Stochastic models for population networks

II: Discrete-time patch occupancy models
[Exact results]

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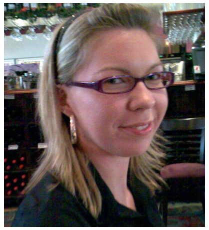
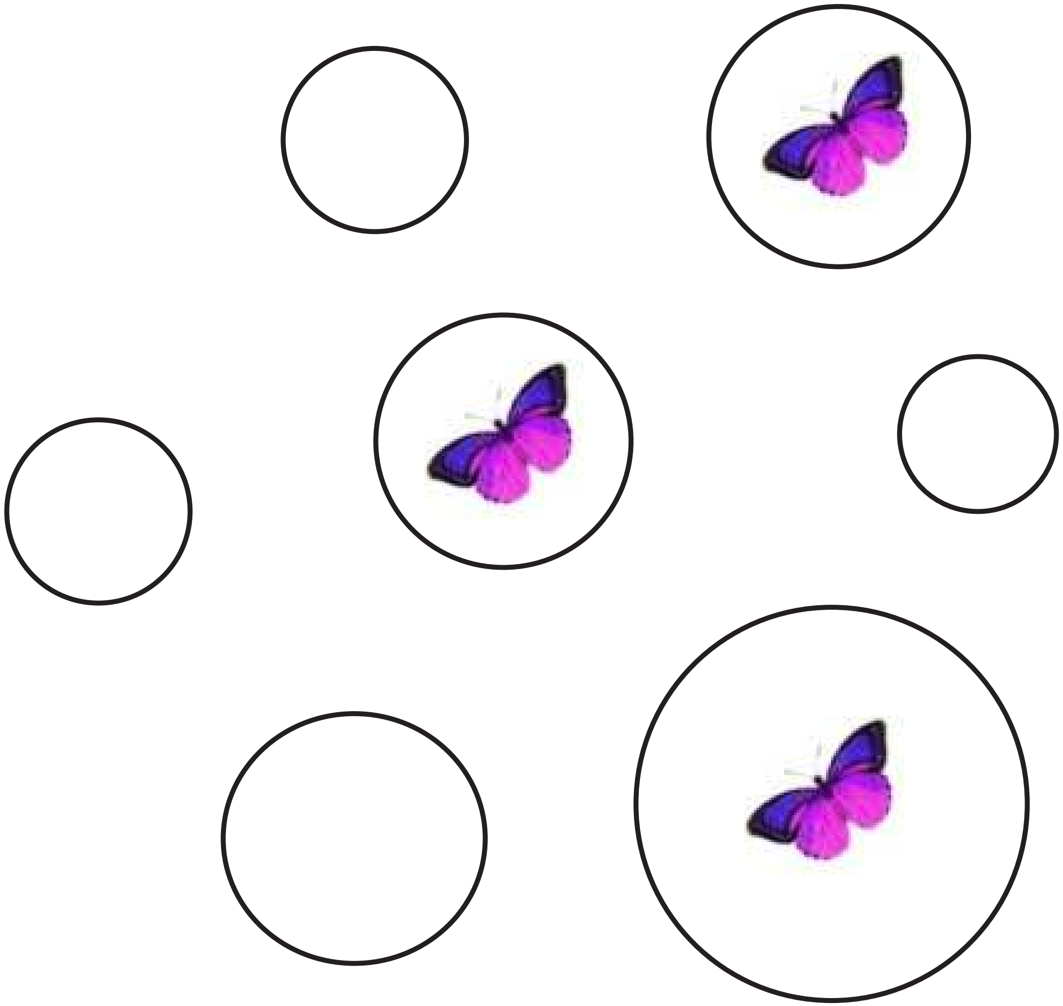


Metapopulations



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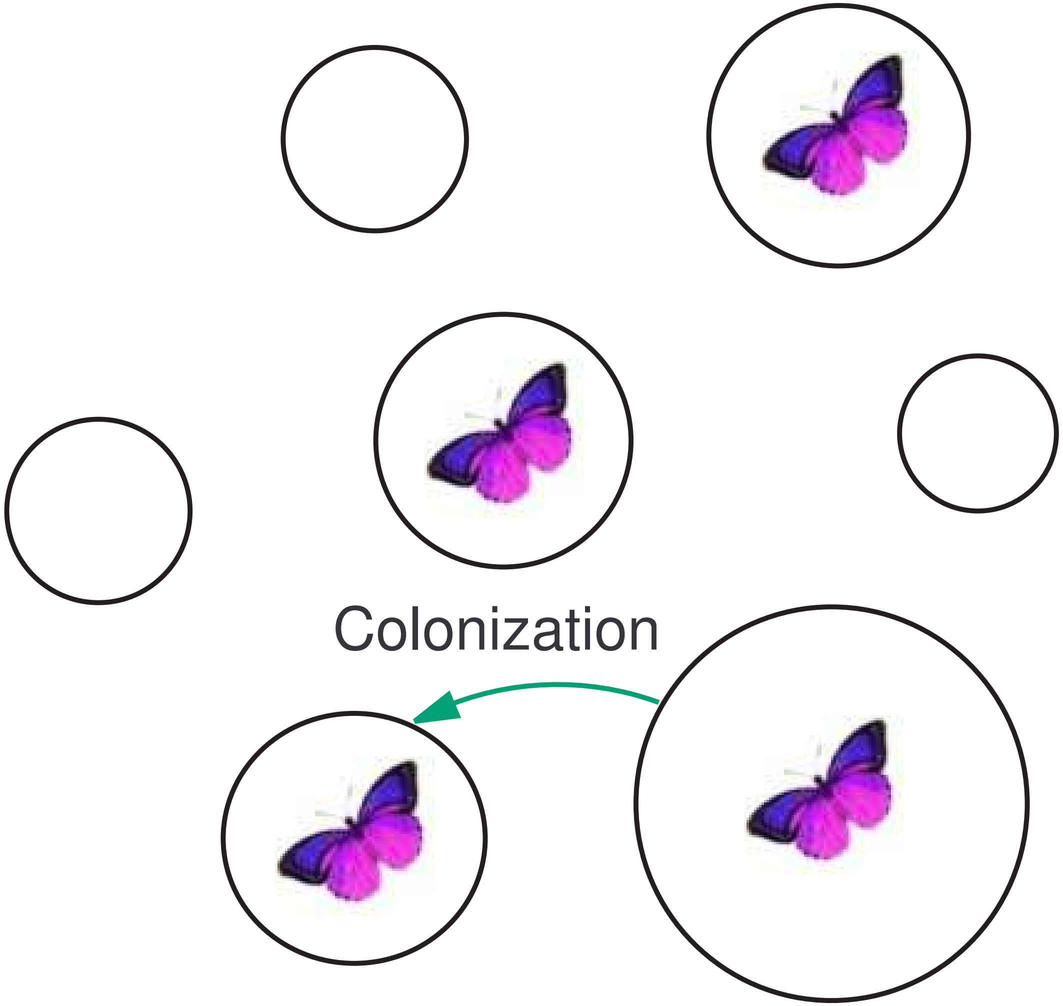

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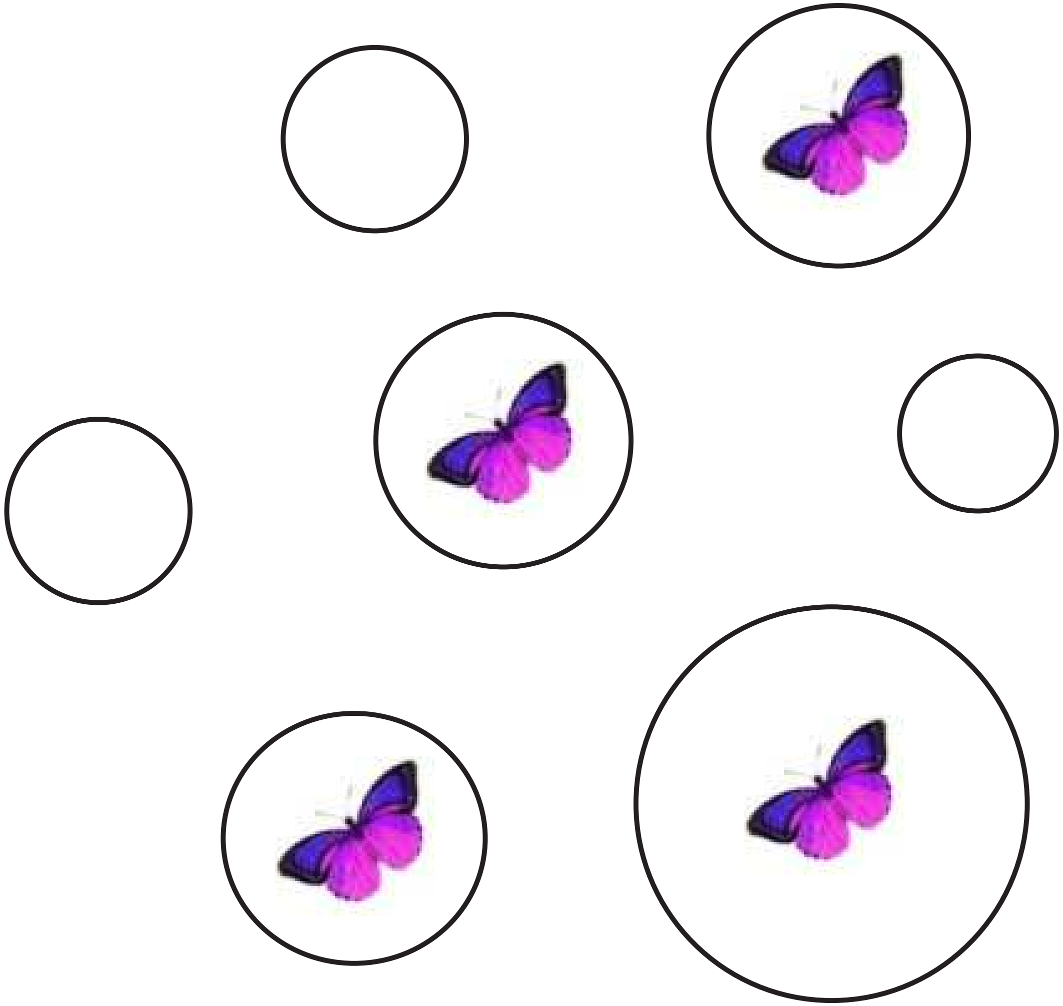

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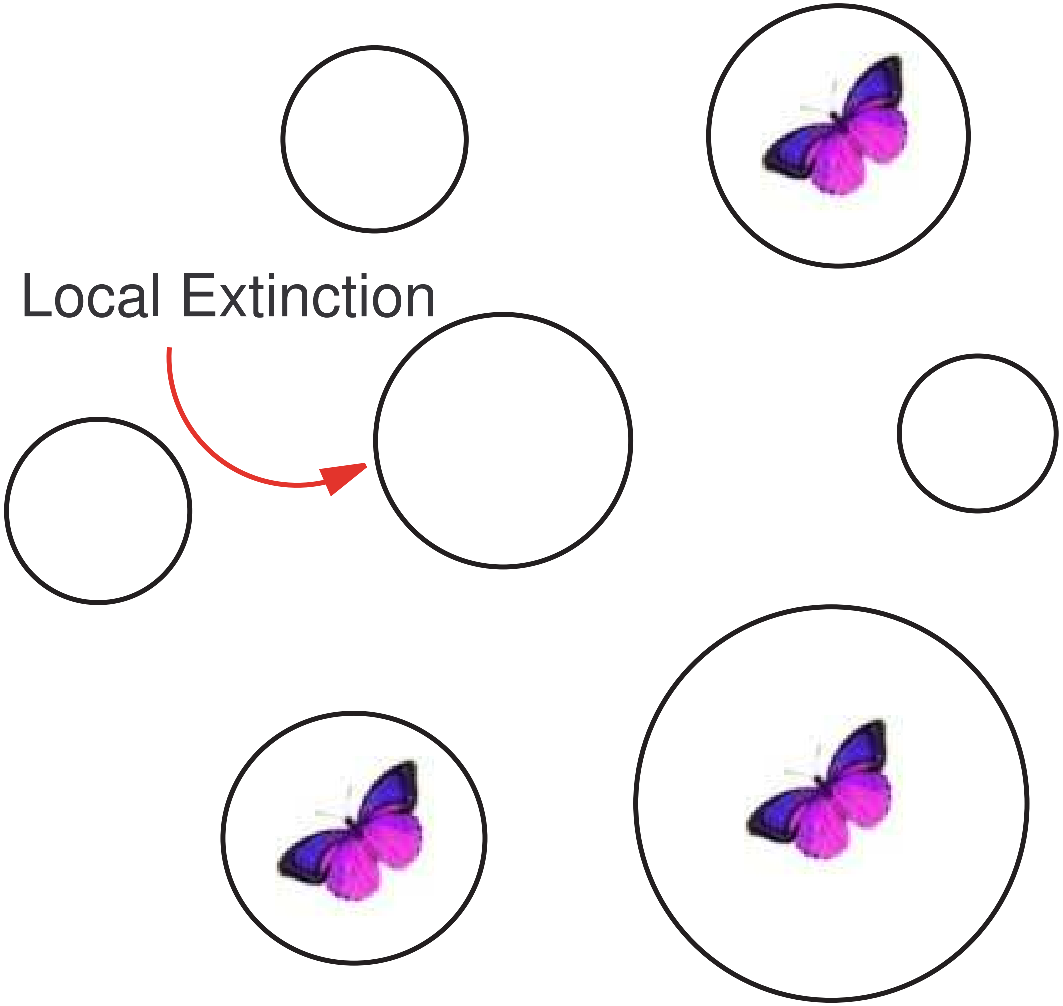

Metapopulations

- 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.

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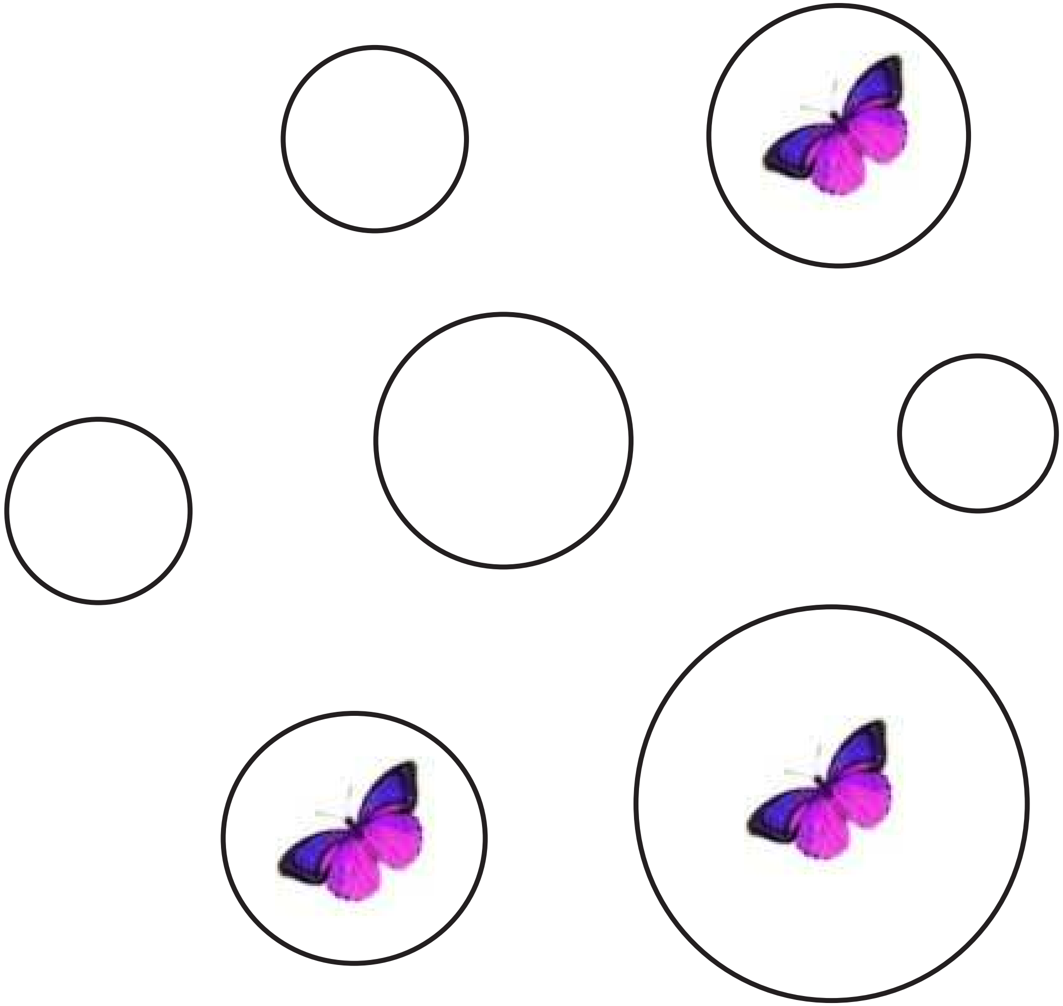

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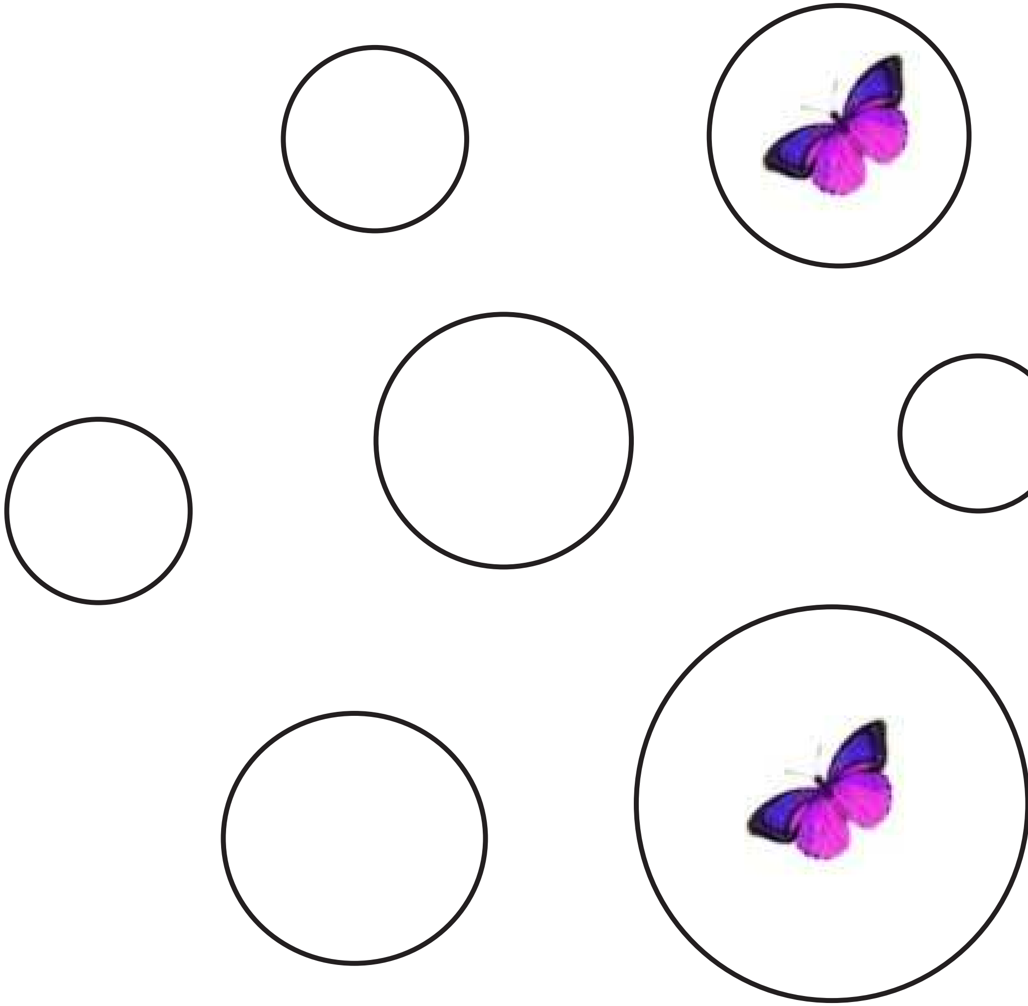

