Stochastic models for population networks

I: Network models

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Metapopulations

Colonization

Local Extinction
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).
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.

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:

\[
\begin{align*}
    n &\to n + 1 \text{ at rate } \frac{c}{J} (J - n) \\
    n &\to n - 1 \text{ at rate } en
\end{align*}
\]

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

The SL model simulation \((c < e)\)

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

Note. This entails a high degree of homogeneity among patches (in particular the colonization and local extinction processes).

The SL model simulation \((c > e)\)

There are many ways to distinguish this behaviour and, at the same time, evaluate some useful quantities.

For example, drift:

\[
E(n_{t+s} - n_t | n_t) = n_t \left( c - e - c \frac{n_t}{J} \right) s + o(s).
\]

So, \(c < e\) implies that the drift is always \(< 0\) (small \(s\)).

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\]

So, \(c < e\) implies that the drift is always \(< 0\) (small \(s\)).

If \(c > e\), then the drift is \(< 0\) when \(n_t > n^* := J(1 - e/c)\) and \(> 0\) when \(n_t < n^*\): the process is “attracted” to \(n^*\).
The SL model

Since the SL model is a birth-death process, we have an explicit expression for the expected time to extinction starting with \( n \) occupied patches:

\[
\tau_n^{(J)} = \frac{1}{c} \sum_{j=1}^{n} \sum_{k=0}^{J-j} \frac{1}{j+k} \prod_{l=0}^{k-1} \left( \frac{J-j-l}{J \rho} \right),
\]

where \( \rho = e/c \).

This expression permits large-\( J \) asymptotics . . . .

The following hold in the limit as \( J \to \infty \). If \( \rho > 1 \) (\( c < e \)),

\[
\tau_1^{(J)} \sim \frac{1}{c} \log \left( \frac{\rho}{\rho - 1} \right)
\]

and, for \( n \geq 2 \),

\[
\tau_n^{(J)} \sim \frac{1}{c(\rho - 1)} \left\{ (\rho^n - 1) \log \left( \frac{\rho}{\rho - 1} \right) - \sum_{k=1}^{n-1} \left( \frac{\rho^n - k}{k} \right) \right\},
\]

while if \( \rho < 1 \) (\( c > e \)),

\[
\tau_n^{(J)} \sim \frac{1}{c(1 - \rho)} \left\{ \left( \frac{1 - \rho^n}{1 - \rho} \right) \left( \frac{e^{ -(1-\rho)}}{\rho} \right)^J \sqrt{\frac{2\pi}{J}} - \sum_{k=1}^{n-1} \left( 1 - \rho^{n-k} \right) \right\}.
\]
Or, we can identify 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

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

namely

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

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 simulation ($c < e$)

The SL model simulation ($c > e$)
The SL model: \( c < e \), \( x = 0 \) stable

\[ x_t = \frac{(1 - \rho)x_0}{x_0 + (1 - \rho - x_0) \exp(-(c - e)t)} \]

\[ 1 - \rho = 1 - e/c = -4.0 \]

\( n(0) = 18 \)

The SL model: \( c > e \), \( x = 1 - e/c \) stable

\[ x_t = \frac{(1 - \rho)x_0}{x_0 + (1 - \rho - x_0) \exp(-(c - e)t)} \]

\[ 1 - \rho = 1 - e/c = 0.8 \]

\( n(0) = 2 \)

This of course is the classical Verhulst* 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 \( \epsilon > 0 \),

\[ \lim_{J \to \infty} \Pr \left( \sup_{s \leq t} \left| X_s^{(J)} - x_s \right| > \epsilon \right) = 0. \]
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 at rate $v$.

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

- $n \rightarrow n + 1$ at rate $v(J - n) + cJn(J - n)$
- $n \rightarrow n - 1$ at rate $en$

Network models

We now record the numbers of individuals in the various patches: a typical state is $n = (n_1, \ldots, n_J)$, 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 $\nu_i$ (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 $\lambda_{i0}$, or proceeds to another patch $j$, with probability $\lambda_{ij}$ (in the closed case we take $\lambda_{i0} = 0$); $\lambda_{ij}$ thus specifies the relative proportion of propagules emanating from patch $i$ that are destined for patch $j$, $\lambda_{i0}$ 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.
Again for simplicity, we shall assume that $\Lambda$ 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 $\Lambda$ is irreducible and, hence, that there is a unique collection $(\alpha_1, \ldots, \alpha_J)$ of strictly positive numbers which satisfy the traffic equations $\alpha_j = \nu_j + \sum_i \alpha_i \lambda_{ij}, j = 1, \ldots, J$ (cf. Kirchhoff’s law). Here we may assume without loss of generality that $\sum_j \alpha_j = 1$.

