Rules of thumb for metapopulation management

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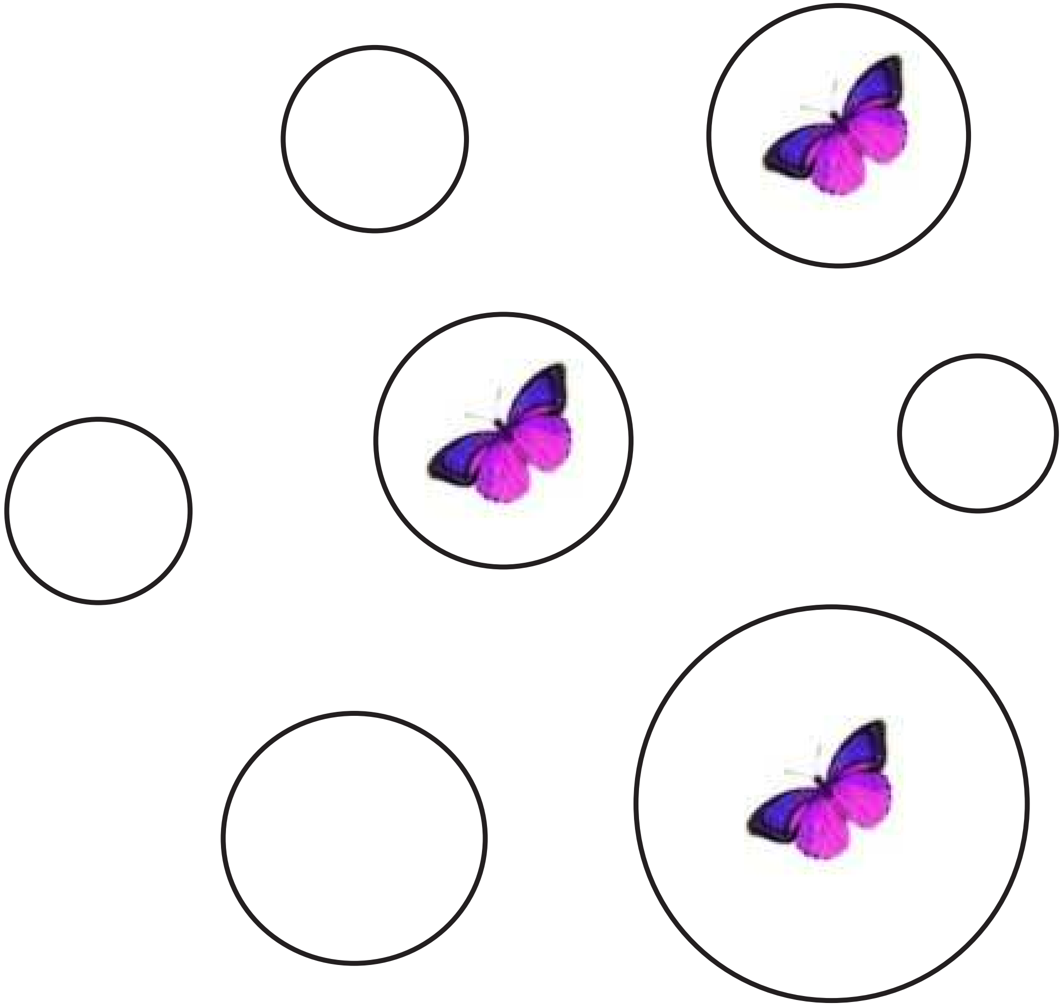
Metapopulations



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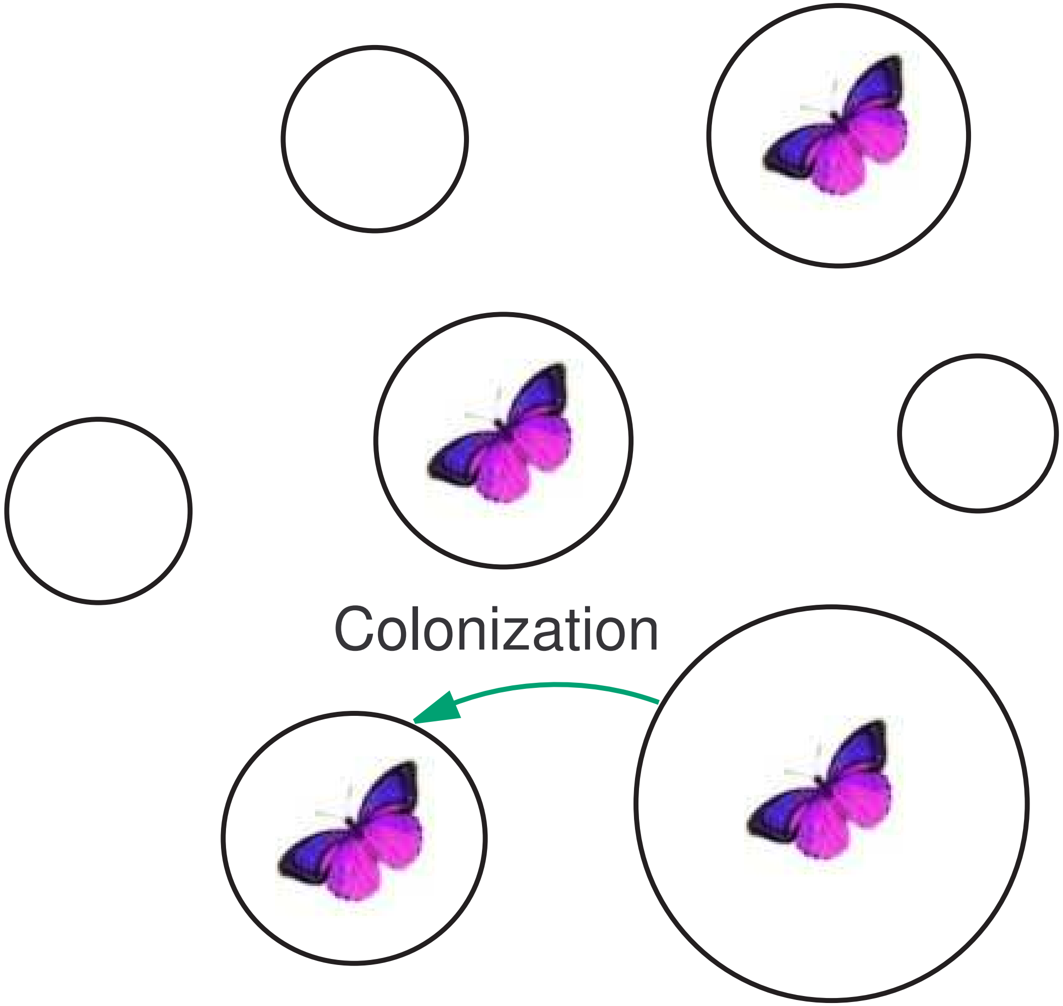