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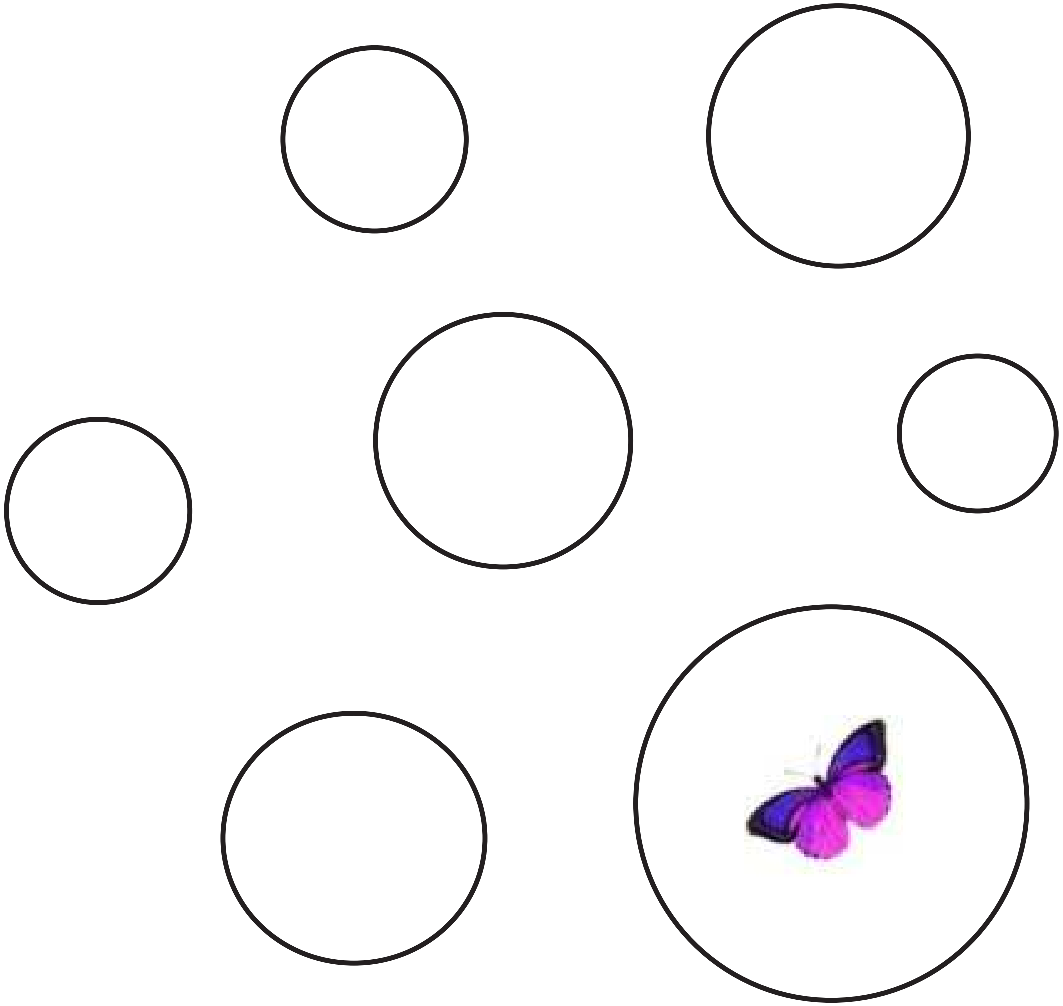

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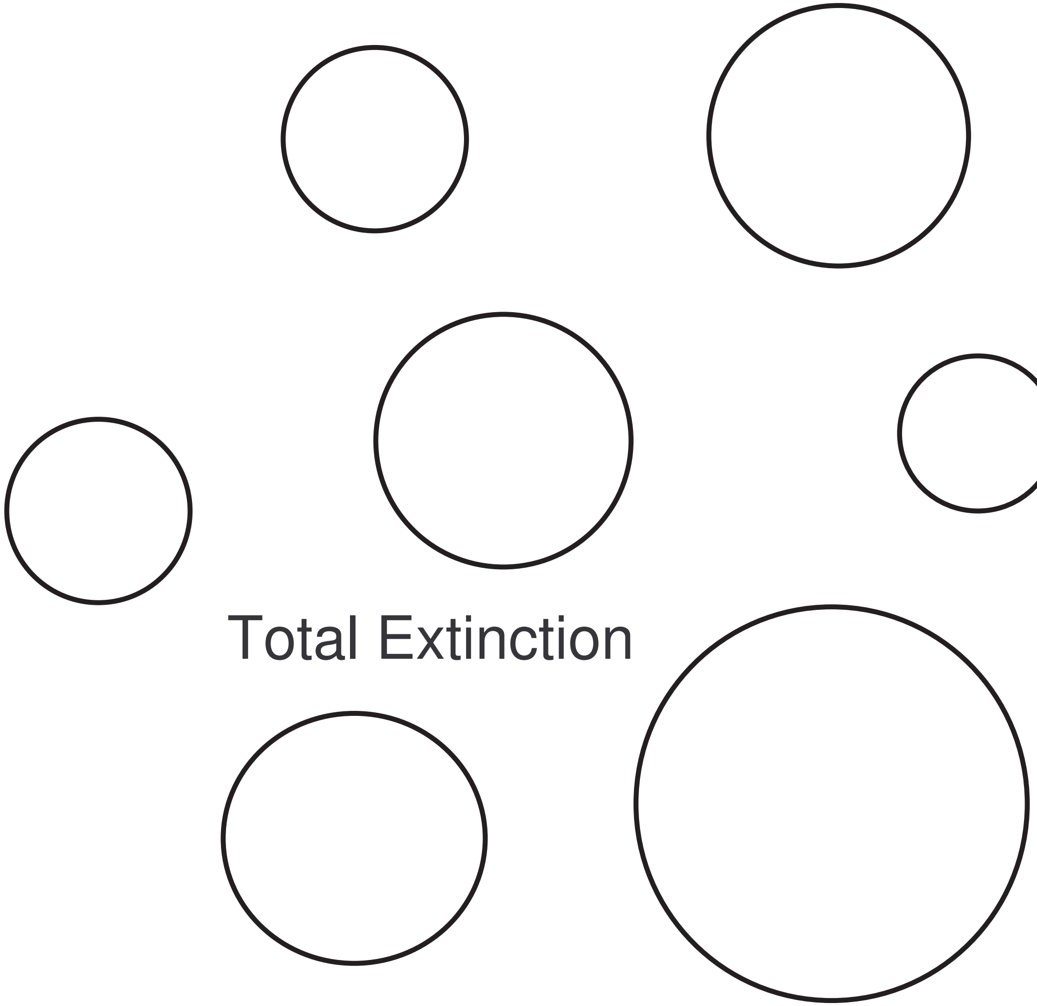

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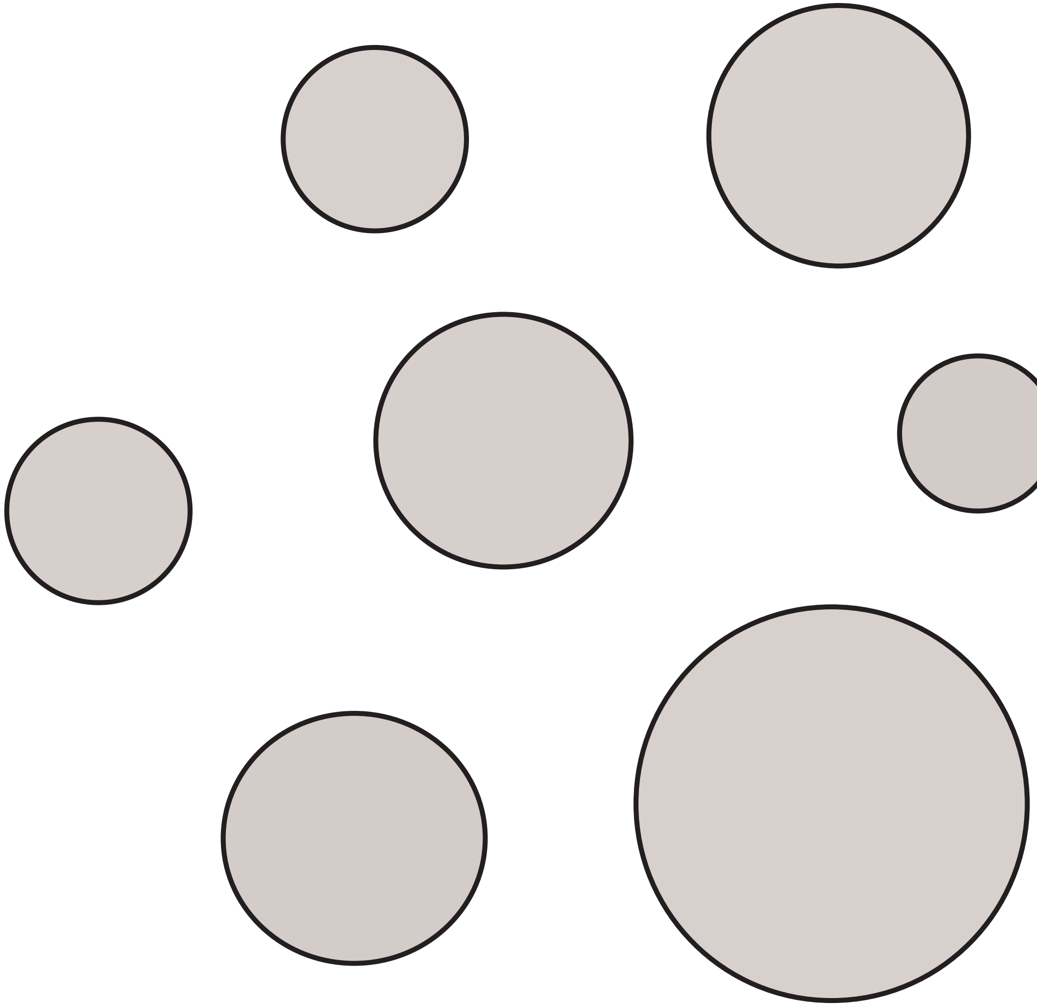

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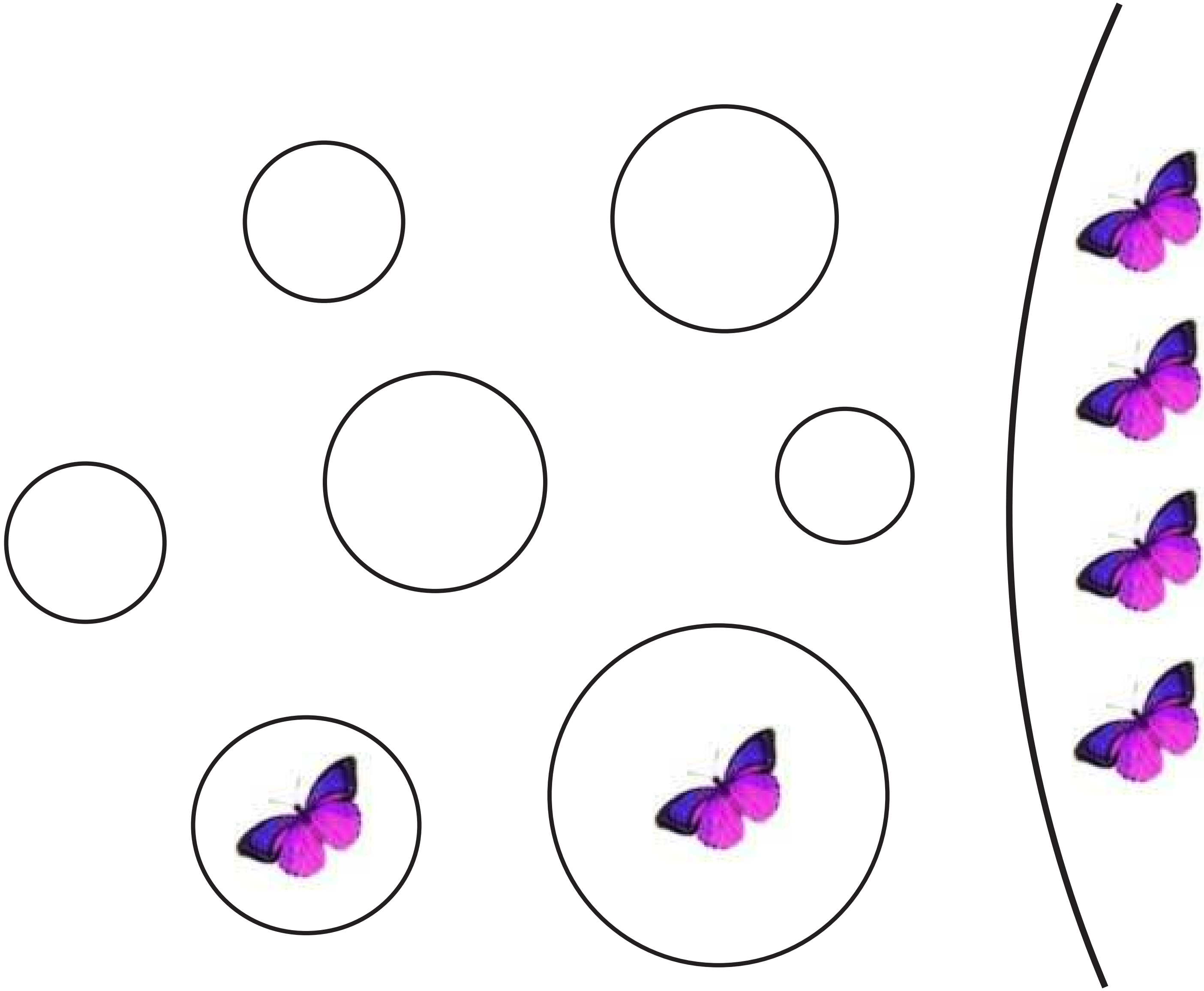
- In some instances there is an external source of immigration (mainland-island configuration).

Mainland-island configuration



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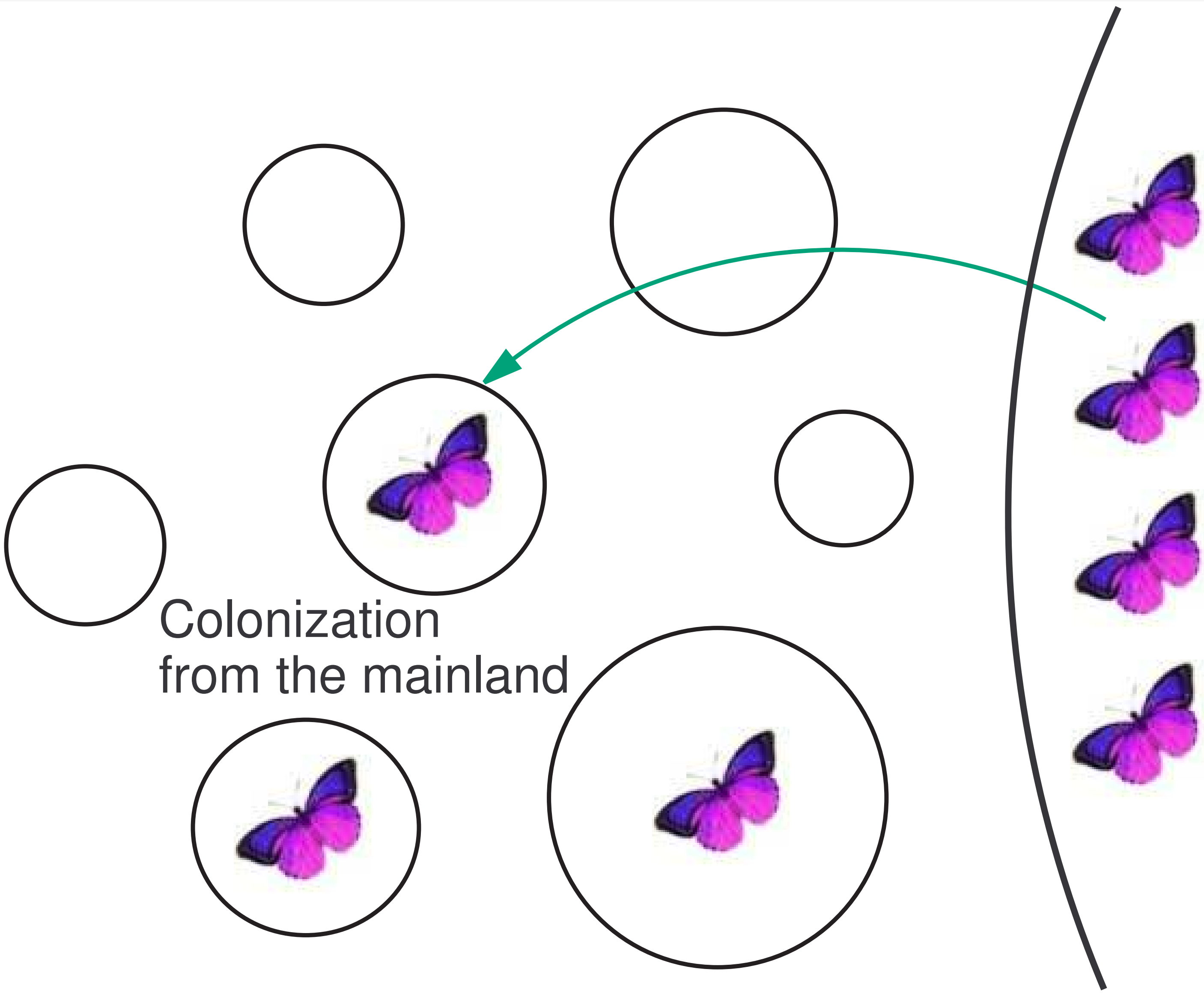

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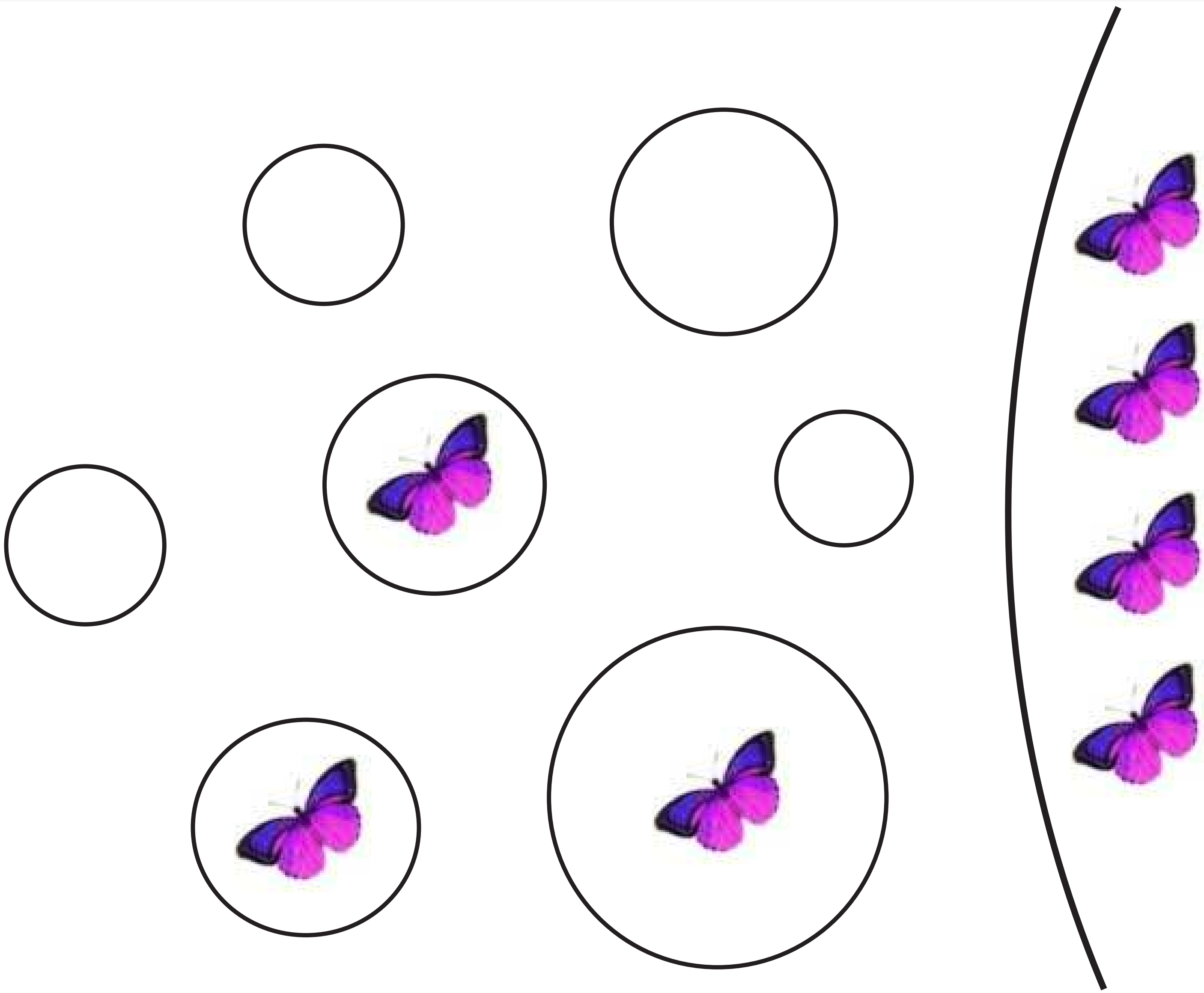

