# Models for Spatially Structured Metapopulations

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Summer Vacation research project - 2005/2006

**Abstract**

A metapopulation is a population which can occupy regions, or 'patches', which are separated geographically. Each patch at any given time can be either occupied or unoccupied by the population. If a patch is empty, it may be colonized by the inhabitants of one (or several) of the other patches through a migration process. So patches in a metapopulation may undergo several local extinctions or recolonizations over time. It is also possible that all patches may become extinct. We may model these dynamics using a Markov chain, as we do in this investigation. First a simple discrete time model is investigated. We adjust this model to create a more realistic model. Several models used by other researchers are also examined. We then look at a continuous time model. Much modelling for metapopulations is done using discrete time Markov chains. However, using continuous time Markov chains can at times be simpler, as we shall see. When applied to a real metapopulation, the models investigated should have the parameters of the model estimated through study of the particular metapopulation. Regrettably, no data was used to estimate parameters in this investigation.

## 1   A Discrete Time Model

First we examine a very simple discrete time Markov chain model of a general metapopulation. This is used when only the number of occupied patches is of importance. Our state space is $S = \{0, 1, \ldots, N\}$, where N is the number of available patches. We wish to create a transition probability matrix $P$ which contains the probabilities of all possible transitions between the numbers of occupied patches in one time period. To simplify this process, here we assume that each population has an equal chance of being colonized by any other patch, and that each patch is equally likely to become extinct in one time period. These are rather poor assumptions, as they would indicate that the patches are equidistant from each other and of equal size, and have equally desirable environmental properties. The tedious counting exercise of creating $P$ can become very difficult for even relatively small numbers of patches. Thus, a method often used by ecologists, and which we adopt here, is to split the matrix P into two transition probability matrices $C$ and $E$, which contain colonization transition probabilities and extinction transition probabilities respectively.

Let $p$ be the probability that a particular occupied patch colonizes a particular unoccupied patch. To create a colonization matrix we use several assumptions:

- Any occupied patch may (but will not necessarily) colonize more than one patch in a single time step.

- More than one patch may colonize an unoccupied patch at the same time.

- Each unoccupied patch is equally likely to be colonized by any of the occupied patches (This assumes that the patches are equidistant and the same size as each other)

Below is the colonization matrix $C$ for a 3 patch system.

$$C = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & (1-p)^2 & 2p(1-p) & p^2 \\ 0 & 0 & (1-p)^2 & 2p(1-p)+p^2 \\ 0 & 0 & 0 & 1 \end{pmatrix}$$

The above matrix was found by counting the number of possible colonizations for each initial state. Note that the number of patches occupied cannot decrease in the colonization transition stage.

The creation of $C$ can be generalised for $N$ patches[1]. Assume that we begin with $i$ occupied patches. If patch $m$ is not occupied, then there is a probability of $(1-p)^i$ that none of the patches will colonize patch $m$. Therefore the probability that at least one of the patches will infect patch $m$ is $1-(1-p)^i$. Initially, $N-i$ patches are not infected. So, the probability that x new patches are infected during one time period is equal to

$$P(\texttt{x new colonies}) = \binom{N-i}{x} \left(1 - (1-p)^i\right)^x ((1-p)^i)^{N-i-x} \tag{1}$$

- a binomial distribution. So to create $C$, since $c_{ij}$ is the probability that $j$ patches will be occupied after a time step if $i$ were initially ocupied, then we can just put $x = j - i$ (with $j \geq i$) in the above formula to find $c_{ij}$ ($j \geq i$). That is,

$$c_{ij} = \binom{N-i}{j-i} \left(1 - (1-p)^i\right)^{j-i} ((1-p)^i)^{N-j} \qquad j \geq i \tag{2}$$

Let $q$ be the probability that an occupied patch goes extinct in a single time period. Then clearly

$$e_{ij} = \binom{i}{i-j} q^{i-j} (1-q)^j \qquad j \leq i \tag{3}$$

Note that 0 is the absorbing state for both C and E.

From these we can create two overall transition probability matrices; either $P = CE$ or $P = EC$. This is a crude method, since this assumes that the colonization and extinction

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[1]Thanks to M. Nester

processes cannot occur at the same time. $P = CE$ assumes that first colonization, then extinction occurs in one time period. This is surely a poor assumption in most cases.

To investigate how the order affects the model, we may look at the distribution $n_t$ at time $t$, given by

$$n_t = n_0 CE$$
$$n_t = n_0 EC$$

where $n_0$ is the initial distribution. A brief investigation showed that this order does affect the result, but affects it most for small numbers of time steps.

