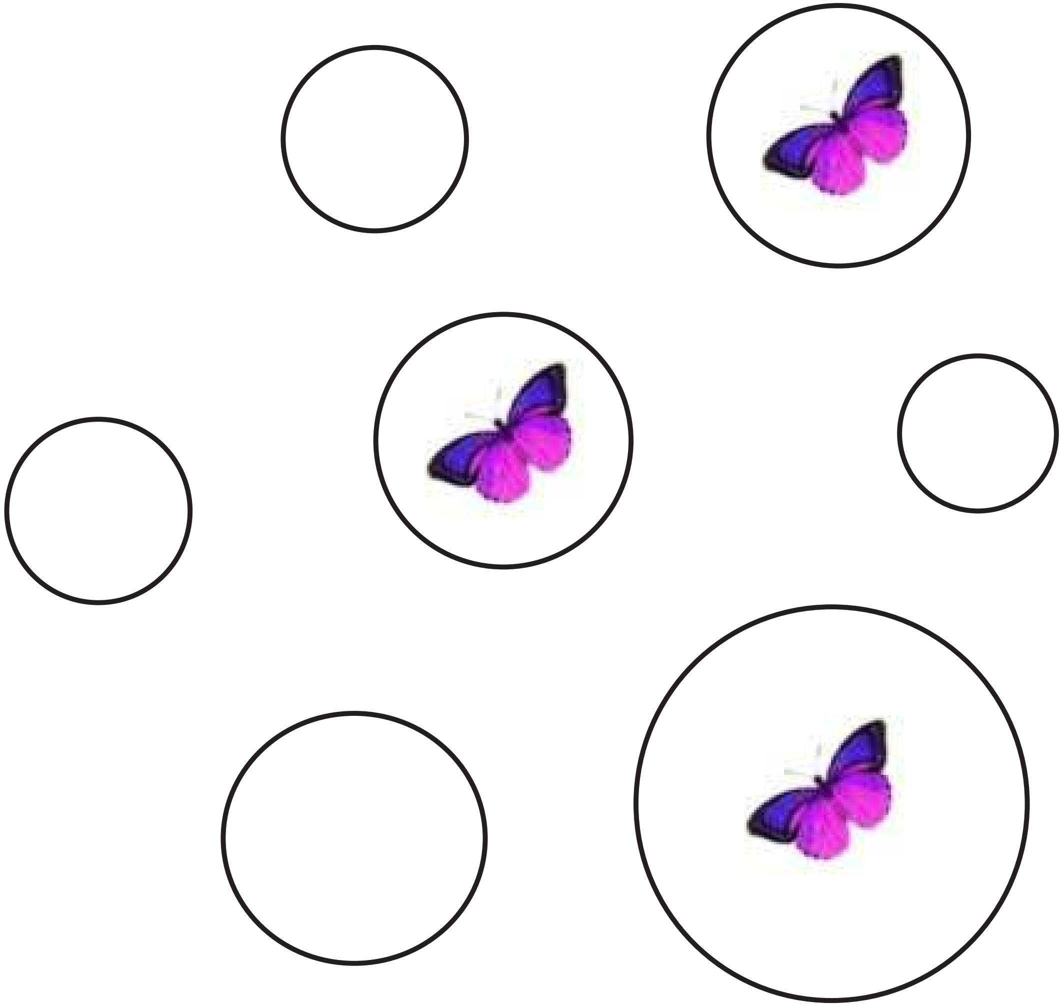
Stochastic models for population networks

Phil Pollett

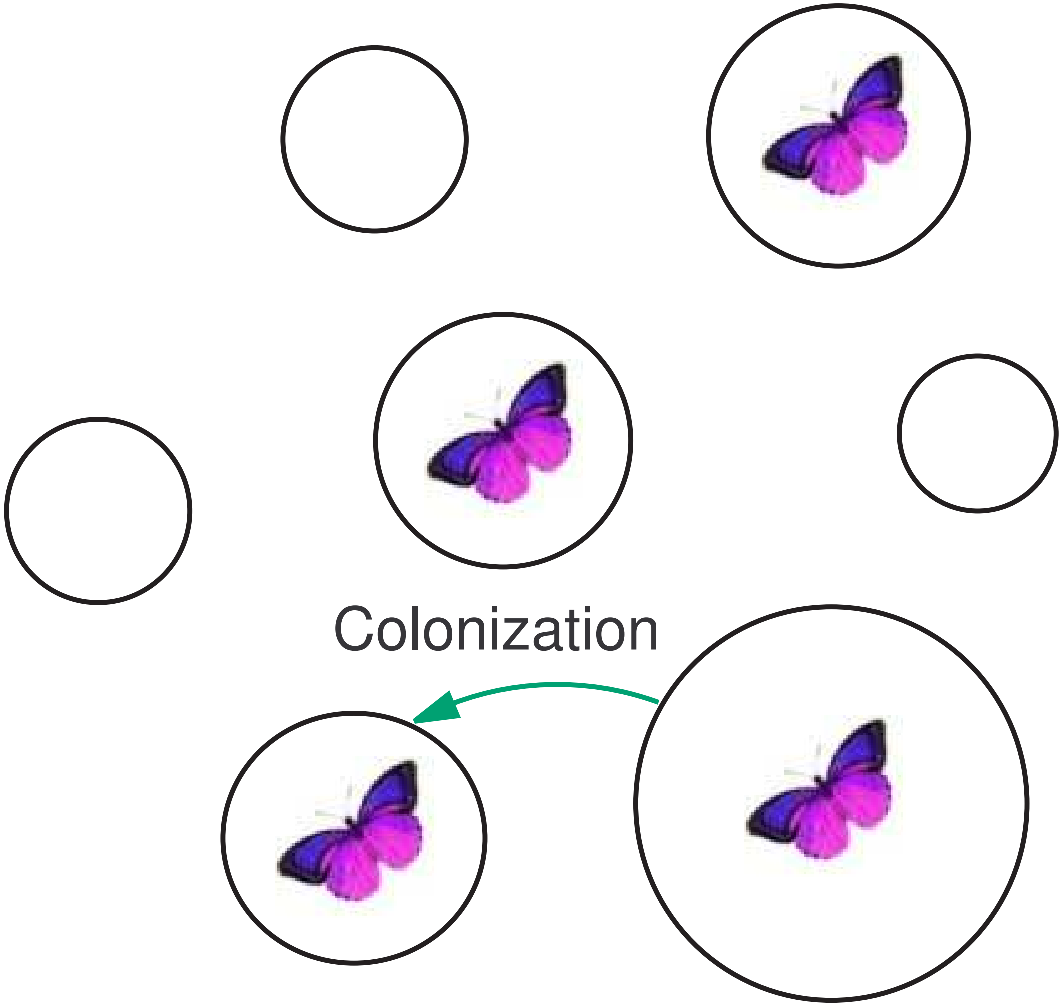
Department of Mathematics
The University of Queensland
`http://www.maths.uq.edu.au/~pkp`

Australian Research Council
Centre of Excellence for Mathematics
and Statistics of Complex Systems

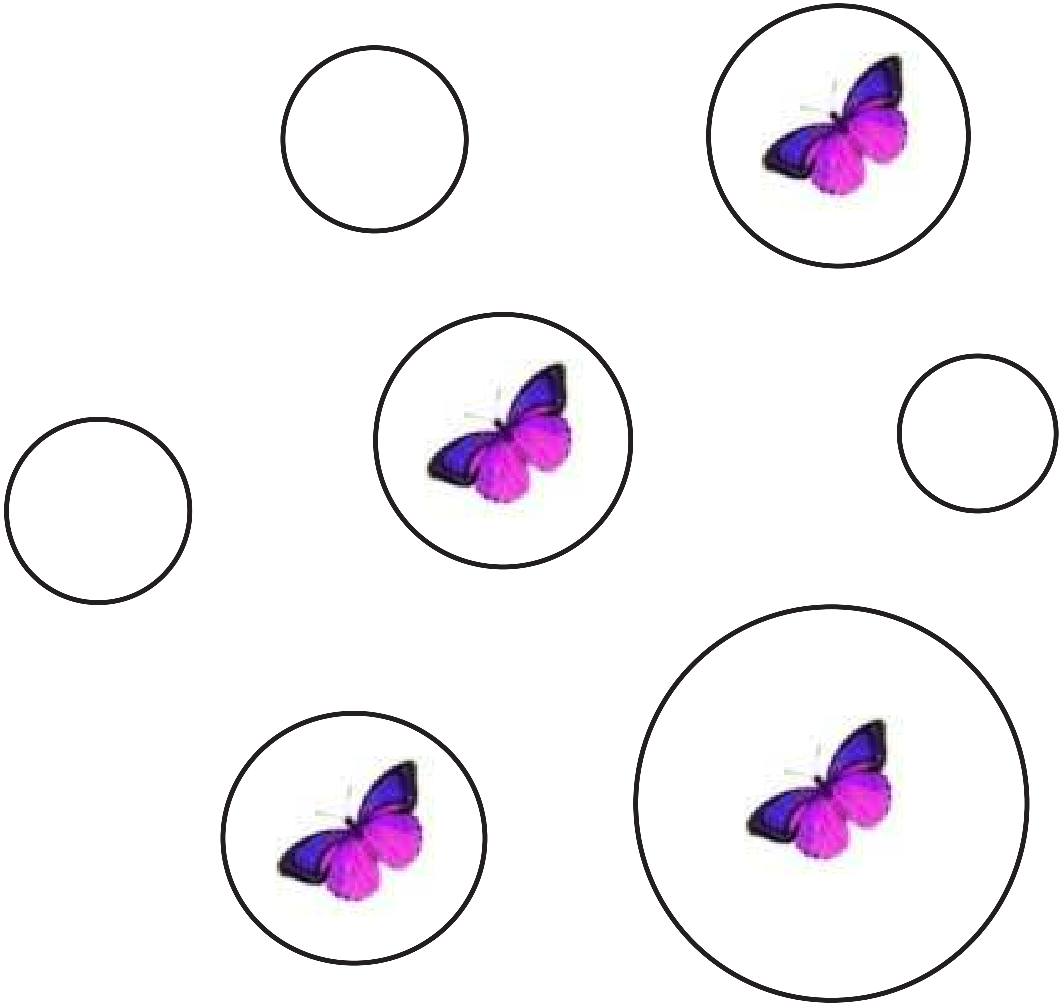
Metapopulations



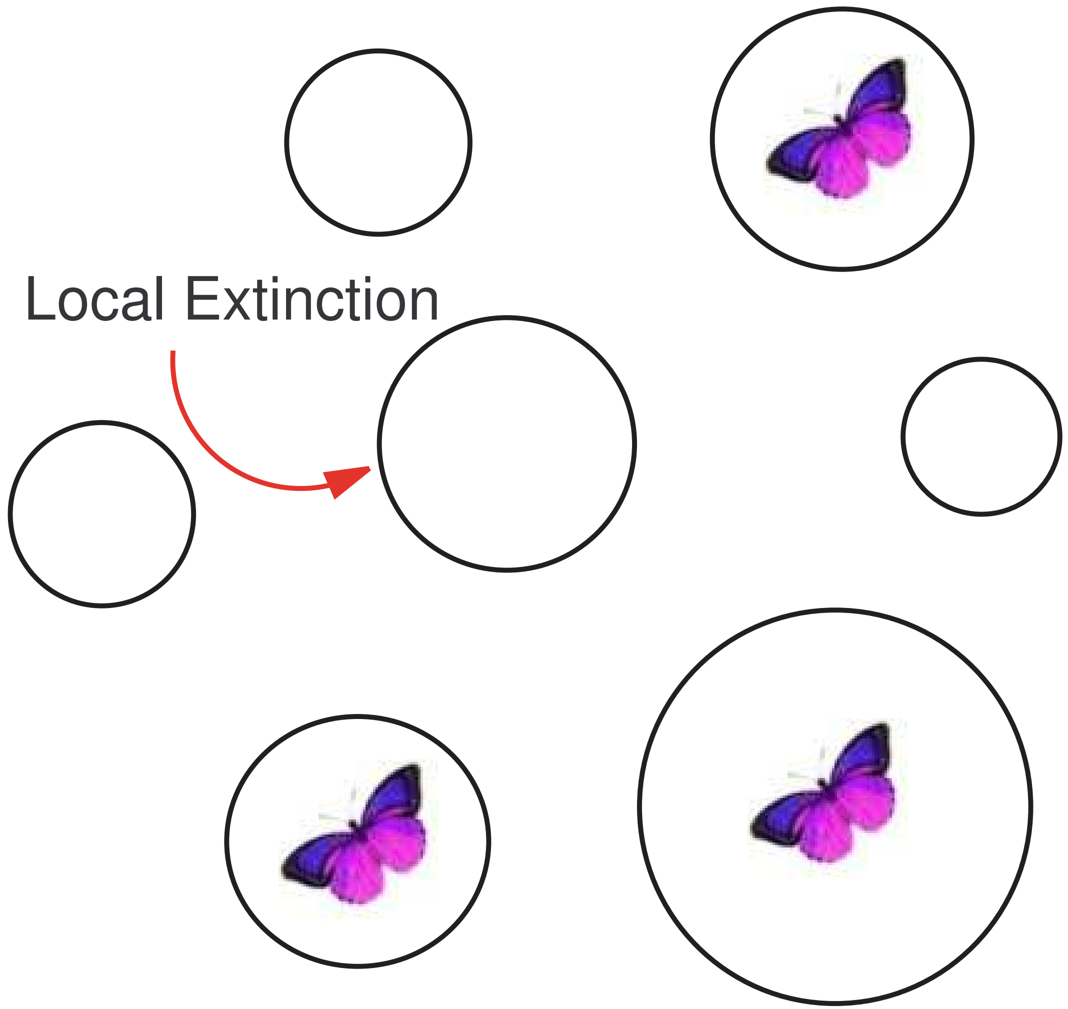
Metapopulations



Metapopulations



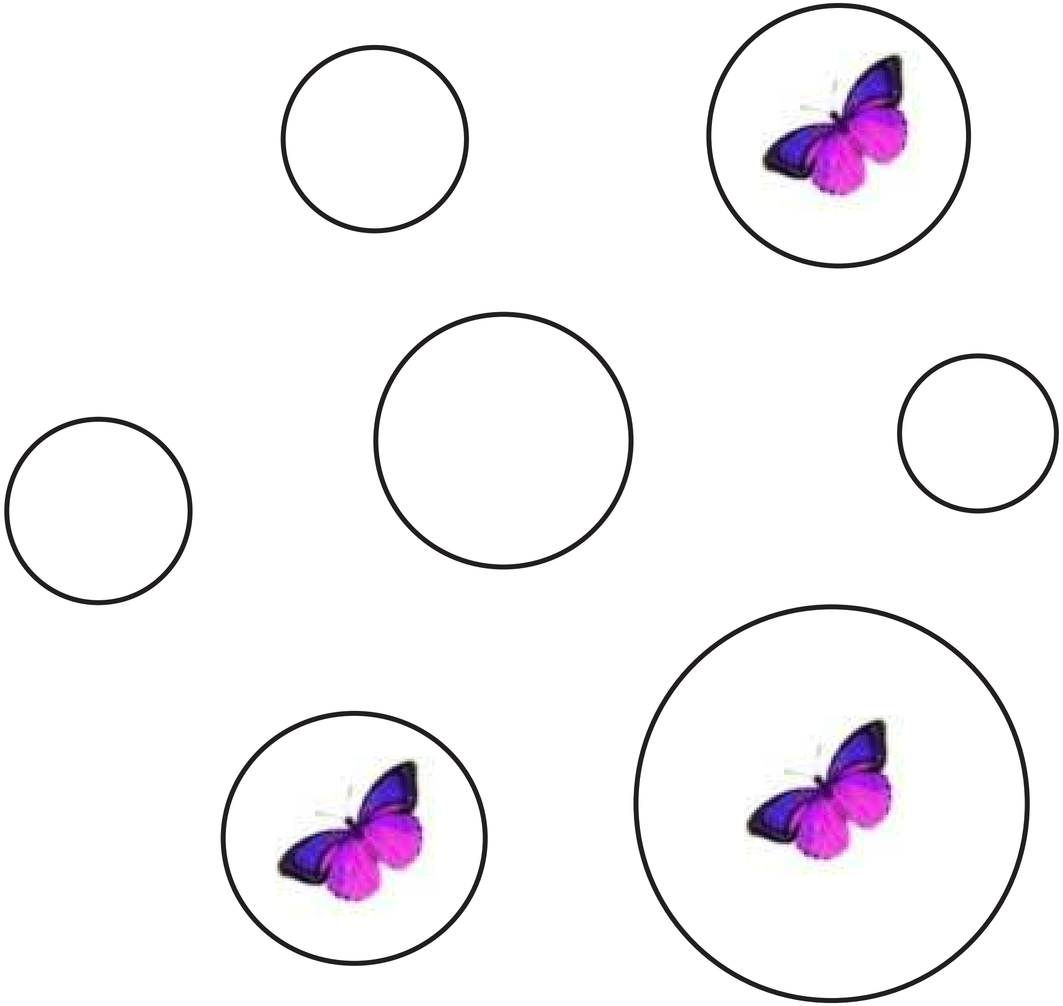
Metapopulations



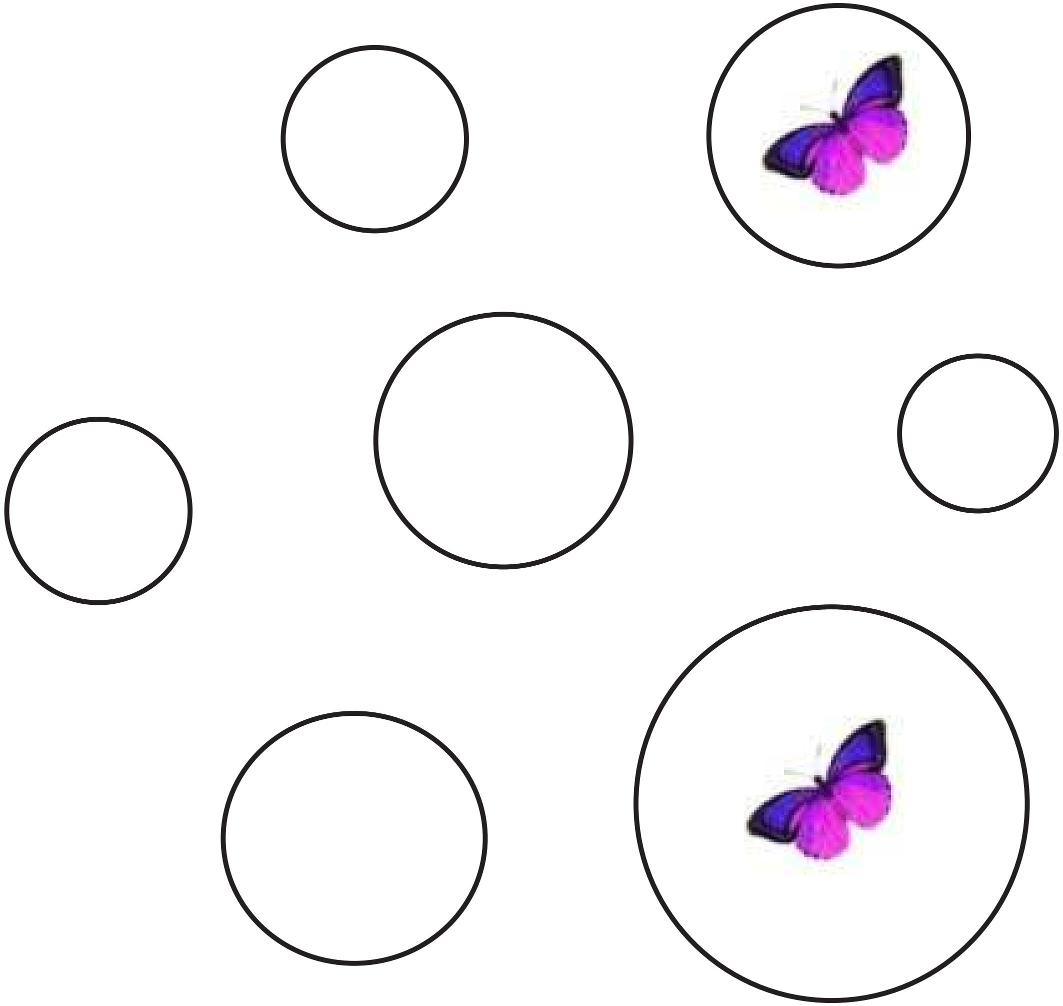
Metapopulations

- 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.