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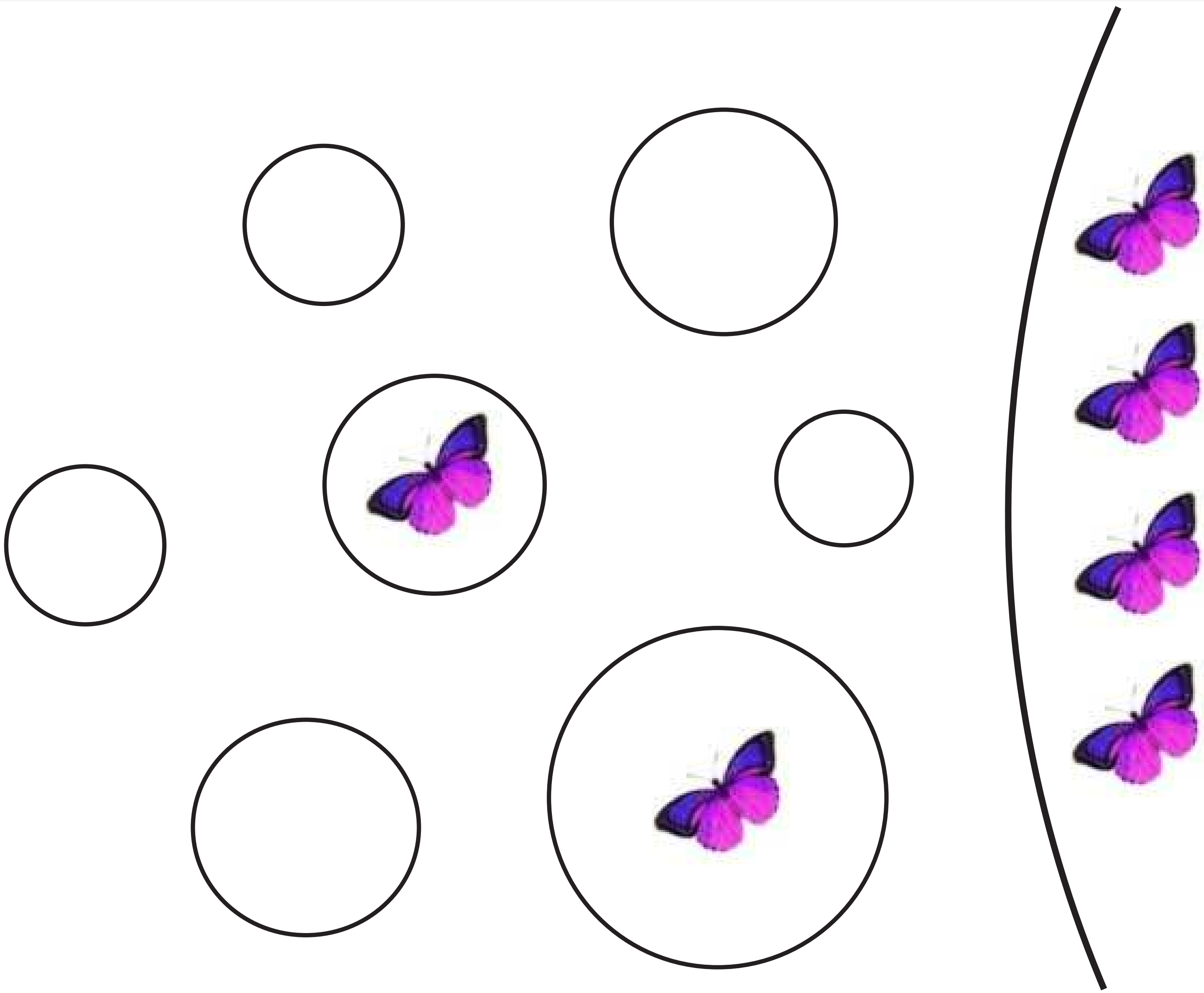

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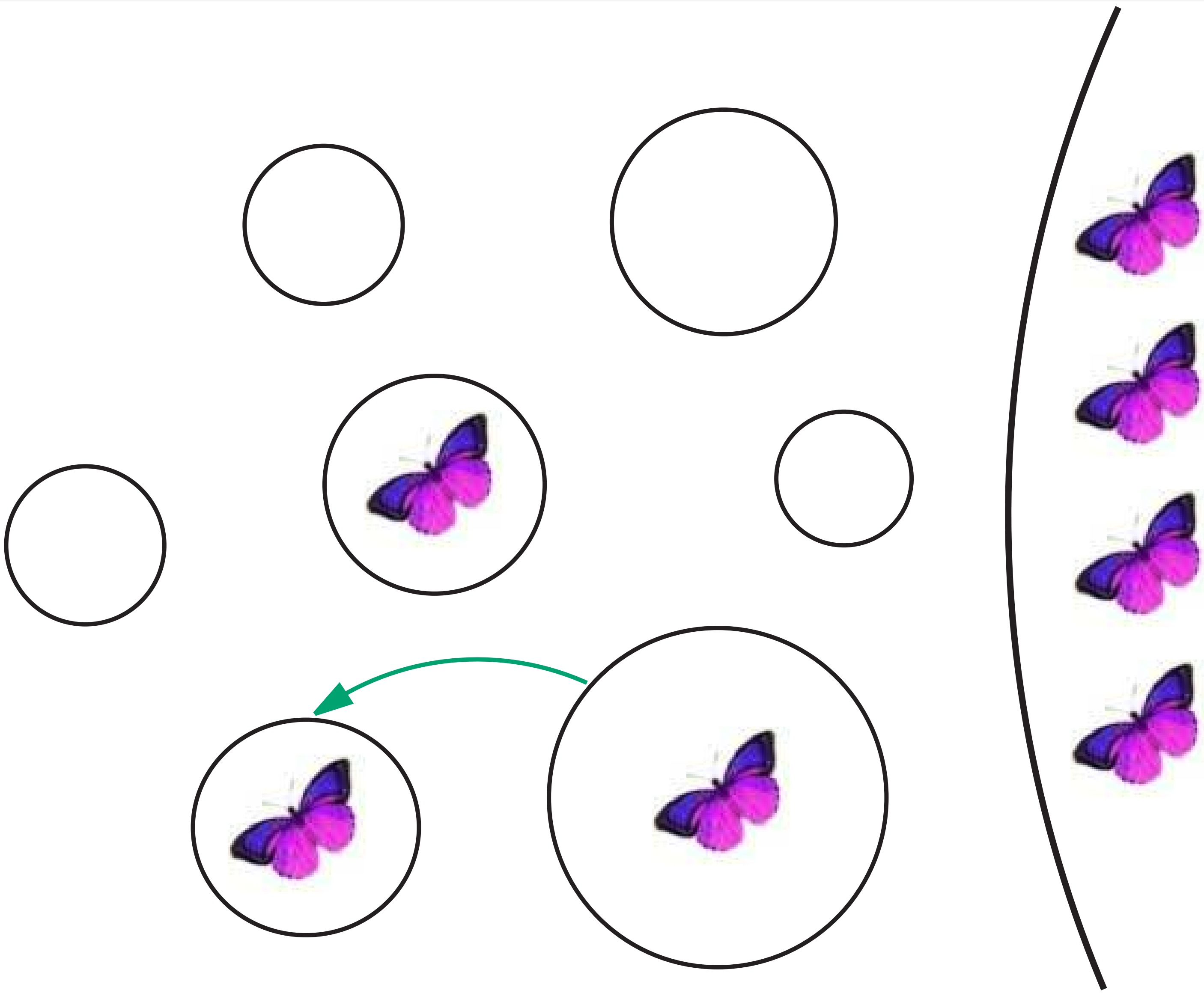

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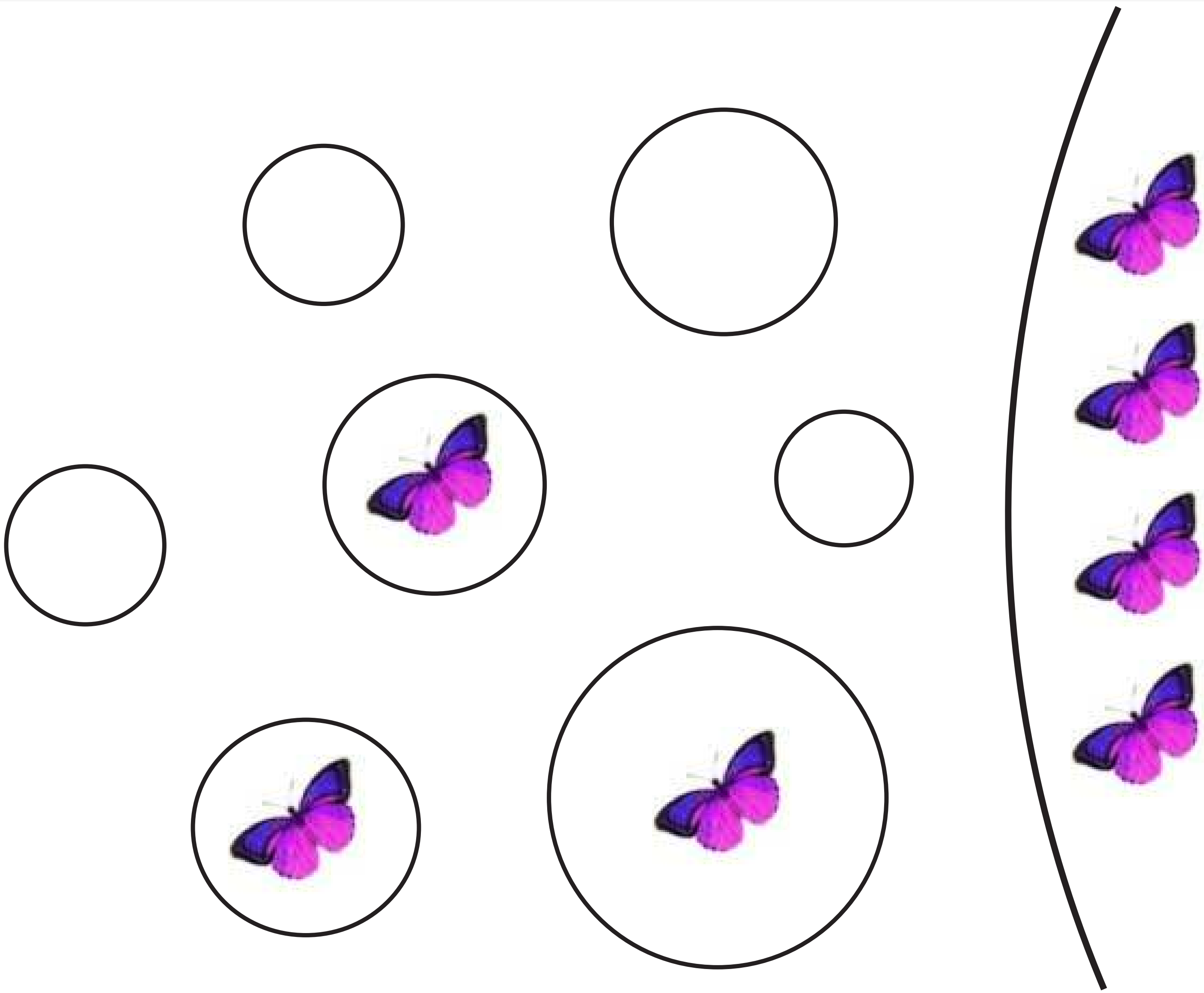

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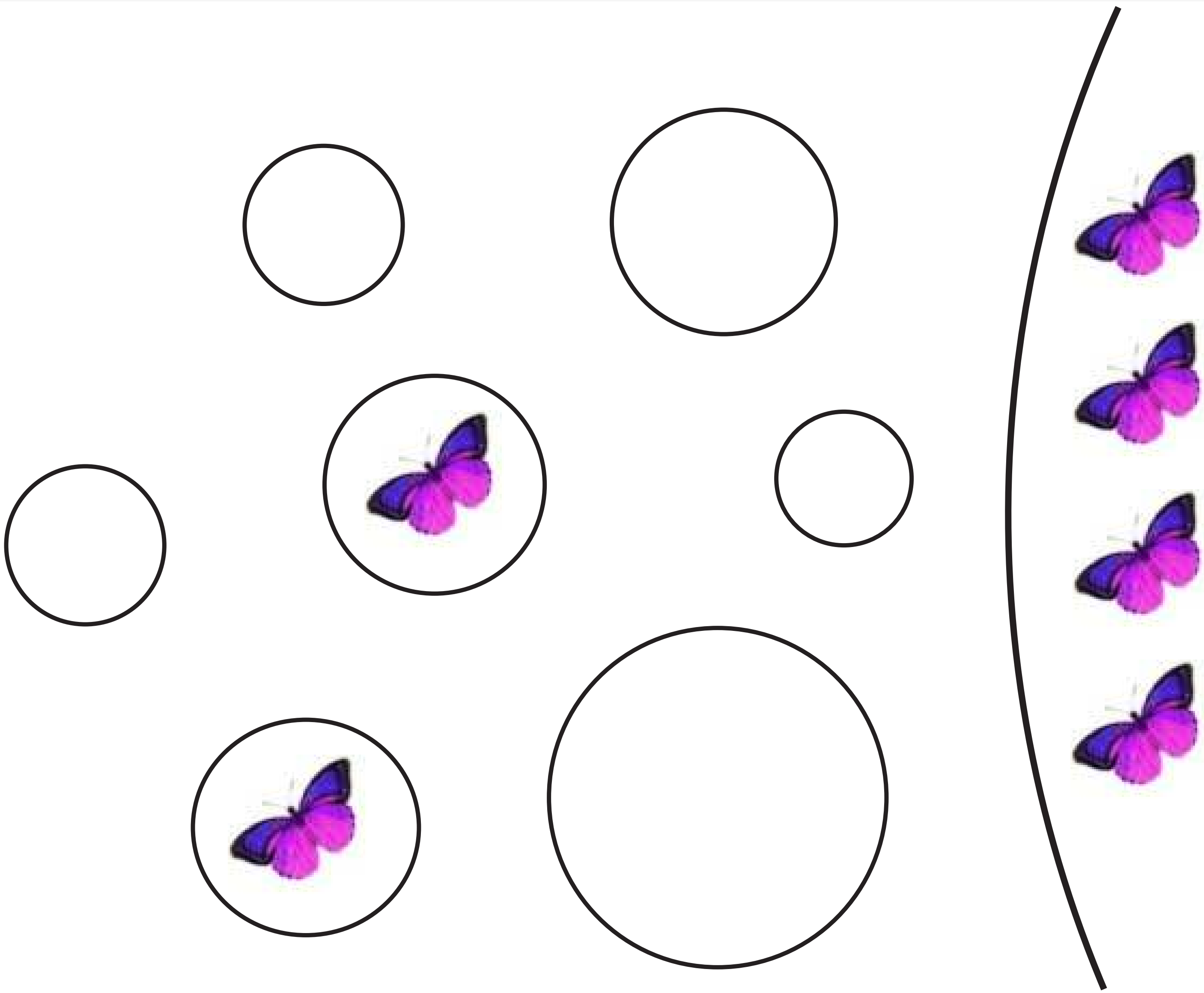

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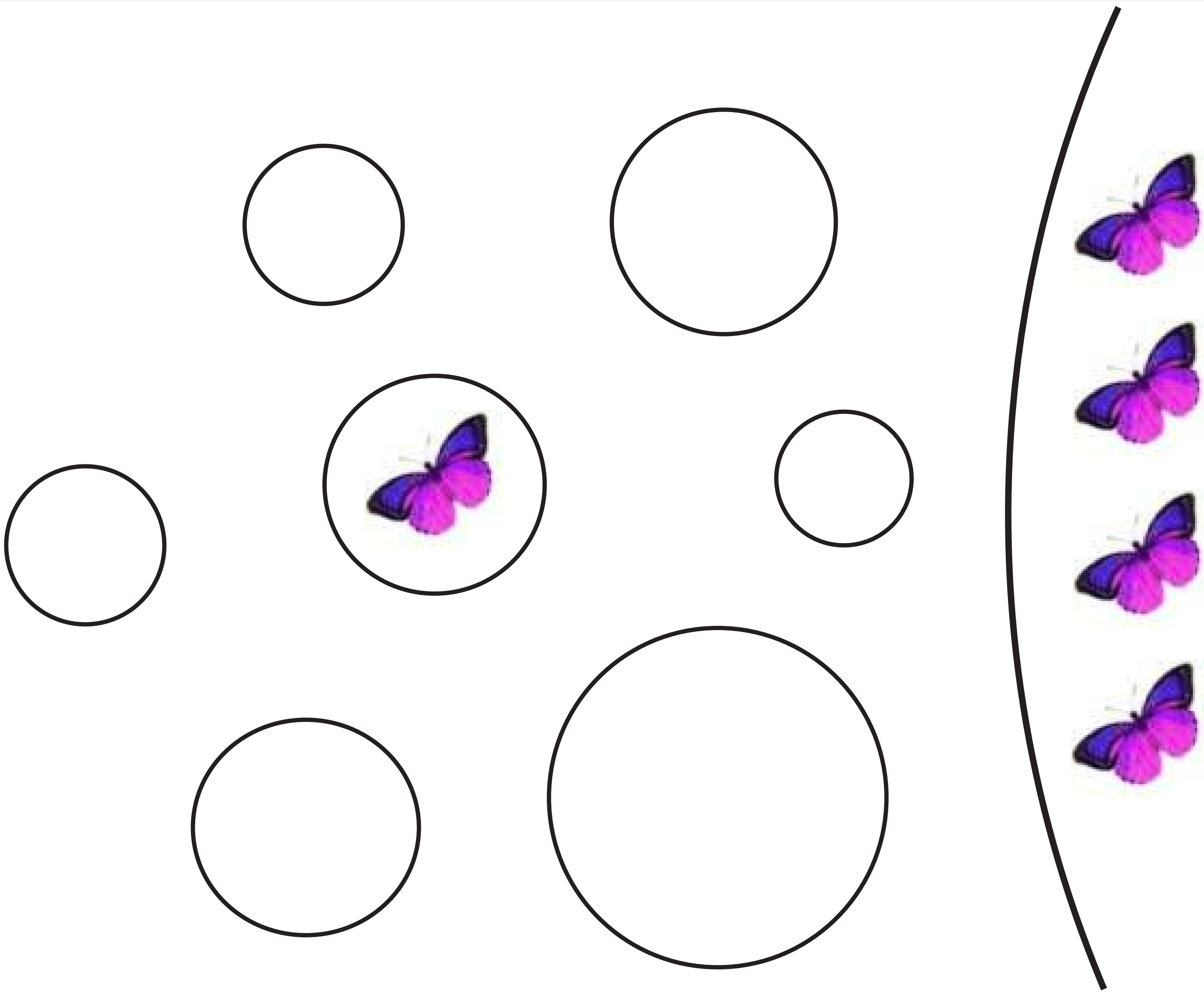