# 2 A Stochastic Metapopulation Model with Variability in Patch Size and Position - J. Day and H. Possingham

The paper *A Stochastic Metapopulation Model with Variability in Patch Size and Position*[2] provides a more realistic model but for a specific metapopulation (malleefowl of South Australia in an eight patch system). This model was used to investigate which patches were occupied, allowing for differences in size and distance between patches. However, the model also used separate transition probability matrices C and E for the colonization and extinction probabilities respectively. The paper uses only the order P = EC.

To investigate the affect that the order would have if CE were to be used, a two patch case was examined, and the same assumptions about extinction and colonizing probabilities as in the paper were made. The same total area was also used in order to preserve as many of the properties as possible. In the paper, the following assumptions were made:

- Annual extinction probabilities $a_i$, for patch $i$ with area $A_i$ is $a_i = 13/A_i$.

- The probability of $i$ colonizing $j$ is given by $b_{ij} = 0.005e^{-1/5\sqrt{d_{ij}}}$ where $d_{ij}$ is the distance between patches $i$ and $j$.

- The model used by the paper keeps track of which patches are occupied, so, in a two patch system, there are actually four possible states.

I created a MATLAB[3] m-file to investigate the difference that the order had on the distribution after different numbers of time periods. In this program I could:

- Alter patch size, so that the patches may or may not be of equal size.

- Alter the distance beween the two patches.

- Alter the initial distribution.

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[2]J. Day, H. Possingham A Stochastic Metapopulation Model with Variability in Patch Size and Position *Theoretical Population biology* Vol 48, pp333-360 (1995) Academic Press, Inc
[3]MATLAB (2004) *The Mathworks, Inc*

I found that using the different orders did not produce very different results for the two patch system. I did find that equal patch sizes decreased the probability of extinction, while increasing the distance between patches only marginally increased the probability of extinction.

# 3   Patches with a nearby mainland

The idea here is to model a metapopulation assuming that there is a 'mainland' nearby. It is assumed that a mainland population never goes extinct, and so there is always a positive probability of an unoccupied patch being colonized. In addition, there is no absorbing state. Further to the assumptions made previously in **Section 1**, we also assume that each patch is equally likely (of probability $a$) to be colonized by the mainland, so all patches are equidistant from the mainland and the probability of the mainland colonizing any of the patches is time independent. The mainland is not considered a patch - it only affects immigration to the patches (so the mainland will not affect the E matrix from our first model; it will only affect C).

Below is the colonization matrix $C$ for a 2 patch system:

$$C = \begin{pmatrix} (1-a)^2 & 2a(1-a) & a^2 \\ 0 & (1-a)(1-p) & (1-a)p + a(1-p) + ap \\ 0 & 0 & 1 \end{pmatrix}$$

The above matrix was found by counting the possibilities. A general formula for filling in the matrix could be found by altering the formula we had for the case without a mainland, but this was not done here. Alternatively, we could make a separate transition probability matrix A for colonizations from the mainland, and so could create $P$ in several ways - $P = ACE$, $P = AEC$, $P = EAC$, $P = ECA$, $P = CEA$, or $P = CAE$. Such a matrix A would be easily constructed, but has not been constructed here. The question of which order to use could be quite difficult, however. This model is even less realistic than the model used in **Section 1**, since we assume here that transitions occur in three separate events - interpatch colonization, extinction and colonization from the mainland - which is surely not the case.

# 4   The quasi-stationary distribution

The quasi-stationary distribution is used to model the behaviour of a Markov chain assuming that extinction has not yet occured. It is the limit of the conditional distribution (conditioned on non-extinction). It is only useful if the Markov chain avoids the absorbing state for a substantial period of time, and when the conditional distribution approaches its limit quickly. Here a model that only kept track of the number of patches that are occupied was used to investigate the quasi-stationary distribution for metapopulations. The quasi-stationary distribution was found using the method described in P. Pollett's *Limiting*

*conditional distributions for stochastic metapopulation models*[4] - the left eigenvector of the transition matrix (with the absorbing state removed) corresponding to the eigenvalue of the largest modulus is the quasi-stationary distribution.

