Metapopulations: from network models to patch occupancy models

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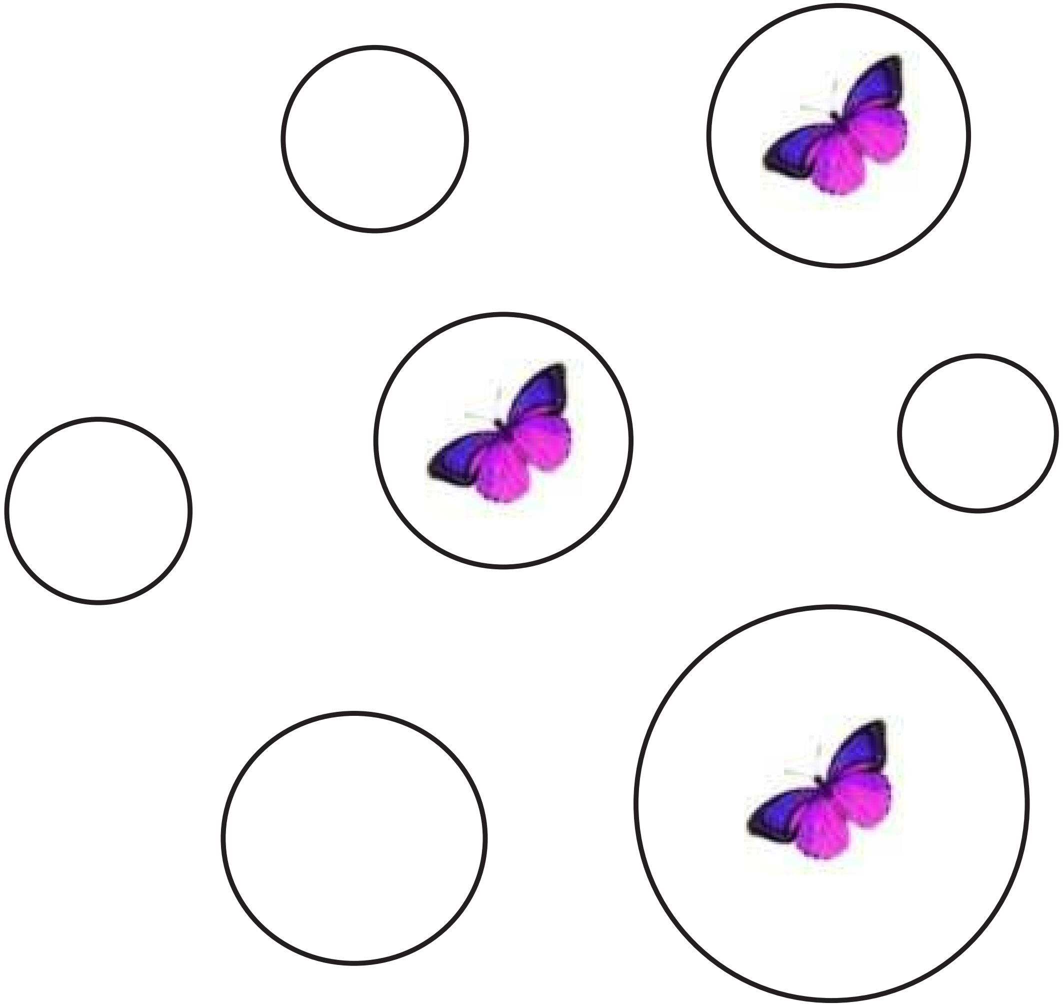
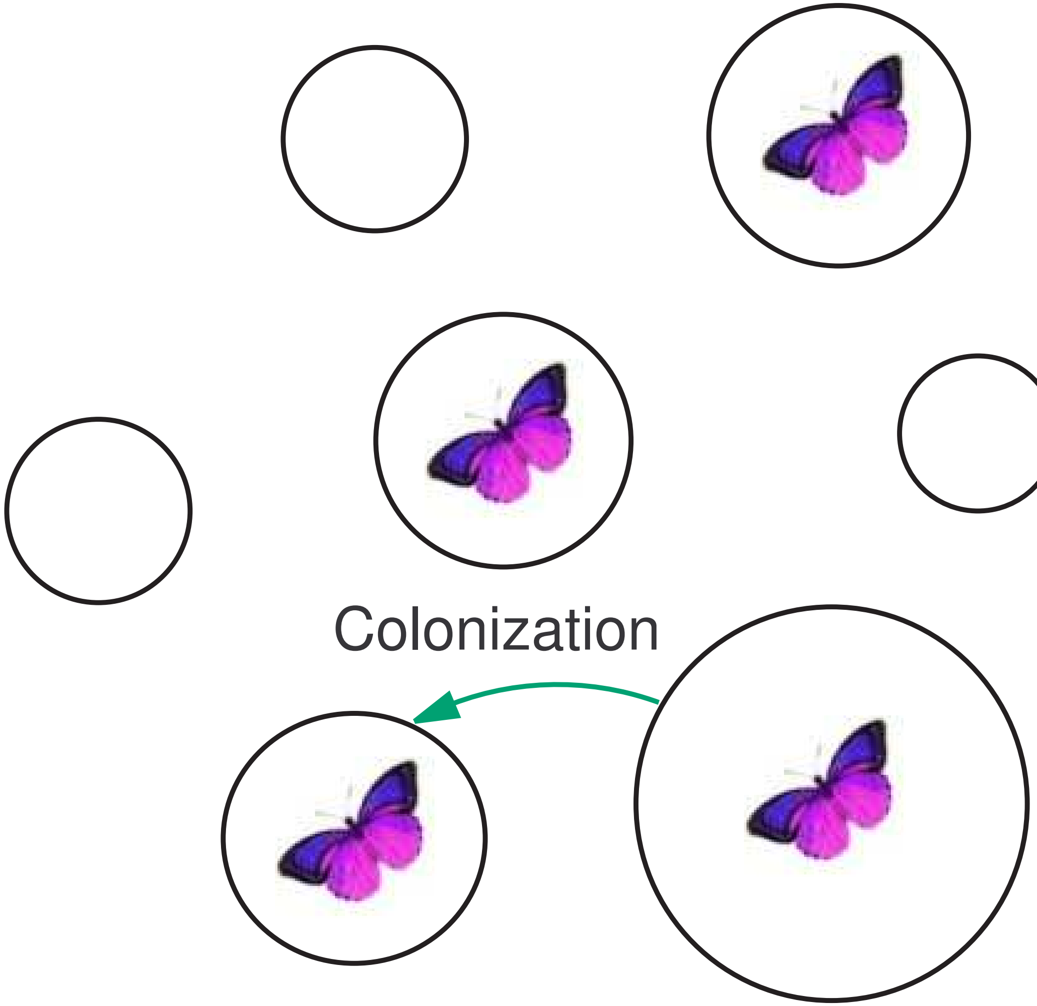
Metapopulations