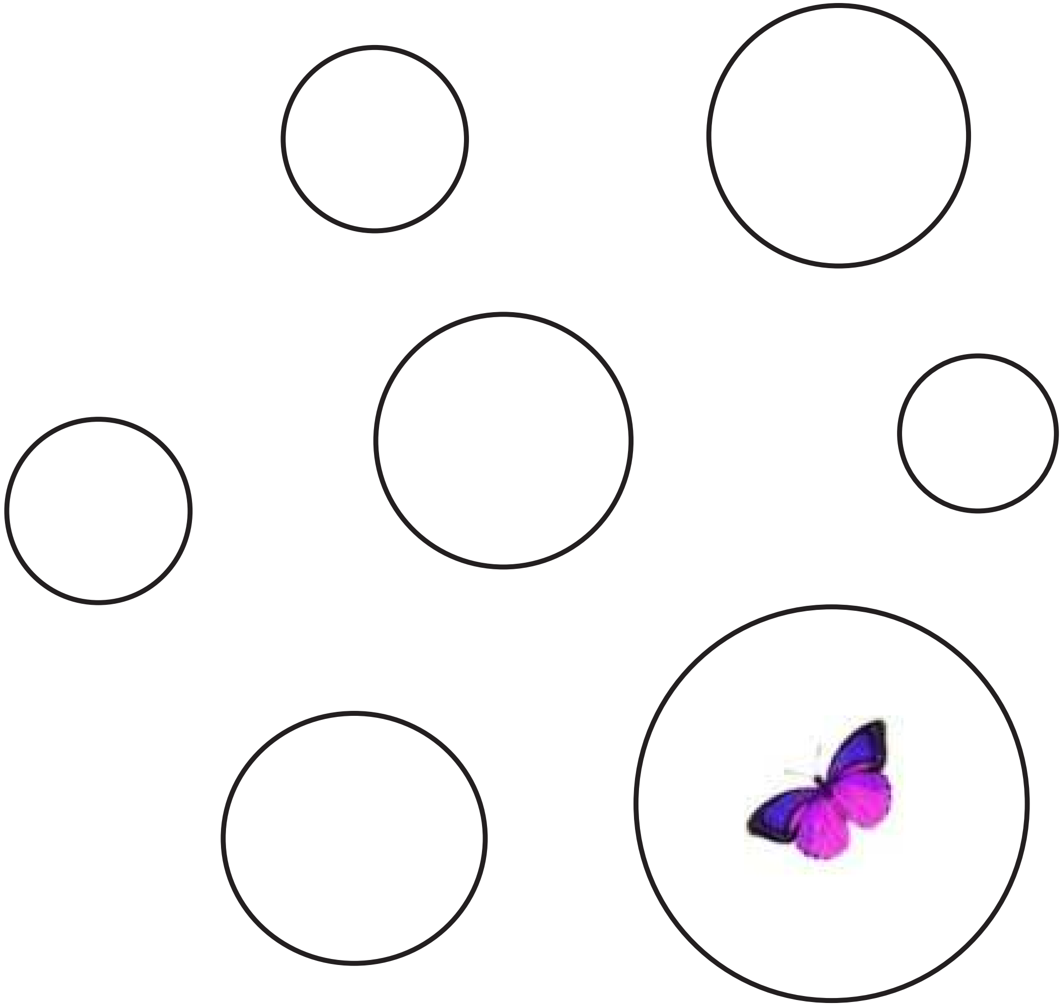
Metapopulations



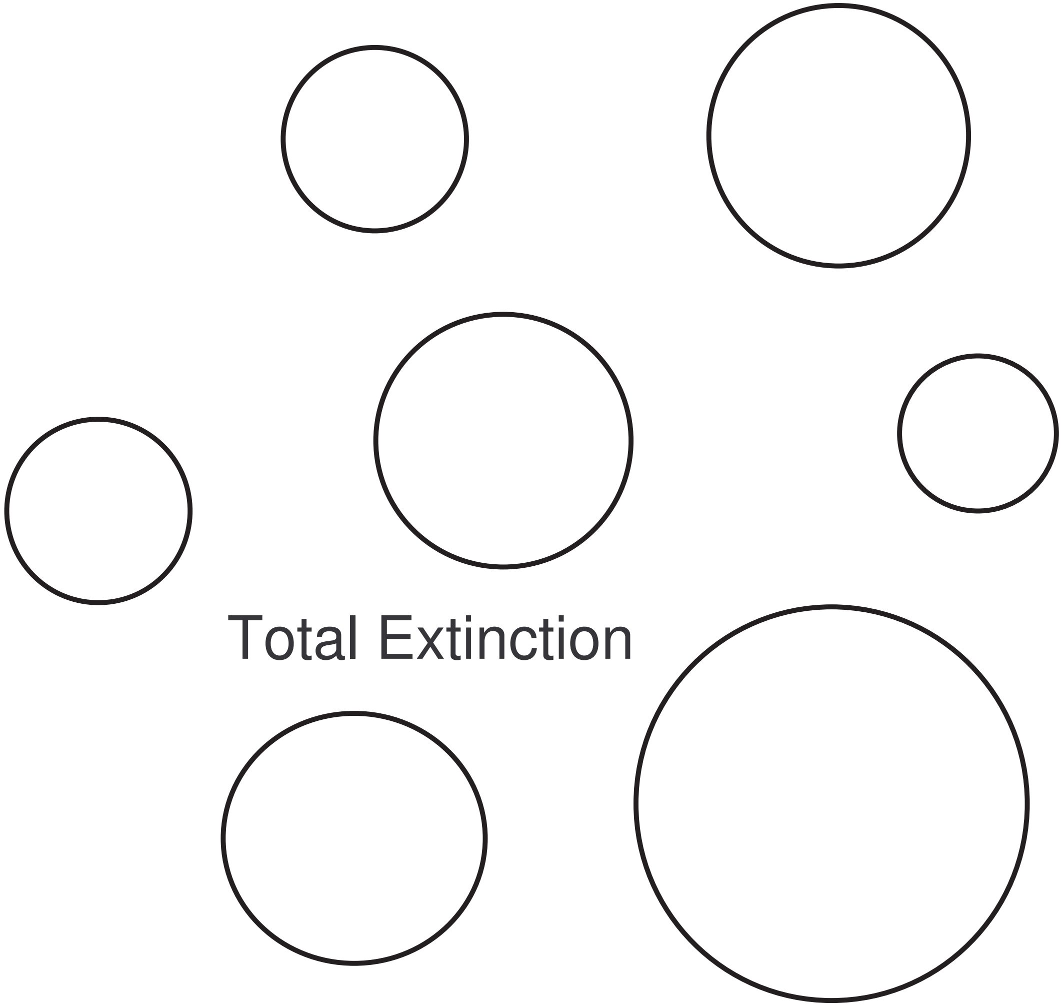
Metapopulations



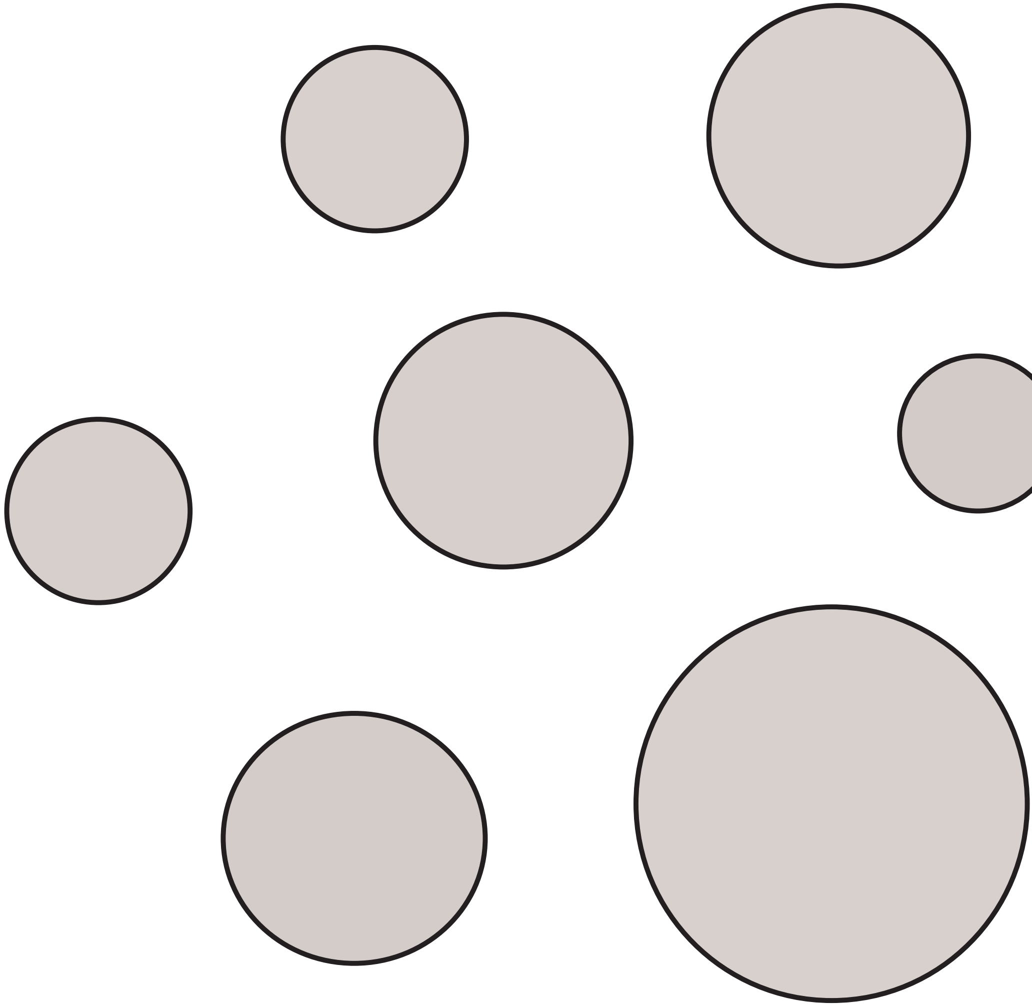
Metapopulations



Metapopulations



Metapopulations



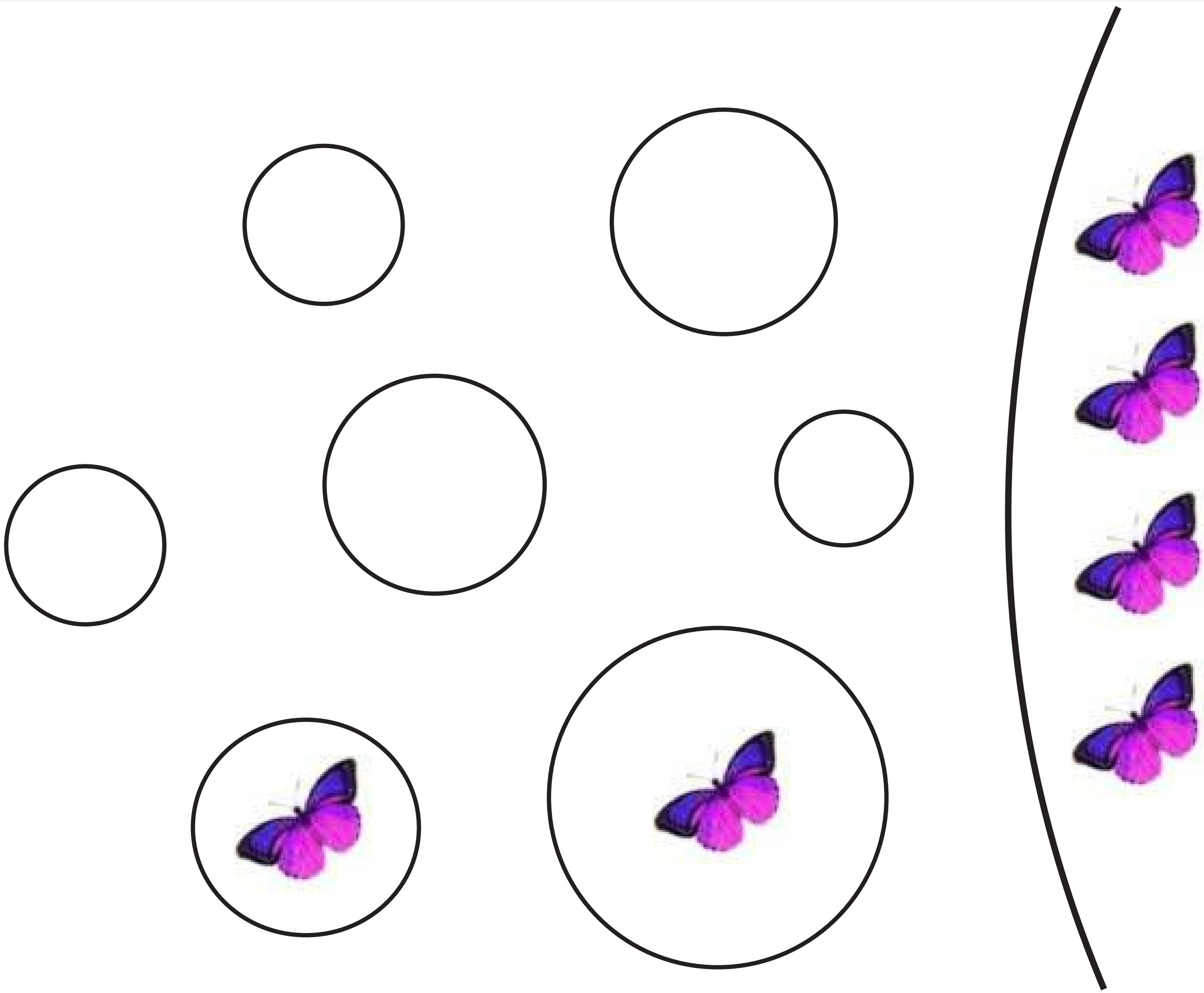
Metapopulations

- 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.

