The limiting behaviour of a patch occupancy model

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AUSTRALIAN RESEARCH COUNCIL
Centre of Excellence for Mathematics
and Statistics of Complex Systems

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Department of Mathematics
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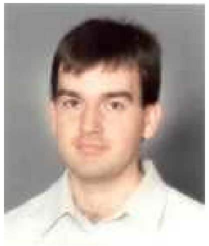


McVinish, R. and Pollett, P.K. (2010) Limits of large metapopulations with patch dependent extinction probabilities. Adv. Appl. Probab. 42, 1172-1186.

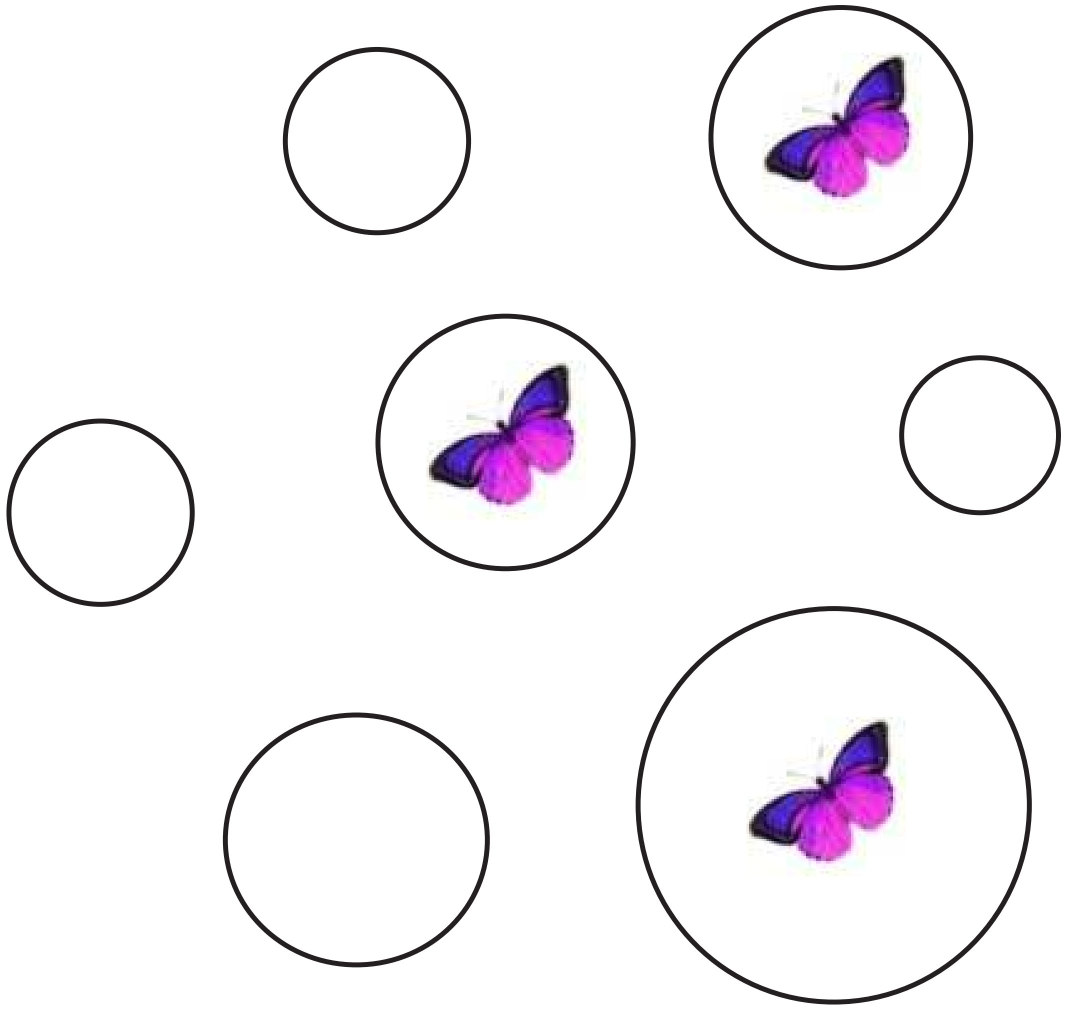
McVinish, R. and Pollett, P.K. (2011) The limiting behaviour of a mainland-island metapopulation. J. Math. Biol. To appear.

McVinish, R. and Pollett, P.K. (2013) Interaction between habitat quality and an Allee-like effect in metapopulations. Ecological Modelling. To appear.

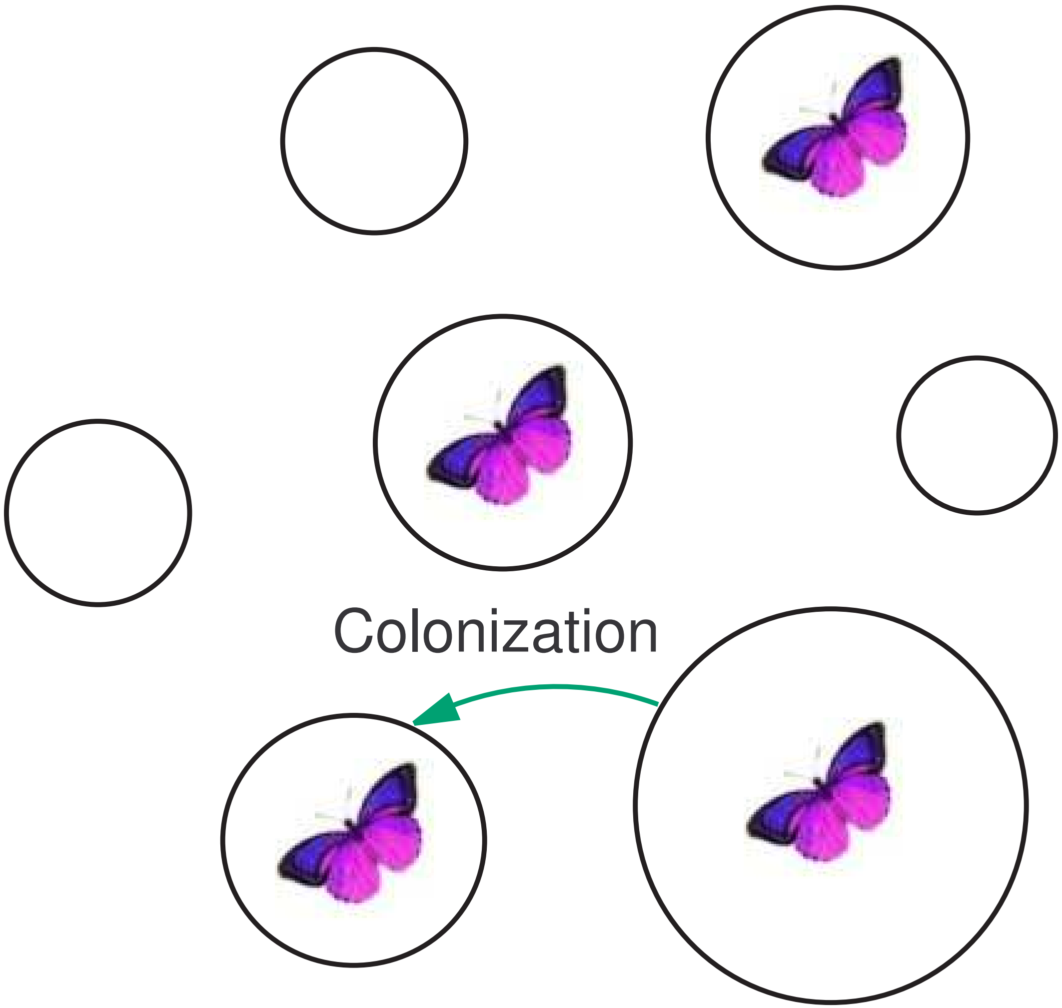
McVinish, R. and Pollett, P.K. (2013) The limiting behaviour of a stochastic patch occupancy model. J. Math. Biol. Under revision.

McVinish, R. and Pollett, P.K. The limiting behaviour of Hanski's incidence function metapopulation model. Submitted.

Metapopulations



Metapopulations



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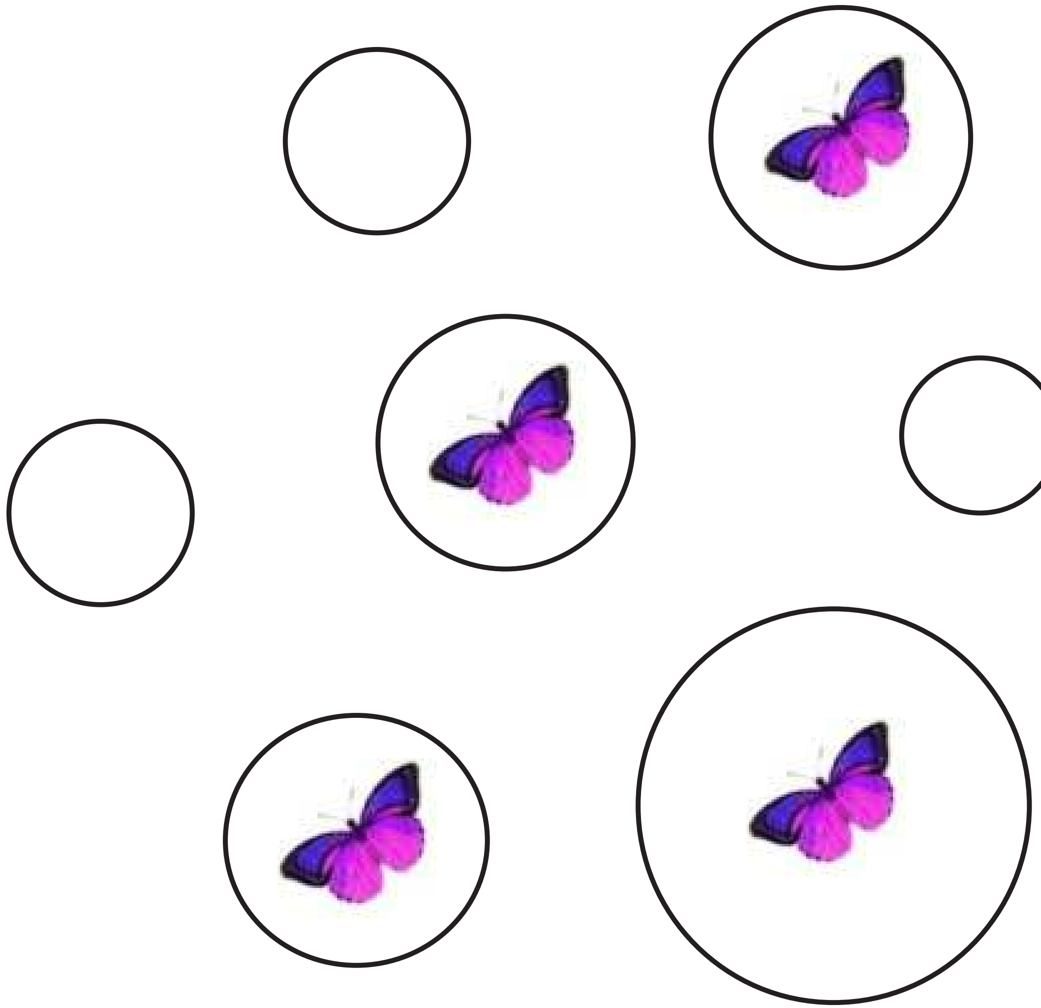