Metapopulations



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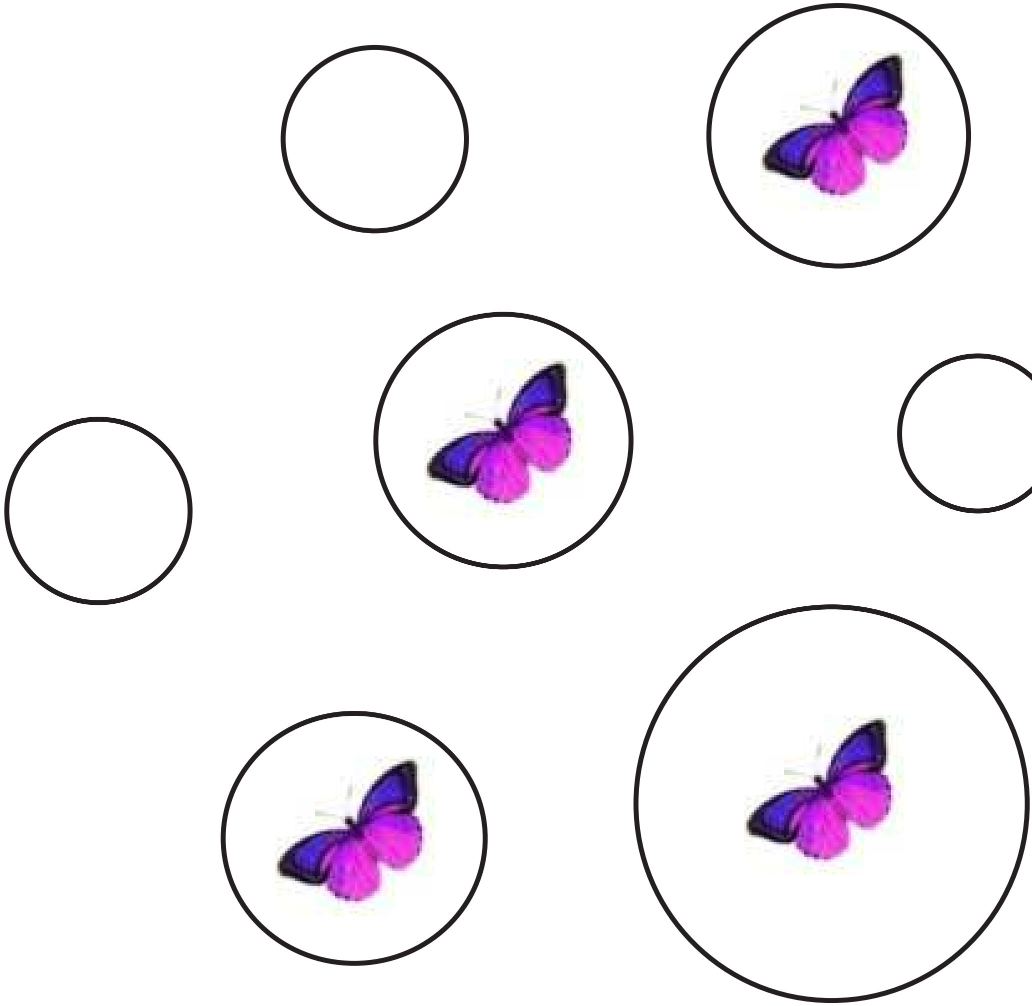

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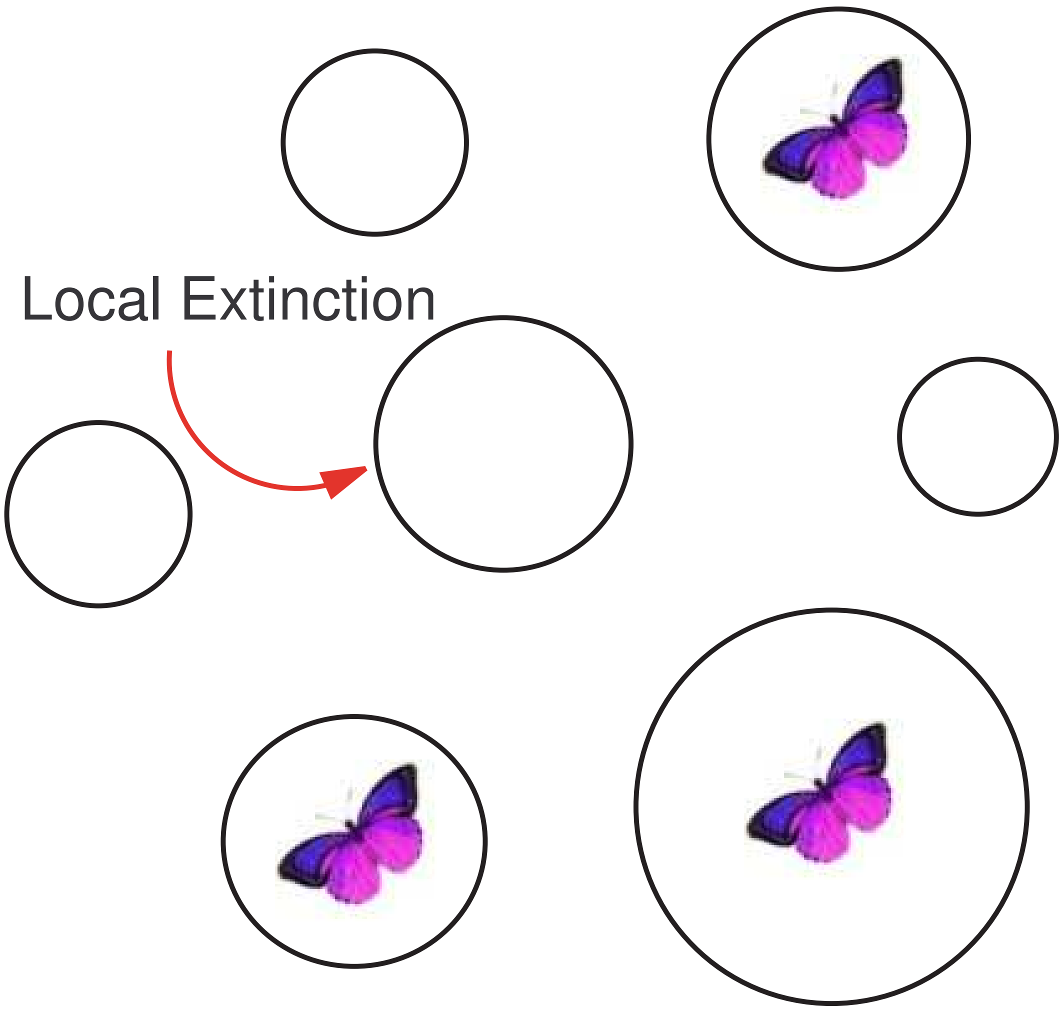
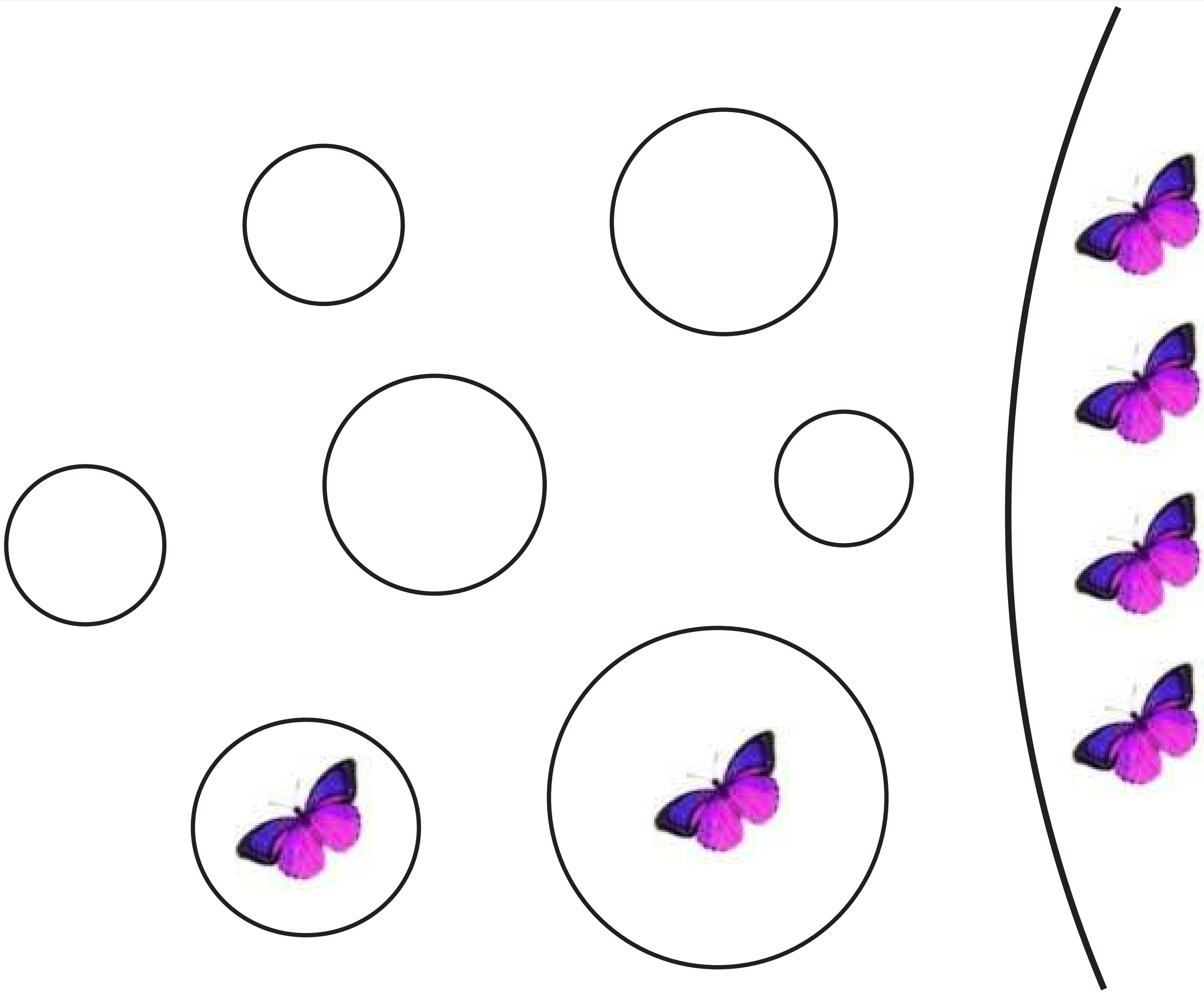


