

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If x_{eq} is a *fixed point* of f, and $\sqrt{N}(X_0^{(N)} - x_{\text{eq}}) \to z_0$, then we might hope that $(Z_t^{(N)}) \stackrel{FDD}{\to} (Z_t)$, 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 $\mathrm{N}(0, s(x_{\text{eq}}))$ 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: $\mathbb{P}_n^{\pi_n} \Rightarrow \mathbb{P}^{\pi}$.

N-patch models: convergence

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

$$(X_{t_1}^{(N)}, X_{t_2}^{(N)}, \dots, X_{t_n}^{(N)}) \xrightarrow{D} (x_{t_1}, x_{t_2}, \dots, x_{t_n}),$$

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

$$f(x) = (1-e)(1+c-c(1-e)x)x \qquad \text{(EC model)}$$

$$f(x) = (1-e)(1+c-cx)x \qquad \text{(CE model)}$$

N-patch models: convergence

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

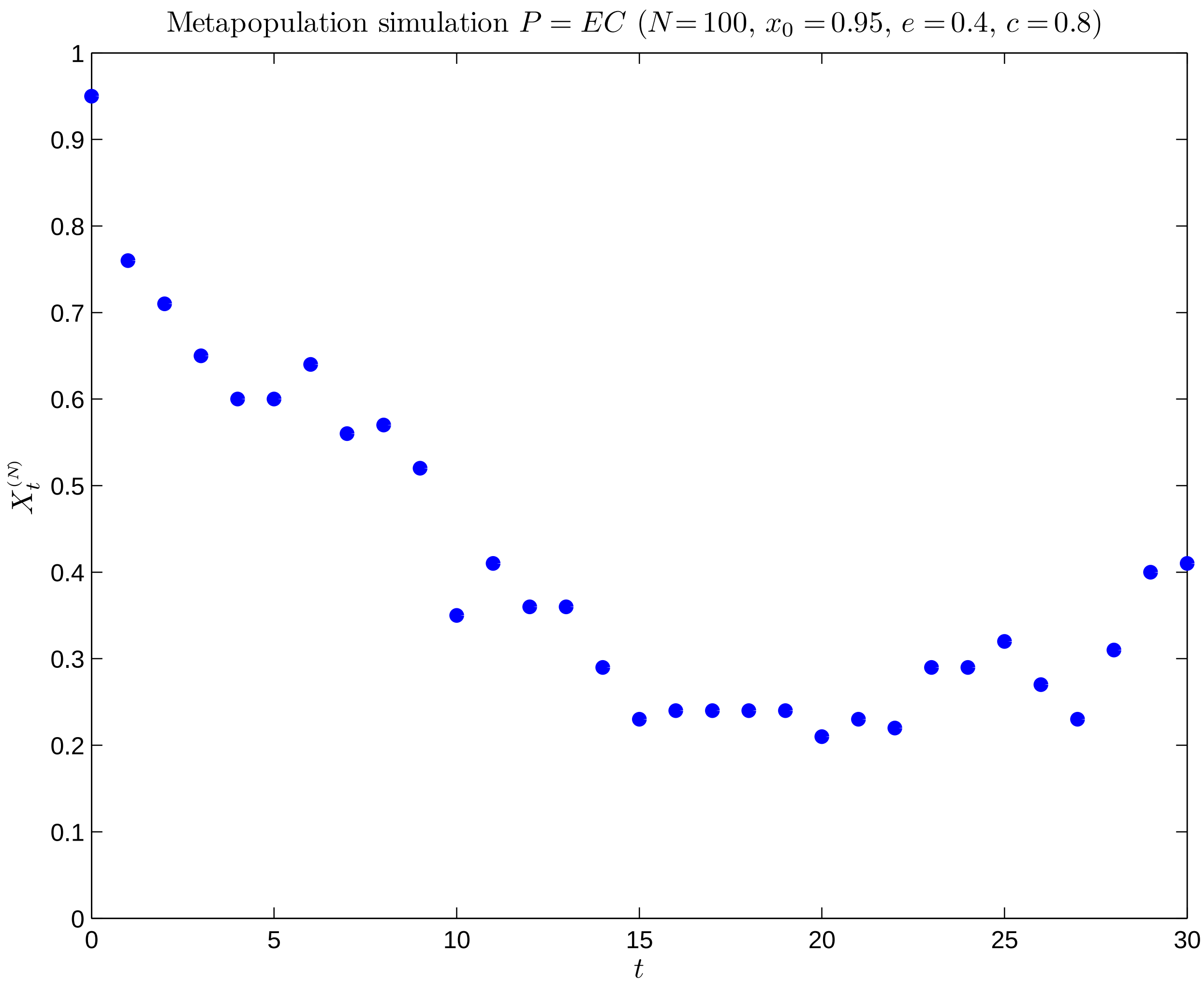
$$Z_{t+1} = f'(x_t)Z_t + E_t \qquad (Z_0 = z_0),$$