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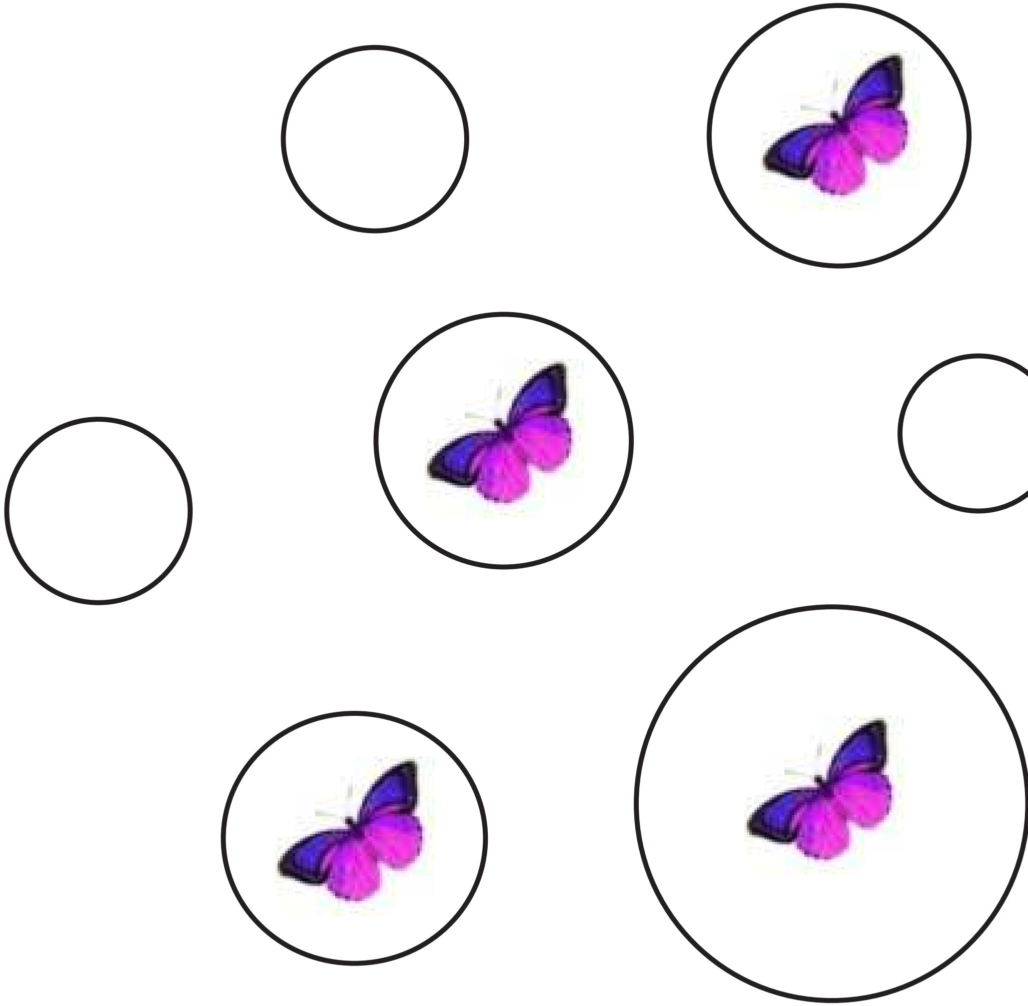

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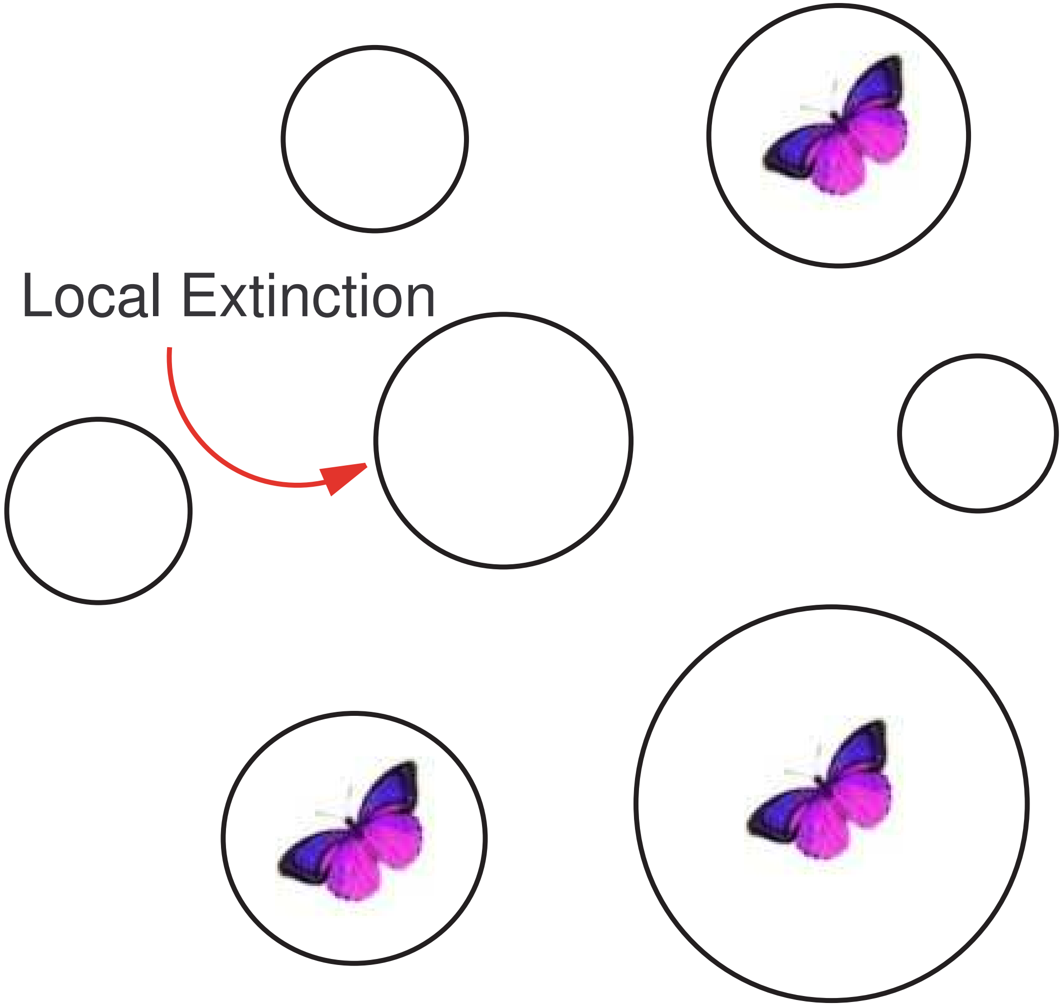