Mainland-island configuration



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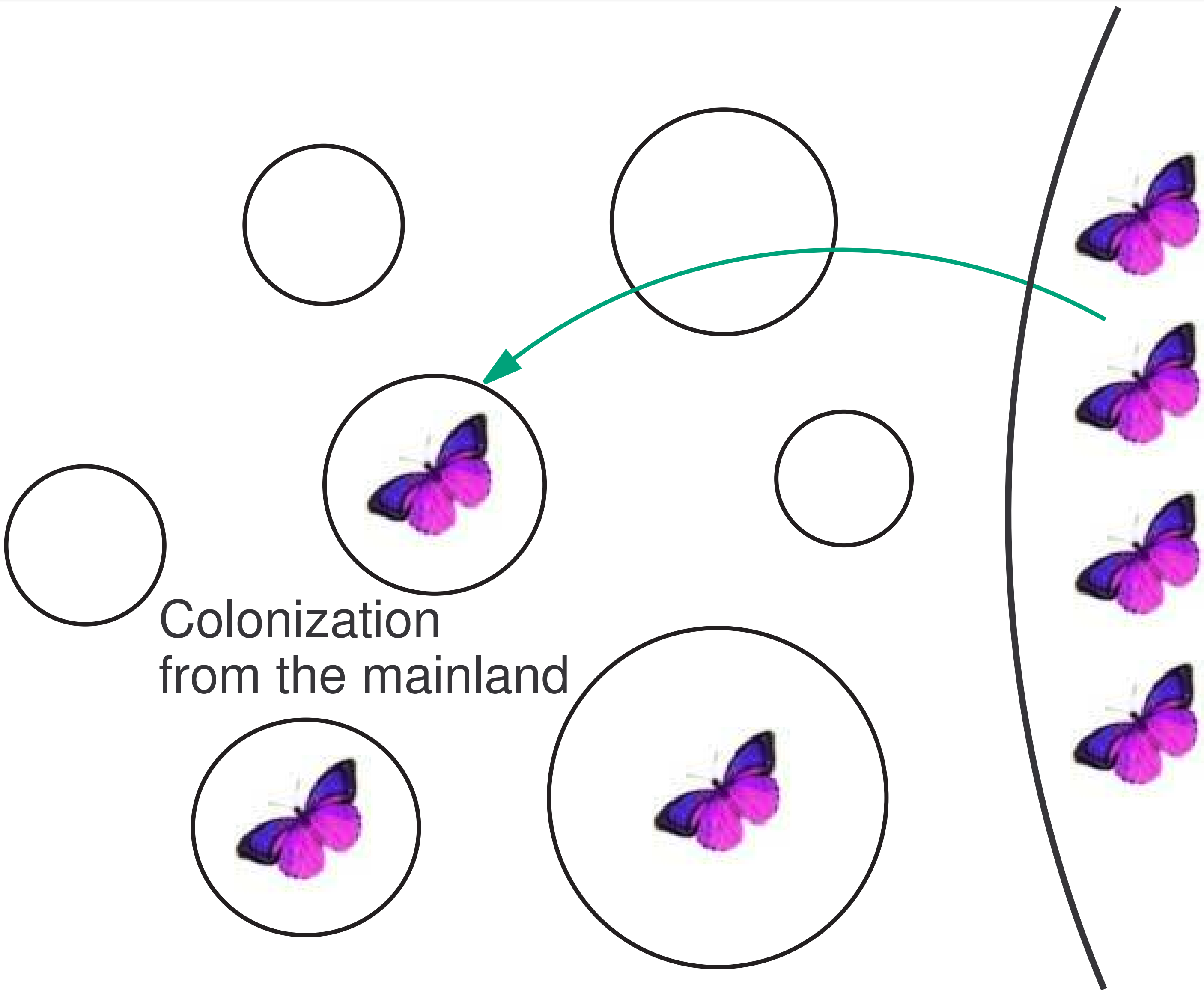

The simplest models

We record the *number* $n(t)$ of occupied patches at each time t.