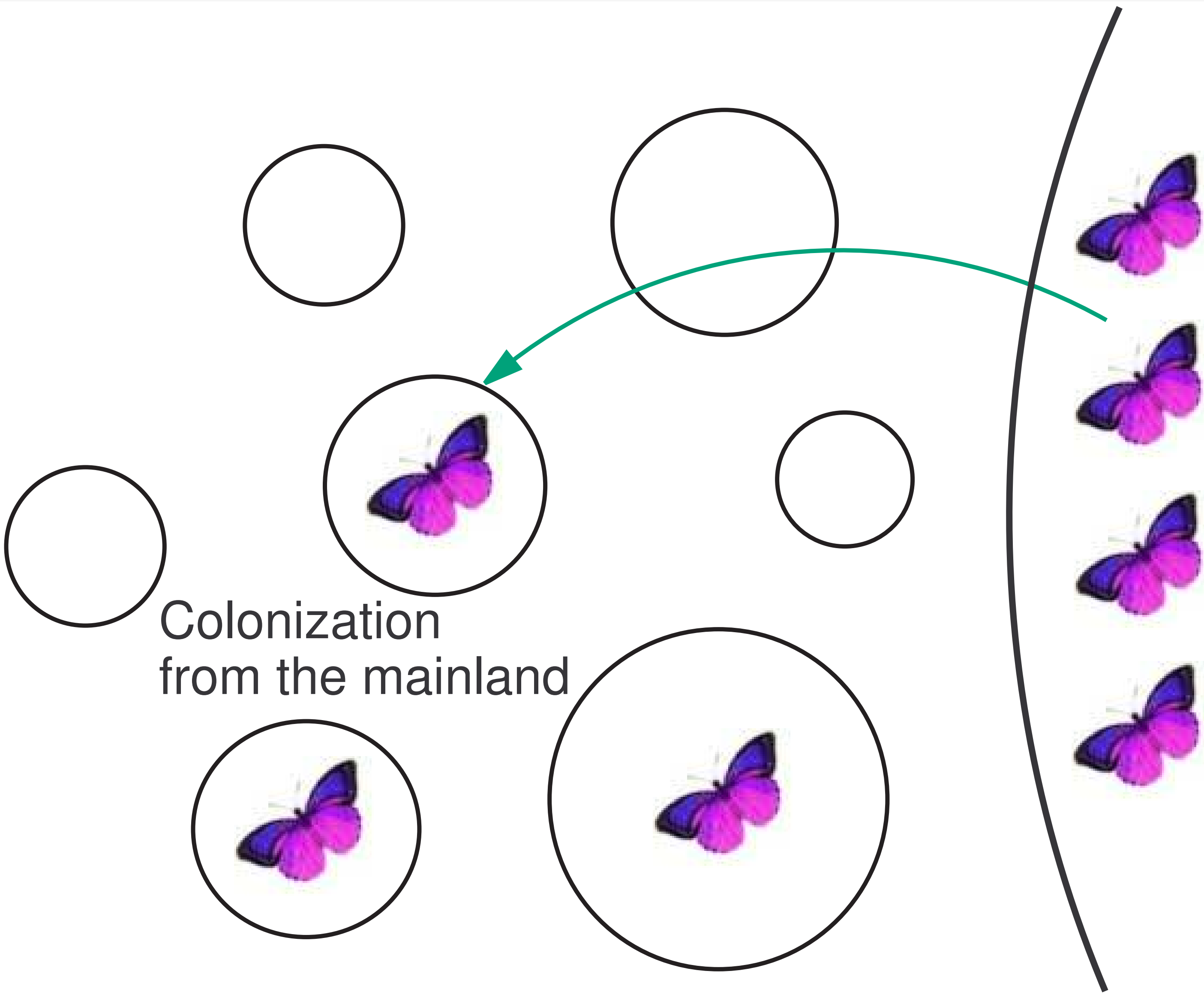
Metapopulations

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

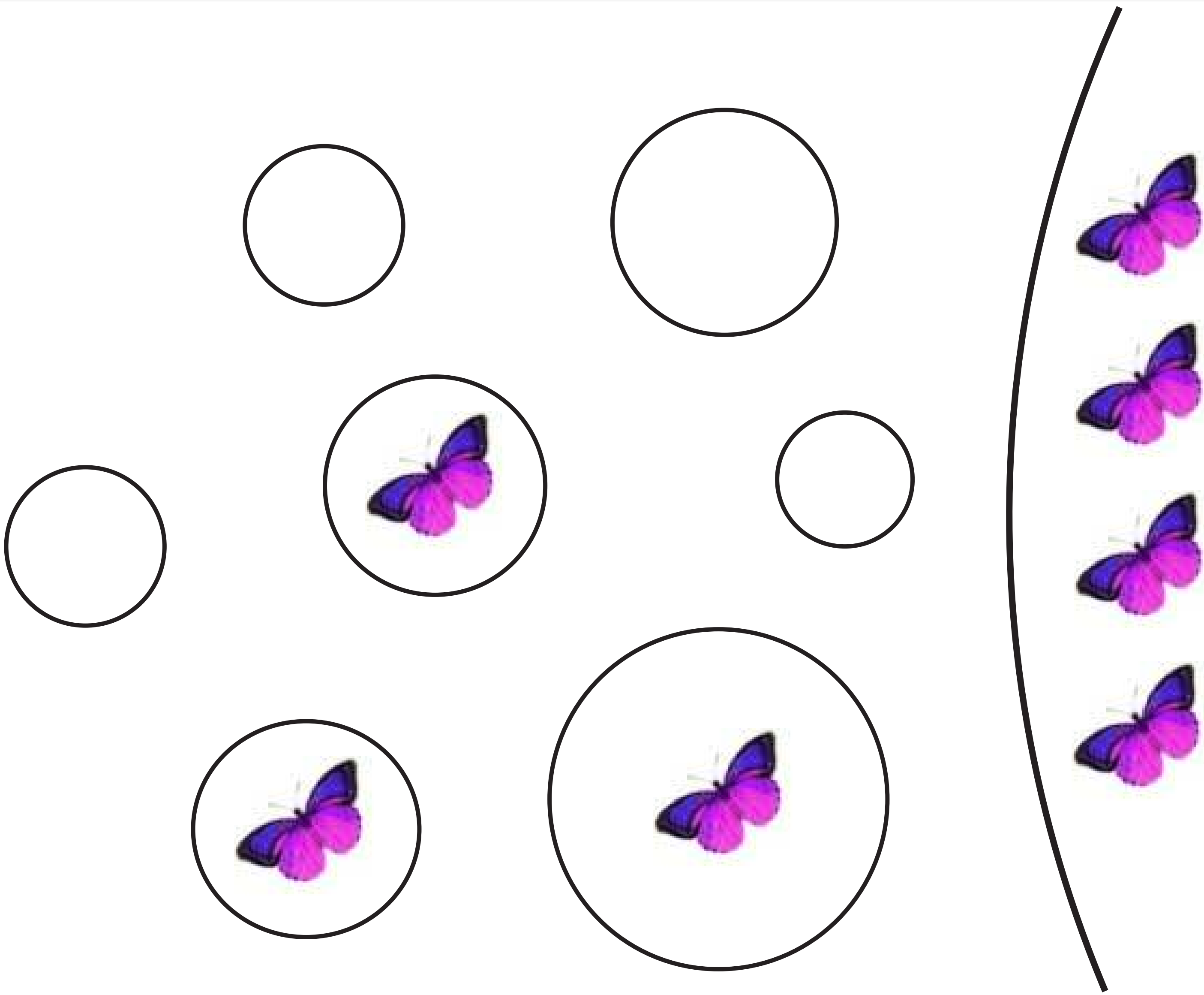
Mainland-island configuration



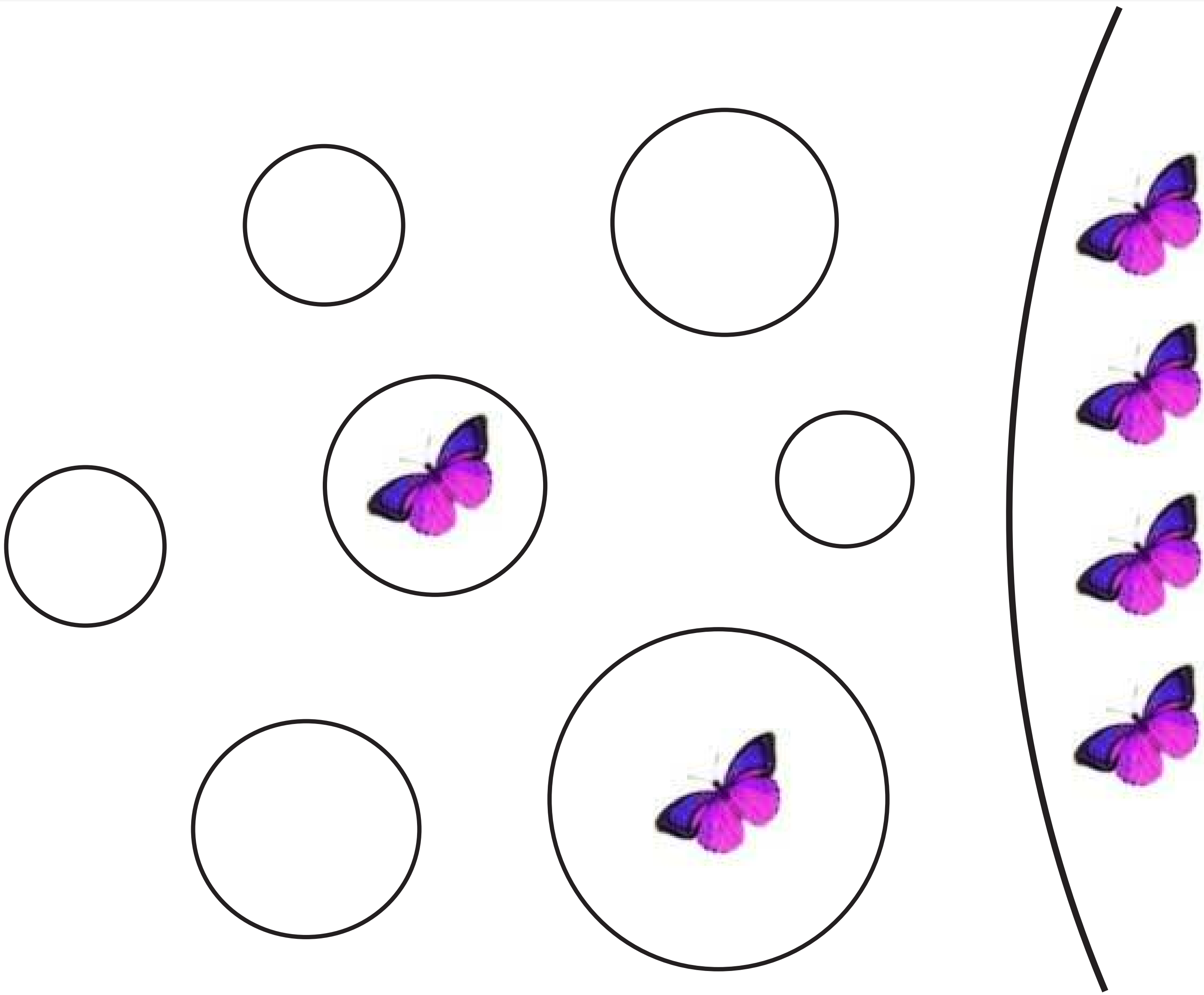
Mainland-island configuration



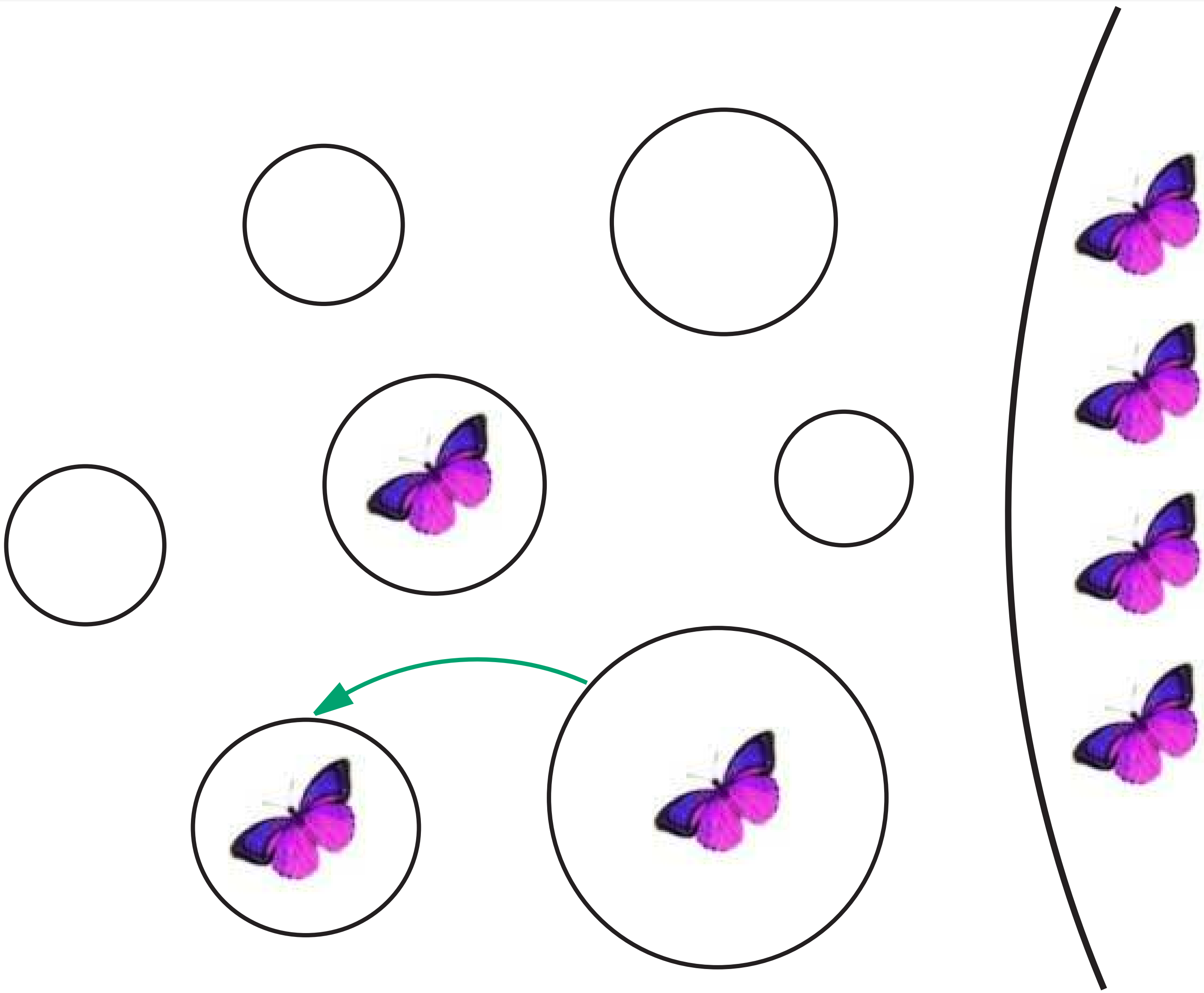
Mainland-island configuration



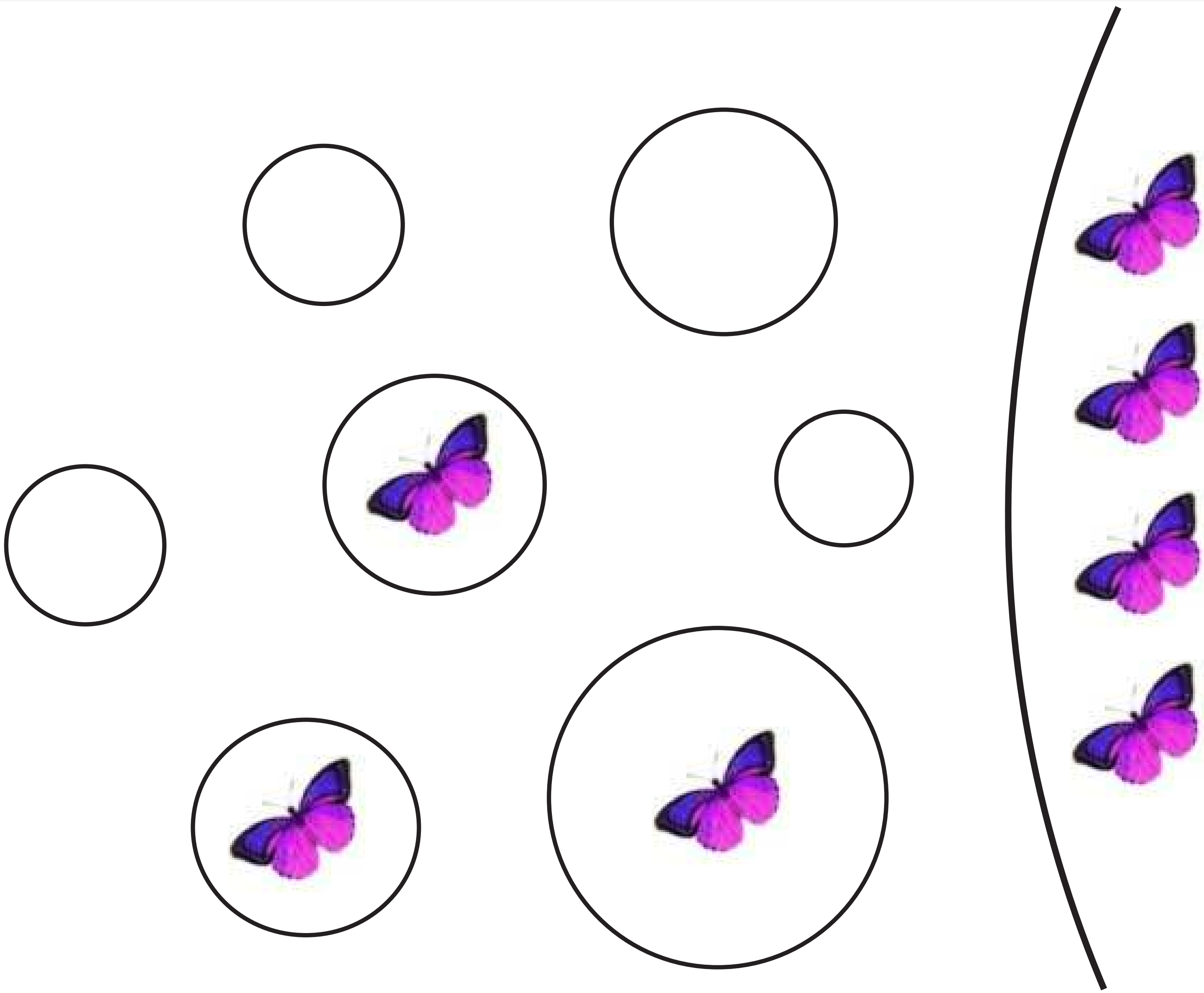
Mainland-island configuration



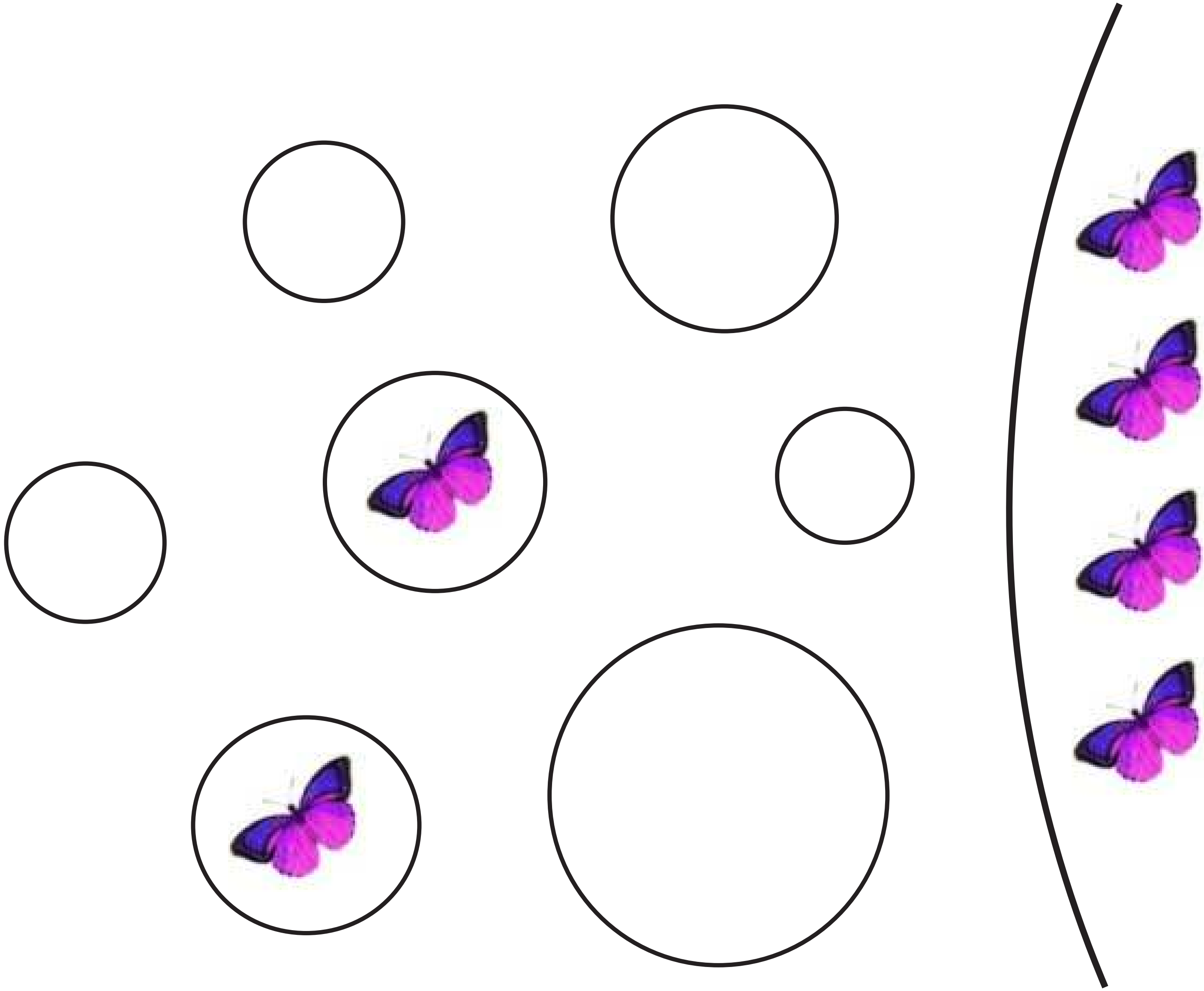
Mainland-island configuration



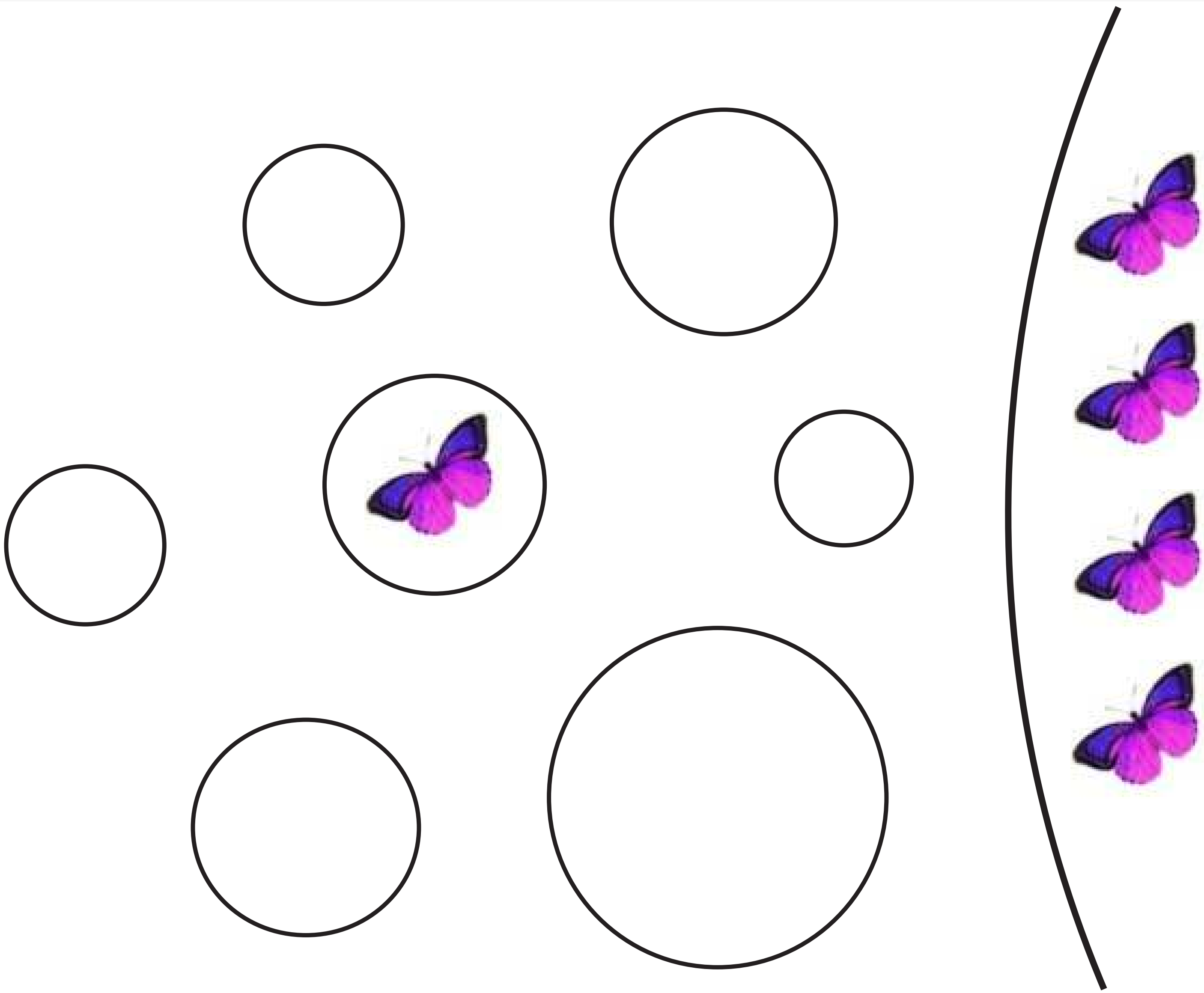
Mainland-island configuration



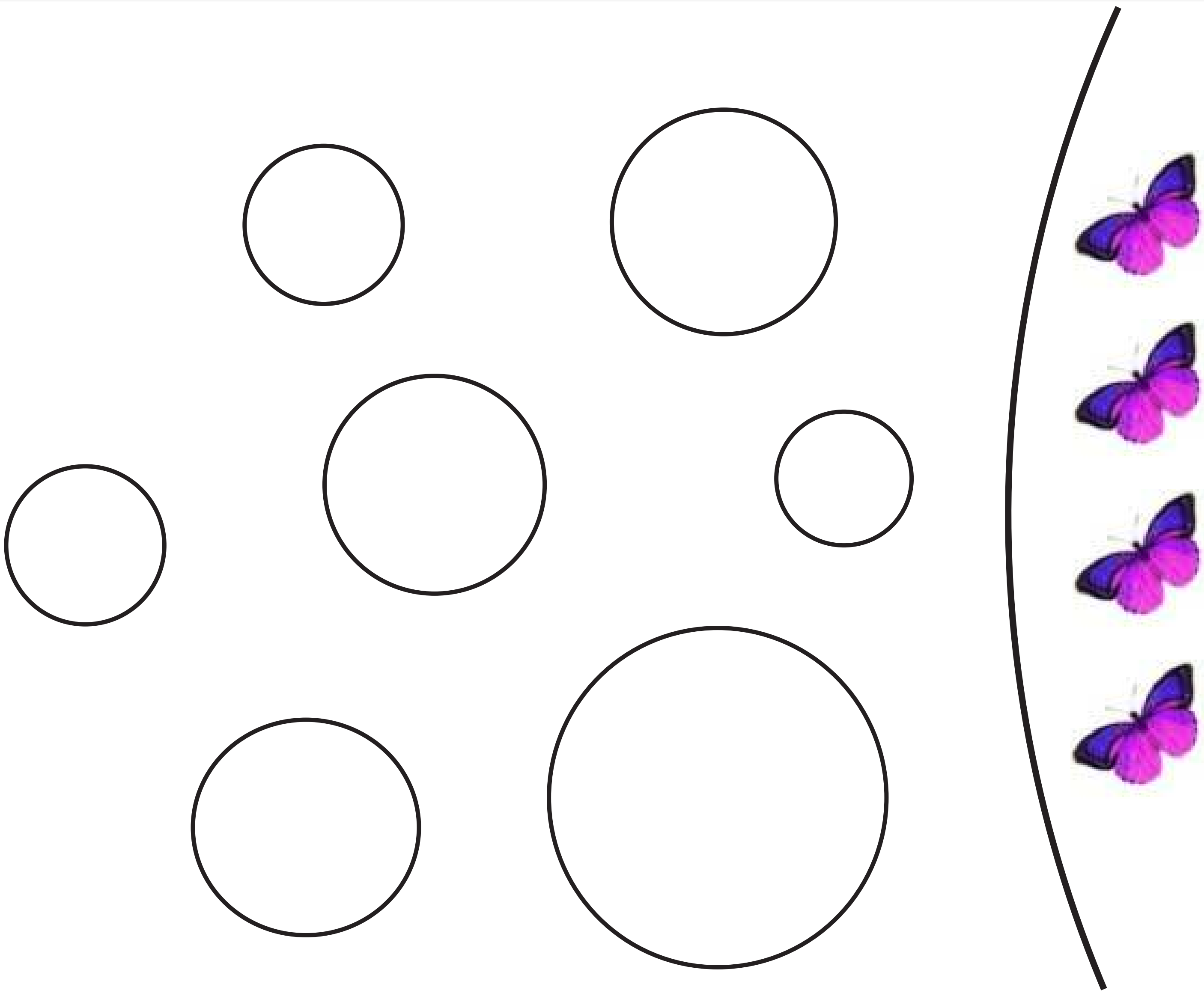
Mainland-island configuration



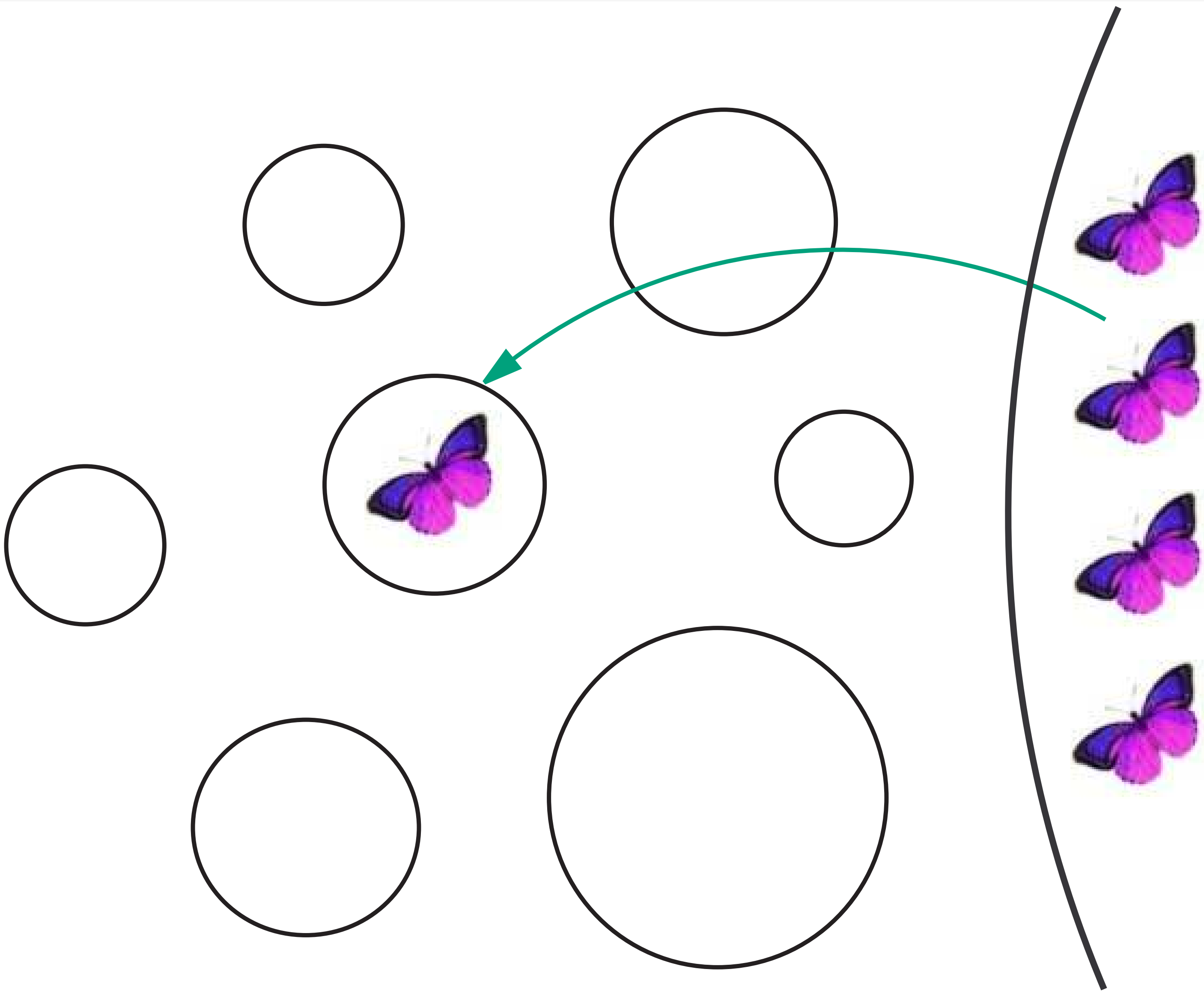
Mainland-island configuration



Mainland-island configuration



Mainland-island configuration



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 ?

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

Patch-occupancy models

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

A typical approach is to suppose that $(n(t), t \geq 0)$ is a Markov chain in discrete or continuous time.

Patch-occupancy models