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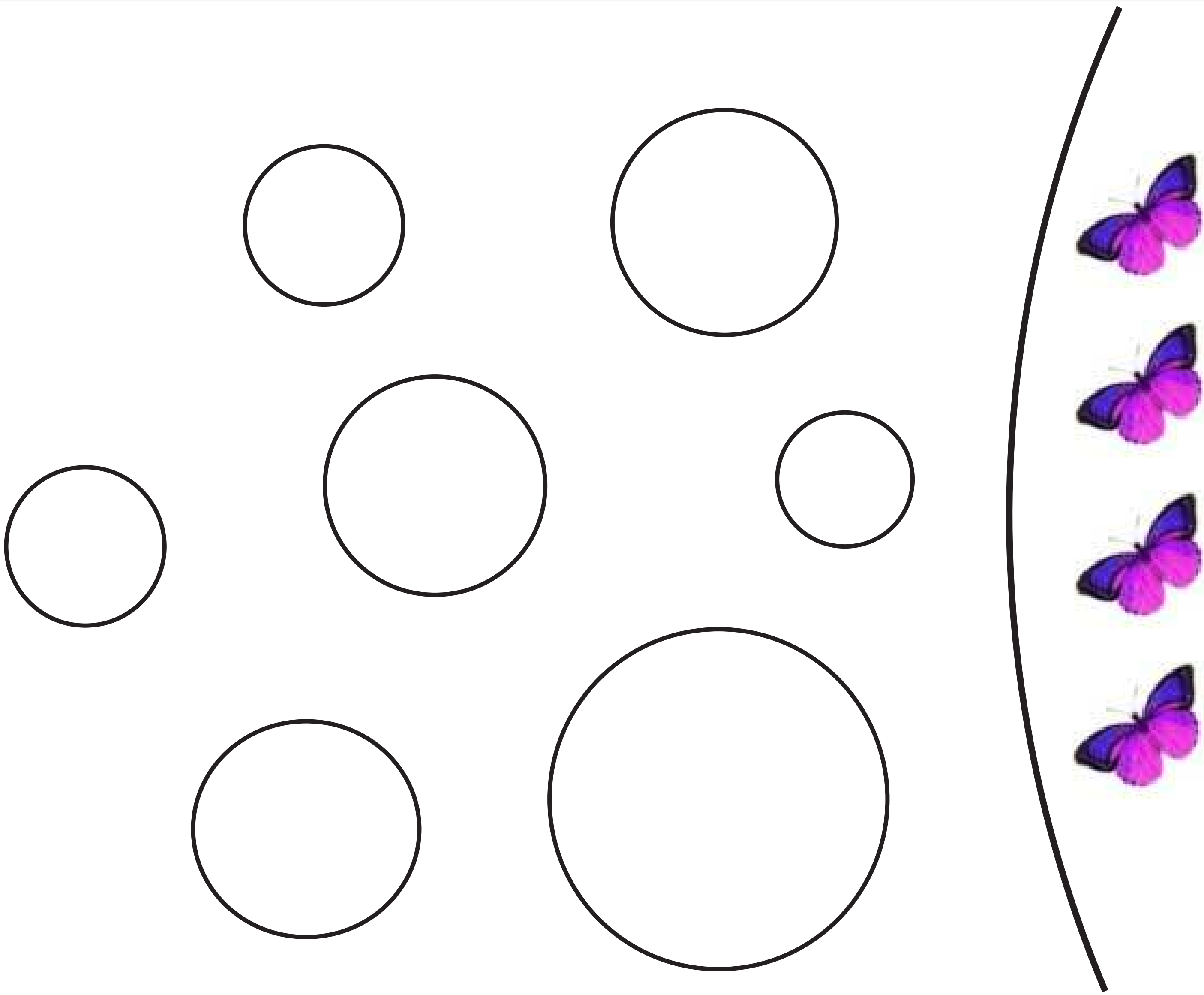

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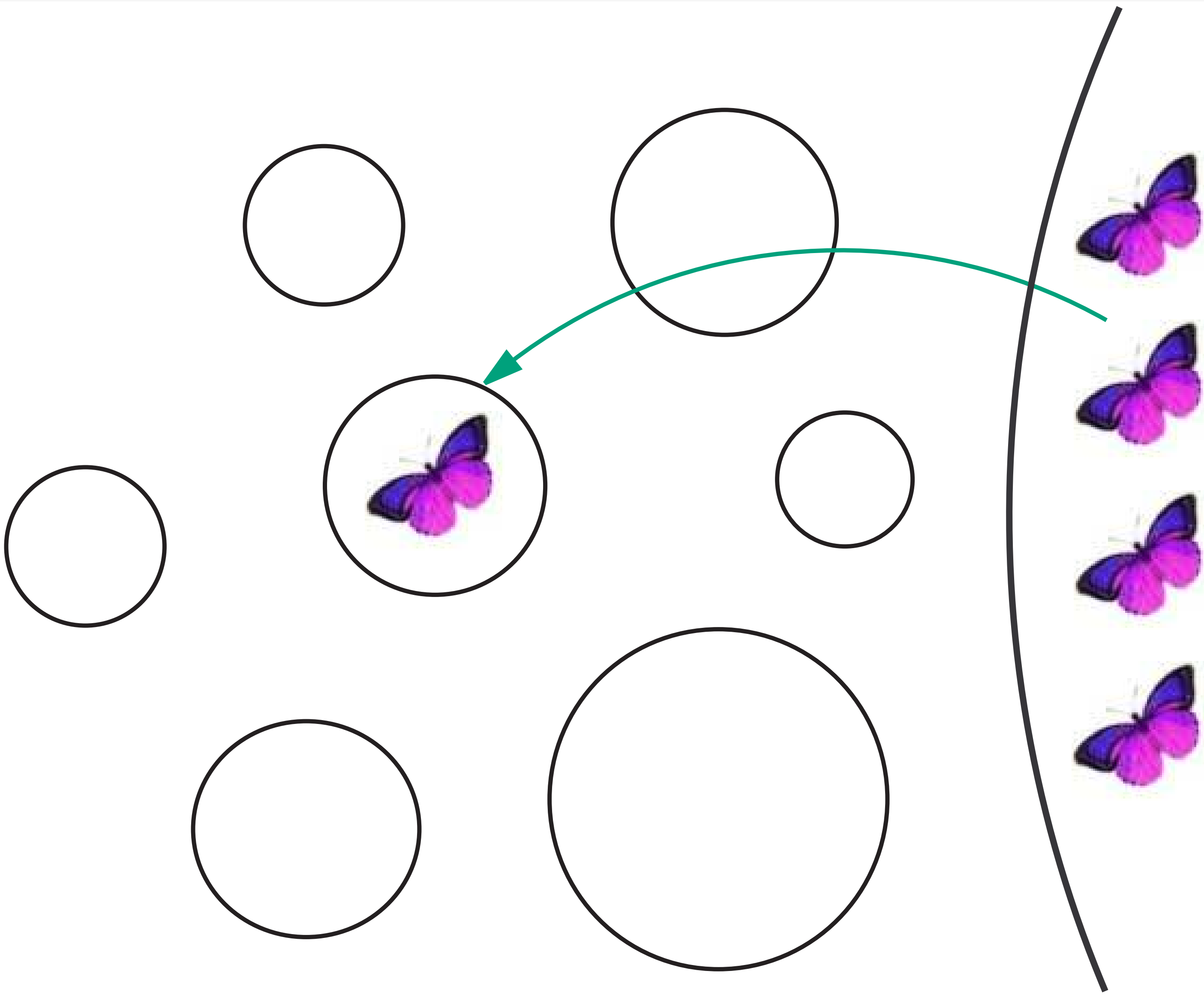

Typical questions

Given an appropriate model . . .

- Assessing population viability:
  - What is the expected time to (total) extinction* ?
  - What is the probability of extinction by time t^* ?
- Can we improve population viability ?
- How do we estimate the parameters of the model ?
- Can we determine the stationary/quasi-stationary distributions ?

*Or *first* total extinction in the mainland-island setup.

Patch-occupancy models

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In Lecture 1 we looked at the *stochastic logistic (SL) model* of Feller*.

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

A continuous-time model

There are J patches. Each occupied patch becomes empty at rate e and colonization of empty patches occurs at rate c/J for each occupied-unoccupied pair.

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

$$n \to n+1 \qquad \text{at rate} \qquad \frac{c}{J} n \,(J - n)$$

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Mainland-island version (v is the immigration rate):

$$n \to n+1 \qquad \text{at rate} \qquad v(J-n) + \tfrac{c}{J} n\,(J-n)$$
$$n \to n-1 \qquad \text{at rate} \qquad en$$

The SL model

We identified an approximating deterministic model for the *proportion*, $X_t^{(J)} = n_t/J$, of occupied patches at time t. A *functional law of large numbers* established convergence of the family $(X_t^{(J)})$ to the unique trajectory (x_t) satisfying

$$x_t' = cx_t(1 - x_t) - ex_t = cx_t\,(1 - \rho - x_t)\,,$$

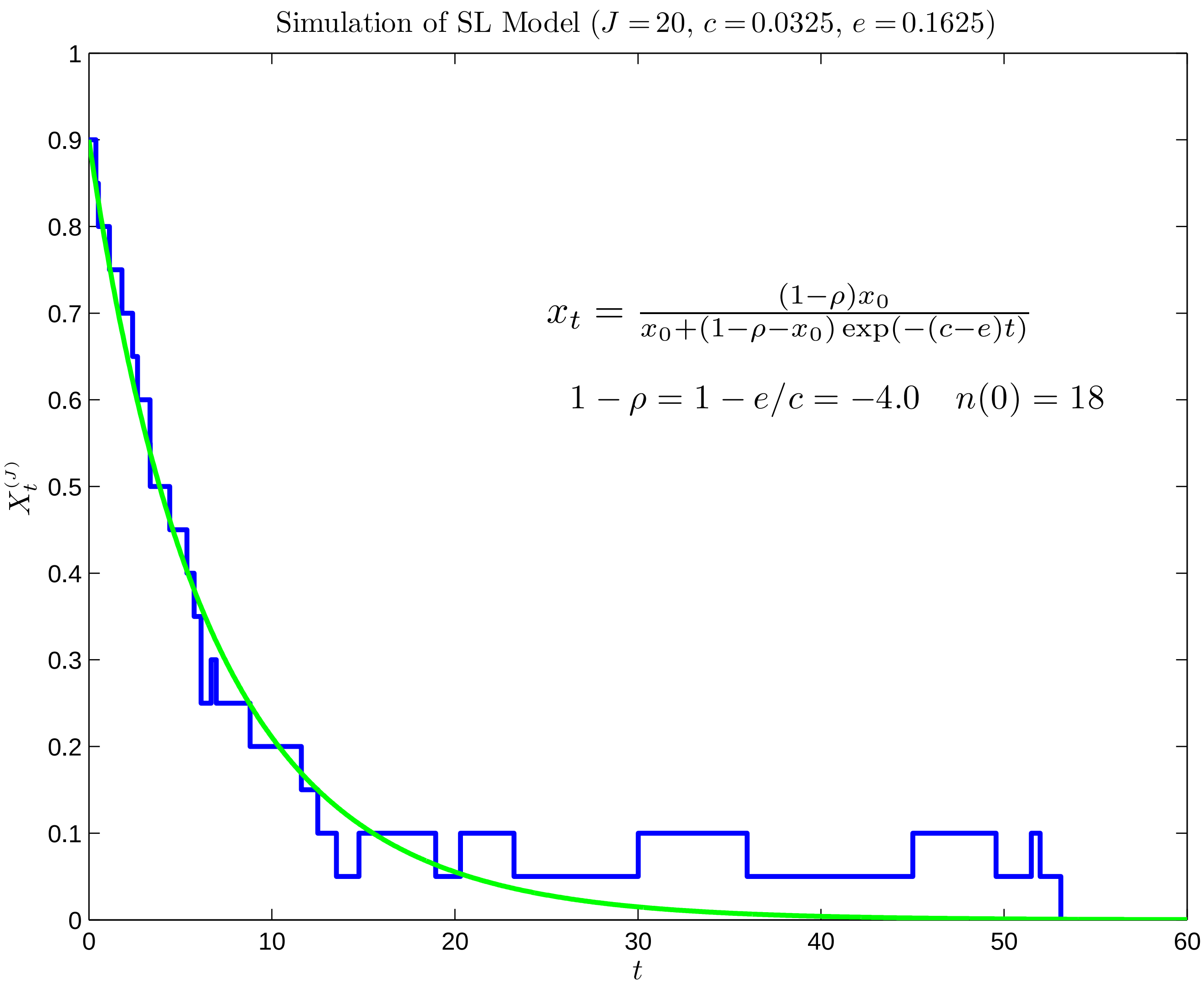
namely

$$x_t = \frac{(1-\rho)x_0}{x_0 + (1 - \rho - x_0)\,e^{-(c-e)t}},$$

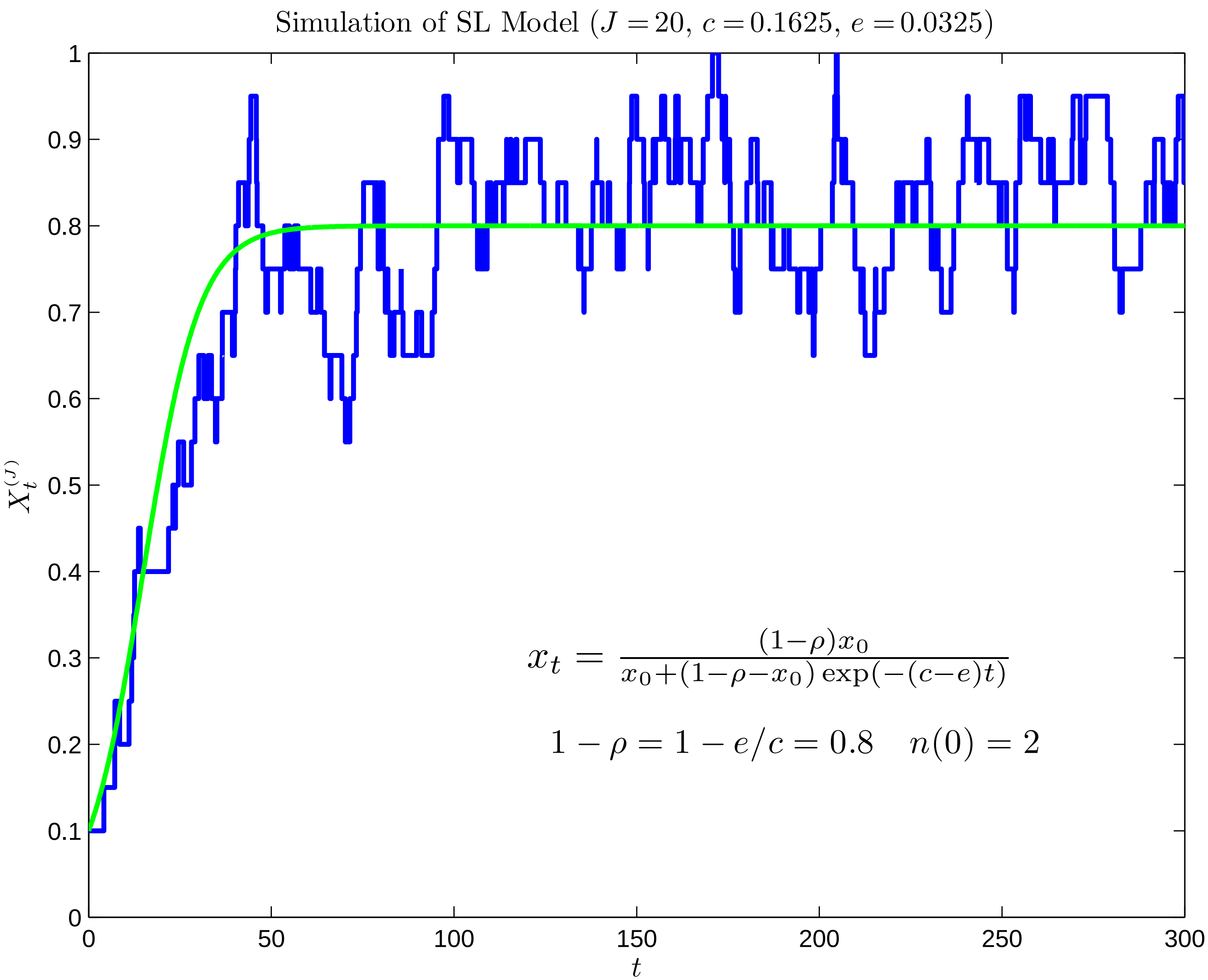
being the classical Verhulst* model.

*Verhulst, P.F. (1838) Notice sur la loi que la population suit dans son accroisement. Corr. Math. et Phys. X, 113–121.

The SL model ($c < e$) $x = 0$ stable



The SL model ($c > e$) $x = 1 - e/c$ stable



The SL model

Theorem If $X_0^{(J)} \to x_0$ as $J \to \infty$, then the family of processes $(X_t^{(J)})$ converges *uniformly in probability* on *finite time intervals* to the deterministic trajectory (x_t): for every $\epsilon > 0$,

$$\lim_{J\to\infty} \Pr\left(\sup_{s\le t} \left| X_s^{(J)} - x_s \right| > \epsilon \right) = 0.$$

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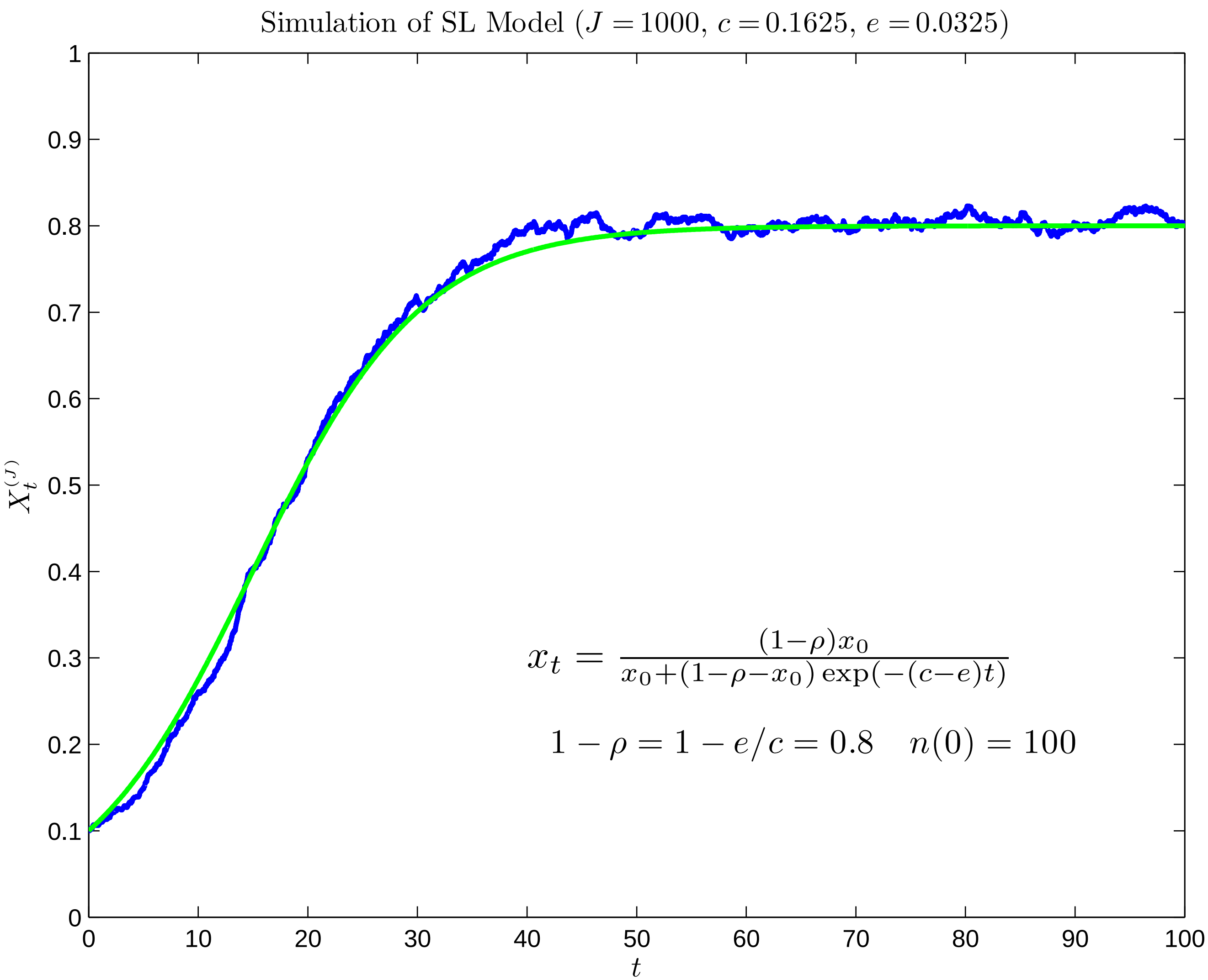

Accounting for life cycle

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.

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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

Butterfly life cycle

Egg $\simeq$ 4 days

Larva (caterpillar) $\simeq$ 14 days

Pupa (chrysalis) $\simeq$ 7 days

Adult (butterfly) $\simeq$ 14 days

Colonization and extinction phases

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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)
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A discrete-time Markovian model

Recall that there are J 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 $S = \{0, 1, \ldots, J\}$ with a 1-step transition matrix $P = (p_{ij})$ constructed as follows.