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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 stochastic mainland-island model

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

$$n \to n+1 \quad \text{at rate} \quad v(N-n) + \frac{c}{N} n\,(N-n)$$

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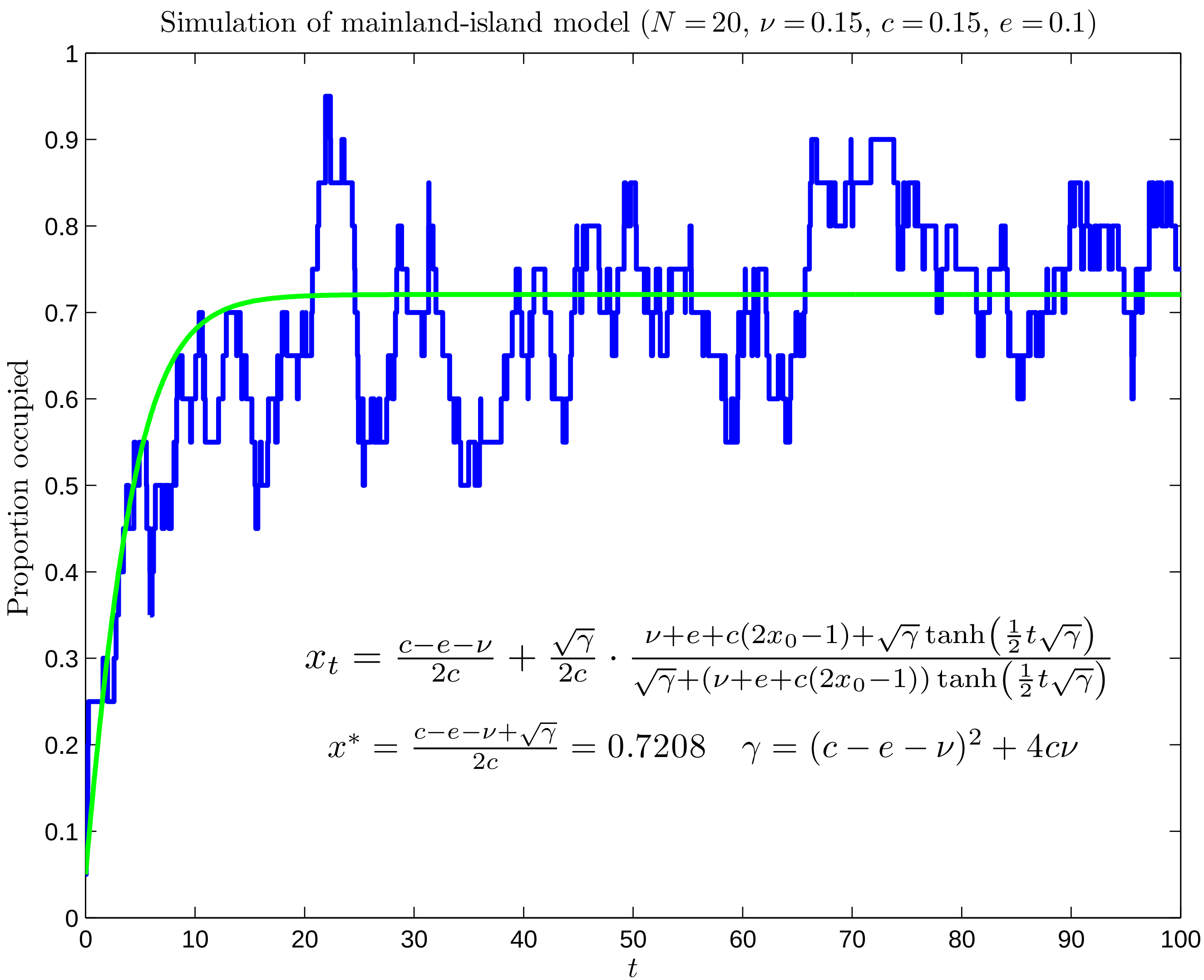
This embellishment of Feller's *stochastic logistic (SL) model* was studied by J.V. Ross.

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.

Simulation of SL model with immigration

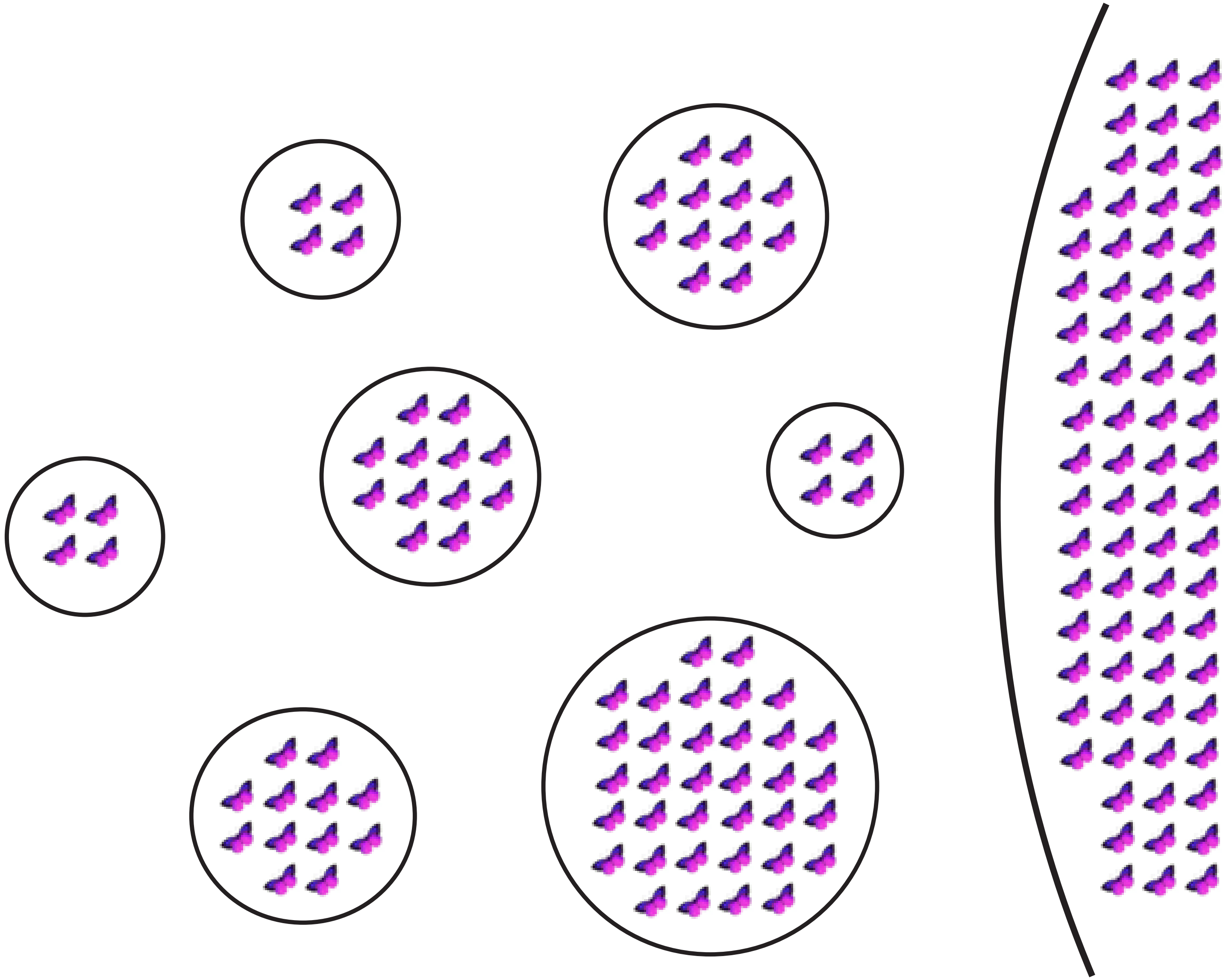


Network model

We now record the *numbers* of individuals in the various patches: a typical state is $\boldsymbol{n} = (n_1, \ldots, n_N)$, where n_j is the number of individuals in patch j.