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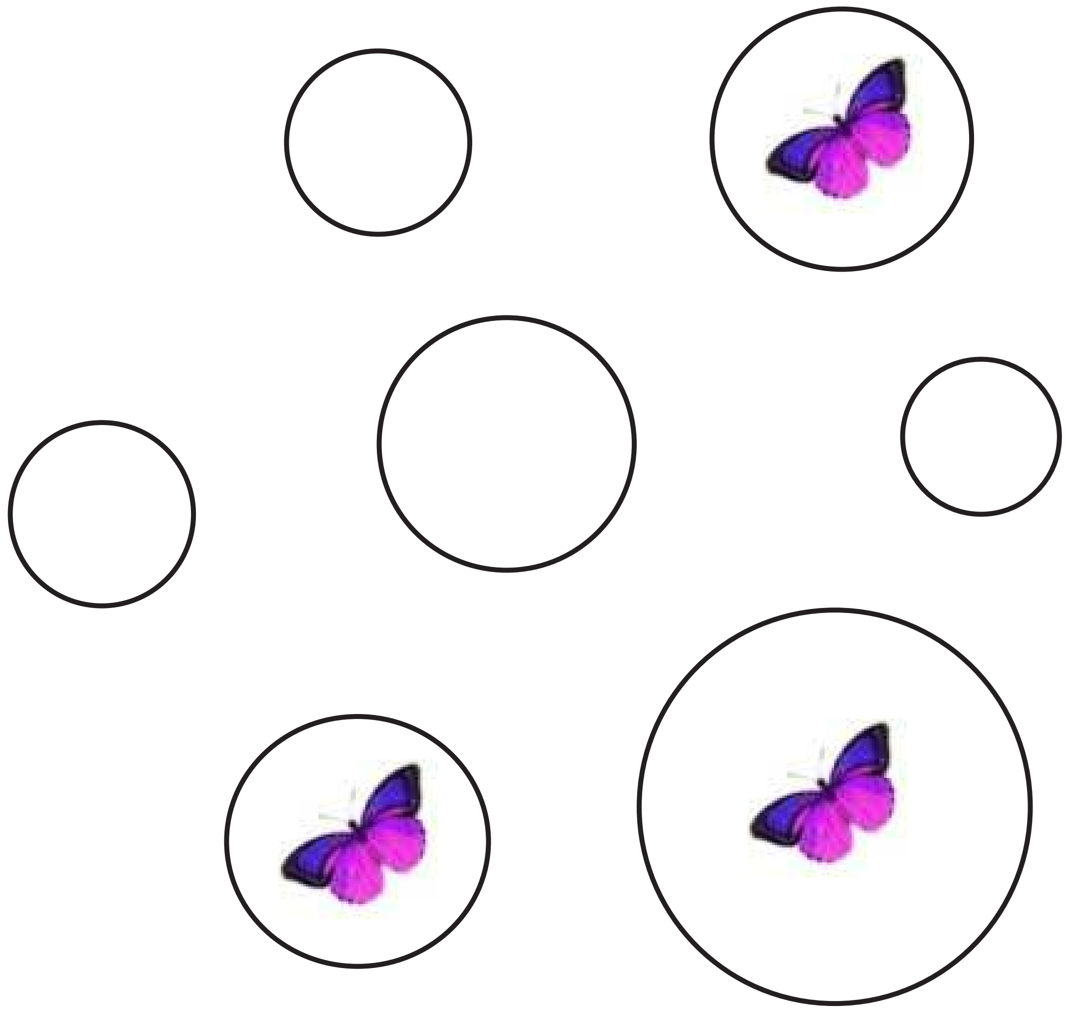

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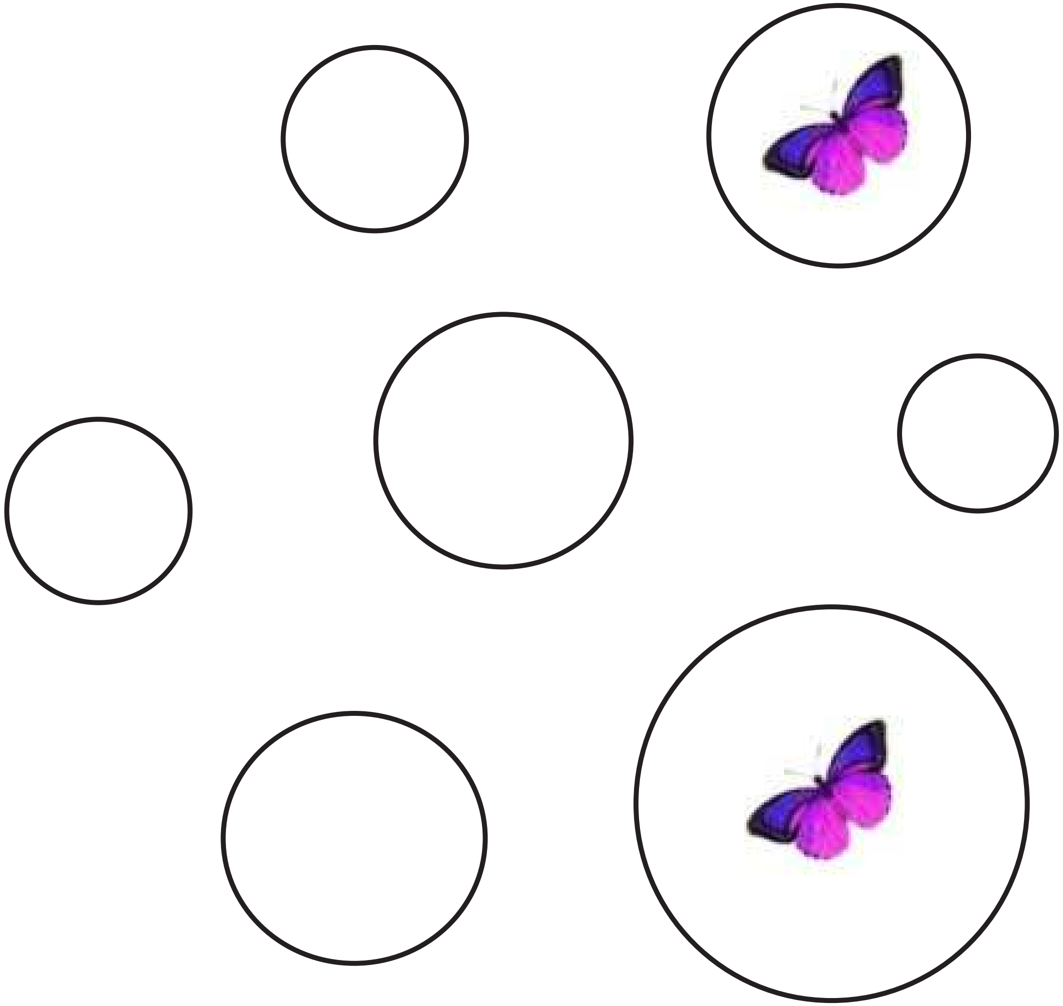