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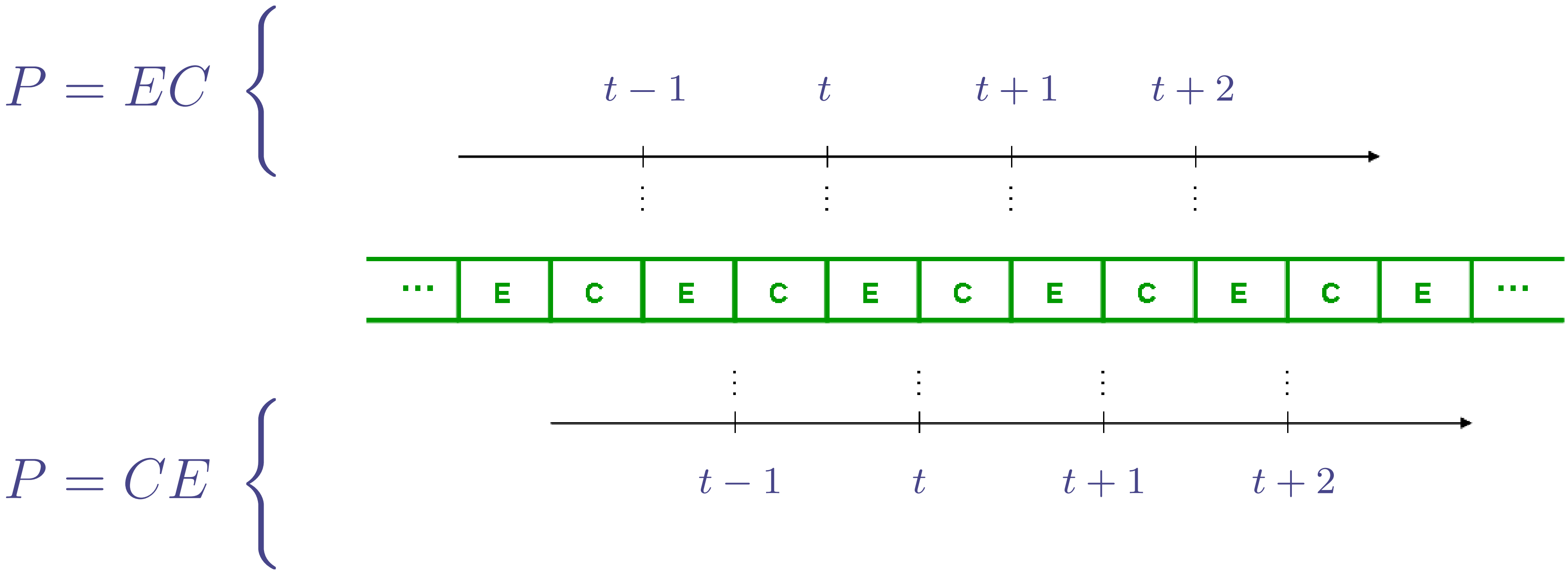
The extinction and colonization phases are governed by their own transition matrices, $E = (e_{ij})$ and $C = (c_{ij})$.

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*



Extinction phase

Suppose that local extinction occurs *at any given patch* with probability e ($0 < e < 1$), independently of other occupied patches. So, the number of extinctions when there are i patches occupied has a binomial *Bin*(i, e) distribution, and therefore

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

We also have $e_{ij} = 0$ if $j > i$.

Colonization phase

Suppose that colonization occurs according to the following mechanism.

If there are i occupied patches, then each unoccupied patch is colonized with probability $c_i = (i/J)c$, where $c \in (0, 1]$ is a *fixed maximum colonization potential*, the (hypothetical) probability that a single unoccupied patch is colonized by the fully occupied network.

So, the unoccupied patches are colonized independently with the same probability, this probability being *proportional to* the number of patches with the potential to colonize.

Colonization phase

Therefore, the number of colonizations when there are i patches occupied has a binomial *Bin*$(J-i, c_i)$ distribution, and so

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

In particular, $c_{0j} = \delta_{0j}$. We also have $c_{ij} = 0$, for $j < i$.

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Notice that 0 is an absorbing state and $C = \{1, \ldots, J\}$ is a communicating class.

There are other sensible choices for c_i: for example $c_i = c(1 - (1 - c_1/c)^i)$ or $c_i = 1 - \exp(-i\beta/J)$.

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$$p_{ij} = \sum_{k=1}^{\min\{i,j\}} \binom{i}{k} (1-e)^k e^{i-k} \binom{J-k}{j-k} c_k^{j-k} (1-c_k)^{J-j}.$$

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If $P = CE$, then $p_{0j} = \delta_{0j}$, and, for $i \geq 1$ and $j \geq 0$,

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In particular, for $i \geq 1$, $p_{i0} = e^i(1 - c_i(1-e))^{J-i}$.

Equivalent independent phases

For the CE-model,

$$\mathsf{E}(z^{n_{t+1}}|n_t = i) = (e + (1-e)z)^i (1 - (1-e)c_i(1-z))^{J-i}.$$

Thus, given $n_t = i$, n_{t+1} has the *same distribution* as $B_1 + B_2$, where B_1 and B_2 are two *independent* random variables with $B_1 \sim \textit{Bin}(i, 1-e)$ and $B_2 \sim \textit{Bin}(J-i, (1-e)c_i)$.

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It is as if each of the i occupied patches remains occupied with probability $1-e$ and each of the $J-i$ unoccupied patches becomes occupied with probability $(1-e)c_i$, all J patches being affected independently.

Equivalent independent phases

For the EC-model, the best we can do is

$$\mathsf{E}(z^{n_{t+1}} | n_t = i) = \mathsf{E}\left\{ z^B \left(1 - c_B(1-z)\right)^{J-B} \right\},$$

where $B \sim \textit{Bin}(i, 1-e)$.

Large-J

However, note the large-J asymptotics when $c_i = ic/J$.
Write $p_i^{(J)}(z) = \mathsf{E}(z^{n_{t+1}} | n_t = i)$.

For the CE-model,

$$\lim_{J \to \infty} p_i^{(J)}(z) = [e + (1-e)z \exp(-c(1-e)(1-z))]^i.$$

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Branching!

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The effect is $\dots$

Theorem Both infinite patch models are Galton-Watson branching processes.

Infinitely many patches - branching

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For the EC-model, $p_{10} = e$ and

$$p_{1j} = (1-e)\exp(-c)\frac{c^{j-1}}{(j-1)!} \quad (j \geq 1),$$

the interpretation being that each individual "dies" with probability e or otherwise is *joined by* a random number of new offspring that follows a *Poisson*(c) law.

Infinitely many patches - branching

For the CE-model, $p_{10} = e\exp(-c(1-e))$ and

$$p_{1j} = (1-e)\exp(-c(1-e))\frac{(c(1-e))^{j-1}}{(j-1)!} + e\exp(-c(1-e))\frac{(c(1-e))^{j}}{j!} \quad (j \geq 1).$$

The individual survives with probability $1-e$ or dies with probability e, and there is a random number of *new* offspring that follows a *Poisson*$(c(1-e))$ law.

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We can now invoke the encylopaedic theory of branching processes.

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Recall that, given $n_0 = i$, E$(n_t) = i\mu^t$ and

$$\text{Var}(n_t) = \begin{cases} i\sigma^2 t & \text{if } \mu = 1 \quad (e = c/(1+c)) \\ i\sigma^2(\mu^t - 1)\mu^{t-1}/(\mu - 1) & \text{if } \mu \neq 1 \quad (e \neq c/(1+c)). \end{cases}$$

Infinitely many patches - total extinction

Theorem For both models extinction occurs with probability 1 if and only if $e \geq c/(1+c)$; otherwise the extinction probability η is the unique solution to $s = p(s)$ on the interval $(0,1)$, where:

EC-model: $p(s) = e + (1-e)s\exp(-c(1-s))$

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And much more ...

- The expected time to extinction.
- Yaglom's theorem on limiting-conditional (quasi-stationary) distributions.

Back to the J-patch models

Recall that ...

In the extinction phase the number of extinctions when there are i patches occupied follows a *Bin*(i, e) law.

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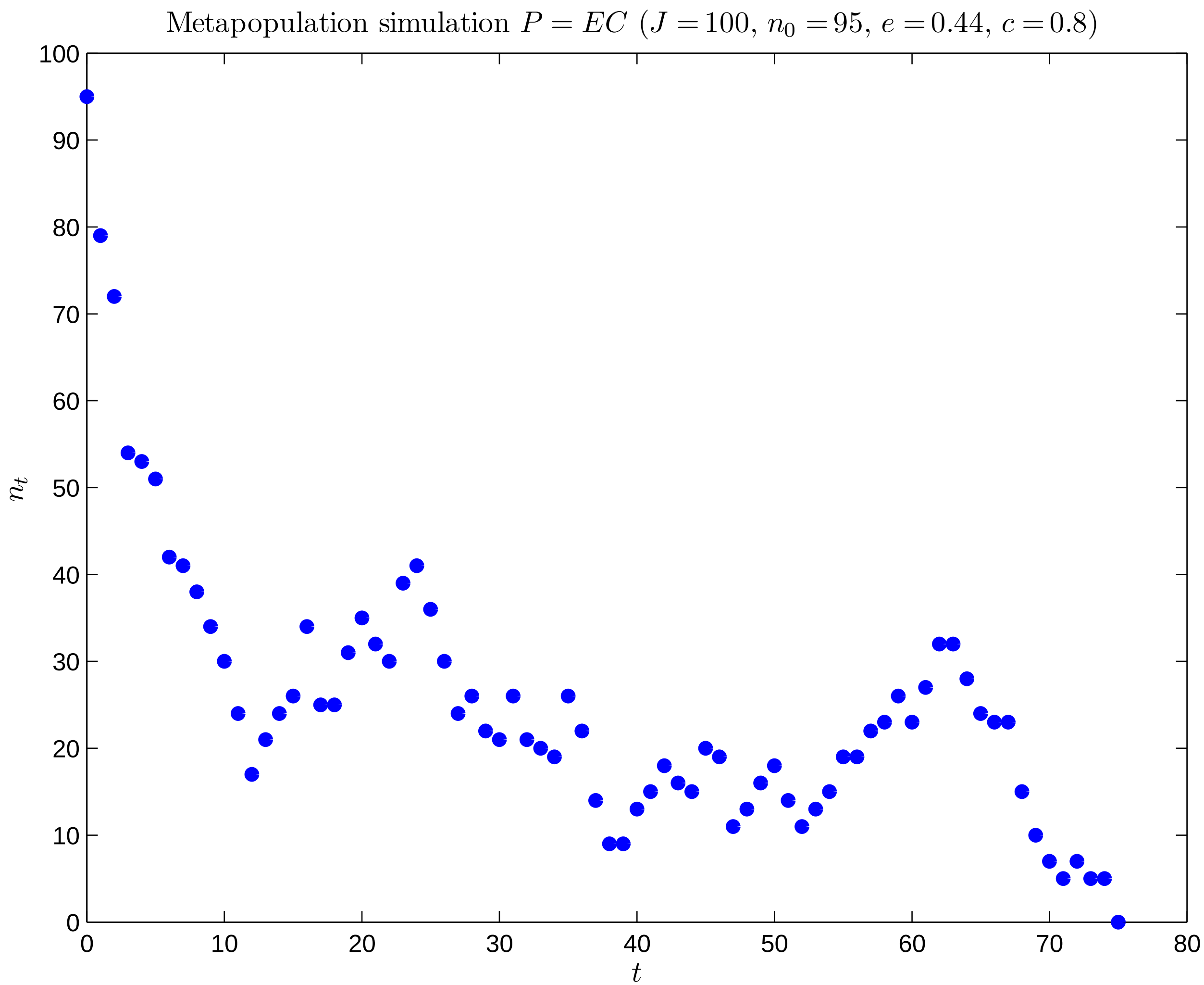
Numerical procedures are routine.

Simulation: $P = EC$



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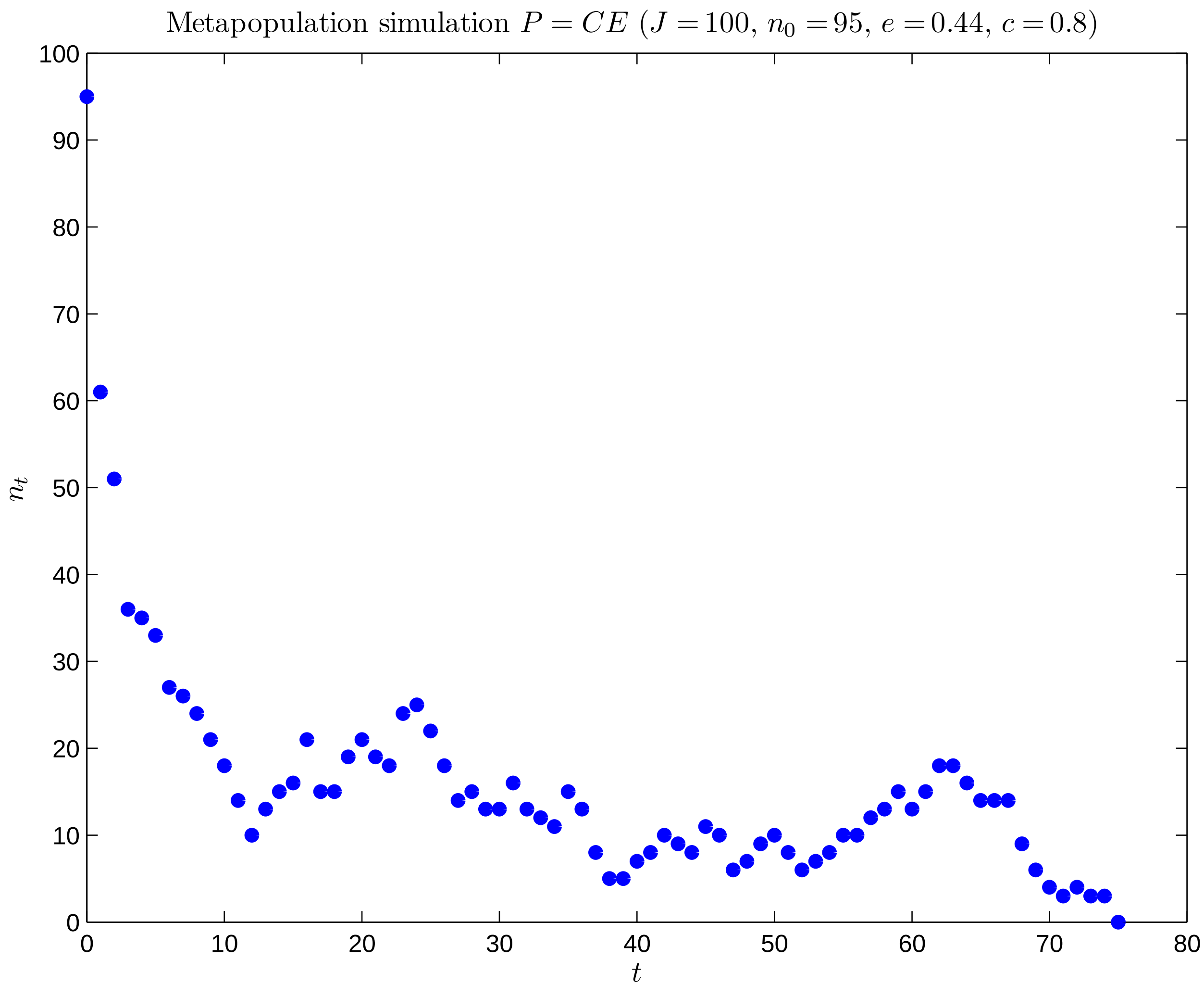
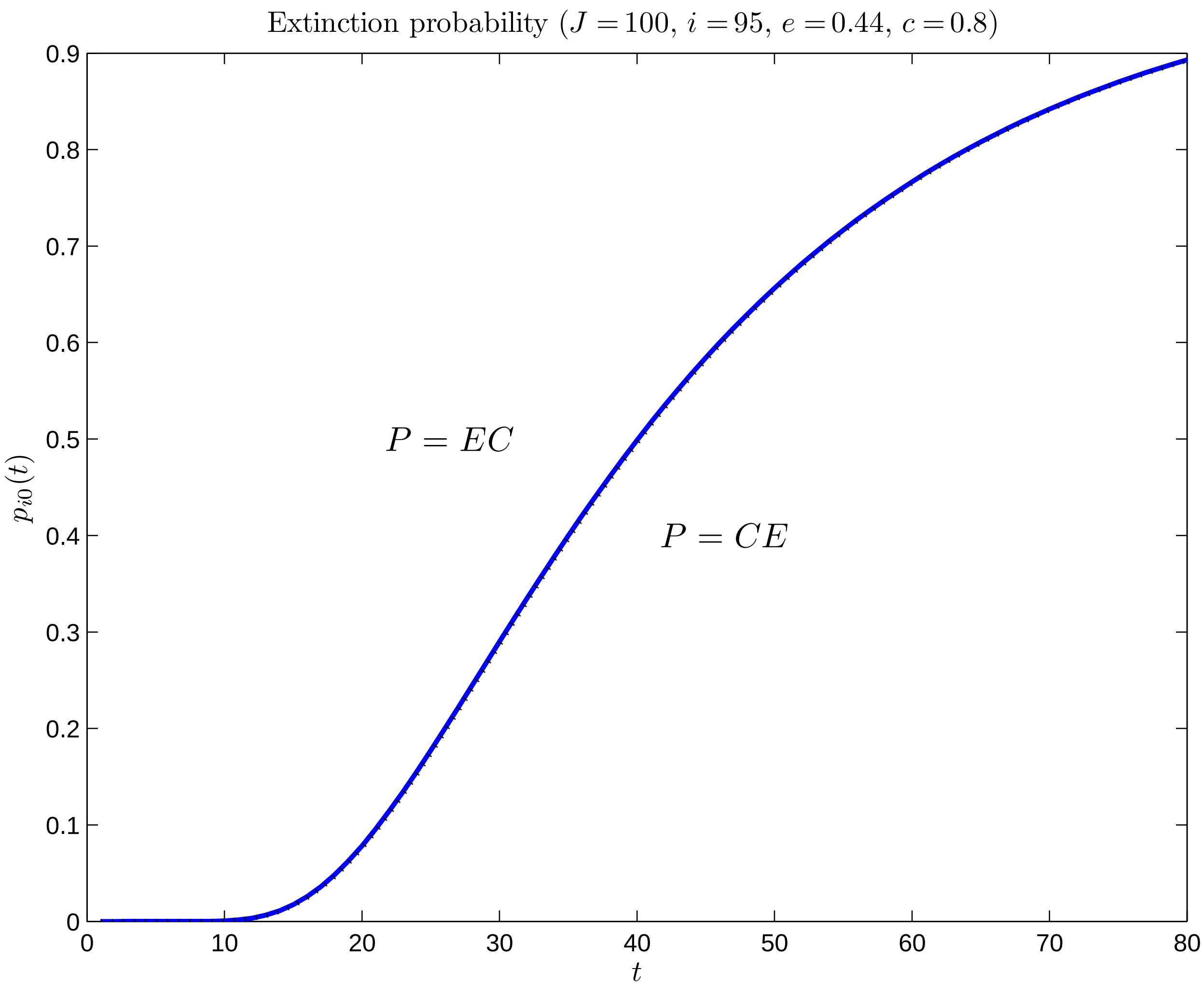
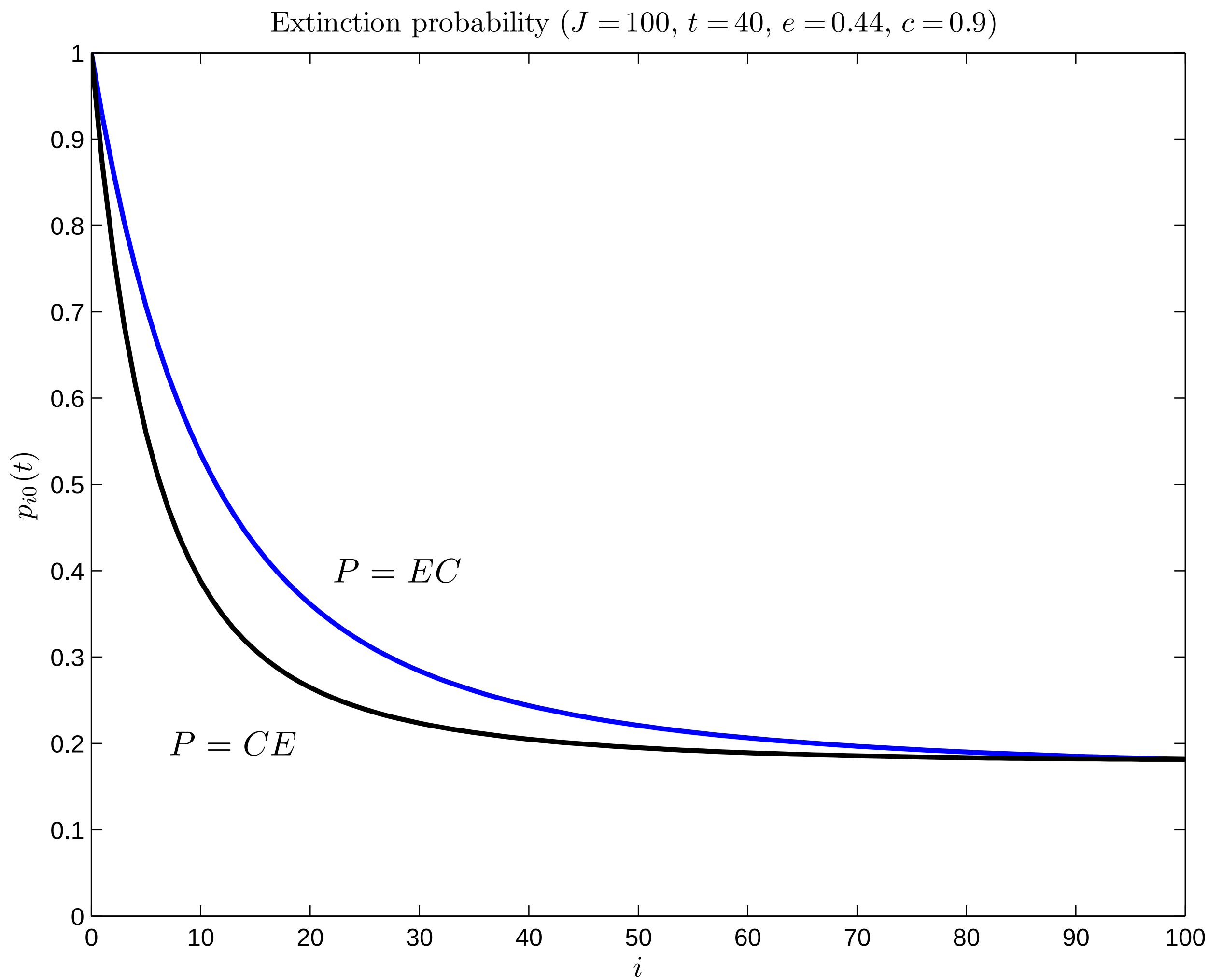