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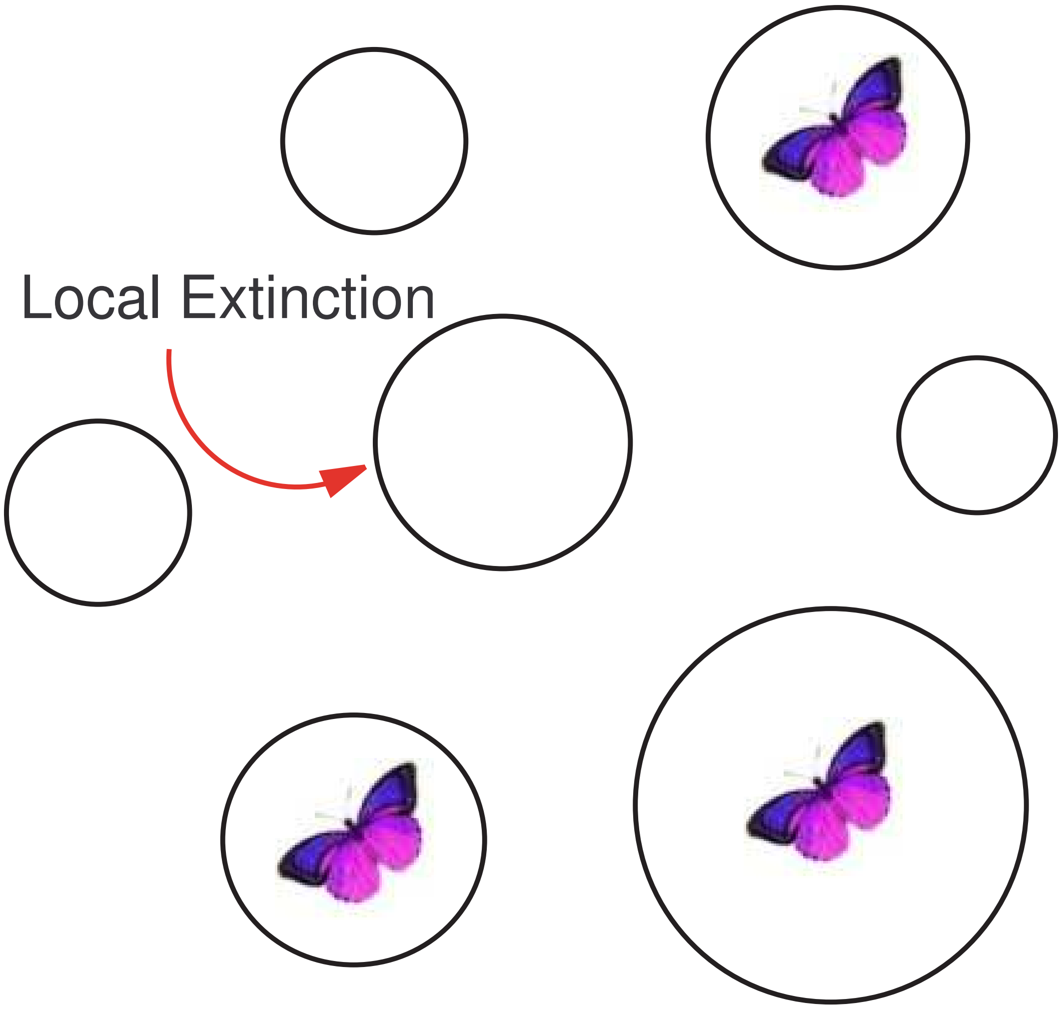

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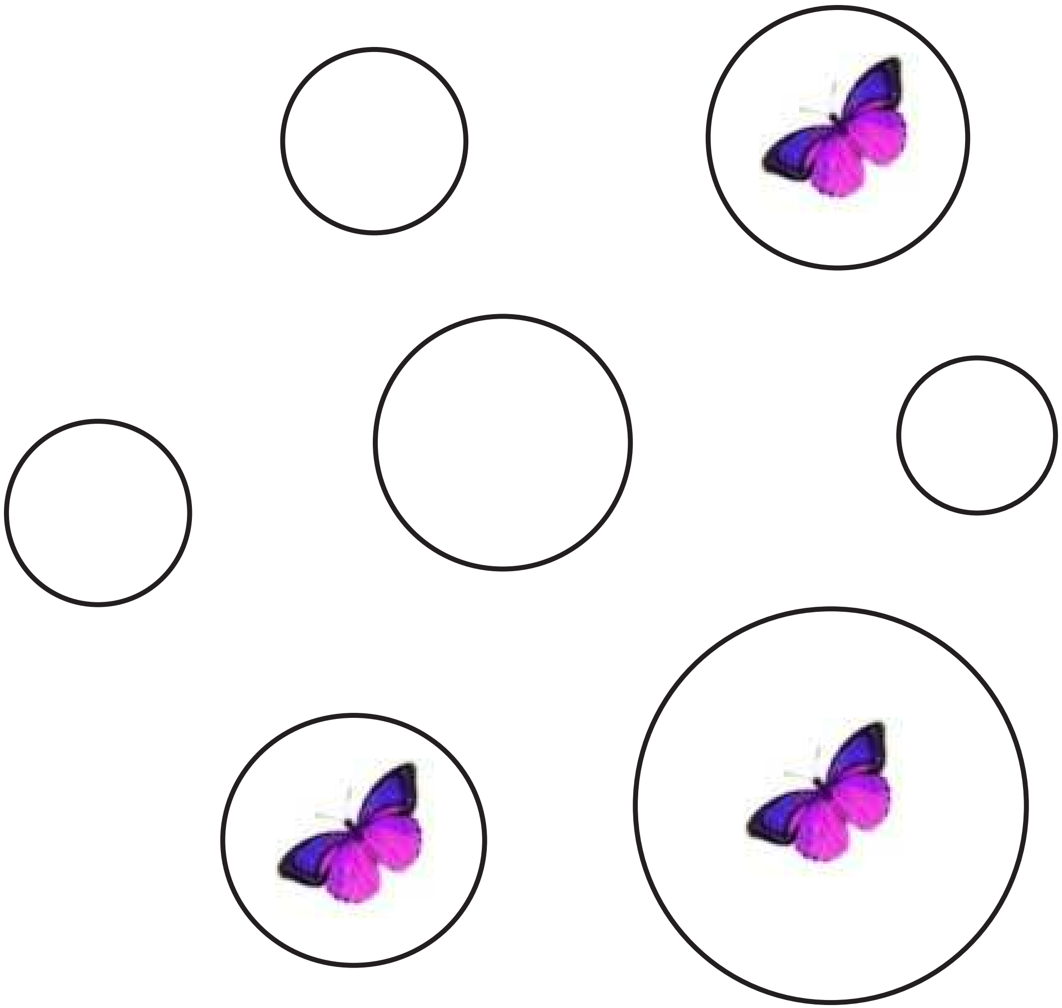

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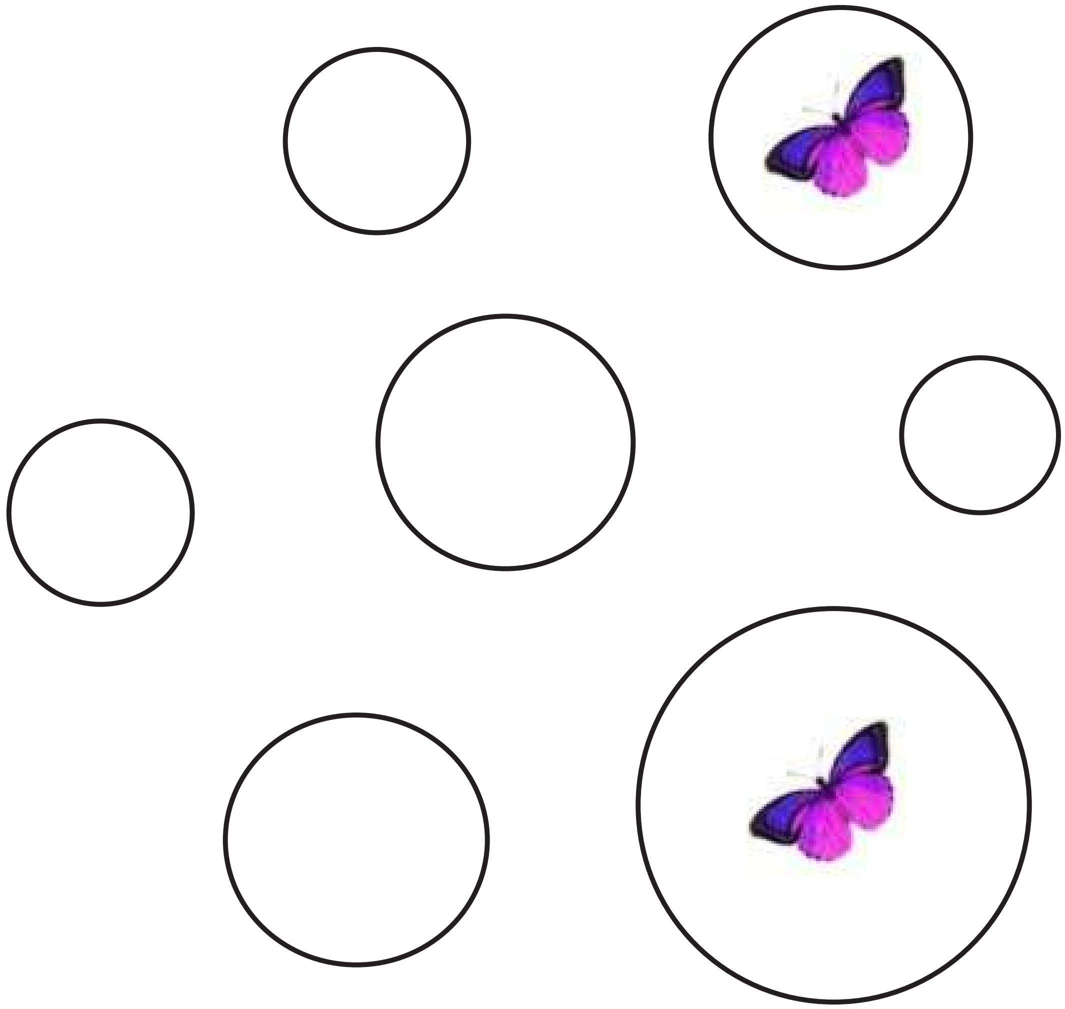