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

In the closed case we simply have

$$q(n, n - e_i + e_j) = \phi_i(n_i)\lambda_{ij} \quad \text{(migration from } i \text{ to } j),$$

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

I have described the migration process of Whittle.*


The Markov chain $(n(t), t \geq 0)$ has state space $S = Z_+^J$ in open case and transition rates

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

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

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

($e_j$ is the unit vector in $Z_+^J$ with a 1 as its $j$-th entry)
Open migration process

**Theorem** An equilibrium distribution exists if
\[ b_{j}^{-1} := 1 + \sum_{n=1}^{\infty} \frac{\alpha_{j}^{n}}{n!} \phi_{j}(r) < \infty \quad \text{for all } j, \]
in which case
\[ \pi(n) = J \prod_{j=1}^{J} \pi_{j}(n_{j}), \quad \text{where} \quad \pi_{j}(n) = b_{j} \frac{\alpha_{j}^{n}}{n!} \phi_{j}(r). \]

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 \( \alpha_{j} \).

Closed migration process (\( N \) individuals)

**Theorem** An equilibrium distribution always exists and is given by
\[ \pi^{(N)}(n) = B^{(N)} \prod_{j=1}^{J} \frac{\alpha_{j}^{n_{j}}}{n_{j}!} \phi_{j}(r) \quad (n \in S^{(N)}), \]
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.

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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) \( \phi_{j}(n) = \phi_{jn}. \)
\[ \pi_{j}(n) = e^{-r_{j}} \frac{r_{j}^{n}}{n!}, \quad \text{where } r_{j} = \frac{\alpha_{j}}{\phi_{j}} \quad (\text{Poisson}). \]

(3) \( \phi_{j}(n) = \phi_{j} \min\{n, s_{j}\} (n \geq 1). \) If \( \rho_{j} := \alpha_{j}/(s_{j}\phi_{j}) < 1, \)
\[ \pi_{j}(n) = \frac{(s_{j}\rho_{j})^{n}}{n!} \quad (n = 1, \ldots, s_{j}) \]
\[ \pi_{j}(n) = \frac{(s_{j}\rho_{j})^{n-s_{j}}}{n-s_{j}!} \quad (n = s_{j} + 1, \ldots). \]

Closed migration process: examples

(1) \( \phi_{j}(n) = \phi_{j} (n \geq 1). \)

The equilibrium distribution is
\[ \pi^{(N)}(n) = B^{(N)} \prod_{i=1}^{J} \rho_{i}^{n_{i}} \quad (n \in S^{(N)}), \]
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 \( \rho_{i} \)'s are distinct).
Closed migration process: examples

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

The equilibrium distribution is \textit{multinomial}:

\[
\pi^{(N)}(n) = \frac{N!}{n_1! n_2! \ldots n_J!} p_1^{n_1} p_2^{n_2} \ldots p_J^{n_J} \quad (n \in S^{(N)}),
\]

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 \textit{binomial}:

\[
\pi_j^{(N)}(n) = \binom{N}{n} p_j^n (1 - p_j)^{N-n} \quad (n = 0, 1, \ldots, N).
\]

Network models: we ask ...

For each of the network models—\textit{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:

\[
\begin{align*}
\text{n} & \rightarrow \text{n + 1} \quad \text{at rate} \quad \frac{c}{J} n (J - n) \\
\text{n} & \rightarrow \text{n - 1} \quad \text{at rate} \quad e n
\end{align*}
\]

(open network)

The SL model: what is \( c \)?

What is the interpretation of \( c \) in the SL model?

\[
\ldots \text{colonization occurred at common rate } \frac{c}{J} \text{ for each of the } n(J - n) \text{ occupied-unoccupied pairs:}
\]

\[
\begin{align*}
\text{n} & \rightarrow \text{n + 1} \quad \text{at rate} \quad \frac{c}{J} n (J - n) \\
\text{n} & \rightarrow \text{n - 1} \quad \text{at rate} \quad e n
\end{align*}
\]

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.

Network models: what are $c$ and $e$?

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

Joshua Ross (2008)* “... $c$ 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.

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 $\phi$) and (ii) “linear” $\phi(n) = \phi n$ ($\phi$ 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.

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

\[
c(m) = \mathbb{E}\left( \sum_j \left( \nu_j + \sum_{i \neq j} \phi_i(n_i(t))\lambda_{ij} \right) 1\{n_j(t)=0\} \mid C(n) = m \right)
\]

\[
= \sum_j \nu_j \Pr(n_j(t) = 0 \mid C(n) = m)
+ \sum_j \sum_{i \neq j} \mathbb{E} \left( \phi_i(n_i(t))1\{n_i(t)=0\} \mid C(n) = m \right) \lambda_{ij}.
\]

(open network)

Which patch-occupancy model?