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

A typical approach is to suppose that $(n(t),\, t \geq 0)$ is a Markov chain in discrete or continuous time.

Warning. This means that knowledge of the just number of occupied patches at any given time t is sufficient to predict what is to happen next, and thus entails some homogeneity among patches (in particular the colonization and local extinction processes).

A continuous-time model

Suppose that there are J patches. Each occupied patch becomes empty at rate e and colonization of empty patches occurs at rate c/J for each suitable pair.

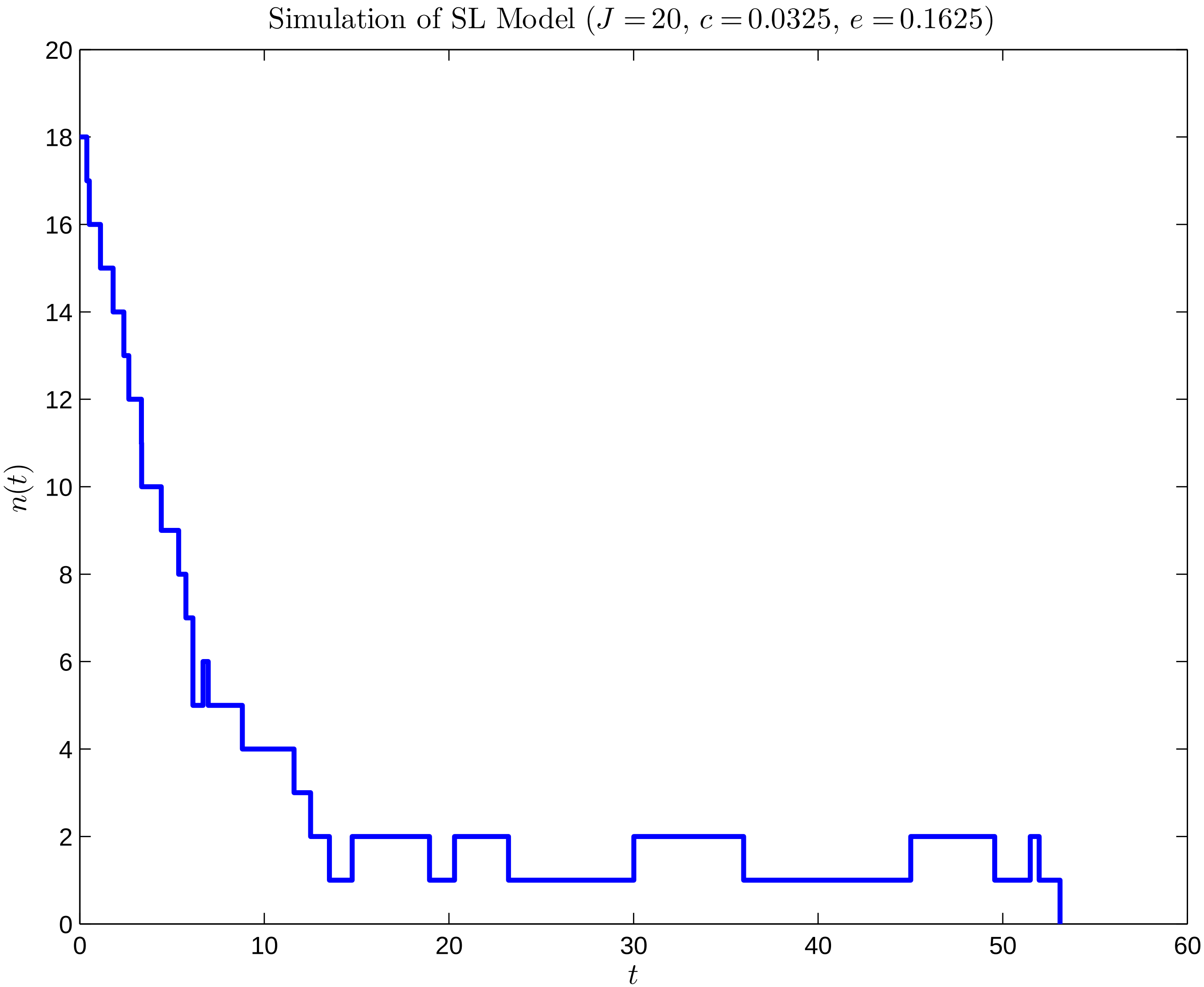
The state space of the Markov chain $(n(t),\, t \geq 0)$ is $S = \{0, 1, \ldots, J\}$ and the transitions are:

$$\begin{array}{lll} n \rightarrow n+1 & \text{at rate} & \frac{c}{J} n\,(J-n) \\ n \rightarrow n-1 & \text{at rate} & en \end{array}$$

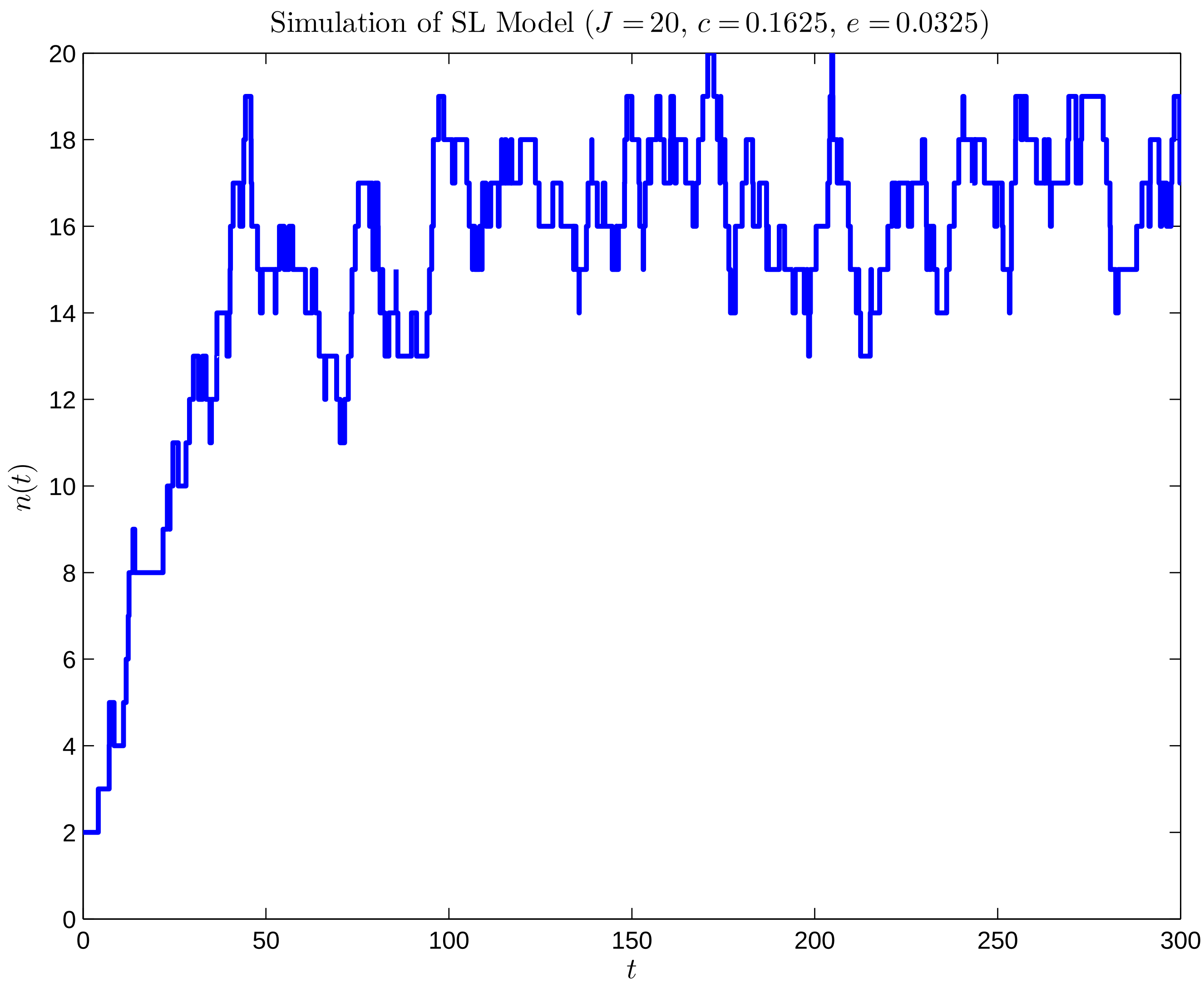
I will call this model the *stochastic logistic (SL) model*, though it has many names, having been rediscovered several times since Feller* proposed it.