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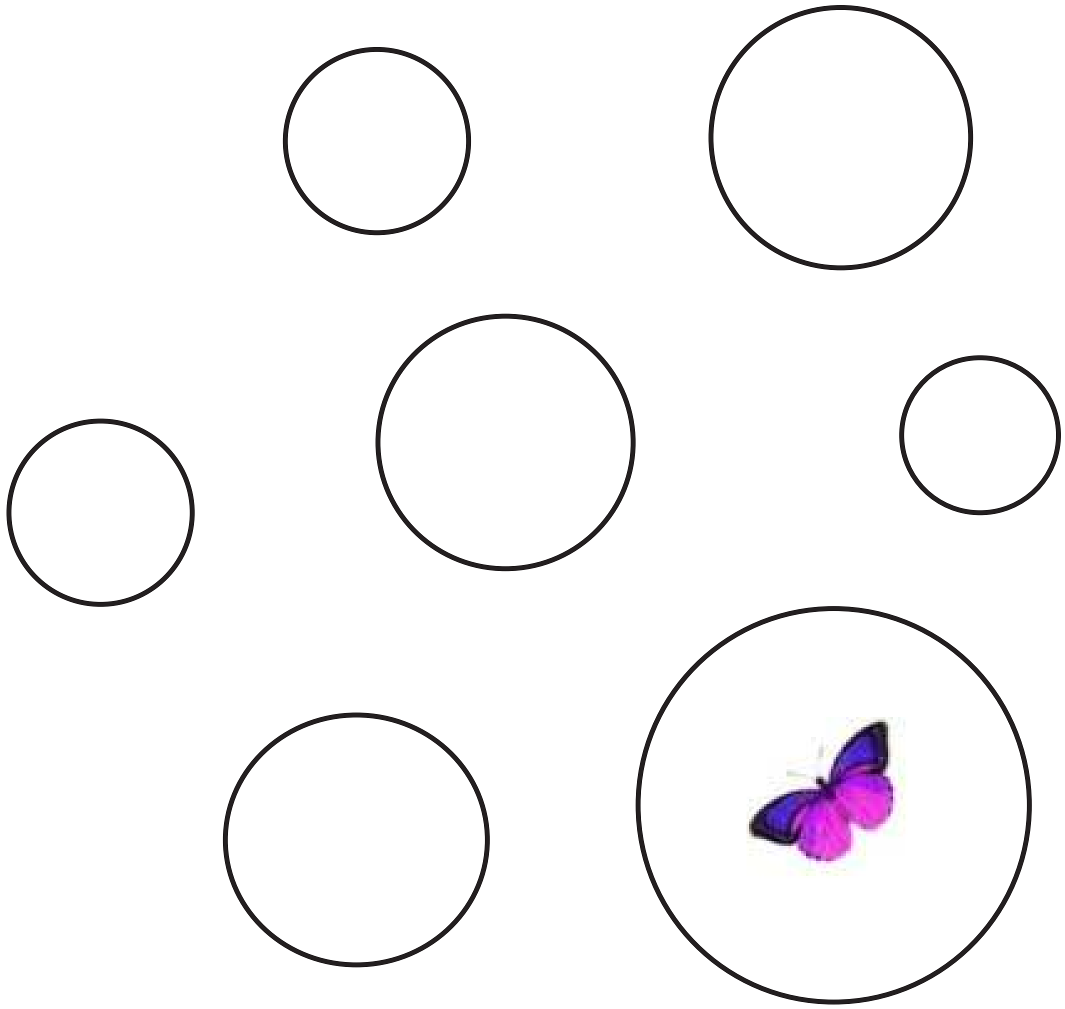

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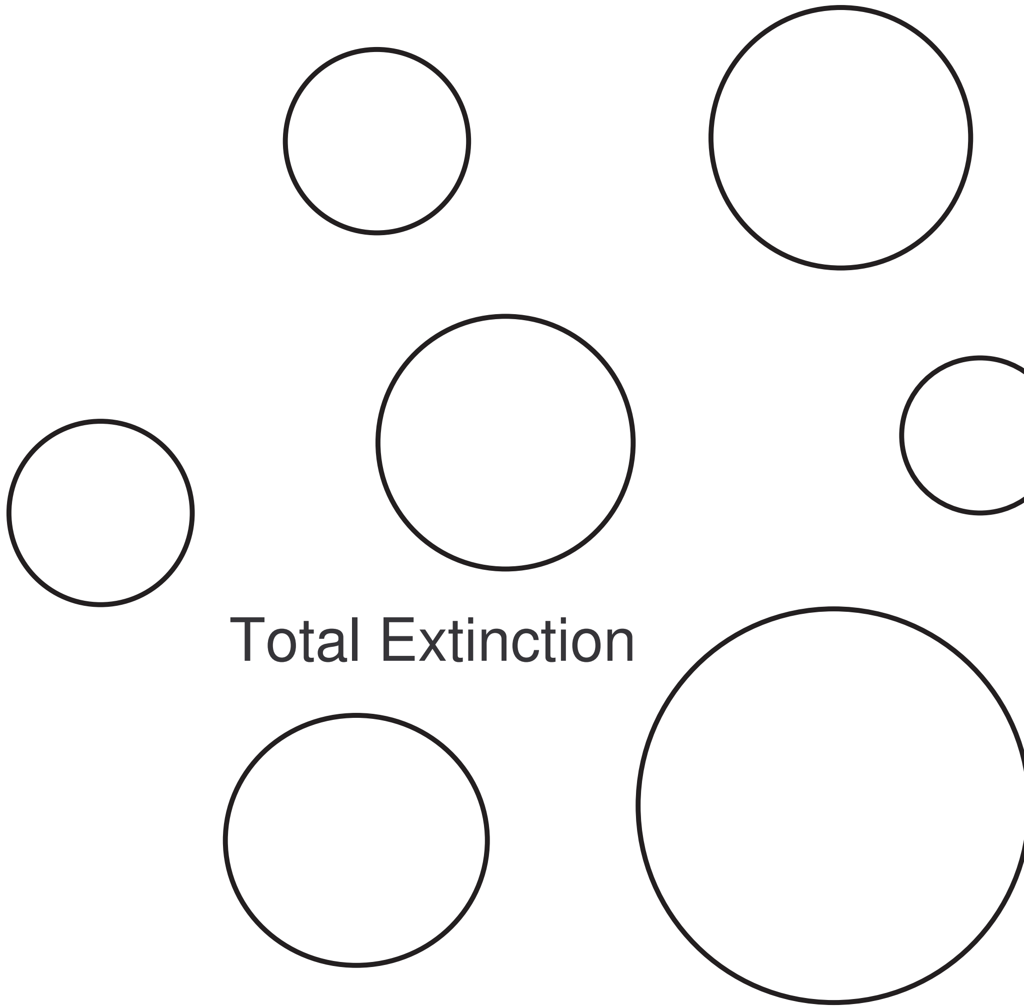

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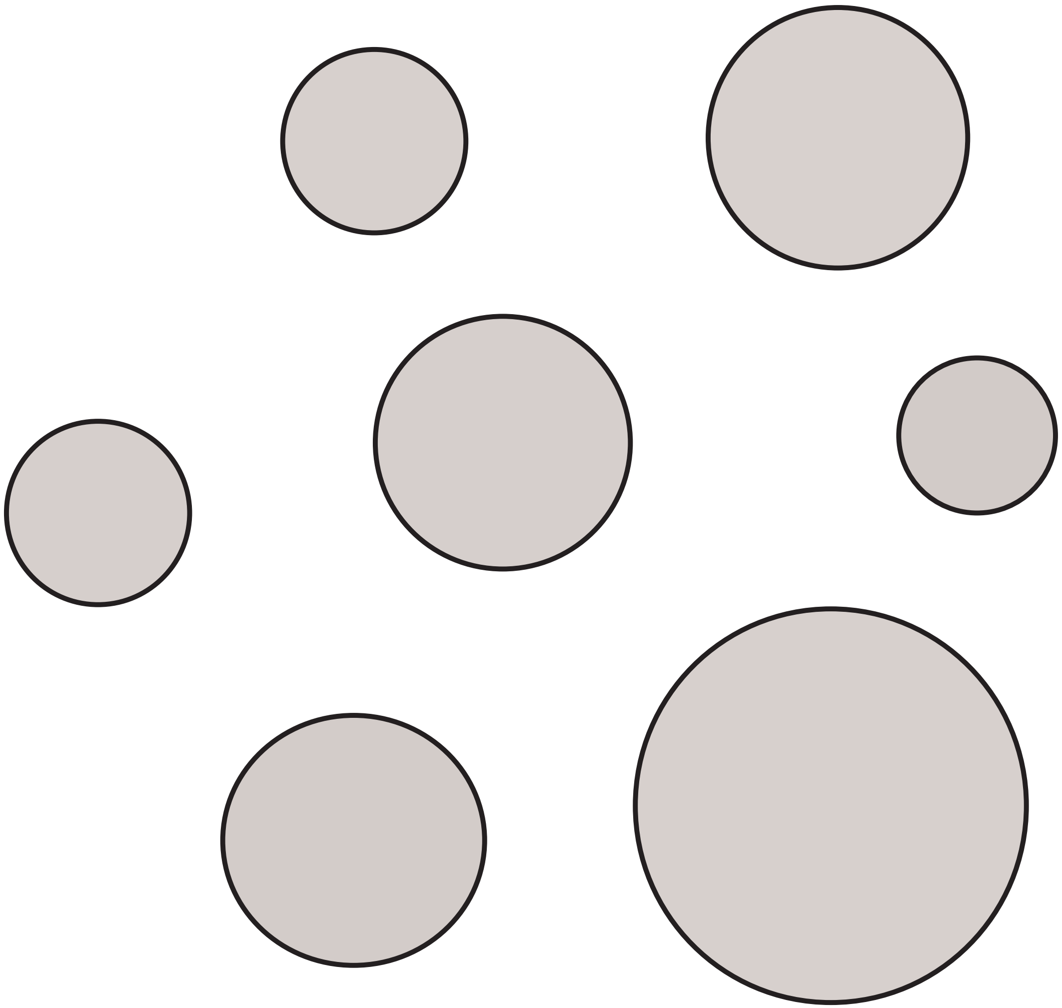
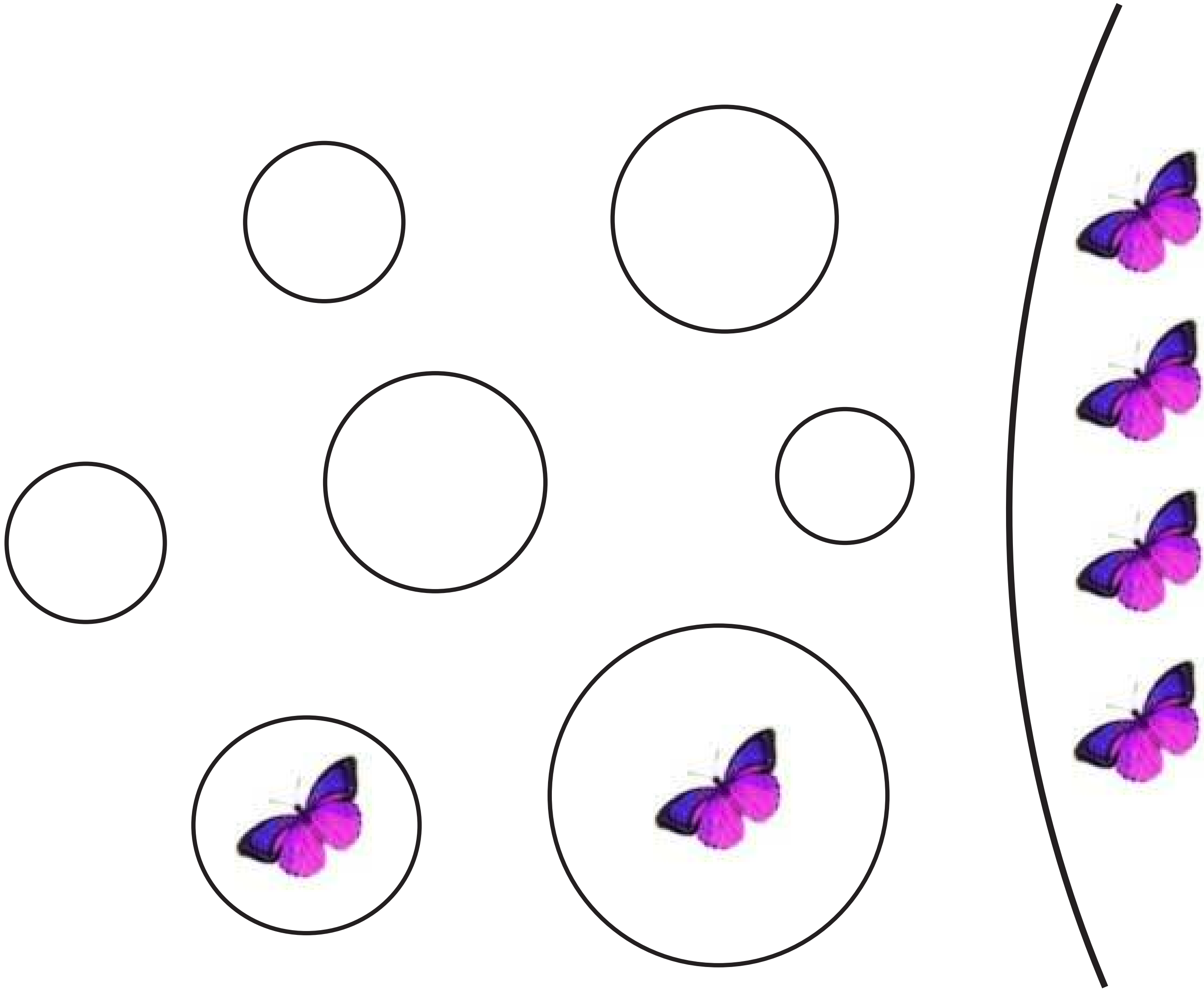