We consider here only *open* systems, where individuals may enter or leave the patch network through external immigration *from the mainland* and external emigration or removal.

Network model



Network model - ingredients

N – number of patches

ν_i – external immigration rate at patch i (independent poisson processes)

$\phi_j(n)$ – propagation rate when n individuals present at patch j – for example:

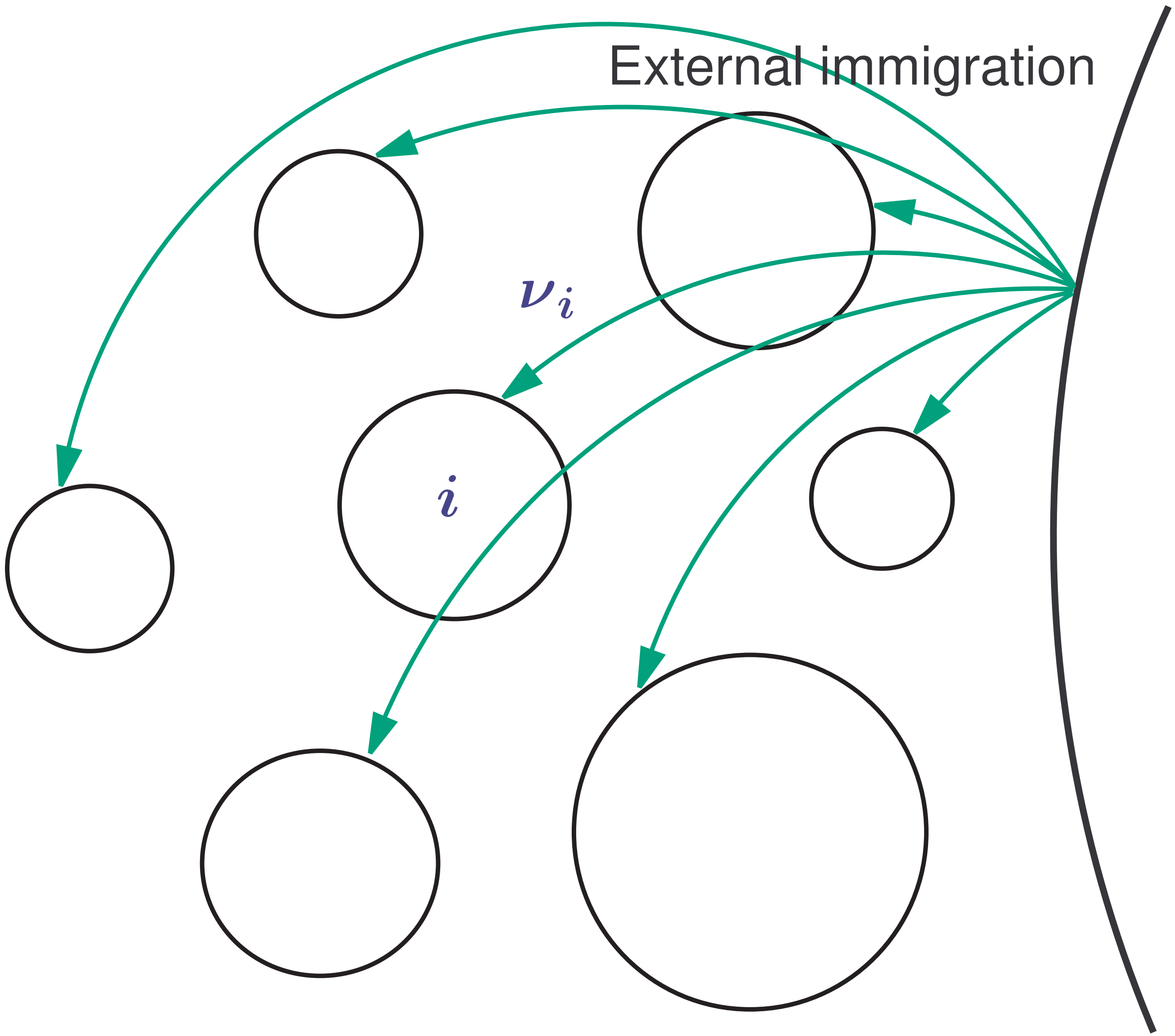
"constant" $\phi_j(n) = \phi_j 1_{\{n>0\}}$

"linear" $\phi_j(n) = \phi_j n$

λ_{ij} – proportion of propagules emanating from patch i that are destined for patch j

λ_{i0} – proportion of propagules emanating from patch i that leave the network

Network model



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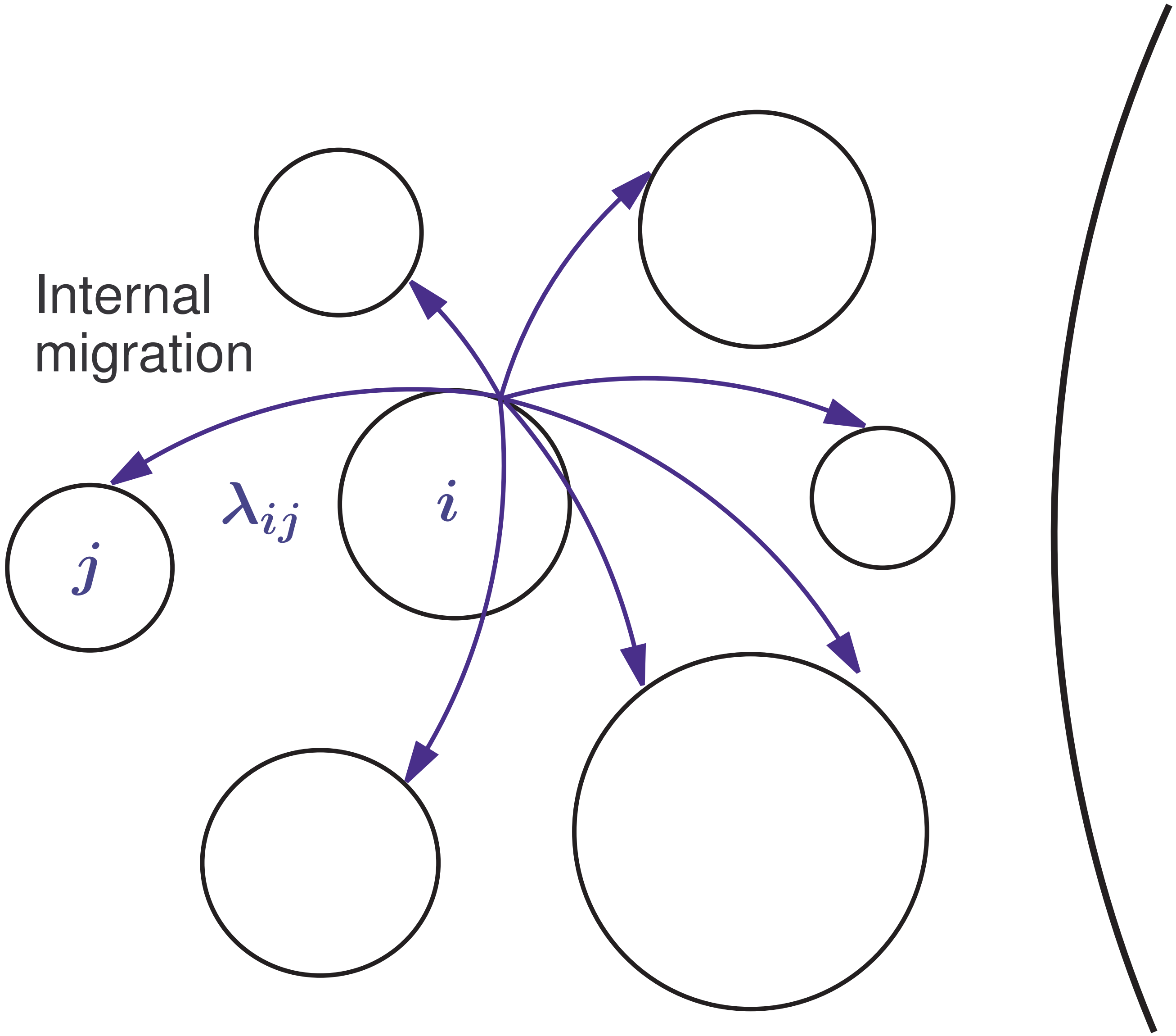