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?

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\]

\[
= \sum_j \nu_j \Pr(n_j(t) = 0 \mid C(n) = m)
+ \sum_j \sum_{i \neq j} \mathbb{E} \left( \phi_i(n_i(t))1\{n_i(t)=0\} \mid C(n) = m \right) \lambda_{ij}.
\]

(closed network)
Which patch-occupancy model?

Owing to the symmetry . . .

c(m) = Jν \Pr(n_1(t) = 0 | C(n) = m)

+ J(J - 1)E(φ(n_1(t))1_{n_2(t)=0} | C(n) = m) \frac{1 - λ_0}{J - 1}

= Jν \left(1 - \frac{m}{J}\right) + (1 - λ_0)JE(φ(n_1(t))1_{n_2(t)=0} | C(n) = m)

(open network)

Which patch-occupancy model?

And, for both the open and closed network,

\[ e(m) = E\left(\sum_i \phi_i(1)1_{n_i(t)=1} | C(n) = m\right) \]

= \sum_i \phi_i(1) \Pr(n_i(t) = 1 | C(n) = m)

= Jφ \Pr(n_1(t) = 1 | C(n) = m)

Before proceeding, recall that . . .

**Open network**

\[ J \] – number of patches

\[ ν \] – common external immigration rate

\[ φ(n) \] – common propagation rate when \( n \) individuals present at that patch – two cases:

- **“constant”** \( φ(n) = φ1_{n>0} \) \( ρ := ν/(φλ_0) \) (< 1)

- **“linear”** \( φ(n) = φn \) \( r := ν/(φλ_0) \)

\[ λ_0 \] – common external emigration/removal probability

\[ λ_{ij} = (1 - λ_0)/(J - 1) \]
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" $\phi(n) = \phi n$
- $\lambda_{ij} = 1/(J-1)$

**Equilibrium distributions**

<table>
<thead>
<tr>
<th>Propagation rates</th>
<th>Open network* $\pi_j(n) ; (n \geq 0)$</th>
<th>Closed network $\pi^{(N)}(n) ; (n \in S^{(N)})$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Constant</strong></td>
<td>$(1 - \rho)\rho^n$</td>
<td>$\left(\frac{N + J - 1}{J - 1}\right)^{-1}$</td>
</tr>
<tr>
<td><strong>Linear</strong></td>
<td>$e^{-r} r^n \frac{n!}{n! n_1! \cdots n_J!} \left(\frac{1}{J}\right)^N$</td>
<td>$\ast n_1, \ldots, n_J \text{ are independent}$</td>
</tr>
</tbody>
</table>

* $n_1, \ldots, n_J$ 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**
$$e(m) = \phi N m \frac{b_{m-1}(N-1)}{b_m(N)} \quad (m = 1, \ldots, J, \; N \geq 2)$$
$$b_m(N) = \sum_{k=0}^{m-1} (-1)^k \binom{m}{k} (m-k)^N \quad (m = 1, \ldots, J) \quad b_0(N) = \delta_{N0}$$

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

**Open linear**
$$e(m) = \phi \left(\frac{r e^{-r}}{1-e^{-r}}\right) m \quad (m = 0, \ldots, J)$$
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
\[ c(m) = \frac{N\phi}{J-1}(J-m) \quad e(m) = \phi N m_{b_{m-1}(N-1)} \]

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

The SL model with immigration

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 \( c_t = \phi(1 - \lambda_0)r_t/(1 - e^{-r_t}) \), \( e_t = \phi r_te^{-r_t}/(1 - e^{-r_t}) \), 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:

\[ q(n, n + e_j) = \nu_j \]
\[ q(n, n - e_i) = d_i n_i + \phi_i(n_i) \lambda_{i0} \]
\[ q(n, n - e_i + e_j) = \phi_i(n_i) \lambda_{ij} \]

per-capita death rate

For example, with linear propagation rates . . .

\[ q(n, n + e_j) = \nu_j \]
\[ q(n, n - e_i) = d_i n_i + \phi_i(n_i) \lambda_{i0} = \phi_i(n_i) \lambda'_{i0} \]
\[ q(n, n - e_i + e_j) = \phi_i(n_i) \lambda_{ij} \]

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

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

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

\[ q(n, n + e_i) = \nu_i + b_i \frac{n_i}{N_i} (N_i - n_i) \]
\[ q(n, n - e_i + e_j) = \phi_i(n_i) \lambda_{ij} \]
\[ q(n, n - e_i) = d_i n_i + \phi_i(n_i) \lambda_{i0} \]

Here \( N_i \) is the population ceiling at patch \( i \).

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