1.0. The Levins Metapopulation model

This is the simplest and classic encapsidation of a metapopulation process due to Levins (1969).

$$\frac{dp}{dt} = mp(1-p) - ep \qquad 1.1$$

p is the proportion of occupied patches, m is the rate of colonization of unoccupied patches per occupied patch, and e is the extinction rate per patch.

There two equilibrium points, the trivial equilibrium point, $p^* = 0$, and by setting the right hand side equal to zero, and solving for p, we get a second 'non-trivial' equilibrium value:

$$p^* = 1 - \frac{e}{m} \qquad 1.2$$

The non-trivial equilibrium is feasible ($p^*>0$) if $e<m$, which makes sense.

Levins, R. (1969), "Some demographic and genetic consequences of environmental heterogeneity for biological control", *Bulletin of the Entomological Society of America* **15**: 237–240

2.0. The demographically stochastic Levins metapopulation model

By recognizing that in reality there will be a discrete and finite number of patches (N_{max}) and that these undergo colonization and extinction, we can reformulate Eq. 1.1, in accordance with the principles of **demographic stochasticity**. Assume that N_t patches are occupied. Then two things may happen. One of the N_t patches may go extinct (at per patch rate e, or total rate eN_t), or one of the N_{max}-N_t unoccupied patches may become colonized (at rate per patch rate $m(1\text{-}p)$, or total rate $m(1\text{-}p)N_t$). Thus

$N_t \longrightarrow N_t + 1$ at rate $m(1\text{-}p)N_t$
$N_t \longrightarrow N_t - 1$ at rate eN_t

Or

$N_t \longrightarrow N_t + 1$ with probability $m(1\text{-}p)N_t\,/\,(m(1\text{-}p)N_t+eN_t)$
$N_t \longrightarrow N_t - 1$ with probability $eN_t\,/\,(m(1\text{-}p)N_t+eN_t)$

The waiting time to the next event is an exponentially distributed random variable with mean equal to the inverse of the sum of the rates. So the faster everything is happening the *less* time between successive events.

So the Gillespie process is an iterative one: 1) Given the state of the system we calculate the rates for every possible event that can occur; 2) we use a random number to determine which event does occur; 3) we use the sum of all the rates to calculate the time increment; 4) we update time and the state of the system given the event that occurred; 4) return to 1.

3.0. The Spatial Patch Occupancy Model – SPOMs

Let us relax the 'Levins' assumptions. Let there be a finite number of patches (N_{max}). Let $P_i = 1$ if the ith patch is occupied, and $P_i = 0$ if it is unoccupied. Let the distance between the ith and jth patch be given by d_{ij}. Let the area of the ith patch be denoted A_i. Let the extinction rate of the ith patch be given by $P_i\, e/A_i$. Let the colonization rate of the ith patch be given by:

Define the dispersal function between patch i and j as :

$$k_{ij} = \exp\left(-a \cdot d_{ij}\right)$$

Define the connectivity function of patch i to be:

$$S_i = \sum_{\substack{j=1 \\ j \neq i}}^{N_{max}} P_j \cdot k_{ij} \cdot A_j^b$$

Define the colonization function of patch i to be:

$$C_i = (1 - P_i)[1 - \exp(-y \cdot S_i)]$$

And the extinction function of patch i to be:

$$E_i = P_i \min\left(1, \frac{u}{A_i^x}\right)$$

We then have total colonization rate of

$$\sum_{\substack{j=1 \\ j \neq i}}^{N_{max}} C_j$$

We then have total extinction rate of

$$\sum_{\substack{j=1 \\ j \neq i}}^{N_{max}} E_j$$

And can apply the Gillespie algorithm on 'N_{max}' possible events.