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

The SL model simulation ($c < e$)



The SL model simulation ($c > e$)



The SL model

We can distinguish this behaviour by identifying an approximating deterministic model.

The SL model

We can distinguish this behaviour by identifying an approximating deterministic model. Let $X_t^{(J)} = n(t)/J$ be the *proportion* of occupied patches at time t.

The SL model

We can distinguish this behaviour by identifying an approximating deterministic model. Let $X_t^{(J)} = n(t)/J$ be the *proportion* of occupied patches at time t. We can prove a *functional law of large numbers* that establishes convergence of the family $(X_t^{(J)})$ to the unique trajectory (x_t) satisfying

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

namely

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

The SL model

We can distinguish this behaviour by identifying an approximating deterministic model. Let $X_t^{(J)} = n(t)/J$ be the *proportion* of occupied patches at time t. We can prove a *functional law of large numbers* that establishes convergence of the family $(X_t^{(J)})$ to the unique trajectory (x_t) satisfying

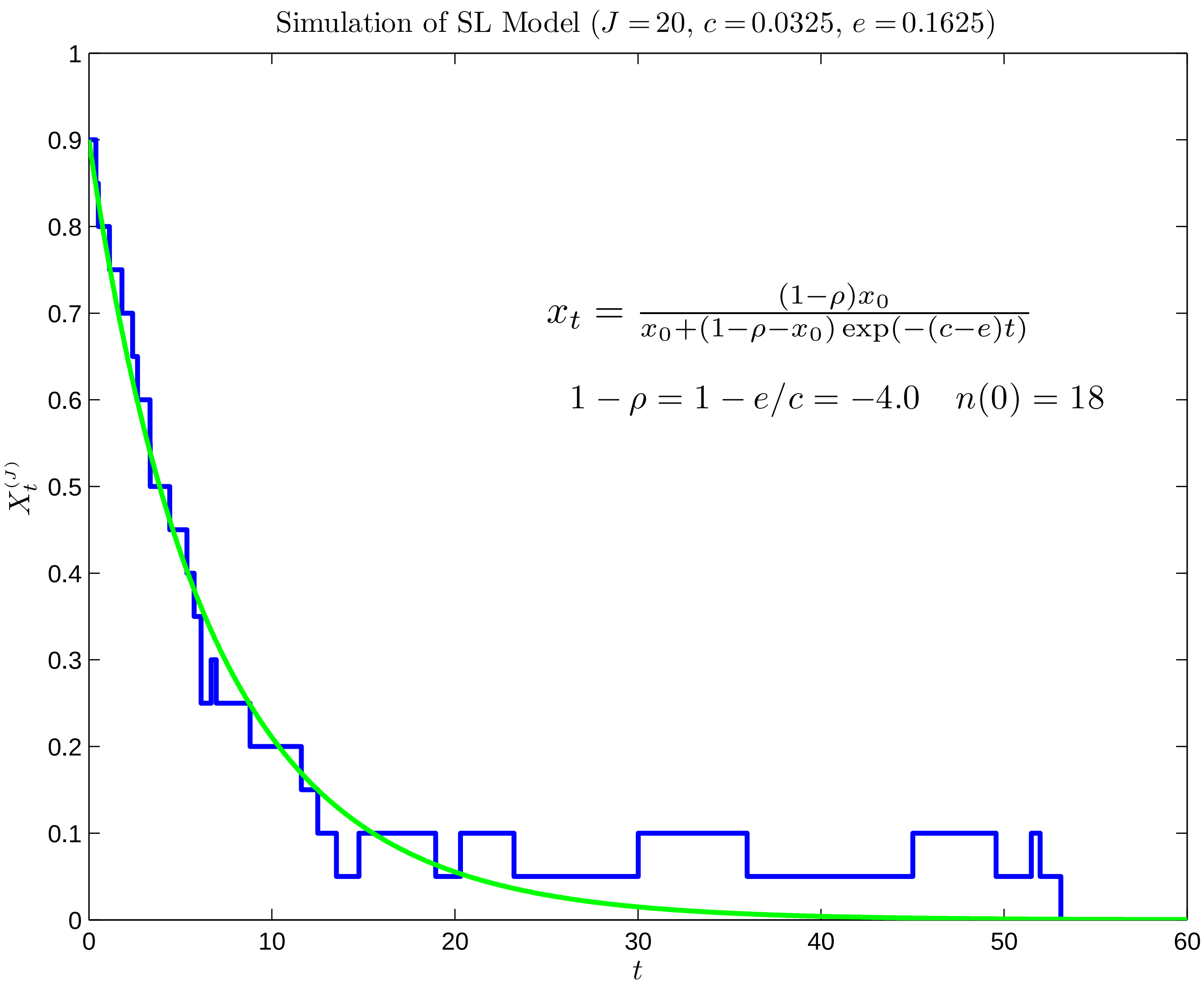
$$x_t' = cx_t(1 - x_t) - ex_t = cx_t\left(1 - \rho - x_t\right),$$

namely

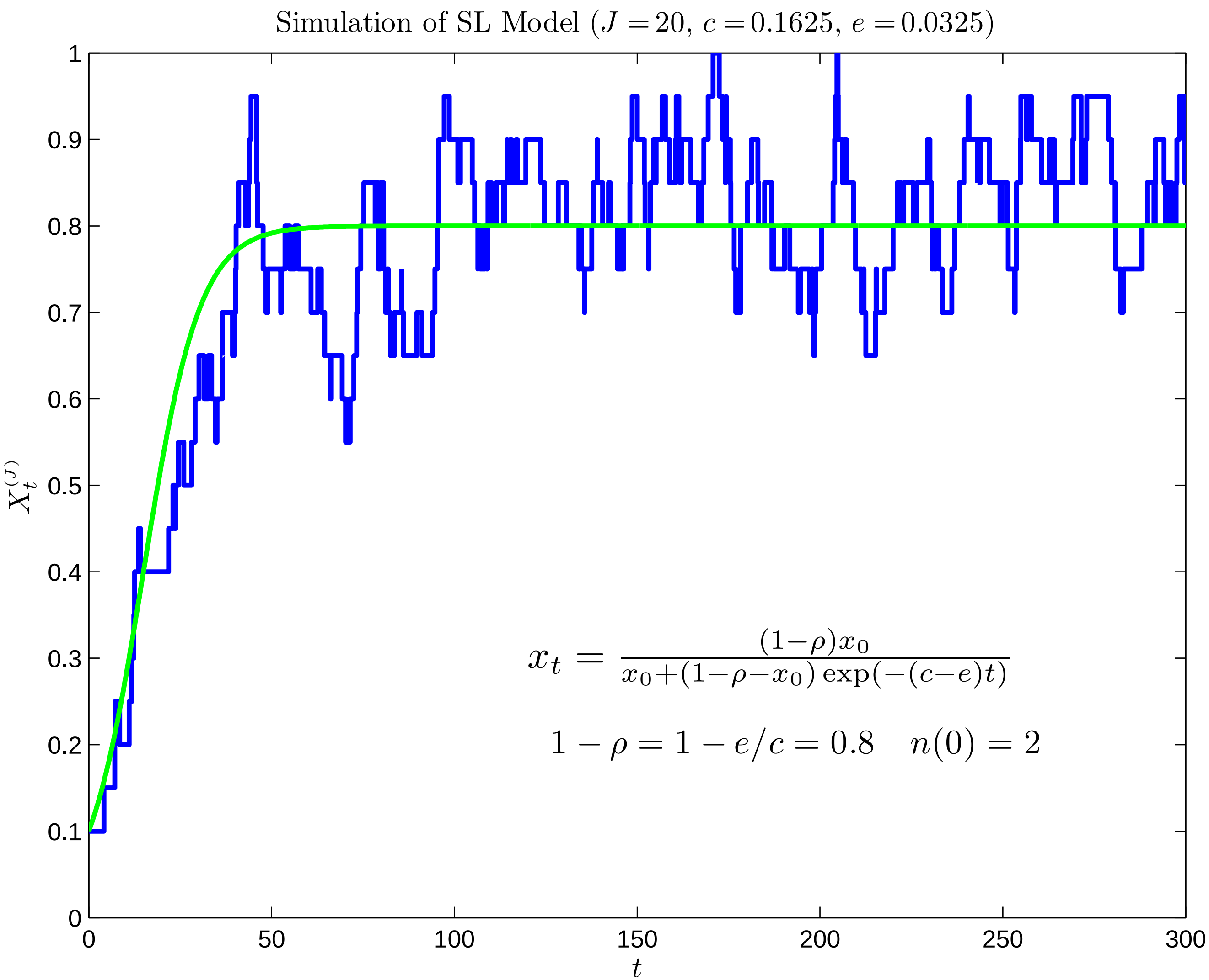
$$x_t = \frac{(1-\rho)x_0}{x_0 + \left(1 - \rho - x_0\right)e^{-(c-e)t}}.$$

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

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



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



The SL model

This of course is 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

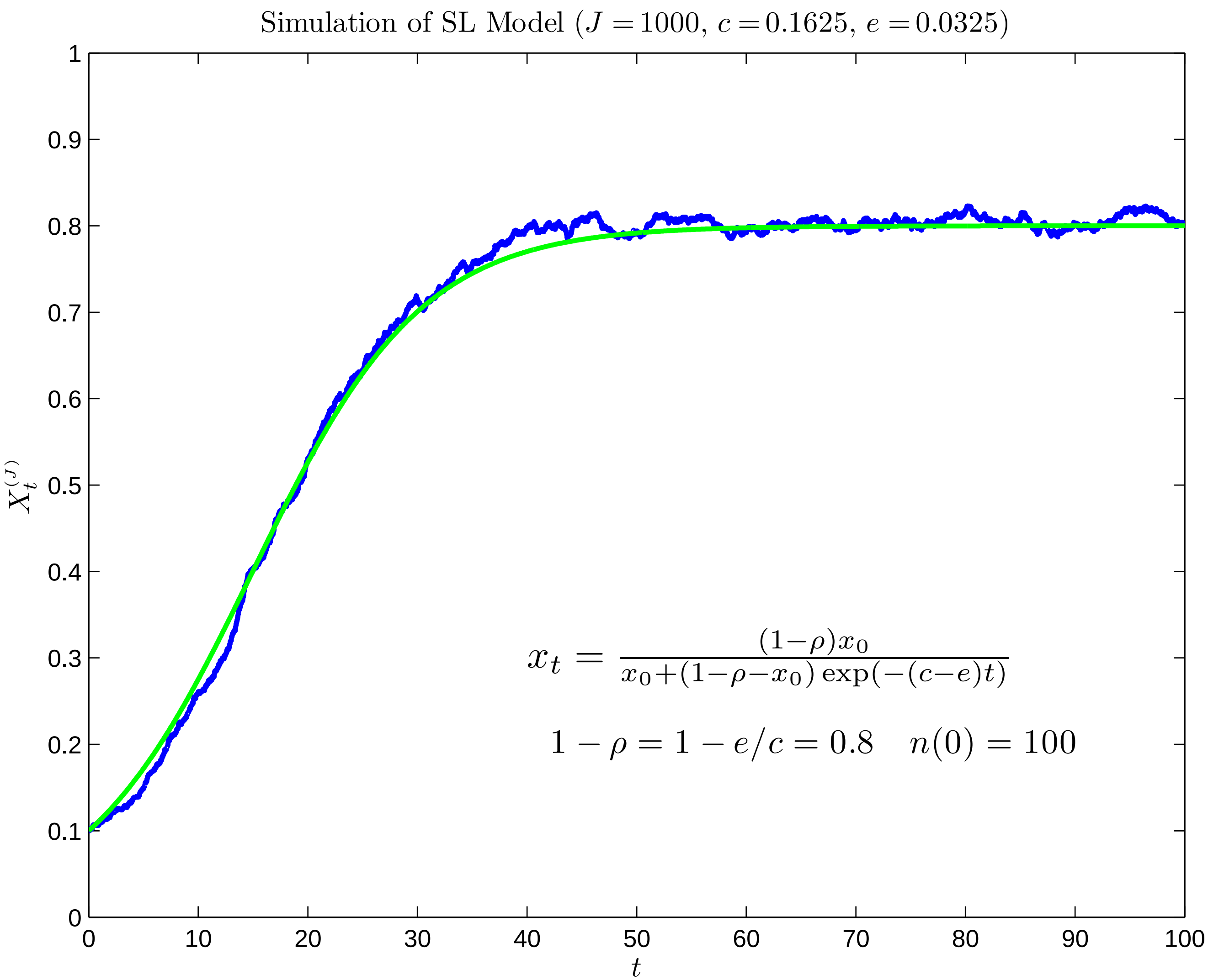
This of course is the classical Verhulst* model.

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

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 $\epsilon > 0$,

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

The SL model ($c > e$) $J \to \infty$



The Mainland-Island model

Recall that there are J patches. Each occupied patch becomes empty at rate e and colonization of empty patches occurs at rate c/J for each suitable pair.

Additionally, immigration from the mainland occurs that rate v.

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

$$\begin{array}{lll} n \to n+1 & \text{at rate} & v(J-n) + \frac{c}{J} n \left(J - n\right) \\ n \to n-1 & \text{at rate} & en \end{array}$$

Network models

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

There are two cases: (1) the *open* system, where individuals may enter or leave the network through external immigration and external emigration or removal, and (2) the *closed* system, where there is a *fixed number* N of individuals circulating.

In the open case individuals are assumed to arrive at patch i from outside the network as a Poisson stream with rate ν_i (if $\nu_i = 0$ there is no external immigration process at that patch).

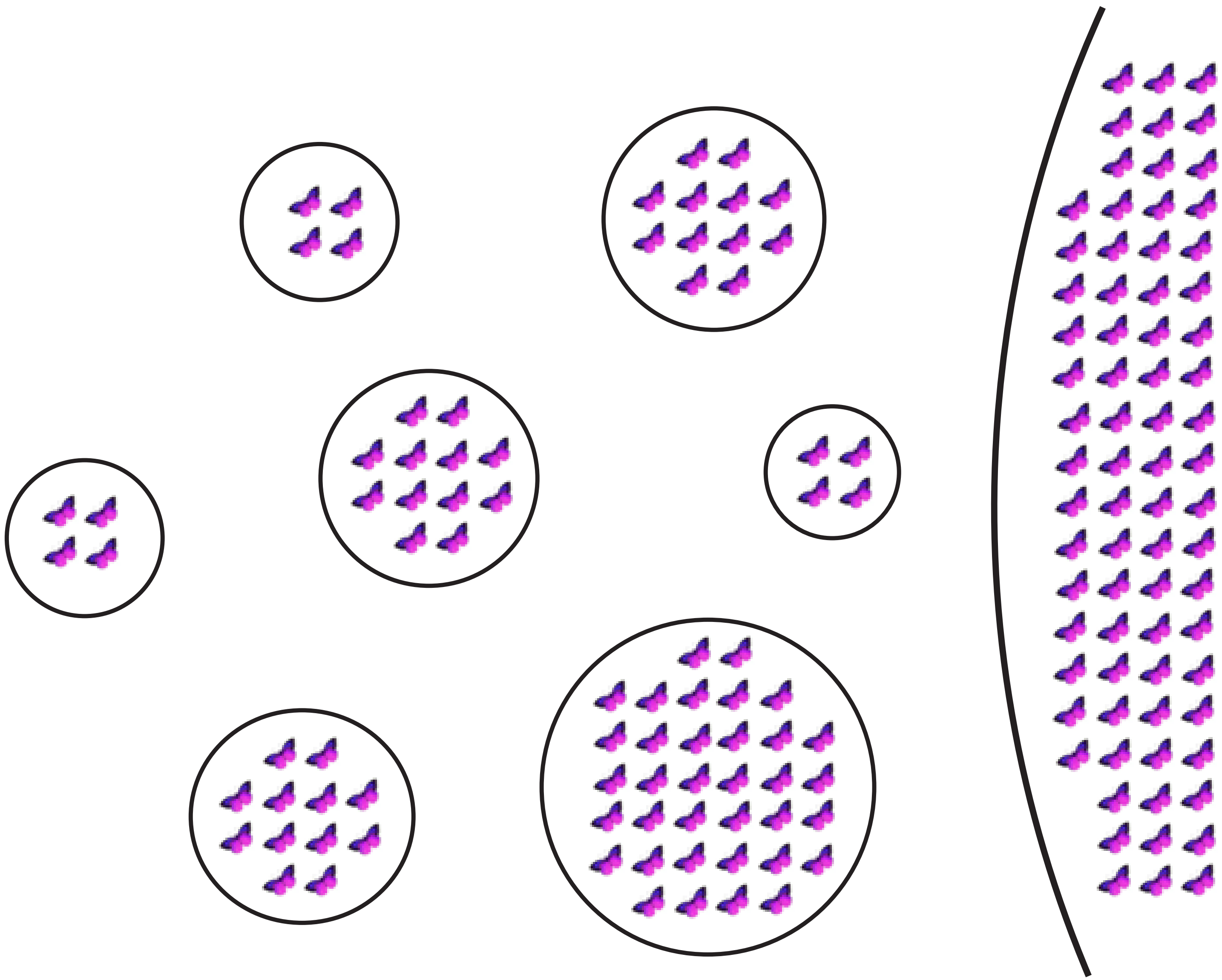
Network models

We account for spatial structure as follows.