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

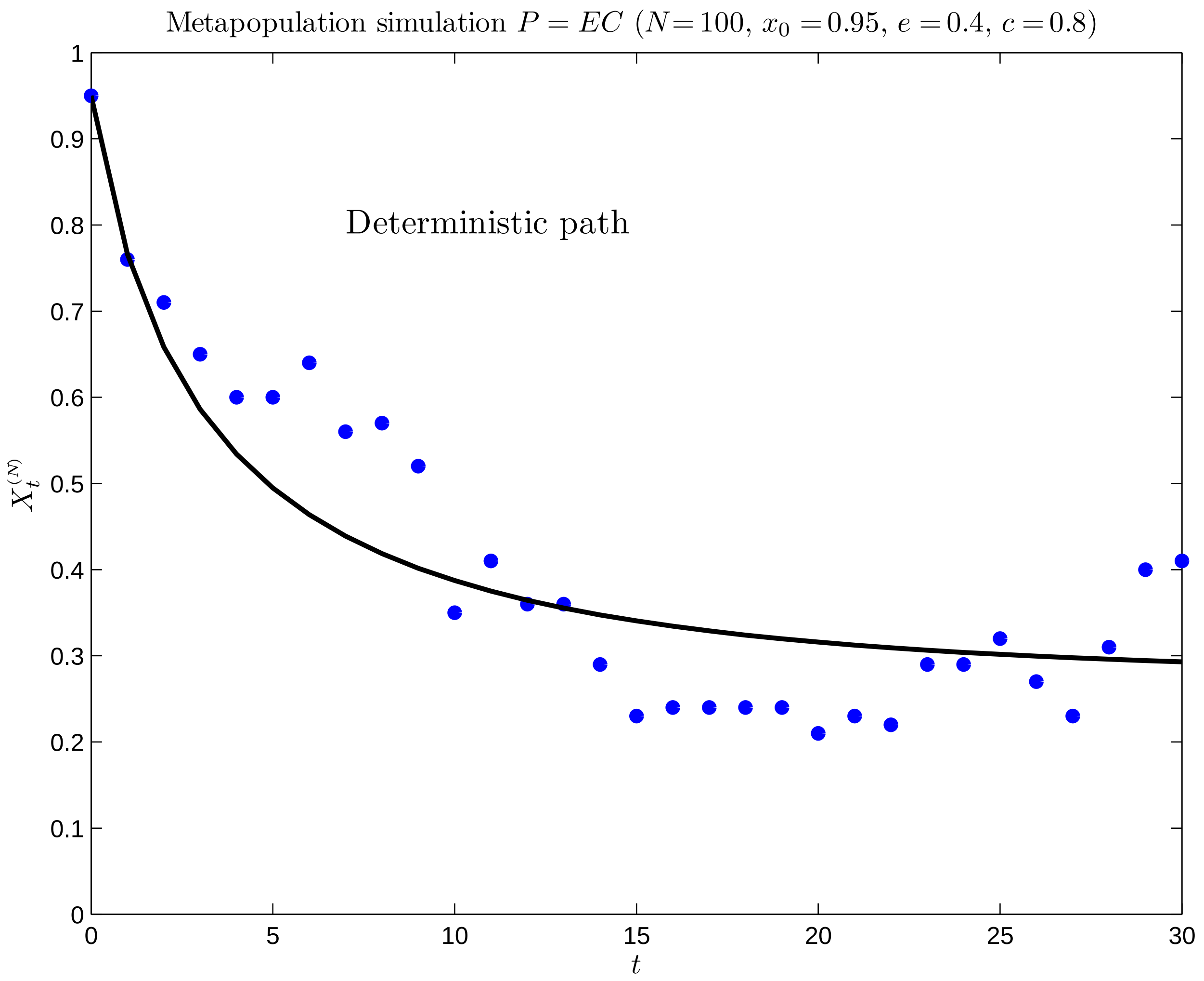
$$s(x) = (1-e)[c(1-(1-e)x)(1-c(1-e)x) + e(1+c-2c(1-e)x)^2]x \qquad \text{(EC model)}$$