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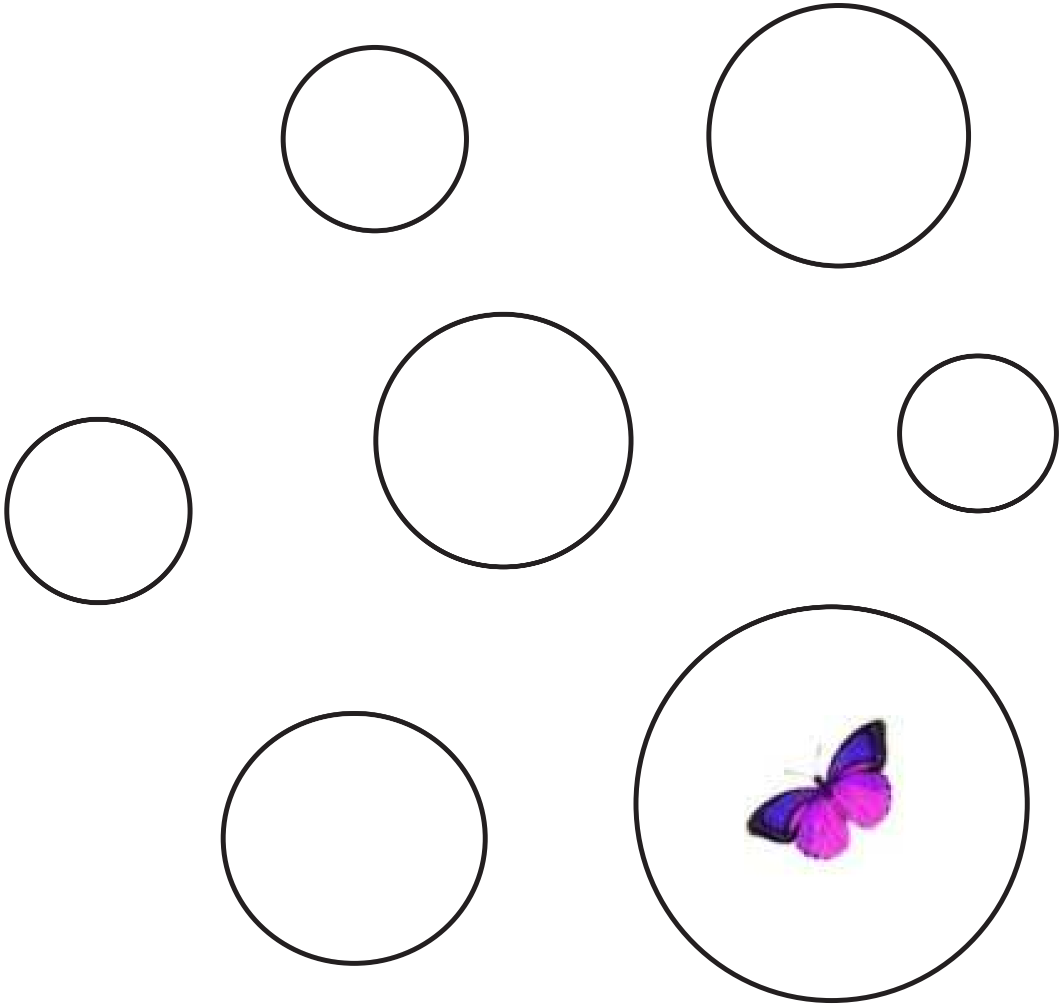

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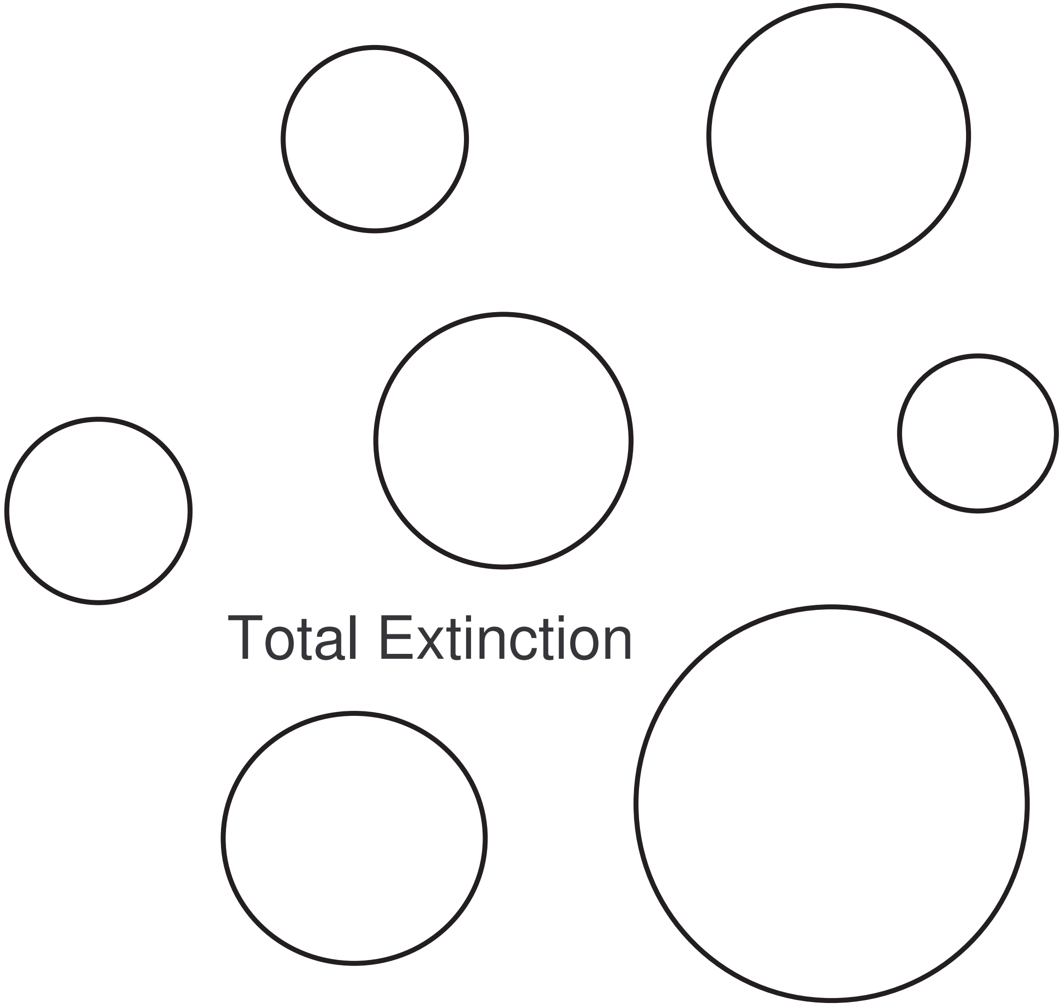