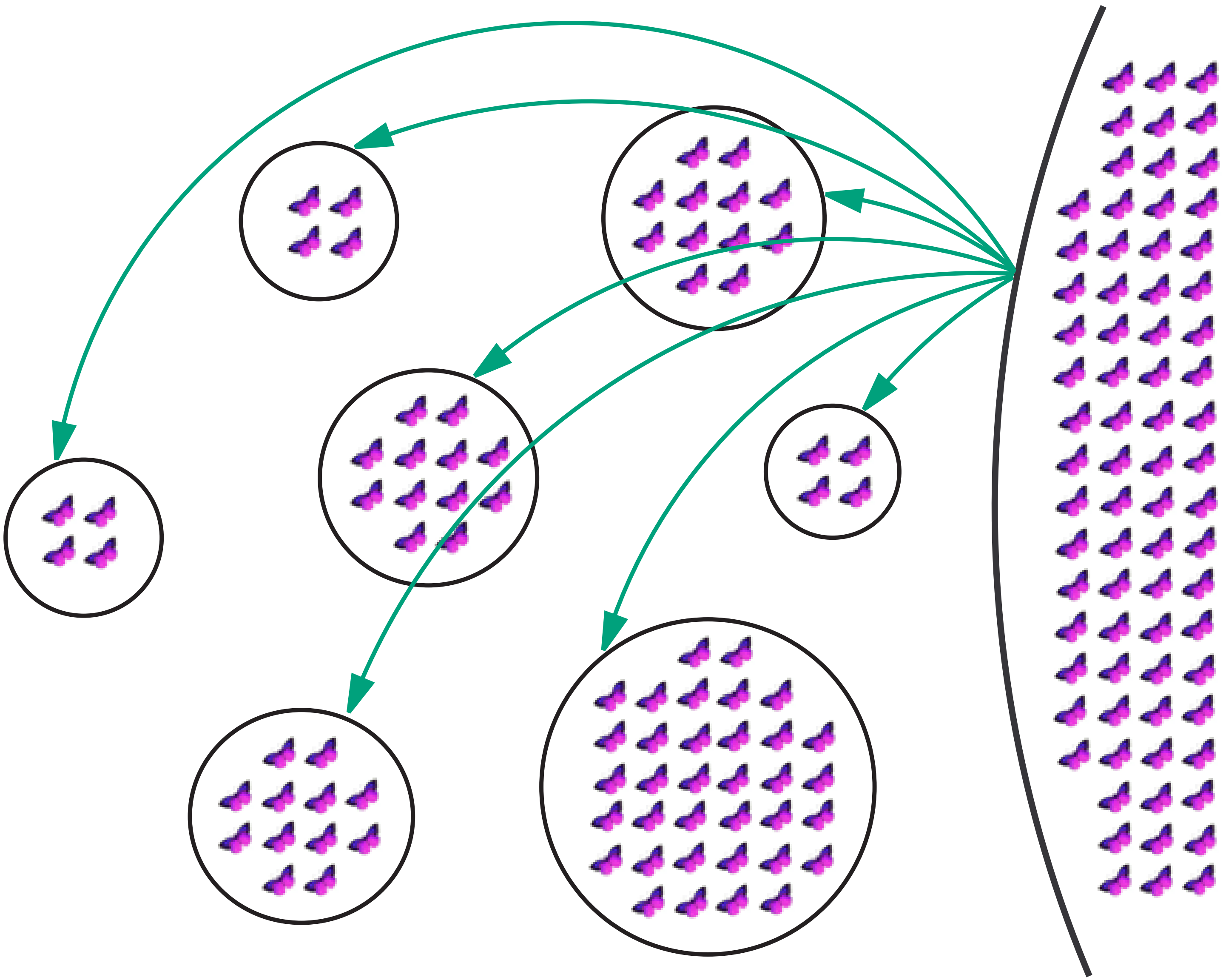
After a sojourn at patch i, an individual either leaves the network, with probability λ_{i0}, or proceeds to another patch j, with probability λ_{ij} (in the closed case we take $\lambda_{i0} = 0$); λ_{ij} thus specifies the relative proportion of propagules emanating from patch i that are destined for patch j, λ_{i0} being the proportion destined to leave the network. For simplicity, we set $\lambda_{ii} = 0$. Clearly $\sum_j \lambda_{ij} = 1$.

The matrix $\Lambda = (\lambda_{ij})$ is termed the *routing matrix*.