$$s(x) = (1-e)[e + c(1-x)(1-c(1-e)x)]x \qquad \text{(CE model)}$$

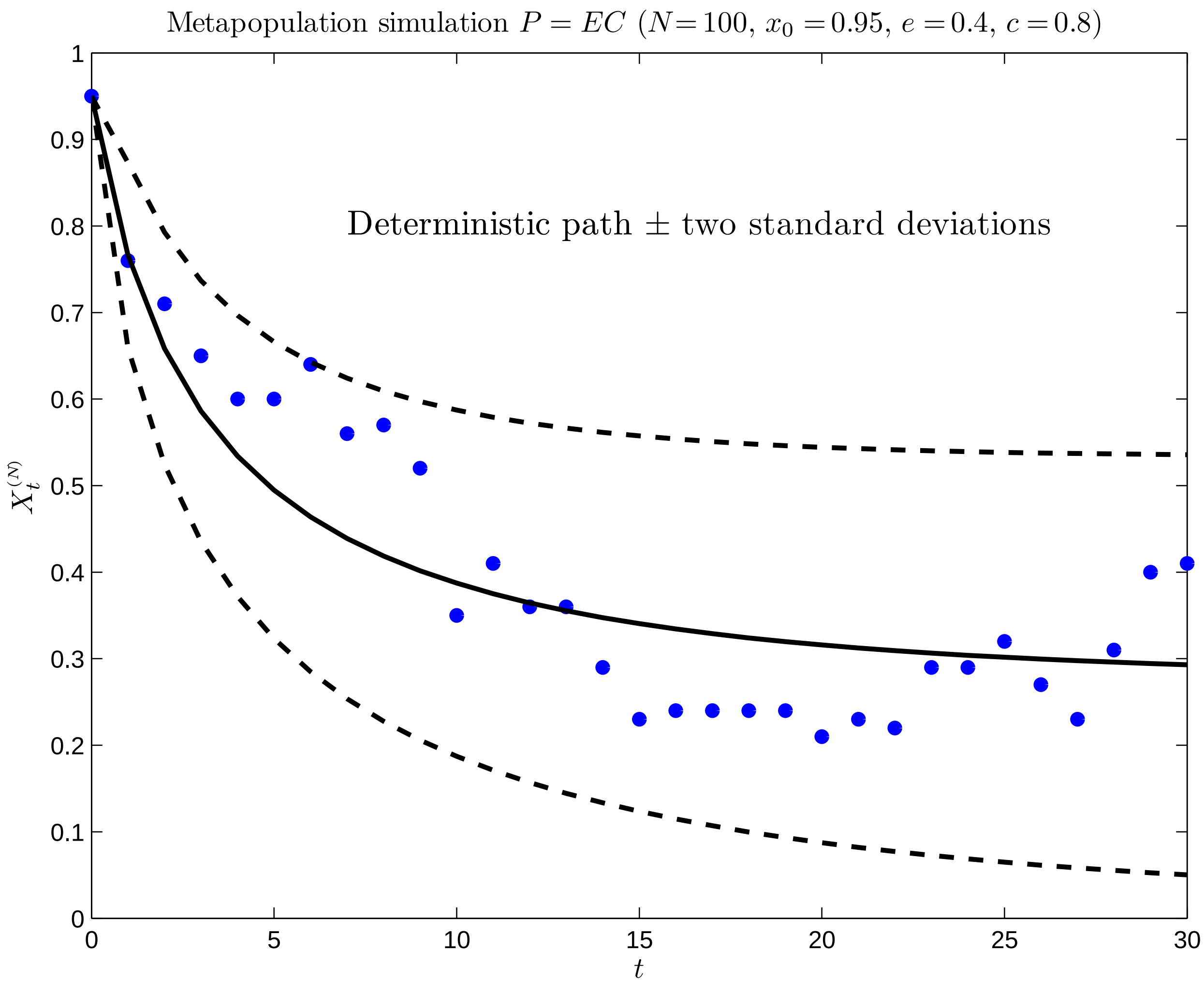
Simulation: EC Model



Simulation: EC Model (Deterministic path)



Simulation: EC Model (Gaussian approx.)