Mainland-island configuration



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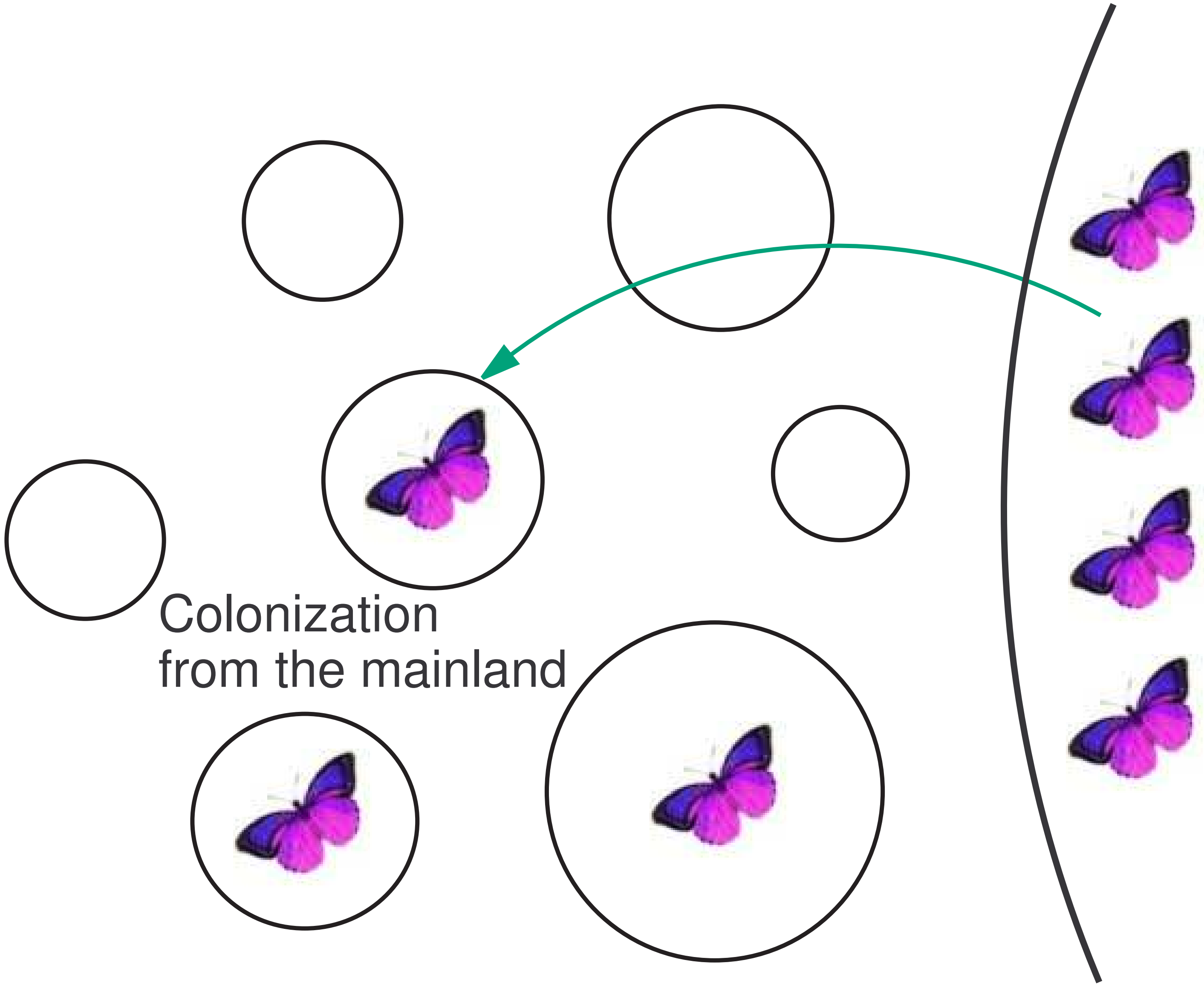

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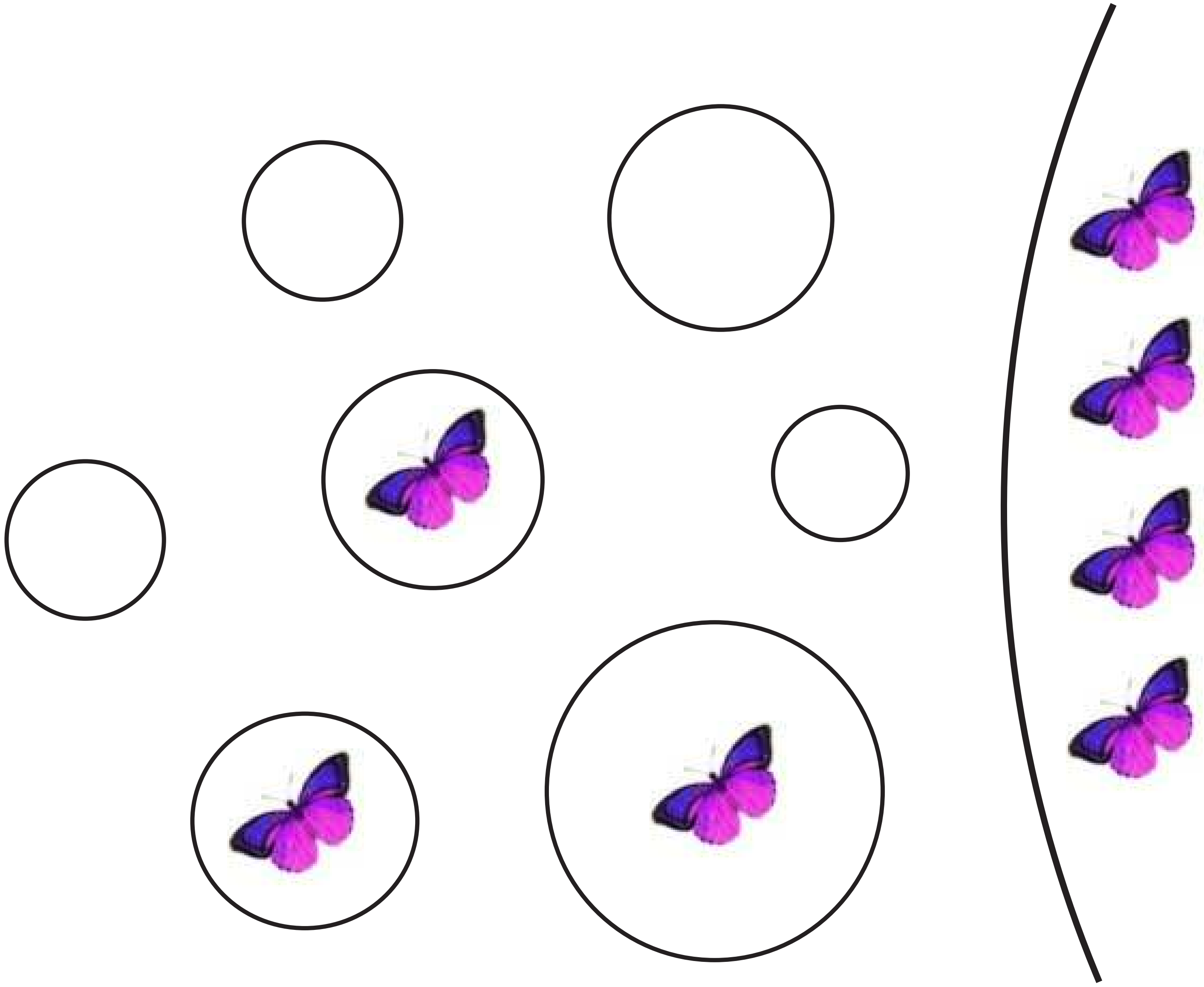

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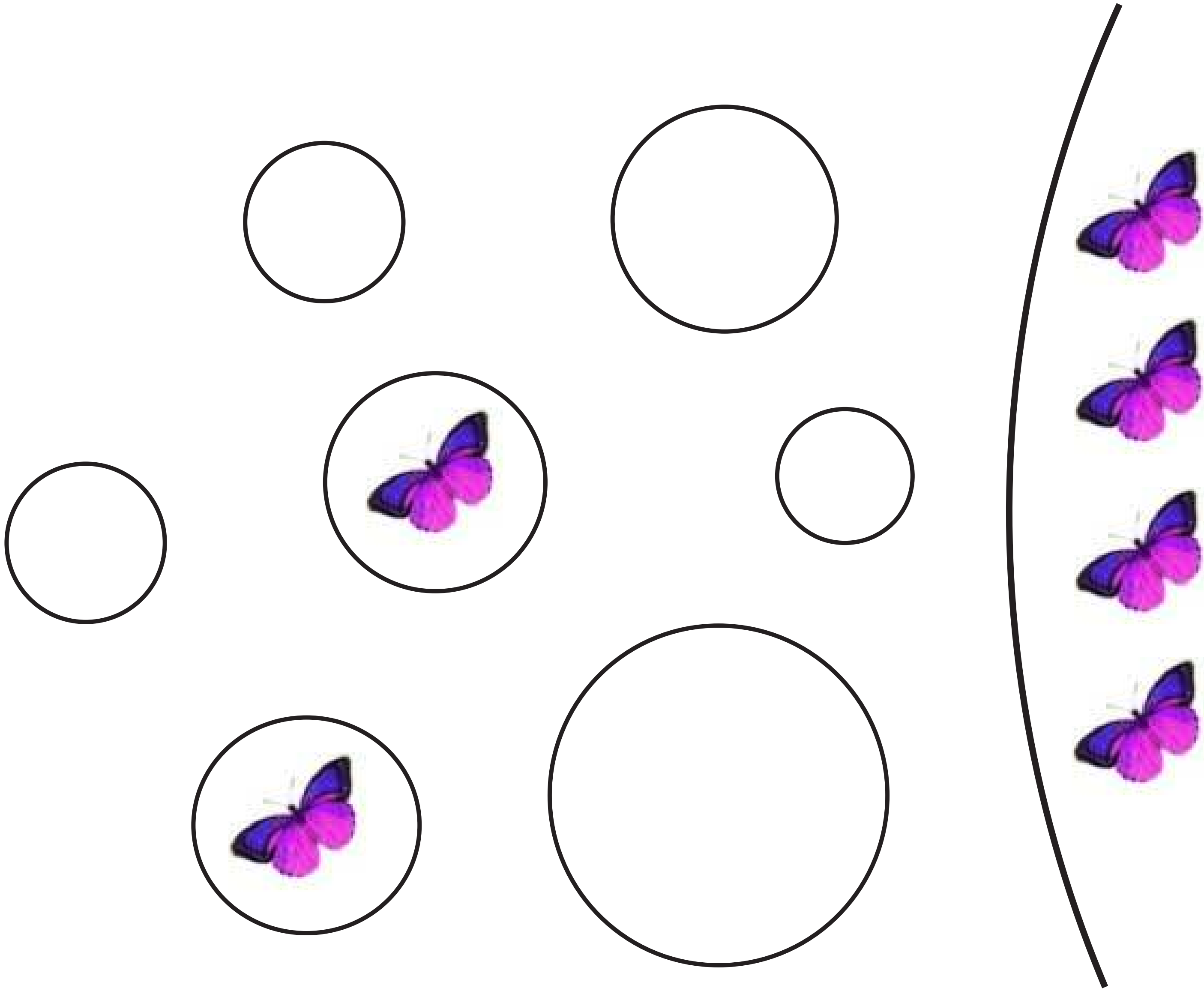