The paper states that the closer the expression $|\rho_2|/\rho_1$ (assuming $\rho_2$ is real) is to 0 and the closer $\rho_1$ is to 1, where $\rho_1$ = the largest eigenvalue of the transition matrix without the absorbing state, and $\rho_2$ = the eigenvalue of the second largest absolute value, the more appropriate is the use of the quasi-stationary distribution. The first expression measures how quickly the conditional distribution approaches the limit, and the closer $\rho_1$ is to 1, the greater the expected time to absorption. The findings just confirmed what one would expect:

- The larger the number of patches, the better and more appropriate is the use of the quasi-stationary distribution (since this would increase the chance of the system avoiding the absorbing state zero) and

- the larger p is compared to q, the better and more appropriate is the use of the quasi-stationary distribution (since there is a higher probability of a higher number of patches being occupied, and thus a higher probability of the system avoiding extinction).

I found that even when the eigenvalues suggest that the quasi-stationary distribution is appropriate, the difference between the EC and CE quasi-stationary distributions can be alarming. For example,

| $n$ | $CE\ QS$ | $EC\ QS$ | $|\rho_2|/\rho_1$ | $\rho_1$ | $p$ | $q$ |
|---|---|---|---|---|---|---|
| 3 | $(0.0074, 0.1375, 0.8551)$ | $(0.0001, 0.0027, 0.9972)$ | 0.0305 | 0.9999 | 0.9 | 0.05 |
| 3 | $(0.5664, 0.3552, 0.0784)$ | $(0.1416, 0.3720, 0.4864)$ | 0.1985 | 0.7754 | 0.5 | 0.5 |

i.e. Assuming that extinction occurs first increases the probability of a higher number of patches being occupied in the quasi-stationary distribution.

# 5    Continuous Time Markov Chains

Instead of viewing this as a discrete time Markov chain we may model it as a continuous time Markov chain. One difference here is that we may calculate probabilities for any time $t \geq 0$, as opposed to the discrete case when we were restricted to finding probabilities after an integer number of time steps. However, one of the more powerful differences between the discrete and the continuous models is that for the continuous case there is no need to split the process up into two processes: colonizations and extinctions. A very brief outline of continuous time Markov chains appears below:

First we define $P_{ij}(t) = P(X(t+s) = j | X(s) = i)$

Conditions used for continuous time Markov chains are:

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[4]P. Pollett Limiting conditional distributions for stochastic metapopulation models *Proceedings of the 3rd Asia-Pacific Conference on Communications*, Vol 3 pp1489-1493 IREE Society of Australia

- $P_{ij}(t) \geq 0$

- $\sum_{j=0}^{N} P_{ij}(t) = 1, i, j = 0, 1, ..., N$

- $P_{ij}(s+t) = \sum_{k=0}^{N} P_{ik}(s)P_{kj}(t)$

- and

$$\lim_{t \to 0+} P_{ij}(t) = \begin{cases} 1, & \text{if } i = j \\ 0, & \text{if } i \neq j \end{cases}$$

One can create a matrix Q describing the process by defining
$q_{ii} = \lim_{h \to 0+} \frac{1 - P_{ii}(h)}{h} =$ infinitesimal probability of leaving state $i$.
$q_{ij} = \lim_{h \to 0+} \frac{P_{ij}(h)}{h} =$ infinitesimal probability of moving from state $i$ to state $j$.
so that

$$P(X(t+h) = j | X(t) = i) = q_{ij}h + o(h) \; for \; i \neq j$$
$$P(X(t+h) = i | X(t) = i) = 1 - q_{ii}h + o(h)$$

o(h) is a neglible remainder term.

From this we create a matrix Q with $-q_{ii}$ along the diagonal and $q_{ij}$ off the diagonal.

But $Q = P'(0) = \lim_{h \to 0+} \frac{P(h) - I}{h}$ So we can write

$$\frac{P(t+h) - P(t)}{h} = \frac{P(t)(P(h) - I)}{h} = P(t)\frac{P(h) - I}{h}$$

Taking the limit, we get $P'(t) = P(t)Q$, the solution of which is $P(t) = \exp(Qt)$

Here we use an SIS model:

$$q(n, n+1) = c\frac{n}{N}(N - n) \tag{4}$$

$$q(n, n-1) = en \tag{5}$$

where n is the number of patches occupied at time t, N is the total number of patches, c is the colonization rate and e is the extinction rate for the system. This is notably different from the model that we used in the discrete time model, since the probability of colonization is inversely proportional to the total number of patches.