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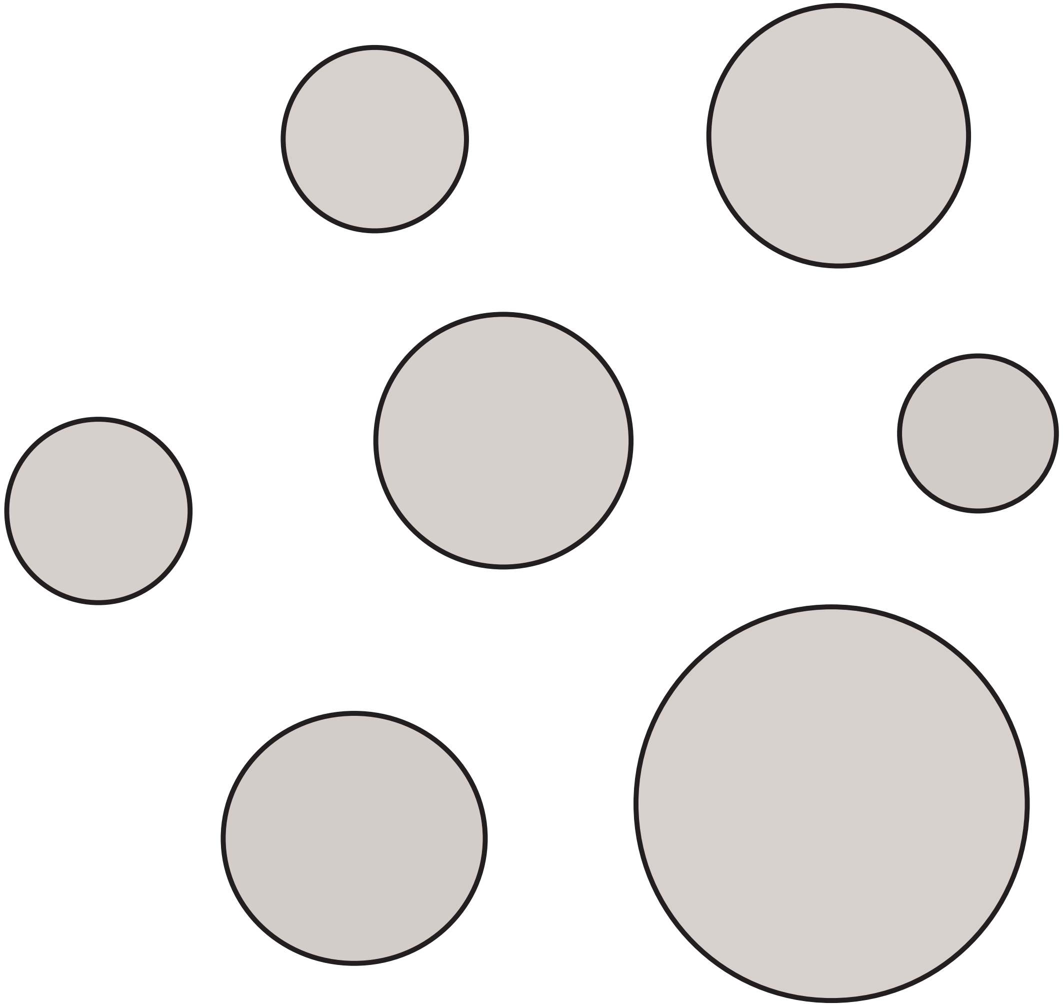

Typical questions

Given an appropriate model . . .

- How do we calibrate the model? (parameter estimation)
- Assessing extinction risk:
  - What is the expected time to (total) extinction?
  - What is the probability of extinction by time t?
- Can we improve population viability (subject to budgetary constraints)?
- Are there simple (but accurate) ‘rules of thumb’?

Rules of thumb: R1

Our first rule (which I shall concentrate on today) is based on exact and approximate formulae for the persistence time (expected time to extinction).

It enables the population manager to form a priority species ranking by identifying those species most at risk of extinction.

Rules of thumb: R2

Our second rule uses R1 to identify an optimal management strategy that specifies how to alter the colonisation rate c (creation or improvement of habitat corridors) and local extinction rate e (restoring habitat quality or expanding habitat) in order to maximise the persistence time under a budgetary constraint.

Rules of thumb: R2

Our second rule uses R1 to identify an optimal management strategy that specifies how to alter the colonisation rate c (creation or improvement of habitat corridors) and local extinction rate e (restoring habitat quality or expanding habitat) in order to maximise the persistence time under a budgetary constraint.

Given a total budget B and costs K_c and K_e for respective (per unit) changes in c and e:

> *If $K_e e - K_c c > B$ then increase c. Otherwise, first reduce e towards its allowable minimum and then increase c if budget permits.*

A simple model

Suppose there are N patches. Let $n(t)$ be the number occupied at time t and suppose that $(n(t),\, t \geq 0)$ is a continuous-time Markov chain with transitions:

Event	Transition	Rate
Colonisation	$n \to n+1$	$\frac{c}{N} n(N-n)$
Local extinction	$n \to n-1$	en

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Colonisation	$n \to n+1$	$\frac{c}{N} n(N-n)$
Local extinction	$n \to n-1$	en

This is the *stochastic logistic (SL) model*, though it has many names, having been rediscovered several times since Feller* proposed it.

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

A simple model

It is a stochastic analogue the classical Verhulst* population model (here, for the *proportion* of occupied patches): $x_t' = cx_t(1 - x_t) - ex_t = cx_t\,(1 - \rho - x_t)$, where $\rho = e/c$, so that

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

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

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There are two equilibria: $x=0$ is stable if $c<e$, while $x = 1-\rho$ $(= 1-e/c)$ is stable if $c>e$.