N-patch models: convergence

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

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

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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.

N-patch models: convergence

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

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

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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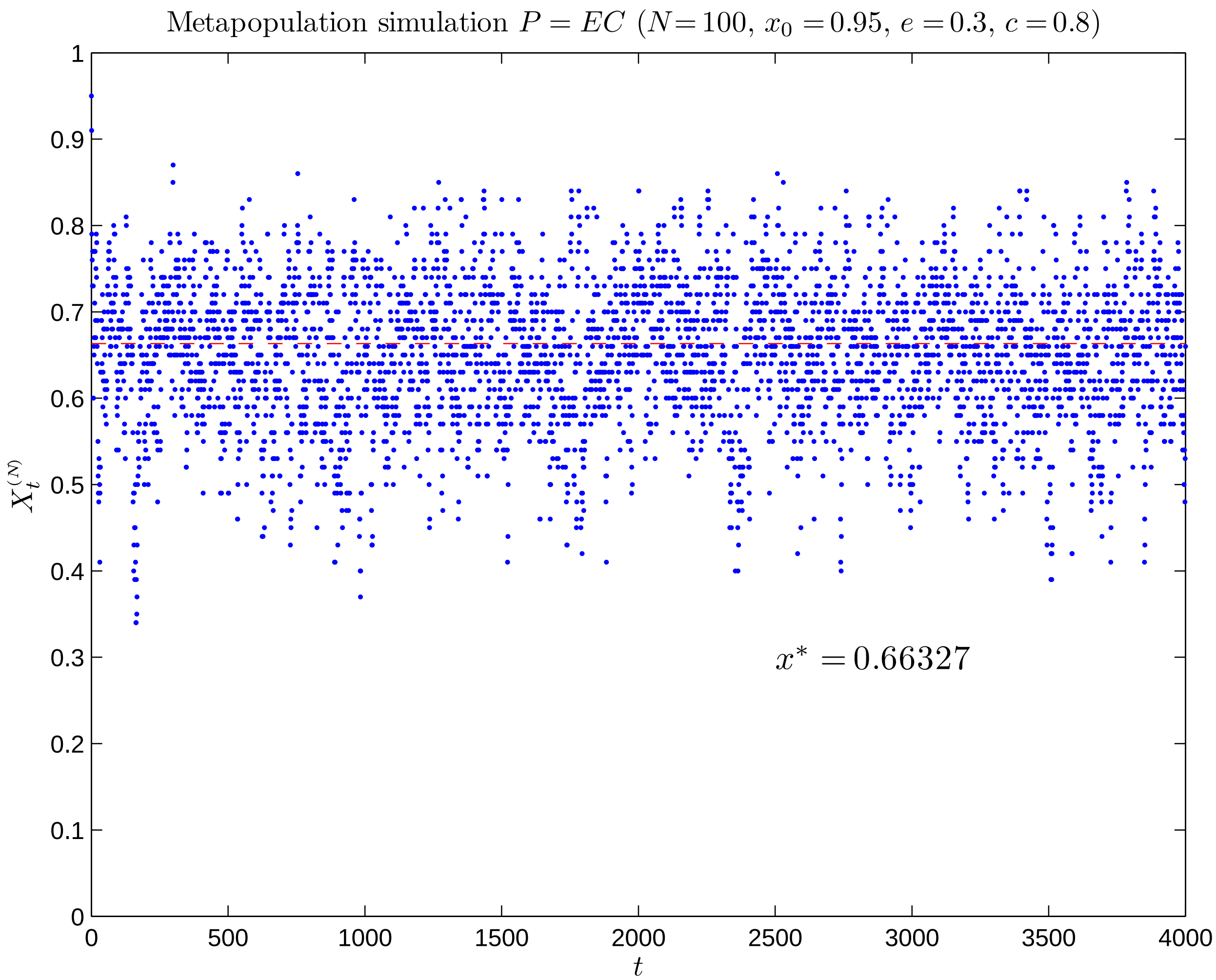