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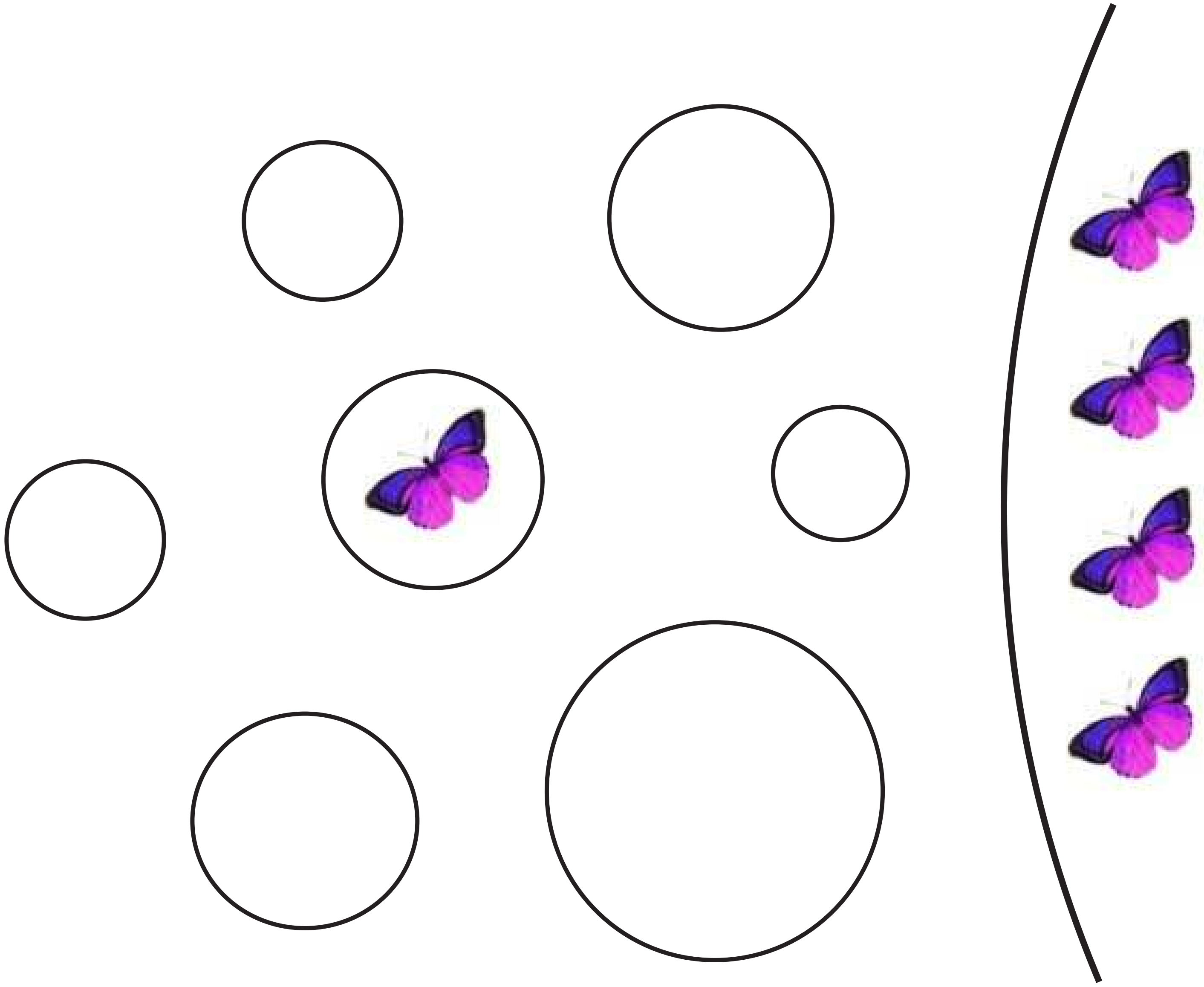

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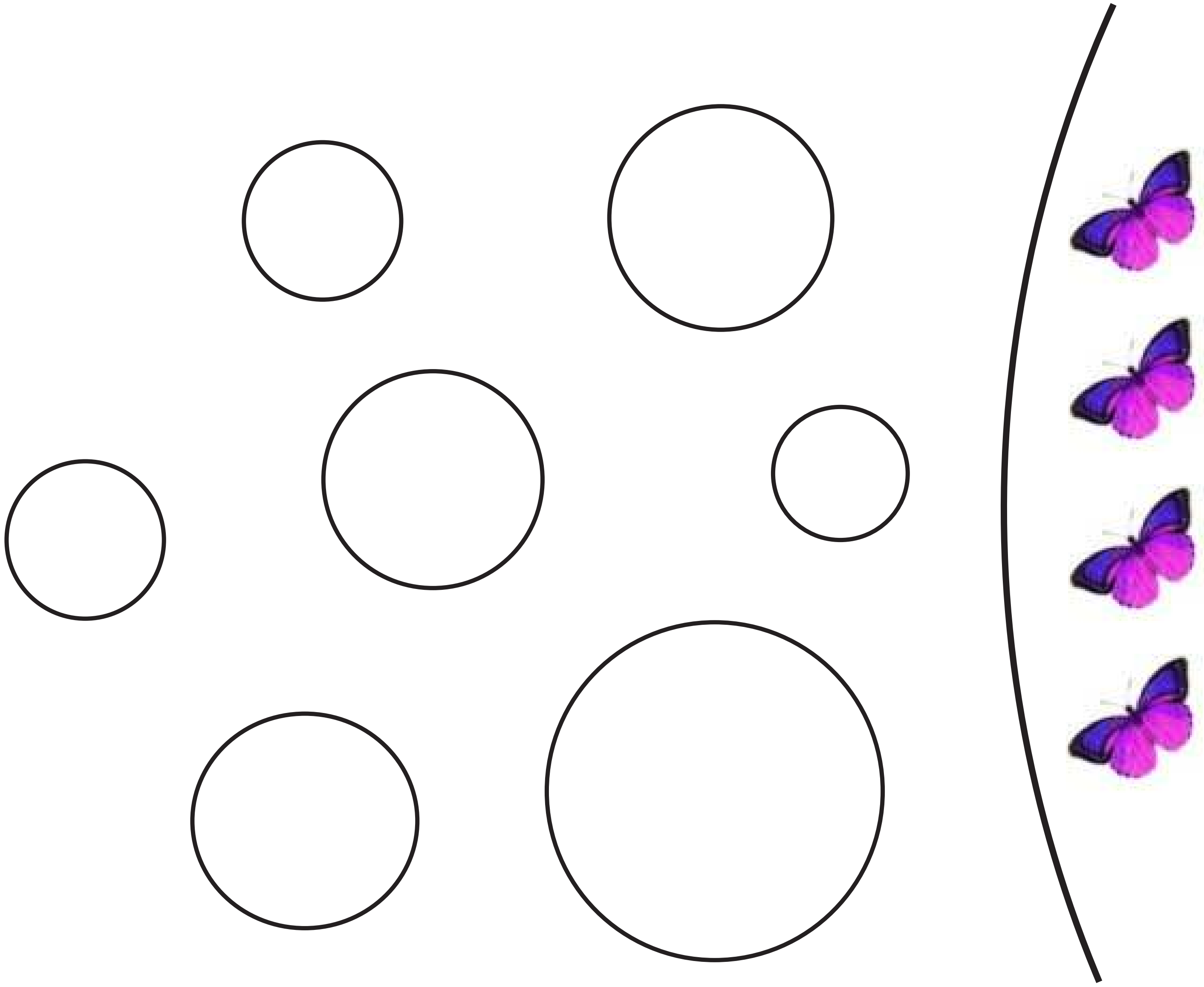

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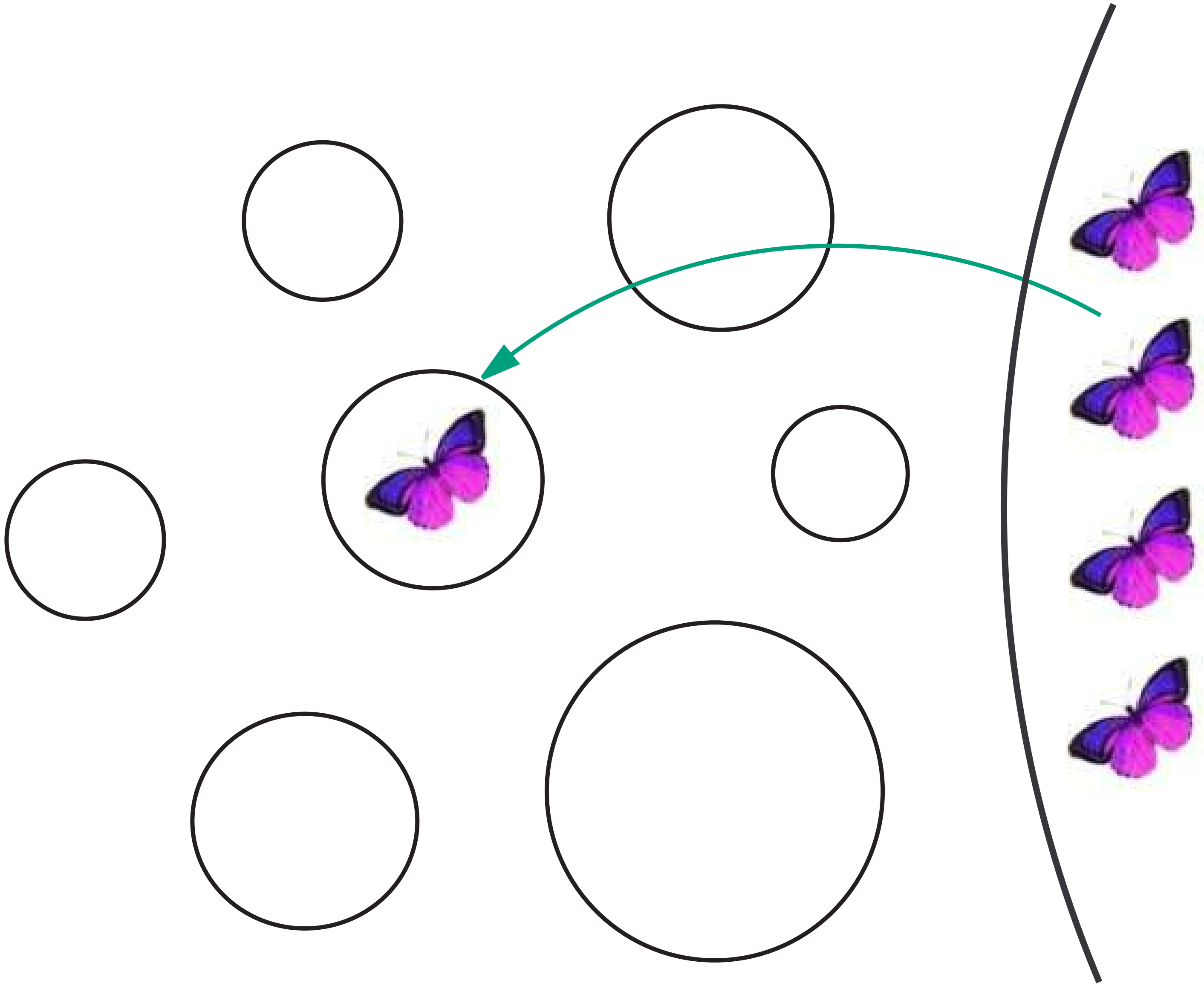