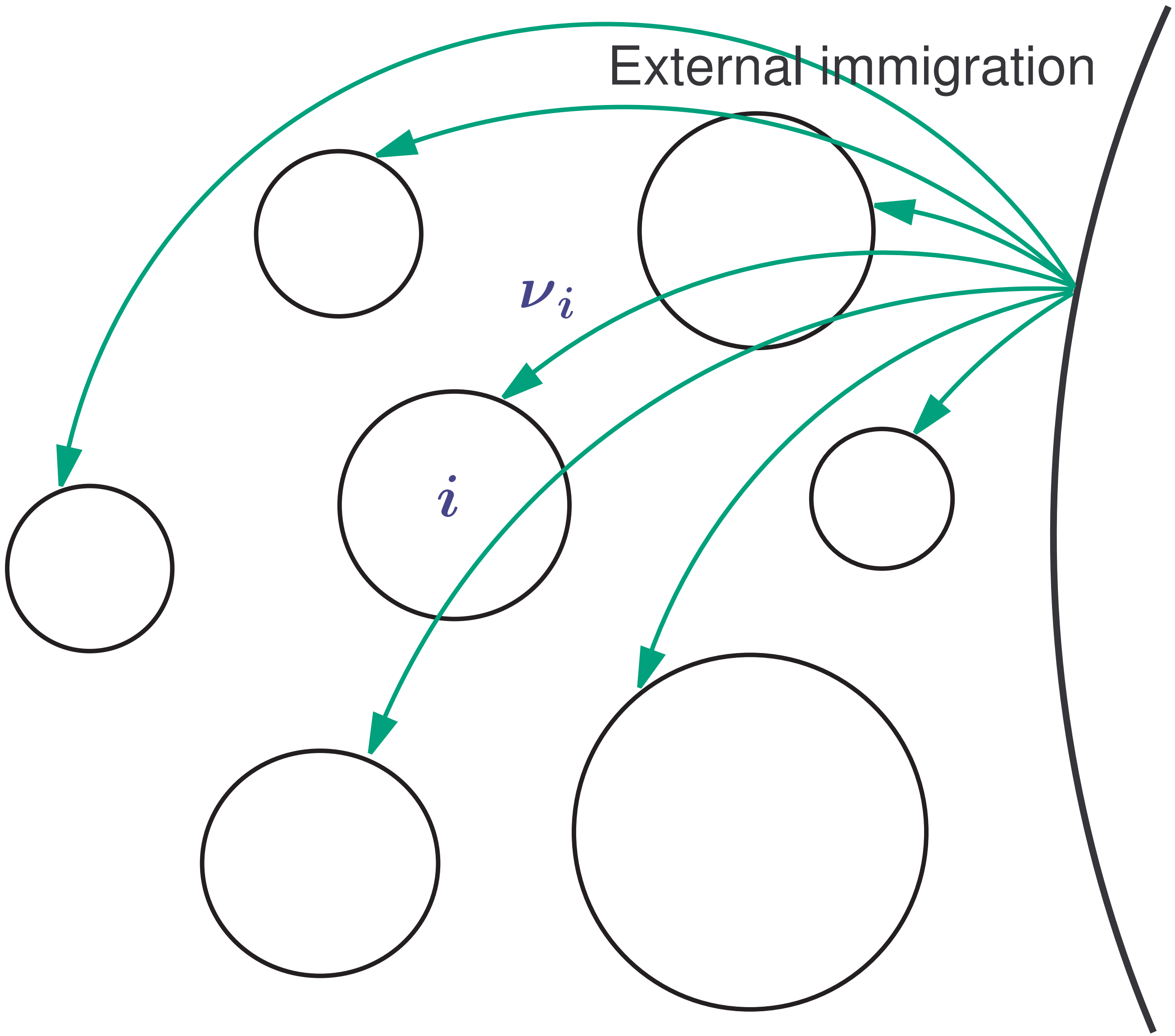
Open network



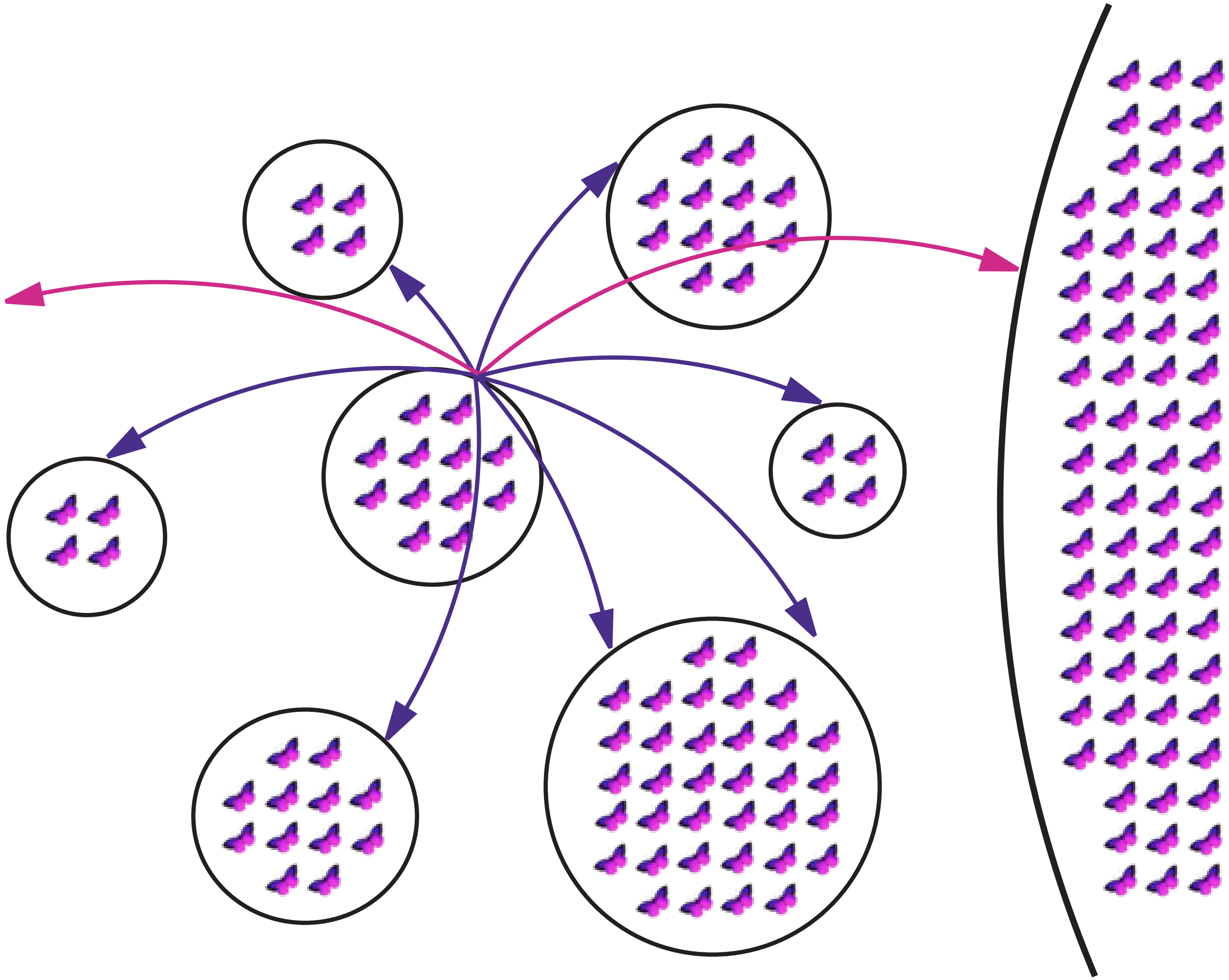
Open network



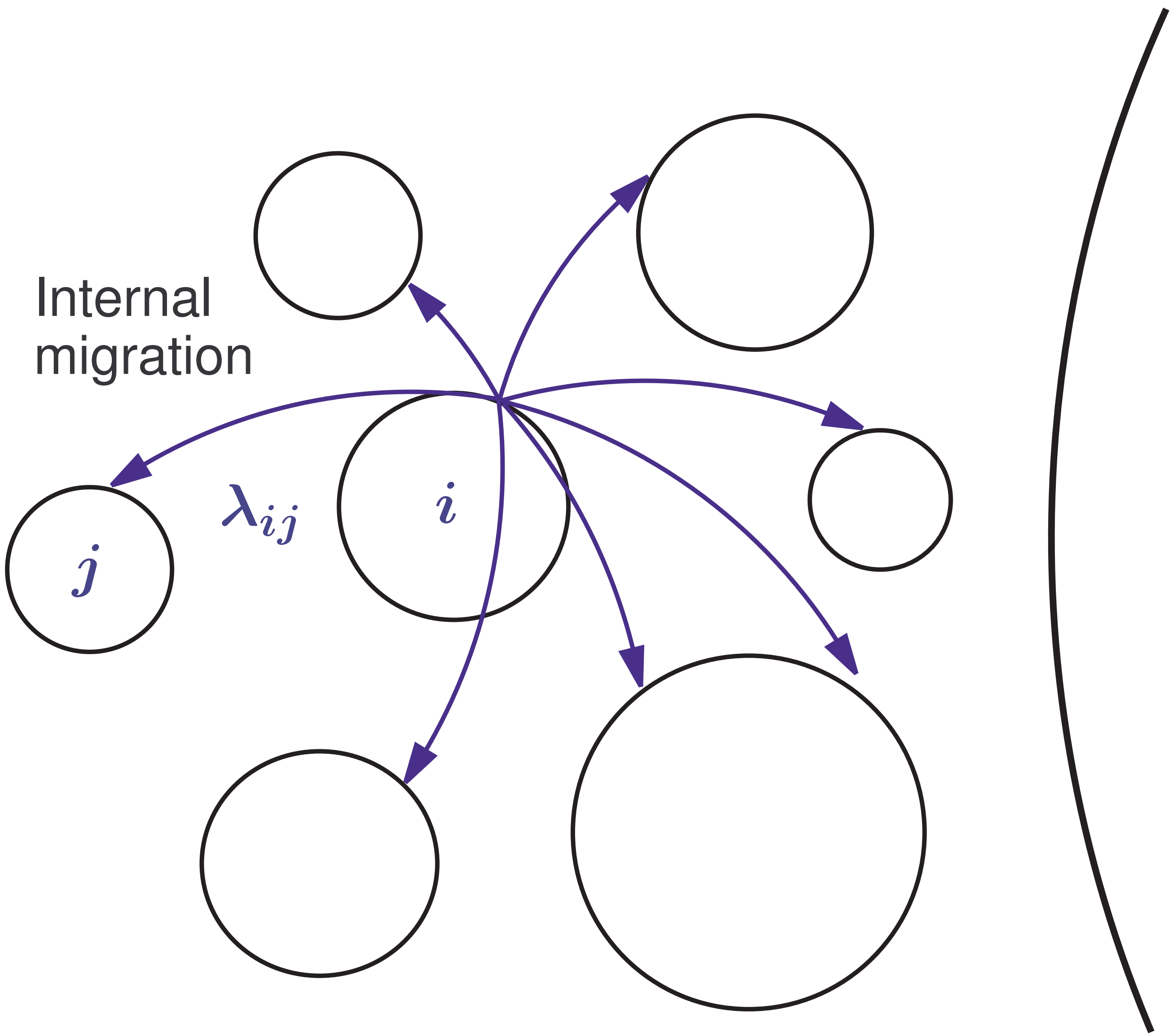
Open network



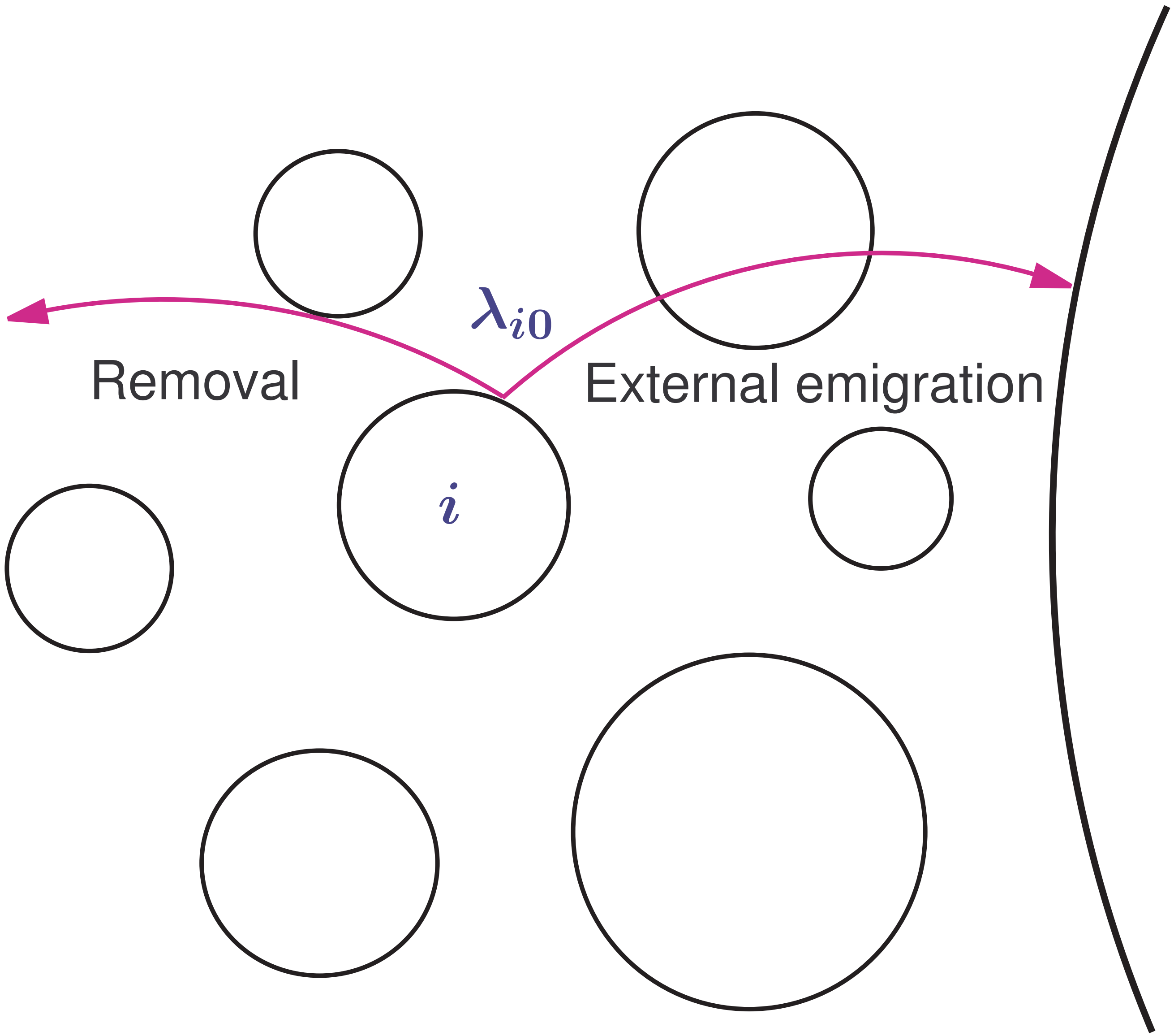
Open network



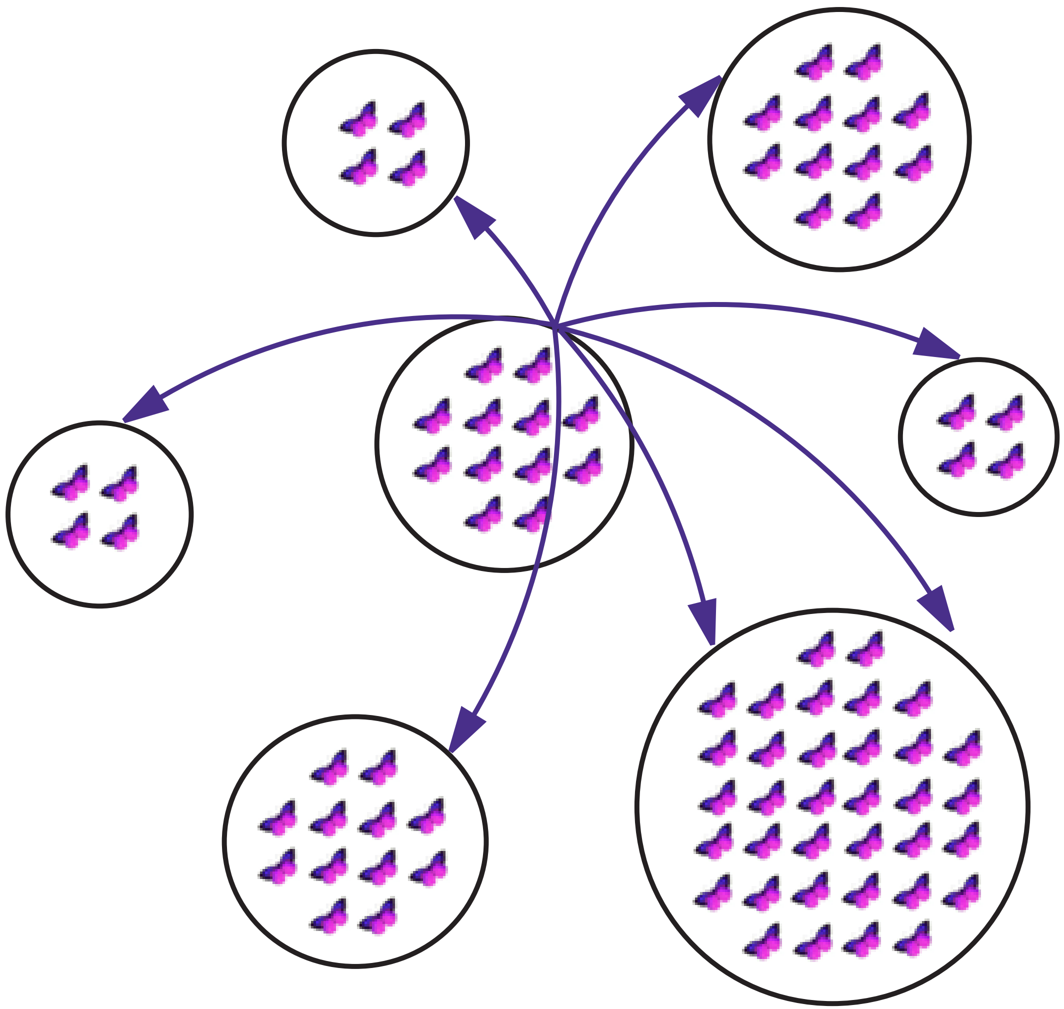
Open network



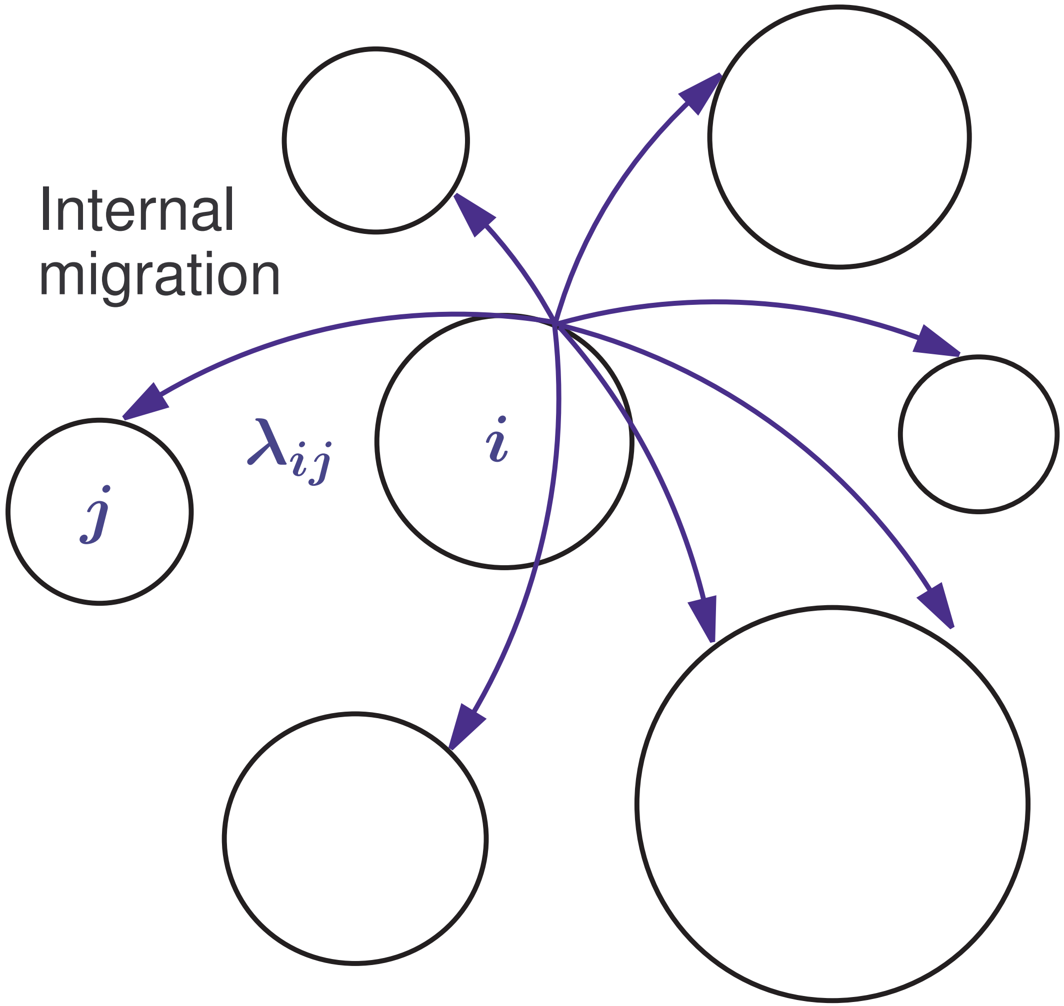
Open network



Closed network



Closed network



Network models

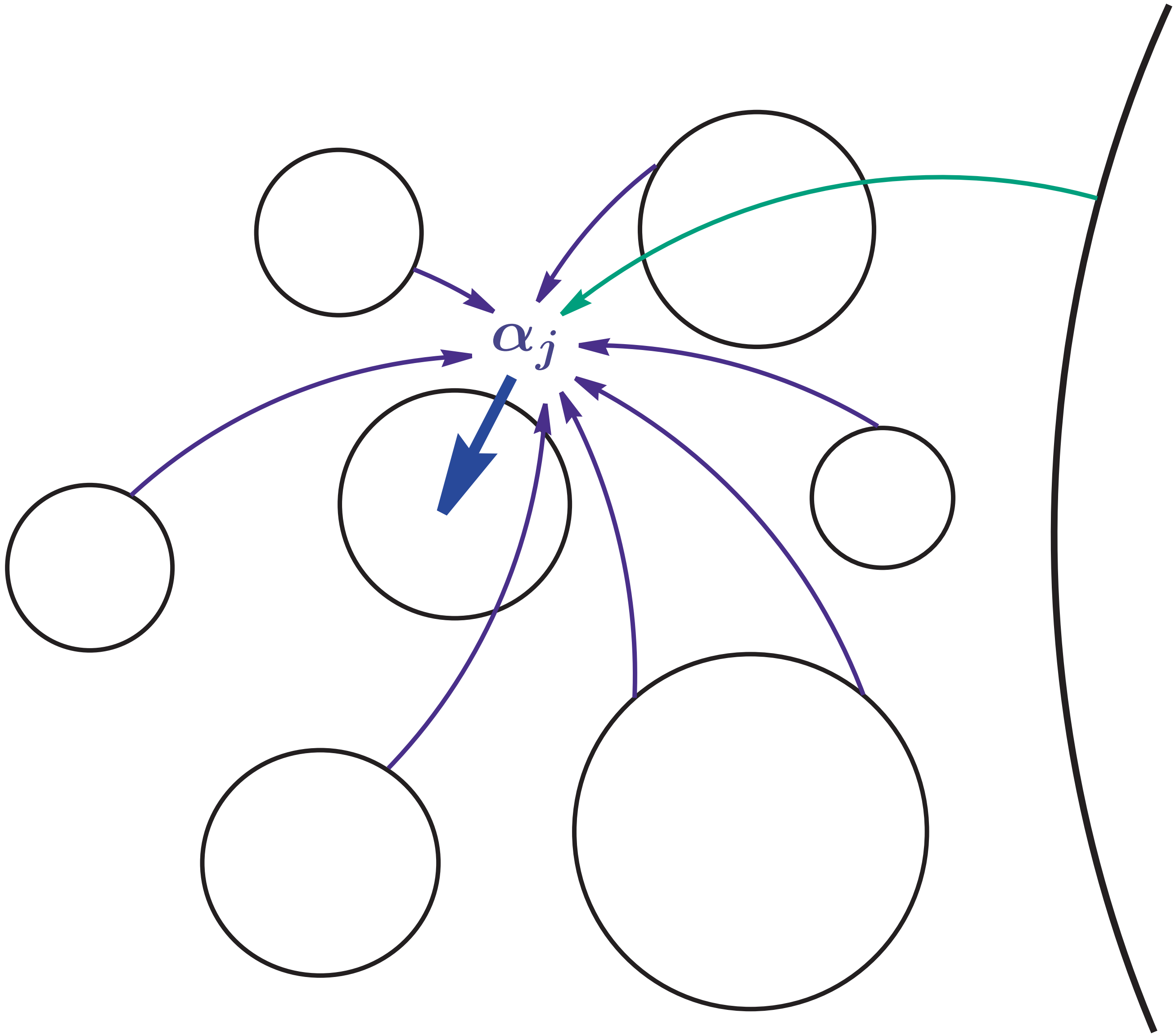
Again for simplicity, we shall assume that Λ is chosen so that an individual can reach any patch from anywhere in the network. In the open case we shall also assume that an individual can reach any patch from outside the network and eventually leave the network starting from anywhere.

In the closed case these conditions ensure that Λ is irreducible and, hence, that there is a unique collection $(\alpha_1, \ldots, \alpha_J)$ of strictly positive numbers which satisfy the *traffic equations* $\alpha_j = \sum_i \alpha_i \lambda_{ij}$, $j = 1, \ldots, J$ (cf. Kirchhoff's law). Here we may assume without loss of generality that $\sum_j \alpha_j = 1$.

Network models

In the open case these conditions ensure that there is a unique positive solution $(\alpha_1, \ldots, \alpha_J)$ to the equations $\alpha_j = \nu_j + \sum_i \alpha_i \lambda_{ij}$, $j = 1, \ldots, J$. In this case α_j is the arrival rate at patch j, while in the closed case α_j is *proportional to* the arrival rate at patch j.

Open network



Network models: propagation

When there are n individuals at patch j, propagation occurs at rate $\phi_j(n)$ (an arbitrary function for each patch). We assume that $\phi_j(0) = 0$ and $\phi_j(n) > 0$ whenever $n \geq 1$.

Network models: propagation

When there are n individuals at patch j, propagation occurs at rate $\phi_j(n)$ (an arbitrary function for each patch). We assume that $\phi_j(0) = 0$ and $\phi_j(n) > 0$ whenever $n \geq 1$. For example,

- $\phi_j(n) = \phi_j \ (n \geq 1)$: the propagation rate is ϕ_j, irrespective of how many individuals are present;
- $\phi_j(n) = \phi_j n$: the propagation rate at patch j is proportion to the number of individuals present;
- $\phi_j(n) = \phi_j \min\{n, s_j\} \ (n \geq 1)$: the propagation rate is proportion to the number of individuals present, but there is a fixed maximum rate.

Network models

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 $S = Z_+^J$ in open case and transition rates

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

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

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

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

Network models

In the closed case we simply have

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

and state state space $S^{(N)}$ is the subset of Z_+^J whose elements satisfy $n_1 + \cdots + n_J = N$.

Network models

In the closed case we simply have

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

and state state space $S^{(N)}$ is the subset of Z_+^J whose elements satisfy $n_1 + \cdots + n_J = N$.

The equilibrium behaviour of migration processes is well understood.

Network models

In the closed case we simply have

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

and state state space $S^{(N)}$ is the subset of Z_+^J whose elements satisfy $n_1 + \cdots + n_J = N$.

The equilibrium behaviour of migration processes is well understood (but apparently not by ecologists).

Network models

In the closed case we simply have

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

and state state space S is the subset of Z_+^J whose elements satisfy $n_1 + \cdots + n_J = N$.

The equilibrium behaviour of migration processes is well understood (but apparently not by ecologists).

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

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

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

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

Open migration process: examples

(1) $\phi_j(n) = \phi_j \ (n \geq 1)$. If $\rho_j := \alpha_j/\phi_j < 1$,

$$\pi_j(n) = (1 - \rho_j)\rho_j^n \quad \text{(geometric)}.$$

Open migration process: examples

(1) $\phi_j(n) = \phi_j \ (n \geq 1)$. If $\rho_j := \alpha_j/\phi_j < 1$,

$$\pi_j(n) = (1 - \rho_j)\rho_j^n \quad \text{(geometric)}.$$

(2) $\phi_j(n) = \phi_j n$.

$$\pi_j(n) = e^{-r_j}\frac{r_j^n}{n!}, \quad \text{where } r_j = \frac{\alpha_j}{\phi_j} \quad \text{(Poisson)}.$$

Open migration process: examples

(1) $\phi_j(n) = \phi_j \ (n \geq 1)$. If $\rho_j := \alpha_j/\phi_j < 1$,

$$\pi_j(n) = (1-\rho_j)\rho_j^n \quad \text{(geometric)}.$$

(2) $\phi_j(n) = \phi_j n$.

$$\pi_j(n) = e^{-r_j}\frac{r_j^n}{n!}, \quad \text{where } r_j = \frac{\alpha_j}{\phi_j} \quad \text{(Poisson)}.$$

(3) $\phi_j(n) = \phi_j \min\{n, s_j\} \ (n \geq 1)$. If $\rho_j := \alpha_j/(s_j\phi_j) < 1$,

$$\pi_j(n) = \pi_j(0)\frac{(s_j\rho_j)^n}{n!} \qquad (n = 1, \dots, s_j)$$

$$\pi_j(n) = \pi_j(s)\rho_j^{n-s_j} \qquad (n = s_j + 1, \dots).$$

Closed migration process (N individuals)

Theorem An equilibrium distribution always exists and is given by

$$\pi^{(N)}(\boldsymbol{n}) = B^{(N)} \prod_{j=1}^{J} \frac{\alpha_j^{n_j}}{\prod_{r=1}^{n_j} \phi_j(r)} \qquad (\boldsymbol{n} \in S^{(N)}),$$

where $B^{(N)}$ is a normalizing constant chosen so that $\pi^{(N)}$ sums to 1 over $S^{(N)}$.

Closed migration process (N individuals)

Theorem An equilibrium distribution always exists and is given by

$$\pi^{(N)}(\boldsymbol{n}) = B^{(N)} \prod_{j=1}^{J} \frac{\alpha_j^{n_j}}{\prod_{r=1}^{n_j} \phi_j(r)} \qquad (\boldsymbol{n} \in S^{(N)}),$$

where $B^{(N)}$ is a normalizing constant chosen so that $\pi^{(N)}$ sums to 1 over $S^{(N)}$.

Note that $n_1, \ldots, n_J$ are *not* independent.

Closed migration process: examples

(1) $\phi_j(n) = \phi_j \ (n \geq 1)$.

The equilibrium distribution is

$$\pi^{(N)}(\boldsymbol{n}) = B^{(N)} \prod_{i=1}^{J} \rho_i^{n_i} \quad (\boldsymbol{n} \in S^{(N)}),$$

where $\rho_i = \alpha_i/\phi_i$.

Closed migration process: examples

(1) $\phi_j(n) = \phi_j \ (n \geq 1)$.

The equilibrium distribution is

$$\pi^{(N)}(\boldsymbol{n}) = B^{(N)} \prod_{i=1}^{J} \rho_i^{n_i} \quad (\boldsymbol{n} \in S^{(N)}),$$

where $\rho_i = \alpha_i/\phi_i$.

The marginal distribution of the number n_j at patch j is messy (the form depends on which of the ρ_i's are distinct).

Closed migration process: examples

(2) $\phi_j(n) = \phi_j n$.

The equilibrium distribution is *multinomial*:

$$\pi^{(N)}(\boldsymbol{n}) = \frac{N!}{n_1!\, n_2! \cdots n_J!}\, p_1^{n_1} p_2^{n_2} \cdots p_J^{n_J} \qquad (\boldsymbol{n} \in S^{(N)}),$$

where $p_i = r_i / \sum_{j=1}^{J} r_j$ and $r_i = \alpha_i / \phi_i$.

Closed migration process: examples

(2) $\phi_j(n) = \phi_j n$.