So I created the Q matrix

$$Q = \begin{pmatrix} 0 & 0 & 0 & 0 \\ e & -(e + \frac{2}{3}c) & \frac{2}{3}c & 0 \\ 0 & 2e & -2(e + \frac{1}{3}c) & \frac{2}{3}c \\ 0 & 0 & 3e & -3e \end{pmatrix}$$

So we have the general formula

$$q_{ij} = \begin{cases} q(n, n+1) = c\frac{n}{N}(N - n) \\ q(n, n-1) = en \\ q(n, n) = -(q(n, n+1) + q(n, n-1)) \end{cases}$$

Note that there is no counting required here as there is in the discrete case. Also, $q(n, n+k)h$ for $k \geq 2$ is $o(h)$.

Now, the transition matrix $P(t)$ is given by

$$P(t) = e^{Qt} = I + \sum_{k=1}^{\infty} \frac{Q^k t^k}{k!}$$

where $I$ is the identity matrix. It is best to make this calculation computationally. In fact, in most cases this cannot be determined analytically. Here, the program *Expokit*[5] was used for the calculation of the matrix exponential.

# 6  Comparing the Continuous Time and Discrete Time Models

Comparing the continuous time and discrete time models could give us an indication of which model is more appropriate. However, a problem with comparing our original model from **Section 1** to the continuous time model from **Section 5** is that in the continuous time model we assume that the probability of colonization is inversely proportional to N, the number of patches available, whereas in the discrete time model we do not. A way to ensure that our continuous and discrete time models are consistent is to alter our discrete time model. Our new model is outlined below[6]:

Assume that in one time step, an unoccupied patch is colonized with probability $c_i = (i/N)c$, where $c$ is a constant which describes the maximum potential for colonization. We then have

$$c_{ij} = \binom{N-i}{j-i} c_i^{j-i} (1 - c_i)^{N-j} \tag{6}$$

We use the same model for the extinction as given by (3). So now we can create transition probability matrices C and E for colonization and extinction respectively. Unfortunately, once again our discrete time Markov chain model uses either the overall transition probability matrix CE or EC, while our continuous model is pleasing in that we do not have this separation between extinction and colonization events. In order to investigate differences between the continuous time and the two discrete time (CE and EC) models, I created a MATLAB[7] m-file which calculated the distibution after an input number of time periods and input c and e, for an input number of patches, using a desired initial distribution. Common sense would suggest that the continuous case is most accurate at giving probabilities - since we make no assumptions about which event - colonization or extinction - occurs first, or indeed, that they occur separately at all. The outcome of the investigation was somewhat surprising, since I found that generally the CE discrete time model gives

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[5]Sidje (1999)

[6]Thanks to P. Pollett

[7]MATLAB (2004) *The MathWorks, Inc.*

a distribution which is closer to the continuous time model. For example, for an 8 patch system with c=0.9, e=0.05, and t=50, then we have

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Assume initial distibution is

v =

     0     1     0     0     0     0     0     0     0

Then the final distribution is
For transition probability matrix CE

ans =

  Columns 1 through 8

    0.0427    0.0000    0.0000    0.0002    0.0016    0.0132    0.0802    0.3077

  Column 9

    0.5544

For transition probability matrix EC

ans =

  Columns 1 through 8

    0.0905    0.0000    0.0000    0.0000    0.0002    0.0015    0.0127    0.1011

  Column 9

    0.7940

Compare this to the continuous calculation

ans =

  Columns 1 through 8

    0.0643    0.0000    0.0000    0.0002    0.0018    0.0131    0.0739    0.2852

  Column 9
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0.5614
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Unfortunately, however, a thorough investigation into the differences between the continuous time model and the discrete time models was not completed. A further study into this may prove helpful. It is important to realize that the continuous time model was more accurate than either of the two discrete time models presented here.

# 7    Acknowledgements

# References

[1] J. Day, H. Possingham A Stochastic Metapopulation Model with Variability in Patch Size and Position *Theoretical Population biology* Vol 48, pp333-360 (1995) Academic Press, Inc

[2] P. Pollett Limiting conditional distributions for stochastic metapopulation models *Proceedings of the 3rd Asia-Pacific Conference on Communications*, Vol 3 pp1489-1493 IREE Society of Australia

[3] H. Taylor, S. Karlin, *An Introduction to Stochastic Modeling* 3rd ed. (1998) Academic Press (USA)

[4] R. Sidje, *Expokit* University of Queensland (1999) Available online http://www.maths.uq.edu.au/expokit/ (Accessed 20/01/06)

[5] MATLAB (2004) *The MathWorks, Inc.*