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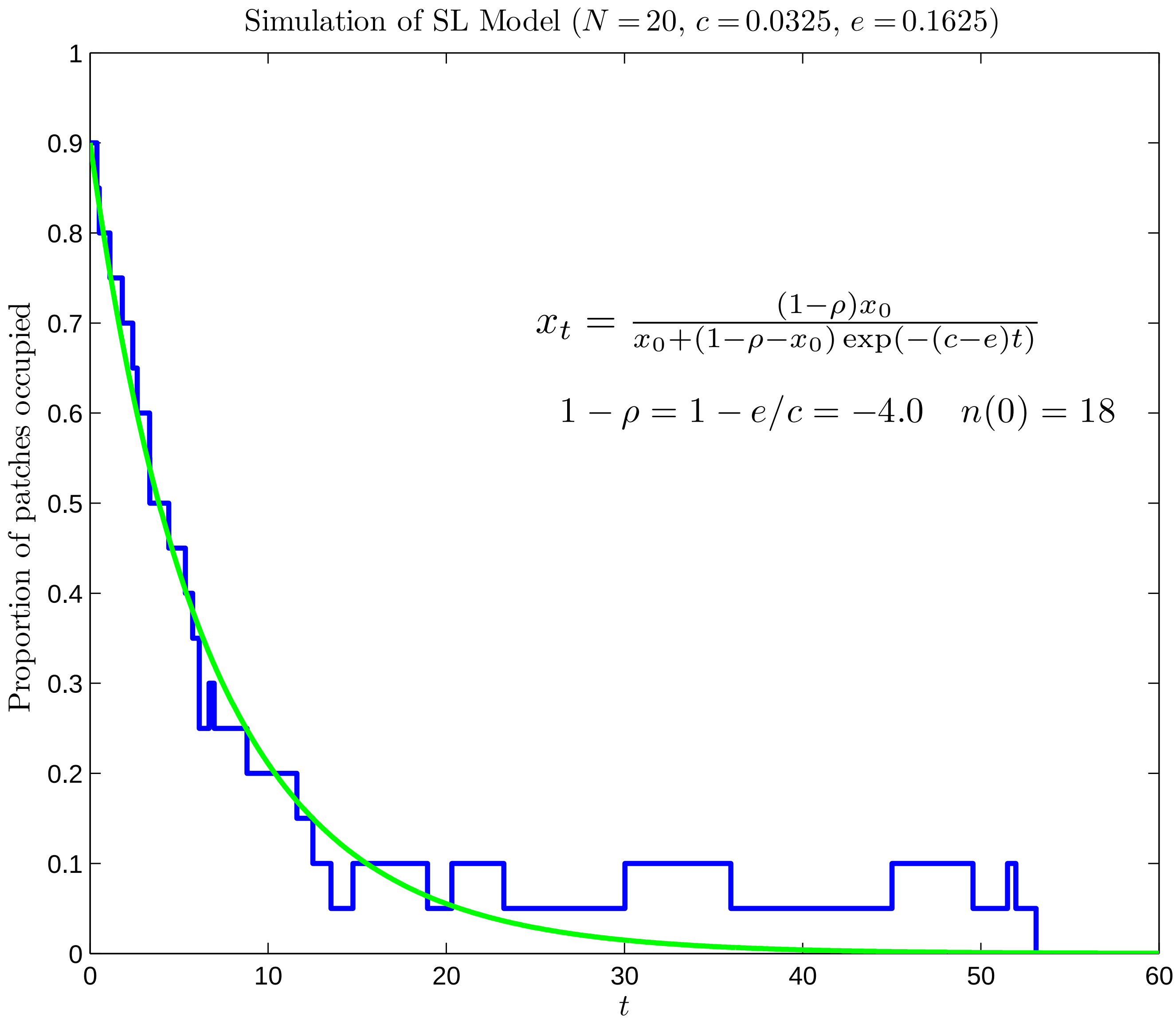
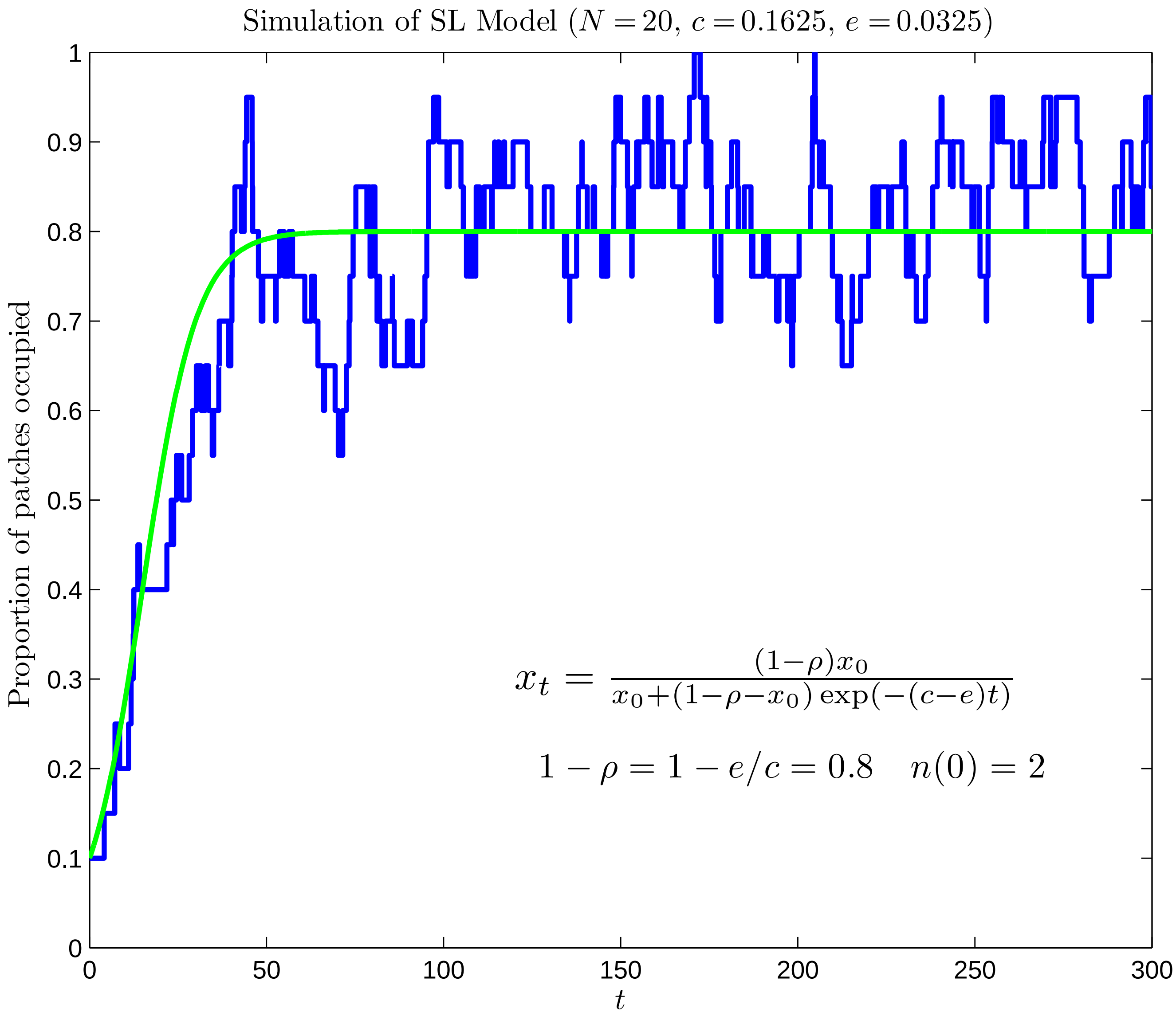
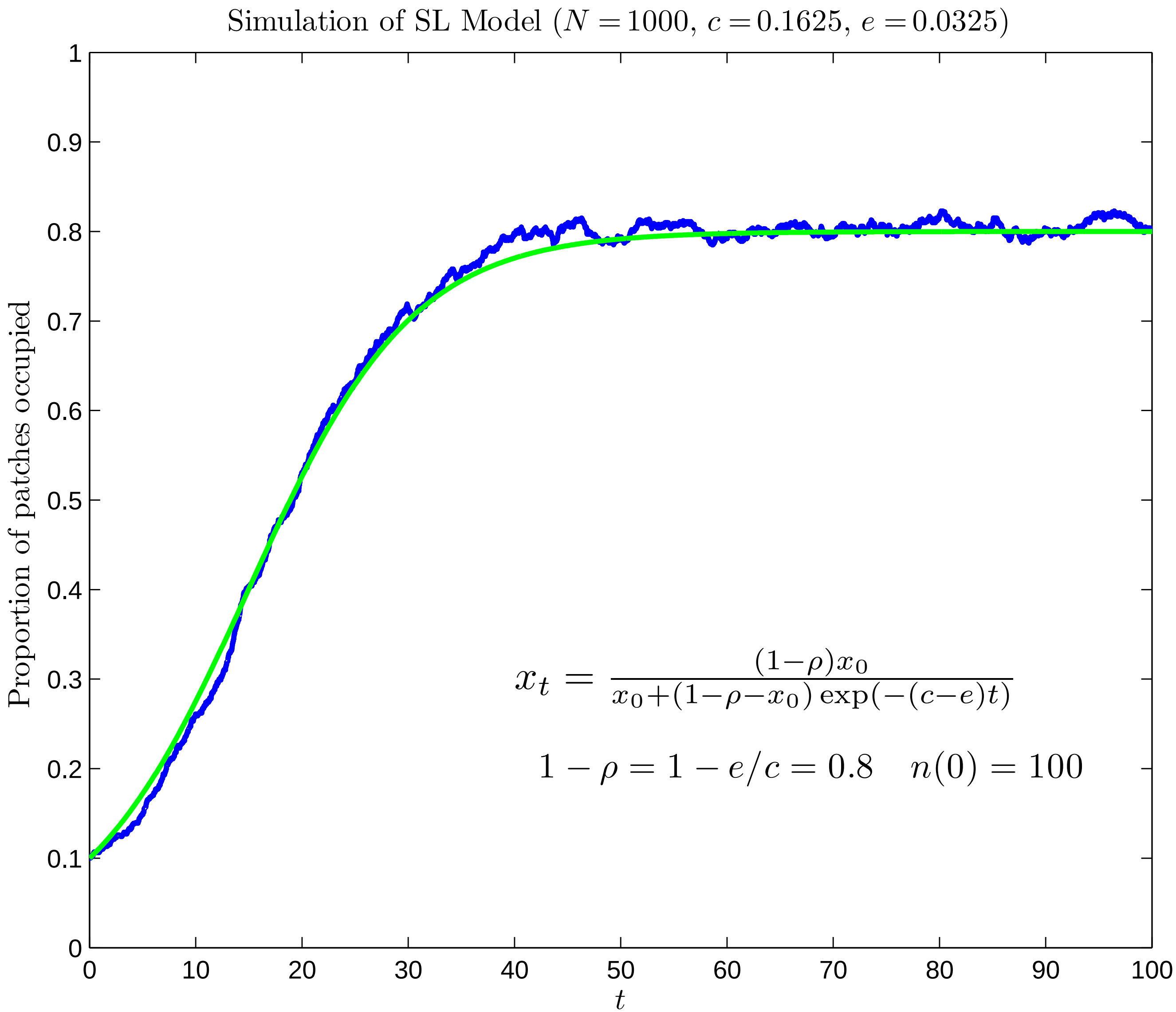
The SL model ($c < e$) $x = 0$ stable