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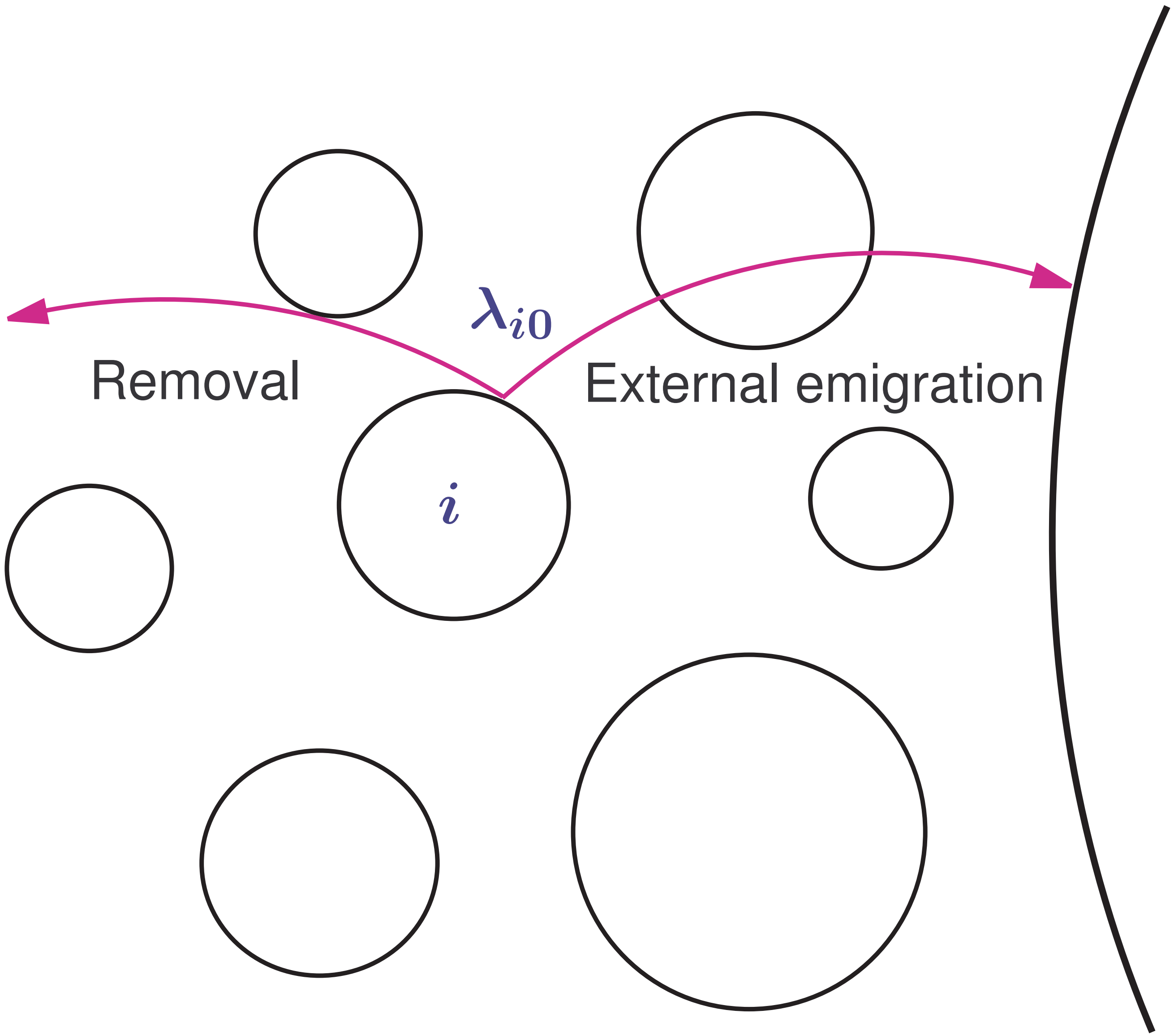

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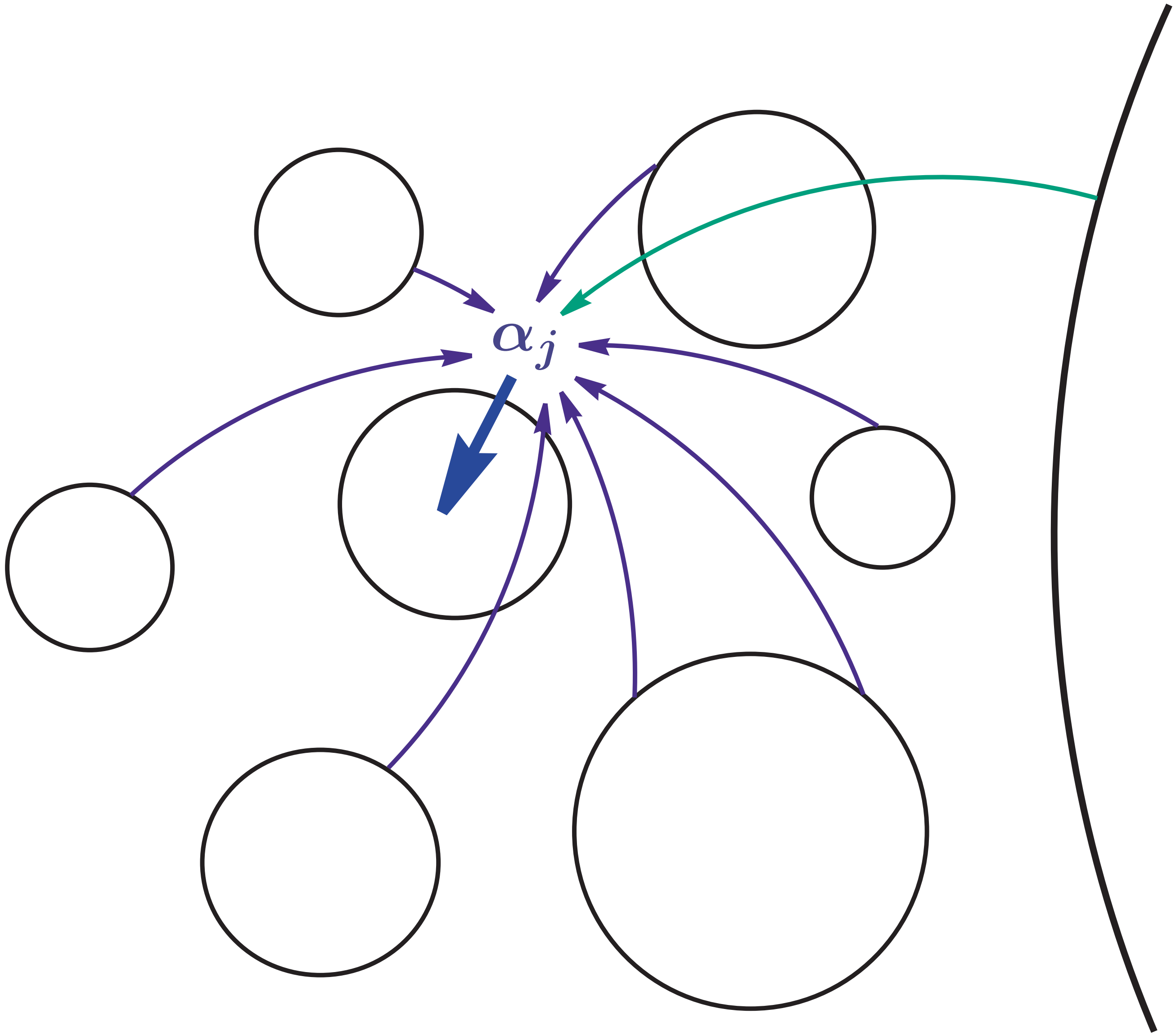