The equilibrium distribution is *multinomial*:

$$\pi^{(N)}(\boldsymbol{n}) = \frac{N!}{n_1!\,n_2!\cdots n_J!}\,p_1^{n_1}p_2^{n_2}\cdots p_J^{n_J} \qquad (\boldsymbol{n} \in S^{(N)}),$$

where $p_i = r_i / \sum_{j=1}^{J} r_j$ and $r_i = \alpha_i/\phi_i$.

The marginal distribution of the number n_j at patch j is *binomial*:

$$\pi_j^{(N)}(n) = \binom{N}{n} p_j^n (1-p_j)^{N-n} \qquad (n = 0, 1, \ldots, N).$$

Network models: we ask ...

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

Network models: we ask ...

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

Do we recover the SL model?

Network models: we ask ...

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

Do we recover the SL model?

Recall that $n(t)$ was the number of occupied patches at time t, that local extinction occurred at common rate e and that colonization occurred at common rate c/J for each of the $n(J-n)$ occupied-unoccupied pairs:

$$\begin{array}{lll} n \to n+1 & \text{at rate} & \frac{c}{J} n\,(J-n) \\ n \to n-1 & \text{at rate} & en \end{array}$$

(closed network)

Network models: we ask ...

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

Do we recover the SL model?

Recall that $n(t)$ was the number of occupied patches at time t, that local extinction occurred at common rate e and that colonization occurred at common rate c/J for each of the $n(J-n)$ occupied-unoccupied pairs:

$$\begin{array}{lll} n \to n+1 & \text{at rate} & v(J-n) + \frac{c}{J} n\,(J-n) \\ n \to n-1 & \text{at rate} & en \end{array}$$

(open network)

The SL model: what is c?

What is the interpretation of c in the SL model?

The SL model: what is c?

What is the interpretation of c in the SL model?

$\ldots$ colonization occurred at common rate c/J for each of the $n(J-n)$ occupied-unoccupied pairs:

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

The SL model: what is c?

What is the interpretation of c in the SL model?

... colonization occurred at common rate c/J for each of the $n(J-n)$ occupied-unoccupied pairs:

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

Even in the epidemiological literature*, where the SL model—called the Susceptible-Infective-Susceptible (SIS) model—is ubiquitous, there is still controversy about interpretation of the ingredients of the model.

*Begon, M., Bennett, M., Bowers, R.G., French, N.P., Hazel, S.M. and Turner, J. (2002) A clarification of transmission terms in host-microparasite models: numbers, densities and areas. Epidemiology and Infection 129, 147–153.

The SL model: what is c?

What is the interpretation of c in the SL model?

$\ldots$ colonization occurred at common rate c/J for each of the $n(J-n)$ occupied-unoccupied pairs:

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

Even in the epidemiological literature*, where the SL model—called the Susceptible-Infective-Susceptible (SIS) model—is ubiquitous, there is still controversy about interpretation of the ingredients of the model.

*Begon, M., Bennett, M., Bowers, R.G., French, N.P., Hazel, S.M. and Turner, J. (2002) A clarification of transmission terms in host-microparasite models: numbers, densities and areas. Epidemiology and Infection 129, 147–153.

Network models: what are c and e?

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

Network models: what are c and e?

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

Joshua Ross (2008)* “$\ldots$ c is the rate of propagation from any given occupied patch”.

*Personal communication

Network models: what are c and e?

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

Joshua Ross (2008)* "$\ldots$ c is the rate of propagation from any given occupied patch".

*Personal communication

We will use the various network models to find out. There are some surprises.

Which patch-occupancy model?

Symmetric networks Suppose that $\phi_j(n) = \phi(n)$ for all j (all patches produce propagules at the same rate). We consider two cases (i) "constant" $\phi(n) = \phi$ $(n \geq 1)$ (constant propagation rate ϕ) and (ii) "linear" $\phi(n) = \phi n$ (ϕ is the *per-capita* propagation rate).

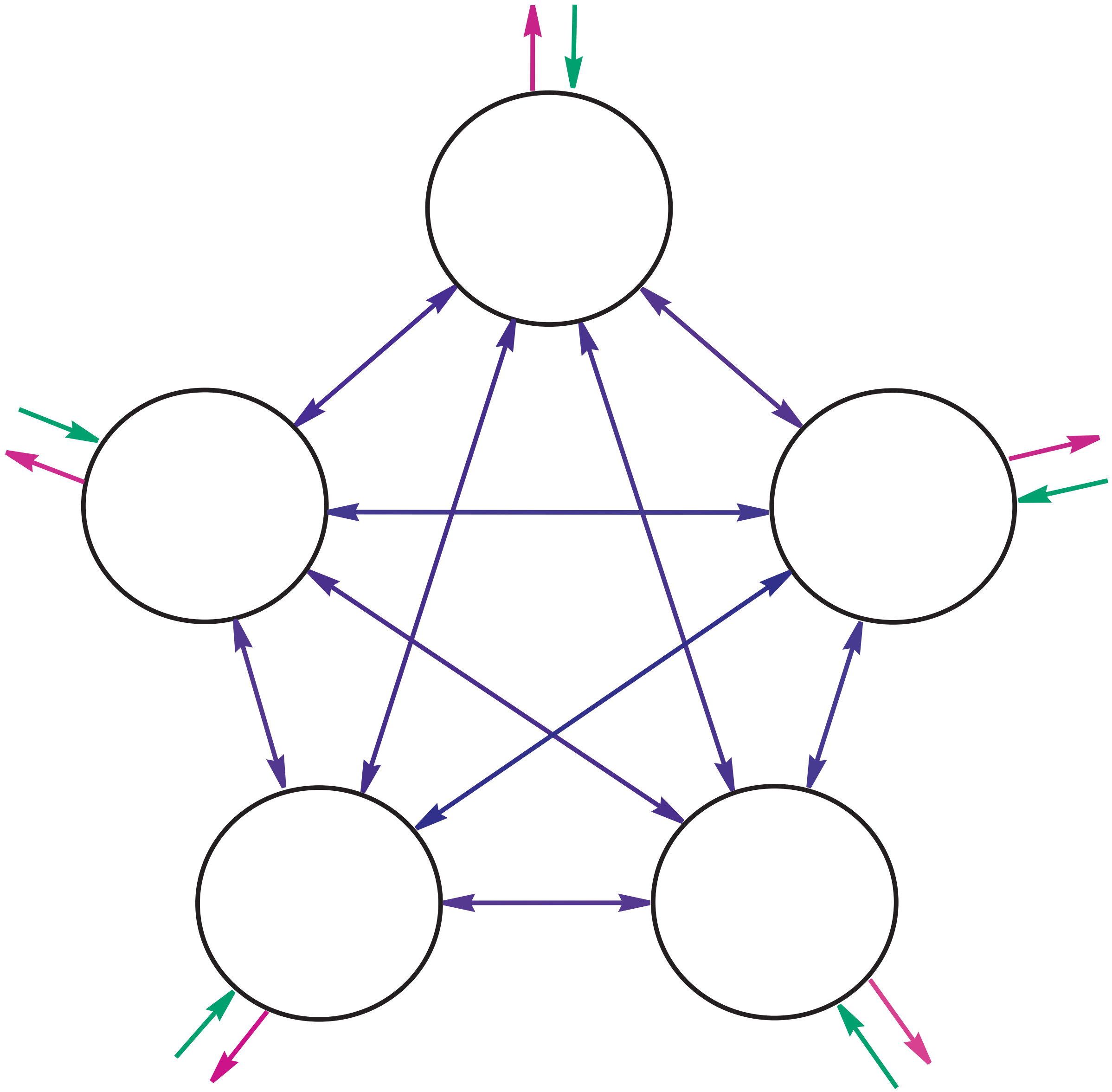
Which patch-occupancy model?

Symmetric networks Suppose that $\phi_j(n) = \phi(n)$ for all j (all patches produce propagules at the same rate). We consider two cases (i) "constant" $\phi(n) = \phi$ $(n \geq 1)$ (constant propagation rate ϕ) and (ii) "linear" $\phi(n) = \phi n$ (ϕ is the *per-capita* propagation rate).

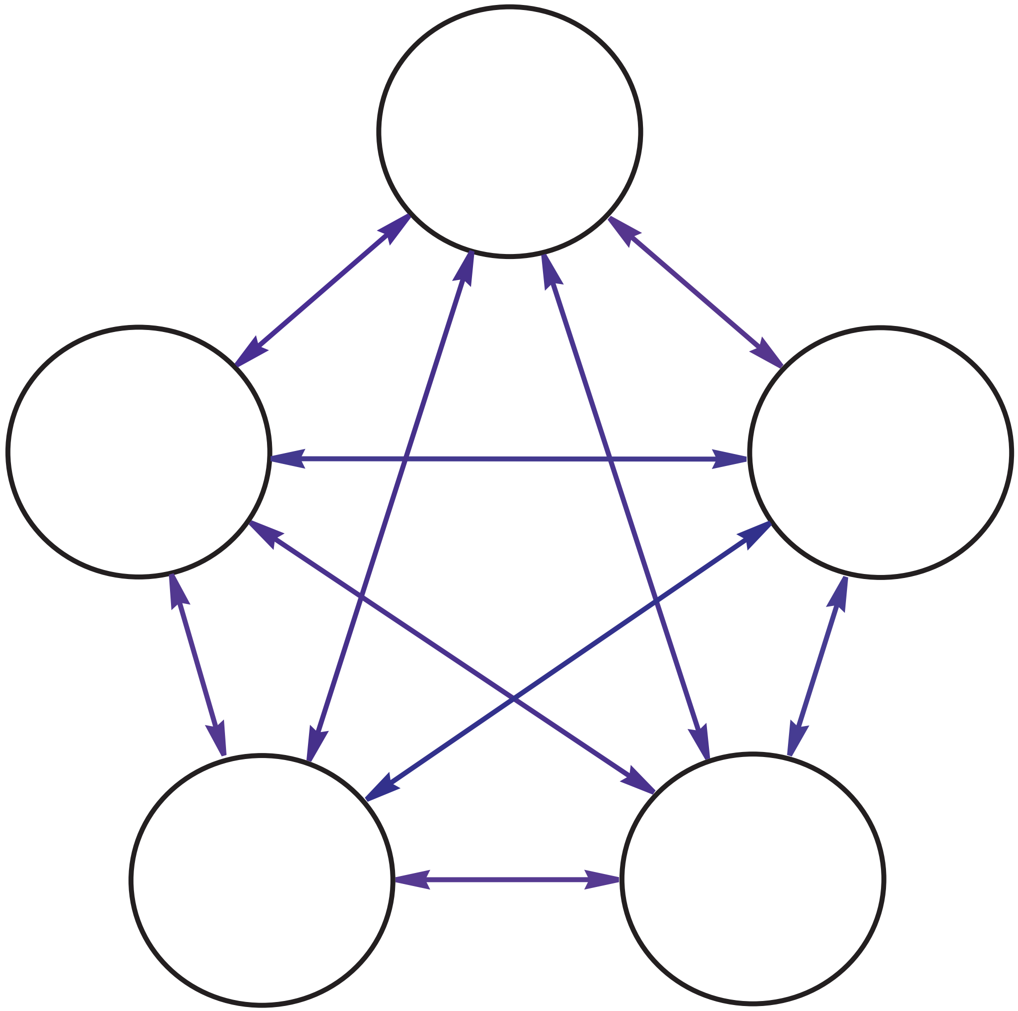
We will also suppose that emigration *to* any patch j is the same *from* all patches i: $\lambda_{ij} = 1/(J-1)$ in the closed network, and, $\nu_i = \nu$, $\lambda_{i0} = \lambda_0$ and $\lambda_{ij} = (1-\lambda_0)/(J-1)$ in the open network.

This is sufficient for $\alpha_j \ (= \alpha)$ to be the same for all j: $\alpha = 1/J$ (closed network) and $\alpha = \nu/\lambda_0$ (open network).

Symmetric network (open)



Symmetric network (closed)



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?

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*.

We might expect that, for some c, e and v,

(i) $c(m) = v(J-m) + \frac{c}{J} m(J-m)$ and (ii) $e(m) = em$.

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*.

External colonization

We might expect that, for some c, e and v,

(i) $c(m) = \boxed{v(J-m)} + \frac{c}{J} m(J-m)$ and (ii) $e(m) = em.$

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*.

Ross (2008)?

We might expect that, for some c, e and v,

(i) $c(m) = v(J - m) + \frac{\phi}{J} m(J - m)$ and (ii) $e(m) = em$.

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,

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

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

(open network)

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,

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

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

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

(closed network)

Which patch-occupancy model?

Owing to the symmetry ...

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

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

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

(open network)

Which patch-occupancy model?

Owing to the symmetry ...

$$
\begin{aligned}
c(m) &= J\nu \Pr(n_1(t) = 0 | C(\boldsymbol{n}) = m) \\
&\quad + J(J-1)\mathsf{E}\left(\phi(n_1(t))1_{\{n_2(t)=0\}} \middle| C(\boldsymbol{n}) = m\right)\frac{1-\lambda_0}{J-1} \\
&= J\nu\left(1 - \frac{m}{J}\right) + (1-\lambda_0) J\,\mathsf{E}\left(\phi(n_1(t))1_{\{n_2(t)=0\}} \middle| C(\boldsymbol{n}) = m\right)
\end{aligned}
$$

(closed network)

Which patch-occupancy model?

And, for both the open and closed network,

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

Which patch-occupancy model?

Before proceeding, recall that ...

Open network

J – 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} = $(1 - \lambda_0)/(J - 1)$

Which patch-occupancy model?

Closed network

J – number of patches

N – number of individuals (fixed)

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

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

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

λ_{ij} = $1/(J-1)$

Equilibrium distributions

Propagation rates	Open network* $\pi_j(n)\ (n \geq 0)$	Closed network $\pi^{(N)}(\boldsymbol{n})\ (\boldsymbol{n} \in S^{(N)})$
Constant	$(1-\rho)\rho^n$	$\binom{N+J-1}{J-1}^{-1}$
Linear	$e^{-r}\dfrac{r^n}{n!}$	$\dfrac{N!}{n_1!\,n_2!\cdots n_J!}\left(\dfrac{1}{J}\right)^N$

*$n_1, \ldots, n_J$ are independent

Which patch-occupancy model? $c(m)$

Closed constant

$$c(m) = \frac{\phi}{J-1} m(J-m) \quad (m = 1, \ldots, J)$$

Closed linear

$$c(m) = \frac{N\phi}{J-1} (J-m) \quad (m = 1, \ldots, J)$$

Open constant

$$c(m) = \nu(J-m) + \frac{\phi(1-\lambda_0)}{(J-1)(1-\rho)} m(J-m) \quad (m = 0, \ldots, J)$$

Open linear

$$c(m) = \nu(J-m) + \frac{\phi(1-\lambda_0)}{J-1} \left(\frac{r}{1-e^{-r}} \right) m(J-m) \quad (m = 0, \ldots, J)$$

Which patch-occupancy model? $e(m)$

Closed constant

$$e(m) = \phi N \frac{m(m-1)}{(N+m-1)(N+m-2)} \quad (m = 1, \ldots, J,\ N \geq 2)$$

Closed linear

$$e(m) = \phi N m \frac{b_{m-1}(N-1)}{b_m(N)} \quad (m = 1, \ldots, J,\ N \geq 2)$$

$$b_m(N) = \textstyle\sum_{k=0}^{m-1} (-1)^k \binom{m}{k} (m-k)^N \ \ (m = 1, \ldots, J) \quad b_0(N) = \delta_{N0}$$

Open constant

$$e(m) = \phi(1-\rho)m \quad (m = 0, \ldots, J)$$

Open linear

$$e(m) = \phi \left(\frac{re^{-r}}{1-e^{-r}} \right) m \quad (m = 0, \ldots, J)$$

Which patch-occupancy model?

Closed constant

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

Closed linear

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

Open

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

Constant $c = \phi(1-\lambda_0)/(1-\rho)$ $\qquad e = \phi(1-\rho)$

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

Which patch-occupancy model?

Closed constant

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

Closed linear

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

“Correct” logistic growth

Open

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

Constant $c = \phi(1-\lambda_0)/(1-\rho)$ $\quad e = \phi(1-\rho)$

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

Which patch-occupancy model?

Closed constant

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

Closed linear

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

Open

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

Constant $c = \phi(1-\lambda_0)/(1-\rho)$ $\quad e = \phi(1-\rho)$

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

Which patch-occupancy model?

Closed constant

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

The SL model with immigration

Closed linear

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

Open

$$\boxed{c(m) = \nu(J-m) + \frac{c}{J-1} m(J-m) \qquad e(m) = em}$$

Constant $c = \phi(1-\lambda_0)/(1-\rho)$ $\qquad e = \phi(1-\rho)$

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

Which patch-occupancy model?

Closed constant

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

Closed linear

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

Open

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

Constant $c = \phi(1-\lambda_0)/(1-\rho)$ $\quad e = \phi(1-\rho)$

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

Which patch-occupancy model?

For the open network with linear propagation rates (only), 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:

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

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 $r_t = \nu(1 - e^{-\phi\lambda_0 t}) / (\phi\lambda_0)$.

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:

$$
\begin{aligned}
q(\boldsymbol{n}, \boldsymbol{n} + \boldsymbol{e}_j) &= \nu_j \\
q(\boldsymbol{n}, \boldsymbol{n} - \boldsymbol{e}_i) &= d_i n_i + \phi_i(n_i)\lambda_{i0} \\
q(\boldsymbol{n}, \boldsymbol{n} - \boldsymbol{e}_i + \boldsymbol{e}_j) &= \phi_i(n_i)\lambda_{ij}
\end{aligned}
$$

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:

$$
\begin{aligned}
q(\boldsymbol{n}, \boldsymbol{n} + \boldsymbol{e}_j) &= \nu_j \\
q(\boldsymbol{n}, \boldsymbol{n} - \boldsymbol{e}_i) &= d_i n_i + \phi_i(n_i)\lambda_{i0} \\
q(\boldsymbol{n}, \boldsymbol{n} - \boldsymbol{e}_i + \boldsymbol{e}_j) &= \phi_i(n_i)\lambda_{ij}
\end{aligned}
$$

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 $\ldots$

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

$$
\begin{aligned}
q(\boldsymbol{n}, \boldsymbol{n} + \boldsymbol{e}_i) &= \nu_i + b_i \tfrac{n_i}{N_i}(N_i - n_i) \\
q(\boldsymbol{n}, \boldsymbol{n} - \boldsymbol{e}_i + \boldsymbol{e}_j) &= \phi_i(n_i)\lambda_{ij} \\
q(\boldsymbol{n}, \boldsymbol{n} - \boldsymbol{e}_i) &= d_i n_i + \phi_i(n_i)\lambda_{i0}
\end{aligned}
$$

Here N_i is the population ceiling at patch i.

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

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

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

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

Here N_i is the population ceiling at patch i.

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