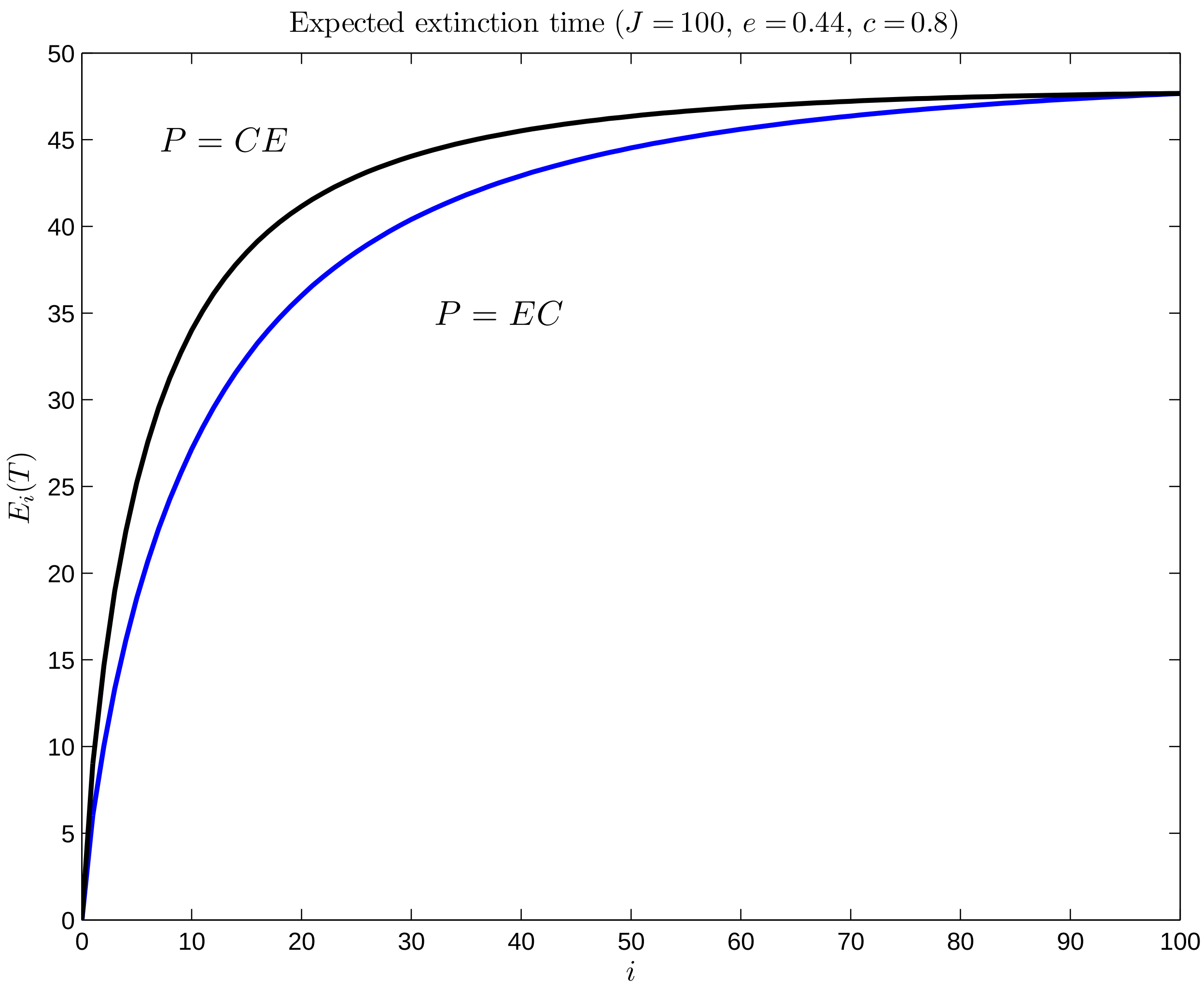
Extinction probability: vary *t*



Extinction probability: vary n_0



Expected extinction time: vary n_0



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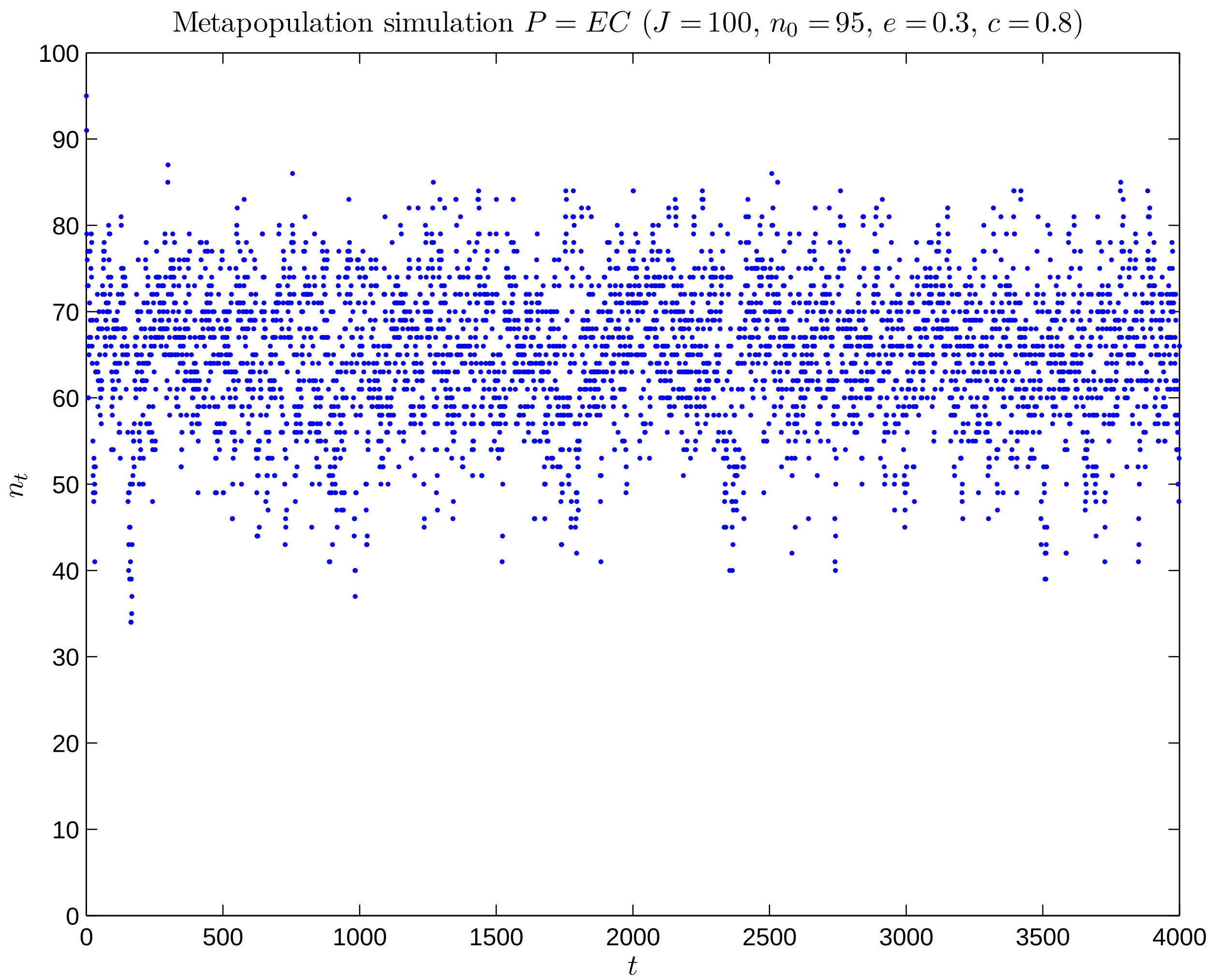

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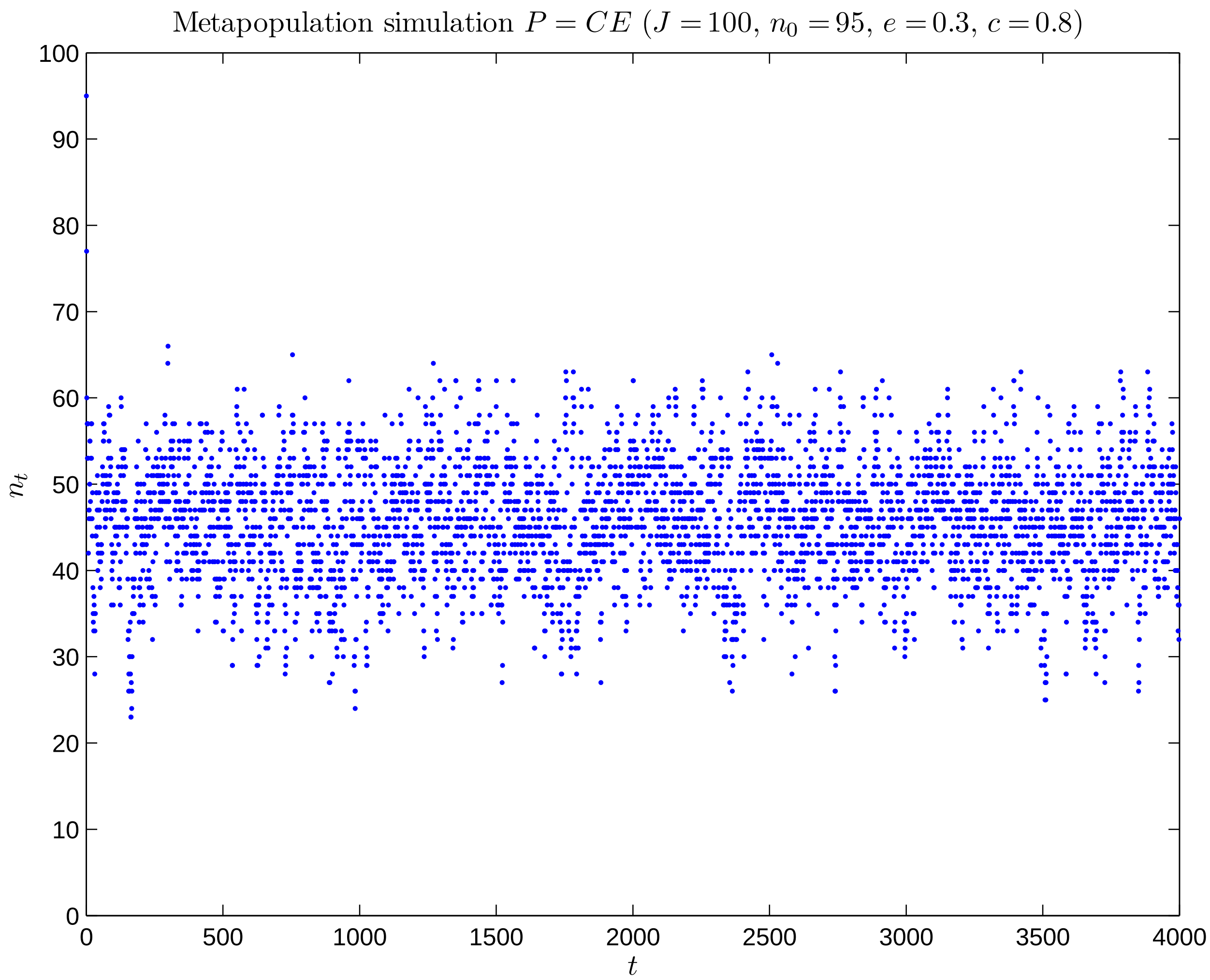

Quasi stationarity

We can model this behaviour using a *limiting conditional distribution* (lcd) $(m_j, j = 1, \ldots, J)$; often called a *quasi-stationary distribution* (qsd)*.

lcd:

$$\lim_{t \to \infty} \Pr(n_t = j | n_t \neq 0) = m_j.$$

qsd:

$$\Pr(n_0 = j) = m_j \implies \Pr(n_t = j | n_t \neq 0) = m_j \quad (\forall t > 0).$$

*In the infinite state space setting, the distinction between lcd and is both subtle and interesting.

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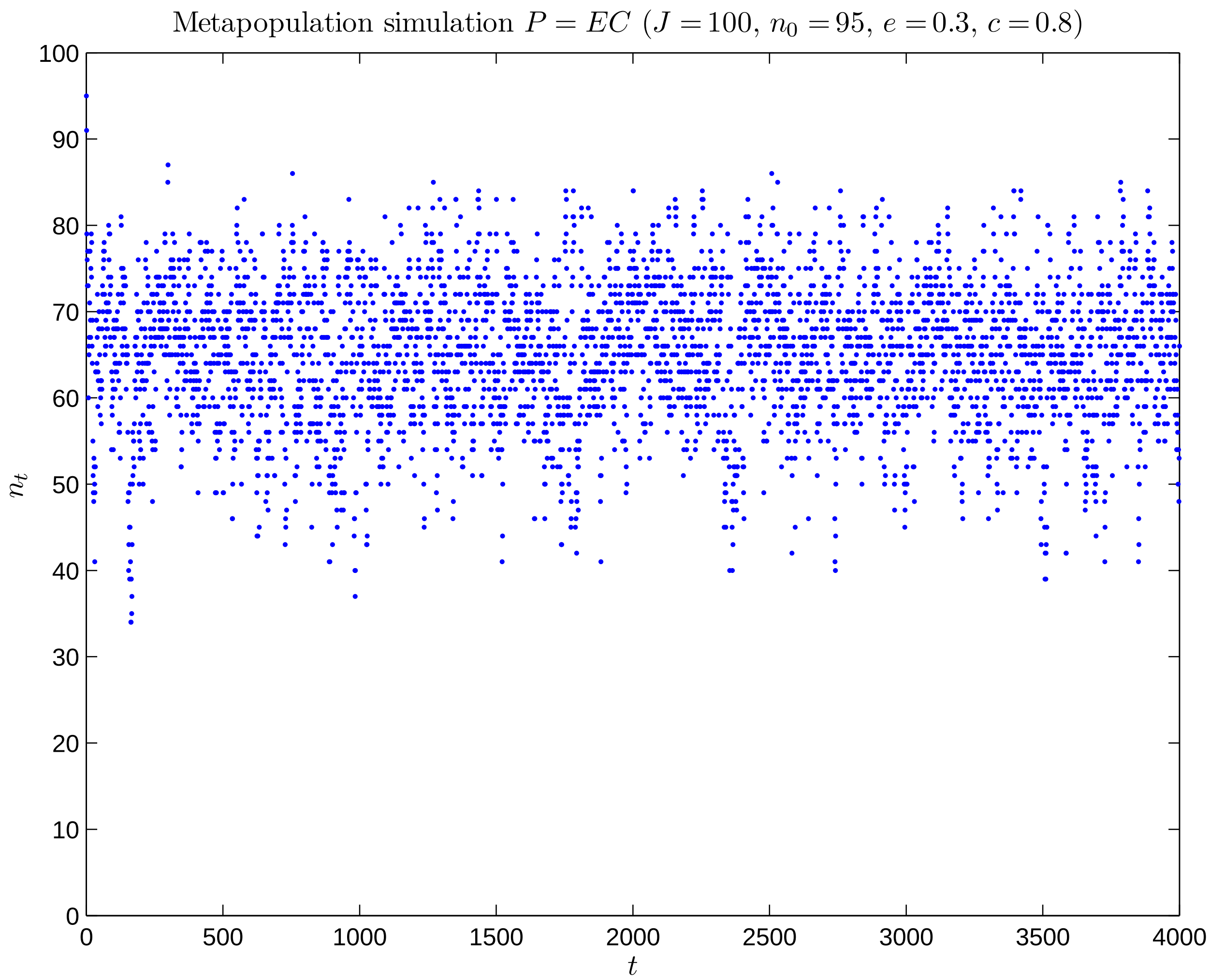
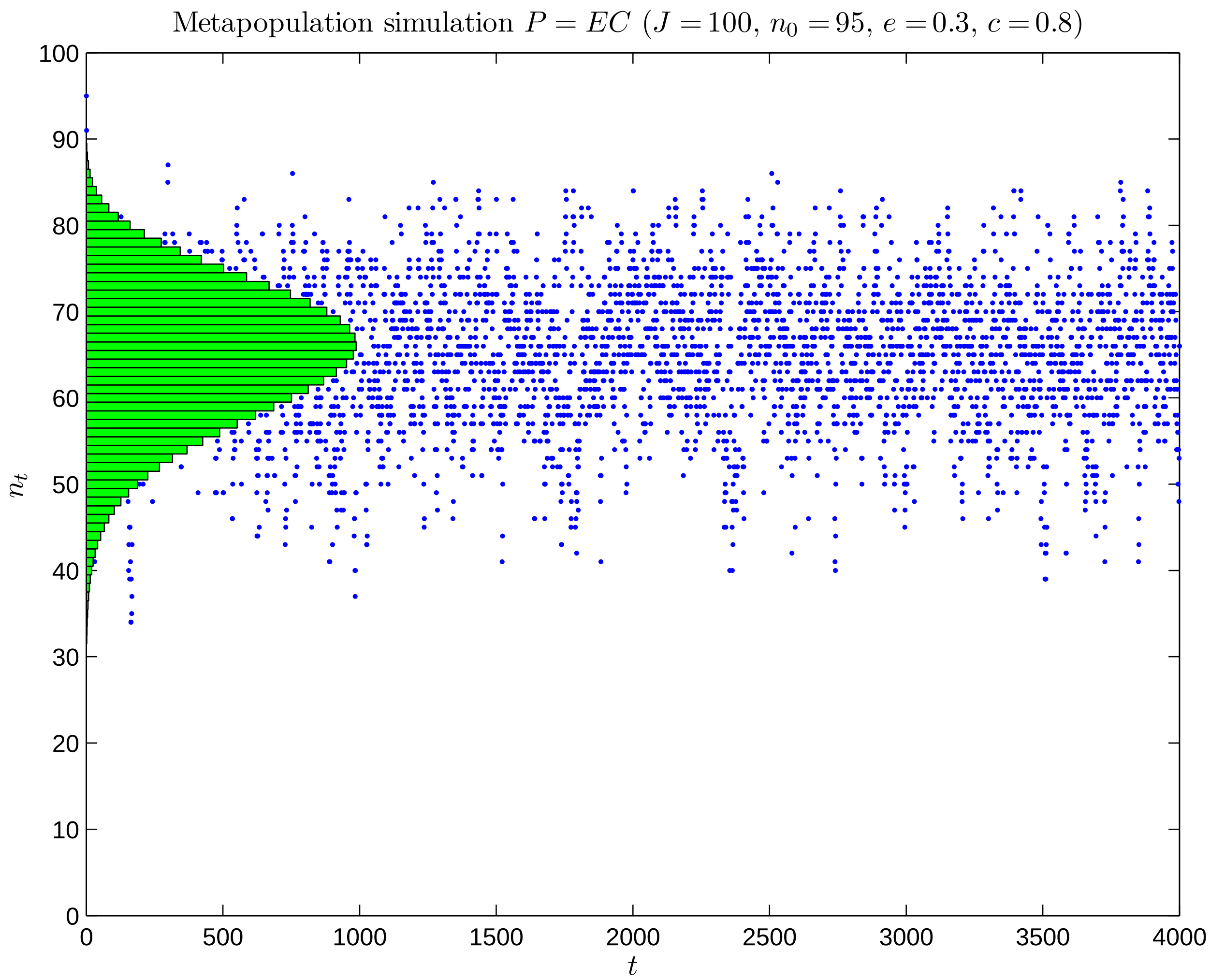