Network model

If the *routing matrix* $\Lambda = (\lambda_{ij})$ is "irreducible", then there is a unique positive solution $(\alpha_1, \ldots, \alpha_N)$ to the equations

$$\alpha_j = \nu_j + \sum_i \alpha_i \lambda_{ij} \quad (j = 1, \ldots, N),$$

and it is easy to show that α_j is the (equilibrium expected) *arrival rate* at patch j.

Network model

I have described the *migration process* of Whittle*.

*Whittle, P. (1967) Nonlinear migration processes. Bull. Inst. Int. Statist. 42, 642–647.

(Constant rates: Jackson, R.R.P. (1954) Queueing systems with phase-type service. Operat. Res. Quart. 5, 109–120.)

The Markov chain $(\boldsymbol{n}(t), t \geq 0)$ has state space $S = Z_+^N$ and transition rates

$$q(\boldsymbol{n}, \boldsymbol{n} + \boldsymbol{e}_j) = \nu_j \quad \text{(external arrival at patch } j\text{)}$$

$$q(\boldsymbol{n}, \boldsymbol{n} - \boldsymbol{e}_i) = \phi_i(n_i)\lambda_{i0} \quad \text{(removal from patch } i\text{)}$$

$$q(\boldsymbol{n}, \boldsymbol{n} - \boldsymbol{e}_i + \boldsymbol{e}_j) = \phi_i(n_i)\lambda_{ij} \quad \text{(migration from } i \text{ to } j\text{)}.$$

($\boldsymbol{e}_j$ is the unit vector in Z_+^N with a 1 as its j-th entry)

Network model

The equilibrium behaviour of migration processes is well understood.

Let $\pi(\boldsymbol{n})$ be the equilibrium probability of configuration $\boldsymbol{n} = (n_1, \ldots, n_N)$.

Open migration process

Theorem An equilibrium distribution exists if

$$b_j^{-1} := 1 + \sum_{n=1}^{\infty} \frac{\alpha_j^n}{\prod_{r=1}^{n} \phi_j(r)} < \infty \quad \text{for all } j,$$

in which case

$$\pi(\boldsymbol{n}) = \prod_{j=1}^{N} \pi_j(n_j), \quad \text{where} \quad \pi_j(n) = b_j \frac{\alpha_j^n}{\prod_{r=1}^{n} \phi_j(r)}.$$

Thus, in equilibrium, $n_1, \ldots, n_N$ are *independent* and each patch j behaves *as if* it were isolated with Poisson input at rate α_j.

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For the network model—*but where there is homogeneity among the patches*—what is the corresponding/appropriate patch-occupancy model?

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Is it the SL model with immigration?

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$$n \to n-1 \quad \text{at rate} \quad en$$

Is there a "network interpretation" of c, e and v?

Which patch-occupancy model?

Symmetric networks

N – number of patches

ν – common external immigration rate

$\phi(n)$ – common propagation rate when n individuals present at that patch – two cases:

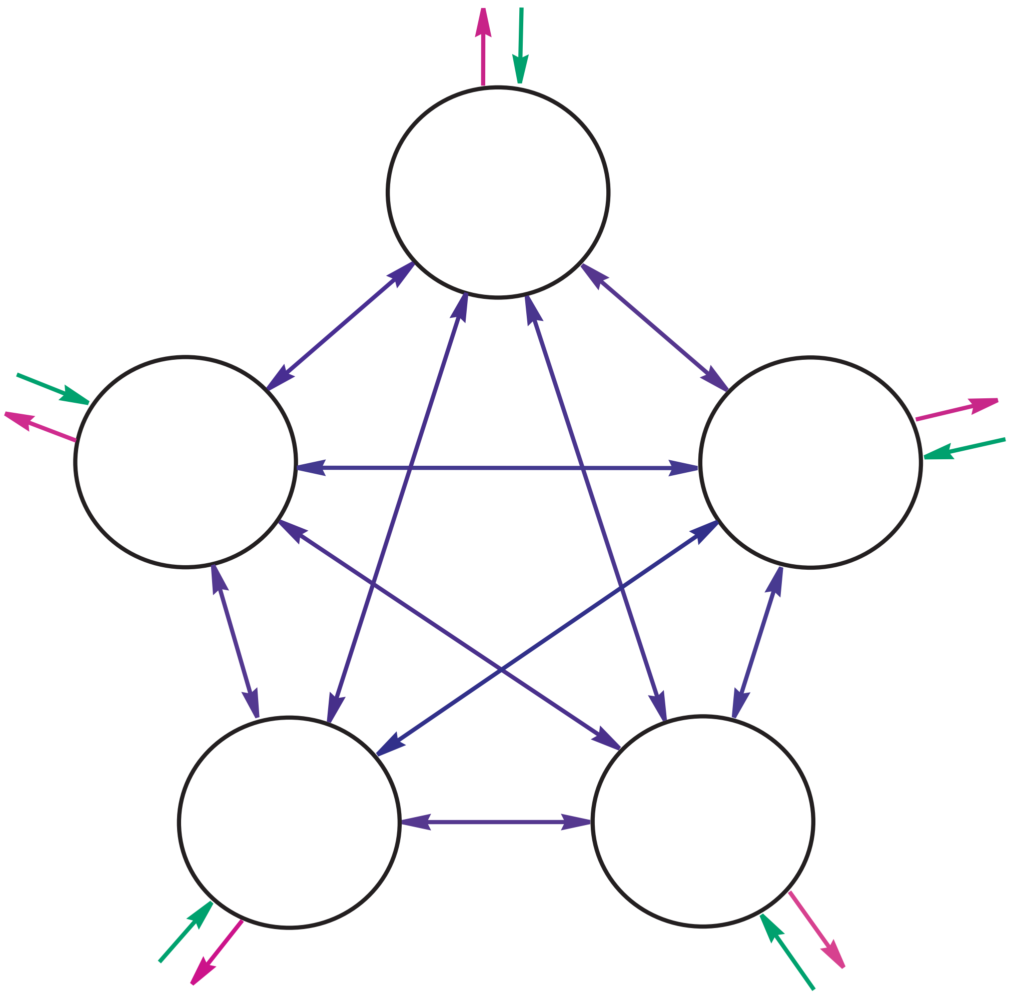
"constant" $\phi(n) = \phi 1_{\{n>0\}}$ $\rho := \nu/(\phi\lambda_0)$ (< 1)

"linear" $\phi(n) = \phi n$ $r := \nu/(\phi\lambda_0)$

λ_0 – common external emigration/removal probability

λ_{ij} = $(1 - \lambda_0)/(N - 1)$

Symmetric network



Which patch-occupancy model?