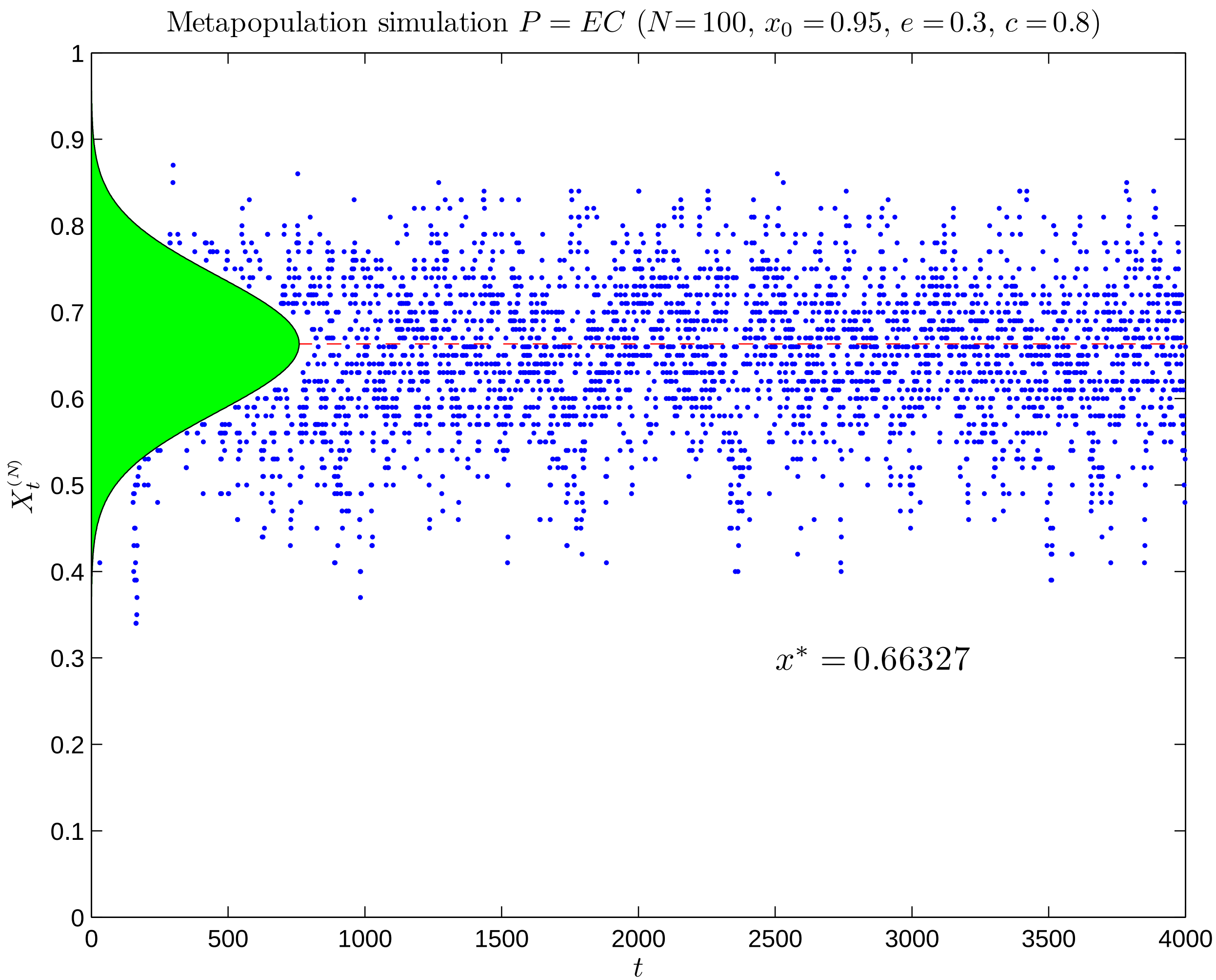
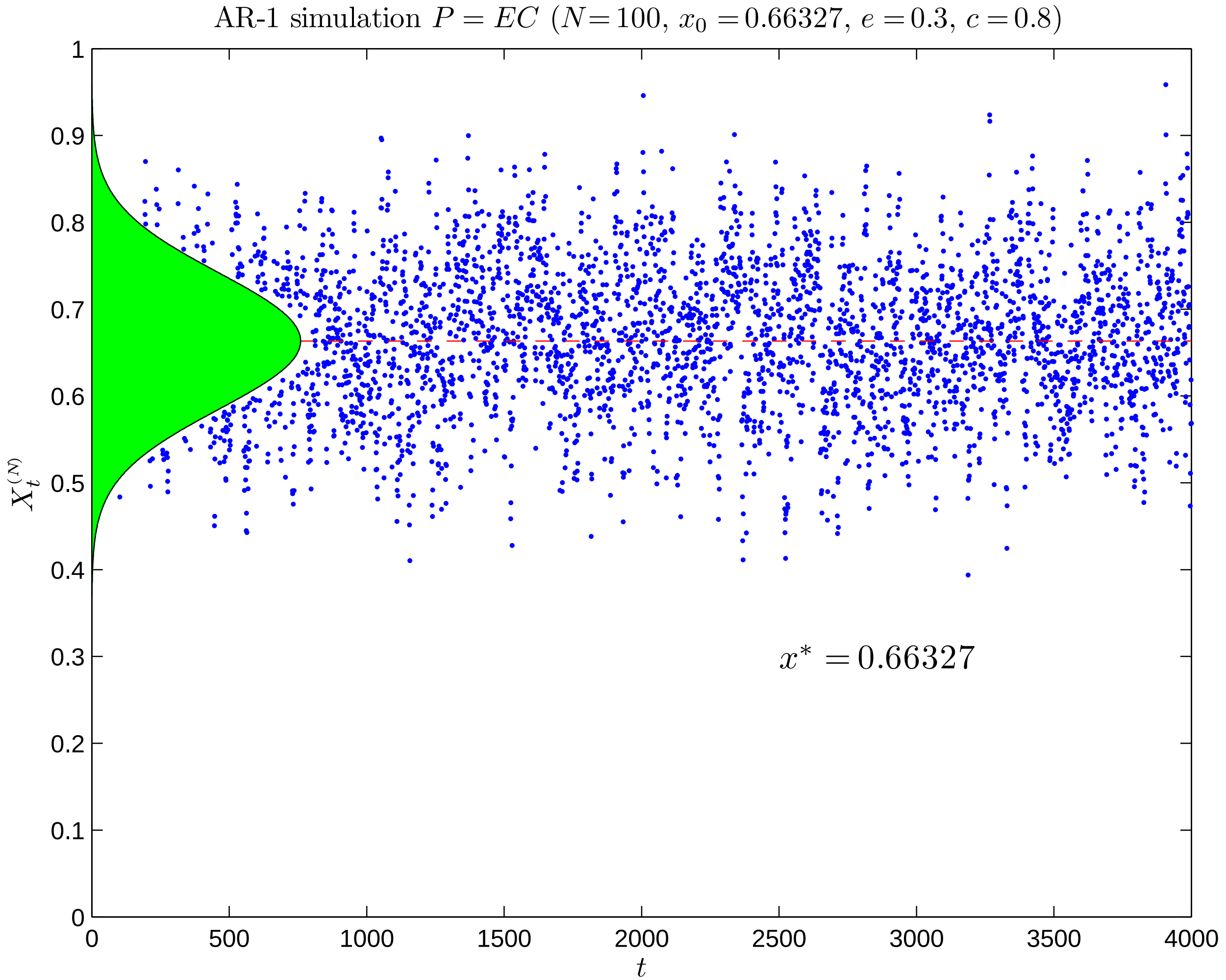
Simulation: EC Model



Simulation: EC Model (AR-1 approx.)



AR-1 Simulation: EC Model



Recent developments

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

$$n_{t+1} = \tilde{n}_t + \textit{Bin}(N - \tilde{n}_t, c(\tilde{n}_t/N)) \quad \tilde{n}_t = n_t - \textit{Bin}(n_t, e) \qquad \text{(EC)}$$

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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 *Bin*$(N-n, c(n/N)) \xrightarrow{D}$ *Poi*(mn) as $N \to \infty$, where $m = c'(0)$.

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$$n_{t+1} = \tilde{n}_t + \textit{Poi}(m\tilde{n}_t) \quad \tilde{n}_t = n_t - \textit{Bin}(n_t, e) \qquad \text{(EC)}$$

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assuming $m(n) = n_0\mu(n/n_0)$. In the limit as $n_0 \to \infty$ $X_t^{(N)} := n_t/n_0$ has a deterministic approximation that can exhibit the full range of dynamic behaviour (including chaos).

Ricker dynamics: $\mu(x) = x \exp(r(1\text{-}x))$