Simulation and qsd: $P = EC$



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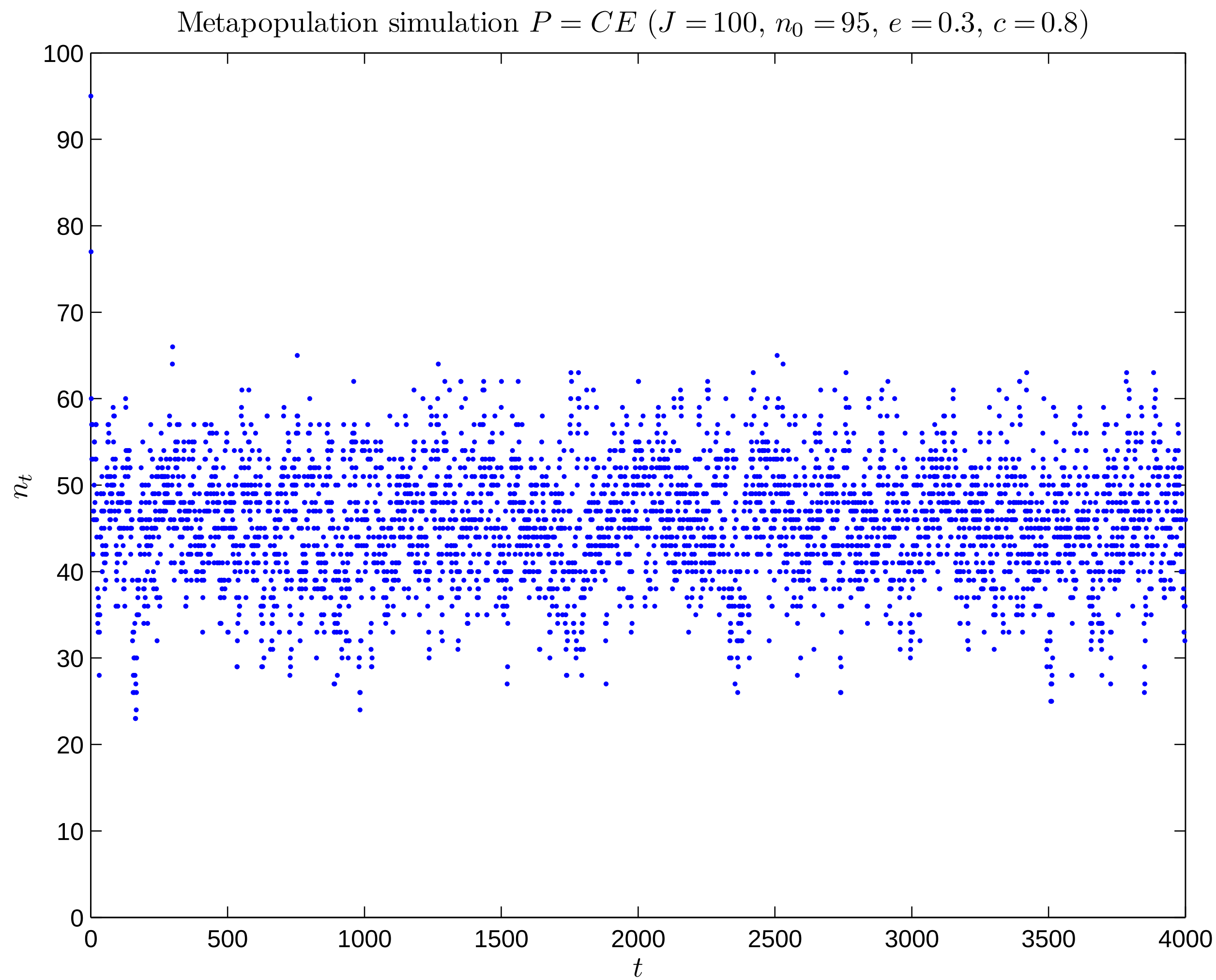

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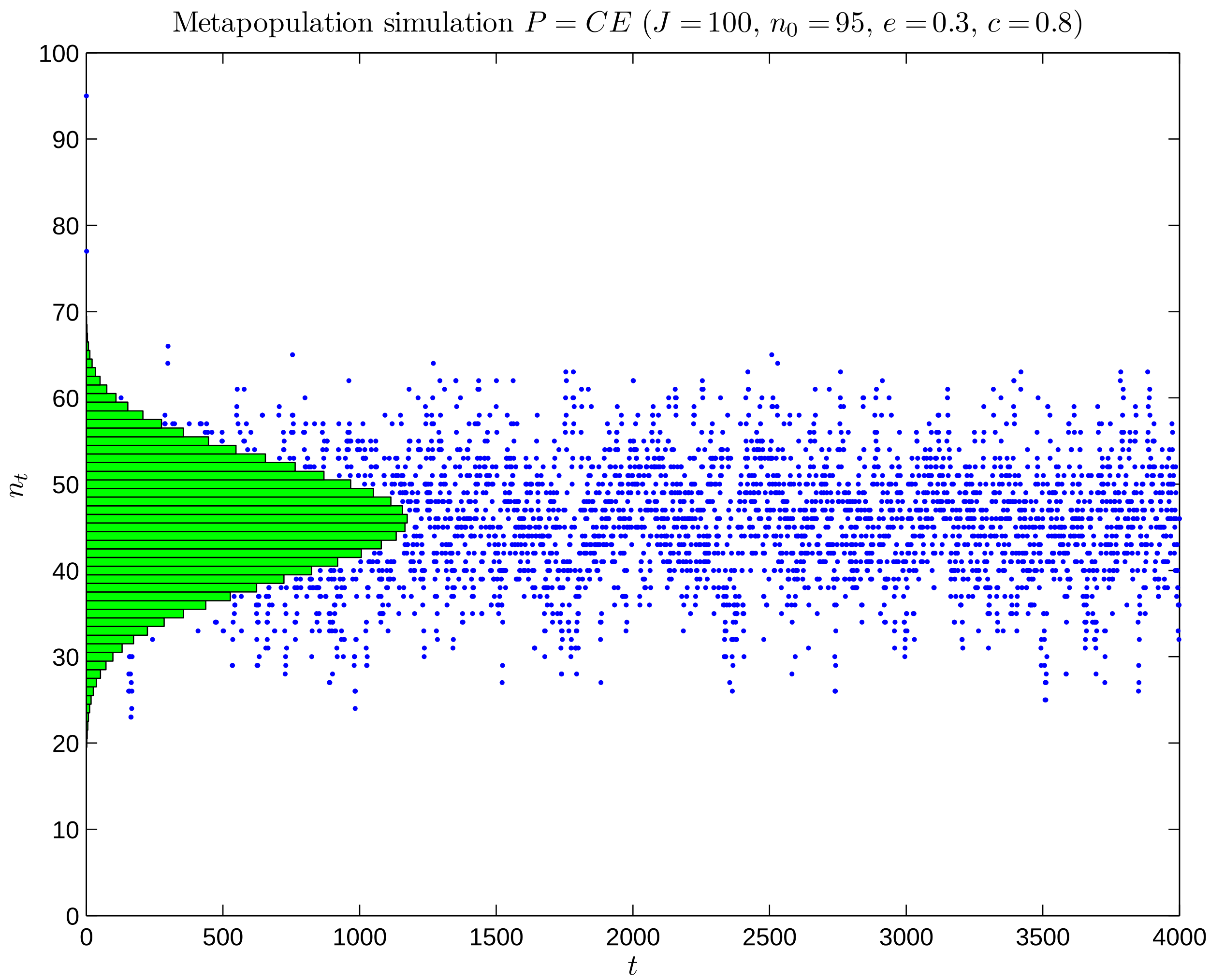

J-patch Mainland-Island models

In the extinction phase the number of extinctions when there are i patches occupied follows a *Bin*(i, e) law.

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This greatly simplifies the analysis!

J-patch Mainland-Island models

The behaviour of both models can be summarized in terms of a single pair of parameters (p, q):

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

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

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We can improve on this result ...

J-patch Mainland-Island models

Reparameterize by setting $a = p - q = (1 - e)(1 - c)$, being the *same* for both models ($0 < a < 1$), and $q^* = q/(1 - a)$. 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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J-patch Mainland-Island models

We have in particular that

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

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

and

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

$$(\to Jq^*(1-q^*) \text{ as } t \to \infty).$$

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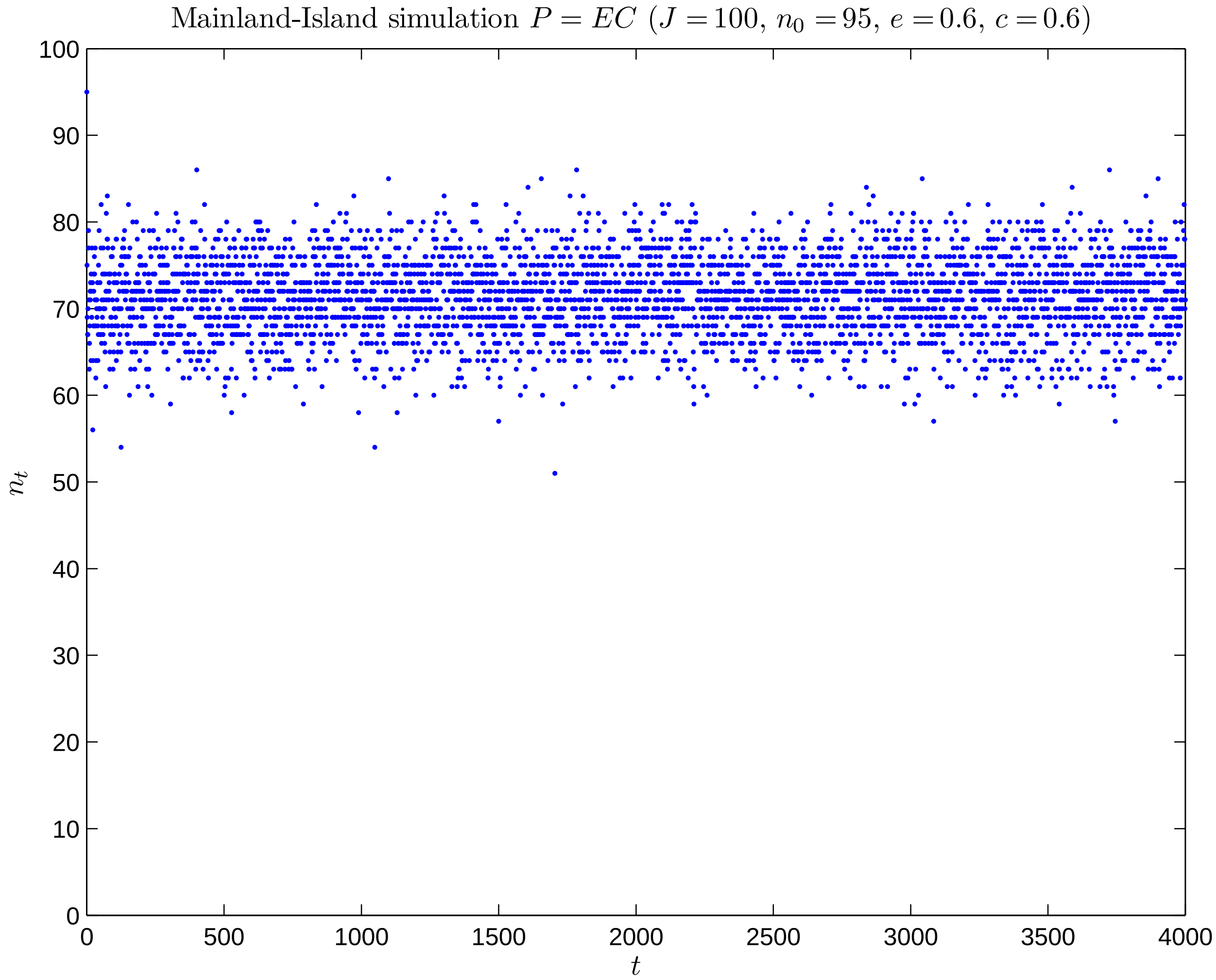

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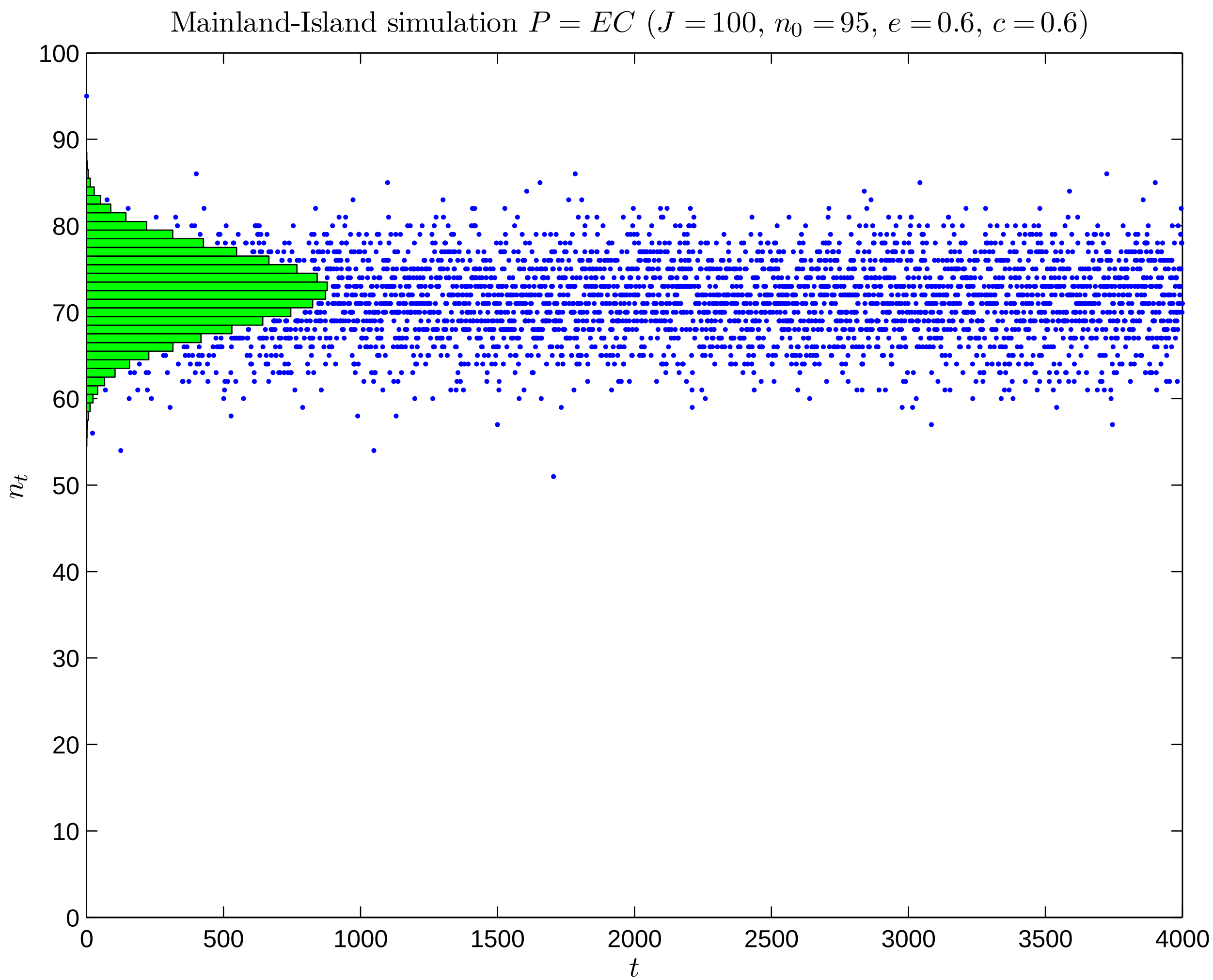

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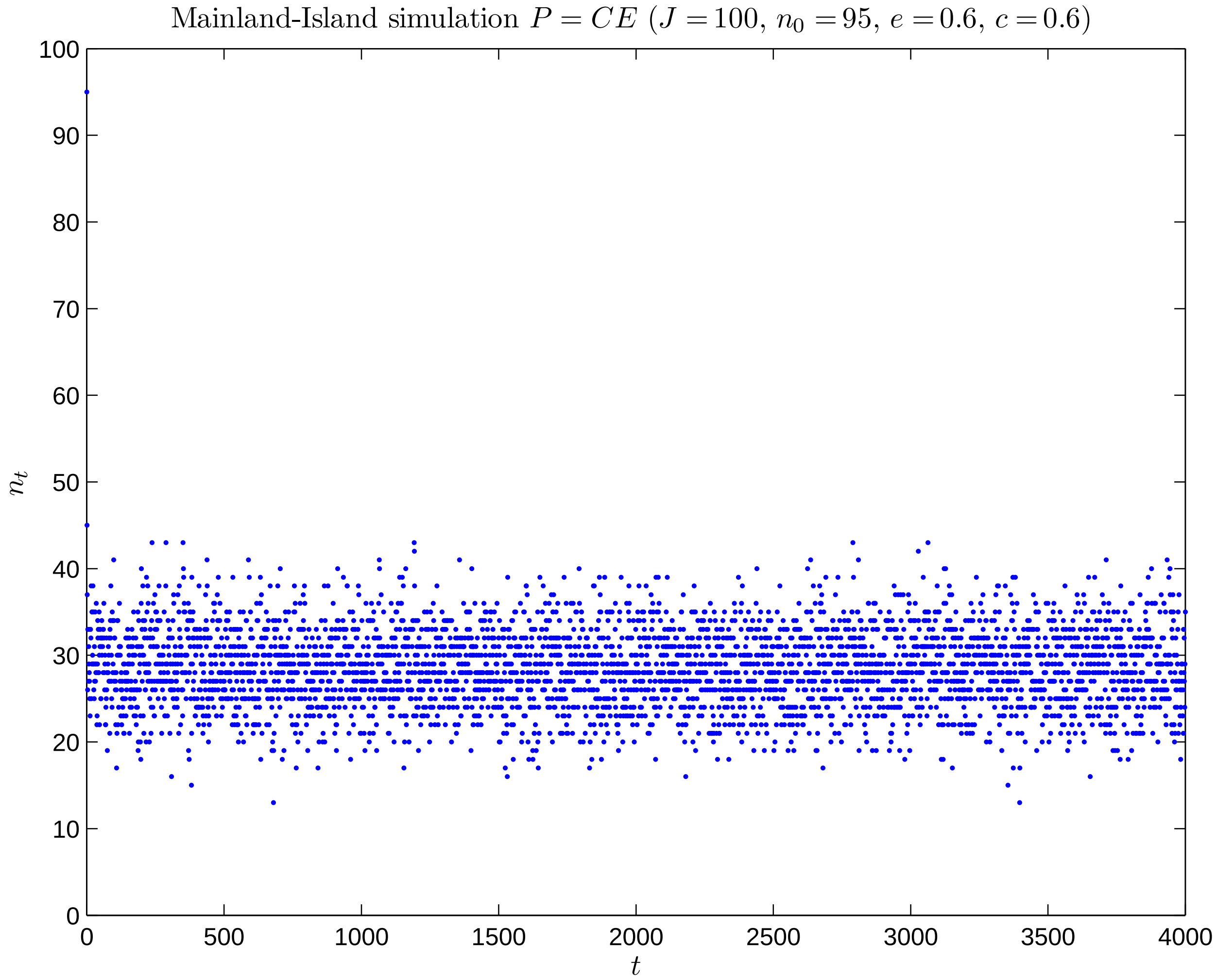

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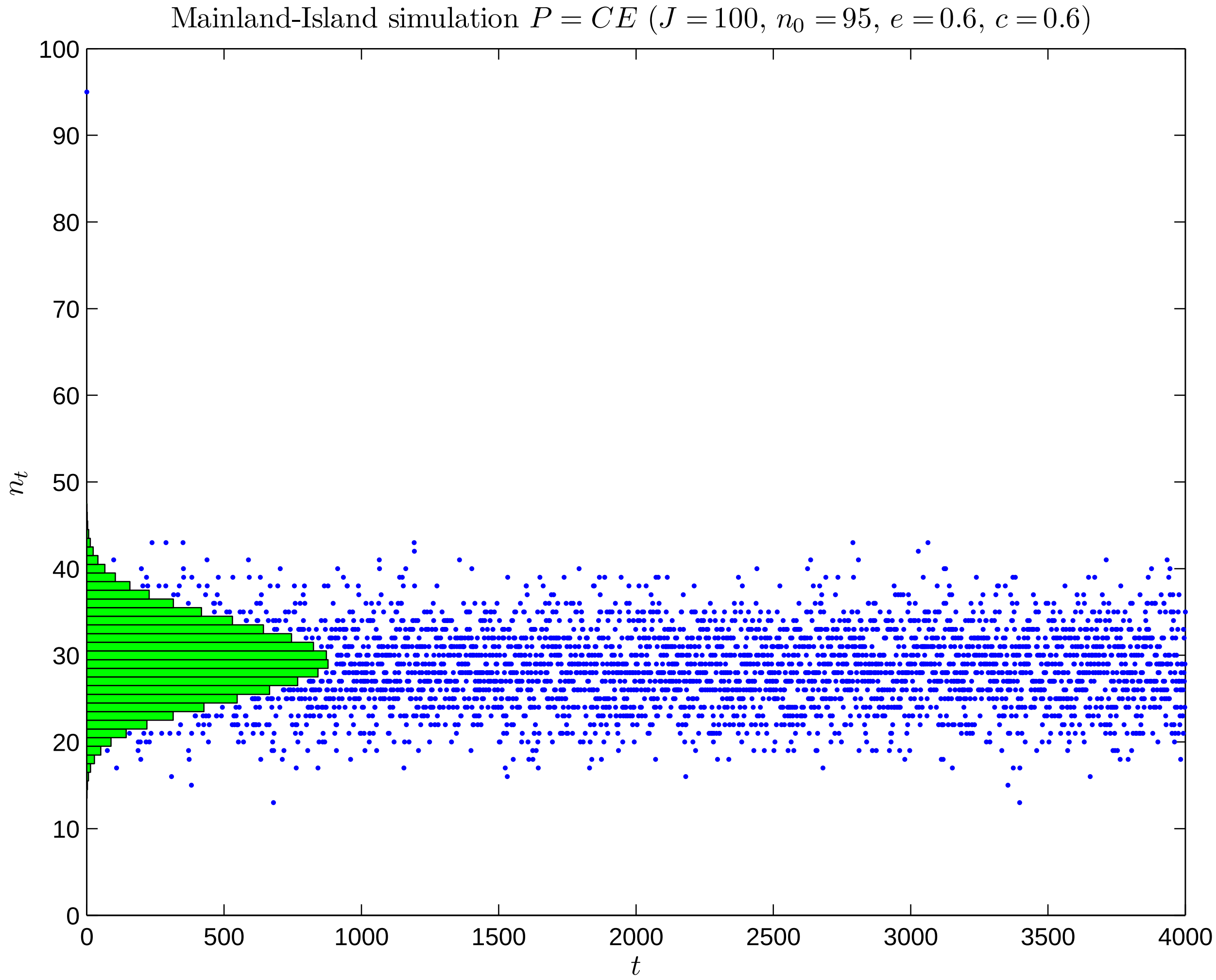

Infinite-patch Mainland-Island models

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Thus, the analogous infinite-patch model has $c_{ij} = 0$ for $j < i$ and $c_{ij} = \exp(-d) d^{j-i}/(j-i)!$ ($j = i, i+1, \ldots$).