We will evaluate

(i) the equilibrium expected colonization rate $c(m)$, that is, *the expected arrival rate at unoccupied patches, conditional on there being m patches occupied*, and,

(ii) the equilibrium expected local extinction rate $e(m)$, that is, *the expected rate at which empty patches appear, conditional on there being m patches occupied*.

Which patch-occupancy model?

Let $C(\boldsymbol{n}) = \sum_k 1_{\{n_k(t)>0\}}$ be the number of occupied patches when the network is in state $\boldsymbol{n}$. Then,

$$c(m) = \mathsf{E}\left(\sum_j \left(\nu_j + \sum_{i\neq j}\phi_i(n_i(t))\lambda_{ij}\right)1_{\{n_j(t)=0\}}\middle| C(\boldsymbol{n}) = m\right)$$

$$= \sum_j \nu_j \Pr(n_j(t) = 0 | C(\boldsymbol{n}) = m)$$

$$+ \sum_j \sum_{i\neq j} \mathsf{E}\left(\phi_i(n_i(t))1_{\{n_j(t)=0\}}\middle| C(\boldsymbol{n}) = m\right)\lambda_{ij}.$$

Which patch-occupancy model?

Owing to the symmetry ...

$$c(m) = N\nu \, \Pr(n_1(t) = 0 | C(\boldsymbol{n}) = m)$$

$$+N(N-1)\mathsf{E}\left(\phi(n_1(t))1_{\{n_2(t)=0\}}\middle|C(\boldsymbol{n}) = m\right)\frac{1-\lambda_0}{N-1}$$

$$= N\nu\left(1 - \frac{m}{N}\right) + (1-\lambda_0)N\,\mathsf{E}\left(\phi(n_1(t))1_{\{n_2(t)=0\}}\middle|C(\boldsymbol{n}) = m\right)$$

Which patch-occupancy model?

$$
\begin{aligned}
e(m) &= \mathsf{E}\left(\sum_i \phi_i(1) 1_{\{n_i(t)=1\}} \middle| C(\boldsymbol{n}) = m\right) \\
&= \sum_i \phi_i(1) \Pr(n_i(t) = 1 | C(\boldsymbol{n}) = m) \\
&= N\phi(1) \Pr(n_1(t) = 1 | C(\boldsymbol{n}) = m)
\end{aligned}
$$

Which patch-occupancy model?

Recall that . . .

N	–	number of patches
ν	–	common external immigration rate
$\phi(n)$	–	common propagation rate when n individuals present at that patch – two cases:

"constant" $\phi(n) = \phi 1_{\{n>0\}}$ $\rho := \nu/(\phi\lambda_0)$ (< 1)

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λ_0	–	common external emigration/removal probability
λ_{ij}	=	$(1 - \lambda_0)/(N - 1)$

Equilibrium distributions

Propagation rates	Open network* $\pi_j(n)$ $(n \geq 0)$
Constant	$(1-\rho)\rho^n$
Linear	$e^{-r}\dfrac{r^n}{n!}$

*$n_1, \ldots, n_N$ are independent

Which patch-occupancy model?

We find that

$$c(m) = \nu(N - m) + \frac{c}{N-1} m(N - m) \quad e(m) = em$$

Constant	$c = \phi(1 - \lambda_0)/(1 - \rho)$	$e = \phi(1 - \rho)$
Linear	$c = \phi(1 - \lambda_0) r/(1 - e^{-r})$	$e = \phi r e^{-r}/(1 - e^{-r})$

Which patch-occupancy model?

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Constant	$c = \phi(1-\lambda_0)/(1-\rho)$	$e = \phi(1-\rho)$
Linear	$c = \phi(1-\lambda_0)r/(1-e^{-r})$	$e = \phi r e^{-r}/(1-e^{-r})$

Thus the SL model with immigration is the appropriate patch occupancy model, and we have provided a "network interpretation" of the parameters c, e and ν.

Which patch-occupancy model?

If the propagation rates are linear, we can do much better.

We can evaluate the expected colonization rate and the expected local extinction rate as *time-dependent quantities*. This yields a corresponding *time-inhomogeneous* SL model with immigration:

$$c_t(m) = \nu(N-m) + \frac{c_t}{N-1} m(N-m) \quad e_t(m) = e_t m.$$

Here $c_t = \phi(1-\lambda_0)r_t/(1-e^{-r_t})$, $e_t = \phi r_t e^{-r_t}/(1-e^{-r_t})$, where $r_t = \nu(1-e^{-\phi\lambda_0 t})/(\phi\lambda_0)$.

Sneak peek - closed network

For the symmetric closed network with a fixed number M of individuals

Closed constant

$$c(m) = \frac{\phi}{N-1} m(N-m) \quad e(m) = \phi M \frac{m(m-1)}{(M+m-1)(M+m-2)}$$

Closed linear

$$c(m) = \frac{M\phi}{N-1}(N-m) \quad e(m) = \phi M m \frac{b_{m-1}(M-1)}{b_m(M)}$$

where

$$b_m(M) = \sum_{k=0}^{m-1} (-1)^k \binom{m}{k} (m-k)^M \ (m = 1, \ldots, N) \ \ b_0(M) = \delta_{M0}$$

Local population dynamics

We have not attempted to account for local population dynamics (within patches).

Here is a simple embellishment that separates emigration from death:

$$q(\boldsymbol{n}, \boldsymbol{n} + \boldsymbol{e}_j) = \nu_j$$

$$q(\boldsymbol{n}, \boldsymbol{n} - \boldsymbol{e}_i) = d_i n_i + \phi_i(n_i)\lambda_{i0}$$

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per-capita death rate

Local population dynamics

For example, with linear propagation rates ...

$$q(\boldsymbol{n}, \boldsymbol{n} + \boldsymbol{e}_j) = \nu_j$$

$$q(\boldsymbol{n}, \boldsymbol{n} - \boldsymbol{e}_i) = d_i n_i + \phi_i n_i \lambda_{i0} = \phi_i n_i \lambda'_{i0}$$

$$q(\boldsymbol{n}, \boldsymbol{n} - \boldsymbol{e}_i + \boldsymbol{e}_j) = \phi_i n_i \lambda_{ij}$$

where $\lambda'_{i0} = \lambda_{i0} + d_i/\phi_i$.

(This can be accommodated within the present setup with some minor adjustments.)

Local population dynamics

And, something a little more complicated ...

Let $S = \{0, \ldots, N_1\} \times \cdots \times \{0, \ldots, N_k\}$ and define non-zero transition rates as

$$q(\boldsymbol{n}, \boldsymbol{n} + \boldsymbol{e}_i) = \nu_i + b_i \frac{n_i}{N_i}(N_i - n_i)$$

$$q(\boldsymbol{n}, \boldsymbol{n} - \boldsymbol{e}_i + \boldsymbol{e}_j) = \phi_i(n_i)\lambda_{ij}$$

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Here N_i is the population ceiling at patch i.

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Local population dynamics are in accordance with the stochastic logistic model.