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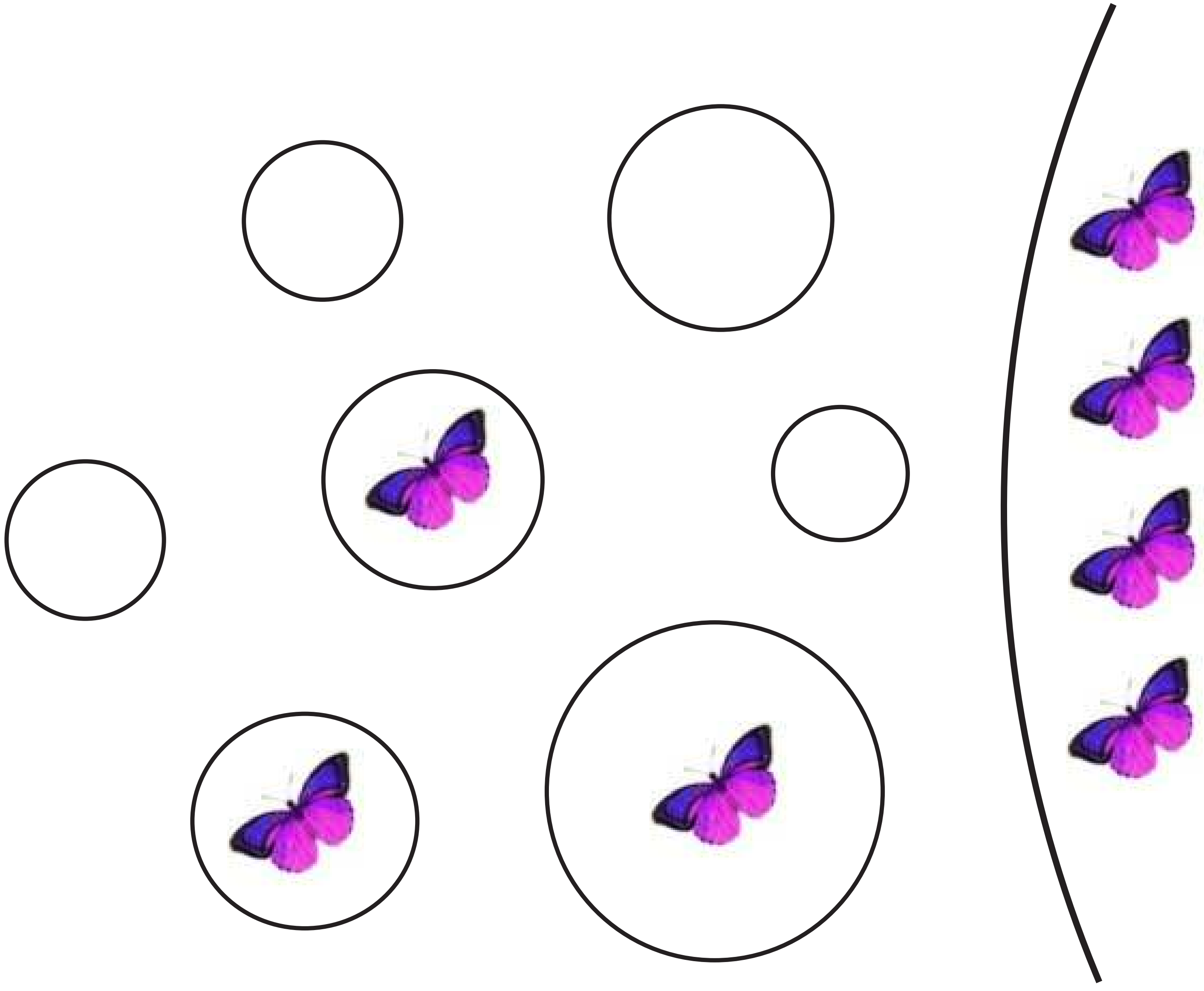

A Stochastic Patch Occupancy Model (SPOM)

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Suppose that there are n patches.

Let $X_t^{(n)} = (X_{1,t}^{(n)}, \ldots, X_{n,t}^{(n)})$, where $X_{i,t}^{(n)}$ is a binary variable indicating whether or not patch i is occupied.

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SPOM - Phase structure

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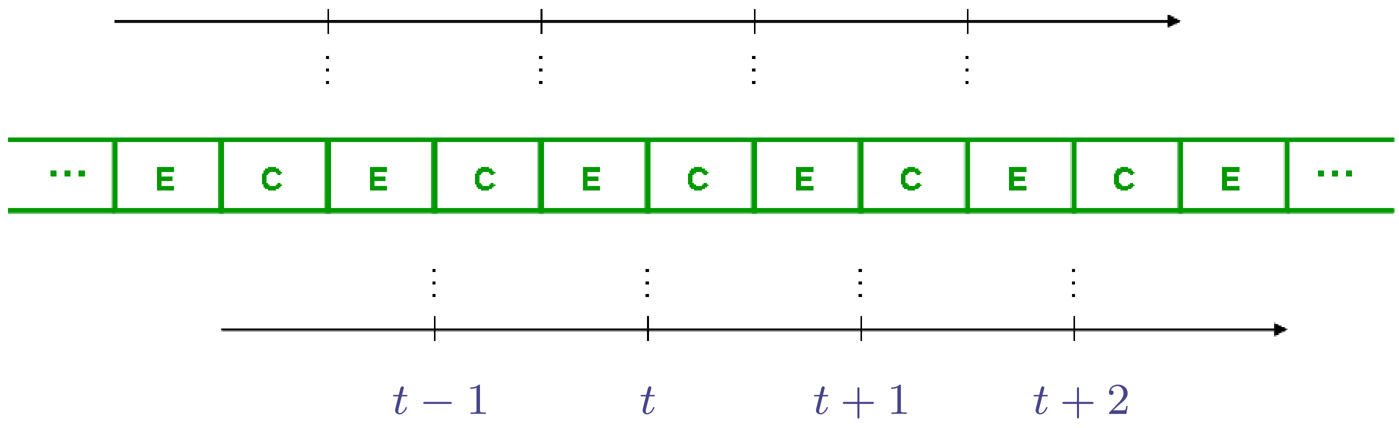

We will we assume that the population is *observed after successive extinction phases* (CE Model).

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Colonization and extinction happen in distinct, successive phases, as independent trials.

Colonization: unoccupied patches become occupied independently with probability $c(n^{-1}\sum_{i=1}^{n} X_{i,t}^{(n)})$, where $c:[0,1]\to[0,1]$ is continuous, non-decreasing and concave.

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[In our most recent work, we allow the patch colonization probability $c(\,\cdot\,)$ to depend on the *positions* of all patches and their *areas*.]

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Thus, we have a *Chain Bernoulli* structure:

$$X_{i,t+1}^{(n)} \stackrel{d}{=} \mathit{Bin}\left(X_{i,t}^{(n)} + \mathit{Bin}\left(1 - X_{i,t}^{(n)}, c\left(\frac{1}{n}\sum_{j=1}^{n} X_{j,t}^{(n)}\right)\right), s_i\right)$$

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SPOM

$n = 30$, $s_i \sim$ Beta$(25.2,\ 19.8)$ $(\mathbb{E}s_i = 0.56)$ and $c(x) = 0.7x$

0 0 0 0 1 0 1 1 0 1 0 1 0 0 0 0 1 1 1 0 1 0 1 0 0 0 1 0 0 0

$c(x) = c(\frac{11}{30}) = 0.7 \times 0.3\dot{6} = 0.25\dot{6}$

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0 0 0 0 1 0 1 1 0 1 0 1 0 0 0 0 1 1 1 0 1 0 1 0 0 0 1 0 0 0

C 1 0 0 0 1 1 1 1 0 1 0 1 0 0 0 0 1 1 1 1 1 1 1 0 0 0 1 0 1 0

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C 1 0 0 0 1 1 1 1 0 1 0 1 0 0 0 0 1 1 1 1 1 1 1 0 0 0 1 0 1 0

0.60 0.56 0.63 0.62 0.52 0.61 0.68 0.49 0.49 0.49 0.50

0.41 0.59 0.63 0.60 0.61

[Survival probabilities listed for occupied patches only]

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  0 0 0 0 1 0 1 1 0 1 0 1 0 0 0 0 1 1 1 0 1 0 1 0 0 0 1 0 0 0
C 1 0 0 0 1 1 1 1 0 1 0 1 0 0 0 0 1 1 1 1 1 1 1 0 0 0 1 0 1 0
E 0 0 0 0 1 0 0 1 0 1 0 1 0 0 0 0 1 0 1 1 1 1 0 0 0 0 0 0 1 0

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	0	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	1	1	1	0	1	0	1	0	0	0	1	0	0	0
C	1	0	0	0	1	1	1	1	0	1	0	1	0	0	0	0	1	1	1	1	1	1	1	0	0	0	1	0	1	0
E	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	1	0

$c(x) = c(\frac{10}{30}) = 0.7 \times 0.\dot{3} = 0.2\dot{3}$

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0 0 0 0 1 0 1 1 0 1 0 1 0 0 0 0 1 1 1 0 1 0 1 0 0 0 1 0 0 0
C 1 0 0 0 1 1 1 1 0 1 0 1 0 0 0 0 1 1 1 1 1 1 1 0 0 0 1 0 1 0
E 0 0 0 0 1 0 0 1 0 1 0 1 0 0 0 0 1 0 1 1 1 1 0 0 0 0 0 0 1 0
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	0	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	1	1	1	0	1	0	1	0	0	0	1	0	0	0
C	1	0	0	0	1	1	1	1	0	1	0	1	0	0	0	0	1	1	1	1	1	1	1	0	0	0	1	0	1	0
E	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	1	0
C	0	0	1	0	1	0	0	1	1	1	0	1	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0

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C	1	0	0	0	1	1	1	1	0	1	0	1	0	0	0	0	1	1	1	1	1	1	1	0	0	0	1	0	1	0
E	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	1	0
C	0	0	1	0	1	0	0	1	1	1	0	1	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0
E	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0

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	0 0 0 0 1 0 1 1 0 1 0 1 0 0 0 0 1 1 1 0 1 0 1 0 0 0 1 0 0 0
C	1 0 0 0 1 1 1 1 0 1 0 1 0 0 0 0 1 1 1 1 1 1 1 0 0 0 1 0 1 0
E	0 0 0 0 1 0 0 1 0 1 0 1 0 0 0 0 1 0 1 1 1 1 0 0 0 0 0 0 1 0
C	0 0 1 0 1 0 0 1 1 1 0 1 0 0 1 0 1 1 1 1 1 1 0 0 0 0 0 0 1 0
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  0 0 0 0 1 0 1 1 0 1 0 1 0 0 0 0 1 1 1 0 1 0 1 0 0 0 1 0 0 0
C 1 0 0 0 1 1 1 1 0 1 0 1 0 0 0 0 1 1 1 1 1 1 1 0 0 0 1 0 1 0
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SPOM - Homogeneous case

In the *homogeneous case*, where $s_i = s$ (non-random) is the same for each i, the *number* $N_t^{(n)}$ of occupied patches at time t is Markovian.