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



The SL model ($c > e$) N large



Spatially realistic models

The state of our Markov chain is now $\boldsymbol{n} = (n_1, \ldots, n_N)$, where $n_i = 1$ if patch i is occupied and $n_i = 0$ if unoccupied. The transitions rates are:

Event	Transition	Rate
Colonisation	$\boldsymbol{n} \to \boldsymbol{n} + \mathbf{1}_i$	$(1 - n_i) \sum_{j \neq i} n_j \lambda_{ji}$
Local extinction	$\boldsymbol{n} \to \boldsymbol{n} - \mathbf{1}_i$	$n_i \lambda_{i0}$

Here $\mathbf{1}_i$ is the unit vector with a 1 as its i-th entry, λ_{ji} is the propagation rate from patch j to patch i and λ_{i0} is the local extinction rate.

Spatially realistic models

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Local extinction	$\boldsymbol{n} \to \boldsymbol{n} - \mathbf{1}_i$	$n_i \lambda_{i0}$

For example, $\lambda_{ij} = g e^{-\beta \sqrt{d_{ij}}}$, where g is the base propagation rate, β is the exponential dispersion parameter and d_{ij} is the distance between patches i and j, and, $\lambda_{i0} = \kappa / A_i$, where A_i is the area of patch i; the rate of colonisation decreases with distance between patches, and the rate of local extinction decreases with patch area.

Persistence times

How do we evaluate the expected time to (total) extinction?

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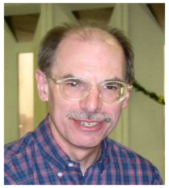
Mangel and Tier's* Fact 2: "There is a simple and direct method for the computation of persistence times that virtually all biologists can use".

*Mangel, M. and Tier, C. (1994) Four facts every conservation biologist should know about persistence. Ecology 75, 607–614.



Persistence times - my take on it

Every undergraduate mathematician is (or should be) familiar with the following:

Theorem For a Markov chain with transition rates $Q = (q(m,n), m, n \in S)$, whose state space S (possibly infinite) includes a subset E which is reached with probability 1, the expected time τ_i it takes to reach E starting in state i is the minimal non-negative solution to $\sum_{i \in S} q(i,j)\tau_j + 1 = 0$, $i \notin E$, with $\tau_i = 0$ for $i \in E$.

For birth-death processes

For birth-death processes (such as the SL model) with birth rates (a_n) and death rates (b_n), the expected time $\tau_i(N)$ it takes to reach (the extinction state) 0 starting in state i is given by

$$\tau_i(N) = \sum_{j=1}^{i} \frac{1}{b_j \pi_j} \sum_{k=j}^{N} \pi_k, \quad \text{with } \tau_0(N) = 0,$$

where the “potential coefficients” (π_j) are given by $\pi_1 = 1$ and $\pi_j = \prod_{k=2}^{j} (a_{k-1}/b_k)$ for $j \geq 2$.

(This formula is valid in the infinite state-space case, replacing N by ∞.)

For the SL model

For the SL model, the expected time to total extinction starting with i patches occupied is given by

$$\tau_i(N) = \frac{1}{e} \sum_{j=1}^{i} \sum_{k=0}^{N-j} \frac{1}{j+k} \prod_{l=0}^{k-1} \left(\frac{N-j-l}{N\rho} \right).$$

(Recall that $\rho = e/c$, where c is the colonisation rate and e is the local extinction rate.)

Whilst this admits further simplification, the form given reflects the algorithm one might use to evaluate $\tau_i(N)$, the product being evaluated recursively, and the sums evaluated in such a way as to minimize round-off error.

For the SL model

This is far from being an explicit formula.

$$\tau_i(N) = \frac{1}{e}\sum_{j=1}^{i}\sum_{k=0}^{N-j}\frac{1}{j+k}\prod_{l=0}^{k-1}\left(\frac{N-j-l}{N\rho}\right).$$

For the SL model ($\rho < 1$)

Note. Tilde ($\sim$) here has the following interpretation:
$a_N \sim b_N$ as $N \to \infty$ means $a_N / b_N \to 1$.