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Note that in contrast with our earlier infinite-state models, state 0 is *no longer absorbing*.

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It is as if each of the i currently occupied patches remains occupied with probability $1 - e$ and a Poisson distributed number of unoccupied patches become occupied, the mean number being m (all patches being affected independently).

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Indeed we observe that ...

Proposition The process (n_t) is a Galton-Watson process with immigration: each occupied patch has a Bernoulli *Bin*$(1, 1-e)$ distributed number of offspring and in each generation there is a *Poisson*(m) number of immigrants. The mean number of offspring is $1-e$ (<1) and the mean number of immigrants is m $(<\infty)$.

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Again we can invoke general theory.

Infinite-patch Mainland-Island models

Theorem For the infinite-patch model with parameters e and m, given $n_0 = i$ patches occupied initially, the number n_t occupied at time t has the same distribution as $B_t + M_t$, where B_t and M_t are two *independent* random variables with $B_t \sim$ *Bin*$(i, (1-e)^t)$ and $M_t \sim$ *Poisson*(m_t), where $m_t = (m/e)(1-(1-e)^t)$. The limiting distribution of n_t is *Poisson*(m/e).

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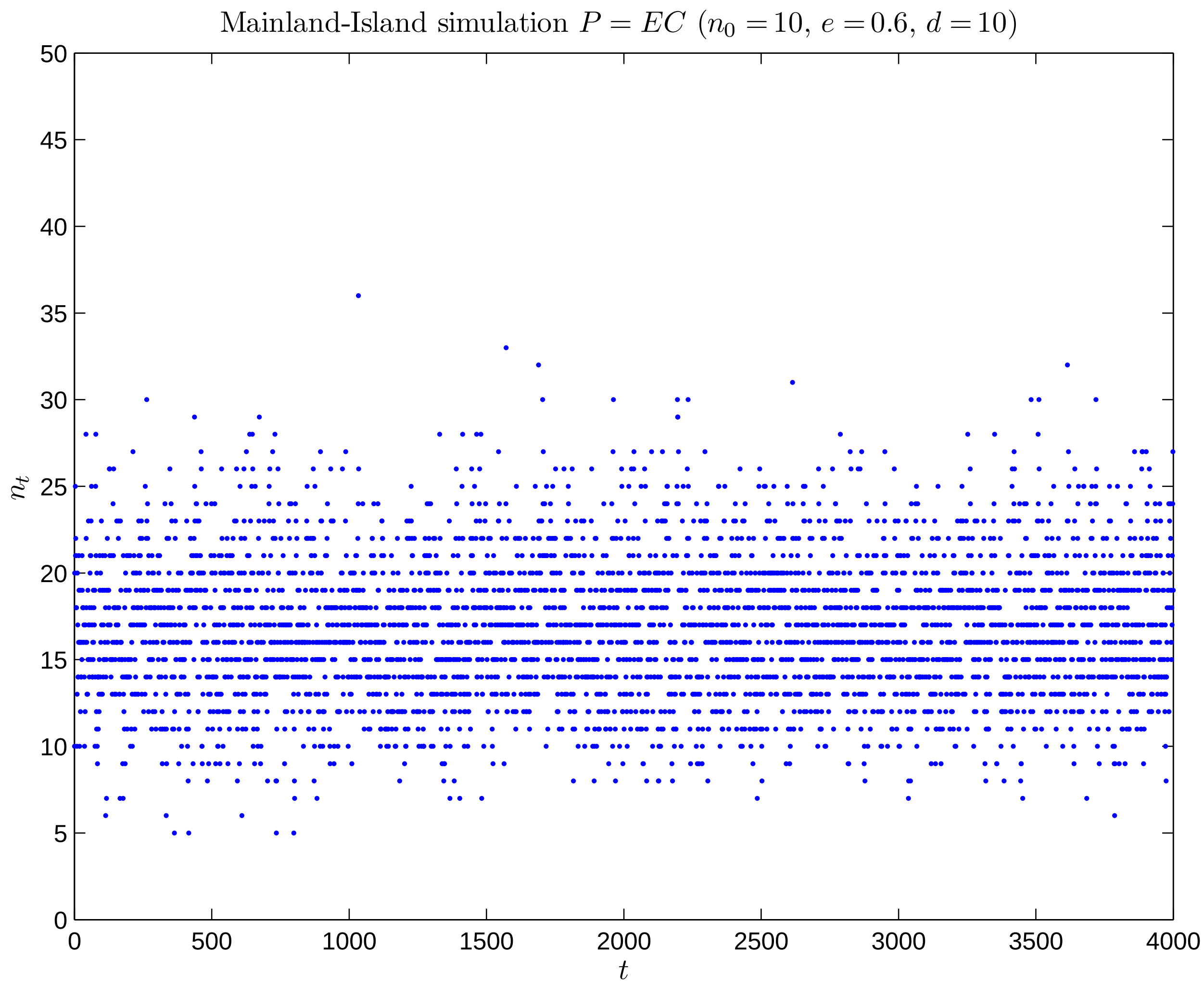

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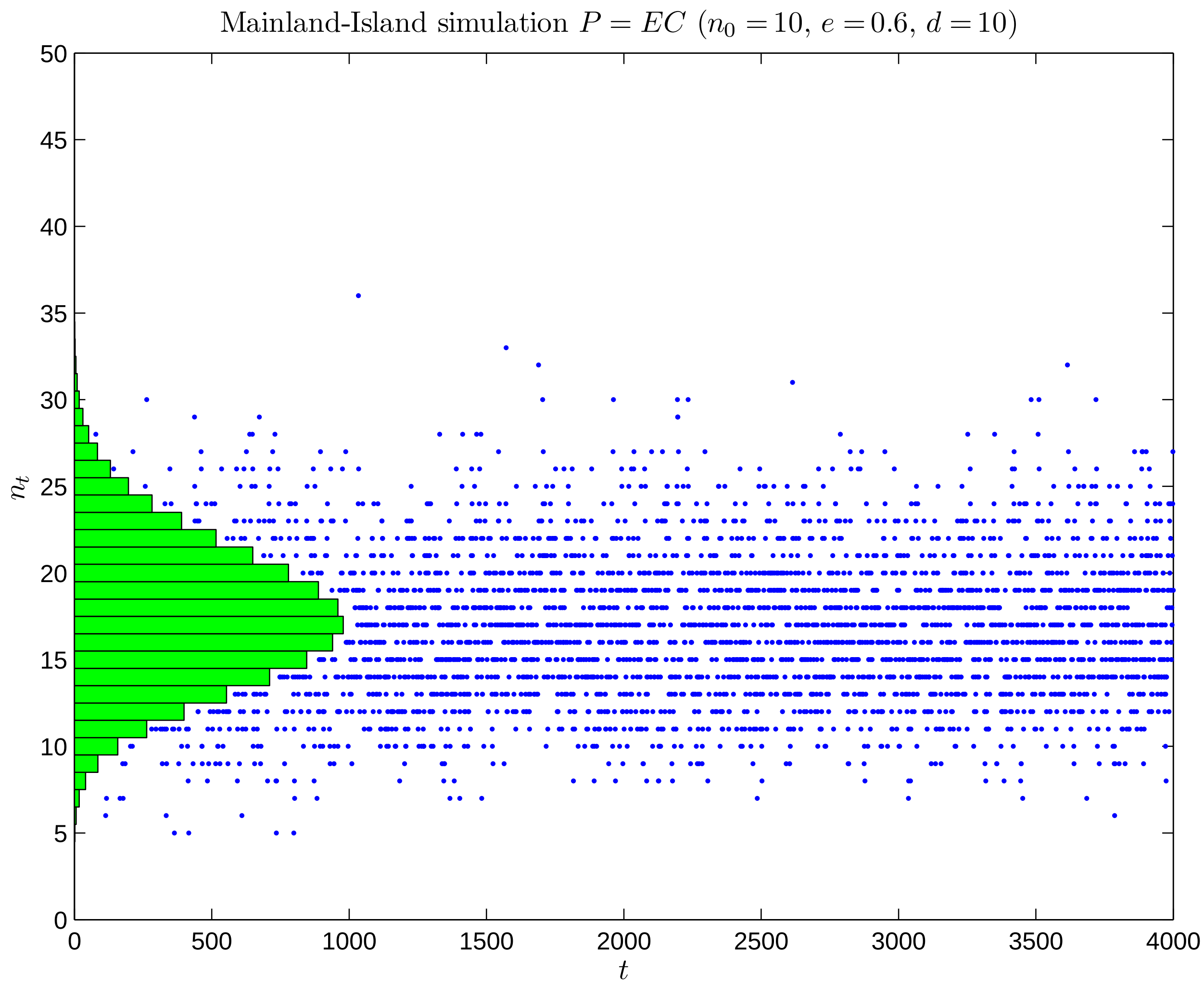

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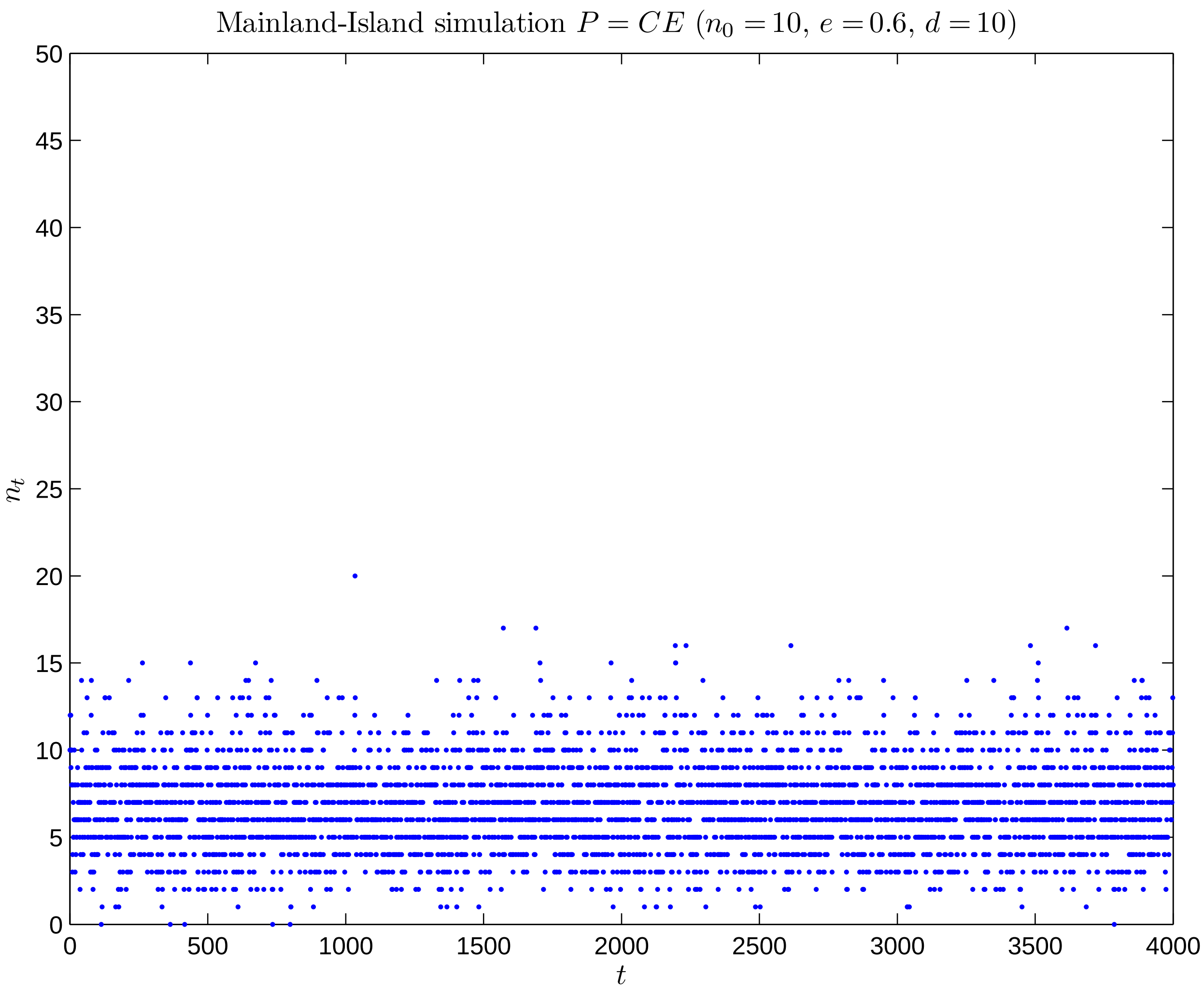

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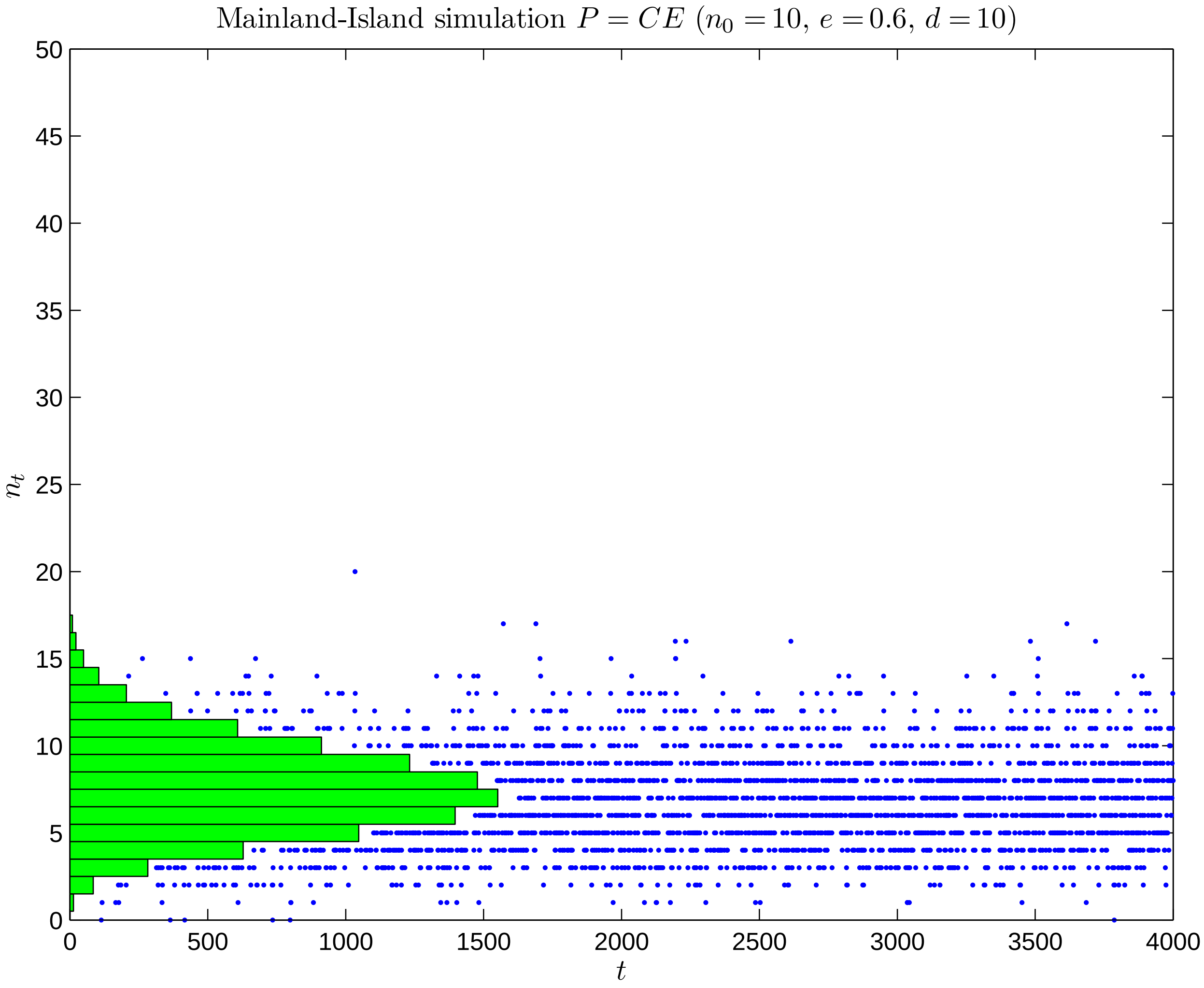

First passage times

A measure of persistence for the Mainland-Island models is the expected time to *first* total extinction of the *island network*.

First passage times

Theorem For the J-patch Mainland-Island model with parameters p and q, given $n_0 = i$ patches occupied initially, the expected time to first enter state 0 is given by

$$\mu_{i0} = \sum_{k=1}^{J} \binom{J}{k} \frac{b^k}{1-a^k} - \sum_{j=0}^{i} \binom{i}{j} (-1)^j \sum_{k=0}^{J-i} \binom{J-i}{k} \frac{b^k (1 - \delta_{j0}\delta_{k0})}{1 - a^{j+k}}$$

$$= \sum_{n=0}^{\infty} \left[(1+ba^n)^J - (1-a^n)^i (1+ba^n)^{J-i} \right],$$

where $a = p - q$ and $b = q/(1-p)$.

First passage times

Theorem For the infinite-patch Mainland-Island model with parameters e and m, given $n_0 = i$ patches occupied initially, the expected time to first enter state 0 is always *finite* and is given by

$$\mu_{i0} = \sum_{j=1}^{i} \binom{i}{j} (-1)^{j+1} \sum_{n=0}^{\infty} (1-e)^{jn} \exp\left(\frac{m}{e}(1-e)^n\right)$$

$$= \sum_{n=0}^{\infty} [1 - (1 - (1-e)^n)^i] \exp\left(\frac{m}{e}(1-e)^n\right).$$