It has the following *Chain Binomial* structure:

$$N_{t+1}^{(n)} \stackrel{d}{=} \textit{Bin}\left(N_t^{(n)} + \textit{Bin}\left(n - N_t^{(n)}, c\left(\tfrac{1}{n}N_t^{(n)}\right)\right), s\right)$$

A deterministic limit

Letting the initial number $N_0^{(n)}$ of occupied patches grow at the same rate as n . . .

Theorem [BP] If $N_0^{(n)}/n \xrightarrow{p} x_0$ (a constant), then

$$N_t^{(n)}/n \xrightarrow{p} x_t, \quad \text{for all } t \geq 1,$$

with (x_t) determined by $x_{t+1} = f(x_t)$, where

$$f(x) = s(x + (1 - x)c(x)).$$

[BP] Buckley, F.M. and Pollett, P.K. (2010) Limit theorems for discrete-time metapopulation models. Probability Surveys 7, 53-83.

Stability

$x_{t+1} = f(x_t)$, where $f(x) = s(x + (1-x)c(x))$.

Stationarity: $c(0) > 0$. There is a unique fixed point $x^* \in [0,1]$. It satisfies $x^* \in (0,1)$ and is stable.

Evanescence: $c(0) = 0$ and $1 + c'(0) \leq 1/s$. Now 0 is the unique fixed point in $[0,1]$. It is stable.

Quasi stationarity: $c(0) = 0$ and $1 + c'(0) > 1/s$. There are two fixed points in $[0,1]$: 0 (unstable) and $x^* \in (0,1)$ (stable).

[Notice that $c(0) = 0$ implies that $c'(0) > 0$.]

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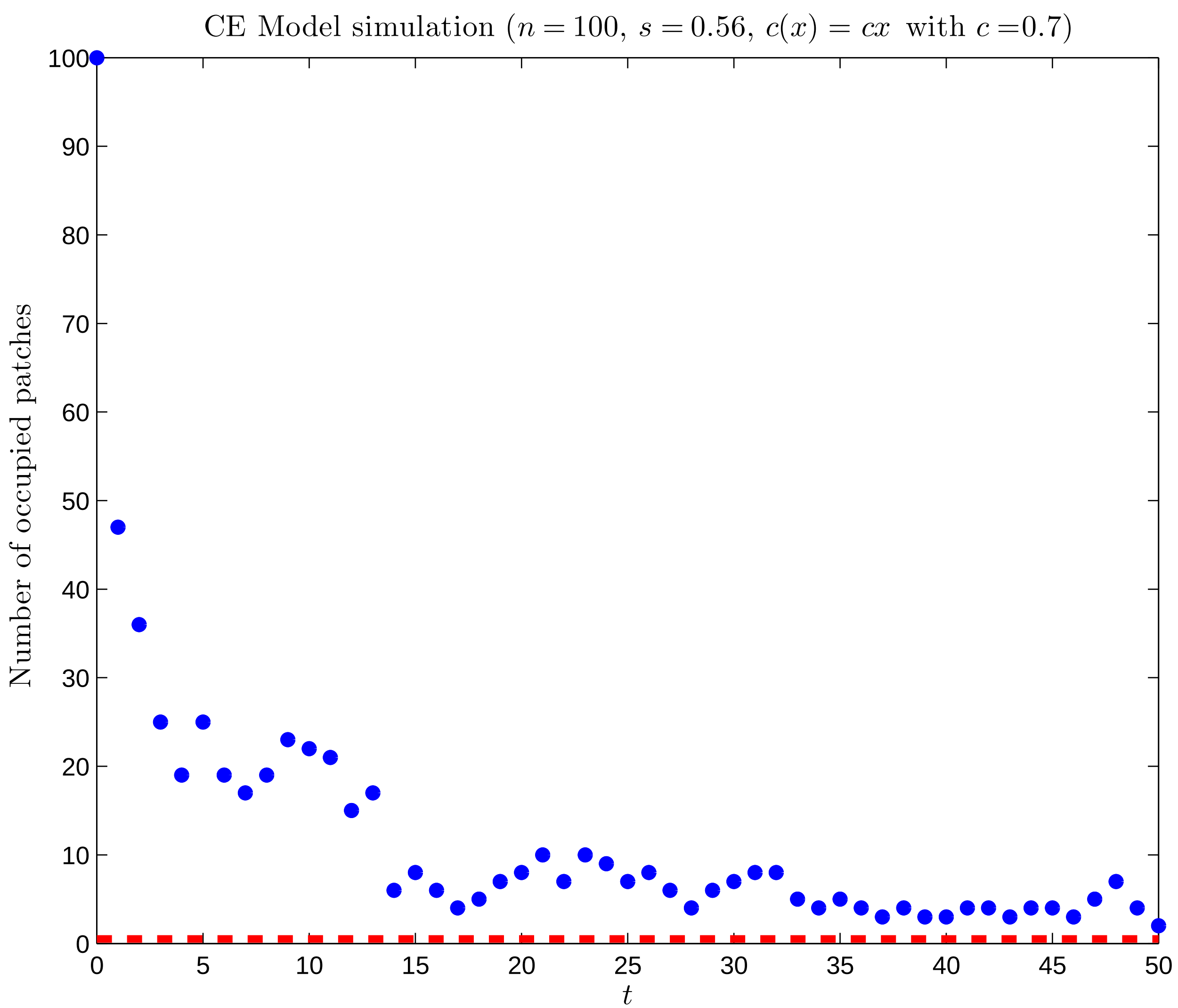
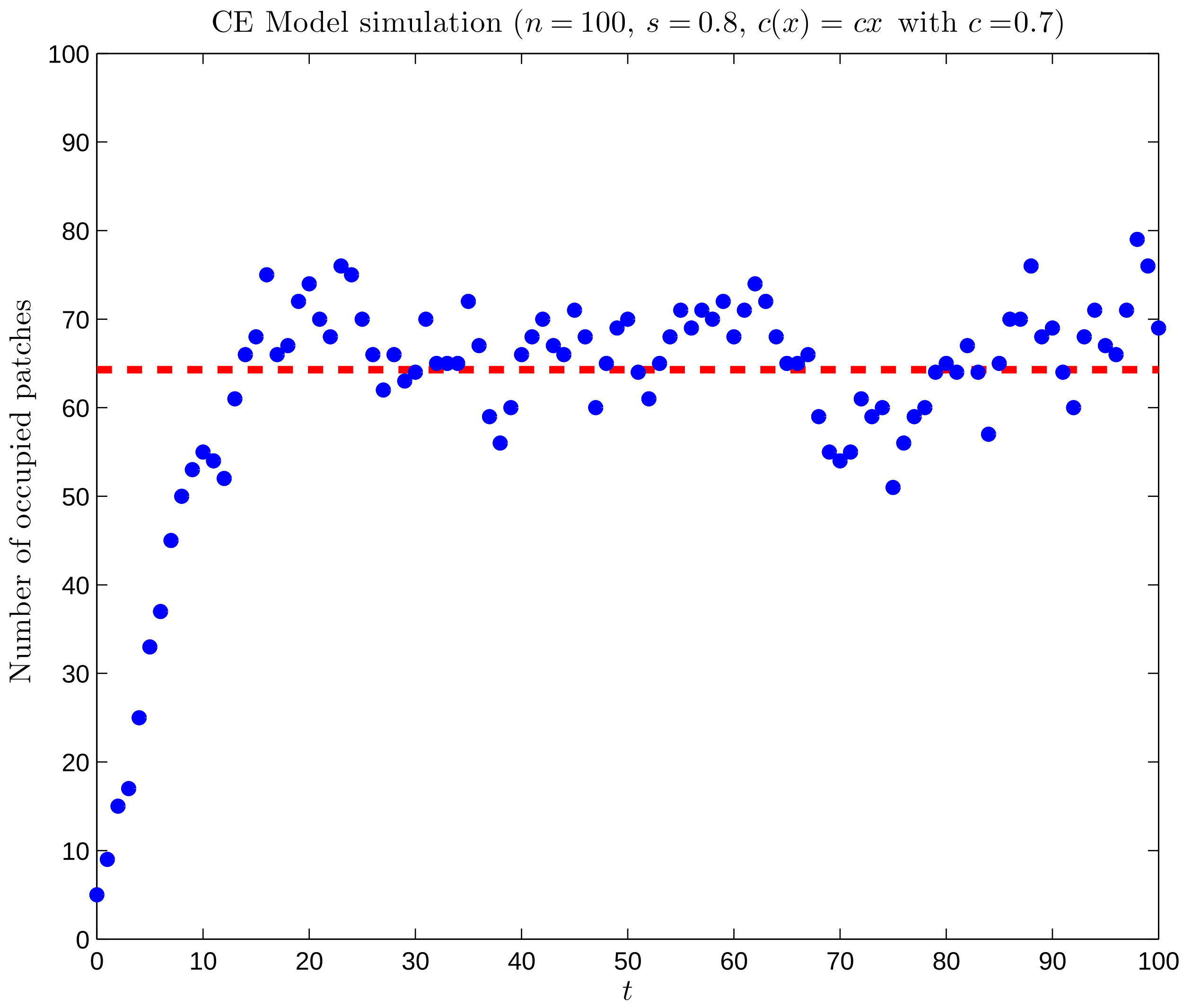
CE Model - Evanescence



CE Model - Quasi stationarity



SPOM - general case

Returning to the general case, where patch survival probabilities (s_i) are *random* and *patch dependent*, and we keep track of which patches are occupied ...

$$X_{i,t+1}^{(n)} \stackrel{d}{=} \mathit{Bin}\left(X_{i,t}^{(n)} + \mathit{Bin}\left(1 - X_{i,t}^{(n)}, c\left(\tfrac{1}{n}\sum_{j=1}^{n} X_{j,t}^{(n)}\right)\right), s_i\right).$$

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Notice that

$$X_{i,t+1}^{(n)} \stackrel{d}{=} \mathit{Bin}\left(X_{i,t}^{(n)}, s_i\right) + \mathit{Bin}\left(1 - X_{i,t}^{(n)}, s_i c\left(\tfrac{1}{n}\sum_{j=1}^{n} X_{j,t}^{(n)}\right)\right).$$

Our approach - Point Processes!

Treat the collection of patch survival probabilities and those of *occupied patches* at time t as point processes on $[0, 1]$.

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Define sequences (σ_n) and $(\mu_{n,t})$ of random measures by

$$\sigma_n(B) = \#\{s_i \in B\}/n, \qquad B \in \mathcal{B}([0,1]),$$

$$\mu_{n,t}(B) = \#\{s_i \in B : X_{i,t}^{(n)} = 1\}/n, \qquad B \in \mathcal{B}([0,1]).$$

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Think of σ as being the distribution of survival probabilities. In the earlier simulation σ was a Beta$(25.2,\ 19.8)$ distribution.

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Treat the collection of patch survival probabilities and those of *occupied patches* at time t as point processes on $[0, 1]$.

Define sequences (σ_n) and $(\mu_{n,t})$ of random measures by

$$\sigma_n(B) = \#\{s_i \in B\}/n, \qquad B \in \mathcal{B}([0,1]),$$

$$\mu_{n,t}(B) = \#\{s_i \in B : X_{i,t}^{(n)} = 1\}/n, \qquad B \in \mathcal{B}([0,1]).$$

We are going to suppose that $\sigma_n \xrightarrow{d} \sigma$ for some non-random (probability) measure σ.

Think of σ as being the distribution of survival probabilities. In the earlier simulation σ was a Beta$(25.2, 19.8)$ distribution.

Our approach - Point Processes!