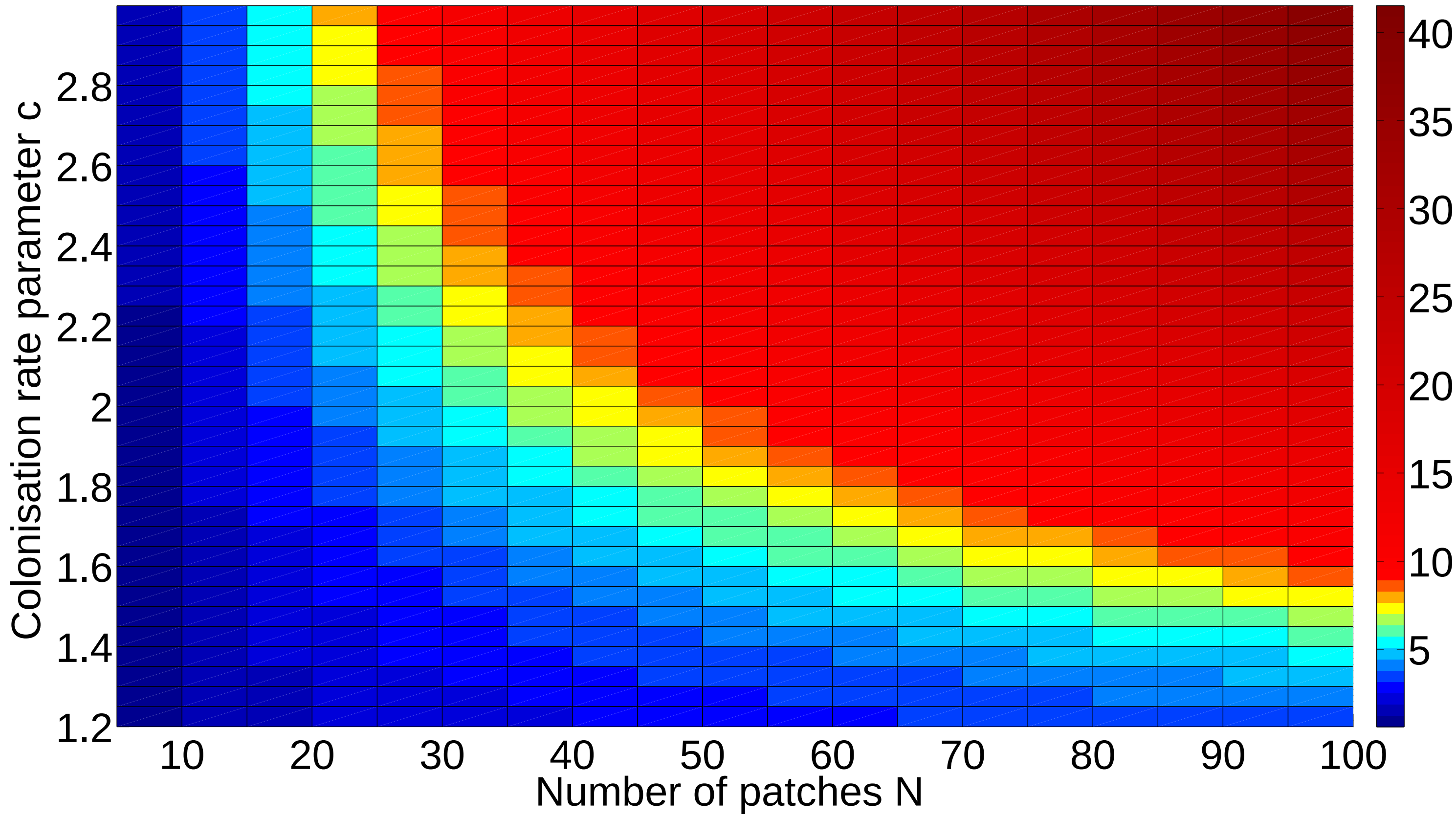
Theorem. If $\rho < 1$, then

$$\tau_i(N) \sim \frac{1-\rho^i}{c(1-\rho)^2}\left(\frac{e^{-(1-\rho)}}{\rho}\right)^N \sqrt{\frac{2\pi}{N}} \quad \text{as } N \to \infty.$$

With correction:

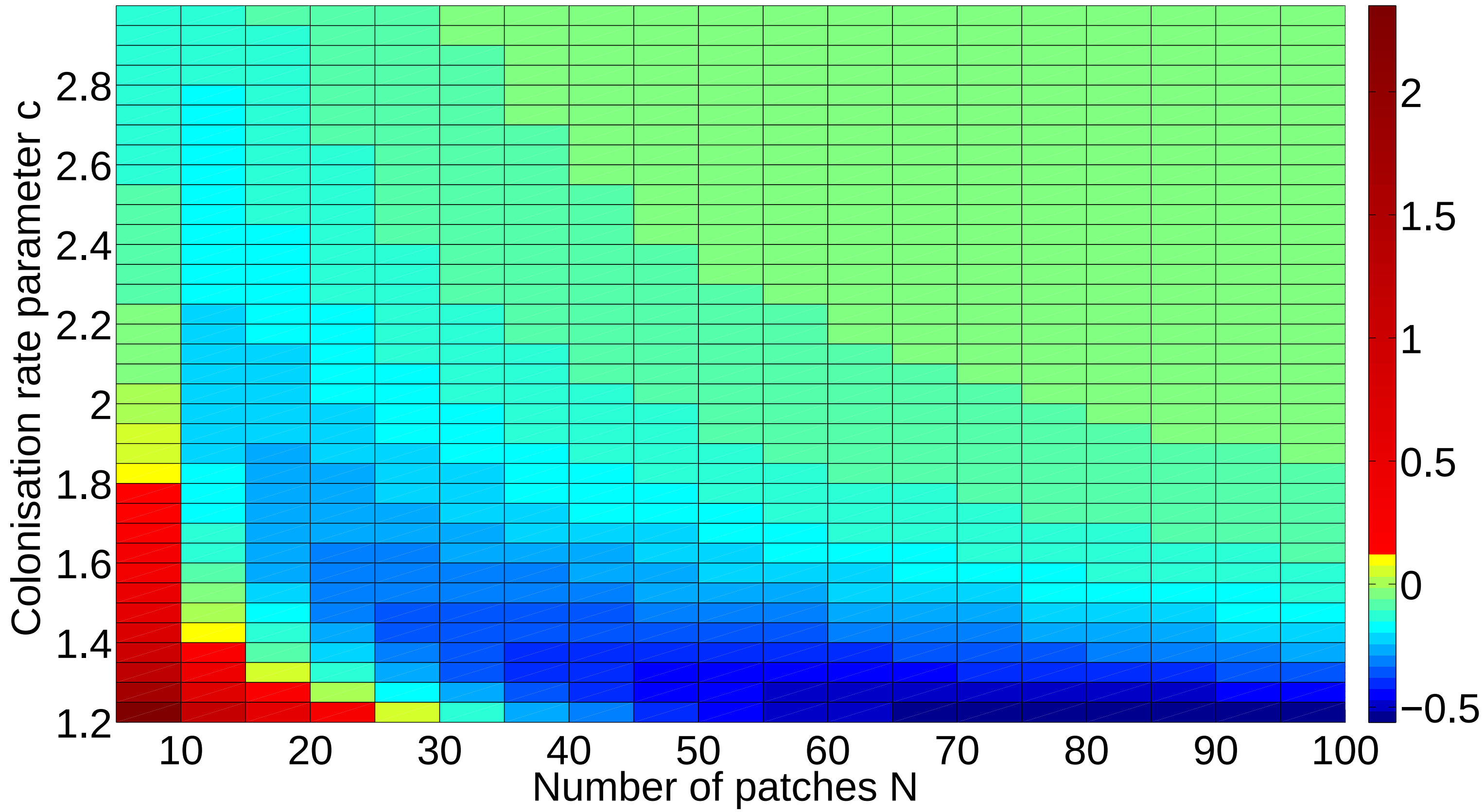
$$\tau_i(N) \simeq \frac{1}{c(1-\rho)}\left\{\left(\frac{1-\rho^i}{1-\rho}\right)\left(\frac{e^{-(1-\rho)}}{\rho}\right)^N \sqrt{\frac{2\pi}{N}} - \sum_{k=1}^{i-1} \frac{(1-\rho^{i-k})}{k}\right\}.$$

The approximation



Log_{10} of approximated expected time to extinction. The initial number of occupied patches is $n(0) = N/5$ and $e = 1$.

The approximation



Relative error in the approximation. The initial number of occupied patches is $n(0) = N/5$ and $e = 1$.

Bonus theorem: for the SL model ($\rho > 1$)

Theorem. If $\rho > 1$, then

$$\tau_i(N) \sim \frac{\rho^i - 1}{c(\rho - 1)} \log\left(\frac{\rho}{\rho - 1}\right) \quad \text{as } N \to \infty.$$

With correction:

$$\tau_i(N) \simeq \frac{1}{c(\rho - 1)} \left\{ (\rho^i - 1) \log\left(\frac{\rho}{\rho - 1}\right) - \sum_{k=1}^{i-1} \frac{(\rho^{i-k} - 1)}{k} \right\}.$$