Equivalently, we may define (σ_n) and $(\mu_{n,t})$ by

$$\int h(s)\sigma_n(ds) = \frac{1}{n}\sum_{i=1}^{n} h(s_i)$$

$$\int h(s)\mu_{n,t}(ds) = \frac{1}{n}\sum_{i=1}^{n} X_{i,t}^{(n)}\, h(s_i),$$

for h in $C^+([0,1])$, the class of continuous functions that map $[0,1]$ to $[0,\infty)$.

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for h in $C^+([0,1])$, the class of continuous functions that map $[0,1]$ to $[0,\infty)$. For example $(h \equiv 1)$,

$$\int \mu_{n,t}(ds) = \frac{1}{n}\sum_{i=1}^{n} X_{i,t}^{(n)} \quad \text{(proportion occupied)}.$$

A measure-valued difference equation

Theorem Suppose that $\sigma_n \xrightarrow{d} \sigma$ and $\mu_{n,0} \xrightarrow{d} \mu_0$ for some non-random measures σ and μ_0. Then, $\mu_{n,t} \xrightarrow{d} \mu_t$ for all $t = 1, 2, \ldots$, where μ_t is defined by the following recursion: for $h \in C^+([0,1])$,

$$\int h(s)\mu_{t+1}(ds) = (1 - c_t) \int sh(s)\mu_t(ds) + c_t \int sh(s)\sigma(ds),$$

where $c_t = c\left(\mu_t([0,1])\right) = c\left(\int \mu_t(ds)\right)$.

Moments

Set $h(s) = s^k$. Then, our recursion is

$$\int s^k \mu_{t+1}(ds) = (1 - c_t) \int s^{k+1} \mu_t(ds) + c_t \int s^{k+1} \sigma(ds),$$

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where $c_t = c\,(\mu_t([0,1])) = c\left(\int \mu_t(ds)\right)$. So, with moments defined by $\bar{\sigma}^{(k)} := \int s^k \sigma(ds)$ and $\bar{\mu}_t^{(k)} := \int s^k \mu_t(ds)$,

$$\bar{\mu}_{t+1}^{(k)} = (1 - \bar{\mu}_t^{(0)})\bar{\mu}_t^{(k+1)} + \bar{\mu}_t^{(0)}\,\bar{\sigma}^{(k+1)},$$

and the theorem allows to conclude that

$$\frac{1}{n}\sum_{i=1}^n s_i^k X_{i,t}^{(n)} \; \left(= \int s^k \mu_{n,t}(ds)\right) \; \to \bar{\mu}_t^{(k)},$$

for example, $\frac{1}{n}\sum_{i=1}^n X_{i,t}^{(n)} \to \bar{\mu}_t^{(0)}$.

Equilibria?

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Let $\mathcal{M}$ be the set of measures that are absolutely continuous with respect to σ and whose Radon-Nikodym derivative is bounded by 1, $\sigma -$ a.e.

We shall be interested in the behaviour of solutions to our recursion starting with $\mu_0 \in \mathcal{M}$.

Equilibria?

"Differentiating" with respect to σ, we see that our recursion can be written

$$\frac{\partial \mu_{t+1}}{\partial \sigma} = s\frac{\partial \mu_t}{\partial \sigma} + sc_t\left(1 - \frac{\partial \mu_t}{\partial \sigma}\right).$$

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Furthermore, a measure $\mu_\infty \in \mathcal{M}$ will be an equilibrium point of our recursion if it satisfies

$$\frac{\partial \mu_\infty}{\partial \sigma} = s\frac{\partial \mu_\infty}{\partial \sigma} + sc_\infty\left(1 - \frac{\partial \mu_\infty}{\partial \sigma}\right),$$

where $c_\infty = c\left(\mu_\infty([0,1])\right)$.

Equilibria?

Theorem Suppose that $c(0) = 0$ and $c'(0) < \infty$. Let ψ^* be a solution to the equation

$$\psi = R_\sigma(\psi) := \int \frac{sc(\psi)}{1-s+sc(\psi)} \sigma(ds). \qquad (1)$$

The fixed points of our recursion are given by

$$\mu_\infty(ds) = \frac{sc(\psi^*)}{1 - s + sc(\psi^*)} \sigma(ds).$$

Equation (1) has the unique solution $\psi^* = 0$ if and only if

$$c'(0) \int \frac{s}{1-s} \sigma(ds) \leq 1.$$

Otherwise, there are two solutions, one of which is $\psi^* = 0$.

Recovery of a near-extinct population

Return to our patch occupancy model . . .

$$X_{i,t+1}^{(n)} \stackrel{d}{=} \textit{Bin}\left(X_{i,t}^{(n)}, s_i\right) + \textit{Bin}\left(1 - X_{i,t}^{(n)}, s_i c\left(\frac{1}{n}\sum_{j=1}^{n} X_{j,t}^{(n)}\right)\right).$$

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Assume now that $c(0) = 0$ (which implies $c'(0) > 0$).

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Fix the initial configuration $X_0^{(n)}$ $(= X_0)$, and let $n \to \infty$.

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First notice that if c has a continuous second derivative near 0, then, for fixed m, *Bin*$(n-m, c(m/n)) \stackrel{d}{\to}$ *Poi*(λm) as $n \to \infty$, where $\lambda = c'(0)$. So, if every patch had the *same survival probability*, then we might expect the number of occupied patches $(N_t^{(n)},\, t = 0, 1, \dots)$ to converge to a Galton-Watson process (see [BP] for details).

Recovery of a near-extinct population

As before, treat the collection of patch survival probabilities of occupied patches at time t as a point process on $[0, 1]$, but now define $(S_t^{(n)}, t \geq 0)$ by $S_t^{(n)} = \{s_i : X_{i,t}^{(n)} = 1\}$.

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The aim is to show that there is a point process S_t such that $S_t^{(n)} \Rightarrow S_t$ as $n \to \infty$ and then to evaluate $\lim_{t\to\infty} \Pr\left(S_t = \varnothing\right)$.

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We now work with the sequence $(\mu_{n,t})$ of random measures defined by $\mu_{n,t}(B) = \#\{s_i \in B : X_{i,t}^{(n)} = 1\}$, $B \in \mathcal{B}([0, 1])$.

Tools*

Define the *probability generating functional* (p.g.fl) of a point process S by

$$G_S[\xi] = \mathbb{E}\Big(\prod_{s\in S} \xi(s)\Big),$$

where $\xi : [0,1] \to [0,1]$ is some Borel function. It determines the point process uniquely. Convergence of $G_{S_t^{(n)}}$ to G_{S_t} establishes that $S_t^{(n)} \Rightarrow S_t$. Furthermore,

$$\Pr(S_t = \varnothing) = \lim_{b\downarrow 0} G_{S_t}[1_b(x)].$$

*Daley, D. J. and Vere-Jones, D. (2008) An Introduction to the Theory of Point Processes. Volume II: General Theory and Structure, 2nd Edn., Springer, New York.

Convergence

Theorem Suppose that $S_0^{(n)}$ converges weakly to a point process S_0 as $n \to \infty$ (its p.g.fl being G_{S_0})*.

Then, $S_t^{(n)}$ converges weakly to a point process S_t whose p.g.fl satisfies the recursion $G_{S_{t+1}}[\xi] = G_{S_t}[h[\xi]]$ $(t \geq 0)$, where $h[\xi]$ is given by

$$h[\xi](s) = (1 - s(1 - \xi(s))) \exp\left(-c'(0) \int y(1 - \xi(y))\,\sigma(dy)\right).$$

*More general than (as earlier) fixing the initial configuration and letting $n \to \infty$.

Interpretation of limit

The limit point process $(S_t, t = 0, 1, \dots)$ is a *multiplicative population chain**, where each member of the population at time t produces offpring independently of the other members of the population. The offspring from the member of the population "located" at s is generated according to an inhomogeneous Poisson process with intensity measure $c'(0)s\sigma(\,\cdot\,)$, and the original member of the population survives to the next generation with probability s.

*Moyal, J.E. (1962). Multiplicative population chains. Proc. R. Soc. Lond. A, 266, 518-526.

Probability of total extinction

Theorem S_t eventually becomes empty with probability 1 ($S_t = \varnothing$ for some $t > 0$) if

$$c'(0)\int \frac{s}{1-s}\sigma(ds) \leq 1.$$

Otherwise, it eventually becomes empty with probability $G_{S_0}[g]$, where $g(s) = \psi(1-s)/(1-\psi s)$, with ψ (< 1) being the unique solution to

$$\psi = \exp\left(-c'(0)\int \frac{(1-\psi)s}{1-\psi s}\,\sigma(ds)\right),$$

that is, with probability

$$\mathbb{E}\left(\prod_{s\in S_0} \frac{\psi(1-s)}{1-\psi s}\right).$$

Example

Suppose that (s_i) are chosen *independently* according to σ and patches are initially occupied independently with probability p_n, where $np_n \to \lambda \ (> 0)$.

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$$G_{S_0^{(n)}}[\xi] = \mathbb{E}\left(\prod_{s\in S_0^{(n)}} \xi(s)\right) = \mathbb{E}\left(\mathbb{E}\left(\prod_{i=1}^{n} \xi(s_i)\middle| X_0^{(n)}\right)\right)$$

$$= \mathbb{E}\left(\prod_{i=1}^{n}(X_{i,0}^{(n)}\xi(s_i) + 1 - X_{i,0}^{(n)})\right) = \left(p_n \int \xi(s)\sigma(ds) + 1 - p_n\right)^n$$

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$$\sim \left(1 - \tfrac{\lambda}{n}\left(1 - \int \xi(s)\sigma(ds)\right)\right)^n \to G_{S_0}[\xi], \quad \text{as } n \to \infty,$$

where

$$G_{S_0}[\xi] = \exp\left(-\lambda\left(\int 1 - \xi(s)\,\sigma(ds)\right)\right).$$

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So, $S_0^{(n)} \Rightarrow S_0$, where S_0 contains a *Poi*(λ) number of points distributed on $[0, 1]$ independently according to σ.

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That is, in the limiting initial patch configuration, there is a *Poi*(λ) number of occupied patches, and the survival probabilities are distributed independently according to σ.

Example - probability of total extinction

In the example, where the limiting $(n$ large$)$ initial patch configuration had a *Poi*(λ) number of occupied patches, and survival probabilities were distributed independently according to σ, the "limiting metapopulation" will eventually go extinct with probability 1 if

$$c'(0)\int \tfrac{s}{1-s}\sigma(ds) \leq 1.$$

Otherwise, it will go extinct with probability

$$\exp\left(-\lambda \int \tfrac{1-s}{1-\psi s}\,\sigma(ds)\right).$$

Example - probability of total extinction

In the case where σ is the beta distribution with parameters α and β (both > 0), that is

$$\sigma(ds) = \frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\Gamma(\beta)} s^{\alpha-1}(1-s)^{\beta-1}\, ds, \qquad s \in [0,1],$$

we have that

$$\int \tfrac{s}{1-s}\sigma(ds) = \begin{cases} \frac{\alpha}{\beta-1} & \text{if } \beta > 1 \\ \infty & \text{if } \beta \leq 1. \end{cases}$$

Example - probability of total extinction

So, the “limiting metapopulation” $(n$ large$)$ will eventually go extinct with probability 1 if $\beta \geq 1 + \alpha c'(0)$. Otherwise, it will go extinct with probability

$$\exp\left(-\lambda \int \frac{1-s}{1-\psi s}\, \sigma(ds)\right),$$

where ψ solves (uniquely)

$$\psi = \exp\left(-c'(0) \int \frac{(1-\psi)s}{1-\psi s}\, \sigma(ds)\right).$$